Hypopterygiaceae of the World

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ABSTRACT

This publication presents a systematic study of the Hypopterygiaceae Mitt. s.l., a small family of pleurocarpous mosses. It includes a taxonomic revision and phylogenetic analyses to clarify the circumscription of the family and the mutual relationships of its genera and species.

The Hypopterygiaceae have a mainly Gondwanan distribution and occur in humid forests of (warm-)temperate to tropical areas of the world. They are characterised by having partly or entirely complanate foliate stems and branches, whereby the leaves are arranged in two rows of asymmetrical, lateral leaves and a single, ventral row of smaller, symmetrical amphigastria. Seven genera are recognised. The c. 160 validly published species and intraspecific taxa are reduced to 21 species. The family shows its greatest diversity in Indo Malaysia (11 species) and Australasia (9 species). Africa and the New World are poor in species with, respectively, 3 and 5 representatives.

In the past, the Hypopterygiaceae were regarded as a monophyletic family, but during the last twenty years this status has frequently been discussed. Several authors suggested the Hypopterygiaceae to be polyphyletic, while others still regarded the family as monophyletic. However, a series of phylogenetic analyses performed in this study – based on 57 morphological characters and, initially, 34 species, including the Hypopterygiaceae and representatives of possibly related families – supports the monophyletic status of the Hypopterygiaceae.

Based on the outcomes of the analyses, the genus *Cyathophorella* (Broth.) M. Fleisch. is united with *Cyathophorum* P. Beauv., which results in the well-supported, monophyletic genus *Cyathophorum* with 7 species. The genus is nested in a monophyletic *Dendrocyathophorum-Lopidium-Cyathophorum* clade. *Lopidium* Hook.f. & Wilson is a well-supported monophyletic genus of two species. *Dendrocyathophorum* Dixon is a monotypic genus that is maintained as a separate genus. One of the most characteristic features of *Dendrocyathophorum*, the central cavity in its axes, is a plesiomorphic condition and a synapomorphy of the *Dendrocyathophorum-Lopidium-Cyathophorum* clade. *Hypopterygium* Brid. is a paraphyletic genus of 7 species, which has a basal position to the *Dendrocyathophorum-Lopidium-Cyathophorum* clade.

The monotypic genera *Catharomnion* Hook.f. & Wilson and *Canalohypopterygium* W. Frey & Schaepe form a monophyletic clade with a basal position to the *Hypopterygium* grade. *Catharomnion* and *Canalohypopterygium* share the – for mosses unique – rudimentary branches and associated cavity system, but are maintained as separate genera, because of distinct morphological differences, in particular in sporophytic characters.

Dendrohypopterygium is a newly described paraphyletic genus of two species, which has a basal position to the Hypopterygiaceae in the obtained phylogenetic trees.

The distribution of extant Hypopterygiaceae is probably the result of a combination of dispersal and continental drift acting as vicariance and speciation events. Dispersal of Hypopterygiaceae occurs by means of detached branch fragments, detached leaves, gemmae, and spores. Vegetative propagulae and a portion of the spores mainly contribute to local dispersal and the maintenance and growth of local populations. Dispersal by spores is most common over longer distances. However, the survival rate of spores of Hypopterygiaceae under conditions occurring during long-distance transport in air streams is low. Effective long-range dispersal is probably rare in Hypopterygiaceae, and may have occurred only few times in the history of the family (e.g. *Hypopterygium sandwicense* on the Hawaiian Islands).

Endemism in New Zealand, Australia, and South America suggests that the origin of the Hypopterygiaceae is situated in East Gondwanaland. The presumably terrestrial, dendroid ancestral species were probably distributed in active mountain ranges on the margin of the continent and faced cool temperate conditions and occupied humid, terrestrial habitats at low altitude. Descendants of the cool-temperate ancestor(s) probably moved to higher altitudes due to climatic changes in the course of the Cretaceous. Speciation was induced as a result of fragmentation of the original distribution area in combination with a change of ecological conditions towards a higher humidity and precipitation. Descendants of the terrestrial ancestral species became epiphytic and epilithic. The rise and radiation of angiosperms have presumably favoured the appearance of epiphytes.

The Hypopterygiaceae are probably at least 84 million years old, but presumably much older. The existence of most extant species and their present distribution can be explained by northwards rafting on drifting fragments of East Gondwanaland during the Cretaceous or Cenozoic period in combination with mainly short range dispersal events.

It seems that Hypopterygiaceae experienced low evolution rates, but part of the family faced probably a Cretaceous radiation event eventually resulting in the appearance of pinnate or simple epiphytic species. Intraspecific variation that is found in some *Hypopterygium*-species (*H. tamarisci*, *H. flavolimbatum*, and *H. didictyon*) is perhaps of Late Cenozoic origin, and may represent an early stage of a second radiation event due to the climatic changes in the Late Cenozoic.

SAMENVATTING

Dit proefschrift omvat een studie naar de systematiek van de bladmossenfamilie Hypopterygiaceae. Hypopterygiaceae zijn mooie mossen en enkele van de grootste en fraaiste mossen die er bestaan behoren tot deze familie. Het boomvormige Nieuw-Zeelandse mos *Dendrohypopterygium filiculiforme* (Fig. 4) kan tot 13 cm hoog worden en vormt opvallende groepen van kleine, rechtopstaande boompjes op de vochtige bosbodem. *Cyathophorum bulbosum* (Fig. 46) kan op Nieuw-Zeeland tot 25 cm lang worden en groeit horizontaal afstaand van rotswanden en op takken en stammen van bomen.

De familie van de Hypopterygiaceae komt voor in de vochtige bossen van (warm) gematigde tot tropische gebieden van de wereld, maar ze kent haar voornaamste verspreiding op het Zuidelijk Halfrond. Vanuit Zuid-Oost Azië bereikt ze noordwaarts Japan en Brits Columbia (Canada). In de Nieuwe Wereld bereikt de familie vanuit de noordelijke Andes van Zuid-Amerika, Midden-Amerika en de Caraïben, zuidelijk Mexico en nipt Florida (Verenigde Staten). In noordelijk en centraal Azië en Europa komt de familie van nature niet voor. De wijdverspreide, vaak op boomvoeten en stammen van boomvarens groeiende soort *Hypopterygium tamarisci* is waarschijnlijk met Australische of Nieuw-Zeelandse boomvarens door de mens geïntroduceerd in Portugal en daardoor ook in kassen in verschillende West-Europese botanische tuinen (bijvoorbeeld Utrecht) te vinden.

Planten van Hypopterygiaceae kennen een opvallende verscheidenheid in bouw. De familie omvat bodembegroeiende soorten met boomvormig vertakte planten, op bomen of rotsen groeiende soorten met waaier- tot veervormig vertakte of onvertakte planten, en op boomvoeten en keien groeiende tussenvormen. Alle Hypopterygiaceae hebben een bijzondere wijze van bebladering met elkaar gemeen. Bij dit type bebladering staan de bladeren in drie rijen en zijn ze als het ware in één vlak samengedrukt (afgeplat bebladerd). De bladeren van de middelste en onderste rij bladeren (de zogenaamde amfigastria) verschillen daarbij bovendien in vorm en grootte van die van de twee zijdelingse rijen (zie Fig. 46). Soorten met waaier- tot veervormige of onvertakte planten zijn bijna altijd geheel op deze wijze drie-rijig bebladerd. Soorten met boomvormige planten hebben ook altijd drie-rijig bebladerde takken. De stam van boomvormige planten is echter vaak (niet bij alle soorten) afwijkend bebladerd met acht rijen gelijke bladeren, die niet zijn samengedrukt.

De Hypopterygiaceae worden beschouwd als een familie waarbinnen veel soorten moeilijk van elkaar te onderscheiden zijn. Over de verwantschapsrelaties tussen de soorten bestaat ook grote onduidelijkheid en de omgrenzing van de familie is onderwerp van discussie. Er bestaan sinds de zeventiger jaren verschillende opvattingen over de omgrenzing van de familie en consensus hierover ontbreekt dus. Men heeft voorgesteld enkele geslachten (groepen van soorten) uit de Hypopterygiaceae te halen en over te brengen naar andere mossenfamilies; de Hookeriaceae worden in dit verband vaak genoemd.

Revisie van de Hypopterygiacea

Om vast te stellen wat goede soorten zijn en welke naam ze moeten krijgen was een taxonomische revisie van de soorten van de Hypopterygiaceae noodzakelijk. Voor de revisie is alle relevante literatuur en een groot aantal herbariumcollecties van Hypopterygiaceae van verschillende herbaria bestudeerd om de variatie binnen de soorten te leren kennen. In het verleden waren ongeveer 160 soorten en lagere eenheden (variëteiten en forma) voor de Hypopterygiaceae beschreven.

Veel soorten bleken echter meer dan eens onder verschillende namen (synoniemen) als nieuwe soorten te zijn beschreven. Het aantal geaccepteerde soorten binnen de Hypopterygiaceae is na de revisie teruggebracht tot 21. Na de revisie is duidelijk geworden, dat het grootste aantal soorten van de familie gevonden wordt in het Indo-Maleise gebied (11 soorten) en Australië en Nieuw-Zeeland (9 soorten). Afrika en de Nieuwe Wereld zijn soortenarm met, respectievelijk, 3 en 5 soorten.

Alle geaccepteerde soorten worden in dit proefschrift beschreven en geïllustreerd. Bij iedere soort worden de typificatie, de synonymie en eerdere illustraties opgegeven en becommentarieerd in noten. De gepresenteerde morfologische variatie, de geografische verspreiding en de standplaatsgegevens zijn gebaseerd op de onderzochte herbariumcollecties. Bij iedere soort wordt een representatieve selectie van het bestudeerde materiaal gepresenteerd.

Omgrenzing van de Hypopterygiaceae en verwantschapsrelaties tussen de soorten

Om meer inzicht te krijgen in de verwantschapsrelaties tussen de soorten van de Hypopterygiaceae en de omgrenzing van de familie werd de hypothetische, evolutionaire geschiedenis van deze familie gereconstrueerd op basis van fylogenetische analyses. Hierbij worden soorten gegroepeerd op grond van gemeenschappelijk bezit van afgeleide ('nieuwe') kenmerktoestanden. Het gemeenschappelijk bezit van afgeleide kenmerken duidt op een gemeenschappelijke voorouder en dus verwantschap. De oplossingen van fylogenetische analyses worden bomen (cladogrammen) genoemd. Ze zijn te vergelijken met stambomen.

De fylogenetische analyses zijn uitgevoerd met alle 21 soorten van de Hypopterygiaceae en een representatieve selectie van mogelijk nauw en ver verwante soorten die tot andere mossenfamilies behoren (waaronder de Hookeriaceae).

De analyses zijn gebaseerd op 57 morfologische kenmerken en werden, in eerste instantie, uitgevoerd met 34 soorten. De resultaten ondersteunen de hypothese, dat alle Hypopterygiaceae van één en dezelfde vooroudersoort afstammen: de familie is monofyletisch.

De resultaten maakten het mogelijk om de soorten van de Hypopterygiaceae onder te brengen (classificeren) in 7 geslachten. De geslachten *Dendrocyathophorum*, *Lopidium*, *Hypopterygium*, *Catharomnion* en *Canalohypopterygium* blijven gehandhaafd. Het geslacht *Cyathophorella* wordt samengevoegd met het (eerder beschreven) geslacht *Cyathophorum*. Twee *Hypopterygium*-soorten worden van het geslacht *Hypopterygium* afgesplitst en ondergebracht in het nieuwe geslacht *Dendrohypopterygium*. Eén van deze twee soorten, *Dendrohypopterygium filiculiforme* (Fig. 4), is van de Hypopterygiaceae waarschijnlijk de soort met de meeste vooroudeerkenmerken.

Geschiedenis en geografische verspreiding

Door gegevens over de verspreidingsgebieden van soorten te combineren met de gereconstrueerde afstammingsgeschiedenis, kan een beeld verkregen worden van wat er in het verleden met de Hypopterygiaceae is gebeurd. De huidige verspreidingsgebieden van de Hypopterygiaceae zijn waarschijnlijk tot stand gekomen door een combinatie van continent verschuiving (met de daarop groeiende mossen) en verspreiding van sporen van Hypopterygiaceae in het verleden. Sporen van Hypopterygiaceae kunnen over grote afstanden worden verspreid door de lucht, maar kunnen door uitdroging en ultraviolette straling een transport over lange afstand niet overleven. Ver afgelegen en geïsoleerde eilanden en door oceanen omgeven landmassa's kunnen slechts bij hoge uitzondering door een levensvatbare spore van Hypopterygiaceae worden getroffen. Zo'n uitzonderlijke gebeurtenis heeft waarschijnlijk geleid tot het ontstaan van de soort *Hypopterygium sandwicense* op Hawaii.

De huidige verspreidingsgebieden van de Hypopterygiaceae wijzen op een oorsprong in Gondwanaland, het grote continent van het Zuidelijk Halfrond in het Krijt (135–65 miljoen jaar geleden). Het bestaan van drie soorten, waaronder *Dendrohypopterygium filiculiforme*, die alleen voorkomen op Nieuw Zeeland en nabij gelegen eilanden wijst er ook op, dat de Hypopterygiaceae heel oud zijn. Nieuw Zeeland is sinds 86–84 miljoen jaar geleden gescheiden van Gondwanaland en is sindsdien geïsoleerd gebleven. De Hypopterygiaceae zijn dan ook waarschijnlijk tenminste 84 miljoen jaar oud; misschien zijn ze veel ouder.

De huidige Hypopterygiaceae stammen waarschijnlijk af van een bodembegroeiende, boomvormige vooroudersoort van koelgematigde bossen op Gondwanaland in het Vroege Krijt of misschien zelfs de Late Jura. Waarschijnlijk trokken afstammelingen van deze vooroudersoort zich in de loop van het Krijt terug naar koelere (zuidelijker) streken en in berggebieden naar grotere hoogtes, als gevolg van het warmer wordende klimaat. De veranderende omstandigheden en opsplitsing van het oorspronkelijke verspreidingsgebied leidde tot de vorming van nieuwe soorten. Voor nieuwe soorten waren, door een hogere luchtvochtigheid en meer neerslag, grotere bladeren mogelijk en kwamen nieuwe, minder beschutte groeiplaatsen beschikbaar. Sommige afstammelingen van de bodembegroeiende, boomvormige, kleinbladige vooroudersoort ontwikkelden zich door deze processen tot bomen of rotsen begroeiende soorten met waaier- tot veervormig vertakte of onvertakte planten met grote bladeren. Mogelijk speelde de snelle opkomst van de bloemplanten in het Krijt met het verschijnen van veel nieuwe boomsoorten een grote rol bij de evolutie van op bomen groeiende Hypopterygiaceae.

De morfologische variatie die binnen sommige *Hypopterygium*-soorten wordt gevonden (*H. tamarisci*, *H. flavolimbatum* en *H. didictyon*) wijst waarschijnlijk op een nieuwe evolutionaire ontwikkeling als gevolg van het koeler wordende klimaat in het Kenozoicum (Tertiair + Kwartair, 65 miljoen jaar geleden tot heden).

Chapter 1

INTRODUCTION

The Hypopterygiaceae are a family of, usually attractive, pleurocarpous mosses. Despite distinct differences in growth habit between genera, the Hypopterygiaceae form a well-defined group of mosses, which is recognisable by a unique combination of features. All Hypopterygiaceae possess a complanate, anisophyllous foliation in, at least, the distal part of stems and branches, whereby the leaves are situated in three ranks: two rows of asymmetrical, lateral leaves, and a single, ventral row of smaller, symmetrical ones.

Hypopterygiaceae generally occur in humid forests, where they often grow on wet or shaded places. On places where Hypopterygiaceae occur abundantly, they especially draw attention by their prominent shape and large size, which results in conspicuous colonies. Most attractive are the large, terrestrial Hypopterygiaceae of southern South America, New Zealand, and the coastal regions of central eastern Australia. They have a striking appearance by a pronounced, dendroid habit, which is accentuated by the distinct, palmate- or umbrella-shaped frond.

The Hypopterygiaceae have a mainly Gondwanan distribution and occur in both the Palaeo- and Neotropics, the warm-temperate regions of the southern hemisphere and eastern Asia, and the more typical temperate areas along the western and north-eastern coast of the Pacific. As treated here, the family consists of 21 species. The greatest diversity of the family is found in Indo Malaysia (11 species) and Australasia (9 species). Africa and the New World are poor in species, with 3 and 5 representatives, respectively.

The low number of species makes it clear that the Hypopterygiaceae are a relatively small family. In the present study, the species are classified in 7 genera, whereby one of the existing genera, *Cyathophorella*, is merged with *Cyathophorum*, and two *Hypopterygium* species are transferred to the new genus *Dendrohypopterygium*. Three genera are monotypic: *Catharomnion*, *Canalohypopterygium*, and *Dendrocyathophorum*. *Lopidium* consists of 2 species. *Cyathophorum* and *Hypopterygium* are the largest genera, each containing 7 species.

The family shows a tremendous variation in morphology among various taxa. The most extreme forms of this variability are found on New Zealand, where the large, dendroid plants of the terrestrial species *Dendrohypopterygium filiculiforme* (Fig. 4) are strikingly different from those of the large, principally simple plants of the epiphytic and epilithic species *Cyathophorum bulbosum* (Fig. 46).

In addition to interspecific variability, several species show a great morphological plasticity, especially in the gametophore. A striking example for this intraspecific variability is found in *Hypopterygium didictyon*, whose dwarfish plants from the northern part of New Zealand differ completely in growth habit from the large and quite robust ones from southern New Zealand and southern Chile.

The high amount of intraspecific and interspecific variability in morphology resulted in the description of numerous superfluous taxa and hampered the systematic understanding and classification of, and within, the Hypopterygiaceae. Hitherto, c. 160 species and intraspecific taxa have been published. Identification proved often to be problematic and confusion on the identity and circumscription of species devalued several bryological studies. Consequently, the taxonomic chaos means a sincere threat for a reliable outcome of molecular studies which try to elucidate the phylogenetic relationships between taxa on the specific and generic level.

Hitherto, a monographic revision of the family as a whole does not exist and the literature is of little help to overcome these problems. Kindberg's (1901) world-wide treatment of the Hypopterygiaceae s.str. can hardly be considered a taxonomic revision, because it is not critical, and it mainly includes an enumeration of species and many subspecies, in particular in the treatment of *Hypopterygium*. Furthermore, Kindberg treated only a part of the family, because he had already excluded the Cyathophoraceae (represented by *Cyathophorum* in the present study) in 1898 (Kindberg, 1898).

Kindberg's (1901) highly hierarchic classification in genera, subgenera, sections, subsections, species, and subspecies reflects a fairly good insight in the systematics of the Hypopterygiaceae s.str. on the generic and subgeneric level, but is inadequate at lower levels. Kindberg's low level classification is highly artificial, whereby species and subspecies, which – in the present study considered to be either closely related or conspecific – were frequently classified in different (sub)sections.

More useful than Kindberg's (1901) 'revision' are several local treatments of the Hypopterygiaceae s.l. (e.g. Fleischer, 1908; Dixon, 1929; Bartram, 1939; Noguchi, 1951, 1952, 1991; Sainsbury, 1955; Matteri, 1973, 1975; Chopra, 1975; Whittier, 1976; Gangulee, 1977). Some of them include a critical revision of the local species (e.g. Fleischer, 1908; Noguchi, 1951, 1952; Matteri, 1973), but most of them are outdated and have limited value, because insight in the delimitations between the species and their mutual relationships from a world-wide view was missing. Brotherus' (1907, 1925) world-wide flora treatments hardly overcome this disadvantage of local floras, because Brotherus' works are not critical and, for the Hypopterygiaceae s.str., mainly based on Kindberg's (1901) 'revision'.

Since the seventies of last century the familial relationships of the Hypopterygiaceae s.l. have been discussed (e.g. Crosby, 1974; Buck & Vitt, 1986; Buck, 1987, 1988; Kruijer, 1995a, b, 1996c; Hedenäs, 1996a, b; Vitt, 1984), which resulted in a lack of consensus on the classification of the Hypopterygiaceae and totally different views on the relationships between the genera of the family and other pleurocarpous genera (see 'Family affairs', p. 20). Most important in this respect are the genera of the Hookeriaceae in the circumscription proposed by Hedenäs (1996b).

The aim of this study is to obtain a better understanding of the Hypopterygiaceae. It includes a phylogenetic study on the relationships within the Hypopterygiaceae s.l., the circumscription of the family, and the relationships of the representatives of the family with, in particular, representatives of the Hookeriaceae. In addition, it presents a world-wide, monographic revision of all extant Hypopterygiaceae based on morphological studies of herbarium material.

Chapter 2

MATERIAL AND METHODS

The present study is entirely based on the examination of herbarium material. In the course of this study over 9,300 dried herbarium specimens were examined from 41 institutional herbaria (abbreviations follow Holmgren et al., 1990): B, BM, BP (1 type), BR, CBG, CHR, COI, DR, E, EGR, F, FH, G, GRO (will become L), HBG, H-BR, HIRO, JE, KLU (2 specimens), KUMAMOTO (2 types), KYO, L, LISU, MEL, MO (4 specimens), NICH, NSW, NY, PC, PE, RO, S, SYD, TDC, U, UPS, W, WELT, Z, ZT, and MACQ (Macquarie University, School of Biological Sciences, Sydney; not listed by Holmgren et al., 1990). The loan from CHR contained a representative selection of their specimens of *Canalohypopterygium*, *Dendrohypopterygium*, and *Hypopterygium*. The loan from SYD included the voucher specimens of Ramsay's (1967a) study on intraspecific levels of polyploidy in *Hypopterygium tamarisci* (as *H. rotulatum*). The material examined includes voucher specimens that were used for molecular studies by Frey and co-workers (Frey et al., 1999; Stech et al., 1999; Pfeiffer, 2000; Pfeiffer et al., 2000) and are preserved in Frey's personal herbarium ('hb. Frey').

Specimens were grouped by similarity and continuity (overlap) in the character states of their morphological characters. Following the rules and recommendations in herbarium taxonomy for plant taxonomists as formulated by Van Steenis (1957), species were distinguished when any two of such groups differ from each other by a perfect morphological discontinuity, i.e. showing morphological gaps between character states, in at least two independent characters. Differentiating characters were assumed a) to be independent in morphological-ontogenetic sense, and b) to represent the same ontogenetic stage. Where possible, species were distinguished by differences in states of both gametophytic and sporophytic characters.

Groups of specimens showing imperfect morphological discontinuities (e.g. low frequencies of overlap) and/or discontinuities based on related characters were considered to be conspecific. These groups include groups of specimens showing only a single morphological discontinuity and those showing a few morphological discontinuities that are almost certainly artificial due to undercollecting of intermediates or overcollecting of asexually reproduced clones. For the recognition of conspecific groups of specimens as formal intraspecific taxa the following criteria were used: 1) the majority of the specimens in the groups of specimens are – as subsets – morphologically distinct and show morphological discontinuity in one or more character states (the minority of the specimens being intermediates or showing overlap), and 2) the groups of specimens show ecological and/or geographical separation (for the recognition of varieties and subspecies).

Unless indicated otherwise, names and combinations cited throughout the present study are understood as in the circumscription of the present study.

Special attention was paid to unravel nomenclatural problems and to give insight in historical and taxonomical confusion. Names and combinations are given in groups of homotypic synonyms. The groups are arranged in order of priority and chronology, whereby the group that includes the correct name or combination is given first, and is followed by groups of taxonomic synonyms. Groups based on illegitimate or invalid names are presented after the legitimate ones. Names and combinations within a group of homotypic synonyms are ordered in a similar way, whereby the basionym (if legitimate) is given first. The first group of homotypic synonyms in a series of taxonomic synonyms is, of course, presented below the correct name or combination of the taxon involved.

The nomenclature was consistently checked from original literature. Valid names or combinations are immediately followed by the citation of the publication (or exsiccata series) in which they were validly published at first and are given in chronological order. Concerning illegitimate and invalid names based on the same original material, only the oldest publication is given, unless the more recent ones are more commonly known or contributed to bryological knowledge or confusion. Abbreviations of authors follow Brummitt & Powell (1992). Abbreviations of book titles follow Stafleu & Cowan (1976–1988); abbreviations of journals follow Lawrence et al. (1968) and Bridson & Smith (1991). The citation of type material is as complete as possible. Nomenclatural notes give additional information. Symbols for and abbreviations of nomenclatural comments follow Van der Wijk et al. (1959–1969).

The treatments of species include references of illustrations published in preceding publications. Every illustration that is cited has been checked and reflects a correct illustration of the species involved, and is based on material that belongs to this taxon. Cited illustrations could beyond any doubt withstand a critical comparison with the taxon involved in the present circumscription. Illustrations that could not pass this test with absolute certainty are marked with a question mark.

Morphological and anatomical research was carried out according to common practice in bryology. Unless indicated otherwise, specimens were examined in moist conditions. Material for slides were soaked in water to obtain detailed measurements and qualitative character states used in the descriptions and the cladistic analyses. The drawings that are given here were made after rehydrated herbarium material. Descriptive terminology follows Magill & Stotler (1990) unless reported otherwise. The features given in the species descriptions are based on the examination of a representative number of specimens, selected from different regions in the distribution area of the species. Aberrant specimens have not been included in the descriptions. Descriptions of higher taxa are composed from the descriptions of the species that they include.

Plant sizes and length of axes are given in centimetres. Four informal categories of plant size have been used: very small (not exceeding 1.0 cm), small (up to 1.5 cm tall), medium-sized (1.5–4.0 cm), large (more than 4.0 cm).

Size and habit features of specimens were examined and analysed with the aid of a stereo microscope and a light microscope. The frond shapes refer to the outline of the fronds (in a single plane). The frond sizes are measured across the longest diameter of the fronds. Axes, leaf arrangement, and leaves from various parts of the gametophores were examined and are treated separately for the various parts in the descriptions where useful and appropriate.

Unless indicated otherwise, the leaf features given in the descriptions refer to leaves that are situated in the middle parts of the stem or branch to which they are attached. Leaf shapes and sizes of acuminate leaves do not include the acumen. The costa length is given as a fraction of the length of the leaf. Protrusions, like serrations and acumina, are measured from where they protrude from the leaf margin to their top.

The shape of leaf cells is given in surface view. The shape of cells in filamentous structures (viz. axillary hairs, gemmae, paraphyses) is given in side view. Sizes of cells and other structures that are only visible at the microscopic level are given in µm. Cell measurements include the lumen and the wall of the measured cell. Descriptive terminology of cell shape and relative cell length (length/width ratio) follows Touw & Rubers (1989). The axis structure was examined by making cross sections of the middle part of the axis by hand using single edged razor blades.

Axillary hairs of stems and branches were described after removing leaves. For practical reasons, no attempt was made to examine axillary hairs that are attached to stolons, because these hairs are almost impossible to find in the tomentum. Unless reported otherwise, features of axillary hairs are given for those in the middle parts of the stem or, when appropriate, in the middle parts of the main frond axes. Cell sizes are only given for the terminal cells of the axillary hairs. Axillary hairs of gametoecia are treated as part of the gametoecia.

Shapes and sizes of leaf cells were obtained from cells that are situated in the median third part of the lamina between the costa and the border (or leaf margin in unbordered leaves), but at least two cell rows besides these leaf structures.

Shapes, sizes, and other features described for gametoecial leaves are obtained from full grown, inner (distal) gametoecial leaves. For the qualitative and quantitative observations of gametoecial axillary hairs, parafyses, and gametangia, the gametoecial leaves were removed from the gametoecial axis.

Sporophyte and calyptra features were obtained by the examination of mature sporophytes. Shapes and sizes given for capsules do not include operculae, which are described separately. Descriptions of the direction of the capsule with respect to the seta follows Touw & Rubers (1989). The terminology of the peristomial layers and the notation of the peristomial formula follows Edwards (1979).

The length of the exostome teeth and the processes are measured from the orifice. Measurements of the thickness of the dorsal and ventral plates of exostome teeth include their ornamentation. The height of the basal membrane is measured from the orifice to the base of the processes. It is given as a relative measure as the proportion of the length of the exostome teeth.

In addition to light microscopic studies, the structure and ornamentation of the peristomes, and the ornamentation of the spores, were examined by using scanning electron microscopy (SEM). To prepare peristomes for SEM selected capsules were soaked in water, and sectioned to obtain relevant parts. The material was preserved in 50% ethyl alcohol for half an hour and, subsequently, brought in dimethoxymethane (DMM) after rinsing the material two times 30 min. with DMM. After treatment in a critical point dryer (Balzers CPD 030), the material was coated with gold using a Polaron SEM Coating Unit E5100 (which has been replaced by a BAL-TEC SCD 005 Sputter Coater during research). SEM observations were made with a JEOL JSM

35 microscope, later on by a JEOL JSM-5300 microscope (15 kV, 20–25 mm). Eastman Kodak Tmax-100 (TMX 120) film (100 ASA/21°) was used for photography.

Reconstructions of the geographical distribution of species are presented in maps and are based on the specimens examined. For taxa of which less than 175 specimens were examined, all specimens are cited. A representative selection is given for species of which a higher number of specimens was examined. Where possible, geographical records of taxa given in bryological literature were checked. In cases where no original material of such records was available, a literature reference was given.

The geographical distributions of all species are listed according to countries, grouped per continent and floristic region and given from north to south and west to east. The geographical names are given as up to date and accurate as possible using various sources of information, including 'The Times Atlas of the World' (mid-century edition, vol. 1–5, 1955–1959; comprehensive editions, 1967, 1992), the United States Office of Geography's 'Official Standard Names' gazetteer volumes for the various countries (1952–1974, and 1999–2000 internet versions: http://164.214.2.59/gns/html/index.html), the 'Australia 1:250,000 Map Series Gazetteer' (1975), and various other atlases and maps. Phytogeographic regions are based on Good (1974: 30–32, pl. 4) with a few modifications based on Van der Wijk et al. (1959), Van Balgooy (1971), Piippo (1992), and Piippo & Koponen (1997) for, in particular, South America, Asia, and Australasia. These modifications result in the following phytogeographic regions: South America: southern South America includes Chile and Argentina; western South America includes Andean South America north of Chile and Argentina and mountaineous NW Colombia and Venezuela; south-eastern South America includes Paraguay, Uruguay, and SE Brazil; South and East Asia: Sino Japan includes China, Taiwan, N and S Korea, SE Siberia, and Japan; Indo Malaysia includes the Indian subcontinent, continental SE Asia (Burma, Thailand, Indochina), and Malesia; Malesia includes Malaysia, Brunei, Indonesia, the Philippines, Papua New Guinea, and the Solomon Islands. As a sequel to this, Australasia (often considered to include New Guinea and the Solomon Is.) is defined here as consisting of Australia, New Caledonia, New Zealand and neighbouring islands. The term Oceania is used for the tropical and near-tropical Pacific Islands north and east of the Solomon Islands and New Caledonia. The subdivision of New Zealand follows Raven & Raven (1976). Old locality names of East Africa were checked using Polhill (1970). Old locality names of the Dutch East Indies were checked using the 'Atlas van Tropisch Nederland' (1938) and Van Steenis-Kruseman (1950).

The ecological data are given here as accurately as possible, but one should bear in mind, that they are obtained from herbarium labels, which often contain insufficient or ambiguous information. Information that with certainty is erroneous was omitted.

Chapter 3

HISTORY

INTRODUCTION

The Hypopterygiaceae were formally established as a separate moss family in 1859 by Mitten, but they had before already been recognised as a distinct taxon by Bridel (1827, 'Hypophyllocarpi') and Müller (1850–1851, 'Tristichophylla'), albeit in a broader sense.

The taxonomic history of the Hypopterygiaceae followed the general trends in bryological history, in particular that of exotic bryophytes, and actually started several decades before, when in the second half of the 18th century the first exotic moss specimens were collected during the world exploring expeditions of the European powers, at that time mainly England and France.

EARLY SPECIMENS

The first scientific collection of a member of Hypopterygiaceae was made by Commerson during the French Bougainville expedition in 1766–1769 (Menzel, 1988; Marticorena, 1995). In the summer of 1767–1768, Commerson collected plants in the coastal regions of the Magellan Straits in southern South America, whereby, in December 1767, he also collected the moss *Dendrohypopterygium arbuscula*, presumably only once and from one single locality. It was, however, not until 1805 before Commerson's finding was published by Palisot de Beauvois, who recognised in this plant a new moss species (Palisot de Beauvois, 1805). Palisot de Beauvois classified his new species in *Hypnum* and described it as *Hypnum arbuscula*, which is nowadays considered an illegitimate homonym.

Less than two years later, Banks and Solander collected a few Hypopterygiaceae on the Eastern Hemisphere during Cook's first voyage, an English expedition during 1768–1771. They collected material of *Dendrohypopterygium filiculiforme* in August 1769 and of *Cyathophorum bulbosum* on an unknown date. The labels of these specimens (in BM) provide no information about their origin, but according to Müller (1850–1851), the collections were made in 'Insulae Australes', which almost certainly denotes New Zealand here. Banks or Solander may also have collected material of *Hypopterygium didictyon* and *Canalohypopterygium tamariscinum* during Cook's voyage. A single specimen of *Hypopterygium didictyon* in the material of BM is attributed to Banks and Solander. This specimen, under the name '*Hypnum rotulatum*', is annotated to come from Tasmania, but Banks and Solander never visited this island, and mislabelling must have taken place. One of two early New Zealand specimens of *Hypopterygium didictyon* in S, likewise labelled '*Hypnum rotulatum*', was apparently a gift from Banks in 1783, but it is not known by whom and when it was collected. The other, present under a herbarium name in Ångström's herbarium, is annotated as being collected by Banks. It is mixed with a scrab of *Canalohypopterygium tamariscinum*. Hence, the possibility that Banks or Solander actually made separate collections of the latter species cannot be ruled out. Three specimens of *Canalohypopterygium tamariscinum* lacking a collector's name in BM (two from Dickson) and W (one from Swartz), possibly represent specimens of such collections.

Between 1768 and 1773, after the Bougainville expedition sailed home to France in 1768–1769, Commerson stayed behind on Mauritius, and collected the first specimens of *Lopidium struthiopteris* on Mauritius ('Ile de France') and Réunion ('Bourbon'). The year, date, and sequences of collecting of these findings are not reported, but it is known that in this period Commerson spent most of his time on Mauritius, from where he visited Madagascar in 1770 and Réunion in 1771. In the latter year he returned to Mauritius, where he stayed till his death in 1773 (Van Steenis-Kruseman, 1950; Stafleu & Cowan, 1976). It is, therefore, highly likely that the material from Réunion, upon which Bridel (1812) based his newly described species *Hypnum struthiopteris*, was collected in 1771.

During Cook's second voyage in 1772–1775, G. Forster collected a few specimens of *Hypopterygium didictyon* in 'Australasia' and *Cyathophorum bulbosum* in Dusky Bay, New Zealand. The specimen of *Hypopterygium didictyon* is nowadays preserved in BM, the one of *Cyathophorum bulbosum* is preserved in S. In the same period, Thunberg collected material of *Lopidium struthiopteris* (Brid.) M.Fleisch. in the Cape of Good Hope (Thunberg, 1800). Swartz collected material of *Hypopterygium tamarisci* on Jamaica between 1784 and 1786 (Swartz, 1788). Based on this material, Swartz described the new species *Hypnum tamarisci* in 1788, by which it is the first species of the present Hypopterygiaceae. Swartz' name is invalid (pre-starting-point), but he validated his species by describing the species again eighteen years later in 1806 (Swartz, 1806), a few years after the starting point of the nomenclature of Musci with the publication of Hedwig's (1801) 'Species muscorum frondosorum'.

Between 1790 and 1800, several collections of Hypopterygiaceae arrived in Europe as a result of collecting activities of Menzies (Vancouver's voyage, 1791–1795), De Labillardière and Ventenat (Bruny d' Entrecasteaux' voyage, 1791–1794), and Thunberg (1772–1775). The diversity of the Hypopterygiaceae is best shown by Menzies' collections, which contain material of *Cyathophorum bulbosum* (New Zealand), *Hypopterygium sandwicense* (Hawaii Is.), *Hypopterygium didictyon* (New Zealand, Australia, Tasmania), *Hypopterygium laricinum* (= *Hypopterygium tamarisci*; Cape of Good Hope), *Lopidium concinnum* (New Zealand), and *Dendrohypopterygium filiculiforme* (New Zealand). De Labillardière (and Ventenat) collected material of *Cyathophorum bulbosum* and *Hypopterygium didictyon* in Australia and Tasmania.

Despite the rather large number of exotic collections made in the 18th century, little is known about the fate of these specimens in the first decades after their arrival in Europe. Swartz (1788) and Thunberg (1800) worked out their own material. Palisot de Beauvois (1804, 1805) remarked, that he once owned specimens of *Cyathophorum bulbosum*, referred to as *Cyathophorum pteridioides* P. Beauv., which he had received from Dickson in 1784. Palisot de Beauvois' material was very probably collected by Banks or Solander, but material that had been collected by R. and G. Forster (Cook's second voyage, 1772–1775) or either Andersson or Nelson (Cook's third voyage, 1776–1780) cannot be ruled out. Most likely, Palisot de Beauvois' specimens came from New Zealand, but Australia is also a possibility.

HEDWIG, AND EARLY BRYOLOGY OF EXOTIC BRYOPHYTES

When the first exotic moss specimens arrived in Europe in the first decades of the second half of the 18th century, bryology was still a young branch of science. Little was known about the European bryophytes, and almost nothing about bryophytes on a world-wide scale. The circumscription and delimitation of the Musci and Hepaticae was still in a state of flux, mainly because the sexual reproduction of bryophytes was a mystery until Hedwig's (1784) microscopical studies on the sexual organs and the ontogeny of the sporophyte and the calyptra unravelled partly the life cycle of bryophytes. Hedwig's work significantly increased the interest in bryophytes in the last decades of the 18th century.

Johann Hedwig (*1730–†1799) was one of the most outstanding and famous bryologists of his time. His work lead to new insights in the systematics of bryophytes, and was followed, amongst others, by Bridel (1797, 1798–1803, 1806, 1812, 1817). Hedwig's classification of bryophytes was published in his posthumous 'Species muscorum frondosorum', which was edited by Schwägrichen and published in 1801. Hedwig described five new species that belong to the present moss family Hypopterygiaceae: *Anictangium bulbosum*, *Pterigynandrum ciliatum*, *Leskea filiculiformis*, *Leskea tamariscina*, and *Leskea rotulata*.

Despite the reasonable number of early collections of exotic bryophytes, the relatively late development of bryology as a botanical science seems to be an explanation for the remarkably low number of publications on exotic mosses in the second half of the 18th century. In addition, the identification of bryophytes – which usually meant the description of an hitherto unknown species – had presumably low priority during working out botanical collections from Africa, South America, the Pacific, and Australasia. The limited economic value of bryophytes may be the main reason for this.

The study and identification of exotic mosses in this early period might also have been hampered by a slow exchange of precious duplicates of bryophyte collections between the few European botanists with an interest in bryology or cryptogamic plants in general. The French Revolution, 1789–1799, and the turbulent period afterwards, caused an economic decline and a difficult period for scientific progress in Europe (cf. Margadant, 1968). During the French Revolutionary Wars, 1792–1801, and the following era of Napoleonic Wars until Napoleon's final defeat in 1815, transport possibilities were limited, resulting in a dramatic reduction of publication facilities, collecting possibilities, and correspondence, in particular between Great Britain and the European continent. Shipping collections was a risky undertaking. For instance, the French expedition of Bruny d' Entrecasteaux, which was joined by De Labillardière and Ventenat, sailed from Brest to the East in search for 'La Pérouse' in 1791 and ended on Java in 1794, where the crew, including De Labillardière and Ventenant, was imprisoned by the Dutch East Indian Government and the ship was captured. De Labillardière's collections, which included Australian material, were sold as war prize to England, but returned to De Labillardière after his repatriation to France in 1796 through Banks (Van Steenis-Kruseman, 1950; Mabberley, 1985). Almost contemporary, Palisot de Beauvois lost several West African, Caribbean, and North American collections in overseas transport (Margadant, 1968).

Consequently, the present Hypopterygiaceae and other exotic mosses, became only slowly better known in the first two decades of the 19th century. Collections of Hypopterygiaceae that were collected in the last decade of the 18th and the first of the 19th century were worked up and published by Bridel (1797, 1798–1803, 1806, 1812, 1817, 1819), De Labillardière (1806), Smith (1808), Schwägrichen (1811, 1816), and Hooker (1818–1820). In this period only a few new species were described. Among them was De Labillardière's *Leskea pennata* from 'Van Diemensland' (Tasmania), which Smith (1808) already recognised as being conspecific with Hedwig's (1801) *Anictangium bulbosum* from 'Insulae Australes'.

In 1804, Palisot de Beauvois, who was opposed to Hedwig's classification system (Palisot de Beauvois, 1804, 1805; Lamy, 1989), described the monotypic genus *Cyathophorum* based on Hedwig's (1801) *Anictangium bulbosum*, but it lasted several years before the genus *Cyathophorum* became generally accepted. Smith (1808) was the first who noticed a resemblance between Hedwig's *Anictangium bulbosum* and Hedwig's *Leskea filiculiformis*, *Leskea tamariscina*, and *Leskea rotulata*, and transferred them to his new genus *Hookeria*.

POST-NAPOLEONIC ERA

After the Napoleonic era in the first decades of the 19th century, the conditions for science improved. West European countries took greater interest in the flora of their colonies, potential colonies, or trading partners overseas. From the 1830s onwards the United States of America became active in the exploration of exotic floras. Throughout the 19th century, bryophyte collections were made in increasing numbers by various collectors (e.g. Andersson, Balansa, Griffith, Hildebrandt, Hooker f., Moritz, Nadeaud, Teijsmann, Thwaites) and were often widely distributed among bryologists.

Most important in this period were the systematic changes. Better understanding of sexual reproduction in bryophytes modified the view about the value of reproductive characters for classification systems. Better microscopes became available (Margadant, 1968), and features of mosses could be studied with greater accuracy and precision. Hence, microscopic features and gametophytic characters, became more and more important in the delimitation of species and classification systems.

Throughout the 19th century, numerous moss species were described. Many of them were based on the examination of only a few specimens. In combination with the often slow access to new literature and probably also due to the disproportional importance that most contemporary bryologists gave to minor microscopical details, this resulted in the description of many local moss 'species'.

An important trend in bryology in the first half of the 19th century was the development of a natural classification, especially in the third decade (cf. Margadant, 1968). Most important for mosses was the work by Bridel (*1761–†1828). Bridel (1797, 1798–1803, 1806, 1812, 1817) first closely followed Hedwig's classification systems (Hedwig, 1785–1787, 1789, 1791–1792, 1797, 1801), but since 1819 he developed a new classification of mosses. In 1827, a year before his death, he proposed a completely new classification system of the mosses in his 'Bryologia universa' (Bridel, 1827).

'BRYOLOGIA UNIVERSA' AND 'SYNOPSIS MUSCORUM FRONDOSORUM'

In his 'Bryologia universa', Bridel (1827) gave an overview of the Hypopterygiaceae that were known by 1827 and came to 9 *Hypopterygium* species and 1 *Cyathophorum* species. Bridel's work had important consequences for the concept of Hypopterygiaceae. He established the genus *Hypopterygium* and accepted Palisot de Beauvois' *Cyathophorum* as a monotypic genus to encompass De Labillardière's *Leskea pennata* and Hedwig's *Anictangium bulbosum*, which he considered conspecific. The correct combination *Cyathophorum bulbosum* was made later on by Müller (1850–1851).

Bridel (1827) also made a first attempt to produce a higher classification. He classified *Hypopterygium* and *Cyathophorum*, together with *Racopilum* P. Beauv., in the 'ordo' Peristomi of his 'classis' Hypophyllocarpi (≡ Hypopterygoc[arpi]), by which Bridel proposed an early delimitation of what later became the family Hypopterygiaceae. He classified *Helicophyllum* Brid. in the same 'classis', but placed this genus in his 'ordo' Gymnostomi (≡ Astomi).

In 1850, Müller (1850–1851) published a detailed and updated overview of the species of the Hypopterygiaceae, and treated 6 species that had been newly described after the publication of Bridel's (1827) 'Bryologia universa'. Müller mainly followed Bridel's classification of the present Hypopterygiaceae, and included *Racopilum* as a separate section in the genus *Hypopterygium*. Müller doubted, however, Bridel's classification of *Helicophyllum*. In 1850, he treated this genus as a 'genus incertum' and eventually excluded *Helicophyllum* from his Tristichophylla (Hypopterygiaceae + *Racopilum*) in his classification scheme of 1851 (Müller, 1850–1851).

THE SPLITTING OF CYATHOPHORUM

In Bridel's (1827) and Müller's (1850–1851) time *Cyathophorum* was generally regarded as a monotypic genus, but after 1854 several new species were placed in this genus. Wilson (1855) recognised three varieties in *Cyathophorum*'s single species of that time. A few years later, Mitten (1859) transferred two *Neckera* species from the East Indies, which had been described by Griffith (1849a, b), to *Cyathophorum*, and described a new one from the Himalayas (*C. intermedium* Mitt.). Shortly after, Van den Bosch & Van der Sande Lacoste (1861) described two new *Cyathophorum* species from Java. In the last three decades of the 19th century, other authors described a few new *Cyathophorum* species from Sri Lanka (Mitten, 1873), New Guinea (Müller, 1896), Tasmania (Brotherus, 1893), and Tahiti (Bescherelle, 1895).

Brotherus (1907) distinguished two separate sections in *Cyathophorum*. He classified the Indo Malaysian and Pacific species – with the exception of the New Guinean species *Cyathophorum loriae* Müll.Hal. – in section *Cyathophorella*, and the Australasian species, including *Cyathophorum loriae*, in section *Cyathophorum* ('*Eu-Cyathophorum*'). Fleischer (1908) raised Brotherus' section *Cyathophorella* to the generic level. Fleischer, furthermore, removed *Cyathophorum loriae* Müll.Hal. from *Cyathophorum*, and suggested that it should be placed in *Cyathophorella*, which suggestion was followed by Brotherus (1925). From 1908 onwards several new Asian and African species have been placed in the *Cyathophorella* lineage by Fleischer and other authors.

The new species were either originally described as *Cyathophorum* species and shortly afterwards transferred to *Cyathophorella*, or directly described as a *Cyathophorella* species. The most recently described *Cyathophorella* species is *Cyathophorella taiwania* by Lai (1976).

THE SPLITTING OF HYPOPTERYGIUM

In 1854, the genera *Catharomnion* and *Lopidium* were separated from Bridel's (1827) *Hypopterygium* by Hooker f. & Wilson (Wilson, 1855), but it lasted several years before these genera became generally accepted. Even Hooker f. (1867) included them in *Hypopterygium* in his 'Handbook of the New Zealand Flora'. Consequently, Mitten (1882) treated *Catharomnion* as a section of *Hypopterygium*. Kindberg (1901) resurrected *Catharomnion* as a separate genus.

Van den Bosch & Van der Sande Lacoste (1861) and Mitten (1869) considered *Lopidium* a subgenus and a section of *Hypopterygium*, respectively. It was not until 1908, before *Lopidium* was resurrected as a separate genus by Fleischer. He distinguished *Lopidium* from *Hypopterygium* by its more or less horizontal gametophore, its leaves with a percurrent (to excurrent) costa, and its small, subcircular laminal cells with incrassate walls. By contrast, he characterised *Hypopterygium* by ascending gametophores and the presence of leaves that have a shorter costa, ending below the leaf apex, and have elliptic-hexagonal to rhomboid thin-walled laminal cells.

Kindberg (1901) proposed a new classification within *Hypopterygium* and recognised 4 subgenera. His subgenus *Hypopterygium* ('*Eu-Hypopterygium*') corresponds with the present genus *Hypopterygium* and is basically artificially divided in 4 sections and 4 subsections. Likewise, subgenus *Lopidium* corresponds with the present genus *Lopidium*. Subgenus *Filiculoides* extended with the South American representative of subgenus *Stephanobasis*, i.e. *Hypopterygium thouini* Schwägr., corresponds with the present genus *Dendrohypopterygium*. The New Zealand representative of subgenus *Stephanobasis*, *H. setigerum* (P. Beauv.) Wilson, belongs to *Canalohypopterygium*, which was recognised as a new, monotypic genus by Frey & Schaepe (1989).

In 1913, Cardot (1912) recognised a new section in *Hypopterygium*, the section *Eurydictyon*. This section was raised to generic level by Horikawa and Noguchi (Noguchi, 1936b) and Dixon (1936), and is known as *Dendrocyathophorum* (Dixon, 1937).

FAMILY AFFAIRS

When Kindberg (1898) proposed a new classification of the pleurocarpous mosses, he separated the Cyathophoraceae Kindb. from the Hypopterygiaceae as a separate, 'analogous' family. Consequently, *Cyathophorum* is not included in Kindberg's (1901) revision of the Hypopterygiaceae s.str. Fleischer (1908) considered Kindberg's families nothing more than two subdivisions within a single family. Fleischer (1908) classified these subdivisions as tribes. Fleischer was followed by Brotherus (1925), who raised Fleischer's tribes to the subfamily level.

In Brotherus' (1925) classification system, the subfamily Hypopterygioideae included the present genera *Canalohypopterygium*, *Catharomnion*, *Dendrocyathophorum*, *Dendrohypopterygium*, *Hypopterygium*, and *Lopidium*, whereas the subfamily Cyathophoroideae (Kindb.) Broth. included the present genus *Cyathophorum*.

In the Fleischer–Brotherus system, the two subdivisions of the family were distinguished by differences in the ramification of the gametophore, the seta length, and the direction of the capsules. The Hypopterygioideae were characterised by pinnately branched stems, long setae, and usually nodding to pendulous capsules. The Cyathophoroideae were characterised by simple or weakly dichotomously branched stems, short setae, and erect capsules. The sporophytic differences observed by Brotherus and Fleischer are mainly a result of differences in the direction of the sporophytes. Sporophytes of Hypopterygioideae are projecting above the gametophore, and are generally ascending or vertical, whereas sporophytes of Cyathophoroideae are generally projecting downwards from the gametophore and are thus horizontal or descending.

Fleischer (1908, 1923a) and Brotherus (1925) placed the Hypopterygiaceae s.l. as a single family within the order of the Hookeriales (M. Fleisch.) M. Fleisch. In their concept, this order included 6 families, of which the Hookeriaceae Schimp. are most important with respect to the discussion on the relationships and the delimitation of the Hypopterygiaceae.

In the Fleischer–Brotherus system, the Hookeriaceae included 35 genera distributed over 4 subfamilies (Daltonioideae, Distichophylloideae, Hookerioideae, Hypnelloideae); an overview was presented by Crosby (1974). Since 1974, several 'hookeriaceous' genera have been proposed as being related to 'hypopterygiaceous' genera: *Achrophyllum* Vitt & Crosby (in the Fleischer–Brotherus system placed in the Hookeriaceae subfam. Distichophylloideae), *Calyptrochaeta* Desv. (subfam. Distichophylloideae), *Hookeria* Sm., and *Schimperobryum* Margad. (both subfam. Hookerioideae).

The Fleischer–Brotherus scheme of the Hypopterygiaceae was followed for nearly 50 years, until 1971, when Miller treated Brotherus' (1925) subfamilies of the Hypopterygiaceae s.l. again as separate families. Miller's (1971) act was, however, nothing more than a change of rank, because he still considered the Cyathophoraceae closely related to the Hypopterygiaceae s.str., and arranged them both in his suborder Hypopterygiineae H.A. Mill. It has to be remarked, however, that Miller apparently overlooked *Dendrocyathophorum*, which among the Hypopterygioideae shows most resemblance with the Cyathophoroideae.

Miller's (1971) publication started a broad discussion about the familial relationships and delimitation of the Hypopterygiaceae s.l., and the systematic position of its genera.

In 1974, Crosby proposed an entirely modified classification. Based on peristome characters, he (1974) transferred the genera *Cyathophorella* and *Catharomnion* to an informal catharomnioid group in the Daltoniaceae Schimp., and the remaining genera of the Hypopterygiaceae, with *Calyptrochaeta* in a cyathophoroid group of the Hookeriaceae.

Vitt (1984), on the other hand, maintained *Cyathophorum* and *Cyathophorella* in the Hypopterygiaceae, but transferred *Dendrocyathophorum* to the Hookeriaceae.

Buck & Vitt (1986) transferred the Hypopterygiaceae, including *Cyathophorum*, to the order of the Bryales M. Fleisch. and placed the family close to the Racopilaceae Kindb. and the Helicophyllaceae Broth. After evaluation of the genera, Buck (1987, 1988) placed *Cyathophorum*, *Cyathophorella*, and *Dendrocyathophorum* in the Hookeriaceae, which included *Achrophyllum*, *Hookeria*, and *Schimperobryum*. Buck (1987) centred the first three genera in a lineage around *Cyathophorum*, and the last three in a lineage around *Hookeria*. It should be remarked, however, that in Buck's studies apparently only *Cyathophorum* and *Hypopterygium* were examined.

Whittemore & Allen (1989), using Buck's (1987) delimitation of the Hookeriales s. str., arranged *Cyathophorum* and *Cyathophorella* in the Daltoniaceae, together with *Achrophyllum*, *Calyptrochaeta*, and other genera. Whittemore & Allen, however, emphasised the similarities between the Hypopterygiaceae and, in particular, *Cyathophorum* and *Cyathophorella*, and remarked that the traditional classification of the Hypopterygiaceae s.str. in the Hookeriales may be correct. In addition, they remarked that *Dendrocyathophorum* further connects *Cyathophorum* and *Cyathophorella* with the Hypopterygiaceae. Tan & Robinson (1990) considered Buck's (1987) classification of *Cyathophorum*, *Cyathophorella*, and *Dendrocyathophorum* as controversial, and preferred to keep these genera in or near the Hypopterygiaceae s.str.

Kruijer's (1995a, b) phylogenetic analyses – early precursors of the phylogenetic studies presented in the chapter 'Phylogeny' (p. 59) of the present study – suggested that the Hypopterygiaceae s.l. are polyphyletic. *Cyathophorum*, represented by *C. bulbosum*, *C. tahitense*, *C. spinosum*, and *C. adiantum*, was found in a terminal position of the trees and nested in a clade which consisted of representatives of Hookeriaceae and Daltoniaceae. The remaining species of the Hypopterygiaceae constituted a distantly related monophyletic group, which included the three species of the former genus *Cyathophorella* (*C. africana*, *C. hookeriana*, *C. parvifolia*). The analyses, however, were hampered by much homoplasy. After re-evaluation of the characters, subsequent cladistic analyses supported the monophyletic status of the Hypopterygiaceae s.l. (Kruijer, 1996c).

Hedenäs (1994, 1995, 1996a, b) analysed the higher level phylogenetic relationships between diplolepidous pleurocarpous mosses by a step by step approach in studies using a balanced selection of various morphological characters of the gametophyte and sporophyte. He found that in the trees the representatives of the Hypopterygiaceae have either a basal position in the pleurocarpous mosses or are connected to the Hookeriaceae. Hedenäs (1994) presented an overview of the relationships within a selected group of basal diplolepidous pleurocarpous mosses, and found *Hypopterygium*, represented here by *H. didictyon* and *H. arbuscula* (≡ *Dendrohypopterygium arbuscula*), to be the sister group of *Cyclodictyon laetevirens* (W. Hook. & Taylor) Mitt., his representative of the Hookeriaceae. This *Hypopterygium–Cyclodictyon* clade is nested in a monophyletic clade with representatives of the Leucodontales (M. Fleisch.) W.R. Buck & Vitt and Hypnales (M. Fleisch.) W.R. Buck & Vitt (sensu Buck & Vitt, 1986). The latter clade was subject of a subsequent study (Hedenäs, 1995), in which the position in the trees of the representative of *Hypopterygium* (*H. arbuscula*) was rather far removed from that of the representatives of the Hookeriaceae (*Distichophyllum mittenii* Bosch & Sande Lac., *Hookeria lucens* (Hedw.) Sm., *Hookeriopsis crispa* (Müll. Hal.) A. Jaeger) and close to that of the representatives of the Leucodontales (*Homalia lusitanica* Schimp.) and Hypnales (*Thamnobryum maderense* (Kindb.) Hedenäs). However, in several trees, Hedenäs found *Hypopterygium arbuscula* in a basal position to all diplolepidous pleurocarpous mosses.

Next, Hedenäs (1996a, b) focussed on the phylogenetic relationships within the Hookeriales, the Sematophyllaceae Broth. and some related taxa. He found that the Hypopterygiaceae – represented by *Cyathophorum bulbosum*, *Hypopterygium arbuscula*, and *H. laricinum* – constitute a monophyletic group, which is nested at a basal position in the Hookeriaceae-clade. Consequently, Hedenäs (1996b) proposed a classification of the taxa of the Hypopterygiaceae within the Hookeriaceae.

Newton & De Luna (1999) studied the transition to pleurocarpy in mosses and used a different selection of species, a partly different set of characters, and a different way of coding than used by Hedenäs. In their phylogenetic trees, they found *Hypopterygium tamarisci* – their only representative of the Hypopterygiaceae – in a basal position to most other pleurocarpous mosses, but at a distant position from *Hookeria*.

The phylogenetic analyses of De Luna et al. (1999), based on *rbcL* sequences and using an almost similar selection of diplolepidous mosses as Newton & De Luna (1999) did, resulted in trees with *Hypopterygium tahitense* (= *H. tamarisci*) and *Hypopterygium tamarisci* in a single clade with *Hookeria*. Analyses of a combined set of the morphological and molecular data of Newton & De Luna (1999) and De Luna et al. (1999) resulted in two most parsimonious trees with *Hypopterygium tamarisci* at a basal position in a clade with *Fontinalis* L. ex Hedw. and *Hookeria*. This clade is nested at a basal position in a clade with representatives of the Leucodontales (*Leucodon* Schwägr., *Neckera* Hedw., *Papillaria* (Müll.Hal.) Müll.Hal., *Prionodon* Müll.Hal., *Pterobryon* Hornsch.) and Hypnales (*Brachythecium* Schimp., *Pleurozium* Mitt., *Thuidium* Schimp.).

Cox et al. (2000), who studied the phylogenetic relationships among diplolepidous-alternate mosses with chloroplast (*rbcL*, *rps4*, and *trnL–trnF*) and nuclear (18S *r*RNA) DNA sequence data, found support for a monophyletic clade consisting of Hookeriales, Hypnales, and Leucodontales (p.p.). They found moderate support for a *Hypopterygium* *–Hookeria* clade (represented by *Hypopterygium tamarisci*, *Hookeria lucens*, and *Hookeria acutifolia* W. Hook. & Grev.) as a sister clade of a clade consisting of 'Leucodontales' (represented by *Fontinalis antipyretica* Hedw.[1]) and Hypnales (*Brachythecium*, *Hypnum lindbergii* Mitt., *Plagiothecium undulatum* (Hedw.) Schimp.).

A phylogenetic study by De Luna et al. (2000) – using chloroplast sequence data – focussed on the phylogeny within the hypnobryalean pleurocarpous mosses (Hypnales, Leucodontales, and Hookeriales). They corroborated that the hypnobryalean pleurocarpous mosses constitute a monophyletic group with two – weakly supported – clades: Hypnales s.l. (= the traditional Hypnales s.str. and Leucodontales, represented by 44 species) and Hookeriales (represented by 4 species: *Hypopterygium tamarisci*, *Hookeria acutifolia*, *Lepidopilum surinamense* Müll.Hal., and *Ptychomnion aciculare* (Brid.) Mitt. [= Leucodontales sensu Buck & Vitt, 1986]).

Buck et al. (2000a) obtained comparable results using chloroplast sequence data from more hypnobryalean pleurocarpous taxa. In most of their phylogenetic analyses, they obtained a monophyletic group of hypnobryalean pleurocarpous mosses. One of the analyses suggested, that the Hypopterygiaceae, represented by *Hypopterygium tamarisci*, are a sister group to the other pleurocarpous mosses. In the other analyses,

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1) Cox et al. (2000) followed Vitt et al. (1998) with the classification of *Fontinalis antipyretica* in the Leucodontales. Buck & Vitt (1986) classified *F. antipyretica* in the Hypnales.

the Hypopterygiaceae are presented within the Hookerialean clade. The Leucodontales and Hypnales (represented by 63 species) were found to be polyphyletic or paraphyletic. The Hookeriales (8 representing species) – Hypopterygiaceae excluded – were found to be monophyletic or paraphyletic. Buck et al. (2000a, b) accepted the latter possibility. They presented *H. tamarisci* in a basal position in a Hookeriales-Ptychomniaceae-Garovagliaceae clade and presented the Hypnales s.l. (= Hypnales and Leucodontales) as the sister group of this clade.

The results of Hedenäs (1994, 1995), De Luna et al. (1999, 2000), Buck et al. (2000a), and Cox et al. (2000) strongly support the hypothesis that the Hypnales, Leucodontales, and Hookeriales constitute a monophyletic group, which includes the Hypopterygiaceae s.l. The position of this family within this monophyletic group is less clear. It was found in a basal position in a Hypnales–Leucodontales–Hookeriales clade (Hedenäs, 1995), or in a basal position in a separate clade with (other) representatives of the Hookeriales (Hedenäs, 1994; De Luna et al., 1999, 2000; Cox et al., 2000). One of the main points of concern is, that only a few representatives of the Hypopterygiaceae were used in the systematic and phylogenetic studies cited above. Deduction of phylogenetic relationships for untreated taxa is, in general, hazardous and may lead to wrong conclusions. This holds, in particular, for Hypopterygiaceae s.l., because the monophyly of this family has been subject of debate (Crosby, 1974; Vitt, 1984; Buck, 1987, 1988). The phylogeny of the Hypopterygiaceae s.l. in their present circumscription is studied in detail in the chapter 'Phylogeny' (p. 59) of this study.

GENERAL TYPIFICATION PROBLEMS

THE TYPIFICATION OF HEDWIG'S SPECIES OF THE HYPOPTERYGIACEAE

Hedwig (1801) described five new species that belong to the present Hypopterygiaceae: *Anictangium bulbosum*, *Pterigynandrum ciliatum*, *Leskea filiculiformis*, *Leskea tamariscina* and *Leskea rotulata*. It is not known by whom and when Hedwig's specimens of these species were collected. It is neither known when they were received and examined by Hedwig, but it is plausible that they were among the collections from Australasia that arrived in Europe between 1790 and Hedwig's death in 1799 (see 'Early specimens', p. 15).

The typification of the five species is problematic, because it is not known where Hedwig's type specimens are preserved at present. Specimens of *Anictangium bulbosum* and *Pterigynandrum ciliatum* are completely absent from the Hedwig–Schwägrichen herbarium kept at G (Geissler in litt.). The material in the Hedwig–Schwägrichen herbarium that is presented as *Leskea filiculiformis*, *Leskea tamariscina*, and *Leskea rotulata* can be discounted as type material. There is no evidence that Hedwig had actually seen the two specimens of *Leskea filiculiformis* and *Leskea rotulata* that are preserved in this herbarium, because they are not labelled with any annotation in Hedwig's handwriting. The label of the specimen that is presented as *Leskea filiculiformis* lacks any information about its origin and collector. The specimen that is presented as *Leskea rotulata* comes from Tasmania and was collected by Brown, probably in 1804 (Mabberley, 1985), but certainly at least a few years after Hedwig's death.

The specimen in the Hedwig–Schwägrichen herbarium that is presented as *Leskea tamariscina* is not the one that is depicted and described by Hedwig, but a specimen that was gathered by Swartz in Jamaica. The true type material of *Leskea tamariscina* is missing. Hedwig erroneously considered his plants of *Leskea tamariscina* from 'Insulae Australes' conspecific with Swartz' (1788) *Hypnum tamarisci* from Jamaica, but Hedwig's *Leskea tamariscina* is solely attached to the material from 'Insulae Australes' (see also Kruijer, 1996a).

The quest for Hedwig's type material is strongly hampered because Hedwig (1801) only gave vague information about the origin of the types. This makes the identification of potential type material almost impossible. Hedwig cited the origin of *Anictangium bulbosum*, *Pterigynandrum ciliatum*, and *Leskea filiculiformis* as 'Insulae Australes', that of *Leskea tamariscina* as 'Insulae Australes et Jamaica', and that of *Leskea rotulata* as 'Insulae Meridionales'. Including the five species of the Hypopterygiaceae, Hedwig described twelve species from 'Insulae Australes', two from 'Insulae Australes et Jamaica', and two from 'Insulae Meridionales'. Other origin citations given by Hedwig are not discussed here.

Although Hedwig (1801) used the locality indication 'Nova Seelandia' for New Zealand twice, Touw's (1971) hypothesis that 'Insulae Australes' denotes New Zealand is almost certainly correct. Touw argued, that the only area that Hedwig's species from 'Insulae Australes' have in common is New Zealand. He pointed out that two species are endemic for this area (by which he probably meant *Pterigynandrum ciliatum* and *Leskea filiculiformis*). Touw's argument is based on ten of Hedwig's twelve species from "Insulae Australes", because he considered Hedwig's *Anictangium planifolium* and *Weissia radians* species of uncertain identity. Fife (1996) resurrected the latter – as *Enthostodon radians* (Hedw.) Müll.Hal. – from obscurity for an Austral species, the distribution of which gives supporting evidence for Touw's hypothesis. Other supporting evidence is obtained from the distribution of *L. tamariscina*, one of the two species that according to Hedwig comes from 'Insulae Australes' and Jamaica, but is shown to come from 'Insulae Australes' (Kruijer, 1996a). It represents an endemic species for New Zealand and the Lord Auckland's group.

Unfortunately, it is not known what Hedwig's 'Insulae Meridionalis', the origin of *L. rotulata*, stands for. The only other species that is indicated by Hedwig (1801) to come from this area ('Insularum Meridionalum Incola') is *Dicranum introflexum* (≡ *Campylopus introflexus* (Hedw.) Brid.). This species is widespread in the southern hemisphere (Frahm, 1975). If Frahm's (1975) citation of the type material of *Dicranum introflexum* is correct, than 'Insulae Meridionalis' may denote Australia. However, another origin cannot be excluded. Hedwig cited the origin of his material of *Bryum macrocarpon* in 1792 as 'Insulis Meridionalibus' (Hedwig 1791–1792) and in 1801 as 'Insulae Australes' (Hedwig, 1801). If Hedwig based his two treatments of this species on the same material, than the possibility that 'Insulae Meridionalis' is a synonym of 'Insulae Australes', and New Zealand, cannot be ruled out.

The missing type specimens of *Anictangium bulbosum*, *Pterigynandrum ciliatum*, *Leskea filiculiformis*, *L. tamariscina*, and *L. rotulata* share presumably a similar, but mysterious history. Several authors (e.g. Touw, 1971, Miller & Manuel, 1982; Fife, 1996) were confronted with missing types and problems in locating potential type material, when they treated Hedwigian species from 'Insulae Australes'. The history of the specimens from 'Insulae Australes' probably became already a mystery with or shortly after Hedwig's death. Schwägrichen (1816), who edited Hedwig's (1801) posthumous book and acquired Hedwig's herbarium, remarked that the type specimen of *Hypnum arcuatum* (currently placed in *Hypnodendron*) is not present in Hedwig's herbarium. Unfortunately, Schwägrichen did not give information on the presence or absence of the five species of the Hypopterygiaceae in Hedwig's herbarium collections.

The collector(s) of Hedwig's material of 'Insulae Australes' and 'Insulae Meridionalis' will probably remain a mystery unless Hedwig's original material will be located. Nevertheless, it is almost certain that Hedwig's material was collected in the second half of the 18th century between the return of the Bougainville expedition to Europe in 1769 and Hedwig's death in 1799.

According to Touw (1971), the material from 'Insulae Australes' was most likely collected by Banks, the Forsters, or Menzies. He discounted Menzies' material, because his bryophyte collections were worked up by Hooker (1818–1820). He found no specimens of Hedwig's species that were collected by the Forsters, as was suggested for *Hypnum microcarpon* by Bridel (1827) and for *Leskea cristata* by Hooker & Greville (1825). In addition, Touw found no evidence that Hedwig has actually seen Bank's material of *Hypnum arcuatum*.

In 1850, Müller (1850–1851) cited collections made by Banks in 'Insulae Australes' of *Hypopterygium filiculiforme* (≡ *Leskea filiculiformis*), *Hypopterygium ciliatum* (Hedw.) Brid. (≡ *Pterigynandrum ciliatum*), and *Hypopterygium rotulatum* (Hedw.) Brid. (≡ *Leskea rotulata*, quod nom.). Müller did not indicate that he had actually seen Hedwig's specimens and he cited another specimen of *Leskea rotulata* than Hedwig. The use of an exclamation mark in Müller's treatment of *Hypopterygium commutatum*, which he placed after the citation of Hedwig's treatment of *Leskea tamariscina*, presumably indicates that Hedwig's illustrations of *Leskea tamariscina* match *Hypopterygium commutatum* (and not the excluded material of *Hypopterygium tamarisci*).

Scott (1977) suggested Banks and Solander as possible collectors of Hedwig's material, and remarked that the specimens were presumably borrowed by Hedwig. Fife (1993) suggested Banks as a possible collector of Hedwig's type material from 'Insulae Australes'. Fife (1996) proposed potential type material for seven Hedwigian species, which was collected by Banks (*Bryum macrocarpon*, *Leskea cristata*, *Neckera planifolia*, *Weissia radians*), Banks & Solander (*Hypnum tenuifolium*), and Menzies (*Anictangium bulbosum*, *Anictangium setosum*).

However, there is no evidence that Hedwig had such early specimens as the ones collected by Banks at his disposal. Kruijer (1996a) argued that the type specimens of the species from 'Insulae Australes' were probably among the collections from New Zealand and Australia that arrived in Europe between 1790 and Hedwig's death in 1799. With the exception of *Bryum macrocarpon*, Hedwig mentioned his species from 'Insulae Australes' and the two from 'Insulae Meridionalis' discussed above only in his posthumous 'Species muscorum frondosorum'. In all probability, he had not seen any specimens of these species until the early nineties of the eighteenth century.

In this period most, if not all, botanical collections from this region were collected by Menzies, De Labillardière, and Ventenat (see 'Early specimens', p. 15). De Labillardière's collections may be discounted, because he paid only a very short visit to

New Zealand (De Labillardière, 1800). Besides, De Labillardière (1806) treated the type of *Leskea pennata* as different from Hedwig's *Anictangium bulbosum*. Comparison of De Labillardière's and Hedwig's illustrations and descriptions showed, that the specimens upon which their protologues are based may safely considered to be different plants.

Touw (1971) discounted the collections made by Menzies as possible types of *Hypnum arcuatum*, because they were worked up by Hooker (1818–1820). Nevertheless, specimens gathered by Menzies were reported by Smith (1808), and duplicates might have been distributed shortly after their arrival in England. Fife (1996) also considered Menzies a possible collector of some of Hedwig's (1801) exotic material. Sastre-De Jesus (1987) cited a specimen in G that was collected by Menzies in New Zealand as the holotype of Hedwig's *Anictangium setosum* (≡ *Cyrtopus setosus* (Hedw.) Hook.f.) from 'Insulae Australes'.

However, despite the rather large number of early collections of Hypopterygiaceae that have been examined during the present study – which includes material collected by Menzies [many], Banks and/or Solander [few], and G. Forster [two] (see 'Early specimens', p. 15) –, no collection was found that was actually seen by Hedwig.

Moreover, in the material examined, only a single specimen was indicated to come from 'Insulae Australes'. This specimen is preserved in Hooker's herbarium in BM. Its label lacks a collector's name and date, and is only provided with name of the species and the abbreviation "Ins. Austr.". The specimen was presented as *Leskea rotulata* Hedw., but according to Hedwig (1801) the original material of this species comes from 'Insulae Meridionalis'. Therefore, the specimen cannot be part of the type material of this species. The specimen belongs to the present species *Hypopterygium didictyon*.

From above it is concluded, that Hedwig's (1801) type material *Anictangium bulbosum*, *Pterigynandrum ciliatum*, *Leskea filiculiformis*, *L. tamariscina*, and *L. rotulata* has to be considered missing. Therefore, it is necessary to select Hedwig's illustrations belonging to the protologue of these species as their lectotypes. In the present study, lectotypes have been selected for *Anictangium bulbosum*, *Pterigynandrum ciliatum*, *Leskea filiculiformis*, and *L. rotulata*. The lectotype of *Leskea tamariscina* had already been selected (Kruijer, 1996a).

Hedwig's (1801) excellent illustrations of *Anictangium bulbosum*, *Pterigynandrum ciliatum*, *Leskea filiculiformis*, and *L. tamariscina* provide sufficient information on the identity of these species. However, the illustrations and the description of *Leskea rotulata* are ambiguous. In the present study, *L. rotulata* is, therefore, treated as a doubtful species.

Confusion about the true identity of *Leskea rotulata* (≡ *Hypopterygium rotulatum*) arose already rather early in history. Wilson (1855) was presumably the first who was aware of this problem. The material examined for the present study that was presented as *Leskea rotulata*, or *Hypopterygium rotulatum*, proved in majority to belong to two distinct, separate taxa (*Hypopterygium didictyon* and *Hypopterygium tamarisci*).

TYPES COLLECTED BY MOTLEY CITED IN THE 'BRYOLOGICA JAVANICA'

Type material of three species of the Hypopterygiaceae that were described by Van den Bosch & Van der Sande Lacoste (1861) (*Cyathophorum parvifolium*, *Hypoptery-*

gium aristatum, *Hypopterygium humile*) includes Javan material.collected by Motley. Van den Bosch & Van der Sande Lacoste linked this and other Motley material with Mitten.

Touw (1979) remarked that he did not find evidence for direct contacts between Van der Sande Lacoste and Mitten, which is remarkable, because both were contemporary and prominent bryologists working in the same field of interest. Nevertheless, it is certain that, for the preparation of the 'Bryologia Javanica', Van den Bosch & Van der Sande Lacoste obtained via Mitten material collected by Motley, which included specimens of Hypopterygiaceae. In return, Mitten also received Javan material that was collected by other collectors, e.g. Kurz, from Van den Bosch & Van der Sande Lacoste.

From the examination of the specimens that are preserved in Mitten's herbarium, nowadays kept in NY, and the information written on their labels, it became clear, that after examination Van der Sande Lacoste returned several of Motley's specimens of Hypopterygiaceae to Mitten. In a few cases, even all the material that Van der Sande Lacoste had in his hands was returned. As a result the major type specimens of Van den Bosch & Van der Sande Lacoste's (1861) new species of the Hypopterygiaceae are preserved in NY.

Despite this exchange of material, Van den Bosch & Van der Sande Lacoste (1861) reported only for a single collection of the Hypopterygiaceae, that it actually came from Mitten ("comm. Mitten"). This collection was made by Motley and is a syntype of *Cyathophorum parvifolium*. A specimen of this collection is preserved in Mitten's herbarium in NY. Another is still present in Van der Sande Lacoste's herbarium in L.

In a few cases, Van den Bosch & Van der Sande Lacoste (1861) indicated in their treatment of the Hypopterygiaceae, that Motley's specimens were preserved in Mitten's herbarium. This is in accordance with where they are nowadays preserved; duplicates are absent from Van der Sande Lacoste's herbarium. The specimens that are of concern here are type material of *Hypopterygium aristatum* Bosch. & Sande Lac. (= *H. flavolimbatum*), *Hypopterygium humile* Mitt. ex Bosch & Sande Lac. (= *H. tamarisci*), and material of *Lopidium struthiopteris*, upon which Hampe (1874a) based *Lopidium javanicum* Hampe.

The type specimens of *Hypopterygium aristatum* and *Lopidium javanicum* do, unfortunately, not reveal direct information whether or not they have been seen by Van den Bosch and/or Van der Sande Lacoste, but there is little doubt that they actually were. The label of the specimen of *Hypopterygium humile* in Mitten's herbarium is provided with few annotations in Dutch, presumably meant for A.J. Kouwels, who was Van den Bosch & Van der Sande Lacoste's (1861) illustrator. It is certain that this specimen represents the holotype of *Hypopterygium humile*.

Although they did not report the species, Van den Bosch or Van der Sande Lacoste must also have seen material of *Cyathophorum hookerianum*. Part of this material is preserved in Van der Sande Lacoste's herbarium. It contains only a few leaves, which were probably used for microscopic examination. The major part of this material is preserved in Mitten's herbarium. The material was annotated to be collected by Motley on Java, but this origin is probably corrupt (see '*C. hookerianum*', note 17, p. 347).

Chapter 4

MORPHOLOGY AND ANATOMY

GAMETOPHORES

Hypopterygiaceae are very variable in size and habit, especially the degree of ramification and foliation may vary considerably within one species giving rise to plants with a completely different appearance within the same species. Inter- and intraspecific variation between Hypopterygiaceae is also found in many other features.

Life form

Hypopterygiaceae grow in open to dense colonies on various, horizontal to vertical substrates. Following Bates' (1998) overview on bryophyte life-forms, Hypopterygiaceae with branched stems are fans or dendroids. Terrestrial species, growing on roughly horizontal substrates, are (nearly) strict dendroids with a distinctly palmate to umbellate habit (Fig. 4). Strictly epiphytic or epilithic species, growing on inclined or vertical substrates, are fans with a pinnate to bipinnate (Fig. 37) or flabellate habit (Fig. 27, 43). Several *Hypopterygium* species may grow on diverse substrates of various inclination, and may, therefore, be fans, dendroids, or intermediates between them.

Plants of *Cyathophorum* have mainly simple stems (Fig. 46). Colonies of *Cyathophorum* usually grow epiphytically or epilithically on sloping or vertical substrates. The basic life form of *Cyathophorum* is, therefore, best described here as being a fan without branches.

Growth form and branching pattern

Shoots of Hypopterygiaceae show determinate growth. The shoots are sympodially branched and form by branching a chain of repeated modules of stolons and stems (Fig. 20; cf. La Farge-England, 1996; Tangley, 1997, f. 4: 1). Each module consists of a creeping, plagiotropic stolon and an (initially) orthotropic stem.

In early bryological literature on Hypopterygiaceae, the stolon and stem were frequently termed, respectively, 'primary' and 'secondary stem', but Argent (1973) correctly pointed out that this terminology is incorrect for mosses which form such a chain of modules.

Prostrate growth takes place through the stolons. The distal part of the stolons detaches from the substrate and turns sharply to roughly 90° away to become an erect, simple or branched, foliate stem (e.g. Fig. 6, 37, 50). In *Catharomnion*, however, the stolon may continue to grow in its original direction and gradually change into the stem (Fig. 13, 14).

New stolons originate in majority from primordia that are situated in the part of the shoot where the stolon changes into the basal part of the stem. This part is bent, and usually one, sometimes two or three, new stolons sprout from primordia that are located at the ventral (substrate) side of the axis in this bend (Fig. 10, 20, 37, 47).

Above the bend, the stem grows with a perpendicular orientation from the substrate in the direction of the light. Prostrate stems of *Catharomnion* and *Cyathophorum bulbosum*, however, continue to grow in the growth direction of the stolon, but become loose or have only limited contact with the substrate.

When growing on a sloping or vertical substrate, the basal part of the stem shows often a rotation on the stem axis with an angle of roughly 90° at most (Fig. 14). This rotation results, ultimately, in the roughly perpendicular orientation of the dorsal faces of the lateral leaves towards incident light[1]. The rotation can be observed in a change of stem compression, a deviation of the phyllotaxis, or, rarely, a change in the orientation of the foliation.

The distal part of the stem is either simple or branched. Normally, stems are simple in *Cyathophorum* and branched in the other genera. In branched Hypopterygiaceae, the stem is differentiated in a simple basal part, termed stipe, and a branched distal part, termed rachis. The branched distal part of the plant, which includes the foliate rachis and its cluster of foliate branches, is termed frond (cf. Tangley, 1997, f. 4: 2; frond axis = rachis). Rachis and the branches are usually glabrous, although the basal part of the rachis and the lower branches may occasionally be set with rhizoids.

In pinnate or flabellate Hypopterygiaceae, the rachis has the same direction as the stipe (Fig. 37). In dendroid Hypopterygiaceae, the rachis undergoes a second change of direction at the point where the lowest first order branches sprout (Fig. 4); it becomes plagiotropic. The plagiotropic rachis of dendroid Hypopterygiaceae in plants growing on a horizontal substrate follows the direction of growth of the stolon. In plants growing on a sloping or vertical substrate it has often an orientation of roughly 90° to the direction of growth of the stolon (cf. Newton & De Luna, 1999). This is a consequence of the roughly horizontal orientation of the stolons under these conditions, and the subsequent rotation on the axis of the basal part of the stems as described above.

In Hypopterygiaceae with a branched foliate stem, the frond forms a complanate surface, which is more or less horizontal and roughly orientated at a right angle to the light. In *Cyathophorum*, which has normally a simple foliate stem, two rows of lateral leaves at both sides of the foliate stem form a large flattened surface. These foliate stems are, likewise, more or less horizontal, although the apical part may sometimes be curved downwards.

Branches are nearly always laterally borne on the main axis (rachis) and sprout usually from primordia that are associated with lateral leaves. The branches are initiated from a cauline primordium (in the definition of La Farge-England, 1996) and are often seemingly positioned in the axils of (lateral) leaves.

Ramification follows a structural hierarchy. Branched stems have, in majority, lateral first order branches, which may in turn be branched by second order branches, those by third order branches, and those by fourth order branches. This branching pattern can be best observed in *Dendrohypopterygium filiculiforme*, which has a bipinnate to tetrapinnate branched frond.

1) The ventral leaves or amphigastria of the prostrate stolon are directed towards the sloping or vertical substrate, while after the rotation those of the stem become directed towards the earth's surface.

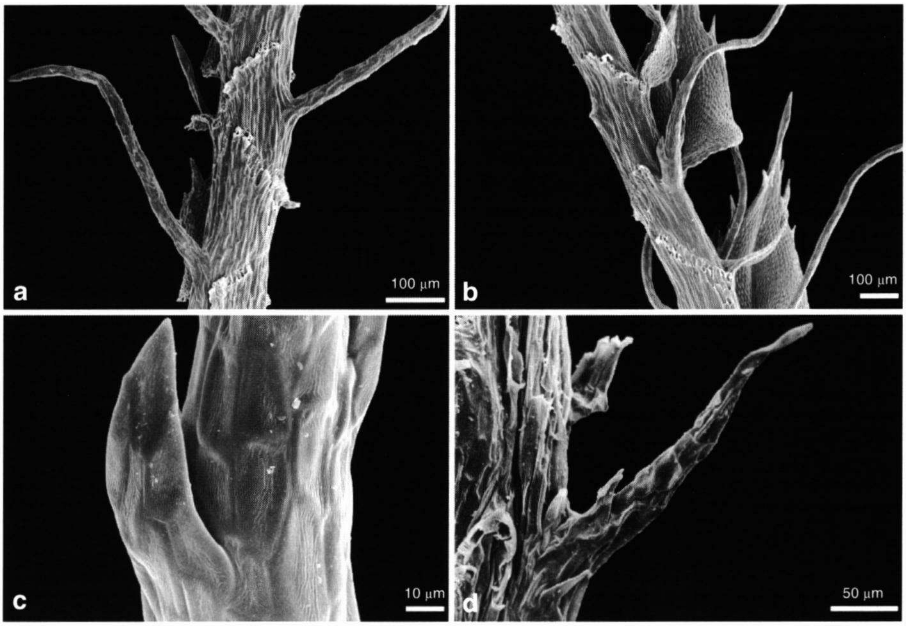

Plate 1. SEM photographs of rudimentary branches. a–c. *Canalohypopterygium tamariscinum* (Hedw.) Kruijer, a. defoliated frond axis (dorsal view) with rudimentary branches, b. defoliated frond axis (dorsal view) with rudimentary branches, one with two scaly leaves at base, c. scaly leaf at base of rudimentary branch (detail of photograph 1b); d. *Catharomnion ciliatum* (Hedw.) Wilson, rudimentary branch with three scaly leaves at base on defoliated frond axis (a–c: *Brownsey s.n.*, '30.09.1983', WELT); d: *Beever 70–26*, CBG).

Canalohypopterygium and *Catharomnion* have two types of branches: normal ones and small, generally leafless, rudimentary branches (Plate 1a, b, d; Reimers, 1953; Frey & Schaepe, 1989) with a distinctly cauline position. Many segments of the rachis and branches of *Canalohypopterygium* and *Catharomnion* bear a single rudimentary branch (Reimers, 1953). The rudimentary branches are a unique feature among mosses and are associated with a cavity system. The rudimentary branches and their associated cavity system are treated in detail under the genus *Canalohypopterygium*, note 3, p. 121. Magill & Stotler (1990) use the term 'axillary bristle' for rudimentary branches, but this terminology is not followed here, because it is to some extent misleading with respect to the position of a rudimentary branch.

Stolons are set with rudimentary leaves and have a moderate to dense tomentum consisting of usually branched rhizoids. The stem is set with conspicuous leaves, although the leaves at the stem base remain usually small and scale-like. The stem base is almost always tomentose. Above the base, the stem is glabrous or beset with a tomentum, which from base to apex decreases in density. Ultimately, the tomentum vanishes, by which the distal part of the stem becomes entirely glabrous. Branches are set with conspicuous leaves, but the base is set with a few small, scaly leaves.

Ontogeny, morphology, and anatomy of stolons, stem, and branches

Ontogeny — Axes of bryophyte gametophores show modular growth and are composed of numerous segments (merophytes), which are placed in a spiral arrangement. The segments form a heteroblastic series. Each segment has determinate growth. In vegetative axes, a mature segment, also termed metamer (Mishler & De Luna, 1991), consists of a single leaf with associated axillary hairs situated in the axil of this leaf, a primordium, and an associated portion of the axis with epidermal, cortical, and, if present, central strand tissue. In Hypopterygiaceae, the heteroblastic, modular nature of axes is often only weakly conspicuous. Usually, the segmented structure of the axes of Hypopterygiaceae is difficult to observe, but it can indirectly be determined by the position of the axillary hairs, leaves, and primordia.

Growth of gametophore axes is initiated by a single apical cell, which, in most mosses, possesses three cutting faces. In pleurocarpous mosses, this apical cell is roughly oblong-ellipsoid (Frey, 1981, cf. Frey et al., 1983). Cell divisions of the apical cell are anticlinal (cf. Berthier, 1972) and roughly parallel to the direction of growth of the axis (cf. Frey et al., 1983). Subsequent divisions follow a clockwise or counterclockwise rotation on the longitudinal axis of the apical cell. A single daughter cell of the apical cell forms, after a series of subsequent divisions (see: Lorch, 1931; Berthier, 1972, and references therein; Frey et al., 1983), a single segment of an axis.

In Hypopterygiaceae, a mature segment includes 3/8 to 1/3 (or nearly so) part of the axis in cross section. In length, a segment reaches from the second row of cells above the leaf insertion of the lower segment till the first row of cells above its own leaf insertion. The basal part of the outer face of a segment contains in Hypopterygiaceae a single primordium (see also: Goebel, 1906; Reimers, 1953), which consists of an apical cell and a few young segments or initial cells of segments. A primordium is either dormant or may form a new axis or gametoecium. The outer face of a segment is glabrous or set with structures, and may be set with a few scaly leaves surrounding the primordium, at tomentose axes set with rhizoids sprouting from epidermis cells, and at gemmiferous axes set with clusters of gemmaphores. Paraphyllia are absent. Every segment contains a single leaf which is attached to the two most distal rows of cells in the segment. A few cells of the most distal row, which is visible at the base of the leaf axil, bear an axillary hair.

Morphology — In most Hypopterygiaceae, the axes of the plants are terete (Fig. 8a, b). *Cyathophorum bulbosum* is the only species which has entirely quadrangular stems (Fig. 48e). *Dendrohypopterygium filiculiforme* has terete axes, but the stipe base is somewhat quadrangular. Stolons, stems, including stipe and rachis, and branches are circular to elliptic in cross section and have either a dorsiventral (Fig. 8a, b) or a lateral (Fig. 28a, b) orientation, which is irrespective of the orientation of the foliation.

Anatomy — The stolons, stems, including stipe and rachis, and branches have a protective epidermis, a cortex, and often a central strand (Fig. 5a, b).

The epidermis of shoot axes is presumably covered by a thin cuticle. A cuticle is present on the surface of leaves and is best developed in leaves with a pronounced glaucous or greyish bloom. Shoot axes of plants with glaucous or greyish leaves are usually tinged with the same colour.

The cortex is frequently differentiated in an outer and an inner cortex (Fig. 19a, 28a). The two layers are not sharply separated. The outer cortex consists of cells with incrassate walls. The inner cortex consists of wider cells with thin or weakly incrassate walls. Epidermis cells are usually almost similar to the outer cortex cells, but have often less incrassate walls. Cortex differentiation is strongest in the stipe and the basal part of the rachis and the basal branches and decreases significantly towards the apices of the frond axes. Colour saturation of the cell wall is generally positively correlated with thickness: thin walls are usually colourless or pale yellow, whereas incrassate walls are often brown, or even dark brown when they are very incrassate. Hence, the basal part of the stem – in branched Hypopterygiaceae the stipe and basal part of the rachis and the lower branches – is usually firm and brown, because of the incrassate and (dark) brown walls of the epidermis and outer cortex cells (Fig. 19a, 28a). The distal part of the stem – frond axes – is usually slender and green, because of the thin and colourless walls of the epidermis and cortex cells (Fig. 19b, 28b).

The strength and colour of shoot axes depends highly on the thickness of the walls of the outer cortex cells and, to a lesser extent, the epidermis cells. Lorch (1931) indicated, that strengthening tissue is not necessarily evenly distributed over the epidermis and the outer cortex of the axes. In most cross sections of shoot axes, however, the outer cortex forms a peripheral ring of more or less evenly distributed strengthening tissue, which may be interrupted by branch primordia. Walls of primordium cells are very thin and colourless.

In the axes of most Hypopterygiaceae, a central strand is present (Fig. 5a,b). When observed in cross section, the strand cells are either roughly equally wide or much narrower than the inner cortex cells. The walls of the strand cells are thin and colourless to brown.

In mosses, the hydroids in the central strand are thought to have a function in water transport. In the final stages of the differentiation process of a hydroid, the protoplast of an elongated central cell in the axis of a moss degenerates in concert with partial hydrolysis of the longitudinal and transverse walls of the cell. Such hydrolysed walls are highly permeable for water and solutes, and contribute to the conduction capacity for water of the hydroids (Hébant, 1977; Frey & Richter, 1982; Schofield & Hébant, 1984). TEM observations (Frey & Richter, 1982) revealed such hydrolysed walls in the hydroids of the central strand of *Dendrohypopterygium filiculiforme.*

According to Hébant (1977) and Schofield & Hébant (1984), the central strand in the stolons of *Hypopterygium* is developed to a lesser extent than the central strand of the stem. This might reflect a general pattern within the Hypopterygiaceae that possess a central strand, if the number of strand cells between stolons and stems are compared, but the differences are usually small.

The central strand in stems and branches of *Canalohypopterygium* (Fig. 12a, b) is rather weak (Reimers, 1953; Frey & Richter, 1982), when compared with that in *Dendrohypopterygium* and *Hypopterygium* species.

In *Cyathophorum africanum* the central strand may be interrupted by a central cavity (Fig. 55a). In mature gametophores of *Dendrocyathophorum*, the central strand, which was probably present in juvenile stages of development of axes or segments, has almost entirely been replaced by a central cavity (Fig. 45a). Replacement of the central strand by a central cavity may also occur in the frond axes of the *Dendrohypopterygium* species (Fig. 5c, d), *Hypopterygium vriesei* (Fig. 28b), and *Hypopterygium sandwicense* (Fig. 36b, c).

A central strand is usually absent from *Lopidium*. Occasionally, a central strand is present in the stipe of *Lopidium struthiopteris*.

Cortex and strand cells of all species of the Hypopterygiaceae may contain inclusions of visible substances (e.g. Fig 19a, b). These inclusions consists of oil-like fluids or fat-like or waxy, amorphous solids. The chemical composition of these inclusions is unknown. In *Cyathophorum bulbosum,* the inclusions, present in the inner cortex cells (Fig. 48e), are sometimes granular starch.

Peculiar structures which occur in several species of the Hypopterygiaceae, are the longitudinal, axial cavities, which may be present in stolons, stems (stipe and rachis), and branches (Noguchi, 1936b; Reimers, 1953; Frey & Richter, 1982; Frey et al., 1983; Whittemore & Allen, 1989; Kruijer, 1995b; Magill & Van Rooy, 1998). The axial cavities are either situated in the cortex (e.g. Fig. 15a, b), whereby they in cross section replace several cortical cells, or have a central position (Fig. 15c, d, 55a), whereby they replace the central strand (if originally present). Axial cavities that are situated in the cortex nearly always correspond with the modular structure of the axes: each segment produces a single cavity.

Dendrocyathophorum and *Cyathophorum africanum* possess a central cavity in the aerial axes (stem and branches). A central cavity is present in most cross sections of *Dendrocyathophorum* (Fig. 45a) and some of the cross sections of *Cyathophorum africanum* (Fig. 55a). In radial view, the central cavity of *Cyathophorum africanum* is interrupted. It could not be determined whether the length of the various parts of this central 'cavity' corresponds with the segment length. In *Dendrocyathophorum,* the central cavity is a duct, which is only rarely interrupted and traverses many segments. In both taxa, the central strand, probably present in early stages of development of the axis, is later partly or entirely replaced by a central cavity.

In *Dendrohypopterygium* (Fig. 5c, d), *Hypopterygium vriesei* (Fig. 28b), and *Hypopterygium sandwicense* (Fig. 36b, c), axial cavities are frequently present as central cavities in the distal part of the rachis and the branches, but they are absent from the lower part of these axes, the stipe, and the stolons.

In *Lopidium concinnum,* axial cavities are often present in the cortex of the stipe, the rachis, and the branches (Fig. 41h), but they become central towards the distal parts of the frond axes. These central cavities in the branches of *L. concinnum* can almost certainly be considered as cortical cavities that are situated in a nearly central position in the relatively narrow branches. In *L. struthiopteris*, axial cavities are, when present, always situated in or near the centre of the stipe, the rachis, and the branches (Fig. 41a).

The stem and branch cavities of *Canalohypopterygium* and *Catharomnion* are situated in the cortex (Fig. 12a, b, 15 a, b; see also: Reimers, 1953; Frey et al.,1983; Frey & Schaepe, 1989). In branches and the distal part of the rachis, the cavities can usually easily be observed through intact axes by light microscope, because the cavities often contain a conspicuous amount of an oil-like substance (Reimers, 1953). The lumen of the cavities is bordered by a usually unicellular layer of thin-walled cells or their remnants, which remind of specialised epithelial cells like the ones found in resin ducts of Gymnosperms and Angiosperms (cf. Reimers, 1953; Frey et al., 1983). Whether the 'epithelium cells' have a similar function and contribute to the accumulation of the substances is still unknown. Each cavity is situated in its own segment (cf. Frey et al., 1983). Many segments, but not all, contain a cavity. Almost every segment of frond axes contains a cavity. Segments with cavities occur less frequently in the stipe and the stolons. The cavities are simple and not connected with each other (Frey et al.,1983).

Studies by Frey et al. (1983) revealed, that in *Canalohypopterygium* a cavity is formed in cortical tissue that originates from the primordium initial cell – which also forms the primordium. The formation of the cavity lumen begins early in the ontogenetic development of a segment and starts simultaneously with the process of central strand differentiation (Frey et al., 1983).

The rudimentary branches contain a central cavity (Reimers, 1953), by which they, in cross section (Fig. 12c, d, 15c, d), resemble the leafy, (third and) fourth order branches of *Dendrohypopterygium filiculiforme* (Fig. 5c, d). The cavity wall in the rudimentary branch is partly or entirely covered with thin-walled cells or their remnants. Each rudimentary branch and its cavity originates from a segment primordium, by which the whole cavity system ontogenetically originates from the primordium initial cell. This explains, why the cortical cavity of the main axis is connected with the central cavity of the rudimentary branch of the same segment. The cavity system of *Canalohypopterygium* and *Catharomnion* is unique among mosses and is treated in more detail under the genus *Canalohypopterygium*, note 3, p. 121.

Like in *Canalohypopterygium* and *Catharomnion*, axial cavities of other Hypopterygiaceae contain usually conspicuous inclusions (Noguchi, 1936b; Kruijer, 1995b). The inclusions consist of droplets or amorphous solids of, respectively, oil-like or wax-like, colourless (white) to reddish brown substances. The lumen of the cavities is also bordered by a usually unicellular layer of thin-walled cells or their remnants, but their resemblance with epithelium cells is often less clear. Consequently, the substances of Hypopterygiaceae (or their precursors) are: 1) formed by tissue cells, which ruptured or disintegrated during the process of cavity formation; 2) formed and secreted into the cavity by specialised cells surrounding the cavity in various degree of specialisation; or 3) formed and secreted into the cavity by non-specialised cells surrounding the cavity. The first hypothesis is most likely, because the inclusions found in cavities physically resemble the inclusions that are found inside living cells of places were the cavities are or may be formed (Fig. 28b, 36c, 55a).

The oil-like inclusions of *Canalohypopterygium* mainly consists of apolar hydrocarbons, some of which are alkanes and fatty acids, including unsaturated fatty acids (Pelser et al., accepted). The chemical composition of the inclusions of other Hypopterygiaceae is not known. The production process of the substances is not known either. It is, therefore, unknown whether the substances are assimilates or dissimilates, hence a distinction in terminology between 'secretion' and 'excretion' (sensu Frey-Wyssling, 1935; Schnepf, 1969) cannot be made.

The ontogenetic processes that are involved in the formation of the lumen of the cavities are not clear. Based on light microscopical observations, Frey et al. (1983) tentatively suggested that the development of the cavity system in *Canalohypopterygium* is schizogenous. The authors remarked that further research is needed to unravel the ontogeny of the cavities, partly because their TEM observations of inclusions of substances or remains of cells in the cavity did not exclude lysigenous processes.

Rhizoids

Rhizoids are produced from the epidermis cells of axes. They mainly project from the stolons and the stem bases – i.e. stipe bases in branched Hypopterygiaceae – and are quite often predominant at the ventral side. Rhizoids may also occur in the distal part of the stipe and the basal part of the rachis, where they are generally evenly distributed around the axis, albeit that some clustering in the distal part of segments may be observed. In some species, rhizoids may also occur at the basal part of the lower branches. *Dendrohypopterygium filiculiforme* is the only species in which rhizoids may also sprout from leaf cells at the base of the stipe leaves.

The rhizoid initial cells are morphologically indistinct from other epidermis (or leaf base) cells, unless rhizoid growth has started. Based on the examination of segments with few, scattered rhizoids, it seems that rhizoid formation is initiated in the distal part of the segments, and then disperses downwards towards the segment base, in particular, along the lateral sides of the segments. The first few rhizoids are apparently formed in the median or lateral part of the distal segment half, often just below the associated leaf. The next ones have a more lateral or basal position, but the first of them are usually still restricted to the distal part of the segment. This ontogenetic pattern may result in some clustering of rhizoids just below the associated leaves in parts of axes where the tomentum is open or scarce. This clustering is most pronounced in *Canalohypopterygium tamariscinum*, where it may also be visible in densely tomentose stolons. In parts of axes of other species with a dense tomentum, rhizoids sprout from every part of the epidermis, but a higher density of rhizoids in the distal part of the segments than in the basal part is often observed.

Rhizoids are over most of their length dark brown to brown, but become pale brown or colourless in the distal part. They are smooth or minutely papillose. Most rhizoids are weakly to strongly, pinnately branched, but in *Cyathophorum bulbosum* dichotomously branched rhizoids may also occur. The rhizoids of *Canalohypopterygium* may either be simple or weakly to strongly branched. Rhizoids are usually soft, but those at the stipe of *Dendrohypopterygium filiculiforme* (Fig. 4) are bristly.

Axillary hairs

Axillary hairs provide useful character states for distinguishing taxa, especially at the species level.

Axillary hairs are situated on the axes of the gametophore. For practical reasons, attention is focussed on the axillary hairs that are situated in the various parts of the stem and branches. The axillary hairs attached to gametoecial branches are treated as a part of the gametoecia.

In most Hypopterygiaceae axillary hairs are persistent, but such hairs are frequently absent from *Cyathophorum bulbosum* and *Catharomnion*. The axillary hairs are associated with leaves. Each axillary hair sprouts from a cell, which belongs to a row of cells that is situated in the leaf axil just above the base of the associated leaf. The number of cells in that row bearing an axillary hair is variable, and may vary between leaves, specimens, and species. Consequently, the number of axillary hairs per associated leaf is variable.

The axillary hairs are simple and hyaline. In other Hypopterygiaceae than *Cyathophorum*, they consist of one to three (rarely four) brown basal cells and a colourless terminal cell (e.g. Fig. 9d–i). The basal cells are sometimes very lightly pigmented. The terminal cell is usually longer than wide, but may show considerable variation in length and shape between species, and sometimes within species. In a few species, e.g. *Hypopterygium didictyon*, the terminal cell may be conspicuously covered with white, waxy substances (Fig. 17d, f).

The axillary hairs of *Cyathophorum* show considerably more intra- and interspecific variation than those of the other Hypopterygiaceae. The number of basal cells varies in *Cyathophorum tahitense*, *C. africanum*, and *C. parvifolium* between one and two, in *C. hookerianum* between one and four, in *C. bulbosum* between two and six, in *C. spinosum* between one and eight, and in *C. adiantum* between one and five. Intermediate cells, which are situated between the basal cells and the terminal cell (Fig. 49n), are commonly present in *C. bulbosum*, C. *tahitense*, *C. spinosum*, and *C. adiantum*, but they are absent in the other three *Cyathophorum* species. The terminal cell may show considerable variation in length and shape between and within species. The circular to elliptic terminal cells of *C. hookerianum* and *C. parvifolium* (Fig. 59d–f, n–p) are unique within the Hypopterygiaceae. In *C. africanum*, the terminal cell may vary from elliptic to short-linear-rectangular (Fig. 55b–d). In the other *Cyathophorum* species, the terminal cell is always longer than wide, varying from oblong-rectangular (Fig. 53o) to linear (Fig. 49o).

Scaly leaves

The primordia of the Hypopterygiaceae are naked or set with scaly leaves. The proportion of naked primordia versus primordia set with scaly leaves shows much intra- and interspecific variation. The definition of scaly leaves follows that of Akiyama & Nishimura (1993).

Phyllotaxis

In most mosses, the daughter cells of the apical cell of an axis, formed after the first anticlinal divisions, are cut off in three directions. Hence, they are initially placed in three ranks. Generally, this three-ranked arrangement will be altered during growth, because: 1) the subsequent anticlinal divisions occur in an order following a clockwise or counterclockwise rotation; 2) the newly formed initial cells and immature segments increase with age in size in all three dimensions. Consequently, initial cells and young segments are unequal in size – older ones being larger than the younger ones. Due to side by side contact, growth of initial cells and very young segments induce peripheral displacement of, in particular, the outer portion of older ones (cf. Frey et al., 1983, f. 4). Growth of older segments, initially mainly by cell division followed by cell elongation, results in distal displacement of the axis apex, and induces, as a consequence of the rotating division sequence of the apical cell, lateral displacement of younger segments[1]. Because these processes take place in a fixed cylindrical space, i.e. the axis, they result in a spiral arrangement of segments along the axis. In most

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1) Possibly, lateral displacement may also occur within a single segment, because the basal part of a young segment is in contact with older and larger segments than the distal part. Lateral displacement within a segment explains the weak spiral that Frey et al. (1983: 315) often observed in the shape of axial cavities in the cortex of *Canalohypopterygium*.

mosses, this process results in a spiral arrangement on axes of segments and leaves in more than three ranks.

The Hypopterygiaceae show a peculiar variation in phyllotaxis. In *Cyathophorum*, *Dendrocyathophorum*, *Lopidium*, and *Catharomnion* the segments and leaves are placed in three ranks (tristichous phyllotaxis, denoted by 1/3; e.g. Fig. 46), which indicates that no displacement of segments took place. A similar tristichous phyllotaxis is also found in *Hypopterygium vriesei* and most plants of *H. discolor* and *H. tamarisci*. In some plants of the latter, the phyllotaxis of the stipe is slightly altered from tristichous, often because of a torsion of the stipe.

The phyllotaxis of *Canalohypopterygium*, *Dendrohypopterygium*, *Hypopterygium didictyon*, *H. elatum*, *H. flavolimbatum*, and *H. sandwicense* is unique among mosses. In these taxa, the segments and leaves of the stolon, the stipe, and the basal part of the rachis are placed in eight ranks (octostichous, denoted by 3/8; e.g. Fig. 11, 23), whereas the leaves of the distal part of the rachis and the branches are placed in three ranks (tristichous, 1/3), like in other Hypopterygiaceae. In *Dendrohypopterygium*, even the branch segments and leaves of the lower branches are placed in eight ranks.

The ontogenetic spiral of the stem of Hypopterygiaceae is clockwise or counterclockwise. According to Reimers (1953) and Berthier (1972), the ontogenetic spiral of branches in Hypopterygiaceae is independent from the ontogenetic spiral of the axis where they originate from. When gametophores of branched Hypopterygiaceae are viewed with the ventral side in an upwards position (base towards and apex away from the observer; cf. Reimers, 1953), the branches sprouting from the left side of the main axis show a clockwise spiral arrangement and those sprouting from the right side of the main axis a counterclockwise arrangement. The occasional dorsal or ventral branches in Hypopterygiaceae with a partly octostichous phyllotaxis may show either rotation type, but a general pattern or rule for their direction of rotation was not found.

Foliation

In Hypopterygiaceae, the foliation of axes, or parts of axes, may be isophyllous or anisophyllous. Axes or parts of axes with an isophyllous foliation are characterised by having monomorphic leaves. Isophylly is indepent of phyllotaxis and occurs in axes or parts of axes with an octostichous phyllotaxis (Fig. 11, 23), but may also occur in those with a tristichous, or nearly tristichous, phyllotaxis (e.g. in some plants of *Lopidium concinnum*). Axes or parts of axes with an anisophyllous foliation (Fig. 46) are characterised by having dimorphic leaves arranged in two rows of asymmetrical, lateral leaves and a single row of symmetrical, ventral leaves, which are termed amphigastria in this study. Anisophylly is, therefore, in Hypopterygiaceae restricted to axes or parts of axes with a tristichous phyllotaxis.

In Hypopterygiaceae, the foliation of stolons is inconspicuous, isophyllous, and not complanate.

The foliation of the stem is more complex. In most species, the foliation is inconspicuous in the basal part of the stem, and becomes conspicuous above. In *Catharomnion*, however, the differences in foliation between the basal and the distal part of the stem (stipe and rachis) are weak or non-existent. Branches have a conspicuous foliation.

The foliation of the stem, above the base, and the branches is partly or entirely anisophyllous.

The dorsiventral orientation of the anisophyllous foliation of stem and branches is almost certainly a consequence of the dorsiventral orientation of the stolons. In plants growing on a sloping or vertical substrate, the basal part of the stem, originating from a horizontal, plagiotropic stolon, often shows a rotation with an angle till roughly 90°. This rotation results in the roughly perpendicular orientation of the dorsal faces of the lateral leaves towards incident light.

In Hypopterygiaceae, anisophylly is associated with a complanate foliation, whereas isophylly is associated with a not complanate foliation. However, a complanate foliation is not fully restricted to parts of axes with anisophylly. In branched Hypopterygiaceae with a partly octostichous phyllotaxis, the foliation of axis parts with an isophyllous foliation may already become complanate under or in the basal part of the zone where the phyllotaxis changes from octostichous to tristichous, which usually takes place in the basal part of the rachis.

Leaves

In Hypopterygiaceae, leaves are distantly placed to closely set. In addition to isophylly and anisophylly and the degree of compression of the foliation, the distance between the leaves strongly affect the appearance of foliate axes. Stolon leaves are distant. Stem leaves are usually distant in the basal part of the stem and become closely set in the distal part. Scale-like stem leaves, however, may be closely set when they are situated at the stem base. The stipe leaves of branched Hypopterygiaceae are distant on the entire stipe or in the basal part of the stipe and closely set above. Rachis and branch leaves are usually closely set. However, plants, including those of *Cyathophorum*, may have an entirely distant foliation, which occurs usually when they are fans.

Leaves are usually broadest at or below mid-leaf. Leaf shape varies in majority from broad-ovate to lanceolate. Vegetative leaves have never distinct alar cell groups. Leaf structures (i.e. apex, margin, border, costa, and areolation) are discussed in detail in connection with the frond leaves.

Leaves of Hypopterygiaceae may be monomorphic or dimorphic. Monomorphic is defined here as being uniform in size and shape and is used when all leaves on the same axis, or in the same part of an axis, are similar. Monomorphic leaves may take every position – i.e. dorsal, ventral, lateral, or in between – on the axis. They are symmetrical, and frequently show a close resemblance with the amphigastria (ventral leaves) of axes with an anisophyllous foliation (see below).

Dimorphic is defined as occuring in two forms, and is used here when on the same axis the lateral and ventral leaves differ in size and shape – and are differentiated in lateral leaves and amphigastria. Lateral leaves (s.str.) have a lateral position on the axis, whereby their antical half is situated at the dorsal side of the axis, and the postical half at the ventral side (Fig. 47). The lateral leaves are curved downwards in longitudinal direction, convex at their abaxial (dorsal) side, incubous, patent tot widely patent, and asymmetrical (Fig. 48b, c, f). The costa is laterally displaced and divides the leaf into two unequal halves, the one situated at the dorsal side of the stem being the largest. Amphigastria have a ventral position at the stem (Fig. 47). They are straight or curved downwards in longitudinal direction, plane or concave at their adaxial side, erecto-patent to widely patent, and symmetrical (Fig. 48d, g). The costa, if present, is positioned along the median longitudinal axis of the amphigastrium.

Stolon leaves — Stolon leaves are monomorphic. They are small, colourless, and scale-like. They are often lost, damaged or difficult to find in the tomentum of the stolon. The features of internal structures frequently show only rudimentary development. Hence, stolon leaves are omitted from the morphological examinations.

Stem leaves — Stem leaves are monomorphic or dimorphic. In general, stem leaves that are situated near the stem base are usually monomorphic, small, scale-like, and inconspicuous. They are usually entire and, like stolon leaves, frequently show only rudimentary development of internal structures. The distal stem leaves are monomorphic or dimorphic. They are – or become – conspicuous and are usually well differentiated. Above the stem base, leaves usually show increased differentiation of internal structures, which are weakest in the basal leaves and become maximally expressed in the distal ones.

However, in *Cyathophorum*, there are only minor differences between the distal stem leaves in the basal part of the stem and those situated in the median or distal part. These differences concern the size – the lowest leaves being smallest – and the shape related to size.

The stem leaves of branched Hypopterygiaceae are differentiated in stipe and rachis leaves. Such differentiation is absent from *Cyathophorum*. Stem leaves of *Cyathophorum* are best compared with the frond leaves of branched Hypopterygiaceae (see below).

Stipe leaves — Stipe leaves occur only in branched Hypopterygiaceae. They increase often gradually in size from stem (stipe) base to frond base. The stipe leaves situated at the stipe base follow the general pattern of stem leaves and are small, scale-like, and inconspicuous. Distal stipe leaves are larger than the basal ones and, except for most distal stipe leaves, they are usually smaller than the basal frond leaves.

Stipe leaves may be considered intermediates between stolon and frond leaves. Generally, leaf structures like the costa, the border, or the acumen are absent or rudimentary in stolon leaves, become weakly developed in stipe leaves, and become fully expressed in frond leaves. In branched Hypopterygiaceae, however, differences between stipe and frond leaves may vary from almost non-existing to distinct. The least differentiation between stipe and frond leaves is found in *Catharomnion*, *Dendrocyathophorum*, and in a few *Hypopterygium* species with mainly three-ranked stipe leaves. The differentiation between stipe and frond leaves is most striking in *Dendrohypopterygium*.

Frond leaves — Frond leaves are monomorphic or dimorphic. Monomorphic frond leaves are almost restricted to frond axes with an octostichous phyllotaxis, i.e. the basal part of the rachis or lower branches of branched Hypopterygiaceae with a partly octostichous phyllotaxis. Monomorphic frond leaves sometimes occur in *Lopidium concinnum*, which has tristichous frond axes. Dimorphic frond leaves are restricted to frond axes with a tristichous phyllotaxis and are present in all Hypopterygiaceae. In branched Hypopterygiaceae with a partly octostichous phyllotaxis, dimorphic frond leaves occur in the distal part of the rachis, the lower branches, and the distal branches.

The dimorphic stem leaves of *Cyathophorum* resemble the dimorphic frond leaves of branched Hypopterygiaceae.

Margin — The margin of the frond leaves is generally set with protrusions. Protrusions may show much variability in length and shape within a single leaf, between leaves of a single specimen, between specimens of a single species, and between species. Protrusions are formed by a small protruding portion of a single border (margin) cell (Fig. 49l), by protruding portions of a few adjacent border cells (Fig. 45k), or by a combination of few partly and entirely protruding adjacent border cells (Fig. 9p, 53l). They may be serrations (Fig. 59k), dents (Fig. 49b), cilia (Fig. 15q, r), or intermediates. Most species of the Hypopterygiaceae have serrate or serrate-dentate leaves. Serrate-dentate leaves are set with serrations (sharp teeth, sharp indentations) and dents (sharp teeth, rounded indentations), or their intermediates. Cilia are the longest and most pronounced protrusions and occur in *Catharomnion* and *Canalohypopterygium* (and rarely *Cyathophorum bulbosum*). Ciliate leaves predominate in *Catharomnion* and occur less often in *Canalohypopterygium.*

Border — Frond leaves of most Hypopterygiaceae are bordered. The extent of the border may vary within a single leaf, between leaves of a single specimen, between specimens of single species, and between species. A border is distinct where it is sharply delimited from the lamina by cells which differ substantially in size, shape, and usually also in colour from the laminal cells (Fig. 42a, b, m, n). A border is faint where border cells and laminal cells are weakly differentiated (Fig. 55g). A border is absent where margin cells and laminal cells are similar (Fig. 55h). The leaf border is usually strongest and widest in the basal half of the leaf and becomes often narrower, fainter, or interrupted over shorter and longer distances in the distal part. At or just above the leaf base a border is commonly absent or faint over a distance of a few cells long. In the leaves of *Dendrohypopterygium filiculiforme*, a border is mainly absent (Fig. 9a–c).

Apex — Frond leaves of Hypopterygiaceae are principally acuminate with a short to long acumen (Fig. 34) and are less often acute or subulate. The leaf border and the costa may, or may not, contribute to the acumen. The acumen itself may possess a few lateral protrusions. The leaves of *Cyathophorum bulbosum* and *C. tahitense* are rarely obtuse or rounded, lacking an acumen.

Costa — Frond leaves of Hypopterygiaceae are basically costate. The costa is single and essentially simple, although it may be weakly forked in the distal part. The length and extent of the costa is very variable, especially in amphigastria (Fig. 58k–m). Occasionally, amphigastria of *Cyathophorum* are ecostate (Fig. 58e) or have a short, double costa.

Areolation — In most Hypopterygiaceae, the areolation of the leaves is entirely prosenchymatous (Fig. 19m–o). In *Hypopterygium didictyon* and *H. discolor*, the areolation of the leaves is more complex, being parenchymatous in the basal part and prosenchymatous in the distal part. The leaves of *Dendrohypopterygium filiculiforme* have weakly parenchymatous areolation near the leaf base. The leaf areolation of *Lopidium* can be characterised as being collenchymatous (Fig. 42a, b, m, n). It is basically prosenchymatous, but the wall of the broad to short laminal cells is distinctly incrassate, in particular in the corners of the cells. A weakly collenchymatous areolation may occasionally be observed in the distal parts of frond leaves of *Hypopterygium flavolimbatum*.

Leaf cells — Leaf cells in outgrown leaves are basically hexagonal having porose walls. Cell length is variable. Laminal cells may vary in length between broader than long to short-linear. Border cells are basically rectangular or rhomboid, and less often hexagonal. They are usually longer than the laminal cells and vary in length from short to linear. Border cells shorter than the adjacent laminal cells are usually restricted to a short portion of the border near the leaf base. Acumen cells resemble border cells in length, but are principally hexagonal and occasionally rhomboid.

Cuticle — It is often difficult to soak specimens of *Canalohypopterygium*, *Catharomnion*, *Lopidium*, *Hypopterygium didictyon*, and *H. flavolimbatum* in water. These taxa are characterised by a frequently glaucous or greyish appearance. Reimers (1953) observed filmy, hyaline structures showing imprints of the areolation of the lateral leaves in slides of *Canalohypopterygium* ('*Hypopterygium setigerum*') in water, and hypothesised the presence of a water-repellent cuticle in *Canalohypopterygium* and *Hypopterygium* species.

The structures observed by Reimers (1953) are almost certainly parts of a cuticle or wax-like layer that have come loose from the leaves. I have frequently found such structures in slides of material of *Canalohypopterygium*, *Catharomnion*, *Lopidium*, and the *Hypopterygium* species *H. didictyon* and *H. flavolimbatum*. Especially in glaucous plants, though with some difficulty, a hyaline layer covering the epidermis can be observed. For *Canalohypopterygium*, Reimers (1953) proposed that rudimentary branches play a role in the production of the cuticle or wax-like layer. However, because *Hypopterygium* and *Lopidium* species lack such rudimentary branches and may be conspicuously glaucous and difficult to soak, it is beyond any doubt that even in *Canalohypopterygium* and *Catharomnion*, leaf cells predominantly contribute to the formation of the water repellent, cuticle.

Vegetative propagation

Vegetative propagation in Hypopterygiaceae may occur by fragments of the gametophore or, in gemmiferous species, by gemmae. After the fragments and gemmae have become detached and dispersed, they may form new protonemata in suitable habitats, which in turn may form new gametophores.

Fragments — Fragments may be formed by accidental fragmentation of the gametophore. In *Dendrohypopterygium*, *Lopidium concinnum*, and most species of *Hypopterygium*, however, distal parts of the frond may act as specialised vegetative propagulae. In such species, entire leaves and/or the distal (apical) foliate part of the outermost frond axes may become loosely attached to the gametophore. As a consequence, they easily detach and become caducous. Leaf detachment occurs by breaking off the leaf from the main axis at the leaf base (following the leaf insertion; Fig. 24, 38b). The detachment of distal parts of frond axes is generally preceded by the occurrence of brown spots on the axes. These brown spots correspond with weak spots, and presumably mark dead or dying epidermal and cortical tissue with disintegrated cell walls[1].

1) After the detachment of the distal part of a frond axis, usually, just under the brown spot, a few tiny branches are formed as new innovations on the basal, remaining part of the axis.

Gemmae — The gemmae are, in fact, specialised secondary protonemata. They are filiform, uniseriate (e.g. Fig. 28m, 39, 53c, m), and form on specialised rhizoids, referred to as gemmaphores, that sprout in clusters from epidermal cells. These epidermal cells are situated in the basal part, and occasionally the middle part, of segments. Consequently, each cluster of gemmae is situated in the axil of a leaf, which in fact, is not the associated leaf, but the one that belongs to the lower segment.

A gemmaphore may be simple and bear one gemma or may be branched to form two or more gemmae. The gemmaphores show often intra- and interspecific variability in length. One of the reasons of this variability is explained by Correns (1899), who observed in *Lopidium struthiopteris*, that, after the detachment of the gemma which it had produced, the distal cell of the gemmaphores continues to grow and usually forms a few new gemmaphore cells, which in turn produce new gemmae. This process probably occurs also in other gemmiferous species of the Hypopterygiaceae.

The gemmae are usually simple and consist of an uniseriate filament of a few to many cells. Gemmae become easily detached, because the connection between a terminal cell of the gemmaphore and basal cell of the gemma becomes weak. Correns (1899) observed that both basal and distal cells of gemmae of the present species *Lopidium struthiopteris* were able to germinate. Because the gemmae of all Hypopterygiaceae are very similar, it seems reasonable to suppose, that gemmae of other species are capable of germinating in two directions as well.

Clusters of gemmae are usually formed in the axils of the lateral leaves and occur somewhat less frequently in the axils of amphigastria. They are usually produced by the distal part of the stem in simple Hypopterygiaceae and by the distal part of the ultimate frond axes in branched Hypopterygiaceae. In *Hypopterygium vriesei* almost every part of the frond axes may be set with clusters of gemmae (Fig. 27). Gemmae are rarely produced by stolons and flagelliform innovations.

THE SEXUAL REPRODUCTIVE PHASE

Reproductive features are important at various taxonomic levels within the Hypopterygiaceae. There is a considerable amount of inter- or intraspecific variation, but most striking is the interspecific variation in peristome and calyptra characters that is found in *Cyathophorum*. Although the sporophytes of *Dendrohypopterygium*, *Canalohypopterygium*, *Hypopterygium*, and *Dendrocyathophorum* show some differences in a few characters, e.g. the number of IPL cells (see p. 52; Edwards, 1979), they are basically similar. The sporophytes of *Catharomnion*, *Cyathophorum*, and, to a lesser extent, *Lopidium* are considerably different.

Fruiting plants have not been found in *Cyathophorum tahitense* and *Hypopterygium vriesei*.

Sexual condition

Fourteen species of Hypopterygiaceae are strictly dioicous and one (*Hypopterygium elatum*) is presumably dioicous. *Dendrocyathophorum decolyi* is the only strictly autoicous species among the monoicous ones. The others are heteroicous with various frequencies of male, female, and bisexual gametoecia. In *Lopidium concinnum* and

Cyathophorum africanum, bisexual gametoecia are rare. Plants of *L. concinnum* may sometimes be strictly unisexual.

Gametoecia

Hypopterygiaceae are pleurocarpous mosses (sensu La Farge-England, 1996). Their gametoecia are formed by lateral primordia and are specialised, short, leafy branches with determinate growth bearing terminal gametangia. The gametoecia are situated as buds on the stem or the first order branches, in majority between the lateral leaves (Fig. 40) or the dorsal leaves, and are rarely situated between ventral leaves or amphigastria. Gametoecia are usually situated in the basal and middle parts of the gametophores. Only in *Catharomnion* (male plants; Fig. 14) and *Cyathophorum*, they are occasionally situated in the distal part of the gametophores. Gametoecia may be either male, termed perigonia, female or bisexual, both termed perichaetia.

Gametoecial branches — The gametoecial branches are usually simple. Primordia of gametoecial branches have not been observed, although they are presumably present and dormant. In some plants of *Dendrohypopterygium filiculiforme* small, subfloral branchlets sprout from the gametoecial stalk.

The axis of a sporophyte-bearing perichaetium is often longer than those of non-sporophyte bearing perichaetia. Apparently, sporophyte growth induces transformation of the perichaetial branch into a stalk.

Gametoecial axillary hairs — Gametoecial axillary hairs are usually present, although sometimes difficult to find. They are not substantially different from axillary hairs of normal axes, but they may show minor differences with the latter in the number per leaf and the number and size of cells. Gametoecial axillary hairs located between the gametangia and the paraphyses at the top of the gametoecial branch are generally somewhat larger than those lower on the gametoecial branch.

Gametoecial leaves — The gametoecial leaves of Hypopterygiaceae are closely set in spirals. They are symmetrical and usually concave. Perichaetial leaves of *Lopidium concinnum*, however, are frequently V-shaped in full-grown perichaetia. The gametoecial leaves differ in size and shape from the normal leaves, including amphigastria. The outer (basal) gametoecial leaves are shorter and narrower than the inner (distal) ones. The most inner (distal) gametoecial leaves are sometimes smallest, presumably because they are still juvenile.

Gametoecial leaves are entire or nearly so, even in species with normal leaves set with distinct protrusions at the margins. Gametoecial leaves lack distinct alar cell groups, except the perichaetial leaves of *Catharomnion*, which may possess a distinct group of alar cells. Gametoecial leaves are shouldered or not, but the apex is always acuminate. Border and costa may be absent or present. The extent of the border and the costa, when present, shows much inter- and intraspecific variation. The areolation is prosenchymatous with hexagonal cells, and sometimes somewhat parenchymatous with rectangular or rhomboid cells. The cell length ranges from short to short-linear.

Paraphyses — In Hypopterygiaceae, paraphyses are absent or present. Paraphyses are usually filiform, hyaline, uniseriate, and few to numerous cells long (Fig. 33f–r). They are entirely colourless, brown in the basal part, or entirely brown (Fig. 49i, j, p, q). Usually, the basal cells of the paraphyses are different from the distal ones and show some resemblance with the basal cells of the axillary hairs. However, cell differentiation is generally less obvious in paraphyses than in axillary hairs.

Paraphyses are usually much longer than the gametoecial axillary hairs and have often longer and, in particular, broader cells. In South American representatives of *Hypopterygium tamarisci* – and perhaps also in Asian and Australasian ones – short paraphyses (Fig. 33f–h) are almost identical with gametoecial axillary hairs (Fig. 33a–d), which may also be placed close to the gametangia. In such cases, it is very difficult to distinguish paraphyses from the gametoecial hairs.

Paraphyses are apparently persistent, and, when present, are found in both young and old gametoecia. In most Hypopterygiaceae, there is apparently neither production of new paraphyses nor growth of existing ones after the formation of ripe gametangia and subsequent ageing of the gametoecia, including development of perichaetia after fertilisation induced by the growth of the sporophyte.

Perichaetial paraphyses of *Lopidium*, however, are an exception and may show additional growth. When present, paraphyses in perichaetia prior to sporophyte development are always filiform and mainly uniseriate (up to 3 cells wide at most, Fig. 42i–k). In full-grown perichaetia, filiform and leaf-like paraphyses may be found. The filiform paraphyses resemble those of the perichaetia prior to sporophyte development. The leaf-like paraphyses, however, are much longer and several cells wide (up to 20 cells in *Lopidium concinnum*, Fig. 42r; up to 5 cells in *L. struthiopteris*, Fig. 42h). It is almost certain that, probably induced by development of the sporophyte after fertilisation, the leaf-like paraphyses in *Lopidium* result from growth of filiform paraphyses. The paraphyses of *Lopidium* are usually entirely colourless or pale brown to brown in the basal and middle parts, but the leaf-like ones are sometimes pale green.

The position of the paraphyses of *Lopidium concinnum* on the perichaetial disc suggest that they are homologous with axillary hairs (see under this species, note 10, p. 263). The paraphyses were often found to be placed just a single cell above the insertion of the distal perichaetial leaves, just like gametoecial axillary hairs, and they are possibly associated with distal perichaetial leaves or their potential positions. In addition, gametoecial axillary hairs of *L. concinnum* – and those of other Hypopterygiaceae – have sometimes a central position on the perichaetial (gametoecial) disc and are placed between the archegonia (gametangia), just like paraphyses. Gametoecial axillary hairs are absent from positions where paraphyses are present. However, the relative position of the paraphyses and gametoecial hairs is sometimes difficult to observe and further anatomical and ontogenetic research on the homology of the paraphyses of *L. concinnum* and other species is necessary.

Gametangia — Gametoecia usually contain few to numerous gametangia. Perigonia contain antheridia; perichaetia contain archegonia and, when bisexual, antheridia. Antheridia and archegonia develop from a single initial surface cell at the apex (disk) of the gametoecial stalk. A detailed description of the development of antheridia and archegonia in *Cyathophorum bulbosum* is given by Burr (1938).

Fertilisation — The process of fertilisation and embryo development in *Cyathophorum bulbosum* (Burr, 1938) represents that of all Hypopterygiaceae. Two or more archegonia in a single perichaetium may be fertilised. Afterwards, the stalk and the venter of the archegonia start to grow. This growth passes synchronously with the growth of the embryo and, later, the young sporophyte. In a single perichaetium, two or more embryos may develop up to a certain stage, but eventually one will outgrow the others; the others stop growing or abort. The surviving embryo forms the mature sporophyte. In association with tissue of the perichaetial disc, the surviving archegonium develops in concert with the embryo or the young sporophyte to form the vaginula (basal part) and the calyptra (distal part). Irrespective of the number of archegonia that a perichaetium contains, all Hypopterygiaceae have usually only a single mature sporophyte per perichaetium.

Vaginula

In Hypopterygiaceae, the foot of the seta is positioned in a distinct vaginula. In most species, the vaginula is developed from the perichaetial disc and the basal part of a fertilised archegonium (cf. Burr, 1938). The vaginula is often set with a few other archegonia (e.g. Burr, 1938) and, if present, with a few to several persistent paraphyses. Sometimes, even a few perichaetial axillary hairs are attached to the vaginula. From this, it is clear that the disc of the perichaetium contributes to the formation of the vaginula.

In *Dendrohypopterygium filiculiforme* and *Lopidium struthiopteris* the archegonium does not contribute to the formation of the vaginula, which, consequently, consists entirely of the outgrown perichaetial disc. Arguments for this are found in the paraphyses that are attached to the basal part of the calyptra in these species (Fig. 5s, 41g). In *Lopidium struthiopteris* the basal part of the calyptra is occasionally even set with a few archegonia. This is only possible, when in the process of calyptra formation the distal part of the perichaetial disc disrupts from the early vaginula and becomes the basal part of the calyptra.

The vaginula is usually very different from the perichaetial stalk in shape and consistence. In *Dendrohypopterygium arbuscula*, however, the vaginula is almost a prolongation of the stalk. In this species, the foot of the sporophyte may even penetrate the top of the perichaetial stalk.

Sporophytes

A detailed description of ontogenetic development of the sporophyte in *Cyathophorum bulbosum* is given by Burr (1938).

In most genera of the Hypopterygiaceae, the sporophyte is usually projecting from the gametophore by an ascending or vertical seta (e.g. Fig. 6). In *Cyathophorum*, however, the sporophytes are usually projecting from beneath the gametophore by a descending seta (e.g. Fig. 50). In some specimens of *Catharomnion*, *Lopidium*, and *Cyathophorum*, the sporophytes are lying in the plane of the gametophore by their horizontally projecting setae. The presence of such horizontal sporophytes is probably caused by an unusual growing direction of the gametophore from a vertical substrate, i.e. in *Catharomnion* and *Lopidium* by a gametophore that is steeply ascending and in *Cyathophorum* by a foliate stem that is steeply hanging.

Setae

The sporophytes of *Dendrohypopterygium*, *Canalohypopterygium*, *Hypopterygium*, and *Dendrocyathophorum* have a cygneous or flexuose to uncinate seta. Their capsules are more or less directed downwards, varying from cernuous (slightly drooping), inclined, nutant (nodding), to pendulous. The sporophytes of *Lopidium* may show similar features, or have a straight seta with an erect capsule. The seta of *Catharomnion* is straight or curved to some extent. The seta of *Cyathophorum* is straight or curved downwards. The capsules of *Catharomnion* and *Cyathophorum* are erect and point to the same direction as the distal part of the seta, even when the seta is curved.

In most genera of the Hypopterygiaceae, the seta has usually no ornamentation. It is occasionally slightly mamillate or weakly rugose at the base of the capsule and, but less often, in the distal part of the seta. By contrast, the seta of *Lopidium* is weakly to distinctly mammillate.

Capsules

The capsules of Hypopterygiaceae are circular in cross section. In most species, the capsules have a more or less rounded outline in side view, but in *Lopidium* and some *Cyathophorum* species the walls of the urn are frequently almost parallel in side view between base and orifice and form a tube, which results in a more or less cylindrical shape of the capsule.

Most capsules are ovoid or ellipsoid or, when the urn narrows abruptly at both ends, barrel-shaped. Most urns are one to two times as long as wide, but in a few species they may become more than twice as long. Such capsules are usually ovoid-oblong or ellipsoid-oblong. Capsules being almost equally long as wide are globose or subglobose.

The shape of the capsule shows most interspecific and in some species also intraspecific variability in *Lopidium*, *Hypopterygium*, and *Cyathophorum*. Their urns may show a gradual or abrupt widening from base to orifice, having their widest part near the orifice, which results in turbinate or cupulate capsules. In *Lopidium*, the urn may also be gradually, but little, widened from base to orifice, resulting in a clavate capsule. Occasionally, the capsule of *Cyathophorum* and *Hypopterygium* is strikingly contracted below the orifice, which results in urceolate capsules.

The capsules of *Catharomnion* are unique among the Hypopterygiaceae, and differ from those of the other species in shape and often also in colour. In *Catharomnion*, the orifice may be oblique or transverse, whereas in the other *Hypopterygiaceae* it is always transverse. The urns of the *Catharomnion* capsules are ovoid to ovoid-oblong and have above their widest point straight to weakly curved, tapering walls which form a narrowing tube (Fig. 13).

The capsule neck is usually conspicuously pustulose in *Dendrohypopterygium* and *Canalohypopterygium* and possesses usually entirely sunken stomata (Fig. 7, 10). In *Hypopterygium*, the surface of the neck shows interspecific and in some species intraspecific variation and varies between smooth with superficial stomata to pustulose with sunken stomata. The neck is weakly pustulose in *Catharomnion* and smooth or nearly so in *Dendrocyathophorum*, *Lopidium*, and *Cyathophorum*. These genera have superficial stomata.

Exothecial cells are extremely variably in shape, and may even show considerable variation within a single urn. The cells may vary in shape from hexagonal to rectangular and in relative length from ovate to elongate. The transverse and longitudinal walls are thin or (partly) incrassate, but the corners are often thickened.

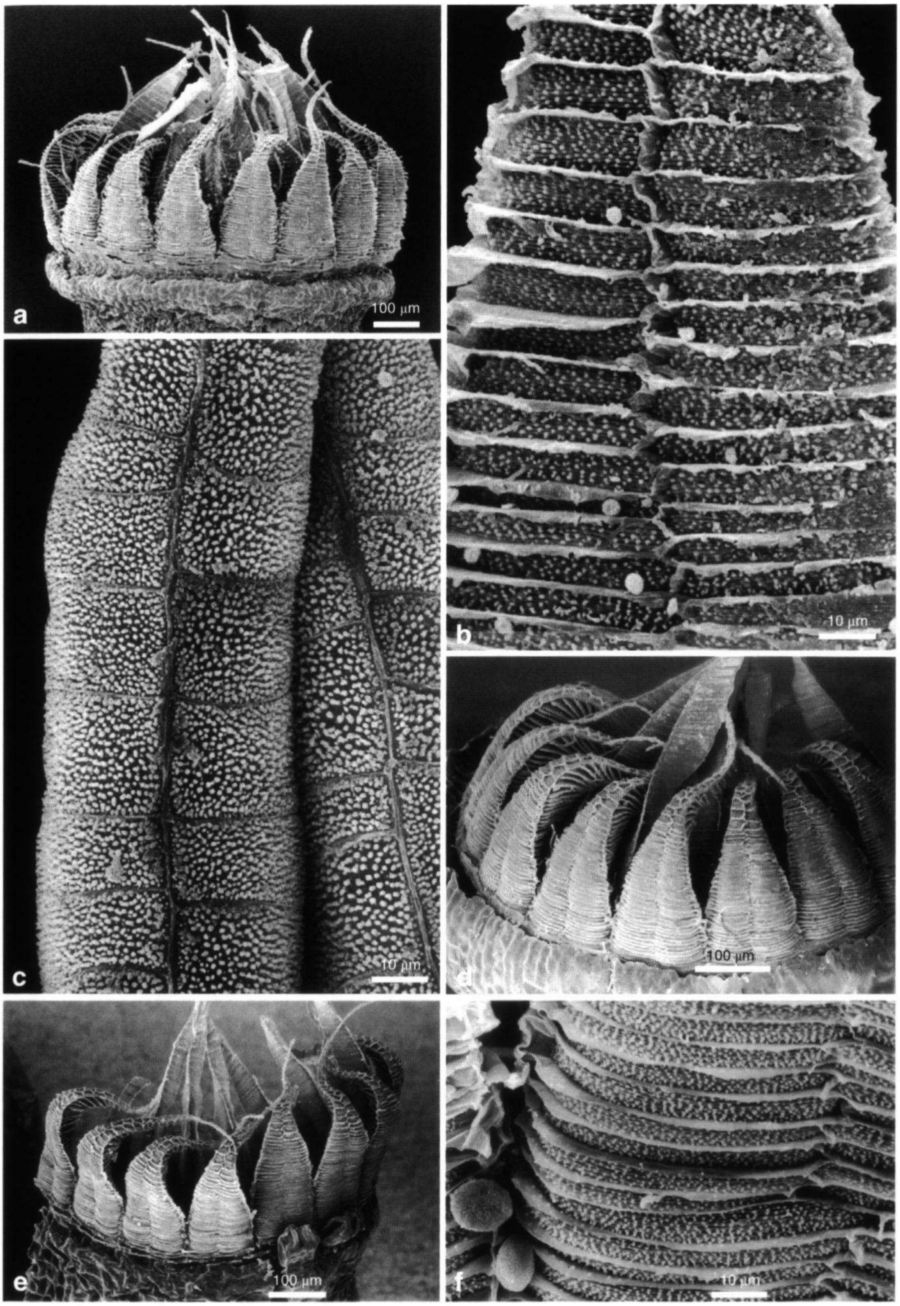


Plate 2. SEM photographs of peristomes. a, b. *Dendrohypopterygium filiculiforme* (Hedw.) Kruijer: a. peristome; b. detail exostome tooth; c. *Catharomnion ciliatum* (Hedw.) Wilson, detail endostome (processes); d. *Canalohypopterygium tamariscinum* (Hedw.) Kruijer, peristome; e, f. *Hypopterygium tamarisci* (Sw.) Brid. ex Müll.Hal.: e. peristome, f. detail basal part of exostome tooth (a, b: *Allison 4257*, JE; c: *Beever 70–26*, CBG; d: *Visch s.n.*, '19.11.1972', L; e, f: *Herzog 2730*, L).

The abscission zone between the urn of the capsule and the operculum may, or may not, be differentiated as a distinct annulus. In *Cyathophorum bulbosum* detachment of the operculum occurs by opening and subsequent recurling of the annulus, whereby the annulus detaches from both the operculum and the urn. Dehiscence of the operculum in *C. africanum* is described under this species, note 1, p. 336. The dehiscence mechanisms of other species of the Hypopterygiaceae have not been observed in detail.

The two *Dendrohypopterygium* species, *Hypopterygium didictyon*, *H. discolor*, and *Cyathophorum bulbosum* have always a distinct annulus. In most of the other species the annulus may display various degrees of development. In *Hypopterygium tamarisci* an annulus is often weakly differentiated or absent. It is always absent in *Lopidium struthiopteris* and the remaining *Cyathophorum* species (except *C. africanum*).

Annular cells are short to oblong and isodiametric to basically triangular or rhomboid-ovate. Adjacent triangular or rhomboid-ovate cells have usually an opposite position like teeth in a zipper, e.g. a triangular or rhomboid-ovate cell is surrounded by two obtriangular or rhomboid-obovate cells. However, even in a single, distinctly differentiated annulus, annular cells may show considerable variation in shape and relative length and isodiametric cells may be alternate (ob)triangular or rhomboid-(ob)ovate.

Peristome

The peristome of the Hypopterygiaceae is diplolepidous – two laterally adjacent columns of cells contribute to the dorsal face of a single exostome tooth (Plate 2b, d) – and is double in all but one genus. A complete peristome consists of an exostome with16 teeth and an endostome with 16 processes (Plate 2a). *Catharomnion* is the only genus which lacks an exostome.

Exostome teeth are formed from cell wall material between the cells of the outer peristomial layer (OPL) and the primary peristomial layer (PPL) (see Edwards, 1979; Mueller & Neumann, 1988). Each tooth is formed by two columns of OPL cells and a single column of PPL cells. The columns are decreasing in size and tapering towards the apex of the capsule. OPL cells produce the dorsal plates of a tooth, PPL cells the ventral ones.

During exostome development, cell wall material is deposited on the adjacent, periclinal walls between the OPL and PPL cells, which become incrassate at both sides, and to a lesser extent, the anticlinal, transverse walls of the PPL cells. Ultimately, the anticlinal, radial and transverse walls of the OPL and PPL cells rupture, which results in formation of free teeth. Each tooth consists of two joined files of periclinal plates on the dorsal (outer) face and a single file of periclinal plates, usually joined with transverse plates, on the ventral (inner) face. The periclinal plates at the outer face are termed dorsal plates, those at the inner face are termed ventral plates. Remnants of transverse and radial cell walls of the OPL cells, which may be visible between the separate dorsal plates, are termed lamellae. The transverse plates at the ventral face (remnants of transverse walls of the PPL cells) are termed trabeculae.

The sizes of the exostome teeth and the ornamentation of the dorsal plates show interspecific and sometimes intraspecific variation (Plate 4e, f, Fig. 59q–s). The dorsal plates usually show ornamentation, which is correlated with the thickness of the plates. The ornamentation is presumably basically papillose. In many species, the dorsal

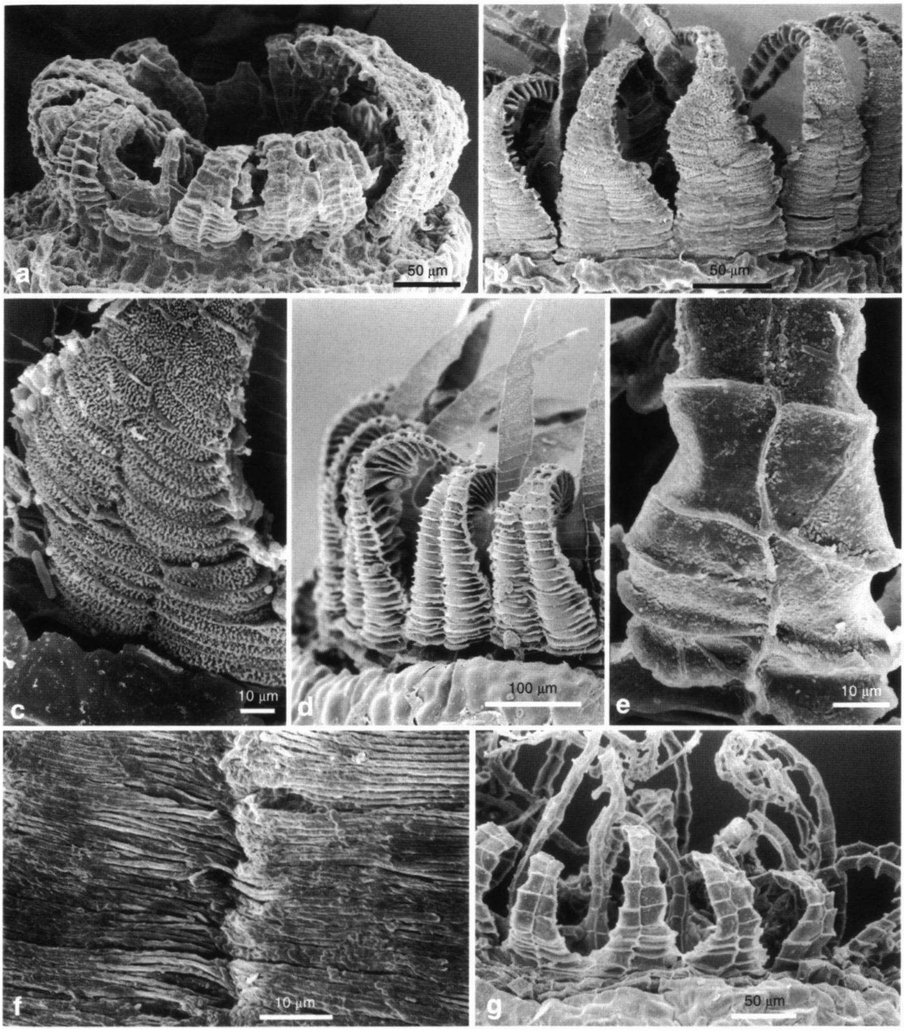
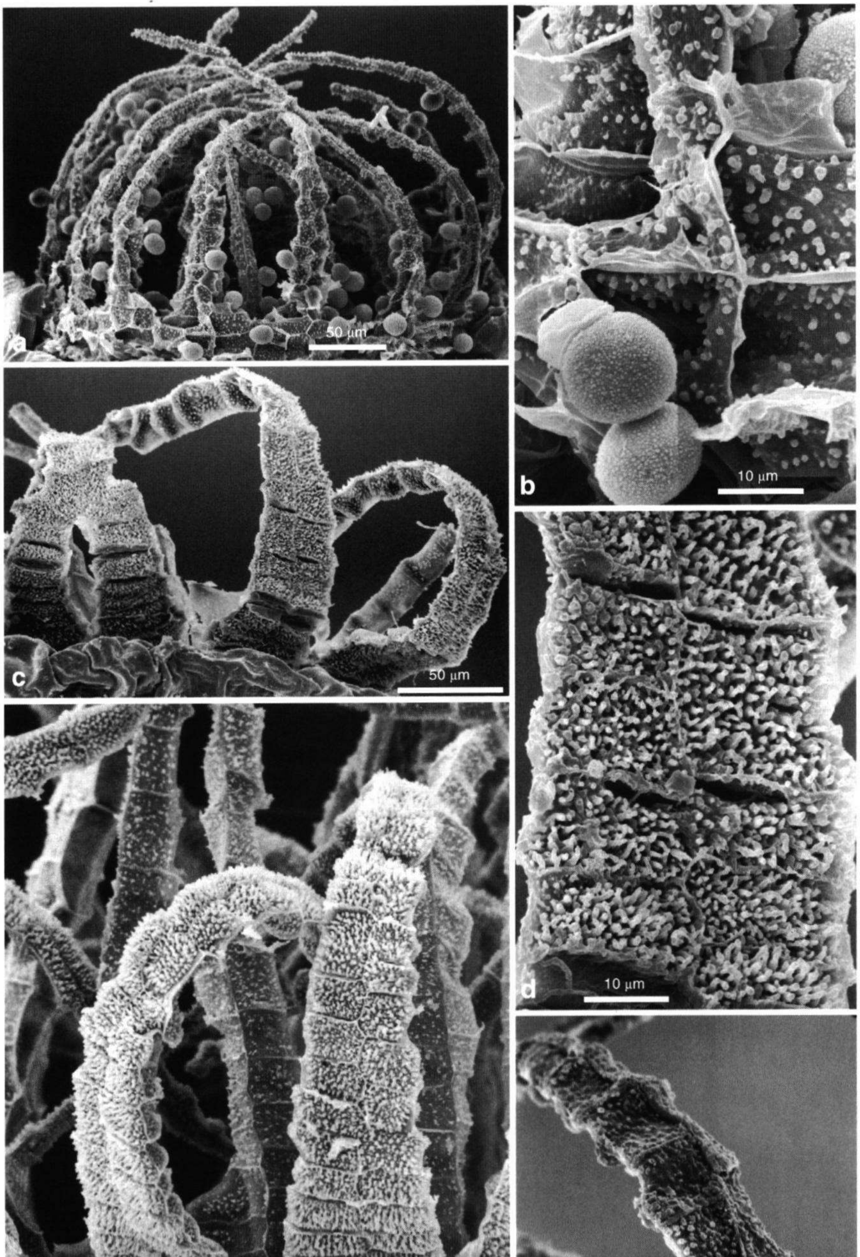


Plate 3. SEM photographs of peristomes. a. *Lopidium struthiopteris* (Brid.) M. Fleisch., peristome (partly covered with debris); b. *L. concinnum* (W. Hook.) Wilson, peristome; c. *Dendrocyathophorum decolyi* (Broth. ex M. Fleisch.) Kruijer, detail exostome; d. *Cyathophorum bulbosum* (Hedw.) Müll. Hal., peristome; e, g. *C. adiantum* (Griff.) Mitt., e. detail basal part of exostome tooth, g. peristome; f. *C. spinosum* (Müll.Hal.) H. Akiyama, detail basal part of exostome tooth. (a: *Streimann 30553*, L; b: *Beckett 854*, L; c: *Meijer B7598*, L; d: *Van Zanten 1285*, L; e, g: *Decoly & Schaul, Bryoth. Levier 2571*, S; f: *Brass 12934*, L).

Plate 4. SEM photographs of peristomes. a, b. *Cyathophorum africanum* Dixon, a. peristome with a few preperistomial thickenings; b. detail base of exostome tooth with spores (background: process of endostome); c, d. *C. parvifolium* Bosch & Sande Lac., c. exostome, d. detail basal part of exostome tooth; e, f. *C. hookerianum* (Griff.) Mitt., e. detail of peristome, f. detail of exostome tooth (a, b: *Pócs & Harris, 6158/B*, EGR; c, d: *Meijer B9095*, L; e: *Williams 1671*, NY; f: *Norkett 7398*, BM).


a
50 µm
b
10 µm
c
50 µm
d
10 µm
e
50 µm
f
10 µm

plates in the basal part of the teeth have become very thick and conspicuously papillose-striate (Plate 2b, f, 3c) or striate (Plate 3f). In other species, the basal dorsal plates remain relatively thin and are papillose (Plate 4b, d, f) or smooth (Plate 3e). In all species, the distal dorsal plates and all ventral plates of exostome teeth are thin and papillose. The median line between the two rows of dorsal plates is zigzag (Plate 2f) and usually easily visible between the dorsal plates, especially when they are (papillose-)striate.

The trabeculae (best visible in Plate 2d and 3d) have a similar ornamentation as the ventral plates of the exostome teeth. The sizes of the exostome teeth and the projection of the trabeculae show interspecific and sometimes intraspecific variation. In exostome teeth with well-pronounced trabeculae, the trabeculae may show considerable variation in length within a single tooth, whereby the protrusion of the trabeculae is strongest in the middle parts of the exostome teeth, and less near the tooth base (Plate 3d). In all types of exostome teeth, the trabeculae in the distal part of the teeth are shortest, and may even become absent at the tooth apex.

Dendrohypopterygium (Plate 2a,b), *Canalohypopterygium* (Plate 2d), *Hypopterygium* (Plate 2e,f), and *Dendrocyathophorum* (Plate 3c) possess a pronounced exostome with thick dorsal plates and firm and distinctly projecting trabeculae. The ornamentation of the dorsal face of the teeth is striate or papillose-striate in, at least, the basal half of the dorsal face, and becomes papillose above. The exostome of *Cyathophorum bulbosum* (Plate 3d), *C. spinosum* (Plate 3f), and *Lopidium concinnum* (Plate 3b) is essentially similar, but trabeculae may become short in *L. concinnum*.

The exostome of *Lopidium struthiopteris* (Plate 3a) and four *Cyathophorum* species (*C. adiantum*, *C. africanum*, *C. hookerianum*, *C. parvifolium*; Plate 3e, g, 4a–f) have relatively thin dorsal and ventral plates and have generally much shorter trabeculae, which is most obvious in the middle part of the teeth. In *Lopidium struthiopteris*, the ornamentation of the dorsal face of the teeth is weakly (papillose-)striate in the basal third of the dorsal face, and becomes papillose above. In the four *Cyathophorum* species, the dorsal face of the exostome teeth is usually entirely conspicuously papillose, but in *Cyathophorum hookerianum* it is occasionally weakly striate in the basal fourth of the teeth and in *C. adiantum* it may be partly or nearly entirely smooth.

Catharomnion lacks an exostome, but pattern of exostome formation is visible at the inner side of the operculum in *Catharomnion*, where a slight thickening of the periclinal and transverse walls of PPL cells, sometimes with few minute papilla, indicates a rudimentary stage in the ontogeny of exostome formation.

The endostome is formed from cell wall material between the cells of the PPL and those of the inner peristomial layer (IPL). The periclinal walls between these layers become less incrassate during peristome development than those between the OPL and the PPL, which are involved in exostome formation (except in *Catharomnion*).

The ratio between the number of PPL and IPL cells is variable and shows inter- and intraspecific variation. In species with intraspecific variation, the number of IPL cells may vary within a single specimen or even urn. The number of IPL cells ranges from four to eight – and in *Cyathophorum bulbosum* occasionally up to ten – per every pair of PPL cells. Most variation is found in *Cyathophorum*.

The endostome of Hypopterygiaceae is minutely to pronouncedly papillose (Plate 2c–e, 4a, e). It is usually papery (membranous) and colourless or pale yellow and hyaline. The endostome of *Catharomnion* (Plate 2c) is, on the other hand, thick and firm and colourless to brown. In every species, the endostome consists of a basal membrane and 16 processes. The basal membrane reaches a third of the length of the exostome teeth or more in species with pronounced exostome teeth and reaches up to a fourth of the length of the exostome teeth at most in species with less incrassate exostome teeth. Endostomial cilia may be present or absent. The number of cilia depends on the number of IPL cells (cf. Edwards, 1979), and shows much interspecific and sometimes intraspecific variation. Cilia are conspicuous in *Dendrohypopterygium*, *Canalohypopterygium*, *Hypopterygium*, *Dendrocyathophorum*, and *Cyathophorum bulbosum*. They are absent or rudimentary in *Lopidium* and five other *Cyathophorum* species.

Cyathophorum africanum is the only species with preperistomial thickenings (Plate 4a) and a few rudimentary teeth between the IPL and the outer perithecial layer.

Operculum

The operculum is rostrate from a conical base. In *Cyathophorum africanum* the operculum is short-rostrate, i.e. the rostrum is approximately equally long as or shorter than the conical part (Fig. 55i). In the other species, the operculum is long-rostrate, i.e. the rostrum is longer than the conical part (Fig. 5r), although short-rostrate operculae occasionally also occur in *Hypopterygium tamarisci* and *Dendrocyathophorum decolyi*.

The rostrum is straight and erect in *Canalohypopterygium*, *Catharomnion*, and *Dendrohypopterygium* (e.g. Fig. 12p). In the other taxa the rostrum is oblique (e.g Fig. 21n, o), although it may occasionally be straight in two *Cyathophorum* species (*C. adiantum* and *C. hookerianum*).

The operculum of *Hypopterygium elatum* is not known.

Calyptra

The shape of the calyptra is variable within the Hypopterygiaceae. The calyptra is strictly mitrate in *Canalohypopterygium*, *Catharomnion*, and three *Cyathophorum* species (e.g. Fig. 12q, 52g, l). It is mitrate to cucullate in *Cyathophorum hookerianum* (Fig. 58p, q), and occasionally mitrate to cucullate in *Hypopterygium flavolimbatum*. In the other Hypopterygiaceae, the calyptra is cucullate (e.g. Fig. 21o, 58g).

A relation between the shape of the calyptra, the portion of the operculum that it covers, and the direction of the rostrum was not found. In most Hypopterygiaceae, the calyptra is entirely covering the operculum. In *Dendrocyathophorum*, the covering by the calyptra is restricted to rostrum and distal part of the operculum.

In most species, the calyptra has no ornamentation and is naked. In species with a naked calyptra, the outgrown archegonium is possibly disrupted into two parts, whereby the distal part of the archegonium becomes the calyptra and the basal part the vaginula. If Burr's (1938) observations on *Cyathophorum bulbosum* are also true for other Hypopterygiaceae with a naked calyptra, the outgrowing archegonium ruptures at the base of the venter, whereby the calyptra originates from the venter and the vaginula from the stalk of the archegonium.

However, the basal, nearly marginal part of the calyptra of *Dendrohypopterygium filiculiforme* and *Lopidium struthiopteris* has an indumentum of a few, but distinct, paraphyses (Fig. 5s, 41g) and in *Lopidium struthiopteris* occasionally of a few archegonia. In these two species, the outgrowing archegonium must have been disrupted in a zone that contains paraphyses (*D. filiculiforme*, *L. struthiopteris*) and (unfertilised) archegonia (*L. struthiopteris*). Consequently, the distal part of the calyptra has to originate from the venter and the stalk of the archegonium and the basal part from a portion of the perichaetial disc.

Apart from indumentum, the surface of the calyptra of Hypopterygiaceae is usually smooth, but it may be slightly mamillate in three *Cyathophorum* species (*C. bulbosum*, *C. spinosum*, *C. adiantum*).

The texture of the calyptra is either entirely membranous, entirely fleshy, or membranous in the basal part and fleshy in the distal part. The apex of the calyptra is always (somewhat) fleshy. All calyptrae are thicker in the distal part (5–8 cell layers) than in the basal part (2–6 cell layers).

The differences in texture are presumably caused by yet unknown ontogenetic processes during growth of the archegonium after fertilisation and/or after the moment of disrupture of the calyptra from the vaginula. Cell elongation during growth of the fertilised archegonium may strongly affect the texture of the calyptra, whereby a strong elongation presumably results in a membranous texture of the calyptra and a weak elongation in a fleshy texture. The (relative) position of the rupture between the early vaginula and the early calyptra, which is ontogenetically determined, plays presumably also an important role. This is suggested by the fleshy calyptra of three *Cyathophorum* species (*C. bulbosum*, *C. spinosum*, *C. adiantum*), which closely resembles the apical part of the calyptra of other Hypopterygiaceae.

The colour of the calyptra shows interspecific variability that is not correlated with shape or texture. Irrespective of the colour of the calyptra, the calyptra apex has generally a darker colour than its lower parts.

The calyptra of *Hypopterygium elatum* is not known.

Spores

The spores are subglobose to short-ellipsoid. The ornamentation is minute and consists of short and granulum- or pilum-like processes (cf. Erdtmann, 1965). A trema is probably lacking, but Erdtman (1965) indicated that he may have seen a thin, trema-like area in the proximal face of spores of *Hypopterygium flavolimbatum*. For the present species *H. flavolimbatum* and *H. tamarisci*, Erdtmann observed the exine to be less than 1 µm thick. Probably, in all spores of Hypopterygiaceae the exine does not exceed 1 µm in thickness.

In particular in *Cyathophorum* species, the spores show much intraspecific variation in size. The variability ranges show usually distinct overlap between (closely related) species.

CYTOLOGY

Chromosome numbers of Hypopterygiaceae are known for 6 species belonging to *Cyathophorum*, *Lopidium*, and *Hypopterygium* (Table 1). The chromosome numbers were obtained from counting chromosomes in mitotic stages in gametophytic material (Shimotomai & Koyama, 1932a, b; Inoue & Uchino, 1969; Newton, 1973; Inoue, 1979)

Table 1. Chromosome numbers of Hypopterygiaceae. *C.* = *Cyathophorum*; *H.* = *Hypopterygium*; *L.* = *Lopidium*.

species	chromosome number(s)	origin of material	literature
C. bulbosum	n = 5	Australia (Victoria)	Ramsay, 1967b, 1974
	n = 5	New Zealand	Newton, 1973
H. didictyon	n = 6	New Zealand	Newton, 1973
H. flavolimbatum	n = 9	Japan	Inoue & Uchino, 1969
	n = 18	Japan, Taiwan	Shimotomai & Koyama, 1932a, b; Inoue & Uchino, 1969; Inoue, 1979
H. tamarisci	n = 18	Venezuela	Inoue, 1979
	n = 9, 18	Japan	Inoue, 1979
	n = 9, 18, c. 27, 36	Australia (New South Wales)	Ramsay, 1967a
L. concinnum	n = 12	Australia (New South Wales)	Ramsay, 1967b, 1974
L. struthiopteris	n = 11	Japan	Inoue, 1979

or meiotic stages of the sporocyte (Ramsay, 1967a, 1974). Chromosome morphology and chromosome behaviour was taken into account in only a few studies (Ramsay, 1967a, 1974; Inoue & Uchino, 1969).

Hypopterygium shows the highest intrageneric variation in chromosome numbers within the family (Table 1). Intraspecific variation in chromosome numbers was found in *H. flavolimbatum* and *H. tamarisci*. The highest variation in ploidy levels was found in *H. tamarisci* in its present circumscription. Ramsay (1967a) found a ploidy series of Australian *H. tamarisci* (Table 1) in plants which were growing in close proximity, some even on the same log.

Intraspecific variability in cytotypes is a generally observed phenomenon in mosses, and is related to polyploidy and/or aneuploidy (cf. Pryzwara & Kuta, 1995). The cytological data presented by Ramsay (1967a) and Inoue & Uchino (1969; see Table 1) provide evidence that the observed polyploids in *Hypopterygium flavolimbatum* and *H. tamarisci* are euploids with the basic chromosome number x = 9. Intraspecific aneuploidy has not been observed within the Hypopterygiaceae with the possible exception of abnormalities found for plants of *H. tamarisci* with chromosome number n = c. 27 by Ramsay (1967a).

Intraspecific chromosome races in moss species are generally morphologically indistinct (Pryzwara & Kuta, 1995), but Ramsay (1967a) found few morphological differences in her ploidy series of plants of *Hypopterygium tamarisci* (see '*H. tamarisci*', note 62, p. 237). The most substantial difference is, that her plants with n = 9 are dioicous, whereas her polyploids are monoicous. This is in accordance with a general pattern found in moss and liverwort species (Pryzwara & Kuta, 1995) and is well explained by a genetically based sexual predetermination, whereby primary dioicy is expressed in the haploid cytotype due to the presence of a single sex chromosome. When polyploids originate from dioicous parents, monoicy due to the presence of both types of sex chromosomes would be expected if the polyploids originate from an unreduced spore (Ramsay & Berrie, 1982). Ramsay (1967a), however, found no evidence for the occurrence of sex chromosomes in *H. tamarisci*.

It is obvious, that intra- and intergeneric aneuploidy occurs within the Hypopterygiaceae (Table 1), but the available cytological data give no insight in the processes that produced this aneuploidy. Ramsay (1974) considered the chromosome number $x = 9$ basic for *Hypopterygium* (cf. Ramsay, 1983), but she was not aware of Newton's (1973) work on *H. didictyon*, which has the chromosome number $n = 6$. The basic chromosome number for the genus is, therefore, presumably $x = 6$. Pryzwara & Kuta (1995) suggest for the Hookeriaceae – which in their circumscription includes the Hypopterygiaceae – the primary basic chromosome number $x = 5$. This number might also be basic for the family Hypopterygiaceae.

Chapter 5

SPECIES AND INTRASPECIFIC VARIATION

In the material examined, 21 morphologically cohesive groups of specimens could be delimited from each other in every arbitrary combination by a monothetic set of character states of two or more independent characters. These groups, therefore, fulfil the criteria for delimitation at the specific level and represent species (see 'Taxonomic treatment', p. 93 and onwards).

Delimitation problems occurred only between *Cyathophorum hookerianum* and *C. parvifolium* (see '*C. parvifolium*', note 11, p. 356), tiny plants of *Hypopterygium flavolimbatum* and *H. tamarisci* (see '*H. flavolimbatum*', note 27, p. 187), and between small, not gemmiferous plants of *Hypopterygium vriesei* and *H. tamarisci* (see '*H. vriesei*', note 12, p. 196)[1]. The problems were mainly due to the difficulty to judge the developmental stage of the problematic specimens.

Intraspecific morphological variation was observed in all species, caused by tremendous phenotypic plasticity in habit (e.g. life form, size, number, and mutual distance of branches) and reproductive structures. Within *Hypopterygium didictyon*, *H. flavolimbatum*, *H. tamarisci*, *Lopidium concinnum* and *L. struthiopteris* groups of specimens were observed, which show a higher morphological homogeneity within the subset than with other subsets of the same species. However, none of these subsets fulfil the criteria for the recognition as formal intraspecific taxa; the subsets represent variants that are treated as informal classes here (see 'Taxonomic treatment', under the pertinent species). The complicated systematics at the specific and intraspecific level of *Hypopterygium tamarisci* is treated in full detail by Pfeiffer et al. (2000).

The observed intraspecific variation within species of the Hypopterygiaceae is mainly regional and is (after Van Steenis, 1957) either: 1) continuous and clinal (to some extent in most species, in its most extreme form observed in *Lopidium concinnum* and Oceanian *Hypopterygium tamarisci*); 2) 'discontinuous' and exclusive (African *H. tamarisci*); or 3) 'discontinuous' and variants sympatric, i.e. occurring in the same area (e.g. *Hypopterygium didictyon* in New Zealand, *H. flavolimbatum* in E Malesia, *H. tamarisci* in Australia, *Lopidium struthiopteris* in Australia and E Malesia).

The two widely distributed variants of *Cyathophorum hookerianum* are best described as ecological variants that are confined to different climate zones and, hence, have a principally different latitudinal-altitudinal distribution (see '*C. hookerianum*', 'Ecological variation', p. 341). This type of intraspecific variation is also regarded 'discontinuous' and exclusive. A local variant of *C. hookerianum* in the eastern Himalayas, which is somewhat intermediate between the two widely distributed forms in morphology and ecology, but shows minor differences in gemmaphores and gemmae, represents to some extent a 'discontinuous' variability within the species with variants occurring in the same area.

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1) The resemblance between medium-sized and large plants of *H. vriesei* and *H. tamarisci* (i.e. 'Oceanian variant 1') from the western Pacific is superficial (see '*H. vriesei*', note 13, p. 197).

Ramsay's (1967a) work indicates that the regional variation of *Hypopterygium tamarisci* in Australia can, at least for a great deal, be explained as a result of the different chromosome races that occur in this area. Ramsay's (1967a) haploid and polyploid plants do not correspond perfectly in morphology with the two Australian variants as defined by Pfeiffer et al. (2000) and the present study, but Ramsay's haploids strongly resemble the strictly dioicous 'Australian' variant and her polyploids strongly resemble the general 'Australasian' variant. This suggests that the other variants within *H. tamarisci* and other *Hypopterygium* species may also have a genetic component that is based on chromosomal races. However, further combined cytological, molecular, and morphological research is needed to test this hypothesis.

Chapter 6

PHYLOGENY

INTRODUCTION

One of the aims of this study is to find the most plausible hypothesis for clarifying the mutual phylogenetic relationships of the species of the Hypopterygiaceae s.l. Results of recent cladistic analyses (Hedenäs, 1994; De Luna et al., 1999, 2000; Cox et al., 2000; see 'Family affairs', p. 20) strongly support the hypothesis that the Hypopterygiaceae s.l. are included in a monophyletic group of pleurocarpous mosses that consists of the Hookeriales, Leucodontales, and Hypnales. The phylogenetic relationships of this family and its representatives within this monophyletic group are, however, less clear due to: a) incongruent results of subsequent studies with respect to the position of the representative(s) of the Hypopterygiaceae s.l. in the phylogenetic trees (Hedenäs, 1994, 1995, 1996a, b; Newton & De Luna, 1999; De Luna et al., 1999, 2000; Cox et al., 2000); and b) the low number of representatives of the Hypopterygiaceae used in these phylogenetic studies. This is also a weak point in the discussion on the classification and relationships of Hypopterygiaceae in the systematic studies by Crosby (1974), Vitt (1984), Buck & Vitt (1986), and Buck (1987, 1988).

MATERIAL AND METHODS

The taxonomic units used for cladistic analyses are species. The selected taxa include all present species of the Hypopterygiaceae s.l. (see 'Taxonomic treatment', p. 93 and onwards). As monophyly of the Hypopterygiaceae s.l. could not be ascertained prior to the analyses (cf. Crosby, 1974; Vitt, 1984; Buck, 1987, 1988; Whittemore & Allen, 1989; Kruijer, 1995a, b, 1996c; Hedenäs, 1996a, b), a selection of species that belong to the following families in the Hookeriales (following Buck, 1988) was included in the ingroup: Adelotheciaceae W.R. Buck (*Adelothecium bogotense* (Hampe) Mitt.), Callicostaceae Crum (*Thamniopsis undata* (Hedw.) W.R. Buck), Daltoniaceae (*Calyptrochaeta apiculata* (Hook.f. & Wilson) Vitt, *Daltonia angustifolia* Dozy & Molk., *Distichophyllum pulchellum* (Hook.f. & Wilson) Mitt.), and Hookeriaceae (*Achrophyllum dentatum* (Hook.f. & Wilson) Vitt & Crosby, *Hookeria lucens* (Hedw.) Sm., *Schimperobryum splendidissimum* (Mont.) Margad.). In addition, as representatives of (more) distantly related taxa to the Hypopterygiaceae and as potential outgroups, a selection of Hypnales (*Pterobryella longifrons* (Müll.Hal.) A. Jaeger, *Hypnum cupressiforme* Hedw.) and Leucodontales (*Leucodon sciuroides* (Hedw.) Schwägr., *Neckera crispa* Hedw.) have been included as well. A representative of the pleurocarpous Bryales (*Racopilum spectabile* Reinw. & Hornsch.) was chosen as the basal outgroup for the initial analysis.

Table 2. Data matrix. Character numbers refer to characters listed in the text; ? = unknown character states; – = unknown character states of the sporogone and the calyptra for species with unknown sporogones.

character:	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57
ingroup																																																									
Cyathophorum bulbosum	1	4	4	4	2	2	2	2	3	2	1	1	?	1	2	2	1	2	1	2	1	3	3	1	3	1	1	2	1	2	2	2	3	3	1	1	2	1	1	1	2	1	1	1	1	1	1	1	1	1	1	3	3	3	3	1	4
Cyathophorum tahitense	1	4	4	4	2	2	2	2	3	3	1	1	?	1	2	1	1	2	2	2	1	3	3	1	3	1	1	1	?	?	?	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Cyathophorum spinosum	1	4	4	4	2	2	2	2	3	3	1	1	?	1	2	1	1	2	1	1	1	3	3	1	3	1	1	2	1	2	3	2	3	3	1	2	2	1	2	1	2	1	1	1	1	1	1	1	1	2	1	3	3	2	3	1	4
Cyathophorum adiantum	1	4	4	4	2	2	2	2	3	2	1	1	?	1	2	1	1	2	1	2	1	3	3	1	3	1	2	3	1	2	2	2	3	2	1	1	2	1	2	1	1	1	2	2	1	2	1	2	3	2	1	1	3	3	3	1	4
Cyathophorum africanum	1	4	4	4	2	2	2	2	3	2	1	2	?	1	1	3	2	1	1	2	1	2	1	1	1	2	3	3	1	2	1	2	3	1	1	2	2	1	2	1	1	1	2	2	1	2	2	2	3	2	2	1	1	1	1	1	1
Cyathophorum hookerianum	1	4	4	4	2	2	2	2	3	2	1	1	?	1	2	3	3	1	1	2	1	3	3	1	3	1	3	3	1	2	3	2	2	1	1	2	2	1	2	1	2	1	2	2	1	2	2	2	3	2	1	2	2	2	1	1	1
Cyathophorum parvifolium	1	4	4	4	2	2	2	2	3	1	1	1	?	1	2	3	3	1	1	1	1	3	3	1	3	1	3	3	1	2	3	2	2	1	1	2	2	1	2	1	2	1	2	2	1	2	2	2	3	2	1	1	1	1	1	1	1
Dendrocyathophorum decolyi	1	3	4	4	2	2	2	2	3	1	1	2	2	1	1	3	2	2	1	2	1	3	2	1	1	2	3	3	1	2	3	1	1	1	1	1	3	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	3	1	1	1
Lopidium struthiopteris	1	3	4	4	1	2	2	2	3	2	2	2	2	1	1	3	3	1	2	2	1	1	1	2	3	1	2	2	2	1	3	1	2	1	2	2	2	1	?	1	2	1	2	1	1	1	1	2	3	2	1	1	1	1	1	3	3
Lopidium concinnum	1	3	4	4	1	2	2	2	3	2	3	3	2	1	1	3	2	1	3	2	1	1	1	2	1	2	3	2	2	1	3	1	3	1	2	1	1	1	1	1	2	1	1	1	1	1	1	2	2	2	1	1	1	1	1	1	3
Dendrohypopterygium filiculiforme	1	1	1	4	1	2	1	2	3	1	1	1	2	1	1	3	2	1	1	1	1	2	1	1	1	1	1	1	1	1	3	1	1	1	1	1	3	2	1	1	2	1	1	1	1	1	1	1	1	1	1	2	1	1	1	2	2
Dendrohypopterygium arbuscula	1	1	1	4	1	2	1	2	3	1	1	1	2	1	1	3	2	2	3	2	1	1	1	1	1	1	1	1	1	2	3	1	2	1	1	1	3	2	1	1	2	1	1	1	1	1	1	1	1	1	1	3	1	1	1	1	2
Hypopterygium sandwicense	1	2	1	4	1	2	1	2	3	2	1	1	2	1	1	3	3	1	2	2	1	2	2	1	1	2	3	3	1	2	3	1	1	1	1	1	3	1	1	1	3	1	1	1	1	1	1	1	2	1	1	1	1	1	1	1	2
Hypopterygium flavolimbatum	1	2	1	4	1	2	1	2	3	1	1	1	1	1	1	3	2	2	3	2	1	2	1	1	2	2	3	3	1	1	3	1	1	1	1	1	3	2	1	1	3	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	3
Hypopterygium didictyon	1	1	1	4	1	2	1	2	3	1	1	1	1	1	1	3	1	2	3	2	1	2	1	1	1	1	3	3	1	1	3	1	1	1	1	1	3	2	1	1	3	1	1	1	1	1	1	1	2	1	1	1	1	1	1	1	2
Hypopterygium discolor	1	1	4	4	1	2	1	2	3	1	1	1	1	1	1	3	2	2	3	2	1	2	1	1	1	1	3	2	1	1	2	1	1	1	1	1	3	1	1	1	3	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	3
Hypopterygium tamarisci	1	2	4	4	1	2	1	2	3	2	1	1	1	1	1	3	3	2	3	2	1	2	1	1	?	2	?	?	1	1	2	1	1	1	1	1	3	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	2	1	1	3
Hypopterygium elatum	1	3	1	4	1	2	1	2	3	1	1	1	1	1	1	3	2	2	3	2	1	1	1	1	1	1	?	3	1	1	3	1	1	1	1	1	2	1	?	1	3	1	1	1	1	1	2	1	2	1	?	?	?	?	?	?	?
Canalohypopterygium tamariscinum	1	2	1	4	1	2	1	2	3	1	1	3	2	2	1	3	2	4	1	2	1	2	1	1	1	1	1	1	1	1	1	1	2	1	1	1	3	2	1	1	3	1	1	1	1	1	1	1	2	1	1	3	3	1	1	1	2
Catharomnion ciliatum	1	2	4	4	2	2	2	2	3	2	1	3	2	2	1	3	2	4	2	2	1	2	1	1	1	1	2	2	1	1	1	1	2	1	1	1	1	1	1	2	1	2	?	?	?	?	?	?	?	2	1	3	3	1	2	1	2
Hypopterygium vriesei	1	3	4	4	1	2	1	2	3	3	1	1	2	1	1	3	2	2	2	2	1	2	1	1	3	1	3	3	?	?	?	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Achrophyllum dentatum	1	4	1	1	1	1	1	1	3	1	1	1	1	1	1	3	2	3	1	1	1	1	2	1	3	1	1	3	1	2	1	1	3	1	1	1	3	2	1	1	1	1	1	2	3	1	1	1	1	2	1	3	3	1	1	1	4
Calyptrochaeta apiculata	1	4	1	1	1	1	1	1	3	1	1	1	?	1	1	1	2	2	3	1	1	3	3	1	3	1	2	2	1	1	1	1	1	3	3	1	3	2	2	1	2	1	2	1	3	1	1	1	1	2	1	3	3	1	1	3	4
Thamniopsis undata	2	4	2	2	2	2	1	1	1	1	3	1	?	1	1	3	2	2	1	1	2	2	2	1	1	2	1	1	1	1	1	1	1	1	1	1	3	2	2	1	2	1	1	1	3	1	1	1	1	2	1	2	2	1	1	2	2
Schimperobryum splendidissimum	1	4	3	3	2	2	1	1	1	1	3	1	?	1	1	1	1	2	1	1	1	3	3	1	3	1	1	1	1	1	1	2	3	1	1	1	2	1	2	1	1	1	1	1	1	1	1	2	3	2	2	1	3	1	1	1	3
Daltonia angustifolia	1	4	1	1	1	1	1	1	1	1	3	1	?	1	2	1	3	1	3	2	1	1	1	1	1	2	3	3	1	1	1	1	2	1	1	1	1	1	2	1	1	1	2	2	2	2	1	2	3	2	1	3	3	1	1	1	2
Distichophyllum pulchellum	2	4	1	1	1	2	1	1	1	1	3	1	?	1	1	1	2	1	3	2	1	1	2	1	1	2	3	3	1	1	1	1	1	1	1	1	2	1	2	1	1	1	?	1	3	1	1	2	1	2	1	1	3	1	2	1	2
Hookeria lucens	2	4	1	2	2	2	1	1	1	2	1	1	?	1	1	2	2	1	1	1	2	3	3	1	1	2	1	3	1	1	1	1	1	3	1	1	3	1	2	1	2	1	1	1	1	1	1	1	1	2	1	2	3	1	1	1	4
Adelothecium bogotense	2	4	2	2	2	2	1	1	1	1	3	1	?	3	1	1	3	1	1	1	1	1	1	2	3	1	3	2	1	1	1	2	3	1	2	2	2	2	2	?	?	1	?	1	2	1	?	2	1	2	1	?	3	1	1	2	3
outgroup																																																									
Leucodon sciuroides	2	3	1	1	1	1	1	1	1	1	1	1	?	1	2	1	2	1	1	1	?	3	3	2	3	1	1	1	1	2	3	1	2	1	1	2	2	1	1	2	1	1	2	1	3	2	2	2	3	2	2	1	1	1	1	1	1
Neckera crispa	?	3	1	1	2	2	1	1	1	1	3	1	?	1	1	1	2	2	1	1	2	3	3	?	1	1	1	1	1	2	3	1	1	1	1	1	2	1	2	1	1	1	2	1	1	2	1	2	3	2	1	1	1	1	1	1	1
Pterobryella longifrons	1	3	1	1	1	2	1	1	1	2	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	1	1	1	2	1	1	1	1	1	1	2	1	1	1	3	?	?	?	?	?
Hypnum cupressiforme	2	4	1	1	2	2	1	1	3	1	1	1	?	1	1	1	1	1	1	1	2	3	3	1	1	1	1	1	1	1	2	1	1	1	1	1	2	1	2	2	3	1	1	1	1	1	1	1	1	1	2	2	1	1	1	1	1
Racopilum spectabile	2	4	1	1	2	2	2	2	2	1	1	1	?	1	1	1	1	3	3	1	1	1	1	1	1	1	?	1	1	1	1	1	1	1	1	2	3	1	1	2	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	3

Characters and character states

The character matrix – containing 34 taxa and 57 characters – used for the analyses is given in Table 2. The characters and states are explained below. More detailed information on the morphology of the Hypopterygiaceae s.l. is given in the chapter 'Morphology and anatomy', p. 29.

Character and character state selection and optimalisation resulted from successive evaluations of earlier analyses (Kruijer, 1995a, b, 1996c). Continuous characters were kept to a minimum, but proved to be useful in selected cases; only few character states were recognised within such characters. Autapomorphies were omitted with two exceptions: a) the gemmiferous rudimentary branches of *Adelothecium bogotense* (character 14, state 3) differ significantly from those of *Catharomnion ciliatum* and *Canalohypopterygium tamariscinum* (character 14, state 2) and had to be coded by a different character state; b) the absence of the exostome in *Catharomnion ciliatum* (character 42, state 2) compensated for the unknown states of exostome characters (characters 43–49) for this species.

Character coding of the individual species of the Hypopterygiaceae s.l. was based on morphological data obtained from the examination of herbarium specimens for the present revision (see 'Taxonomic treatment', p. 93 and onwards). Character coding of species that are not treated here, viz. those belonging to the Daltoniaceae, Hookeriaceae, and the outgroups, was based on the study of herbarium specimens and literature (listed in Table 3).

Characters were defined as multi-state characters. Character states were numbered 1, 2, etc. Characters and character states were treated as unordered. Two different types of polymorphy were recognised (see De Jong et al., 2000). Species may show a gradual overlap between two defined character states of a particular character, because they express a character state with a broad amplitude; such a state is coded as a separate state. Species may also show two distinct discontinuous character states of a particular character (one of the states is often rare). The plesiomorphic character state of such characters is usually not known (cf. Turner, 1995). In this study, qualitative polymorphic character states were treated as such and were basically coded as unknown. Analyses based on coding such states as polymorphisms were used for comparison only.

Definition of characters and character states

Characters of the gametophore:

1. Ramification: 1 = sympodial; 2 = monopodial.
   Like in other Neckeraceae (cf. Nelson, 1973; Enroth, 1994), the ramification pattern of *Neckera crispa* is flexible and includes both sympodial and monopodial ramification (state 1 & 2); for this species the character state is coded as unknown.
2. Habit: 1 = strictly palmate or umbellate; 2 = pinnate, bipinnate, or flabellate to palmate or umbellate; 3 = pinnate to bipinnate or flabellate (occasionally somewhat dendroid); 4 = usually simple, less often set with a few innovations or weakly branched (branches may function as new shoots).
3. Phyllotaxis of the basal part of the stem (stipe): 1 = 3/8; 2 = 5/13; 3 = 2/5; 4 = 1/3 or nearly so (i.e. 4/11, or 8/21).
4. Phyllotaxis of the distal parts of the stem (distal parts of the rachis and branches): 1 = 3/8; 2 = 5/13; 3 = 2/5; 4 = 1/3 or nearly so (i.e. 4/11, or 8/21).

Table 3. Selected specimens examined and literature consulted to assign or checking character states for species given in the data matrix of Table 2 that do not belong to the Hypopterygiaceae s.l. The specimens are preserved in L, unless indicated otherwise.

species	specimens	literature
ingroup		
Achrophyllum dentatum	Kantak & Churchill 124; McDonnell 304A; Streimann HS 1025; Touw 18747, 18842	Streimann, 1997
Calyptrochaeta apiculata	Huntley 846; Ratowsky H667	
Thamniopsis undata	Davidse, Herrera & Grayum 28815; Yano 173 (GRO); unknown collector (165)	Churchill & Linares, 1995
Schimperobryum splendidissimum	Crosby 11625, 11990, 12028, 12064, 12282, 12339, 12466, 12508, 12975, 13053; Deguchi BSE 842; Landrum CE 4773	Whittemore & Allen, 1989
Daltonia angustifolia	Brass 30248; Doctors van Leeuwen 11918, 12415; Robbins 3197; Schiffner 12722; Van Steenis 17959; Touw & Snoek 23165, 23174	Tan & Robinson, 1990
Distichophyllum pulchellum	Streimann HS 1358, HS 3808, 6071, 7059; Visch s.n. (New Zealand, 22/02/1975); Zanten 7401496 p.p.	
Hookeria lucens	Balle s.n. (Norway: Bergen, 25/03/1975); Groenhuizen s.n. (Germany: Eifel, 01/05/1981); Kruijer & Brodt 98.01.01; Le Jolis? s.n. (France: Cherbourg, 16/2/1885); Luitingh 65-5-1; Montange s.n. (Belgium: Ardennes); Nannenga-Bremekamp 1424; Schofield 64049; Touw 6901; Vellinga 1718	Touw & Rubers, 1989
Adelothecium bogotense	Crosby & Crosby 6804; Herzog 4582; Korthals s.n. (Venezuela); Nichols 181; Puiggari s.n. (S. Paulo, 1879); Robbins 66; unknown collector s.n. (Nova Granata)	Mitten, 1869; Brotherus, 1907; Welch, 1966; Crosby, 1974; Whittemore & Allen, 1989; Ochyra et al. 1992; Churchill & Linares, 1995
outgroup		
Leucodon sciuroides	Audiffred 2; Jalink 8067	Touw & Rubers, 1989; Hedenäs, 1989
Neckera crispa	Froelich s.n. (Österreich: Johnsbachtal, 04/10/1931); Gravet MA 80; Luitingh 77.10.19; Touw 2750, 6044; Vellinga 1660, 1724	Touw & Rubers, 1989; Hedenäs, 1989
Pterobryella longifrons	Edaño PNH 4056; Elmer 7777; Foxworthy BS 2426; Jacobs B 174, B 177, B 220, B, 358, B 396, B 405	Brotherus, 1925
Hypnum cupressiforme	Kern & Reichelt s.n. (Netherlands: Ubbergen, 31/12/1928); Kruijer 90.03.01; Lako s.n. (Netherlands: Zwolle, 2/1904); Molkenboer s.n. (Netherlands: Beekbergerwoud, 1845); Weeda s.n. (Netherlands: Katwijk, 23/10/1979)	Touw & Rubers, 1989
Racopilum spectabile	Koie & Sandermann Olsen 2067; Meijer B 11309; Wijk 1914; Wilde (836a), (838), (857); Zanten 303, 511, 890	

5. Foliation of the basal part of the stem (stipe): 1 = not or weakly complanate; 2 = distinctly complanate.
6. Foliation of the distal parts of the stem (distal parts of the rachis and branches): 1 = not or weakly complanate; 2 = distinctly complanate.
7. Foliation of the basal part of the stem (stipe): 1 = isophyllous; 2 = anisophyllous.
8. Foliation of the distal parts of the stem (distal parts of the rachis and branches): 1 = isophyllous; 2 = anisophyllous.
9. Orientation of the foliation: 1 = not orientated in any direction or dorsiventral; 2 = dorsal; 3 = ventral.
10. Compression of the non-gemmiferous parts of the stem (stipe and rachis): 1 = entirely dorsiventral or partly uncompressed; 2 = mainly dorsiventral, but partly lateral (near the stipe base) in a few specimens of the species at least; 3 = lateral.
11. Central strand cells (in cross sections without central cavities): 1 = present; 2 = occasionally present; 3 = absent.

    In *Lopidium struthiopteris*, central strand cells are present in the stipe, but are absent from the rachis; the state is coded as state 2. In *Pterobryella longifrons*, central strand cells were only observed in the stipe and the rachis of a single specimen; the state is coded as state 2. The central strand of *Hypnum cupressiforme* is present in all axes, but it is weakly differentiated and often obsolete in cross sections of young innovations; the state is coded as state 2.
12. Axial cavities in the basal and middle parts of the stem (the stipe and the basal and middle parts of the rachis): 1 = absent; 2 = central; 3 = cortical.

    Species for which the character state of this character is coded as state 2 or 3 do not necessarily possess cavities in every cross section.
13. Axial cavities in ultimate branches: 1 = absent; 2 = present.

    This character state is coded as unknown for species lacking ultimate branches, viz. for species lacking any ramification, for species usually lacking ramification in which the rare branches are similar to the main axis or show indeterminate growth, and for species with indeterminate growth of branches.
14. Rudimentary branches: 1 = absent; 2 = present, not gemmiferous but naked or only set with a few scaly leaves; 3 = present, gemmiferous.
15. Scaly leaves at primordia: 1 = occasionally present at least; 2 = absent.

    Scaly leaves are absent from dormant stem primordia of *Cyathophorum bulbosum* (coded as state 2), but the absence or presence of scaly leaves was sometimes difficult to ascertain. Scaly leaves might rarely be present at the perichaetial primordia of this species.
16. Intermediate cells of axillary hairs (at stipe, rachis, or branches): 1 = present; 2 = occasionally present; 3 = absent.
17. Terminal cell of axillary hairs (at stipe, rachis, or branches): 1 = short-linear to linear and rectangular; 2 = short-elliptic to elongate-rectangular; 3 = short and elliptic, subcircular, or circular.

    In *Dendrohypopterygium filiculiforme* and *D. arbuscula*, the length of the terminal cell and hence its outline strongly depends on the position of the axillary hair on the gametophore. Axillary hairs on the stipe have generally a (much) longer terminal cell than those on the frond axes. In *D. filiculiforme*, the axillary hairs in the basal part of the rachis and the lower first order branches have generally a (much) longer terminal cell than those on the distal frond axes. For both species the character state is coded as state 2. The terminal cells of the axillary hairs of *Leucodon sciuroides* are short-ovate to short-linear-rectangular in outline and those of *Neckera crispa* are elongate-elliptic to short-linear-rectangular in outline; for both species the character state of this character is coded as state 2.

18. Margin of lateral leaves in the distal part of the frond: 1 = entire or truly serrate; 2 = entire or serrate-dentate; 3 = dentate; 4 = partly dentate-ciliate at least.
    Serrate leaves are set with serrations (sharp teeth, sharp indentations: Fig. 59k). Dentate leaves are set with dents (sharp teeth, rounded indentations: Fig. 49b). Serrate-dentate leaves are set with serrations and dents, or their intermediates. Dentate-ciliate leaves are set with dents and cilia (very long and pronounced protrusions: Fig. 15q, r).
    The leaves of *Cyathophorum bulbosum* are normally weakly to coarsely serrate-dentate and only by exception set with a few cilia; for this species the character state is coded as state 2. The protrusions at the leaf margin of *Neckera crispa* are very short and are intermediate between serrations and dents; for this species the character state is coded as state 2.
19. Border of lateral leaves (above the leaf base) in the distal part of the frond: 1 = absent or interrupted; 2 = interrupted or continuous, but never absent and interrupted in a few leaves at least; 3 = always continuous.
    The border of the lateral frond leaves of *Lopidium concinnum* is occasionally somewhat interrupted near the leaf apex. Nevertheless, the character state is coded as state 3 for this species.
20. Border of lateral leaves (above the leaf base) in the distal part of the frond: 1 = up to 2 cells wide at most; 2 = at least partly more than 2 cells wide.
21. Leaf costa of frond leaves: 1 = single; 2 = double or forked at base.
22. Leaf costa of lateral leaves in the distal part of the frond: 1 = reaching 4/5 of the length of the leaf at least; 2 = reaching 1/2–4/5 of the length of the leaf; 3 = reaching up to 1/2 of the length of the leaf at most.
23. Leaf costa of amphigastria (or ventral leaves) in the distal part of the stem (rachis) and branches: 1 = reaching 1/2 of the length of the amphigastrium and at least occasionally percurrent or nearly so; 2 = reaching 1/3 of the length of the amphigastrium at least, but never percurrent; 3 = reaching up to 1/2 of the length of the amphigastrium at most and at least occasionally shorter than 1/3 of the length of the leaf.
24. Laminal cells in frond leaves: 1 = cell walls thin or weakly incrassate (prosenchymatous or in parts of the leaf parenchymatous); 2 = cell walls distinctly incrassate (collenchymatous).
    In *Neckera crispa* both character states may occur in a single leaf (state 1 & 2); for this species, the character state is coded as unknown.
25. Gemmae: 1 = absent; 2 = not common, present in only a few specimens; 3 = common.
    Character state 2 intends to code for species of which plants usually lack gemmae, but may occasionally be gemmiferous under specific (e.g. traumatic) conditions.

In the species that are coded here with character state 2, the majority of the specimens lack gemmae, while the few gemmiferous plants are often – but not always – damaged. It is plausible, that in these species gemmae are only produced under certain, but yet unknown, conditions of stress. Two regional variants of *Hypopterygium tamarisci* – the 'African' and 'Australian' variant – are strictly non-gemmiferous (state 1), whereas the other variants are occasionally or frequently gemmiferous (state 2, 3). The character state for this species is coded as unknown.

26. Sexuality: 1 = strictly dioicous; 2 = partly or strictly monoicous.

    In two specimens of *Achrophyllum dentatum* (*Streimann HS 1025*, *Touw 18747*), male and female plants were found intermingled, but according to Streimann (1997) *A. dentatum* is dioicous.

27. Paraphyses in perigonia: 1 = always present; 2 = present or absent; 3 = always absent.

    Perigonial paraphyses are present in one regional variant of *Hypopterygium tamarisci* – the 'New World' variant – and absent from the others (state 1, 3). The character state for this species is coded as unknown.

    Only two of the specimens of *Achrophyllum dentatum* examined (*Streimann HS 1025*, *Touw 18747*) have perigonia. The perigonia of *Streimann HS 1025* contain many paraphyses, the perigonia of *Touw 18747* only a few.

28. Paraphyses in perichaetia: 1 = present; 2 = present or absent (either in perichaetia prior to sporophyte development or in full grown ones); 3 = absent.

    In *Dendrocyathophorum decolyi* only once a single (damaged) paraphysis was observed after examination of over 50 perigonia. Paraphyses are principally absent in this species, hence its character state is coded as state 3. In *Hypopterygium tamarisci*, perichaetial paraphyses are present in one regional variant – the 'New World' variant –, present or absent in four other regional variants of this species – the 'African', 'Asian', and the two 'Oceanian' variants –, and absent in the two 'Australian' variants (states 1, 2, and 3). The character state for this species is coded as unknown.

    None of the specimens of *Achrophyllum dentatum* examined contained perichaetial paraphyses. Streimann (1997) described the perigonial paraphyses of this species as being distinct, but he gave no description of perichaetial paraphyses. Probably, perichaetial paraphyses are absent from this species, or at most rare. Hence, the character state for this species is coded as state 3.

29. Leaf-like paraphyses in full grown perichaetia: 1 = absent; 2 = occasionally present.
30. Stalk of full grown perichaetia: 1 = at least occasionally set with rhizoids; 2 = glabrous.
31. Vaginula length: 1 = short, 0.8 mm long at most; 2 = intermediate in length, both shorter and longer than 0.8 mm present; 3 = long, 0.8 mm long at least.

Characters of the sporophyte and the calyptra:

32. Direction of the sporophyte: 1 = usually projecting above the gametophore; 2 = usually projecting beneath the gametophore.
33. Seta: 1 = 10.0 mm long at least; 2 = intermediate in length, between 4.5 mm and 10 mm long; 3 = short, 4.5 mm long at most.
34. Seta base: 1 = narrow; 2 = narrow or widened; 3 = widened.

35. Seta surface: 1 = smooth or nearly so; 2 = weakly to moderately mammillate; 3 = coarsely mammillate.
36. Capsule: 1 = subglobose to barrel-shaped, never cylindrical; 2 = (occasionally) cylindrical.
    Character state 1 includes ovoid, ellipsoid, and turbinate capsules.
37. Angle of the capsule with the direction of the seta: 1 = variable, erect to pendulous; 2 = erect to horizontal; 3 = horizontal to pendulous.
    The capsules of *Catharomnion ciliatum* are erect to drooping, but in a few sporophytes the seta and capsule are both weakly curved in the same direction, which may result in a horizontal position of the (distal part of the) capsule with respect to the basal part of the seta. The capsules of *Distichophyllum pulchellum* are inclinate to horizontal. For both species the character state is coded as state 2.
38. Capsule neck: 1 = smooth or nearly so; 2 = pustulose.
39. Annulus: 1 = (occasionally) present; 2 = absent.
40. Orifice: 1 = always transverse; 2 = transverse or oblique.
41. Number of IPL-cells in the peristome: 1 = strictly 4; 2 = variable, 4–8(–10); 3 = several, 6–10.
42. Exostome teeth: 1 = present; 2 = absent.

In *Catharomnion ciliatum*, the exostome is absent. Therefore, the character states of characters 43–49 are coded as unknown for this species.

43. Exostome teeth: 1 = 70 µm wide at least; 2 = 70 µm wide at most.
44. Exostome teeth: 1 = partly or entirely bordered above the base; 2 = not bordered or slightly bordered.
45. Median line: 1 = not furrowed; 2 = not or interuptedly furrowed; 3 = distinctly furrowed.
46. Ornamentation of the dorsal plates in the basal 1/3 of the exostome teeth: 1 = conspicuously striate (striae set with papillae or not); 2 = smooth, papillose, or weakly striate near the tooth base.
47. Papillae on the dorsal plates of the exostome: 1 = strictly low; 2 = (occasionally) high.
48. Trabeculae in the middle parts of the exostome teeth: 1 = short to strongly protruding and closely set; 2 = very short to short and distant.
49. Height of the basal membrane of the endostome beyond the orifice: 1 = projecting 1/3–1/2 of the length of the exostome teeth; 2 = projecting c. 1/3 of the length of the exostome teeth; 3 = projecting 1/3 of the length of the exostome teeth at most.
50. Endostomial cilia: 1 = (occasionally) present and parts of several plates long; 2 = absent or present as a part of single plate.
    In the material of *Calyptrochaeta apiculata* only a single short cilium was observed and the character state for this species is coded as state 2.
51. Operculum: 1 = long-rostrate; 2 = short-rostrate.
52. Rostrum: 1 = oblique; 2 = oblique or straight; 3 = straight.
53. Calyptra: 1 = cucullate; 2 = cucullate to mitrate: 3 = mitrate.
54. Calyptra: 1 = completely covering the operculum; 2 = partly or completely covering the operculum; 3 = partly covering the operculum.

55. Colour of the calyptra below the apex: 1 = white, or pale ochraceous to pale brown; 2 = ochraceous or pale brown to brown; 3 = brown to dark brown.
56. Paraphyses on the calyptra: 1 = absent; 2 = present and short; 3 = present and long.
    The hairs on the calyptrae in *Daltonia angustifolia*, *Distichophyllum pulchellum*, and *Calyptrochaeta apiculata* proceed from the calyptra. They are not paraphyses.
57. Texture of the calyptra: 1 = entirely membranous; 2 = membranous and slightly fleshy near the apex; 3 = membranous in the basal part and at some distance from the base becoming fleshy in the distal part; 4 = entirely fleshy.
    In *Achrophyllum dentatum* and *Hookeria lucens* the texture of the calyptra varies between partly fleshy to entirely fleshy. In *Calyptrochaeta apiculata* the calyptra is almost entirely fleshy and only membranous near the base. For these species the character state is coded as state 4.

Programme choice and analytical protocol

The PAUP software package version 4.0b1a (Swofford, 1998) was used for the phylogenetic analyses. The large number of taxa and characters in the data matrix precluded exhaustive searches. Hence, cladograms were obtained by computing a set of most parsimonious trees (MPTs) using heuristic search strategies, which involved building starting trees using random addition of taxa followed by branch swapping using tree bisection-reconnection (TBR). Bootstrap values (Felsenstein, 1985; 1000 replicates, < 50% not shown) and Bremer indices (Bremer, 1988; Källersjö et al., 1992) were computed as indicators of tree stability. Bremer indices were calculated using the computer program AutoDecay version 4.0.2' (Eriksson, 1998; 1000 replicates) and PAUP. All characters and character states were treated as unordered and unweighted. Character state changes were evaluated using MACCLADE version 3.0.8 (Maddison & Maddison, 1992).

RESULTS

Phylogenies obtained from four different analyses with polymorphic character states coded as unknown[1] are depicted in Fig. 1. When all taxa were used in the analysis, the phylogenetic analysis resulted in 2 completely resolved most parsimonious trees (length 324 steps, CI = 0.287, RI = 0.561), of which the combined majority rule with superimposed strict consensus tree is shown in Fig. 1a. When *Racopilum spectabile* was omitted from the analysis, the phylogenetic analysis resulted in 14 completely resolved

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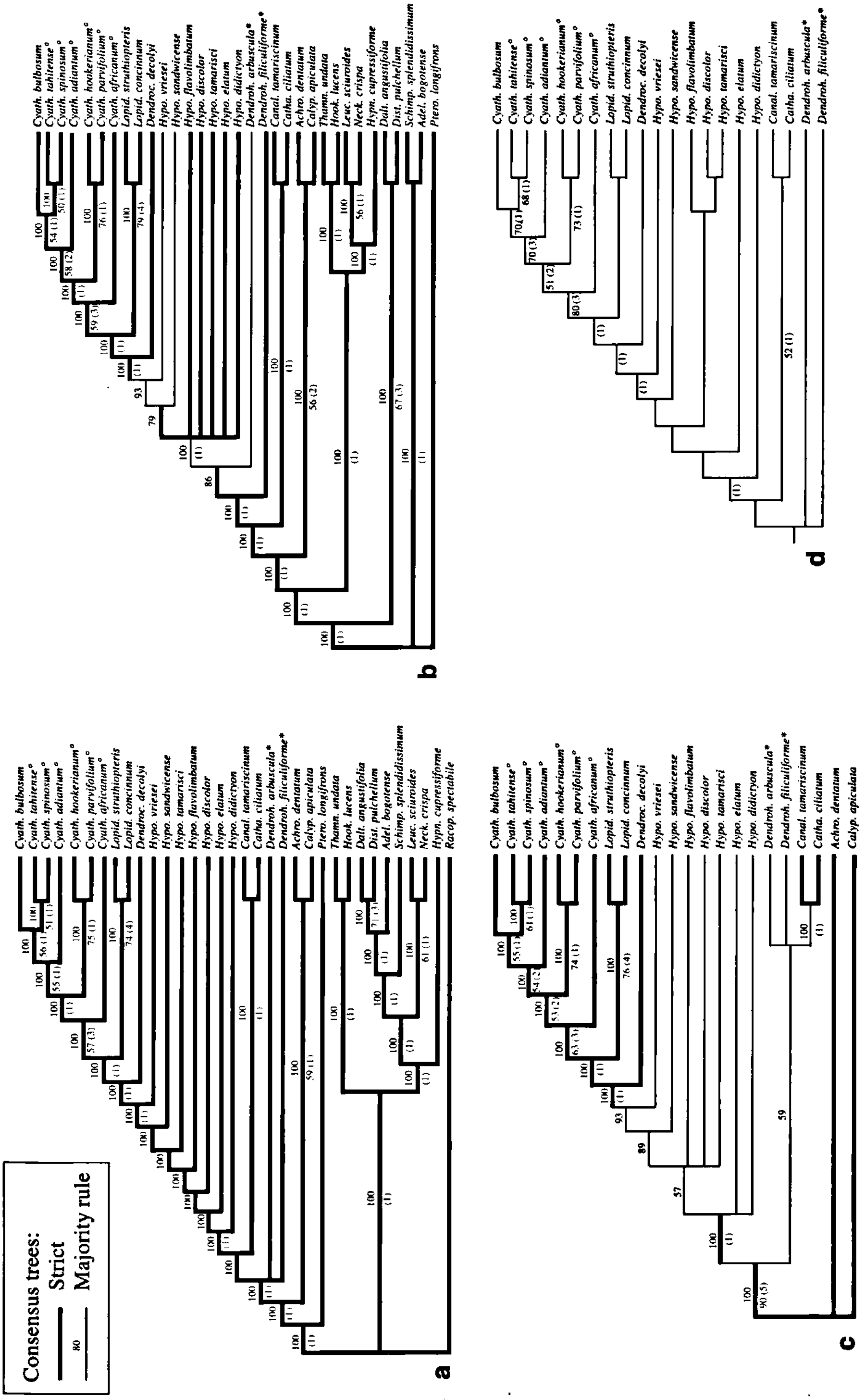
[1] The results of similar analyses with polymorphic character states coded as polymorphisms (not shown) are essentially similar to the four described above. The MTPs resulting from these analyses are equal in length, almost identical in topology, and have similar CI and RI values as those from the corresponding analyses with polymorphic character states coded as unknown. However, when polymorphic characters are coded as polymorphisms, the basal polytomies in the trees of Fig. 1 became resolved (with the outgroup in a basal position). When all taxa were used in the analysis (cf. Fig. 1a), the analysis resulted in a *Hypopterygium flavolimbatum–H. tamarisci–H. discolor* clade, which was nested in a paraphyletic *Hypopterygium* s.str. grade. That clade was absent from the tree resulting from the analysis with Hypopterygiaceae (cf. Fig. 1d), where *Hypopterygium* s.str. was a resolved, paraphyletic grade.


Consensus trees:
Strict
80 Majority rule
a
Cyath. bulbosum
Cyath. tahitense°
Cyath. spinosum°
Cyath. adiantum°
Cyath. hookerianum°
Cyath. parvifolium°
Cyath. africanum°
Lopid. struthiopteris
Lopid. concinnum
Dendroc. decolyi
Hypo. vriesei
Hypo. sandwicense
Hypo. tamarisci
Hypo. flavolimbatum
Hypo. discolor
Hypo. elatum
Hypo. didictyon
Canal. tamariscinum
Catha. ciliatum
Dendroh. arbuscula*
Dendroh. filiculiforme*
Achro. dentatum
Calyp. apiculata
Ptero. longifrons
Thamn. undata
Hook. lucens
Dalt. angustifolia
Dist. pulchellum
Adel. bogotense
Schimp. splendidissimum
Leuc. sciuroides
Neck. crispa
Hypn. cupressiforme
Racop. spectabile
b
Cyath. bulbosum
Cyath. tahitense°
Cyath. spinosum°
Cyath. adiantum°
Cyath. hookerianum°
Cyath. parvifolium°
Cyath. africanum°
Lopid. struthiopteris
Lopid. concinnum
Dendroc. decolyi
Hypo. vriesei
Hypo. sandwicense
Hypo. flavolimbatum
Hypo. discolor
Hypo. tamarisci
Hypo. elatum
Hypo. didictyon
Dendroh. arbuscula*
Dendroh. filiculiforme*
Canal. tamariscinum
Catha. ciliatum
Achro. dentatum
Calyp. apiculata
Thamn. undata
Hook. lucens
Leuc. sciuroides
Neck. crispa
Hypn. cupressiforme
Dalt. angustifolia
Dist. pulchellum
Schimp. splendidissimum
Adel. bogotense
Ptero. longifrons
c
Cyath. bulbosum
Cyath. tahitense°
Cyath. spinosum°
Cyath. adiantum°
Cyath. hookerianum°
Cyath. parvifolium°
Cyath. africanum°
Lopid. struthiopteris
Lopid. concinnum
Dendroc. decolyi
Hypo. vriesei
Hypo. sandwicense
Hypo. flavolimbatum
Hypo. discolor
Hypo. tamarisci
Hypo. elatum
Hypo. didictyon
Dendroh. arbuscula*
Dendroh. filiculiforme*
Canal. tamariscinum
Catha. ciliatum
Achro. dentatum
Calyp. apiculata
d
Cyath. bulbosum
Cyath. tahitense°
Cyath. spinosum°
Cyath. adiantum°
Cyath. hookerianum°
Cyath. parvifolium°
Cyath. africanum°
Lopid. struthiopteris
Lopid. concinnum
Dendroc. decolyi
Hypo. vriesei
Hypo. sandwicense
Hypo. flavolimbatum
Hypo. discolor
Hypo. tamarisci
Hypo. elatum
Hypo. didictyon
Canal. tamariscinum
Catha. ciliatum
Dendroh. arbuscula*
Dendroh. filiculiforme*

MPTs (length 312 steps, CI = 0.295, RI = 0.567), of which the combined consensus tree is shown in Fig. 1b. When, in addition, *Hookeria lucens*, *Thamniopsis undata*, *Adelothecium bogotense*, *Schimperobryum splendidissimum*, *Daltonia angustifolia*, *Distichophyllum pulchellum*, *Pterobryella longifrons*, *Hypnum cupressiforme*, *Leucodon sciuroides*, and *Neckera crispa* were omitted, the phylogenetic analysis resulted in 46 completely resolved MPTs (length 195 steps, CI = 0.426, RI = 0.607) of which the combined consensus tree is shown in Fig. 1c. When non-hypopterygiaceae were excluded from the analysis (Fig. 1d), the phylogenetic analysis resulted in a single completely resolved MPT (length 165 steps, CI = 0.467, RI = 0.639). This MPT has been accepted as the best possible reconstruction of phylogenetic relationships within the Hypopterygiaceae based on morphological and anatomical data. This MPT has been used for plotting character transformation in Fig. 2.

In the combined consensus trees resulting from the three analyses including non-hypopterygiaceous taxa (Fig. 1a–c), the Hypopterygiaceae constitute a single terminal clade with the *Achrophyllum dentatum–Calyptrochaete apiculata* clade as their sister group.

The topology of the Hypopterygiaceae clade is remarkably similar in all four trees of Fig. 1. *Dendrocyathophorum decolyi*, the *Lopidium* species, and the *Cyathophorum* species form a terminal clade in all trees. *Dendrohypopterygium filiculiforme*, *D. arbuscula*, and the clade *Canalohypopterygium tamariscinum–Catharomnion ciliatum* have always a basal position within the Hypopterygiaceae, although their mutual arrangement show some differences between the various trees.

Phylogenetic relationships of *Hypopterygium* species in strict sense (*H. didictyon*, *H. elatum*, *H. tamarisci*, *H. discolor*, *H. flavolimbatum*, *H. sandwicense*, and *H. vriesei*) are weakly supported. The species form a mainly paraphyletic assemblage of single branches (Fig. 1a–d), polytomies of different configuration (Fig. 1a–c), and a monophyletic clade of three species (Fig. 1c) between the basal group of Hypopterygiaceae and the terminal clade of the Hypopterygiaceae (see Fig. 1). In all four trees of Fig.1, the internal branches of this (paraphyletic) group of species obtain no satisfactory bootstrap values and no, or only weak, Bremer support.

In the two analyses that include a selection of representatives of the Hookeriales, the Hypnales, and Leucodontales (Fig. 1a, b), the Hypopterygiaceae clade is defined by 5 (Fig. 1a) or 4 (Fig. 1b) synapomorphies resulting from unambiguous characters state changes (not shown). In both analyses (Fig. 1a, b), these synapomorphies include the tristichous phyllotaxis and the anisophyllous foliation in the distal parts of the stem or rachis and branches (character 4: state 4, character 8: state 2), and the presence of axial cavities (character 13: state 2). The two analyses differ in the other synapomorphies for the Hypopterygiaceae clade. In the analysis with all taxa (Fig. 1a), the

Fig. 1. Four phylogenies of the Hypopterygiaceae. Taxa correspond with those in Table 2. — a–c: consensus trees (combined majority rule with superimposed strict); d: single MPT of the analysis with Hypopterygiaceae only (see text). — Numbers under branches refer to bootstrap values and, when between parentheses, Bremer support values. * = *Dendrohypopterygium filiculiforme* and *D. arbuscula* were formerly classified in *Hypopterygium*; ° = *Cyathophorum spinosum*, *C. tahitense*, *C. adiantum*, *C. hookerianum*, and *C. parvifolium* were formerly classified in *Cyathophorella*; *C. spinosum* was only recently transferred to *Cyathophorum* by Akiyama (1988, 1992).

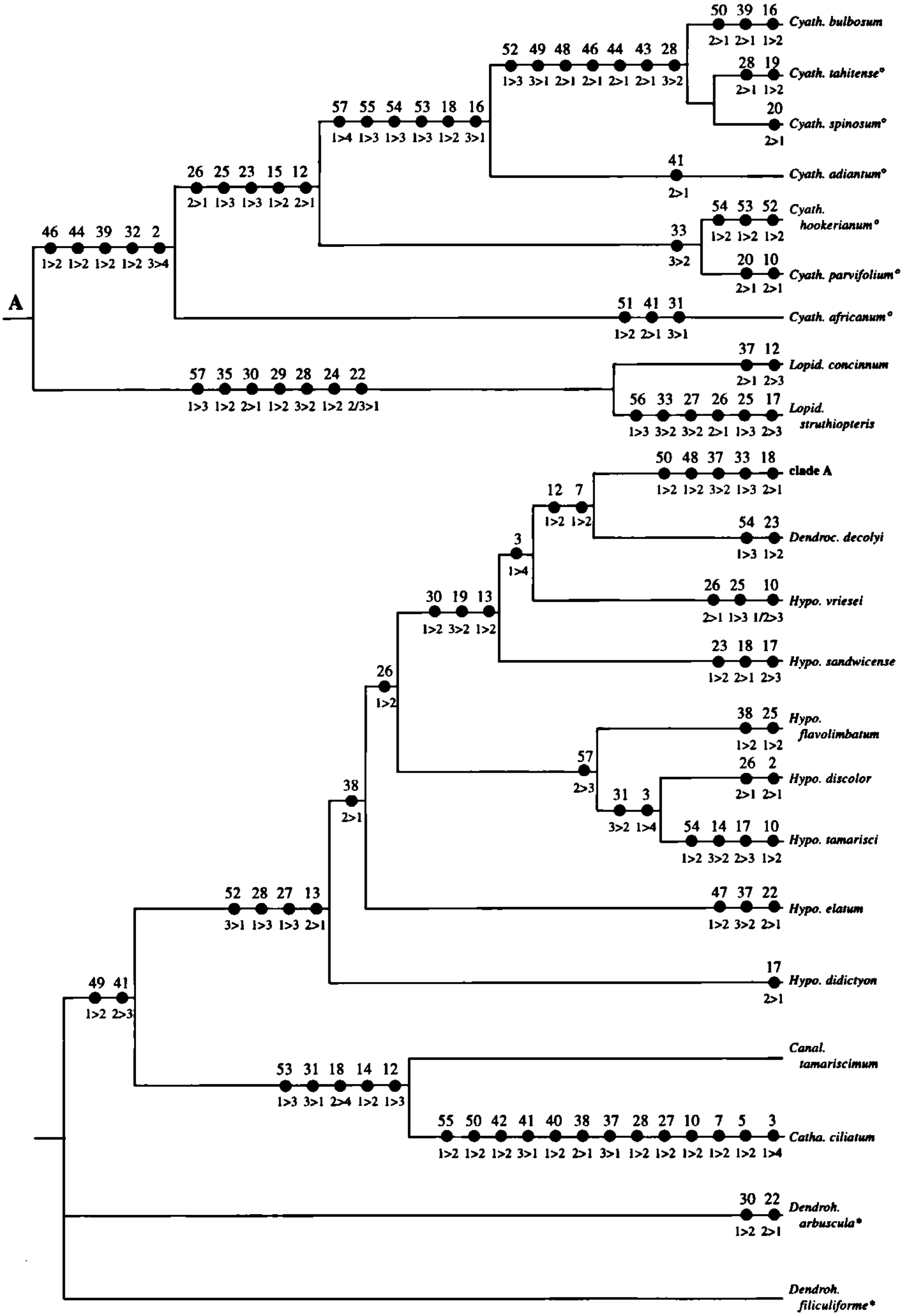


Fig. 2. Distribution of unambiguous character state changes on the tree of Fig. 1d. ● = synapomorphies. Numbers above the dots = characters listed in Table 2; figures below the dots = character state changes. The meaning of symbols * and ° is explained in Fig. 1.

other synapomorphies are the strictly dendroid habit (character 2: state 1) and the long vaginula (character 31: state 3). When *Racopilum spectabile* is omitted from the analysis (Fig. 1b), the other synapomorphy is in 12 of the resulting trees the intermediate costa length of the lateral frond leaves (character 22: state 2) and in the two other trees the – at least partly – more than 2 cells wide border of the lateral frond leaves (character 20: state 2).

In the analysis with the Hypopterygiaceae, *Achrophyllum dentatum*, and *Calyptrochaete apiculata* (Fig. 1c), the Hypopterygiaceae clade is not defined by any synapomorphies, while *Achrophyllum dentatum* and *Calyptrochaete apiculata* are well supported by apomorphic character states. The lack of synapomorphies for the Hypopterygiaceae clade results from the unknown ancestral state of characters 2, 4, 6, 8, 13, 16, 18, 19, 22, 23, 25, 27, 28, 30, 33, 34, 35, 39, 41, 43, 44, 45, 50, 56, and 57. The ancestral states of these characters could not be calculated, because of data conflict between and uncertainty on the states of these characters within the outgroup, between the basal taxa of the ingroup, or between the (basal taxa of) the ingroup and the outgroup (not shown).

In all four analyses, bootstrap values (1000 replicates, < 50% not shown) are generally low for most branches. However, the application of this method on morphological data matrices with a relatively low character to taxon ratio has limited use, because the number of (syn)apomorphies on each branch is often low (≤ 3), and confidence levels of clades are directly proportional to the number of character states appearing along the branches below the clades (Felsenstein, 1985; Sanderson, 1989). Best support is found for internal branches within the *Lopidium–Cyathophorum* clade (Fig. 1), which is related to the relatively high number of supporting (syn)apomorphies on the particular branches. Among the non-hypopterygiaceae, the highest bootstrap value is obtained for the *Daltonia angustofolia–Distichophyllum pulchellum* clade, the *Leucodon sciuroides–Neckera crispa* clade (Fig. 1a, b), and the *Achrophyllum dentatum–Calyptrochaeta apiculata* clade (Fig. 1a, b), resulting in the strong support for the basal branch of the Hypopterygiaceae clade in Fig. 1c.

Likewise, Bremer support is low for most internal branches of all trees in Fig. 1. Best Bremer support is found for the *Lopidium* clade, the *Cyathophorum* clade, and some of its internal branches. Among the non-hypopterygiaceae, the best Bremer support is obtained for the *Daltonia angustofolia–Distichophyllum pulchellum* clade and the *Achrophyllum dentatum–Calyptrochaeta apiculata* clade (Fig. 1a, b), resulting in the strong support for the basal branch of the Hypopterygiaceae clade in Fig. 1c.

DISCUSSION

Despite the use of different outgroups and different selections of (ingroup) taxa, the hypotheses of the phylogeny of the Hypopterygiaceae resulting from the four analyses are remarkably congruent. The combined consensus trees of the three analyses including non-hypopterygiaceae provide strong support for the hypothesis, that the Hypopterygiaceae form a monophyletic group with a group formed by *Achrophyllum* and *Calyptrochaeta* as its sister group. Other Daltoniaceae and Hookeriaceae are more distantly related. The Adelotheciaceae, the Callicostaceae, the Hypnales, and the Leucodontales are likewise distantly related to the Hypopterygiaceae.

The MPT presented in Fig. 1d and 2 shows the best possible outcome for the Hypopterygiaceae of the phylogenetic analyses with the available morphological data set. The low bootstrap values and the weak Bremer support for several internal branches in the trees presented in Fig. 1 indicate low stability for parts of the tree, i.e. those consisting of unstable branches. Branch stability is, in particular, low for the species in the *Hypopterygium* s.str. grade, and the configuration of the basal clades of the Hypopterygiaceae (*Dendrohypopterygium filiculiforme*, *D. arbuscula*, and the *Canalohypopterygium tamariscinum–Catharomnion ciliatum* clade). This is possibly related to the low number of supporting (syn)apomorphies on the branches (cf. Sanderson, 1989), and may represent two radiation events.

The CI and RI values obtained for the results of the four analyses indicate substantial homoplasy among the character states, which is the underlying problem of branch and tree stability. The amount of homoplasy is positively correlated with the number of taxa used in cladistic analyses (Sanderson & Donoghue, 1989). In addition, the amount of homoplasy may be exceptionally large in a morphological data set, when several (distant or closely related) taxa that are adapted to a similar habitat and show similar – reproductive – ecology (e.g. epiphytes) are included in the cladistic analyses. A combination of an overall higher number of taxa and a higher number of taxa that occupy similar habitats and show similar ecology may explain the relatively low CI and RI values (cf. Sanderson & Donoghue, 1989) of the analyses including representatives of the Hookeriales, Hypnales, and Leucodontales in Fig. 1a, b. The high number of taxa that grow in similar habitats and show similar ecology also contributes to the amount of homoplasy that exists among the Hypopterygiaceae themselves. Nevertheless, the amount of homoplasy found for the analyses of Fig. 1c, d is not exceptionally high. The CI indices obtained for these analyses are – for their number of taxa – within the variation range of CI indices (Sanderson & Donoghue, 1989).

Although the *Achrophyllum dentatum–Calyptrochaeta apiculata* clade (Fig. 1a–c) and the Hypopterygiaceae clade represent close relatives, the high number of equivocal ancestral character states between these groups (not shown) suggests, that the two are quite distantly related. The high number of equivocal ancestral character states is a source of uncertainty, which in analyses mostly affect the supposed character state changes in the basal part of the Hypopterygiaceae clade, and hence its topography. This effect can be seen when the configuration of the *Dendrohypopterygium filiculiforme*, the *D. arbuscula*, and the *Canalohypopterygium–Catharomnion* clades in Fig. 1a–c are compared with each other. Unfortunately, this problem cannot be solved, because extant mosses more closely related to the Hypopterygiaceae than *Achrophyllum* or *Calyptrochaeta* are still unknown.

Despite this uncertainty in configuration of the basal part of the Hypopterygiaceae clade, and hence the correct position of the root, the results of the series of analyses provide strong support for a basal position of the *Dendrohypopterygium* grade and the *Canalohypopterygium–Catharomnion* clade in the Hypopterygiaceae. Plausibly, *Dendrohypopterygium filiculiforme* is, among the extant Hypopterygiaceae species, the one showing most plesiomorphies.

Stech et al. (1999) also presumed an ancient status of *Dendrohypopterygium filiculiforme* (as *Hypopterygium filiculiforme*), but found no evidence for a basal position of the two *Dendrohypopterygium* species and the *Canalohypopterygium–Catharomnion* clade based on *trnL* intron sequence data.

The general pattern of character state changes within the Hypopterygiaceae is from complex to simple. Epiphytic or epilithic species with simple gametophores or pinnate fans have been derived from terrestrial dendroid ancestors (character 2: state 1 → 3 or 4) firstly by the reduction of the number of branches and secondly by the reallocation of the photosynthetic surface from numerous, small leaves to a fewer number of large(r) leaves. The best evidence for this overall process is found in the differences between the gametophores of *Dendrohypopterygium filiculiforme* and *Cyathophorum bulbosum*. The occurrence of rudimentary branches in *Canalohypopterygium* and *Catharomnion* (character 14: state 2) with their central axial cavity (character 13: state 2) fits perfectly in this process, whether or not they have been derived from the ultimate branches with a central cavity like the ones in *Dendrohypopterygium* (character 13: state 2) or from first orders branches. The first hypothesis is most plausible, because in *Dendrohypopterygium* axial cavities are absent from the stipe, the basal and middle parts of the rachis, and the basal and middle parts of the lower branches.

The shift from an octostichous phyllotaxis of the basal part of the stem (stipe) to a tristichous phyllotaxis (character 3: state 1 → 4) has occurred, at least, three times independently. All epiphytes and epilithic plants – the fans – have a stipe or a basal part of the stem with a tristichous phyllotaxis, which suggests a correlation. However, a tristichous phyllotaxis of the stipe also occurs in the dendroids *Hypopterygium discolor* and *H. tamarisci*. These two constitute a clade that is nested in a monophyletic clade together with *H. flavolimbatum* (Fig. 1d, 2). This arrangement suggests that the occurrence of a tristichous or nearly tristichous phyllotaxis of the stipe in tiny plants of *H. flavolimbatum* – as such not used in the analyses – may not be accidental or indetectable due to size, but may in fact reflect a rare state of polymorphism, which represents the plesiomorphic condition of the *H. flavolimbatum – H. discolor–H. tamarisci* clade.

The shift from an isophyllous foliation of the basal part of the stem (stipe) (character 7: state 1) to an anisophyllous one (character 7: state 2) is superimposed on the shift from terrestrial dendroids towards epiphytic fans. The shift from cygneous or uncinate sporophytes that are projecting above the gametophores (character 32: state 1) to straight or curved ones that are projecting beneath the gametophore (character 32: state 2) is, to a lesser extent, superimposed on the shift from terrestrial dendroids towards epiphytic fans.

Peristome reductions, on the other hand, are only partly explained by either the shift from terrestrial dendroids to epiphytic fans or the shift from sporophytes that are projecting above the gametophores to ones that are usually projecting beneath the gametophore. Reduced peristome structures (character 42: state 2; character 43: state 2; character 44: state 2; character 46: state 2; character 48: state 2; character 49: state 3; character 50: state 2) are restricted to epiphytes (and epilithic plants), but are basically absent from *Hypopterygium vriesei*, *Dendrocyathophorum decolyi*, *Lopidium concin-*

num (major peristome character states plesiomorphic) and *Cyathophorum bulbosum* and *C. spinosum* (major peristome character state synapomorphic).

The hypothesised relationships among the Hookeriales – other than *Achrophyllum* or *Calyptrochaeta* –, the Leucodontales, and Hypnales that were used in the analyses have limited value, because in the present study only a small selection of – for these orders non-representative – species was used. Likewise, the present study does not give a clear answer to the taxonomic position of the Hypopterygiaceae in the pleurocarpous mosses. Nevertheless, it is clear that Hypopterygiaceae form a monophyletic group and that they, as a whole, are well nested in the Hookeriales–Leucodontales–Hypnales clade, in particular because of the strong sister group connection between the *Achrophyllum–Calyptrochaeta* clade and the Hypopterygiaceae clade. In Hedenäs' (1996a) and, in particular, Hedenäs' (1996b) cladistic studies, *Calyptrochaeta* and *Achrophyllum* were also found in a position close to representatives of the Hypopterygiaceae, albeit in a paraphyletic grade. These results confirm Hedenäs' (1996a) conclusion, that the Hypopterygiaceae do not belong to the Bryales as was suggested by Buck (1987, 1988).

Hedenäs' (1995) and Newton & De Luna's (1999) morphological studies indicated that the Hypopterygiaceae, represented by *Hypopterygium arbuscula* (≡ *Dendrohypopterygium arbuscula*) and *H. tamarisci* ('*tamariscinum*') are basal to the pleurocarpous mosses. Based on his morphological studies (Hedenäs, 1996a, b), Hedenäs (1996b) suggested that the Hypopterygiaceae constitute a basal monophyletic group within the Hookeriaceae. This view is to some extent supported by analyses of molecular data. Studies by De Luna et al. (1999) and Cox et al. (2000) indicated that the Hypopterygiaceae, represented by two *Hypopterygium* 'species' (= *H. tamarisci*), constitute a monophyletic group with the Hookeriaceae, represented by *Hookeria*, which is basal to the Leucodontales and the Hypnales. From subsequent analyses based on molecular data, De Luna et al. (2000) obtained a monophyletic group of Hypopterygiaceae and Hookeriales, represented by *Hypopterygium*, *Ptychomnion* (Hook.f. & Wilson) Mitt., *Lepidopilum* Müll.Hal., and *Hookeria*. The Hypopterygiaceae possess a basal position in this monophyletic group, which is presented as the sister group of the Hypnales and the Leucodontales (Hypnales s.l. in De Luna et al., 2000). Buck et al. (2000a, b) obtained comparable results in most of their analyses based on molecular data, which include many more taxa, especially from the Hypnales and Leucodontales, but still only one representative of the Hypopterygiaceae (*Hypopterygium tamarisci*).

The trees obtained from the present analyses, depicted in Fig. 1a and 1b, suggest that Hypopterygiaceae constitute a terminal clade. However, a basal position of the Hypopterygiaceae may very well be correct, if we assume that the trees including non-hypopterygiaceae have an ancestral root near the base of the Hypopterygiaceae clade. The incongruence between the trees obtained from the present analyses, depicted in Fig. 1a and 1b, with the studies by Hedenäs (1995; 1996a, b) and Newton & De Luna (1999) based on morphological data, and the mutual incongruence between Hedenäs' own trees, show that this rooting problem can only be solved when a sufficient and well balanced sampling of a high number of, preferably revised, taxa of the Adelotheciaceae, Callicostaceae, Daltoniaceae, Hookeriaceae, Hypopterygiaceae, Leucodontales, and Hypnales are analysed in a single cladistic analysis. Such an analysis will be a complicated one when it is based on morphological data, because in mosses a high amount of homoplasy may be expected due to convergence as a result of reduction of morphological characters. Recent molecular studies (Buck et al., 2000a, b; De Luna et al., 2000) indicate that representatives of the Ptychomniaceae M. Fleisch. and Garovagliaceae (M. Fleisch.) W.R. Buck & Vitt (both Leucodontales) should be included in the analysis.

SYSTEMATIC IMPLICATIONS AND SUBFAMILIAL CLASSIFICATION

The Hypopterygiaceae constitute a monophyletic group that is best retained as a separate family. It is provisionally maintained in the Hookeriales, but the higher phylogenetic relationships of the family with the Hookeriales, Leucodontales, and Hypnales need further study. The results obtained in the present study do not justify merging the Hypopterygiaceae with the Hookeriaceae as suggested by Hedenäs (1996b).

The Hypopterygiaceae are characterised by – at least – 3 synapomorphies, which include the tristichous phyllotaxis and anisophyllous foliation of the distal parts of the stem or the distal parts of the rachis and the branches (character 4: state 4, character 8: state 2), and the axial cavities in the ultimate branches (character 13: state 2). All 3 synapomorphies contribute to the morphological differentiation between the basal and distal parts of the gametophore of the Hypopterygiaceae.

The proposed phylogenetic relationships between the species of the Hypopterygiaceae (Fig. 1d, 2) do not justify a subdivision of the family at the subfamily or tribus level, but unfortunately leaves classification on the genus level quite complicated. A strictly cladistic classification for the generic subdivision of the Hypopterygiaceae, which only allows monophyletic groups, would not lead to a better classification. The classification of all Hypopterygiaceae species in a single, large, monophyletic genus does not do justice to the tremendous, discontinuous morphological diversity that is present within the family. For instance, the mainly simple, epiphytic plants of *Cyathophorum bulbosum* with very large leaves are very different from the terrestrial dendroids of *Dendrohypopterygium filiculiforme* with its small leaves and three to four times pinnately branched frond. In addition, there are no extant intermediate species or groups of species that, to some extent, fill the morphological gaps between *Canalohypopterygium tamariscinum* and *Catharomnion ciliatum*. Recognition of smaller monophyletic groups than all species in a single group results in the formation of either one or two paraphyletic groups, a single polyphyletic group, or many monophyletic groups (i.e. monotypic genera) at the base of the Hypopterygiaceae. The formation of a polyphyletic group or many monophyletic groups is undesirable, but the formal classification of a paraphyletic group is acceptable. In the proposed classification, changes with respect to the traditional classification are kept to a minimum.

The genus *Cyathophorella* is united with *Cyathophorum*. In Fleischer's (1908) concept, *Cyathophorella* is a polyphyletic group. In a smaller concept, including the *Cyathophorum africanum–C. hookerianum–C. parvifolium* grade, *Cyathophorella* becomes paraphyletic, but only arbitrary decisions would decide whether or not *Cyathophorum adiantum* should be included in *Cyathophorella* or *Cyathophorum*.

In its present circumscription, *Cyathophorum* is supported by 5 synapomorphies (Fig. 2): the usually simple plants (character 2: state 4); the sporophyte that is usually projecting beneath the gametophore (character 32: state 2); the absence of an annulus (character 39: state 2); the mainly absence of a border in exostome teeth (character 44: state 2); and the smooth, papillose, or weakly striate ornamentation of the basal dorsal face of exostome teeth (character 46: state 2). For the *Cyathophorum bulbosum–C. tahitense–C. spinosum* clade, the latter two character states reverse to their plesiomorphic conditions: the exostome teeth being partly bordered above the base at least (character 44: state 1) and the exostome teeth being conspicuously striate on the basal dorsal face (character 46: state 1). It should be kept in mind, however, that the sporophyte of *C. tahitense* is yet unknown.

Lopidium is a monophyletic group including *Lopidium concinnum* and *L. struthiopteris.* It is supported by 7 synapomorphies (Fig. 2): the long costa in the lateral leaves in the distal part of the frond, reaching 4/5 of the length of the leaf at least (character 22: state 1); the incrassate walls of the laminal cells of the frond leaves (character 24: state 2); the occasional presence of perichaetial paraphyses (character 28: state 2); the occasional presence of leaf-like perichaetial paraphyses (character 29: state 2); the rhizoids at the stalk of full grown perichaetia (character 30: state 1); the weakly to moderately mamillate seta (character 35: state 2); and the texture of the calyptra, being membranous in the basal part and becoming fleshy in the distal part at some distance from the apex (character 57, state 3). Among the Hypopterygiaceae, the states of character 24, 29, and 35 are truly unique for *Lopidium.* The state of character 30 is a reversal to a plesiomorphic condition. The states of character 22, 28, and 57 have analogies in other clades. Studies based on *trnL* intron sequences carried out by Stech et al. (1999) and Pfeiffer (2000) provide further supporting evidence for a distinct *Lopidium* clade within the Hypopterygiaceae.

Dendrocyathophorum is maintained as a separate monotypic genus, although the *Dendrocyathophorum decolyi* clade is supported by only two apomorphies: the costa of the amphigastria reaches more than 1/3 of the length of the amphigastrium, but becomes never percurrent (character 23: state 2), and the calyptra is partly covering the operculum (character 54, state 3). State 2 of character 23 is also found in *Hypopterygium sandwicense*, whereas state 3 of character 54 occurs in two *Cyathophorum* species. One of the main characteristic features of *Dendrocyathophorum*, the central axial cavity in the stipe and rachis, is given as a synapomorphy of the *Dendrocyathophorum decolyi–Lopidium–Cyathophorum* clade (Fig. 2) and as a plesiomorphic condition for *Dendrocyathophorum* (character 12: state 2). Likewise, the anisophyllous foliation of the basal part of the stipe is given as a synapomorphy of the *Dendrocyathophorum decolyi–Lopidium–Cyathophorum* clade and as a plesiomorphic condition for *Dendrocyathophorum* (character 7: state 2). These two synapomorphies give strong support for the delimitation of the *Dendrocyathophorum decolyi–Lopidium–Cyathophorum* clade from the *Hypopterygium* s. str. grade. State 2 of character 12 is not found outside this clade and state 2 of character 7 is elsewhere only found in *Catharomnion ciliatum.* Consequently, *Dendrocyathophorum* cannot be included in *Hypopterygium* s. str., and it does not belong to *Lopidium* and *Cyathophorum* in their present circumscription.

In all trees of Fig. 1, *Canalohypopterygium* and *Catharomnion* are arranged in a single clade. Studies based on *trnL* intron sequences carried out by Stech et al. (1999) provide further supporting evidence for a distinct *Canalohypopterygium–Catharo-*

mnion clade within the Hypopterygiaceae. Nevertheless, *Canalohypopterygium* and *Catharomnion* are kept separate as monotypic genera (see also Stech et al., 1999). They differ substantially qualitatively and quantitatively in many gametophytic and sporophytic features from each other. Striking qualitative differences, amongst others, are for *Canalohypopterygium tamariscinum*: the octostichous phyllotaxis of the stipe (character 3: state 1); the not complanate and isophyllous foliation of the stipe (character 5: state 1; character 7: state 1); the uncinate sporophyte with its horizontal to pendulous capsule (character 37: state 3); and the presence of an exostome (character 42: state 1), and for *Catharomnion ciliatum*: the tristichous phyllotaxis of the stipe (character 3: state 4); the complanate, anisophyllous foliation of the stipe (character 5: state 2; character 7: state 2); the straight or curved sporophyte with its principally erect capsule (character 37: state 2); and the absence of the exostome (character 42: state 2). Quantitative differences in polymorphic character states were not used in the analyses, but differences, e.g. in habit and dentation of the leaf margin, emphasise the differences between *Canalohypopterygium* and *Catharomnion*. The *Catharomnion ciliatum* clade is supported by 13 synapomorphies, which include the character states cited above (Fig. 2). *Canalohypopterygium tamariscinum* maintained the plesiomorphic conditions of the common ancestor of *Canalohypopterygium* and *Catharomnion*. *Catharomnion ciliatum* is most derived from this ancestor.

The *Canalohypopterygium–Catharomnion* clade is well separated from the *Hypopterygium* s.str. and the *Dendrohypopterygium* grades. The *Canalohypopterygium–Catharomnion* clade is supported by 5 synapomorphies, among which the for all mosses unique synapomorphies of having rudimentary branches (character 14: state 2) and the presence of cortical axial cavities in the stipe and the basal and middle parts of the rachis (character 12: state 3), which are connected with the central cavity of the rudimentary branches. The other synapomorphies are the at least partly dentate-ciliate margin of the lateral leaves in the distal part of the frond (character 18: state 4), the short vaginula (character 31: state 1), and the mitrate calyptra (character 53: state 3). Analogies of the latter two are also found in some *Cyathophorum* species.

The *Hypopterygium* s.str. grade is a paraphyletic core of 7 species (*H. didictyon*, *H. elatum*, *H. tamarisci*, *H. discolor*, *H. flavolimbatum*, *H. sandwicense*, and *H. vriesei*), which is treated here as a separate genus. In Fig. 2, the base of the grade is supported by 4 synapomorphies: the absence of axial cavities in ultimate branches (character 13: state 1); the absence of paraphyses in perigonia and perichaetia (character 27 and 28: state 3); and the oblique rostrum (character 52: state 1). The plesiomorphic condition of character 27 and 28 reappears as a state of polymorphism within *Hypopterygium tamarisci*. Character 13 reverses to its plesiomorphic state within *Hypopterygium* as a synapomorphy for the terminal clade including *H. sandwicense* and *H. vriesei*. The state of character 52 changes within *Cyathophorum* to, respectively, state 2 and the plesiomorphic state 3.

Dendrohypopterygium forms the paraphyletic, basal group of the Hypopterygiaceae (Fig. 1d, 2). The two species of this genus were formerly classified in *Hypopterygium*, but must be transferred from this genus as a consequence of the generic status of *Canalohypopterygium* and *Catharomnion*. The inclusion of the two *Dendrohypopterygium* species in *Hypopterygium* would result in a paraphyletic genus *Hypopterygium* in the combined consensus tree of Fig. 1b, and in a polyphyletic one in the trees of Fig. 1a, 1c and in the accepted phylogenies of Fig. 1d and 2.

The differences between the trees of Fig. 1 at the base of the Hypopterygiaceae show, that the phylogenetic relationships between the basal species are not completely resolved. Apart from outgroup problems (see discussion), this is due to the high number of (potentially) plesiomorphic character states of the family that are expressed in both *Dendrohypopterygium* species. In fact, all other Hypopterygiaceae have been derived from the ancestor of *Dendrohypopterygium filiculiforme*, *D. arbuscula*, or both. Retained or regained plesiomorphic character states can be found scattered throughout the descendents of this *Dendrohypopterygium* ancestor. This makes it almost impossible to find a better resolved phylogenetic reconstruction of the (basal) Hypopterygiaceae based on morphology.

Chapter 7

DISTRIBUTION AND BIOGEOGRAPHY

DISPERSAL AND DISTRIBUTION

The present geographic distribution areas of the Hypopterygiaceae (see the various maps in 'Taxonomic treatment', p. 93 and onwards) are the result of a combination of factors acting in time, which include dispersal, vicariance, and speciation events. Dispersal events result from dispersal of diaspores, which may occur over various distances. Vicariance events are a result of fragmentation of a, formerly continuous, distribution area and are, for Hypopterygiaceae, mainly a result of plate tectonics and continental drift. Speciation events may follow after dispersal and vicariance events.

Diaspores

Dispersal of Hypopterygiaceae occurs by means of detached branch fragments, detached leaves, gemmae, and spores.

Vegetative propagation by means of detached branch fragments or leaves is found in *Dendrohypopterygium* (*D. filiculiforme*, and perhaps *D. arbuscula*), *Hypopterygium* (*H. didictyon*, *H. discolor*, *H. flavolimbatum*, *H. vriesei*, *H. tamarisci*, *H. sandwicense*), and a single *Lopidium* species (*L. concinnum*). Fragmenting axes and caducous leaves are usually restricted to the distal parts of the fronds of the gametophores. The frequency of appearance of caducous (distal) branch fragments and frond leaves may differ between species, and between variants within species (*H. flavolimbatum*, *H. tamarisci*, *L. concinnum*; see 'Taxonomic treatment', p. 93 and onwards).

Vegetative propagation by means of gemmae is found in *Hypopterygium discolor*, *H. flavolimbatum*, *H. vriesei*, *H. tamarisci*, *Lopidium struthiopteris*, *Cyathophorum hookerianum*, *C. parvifolium*, *C. adiantum*, *C. bulbosum*, *C. spinosum*, and *C. tahitense*. The production of gemmae is, like the occurrence of fragmenting axes and caducous leaves, usually restricted to the distal parts of the fronds or foliate stems of the gametophores. The frequency of gemmiferous plants may differ between species, and between variants of species (e.g. *H. tamarisci*). The production of gemmae is most frequent and a normal condition in the mainly epiphytic and epilithic species *Lopidium struthiopteris*, *Hypopterygium vriesei*, *Cyathophorum hookerianum*, *C. parvifolium*, *C. adiantum*, *C. spinosum*, and *C. tahitense*, and to some extent *C. bulbosum*. In *Hypopterygium discolor* and *H. flavolimbatum* the occurrence of gemmiferous gametophores is a rare or an occasional phenomenon, whereby the production of gemmae is (usually) a reaction on damage to frond axes.

Sporophytes of *Hypopterygium vriesei* and *Cyathophorum tahitense* have not been found, which suggests that these species mainly reproduce vegetatively by means of gemmae. In herbarium material of *Lopidium struthiopteris*, *Cyathophorum hookerianum*, *C. parvifolium*, *C. adiantum*, *C. spinosum*, and *C. tahitense*, fruiting specimens and sporophytes are rare to such a degree, that vegetative propagation by means of gemmae will also be a main factor of reproduction and dispersal for these species.

The other species of the Hypopterygiaceae have fruiting specimens in various frequencies of occurrence. The occurrence of fruiting specimens may show local variation within species (e.g. *C. bulbosum*, *H. tamarisci*, *L. concinnum*).

Transport of vegetative propagula

Gemmae, branch fragments, and detached leaves are transported by air streams or water currents. It is generally assumed that particles smaller than 25 μm in diameter can horizontally be dispersed over hundreds of kilometres or more by air streams (cf. Van Zanten & Pócs, 1981; Van Zanten & Gradstein, 1988). Vegetative propagula are usually much larger in at least one dimension, which significantly decreases the possibility for transport by air streams. Transport of vegetative propagula by air streams usually results in dispersal over only a very short distance, which in forests and open habitats will generally not exceed a few decametres as a result of whirling downwards from a site on a phorophyte (i.e. tree or tree fern) or other high point of release. However, strong winds may increase the transport distances considerably and the possibility of transport over hundreds of kilometres or more by air streams cannot be excluded.

Most vegetative propagula that are transported by water will be transported by surface flow over distances of a few decametres at most. Transport by water currents, usually streams, may occasionally occur over much longer distances. Effective dispersal by ocean currents, however, seems unlikely.

Regardless of the transport vector, vegetative propagation will generally result in local dispersal and mainly contributes to the maintenance, the growth, or the expansion of the local population. Nevertheless, rare, exceptional events of propagula transport over larger distances may occasionally result in the establishment of new, viable populations. The chance that a rare transport event will have taken place increases with time.

Transport of spores

Spores may contribute to dispersal over much longer distances. The spores of Hypopterygiaceae vary between 9 μm and 25(−35) μm in diameter. They are much smaller than the vegetative propagula and are assumed to be mainly dispersed by air streams. Being in majority smaller than c. 25 μm in diameter, they are generally small enough to be transported up to several thousands of kilometres in air streams (cf. Van Zanten & Pócs, 1981, Van Zanten & Gradstein, 1988). The number of dispersed spores after release is inversely correlated with distance, whereby a significant portion of the released spores is dispersed over only a short distance and lands usually within a few metres after release depending on the height of the point of release and spore size (e.g. McQueen, 1985; Miles & Longton, 1992; Stoneburner et al.,1992) and the openness of the environment. However, a considerable number of spores remain airborne over longer distances (Miles & Longton, 1992; Stoneburner et al.,1992) and it is therefore assumed that they reach higher air streams and travel over long distances.

Local dispersal

Vegetative propagula and a portion of the spores mainly contribute to local dispersal. Local dispersal contributes to the maintenance and growth of local populations. Steady growth of local populations, usually in combination with short-range dispersal events, may result in time in considerable increase of the distribution area of the species. This process probably played an important role for most species of the Hypopterygiaceae in the warm periods of the Pleistocene, following a cold one after a climatic change. In addition, vegetative propagation increases the chance of survival of populations under (temporarily) unfavourable conditions and the chance of quick recovery after conditions have become more favourable.

Short-range dispersal

Based on Van Zanten's (1978) and Van Zanten & Pócs' (1981) definition of long-range dispersal, short-range dispersal is defined here as dispersal up to c. 2000 km, which may result in the colonisation of unoccupied habitats and the founding of new populations. Schuster's (1983) definition of short-range dispersal, up to 300 km, is not adopted here.

Due to their size, short-range dispersal by vegetative propagula is probably a rare event. Short-range dispersal by spores is more common and may be most effective in a range of a few hundreds of kilometres from the point of release, which may indirectly lead to transport over much larger distances by serial short-range dispersal events by island- or mountain-hopping.

Thus far, colonisation following a transport event over a short distance has been observed for the Hypopterygiaceae only once. In 1979, *Hypopterygium vriesei* and *Cyathophorum spinosum* were found on the Krakatau Islands (see '*H. vriesei*', note 9, p. 195). The Krakatau eruptions of 1883 completely destroyed the flora and fauna on the remains of the Krakatau Island group, and left for years no suitable habitat for rain forest mosses like *H. vriesei* and *C. spinosum*. The surviving parts of the island group, and Anak Krakatau after its emergence in 1930, were recolonised by floristic elements from Sumatra and Java. The Krakatau Islands are located at c. 19 km distance from the nearest island (Sebesi Is.) and c. 40 km from the nearest land from Java and Sumatra. It is not known how, from where, and by which diaspores (gemmae or spores; less likely plant fragments) *H. vriesei* and *C. spinosum* reached the Krakatau Islands. Transport by spores seems most likely, but the fact that spore production is rare in both species, suggests that incidental dispersal of gemmae from Java, or Sumatra, by strong air streams – or perhaps by birds? – over a distance of ten to forty kilometers overseas cannot be excluded.

The best examples of step-by-step short-range dispersal are the distributions of *Hypopterygium flavolimbatum* along the northern Pacific coast, and *H. tamarisci* on the Pacific Islands.

Long-range dispersal

Following Van Zanten's (1978) and Van Zanten & Póc's (1981) definition, long-range dispersal is defined here as dispersal beyond c. 2000 km, which may result in the colonisation of unoccupied habitats and the founding of new populations. Essential for an expansion of the distribution area of a species after such long-range transport is, that: a) the spores survive the hazardous conditions, e.g. desiccation, UV irradiation, frost, during the transport; and b) that after the transport, they are deposited in a habitat which is suitable for germination and subsequent colonialisation by growth and local or short-range dispersal of diaspores. The problems associated with long-range dispersal of bryophyte spores have been thoroughly investigated and discussed by Van Zanten (1976, 1978, 1983, 1992), Van Zanten & Pócs (1981), and Van Zanten & Gradstein (1988). Van Zanten's experiments showed, that resistance to UV irradiation is the limiting factor in aerial long-range dispersal by bryophyte spores. Resistance to desiccation is correlated with resistance to UV irradiation (Van Zanten, pers. comm.).

Possibilities for Hypopterygiaceae of effective short- and long-range dispersal by spores

In his experiments to resistance of moss spores to drought, frost, and UV irradiation, Van Zanten tested spores of a few species of the Hypopterygiaceae, which he obtained from Australian, New Zealand, and South American material (Van Zanten, unpublished data[1]). The survival rate of the spores to the conditions occuring during long-distance transport in air streams was low.

Van Zanten's experiments showed that spores of the South American endemic *Dendrohypopterygium arbuscula* had very low resistance to UV irradiation (less than a single day of UV light exposure at sea level in June, if any). Spores of the Austral species *Hypopterygium didictyon* had also very low resistance to UV irradiation (less than a single day of UV light exposure at sea level in November and January, if any). Spores of the endemic species *Catharomnion ciliatum*, distributed in New Zealand and the Chatham Is., and *Cyathophorum bulbosum*, distributed in eastern Australia, New Zealand, and Papua New Guinea, were somewhat more resistent to UV irradiation. Roughly 10% of the spores remained viable after 1 day of exposure to daylight at sea level at c. 53.1° N, 6.7° E in autumn and winter – November to January –, but none of the spores survived 2 days of exposure. Spores of one of the two samples of *Catharomnion ciliatum* did not survive a day of UV light exposure at sea level. Spores from New Zealand material of the widely distributed *Hypopterygium tamarisci* showed the highest resistance to UV irradiation, whereas Australian material of this species had a low resistance. Roughly 50% of the New Zealand spores remained viable after 2 days of exposure at sea level; none of the New Zealand spores survived 3 days of exposure. The Australian spores did not survive a single day of UV light exposure at sea level.

The results of Van Zanten's experiments indicate, that effective long-range transport of spores is possible for *Cyathophorum bulbosum, Catharomnion ciliatum*, and *Hypopterygium tamarisci* within Australasia (e.g. between Tasmania and New Zealand), most likely during winter in streams with moist air (Van Zanten, pers. comm.). It is, however, unlikely that spores of these species survive aerial long-range transport from Australasia to southern South America. The prevailing westerly winds probably prevent spores of New Zealand *Catharomnion ciliatum* to reach suitable habitats in Tasmania and south-eastern Australia, but the westerly winds may explain the occurrence of the

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1) Drought tolerance of viable spores of *Catharomnion ciliatum, Cyathophorum bulbosum, Dendrohypopterygium arbuscula, Hypopterygium didictyon, H. tamarisci*, and *Lopidium concinnum* was tested principally following the method described by Van Zanten & Gradstein (1988). Resistance to UV irradiation was tested by exposing viable spores of *Catharomnion ciliatum, Cyathophorum bulbosum, Dendrohypopterygium arbuscula, Hypopterygium didictyon*, and *H. tamarisci* to daylight (indirect sunlight) at sea level at c. 53.1° N, 6.7° E in June (*Dendrohypopterygium arbuscula, Hypopterygium didictyon*), and November–January (*Catharomnion ciliatum, Cyathophorum bulbosum, Hypopterygium didictyon, H. tamarisci*); see Meesters & Van Zanten (1988) for a description of the test device used for the experiment.

species on the Chatham Islands; these are remnants of Late Cretaceous volcanic islands and have been isolated for at least 70 million years (Campbell et al., 1993; Stilwell, 1997).

Van Zanten's experiments showed much variation in the survival of spores of the same species under the same (harsh) conditions. Nevertheless, his results convincingly suggest that effective long-range dispersal by spores is a rare process in Hypopterygiaceae, which may have occurred only a few times in the history of the family. The occurrence of *Hypopterygium sandwicense* on the Hawaiian Islands is perhaps best explained by such a rare event.

PLATE TECTONICS AND DISTRIBUTION

Endemism in New Zealand, Australia, and South America strongly suggests that plate tectonics and continental drift played a significant role in the biogeographic history of the Hypopterygiaceae. The low possibilities of effective long-range dispersal for Hypopterygiaceae, as is shown and hypothesised in the previous section, indicate further that long-range dispersal events are rare and are superimposed on biogeographical events as vicariance and speciation caused by plate tectonics.

If so, the speciation events shown in the reconstructed phylogeny of the Hypopterygiaceae (Fig. 1d) are mainly related to geological events. A reconstruction of the biogeographical history of the Hypopterygiaceae is given below and is based on the present distribution areas of the extant species in relation to the phylogeny of the species (Fig. 3).

The origin of the Hypopterygiaceae is situated in Gondwanaland[1]. This hypothesis is supported by: a) the occurrence of basal Hypopterygiaceae (*Dendrohypopterygium filiculiforme*, *Canalohypopterygium*, *Catharomnion*) as New Zealand endemics (Fig. 3, Map 4, 6–8); b) the occurrence of *Dendrohypopterygium arbuscula* as a South American endemic (Fig. 3, Map 5); c) the high diversity at generic and specific level of the family in New Zealand (Map 2) and at the specific level in Australasia and Indo Malaysia (Map 1); and d) the present distribution of the *Hypopterygium*, *Lopidium*, *Dendrocyathophorum*, and *Cyathophorum* species on fragments of Gondwanaland origin (Map 9–26).

The occurrence of the New Zealand endemics suggests, furthermore, that the basal Hypopterygiaceae have their origin in (south-)eastern Gondwanaland. Before the break-up of East Gondwanaland, New Zealand had a position adjacent to, what is nowadays, Marie Byrd Land in West Antarctica (Stilwell, 1997; Grunow, 1999; Storey et al., 1999). Hence, the ancestral species of the basal Hypopterygiaceae were probably distributed in active mountain ranges on the margin of the continent. They faced cool

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1) Examples of other moss families with a distribution pattern that is related to the break-up of East Gondwanaland are the Hypnodendraceae Broth. (Ramsay 1983, 1987; Touw, cf. 1971, 1992b) and the Garovagliaceae (M. Fleisch.) W.R. Buck & Vitt (During, 1977). *Trachyloma* Brid., and possibly *Racopilum* P. Beauv., are such examples on the generic level (Miller & Manuel, 1982; cf. De Vries et al., 1989). Other examples of liverwort and moss taxa and an ample discussion on distribution patterns that are assumed to be a result of the break-up of East Gondwanaland were given by Schuster (1982, 1983).

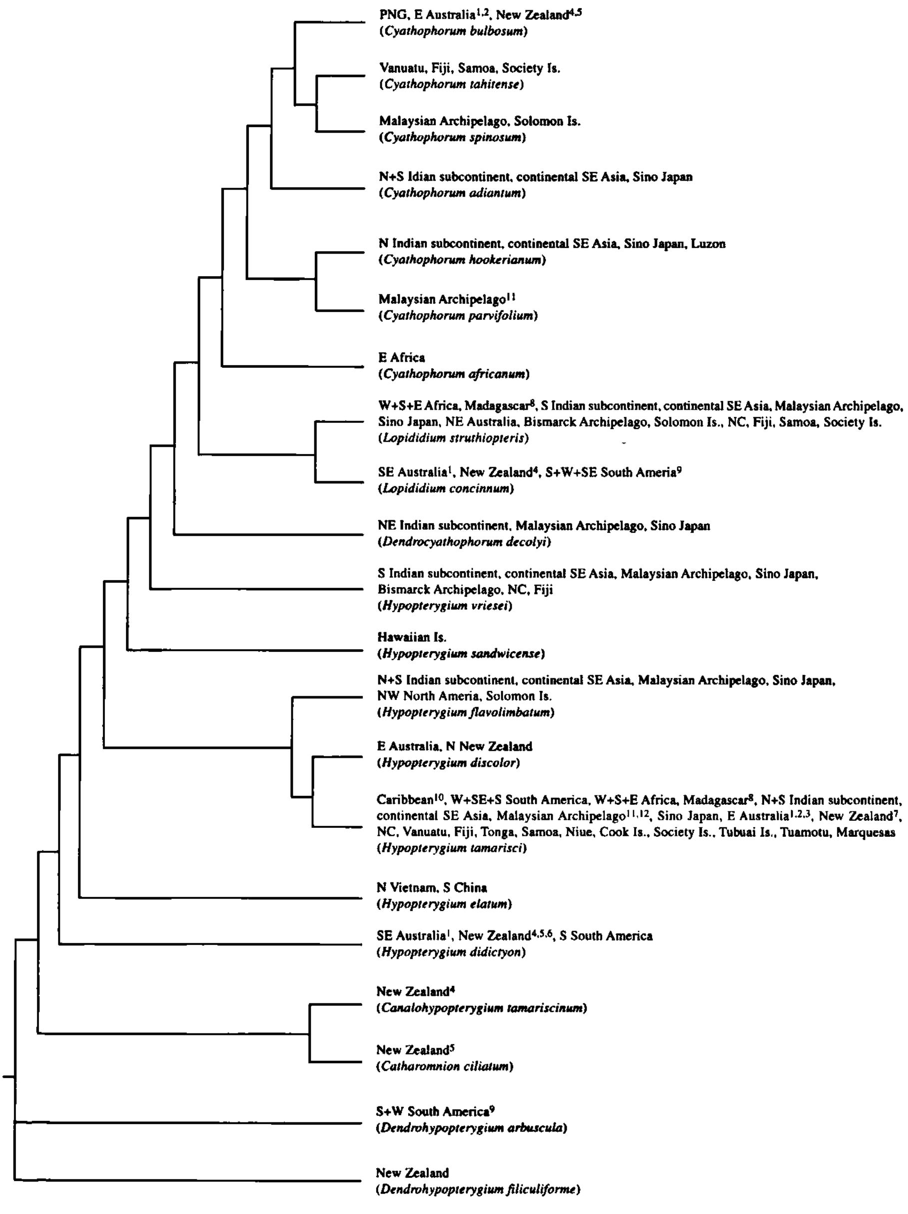

Fig. 3. Area cladogram of Hypopterygiaceae showing the distribution areas of species related to the phylogeny of the family presented in Fig. 1d. NC = New Caledonia; PNG = Papua New Guinea.

Notes: 1) Australia incl. Tasmania; 2) Australia incl. Lord Howe Is.; 3) Australia incl. Norfolk Is.; 4) New Zealand incl. Auckland Is.; 5) New Zealand incl. Chatham Is.; 6) New Zealand incl. Campbell Is.; 7) New Zealand incl. Kermadec Is.; 8) Madagascar incl. Mascarenes; 9) South America incl. Juan Fernandez Is.; 10) Carribean incl. Central America and Mexico; 11) Malaysian Archipelago without Luzon, Palawan, and Borneo; 12) Malaysian Archipelago without Visayas and Mindanao. See 'Taxonomic treatment', p. 93 and onwards, for more detailed information on the distribution areas of the various species.

temperate conditions[1] and occupied humid, terrestrial habitats at low altitude much like the terrestrial *Dendrohypopterygium* and *Canalohypopterygium* species of today (cf. Frey & Beever, 1995). Since the New Zealand mirco-continent separated from Gondwanaland c. 86–84 million years ago (Ma) (Storey et al., 1999; O'Sullivan et al., 2000) in the Late Cretaceous, the Hypopterygiaceae are at least 84 million years old.

The separation of the New Zealand mirco-continent is one of the events in the stepwise break-up of East Gondwanaland since the Late Jurassic (Gnos et al., 1997). The break-up of Gondwanaland started at c.158 Ma with the separation of West Gondwana and East Gondwana (Gnos et al., 1997). The break-up of West Gondwana (South America and Africa) started c. 130 Ma with rifting and formation of the Southern Atlantic Ocean (Deckart et al., 1998).

Almost simultaneously, the break-up of East Gondwanaland (East and West Antarctica, Australia, India, and Madagascar) started with westwards rifting along the margin of present Antarctic plates and subsequent northwards drifting of the separated fragments and continents. India and Madagascar separated between 140–130 Ma from Australia (Gnos et al., 1997; Song & Cawood, 2000), which was still joined with Antarctica and New Zealand. Australia separated at c. 95 Ma from Antarctica (O'Sullivan et al., 2000). New Zealand was the last continental fragment that separated from Antarctica (Storey et al., 1999).

After the New Zealand microcontinent had separated from Gondwanaland, it slowly sank below sea level in the latest Cretaceous while drifting northwards, until a vast continental shelf with a few low islands remained (Campbell et al., 1993; Norris, 1999). In the Miocene the Alpine Fault through South Island was formed (c. 25 Ma) due to the northwards drift of Australia. A long period of movement, compression, uplift, and expansion of land areas close to the fault resulted in the shaping of present-day New Zealand (Heads, 1998; Norris, 1999). The combination of marine transgression, which resulted in the formation of low islands, and isolation provided favourable conditions for vicariance events and subsequent speciation, and may partly explain the high amount of endemism in New Zealand. *Catharomnion ciliatum* is plausibly one of the endemics that have come into existence during, or after, the transgression period. *Dendrohypopterygium filiculiforme* and *Canalohypopterygium tamariscinum* are probably older (see below) and survived on (some) islands.

The present distribution pattern of *Catharomnion ciliatum* suggests (Fig. 3, Map 6b, 8), that it has its origin east of the Alpine Fault, but this is not certain. *Catharomnion ciliatum* is absent from the south-eastern part of South Island (Map 8). Heads (1998) suggested that such a distribution pattern may be affected by movements along the Alpine Fault. However, it is difficult to believe that *C. ciliatum* has been able to reach the Chatham Is. by a dispersal event, while it is not capable to disperse itself further into South Island. The present distribution pattern of the species is probably determined by present day climatic factors, of which temperature may be the main factor.

The New Zealand drift scenario implies that the ancestor species of the other Hypopterygiaceae remained on Gondwanaland. The phylogenetic relationships of the New

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1) Palaeoclimatological data for the Early Cretaceous period are obtained from Scotese et al. (1999); palaeoclimatological data for the Late Cretaceous and Cenozoic period are obtained from their website (www.scotese.com).

Zealand species with the South American *Dendrohypopterygium arbuscula* (Fig. 1d, 2; see also Fig. 3) suggest, that part of the speciation processes had already taken place before the New Zealand microcontinent separated from Gondwanaland. *Dendrohypopterygium arbuscula*, or its immediate ancestors, then would have remained on Gondwanaland, mainly in what is, nowadays, West Antarctica. This subcontinent has been assembled of smaller fragments that have moved relative to each other and to East Antarctica (Dalziel & Elliot, 1982; Grunow, 1999; Cande et al., 2000), and may have included islands or groups of islands in the Late Cretaceous and Early Cenozoic. During the accretion of the West Antarctic subcontinent, *D. arbuscula*, or its immediate ancestors, may have become dispersed by local and short-range dispersal through the cool temperate forests of West Antarctic fragments, and finally may have reached southern South America by a short-range dispersal event, either by spore dispersal directly over sea or by island hopping. This event took probably place in the period from the Late Cretaceous to the Oligocene, when southern South America and West Antarctica, part of Gondwana as an assemblage of fragments, were connected or at least at a short distance from each other (Hill & Scriven, 1995).

After the Eocene, the Antarctic climate became too cold for Hypopterygiaceae due to the northward drift of Australia and consequent insulation of Antarctica by a cold circumpolar ocean current. However, a floristic migration route between Australia and South America, through Antarctica, may have been periodically available during interglacial periods until the Miocene (Drinnan & Crane, 1990). If so, the fact that *Dendrohypopterygium* and *Canalohypopterygium* are unknown from Australia (Map 3, 6a) needs further explanation.

The theory of early speciation on East Gondwanaland, i.e. before the drift of the New Zealand microcontinent, is supported by the phylogeny and the distribution of *Hypopterygium*, *Lopidium*, *Dendrocyathophorum*, and *Cyathophorum* species (Fig. 3). If these species were transported northwards by fragments of this supercontinent, the Hypopterygiaceae may have originated much earlier. In the early-origin scenario, the extant species would be descendants from a cool-temperate, terrestrial ancestral species, which came into existence in the Late Jurassic or in the Early Cretaceous, i.e. after the separation of West-Gondwana and before the final break-up of East Gondwana, when Australia, New Zealand and Antarctica were still joined and India and other fragments that were separated in the Late Jurassic–Early Cretaceous were still in close proximity of the shores of what is nowadays Australia.

When in the course of the Cretaceous period an increasing area of East Gondwanaland and its separated fragments became warm-temperate, descendants of this cool-temperate ancestor that came in the warm-temperate climate zone moved to higher altitudes. Speciation was probably induced by fragmentation of the original distribution area (vicariance) in combination with a change of ecological conditions towards higher humidity and precipitation. This meant for the Hypopterygiaceae, that more exposed habitats could be occupied and that larger leaves were possible. As a consequence, descendants of terrestrial species became epiphytic and epilithic, whereby an accessory change in plant morphology occurred: dendroid plants became pinnate or simple. Species with dendroid to flabellate plants growing on tree bases and boulders may have appeared first.

The appearance of epiphytes have probably been favoured by the rise, radiation and south- and eastwards migration of angiosperms from the low-latitudinal, north-western Gondwana/south-western Laurasia area to the high latitudes of East Gondwanaland during the Cretaceaous (Drinnan & Crane, 1990; Hill & Scriven, 1995; Morley, 1998), by which new potential host plants became available to early Hypopterygiaceae and other mosses.

In the early-origin scenario, *Dendrohypopterygium* and *Canalohypopterygium* are early descendants of an Hypopterygiaceae ancestor, and changed only very slowly after they came into existence at, presumably, high latitudes of East Gondwanaland in the Early Cretaceous.

Extant *Hypopterygium* species reflect several later stages in the speciation process that occurred during the Cretaceous.

In Cretaceous times, the Austral *Hypopterygium didictyon* was probably distributed in the cool-temperate climate zones of East Gondwanaland. Its geographic history can be compared with that of *Dendrohypopterygium* (Fig. 3, compare Map 3 and 10), but the species reached Australia from East Antarctica (when it originated in southern Gondwanaland) or remained in Australia and reached West Antarctica through East Antarctica (when it originated in northern Gondwanaland).

Hypopterygium elatum, *H. flavolimbatum*, *H. vriesei*, and *Dendrocyathophorum decolyi*, but most likely their immediate ancestors, came probably in existence in the Early Cretaceous. They presumably evolved at higher altitudes under humid conditions on the warm-temperate, northern shores of East Gondwanaland, the Indian subcontinent, or on other fragments that had separated from the supercontinent in the Late Jurassic–Early Cretaceous and were still at a short distance from its shores. The species, or their ancestors, were transported to Asia by northwards drift of the occupied continental fragment. The precise migration route or route of the continental fragment transporting these species is unknown and cannot be reconstructed from the present distribution area of the species. However, there are two plausible possibilities for Cretaceous–Cenozoic migration routes towards Asia: a) the species or their ancestors were transported towards Asia by the Indian subcontinent, which they may have reached after it separated from Madagascar, c. 84 Ma (Gnos et al., 1997), or earlier, assuming that they became extinct in Madagascar or did not reach it, e.g. because the species were restricted to the north-eastern part of the Indian subcontinent; b) the species or their ancestors reached the proto-Malaysian Archipelago and Asia by step-by-step short-range dispersal through (volcanic) islands associated with the arc systems on the Australian Plate, Pacific Plate, Caroline Plate, and Philippine Sea Plate boundaries. Another Cretaceous–Cenozoic migration route by continental fragments that separated from the northern margin of what is nowadays Australia is unlikely, because other Late Jurassic–Cretaceous continental fragments which may have acted as a transport vector, for instance West Burma, were or became submerged during the Cretaceous (Metcalfe, 1998), and can be excluded as possible migration vectors.

India collided with Eurasia in the Eocene, c. 50–56 Ma (Briggs, 1989; Daly et al., 1991; Thewissen & McKenna, 1992), but contacts with Asia may have existed since the early Paleocene (Rage, 1988; Patterson & Owen, 1991). Migration through island arcs between the outer Pacific (Melanesian) arc of Australian origin and the proto-Malaysian Archipelago have become possible since the Early Miocene, c. 25–20 Ma, and possibly since the mid-Oligocene, c. 30 Ma (cf. Hall, 1998). The present distribution areas of *Hypopterygium flavolimbatum* (Fig. 3, Map 13), *H. vriesei* (Fig. 3, Map 14), and *Dendrocyathophorum decolyi* (Fig. 3, Map 20) can best be explained by a combination of local growth in eastwards migrating forests and eastwards short distance dispersal after the collision of India, like many other plants (cf. Morley, 1998) or westwards short distance dispersal after migration into the proto-Malaysian Archipelago. The present distribution area of *H. elatum* (Fig. 3, Map 11) is presumably a relic of a much larger distribution area in the past.

Hypopterygium sandwicense must have reached the Hawaiian Archipelago (Fig. 3) by a single long range dispersal event of (dia)spore(s) from its common ancestor with *H. flavolimbatum*, probably after the latter became dispersed out of the various fragments that assembled in South and South-East Asia into the continental margin of East Asia and the island arcs system of East Asia. The Hawaiian–Emperor hotspot has been producing oceanic islands since 81 Ma (DiVenere & Kent, 1999).

The widely distributed *Hypopterygium tamarisci* (Fig. 3, Map 15) and the Australasian endemic *H. discolor* (Fig. 3, Map 12) occur both in Australia and New Zealand. The distribution areas of the species suggest that they came into existence before New Zealand separated from Gondwanaland. *Hypopterygium discolor* may be regarded as a low-altitude, warm-temperate, terrestrial relic species. There are no experimental data of UV irradiation resistance of *H. discolor* spores, but the spores have presumably low resistance to UV irradiation, which would hamper effective spore dispersal.

The data of UV irradiation resistance of spores for *Hypopterygium tamarisci* indicate, that this species is capable of long-range dispersal over c. 2000 km at c. 50° S. Although this range is probably shorter at lower latitudes, long-range dispersal may have contributed to the present distribution area of the species. Whether or not *H. tamarisci* came into existence before or after the separation of New Zealand, it probably reached Oceania and Asia by northwards drifting fragments of Gondwanaland, which may have included the Indian subcontinent, from where it dispersed into adjacent areas. The species presumably reached Africa and Madagascar in the Late Cretaceous or the Cenozoic via India, before or after the collision with Asia. During the Late Cretaceous – Palaeocene short-distance dispersal may have well been possible, because India remained close to or even in contact with Africa (Briggs, 1989; Weijermars, 1989), although this position is not generally accepted (see e.g. Patterson & Owen, 1991).

Hypopterygium tamarisci may have reached Neotropical South America through Africa. The northern part of South America was in the early Cenozoic close to the western part of Africa (Rage, 1988; Weijermars, 1989; Drinnan & Crane, 1990). Short-range dispersal may have been possible in the Paleocene and long-range dispersal may have been possible in later periods. However, a dispersal event through West Antarctica and southern South America in the early Cenozoic cannot be excluded.

The present distribution of the two *Lopidium* species (Fig. 3, Map 16–18) reflects the climatic conditions of Gondwanaland during the Early Cretaceous period. *Lopidium struthiopteris* occurred in the warm-temperate areas of the north, and *L. concinnum* in the cool temperate areas of the south. Consequently, the distribution of the former is best explained by the northwards drift of Gondwanaland fragments, most likely the Indian subcontinent, and dispersal to Africa and Madagascar in the Late Cretaceous or the Cenozoic, before or after the collision of India with Asia. The geographic history of the Austral *L. concinnum* follows in principle that of *Hypopterygium didictyon* (compare Map 10 and 17).

The distribution of *Cyathophorum* (Fig. 3, Map 21) indicates that its geographic history is a variant of that of *Lopidium*. *Cyathophorum* presumably originated on the warm-temperate northern shores of Gondwanaland in the Early Cretaceous. Comparable with *L. struthiopteris*, descendants of the ancestral species of *Cyathophorum* (*C. africanum*, *C. hookerianum*, *C. parvifolium*, *C. adiantum*, or their immediate ancestors) at the north-western shores moved northwards during the Late Cretaceous by drifting fragments of Gondwanaland, of which the Indian subcontinent is the most important vector. *Cyathophorum africanum* reached Africa (Map 25) by short-range dispersal through India in the Early Cenozoic before or after the collision with Asia or in the Late Cretaceous, if we assume that the species became extinct in Madagascar. The other species reached southern Asia and migrated by short-range dispersal into the Malaysian Archipelago and the island arc system at the margin of East Asia. The sister species *C. hookerianum* and *C. parvifolium* are presumably young species, which came into existence after the docking of India as a result of climatic changes in the Late Cenozoic (Neogene). Vicariance is the plausible explanation for their present distribution areas (Fig. 3, Map 26). Cenozoic climatic changes might also be responsible for the present distribution area of *C. adiantum* (Fig. 3, Map 24), but I found no explanation for its absence from the Malaysian Archipelago.

The ancestor of the *Cyathophorum* species (*C. bulbosum*, *C. spinosum*, *C. tahitense*) remaining in Gondwana reached the eastern margin of East Gondwanaland in the Late Cretaceous or the early Cenozoic. Up to the Late Cretaceous, the New Zealand area, New Guinea, the Solomon Islands, Vanuatu, and Fiji had formed a single geographical unit adjacent to eastern Australia (Michaux, 1989). After the ancestral species of *Cyathophorum* occupied this area, the area rifted from Australia from roughly south with the opening of the Tasman Sea, c. 86–84 Ma, to north with the opening of the Coral Sea, c. 62 Ma (O'Sullivan et al., 2000) and broke up. The separation from Australia became complete in the Palaeocene (c. 60 Ma). *Cyathophorum* may have reached the eastern margin of East Gondwanaland just in time for migration over land towards New Zealand, or it may have reached the New Zealand microcontinent and some other fragments after separation by short-range spore dispersal at high latitudes from Australia in the Early Cenozoic.

After separation of New Zealand and other fragments, two parallel arc systems were formed in the Eocene (c. 45–40 Ma): 1) an inner Pacific (Melanesian) arc, which includes the Arfak Mts in the Vogelkop, the Central Highland region and the southeast peninsula of Papua New Guinea, New Caledonia, the Norfolk and Lord Howe Ridges, and extends into New Zealand; and 2) an outer Pacific (Melanesian) arc, which includes northern New Guinea, the Huon Peninsula, the Bismarck Archipelago, the Solomon–Vanuatu Ridge, Fiji, Samoa, Tonga, and extends into the New Zealand area (Michaux, 1989, 1994; cf. Hall, 1998). *Cyathophorum bulbosum* occupied the inner Pacific arc, the ancestor of *C. tahitense* and *C. spinosum* the outer one.

Cyathophorum bulbosum remained in areas that originally belonged to the inner Pacific arc (Fig. 3, Map 22). The ancestral species of *C. tahitense* and *C. spinosum* probably migrated northwards and later westwards along the outer Pacific arc (sensu

Michaux, 1989) and the island arc system at the western margin of the Pacific and Philippine Plate by short-range dispersal. *Cyathophorum tahitense* split off in or after the Late Miocene, when Vanuatu and Fiji separated from the Solomon Islands (Burrett et al., 1991). The species may have reached Samoa and the Society Islands (Fig. 3, Map 23) by a combination of step-by-step short-range dispersal through islands of volcanic origin or crustal material that have now disappeared (Michaux & White, 1999) or by rare long-range dispersal events. The distribution of *C. spinosum* (Fig. 3, Map 24) can be explained by a combination of westwards migration into the Malaysian Archipelago by short-range dispersal, favoured by the prevailing easterly winds, and westwards motion of occupied terranes (= structural units of the earth's crust).

Evolution rate

The palaeogeographic history of the Hypopterygiaceae as hypothesised above implies that the evolution rate of the species must be very low. Bryophytes in general are often assumed to have low evolution rates, because of their predominantly haploid life cycle, the high incidence of inbreeding in monoicous taxa, the assumed low levels of sexual reproduction in dioicous taxa, and the importance of asexual reproduction (e.g. Anderson, 1963; Crum, 1972; Longton, 1976). Schuster (1983) and Van Zanten & Pócs (1981) argued, however, that evolution rates of bryophytes may vary among families, genera, and species. For example, high levels of genetic variation, indicating high evolution rates, are reported for four *Racopilum* species (De Vries et al., 1989).

Results of molecular research indicate that evolution rates of Hypopterygiaceae are truly very low. Frey et al. (1999) observed hardly any genetic divergence for the non-coding chloroplast DNA region *trnT–trnF*, incorporating the *trnT–trnL* spacer, the *trnL* intron, and the *trnL–trnF* spacer, between populations of *Lopidium concinnum* from South America (Brazil, Chile), and New Zealand, which separated c. 86–84 Ma. Likewise, Pfeiffer (2000) found no differences for the *trnL* intron between a population of *Hypopterygium didictyon* from Chile (examined by Stech et al., 1999) with nine out of ten of its New Zealand ones. She observed, however, a low genetic difference, corresponding at intraspecific level, between her two populations from Tasmania and those from New Zealand and Chile. This is remarkable, because a floristic migration route between Australia and South America, through Antarctica, existed in the Early Cenozoic, possibly even until the Miocene, and postdated the separation of New Zealand. In addition, I found no morphological differences between Tasmanian and New Zealand–South American specimens that would justify the delimitation of intraspecific taxa (see '*H. didictyon*', 'Geographical variation', p. 151).

The sequence similarity of the *trnL* intron of Pfeiffer's (2000) tenth New Zealand population ('NZ10') of *Hypopterygium didictyon* was found to be closest to the Tasmanian ones. The *trnL* intron of 'NZ10' shares an indel with *H. tamarisci*, but it is clearly differentiated from this species by a much lesser degree of sequence identity (Pfeiffer, 2000; see '*H. didictyon*', note 20, p. 156). It would be of great interest to know, whether the Tasmanian/NZ10 similarity is a result of a dispersal event, which may have been a long-distance one in recent times, or a short-distance one much longer ago.

It is remarked that Frey et al. (1999) and Pfeiffer (2000) sampled only a few populations. Besides, the *trnL* intron, being a group I intron, possesses few sites that are free to vary due to a highly constrained secondary structure (Cech, 1988). Furthermore, loops that can be highly polymorphic in Angiosperms show little variation in Hypopterygiaceae (Grob, pers. comm.). The low genetic divergence observed for separated populations of *Lopidium concinnum* and *Hypopterygium didictyon* needs confirmation based on more DNA sequence data from specimens of more populations.

Concluding remarks

The Hypopterygiaceae are a moss family with a long history, which presumably goes back to the Late Jurassic. They probably came into existence in cool-temperate East Gondwanaland as terrestrial dendroids growing on forest floors and river banks in mountaineous areas, presumably consisting of active mountain ranges in subduction zones.

The Hypopterygiaceae are characterised by low evolution rates, but part of the family went through a radiation event in the (Early) Cretaceous. This radiation event eventually resulted in the appearance of pinnate or simple epiphytic species. The event was probably induced by a climatic change towards a warm-temperate climate and the arrival of early Angiosperms.

Most species are stenoevolutionary taxa, which are defined as taxa without or with only little genetic divergence between populations and no speciation after separation of populations in geological times (after Frey et al., 1999).

The intraspecific variation that is found in, in particular, *Hypopterygium tamarisci*, *H. flavolimbatum*, and *H. didictyon* is perhaps of Late Cenozoic origin, and may represent an early stage of a second radiation event due to the climatic changes in the Late Cenozoic.

The distribution pattern of species is best explained by plate tectonics and rafting on drifting continental fragments, followed by local dispersal and short-distance dispersal events. The best example of long-range dispersal, however, is the occurrence of *Hypopterygium sandwicense* on the Hawaiian Islands.

Chapter 8

TAXONOMIC TREATMENT

(In order of increasing simplicity)

HYPOPTERYGIACEAE Mitt. — Map 1, 2

Hypopterygiaceae Mitt., J. Proc. Linn. Soc., Bot., Suppl. 1 (1859) 147. — Hypopterygiaceae Müll.Hal., Syn. Musc. Frond. 2 (1850) 3, pro parte, nom. inval., misplaced rank. — Hypopterygieae A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1874–75 (1876) 139 (Gen. Sp. Musc. 2 (1876) 55), pro parte, nom. nud. and misplaced rank. — Hypopterygieae Sull., U.S. Expl. Exped., Musc. (1860) 25 (97), nom. nud., misplaced rank? — Hypopterygiaceae Kindb. ex Crosby, J. Hattori Bot. Lab. 38 (1974) 134, hom. illeg. — Hypopterygiaceae sect. Hypopterygioideae Gangulee, Mosses of Eastern India (1977) 1540, nom. inval., misplaced rank, '-ioideoe'. — Type: *Hypopterygium* Brid.

Cyathophoraceae Kindb., Bot. Centralbl. 76 (1898) 85. — Hypopterygiaceae Mitt. tribus Cyathophoreae (Kindb.) M. Fleisch., Musc. Buitenzorg 3 (1908) 1066. — Hypopterygiaceae Mitt. subfam. Cyathophoroideae (Kindb.) Broth. in Engler *&* Prantl, Nat. Pflanzenfam. ed. 2, 11 (1925) 276. — Cyathophoreae A. Jaeger, Ber. Thät. St. Gall. Naturw. Ges. 1874–1875 (1876) 152 (Gen. Sp. Musc. 2 (1876) 68), nom. inval., nom. nud. and misplaced rank. — Cyathophoraceae Brizi, Atti Reale Accad. Lincei, Rendiconti Cl. Sci. Fis., Ser. 5, 2 (1893) 103, nom. nud.; Annuario Reale Ist. Bot. Roma 6 (1897) 355, nom. nud. — Cyathophoraceae H. A. Mill., Phytologia 21 (1971) 251, hom. illeg. — Hypopterygiaceae sect. Cyathophoroideae Gangulee, Mosses of Eastern India (1977) 1531, nom. inval., basionym not given and misplaced rank. — Type: *Cyathophorum* P. Beauv.; fide Kindberg l.c.: 86.

Hypopterygiineae H. A. Mill., Phytologia 21 (1971) 251. — Type: Hypopterygiaceae Mitt. s. str.

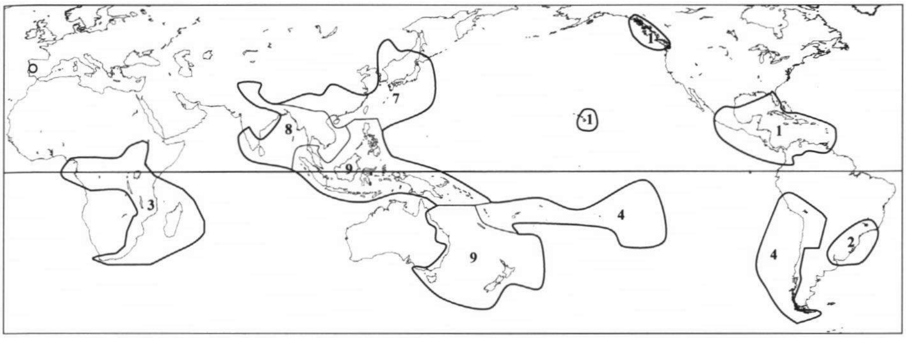
Lopidiaceae Brid. ex Rodway, Pap. *&* Proc. Roy. Soc. Tasmania 1913 (1914) 236, 'Lophidiaceae', pro parte, nom. illeg. incl. fam. prior. (Hypopterygiaceae Mitt.). — Type: *Lopidium* Hook.f. *&* Wilson in Hook.f. ('*Lophidium* Bridel').

Hypophyllocarpi Brid., Bryol. Univ. 2 (1827) 709, pro parte, nom. inval., nom. nud., misplaced name and misplaced rank. — Hypopterygocarpi Brid., Bryol. Univ. 2 (1827) 710, pro parte, nom. inval., err. pro Hypophyllocarpi Brid., given in the header of Bridel's l.c. treatment of Hypophyllocarpi Brid. — Genera included: *Hypopterygium* Brid., *Racopilum* P. Beauv., *Cyathophorum* P. Beauv.

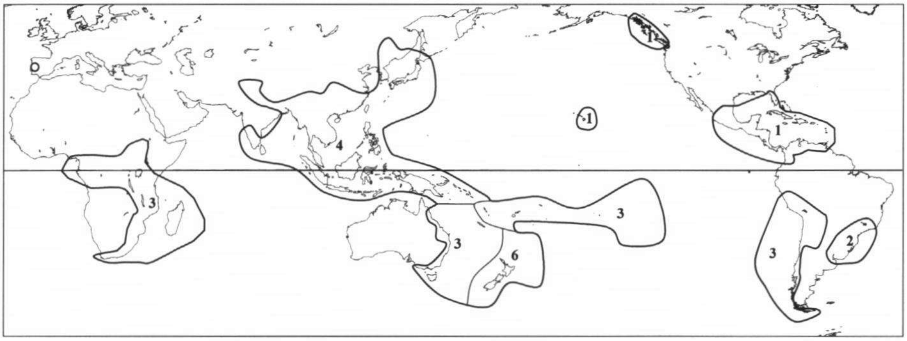
Tristichophylla Müll.Hal., Syn. Musc. Frond. 2 (1850) 3, pro parte, nom. inval., misplaced name of uncertain rank.

Hypopterygiaceae A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1874–75 (1876) 138 (Gen. Sp. Musc. 2 (1876) 54), pro parte, nom. nud. and misplaced rank. — Invalid taxa included: Helicophylleae A. Jaeger, Hypopterygieae A. Jaeger, Cyathophoreae A. Jaeger

Plants pleurocarpous, dull or weakly glossy (frequently very glossy in *Cyathophorum bulbosum*), gemmiferous or not gemmiferous. *Shoots* differentiated in stolons and stems. *Stolons* creeping, sympodially branched, becoming branched and ascending in distal part (where changing into stem), tomentose; rhizoids weakly to distinctly pinnate, brown, smooth to minutely verrucose or papillose. *Stem* simple or branched, when simple not differentiated and more or less horizontal, when branched usually differentiated in a vertical or ascending stipe and a more or less horizontal rachis set with more or less horizontal branches. *Branches* ± identical to middle and distal part of rachis, usually arranged between lateral frond leaves, rarely between amphigastria or ventral



Map 1. Overall distribution of the Hypopterygiaceae Mitt. The figures represent the number of species in a given area.



Map 2. Overall distribution of the Hypopterygiaceae Mitt. The figures represent the number of genera in a given area. Notice the high diversity at the generic level in the New Zealand area.

leaves near frond base, similar in phyllotaxis, foliation, and anatomy to distal part of rachis. *Axillary hairs* usually on stem, branches, and gametangiophores near and above leaf insertion, usually long-persistent, simple, filiform, hyaline; basal cells transverse to elongate, trapiziform to rectangular, usually brown, rarely colourless, walls thin; intermediate cells absent or present, when present short to short-linear, elliptic to rectangular, colourless, walls thin; terminal cell short to linear, (sub)circular to nearly rectangular, colourless, usually smooth, less often weakly verrucose in *Canalohypopterygium tamariscinum* and *Cyathophorum spinosum* (distinctly verrucose in *Cyathophorum hookerianum* and *C. parvifolium*; conspicuously covered with substances in *Hypopterygium didictyon*), apex rounded (rarely truncate in *Dendrohypopterygium arbuscula*), walls thin or incrassate.

Phyllotaxis: variable; of stolons octostichous or tristichous; of stem either octostichous in basal part of stem (stipe) and becoming tristichous in distal part (rachis) or entirely tristichous (or nearly so); of branches usually entirely tristichous, occasionally in basal frond branches octostichous in basal part of branch and becoming tristichous in distal part. *Foliation*: variable, complanate or not complanate, but not or weakly complanate only in combination with octostichous phyllotaxis; of stolons not complanate; of stems not or weakly complanate at base, becoming distinctly complanate in distal part (with a tristichous phyllotaxis); of branches (when present) usually distinctly complanate, occasionally not complanate in basal parts with an octostichous phyllotaxis. *Leaves* variable in direction, size, and shape; border absent or present; costa variable in length and degree of development, single, simple or weakly forked in distal part, occasionally absent or double in amphigastria in *Cyathophorum* species; laminal cells prosenchymatous (or partly parenchymatous in *Hypopterygium didictyon* and *H. discolor*; somewhat parenchymatous near leaf base in *Dendrohypopterygium filiculiforme*), basically hexagonal, walls porose. *Stolon leaves* smaller than stem leaves, symmetrical, monomorphic, hyaline, often damaged. *Basal stem (stipe) leaves* appressed to widely patent, symmetrical or asymmetrical, monomorphic or dimorphic, concolorous or paler than distal ones. *Distal stem (stipe, rachis, or distal rachis) leaves* arranged in two lateral rows and a single abaxial row, usually distinctly dimorphic (occasionally almost monomorphic in *Lopidium*), coloured in various shades of green (see below species). *Distal lateral stem (rachis) leaves* incubous, patent tot widely patent, asymmetrical; insertion weakly to distinctly concave, oblique and descending at dorsal side of stem (but transverse to oblique at this side in *Catharomnion*), and descending, transverse, or ascending at ventral side; base either not decurrent or decurrent at ventral side of stem (or at dorsal side in *Catharomnion*); border absent or present, when present interrupted or continuous, generally most pronounced in basal half of leaf; dentation absent or present, when present most pronounced in distal half of leaf. *Distal stem (rachis) amphigastria* erecto-patent to widely patent, symmetrical, concolorous with lateral leaves (often discolorous in *Cyathophorum parvifolium*); insertion convex to concave; basal part of lamina usually almost plane or smoothly curved (bulging in *Cyathophorum* species, saccate in *Cyathophorum tahitense*). *Branch leaves* when present equally large as or smaller than those in a similar row in distal part of rachis, otherwise similar.

Gemmae clusters when present usually in distal part of stem or rachis and branches (where applicable), rarely on stolons, flagelliform innovations, or basal part of stem (or stipe where applicable), in or above leaf axils, usually between lateral leaves, less frequently between amphigastria. *Gemmaphores* present, simple or branched; cells short to short-linear, rectangular to rhomboid, smooth. *Gemmae* filiform; cells short to oblong, rectangular or truncate-elliptic, inflated or not, smooth (or roughly verrucose in *Lopidium struthiopteris*); terminal cell short to oblong, triangular to elliptic, rounded or gradually attenuate, inflated or not.

Monoicous or *dioicous*. *Gametoecia* usually on lateral side of main axis, occasionally on dorsal or ventral side, usually between (dorsal-)lateral leaves, rarely between amphigastria or ventral leaves, bud-like, consisting of a very short, foliate gametangiophore (axis with terminal gametangia). *Axillary hairs at gametangiophores* present, persistent, associated with gametoecial leaves, in structure and morphology similar to or a few cells longer than those on stem and branches. *Gametoecial leaves* concave; outer leaves smaller or somewhat smaller than inner ones; margin ± entire; apex usually abruptly acuminate, occasionally gradually acuminate; laminal cells prosenchymatous, occasionally somewhat parenchymatous, short- to short-linear, usually hexagonal, occasionally somewhat rectangular or rhomboid. *Gametoecial axillary hairs* few to numerous on the gametoecial disc, persistent, associated with gametoecial leaves (or leaf primordia in centre of gametoecium), in structure and morphology similar to, a few cells longer, or somewhat larger than those on stem and branches. *Paraphyses* present or absent, when present filiform (or leaf-like in *Lopidium*), hyaline, colourless or pale brown (or pale green when leaf-like in *Lopidium*); cells inflated or not, smooth; basal cells oblate to oblong, rectangular or quadrate to trapeziform, elliptic, or obovate (or short-linear-rectangular in full-grown perichaetia of *Dendrohypopterygium arbuscula*); intermediate cells short to short-linear, rectangular to elliptic; terminal cell (oblate to) short to short-linear, subcircular or triangular, ovate, or elliptic to rectangular, apex gradually attenuate or rounded. *Antheridia* oblong to short-linear, ellipsoid to more or less fusiform, when old becoming flat and roughly ellipsoid or fusiform to obovate with a truncate apex, straight to weakly curved, colourless to brown; stalk colourless to brown. *Archegonia* filiform with an expanded venter, colourless to reddish brown; stalk colourless to pale brown.

Sporophytes exserted, usually one per perichaetium. *Seta* straight to uncinate. *Capsule* subglobose to oblong-ovoid; orifice transverse (or oblique in *Catharomnion*). *Peristome* diplolepideous, double (single in *Catharomnion*). *Exostome* present (absent in *Catharomnion*); teeth 16; median line at dorsal side of exostome teeth zig-zag or straight, not furrowed. *Endostome* membraneous, hyaline; basal membrane low or high; processes 16; cilia absent or present. *Operculum* rostrate, ochraceous to brown, occasionally somewhat tinged with red. *Calyptra* cucullate or mitrate. *Spores* (sub) globose or short-ellipsoid, scabrous.

KEY TO THE GENERA

1a. Stem mainly simple, occasionally with a few innovations or a few distant branches, but not differentiated in stipe and rachis. Sporophyte (in or) projecting beneath plane of gametophore . . . . **7. Cyathophorum**
b. Stem branched, differentiated in stipe and rachis. Sporophyte projecting above plane of gametophore 2
2a. Rudimentary branches present. Frond leaves at least partly dentate-ciliate . . . 3
b. Rudimentary branches absent. Frond leaves entire, serrate, or serrate-dentate (never ciliate) 4
3a. Stipe up to 5.5 cm long, but usually longer than 1.5 cm. Stolon leaves and stipe leaves arranged in eight ranks. Exostome present. Endostomial cilia distinct . . . . **2. Canalohypopterygium**
b. Stipe up to 1.5 cm long. Stolon leaves and stipe leaves arranged in three ranks. Exostome absent. Endostomial cilia absent . . . . **3. Catharomnion**
4a. Laminal leaf cells collenchymatous; walls incrassate, especially in cell corners. Stipe leaves always arranged in three ranks. Costa of lateral frond leaves percurrent. Seta mamillate . . . . **5. Lopidium**
b. Laminal leaf cells prosenchymatous, walls thin or weakly and evenly incrassate. Stipe leaves arranged in eight ranks or three ranks, or number of ranks difficult to observe (usually eleven or more). Costa of lateral frond leaves reaching up to 4/5 of leaf length at most. Seta smooth. 5

5a. Stipe cavity central. Stipe leaves arranged in three ranks. Border of lateral frond leaves absent or interrupted .... **6. Dendrocyathophorum**

b. Stipe cavities absent. Stipe leaves arranged in eight ranks or three ranks, or number of ranks difficult to observe (usually eleven or more). Border of lateral frond leaves continuous (absent or interrupted in *Dendrohypopterygium filiculiforme*) ... 6

6a. Plant usually palmate or umbellate (rarely flabellate), not gemmiferous. Stipe usually longer than 3.5 cm. Axial cavities central in distal part of rachis and distal branches. Apex of basal and middle stipe leaves obtuse, rounded, truncate, or eroded (apex of distal stipe leaves occasionally gradually or abruptly acuminate). Terminal cell of axillary hairs of stipe and basal part of rachis longer than those in distal part of frond. Capsule neck distinctly pustulose .... **1. Dendrohypopterygium**

b. Plant pinnate, flabellate, palmate, or umbellate, gemmiferous or not. Stipe shorter than 3.5 cm when palmate or umbellate, up to 4.5 cm long when pinnate or flabellate. Axial cavities absent or central in distal part of rachis and branches. Apex of stipe leaves acute or acuminate (rounded or emarginate in *H. elatum*). Terminal cell of axillary hairs variable in length, but on average equally long in various parts of frond. Capsule neck smooth or weakly pustulose .. **4. Hypopterygium**

REGIONAL KEYS TO THE SPECIES

AFRICA

1a. Stem mainly simple, occasionally with a few innovations or a few distant branches, but not differentiated in stipe and rachis. Gemmae absent. Capsules projecting beneath lateral leaves. Operculum short-rostrate **7.5. Cyathophorum africanum**

b. Stem strongly branched, differentiated in stipe and rachis. Gemmae present or absent. Capsules (when present) projecting above lateral leaves. Operculum long-rostrate 2

2a. Ramification pinnate to bipinnate. Laminal leaf cells collenchymatous; walls incrassate, especially in cell corners. Costa of lateral frond leaves percurrent or nearly so. Gemmae frequently present .... **5.2. Lopidium struthiopteris**

b. Ramification usually dendroid, occasionally pinnate or flabellate. Laminal leaf cells not collenchymatous; walls thin. Costa of lateral frond leaves reaching 4/5 of leaf length at most. Gemmae absent .... **4.7. Hypopterygium tamarisci** ('African' variant)

INDO MALAYSIA AND SINO JAPAN

(Indian subcontinent, temperate East Asia, continental South East Asia, and Malesia including the Solomon Islands)

1a. Stem mainly simple, occasionally with a few innovations or a few distant branches, but not differentiated in stipe and rachis. Sporophytes (in or) projecting beneath plane of gametophore.. 2

b. Stem branched, differentiated in a stipe and a rachis. Sporophytes projecting above plane of gametophore.. 6

2a. Leaves strikingly serrate-dentate. Calyptra mitrate, pale brown to dark brown, fleshy. Intermediate cells in axillary hairs usually present, occasionally absent. Paraphyses present or absent 3

b. Leaves entire or serrate. Calyptra cucullate or mitrate to cucullate, nearly white to pale ochraceous, membranous. Intermediate cells in axillary hairs absent. Paraphyses always absent 5

3a. Stem quadrangular. Endostomial cilia usually distinct, rarely absent or rudimentary .... **7.1. Cyathophorum bulbosum**

b. Stem rounded in cross section. Endostomial cilia absent or rudimentary, never distinct 4

4a. Gemmae when coloured frequently orange to orange-brown, occasionally brown or dark brown. Stems entirely laterally compressed, in distal part only regularly dorsiventrally compressed when gemmiferous. Perigonial paraphyses present. Perichaetial paraphyses present or absent. Exostome teeth in basal half of dorsal side striate .... **7.3. Cyathophorum spinosum**

b. Gemmae when coloured usually brown to dark-brown, never orange or orange-brown. Stems laterally compressed up to 4/5 of stem length at most, in distal part dorsiventrally compressed. Perigonial paraphyses present or absent. Perichaetial paraphyses absent. Exostome teeth in basal half of dorsal side smooth or papillose .... **7.4. Cyathophorum adiantum**

5a. Stems entirely laterally compressed to entirely dorsiventrally compressed. Leaf border up to 4 cells wide, usually continuous, occasionally absent in distal third of leaf. Leaves and amphigastria concolourous, never discolourous .... **7.6. Cyathophorum hookerianum**

b. Stems usually entirely dorsiventrally compressed, occasionally not compressed below, never laterally compressed. Leaf border up to 2 (or 3) cells wide, interrupted, usually absent but occasionally interrupted in distal third of leaf. Leaves and amphigastria discolourous or concolourous ...... **7.7. Cyathophorum parvifolium**

6a. Laminal leaf cells collenchymatous; walls incrassate especially in cell corners. Stipe leaves always and clearly arranged in three ranks. Costa of lateral frond leaves percurrent. Gemmae present. Seta mamillate...................... .... **5.2. Lopidium struthiopteris**

b. Laminal leaf cells prosenchymatous; walls thin or weakly and evenly incrassate. Stipe leaves arranged in eight ranks or three ranks, or number of ranks difficult to observe (usually eleven or more). Costa of lateral frond leaves reaching up to 4/5 of leaf length at most. Gemmae present or absent. Seta smooth 7

7a. Stipe cavity central. Stipe leaves and basal frond leaves arranged in three ranks; dorsal leaves absent. Border of lateral frond leaves absent or interrupted .... **6.1. Dendrocyathophorum decolyi**

b. Stipe cavities absent. Stipe leaves and basal frond leaves arranged in eight ranks (or in three ranks in small plants); dorsal leaves present in basal part of frond (absent from small plants). Border of lateral frond leaves continuous 8

8a. Frond leaves loosely attached and frequently caducous; margin entire to weakly crenulate or weakly serrate .... **4.4. Hypopterygium flavolimbatum** ('East Malesian' variant)

b. Frond leaves mainly firmly attached and persistent, only occasionally caducous when situated near apices of rachis or branches; margin entire, serrate, or serrate-dentate, but not crenulate 9

9a. Dorsal frond leaves present in basal part of rachis. Stipe leaves and basal rachis leaves arranged in eight ranks 10

b. Dorsal frond leaves absent. Stipe leaves and basal rachis leaves arranged in three ranks or number of ranks difficult to observe (usually eleven or more) 11

10a. Plant not gemmiferous. Apex of stipe leaves rounded or emarginate. Stipe dorsiventrally compressed, tomentose at base at most. Dioicous(?) .... **4.2. Hypopterygium elatum**

b. Plant gemmiferous or not. Apex of stipe leaves abruptly acuminate. Stipe generally not compressed, occasionally dorsiventrally compressed, tomentose in basal fourth at least. Monoicous or dioicous .. **4.4. Hypopterygium flavolimbatum**

11a. Plant usually pinnate to flabellate, usually conspicuously gemmiferous with crowded clusters of gemmae in axils of frond leaves (examine several gametophores). Stipe entirely laterally compressed or dorsiventrally compressed in basal part. Branches not caducous (brown spots absent). Axial cavities central in distal part of rachis and branches. Frond leaves pronounced serrate-dentate; teeth frequently much longer than 40 µm. Dioicous ..... **4.5. Hypopterygium vriesei**

b. Plant usually palmate or flabellate, rarely gemmiferous (usually when damaged), with scattered gemmae or open clusters of gemmae. Stipe entirely dorsiventrally compressed or laterally compressed in basal part. Branches partly caducous or not (brown spots often present). Axial cavities absent. Frond leaves entire, serrate, or serrate-dentate; teeth shorter than 40 µm. Monoicous or dioicous .... **4.6. Hypopterygium tamarisci** ('Asian' variant)

AUSTRALASIA

(Australia, New Caledonia, New Zealand, and neighbouring islands)

1a. Rudimentary branches present. Frond leaves at least partly dentate-ciliate ... 2

b. Rudimentary branches absent. Frond leaves entire, serrate, or serrate-dentate 3

2a. Plants usually forming groups of dendroids (rarely fans). Stipe up to 5.5 cm long, usually longer than 1.5 cm. Stolon leaves and stipe leaves arranged in eight ranks. Exostome present. Endostomial cilia distinct .... **2.1. Canalohypopterygium tamariscinum**

b. Plants forming mats or groups of fans. Stipe up to 1.5 cm long at most. Stolon leaves and stipe leaves arranged in three ranks. Exostome absent. Endostomial cilia absent .... **3.1. Catharomnion ciliatum**

3a. Stem simple, or with a few innovations or branches, not differentiated in stipe and rachis. Capsules projecting beneath plane of gametophore .... **7.1. Cyathophorum bulbosum**

b. Stem branched, differentiated in stipe and rachis. Capsules projecting above plane of gametophore 4

4a. Plant pinnate to bipinnate. Laminal leaf cells collenchymatous; walls incrassate. Costa of lateral frond leaves percurrent or nearly so. Seta mamillate. Calyptra naked or with long paraphyses of several cells wide 5

b. Plant usually palmate or umbellate, less often pinnate or flabellate. Laminal leaf cells not collenchymatous; walls thin. Costa of lateral frond leaves reaching 4/5 of leaf length at most. Seta smooth. Calyptra naked or with short, uniseriate paraphyses 6

5a. Gemmae absent. Monoicous. Paraphyses absent or present in full-grown perichaetia, immersed. Exostome teeth 70 µm wide at least. Calyptra naked .... **5.1. Lopidium concinnum**

b. Gemmae present. Dioicous. Paraphyses present in full-grown perichaetia, frequently exserted. Exostome teeth less than 70 µm wide. Calyptra with paraphyses .... **5.2. Lopidium struthiopteris**

6a. Ramification of frond bipinnate to tetrapinnate. Axial cavities central in distal part of branches. Border of frond leaves absent or interrupted. Calyptra with short and uniseriate paraphyses .... **1.1. Dendrohypopterygium filiculiforme**

b. Ramification of frond pinnate to bipinnate (or partly tripinnate). Axial cavities absent. Border of frond leaves continuous. Calyptra naked 7

7a. Stipe and basal frond leaves arranged in eight ranks; dorsal leaves present in basal part of rachis. Laminal leaf cells parenchymatous to prosenchymatous, rectangular or hexagonal. Terminal cell of axillary hairs predominately short-linear to linear, frequently distinctly covered with white substances (visible as white dots with hand lens or stereomicroscope), less often smooth .... **4.1. Hypopterygium didictyon**

b. Stipe and basal frond leaves arranged in three or eleven (or more) ranks; dorsal leaves absent. Laminal leaf cells prosenchymatous, hexagonal. Terminal cell of axillary hairs short to elongate, never short-linear or linear, usually smooth, less often weakly covered with white substances (only visible with light microscope) 8

8a. Plant usually distinctly palmate or umbellate, rarely flabellate, never (tri)pinnate, not gemmiferous. Stipe frequently longer than 1.5 cm. Distal frond leaves coarsely serrate-dentate; teeth usually more than 20 in number; border green. Dioicous .... **4.3. Hypopterygium discolor**

b. Plant either weakly palmate to umbellate or (tri)pinnate, gemmiferous or not. Stipe up to 1.5 cm long at most. Distal frond leaves entire or weakly serrate to weakly serrate-dentate; teeth less than 20 in number; border colourless. Monoicous or dioicous .... **4.6. Hypopterygium tamarisci** ('Australasian' and 'Australian' variants)

OCEANIA

(Tropical and near-tropical Pacific Islands north and east of the
Solomon Islands and New Caledonia)

1a. Stem simple or with a few innovations. Amphigastrium pouch present....... .... **7.2. Cyathophorum tahitense**

b. Stem branched. Amphigastrium pouch absent 2

2a. Laminal leaf cells collenchymatous; walls incrassate, especially in cell corners. Stipe leaves always arranged in three ranks. Costa of lateral frond leaves percurrent. Gemmae present. Seta mamillate .... **5.2. Lopidium struthiopteris**

b. Laminal leaf cells prosenchymatous; walls thin. Stipe leaves arranged in eight ranks or three ranks, or number of ranks difficult to observe (usually eleven or more). Costa of lateral frond leaves reaching up to 4/5 of leaf length at most. Gemmae present or absent. Seta smooth 3

3a. Dorsal frond leaves present in basal part of frond. Stipe and basal frond leaves arranged in eight ranks . . . . **4.9. Hypopterygium sandwicense**

b. Dorsal frond leaves absent. Stipe and basal frond leaves arranged in three ranks, or number of ranks difficult to observe (usually eleven or more) 4

4a. Plant usually gemmiferous with crowded clusters of gemmae in axils of frond leaves (examine several gametophores). Stipe entirely laterally compressed or dorsiventrally compressed in basal part. Axial cavities central in distal part of rachis and branches. Frond leaves pronounced serrate-dentate; teeth frequently much longer than 40 μm. Dioicous . . . . **4.5. Hypopterygium vriesei**

b. Plant not gemmiferous or rarely gemmiferous (usually when damaged) with scattered gemmae or open clusters of gemmae. Stipe entirely dorsiventrally compressed or not compressed in basal part. Axial cavities absent. Frond leaves entire, serrate, or serrate-dentate; teeth shorter than 40 μm. Monoicous or dioicous . . . . **4.6. Hypopterygium tamarisci** ('Oceanian' variants 1 and 2)

SOUTH AMERICA

1a. Plant pinnate to bipinnate. Laminal leaf cells collenchymatous; walls incrassate, especially in cell corners. Costa of lateral frond leaves percurrent or nearly so. Seta mamillate . . . . **5.1. Lopidium concinnum**

b. Plant usually palmate or umbellate, less often pinnate or flabellate. Laminal leaf cells prosenchymatous; walls thin. Costa of lateral frond leaves reaching 4/5 of leaf length at most. Seta smooth 2

2a. Stipe leaves obtuse, rounded, or truncate, usually appressed. Frond leaves not bordered or with an interrupted border. Ramification of frond bipinnate to tetrapinnate. Axial cavities central in distal part of branches . . . . **1.2. Dendrohypopterygium arbuscula**

b. Stipe leaves acuminate, usually erecto-patent to patent. Frond leaves continuously bordered or mainly so. Ramification of frond pinnate to bipinnate (or partly tripinnate). Axial cavities absent 3

3a. Stipe and basal frond leaves arranged in three or eleven (or more) ranks; dorsal leaves absent. Laminal leaf cells prosenchymatous, hexagonal. Terminal cell of axillary hairs short to elongate, never short-linear or linear, smooth or nearly so (only visible with light microscope). Gemmae present or absent. Monoicous or dioicous . . . . **4.8. Hypopterygium tamarisci** ('New World' variant)

b. Stipe and basal frond leaves arranged in eight ranks; dorsal leaves present in basal part of rachis. Laminal leaf cells parenchymatous to prosenchymatous, rectangular or hexagonal. Terminal cell of axillary hairs predominately short-linear to linear, often distinctly covered with white substances (visible as white dots with hand lens or stereomicroscope), less often smooth. Gemmae absent. Dioicous . . . . **4.1. Hypopterygium didictyon**

NORTH AMERICA, CENTRAL AMERICA, AND THE CARIBBEAN

1a. Dorsal frond leaves present in basal part of rachis. Stipe leaves and basal frond leaves arranged in eight ranks. Paraphyses absent .... **4.4. Hypopterygium flavolimbatum**

b. Dorsal frond leaves absent. Stipe leaves and basal frond leaves arranged in three ranks or number of ranks difficult to observe (usually eleven or more). Paraphyses present, but frequently similar to axillary hairs when short .... **4.8. Hypopterygium tamarisci** ('New World' variant)

TREATMENT OF GENERA

1. DENDROHYPOPTERYGIUM Kruijer, *gen. nov.* — Map 3

From the Greek δενδρον (dendron, tree) and the genus name *Hypopterygium.*

Hypopterygio similis, statura plerumque altiore, praecipue et in habitu fere semper palmato vel umbellato quid plerumque distinctius (raro flabellatus in *Dendrohypopterygio arbuscula*) ac cavitatis centralibus in parte distali rhachidis et ramis distalibus, sed praeterea apice foliorum stipitis plerumque obtuso, rotundo, truncato, vel praemorso (apex foliorum distalium stipitis interdum gradatim vel abrupte acuminatus in *D. arbuscula*), cellula terminali pilorum axillarium differenti in longitudini inter partem plantae basalem et distalem, et thecae collo distinctius pustuloso differt. — Type: *Dendrohypopterygium filiculiforme* (Hedw.) Kruijer (≡ *Hypopterygium filiculiforme* (Hedw.) Brid.).

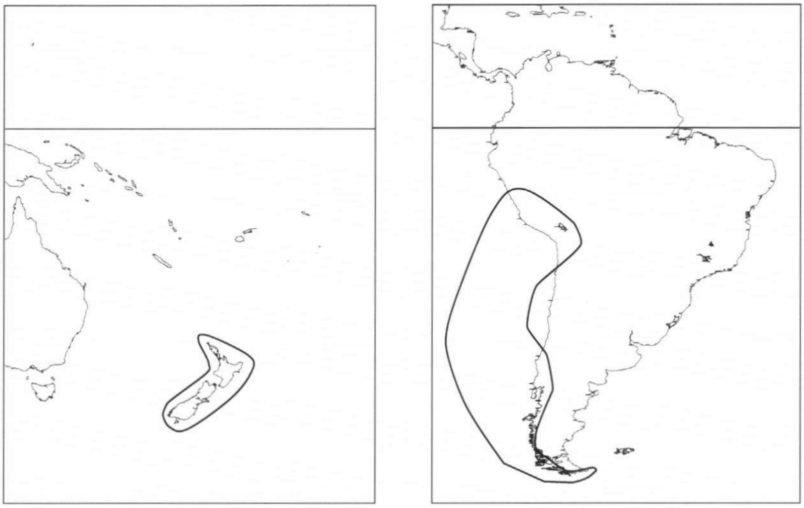
Hypopterygium Brid. subgen. *Filiculoides* Kindb., Hedwigia 40 (1901) 279. — *Hypopterygium* Brid. sect. *Filiculoides* (Kindb.) M. Fleisch., Musc. Buitenzorg 3 (1908) 1087. — Type: *Hypopterygium filiculiforme* (Hedw.) Brid. (≡ *Dendrohypopterygium filiculiforme* (Hedw.) Kruijer).

Hypopterygium Brid. subgen. *Stephanobasis* Kindb., Hedwigia 40 (1901) 279. — *Hypopterygium* Brid. sect. *Stephanobasis* (Kindb.) M. Fleisch., Musc. Buitenzorg 3 (1908) 1087, nom. illeg. incl. sect. prior. (*Hypopterygium* Brid. sect. *Perlimbata* Broth.). — Lectotype: *Hypopterygium thouinii* (Schwägr.) Mont. (≡ *Dendrohypopterygium arbuscula* (Brid.) Kruijer); designated here. — See note.

Hypopterygium Brid. sect. *Perlimbata* Broth. in Engler & Prantl, Nat. Pflanzenfam. ed. 1, 3 (1907) 972. — *Hypopterygium* Brid. subsect. *Perlimbata* (Broth.) Broth. in Engler & Prantl, Nat. Pflanzenfam. ed. 2, 11 (1925) 275. — Type: *Hypopterygium thouinii* (Schwägr.) Mont. (≡ *Dendrohypopterygium arbuscula* (Brid.) Kruijer).

Plants usually forming open groups of dendroids (occasionally forming dense groups in *D. filiculiforme*), branched, dull, yellowish green to blackish green, not gemmiferous; ramification usually palmate or umbellate (rarely flabellate in *D. arbuscula*). *Stems* differentiated in stipe and rachis. *Stipe* usually vertical, less often ascending, straight, becoming curved near frond base, partly or entirely tomentose, usually dark brown to brown or partly green in distal part, occasionally entirely green or tinged with red. *Frond* suborbicular to ovate-oblong, ± complanate; rachis and branches horizontal, straight or weakly curved downwards, usually glabrous (rachis and lower first-order branches occasionally tomentose at base in *D. filiculiforme*), brown, reddish brown, or green to pale green; branches distant or closely set, erecto-patent to widely patent or recurved in umbellate plants; apex of foliate rachis and branches rounded (or gradually attenuate in *D. arbuscula*). *Rudimentary branches* absent. *Stipe, rachis, and branches* terete (but weakly quadrangular near stipe base in *D. filiculiforme*). *Epidermis* ± similar in cellular structure to (outer) cortex. *Cortex* of stipe and basal part of frond axes differentiated, in distal part of frond axes less or not differentiated. *Central strand* present, but absent from frond axes when replaced by a central cavity. *Axial cavities* absent from stipe and basal and middle part of rachis and lower branches, absent or central in distal part of rachis and branches, becoming more frequent towards apex of these frond axes. *Axillary hairs* present; basal cells colourless or brown; intermediate cells absent; terminal cell straight or recurved, colourless, smooth. *Phyllotaxis*: of stipe and basal part of rachis and lower first-order branches usually octostichous (occasionally irregular or tristichous in distal part of stipe in *D. arbuscula*); of distal part of rachis and branches tristichous. *Foliation*: of stipe isophyllous, not complanate; of frond either isophyllous and not complanate or weakly anisophyllous and weakly complanate in basal parts with an octostichous phyllotaxis, complanate and anisophyllous in distal parts (with a tristichous phyllotaxis). *Leaves* when moist smooth or weakly wrinkled, when dry smooth or weakly twisted to strongly crisped; insertion concave, transverse, or convex; base not decurrent; margin entire, serrate, or serrate-dentate (or weakly crenate to roughly eroded in stipe leaves of *D. arbuscula*); apex rounded or obtuse in stipe leaves (but also truncate, and occasionally gradually acuminate or abruptly acuminate in stipe leaves of *D. arbuscula*), gradually or abruptly acuminate in frond leaves; costa absent from stipe leaves of *D. filiculiforme*, faint to distinct in stipe leaves of *D. arbuscula*, distinct in frond leaves, simple or somewhat forked in distal part; laminal cells prosenchymatous (or somewhat parenchymatous), short to elongate, usually hexagonal, occasionally rhombic to rectangular in parts of leaves, walls thin or incrassate, not porose in *D. filiculiforme* and porose in *D. arbuscula*: costa cells longer than adjacent laminal cells, short-linear to linear, hexagonal or rhomboid, walls thin or incrassate; border and acumen cells (where present) longer than adjacent laminal cells, elongate to linear, hexagonal or rhomboid, walls incrassate. *Stipe leaves* monomorphic or weakly dimorphic, scale-like or leaf-like, appressed to erecto-patent, straight. *Frond leaves* monomorphic or weakly dimorphic in basal part of frond and dimorphic in distal part. *Basal frond leaves* erect to widely patent, symmetrical or weakly asymmetrical, broad-ovate or (short-)ovate; costa reaching c. 4/5 of leaf length. *Distal lateral frond leaves* patent to widely patent, asymmetrical, short-ovate or ovate; costa reaching 2/3–4/5 of leaf length (*D. filiculiforme*) or 4/5 of leaf length to almost percurrent in (*D. arbuscula*). *Frond amphigastria* symmetrical, erecto-patent to patent, short-ovate to short-elliptic (*D. filiculiforme*) or ovate (*D. arbuscula*); costa reaching 2/3 of amphigastrium length to percurrent.

Dioicous. *Gametoecia* in basal and middle part of rachis and basal half of lower first-order branches. *Gametoecial leaves* concave, not or weakly shouldered, triangular to oblong; outer ones usually smaller than inner ones; margin ± entire; border absent, faint, or distinct in basal half of leaf, faint to distinct in distal part, entire or interrupted in basal part of leaf or near acumen; apex gradually to abruptly acuminate (or obtuse or rounded in perigonial leaves); costa absent, faint, or distinct in perigonia, faint to distinct in perichaetia; laminal cells prosenchymatous or partly parenchymatous, short to short-linear, hexagonal in prosenchymatous leaf parts, rectangular in parenchymatous parts; border cells short to linear, rectangular to rhomboid (or oblong-hexagonal);



Map 3. Distribution of *Dendrohypopterygium* Kruijer.

acumen cells short to linear, hexagonal; walls of gametoecial leaf cells thin or incrassate in border and acumen cells. *Paraphyses* present, filiform, simple, hyaline.

Sporophyte projecting above frond (rarely lying in the frond in *D. arbuscula*). *Seta* ascending or vertical, cygneous to uncinate, smooth or weakly rugose near base of the capsule in *D. arbuscula*; base narrow. *Capsule* nodding to pendulous, ovoid, ellipsoid or barrel-shaped; orifice transverse. *Peristome* double. *Exostome* present, yellow to reddish brown; teeth bordered, weakly shouldered; dorsal side striate in basal half of teeth, becoming papillose in distal part; median line zig-zag, not furrowed; lamellae weakly projecting or not; papillae low, simple; striae distinctly papillose; dorsal plates equally wide as or broader than ventral ones; ventral plates weakly and minutely papillose; trabeculae short in basal third of teeth, very pronounced in distal part, very short near apex. *Endostome* colourless to pale yellow, perforate or not, papillose at both faces; papillae low, simple; processes distinctly keeled; cilia present. *Operculum* long-rostrate from a low or high conical base, pale ochraceous to brown; rostrum straight or oblique. *Calyptra* cucullate, entirely covering operculum, entirely ochraceous or brown in distal half, membranous but somewhat fleshy in distal half, naked or set with paraphyses; apex dark brown, fleshy.

A genus of 2 species.

Distribution — New Zealand, South America: Juan Fernandez Islands, C and SW Andes.

Habitat & Ecology — In forests, especially in moist or wet, shaded places. Terrestrial, on rocks, or rotting logs; also on tree trunks.

Note:

Kindberg's (1901) *Hypopterygium* subgen. *Stephanobasis* accommodated the South American *H. thouinii* (≡ *Dendrohypopterygium arbuscula*) and the New Zealand *H. setigerum* (≡ *Canalohypopterygium tamariscinum*) on account of the bordered leaves, the capsule neck that is set with a whorl of protrusions, and the minute orifice. Frey & Schaepe (1989) transferred the New Zealand species (as *Hypopterygium commutatum* ≡ *Canalohypopterygium tamariscinum*), to their new genus *Canalohypopterygium*, and this is followed here. They maintained the South American species in *Stephanobasis* (as a section of *Hypopterygium*).

Kindberg (1901) did not indicate a holotype for his subgenus *Stephanobasis*, and *Hypopterygium thouinii* is chosen as lectotype here. The species corresponds best with Kindberg's diagnosis, because of its distinctly coroniform, pustulose capsule neck (cf. Matteri, 1973: pl. 4, f. 8) and its – almost always – distinctly and entirely bordered frond leaves. Because the species is transferred to the genus *Dendrohypopterygium*, the subgenus is placed in the synonymy of the latter.

KEY TO THE SPECIES

1a. Frond bipinnate to tetrapinnate. Stipe entirely tomentose. Terminal cell of axillary hairs straight. Stipe leaves broad-deltoid or nearly so, often with bristly rhizoids at base; margin entire, frequently revolute to recurved. Calyptra with few to several paraphyses .... **1.1. D. filiculiforme**

b. Frond pinnate to bipinnate. Stipe tomentose in the basal third at most and glabrous upwards. Terminal cell of axillary hairs usually curved downwards, rarely straight. Stipe leaves broad-ovate or ovate, without rhizoids; margin frequently weakly crenate or roughly eroded near the apex, flat or incurved. Calyptra naked .... **1.2. D. arbuscula**

1.1. **Dendrohypopterygium filiculiforme** (Hedw.) Kruijer, *comb. nov.* — Fig. 4, 5, 9A; Map 4; Plate 2a, b

Leskea filiculiformis Hedw., Sp. Musc. Frond. (1801) 212, t. 50, f. 1–5, '*filiculaeformis*'. — *Hypnum filiculiforme* (Hedw.) P. Beauv., Prodr. (1805) 64, '*filiculaeforme*'. — *Hookeria filiculiformis* (Hedw.) Sm., Trans. Linn. Soc. London 9 (1808) 278. — *Pterygophyllum filiculiforme* (Hedw.) Brid., Muscol. Recent. Suppl. 4 (1818, '1819') 151, '*filiculaeforme*'. — *Hypopterygium filiculiforme* (Hedw.) Brid., Bryol. Univ. 2 (1827) 712. — *Leskea filiculaefolia* Hedw. ex Touw, Blumea 19 (1971) 271, nom. inval., err. pro *Leskea filiculiformis* Hedw. — Type: "Insulae Australes" (material absent from Hedwig's herbarium in G, elsewhere not found; see 'General typification problems', p. 24); lectotype: Hedwig, Sp. Musc. Frond. (1801) t. 50 f. 1–5; designated here.

Illustrations: Hedwig, Sp. Musc. Frond. (1801) 212, t. 50, f. 1–5. — Schwägrichen, Sp. Musc. Frond., Suppl. 3, 2 (1830) t. 281a. — Brotherus in Engler & Prantl, Nat. Pflanzenfam. ed. 1, 3 (1907) f. 708; ed. 2, 11 (1925) f. 629. — Sainsbury, Roy. Soc. N. Z. 5 (1955) pl. 67, f. 2. — Allison & Child, Mosses of New Zealand (1971) p. 124, pl. 29. — Beever et al., Mosses of New Zealand (1992) pl. 70, f. 72 a, c–g. — B. & N. Malcolm, Mosses and other Bryophytes (2000) 30, ?37, ?63.

Plants forming open (to dense) groups of dendroids, (small to) medium-sized to large; ramification palmate to umbellate. *Stipe* up to 10(–13) cm long, dorsiventrally compressed, entirely tomentose (but often glabrous in middle and distal part when old); rhizoids dark brown to reddish brown; distal part densely branched, often damaged and lost; basal (remaining) part erect, simple, bristly. *Frond* suborbicular to oblong-ovate, up to 6.5(–9.0) cm in diameter; ramification bipinnate to tetrapinnate; rachis and branches dorsiventrally compressed, usually glabrous, occasionally tomentose at base of rachis or lower branches, not caducous in young gametophores, becoming frequently caducous in distal part of frond in older gametophores; first-order branches up to 4.5 cm long; higher order branches in majority much shorter, when very short often pointing above or below plane of frond (see note 1), not caducous in young gametophores, becoming frequently caducous in older ones. *Primordia* frequently set

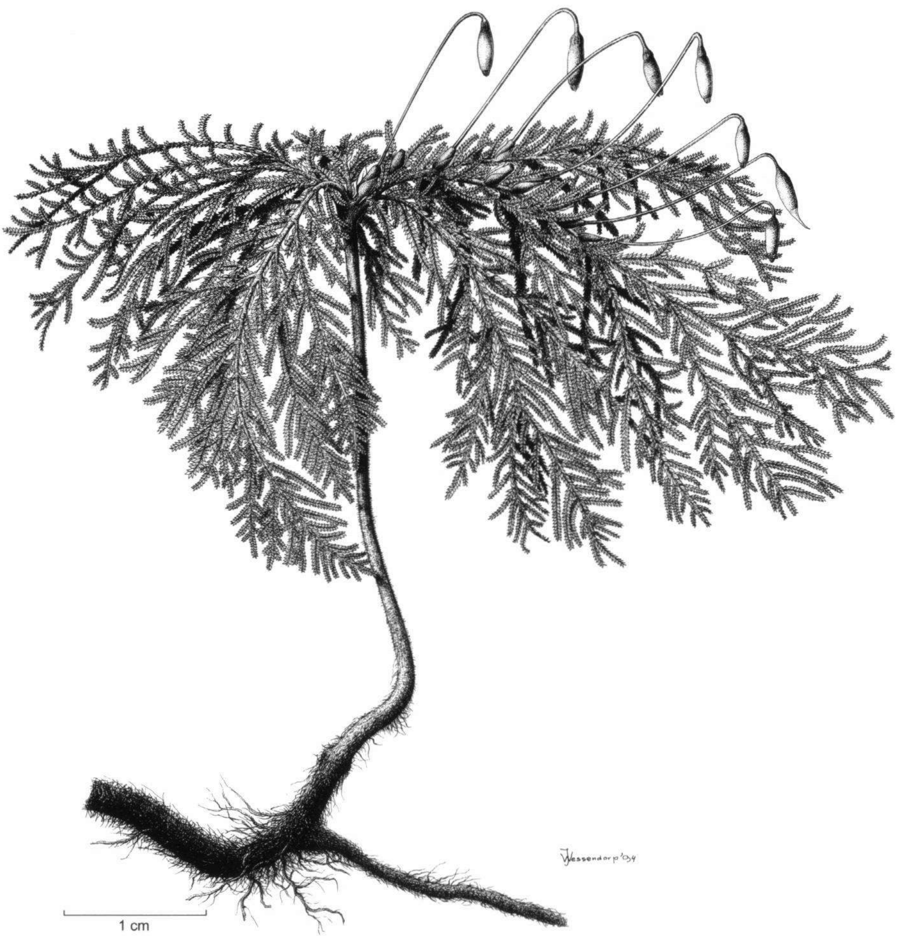


Fig. 4. *Dendrohypopterygium filiculiforme* (Hedw.) Kruijer. Habit (*Hamlin 2266*, WELT).

with scaly leaves; scaly leaves deltoid to ovate, margin entire. *Shoot axes* terete but somewhat quadrangular near stipe base. *Epidermis cells and cortical cells of stipe, rachis, and branches* equally wide or (inner) cortical ones wider; walls thin or incrassate (especially in ring of cortex cells at some distance from centre of stipe and basal frond axes), reddish brown to colourless when located in stipe, becoming entirely colourless towards distal part of rachis and branches; inclusions absent; cortical cells differentiated in outer, middle, and inner ones in stipe, becoming less differentiated or not differentiated in frond axes. *Central strand* present, but absent from frond axes when replaced by a central cavity cavity; cells narrow to broad in stipe, becoming narrow in frond axes; walls thin, brown to colourless in stipe, becoming colourless in axes in distal part of frond; inclusions absent from stipe, absent or present in frond axes as tiny, colourless to very pale yellow, oil-like droplets. *Axial cavities* absent from stipe and frond axes in basal (central) part of frond, absent or central in frond axes of distal part of frond, central in ultimate branches; inclusions present as colourless or white to reddish brown, oil- or fat-like droplets, wax-like plates, or crusts. *Axillary hairs* up to 2 per leaf, 2- or 3-celled; basal cells 1 or 2; terminal cell oblong-elliptic to nearly elongate-rectangular on stipe and parts of frond axes in basal (central) part of frond, becoming circular to elliptic in parts of frond axes in distal part of frond, straight, 25–40 μm long and 9–15 μm wide at stipe and parts of frond axes in basal part of frond, becoming 10–25 μm long and wide at parts of frond axes in distal part of frond, smooth, walls thin or incrassate. *Leaves* distant at stipe, closely set in frond, yellowish green to dark green, occasionally tinged with red; insertion concave; laminal cells prosenchymatous, short, hexagonal, 10–40 μm long and 5–20 μm wide, walls thin or incrassate, not porose. *Basal and distal stipe leaves* monomorphic, not differentiated, erect to erecto-patent, symmetrical, straight, scale-like to leaf-like, ± broad-deltoid, 0.5–1.5 mm long and 0.5–1.5(–2.0) mm wide, often with bristly rhizoids at base; margin entire, frequently revolute to recurved; border absent; apex rounded to obtuse; costa absent. *Frond leaves* partly monomorphic and partly dimorphic, not caducous or caducous at axial apices; margin ± entire in basal frond leaves, entire to moderately serrate in distal ones, flat or nearly so (to partly recurved); teeth 1–3-celled, up to 15 μm long, uniseriate or 2 (or 3) cells wide at base, projecting up to 1 cell; border absent or faint and interrupted in basal frond leaves and amphigastria, absent from distal lateral frond leaves, up to 2 cells wide; apex gradually or abruptly acuminate; acumen up to 0.2 mm long in basal and lateral frond leaves, up to 0.4 mm long in amphigastria. *Basal frond leaves* symmetrical, erecto-patent to patent, broad-ovate, 0.5–1.5 mm long and 0.5–2.0 mm wide, straight; costa distinct, reaching 4/5 of leaf length, conspicuously widened at base. *Lateral frond leaves (in distal part of frond)* asymmetrical, short-ovate, 0.5–1.5 mm long and 0.4–1.0 mm wide; costa distinct, reaching 2/3–4/5 of leaf length. *Frond amphigastria (in distal part of frond)* symmetrical, short-ovate to short-elliptic, 0.2–1.0 mm long and 0.2–1.0 mm wide; costa distinct, reaching 2/3 of amphigastrium length to percurrent.

Dioicous. *Gametoecia* in basal and middle part of rachis and basal half of lower first-order branches. *Gametoecial leaves* green; margin entire; border faint to distinct, or absent near leaf base, (0–)1–2 cells wide; costa absent, faint, or distinct in perigonia, faint to distinct in perichaetia, reaching 2/3–4/5 of leaf length. *Inner leaves*: of perigonia ovate to elliptic, up to 0.9 mm long and 0.6 mm wide, acumen up to 0.3 mm long; of perichaetia prior to sporophyte development triangular to elliptic, up to 1.1 mm long and 0.8 mm wide, acumen up to 0.9 mm long; of perichaetia of full grown perichaetia triangular to elliptic, up to 2.5 mm long and 0.9 mm wide, acumen up to 0.6 mm long. *Antheridia* 0.5–0.9 mm long. *Stalk in full grown perichaetia* 0.7–0.9 mm long, densely tomentose with brown rhizoids. *Archegonia* 0.5–0.7 mm long. *Vaginula* 0.9–1.5 mm long. *Gametoecial axillary hairs* up to 4 per gametoecial leaf (number difficult to observe), 2–6-celled; basal cells 1–5, brown; intermediate cells absent; terminal cell short to elongate, ovate to elliptic, (15–)20–45(–65) μm long and 10–15 μm wide, smooth, colourless, apex rounded. *Paraphyses* few to numerous, persistent, 9–15 cells long, uniseriate (or partly 2 cells wide), colourless or pale brown at base; basal cells 1–4; intermediate cells short to short-linear, rectangular or somewhat elliptic; terminal cell short to elongate, triangular, ovate, or elliptic to rectangular, somewhat inflated or not.

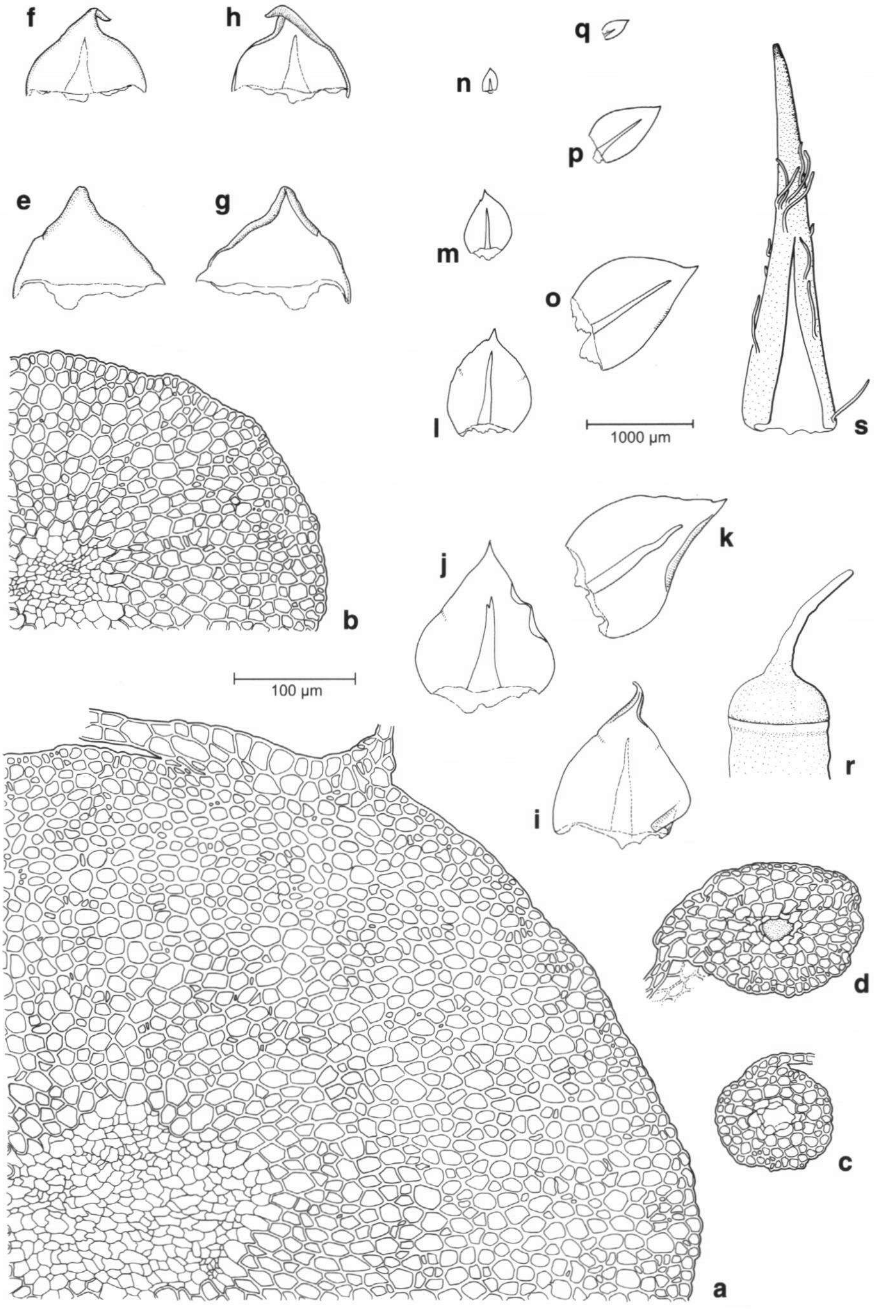


Fig. 5. *Dendrohypopterygium filiculiforme* (Hedw.) Kruijer. a. Rachis (cross section dorsal quadrant); b. branch (cross section dorsal quadrant); c, d. ultimate branches with central cavity (cross section) without (c) and with inclusions (d); e–h. stipe leaves in adaxial (e, f) and abaxial view (g, h); i–k. rachis leaves (i. dorsal, j. ventral, k. lateral); l–q. branch leaves (l–n. amphigastria, o–q. lateral); r. operculum; s. calyptra (a–q: *Hamlin 2266*, WELT; r–s: *Ruinard 98.10.31.02*, L).

Sporophytes up to 9 per frond. *Seta* (ascending or) vertical, uncinate, 12.0–16.5 mm long, nearly white or pale ochraceous to brown, frequently tinged with ochraceous or red at base. *Capsule* horizontal to pendulous, ellipsoid to barrel-shaped, 1.5–3.0 mm long and 1.0–1.5 mm wide, ochraceous to brown, regulary tinged with red; neck distinctly pustulose, occasionally weakly pustulose or nearly smooth; annulus distinct. *Peristomial formula OPL:PPL:IPL* = 4:2:(4–)6c. *Exostome* yellow; teeth 660–720 µm long and 125–160 µm wide, entirely weakly bordered, weakly shouldered; dorsal side striate in basal half of teeth, becoming moderately to coarsely papillose in distal part; dorsal plates broader than ventral ones,14–19 µm thick; ventral plates 26–30 µm thick. *Endostome* not perforate, papillose at both faces; basal membrane reaching 1/3–1/2 of length of exostome teeth; processes 420 µm long beyond orifice and 60–80 µm wide at base, often becoming much shorter and truncate by damage, not nodulose, not appendiculate; cilia distinct, 1 or 2(or 3), 8 or 9 cell plates long and 1–3 cell plates wide, nodulose or not, appendiculate with lateral appendages or not. *Operculum* 1.2–1.5 mm long, with a low conical base; rostrum straight to oblique. *Calyptra* 2.5–3.0 mm long, ochraceous or brown in distal half (when young green in basal half), membranous but somewhat fleshy in distal half, set with a few paraphyses, smooth; margin entire or with few, shallow incisions; paraphyses short. *Spores* 10–16 µm.

Distribution — New Zealand (North Island, South Island, Stewart Island), Australia? (New South Wales?; see note 3), Norfolk Island? (see note 3). The species occurs probably throughout New Zealand. The present distribution pattern (Map 4) is probably biased by undercollecting, especially on South Island. Nevertheless, the species might be absent or rare in the non-coastal areas east and southeast of the higher mountain ranges of South Island.

Habitat & Ecology — In forests, especially in damp or wet places, usually on wet forest floors or on banks of streams and gullies, frequently in dense shade. Terrestrial, often on clay or silty soils; less often on rocks, and rotting logs, occasionally also on tree trunks. Altitude: 0–750 m; 150–750 m on North Island and 0–500 m on South Island.

Map 4. Distribution of *Dendrohypopterygium filiculiforme* (Hedw.) Kruijer.

Groups entirely composed of dendroids of this species may occupy extensive areas of a few to several square metres on stream banks and forest floors of gullies (Klazenga, pers. comm).

According to Frey & Beever (1995) the species is found in very wet and totally shaded sites in various forest types, and often on loamy ground. They reported that the forest types include *Agathis* forests, mixed podocarp/broad-leaved and broad-leaved forests, and *Nothofagus* forests.

In wet, densely shaded sites the species grows in association with *Monoclea forsteri* W. Hook. (Monocleales Schust., Hepaticae); on drier sites and at higher elevations it is often found with *Achrophyllum dentatum* (Hook.f. & Wilson) Vitt & Crosby (Frey & Beever, 1995).

Geographical & Ecological variation — Not found.

Chloroplast DNA sequences — *trnL*$_{\mathrm{UAA}}$ intron, 304 bp, deposited in GenBank database under accession number AF134638, see Stech et al. (1999: 361). — Voucher: *Frey 94-76* (hb. Frey n.v., CHR n.v.), New Zealand; see Pfeiffer et al. (2000: 57).

Notes:

Description — 1. Frequently, small (ultimate) branches sprout directly from the basal and middle part of the rachis and first-orderbranches. They are associated with dorsal, lateral, or ventral leaves (or amphigastria). In some plants such small branches are borne on the gametoecial stalk.

Reproduction — 2. There were 89 fruiting specimens among the specimens examined (c. 22%, n = 401).

Distribution — 3. *Dendrohypopterygium filiculiforme* is almost certainly endemic for New Zealand. The species has doubtfully been reported from areas outside New Zealand and among the material examined there were only four old specimens labelled with another origin. Two specimens were indicated to come from Australia (*[uninterpretable] Banks s.n.*, BM; *Collie s.n.*, NY) and two specimens from Norfolk Island (*Moore? s.n*, *unknown collector 333/246 b*; W). It is very likely, that the origin of these specimens has been mislabelled. Streimann, who made thousands of bryophyte collections in Australia and hundreds on Norfolk Island did not find the species there. In BM there are four more specimens of *D. filiculiforme* gathered by Leichardt and labelled "Australia & New Zealand", but it is presumed that these are New Zealand specimens.

Other — 4. Sainsbury (1955) described a plant of *Hypopterygium filiculiforme* with normal and abnormal shoots from Poverty Bay, Wharerata Hill, North Island, New Zealand. The described plant is probably *Sainsbury 15422*. The abnormal appearance of some of its shoots can be explained by assuming the occurrence of juvenile stages in the tomentum of the stipe and the ramification of the outer branches. The abnormal shoots have a smooth or weakly tomentose stipe, whereby the tomentum is restricted to the basal part of the stipe. The ramification of the frond is entirely bipinnate with first-order branches of usual length and unusually short second-order ones.

Selected specimens (from 401 specimens examined):

NEW ZEALAND: *Lyall s.n. (113?)* (L, s.loc.). - North Island. North Auckland L.D.: *Allison 790* (CHR), *Van Zanten 7401281* (B, EGR, GRO, L, NICH), Waipoua forest; *Hamilton s.n.* (WELT), *Braggins & Beever 80/209* (CHR), Little Barrier Is. - South Auckland L.D.: *Hamlin 2266* (WELT), Kamai Ra.; *Jardine & Sainsbury s.n.* (BM, BR, L, NY, UPS, W), *Poole s.n.* (CHR), Mamaku Hill; *Allison 2927* (CHR), *4257* (JE), Lake Rotoehu. - Gisborne L.D.: *Van Zanten 7402585a* (GRO), Lake Waikaremoana; *Sainsbury 15422* (CHR, WELT, sub no. M 1549), Poverty Bay, Wharerata Hill. - Hawke's Bay L.D.: *Hodgson MENZ 40* (BM, CHR, FH, S, WELT), Wairoa; *Beckett 848* (BM, CHR, NSW, NY, UPS), Seventy Mile Bush, Piri-Piri. - Taranaki L.D.: *Fleischer B 187* (B), Mt Taranaki ('Mt Egmont'); *Martin s.n.* (CHR), Stratford. - Wellington L.D.: *Mundy 37* (CHR, WELT), Ohakune; *Brownsey s.n.* (WELT), Akatarawa Saddle; *Lyall 125* (BM), Hutt Valley. - South Island. Nelson L.D.: *Fife 6576* (CHR), Porarari River. - Marlborough L.D.: *Fife 5661* (CHR), Pelorus River; *Joliffe s.n.* (NY), Queen Charlotte Sound; *Beckett 767* (CHR), Mt Fyffe. - Westland

L.D.: *Berggren 1974* (B, S, UPS), Taramakau ('Teremakau'); *Beckett 954* (BM, CHR, FH, JE, NICH, NSW, NY, S, W), 'West Coast Road below Jacksons'; *Ruinard 98.10.31.02* (L), Fox Glacier; *Brownlie 378* (CHR), *Child 1990* (BM), Franz Josef. - Canterbury L.D.: *Beckett s.n.* (FH), Christchurch; *Beckett s.n.* (CHR), *G. & D. Kelly s.n.* (CHR, 'F/10/71/12'), Banks Peninsula. - Otago L.D.: *Berggren 1973* (B, BR, HBG, NY, S, UPS, W), *Child 1200* (BM), *Thomson s.n.* (CHR), Dunedin; *Child 5407* (BM, CHR); Morrisons Creek. - Southland L.D.: *Simpson s.n.* (CHR, WELT), Doubtful Sound; *Simpson s.n.* (WELT), Dusky Sound. - Stewart Is.: *Smith 213* (CHR).

DUBIOUS ORIGIN: *[uninterpretable] Banks s.n.* (BM, 'New Holland'), *Collie s.n.* (NY, 'Sydney'), *Moore? s.n* (W, 'Norfolk Is.'), *unknown collector 333/246 b* (W,'Norfolk Is.'); see note 3.

1.2. Dendrohypopterygium arbuscula (Brid.) Kruijer, *comb. nov.* — Fig. 6–8, 9B; Map 5

Hypopterygium arbuscula [P. Beauv.] Brid., Bryol. Univ. 2 (1827) 717. — *Hypnum thouinii* Schwägr., Sp. Musc. Frond, Suppl. 3, 2 (1830) 289, '*thouini*'. — *Hypnum arbuscula* P. Beauv., Prodr. (1805) 61, hom. illeg. [non Brid., Muscol. Recent. 2, 2 (1801) 96, nom. illeg. incl. spec. prior. (*Hypnum alopecurum* L. ex Hedw.); nec (Sm.) W. Hook., Musc. Exot. 2 (1819) 112, hom. illeg.] — *Hypopterygium thouinii* (Schwägr.) Mont., Ann. Sci. Nat. Bot. Ser. 3, 4 (1845) 86, '*thouini*', nom. illeg. incl. spec. prior; see note 1. - *Hypopterygium douini* K.I. Goebel, Organogr. Pfl. 1, ed. 2 (1913) f. 225iii, nom. inval., err. pro *Hypopterygium thouinii* (Schwägr.) Mont. Type: *Commerson s.n.* (G holo n.v.; BM, PC), Chile, Magallanes Prov., Magellan Straits, 1767; possible isotype: *unknown collector (Commerson?) (H. 1533)* (BM, "Magellan", "Jussieu"), Magellan Straits; see note 2. — The isotypes in PC were, together, superfluously designated as the lectotype by Menzel, Willdenowia 18 (1988) 304; see note 3.

Hypopterygium speciosum Müll.Hal., Linnaea 18 (1845, '1844') 683. — *Hypnum speciosum* Müll.Hal. ex Paris, Index Bryol. (1896) 684., hom. illeg. [non Brid., Muscol. Recent. Suppl. 2 (1812) 105], probably error for *Hypopterygium speciosum* Müll.Hal. — Type: *Philippi s.n.* (B holo, destroyed; BM lecto, designated here; S), Chile. — Merged with *Hypopterygium arbuscula* Brid. and synonymised with *Hypopterygium thouinii* (Schwägr.) Mont. by Müller, Syn. Musc. Frond. 2 (1850) 5. and with *Hypopterygium arbuscula* Brid. by Matteri, Bol. Soc. Argentina Bot. 15 (1973) 244, 247.

Hypopterygium wolffhuegelii Herzog, Hedwigia 64 (1923) 15, f. 5., '*wolffhügelii*'. — Type: *Wolffhügel s.n.* (JE holo n.v., hb. Herzog sub no. *5333*), Chile, Llanquihue Prov., Lago Todos los Santos ["An Bäumen im Urwald des Lago Todos Santos bei Osorno"], Febr. 1914. — Synonymised with *Hypopterygium arbuscula* Brid. by Matteri, Bol. Soc. Argentina Bot. 15 (1973) 244.

Hypopterygium pachyloma Dixon ex R.S. Chopra, Bot. Monogr. Council Sci. Industr. Res., India 10 (1975) 399, nom. nud.; syn. nov. — Original material: *unknown collector s.n.* (BM), "Bengal" ["West Bengal"]. — See note 4.

Illustrations: Schwägrichen, Sp. Musc. Frond., Suppl. 3, 2 (1830) t. 289. — Montagne in Gay, Fl. Chil., Atlas 1 (1854, '1850') t. 2, f. 4. — Goebel, Organogr. Pfl. 1, ed. 2 (1913) f. 225iii. — Brotherus in Engler & Prantl, Nat. Pflanzenfam. ed. 1, 3 (1907) 971, f. 707.; ed. 2, 11 (1925) 274, f. 628. — Frey & Richter, J. Hattori Bot. Lab. 51 (1982) 58, f. 12. — Herzog, Hedwigia 64 (1923) 16, f. 5. — Matteri, Bol. Soc. Argentina Bot. 15 (1973) 246, t. 4.; Flora Criptogámica de Tierra del Fuego 14 (9) (1975) pl. 15. — Menzel, Willdenowia 18 (1988) 303–306, f. 2–5.

Plants forming open groups of dendroids, medium-sized to large; ramification usually palmate to umbellate, rarely flabellate. *Stipe* up to 6.0(–9.0) cm long, not compressed to laterally or dorsiventrally compressed, tomentose in basal fifth to third, glabrous above, rhizoids reddish brown to brown, becoming pale brown or colourless at apex, weakly to densely branched from base, erect at base, soft, not differentiated in a basal and distal part. *Frond* suborbicular to ovate, up to 4.0(–5.0) cm in diameter; ramification

Fig. 6. *Dendrohypopterygium arbuscula* (Brid.) Kruijer. Habit (*Van Zanten & Kruijer 86.02.1137*, GRO).

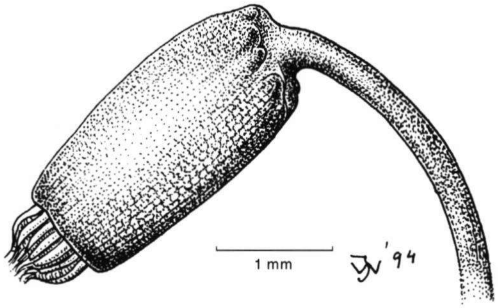


Fig. 7. ***Dendrohypopterygium arbuscula*** (Brid.) Kruijer. Capsule (*Van Zanten & Kruijer 86.02.1137*, GRO).

pinnate to bipinnate (or tripinnate); rachis and branches dorsiventrally compressed, glabrous, not caducous; branches up to 2.5 cm long. *Primordia* set with scaly leaves; scaly leaves deltoid to narrowly triangular or ovate, margin entire or crenulate. *Shoot axes* terete. *Epidermis and cortical cells of stipe, rachis, and branches* equally narrow or cortical cells wider; walls thin or incrassate, colourless to brown; inclusions absent. *Central strand cells* narrow to broad; walls brown in stipe and basal part of rachis, becoming colourless in distal part of rachis and branches; inclusions absent (present in central strand cells of stipe?). *Axial cavities* absent (or present as small cavities?) in central strand of stipe and basal part of rachis, absent or central in distal part of rachis or branches; inclusions present, small oil-like or fat-like droplets, colourless or pale brown. *Axillary hairs* up to 8 per leaf, 2–4-celled; basal cells 1–3; terminal cell short-elliptic to elongate-rectangular at stipe, suborbicular to oblong at frond axes, usually recurved, rarely straight, 15–40 µm long and 10–20 µm wide, apex usually rounded, rarely truncate; wall thin. *Leaves* distant or closely set at stipe, usually closely set, occasionally distant in distal part of frond axes, yellowish green to blackish green; insertion usually concave, transverse, or convex in stipe leaves, transverse or concave in frond leaves; laminal cells prosenchymatous (or somewhat parenchymatous in frond leaves), short to elongate, predominantly hexagonal, occasionally rhombic to rectangular in frond leaves, (10–)15–90 µm long and 10–25 µm wide; walls thin or weakly incrassate, porose. *Basal and distal stipe leaves* weakly differentiated in basal and distal ones or not differentiated, appressed to erecto-patent, symmetrical, broad-ovate to ovate; margin usually entire but weakly crenate to roughly eroded near apex, less often irregularly crenate or eroded in distal half of basal stipe leaves, occasionally coarsely serrate-dentate in distal ones; border usually absent, occasionally faint to distinct in distal stipe leaves, entire or interrupted, 1–6 cells wide; apex usually obtuse, rounded, or truncate, occasionally gradually or abruptly short-acuminate in distal stipe leaves, plane or incurved; costa faint to distinct, reaching 1/3 of leaf length to nearly percurrent. *Basal stipe leaves* scale-like to leaf-like, 1.0–2.5 mm long and 0.5–2.0 mm wide, usually damaged. *Distal leaves* 1.0–2.5 mm long and 0.5–1.5(–2.0) mm wide. *Frond leaves* monomorphic or weakly dimorphic in basal part of rachis or at base of lower branches, becoming dimorphic in distal part, probably occasionally caducous at apex of frond axes; margin moderately to coarsely serrate-dentate; teeth uniseriate or 2 (or 3) cells wide, 1–6-celled, up to 160 µm long, projecting up to 4 cells, in distal frond leaves shorter than in basal (central) frond leaves, and in lateral leaves shorter than in amphigastria; border distinct and entire, but in basal (central) frond leaves often faint or absent near base and occasionally absent near apex, 1–7 cells wide; apex rounded, gradually acuminate, or abruptly acuminate in basal (central) frond leaves, becoming

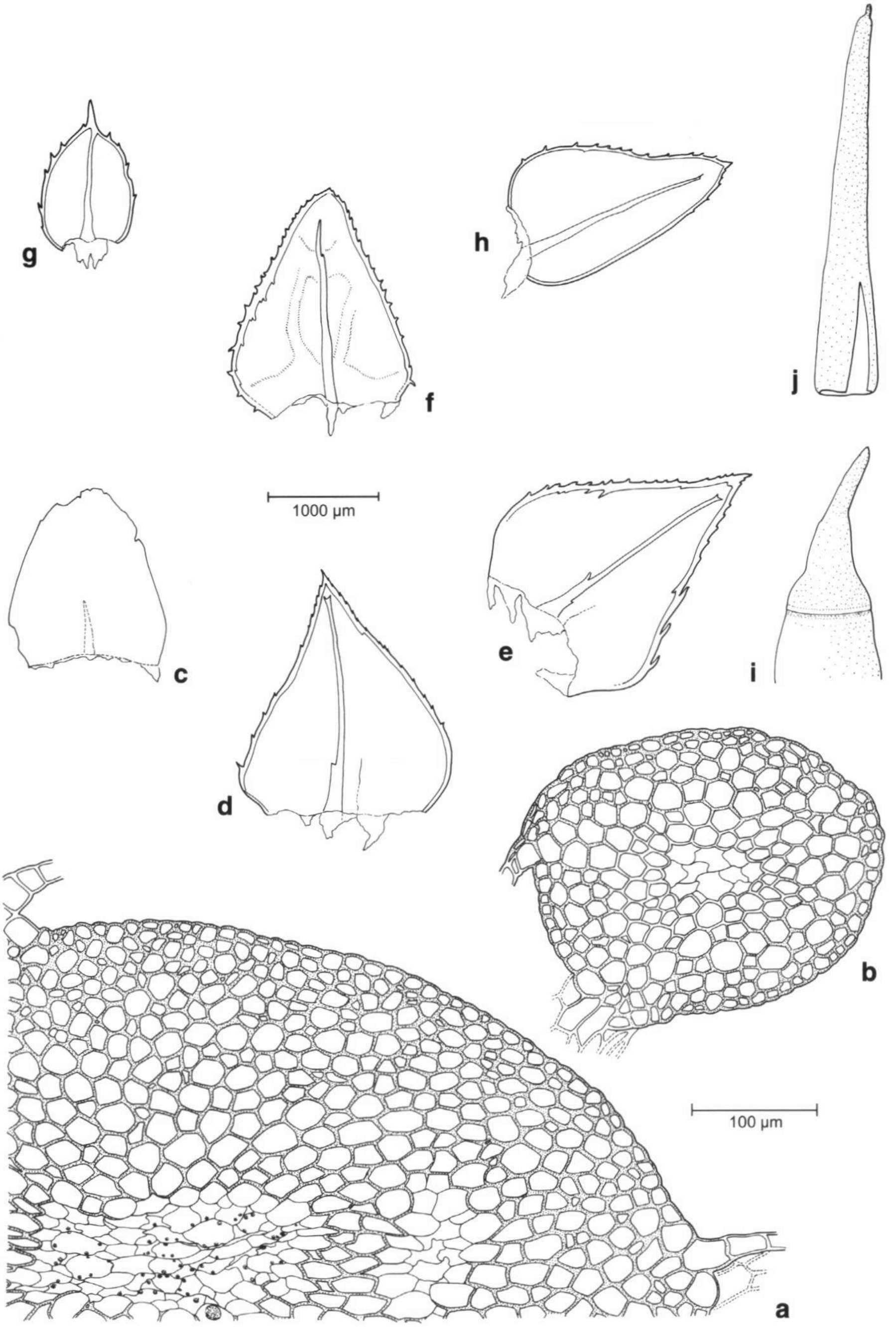
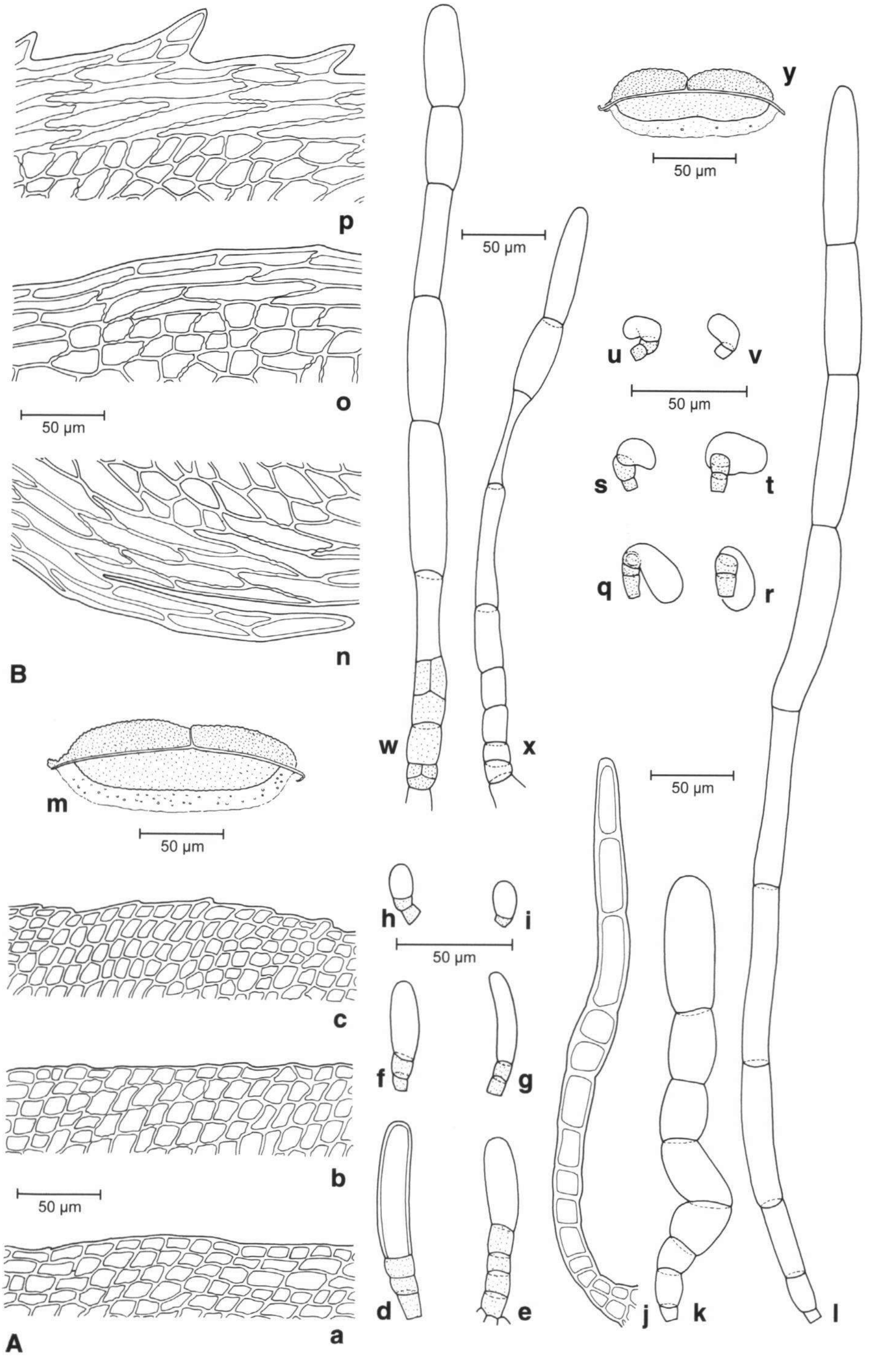


Fig. 8. ***Dendrohypopterygium arbuscula*** (Brid.) Kruijer. a. Rachis (cross section dorsal quadrant); b. branch (cross section); c. stipe leaf; d–f. rachis leaves (d. dorsal, e. ventral, f. lateral); g, h. branch leaves (g. amphigastria, h. lateral); i. operculum; j. calyptra (a–h: *Van Zanten & Kruijer 86.02.1137*, GRO; i: *Schmitz? s.n.*, HBG; j: *Neger 40*, L).

entirely abruptly acuminate in distal ones, occasionally weakly incurved when rounded; acumen up to 0.3 mm long. *Basal frond leaves* symmetrical, ovate, 1.5–2.5 mm long and 1.0–1.5 mm wide; costa distinct, reaching c. 4/5 of leaf length. *Lateral frond leaves (in basal and distal part of frond)* asymmetrical, ovate, 1.0–2.5 mm long and 0.5–2.0 mm wide, straight or weakly secund-falcate; costa distinct, reaching 4/5 of leaf length to nearly percurrent. *Frond amphigastria (in basal and distal part of frond)* symmetrical, ovate, (0.5–)1.0–2.5 mm long and 0.5–1.5 mm wide, straight or weakly secund-falcate; costa distinct, reaching 4/5 of amphigastrium length to percurrent.

Dioicous. *Gametoecia* most frequently in basal part of rachis, less often in basal part of lower branches. *Gametoecial leaves* green; margin ± entire; border faint to distinct or absent in basal half of leaf, frequently interrupted near acumen, 1–4 cells wide; costa absent or faint to distinct in perigonia, faint to distinct in perichaetia, reaching 1/2–4/5 of leaf length in perigonia and perichaetia prior to sporophyte development, becoming nearly percurrent in full grown perichaetia. *Inner leaves*: of perigonia broad-elliptic to elliptic, up to 1.2 mm long and 1.0 mm wide, apex gradually to abruptly acuminate or weakly rounded, acumen up to 0.2 mm; of perichaetia prior to sporophyte development ovate to oblong-ovate, up to 0.9 mm long and 0.6 mm wide, inner most ones frequently much smaller, apex gradually to abruptly acuminate, acumen up to 0.3 mm; of full grown perichaetia ovate to oblong, up to 2.0 mm long and 1.0 mm wide, apex gradually to abruptly acuminate, acumen up to 0.7 mm. *Antheridia* c. 0.7 mm long. *Stalk in full grown perichaetia* 1.1–1.3 mm long. *Archegonia* c. 0.7 mm long. *Vaginula* 1.1–1.3 mm long, little different from stalk. *Gametoecial axillary hairs* up to 3 per gametoecial leaf, 2–4-celled, simple; basal cells 1–3, pale brown to brown; intermediate cells absent; terminal cell oblong to elongate or nearly rectangular, obovate to narrowly elliptic, 20–40 µm long and 9–12 µm wide, smooth, colourless, apex rounded. *Paraphyses* few to numerous in perigonia, few in perichaetia, persistent (or becoming detached in full grown perichaetia?), 8–12 cells long in perigonia, 4–10 cells long in perichaetia, colourless or brown at base; basal cells 1 or 2; intermediate cells short to short-linear, rectangular to elliptic, not inflated; terminal cell short to short-linear, ovate, elliptic or nearly rectangular, inflated or not.

Sporophytes up to 14 per frond, usually projecting above the frond, rarely lying in the frond. *Seta* (ascending or) vertical, cygneous to uncinate, 8.0–10.0 mm long, ochraceous to reddish brown. *Capsule* horizontal to pendulous, ovoid to ellipsoid, 1.5–2.0 mm long and 0.5–1.0 mm wide, ochraceous to dark brown, smooth; neck distinctly pustulose; annulus distinct. *Peristomial formula OPL:PPL:IPL* = 4:2:(4–)6–8c. *Exostome* yellow to reddish brown; teeth 510–660 µm long and 110–120 µm wide, entirely and distinctly bordered, weakly shouldered; dorsal side striate in basal third to half of teeth, becoming moderately to coarsely papillose in distal part; dorsal plates 13–16 µm thick; ventral plates 15–17 µm thick. *Endostome* perforate, weakly papillose at outer face, densely and minutely papillose at inner face; basal membrane reaching 1/3–1/2 of length of exostome teeth; processes c. 450 µm long beyond orifice and 40–60(–90) µm wide at base, distinctly keeled, not nodulose, not appendiculate; cilia 1 or 2, 7–11 cell plates long and 1–3 cell plates wide, nodulose or not, regularly appendiculate with lateral or ventral, trabeculiform appendages. *Operculum* 1.0–1.5 mm long, with a high and weakly oblique conical base, ochraceous (see note 7);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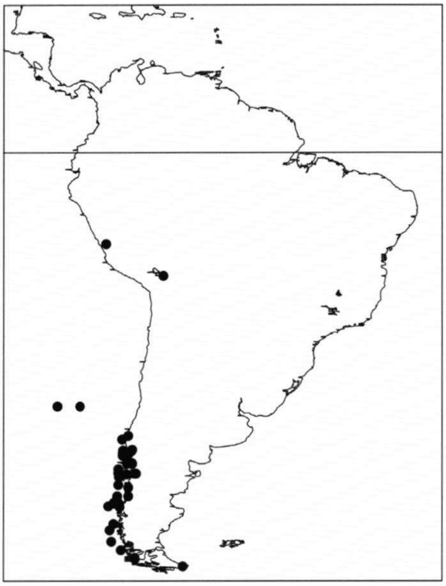


Map 5. Distribution of *Dendrohypopterygium arbuscula* (Brid.) Kruijer.

rostrum weakly oblique. *Calyptra* 3.0–3.5 mm long, pale ochraceous, membranous but somewhat fleshy in distal half, naked, smooth; margin entire. *Spores* 15–16 µm.

Distribution — Peru, Bolivia, Chile (Juan Fernandez Islands, Colchagua, Arauco, Cautín, Valdivia, Osorno, Llanquihue, Chiloé, Aisén, Magellanes), Argentina (Neuquén, Chubut, Tierra del Fuego). Most common in southern-central and southern Chile.

According to Matteri (1973) in the Argentinian Andes also in Rio Negro and Santa Cruz.

Habitat & Ecology — In forests, frequently in moist and shaded places. Terrestrial, on rocks, and rotting logs; also on tree trunks. Altitude: 10–560 m; in Peru 2650–3350 m. The altitudinal distribution for Bolivia is not known, but there is no reason to suppose it to be different from that of Peru. Pearie collected a specimen of *Lopidium concinnum* at 3350 m at the same locality in Bolivia, Unduavi, where he gathered a specimen of *D. arbuscula*.

Groups entirely composed of dendroids of this species may occupy extensive areas of a few to several square metres on forest floors.

Fig. 9. — A. *Dendrohypopterygium filiculiforme* (Hedw.) Kruijer. a–c. Leaf cells of lateral frond leaves: a, b. rachis leaf (a: basal part of antical side; b: distal part of antical side); c. branch leaf (distal part of antical side); d–i. axillary hairs (d. rachis, e–g. branch, h, i. ultimate branch); j–l. paraphyses (j. on calyptra; k, l. in perigonium); m. exostome tooth (cross section). — B. *D. arbuscula* (Brid.) Kruijer. n–p. Leaf cells of lateral frond leaves: n, p. rachis leaf (n. basal part of postical side, p. basal part of antical side), o. branch leaf (distal part of antical side); q–v. axillary hairs (branches); w–x. paraphyses (full grown perichaetia); y. exostome tooth (cross section) (A. a–i, k, l: *Hamlin 2266*, WELT; j: *Ruinard 98.10.31.02*, L; m: *Lyall s.n. (113?)*, L); B. n–x: *Van Zanten & Kruijer 86.02.1137*, GRO; y: *Lechler, PC 3063a*, L).

Geographical variation — The habitus of most plants is distinctly dendroid, and varies between palmate and umbellate. In two collections from, respectively, the Juan Fernandez Islands (*Sparre M356*) and Peru (*Hamilton (493)*) the dendroid shape of the plants was less pronounced and flabellate plants, with striking strongly twisted dry leaves, predominated.

Ecological variation — Not found.

Chloroplast DNA sequences — *trnL*$_{\mathrm{UAA}}$ intron, 256 bp, deposited in GenBank database under accession number AF134637, see Stech et al. (1999: 361). — Voucher: *H.& W. Frey 95–17* (hb. Frey), Chile, Osorno Prov., Parque Nacional Puyehue.

Notes:

Nomenclature — 1. *Hypopterygium arbuscula* is a legitimate name, which was published by Bridel (1827) as a new combination based on Palisot de Beauvois' (1805) illegitimate homonym *Hypnum arbuscula*. Schwägrichen's (1830) *Hypnum thouinii* is the legitimate name of the species when placed in *Hypnum* Hedw. Montagne's (1845) new combination *Hypopterygium thouinii* is illegitimate, because it is superfluous. It is based on *Hypnum thouinii* and inherits the type of *Hypopterygium arbuscula* Brid.

Menzel (1988) erroneously considered *Hypopterygium thouinii* to be a species introduced by Montagne (1845), although Montagne evidently had based his name on *Hypnum thouinii*. Menzel proceeded to designate Montagne's material, gathered by Gay in Chile, as the lectotype of *Hypopterygium thouinii* (PC, not seen; photographed by Menzel, 1988: 306, f. 5). Since *Hypopterygium thouinii* is a new combination and inherits the type of *Hypnum thouinii*, Menzel's typification is superfluous.

2. All specimens of *Dendrohypopterygium arbuscula* collected by Commerson near the Magellan Straits, including the holotype of this species, come from a single collection.

3. The lectotypification of *Hypopterygium arbuscula* by Menzel (1988) is superfluous and incorrect. He misjudged the name given by Bridel (1827) to be the first name of this species that was validly published. Bridel (1827) clearly based the name on *Hypnum arbuscula* P. Beauv., which is an illegitimate homonym, but had, nevertheless, been validly published. Consequently, *Hypnum arbuscula* P. Beauv. is attached to a type and *Hypopterygium arbuscula* inherits it.

However, if a lectotype had to be selected for *Hypopterygium arbuscula*, it should have only been the specimen that was gathered by Commerson, now kept in PC, which is labelled "*Leskea Hookeria rotulata?Hypnum arbuscula* P.B." and "Magallan. Juss." in Palisot de Beauvois' script. This specimen is the only one that is presented as *Hypnum arbuscula* P. Beauv., and it is best in accordance with Palisot de Beauvois' (1805) protocol, in which he stated that he received a plant from Jussieu under the name *Hypnum rotulatum* [(Hedw.) P. Beauv.], but that the plant is much taller and different because of its leaves.

Synonymy — 4. The original material of *Hypopterygium pachyloma* in Dixon's herbarium (BM) has almost certainly been mislabelled. It is indicated to come from 'Bengal', but its label bears no collector's name, and it is the only collection from outside South America that was found. The possibility of mislabelling escaped Chopra (1975), who did not realise that the material belongs to a South American species.

Description — 5. The terminal cells of the axillary hairs of the stipe are considerably longer than those of the axillary hairs of the rachis. However, the differences in length and, consequently, shape of the terminal cells are less pronounced than in *Dendrohypopterygium filiculiforme*.

6. The crenate or eroded parts in the margin of borderless stipe leaves are caused by the very thin walls of the margin cells, which make them very vulnerable to damage, rupture, or even loss. Such thin-walled margin cells occur, in particular, in the distal part of the stipe leaves, and most frequently in the leaves in basal and middle part of the stipe.

7. Mature operculae were found in only a single specimen (*Schmitz s.n.*, HBG). The given range of operculum length is based on the examination of the mature operculae in Schmitz' specimen and immature operculae of other collections that were almost certainly outgrown in length.

Reproduction — 8. There were 57 fruiting specimens among the specimens examined (c. 34%, n = 181).

Distribution — 9. *Dendrohypopterygium arbuscula* is a temperate to warm-temperate species. It occurs most frequently in the areas of Chile and southern Argentina (cf. Matteri, 1973) with abundant rainfall and a temperate or warm-temperate climate. In tropical South America, i.e. in Peru and probably also in Bolivia, the species is probably restricted to high elevations in mountainous areas.

Selected specimens (from 181 ones examined):

PERU: *Cuming s.n.* (BM, s.loc.). – Lima Prov.: *Hamilton (493)* (BM), W of Lima. — BOLIVIA: La Paz: *Pearie s.n.* (BM), Yungas, Unduavi.

CHILE: *Gay s.n.* (BM, L; s.loc.), *Philippi s.n.* (BM, S; s.loc.). – Juan Fernandez Is.: *Skottsberg & Skottsberg, SPE 334* (BM, S), Alejandro Selkirk ('Masafuera'); *Kunkel & Skottsberg M 342* (S), *Sparre M 356* (FH, S, UPS), Robinson Crusoe ('Masatierra'). – Colchagua Prov.: *unknown collector 28* (BM). – Arauco Prov.: *Crosby 13032* (CHR, GRO), Lago Lanalhue, Fundo Tranquivora. – Cautín Prov.: *Neger 40* (L), *s.n.* (S), Villarica; *unknown collector s.n.* (BM), Calafquén. – Valdivia Prov.: *Dusén, MC 72* (BM, S, ZT), *Krause (2)* (HBG), *Thilling (64?)* (HBG), Corral; *Schmitz s.n.* (HBG), Fundo San Martín; *Crosby 11571* (GRO, L, S), Lago Riñihue; *Lechler LPC 3063a* (BM, L, S), Arique. – Osorno Prov.: *H.& W. Frey 95–17* (hb. Frey), *Blöcher 176-1-Ha-c* (L), Parque Nac. Puyehue. – Llanquihue Prov.: *Dusén s.n.* (S), *Roth s.n.* (ZT), *Schmitz s.n.* (HBG), *Van Zanten & Kruijer 86.01.836* (GRO p.p.), *Wall s.n.* (S), Ensenada; *Van Zanten 79.01.118* (GRO), Saltos de Petrohué; *Reichert s.n.* (S, ZT), Lago Todos los Santos; *Van Zanten 79.01.573*, *Van Zanten & Kruijer 86.02.988* (GRO), Punta Huano; *Van Zanten 79.01.372* (GRO), *Van Zanten & Kruijer 86.02.1137* (GRO), Pto. El Manzano; *Andreas 5b + 6c* (GRO), Peulla. – Chiloé Prov.: *Lechler, LPC 594* (BM, BR, L, RO), *(972)* (HBG), Morro Gonzales; *Zöllner 4898* (L), Chiloé Is., Ancud; *Crosby 12506* (GRO, L), Puente San Juan. – Aisén Prov.: *Darwin 463?* (BM), *464* (BM), Chonos Archipelago; *Crosby 16211* (L), Taitoa Peninsula. – Magellanes Prov.: *Cunningham 243* (BM), Wellington Is., Pto. Edén ('Eden Harbour'); *Greene B1791* (CHR), Virtudes Is.; *Skottsberger, Exp. Suec. 957* (S), Canal Smyth, Muñoz Gamero; *Commerson s.n.* (PC, BM), *unknown collector (Commerson?) (1533)* (BM), Magellan Straits. — ARGENTINA: Neuquén: *Dusén 775* (S), Pto. Blest. – Chubut: *Kühneman s.n.* (S), Lago Menéndez. – Tierra del Fuego: *Matteri & Schiavone, CM 3685* (S; U, *MFE 36*), Ushuia, Mt Noroeste.

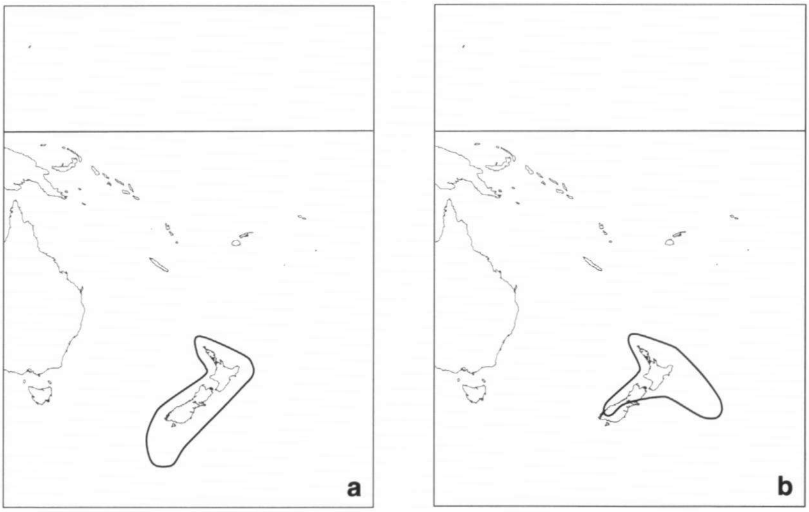
DUBIOUS ORIGIN: *unknown collector s.n.* (BM, 'Bengal'; see note 4); *Hooker f.? s.n.* (BM, 'Nepal Or.'); *Douglas s.n.*, (BM, 'New Zealand'); *unknown collector s.n.* (BR, 'New Zealand').

2. CANALOHYPOPTERYGIUM W. Frey & Schaepe — Map 6a

Canalohypopterygium W. Frey & Schaepe, J. Hattori Bot. Lab. 66 (1989) 269; from the Latin *canalis* (a canal) and the genus name *Hypopterygium*. — Type: *Canalohypopterygium commutatum* (Müll.Hal.) W. Frey & Schaepe, nom. illeg. ≡ *Canalohypopterygium tamariscinum* (Hedw.) Kruijer.

Hypopterygium Brid. sect. *Semilimbata* Broth. in Engler & Prantl, Nat. Pflanzenfam. ed. 1, 3 (1907) 972. — *Hypopterygium* Brid. subsect. *Semilimbata* (Broth.) Broth. in Engler & Prantl, Nat. Pflanzenfam. ed. 2, 11 (1925) 276. — Type: *Hypopterygium setigerum* (P. Beauv.) Wilson in Hook.f. ≡ *Canalohypopterygium tamariscinum* (Hedw.) Kruijer.

Plants usually forming open to dense groups of dendroids, rarely forming groups of fans or fans growing intermingled with dendroids, branched, dull, dark or olive-green to glaucous green (see note 3), not gemmiferous; ramification palmate or umbellate (rarely flabellate). *Stems* differentiated into stipe and rachis. *Stipe* straight, but curved at base and curved near frond base, usually vertical, less often ascending from substratum, becoming horizontal when changing into rachis, tomentose or set with scattered rhizoids at base, glabrous in distal part, entirely blackish brown to pale green in distal part. *Frond* suborbicular to short-ovate, ± complanate; rachis and branches roughly horizontal, straight or curved downwards, brown to pale green (usually brown or green at frond base, becoming green to pale green in distal part of frond), not caducous; rachis bent from stipe to roughly horizontal, glabrous; branches distant or closely set, patent to recurved; apex of foliate rachis and branches usually ± rounded. *Rudimentary branches* present (see note 3). *Stipe, rachis, and branches* terete or stipe quadrangular. *Epidermis* ± similar in cellular structure to (outer) cortex. *Cortex* differentiated in stipe and basal part of frond axes, becoming less differentiated or not differentiated in distal part of frond axes. *Central strand* present. *Axial cavities* present, located in cortex of stolon, stipe, rachis, and branches, and central in rudimentary branches (see note 3). *Axillary hairs* present; basal cells colourless to brown; intermediate cells absent; terminal cell straight, colourless, smooth. *Phyllotaxis*: of stipe and basal and middle part of rachis octostichous; of distal part of rachis and branches tristichous. *Foliation*: of stipe isophyllous, not complanate; of frond isophyllous and not complanate in basal parts with octostichous phyllotaxis, anisophyllous and complanate in distal part (with a tristichous phyllotaxis). *Leaves* when moist ± flat, when dry weakly to moderately crisped or twisted; insertion concave; base not or weakly decurrent; margin entire to dentate-ciliate; border faint to distinct, but at antical side of lateral leaves also absent or in traces, interrupted or continuous; apex abruptly acuminate (or gradually acuminate in amphigastria); costa absent or faint in stipe leaves, distinct in frond leaves (or faint in basal frond leaves), simple or somewhat forked in distal part; laminal cells prosenchymatous, short, hexagonal,walls incrassate, porose; costa cells longer than adjacent laminal cells, elongate to linear, rectangular to rhomboid, walls thin or weakly incrassate, porose; border and acumen cells longer than adjacent laminal cells, rhomboid or hexagonal, oblong to short-linear, walls thin or incrassate, porose. *Stipe leaves* monomorphic, scale-like or leaf-like, appressed to widely patent, straight. *Frond leaves* monomorphic in basal part of frond and dimorphic in distal part, straight or curved downwards. *Basal frond leaves* patent to widely patent, symmetrical, sub-



Map 6. Distribution of the two endemic genera of New Zealand and adjacent islands. a. Distribution of *Canalohypopterygium* W. Frey & Schaepe. b. Distribution of *Catharomnion* Hook.f. & Wilson.

orbicular to broad-ovate; *costa* reaching up to 3/4 of leaf length. *Distal lateral frond leaves* patent to widely patent, asymmetrical, short-ovate to ovate; costa reaching c. 3/4 of leaf length. *Frond amphigastria* symmetrical, erecto-patent to patent, short-ovate to ovate; basal part of lamina nearly flat or smoothly curved; costa reaching 3/4 of amphigastrium length to percurrent.

Dioicous. Gametoecia in basal part of rachis. *Gametoecial leaves* concave, shouldered, subcircular or broad-elliptic to ovate or oblong; outer ones usually smaller than inner ones; margin ± entire; border faint to distinct, interrupted or continuous; apex abruptly acuminate or subulate; costa absent or faint in full-grown perichaetia; laminal cells prosenchymatous, elongate to shortly linear, hexagonal or somewhat rhomboid; border cells shorter or longer than adjacent laminal cells, short to linear, quadrate or rectangular, becoming rhomboid or hexagonal in acumen; acumen cells elongate to linear, hexagonal; walls of gametoecial leaf cells thin or incrassate, porose. *Paraphyses* present, filiform, simple, hyaline.

Sporophyte projecting above frond. *Seta* ascending or vertical, uncinate, smooth; base narrow or somewhat widened. *Capsule* horizontal to nodding, ovoid to ellipsoid, smooth; orifice transverse. *Peristome* double. *Exostome* present, pale yellow to reddish brown; teeth distinctly bordered in basal half, not bordered in distal part, not shouldered; dorsal side striate in basal half of teeth, becoming papillose in distal part; median line zig-zag, not furrowed; lamellae weakly projecting or not; papillae low, simple; striae weakly papillose; dorsal plates broader than ventral ones; ventral plates smooth or papillose; trabeculae short in basal fourth of tooth, becoming very pronounced in distal part, becoming very short near apex. *Endostome* colourless, perforate or not, papillose at both faces; papillae low, simple; processes distinctly and conspicuously keeled; cilia present. *Operculum* long-rostrate, ochraceous; rostrum straight. *Calyptra* mitrate, entirely covering operculum, ochraceous, membranous but somewhat fleshy in distal part, naked, smooth; apex dark brown, somewhat fleshy.

Monotypic.

Distribution — See below the species.

Habitat & Ecology — See below the species.

Notes:

1. Fleischer (1908) suggested that *Hypopterygium setigerum* should be accommodated in a genus of its own, but made no final decision because he had no fruiting material at his disposal.

2. Kindberg (1901) classified *Hypopterygium setigerum* in *Hypopterygium* Brid. subgen. *Stephanobasis* Kindb., but it does not belong there (see '*Dendrohypopterygium*', note, p. 104).

3. The rudimentary branches of *Canalohypopterygium* (Plate 1a, b, p. 31; e.g. Reimers, 1953, f. 1–5; Frey & Schaepe, 1989, f. 1–3) and *Catharomnion* (Plate 1d; e.g. Frey & Schaepe, 1989, f. 7; Sainsbury, 1955, pl. 67, f. 1) are similar in morphology and anatomy, and are unique among mosses. These branches are leafless, but, exceptionally, may bear a few scaly leaves at base (Plate 1c, d; Reimers, 1953, f. 5). Rudimentary branches with scaly leaves occur most frequently in *Catharomnion*.

Rudimentary branches contain a central cavity, which is connected with a cavity in the cortex of the axis bearing the rudimentary branch (see also: Reimers, 1953; Frey et al., 1983; Frey & Schaepe, 1989; Kruijer, 1995b; Pelser et al., accepted). According to Frey et al. (1983) the development of the cavity system is probably schizogenous (in *Canalohypopterygium*), but perhaps lysigenous processes may occur as well.

The cavity system contains oil-like inclusions, which are colourless to pale yellow in *Catharomnion*, and yellow to pale brown in *Canalohypopterygium*. Inclusions in the cavity system were even found in the oldest material of *Canalohypopterygium* and *Catharomnion*, which is at least over 150 years to more than 200 years old (cf. Kruijer, 1995b). According to Pelser et al. (accepted), the inclusions in the cavity system of *Canalohypopterygium* mainly consists of apolar hydrocarbons, some of which are alkanes and fatty acids, including unsaturated fatty acids. They also found some evidence for the presence of compounds with an aromatic ring moiety.

Kindberg (1901), Brotherus (1907, 1925), and Sainsbury (1955, 1956) interpreted the rudimentary branches as bristle-like amphigastria or leaves, but Reimers (1953) showed that the rudimentary branches of *Canalohypopterygium* are modified branches ('Kurzäste'). Each rudimentary branch is associated with a superposed leaf or amphigastrium. Almost every frond leaf is associated with a rudimentary branch, a normal branch, or a gametoecium, whereby associations with rudimentary branches predominate. In *Catharomnion* the stipe leaves are occasionally also associated with a rudimentary branch. Amphigastria are less often associated with a rudimentary branch, although they are more frequently associated with rudimentary branches in *Canalohypopterygium* than in *Catharomnion*. Rudimentary branches associated with amphigastria are usually shorter than those associated with lateral leaves (see also: Reimers, 1953). The functions of the rudimentary branches and the inclusions of the cavity system are unknown (see for a discussion: Pelser et al., accepted).

2.1. **Canalohypopterygium tamariscinum** (Hedw.) Kruijer — Fig. 10–12; Map 7; Plate 1a–c, 2d

Canalohypopterygium tamariscinum (Hedw.) Kruijer, Lindbergia 20 (1996) 87; (Hedw.) Kruijer ex W. Frey & Beever, Nova Hedwigia 61 (1995) 352, nom. inval., basionym not given. — *Leskea tamariscina* Hedw., Sp. Musc. Frond. (1801) 212, t. 51, f. 1–7. — *Hookeria tamariscina* (Hedw.) Sm., Trans. Linn. Soc. 9 (1808) 279, quod nom. — *Hypopterygium tamariscinum* (Hedw. ["Swartz. Hedw."]) Brid., Bryol. Univ. 2 (1827) 715, pro parte, quod nom.? — *Hookeria tamarisci* (Hedw.) Sm. ex Arn., Disposition Méth. Espèc. Mousses (preprint) (1825 [= 1826?]) 56; Mém. Soc. Hist. Nat. Paris 2, 2 (1826) 305, nom. illeg. orthogr. err. pro *Hookeria tamariscina* (Hedw.) Sm. — *Pterygophyllum tamarisci* (Hedw. ["Swartz. Hedw."]) Brid., Muscol. Recent. Suppl. 4 (1818, '1819') 151, 'Pterigophyllum', pro parte, err. pro *Pterygophyllum tamariscinum* (Hedw.) Brid.; corr. Bridel, Bryol. Univ. 2 (1827) 715. — *Pterygophyllum tamariscinum* (Hedw.) Brid., Bryol. Univ. 2 (1827) 715, nom. inval. in syn. — Type: "Insulae Australes et Jamaica" (material from 'Insulae Australes' absent from Hedwig's herbarium in G, elsewhere not found; Jamaican material excluded; see 'General typification problems', p. 24); lectotype: Hedwig, Spec. Musc. (1801) t. 51, f. 1–7. — Lectotype designated by Kruijer, Lindbergia 20 (1996) 87. See Kruijer l.c. 85–88, for problems concerning the typification of *Leskea tamariscina* Hedw. — See also notes 1, 2, and 3.

Hypnum setigerum P. Beauv., Prodr. (1805) 70. — *Hypopterygium setigerum* (P. Beauv.) Wilson in Hook.f., Fl. Nov. Zel. 2 (1854, '1855') 118, nom. illeg. incl. spec. prior. (*Leskea tamariscina*). — See Kruijer, Lindbergia 20 (1996) 86.

Hypnum flabelliforme Brid., Muscol. Recent. Suppl. 2 (1812) 85, pro parte, nom. illeg. incl. spec. prior. (*Leskea tamariscina*). — *Hypnum flabelliforme* Brid. includes *Leskea tamariscina* Hedw. and *Hypnum tamarisci* Sw. — According to Kruijer, Lindbergia 20 (1996) 86, best assigned to *L. tamariscina* Hedw.

Hypopterygium commutatum Müll.Hal., Syn. Musc. Frond. 2 (1850) 6, nom. illeg. incl. spec. prior. — *Canalohypopterygium commutatum* (Müll.Hal.) W. Frey & Schaepe, J. Hattori Bot. Lab. 66 (1989) 269, nom. illeg. incl. spec. prior. (*Leskea tamariscina*). — Frey & Schaepe, J. Hattori Bot. Lab. 66 (1989) 269, overlooked the fact that *Hypopterygium commutatum* Müll.Hal. includes *Leskea tamariscina* Hedw. and superfluously chose a neotype; see Kruijer, Lindbergia 20 (1996) 85.

Hypopterygium elegantulum Colenso, Trans. & Proc. New Zealand Inst. 20 (1888) 242. — Type: *Colenso s.n.* (WELT holo, BM), New Zealand, North Island, Hawke's Bay L.D., ["On the ground, shady ravines, forest South of Dannevirke, County of Waipawa"], 1887. — Merged with *Hypopterygium setigerum* (P. Beauv.) Wilson in Hook.f. by Brotherus, Nat. Pflanzenfam. ed. 1, 3 (1907) 972. — The holotype is preserved in Colenso's herbarium kept at WELT. An isotype is present in Sainsbury's herbarium, which is also kept in WELT. Both specimens are labelled with the (herbarium) number *4191*, but it is not known by whom. Possibly, it is an herbarium or collection number that was given by Colenso, but it cannot be ruled out that it is by the hand of Dixon or Sainsbury. The holotype is also labelled with the (herbarium) number *M. 72*. The specimen in BM was sent to England by Colenso in 1890. It is not labelled with a collection or herbarium number.

Hypopterygium setosum Wilson ex Müll.Hal., Syn. Musc. Frond. 2 (1851) 659, nom. nud. in syn. (*Hypopterygium commutatum* Müll.Hal.). — Original material: *Stephenson s.n.* (B destroyed), New Zealand, 1843; possible duplicate: *Stephenson 11* (BR, NY; G n.v., according to Frey & Schaepe, J. Hattori Bot. Lab. 66 (1989) 269, as 'neotype' of *Hypopterygium commutatum* Müll.Hal.), New Zealand, 1843–4.

Hypopterygium huttonii Schimp. & Hampe ex Kindb., Hedwigia 40 (1901) 279, nom. nud. in syn. (*Hypopterygium setigerum* (P. Beauv.) Wilson). — Original material: *Hutton s.n.* (BM), New Zealand.

Illustrations: Hedwig, Sp. Musc. Frond. (1801) t. 51, f. 1–7. — Brotherus in Engler & Prantl, Nat. Pflanzenfam., ed. 1, 3 (1925) f. 704A. 1907; ed. 2, 11: f. 626A. — Reimers, Ber. dtsch. Bot. Ges. 66 (1953) 412, 414–415, f. 1–8. — Berthier, Rev. Bryol. Lichénol. 38 (1972) 547, pl. 28 f. J. — Frey & Richter, J. Hattori Bot. Lab. 51 (1982) 58, f. 13–17. — Frey et al., J. Hattori Bot. Lab. 54 (1983) 308–318, f. 1–8. — Frey & Schaepe, J. Hattori Bot. Lab. 66 (1989) 266, f. 1–6. — Beever et al., Mosses of New Zealand (1992) f. 72 h.— B. & N. Malcolm, Mosses and other Bryophytes (2000) 14, 101, 183.

Plants medium-sized, not gemmiferous. *Stipe* up to 5.5 cm long, lateraly compressed. *Frond* suborbicular to short-ovate, up to 4.5 cm in diameter; rachis and branches dorsiventrally compressed; branches up to 3.0 cm long. *Rudimentary branches* between frond leaves, arranged in 8 rows in basal part of rachis and lower branches, arranged in 3 rows in distal part of frond (but less frequently between amphigastria), up to 1.5 mm long, leafless but occasionally bearing scaly leaves near base; axial cavity single, central, connected with a cortical cavity in rachis or branch. *Primordia* set with scaly leaves; scaly leaves short-filiform or narrowly triangular to broad-ovate, margin ± entire. *Epidermal and cortical cells of stipe, rachis, and branches* equally narrow or cortical cells wider; walls thin or incrassate, colourless to pale brown; inclusions absent or perhaps present in cortical cells near developing cavities. *Central strand cells* very narrow; walls thin, colourless; inclusions absent. *Axial cavities* 8–10 per cross section in stipe, 4 or 5 per cross section in lower part of rachis and 3 or 4 per cross section in its distal part, (1–)3 per cross section in branches, and 1 per cross section in rudimentary branches; inclusions filling axial cavity for most part, yellow to pale brown, consisting of oil-like droplets. *Axillary hairs* up to 2 per leaf, 3-celled; basal cells 2; terminal cell elongate to short-linear, elliptic to rectangular, 25–100 µm long and 10–17 µm wide, smooth or weakly verrucose, wall thin or incrassate at cell apex. *Leaves* distant at stipe, becoming closely set in frond, dark or olive-green to glaucous green; insertion concave; laminal cells prosenchymatous, short, hexagonal, 10–35 µm long and 10–15 µm wide; walls incrassate, porose. *Basal and distal stipe leaves* monomorphic, differentiated in basal ones and distal ones, appressed to widely patent, symmetrical, short-ovate to broad-obovate; margin entire; border absent or faint and interrupted, up to 5 cells wide; apex abruptly acuminate; acumen up to 1.0 mm long; costa absent or faint, reaching (up to) 1/5 of leaf length. *Basal stipe leaves* scale-like to leaf-like, up to 1.0 mm long and 1.0 mm wide, often damaged. *Distal stipe leaves* 0.9–1.2 mm long and 0.9–1.2 mm wide. *Frond leaves* monomorphic in

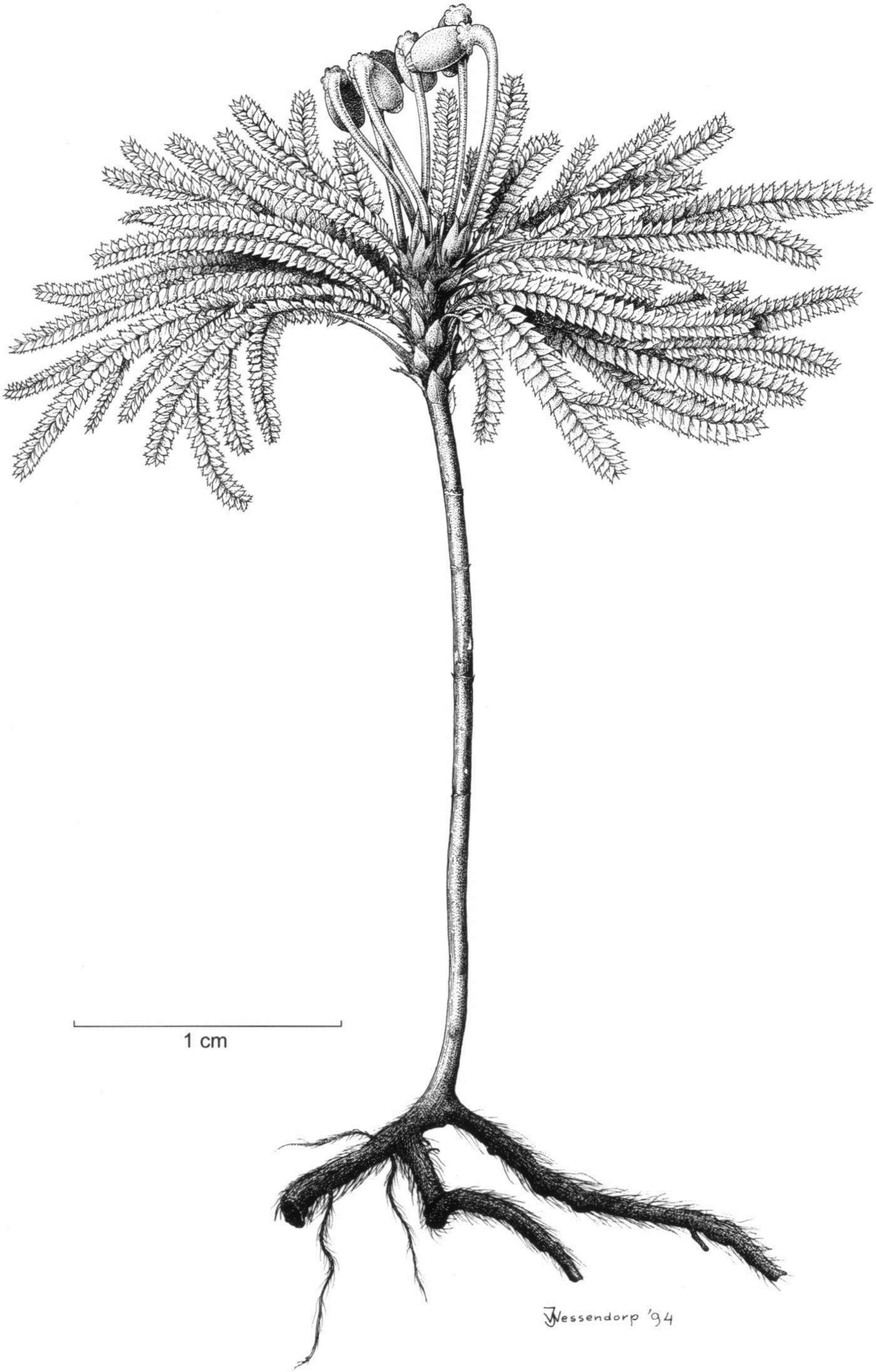


Fig. 10. ***Canalohypopterygium tamariscinum*** (Hedw.) Kruijer. Habit (*Visch s.n.*, '19.11.1972', L).

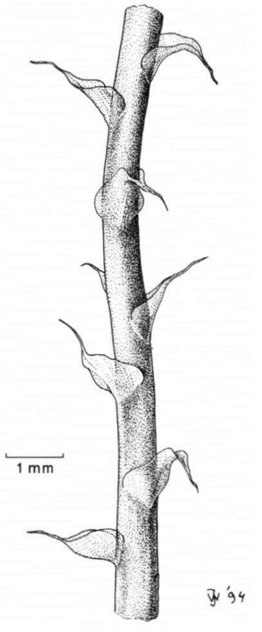
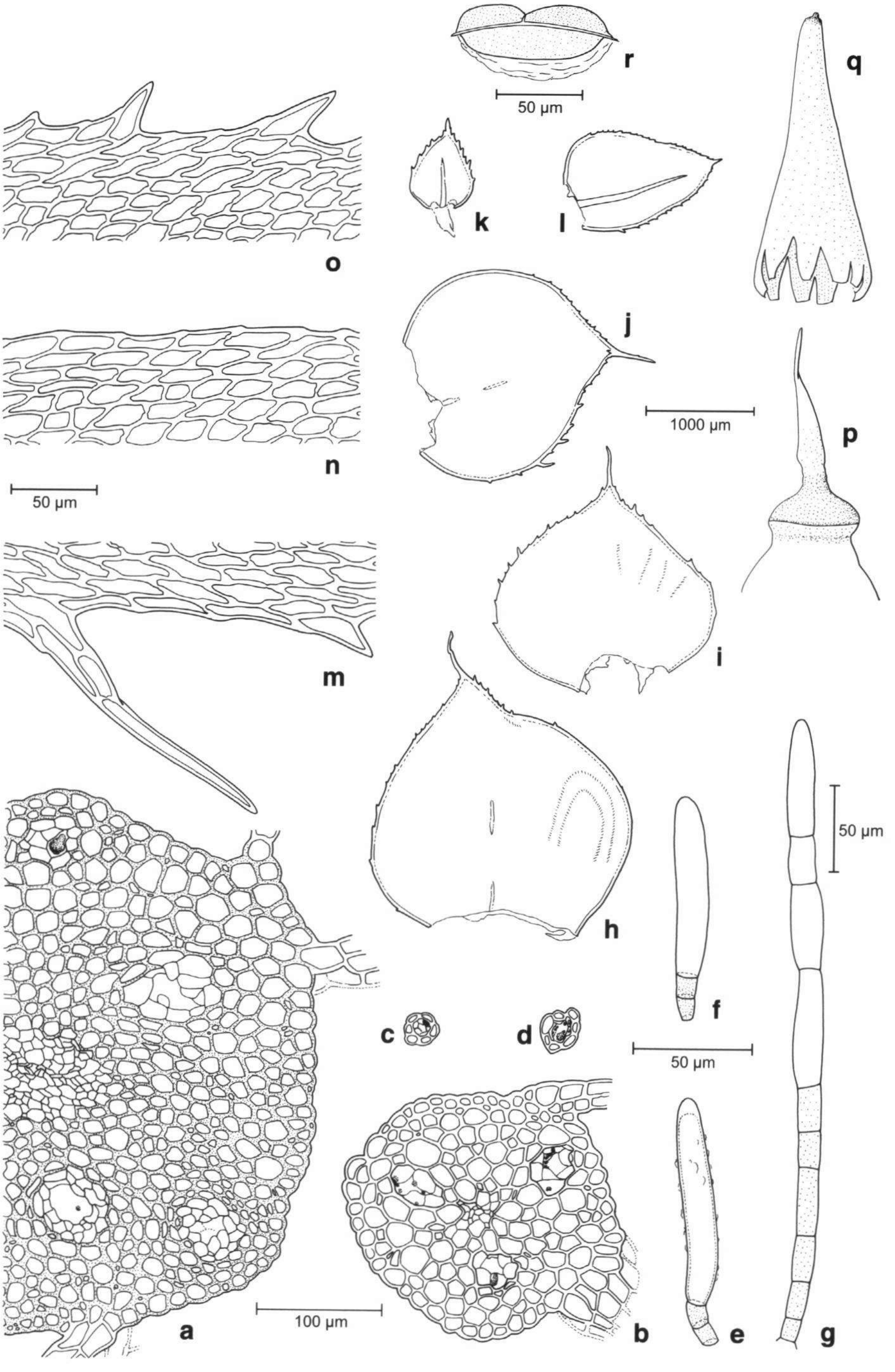


Fig. 11. *Canalohypopterygium tamariscinum* (Hedw.) Kruijer. Stipe (*Visch s.n.*, '19.11.1972', L).

basal part of frond, becoming dimorphic in distal part, not caducous; margin entire to serrate-dentate or dentate-ciliate; teeth 1- or 2-celled at antical side of lateral leaves and here up to 25 µm long, uniseriate or biseriate, projecting up to 1 cell, 1–12-celled at postical side of lateral leaves or amphigastria and here up to 360 µm long, uniseriate or several cells wide at base, projecting up to 5 cells, up to 40 at lateral leaves and 20 at amphigastria; border faint to distinct, but at antical side of lateral leaves also absent or in traces, interrupted or continuous, up to 6 cells wide, pale green to green; apex abruptly acuminate; acumen 0.3–0.8 mm long in lateral leaves, 0.2–0.4 mm long in amphigastria. *Basal frond leaves* symmetrical, suborbicular to broad-ovate, 1.5–2.0 mm long and 1.5–2.5 mm wide; *costa* faint, reaching up to 3/4 of leaf length. *Lateral frond leaves (in distal part of frond)* asymmetrical, short-ovate to ovate, 1.0–1.5 (–2.0) mm long and 0.5–1.5 mm wide; costa distinct, reaching up to 3/4 of leaf length. *Frond amphigastria (in distal part of frond)* symmetrical, short-ovate to ovate, 0.4–1.1 mm long and 0.4–1.1 mm wide; costa distinct, simple or forked, reaching 3/4 of amphigastrium length to percurrent.

Dioicous. Gametoecia in basal part of rachis. *Gametoecial leaves* green or brown at base; margin entire; border up to 4 cells wide in basal half of leaf, up to 2 cells wide in distal half; costa absent or faint in full-grown perichaetia, reaching 1/2 of leaf length. *Inner leaves*: of perigonia broad- to short-elliptic, up to 1.1 mm long and 1.2 mm wide, acumen up to 0.4 mm long; of perichaetia prior to sporophyte development suborbicular to elliptic, up to 0.8 mm long and 0.7 mm wide, acumen up to 1.1 mm long; of full-grown perichaetia short-ovate to oblong, up to 3.0 mm long and 2.0 mm wide, acumen up to 0.9 mm long. *Antheridia* up to 0.7 mm long. *Stalk in full-grown perichaetia* 0.7 mm long, set with rhizoids near base. *Archegonia* 0.3–0.4 mm long. *Vaginula* 0.6 mm long. *Gametoecial axillary hairs* 2 (or more?) per gametoecial leaf, 3–5-celled, simple; basal cells 2 or 3, (colourless or) brown; intermediate cells absent or present, short to oblong, ± rectangular, colourless; terminal cell elongate to short-linear, elliptic to narrowly ovate, 25–110 µm long and 10–15 µm wide, smooth, colourless. *Paraphyses* few, 7–13 cells long, colourless to pale brown; basal cells 2 or 3 (or 4) in perigonia, (1? or) 2 in perichaetia; intermediate cells short to short-linear, elliptic to rectangular; terminal cell elongate to linear, rectangular or somewhat attenuate.

Sporophytes up to 10 per frond. *Seta* (ascending or) vertical, uncinate, (4.5–)7.0–8.5 mm long, ochraceous, tinged with red, often swollen in distal part just below capsule. *Capsule* horizontal to pendulous, ovoid to ellipsoid, (1.5–)2.0–2.5 mm long and 1.0–1.5 mm wide, ochraceous to brown, often tinged with red; neck usually distinctly pustulose, occasionally weakly pustulose or almost smooth; annulus indistinct. *Peristomial formula OPL:PPL:IPL* = 4:2:6–8c. *Exostome* pale yellow to reddish brown;


r
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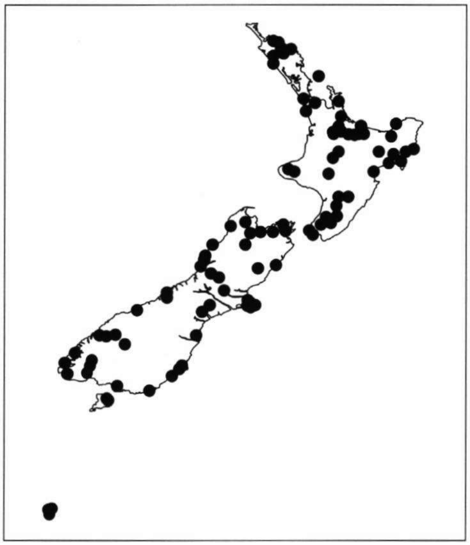


Map 7. Distribution of *Canalohypopterygium tamariscinum* (Hedw.) Kruijer.

teeth 600–630 µm long and 100–110 µm wide, distinctly bordered in basal half of tooth only, not shouldered; dorsal side striate in basal half of teeth, becoming moderately to coarsely papillose in distal part; dorsal plates broader than ventral ones, 13–14 µm thick; ventral plates 18–19 µm thick. *Endostome* occasionally perforate, papillose at both faces; basal membrane reaching 1/3 of length of exostome teeth; processes projecting 570 µm beyond orifice and 50–60 µm wide at base, not nodulose, not appendiculate; cilia 1–3, c. 8 cell plates long and 1–3(–4) cell plates wide, nodulose or not, not or weakly appendiculate. *Operculum* 1.3–1.4 mm long. *Calyptra* 2.0–2.5 mm long, membranous but somewhat fleshy in distal part; margin lobed, usually with distinct lobes, occasionally with indistinct, small or very short lobes. *Spores* 10–15 µm.

Distribution — New Zealand (North Island, South Island, Stewart Island; Auckland Islands: Enderby Island, Auckland Island); see note 6.

According to Vitt (1979) rare on the Auckland Islands, and also found on Adams Island. As yet not found in the southern part of Stewart Island (cf. Martin, 1950).

Habitat & Ecology — In various forests, often in wet or damp places, especially near streams on banks and wet boulders, in wet ravines or damp gullies; frequently in

Fig. 12. *Canalohypopterygium tamariscinum* (Hedw.) Kruijer. a. Rachis (cross section lateral half with three cavities and a cavity in process of formation); b. branch (cross section with three cavities, cavities partly in process of formation); c, d. rudimentary branches with central cavity (cross section: c. 'epithelium cells' intact, d. 'epithelium cells' degenerating); e, f. axillary hairs; g. paraphyse; h–j. rachis leaves (h. ventral, i. dorsal, j. lateral); k, l. branch leaves (k. amphigastria, l. lateral); m–o. leaf cells of lateral frond leaves: m, n. rachis leaf (m. basal part of postical side, n. basal part of antical side), o. branch leaf (distal part of antical side); p. operculum; q. calyptra; r. exostome tooth (cross section) (a–d, h–o: *Visch s.n.*, '19.11.1972', L; e, f, p, q: *Martin 274.9*, CHR; g: *Vitt 8537*, NY; r: *Fife 4580*, NY).

dense shade. Terrestrial on soil (often clay or silt), humus or litter, rocks (greywacke, limestone, granite), and exposed roots; also on tree trunks and rotting logs. Altitude: 100–850 m on North Island, 0–600 m on South Island.

Groups entirely composed of dendroids of this species usually occupy areas of up to a few square decimetres, and rarely occupy larger areas of up to 2 m^2 (Glenny, pers. comm.; Klazenga, pers. comm.). According to Frey & Beever (1995) the species forms extensive pure stands with few other bryophytes in wetter sites of various forests, especially on loamy ground. The forest types they reported for the species include *Agathis* forests, mixed podocarp/broad-leaved and broad-leaved forests dominated by species as *Vitex lucens* Kirk, *Beilschmiedia tarairi* Kirk, *B. tawa* Kirk or *Weinmannia racemosa* L.f., and *Nothofagus* forests. The species is probably restricted to low elevations on the Auckland Islands (Vitt, 1979), where it was found on humus and moist peaty soil in lowland *Dracophyllum–Metrosideros* forests. Vitt's collection on Adams Island was found on gravelly soil in a *Dracophyllum* forest.

Geographical & Ecological variation — Not found.

Chloroplast DNA sequences — *trnL*$_{\mathrm{UAA}}$ intron, 274 bp, deposited in GenBank database under accession number AF134632, see Stech et al. (1999: 361). — Voucher: *Frey 94–79* (hb. Frey n.v., CHR n.v.), New Zealand; see Pfeiffer et al. (2000: 57).

Notes:

Nomenclature — 1. The typification of *Leskea tamariscina* Hedw. and *Hypnum tamarisci* [Sw. ex] Sw. and the similarity between their epithets have caused much confusion. *Leskea tamariscina* and *Hypnum tamarisci* are two separate species, i.e. *Canalohypopterygium tamariscinum* (Hedw.) Kruijer and *Hypopterygium tamarisci* (Sw.) Brid. ex Müll.Hal., but quite a few authors used the wrong name or combination for the species they had in mind, especially when the species were placed in *Hypopterygium*.

When Hedwig (1801) published *Leskea tamariscina*, he erroneously considered his plants from 'Insulae Australes' conspecific with *Hypnum tamarisci* described by Swartz (1788) from Jamaica. Swartz (1806) created *Hypnum tamarisci* [Sw. ex] Sw., thereby validating his (1788) pre-starting-point name by means of a direct reference. Kruijer (1996a) showed that Hedwig's *Leskea tamariscina* is only attached to the material from 'Insulae Australes', whereas Swartz' *Hypnum tamarisci* did not include *Leskea tamariscina*, and is attached to material from Jamaica.

Leskea tamariscina is endemic to New Zealand and the Auckland Islands and Hedwig's 'Insulae Australes' almost certainly denotes New Zealand (Kruijer, 1996a; Touw, 1971). Swartz' *Hypnum tamarisci* is restricted to the Neotropics.

2. Van der Wijk et al. (1967) erroneously considered *Pterygophyllum tamarisci* (Hedw.) Brid. 1819 ('*P. tamariscinum* (Hedw.) Brid.') a homotypic synonym of *Thuidium tamariscinum* (Hedw.) Schimp. In 1969 they corrected this error while making a new mistake, and considered *P. tamarisci* ['(Sw.) Brid.'] to be based on *Hypnum tamarisci* [Sw. ex] Sw. and a heterotypic synonym of *Hypopterygium tamariscinum* (Hedw.) Brid. 1827. Kruijer (1996a) showed that Bridel (1819, 1827) had included *Leskea tamariscina* Hedw. 1801 in his concept of *P. tamarisci* and *Hypopterygium tamariscinum*.

Synonymy — 3. Sprengel (1820) may have had the South American *Hypnum tamarisci* Sw. in mind, when he considered *Hypnum laricinum* Hook., *Leskea tamariscina* Hedw., and *L. rotulata* Hedw. conspecific (in *Hypnum* Hedw.).

4. Bridel (1827) gave two, nowadays dubious, names in the synonymy of *Hypopterygium tamariscinum*: *Hypnum umbraculum* Brid., nom. nud. in syn., and *Pterygophyllum jungermannioides* Brid. These doubtful species are, in all probability, not conspecific with the present species and must be excluded from *Hypopterygium tamariscinum*. *P. jungermannioides* is probably conspecific with either *Hypopterygium tamarisci* or *H. didictyon*. Little is known about the identity of *Hypnum umbraculum* (see under the doubtful species of *Hypopterygium*, p. 249).

Reproduction — 5. There were 124 fruiting specimens in the material examined (c. 28%, n = 441). Sporulation is apparently somewhat more frequent on North Island (c. 31% of the specimens in fruit, n = 152), than on South Island (c. 25% of the specimens in fruit, n = 198).

In a sample of 62 collections of fertile plants, of which 14 contained a mixed collection of male and female plants, c. 34% (n = 26) of the plants were male and c. 66% (n = 50) were female. Apparently, the male–female ratio equals roughly 1:2.

Distribution — 6. Sainsbury (1955) reported *Canalohypopterygium tamariscinum* (as *Hypopterygium setigerum*) from Australia and Tasmania, but I doubt whether it actually occurs there (cf. Scott & Stone, 1976; as *H. commutatum*). There was no specimen of this species from Australia or Tasmania in the material received on loan from Australian herbaria. According to Dalton et al. (1991), who reviewed the reports of Tasmanian records and rejected this species from the Tasmanian moss flora, there are no collections of this species held in HO. A specimen from Tasmania ("Van D'^{s}.L^{d}.") in FH (*Gunn s.n.*, hb. James), which was presented as '*Hypopterygium tamariscinum* Brid.', is a misidentification of *Hypopterygium tamarisci*. The collection *Petrie s.n.* in BM is labelled to come from Mt Cargill, "NSW", but has almost certainly been mislabelled, since Mt Cargill is located in Dunedin, New Zealand. A re-examination of the collections that were reported by me (Kruijer, 1996a) as assumed to come frome Australia (*De Labillardière s.n.*, L, "N. Hollandia") and (*Menzies s.n.*, FH, "New Holland", mounted on a sheet with a specimen from "Macquairy River") revealed that they were misidentified and belong to *Hypopterygium didictyon*. A specimen in BM collected by Leichardt is labelled "Australia & New Zealand", and comes presumably from New Zealand.

A specimen in FH that is indicated to come from the "Philippine Islands" has been mislabelled. The text on its original label has been misinterpreted while the text was copied on a new label. The original text could not be deciphered, but it does not stand for "Philippine Islands" or one of the major islands in the Philippines or the Pacific Ocean.

Other — 7. Up to now, the species is undercollected in autumn, winter, and early spring. On North Island, only very few collections were gathered in the period from March up to and including September. On South Island, the period of undercollecting is shorter and covers the period from June up to and including September.

Selected specimens (from 441 ones examined):

NEW ZEALAND: *Stephenson 11* (BR, NY; s.loc.). – North Island. North Auckland L.D.: Waipoua Forest, *Allison 791* (WELT); Puketi State Forest, *Brownsey s.n.* (WELT); Ohaeawai, *Berggren 2021* (S, UPS); Little Barrier Is., *Molesworth 321* (WELT), *Petrie s.n.* (BM, CHR p.p., NSW), *Wormald 3b* (CHR). – South Auckland L.D.: Matamata, *Jardine & Sainsbury s.n.* (BM, BR, L, NY, UPS, W); Rotorua, Mt Nongataha, *Child 416* (BM, CHR), *Walker 4395* (S); Puaiti Bush, *Allison 2935* (CHR). – Gisborne L.D.: Toatoa, *Haskell s.n.* (CHR, sub no. *3587*, WELT); Lake Waikaremoana, Hopuruahine, *Sainsbury 8714* (NY, WELT). – Hawke's Bay L.D.: Morere, *Van Zanten 1416* (B, GRO, L, NICH, S, U, WELT); White Pine Bush, *Van Zanten 731269* (EGR, GRO, L, S, U); Mangapaieke, *Sainsbury 3594* (CHR, WELT); Wairoa, *Sainsbury s.n.* (FH, S); Dannevirke, *Colenso s.n.* (BM, WELT). – Taranaki L.D.: Mt Taranaki (Mt Egmont), *Gray 126* (BM); Stratford, *Martin 274.6* (CHR). – Wellington L.D.: Ohakune, *Mundy 24* (CHR), *s.n.* (WELT); Hutt Valley, *Brownsey s.n.* (WELT); Silver Creek, *Kirk s.n.* (CHR). – South Island. Nelson L.D.: Nelson, *Grant s.n.* (CHR); Oparara River, *Fife et al. 9439* (CHR); Reefton, *Ruinard 98.10.26.02/2* (L). – Marlborough L.D.: Pelorus Bridge Scenic Reserve, *Brownsey s.n.* (30.09.1983, WELT); Queen Charlotte Sound, Endeavour Inlet, *Brownlie 538* (CHR); Mt Fyffe, *Beckett s.n.* (CHR). – Westland L.D.: Barrytown, *Fife 4580* (NY); Kelly's Ra., above Jacksons, *Beckett 1013* (BM, CHR, FH, HBG, JE, NSW, S); Fox Glacier, *Lewinsky 2240* (CHR, L); Lake Matheson, *Prud'homme van Reine M 7a* (L); Lower Haast Valley, *Schofield 49018* (HIRO, U). – Canterbury L.D.: Waimate, *Beckett s.n.* (BM, JE, NICH, NY); Lyttleton, *Berggren 2008* (NY, S, UPS); Banks Peninsula, *Visch s.n.* (19.11.1972, L); Little River, *Berggren 2009* (UPS), *2024* (UPS). – Otago L.D.: Queenstown, *Fleischer B 8* (B, BR, GRO, NICH, L); Dunedin, Mt Cargill, *Petrie (38)* (CHR), *s.n.* (BM, "NSW"); Leith Valley, *Vitt 8537* (NY); Taieri mouth, *Allison 5846* (S), *Martin s.n.* (CHR). – Southland L.D.: Dusky Sound, Indian Is., *Brownsey s.n.* (WELT); Tuatapere Domain, *Martin 274.9* (CHR);

The Chaslands, *Visch s.n.* (FH, GRO, L, NICH, S). – Stewart Is.: Halfmoon Bay, *Martin 274.1* (CHR, 'Oban'), *Parsons s.n.* (CHR); Ringaringa, *Kirk s.n.* (WELT). – Auckland Is. Enderby Is.: *Fineran 1600* (CHR). Auckland Is.: *Lyall 56* (BM); North Harbour, *Macmillan 83/166* (CHR); Tandy Inlet, *Vitt 10102* (CHR).

DUBIOUS ORIGIN: *unknown collector (Vasey?) s.n.* (FH, "Philippine Islands"); *Leichardt s.n.* (BM, "Australia & New Zealand").

3. CATHAROMNION Hook.f. & Wilson — Map 6b

Catharomnion Hook.f. & Wilson in Hook.f., Bot. Antarct. Voy. 2(2) (1854, '1855') 119; from the Greek *καθαρος* (catharos, neat) and *μνιον* (mnion, sea grass; used by Dillenius, Hist. Musc. (1741) 229, for his new [pre-starting point] moss genus *Mnium*). — *Hypopterygium* sect. *Catharomnion* (Hook.f. & Wilson) Mitt., Trans. & Proc. Roy. Soc. Victoria 18 (1882) 76. Type: *Catharomnion ciliatum* (Hedw.) Wilson in Hook.f.

Plants usually forming dense, soft mats, less often forming looser mats or groups of fans, usually branched but occasionally simple when male, weakly glossy, yellowish-green to green or somewhat glaucous-green, not gemmiferous; ramification usually pinnate to flabellate, occasionally somewhat palmate. *Stems* usually differentiated into stipe and rachis, occasionally not differentiated in male plants. *Stipe* creeping, horizontal or ascending, straight or weakly curved near frond base, tomentose with brown rhizoids, dark brown to pale green. *Frond* ovate to elliptic, ± complanate; rachis and branches usually glabrous, occasionally creeping at base, straight or curved downwards, pale green, not caducous; rachis following direction of stipe or roughly so; branches distant or closely set, patent to widely patent; apex of foliate rachis and branches rounded. *Rudimentary branches* present (see note 2). *Stipe, rachis, and branches* terete. *Epidermis* ± similar in cellular structure to (outer) cortex. *Cortex* weakly (to distinctly) differentiated in stipe and basal part of frond axes, weakly differentiated or not in distal part of frond axes. *Central strand* present. *Axial cavities* present, located in cortex of stolon, stipe, rachis, and branches, and central in rudimentary branches (see note 2). *Axillary hairs* present or absent; basal cells colourless to brown; intermediate cells absent; terminal cell straight, colourless, smooth. *Phyllotaxis* tristichous. *Foliation*: of stipe complanate or not, isophyllous or anisophyllous; of frond complanate and anisophyllous, in dorsal view usually julaceous. *Leaves* when moist smooth or nearly so, when dry smooth to weakly crisped or twisted; *insertion* oblique to concave in lateral leaves, concave in amphigastria; base not decurrent to distinctly decurrent; margin dentate-ciliate; border distinct, often becoming faint or absent near leaf apex, usually continuous, less often interrupted; apex abruptly acuminate (or gradually acuminate in amphigastria); costa distinct, simple or somewhat forked in distal part; laminal cells prosenchymatous, short, hexagonal, walls thin or incrassate, porose; costa cells longer than adjacent laminal cells, elongate to linear, hexagonal to rhomboid, walls thin or incrassate, porose; border and acumen cells longer than adjacent laminal cells, elongate to linear, most frequently rhomboid, less often rectangular or hexagonal, walls incrassate, porose. *Stipe leaves* monomorphic or dimorphic, leaf-like, patent to widely patent; lateral ones symmetrical or asymmetrical, straight or curved downwards; amphigastria symmetrical, straight. *Frond leaves* dimorphic. *Lateral frond leaves* patent to widely patent, asymmetrical, short-ovate to ovate, curved downwards; costa reaching 2/3–4/5 of leaf length. *Frond amphigastria* widely patent, symmetrical, ovate, straight; basal part flat or smoothly curved; *costa* reaching 4/5 of amphigastrium length to percurrent.

Dioicous. Gametoecia in basal and middle part of rachis; in simple stems of male plants located in middle part to distributed over nearly entire stem. *Gametoecial leaves* concave, shouldered or not, ovate to elliptic; outer ones smaller than inner ones; margin ± entire (often dentate-ciliate in basal gametoecial leaf); border distinct or faint near leaf base, continuous but absent from alar cell groups in perichaetial leaves; apex abruptly acuminate or subulate; costa absent; laminal cells prosenchymatous or somewhat parenchymatous in basal half, elongate to shortly linear, hexagonal or rhomboid; border cells equally long or longer than adjacent laminal cells, oblong to linear, rectangular or nearly so; acumen cells elongate to linear, hexagonal; walls of gametoecial leaf cells thin or incrassate, thin in alar cells. *Paraphyses* present, filiform, simple, hyaline.

Sporophyte projecting above or lying in plane of frond. *Seta* horizontal to ascending, straight to curved, smooth or nearly so; base narrow. *Capsule* erect, straight or weakly curved (see note 3); orifice transverse or oblique. *Peristome* simple. *Exostome* absent. *Endostome* colourless to brown, not perforate, papillose at both faces; papillae low, simple; processes somewhat keeled to weakly caniculate; cilia absent. *Operculum* long-rostrate, brown; rostrum straight. *Calyptra* mitrate, entirely covering operculum, pale brown to brown, membranous, naked, smooth; apex dark brown, somewhat fleshy.

Monotypic.

Distribution — See below the species.

Habitat & Ecology — See below the species.

Notes:

Nomenclature — 1. Several authors, among them Paris (1904), Reimers (1953), and Frey & Schaepe (1989), spelled the name *Catharomnium*, an invalid, later orthographic variant for *Catharomnion*.

Description — 2. For the morphology, anatomy, and functions of the rudimentary branches (and their inclusions) see '*Canalohypopterygium*', note 3, p. 121.

3. The capsule points in the same direction as the seta or, when the seta is curved, as the top of the seta.

3.1. Catharomnion ciliatum (Hedw.) Wilson — Fig. 13–15; Map 8; Plate 2d

Catharomnion ciliatum (Hedw.) Wilson in Hook.f., Bot. Antarct. Voy. 2(2) (1854, '1855') 119. — *Pterigynandrum ciliatum* Hedw., Sp. Musc. Frond. (1801) 84, t. 17 f. 7–13. — *Pterogonium ciliatum* (Hedw.) Schwägr., Sp. Musc. Frond., Suppl. 1, 1 (1811) 108. — *Maschalocarpus ciliatus* (Hedw.) Spreng., Syst. Veg. 4, 1 (1827) 160, (Jan.). — *Hypopterygium ciliatum* (Hedw.) Brid., Bryol. Univ. 2 (1827) 710. (Nov.). — Type: "Insulae australes", (material absent from Hedwig's herbarium in G, elsewhere not found; see 'General typification problems', p. 24); lectotype: Hedwig, Sp. Musc. Frond. (1801) t. 17 f. 7–13; designated here.

Illustrations: Hedwig, Sp. Musc. Frond. (1801) t. 17 f. 7–13. — Brotherus in Engler & Prantl, Nat. Pflanzenfam. ed. 1 (1907) f. 705.; ed. 2 (1925) f. 627. — Noguchi, J. Hattori Bot. Lab. 6 (1951) 25, f. I-3–4, III-2. — Sainsbury, Roy. Soc. New Zeal. Bull. 5 (1955) pl. 67, f. 1. — Allison & Child, Mosses of New Zealand (1971) 122. — Frey & Schaepe, J. Hattori Bot. Lab. 66 (1989) 267, f. 7–10. — Beever et al., Mosses of New Zealand (1992) f. 70. — B. & N. Malcolm, Mosses and other Bryophytes (2000) 13, 15, 44, 84, 88, 147.

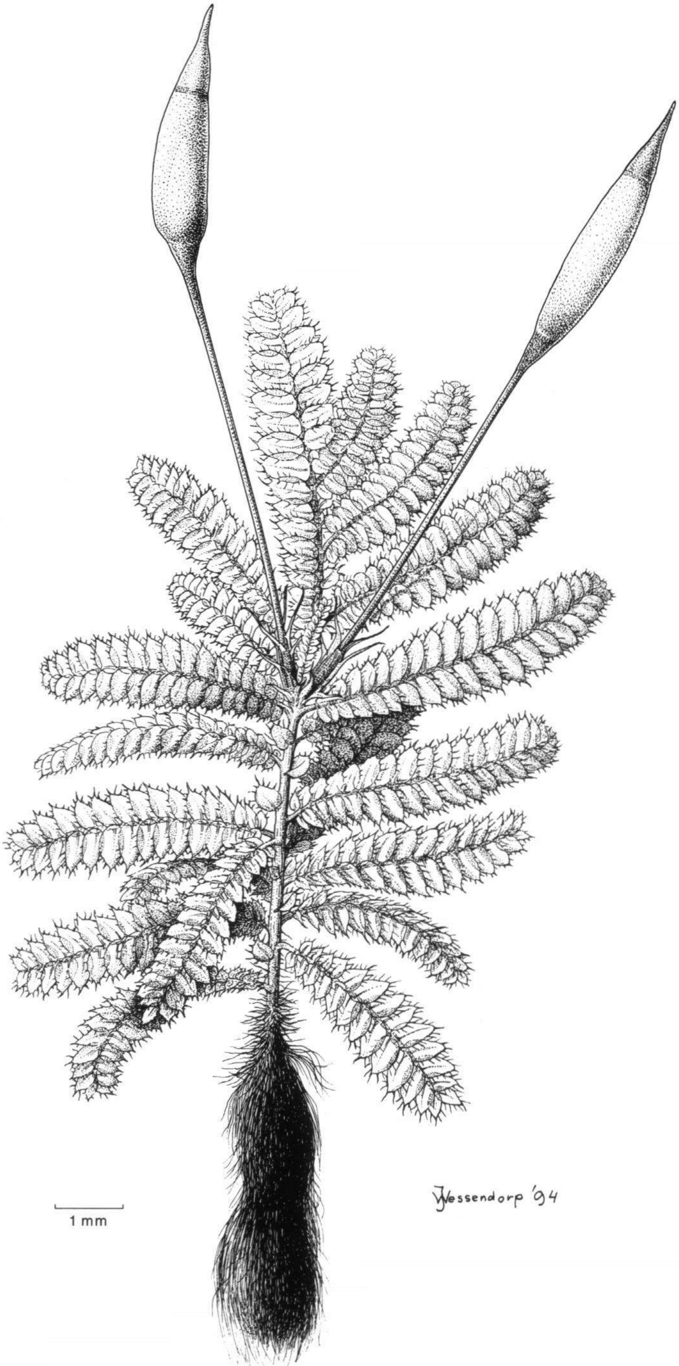
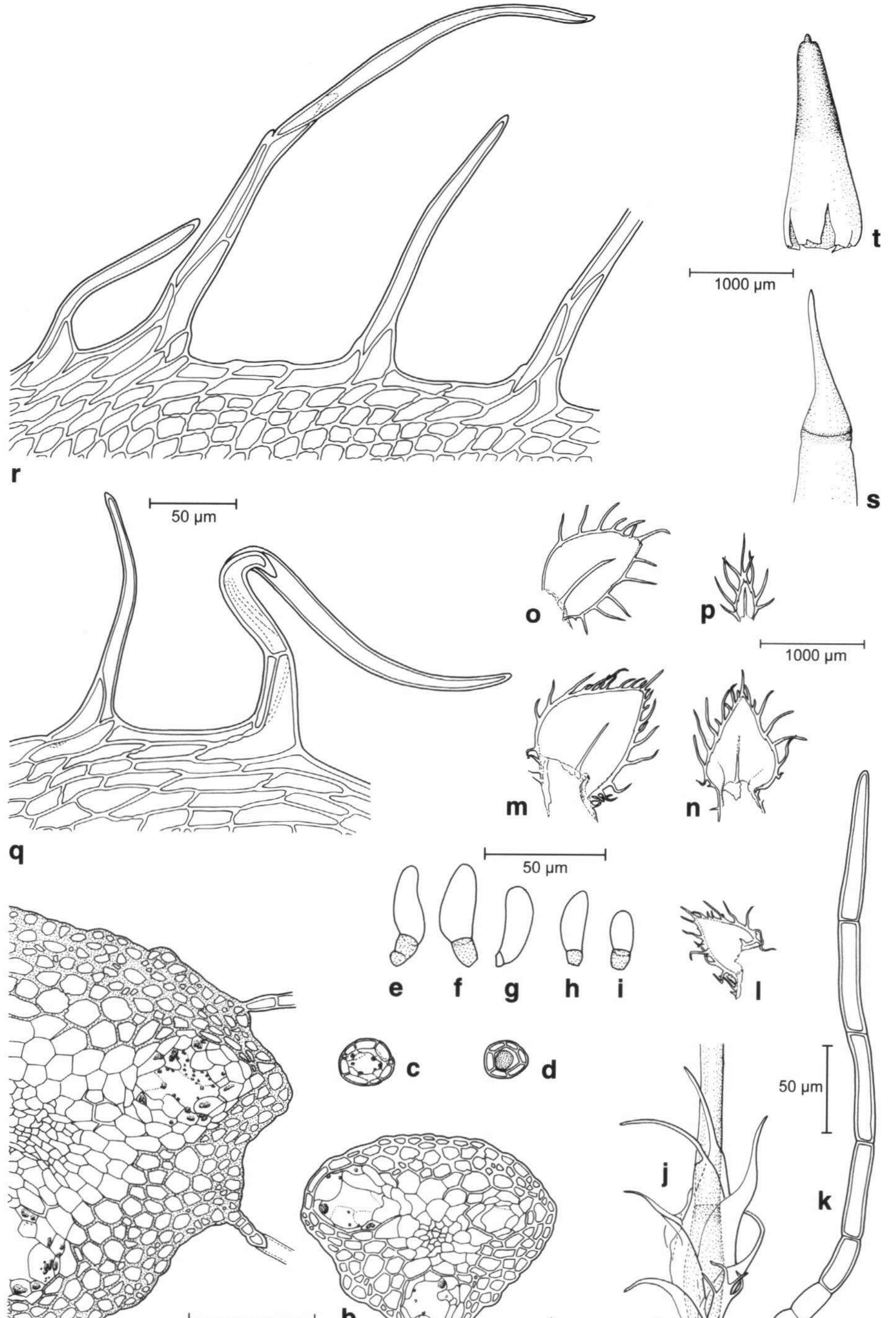


Fig. 13. ***Catharomnion ciliatum*** (Hedw.) Wilson. Habit female plant (dorsal view, ***Beever 70–26***, CBG).

Fig. 14. *Catharomnion ciliatum* (Hedw.) Wilson. Habit male plant (ventral view, *Beever 70–26*, CBG).

Plants small (to medium-sized), not gemmiferous. *Stipe* up to 1.5 cm long, laterally compressed. *Frond* ovate to elliptic, up to 1.0(–1.5) cm in diameter; rachis and branches dorsiventrally compressed; branches up to 0.7 cm long. *Rudimentary branches* usually between frond leaves, less frequently between stipe leaves, usually arranged in 2 lateral rows, less frequently in 3 rows with third row between amphigastria, up to 0.5 mm long, leafless but occasionally bearing scaly leaves at base; axial cavity single, central, connected with a cortical cavity in stipe, rachis, or branch. *Primordia* usually set with scaly leaves; scaly leaves short-filiform or narrowly triangular to elliptic, margin dentate-ciliate. *Epidermis and cortical cells of stipe, rachis, and branches* equally narrow or cortical cells wider; walls thin or incrassate, colourless, yellow, or pale brown; inclusions absent. *Central strand cells* very narrow; walls thin, colourless; inclusions absent. *Axial cavities* (1 or) 2 (or 3) per cross section in stipe, rachis, and branches, arranged in 2 lateral rows and a single ventral row, 1 per cross section in rudimentary branches; inclusions filling axial cavity for a considerable part, consisting of large oil-like droplets, colourless to pale yellow. *Axillary hairs* 0–4 per leaf, 2- or 3-celled; basal cells 1 or 2 in number; terminal cell short to elongate, ovate to elliptic or obovate, 15–35 μm long and (5–)7–15 μm wide, smooth, wall thin. *Leaves* distant to closely set, but usually closely set in frond, yellowish-green to green or somewhat glaucous-green, weakly glossy; laminal cells prosenchymatous, short, hexagonal, 20–30(–40) μm long and 10–15 μm wide; walls incrassate, porose. *Stipe leaves* not differentiated in basal and distal ones, dimorphic, patent to widely patent, short-ovate to ovate,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0.4–0.7 mm long and 0.4–0.8 mm wide; margin dentate-ciliate; apex abruptly acuminate; acumen 0.1–0.3 mm long; costa faint, reaching 2/3–4/5 of leaf length; lateral leaves and amphigastria equally large or amphigastria smaller, often similar to basal frond leaves when located in distal part of stipe; lateral leaves symmetrical or asymmetrical; amphigastria symmetrical. *Frond leaves* dimorphic, not caducous; margin coarsely dentate-ciliate; teeth 1–12-celled (up to 8-celled in amphigastria), up to 600 µm long, uniseriate or several cells wide at base, projecting up to 6 cells; border distinct, but often absent or faint near leaf apex, continuous or interrupted, (up to) 1–6 cells wide, narrowest near leaf apex, colourless; apex abruptly acuminate (or gradually acuminate in amphigastria); acumen 0.2–0.4 mm long in lateral leaves, 0.2–0.6 mm long in amphigastria. *Lateral frond leaves* asymmetrical, short-ovate to ovate, 0.7–1.2 mm long and 0.5–1.1 mm wide; costa distinct, reaching 2/3–4/5 of leaf length. *Frond amphigastria* symmetrical, ovate to oblong-ovate, 0.3–0.8 mm long and 0.1–0.6 mm wide; costa distinct, simple or forked, reaching 4/5 of amphigastrium length to percurrent.

Dioicous. *Gametoecial leaves* green in perichaetia, usually reddish-brown in basal part and green or colourless in distal half to third of leaf and occasionally entirely green in perigonia; alar cells absent or present in perichaetial leaves; margin ± entire (except for the basal gametoecial leaf, see note 2), border 1 or 2 cells wide, but absent from alar cell groups in perichaetial leaves. *Inner leaves*: of perigonia ovate to obovate, up to 0.8 mm long and 0.4 mm wide, acumen up to 0.6 mm long; of perichaetia prior to sporophyte development ovate to elliptic, up to 1.0 mm long and 0.7 mm wide; acumen up to 0.8 mm long; of full-grown perichaetia ovate to elliptic, up to 1.3 mm long and 0.8 mm wide, *acumen* up to 0.5 mm long. *Antheridia* up to 0.4 mm long. *Stalk in full-grown perichaetia* 0.2–0.3 mm long, glabrous. *Archegonia* 0.4 mm long. *Vaginula* 0.7 mm long. *Gametoecial axillary hairs* c. 1 per gametoecial leaf, 2–4-celled, simple; basal cells 1–3, brown; intermediate cells absent; terminal cell elongate to short-linear, narrowly ovate to narrowly elliptic, 65–85 µm long and 10–12 µm wide, smooth, colourless. *Paraphyses* absent or few, most frequently found in perigonia, 7–10 cells long, colourless or brown; basal cell 1; intermediate cells elongate to short-linear, rectangular; terminal cell short-linear, rectangular.

Sporophytes up to 3 per frond. *Seta* horizontal to ascending, straight to curved, 5.0–9.0 mm long, brown. *Capsule* erect, straight or weakly curved, ovoid to ovoid-oblong, 0.7–2.2 mm long and 0.3–0.8 mm wide, ochraceous or whitish brown to brown, occasionally tinged with red, smooth but somewhat plicate beneath orifice or not; neck weakly pustulose or not; annulus indistinct. *Peristomial formula OPL:PPL:IPL* = [4:]2:4c. *Exostome* absent (see note 3). *Endostome* not perforate, coarsely papillose at both faces; papillae low, simple; basal membrane projecting 80 µm beyond orifice;

Fig. 15. *Catharomnion ciliatum* (Hedw.) Wilson. a. Rachis (cross section lateral half with two cavities); b. branch (cross section with three cavities); c, d. rudimentary branches with central cavity (cross section: c. 'epithelium cells' intact, d. 'epithelium cells' degenerating); e–i. axillary hairs; j. perichaetium; k. paraphyse; l. stipe leaf; m, n. rachis leaves (m. lateral, n. amphigastrium); o, p. branch leaves (o. lateral, p. amphigastrium); q, r. leaf cells of lateral frond leaves: q. rachis leaf (basal part of antical side), r. branch leaf (distal part of antical side); s. operculum; t. calyptra (a–j, l–t: *Beever 70–26*, CBG, L; e–i: *Van Zanten 7401243*, L).

Map 8. Distribution of *Catharomnion ciliatum* (Hedw.) Wilson.

processes projecting 380 µm beyond orifice and 55–60 µm wide at base, not nodulose, not appendiculate; cilia absent. *Operculum*1.3–1.4 mm long. *Calyptra* 1.9 mm long, membranous but somewhat fleshy near apex; margin lobed, usually with distinct lobes, occasionally provided with a few incisions of irregular depth, resulting in indistinct, broad and short, truncate lobes. *Spores* 12–17 µm.

Distribution — New Zealand (North Island, South Island, Chatham Is.); see notes 5 and 6.

Habitat & Ecology — In forests, frequently in shaded places. Predominantly epiphytic and most frequently on tree ferns; less often on tree trunks and palms. Also occasionally on soil, rocks, litter, and rotting wood, especially in wet or damp places. Altitude 0–500 m. On tree ferns frequently associated with *Hymenodon pilifer* Hook.f. & Wilson.

According to Beever (1984) most frequently found on the tree fern species *Sphaeropteris medullaris* (G. Forst.) Bernh. (≡ *Cyathea medullaris* (G. Forst.) Sw.). Also epiphytic on the trunks of the tree ferns *Alsophila smithii* (Hook.f.) R.M. Tryon (≡ *C. smithii* Hook.f.), *A. cunninghamii* (Hook.f.) R.M. Tryon (≡ *C. cunninghamii* Hook.f.) and rarely on *Dicksonia squarrosa* (G. Forst.) Sw. The species occurs also on trunks of trees and palms, including *Leptospermum scoparium* J.R. Forst. & G. Forst., *Pseudopanax arboreus* (Murray) Philipson, and *Rhopalostylis sapida* H. Wendl. & Drude.

In the material examined, the type of rock has been reported for only a single collection, which was found on limestone (*Gray (58)*). Beever (1990) reported a plant that was growing on limestone and adjacent soil and humus. When growing on rock, the species occurs on shaded vertical rock faces, including both greywacke and limestone (Fife, pers. comm.).

Geographical variation — Not found.

Ecological variation — Epiphytic plants of *Catharomnion ciliatum* grow generally in compact groups of fans or mats. The plants are strongly and closely branched, which results in a dense frond with many branches. When growing on rocks or soil, the plants grow in looser groups and show a more open branching pattern, having distant branches.

On tree ferns, patches nearly entirely composed of fans of this species may cover the exposed side of the caudices up to over a length of over 1 m (Klazenga, pers. comm.). Nearly pure mats may cover over 1 by 0.5 m^2 on limestone (Fife, pers. comm.).

Chloroplast DNA sequences — *trnL*$_{\mathrm{UAA}}$ intron, 274 bp, deposited in GenBank database under accession number AF134633, see Stech et al. (1999: 361). — Voucher: *Van Zanten 7401243* (B), New Zealand, North Island, North Auckland L.D., N.W. of Dargaville; wrongly cited '7407243' by Pfeiffer et al. (2000: 57).

Notes:

Synonymy — 1. Probably based on a similarity in leaf dentation, *Pterogonium ciliatum* (Hedw.) Schwägr. was erroneously given in the synonymy of *Hookeria tamariscina* (Hedw.) Sm. (as *H. tamarisci* (Hedw.) Sm. ex Arn., nom. illeg. ≡ *Canalohypopterygium tamariscinum* (Hedw.) Kruijer) by Arnott (1825, 1826).

Description — 2. The basal leaf of the gametoecia is often different from the other gametoecial leaves in leaf dentation. The margin of the basal gametoecial leaf is often dentate-ciliate, whereas it is always entire in the distal gametoecial leaves.

It is almost certain, that the basal gametoecial leaf is actually an outgrown scaly leaf. The basal gametoecial leaf is situated at the abaxial side of the gametoecia, by which it has a similar position as the basal leaf of the branches (cf. cataphyll α, sensu Berthier, 1972). The similarity between the basal leaves of gametoecia and those of the branches is sometimes striking. The basal leaf of the gametoecia is occasionally distinctly dentate-ciliate and very small, by which it is in shape and leaf dentation hardly different from the basal leaves of some branches.

3. *Catharomnion ciliatum* is the only species in the Hypopterygiaceae that has no exostome. The OPL cells and the outer portion of the PPL cells remain attached to the operculum. However, exostomial development is not entirely absent in the ontogeny of the sporophyte. The inner tangential cell walls of the OPL cells near the orifice, which are homologous with the dorsal plates of exostome teeth, are ornamented with very few to numerous small papillae. The outer tangential cell walls of the PPL cells, which are connected with the inner ones of the OPL cells, are very weakly to moderately papillose, and might also be somewhat incrassate. Furthermore, trabeculae, i.e. parts of transverse cell walls of the PPL cells, can frequently be observed at the inside of the operculum, where they are attached to the outer tangential walls of the PPL cells. Because of this very weak exostomial development, the exostome of *C. ciliatum* is considered strongly reduced.

Reproduction — 4. There were 100 fruiting specimens among the specimens examined (c. 52%, n = 194). The fruiting specimens came in majority from North Island, where c. 53% of the specimens were found in fruit (and where most collections were made, n = 118). The production of sporophytes is probably less frequent on South Island and the Chatham Is., where, respectively, c. 32% (n = 22) and c. 29% (n = 7) of the specimens where found in fruit, but these figures are probably biased by under collecting.

In a representative sample of 83 specimens, 47 (57%) contained fruiting material. The non-fruiting material consist of 9 female plants (11%), 17 male plants (20%), and 10 sterile plants (12%), which were often small. Approximately half of the collections with fruiting material contained mixed collections, in which both male and female plants occur intermingled. In total, 56 specimens were female (58%, including the female plants from 23 mixed collections) and 40 specimens were male (42%, including the male plants from the 23 mixed collections).

Distribution — 5. Sainsbury (1955) and Beever et al. (1992) reported *Catharomnion ciliatum* as being distributed throughout New Zealand, but this is not completely true. The species is more or less a warm-temperate species that occurs throughout North Island, but on South Island it is almost restricted in its distribution to the mountain ranges of the western and the northwestern part.

The species is most abundant on North Island and the northwestern part of South Island – with the exception of northern Nelson, which might be due to undercollecting.

In the southern half of South Island, south of the line Hokitika–Kaikoura, the species is rare and has, so far, not been recorded from southeastern Marlborough, Canterbury, and eastern Otago. The species reaches as far south as central Fiordland National Park, in W Southland (Beever, 1990).

6. *Catharomnion ciliatum* is almost certainly endemic for New Zealand and the Chatham Islands. Among the examined collections only five were indicated to come from either Australia or Tasmania. Two of them were labelled 'Australia', nonetheless their origin is questionable, as neither collectors nor collecting localities are known. The remaining three were reported to be gathered by Gunn on Tasmania ("V.D.L^{d}.").

The first Tasmanian record of *Catharomnion ciliatum* was made by Wilson (1860) based on this material gathered by Gunn. Several other authors (e.g. Mitten, 1882; Bastow, 1887; Dixon, 1927; Sainsbury, 1955; Streimann & Curnow, 1989) reported *C. ciliatum* from Tasmania as well, but they probably based their records either on Wilson's record or directly on the material gathered by Gunn. However, according to Rodway (1913), followed by Sainsbury (1956), the occurence of *C. ciliatum* on Tasmania is doubtful. Dalton et al. (1991) reviewed the reports of Tasmanian records, and rejected this species from the Tasmanian moss flora.

In addition, there was no other Tasmanian plant among the collections examined, and it is very doubtful whether Gunn's collections themselves actually came from Tasmania. According to Touw (1971) there is similar doubt on the origin of Gunn's Tasmanian collections of *Hypnodendron colensoi* (Hook.f. & Wilson) Mitt. and *Hypnodendron menziesii* (W. Hook.) Paris subsp. *menziesii*, both probably endemic for New Zealand. Therefore, there is little likelihood that *Catharomnion ciliatum* actually occurs on Tasmania. Gunn's collections are almost certainly mislabelled and probably came from New Zealand.

Hampe (1880) recorded the species for continental Australia based on collections made by F. von Mueller. However, such collections were not found among the material examined. Furthermore, there were no other collections that with any certainty originated from Australia, and there is little likelihood that *Catharomnion ciliatum* actually occurs there.

Selected specimens (from 194 specimens examined):

NEW ZEALAND: North Island. North Auckland L.D.: NW of Dargaville, *Van Zanten 7401243* (B, L, NICH); Bay of Islands, *Kerr s.n.* (BM, NY); Waitakeri Ra., *Van Zanten 93.09.905* (GRO); Auckland, *Knight s.n.* (B); Rangitoto Is., *Robbins s.n.* (L). – South Auckland L.D.: Dunphail, *Petrie s.n.* (WELT); Coromandel, Tararu, *Van Zanten 93.09.947* (GRO); Tauranga, *Berggren 2045* (S); Rotorua, *Allison 158* (WELT); Motuhora ('Whale') Is., *Brownsey s.n.* (WELT); Mt Pirongia, *Sainsbury s.n.* (FH, NY). – Gisborne L.D.: Gisborne, *Colenso? 2948* (WELT). – Hawke's Bay L.D.: Puketitiri, *West s.n.* (WELT). – Taranaki L.D.: Mt Taranaki (Mt Egmont), *Fleischer B 84* (B, BR, L, NICH, NY), *B 185* (B). – Wellington L.D.: Ohakune, *Mundy s.n.* (WELT); Kapiti Is., *McKenzie s.n.* (WELT); Mauriceville, *Gray (58)* (BM); Wellington, *Berggren 2043* (NY, S, UPS). – South Island. Nelson L.D.: Hira State Forest, *Beever 70–26* (CBG), *Streimann, MAE 262* (L). – Marlborough L.D.: Picton, *McMahon s.n.* (WELT). – Westland L.D.: Paparoa Coast, Fox River, *Fife 4571* (NY); Punakaiki area, Bullock Creek, *Fife 4744* (NY). – Otago L.D.: Beans Burn, *Child 3442* (BM). – Chatham Is.: *Travers s.n.* (WELT), *s.n.* (BM); Te Awainanga River, *Hamlin 1975* (WELT).

DUBIOUS ORIGIN: *Gunn s.n.* (BM; "V.D.L^{d}." = Van Diemens Land); *Leichardt s.n.* (BM, 'Australia & New Zealand'); *unknown collector s.n.* (JE, MEL; 'Australia').

4. HYPOPTERYGIUM Brid. — Map 9

Hypopterygium Brid., Bryol. Univ. 2 (1827) 709; from the Greek *υπο* (hypo-, under) and *πτερυγιον* (pterygion, a little wing). *Hypopterygium* Brid. sect. *Euhypopterygium* Müll.Hal., Syn. Musc. Frond. 2 (1850) 3, nom. illeg. (*Hypopterygium* Brid. sect. *Hypopterygium*). — *Hypopterygium* Brid. subgen. *Euhypopterygium* Bosch & Sande Lac., Bryol. Jav. 2 (1861) 10, nom. illeg. (*Hypopterygium* Brid. subgen. *Hypopterygium*); according to Van der Wijk et al., Regnum Veg. 33 (1964) 178, based on *Hypopterygium* Brid. sect. *Euhypopterygium* Müll.Hal. — Lectotype:

Hypopterygium laricinum (W. Hook) Brid. (= *Hypopterygium tamarisci* (Sw.) Brid. ex Müll.Hal.); syntype: *H. rotulatum* (Hedw.) Brid. (doubtful species). — New lectotype proposed here. — See notes 1, 2 and 3.

Hookeria sect.? *Dendroideae* Arn., Disposition Méth. Espèc. Mousses (preprint) (1825 [= 1826?]) 56; Mém. Soc. Hist. Nat. Paris 2, 2 (1826) 305; rank not indicated. — Lectotype: *Hookeria laricina* (W. Hook.) W. Hook. & Grev. (= *Hypopterygium tamarisci* (Sw.) Brid. ex Müll.Hal.); syntypes: *Hookeria arbuscula* Arn. non Sm. (≡ *Hypopterygium tamarisci* (Sw.) Brid. ex Müll. Hal.), and provisionally the doubtful species: *Hookeria rotulata* (Hedw.) Sm., and *Hookeria jungermannoides* (Brid.) Steud. — Lectotype designated here. — See note 4.

Hypopterygium Brid. sect. *Lopidioidea* Kindb., Hedwigia 40 (1901) 284; sect. *Lopidioideum* (Kindb.) M. Fleisch., Musc. Buitenzorg 3 (1908) 1080, hom. illeg. — Lectotype: *Hypopterygium vriesei* Bosch & Sande Lac.; syntype: *Hypopterygium philippinense* Hampe ex Kindb. (≡ *Hypopterygium micholitzii* Paris = *Hypopterygium vriesei* Bosch. & Sande Lac.); designated here.

Hypopterygium Brid. sect. *Aristifolia* Kindb., Hedwigia 40 (1901) 285. — *Hypopterygium* Brid. subsect. *Aristifolia* (Kindb.) M. Fleisch., Musc. Buitenzorg 3 (1908) 1080. — Lectotype: *Hypopterygium aristatum* Bosch & Sande Lac. (= *Hypopterygium flavolimbatum* Müll.Hal.); other syntypes: *Hypopterygium fauriei* Besch. (= *Hypopterygium flavolimbatum* Müll.Hal.), *Hypopterygium tibetanum* Mitt. (= *Hypopterygium flavolimbatum* Müll.Hal.), *Hypopterygium apiculatum* Thwaites & Mitt. (= *Hypopterygium flavolimbatum* Müll.Hal.). — Lectotype designated here. — See note 5.

Hypopterygium Brid. sect. *Pseudo-tamariscina* Kindb., Hedwigia 40 (1901) 285, '*Pseudo-Tamariscina*'. — *Hypopterygium* Brid. subsect. *Pseudo-tamariscina* (Kindb.) M. Fleisch., Musc. Buitenzorg 3 (1908) 1080, '*Pseudo-Tamariscina*'. — Type: *Hypopterygium tasmanicum* Kindb. (= *H. didictyon* Müll.Hal.).

Hypopterygium Brid. subgen. *Euhypopterygium* Kindb., Hedwigia 40 (1901) 284, nom. illeg., incl. type of *Hypopterygium* Brid. — *Hypopterygium* Brid. sect. *Euhypopterygium* (Kindb.) M. Fleisch., Musc. Buitenzorg 3 (1908) 1080, nom. illeg., incl. type of *Hypopterygium* Brid.

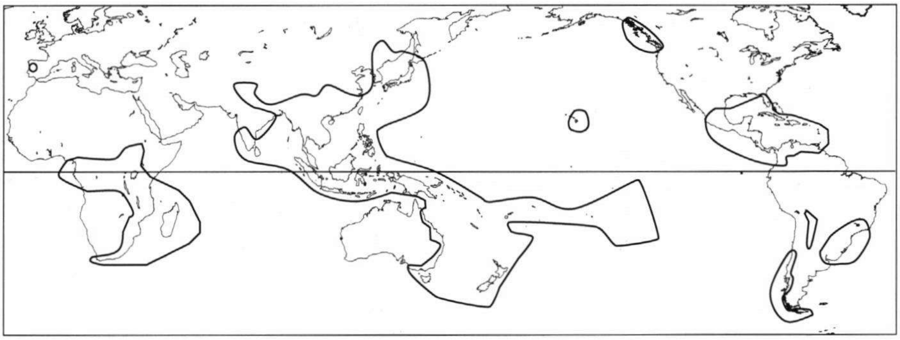
Hypopterygium Brid. sect. *Tamariscina* Kindb., Hedwigia 40 (1901) 287, nom. illeg., incl. type of *Hypopterygium* Brid. — *Hypopterygium* Brid. subsect. *Tamariscina* (Kindb.) M. Fleisch., Musc. Buitenzorg 3 (1908) 1083, nom. illeg., incl. type of *Hypopterygium* Brid.

Note:

The names of Kindberg's (1901) subsections in *Hypopterygium* Brid. sect. *Tamariscina* Kind. are not in accordance with the nomenclatural rules. Taxonomically, Kindberg's sections and subsections represent a highly artificial classification, whereby species and subspecies, which in the present study are considered to be closely related or even conspecific, were frequently classified by Kindberg in different (sub)sections.

Plants forming loose to dense groups of dendroids or fans, usually branched, rarely simple, dull or weakly shiny, dark green to yellowish green, often glaucous green, or greyish green in *H. didictyon* and *H. flavolimbatum* (see note 6), gemmiferous or not gemmiferous; ramification pinnate to bipinnate (or tripinnate), flabellate, palmate, or umbellate, two- or three-dimensional. *Stems* differentiated into stipe and rachis, vertical or ascending from substratum, becoming horizontal when changing into rachis. *Stipe* straight, but curved at base and in dendroid plants also curved near frond base, tomentose at base, glabrous or partly to entirely tomentose in distal part, dark brown to pale green, usually most saturated in colour in basal part. *Frond* horizontal, subcircular, triangular, or transverse-(ob)ovate to lanceolate, ± complanate; rachis and branches occasionally with flagelliform innovations, straight, flexuose, or curved downwards, brown to pale green (usually brown or green at frond base, becoming green to pale green in distal part of frond), partially caducous in middle or distal part or not; rachis erect to roughly at right angle with stipe, glabrous or tomentose at base; branches distant or closely set, erecto-patent to widely patent or recurved, usually glabrous, rarely tomentose at base, straight or curved downwards; apex of foliate rachis and branches usually rounded, occasionally attenuate or caudate by a flagelliform innovation (see note 7). *Rudimentary branches* absent. *Stipe, rachis, and branches* terete. *Epidermis* ± similar in cellular structure to (outer) cortex. *Cortex* weakly to distinctly differentiated in stipe and basal part of frond axes, becoming less or not differentiated in distal part of frond axes. *Central strand* present (but absent where replaced by a central axial cavity in *H. vriesei*, and *H. sandwicense*). *Axial cavities* absent (or central in distal part of frond axes in *H. vriesei* and *H. sandwicense*). *Axillary hairs* present; basal cells pale brown to brown; intermediate cells absent; terminal cell straight (or weakly curved in *H. elatum*), colourless, smooth, verrucose, or covered with white substances. *Phyllotaxis*: of stipe entirely octostichous, entirely tristichous, or with various other leaf arrangements close to tristichous (4/11, 7/18, or 8/21) in the basal part and tristichous upwards; of rachis and lower branches entirely tristichous or octostichous in basal and middle part and becoming tristichous in distal part; of distal branches entirely tristichous. *Foliation*: of stipe complanate or not, isophyllous or anisophyllous; of frond axes not complanate and ± isophyllous in parts with octostichous phyllotaxis, complanate and anisophyllous in parts with tristichous phyllotaxis. *Leaves* when moist smooth (or weakly crisped), when dry weakly to strongly crisped or twisted; insertion transverse, transverse-flexuose, oblique, or concave; base not or weakly decurrent; margin entire or serrate-dentate, (or serrate in *H. flavolimbatum* and *H. sandwicense*, bitten or crenulate in stipe leaves of *H. elatum*); border absent, faint and interrupted, or distinct and continuous in stipe leaves, usually distinct and continuous in frond leaves; apex acute, gradually acuminate, or abruptly acuminate in stipe leaves (rounded or emarginate in stipe leaves of *H. elatum*), gradually or abruptly acuminate in frond leaves; costa usually distinct, less often faint or absent in stipe leaves, basal frond leaves, or amphigastria, simple or somewhat forked in distal part; laminal cells prosenchymatous (or partly parenchymatous in *H. didictyon* and *H. discolor*), short to short-linear, hexagonal (or rectangular in *H. didictyon* in leaf parts with a parenchymatous areolation), walls thin or incrassate, porose (or not); border and acumen cells longer than adjacent laminal cells, rectangular, rhomboid, or hexagonal, short to linear, often with a rectangular or rhomboid outline near leaf margin and a hexagonal outline in acumen, walls incrassate, porose. *Stipe leaves* monomorphic or dimorphic, scale- or leaf-like, appressed to squarrose-recurved. *Frond leaves* dimorphic or monomorphic when situated in basal frond parts with octostichous phyllotaxis, straight or curved downwards. *Lateral frond leaves* patent to widely patent, asymmetrical (symmetrical in basal frond parts with octostichous phyllotaxis), broad-ovate to oblong; costa reaching (1/4–)1/2–4/5 of leaf length (to percurrent). *Frond amphigastria* symmetrical, erecto-patent to patent, broad-ovate, subcircular, (ob)ovate, or elliptic to oblong; base not or weakly decurrent; basal part of lamina nearly plane or smoothly curved; costa reaching 1/4 of amphigastrium length to excurrent.

Monoicous or *dioicous*. *Gametoecia* on frond axes, usually in basal and middle part of rachis, less often in basal and middle part of lower branches, usually between lateral or dorsal leaves, rarely between amphigastria. *Gametoecial leaves* concave, shouldered or not, subcircular or ovate to oblong, obovate, or somewhat lingulate;



Map 9. Distribution of *Hypopterygium* Brid.

outer ones usually smaller than (but occasionally equally wide as) inner ones, central ones occasionally very narrow in immature gametoecia; margin ± entire (or weakly crenate in *H. elatum*); border faint to distinct, continuous, interrupted or partly absent, up to 1 or 2 cells wide; apex acuminate or subulate; costa absent, obsolete, faint, or distinct, simple or somewhat forked in distal part, in traces or of various length from 1/5 of leaf length to percurrent; laminal cells entirely prosenchymatous or weakly parenchymatous in basal third or central part of leaf, oblong to short-linear, rectangular when situated in parenchymatous leaf parts, rhomboid to hexagonal when situated in prosenchymatous leaf parts; border cells shorter or longer, short to linear, rhomboid to rectangular; acumen cells oblong to short-linear, hexagonal to rhomboid; walls of gametoecial leaf cells thin or incrassate. *Gametoecial axillary hairs* present; basal cells pale brown to brown; intermediate cells absent or present, colourless; terminal cell straight or weakly curved, colourless, smooth. *Paraphyses* absent or present, filiform, simple, hyaline.

Sporophyte projecting above frond (see note 8). *Seta* (horizontal to) ascending to vertical, usually uncinate, occasionally weakly curved or flexuose, smooth (or weakly mamillose near capsule base in *H. elatum*); base narrow. *Capsule* cernuous to pendulous, subglobose, ovoid, ellipsoid, barrel-shaped, urceolate, or cupulate, smooth (or weakly mamillose in *H. elatum* and *H. flavolimbatum*); orifice transverse. *Peristome* double. *Exostome* present, pale yellow to (reddish) brown; teeth bordered or not, shouldered or not; dorsal side striate in basal half of teeth, becoming papillose in distal part; median line zig-zag, not furrowed; lamellae projecting or partly not projecting; papillae low, simple; striae minutely papillose; dorsal plates broader than or equally wide as ventral ones; ventral plates papillose; trabeculae short in basal third to half of teeth, becoming very pronounced in distal part (short to pronounced in *H. elatum*), becoming very short towards apex, papillose. *Endostome* colourless or pale yellow, perforate or not, papillose at both faces or partly smooth; papillae low, simple; processes distinctly keeled; cilia present. *Operculum* usually long-rostrate (occasionally short-rostrate in *H. tamarisci*), ochraceous to brown, often becoming pale near apex; rostrum oblique. *Calyptra* cucullate (occasionally mitrate to cucullate in *H. flavolimbatum*), entirely covering operculum (or nearly so in *H. flavolimbatum*; partly or entirely covering operculum in *H. tamarisci*), usually colourless, white, or ochraceous, rarely pale green, entirely membranous or fleshy in distal half to third, naked, smooth; apex dark brown or brown, ± fleshy.

A genus of 7 species.

Distribution — Subsaharan Africa, Indo Malaysia, Sino Japan, E Australasia, SW, S, and C Polynesia, NW coast of North America, South and Central America.

Habitat & Ecology — In open to dense (rain) forests, less often in open or scrub woodland, usually near streams or in humid habitats, frequently shaded, occasionally exposed. Substratum and altitude: various, see under the species.

Notes:

Nomenclature and classification — 1. Matteri (1976: 189) proposed *Hypopterygium rotulatum* (Hedw.) Brid. as the lectotype of *Hypopterygium* Brid. She was not aware that *H. rotulatum* is a dubious species and may be conspecific with either *H. didictyon* or *H. tamarisci* (see 'Doubtful Hypopterygium species', p. 249). This uncertainty increases the confusion on the true identity of *Hypopterygium* in the future. Hence, *H. rotulatum* is not a suitable lectotype.

Matteri (1976) rejected *Hypopterygium laricinum* as a suitable lectotype, because it was originally based on specimens from South Africa and South America. However, *H. laricinum* has, since long, been firmly attached to the South African material, and lectotypification by Pfeiffer et al. (2000) has overcome this problem. There is no objection to select *H. laricinum* as the lectotype of *Hypopterygium.*

2. *Hypopterygium* was originally proposed for 9 species (Bridel, 1827). The following species are excluded and have been transferred to other genera: *Hypopterygium ciliatum* (Hedw.) Brid. (≡ *Catharomnion ciliatum* (Hedw.) Wilson), *H. concinnum* (W. Hook.) Brid. (≡ *Lopidium concinnum* (W. Hook.) Wilson), *H. filiculiforme* (Hedw.) Brid. (≡ *Dendrohypopterygium filiculiforme* (Hedw.) Kruijer); *H. tamariscinum* (Hedw. ["Swartz. Hedw."]) Brid. (≡ *Canalohypopterygium tamariscinum* (Hedw.) Kruijer), *H. struthiopteris* (Brid. ["Comm."]) Brid. (≡ *Lopidium struthiopteris* (Brid.) M. Fleisch.), and *H. penniforme* (Thunb. ex Brid.) Brid. (= *Lopidium struthiopteris* (Brid.) M. Fleisch.).

3. Bridel (1827) referred to an illustration of *Hypopterygium* (as "*Pterygophyllum*") in his 't. 7', but this reference is incorrect; the plate contains illustrations of sporophytes of other mosses. In fact, Bridel did not depict a sporophyte of *Hypopterygium* at all – neither in 't. 10' under the name of "*Pterygophyllum*" nor in his other plates.

4. *Hookeria* sect.? *Dendroideae* accommodated 8 species (Arnott, 1825, 1826). The following species do not belong here, because they have been transferred to other genera: *Hookeria tamarisci* (Hedw.) Sm. ex Arn. (≡ *Canalohypopterygium tamariscinum* (Hedw.) Kruijer), *Hookeria filiculiformis* (Hedw.) Sm. (≡ *Dendrohypopterygium filiculiforme* (Hedw.) Kruijer), *Hookeria concinna* (W. Hook.) W. Hook. & Grev. (≡ *Lopidium concinnum* (W. Hook.) Wilson), and *Hookeria struthiopteris* (Brid.) Arn. (≡ *Lopidium struthiopteris* (Brid.) M. Fleisch.).

5. *Hypopterygium levieri* Broth. ex Kindb. (= *Hypopterygium tamarisci* (Sw.) Brid. ex Müll.Hal.) is excluded from *Hypopterygium* sect. *Aristifolia.*

Description — 6. The glaucous or greyish and dull colours of the plants are caused by the cuticle or wax-like surface layer that covers the leaves and amphigastria (see 'Morphology', 'Cuticle', p. 42).

7. In species with caducous frond leaves and partially caducous ultimate frond axes, the apex of the remaining part of the foliate frond axes becomes truncate after its distal leaves or distal part has become detached.

8. The sporophyte of *Hypopterygium vriesei* is unknown.

KEY TO THE SPECIES

1a. Frond leaves loosely attached and frequently caducous over the entire length of the (distal half of) rachis and branches; margin entire, weakly crenulate, or weakly serrate . . . . **4.4. H. flavolimbatum** ('East Malesian' variant)

b. Frond leaves principally firmly attached and persistent, partly caducous when situated at the apices of the rachis or ultimate branches or not caducous; margin entire, serrate, or serrate-dentate, but not crenulate 2

2a. Dorsal frond leaves present in the basal part of the frond. Stipe and basal frond leaves situated in eight ranks 3

b. Dorsal frond leaves absent. Stipe and basal frond leaves situated in three ranks or number of ranks difficult to observe (usually eleven or more) 6

3a. Laminal leaf cells parenchymatous to prosenchymatous, rectangular or hexagonal. Terminal cell of axillary hairs predominately short-linear to linear, smooth or covered with white substances (visible as white dots with hand lens or stereomicroscope). Plant palmate or umbellate .... **4.1. H. didictyon**

b. Laminal leaf cells prosenchymatous, always hexagonal. Terminal cell of axillary hairs short to elongate, never short-linear or linear, ± smooth (only visible with light microscope). Plant pinnate, flabellate, or palmate 4

4a. Axial cavities central in the distal part of the rachis and the branches. Capsule shorter than 2.0 mm .... **4.7. H. sandwicense**

b. Axial cavities absent. Capsule longer than 2.0 mm 5

5a. Plant gemmiferous or not. Apex of stipe leaves abruptly acuminate. Stipe usually not compressed, occasionally dorsiventrally compressed, tomentose in the basal fourth at least. Monoicous or dioicous .... **4.4. H. flavolimbatum**

b. Plant not gemmiferous. Apex of stipe leaves rounded or emarginate. Stipe dorsiventrally compressed, tomentose at the base at most. Dioicous(?) .... **4.2. H. elatum**

6a. Gametoecia bisexual or both male and female gametoecia present on the same shoot .... **4.6. H. tamarisci**

b. All gametoecia on a shoot belonging to the same gender or gametoecia absent 7

7a. Plant usually gemmiferous (examine several gametophores). Stipe entirely laterally compressed or dorsiventrally compressed in the basal part. Axial cavities central in the distal part of rachis and branches. Frond leaves pronouncedly serrate-dentate; teeth frequently much longer than 40 μm .... **4.5. H. vriesei**

b. Plant not gemmiferous (or rarely gemmiferous when damaged). Stipe entirely dorsiventrally compressed or laterally compressed in the basal part. Axial cavities absent. Frond leaves entire, serrate, or serrate-dentate; teeth shorter than 40 μm 8

8a. Plant usually distinctly palmate to umbellate, rarely flabellate, never (tri)pinnate. Distal frond leaves coarsely serrate-dentate; teeth usually more than 20 in number; border green .... **4.3. H. discolor**

b. Plant (bi- or tri-)pinnate to palmate or umbellate. Distal frond leaves entire or weakly serrate to coarsely serrate-dentate; teeth usually less than 20 in number; border colourless .... **4.6. H. tamarisci**

4.1. Hypopterygium didictyon Müll.Hal. — Fig. 16, 17; Map 10

Hypopterygium didictyon Müll.Hal., Syn. Musc. Frond. 2 (1850) 9. — *Hypopterygium didyctium* Müll.Hal. ex Berthier, Rev. Bryol. Lichénol. 38 (1972) 546, nom. inval., err. orthogr. pro *Hypopterygium didictyon* Müll.Hal. — *Hypopterygium laricinum* auct. non (W. Hook.) Brid.: Wilson & Hooker f., Bot. Antarct. Voy. 1(2) (1847) 428; corr. Müller, Syn. Musc. Frond. 2 (1850) 9. —

Type: *Hooker s.n.* (B holo, destroyed; L lecto, designated here; BM sub no. *163*, and sub no. *W. 154*; E n.v., H n.v.; S, sub nos. *23* and *24* in hb. Kindberg; BR, TDC), Chile, Magallanes Prov., Hermite Island, Cape Horn, Antarct. Exp. 1839–43. — See note 1.

Hypopterygium novaeseelandiae Müll.Hal., Bot. Zeit. 9 (1851) 562, '*novae-seelandiae*'. — *Hypopterygium novae-seelandicum* Müll.Hal. ex Burges, Proc. Linn. Soc. New South Wales 60 (1935) 88, nom. inval., err. orthogr. pro *Hypopterygium novaeseelandiae* Müll.Hal. — Type: *Mossman 722* (B holo, destroyed; NY lecto, designated here; BM?, FH?, both sub no. *22*, which is probably an error for *722*; JE?, s.n., s.loc.), New Zealand, North Island, North Auckland L.D., Kiapara Harbour, "Wairoa forests Kiapara", ["ad corticem arborum dejectarum sylvarum prope Kaipara", "Bartramia Coll. No. 722"], 1850. — There are a few other, later and invalid orthographic variants that vary in the spelling of the epithet. — Synonymised with *Hypopterygium smithianum* Hook.f. & Wilson by Wilson in Hooker f., Bot. Antarct. Voy. 3(2) (1859, '1860') 217, who overlooked that the name *Hypopterygium novaeseelandiae* Müll.Hal. has priority over *Hypopterygium smithianum* Hook.f. & Wilson; Wilson's mistake was corrected by Hooker f., Handb. N. Zeal. Fl. (1867) 487. — Synonymised with *Hypopterygium didictyon* Müll.Hal. by Matteri, Bol. Soc. Argentina Bot. 15 (1973) 240.

Hypopterygium smithianum Hook.f. & Wilson in Wilson in Hook.f., Bot. Antarct. Voy. 2 (2) (1854, '1855') 118. — *Hypopterygium smithii* Wilson ex Kindb., Enum. Bryin. Exot. (1888) 20, nom. inval., err. orthogr. pro *Hypopterygium smithianum* Hook.f. & Wilson. — *Hookeria rotulata* auct. non Hedw.: Smith, Trans. Linn. Soc. London 9 (1808) 279; according to Hooker f. & Wilson, Bot. Antarct. Voy. 2 (2) (1854, '1855') 118; Smith l.c. identified a plant from New Zealand that was collected by A. Menzies, which was almost certainly a syntype of *H. smithianum*. — Syntypes: *Menzies 74* (BM lecto, designated here), New Zealand, South Island, Southland L.D., Dusky Sound ["Dusky Bay"]; *Cunningham s.n.* (not found), and other collector's (names not cited by Hooker f & Wilson l.c.), *Colenso s.n.* (not found with certainty: probably *Colenso 2535* (BM) and *Colenso 2560* (BM), both s.loc.), *Sinclair s.n.* (not found with certainty, presumably the original material of *Hypopterygium pallidisetum* Wilson, nom. nud. in syn., which is preserved in Wilson's herbarium kept in BM), North Island, Bay of Islands; New Zealand, North Island, East Coast and interior; *Lyall 80* (BM), New Zealand, Stewart Island, Port William, 1850. — Synonymised with *Hypopterygium novaeseelandiae* Müll.Hal. by Mitten, J. Proc. Linn. Soc., Bot. 4 (1860) 96. — See notes 2, 3, and 4.

Hypopterygium glaucum Sull., Proc. Amer. Acad. Arts. 3 (1855) 184. — *Hypopterygium novaeseelandiae* Müll.Hal. var. *glaucum* (Sull.) Dixon, New Zealand Inst. Bull. 3, 5 (1927) 295. — *Hypopterygium novaeseelandiae* Müll.Hal. fo. *glaucum* (Sull.) Vitt, New Zealand J. Bot. 12 (1974) 205. — Type: *U.S. Exploring Exp. Wilkes 1838–42* (FH holo?, not found; BM, NY), New Zealand. — Synonymised with *Hypopterygium didictyon* Müll.Hal. by Streimann & Curnow, Australian Flora and Fauna Series 10 (1989) 212. — See note 5.

Hypopterygium novaeseelandiae Müll.Hal. ["Hpe."] var. *chilensis* Lorentz, Bot. Zeit. 24 (1866) 187. — *Hypopterygium krauseanum* Müll.Hal. ex Kindb., Hedwigia 40 (1901) 292, nom. nud. in syn. (*Hypopterygium novaeseelandiae* Müll.Hal. subsp. *viridulum* Mitt. ex Kindb.). — Type: *Krause s.n.* (M holo, n.v.; B destroyed; S, sub no. *37* in hb. Kindberg), Chile, Valdivia, Corral, ["auf Steinen und Wurzeln an Bachrändern in dunklen feuchten Schluchten"]. — Synonymised with *Hypopterygium novaeseelandiae* Müll.Hal. subsp. *viridulum* Mitt. ex Kindb. by Kindberg, Hedwigia 40 (1901) 292. — Synonymised with *Hypopterygium didictyon* Müll.Hal. by Matteri, Bol. Soc. Argentina Bot. 15 (1973) 240.

?: *Hypopterygium hillii* Colenso, Trans. & Proc. New Zealand Inst. 19 (1887) 277. — Syntypes: *Hill s.n.* (not found), New Zealand, North Island, Hawke's Bay L.D., Dannevirke, ["Forests, Daneverke, County of Waipawa"], 1885; *Colenso s.n.* (not found), Hawke's Bay L.D., Norsewood, ["forests near Norsewood, same county"], 1886. — Synonymised with *Hypopterygium novaeseelandiae* Müll.Hal. by Dixon, New Zealand Inst. Bull. 3, 5 (1927) 294. — See note 6.

Hypopterygium pachyneuron Colenso, Trans. & Proc. New Zealand Inst. 19 (1887) 277. — Type: *Hamilton s.n.* (WELT holo, sub no. *820* in hb. Colenso, also presented sub no. *3108*, p.p., mixed with material of *Hypopterygium tamarisci* (Sw.) Brid. ex Müll.Hal.; WELT, sub nos.

820 and *3108* in hb. Sainsbury; BM, sub no. *3108*, "Colenso"), New Zealand, North Island, Hawke's Bay L.D., Putere ["near Wairoa"], Xmas, 1885. — Synonymised with *Hypopterygium novaeseelandiae* Müll.Hal. by Dixon, New Zealand Inst. Bull. 3, 5 (1927) 295. — The type is annotated, presumably by Sainsbury, with the remark: "Wrapping of bundle whence this packet had annotation '*Hypopterygium pachyneuron* sp nov is 820'". — According to annotations on the label of the holotype duplicate specimens were sent to Reader, sub no. *820*, and to K, sub no. *3108*. However, in the material of *Hypopterygium tamarisci* (Sw.) Brid. ex Müll.Hal. and *H. didictyon* Müll.Hal., including material from BM and MEL, no specimen was found that had been sent to Reader. The material that was sent to K is now preserved in BM. It is presented under Colenso's name as *Hypopterygium pachyneuron*. See note 7.

Hypopterygium marginatum Colenso, Trans. & Proc. New Zealand Inst. 21 (1889) 44, syn. nov. Type: *Hill s.n.* (WELT holo), New Zealand, North Island, Wellington L.D., ["sides of Mount Tongariro"], "Hill's among rubbish", ["1887"]. — See notes 8 and 9.

Hypopterygium vulcanicum Colenso, Trans. & Proc. New Zealand Inst. 21 (1889) 43. — Type: *Owen s.n.* (WELT holo), New Zealand, North Island, Wellington L.D., County of East Taupo, ["among stones and pumice, sides of Mount Tongariro"], "Owen's lot scraps", ["1887"]. — Synonymised with *Hypopterygium novaeseelandiae* Müll.Hal. by Dixon, New Zealand Inst. Bull. 3, 5 (1927) 295. — See notes 9 and 10.

Hypopterygium novaeseelandiae Müll.Hal. subsp. *viridulum* Mitt. ex Kindb., Hedwigia 40 (1901) 292, syn. nov. — Syntypes: *Knight s.n.* (S lecto, designated here), New Zealand, North Island, North Auckland L.D., Auckland, "ex hb. S.O. Lindberg"; *unknown collector [Beckett?] s.n.* (S), New Zealand, South Island, Canterbury L.D., Mt Torlesse, April 1892; both syntypes sub nos. *26* and *37* in hb. Kindberg. — Erroneously considered to be based on *Hypopterygium viridulum* Mitt. (= *Hypopterygium tamarisci* (Sw.) Brid. ex Müll.Hal.) by Van der Wijk et al., Regnum Veg. 33 (1964) 181; see note 11.

Hypopterygium tasmanicum Müll.Hal. ex Kindb., Hedwigia 40 (1901) 285, syn. nov. — Type: Australia, Tasmania, May, 1890, *Borchard s.n.* (S holo, sub no. *12* in hb. Kindberg; B destroyed). — See note 12.

Hypopterygium novaeseelandiae Müll.Hal. var. *nudicaule* Dixon, New Zealand Inst. Bull. 3, 5 (1927) 295, syn. nov. — Syntypes: *Berggren 2004* (BM lecto, designated here; S, UPS), New Zealand, South Island, Otago L.D., Waititi, Blueskin; *Berggren 2239* (BM), North Island, South Auckland/Taranaki L.D., Papakauri; *Gray 277* (BM p.p., mixed with *Hypopterygium tamarisci* (Sw.) Brid. ex Müll.Hal.), North Island, Wellington, Wairarapa, Mauriceville. — According to Dixon's l.c. annotations on the sheet with the syntypes the variety is mainly based on Berggren's specimens. — Proposed in the synonymy of *Hypopterygium novaeseelandiae* Müll.Hal. by Sainsbury, Roy. Soc. New Zeal. Bull. 5 (1955) 413. — See note 13.

Hypopterygium pallidisetum Wilson in Hook.f., Bot. Antarct. Voy. 2(2) (1854, '1855') 118, nom. nud. in syn. (*Hypopterygium smithianum* Hook.f. & Wilson). — Original material: *Sinclair s.n.* (BM), New Zealand, 1850.

Hypopterygium smithianum Hook.f. & Wilson var. *minus* Wilson in Hook.f., Bot. Antarct. Voy. 2 (2) (1854, '1855') 118, nom. nud. in syn. (*Hypopterygium rotulatum* (Hedw.) Brid. var. *incurvum* Brid.). — Original material: *Hooker f. s.n.* (not found with certainty), New Zealand, North Island, North Auckland L.D., Bay of Islands, ["at the roots of trees"]; *Sinclair s.n.* (not found), Wellington L.D., Wellington, Port Nicholson; *Colenso s.n.* (not found with certainty), Wellington L.D., Rangitikei River; probable original material: *Hooker f. 384* (BM, FH), *s.n.* (TDC), New Zealand, Antarct. Exp. 1839–43; *Colenso 394* (BM, "ß *1*"; NY), New Zealand, probably North Island. — Wilson l.c. expressed some taxonomic doubt on the synonymy of his variety with *Hypopterygium rotulatum* (Hedw.) Brid. var. *incurvum* Brid., but he clearly published and accepted this taxonomic synonymy, by which his variety has become invalid. — Synonymised with *Hypopterygium glaucum* Sull. by Hooker f., Handb. N. Zeal. Fl. (1867) 488. — Synonymised with the species (*Hypopterygium smithianum* Hook.f. & Wilson) by Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1874–75 (1876) 149. (Gen. Sp. Musc. 2 (1876) 65). Jaeger did not explicitely give the name of the variety that he synonymised, but it is certain that *Hypopterygium smithianum* Hook.f. & Wilson var. *minus* Wilson is concerned here. — See note 5.

Hypopterygium concinnum auct. non (W. Hook.) Wilson: Schimp. ex Hohen., *W. Lechler plantae chilenses: 595*; exsiccata presumably distributed between Sept. 1853 and May 1854, nom. nud.; Bot. Zeit. 12 (1854) 349, (May), nom. nud. — Original material: *Lechler, LPC 595* (B destroyed; BM, BR, L, NY, RO, S, W), Chile, Chiloé Prov., "ad truncos arborum pr. Morro Gonzales", Dec., 1850. — Mitten, J. Linn. Soc., Bot. 12 (1869) 330, correctly identified *Lechler, LPC 595* from Morro Gonzales as *Hypopterygium didictyon* Müll.Hal.; Kindberg, Hedwigia 40 (1901) 291, synonymised *Hypopterygium concinnum* Schimp. ex Hohenacker with *Hypopterygium didictyon* Müll.Hal.

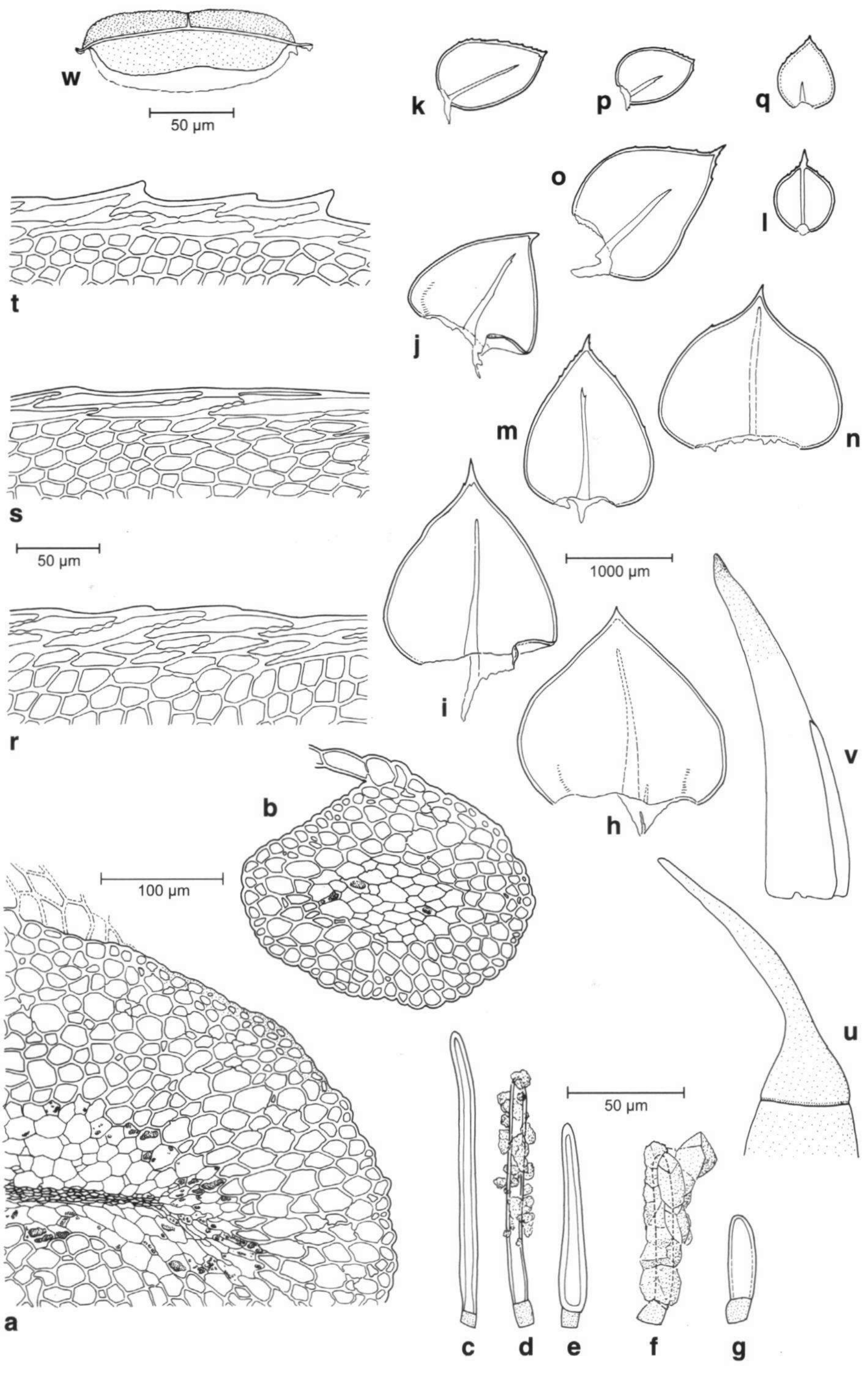
Hypopterygium chrysopus Müll.Hal. ex Kindb., Hedwigia 40 (1901) 292, nom. nud. in syn. (*Hypopterygium novaeseelandiae* Müll.Hal. subsp. *viridulum* Mitt. ex Kindb.). — Original material: *Helms s.n.* (S, s.loc., sub nos. *1* and *37* in hb. Kindberg, for the part [sub no. *1*] that was identified by Müller), New Zealand; *Reader s.n.* (not found), New Zealand; perhaps also: *Helms s.n.* (W sub no. *381*), New Zealand, South Island, Canterbury L.D., Little Kowai, Mt Torlesse.

Illustrations: Sainsbury, Roy. Soc. New Zealand Bull. 5 (1955) pl. 67, f. 1. — Allison & Child, Mosses of New Zealand (1971) pl. 29. — Berthier, Rev. Bryol. Lichénol. 38 (1972) 547, pl. 28, f. F. — Matteri, Bol. Soc. Argent. Bot. 15 (1973) 242, pl. 3; Flora Criptogámica de Tierra del Fuego 14 (9) (1975) pl. 14. — Newton, J. Bryol. 7 (1973) 401, f. 3. (karyotype).

Plants in groups of dendroids, palmate to umbellate, very small to medium-sized (rarely large), not gemmiferous; small projecting shoots occasionally not differentiated in stipe and frond when originating from thin stolons. *Stipe* up to 2.5(–4.0) cm long, usually ascending or vertical, occasionally creeping, not compressed to entirely dorsiventrally compressed, usually entirely tomentose, less frequently set with a few rhizoids in distal part, glabrous when young (but see 'Geographical variation'). *Frond* subcircular or short-ovate to elliptic, up to 2.5 cm in diameter; rachis and branches entirely dorsiventrally compressed or not compressed in basal third to half, glabrous or weakly to distinctly tomentose at frond base, entirely glabrous when young, caducous near apex or not; rachis bend from stipe to roughly horizontal, branches up to 1.5 cm long. *Primordia* frequently set with scaly leaves; scaly leaves deltoid to oblong, margin entire. *Epidermis cells and cortical cells of stipe, rachis, and branches* equally narrow or cortical ones wider; walls thin or weakly incrassate, colourless to brown; inclusions absent. *Central strand* present; cells equally wide as cortical ones or narrower, walls thin, colourless (occasionally brown?); inclusions frequently present in outer strand cells, less frequently in inner ones, fat-like granules, colourless (white). *Axial cavities* absent. *Axillary hairs* 3–5 per leaf, 2- (or 3-)celled; basal cells 1 (or 2) ; terminal cell (elongate or) short-linear to linear, usually ± rectangular, rarely elliptic, somewhat attenuate or not, 40–95 μm long and 5–15 μm wide, smooth or covered with white and wax-like substances, wall incrassate. *Phyllotaxis*: of stipe octostichous; of rachis octostichous in basal part, becoming tristichous in distal part; of branches tristichous. *Foliation*: of stipe isophyllous or weakly anisophyllous, not complanate; of rachis isophyllous or weakly anisophyllous and not complanate or weakly complanate in basal third to half, distinctly anisophyllous and complanate in distal part, in dorsal view often julaceous; of branches distinctly anisophyllous, complanate, in dorsal view often julaceous. *Leaves* distant at stipe, usually closely set but occasionally distant in frond, yellowish green to green or glaucous green, dull; insertion concave; laminal cells short to short-linear, parenchymatous and rectangular to prosenchymatous and hexagonal, 20–95 μm long and 5–30 μm wide, walls thin or incrassate, porose. *Basal and distal stipe leaves* monomorphic, weakly differentiated in basal and distal ones or

Fig. 16. *Hypopterygium didictyon* Müll.Hal. Habit (*Streimann 51282*, L).

not, appressed to widely patent, symmetrical, deltoid to broadly ovate; margin entire; border faint to distinct, continuous or interrupted, 1–5 cells wide; apex acute, gradually acuminate, or abruptly acuminate; acumen up to 0.2 mm long; costa absent, faint, or distinct, reaching c. 4/5 of leaf length. ***Basal stipe leaves*** scale- to leaf-like, 0.4–0.5 mm long and 0.2–0.5 mm wide, often hidden in tomentum of stipe. ***Distal stipe leaves***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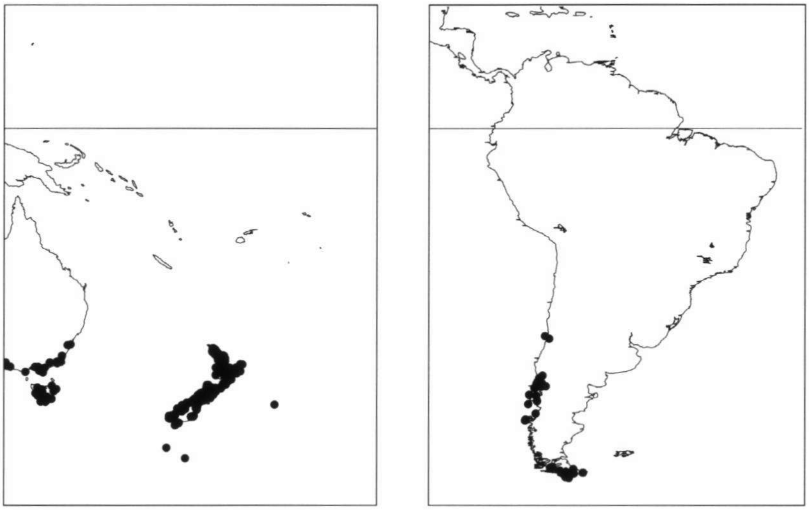
leaf-like, 0.5–1.0(–1.5) mm long and 1.0–1.5 mm wide. *Frond leaves* dimorphic, but ± monomorphic in basal part of rachis, occasionally caducous at apices of ultimate frond axes; margin ± entire in basal leaves, usually becoming weakly to coarsely serrate or serrate-dentate in distal ones, frequently partly recurved in basal part of basal leaves; teeth 1-celled, up to 20 μm long, projecting up to 1/2 of cell length, in distal lateral frond leaves up to 20; border distinct, continuous, 1–4 cells wide; apex abruptly acuminate; acumen 0.05–0.3 mm long. *Basal frond leaves* symmetrical or weakly asymmetrical, broad-ovate to short-ovate, 0.5–1.5 mm long and 1.0–1.5(–2.0) mm wide, straight; *costa* absent, faint, or distinct, reaching 2/3 of leaf length to percurrent. *Lateral frond leaves (in central and distal part of frond)* asymmetrical, ovate to oblong, 0.5–2.0 mm long and 0.2–1.5 mm wide, straight or curved downwards; *costa* distinct, reaching 2/3–4/5 of leaf length. *Frond amphigastria (in central and distal part of frond)* symmetrical, subcircular or short-ovate to oblong, 0.2–1.5 mm long and 0.2–1.0(–1.5) mm wide, straight; costa distinct, generally percurrent or excurrent, occasionally shorter but reaching 1/2 of amphigastrium length at least.

Dioicous. *Gametoecia* in basal and middle part of rachis. *Gametoecial leaves* green, rarely pale brown to brown in perigonia; margin entire; border faint to distinct, continuous or absent or faint near leaf base, 1 or 2 cells wide; apex gradually or abruptly acuminate; costa absent, faint or distinct, reaching 1/3–2/3 of leaf length, frequently becoming percurrent in full-grown perichaetia; laminal cells parenchymatous to prosenchymatous in basal 1/4–1/2 of leaf, becoming prosenchymatous in distal part, short to short-linear, hexagonal to rectangular. *Inner leaves*: of perigonia elliptic to obovate, up to 1.3 mm long and 1.0 mm wide, acumen up to 0.4 mm long; of perichaetia prior to sporophyte development and full-grown perichaetia almost similar, ovate to ovate-lanceolate, up to 1.7 mm long and 0.7 mm wide, acumen up to 0.7 mm long. *Antheridia* 0.6–0.7 mm long. *Stalk in full-grown perichaetia* c. 0.5 mm long, set with rhizoids. *Archegonia* 0.5–0.6 mm long. *Vaginula* 1.0–1.5 mm long. *Gametoecial axillary hairs* 2–4 per gametoecial leaf, 3- (or 4-)celled; basal cells 2, usually brown, rarely colourless; intermediate cells usually absent, rarely present, short, rectangular; terminal cell elongate to short-linear, ovate to rectangular, 25–100 μm long and 9–10 μm wide, smooth, apparently often somewhat collapsed, walls thin. *Paraphyses* absent.

Sporophytes up to 5 per frond. *Seta* ascending or vertical, cygneous to uncinate, 7.0–18.0 mm long, ochraceous to reddish brown. *Capsule* horizontal to pendulous, ellipsoid, 0.8–2.4 mm long and 0.6–1.5 mm wide, brown; neck weakly pustulose; annulus distinct. *Peristomial formula OPL:PPL:IPL* = 4:2:6–8c. *Exostome* yellow to brown; teeth (440?–)630–640 μm long and (120–)140–160 μm wide, not bordered or partly to entirely bordered, weakly shouldered or not; dorsal side striate in basal

Fig. 17. *Hypopterygium didictyon* Müll.Hal. a. Rachis (cross section dorsal quadrant); b. branch (cross section); c–g. axillary hairs (c–e. 'normal' variant, f, g. 'Northern New Zealand' variant); h–j. rachis leaves 'normal' variant (h. dorsal, i. ventral, j. lateral); k, l. branch leaves 'normal' variant (k. lateral, l. amphigastrium); m–o. rachis leaves 'Northern New Zealand' variant (m. ventral, n. dorsal, o. lateral); p, q. branch leaves 'Northern New Zealand' variant (p. lateral, q. amphigastrium); r–t. leaf cells of lateral frond leaves: r, s. rachis leaf (r. basal part of antical side, s. distal part of antical side), t. branch leaf (distal part of antical side); u. operculum; v. calyptra; w. exostome tooth (cross section) (a–e, h–l, r–t: *Streimann 51282*, L; f, g, m–q: *Fleischer B76*, L; u, w: *Allison s.n*, FH, hb. Bartram sub no. *6456*; v: *Weymouth s.n.*, FH, hb. Bartram sub no. *6457*).



Map 10. Distribution of *Hypopterygium didictyon* Müll.Hal.

half of teeth, becoming papillose in distal part; dorsal plates broader than ventral ones, 13–14 µm thick; ventral plates 20–21 µm thick. *Endostome* perforate, weakly papillose at both faces; basal membrane reaching c. 1/3 of length of exostome teeth; processes projecting 520–600 µm long beyond orifice and 60–70 µm wide at base, nodulose, not appendiculate; cilia 1–3, 1–3 cells wide, up to 15 cells long, not nodulose, not appendiculate. *Operculum* c. 2.5 mm long. *Calyptra* c. 3.9 mm long, membranous. *Spores* 9–16 µm.

Distribution — Australia (New South Wales, Victoria, South Australia, Tasmania), New Zealand (North Island, South Island, Stewart Island; Auckland Islands; Campbell Island; Chatham Islands), Chile (Valparaiso, Santiago, Cautín, Valdivia, Osorno, Llanquihue, Chiloé, Aisén, Magellanes), Argentina (Río Negro, Neuquén, Tierra del Fuego). See note 15.

According to Matteri (1973), the species also occurs in the Argentinian Andes of Chubut and Santa Cruz.

On the Australian continent, the species is restricted to southeastern Australia, where it occurs south and east of the Australian Alps. It is distributed almost throughout Tasmania, but is mainly absent in the northern central part of Tasmania (north of the Western Tiers).

In New Zealand south of Auckland the species is usually found in mountain ranges and mountainous areas. The species is abundant in large parts of North Island, but has, thusfar, not been found in the coastal areas of the southwestern part of the island or in the lowlands and low mountainous areas of the southwestern part (i.e. most of Taranaki and the northwestern coast of Wellington), the coast of Bay of Plenty, and the Waikato region. On South Island, it is abundant in and on the western side of the Southern Alps. The species is apparently less abundant in the southeastern part of the island, where it occurs in only a few areas at the southeast coast. According to Martin (1949, 1950) the species is common on Stewart Island.

In South America the species is distributed in the southern part of Chile and adjacent areas of Argentina. Most specimens are found in and south of the Chilean province of Cautín. Thusfar the species is not known from the northwestern part of the Chilean province of Magellanes.

Habitat & Ecology — In forests and scrub woodland, frequently near streams and in humid habitats. Terrestrial, on rocks, rotting logs, and tree trunks. Altitude: 15–1400(–2000) m in New Zealand; up to 1160 m in Australia and up to 900 m in South America. Found twice at 2000 m in New Zealand (*Buck 7072, 7083*).

The species is principally a cool- to warm-temperate species (see note 16) that occurs in regions with sufficient rainfall throughout the year.

According to Martin (1949, 1950), the species grows on Stewart Island on rocks and stones, and on stumps and logs in the wetter areas on the forest floor, especially in places where water tends to lie after rainfall and on banks of clay or sand that are perpetually kept moist by seepage, often in association with other mosses, e.g. *Dicranoloma billardieri* (Brid.) Paris.

According to Vitt (1979) the species grows on the Auckland Islands on humus and soil in dense forests, and occurs here at higher elevations beneath rock overhangs or overhanging vegetation, which is also the common habitat on Campbell Island.

Geographical variation — Small and medium-sized plants occur throughout the distribution area of the species. Large plants have a more restricted distribution and occur only in southern Chile and southern New Zealand. The plants from the Valdivian region and the Chonos Archipelago, southern Chile, and those from southern New Zealand are often quite robust and up to 4.5(–5.5) cm tall. These plants are palmate and grow in dense, cushion-like to somewhat loose groups. The stipe of these plants is often quite long and measures up to 4.0 cm in height. The stipe of juvenile plants is frequently densely tomentose in the basal half, and it becomes entirely tomentose in older ones. Stipes that are entirely glabrous are rare. The robust plants have often a frond with a dense ramification of closely set branches.

Most striking differences in size and appearance are found in New Zealand. The South American plants express less variability, the lowest variability in size and shape of the plant is found in Australia. The largest plants from Australia are smaller and grow in less dense cushion-like groups than the largest from New Zealand. The smallest plants from Australia are larger than the smallest from New Zealand.

In New Zealand, two variants of *Hypopterygium didictyon* can be recognised:

'Normal' variant: Plants growing in somewhat loose or dense, cushion-like groups, palmate to umbellate, small to medium-sized, 1–4.5(–5.5) cm tall. Stipe 7.0–25 mm long. Rachis 10.0–25 mm long. Branches (up to) 7.0–15 mm long. Lateral frond leaves 0.7–2.0 mm long and 0.4–1.5 mm wide; amphigastria 0.4–1.5 mm long and 0.4–1.0(–1.5) mm wide. Seta 11–18 mm long. Capsule 1.0–2.4 mm long and (0.6–)0.8–1.5 mm wide. — Distribution: throughout the distribution area of the species.

'Northern New Zealand' variant: Plants growing in dense, almost mat-like groups, usually umbellate, less often palmate, dwarfish, less than 1 cm tall. Stipe 2.0–7.0 mm long. Rachis 4.0–11 mm long. Branches up to 7.0 mm long, usually simple, less often weakly branched. Lateral frond leaves 0.5–1.0 mm long and 0.2–1.0 mm wide; amphigastria 0.2–1.0 mm long and 0.2–1.0 mm wide. Seta 7.0–12 mm long. Capsule 0.8–

1.1 mm long and 0.6–0.8 mm wide. — Distribution: New Zealand: North Island (throughout), South Island (northern Nelson). Rare in the northern part in the Nelson area, and increasing in abundancy northwards on North Island. Most common in North Auckland L.D., but even here less abundant than the small or medium-sized plants of the 'normal' variant of the species.

The tiny plants of the 'Northern New Zealand' variant differ strongly from the 'normal' variant of *Hypopterygium didictyon*, because of their small size, their occurrence in low, almost mat-like groups, and, despite this, their strikingly umbellate habitus with a short stipe, short, deflexed frond axes, and usually simple, and only incidently branched, branches. Sullivant (1855) and Wilson (1855) considered the dwarfish plants to belong to a separate taxon (see note 5), but this is not correct. Despite their different appearance, the two variants of *H. didictyon* in New Zealand are not sharply defined. Plants that are intermediate in size and shape occur throughout New Zealand, whereby plants with intermediate features are most frequently found in and northwards of South Auckland. Hence, a separate taxonomical status for the dwarfish form is not required.

Some New Zealand plants that belong to the 'normal' variant of the present species are not or weakly glaucous, densely branched with numerous branches, and have inconspicuous axillary hairs with narrow and smooth terminal cells. These plants may belong to another variant of the species, but it proved to be impossible to find a distinctive combination of characters states for delimiting this variant from the others. Nevertheless, Pfeiffer's molecular data indicate, that this morphological variant may have a genetic base (Pfeiffer, 2000: *Frey & Pfeiffer 98-Mo 52* from population 'NZ10'; see also note 20).

Ecological variation — Unclear. The Northern New Zealand variant of *H. didictyon* in New Zealand (see 'Geographical variation') is presumably a lowland form of the species, but this could not be confirmed due to insufficient information.

Chromosome numbers — n = 6, see Newton (1973: 399, '*Hypopterygium novaeseelandiae*'). — Voucher: *Greene* (AAS? n.v.; collection number not given), New Zealand, Otago L.D., Dunedin.

Chloroplast DNA sequences — *trnL*$_{\mathrm{UAA}}$ intron, 296 bp, deposited in the GenBank database under accession numbers AF134636–39, see Stech et al. (1999: 361), AF170585–95, see Pfeiffer (2000: 294, 295). — Vouchers: *H. & W. Frey 95–13* (hb. Frey), Chile, Osorno Prov., Parque Nac. Puyehue: AF134639; *Pfeiffer 98-Mo 62* (hb. Frey n.v., CHR n.v.; 'NZ1'), New Zealand, North Is., Gisborne L.D., Lake Waikareiti: AF170585; *Frey 92–45* (hb. Frey, CHR n.v.; 'NZ2'): AF134636, *Pfeiffer 98-Mo 54* (hb. Frey n.v., CHR n.v.; 'NZ3'): AF170586, both from New Zealand, North Is., Wellington L.D., Mt Ruahepu; *Frey & Pfeiffer 98-Mo 40* (hb. Frey n.v., CHR n.v.; 'NZ4'), New Zealand, South Is., Nelson L.D., Mt Stormy: AF170587; *H. & W. Frey 94–138* (hb. Frey n.v., CHR n.v.; 'NZ5'), New Zealand, South Is., Nelson L.D., Lake Rotoiti: AF170588; *Frey 98-Mo 68* (hb. Frey n.v., CHR n.v.; 'NZ6'), New Zealand, South Is., Westland L.D., Bruce Bay: AF170589; *Frey & Pfeiffer 98-Mo 18* (hb. Frey n.v., CHR n.v.; 'NZ7'), New Zealand, South Is., Westland L.D., Robinson Creek: AF170590; *Frey & Pfeiffer 98-Mo 19* (hb. Frey n.v., CHR n.v.; 'NZ8'), New Zealand, South Is., Haast Pass Road, Roaring Billy Bush Walk: AF170591; *Frahm 9–7* (hb. Frey, BONN n.v., CHR n.v., 'NZ9'), New Zealand, South Is., Westland L.D., S of

Haast: AF170592; *Frey & Pfeiffer 98-Mo 52* (hb. Frey, CHR n.v.; 'NZ10'), New Zealand, South Is., Nelson L. D., Waikoropupu Springs: AF170595; *Jarman HO 52617* (hb. Frey, HO n.v.; 'TAS1'), Tasmania, Bermuda Road: AF170593; *Jarman HO 64727* (hb. Frey, HO n.v.; 'TAS2'), Tasmania, Manuka Road: AF170594.

Notes:

Nomenclature and synonymy — 1. The type of *Hypopterygium didictyon* was originally misidentified and distributed as *Hypopterygium laricinum* (W. Hook.) Brid. Two type specimens in BM are actually labelled with this name. The labels of the other type specimens bear a herbarium name that is based on the basionym of *Hypopterygium laricinum*, when transferred to *Leskea* Hedw. According to Hooker f. (1845) the type material was collected in September or October 1842.

2. Smith (1808) identified a New Zealand plant that was collected by Menzies. This plant was almost certainly Menzies' syntype of *H. smithianum* from Dusky Bay. Attached to a specimen of this syntype in Wilson's herbarium, kept at BM, Wilson annotated that Smith had earlier identified this specimen as *H. rotulatum* (Hedw.) Brid.

Hooker f. & Wilson (in Wilson, 1855) named their new species *H. smithianum* after Smith.

3. Jaeger's (1876) opinion on *H. smithianum* is contradictory. He treated *H. smithianum* as a taxonomic synonym of *H. novae-seelandiae*, but he treated *H. smithianum* also as a separate species. Jaeger attributed his taxonomic synonym to Hooker f. & Wilson (in Wilson, 1855), but referred the species to Wilson (1860). When he made this reference, Jaeger was probably confused, because he accredited the species to Hooker f. & Wilson, instead of Wilson, and apparently overlooked, that Wilson himself referred *H. smithianum* to Hooker f. & Wilson (in Wilson, 1855).

4. The syntypes collected by Colenso include probably *Colenso 2535* (BM) and *Colenso 2560* (BM, s.loc.), which are preserved in Wilson's and Hooker's herbaria, both kept at BM. *Colenso 2560* is presented as *Hypopterygium smithianum. Colenso 2535* is not labelled with the name of a species, but in annotations attached to this material Wilson and Hooker clearly indicate that both collections are similar.

5. The type of *Hypopterygium glaucum* Sull. and the original material of *H. smithianum* Hook.f. & Wilson var. *minus* Wilson belong to the 'Northern New Zealand' variant of *H. didictyon* Müll.Hal. (see 'Geographical variation', p. 151).

6. It is not known where the type material of *Hypopterygium hillii* Colenso is preserved, if still in existence. The collection made by Hill is apparently missing; I did not find it in WELT, BM, or other herbaria. There are numerous collections made by Colenso in WELT and BM, but none of them is provided with sufficient information to identify them as type material. Colenso (1887) did not give collection numbers for his type material.

Based on Colenso's description, Dixon (1927) synonymised *H. hillii* with *H. novaeseelandiae* Müll.Hal. I found no reasons to object to Dixon's decision. Colenso's description is pretty close to *H. didictyon*, with the exception for the description of his 'dorsal leaves'. With the latter, Colenso was almost certainly mistaken in the orientation of his mosses when he examined them, because he also described such 'dorsal leaves' for his new species *H. pachyneuron*, which most certainly belongs to *H. didictyon*. Hence, in all probability Colenso's 'dorsal leaves' correspond to amphigastria here.

7. The holotype of *Hypopterygium pachyneuron* Colenso is a mixed collection of *H. tamarisci* (Sw.) Brid. ex Müll.Hal. and *H. didictyon* Müll.Hal. Plants that belong to the latter species form a substantial part of this type, but the majority of the plants in the holotype belongs to *H. tamarisci*, and is excluded here. All the material of the isotypes in WELT and BM belong to *H. didictyon*.

Apparently, Colenso was unaware that Hamilton's material was a mixed collection of two *Hypopterygia*, and his description of *H. pachyneuron* (1887) as a new species is probably based on plants from both species. Evidence that the description is partly based on plants of *Hypopterygium tamarisci* is provided by the costa length of the amphigastria. Colenso described the costa of the 'dorsal leaves', by which he meant amphigastria, as "vanishing beyond the middle". The amphigastrium costae in the plants of *H. tamarisci* perfectly match Colenso's description. Those in the plants of *H. didictyon* are, on the other hand, distinctly excurrent. Elements of *H. didictyon*, are, amongst others, found in the degree of development of the leaf costa of the lateral frond leaves. In the plants of *H. didictyon* this leaf costa agrees perfectly well with Colenso's description, who described it as "very stout and broad at base". The costa in the lateral leaves of the plants of *H. tamarisci*, on the other hand, is thin and much less pronounced. In addition, Colenso's description of the number of 8 or 9 sporophytes per plant is, in all probability, based on a plant of *H. tamarisci*, whereas he presumably examined only the sporophytes of *H. didictyon* in detail. Enclosed with Hamilton's material I found a separate convolute with a branch fragment, the remains of a perichaetium, and three sporophytes of *H. didictyon* that were selected by Colenso on Sept. 28, 1886.

It was difficult to decide to which plants in Colenso's original collection *Hypopterygium pachyneuron* is best attached, because Colenso's description and protocol give no decisive clue. However, in my opinion *H. pachyneuron* is best attached to the plants in the original collection that belong to *H. didictyon*, because the isotype in BM, which was sent to K by Colenso himself, contains only material of *H. didictyon*. Besides, Dixon (1927) already placed the species in the synonymy of *H. novaeseelandiae*. By this, the specimens in BM and WELT must be considered isotypes of *H. pachyneuron*.

8. The type of *Hypopterygium marginatum* Colenso consists of a single gametophore. According to Colenso (1889) his material was a single specimen from Mt Tongariro that was picked out from among a lot of scrap and damaged mosses.

9. Colenso (1889) did not compare *Hypopterygium marginatum* and his two other newly described New Zealand *Hypopterygium* species, *H. vulcanicum* and *H. flaccidum*, with known *Hypopterygia* or other mosses from New Zealand. By this *H. marginatum* and *H. vulcanicum*, both from Mt Tongariro, were superfluously described as new species, because they do not substantially differ from each other and neither from, e.g. *H. novaeseelandiae* Müll.Hal. and *H. smithianum* Hook.f. & Wilson. Because of the octostichous phyllotaxis of the stipe and the basal part of the rachis and the long terminal cell of the axillary hairs with the incrassate walls, its beyond doubt that *H. marginatum* and *H. vulcanicum* are conspecific with *H. didictyon*.

Colenso's *Hypopterygium flaccidum* belongs to *Hypnodendron arcuatum* (Hedw.) Lindb. ex Mitt. (see 'Taxa excluded from the Hypopterygiaceae', p. 358).

10. The holotype of *Hypopterygium vulcanicum* Colenso had apparently not been presented with this name. In annotations attached to the specimen concerned, Sainsbury stated on 21-9-1947, that the specimen is "evidently the *H. vulcanicum* published on p. 43 of Vol. 21 Trans. N.Z. Inst.", viz. Colenso's (1889) original publication on *H. vulcanicum*. There is no reason to question Sainsbury's observation. The *H. vulcanicum* specimen is, nowadays, separately preserved in WELT, but when Sainsbury examined this specimen it was preserved together with four other mosses, which were also newly described by Colenso (1889). Among them were the types of *H. marginatum* Colenso and *H. flaccidum* Colenso.

11. There is no evidence that Kindberg (1901) actually based his subspecies on Mitten's (in Hooker f., 1867) species *Hypopterygium viridulum*. According to Kindberg, he based the name of his subspecies on herbarium material that came from Lindberg's herbarium and was identified by Mitten. He did not give a reference to Mitten's original publication or any of Mitten's specimens. Both syntypes are non-fruiting plants and belong beyond any doubt to *H. didictyon*.

12. Kindberg (1901) did not only describe *Hypopterygium tasmanicum* as a new species, but classified it also in its own section, *Hypopterygium* sect. *Pseudo-Tamariscina*, whereas he treated *H. didictyon* and *H. novaeseelandiae* as separate species in *Hypopterygium* sect. *Tamariscina*. I do not understand Kindberg's considerations for the classification of a new species in its own section, because the type of *H. tasmanicum* is very similar to that of *H. novaeseelandiae*. In addition, the differences between Kindberg's sections are small and represent differences between specimens rather than differences between taxa.

It is beyond any doubt that *H. tasmanicum* belongs to *H. didictyon*, because of its octostichous phyllotaxis of the stipe and basal part of the frond and its 2-celled axillary hairs, which have long, cylindrical terminal cells with somewhat incrassate walls.

13. Sainsbury (1955) proposed Dixon's variety to be synonymous with *Hypopterygium novaeseelandiae* Müll.Hal., but did not explicitly formalise this synonymy. This was probably because Sainsbury struggled with the delimitation between *H. didictyon* and *H. rotulatum* (Hedw.) Brid. (see note 17).

Nevertheless, Sainsbury's remark, that Dixon's variety could not stand, because it can not satisfactorily be delimited from the species, is correct. Dixon (1927) distinguished his new New Zealand variety *Hypopterygium novaeseelandiae* Müll.Hal. var. *nudicaule* Dixon from the species by its glabrous stipe, but this does not justify the recognition of a separate taxon within *H. didictyon.*

In great majority the stipe of *H. didictyon*, from New Zealand and other regions, is largely or entirely tomentose, but the stipe shows much variation in its tomentum within and between specimens, and may vary from glabrous to densely tomentose. There are no sharp delimitations and almost every possible intermediate in the covering of the stipe occurs. In *Berggren 2239*, the stipe is glabrous with the exception of a few rhizoids in the basal part. The tomentum of the stipe of Gray's material that belongs to the present species (*Gray 277* p.p.) is almost identical. By contrast, in Berggren's material (*Berggren 2004*) from Blueskin, Waitati, it varies from set with a few rhizoids to being tomentose in the basal half.

Reproduction — 14. There were 494 fruiting specimens among the specimens examined (c. 42%, n = 1184). Fruiting specimens are less common in South America (16%, n = 134) than in Australia (46%, n = 253) and New Zealand (45%, n = 774). Within Australia and New Zealand fruiting specimens are more common in the northern areas (respectively, 57% in continental Australia, n = 47, and 47% on North Island, n = 362) than in the southern areas (44% on Tasmania, n = 188, and 37% on South Island and Stewart Island, n = 290).

In a representative sample of 20 specimens from the whole distribution area, 9 (45%) were fruiting female plants, 4 (20%) non-fruiting female plants, and 7 (35%) were male plants.

Distribution — 15. Three specimens from a collection that was made by an unknown collector were indicated to come from Norfolk Island. They are presented under number *H. 2181* in Wilson's herbarium that is kept in BM. These old collections are almost certainly mislabelled, because I found no other specimens of *H. didictyon* from Norfolk Island. Every other specimen of the numerous *Hypopterygia* from Norfolk Island, in majority collected by Streimann in 1984, belongs to *Hypopterygium tamarisci* (Sw.) Brid. ex Müll.Hal. ('Australasian' variant).

16. The material examined contained only two specimens that came from a region with a mediterranean climate. They were found in Valparaiso (*De Notaris s.n.*) and "Corra Jeune", near Santiago (*Wall s.n.*), Chile. There are no reasons to believe that these specimens have been mislabelled.

Identification — 17. Bryologists treating Australasian material often confused the present species *Hypopterygium didictyon* with *H. tamarisci*. In addition, New Zealand (and Australian) specimens that belong to *H. didictyon* were often identified as *H. rotulatum* (Hedw.) Brid., which is a doubtful species in *Hypopterygium.*

Hampered by the absence of type material of *H. rotulatum*, Dixon (1927) had almost certainly New Zealand representatives of *H. tamarisci* in mind in his treatment of *H. rotulatum*. He attempted to separate *H. rotulatum* from *H. novaeseelandiae* (= *H. didictyon*), but used characters in which *H. tamarisci* and *H. didictyon* are not substantially different. His delimiting features in habitus, ramification, and colour of the plant, the covering of the stipe, and the direction of the stipe leaves are principally correct, but represent only quantitative differences. In his discussion on the synonymy of *H. viridulum* (= *H. tamarisci*) and *H. oceanicum* (= *H. tamarisci*), Dixon came to the conclusion that *H. rotulatum* is dioicous, probably because he overlooked the variability in sexuality in the material that he examined. Because he also merged the dioicous *H. discolor* with *H. rotulatum*, Dixon made it very difficult for later bryologists to separate *H. didictyon* from New Zealand or other Australasian representatives of *H. tamarisci.*

Sainsbury (1955) struggled with the delimitation between *Hypopterygium didictyon* and *H. rotulatum*, by which he had also New Zealand representatives of *H. tamarisci* in mind. About half of the specimens in his herbarium that Sainsbury identified as *H. novaeseelandiae* var. *nudicaule* belongs to *H. tamarisci*, the other half belongs to *H. didictyon.*

Beever et al. (1992) treated *Hypopterygium didictyon* (as *H. novaeseelandiae*) under *H. rotulatum* and probably considered it conspecific with *H. tamarisci*. Frey & Beever (1995) included both *H. didictyon* and *H. tamarisci* in their circumscription of *H. rotulatum.*

It is not known with certainty which Australian *Hypopterygium* species, presumably *Hypopterygium didictyon* or *H. tamarisci*, Catcheside (1980: 305, f. 185) had in mind when he treated *H. rotulatum*. It is not known to which species the photographs made by B. & N. Malcolm (1989: 55) correspond.

Hypopterygium tamarisci can easily be recognised from *H. didictyon* by its tristichous (or nearly so) phyllotaxis at the stipe and the basal part of the frond, the absence of dorsal leaves in the basal part of the frond, and the relatively short, smooth terminal cells of the axillary hairs. *H. didictyon*, on the other hand, is characterised by an octostichous phyllotaxis at the stipe and the basal part of the frond, the often easily observable dorsal leaves in the basal part of the frond, and the long terminal cells of the axillary hairs, which are often covered with white substances. The latter can quickly and easily be observed with an ordinary stereomicroscope (with 8×4 or 8×8 magnification) used in daily bryological practise as white dots or white hairs in the axils of the lateral leaves, when observed from the ventral side.

Other — 18. The collection from Mt Gambier, South Australia that is preserved in RO, is accredited to F. von Mueller, but was probably collected by Wilhelmi (cf. Hampe, 1856).

19. Thus far, *Hypopterygium didictyon* was introduced only once in an European greenhouse (Kruijer, 1997b). The moss was found on a trunk of *Dicksonia antarctica* Labill. in a greenhouse in Neuilly near Paris, France (*Eloc s.n.*, S).

20. The molecular sequence data (see 'Chloroplast DNA sequences', p. 152) obtained by Stech et al. (1999) and Pfeiffer (2000) support the present circumscription of *Hypopterygium didictyon*. Stech et al. (1999) found, that the *trnL* intron sequences of a New Zealand and Chilean specimen of the species are completely identical. In their opinion, this indicates that *H. didictyon* is a 'stenoevolutionary taxon' sensu Frey et al. (1999) and experienced no relevant genetic divergence after the disruption and separation of its populations, which probably started 86–84 million years ago with the separation of the New Zealand microcontinent from Gondwanaland (Storey et al., 1999; O'Sullivan et al., 2000).

Pfeiffer (2000) found no differences for the *trnL* intron between a Chilean specimen of *Hypopterygium didictyon* (examined by Stech et al., 1999) with nine New Zealand specimens from different populations. She found, however, a low genetic divergence, corresponding at intraspecific level, between two specimens from different populations from Tasmania and a specimen from a tenth population from New Zealand ('NZ10', *Frey & Pfeiffer 98-Mo 52*) with the specimens from the other populations from New Zealand and Chile.

According to Pfeiffer (2000), the *trnL* intron sequence of *Frey & Pfeiffer 98-Mo 52* is closest to the Tasmanian specimens (98.6% of similarity), followed by the other New Zealand/Chilean specimens (98.3%). *Frey & Pfeiffer 98-Mo 52* shares an indel with *H. tamarisci*, but it is clearly differentiated from this species by a much lesser degree of sequence identity (96–96.3%). Interestingly, *Frey & Pfeiffer 98-Mo 52* differs in habit from most plants of *H. didictyon*, including the other specimens sequenced by Pfeiffer (2000), by its strongly branched frond and green colour, by which it superficially resembles *H. tamarisci*.

Stech et al. (1999) and Pfeiffer (2000) sampled only a few populations. Hence, more molecular sequence data of, in particular, nuclear DNA are needed to get a better understanding of the genetic variation within *H. didictyon*, the genetic base of its morphological variation, and to confirm the low genetic divergence between separated populations of the species claimed by Stech et al. (1999) and Pfeiffer (2000); see also 'Evolution rate', p. 90.

Selected specimens (among 1184 specimens examined):

AUSTRALIA: *De Labillardière s.n.* (L, '*Leskea tamariscina*', s.loc.). – New South Wales: *Willis s.n.* (MEL), White Rock Mt, Rockton; *Thorpe (161)* (MEL), Cambewarra; *Streimann 40190* (CBG), Badja Sate Forest. – Victoria: *Baüerlen 219* (JE), *s.n.* (JE), Bonang River; *Streimann 36592* (B, CBG, NY), Errinundra River; *Von Mueller 102* (BM, NY, MEL p.p.), Tarwin; *Von Mueller 169* (BM, NY, *179?*), *179* (NY, MEL), Wilson's Promontory, Sealer's Cove; *Beauglehole 442* (MEL), *1370* (MEL), *1373* (MEL), *73422* (MEL), Lower Glenelg Nat. Park; *Walker s.n.* (BM, MEL), Cape Otway–Cape Patten. – South Australia: *Wilhelmi s.n.* (BM, RO, see note 18), Mt Gambier. – Tasmania: *Moscal 4235* (CBG, NY), Clifton Creek; *Davies & Ollerenshaw 1121* (CBG, L), Hellyer Gorge; *Seppelt 12900* (B, NICH, NY), *12904* (B, NICH, NY), Western Tiers, Projection Bluff; *Jarman (HO 52617)* (hb. Frey), Bermuda Road; *Jarman (HO 64727)* (hb. Frey), Manuka Road; *Tindale (M 10297)* (NSW), *Weymouth 724a* (BM, NY), *Willis s.n.* (MEL), Russell Falls; *Bastow 147* (NSW, MEL), *s.n.* (CHR), *Fleischer B 2038* (B), *Seppelt 11455* (B), *Weymouth 166* (FH), *2200* (JE, NY), *(6457)* (FH), Mt Wellington; *D.A. & A. V. Ratowsky B44e* (CBG, CHR, GRO, NY), Wylds Graig; *Downing 0990* (MACQ), Harz Mts; *Downing 0898* (MACQ), Hastings Caves. — NEW ZEALAND: *Hooker f. 384* (BM, s.loc.), *s.n.* (TDC, s.loc.); *Colenso 394* (BM, “ß *1*”; NY, s.loc.). – North Island. North Auckland L.D.: *Allison 733* (CHR), *735* (WELT), *Van Zanten 7401245* (GRO, L, NICH), Waipoua Forest; *Mossman 722* (NY), Kiapara Harbour, Wairoa forests; *Jupp s.n.* (NY), Mt Eden; *Moore 75* (CHR, WELT), Rangitoto Is.; *Moore 56a* (CHR), *s.n.* (WELT), Little Barrier Is.; *Medway (3576)* (CHR), Great Barrier Is. – South Auckland L.D.: *Fleischer B 76* (B, BR, L), *Poole 23* (CHR), Mamaku; *Allison (6456)* (FH), Rotorua, Kaingaroa Plains. – Gisborne L.D.: *Whitehouse 29329* (L, NICH), *Sainsbury 181* (CHR), Lake Waikaremoana; *Sainsbury s.n.* (WELT), Gisborne. – Hawke’s Bay L.D.: *Hamilton s.n.* (WELT), Wairoa; *Van Zanten 1260* (B, GRO, L, NICH, U, WELT) Mt Titiokura; *Colenso 4161* (WELT), Norsewood; *Colenso 2522* (BM, WELT), Dannevirke; *Beckett 847* (BM, CHR, FH, S), *s.n.* (NSW, UPS, W), Seventy Mile Bush, Piri-Piri. – Taranaki L.D.: *Lewinski 1994* (CHR, L), Mt Taranaki (Mt Egmont); *Ruinard 98.12.04.01* (L), Mt Messenger. – Wellington L.D.: *Robbins 52* (WELT), Tongariro Nat. Park; *Hill s.n.* (WELT), *Owen s.n.* (WELT), Mt Tongariro; *Frey 92–45* (hb. Frey), Mt Ruapehu; *Sainsbury 3564* (CHR, WELT), Ohakune; *Gray 277* (BM p.p., mixed with *H. tamarisci*), *s.n.* (WELT), Mauriceville. – South Island. Nelson L.D.: *Frey & Pfeiffer 98-Mo 52* (hb. Frey), Waikoropupu Springs; *Streimann 51282* (L), NW Nelson Forest Reserve; *Sainsbury 8015* (WELT), Lake Rotoiti. – Marlborough L.D.: *Lewington s.n.* (WELT), Mt Richmond. – Westland L.D.: *Helms 29* (B, FH, NY, UPS), *s.n.* (FH, JE, W), Greymouth; *Beckett 914* (BM, CHR, FH, JE, NICH, NSW, S), Taramakau (‘Teremakau Bush’); *Child 5674* (BM), *Frahm 5–12* (hb. Frey), Fox Glacier; *Prud’homme van Reine M 5a* (L), Lake Matheson; *Frahm 9–7* (hb. Frey), S of Haast. – Canterbury L.D.: *Buck 7072* (NY), *7083* (NY), Lewis Pass Scenic Reserve; *Child 1905* (BM), *Whitehouse 29519* (GRO, NICH, U), *Lewinsky 74-323* (BR), Arthur’s Pass; *Berggren 136* (B, FH, LISU, UPS, W), Castle Hill; *Beckett 381* (CHR); *Helms s.n.* (S; W sub *no. 381*), Mt Torlesse. – Otago L.D.: *Fleischer B 6* (L), Queenstown; *Child 2420* (BM), Mt Cargill. – Southland L.D.: *Vitt 10403* (L), Milford Sound; *Menzies 74* (BM), *s.n.* (BM), *Brownsey s.n.* (WELT), Dusky Sound (‘Dusky Bay’); *Johnson s.n.* (CHR), Solander Is. – Stewart Is.: *Brown ter.* (BM); *Chase 324b* (FH), Halfmoon Bay; *Lyall 80* (BM), Port William; *Vitt 10297* (B), Port Pegasus. – Auckland Islands. Auckland Island: *Dawbin s.n.* (CHR), Waterfall Inlet. – Campbell Is. Lyall Ridge, *Vitt 2853* (B, NICH, NY); Mt Fizeau, *Vitt 3141* (S). – Chatham Islands. Chatham Island: *Kirk s.n.* (CHR).

CHILE: Valparaiso Prov.: *De Notaris s.n.* (S), Valparaiso. – Santiago Prov.: *Wall s.n.* (S, ‘Corra Jeune’). Cautín Prov.: *Crosby 11923* (L), Salto Palguín; *Neger 105* (L), Villarica. – Valdivia Prov.: *Neger 101* (S), Valdivia; *Crosby 12203* (L), Planta Hydroeléctrica Pilmaiquén; *Krause s.n.* (BM, sub no. *7* ex hb. Kindberg; S), *Dusén 283* (S, Z), Corral. – Osorno Prov.: *Crosby 12138* (L), Refugio; *Crosby 12257* (L), Anticura; *H. & W. Frey 95–13* (hb. Frey), Parque Nacional Puyehue. – Llanquihue Prov.: *Dusén A.67* (BM, HBG, L, S), Lago Llanquihue; *Van Zanten & Kruijer 86.01.836* (GRO p.p.), Ensenada; *Van Zanten 79.01.119* (GRO), Saltos de Petrohué; *Wolffhügel s.n.* (S), Lago de Todos los Santos. – Chiloé Prov.: Chiloé Is., *Crosby 12429* (L), Cordillera San Pedro; *Lechler, LPC 595* (BM, BR, L, NY, RO, S, W), Morro Gonzales. Aisén Prov.: *Darwin 463* (BM), Chonos Archipelago; *Crosby 16203* (L), Taitao Peninsula. – Magellanes Prov.: *Santesson 528* (S), Pto. Yartou; *Hooker s.n.* (BM, BR, L, TDC; BM, sub nos. *163* and *W. 154*; S, sub nos. *23* and *24* in hb. Kindberg), Cape Horn, Hermite Is. ARGENTINA. Río Negro: *Moreau (4667)* (CHR), Lago Frías. – Neuquén: *Moreau 6000* (S), Lago Espejo Grande; *Ljunger 1340* (S), Lago Nahuel Huapi. – Tierra del Fuego: *Skottsberg, Svenska Sydpolar Exp. 191* (S), Ushuaia; *Halle & Skottsberg 955* (BM, S), Lago Fagnano; *Matteri & Schiavone, MFE 46* (S, U), *MFE 51* (CHR), Bahia Buen Suceso; *Hettermite? s.n.* (BM), Fondeadero San Martín (‘Bay St. Martin’).

DUBIOUS ORIGIN: *unknown collector (H. 2181)* (BM; ‘Norfolk Is.’, see note 15); *unknown collector s.n.* (NY, “Figi”); *Tilden 324b* (BM, ‘Tahiti’).

4.2. **Hypopterygium elatum** Tixier — Fig. 18, 19; Map 11

Hypopterygium elatum Tixier, Rev. Bryol. Lichénol. 34 (1966) 152, f. 15. — Type: *Pételot 8* (PC holo?, not found), Vietnam, Hoang Liên So’n, Sa-Pâ, “Environs de Chapa”, Aug., 1927; lectotype: Tixier, Rev. Bryol. Lichénol. 34 (1966) f. 15; designated here; see notes 1 and 2.

Illustrations: Tixier, Rev. Bryol. Lichénol. 34 (1966) 153, f. 15.

Plants in groups of fans, pinnate to bipinnate or weakly palmate, medium-sized to large, not gemmiferous. *Stipe* up to 4.0 cm long, ascending (from probably a vertical substratum), dorsiventrally compressed (occasionally weakly irregularly compressed?), entirely glabrous or tomentose at base. *Frond* short-ovate to oblong, up to 6.0 cm in diameter; rachis and branches dorsiventrally compressed, glabrous; rachis growing in direction of stipe, (probably) roughly horizontal; branches up to 3.5 cm long. *Primordia* regularly set with scaly leaves; scaly leaves (deltoid to) ovate to oblong, margin entire. *Epidermis cells and cortical cells* equally wide or cortical ones wider; walls thin or incrassate, brown, yellow, or colourless; inclusions usually absent, occasionally present in cortex, tiny droplets, oil-like, colourless. *Central strand* present; cells equally wide to cortical ones or narrower, walls thin, brown, yellow, or colourless; inclusions absent or present, granules or clumps, fat-like, colourless (white). *Axial cavities* absent. *Axillary hairs* 2 or 3 per leaf, 2–4-celled; basal cells 1–3; terminal cell short to short-linear, ovate, elliptic, or obovate to nearly rectangular, straight or weakly curved, 35–80 μm long and 10–25 μm wide, ± smooth, walls thin. *Phyllotaxis*: of stipe octostichous; of rachis octostichous in basal and middle part, becoming tristichous in distal part; of branches tristichous. *Foliation*: of stipe isophyllous and not complanate; of rachis isophyllous or weakly anisophyllous and weakly complanate in basal part, distinctly anisophyllous and complanate in distal part; of branches distinctly anisophyllous, complanate. *Leaves* distant to closely set at stipe, closely set in frond, colourless (or brown near leaf base) in basal and middle part of stipe, colourless or green in distal part of stipe, green to dark green in frond, dull; insertion transverse in stipe leaves, becoming oblique or concave in frond leaves; laminal cells prosenchymatous or partly parenchymatous in basal half of stipe leaves, hexagonal to elongate-hexagonal, rectangular in leaf parts with a parenchymatous areolation, 20–50 μm long and 10–20 μm wide, walls thin, often very thin in stipe leaves (note 4). *Basal and distal stipe leaves* monomorphic, weakly or distinctly differentiated, appressed to erecto-patent, symmetrical, frequently damaged or lost; margin entire or weakly bitten or crenulate near apex to roughly bitten (note 4); border absent or faint near base, faint to distinct in distal part, 1–3 cells wide; apex rounded or emarginate; costa absent or faint, short, hardly extending leaf insertion. *Basal stipe leaves* scale-like, half-suborbicular to ovate, (0.5?–)1.0–1.5 mm long and 0.5–1.0 mm wide, usually damaged in distal part and then half transverse-elliptic and 0.2–0.5 mm long and 0.8–1.0 mm wide. *Distal stipe leaves* leaf-like, half transverse-elliptic to half-suborbicular, ovate, or elliptic, 0.5–2.0 mm long and 0.5–1.0 mm wide. *Frond leaves* partly monomorphic and partly dimorphic, probably frequently caducous at apex of ultimate frond axes; margin ± entire in basal leaves, becoming moderately serrate-dentate in distal ones; teeth 1-celled, up to 40 μm long, projecting up to 1/2 of cell length, up to 30; border distinct, continuous, 1–5 cells wide; apex gradually to abruptly acuminate; acumen 0.05–0.4 mm long. *Basal frond leaves* symmetrical or weakly asymmetrical, (short-ovate to) ovate, 1.0–3.0 mm long and 1.0–3.0 mm wide; costa distinct, reaching 4/5 of leaf length to percurrent. *Lateral frond leaves (in distal part of frond)* asymmetrical, ovate, 0.5–3.0 mm long and 0.5–1.5 mm wide; costa distinct, reaching 4.5 of leaf length to percurrent.

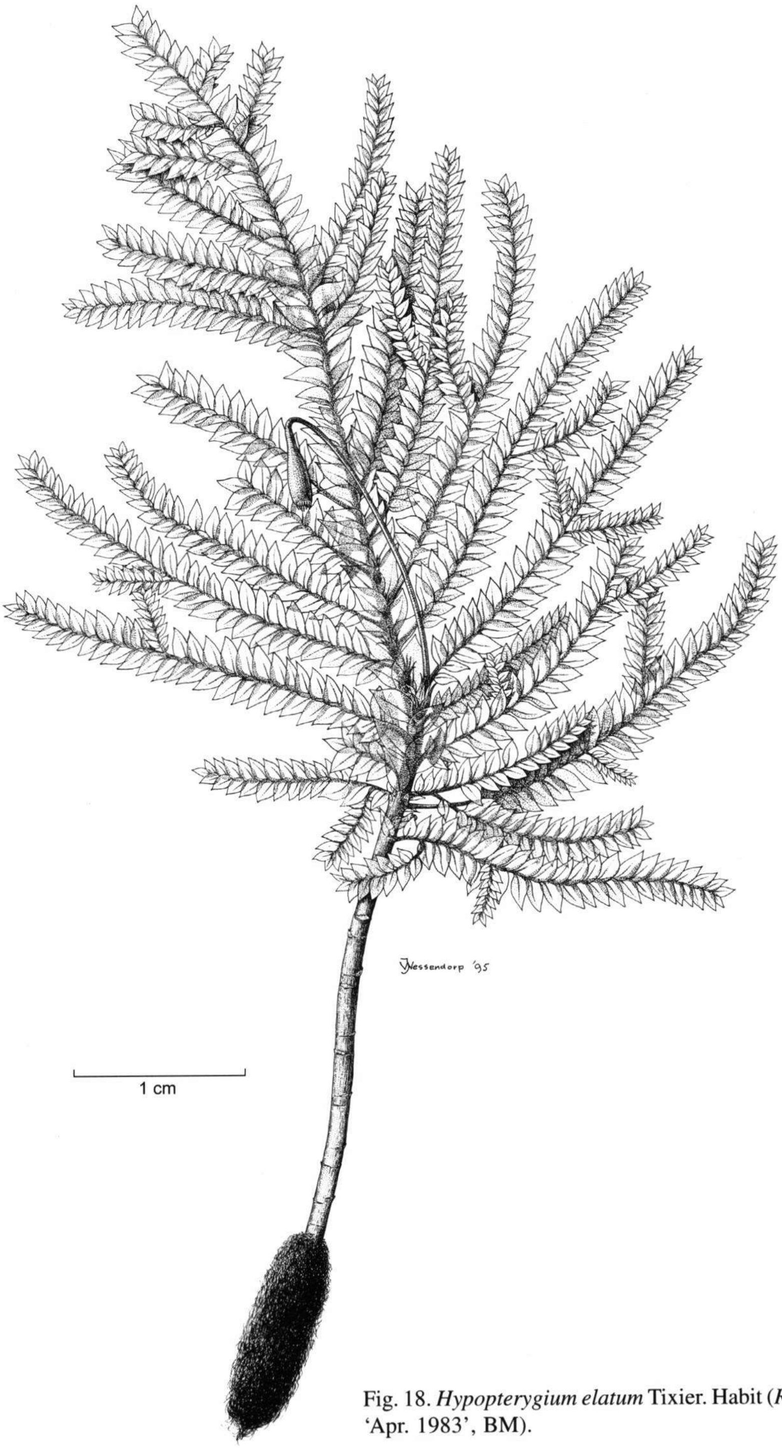


Fig. 18. *Hypopterygium elatum* Tixier. Habit (*Ratcliff s.n.,* 'Apr. 1983', BM).

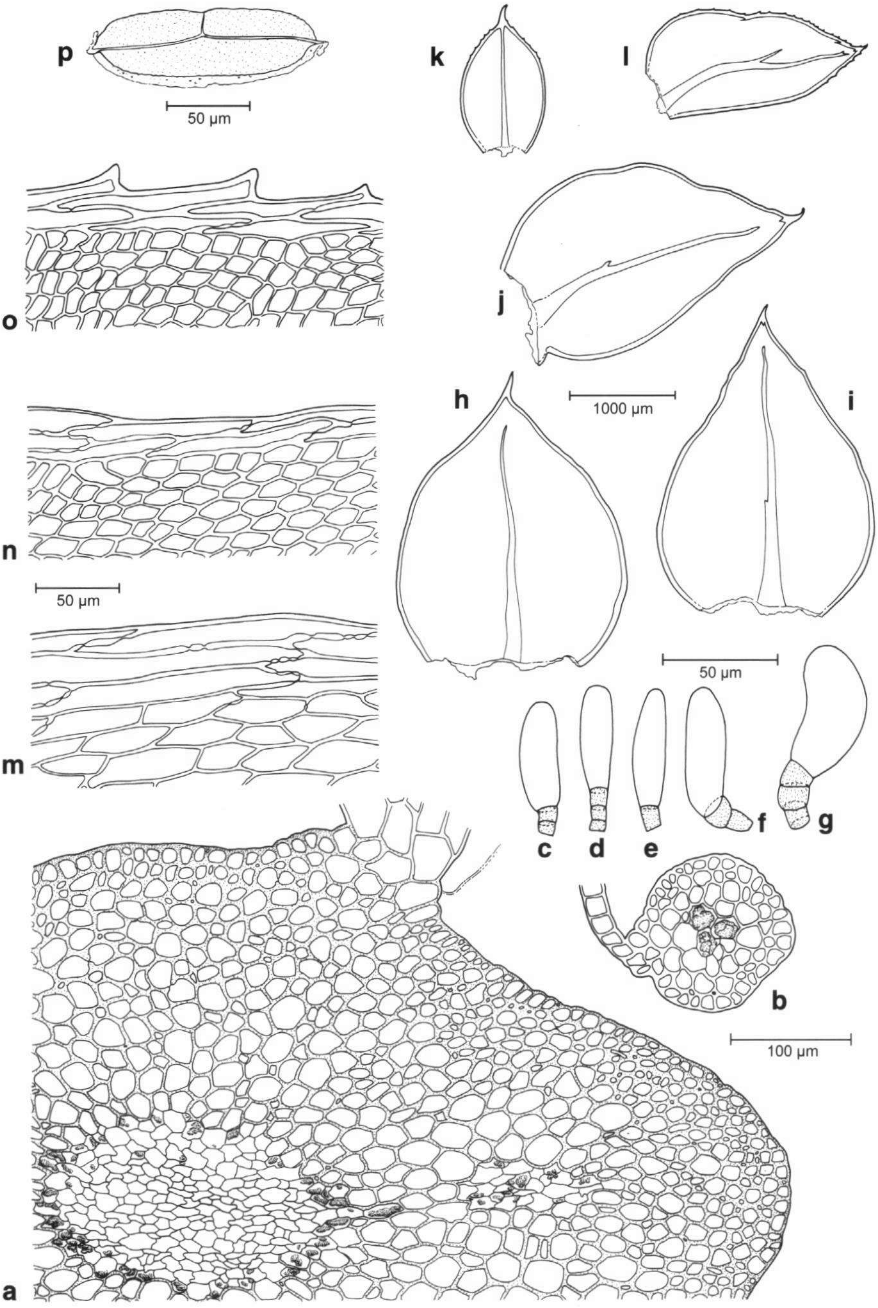
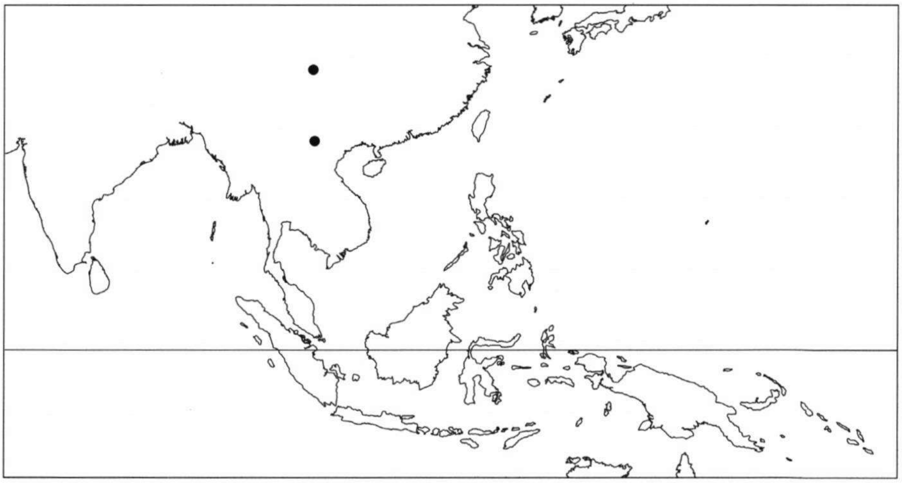


Fig. 19. *Hypopterygium elatum* Tixier. a. Rachis (cross section dorsal quadrant); b. branch (cross section); c–g. axillary hairs; h–j. rachis leaves (h. ventral, i. dorsal, j. lateral); k, l. branch leaves (k. amphigastrium, l. lateral); m–o. leaf cells of lateral frond leaves: m. rachis leaf (m. basal part of antical side, n. distal part of antical side), o. branch leaf (distal part of antical side); p. exostome tooth (cross section) (a–p: *Ratcliff s.n.*, 'Apr. 1983', BM).

Frond amphigastria (in distal part of frond) symmetrical, ovate to elliptic (or obovate), 0.5–2.5 mm long and 0.5–2.0 mm wide; costa distinct, reaching 4/5 of amphigastrium length to percurrent in basal part of rachis, percurrent in distal part of frond.

Dioicous(?). *Perigonia* not seen. *Perichaetia* in basal and middle part of rachis. *Perichaetial leaves* green; margin entire or weakly crenate; border absent or faint near leaf base, faint or distinct in distal part, but interrupted or not in acumen, 1–4 cells wide; apex gradually acuminate or subulate; costa faint to distinct, percurrent; laminal cells prosenchymatous or weakly parenchymatous near leaf base, prosenchymatous in distal part, short to elongate, hexagonal or somewhat rectangular in parenchymatous leaf parts. *Perichaetial stalk* 0.8–1.2 mm long, set with rhizoids at base. *Inner leaves*: of perichaetia short-ovate to elliptic; of perichaetia prior to sporophyte development up to 0.9 mm long and 0.9 mm wide, inner most ones frequently shorter or narrower, acumen up to 0.8 mm long; of full-grown perichaetia up to 2.0 mm long and 1.5 mm wide, acumen up to 1.1 mm long. *Archegonia* 0.4–0.8 mm long. *Vaginula* 1.4–1.7 mm long. *Gametoecial axillary hairs* c. 2 per gametoecial leaf (few observed), 3- or 4-celled; basal cells 2 or 3, brown; intermediate cells absent; terminal cell elongate (to short-linear?), ovate to elliptic, 65–80 µm long and 20–25 µm wide, colourless or pale brown, smooth, wall thin. *Paraphyses* absent.

Sporophytes up to 5 per frond. *Seta* ascending, uncinate, c. 17 mm long, ochraceous, smooth or weakly mamillate near base of capsule. *Capsule* inclined to horizontal, oblong-ellipsoid, 2.0–3.0 mm long and 1.0–1.5 mm wide, smooth or weakly mamillate, ochraceous; neck ± smooth; annulus unknown. *Peristomial formula OPL:PPL:IPL* = 4:2:6–8(–10)c. *Exostome* ochraceous; teeth 590–675 µm long and 150–160 µm wide, entirely bordered, not shouldered; dorsal side cross-striate in basal half of teeth, becoming coarsely papillose above; dorsal plates broader than ventral ones, 15–23 µm thick; ventral plates 20–23 µm thick. *Endostome* perforate, moderately to densely papillose; basal membrane reaching 1/3 of length of exostome teeth; processes project-



Map 11. Distribution of *Hypopterygium elatum* Tixier.

ing 590–600 µm beyond orifice and 85–100 µm wide at base, not nodulose, not appendiculate; cilia 1–4 cells wide, up to 10 cells long at least, weakly nodulose or not, laterally appendiculate by plate parts of a single cell or not. *Operculum and calyptra* unknown. *Spores* 12–17 µm.

Distribution — China (Sichuan), Vietnam.

Habitat & Ecology — Not known.

Geographical variation — With only 6 specimens known from only 2 localities, *H. elatum* is the least well-known *Hypopterygium* species. Plants from the same locality are very similar, but show minor differences with the plants from the other locality.

The frond leaves of the Vietnamese plants are more closely set than those of the Chinese plants. In addition, the Vietnamese specimens have a slightly longer stipe, a slightly shorter rachis, and slightly shorter branches. These stem parts measure, respectively, up to 4.0 cm, 4.5 cm, and 2.5 cm in length in the Vietnamese plants, and up to 3.0 cm, 5.6 cm, and 3.5 cm in Chinese plants.

Notes:

Nomenclature — 1. The type collection of *H. elatum* was not found. Tixier (1966) based his study on specimens preserved in the herbaria of Henry and Thériot (see also note 2), which are kept in PC. However, the type was neither found among the material on loan from PC nor during visits to PC. It is absent in the general herbarium of PC and Thériot's herbarium, but perhaps it has been mislaid in Henry's herbarium. Tixier (in litt.) suggested to select a neotype. In the present study the type material of *H. elatum* is considered missing, but because Tixier's (1966) original description of the species is provided with illustrations, the selection of these illustrations as the lectotype is sufficient.

2. The name *H. elatum* is almost certainly based on a provisional name given by Thériot and Henry. Tixier's (1966) publication was partly based on Henry's studies of mosses from Tonkin. Henry's (1928) Tonkinese material was mainly gathered by V. Demange and A. Pételot. Largely based on this material Henry published a paper on the mosses of the Far East in 1928 with the assistence of Thériot (Gaume, 1963; Tixier, 1966). Henry prepared a second paper on this subject (Gaume, 1963; Tixier, 1966), which should have been published in 1932. Henry's unfinished work was revised by Tixier, who remarked that certain names for new species of mosses in Henry's work were similar to herbarium names in Thériot's herbarium, kept in PC. This is, with great certainty, also true for *H. elatum*, for Thériot and Henry labelled *Pételot 173*, which comes from Henry's herbarium and is kept in Thériot's, as a new species with the same name.

3. Although the holotype was not found (see note 1), it is almost certain that the specimens examined belong to this species. In particular, the specimens from Vietnam agree perfectly well with Tixier's (1966) description and illustrations. Moreover, they were gathered by Pételot on the same locality as the holotype, but one month earlier.

Description — 4. The stipe leaves at the basal and middle part of the stipe are almost always damaged or lost. Usually, when the stipe leaves are present, their distal part has totally disappeared or can be observed as slimy remains. This is caused by the degeneration of the very thin-walled margin cells and laminal cells in the distal part of the leaf, which during degeneration apparently become slimy. This degeneration may also result in a bitten margin and an emarginate apex.

Reproduction — 5. There was only a single fruiting specimen among the specimens examined (*Ratcliff s.n.*, Apr., 1983), which was found on Mt Emei, China.

Other — 6. Tixier (1966) classified this species in *Hypopterygium* sect. *Tamariscina* Kindb.

Specimens examined (6 specimens):

CHINA: Sichuan ('Szechwan'). *Ratcliff s.n.* (BM, 'Apr., 1982'), *s.n.* (BM, 'Apr., 1982'), *s.n.* (BM, 'Apr., 1983'), Mt Emei ('Omei'). — VIETNAM: Hoang Liên So'n: *Pételot 9* (PC), *173* (PC), *s.n.* (S), Sa-Pâ.

4.3. Hypopterygium discolor Mitt. in Hook.f. — Fig. 20, 21; Map 12

Hypopterygium discolor Mitt. in Hook.f., Handb. N. Zeal. Fl. 2 (1867) 488, pro parte. — Syntypes: *Mossman s.n.* (NY lecto, designated here), New Zealand, North Island, North Auckland L.D., Kiapara Harbour ["Kiapara"], "Wairoa forests Kiapara"; *Knight s.n.* (not found), New Zealand, North Island, North Auckland L.D., Auckland; excluded from syntypes: *Jupp s.n.* (NY), New Zealand, North Island, North Auckland L.D., Auckland. — Merged with *Hypopterygium scottiae* Müll.Hal. by Mitten, Trans. & Proc. Roy. Soc. Victoria 18 (1882) 76. — Synonymised with *Hypopterygium rotulatum* (Hedw.) Brid. by Dixon, New Zealand Inst. Bull.3, 5 (1927) 296. See notes 1 and 2.

Hypopterygium scottiae Müll.Hal., Linnaea 35 (1868) 619. — Syntypes: *Scott s.n.* (B destroyed; BM lecto, designated here; NY), Australia, Queensland, Hunter River, Ash Is. "Ash Island ad or. flum. Hunter litor. orient. Novae Hollandiae"; *Dietrich s.n.* (B destroyed; BM; BM, '1864'; HBG, sub no. *7645*, '1863–1865'; JE; JE, '1865'; NY; MEL, sub no. *451*; S, '1864', ex hb. Müller, sub nos. *2*, *25*, and *34* in hb. Kindberg; S, W), Australia, Queensland "Austral. or. aeq.", Brisbane River. — See note 3. — Merged with *Hypopterygium discolor* Mitt. in Hook.f. by Mitten, Trans. & Proc. Roy. Soc. Victoria 18 (1882) 76. — Based on Mitten's l.c. synonymy, merged with *Hypopterygium rotulatum* (Hedw.) Brid. by Dixon, New Zealand Inst. Bull.3, 5 (1927) 296; inclined to be merged with *Hypopterygium muelleri* Hampe by Dixon, Proc. Roy. Soc. Queensland 53 (1941) 36. — See note 4.

Illustrations: none.

Plants usually in groups of dendroids and palmate to umbellate, rarely in groups of fans and flabellate, medium-sized to large, usually not gemmiferous, rarely gemmiferous (note 5). *Stipe* up to 3.0 cm long, usually (ascending to) vertical, rarely horizontal, entirely dorsiventrally compressed or laterally compressed in basal third, glabrous but tomentose at base. *Frond* subcircular to elliptic, up to 3.5 cm in diameter; rachis and branches dorsiventrally compressed, glabrous, occasionally caducous near apex; rachis bend from stipe to roughly horizontal; branches up to 2.5 cm long. *Primordia* occasionally set with scaly leaves; scaly leaves deltoid to triangular or oblong-ovate, margin entire. *Epidermis cells and cortical cells of stipe, rachis, and branches* equally wide or epidermis cells (of rachis and branches) and outer cortical cells (of stipe, rachis, and branches) narrower than inner cortical ones; walls thin or incrassate in epidermis cells and outer cortical cells, thin in inner cortical cells, brown to yellow in stipe, yellow or colourless in rachis and branches; inclusions absent. *Central strand* present; cells narrow, walls thin or incrassate in stipe, thin in rachis and branches, ochraceous in stipe, colourless in rachis and branches; inclusions frequently present in outer strand cells, less frequently in inner ones, plates, granules, or droplets, fat-like, colourless (white or hyaline). *Axial cavities* absent. *Axillary hairs* 2–4 per leaf, 2- or 3-celled; basal cells 1 or 2; terminal cell short to elongate, elliptic to ovate or rectangular, 30–70 μm long and 10–30 μm wide, colourless, smooth or verrucose and weakly covered with colourless (white) and wax-like substances, wall thin or incrassate. *Phyllotaxis*: of stipe tristichous or nearly so (4/11) in basal third; of rachis, and branches tristichous. *Foliation*: of stipe isophyllous, not complanate in basal part, weakly complanate or not in distal fourth; of rachis and branches anisophyllous, weakly to distinctly complanate in basal third of rachis, distinctly complanate in distal part of rachis and at branches. *Leaves* distant at stipe, becoming closely set in frond, usually green to dark green, rarely yellowish green, dull or weakly glossy; insertion transverse, oblique, or concave, becoming concave in lateral frond leaves, usually becoming trans-

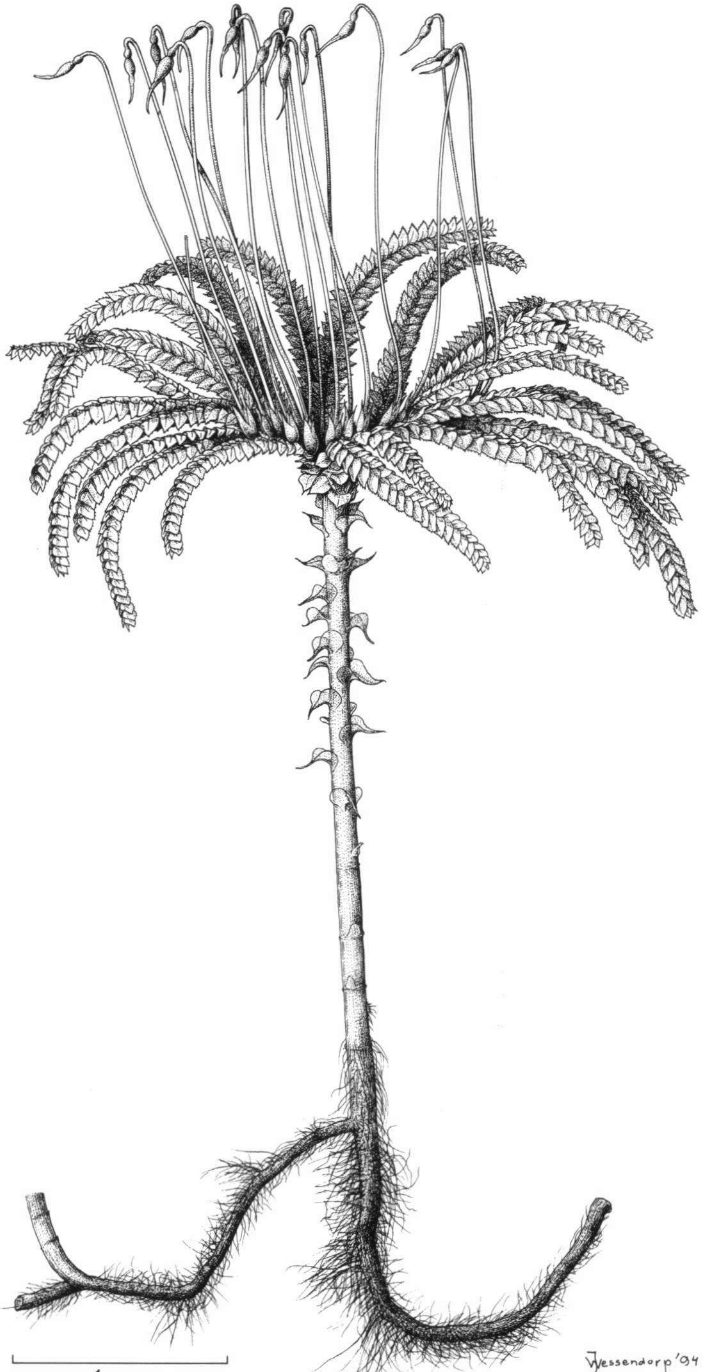


Fig. 20. *Hypopterygium discolor* Mitt. Habit (*Dietrich s.n.*, S).

verse or transverse-flexuose in frond amphigastria; laminal cells prosenchymatous or weakly parenchymatous near base of stipe leaves, hexagonal, short to elongate, 15–60 µm long and 15–25 µm wide; walls thin, weakly porose or not. *Basal and distal stipe leaves* monomorphic or mainly so, not or weakly differentiated, erecto-patent to widely patent or weakly recurved, symmetrical, straight or weakly recurved, broad-ovate to short-ovate; margin ± entire, partly recurved or not; border distinct, continuous, 2–4 cells wide; apex abruptly acuminate; acumen 0.15–0.4 mm long; costa distinct, reaching 1/2–2/3 of leaf length. *Basal stipe leaves* (scale- to) leaf-like, 0.5–0.7 mm long and 0.5–1.0 mm wide. *Distal stipe leaves* leaf-like, 0.7–1.5 mm long and 1.0–1.5 mm wide. *Frond leaves* dimorphic, occasionally caducous in distal part of ultimate frond axes; margin entire or weakly serrate-dentate in basal rachis leaves, (weakly to) coarsely serrate-dentate in distal frond leaves; teeth 1- (or 2-)celled, uniseriate, up to 40 µm long, projecting up to 1/3 of cell length, in distal lateral frond leaves 25–35; border distinct, but frequently becoming faint or narrow in distal part of leaf, 1–4 cells wide, green to dark green; apex abruptly acuminate; acumen 0.05–0.1 mm long in lateral leaves, 0.15–0.4 mm long in amphigastria. *Lateral frond leaves (in basal and distal part of frond)* asymmetrical, broad-ovate to short-ovate in basal part of frond, becoming short-ovate (or elliptic) in distal part, (0.5–)1.0–1.5 mm long and 0.5–1.5 mm wide; *costa* distinct, reaching c. 2/3 of leaf length. *Frond amphigastria (in basal and distal part of frond)* symmetrical, broad-ovate to short-elliptic, 0.5–1.0(–1.5) mm long and 0.5–1.5 mm wide; costa distinct, reaching 1/2 of amphigastrium length to percurrent. *Gemmae clusters* (when present) located in distal half of rachis or branches, in particular at damaged plants, reaching up to entire length of covering lateral leaves or somewhat longer. *Gemmaphores* 3–6 cells long, branched, brown. *Gemmae* simple, 6 cells long at least, colourless or brown; cells 15–45 µm long and 10–30 µm wide.

Dioicous. *Gametoecia* in basal and middle part of rachis and branches. *Gametoecial leaves* green; margin entire; border distinct, but frequently absent or faint in acumen, continuous or interrupted, 1–3 cells wide; apex gradually or abruptly acuminate; costa absent from perigonial leaves, absent or faint in perichaetial leaves and reaching 1/3–4/5 of leaf length; laminal cells prosenchymatous, short to short-linear, hexagonal. *Inner leaves*: of perigonia suborbicular to elliptic, up to 1.2 mm long and 1.2 mm wide, acumen up to 0.3 mm long; of perichaetia prior to sporophyte development ovate, up to 0.7 mm long and 0.6 mm wide, acumen up to 0.3 mm long; of full-grown perichaetia ovate to elliptic, up to 1.7 mm long and 1.6 mm wide, acumen up to 0.4 mm long. *Antheridia* c. 0.7 mm long. *Stalk in full-grown perichaetia* 0.8–1.0 mm long, set with rhizoids. *Archegonia* c. 0.5 mm long. *Vaginula* 0.6–1.0 mm long. *Gametoecial axillary hairs* up to 3 per gametoecial leaf, 2- or 3-celled, simple; basal cells 1 or 2; intermediate cells absent; terminal cell short to elongate, elliptic to obovate, 35–65 µm long and 14–22 µm wide, smooth, wall thin (or incrassate). *Paraphyses* absent from perigonia, absent or few and persistent in perichaetia, 8–10 cells long, colourless or pale brown; basal cells 1 or 2; intermediate cells transverse to short-linear, elliptic to rectangular; terminal cell oblong to short-linear, ovate to rectangular, 45–80 µm long and 10–20 µm wide, inflated or not.

Sporophytes up to 30 per frond. *Seta* ascending or vertical, straight to flexuose, uncinate, 9–40 mm long, ochraceous to brown. *Capsule* horizontal to pendulous,

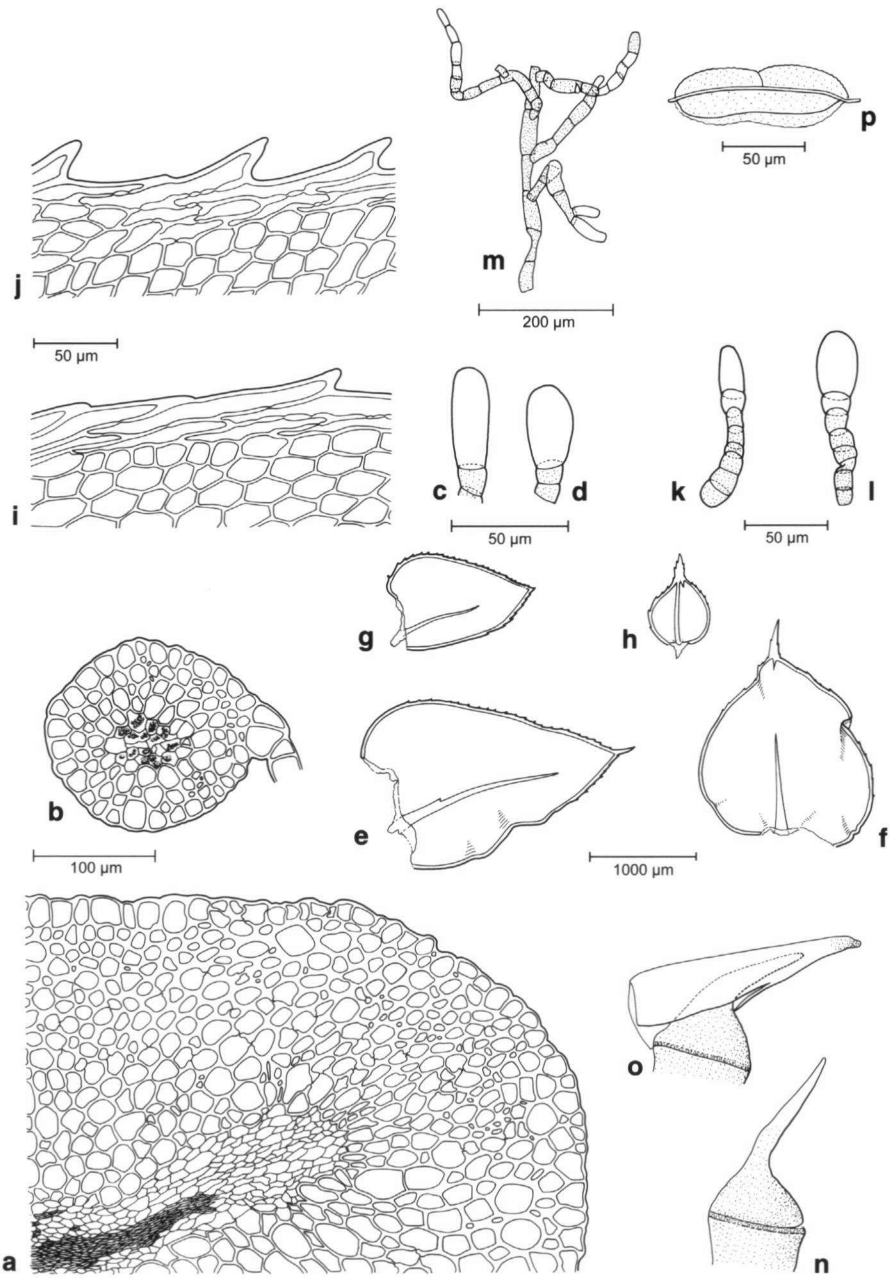


Fig. 21. *Hypopterygium discolor* Mitt. a. Rachis (cross section dorsal quadrant, tissue of central strand partly compressed); b. branch (cross section); c, d. axillary hairs; e, f. rachis leaves (e. lateral, f. amphigastrium); g, h. branch leaves (g. lateral, h. amphigastrium); i, j. leaf cells of lateral rachis leaf (i. basal part of antical side, j. distal part of antical side); k, l. paraphyses; m. part of a gemmaphore with gemmae; n. operculum; o. calyptra; p. exostome tooth (cross section) (a–m: *Robbins 3946*, L; n, o: *unknown collector s.n.*, L, ex hb. Mitten; p: *Wild s.n.*, MEL).

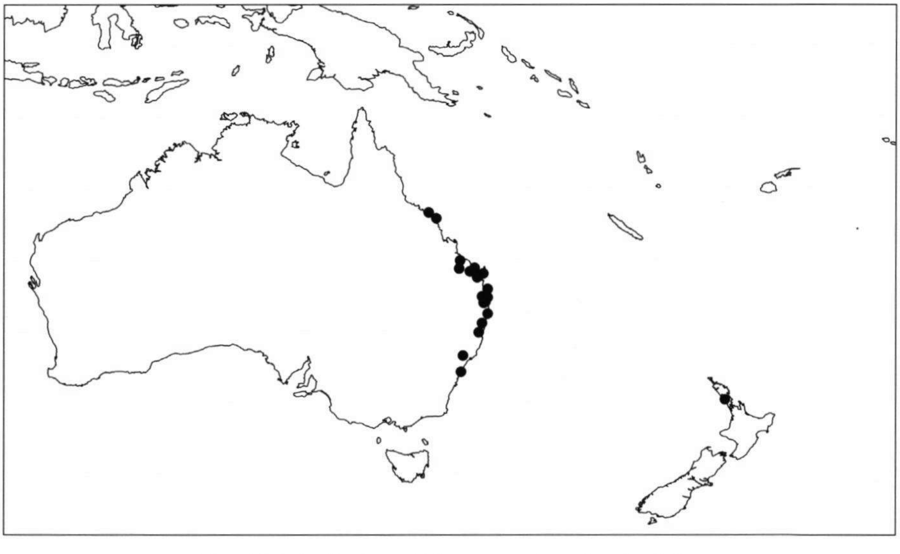
barrel-shaped to narrowly ellipsoid, 1.4–2.0(–2.5) mm long and 0.9–1.5 mm wide, brown; neck weakly pustulose or not; annulus distinct.

Peristomial formula OPL:PPL:IPL = 4:2:6–10c. *Exostome* yellow; teeth 540–640 µm long and 125–160 µm wide, entirely bordered, weakly shouldered or not; dorsal side striate in basal half of teeth, becoming coarsely papillose in distal part; dorsal plates broader than or equally wide as ventral ones, 10–12 µm thick; ventral plates 14–22 µm thick. *Endostome* perforate, weakly to densely papillose at both faces; basal membrane reaching c. 1/2 of length of exostome teeth; processes c. 490 µm projecting beyond orifice and 55–60 µm wide at base, not nodulose, not appendiculate; cilia 1–4, 1–4 cells wide, up to 15 cells long, nodulose or not, laterally appendiculate by (parts of) plates of a single or a few cells. *Operculum* 1.5–2.0 mm long. *Calyptra* 2.0–2.5(–3.0) mm long, membranous in basal half, becoming fleshy in distal half. *Spores* 10–15 µm.

Distribution — Australia (Queensland, New South Wales), New Zealand (North Island). Restricted to the eastern coastal regions of Queensland and New South Wales in Australia, and the northern part of North Island in New Zealand.

In New Zealand the species was found in the Wairoa forests near Kiapara Harbour, but the origin of the New Zealand specimens was only recorded for the lectotype of *H. discolor*. Recent collections of *H. discolor* from New Zealand are absent from the material examined. It is not known whether the species has become extinct in New Zealand, or if the old specimens from New Zealand are mislabelled.

Habitat & Ecology — In riverine rain forests, monsoon forests with dense shrubby understorey, and dry monsoon scrubs, also found in 'native vineyards', most frequently in shade, near streams or in damp places, also in dry places, once found on semi-shaded grassy ground, once found on dunes. Terrestrial, frequently found on sandy soil, once found on tree roots. Altitude: 40–330 m.



Map 12. Distribution of *Hypopterygium discolor* Mitt.

Most collection sites are very close to the coast or to estuaries. The species occurs in Australia at the east coast between Port Denison and Parramatta, and, in Queensland, a little more land inwards in the monsoon forests near Calliope and Monto, where it grows near streams and gullies. See also note 7 and 8.

Variability — The species shows most variation in stipe length and frond diameter. The number of branches and sporophytes per gametophore is also highly variable.

Geographical variation — Not found.

Ecological variation — Not found (insufficient data).

Notes:

Nomenclature — 1. The typification of *Hypopterygium discolor* is difficult. Types that are presented as *H. discolor* were not found in Mitten's (NY) nor in Hooker's (BM) herbarium. In these herbaria there are only a few collections that are labelled as *H. discolor*, and not one of these were gathered by Knight, Jupp, or Mossman.

Among all the material that is of concern here, no collection was found that was made by Knight and might be of any importance in the typification of *Hypopterygium discolor*.

However, among the collections in Mitten's herbarium that are attached to a sheet bearing the name of *Hypopterygium scottiae* Müll.Hal., there is a collection from Auckland made by Jupp, and another one from the Wairoa forests near Kiapara Harbour made by Mossman. Because Mitten (1882) himself merged his *H. discolor* with *H. scottiae* it can be safely assumed that these specimens represent two of the syntypes.

Jupp's specimen, however, belongs to *Hypopterygium didictyon* Müll.Hal., and is not conspecific with Mossman's plant. Although Mitten's description of *H. discolor* does not allow the reader to differentiate it clearly from *H. didictyon* (see note 2), the species that Mitten (in Hooker f., 1867) had in mind is entirely different from the latter. Mitten not only distinguished his species from *H. novaeseelandiae* Müll.Hal., which is conspecific with *H. didictyon*, but he also stated that his *H. discolor* is larger and does not turn yellow when dry. These differences represent indeed characters that generally can be used to distinguish these species. In addition, among all specimens examined three were found that were actually seen by Mitten, and are presented as *H. discolor*. These are not conspecific with *H. didictyon*, and definitely belong to a separate species. At least one of these specimens (*unknown collector s.n.*, BM), which comes from Ash Island, Australia, was identified by Mitten himself, in 1891. The other two, which are duplicates and have an unknown origin (*unknown collector s.n.*, L, NY), were possibly also identified by Mitten. They come originally from his herbarium, and were preserved in Elizabeth Britton's herbarium (NY). Mossman's plant is conspecific with these three specimens, and agrees best with Mitten's description. Therefore, Jupp's specimen must be excluded as a syntype of *H. discolor*, and Mossman's was designated as its lectotype.

2. Because two specimens that belong to different species were included in the type material of *Hypopterygium discolor* (see note 1), Mitten's (in Hooker f., 1867) description is almost certainly partly based on *H. novaeseelandiae* Müll.Hal. (= *H. didictyon* Müll.Hal.). The description of the perichaetia and the sporophyte is possibly based on Jupp's fruiting specimen, which belongs to *H. didictyon*, because Mossman's plant, which is the lectotype of *H. discolor*, bears no sporophytes and was almost certainly sterile.

Mitten's error is understandable with regard to the types examined. Both specimens are rather small for their species. Mossman's single plant is c. 2.0 cm tall, whereas the plants in Jupp's specimen measure c. 1.0 cm at most. The gametophore of these types have a similar appearance in habitus. Both are palmate, and greyish green, although in Jupp's specimen parts of the frond are often also weakly yellowish green. Besides, most of the characters that were studied by Mitten are not at all distinctive, whereas Mitten's most useful features, i.e. differences in size and colour, only distinguish between the two species in general. Mitten described *H. discolor* as being larger than *H. novaeseelandiae*, and not turning yellow when dry.

3. The lectotype of *Hypopterygium scottiae*, collected by Helen Scott, is preserved in Hampe's herbarium kept in BM. It belongs to a set of three specimens, which are attached to the same sheet,

and are labelled in the same script. Two of them were gathered by Miss A. Dietrich near the Brisbane River, and are also syntypes of *H. scottiae.*

All three specimens are labelled as "*Hypopterygium scottiae* mihi". One of the two collected by Dietrich is labelled to come from Müller's herbarium, and it is certain that "mihi" stands for Müller here. Therefore, it is almost certain, that the other two collections, including the lectotype, were also seen by Müller.

One of the three specimens in JE that were gathered by Dietrich is the only other specimen among the ones examined that with certainty came from Müller's herbarium.

The other specimens cited as type specimens of *H. scottiae* in this study perfectly comply with the types cited by Müller (1868), and their plants match Müller's description perfectly well. They almost certainly belong to the set of syntypes, but there is no certainty that they actually belong to the collections that were studied by Müller.

Synonymy — 4. Dixon (1927) could not find features that separate *Hypopterygium discolor,* which included *H. scottiae,* from *H. rotulatum,* by which he had almost certainly *H. tamarisci* in mind. In 1941, Dixon suggested that *H. scottiae* is conspecific with *H. rotulatum,* because he could not find clear differences in the dentation of the leaves and amphigastria between the two species. However, *Hypopterygium discolor,* including *H. scottiae,* is very distinct from (Australasian and Australian) *H. tamarisci* by its often large and strikingly dendroid habit, and its persistent, coarsely serrate-dentate distal frond leaves with a green border. Plants of *H. tamarisci* are usually smaller and are either fans or less conspicuously dendroid. The distal frond leaves of *H. tamarisci* are usually entire or weakly serrate-dentate, and only rarely coarsely serrate-dentate, and have a colourless border.

Description — 5. In the material examined, gemmiferous plants were only observed in a few collections with damaged material, where the gemmae were usually found at damaged gametophores.

Reproduction — 6. There were 51 fruiting specimens among the specimens examined (c. 55%, including 2 plants with fertilised archegonia; n = 94). In 5 of them the female plants are mixed with male plants. The male/female ratio is approximately 0.41. In most collections with female plants fruiting plants were present.

Distribution — 7. *Hypopterygium discolor* was erroneously reported from Tasmania by Lett (1904) based on a plant that actually belongs to *H. tamarisci* (*unknown collector s.n.*, TDC).

8. According to Mitten (1882) the species also occurs on Mt Gambier, South Australia. This could not be verified, because Mitten's specimens from Mt Gambier were not found in the material examined.

Identification — 9. *Hypopterygium discolor* can usually easily be recognised from the other Australian and New Zealand *Hypopterygium* species by its persistent, coarsely serrate-dentate distal frond leaves and their green border. The distal frond leaves of both *H. tamarisci* and *H. didictyon* have a colourless border, and are usually entire or weakly serrate-dentate and less often, and less striking, coarsely serrate-dentate.

Hypopterygium discolor's larger, and striking, palmate to umbellate habitus separates it further from *H. tamarisci,* and prevents, in addition to the colour of the border, misidentification of the few plants of the latter species with coarsely serrate-dentate leaves.

The usually dark green to green colour of *Hypopterygium discolor* separates it further from *H. didictyon.* The few yellowish plants of *H. discolor* can easily be distinguished from those of *H. didictyon* by the tristichous (or nearly so) phyllotaxis of the stipe and basal part of the rachis and their elliptic to elongate-rectangular terminal cell of the axillary hairs, whereas in *H. didictyon* the stipe and the basal part of the rachis is octostichous and the terminal cell of the axillary hairs is usually short-linear-rectangular to linear. The few dark green plants of *H. didictyon* can easiliy be identified by these features.

Specimens examined (94 specimens):

AUSTRALIA: *Bauer s.n.* (W, s.loc.); *Eaves s.n.* (BM, MEL, S; 'Subtropical East Australia', s.loc.), *unknown collector (Eaves?) s.n.* (BM, FH; 'Subtropical East Australia', s.loc.); *unknown collector s.n.* (BM), Dangar? – Queensland: *Bailey s.n.* (MEL, s.loc.), *Fleischer? s.n.* (FH, s.loc.), *Simmonds*

(Q.87) (NSW, s.loc.), *Wild s.n.* (MEL, s.loc.), *unknown collector (Dietrich?) s.n.* (BM, s.loc.), *unknown collector s.n.* (CHR, s.loc.); *Tryon s.n.* (MEL), Inskip Point(?);*Tryon s.n.* (CHR, MEL), Ennogera Scrub(?); *Wild? s.n.* (MEL), Port Denison; *Van Zanten et al. 93.10.2806* (GRO), Whitsunday Coast; *Streimann 52517* (L), Calliope, Pine Mt; *Streimann 52819* (L), *52830* (L), Monto, Coominglah State Forest; *Smithurst 270* (MEL, NSW), *s.n.* (MEL, S), Bundaberg; *Forster 3273* (CBG), St. Agnes Creek; *Carriage s.n.* (CBG), Mary River, Maryborough; *Robbins 3946* (L), N of Gympie, Ramsay's Scrub; *Borough 4* (CBG, L), Fraser Is., Bogimbah Scrub; *Van Zanten et al. 93.10.2339* (GRO), Jandina–Northarum; *Bailey s.n.* (MEL), *Dietrich s.n.* (BM, JE, NY, W, S; HBG, sub no. *7645*; MEL, sub no. *451*), *Scott s.n.* (NY), Brisbane River; *McLeay s.n.* (NY), *Scott s.n.* (BM), *s.n.* (NY), *unknown collector s.n.* (BM), Hunter River, Ash Is.; *Kelleway s.n.* (MEL), *Von Mueller s.n.* (BM), *Muller s.n.* (NY), *unknown collctor s.n.* (BM), Moreton Bay; *Wild s.n.* (CHR, MEL), *s.n.* (MEL), Pimpama [Scrub]; *Simmonds (Q.137)* (NSW), Tambourine. – New South Wales: *Woolls s.n.* (W, s.loc.); *Watts 1028* (Z), *3409* (CHR), *3412* (NSW), *s.n.* (BM, S), *s.n.* (S), Ballina; *Camara s.n.* (MEL), *Stackhouse M6* (JE, MEL), *s.n.* (JE, S), *unknown collector (20)* (S, W), Richmond River; *Von Mueller s.n.* (BM), *Watts 143* (CHR), Clarence River; *Rudder s.n.* (MEL), Bellingen & Macleay Rivers; *Von Mueller s.n.* (BM), *s.n.* (MEL), *s.n.* (NY), Paramatta; *Woolls s.n.* (MEL), Cabramatta. — NEW ZEALAND: *Knight 53* (BM, NY; s.loc.), *Reader s.n.* (NY p.p., s.loc.). – North Island. North Auckland L.D.: *Mossman s.n.* (NY), Kaipara Harbour, Wairoa forests.

ORIGIN UNKNOWN: *Henderson s.n.* (NY p.p.), *unknown collector s.n.* (L, NY; "Ex herb. Wm. Mitten"), *unknown collector s.n.* (S).

4.4. **Hypopterygium flavolimbatum** Müll.Hal. — Fig. 22–26; Map 13

Hypopterygium flavolimbatum Müll.Hal., Syn. Musc. Frond. 2 (1850) 10, '*flavo-limbatum*'. — Type: collector's name not cited (B holo, destroyed), Nepal; *Wallich s.n.* (NY neo, designated here), Nepal; possible duplicates of the neotype: *Wallich s.n.* (FH, hb. Sullivant), Nepal. — No original type material was found and it is not known where specimens of this type material might be preserved, if still in existence. — See notes 1 and 2.

Hypopterygium tibetanum Mitt., J. Proc. Linn. Soc., Bot., Suppl. 1 (1859) 148, syn. nov. — Types: *Thomson 682* (NY holo, BM, W?), India, Jammu & Kashmir, Ladakh ["Tibet"], Nubra, alt. 11,000 ft, ["occid. reg. temp."], Sept. 1, (18)49; probable isotype: *Thomson s.n* (NY), India, Jammu & Kashmir, Ladakh ["Tibet"], Nubra, alt. 11,000 ft. — The specimen that is preserved in W comes from Hooker f. and Thomson's East Indian herbarium. Its label bears the number *682*, but lacks a collector's name and information about when and where the specimen was collected. — A specimen collected by Thomson in western "Tibet" that is preserved in Kindberg's herbarium (S) might also be type material, but there is no evidence to prove this. — Ladakh is also known as Little Tibet. — See note 3.

Hypopterygium aristatum Bosch & Sande Lac., Bryol. Jav. 2 (1861) 12, t. 141, syn. nov. — Syntypes: *unknown collector s.n.* (L lecto, designated here), Indonesia, Java, s.loc., "Inter specimina *H. struthiopteris* Hb. Dz. & Mb." ["inter specimina *H. struthiopteris* in m. Gede lecta, Herb. Dz. & Mb."], "al wat wij bezitten! Niets verloren gegaan"; *Motley s.n.* (NY), Indonesia, Java, Mt Pangerango, "Java in regione super[iore] montis Pangerongo alt. 7–10,000"'. — The Dutch remark on the label of the lectotype "al wat wij bezitten!" (all what we possess) is probably by the hand of Van den Bosch, and the remark "Niets verloren gegaan" (nothing lost) is written by Van der Sande Lacoste. — See note 4.

Hypopterygium japonicum Mitt., J. Linn. Soc., Bot. 8 (1864, '1865') 155, syn. nov. — *Hypopterygium tamarisci* (Sw.) Brid. ex Müll.Hal. subsp. *japonicum* (Mitt.) Kindb., Hedwigia 40 (1901) 288. — Type: *Oldham s.n.* (NY holo, FH, S; BM n.v.), Japan, Nagasaki Pref., Nagasaki, ["1861"]. — Mitten, J. Linn. Soc., Bot. 8 (1864) 148, reported that Oldham's material was deposited in Hooker's herbarium, which is nowadays kept in BM. I could not trace this material. — See notes 5 and 6.

Hypopterygium apiculatum Thwaites & Mitt. in Mitt., J. Linn. Soc., Bot. 13 (1873) 309, syn. nov. — *Hypopterygium spiculatum* Erdtman, An Introduction to Palynology 3 (1965) 122, nom.

inval., err. typogr. pro *Hypopterygium apiculatum* Thwaites & Mitt. — Type: *Thwaites CM 129* (NY holo, BM, S, W), Sri Lanka ["Ceylon"], Central Prov. — According to Mitten, J. Linn. Soc., Bot. 13 (1873) 294, the description of the species has been written by himself. — Thwaites & Mitten, in Mitten, J. Linn. Soc., Bot. 13 (1873) 309, did not indicate a collector's number for Thwaites' type collection. — See note 7.

?: *Hypopterygium fauriei* Besch., Ann. Sci. Nat. Bot. 7, 17 (1893) 391. — Syntypes: *Faurie 896* (not found), N Japan, Aomori Pref., Mt Koibashi, July, 1886; *Textor s.n.* (not found), Japan, exact locality not given. — Suggested in the synonymy of *H. japonicum* Mitt. by Tan et al., Bryologist 97 (1994) 132. — There is a possibility that syntypes are still in existence in Bescherelle's herbarium, kept in BM, but they were not in the material that I have examined; duplicate specimens were also not found in the material from other herbaria. — Noguchi, J. Hattori Bot. Lab. 7 (1952) 5, cited *Faurie 986* as type material, but this is incorrect if this collection has not been mislabelled. It is true that this collection was made by Faurie in northern Japan, presumably in July 1886, in the Aomori Pref., but it comes from a different locality, which is Mt Hakkoda. Material of *Faurie 986* is preserved in FH, PC, and S. — See notes 5, 8, and 9.

Hypopterygium canadense Kindb., Rev. Bryol. 26 (1899) 46. — Type: *Newcombe (365)* (S holo, sub no. *22* in hb. Kindberg; S, *s.n.*), Canada, British Columbia, Queen Charlotte Islands, on limestone rocks with *Asplenium viride* Huds. ["sur les rochers avec la fougère boréale *Asplenium marinum*"]. — Synonymised with *Hypopterygium japonicum* Mitt. by Holzinger, Bryologist 17 (1914) 44. — Synonymised with *Hypopterygium fauriei* Besch. by Lawton, Moss Flora of the Pacific North West (1971) 247. — See note 10.

Hypopterygium fauriei Besch. subsp. *solmsianum* Müll.Hal. ex Kindb., Hedwigia 40 (1901) 286. — ***Hypopterygium solmsianum*** (Müll.Hal. ex Kindb.) M. Fleisch., Musc. Buitenzorg 3 (1908) 1081, nom. nud. in syn. (*Hypopterygium aristatum* Bosch & Sande Lac.). — Type: *Solms-Laubach s.n.* (S holo; B destroyed; FH, 'Solms'), Indonesia, Java, Mt Gedeh (G. Gedé). — Synonymised with *Hypopterygium aristatum* Bosch & Sande Lac. by Fleischer l.c. — Van der Wijk et al., Regnum Veg. 33 (1964) 183, erroneously regarded Kindberg's l.c. subspecies as a species given in the synonymy of *Hypopterygium fauriei* Besch. and hence treated it as a nomen nudum.

Hypopterygium delicatulum Broth., Leafl. Philipp. Bot. 2 (1909) 656, syn. nov. — Type: *Elmer 10386* (H-BR holo, BM, FH, JE, L, NY, S, W, Z; '10385'), Philippines, Negros, Negros Oriental, Cuernos Mts, Dumaguete, ["ad truncos putridos"], June, 1908. — It is almost certain that Brotherus, Leafl. Philipp. Bot. 2 (1909) 656, erroneously cited the collection number of Elmer's type as "10385". — See notes 11, 12, and 13.

?: *Hypopterygium formosanum* Nog., Trans. Nat. Hist. Soc. Formosa 26 (148) (1936) 40, f. 3, 9–13, syn. nov. — Type: *Noguchi 7200* (NICH holo? not found), Taiwan ("Formosa"), Tainan Prov., Mt Kodama, on the moist soil in the forest, Aug., 1932. — The type is also depicted by Noguchi, J. Hattori Bot. Lab. 7 (1952) 6, f. 7. — See notes 14 and 15.

Hypopterygium sasaokae Dixon, Rev. Bryol. Lichénol. 13 (1942) 15. — Type: *Sasaoka 4648* (BM holo, TNS n.v.), Japan, Kyushu, Kumamoto Pref. (Higo Prov.), Aida, on ground; paratype: *Sasaoka 5371* (BM, TNS n.v.), Japan, Honshu, Nara Pref. (Yamoto Prov.), Mt Oodaigahara, on ground. — Synonymised with *Hypopterygium japonicum* Mitt. by Noguchi, J. Jap. Bot. 29 (1954) 85; Noguchi l.c. identified the paratype as *H. fauriei* Besch. — See note 16.

Hypopterygium acuminatum Dixon, Rev. Bryol. Lichénol. 13 (1942) 15, syn. nov. — *Hypopterygium japonicum* Mitt. var. *acuminatum* (Dixon) Nog., J. Hattori Bot. Lab. 7 (1952) 22. — Type: *Sasaoka 6047* (BM holo, TNS? n.v.), Japan, Ryukyu Arch., Okinawa Island, Oogimi, ["rock"], Dec. 27, 1930. — Dixon, Rev. Bryol. Lichénol. 13 (1942) 16, erroneously cited the type as being labelled "6097". — See note 17.

Hypopterygium vietnamicum Pócs, Rev. Bryol. Lichénol. 34 (1967, '1966') 806, pl. (3) 49, syn. nov. — Type: *Pócs 2574/a* (BP holo, GRO), NW Vietnam, Hoang Liên So'n, "Ad truncos Quercorum in silvis montanis, ad cacumine supra opp. SAPA / etiam in rupibus calcareis umbrosis/." ["in rupibus calcareis umbrosis & ad corticem Quercus in silva saxosa suppra opp. Sa-pa"], alt. 1785 m ["1700 m"], Sept. 27, 1963 ["Legi 28.X.1963"]. — See notes 18 and 19.

?: *Hypnum rotulatum* auct. non Hedw.: Griffith, Notul. Pl. As. 2 (1849) 478; Icon. Pl. As. 2 (1849) pl. 98, f. 1. — See note 20.

Hypopterygium aristatum Dozy & Molk. ex M. Fleisch., Musci Frond. Archipelagi Indici, Serie 2 (1899) 100, nom. nud., probably err. pro *Hypopterygium aristatum* Bosch & Sande Lac. Original material: *Fleischer, MFAI 100* (BM, FH, JE, L, NY, U, Z), Indonesia, W Java (Jawa Barat), "Bei Tjibodas im Urwald an Stämmen", alt. 1500 m, March 1899.

Hypopterygium emodi Müll.Hal. ex Kindb., Hedwigia 40 (1901) 292, nom. nud. in syn.; Müll.Hal. in Levier, Bryoth. Levier (1899–1908) 1333, nom. nud., year and date of distribution not found, presumably distributed before 1901. — Original material: *Gollan, Bryoth. Levier 1333* (BM; FH, '1894'; FH, '5500 ft'; NY; S), India, Uttar Pradesh, NW Himalaya, Dehra Dun, Mussooree (Mussoorie), Arnigadh, alt. 6000–7000 ft, June 23, 1895. — Synonymised with *Hypopterygium flavolimbatum* Müll.Hal. by Kindberg l.c. — Three other collections in this exsiccata series are also presented as material of the 'new' species *Hypopterygium emodi* Müll.Hal. Specimens of these collections were distributed with higher collection numbers than Gollan's material in *Bryotheca Levier 1333* and hence were presumably later included in this exsiccata series. The collections – *Gollan, Bryoth. Levier 1893* ('Sept. 11, 1900'), *Gollan, Bryoth. Levier 5770* ('Nov. 26, 1903') and *Bahadru, Bryoth. Levier 6029* ('Febr. 22, 1904') – were made in or near Mussooree and were identified by Brotherus after Müller's death (see also homonym below).

Hypopterygium emodi Müll.Hal. ex Broth. in Levier, Bryoth. exotica (1907) 50, nom. nud.; Müll.Hal. in Levier in Brühl, Records Bot. Survey India 13 (1931) 121, nom. nud. — Original material: *Gollan, Bryoth. exotica 50* (BM, FH, NY, S, Z), India, Uttar Pradesh, NW Himalaya, Dehra Dun, Mussooree (Mussoorie), Arnigadh, alt. 1770 m (5800 p.), Nov. 26, 1903.

Illustrations: Van der Sande Lacoste, Ann. Mus. Lugd.-Bat. 2 (1866) t. 9; see note 30. — Holzinger, Bryologist 17 (1914) pl. 9. — Shimotomai & Koyama, Bot. Mag. (Tokyo) 46 (1932) 388, f. 3a; J. Sci. Hiroshima Univ., Ser. B., Div. 2, Bot. 1 (1932) 98, f. 19 (karyotypes). — Grout, Moss Flora of North America 3 (1934) pl. 66, f. 1–3. — Noguchi, Trans. Nat. Hist. Soc. Formosa 26 (148) (1936) 40, f. 3. 9–13; (as *H. formosanum*). — Bartram, Philipp. J. Sci. 68 (1939) f. 356. — Okamura in Makino, Illustrated Flora of Japan (1940) f. 2941; revised edition (1954) f. 2941. — Noguchi, J. Hattori Bot. Lab. 6 (1951) 25, 27, 28, f. 1.5, 2.3, 3.3. — Noguchi, J. Hattori Bot. Lab. 7 (1952) 4, f. 6, 6, f. 7, 8, f. 8. — Sakurai, Muscol. Jap. (1954) pl. 42, a, k. — Pócs, Rev. Bryol. Lich. 34 (1967) pl. (3) 49. — Noguchi, Misc. Bryol. Lichenol. 5 (1969) 31, f. 146, 1 & 2, (as 1. *H. fauriei* and 2. *H. japonicum*). — Inoue & Uchino, Bot. Mag. (Tokyo) 82 (1969) 361, f. 3–8; 366, f. 36, (karyotype, as *H. fauriei* and *H. japonicum*). — Lawton, Moss Flora of the Pacific North West (1971) pl. 136, f. 1–6. — Lin & Li(?), in: Li et al., Bryoflora of Xizang (1985) pl. 125, f. 1–11 (as *H. japonicum* and *H. fauriei*). — ?Lin, Introduktion to the Bryophytes (1988) 36. — Mohamed & Robinson, Smithsonian Contrib. Bot. 80 (1991) f. 131–140. — Noguchi, Moss Flora of Japan 4 (1991) f. 336, 337. — Anonymous, Plants of the World 136 (1996) 12/118–119, (text in Japanese). — ?B. & N. Malcolm, Mosses and other Bryophytes (2000) 24, 59.

Some references to Japanese literature given by Iwatsuki & Noguchi (1973) for the present species could not be verified, because the publications were not at my disposal.

Plants in groups of dendroids or fans, occasionally growing in dense, turf- or cushion-like groups, pinnate to flabellate or palmate, small to medium-sized, usually not gemmiferous, occasionally gemmiferous (see 'Geographical variation' and note 23). *Stipe* up to 3.0 cm long, creeping to ascending, not compressed or dorsiventrally compressed, entirely tomentose or tomentose in basal part. *Frond* broad-ovate to oblong, up to 2.5 cm in diameter; rachis and branches entirely dorsiventrally compressed or not compressed in basal part, glabrous, caducous in distal part or not; rachis growing in direction of stipe or bend from stipe and becoming roughly horizontal; branches up to 1.2 cm long, patent to widely patent, but frequently erect when small. *Primordia* frequently set with scaly leaves; scaly leaves deltoid to narrowly triangular, margin ± entire. *Epidermis cells and cortical cells of stipe, rachis, and branches* equally wide or cortical

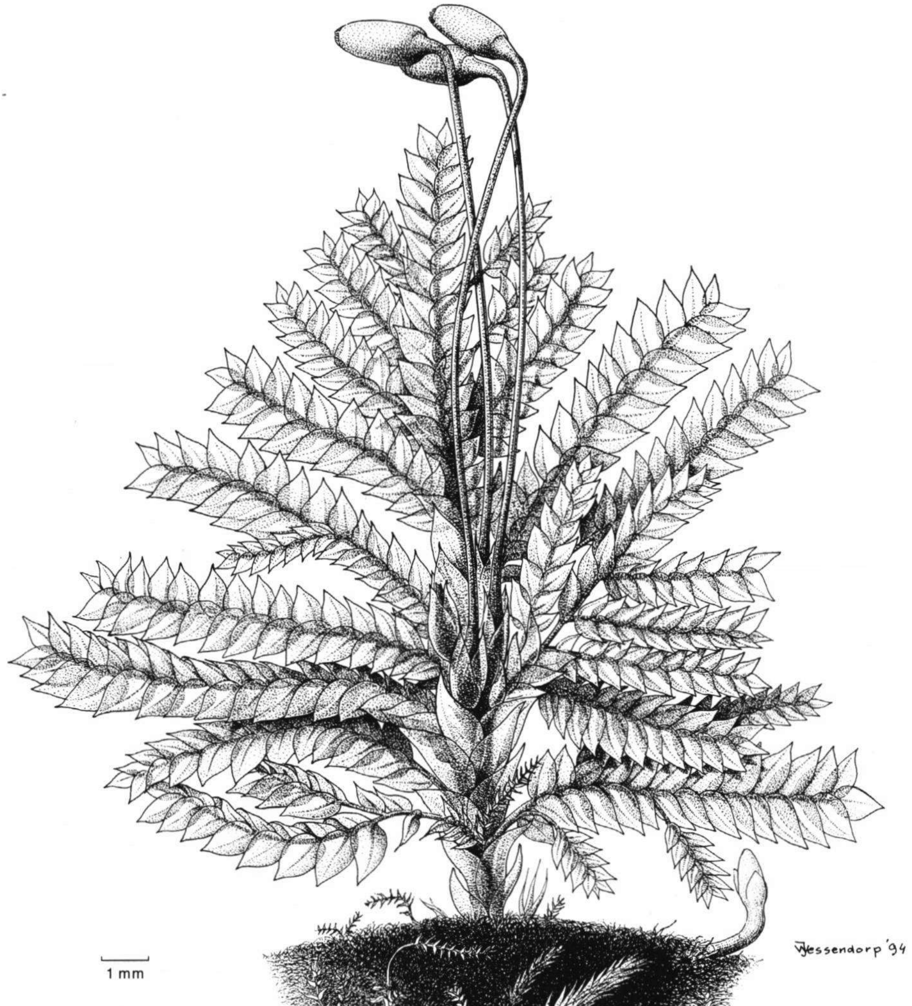


Fig. 22. ***Hypopterygium flavolimbatum*** **Müll.Hal. Habit 'normal' variant (*Long 18911*, E).**

ones wider; walls thin or incrassate, colourless to dark brown; inclusions absent. *Central strand* present; cells equally wide as cortical ones or narrower, walls thin, colourless; inclusions frequently present, granules, clumps or crystalline plates, fat-like, colourless (white). *Axial cavities* absent (see note 22). *Axillary hairs* 1–3 per leaf, (2- or) 3-celled; basal cells (1 or) 2 ; terminal cell short to elongate, (suborbicular or) elliptic to rectangular, (10–)25–60 µm long and 10–25 µm wide, ± smooth, wall thin or incrassate. *Phyllotaxis*: of stipe octostichous (see note 21); of rachis octostichous in basal part, tristichous in distal part; of branches tristichous. *Foliation*: of stipe entirely isophyllous and not complanate or weakly anisophyllous and weakly complanate in distal

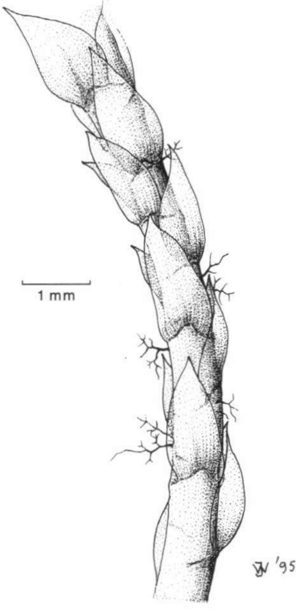


Fig. 23. *Hypopterygium flavolimbatum* Müll.Hal. Stipe 'normal' variant (*Long 18911*, E).

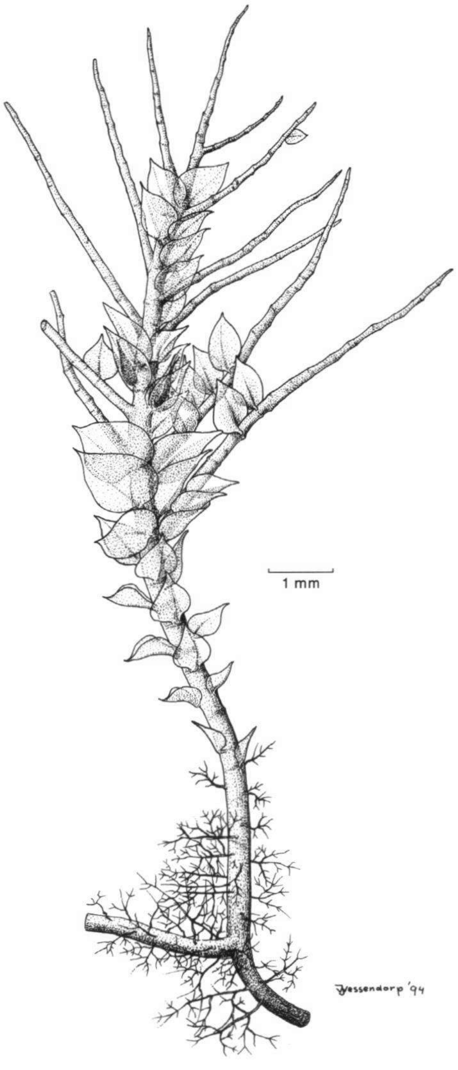


Fig. 24. *Hypopterygium flavolimbatum* Müll.Hal. Habit 'East Malesian' variant (*Streimann 26509*, CBG).

part, occasionally partly or entirely julaceous; of rachis isophyllous and not complanate or weakly anisophyllous and weakly complanate in basal part, distinctly anisophyllous and complanate in distal part; of branches distinctly anisophyllous, complanate. *Leaves* distant or closely set, yellowish green to dark green or glaucous green, dull; insertion concave (to transverse); laminal cells usually prosenchymatous, occasionally weakly collenchymatous in distal part of leaf, hexagonal, short to oblong (to elongate), 15–60 µm wide and 10–25 µm wide, walls thin or incrassate, thin in cells at leaf base of caducous leaves, porose. *Basal and distal stipe leaves* monomorphic, not or weakly

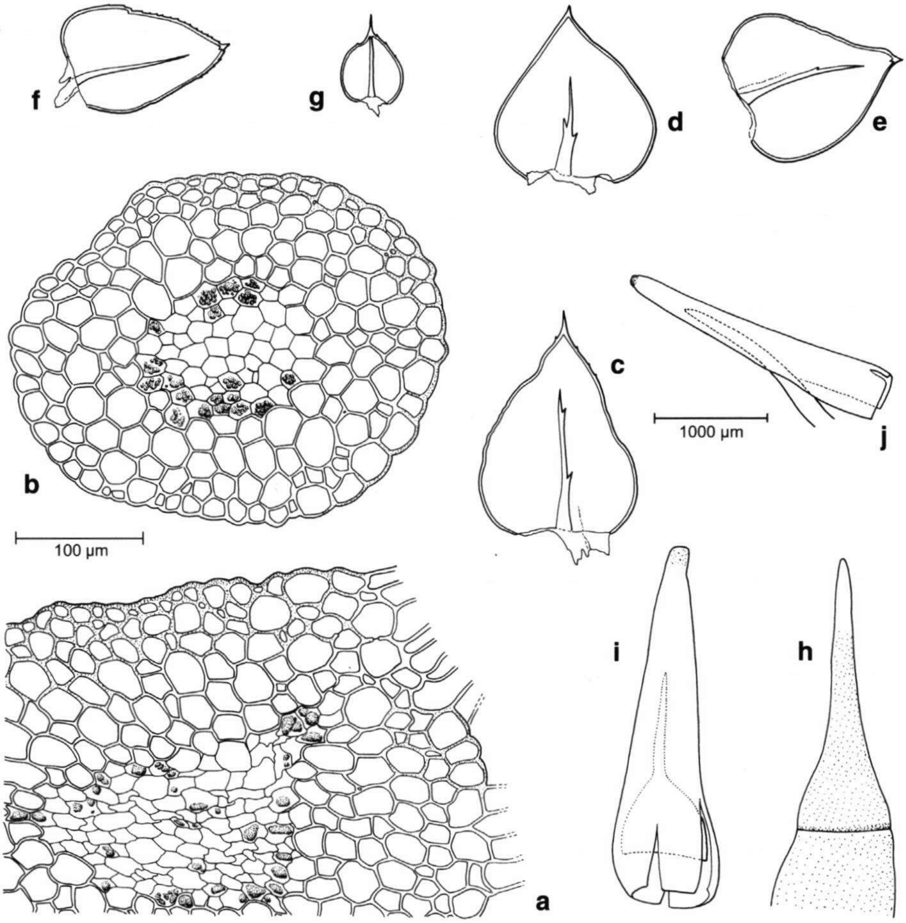


Fig. 25. *Hypopterygium flavolimbatum* Müll.Hal. a. Rachis (cross section dorsal quadrant); b. branch (cross section); c–e. rachis leaves (c. dorsal, d. ventral, e. lateral); f, g. branch leaves (f. lateral, g. amphigastrium); h. operculum; i, j. calyptra (a–g: *Igbal 646*, L; h, i: *Schiffner 12924*, L; j: *Ahmad 682*, L).

differentiated in basal and distal ones, appressed to widely patent, ± symmetrical, straight, weakly or strongly concave, short-ovate to ovate, rarely caducous in Malesian plants (see 'Geographical variation', 'East Malesian' variant); margin entire; border distinct or faint near acumen, 1–3 cells wide; apex (gradually or) abruptly acuminate; acumen (up to) 0.05–0.4(–0.7) mm long; costa (faint to) distinct, occasionally absent in small basal stipe leaves, reaching (up to) 2/3–4/5 of leaf length (to excurrent). *Basal stipe leaves* scale-like to leaf-like, 0.4–0.8 mm long and 0.4–0.7 mm wide. *Distal stipe leaves* leaf-like, 0.6–1.5 mm long and 0.4–1.0 mm wide. *Frond leaves* dimorphic but (weakly) monomorphic in basal part of rachis, frequently caducous at (basal and) distal part of ultimate frond axes in East Malesian plants (see 'Geographical variation', 'East Malesian' variant), less often caducous in plants from tropical areas

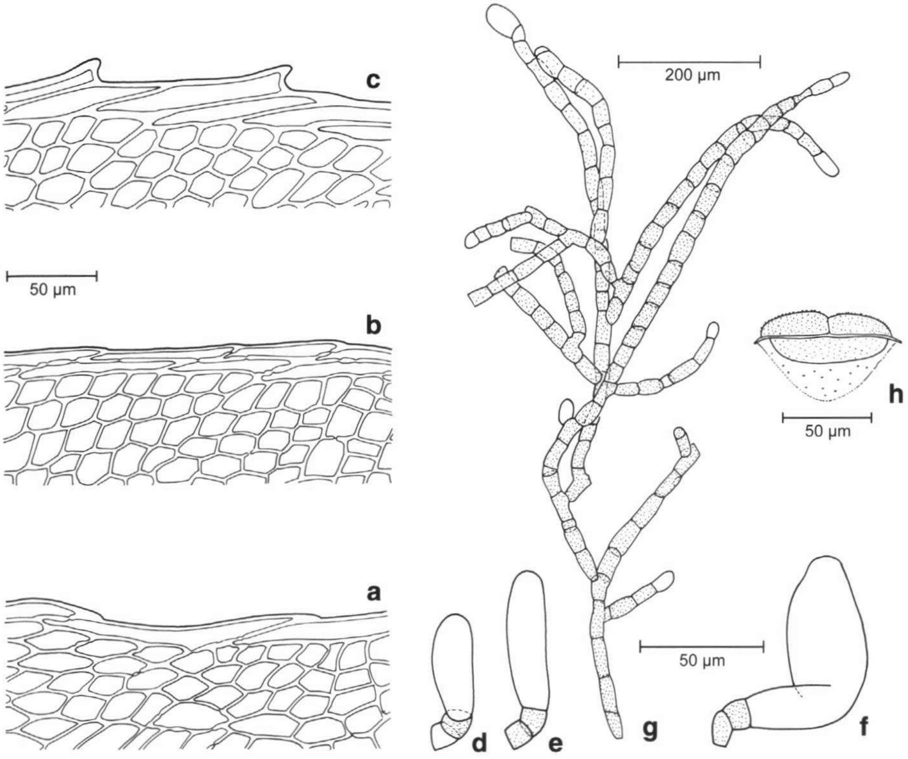


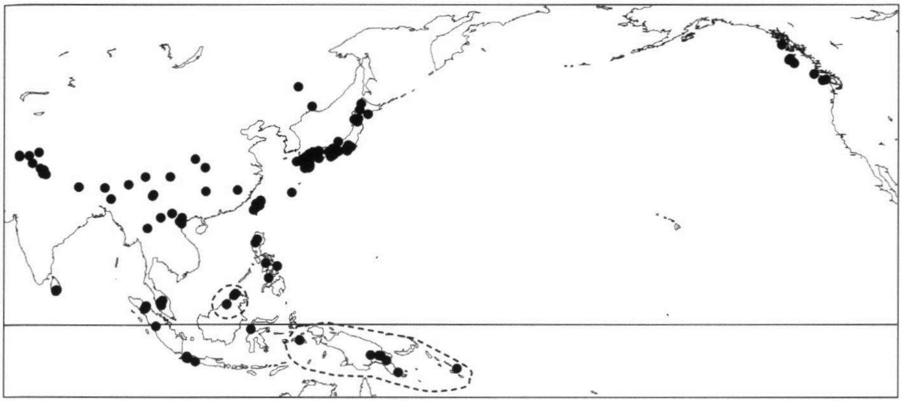
Fig. 26. *Hypopterygium flavolimbatum* Müll.Hal. a–c. Leaf cells of lateral frond leaves: a, b. rachis leaf (a. basal part of antical side, b. distal part of antical side), c. branch leaf (distal part of antical side); d–f. axillary hairs; g. gemmaphore with gemmae; h. exostome tooth (cross section) (a–f: *Igbal 646*, L; g: *Touw 19795*, L; h: *Schmutz 7152*, L).

outside Malesia, rarely caducous in temperate plants; margin ± entire in basal leaves, usually becoming moderately to coarsely serrate or serrate-dentate in distal ones; teeth 1-celled, up to 25 µm long, projecting up to 1/5 of length of a cell, rarely with two apices, up to 20; border distinct, occasionally becoming faint near apex, continuous, 1–3 cells wide; apex abruptly acuminate; acumen 0.05–0.3 mm long in lateral leaves and 0.2–0.5 mm long in amphigastria. *Basal frond leaves* symmetrical, (suborbicular to) ovate to oblong-elliptic, 0.5–1.7 mm long and 0.4–1.4 mm wide; costa (absent or faint to) distinct, reaching (1/2–)4/5 of leaf length (to nearly excurrent). *Lateral frond leaves (in central and distal part of frond)* asymmetrical, short-ovate to elliptic, 0.5–1.7 mm long and 0.4–1.4 mm wide; costa (absent or faint to) distinct, reaching (1/2–)2/3–4/5 of leaf length. *Frond amphigastria (in central and distal part of frond)* symmetrical, transverse-elliptic to ovate or elliptic, 0.3–1.5 mm long and 0.3–0.8 mm wide, occasionally very narrow in distal part of frond, straight; costa (faint or) distinct, reaching (1/2–2/3 to) excurrent, whereby most frequently reaching 2/3–4/5 of amphigastrium length in basal part of frond and excurrent in distal part of frond. *Gemmae clusters* located in distal part of frond axes, reaching 1/2 to 3 times length of covering (lateral) leaf. *Gemmaphores* (simple or) branched, (1?–)2–33 cells long, shiny, brown, frequently becoming pale brown at apex of gemmaphore. *Gemmae* simple, up to 20 cells long, brown; cells 20–40 µm long and 15–30 µm wide.

Heteroicous. *Gametoecia* in basal and middle part of rachis and branches, generally bisexual, less often unisexual; perigonia situated above perichaetia. *Gametoecial leaves* green; margin entire; border absent or faint near leaf base, distinct in distal part, but frequently faint in acumen, continuous; apex abruptly acuminate; costa absent, faint, or distinct, reaching 2/3 of leaf length to nearly percurrent; laminal cells entirely prosenchymatous or parenchymatous in basal third of leaf, short to elongate, rectangular when situated in parenchymatous leaf parts, hexagonal when situated in prosenchymatous leaf parts. *Inner leaves*: of perigonia ovate, up to 0.6 mm long and 0.5 mm wide, acumen up to 0.3 mm; of perichaetia prior to sporophyte development elliptic to obovate, up to 1.0 mm long and 0.7 mm wide, acumen up to 0.7 mm long; of full-grown perichaetia elliptic to obovate, up to 1.6 mm long and 1.0 mm wide, *acumen* up to 0.6 mm long. *Antheridia* 0.5–0.6 mm long. *Stalk in full-grown perichaetia* 0.3–0.9 mm long. *Archegonia* 0.5–0.6 mm long. *Vaginula* 1.0–1.3 mm long. *Gametoecial axillary hairs* 1–4 per gametoecial leaf, 3- (or 4-)celled; basal cells 2 (or 3); intermediate cells absent; terminal cell (short or) oblong to elongate, (subcircular or) elliptic or obovate to rectangular, (15–)20–75 µm long and 10–25 µm wide, smooth, wall thin or incrassate. *Paraphyses* absent.

Sporophytes up to 9 per frond. *Seta* nearly horizontal to vertical, uncinate, 2.5–30.0 mm long, ochraceous to brown or red, smooth or weakly mammilose near base of capsule. *Capsule* barrel-shaped to ellipsoid, (cernuous to) horizontal to pendulous, 2.5–3.1 mm long and 1.1–1.3 mm wide, ochraceous to pale brown, smooth; neck pustulose or not; annulus indistinct to distinct. *Peristomial formula OPL:PPL:IPL* = 4:2:6(–8?)c. *Exostome* reddish brown; teeth 470–600 µm long and 120–140 µm wide, entirely bordered, not shouldered; dorsal side striate in basal half of teeth, becoming papillose in distal part; dorsal plates broader than ventral plates, 13–16 µm thick; ventral plates 12–15 µm thick. *Endostome* weakly perforate or not, weakly to moderately papillose at both faces; basal membrane reaching 1/3–1/2 of length of exostome teeth; processes c. 530 µm long beyond orifice and c. 70 µm wide at base, not nodulose, not appendiculate; cilia 2 or 3, 1 (or 2) plate(s) wide, up to 10 cells long, nodulose, laterally appendiculate or not by plate parts of a single cell. *Operculum* 1.3–3.0 mm long. *Calyptra* usually cucullate, occasionally mitrate to cucullate, ± entirely covering operculum, 1.7–3.6 mm long, usually almost colourless to ochraceous, occasionally pale green, usually membraneous in basal 1/3–2/3 and becoming fleshy in distal part, occasionally entirely fleshy. *Spores* 12–21 µm.

Distribution — Nepal, Bhutan, Pakistan (NW Frontier Prov., Punjab), India (Jammu & Kashmir, Himachal Pradesh, Uttar Pradesh, Meghalaya, Arunachal Pradesh), Sri Lanka, Russia (Primor'ye), China (Heilongjiang, Shaanxi, Sichuan, Yunnan, Hubei, Hunan, Fujian), Japan (Hokkaido, Honshu, Shikoku, Kyushu, Ryukyu Islands), Taiwan, Thailand, Vietnam, Philippines (Luzon, Sibuyan?, Negros, Samar), Malaysia (Peninsular Malaysia, Sarawak, Sabah), Indonesia (Sumatra, Java, Kalimantan, Sulawesi, Moluccas: Seram), Papua New Guinea, Solomon Islands (Malaita), USA (Alaska: Alexander Archipelago), Canada (British Columbia: Queen Charlotte Islands).



Map 13. Distribution of *Hypopterygium flavolimbatum* Müll.Hal. The broken line indicates the area where the 'East Malesian' variant occurs. On Borneo, Seram, and New Guinea both variants of *H. flavolimbatum* (see text) are found.

Reported from the Chinese Provinces of Anhui, Zhejiang (Hu Renliang & Wang Youfang, 1987; as *H. fauriei*, *H. formosanum*, *H. japonicum*), and Guizhou (Tan et al., 1994). Reported from the Korean Peninsula by Okamura (1915), Horikawa (1934b), and from the Kumgang Mts, North Korea, by Kim et al. (1995). Reported from Tanegashima Island, Ryukyu Islands, Kagoshima Pref., Japan (as *H. japonicum*) by Deguchi & Kariyasaki (1991).

Hypopterygium flavolimbatum Müll.Hal. is the most widespread *Hypopterygium* species on the northern hemisphere. It has its most northwestern localities in the Nubra Valley, south of the Karakorum Range, in NW India, and the southern flanks of the western Himalayas in NE Pakistan and NW India. The species occurs eastwards on the southern flanks and in valleys along the entire Himalaya Range. Although the species is also found on Sri Lanka, it is not known from the Indian plains and the higher and lower mountains south of the Himalayas, with the exception of the Khasi Hills. Eastwards, the species is widely distributed in China south of the Qinling Range and occurs also in northern Vietnam and northern Thailand. The species is, however, not known from Myanmar and central and southern continental SE Asia, nor is it known from Hainan and other coastal areas in SE China.

The species is very common and widely distributed in Taiwan and Japan, where it reaches SE Hokkaido. It is also known from continental coastal areas of the Japanese Sea and from a single location in NE China. The species occurs also on the Pacific coast of SE Alaska and British Columbia.

In Malesia, the species is distributed from northern Sumatra and Peninsular Malaysia towards the Philippines and the Solomon Islands. A large number of specimens were collected on West Java, but the species seems to be generally rare in the Malaysian Archipelago. The species is absent from the Lesser Sunda Islands and not known from the northern Moluccas, West Papua, and large areas of Papua New Guinea.

Habitat & Ecology — In evergreen, broad-leaved or coniferous forests, especially in humid places and near and along streams, usually in partially or fully shaded places, occasionally in open, humid habitats, rarely in dry habitats or on sunny and open places. Terrestrial, on rocks (mostly on limestone, marble, or cement, less often on sandstone), tree trunks, and rotten logs, less often on shrubs and climbers. In North America at the Pacific coast often found on calcareous cliffs. On Malaita, Solomon Islands, in or near limestone caves. Altitude: 100–2500(–3330) m in tropical areas but here most frequently found between 1000 and 1850 m, 1430–3670 m in the Himalayas, 650–3170 m in China, (200–)1100–2500 m in Taiwan, and 50–800 (–1240) m in southern and central Japan; probably near sea level in the coastal regions of (cool-) temperate, continental E Asia, northern Japan, and the Pacific coast of (warm-)temperate NW North America. According to Noguchi (1952), in Taiwan found between sea level and 2500 m altitude (as *H. formosanum* and *H. japonicum*).

Akiyama (1992) remarked that on Seram *H. aristatum* is confined to higher elevations than other *Hypopterygium* species. For the present species, however, Akiyama's conclusion is incorrect, because he misidentified several of his specimens that were found on lower altitudes and belong to the 'East Malesian' variant (see under 'Geographical variation' and note 28), as *H. humile* Mitt. ex Bosch & Sande Lac. On Seram the present species was found between 430 and 2000 m.

Hypopterygium flavolimbatum was often found on other substrates than rock. However, it occurs probably predominantly in limestone areas or other calcareous areas. This was also noticed by other authors. Noguchi (1952) reported that in Japan it is often distributed in limestone areas (as *H. japonicum*). Mohamed & Robinson (1991) remarked that on Peninsular Malaysia the species (as *H. aristatum*) grows mostly on rocks and sometimes on logs at altitudes above 1000 m, but it is confined to limestone at altitudes at or near 200 m. Akiyama (1992) reported that on Seram it is confined to limestone boulders.

The present species is principally a warm-temperate to temperate species, but it also occurs in tropical areas with sufficient rainfall throughout the year. The species is mainly absent in (sub)tropical areas with a monsoon climate. In the cool temperate climates of NE Asia and NW North America the species is restricted to sheltered areas or areas where the macroclimate is tempered by warm ocean currents.

Variation — *Hypopterygium flavolimbatum* is distributed over a large distribution area, which includes different climates that vary from cool temperate to tropical. Hence, the species shows great morphological variation and consists of many forms. These forms, however, cannot satisfactorily be separated and show no morphological discontinuities between each other.

Pronounced variation is found in the shape of the plant and the hair-covering of the stipe. However, no segregate forms that are based on these features could be found. Evidence for a geographical or ecological component of the variability in these features was not obtained.

Pronounced variation is also found in the degree of defoliation of the plant caused by the absence or presence of caducous leaves. This variability shows a clear correlation with geography (see 'Geographical variation'). In gametophores with caducous or loosely attached leaves, these leaves, which include amphigastria, occur usually at the distal part of the rachis and branches and less often at the basal part of these axes. Caducous or loosely attached stipe leaves occur usually only in highly defoliated plants. In gametophores with caducous or loosely attached leaves, all leaves are probably potentially caducous, but those at the stipe and the basal part of the rachis detach less easily from the axes than those at the branches and the distal part of the rachis. The caducous or loosely attached leaves break off at the leaf. This is caused by the thin to very thin walls of the leaf cells, even in the border and costa cells, that are situated at the insertion of the leaf.

The present species shows much variation in sexuality. It is heteroicous and monoicous and dioicous plants occur. In monoicous material, the frequency of unisexual (male, female) and bisexual gametoecia shows considerable variation between specimens and gametophores.

Geographical variation — Within *Hypopterygium flavolimbatum* two variants can be recognised based upon the absence or presence of caducous or loosely attached frond leaves:

'Normal' variant: Plants with only entirely foliated branches or up to two partly defoliated branches at most. Stipe usually not compressed, occasionally dorsiventrally compressed. Frond leaves more or less firmly attached. — Distribution: throughout the distribution area of the species, but thus far not known from the Solomon Islands.

'East Malesian' variant: Plants with two or more mainly defoliated branches. Stipe not compressed in the basal half or entirely dorsiventrally compressed. Frond leaves frequently caducous or loosely attached. Highly defoliated plants are often small, and have thus far not been found in fruit. — Distribution: Malaysia (NE Borneo: Sarawak, Sabah), Indonesia (Moluccas: Seram), Papua New Guinea, Solomon Islands (Malaita).

The laminal leaf cells of the frond leaves of 'East Malesian' variant are generally somewhat shorter than those of the 'normal' variant (and other *Hypopterygium* species). Because of their incrassate walls, these short cells sometimes result in a weakly collenchymatous areolation, which then usually occurs in distal parts of the leaf, but this type of collenchymatous areolation is less striking than that of *Lopidium* species.

Despite the fact that highly defoliated plants show often a strikingly different appearance from plants with mainly entirely foliated fronds and at most a few partly defoliated branches, the separation between the two variants is highly artificial. Attempts to find more natural delimitations between the two forms failed, because there is a wide range of all kinds of intermediates between completely foliated plants and largely defoliated ones. Hence, the two variants are not sharply defined, and need no nomenclatural status.

Nevertheless, the 'East Malesian' variant has a much more restricted – i.e. mainly East Malesian – distribution than the 'normal' variant of *H. flavolimbatum*, which is found in almost the entire distribution area of the species. In a broader context, the occurrence of plants with caducous or loosely attached frond leaves shows a correlation with geography. Plants with at least a few caducous or loosely attached frond leaves occur often in Malesia, but are rare in temperate areas, the Indian subcontinent, and continental SE Asia. Malesian plants with caducous leaves show also often a higher degree of defoliation. In Malesia, the degree of defoliation that was found in plants with caducous leaves increases from west to east. The most strongly defoliated plants are found in SE Malesia (the Philippines excluded). The 'East Malesian' variant of *H. flavolimbatum* includes the plants with strongest defoliated fronds of the species and is, hence, restricted to this area.

In addition to the differences in persistence of the frond leaves between Malesian plants and plants from other parts of the distribution area of the species, there are a few other minor differences between tropical plants and temperate ones. Tropical plants are more often and generally more strongly gemmiferous than temperate plants, almost certainly because tropical plants have more often partially caducous branches than temperate ones.

Other geographical variation — A weak correlation between geography and variability was found for the direction and shape of the stipe leaves, the length of the amphigastrium costa, the size of the gametoecia, and the length of the seta.

In the plants of the cool-temperate western Himalayas, continental northeastern Asia, and northwestern North America the foliation of the stipe is often julaceous in the distal part of the stipe, or even entirely julaceous. The Himalayan plants have appressed to erecto-patent stipe leaves, while the North American and NE Asian plants have mainly erecto-patent to erect ones. The stipe leaves of the North American and NE Asian plants are often strongly concave. The concave shape is less pronounced in the stipe leaves of the Himalayan plants. In addition, the acumen of the stipe leaves is 0.2–0.3 mm long in the North American and NE Asian plants and 0.05–0.15 mm long in the Himalayan plants.

Plants from tropical and warm-temperate areas, including most Japanese ones, have no julaceous foliation at the stipe. Only in a few Japanese plants a weak julaceous foliation could be observed, mainly in the basal part of the stipe. The stipe leaves of tropical plants are usually erecto-patent to patent and less often widely patent, and only occasionally erect and rarely appressed. Erect and appressed stipe leaves are more frequently found in Taiwanese and Japanese plants, where they occur usually in the basal part of the stipe. In tropical and warm-temperate plants the acumen of the stipe leaves varies usually between 0.15 and 0.4 mm. In a few Japanese specimens, the acumen of the stipe leaves varied between 0.2 to 0.7 mm long.

In the whole distribution area of the species, the length of the costa shows little variation in stipe and lateral frond leaves, and mainly varies between 2/3 and 4/5 of the length of the leaf. In the ventral leaves of the distal part of the stipe and the basal part of the frond the costa is often equally long, but occasionally longer, up to percurrent or excurrent. The costa shows more variation in length in the true amphigastria of the distal part of the frond. In most of the distal amphigastria, the costa is distinctly excurrent, but occasionally, especially when it is faint, the costa is interrupted or only reaching 1/2 to 4/5 of the length of the amphigastrium.

Plants from continental northeastern Asia and northwestern North America have often very small gametoecia, which are situated in the distal part of the stipe and the basal part of the rachis. Most small gametoecia are perigonia, but small perichaetia occasionally also occur. The leaves of the small gametoecia are up to 0.6 mm long and 0.2 mm wide and have an acumen, which is up to 0.15 mm long.

The seta shows much continuous, variation in length, especially in Japan, Taiwan, and southern China. The seta varies between 2.5 and 30 mm in length in Japanese plants, and between 9 and 23 mm in Taiwanese and South Chinese plants. In other parts of the distribution area, seta lengths between 8 and 17 mm were observed. Noguchi (1991) distinguished two – principally Japanese – taxa that are included in the present species, which he separated by their seta length being either shorter or longer than 20 mm. However, in the material examined no groups of specimens from Japan or abroad could be made and delimited based on differences in seta length as a single character or in combination with other features (see note 9).

Setae may superficially show striking differences in thickness. Long setae may look very thin and short ones may look rather thick. However, thin and thick setae may be attached to the same plant, and the actual differences in thickness are rather small. The seta diameter varies between approximately 0.15 and 0.20 mm. Differences in thickness of the seta are presumably partly caused by the age of the sporophytes.

Ecological variation — Despite the variability in morphological features, no variation was found that shows a correlation with habitat, the type of substratum, or altitude. Variability that is caused by climatic conditions is included in the treatment of 'Geographical variation'.

Chromosome numbers — n = 9, 18, see Shimotomai & Koyama (1932a: 391; 1932b: 95–101; '*Hypopterygium japonicum*', n = 18), Inoue & Uchino (1969: 361, f. 3-8; 366, f. 36; '*H. fauriei*' and '*H. japonicum*', n = 9, 18), Inoue (1979: 111; '*H. formosanum*, n = 18). Karyotype formulas given by Inoue & Uchino l.c.: K(n) = 9 = [V(H)+2V+J+4(2v+2j)+m(h)]; K(n) = 18 = [2V(H)+4V+2J+8(4v+4j)+2m(h)]. — Vouchers: *?Shimotomai & Koyama s.n.*, (n.v.), Japan, 'surroundings of Hiroshima': n = 18; *?Inoue & Uchino s.n.* (n.v.), Japan, Kumamoto Pref., Kikuchi-suigen: n = 9; *?Inoue & Uchino s.n.* (n.v.), Japan, Kumamoto Pref., Mizukoshi: n = 9; *?Inoue & Uchino s.n.* (n.v.), Japan, Kagoshima Pref., Mt Shibi: n = 9; *?Inoue & Uchino s.n.* (n.v.), Japan, Yamaguchi Pref., Akiyoshi-dai: n = 9; *?Inoue & Uchino s.n.* (n.v.), Japan, Kumamoto Pref., Kikuchi-suigen: n = 18; *Iwatsuki et al. 145* (n.v.), Taiwan, Chia-yi Co., Mt Ali: n = 18.

Notes:

Nomenclature and synonymy — 1. Müller (1850) did not indicate the collector of his original material. The collector may have been Wallich, who collected in Nepal in 1820 (Wallich, 1830), but other collectors (see e.g. Hooker, 1820: 146; Hooker & Thomson, 1855: 48, 184) cannot be excluded.

2. The neotype of *Hypopterygium flavolimbatum* matches with Müller's (1850) original description of the species fairly well. The specimen is a female plant with numerous flabellate to palmate gametophores, which vary in size between 1.4 to 3.1 cm. The stipe is rather short and varies in length between 0.2 to 0.8 cm; the rachis varies in length between 0.6 to 2.2 cm. The stipe leaves and lateral frond leaves are ovate and between 0.7 and 1.4 mm long and 0.4 and 0.9 mm wide; the ventral leaves and amphigastria in the frond are short-elliptic to ovate and are between 0.5 to 1.2 mm long and 0.3 to 0.7 mm wide.

Several gametophores of the neotype bear sporophytes (up to 9 per gametophore). The capsules are in various stages of development and are short-elliptoid. Several capsules are heavily damaged or even missing. All undamaged capsules are still in possession of their operculum. Müller's material apparently lacked operculae, because Müller (1850) gave a full description of the peristome and a description of the operculum is lacking.

3. When Mitten (1859) described the new, monoicous species *Hypopterygium tibetanum*, he compared it with *H. rotulatum* (a doubtful *Hypopterygium* species). He did not compare it with Müller's (1850) species *H. flavolimbatum*, which he reported in the same publication, probably because Müller had described *H. flavolimbatum* as dioicous. Monoicy, however, is not a differentiating character state here.

When Mitten compared *Hypopterygium tibetanum* with *H. rotulatum*, he had probably (Asian) *H. tamarisci* in mind. He distinguished *H. tibetanum* by its more completely serrate leaf margin, its more translucent leaf cells, its rough seta near the capsule neck, and its, long extending operculum.

These features do not fully separate *H. tibetanum* from (Asian representatives of) *H. tamarisci*, although they, except for translucency, are generally correct, when plants of *H. flavolimbatum* are compared with those of *H. tamarisci*.

Chopra (1975) distinguished *Hypopterygium tibetanum* from *H. flavolimbatum* by the direction of the stipe leaves. He described moistened stipe leaves of the former as being appressed, and those of the latter as spreading. This is, however, not a substantial difference. In the present species, even in a single specimen, the direction of the stipe leaves varies from appressed to widely patent. The stipes of cool-temperate plants of the present species *H. flavolimbatum* are set with principally appressed to erecto-patent leaves and are often partly or entirely julaceous, whereas the leaves of warm-temperate or tropical plants are not julaceous and mainly erecto-patent to widely patent.

The holotype of *Hypopterygium tibetanum* is a pinnate to weakly palmate, fruiting plant of up to 3.2 cm tall. It is a monoicous plant with entirely female gametophores and gametophores that are set with male and female gametoecia. The leaves of the stipe and the lower part of the frond are situated in eight ranks and dorsal leaves are present. The setae are 8 to 10 mm long. There is no doubt that the holotype belongs to *H. flavolimbatum*.

4. Motley's collection is absent from L. According to Van den Bosch & Van der Sande Lacoste (1861), Motley's specimen is preserved in Mitten's herbarium, which is nowadays kept in NY. Plausibly, Mitten sent Motley's material to Van den Bosch & Van der Sande Lacoste, who after examination returned it without making a duplicate.

5. In the material from BM that I had on loan, I found only a few specimens from Japan that belong to the present species. All of them were collected by Sasaoka, and are preserved in Dixon's herbarium (kept in BM).

6. Mitten (1864) remarked that his new species *Hypopterygium japonicum* very closely resembled his *H. tibetanum* in size, colour, and appearance. He separated his species from the latter by non-reliable characters: the more regularly ovate leaves with their longer costa, the smaller [laminal] leaf cells, and the shape of the capsule.

Although Mitten's observations are principally correct, I found no substantial differences in the type material of Mitten's two species. The material of *Hypopterygium japonicum* has generally longer lateral frond leaves with shorter leaf cells than the material of *H. tibetanum*. The capsules of *H. tibetanum* are longer and generally wider than those in the type material of *H. japonicum*. Mitten correctly remarked that the capsules of *H. japonicum*, when dry, very much shrivel up, whereas those of *H. tibetanum* retain the same shape. Therefore, the differences in capsule shape between the two species of Mitten are best regarded as differences in the degree of development of the capsules.

Mitten described *Hypopterygium japonicum* as being synoicous, but it is better described as being heteroicous, because the type material is set with both unisexual and bisexual gametoecia.

The type material of *Hypopterygium japonicum* is a pinnate to flabellate or weakly palmate plant of up to 2.7 cm tall. The holotype in NY and the isotype in FH are fruiting plants; the type material in S lacks sporophytes. The type material of *H. japonicum*, like that of *H. tibetanum*, belongs evidently to the present species *H. flavolimbatum*, because of the dorsal leaves and the octostichous foliation of the stipe and the basal part of the frond.

7. Thwaites & Mitten (in Mitten, 1873) considered their new species *Hypopterygium apiculatum* to be very similar with *H. aristatum*, but different by the smaller size of its leaf cells. The size of the leaf cells, however, is not a reliable character for the separation of species in *Hypopterygium*. In addition, I did not find any substantial difference in the size of the leaf cells between *H. apiculatum* and *H. aristatum* or in any other character.

Thwaites & Mitten (in Mitten, 1873) erroneously described their species as dioicous. The type material of *H. apiculatum* is, in fact, monoicous. Possibly, Thwaites & Mitten have overlooked the few bisexual gametoecia in their type material, for most of its gametoecia are female. Perigonia are absent from the type material.

The type material of *Hypopterygium apiculatum* is fruiting. It consists of pinnate to weakly palmate, fruiting gametophores, which are up to 2.7 cm tall. The stipe and lower part of the frond have dorsal leaves and an octostichous foliation, and there is no doubt that *H. apiculatum* is conspecific with *H. flavolimbatum*. This is emphasised by the distinct and excurrent amphigastrium costae. The costae of the leaves in the lower part of the frond are rather long and often percurrent.

8. In the material examined there were no specimens that with certainty could be identified as authentic type material of Bescherelle's (1893) species *Hypopterygium fauriei*. Although the search for type material was hampered by the lack of information given by the labels attached to the specimens, most specimens that were collected by Faurie could be excluded as potential types, because they were collected on a different place or at a different time than the type material. Other potential type specimens, either collected by Faurie or collected by Textor, could be discarded because they are fruiting plants, where Bescherelle (1893) clearly described non-fruiting ones.

A duplicate specimen of a collection in Bescherelle's herbarium that was made by Faurie in 1886 is preserved in W and is presented as *Hypopterygium fauriei*. This specimen contains a fruiting plant, which clearly belongs to the present species.

However, if Bescherelle's (1893) authentic material actually belongs to the present species, it is curious that he described the amphigastrium costa as reaching 2/3 of the length of the amphigastrium. In addition, when he compared his species with *Hypopterygium tibetanum*, he described the amphigastrium costa of *H. fauriei* as fading far beneath the narrowing part of the amphigastrium. Such short amphigastrium costae suggest a relationship with *H. tamarisci*. It is possible, however, that Bescherelle either had at his disposal plants with exceptionally short costae in all amphigastria or he may have overlooked amphigastria with costae that reach the acumen, for instance when he only examined the ventral leaves or amphigastria from the basal part of the frond. The latter possibility is more plausible, because Salmon (1900), who examined an authentic specimen of *H. fauriei* which he received from Bescherelle himself, observed in this specimen amphigastrium costae that vary in length between, nearly always, excurrent and, rarely, vanishing at the base of the acumen. Noguchi (1952) also assumed that Bescherelle observed amphigastria from the base of the frond and Salmon amphigastria from the distal part of the frond. Based on *Faurie 986*, which he considered type material of *H. fauriei*, he illustrated this by depicting a amphigastria from the basal and the median part of the frond with a costa that vanishes well below the acumen and an amphigastrium of the distal part of the frond with an excurrent costa.

9. The characters used by Bescherelle (1893) to distinguish *Hypopterygium fauriei* from *H. japonicum* and *H. tibetanum* are not reliable and do not delimit them as separate species. Likewise, the characters used by Noguchi (1952, 1991) to distinguish *H. fauriei* from *H. japonicum* are not reliable and do not represent discriminating characters. Noguchi's (1991) treatment of the Hypopterygiaceae was mainly based on his earlier work (Noguchi, 1951, 1952). Hence, he probably missed the more recent doubts on the taxonomic status of *H. fauriei*, as put forward by Lin & Li (1985) and Tan et al. (1994). None of these authors compared *H. fauriei* with *H. flavo-limbatum*.

10. Macoun (1902) reported that material of *Hypopterygium canadense* was collected by Newcombe on the Queen Charlotte Islands near Skiddegate in June 1898. Presumably, the type of *H. canadense* was of concern here.

11. Specimens collected by Elmer and are labelled "*10385*" were absent from Brotherus' material that I received on loan from H-BR and other herbaria. The two *Elmer* specimens in Brotherus' herbarium kept in H that are presented as "*Hypopterygium delicatulum* Broth. n. sp." are both labelled with the number *10386*. One of them was clearly indicated as a duplicate from the original.

12. Brotherus (1909) apparently overlooked the gametoecia in the type material of *Hypopterygium delicatulum*. Most of these gametoecia are unisexual, female perichaetia, but in one gametoecium several mature archegonia were mixed with a single, young antheridium. The type of *H. delicatulum* is a small, pinnate (to weakly palmate) plant with a loosely to strongly branched frond. Bartram (1939) described *H. delicatulum* as synoicous, but I observed only female perichaetia in his type specimen.

13. Brotherus (1909) and Bartram (1939) compared *Hypopterygium delicatulum* with *H. ceylanicum* (= *H. tamarisci*), but apparently did not realise that *H. delicatulum* is very similar to *H. aristatum*, which was already known from Java. *H. delicatulum* and *H. aristatum* are typical Malesian plants of *H. flavolimbatum*.

14. Noguchi (1936a, 1952) cited *Noguchi 7200* as the type of *Hypopterygium formosanum*, but this collection has not been found and it is not known where it is preserved. It is not in Noguchi's herbarium, kept in NICH. In this herbarium only a single collection is presented as *H. formosanum*:

Formosa, Tainan Prov., Mt Kodama, (on moist soil), Aug. 18, 1932, *Noguchi 6754*. There is no evidence that this specimen, which belongs evidently to the present species *H. flavolimbatum*, is labelled with the wrong collection (or herbarium) number. There is a possibility that Noguchi's type material is present in KUMAMOTO, but this could not be confirmed.

15. Noguchi (1936a, 1951) considered *Hypopterygium formosanum* related to *H. fauriei*, but treated them as separate species. Dixon (1942) considered *H. formosanum* more closely related to *H. japonicum*. Noguchi did not compare *H. formosanum* with the latter, except for a short remark in his treatment of *H. formosanum* (Noguchi, 1952), where he stated that the leaf acumina of *H. formosanum* are shorter than those of *H. fauriei* and *H. japonicum*.

In his original paper, Noguchi (1936a) distinguished *Hypopterygium formosanum* from *H. fauriei* by its taller size of the plant and its longer stipe. Noguchi (1952) considered the two similar, but maintained *H. formosanum* as a separate species because of minor differences with *H. fauriei*, i.e. the larger size of the plant, the frequent branching, the wider lateral branch leaves, the blunter leaf apices, and the shorter leaf acumina. Furthermore, Noguchi (1952) stated that fruiting material of *H. formosanum* contains generally several (up to 8) sporophytes per frond, whereby the seta length in *H. formosanum* is generally shorter than that in *H. fauriei*. These characters, however, are within the range of variability within the present species and do not distinguish *H. formosanum* from *H. fauriei*.

Noguchi's descriptions and illustrations produced in 1936 and 1952 give a fairly good picture of his *Hypopterygium formosanum*. Despite the fact, that Noguchi's original material was not at my disposal (see note 14), it is almost certain that Noguchi's *H. formosanum* resembles other Sino Japanese material of *H. flavolimbatum*.

16. Dixon (1942) distinguished *Hypopterygium sasaokae* from *H. formosanum* and *H. japonicum* by its smaller [leaf] cells, the somewhat more distinct border, and the often somewhat longer [lateral? leaf] costa, which does not reach the acumen. Dixon's features, however, do not delimit these *Hypopterygia* as separate taxa. The size of these leaf cells are within the range of variability of the present species, and the other features do not represent reliable, discontinuous character states. Dixon did not compare his new species with *H. fauriei*.

Noguchi (1954) regarded Dixon's types of *Hypopterygium sasaokae* as to belong to two different species. Although he included features of the leaves in his comparison, his decision is presumably mainly based on differences in sporophytic characters (cf. Noguchi, 1991), i.e. the length and possibly the colour of the seta of the material in TNS.

Noguchi (1954) considered the isotype of *Hypopterygium sasaokae* to belong to *H. japonicum*, and the paratype material to *H. fauriei*. Noguchi reported the seta of the isotype as being 1.3–1.7 cm long, and that of the paratype as being more than 2.0 cm long. Dixon, who may not have seen the material that is preserved in TNS, described the seta length of *H. sasaokae* as varying between 1.5–2.0 cm. The actual seta length of Dixon's material, however, is 1.3–1.8 cm for the holotype and 2.0–2.5 cm for the paratype. Noguchi did not specify the differences in leaf characters upon which he based his decision, and he did not give features of the leaves of the paratype material that he examined.

17. The diagnostic features given by Dixon (1942) to distinguish *Hypopterygium acuminatum* does not separate the latter from *H. flavolimbatum*.

Based on Dixon's miscitation of the type, Inoue (1987) regarded a specimen in TNS that was collected by Takaesu near Oogimi on Okinawa Island, which is preserved sub no. *6097* in Sasaoka's herbarium, as the isotype of *Hypopterygium acuminatum*.

18. The specimens in BP, EGR, and GRO that are presented as type material of *Hypopterygium vietnamicum* do not completely correspond with Pócs' (1966) circumscription of the type.

The material that is preserved in EGR, *Pócs 2576/a*, was collected on Sept. 28, 1963, at 1700 m altitude "in rupibus calcareis umbrosis in decl. occid., silcaticis supra opp. Sapa", and was not found on *Quercus*. The annotations on habitat, ecology, and substrate on the labels of the specimens in BP and GRO correspond well with Pócs' circumscription of the type, but differ from the latter in collection date and altitude. Because Pócs cited BP as the herbarium in which the type is conserved, the specimen preserved in EGR is excluded from the type material.

19. Pócs (1966) compared *Hypopterygium vietnamicum* with *H. ceylanicum* (= *H. tamarisci*), but apparently overlooked *H. flavolimbatum*, with which it is conspecific. Pócs erroneously described *H. vietnamicum* as dioicous. It is actually monoicous, although most of its gametangia are female perichaetia.

20. Mitten (1859) considered Griffith's *Hypnum rotulatum* a misidentification of *Hypopterygium flavolimbatum*. Although parts of the plants that are depicted by Griffith (1849b) show no features that are decisive for a good identification, Mitten's judgement is strongly supported by the depiction of aristate amphigastria having an almost percurrent to excurrent costa and lateral leaves that are provided with pronounced serrations at the margin.

Unfortunately, it is not precisely known upon which material Griffith (1849a, b) based his *Hypnum rotulatum*. Griffith (1849a) referred to his material with "It. Ass. 531" and indicated that his specimens came from Moosmai and Mumbree. However, none of his collections were labelled as "It. Ass 531", and the specimens can probably be found among other *Hypopterygium* material that was collected by Griffith.

The search for specimens that are of concern here, however, was hampered by the lack of information on the origin of most of Griffith's *Hypopterygia*. Hence, Griffith's original material of his *Hypnum rotulatum* could not be traced with certainty.

There is only one specimen in Griffith's material that was labelled as *Hypnum rotulatum* (*Griffith 28*, TDC). Such specimens were absent from Griffith's own herbarium (BM), where a single specimen that was presented as *Hookeria rotulata* (*Griffith? s.n.*, BM) came nearest to this presentation. Both specimens belong to *Hypopterygium flavolimbatum*. They are not labelled with information on their origin.

In Griffith's *Hypopterygium* material three specimens are indicated to come from Moosmai. They are all three presented as *Hypopterygium flavolimbatum*. However, one of them, which is preserved in Hampe's herbarium (BM), is a specimen that belongs to *H. tamarisci* (*Griffith 1110*). The other two, which are preserved in Mitten's herbarium (NY), belong truly to *H. flavolimbatum* (*Griffith 280, 340*). In Griffith's own herbarium (BM), I found no specimens of *Griffith 280* and *1110*, but only a single specimen of *Griffith 340*. This specimen had originally been labelled "*Climacium*" and lacks information on its origin. None of Griffith's *Hypopterygium* specimens were labelled to come from Mumbree.

Description — 21. In tiny plants the phyllotaxis of the stipe is difficult to ascertain, and is often not distinguishable from tristichous.

22. In a few defoliated branches of plants that belong to the 'East Malesian' variant of the present species (see under 'Geographical variation', p. 180), it was very difficult to ascertain, whether or not central strand cells were replaced by a central cavity. This problem was caused by the large amount of inclusions, mainly consisting of large droplets of colourless to olivaceous, oil-like substances, which troubled the visibility of cross sections. However, in several other defoliated branches, even in completely defoliated ones, central strands containing cells with large amounts of colourless, granular, fat-like inclusions were observed to be intact.

23. Gemmae occur usually on damaged stems.

Reproduction — 24. There were 314 fruiting specimens among the specimens examined (c. 56%, n = 563), but regional differences in fertility were observed. In the Indian subcontinent (including Sri Lanka; n = 125) and China (n = 18) a majority of the specimens were found in fruit (both c. 61%). A vast majority of fruiting specimens was found on Taiwan (92%, n = 23). Along the northwestern coast of the Pacific (Japan, Russia) and adjacent NE China 72% (n = 183) of the specimens were found in fruit, whereas along the Pacific coast of North America only a small minority of the specimens were found in fruit (15%; n = 40).

In continental South East Asia the percentage of fruiting specimens was highest for Vietnam (50%, n = 12); fruiting specimens are not known from Thailand (n = 2). Only a single fruiting specimen is known from Peninsular Malaysia (c. 15%, n = 7).

A low frequency of fruiting specimens was found for Malesia (incl. Malay Peninsula and Solomon Islands), where 39% (n = 159) of the specimens were found in fruit. The fruiting specimens from this area came in majority from W Java, where c. 62% (n = 86) of the specimens were found in fruit. Approximately 16% (n = 18) of the specimens from the Moluccas were fruiting ones. They all came from Seram and were collected by Akiyama, who collected large numbers of mosses there. Only two fruiting specimens came from the Philippines (c. 9%, n = 23); both were found on Luzon. Such a low number of fruiting specimens is also known for Sumatra (25%, n = 8) and Papua New Guinea (c. 29%, n =7). There are no fruiting specimens known from Borneo (n = 10), Sulawesi (n = 1), and the Solomon Islands (n = 1).

The low frequencies found for the Malesian regions outside Java and Seram are almost certainly biased by undercollecting. Nevertheless, the reliable low percentage of fruiting specimens found for Seram suggests that frequency of fruiting specimens may actually be very low in eastern Malesia, and perhaps also in western Malesia outside Java.

Plants that belong to the 'East Malesian' variant, which are conspicuously defoliated, but also less defoliated plants have, thus far, not been found in fruit.

25. Noguchi (1991) observed for *Hypopterygium fauriei* that female plants are common and male plants are rare. In *H. flavolimbatum* purely male plants are indeed rare. In a representative sample of 71 specimens, 2 specimens (3%) were male, 28 were female (39%), and 41 bisexual (58%). Female plants are more often found in temperate areas (44% of the temperate plants, n = 43) of the distribution area of the species than in tropical areas (28%, n = 28). Among the bisexual (monoicous) plants 36% (n = 41) have monosexual gametoecia and 63% have at least a few bisexual gametoecia. Autoicy and heteroicy is also not evenly distributed. In monoicous material from temperate areas 62% (n = 24) of the plants are autoicous, whereas in tropical monoicious material all plants are heteroicous (n = 17).

Distribution — 26. Akiyama (1992) reported that the species is rare on Ambon, Moluccas. I have seen no material or other record of this species from that island.

Identification — 27. The distribution area of *Hypopterygium flavolimbatum* largely overlaps that of *H. tamarisci* in Asia. Occasionally, the two taxa have been confused, but, except for tiny plants, they can easily be distinguished. *H. flavolimbatum* can be recognised by the octostichous leaves in the stipe and the basal part of frond. This results in the occurrence of dorsal leaves, which can best be observed in the basal part of the frond. The foliation of *H. tamarisci* is entirely tristichous or nearly so at the stipe and dorsal leaves are entirely absent.

In addition, the amphigastria of *Hypopterygium flavolimbatum* in the distal parts of the frond are often more abruptly acuminate than in *H. tamarisci* and have usually a more pronounced, excurrent costa, which results in an often long, aristate acumen. In *H. flavolimbatum*, the acumen is at least 0.2 mm long. In distal frond parts of *H. tamarisci* the amphigastrium costa becomes usually fainter in the distal part of the acumen and often does not reach the apex of the amphigastrium. The acumen is shorter, up to 0.15 mm long at most.

Other — 28. Akiyama (1988, 1992) misidentified several specimens, which actually belong to the 'East Malesian' variant of *H. flavolimbatum*, i.e. *Akiyama C-10533, C-16027, C-16090, C-16280, C-16306*, as *H. humile* Mitt. ex Bosch & Sande Lac.

29. Akiyama (1988, 1992) reported the present species (as *Hypopterygium aristatum*) as the only fruiting *Hypopterygium* species that was found on Seram.

30. Van der Sande Lacoste's (1866) illustrations of *Hypopterygium japonicum* ('*iaponicum*') are based on material that was collected by or for Von Siebold in Japan. The octostichous phyllotaxis and the presence of a few dorsal leaves cannot be observed in Van der Sande Lacoste's illustrations. Probably, these character states were overlooked by the author and his artist, for these features are weakly developed in Von Siebold's material.

Selected specimens (among 563 specimens examined):

NEPAL: *Hooker s.n.* (NY, s.loc.), *Hooker f.? H. 1541* (BM, s.loc.), *Wallich s.n.* (FH, NY, s.loc.). – Bagmati: *Schmutz 7152* (L), Kathmandu, Gokarna Forest. BHUTAN: *Griffith s.n.* (NY), Tongsa. — PAKISTAN: NW Frontier Prov. Hazara: *Ahmad 682* (L), Shogran; *Igbal 646* (L), Bara Gali. – Punjab. Rawalpindi: *Hamid 4* (FH), *Stewart 3846* (BM), Murree Hills; *Ahmed 492* (L), Chora Gali. — INDIA: Jammu & Kashmir. Kashmir South: *Khan, Bryoth. Levier 2898* (BM, FH), Lidar Valley, Arroo; *Garrett 2394* (BM), *Stewart 8215* (BM), Pahlgam. – Ladakh ('Tibet'): *Thomson 682* (BM, NY, W), Nubra. – Himachal Pradesh. Chamba: *Badhwar 396* (BM), Dalhousie–Kajiar. – Simla: *Koelz 3195* (NY), Rampur-Bushahr, Dorkali. – Uttar Pradesh. Kumaun. Dehra Dun: *Bahadru, Bryoth. Levier 6029* (BM, S), *Gollan, Bryoth. Levier 5770* (S), Mussooree ('Mussoorie');

Gollan, Bryoth. Levier 1333 (BM, FH, NY, S), *Bryoth. Levier 1893* (NY), *BE 50* (BM, FH, NY, S, Z), Arnigadh. – Tehri Garhwal: *Duthie 13* (HBG), *s.n.* (S), *s.n.* (W), Phedi. – Uttarkashi?: *Duthie 17946* (BM), Jaunsar; *Duthie 12970* (BM), Mandali. – Meghalaya: *Hooker & Thomson 689* (BM, NY), *s.n.* (NY), Khasi Hills ('Khasia'); *Griffith 280* (NY), *340* (BM, NY), Moosmai. – Arunachal Pradesh. Siang Frontier Div. ('Assam, Abor Distr.'): *Burkill 37319* (BM), Serpo River; *Burkill 36236a* (BM), S of Rotung. — SRI LANKA: Central Prov.: *Thwaites CM 129* (BM, NY, W, S); *Fleischer s.n.* (FH), Mt Hakgala; *Beckett s.n.* (BM), Uda Pussellawa; *Binstead 61* (BM), Nuwara Eleya; *Herzog s.n.* (JE), Horton Plains.

RUSSIA: Primor'ye: *Lazarenko s.n.* (EGR, L, NICH, NY), Suputinka River. — CHINA: Heilongjiang: *[uninterpr.] (B. Bryo 84014)* (B), Wu-jing. – Shaanxi: *Chen Pang-Chieh et al. 417* (NY), Ning-shan Hsien, Qinling Mts – Sichuan: *Touw 23909* (L), *Lin Pang-juan 51* (NICH, NY), *Redfearn jr. et al. 34713* (NY), Mt Emei ('Omei'). – Yunnan: *Long 18911* (E), Yulong Shan, Baishui, Lijang; *Touw 23630* (L), Xishuangbanna, Mengla; *Redfearn jr. & Su 986* (NY), Yangi Hsien, Dajiuping. – Hubei: *Sino-Amer. Exp. 286A* (NY), Mt Huanghunling. – Hunan: *Von Handel-Mazzeti, It. Sin. 12194* (W, S), Yün-schan. – Fujian: *Lin Pang-juan 448b* (NICH, NY), Mt Wuyishan. — JAPAN: *Faurie s.n.* (W, s.loc.), *s.n.* (S, s.loc.), *Textor s.n.* (L, S; s.loc.), *Von Siebold* (L, S; s.loc.). – Hokkaido. Rumoi Pref.: *Ishikawa (90)* (S), Yezo, Kotambetsu-gawa ('Kotanbetzu River'). – Ishikari Pref.: *Arimoto s.n.* (FH), Sapporo, Mt Moiwa. – Hidaka: *Kobayashi s.n.* (S), Samani-cho. – Honshu. Aomori Pref.: *Faurie 986* (FH, PC), Mt Hakkoda; *Faurie s.n.* (FH), Osoresan; *Mori 6* (NICH), Kitatsugaru-gun. – Saitama Pref.: *Nagano 86 09* (UPS), Chichibu. – Tokyo Pref.: *Mizushima, CJE 25* (NY), *4158* (S), Minamitama, Yokoyama-mura. – Yamanashi Pref.: *Smith J-351* (NY), Fuketsu. – Shizuoka Pref.: *Mizutani s.n.?* (NICH), Izu Peninsula, Yugashima. – Aichi Pref.: *Iwatsuki, MJ 429* (B, BR, GRO, L, NY, S, U, W), Miwa. – Gifu Pref.: *Mizutani 14072* (L, NY), Gujo-gun, Hachiman-cho. – Mie Pref.: *Iwatsuki 3976* (NICH), Nabari-shi; *Inoue, BSE 637* (B, EGR, GRO, L, S, U), Owase. – Nara Pref.: *Mizutani 311* (NICH), Mt Tabugamine; *Sasaoka 5371* (BM), Mt Oodaigahara. – Wakayama Pref.: *Iwatsuki 591c* (NICH p.p., mixed with *Hypopterygium tamarisci*). – Tottori Pref.: *Arimoto s.n.* (FH). – Hyogo Pref.: *Kodama, MJ 1127* (B, EGR, GRO, HIRO, JE, L, NY, S), Kobe. – Hiroshima Pref.: *Higuchi 3451* (HIRO), Taishaku River. – Shimane Pref.: *unknown collector s.n.* (S), Mt Kasugayama. – Yamaguchi Pref.: *Watanabe 21723* (NICH), *21909* (NICH), Akiyoshidai; *Shiomi, BE 20* (B, BR, CBG, EGR, GRO, L, U, Z), Sayama. – Shikoku. Kochi Pref.: *Iwatsuki M 44752* (NICH), Mt Honokawa; *Okamura s.n.* (FH, NY, S), Mt Washio-yama. – Kyushu. Fukuoka Pref.: *Kuwahara 2731* (NY), Mt Kawara, Ichinotake. – Nagasaki Pref.: *Iwatsuki 6878* (NICH), Goto Is., Fukue-jima; *Faurie 15422* (JE), *Oldham s.n.* (FH, NY, S), Nagasaki. – Kumamoto Pref.: *Mayebara, MJ 222* (B, BR, GRO, L, S, W), Kumamoto, Kuma-gun; *Sasaoka 4648* (BM), Aida. – Miyazaki Pref.: *Hattori & Kurata, MJ 84* (B, EGR, FH, GRO, JE, L, S, U), Minaminaka; *Inoue, BSE 489* (EGR, GRO, JE, L, S, U), Kushima. – Ryukyu Archipelago. Kagoshima Pref.: *Iwatsuki & Sharp 15449* (NICH), Yakushima Is.; *Iwatsuki & Suzuki, MJE 1327* (B, CBG, EGR, GRO, L, NY, S, U), Hana-age-gawa. – Okinawa Pref.: *Sasaoka 6047* (BM), Okinawa Is., Oogimi. — TAIWAN ('FORMOSA'): T'aichung Co.: *Lin, BT 174* (L). T'aitung Co.: *Ching-Chang Chuang 5139* (NY), Pa-yu Lake. – Tainan Co.: *Noguchi 6754* (NICH), Mt Kodama. – Chiayi Co.: *Ching-Chang Chuang 6418* (NY), Mt A-li. – Nantou Co.: *Lai 11542* (B, FH, GRO, L, NICH, NY, U, UPS), Chitou. – Ilan Co.: *Lin, BT 173* (L), Nan-shan Tsun, Nanhuta Shan. – Taipei Co. ('Taihoku Prov.'): *Noguchi 7068* (NICH), Tensonpi(?); *DeVol 1009* (B), Kan-kou.

THAILAND: Payap ('Chiang Mai'): *Touw 3680* (L), *Robbins 3680* (L), Doi Chiang Dao. — VIETNAM. Hoang Liên So'n: *Pételot s.n.* (S), *Pócs 2574/a* (BP. GRO). *2576/a* (EGR).*2577/a* (EGR), *2578/2* (EGR, GRO), Sa Pâ. – Vinh Phu-Bac Thai: *Tran Ninh 68 334a* (EGR), Tam Dao. – Ha So'n Binh: *Pócs et al. 3206/a* (EGR), Núi Biêù Mts, Giàng Sèo. – Ha Nam Ninh: *Pócs 2621* (EGR), *Pócs et al. 3017/d* (EGR), Cúc-phu'o'ng.

PHILIPPINES: Luzon. Mountain Prov.: *Del Rosario & De La Cruz 15047* (GRO), Bontoc, Mt Data. – Benguet Prov.: *Williams 1879* (FH). – Sibuyan?: *Elmer 10386* (U), Magallanes (Mt Giting-giting). – Negros. Negros Oriental: *Elmer 10386* (BM, FH, H-BR, HBG, JE, L, NY, S, W, Z), *10387* (FH p.p.), Cuernos Mts, Dumaguete. – Samar: *Tan 75-335* (GRO), Hinabaryan?, Concord. Barrio. — MALAYSIA: Peninsular Malaysia. Perak: *Spare 2565* (BM). – Kelantan: *Chin 1572* (GRO, KLU, L), Gua Nusang. – Selangor–Pahang: *Hedenäs 92-545* (S), Fraser's Hill–Gap. – Pahang:

Mohamed & Zamzuri 1140 (L), Cameron Highlands. – Borneo. Sarawak: *Touw 19767* (L), *19795* (L), *Klazenga (340)* (L), G. Mulu Nat. Park. – Sabah: *Tan 89-836* (L), *Enriguez 18115* (BM), Mt Kinabalu; *Meijer B 11343* (L), Mt Tam-buyukon; *Wood 1520* (BM, GRO), Tambunan Distr., Kaingaran. — INDONESIA: Sumatra. N Sumatra (Sumatera Utara): *Touw & Snoek 25320* (L), Mt Sinabung; *Staal 192* (EGR, GRO, L), Bandarbaru. – W Sumatra (Sumatera Barat): *Meijer B 9712* (L), Payakumbuh, Halaban, Mt Kapur. – Java. W Java (Jawa Barat): *Kurz (?) 827* (BM), Mt Megamendong; *Fleischer, MFAI 50* (JE, NY; H-BR p.p., L p.p., Z p.p., mixed with *Hypopterygium tamarisci*), *MFAI 100* (BM, FH, JE, L, NY, U, S, Z), *Schiffner 12924* (L, W), Tjibodas; *Nyman 561* (BM, FH, L, NICH, S, UPS), Salak; *Solms-Laubach s.n.* (FH, '*Solms*'; S), Mt Gedé; *Motley s.n.* (NY), Mt Pangarango. – Kalimantan. *Korthals s.n.* (L, s.loc.). – Sulawesi: *Hennipman 5503* (L), Roroka Timbu. – Moluccas (Maluku). Seram: *Akiyama C-8768* (KYO, L), *C-9204* (KYO), *C-9164* (KYO p.p.), *C-9859* (KYO), *C-10533* (KYO), *C-15194* (KYO, L), *C-16027* (KYO), *C-16090* (KYO, L), *C-16280* (KYO), *C-16306* (L), *C-16509* (KYO, L), Manusela Nat. Park. — PAPUA NEW GUINEA: Eastern Highlands: *Streimann 18802* (CBG), Mt Michael; *Streimann 32847* (CBG), Det Mission, SSW of Mendi. – Southern Highlands Prov.: *Streimann 26509* (CBG, L), Andawe River. – Morobe Prov.: *Streimann 13739* (CBG), Kaisinik. – Milne Bay Prov.: *Stevens (LAE 55715)* (BM, L), Mt Suckling. — SOLOMON IS.: Malaita: *Braithwaithe, Roy. Soc. Exp. 4858* (GRO).

USA: Alaska: *Worley 7320* (U), Alexander Archipelago, Kosciusko Is., Mt Francis; *Foster s.n.* (ZT), Coronation Bay, Egg Harbour. — CANADA: British Columbia. Queen Charlotte Is.: *Newcombe (365)* (S). Graham Is.: *Schofield 15635* (S), Trounce Inlet; *Schofield 15184* (BR, GRO, S, U), Moresby Is., Cumshewa Inlet; *Schofield, BC 21 (15490)* (GRO, L, MEL, S, U), Hibben Is.; *Schofield 44626* (S, U), Huxley Is. – Vancouver Is.: *Halbert 72 47* (S, U), Kashult Inlet; *Macoun s.n.* (S), Ucluelet.

4.5. **Hypopterygium vriesei** Bosch & Sande Lac. — Fig. 27, 28; Map 14

Hypopterygium vriesei Bosch & Sande Lac., Bryol. Jav. 2 (1861) 11, t. 140. — Type: *De Vriese,* (L holo, FH?, NY), Indonesia, Moluccas, Seram, "Iter Indicum 1858–60".

Hypopterygium chamaedrys Bosch & Sande Lac., Bryol. Jav. 2 (1861) 10, t. 139, syn. nov. — *Hypopterygium vriesei* Bosch & Sande Lac. subsp. *chamaedrys* (Bosch & Sande Lac.) Kindb., Hedwigia 40 (1901) 284. — Syntypes: *Holle s.n.* (L lecto, designated here; NY), Indonesia, Java, ["Gedok"]; *Teijsmann s.n.* (L), Java, W. Java (Jawa Barat), "in m. Gedé et Salak", ["in m. G. Gedé, (inter alios muscos)"]; *Amann 'Aman' [= Kurz] s.n.* (L, sub no. *147*), Java, W Java (Jawa Barat), Mt Salak, on tree trunks, alt. 6000 ft., July 17, (18)60; possible syntype: *Kurz s.n.* (L), Indonesia, Java, W Java (Jawa Barat), Mt Salak, alt. 6000 ft., July 17, (18)60. — See notes 1 and 2.

Hypopterygium micholitzii Paris, Index Bryol. Suppl. (1900) 216, syn. nov. — *Hypopterygium nematosum* Müll.Hal., Flora 82 (1896) 456, hom. illeg., [non Müll.Hal., J. Mus. Godeffroy 3 (6) (1874) 80, (≡ *Lopidium nematosum* (Müll.Hal.) M. Fleisch., Hedwigia 63 (1922) 213)]. — *Hypopterygium philippinense* Hampe ex Kindb., Hedwigia 40 (1901) 285, nom. illeg. incl. spec. prior. (*Hypopterygium micholitzii* Paris). — Type: *Micholitz s.n.* (B holo, destroyed; S lecto, designated here, ex hb. C. Müller; BM, FH, GRO, S), Indonesia, West Papua (Papua, Irian Jaya), Onin Peninsula, Fakfak, "Mc. Cluer Gulf" (= Teluk Berau), "Skroe" (= Sekru). — See notes 3 and 4.

Hypopterygium pernanum Müll.Hal. ex Kindb., Hedwigia 40: 294. 1901; Müll.Hal. in Levier, Bryoth. Levier (1899–1908) 1596, nom. nud., year and date of distribution not found, presumably distributed before 1901. — Type: *Loria s.n.* (S holo, sub nos. *31* and *57* in hb. Kindberg), New Guinea, "(ad C.M. misit Levier)", Aug., 1893; *Loria, Bryoth. Levier 1596* (FH iso), Papua New Guinea, Central, Mt Moroko, "Nova Guinea austro-orient. Brit. in montosis Mo-roka, 1300 m. (distr Moresby)", July–Aug., 1893. — It is certain that the specimens in S and FH are duplicate specimens of the same collection. — Synonymised with *Hypopterygium ceylanicum* Mitt. by Fleischer, Musc. Buitenzorg 3 (1908) 1084. — See note 5.

Hypopterygium semperanum Hampe ex Kindb., Hedwigia 40 (1901) 285, nom. nud. in syn. (*Hypopterygium philippinense* Hampe ex Kindb.). — Original material: *Semper s.n.* (BM, GRO, S, sub nos. *11* and *14* in hb. Kindberg), Philippines, Luzon. — Given in the synonymy of *Hypopterygium philippinense* Hampe ex Kindb. by Kindberg l.c. with *Hypopterygium nematosum* Müll.Hal., hom. illeg.

Hypopterygium borneense Broth., Mitteil. Inst. Allg. Bot. Hamburg 7 (1928) 128, syn. nov. — Type: *Winkler 3022* (H-BR holo), Indonesia, Kalimantan Barat, "West-Borneo: am Sungai Gulu", alt. 150 m, Nov. 16, 1924. — See note 6.

Illustrations: Fleischer, Musc. Buitenzorg 3 (1908) f. 182. — Rosario, Moss Flora Nat. Bot. Garden Quezon Prov. (1979) f. 64.

Plants in loose groups of fans, usually pinnate to bipinnate, flabellate, or weakly palmate, occasionally simple, medium-sized to large, usually gemmiferous. *Stipe* up to 2.5(–4.5) cm long, usually ascending, rarely partly creeping, entirely laterally compressed or dorsiventrally compressed in basal fourth to half, usually tomentose at base and glabrous above, occasionally partly tomentose in distal part or entirely tomentose. *Frond* usually ovate to narrowly elliptic, occasionally irregulary transverse-elliptic, subcircular or triangular, up to 3.5 cm in diameter; rachis and branches laterally or dorsiventrally compressed (rachis frequently dorsiventrally compressed or not compressed in basal fourth), laterally compressed in gemmiferous part, growing in stipe direction and roughly horizontal, occasionally caducous near apex (see note 7), glabrous; branches up to 1.7 cm long. *Primordia* occasionally set with scaly leaves; scaly leaves ovate to elliptic, margin entire. *Epidermis cells and cortical cells of stipe, rachis, and branches* equally wide or cortical ones wider; walls incrassate in epidermis cells and outer cortical cells, thin in inner cortical cells, yellow to brown in epidermis cells and outer cortical cells, yellow in inner cortical cells; inclusions absent. *Central strand* present in stipe and basal part of rachis, absent from distal part of rachis and branches (replaced by a central cavity); cells narrower than inner cortical ones, walls thin, yellow; inclusions present in outer strand cells but less frequently in inner ones, clumps or plates, fat-like (or crystalline when plates?), colourless. *Axial cavities* absent from stipe and basal part of rachis, central in distal part of rachis and branches; inclusions present, similar to those of central strand cells. *Axillary hairs* 2–4 per leaf, 2- or 3-celled; basal cells 1 or 2 ; terminal cell elliptic to obovate, 40–75 µm long and 25–35 µm wide, smooth or slightly verrucose, wall (thin or) incrassate. *Phyllotaxis of stipe, rachis and branches* tristichous. *Foliation*: of stipe isophyllous and not complanate in basal part of stipe, weakly or distinctly anisophyllous and complanate in distal part; of rachis and branches distinctly anisophyllous and complanate. *Leaves* distant at stipe, distant or closely set in frond, yellowish green to dark green, dull; insertion concave; laminal cells prosenchymatous, hexagonal, short to elongate, 20–85 µm long and 20–30 µm wide, walls thin, porose. *Basal and distal stipe leaves* dimorphic or monomorphic, weakly or distinctly differentiated, appressed to squarrose-recurved, symmetrical or asymmetrical, ovate; margin entire, weakly serrate, or weakly serrate-dentate; teeth 1-celled, uniseriate, up to 20 µm long; border faint to distinct, continuous or interrupted, 1 or 2 cells wide, colourless; apex acute, gradually acuminate, or abruptly acuminate; acumen up to 0.3 mm long; costa faint to distinct, reaching 1/2 of leaf length to percurrent. *Basal stipe leaves* scale-like (or leaf-like), appressed to squarrose-recurved, ovate, up to 1.0 mm long and 0.3 mm wide, frequently damaged. *Distal stipe leaves* leaf-like, ± similar to basal frond leaves; lateral ones patent to widely patent, short-ovate to ovate, 1.0–2.5 mm long and 0.5–2.0 mm wide; stipe amphigastria

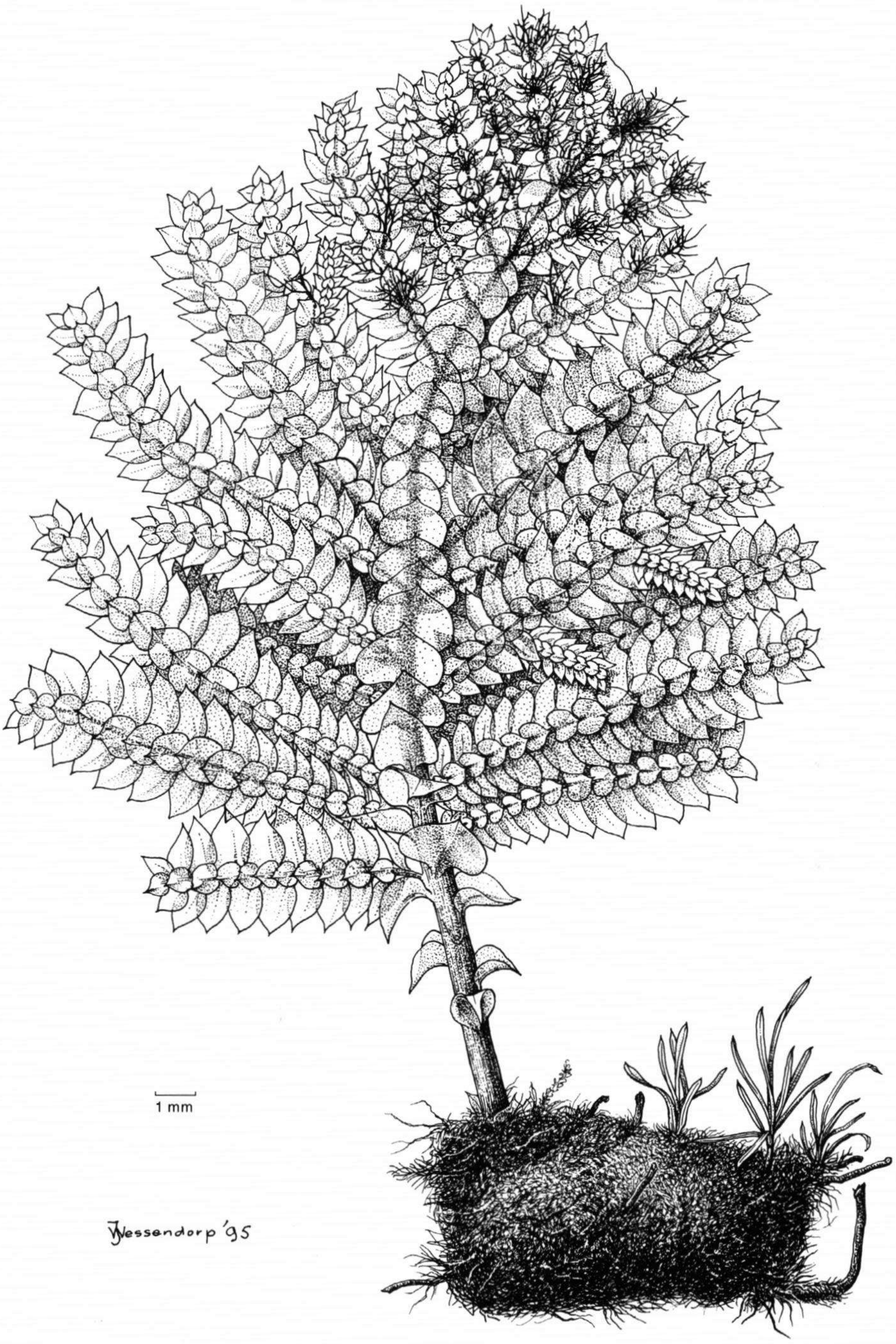


Fig. 27. ***Hypopterygium vriesei*** Bosch & Sande Lac. Habit (ventral view, *Touw 19636*, L).

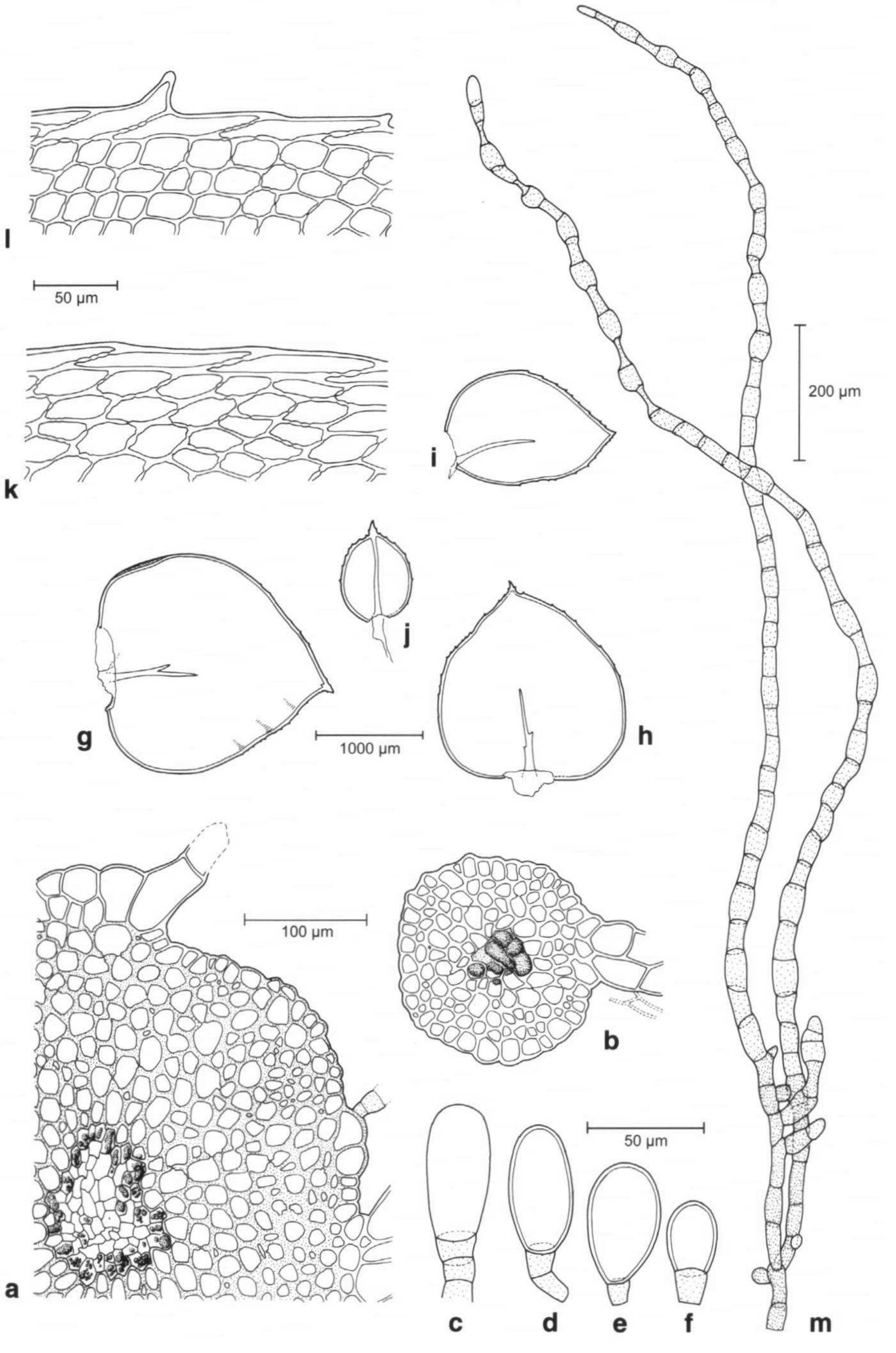


Fig. 28. *Hypopterygium vriesei* Bosch & Sande Lac. a. Rachis (cross section dorsal quadrant); b. branch (cross section); c–f. axillary hairs; g, h. rachis leaves (g. lateral, h. amphigastrium); i–j. branch leaves (i. lateral, j. amphigastrium); k–l. leaf cells of lateral rachis leaf (k. basal part of antical side, l. distal part of antical side); m. gemmaphore with gemmae (a–m: *Touw 19636*, L).

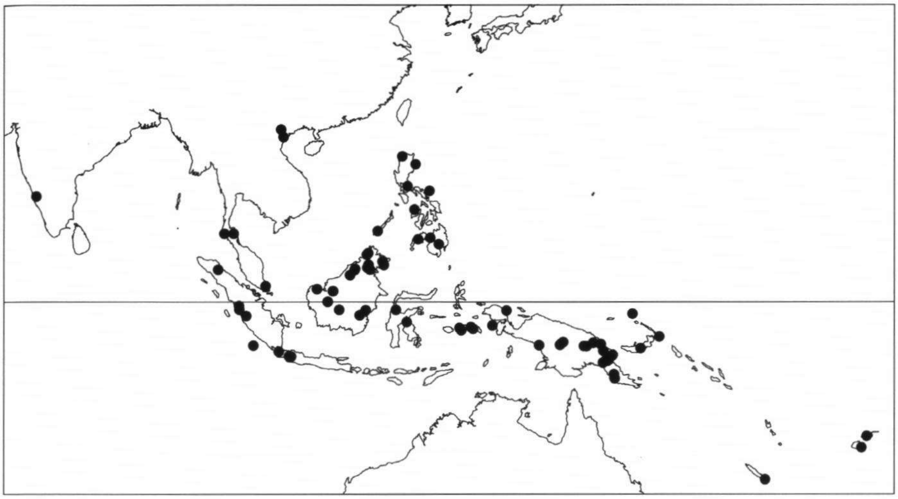
erect to patent, broad-ovate to elliptic, 0.5–1.5 mm long and 0.5–1.5 mm wide. *Frond leaves* dimorphic, not caducous or caducous when situated at apex of (ultimate) branches; margin moderately to coarsely serrate-dentate; teeth 1- (or 2-)celled, usually uniseriate, occasionally 2 cells wide at base, occasionally forked near tooth apex, up to 100 μm long, projecting up to 3/4 of cell length, up to 15–35; border faint or distinct, continuous or interrupted near apex, 1–4 cells wide, colourless; apex (gradually or) abruptly acuminate; acumen 0.1–0.3 mm long. *Lateral frond leaves (in basal and distal part of frond)* asymmetrical, ovate, 1.0–2.5 mm long and 0.5–2.0 mm wide, often appearing as squarrose-recurved when dry; costa distinct, reaching 1/2–3/4 of leaf length. *Frond amphigastria (in basal and distal part of frond)* symmetrical, broad-ovate, subcircular, ovate, or elliptic, 0.3–1.5 mm long and 0.2–1.5 mm wide; costa faint or distinct, reaching 1/3 of amphigastrium length to excurrent. *Gemmae clusters* in various parts of frond axes, most frequently on branches, less often on rachises, often conspicuous and crowded, usually reaching up to 4/5 of length of associated lateral leaves, exceptionally up to 2 times as long. *Gemmaphores* branched, 3–10 cells long, brown. *Gemmae* simple (or branched when long), usually up to 25 cells long, exceptionally up to 85 cells long, brown (or colourless at apex); cells 25–60 μm long and 25–45 μm wide.

Dioicous. Gametoecia in basal and middle part of rachis; *full-grown perichaetia* unknown. *Gametoecial leaves* green; margin ± entire; border distinct and continuous, or partly distinct and faint or interrupted near leaf base or in acumen, up to 3 cells wide; apex gradually or abruptly acuminate; costa usually absent, less often faint, reaching 1/5 of leaf length; laminal cells entirely prosenchymatous or parenchymatous near leaf base, short to short-linear, rectangular when situated in parenchymatous leaf parts, hexagonal or rhomboid when situated in prosenchymatous leaf parts. *Inner leaves*: of perigonia short-ovate to oblong, up to 1.0 mm long and 0.9 mm wide, acumen up to 0.3 mm long; of perichaetia prior to sporophyte development ovate to nearly short-lingulate, up to 0.7 mm long and 0.5 mm wide, acumen up to 0.3 mm long. *Antheridia* 0.4–0.6 mm long. *Archegonia* 0.4–0.5 mm long. *Vaginula* unknown. *Gametoecial axillary hairs* up to 2 (or more?) per gametoecial leaf, 2- (or 3-)celled; *basal cells* 1 (or 2) ; *intermediate cells* absent; *terminal cell* short to elongate, ovate to elliptic or rectangular, 30–65 μm long and 14–25 μm wide, smooth, wall thin or incrassate. *Paraphyses* absent. *Sporophyte* unknown.

Distribution — India (Karnataka), Thailand, Vietnam, Philippines (Luzon, Catanduanes, Palawan, Panay, Mindanao), Malaysia (Johore, Sarawak, Sabah), Indonesia (Sumatra, Enggano, Krakatau, Java, Kalimantan, Sulawesi, Moluccas: Ambon, Seram; West Papua), Papua New Guinea, Bismarck Archipelago (Mussau, New Ireland, New Britain), Vanuatu (Espiritu Santo), Fiji (Viti Levu, Vanua Levu), New Caledonia. See notes 9–11.

Apparently absent from areas with a monsoon climate. Rare in continental Asia north of the Isthmus of Kra. Absent from southern China. Not known from Central and E Java and the Lesser Sunda Islands, Indonesia (cf. Touw, 1992a), and the northern Moluccas. Not known from the Solomon Islands and Vanuatu.

Ecology — In forests; in humid places or near streams, in open, sunny habitats to fully shaded. On rocks and boulders (mostly limestone, less often on ultrabasic, volcanic, or non-calcareous rock like sandstone, possibly also on granite), stem bases, tree



Map 14. Distribution of *Hypopterygium vriesei* Bosch & Sande Lac.

trunks, branches, twigs, and rotten logs; rarely epiphyllous. Altitude: 60–2200 m, most frequently found below 900 m, rarely above 1500 m. Above 900 m usually found on tree trunks, branches, and twigs.

According to Akiyama (1992) the present species (as *Hypopterygium chamaedrys*) forms extensive populations especially on limestone.

Geographical & Ecological variation — Not found.

Notes:

Nomenclature and synonymy — 1. Van den Bosch & Van der Sande Lacoste (1861) distinguished *Hypopterygium vriesei* from *H. chamaedrys* by differences in habit, i.e. the shape of the frond, the foliation of the stipe, the size of the amphigastria and the length of the costa, the ramification of gemmae, the size of the [leaf]cells and the size of the perigonia. These differences, however, are not substantial.

There is considerable overlap in the size of the amphigastria, the perigonial leaves, and the leaf cells. Only the largest amphigastria of *Hypopterygium vriesei* are somewhat longer than those in the lectotype and Teijsmann's syntype of *H. chamaedrys*, whereas only the shortest amphigastria of *H. vriesei* are somewhat shorter than in Amann's syntype of *H. chamaedrys*. The perigonial leaves of *H. vriesei* are generally longer than those of *H. chamaedrys*, but among its syntypes only the lectotype is fertile. The laminal cells of the frond leaves of *H. vriesei* are generally smaller than in *H. chamaedrys*, but overlap occurs.

Van den Bosch & Van der Sande Lacoste (1861) described the frond of *Hypopterygium vriesei* as ovate to oblong-lanceolate and that of *H. chamaedrys* as triangular to ovate. The fronds are, in fact, broadly ovate to oblong in *H. vriesei* and subcircular, ovate, or oblong, and occasionally irregulary obovate, in the syntypes of *H. chamaedrys*.

The authors described the stipe of *Hypopterygium vriesei* as foliose, and that of *H. chamaedrys* as non-foliose over a long distance. They overlooked that in the syntypes of *H. chamaedrys* occasionally all stipe leaves, but more often the basal ones, are small and scale-like and often damaged or lost. Damaged and scale-like stipe leaves occur also in the types of *H. vriesei*, but are less pronounced.

Van den Bosch & Van der Sande Lacoste (1861) described the amphigastrium costa as vanishing halfway the amphigastrium in *Hypopterygium vriesei* and as excurrent in *H. chamaedrys*. However, there is considerable overlap between these two in the length of the amphigastrium costa. In *H. vriesei* the costa reaches generally between 1/3 to 4/5 of amphigastrium length and is, less often, excurrent. In *H. chamaedrys* the costa reaches at least halfway the amphigastrium and is frequently excurrent. In Amann's syntype, however, excurrent amphigastrium costae predominate. The mutual differences between the syntypes of *H. chamaedrys* are more significant than those between *H. vriesei* and *H. chamaedrys.*

Former authors considered the gemmae and gemmaphores ("pili in axillis foliorum") in *Hypopterygium vriesei* as moderately dichotomous and those in *H. chamaedrys* as rigid and much-branched. The gemmaphores in the two gemmiferous syntypes of *H. chamaedrys* (*Holle s.n.* and *Teijsmann s.n.*) are generally somewhat shorter and more strongly, alternately branched than those at *H. vriesei,* which are occasionally dichotomously branched or even simple. In both taxa the gemmae are filiform and simple, but are mostly broken off from the gemmaphores.

2. Akiyama (1992) considered *Hypopterygium vriesei* and *H. chamaedrys* to be closely related, because of their filamentous gemmae in the leaf axils, their widely ovate lateral leaves, and their strongly serrate amphigastria. Nevertheless, he distinguished them by differences in the morphology of the amphigastria. He described the amphigastria of *H. vriesei* having a gradually narrowed, acute apex that is not reached by the costa, whereas he considered the amphigastria of *H. chamaedrys* to be more or less retuse and often having costate aristae.

However, these differences do not exist as distinctive features. In Akiyama's material of both *Hypopterygium vriesei* and *H. chamaedrys,* I found that the amphigastria are usually abruptly acuminate and occasionally gradually acuminate. The amphigastria situated in the basal part of the stipe are occasionally rounded-obtuse or nearly so and have a short to long acumen. As shown above, the length of the amphigastrium costa is not a discriminating feature between *H. vriesei* and *H. chamaedrys.*

3. The lectotype of *Hypopterygium micholitzii,* which is preserved in Kindberg's herbarium (S), includes a gemmiferous plant that lost most of its stipe and a fragment of a plant. It is the only specimen that comes evidently from Müller's herbarium.

The lectotype is labelled with the number *14,* which is written in red ink and striked out with black. It is not known what this number stands for. Presumably, it represents an herbarium number for the species, i.e. *H. philippinense,* for Kindberg's specimen of *H. semperanum* is also labelled with this number. The isotypes in BM, GRO, and S that were distributed by Brotherus are labelled as *H. nematosum* with species number *14.*

One of the two type collections in BM and the one in GRO contain gemmiferous fragments of a plant.

4. The type material of *Hypopterygium micholitzii* is strongly gemmiferous. The plants are up to 2.5 cm tall. It is beyond any doubt that *H. micholitz* is conspecific with *H. vriesei.*

5. The type of *Hypopterygium pernanum* is a frond fragment of a small plant of *Hypopterygium vriesei* bearing gemmaphores.

6. The holotype of *Hypopterygium borneense* is a medium-sized, gemmiferous plant with a pinnate ramification and three-ranked leaves, and it is beyond any doubt conspecific with *H. vriesei.* According to an identification label from 1976 that is attached to the holotype of *H. borneense,* Iwatsuki also identified the holotype as *H. vriesei.*

Description — 7. In some rachises and branches with lost apices growth is overtaken by one or two subapical branches.

Reproduction — 8. To date fruiting specimens have not been found, despite the fact that approximately 50% of the specimens were fertile (n = 55). Among the fertile plants, plants containing only a few gametoecia have a small majority (60%) over those containing numerous gametoecia (n = 20). Approximately 70% of the fertile material (n = 20) were female plants.

Approximately 93% of the specimens is gemmiferous material (n = 169). Fertile specimens are also very often gemmiferous.

Distribution — 9. To my knowledge, Flenley's findings of *Hypopterygium vriesei* (*KCE 425*) and *Cyathophorum spinosum* (*KCE 475*) in September 1979 on Rakata (Pulau Rakata Besar) are the first records of Hypopterygiaceae found on the Krakatau Islands. Flenley's collection of *H. vriesei* is a gemmiferous, sterile plant; his collection of *C. spinosum* is a gemmiferous, male plant. Both mosses were collected at 671 m altitude in a very mossy secondary forest with a high percentage of *Ficus ribes* Reinw. ex Blume and with luxuriant growth of epiphytic mosses on tree trunks, branches and twigs (cf. Forster, 1982; Whittaker, 1982; 'Ecological plot 8'). *Hypopterygium vriesei* was collected by Flenley from the base of a living tree trunk, *Cyathophorum spinosum* was found on trunks of dead trees, whereby it was restricted to the trunk base up to 50 cm above ground. Forster (1982) reported Flenley's finding of *Hypopterygium vriesei* as an unidentified *Hypopterygium* (species nr. *KCE 423*) and reported it also from another place ('plot 1840'), but I have not seen material from this locality. Flenley's finding of *C. spinosum* is not recorded by Forster or other authors of the Final Report of the Krakatao Centenary Expedition.

Both moss species were able to reach the island group of Krakatau within a century after the volcano's famous eruptions, followed by the explosion, in 1883. The Krakatau group of islands is located at c. 19 km distance from the nearest island (Sebesi Is.) and c. 40 km from Java and Sumatra. It is assumed (cf. Thornton, 1996), that the events in 1883 almost completely destroyed the entire flora and fauna on the Krakatau Islands, and left for years no suitable habitat for rain forest mosses like *Hypopterygium vriesei* and *Cyathophorum spinosum*. After the cataclysm, the surviving parts of the island group, and Anak Krakatau after its emergence in 1930, were recolonised from Sumatra and Java.

Three years after the eruptions Treub (1888) found Krakatau predominantly recolonised by ferns. He collected only two, unidentified mosses, which probably did not grow there in large quantities (cf. Docters van Leeuwen, 1936). Ernst (1908) collected only two acrocarpous mosses in 1906. Docters van Leeuwen (1936; Fleischer, 1923b) collected numerous mosses on the Krakatau Islands between 1919 and 1929, but did not find *Hypopterygium vriesei* and *Cyathophorum spinosum.*

It is not known by which type of diaspores (gemmae or spores; less likely plant fragments) these moss species have reached the Krakatau Islands. The spores of *Cyathophorum spinosum* are much smaller than its gemmae and are much easier dispersed by air streams. However, the dispersal of *C. spinosum* by gemmae from Java or Sumatra, by air streams – or by birds – over such a relatively short distance overseas can not be excluded. According to Thornton (1996), airborne diaspores may reach the Krakatau Islands from Java or Sumatra on average in about 2 hours or less at times of strong winds.

However, in contrast to *Cyathophorum spinosum*, sporophytes of *Hypopterygium vriesei* are further unknown and its dispersal by the means of spores seems unlikely. There is thus a greater likelihood that *H. vriesei* reached Krakatau and colonised Rakata by means of its gemmae. Most plants of *H. vriesei* are gemmiferous and produce large quantities of filamentous gemmae, which are much shorter than those of *Cyathophorum spinosum.*

10. The species is remarkably little collected on Java. The species is rare on Ambon (cf. Akiyama, 1992).

11. A non-gemmiferous plant that was found growing intermingled in small quantity with material of *Hypopterygium tamarisci* from Mt Kudremukh, Western Ghats, India (*Gleiderer (6457)*, BM p.p.), shows such a close resemblance with *H. vriesei*, that in my opinion it belongs here. Gleiderer's collection is the first record of the species for India.

Identification — 12. Flabellate to palmate plants of *Hypopterygium vriesei* with closely set leaves that are up to 2.0 cm tall may easily be confused with Indo Malaysian plants of *Hypopterygium tamarisci*, especially when they come from New Guinea.

When the plants are gemmiferous, they can be recognised by short clusters of gemmae placed in the axils of usually numerous lateral leaves. Otherwise, identification is more difficult. The amphigastria of the basal part of the rachis are usually longer than wide in *Hypopterygium vriesei* and usually more or less equally long and wide or even shorter than wide in *H. tamarisci.*

In addition, the stipe of small plants of *Hypopterygium vriesei* is usually laterally compressed. This compression is stronger than in small, Indo Malaysian plants of *H. tamarisci*, in which the stipe is, moreover, often dorsiventrally compressed. Besides, when in *H. vriesei* the stipe of a plant is partly dorsiventrally and partly laterally compressed, the dorsiventral compression is restricted to the basal fourth to half of the stipe, whereas in similar cases in Indo Malaysian *H. tamarisci* the distal half of the stipe is dorsiventrally compressed.

13. Medium-sized to large plants of *Hypopterygium vriesei* from the western Pacific may easily be confused with large plants of *H. tamarisci* in this area, i.e. 'Oceanian variant 1' of this species. Plants of the former species can be identified by the central cavities in the distal part of the frond axes, the strikingly regulary, and usually densely, branched, pinnate frond, which is usually clearly longer than wide, and – when present – the short, brown clusters of gemmae placed in the axils of lateral leaves (and amphigastria) over the full length or most of it of the rachis or the branches. The gemmae clusters do usually not exceed 1/3 of the length of the associated lateral leaf.

Plants of the 'Oceanian variant 1' of *Hypopterygium tamarisci* can be identified by the absence of central cavities in frond axes, provided that the material is not too old, the often irregulary, loosely branched, flabellate frond, which is almost equally long as wide or broader because of its strinkingly long, mainly simple branches. Gemmae occur less often, and are usually located on damaged branches or on branches with a detached distal part. The gemma clusters in *H. tamarisci* are located in the distal part of branches, are usually longer, reach at least half of the length of the associated lateral leaf, and have a paler brown colour than those in *H. vriesei.*

In addition, *Hypopterygium vriesei* is dioicous, whereas both Oceanian variants of *H. tamarisci* are monoicous. However, plants of 'Oceanian variant 1' of *H. tamarisci* often lack gametoecia or bear only gametoecia of a single gender, usually female. Hence, sexuality is often a feature of little value for identification in the western Pacific.

Other — 14. In 1996 Urmi found an etiolated, but highly gemmiferous plant of this species in the new Botanic Garden of Zurich, Switzerland (*Urmi s.n.*, Z). This accidently introduced moss was found in a subtropical green house on living and dead fern trunks on moist calcareous stones.

15. A specimen from the Eipomek Valley in West Papua, Indonesia (*Hiepko & Schultze-Motel 2006*, B), has provisionally been placed here. The moss is a flabellate to palmate, male plant. A few gametophores that are set with numerous perigonia are simple. The plant is very small, up to 1.0 cm tall, and was found on the trunk of a tree fern at 1900 m altitude. It is strongly gemmiferous. The gemmaphores are shiny and brown, and are clustered in small groups of a few gemmaphores that are situated just below the lateral leaves and amphigastria of rachises and branches. Clusters of gemmaphores are found at almost the entire length at the ventral or dorsi-lateral side of almost every rachis or branch. The gemmae are filiform, brown, and approximately 6 to 17 cells long. As most gemmae are lost or detached, the bristle-like gemmaphores, which are almost equally long as the leaves, are easily visible and striking.

Undoubtedly, the moss belongs to *Hypopterygium*. It has an entirely tristichous phyllotaxis. Although the stipe is laterally compressed in the basal part and dorsiventrally compressed in the distal part (compare note 12), the moss shows most affinity to *H. vriesei*, because of its numerous gemmaphores. However, the long gemmaphores, the location of the gemmaphore-clusters just below the frond leaves, and the dorsiventral location of the gemmaphore-clusters that are associated with the lateral leaves, suggest that this moss either belongs to an undescribed species or represents a still unknown, New Guinean variant of *H. vriesei*. In the present study, the specimen is not transferred to a new taxon, because it is a single collection and the status of the possible taxon whereto it might belong is very uncertain.

Selected specimens (from 250 examined):

INDIA: Karnataka. *Gleiderer (6457)* (BM p.p., intermingled with *Hypopterygium tamarisci*), Mt Kudremukh, see note 11.

THAILAND: Phuket: *Touw 11319*, Khao (Mt) Nang Hong. – Nakhon Si Thammarat: *Touw 11997* (BM, BR, EGR, GRO, L, NY), Khao (Mt) Luang. VIETNAM. Vinh Phu: *Tran Ninh 69 261* (EGR), *74 221* (EGR), Tam Dao. – Ha Nam Ninh Prov. ('Ninh Binh'): *Pócs et al. 3010/c* (EGR), *3102/1* (EGR), Cúc-Phuong Reserve.

PHILIPPINES: *Micholitz s.n.*. (BM, s.loc.). – Luzon: *Semper s.n.* (BM, S, sub nos. *11* and *14*; s.loc.). – Ilocos Norte Prov.: *Semper s.n.* (BM, GRO s.loc.), Cordillera Central, Mariquet. – Isabela Prov.: *Tan 91 155* (FH), Palanan, Sitio Dipaquiden, Barangay San Isidro. – Quezon Prov.: *Boeken 81.02.1141* (GRO), Siniloan, Botanic Garden; *Robinson 9477* (FH, NY), Siniloan Trail. – Catanduanes: *Van Zanten 80.02.879* (GRO), Balongbong. – Palawan: *Tan 91 256* (FH), *91 262* (FH), Mt Matalinghan. – Panay. Capiz Prov.: *Paniza 9275* (GRO), *9278* (GRO), Mt Upao. – Mindanao. Zamboanga: *Ebalo? 672* (FH), Kabasalan, Mt Lilimbrog. – Lanao del Sur: *Bartlett*

15878a (FH), Marawi ('Dansalan'). – Davao del Sur: *Van Zanten 80.01.723* (GRO), *80.01.728B* (GRO), Malagos Calinan. — MALAYSIA: Peninsular Malaysia. Johore: *Chin 700* (KLU, L), Mt Sumalayang. – Borneo. Sarawak: *Everett s.n.* (NY), Sibu Is.; *Koops & Gravendeel CGK 1846* (L), Lanjak–Entimau Wildlife Sanct.; *Klazenga 340* (L), *345*, *(64k)* (L), *(82)* (L), Batu Kalulong; *Touw 19636* (L), G. Mulu Nat. Park, Gua Payau; *Klazenga (277)* (L), Sungei Melinau; *Richards 1117* (BM, FH, GRO, NICH), *1357* (BM, GRO), *2553* (BM), Mt Dulit; *Ridley s.n.* (BM), Mt Matang. – Sabah: *Tan 89 1020* (L), Mt Kinabalu; *Meijer B 12.899* (L), Silabukan Forest Res.; *Keith 7358* (BM), Semporna, Timbun Mata Is.; *Klazenga (745)* (L), Batu Tinhar. — INDONESIA: Sumatra. N Sumatra (Sumatera Utara): *Koop 17B* (L), G. Leuser Nat. Park, Ketambe; *Bartlett 7686* (BM), Asahan. – W Sumatra (Sumatera Barat): *Van Borssum Waalkes 2742* (GRO, L), Indarung. – Enggano: *Lütjeharms 4594H* (L), Buah-Buah. – Krakatau: *Flenley KCE 423* (L), Pulua Rakata Besar. – Java. W Java (Jawa Barat): *Aman [=Kurz] s.n.* (L), *s.n.* (S); *Nyman 560* (NICH p.p., S), *Schiffner 12931* (L, S), Mt Salak; *Schultze-Motel 5113* (B p.p.), Tjibodas. – Kalimantan: *Jaheri s.n.* (L, s.loc.), *Nieuwenhuis [= Jaheri?] (2563)* (BM, s.loc.). – W Kalimantan (Kalimantan Barat): *Winkler 3022* (H-BR), Sungei Gulu. – C Kalimantan (Kalimantan Tengah): *Veldkamp 8099 D* (L), Tumbang Habangoi. – E Kalimantan (Kalimantan Timur): *Meijer B 4562* (GRO, L), Tarakan, Nunukan Timur ('Nunukan'); *Amdjah 301* (GRO, L), Labang; *Meijer B 2370* (L), Mt Balikpapan. – S Kalimantan (Kalimantan Selatan): *Dransfield 2348* (L), Mt Sarempaka. – Sulawesi. S Sulawesi (Sulawesi Selatan): *Van Balgooy 3917 C* (L, NICH, S), Soroako–Wasuponda Road. – C Sulawesi (Sulawesi Tengah): *Hennipman 5103 H* (L), Sopu Valley. – Moluccas (Maluku). Ambon: *Robinson 2332* (NY); *Akiyama A-14511* (KYO), Liang. – Seram: *De Vriese s.n.* (FH, L, NY); *Akiyama C-15605* (KYO), Tanah-goyang–Mt Sia-Pu; *Akiyama C-8588* (KYO, L), Manusela National Park. – West Papua (Papua, Irian Jaya). Manokwari: *Beccari 197* p.p. (GRO, L), Mt Arfak, Putat. – Fakfak: *Micholitz (14)* (BM, GRO, S), *s.n.* (FH), Onin Peninsula, Sekru ('Skroe'). – Merauke: *Von Römer 108* (GRO, L), Sungai Lorentz ('Noordrivier'); *Van Zanten 280c* (GRO, L), Amiol. — PAPUA NEW GUINEA: West Sepik: *Touw 15066* (L), Star Mts, Busilmin. – Enga: *Robbins 3014* (FH, L), Wabag area. – Western Highlands: *Streimann 21079* (CBG), N of Mt Hagen; *Thiers 3589* (NY), *Van Zanten 68857* (GRO p.p., mixed with *Hypopterygium tamarisci*), Baiyer River. – Eastern Highlands: *Streimann & Umba 11537* (CBG), Kassam Pass, Yati River. – Madang: *Robbins 1421a* (FH, L), Aiome, Asai River Gorge. – Morobe: *Streimann & Bellamy 13173A* (CBG), Buldo; *Streimann 33564* (CBG), Mumeng. – Central: *Loria, Bryoth. Levier 1596* (FH), Mt Moroko ('Moroka'); *Robbins 4135* (L), Musgrave River; *Van Zanten 68061* (GRO), Sogeri Plateau. – Gulf: *Streimann 33782* (CBG), Kaintiba, Hepataewa. – Bismarck Archipelago. Mussau: *Køie & Sandermann Olsen 2059* (GRO, L, NY). – New Ireland: *Eddy 6119* (BM), Danfu Valley. – New Britain: *Streimann 40244* (L), *40888* (L). Lakum River.

VANUATU: Espiritu Santo: *Bowie (72)* (BM); *Bowie s.n.* (MEL), Tangoa. — FIJI: Viti Levu: *Mead 32* (WELT), Suva. – Vanua Levu: *Smith 6845* (BM, BR, FH, L, NY, S, W), Mathuata.

NEW CALEDONIA: *Robbins 3764* (L p.p.), Mt Dzumac, Ouinne Valley.

4.6. **Hypopterygium tamarisci** (Sw.) Brid. ex Müll.Hal. — Fig. 29–34; Map 15; Plate 2e–f

Hypopterygium tamarisci (Sw.) Brid. ex Müll.Hal., Syn. Musc. Frond. 2 (1850) 8. — *Hypnum tamarisci* [Sw. ex] Sw., Fl. Ind. Occ. 3 (1806) 1825; Sw., Prodr. (1788) 141, nom. inval. (pre-starting-point). — *Hookeria arbuscula* Arn., Disposition Méth. Espèc. Mousses (preprint) (1825 [= 1826?]) 56; Mém. Soc. Hist. Nat. Paris 2, 2 (1826) 305, hom. illeg., [non Sm., Trans. Linn. Soc. London 9 (1808) 280, t. 23 f. 3 (≡ *Camptochaete arbuscula* (Sm.) Reichardt)]. — Type: *Swartz s.n.* (UPS holo, n.v.; S, G; W, damaged, only a part of the stolon is preserved on the sheet, the other parts of this specimen are completely lost), Jamaica. — See notes 1 and 2.

Hypnum laricinum W. Hook., Musci Exot. 1 (1818) t. 35. — *Hookeria laricina* (W. Hook.) W. Hook. & Grev., Edinburgh J. Sci. 2 (1825) 234. — *Hypopterygium laricinum* (W. Hook.) Brid., Bryol. Univ. 2 (1827) 714. — Syntypes: *Menzies 75* (BM lecto, also sub no. *H. 1532*), South Africa, Cape of Good Hope, 1791; *Humboldt ['Humboldt & Bonpland'] 92* (BM, also sub no. *H. 1531*), South America, "in jugis Andium region temperata". — Lectotype designated by

Pfeiffer et al., J. Hattori Bot. Lab. 89 (2000) 65. — Synonymised with *Hypopterygium tamarisci* (Sw.) Brid. ex Müll.Hal. by Pfeiffer et al., l.c. — According to annotations in Wilson's herbarium, Hooker's illustrations of *Hypnum laricinum* in Musci Exot. 1 (1818) t. 35 are based on the South American material.

Hypopterygium rotulatum (Hedw.) Brid. var. *incurvum* Brid., Bryol. Univ. 2 (1827) 714, syn. nov. — Type: *De Candolle s.n.* (B holo; JE, collector's name and year not given), Australia ('Nova Hollandia'), 1822. — The specimen that is preserved in JE comes from Bridel's herbarium. — See note 3.

Hypopterygium flavescens Hampe, Linnaea 20 (1847) 95, syn. nov. — *Hypopterygium tamarisci* (Sw.) Brid. ex Müll.Hal. subsp. *flavescens* (Hampe) Kindb., Hedwigia 40 (1901) 288. — Type: *Moritz 70* (BM holo, n.v.; S; ?S '1844'; ?S, both sub no. *30* in hb. Kindberg, but without a collection number), Venezuela ["Columbia"], Mérida, ["intermixtum"]. — See notes 4 and 5.

Hypnum scutellatum Taylor, London J. Bot. 6 (1847) 338. — *Hypopterygium scutellatum* (Taylor) Müll.Hal., Syn. Musc. Frond. 2 (1850) 7. — Type: *Jameson s.n.* (FH holo, n.v.; BR, sub no *81*; BM not found, NY n.v.), Ecuador, Pichincha Prov., Mt Pichincha ("on Pichincha"), near Quito, Nov., 1846. — Synonymised with *Hypopterygium tamarisci* (Sw.) Brid. ex Müll.Hal. ["Sw., *Hypnum*; Hedw. Musc. Frond. t. 51, *Leskea*"] by Mitten, J. Linn. Soc., Bot. 12 (1869) 330. — Müller l.c. did not cite Taylor's l.c. name, but from Müller's protologue it becomes clear that *Hypopterygium scutellatum* (Tayl.) Müll.Hal. is a new combination based on *Hypnum scutellatum* Tayl. — See notes 6 and 7.

Hypopterygium incrassatolimbatum Müll.Hal., Syn. Musc. Frond. 2 (1850) 8, '*incrassato-limbatum*', syn. nov. — *Hypopterygium laricinum* (W. Hook.) Brid. subsp. *incrassatolimbatum* (Müll.Hal.) Kindb., Hedwigia 40 (1901) 291, '*incrassato-limbatum*'. — *Hypopterygium laricinum* (W. Hook.) Brid. ["Hook."] var. *incrassatolimbatum* (Müll.Hal.) W. Krieg. & Broth., Hedwigia 43 (1904) 349, '*incrassato-limbatum*'. — *Hypopterygium incrasso-limbatum* Erdtman, An Introduction to Palynology 3 (1965) 122, nom. inval., err. typogr. pro *Hypopterygium incrassatolimbatum* Müll.Hal. — Type: *Pabst s.n.* (B destroyed; S lecto, designated here, in hb. Ångstrom; S, sub no. 54 in hb. Kindberg), Brazil, Santa Catarina, "ad flum. Itajahi in silvis montosis ad lapides" ["ad truncos arborum sylvarum ad flum. Itajahi, lapides sylvarum montos. habitans. Jul. Oct. 1847"], 1847. — See note 8.

Hypopterygium tenellum Müll.Hal., Bot. Zeit. 12 (1854) 557. — *Hypopterygium rotulatum* auct. non Hedw.: Montagne, Ann. Sci. Nat. Bot. 2, 17 (1842) 243; according to Müller, Bot. Zeit. 12 (1854) 558. — *Hypopterygium rotulatum* Mont. in Okamura, J. Coll. Sci. Imp. Univ. Tokyo 36, 7 (1915) 25, nom. nud. in syn. (*Hypopterygium tenellum* Müll.Hal.); given as a synonym, but probably meant as a misidentification. — Syntypes: *Schmid s.n.* (B destroyed; JE lecto, BM, NY), India, Tamil Nadu, Nilgiri Hills; *Perrottet s.n.* (B destroyed; BM, s. coll., s.loc., 'Neel-Gherries'), India, Tamil Nadu, Nilgiri Hills, ["In cortice arborum una cum Hypopt. Struthiopteris circa Ootacamund"]; possible syntypes: *Perrottet 1522* (BM, RO, UPS), *1565* (BM), *s.n.* (BM, "Neelgherries"; NY), India, Tamil Nadu, Nilgiri Hills; *Perrottet s.n.* (NY, s.loc.), India. — Lectotype designated by Pfeiffer et al., J. Hattori Bot. Lab. 89 (2000) 65–66. Typification is discussed by Pfeiffer et al., l.c.: 68. — Synonymised with *Hypopterygium tamarisci* (Sw.) Brid. ex Müll.Hal. by Pfeiffer et al., l.c.: 65. — See note 9.

Hypopterygium brasiliense Sull., Proc. Amer. Acad. Arts. 3 (1855) 184. — Type: *US Exploring Exp. (Wilkes)*, 1838–1842 (n.v.), Brazil, Organ Mts — Synonymised with *Hypopterygium tamarisci* (Sw.) Brid. ex Müll.Hal. ["Sw., *Hypnum*; Hedw. Musc. Frond. t. 51, *Leskea*"] by Mitten, J. Linn. Soc., Bot. 12 (1869) 330. — Synonymised with *Hypopterygium incrassatolimbatum* by Piovano, Sellowia 9 (1958) 109. — See note 10.

Hypopterygium muelleri Hampe, Linnaea 28 (1856) 215. — *Pterobryon muelleri* (Hampe) Mitt., Trans. & Proc. Roy. Soc. Victoria 19 (1882) 81. — Type: *Von Mueller s.n.* (BM holo not found; MEL holo?, sub no. *40*; MEL and WELT iso, sub no. *40* and (exchange) no. *111*), Australia, E. Victoria: Austr. felix., In lapidibus ad ripam fluminis Buchan humidam ("Ad ripas flum. Buchan-river"), March, 1854. — Typification is discussed by Kruijer, Glasgow Naturalist 23, 2 (1997) 16: see also Pfeiffer et al., J. Hattori Bot. Lab. 89 (2000) 68. — Synonymised with *Hypopterygium tamarisci* (Sw.) Brid. ex Müll.Hal. by Pfeiffer et al., l.c.: 66.

Hypopterygium ceylanicum Mitt., J. Proc. Linn. Soc., Bot., Suppl.1 (1859) 148. — *Hypopterygium rotulatum* auct. non (Hedw.) Brid.: Wilson ex Mitten, J. Proc. Linn. Soc., Bot., Suppl. 1 (1859) 148. — Syntypes: *Gardner 691* (NY, BM, s.loc.; both also sub no. *18*), Sri Lanka ["Ceylon"], Central. Prov., Ramboda "Ramboddi"; *Gardner 692* (NY lecto, designated here, s. coll.; BM; both specimens also sub no. *86*), Sri Lanka ["Ceylon"]. — Drawings of *Hypopterygium ceylanicum* Mitt. by the hand of Mitten are attached to the lectotype. Although the label of the lectotype lack's a collector's name, it is certain that it was collected by Gardner. — Synonymised with *Hypopterygium tenellum* Müll.Hal. by Van den Bosch & Van der Sande Lacoste, Bryol. Jav. 2 (1861) 13. Also proposed in the synonymy of *Hypopterygium tenellum* Müll.Hal. by Cardot in Renauld & Cardot in A. & G. Grandidier, Hist. Phys. Madagascar 39, Mousses (1915) 422.

Hypopterygium humile Mitt. ex Bosch & Sande Lac., Bryol. Jav. 2 (1861) 15 t. 143, syn. nov. — *Hypopterygium ceylanicum* Mitt. subsp. *humile* (Mitt. ex Bosch & Sande Lac.) Kindb., Hedwigia 40 (1901) 290. — Type: *Motley s.n.* (NY holo; L not found), Indonesia, Java, W Java, Mt Megamendong, alt. 4–6000 ft. — See notes 11 and 12.

Hypopterygium oceanicum Mitt. in Hook.f., Handb. N. Zeal. Fl. (1867) 487, syn. nov. — *Hypopterygium muelleri* Hampe subsp. *oceanicum* (Mitt.) Kindb., Hedwigia 40 (1901) 296. — *Hypopterygium rotulatum* (Hedw.) Brid. var. *oceanicum* (Mitt.) Dixon, New Zealand Inst. Bull. 3, 5 (1927) 296. — *Hypopterygium novaeseelandiae* Müll.Hal. var. *oceanicum* (Mitt.) Dixon, New Zealand Inst. Bull. 3, 6 (Index) (1929) xiii, nom. inval., err. pro *Hypopterygium rotulatum* (Hedw.) Brid. var. *oceanicum* (Mitt.) Dixon. — Syntypes: *Milne 75* (NY lecto, designated here, '1855'; BM, "trees summit mountain not frequent in fruit", "HMS Herald 1855"), Kermadec Islands, Raoul Island ["Sunday Island"], Summit of Mountain, July 1854; *McGillivray s.n.* (BM, NY), Kermadec Islands, Raoul Island, on trees, July 1854. — See notes 13, 14, and 15.

Hypopterygium viridulum Mitt. in Hook.f., Handb. N. Zeal. Fl. 2 (1867) 487. — *Hypopterygium rotulatum* auct. non (Hedw.) Brid.: Hooker f. & Wilson, Bot. Antarct. Voy. 2 (2) (1854, '1855') 118, according to Mitten l.c. — Syntypes: *Stephenson s.n.* (not found), New Zealand, North Island, Wellington L.D., Wellington; *Kerr s.n.* (not found), New Zealand, North Island, North Auckland L.D., Whangaroa ["Wangaroa"]; *Kerr s.n.* (NY lecto, designated here), New Zealand, South Island ["Middle Island"], Canterbury L.D., Banks Peninsula, Akaroa; probable syntypes: *Stephenson 20* (BM, NY), *11b* (NY), *s.n.* (NY), New Zealand. — Synonymised with *Hypopterygium rotulatum* (Hedw.) Brid. by Dixon, New Zealand Inst. Bull. 3, 5 (1927) 296. — Should not be confused with *Hypopterygium novaeseelandiae* Müll.Hal. subsp. *viridulum* Mitt. ex Kindb. (= *Hypopterygium didictyon* Müll.Hal.). — See notes 15 and 16.

Hypopterygium debile Reichardt, Verh. Zool. Bot. Ges. Wien 18 (1868) 197; Hedwigia 7 (1868) 191. — *Hypopterygium rotulatum* (Hedw.) Brid. subsp. *debile* (Reichardt) Kindb., Hedwigia 40 (1901) 294. — Synonymised with *Hypopterygium tamarisci* (Sw.) Brid. ex Müll.Hal. by Pfeiffer et al., J. Hattori Bot. Lab. 89 (2000) 66. — Type: *Jelinek 125*, (W holo, S; "Exped. Novara"), Society Islands, Tahiti, Fataua, "Im Urwald auf feuchten Abhängen". — See note 17.

Hypopterygium rigidulum Mitt., J. Linn. Soc., Bot. 12 (1869) 329. — Type: *Weir 348* (NY holo n.v.), "Colombia: Andes Bogotenses, in sylvis prope Bucamaranga & Pacho, alt. 6000–7000 ft.". — Mitten, J. Linn. Soc., Bot. 12 (1869) 330, cited the type under material of *Hypopterygium tamarisci* (Sw.) Brid. ex Müll.Hal., but it was formally synonymised with *Hypopterygium tamarisci* (Sw.) Brid. ex Müll.Hal. ('*Hypopterygium tamariscinum* (Hedw.) Brid.') by Churchill, Bryologist 91 (1988) 117.

Hypopterygium sylvaticum Mitt., J. Linn. Soc., Bot. 12 (1869) 329. — *Hypopterygium silvaticum* Mitt. ex Kindb., Hedwigia 40 (1901) 289, nom. inval., err. orthogr. pro *Hypopterygium sylvaticum* Mitt. — Syntypes: *Funck & Schlim 356* (L, s.loc., '*Hypopterygium tamariscinum*'; NY n.v.), Venezuela; *Birschel s.n.* (NY n.v.), Venezuela, Caracas; *Spruce 1490* (NY n.v.), Peru, ["Andes Peruvianae, in monte Guayrapurina ad corticem (3000 ped.)"]; *Macrae s.n.* (NY n.v.), Brazil, Santa Catarina; *Gardner 90* (NY? n.v.), Brazil, Sierra dos Orgãos; *Weir, MB 55* (S, sub nos. *56* and *20* in hb. Kindberg, NY lecto, designated here, n.v.), Brazil, Paraná et S. Paulo, ["in sylvis passim ad arbores & lapides (1500–2200)"]. — Proposed in the synonymy of *Hypopterygium serrulatum* Lindb. in Ångstr., nom. nud., by Ångström, Oefvers. Förh. Kongl. Svenska Vetensk.-Akad. 33 (1876) 21. — Synonymised with *Hypopterygium flavescens* Hampe by Hampe, Vidensk.

Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1879–80 (1879) 162. — Synonymised with *Hypopterygium tamarisci* (Sw.) Brid. ex Müll.Hal. (‘*Hypopterygium tamariscinum* (Hedw.) Brid.’) by Churchill, Bryologist 91 (1988) 117.

Hypopterygium flaccidum Mitt. in Seem., Fl. Vit. (1873) 390, (Febr.), syn. nov., non Sull., U.S. Expl. Exped., Musc. (1860) 27 (102), nom. nud. in syn. (≡ *Hypopterygium flavescens* Hampe = *Hypopterygium tamarisci* (Sw.) Brid. ex Müll.Hal.). — Type: *unknown collector s.n.* (NY holo), Pacific Islands. — See note 18.

Hypopterygium neocaledonicum Besch., Ann. Sci. Nat. Bot. 5, 18 (1873) 222, ‘*neo-caledonicum*’. — Type: *Balansa 2551* (BM holo, L), New Caledonia, Mt Cougui, humid rocks, [“ad rupes humidas montis Cougui”], 1869. — Synonymised with *Hypopterygium ceylanicum* Mitt. by Kindberg, Hedwigia 40 (1901) 289; synonymised with *Hypopterygium tenellum* Müll.Hal. by Schultze-Motel, Willdenowia 7 (1973) 67. — See notes 19 and 20.

Hypopterygium tahitense Ångstr., Oefvers. Förh. Kongl. Svenska Vetensk.-Akad. 30, 5 (1873) 121, syn. nov. — Type: *Andersson s.n.* (S holo), Society Islands, Tahiti, Sept., 1852. — Synonymised with *Hypopterygium muelleri* Hampe by Kindberg, Hedwigia 40 (1901) 296. — See notes 21 and 22.

Hypopterygium pseudotamarisci Müll.Hal., Linnaea 38 (1874) 645, ‘*pseudo-tamarisci*’. — *Hypopterygium tamarisci* (Sw.) Brid. ex Müll.Hal. subsp. *pseudotamarisci* (Müll.Hal.) Kindb., Hedwigia 40 (1901) 288, ‘*pseudo-tamarisci*’. — *Hypopterygium tamarisci* auct. non. (Sw.] Brid. ex Müll.Hal.: Besch., Mém. Soc. Nat. Sci. Nat. Cherbourg 16 (1871 [= 1872?]) 111, according to Müller, Linnaea 38 (1874) 645, and Kindberg, Hedwigia 40 (1901) 288. — Syntypes: *Von Chrismar s.n.* (B destroyed; S lecto, designated here, sub no. *28* in hb. Kindberg), Mexico, Veracruz, Jalapa (‘Xalapa’), [“in lapidibus & arboribus”], 1849; *Müller s.n.* (B destroyed), Mexico, Veracruz, Mt Orizaba [= Citlaltépetl]; *Mohr s.n.* (B destroyed), Mexico, [“in sylvis opacis montosis ad loca humida in ligno putrido vel in terra humosa montis San Cristobal haud frequens, inter 6000–6500 pedes elevationis”], 1857; *Mohr s.n.* (B destroyed), Mexico, [“in sylvis profundis ad arbores muscosas & ligna valde putrida regionis temperatae montosa prope Mirador, haud raro, inter 4–5000 pedes altitudinis”], 1857. — Synonymised with *Hypopterygium tamarisci* (Sw.) Brid. ex Müll.Hal. by Britton, Bull. Torr. Bot. Cl. 40 (1914, ‘1913’) 666. — The lectotype is damaged and consists of only the frond of a plant.

?: *Hypopterygium monoicum* Hampe in Warm., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 3, 6 (1875, ‘1874’) 177, syn. nov. — *Hypopterygium rigidulum* Mitt. subsp. *monoicum* (Hampe) Kindb., Hedwigia 40 (1901) 295. — Type: *Glaziou 7189* p.p. (n.v.), Brazil, Rio de Janeiro, vicinity of Rio de Janeiro. — According to Hampe l.c.: 178, the type was sparingly mixed with *Hypopterygium incrassatolimbatum* Müll.Hal. — See note 23.

Hypopterygium macrorhynchum Ångstr., Oefvers. Förh. Kongl. Svenska Vetensk.-Akad. 33 (1876) 21, syn. nov. — *Hypopterygium rigidulum* Mitt. subsp. *macrorhynchum* (Ångstr.) Kindb., Hedwigia 40 (1901) 295. — Type: *Widgren s.n.* (S holo; S, sub no. *10*), Brazil, Minas Geraïs, “Caldas Brasilia”, [“inter *H. regnelii* specimina pauca carpsi”]. — Identified as *Hypopterygium flavescens* Hampe by Hampe, Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1879–80 (1879) 162. — See note 24.

Hypopterygium viridissimum Müll.Hal., Linnaea 40 (1876) 255, syn. nov. — Type: *Hildebrandt s.n.* (B holo destroyed; S lecto, designated here, sub nos. 35 and 52 in hb. Kindberg), Comoro Islands, Anjouan [“Johanna”], [“inter *Rhizogonium spiniforme*, 800 m. supra mare ad truncos arborum”], 1875. — The lectotype is a fragment of a small plant; only the frond of this plant has been preserved. — See note 25.

Hypopterygium pygmaeum Müll.Hal., Linnaea 40 (1876) 256; Müll.Hal. ex Kindb., Hedwigia 40 (1901) 290, nom. nud. in syn. (*Hypopterygium ceylanicum* Mitt.). — Based on: *Hypopterygium tenellum* auct. non Müll.Hal.: Van den Bosch & Van der Sande Lacoste, Bryol. Jav. 2 (1861) t. 142. — Type: Van den Bosch & Van der Sande Lacoste, Bryol. Jav. 2 (1861) t. 142; based on (syntypes): *Wiltens s.n.* (L lecto, designated here; H-BR, L, ‘Padang’; BM, ‘Sumatra’, s. coll. in hb. Hampe, ex hb. Van der Sande Lacoste), Indonesia, Sumatra, “prope Padang in regionibus superioribus ad corticum cespitosum”; *Junghuhn s.n.* (L, ‘*Hypopterygium medinense* Dz. & Mb.’; L), Java, Medini [“pr. Medini Prov. Samarang in m. Oengarang”], alt. 3–4000', June. — See notes 26, 27, and 28.

Hypopterygium argentinicum Müll.Hal. in Besch., Mém. Soc. Nat. Sci. Nat. Cherbourg 21 (1877) 266, syn. nov. — Type: *Balansa, PP 1246* (BM holo, n.v.; B destroyed, PC), Paraguay, Guaira, Villarrica, "Forêts à l'Est de la Cordillère de Villa-Rica – Tronc des arbres" ["forêts à l'est de la Cordillère, sur les arbres"]. — See note 29.

Hypopterygium torulosum Schimp. ex Besch., Ann. Sci. Nat. Bot. 6, 10 (1880 [= 1881?]) 326, syn. nov. — *Hypopterygium sylvaticum* Mitt. subsp. *torulosum* (Schimp. ex Besch.) Kindb., Hedwigia 40 (1901) 289. — Syntypes: *Bory s.n.* (PC n.v.), Réunion, ["Lieux & rochers humides, sur les vieux troncs d'arbres, dans les bois & les ravines obscures & ombragées"], ["hb. Cosson"]; *Richard 303, 574* (PC n.v.), Réunion; *De l'Isle 202* (BM lecto, designated here), Réunion, Plaine des Palmistes ["sur les arbres, petit bras de Caverne & plaine des Palmistes"]; *Lépervanche s.n.* (BM, S), Réunion, ["sommet de Brûlé de Saint-Denis"]; *Commerson s.n.* (BM not found, PC n.v.), Mauritius, ["associé à *H. struthiopteris*"]; *Pervillé 834* (PC n.v.; L?, s. coll., sub no. *834*, ex PC), Malagasy Republic, ["N.O. de Madagascar"], 1841. — See notes 30, 31, and 32.

Hypopterygium torulosum Schimp. ex Besch. var. *nossibeanum* Besch., Ann. Sci. Nat. Bot. 6, 10 (1880 [= 1881?]) 326, syn. nov., '*Nossi-Beanum*'. — *Hypopterygium nossi-beanum* Müll.Hal. in Besch., Ann. Sci. Nat. Bot. 6, 10 (1880 [= 1881?]) 327, nom. nud. in syn. (*Hypopterygium torulosum* Schimp. ex Besch. var. *nossibeanum* Besch.), quod. nom., possibly based on *Hypopterygium nossibeanum* Müll.Hal. in Besch., Rev. Bryol. 4 (1877) 15, nom. nud. — *Hypopterygium torulosum* Schimp. ex Besch. var. *nossianum* Besch. ex Renauld, Prodr. Fl. Bryol. Madagascar (1898, '1897') 271, nom. inval., err. pro *Hypopterygium torulosum* Schimp. ex Besch. var. *nossibeanum* Besch. — Type: *Pervillé s.n.* (BM holo, PC n.v.), Malagasy Republic, Antsiranana Prov., Nosy Be. — See note 33.

Hypopterygium mauritianum Hampe ex Besch., Ann. Sci. Nat. Bot. 6, 10 (1880 [= 1881?]) 327. — Syntypes: *Boivin s.n.* (BM), Mauritius, ["montagne de la Rivière Noire"], 1847; *Andersson s.n.* (BM? not found; S, s.loc.; S, s.loc., sub nos. *54* and *49*? in hb. Kindberg), Mauritius; *Darnty (1)* (BM lecto, designated here), Mauritius, Mt Bambou, "rochers humides", June 17, 1874. — Synonymised with *Hypopterygium laricinum* (W. Hook.) Brid. subsp. *incrassatolimbatum* (Müll.Hal.) Kindb. by Kindberg, Hedwigia 40 (1901) 291. — Synonymised with *Hypopterygium laricinum* (W. Hook.) Brid. by Renauld & Cardot in A. & G. Grandidier, Hist. Phys. Madagascar, Vol. 39, Mousses (1915) 418. — See note 34.

Hypopterygium mauritianum Hampe ex Besch. var. *nanum* (Müll.Hal. in Geh.) Besch., Ann. Sci. Nat. Bot. 6, 10 (1880 [= 1881?]) 327. — *Hypopterygium nanum* Müll.Hal. in Geh., Rev. Bryol. Lichénol. 5 (1878) 59, nom. nud. — Type: *De Robillard s.n.* (BM holo, S; B destroyed), Mauritius, 1876. — Synonymised with *Hypopterygium laricinum* (W. Hook.) Brid. subsp. *incrassatolimbatum* (Müll.Hal.) Kindb. by Kindberg, Hedwigia 40 (1901) 291. — See note 35.

Hypopterygium uliginosum Müll.Hal., Linnaea 43 (1882) 470. — Type: *Schnyder s.n.* (B destroyed; S lecto, designated here, sub nos. *29* and *55* in hb. Kindberg), Argentina, Buenos Aires, ["Argentinia temperata Buenos-Airensis, in paludibus prope Maciel in trunco Salicis putrido"], Febr. 14, (18) 81. — Synonymised with *Hypopterygium rotulatum* (Hedw.) Brid. by Kindberg, Hedwigia 40 (1901) 293.

Hypopterygium falcatum Müll.Hal., Flora 69 (1886) 514. — Type: *Mönkemeyer s.n.* (B holo destroyed; S lecto, designated here, sub nos. *21* and *52* in hb. Kindberg; S; JE, sub no. *9*?), Equatorial Guinea ["Africa occid. tropica"], Bioko (Fernando Poó), in terra, May, 1885. — Synonymised with *Hypopterygium ceylanicum* Mitt. (= *Hypopterygium tamarisci* (Sw.) Brid. ex Müll.Hal.) by Kindberg, Hedwigia 40 (1901) 290. — The lecotype is small plant that is up to 1.2 cm tall and comes closest to Müller's, Flora 69 (1886) 514, description of the species as being "humile tenellum vix semipollicare". — See notes 36 and 37.

Hypopterygium sphaerocarpum Renauld, Rev. Bryol. Lichénol. 16 (1889) 86, syn. nov. — Type: *De Robillard s.n.* (PC holo; BR; S, sub nos. *22* and *35* in hb. Kindberg), Mauritius, ["1876"]. — Type information was given by Renauld, Rev. Bryol. Lichénol. 15 (1888) 87. — See note 38.

Hypopterygium brevifolium Broth., Bol. Soc. Brot. 8 (1890) 188, syn. nov. — *Hypopterygium laricinum* (W. Hook.) Brid. fo. *nana* Kindb., Hedwigia 40 (1901) 291, nom. nud.; *Hypopterygium falcatum* auct. non Müll.Hal.: Kindb., Hedwigia 40 (1901) 291. — Type: *Quintas (25)* (H-BR holo p.p., mixed with *Lopidium struthiopteris* (Brid.) M. Fleisch.; COI, sub no. *1448*; S; S, sub no. *53* in hb. Kindberg; S?, sub nos. *52* and *23* in hb. Kindberg), São Tomé e Príncipe, "Afr. occ., Ins. S. Thomé", alt. 1000 m. — Annotations on the labels of one of the two isotypes in COI indicate that these mosses were collected from tree trunks in April 1889. The label of one of them is annotated with the quotation 25/4-89, which presumably stands for the date of collecting. — See note 39.

Hypopterygium sinicum Mitt., Trans. Linn. Soc. London, Bot. 2, 3 (1891) 169, (June), syn. nov. Type: *Bowring s.n.* (NY holo), China, Hong Kong. — See note 40.

Hypopterygium subhumile Renauld & Cardot in Renauld, Rev. Bot. Bull. Mens. 9 (1891) 400, syn. nov. — *Hypopterygium tenellum* Müll.Hal. subsp. *subhumile* (Renauld & Cardot) Kindb., Hedwigia 40 (1901) 293. — Type: *Chenagan s.n.* (PC holo?, n.v.; S, sub no. *46* in hb. Kindberg), Malagasy Republic, Madagascar, Antsiranana Prov., Antsiranana ["Diego Suarez"], 1890. — Renauld & Cardot l.c. provided the species with a very short diagnosis. More extended descriptions were given by Renauld & Cardot, Bull. Soc. Roy. Bot. Belgique 32 (1893) 27; Renauld, Prodr. Fl. Bryol. Madagascar (1898, '1897') 273; and Cardot in Renauld & Cardot in A. & G. Grandidier, Hist. phys. Madagascar 39, Mousses (1915) 422. — See note 41.

?: *Hypopterygium pirottae* Brizi, Annuario Reale Ist. Bot. Roma 2, 5 (1893) 80, syn. nov. — Type: *Ragazzi s.n.* (RO holo, not found; FT? n.v., PAD? n.v.), Ethiopia, Shoa, forest of Fekeriè-Ghemb, April 27, 1885. — According to Brizi's description and diagnosis his new *Hypopterygium* species closely resembles *Hypopterygium laricinum* (W. Hook.) Brid. The features by which Brizi distinguished his new species from the latter are, however, not decisive and do not justify the recognition of a separate taxon.

Hypopterygium grandistipulaceum Renauld & Cardot, Bull. Soc. Roy. Bot. Belgique 32 (1893) 28. — Syntypes: *Besson 348* (PC lecto, designated here; S, without a collection number, but ex hb. Renauld, sub no. *47* in hb. Kindberg), Malagasy Republic, Madagascar, Fianarantsoa Prov., "entre Vinanintelo et Ikongo", ["ad truncos putridos inter Vinanintelo & Ikongo"], 1892; *Camboué s.n.* (n.v.), Malagasy Republic, Madagascar, Toamasina Prov., ["in silva Analamazoatra"]. — Synonymised with *Hypopterygium laricinum* (W. Hook.) Brid. subsp. *incrassato-limbatum* (Müll.Hal.) Kindb. by Kindberg, Hedwigia 40 (1901) 291.

Hypopterygium torulosum Schimp. ex Besch. var. *kameruniae* Broth. in Engler, Bot. Jahrb. Syst. 20 (1894) 217. — Type: *Preuss 1047* (H-BR holo, n.v.), Cameroon, South West Prov., ["Urwald bei Buea"], alt. 2000 m. — Synonymised with *Hypopterygium sylvaticum* Mitt. subsp. *torulosum* (Schimp. ex Besch.) Kindb. by Kindberg, Hedwigia 40 (1901) 289. — See note 42.

Hypopterygium lehmannii Besch., Bull. Herb. Boissier 2, 6 (1894) 399, syn. nov. — *Hypopterygium sylvaticum* Mitt. subsp. *lehmannii* (Besch.) Kindb., Hedwigia 40 (1901) 289. — Type: *Lehmann 684* (BM holo, n.v.; G n.v.; PC), Ecuador, Carchi Prov., ["Am Fusse von Bäumen und auf verwitterten Holze in schattigen, feuchten Wäldern am Rio Pun, Ostgehänge der Cordilleren von Tulcan. 3000 m. Ecuador Septent."], Febr. 4, 1881. — See note 43.

Hypopterygium nadeaudianum Besch., Ann. Sci. Nat. Bot. 7, 20 (1895) 58, syn. nov. — *Hypopterygium rigidulum* Mitt. subsp. *nadeaudianum* (Besch.) Kindb., Hedwigia 40 (1901) 295. — *Hypopterygium nadeaudii* Besch. ex Besch., Bull. Soc. Bot. France 48 (1901) 12, nom. inval., err. orthogr. pro *Hypopterygium nadeaudianum* Besch. — *Hypopterygium filiculiforme* auct. non (Hedw.) Brid.: Nadeaud, Enum. Pl. Indig. Tahiti (1873) 13; corr. by Bescherelle, Ann. Sci. Nat. Bot. 7, 20 (1895) 9. — Type: *Nadeaud 65* (BM holo), Society Islands, Tahiti, ["vallées humides, vers le Marau & spécialement dans la vallée cratériforme du Mamano, à 900 mètres d'altitude, sur des argiles calcinées"]. — There are two specimens of *Nadeaud 65* in BM, which apparently belong to different Oceanian variants of *Hypopterygium tamarisci* (Sw.) Brid. ex Müll.Hal. (see 'Variation', p. 219). It is almost certain that Bescherelle's description is based on the specimen preserved in his herbarium kept in BM. Hence, the other specimen is excluded here. — See notes 21, 22, and 44.

Hypopterygium squarrulosum Müll.Hal., Hedwigia 36 (1897) 106. — Type: *Arechavaleta s.n.* (S holo?, sub nos. *32 1/2* and *22* in hb. Kindberg; B destroyed, if ever present), Uruguay, Canelones, Montevideo, Camino de Carrasco, ["Sept., 1876"]. — Proposed in the synonymy of *Hypopterygium sphaerocarpum* Renauld by Kindberg, Hedwigia 40 (1901) 290. According to Müller l.c. the type specimen is preserved in "Hb. Lund". This specimen is presumably the one that is nowadays preserved in Kindberg's herbarium in S. — See notes 45 and 46.

Hypopterygium arbusculosum Besch., Bull. Soc. Bot. France 45 (1898) 127, syn. nov. — *Hypopterygium tamarisci* (Sw.) Brid. ex Müll.Hal. subsp. *arbusculosum* (Besch.) Kindb., Hedwigia 40 (1901) 288. — Type: *Nadeaud 440* (holo not found; PC, BM, S, W), Society Islands, Tahiti, ["Extrémité supérieure de la vallée de Puaa, ravin de Tearapau, & du mont Ereeraoe, au-dessus de Papeete à 1000 mètres & au delà (1re herbor., no 440)"], Apr. 1, 1896. — Type material of *Hypopterygium arbusculosum* Besch. was not found in Bescherelle's herbarium preserved in BM. The isotypes in BM and W are presented as "Mousses de Tahiti. Collon 2". — See note 22.

Hypopterygium bouvetii Besch., Bull. Soc. Bot. France 45 (1898) 490. — Type: *Bouvet s.n.* (BM holo not found; PC, mixed with *Racopilum* spec.), France, Maine-et Loire, Angers, sur les troncs de fougères arborescente dans les serres de M. Fargeton ["dans les serres des établissements horticoles, sur vieux stipes de Balantium antarcticum"], July 29, 1897. — Synonymised with *Hypopterygium muelleri* Hampe by Kruijer, Glasgow Naturalist 23, 2 (1997) 16. — See note 47.

Hypopterygium kaernbachii Broth. in K. Schum. & Lauterb., Fl. Deutsch. Schutzgeb. Südsee (1900, '1901') 104, syn. nov. — Type: *Kaernbach 36* (H-BR holo p.p., mixed with *Lopidium struthiopteris* (Brid.) M. Fleisch.; S; ?S, sub no. *40* in hb. Kindberg), Papua New Guinea ["Kaiser Wilhelmsland"], Morobe Prov., Sattelberg, Nuselang, "Bäume im Walde", alt. 2630 ft. ["800 m"], Dec. 9, 1893. — Dixon, J. Bot. 80 (1942) 29, considered *Hypopterygium kaernbachii* Broth. scarcely separable from *Hypopterygium ceylanicum* Mitt., but did not synonymise the former with the latter. — See note 48.

Hypopterygium levieri Broth. ex Kindb., Hedwigia 40 (1901) 286. — Type: *Ferrié, Bryoth. Levier 160* (S holo, sub no. *16* in hb. Kindberg; H-BR), Japan, Ryukyu Archipelago, "Archip. Liu-Kiu (Japon. mer.) prope Naze in insula Amami.Oshima", Dec. 27, 1897. — Proposed in the synonymy of *Hypopterygium ceylanicum* Mitt. by Noguchi, J. Hattori Bot. Lab. 7 (1952) 11. — Synonymised with *Hypopterygium tenellum* Müll.Hal. by Iwatsuki & Noguchi, J. Hattori Bot. Lab. 37 (1973) 359. — See note 49.

Hypopterygium tamarisci (Sw.) Brid. ex Müll.Hal. subsp. *hildebrandtii* Müll.Hal. ex Kindb., Hedwigia 40 (1901) 288. — Syntypes: *Hildebrandt s.n.* (B destroyed; S lecto, designated here; L, W, ZT), *(FCM) 2093* (COI, S, W), Malagasy Republic, C Madagascar, Fianarantsoa Prov., "Süd-Betsiléo", "Urwald von Ankafina", March, 1881; *Sikora ['Tikora'] s.n.* (B destroyed; PC? n.v.; BR, *s.n.*; S; S, sub no. *48* [in hb. Kindberg?]), *(14310)* (W, also sub no. *34*), Malagasy Republic, Madagascar, Antananarivo Prov., Andrangolaoka, "Wald bei Andrangoloake an Bäumen", March, 1891. — Synonymised with *Hypopterygium laricinum* (W. Hook.) Brid. by Cardot in Renauld & Cardot in A. & G. Grandidier, Hist. Phys. Madagascar 39, Mousses (1915) 418. — Kindberg (1901) did not cite any collection numbers, but it is almost certain that *Hildebrandt 2093* and *Sikora (14310)* represent syntypes.

Hypopterygium jungermannioides Müll.Hal. ex Kindb., Hedwigia 40 (1901) 294, syn. nov. — Type: *Beccari s.n.* (S holo; B destroyed), Indonesia, Moluccas, Ternate, "(ad C.M. misit Levier)", Febr., 1876. — See note 50.

Hypopterygium rigidulum Mitt. subsp. *balantii* Müll.Hal. ex Kindb., Hedwigia 40 (1901) 295. — *Hypopterygium rigidulum* Mitt. var. *balantii* Kindb. ex Streimann & Curnow, Australian Flora and Fauna Series 10 (1989) 213, nom. inval., err. pro (*Hypopterygium rigidulum* Mitt. subsp. *balantii* Müll.Hal. ex Kindb.). — Syntypes: *Graef s.n.* (B destroyed; S lecto, sub nos. *45* and *33* in hb. Kindberg; JE), Germany, Berlin, Charlottenburg, Botanical Garden of Berlin: palm house of the 'Flora', "ad truncum *Balantii antarctii*", Nov. 13, 1885; *Graef s.n.* (B destroyed; S, sub nos. *45* and *33*, JE), Germany, Berlin, Charlottenburg, Botanical Garden of Berlin: palm house of the 'Flora', "ad truncum [putrid.?] *Balantii antarctii*", Nov. 1888. — Lectotype designated by Kruijer, Glasgow Naturalist 23, 2 (1997) 16. — Synonymised by Kruijer l.c. — The syntype in S that was collected by Graef in 1888 is preserved in Möller's herbarium. There is no direct evidence that Kindberg l.c. saw this material, but it is almost certain he examined it for his revision of 1901. — See note 47.

Hypopterygium scottiae Müll.Hal. subsp. *denticulatum* Kindb., Hedwigia 40 (1901) 296, syn. nov. — Type: *Hartmann s.n.*, "*distr. Rehmann n. 20*" (S holo), Australia, Tasmania ('Van Diemensland'), Toowoomba. — See note 51.

Hypopterygium immigrans Lett, J. Bot. 42 (1904) 249, t. 463. — Type: *Pim s.n.* (not found), Ireland, Co. Dublin, Monkstown, Easton Lodge, ["On surface of earth in pots and rock-work in cold fernhouse"], 1887. — Synonymised with *Hypopterygium muelleri* Hampe by Kruijer, Glasgow Naturalist 23, 2 (1997) 16. — See note 47.

Hypopterygium bolivianum Herzog, Beih. Bot. Centralbl. 26 (1910 [= 1909?]) 81, syn. nov. — Type: *Herzog s.n.* (JE holo, n.v.; S), Bolivia, Cochabamba, "Bergurwald bei Incacorra", alt. 2200 m, January, 1908. — See note 52.

?: *Hypopterygium mildbraedii* Broth. in Mildbr., Wiss. Ergeb. Deut. Zentr.-Afr. Exped., Bot. (1910) 167, syn. nov. — Type: *Mildbraed 2054* (H-BR holo, n.v.), Democratic Republic of Congo (Zaire), Kivu, ["Vulkan-Gebiet: Bambuswald am Südfuß des Karisimbi auf Lava-blöcken, ca. 2500 m. ü. M."], Sept. 1907. — Material of *Hypopterygium mildbraedii* Broth. that was collected by Mildbraed in the 'Vulkan Gebiet' was apparently sent by Brotherus to BR and PC. The duplicate in BR is not provided with a collection number and has lost all its material. The condition of the specimen in PC is unknown (n.v.). — See note 53.

Hypopterygium usambaricum Broth. in Brunnth., Denkschr. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl. 88 (1913) 741, syn. nov. — Type: *Brunnthaler s.n.* (H-BR holo), Tanzania, Tanga ['Deutsch Ost-Afrika: Ost-Usambara'], Amani, Kwamkoroweg, "auf Gneissfelsen", alt. 800 m, Aug. 5, 1909. — See note 39.

Hypopterygium bowiei Broth. & Watts, J. R. Soc. N. S. Wales 49 (1915) 147, syn. nov. — Type: *Bowie, Hb. Watts 73* (H-BR lecto, designated here; BM, NSW n.v.), Vanuatu ('New Hebrides'), Espíritu Santo Is. ["Isl. of Santo"], Tangoa. — See note 54.

Hypopterygium atrotheca Dixon, J. Bot. 66 (1928) 350. — Type: *Grierson s.n.* (BM holo n.v., W), United Kingdom, Scotland, Glasgow Botanic Gardens, Kibble Palace Fernery, tree ferns, "Origin unknown. But soc. cum *Pterygophyllo dentato*", Febr. 1927. — Synonymised with *Hypopterygium muelleri* Hampe by Kruijer, Glasgow Naturalist 23, 2 (1997) 16. — See note 47.

?: *Hypnum frondiferum* Brid., Muscol. Recent. Suppl. 2 (1812) 87, nom. nud. in syn. — Original material: "Parisiis ex Insulâ Borboniâ allatum vidi" (B n.v., probably destroyed). — Given in the synonymy of *Hypnum flabilliforme* Brid. (nom. illeg. incl. spec. prior. *Leskea tamariscina* Hedw., 1801 ≡ *Canalohypopterygium tamariscinum* (Hedw.) Kruijer) by Bridel l.c. — See note 55.

Hypopterygium nivale Müll.Hal., Syn. Musc. Frond. 2 (1850) 9, nom. illeg. incl. spec. prior. (*Hypopterygium flavescens* Hampe). — *Hypopterygium tamariscinum* auct. non (Hedw.) Brid.: Müll.Hal., Linnaea 19 (1847) 213; corr. C. Müller, Syn. Musc. Frond. 2 (1850) 9. — Syntypes: *Moritz 70*, (B destroyed; L, "Caripe, Colona Tovar, Covollar, Caracas"; S, s.loc.), Venezuela, ["in montibus nivalibus prov. Meridae"], Mérida; *Moritz 150* (L), Venezuela , Japé; and also: *Moritz s.n.* (S, sub no. *30* in hb. Kindberg), Venezuela, Mérida. — Synonymised with *Hypopterygium tamarisci* (Sw.) Brid. ex Müll.Hal. subsp. *flavescens* (Hampe) Kindb. by Kindberg, Hedwigia 40 (1901) 288. — Contrary to Hampe, Linnaea 20 (1847) 95, Müller, Syn. Musc. Frond. 2 (1850) 9, did not consider *Moritz 70* to be a mixed collection of two species. Hence, Hampe's *Hypopterygium flavescens* is included in Müller's species. — See note 5.

Hypopterygium capense Schimp. in Breutel, Musci Capenses (1859?), nom. nud.; Schimp. ex A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1874–1875 (1876) 152 (Gen. Sp. Musc. 2 (1876) 68), nom. nud.; Schimp. ex Kindb., Hedwigia 40 (1901) 291, nom. nud. in syn. (*Hypopterygium laricinum* (W. Hook.) Brid.). — Original material: *Breutel, MC s.n.* (L, S), South Africa, Western Cape Prov. [Cape of Good Hope], Genadendal ["Gnadenthal"]. — Given in the synonymy of *Hypopterygium laricinum* (W. Hook.) Brid. by Kindberg l.c. and Sim, Trans. Roy. Soc. South Africa 15 (1926) 446. — See note 56.

Hypopterygium flaccidum Sull., U.S. Expl. Exped., Musc. (1860) 27 (102), nom. nud. in syn. (*Hypopterygium flavescens* Hampe). — Original material: collector's name not not cited (n.v.), Brazil.

Hypopterygium tenellum auct. non Müll.Hal.: Van den Bosch & Van der Sande Lacoste, Bryol. Jav. 2 (1861) t. 142, according to Müller, Linnaea 40 (1876) 256, according to Kindberg, Hedwigia 40 (1901) 290; Bryol. Jav 2 (1861) 13, t. 142, according to Fleischer, Musc. Buitenzorg 3 (1908) 1084. — Müller l.c. based *Hypopterygium pygmaeum* Müll.Hal. on Van den Bosch & Van der Sande Lacoste l.c. supposed misidentification.

Hypopterygium medinense Dozy & Molk. ex Bosch & Sande Lac., Bryol. Jav. 2 (1861) 13, nom. nud. in syn. (*Hypopterygium tenellum* Müll.Hal.); Dozy & Molk. ex M. Fleisch., Musc. Buitenzorg 3 (1908) 1084, nom. nud. in syn. (*Hypopterygium ceylanicum* Mitt.). — Original material: *Junghuhn s.n.* (L), Indonesia, Java, Medini ["pr. Medini Prov. Samarang in m. Oengarang"], alt. 3–4000', June. — See note 28.

Hypopterygium norfolkianum Müll.Hal. in A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1874–75 (1876) 148. (Gen. Sp. Musc. 2 (1876) 64), nom. nud.; Müll.Hal. in Kindb., Hedwigia 40 (1901) 296, nom. nud. in syn. (*Hypopterygium muelleri* Hampe subsp. *oceanicum* (Mitt.) Kindb.). — Original material: *unknown collector s.n.* (NY), "Norfolk Isl.: Hb. Melbourne. Rarissimum". — Synonymised with *Hypopterygium oceanicum* Mitt. by Mitten, Trans. & Proc. Roy. Soc. Victoria 19 (1882) 76.

Hypopterygium serrulatum Lindb. in Ångstr., Oefvers. Förh. Kongl. Svenska Vetensk.-Akad. 33 (1876) 21, nom. nud. and incl. spec. prior. (*Hypopterygium sylvaticum* Mitt.); Lindb. in Kindb., Hedwigia 40 (1901) 295, nom. nud. in syn. (*Hypopterygium rigidulum* Mitt. subsp. *monoicum* (Hampe) Kindb.). — Original material: *Regnell 29* (S), *Widgren s.n.* (S), *Lindberg s.n.* (S), Brazil, Minas Geraïs, "Caldas Brasiliae".

Hypopterygium nossibeanum Müll.Hal. in Besch., Rev. Bryol. 4 (1877) 15, nom. nud.; Müll.Hal. ex Melvill, Mem. & Proc. Manchester Lit. Soc. 4, 1 (1888) 102, nom. nud. in syn. (*Hypopterygium pugiunculum* Bosw. in Melvill, nom. nud.); Müll.Hal. in Kindb., Hedwigia 40 (1901) 291, nom. nud. in syn. (*Hypopterygium sylvaticum* Mitt. subsp. *torulosum* (Schimp. ex Besch.) Kindb.). — Original material: *Boivin s.n.* (B destroyed, BM), Malagasy Republic, Antsiranana Prov., Nosy Be.

Hypopterygium argentinicum Lorentz ex Müll.Hal., Linnaea 42 (1879) 404, hom. illeg., syn. nov. — *Hypopterygium tamarisci* (Sw.) Brid. ex Müll.Hal. subsp. *argentinicum* (Lorentz ex Müll.Hal.) Kindb, Hedwigia 40 (1901) 288. — Syntypes: *Lorentz s.n.* (B destroyed; S lecto, designated here, sub no. *33* in hb. Möller [hb. Kindberg?]; S; S in hb. Dusén, wrongly labelled "18.VII.1873"), Argentina, Salta Prov.? ["Argentina subtropica"], Cuesta de Santa Rosa, ["cum *Mnio & Racopilo tomentoso*"] June 18, 1873; *Lorentz s.n.* (B destroyed; not found), Argentina, Tucumán Prov. ["Sierra de Tucumán"], Siambon, January 1874. — The lectotype of *Hypopterygium argentinicum* Lorentz ex Müll.Hal. contains only few material with two sporophytes, but among the syntypes its origin is most certain and hence it is designated as the lectotype. — See notes 57 and 58.

?: *Hypopterygium pugiunculum* Bosw. in Melvill, Mem. & Proc. Manchester Lit. Soc. 4, 1 (1888) 102, nom. nud.; '*pugiunculus*'. — Original material: collector's name not given (OXF n.v.), Mauritius, 1887?. — Proposed in the synonymy of *Hypopterygium sylvaticum* Mitt. subsp. *torulosum* Schimp. ex Besch. by Kindberg, Hedwigia 40 (1901) 289. — Boswell l.c. considered it possibly conspecific with *Hypopterygium nossibeanum* Müll.Hal. ex Melvill.

?: *Hypopterygium longirostrum* Schimp. ex C.H. Wright, J. Bot. 26 (1888) 268, nom. nud. — Original material: *Pervillé 805* (not found with certainty), Malagasy Republic, Madagascar. — Based on the examination of other material synonymised with *Hypopterygium sphaerocarpum* Renauld by Cardot in Renauld & Cardot in A. & G. Grandidier, Hist. Phys. Madagascar 39, Mousses (1915) 421. — See note 59.

Hypopterygium hildebrandtii Müll.Hal. in C.H. Wright, J. Bot. 26 (1888) 268, nom. nud., ('-i'); Müll.Hal. in Paris, Index Bryol. ed. 2, 3 (1905) 111, nom. nud., ('-i'). — Original material: *Hildebrandt 2094* (B destroyed; not found), Malagasy Republic, C Madagascar, Fianarantsoa Prov., S Betsileo. — According to Paris, Index Bryol. ed. 2, 3 (1905) 111, the original material comes from "Madagasc. merid.", but it is almost certain that Paris' material is identical with Wright's, J. Bot. 26 (1888) 268, material. — Wright's name was synonymised with *Hypopterygium laricinum* (W. Hook.) Brid. by Cardot in Renauld & Cardot in A. & G. Grandidier, Hist. Phys. Madagascar 39, Mousses (1915) 418.

Hypopterygium cameruniae Müll.Hal. in Dusén, Musci Africani in Camurunia a P. Dusén collecti (1893) 38, nom. nud.; Müll.Hal. in Paris, Index Bryol. (1896) 699, nom. nud.; Müll.Hal. in Kindb., Hedwigia 40 (1901) 291, nom. nud. in syn. (*Hypopterygium sylvaticum* Mitt. subsp. *torulosum* (Schimp. ex Besch.) Kindb.). — Original material: *Dusén, MAC 38* (PC, S, ZT), Cameroon, South West Prov., "In montibus Camerunensibus ad Bomanam pagum c. 670 metra supra mare in saxis rivalibus die 5 m.", Dec. 1890; *Dusén, MAC 38* (S; S?, without the distribution number of the exsiccata series), "In montibus Camerunensibus supra Bueam pagum inter 950 & 1840 metra supra mare in saxis rivalibus die 10 m.", July, 1891.

Hypopterygium semiglobosum Müll.Hal. in Broth., E. Ule: Bryoth. Brasiliensis (1895) 153, nom. nud.; Müll.Hal. in Paris, Index Bryol. (1896) 702, nom. nud.; Müll.Hal. in Kindb., Hedwigia 40 (1901) 290, nom. nud. in syn. (*Hypopterygium sphaerocarpum* Renauld). — Original material: *Ule, Bryoth. brasil. 153* (BR, L, S), Brazil, Rio de Janeiro, Corcovado, "ad aquaeductum", July, 1893. — See note 46.

Hypopterygium balantii Müll.Hal. ex Baenitz, *Herbarium europaeum*, series number not known, collection no. *8088*, "Flora Marchica, 1891–93"; exsiccata presumably distributed between 1893 and in or before 1896, nom. nud. — *Hypopterygium banlatii* Müll.Hal. ex Amann, Rev. Bryol. 40 (1913) 24, nom. inval., err. typogr. pro *Hypopterygium balantii* Müll.Hal. ex Baenitz, fide Amann l.c. — Original material: *Sydow s.n.* (B destroyed; JE *s.n.*, L *s.n.*, S, Z *s.n.*), Germany, Berlin, Charlottenburg, 'Flora'. — Synonymised with *Hypopterygium muelleri* Hampe by Kruijer, Glasgow Naturalist 23, 2 (1997) 17. — It is not known with certainty whether Müller actually identified Sydow's material. — The series number and the date or year of distribution of the original material of *Hypopterygium balantii* Müll.Hal. ex Baenitz are not known and could not be traced; the collection number was given for only a single specimen (in S). — Nomenclature is discussed by Kruijer, l.c.: 16, 17. — See note 47.

Hypopterygium rotundostipulatum Müll.Hal., Hedwigia 36 (1897) 106, nom. illeg. incl. spec. prior. (*Hypopterygium argentinicum* Müll.Hal. in Besch.), '*rotundo-stipulatum*', syn. nov. — *Hypopterygium sylvaticum* Mitt. subsp. *rotundostipulatum* (Müll.Hal.) Kindb., Hedwigia 40 (1901) 289, '*rotundo-stipulatum*'. — Syntypes: *Balansa, PP 3629* (B destroyed; L lecto, designated here; COI, sub *Hypopterygium argentinicum* Lorentz ex Müll.Hal.; S, without a distribution number, sub nos. *52* and *32* in hb. Kindberg), Paraguay, Paraguirí, "Cordillère de Ubatobi, près de Paraguari, sur les roches humides", June, 1881; *Balansa, PP 3628a* (B destroyed; COI, PC, both sub *Hypopterygium argentinicum* Lorentz ex Müll.Hal.), Paraguay, "Guarapi, dans les forêts, sur le tronc des arbres", July–August, 1879; *Balansa, PP 1246* (B destroyed; BM n.v.; PC), Paraguay, Guaira, Villarrica ["Villa Rica"], "Forêts à l'Est de la Cordillère de Villa-Rica – Tronc des arbres", Sept., 1874. — See note 60.

Hypopterygium balantii Müll.Hal. ex Bouvet, Bull. Soc. Étude. Scient. Angers 27 (1898) 138, nom. nud. — Presumably based on *Hypopterygium balantii* Müll.Hal. ex Baenitz. — Synonymised with *Hypopterygium muelleri* Hampe by Kruijer, Glasgow Naturalist 23, 2 (1997) 17. — Nomenclature is discussed by Kruijer, l.c.: 15, 16. — See note 47.

Hypopterygium balantii Müll.Hal. ex Warnst., Verh. Bot. Vereins Prov. Brandenburg 41 (1899, '1900') 66, nom. nud.; Müll.Hal. ex Warnst. in Loeske, Moosfl. Harz. (1903) 333, nom. nud.; Müll.Hal. ex Warnst., Kryptogamenflora Mark Brandenburg (1905) 659, nom. nud. — Original material: *Graef s.n.* (B destroyed; S, sub nos. *45* and *33* in hb. Kindberg; JE), Germany, Berlin, Charlottenburg, Botanic Garden of Berlin: palm garden 'Flora', "ad truncum *Balantii antarctii*", Nov. 13, 1885. — Synonymised with *Hypopterygium muelleri* Hampe by Kruijer, Glasgow Naturalist 23, 2 (1997) 17. — The original material is a syntype of *Hypopterygium rigidulum* Mitt. subsp. *balantii* Müll.Hal. ex Kindb. — Nomenclature is discussed by Kruijer, l.c.: 16, 17. — See note 47.

Hypopterygium sikorae Müll.Hal. in Paris, Index Bryol. Suppl. (1900) 217, nom. nud. — *Hypopterygium tikorae* Müll.Hal. ex Kindb., Hedwigia 40 (1901) 288, nom. nud. in syn. (*Hypopterygium tamarisci* (Sw.) Brid. ex Müll.Hal. subsp. *hildebrandtii* Müll.Hal. ex Kindb.), err. typogr. pro *Hypopterygium sikorae* Müll.Hal. in Paris; corr. by Cardot? in Renauld & Cardot in A. & G. Grandidier, Hist. Phys. Madagascar 39, Mousses (1915) 418. — Original material: *Sikora (14310)* (B destroyed; PC? not found; BR, *s.n.*; S, *s.n.*; S, '*Tikorae*', sub no. *48* [in hb. Kindberg?]; W, sub no. *34*), Malagasy Republic, Madagascar, Antananarivo Prov., Andrangolaoka, "Wald bei Andrangoloake an Bäumen", 1891. — It is almost certain that Sikora's material was distributed under number *14310*. — The original material is a syntype of *Hypopterygium tamarisci* (Sw.) Brid. ex Müll.Hal. subsp. *hildebrandtii* Müll.Hal. ex Kindb. — Synonymised with *Hypoptery-*

gium grandistipulaceum Renauld & Cardot by Renauld & Cardot in A. & G. Grandidier, Hist. phys. Madagascar 39, Mousses (1915) 419.

Hypopterygium cubense Müll.Hal. in Kindb., Hedwigia 40 (1901) 287, nom. nud. in syn. (*Hypopterygium tamarisci* (Sw.) Brid. ex Müll.Hal.). — Original material: *Wright, MC 130* (HBG, L, S), Cuba, rocks in dense woods. — Sullivant, Musci Cubenses (1861) 130, and Proc. Amer. Acad. Arts. 5 (1861) 290, identified Wright's plant as *Hypopterygium brasiliense* Sull.

?: *Hypopterygium brachypodium* Müll.Hal. in Kindb., Hedwigia 40 (1901) 288, nom. nud. in syn. (*Hypopterygium tamarisci* (Sw.) Brid. ex Müll.Hal. subsp. *pseudotamarisci* (Müll.Hal.) Kindb.). — Original material: *Puiggari* (B destroyed, S not found), Brazil.

?: *Hypopterygium tenuisetum* Müll.Hal. in Kindb., Hedwigia 40 (1901) 290, nom. nud. in syn. (*Hypopterygium sphaerocarpum* Renauld). — Original material: *Puiggari* (B destroyed, S not found), Brazil. — See note 46.

?: *Hypopterygium pallidum* Hampe in Müll.Hal. in Kindb., Hedwigia 40 (1901) 291, nom. nud. in syn. (*Hypopterygium laricinum* (W. Hook.) Brid. subsp. *incrassatolimbatum* (Müll.Hal.) Kindb.). — Original material: *Döring s.n.* (B destroyed, S not found), Brazil.

Hypopterygium brevipes Broth. in Paris, Bull. Herb. Boissier 2, 2 (1902) 993, nom. nud. — Original material: *Ferrié, Bryoth. Levier 160b* (H; PC, sub no. *160*; S; S, sub no. *63* in hb. Kindberg), Japan, Ryukyu Archipelago, "Archip. Liu-Kiu (Japonia merid.) in insula Amani-Oshima prope Naze", ["Oho-Sima"], March 29, 1898. — Proposed in the synonymy of *Hypopterygium ceylanicum* Mitt. by Noguchi, J. Hattori Bot. Lab. 7 (1952) 11. — Synonymised with *Hypopterygium tenellum* Müll.Hal. by Iwatsuki & Noguchi, J. Hattori Bot. Lab. 37 (1973) 359.

Hypopterygium laricinum (W. Hook.) Brid. fo. *depauperata* Rehm. ex Dixon & Gepp, Bull. Misc. Inform. 1923 (1923) 210, nom. nud. — Original material: *Rehmann, MAA 298c* (BM n.v., L), South Africa, Western Cape Prov., Rondebosch, 1875–1877.

Hypopterygium sinicum auct. non Mitt.: Sakurai, Bot. Mag. (Tokyo) 47 (1933) 337; Muscol. Jap. (1954) 112, pl. 42, h; according to Iwatsuki & Sharp, J. Hattori Bot. Lab. 30 (1967) 294. — Identified as *Hypopterygium tenellum* Müll.Hal. by Iwatsuki & Sharp l.c., see also Iwatsuki & Noguchi, J. Hattori Bot. Lab. 37 (1973) 360.

Illustrations: Hooker, Musci Exot. 1 (1818) t. 35. — Van den Bosch & Van der Sande Lacoste, Bryol. Jav. 2 (1861) t. 142–143. — Reichardt in Fenzl, Reise Novara 1, 3 (1870) t. 35. — Sullivant, U.S. Expl. Exped., Musc. (1874) pl. 26B, (n.v.). — Fleischer, Musc. Buitenzorg 3 (1908) f. 183; Abeywickrama, Ceylon J. Sci., Biol. Sci. 3 (1960) 100, f. 119a–b; Chopra, Bot. Monogr. Council Sci. Industr. Res., India 10 (1975) f. 100. — Lorch, Anatomie der Laubmoose (1931) f. 23. — ?: Bailey, Compr. Cat. Queensland Pl. (1913) pl. 158, f. 635. — Marloth, Fl. S. Afr. 1 (1913) pl.7, F. — Herzog, Geographie der Moose (1926) 66. — Sim, Trans. Roy. Soc. South Africa 15 (1926) 446 (left). — Bartram, Philipp. J. Sci. 68: f. 355. 1939. — Sakurai, Muscol. Jap. (1954) pl. 42, h. — Breen, Mosses of Florida (1963) pl. 102, f. 1–5. — Landwehr, Atlas Nederlandse Bladmossen (1966) 379, f. 330; 2nd ed. (1974); 3rd ed. (1978); based on *Wachter s.n.* (L). — Iwatsuki & Sharp, J. Hattori Bot. Lab. 30 (1967) 295, f. 3. — Ramsay, Proc. Linn. Soc. New South Wales 91 (1967) 222, f. 1–11, pl. 6–9, (karyotypes in f. 1–11 and pl. 6–7). — Whittier, Mosses of the Society Islands, Preliminary Studies (1968) pl. 60; Mosses of the Society Islands (1976) f. 80, 81 A–Q. — Noguchi, Misc. Bryol. Lichenol. 5 (1969) 30, f. 145, 2. — Sehnem, Pesquisas, Botânica 27 (1969) pl. 5, f. 9. — Petit, Bull. Jard. Bot. Belg. 48 (1978) 167, f. 44. — Ramsay in Schuster, New Manual of Bryology 1 (1983) 160, f. 40 & 41; 193, f. 116–117, (karyotypes; f. 40 & 41, probably from Ramsay, Proc. Linn. Soc. New South Wales 91 (1967) pl. 6 f. 2, pl. 9 f. 3). — Vitt in Schuster, New Manual of Bryology 2 (1984) 734, f. 62. — ?: Lin, Introduktion to the Bryophytes (1988) p. 36. — Mohamed & Robinson, Smithsonian Contrib. Bot. 80 (1991) f. 141–150. — Noguchi, Moss Flora of Japan 4 (1991) f. 338. — Sharp et al., Moss Flora of Mexico (1994) f. 632. — So, Mosses and Liverworts of Hong Kong (1995) f. 53. — Duarte Bello, Fontqueria 47 (1997) pl. 248. — Kruijer, Glasgow Naturalist 23, 2 (1997) 13, f. 1. — Schenk, Moss Gardening (1997) pl. 21. — Condy in Magill & Van Rooy, Flora of Southern Africa 1, 3 (1998) f. 171, 1–13. — ?B. & N. Malcolm, Mosses and other Bryophytes (2000) 110, 127. — ?: Henseler & Frahm, Nova Hedwigia 71 (2000) 530, f. 13. — Gradstein et al., Mem. New York Bot. Gard. 86 (2001) f. 143 L–Q (habit shown in f. 143 L atypical).

According to annotations in Wilson's herbarium, Hooker's (1818) illustrations of *Hypnum laricinum* are based on Hooker's South American material, i.e. *Humboldt 92*. Several authors erroneously cited Hedwig's (1801) illustrations (t. 51 f. 1–7) for the present species. Hedwig's illustrations are based on material from 'Insulae Australes', i.e. *Canalohypopterygium tamariscinum*, and are not based on Swartz' material of *Hypopterygium tamarisci* from Jamaica.

See Pfeiffer et al. (2000) for a discussion on the circumscription of the present species.

Plants in groups of dendroids or fans, pinnate (to bipinnate), flabellate, palmate, or umbellate, small to large, gemmiferous or not. *Stipe* up to 3.4 cm tall, ascending or vertical, laterally or dorsiventrally compressed, tomentose at base and glabrous above or entirely tomentose. *Frond* broad or short (to lanceolate), subcircular, (ob)ovate, or elliptic, up to 3.5 cm in diameter; rachis and branches laterally compressed, not compressed, or dorsiventrally compressed, growing in direction of stipe or bend from stipe with a roughly horizontal orientation, glabrous (or set with few rhizoids), caducous in middle or distal part or not caducous, occasionally with a few flagelliform innovations; branches up to 1.7 cm long, up to 85. *Primordia* occasionally or frequently set with scaly leaves, especially at lateral primordia; scaly leaves short, deltoid to oblong-ovate, elliptic, or narrowly triangular, margin usually entire, occasionally with a few serrations. *Epidermis cells and cortical cells of stipe, rachis, and branches* equally wide or inner cortical ones wider; walls thin in epidermis cells and inner cortical cells, thin or incrassate in outer cortical cells, colourless when thin, becoming brown when incrassate; inclusions absent. *Central strand* present; cells equally wide as inner cortical ones or narrower, walls thin, brown in central strand cells stipe, becoming colourless in those of rachis; inclusions absent or present, most frequently present in outer strand cells, less frequently in inner ones, clumps, plates (or crystals?), granules, or droplets, fat-like, colourless (white). *Axial cavities* absent. *Axillary hairs* (0?–)2–6 per leaf, 2–4-celled; basal cells 1–3; terminal cell short to elongate, subcircular to elliptic, occasionally short-obovate, 20–75 µm long and 8–30 µm wide, smooth (or weakly verrucose), wall thin or incrassate. *Phyllotaxis*: of stipe entirely tristichous or nearly so (irregular, 4/11, or rarely 7/18 or 8/21) in basal third to half; of rachis and branches tristichous. *Foliation*: of stipe frequently isophyllous in basal fourth to half and becoming anisophyllous in distal part, less often entirely isophyllous, where isophyllous not or weakly complanate, where anisophyllous complanate; of rachis and branches anisophyllous, complanate. *Leaves* distant at stipe, (distant or) closely set in frond, yellowish green to dark green, dull; insertion transverse, transverse-flexuose, oblique, or concave in stipe leaves, concave in lateral frond leaves, and transverse to transverse-flexuose or concave in amphigastria; laminal cells prosenchymatous, hexagonal, short to elongate, 15–60 µm long and 10–25 µm wide, walls thin, porose or not. *Stipe leaves* monomorphic or partly dimorphic, differentiated in basal and distal ones or not, (appressed to) erecto-patent to (squarrose-)recurved, symmetrical or lateral ones in distal part of stipe asymmetrical, broad-ovate to triangular, ovate, or elliptic (or short-lingulate); margin entire or weakly serrate, frequently partly or entirely recurved in basal stipe leaves, frequently plane in distal ones; border distinct or faint, interrupted or continuous, 1–5 cells wide, colourless; apex (acute or) abruptly acuminate; acumen 0.05–0.5 mm long; costa (faint to) distinct, reaching (1/5–)1/2–4/5 of leaf length. *Basal stipe leaves* scale-like to leaf-like, 0.3–1.0 mm long and 0.2–1.0 mm wide, frequently damaged or lost. *Distal stipe leaves* leaf-like, often differentiated

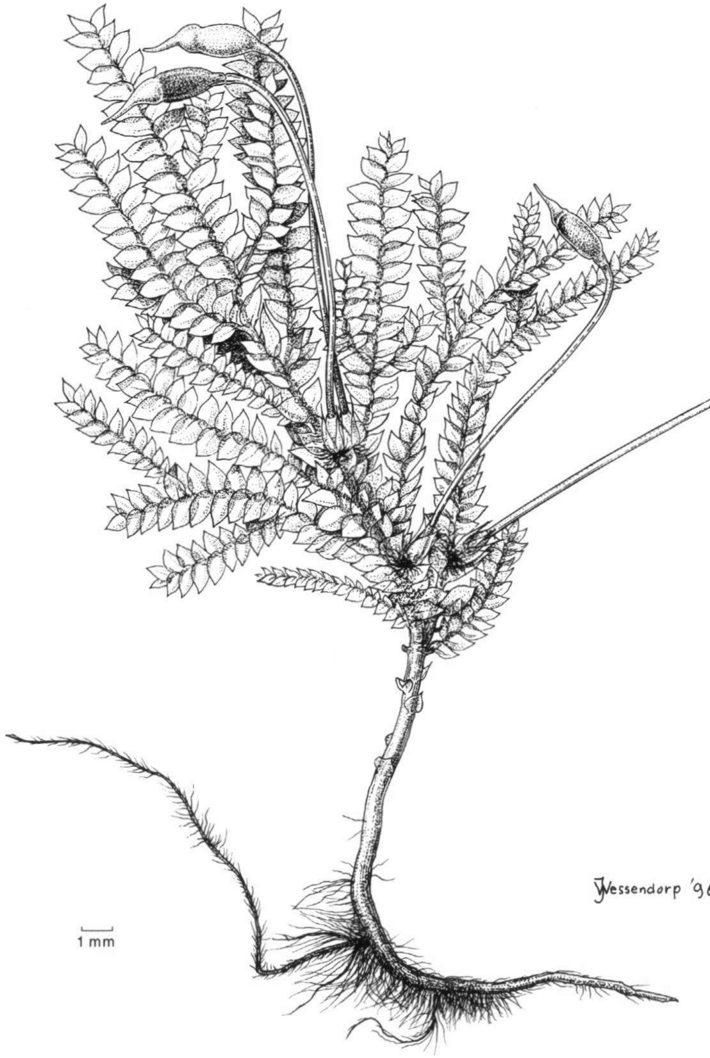


Fig. 29. *Hypopterygium tamarisci* (Sw.) Brid. ex Müll.Hal. Habit 'Asian' variant (*Robbins 3600*, L).

in lateral leaves and amphigastria, 0.9–1.5 mm long and 0.8–1.3 mm wide. ***Frond leaves*** dimorphic, not caducous or caducous near apex of ultimate frond axes; margin entire to coarsely serrate or serrate-dentate; teeth 1- (or 2-)celled, usually uniseriate, occasionally 2 cells wide at base, up to 50 µm long, usually much shorter, projecting up to 1/2 of cell length, up to 20; border usually distinct, occasionally faint near leaf base and apex, continuous, 1–5 cells wide, colourless; apex gradually to abruptly acuminate (rarely rounded and set with a short acumen); acumen 0.05–0.4 mm long. *Lateral frond leaves (in basal and distal part of frond)* asymmetrical, short-ovate, 0.7–2.0 mm long and 0.3–1.5 mm wide; costa (faint to) distinct, reaching 1/3–4/5 of

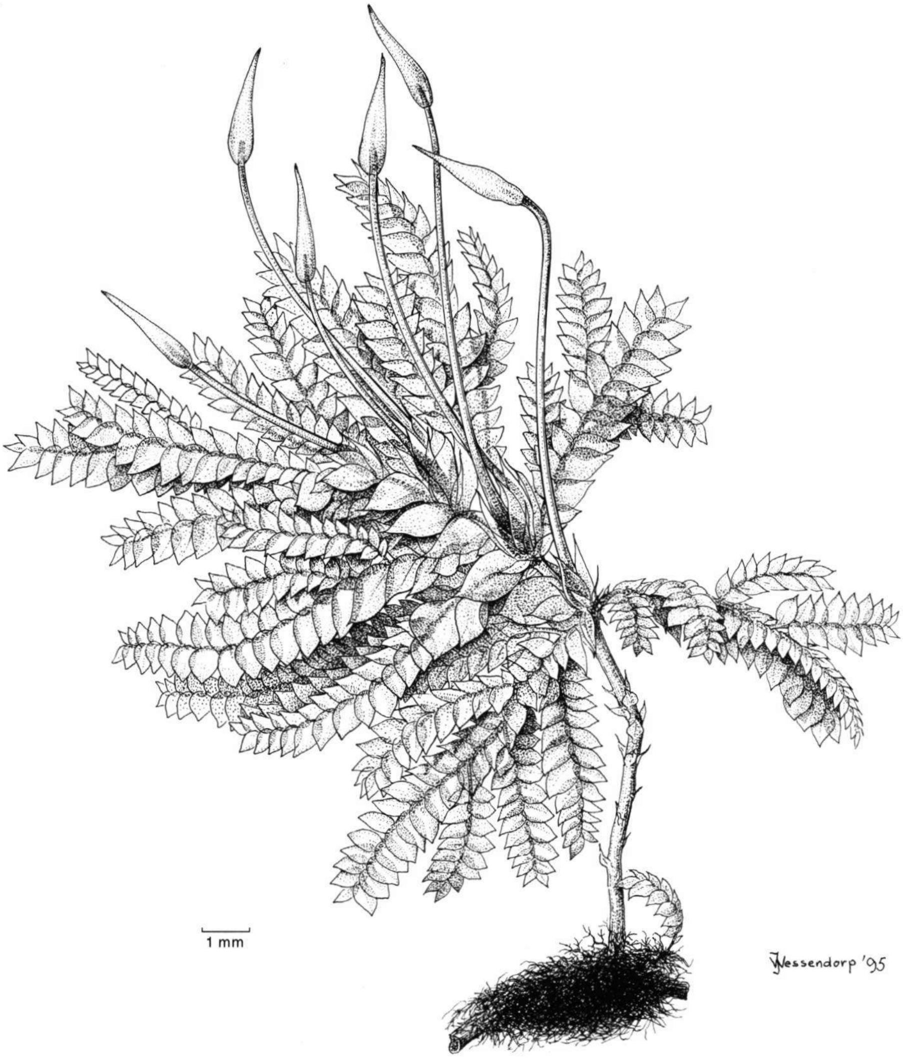


Fig. 30. *Hypopterygium tamarisci* (Sw.) Brid. ex Müll.Hal. Habit 'Australasian' variant (*Streimann HS 1065*, L).

leaf length. *Frond amphigastria (in basal and distal part of frond)* symmetrical, circular to broad-ovate, short-elliptic, or ovate, 0.1–1.7 mm long and 0.1–2.5 mm wide; costa faint to distinct, reaching 1/4 of amphigastrium length to being excurrent (thereby frequently reaching 1/3–2/3 of amphigastrium length in basal part of frond and reaching 1/2 of amphigastrium length to excurrent in distal part of frond). *Gemmae clusters* located in distal half of rachis or branches (rarely on flagelliform innovations or at dorsal side of stolons), reaching 1/3 to 1 1/2 times of length of covering lateral leaves. *Gemmaphores* simple or branched, 3–16 cells long, brown, frequently colourless near apex. *Gemmae* up to 16 cells long, colourless to brown (rarely green), gradually atten-

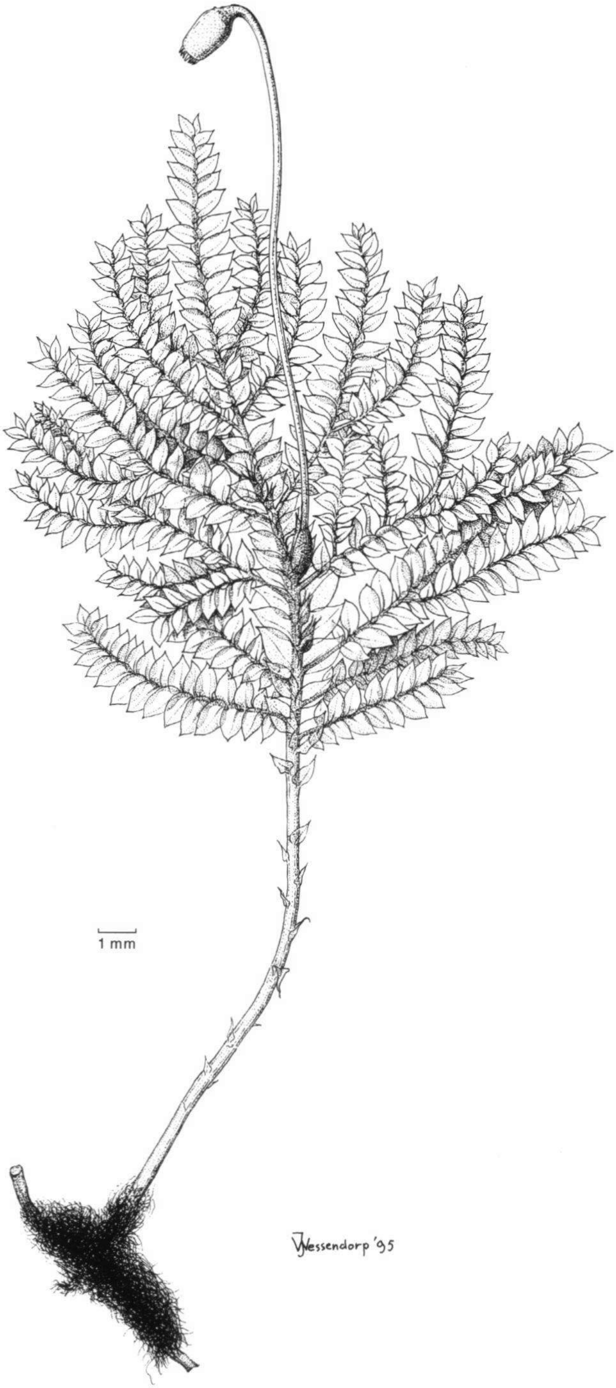


Fig. 31. *Hypopterygium tamarisci* (Sw.) Brid. ex Müll.Hal. Habit 'Oceanian variant 2' (*Robbins 3851*, L).

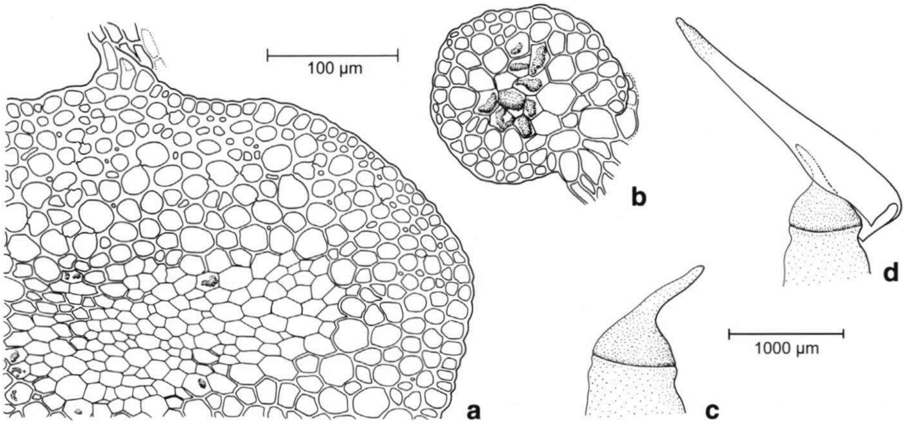


Fig. 32. *Hypopterygium tamarisci* (Sw.) Brid. ex Müll.Hal. a. Rachis (cross section dorsal quadrant); b. branch (cross section); c. operculum; d. calyptra ('Asian' variant: a, b: *Touw & Snoek 22689*, L; c, d: *Touw 10444*, L).

uate when situated on stolons; cells (15–)20–95 µm long and 12–40 µm wide, occasionally almost indistinct from those of gemmaphores.

Heteroicous (or *dioicous*). *Gametoecia* in basal and middle part of rachis and branches; most frequently unisexual, less often bisexual; perigonia situated below, among, or above perichaetia. *Gametoecial leaves* green; margin ± entire; border faint or absent in basal half of leaf, becoming faint or distinct in distal part, interrupted or continuous, 1 or 2 cells wide; apex gradually or abruptly acuminate; acumen up to 0.5 mm long (in leaves of full-grown perichaetia of the 'African' variant up to 0.8 mm long); costa absent, faint, or distinct, reaching 1/4–4/5 of leaf length; laminal cells prosenchymatous or parenchymatous when situated in basal third or central part of leaf, prosenchymatous when situated in the distal part, short to short-linear and rectangular when parenchymatous, short to elongate and hexagonal when prosenchymatous. *Inner leaves*: of perigonia short-elliptic to ovate or lingulate, up to 1.0 mm long and 0.7 mm wide; of perichaetia prior to sporophyte development short-ovate to elliptic, up 1.0 mm long and 0.7 mm wide; of full-grown perichaetia short-lingulate to ovate, up to 2.0 mm long and 1.4 mm wide. *Antheridia* 0.4–0.7 mm long. *Stalk in full-grown perichaetia* 0.3–0.8 mm long, set with rhizoids. *Archegonia* 0.4–0.7 mm long. *Vaginula* 0.5–1.2 mm long. *Gametoecial axillary hairs* 1–5 per gametoecial leaf, 2–4-celled, simple; basal cells 1–3; intermediate cells usually absent, occasionally present, transverse to oblong, elliptic, obovate, or rectangular; terminal cell short to elongate, ovate to elliptic, obovate, or rectangular, 15–85(–115) µm long and 10–30 µm wide, ± smooth, wall thin or incrassate. *Paraphyses* absent or present, 2–10-celled, frequently similar to gametoecial axillary hairs when short; basal cells 1–3, colourless or brown; intermediate cells absent or present, transverse to elongate, rectangular to elliptic or obovate, distinct from basal cells or not, colourless or brown; terminal cell short to short-linear, ovate to elliptic to rectangular or somewhat rhomboid, (15–)35–160 µm long and (10–)15–35 µm wide, weakly inflated or not, colourless (becoming brown in old perigonia), smooth, wall incrassate or not.

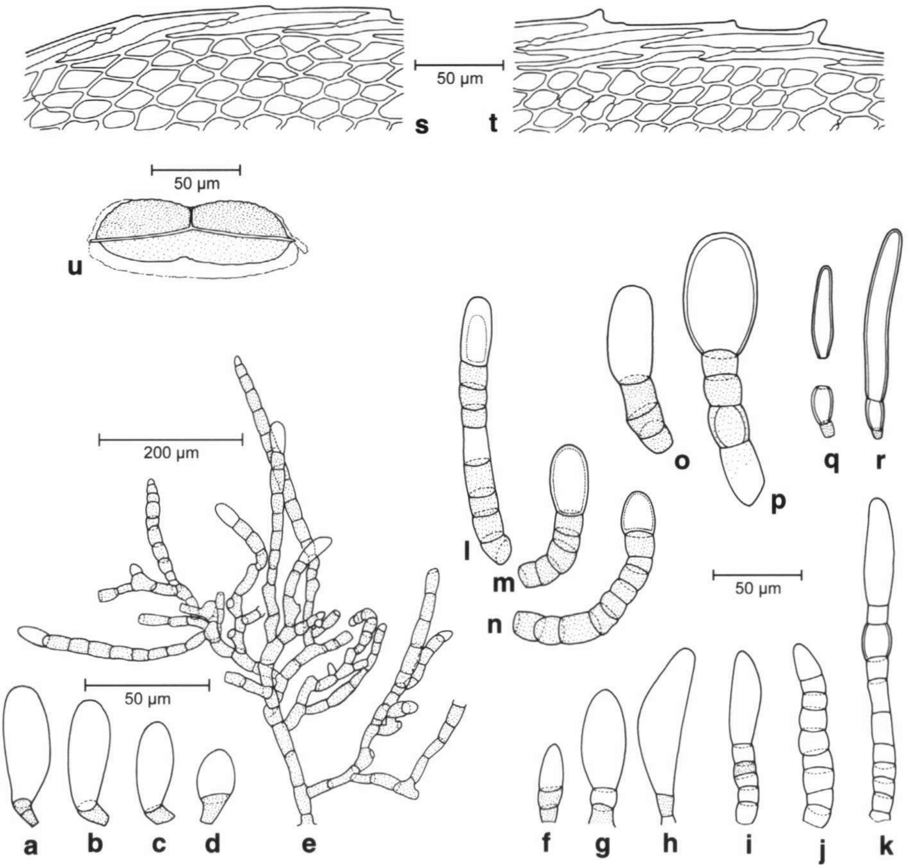


Fig. 33. *Hypopterygium tamarisci* (Sw.) Brid. ex Müll.Hal. a–d. Axillary hairs; e. gemmaphore with gemmae; f–r. paraphyses; s, t. leaf cells of lateral rachis leaf (s. basal part of antical side, t. distal part of antical side); u. exostome tooth (cross section) ('Oceanian variant 2': a–d: *Robbins 3523*, L; l–n: *Nadeaud 440*, W. — 'Asian' variant: e: *Touw & Snoek 22689*, L; s, t: *Robbins 3600*, L; u: *Staal 375*, L. — 'New World' variant: f–k: *Rossato et al. 3307*, L; o, p: *Herzog 2730*, L; q, r: *Allen 8846*, L).

Sporophytes up to 20 per frond, rarely 2 per perichaetium. *Seta* ascending or vertical, uncinate, occasionally weakly curved or flexuose, 6.0–25.0 mm long, ochraceous to reddish brown (or red). *Capsule* (cernuous or) horizontal to pendulous, globose to barrel-shaped, narrowly ellipsoid, urceolate, cupulate, or ovoid, 0.5–2.3 mm long and 0.4–1.3 mm wide, ochraceous to brown; neck smooth or weakly pustulose; annulus absent, indistinct, or distinct.

Peristomial formula OPL:PPL:IPL = 4:2:4–8(–10)c. *Exostome* pale yellow to ochraceous; teeth 360–720 µm long and 95–135 µm wide, entirely bordered, not shouldered; dorsal side striate in basal 2/3 of teeth, becoming papillose in distal part; dorsal plates equally wide or broader than ventral ones, 11–21 µm thick; ventral plates 12–22 µm thick. *Endostome* perforate or not, minutely to moderately papillose at both faces or smooth at outer face of basal membrane; basal membrane reaching 1/3–1/2(–2/3) of length of exostome teeth; processes 300–540 μm long beyond orifice and 40–80 μm wide at base, not nodulose, not appendiculate; cilia 1–4, 1–3 plates wide, up to 9 plates long but often reduced in length, nodulose or not, apendiculate or not; appendages occasionally present, lateral or ventral; lateral ones consisting of 1 or 2 plates or parts of plates; ventral ones consisting of short trabeculiform plates. *Operculum* 0.7–2.2 mm long, (short- to) long-rostrate. *Calyptra* 1.0–3.0 mm long, colourless to ochraceous, occasionally brown in distal part or pale green when dry, entirely membranous or becoming fleshy in distal third to half, partly or entirely covering operculum (in 'African' variant frequently detached prior to thickening of the capsule; see also note 61). *Spores* 11–17 μm.

Distribution — A widely distributed, mainly pantropical and warm-temperate species. Occurs in Africa, Asia, Australasia, Oceania, and the New World. Newly introduced in Europe.

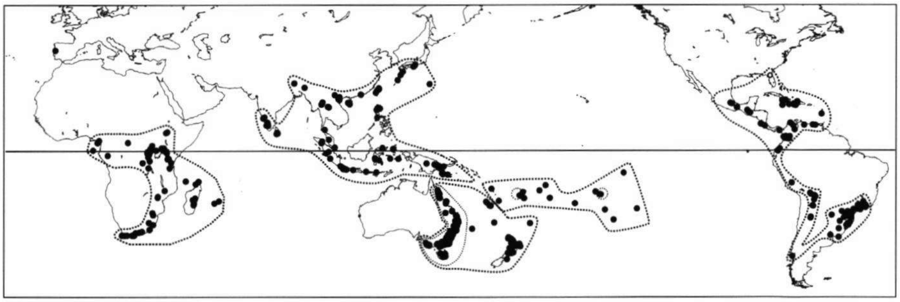
AFRICA: São Tomé e Príncipe, Equatorial Guinea (Bioko), Cameroon, Gabon, Ethiopia, Kenya, Uganda, Democratic Republic of Congo, Rwanda, Burundi, Tanzania, Malawi, Zimbabwe, South Africa, Comoros (Anjouan), Malagasy Republic (Madagascar, Nosy Be), Mascarenes (Réunion, Mauritius). Absent from the Congo Basin.

According to Cufodontis (1951) also found in Schoa, Ethiopia, and possibly also in Eritrea (as *H. pirottae*).

ASIA: Nepal, India (Meghalaya, Karnataka, Kerala, Tamil Nadu), Sri Lanka, China (Hongkong, Hainan), Taiwan, Japan (Honshu, Kyushu, Ryukyu Archipelago, Bonin Islands), Thailand, Vietnam, Philippines (Luzon, Mindoro), Malaysia (Pahang), Singapore, Indonesia (Sumatra, Java, Sulawesi; Moluccas: Buru, Seram, Ternate, Tidore; Lombok, Flores, West Papua), Papua New Guinea.

Reported from southern Vietnam by Tixier (1970). The species is, however, apparently absent from the monsoon forests of the lower mountainous regions of continental SE Asia and the Indian subcontinent.

Reported from Zhejiang, China, by Hu Renliang & Wang Youfang (1987), but remarkably rare in China and restricted to the coastal regions of SE China. The species is more common on Taiwan, where it mainly occurs in the northern and northwestern part of the country.



Map 15. Distribution of *Hypopterygium tamarisci* (Sw.) Brid. ex Müll.Hal. The distribution areas of regional variants (see text) are indicated by a dashed line (......), local variants are indicated by a dotted line (......). The reported locality in Florida is indicated by an open dot (○); the introduction locality of the species in Portugal is indicated by a closed dot (●). See text for further details.

In Japan restricted to the Ryukyu Archipelago and coastal regions of south-eastern Kyushu and Honshu. In the Ryukyu Archipelago it occurs on Amami-Oshima Island, but it was also reported from Iriomote Island by Inoue (1979), and Tanega-shima Island by Deguchi & Kariyasaki (1991). The species finds its most remote occurrence on Haha-jima Island, Bonin Islands.

Erroneously reported from Borneo by Dixon (1935), see note 74. The species is absent from Borneo and, thusfar, not known from Palawan, Midanao, and the islands of Visayas southeast of Mindoro.

AUSTRALASIA: Australia (Queensland, New South Wales, ACT, Victoria, South Australia, Tasmania, Lord Howe Island, Norfolk Island), New Zealand (North Island, South Island, Kermadec Islands), New Caledonia. Presumably also on Île des Pins (Paris, 1910).

In Australia mainly east and south of the Great Dividing Range. Rare in Tasmania and only found in coastal areas of the eastern part of the island. In New Zealand also rather rare and mainly found in the coastal areas of the western and northern part of North Island. On South Island apparently restricted to the north-eastern coast at the Cook Strait and its offsshore islands (Rangitoto Island), and the Banks Peninsula. The low abundancy of the species in Tasmania and South Island of New Zealand is presumably caused by climatological conditions.

OCEANIA: Vanuatu (Espiritu Santo, Aneityum), Fiji (Vanua Levu, Viti Levu, Matuku), Tonga (Tafahi), Samoa Islands (Upolu), Niue, Cook Islands (Rarotonga), Society Islands (Raiatea, Bora Bora, Moorea, Tahiti), Tubuai Islands (Raivavae, Rapa Iti), Tuamotu (Mangareva), Marquesas (Nuku Hiva).

Reported from Raiatea, Society Islands (Bartram, 1931).

NEW WORLD: Cuba, Jamaica, Haiti, Dominican Republic, Martinique, Mexico (Vera Cruz, Chiapas), Guatemala, Costa Rica, Panama, Colombia, Venezuela, Ecuador, Peru, Bolivia, Chile (see note 67), Argentina (Salta?, Tucumán, Buenos Aires), Brazil (Minas Geraïs, Rio de Janeiro, São Paolo, Paraná, Santa Catarina, Rio Grande do Sul), Paraguay, Uruguay. Not known from the Lesser Antilles, the Guyanas, the Guiana Highlands and Llanos in Venezuela and Colombia, the lowlands of the Amazon basin, the highlands of Central and NE Brazil, and the Gran Chaco.

Reported from one locality in Alachua County, Florida, USA, by Diddel & Shields (1943; cf. Grout, 1943; Breen, 1953, 1963). This plant was found on limestone in a lime sink near Newberry on more or less vertical, lower, cool and moist walls (Diddel & Shields, 1943; Breen, 1953). According to Steinman (pers. comm.) suitable habitats have nowadays probably disappeared from this area due to agricultural landuse. Hence, the species has probably become extinct in the USA.

According to Duarte Bello (1997), more widespread on Cuba than given here, and along the southern coast also found in La Habana, Sancti Spíritus, and Guantánamo. Reported from Puerto Rico by Kindberg (1901) and Britton (1913). For Mexico also reported from Hidalgo, Oaxaca, Puebla, San Luis Potosí, and Tamaulipas (Sharp et al., 1994). Reported from Prov. del Oriente, Ecuador, by Brotherus (1920a).

EUROPE: Introduced in Portugal in the Bussaco Forest Arboretum (Allorge, 1974; Kruijer, 1997b), which is the only locality known in Europe where the species grows outdoors (see note 47).

Habitat & Ecology — Usually in dry to wet forests, occasionally in half-open areas with scattered trees and grasses, frequently near streams, in moist or wet places, or in partially to fully shaded habitats. On rocks (basalt, sandstone, limestone, granite, conglomerate, and gneiss?), trunks of trees and palms, tree bases, rotten logs, less often terrestrial or on tree roots, shrubs, tree ferns (but in Australasia frequently on tree ferns), vines, and climbers. Altitude in (sub)tropical areas: 600–3160 m in the Neotropics: 1350–3160 m in the Andes, 600–1950 m in Central America and the Caribbean; 0–4160 m in the Palaeotropics: 650–4160 m in tropical Africa, (0–)600–2330(–2500) m in Indo Malaysia and Oceania; 0–1660 m in (sub)tropical Australasia; 330–660 m on New Caledonia. Altitude in (warm)temperate areas: 0–1550 m for (warm-)temperate areas as a whole: 20–1100 m in SE Brazil and adjacent areas; (50–)100–1550 m in South Africa; 150–1400 m in China and Taiwan; up to 500 m in Japan, Victoria, Tasmania, and New Zealand; 90–295 m on Norfolk Island; found near sea level on Lord Howe Island. Poorly recorded for the Comoro Islands (800 m), the Malagasy Republic (100–1200 m), and the Mascarenes (1350 m on Réunion). According to Hodgetts et al. (1999) found at 1750 m in the Drakensberg Mts, KwaZulu-Natal, South Africa.

The species is principally restricted to humid climates and is not known from deserts and semi-arid areas. In relatively dry habitats of eastern Australia the species is occasionally found in caves and other moist, sheltered environments (cf. Downing et al., 1997).

The widest range of altitudinal distribution is found in the tropics, in particular tropical South America (1350–3160 m) and tropical Africa (650–4160 m). The species is mainly absent from tropical lowlands (e.g. Amazone Basin, Congo Basin; Map 15). In areas with unfavourable ecological conditions (e.g. open or dry forest, low elevations and high temperatures in the tropics, low temperatures in areas with high latitude) the species is usually confined to sheltered places (e.g. rocks in stream beds, rocky slopes of narrow and humid valleys, caves, full shade).

Ecology of this species is poorly known for the West African Islands, the Comoro Islands, the Malagasy Republic, the Mascarenes, and New Caledonia. The ecology of African plants is best known for the plants from South Africa, Malawi, and Uganda (Kruijer, 1997a; Magill & Van Rooy, 1998; Porley et al., 1999; as *Hypopterygium laricinum*).

In South America, the species is occasionally found in *Araucaria* forests. In the Central Cordillera of the northern Andes of Colombia, Wolf (1993c) found *Hypopterygium tamarisci* from 1725 m up to 2460 m. Between 1725 and 1980 m altitude in this area, Wolf (1993a) found *H. tamarisci* forming a tree base moss community that mainly consists of this species, but at lower and higher elevations he regulary observed the species growing on organic soil (pH 7.1) and dead logs, and once above the tree base in a *Bryopteris filicina* community. At higher elevations *H. tamarisci* was accidentally seen in the tree base *Mittenothamnium reptans* community (Wolf, 1993b).

In Africa the species is below 1050 m altitude predominantly found on rocks and above 1050 m even frequently on rocks, tree trunks, tree bases, and other substrates (Kruijer, 1997a). South African plants frequently occur on rocks, stones, litter, or humus, but Sim's (1918) observation, that the species is usually found on stones or accumulated humus overestimates the frequency of occurrence on these substrates.

Table 4. Character state distribution of relevant characters of the variants within *Hypopterygium tamarisci* modified from Pfeiffer et al. (2000). + = presence of a character (state); – = absence of a character (state); × = unknown character state due to absence of the character; brackets indicate infrequent presency.

variant character	New World	African	Asian	Austral-asian	Australian	Oceanian 1	Oceanian 2
life form							
dendroid	+	+	+	+	–	–	+
fan	+	+	+	(+)	+	+	+
plant size							
stipe length							
(max.) ≥ 1.5 cm	+	+	+	–	–	+	–
rachis length							
(max.) ≥ 1.5 cm	+	+	+	(+)	+	+	–
branches / frond leaves							
closely set	+	+	+	+	+	–	+
distant	+	+	+	+	+	+	–
axillary hairs							
number per leaf 1	+	+	+	–	–	+	+
2	+	+	+	+	+	+	+
3	+	+	+	+	+	–	–
4	–	–	(+)	+	+	–	–
5	–	–	–	+	+	–	–
6	–	–	–	+	+	–	–
shape terminal cell							
subcircular	–	+	–	+	+	+	+
elliptic	+	+	+	+	+	+	+
obovate	–	–	–	+	+	+	+
lateral frond leaf							
leaf length							
(max.) ≥ 1.5 mm	+	+	(+)	–	–	+	–
costa < 4/5	+	+	+	–	–	+	+
c. 4/5	–	–	+	+	+	–	–
frond amphigastrium							
costa < 2/3	+	+	+	+	–	+	+
> 2/3	+	+	+	(+)	+	(+)	(+)
asexual propagation							
caducous branches	+	–	+	+	–	+	+
gemmae	(+)	–	+	+	–	+	+
gemmaphores							
simple	–	×	+	–	×	+	+
branched	+	×	+	+	×	+	+
paraphyses							
in perigonia	+(/–?)	–	–	–	–	–	–
in perichaetia	+	+/–	(+)	–	–	(+)	(+)
terminal cell > 50 µm	+(/–)	–	–	×	×	–	–
persistent	–	+	+	×	×	+	+
sexuality							
heteroicous	+	+	+	+	–	+	+
strictly dioicous	–	–	–	–	+	–	–
capsule shape							
(sub)globose	+	(+)	(+)	–	–	–	–
other	+	+	+	+	+	+	+
calyptra							
persistent	+	–	+	+	+	+	+

In Japan and Taiwan the species is predominantly found on rocks. In other parts of Asia, plants occur equally frequently on rocks and tree trunks.

For Oceania, the type of rocks was recorded only once (*St. John 14515*), but according to Whittier (1968, 1976) the species (as *H. tahitense*) is common on wet basaltic rock.

Variation — *Hypopterygium tamarisci* is a wide-spread species, whose distribution area includes different climates varying from temperate to tropical. Hence, the species shows great morphological variation. Regional and some ecological variation was especially observed in life form, size, sexuality, and the presence or absence of reproductive structures and characters (Pfeiffer et al., 2000). Variation was also found in the number of axillary hairs per associated leaf, the shape of the terminal cell of the axillary hair, and the length of the costa of the lateral leaves and amphigastria. Pfeiffer et al. (2000) proposed an artificial classification of informal regional variants, which is followed here to describe the observed geographic variation.

In short, the hypothetic general form of *H. tamarisci* is characterised by small to medium sized, palmate to umbellate plants with a tristichous leaf arrangement and entire or weakly serrate-dentate, acuminate frond leaves with up to 25 µm long marginal protrusions. The general form is heteroicous. Monoicous plants predominate, but dioicous ones are common. Specimens containing both monoicous and dioicous gametophores are also common; in such specimens gametophores with different sexuality are sometimes attached to each other. In monoicous material, the frequency of unisexual (male, female) and bisexual gametoecia shows considerable variation between specimens and gametophores.

Regional variants deviate in one or more character states from the other variants (Table 4). Other geographical and ecological variation is treated in the following subsection under the variants:

'New World' variant: The main characteristic of this variant is the presence of paraphyses in both perigonia and perichaetia. The paraphyses are 2- or 3-celled in perigonia and 2–10-celled in perichaetia. The terminal cell is (15–)60–160 µm long and (10–) 15–35 µm wide, and is frequently easily detached. Among the variants, the 'New World' variant shows most variation in marginal protrusions. Frond leaves are usually weakly to coarsely serrate or serrate-dentate and are only occasionally entire. The protrusions are up to 35 µm long.

Distribution: The variant occurs in southern North America (Mexico), Central America, the Caribbean, western and southeastern South America.

Geographical variation: Observed in the sizes of the plant and is weakly present in capsule size. There is no correlation between these features.

Plants of 4.5–5.5 cm tall were frequently found among the material from the Caribbean, the Andes, and south-eastern Brazil and adjacent areas, but were less often found in Central America. Plants up to 4.5 cm occur in every area.

Most striking in the New World plants is the variability of capsule size. The majority of the fruiting plants have small capsules (up to 1.0 mm long and 0.8 mm wide). Plants with small capsules are found throughout the distribution area. Plants with large capsules (exceeding 1.0 mm long and 0.8 mm wide) are most frequently found

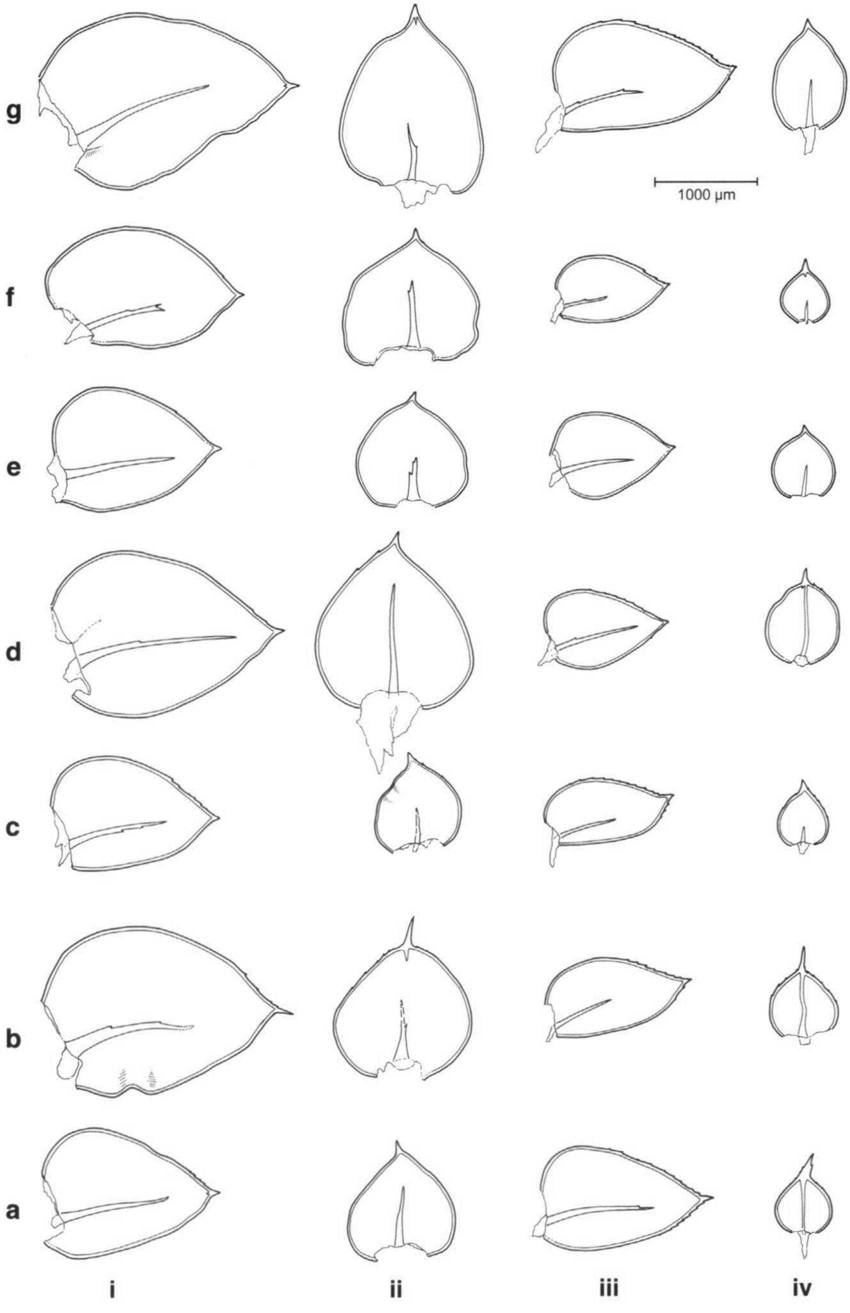


Fig. 34. *Hypopterygium tamarisci* (Sw.) Brid. ex Müll.Hal. Frond leaves: i. lateral rachis leaves; ii. rachis amphigastria; iii. lateral branch leaves; iv. branch amphigastria; a. 'New World' variant (*Harris s.n.*, L); b. 'African' variant (*De Wilde-Duyfjes 11587A*, L); c. 'Asian' variant (*Robbins 3600*, L); d. 'Australian' variant (*Verdon 1253*, L); e. 'Australasian' variant (*Streimann 3807*, L); f. 'Oceanian variant 2' (*Robbins 3523*, L); g. 'Oceanian variant 1' (*Sloover 20.946*, L).

in the Andes and SE Brazil and adjacent areas. Sometimes small and large capsules may be present in a single specimen.

Ecological variation: Not found. A correlation between plant size and capsule size with altitudinal distribution or type of substrate did not exist. Other ecological variation may have been overlooked because of insufficient data.

'African' variant: The main characteristic of this variant is the absence of asexual propagulae and the loosely attached calyptra.

Sim (1926) described the calyptra of South African plants as rather persistent. However, in the vast majority of African specimens – including those from South Africa – calyptrae were often found to be detached from the sporophytes. Almost every mature and immature sporophyte of African plants has lost its calyptra. Presumably, calyptrae of African plants usually become detached before or shortly after the thickening of the capsules. An explanation for this phenomenon was not found.

According to Sim (1926), South African plants are often very scattered, but sometimes caespitose. Most plants from South Africa and tropical Africa, however, grow in dense to very dense, and then weft-like, groups or patches.

Distribution: The variant occurs in Subsaharan Africa, including the West and East African Islands and Madagascar.

Geographical variation: Observed in the size of the plant, the development of the border of the lateral leaves, and the shape and size of the capsule. There is no correlation between these features.

Plants from tropical Africa, including the East African islands, are between 1.0 and 6.5 cm tall. The majority of the plants do not exceed 3.0 cm in height, and are usually much smaller. In most tropical plants, almost every lateral leaf is provided with a distinct and continuous border. The plants from South Africa are generally smaller than the tropical ones and are between 0.5–3.0 cm tall. The leaf border of the lateral leaves in the South African plants is frequently partly faint or interrupted.

The plants from the West African islands differ from the plants of continental (tropical) Africa in size and shape of the capsules. The continental capsules are usually ellipsoid to weakly cupulate. The few 'mature' capsules found in the fruiting material from São Tomé are urceolate to subglobose. In addition, these capsules are smaller, approximately 1.0 mm long and 0.7 mm wide. The majority of the sporophytes in the fruiting material of São Tomé is immature and it was difficult to ascertain whether the 'mature' capsules were truly fully ripe. Nevertheless, the 'mature' capsules in the West African island plants show a remarkable resemblance with the small capsules of the 'New World' variant. If the small size of the 'mature' capsules of the West African plants is natural, than this resemblance may indicate an ecological or historical factor that plants from the West African islands and those from the New World have in common. All fruiting specimens from São Tomé examined were collected by Quintas and are preserved in S (sub no. *(25)*) and COI (sub no. *1448*).

Ecological variation: Observed in the size of the plant. The plants from the East African Islands and Madagascar are not significantly different from those from continental (tropical) Africa and they show a similar variation. However, the plants from Mauritius are small and the size of the plants shows less variation than present on other African islands and on the African continent. This is due to the relatively low elevation of Mauritius: in tropical Africa medium sized and large plants only occur above the 1050 m level, while Mauritian mountains do not exceed 820 m altitude.

In tropical Africa, small plants are found at every level within the altitudinal distribution. Very small plants (less than 1.5 cm tall) are only found below 1050 m (Kruijer, 1997a). Plants between 1.5 and 4.5 cm tall are nearly all found above 1050 m. A single collection, from 2220 m altitude origin, contains among several small and medium sized gametophores a few that are up to 6.5 cm tall

In South Africa, a correlation of size with altitudinal distribution was not found. Small and medium sized plants seemingly occur throughout the altitudinal distribution of the species. Large plants are not known from South Africa.

'Asian' variant: A less characteristic variant of the species and it may be considered intermediate between the variants. Important character states are the frequently caducous branches, the 1–3(–4) axillary hairs per leaf having a strictly elliptic, smooth terminal cell of 20–75 μm long and 8–30 μm wide, the variable length of the costa of the lateral frond leaves (reaching 1/2–4/5 of leaf length), and the simple or branched gemmaphores.

Distribution: This variant occurs in Indo Malaysia, and Sino Japan.

Geographical variation: Plants from (sub)tropical areas are between 0.8 to 4.3 cm tall. The largest plants were found in northern Thailand, which are up to 4.3 cm, and on Peninsular Malaysia. The SE Asian plants are in majority between 2.0 and 3.2 cm tall. New Guinean plants are generally shorter than 2.0 cm, but are occasionally up to 3.1 cm tall. Plants from other tropical areas are up to 2.5 cm tall, but are often shorter than 2.0 cm.

Taiwanese and Chinese plants are usually shorter than 2.0 cm, but a few plants from northern and western Taiwan are between 2.5 and 3.0 cm tall. Taiwanese plants are nearly always palmate. Japanese plants are smaller than the Taiwanese plants. They are maximally 2.6 cm tall, but in majority much shorter than 1.7 cm. They are almost always palmate.

In most Asian specimens, the margin of the frond leaves is entire or weakly serrate-dentate and set with a few protrusions not exceeding 15 μm in length. In a few specimens, from southern India (*Foreau 539*, BM; *Gardner 3b*, BM), Sulawesi (*Touw & Snoek 24490*, L), and Papua New Guinea (*Hovenkamp 91/88*, L; *Streimann & Umba 11462*, CBG), a moderately serrate-dentate leaf margin with more and longer protrusions was observed. The largest protrusions were found in the specimen from Sulawesi, which are up to 35 μm in length.

Ecological variation: In tropical Indo Malaysia, the plants are in majority palmate. Pinnate and flabellate plants grow epiphytic or epilithic on inclined or vertical substrates, whereas umbellate plants are predominantly terrestrial or on rocks on roughly horizontal surfaces. Palmate plants may grow on various substrates of various inclination, and grow often intermingled with pinnate, flabellate, or umbellate plants. Palmate, pinnate, and flabellate plants are found at every altitude. Umbellate plants are found below 1500 m altitude and occur intermingled with palmate ones.

'Australasian' variant: The main characteristics of this heteroicous variant are the 2–6 axillary hairs per leaf, the long costa of the lateral frond leaves (reaching c. 4/5 of leaf length), the branched gemmaphores, and the absence of paraphyses.

Plants of this variant are occasionally very small and may even be dwarfish.The variant is most frequently found on rocks, tree trunks, saplings, or tree ferns, and less often found on soil and rotten logs.

Distribution: The variant is distributed throughout Australasia, including the Kermadec Islands and New Caledonia.

Geographical variation: Variation correlated with geography is remarkably low, and principally found in size of the gametophores. Australasian plants are between 0.5 and 3.5 cm tall, but the majority is shorter than 1.5 cm. In Australia, including Tasmania, plants do not exceed 2.5 cm in height. New Zealand and New Caledonian plants are up to 3.5 cm tall, those from Lord Howe Island, Norfolk Island, and the Kermadec Islands are generally smaller and up to 2.0 cm tall, whereby plants smaller than 1.5 cm predominate. Plants from Raoul Island, Kermadec Islands, and New Caledonia show closest resemblance with the plants from NE Australia.

In most Australasian specimens, the margin of the frond leaves is set with a few protrusions not exceeding 15 µm in length. A few plants from two localities near Proserpine, Queensland, Australia (*Streimann 37397*, B, CBG, NY; *37628*, CBG), and from Mt Mouè, New Caledonia (*Le Rat s.n.*), have moderately to coarsely serrate-dentate frond leaves, which are set with several protrusions up to 30 µm long. An (ecological) explanation for the pronounced leaf dentation in these plants was not found.

Monoicy occurs in a remarkable low frequency on Norfolk Island (c. 25% of the specimens; n = 36). Gemmiferous plants are rather rare in New Zealand (c. 12%; n = 12).

Ecological variation: Only observed for size related to altitude in SE New South Wales, Victoria, Tasmania, and New Zealand. In these areas small and medium-sized plants occur equally frequent at every altitude, although the smaller ones seem occasionally to be somewhat more abundant. In the material from Lord Howe Island and Norfolk Island small plants predominate. In Queensland and north-eastern New South Wales, Australia, medium-sized plants occur mainly between 500–1000 m altitude.

'Australian' variant: The variant resembles the 'Australasian' variant, but it differs in habit (fans), the absence of asexual propagulae, the length of the amphigastrium costa (reaching at least 2/3 of amphigastrium length to excurrent), and its strict dioicy.

Plants of the 'Australian' variant are generally larger than those of the 'Australasian' variant and may occasionally become 3.0 cm tall and rarely 5.0 cm tall.

Habitat & Ecology: The Australian variant is most frequently found on rocks and it is less often found on the ground, tree trunks, treelets, or tree ferns, and rotten logs.

Distribution: The variant is distributed throughout E Australia, including Tasmania. It is most common in SE New South Wales and Victoria, where it occurs equally frequent as or somewhat more abundant than the 'Australasian' variant. The latter predominates in Queensland and NE New South Wales.

Geographical and Ecological variation: Not found.

'Oceanian variant 1': The main characteristics of this variant are its size and habit. Plants of this variant are fans up to (2.5–)3.0–4.5 cm tall. The rachis reaches up to 2.7 cm. The branches are distant. There are 1 or 2 axillary hairs per leaf. The smooth or weakly verrucose terminal cell is subcircular, obovate, or elliptic. The frond leaves are large and distant when dry. The lateral leaves are 1.0–2.0 mm long and 0.5–1.5 mm wide and are usually remarkably similar in size and shape within a frond. The costa of the lateral leaves reaches 1/3–2/3 of the length of the leaf. Paraphyses are usually absent, but occasionally present in full-grown perichaetia and 6–10 cells long; the terminal cell is 15–35 µm long and 10–25 µm wide.

Habitat & Ecology: The variant is only known from rocks below 1000 m altitude. Fruiting specimens were not found below 500 m.

Distribution: The variant is known from the Society Islands and Viti Levu (Fiji).

Geographical variation and Ecological variation: not found (insufficient data).

'Oceanian variant 2': This variant resembles the 'Asian' and 'Australasian' variants but has with 'Oceanian variant 1' in common the number of axillary hairs per leaf, the shape and ornamentation of the terminal cell of the axillary hairs, the length of the costa of the lateral leaves, and the characteristics of the paraphyses. 'Oceanian variant 1' differs from 'Oceanian variant 2' by its growth habit and size. Plants of 'Oceanian variant 2' are fans or dendroids with closely set branches. The plants are up to 3.0 cm tall, but are usually much shorter with a rachis that is up to 1.5 cm long. The frond leaves are closely set when dry. The lateral leaves are up to 1.2 mm long and 0.8 mm wide.

Habitat & Ecology: Fruiting specimens were not found below 500 m altitude.

Distribution: The variant is distributed on Melanesian and Polynesian Islands from Vanuatu to the Marquesas.

Geographical variation and Ecological variation: Not found (insufficient data).

Chromosome numbers — n = 9, 18, c. 27, and 36; see Inoue (1979: 111–112, '*Hypopterygium tamariscinum*'); Ramsay (1967: 221; 1974: 295; '*H. rotulatum*'). — Vouchers: *Sharp X-763* (n.v.), Venezuela, Parque Nac. H.P. Araqua: n =18; *Inoue 2416* (n.v.), Japan, Okinawa Pref, Iriomoto Island, Nakamagawa: n = 9; *Iwatsuki 1629* (n.v.), Japan, Miyazaki Pref., Nichinan: n = 18; *Ramsay 8/64* (SYD), *36/65* (SYD): n = 9; *Ramsay 8a/64* (SYD), *33/64* (SYD), *33a/64* (SYD), *33b/64* (SYD): n = 18, *Ramsay 8d/64* (SYD), *22/64* (SYD): n = c. 27; *Ramsay 8b/64* (SYD), *8c/64* (SYD), *8e/64* (SYD), *8f/64* (SYD), *16/64* (SYD): n = 36; all vouchers collected by Ramsay from Australia, New South Wales, Mt Wilson; see note 62; *Ramsay 4/72* (UNSW?, n.v.), Australia, New South Wales, Royal Nat. Park: n = 18.

Chloroplast DNA sequences — *rbcL*, 1297 bp, deposited in the GenBank database under accession number AF158171, see De Luna et al. (1999: 635, '*H. tamariscinum*'); 1303 bp, AF232695, Cox et al. (2000: 229). — *rps4*, 614 bp, AF143077, see Buck et al. (2000: 182), Cox et al. (2000: 229). — *trnL–trnF* intergenic spacer, AF161170, see Buck et al. (2000:182), Cox et al. (2000: 229). — *trnL*$_{UAA}$ intron, 296 bp, AF134635, see Stech et al. (1999: 361), AF170596–600, AF265218, Pfeiffer (2000: 297), Pfeiffer et al. (2000: 59); 297 bp, AF265217, AF265219, Pfeiffer et al. (2000: 59); 298 bp, AF170601, Pfeiffer (2000: 297). — Vouchers: *Schultze-Motel 3300* (B), Samoa Is., Western Samoa, Upolu, Mt Fiamoe – Lake Lamoto'o: AF134635; *De Luna 2236* (XAL n.v.), Mexico, Veracruz, Jardin Botanico Clavijero: AF158171; *Churchill & Betancur 18102* (NY n.v.), locality not cited: AF143077, AF161170; *Brownsey s.n.* (WELT, sub no. M029155; hb. Frey, 'Hm 1'), New Zealand, North Is., Wellington L.D., Upper

Hutt, Kaitoke Waterworks: AF170596; *Brownsey s.n.* (WELT, sub no. M028292; hb. Frey, 'Hm 2'): AF170597, [ex] *Streimann 51393* (L p.p.; hb. Frey, 'Hm3', picked out of a collection of *Canalohypopterygium tamariscinum*): AF170598, both from New Zealand, South Is., Nelson L.D., Hira Sate Forest; *Streimann 63472* (hb. Frey, 'AUS 2'; CANB n.v.), Australia, New South Wales, Marble Arch: AF170599; *Streimann 49667* (L; hb. Frey, 'Hm NORF'), Norfolk Is.: AF170600; *Streimann 63471* (hb. Frey, 'AUS 1'; CANB n.v.), Australia, New South Wales, Nadgee State Forest: AF170601; *O'Shea 99E28a* (hb. Frahm, n.v.), South Africa: AF265217; *Koops CGK 1828* (L), Malaysia, Pahang, Cameron Highlands, Tanah Rata: AF265218; *Maitland 1A* (L), Bolivia, Santa Cruz, Samaipata, Amboro Park: AF265219.

Nuclear DNA sequences — 18S *r*RNA gene, 1771 bp (partial sequence), deposited in GenBank database under accession number AF229923, see Cox et al. (2000: 229).

Cox et al's (2000) indirect reference to the voucher material of their *rbcL* and 18S *r*RNA gene sequences revealed no further information on voucher identity and location.

Notes:

Nomenclature and synonymy — 1. In neotropical botanical literature, several authors erroneously used the name *Hypopterygium tamariscinum* (Hedw.) Brid. for this widely distributed species. Kruijer (1996a) showed, however, that *Hypopterygium tamarisci* (Sw.) Brid. ex Müll.Hal. is the correct name for this species. Van der Wijk et al. (1964) erroneously considered *Hypnum tamarisci* Sw. 1806 an illegitimate name that is based on *Leskea tamariscina* Hedw. 1801. Kruijer (1996a) pointed out that Hedwig's (1801) species is not included in Swartz' (1806) concept of *Hypnum tamarisci* Sw. 1806. Swartz' description is solely based on the Jamaican material of *Hypnum tamarisci* Sw. 1788. Swarz may have cited Hedwig's name only because Hedwig listed *Hypnum tamarisci* Sw. 1788. in the synonymy of *L. tamariscina.* Swartz (1806) did not cite the material from 'Insula Australes' upon which Hedwig based his *L. tamariscina.*

The names *Leskea tamariscina* and *Hypopterygium tamariscinum* represent a – distantly related – New Zealand species, which has been transferred to the monotypic genus *Canalohypopterygium* Frey & Schaepe (Frey & Schaepe, 1989; Kruijer, 1996a; see also '*Canalohypopterygium tamariscinum*', p. 122).

2. The type material of *Hypopterygium tamarisci* (Sw.) Brid. ex Müll.Hal. consists of medium-sized to large, flabellate plants with a nearly entirely tomentose stipe. Stipe and rachis measure up to slightly more than 2.0 cm in length.

Swartz (1806) described *Hypnum tamarisci* Sw. as a monoicous species. Müller (1850) considered it erroneously to be dioicous. Swartz' material is autoicous. Most of its gametoecia are unisexual; a gametoecium that is attached to the specimen, preserved in G, may be bisexual, but I could not observe this with certainty. The material did not bear sporophytes, but a few perichaetia contained fertilised archegonia.

3. The type of *Hypopterygium rotulatum* var. *incurvum* Brid. is a very small plant that is up to 1.4 cm tall, which beyond any doubt belongs to the present species.

4. Hampe (1847) considered *Moritz 70* from Mérida, Venezuela, to be a mixed collection of fruiting plants that belong to two species: the American form (no formal status) of *Hypopterygium laricinum* and Hampe's new species *H. flavescens.* Hampe compared his new species with *H. laricinum*, and not with *H. tamarisci*, although he reported the latter also from Mérida (*Moritz 150*; as *H. tamariscinum*).

Hampe distinguished *Hypopterygium flavescens* from *H. laricinum* and *H. rotulatum* by non-substantial differences, including the yellow colour, the kidney-shaped amphigastria with a thick, excurrent costa, and the relative length of the acumen, given as a third to half times the amphigastrium length. Hampe described the capsule of *H. flavescens* as oblong-cylindrical, attenuate at both sides, and having a conical-subulate operculum. On the other hand, he described the capsule of his material of "*H. laricinum*" from Venezuela as subglobose and the base of its operculum as thick.

Hypopterygium flavescens is best assigned to the 'New World' variant of *H. tamarisci.*

Hampe (1847) cited only a portion of *Moritz 70* as *Hypopterygium flavescens*. It remains unclear whether a specimen in L (*Moritz 70*, 'Caripe, Colona Tovar, Covollar, Caracas') is a duplicate of the portion cited by Hampe and type material of this species.

5. Moritz' collections (*Moritz 70*, *Moritz 150*) from Mérida, Venezuela, were examined by Müller (1850), who, contrary to Hampe (1847), considered them conspecific. Based on both, i.e. *Moritz 70* and *150*, Müller described his new species *Hypopterygium nivale*, apparently unaware of Hampe's new species *H. flavescens* (see above, note 4). Although Müller (1850) did not recognise *Moritz 70* as a mixed collection, he did notice differences in the colour intensity of the leaf cells.

Müller (1850) compared his *Hypopterygium nivale* with his other new species *H. incrassatolimbatum* and with *H. tamarisci*, whereby he especially considered leaf features. He described *H. nivale* as more robust having larger leaves than *H. incrassatolimbatum*. In addition, he described the leaf border in *H. nivale* as laxer and less incrassate, the costae as longer and forked, and the laminal cells as less green or even colourless. Müller described the amphigastria of *H. nivale* as wider cordate than in *H. incrassatolimbatum*, less serrate, and continuously bordered.

Müller's observation that the type material of *Hypopterygium nivale* is generally more robust and larger than the type material of *H. incrassatolimbatum* is correct, for the gametophores of the latter are 2.3 to 3.1 cm tall and the lateral frond leaves are 0.8–1.2 mm long and 0.5–0.7 mm wide. These differences in size are, however, not substantial. The costae in the lateral leaves of *Moritz 150* are well pronounced. Although they are often forked in their apical part, they are essentially simple. In *Moritz 70* the costae are less pronounced and almost entirely simple. The 'forked' leaf costae found in *Moritz 150* do not justify the separation of *H. nivale* as a distinct species. Nor does the width of the base of the amphigastrium, the degree of dentation, and degree of development of the border of the amphigastria justify such a separation.

Müller distinguished *Hypopterygium nivale* from *H. tamarisci* by its wider laminal leaf cells and laxer areolation of the leaves. The differences in the "utriculo primoridiali", by which Müller meant the plasmolysed protoplasts in the lumen of dry or plasmolysed cells, must be considered artefacts. None of the differences given by Müller are substantial and legitimate the distinction of *H. nivale*, *H. incrassatolimbatum*, and *H. tamarisci* as separate species.

The syntypes of *Hypopterygium nivale* are flabellate to palmate plants, which are (small to) medium-sized to large. The gametophores in *Moritz 70* are (1.5–)2.0 cm to 4.5 cm tall and are generally less robust than those of *Moritz 150*, whose gametophores are 2.0 to 5.5 cm tall. The leaves of *Moritz 70* are also generally smaller than in *Moritz 150*. The lateral frond leaves, for instance, are 0.8–1.8 mm long and 0.7–1.0 mm wide in *Moritz 70* and 1.4–2.3 mm long and 0.7–1.4 mm long in *Moritz 150*. *Moritz 70* possesses only a few old gametoecia, whose paraphyses have presumably been detached or damaged. The specimen of *Moritz 70* kept in L possesses a subglobose capsule being 0.8 mm long and 0.7 mm wide. The capsules in *Moritz 150* are larger, being 1.2–1.3 mm long and 0.8–1.1 mm wide, and are subglobose to barrel-shaped. The terminal cell of the paraphyses found in a few perichatia of this type vary between 58 to 84 µm in length.

6. When Hooker (1818) described *Hypnum laricinum*, he considered the material collected in South America by Humboldt and Bonpland to be conspecific with the material collected by Menzies from the Cape of Good Hope. Taylor (1847) suggested, that his specimen of *Hypnum scutellatum* from Mt Pichincha, near Quito, collected by Jameson is conspecific with Hooker's material of *Hypnum laricinum* from the Andes, but not with that of Menzies from the Cape of Good Hope. Müller (1850) excluded the Andean specimens from *Hypopterygium laricinum* and included these in his concept of *Hypopterygium scutellatum*.

Müller also excluded Hooker's illustrations in t. 35[1] from *Hypopterygium scutellatum*, because he was unaware that, according to annotations in Wilson's herbarium, Hooker's illustrations of *Hypnum laricinum* are based on Hooker's South American material, i.e. *Humboldt 92*.

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1) Müller referred to t. 34, but it is safe to consider Müller's reference an error for Hooker's t. 35 ('*Hypnum laricinum*'), because Hooker's t. 34 contains illustrations of *Leskea concinna* W. Hook. (= *Lopidium concinnum* (W. Hook.) Wilson).

7. Taylor (1847) did not report a collection number for Jameson's material, but it is almost certain that the specimen in BR that is labelled with the number *81* is a part of the type material of *Hypopterygium scutellatum* (Tayl.) Müll.Hal.

According to Sayre (1975), Jameson sent his plants to W.J. Hooker at Kew in 1840, who sent some of the bryophytes to Taylor and some to Wilson. After Taylor's death in 1848 his specimens, or part of them, came to Mitten, who (1851) apparently prepared Jameson's collections for distribution. Mitten (1851) adopted the numbers used by Wilson in an unpublished list of Jameson's collections, but used Taylor's published names, and some of Wilson's unpublished ones, with Mitten's own interpretations. Mitten accepted Müller's transfer (1850) of Taylor's species *Hypnum scutellatum* to *Hypopterygium*. He listed *Hypopterygium scutellatum* under number *81* and he gave Taylor's species as a synonym.

8. Müller (1850) recognised *Hypopterygium tamarisci* from Jamaica as a distinct species, but nevertheless described three new *Hypopterygium* species from South America, of which two, *H. incrassatolimbatum* and *H. nivale*, are conspecific with *H. tamarisci* in its present circumscription.

Müller defined *Hypopterygium incrassatolimbatum* from Brazil to be similar to *H. laricinum* from the Cape of Good Hope and Mauritius, but being somewhat more robust with broader amphigastria and longer acuminate perichaetia. In addition, he described the leaf areolation in *H. incrassatolimbatum* as denser, consisting of smaller cells with more incrassate walls. He also described the leaf border as incrassate and denticulate at the leaf apex and the contents of the leaf cells ("utriculo primoridiali") as green.

Hypopterygium incrassatolimbatum is best assigned to the 'New World' variant of the present species. The type of *H. incrassatolimbatum* is a small to medium-sized plant that is up to 3.3 cm tall. It is weakly palmate, autoicous, and fruiting plant with small, subglobose capsules that are approximately 0.8 mm long and 0.6 mm wide.

9. Müller (1854) defined his new species *H. tenellum* as dioicous, but several type specimens and potential type specimens proved to be monoicous.

10. Sullivant (1874) considered his (1855) species *Hypopterygium brasiliense* closely related to *Hypopterygium scutellatum*, *H. incrassatolimbatum*, and *H. nivale*, but treated them as separate species. However, the characters he used are not sufficiently distinctive to separate them from *H. tamarisci*.

Sullivant (1855) described *Hypopterygium brasiliense* as monoicous with simple costae in the lateral leaves and percurrent or excurrent ['continuous'] costae in amphigastria.

Sullivant (1874) distinguished *Hypopterygium incrassatolimbatum* from *H. brasiliense* by its dioicy and its thicker and wider leaf border. However, the type of sexuality is not suitable to discriminate *Hypopterygium* species that are closely related to *H. tamarisci*, because of its variability. Dioicy is a common feature, even though the plants are predominantly monoicous. Also, the degree of development of the leaf border is not essentially different between Sullivant's species and *H. incrassatolimbatum*, and does not represent a differentiating character.

Sullivant (1874) erroneously distinguished *Hypopterygium nivale* from *H. brasiliense* by its forked leaf costa and the length of its amphigastrium costa. Although in *H. nivale* the costae are often forked in the apical part, they are essentially simple.The amphigastrium costa is variable in length. It may reach 1/2 of amphigastrium length, but it is in both types of *H. nivale* often excurrent.

Sullivant distinguished *Hypopterygium scutellatum* from *H. brasiliense* by its shorter, thicker setae and its shorter amphigastrium costae. He also remarked, that, contrary to *H. brasiliense* and *H. nivale*, *H. scutellatum* does not stain water yellow. These differences are not important as taxonomic characters.

Sullivant did not compare his species with *Hypopterygium tamarisci*, but emphasised that his and other South American species altogether differ from the New Zealand *H. tamariscinum* (Hedw.) Brid. (≡ *Canalohypopterygium tamariscinum* (Hedw.) Kruijer), because they do not posses the rudimentairy branches ('setulae') of the latter.

11. Van den Bosch & Van der Sande Lacoste (1861) indicated that Motley's material of *Hypopterygium humile* is preserved in Mitten's herbarium, which is now kept in NY. Type material of *H. humile* is absent from L. The holotype is provided with few annotations in Dutch, presumably meant as instructions for the author's illustrator A.J. Kouwels. See further 'Types collected by Motley cited in the 'Bryologica javanica', p. 27.

12. The holotype of *Hypopterygium humile* is an autoicous, fruiting plant, which closely resembles the type material of *H. tenellum* and *H. ceylanicum* and evidently belongs to the 'Asian' variant of the present species.

Van den Bosch & Van der Sande Lacoste (1861) distinguished *Hypopterygium humile* from *H. tenellum* (= *H. tamarisci*) by its smaller size, its slender habitus, its larger lateral leaves, its smaller and narrower amphigastria, its distinctly larger basal leaf cells, and its larger, cylindrical capsule having a more robust peristome. In my opinion, these features do not separate *H. humile* and *H. tenellum* at specific or infraspecific level. The differences given by Van den Bosch & Van der Sande Lacoste are based on the examination of a few specimens only. My examination of many more specimens showed that the diagnostic features given by Van den Bosch & Van der Sande Lacoste show much more variation than they were aware of, and show considerable variation in their discriminating character states.

Fleischer (1908) erroneously distinguished *Hypopterygium humile* from *H. ceylanicum* by its entire leaf margins. The degree of serration [dentation] of the leaf margin is not a reliable character to distinguish species that resemble *H. tamarisci.* This was also concluded by Akiyama (1992), who observed a high variability in serration in his plants from Seram. It should be noted, however, that Akiyama included several specimens of the 'East Malesian' variant of *H. flavolimbatum* Müll.Hal. (see '*H. flavolimbatum*', note 28, p. 187) in his concept of *H. humile.*

13. Despite the fact that the labels of the two specimens of Milne's syntype of *Hypopterygium oceanicum* are provided with the annotation "1855", it is certain that all the type material of *H. oceanicum* was collected in July, 1854, presumably even on the same day and shortly before the 24th of July of that year.

The ship "Herald" reached Raoul Island on July 2nd (McGillivray, 1855). It left the island for sailing to the Minerva Reefs and the Fiji Islands on July 24th (McGillivray, 1855; Milne, 1855). McGillivray and Milne did not mention the year in which the island was visited, but according to Hooker (1857) this took place in 1854. Milne (1855) reported that during their stay on Raoul Island he and McGillivray made an excursion towards the summit of the mountain of the island, at c. 518 m altitude (Mueller-Dombois & Fosberg, 1998), during which they collected phanerogams, lichens, liverworts, mosses, and other organisms. Among the "*Hypna*" that were collected by Milne on the summit was presumably the syntype of *Hypopterygium oceanicum.* Milne did not report the actual date of collecting, but his report suggests that the excursion took place shortly before the sailing from Raoul Island.

14. Mitten (in Hooker, 1867) described *Hypopterygium oceanicum* as monoicous, but it is defined as dioicous in Hooker's (1867) key. In both type collections of *H. oceanicum* male and female plants are intermingled. Both collections contain fruiting material.

Hooker (1867) distinguished *Hypopterygium oceanicum* from *H. viridulum* by the length and thickness of the seta, but these features are variable within the species and do not delimit taxa.

The syntypes of *Hypopterygium oceanicum* (*Milne 75, McGillivray s.n.*) are intermediates between the regional variants of *H. tamarisci* (viz. 'Asian' variant, 'Australasian' variant, 'Oceanian variant 2'). The syntypes share their dorsiventrally to laterally compressed stipe and their partially caducous branches with the 'Asian' and 'Australasian' variants. The short leaf costae, reaching between 1/3 to 1/2(–4/5) of leaf length, and the small number of axillary hairs, usually 1 per leaf, have the syntypes in common with the 'Oceanian variant 2' and 'Asian' variant. The shape of the terminal cell of the axillary hairs, elliptic to almost elongate, fits best with 'Australasian' variant. However, the fact that the terminal cell in *McGillivray s.n.* is occasionally nearly obovate suggests a link with 'Oceanian variant 2'.

The gemmaphores of *Milne 75* are branched. Those of *McGillivray s.n.* are also branched, but it could not be acertained whether or not among the short gemmaphores a few simple ones were present. The calyptra, present in Milne's collection of *Hypopterygium oceanicum*, is completely covering the operculum, which is approximately 1.3 mm long. A single operculum in this collection was shorter, 0.9 mm long, but it was strongly curved and probably aberrant. In McGillivray's collection the operculum was approximately 1.6 mm long, which links it with 'Oceanian variant 2' and 'Australasian' variant. Because of the pronounced and excurrent costa in almost every amphigastrium of their distal frond parts and their overall appearance, the syntypes of *H. oceanicum* show closest resemblance with 'Australasian' variant. Likewise, other specimens from the Kermadec Islands, match the 'Australasian' variant best.

15. Dixon (1927) assigned *Hypopterygium discolor* Mitt., *H. scottiae* Müll.Hal., and *H. viridulum* to his concept of the dubious species *H. rotulatum* (see 'Doubtful Hypopterygium species', p. 249) and changed the rank of *H. oceanicum* to a variety of this species. Dixon's concept of *H. rotulatum* corresponds with the 'Australasian' variant of *H. tamarisci.*

16. Dixon (1927) erroneously considered Mitten's type material of *Hypopterygium viridulum* to include two species: *H. novaeseelandiae* (= *H. didictyon*) and *H. rotulatum* (see 'Doubtful Hypopterygium species', p. 249), by which he meant the 'Australasian' variant of *H. tamarisci.*

17. Reichardt (1868, 1870) considered *Hypopterygium debile* a dioicous species and described the type of *H. debile* as a male plant with ecostate amphigastria. The type of *H. debile* is, in fact, monoicous, and has male and female, unisexual gametoecia. Furthermore, its amphigastria are actually costate with a faint to distinct costa, which usually reaches 1/3–1/2 of amphigastrium length.

18. The type of *Hypopterygium flaccidum* from "Pacific Islands" belongs to 'Oceanian variant 1' of *H. tamarisci.* It contains 3 gametophores and a branch fragment material of a medium-sized to large, non-fruiting female plant with rather old perichaetia. The plant is basically flabellate. Two of the gametophores are more or less intact, but one of them bears a few innovations in the distal part of the stipe. The gametophores are 4.0 to 5.0 cm tall and have a stipe that measures, respectively, 2.0 and 3.0 cm in length. The frond leaves are rather distant and large. They measure 1.7–2.0 mm in length and 0.9–1.0 mm in width for the lateral ones and 0.8–1.4 mm in length and 0.7–1.2 mm in width for the amphigastria.

19. The holotype of *Hypopterygium neocaledonicum* Besch., which is preserved in Bescherelle's herbarium (BM), lacks the name of its collector. However, because this specimen is the only specimen of *H. neocaledonicum* in Bescherelle's herbarium and seeing that all other data are in accordance with the information given by Bescherelle (1873), it is beyond any doubt that the holotype is concerned here.

20. The type of *Hypopterygium neocaledonicum* is conspecific with *H. tamarisci* and shows closest similarity with the 'Australasian' variant of this species. The type is a fruiting plant with a few sporophytes lacking a calyptra. The plant is palmate and up to 2.5 cm tall, whereby its stipe is up to 1.6 cm tall and its rachis up to 1.2 cm long. The basal part of the stipe is laterally compressed to not compressed. The plant is autoicous and gemmiferous. The amphigastria costa reaches from 1/2 of amphigastrium length to excurrent.

Like the plants from the Kermadec Islands (note 14), the New Caledonian plants including the type of *Hypopterygium neocaledonicum* can be considered intermediates between the regional variants of *H. tamarisci* (viz. 'Asian' variant, 'Australasian' variant, 'Oceanian variant 2'). The New Caledonian plants are flabellate to palmate and frequently gemmiferous. They are up to 2.3 cm tall, but are frequently much smaller. The basal third of the stipe of the New Caledonian plants is not compressed or laterally compressed. The primordia are frequently set with scaly leaves. There are 1–4 axillary hairs per leaf. The terminal cells of the axillary hairs are usually elliptic to elongate-elliptic and rarely short-elliptic. The distal part of the branches is frequently caducous. The leaf costa reaches 1/2–2/3 of the length of the leaf. The amphigastrium costa reaches 1/4–1/2 of the length of the amphigastrium, but is frequently excurrent. The gemmae are borne on branched gemmaphores.

Almost every plant on New Caledonia is monoicous, whereby unisexual gametoecia occur more frequently than bisexual ones. Paraphyses were not found. In the New Caledonian material the number of sporophytes per frond reaches up to 12. The dorsal plates of the exostome teeth are 12–17 µm thick and the ventral ones 17–22 µm thick. The calyptra of the New Caledonian material is completely covering the operculum and fleshy in the distal half.

When compared with the variants of *H. tamarisci*, the New Caledonian material matches best with the 'Australasian' variant, in particular with the plants from Queensland and northern New South Wales.

21. Bescherelle (1895) distinguished *Hypopterygium debile* from *H. tahitense* by its ovate-acuminate, ecostate amphigastria. He described the amphigastria of *H. tahitense* as orbicular-cuspi-

date and costate, having a costa that vanishes halfway the amphigastrium. Bescherelle described the amphigastria of *H. nadeaudianum* as rotundate-ovate that are moderately long cuspidate with a short costa. However, *H. debile*, *H. nadeaudianum*, and *H. tahitense* do not substantially differ in the shape of the amphigastria, the length of the amphigastrium costa, and the shape and length of the amphigastrium apex.

22. Whittier (1976) recognised *Hypopterygium arbusculosum*, *H. nadeaudianum*, *H. tahitense* as separate species, but his delimitations are based on non-discriminating characters and non-existing differences. Whittier distinguished these three species from *H. debile* by their monoicy, their costate amphigastria, and their short 'secondary stems' (i.e. stipes[1]), which he described as 1.5 cm long in *H. arbusculosum*, 1 to 2 cm long in *H. tahitense*, and (presumably) 1–3 cm long in *H. nadeaudianum*. Whittier considered *H. debile* to be dioicous with ecostate amphigastria and having a longer 'secondary stem', which reaches up to 5 cm.

Whittier based his description of *Hypopterygium debile* on Reichardt's (1868), who erroneously considered *H. debile* to be dioicous having ecostate amphigastria (see note 17). In addition, differences in stipe (and rachis) length between *H. debile*, *H. arbusculosum*, *H. nadeaudianum*, and *H. tahitense* are not substantial. The types of *H. debile* and *H. arbusculosum* are small plants, which are respectively up to 1.5(–1.7) cm and 1.5(–2.2) cm tall. Hence, they have short stipes and rachises, whereas the plants of the other two are larger and have generally longer stipes and longer rachises.

Differences in the width of the frond are basically correlated with the size of the plant, especially the length of the rachis. Hence, Whittier's attempt to separate *Hypopterygium nadeaudianum* and *H. tahitense* by differences in the width of the frond (given as up to 2.5 cm wide in *H. nadeaudianum* and up to 1.0 cm wide in *H. tahitense*, but in fact approximately 1.0 to 4.0 cm wide in the former and 0.7 to 1.5 cm wide in the latter) also fails. The type of *H. tahitense* is a medium-sized, male plant that is up to 2.6 cm tall. It is somewhat scanty material, which is almost identical to the type of *H. debile* and belongs to 'Oceanian variant 2' of *H. tamarisci*.

The type of *H. nadeaudianum* is larger. It is a medium-sized plant with 2.3 to 3.5 cm tall, flabellate gametophores. A few gametophores are damaged. The undamaged gametophores closely resemble that of *H. flaccidum*. Because of the size and the shape of the gametophores, its long, mainly distant branches and its large, distant leaves the type of *H. nadeaudianum* belongs to 'Oceanian variant 1' of *H. tamarisci*. The type of *Hypopterygium arbusculosum* is a fruiting specimen of up to 1.5(–2.2) cm tall, whose gametophore is very similar to that of the non-fruiting type of *H. debile*. Whittier (1976) distinguished *H. arbusculosum* from *H. nadeaudianum* and *H. tahitense* by the entire versus toothed leaf margin. *H. arbusculosum* has, in fact, only a few entire leaves. Most of its leaves are weakly or moderately serrate-dentate, however.

23. Hampe's (1874b) description of the new species *Hypopterygium monoicum* does not separate it adequately from *Hypopterygium tamarisci*. Hampe considered *Glaziou 7189* a mixed collection of his species *H. monoicum* and Müller's (1850) *H. incrassatolimbatum*.

Although Hampe's observation of a mixed collection might be correct, the differentiating characters given by Hampe do not separate *Hypopterygium monoicum* from *H. incrassatolimbatum*. These characters pertain to stature, the ornamentation of the stipe, the shape and colour of the frond, the shape and colour of the perichaetial leaves, and the length of the operculum. The long neck of the capsules of *H. monoicum*, as described by Hampe, is probably an effect that is caused by the young age of the capsules.

Hampe's most substantial difference between *Hypopterygium monoicum* and *H. incrassatolimbatum*, whereby he considered the former a monoicous species and the latter a dioicious one, does not separate these two from *H. tamarisci*, because of variability (see 'Variation', p. 219).

24. Ångström (1876) distinguished his new species *Hypopterygium macrorhynchum* from *H. serrulatum* Lindb. in Ångstr., nom. nud., and hence probably also from *H. sylvaticum* Mitt., by its smaller size and the dense, complanate foliation with shorter and wider leaves. The type is,

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1) It is not clear whether or not in Whittier's terminology the rachis is included in the 'secondary stem'.

indeed, a small plant, which has very small to small capsules. The capsules are subglobose to barrel-shaped and vary in size from 0.6 mm long and 0.6 mm wide to 1.3 mm long and 1.0 mm wide. There is no doubt, that this plant belongs to *H. tamarisci.*

In the type material only two opercula could be found. In contrast with the epithet of the species name, they are short-rostrate. However, Ångström may have observed opercula with a much longer rostrum, because the rostrum of at least one of the two opercula was damaged and he described the apex of the opercula as fragile.

25. The lectotype of *Hypopterygium viridissimum* Müll.Hal. shows only minor differences with *H. laricinum.* The border of frond leaves is entirely distinct in *Hypopterygium viridissimum,* whereas it is faint at the anterior of lateral leaves and entirely faint in amphigastria in *H. laricinum.* In addition, in *H. viridissimum* the leaves are less pronounced serrate-dentate than in *H. laricinum.*

26. According to Müller (1876: 256), he examined authentic material from Van den Bosch & Van der Sande Lacoste (1861: t. 142) – or their predecessors. This could not be verified, because Müller's herbarium, which was kept in B, has been destroyed during World War II.

Among the remaining specimens of the type material that were preserved in other herbaria, the specimen in BM is the only specimen that is presented as '*Hypopterygium pygmaeum* C. Müll. n. sp.'. It is almost certain that it was collected by Wiltens near Padang.

27. Kindberg (1901) and Fleischer (1908) apparently followed Müller's (1876) misinterpretation of Van den Bosch & Van der Sande Lacoste's (1861) *Hypopterygium tenellum* Müll.Hal. as a misidentification of *H. ceylanicum.*

28. The habitus and detailed illustrations of *Hypopterygium tenellum* made by Kouwels in Van den Bosch & Van der Sande Lacoste's (1861: t. 142) Bryologia Javanica 2 are probably drawn after material selected by Van der Sande Lacoste from both Junghuhn's and Wiltens' specimens (preserved in Van der Sande Lacoste's herbarium, L). For none of the illustrations, however, the original material that was used by Kouwels could be found with certainty. The habitus illustrations are probably based on Wiltens' material, because of the size of his plants. Although Van den Bosch & Van der Sande Lacoste (1861: t. 142) depicted fruiting material in a few illustrations, in none of the four specimens of Junghuhn and Wiltens in L a sporophyte was found. In the icones collection of L sketchy outlines for Bryologia Javanica 2 are preserved that are made after parts of Junghuhn's and Wiltens' collection. Outlines of leaves have been drawn after Wiltens' material. Outlines of leaves, areolation of leaf parts, a distal part of a branch (not as such depicted in the Bryologia Javanica), and archegonia have been drawn after Junghuhn's material (as *H. medinense*).

Archegonia are depicted in a few of Van den Bosch & Van der Sande Lacoste's (1861: t. 142) illustrations of *Hypopterygium tenellum,* but it is uncertain whether all are based on Junghuhn's material. It is, nevertheless, almost certain that one of the detailed illustrations, which depicts two antheridia, is based on Wilten's material, because only in this material male and synoicious gametoecia were found.

29. The description of *Hypopterygium argentinicum* Müll.Hal. in Bescherelle (1877) is very similar to that of Mitten's (1869) *H. sylvaticum.* The main difference is the length of the amphigastrium costa, which Müller described in *H. argentinicum* as being often obsolete in the distal half of the amphigastrium to excurrent. Mitten defined the amphigastrium costa of *H. sylvaticum* as excurrent.

Actually, the length of the amphigastrium costa of *Hypopterygium sylvaticum* varies between 2/3 of amphigastrium length to excurrent, whereas in most amphigastria of *H. argentinicum* the costa is excurrent. The difference in costa length is certainly not substantial. In other respects, the types of *H. argentinicum* and *H. sylvaticum* are very similar.

Because of the long terminal cells of the paraphyses, which are 50 to 70 µm long (and perhaps longer) and the small, urceolate to short barrel shaped capsules, it is beyond doubt that *Hypopterygium argentinicum* is conspecific with *H. tamarisci.* The paraphyses of the isotype of *H. sylvaticum* could not be observed, because it would have damaged the scarce material in S.

30. Bescherelle (1880) based *Hypopterygium torulosum* on material from Réunion, Mauritius, and Madagascar. Bescherelle considered part of Bridel's (1827) *H. tamariscinum* (Hedw.) Brid. conspecific with his new species, whereby he probably had Bridel's records from Réunion and

Mauritius in mind. Bescherelle did not include the type of *H. tamariscinum* in his concept of *H. torulosum*.

31. When Bescherelle (1880) described *Hypopterygium torulosum*, he referred to a name used by Schimper in "Musc. Boryanis". However, I did not find an earlier use of the name *H. torulosum* in publications or exsiccata series than the one published by Bescherelle, and do not know whether they exist.

32. Bescherelle (1880) compared *Hypopterygium torulosum* from Réunion with *H. mauritianum* from Mauritius. He described the leaves of *H. torulosum* as serrate in the distal half and the amphigastrium costa as thick and long excurrent. He set *H. mauritianum* against *H. torulosum* by its smaller stature, its hardly denticulate leaves and its often faint amphigastrium costa that vanishes above the middle of the amphigastrium. In addition, he described *H. mauritianum* as a dioicous species, and *H. torulosum* as a monoicous one.

Bescherelle's differences are not substantial and do not justify the recognition of separate taxa on Réunion and Mauritius. His material of *H. torulosum* and that of *H. mauritianum* belong both to 'African' variant of *H. tamarisci*. In the latter, the degree of dentation in the leaves and amphigastria and the length of the amphigastrium costae are very variable. As said before, monoicy or dioicy is not a differentiating feature. Bescherelle's plants from Mauritius are just smaller than the ones he had obtained from Réunion.

33. Bescherelle (1880) separated *Hypopterygium torulosum* var. *nossibeanum* from his concept of the species by its smaller and more slender stipe, the more serrate leaves, and the broadly ovate amphigastria with a costa often vanishing in the acumen. The species was described with a stipe of 3–5 cm long and rounded amphigastria with a thick, and long excurrent costa.

Bescherelle (1880) apparently included the rachis in his definition of the stipe, because he described the 'stipe' of the variety as branched and that of the species as dendroid. These descriptions do not exclude each other, and it is not clear which difference between the stipes of the variety and the species Bescherelle actually had in mind. Bescherelle's (1880) other reported differences are not substantial. The degree of dentation in the leaves and amphigastria and the length of the amphigastrium costae are very variable in the 'African' variant of *Hypopterygium tamarisci*, whereto Bescherelle's variety evidently belongs. The type of the variety is a non-fruiting, autoicous plant up to 2.1 cm tall with ovate amphigastria, which, in contrast to Bescherelle's (1880) judgement, has an excurrent costa. The type is smaller than the plants from the East African islands which Bescherelle identified as *H. torulosum*.

34. Bescherelle (1880) clearly based *Hypopterygium mauritianum* on material from Mauritius. Although Bescherelle considered part of *H. laricinum* (W. Hook.) Brid. sensu Müller (1850) conspecific with his new species, he did not include the type of *H. laricinum* from the Cape of Good Hope or any other South African material in his concept of this new species.

Sim (1926), apparently following Bescherelle, considered *Hypopterygium mauritianum* and *H. laricinum* separate species and remarked that Bridel (1827) and Müller (1850) included *H. mauritianum* in their descriptions of *H. laricinum*. He distinguished *H. mauritianum* from *H. laricinum* by leaf border width, defined as only 1 cell wide in the former species and 2 or 3 cells wide in the latter, and the length of the amphigastrium costa, defined as almost absent in *H. mauritianum* and reaching at least halfway the amphigastrium in *H. laricinum*.

However, in Mauritian plants, border width of the lateral leaves varies between 1 and 3 cells wide and the length of the amphigastrium costa varies between 1/3 of amphigastrium length to excurrent. This variation may even occur within a single specimen. Hence, the differences given by Sim, if based on correct observations, are not substantial and do not justify the separation of any Mauritian, or even Mascarenian, taxon from *H. laricinum*, and the 'African' variant of *H. tamarisci*.

35. Bescherelle (1880) described *H. mauritianum* var. *nanum* with a short stipe and minor leaves. This variety is a very small plant that belongs to the 'African' variant of *H. tamarisci*.

36. When he treated *Hypopterygium falcatum*, Müller (1886) referred to Mitten's (1864) record of *H. laricinum* from Bioko ("Fernando Poo") and São Tomé. Müller remarked that the latter had been described as monoicous, but he did not make it clear whether he considered Mitten's material from the West African Islands as misidentified specimens of his *H. falcatum* or not. It is unlikely, that Müller had actually examined Mitten's material, because he did not cite any of Mitten's specimens.

37. Müller (1886) considered his West African species *Hypopterygium falcatum* distinct from *H. laricinum* because of the smaller and more slender stature of the former. These differences are not substantial and represent variation within a single species. In fact, here they even represent variability within a single patch of moss. Müller's species belongs to the 'African' variant of *H. tamarisci*. The type material that Müller had at his disposal contained probably only small plants – just like the lectotype –, while the isotype in S consists of slightly to much larger plants, which are even up to 3.0 cm tall.

38. Renauld (1889) compared his new species *Hypopterygium sphaerocarpum* from Mauritius with Bescherelle's (1880) *H. mauritianum* from Mauritius and *H. torulosum* from Réunion, Mauritius, and Madagascar. Renauld justified the separation of his new species by a combination of features, i.e. the size of the plant and its sexuality. He described his plants of *H. sphaerocarpum* as monoicous with about the same stature as the dioicous *H. mauritianum*. Compared with the monoicous *H. torulosum*, his plants are much smaller with smaller and usually globose capsules. *Hypopterygium sphaerocarpum* is just another representative of *H. tamarisci* from the East African islands. The type material of *H. sphaerocarpum* consists of small to medium-sized plants up to 1.8 cm tall. The material is autoicous. Renauld reported that by way of exception he found a bisexual gametoecium, but I did not find it. The type material contained immature capsules.

Renauld distinguished *H. tenellum* from Sri Lanka from his new species by its smaller leaves having a thick, continuous, yellowish border. The differences are not substantial.

39. The types of *H. brevifolium* and *H. usambaricum* are just small plants of the 'African' variant of *H. tamarisci*.

40. In his enumeration of Japanese bryophytes, Mitten (1891) newly described *Hypopterygium sinicum* as a species from Hong Kong. He compared his new species briefly with *H. japonicum* Mitt. (= *H. flavolimbatum*), which was at that time the only *Hypopterygium* species that was known from Japan and E Asian mainland. However, Mitten did not compare his new species with other *Hypopterygia*, viz. *H. tenellum*, *H. ceylanicum*, *H. humile*, and *H. pygmaeum*, known from British India, Ceylon, and the Dutch East Indies.

The holotype of *Hypopterygium sinicum* is a typical East Asian plant that belongs to the 'Asian' variant of *H. tamarisci*. The holotype is a non-fruiting, female plant up to 1.8 cm tall with an entirely tristichous phyllotaxis. The amphigastrium costa is distinct, and reaches from a third of the amphigastrium to the apex.

41. Renauld & Cardot (in Renauld, 1891) distinguished *Hypopterygium subhumile* from *H. torulosum* and *H. mauritianum* from the Mascarenes by its entire leaf margins. However, the degree of dentation of the leaf is not a differentiating character and do not justify the recognition of *H. subhumile* as a separate from *H. tamarisci*. They considered their new species closely related with *H. humile* from Java, but distinguished their species by its dense areolation in the basal part of the branch leaves and its relatively large, suborbicular amphigastria having a ('ob')cordate base and a long, cuspidate apex. These differences are not substantial and do not separate *H. subhumile* from *H. humile*.

Renauld & Cardot (1893), followed by Renauld (1897), considered *Hypopterygium subhumile* very closely related to *H. tenellum*. They compared the former with Müller's (1876) description of *H. viridissimum*, which they also considered to be very closely related to *H. tenellum*. They concluded that Müller's features do partly not apply to their *H. subhumile* and remarked, that the differences between *H. subhumile* and *H. viridissimum* are trivial and may signify differences between regional races. Nevertheless, they maintained *H. subhumile* as a separate species.

Cardot (in Renauld & Cardot, 1915) distinguished *H. subhumile* from *H. tenellum* and *H. humile*, because of its dioicy. Cardot considered the latter two (and *H. ceylanicum*, which he proposed in the synonymy of *H. tenellum*) as monoicous. In addition, he distinguished *H. subhumile* from *H. tenellum* because of its much smaller stature and amphigastria and from *H. humile* because of its entire leaves.

42. Brotherus (1894) considered *Hypopterygium torulosum* var. *kameruniae* a West African variety of *H. torulosum* with shorter setae and small capsules. Kindberg (1901) reduced the variety with the species, which, subsequently, was treated as a subspecies of the South American *H. sylvaticum*. Obviously, Brotherus and Kindberg considered the variety very similar to African material

that had been identified as *H. torulosum*. Because seta length and capsule size show great variability in *H. tamarisci* in its present circumscription, it is safe to assume that the variety is also conspecific with the latter.

43. Bescherelle (1894) separated his new species *Hypopterygium lehmannii* from *Hypopterygium sylvaticum* Mitt. by its larger, double sized and suborbicular leaves, its stronger serrate branch leaves, whereby the serrations are especially pronounced near the leaf apices, and the orbicular amphigastria having a percurrent costa. He distinguished *H. lehmannii* from *H. tamarisci* by the monoicy and the orbiculate shape of the amphigastria of the former, but such differences do not exist. *H. tamarisci* is predominantly monoicous and the shape of the amphigastria vary from transverse ovate to short-elliptic or ovate. Swartz described *H. tamarisci* (as *Hypnum tamarisci*) as monoicous and the shape of its amphigastria as suborbicular, being cordate at base (Swartz, 1788, 1806). Müller (1850), however, described *H. tamarisci* as dioicous with ovate amphigastria. Hence, it becomes clear that Bescherelle's understanding of this species has been based on Müller's erroneous description.

The type material of *Hypopterygium lehmannii* that I had at my disposal is sterile and has ovate amphigastria. The amphigastrium costa varies in length, and may be as short as 1/3 of the length of the amphigastria, but is often longer and can be excurrent. The type material is a medium-sized plant and there are no features that distinguish it from *Hypopterygium tamarisci*.

44. Bescherelle (1895) erroneously described the calyptra of *Hypopterygium nadeaudianum* as mitriform. His observation is based on a calyptra that is attached to an immature sporophyte.

45. The type specimen of *Hypopterygium squarrulosum* in S contains a small, young gametophore and a frond fragment of a sterile plant. Müller (1897) distinguished *H. squarrulosum* from his other newly described species *H. rotundostipulatum* – which is also conspecific with *H. tamarisci* (see note 60) – by, to my opinion, non-differentiating characters like a longer stipe, a flabellate habit with more closely set, shorter, subsecund branches, and a less complanate foliation and perfect symmetrical leaves.

The flabellate habit of *H. squarrulosum* reminded Müller (1850) of *Hypopterygium pallens* (Hook.f. & Wilson) Mitt. (= *Lopidium concinnum* (W. Hook.) Wilson) from Brazil, with which it has, for the rest, little in common.

46. Kindberg (1901) included the South American *Hypopterygium squarrulosum*, *H. semiglobosum*, and *H. tenuisetum* in the synonymy of the *H. sphaerocarpum* from Mauritius. He distinguished *H. sphaerocarpum* from *H. tamarisci* by its globose or subglobose capsules and its darker and greener laminal leaf cells. These characters, however, do not separate Kindberg's South American material of *H. sphaerocarpum* from *H. tamarisci*.

Except for material from São Tomé, I did not find globose or subglobose capsules in the African and Mascarenian material. Kindberg's description of the capsule shape of *Hypopterygium sphaerocarpum* is not based on his Mauritian material (*Robillard s.n.*, S), because it is a non-fruiting specimen. It may be based on the South American material that he identified as *H. sphaerocarpum* or Renauld's (1889) description of *H. sphaerocarpum*. Renauld's material, however, contains only immature capsules (*Robillard s.n.*, PC).

47. The present species has been several times accidently introduced in glasshouses of European botanic and private gardens in the second half of the nineteenth century and the first decades of the twentieth century. Several of these introduced mosses have been described as new taxa (*Hypopterygium bouvetii*, *H. rigidulum* subsp. *balantii*, *H. immigrans*, *H. atrotheca*). Most introduced plants belong to the 'Australasian' variant of *H. tamarisci*. The species was also introduced in the Bussaco Forest Arboretum in Portugal (Allorge, 1974), which is the only locality known in Europe where the species grows outdoors.

The history, 'true' origin, and relationships of the plants that were introduced in the Bussaco Forest, private glasshouses in Monkstown and Angers, and the botanic gardens of Berlin, Glasgow, and some other European cities are discussed by Kruijer (1997b). Additions to Kruijer's list of specimens are given in note 79.

48. Brotherus (1901, 1907) erroneously described *Hypopterygium kaernbachii* as dioicous, where it is, in fact, heteroicous. He corrected this in 1925 (Brotherus, 1925).

Because of its assumed dioicy, Brotherus (1901) compared *Hypopterygium kaernbachii* with a the dioicous species *H. chamaedrys* (= *H. vriesei*) and overlooked that *H. kaernbachii* shows a closer resemblance with e.g. *H. tenellum* and *H. humile*. The latter were described by Van der Bosch & Van der Sande Lacoste (1861) as monoicous and were already known for the Malaysian Archipelago.

The type of *Hypopterygium kaernbachii* is a non-fruiting plant that belongs to the 'Asian' variant of *H. tamarisci*. The plant does not exceed 2.0 cm height. The stipe is up to 0.7 cm and the rachis up to 1.4 cm long. The stipe is entirely dorsiventrally compressed or laterally compressed in the basal third. The costa reaches 1/2–2/3 of leaf length in the lower part of the frond and 2/3 in the distal part. The amphigastrium costa reaches 1/3–1/2 of amphigastrium length in the lower part of the frond and is occasionally excurrent in the distal part. A single, damaged shoot in the isotype preserved in S is gemmiferous, but the holotype is not so.

49. Kindberg (1901) classified *Hypopterygium levieri* in *Hypopterygium* Brid. sect. *Aristifolia* Kindb. and, hence, compared this species with *H. aristatum* Bosch & Sande Lac. (= *H. flavolimbatum*). He overlooked the close affinity of *H. levieri* with *H. ceylanicum* and *H. tenellum* – with which it is evidently conspecific – because he classified the latter two in *Hypopterygium* sect. *Tamariscina* Kindb. in separate subsections.

The type of *Hypopterygium levieri* Kindb. is a small to medium-sized, pinnate to palmate plant that belongs to the 'Asian' variant of *H. tamarisci*. It is up to 2.6 cm tall. It is monoicous, having unisexual gametoecia and probably a few fertilized bisexual ones.

50. The holotype of *Hypopterygium jungermannioides* Müll.Hal. ex Kindb. consists of sterile scrap of a loosely branched frond of a plant that belongs to *H. tamarisci*. There is no evidence that *H. jungermannioides* is based on the earlier described *Pterygophyllum jungermannioides*, which was presumably erroneously given by Bridel (1827) in the synonymy of *H. tamariscinum* (≡ *Canalohypopterygium tamariscinum*; but see for *P. jungermannioides* in 'Doubtful Hypopterygium species', p. 249).

Beccari visited Ternate four times, in 1873, 1874, 1875, and 1876 (Martelli, 1921). The holotype of *Hypopterygium jungermannioides* was collected during Beccari's fourth visit to Ternate. The material of Beccari's second visit (*Beccari s.n., 121*) was collected from the old crater of Ternate in November 1874 (see also Martelli, 1921). The fronds of the plants in this material closely resemble that of the holotype of *H. jungermannioides*, but the plants are complete and better conserved. The plants belong the present species. They are up to 2.2. cm tall and are weakly to distinctly palmate. The stipes and rachises have an entire tristichous phyllotaxis and are entirely dorsiventrally compressed. Three specimens are fruiting plants bearing a few sporophytes. The two specimens of *Beccari 121* are presented with Müller's herbarium name.

51. The holotype of *Hypopterygium scottiae* subsp. *denticulatum* is a small, fruiting plant that is rather similar to the type material of *H. muelleri* and *H. viridulum*. The plant is autoicous and has percurrent amphigastrium costae, by which it is intermediate between the two variants of *H. tamarisci* that occur in Australia. The plant shows closest affinity to the 'Australasian' variant.

52. The type of *Hypopterygium bolivianum* is a medium-sized, fruiting plant with a single sporophyte that certainly belongs to *H. tamarisci*. The capsule is intermediate in size and shape between typical small capsules and typical large ones. It is c. 1.3 mm long and 0.9 mm wide at most, but consists of a long neck that has about the same length as the subglobose urn.

Herzog (1910) classified his new species in *Hypopterygium* Brid. sect. *Tamariscina* Kindb., but he did not compare his species with a South American representative of this section or any other Hypopterygiaceae.

53. Enroth (1993) compared *Hypopterygium mildbraedii* with *H. torulosum* and *H. torulosum* var. *kameruniae*. He judged their differences as not very convincing, but described the former by having slightly narrower amphigastria with shorter acumina than present in the latter two.

Hypopterygium mildbraedii is conspecific with *H. tamarisci*. The differentiating character states that were given by Brotherus (1910) to distinguish *H. mildbraedii* from *H. laricinum* do not separate them as different species. Brotherus' extended description of *H. mildbraedii* included a large, autoicous plant that is very similar to the 'African' variant of *H. tamarisci*.

54. The type of *Hypopterygium bowiei* is a medium-sized plant that is up to 3.2 cm tall and has a rachis up to 1.7 cm long. Its frond leaves are weakly to moderately serrate-dentate. The amphigastrium costa is distinct and reaches at least 1/2 of amphigastrium length and is frequently excurrent. The type matches best the 'Oceanian variant 1' of *H. tamarisci*, although its branches and leaves are less distant than usual in this form.

Brotherus & Watts (1915) separated *Hypopterygium bowiei* from *H. tahitense* by its dense pinnate ramification, but they overlooked the fact that the type of *H. tahitense* is a little scanty. *H. bowiei* is actually flabellate to (bi)pinnate or weakly palmate.

Brotherus & Watts erroneously considered the type of *Hypopterygium bowiei* a male plant, and described *H. bowiei* as dioicous. It is, in fact, monoicous. The type is set with numerous unisexual gametoecia. Most stems are either male or female, but a few stems have both male and female gametoecia.

55. Bridel's (1812) description is not accurately decisive for the actual identity of *Hypnum frondiferum*. The name is not used in Bridel's (1819, 1827) later publications.

Bridel (1812) included *Hypnum frondiferum* in the synonymy of *Hypnum flabelliforme*. The latter is best assigned to *Canalohypopterygium tamariscinum* (Kruijer, 1996a). However, because Bridel did not report rudimentary branches – a pronounced feature of *C. tamariscinum* – for *Hypnum frondiferum* and mentioned Réunion ("ex Insulâ Borboniâ") as its origin, it is safe to assume that *Hypnum frondiferum* is conspecific with *Hypopterygium tamarisci*.

56. Breutel's original material of *Hypopterygium capense*, which is distributed in the exsiccata series 'Musci Capenses', is undated and lacks a collector and exsiccata number. According to Sayre (1975), Breutel's South African mosses were collected 1853–54 and offered for sale by Hohenacker in 1859 as 'Musci Frondosi Africae Australis' with the numbers 47–100. Sayre's view that this exsiccata series is identical with 'Musci Capenses' is probably correct. Breutel's *Hypopterygia* are either presented as specimens of 'Musci Capenses' or are not presented as specimens of an exsiccata series. Apart from Hohenacker's advertisement, I found no other offers on Breutels' South African mosses. I did not find specimens that are presented as specimens of Hohenacker's exsiccata series 'Musci Frondosi Africae Australis'.

57. The type material of *Hypopterygium argentinicum* Lorentz ex Müll.Hal. from Cuesta de Santa Rosa, Argentina, consists of green to dark green, palmate, fruiting plants. The lectotype contains a single sporophyte with a small, damaged capsule. It also contains one detached sporophyte with a small, intact, urceolate capsule, c. 0.8 mm long and 0.4 mm wide. A specimen in Dusén's herbarium (S) contains more sporophytes. The size of its capsules varies between 0.8–1.5 mm long and 0.7–1.3 mm wide, whereby the shape of the capsules varies between subglobose to barrel shaped. The other syntypes kept in S contain few material, only one of them is a fruiting specimen and bears a single sporophyte with a barrel shaped capsule, c. 1.4 mm long and 1.0 mm wide. The number of gametoecia in the lectotype (S, hb. Möller) was actually too few for a reliable examination of the presence of paraphyses. Only a single perigonium could adequately be studied. In Dusén's material (S), 3–9-celled paraphyses were with certainty observed in a fertilised archegonium. The size of the terminal cells of these paraphyses range from 24–96 μm long and 19–24 μm wide. Lorentz' material showed no substantial differences with the 'New World' variant of *H. tamarisci*.

58. I found a single specimen that was collected by Lorentz in Siambon, Argentina. It is preserved in S under the name *Hypopterygium argentinicum* Lorentz ex Müll.Hal. ['Lor.'], but it is not a syntype of the latter, because it was collected in March of an unknown year in the 1870s. Müller's (1879) syntype of *H. argentinicum* from Siambon was collected in January, 1874. The specimen of March has probably not been mislabelled. Although Müller (1879) did not report this specimen in his treatment of *H. argentinicum*, it is certain that Lorentz collected mosses in 1872 and 1873 in March in or near Siambon according to the data that was given by Müller for other mosses.

59. I found a single specimen under the name *Hypopterygium longirostrum* (BM), but this specimen was collected by Darnty on Mauritius and cannot represent the original material of *Hypopterygium longirostrum* Schimp. ex C.H. Wright. Potentially original material was found in Bescherelle's herbarium (BM), where a non-fruiting specimen, collected by Pervillé on Madagascar, is preserved under the names of *Hypopterygium nossibeanum* and *H. laricinum*. It is labelled as "*805* ex parte". A fruiting specimen from Madagascar (in L, ex PC) under the name of *H. torulosum* may also represent original material, but its label lacks a collector's name.

60. In my opinion, Müller's (1850) diagnosis of *Hypopterygium rotundostipulatum* does not justify its separation from *H. tamarisci*. He indicated the strongly asymmetrical shape of the lateral leaves to be responsible for parting his new species from the other American ones, but the leaves of the syntypes of *H. rotundostipulatum* are actually not exceptionally asymmetric. Besides, such a feature is not a differentiating character within the Hypopterygiaceae. The type material of *H. rotundostipulatum* contains small to medium-sized plants. *Balansa, PP 3628a* is up to 2.0 cm tall and generally smaller and somewhat less robust than *Balansa, PP 3629*, which is up to 3.0 cm tall. Both are fruiting specimens with small to large capsules. The syntype in S, lacking a distribution number, is also a fruiting with small capsules. The syntype *Balansa, PP 1246* (PC) is an isotype of *H. argentinicum* Müll.Hal. in Besch. It is a small to medium-sized, fruiting plant. The gametophores are up to 2.0 cm tall, but are somewhat less robust than those of *Balansa, PP 3628a.*

Description — 61. Sim (1926) remarked, that the calyptra is sometimes placed sideways on the operculum. The relative orientation of the calyptra proves to vary from normal, that is with a downwards orientation of the slit of calyptra, to upside down, i.e. with an upwards orientation of the slit of the calyptra.

62. Ramsay's (1967a) chromosome study was based on material of *Hypopterygium tamarisci* from Mt Wilson, New South Wales, collected at c. 1070 m. altitude. She presented her material under the name *H. rotulatum* (Hedw.) Brid. (a dubious name, see 'Doubtful Hypopterygium species', p. 249).

Except for the size of the laminal cells of the lateral leaves and amphigastria, Ramsay's morphological data of her voucher material (1967a: t. 2) agree well with those of the present revision of *Hypopterygium tamarisci*. The size of the laminal cells are puzzling, and almost certainly incorrect. The correct figures are given in Table 5.

The width of the amphigastrium cells in the haploid voucher *Ramsay 8/64* is significantly different from those of the other haploid voucher (*Ramsay 36/65*) and the diploid and tetraploid vouchers (Student t-test, $p < 0.05\%$). Other significant differences in cell size between vouchers and chromosomal races were not found.

Among the chromosomal races substantial differences in size of the plant were not observed. Most plants are up to 2.5 cm tall, whereby those in voucher *Ramsay 22/64* (chromosome number: n = c. 27) are smallest and 1.5 cm tall at most, and those in *Ramsay 33b/64* (n = 18) and *Ramsay 8b/64* (n = 36) are tallest and reach up to, respectively, 2.9 and 3.6 cm. No substantial differences were observed in shape of the plant, leaf size and costa length, although amphigastrium costae shorter than 2/3 of amphigastrium length were only found in polyploid vouchers.

The few gemmiferous plants were only found among the polyploids. The plant of voucher no. *Ramsay 16/64* (chromosome number: n = 36) contains a few branches with numerous gemmae. The plants of vouchers no. *Ramsay 33a/64* (n = 18) and *Ramsay 8d/64* (n = c. 27) bear a few branches scarcely set with gemmaphores.

Ramsay's haploid and polyploid plants do not correspond perfectly with the two variants of the present species in Australia, but her haploid plants resemble the 'Australian' variant and her polyploid ones resemble the 'Australasian' variant to a great extent. Ramsay's haploid plants are pinnate to palmate, dioicous and not gemmiferous. The amphigastrium costa reaches 2/3 of amphigastrium

Table 5. The size of the laminal cells of the leaves and amphigastria of the vouchers given by Ramsay (1967a, t. 2) and her voucher no. *36/65*. Data obtained after re-examination of the voucher material for the present study.

voucher (chromosome numbers given between brackets)	mean sizes of laminal cells of lateral leaves (in µm; length × width)	mean sizes of laminal cells of amphigastria (in µm; length × width)
Ramsay 8/64 (n = 9)	25.8(± 6.8) × 12.8(± 1.8)	27.0(± 6.1) × 12.4(± 1.3)
Ramsay 36/65 (n = 9)	27.3(± 8.4) × 14.9(± 4.6)	29.3(± 7.3) × 16.7(± 2.2)
Ramsay 33/64 (n = 18)	30.4(± 5.0) × 17.3(± 5.5)	29.8(± 10.0) × 15.9(± 1.9)
Ramsay 22/64 (n = c. 27)	32.4(± 4.4) × 13.9(± 1.8)	31.5(± 5.2) × 14.7(± 2.3)
Ramsay 8f/64 (n = 36)	25.8(± 7.1) × 15.0(± 2.3)	29.1(± 8.5) × 16.3(± 2.4)

length to excurrent. Ramsay's polyploid plants are monoicous, generally palmate or umbellate and occasionally pinnate or flabellate. Few of them are gemmiferous. The amphigastrium costa reaches 1/2 of amphigastrium length to excurrent.

Reproduction — 63. There were 934 fruiting specimens among the specimens examined (44%, n = 2123; specimens from botanic gardens were omitted). Regional differences in fertility were observed:

a) New World: the material contained 222 fruiting specimens (c. 65%, n = 341). The majority of the specimens from SE Brazil and adjacent areas (c. 76%, n = 160) was in fruit. In the Caribbean material a minority of the specimens was in fruit (c. 45%, n = 56). Intermediate percentages were found for the Central and NE Andean Ranges (c. 59%, n = 92) and Central America (63%, n = 30).

b) Africa: the material contained 118 fruiting specimens (c. 36%, n = 335). Fruiting specimens are less common in South Africa (c. 29%, n = 23) than in the other parts of Africa and the African islands (c. 39%, n = 312).

c) Asia: the material contained 226 fruiting specimens (c. 44%, n = 520). The percentages of fruiting specimens vary between c. 29% for Sumatra (n = 28) and New Guinea (n = 38) to 61% for Sri Lanka (n = 44). Low frequencies were obtained for India and Nepal (36%, n = 100), Taiwan and China (35%, n = 26), and Japan (31%, n = 48). High percentages were found for Java (50%, n = 131) and continental SE Asia (c. 51%, n = 59). For the other areas, the percentages of fruiting specimens are not reliable because of the low numbers of specimens collected there.

d) Australasia: the material contained 361 fruiting specimens (c. 46%, n = 773). The highest percentage of fruiting specimens was found on New Zealand (c. 70%, n = 135), in particular North Island (c. 77%, n = 82), followed by New Caledonia (c. 68%, n = 37), the Kermadec Islands, and Lord Howe Island (both 54%, respectively n = 14 and n = 28). Low percentages were found for Australia (c. 40%, n = 478), and Norfolk Island (c. 39%, n = 89). In Australian material, the highest percentage fruiting specimens was obtained for New South Wales and the Australian Capital Territory (c. 45%, n = 276). The percentages for Queensland, Victoria are lower (respectively c. 35%, n = 100, and 33%, n = 72). The lowest percentage was obtained for the Tasmanian material (c. 18%, n = 17), but this percentage might be biased by the low number of specimens collected. The Australian figures are only partly affected by the sympatric occurrence of two variants with different sexuality and differences in abundancy. The dioicous 'Australian' variant is less often found in fruit (34%, n = 32) than the monoicous 'Australasian' variant (48%, n = 104). The 'Australian' variant is most common in SE New South Wales and Victoria, where it is equally abundant as the 'Australasian' one. The latter is predominant in Queensland and NE New South Wales. These differences in abundancy may explain the low percentages of fruiting specimens for Victoria and Tasmania and the high percentage found for New South Wales. The low percentage of fruiting specimens obtained for Queensland is probably caused by ecological factors.

e) Oceania: the material contained 49 fruiting specimens (c. 30%, n = 165). They came in majority from Fiji and Society Islands. The Fijian material came in majority from Viti Levu and contained 22 fruiting specimens (c. 48%). The material from the Society Islands came in majority from Tahiti, where all 22 fruiting specimens came from (c. 43%). A few fruiting specimens came from Vanuatu (3 specimens; c. 43%) and Western Samoa (2 specimens, c. 14%). Fertility differences between the two 'Oceanian' variants were not observed.

Fertility showed a correlation with altitudinal distribution in tropical Asia. Highest percentages of fruiting specimens were obtained for Asian specimens collected between 1000 and 1500 m (35%, n = 133) and between 1500 and 2000 m altitude (35%, n = 106). Between 500 and 1000 m altitude 9% of the specimens were found in fruit (n = 32), whereas between 2000 and 2500 m 25% of the specimens were found in fruit (n = 20). A correlation between fertility and altitudinal distribution could not be found in material from temperate Asia, for Chinese and Taiwanese specimens lack sufficient ecological information. Ecological data provided with Japanese fruiting material is only slightly better. All Japanese specimens were found below (or at) 500 m altitude and it seems that in Japan fruiting specimens are restricted to lower altitudes (below 130 m).

64. In variants with heteroicous sexuality, monoicy predominates. The proportion monoicous plants among fertile plants varies between 80% (Queensland, NE New South Wales, Melanesia, Polynesia) to 88% (Lord Howe Island, New Zealand). The other specimens are usually female.

The percentage monoicous plants from Norfolk Island is rather low (c. 25%). Dioicous plants of the 'Australasian' variant grow less often epiphytically than monoicous plants, and show preference for growing on rocks.

In the 'New World' variant, plants with bisexual gametoecia are rare. In the 'African' variant, plants with bisexual gametoecia are common (c. 34%), but even in plants with a few bisexual gametoecia the unisexual ones usually predominate.

In the 'Asian' variant, the majority of the monoicous specimens posses at least one, but often more, bisexual gametoecia. Bisexual gametoecia were less frequently found in the material from continental South East Asia than in material from the other parts of the distribution area.

In the 'Australasian' and 'Oceanian' variants gametophores bearing bisexual gametoecia are common, but occur less frequently than in the 'Asian' variant. In the 'Oceanian' variants gametophores bearing only unisexual gametoecia occur almost equally frequently as ones having at least a single bisexual gametoecium. In the 'Australasian' variant gametophores bearing only unisexual gametoecia predominate.

65. Plants of the 'New World' variant are rarely gemmiferous. Gemmiferous plants of the 'Asian' variant occur more commonly (c. 24%, n = 157). In both variants, gemmiferous plants are usually old or damaged. In Asia, the percentages of gemmiferous plants are somewhat higher in tropical areas (19–45%, n = 125) than in temperate areas (11–15%, n = 32). In the 'Australasian' variant, c. 53% (n = 66) of the plants from Queensland and NE New South Wales are gemmiferous, against 24% (n = 55) of those from SE New South Wales, ACT, Victoria, and Tasmania. There is no substantial difference in the percentage of gemmiferous plants between monoicous and dioicous plants from Queensland and NE New South Wales. In the material of the 'Australasian' variant from SE New South Wales, ACT, Victoria, and Tasmania c. 45% (n = 20) monoicous specimens are gemmiferous, against c. 9% (n = 24) dioicous ones. Almost all plants from Lord Howe Island are gemmiferous. The majority of the plants from Norfolk Island is gemmiferous (75%, n = 36). In New Zealand only c. 12% (n = 17) of the plants are gemmiferous. No substantial differences in the percentage gemmiferous plants were found here between monoicous and dioicous plants. In the 'Oceanian' variants, c. 64% (n = 33) of specimens are gemmiferous. Gemmae are usually present at damaged stems and branches.

66. Van Balgooy collected plants of both 'Oceanian' variants on the same locality on Bora Bora (*Van Balgooy 1979A*, *1979B*, L). Nadeaud collected both variants on Tahiti, presumably once in the same locality (*Nadeaud 65*). The two specimens of this collection are preserved in BM. The one in Bescherelle's herbarium – the holotype of *H. nadeaudianum* Besch. – belongs to 'Oceanian variant 1', the other resembles 'Oceanian' variant 2'.

Distribution — 67. *Hypopterygium tamarisci* is rare in Chile. The two specimens that are known from this country are parts of presumably the same collection. They were collected by Lechler and included in Hohenacker's exsiccata series 'W. Lechler pl. chilenses' under number *595* (*Lechler, LPC 595*). All specimens of this collection were identified – possibly by W.P. Schimper – as *Hypopterygium concinnum* (≡ *Lopidium concinnum*), but belong in fact to *H. didictyon*, except for the two specimens of *H. tamarisci*. The two Chilean specimens of *H. tamarisci* were indicated to come from Morro Gonzales (mainland Chiloé Prov.), like the majority of *Lechler, LPC 595*. The specimen in PC was, almost certainly by Cardot, picked out of another specimen of *Lechler, LPC 595*. The specimen in BR is an original specimen of the exsiccata series and contains much and well developed, fruiting material of *H. tamarisci* that, amongst other mosses, grew intermingled with *Racopilum* cf. *tomentosum* (Hedw.) Brid. This mainly neotropical species was thus far not known from this part of South America (Van Zanten, pers. comm.).

68. Brotherus & Watts (1915) reported a few collections of *Hypopterygium neocaledonicum* that were made by Gunn in Vanuatu on the islands of Aneityum and Futuna. I have only found a single specimen of these collections, which was collected by 'native collectors' for Gunn on Aneityum. It is presented under number *427* in BM. It is a small to medium-sized, fruiting plant, which shows no substantial differences with other material examined of *H. tamarisci* from Vanuatu. I have not seen any material from Futuna.

Identification — 69. In Indo Malaysia small (to medium-sized) plants of the 'Asian' variant of *Hypopterygium tamarisci* with closely set leaves may be confused with similar plants belonging to *H. vriesei*. See under the latter, note 12, p. 196.

70. Bryologists treating Asian material occasionally confused the 'Asian' variant of *Hypopterygium tamarisci* with the present species *H. flavolimbatum*. See under the latter, note 27, p. 187.

71. In the past several bryologists confused the Australasian representatives of the present species *Hypopterygium tamarisci* with the present species *H. didictyon*. This has partly been caused by the doubtful status of *H. rotulatum* (Hedw.) Brid. (see 'Doubtful Hypopterygium species', p. 249). However, the present taxa can usually easily be distinguished from each other: see under *H. didictyon*, note 17, p. 155.

72. Plants of 'Oceanian' variant 1 of *Hypopterygium tamarisci* may easily be confused with medium-sized to large plants of *H. vriesei* from the eastern Pacific; see under the latter, note 13, p. 197.

Other — 73. The African material examined contained only three specimens from Uganda. Recently, 12 new Ugandese collections of *Hypopterygium laricinum* have been made in Kabale, Kabarole, and Rukungiri (Porley et al., 1999) during the expeditions of the Tropical Bryology Group of British Bryological Society in Uganda (Wigginton et al., 1999). These were not included in the present study.

74. Dixon's (1935) record of *Hypopterygium ceylanicum* for Borneo is incorrect, because it is based on misidentified specimens of *Hypopterygium vriesei* (*Richards 1117, 2553*), and presumably also of *H. flavolimbatum*.

75. Kindberg (1901) synonymised *Hypopterygium neocaledonicum* with *H. ceylanicum*, and hence recorded the latter from New Caledonia. Later authors followed Kindberg. Based on the generally accepted synonymy of *H. ceylanicum* with *H. tenellum*, Pursell & Reese (1982) reported *H. tenellum* from New Caledonia

76. Kindberg (1901) synonymised *Hypopterygium tahitense* with *H. muelleri*. Hence, he reported the latter from Tahiti. Based on Kindberg's synonymy, Whittier (1968) and De Sloover (1994) recorded *H. muelleri* for Tahiti and other Melanesian and Polynesian islands. Whittier (1973, 1975, 1976) and Whittier & Whittier (1974), however, used the name *H. tahitense*. Most of the material, which these authors referred to, has been examined during the present study, and is identified as *Hypopterygium tamarisci*.

77. *Hypopterygium oceanicum* was reported from Fiji by Gibbs (1909) and Dixon & Greenwood (1930).

78. Dixon (1941) erroneously supposed *Hypopterygium muelleri* (= *H. tamarisci*) to be specifically indistinct from *H. scottiae* Müll.Hal. (= *H. discolor*). He observed such a great variability in the denticulation of the leaves and amphigastria, that he could not distinguish these two species. He did not find any other discriminating features. Dixon's judgement is probably based on the examination of a few specimens that are attached to the same sheet in Dixon's herbarium (BM). They are present under the name *H. muelleri* and include the specimens *Henry 3960, 6734*, which are treated in Dixon's (1941) study, *Hubbard s.n.* (Queensland), and *Watts 1319* (New South Wales). Dixon misidentified the specimen collected by Hubbard, which in fact belongs to *H. discolor*. Hubbard's plant has coarsely serrate-dentate leaves and amphigastria and is much larger than Dixon's other, correctly identified specimens, which have entire or weakly to moderately serrate leaves and amphigastria. Hubbard's plant was presumably included in Dixon's concept of *H. muelleri*. However, Dixon did recognise the difference in size between Hubbard's plant and his other ones and labelled Hubbard's specimen – and a duplicate specimen that is also preserved in BM – with an unpublished name with the rank of forma.

79. Additions to the specimens of *Hypopterygium muelleri* listed by Kruijer (1997b) that were collected in European botanic gardens and belong to the present species *H. tamarisci*: Amsterdam: *Margadant s.n.*, on tree fern (1942, L), *Marcel Arens s.n.*, in a green house at a palm (1945, L), *s.n.* (1948, L); Baarn (Cantonspark): *Max Arens s.n.*, in green house (1944, L), *Kreulen s.n.*, on boulders of lava in green house (1967, GRO, L; 1971, L); Berlin-Dahlem: *unknown collector s.n.*, from New South Wales (?; FH). Cambridge: *Holmes s.n.*, on tree fern (?; NY). Leiden: *La Rivière s.n.* (1912, L); *Barkman s.n.* (1940, L); *Wachter s.n.* (1940, L); *Meeuse & Van Oostroom 7627* and *7628*, on trunk and tub of *Sphaeropteris medullaris* (G. Forst.) Bernh. (1942, L); *Meeuse & Van Oostroom 7649* (?; L); *Meeuse & Van Oostroom 7654*, on cinder (?; L). Utrecht: *Van Oostroom 2941* and *s.n.*, in fern house on boulders and on the wall (1930, L); *Aptroot 26699*, in green house

of 'De Uithof' (1985–95?, U). Wernigerode: *Mönkemeijer s.n.*, in palm house of the "*Hofgärtnerei*" on trunks of tree ferns (1898, HBG; 1900, HBG).

Most specimens come closest to the 'Australasian' variant and provide further evidence for Kruijer's (1997b) hypothesis, that a great majority of the introduced *Hypopterygia* were imported together with tree ferns and originally came from (SE) Australia or New Zealand.

Selected specimens (among 2206 specimens examined):

SÃO TOMÉ E PRÍNCIPE: São Tomé: *Mann s.n.* (S). *Quintas (25)* (H-BR p.p., S), *1448* (COI). EQUATORIAL GUINEA: Bioko ('Fernando Poó'): *Mönkemeyer s.n.* (S), *s.n.* (JE); *Müller B115* (L), *B271* (L), Luba. — CAMEROON: South West Prov.: *Dusén, MAC 38* (PC, S, ZT), Mt Cameroon, Bomana; *Dusén, MAC 38* (S), Buea. GABON. Ogooué-Lolo: *Le Testu s.n.* (S), Levata. — ETHIOPIA: Kefa ('Kaffa') Prov.: *De Wilde-Duyfjes 11587 A* (L), Jimma; *De Wilde-Duyfjes 11552 A* (L), Bellete State Forest; *Friis et al. B118a* (BR), Bonga Forest. — KENYA: Western Prov.: *Granvik s.n.* (S), Mt Elgon. – Nyanza/Rift Valley Prov.: *Davidse 7118* (L), S of Nandi Hills. – Rift Valley Prov.: *Maas Geesteranus 10306 A* (L), Cherangi. – Central Prov.: *Hedberg 1409a* (S), Aberdare Ra. — UGANDA: *Lorenz U1* (DR), Ruwenzori Mts – Kabarole: *Lisowski 3363* (BR), Ruwenzori Mts, Mubuku Valley. – Mpigi: *Arnstein Lye & Morrison LY-B304* (BR), SW of Mpigi. — DEMOCRATIC REPUBLIC OF CONGO (ZAIRE): Équateur: *Schouteden 24* (BR), Businga. – Haut-Zaire: *Lisowski 6757* (BR), Ituri, Mt Hoyo. – Kivu: *Bequaert 4329* (BR), Ruwenzori, *Lisowski 3937* (BR); *Müller Z387* (DR), Pinga; *Müller Z430* (DR), Mitumba Mts; *Germain 1416* (BR), Nyamlagyra; *Leroy 100* (BR), Kikomero. – Shaba: *Lisowski 4951* (BR), Muhila Plateau. — RWANDA: Gisenye Pref.: *De Sloover 18581* (L), *18769* (CBG), Gikunga. – Cyangugu Pref.: *De Sloover 19410* (CBG, L), Butare–Cyangugu road. — BURUNDI: Muyinga Prov.: *Petit 2177* (BR), Bururi, Sikuvyage River. — TANZANIA: Kilimanjaro: *Hedberg 1160c* (BR, S), Mt Kilimanjaro. – Arusha: *Pócs 6983/B* (GRO), *Crosby & Crosby 8716* (L, S), Meru Crater, Ngarenanynki River. – Tanga: *Brunnthaler s.n.* (H-BR), Usambara Mts, Amani; *Holst 9199* (COI, HBG, S, Z), 'Kwa Mshuza'. – Morogoro: *Crosby & Crosby 8707* (L), Uluguru Mts, Morogoro; *Pócs & Harris CE 4886 (6185/E)* (BR, L, S), Mt Bondwa. — MALAWI: Southern Prov.: *Feijen & Feijen s.n.* (L), *Hodgetts M2402b* (E), *Longton M8611a* (E), *O'Shea M7561a* (E), *Magombo & Longton M4217* (E), *Wigginton M1383a* (E), Mulanje Mt. — ZIMBABWE: Manicaland: *Müller 2533* (L), Rupere, Stapleford Forest; *Müller 2604* (L), Benti Forest Reserve; *Müller 2626* (L), Little Inyangani. — SOUTH AFRICA: Cape of Good Hope: *Menzies 75* (BM, s.loc.). – Mpumalanga (Eastern Transvaal): *Oliver 7125* (L), Barberton; *Vorster 1440b* (L), Mariepskop. – KwaZulu-Natal: *Crosby 7906* (L), Cathkin Peak Forest; *Greinzius s.n.* (W), Durban ('Port Natal'); *Van Zinderen Bakker 343b* (GRO), Bergville, Little Switzerland. – Eastern Cape Prov.: *Schelpe 7516* (BR, GRO, S), Port St. Johns; *McOwan, Bryoth. Europ. 1412* (L, S, Z), Somerset-East, Mt Boschberg. – Western Cape Prov.: *Crosby & Crosby 8100* (L), George, Groenkop Forest Reserve; *Breutel s.n.* (L, S), Genadendal ('Gnadenthal'); *Arts RSA 08/01* (BR, Table Mountain; *Rehmann MAA 298c* (L), Rondebosch. — COMORO IS.: Anjouan ('Johanna'): *Hildebrandt s.n.* (S, sub nos. *35* and *52* in hb. Kindberg). — MALAGASY REPUBLIC: Madagascar: *Pervillé 805* p.p. (BM; s.loc.). – Antsiranana Prov.: *Chenagan s.n.*, Antsiranana; *Boivin s.n.* (BM), *Pervillé s.n.* (BM), Nosy Be. – Antananarivo Prov.: *Sikora 14310* (W), *s.n.* (BR, S, S, sub no. *48* in hb. Kindberg?), Andrangolaoka; *Cremers 1681* (BR), Ankaratra Mts, Manjakatompo. – Fianarantsoa Prov.: *Touw & Snoek 25077* (L), Ranomafana; *Hildebrandt s.n.* (L, S, W), *(FCM) 2093* (COI, S, W), S Betsiléo, Ankafina; *Besson 248* (PC, S, sub no. *47* in hb. Kindberg), Vinanintelo–Ikongo. — MASCARENES: Mauritius ('Île de France'): *Balfour s.n.* (L), *Onraedt 71 Ma 187* (BR), *De Robillard s.n.* (BM, S), *s.n.* (BR, PC, S; HBG, sub no. *23*); *De Robillard s.n.* (BM, PC), "montagne de la Rivière Noire"; *M.R. & C.A. Crosby 8607* (GRO p.p.), Basin Anglais. – Réunion ('Bourbon'): *Polly & Van Dam s.n.* (L, S); *Rodriguez s.n.* (S), *Onraedt 69 R 953* (BR), St. Philippe; *De Sloover 17694* (CBG), Bebour.

NEPAL: *Hooker f. s.n.* (BM, G), 'E Nepal'. — INDIA: Meghalaya: *Griffith 1110* (BM), Moosmai. – Karnataka: *Gleiderer (6457)* (BM p.p., mixed with *Hypopterygium vriesei*), *Gleiderer? (6459)* (JE), Mt Kudremukh; *Law s.n.* (NY), Bababudan Ra. – Kerala: *Barnes 51* (BM), High Ra. – Tamil Nadu ('Madras'): *Beddome 160* (BM, NY), *226* (BM, NY), *Gardner 3b* (BM), *Schmid s.n.* (JE, BM, NY), *(45)* (HBG), Nilgiri Hills; *Perrottet 1513* (BR), *1522* (BM, RO, UPS), *1565* (BM), *s.n.* (BR, BM), *s.n.* (NY), Ootacamund?; *Gambler (16883)* (H-BR), Conoor; *Lüthi (7330)* (JE), Kotagiri; *Nurayanasewami 2B* (BM), Coimbatore, Bellaji Shola; *Beddome 700* (BM), Anamallai Hills

('Anamallags'); *Foreau MM(IME) 3* (BR, FH, S), *Foreau & Roiné 453* (NY, also sub no. *255*), Palni Hills, Shembaganur; *Foreau, MMIME 255* (B, L, NICH, S), *110* (NY, also sub no. *255*), Perumalmalai; *Foreau 424* (NY, also sub no. *255*), Sirumalai Hills; *Foreau 523* (NY, also sub no. *255*), Malanur; *Foreau 539* (BM), Jogarivarai Shola. — SRI LANKA ('CEYLON'): *Gardner 692* (BM, NY; s.loc.). – Central Prov.: *Thwaites CM 130* (BM, NY; H-BR, S; W, s. coll.); *Gardner 691* (NY), Ramboda ('Ramboddi'); *Binstead 335* (BM), Nuwara Eliya; *Fleischer s.n.* (FH), *Onraedt 76.L.2757* (BR), *Ruinard 19/111.2* (L), Mt Hakgala; *Beccari 54* (GRO, L), Mt Pidurutalagala ('Pedrotallagalla').

CHINA: Hongkong: *Bowring s.n.* (NY). – Hainan: *Redfearn jr. et al. 36234* (NY), San Jian Shan; *Redfearn jr. et al. 35753* (NY), Bawanglin Forest Reserve. — JAPAN: Honshu. Mie Pref.: *Takaki 20967* (NY), Minamimuro-gun; *Magohuku 4082* (S), Owase. – Wakayama Pref.: *Iwatsuki 591c* (NY; NICH p.p., mixed with *Hypopterygium flavolimbatum*), Mt Nogi. – Kyushu. Miyazaki Pref.: *Hattori & Toyama, MJ 19* (B, GRO, JE, L, NY, S, W), Minaminaka, Udo; *Iwatsuki et al., MJ 779* (EGR, HIRO, JE, L, NY, S), Nichinan. – Kagoshima Pref.: *Iwatsuki & Sharp 15516* (NICH), *Smith J-1263* (NY), *J-1339* (NY), Yaku-shima Is. – Ryukyu Archipelago. Amami-Oshima Is.: *Ferrié, Bryoth. Levier 160* (H-BR, S), *Ferrié, Bryoth. Levier 160b* (H-BR, PC, sub no. *160*; S; S, sub no. *63* in hb. Kindberg), *Iwatsuki, MJE 1675* (B, GRO, HIRO, L, S, U), Naze. – Bonin Is. Haja-jima Is.: *Inoue, BSE 85* (GRO, JE, L, S, U, WELT). — TAIWAN: Kaohsiung Co. ('Takao Prov.'): *Kodaira 672* (NICH), "Mt. Daibu". – Tainan Co.: *Chiang 5541* (B, Z), Ta-don Shan. – Nantou Co.: *Chiang 5300* (B), Chitou. – Taichung Co.: *Lai 3200* (NICH), Pasienshan. – Miaoli Co.: *Lin, BT 125* (L), Manabang Shan. – Taipei Co. ('Taihoku Prov.'): *Noguchi (5863)* (NICH), Hsinhsien ('Rahoa'); *Noguchi (5910)* (NICH), Tiensungpai ('Tensonpi'); *Lai 11316* (B, L, NICH, NY, UPS), Wulai ('Urai'); *Chuang 5345* (HIRO, NY), Kan-kou.

THAILAND: Payap ('Chiang Mai'): *Touw 9229* (BM, BR, EGR, FH, GRO, L, NY), Doi (Mt) Chiang Dao; *Robbins 3600* (L), *Thaithong 73* (NICH), Doi (Mt) Inthanon. – Phitsanulok: *Larsen & al 1062* (EGR, GRO, JE, L, NICH, NY, S, U), Puh Mieng Mt – Udawn ('Loei'): *Touw 10444* (BM, BR, FH, GRO, L, NY), Phu (Mt) Luang; *Kerr 101* (BM), Phu Tong ('Po-Jong'). – Nakhon Si Thammarat: *Touw 11973* (BM, BR, L, NY), Khao (Mt) Luang. — VIETNAM: Hoang Liên So'n: *Pételot s.n.* (S, PC), Sa-Pâ. – Vinh Phu: *Tran Ninh 67 137* (EGR), Tam Dao. – Ha Nam Ninh ('Ninh Binh'): *Pócs et al. 3016/b* (EGR, GRO, NICH), Cuc-Phuong Reservate. – Ha So'n Binh ('Hoa Binh'): *Pócs et al. 3156/r* (EGR), Mt Nui Cai.

PHILIPPINES: Luzon. Benquet Prov.: *Williams 1879* (FH, NY), Baguio; *Del Rosario 7429C* (GRO), La Trinidad. – Mountain Prov.: *Boeken 81.03.2486* (GRO), *Hoogstraal et al. 13006* (GRO; HIRO, *s.n.*), Mt Data. – Isabela Prov.: *Tan 91-0105* (FH), San Mariano. Mindoro: *Bartlett 13853* (FH), Pto. Galera, Mt Malasimba. — MALAYSIA: Peninsular Malaysia. Pahang: *Hedenäs MY 92-257* (S), *MY 92-385* (S), *MY 92-353* (S), *MY 92-367* (S), *MY 92-405* (S), Cameron Highlands; *Koops CGK 1828* (L), Tanah Rata. — SINGAPORE: *Schotmüller s.n.* (H-BR, S). — INDONESIA: Sumatra. N Sumatra (Sumatera Utara): *Staal 191* (GRO; L p.p., mixed with *Hypopterygium flavolimbatum*), Deli Sungai ('Petani'); *Touw & Snoek 25340* (L), *25350* (L), Mt Sinabung; *Staal 121* (GRO, L), *375* (L), Berastagi. – W Sumatra (Sumatera Barat): *Wiltjens s.n.* (H-BR, L); *Schiffner, It. Ind. 12930* (BM, GRO), Mt Singalang. – Bengkulu: *Meijer B6460 A* (L), Mt Sago. – Java. W Java (Jawa Barat): *Motley s.n.* (NY), Mt Megamendong; *Fleischer, MFAI 50* (BM, FH, GRO, HBG, JE, NY, S, U, Z; H-BR p.p., L p.p, Z p.p., mixed with *Hypopterygium flavolimbatum*), *Nyman 420* (FH, H-BR, NICH, S, U, UPS), *Schiffner, It. Ind. 12928* (BM, L, NY, S, W), Tjibodas; *Verdoorn 1810* (BM), *AM 60* (FH, L), Mt Patuha; *Junghuhn s.n.* (L), Medini. – E Java (Jawa Timur): *Clason 10* (GRO, L), Sarangan. – Sulawesi. N Sulawesi (Sulawesi Utara): *Hose s.n.* (BM), Mt Masarang. – S Sulawesi (Sulawesi Selatan): *Eddy 5298* (BM), Latimojong Mts, Rantelemo; *Touw & Snoek 24469* (L), *24490* (L), *24516* (L), Tana Toraja. – SE Sulawesi (Sulawesi Tenggara). *Kjellberg 10* (BM, GRO, L, S), B.T. Watuwilla. – Moluccas (Maluku). Buru: *Saprin 2112* (BM, L), *s.n.* (GRO, L); *Van Balgooy 5023B* (L), S of Bara. – Seram: *Akiyama C-9390* (KYO), *C-9576* (NY), *C-14617* (KYO, L), Manusela Nat. Park. – Ternate: *Beccari s.n.* (S, '1876'); *Beccari 121* (L, GRO; '1874'), *s.n.* (L, GRO; '1874'), old crater. – Tidore: *Alston 16679b* (BM), *16713b* (BM), Mt Krematuba. – Lesser Sunda Is. (Nusa Tenggara). Lombok: *Touw & Snoek 22273* (L), Mt Rinjani; *Balázs 44/e* (L), Mt Pusuk. – Flores: *Schmutz 5346A* (L), Manggarai, Pahu; *Veldkamp 6987Q* (L), SW of Ruteng; *Touw & Snoek 22689* (L), *22700* (L), Ranggawata. – West Papua (Papua, Irian Jaya). Jayawijaya/Merauke: *Van Zanten 715a* (BM, GRO, NY), 'Camp 36'. — PAPUA NEW GUINEA: Western Highlands: *Streimann 21788* (CBG), NE of Mt Hagen, Gumants River; *Van Zanten 68857* (GRO p.p., mixed with *Hypopterygium vriesei*), Baiyer River. – Eastern Highlands: *Argent, NGBF 11/6/72/6* (L), Habi'ina; *Van Zanten 68377* (GRO), Goroka; *Streimann & Umba 11462* (CBG), Kassam Pass. – Morobe Prov.: *Nyman 179* (UPS), *Kaernbach s.n.* (FH), Sattelberg; *Kaernbach 36* (H-BR p.p., mixed with *Lopidium struthiopteris*, S), *40* (S), Nuselang; *Van Zanten 68211* (GRO), Wau; *McVean 268155* (CBG), Mt Kaindi. – Central Prov.: *Hovenkamp 91/88* (L), Varirata Nat. Park; *Van Zanten 68857* (GRO p.p., mixed with *Hypopterygium vriesei*), *683752* (GRO p.p., mixed with *Lopidium struthiopteris*), *683778* (GRO), Owen Stanley Ra., Mission Ridge. – Milne Bay Prov.: *Brass 22475* (FH).

AUSTRALIA: *De Candolle s.n.* (B, s.loc.). – Queensland: *Van Zanten 68.1233* (GRO), Atherton; *Streimann 36997* (CBG), Paluma Ra.; *Streimann 52097* (L), *Van Zanten 93.10.2896* (GRO), Carnervon Nat. Park; *Streimann 37397* (B, CBG, NY), Conway State Forest; *Streimann 9935* (CBG, L), Six Mile Creek; *Thiers & Halling 2820* (NY), *Tindale (11031)* (FH, WELT; BM, *s.n.*), *Van Zanten 93.10.2983 (GRO)*, Lamington Nat. Park. – New South Wales: *Guilfoyle s.n.* (MEL), Tweed Heads; *Watts 80* (CHR, NSW), *364* (NSW), *480* (NSW), *611* (CHR), *1319* (BM), *1397* (NSW), *1450* (NSW), *1453* (Z), *1783* (NSW), *2191* (NSW), *2968* (NSW), *3028* (BM), *3054* (NSW), *4371* (NSW), *5210* (NSW), Richmond River; *Boorman 1528* (NSW), Dorrigo; *Von Mueller s.n.* (BM), *s.n.* (MEL), Paramatta; *Ramsay 8/64* (SYD), *8a/64* (SYD), *8b/64* (SYD), *8c/64* (SYD), *8d/64* (SYD), *8e/64* (SYD), *8f/64* (SYD), *16/64* (SYD), *33/64* (SYD), *33a/64* (SYD). *33b/64* (SYD), *36/65* (SYD), *s.n.* (SYD), Mt Wilson; *Streimann 15879* (CBG, L, NICH, NY), *Tindale s.n.* (MEL), Diamond Creek; *Reader s.n.* (MEL, NY), Mt Dromedary; *Downing 0987* (MACQ), Jenolan Caves; *Streimann 63472* (hb. Frey), Marble Arch; *Streimann 3807* (CBG, L), Wadbilligia River; *Downing 0808* (MACQ), Yarangobilly Caves; *Streimann 63471* (hb. Frey), Nadgee State Forest. – ACT: *Beeton 45198* (L), *Streimann 1065* (B, CBG, L), Tindbilla Nature Reserve; *Streimann 5045* (BM, CBG, L, NY), Jervis Bay. – Victoria: *Streimann 39233* (CBG), Club Terrace; *Verdon 1253* (CBG, L, NY), *Willis s.n.* (MEL), Mt Drummer; *Von Mueller 40* (MEL, WELT), *s.n.* (BM), Buchan River; *Von Mueller? s.n.* (BM), Mt Juliette, Sources of the Yarra; *Beaglehole 3905* (MEL), *3908* (MEL), Mt Napier State Park; *Beauglehole 4395* (MEL), *4396* (MEL), Heywood, Cave Hill; *Beauglehole 1323* (MEL), *1372* (MEL), *4493* (MEL), *4542* (MEL), Lower Glenelg Park. – South Australia: *Wilhelmi s.n.* (BM), 'cave near Mt Gambier'; *Downing 0944* (MACQ), Naracoorte Caves. – Tasmania: *Hartmann, (20)* (S), 'Toowoomba'; *Curnow 2448* (CBG), St. Marys; *Weymouth s.n.* (BM), Mersey River; *Bastow 677* (MEL), Maria Is. – Lord Howe Is.: *Beauglehole 73596* (MEL), *Fullager s.n.* (MEL), Mt Lidgbird; *Fullager s.n.* (BM, NY, RO, S), *Streimann 56043* (CBG), Mt Gower; *Vitt 28686* (CBG), Middle Beach. – Norfolk Is.: *Cunningham (H. 3319)* (BM), *Milne 28* (BM), *unknown collector s.n.* (NY); *Streimann 31912* (B, CBG, NY), *32100* (CBG, NY), Mt Pitt Reserve; *Streimann 34904* (B, CBG, NY), Bird Rock Track; *Henderson 9519* (BM, MEL, NY); *Streimann 53753* (CBG, L), Selwyn Pine Road. NEW ZEALAND: *Stephenson 20* (BM, NY; s.loc.), *11b* (NY, s.loc.), *s.n.* (NY, s.loc.). – North Island. North Auckland L.D.: *Joliffe s.n.* (BM), Hokianga; *Berggren 2005* (UPS, W), Whangaroa; *Lyall H. 3854* (BM), Auckland; *Chambers (181)* (L), *Robbins 181* (WELT), Mt Eden; *Moore (3578)* (WELT), Rangitoto Is.; *Moore 538* (CHR), Taranga ('Hen') Is.; *Lush s.n.* (WELT, sub no. *M 8066*), *Petrie s.n.* (CHR), Little Barrier Is.; *Kirk 58* (NY), Great Barrier Is. – South Auckland L.D.: *Allison 2255* (WELT), *(3572)* (CHR), *20.391* (WELT), Atiamuri; *Cheeseman 65* (CHR, WELT), Coromandel; *Beever 34-95* (WELT), Motuhora ('Whale ') Is. – Gisborne L.D.: *Kantak & Churchill 108* (CBG, NY), Opotiki; *Hamlin 2180* (WELT), *2182* (WELT), *2184* (WELT), Whanarua Bay; *Sainsbury 3573* (CHR, WELT), Poverty Bay, Panikau. – Hawke's Bay L.D.: *Van Zanten 73.12.48* (GRO), Tongiro Reserve. – Taranaki L.D.: *Gray 126a* (BM), Mt Taranaki ('Mt Egmont'). – Wellington L.D.: *Gray 277* (BM, mixed with *Hypopterygium didictyon*), Wairarapa, Mauriceville; *Brownsey s.n.* (WELT), Upper Hutt, Kaitoke Waterworks; *Berggren 2731* (UPS), Wellington; *Mason s.n.* (CHR), Wiltons Bush. – South Island: *Lyall 170* (BM; s.loc.), *290* (BM; s.loc.). – Nelson L.D.: *unknown collector s.n.* (W), Cook Strait, Rangitoto Is.; *Streimann 51113* (CBG), Cable Bay; *Streimann 51393* (L), Hira Forest. – Marlborough L.D.: *McMahon (10369)* (WELT), Picton. – Canterbury L.D.: *Kerr s.n.* (NY), Banks Peninsula, Akaroa. – Kermadec Is.

Raoul ('Sunday') Is.: *Cheeseman s.n.* (S, CHR, WELT; WELT, *10.366*), *(36)* (HBG), *273a.2* (CHR), *McGillivray s.n.* (NY; BM, FH, *s. coll.*); *Milne 75* (NY), *s.n.* (BM), 'Summit of Mountain'. — NEW CALEDONIA: *Le Rat s.n.* (S, loc. uninterpr.); *Balansa 2551* (BM, L), Mt Cougui; *Le Rat s.n.* (L), Mt Moné ('Mouè'); *Franc, MHNCE 159* (FH, L, W, S, Z), Nouméa; *Franc s.n.* (S), *Franer?, Filic. Novae-Caled. 50* (p.p.?) (S), *Robbins 3775* (L), *Hürlimann 2113* (Z), Mt Koghis; *Le Rat s.n.* (Z), *Robbins 3764* (L p.p.), Mt Dzumac; *Franc s.n.* (S), Mt Moriè; *Hürlimann 2998* (Z), Rivière Bleu; *MacKee (2708)* (MEL), Mt Des Sources.

PACIFIC ISLANDS: *unknown collector s.n.* (NY). — VANUATU: Espiritu Santo: *Robbins 3851* (L), Santo Peak; *Bowie, Hb. Watts 73* (BM, H-BR), *518* (BM), Tangoa. – Aneityum: *native collectors* for *Gunn (427)* (BM); *unknown collector 17c* (BM), Anelquahat. — FIJI: *Moore s.n.* (S, s.loc.). – Vanua Levu: *Robbins 3523* (L), Mt Delaikoro; *Smith 467a (407a?)* (NY), Mt Mariko. – Viti Levu: *Degener 14569.1* (FH), *14778.1* (FH), Mt Matomba; *Greenwood 8* (BM), *F 28* (BM), *(F) 54* (BM), *280* (BM), *318* (BM), *1099* (BM), Lautoka, Mt Evans; *Greenwood 1048* (FH), Nasinu; *Wimmer 56* (L), *188* (L), *214* (L), Nadala; *Gibbs 643* (BM, FH?, s.coll.), *676* (BM, WELT s.coll.), *719* (BM), *812* (BM), *s.n.* (BM), Nadarivatu; *Greenwood s.n.* (FH), Tomanivi ('Mt Victoria'); *Smith 5516* (BM, FH, L, NY, S), Nandronga & Navosa; *Smith 5731* (BM, FH, L, NY, S), Ra; *Mead 1326* (FH), Suva. – Matuku: *Milne s.n.* (BM). — TONGA: Tafahi: *Hürlimann T 911* (Z), Mt Piu'o Tafahi. — SAMOA IS.: *Reinecke 333* (W). – Western Samoa. Upolu: *Fleischer B1117* (B, CBG, NY), Mt Lanutoo; *Schultze-Motel 3300* (B, L, NICH), Mt Fiamoe–Lake Lamoto'o; *Hills 27* (BM), Malua; *Weber s.n.* (HBG), Fakalili. — NIUE: *Irwin 411* (WELT), Alofi. — COOK IS.: Rarotonga: *Graham 32* (BM), *(14351)* (WELT), *Hamilton (14350)* (WELT), *Taverner 709* (BM), *(14349)* (WELT); *Parks & Parks 22378* (FH), Mt Maungatea. — SOCIETY IS.: Raiatea: *Moore 46d* (FH), Temahaui Ra. – Bora Bora: *Van Balgooy 1979A* (L), *1979B* (L), Pahia. – Moorea: *De Sloover 20.946* (NY), *21.017* (BR, GRO, EGR, S), *Temarii s.n.* (FH); *De Sloover 20946* (L, S), Toto Valley. – Tahiti: *Andersson s.n.* (S), *Challenger Exp. s.n.* (BM, NY), *Nadeaud 434* (S, W), *434+435* (FH), *436* (BM, S), *438* (S), *439* (BM, FH, S, W); *Van Balgooy 1863* (L), Aorai; *Nadeaud 65* (BM), Marau, Mamano; *Nadeaud 437* (FH, s.loc.; S), Papenoo Valley; *Nadeaud 440* (BM, FH, PC, W, S), Mt Pinai, Puaa Valley; *Hürlimann T 911* (FH), Piu 'o Tafahi; *Jelinek 125* (S, W), Fataua; *Temarii [Nadeaud] s.n.* (S), Rahi; *Temarii s.n.* (FH), Miaa. — TUBUAI IS.: Raivavae: *Fosberg 11712* (BM, FH, L), Mt Muanui. – Rapa Iti ('Rapa'): *Fosberg, MSC 274* (BR, BM, FH, GRO, HBG, JE, L, NY, S, U, WELT, Z), Mt Morongota; *Cook s.n.* (FH), Mt Oranga. — TUAMOTU: Mangareva: *St. John 14515* (FH, L), Mt Duff. — MARQUESAS: Nuku Hiva: *Erikson 27* (FH, S), Taipi.

ANTILLES: *Ruhard 51* (G, s.loc.). — CUBA: *Wright, MC 130* (HBG, L, S; s.loc.). – Granma?: *Hazen 12251* (S), Rio Santa Rita. – Santiago de Cuba: *Hioram s.n.* (S, '7-1933'), Ioma San Juan, *Ekman PIR 5240* (S), Punta de Palma Mocha. — JAMAICA: *Swartz s.n.* (G, S; s.loc.). – Surrey: *Robbins 69* (L), Blue Mts; *Harris s.n.* (L, MEL, S), Cinchona–Morce's Gap; *Crosby 3559* (S), Morce's Gap–Clydesdale. — HAITI: Sud: *Ekman PIO H512a* (S), Massif de la Hotte, Ma Blanche. – Ouest: *Ekman PIO H8015* (S), Massif de la Selle, Marigot. — DOMINICAN REPUBLIC: Santiago Prov.: *Zanoni et al. 26807A* (U), Ioma Diego de Ocampo. – La Vega Prov.: *Buck 7923* (U), Constanza. – Pedernales Prov.: *Smith 10067* (U), Las Abejas. – Barahona Prov.: *Zanoni et al. 18928Z* (U), Monteada Nueva. — MARTINIQUE: *Perrotet s.n.* (BR; s.loc.).

MEXICO: Veracruz: *Pringle, PM 10497* (L, S), *Von Chrismar s.n.* (S, sub no. *28* in hb. Kindberg), Jalapa; *Purpus (385)* (HBG), *Sartorius, PM s.n.* (S, W), Mirador. – Chiapas: *Zamudio, PM 1526* (U), Tecpatán; *Den Held & Van Rijn HH 68* (U), Tziscao. — GUATEMALA: Aeta Vera Paz: *Von Türckheim, Bryoth. Levier (25)* (S), Cobán. – Zacapa: *Steyermark 29926* (S), Sierra de las Minas, Finca Alejandria. — COSTA RICA: *Breues 32* (HBG), 'Collines' de Santiago. – Alajuela: *Liesner 5087* (U), Santa Maria Nat. Park. – Cartago: *Maas 799* (U), Turrialba, Finca La Palmira. — PANAMA: Darién Prov.: *Allen 8846* (L), Pirre Massif.

ANDES: *Humboldt ('Humboldt & Bonpland') 92* (BM, s.loc.). — COLOMBIA: Dept. Magdalena: *Griffin III et al., 50.036* (U), Parque Nac. de la Sierra Nevada de Santa Maria. – Dept. Antioquia: *Churchill et al. 15529* (U), Sonson. – Dept. Santander: *Van der Hammen & Jaramillo 1868* (U), Carretera San Joaquin–Mogotes. – Dept. Boyaca: *Van der Hammen et al. 2837* (U), Carretera Chiquinquira–Pauna. – Int. Casanare: *Aquirre et al. 3108* (U), Sacana, Macueque, Río Sácana. – Dept. Risaralda: *Van Reenen et al. 1548* (U), Sta. Rosa de Cabal. – Dept. Caldas: *Churchill & Arbelaez 15649* (U), Vereda el Tabor. – Dept. Cundinamarca: *Cleef 8472* (S, U), Páramo de Sumapaz;

Van der Hammen & Jaramillo 2649 (BR, S, U), Sasaima. – Dept. Tolima: *Van Reenen & Cleef 2268* (U), Sta. Isabel. – Dept. Valle del Cauca: *Aguirre & Van Reenen 4176* (U), Anserma. – Dept. Cauca: *Bischler 1095* (U), Macizo Colombiano. – Dept. Huila: *Van Zanten et al. 84.09.722* (GRO), Merenberg. — VENEZUELA: *Funck & Schlim 356* (L, s.loc.). – Zulia: *Dana Griffin III 101* (BR), Sierra de Perija, San José de los Altos–Topochalito. – Mérida: *Moritz 70* (L; S, s.loc.) Tovar; *Griffin et al. 766* (U), Chana River. – Carabobo: *Fendler s.n.* (S, in hb. Kindberg sub no. *59*), Valencia. – Aragua: *Mägdefrau 75* (U), Los Guayabitos. – Distr. Federal: *Funck & Schlim (18)* (HBG), Caracas. — ECUADOR: Carchi: *Lehmann 684* (PC), Tulcan, Rio Pun. – Pichincha: *Spruce 1489* (S), *Jameson 81* (BR), Quito; *Frahm et al. 131* (U), Lloa. — PERU: *Spruce 1491* (S, s.loc.). – Ayacucho: *Frahm (16)* (NY), Huanta–San Fransisco. — BOLIVIA: Cochabamba: *Herzog 2730* (L, S), Espiritu Santo; *Herzog s.n.* (S), Incacorral; *Lewis 83-1972* (F, L), Río Monte Puncu, Estancia Sehuenca. – Santa Cruz: *Maitland 1A* (L), Samaipata, Amboro Park; *Herzog 3650* (L, S), Florida ('Florida de San Mateo'). – Chuquisaca: *Lewis 84-918* (F, L), W of Monteagudo. – Tarija: *Lewis 84-2207* (F, L), Cerro Nogal.

CHILE: Chiloé Prov.: *Lechler, LPC 595* (BR, PC; see note 67), Morro Gonzales. — ARGENTINA: Salta?: *Lorentz s.n.* (S, sub no. *33* in hb. Kindberg; S; S, wrongly labelled '18.VII.1873'), Cuesta de Santa Rosa. – Tucumán: *Kühn s.n.* (BM) *s.n.* (S), *s.n.* ZT), Quebrada de Acheral; *Hichen 988* (ZT), Yerba Buena. – Buenos Aires: *Schnyder s.n.* (S); *Kühnemann 77* (S), Isla Martin Garcia.

BRAZIL: Minas Geraïs: *Mosén 369* (S, Z?, 'Hj. Mateùs'), *Lindberg s.n.* (L, RO, S, U), *Regnell 29* (S), *Widgren s.n.* (S), Caldas. – Rio de Janeiro: *Gaudichaud s.n.* (L), Rio de Janeiro; *Frahm 1334* (U, S), Teresópolis; *Ule, Bryoth. Brasil. 153* (BR, HBG, L, S), *Herbar Brasil. 1068* (HBG), Mt Corcovado. – São Paolo: *Puiggari (33)* (HBG), *54* (L), *190* (L, S), *897* (L), Apiai ('Apiahy'); *Hoehne 255* (ZT), Morro do Taraqua; *Schiffner 222* (L, S), *MB55* (S), Itapecirica, Barra Mansa. – Paraná: *Dusén 8373* (S), *Hatschbach 17443* (L), Ponta Grossa; *Cordeiro 1031 & Polquesi* (BR, ZT), Bocaivu do Sul, Estrada da Ribeira, Serra de Santana. – Santa Catarina: *Ule, Herbar Brasil. 48* (HBG), São Francisco Is.; *Frahm, BNE 163* (L, S, U), Serra do Espigao; *Reitz 2224* (U, Z), Azambuja, Brusque; *Ule, Bryoth. Brasil. 154* (HBG, L, S), Serra Geral; *Pabst s.n.* (S), Itajahi. – Rio Grande Do Sul: *Lindeman et al. s.n.* (U), Rio Camaqua; *Rossato et al. 3307* (L), Esmeralda; *Lindman B54* (S), *Reineck s.n.* (HBG), Pôrto Allegre; *Reineck & Germak, MA 42* (S), Belém Velho; *Poloni et al. 2392* (L), São Francisco de Paula-Carapina. — PARAGUAY: *Balansa, PP 3628a* (COI, PC), Guarapi. – Paraguirí: *Balansa, PP 3629* (COI, L), *s.n.* (S, sub nos. *52* and *32* in hb. Kindberg), Cordillère de Ubatobi, Paraguirí. – Guaira: *Balansa, PP 1246* (PC), Villarrica. — URUGUAY: Canelones: *Arechavaleta s.n.* (S, sub no. *32 1/2* in hb. Kindberg), Montevideo, Camino de Carrasco.

PORTUGAL: (introduced, see note 47). Beira Litoral: *P. & V. Allorge, Bryoph. Iber. 146* (BM, *s.n.*; L, S, ZT); *Florin s.n.* (S), *Rozeira s.n.* (S), *Sérgio 2259* (L, LISU), *Kruijer & Felëus 97.09.01* (L), Mata do Bussaco.

4.7. **Hypopterygium sandwicense** Broth. — Fig. 35, 36

Hypopterygium sandwicense Broth., Bishop Mus. Bull. 40 (1927) 25. — Type: *Baldwin 104 (Bryoth. Levier 533)* (H-BR holo; FH, NY, both with the collector's number only; FH, S, both with exsiccate series number only), USA, Hawaiian Islands: "Insulae Sandwich", West Maui, "in faucibus montium, 5000 p. in arboribus humilibus" ["mountain ravines, on small trees, elevation 1500 m"], Aug., 1875.

Illustrations: Bartram, Bishop Mus. Bull. 101 (1933) f. 145.

Plants in groups of fans (or dendroids?), pinnate to flabellate or weakly palmate, small to medium-sized, not gemmiferous. *Stipe* short, up to 0.9 cm long, ± horizontal, straight, dorsiventrally or laterally compressed in basal half, dorsiventrally compressed in distal part, entirely tomentose or scattered with a few rhizoids in distal part. *Frond* short-elliptic or rhombic to short-obovate, up to 2.5 cm in diameter; rachis and branches dorsiventrally compressed, glabrous or scattered with rhizoids (or tomentose) in basal part; rachis roughly growing in direction of stipe, roughly horizontal; branches up to

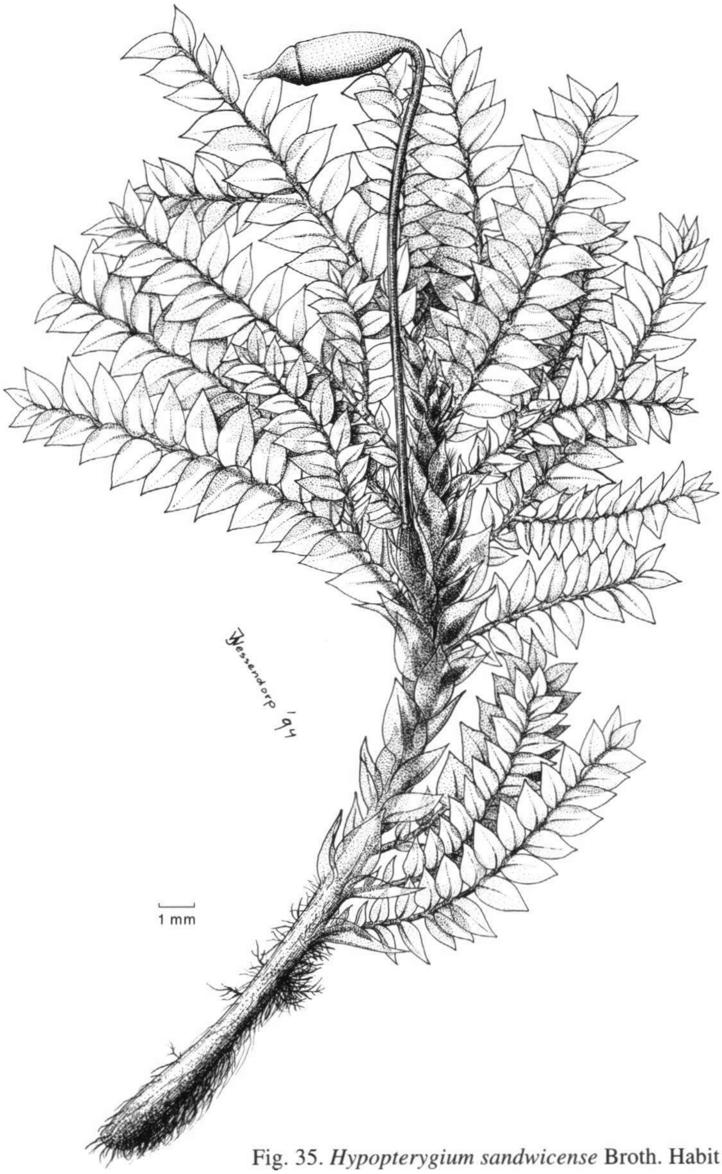


Fig. 35. *Hypopterygium sandwicense* Broth. Habit (***Baldwin 104***, **FH**).

0.8 cm long. *Primordia* regulary set with scaly leaves; scaly leaves triangular to elliptic or ovate, margin entire. *Epidermis cells and cortical cells of stipe, rachis, and branches* equally wide or cortical ones wider; walls incrassate in epidermis cells and outer cortical cells, thin in inner cortical cells, when incrassate yellow to brown, when thin pale yellow; inclusions absent. C*entral strand* present in stipe and lower and middle part of rachis, present or absent in distal part of rachis (where replaced by a central cavity); cells narrow, walls thin, colourless to yellow; inclusions present, granules to clumps, fat-like, colourless (white). *Axial cavities* absent from stipe and basal part of rachis and branches, central in distal part of rachis and branches; inclusions present, similar to those in central strand cells, but more frequently found as clumps. *Axillary hairs* up to 3 per leaf, 3- or 4-celled; basal cells 2 or 3; intermediate cells absent; terminal cell elliptic to narrowly elliptic, 25–40 µm long and 10–15 µm wide, ± smooth, wall thin. *Phyllotaxis*: of stipe octostichous; of rachis octostichous in basal part, becoming tristichous in distal part; of branches tristichous. *Foliation*: of stipe usually isophyllous and not complanate, occasionally weakly anisophyllous and weakly complanate in distal part; of rachis usually isophyllous and not complanate and occasionally weakly anisophyllous and weakly complanate in basal part, becoming distinctly anisophyllous and complanate in distal part; of branches distinctly anisophyllous and complanate. *Leaves* distant or closely set at stipe, becoming closely set in frond, yellowish green, dull; insertion transverse, becoming concave in distal frond leaves; laminal cells prosenchymatous, hexagonal, short, 25–50 µm long and 15–25 µm wide, walls incrassate, porose. *Basal and distal stipe leaves* monomorphic, usually not differentiated, occasionally differentiated in basal ones and distal ones, appressed to patent, symmetrical or weakly asymmetrical, ovate to elliptic; margin entire; border faint to distinct, interrupted (to continuous?), up to 2 cells wide; apex acute to gradually acuminate; costa faint to distinct, reaching up to 2/3 of leaf length. *Basal stipe leaves* scale-like, similar in size as distal ones or smaller. *Distal stipe leaves* scale- to leaf-like, 0.5–2.0 mm long and 0.5–1.5 mm wide. *Frond leaves* monomorphic in basal and middle part of rachis, becoming dimorphic in distal part of rachis and branches, not caducous or becoming caducous when situated at apex of ultimate frond axes; margin entire or weakly to coarsely serrate; teeth 1-celled, up to 25 µm long (up to 8 µm long in amphigastria), projecting up to 1/4 of cell length, up to 20; border (faint to) distinct, frequently faint or interrupted near apex, 1–3 cells wide; apex gradually to abruptly acuminate in basal frond leaves, becoming abruptly acuminate in distal ones; acumen up to 0.3 mm long. *Basal and central rachis leaves* ± symmetrical, ovate to elliptic, 1.5–2.0 mm long and 1.0–1.5 mm wide; costa distinct, reaching 1/4 –2/3 of leaf length. *Lateral frond leaves (in distal part of frond)* asymmetrical, ovate to elliptic, 1.5–2.0 mm long and 1.0–1.5 mm wide; costa distinct, reaching 1/2–4/5 of leaf length. *Frond amphigastria (in distal part of frond)* symmetrical, short-ovate to elliptic, 0.5–1.5 mm long and 0.5–1.5 mm wide; costa distinct, reaching 1/2–4/5 of amphigastrium length.

Heteroicous. *Gametoecia* in basal and middle part of rachis; perigonia placed below perichaetia. *Gametoecial leaves* green; margin entire; border faint to distinct, frequently absent near base or faint and interrupted in acumen, 1 or 2 cells wide; apex acute or gradually to abruptly acuminate; costa absent, faint, or distinct, reaching 2/3–4/5 of leaf length. *Inner leaves*: of perigonia ovate to elliptic, up to 0.8 mm long and 0.6 mm wide, but frequently much smaller, acumen up to 0.4 mm long; of perichaetia prior to sporophyte development ovate to elliptic, up to 0.8 mm long and 0.6 mm wide, acumen up to 0.4 mm long; of full-grown perichaetia ovate to elliptic or weakly lingulate, up to 1.7 mm long and 0.8 mm wide, acumen up to 0.8 mm long. *Antheridia* 0.5 mm long. *Stalk in full-grown perichaetia* 0.3–0.4 mm long. *Archegonia* 0.5–0.6 mm long. *Vaginula* 1.0–1.3 mm. *Gametoecial axillary hairs* up to 4 per gametoecial leaf, 2- or 3-celled, simple; basal cells 1 or 2, pale brown to brown; intermediate cells absent;

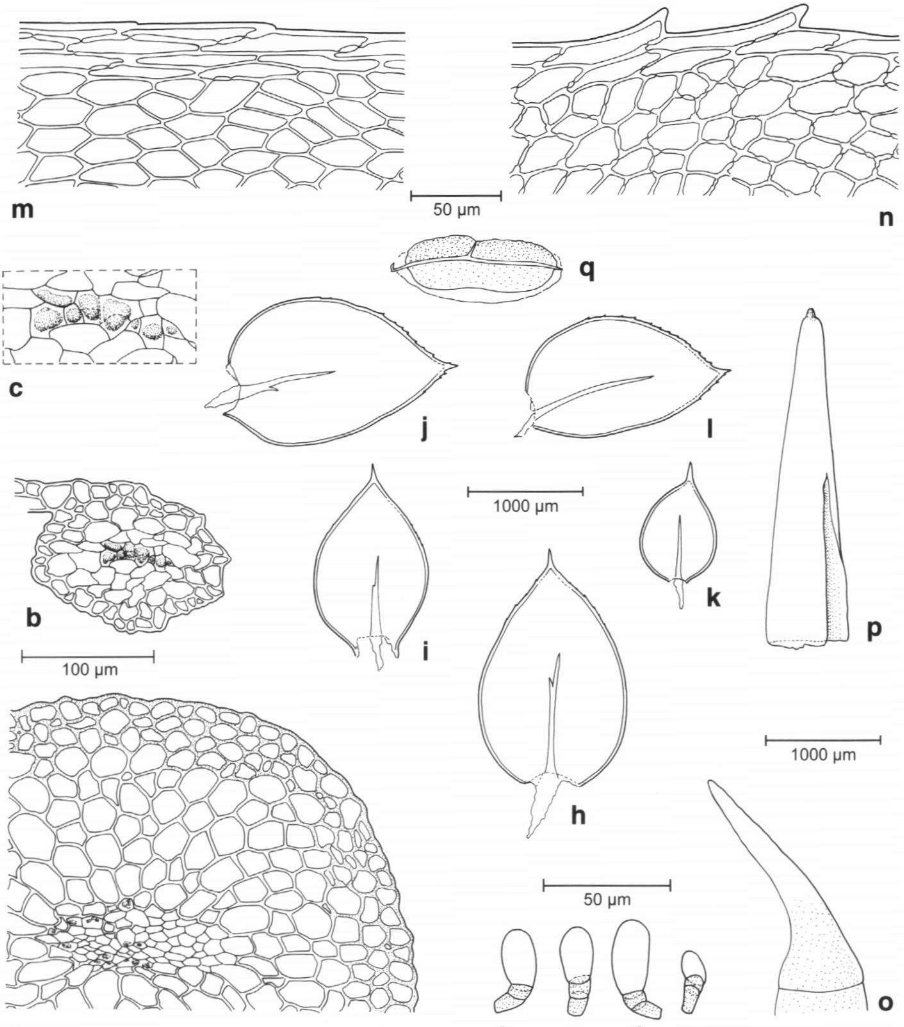


Fig. 36. *Hypopterygium sandwicense* Broth. a. Rachis (cross section dorsal quadrant); b, c. branch (b. cross section, c. central cavity in process of formation: degenerating strand cells); d–g. axillary hairs; h–j. rachis leaves (h. dorsal, i. ventral, j. lateral); k, l. branch leaves (k. amphigastrium, l. lateral); m, n. leaf cells of lateral rachis leaf (m. basal part of antical side, n. distal part of antical side); o. operculum; p. calyptra; q. exostome tooth (cross section) (a–n: *Hoe 704.0*, NICH; o–p: *Baldwin 104*, FH isotype; q: *Baldwin MH 461*, S).

terminal cell short to elongate, elliptic to nearly rectangular, 25–45 µm long and 9–14 µm wide, smooth, wall thin or incrassate. *Paraphyses* absent.

Sporophytes up to 3(?) per frond. *Seta* ascending, uncinate and weakly flexuose, 10.0–15.0 mm long, ochraceous to brown. *Capsule* horizontal to pendulous, ellipsoid, 1.0–1.7 mm long and 0.7–0.8 mm wide, ochraceous to brown; annulus (indistinct to) distinct. *Peristomial formula OPL:PPL:IPL* = 4:2:6–8c. *Exostome* yellow to brown;

teeth 510–540 µm long and 105–110 µm wide, entirely bordered, not shouldered; dorsal side striate in basal half to 2/3 of teeth, becoming densely papillose in distal part; dorsal plates broader than ventral ones, 7–10 µm thick; ventral plates 23 µm thick. *Endostome* probably not perforate, smooth or minutely to moderately papillose; basal membrane reaching 1/3 of length of exostome teeth; processes 360 µm long beyond orifice and 55 µm wide at base, not nodulose, not appendiculate; cilia (1? or) 2 or 3 cell plates wide and up to 14 cell plates long, not nodulose, appendiculate or not; appendages lateral. *Operculum* 1.3–1.8 mm long; rostrum conspicuously broad and flattened in distal half. *Calyptra* 2.0–2.8 mm long, ochraceous, membranous. *Spores* 15–16 µm.

Distribution — Hawaiian Islands (Maui, Hawaii). Endemic. According to Bartram (1933) rare on Maui. According to Hoe (annot. at *Hoe 704.0*) locally abundant on Hawaii.

Habitat & Ecology — Poorly known. In (dense *Cibotium–Metrosideros*) forests, probably often in mountain ravines, in moist or wet habitats. On tree trunks and on rocks. Altitude: 1500–1700 m. According to Bartram (1933) found in wet forests.

Geographical variation — Not found.

Ecological variation — Not found (insufficient data?).

Notes:

Description — 1. Brotherus (1927) and Bartram (1933) erroneously defined *Hypopterygium sandwicense* as an autoicous species. The species is, however, actually heteroicous, but plants bearing only female or both male and female gametoecia often occur. One of the two Mauiian specimens that were examined by Bartram (*Bartram 461*) is an example of a female plant. The other, the isotype in Bartram's herbarium kept in FH, bears female gametoecia, but has also a single hermaphroditic gametoecium, which Bartram apparently had overlooked.

2. In few plants the basal part of the rachis bears no branches and only a few gametoecia.

3. Because of the horizontal orientation of the plant, the basal part of the lower branches may occasionally become tomentose. In addition, the lower branches may be more developed than usual. Because in such plants, the stipe and lower part of the rachis are often distinctly tomentose and, consequently, hardly visible, the lower branches may easily be confused with an entire plant. The basal part of such branches may even strongly resemble a stipe. These typical lower branches, however, can be distinguished from the entire plant by the tristichous phyllotaxis and by the complanate foliation with distinctly dimorphic leaves in their basal part.

Reproduction — 4. Presumably, sporophytes are frequently found in *Hypopterygium sandwicense*, but the frequency of fruiting specimens in the material examined may be biased by the low number of collections and the overcollecting of fruiting plants. There were 10 fruiting specimens among the specimens examined (c. 77%, n = 13).

Specimens examined (13 specimens):

USA: Hawaiian ('Sandwich') Is.: *Baldwin 201* (NY; s.loc.). – Maui: *Baldwin 104* (FH, H-BR, NY), *Bryoth. Levier 533* (FH, S), W Maui; *Bartram 461* (FH, S), Nakalalua. – Hawaii: *Menzies (6)* (BM); *Hoe 704.0* (NICH), Kulani Honor Camp; *Degener 19929* (FH, NY), Saddle Road, 21 miles from Hilo.

DOUBTFUL HYPOPTERYGIUM SPECIES

Hypnum umbraculum Brid., Muscol. Recent. Suppl. 2 (1812) 86, nom. nud. in syn. — Original material: collector's name not given (B not found, probably destroyed), "In Phytophylaciis Parisiensibus vidi". — Given in the synonymy of *Hypnum flabilliforme* Brid., nom. illeg., incl. spec. prior. (*Leskea tamariscina* Hedw., 1801 ≡ *Canalohypopterygium tamariscinum* (Hedw.)

Kruijer) by Bridel l.c.; given in the synonymy of *Hypopterygium tamariscinum* (Hedw.) Brid. by Bridel, Bryol. Univ. 2 (1827) 715.

Note — Bridel's (1812) description is not decisive for the identity of *Hypnum umbraculum*. There is no evidence for his opinion (1827) that it belongs to *Hypopterygium tamariscinum* (Hedw.) Brid. (≡ *Canalohypopterygium tamariscinum* (Hedw.) Kruijer), because Bridel's (1812) description does not mention rudimentary branches that are so characteristic for the latter species. It is, therefore, most likely that *Hypnum umbraculum* actually belongs to one of the *Hypopterygium* species.

Hypopterygium rotulatum (Hedw.) Brid., Bryol. Univ. 2 (1827) 713. — *Leskea rotulata* Hedw., Sp. Musc. Frond. (1801) 213, t. 51, f. 8–13. — *Hypnum rotulatum* (Hedw.) P. Beauv., Prodr. (1805) 69. — *Hookeria rotulata* (Hedw.) Sm., Trans. Linn. Soc. London 9 (1808) 279; quod nom., fide Wilson & Hooker f. in Hooker f., Bot. Antarct. Voy. 2 (2) (1854, '1855') 118. — *Pterygophyllum rotulatum* (Hedw.) Brid., Muscol. Recent. Suppl. 4 (1818, '1819') 151. — Type: "Insulae meridionales", (material absent from Hedwig-Schwaegrichen's herbarium kept in G, elsewhere not found; see 'General typification problems', p.24); lectotype: Hedwig, Sp. Musc. Frond. (1801) t. 51, f. 8–13; designated here.

Note — Hedwig's (1801) *Leskea rotulata* is clearly a *Hypopterygium* species, but, unfortunately, his description and illustrations lack differentiating character states at the specific level. In the material that I examined, all specimens collected before 1800 prove to belong to *Hypopterygium didictyon*, but there was no evidence, or even indication, that this set of specimens includes Hedwig's type material. Bridel (1812, 1819) and Schwägrichen (1816) followed Hedwig's inadequate circumscription of *Leskea rotulata*. Bridel (1827) presumably included Australasian representatives of *H. didictyon* and *H. tamarisci* in *H. rotulatum*. Hooker's (1818) interpretation of *L. rotulata* corresponds with *H. tamarisci*. His interpretation was followed by, amongst others, Sprengel (1820), Hooker & Greville (1825), and Wilson (1855). Müller's (1850) interpretation of Hedwig's species probably corresponds with *H. didictyon*.

Mitten's (in Hooker f., 1867) interpretation of Hedwig's *Leskea rotulata* is very confusing. He considered Wilson's (1855) interpretation of this species to be incorrect and referred his *L. rotulata* to *Hypopterygium viridulum* Mitt. (= *H. tamarisci*). Mitten examined a specimen that was collected by Kerr in Whangaroa, New Zealand. If Kerr's specimen from Whangaroa, New Zealand, present as '*Hypopterygium rotulatum*' in Mitten's herbarium (NY), is the one to which Mitten referred to, than Mitten included *H. didictyon* in his concept of the species. His description of the species, however, corresponds well with *H. tamarisci*.

See for a comparison of *Hypopterygium didictyon* with *H. tamarisci* further '*H. didictyon*', note 17, p. 155.

Pterygophyllum jungermannioides Brid., Muscol. Recent. Suppl. 4 (1818, '1819') 152, '*Pterigophyllum*'. — *Hookeria jungermannioides* (Brid.) Steud., Nomencl. Bot. 2 (1824) 201, '*jungermannoides*'. — Type: collector's name not given (B holo not found, probably destroyed), "E Novâ Hollandiâ allatum clar. Desfontaines sub nomine Jungermanniae communicavit.". — Given in the synonymy of *Hypopterygium tamariscinum* (Hedw.) Brid. by Bridel, Bryol. Univ. 2 (1827) 715.

Note — Bridel's (1819) description of *Pterygophyllum jungermannioides* and his reported origin of its type give insufficient support for Bridel's (1827) opinion that *P. jungermannioides* is conspecific with *Hypopterygium tamariscinum* (Hedw.) Brid. (≡ *Canalohypopterygium tamariscinum* (Hedw.) Kruijer). The description of *P. jungermannioides* does not mention rudimentary branches that are so characteristic for *Canalohypopterygium tamariscinum*. It is, therefore, more likely, that *P. jungermannioides* is conspecific with either *H. tamarisci* or with *H. didictyon*.

5. LOPIDIUM Hook.f. & Wilson — Map 16

Lopidium Hook.f. & Wilson in Hook.f., Bot. Antarct. Voy. 2(2) (1854, '1855') 119; from the Greek λοπις (lopis, a scale). — *Hypopterygium* subgen. *Lopidium* (Hook.f. & Wilson) Bosch & Sande Lac., Bryol. Jav. 2 (1861) 8. — *Hypopterygium* sect. *Lopidium* (Hook.f. & Wilson)

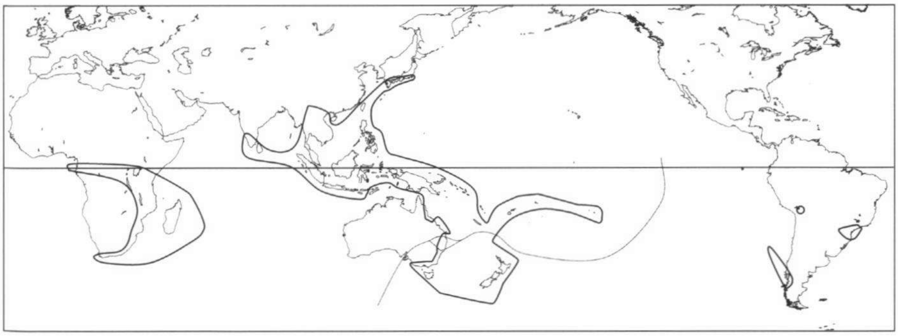
Mitt., J. Proc. Linn. Soc., Bot. 12 (1869) 329. — *Lophidium* Brid. ex Rodway, Pap. & Proc. Roy. Soc. Tasmania 1913 (1914) 237, nom. illeg. incl. gen. prior, err. pro *Lopidium* Hook.f. & Wilson. — Lectotype: *Lopidium concinnum* (W. Hook.) Wilson in Hook.f. — Lectotype designated by Matteri, Bol. Soc. Argent. Bot. 15 (1973) 234, who erroneously accredited the selection of the lectotype to Dixon, New Zealand Inst. Bull. 3, 5 (1927) 293. — Resurrected as a separate genus by Fleischer, Musc. Buitenzorg 3: 1067. 1908; see note 6.

Plants forming loose to dense groups of fans, usually branched, rarely simple, dull, frequently glaucous or greyish green (see note 1), less often yellowish green or blackish green, gemmiferous or not; ramification usually pinnate to bipinnate (or tripinnate), occasionally weakly flabellate, usually two-dimensional with all branches in a single plane, occasionally weakly three-dimensional with several branches projecting in other directions than lateral (ascending or descending; see note 2). *Stems* differentiated into stipe and rachis, ascending from substratum and becoming horizontal (see note 3). *Stipe* straight, entirely glabrous or tomentose at base, reddish brown to blackish brown in basal part, becoming green to dark brown and less saturated in colour in distal part. *Frond* ± complanate, horizontal (see note 3), usually ovate to short-linear-elliptic, occasionally rhombic (in *L. concinnum*); rachis and branches occasionally with flagelliform innovations (see note 4), glabrous, pale green to blackish-brown, in basal part often with a darker and more saturated colour than in distal part; rachis horizontal or curved downwards towards apex; branches distant or closely set, erecto-patent to widely patent, straight or curved downwards; apex of foliate rachis and branches usually rounded, occasionally attenuate or caudate by a flagelliform innovation. *Rudimentary branches* absent. *Shoot axes* terete. *Epidermis* ± similar in cellular structure to (outer)cortex. *Cortex* differentiated in stipe and basal part of frond axes, becoming weakly differentiated or not differentiated in distal part of frond axes. *Central strand* absent (absent or present in stipe of *L. struthiopteris*). *Axial cavities* absent or present, either (sub)central or situated in cortex of stipe, rachis, or branches; inclusions present. *Axillary hairs* present; basal cells brown; intermediate cells absent; terminal cell straight (to recurved in *L. struthiopteris*), colourless, smooth. *Phyllotaxis* tristichous. *Foliation*: in basal part of stipe and of flagelliform innovations isophyllous and not complanate or weakly anisophyllous and weakly complanate; in distal part of stipe and of rachis and branches usually distinctly anisophyllous and complanate, less often weakly anisophyllous and weakly complanate (occasionally isophyllous and not complanate at all axes in *L. concinnum*). *Leaves* smooth or weakly wrinkled when moist, moderately crisped or twisted when dry; margin entire or partly serrate to serrate-dentate; border distinct (or faint or interrupted near leaf base or apex); apex usually acute or acuminate, occasionally subulate (rarely obtuse in *L. struthiopteris*); costa distinct, simple (rarely weakly forked in distal part); laminal cells collenchymatous, isodiametric, transverse-hexagonal or hexagonal, walls incrassate, in particular in corners of the cell; costa cells longer than adjacent laminal cells, short-linear to linear, hexagonal or rectangular to rhomboid in basal part of costa, walls incrassate, porose; border and acumen cells usually longer, hexagonal to linear, often with a rhomboid outline near leaf margin, walls incrassate, porose. *Basal stipe leaves* monomorphic, scale-like or leaf-like, appressed to erecto-patent. *Distal stipe leaves and frond leaves* dimorphic (or monomorphic in *L. concinnum*), straight or falcate-secund. *Lateral stipe and frond leaves* (appressed or) erecto-patent to widely patent, asymmetrical (or symmetrical in

L. concinnum), short-ovate to lanceolate-ovate; insertion concave or nearly oblique, descending at dorsal side of axis, descending to ascending at ventral side; base not decurrent or decurrent at ventral side of axis; costa usually ± percurrent. *Amphigastria* symmetrical, appressed to patent, broad-ovate, subcircular, or ovate; basal part (nearly flat or) smoothly curved; insertion concave, transverse-flexuose, transverse, or convex; base decurrent or not; basal part of lamina nearly flat or smoothly curved; costa ± percurrent (to excurrent in *L. concinnum*).

Monoicous or *dioicous*. *Gametoecia* in basal or middle part of frond axes, most frequently at rachis, occasionally at branches. *Gametoecial leaves* usually concave (or frequently V-shaped in cross section in full-grown perichaetia of *L. concinnum*), subcircular or short-ovate to lanceolate-obovate, or weakly lingulate to weakly ligulate; margin ± entire; border interrupted or continuous, faint or distinct; apex acuminate or subulate; costa absent, faint, or distinct; laminal cells prosenchymatous or weakly parenchymatous in basal part of leaf, when prosenchymatous short to short-linear and hexagonal, when parenchymatous transverse-rectangular to short-linear-rectangular; border cells transverse-rectangular to linear, occasionally weakly rhomboid; acumen cells short to short-linear, hexagonal; costa cells short to short-linear, rectangular, rhomboid, or hexagonal; walls of gametoecial leaf cells thin or incrassate. *Paraphyses* absent or present, simple, filiform or partly to almost entirely widened and leaf-like.

Sporophyte projecting above or lying in plane of frond. *Seta* horizontal or ascending, straight to uncinate, weakly to distinctly mamillate; base narrow. *Capsule* erect to pendulous, subglobose to elongate-cylindrical, smooth; neck ± smooth; orifice transverse. *Peristome* double. *Exostome* present, colourless or yellow; teeth entirely bordered, not shouldered; dorsal side striate in basal part of teeth, becoming papillose above; median line zig-zag in *L. concinnum* and present as a roughly straight border in *L. struthiopteris*, not furrowed; lamellae weakly or distinctly projecting or not; papillae low, simple; striae papillose or not; dorsal plates broader than ventral plates; ventral plates and trabeculae smooth or minutely papillose. *Endostome* colourless, perforate or not, smooth or papillose at both faces; papillae low, simple; processes distinctly keeled; cilia absent or rudimentary and consisting of parts of 1 (or 2) plates. *Operculum* long-rostrate, ochraceous to dark brown; rostrum oblique. *Calyptra* cucullate, entirely covering operculum, pale ochraceous or partly colourless in basal part or partly brown



Map 16. Distribution of *Lopidium* Hook.f. & Wilson. The dotted lines represent the border between the areas of the two species.

in distal third, naked (in *L. concinnum*) or set with paraphyses (in *L. struthiopteris*), membranous in basal part, becoming fleshy in distal third, smooth; apex dark brown or reddish brown.

A genus of 2 species.

Distribution — Subsaharan Africa, Indo Malaysia, Sino Japan, E Australasia, SW Polynesia, and mainly non-tropical South America. See note 5.

Habitat & Ecology — In forests, often in shaded or wet habitats. Usually on tree trunks, stem bases, saplings, tree branches, and climbers; less often on tree ferns, rocks, rotting logs; infrequently (*L. concinnum*) or rarely (*L. struthiopteris*) terrestrial.

Notes:

Description — 1. The glaucous or greyish and dull colours of the plants are caused by the wax-like surface layer that covers the leaves and amphigastria (see 'Morphology', 'Cuticle', p. 42).

2. The fronds of *Lopidium* plants with a weak, three-dimensional ramification have short, ventral branches that are situated between the amphigastria. These branches are usually descending and occur in between the, usually much larger, 'normal' lateral branches, which are associated with the lateral leaves. The lateral branches are usually more or less horizontal, but are occasionally ascending or descending. In both *Lopidium* species, only a small minority of the plants have a frond with a three-dimensional ramification. Such plants occur most frequently in *L. concinnum*, but are rare in *L. struthiopteris*.

3. The stem of *Lopidium* plants grows generally horizontally or pendulously from a more or less vertical substrate (cf. Fleischer, 1908; Allison & Child, 1971; Scott & Stone, 1976), whereby most of the lateral branches are arranged in a more or less flat and horizontal, or roof-like frond, which is inclined at both sides of the rachis.

Hooker f. & Wilson (in Wilson, 1855), Kindberg (1901), and Brotherus (1907) incorrectly described the frond as growing erect.

4. Plants of *L. struthiopteris* have more often flagelliform innovations than those of *L. concinnum*.

Distribution — 5. The two *Lopidium* species have an almost allopatric distribution. The two species occur in entirely separate areas, except for a narrow zone in Australia, where a small overlap in the distribution area exists near the Queensland and New South Wales border.

In New South Wales *Lopidium struthiopteris* reaches Briggsvale (north of Dorrigo) to the south, whereas *L. concinnum* reaches Point Lookout (south of Dorrigo) to the north. It is not known whether they actually occur together at the same locality. *L. concinnum* may have reached Queensland, for a single specimen is attributed to Moreton Bay, near Brisbane, but this record is dubious.

Delimitation and identification — 6. When Fleischer (1908) resurrected *Lopidium*, he made clear that in his opinion the genus represents a natural genus, which is distinctly separated from *Hypopterygium*. He distinguished the former genus from the latter by several gametophytic and sporophytic characters: the anatomy and growth direction of the stem, the shape and areolation of the leaves, and the extent of peristome development. Fleischer (1908) described the stem ("secundäre Stengel") of *Lopidium* as growing more or less horizontally from a vertical substrate, lacking a central strand, and having an undifferentiated cortex consisting of cells with incrassate walls, which become almost stereids in the outer cortex. The [frond] leaves were described as being "oval-bis lanzettzungenförmig" (ovate to lanceolate-lingulate) and having a percurrent (to excurrent) costa, and small, subcircular laminal cells with incrassate walls.

By contrast, Fleischer (1908) described the stem of *Hypopterygium* as being ascending or vertical and having a distinct central strand and a differentiated cortex (with, in the rhizome and the basal part of the stem, three layers of cells: two layers of thin-walled cells, one surrounding the central strand and one situated just below the epidermis, with an intervening layer of thick-walled cells). The lateral frond leaves were described as being "schmal-oval bis sehr breit-oval" (narrow- to broad-ovate), and having a costa that ends well before the apex. The amphigastria were described as more or less broad-elliptic.

Fleischer's (1908) discriminating characters of the gametophore are not always correct, as he overlooked that the stem of *Hypopterygium vriesei* may grow horizontally from a vertical substrate.

He also overlooked the occasional presence of a central strand in the stipe of *Lopidium struthiopteris*, and overestimated the differentiation of the cortex in *Hypopterygium*. However, he emphasised the differences between *Lopidium* and *Hypopterygium* in the shape of the frond leaves and their areolation, and these differences are striking. Generally, the ratio of length to width in the frond leaves is higher in *Lopidium* than in *Hypopterygium* and the frond leaves of *Lopidium* have more distinctly parallel sides. Often, plants of *Lopidium* can easily be recognised by their dull, often greyish-green and falcate-secund lateral frond leaves.

In *Lopidium*, the costa of the lateral frond leaves is almost always percurrent or nearly so. In *Hypopterygium*, the length of the costa in the lateral frond shows usually more variation, but in most species does not extend beyond 4/5 of leaf length. In two *Hypopterygium* species percurrent costae may be observed in some lateral frond leaves, but the same frond always contains leaves with costae that end well below the apex. The laminal leaf cells of *Lopidium* vary in shape from transverse-hexagonal to hexagonal, but are generally more or less isodiametric. The wall of laminal leaf cells in *Lopidium* is usually incrassate, and generally most distinctly incrassate near the angles of the cell, which contributes to a collenchymatous areolation of the lamina.

The laminal leaf cells of *Hypopterygium* are short- to elongate-hexagonal. They are generally longer than those of *Lopidium*, and have considerably thinner walls. A pronounced thickening of the cell walls at the angles of the laminal leaf cells is usually absent from *Hypopterygium*. A distinct collenchymatous leaf areolation does not occur in this genus. In fact, most *Hypopterygium* species show no collenchymatous leaf areolation whatsoever, although a weak collenchymatous areolation was found in the distal part of frond leaves of the 'East Malesian' variant of *H. flavolimbatum*.

Fleischer's differentiating sporophytic characters are only partly correct. He characterised *Lopidium* by its short seta and its less-developed, non-ciliate peristome ("leskeaartig"), and *Hypopterygium* by its longer seta and its well-developed, ciliate peristome ("hypnumartig"). Fleischer's judgment on the presence or absence of endostomial cilia as differentiating character states is essentially correct, but there exists considerable overlap in seta length between *Lopidium* and *Hypopterygium*. Fleischer overlooked that the seta is smooth in *Hypopterygium*, and mamillate in *Lopidium*.

KEY TO THE SPECIES

1a. Gemmae absent. Monoicous. Paraphyses in full-grown perichaetia absent or present, immersed. Exostome teeth 70 μm wide at least. Calyptra naked .... **5.1. L. concinnum**

b. Gemmae (almost always) present. Dioicous. Paraphyses in full-grown perichaetia present and frequently partly exserted. Exostome teeth less than 70 μm wide. Calyptra with paraphyses .... **5.2. L. struthiopteris**

Notes on identification:

1. *Lopidium struthiopteris* is strictly dioicous. *L. concinnum* is monoicous, but shows some variability in sexuality. Most of its plants are bisexual, but occasionally unisexual plants occur. These plants are often characterised by their monomorphic or weakly dimorphic frond leaves, by which they can be distinguished from the unisexual plants of *L. struthiopteris*.

The bisexual plants of *Lopidium concinnum* have in majority unisexual gametoecia (male and female), and bear rarely a few bisexual gametoecia.

2. Sporophytes are rare in *Lopidium struthiopteris*, but occur frequently in *L. concinnum*.

5.1. **Lopidium concinnum** (W. Hook.) Wilson — Fig. 37, 38, 41B, 42B; Map 17; Plate 3b

Lopidium concinnum (W. Hook.) Wilson in Hook.f., Bot. Antarct. Voy. 2(2) (1854, '1855') 119. — *Leskea concinna* W. Hook., Musci Exot. 1 (1818) t. 34. — *Hookeria concinna* (W. Hook.) W. Hook. & Grev., Edinburg J. Sci. 2 (1825) 232. — *Hypopterygium concinnum* (W. Hook.) Brid., Bryol. Univ. 2 (1827) 711. — Type: *Menzies s.n.* (BM holo, sub nos. *84* and *H. 1529a*; BM, fragments sub no. *H. 1529b*; G? n.v., S), New Zealand, South Island, Southland L.D., Dusky Sound ["Dusky Bay"], 1791; potential isotype: *Menzies s.n.* (NY, hb. Mitten, s.loc.). — See note 1.

Lopidium pallens Hook.f. & Wilson in Hook.f., Bot. Antarct. Voy. 2(2) (1854, '1855') 119. — *Hypopterygium pallens* (Hook.f. & Wilson) Mitt., Hooker's J. Bot. Kew. Gard. Misc. 8 (1856) 265. — *Hypopterygium pallens* (Hook.f. & Wilson) Reichardt in Fenzl, Reise Novara, Bot., Bd. 1 (1870) 194, hom. illeg. — Syntypes: *Sinclair s.n.* (BM; see note 2), New Zealand, Waikehi; *Lyall s.n.* (BM), New Zealand, Ship Cove; *Hooker 386* (BM, "New Zealand, Antarct. Exp. 1839–1843", see note 2), New Zealand, North Island, North Auckland L.D., Bay of Islands; *Sinclair s.n.* (BM), New Zealand, North Island, North Auckland L.D., Auckland; *Lyall 126* (BM lecto, designated here), New Zealand, North Island, Wellington L.D., Hutt Valley; *Lyall 112* (BM), New Zealand, North Island, Wellington L.D., Wellington; *Lyall 23* (BM), New Zealand, South Island, Southland L.D., Milford Sound; *Lyall 184* (BM), New Zealand, South Island, Southland L.D., Bligh's Sound. — Erroneously merged with *Hypopterygium struthiopteris* (Brid.) Brid. by Mitten, J. Linn. Soc., Bot. 4 (1860) 96. — Synonymised with *Hypopterygium concinnum* (W. Hook) Brid. by Dixon, New Zealand Inst. Bull. 3, 5 (1927) 292. — See note 3.

Hypopterygium plumarium Mitt., J. Linn. Soc., Bot. 12 (1869) 329. — *Lopidium plumarium* (Mitt.) Hampe, Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn. 1879 (1879) 162. — *Hypopterygium pallens* (Hook.f. & Wilson) Mitt. ssp. *plumarium* (Mitt.) Kindb., Hedwigia 40 (1901) 281. — Syntypes: *Weir 1* (BM lecto, designated here, s.loc.; S, also sub no. *12* in hb. Kindberg; H n.v., JE n.v., TNS n.v.), Brazil, Paraná, ["in sylvulis 'çapaos' planitierum 'campos' ad arborum truncos, etiam Fazenda do Lageado prope Corritiba" (= Curitiba), alt. 2000 ft.; *Lobb s.n.* (n.v.), Chile, Chiloé Island ["Chiloé"]; *Hooker s.n.* (not found with certainty), New Zealand, Auckland Islands(?), ["ins. Auckland"]; possible syntypes: *Lobb 45* (BM), Chile, Chiloé Island ["Chiloé"]; *Hooker 90* (BM; BM, sub no. *W. 90*; ?: BM, NY, s. coll. (Hooker?), sub no. *W. 90*), New Zealand, Auckland Islands, see note 4. — Synonymised with *Lopidium concinnum* (W. Hook.) Wilson by Thériot, Rev. Chil. Hist. Nat. 38 (1934) 84. — See note 5.

Hypopterygium flexisetum Hampe ex Lor., Bot. Zeitung (Berlin) 24 (1866) 187, nom. nud. — *Hypopterygium flexisetum* Hampe ex Kindb., Hedwigia 40 (1901) 281, nom. nud. in syn. (*Hypopterygium concinnum* (W. Hook.) Brid.). — *Lopidium flexisetum* M. Fleisch., Hedwigia 63 (1922) 213, nom. nud. — Original material: *Krause s.n.* (BM, 'reflexisetum'; L, S, *s.n.*; S, sub nos. *5* and *10* in hb. Kindberg; B destroyed), Chile, Valdivia, Corral, "in sylvis umbrosis ad arborum truncos", alt. 500 ft. — The original material was collected before 1865, see Lorentz l.c. — Synonymised with *Lopidium plumarium* (Mitt.) Hampe by Reimers, Hedwigia 66 (1926) 69. — Given in the synonymy of *Hypopterygium concinnum* (W. Hook.) Brid. by Kindberg l.c., and Thériot, Revista Chilena Hist. Nat. 38 (1934) 85.

Lopidium aristatulum Müll.Hal. in Ule, Bryoth. Brasil. (1891) 66, nom. nud.; Hedwigia 38 (Beibl.) (1899) 58., nom. nud. — *Hypopterygium aristatulum* Müll.Hal. ex Kindb., Hedwigia 40 (1901) 281, nom. nud. in syn. (*Hypopterygium pallens* (Hook.f. & Wilson) Mitt. ssp. *plumarium* (Mitt.) Kindb.). — Original material: *Ule, Bryoth. Brasil. 66* (B destroyed; L, PC, S), Brazil, Santa Catharina, Pedro Grandes, Aug., 1890; *Ule, Bryoth. Brasil. 66* (B destroyed; BM, BR, H n.v., HBG, JE n.v., S, UPS n.v.), Pedro Geral, Aug., 1890; *Ule, Bryoth. Brasil. 66* (B destroyed; L, S), Blumenau, July, 1898. — Given in the synonymy of *Lopidium plumarium* (Mitt.) Hampe by Fleischer, Musc. Buitenzorg 3 (1908) 1073.

Hypopterygium araucarieti Müll.Hal. ex Kindb., Hedwigia 40 (1901) 281, nom. nud. in syn. (*Hypopterygium pallens* (Hook.f. & Wilson) Mitt. ssp. *plumarium* (Mitt.) Kindb.). — *Lopidium araucarieti* M. Fleisch., Hedwigia 63 (1922) 213, nom. nud. — Original material: *Ule s.n.* (B destroyed; S, sub no. *12* in hb. Kindberg), Brazil, Apr. 1889; possible original material: *Ule, Herbar Brasil. 542* (H n.v., PC), Brazil, Santa Catharina, "Entroncos do mato dos pinheiros azima da Serra Geral", Apr., 1889; *Ule, Herbar Brasil. 542* (HBG), Brazil, Santa Catharina, "An Baumstämmen im Araucarienwalde auf der Serra do Oratorio", Apr., 1889. — Given in the synonymy of *Lopidium concinnum* (W. Hook.) Wilson by Matteri, Bol. Soc. Argent. Bot. 15: (1973) 234.

Hypopterygium hyalinolimbatum Müll.Hal. ex Kindb., Hedwigia 40 (1901) 281, nom. nud. in syn. (*Hypopterygium pallens* (Hook.f. & Wilson) Mitt. ssp. *plumarium* (Mitt.) Kindb.), '*hyalino-limbatum*'; syn. nov. — *Lopidium hyalinolimbatum* M. Fleisch., Hedwigia 63 (1922) 213, '*hyalino-limbatum*'; nom. nud. — *Hypopterygium hyalo-limbata* Müll.Hal. ex Burges, Proc. Linn. Soc. New South Wales 60 (1935) 88, nom. illeg. orthogr. err. pro *Hypopterygium hyalinolimbatum* Müll.Hal. ex Kindb. — Original material: *Whitelegge s.n.* (S; MEL, sub no. *189*, "on rocks", Nov. 8), Australia, New South Wales, Mossvale, Nov., 1884.

Illustrations: Hooker, Musci Exot. 1 (1818) t. 34. — Schwägrichen, Sp. Musc. Frond., Suppl. 3, 2 (1829) t. 269.— Brotherus in Engler & Prantl, Nat. Pflanzenfam., ed. 1: f. 706. 1907; ed. 2, 11 (1925) f. 625. — Noguchi, J. Hattori Bot. Lab. 6 (1951) 27. f. 2.1, (seta in cross section, see note 6; as *L. plumarium*). — Sehnem, Pesquisas, Bot. 27 (1969) pl. 5, f. 8. — Allison & Child, Mosses of New Zealand (1971) p. 123 & pl. 28. — Matteri, Bol. Soc. Argent. Bot. 15 (1973) 236, pl. 1. — Ramsay, Austral. J. Bot. 22 (1974) 327, f. 107, (karyotype). — B. & N. Malcolm, The Forest Carpet (1989) 57. — Beever et al., Mosses of New Zealand (1992) pl. 69 & f. 71. — B. & N. Malcolm, Mosses and other Bryophytes (2000) 1, 78, 86, 156. — Gradstein et al., Mem. New York Bot. Gard. 86 (2001) f. 144 A–C.

Plants medium-sized to large, not gemmiferous (see note 7). *Stipe* up to 3.0(–5.0) cm long, entirely dorsiventrally compressed or laterally compressed in basal part and dorsiventrally compressed above. *Frond* up to 10.5 cm in diameter; rachis dorsiventrally compressed; branches up to 3.0 cm long, frequently tinged red when set with caducous leaves. *Primordia* naked or set with scaly leaves; scaly leaves deltoid to ovate-oblong, margin entire. *Epidermis cells and cortical cells of stipe, rachis, and branches* equally narrow or cortical ones wider; walls thin or incrassate, colourless to dark brown; inclusions absent. *Central strand* absent. *Axial cavities* absent or situated in cortex of stipe, rachis, and branches, occasionally becoming central in distal part of rachis and branches, more frequently central in ultimate branches, in cross-section up to 9 in stipe and basal part of rachis, up to 5 in distal part of rachis and branches (see note 8); inclusions droplets or amorphous solids, oil-like or wax-like, colourless (white) to olivaceous or reddish brown. *Axillary hairs* up to 2 per leaf, 2–4-celled; basal cells 1–3; terminal cell short to elongate, usually elliptic to rectangular, occasionally subcircular to obovate, straight, (10–)15–35 µm long and (7–)10–15 µm wide. *Leaves* distant or closely set; laminal cells 7.0–20.0 µm long and 7.0–20.0 µm wide. *Basal stipe leaves* small, monomorphic or dimorphic, few in number; apex gradually or abruptly acuminate. *Distal stipe leaves* monomorphic or dimorphic; margin entire or weakly serrate-dentate to moderately serrate. *Lateral stipe leaves* asymmetrical or symmetrical, ovate to oblong-ovate, 1.0–3.0 mm long and 0.5–1.5 mm wide; apex gradually or abruptly acuminate; costa ± percurrent. *Stipe amphigastria* symmetrical, usually broad-ovate to ovate, occasionally subcircular, 0.5–2.5 mm long and 0.5–1.5 mm wide; apex usually gradually or abruptly acuminate, occasionally subulate; costa almost percurrent to excurrent. *Frond leaves* monomorphic or dimorphic, occasionally caducous in apical part of rachis, more frequently caducous in distal part of branches; margin weakly serrate-dentate to moderately serrate; teeth 1-celled, up to 40 µm long, projecting up to 1/2 of its length; border distinct, continuous (or narrow, faint, or interrupted near leaf apex), 1–5 cells wide; branch leaves almost similar to rachis leaves or smaller. *Lateral frond leaves* asymmetrical or symmetrical, ovate to lanceolate-ovate, 0.5–3.5 mm long and 0.4–1.5 mm wide; apex gradually or abruptly acuminate or acute; acumen 0.05–0.5 mm long; costa ± percurrent. *Frond amphigastria*

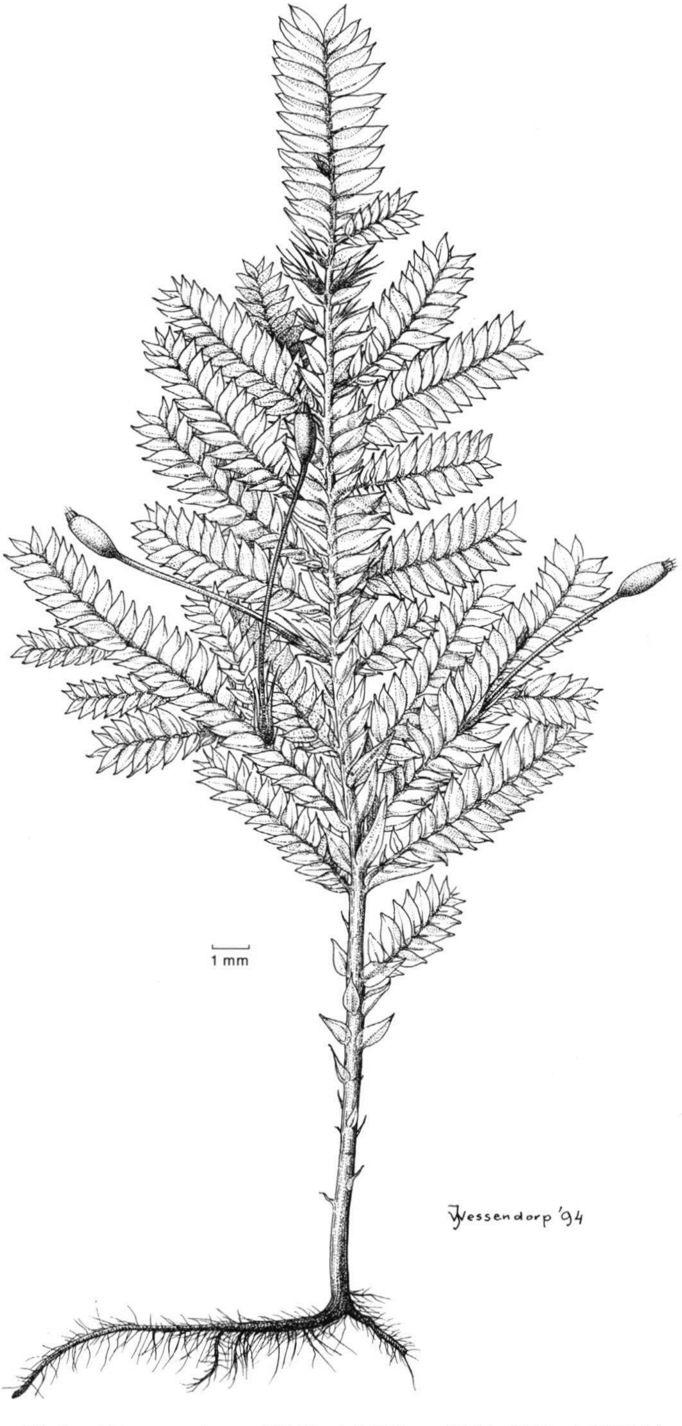


Fig. 37. *Lopidium concinnum* (W. Hook.) Wilson. Habit (*Telford 4207*, L).

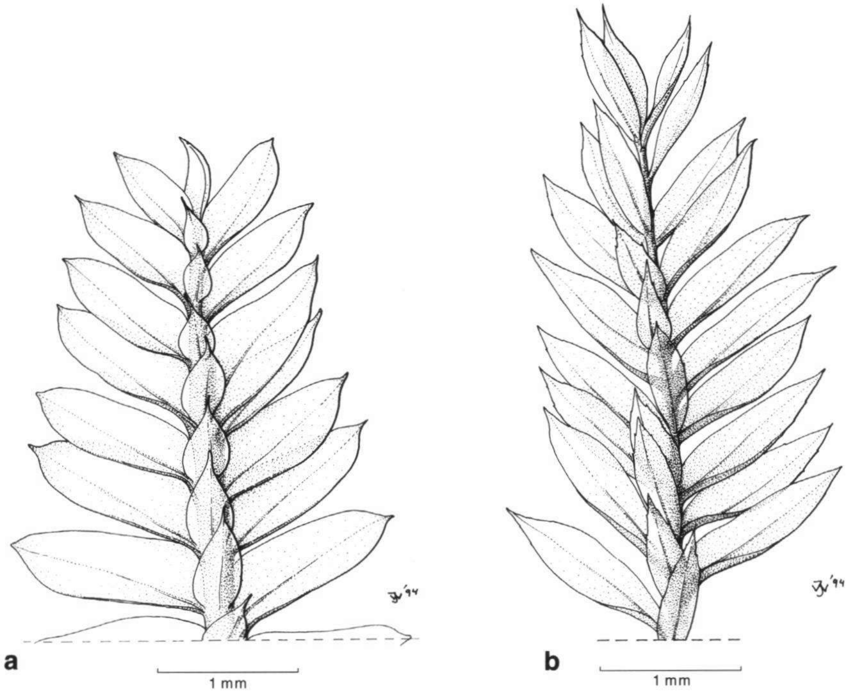


Fig. 38. *Lopidium concinnum* (W. Hook.) Wilson. Distal part of frond axes (ventral view): a. foliated with anisophyllous foliation; b. partly defoliated and with anisophyllous to isophyllous foliation (a: *Telford 4207*, L; b: *Crosby 12450*, L).

symmetrical, ovate to oblong-ovate, 0.3–3.0 mm long and 0.2–1.5 mm wide; apex gradually or abruptly acuminate or acute; acumen 0.1–0.3 mm long; costa almost percurrent to excurrent.

Autoicous, but occasionally dioicous, and rarely heteroicous (see note 9). *Gametoecia* in basal and middle part of frond axes, usually unisexual, rarely bisexual. *Perigonia* placed among perichaetia. *Inner leaves*: of perigonia short-ovate to elliptic, obovate, or weakly lingulate, up to 0.5 mm long and 0.5 mm wide, acumen up to 0.3 mm long, costa absent; of perichaetia prior to sporophyte development usually ovate to elliptic, occasionally subcircular and subulate, up to 1.0 mm long and 0.6 mm wide, acumen up to 1.5 mm long, costa absent, faint, or distinct, but frequently absent near leaf base, when present ± percurrent; of full-grown perichaetia oblong or weakly lingulate to lanceolate-obovate, up to 1.5 mm long and 0.6 mm wide, acumen up to 0.6 mm long, costa distinct, reaching 2/3 of leaf length to excurrent. *Antheridia* c. 0.3 mm long. *Stalk in full-grown perichaetia* 0.2–1.1 mm long. *Archegonia* 0.3–0.4 mm long. *Vaginula* 0.8–1.1 mm long, occasionally set with paraphyses (see note 10). *Gametoecial axillary hairs* up to 3 per gametoecial leaf, 3- or 4-celled; basal cells 2 or 3, brown; intermediate cells absent; terminal cell short to elongate, subcircular or elliptic to obovate, 10–40 μm long and 8–20 μm wide, smooth. *Paraphyses* absent from perigonia, absent or few in perichaetia (see note 10), simple, usually entirely colourless or pale brown to brown in basal and middle part when filiform, occasionally pale green (chloroplasts visible) when leaf-like, smooth or weakly verrucose in basal part; basal cells 1–3; intermediate cells short to short-linear, rectangular or truncate-elliptic in filiform parts of paraphyses, rectangular to hexagonal in leaf-like parts; terminal cell short to oblong, deltoid to elliptic, 20–35 µm long and 10–20 µm wide; *paraphyses in perichaetia prior to sporophyte development* filiform, 4–8 cells long and 1 or 2 cells wide; *paraphyses in final stages of sporophyte development* filiform or leaf-like, situated on vaginula, absent from calyptra, numerous cells long and (1–)2–20 cells wide, reaching up to 1.3 mm long and 0.2 mm wide, shorter than perichaetial leaves, straight or capricious in direction, occasionally mamillate.

Sporophytes up to 20 per frond, ochraceous to brown, frequently tinged with red. *Seta* 2.5–9.5 mm long. *Capsule* subglobose, turbinate, ellipsoid, clavate, or cylindrical, 0.7–2.0 mm long and 0.4–1.0 mm wide; annulus indistinct to distinct. *Peristomial formula OPL:PPL:IPL* = 4:2:4–6c. *Preperistome* absent. *Exostome* yellow; teeth 390–600 µm long and 75–90 µm wide; dorsal side striate in basal third to half of teeth, becoming moderately to coarsely papillose above; median line zig-zag; lamellae weakly projecting or not in basal half of teeth, distinctly projecting in distal part; striae distinctly papillose; dorsal plates 9–16 µm thick; lamellae not projecting; ventral plates 12–16 µm thick; trabeculae short in basal fourth of teeth, short to pronounced in middle part of teeth, becoming very short near apex. *Endostome* weakly papillose or not; basal membrane reaching c. 1/3 of length of exostome teeth; processes projecting 290–540 µm beyond orifice and 35–60 µm wide at base, not keeled, weakly nodulose or not, occasionally appendiculate with a few lateral appendages or not. *Operculum* 0.9–1.4 mm long. *Calyptra* 1.2–2.5 mm long, naked; margin entire; paraphyses absent. *Spores* 11–20 µm.

Distribution — Australia (Queensland, New South Wales, Victoria, Tasmania), Norfolk Island?, New Zealand (North Island, South Island, Stewart Island, Auckland Islands), Bolivia, Chile (Juan Fernandez Islands, mainland), Brazil (Minas Geraïs, São Paulo, Paraná, Santa Catarina). See note 12–14.

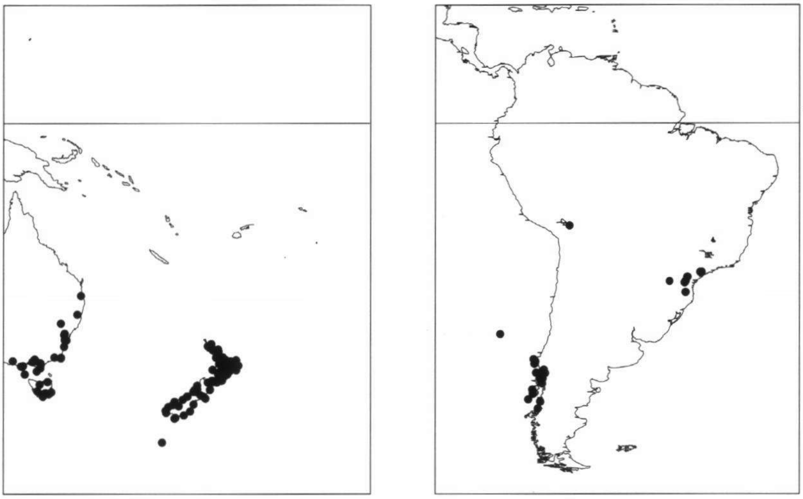
In Brazil also reported from Rio Grande do Sul (Sehnem, 1969; Matteri, 1973). According to Burges (1935) common in rain forests on the coast of New South Wales, Australia.

Habitat & Ecology — In forests, often in shaded or wet habitats. Generally on trunks, stem bases, or branches of trees, but also on tree ferns and rocks (basalt, granite, volcanic); less frequently terrestrial or on exposed roots; rarely epiphyllous.

In New Zealand, patches of fans growing intermingled with other mosses may cover trunks and branches to a length of over 1 m (Klazenga, pers. comm).

According to Beever (1984), in New Zealand mainly epiphytic on seed plants, but also on tree ferns and then most frequently on *Sphaeropteris medullaris* (G. Forst.) Bernh. (≡ *Cyathea medullaris* (G. Forst.) Sw.), and less often on *Dicksonia squarrosa* (G. Forst.) Sw. In Paraná, Brazil, once found on the skin of a mammal (*Robert s.n.*), possibly a sloth (*Bradypodidae* species).

Altitude: 0–1130 m in continental Australia and New Zealand, up to 500 m in Tasmania; 0–650 m in southern Chile and Juan Fernandez Islands; poorly recorded for Brazil, but found up to 1100 m. Once collected in Bolivia and found at 3350 m.



Map 17. Distribution of *Lopidium concinnum* (W. Hook.) Wilson.

According to Matteri (1973) found between 250–1000 m in the distribution area of *Araucaria angustifolia* (Bertol.) Kuntze in SE Brazil; according to Sehnem (1969) found there between 250–1200 m. According to Matteri (1973) up to 700 m on the Juan Fernandez Islands. According to Vitt (1979) absent from the low elevation forests on the Auckland Islands, but found there between 430–470 m altitude in the tussock-grassland zone, in crevices, under rock overhangs, and the bases of rock outcrops; this is in accordance with Wilson & Hooker f.'s (1845) findings, who reported the species from the top of hills growing on shady rocks between 400–465 m altitude.

Variability — The species is very variable in morphology of the gametophore, viz. in the size of the plant, the length of the stipe and the rachis, and the number of branches and their mutual distance, which in turn highly affects the shape of the frond. In addition, there is much variation in the distance between the leaves and amphigastria, their length, and the curve of their insertion. This variation shows, however, no apparent relation to geography or ecology.

There is also much variation in the symmetry and dimorphy of the leaves. Most plants of *Lopidium concinnum* belong to the usual, 'anisophyllous' variant of this species with dimorphic and asymmetrical distal stipe and frond leaves, which are ovate to oblong-ovate.

However, a minority of the plants have monomorphic and symmetrical leaves, which are frequently longer than in the normal variant and are ovate to lanceolate-ovate. The monomorphic leaves occur most frequently at the basal part of the stipe and the middle or distal part of the frond, and less often in the distal part of the stipe and the basal part of the frond.

Plants that belong to this 'isophyllous' variant of *L. concinnum* frequently have caducous leaves in the distal part of the frond, and are often unisexual (and mostly male, see note 9). In the 'anisophyllous' variant of *L. concinnum*, plants with caducous leaves and unisexual plants occur less frequently.

Between the two variants there is considerable overlap in these features. The number of branches with caducous leaves and the number of caducous leaves are very variable in both variants, and even in the 'isophyllous' variant specimens with entirely persistent frond leaves were found. Most plants of the 'anisophyllous' variant of *L. concinnum* are bisexual, but some have a few unisexual stems or are even entirely unisexual. In addition, there are also plants that are intermediates between the two variants by having partly monomorphic and partly dimorphic distal stipe and frond leaves, either in the same stem, or in different ones. The two variants are, therefore, not sharply defined, and no nomenclatural status is needed. The occurrence of the two forms shows no apparent relation to geography or ecology.

Geographical variation — Observed in sexuality, and length and shape of the seta and the capsule.

In nearly all fertile plants of *Lopidium concinnum*, bisexual and unisexual plants alike, the gametoecia are unisexual. However, in the Brazilian material a single bisexual gametoecium was found once on a bisexual plant which for the rest bears unisexual gametoecia.

South American material possesses a generally shorter, stronger curved to flexuose seta than fruiting material from New Zealand and Australia. In South American material the seta is about 2.0–4.5 mm long, whereas it is 3.5–6.0 mm long in Australian and 3.0–9.5 mm long in New Zealand material.

In Brazilian plants the capsule is more often subglobose or short-ellipsoid, about 0.7–1.3 mm long and 0.6–0.9 mm wide, thus generally shorter than in other areas.

Ecological variation — Not found except for plants growing in dense shade.

Densely shaded plants have often distant leaves and amphigastria, and are frequently weakly branched with a few, short, and very distant branches. According to Allison & Child (1971) plants growing in very shaded habitats are sometimes yellowish green, but the herbarium material showed no apparent correlation between shade and the colour of the plant.

Chromosome number — n = 12; see Ramsay (1967b: 559; 1974: 327, 328), Scott & Stone (1976: 401). — Voucher: *Ramsay 25/63* (SYD n.v.), Australia, New South Wales, Zircon Creek.

Chloroplast DNA sequences — *trnT*$_{UGU}$–*trnL*$_{UAA}$ 5' exon intergenic spacer, 295 bp, 299 bp, or 311 bp, deposited in GenBank database under accession numbers AF033225–29, see Frey et al. (1999: 70); *trnL*$_{UAA}$ intron, 304 bp, AF033230–34, see Frey et al. (1999: 70), Stech et al. (1999: 361); *trnL*$_{UAA}$ 3' exon–*trnF*$_{GAA}$ spacer, 61 bp, AF033235–39, see Frey et al. (1999: 70). — Vouchers: *Frey 92–72* (hb. Frey n.v., CHR n.v.; 'NZL 1'), New Zealand, North Is., Wellington L.D., Mt Hauhungatahi, Nov. 29th, 1992: AF033228, AF033233, AF033238, see Pfeiffer et al. (2000: 57); *Frey? 94–136* (hb. Frey n.v., CHR n.v.; 'NZL 2'), New Zealand, South Is., Nelson L.D., W Pakawau, Cape Farewell, March 5th, 1994: AF033229, AF033234, AF033239; *Frey? 95–62* (hb. Frey n.v.; 'CHI 1'), Chile, X. Region, Llanquihue, SE Puerto Montt, Hornopirén, Dec 3rd, 1995: AF033226, AF033231, AF033236; *Frey? 95–20* (hb. Frey n.v.; 'CHI 2'), Chile, X. Region, Valdivia/Osorno, Puyehue, Aguas Calientes, Nov. 29th, 1995: AF033227, AF033232, AF033237; '*8224*' (hb. Frey n.v., B n.v.; 'BRA'; collector's name not cited), Brazil, Rio Grande do Sul, Porto Alegre, Jan. 20th, 1987: AF033225, AF033230, AF033235.

Notes:

Nomenclature and synonymy — 1. The specimens under number *H. 1529b* in Hooker's and Wilson's herbaria (BM) are almost certainly duplicates of the holotype, because several annotations attached to these specimens in Wilson's herbarium (BM) refer to them as original specimens.

2. The two specimens collected by Sinclair at Waikehi, New Zealand (BM) are without a species name. On the label of one the name *Hypopterygium concinnum* is struck out. Both specimens are attached to a sheet on which some specimens are labelled *Lopidium pallens*, while others are labelled *L. concinnum*. The sheet itself is labelled with the names *Hypopterygium pallens* and *L. concinnum*, so there is little doubt that the sheet contains the type specimens of *Lopidium pallens*.

According to Hooker f. & Wilson (in Wilson, 1855) the syntype of *Lopidium pallens* that was collected by Hooker f. comes from the Bay of Islands, New Zealand, but specimens that are labelled and presented as such are absent from the material examined. However, in Hooker's and Wilson's herbaria (BM) a few specimens of *Hooker f. 386* are presented as *L. pallens*. This collection was made in New Zealand during the Antarctic Voyage in 1839–1843, but none of its parts describe precisely where it was found. Annotations in Wilson's herbarium show, however, that Wilson compared his specimen of *Hooker f. 386* with one of his specimens of *L. concinnum* (see note 3), strongly suggesting that *Hooker f. 386* is a syntype of *L. pallens*.

3. Hooker f. & Wilson (in Wilson, 1855) treated *Lopidium pallens* and *L. concinnum* as two separate species, essentially relying on the differences in sexuality among their own specimens. They considered *L. pallens* to be a monoicous species, and *L. concinnum* a dioicous one. In addition, they distinguished *L. pallens* from *L. concinnum* by differences in the sporophyte. They characterised the sporophyte of the latter as having a short, thick, and nearly smooth seta, a peristome with a low basal membrane, and small exostome teeth possessing distant trabeculae. By contrast, they characterised the sporophyte of *L. pallens* as having a long, thin, and rough, seta and a peristome with a higher basal membrane, longer processes, and larger exostome teeth possessing more closely set trabeculae.

Dixon (1927), however, argued correctly that the differences in length, stoutness, and degree of ornamentation of the seta between *Lopidium pallens* and *L. concinnum* do not represent differentiating character states. There is considerable variation in these characters in *L. concinnum*, and the character states found for the type material of *L. pallens* are within the range of variability of those in *L. concinnum*. The size of the exostome teeth, the distance between their trabeculae, the height of the basal membrane, and the length of the processes are likewise very variable, and do not distinguish *L. pallens* from *L. concinnum*. Nor does the concept of the sexuality of the plants differentiate between *Lopidium concinnum* and *L. pallens*. In the present circumscription of *L. concinnum*, both unisexual and bisexual plants occur.

Besides, the possibility that the type material of *L. concinnum* is partly bisexual cannot be ruled out. The type specimens of Menzies' collection from "Dusky Bay", New Zealand, in BM (Wilson's and Hooker's herbaria) and S have only female gametoecia, which supports Wilson's (1855) diagnosis of *L. concinnum* as a dioicous species. Schwägrichen (1829), however, reported Menzies' plant as being monoicous.

As a consequence of their circumscriptions of the two *Lopidium* species, Hooker f. & Wilson (in Wilson, 1855) incorrectly considered Schwägrichen's (1829) *Leskea concinna* to belong to their new species *Lopidium pallens*. Schwägrichen's plant is type material of *Lopidium concinnum* (see also Dixon, 1927).

4. Presumably, Mitten (1869) referred to the Auckland Islands when he reported the origin of Hooker's collection of *Hypopterygium plumarium* as "ins. Auckland". However, in Mitten's herbarium (NY) there is no Auckland Islands collection that is explicitely attributed to J.D. Hooker. In fact, only a single collection in this herbarium may be relevant in this respect, viz. one labelled "*Leskea concinna*" preserved below the reference number *W. 90*. Though its label lacks a collector's name, it almost certainly came from Wilson's herbarium (BM). The original specimen is probably one of the two collections of *Leskea concinna* from the Auckland Islands in this herbarium that are labelled with the number *W. 90*.

There is, furthermore, a suggestive coincidence in numbering between the specimens given above and the other specimens of *Lopidium concinnum* from the Auckland Islands that were examined. All of them, except a single one in BM that lacks a collection number and a collector's name, were gathered by Hooker f. during the Antarctic Voyage in 1839–1843. The ones that are kept in Wilson's and Hooker's herbaria are labelled as *Leskea concinna* with collection number *90*. It is plausible, that the specimens in Wilson's and Mitten's herbaria numbered *W. 90* are actually duplicates of *Hooker f. 90*. Consequently, if Mitten's "ins. Auckland" stands for the Auckland Islands, they might belong to the type material of *Hypopterygium plumarium*.

5. According to Sayre (1975), the Brazilian material collected by Weir is collected between 1861 and 1863. The Chilean material collected by Lobb is collected between 1840 and 1848.

Description — 6. The cavity in the cross section of the seta that is illustrated by Noguchi (1951) is probably an artefact, as the walls of the central seta cells are often very thin, and may easily be torn during cutting.

7. Sainsbury (1955) reported gemmae in one of the specimens of *L. concinnum* from New Zealand. However, in all the New Zealand material of *Lopidium* examined, including the material that is preserved in Sainsbury's herbarium, housed in WELT, no gemmiferous plants were found.

8. In plants of *Lopidium concinnum*, the central axial cavities that were sometimes observed in the distal part of the rachis and branches, and even more frequently in the ultimate branches, are cortical cavities in origin that have got a central position during cavity development.

Cavities with a central position are absent from the stipe and in the basal part of the rachis and inner branches. In these axes and parts of axes, all cavities are situated in the cortex. The distal part of the rachis and branches is, however, narrower then the basal part, and, in addition, the ultimate branches are narrower than the inner ones or the rachis. The presence of a central cavity is restricted to such narrow axes and parts of axes. A central cavity is usually accompanied by cortical ones. Apparently, what are now a central cavities in narrow axes used to be a cortical ones, that were situated close to the axial centre, which due to the small width of the axes during cavity development moved towards a central position.

9. Most plants of *Lopidium concinnum* are bisexual, but some have a few unisexual stems or are even entirely unisexual. These unisexual plants usually belong to the variant of *L. concinnum* with weakly dimorphic or monomorphic frond leaves, and are male in most cases.

10. The paraphyses in *Lopidium concinnum* are possibly associated with distal perichaetial leaves or their – potential – positions. Often, the paraphyses were observed to be situated just a single cell above the insertion of the distal perichaetial leaves. In such cases a few paraphyses were found per leaf, and, in addition, they were often found to be attached to the leaf base by the cell or a row of cells that are situated directly above the insertion of the leaf. Paraphyses were also found in positions in between the archegonia (in between which perichaetial leaves are almost always absent) near positions where phyllotaxis would lead one to expect a perichaetial leaf.

The position of the paraphyses that are attached to perichaetial leaves suggests that the paraphyses are homologous with axillary hairs, which (in gametoecia) are also associated with the gametoecial leaves. These axillary hairs are numerous in the perichaetia and they also occur in between the archegonia. At the base of the perichaetial leaves, axillary hairs were not found at positions where paraphyses were present. However, the position of the paraphyses is sometimes difficult to ascertain and further anatomical and ontogenetic research on the paraphyses is necessary to unravel this homology problem.

In full-grown perichaetia, the occurrence of paraphyses is probably correlated with the position of the remaining, unfertilised or not outgrown, archegonia on the vaginula. Paraphyses are absent from full-grown perichaetia if the remaining archegonia are situated at the base of the vaginula, and were most frequently present if the remaining archegonia are situated at the apical part of the vaginula.

Reproduction — 11. There were 611 fruiting specimens among the specimens examined (c. 69%, n = 631), but some regional differences in fertility were observed. The highest percentages of fruiting specimens were found for Australia (72%, n = 230), New Zealand (70%, n = 527), and mainland Chile (76%, n = 67). The lowest percentages of fruiting specimens were found for Brazil (48%, n = 58), the Auckland Islands (18%, n = 11), and the Juan Fernandez Islands (0%, n = 17).

Distribution — 12. In Brazil, *Lopidium concinnum* is restricted to the south east, where the climate is intermediate between warm temperate to humid tropical. Outside Brazil, the species is almost confined to temperate and warm-temperate climates.

With the exception of a single dubious finding (see note 13), all specimens from Australia were found south of the border between Queensland and New South Wales. In continental Australia the species is restricted to the east and south side of the Great Dividing Range and the coastal regions of New South Wales and Victoria.

In Chile most specimens were found in the warm temperate and temperate areas of southern Chile. Only a few specimens were found north of c. 39° S, where the warm-temperate macroclimate gives way to the mediterranean. These specimens were found quite close to the coast.

The species is distributed throughout New Zealand, although most specimens came from North Island. The species is presumably more abundant in the coastal areas than in the central parts, most notably in South Island. However, the observed distribution may reflect undercollecting in the central areas of New Zealand.

13. There is some doubt about the occurrence of *Lopidium concinnum* in Queensland; the label of the single specimen examined did not have a collector's name. The specimen was annotated to come from Moreton Bay near Brisbane, which is outside the known distribution area of the species.

14. Two specimens collected by A. Cunningham were indicated to come from Norfolk Island (*Cunningham s.n.*, FH). Their origin is dubious, because all the species that Cunningham supposedly collected from Norfolk Island – which include hardy species with conspicuous plants – have never been collected there again (Streimann, pers. comm; cf. Touw, 1971). Streimann, who made many bryophyte collections on Norfolk Island in the nineties of last century and nearly completed a moss flora for this island[1], did not find the species there (Streimann, pers. comm.).

Other — 15. The molecular sequence data obtained by Frey et al. (1999) – and the phylogenetic analyses partly based on their data by Stech et al. (1999) – support the present circumscription of the species. According to Frey et al. (1999), three non-coding cpDNA sequences (*trnT–trnL* spacer, *trnL* intron, *trnL–trnF* spacer) of specimens of *Lopidium concinnum* from Chile and Brazil are almost identical. In addition, they found only minimal genetic divergence between their New Zealand and South American specimens of the species and concluded, that no remarkable genetic changes and no speciation have occurred since the disruption of *L. concinnum* populations c. 80–60 million years ago. Frey et al. (1999) defined this phenomenon as 'stenoevolution'.

The morphological similarity between New Zealand and South American plants of *Lopidium concinnum* supports Frey et al.'s (1999) hypothesis, but the period of 'stenoevolution' may have started earlier, because the New Zealand microcontinent separated from Gondwanaland c. 86–84 million years ago (Storey et al., 1999; O'Sullivan et al., 2000).

However, Frey et al.'s (1999) assumption that separated *L. concinnum* populations remained almost unchanged at DNA level is premature. They sampled only a few populations and the *trnL* intron, and probably the entire *trnT–trnF* region, is constrained against substitutions; see also 'Evolution rate', p. 90. Hence, more molecular sequence data are needed to confirm the low genetic divergence between separated populations of the species claimed by Frey et al. (1999).

Selected specimens (from 921 ones examined):

AUSTRALIA: Queensland?: *unknown collector s.n.* (MEL, see note 13), Brisbane, Moreton Bay. – New South Wales: *McVean 267466* (CBG), Point Lookout; *Streimann 38183* (CBG, NY), Nadgee State Forest; *Downing & Ramsay 0991* (MACQ), Mt Wilson; *Whitelegge s.n.* (MEL, S), Mossvale; *Telford 4207* (L), Mt Durras. – Victoria: *Streimann MAE 485* (L), *58392* (L), Melba State Park; *Scott, BSE 638* (B, EGR, GRO, L, NICH, S, U), Otways, Turtons Track; *Streimann 2396* (L), Turtons Pass; *Streimann 58639* (L), Apollo Bay. – Tasmania: *Weber & McVean B-33365* (GRO, NICH, NY), Hellyer Gorge; *Fleischer B 2116* (B, GRO, L, NICH), Mt Wellington; *Curnow 2132* (CBG), Great Western Tiers. — NEW ZEALAND: *Sinclair s.n.* (BM), Waikiki; *Sinclair s.n.* (BM), Ship Cove. – North Island. North Auckland L.D.: *Allison 734* (WELT), *Van Zanten 82.02.351d* (GRO), Waipoua Forest; *Berggren 2038* (NY, S), Hokianga; *Petrie s.n.* (WELT), Northcote; *Sinclair s.n.* (BM), Auckland; *Lush s.n.* (WELT), Little Barrier Is. – South Auckland L.D.: *Molesworth 198* (WELT), Mt Pirongia; *Jardine & Sainsbury s.n.* (BR, L, NY, UPS), Matamata, Peria Reserve; *Van Zanten 93.09.1161* (GRO), Thames; *Berggren 2036* (BR, NY, S, UPS, W), *2737* (B, S, UPS, W),

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[1] Sadly, Streimann passed away on August 29th, 2001.

Tauranga; *Brownsey s.n.* (WELT), Motuhora ('Whale') Is. – Gisborne L.D.: *Sainsbury 15371 (M 15244)* (WELT), Gisborne. – Hawke's Bay L.D.: *Van Zanten 1143a* (B, GRO, NICH, S), White Pine Reserve. – Taranaki L.D.: *Fleischer B 231* (B), Mt Egmont. – Wellington L.D.: *Mundy 23* (WELT), Ohakune; *Wilkinson s.n.* (WELT), Kapiti Is.; *Brownsey s.n.* (WELT); *Lyall 126* (BM), Hutt Valley; *Berggren 2032* (B, HBG, NY, S, UPS); *Lyall 112* (BM), Wellington. – South Island. Nelson L.D.: *Glenny s.n.* (WELT), Mt Burnett. – Marlborough L.D.: *McMahon s.n.* (WELT), *Streimann 51431* (CBG), Mt Stokes; *Kantak & Churchill 20* (CHR), S of Kaikoura. – Westland L.D.: *Helms 32* (NY), *s.n.* (JE), Greymouth; *Vitt 29702* (CBG), Fox Glacier. – Canterbury L.D.: *Lewinsky 1347* (L), Banks Peninsula, Otepatotu; *Beckett s.n.* (FH, HBG, JE, NY, S, UPS, W), Waimate. – Otago L.D.: *Berggren 2735* (BR, HBG, NY, S, UPS, WELT), Dunedin; *Fleischer B 258* (B), Queenstown. – Southland L.D.: *Hutton 399* (FH, S; *s.n.*: FH, NICH), Martins Bay; *Lyall 23* (BM), Milford Sound; *Lyall 184* (BM), Bligh's Sound; *Menzies s.n.* (BM, sub nos. *84, H. 1529a*, and *H. 1529b*; S), Dusky Sound; *Brownsey s.n.* (WELT), Anchor Is. – Stewart Is.: *Martin 326* (WELT), Garden Mound; *Doore et al. 362* (S, 'Oban'), Halfmoon Bay. – Auckland Is.: *Hooker 90* (BM, BM, sub no. *W. 90*), *s.n.* (BR, TCD); *unknown collector (Hooker?) (W. 90)* (BM, NY).

BOLIVIA: La Paz: *Pearie s.n.* (BM), Yungas, Unduavi.

CHILE: Juan Fernandez Is.: *Skottsberg & Skottsberg, Svenska Pacific Exp. 332* (BM, FH, UPS), *M213* (S), *M252* (S), Robinson Crusoe ('Masatierra'). – Colchagua Prov.: *unknown collector 29* (BM). – Arauco Prov.: *Crosby 13043* (L), Cordillera Nahuelbuta. – Cautín Prov.: *Crosby 11965*, Lago Villarica. – Valdivia Prov.: *Krause s.n.* (BM, L), *Dusén 63* (S), Valdivia, Corral. – Osorno Prov.: *Crosby 12260* (L), Anticura. – Llanquihue Prov.: *Egerdam & Beetle 24595* (BM), Lago Todos Los Santos; *Van Zanten 79.01.255* (GRO), *Van Zanten & Kruijer 86.01.987* (GRO), Punta Huano. – Chiloé Prov.: *Lobb 45* (BM, 'Chiloe'), Chiloé Is.; *Crosby 12450* (L), Cordillera San Pedro; *Dusén 649* (BM, S), *s.n.* (BR, L), Guaitecas Is. – Aisén Prov.: *Halle, Exp. Suec. 960* (S), Canal Moraleda, Pto. Chacabuco.

BRAZIL: Minas Geraïs: *Zitran (236)* (BM), Passa Zerato. – São Paulo: *Puiggari 23* (BM); *s.n.* (L), Apiai ('Apiahy'). – Paraná: *Weir 1* (BM, S), Curitiba ('Corritiba'); *Robert s.n.* (BM), Boca Nova; *Poliguesi & da Cruz 232* (ZT), Bocaiúva do Sul, Rio Capivari. – Santa Catarina: *Ule, Bryoth. Brasil. 66* (L, PC, S), Pedro Grandes; *Ule, Bryoth. Brasil. 66* (BM, BR, HBG, S), Pedro Geral; *Ule, Bryoth. Brasil. 66* (L, S), *Herbar Brasil. 316* (HBG, MO), Blumenau; *Ule, Herbar Brasil. 542* (PC), Serra Geral; *Ule, Herbar Brasil. 542* (HBG), Serra do Oratorio.

DUBIOUS ORIGIN: *Cunningham s.n.* (FH, 'Norfolk Is.'; see note 14).

5.2. **Lopidium struthiopteris** (Brid.) M. Fleisch. — Fig. 39, 40, 41A, 42A; Map 18; Plate 3a

Lopidium struthiopteris (Brid.) M. Fleisch., Musc. Buitenzorg 3 (1908) 1073. — *Hypnum struthiopteris* Brid., Muscol. Recent. Suppl. 2 (1812) 87. — *Pterygophyllum struthiopteris* (Brid.) Brid., Muscol. Recent. Suppl. 4 (1818, '1819') 151. — *Hookeria struthiopteris* (Brid.) Arn., Disp. Méth. Mousses (preprint) (1825 [= 1826?]) 56; Mém. Soc. Hist. Nat. Paris 2, 2 (1826) 305. — *Hypopterygium struthiopteris* (Brid. ["Comm."]) Brid., Bryol. Univ. 2 (1827) 716. — Type: *Commerson(?) s.n.* (B destroyed, isotype not found with certainty), Réunion ["In Insula Borboniâ hâbitat. ex herbario suo clar. Decandolle sed absque fructu communicavit."]; possible isotypes: *Commerson s.n.* (BM neo, designated here, '*Hypopterygium struthiopteris*'), Réunion; *Commerson? (15)* (BR, PC n.v.), Réunion ('Ile Bourbon'). — See note 1.

Hypnum penniforme Thunb. ex Brid., Muscol. Recent. Suppl. 2 (1812) 96, syn. nov., '*pennaeforme*'; Thunb., Prodr. Fl. Cap., 2 (1800) 175, nom. inval., published before starting point, '*pennaeforme*'. — *Hypopterygium penniforme* (Thunb. ex Brid.) Brid., Bryol. Univ. 2: (1827) 717. — *Lopidium penniforme* (Brid.) M. Fleisch., Musc. Buitenzorg 3 (1908) 1073, '*pennaeforme*'. — *Hypopterygium penniforme* (Thunb.) Müll.Hal. ex M. Fleisch., Hedwigia 63 (1922) 213, nom. nud. in syn. (*Lopidium penniforme* (Brid. ["Thb."]) M. Fleisch.). — Type: *Thunberg s.n.* (B destroyed?; BM lecto, designated here, 'Cap. bon. spei', sub nom. '*Hypopterygium pennaeforme* (Thunb.)'; L, "In m. Tafelberg Prom. b. Spei"; L, s. coll., s.loc., "sp. authent."; S; almost certainly also in Thunberg's herbarium in UPS, seen on microfiche, IDC 1036), South Africa, Cape of Good Hope ["In Promontorio Bonae Spei habitat"]. — See notes 2, 3, and 18.

Hypopterygium trichocladon Bosch & Sande Lac., Bryol. Jav. 2 (1861) 9, t. 138, syn. nov. — *Hypopterygium struthiopteris* (Brid.) Brid. subsp. *trichocladon* (Bosch & Sande Lac.) Kindb., Hedwigia 40 (1901) 283. — *Lopidium trichocladon* (Bosch & Sande Lac.) M. Fleisch., Musc. Buitenzorg 3 (1908) 1069. — *Lopidium trichodon* (Bosch & Sande Lac.) M. Fleisch. ex Sakurai, Muscol. Jap. (1954) 112, nom. inval., err. pro *Lopidium trichocladon* (Bosch & Sande Lac.) M. Fleisch. — *Lopidium trichocladum* (Bosch & Sande Lac.) M. Fleisch. ex Touw, J. Hattori Bot. Lab. 71 (1992) 329, typ. err. pro *Lopidium trichocladon* (Bosch & Sande Lac.) M. Fleisch. — Syntypes: Indonesia: *Aman [= Kurz] s.n.* (L lecto, designated here, sub no. *85*; NY), Indonesia, Java, W Java (Jawa Barat), Bogor, G. Salak, ["ad arborum truncos pr. Bogor in m. Salak"], alt. 2000 ft; *De Vriese s.n.* (L, S?), Indonesia, Maluku [Moluccas], Halmahera ["Halmateira"]; probable syntype: *Kurz s.n.* (L), Indonesia, Java, W Java (Jawa Barat), "An [uninterpr.] von N. Abhang [uninterpr.] Salak bei Bogor", alt. 2000 ft., "85. *Neckera*", May 13, 1860. — See notes 4 and 5.

?: *Hypopterygium limbatulum* Müll.Hal., Linnaea 36 (1869) 11 & 27, syn. nov. — *Hypopterygium struthiopteris* (Brid.) Brid. subsp. *limbatulum* (Müll.Hal.) Kindb., Hedwigia 40 (1901) 283. — *Lopidium limbatulum* (Müll.Hal.) M. Fleisch., Hedwigia 63 (1922) 213. — Type: *Nietner*, sub *no. 60* in Müller's (l.c.: 11) enumeration of species (B holo destroyed; isotypes not found), Sri Lanka ["Ceylon"]. — See notes 5 and 6.

Hypopterygium semimarginatulum Müll.Hal., J. Mus. Godeffroy 3, 6 (1874) 80, syn. nov. — *Hypopterygium struthiopteris* (Brid.) Brid. subsp. *semimarginatulum* (Müll.Hal.) Kindb., Hedwigia 40 (1901) 283, erroneously cited as Müller's herbarium name and by indirect reference based on *Hypopterygium semimarginatulum* Müll.Hal. — *Lopidium semimarginatulum* (Müll.Hal.) Wijk & Margad., Taxon 9 (1960) 190, '*semi-marginatulum*'. — *Hypopterygium semi-marginatum* Müll.Hal. ex Paris, Index bryol. ed. 2, 3 (1905) 113, nom. inval., err. pro *Hypopterygium semimarginatulum* Müll.Hal. — *Lopidium semimarginatum* (Müll.Hal.) M. Fleisch., Musc. Buitenzorg 3 (1908) 1073, nom. illeg. incl. spec. prior. — Syntypes: *Graeffe s.n.* (B destroyed; S lecto, designated here), Fiji, Ovalau, ["inter alios muscos"], 1864; *Graeffe s.n.* (B destroyed; iso not found), Samoa Is., Western Samoa, Upolu, ["ad frondem *Spiridentis aristifolii*"], 1864. — See note 5 and 18.

Lopidium pinnatum Hampe, Linnaea 38 (1874) 672, syn. nov. — *Hypopterygium pinnatum* (Hampe) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1874–75 (1876) 150 (Gen. Sp. Musc. 2 (1876) 66). — *Hypopterygium struthiopteris* (Brid.) Brid. subsp. *pinnatum* (Hampe) Kindb., Hedwigia 40 (1901) 282. — ?: *Hypopterygium planatum* Müll.Hal. ex Mitt. ex F. Muell., Fragm., Suppl. 11 (1881) 114, nom. inval., err. pro *Hypopterygium pinnatum* (Hampe) A. Jaeger? — *Hypopterygium planatum* Hampe ex Mitt., Trans. & Proc. Roy. Soc. Victoria 18 (1882) 76, nom. inval., err. pro *Hypopterygium pinnatum* (Hampe) A. Jaeger — Type: *Fitzalan s.n.* (BM holo), Australia, Queensland, Mt Elliot; probable isotypes: *Fitzalan s.n.* (MEL, "parce intermixtum"; S, sub no. *8*), Australia, Queensland, Mt Elliot. — See note 5 and 7.

Lopidium javanicum Hampe, Linnaea 38 (1874) 672, based on *Hypopterygium struthiopteris* auct. non (Brid.) Brid.: Bosch & Sande Lac., Bryol. Jav. 2 (1861) 8, t. 137. — *Hypopterygium javanicum* (Hampe) A. Jaeger, Ber. Thätigk. St. Gallischen. Naturwiss. Ges. 1874–75 (1876) 150. (Gen. Sp. Musc. 2 (1876) 66). — *Hypopterygium javense* Broth. & Watts, J. Roy. Soc. New South Wales 49 (1915) 147, nom. inval., err. pro *Hypopterygium javanicum* (Hampe) A. Jaeger. — *Hypopterygium subpenniforme* Kindb., Hedwigia 40 (1901) 282, '*subpennaeforme*', nom. illeg. incl. spec. prior. (*Lopidium javanicum* Hampe), based on *Hypopterygium struthiopteris* auct. non (Brid.) Brid.: Bosch & Sande Lac., Bryol. Jav. 2 (1861) 8, t. 137. — *Lopidium struthiopteris* (Bosch & Sande Lac. ex Horik.) Horik., Bot. Mag. (Tokyo) 48 (1934) 607, hom. illeg., nom. illeg. incl. spec. prior. (*Lopidium javanicum* Hampe); *Hypopterygium struthiopteris* Bosch & Sande Lac. ex Horik. l.c., nom. nud. in syn. — *Hypopterygium struthiopteris* auct. non (Brid.) Brid.: Bosch & Sande Lac., Bryol. Jav. 2 (1861) 8, t. 137, according to Hampe l.c., Kindberg l.c., and Fleischer, Musc. Buitenzorg 3 (1908) 1071; Mitten, J. Linn. Soc., Bot., Suppl. 1 (1859) 149, according to Fleischer, Musc. Buitenzorg l.c.; Fleischer, Musc. Archip. Ind., Serie 2, (1899) No. 99, according to Fleischer, Musc. Buitenzorg l.c. — Syntypes: *Teijsmann s.n.* (L lecto, designated here; S), Indonesia, W Java (Jawa Barat), "G. Gedé et G. Salak"; *De Vriese s.n.* (L not found?, see possible syntypes), *Motley s.n.* (NY), Indonesia, W Java (Jawa Barat), Mt Pangerango ["in m. Pangerango regione superiore altit. 7–10,000'"]; *Teijsmann s.n.* (L), Indonesia, Sumatra, "An lithis occidentale Sumatrae" ["in littore occidentali Sumatrae"]; possible syntypes: *unknown collector s.n.*, "(voor de bladeren en okselharen)" (L, s.loc.); *De Vriese s.n.* (L, It. Ind. 1858–60, s.loc.), Indonesia, Java. — See notes 8–12 and 18. — Synonymised with *Lopidium struthiopteris* (Brid.) M. Fleisch. by Van der Wijk et al., Regnum Veg. 33 (1964) 180, 310, who erroneously referred to Horikawa, Bot. Mag. (Tokyo) 48 (1934) 607; also given in the synonymy of *Lopidium struthiopteris* (Brid.) M. Fleisch. by Noguchi, Moss Flora of Japan 4 (1991) 762.

?: *Hypopterygium hemiloma* Müll.Hal., Linnaea 40 (1876) 256, syn. nov. — *Hypopterygium struthiopteris* (Brid.) Brid. subsp. *hemiloma* (Müll.Hal.) Kindb., Hedwigia 40 (1901) 283. — *Lopidium hemiloma* (Müll.Hal.) M. Fleisch., Hedwigia 63 (1922) 213. — Type: *Hildebrandt(?) s.n.* (B holo destroyed; S?, isotypes not found), "Comoro-insula Johanna inter alios muscos ad filices arborescentes involvendas", 1875. — See notes 5 and 13.

Hypopterygium subtrichocladum Broth., Bol. Soc. Brot. 8 (1890) 189, syn. nov. — *Hypopterygium struthiopteris* (Brid.) Brid. subsp. *subtrichocladum* (Broth.) Kindb., Hedwigia 40 (1901) 283, '*subtrichocladon*'. — *Lopidium subtrichocladum* (Broth.) M. Fleisch., Hedwigia 63 (1922) 213. — Type: *Quintas s.n.* (H holo, n.v.; COI, S), São Tomé e Principe, ["Ins. S. Thomé, ubi ad corticem arborum specimina perfecta sterila"]. — See note 5 and 14.

Hypopterygium campenonii Renauld & Cardot in Renauld, Rev. Bot. Bull. Mens. 9 (1891) 400, syn. nov., '*campenoni*'. — *Lopidium campenonii* (Renauld & Cardot) M. Fleisch., Musc. Buitenzorg 3 (1908) 1073, 'Campenoni'. — *Lopidium struthiopteris* (Brid.) M. Fleisch. var. *campenonii* (Renauld & Cardot) Bizot in Bizot & Pócs, Acta Bot. Acad. Sci. Hung. 28 (1982) 43. — Syntypes: *Campenon s.n.* (PC lecto, ex herb. Renauld; PC, ex herb. Cardot; S, sub nos. *5 & 9*), Madagascar, Antananarivo Prov., Imerina, "Fôret d'Amperifery", alt. 1300–1400 m. — Cardot's specimen contains only a single, small branch. — See note 18.

Hypopterygium daymanianum Broth. & Geh. in Broth., Oefvers. Förh. Finska Vetensk.-Soc. 40 (1898) 193, syn. nov. — *Hypopterygium struthiopteris* (Brid.) Brid. subsp. *daymanianum* (Broth. & Geh.) Kindb., Hedwigia 40 (1901) 283. — *Lopidium daymanianum* (Broth. & Geh.) M. Fleisch., Musc. Buitenzorg 3 (1908) 1071. — Type: *Armit Jr. s.n.* (H n.v.; FH, ex herb. Geheeb; S, sub *(658)*, ex herb. Brotherus), Papua New Guinea, Milne Bay Prov., Mt Dayman, 1894? — See notes 5 and 15.

Hypopterygium trichocladulum Besch., Bull. Soc. Bot. France 45 (1898) 127, syn. nov. — *Hypopterygium struthiopteris* (Brid.) Brid. subsp. *trichocladulum* (Besch.) Kindb., Hedwigia 40 (1901) 283. — *Lopidium trichocladulum* (Besch.) M. Fleisch., Musc. Buitenzorg 3 (1908) 1071. — Type: *Nadeaud 441* (PC? n.v.), Society Islands, Tahiti, ["montagnes de Hitiaa et du bord de la mer, celles de Faaiti, au pied de l' Aorai, ainsi que celles de la vallée de Tipaeaui"], ["June 22, 1896"]; almost certainly isotype: *Nadeaud s.n.* (S, sub no. *1*, "ad C. M. misit Besch."), Society Islands, Tahiti. — See notes 5, 16, and 18.

Lopidium javanicum Hampe fo. *acutifolium* M. Fleisch., Musc. Buitenzorg 3 (1908) 1073, syn. nov. — *Hypopterygium javanicum* (Hampe) A. Jaeger fo. *acutifolium* (M. Fleisch.) Dixon, Ann. Bryol. 5 (1932) 17–50, '*acutifolia* Fleisch.'. — Syntypes: *Fleischer s.n.* (FH), Indonesia: Java, W Java (Jawa Barat), G. Gedé, Tjibodas, July, (18)98; *Fleischer s.n.* (FH lecto, designated here), Mt Megamendong, Lemoe, "sehr lang zugespitzt", alt. 1600 m, July, 1901; *Fleischer? s.n.* (FH), Philippines, Mindanao, Mt Batangan. — See note 18.

Hypopterygium nazeense Thér., Bull. Acad. Int. Géogr. Bot. 19 (1909) 17, syn. nov. — *Lopidium nazeense* (Thér.) Broth. in Engler & Prantl, Nat. Pflanzenfam. ed. 2, 11 (1925) 271. — Type: *Ferrié s.n.* (PC holo, S), Japan, Ryukyu Archipelago, "Arch. Liu-Kiu", Kagoshima Pref., Amami-oshima Island, Naze, Nov., 1899. — See note 17 and 18.

Hypopterygium francii Thér., Bull. Acad. Int. Géogr. Bot. 19 (1909) 22, ('-i'), syn. nov. — *Lopidium javanicum* Hampe var. *francii* (Thér.) Thér., Musci & Hep. Novae-Caledoniae Exsicc. (1913) no. 161, ('-i'). — *Lopidium francii* (Thér.) Broth. in Engler & Prantl, Nat. Pflanzenfam. ed. 2, 11 (1925) 271. — Type: *Franc s.n.* (PC holo), New Caledonia, Mt Dzumac, forest, "avec *Bescherellia elegantissima*", alt. 900 m, Aug. 15, (19)08. — See note 18.

Hypopterygium bonatii Thér., Bull. Acad. Int. Géogr. Bot. 19 (1909) 23, syn. nov. — *Lopidium bonatii* (Thér.) Broth. in Engler & Prantl, Nat. Pflanzenfam. ed. 2, 11 (1925) 271. — Type: *Franc s.n.* (PC holo, "Comm. Bonati"; FH), New Caledonia, ["environ de Nouméa, croissant parmi les touffes de *Bescherellia elegantissima*"], "[uninterpr.] i *Bescherellia elegantissima*", 1906. — See note 18.

Hypopterygium parvulum Broth. & Paris in Broth., Oefvers. Förh. Finska Vetensk.-Soc. 53A, 11 (1911) 31, syn. nov. — *Lopidium parvulum* (Broth. & Paris) Broth. in Engler & Prantl, Nat. Pflanzenfam. ed. 2, 11 (1925) 271. — Type: *Le Rat s.n.* (H n.v.; PC lecto, designated here, "comm. Brotherus"), New Caledonia, "In jugo Dogny", "Etiq. Paris (N^{o}. 1690): 'an Fissidentacies[?] genus novum proximum? lamina apicali deest.'", alt. 1045 m, Sept., 1909. — See note 18.

Cyathophorella doii Sakurai, Bot. Mag. (Tokyo) 46 (1932) 376. — Type: *Doi 2106* (holo, not found; iso not found), Japan, Kyushu, Kumamoto Pref. [Higo Prov.], Mt Ichibusa [= Mt Ichifusa?], ["am Stamme eines alten Baumes"], Aug. 10, 1930; *Doi 2107* (para, not found), Kagoshima Pref., Satsuma-Hanto ["Satsuma Prov."], Mt Kammuri, "an der Rinde", May, 1930. — Synonymised with *Lopidium nazeense* (Thér.) Broth. by Noguchi, Trans. Nat. Hist. Soc. Taiwan 24 (1934) 292; also given in the synonymy of *Lopidium nazeense* (Thér.) Broth. by Noguchi, J. Hattori Bot. Lab. 6 (1951) 30, and Sakurai, Muscol. Jap. (1954) 112. — It is not known where the types of *Cyathophorella doii* Sakurai are preserved; they are not present in MAKINO, and they were not found among the material on loan from NICH and HIRO.

Hypopterygium polythrix Dixon, Kongel. Norske Vidensk. Selsk. Skr. (Trondheim) 1932, 4 (1932) 15. — Syntypes: *Høeg 127* (BM lecto, BR), *149* (BM), South Africa, KwaZulu-Natal, "In forest, Eshowe, Zululand, Natal", Aug. 22, 1927. — Lectotype designated by Magill & Van Rooy, Flora of Southern Africa 1, 3 (1998) 617. — Synonymised with *Lopidium penniforme* (Brid.) M. Fleisch. by Magill & Van Rooy l.c. — See note 18.

Hypopterygium congoanum Dixon & Thér., Rev. Bryol. Lichénol. 12 (1942) 75, syn. nov. — Type: *Bequaert 8067* (BM lecto, BR, PC? n.v.), Democratic Republic of Congo [Zaire], ["Congo Belge"], Kivu Prov., Masisi, Dec., 1914. — See note 18.

Hypnum javanicum Dozy & Molk. ex Bosch & Sande Lac., Bryol. Jav. 2 (1861) 8, nom. nud. in syn. (*Hypopterygium struthiopteris* (Brid.) Brid.). — Original material: *unknown collector s.n.* (L), Indonesia, Java, s.loc., "H. javanicum Dz. et Mb. Herb.". — The original material includes two specimens that are preserved in Van der Sande Lacoste's herbarium kept in L. One of them contains a well-developed plant, the other contains only a few leaves and perigonia, which almost certainly derive from the former. — See notes 8, 9, and 10.

Illustrations: Van den Bosch & Van der Sande Lacoste, Bryol. Jav. 2 (1861) t. 137, 138. — Fleischer, Musc. Buitenzorg 3 (1908) f. 181a–e.; Chopra, Bot. Monogr. Council Sci. Industr. Res., India 10 (1975) f. 99. — Sim, Trans. Roy. Soc. South Africa 15 (1926) 446 (right). — Bartram, Philipp. J. Sci. 68 (1939) pl. 21, f. 352–353. — Noguchi, J. Hattori Bot. Lab. 6 (1951) 1, f. 4. — Noguchi, J. Hattori Bot. Lab. 7 (1952) 1, f. 5. — Sakurai, Muscol. Jap. (1954) pl. 2 f. f, pl. 42 f. b & f. — Abeywickrama, Ceylon J. Sci., Biol. Sci. 3 (1960) 100 f. 118a–c. — Noguchi, Misc. Bryol. Lichenol. 5 (1969) 30, f. 145, 1. — Iwatsuki & Mizutani, Coloured illustr. bryoph. Japan (1972) pl. 25, f. 359.— Petit, Bull. Jard. Bot. Belg. 48 (1978) 167, f. 43. — Mohamed & Robinson, Smithsonian Contr. Bot. 80 (1991) f. 151–168. — Noguchi, Moss Flora of Japan 4 (1991) f. 334.B, f. 335.— So, Mosses and Liverworts of Hong Kong (1995) f. 61. — Condy in Magill & Van Rooy, Flora of Southern Africa 1, 3 (1998) 616, f. 14–25.

Plants medium-sized to large, usually gemmiferous. *Stipe* up to 3.0 cm long, dorsiventrally or laterally compressed in basal third, usually dorsiventrally compressed but occasionally laterally compressed in distal part. *Frond* up to 12.5 cm in diameter; rachis usually dorsiventrally compressed, rarely laterally compressed in basal half; branches up to 2.5 cm long. *Primordia* naked or set with scaly leaves; scaly leaves deltoid to narrowly triangular, ovate-oblong, or subcircular, margin ± entire. *Epidermis cells and outer cortical cells of stipe, rachis, and branches* equally narrow or cortical

Fig. 39. *Lopidium struthiopteris* (Brid.) M. Fleisch. Distal part of gemmiferous frond axis (*Van Zanten 68.1390 D*, GRO).

ones wider; walls thin or incrassate, colourless to dark brown; inclusions usually absent, but occasionally present in inner cortical cells, tiny to large droplets, oil-like, pale olivaceous. *Central strand* absent or present in stipe, absent from rachis and branches; cells broad; walls thin, colourless; inclusions absent. *Axial cavities* absent, subcentral, or central in stipe, rachis, and branches, in cross section usually 1 and central, occasionally 2 in or near centre of stipe, rachis, or branches; inclusions tiny to large droplets, granules, clumps, or crusts, oil-like to fat-like, colourless to dark olivaceous. *Axillary hairs* up to 8 per leaf, 2- or 3-celled; basal cells 1 or 2; terminal cell subcircular to narrowly elliptic, straight to recurved, 10–20 µm long and 7–15 µm wide. *Leaves* closely set; laminal cells 5–20(–25) µm long and 5–15 µm wide. *Basal stipe leaves* small,

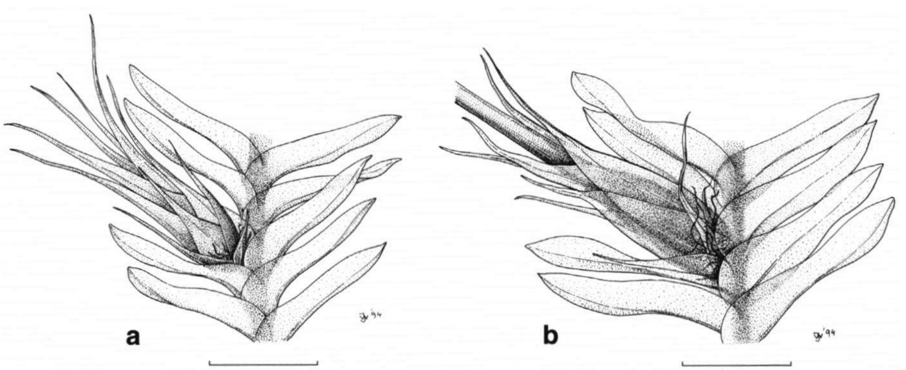


Fig. 40. *Lopidium struthiopteris* (Brid.) M. Fleisch. Perichaetia: a. prior to sporophyte development, b. full-grown (*Van Zanten 68.1390 D*, GRO).

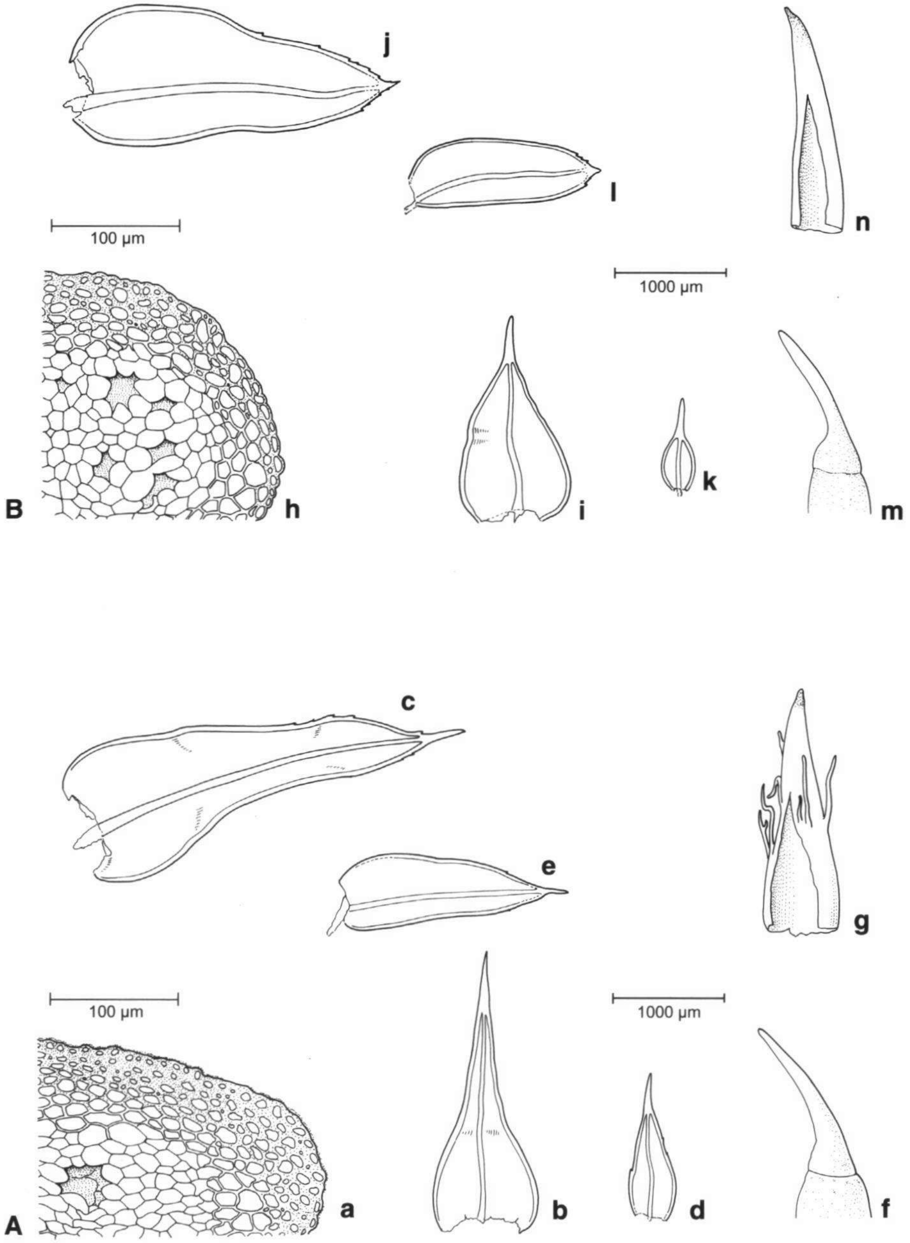
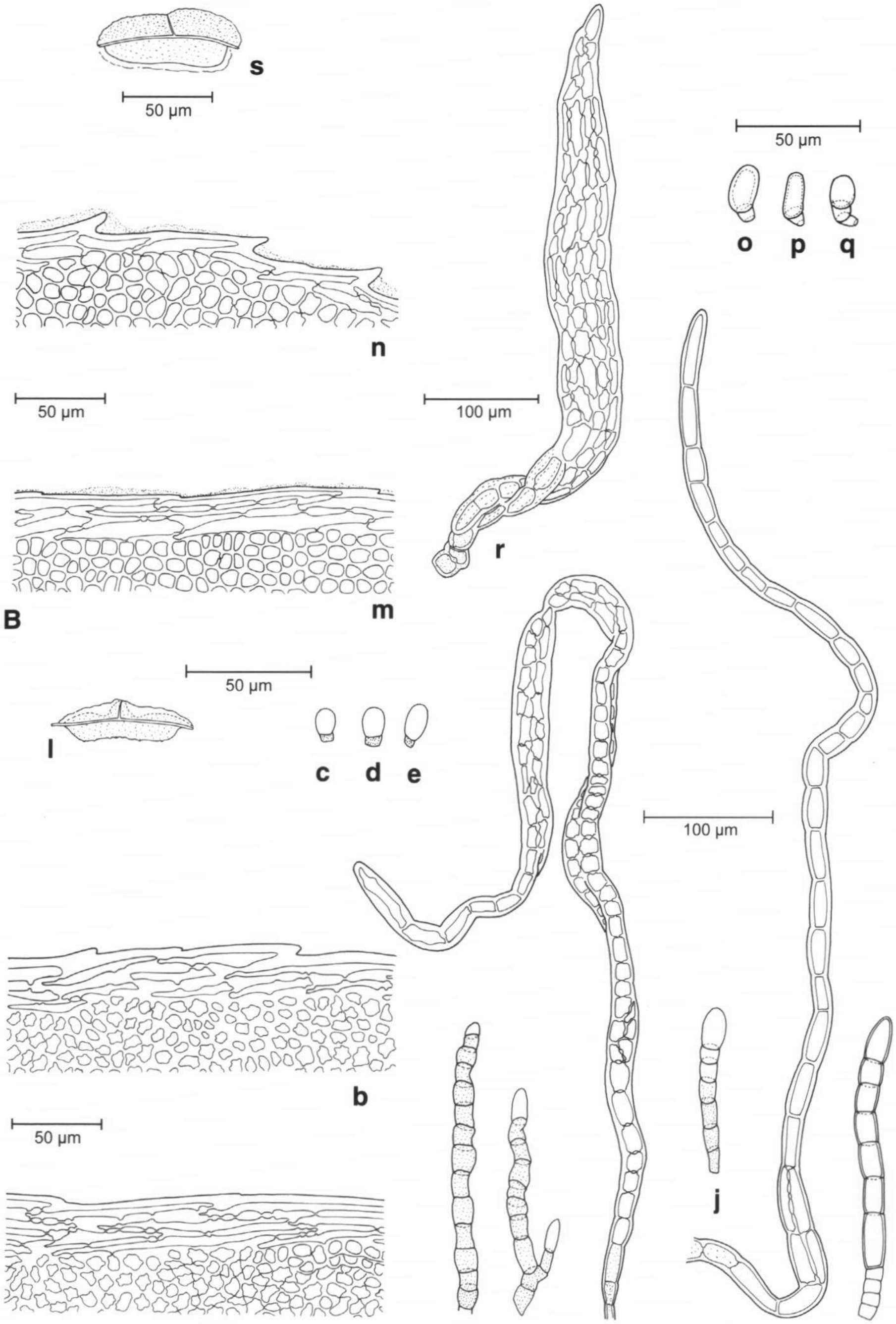


Fig. 41. — A. *Lopidium struthiopteris* (Brid.) M. Fleisch. a. Rachis (cross section dorsal quadrant, with central cavity); b, c. rachis leaves (b. amphigastrium, c. lateral); d, e. branch leaves (d. amphigastrium, e. lateral); f. operculum; g. calyptra set with paraphyses. — B. *L. concinnum* (W. Hook.) Wilson. h. Rachis (cross section dorsal quadrant, with cortical cavities); i, j. rachis leaves (i. amphigastrium, j. lateral); k, l. branch leaves (k. amphigastrium, l. lateral); m. operculum; n. calyptra (A. a–e: *Van der Wijk 453*, L; f, g: *Streimann 30553*, L); B. h–k: *Telford 4207*, L; m–n: *Streimann 2396*, L).

dimorphic, few in number; apex acute, gradually or abruptly acuminate, or subulate. *Distal stipe leaves* dimorphic; margin ± entire. *Lateral stipe leaves* asymmetrical, short- to oblong-ovate, 0.4–2.0 mm long and 0.3–1.5 mm wide; apex usually gradually or abruptly acuminate, occasionally acute, rarely obtuse; costa usually percurrent, occasionally reaching 1/4 of leaf length. *Stipe amphigastria* symmetrical, broad- to oblong-ovate, 0.4–1.5 mm long and 0.3–1.0 mm wide; apex gradually or abruptly acuminate; costa ± percurrent. *Frond leaves* dimorphic, not caducous; margin entire or weakly serrate to moderately serrate-dentate; teeth 1- or 2-celled, up to 18 μm long, projecting up to length of a single cell; border (above leaf base) faint or distinct, continuous, in lateral leaves frequently absent in apical third or absent or interrupted at one side of lamina (see 'Variability'), 1–4 cells wide; branch leaves similar to rachis leaves or smaller. *Lateral frond leaves* asymmetrical, ovate to lanceolate-ovate, 1.0–2.5 mm long and 0.4–1.0 mm wide; apex usually gradually or abruptly acuminate or acute, rarely obtuse; acumen up to 0.3 mm long in rachis amphigastria and up to 0.1 mm long in branch amphigastria; costa ± percurrent. *Frond amphigastria* symmetrical, broad- to oblong-ovate, 0.3–2.0 mm long and 0.1–1.0(–1.5) mm wide; apex acute or gradually to abruptly acuminate; acumen up to 0.2 mm long in rachis amphigastria and up to 0.05 mm long in branch amphigastria; costa ± percurrent. *Gemmae clusters* frequently present, usually on branches and flagelliform innovations, less frequently on rachis and rarely on stipe, usually reaching 1/4–2/3 of length of associated lateral leaves and occasionally roughly equally long when situated in middle part of frond axes, often longer and up to 1 1/2 times as long when located at apex of frond axes, reaching up to 3 times leaf length of associated leaves when borne on flagelliform innovations. *Gemmaphores* simple or branched, 1–25 cells long, brown to dark brown. *Gemmae* simple (or weakly branched), up to 25(–55) cells long, pale brown to brown, smooth or roughly verrucose, occasionally continuing in short rhizoids of c. 5 cells long; cells 10–40 μm long and 10–25 μm wide.

Dioicous. *Inner leaves*: of perigonia elliptic or weakly lingulate, up to 1.1 mm long and 1.0 mm wide, acumen up to 1.1 mm long, costa absent, faint, or distinct and interrupted, reaching 3/4 of leaf length to percurrent; of perichaetia prior to sporophyte development ovate to oblong, somewhat subulate or not, up to 1.3 mm long and 0.8 mm wide, acumen up to 1.4 mm long, costa absent, faint, or distinct and interrupted, obsolete to percurrent; of full-grown perichaetia (ovate to) elliptic to elliptic-lanceolate or weakly lingulate to weakly ligulate, up to 1.6 mm long and 0.6 mm wide, acumen up to 1.6 mm long, costa (absent or) faint or distinct and interrupted, obsolete to percurrent. *Antheridia* 0.6–0.8 mm long. *Perichaetia* situated in distal half of rachis. *Perichaetial stalk* 0.6–1.4 mm long. *Archegonia* 0.3–0.7 mm long. *Vaginula* 0.8–1.0 mm long, set with paraphyses. *Gametoecial axillary hairs* up to 3 per gametoecial leaf, 2- or 3-celled; simple; basal cells 1 or 2; intermediate cells absent; terminal cell short to oblong, elliptic to rectangular, 14–25 μm long and 9–15 μm wide, smooth. *Paraphyses* absent or few in perigonia, usually few but occasionally absent in perichaetia prior to sporophyte development, numerous in full-grown perichaetia, filiform or leaf-like, usually entirely colourless or pale brown to brown in basal and middle part when filiform or leaf-like, occasionally pale green (chloroplasts visible) when leaf-like; basal cells 1–4; intermediate cells short to short-linear, rectangular to truncate-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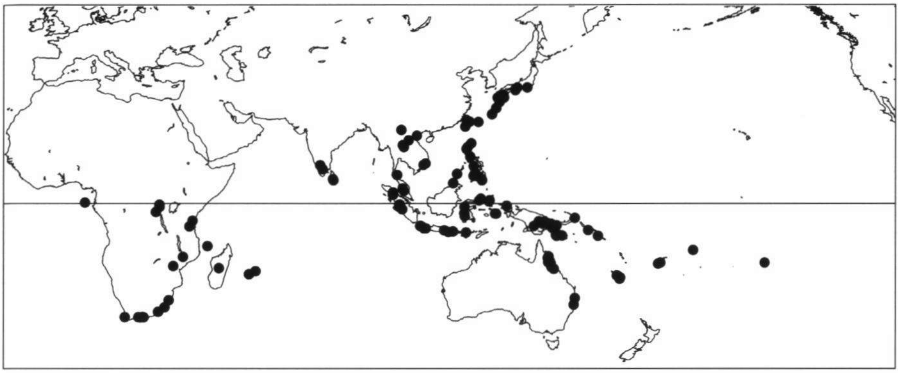
elliptic in filiform parts of paraphyses, rectangular to hexagonal in leaf-like parts; terminal cell short to short-linear, subcircular, elliptic to ovate (or rectangular), 15–55 µm long and 14–25 µm wide; *paraphyses of perigonia and perichaetia prior to sporophyte development* filiform or occasionally widened in lower and middle part, uniseriate or up to 3 cells wide in lower and middle part, (2–)5–42 cells long; *paraphyses in final stages of sporophyte development* filiform or leaf-like, situated on vaginula and calyptra, several to numerous cells long and up to 5 cells wide, reaching up to 2.5 mm long and 0.05 mm wide, shorter or longer than perichaetial leaves and frequently partly exserted, ± straight.

Sporophytes up to 4 per frond, ochraceous to brown or with a dark brown capsule, occasionally tinged with some red (see note 19). *Seta* 4.0–10.0 mm long. *Capsule* barrel-shaped to elongate-cylindrical, 1.9–3.1 mm long and 0.6–1.0 mm wide; annulus absent. *Peristomial formula OPL:PPL:IPL* = 4:2:(4?–)6–8c. *Preperistome* absent or present(?). *Exostome* colourless; teeth 300–345 µm long and 50–60 µm wide; dorsal side weakly cross-striate in basal third of teeth, becoming minutely papillose above; median line present as a roughly straight border; lamellae weakly to distinctly projecting in basal half of teeth, weakly projecting or not in distal half; striae weakly papillose or not; dorsal plates 5–8 µm thick, occasionally conspicuously incrassate along transversal walls and inner radial ones; lamellae distinctly projecting in basal third of teeth, not projecting in distal part; ventral plates 7–10 µm thick; trabeculae very short, somewhat more pronounced in middle part of teeth. *Endostome* weakly to moderately papillose; basal membrane reaching 1/10–1/9 of length of exostome teeth; processes projecting 130–270 µm beyond orifice and 15–25 µm wide at base (see note 20), distinctly keeled, weakly nodulose or not, not appendiculate or with lateral appendages by parts of a single cell. *Operculum* 1.2–2.0 mm long. *Calyptra* 2.1–2.5 mm long, set with a few to numerous paraphyses, occasionally set with a few archegonia; margin provided with a few incisions of irregular depth. *Spores* 13–19 µm.

Distribution — São Tomé e Principe, Democratic Republic of Congo, Tanzania, Malawi, Zimbabwe, South Africa, Comoros (Grande Comore), Malagasy Republic (Madagascar), Mascarenes (Réunion, Mauritius), India (Tamil Nadu), Sri Lanka, China (Yunnan), Taiwan, Japan (Honshu, Shikoku, Kyushu, Ryukyu Archipelago), Thailand, Laos, Vietnam, Philippines (Luzon, Negros, Mindanao, Palawan), Malaysia (Peninsular Malaysia: Pahang; Sabah), Indonesia (Sumatra, Java, Kalimantan, Sulawesi; Moluccas: Tidore, Halmahera, Seram; Bali, Lombok, Flores, West Papua), Papua New Guinea, Bismarck Archipelago (New Ireland), Australia (Queensland, New South Wales), Solomon Islands (Guadalcanal), New Caledonia, Fiji (Viti Levu, Ovalau), Samoa Islands (Upolu), Society Islands (Tahiti).

Fig. 42. — A. *Lopidium struthiopteris* (Brid.) M. Fleisch. a, b. Leaf cells of lateral rachis leaf (a. basal part of antical side, b. distal part of antical side); c–e. axillary hairs; f–g. gemmaphores with gemmae; h–k. paraphyses (h. leaf-like, i–k. filiform); l. exostome tooth (cross section). — B *L. concinnum* (W. Hook.) Wilson. m, n. Leaf cells of lateral rachis leaf (m. basal part of antical side, n. distal part of antical side); o–q. axillary hairs; r. leaf-like paraphyse; s. exostome tooth (cross section) (A. a–g: *Van der Wijk 453*, L; h–k: *Streimann 30553*, L; l: *Streimann 37033*, CBG; B. m–q, s. *Telford 4207*, L; r. *Streimann 58659*, L).



Map 18. Distribution of *Lopidium struthiopteris* (Brid.) M. Fleisch.

For Africa also reported from Mt Kenya, Kenya (Bizot & Pócs, 1982) and Kabarole and Rukungiri, Uganda (Porley et al., 1999).

For continental SE Asia reported from Negri Sembilan, Singapore (Dixon, 1926), Perak and Tioman Island, Malaysia (Mohamed & Robinson, 1991), Cambodia (Tixier 1970, 1971a, b), and southern Vietnam (Tixier, 1970). For Indonesia reported from the Mentawai Islands (Touw, 1968) and Batjan, Maluku (Horikawa, 1934b). Also reported from Ogasawara Gunto, Bonin Islands (Lai, 1976) and from Aneityum, Vanuatu (Brotherus & Watts, 1915). See further notes 23–25.

Habitat & Ecology — In forests, in wet, damp, or dry places, usually in shade or partial shade, occasionally in open habitats. On tree trunks; also on saplings, branches, and climbers, occasionally on tree ferns, rocks (granite, limestone, conglomerate, and sandstone), and rotting logs, rarely terrestrial. Once found submerged (*Akiyama C-14890*). In Japan (Noguchi, 1951) and Taiwan (Noguchi, 1952) found in evergreen forests. Altitude: 300–3300 m in the palaeotropics, 360–1200 m in Australia, 200–560 m in South Africa, and 120–500 m in Japan; found between 720–740 m in China. According to Noguchi (1951) in Japan also found at 1000 m at Mt Ichifusa, Kyushu. See also note 23.

Except for South Africa, the altitudinal distribution in Africa is poorly known. The few records and the data provided by Bizot & Pócs (1982), Kruijer (1997a), and Porley et al. (1999) indicate, that the altitudinal distribution ranges between 800 and 2100 m.

Variability — The species shows a remarkable morphological plasticity in the gametophore with great variability in the size of the plant, the degree of ramification, and the growth direction of the branches, which in turn highly affects the shape of the frond, and the direction of the lateral leaves. There is also great variability in the sizes of the leaves and the amphigastria, the evenness of the leaf surfaces, the extent of the leaf border, and the shape of the leaf apices. The limited data available suggest that the variability in the size of the plant is correlated with geography, and perhaps also with altitude, but not with ecological factors. The variation in the degree of ramification, the direction of the branches, and the direction of the lateral leaves is influenced by geography and, perhaps, by ecology. No correlations were found between the variabilities in the extent of the leaf border or other features and ecology or geography.

The vast majority of the leaves of the plants of *Lopidium struthiopteris* possesses a clearly visible leaf border. However, the extent of the leaf border is very variable, especially in the lateral leaves. When Baumgartner (in Froehlich, 1953) discussed the differences between *L. trichocladon* and *L. struthiopteris* (as *L. javanicum*; see also note 4), he observed that differences in extent of the leaf border may occur not only between different plants, but also between plants or shoots of the same collection, and between leaves situated on the same stem. He noted that, especially, in small, flabellate plants the leaf border is faint or absent. Touw (1992a) reported that plants assigned to *L. trichocladon*, which are smaller than plants assigned to *L. struthiopteris* and have a faint or (partly) absent border in the lateral frond leaves (cf. Fleischer, 1908), are generally from lower altitudes. Both Baumgartner (in Froehlich, 1953) and Touw (1992a) suggested that plants assigned to *L. trichocladon* are juvenile or suboptimal forms of *L. struthiopteris*. Unfortunately, the ecological data provided with the specimens examined were insufficient to find any correlation between growing conditions, in particular in micro habitat, and the size of the plant or the extent of the lateral leaf border.

Furthermore, a correlation between plant or shoot size and the extent of the border of the lateral frond leaves is more complex than was hypothesised by Baumgartner and Touw. Shoots or foliate stems of plants taller than 0.5 cm, which includes the vast majority of the material examined, almost always possess lateral frond leaves that have at least a trace of a distinct border. Neither the length of the border, the proportion of the leaf with a border, nor the extent of the border showed any correlation with the plant or shoot size. The complete absence of a leaf border, the presence of only traces of a leaf border, or the occurrence of a continuously faint border, is usually restricted to minute, often simple, plants that are up to 0.5 cm tall. Similar borderless or nearly borderless leaves may occasionally also be attached to the minute foliate stems that are sometimes found between much larger ones in collections of medium-sized or large plants.

In amphigastria a distinct border is usually present on both sides in the middle part of the amphigastrium. However, in the basal and distal part of the amphigastrium a border may be absent or present in various degrees of extent, ranging from faint and in traces to being distinct and continuous. In the lateral leaves, a border is nearly always distinct in the basal and middle part of the postical side of the leaf, but it may be present in various degrees of extent or even absent in the other leaf parts. Most variation in the extent of the border occurs near the leaf apex and at the antical side of the lateral leaves, where a border may be entirely absent, interrupted, faint, or even entirely distinct. The border of branch leaves, which include amphigastria, is often less well-developed and is more often interrupted or partly absent than in rachis leaves.

Geographical variation — Observed in the size of the plant (viz. length of the stipe, the rachis, and the branches), the degree of ramification (the number of branches, their mutual distance), the direction of the branches, and the direction of the lateral leaves.

Most plants of the species are small to medium-sized, but they are occasionally large when they come from rain forest areas of Indo Malaysia, Australia, and New Caledonia. Plants from these areas have a stipe that is up to 3.0 cm long and a rachis that is up to 6.0 cm long. The largest plants were found in W Malesia, in which the rachis reaches even up to 12.5 cm.

Plants from Africa, Taiwan, Japan, and SW Polynesia are generally smaller than those from the other areas, and have a stipe that is up to 1.5 cm long, and a rachis that is up to 4.0 cm long. Branch length shows a similar correlation with geography and is closely correlated with the length of the stipe.

Within *Lopidium struthiopteris* two variants can be recognised based upon differences in the ramification pattern and the direction of the lateral frond leaves:

'Normal' variant: Plants moderately to densely branched. Branches (few to) numerous, more or less closely set, patent to widely patent. Lateral frond leaves predominantly patent to widely patent, infrequently erecto-patent. — Distribution: Palaeotropics, Sino Japan, Australia (Queensland, northern New South Wales).

'Queensland' variant: Plants scarcely branched. Branches few, very distant, erecto-patent. Lateral frond leaves erecto-patent. The variant can often easily be recognised and distinguished from the 'normal' variant by the more or less slender appearance of its plants. — Distribution: Australia (Queensland), Philippines (Mindanao), Solomon Islands (Kolombangara).

The 'normal' variant occurs in the entire distribution area of the present species, and is the predominant variant in most regions. The 'Queensland' variant is most frequently found in Queensland, Australia, where it is the most abundant variant of the species, but occurs also, though much less frequently, in other parts of the distribution area of the species, viz. the Philippines and the Solomon Islands The plants of the 'Queensland' variant are medium-sized to large. They have a stipe that is up to 2.0 cm long and a rachis that is 2.0 to 6.0 cm long. The branches are up to 2.0 cm long. These sizes are within the range of variability of those of the 'normal' variant. Other differences between the 'Queensland' variant and the 'normal' variant were not found. In both variants the number of branches, their mutual distance, and their direction is very variable. Between the two variants the variation in these features shows considerable overlap. Intermediates between the two variants have occasionally been found in Malesia, while in Queensland and elsewhere the two variants are not sharply defined. Hence, the variants need no nomenclatural status.

Ecological variation — Under moist (sub)tropical conditions a correlation between altitudinal distribution and plant size may exist. According to Fleischer (1908), Mohamed & Robinson (1991), and Touw (1992a, pers. comm.) small plants (assigned to *Lopidium trichocladon*) are generally from lower altitudes than larger ones (assigned to *L. struthiopteris*). Their hypothesis looks plausible and may be observed when climbing a (sub)tropical mountain, but the herbarium material examined provided no supporting evidence. Indeed, plant sizes obtained for the whole tropical area indicate that a correlation between size and altitudinal distribution is absent.

It is not known whether the occurrence of the 'Queensland' variant (see 'Geographic variation') is correlated with ecological factors. However, the characteristic morphology of the 'Queensland' variant might be correlated with seasonal drought, as this variant occurs in the wetter regions of Queensland and in the Malesian area in regions with monsoon influences.

Chromosome number — n = 11, see Inoue (1979: 109–113). — Voucher: *Taguchi 2129* (n.v.), Japan, Kyushu, Kagoshima Pref., Kumage-gun, Yakushima Is., Suzukawa.

Chloroplast DNA sequences — *trnT*$_{UGU}$–*trnL*$_{UAA}$ 5' exon intergenic spacer, 309 bp, deposited in GenBank database under accession number AF034834, see Frey et al. (1999: 70); *trnL*$_{UAA}$ intron, 304 bp, GenBank accession number AF034835, see Frey et al. (1999: 70), Stech et al. (1999: 361); *trnL*$_{UAA}$ 3' exon–*trnF*$_{GAA}$ spacer, 61 bp, GenBank accession number AF034836, see Frey et al. (1999: 70). — Voucher: *Frey & Kürschner 6701* (hb. Frey; 'AFR'), Democratic Republic of Congo (Zaire), Kivu Prov., Irangi Forest, Mt Ilimo, Aug. 23, 1991: AF034834–36.

Remark — As shown, *Lopidium struthiopteris* is a very variable species in terms of habit, size, and leaf characters. Many formerly separate taxa are now considered synonyms.

Notes:

Nomenclature and synonymy – 1. Bridel (1812) did not report the collector of the type of *Hypnum struthiopteris*. Nevertheless, it is almost certain that the type material was gathered by Commerson, for he was reported as the collector of the material from Réunion by Bridel (1819, 1827), Müller (1850), and Schwägrichen (1816). Commerson visited this island in 1771 (Stafleu & Cowan, 1976).

2. According to Thunberg (1823) his plants of *Hypnum penniforme* grew "in sylvis Houtniquas" in Cape of Good Hope. However, none of the specimens examined that are relevant here are labelled with the name of a locality. Material from Thunberg's own herbarium kept in UPS was not accessible, but the microfiche-series that was made from his herbarium (IDC 1036) shows that the origin of the two specimens of *H. penniforme* is indicated as "Cap. b. Spei", without further elaboration of locality.

3. A specimen in L that is indicated to be an authentic specimen contains only a few leaves and a few perichaetia. It is almost certain that they are taken from the other type specimen of *Hypnum penniforme* Thunb. ex Brid. that is preserved in L.

4. *Lopidium trichocladon* has been distinguished from *L. struthiopteris*, but its separate status was questioned by Bartram (1939), Baumgartner (in Froehlich, 1953), Mohamed & Robinson (1991), and Touw (1992a). Van den Bosch & Van der Sande Lacoste (1861) separated *Hypopterygium trichocladon* from *H. struthiopteris* by the smaller size of the former. They also treated the border of the lateral frond leaves of *H. trichocladon* as narrower ("limbum angustum tenuem efficientibus") than that of *H. struthiopteris* ("limbum tenuem efficientibus").

Fleischer (1908) distinguished *Lopidium trichocladon* from *L. javanicum* (≡ *H. struthiopteris* sensu Van den Bosch & Van der Sande Lacoste) by the small(er) size of the plant in combination with the partly bordered lateral frond leaves. He described the plants of *L. javanicum* as being tall(er) with continuously bordered lateral frond leaves. Other authors (e.g. Bartram, 1939; Mohamed & Robinson, 1991) followed Fleischer, but emphasised the difference in continuity and the extent of the border of the lateral frond leaves. However, differences in stature and the extent of the leaf border are not substantial (see 'Variability', p. 274 and 'Ecological variation', p. 276). *Lopidium trichocladon* is an artificial subset of the present species *L. struthiopteris*.

Akiyama (1988, 1992) added another discriminating character to the two discussed above. According to him, the amphigastria should be recurved in *Lopidium trichocladon* and planar in *L. struthiopteris*. However, there is too much variation in the evenness of the lateral leaves and amphigastria. Van den Bosch & Van der Sande Lacoste (1861) described the costa of the lateral (frond) leaves as being excurrent in *Lopidium struthiopteris* (as *Hypopterygium struthiopteris*), and vanishing beneath the leaf apex in *L. trichocladon* (as *H. trichocladon*), but this is incorrect. The costa shows little variation in length in these taxa and is never excurrent in their lateral leaves. In the present species, the costa of the lateral frond leaves may vary in and among plants from ending just below the apex to being percurrent. The costa length is more variable in the stipe leaves.

5. Kindberg (1901) used the differences in the extent of the leaf border, the dentation of the leaves, the length of the acumen, and the size of the plant to distinguish nine subspecies in *Lopidium*

struthiopteris (as *Hypopterygium struthiopteris*). However, no forms can be sharply defined by these features, because of their high variability (see 'Variability', p. 274).

6. According to Müller (1869: 28), *Hypopterygium limbatulum* is a possible synonym of *Hypopterygium struthiopteris* (Brid.) Brid. sensu Mitten (1859) and that opinion is followed here.

7. The holotype of *Lopidium pinnatum* is a medium-sized, female plant. The frond consists of a scarcely to moderately branched rachis and few, short, very distant to closely set branches, which are erecto-patent. The lateral frond leaves are also erecto-patent. It cannot be ascertained, whether the holotype is gemmiferous. Gemmaphores are absent from most parts of the plant, but a few gemmaphores seem to be present at a single, flagelliform innovation that is set with longer rhizoids. The probable isotype in S is not gemmiferous; the one in MEL, which is a larger plant, is clearly gemmiferous. The holotype is very similar to other, frequently gemmiferous specimens of *L. struthiopteris* from Queensland, and because of the features given above it shows most resemblance to the 'Queensland' variant of this species (see 'Geographical variation', p. 275).

8. Hampe (1874a) did not provide *Lopidium javanicum* with a description, but it was validated by Hampe's indirect reference "*Hypopterygium struthiopteris* B.J." (= Bryologia javanica) to Van den Bosch & Van der Sande Lacoste's (1861) description of *Hypopterygium struthiopteris*. Hampe (1874a) considered Van den Bosch & Van der Sande Lacoste's (1861) description of *H. struthiopteris* a new species, which Hampe named himself *Lopidium javanicum*. As Hampe failed to designate any material as its type, *L. javanicum* is typified by the material that was given or cited by Van den Bosch & Van der Sande Lacoste.

Syntypes are present in L, NY, and S. They were not found in Hampe's herbarium (BM). Few specimens in this herbarium are preserved as "*Hypopterygium struthiopteris* Brid." and at least one of them comes from Van der Sande Lacoste (Java, *unknown collector "Lacoste" s.n.*, BM), but none are labelled as *L. javanicum* (or *H. javanicum*), and none could be identified as type material of *L. javanicum*. Lai (1976) erroneously considered *Lopidium javanicum* to be a nomen nudum.

9. The labels of the original material of *Hypnum javanicum* Doz. & Molk. ex Bosch & Sande Lac. lack the names of a collector and the locality of origin. The epithet indicates that the material comes from Java, but only circumstantial evidence can point to the collector. When Van de Bosch & Van der Sande Lacoste (1861) gave the name *Hypnum javanicum* in the synonymy of *Hypopterygium struthiopteris*, they cited specimens from W Java, that were collected by Teijsmann, De Vriese, and Motley. It is almost certain, that the collector of Dozy and Molkenboer's original material is among them. De Vriese collected in the Indonesian Archipelago after Molkenboer's death in 1854 (Touw, 1979). Motley visited Java in 1854 (Van Steenis-Kruseman, 1950), but it is unlikely that his material reached Molkenboer before his death. Teijsmann, however, came to Java in 1830 and collected there (and elsewhere in the Dutch Indies) from at least 1842 until a few years before his death in 1882 (Van Steenis-Kruseman, 1950). Teijsmann is, therefore, the most likely collector.

10. The detailed anatomical illustrations of leaf and perigonial structures referred to as *Hypopterygium struthiopteris* and depicted in Van den Bosch & Van der Sande Lacoste's (1861) t. 137, f. 18–22, 23?, and 25–36, are based on the original material of *Hypnum javanicum* Doz. & Molk. ex Bosch & Sande Lac. The habitus depicted in f. 2 and the distal part of a frond depicted in f. 4 are based on material from one of the collections cited by Van den Bosch & Van der Sande Lacoste for *Hypopterygium struthiopteris* (upon which *Lopidium javanicum* is based, see note 8). This material is preserved in Van der Sande Lacoste's herbarium kept in L. Although it is labelled neither with a collector's name nor with a locality, annotations in Dutch – 'voor de bladeren en okselharen' – indicate that it was used by Van den Bosch & Van der Sande Lacoste's artist Kouwels for making drawings of the leaves and gemmaphores (f. 5–17, 24). Evidence that the material was actually used for this purpose is provided by the fact that amphigastria and a branch with numerous gemmaphores are preserved in small, separate envelopes with the selected plant in the same convolute. It was impossible to ascertain on which material the habitus illustrations f. 1 and 3 are based.

11. Kindberg (1901) distinguished *Hypopterygium subpenniforme*, based on *H. struthiopteris* sensu Van den Bosch & Van der Sande Lacoste (1861), from *H. struthiopteris* (Brid.) Brid. (1827) by its taller growth habit and its continuously bordered lateral leaves and amphigastria. However, Kindberg's features do not represent discriminating characters between the two taxa, nor can they

be separated by other features. Kindberg's *H. subpenniforme* represents principally a selection of well-developed Indo Malaysian plants of the present species.

12. Van den Bosch & Van der Sande Lacoste (1861) indicated that Motley's material of *Hypopterygium struthiopteris* (Brid.) Brid. is preserved in Mitten's herbarium (NY). A specimen that was collected by Motley and was identified as *H. struthiopteris* is present in this herbarium. Such specimens are absent from Van der Sande Lacoste's herbarium (L). Hence, the specimen in NY must be the one that was actually examined, identified, and cited by Van den Bosch & Van der Sande Lacoste (see also 'Types collected by Motley cited in the 'Bryologia Javanica',' p. 27).

13. According to Müller (1876), *Lopidium hemiloma* is close to *Hypopterygium trichocladon*, and therefore it is probably conspecific with *L. struthiopteris*, the only *Lopidium* species known from Africa. *Lopidium hemiloma* was reported from Tanzania by Bizot & Pócs (1982) and from Kahuzi-Biega, Democratic Republic of Congo (Zaire), by Enroth (1993).

14. The type of *Hypopterygium subtrichocladum* (São Tomé e Principe) is a small to medium-sized, gemmiferous plant that shows a great similarity with the type of *Lopidium struthiopteris*. In addition, Brotherus' (1890) diagnostic differences between *H. subtrichocladum* and *H. trichocladon* do not separate the former from the latter.

15. The type of *Hypopterygium daymanianum* is a medium-sized, distinctly gemmiferous, female plant with only a single perichaetium. Although its branches and lateral frond leaves are more frequently patent, it shows a close resemblance to the type of *Lopidium pinnatum* (see note 7), and hence closely resembles the 'Queensland' variant of *L. struthiopteris* (see 'Geographical variation').

16. Fleischer (1908) remarked that *Lopidium trichocladulum* and *L. daymanianum* are very similar to *L. trichocladon* and should be distinguished from the latter at the level of subspecies or below, but he did not actually change their taxonomic status.

17. According to Noguchi (1951), the major differences between *Lopidium nazeense* and *L. javanicum* are the size of the mid-leaf cells (of the lateral leaves) and the development of the border in the lateral leaves. However, these features show much variation and overlap. There are no clear-cut differences in other features, especially when *L. nazeense* is compared to Chinese and Indo Malayan representatives of the present species.

18. The types of *Hypopterygium penniforme* (South Africa), *Lopidium javanicum*, *L. javanicum* fo. *acutifolium* (Malesia), *H. bonatii*, and *H. francii* (New Caledonia) are medium-sized (*H. penniforme*) or large plants (others). They are gemmiferous and show a great similarity to the type of *L. struthiopteris*, which itself is a medium-sized plant.

Sim (1926) treated *Hypopterygium penniforme* as distinct from *H. struthiopteris*, but he erroneously considered the latter species to have simple stems. His description of *H. penniforme* does not separate it from *Lopidium struthiopteris*.

The types of *Hypopterygium campenonii* (Madagascar), *H. congoanum*, *H. polythrix* (Africa), *H. nazeense* (Japan), *H. semimarginatulum* (Fiji), and *H. parvulum* (New Caledonia) are small, gemmiferous plants that show such great similarity with *Lopidium struthiopteris*, that they must be considered conspecific with the latter. The presumed isotype of *H. trichocladulum* from Tahiti in S is also a small, gemmiferous plant that belongs to the present species.

Description — 19. None of the types are fruiting plants. The sporophyte of *Lopidium struthiopteris* is newly described here.

20. The processes are rather irregular in length. This is probably caused by irregular tearing and subsequent detachment of their distal part, whose narowness may increase the chance of rips in the tangential walls of the cells in the PPL and IPL layer during the final stages of peristome development.

Reproduction — 21. Almost every plant of *L. struthiopteris* is gemmiferous having at least a few gemmae at a few branches or flagelliform innovations.

22. There were 20 fruiting specimens among the specimens examined (c. 2%, n = 947). The majority of the fruiting specimens came from Queensland and Mindanao, where, respectively, 11 and 7 fruiting specimens were found (c. 13% of the plants in Queensland, n = 86, and c. 22% in Mindanao, n = 32). One fruiting plant came from Papua New Guinea (c. 1%, n = 82) and one came from Luzon (c. 2%, n = 55). Three plants from Java contain a few fertilised archegonia (c. 1%, n = 252), but there were no Javan plants actually bearing sporophytes. Fruiting plants are not known from other areas.

The occurrence of fruiting specimens might be correlated with ecological factors, but the ecological data with the specimens examined are scant. Nevertheless, it appears that fruiting specimens usually occur in relatively open habitats and in trees at elevated places.

The distribution of fruiting specimens in Queensland and the Philippines shows a remarkable correspondence with the distribution of the 'Queensland' variant of *Lopidium struthiopteris* (see 'Geographic variation', p. 275). However, a correlation between the frequency of fruiting and this variant have not been found. Sporulating plants that belong to the 'normal' variant are also known from Queensland and the Philippines. The restricted distribution of fruiting specimens suggest that sporophyte formation is correlated with, and perhaps even induced, by seasonal drought, but more research is needed to test this hypothesis.

Distribution — 23. *Lopidium struthiopteris* is basically a tropical species, but occurs also in warm-temperate areas of Japan and the warm-temperate and mediterranean areas of South Africa (cf. Magill & Van Rooy, 1998). In both countries, the species is restricted to the coastal regions of the southern and south-eastern parts.

In tropical areas, *Lopidium struthiopteris* occurs mainly in areas or habitats where there is sufficient rainfall or humidity throughout the year. In Australia it is restricted to the coastal regions east of the Great Dividing Range. In Africa, *Lopidium struthiopteris* is confined to mountainous areas. It is found on the West African island São Tomé at high elevations, in the mountains of East and Southeast Africa, in the coastal ranges of South Africa, and in the central highlands of Madagascar. The species is also found on Mt Khartala on Grande Comore, in the low mountains of Mauritius and the high ones of Réunion. The species is absent from the Congo Basin and adjacent areas. In Indo Malaysia and the Polynesian islands, the species is also mainly confined to mountainous areas.

In areas with a warm-temperate or a mediterranean climate, the species distribution is apparently limited by temperature, or humidity, and precipitation. In Japan, the distribution of *Lopidium struthiopteris* is probably limited by temperature and it is restricted to a few regions at or near the south-eastern coast. In southern Japan, precipitation occurs throughout the year, and the climate is very humid in summer. The species occurs in areas where the mean temperature is at least 4° C in winter (cf. Noguchi, 1951), and does not drop below –7° C. In South Africa, the distribution of the species is apparently determined by humidity, for the mean temperatures in winter are several degrees higher than the highest winter temperatures in Japan. Precipitation is sufficient throughout the year in South Africa's warm-temperate climate zone, but there is seasonal summer drought in the mediterranean climate zone. In the latter area the species occurs probably only in mountainous habitats with a relatively short period of seasonal drought, or with sufficient humidity and precipitation in summer on account of fog or rain.

24. *Hypopterygium struthiopteris* was incorrectly reported for Tasmania by Mitten (1860) and for New Zealand, Tasmania, and Chile, by Hooker f. (1867), because they considered this species conspecific with *Lopidium pallens*.

25. A single specimen under the name *Hypopterygium pallens* Hook.f. & Wilson – and two misapplied names – from Palisot de Beauvois in Hooker's herbarium (BM) was labelled to come from the United States, which is almost certainly incorrect.

Selected specimens (from 947 ones examined):

SÃO TOMÉ E PRINCIPE: *Quintas s.n.* (COI, S), *(25)* (H-BR p.p.). — DEMOCRATIC REPUBLIC OF CONGO (ZAIRE): Kivu Prov.: *Bequaert 8067* (BM, BR), Masisi; *Müller Z263* (DR), *Z264* (DR), *400* (DR), Pinga; *Frey & Kürschner 6701* (hb. Frey), Irangi Forest, Mt Ilimo. — TANZANIA: Tanga: *Hedberg 2036a* (S), Usambara Mts, Amani. – Morogoro Prov.: *Crosby et al. 8712* (L), Uluguru Mts, Morogoro; *Pócs et al. 6066/Q* (L), Mt Lupanga; *Thomas s.n.* (MO), Sanje. — MALAWI: Southern Prov.: *Porley M22a* (E), *Wigginton M1709a* (E), Mulanje Mt. — ZIMBABWE: E Mashonaland: *Müller 2544* (L), Stapleford Forest, Rupere. — SOUTH AFRICA: Cape of Good Hope: *Thunberg s.n.* (BM, L, S). – Western Cape Prov.: *Crosby & Crosby 8121* (L), Table Mountain; *Taylor 488* (BM, BR, GRO, MEL, S), Sourflats Forest; *Rehman MAA 301* (COI, S), *901* (BM, L), Blanco. – Eastern Cape Prov.: *Müller SA1* (DR), *SA2* (DR), ENE of Plettenberg Bay; *Lübenau 8* (Z p.p.), Tsitsikama Nat. Res., Storms River State Forest. – KwaZulu-Natal: *Crosby & Crosby 7780* (L), Dhlinza Forest Reserve; *Høeg 127* (BM), *149* (BM), Zululand, Eshowe. — COMOROS IS.: Grande

Comore (Njazidja): *Hunter 92.18* (MO), *Magill & Pócs 11057* (MO), Mt Khartala. — MALAGASY REPUBLIC: Madagascar. Antananarivo Prov.: *Campenon s.n.* (PC, S), Imerina, Amperifery. — MASCARENES: Mauritius ('Île de France'): *Commerson s.n.* (BM), *unknown collector s.n.* (S). – Réunion ('Bourbon'): *Commerson s.n.* (BM), *Commerson? (15)* (BR), *unknown collector s.n.* (L).

INDIA: Tamil Nadu ('Madras'): *Schmid s.n.* (BM, JE, S), *Norkett 11209A* (BM), *Beddome 140* (NY), *s.n.* (BM), Nilgiri Mts; *Foreau MM(IME) 13* (BM, BR, FH, S), Palni Hills, Shembaganur. — SRI LANKA ('CEYLON'): Central Prov.: *Thwaites CM 131* (BM, NY, S, W). – Kandy: *Fleischer B 3626* (B), Peradeniya. – Nuwara Eliya: *Binstead 160* (BM), *331* (BM), Nuwara Eliya.

CHINA: Yunnan: *Redfearn et al. 33684* (BM), Xishuangbanna. — JAPAN: Honshu. Shizuoka Pref.: *Mizutani s.n.* (NICH), Izu Peninsula. – Mie Pref.: *Iwatsuki MJE 1480* (B, CBG, GRO, EGR, L, NY, S), Kumano-shi. – Wakayama Pref.: *Iwatsuki 595b* (NICH), Mt Nachi. – Shikoku. Tokushima Pref.: *Kodama s.n.* (EGR), Kaiba-gun. – Kyushu. Miyazaki Pref.: *Noguchi & Hattori MJ 3* (B, BM, GRO, JE, L, NY, S, W), Minaminaka-gun, Sakatani; *Iwatsuki et al. MJ 784* (BM, EGR, JE, L, NY, S, W), Nichinan, Gongen-dani valley. – Kagoshima Pref.: *Doi 1343* (S), Koshiki Is. – Ryukyu Archipelago. Kagoshima Pref.: *Iwatsuki et al. J-1093* (NY), Yakushima Is.; *Iwatsuki & Sharp 14899* (NICH), *15727* (NICH), *Mayebara 1533* (NICH), Amami-oshima Is.; *Ferrié s.n.* (PC, S), Naze. – Okinawa Pref.: *Higuchi 4325* (HIRO), Okinawa Is., Mt Yonaha-dake; *Watanabe 21465* (NICH), Ishigaki Is. — TAIWAN ('FORMOSA'): Tainan Co.: *Chiang 5659* (B), Ta-don shan. – Nantou Co.: *Lai 9210* (FH, NY), Chitou. – Taoyuan Co.: *Lai & Lewis 0295* (B, NICH, NY, FH), Mt Peitsatienshan. – Taipei Co. ('Taihoku Prov.'): *Noguchi (10116)* (NICH), Wulai ('Urai').

THAILAND: Udawn (Loei): *Touw 10949* (BM, L), Phu (Mt) Luang; *Touw 11052* (BM, BR, EGR, GRO, L, NY), Phu (Mt) Kradung ('Krading'). – Nakhon Si Thammarat: *Touw 11572* (BM, BR, EGR, GRO, FH, L, NY), Khao (Mt) Luang. — LAOS: Xieng Khouang: *Kerr 511c* (BM), Pu Muten. — VIETNAM: Ha Nam Ninh Prov.: *Pócs et al. CE(MHNV) 4793* (B, BM, EGR, L, NICH, S, UPS, W), Cúc-Phuong Reserve. Lâm Dông Prov.: *Tixier s.n.* (EGR), Bao-Lôc.

PHILIPPINES: Luzon. Cagayan Prov.: *Edaño (PBS 79805)* (BM, FH), Mt Babatngin(?). – Benguet Prov.: *Del Rosario 7327D* (GRO), *13000E* (GRO), *Tan et al. 81-330* (B, EGR, GRO, L, NICH, S), Mt Sto. Tomas. – Mountain Prov.: *Van Zanten 683949* (GRO), Mt Data. – Quezon Prov.: *Tan 75-292a* (NICH), *84-128* (NICH p.p.), Mt Banahao. Negros: *Van Zanten 80.01.285* (GRO), Mt Talinis. – Mindanao. Misamis Occ.: *Reyes (2925)* (NY), Mt Malindang. Lanao del Norte: *Bartlett 15942* (FH), Palao Amopo. Lanao del Sur?: *Fleischer s.n.* (FH), Mt Batangan. Davao del Sur: *Edaño (PNH 12950)* (GRO, L), Mt Apo; *Elmer 11409* (BM, FH, HBG, NY, U, W), Todaya; *Van Zanten 81.02.1801* (GRO), *81.02.1673* (GRO p.p.), Mt Talamo. – Palawan: *Edaño (PBS 80840)* (BM, FH), Mt Mantalingahan; *Van Zanten 89.02.540* (GRO), Mt Kalantian. — MALAYSIA: Peninsular Malaysia. Pahang: *Hedenäs MY92-513* (S), *MY92-514* (S), *Allen 628* (GRO, WELT), Fraser's Hill. – Borneo. Sabah: *Richards R. 5752* (L), Mt Kinabalu; *Meijer B. 10165* (L), Mt Templer.

INDONESIA: Sumatra: *Teijsmann s.n.* (L, "An lithis occidentale Sumatrae"). – N Sumatra (Sumatera Utara): *Staal 269* (GRO), Sibajak; *Holttum 15500b* (BM), *15480* (BM), Berastagi; *Touw & Snoek 25304* (L), Mt Sinabung; *Staal 357* (L), Deleng Salit ('Tongkok'); *Alston 14862b* (BM), Parbuluan. – W Sumatra (Sumatera Barat): *Schiffner 12912* (L, S), Mt Singalang; *Alston 14217* (BM), Mt Korinchi; *Meijer B9086* (L), Mt Tudjuh. – Java: *unknown collector s.n.* (L, s. loc, "*H. javanicum* Dz. et Mb. Herb."), *De Vriese s.n.* (L, s.loc.). – W Java (Jawa Barat): *Fleischer s.n.* (FH), Mt Megamendong, Lemoe; *Teijsmann s.n.* (L, S), "in m. Gedé et Salak"; *Fleischer s.n.* (FH), *MFAI 99* (BM, FH, GRO, JE, L, NY, S, U), *Schiffner CE(MHNV) 3970* (B, BM, BR, EGR, L, NICH, NY, UPS, W), Tjibodas; *Van der Wijk 453* (GRO, L), Kandangbadak; *Aman 85* (L), *s.n.* (NY), *Kurz s.n.* (L), Mt Salak. – E Java (Jawa Timur): *Gandrup 520* (FH), *Fleischer 94* (FH p.p.), Idjen Plateau. – Kalimantan. *Korthals s.n.* (L, s.loc.; presumably from SE Kalimantan, cf. Van Steenis-Kruseman, 1950). – Sulawesi. N Sulawesi (Sulawesi Utara): *Touw & Snoek 24362* (L), Minahassa, Mt Mahawu; *Alston 15919* (BM, FH), Mt Minimporok. – C Sulawesi (Sulawesi Tengah): *De Joncheere 1166 D* (L), Sopu Valley. – S Sulawesi (Sulawesi Selatan): *Eddy 5432* (BM), Latimojong Mts, Rantelemo; *Kofman 255N* (L), Mt Rantemario. – Moluccas (Maluku). Tidore: *Alston 16719d* (BM), Mt Kiematulu. – Halmahera: *De Vriese s.n.* (L), *s.n.* (S). – Seram: Manusela Nat. Park, *Akiyama C-9392* (KYO). – Bali: *Touw & Snoek 24781* (L), Mt Catur. – Lombok: *Touw & Snoek 22263* (L), Mt Rinjani. – Flores. Manggarai Prov.: *Touw & Snoek 22865* (L), Golo (= Hill) Lusang; *Schmutz 6716* (L), Mt Desu. – West Papua (Papua, Irian Jaya). Sorong: *Van der Zon* (L), Tamrau Ra., Mt

Bagimana. — PAPUA NEW GUINEA: West Sepik: *Hoffmann 90-192* (CBG, L), *90-308* (CBG, L), Oksapmin. – Enga: *Robbins 3143* (B, FH, L), Lai-Ambum Divide. – Western Highlands: *Van Zanten 68861* (L), Baiyer River. – Eastern Highlands: *Hoffmann 89-422* (CBG), *McVean 268233* (CBG), *Streimann 18123* (CBG), Daulo Pass. – Southern Highlands: *Streimann 24360* (CBG), Margarima. – Morobe: *Kaernbach 36* (H-BR p.p.), *Nyman 109* (NY, S, UPS), Sattelberg; *Weber & McVean B-34978* (CBG), Mt Kaindi. – Central: *Robbins 4107* (L), Sogeri Plateau; *Streimann & Naoni 14922* (CBG), Dabamura. – Milne Bay: *Armit Jr. s.n.* (FH, S), *Brass 23173* (FH), Mt Dayman. – Bismarck Archipelago. New Ireland: *Eddy 6162* (BM), E Coast, Danfu Valley. — SOLOMON IS.: Kolombangara: *Glenny 2290* (CHR), *Spearpoint 76* (CHR), Poitete. – Guadalcanal: *Robbins 4310* (L), Malakuna; *Van Zanten 682543* (GRO), *682526b* (GRO p.p.), Mt Popomanaseu.

AUSTRALIA: Queensland: *Brass 20093* (FH), *Streimann 57151* (CBG), Mt Finnegan; Mt Lewis, *Van Zanten 68.1390D* (GRO); *Downing 0353* (MACQ), Atherton Tablelands; *Streimann 30553* (CBG, L, NY), *57122* (CBG), Walter Hill Ra.; *Streimann 37033* (B, CBG), Paluma Ra.; *Fitzalan s.n.* (BM), *s.n.* (MEL; S, sub no. *8*), Mt Elliot; *Thiers 1205* (NY), Lamington Nat. Park. – New South Wales: *Doing M 135* (L), 'NE New South Wales'; *Streimann 6633* (CBG, L), Briggsvale. — NEW CALEDONIA: *Franc MHNCE 60* (FH, L, S, W), Mt Koghis; *Franc s.n.* (PC), *s.n.* (S), Mt Dzumac; *Franc s.n.* (PC, FH), *MHNCE 161* (FH, L, S, W), Nouméa; *Le Rat s.n.* (PC), "in jugo Dogny". – Île des Pins: *unknown collector s.n.* (NY).

FIJI: Viti Levu: *St. John 18350* (FH), Wainimala Valley. Ovalau: *Graeffe s.n.* (S). — SAMOA IS.: Western Samoa. Upolu: *K. & L. Rechinger 3063* (S, W), Tiavi; *Fleischer B1107* (B, FH, s.n.; NY), Mt Lanutoo. — SOCIETY IS.: Tahiti: *Nadeaud s.n.* (S, sub no. *1*); *Temarii [Nadeaud] s.n.* (FH), Miaa.

DUBIOUS ORIGIN: *unknown collector s.n.* (BM, 'Etats Units'; see note 25).

DOUBTFUL LOPIDIUM SPECIES

Lopidium nematosum (Müll.Hal.) M. Fleisch., Hedwigia 63 (1922) 213. — *Hypopterygium nematosum* Müll.Hal., J. Mus. Godeffroy 3 (1874) 80. — *Hypopterygium struthiopteris* (Brid.) Brid. subsp. *nematosum* (Müll.Hal.) Kindb., Hedwigia 40 (1901) 282. — Type: *Kaysser s.n.* (B holo destroyed; isotypes not found), Australia, New South Wales.

Note — *Lopidium nematosum* is conspecific with either *L. struthiopteris* (Brid.) M. Fleisch. or *L. concinnum* (W. Hook.) Wilson. In Müller's (1874) original description *Hypopterygium nematosum* was reported as being dioicous. This weakly supports synonymy with *L. struthiopteris*, for unisexual plants occur more frequently in *L. struthiopteris* than in *L. concinnum*. Differentiating character states were, unfortunately, not explicitly given in Müller's description.

Although Kindberg (1901) considered *Hypopterygium nematosum* Müll.Hal. to be a subspecies of *Hypopterygium struthiopteris* (Brid.) Brid., it cannot be ruled out that *Lopidium nematosum* actually belongs to *L. concinnum*. Müller (1874) did not report gemmae or paraphyses for *L. nematosum*, which are so characteristic for *L. struthiopteris*. Moreover, *L. concinnum* is more abundant in New South Wales than *L. struthiopteris*.

6. DENDROCYATHOPHORUM Dixon — Map 19

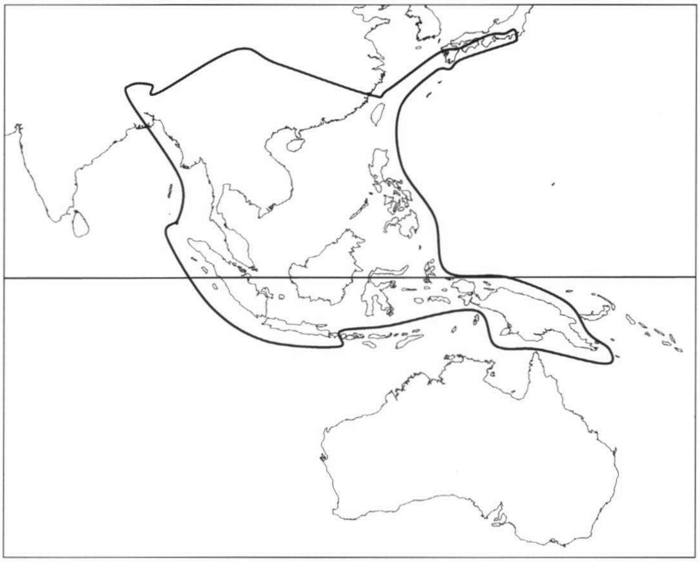
Dendrocyathophorum Dixon, J. Bot. 74 (1936) 7, (January); from the Greek *δενδρον* (dendron, tree) and the genus name *Cyathophorum*. — *Dendrocyatophorum* Dixon ex Sakurai, Muscol. Jap. (1954) 112, nom. inval., orthogr. err. pro. *Dendrocyathophorum* Dixon — Type: *Dendrocyathophorum assamicum* Dixon (= *Dendrocyathophorum decolyi* (Broth. ex M. Fleisch.) Kruijer).

Hypopterygium sect. *Eurydictyon* Cardot, Bull. Soc. Bot. Genève, Sér. 2, 4 (1913, '1912') 378. — *Eurydictyon* (Cardot) Horik. & Nog., J. Sci. Hiroshima Univ, Ser. B, Div. 2, Bot. 3 (1936) 22, (March). — *Eurydyction* (Cardot) Horik. & Nog. ex Sakurai, Muscol. Jap. (1954) 113, nom. inval., orthogr. err. pro *Eurydictyon* (Cardot) Horik. & Nog. — Type: *Hypopterygium paradoxum* Broth. (= *Dendrocyathophorum decolyi* (Broth. ex M. Fleisch.) Kruijer). — Merged with *Dendrocyathophorum* by Dixon, J. Bot. 75 (1937) 126; see note 1.

Plants forming loose to dense groups of fans, usually branched, frequently simple when small, dull or weakly glossy, pale green to dark green, not gemmiferous; ramification pinnate or irregular when weakly branched. *Stems* differentiated into stipe and rachis (when branched), ascending from substratum and becoming horizontal. *Stipe* straight, entirely glabrous or weakly tomentose at base, blackish brown to (reddish) brown at base, becoming brown to green in distal part. *Frond* horizontal, ovate or elliptic to lanceolate-ovate, lacking flagelliform innovations; rachis and branches usually glabrous, occasionally creeping at base, green to brown straight, occasionally weakly curved upwards or downwards; rachis horizontal; branches distant, patent to widely patent, straight; apex of foliate rachis and branches rounded or gradually attenuate. *Rudimentary branches* absent. *Shoot axes* terete. *Epidermis and cortex* ± similar in cellular structure to outer cortex. *Cortex* weakly differentiated. *Central strand* absent (where replaced by a central cavity) or present. *Axial cavities* present in all axes, central; inclusions present. *Axillary hairs* present; basal cells pale brown to brown; intermediate cells absent; terminal cell straight, smooth or covered with substances. *Phyllotaxis* tristichous. *Foliation* anisophyllous and complanate. *Leaves* when moist usually smooth, occasionally somewhat twisted, when dry weakly wrinkled to crisped or weakly twisted; margin serrate or serrate-dentate; border faint or distinct in basal part of leaf, becoming faint and interrupted or absent in distal part; apex gradually or abruptly acuminate; costa distinct, simple (occasionally forked); laminal cells prosenchymatous, short to elongate, hexagonal, walls thin or weakly incrassate, porose; costa cells longer than adjacent laminal cells, elongate to linear, hexagonal (to rhomboid), walls thin or incrassate, porose; border and acumen cells shorter or longer than laminal cells, short to linear, hexagonal, but often rectangular or rhomboid near leaf margin, walls thin or weakly incrassate, porose. *Basal stipe leaves* monomorphic to dimorphic, leaf-like, ovate to oblong-ovate, small, few; lateral ones symmetrical to asymmetrical, patent to squarrose-recurved; amphigastria symmetrical, erecto-patent. *Distal stipe leaves and frond leaves* dimorphic, straight. *Lateral stipe and frond leaves* patent to widely patent (to squarrose-recurved), asymmetrical, ovate to lanceolate-ovate; insertion concave, descending at dorsal side of axis, transverse or ascending at ventral side; base not decurrent; costa reaching 1/2 of leaf length at most. *Amphigastria* symmetrical, patent to widely patent, ovate; basal part smoothly curved; insertion concave; base not decurrent or weakly decurrent; costa reaching 2/3 of length of amphigastrium at most.

Monoicous. *Gametoecia* on rachis. *Gametoecial leaves* concave, elliptic to oblong, shouldered; margin ± entire; border distinct, becoming faint in acumen; apex abruptly acuminate; costa absent or faint; laminal cells prosenchymatous or somewhat parenchymatous, oblong to short-linear, hexagonal, occasionally somewhat rectangular; border cells oblong to linear, rectangular, occasionally elongate-rhomboid near shoulders; acumen cells oblong to short-linear, hexagonal; walls of leaf cells thin or incrassate. *Paraphyses* absent (see note 2).

Sporophyte projecting above frond. *Seta* horizontal to ascending, straight to uncinate, smooth; base narrow. *Capsule* erect to pendent, smooth; neck ± smooth; orifice transverse. *Peristome* double. *Exostome* present, pale yellow; teeth not or partly bordered, not shouldered; dorsal side striate in basal half of teeth, becoming papillose above;



Map 19. Distribution of *Dendrocyathophorum* Dixon.

papillae low to high, simple; striae papillose; median line zig-zag, not furrowed; dorsal plates broader than ventral ones; ventral plates and trabeculae nearly smooth to coarsely papillose. *Endostome* colourless, perforate or not, papillose at both faces; papillae low, simple; processes keeled, cilia present. *Operculum* usually long-rostrate, occasionally somewhat short-rostrate, ochraceous to brown, occasionally tinged with red; rostrum oblique. *Calyptra* probably cucullate (see note 3), partly covering operculum, colourless below, becoming pale brown in distal part, naked, membranous, smooth; apex pale brown.

Monotypic.

Distribution — See below the species.

Habitat & Ecology — See below the species.

Notes:

Nomenclature — 1. Dixon (1937) did not explicitly include *Hypopterygium* sect. *Eurydictyon* in the synonymy of *Dendrocyathophorum*. He considered their types conspecific, and admitted that when he described *Dendrocyathophorum* (Dixon, 1936) he had overlooked the existence of *Hypopterygium paradoxum*. He also remarked, that *Dendrocyathophorum* Dixon precedes *Eurydictyon* (Cardot) Horik. & Nog. by two months.

Description — 2. Extensive examination of numerous gametoecia in many specimens revealed no paraphyses.

3. The definite shape of the calyptra is poorly known. Though many plants were fruiting only a few calyptrae were found and only one of them, of *Boeken 81.03.2587* (Luzon), was situated on a fully developed capsule. This calyptra covers the rostrum and the uppermost conical part of the operculum and is slightly cucullate. Horikawa & Noguchi (in Noguchi, 1936b) and Noguchi (1952, 1991) also reported cucullate calyptrae, and this shape was confirmed by Noguchi's (1991) illustration (f. 339.A.i).

6.1. Dendrocyathophorum decolyi (Broth. ex M. Fleisch.) Kruijer — Fig. 43–45; Map 20; Plate 3c

Dendrocyathophorum decolyi (Broth. ex M. Fleisch.) Kruijer, Lindbergia 20 (1996) 90. — *Hypopterygium decolyi* Broth. ex M. Fleisch., Musc. Buitenzorg 3 (1908) 1079; Broth. in Levier, Bryoth. Levier (1899–1908) 339, nom. nud., precise year and date of distribution not found. — Type: *Decoly & Schaul, Bryoth. Levier 339* (FH holo, BM, H-BR, JE, UPS; S? *s.n.*), India, Bengal Jalpaigura, Karsiyang, "Sikkim-Himalaya, prope Kurseong", Sepoydura Forest, alt. 6800 ft, Oct. 20, 1898. — Merged with *Dendrocyathophorum paradoxum* (Broth.) Dixon and *D. assamicum* Dixon sub *Dendrocyathophorum intermedium* (Mitt.) Herzog (≡ *Cyathophorella intermedia* (Mitt.) Broth.) by Chopra, Bot. Monogr. Council Sci. Industr. Res., India 10 (1975) 399; given in the synonymy of *Dendrocyathophorum paradoxum* (Broth.) Dixon by Gangulee, Mosses of Eastern India (1977) 1542.

Hypopterygium paradoxum Broth. in Cardot, Bull. Soc. Bot. Genève, Sér. 2,4 (1913, '1912') 378. — *Eurydictyon paradoxum* (Broth.) Horik. & Nog. in Nog., J. Sci. Hiroshima Univ., Ser. B, Div. 2, Bot. 3 (1936) 22. — *Dendrocyathophorum paradoxum* (Broth.) Dixon, J. Bot. 75 (1937) 126. — Syntypes: *Matsumura s.n.* (H-BR lecto, sub no. *51*), Japan, Shikoku, Kochi Pref. ["Tosa"]; *Okamura 115* (H-BR, TNS n.v.), Japan, Shikoku, Kochi Pref. ["Tosa"], Mt Yokogura, Apr. 30, 1904; possibly also: *Okamura s.n.* (S), Japan, Shikoku, Kochi Pref. ["Tosa"], Mt Yokogura, March 30, 1904. — Lectotype designated by Kruijer, Lindbergia 20 (1996) 90. — Merged with *Hypopterygium decolyi* Broth. ex M. Fleisch. and *Dendrocyathophorum assamicum* Dixon sub *Dendrocyathophorum intermedium* (Mitt.) Herzog (≡ *Cyathophorella intermedia* (Mitt.) Broth.) by Chopra, Bot. Monogr. Council Sci. Industr. Res., India 10 (1975) 399; merged with *Hypopterygium decolyi* Broth. ex M. Fleisch. and *Dendrocyathophorum assamicum* Dixon by Gangulee, Mosses of Eastern India (1977) 1542; given in the synonymy of *Dendrocyathophorum decolyi* (M. Fleisch.) Kruijer by Kruijer l.c.

Cyathophorella aoyagii Broth., Oefvers. Förh. Finska Vetensk.-Soc. 62A, 9 (1920) 31. — Type: *Aoyagi ["Herb. Iishiba"] 572* (H-BR holo, TNS n.v.), Japan, Honshu, Rendaijimura ["Hondo: Prov. Izu, Rendaijimura"] (Shizuoka Pref.: Izu Peninsula). — Merged with *Hypopterygium paradoxum* Broth. by Horik. & Noguchi in Noguchi, J. Sci. Hiroshima Univ., Ser. B, Div. 2, Bot. 3 (1936) 22. — Synonymised with *Dendrocyathophorum decolyi* (M. Fleisch.) Kruijer by Kruijer, Lindbergia 20 (1996) 90.

Dendrocyathophorum assamicum Dixon, J. Bot. 74 (1936) 7, pl. 610 f. 5. — Type: *Bor 95* (BM holo), India, Arunachal Pradesh ["Assam"], Him Parbat, alt. 6500 ft, March 21, 1934. — Merged with *Hypopterygium paradoxum* Broth. by Dixon, J. Bot. 75 (1937) 126. — Synonymised with *Dendrocyathophorum decolyi* (M. Fleisch.) Kruijer by Kruijer, Lindbergia 20 (1996) 90.

Hypopterygium novaeguineae E.B. Bartram, Rev. Bryol. Lichénol. 30 (1962) 201, '*novae-guineae*'. — Type: *Robbins 3142* (FH holo; B, labelled "near Wabag Govt. station"; GRO, L), Papua New Guinea, Enga ["Western Highlands"], Wabag area, Lai-Ambum Divide, track from Londau in Upper Ambum Valley to Sirunki, mixed *Nothofagus* lower montane rain forest, alt. 8800 ft, corticolous, July 28, 1960. — Synonymised with *Dendrocyathophorum decolyi* (M. Fleisch.) Kruijer by Kruijer, Lindbergia 20 (1996) 90.

Dendrocyathophorum herzogii Gangulee, Mosses of Eastern India: 1541, f. 772. iii. 1977. — Type: *Schwabe-Behn s.n.* (JE holo), Taiwan ["Formosa"], "loco incerto, inter hepaticas", 1947. — Synonymised with *Dendrocyathophorum decolyi* (M. Fleisch.) Kruijer by Kruijer, Lindbergia 20 (1996) 90. — See note 1.

Illustrations: Dixon, J. Bot. 74 (1936) pl. 610 f. 5. — Horikawa & Noguchi in Noguchi, J. Sci. Hiroshima Univ., Ser. B, Div. 2, Bot. 3 (1936) 23 f. 7, pl. 1. — Sakurai, Muscol. Jap. (1954) pl. 42, f. d & g. — Gangulee, Mosses of Eastern India (1977) f. 772. iii, f. 773, f. 774. — Lin P.J. & Li Z.H.(?), in: Li et al., Bryoflora of Xizang (1985) pl. 124, f. 6–10. — Noguchi, Moss Flora of Japan 4 (1991) f. 339.A. — Kruijer, Buxbaumiella 31 (1993) 33, f. 2.

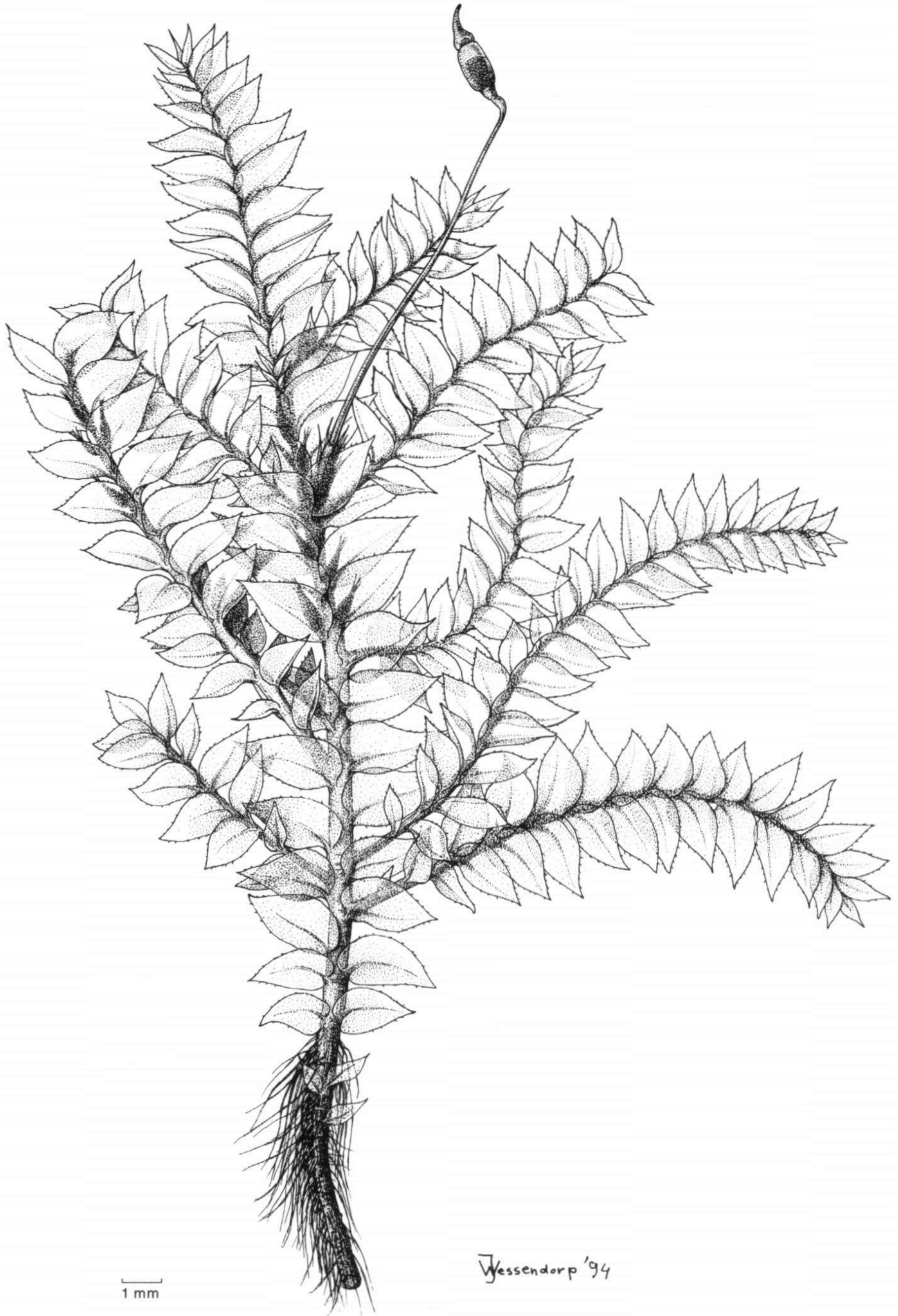


Fig. 43. *Dendrocyathophorum decolyi* (Broth. ex M. Fleisch.) Kruijer. Habit (*Meijer B7598*, L).

Plants small to medium-sized. *Stipe* up to 1.3 cm long, dorsiventrally compressed. *Frond* up to 3.2 cm in diameter; rachis and branches dorsiventrally compressed; branches up to 2.0 cm long. *Primordia* naked or set with scaly leaves; scaly leaves broadly ovate or deltoid to narrowly triangular; margin entire. *Epidermis cells and cortical cells of stipe, rachis, and branches* equally narrow or cortical ones wider; walls thin or incrassate, colourless to brown; inclusions usually absent, but probably occasionally present in inner cortical cells, consisting of oil-like droplets, ± colourless (see note 2). *Central strand* absent, fragmentary, or interrupted (see note 3); cells narrow, walls thin, colourless. *Axial cavities* present in most cross sections, central in all axes, 1 per cross section; inclusions usually present, consisting of large oil-like droplets or wax-like crusts, mostly colourless or ochraceous and occasionally red when oil-like, red to reddish brown when wax-like. *Axillary hairs* 2–6 per leaf, 2–4-celled; basal cells 1–3; intermediate cells absent; terminal cell elongate-ovate to short-linear-rectangular, straight, 70–110(–120) µm long, 14–22 µm wide, usually smooth, occasionally covered with colourless (white) crust-like substances, wall thin. *Leaves* usually closely set, less often distant, pale green to green, occasionally tinged with brown near costa base; laminal cells 35–75 µm long and 15–25 µm wide. *Basal stipe leaves* small, dimorphic, several in number; apex acute or gradually acuminate. *Distal stipe leaves* similar to frond leaves. *Frond leaves* dimorphic, not caducous; margin usually moderately serrate-dentate, occasionally moderately serrate; teeth 1-celled, up to 25 µm long, projecting up to 2/3 of its length; border faint or distinct in basal third of leaf, faint and interrupted, or absent in distal part, up to 3 cells wide. *Lateral stipe and frond leaves* asymmetrical, usually ovate to oblong-ovate, occasionally lanceolate-ovate, (1.3–)1.5–3.5 mm long and (0.4–)1.0–1.5 mm wide; apex gradually or abruptly acuminate; acumen 0.2–0.5 mm long; costa reaching 1/4–1/2 of leaf length. *Frond amphigastria* ovate to oblong-ovate, 0.4–0.9 mm long and 0.3–0.8 mm wide; apex (gradually or) abruptly acuminate; acumen 0.3–0.7 mm long; costa reaching 1/3–2/3 of amphigastrium length.

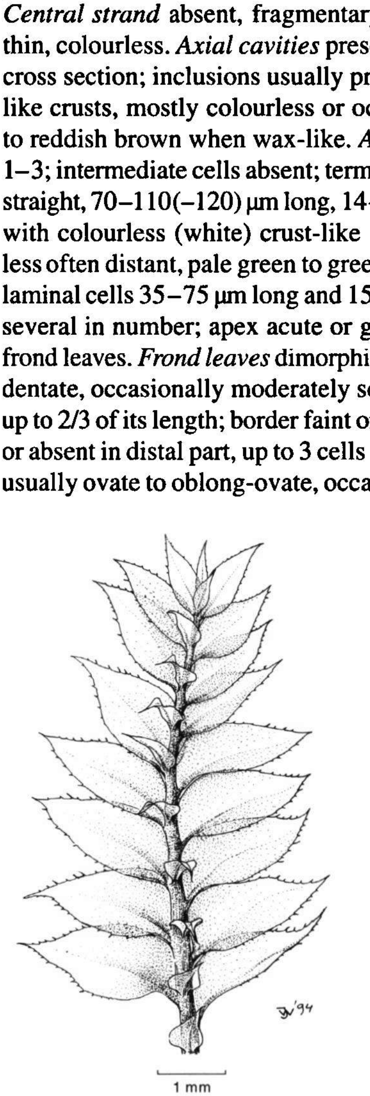


Fig. 44. *Dendrocyathophorum decolyi* (Broth. ex M. Fleisch.) Kruijer. Distal part of frond axis (ventral view, *Meijer B7598*, L).

Autoicous. Gametoecia in basal and middle parts of rachis, unisexual. *Perigonia* usually placed below perichaetia, occasionally among them. *Leaves* ovate or elliptic to oblong, but lingulate to ovate in full-grown perichaetia; costa absent or faint, reaching 1/8–1/5 of leaf length. *Inner leaves*: of perigonia up to 0.7 mm long and 0.4 mm wide, acumen up to 0.5 mm long; of perichaetia prior to sporophyte development up to 1.0 mm long and 0.5 mm wide, acumen up to 0.6 mm long; of full-grown perichaetia up to 1.3 mm long and 0.5 mm wide, acumen up to 0.5 mm long. *Antheridia* 0.4–0.5 mm long. *Stalk in full-grown perichaetia* 0.2–0.9 mm long. *Archegonia* 0.4–0.5 mm

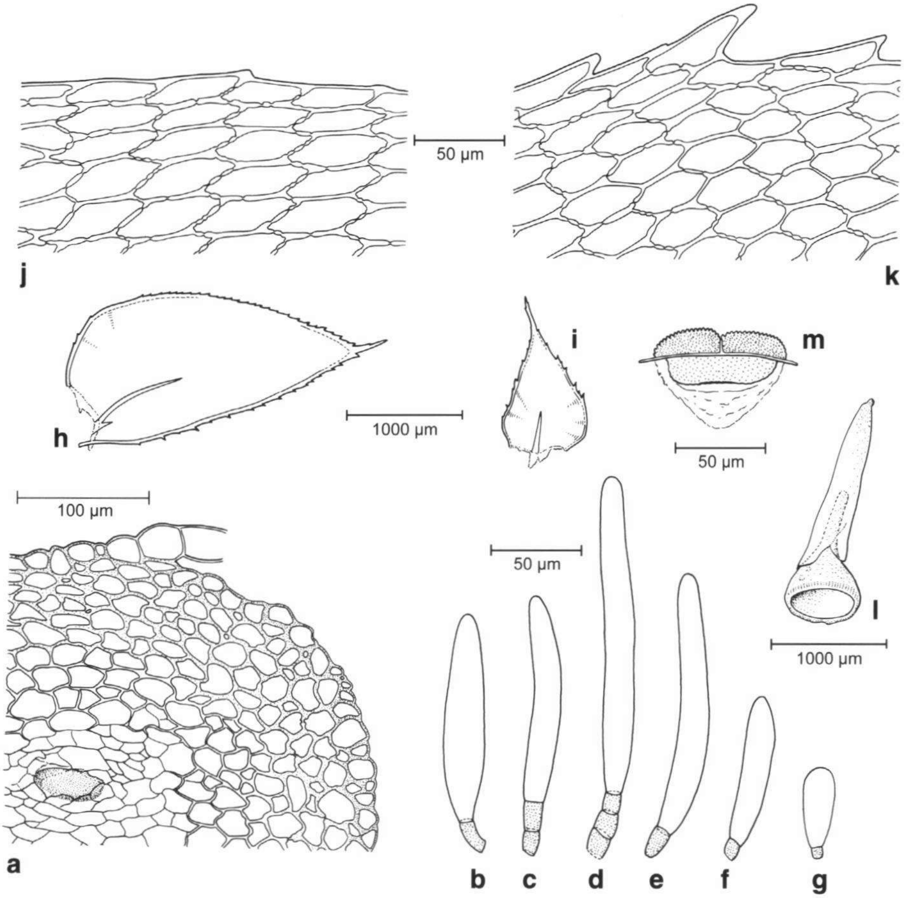
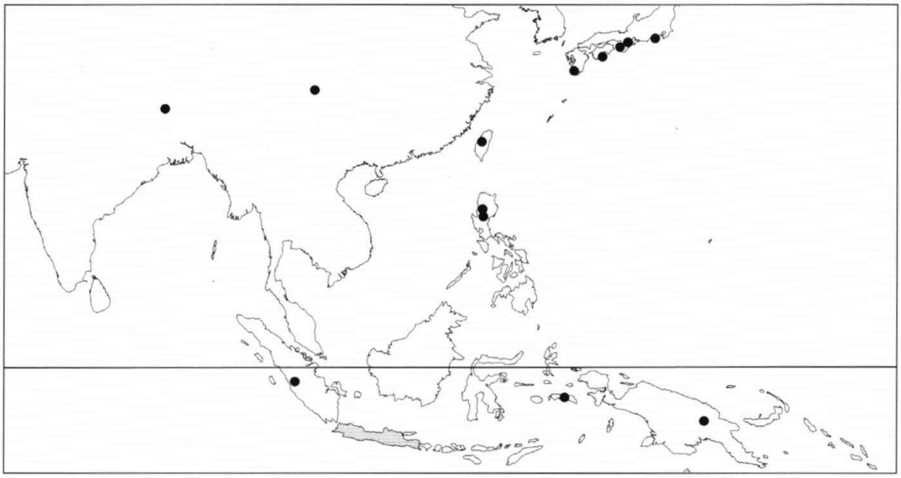


Fig. 45. *Dendrocyathophorum decolyi* (Broth. ex M. Fleisch.) Kruijer. a. Rachis (cross section dorsal quadrant); b–g. axillary hairs; h, i. rachis leaves (h. lateral, i. amphigastrium); j, k. leaf cells of lateral rachis leaf (j. basal part of antical side, k. distal part of antical side); l. operculum with calyptra; m. exostome tooth (cross section) (a, h–k, m: *Meijer B7598*, L; b, c: *Bor 95*, BM; d–g, l: *Boeken 81.03.2587*, GRO).

long. *Vaginula* 0.8–1.2(–2.1) mm long. *Gametoecial axillary hairs* up to 7 per gametoecial leaf, 2–6(–7?)-celled (see note 4); simple; basal cells 1–4, colourless to brown; intermediate cells absent or present, truncate-elliptic, colourless; terminal cell oblong to linear, elliptic to rectangular, 40–140 µm long and 10–25 µm wide, smooth.

Sporophytes up to 3 per frond, ochraceous to brown. *Seta* 4.5–13.5 mm long. *Capsule* usually ovoid to ellipsoid, occasionally turbinate, 0.8–1.8 mm long and 0.4–0.9 mm wide, occasionally tinged with red; annulus (indistinct or) distinct. *Peristomial formula OPL:PPL:IPL* = 4:2:4–6c. *Preperistome* absent. *Exostome* pale yellow; teeth 330–480 µm long and 70–95 µm wide; lamellae weakly projecting or not in basal half of teeth, distinctly projecting in distal part; dorsal plates 11–17 µm thick; ventral plates 15–19 µm thick; trabeculae short in basal third to half of teeth, pronounced to



Map 20. Distribution of *Dendrocyathophorum decolyi* (Broth. ex M. Fleisch.) Kruijer.

strongly pronounced in distal part of teeth, becoming very short near apex. *Endostome* weakly to moderately papillose; basal membrane reaching 1/3–1/2 of length of exostome teeth; processes projecting 340–480 µm long beyond orifice and 40–90 µm wide at base, weakly keeled or not, neither nodulose nor appendiculate; cilia (1 or) 2, 8–10 cell plates long and 1–3 cell plates wide, nodulose or not, frequently bearing trabeculiform appendages at inner face. *Operculum* 0.6–1.1 mm long. *Calyptra* c. 1.7 mm long (see note 5); margin probably ± entire. *Spores* 11–20(–25) µm.

Distribution — India (Bengal Jalpaigura, Arunachal Pradesh), China (Sichuan), Japan (Honshu, Shikoku, Kyushu), Taiwan, Philippines (Luzon), Indonesia (Sumatra, Java, Moluccas: Seram), Papua New Guinea.

In Japan restricted to areas near the southern and southeastern shores of Central Honshu, Shikoku, and Kyushu. Reported from Vietnam (Tixier, 1966) and Thailand (Noguchi, 1973). According to Tan et al. (1994) also found in Guizhou, China.

Habitat & Ecology — In forests. On rocks, and trunks or branches of trees and shrubs; occasionally on rotting wood. Rock type might be limestone, but has been recorded for a single collection (*Akiyama C-15313a*, Seram) only. Altitude: 1600–2260 m in tropical Asia; 1000–1200 m in China and Taiwan, and 30–600 m in Japan. Once found at 2930 m in Papua New Guinea.

Variability — In most plants almost every leaf is serrate-dentate, whereby 'true' serrations frequently predominate, and most to all of their processes lack perforations. The only plant known from New Guinea (*Robbins 3142*), found at 2930 m in Papua New Guinea, has leaves that are either serrate or serrate-dentate. In addition, numerous processes are perforate. It is not known whether these minor differences reflect geographical or altitudinal variation.

Geographical variation — Not found, except for the differences between the plant from Papua New Guinea and plants from other parts of the distribution area (see 'Variability').

Ecological variation — Not found, perhaps except for altitude (see 'Variability').

Notes:

Nomenclature — 1. The type of *Dendrocyathophorum herzogii* is preserved in Herzog's herbarium (JE) and is labelled as *Cyathophorella intermedia* (Mitt.) Broth. (Kruijer, 1996b). The type consists of small, partly damaged plants with a single fertilised archegonium. When Herzog (in Herzog & Noguchi, 1955) examined this specimen in a study on collections from Formosa made by Schwabe, he misinterpreted *Cyathophorum intermedium* Mitt., and erroneously transferred *Cyathophorella intermedia* (Mitt.) Broth. to *Dendrocyathophorum*, making the combination *D. intermedium* (Mitt.) Herzog (Gangulee, 1977; Kruijer, 1996b). Herzog's mistake was corrected by Gangulee (1977), who interpreted Herzog's material as a new *Dendrocyathophorum* species, which he named after Herzog.

Description — 2. Oil-like droplets or wax-like crusts are present in the central cavity. Whether oil-like droplets also occur in the inner cortical cells could not be determined with certainty, as they could have been disposed by sectioning.

3. The central strand is probably present in early stages of development of the axis and is later partly or entirely replaced by a central cavity.

4. A vast majority of the gametoecial hairs that were observed were 5 cells long or shorter, having 1 to 3 basal cells. Only a few hairs were 6 cells long or longer, having 3 or 4 basal cells. The maximum length of the gametoecial hair is not precisely known, because the distal cell(s) of the axillary hairs of 6 cells long or longer are frequently lost.

5. It is remarked that calyptrae are often absent in fruiting specimens, probably because they are loosely attached to the operculum. Perhaps this is why the (juvenile) calyptra Dixon (1936) described in the type collection of *D. assamicum* is now missing.

Reproduction — 6. There were 41 fruiting specimens in the material examined (57%, n = 71).

Other — 7. In *Iwatsuki 906* (B, NY) gall-like structures of leaves were found at the apex of a few branches, but parasites were not observed.

Specimens examined (71 specimens examined):

INDIA: Bengal Jalpaigura ('Sikkim-Himalaya'). *Decoly & Schaul, Bryoth. Levier 678* (PC, S), Karsiyang ('Kurseong'); *Decoly & Schaul, Bryoth. Levier 339* (BM, FH, H-BR, JE, UPS), *Bryoth. Levier s.n.* (S), Sepoydura Forest; *Decoly & Schaul, Bryoth. Levier 678c* (S), Chuttakpur. – Arunachal Pradesh: *Bor 95* (BM), Him Parbat.

CHINA: Sichuan: *Lin 119* (NY), *Ratcliff s.n.* (BM), *Touw 23968* (L), *23975* (L), *24001* (L), Mt Emei (Omei). — JAPAN: Honshu. Shizuoka Pref.: *Nomusa 7463* (S), Izu Peninsula; *Aoyagi ["Herb. Iishiba"] 572* (H-BR), Rendaijimura. – Mie Pref.: *Takaki 20947* (NY), Minami-Muro-gun; *Koide s.n.* (S), Kumano city. – Wakayama Pref.: *Iwatsuki, MJ 906* (B, BM, EGR, GRO, HIRO, JE, L, NY, S), Kumanogawa. – Shikoku. Kochi Pref. ('Tosa'): *Matsumura s.n.* (H-BR sub no. *51*); *Higuchi s.n.* (HIRO), *Okamura 115* (H-BR), *s.n.* (S), Mt Yokogura; *Watanabe s.n.* (FH), Nanokawa. – Kyushu. Kagoshima Pref.: *Mizutani, MJ 512* (B, BM, BR, JE, L, NY, S), Izumi. — TAIWAN: *Schwabe-Behn s.n.* (JE, s.loc.). – Nantou Co.: *Chuang & Schofield 648* (NY), *Lai 8199* (B, FH, NICH, NY), *8200* (B, NICH); *8203* (NICH); *11537* (B, NICH), *11542* (L p.p.), Chitou.

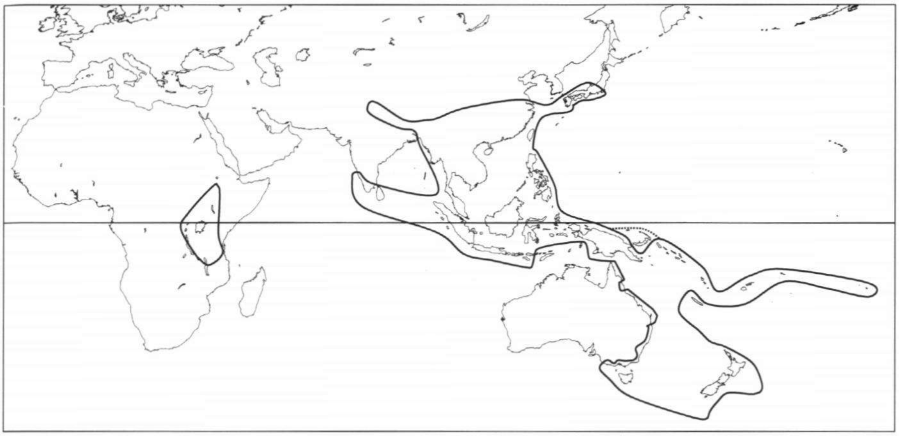
PHILIPPINES: Luzon. Benguet Prov.: *Del Rosario 7472* (GRO), Mt Sto. Tomas; *Del Rosario et al. 12126 A* (GRO p.p., mixed with *Cyathophorum hookerianum*), Mt Pulog. – Mountain Prov.: *Boeken 81.03.2586* (GRO p.p., mixed with *C. hookerianum*); *81.03.2587* (GRO); *Del Rosario 15063 B* (GRO p.p., mixed with *C. hookerianum*), Mt Data. — INDONESIA: Sumatra. W Sumatra (Sumatera Barat): *Alston 13999a* (BM, FH), *Meijer B7598* (L), Mt Kerintji. – Java: *Horsfield s.n.* (NY, s.loc.). – Moluccas (Maluku). Seram: *Akiyama C-15313a* (KYO, L), Manusela Nat. Park. — PAPUA NEW GUINEA: Enga: *Robbins 3142* (B, FH, GRO, L), Lai-Ambum Divide.

7. CYATHOPHORUM P. Beauv. — Map 21

Cyathophorum P. Beauv., Mag. Encycl. 9, 5 (1804) 324; from the Greek κυαθος (cyathos, a cup) and φορεω (phoreo, to bear). — *Hookeria* Sm. sect. *Cyathophorum* (P. Beauv.) Arn., Disposition Méth. Espèc. Mousses (preprint) (1825 [= 1826?]) 56; Mém. Soc. Hist. Nat. Paris 2 (2) (1826) 305. — *Cyathophorum* P. Beauv. sect. *Eu-Cyathophorum* Broth. in Engler & Prantl, Nat. Pflanzenfam. ed. 1, 3 (1907) 966; nom. illeg. pro *Cyathophorum* P. Beauv. sect. *Cyathophorum*. — *Cyathophonom* P. Beauv. ex Brid., Muscol. Recent. Suppl. 4 (1818, '1819') 149, nom. inval., err. pro *Cyathophorum* P. Beauv. — *Cyathopterygium* Brid. ex Mitt., J. Proc. Linn. Soc., Bot., Suppl. 1 (1859) 6, nom. inval., err. pro *Cyathophorum* P. Beauv.; corr. Mitten l.c.: 158. — Type: *Cyathophorum pteridioides* P. Beauv., nom. illeg. incl. spec. prior. (*Anictangium bulbosum* Hedw.) ≡ *Cyathophorum bulbosum* (Hedw.) Müll.Hal.

Cyathophorum P. Beauv. sect. *Cyathophorella* Broth. in Engler & Prantl, Nat. Pflanzenfam. ed. 1, 3 (1907) 965, syn. nov. — *Cyathophorella* (Broth.) M. Fleisch., Musc. Buitenzorg 3 (1908) 1088, [non *Cyathophorella* Müll.Hal. in Paris, Index Bryol. Suppl. (1900) 106, nom. nud. (= *Calyptrochaeta* Desv., see 'Taxa excluded from the Hypopterygiaceae', p. 358)]. — *Cyatophorella* (Broth.) M. Fleisch. ex Sakurai, Bot. Mag. (Tokyo) 50 (1936) 519, f. 7; Sakurai, Muscol. Jap. (1954)113, nom. inval, orthogr. err. pro *Cyathophorella* (Broth.) M. Fleisch. — Lectotype: *Cyathophorella hookeriana* (Griff.) M. Fleisch.; designated here.

Plants forming open to dense groups of fans (or smooth mats in *Cyathophorum bulbosum*) (see note 1), usually simple, occasionally weakly branched or set with a few branch-like innovations (see note 2), gemmiferous in various frequencies (not gemmiferous in *C. africanum*, see note 3). *Stems* not differentiated, usually ascending from substratum and becoming horizontal, occasionally slightly creeping in distal part, straight or curved in distal half, tomentose at base and glabrous above, weakly tomentose where creeping. *Foliate stems* strongly complanate, (oblong to) lanceolate to linear; base tapered (or rounded); apex rounded or tapered and gradually attenuate or caudate by a flagelliform innovation. *Rudimentary branches* absent. *Shoot axes* usually terete, but quadrangular in *C. bulbosum*. *Epidermis* ± similar in cellular structure to outer cortex. *Cortex* differentiated. *Central strand* present (occasionally replaced by a central cavity in *C. africanum*). *Axial cavities* absent (absent, but occasionally present, central, and with inclusions in *C. africanum*). *Axillary hairs* usually present, occasionally absent or lost (see note 4); basal cells colourless or brown; intermediate cells absent or present, colourless; terminal cell straight, colourless, smooth or verrucose. *Phyllotaxis* tristichous. *Foliation* anisophyllous and complanate. *Leaves* when moist smooth to weakly wrinkled, moderately twisted, or strongly crisped, when dry weakly wrinkled to moderately twisted or strongly crisped; margin entire, serrate, or serrate-dentate (rarely ciliate in *C. bulbosum*); border faint or distinct, interrupted; apex usually acuminate, less often acute in a few species (rarely obtuse or rounded in *C. bulbosum* and *C. tahitense*); costa faint or distinct, simple or forked in distal part; laminal cells prosenchymatous, short to short-linear, hexagonal, walls thin or incrassate, porose; border and acumen cells usually longer or narrower than adjacent laminal cells, short to linear, quadrate or rectangular to hexagonal, often with a rectangular or rhomboid outline near leaf margin and a hexagonal outline in acumen, walls thin or incrassate, porose. *Basal leaves* scale- or leaf-like, monomorphic, symmetrical, small, few to numerous. *Distal leaves* dimorphic, not caducous. *Distal lateral leaves* patent to widely patent, asymmetrical, ovate to short-linear; insertion concave or nearly oblique, descending at dorsal side of axis, descending, transverse or ascending at ventral side (see note 5); base decurrent or not; costa reaching 1/2 of leaf length at most. *Distal amphigastria* symmetrical, appressed to patent, circular to lanceolate; basal part nearly plane, smoothly curved, or weakly bulging (usually saccate and weakly to strongly bulging in *C. tahitense*); insertion usually concave or straight, rarely weakly convex or oblique; base decurrent or not; costa reaching 1/2 of amphigastrium length at most.



Map 21. Distribution of *Cyathophorum* P. Beauv. The broken line indicates the area where the occurrence of the genus is dubious.

Dioicous or *monoicous*. *Gametoecia* in basal, middle, or distal part of stem. *Gametoecial leaves* concave, subcircular to ovate or elliptic (or obovate), shouldered; margin entire or weakly serrate-dentate; border faint or distinct, continuous or interrupted; apex acute, or gradually to abruptly acuminate, or subulate; costa absent (or faint); laminal cells prosenchymatous, short to linear, hexagonal; border cells short to linear, usually rectangular or rhomboid, occasionally hexagonal; acumen cells short-hexagonal to short-linear-rhomboid; walls of gametoecial leaf cells thin. *Paraphyses* absent or present, simple or branched, filiform.

Sporophytes usually projecting beneath foliate stem, occasionally lying in or immediately projecting above plane of foliate stem (see notes 6 and 7). *Seta* horizontal or descending and directed downwards, straight or curved, smooth; base narrow or widened. *Capsule* erect, subglobose, cupulate, ellipsoid, or cylindrical; neck ± smooth; orifice transverse. *Peristome* double, showing distinct morphological differences between species. *Exostome* present, yellow to reddish brown; teeth bordered or not, not shouldered (or shouldered in *C. bulbosum*); dorsal side partly or entirely papillose (striate in basal half of teeth in *C. bulbosum*, *C. spinosum*, and to some lesser extent in *C. hookerianum*); papillae low or high, simple or branched; dorsal plates broader than or equally wide as ventral ones, papillose (or striate); ventral plates and trabeculae smooth or papillose. *Endostome* colourless or very pale yellow, not perforate, smooth or papillose; papillae low, simple; processes distinctly keeled (or weakly keeled in *C. hookerianum*, not keeled in *C. africanum*); cilia absent or rudimentary and consisting of parts of 1 or 2 cell plates (present in *C. bulbosum*). *Operculum* long-rostrate (short-rostrate in *C. africanum*), ochraceous to brown, becoming paler towards apex; rostrum straight or oblique. *Calyptra* mitrate, brown, and fleshy (*C. bulbosum*, *C. spinosum*, *C. adiantum*) or (mitrate to) cucullate, white or pale ochraceous, and membranous (*C. africanum*, *C. hookerianum*, *C. parvifolium*), partly or completely covering operculum, naked, smooth or slightly mamillate; apex deep dark brown to red.

A genus of 7 species.

Distribution — E Africa, Sino Japan, Indo Malaysia, E Australasia, and SW Polynesia. Dubious for the Bismarck Archipelago. Absent from New Caledonia.

Habitat & Ecology — In humid to wet, usually evergreen, temperate or tropical (rain) forests, less often in fern thickets (*Cyathophorum bulbosum*) or monsoon forests (*C. adiantum, C. hookerianum*), frequently in moist or wet, shaded places, in particular near streams or waterfalls. On tree trunks, tree ferns (*C. bulbosum*), branches, and twigs, terrestrial, or growing on rocks and rotten logs. Altitude: various distributions; see below the species.

Cyathophorum species occur most frequently epiphytically at low latitudes and low altitudes, and become more abundant on litter, soil, and rocks at high latitudes and high altitudes, but the transition zones, if detectable, are highly dependent on the species.

Notes:

Description — 1. Colonies of *Cyathophorum* are very variable in shape. Most colonies are growing on a surface with a steep slope (e.g. tree trunks, branches, rock faces), and hence consist of fans. *Cyathophorum bulbosum* is also found terrestrially on horizontal surfaces (e.g. soil, litter), where it frequently forms smooth mats.

Depending on differences in structure, colonies may show a quite different appearance. Pure colonies of *Cyathophorum* with an open structure are turf-like, whereas dense colonies may resemble cushions, in particular when they, compared to the size of the plants, occur on large surfaces (e.g. tree bases, tree trunks, boulders, or rock faces). When pure colonies of *Cyathophorum* grow under wet conditions on smaller surfaces (e.g. small stems, thin branches, and climbers), a colony in itself may have a fan-like appearance.

2. Damaged stems and, probably less often, fully outgrown ones have frequently a few innovations.

3. Gemmiferous plants of *Cyathophorum tahitense, C. spinosum*, and, to a lesser extent, *C. adiantum* look often attractive by the presence of numerous, usually coloured, gemmae which occur in clusters in the distal part of the foliate stem, giving it often a brush-like appearance. The colour of the gemmae and gemmaphores depends largely on the pigmentation of their cell walls. Cells of gemmae with colourless cell walls contain frequently visible chloroplasts, which results in a greenish colour of the gemmae.

Cyathophorum africanum is the only monoicous *Cyathophorum* species and the only one that is never gemmiferous. The other *Cyathophorum* species are dioicous and either occasionally or frequently gemmiferous.

4. The distal cells of the axillary hairs placed at the stem of species with long, multicellular axillary hairs with intermediate cells (i.e. *Cyathophorum bulbosum, C. tahitense, C. spinosum*, and *C. adiantum*) are often damaged or lost.

5. The insertion of the first basal lateral leaves is more often descending at the ventral side of the stem (hence oblique) than that of the more distally placed lateral leaves.

6. Sporophytes that are immediately projecting above or are lying in the plane of the foliate stem occur presumably when the gametophore is sharply growing downwards.

7. The sporophyte of *Cyathophorum tahitense* is unknown.

KEY TO THE SPECIES

1a. Leaves serrate-dentate. Calyptra mitrate, pale brown to dark brown, fleshy. Intermediate cells in axillary hairs usually present, occasionally absent. Paraphyses present or absent 2

b. Leaves entire or serrate. Calyptra cucullate (or mitrate), nearly white to pale ochraceous, membranous. Intermediate cells in axillary hairs absent. Paraphyses always absent 5

2a. Amphigastrium pouch present .... **7.2. C. tahitense**
b. Amphigastrium pouch absent 3
3a. Stem quadrangular. Cilia of endostome usually distinct, rarely absent or rudimentary .... **7.1. C. bulbosum**
b. Stem terete. Cilia of endostome absent or rudimentary, never distinct 4
4a. Gemmae when coloured usually orange to orange-brown, occasionally brown or dark brown. Stem entirely laterally compressed (but when gemmiferous regulary laterally compressed in the basal and middle part and dorsiventrally compressed in the distal, gemmiferous part). Perigonial paraphyses present. Perichaetial paraphyses present or absent. Dorsal side of exostome teeth striate in the basal half .... **7.3. C. spinosum**
b. Gemmae when coloured usually brown to dark-brown, never orange or orange-brown. Stem always partly laterally and dorsiventrally compressed, whereby laterally compressed in the basal part up to 4/5 of the length of the stem at most and dorsiventrally compressed in the distal part. Perigonial paraphyses present or absent. Perichaetial paraphyses absent. Dorsal side of exostome teeth smooth or papillose in the basal half .... **7.4. C. adiantum**
5a. Plant never gemmiferous. Monoicous. Axial cavities occasionally present. Operculum short-rostrate .... **7.5. C. africanum**
b. Plant often gemmiferous. Dioicous. Axial cavities absent. Operculum long-rostrate 6
6a. Stem entirely laterally compressed to entirely dorsiventrally compressed. Leaf border up to 4 cells wide, usually continuous, occasionally absent in the distal third of the leaf. Lateral leaves and amphigastria concolourous............ .... **7.6. C. hookerianum**
6b. Stem usually entirely dorsiventrally compressed, sometimes not compressed below, never laterally compressed. Leaf border up to 2 (or 3) cells wide, interrupted, usually absent and occasionally interrupted in the distal third of the leaf. Lateral leaves and amphigastria discolourous or concolourous ... **7.7. C. parvifolium**

Notes on identification:

1. Less developed plants of *Cyathophorum tahitense* resemble sometimes very much small plants of *C. spinosum*. Their differences are discussed under the first species, note 7, p. 311.

2. The identification of non-fruiting plants belonging to either *Cyathophorum adiantum* or *C. spinosum* is sometimes very difficult. The differences between the two species are discussed under the last species, note 15, p. 318.

3. *Cyathophorum hookerianum* and *C. parvifolium* are very similar and closely related species, between which discrimination can be very difficult. The differences between them are discussed under the last species, note 11, p. 356.

7.1. **Cyathophorum bulbosum** (Hedw.) Müll.Hal. — Fig. 46, 48B, 49B; Map 22; Plate 3d

Cyathophorum bulbosum (Hedw.) Müll.Hal., Syn. Musc. Frond. 2 (1850) 14. — *Anictangium* (nom. rejec.) *bulbosum* Hedw., Sp. Musc. Frond. (1801) 43, t. 6, f. 1–5. — *Hedwigia bulbosa* (Hedw.) Brid., J. Bot. (Schrader) 1 (1801, '1800') 272. — *Anoectangium* (nom. cons.) *bulbosum* (Hedw.) Schwägr., Sp. Musc. Frond. Suppl. 1, 1 (1811) 36. — *Cyathophorum pteridioides* P. Beauv., Mag. Encycl. 9, 5 (1804) 324, nom. illeg. incl. spec. prior. (*Anictangium bulbosum*

Hedw.). — Type: "Insulae Australes", (absent from Hedwig's herbarium in G, elsewhere not found; see 'General typification problems', p. 24); lectotype: Hedwig, Sp. Musc. Frond. (1801) t. 6, f. 1–5; designated here; see note 1.

Leskea pennata Labill., Nov. Holl. Pl. 2 (26) (1807, '1806') 106, t. 253, f. 1. — ***Hookeria pennata*** (Labill.) Sm., Trans. Linn. Soc. London 9 (1808) 277, nom. illeg. incl. spec. prior. (***Anictangium bulbosum*** Hedw.). — *Leskea* ('*Leskia*') *pennata* Labill. sensu Brid., Muscol. Recent. Suppl. 2 (1812) 49, nom. illeg. incl. spec. prior. (***Anictangium bulbosum*** Hedw.). — ***Pterigophyllum pennatum*** (Labill.) Brid., Muscol. Recent. Suppl. 4 (1818, '1819') 151, nom. illeg. incl. spec. prior. (***Anictangium bulbosum*** Hedw.). — ***Cyathophorum pennatum*** (Labill.) Brid., Bryol. Univ. 2 (1827) 722, nom. illeg. incl. spec. prior. (***Anictangium bulbosum*** Hedw.). — ***Hypnum pennatum*** (Labill.) Poir. ["Poir."] in Steud., Nomencl. Bot. 2 (1824) 201, nom. nud. in syn. (***Hookeria pennata*** (Labill.) Sm.). — Type: *De Labillardière* (BM?, FI?; not seen with certainty), Australia, Tasmania ["in capite Van Diemen"]. — Merged with ***Anictangium bulbosum*** Hedw. to ***Hookeria pennata*** (Labill.) Sm. nom. illeg. by Smith l.c.; see notes 2, 3, and 4.

Hookeria pennata (Labill.) Sm. (nom. illeg.) var. ***minor*** Wilson & Hook.f., Bot. Antarct. Voy. 1 (1845) 143, t. 62, f. 3. — ***Cyathophorum pennatum*** (Labill.) Brid. (nom. illeg.) var. ***minus*** (Wilson & Hook.f.) Wilson in Hook.f., Bot. Antarct. Voy. 2 (2) (1854, '1855') 120. — ***Cyathophorum bulbosum*** (Hedw.) Müll.Hal. var. ***minus*** (Wilson & Hook.f.) Paris, Index Bryol. (1894) 294. — ***Cyathophorum pennatum*** (Labill.) Brid. (nom. illeg.) fo. ***minus*** (Wilson & Hook.f.) Brizi, Atti Reale Accad. Lincei, Rendiconti Cl. Sci. Fis., Ser. 5, 2 (1893) 103, '***minor***', nom. nud.; Annuario Reale Ist. Bot. Roma 6: 352. 1897, '***minor***'. — ***Cyathophorum minus*** (Wilson & Hook.f.) M. Fleisch., Musc. Buitenzorg 3 (1908) 1097, nom. illeg. incl. spec. prior. (***Cyathophorum densirete*** Broth.). — Type: ***Hooker s.n.*** (BM holo, sub no. ***W 86.b***; BR, FH, L, NY), New Zealand, Auckland Islands ["Lord Auckland's Is."], [on decaying stumps of trees by a water-course, also barren], Antarct. Exp. 1839–1843. — Synonymised with *Cyathophorum densirete* Broth. by Brotherus in Engler & Prantl, Nat. Pflanzenfam. ed. 1 (1907) 966. — Treated as a variety of *Cyathophorum bulbosum* (Hedw.) Müll.Hal. by Dixon, New Zealand Inst. Bull. 3, 5 (1927) 295; Bot. Not. 1937 (1937) 80, who, however, considered the segregation of the variety with the species ill defined. — The type is a small plant of *Cyathophorum bulbosum* (Hedw.) Müll.Hal. with dark olive-green leaves. Its colour is almost certainly caused by growing under wet conditions. — See note 10.

Cyathophorum pennatum (Labill.) Brid. (nom. illeg.) var. *apiculatum* Wilson in Hook.f., Bot. Antarct. Voy. 2 (2) (1854, '1855') 120. — *Cyathophorum bulbosum* (Hedw.) Müll.Hal. var. *apiculatum* (Wilson in Hook.f.) Paris, Index Bryol. (1894) 294. — Type: *Lyall 285* (BM holo), New Zealand, South Island ["Middle I."]; see note 5. — Synonymised with *C. pennatum* (Labill.) Brid. (nom. illeg.) fo. ***minus*** (Wilson & Hook.f.) Brizi by Brizi, Annuario Reale Ist. Bot. Roma 6 (1897) 352.

Cyathophorum novaezealandiae Colenso, Trans. & Proc. New Zealand Inst. 18 (1886) 226, '*novae-zealandiae*'. — Type: ***Colenso s.n.*** (WELT holo), New Zealand, North Island, Hawke's Bay Land District, [In damp, shady woods, generally scattered among other mosses, etc., on rotten logs, both patent, and pendulous; Seventy-mile Bush, County of Waipawa; 1879–1885], 1885. — Three small sheets that are labelled "*Cyathophorum novae-zealandiae*", not bearing a collector's name or other original indications, agree very well with Colenso's description. — See note 12.

Cyathophorum ('*Cyatophorum*') ***densirete*** Broth., Oefvers. Förh. Finska Vetensk.-Soc. 35 (1893) 51. — Type: *Weymouth 862* (H-BR holo, n.v.; BM, JE, NY), Australia, Tasmania, Circular Head, South Road Forest, on small trees, Apr. 21, (18)92. — Merged with ***Cyathophorum bulbosum*** (Hedw.) Müll.Hal. var. ***minus*** (Wilson & Hook.f.) Paris to ***C. minus*** (Wilson & Hook.f.) M. Fleisch., nom. illeg., by Fleischer, Musc. Buitenzorg 3 (1908) 1097; synonymised with ***Cyathophorum bulbosum*** (Hedw.) Müll.Hal. var. ***minus*** (Wilson & Hook. f.) Paris by Dixon, New Zealand Inst. Bull. 3, 5 (1927) 290; see note 6 and 12.

?: *Cyathophorum pennatum* (Labill.) Brid. (nom. illeg.) fo. ***majus*** Brizi, Atti Reale Accad. Lincei, Rendiconti Cl. Sci. Fis., Ser. 5, 2 (1893) 103, '***major***', nom. nud.; Annuario Reale Ist. Bot. Roma 6: 353. 1897, '***major***'. — Type: not indicated; see note 7.

Cyathophorum heterophillum P. Beauv., Mém. Soc. Linn. Paris 1 (1822 [=1823?]) pl. 8, f.6., nom. inval.? — Original material: not indicated. — Probably an error for *C. pteridioides* P. Beauv.; see note 8.

Cyathophorum planum Müll.Hal. ex Brizi, Annuario Reale Ist. Bot. Roma 6 (1897) 354, nom. nud. in syn. — Original material: *Chevalier de Camora s.n.* (RO, JE; B destroyed), Australia, Lord Howe Island, "Lord Howe's Is. Australiae orientalis", "Herb. C. Müller", 1882; see note 9.

Illustrations: Hedwig, Sp. Musc. Frond. (1801) t. 6, f. 1–5. — De Labillardière, Nov. Holl. Pl., Bd. 2 (1807, '1806') t. 253 f. 1. — Hooker, Musc. Exot. 2 (1819) t. 163. — Palisot de Beauvois, Mém. Soc. Linn. Paris 1 (1822) pl. 8, f. 6. — Bridel, Bryol. Univ. 2 (1827) t. suppl. 3. — Wilson & Hooker f., Bot. Antarct. Voy. 1 (1845) t. 62, f. 3. — Brizi, Annuario Reale Ist. Bot. Roma 6 (1897) t. 22–26 f. 12, t. 27 f. 1–9, t. 28–29 f. 26, t. 30; most figures not important. — Goebel, Organogr. Pfl. 1 (1913) f. 54. 1898; ed. 2: f. 230. — Goebel, Flora 96 (1906) 76–85, f. 52–57; Organogr. Pfl. 2, 1, ed. 2 (1915) f. 810, 847. — Brotherus in Engler & Prantl, Nat. Pflanzenfam. ed 1 (1907) f. 703.; ed. 2 (1925) f. 630. — Burr, Trans. & Proc. Roy. Soc. New Zealand 68 (1938) f. 1–88; f. 1 (gametophore), f. 2–88 (stages in ontogeny of gametangia and sporogonium). — Sainsbury, Roy. Soc. New Zealand Bull. 5 (1955) pl. 65, f. 2. — Smith, Cryptogamic Botany 2 (1955) f. 66D & 73. — Allison & Child, The Mosses of New Zealand (1971) pl. 28 f. p. 125. — Ramsay, Austral. J. Bot. 22 (1974) 327 f. 108–111, 332 f. 133.7 (karyotype). — Scott & Stone, Mosses of Southern Australia (1976) pl. 75. — Ramsay in Schuster, New Manual of Bryology 1 (1983) 193, f. 115 (karyotype). — Schofield & Hébant in Schuster, New Manual of Bryology 2 (1984) 633, f. 2.10; Schofield, Introduction to Bryology (1985) f. 8–5. — Vitt in Schuster, New Manual of Bryology 2 (1984) 734, f. 62.— B. & N. Malcolm, The Forest Carpet (1989) 50, 51. — Beever et al., Mosses of New Zealand (1992) f. 73. — Pfeiffer & Frey, Bryol. Rundbriefe 27 (1999) 8. — B. & N. Malcolm, Mosses and other Bryophytes (2000) 10, 37, 71, 152, 203.

Plants in groups of fans or smooth mats, small to large and robust, occasionally gemmiferous, dull to distinctly glossy. *Stems* up to 16.0(–25.0) cm tall, usually quadrangular, occasionally somewhat terete, usually entirely laterally compressed, occasionally not compressed or dorsiventrally compressed in distal half, blackish brown (at base) to brown or green (at top), usually strikingly glossy when blackish. *Primordia* naked. *Epidermis cells and cortical cells of stem* equally narrow or cortical ones wider; walls incrassate or thin, blackish brown to colourless; inclusions absent from epidermis cells and outer cortical cells, absent or present in inner cortical cells, usually amorphous and fat-like plates or crusts, occasionaly oil-like droplets?, occasionally granular starch. *Central strand* present; cells narrow, walls thin, yellow, inclusions absent. *Axial cavities* absent. *Axillary hairs* up to 2 per leaf, 4–11-celled, simple (see note 13); basal cells 2–6, rarely longitudinally divided into 2 cells, colourless? to pale brown; intermediate cells absent or present, elongate to short-linear, rectangular; terminal cell elongate-rectangular to linear, 55–95 µm long and 8–15 µm wide, smooth. *Leaves* distant or closely set, usually pale green to dark green, occasionally tinged with red, rarely blackish green, occasionally slightly brown near base. *Basal leaves* ovate to elliptic; apex gradually acuminate. *Distal leaves* in gemmiferous and non-gemmiferous stem parts similar in size; margin usually weakly to coarsely serrate-dentate, rarely ciliate; teeth 1–4(–7)-celled, up to 150(–400) µm long in lateral leaves and up to 100(–260) µm long in amphigastria, projecting up to 3(–5) cells; border absent, faint, or distinct near leaf base, becoming faint and interrupted in distal part, up to 4 (or 5) cells wide; laminal cells 45–205 µm long and 20–50 µm wide. *Distal lateral leaves* ovate to lanceolate, 3.0–10.5 mm long and 1.0–4.0 mm wide; apex gradually or abruptly acuminate, occasionaly nearly rounded; acumen 0.1–0.5 mm long; costa reaching 1/6–1/2 of leaf length. *Distal amphigastria* erecto-patent to erect, circular to oblong, 1.0–4.0 mm long and 0.5–4.0 mm wide; basal part ± flat or smoothly curved, occasionally weakly bulging; insertion usually weakly concave to straight, rarely weakly convex; apex usually (gradually or) abruptly acuminate; acumen 0.2–0.7 mm long; costa faint to distinct, reaching 1/6–1/3 of amphigastrium length. *Gemmae clusters* located in distal half to third of stem, placed in axils of lateral leaves and amphigastria, reaching 1/3 of length of covering lateral leaves at most. *Gemmaphores* dichotomously branched or penicillate, 5–11 cells long, entirely brown or colourless in distal part. *Gemmae* simple, up to 10 cells long, usually colourless, occasionally brown; cells 20–55 μm long and 10–35 μm wide.

Dioicous. *Gametoecia* in middle part of stem. *Leaves* subcircular, ovate, elliptic, or obovate, green to brown in basal half; margin entire or serrate-dentate in distal part; border faint to distinct, interrupted or continuous, up to 1 or 2 (to 4?) cells wide; costa absent, occasionally faint in perichaetial leaves and reaching up to 2/3 of leaf length. *Inner leaves*: of perigonia up to 1.6 mm long and 1.4 mm wide, acumen up to 0.4 mm long; of perichaetia prior to sporophyte development up to 0.7 mm long and 0.6 mm wide, acumen up to 1.2 mm long; of full-grown perichaetia up to 0.9 mm long and 0.8 mm wide, acumen up to 1.1 mm long. *Antheridia* up to 0.8 mm long. *Stalk of full-grown perichaetia* up to 0.3 mm long. *Archegonia* up to 0.8 mm long. *Vaginula* 0.6–1.2 mm long. *Gametoecial axillary hairs* up to 6 per gametoecial leaf, 3–6-celled, simple (see note 13); basal cells 2–4, brown; intermediate cells usually present, occasionally absent, elongate to short-linear, ± rectangular, colourless (to pale brown); terminal cell (short to) elongate to linear, ovate to narrowly elliptic, (20–)50–115 μm long and 9–20 μm wide, smooth, colourless. *Paraphyses* several to numerous in perigonia, absent or few in perichaetia, 8–11 cells long, usually simple, occasionally branched at base (in perigonia); basal cells 1–3, brown; intermediate cells truncate-elliptic to elongate-rectangular, colourless or brown, often little distinct from basal cells; terminal cell triangular to obovate or elongate-elliptic, 30–230 μm long and (20–)25–85 μm wide, colourless or brown, inflated or not.

Sporophytes up to 14 per stem. *Seta* 0.8–3.0 mm long, ochraceous (to brown when old), occasionally tinged with red; base widened. *Capsule* subglobose to ellipsoid, often narrowed near orifice, 1.2–2.3 mm long and 1.0–1.3 mm wide, ochraceous or red-ochraceous; annulus distinct. *Peristomial formula OPL:PPL:IPL* = 4:2:4–8(–10)c. *Exostome* yellow to reddish brown; teeth 290–510 μm long and 70–140 μm wide, shouldered or not; dorsal side striate in basal half of teeth, becoming moderately papillose in distal part; median line slightly furrowed or not; dorsal plates broader than or equally wide as wide ventral ones, 17–22 μm thick; papillae low, simple; striae minutely papillose or not; lamellae distinctly projecting in basal half of teeth, becoming indistinctly projecting in distal part; ventral plates 9–13 μm thick, smooth or weakly papillose in basal part of teeth, becoming moderately papillose in distal part; papillae low, simple; trabeculae short to pronounced basal fourth of teeth, becoming very pronounced distal part. *Endostome* weakly to moderately papillose at outer face, weakly to coarsely papillose at inner face; papillae low, simple; basal membrane reaching 1/3–1/2 of length of exostome teeth; processes projecting 320–380 μm beyond orifice and 40–55 μm wide at base, distinctly keeled, not nodulose, occasionally containing a few fragmentary lateral appendices; cilia usually present,

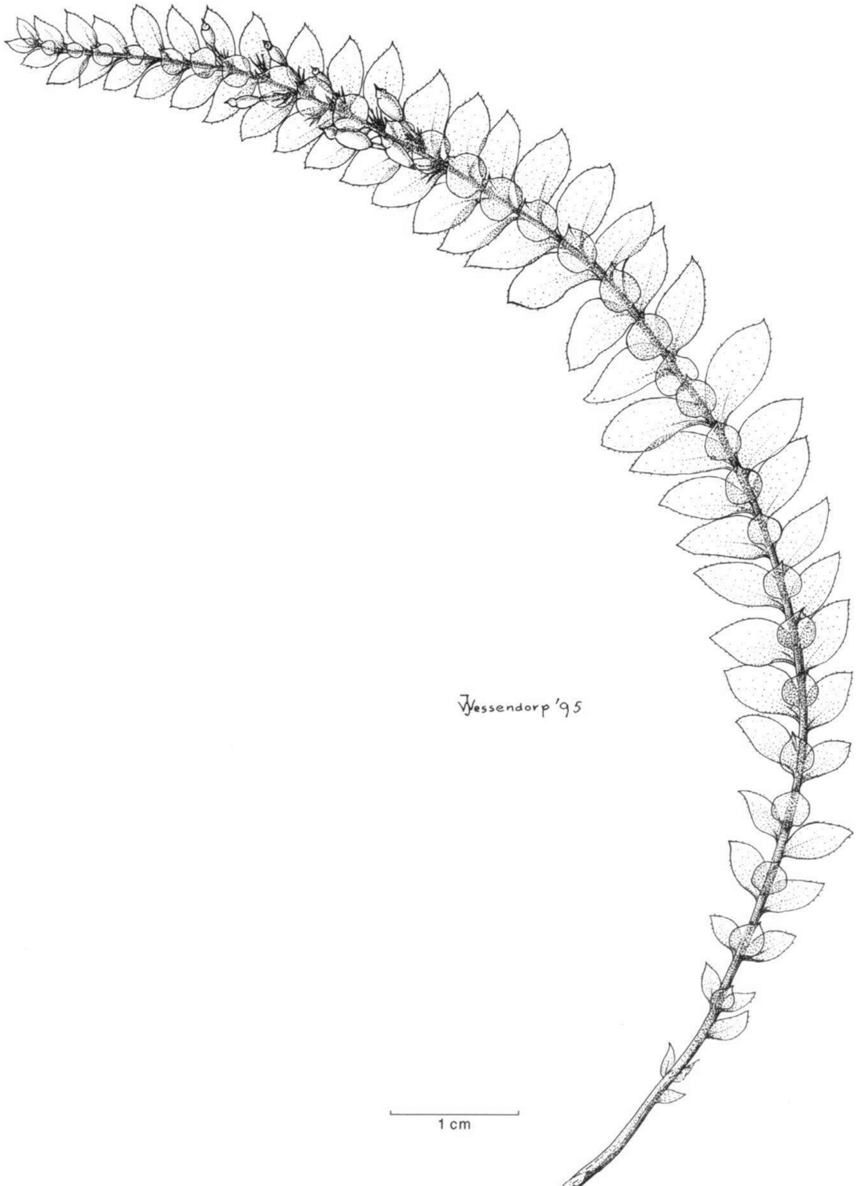
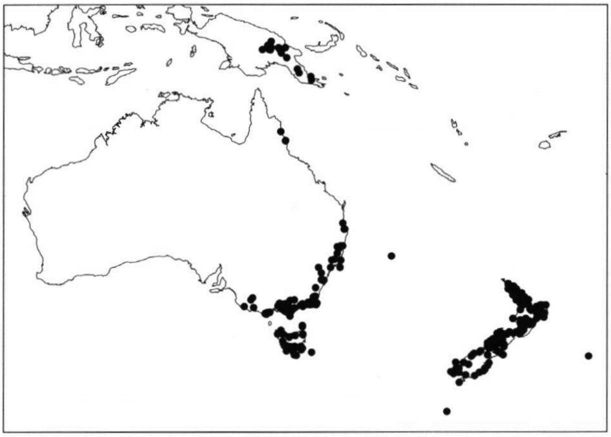


Fig. 46. *Cyathophorum bulbosum* (Hedw.) Müll.**Hal**
Habit (ventral view, *Streimann 51671*, L).



Map 22. Distribution of *Cyathophorum bulbosum* (Hedw.) Müll.Hal.

rarely partly rudimentary or absent, (0–)1–3(–4), 4–15 cell plates long and 1 or 2 (or 3?) cell plates wide, not nodulose, bearing trabeculiform appendages at inner face or not. *Operculum* long-rostrate, 0.8 mm long; rostrum straight. *Calyptra* mitrate, partly covering operculum, 0.4–0.6 mm long, pale brown to dark brown, fleshy; margin entire or weakly bicrenate. *Spores* 10–25 μm.

Distribution — New Ireland?, Papua New Guinea, Australia (Queensland, New South Wales, Victoria, South Australia, Tasmania, Lord Howe Island, Norfolk Island?), New Zealand (North Island, South Island, Stewart Island; Auckland Islands: Auckland Island; Chatham Islands: Chatham Island). See notes 17 and 18.

Habitat & Ecology — In forests and fern thickets, frequently in moist, shaded places, especially in gullies and near streams. Terrestrial (often on banks or slopes of moist to wet, humus rich soil), on rock (basalt, sandstone, granite, limestone), rotting logs (sides), stem bases and trunks of trees, and trunks of tree ferns; less often on branches of trees. Twice found submerged in a stream near the water line. Altitude: 0–1670 m; in New Guinea: 2195–3400 m.

In New Zealand, according to Burr (1938), found in mixed wet forests and absent from or, much less common, in the drier *Nothofagus* forests. According to Beever (1984), in this country with a preference for tree fern species with exposed, hard sclerenchymatous stem surfaces, i.e. *Sphaeropteris medullaris* (G. Forst.) Bernh. (≡ *Cyathea medullaris* (G. Forst.) Sw.).

On Stewart Island, according to Martin (1949), common on rocks that emerge from water, but periodically becoming submerged in flood periods. On the forest floor, the species is more common on roots and stones than on soil or logs.

On the Auckland Islands, according to Vitt (1979), on rocks, small boulders, and tree roots in and near streams at, and just above, the sea level.

Geographical variation — Plants from Papua New Guinea and Queensland show a predominance of unicellular teeth at the margin of their leaves and amphigastria, and are not gemmiferous. Plants from southern areas show a predominance of multicellular teeth at the margin of their leaves and amphigastria, and are occasionally gemmiferous.

Ecological variation — Not found.

Chromosome number — n = 5, see Ramsay (1967b: 559; 1974: 328); Newton (1973: 399). Vouchers: *Ramsay 1/66* (SYD n.v.), Australia, Victoria, Healesville; *Ramsay 8/66* (SYD n.v.), Australia, Victoria, Sherbrook Forest; *Greene* (AAS? n.v.; collection number not given), New Zealand, South Island, Otago L.D., Dunedin.

Chloroplast DNA sequences — *trnL*$_{\mathrm{UAA}}$ intron, 299 bp, deposited in the GenBank database under accession number AF134634, see Stech et al. (1999: 361). Voucher: *'1-4901'*, New Zealand (CHR n.v., hb. Frey n.v.).

Notes:

Nomenclature — 1. I have not seen the specimens concerned, but according to their descriptions and remarks it is virtually certain that Palisot de Beauvois (1804) examined other material than Hedwig (1801). It is, however, beyond any doubt that Hedwig's *Anictangium bulbosum* is included in Palisot de Beauvois' *Cyathophorum pteridioides*, because Palisot de Beauvois (1804) cited Hedwig's (1801) species and regarded *Cyathophorum* as a monotypic genus.

2. In a note, where he briefly discussed the establishment of the genus *Cyathophorum* with a reference to Palisot de Beauvois (1805), De Labillardière (1806) indicated that there exists a relation between his *Leskea pennata* and Hedwig's *Anictangium bulbosum*. However, he did not actually base *L. pennata* on *A. bulbosum*, and they must be considered different names.

3. Hooker (1819) erroneously listed the name *Pterigophorum pennatum* as a synonym of *Hookeria pennata*, with references to Bridel (1819) and Schwägrichen (1816). In subsequent text, however, he uses the name *Pterigophyllum*, and from this it becomes clear that *Pterigophorum pennatum* is an error for *Pterigophyllum pennatum* Brid. The name *Pterigophorum* is therefore invalid.

4. Since Smith (1808) it has been generally accepted that the types of *Anictangium bulbosum* and *Leskea pennata* are conspecific. Schwägrichen (1811) referred only to *Anoectangium bulbosum*, but in 1816 he included the latter in the synonymy of *Leskea pennata*.

I have not seen the type of *Leskea pennata*, but it is certain that *L. pennata* is conspecific with *Cyathophorum bulbosum*. The illustrations given by De Labillardière (1806) clearly show a plant that belongs to *C. bulbosum*.

5. The type of *Cyathophorum bulbosum* var. *apiculatum* is a small plant of *C. bulbosum*. The features given by Wilson (1855) and Hooker f. (1867) entirely fail to distinguish the variety from the species.

6. In the type of *Cyathophorum densirete* male and female plants are mixed, but they show no substantial differences in morphological characters.

7. The type of *Cyathophorum pennatum* fo. *majus* is unknown. Brizi (1893, 1897) cited neither collections nor literature on which he based his forma. Specimens under the name *C. pennatum* fo. *majus* were not found either.

Nevertheless, Brizi's forma is listed here in the synonymy of *Cyathophorum bulbosum*. According to his brief diagnosis in 1897, he must have had large plants of *C. bulbosum* in mind as his *C. pennatum* fo. *majus*. All the material in RO under the name *C. pennatum* belongs to *C. bulbosum*, among them many specimens that are listed by Brizi (1897), and even one that is identified by him.

8. Palisot de Beauvois (1804, 1805) regarded *Cyathophorum* as a monotypic genus with *C. pteridioides* (see also note 1) as the only species. He stated this again in 1822, but used the name of *C. heterophillum* for figure 6 in the legend of plate 8. This name must be regarded as an error for *C. pteridioides*.

9. Brizi (1897) presented the name *Cyathophorum planum* as a nomen nudum with a reference to C. Müller (Halle), but without a citation of the collection on which he based this name. However, in RO the only specimen from C. Müller's herbarium is labelled "*Cyathophorum planum* n. sp. ?". This is almost certainly the original material on which Brizi based *C. planum*. In JE there are two specimens labelled "*Cyathophorum planum* C. Müll. n. sp.", and it is almost certain that they are duplicates of the destroyed original in C. Müller's herbarium, which was kept in B.

The original material of *C. planum* is a non-fruiting plant, which, because of its angular stems, evidently belongs to *C. bulbosum*.

Synonymy — 10. According to Wilson & Hooker f. (1845) *Hookeria pennata* var. *minor* has inwardly curved, rounded leaves. They depicted, however, a plant with gradually, short-acuminate leaves. Wilson (1855, 1860) and Hooker f. (1867) stated that the leaves of this variety are acute. Although, very occasionally, the leaves of *H. pennata* var. *minus* seem to be rounded when dry, they are in fact always gradually acuminate and have a short acumen.

Wilson (1855) indicated that the fruiting stems of *Hookeria pennata* var. *minus* are two inches long at most, whereas the fruiting stems of *Cyathophorum bulbosum* are two inches long at least. In addition, he distinguished *H. pennata* var. *minus* from *C. bulbosum* by its more distant leaves. However, Wilson's features cannot be used to define an infraspecific taxon within *C. bulbosum*, because they basically reflect differences between individual specimens.

Dixon (1927) merged *Cyathophorum densirete* with *C. bulbosum* var. *minus*, but remarked that the variety is difficult to define. Brotherus (1893) distinguished *C. densirete* from *C. bulbosum* by its much smaller size, the very short [leaf] costa, and the much denser areolation [of the leaves] (see note 12). Dixon tested Brotherus' criteria, and pointed out that there is no relation between the size of the [leaf] cells and the size of the plant. Sainsbury (1955) confirmed Dixon's observation for New Zealand specimens, but was in doubt whether *C. bulbosum* var. *minus* actually occurs in New Zealand. Nevertheless, he maintained the variety, because of the smaller areolation recorded for Australian specimens.

There is not any substantial difference in character states between *Hookeria pennata* var. *minus* and *Cyathophorum bulbosum*, and there is no need to separate them. There are no characters nor combinations of character states that can be used to distinguish infraspecific taxa within *C. bulbosum*.

11. The character states given by Colenso (1886) do not delimit *Cyathophorum novaeealandiae* from *C. bulbosum*. The two vertical lines on the exostome teeth of *C. novaezealandiae* reported by Colenso are in fact only one. The dorsal plates of these teeth in *C. novaezealandiae* are slightly less developed along the median line than is usual in *C. bulbosum*, and the median line appears as a weak groove. Colenso indicated that the rostrum of the operculum in *C. novaezealandiae* is recurved, but in its type operculae with a slightly curved rostrum can be observed. *C. novaezealandiae* evidently belongs to *C. bulbosum*.

12. The type of *Cyathophorum densirete* is a medium-sized, fruiting plant that also belongs to *C. bulbosum*. Brotherus (1893) distinguished *C. densirete* from *C. pteridioides* by its much smaller size, the much denser areolation [of the leaves], and the very short [leaf] costa. These character states are discussed by Dixon (1927), who stated that the length of the costa is very variable and not related to other characters. He compared the [leaf] cell width of *C. densirete*, as given by Brotherus, with that of the 'type form', where he probably had *C. bulbosum* var. *minus* in mind. He concluded that the cells of the latter are broader than those of *C. densirete*, but argued that the size of the [leaf] cells is not related to the size of the plant, and then merged *C. densirete* with *C. bulbosum* var. *minus*. In my opinion his argumentation is correct.

Furthermore, Dixon (1927) overlooked the considerable overlap that exists in the length and width of the laminal leaf cells. The laminal leaf cells of *Cyathophorum densirete* are 45–75 μm long and 20–30 μm wide, i.e. longer and slightly broader than described by Brotherus, whereas they are 65–110 μm long and 20–30 μm wide in *C. bulbosum* var. *minus*.

The peristomial formula for the type of *Cyathophorum densirete* is 4:2:4–6c. The cilia of its endostome are up to two cell plates wide and up to 8 cell plates long, but are often rudimentary or even absent. In this respect, *C. densirete* differs from most other specimens of *C. bulbosum*, whose endostomes are usually entirely ciliate. This difference is, however, not substantial. In *C. bulbosum* the number of the cilia and their development is highly variable. I agree, therefore, with Dixon's reduction of *C. densirete*, while I see no need to distinguish infraspecific taxa within *C. bulbosum*. Accordingly *C. densirete* is here merged with *C. bulbosum*.

Description — 13. The axillary hairs that are situated on stems are especially difficult to observe. In addition, they are often damaged or absent and probably lost.

The axillary hairs in gametoecia are less difficult to find, but these hairs are easily damaged by preparation. In addition, observation of these axillary hairs is often hampered by the brown colour of the gametoecial stalk, the brownish, sometimes hair-like, scaly leaves in the basal part of the stalk, and the presence of paraphyses.

14. In *C. bulbosum* inclusions are not restricted to the cortical cells. Burr (1938) observed large droplets of oil in the apex of the perigonial and perichaetial branches, the wall cells of the archegonia, and the calyptrae. I did not observe such oil-like droplets in the wall cells of the archegonia, but observed occasionally oil-like droplets in the calyptra cells.

Oil-like droplets are probably absent from the sporophyte. Burr (1938) did not observe oil droplets in embryo cells, and I did not observe inclusions in the cells of outgrown sporophytes.

15. De Labillardière (1806) and Palisot de Beauvois (1822) depicted entirely non-ciliate endostomes of their specimens of *Cyathophorum bulbosum*. However, in *C. bulbosum* most endostomes are entirely ciliate, and only occasionally partly non-ciliate. I have never encountered material with entirely non-ciliate endostomes. This suggests, that the observations by De Labillardière (1806) and Palisot de Beauvois (1822) are incorrect. I have not seen Palisot de Beauvois' material, but the sporophytes of the fruiting plants that were collected by De Labillardière actually have ciliate endostomes.

Reproduction — 16. The material of *Cyathophorum bulbosum* examined contained 220 fruiting specimens (c. 23%, n = 977). They came in vast majority from Victoria, Tasmania (Australia), North Island, and South Island (New Zealand). Sporophytes were absent from plants from Papua New Guinea, but a single specimen from this area contained an old vaginula. Very few collections from Queensland, New South Wales (Australia), and Stewart Island (New Zealand) contained fruiting plants. Thus far, fruiting specimens are not known from South Australia, Chatham Island, Lord Howe Island and the Auckland Islands The collections that might come from New Ireland or Norfolk Island (see note 17) contain no fruiting material.

According to Burr (1938) c. 10% of the plants of *C. bulbosum* from New Zealand bear fruits. In the specimens examined c. 25% were fruiting plants. This percentage is, however, probably biased by the preference of collectors for fruiting material.

Burr (1938) related the low percentage of fruiting plants to the separation of sexes and reported that male and female plants do not often grow sufficiently intermingled for the production of sporophytes. His observation is probably correct. Among the material examined most collections contain either male or female plants.

Burr's hypothesis saying that the distribution of antherozoids is the limiting factor in fertilisation, is in all probability correct. If his hypothesis is correct, the actual percentage of fruiting plants must be lower than the percentage of male plants. In a sample of fertile, non-fruiting plants of the specimens examined (i.e. female plants under-estimated by omitting fruiting ones; n = 76) c. 40% of the plants were male, where in a sample of both fruiting and non-fruiting plants (i.e. female plants over-estimated by collector bias; n = 240) c. 25% of the plants were male. The actual percentage of male plants is probably in between. Hence, the percentage of fruiting plants (10–25%, see above) is lower than the percentage male plants.

Fructification in a dioicous species must also depend on spatial separation. *Cyathophorum bulbosum* is much more abundant in Victoria (n = 191), Tasmania (n = 139), and the North Island (n = 186) and South Island (n = 187) of New Zealand than elsewhere, and also more frequently found in fruit. In these places 23–30% of the specimens were found in fruit, whereas in other places (Queensland, n = 11; New South Wales, n = 49; Stewart Island, n = 12) only 4–11% of the specimens were found in fruit.

Distribution — 17. I have seen only a single collection of *Cyathophorum bulbosum* from New Ireland. This collection contains two different stems attached to a single sheet labelled "N.^{lle} Irlande", and it may in fact consist of two different specimens. The plants were collected by De Labillardière, who actually visited New Ireland (De Labillardière, 1800). However, mislabelling cannot be ruled out.

The origin "Lord Howe", which was recorded on the label of the only collection from Norfolk Island (*unknown collector s.n.*, W) has been struck out and replaced with "Norfolk". The actual origin of this collection is, therefore, doubtful.

A collection of *Cyathophorum bulbosum* in FH made by an unknown collector is labelled "Philippine Is.". This annotation is almost certainly a mistake. I have not seen any other collection of *C. bulbosum* from the Philippines, nor any specimen gathered north of Papua New Guinea. Therefore, there is little likelihood that *C. bulbosum* actually occurs in the Philippines.

The collection *Chevalier de Camera s.n.* preserved in NY is labelled "Lord Howes Island", but also contains a piece of paper on which is written "Mt Dromedary" and "Reader". Despite this annotation, which suggests Cape Dromedary in New South Wales, Australia, as the collection locality, it is most likely that the collection originates from Lord Howe Island

18. Shaw's (1878) record of *Cyathophorum bulbosum* (Hedw.) Müll.Hal. from South Africa is almost certainly based on misidentified material. I have not seen this material, and do not know to which species it belongs. It might be *C. africanum*, but this species is not known from South Africa. Sim (1926) suggested *C. africanum* and *Distichophyllum* species as possibilities.

Other — 19. *Cyathophorum bulbosum* was collected a few times in greenhouses of botanic gardens in Sweden and Germany, where they may have grown for several years. Plants have been found in the following botanic gardens: Sweden: Uppsala, *Harold Lindberg? s.n.* (S, 'Julii/[18]80'), *Nyman s.n.* (S, '1891'); Germany: Charlottenburg, *Graef s.n.* (HBG, JE; '13 Nov. [18]86'), *Lucas s.n.* (W p.p., '11/87'); Munich: *Dohl s.n.* (GRO, '8-1906'); *unknown collector s.n.* (JE, '21.9.1904'), *s.n.* (JE, 'Aug. 1906'); Wernigerode: *Mönkemeijer s.n.* (HBG, 'Juli 1898'), *s.n.* ('Juli 1901'). The mosses grew on the stems of tree ferns (e.g. *Dicksonia antarctica* Labill.) and, almost certainly, were carried along with these tree ferns from elsewhere. The labels of the two collections made in Uppsala indicate that the phorophytical tree ferns – or a single tree fern – came from New Zealand. The label of one of the two collections made in Munich reports Australia as the origin of the tree fern. The origin of the other collections is not given.

Selected specimens examined (from 977 examined):

?NEW IRELAND: *De Labillardière s.n.* (G). — PAPUA NEW GUINEA: Western Highlands: *Van Zanten 68921* (GRO), Mt Hagen; *Streimann 21226* (CBG), Mur Mur Pass. – Simbu: *De Sloover 42.948* (L), Mt Wilhelm; *Van Balgooy 217* (L), Kombugomambuno. – Eastern Highlands: *Hoffmann 89-481* (CBG), Mt Michael. – Southern Highlands: *Kalkman 5044* (L), Mt Ambua; *De Sloover 42.188* (L), Mt Giluwe. – Morobe: *Robbins 3933* (L), Schrader Ra., Girikum Valley. – Central: *Van Royen 10994* (L), Mt Victoria; *Robbins 4239* (L), Woitape. – Milne Bay: *Brass 22856* (FH), Mt Dayman.

AUSTRALIA: *De Labillardière* (B, BR, G, L; s.loc.). – Queensland: *P[uninterpretable] s.n.* (NY), Daintree; *Streimann 27380* (CBG), Mt Bellenden Ker. – New South Wales: *Weber & McVean B 31266* (NICH, UPS, W), *B 32547* (GRO, FH, NY, S), Point Lookout; *Streimann 7257* (CBG, L, NY), Mt Boss State Forest; *Staer s.n.* (NSW), Guy Fawkes; *Von Mueller s.n.* (MEL), Mittagong; *Streimann 16716* (CBG, NICH, NY), Rutherford Creek. – Victoria: *Streimann 36656* (B, CBG, NY), SSE of Bendoc; *Von Mueller* (BM, MEL, W), 'sources of the Yarra Yarra'; *Von Mueller s.n.* (BM, MEL), *Sullivan s.n.* (MEL), Mt Juliette; *Streimann 36266* (B, CBG, FH), *Van Zanten 68.1723* (GRO), Warburton; *Streimann 51671* (L), Bulga Nat. Park; *Streimann 36238* (B, CBG, FH), Healesville, Myrtle Creek; *Thies FN 1501M* (MEL), Mt Donna Buang; *Mauritzon s.n.* (S, UPS), *Von Mueller s.n.* (RO), *Walter s.n.* (BR, COI, FH, MEL), Dandenong; *Beauglehole 74294* (MEL), Arkins Creekwater Supply Reserve; *Watts v.1166* (NSW), Lorne; *Von Mueller s.n.* (MEL), Apollo Bay; *Streimann 58826* (L), Otway State Forest; *Curnow & Lepp 1395* (CBG), Beauty Spot; *Reader s.n.* (MEL), Mt Arapiles. – South Australia: *Von Mueller s.n.* (MEL), Mount Gambier. – Tasmania. Furneaux Group. Flinders Is.: *Whinray s.n.* (MEL), Earling Ra.; *Gabriel s.n.* (MEL), *Willis s.n.* (MEL), Strzelecki Peak. – Tasmania: *Gunn 1603* (FH, RO; s.loc.), *s.n.* (NSW, NY, RO; s.loc.), *De Labillardière s.n.* (BM, s.loc.), *s.n.* (RO, s.loc.); *Ventenat & De Labillardière s.n.* (G, s.loc.), *Weymouth 862* (BM, JE, NY); Circular Head; *Gunn 1589* (NY), St. Patricks River; *Curnow 2134* (CBG, L), SW of Deloraine; *Bastow s.n.* (MEL, 'Sept. 1885'), *Beccari 33*, (GRO; JE, S, *s.n.*), *Fleischer B 2039* (B, L, NICH), *Hooker f. 1353* (BM), *Oldfield s.n.* (MEL), *Weymouth 2667* (CBG, NY), Mt Wellington; *Seppelt 12966* (B, NICH, NY), Geeveston; *Weymouth s.n.* (CBG, NY), Tasman Peninsula; *Perrin s.n.* (MEL), Maria Is. – Lord Howe Is.: *Chevalier de Camera s.n.* (JE, NICH, NY, RO); *Crisp 4550* (CBG), Mt Gower; *Beauglehole 73523* (MEL), Mt Lidgbird. — NEW ZEALAND: *Buchanan s.n.* (UPS, 'Otago & Wellington'). – North Island. North Auckland L.D.: *Matthews 208* (WELT), *s.n.* (FH), Mangonui; *Allison 711* (WELT), *Child 4161* (BM), *Schofield 48126* (S), *Van Zanten 7401240* (GRO), Waipoua Forest; *Berggren 2221* (S, UPS, W), Ohaeawai; *Bolton s.n.* (BM), *Kirk 180* (BM, NY), *Sinclair s.n.* (BM), Auckland; *Hamilton s.n.* (WELT), Little Barrier Is. – South Auckland L.D.: *Berggren s.n.* (GRO, S), *Hochstetter 241* (W), Coromandel;

Van Zanten 93.09.1064 (GRO), Thames; *Allison 15* (WELT), *Child 367* (BM), Rotorua; *Brownsey s.n.* (WELT), Motuhora ('Whale') Is. – Gisborne L.D.: *Haskell s.n.* (WELT), Toatoa; *Van Zanten 1285* (B, GRO, L, NICH, S, WELT), Lake Waikaremoana; *Sainsbury s.n.* (S), Ngamako. – Hawke's Bay L.D.: *Van Zanten 731268* (GRO, L, NICH), White Pine Bush; *Van Zanten 1451* (B, GRO, L, NICH, S, WELT), Norsewood; *Colenso s.n.* (WELT), Seventy Mile Bush, Waipawa Distr. ["County of Waipawa"]; *Beckett s.n.* (BM, FH, HBG, NY, NSW, S), Te Ohu; *Colenso 2674* (WELT), Dannevirke. – Taranaki L.D.: *Edwards 37* (FH), *53* (FH), *75* (FH), *96a* (FH), *Meebold 21* (JE), *Ratcliff s.n.* (BM), *Svihla & Lawton 5014* (NICH), Mt Egmont; *Lewinsky 2021* (L), *Sainsbury s.n.* (WELT), Dawson Falls. – Wellington L.D.: *Mundy 56* (WELT), Ohakune; *Child 1242* (BM), *Druce 388* (WELT), Pohangina; *Brownsey s.n.* (WELT), Akatarawa Saddle; *Brownsey s.n.* (WELT), Kaitoke Waterworks; *Heine s.n.* (WELT), Kapiti Is.; *Berggren 2226* (NICH, NY, S, UPS, W), Wellington. – South Island: *Lyall 284* (BM, 'Middle Is.'), *285* (BM, 'Middle Is.'). – Nelson L.D.: *Glenny s.n.* (WELT), Anatoki River; *Fife 4734* (CBG, NY), Bullock Creek; *Child 5194* (BM), Mt Duppa. – Marlborough L.D.: *Home s.n.* (BM), Queen Charlotte Sound; *McMahon s.n.* (WELT), Awatere [River]. – Westland L.D.: *Helms 28* (B, FH, NY, UPS), Greymouth; *Berggren 2222* (BM, HBG, NY, S, UPS, W), Blake's–Arahura; *Beckett s.n.* (NY, S), *Berggren 2219* (NY, S, UPS), Taramakau ('Teremakau'); *Beckett 969* (FH, HBG, JE, NSW, WELT, S), Kelly's Ra.; *Child 5670* (BM), Fox Glacier; *Child 1991* (BM), *Prud'homme van Reine M 4a* (L), Franz Josef. – Canterbury L.D.: *Buck 6927* (NY), Hanmer Springs; *Beckett s.n.* (JE, NY, S; 'May 1901'), Waimate; *Berggren 2220* (NY, S, UPS), Little River; *Beckett s.n.* (NY, S; 'May 1895'), Oxford; *Beckett s.n.* (BM, NSW, NY; 'Jan. 1900'), Mt Peel. – Otago L.D.: *Fleischer B 168* (B), Queenstown; *Beverly s.n.* (FH), *Burr s.n.* (WELT), Dunedin; *Petrie s.n.* (BM), Mt Cargill; *Petrie s.n.* (BM), Leith Valley; *Brownsey s.n.* (L), Papatowai. – Southland L.D.: *Brownsey s.n.* (WELT); *Menzies 2* (S, 'Dusky Bay'), Dusky Sound; *Allan s.n.* (WELT), Chalky Inlet; *Allan s.n.* (WELT), Preservation Inlet; *Child 3800* (BM), Lake Hauroko. – Stewart Is.: *Doore et al. 362* (BM, 'Oban'), Halfmoon Bay; *Martin 330* (WELT), Garden Mound; *Vitt 10318* (L), Port Pegasus. – Auckland Islands: *Hooker s.n.* (BM, sub no. *W. 86.b*; BR, FH, L, NY); *Lyall s.n.* (BM). – Auckland Island: *Johnson 21/36* (WELT); *Tennand 51* (WELT), Carnley Harbour. – Chatham Islands. Chatham Island: *Travers s.n.* (WELT).

DUBIOUS ORIGIN: *unknown collector s.n.* (FH, 'Philippine Is.'), *unknown collector s.n.* (W, 'Norfolk Is.'), *unknown collector s.n.* (JE, 'Ins. Austr.').

7.2. **Cyathophorum tahitense** Besch. — Fig. 47, 48A, 49A; Map 23

Cyathophorum tahitense Besch., Ann. Sci. Nat. Bot. 7, 20 (1895) 59. — *Cyathophorella tahitensis* (Besch.) M. Fleisch., Musc. Buitenzorg 3 (1908) 1096. — *Cyathophorum* ('*Cyatophorum*') *taitense* Besch. ex Paris, Index Bryol. (1894) 294, nom. nud.; see note 1. — Type: *Vesco s.n.* (PC holo, BM iso),Tahiti ('Taïti'), 1847.

?: *Cyathophorum bulbosum* Nadeaud non (Hedw.) Müll.Hal., Énum. Pl. Indig. Tahiti (1873) 13; syn. nov. — Original material: *Nadeaud (67?)* (n.v.),Tahiti, ["sur les arbres des crêtes au-dessus de 1000 mètres"]; see notes 2 and 3.

?: *Cyathophorum pennatum* (Labill.) Brid. fo. *aurea* Brizi, Atti Reale Accad. Lincei, Rendiconti Cl. Sci. Fis., ser. 5, 2 (1893) 103, nom. nud., name only; Annuario Reale Ist. Bot. Roma 6 (1897) 353, nom. dub.; synonymised by Fleischer, Musc. Buitenzorg 3 (1908) 1096; see note 4.

Illustrations: Brotherus, in Engler & Prantl, Nat. Pflanzenfam. ed. 1, 3 (1907) f. 704 D; id. ed. 2, 11 (1925) f. 626 D. — Fleischer, Musc. Buitenzorg 3 1908) f. 184x–z. — Whittier, Mosses of the Society Islands: Preliminary Studies (1969) pl. 61, 62; Mosses of the Society Islands (1976) f. 82.

Plants in groups of fans, small to medium-sized, frequently gemmiferous, dull or weakly glossy. *Stems* up to 5.0 cm tall, terete, usually entirely laterally compressed, but laterally or dorsiventrally compressed in gemmiferous stem parts, deep dark brown (at base) to pale green (at top), not glossy. *Primordia* naked. *Epidermis cells and cortical cells of stem* equally narrow or outer cortical ones narrower or inner cortical ones wider; walls thin or incrassate, pale yellow to brown; inclusions absent. *Central*

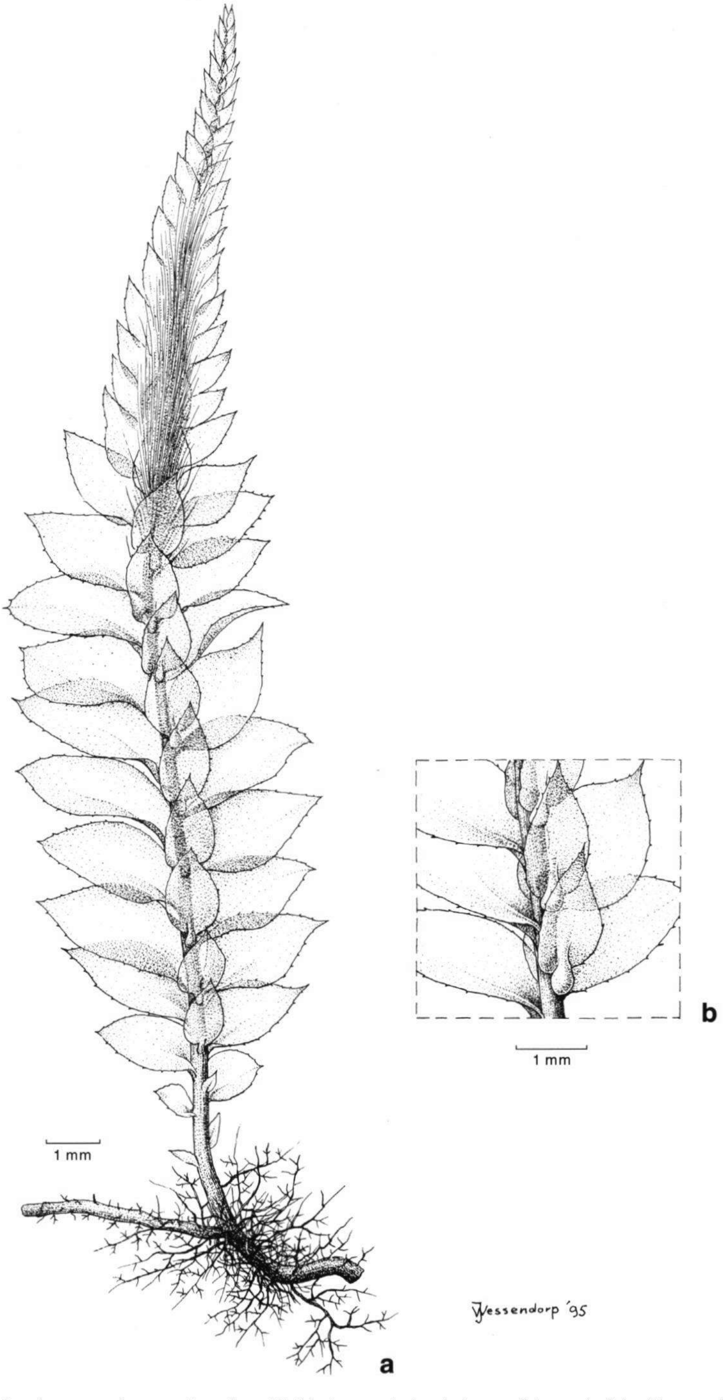


Fig. 47. *Cyathophorum tahitense* Besch. a. Habit (ventral view); b. amphigastria (*De Sloover 21.115*, GRO).

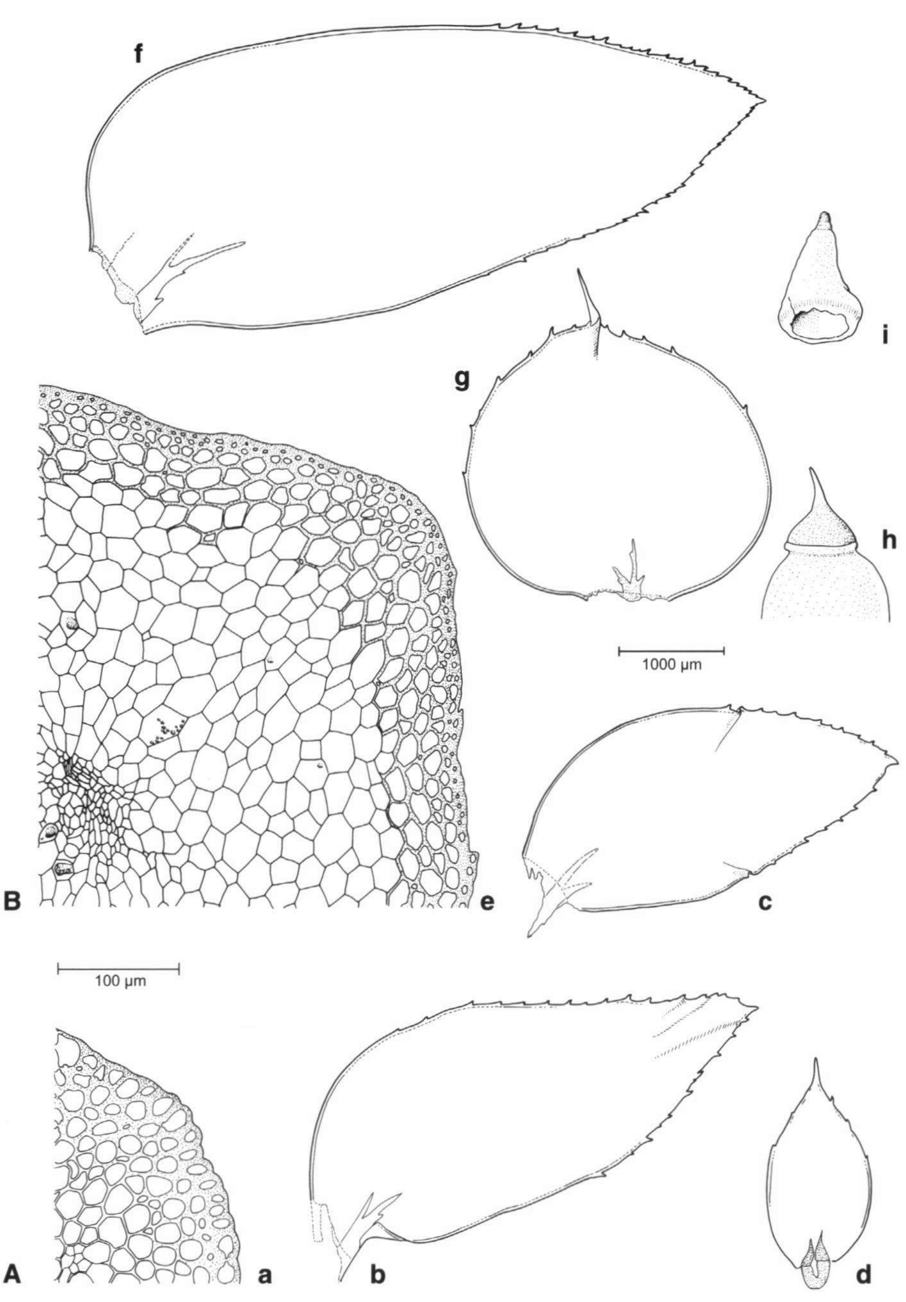
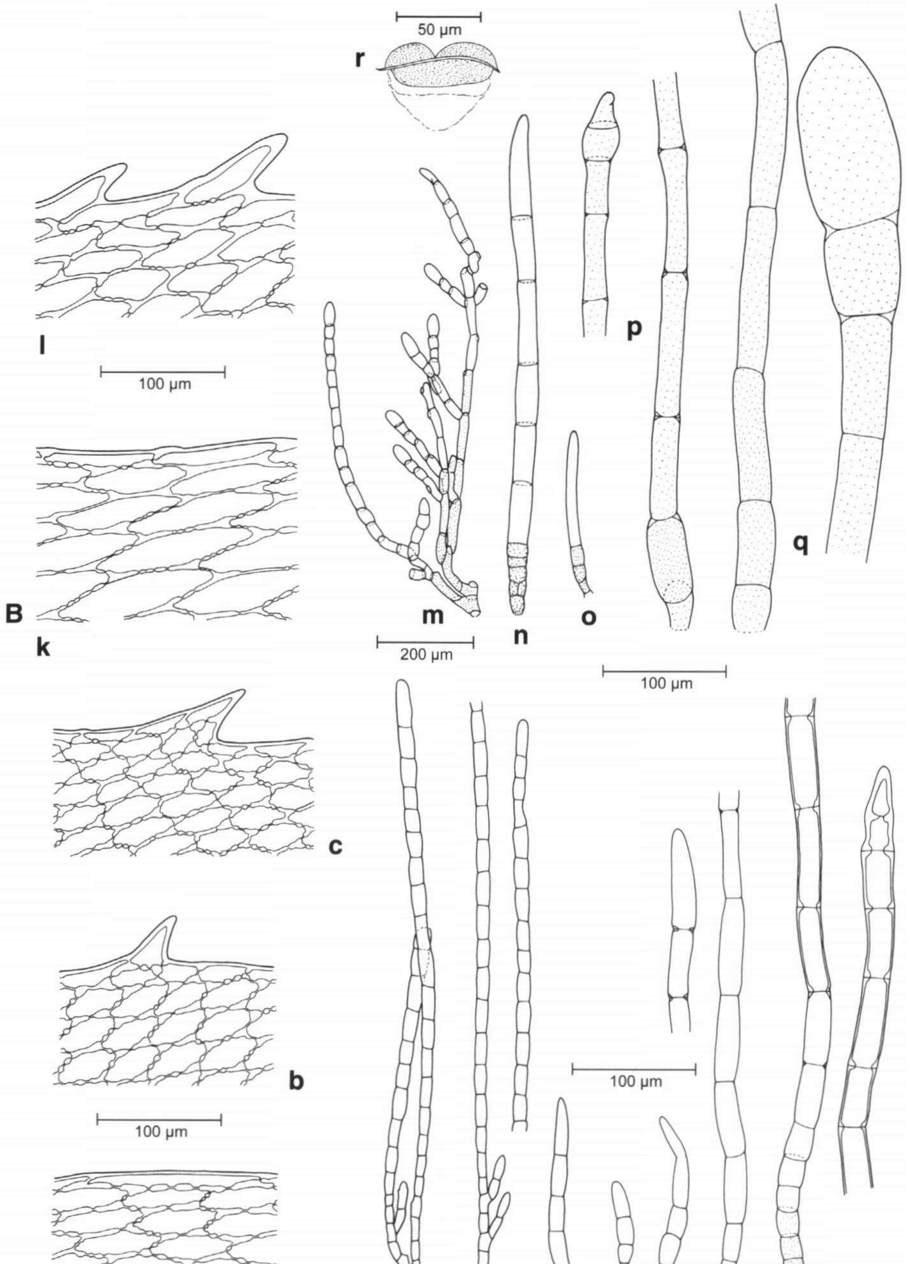


Fig. 48. — A. *Cyathophorum tahitense* Besch. a. Rachis (cross section dorsal quadrant); b–d. leaves (b, c. lateral, d. amphigastrium). — B. *C. bulbosum* (Hedw.) Müll.Hal. e. Rachis (cross section dorsal quadrant); f, g. leaves (f. lateral, g. amphigastrium); h. operculum; i. calyptra (A. a–d: *Nadeaud 452*, S; B. e–i: *Streimann 51671*, L).

strand present; cells narrow, walls thin, pale yellow to brown, inclusions absent. *Axial cavities* absent. *Axillary hairs* 1–7 per leaf, 4–9-celled, simple; basal cells 1 or 2, pale brown or brown; intermediate cells present, rectangular to oblong-rectangular; terminal cell oblong-rectangular to short-linear-rectangular, gradually attenuate or not, 24–65 µm long and 10–17 µm wide, smooth. *Leaves* distant or closely set, yellowish green to dark green, occasionally tinged with red, occasionally brown near base. *Basal leaves* triangular to ovate; apex acute to abruptly acuminate. *Distal leaves* in gemmiferous stem parts generally smaller than those in non-gemmiferous stem parts; margin entire or weakly to coarsely serrate-dentate, usually stronger serrate-dentate in lateral leaves than in amphigastria, serrate-dentate in basal leaves of gemmiferous stem parts, becoming entire in distal ones; teeth 1–5-celled in lateral leaves, usually unicellular and less often 2- or 3-celled in amphigastria, up to 75 µm long, projecting up to 2 cells; border faint to distinct, interrupted, 1–3 cells wide near leaf base and up to 2 cells wide in distal part of leaf; laminal cells 40–105 µm long and 15–30 µm wide. *Distal lateral leaves* usually ovate to oblong, rarely obovate, 1.9–3.9 mm long and 0.9–1.7 mm wide, ovate to ovate-lanceolate in gemmiferous part of stem; apex usually acute or gradually acuminate, rarely obtuse or rounded; acumen up to 0.2 mm long; costa reaching up to 1/6(–1/3) of leaf length. *Distal amphigastria* appressed to erect, ovate to oblong, 0.7–1.9 mm long and 0.3–1.3 mm wide, elliptic to ovate-lanceolate in gemmiferous part of stem; basal part usually saccate having a pouch (see note 5), weakly to strongly bulging, in tiny stems occasionally flat or smoothly curved, being neither saccate nor bulging; insertion usually distinctly concave to straight, in tiny stems occasionally oblique; apex acute or gradually acuminate; acumen up to 0.2 (–0.4) mm long; costa usually absent, rarely faint, reaching up to 1/10 of amphigastrium length. *Gemmae clusters* located in distal (half to) third of stem, placed in and above axils of leaves and amphigastria, reaching 1/4 of length of covering lateral leaves to 4 times as long. *Gemmaphores* simple or penicillate, 1–7 cells long, colourless to brown. *Gemmae* simple or branched at base, up to 50 cells long, colourless to orange-brown; cells 30–65 µm long and 15–30 µm wide.

Dioicous. Perigonia in distal half of stem. *Perichaetia* in basal and middle part of stem. *Gametoecial leaves* ovate or elliptic, green; margin entire, minutely serrate-dentate below apex in pergonial leaves, or dentate in distal half of perichaetial leaves; border faint to distinct in basal third to half of leaf, absent or faint and interrupted in distal part, up to 3 cells wide; costa absent. *Inner leaves*: of perigonia up to 1.4 mm long and 0.7 mm wide, acumen up to 0.5 mm long; of perichaetia prior to sporophyte development up to 0.9 mm long and 0.8 mm wide, acumen up to 1.0 mm. *Antheridia* 0.4–0.5 mm long. *Stalk of full-grown perichaetia* not seen. *Archegonia* 0.4–0.5 mm long. *Mature perichaetia (including vaginula)* unknown. *Gametoecial axillary hairs* (few examined) up to 4 per gametoecial leaf, c. 5-celled, simple; basal cells 2, brown; intermediate cells present, elongate, rectangular or weakly narrowly truncate-elliptic, colourless; terminal cell elongate-ovate, 45–50 µm long and c. 12 µm wide, smooth, colourless. *Paraphyses* numerous in perigonia, absent or few to numerous in perichaetia, c. 13 cells long in perigonia, 10–21 cells long in perichaetia, simple; basal cells 1–4 and pale brown to brown in perigonia, 1–6 and colourless to pale brown in perichaetia; intermediate cells truncate-elliptic to elongate-rectangular, colourless or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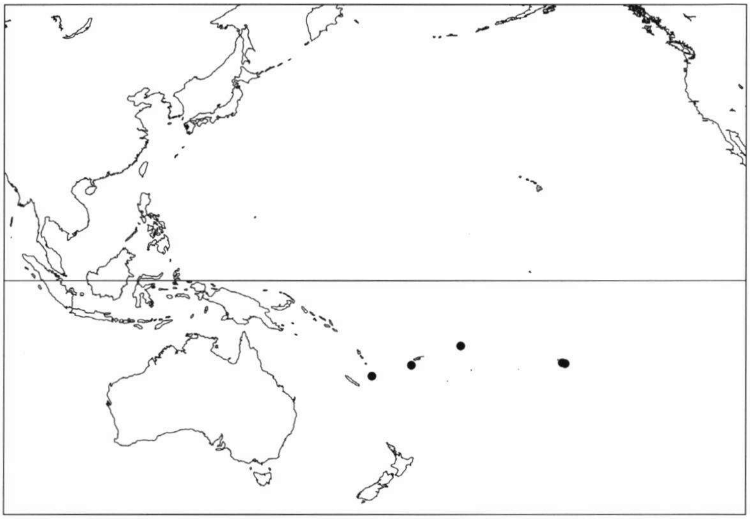


Map 23. Distribution of *Cyathophorum tahitense* Besch.

very pale brown; terminal cell triangular to elongate-ovate, 40–90 µm long and 20–30 µm wide, colourless or nearly so, not inflated. *Sporophytes* unknown. *Calyptra* unknown.

Distribution — Vanuatu (Aneityum), Fiji (Viti Levu), Samoa Islands (Upolu), Society Islands (Moorea, Tahiti). According to Tixier (1974) also found on Espiritu Santo, Vanuatu.

Habitat & Ecology — In forests. On stem bases, trunks, and branches of trees; on logs, litter, and rocks. Altitude: 115–1100(–2500) m (see note 6).

According to Whittier (1976) in habitats with a consistently high humidity. Reported from 1325–1400 m altitude on Mt Tabewasama, Espirutu Santo, Vanuatu, by Tixier (1974).

Geographical variation — Not found; possibly insufficient data. Only a few collections have been made outside the Society Islands.

Ecological variation — Not found; insufficient data, especially for altitudinal distribution.

Fig. 49. — A. *Cyathophorum tahitense* Besch. a–c. Leaf cells of lateral leaves (a. basal part of antical side, b, c. distal part of antical side); d, e. gemmaphores with gemmae; f–h. axillary hairs; i, j. paraphyses. — B. *C. bulbosum* (Hedw.) Müll.Hal. k, l. Leaf cells of lateral leaf (k. basal part of antical side, l. distal part of antical side); m. gemmaphore with gemmae; n, o. axillary hairs; p, q. paraphyses; r. exostome tooth (cross section) (A. a, b, j: *Nadeaud 452*, S; c: *De Sloover 21.115*, GRO; d, e: *De Sloover? 21.035*, NY; f: *Vesco s.n.*, PC; g, h: *Whittier 2501*, BM; i: *Buck 7249*, NY; B. k, l: *Streimann 51671*, L; m: *Streimann 7257*, L; n: *Streimann (field no. 1)*, L; o: *Van Balgooy 217*, L; p: *Van Zanten 68.3008a*, GRO; q: *Willis s.n.*, MEL; r: *Buchanan s.n.*, UPS).

Notes:

Nomenclature and synonymy — 1. Paris (1894) referred the name *Cyathophorum taitense* nom. nud. to a publication by Bescherelle in Ann. Sci. Nat. Bot. in 1894. Although Paris usually gave a full citation, here he omitted to give page numbers. Since there is no publication by Bescherelle present in the 1894 issues of this journal, it is almost certain that Paris referred to Bescherelle's paper in press, which has actually appeared in the 1895 volume of the journal.

2. In his enumeration of mosses from Tahiti, Nadeaud (1873) listed *Cyathophorum bulbosum* var. *bulbosum* and *C. bulbosum* var. *tahitense* as two varieties of *C. bulbosum*. Both varieties were listed below species number *67* in his list of Tahitian mosses. Nadeaud explicitly considered *C. bulbosum* var. *bulbosum* identical with the original species and he gave an indirect, but clear, reference to Müller (1850). Nadeaud described *C. bulbosum* var. *tahitense* as a new variety.

The identity of Nadeaud's varieties is somewhat problematic, but it is almost certain that Nadeaud's *Cyathophorum bulbosum* var. *bulbosum* is conspecific with *C. tahitense*, whereas his *C. bulbosum* var. *tahitense* belongs to *Garovaglia* Endl. and is, therefore, excluded from the Hypopterygiaceae here (see under this variety in 'Taxa excluded from the Hypopterygiaceae', p. 358).

This view is in contrast with that of Bescherelle (1895), who re-identified a collection of *Cyathophorum bulbosum* from Tahiti – made and identified by Nadeaud (*Nadeaud 67*) – as his new species *Garovaglia tahitensis*. Bescherelle (1895) came to the conclusion, that both Nadeaud's varieties occur in the same tuft, and that represent two 'forms' of *G. tahitensis* in different degree of development (growth stages).

However, Bescherelle (1895) did not receive all the mosses that were listed by Nadeaud (1873), and it is very well conceivable that his material of *Nadeaud 67* was incomplete. In particular, because 1) Nadeaud reported, that his varieties came from different locations, which excludes the occurrence of the two varieties in a single tuft, and 2) Nadeaud's descriptions indicate that the two varieties are entirely different.

Nadeaud (1873) described the foliation of *Cyathophorum bulbosum* var. *bulbosum* as: "jungermannoïdeo-foliosos". This matches perfectly well with *Cyathophorum*, but does not match at all with the foliation of *Garovaglia*. That Nadeaud (1873) had a *Cyathophorum* species in mind is emphasised by his statement that the stems of *C. bulbosum* var. *bulbosum* are simple. By contrast, Nadeaud described the stem of *Cyathophorum bulbosum* var. *tahitense* as being often branched. This does not match with *Cyathophorum*, but agrees perfectly well with *Garovaglia*.

In all probability, Bescherelle (1895) saw only a single collection of '*C. bulbosum*' (i.e. *C. bulbosum* var. *tahitense*) from Tahiti, which proved to be *Garovaglia tahitensis*. He had no disposal of the other material of Nadeaud's (1873) *C. bulbosum* (i.e. *C. bulbosum* var. *bulbosum*) and erroneously assumed that Nadeaud's varieties were mixed in a single collection. Hence, Bescherelle also combined Nadeaud's locality descriptions of his two varieties for the original locality of his *G. tahitensis*.

Nadeaud's (1873) description indicates, that his *Cyathophorum bulbosum* is very probably a *Cyathophorum* species, and most likely *C. tahitense*, which is the only representative of the present genus *Cyathophorum* on the Society Islands Unfortunately, I have not seen not any specimen from Tahiti under the name *Cyathophorum bulbosum* (var. *bulbosum*).

3. The presentation of Nadeaud's (1873) *Cyathophorum bulbosum* and the typification problems concerning his varieties *Cyathophorum bulbosum* var. *bulbosum* and *C. b.* var. *tahitense* caused confusion in the publications cited below.

Fleischer (1908), Van der Wijk et al. (1959), Whittier (1968, 1976), and Whittier & Whittier (1974) incorrectly included Nadeaud's (1873) *Cyathophorum bulbosum* var. *tahitense*, which belongs to a *Garovaglia* species, in the synonymy of *Cyathophorella tahitensis*.

Based on Bescherelle (1895), Miller et al. (1978) incorrectly merged Nadeaud's (1873) *Cyathophorum bulbosum* with *Garovaglia plicata* (Brid.) Bosch & Sande Lac. in their catalogue of Polynesian mosses. They were apparently not aware that Nadeaud's *Cyathophorum bulbosum* includes the two varieties and almost certainly represent two separate taxa.

None of the authors from the 20th century reported that they have actually seen the type material of Nadeaud's two varieties. See for a discussion on Nadeaud's varieties of *Cyathophorum bulbosum* note 2 above and 'Taxa excluded from the Hypopterygiaceae', p. 358, under *Cyathophorum bulbosum* var. *tahitense*.

4. No collection was found with any reference to Brizi's (1893) forma *Cyathophorum pennatum* fo. *aurea*. Fleischer (1908) wrote that he had examined the original material of this forma and reduced it to a synonym of *Cyathophorella tahitensis*. Accordingly, it is listed here as a doubtful name in the synonymy of *Cyathophorum tahitense*.

Brizi validated his forma in 1897, and based it on *Cyathophorum tahitense* as well as *Cyathophorum bulbosum* var. *tahitense*. Probably, Brizi did not actually see the latter variety, because it almost certainly belongs to *Garovaglia* Endl. (see note 2 and Taxa excluded from the Hypopterygiaceae, p. 358).

Brizi (1893, 1897) very probably had *Cyathophorum tahitense* in mind as his *Cyathophorum pennatum* fo. *aurea*, but his account is not clear. When Brizi (1897) gave a survey of the distribution of *Cyathophorum pennatum*, he presented a list of collections, which included one from Tahiti made by Nadeaud – probably received from Bescherelle. This collection is probably linked with Brizi's forma. Several of Brizi's collections are known to be kept at RO, and contain plants that belong to *Cyathophorum bulbosum*. Others could not be found, including the collection from Tahiti made by Nadeaud.

Description — 5. Fleischer (1902, 1908), followed by Brotherus (1907, 1925) and other authors, called the sac-like structure at the base of the amphigastria of *Cyathophorum tahitense* 'Wassersack'. As the function of this structure is unknown, I refer to it simply as a 'pouch', a term also used by Whittier (1976).

Ecology — 6. Only a single collection of *Cyathophorum tahitense*, from Fiji (*Buck 7249*), was found above 1100 m, at an altitude of c. 2500 m.

Other — 7. According to Bescherelle (1895) *Cyathophorum tahitense* is quite similar to *C. spinosum* (as *C. adiantum* from Java), but distinct from the latter on account of the pouches at the base of its amphigastria. This is confirmed here. Bescherelle (1895) also noted differences in dentation and nervation of the leaves, but the variability range of these features in *C. tahitense* are within their variability range in *C. spinosum*.

The pouch at the base of the amphigastria in *C. tahitense* is, however, occasionally absent in scanty plants. Such plants can be distinguished from small plants of *C. spinosum* by the relative length of the acumen cells in the lateral leaves. In *C. tahitense* these acumen cells are short to narrowly elongate, but never short-linear or linear. In *C. spinosum* they are oblong to linear, but never short.

8. Localities for *Nadeaud 450, 451* and *452* were obtained from Bescherelle (1898a, b).

Specimens examined (40 in number):

Vanuatu ('New Hebrides'): Aneityum: *Cheesman s.n.* (BM), *collector for Gunn (337)* (BM), *unknown collector [Cheesman?] s.n.* (BM); *unknown collector (148)* (BM), *(165)* (BM), Banges. — Fiji. Viti Levu: *Buck 7249* (NY), W of Nandarivatu. — Samoa Is.: Western Samoa. Upolu: *Schultze-Motel 3231* (B), Mt Fiamoe. — Society Is.: Moorea: *Nadeaud s.n.* (FH), *Temarii [= Temarii Nadeaud] s.n.* (FH, S); *Nadeaud [= Temarii Nadeaud] s.n.* (S), Mt Suira; *De Sloover 21.115* (BR, EGR, GRO, NICH, S), *21.036* (NY), *21.111* (NY), Toto Valley. – Tahiti: *Nadeaud s.n.* (NY, S), *Temarii [= Temarii Nadeaud] s.n.* (JE), *(50/374?)* (GRO), *Vesco s.n.* (BM, PC), *unknown collector s.n.* (BM); *Nadeaud 451* (S), Hitiaa Mts; *Nadeaud 450* (BM), Marciati Mts; *Whittier 2184* (NY), *2187* (NY), *2501* (B, BM, NICH, NY), *2510* (NY), Taiarapu Peninsula; *Nadeaud 452* (FH, S; W), Tipaeaui, Puaa Valley; *Erikson s.n.* (FH), road to Vahira.

7.3. **Cyathophorum spinosum** (Müll.Hal.) H. Akiyama — Fig. 50, 52B, 53B; Map 24; Plate 3f

Cyathophorum spinosum (Müll.Hal.) H. Akiyama, Acta Phytotax. Geobot. 43 (1992) 114; (Müll. Hal.) H. Akiyama in Kato, Taxon. Studies of the Plants of Seram I (1988) 43, nom. inval., basionym not given. — *Hookeria spinosa* Müll.Hal., Syn. Musc. Frond. 2 (1851) 677. — *Lepidopilum spinosum* (Müll.Hal.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1875–76 (1877) 328 (Gen. Sp. Musc. 2 (1877) 232). — *Cyathophorella spinosa* (Müll.Hal.) M. Fleisch., Musc. Buitenzorg 3 (1908) 1091. — *Cyathophorum spinosum* (Müll.Hal.) M. Fleisch., Musci Frond. Arch. Ind. ser. 5 (1902) no. 249, nom. nud.; Musc. Buitenzorg 3 (1908) 1091, nom.

inval. in syn. (*Cyathophorella spinosa* (Müll.Hal.) M. Fleisch.). — Types: *Blume s.n.* ["Hb. Al. Braun"] (B holo destroyed), Indonesia, Java; *Schiffner 12938* (L neo, designated here; BM, S, W), Indonesia, Java, W Java (Jawa Barat), "Preanger Prov.", "In silvis primigeniis supra locum dictum "Tjiburrum" prope Tjibodas. Regio nubium", alt. 1590 m, May 2, 1894. — See note 1.

Cyathophorum loriae Müll.Hal., Flora 82 (1896) 456, syn. nov. — *Cyathophorella loriae* (Müll.Hal.) M. Fleisch. ex Broth. in Engler & Prantl, Nat. Pflanzenfam. ed. 2, 11 (1925) 278. — Type: *Loria, Bryoth. Levier 727* (B holo destroyed; NY lecto, designated here; BM, FH; GRO, sub no. *963*, 'Aug. 1893'; JE, S, W), SE Papua New Guinea, Central, Mt Moroko, "Nova Guinea austro-orient. Brit. in montosis Mo-roka, 1300 m (distr. Moresby)", Jul./Aug. 1893. — See note 5.

Cyathophorum penicillatum Müll.Hal., Flora 82 (1896) 457, syn. nov. — *Cyathophorella penicillata* (Müll.Hal.) M. Fleisch., Hedwigia 63 (1922) 212. — Type: *Micholitz s.n.* (B holo destroyed, BM lecto, designated here; JE, W), New Guinea, Cloudy Mts ["Clouth Mountains"], alt. 4000 ft., [S. Hb. Stephani], Nov. 1894; see note 2. — See note 5.

Cyathophorella adianthoides Broth., Philipp. J. Sci. 8C (1913) 84. — Type: *Ramos BS 13642* (H holo, BM, FH, GRO, NY, TNS n.v.), Philippines, Luzon, Rizal Prov., [on branches of trees], Aug. 1911; see note 3. — Synonymised to *Cyathophorella adiantum* E.B. Bartram non (Griff.) M. Fleisch. by Bartram, Philipp. J. Sci. 68 (1939) 281. — According to Bartram, Philipp. J. Sci. 68: 281. 1939, the type of *Cyathophorella adianthoides* Broth. was collected on Mt Susong-Dalaga. None of the specimens examined are annotated with this locality.

Cyathophorum adiantum Bosch & Sande Lac., Bryol. Jav. 2 (1861) 4, t. 134, non (Griff.) Mitt., J. Proc. Linn. Soc., Bot., Suppl. 1 (1859) 147. — Synonymised with *Cyathophorella spinosa* (Müll.Hal.) M. Fleisch. by Fleischer, Musc. Buitenzorg 3 (1908) 1091; see note 4.

Cyathophorella adiantum E.B.Bartram, Philipp. J. Sci. 68 (1939) 281, pl. 21 f. 358, non (Griff.) M. Fleisch., Musc. Buitenzorg 3 (1908) 1094; syn. nov.; see note 3.

Illustrations: Van den Bosch & Van der Sande Lacoste, Bryol. Jav. 2 (1861) t. 134 (as *Cyathophorum adiantum*). — Fleischer, Musc. Buitenzorg 3 (1908) f. 184a–d. — Bartram, Philipp. J. Sci. 68 (1939) pl. 21 f. 357, 358. (as *Cyathophorella spinosa* and *C. adiantum*). — Akiyama in Kato, Taxon. Studies of the Plants of Seram I. (1988) 59, f. 6. — Mohamed & Robinson, Smithsonian Contr. Bot. 80 (1991) f. 122–130. — Akiyama, Acta Phytotax. Geobot. 43 (1992) 113, f. 1i–s.

Plants in groups of fans, (small to) medium-sized to large and robust, frequently gemmiferous, dull or weakly glossy. *Stems* up to 8.2 cm tall, terete, usually entirely laterally compressed, but laterally or dorsiventrally compressed in gemmiferous stem parts, deep dark brown (at base) to dark brown to green (at top), not glossy. *Primordia* naked. *Epidermis cells and cortical cells of stem* equally narrow or cortical ones wider; walls incrassate or thin, dark brown to colourless; inclusions absent from epidermis cells and outer cortical cells, absent or present in inner cortical cells, amorphous solids or tiny oil-like droplets. *Central strand* present; cells narrow, walls pale yellow to red or deep brown, inclusions tiny oil-like droplets. *Axial cavities* absent. *Axillary hairs* 1–8 per leaf, 4–17-celled, simple or branched; basal cells 1–8, colourless to brown; intermediate cells present (or absent from green stem parts), truncate-elliptic to elongate-rectangular; terminal cell usually oblong to short-linear and ± rectangular, occasionally elliptic at green (young) stem parts near apex, (25–)35–130 μm long and 7–25(–30) μm wide, usually smooth, occasionally slightly verrucose. *Leaves* distant or closely set, usually yellowish green to dark green, occasionally tinged with red or reddish brown, usually brown near base. *Basal leaves* triangular to elliptic; apex acute to abruptly acuminate. *Distal leaves* smaller in gemmiferous stem parts than in non-gemmiferous stem parts; margin usually coarsely serrate-dentate, occasionally moderately serrate-dentate in amphigastria, serrate-dentate in basal leaves of gemmiferous stem parts and becoming entire in distal ones; teeth 1–9-celled, but in amphigastria

1–4-celled and usually unicellular, in lateral leaves up to 290 µm long and projecting up to 3 cells, in amphigastria shorter, up to 100 µm long and projecting up to a single cell length at most; border faint to distinct, interrupted, up to 2(–4) cells wide near leaf base, upwards up to 2 cells wide; laminal cells 45–150 µm long and (10–)15–40 µm wide. *Distal lateral leaves* ovate to lanceolate, rarely short-linear, 2.5–6.5 mm long and 0.6–3.8 mm wide, ovate-lanceolate in gemmiferous part of stem; apex usually gradually or abruptly acuminate, occasionally acute; acumen 0.2–0.7 mm long; costa reaching up to 1/3 of leaf length. *Distal amphigastria* appressed to patent, usually subcircular or ovate to lanceolate, rarely obovate, 1.1–3.9 mm long and 0.4–3.2 mm wide; subcircular to elliptic or ovate-lanceolate in gemmiferous part of stem; basal part ± flat or smoothly curved, weakly bulging or not; insertion distinctly concave; apex gradually or abruptly acuminate; acumen 0.1–0.8 mm long; costa faint to distinct, reaching up to 1/2 of amphigastrium length. *Gemmae clusters* usually located in distal fourth of stem, in short stems located in distal half of stems, placed in and above axils of leaves and amphigastria, reaching 1/4 of length of covering lateral leaves to 1 1/2 times as long. *Gemmaphores* simple or penicillate, 1–9 cells long, colourless to brown. *Gemmae* simple or branched at base, up to 50 cells long, usually colourless to orange-brown, occasionally brown to dark brown; cells 30–80 µm long and 15–40 µm wide.

Dioicous. Gametoecia in middle or distal part of stem. *Leaves* short-elliptic to ovate, becoming short-elliptic in full-grown perichaetia; margin entire, occasionally moderately dentate in distal third of perichaetial leaves; border faint to distinct, interrupted, occasionally absent in distal half of leaf, up to 4 cells wide in basal half of leaf, up to 1 cell wide in distal half; costa absent, occasionally faint in perichaetial leaves and reaching up to 1/6 of leaf length. *Inner leaves*: of perigonia up to 1.6 mm long and 1.1 mm wide, acumen up to 0.4 mm long; of perichaetia prior to sporophyte development up to 1.8 mm long and 0.8 mm wide, acumen 0.6–0.8 mm long; of full-grown perichaetia up to 1.5 mm long and 1.5 mm wide, acumen up to 0.7 mm long. *Antheridia* 0.4–0.7 mm long. *Stalk of full-grown perichaetia* up to 0.4 mm long. *Archegonia* 0.6–0.8 mm long. *Vaginula* 0.8–1.3 mm long. *Gametoecial axillary hairs* c. 3 per gametoecial leaf, c. 5-celled, simple, fragile; basal cells 2, brown; intermediate cells present, elongate to short-linear, ± rectangular, colourless; terminal cell short-linear-rectangular, c. 105 µm long and c. 12 µm wide, smooth, colourless. *Paraphyses* numerous in perigonia, absent or few to numerous in perichaetia, 7–11 cells long, usually simple, occasionally branched (in perichaetia); basal cells 1 in perigonia, 1–3 in perichaetia, (colourless or) brown; intermediate cells truncate-elliptic to elongate-rectangular, occasionally longitudinally divided in 2 cells, colourless or pale brown; terminal cell transverse-ovate to oblong-ovate or oblong-elliptic, 35–120 µm long and 35–55 µm wide, colourless (or pale brown?), inflated or not.

Sporophytes up to 6 per stem, pale yellow to brown, frequently tinged with red. *Seta* 2.0–3.3 mm long; base widened. *Capsule* cylindrical to ellipsoid, 1.7–3.4 mm long and 0.6–1.3 mm wide, often more saturated in colour than seta; annulus absent. *Peristomial formula OPL:PPL:IPL* = 4:2:4–6c. *Exostome* brown; teeth 540–800 µm long and 90–140 µm wide, not shouldered; dorsal side striate in basal and middle part of teeth, becoming moderately papillose in distal part; median line not furrowed; dorsal plates broader than or equally wide as ventral ones, 14–26 µm thick; papillae low, simple, mainly located near lamellae; striae minutely papillose; lamellae distinctly

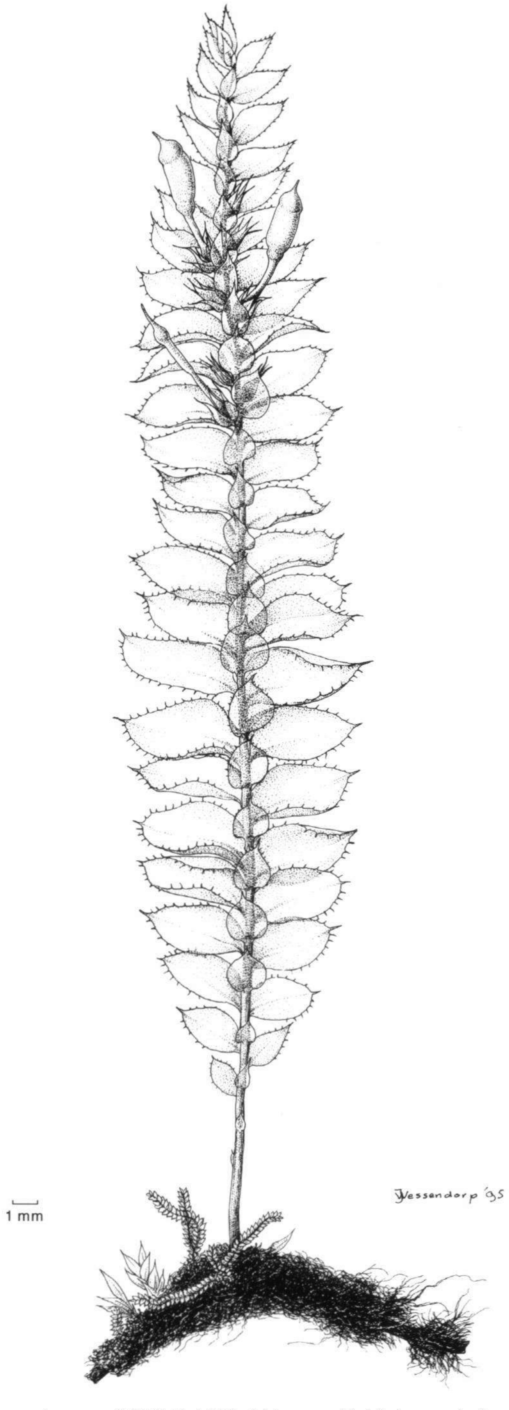
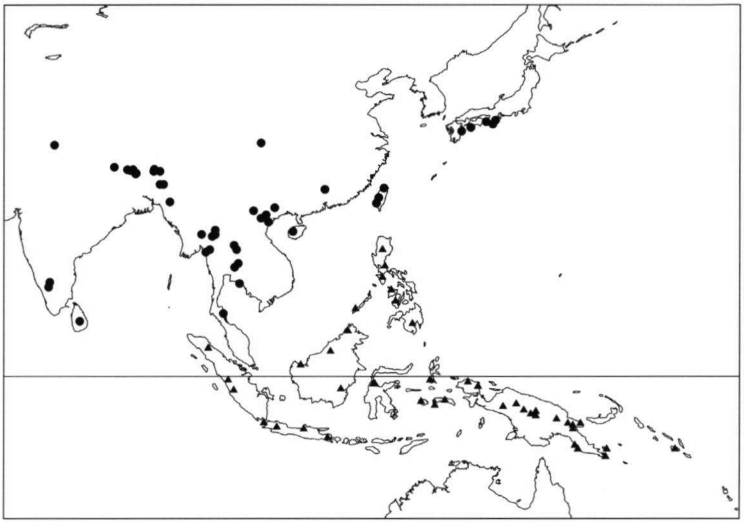


Fig. 50. *Cyathophorum spinosum* (Müll.Hal.) H. Akiyama. Habit (ventral view, *Hoogland & Craven 11.029*, L).



Map 24. Distribution of *Cyathophorum spinosum* (Müll.Hal.) H. Akiyama. (▲) and *C. adiantum* (Griff.) Mitt. (●).

projecting near base of teeth, becoming indistinctly projecting or not projecting above; ventral plates very thin, smooth or weakly papillose; papillae low, simple; trabeculae short to very pronounced up to apex of teeth. *Endostome* smooth or weakly papillose at both faces; papillae low; basal membrane reaching 1/3–1/2 of exostome teeth; processes 480–800 μm long beyond orifice and 60–80 μm wide at base, distinctly keeled, not nodulose, not appendiculate; cilia absent or rudimentary and consisting of parts of 1 or 2 cell plates, 1 cell plate wide. *Operculum* long-rostrate, 0.8–1.5 mm long; rostrum straight. *Calyptra* mitrate, completely or partly covering operculum, 0.8–1.2 mm long, brown to dark brown, fleshy; margin ± entire. *Spores* 17–35 μm.

Distribution — Philippines (Luzon, Mindoro, Palawan, Panay, Negros, Mindanao), Malaysia (Sarawak, Sabah), Indonesia (Sumatra, Krakatau, Java, Kalimantan, Sulawesi; Moluccas: Batjan, Buru, Ambon, Seram; West Papua), Papua New Guinea, Solomon Islands: Guadalcanal. According to Mohamed & Robinson (1991), *Cyathophorum spinosum* is also found in Peninsular Malaysia (see note 13).

Habitat & Ecology — In rain forests. On trunks and branches of shrubs, trees, and climbers; also on rotting wood and less frequently terrestrial. Twice found on rocks and once found on woody grasses; also found on leaves once in Seram (cf. Akiyama, 1988). According to Akiyama (1988, 1992), Fleischer (1908), and Noguchi & Iwatsuki (1972) *Cyathophorum spinosum* often grows in humid places. Akiyama (pers. comm.) states further that the plants often sporulate when growing near streams and rivers. Altitude: 10–2300 m.

Geographical variation — Not found. However, numerous collections from Seram show a relation between the dentation at the leaf margin and altitudinal distribution (see 'Ecological variation'). Such a correlation was not observed outside Seram (but see note 14).

Ecological variation — Plants growing on twigs appear to be generally smaller than those growing on rotten logs and the lower parts of tree trunks. Plants growing near streams and rivers may be less robust than those found further into the forest.

In Seram plants growing below or at 1350 m altitude have the usual type of leaf dentation, with 1–6-celled teeth varying irregularly in cell number. Plants growing at or above 1390 m altitude have usually 1–3-celled teeth, but unicellular teeth predominate. In a few plants multicellular teeth are (almost) absent from the leaf margin.

Notes:

Nomenclature and synonymy — 1. The holotype of *Cyathophorum spinosum* – collected by Blume on Java – in C. Müller's herbarium (B) has been destroyed, and no isotypes were found. The holotype might have been present in the herbarium of Braun – which is incorporated in Mitten's herbarium (NY) –, but the label of the only Javan collection of this species in this herbarium bears no collector's name nor any references to Müller. The only specimen of this species that was gathered by Blume and that I have found in the material examined comes from Java, but is presented as "*C. adiantum*" (*Blume s.n.*, BR).

As the neotype of *C. spinosum*, a Javan collection with widely distributed duplicate specimens has been designated here.

2. Müller (1896) did not mention the collector of the type of *Cyathophorum penicillatum*, and stated only that he had obtained his specimen through Stephani. The original labels of the specimens of the type *C. penicillatum* in BM, JE, and W bear no collector's name. The collection in W is labelled with the name "Micholitz", but in a different script from that of the other annotations, and this name may have been added later. However, Micholitz is the only collector known to have visited the Cloudy Mts in 1894, and it is likely that he collected this type.

3. Brotherus (1913) established *Cyathophorella adianthoides* as a separate species and compared it with *Cyathophorella spinosa* and *Cyathophorella adiantum* (Griff.) M. Fleisch. Several years later he apparently doubted the status of *Cyathophorella adianthoides* since this name is not listed in his enumeration of species in 1925. Brotherus (1925) may actually be referring to the type of *Cyathophorella adianthoides*, when he cites a collection of *Cyathophorella adiantum* from Luzon.

Bartram (1939) reduced *Cyathophorella adianthoides* to a synonym of *Cyathophorella adiantum*, but *Cyathophorella adianthoides* is conspecific with *Cyathophorum spinosum*. The non-gemmiferous stems of the holotype of *Cyathophorella adianthoides* are entirely laterally compressed, and its gemmae are colourless or orange.

Bartram's (1939) description of *Cyathophorella adiantum* is almost certainly based on two specimens of *Cyathophorum spinosum*, which are are very similar to the holotype of *Cyathophorella adianthoides*; in fact one of them is an isotype of the latter. Bartram's plants differ only in the colour of the gemmae. In his isotype most of the gemmae are colourless, and a few are tinged orange, whereas in his other plant (*Williams 1672*) the gemmae are evidently coloured orange to orange-red.

Brotherus (1913) distinguished *Cyathophorella adianthoides* from *Cyathophorella spinosa* by the shape of the leaves, and the widely acuminate amphigastria, which are sparingly and minutely dentate in the distal part. However, these character states are within the variability of *Cyathophorum spinosum*, and there are no substantial differences between the type material of *Cyathophorella adianthoides* and *Cyathophorum spinosum*.

4. Fleischer (1908) already remarked that Van den Bosch & Van der Sande Lacoste (1861) had confused *Cyathophorum spinosum* with *C. adiantum* (Griff.) Mitt. In all probability their descriptions and figures were almost entirely based on the Javan specimens that were collected by Teijsmann and belong to *C. spinosum*. This is supported by their description and illustrations of obovate amphigastria and perichaetial paraphyses. Such features occur in *C. spinosum* and in Teijsmann's material that is preserved in Van der Sande Lacoste's herbarium kept in L, but are absent in *C. adiantum*.

The description of the amphigastrium costa by Van den Bosch & Van der Sande Lacoste of *Cyathophorum adiantum* non (Griff.) Mitt. might be based on the description of *C. adiantum* (Griff.) Mitt. by Mitten (1859). Nonetheless, Van den Bosch & Van der Sande Lacoste described the amphigastria of their species as (almost) ecostate and depicted an amphigastrium with a short, faint, and forked costa. Such costae do occur in the Teysmann material, but the amphigastrium costa is more often distinct, single, and reach up to 1/3 of amphigastrium length. Ecostate amphigastria, however, were not observed. Nor do they occur in specimens of *C. adiantum* (Griff.) Mitt. in Van der Sande Lacoste's herbarium, although the amphigastrium costa in these specimens is usually shorter and less developed than in the Teijsmann material of *C. spinosum.*

5. *Cyathophorum loriae* and *Cyathophorum penicillatum* are quite similar and are based on non-fruiting plants from New Guinea. Fleischer (1908) and Dixon (1922) emphasized the close resemblance between *Cyathophorum loriae* and *Cyathophorella spinosa.* Dixon considered *Cyathophorum loriae* a less developed form of *Cyathophorella spinosa,* but did not explicitly reduce *Cyathophorum loriae.* Fleischer (1908) did not reduce *Cyathophorum loriae* either, because its sporophyte has been unknown. Nevertheless, the collection made by Loria that is listed by Fleischer (1908) below *Cyathophorella spinosa* may be an isotype of *Cyathophorum loriae.*

The types of *Cyathophorum loriae* and *Cyathophorum penicillatum* differ mainly in average leaf width, but there is considerable overlap. Their features are within the variability of *Cyathophorum spinosum* and accordingly *Cyathophorum loriae* and *Cyathophorum penicillatum* are reduced here.

Description — 6. Dorsiventrally compressed non-gemmiferous stem parts were observed in one collection only: *Edaño, PNH 20215* (L). It shows a single stem that is dorsiventrally compressed in the distal half, where it is translucent and abnormally thin. A disturbance during the growth of the plant is suggested by a degree of rotation in a few stems as seen in a duplicate specimen (HIRO). Where in addition the lateral compression of the stem is slightly irregular, as in a few stems in *Raap 193* (occasionally vague near the apices of few stems as in *Iwatsuki 251943, 251944*), the dorsiventrally, non-gemmiferous compressed stem parts may be teratological in *Cyathophorum spinosum.*

7. Fleischer (1908) illustrated gemmaphores that measure c. 20 cells, but I have not seen any longer than 9 cells.

8. In *Akiyama C-10507* strongly branched gemmaphores that sprout near lateral primordia were observed along the distal half of a damaged stem.

9. In some plants a few filamentous to leaf-like enations (= green protrusions arising from stem epidermis) were observed at perichaetia bearing stems. These enations are single and are placed between the lateral leaves. They are up to 3.6 mm long, and 0.5 mm wide.

10. In *Hoogland & Craven 11.029* occasionally an additional row of exostomial cell plates that is connected to an ordinary exostome tooth was observed. These additional rows measure up to 1/4 of the length of the exostome teeth.

Reproduction — 11. Among the collections examined there are only 9 that contain fruiting plants: a single collection from Java (*unknown collector s.n.,* S), 4 from Seram (*Akiyama C-9857, C-16034, C-16240, C-16641* p.p.) and 4 from New Guinea (*Brass 12934, 25066, Hoogland & Craven 11.029, Van Zanten 448*). The sporophyte of *Cyathophorum spinosum* was first described by Akiyama (1988).

Distribution — 12. To my knowledge, Flenley's collections of *Cyathophorum spinosum* (Müll. Hal.) H. Akiyama (*KCE 475*) and *Hypopterygium vriesei* (*KCE 425*) in September 1979 on Rakata (Pulau Rakata Besar) are the first records of Hypopterygiaceae found on the Krakatau islands (see under '*H. vriesei*', note 9, p. 195).

13. Mohamed & Robinson (1991) reported *Cyathophorum spinosum* (as *Cyathophorella spinosa*) from Peninsular Malaysia. Their collection was not at my disposal, nor any other specimen of this species from this area. However, the description of the species and illustrations by Mohamed & Robinson very much resemble *Cyathophorum spinosum,* especially the smaller plants from Sumatra.

Ecology — 14. In two collections of *Cyathophorum spinosum* from Mt Kinabalu, Borneo, (*Iwatsuki 251943, 251944*; see also notes 6 and 16) a predominance of unicellular teeth was observed. Interestingly, they were found between 1350 and 1400 m altitude. In this particular zone on Seram the occurrence of plants of *Cyathophorum spinosum* changes from ones that are characterised by several multi-cellular teeth at the leaf margin to plants with a predominance of unicellular teeth. Some collections from Mt Kinabalu were also found at this altitude, but they contain plants with several multi-cellular teeth at the leaf margin. Specimens from Mt Kinabalu collected at lower or higher altitudes were not at my disposal, and a possible relation between leaf dentation and altitude in *C. spinosum* on this mountain remains unclear.

Identification — 15. It is rather easy to discriminate fruiting material of *Cyathophorum spinosum* and *C. adiantum* (Griff.) Mitt., but identification of non-fruiting material is often very difficult. Unfortunately, most of the collections that belong to these species contain non-fruiting plants.

The gametophores of *Cyathophorum spinosum* and *C. adiantum* are very similar and show mainly quantitative differences in the dentation of the leaves and amphigastria, the length of the gametoecial leaves, and the occurrence of paraphyses.

The two species show differences in the occurrence and morphology of multi-cellular teeth. In *Cyathophorum spinosum* most plants have lateral leaves with at least a few, up to 9-celled multi-cellular teeth. Plants with leaves that have only unicellular teeth are rare in this species, but predominate in *C. adiantum*. Multi-cellular teeth in *C. adiantum* consist of maximally 5 cells. The multi-cellular teeth in *Cyathophorum spinosum* are also slightly different from those in *C. adiantum*. In the teeth of *C. spinosum* a leaf border is absent or only present in faint traces, whereas in *C. adiantum* the leaf border often continues distinctly into its multi-cellular teeth. It is obvious, though, that these species show some overlap in the features of the dentation of the leaves.

Unicellular teeth in *Cyathophorum spinosum* measure up to 70 µm, whereas they are 70 µm long at least in *C. adiantum*.

Cyathophorum spinosum exhibits further differences from *C. adiantum* in the length of the gametoecial leaves, which are generally longer in the former than in the latter species. The perigonial leaves measure up to 1.1 mm in *C. adiantum*, and up to 1.6 mm in *C. spinosum*. The perichaetial leaves measure up to 1.0 mm in *C. adiantum*, while they are up to 1.8 mm long in *C. spinosum*.

Cyathophorum spinosum differs also from *C. adiantum* by the presence of paraphyses. Perigonial paraphyses are always observed in *C. spinosum*, but are frequently absent in *C. adiantum*. Perichaetial paraphyses were frequently observed in the female plants of *C. spinosum*, but were not found in *C. adiantum*.

In addition, *Cyathophorum spinosum* very often differs from *C. adiantum* in the colour of the gemmae. When coloured the gemmae are mostly orange to orange-brown, and only occasionally brown to dark-brown in the former species, but always brown to dark-brown in the latter.

16. Two collections from Mt Kinabalu, Borneo (*Iwatsuki 251943, 251944*) are given as collections of *Cyathophorella tonkinensis* (Broth. & Paris) Broth. by Noguchi & Iwatsuki (1972). Although these non-fruiting specimens strongly resemble *Cyathophorum adiantum* (Griff.) Mitt., they undoubtedly belong to *Cyathophorum spinosum*. The plants are similar to *Cyathophorum adiantum* in the leaves with predominantly unicellular teeth and few multicellular teeth, up to 5 cells, and with traces of the leaf border. However, although the stem compression is occasionally somewhat irregular or faint and only a few gemmae are present in *Iwatsuki 251944*, the plants show the closest similarity to *Cyathophorum spinosum* by their entirely laterally compressed stems, and their pale orange-brown gemmae.

Other — 17. Dixon (1932, 1935) incorrectly reported *Cyathophorella spinosa* from Thailand based on *Kerr 435b*, though the material evidently belongs to *Cyathophorum adiantum* (Griff.) Mitt.

Noguchi (1973) also reported *Cyathophorum spinosum* from Thailand based on several collections from Northern and Peninsular Thailand. His collections were not at my disposal, but I have not seen any collection of *Cyathophorum spinosum* from either Northern or Peninsular Thailand. Touw (1968) correctly stated that *Cyathophorella tonkinensis* (Broth. & Paris) Broth., which belongs to a variant of *Cyathophorum adiantum*, is common in the mountain forests of North, Northeast, and East Thailand. There is a close similarity in gametophytic features between *Cyathophorum spinosum* and, especially, this variant of *Cyathophorum adiantum* - which has leaf margins with both unicellular and multi-cellular teeth. It cannot be ruled out that the collections of *Cyathophorum spinosum* from Northern Thailand described by Noguchi belong to *Cyathophorum adiantum*. However, there is a great possibility that Noguchi correctly identified his material from Peninsular Thailand as *Cyathophorum spinosum* (as *Cyathophorella spinosa*), because this species probably occurs in Peninsular Malaysia (see note 13).

Tixier (1979) reported *Cyathophorum spinosum* (as *Cyathophorella spinosa*) from Cambodia (Kampuchea) based on three collections that he had made himself. Of these collections I have only seen *Tixier 2989* (HIRO), which actually belongs to *Cyathophorum hookerianum* (Griff.) Mitt.

According to Chen et al. (1978) *Cyathophorum spinosum* (as *Cyathophorella spinosa*) occurs in Yunnan, China. I have not seen any specimen from China that is presented as *Cyathophorella spinosa*, and none of the specimens from China that I have examined belongs to *Cyathophorum spinosum*. Chen et al. (1978) were probably confused by the close similarities in gametophytic characters between *Cyathophorum spinosum* and *Cyathophorum adiantum*, and their record of *Cyathophorum spinosum* from China might, therefore, actually be a record of *Cyathophorum adiantum*.

According to Brotherus & Watts (1915) *Cyathophorum spinosum* (also as *Cyathophorella spinosa*) occurs in Vanuatu. I have not seen any collection from Vanuatu that belongs to this species, and *Cyathophorum spinosum* probably does not occur in this archipelago.

Selected specimens (from 196 examined):

PHILIPPINES: Luzon. Benguet Prov.: *Elmer 8544* (BM p.p.), *Williams 1672* (FH, NY p.p.), Baguio. – Rizal Prov.: *Ramos BS 13642* (BM, FH, GRO, H, NY); *Loher s.n.* (NY), Paningtingan. – Mindoro: *Bartlett 13694* (FH), Mt Alingiyaban. – Palawan: *Sandermann Olsen 2148* (GRO, L), Penigisan. – Panay. Capiz Prov.: *Paniza 9285* (GRO, L), Mt Upao. – Negros: *Edaño, PNH 20215* (HIRO, L), Kinabkaban (=? Binalbagan) River. – Mindanao: *Van Zanten et al. 81.02.1750* (GRO), *Robbins 3962* (L), Mt Talamo. — MALAYSIA: Borneo. Sarawak: *Everett s.n.* (NY), Mt Matang. – Sabah: *Iwatsuki 250203a* (NICH), *251943* (NICH), *251944* (NICH), *253458* (NICH), Mt Kinabalu; *Meijer B 10.168* (L), Mt Templer. — INDONESIA: Sumatra: W Sumatra (Sumatera Barat, 'Padang Prov.'): *Wiltens s.n.* (L); *Meijer B 7113* (S), Pajakumbuh, Mt Sago. – Jambi(?): *Meijer B 9095* (L p.p.), Korinchi region, Mt Tudjuh. – Krakatau: *Flenley KCE 475* (L), Pulua Rakata Besar. – Java: *unknown collector s.n.* (NY, ex hb. Braun, s.loc.); *Blume s.n.* (BR), "Gandoger M.". – W Java (Jawa Barat): *Raap 193* (GRO, L), Mt Salak; *Teijsmann s.n.* (L), Mt Gedeh; *Fleischer, MFAI 249* (FH, NY), Telaga Warna; *Schiffner 12938* (L, BM, S, W), Tjiburrum. – C Java (Jawa Tengah): *Junghuhn s.n.* (L), Ungarang. – E Java (Jawa Timur): *Gandrup 539* (FH), Idjen Plateau. – Borneo. South Kalimantan (Kalimantan Selatan): *Dransfield 2344* (L), Mt Serempaka. – Sulawesi. C Sulawesi (Sulawesi Tengah): *Hennipman 5125b* (L), Sopu Valley. – Moluccas (Maluku). Batjan: *Alston 16971c* (BM, FH), Mt Sibeloe. – Buru: *Van Balgooy 5008* (L), Waeduna River. Ambon: *Karsten 13* (FH), Tolepocl?. – Seram: *Akiyama C-10507* (KYO), *C-16034* (KYO), *C-16547* (KYO), Manusela National Park. – West Papua (Papua, Irian Jaya). Sorong: *Royen & Sleumer 7704e* (L), Tamrau Range, Mt Kusemun; – Manokwari: *Beccari s.n.* (GRO), Mt Arfak-Putat. – Paniai: *Kloss 9* (BM), Puncak Jaya ('Mt Carstensz'), 'Camp VIb'. – Jayawijaya: *Brass 12934* (FH, GRO, L), Sungai Taritatu ('Idenburg River'), 'Bernhard Camp'. – Merauke: *Van Zanten 300e* (GRO, L p.p.), Pegunungan Sterren ('Star Mts'), Ariemkop; *Van Zanten 448* (L), Antares. — PAPUA NEW GUINEA: West Sepik: *Touw 15074* (L), Star Mts, Busilmin; *Hoogland & Craven 11.029* (L, MEL), Mt Hunstein. – Western Highlands: *Streimann 22243* (CBG), Jimi Valley. – Madang: *Werner s.n.* (JE), Finisterre Range. – Morobe: *Nyman 113* (S), Sattelberg. – Central: *Loria, Bryoth. Levier 727* (BM, FH, GRO, JE, NY, S, W), Mt Moroko ('Mo-roka'). – Milne Bay: *Micholitz s.n.* (BM, JE, W), Cloudy Mts – Papuan Is.: *Brass 24970* (FH), *25066* (FH), Goodenough Is. — SOLOMON IS.: Guadalcanal: *Van Zanten 682526b* (GRO p.p.), Mt Popomanaseu.

7.4. **Cyathophorum adiantum** (Griff.) Mitt. — Fig. 51, 52A, 53A; Map 24; Plate 3e, g

Cyathophorum adiantum (Griff.) Mitt., J. Proc. Linn. Soc., Bot., Suppl. 1 (1859) 147. — *Neckera adiantum* Griff., Notul. Pl. As. 2: 464. 1849; Icon. Pl. As. 2 (1849) pl. 85 f. 2–2'. — *Cyathophorella adiantum* (Griff.) M. Fleisch., Musc. Buitenzorg 3 (1908) 1094. — Type: *Griffith 221* (BM lecto, designated here, s.loc.; BM; BM, also sub no. *511*), India, Meghalaya, Khasi Hills ["Khasia"]; potential isotypes: *Griffith 221.185* (BM, NY; both specimens also sub no. *511*), India, Meghalaya, Khasi Hills ["Khasia"], Maamloo. — See note 1.

Cyathophorum sublimbatum Thwaites & Mitt. in Mitt., J. Linn. Soc., Bot. 13 (1873) 309, syn. nov. — *Cyathophorella sublimbata* (Thwaites & Mitt.) M. Fleisch., Musc. Buitenzorg 3 (1908) 1094. — Type: *Thwaites CM 127* (NY holo, BM, W), Sri Lanka ["Ceylon"], Central Prov.; potential isotypes: *Thwaites s.n.* (RO, S); see note 2. — According to Mitten, J. Linn. Soc. Bot. 13: 294. 1873, the description of the species has been drawn up by himself. — Thwaites & Mitten, in Mitten, J. Linn. Soc. Bot. 13 (1873) 309, did not indicate a collector's number for Thwaites' type collection.

Cyathophorum tonkinense Broth. & Paris in Paris, Rev. Bryol. Lichénol. 35 (1908) 46, syn. nov. — *Cyathophorella tonkinensis* (Broth. & Paris) Broth. in Engler & Prantl, Nat. Pflanzenfam. ed. 2, 11 (1925) 278. — *Cyathophorella japonica* (Broth. ex Paris) Thér. & R. Henry in R. Henry (hom. illeg.) var. *tonkinensis* (Broth. & Paris in Paris) Thér. & R. Henry in R. Henry, Rev. Bryol. Lichénol. 1 (1928) 45, nom. illeg. prior. ut spec.; see notes 3, 9, and 10. — Type: *Eberhardt s.n.* (PC holo), Vietnam, Vinh Phu, Tam Dao Range, alt. 1100 m, [aux bords ou dans les environs immédiats de la cascade d'Argent, dans la chaîne du Tam Dao, province de Vinh Yen, S.E. du Tonkin], July 1907.

?: *Cyathophorum japonicum* Broth. ex Paris, Rev. Bryol. Lichénol. 35 (1908) 47, syn. nov. — *Cyathophorella japonica* (Broth. ex Paris) Broth. ex Thér. & R. Henry in R. Henry, Rev. Bryol. Lichénol. 1 (1928) 45, hom. illeg. — Type: not indicated; see note 4, 9, and 11.

Cyathophorum japonicum Broth. in Cardot, Bull. Soc. Bot. Genève, 2, 3 (1911) 279, hom. illeg. — Syntypes: *Okamura s.n.* (H n.v.; NY, S; FH, S, both p.p. and sub no. *317*), Japan, Shikoku, Tokushima Pref. ['Awa'], Karei, Dec. 30, 1905; *Gôno s.n.* ["hb. Holzinger"] (MIN? n.v., FH? p.p., sub no. *242*), Japan, Shikoku, Kochi Pref. ['Tosa']; potential syntype: *Gôno s.n.* (UPS), Japan, Shikoku, Kochi Pref. ['Tosa'], Mt Hônokawa. — Although collection numbers are not indicated for the type material, it is almost certain that the collections provided with a number are syntypes. Among all the material examined no other collections made by Okamura or Gôno at the localities given above were found; see also note 5. — See notes 4 and 10. — Synonymised with *Cyathophorella tonkinensis* (Broth. & Paris) Broth. by Noguchi, J. Hattori Bot. Lab. 2 (1947) 80.

Cyathophorella japonica Broth., Oefvers. Förh. Finska Vetensk.-Soc. 62A (1920) 31. — Type: *Okamura 673* (H holo p.p., mixed with *Lopidium struthiopteris* (Brid.) M. Fleisch.; NY), Japan, Shikoku, Kochi Pref. ['Tosa'], Mt Hônokawa, Dec. 31, 1907. — See notes 4, 10, and 11. — Synonymised with *Cyathophorella tonkinensis* (Broth. & Paris) Broth. by Noguchi, J. Hattori Bot. Lab. 2 (1947) 80.

Cyathophorella tonkinensis (Broth. & Paris in Paris) Broth. var. *minor* Nog., J. Hattori Bot. Lab. 2 (1947) 80, syn. nov. — Type: *Kamimura 5000* p.p. (NICH holo, KUMAMOTO), Japan, Shikoku, Kochi Pref. ['Tosa'], Mt Yokogura, July 1937; see notes 6 and 12.

Cyathophorella subspinosa P.C. Chen, Feddes Repert. Spec. Nov. Regni Veg. 58 (1955) 31, syn. nov. — Type: *Chen 25* (PE holo; JE, *s.n.*; S, *s.n.*; isotypes in JE and S presented sub *MSE 92*), China, Guangxi, Longzhou ["Li-kiang (Lung-tschou)"], De-ching-shan, alt. c. 800 m, on rock, Jan. 4, 1952. — See note 13.

Cyathophorum griffithii Wilson in Mitt., J. Proc. Linn. Soc., Bot., Suppl. 1 (1859) 147, nom. nud. in syn. (*Cyathophorum adiantum* (Griff.) Mitt.). — Original material: *Hooker f. & Thomson 715* (BM), India, Assam, Khasi Hills, Myrung.

Cyathophorum kurzianum Hampe ex Mitt. in C.(?S.P.) Parish in F. Mason ex W. Theob., Burma, its People and Productions 2, Botany (1883) 51, nom. nud. — *Cyathophorum kurzeanum* Hampe ex Paris, Index Bryol. Suppl. (1900) 107, nom. nud. — *Cyathophorella kurzeana* (Hampe ex Paris) M. Fleisch., Hedwigia 63 (1922) 212, nom. nud. — Original material: *Kurz 3029* (B, destroyed; BM), Myanmar (Burma) ["Birman"], Karenni, Karen Hills, top of 'Nattoung' (= Mt Nattaung), alt. 7000 ft. — Synonymised with *Cyathophorella adiantum* (Griff.) M. Fleisch. by Fleischer, Musc. Buitenzorg 3 (1908) 1094.

?: *Cyathophorum japonicum* Broth. in Engler & Prantl, Nat. Pflanzenfam. ed. 1, 3 (1907) 966, nom. nud., syn. nov. — Original material: Japan (not known with certainty); see note 7.

Cyathophorella serrulata P.C. Chen, Feddes Repert. Spec. Nov. Regni Veg. 58 (1955) 31, nom. nud. — Original material: *Chen s.n.* (PE, sub no. *05179*), China, Guangdong, Beijang Co.; see note 8 and 13. — Synonymised with *Cyathophorella tonkinensis* (Broth. & Paris) Broth. by Chen et al., Gen. Musc. Sin. 2 (1978) 134. — See note 14.

Illustrations: Griffith, Icon. Pl. As. 2 (1849) pl. 85 f. 2–2'. — Fleischer, Musc. Buitenzorg 3 (1908) f. 184, 1–3. — Noguchi, J. Hattori Bot. Lab. 7 (1952) 14, f. 10; 16, f. 11. — Sakurai, Muscol. Jap. (1954) pl. 42, c, j. — Noguchi, Misc. Bryol. Lichenol. 5 (1969) 31, f. 147. — Yang, Taiwania 16 (1971) pl. 1 f. 1–10. — Iwatsuki & Mizutani, Coloured Illustr. Bryoph. Japan (1972) pl. 25, f. 363. — Gangulee, Mosses of Eastern India (1977) f. 769. — Noguchi, Moss Flora of Japan 4 (1991) f. 340. — Yamaguchi, Bryological Research 7 (2001) 393, f. 1 (leaf dentation not shown in f. 1a).

Plants in groups of fans, small to large, dull or weakly glossy, frequently gemmiferous. *Stems* up to 6.5 cm tall, terete, usually laterally compressed below in basal 1/3–2/3 (–4/5) and dorsiventrally compressed above, occasionally entirely dorsiventrally compressed above base, dorsiventrally compressed in gemmiferous stem parts, deep dark brown or brown (at base) to brown or pale green (at top), glossy when brown or not. *Primordia* naked. *Epidermis cells and cortical cells of stem* equally narrow or cortical ones wider; walls thin or incrassate, colourless to deep dark brown; inclusions absent from epidermis cells and outer cortical cells, absent or present in inner cortical cells, tiny crusts of amorphous solids or tiny oil-like droplets. *Central strand* present; cells narrow, walls colourless to (reddish) brown, inclusions absent. *Axial cavities* absent. *Axillary hairs* 1–4 per leaf, 2–8-celled, simple; basal cells 1–5, colourless to brown; intermediate cells usually present, occasionally absent, oblong-rectangular to elongate-rectangular; terminal cell oblong to short-linear, ± rectangular, 23–85 μm long and 8–17 μm wide, smooth. *Leaves* distant or closely set, yellowish green to dark green, occasionally tinged with red, frequently brown near basal angles. *Basal leaves* deltoid to narrowly triangular or elliptic; apex acute or gradually acuminate. *Distal leaves* smaller in gemmiferous stem than in non-gemmiferous stem parts; margin moderately to coarsely serrate-dentate, occasionally entire in amphigastria, serrate-dentate in basal leaves of gemmiferous stem parts, becoming entire in distal ones; teeth 1–5-celled, but in amphigastria 1- or 2-celled and usually unicellular, in lateral leaves up to 205 μm long, in amphigastria shorter, up to 100(–160) μm long, projecting up to 1 (or 2) cell(s); border faint to distinct, but absent or faint near leaf base and frequently interrupted near teeth or just below leaf apex, up to 3 cells wide; laminal cells 35–135 μm long and 6–40 μm wide, occasionally sinuate when narrow. *Distal lateral leaves* ovate-oblong to short-linear, (1.5–)2.0–5.5 mm long and 0.3–2.0 mm wide, elliptic to linear in gemmiferous part of stem; apex acute or gradually to abruptly acuminate; acumen 0.3–0.6 mm long; costa reaching up to 1/3 of leaf length. *Distal amphigastria* appressed to patent, ovate to narrowly lanceolate, (0.5–)0.7–3.5 mm long and (0.2–)0.3–2.0 mm wide, ovate to linear in gemmiferous part of stem; basal part nearly flat or smoothly curved, weakly bulging or not; insertion distinctly concave to straight; apex acute or gradually to abruptly acuminate; acumen 0.1–0.7 mm long; costa absent, faint to distinct, reaching up to 1/4 of amphigastrium length. *Gemmae clusters* located in distal half to third of stem, placed above axils of lateral leaves and amphigastria, reaching 1/5 of length of covering lateral leaves to ± equally long. *Gemmaphores* penicillate, 1–7 cells long, colourless to brown. *Gemmae* usually simple, rarely branched (at base), up to 25 cells long, colourless to dark brown; cells 19–72 μm long and 17–48 μm wide.

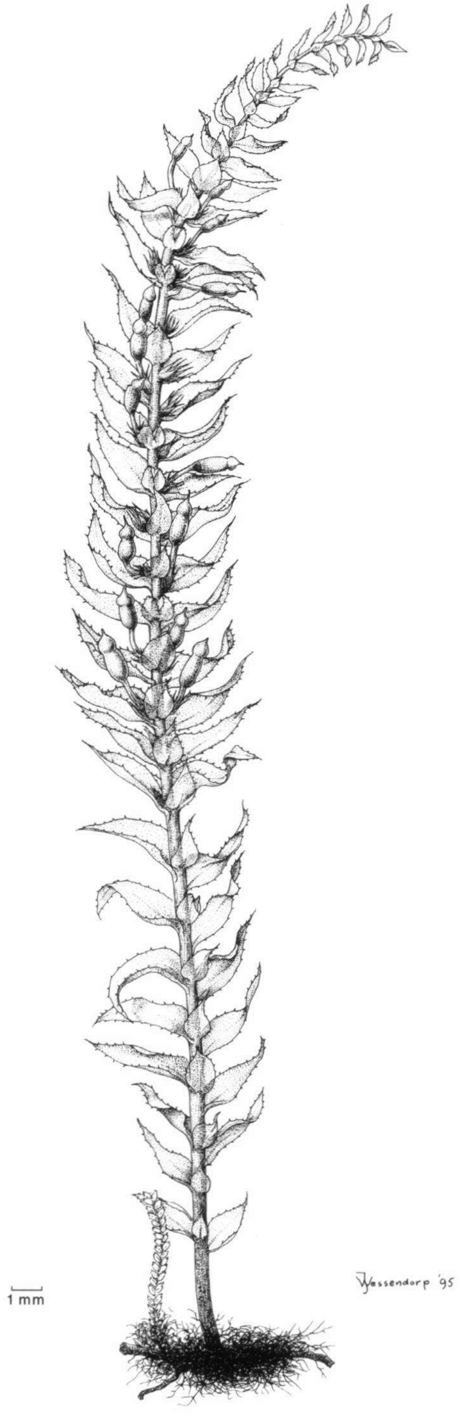


Fig. 51. *Cyathophorum adiantum* (Griff.) Mitt. Habit (ventral view, *Touw 9198*, L).

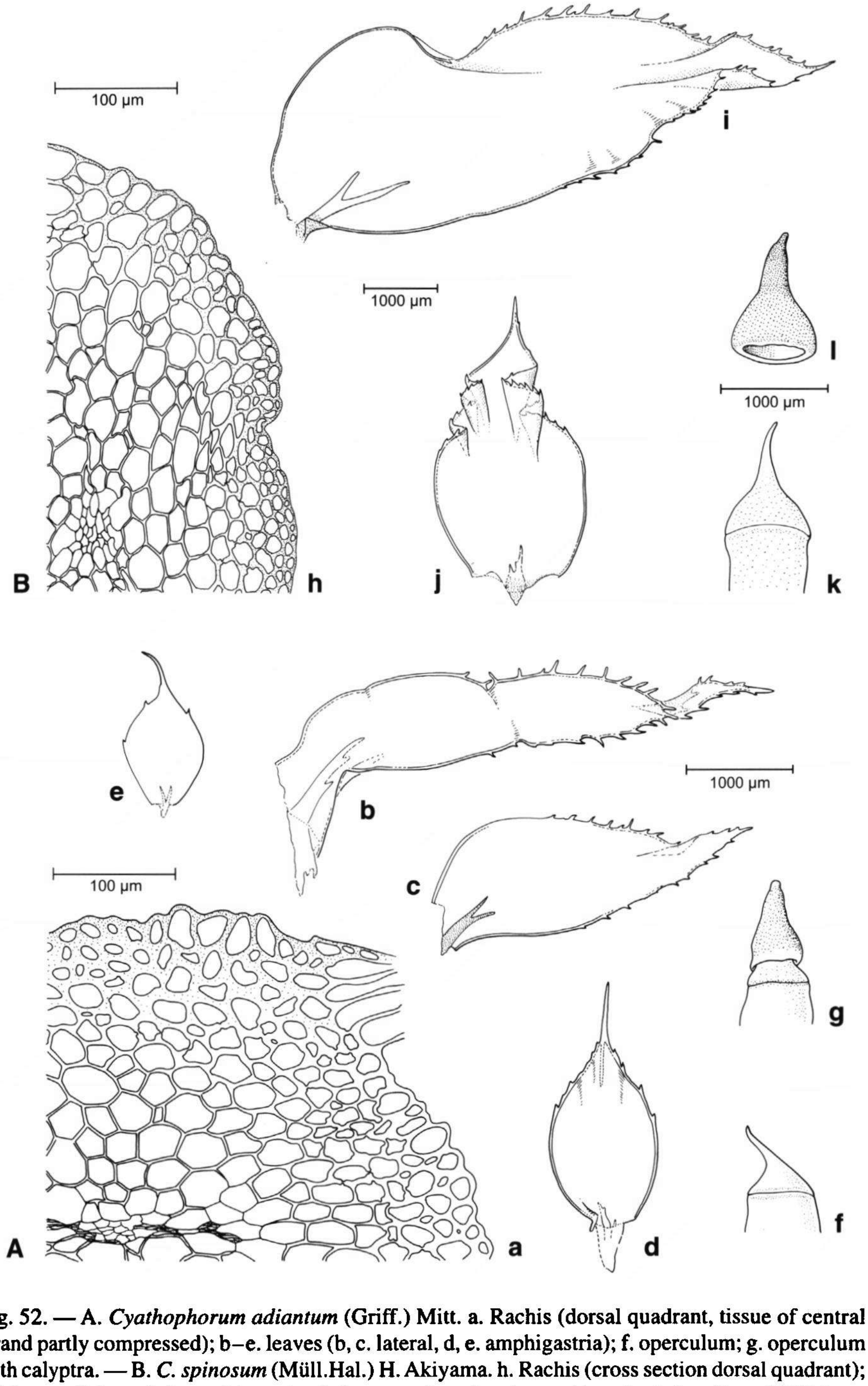
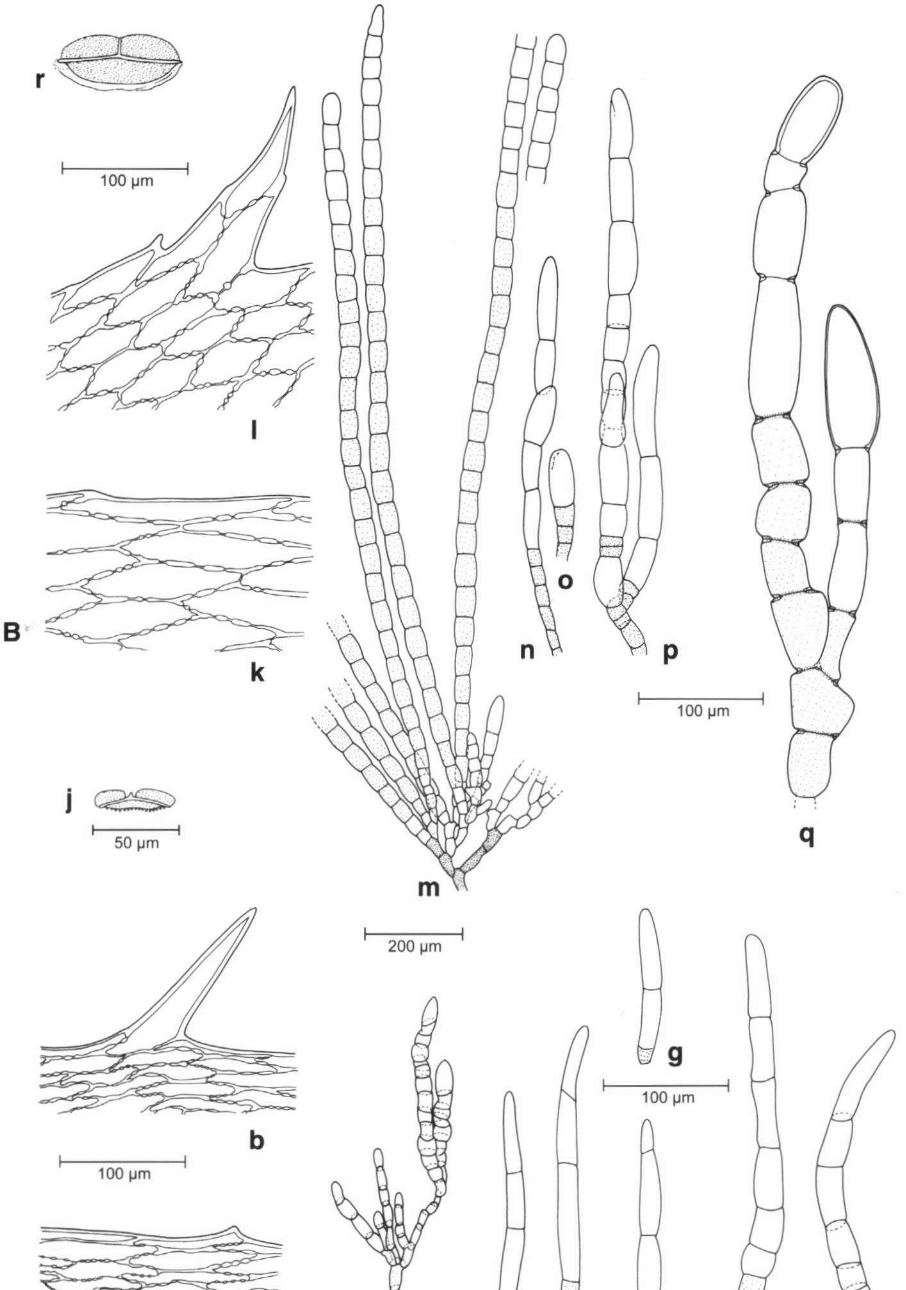


Fig. 52. — A. *Cyathophorum adiantum* (Griff.) Mitt. a. Rachis (dorsal quadrant, tissue of central strand partly compressed); b–e. leaves (b, c. lateral, d, e. amphigastria); f. operculum; g. operculum with calyptra. — B. *C. spinosum* (Müll.Hal.) H. Akiyama. h. Rachis (cross section dorsal quadrant); i, j. leaves (i. lateral, j. amphigastrium); k. operculum; l. calyptra (A. a, b, d, f, g: *Touw 9198*, L; c, e: *Fea BL 687*, BM; B. h–j: *Schiffner 12938*, L; k, l: *Akiyama C-16034*, L).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Dioicous. *Gametoecia* in middle or distal part of stem. *Leaves* short-ovate to elliptic in perigonia, triangular to oblong in perichaetia; margin entire (or serrate-dentate in distal part of leaf in perichaetial leaves); border faint to distinct, frequently faint, interrupted, or absent in distal half of leaf, up to 1 (or 2) cell(s) wide; costa absent. *Inner leaves*: of perigonia up to 1.1 mm long and 1.0 mm wide, acumen up to 0.5 mm long; of perichaetia prior to sporophyte development up to 0.9 mm long and 0.7 mm wide, acumen up to 0.8 mm; of full-grown perichaetia up to 1.0 mm long and 0.6 mm wide, acumen up to 1.1 mm long. *Antheridia* 0.6–0.8 mm long. *Stalk in full-grown perichaetia* up to 0.2 mm long. *Archegonia* 0.5–0.8 mm long. *Vaginula* 0.6–1.0 mm long. *Gametoecial axillary hairs* 0–2 per gametoecial leaf, 3- or 4-celled, simple; basal cells 2, brown; intermediate cells absent or present, elongate, ± rectangular, colourless; terminal cell oblong-elliptic to short-linear-rectangular, 35–80 µm long and 10–15 µm wide, smooth, colourless. *Paraphyses* absent or few in perigonia, absent in perichaetia, 7–10 cells long, simple; basal cells 3 or 4, colourless to brown; intermediate cells short to oblong, rectangular (or somewhat truncate-elliptic), colourless to pale brown; terminal cell elongate-ovate to elongate-rectangular, approximately 65–90 µm long and 15–20 µm wide, colourless.

Sporophytes up to 4 per stem. *Seta* 1.0–2.1 mm long, white to ochraceous; base narrow or widened. *Capsule* cupulate to ellipsoid, 1.2–2.2 mm long and 0.6–1.2 mm wide, yellow-ochraceous to ochraceous, frequently tinged with red; annulus absent. *Peristomial formula OPL:PPL:IPL* = 4:2:(3–)4c. *Exostome* colourless to pale yellow; teeth 140–340 µm long and 30–65 µm wide, occasionally slightly perforate or with a single row of dorsal plates in distal half; dorsal side smooth or weakly papillose in basal third of teeth, smooth or weakly to coarsely papillose above; median line not furrowed; dorsal plates broader than or equally wide as ventral ones, 7–8 µm thick; papillae low, simple; lamellae weakly to distinctly projecting; ventral plates very thin and probably c. 3 µm thick, smooth or weakly papillose; papillae low, simple; trabeculae very short in basal fourth of teeth, short to pronounced in distal part. *Endostome* smooth to moderately papillose at both faces, colourless to pale yellow; papillae low, simple; basal membrane reaching up to 1/5 of length of exostome teeth; processes projecting 200–360 µm beyond orifice and 19–30 µm wide at base, distinctly keeled, weakly nodulose or not, appendiculate or not with a few lateral appendages consisting of parts of a cell plate; cilia absent or rudimentary and consisting of parts of a single cell, 1 cell plate wide, not appendiculate. *Operculum* long-rostrate, 0.7–1.1 mm long, ochraceous to pale brown; rostrum nearly straight to oblique. *Calyptra* mitrate, partly covering operculum, 0.7–1.1 mm long, brown to dark brown, fleshy; margin entire. *Spores* 16–26 µm.

Fig. 53. — A. *Cyathophorum adiantum* (Griff.) Mitt. a, b. Leaf cells of lateral leaf (a. basal part of antical side; b. distal part of antical side); c. gemmaphore with gemmae; d–g. axillary hairs; h, i. paraphyses; j. exostome tooth (cross section). — B *C. spinosum* (Müll.Hal.) H. Akiyama. k, l. Leaf cells of lateral leaf (k. basal part of antical side, l. distal part of antical side); m. gemmaphore with gemmae; n–p. axillary hairs; q. paraphyse; r. exostome tooth (cross section) (A. a–c, f, h–j: *Touw 9198*, L; d, g: *Chen, MSE 92*, S; e: *Griffith 185/509?*, BM; B. k, l, q: *Schiffner 12938*, L; m: *Brass 24970*, FH; n, o: *Brass 12934*, FH; p: *Brass 25066*, FH; r: *Hoogland & Craven 11.029*, MEL).

Distribution — Nepal, Bhutan, India (Uttar Pradesh, Sikkim, Bengal Jalpaiguri, Meghalaya, Mizoram, Karnataka, Tamil Nadu), Sri Lanka, China (Sichuan, Yunnan, Guanxi, Guangdong, Hainan), Japan (Honshu, Shikoku, Kyushu), Taiwan, Myanmar, Thailand, Vietnam.

In Japan restricted to coastal regions of south-eastern Kyushu, Shikoku, and Honshu. Reported from the Ryukyu Archipelago, Japan, by Noguchi (1947), Horikawa (1955), and Yamaguchi (2001) (as *C. tonkinensis*).

Reported from Chinese provinces of Zhejiang (Hu Renliang & Wang Youfang (1987) and Guizhou (Tan et al., 1994), China (as *C. tonkinensis*).

Habitat & Ecology — In dense to open evergreen forests. On trunks, branches, and on rocks (granite, quartzite), especially in humid or shaded places near streams or waterfalls. Less frequently on twigs of trees and shrubs, rotten logs, and soil. Rarely on leaves. Once found on *Hymenophyllum* species (*Univ. Tokyo Bot. Exp. 307*; cf. Noguchi in Hara, 1966). Altitude: 400–3500 m; in SE Japan from sea level up to 640 m, but in Honshu up to only 250 m.

In Japan, Taiwan, and China usually found on rocks, frequently found on rocks in other areas. Incorrectly reported to be rarely found on rocks by Noguchi (1991, as *Cyathophorella tonkinensis*).

Variability — Within the species two morphological variants can be recognised. The variants are not sharply defined, and no nomenclatural status is needed.

The typical variant of *C. adiantum* is characterised by leaves set with only unicellular teeth at the leaf margin, whereas the other variant is characterised by at least a few multicellular teeth among the unicellular teeth at the leaf margin. The leaves in the former variant are somewhat more distant, and more strongly crisped than the leaves in the latter. However, considerable overlap in these features exists, even in the dentation of the leaves. Teeth range from unicellular, unicellular with a portion of a border cell near the base of the terminal cell, to truly multicellular. In unicellular teeth the, usually long, projecting cell is based in the leaf margin, and border cells do not continue into the tooth. In multicellular teeth the most projecting cell, based or not based in the leaf margin, has a few, partly or nearly entirely adjacent border cells. The adjacent part of these partly projecting border cells is very variable. In the most pronounced multicellular teeth a few cells adjacent to the most projecting one are not even based in the leaf margin. Furthermore, there is much variation in the number of cells in the multicellular teeth, even in a single leaf.

Geographical variation — Not found.

Ecological variation — Not found with certainty, insufficient data. The variant that is characterised by at least a few multicellular teeth at the leaf margin might be a modification of humid and shaded places.

Notes:

Nomenclature — 1. *Neckera adiantum* has not been typified before, and a lectotype was designated here. There are four collections attached to the sheet that is labelled "*adiantum*, Griff." in the herbarium of Griffith/East India Company (BM). The origin of these collections is not indicated. *Griffith 262*, which is also labelled with the numbers *29/125*, is presented as "*Hypnum*". *Griffith 179* is labelled "*Neckera adiantum*". In both collections a few stems of *Cyathophorum adiantum* are mixed with several stems of *C. hookerianum*. The plants of *C. adiantum* are sterile. Griffith (1849b), however, presented a female plant of *N. adiantum*. Therefore, neither of these two collections represents type material of *N. adiantum*.

The remaining two collections contain only female plants of *Cyathophorum adiantum*. In *Griffith 102*, labelled "*Neckera*", a few non-fruiting stems of *C. adiantum* are mixed with other mosses. *Griffith 221* is labelled with a herbarium name (epithet "*adiantum*"), and contains a fruiting plant. Although Griffith's illustrations show no sporophytes, one of them shows a fertilised archegonium among non-fertilised ones. Only in *Griffith 221* were such fertilised archegonia observed. This indicates that the fruiting plant is closest to Griffith's concept of *N. adiantum*. Therefore, this collection has been designated as the lectotype.

There are several specimens collected by Griffith that were distributed in 1875 by the Royal Botanic Gardens in Kew, which are, or may be, duplicates of the lectotype. Such a duplicate is another specimen of *Griffith 221* in BM, which contains a non-fruiting, female plant of *Cyathophorum adiantum*. It is labelled "*Cyathophorum adiantum* (Griff.)", and comes from the Khasi Hills, India, making it almost certain that the lectotype also originates there. Another specimen in BM carrying the two numbers *221* and *511* is in all probability also a duplicate of the lectotype. The number *221* may be equivalent to a collection number. The number *511* is probably either the number of the specimen in the East India Company's herbarium or the number under which it was distributed at Kew. The specimen is a fruiting plant. In BM and NY there are a few other specimens that contain fruiting plants. These specimens, which carry the numbers *221.185*, and *511*, may also be duplicates of the lectotype, although this is not known with certainty. The significance of the number *185* is also unknown, although a collection from Bhutan made by Griffith (see below) is also labelled with the number *185*. Parts of *Griffith 221.185* were regarded as potential isotypes here. If *Griffith 221* was kept or distributed under the number *511*, the parts of *Griffith 511* (RO, UPS) might also be duplicates of the lectotype. However, a clear, direct reference to *Griffith 221* is missing and they are not listed as potential isotypes.

Nevertheless, the hypothesis that collections made by Griffith have been identified with herbarium or distribution numbers seems plausible. Double numbering is also found in other collections made by Griffith. *Griffith 171* and *Griffith 187*, for example, are both labelled with the number *508*, which is probably the suggested herbarium or distribution number. These collections, presented as *Cyathophorella hookeriana*, are in fact mixed and contain material of *Cyathophorum adiantum*. A collection of *Cyathophorum adiantum* from Bhutan made by Griffith (NY) is labelled with the numbers *185* and *509*, and again the latter is probably the herbarium or distribution number.

2. Mitten (1873) neither reported the locality, nor the altitude for the type of *Cyathophorum sublimbatum*, but several type specimens are labelled as coming from the Central Prov. of Ceylon. The altitude is recorded for only one isotype in BM, which was found at 5000–7000 ft.

3. Thériot & Henry (in Henry, 1928) did not indicate whether they examined the types of *Cyathophorum japonicum* Broth. ex Paris and *C. tonkinense*, or at least the type of the latter. It is very probable, though, that they did. They examined the characters that were used by Paris (1908) to distinguish *C. japonicum* Broth. ex Paris from *C. tonkinense*: "Les charactères invoqués par Paris [Rev. Bryol., p. 46, 1908] pour distinguer la plante du Tonkin de celle du Japon s'évanouissent à l'examen, ...", and stated that the acumina of the leaves are narrower, and that those of the amphigastria are narrower and longer in *C. japonicum* Broth. ex Paris than in *C. tonkinense*. Moreover, the type of *C. tonkinense* is in Thériot's herbarium (PC). It can be safely assumed that the reduction of *C. tonkinense* by Thériot & Henry is based on the examination of its type, and probably also on the examination of the type of *C. japonicum* Broth. ex Paris. Although they also included in their study a collection that was made by Demange at Tam-Dao, Vietnam, there is no need to consider the variety of Thériot & Henry as another name based on a different type.

4. The names *Cyathophorum japonicum* and *Cyathophorella japonica* have been used in a fairly confusing way. In 1907 *Cyathophorum japonicum* was published by Brotherus as a nomen nudum. A year later *Cyathophorum japonicum* Broth. ex Paris was published by Paris (1908). According to Noguchi (1952) this name is a nomen nudum, and it is not given by Van der Wijk et al. (1959). However, when Paris compared it with *Cyathophorum tonkinense*, he provided *Cyathophorum japonicum* Broth. ex Paris with a brief diagnosis. In 1911 *Cyathophorum japonicum* was also described by Brotherus in Cardot (1911).

Several years later, Brotherus (1920b) described *Cyathophorella japonica* as a new species. Unfortunately, Brotherus (1907) and Paris (1908) gave no references to collections on which they based their *Cyathophorum japonicum*. Although it is conceivable that Paris saw material under the name of *Cyathophorum japonicum* that had been distributed by Brotherus, I have not seen any collection with this name that could have been seen by Paris. Therefore, I consider *Cyathophorum japonicum* Broth. ex Paris based on other collections than *Cyathophorum japonicum* Broth., *Cyathophorum japonicum* Broth. in Cardot, and *Cyathophorella japonica* Broth.

Cyathophorum japonicum Broth. in Cardot. is probably based on other material than *Cyathophorum japonicum* Broth. ex Paris. Paris (1908) stated, that the leaves of *Cyathophorum japonicum* Broth. ex Paris are not recurved when dry, and have a short, but double, leaf costa. In the syntypes of *Cyathophorum japonicum* Broth. in Cardot, however, I observed the dry leaves to be curved from patent to widely patent. In Okamura's material the leaf costa is short, often single, and occasionally forked. In Gôno's material the costa is usually short and forked, but occasionally rather long and nearly simple. *Cyathophorum japonicum* Broth. in Cardot, therefore, must be considered an illegitimate homonym of *Cyathophorum japonicum* Broth. ex Paris.

The combination *Cyathophorella japonica* (Broth.) Broth. used by Thériot & Henry (in Henry, 1928) is evidently based on *Cyathophorum japonicum* Broth. ex Paris. They ascribed this combination to Brotherus by mistake, and their combination is an illegitimate homonym of *Cyathophorella japonica* Broth.

5. The number *317* of the two isotypes of *Cyathophorum japonicum* Broth. in Cardot collected by Okamura at Karei (Kochi Pref., Japan) in Dec. 1905, seems to refer to the name '*Cyathophorum japonicum*', and was probably added later for further distribution of the specimens and does not represent a collection number given by Okamura. In both isotypes *Cyathophorum japonicum* Broth. in Cardot is mixed with *Cyathophorum hookerianum*. Okamura's isotype in FH was distributed from Brotherus' herbarium. It is labelled "*Cyathophorum japonicum* Broth. n. sp.". On this specimen no date was recorded, but the specimen in S was collected on Dec. 30, the same date as reported for the other isotypes collected by Okamura.

Gôno 242 is labelled "*Cyathophorum japonicum* Broth. ms" and was identified by Cardot. Although the collection is almost certainly cited as type material of *Cyathophorum japonicum* Broth. in Cardot, there is no certainty that it was actually seen by Brotherus. The collection also contains *C. hookerianum*.

Brotherus (in Cardot, 1911) description of *Cyathophorum japonicum* is short, and there is no indication that it is partly based on material of *C. hookerianum*.

6. The type of *Cyathophorella tonkinensis* var. *minor* is mixed with *Cyathophorum hookerianum*, but in all probability the description of *Cyathophorella tonkinensis* var. *minor* is exclusively based on the plant that belongs to *Cyathophorum adiantum*.

7. It is not known with certainty upon which collections Brotherus (1907) based his *Cyathophorum japonicum*. The holotype of *Cyathophorella japonica* Broth. (*Okamura 673*) can safely be ruled out, because it was collected on Dec. 31, 1907, but at least two other possibilities remain. The first is Okamura's syntypes of *Cyathophorum japonicum* Broth. in Cardot (1911), i.e. *Okamura s.n. (317)*, which were collected in 1905. Such syntypes were not among the material on loan from Brotherus' herbarium (H-BR), but according to Cardot (1911) a syntype had been present in Brotherus' herbarium. The second possibility is another collection in Brotherus' herbarium that is presented as "*Cyathophorum japonicum* Broth. n. sps.", and was also collected in 1905 by Okamura (*Okamura 240*, Japan, Shikoku, Kochi Pref. ('Tosa'), Mt Imano, Aug. 12, 1905). There is no evidence that Brotherus' (1907) *Cyathophorum japonicum* is based on either one or both of these collections, but bet it is. Since the material of both collections is conspecific with *Cyathophorum adiantum*, *Cyathophorum japonicum* Broth. can almost certainly be merged with *Cyathophorum adiantum*.

8. Crosby & Bauer (1987) overlooked the paper by Chen (1955), and erroneously cited Chen et al. (1978) as the first publication, in which the name *Cyathophorella serrulata* was used. Indeed, Chen may have published the name as early as 1946 (J. West. China Bord. Res. Soc., ser. B: 142–148), but this paper could not be found, and accordingly 1955 has been regarded as the date of first publication

Synonymy — 9. Thériot & Henry (in Henry, 1928) concluded that the features Paris (1908) used to discriminate between *Cyathophorum japonicum* Broth. ex Paris and *Cyathophorum tonkinense* are very variable. They considered them to be most different in the width and the length of the acumen of leaves and amphigastria, but considered the variability to be no more than between varieties of a single species. I have not seen the type of *Cyathophorum japonicum* Broth. ex Paris, but all the material examined that is presented as *Cyathophorum japonicum, Cyathophorella japonica*, or *Cyathophorella tonkinensis* is very similar. The features given by Thériot & Henry do not separate *Cyathophorum japonicum* Broth. ex Paris and *Cyathophorum tonkinense* at the level of variety or other infraspecific level.

10. Based on the study of their original descriptions, and the examination of other specimens from the type location of *Cyathophorum tonkinense* and various localities in Japan, Noguchi (1947) merged *Cyathophorella tonkinensis, Cyathophorum japonicum* Broth. in Cardot, and *Cyathophorella japonica.* Although he did not examine the type material, I agree with his judgement that they are conspecific. Noguchi indicated a considerable variability in the shape of the leaves, in the shape and the size of the amphigastria, and, though less emphatically, in the direction of the teeth projecting at the leaf margin. The ranges of these characters show also overlap in the type material. Noguchi (1952) further argued that the criteria given by Paris (1908) are not sufficient to distinguish '*Cyathophorella japonica*' from *Cyathophorella japonica* var. *tonkinensis.* This was based on material which he said was from the type locality of *Cyathophorum tonkinense.* Noguchi (1952) probably referred to a collection made by Demange, which is very similar to the types, and other material, of *Cyathophorella tonkinensis, Cyathophorum japonicum* Broth. in Cardot, and *Cyathophorella japonica.* Based on Demange's material Thériot & Henry (in Henry, 1928) considered *Cyathophorum tonkinense* a variety of *Cyathophorella japonica* (Broth. ex Paris) Thér. & Henry.

11. Brotherus (in Cardot, 1911) separated *Cyathophorum japonicum* Broth. in Cardot from *Cyathophorum adiantum* by its longer leaves, which are strongly patent-falcate, longer acuminate, and less strongly dentate. However, in all the material presented as *Cyathophorum japonicum*, including the syntypes of *Cyathophorum japonicum* Broth. in Cardot, these features are within the range of variability in *Cyathophorum adiantum.*

According to Brotherus (1920b) *Cyathophorella japonica* differs from *Cyathophorella adiantum* by its entire and ecostate amphigastria. This claim is mistaken, because in the type of *Cyathophorella japonica* the amphigastria are weakly to moderately serrate-dentate and the ecostate amphigastria are within the range of variability in *Cyathophorum adiantum.*

According to Noguchi (1952) *Cyathophorella tonkinensis* (in which he included *Cyathophorum japonicum* Broth. in Cardot and *Cyathophorella japonica*), differs from *Cyathophorella adiantum* by its narrower, more closely set lateral leaves and the larger ratio of the size of the lateral leaf to that of the amphigastria. In addition, he described the amphigastria as commonly ecostate and obovate or oblong in *Cyathophorella tonkinensis* and rounded ovate in *Cyathophorella adiantum.* However, such obovate amphigastria were not observed, and *Cyathophorella tonkinensis* does not substantially differ from *Cyathophorum adiantum* in any of the features he noted.

Noguchi (1952) distinguished *Cyathophorella tonkinensis* from *Cyathophorella spinosa* (Müll.Hal.) M. Fleisch. and *Cyathophorella adiantum* by differences in the dentation of the leaves. There are significant differences between *Cyathophorella tonkinensis* and *Cyathophorum spinosum*, but not between *Cyathophorella tonkinensis* and *Cyathophorum adiantum. Cyathophorum adiantum* has leaves that are set with unicellular teeth, and *Cyathophorum tonkinense* has leaves that are set with both unicellular and multicellular teeth, although multicellular ones are rare.

In the dentation of the leaves, *Cyathophorum japonicum* Broth. in Cardot and *Cyathophorella japonica* resemble *Cyathophorum tonkinense* and show no substantial differences from *Cyathophorum adiantum.* The multicellular teeth in the type of the first have at most 2 cells.

Neither the type nor the original material of, respectively, *Cyathophorum japonicum* Broth. ex Paris (1908) and *Cyathophorum japonicum* Broth. (1907) were found. Thériot & Henry (in Henry, 1928) may have examined the type of *Cyathophorum japonicum* Broth. ex Paris (see note 3). They merged *Cyathophorum japonicum* Broth. ex Paris with *Cyathophorum tonkinense*, both of which belong to *Cyathophorum adiantum.*

All the material examined that is presented as *Cyathophorum japonicum, Cyathophorella japonica*, and *Cyathophorella tonkinensis* belongs to *Cyathophorum adiantum.* Since the material includes collections that came from Brotherus' herbarium and no misidentifications were observed, it is very probable that both *Cyathophorum japonicum* Broth. ex Paris (1908) and *Cyathophorum japonicum* Broth. (1907) belong to *Cyathophorum adiantum.*

12. *Cyathophorella tonkinensis* var. *minor* is nothing but a small form of *Cyathophorum adiantum*.

13. The types of *Cyathophorum sublimbatum* and *Cyathophorella subspinosa* are very similar to the types of *Cyathophorum japonicum* Broth. in Cardot, *Cyathophorella japonica*, and *Cyathophorum tonkinense*, and belong to *Cyathophorum adiantum*. The type of *Cyathophorum sublimbatum* has unicellular and occasionally 2-celled teeth at the leaf margin. In the type of *Cyathophorella subspinosa* the teeth at the leaf margin are frequently multicellular and are not substantially different from the type of *Cyathophorum adiantum*, though there the teeth are exclusively unicellular.

Chen (1955) stated that *Cyathophorella subspinosa* has 2- or 3-celled teeth at the leaf margin, whereas they are actually up to 4-celled. He distinguished *Cyathophorella subspinosa* from the unicellular serrate-dentate *Cyathophorella serrulata* by its multicellular teeth, and its occasionally simple leaf costa. However, the latter difference was not found. Both forked and simple leaf costae were found in the original material of *Cyathophorella serrulata*.

14. The original material of *Cyathophorella serrulata* belongs to *Cyathophorum adiantum*. It contains stems that, except for the unicellular teeth at the margin of their leaves, resemble the type of *Cyathophorum tonkinense*, and stems that resemble the type of *Cyathophorum adiantum*.

15. The lectotype of *Neckera adiantum* belongs to the variant of *Cyathophorum adiantum* that is characterised by having only unicellular teeth at the leaf margin. The original material of *Cyathophorum kurzianum* belongs also to this variant. The types of *Cyathophorum sublimbatum*, *Cyathophorum tonkinense*, *Cyathophorum japonicum* Broth. in Cardot, *Cyathophorella japonica*, and *Cyathophorella subspinosa* belong to the variant of *Cyathophorum adiantum* that is characterised by the presence of at least a few multicellular teeth at the leaf margin. The original material of *Cyathophorella serrulata* is intermediate between these two variants.

Description — 16. Entirely laterally compressed stems are probably teratological in *Cyathophorum adiantum*. A few laterally compressed stems were found in the original material of *Cyathophorella serrulata*, but these stems are either rotated near the base or near the apex or damaged at the apex suggesting that the plant was disturbed during its growth.

Hooker f. s.n. (NY) has rounded stems, but a few stems are occasionally somewhat quadrangular.

17. The lumen of narrow leaf cells contains frequently granulate, probably glutinous inclusions.

Reproduction — 18. Sporophytes are rare. They were found in Sikkim (*Decoly & Schaul, Bryoth. Levier 2571, 2571b, 265b, s.n.*), E Nepal (*Norkett 7953*), the Khasi Hills (*Griffith 221, 221 (511), 221.185 (511), s.n.* 'Assam'; *Hooker f. & Thomson 703*), Myanmar (*Kurz 3029*), and Thailand (*Touw 9198*). Griffith's numbered specimens are very probably duplicates of the same collection. *Decoly & Schaul Bryoth. Levier 2571, 2571b* may also be duplicates. The other collections from Sikkim and the Khasi Hills are possibly different samples from a single population.

Yamaguchi (2001) reported a fruiting specimen (as *Cyathophorella tonkinensis*) from Amami-oshima Island, Ryukyu Archipelago, Japan.

Distribution — 19. All the material from Malesia, presented as *Cyathophorum adiantum* or its synonyms, belongs to *Cyathophorum spinosum* (or else consists of misidentified specimens of other mosses).

Noguchi & Iwatsuki's (1972) record of *Cyathophorella adiantum* from Mt Kinabalu, Borneo, (*Iwatsuki 251428*) is based on a misidentification of a *Calyptrochaeta* species. Their records of *Cyathophorella tonkinensis* from this locality are also incorrect and are based on material of *Cyathophorum spinosum*.

Identification — 20. The differences between *Cyathophorum adiantum* and *C. spinosum* are discussed under the latter species, note 15, p. 318.

Other — 21. The descriptions and illustrations of *Cyathophorum adiantum* presented by Van den Bosch & Van der Sande Lacoste (1861) and Bartram (1939) refer to *C. spinosum* (see under the latter, notes 3 and 4, p. 316).

22. Motley's collection from Mt Megamendong, Java, which is preserved in Mitten's herbarium (NY) is a mixed collection, in which *Cyathophorum adiantum* is intermingled with *Cyathophorum hookerianum*. The collection contains the only specimen of *Cyathophorum adiantum* for which an origin in Malesia is claimed. It is virtually certain, that this collection is mislabelled, because the origin of *Cyathophorum hookerianum* in Malesia is also highly questionable (see under the latter

species, note 17, p. 347). The conclusion must be, that the collection comes from a locality outside Malesia, and presumably from continental SE Asia or, but then made by another collector, from northern India.

Selected specimens (from 271 examined):

NEPAL: Bagmati: *Long 22273* (E p.p.), Sheopuri Lake–Mulkharka. – Kosi: *Norkett 7953* (BM), Sanghu Downs. – Mechi: *Long 17302 a* (E p.p.), Dobala Danda. — BHUTAN: *Griffith s.n.* (BM); *Griffith 102* (BM), *65* (NY), Tongsa; *Long 10761* (E), S of Shamgong; *Griffith 185 (509)* (NY), towards Balfai ('Bailfa'). — INDIA: *unknown collector[Beddome?] s.n.* (BM, s.loc.). – Uttar Pradesh ('Kumaun'). Dehra Dun: *Gollan 3683b* (BM, S), Mussooree ('Mussoorie'). – Sikkim: *Univ. Tokyo Bot. Exp. 307* (NICH), Tingling Bridge–Yoksam; *Long 23003-a* (E), Kabi. – Bengal Jalpaiguri. Darjeeling ('Sikkim'): *Decoly & Schaul, Bryoth. Levier 2571* (NY p.p., S, UPS), Karsiyang ('Kurseong'); *Hooker 704* (BM, NY p.p.), Mt Tonglu ('Tonglo'); *Long 23025* (E), Mungpoo. – Meghalaya. Khasi Hills: *Griffith 221* (BM; BM, also sub no. *511*; see note 1), *511* (RO, UPS; see note 1), *s.n.* (BM, 'Assam'); *Hooker f. & Thomson 701* (BM p.p., NY p.p.), Nongkhlao ('Nunklow'); *Hooker f. & Thomson 703* (BM, NY), Kollong Hill; *Hooker f. 704b* (BM, NY p.p.), Moflong; *Griffith 221.185* (BM, NY; both also sub no. *511*, see note 1), *unknown collector s.n.* (LISU), Maamloo; *Griffith 171 (508)* (BM p.p.), Moosmai; *Griffith s.n.* (NY), Cherrapunji ('Churra'). – Jaintia Hills: *Mann s.n.* (BM), Jakoroing Peak. – Mizoram. Lushai Hills: *Wenger s.n.* (BM). – Karnataka. Kodagu ('Coorg'): *Walker 314* (FH, NY), Tadiandamol Peak. – Tamil Nadu ('Madras'). Wynaad: *Bor 473* (BM), Chandanathode. — SRI LANKA ('CEYLON'): Central Prov.: *Thwaites CM 127* (NY, BM, W), *s.n.* (RO, S).

CHINA: Sichuan: *Hu 0857* (PE p.p.), Mt Jinfu. – Yunnan: *Zhu 57a* (PE), Hekou. – Guangxi: *Chen 25* (PE; JE, S, both sub *MSE 92*), Longzhou, De-ching-shan. – Guangdong: *Chen (05179)* (PE), Beijiang Co. – Hainan: *Chen s.n.* (PE), Mt Jiangfeng; *Lin & Zhang (BSC 10)* (PE), Bawangling. — JAPAN: Honshu. Mie Pref.: *Iwatsuki 3452* (NICH), Owase-shi, Kuki. – Wakayama Pref.: *Nakajima, MJ 807* (HIRO), Higashimuro-gun, Komorigawa.– Shikoku. Tokushima Pref. ('Awa'): *Okamura (317)* (FH p.p., S p.p.), *s.n.* (NY, S), Karei. – Kochi Pref. ('Tosa'): *Gôno 242* (FH p.p.); *Gôno s.n.* (UPS), *Okamura 673* (H p.p., NY), *s.n.* (JE p.p.), Mt Hônokawa; *Kamimura 5000* (NICH p.p., KUMAMOTO p.p.), Mt Yokogura; *Okamura 240* (H), Mt Imano. – Kyushu. Miyazaki Pref ('Hyûga Prov.'): *Noguchi & Hattori, MJ 4* (BM, L p.p.), Minaminaka-gun, Sakatani. — TAIWAN ('FORMOSA'): Tainan Co.: *Chiang 5663* (B), Ta-don shan. – Taoyuan Co.: *Lai & Lewis 0293* (NY), Mt Peitsatienshan. – Chiayi Co.: *Lin, BTE 10* (L), Fenchihu. – Taipei Co. ('Taihoku Prov.'): *Shimada 276* (NICH), Wulai ('Urai'); *Noguchi (6195)* (NICH), Hsinhsien? ('Rahau').

MYANMAR ('BURMA'): Karen State: *Kurz 3029* (BM; BM *s.n.*), Mt Nattaung ('Nattoung'). – Tenasserim: *Parish 121* (NY), Moulmein; *Fea, Bryoth. Levier 687* (BM, FH, PC), Dawna Range, Mulayit Toung ('Mont. Moolegit'). — THAILAND: Payap ('Chiang Mai'): *Touw 9198* (BR, EGR, GRO, L, NY), Doi (Mt) Chiang Dao; *Touw 9545* (BR, EGR, FH, GRO, L, NY), Doi (Mt) Inthanon. – Udawn ('Loei'): *Touw 11055* (L), Phu (Mt) Krading. – Rachasima ('Nakhon Ratchasima'): *Smitinand 8405 A* (L), *Touw 12096* (L), Khao Yai Nat. Park, Khao Khaeo ('Khio'). – Chanthaburi ('Krat'): *Kerr 435b* (BM), Chantabun River, Panom Tom ('Krat, Kao Kuap'). – Nakhon Si Thammarat: *Touw 11568* (L), Khao (Mt) Luang. — VIETNAM: *Acker 2* (HBG), 'Nien-San'. – Hoang Liên So'n: *Ninh 71 54* (EGR), Sa-Pâ. – Vinh Phu: *Eberhardt (952)* (S), *s.n.* (PC), *Demange s.n.* (PC), Tam Dao. – Ha Nam Ninh Prov. ('Ninh Binh'): *Pócs et al. 3010/o* (EGR), Cúc-Phuong Reserve. – Ha So'n Binh ('Hoa Binh'): *Pócs et al. 2371* (EGR), Mt Nui Cai.

DUBIOUS ORIGIN: *Motley s.n.* (NY p.p., "Java, M. Megamendong"; see note 22). — ORIGIN NOT GIVEN: *Griffith 179* (BM p.p.), *187* (NY p.p., also sub no. *508*; see note 1), *262* (BM p.p., also sub no. *29/125*).

7.5. Cyathophorum africanum Dixon — Fig. 54, 55; Map 25; Plate 4a, b

Cyathophorum africanum Dixon, Smithsonian Misc. Collect. 69(8) (1918) 5, pl. 1, f. 3 a–d. — *Cyathophorella africana* (Dixon) Broth. in Engler & Prantl, Nat. Pflanzenfam. ed. 2, 11 (1925) 278. — Type: *Dümmer 721* (BM holo), Uganda, Mukono, Kipayo, tree trunk in forest, alt. 4000 ft., March, 1914.

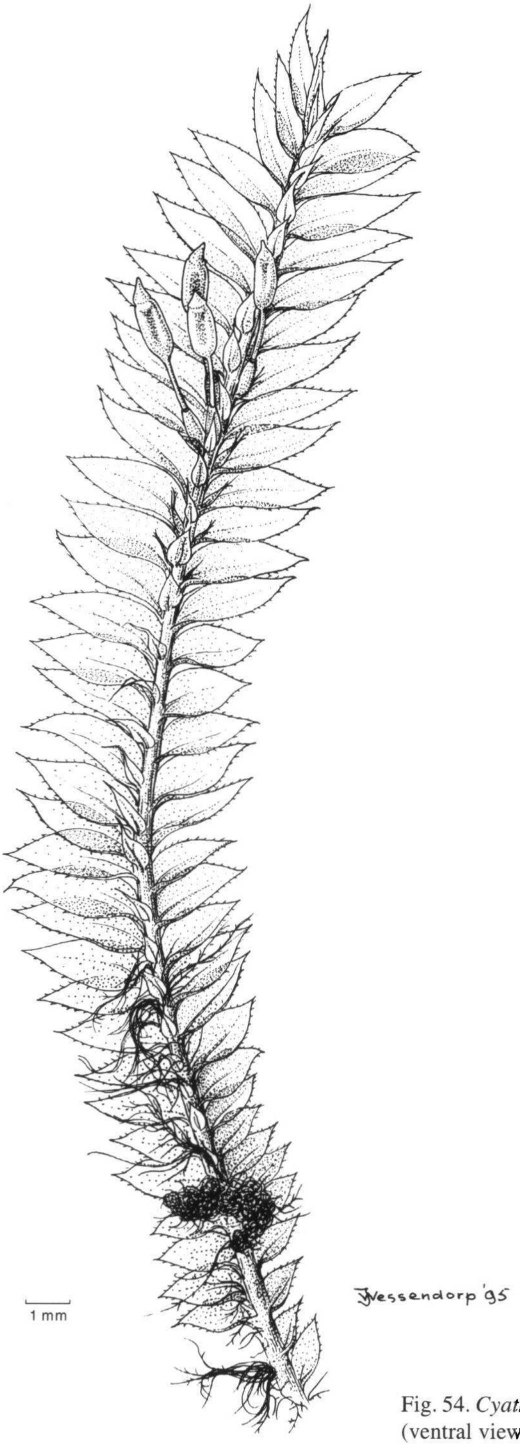


Fig. 54. *Cyathophorum africanum* Dixon. Habit (ventral view, ***Pocs & Harris 6158/B***, L).

Illustrations: Dixon, Smithsonian Misc. Collect. 69(8) (1918) pl. 1, f. 3a–d. — De Sloover, Bull Jard. Bot. Belg. 45 (1975) 319, f. 34–49. — Petit, Bull. Jard. Bot. Belg. 48 (1978) 167, f. 45.

Plants in groups of fans, medium sized, not gemmiferous. *Stems* up to 4.5 cm tall, terete, usually entirely dorsiventrally compressed, occasionally laterally compressed below and dorsiventrally compressed in apical fifth, occasionally partly creeping, dark brown to brown in basal part, becoming green near apex, dull. *Primordia* naked or set with scaly leaves; scaly leaves broadly to narrowly triangular (to linear), margin entire. *Epidermis cells and cortical cells of stem* equally narrow or cortical ones wider (outer cortex) or narrower (inner cortex); walls thin or incrassate, colourless to dark brown; inclusions absent from epidermis cells and outer cortical cells, absent or present in inner cortical cells, tiny oil-like droplets or tiny amorphous crusts. *Central strand* present or absent (where replaced by a central cavity); cells narrow, walls brown, inclusions tiny to large yellow-brown oil-like droplets. *Axial cavities* frequently absent, occasionally central and interrupting central strand, containing inclusions; inclusions amorphous crusts or pale olivaceous-yellow to red oil-like droplets. *Axillary hairs* 2–7 per leaf, 2- or 3-celled, simple; basal cells 1 or 2, pale brown to brown; intermediate cells absent; terminal cell elliptic to short-linear-rectangular, 40–100 μm long and 13–21 μm wide, smooth. *Leaves* closely set, pale green to dark green, frequently slightly brown at base. *Basal leaves* broad-elliptic to ovate; apex gradually or abruptly acuminate. *Distal leaves* between stem base and stem apex similar in size, only becoming smaller when closer to stem apex; margin coarsely serrate in lateral leaves, weakly to moderately serrate in amphigastria; teeth 1–4-celled, predominantly unicellular in amphigastria, up to 115 μm long and projecting up to 2 cells in lateral leaves, up to 70 μm long and projecting up to 2/3 of cell length in amphigastria; border faint to distinct, but absent or faint near leaf base and faint in distal part, in amphigastria absent from acumen, interrupted, up to 4 cells wide; laminal cells 40–120 μm long and 15–25 μm wide, generally longer and wider in amphigastria than in lateral leaves. *Distal lateral leaves* ovate to oblong, 2.5–4.1 mm long and 0.9–2.0 mm wide; *apex* acute or gradually acuminate; acumen 0.2–0.7 mm long; costa reaching 1/3–2/3 of leaf length. *Distal amphigastria* erecto-patent, ovate to ovate-oblong, occasionally somewhat narrowly triangular, 0.5–1.6 mm long and 0.4–0.8 mm wide; basal part smoothly curved; insertion concave; apex usually gradually or abruptly acuminate, occasionally somewhat acute; acumen 0.6–1.2 mm long; costa distinct, reaching 2/3 of amphigastrium length to faintly percurrent.

Autoicous (or *heteroicous*). *Gametoecia* usually unisexual, rarely bisexual, in middle and distal part of stem; perigonia placed below perichaetia. *Leaves* triangular to ovate-oblong; *margin* entire or weakly serrate in acumen; *border* faint to distinct, often less pronounced at shoulders and acumen; *costa* absent or faint, reaching 1/3–1/2 of leaf length. *Inner leaves*: of perigonia up to 0.8 mm long and 0.3 mm wide, acumen up to 0.8 mm long; of perichaetia prior to sporophyte development up to 0.5 mm long and 0.3 mm wide, acumen up to 0.4 mm long; of full-grown perichaetia up to 0.5 mm long and 0.5 mm wide, acumen up to 0.4 mm long. *Antheridia* 0.3–0.4 mm long. *Stalk in full-grown perichaetia* 0.1–0.3 mm long. *Archegonia* 0.3–0.4 mm long. *Vaginula* 0.5–0.8 mm long. *Gametoecial axillary hairs* 1–5 per gametoecial leaf, 3- (or 4-)celled,

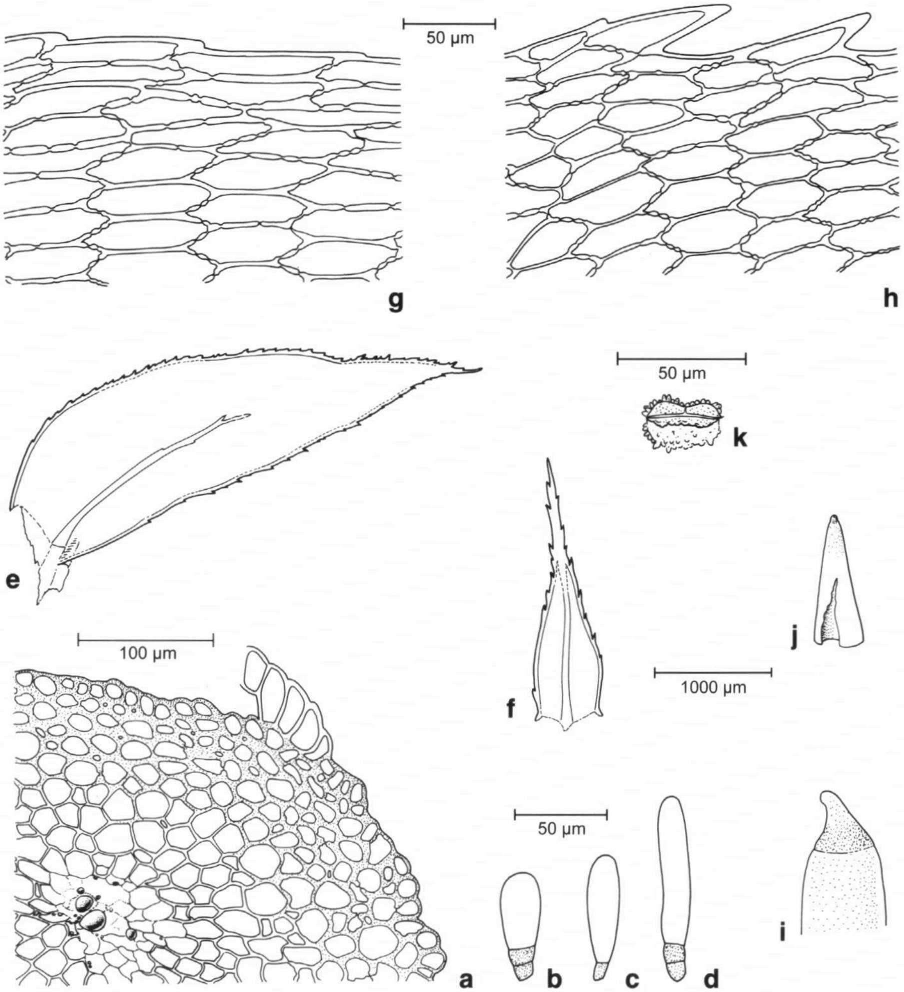
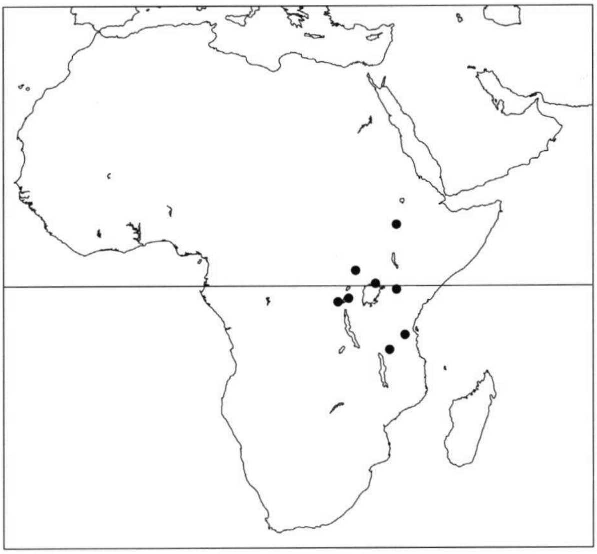


Fig. 55. *Cyathophorum africanum* Dixon. a. Rachis (cross section dorsal quadrant with central cavity in process of formation); b–d. axillary hairs; e, f. leaves (e. lateral, f. amphigastrium); g, h. leaf cells of lateral leaf (g. basal part of antical side, h. distal part of antical side); i. operculum; j. calyptra; k. exostome tooth (cross section) (a, e–k: *Pocs & Harris 6158/B*, L; b–d: *Crosby & Pócs 8711*, L).

simple; basal cells 2 (or 3), brown; intermediate cells absent; terminal cell oblong-elliptic or oblong-obovate to short-linear-rectangular, 50–105 µm long and 12–30 µm wide, smooth. *Paraphyses* absent.

Sporophytes up to 7 per stem. *Seta* 1.2–2.0 mm long, pale or dark yellowish white. *Capsule* ellipsoid or barrel-shaped to oblong-ovoid, 0.8–1.6 mm long and 0.5–0.8 mm wide, pale green to green when young, becoming pale yellow to pale ochraceous, frequently slightly tinged red; annulus distinct, partly indistinct, or partly absent (see note 1). *Peristomial formula [OPL3:OPL2:]OPL:PPL:IPL* = [(4:)4:]4:2:(3–)4c (see



Map 25. Distribution of *Cyathophorum africanum* Dixon.

note 2). ***Preperistome*** rudimentary, consisting of 1 (or 2) whorl(s) of irregulary shaped, papillose cell plates at dorsal base of exostome. ***Rudimentary teeth between IPL and outer endothecial layer*** few in number. ***Exostome*** colourless to pale yellow; teeth 280–300 μm long and 20–30 μm wide; dorsal side (weakly to) moderately to coarsely papillose; median line not furrowed; dorsal plates (probably) broader than or equally wide as ventral ones, 2 μm thick; papillae low to high, broad, simple or branched; lamellae weakly projecting; ventral plates 4 μm thick at most, moderately papillose; papillae low to high, broad, simple or branched; trabeculae very short in basal fourth of teeth, short in distal part. ***Endostome*** weakly to coarsely papillose, colourless to pale yellow; papillae low, simple; basal membrane very low and not extending orifice; processes 235–285 μm long beyond orifice and 10–20 μm wide at base, not keeled, weakly nodulose or not, occasionally appendiculate with a few lateral appendages consisting of parts of a single or a few cells; papillae low to high, simple or branched; cilia absent or rudimentary and consisting of parts of a single cell, 1 cell plate wide. ***Operculum*** short-rostrate, 0.2–0.5 mm long, ochraceous; rostrum oblique. ***Calyptra*** cucullate, completely covering operculum, 0.6–1.0 mm long, pale ochraceous, membranous; margin entire. ***Spores*** 12–19 μm.

Distribution — Ethiopia, Uganda, Kenya, Tanzania, Rwanda, Democratic Republic of Congo (Haut-Zaire, Kivu).

Habitat & Ecology — In wet, submountainous, and mountainous rain forests. On tree bases, tree trunks, and rocks, especially near streams; also on branches, litter, and soil. Altitude: 1330–2500 m.

Geographical variation — Not found.

Ecological variation — Not found; insufficient data.

Notes:

Description — 1. The annulus is a ring of differentiated cells between the capsule urn and the operculum, which is 1 cell wide where the annulus is distinct and 2 or 3 cells wide where it is indistinct.

A distinct annulus or distinct part of an annulus consists of a ring of cells, which possesses slightly thicker radial walls and are about half as wide as the adjacent cells of the capsule urn and the operculum. Such annular cells are in majority rectangular and 2–4 times longer than wide. If and where an annulus is less differentiated, the annular cells are usually much shorter, and often become quadrate or transverse-rectangular. Radial walls of such short cells are hardly thicker than in cells of the capsule urn and the operculum.

The capsule opens with the dehiscence of the operculum. Dehiscence occurs, when the basal cells of the operculum become detached from the (distal) annulus cells. As a result of this process, the annulus remains attached to the capsule urn, although it in turn may eventually become detached from the capsule urn.

2. In the type of *Cyathophorum africanum* Dixon (1918) found only two sporophytes with a peristome in a good condition and he erroneously described the peristome as having only a single row of teeth: the exostome. Dixon was probably confused by the close similarities between the exostome and endostome in *C. africanum*, for the sporophytes concerned here clearly possess a double peristome. In addition, he described one of the two peristomes in good condition as entirely, densely, and coarsely papillose, while the other was absolutely smooth. Examination of the peristomes of the type showed, that the ornamentation of most peristomes is moderately to densely and coarsely papillose. In only a single peristome, where was the ornamentation difficult to observe, did it prove to be weakly to moderately papillose. Smooth peristomes were not found.

3. Despite the large number of sporophytes of *Cyathophorum africanum* observed in the material examined, a few mature calyptrae were found in only a single specimen (*Pócs & Harris 6158/B*, EGR). A few immature calyptrae were found twice (*Pócs & Harris 6158/B*, EGR; *Crosby & Pócs 8711*, L).

Whittemore & Allen (1989) described the calyptra of *Cyathophorella africana* as mitrate, but the calyptrae found here were clearly cucullate.

Reproduction — 4. In *Cyathophorum africanum* fruiting specimens commonly occur. Almost every plant examined bears a few sporophytes.

Distribution — 5. *Cyathophorum africanum* is apparently not restricted to the old crystalline massives of East Africa, but occurs also on volcanic mountains like the Aberdare Ra., Kenya. Surprisingly, the species is not known from Mt Kilimanjaro, Tanzania.

Identification — 6. *Cyathophorum africanum* is the only species in the Hypopterygiaceae with a short-rostrate operculum. Its operculum measures 0.5 mm at most, including the rostrum, whereas the operculum is at least 0.6 mm long in the other species of the Hypopterygiaceae, and at least 0.7 mm long in other *Cyathophorum* species.

The exostome teeth and the processes of *Cyathophorum africanum* are the narrowest among the Hypopterygiaceae. The exostome teeth are 20–30 μm and the processes 10–20 μm wide. In *Lopidium struthiopteris* the processes are also very narrow, measuring 15–25 μm in width, but the exostome teeth are considerably broader and 50–60 μm wide. There is a very weak overlap in width with the processes of *C. adiantum*, where the exostome teeth are 30–65 μm wide and the processes 19–30 μm wide. In the other Hypopterygiaceae, including the other *Cyathophorum* species, the exostome teeth are at least 35 μm wide and the processes at least 25 μm wide.

Cyathophorum africanum has also the shortest exostome teeth among the Hypopterygiaceae. Its teeth are up to 300 μm long, whereas they are at least 300 μm long in the other species.

Cyathophorum africanum differs most substantially from its closest allies *C. hookerianum* and *C. parvifolium* in its autoicous sexuality and the partly present central cavity in the stem. The other two species are dioicous, and lack stem cavities.

In addition, *Cyathophorum africanum* can usually be distinguished from the two other species by its distinctly costate amphigastria, reaching at least 2/3 of the length of the amphigastrium, its short gametoecial leaves, and its relatively short capsule. In the other two species an amphigastrium costa is either absent, faint, or, less often, distinct. When present, their costa usually reaches up to 1/2 of the length of the amphigastrium, but it is occasionally percurrent.

In *Cyathophorum africanum* the inner gametoecial leaves (acumen excluded) are never longer than 0.8 mm, whereas those of *C. hookerianum* and *C. parvifolium* are often much longer.

Specimens examined (28 in number):

ETHIOPIA: Wollega Prov.: *Bazzacco s.n.* (EGR), Argio. — UGANDA: Mukono: *Dümmer 721* (BM), Kipayo. — KENYA: Central Prov.: *Stedborg? 1490b* (BR), Aberdare Ra. — TANZANIA: Morogoro Prov: *Pócs 6966/B* (EGR), *Crosby & Pócs 8711* (L), *8713* (L), *Pócs et al. 6854/D* (EGR, GRO, L), *Pócs & Harris CE 4771 (6158/B)* (BM, BR, EGR, L), Uluguru Mts, Morogoro; *Pócs & Mwanjabe 6558/F* (EGR), Tangeni, Mlulu Valley. - Southern Highlands: *Jones et al. 6318/AA* (EGR), Mufundi Escarpment, Lupeme Estate; *Pócs & Jones 6321/E* (EGR), Mufundi Scarp Forest Reserve, Kilima Tea Factory. — RWANDA: Edward and Kivu Lakes Distr.: *De Sloover 18678* (BM, BR, EGR, LISU), Gisenyi ('Kisenyi') Pref., Valley of the Bikoneko. — DEMOCRATIC REPUBLIC OF CONGO (ZAIRE): Haut-Zaire: *Leroy 30E* (BR), Nioka. - Kivu Prov.: *Pócs 6553* (EGR), *6572* (EGR), *7284* (EGR), *7095* (EGR), *7830* (EGR), *7849* (EGR), Kahuzi-Biega Nat. Park.

7.6. **Cyathophorum hookerianum** (Griff.) Mitt. — Fig. 56, 58B, 59B; Map 26; Plate 4e, f

Cyathophorum hookerianum (Griff.) Mitt., Proc. J. Linn. Soc., Bot., Suppl. 1 (1859) 147. — *Neckera hookeriana* Griff., Notul. Pl. As. 2 (1849) 464; Icon. Pl. As. 2 (1849) pl. 84, f. 2–2a. — *Cyathophorella hookeriana* (Griff.) M. Fleisch., Musc. Buitenzorg 3 (1908) 1094. — *Cyathophorum hookeri* Griff. ex Kindb., Enum. Bryin. Exot. (1888) 10, nom. illeg., incl. spec. prior. — *Cyathophorella hookeri* Herzog, Geographie der Moose (1926) 343, err. pro *Cyathophorella hookeriana* (Griff.) M. Fleisch. — Types: *Griffith, It. Ass. 577* (type not found, see note 1), India, Assam; *Griffith s.n.* (NY lecto p.p., designated here, labelled "Fruct. *Neckera hookeriana* Griff!"; see note 1).

Cyathophorum intermedium Mitt., J. Proc. Linn. Soc., Bot., Suppl. 1 (1859) 148, syn. nov. — *Cyathophorella intermedia* (Mitt.) Broth. in Engler & Prantl, Nat. Pflanzenfam. ed. 2, 11 (1925) 277. — *Dendrocyathophorum intermedium* (Mitt.) Herzog in Herzog & Nog., J. Hattori Bot. Lab. 14 (1955) 65, quod nom.; see note 3. — Type: *Strachey & Winterbottom 70* (NY holo; BM), India, Uttar Pradesh, NW Himalaya, Kumaun; see notes 2, 3 and 5.

Cyathophorum philippinense Broth., Leafl. Philipp. Bot. 2 (1909) 657. — *Cyathophorella philippinense* (Broth.) E.B. Bartram, Philipp. J. Sci. 68 (1939) 427, nom. inval. in syn. — Type: *Elmer 8544* (H holo, n.v.; BM, FH, GRO, L, S), Philippines, Luzon, Benguet Prov., Baguio, March, 1907. — The isotypes in FH, GRO, and S are dated January; an isotype in BM is dated February. — Synonymised with *Cyathophorella hookeriana* (Griff.) M. Fleisch. by Bartram, Philipp. J. Sci. 68 (1939) 282; see note 6.

Cyathophorum burkillii Dixon, Rec. Bot. Surv. India 6 (1914) 67, pl. 1 f. 1, pl. 2 f. 9, syn. nov. — *Cyathophorella burkillii* (Dixon) Broth. in Engler & Prantl, Nat. Pflanzenfam. ed. 2, 11 (1925) 278.— Type: *Burkill 37737* (BM holo), India, Arunachal Pradesh, Siang Frontier Div. ["Assam, Abor Distr."], hill south of the Rebang, alt. 2800 ft, "moss near the ground in deep forest - on a trunk -, grows horizontally", Jan. 8, 1912; see notes 4 and 7.

Cyathophorella densifolia Horik., Bot. Mag. (Tokyo) 48 (1934) 460, f. 3. — Type: *Horikawa s.n.* (holo n.v., absent from HIRO), Taiwan ["Formosa"], Taitung Co. ["Taitô Prov."], Chinshui ["Shinsuiei"], Jan. 3, 1933. — Although it is not known where the type is preserved, it may still be in existence, for it was examined by Noguchi, J. Hattori Bot. Lab. 7: 20. 1952. — Synonymised with *C. hookeriana* (Griff.) M. Fleisch. by Noguchi, J. Hattori Bot. Lab. 7: 18. 1952. — See note 8.

Cyathophorella kyusyuensis Horik. & Nog. in Nog., J. Sci. Hiroshima Univ., Ser. B, Div. 2, Bot. 3 (1936) 25 pl. 2, syn. nov. — *Cyathophorella kyushuensis* Horik. & Nog. ex Nog., Moss Flora of Japan 4 (1991) 771, nom. inval., orthogr. err. pro *Cyathophorella kyusyuensis* Horik. & Nog. — Type: *Noguchi 236* (HIRO holo, KUMAMOTO; NICH, 'Aug. 3, 1931'), Japan, Kyushu, Miyazaki Pref. ["Hyûga Prov."], Mt Aoidake, on bark, Aug. 8, 1931. — A specimen in JE, which was found by Noguchi in the same locality growing on bark, is presumably wrongly labelled and may also be an isotype. This specimen is labelled with the number *256* and its collection date is given as Aug. 8, 1929. The specimen comes from Noguchi's herbarium, but there is no original specimen in this herbarium that is similarly labelled. — See note 9.

Cyathophorella grandistipulacea Dixon & Sakurai in Sakurai, Bot. Mag. (Tokyo) 50 (1936) 519, f. 7, '*Cyatophorella grandistiipulacea*', syn. nov. — *Cyathophorella kyusyuensis* Horik. & Nog. in Nog. var. *grandistipulacea* (Dixon & Sakurai) Nog., J. Hattori Bot. Lab. 7 (1952) 18. Type: *Kaneda 7025* (MAKINO holo, sub no. *7025*, and labelled "*Kaneda 192*"; BM, TNS n.v.), Japan, Kyushu, Kumamoto Pref. ["Higo Prov."], Mt Ichibusa, on rotten wood, Jul. 25, (19)35. — See note 9.

Cyathophorella anisodon Dixon & Herzog in Herzog, Ann. Bryol. 12 (1939) 92, syn. nov. — Syntypes: *Kerstan 13/c ["13 a"]* (JE lecto, designated here; BM), India, Bengal Jalpaiguri ["Sikkim Himalaya"], Darjeeling, Nov., 1935; *Troll s.n.* (JE sub no. *91*), India, Sikkim, alt. 3600–3900 m, "An der Waldgrenze mit *Abies densa* u. *Rhododendron*", ["Tsomgo Lake, zwischen Gangtok und Natu La"], Aug., (19)37. — See note 10.

?: *Cyathophorella taiwaniana* M.J.Lai, Taiwania 21 (1976) 152 pl. 1. — Type: *Lai 333* (TAI holo n.v., see note 11), Taiwan, Chiayi Co., Mt Alishan, Oct. 14, 1970.

Cyathophorum marginatum Wilson ex Mitt., J. Proc. Linn. Soc., Bot., Suppl. 1 (1859) 147, nom. nud. in syn. — Original material: *Hooker f. & Thomson 701* (BM p.p., NY p.p.), India, Meghalaya, Khasi Hills, Nongkhlao ["Nunklow"], alt. 4000 ft, "regio subtrop.".

Cyathophorella subpilifera (Hampe ex M. Fleisch.) M. Fleisch., Hedwigia 63 (1922) 212, nom. nud., syn. nov. —*Cyathophorum subpiliferum* Hampe ex M. Fleisch. l.c., nom. nud. in syn. Original material: *unknown collector s.n.* (BM), Myanmar (Burma), Karen State, Karen Hills, Mt Nattaung ('Nattoung'), alt. 7000 ft. — See note 12.

Cyathophorella rigidula P.C. Chen in Chen et al., Gen. Musc. Sin. 2 (1978) 135, nom. nud. in syn. — Original material: *Chen 1575* (PE), China, Sichuan, Mt Jinfu, Apr. 9, (19)35; see note 13.

Illustrations: Griffith, Icon. Pl. As. 2 (1849) pl. 84 f. 2–2a. — Dixon, Rec. Bot. Surv. India 6 (1914) pl. 1 f. 1, pl. 2 f. 9. — Horikawa, Bot. Mag. (Tokyo) 48 (1934) 460, f. 3. — Noguchi, J. Sci. Hiroshima Univ., Ser. B, Div. 2, Bot. 3 (1936) pl. 2. — Sakurai, Bot. Mag. (Tokyo) 50 (1936) 519, f. 7. — Bartram, Philipp. J. Sci. 68 (1939) pl. 21 f. 360. — Noguchi, J. Hattori Bot. Lab. 7 (1952) 19, f. 12; 21, f. 13. — Sakurai, Muscol. Jap. (1954) pl. 42 e & i (specimen depicted with rather short lateral leaves and slender foliated stems). — Van der Wijk, Acta Bot. Neerl. 6 (1957) f. 5c. — Iwatsuki & Mizutani, Coloured Illustr. Bryoph. Japan (1972) pl. 25 f. 364. — Lai, Taiwania 21 (1976) 153, pl. 1. — Gangulee, Mosses of Eastern India (1977) f. 768, f. 770–771, f. 772 1–2. — Chen et al., Gen. Musc. Sin. 2 (1978) f. 275. — Lin P.J. & Li Z.H.(?), in: Li et al., Bryoflora of Xizang (1985) pl. 124, f. 1–5. — Mohamed & Robinson, Smithsonian Contr. Bot. 80 (1991) f. 99–109, f. 110–121. — Noguchi, Moss Flora of Japan 4 (1991) f. 339.B, 341.

Plants in groups of fans or growing intermingled with other (epiphytic) bryophytes, usually small to medium sized, occasionally large and slightly robust, frequently gemmiferous. *Stems* up to 5.0 cm tall, terete, usually entirely dorsiventrally compressed, occasionally laterally compressed in basal and middle part, occasionally partly creeping, dark brown to brown in basal part, becoming green in distal part, dull. *Primordia* naked. *Epidermis cells and cortical cells of stem* equally narrow or cortical ones wider (inner cortex) or narrower (outer cortex); walls thin or incrassate, yellow to dark brown; inclusions absent from epidermis cells and outer cortical cells, usually absent but occasionally present in inner cortical cells, tiny oil-like droplets. *Central strand* present; cells narrow, walls colourless to brown, inclusions absent. *Axial cavities* absent. *Axillary hairs* (0–)1–4 per leaf, 2–5-celled, simple; basal cells 1–2(–4), pale brown to brown; intermediate cells absent; terminal cell usually circular to elliptic, rarely transverse-elliptic, 16–46 μm long and 12–36 μm wide, usually smooth to densely verrucose, occasionally somewhat striate. *Leaves* distant to closely set, usually pale

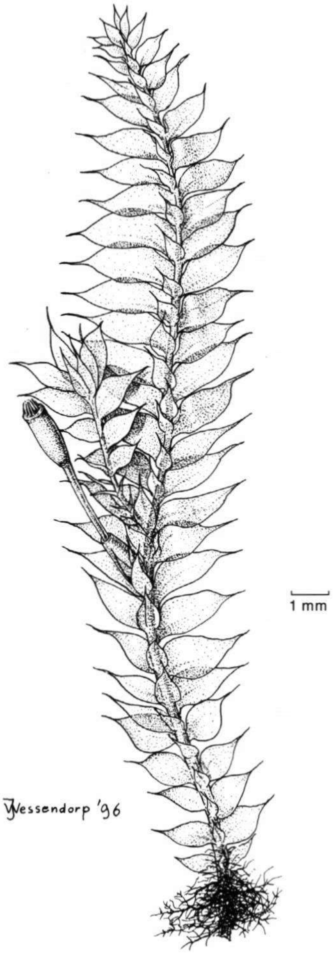
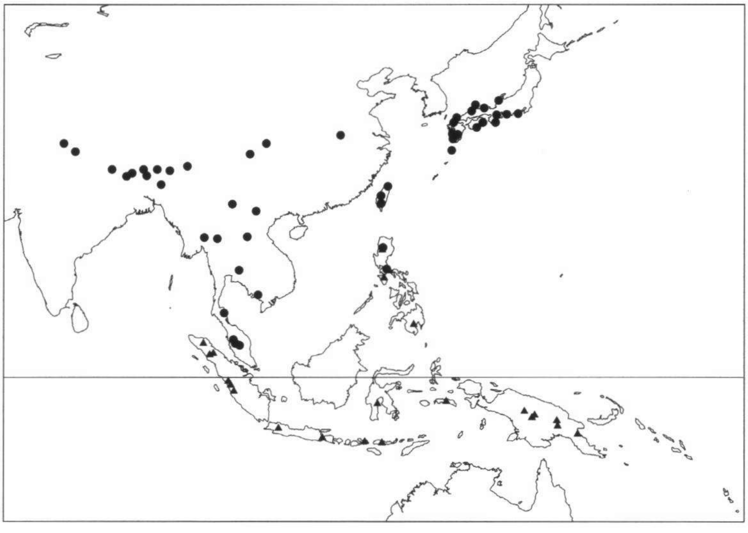


Fig. 56. *Cyathophorum hookerianum* (Griff.) Mitt. Habit (ventral view, *Boele & Boeken 81.03.2586*, GRO).

yellowish green to dark green, rarely nearly colourless. *Lateral leaves and amphigastria* concolourous. *Basal leaves* short-elliptic to ovate-lanceolate; apex acute to gradually acuminate. *Distal leaves* generally much smaller when located in gemmiferous stem parts than when located in non-gemmiferous stem parts; margin usually weakly to coarsely serrate, rarely entire in lateral leaves, occasionally dentate, crenulate or duplicate crenulate in amphigastria, serrate in basal leaves of gemmiferous stem parts, becoming entire in distal ones; teeth unicellular, up to 80 µm long in lateral leaves and up to 20 (–60) µm long in amphigastria, usually projecting up to 1/2 of cell length in lateral leaves and 1/4 of cell length in amphigastria, rarely projecting an entire cell; border absent, faint, or distinct, but faint near leaf base and frequently becoming less pronounced in apical third, continuous or interrupted, up to 4 cells wide; laminal cells 40–160 µm long and 15–40 µm wide, generally longer and wider in amphigastria than in lateral leaves. *Distal lateral leaves* ovate to ovate-lanceolate, 1.1–5.1 mm long and 0.5–2.4 mm wide, in gemmiferous part of stem ovate-oblong to oblong; apex (abruptly or) gradually acuminate; acumen (0.1–)0.3–0.9 mm long; costa occasionally obsolete, reaching (1/10–)1/5–1/3(–1/2) of leaf length. *Distal amphigastria* appressed to patent, usually suborbicular or ovate to lanceolate, occasionally obovate in non-gemmiferous stem parts, occasionally short-linear in gemmiferous stem parts, 0.5–2.7 mm long and 0.2–2.0(–2.5) mm wide; basal part nearly plane or smoothly curved; insertion weakly convex to concave; apex (gradually or) abruptly acuminate; acumen 0.1–1.1 mm long; costa absent, faint, or distinct, usually reaching 1/5–1/3(–1/2) of amphigastrium length, occasionally percurrent. *Gemmae clusters* located in distal half to third of stem, placed in and above axils of leaves and amphigastria, reaching 1/5–2/3 of length of associated leaves. *Gemmaphores* penicillate, (1?–)4–12 cells long, colourless to brown. *Gemmae* simple, up to 20 cells long, colourless to brown, but then often colourless at both ends; cells 25–80 µm long and 15–45 µm wide.

Dioicous. *Gametoecia* in all stem parts; perigonia in middle or distal part of stem; perichaetia in basal or middle part. *Leaves* subcircular to elliptic, frequently becoming ovate-oblong to elliptic-lingulate in full-grown perichaetia; margin entire; border absent, faint, or distinct, up to 2 cells wide; costa absent, in full-grown perichaetial leaves absent, faint or distinct, reaching up to 1/2 of leaf length. *Inner leaves*: of perigonia to 1.5 mm long and 0.9 mm wide, acumen up to 0.5 mm long; of perichaetia prior to sporophyte development up to 1.0 mm long and 0.5 mm wide, acumen up to 0.5–0.8 mm long; of full-grown perichaetia up to 1.7 mm long and 1.1 mm wide, acumen up to 1.1 mm long. *Antheridia* 0.3–0.6 mm long. *Stalk in full-grown perichaetia* 0.1–0.8 mm long. *Archegonia* 0.4–0.8 mm long. *Vaginula* 0.9–1.5 mm long. *Gametoecial axillary hairs* c. 1 per gametoecial leaf, 2-celled, simple; basal cell 1, colourless to brown; intermediate cells absent; terminal cell subglobose to elliptic, 15–35 µm long and 14–25 µm wide, smooth. *Paraphyses* absent.

Sporophytes up to 4 per stem. *Seta* 2.0–6.6 mm long, white to ochraceous, smooth or slightly mamillate in distal fourth. *Capsule* usually cylindrical-ellipsoid to cylindrical, occasionally slightly ovoid, 0.7–3.1 mm long and 0.3–1.0 mm wide, pale yellow to brown, occasionally tinged with red; annulus absent. *Peristomial formula OPL: PPL:IPL* = 4:2:4–6c. *Exostome* pale yellow to dark brown; teeth 300–660 µm long and 45–70 µm wide; dorsal side weakly to coarsely papilose, but occasionally weakly striate in basal fourth of teeth (see note 14); median line not furrowed; dorsal plates broader than or equally wide as ventral ones, 3–17 µm thick; papillae high on basal dorsal plates, low or high on distal ones, simple or branched; lamellae not projecting or distinctly projecting in basal fourth of teeth; ventral plates 4–7 µm thick, weakly to moderately papillose; papillae low to high, simple; trabeculae very short in basal fourth of teeth, short to pronounced above (see note 14). *Endostome* colourless to pale yellow, weakly to coarsely papillose at both faces (see note 14); papillae low to high, simple; basal membrane reaching 1/8–1/4 of length of exostome teeth; processes projecting 360–480 µm beyond orifice and 25–45 µm wide at base, weakly or distinctly keeled, weakly nodulose or not, usually lacking lateral appendages, occasion-



Map 26. Distribution of *Cyathophorum hookerianum* (Griff.) Mitt. (●) and *C. parvifolium* Bosch & Sande Lac. (▲).

ally containing a few lateral appendages consisting of parts of a single cell; cilia absent or rudimentary and consisting of parts of 1 or 2 cells, 1 or 2 cell plates wide. *Operculum* long-rostrate, 0.8–1.7 mm long, pale yellow to brown; rostrum straight to oblique. *Calyptra* mitrate to cucullate, partly to completely covering operculum, 1.0–2.0 mm long, nearly white, membraneous; margin nearly entire to weakly sinuate or provided with a few incisions of irregular depth. *Spores* 10–23 µm.

Distribution — Nepal, Bhutan, India (Uttar Pradesh, Sikkim, Arunachal Pradesh, Meghalaya), China (Sichuan, Yunnan, Guizhou, Anhui), Japan (Honshu, Shikoku, Kyushu), Taiwan, Myanmar, Thailand, Cambodia, Laos, Vietnam, Philippines (Luzon), Malaysia (Peninsular Malaysia: Perak, Pahang; Sarawak), ?: Indonesia (Java). Also reported from the Chinese provinces of Zhejiang (Hu Renliang & Wang Youfang, 1987), Fujan, and Hunan (Koponen et al., 2000).

Habitat & Ecology — In evergreen forests. Usually on twigs and tree trunks; very rare on woody grass stems and litter. Often on rocks in Japan, once found on rocks outside Japan. Altitude: 900–2450 m; in China: 600–1980 m, and Japan (Honshu): 160–300 m.

Ecological variation — Two morphological variants of *Cyathophorum hookerianum* can be recognised, and they generally grow under different macro-ecological conditions. One variant generally prefers a warm-temperate environment, the other a more tropical one and mainly occurs in humid – riverine and mountainous – monsoon forests, but considerable overlap in distribution between the two variants exists.

The plants that belong to the monsoon variant are generally taller and are slightly more robust with stems up to 5.0 cm tall. They grow in more or less open groups with often a fan-like appearance. The plants are straight or only slightly curved in the gemmiferous parts. They have also more distantly foliated stems and show at least distant leaves when dry material is observed. The leaves are up to 5.1 mm long, and usually gradually acuminate (occasionally abruptly acuminate). The leaf border is faint to distinct, is usually continuous, and reaches the acumen. However, in very acuminate leaves, the border may occasionally be obsolete and interrupted in the distal half of the leaf. The amphigastria at the base of gemmiferous stem parts are ovate and occasionally elliptic. The gemmaphores, usually placed in the axils of leaves and amphigastria, and only occasionally scattered along the stem, are 4–12 cells long and bear lateral and terminal gemmae. The terminal cells of the axillary hairs are (19–)28–46 µm long and (14–)17–36 µm wide.

The plants that belong to the warm-temperate variant are small to medium sized. The stems are up to 3.0(–4.3) cm tall and are curved to falcate. They grow in dense, cushion-like groups. The leaves are closely set (when dry) and are generally shorter, being 3.5 mm long at most. The leaves are usually abruptly and sometimes gradually acuminate. They have in majority a faint border that reaches the acumen. In some leaves the border possesses distinct traces, whereas in others the border may be interrupted or even absent in the distal third of the leaf, especially at the antical side of the leaf. The amphigastria at the base of gemmiferous stem parts are subcircular to elliptic. The gemmaphores, only placed in the axils of leaves and amphigastria, are 2–5 cells long and bear terminal gemmae. The terminal cells of the axillary hairs are (16–)20–29 µm long and (12–)17–24 µm wide.

Because there is considerable overlap between the features that characterise the two ecological variants, the variants are not sharply defined, and no nomenclatural status is required.

The monsoon variant occurs in tropical to warm-temperate eastern Asia and the eastern Himalayas. It grows generally at lower altitudes than the warm-temperate variant: between 600–2450 m in tropical Eastern Asia, China, and Taiwan, and between 160–300 m in Japan, but it was once found at 3000 m in the Himalayas. The monsoon variant is less abundant in the warm-temperate regions in the distribution area of the species than the warm-temperate variant.

The warm-temperate variant occurs in warm-temperate Sino Japan and the Northwestern Himalayas. It is very abundant in Japan, but it is absent from tropical, continental SE Asia. In its typical form, it was once found in Luzon (*Boeken 81.3.2497c*), where the monsoon variant (e.g. *Boeken 81.03.2586*, *Williams 1671*) and intermediates between the two variants also occur (e.g. *Van Zanten 684036g*). The warm-temperate variant grows between 2000–3900 m altitude in the Himalayas, where it may occur up to the tree line, and between 40–950 m altitude in Japan. In China and Taiwan the warm-temperate variant has roughly the same altitudinal distribution as the tropical variant.

The warm-temperate variant seems to grow slightly more frequently on rotten log or soil than the monsoon variant, but the ecological data are insufficient to confirm this.

Noguchi (1952) surmised that the development of the leaf border is related to humidity. He reported that plants from Southern Japan, especially those found in arid places, have well developed leaf borders, which are also often coloured pale yellow to yellow. However, the ecological information is insufficient to support a correlation between the development of the leaf border and humidity.

In four locations both variants occur together: Mt Emei in Sichuan, China, Mewa Khola Gorge in E Nepal, Tsuifeng in Taiwan, and Mt Data in Luzon. In two collections the two variants are even mixed. *Lin, BTE 61* (NICH), Taiwan, contains a male plant that belongs to the monsoon variant, and a non-fruiting female plant that belongs to the warm-temperate variant. In *Norkett 9356* (BM), E Nepal, the two variants are mixed with a local variant known from Sikkim and Nepal (see geographical variation).

Geographical variation — Plants from China, Taiwan, and Japan that belong to the monsoon variant frequently have very gradually acuminate leaves that possess a very faint and interrupted border in the apical half of the leaf.

A local variant that is somewhat intermediate between the monsoon and the warm-temperate variant of *Cyathophorum hookerianum* occurs in the Eastern Himalayas between 2000–2750 m altitude. Several plants from E Nepal and Sikkim have distant to closely set leaves, which are gradually acuminate, and are continuously and distinctly bordered. The border is 2 or 3 cells wide. The plants most closely resemble the monsoon variant of *C. hookerianum*, but the terminal cells of the axillary hairs are generally smaller, and in this respect they resemble the warm-temperate variant. The local variant differs generally from both widely distributed variants by its longer gemmaphores, which are 8–12 cells long, and the relatively short gemmae, which are 6–10 cells long. In the monsoon variant the gemmaphores are 4–9 cells long, and the gemmae

6–19 cells long, whereas they are, respectively, 2–5 and 7–21 cells long in the warm-temperate variant. Because overlap exists in all features states, the local variant is not sharply defined, and no nomenclatural status is required. To this local variant belong: *Norkett 9356* (BM, mixed with the warm-temperate variant and the monsoon variant), *9424A* (BM), *Decoly & Schaul, Bryoth. Levier s.n.* (S p.p.), *Decoly & Schaul s.n.* (FH), *unknown collector 1141* (NY), *unknown collector s.n.* (BM, labelled "*Neckera hookeriana* Griff. Mss. Not in It. Musc. Assam."), and the sterile plants of the collections that were made by *Griffith* or probably so (see note 1).

The Himalayan plants that belong to the warm-temperate variant of *Cyathophorum hookerianum* are generally larger, and show slightly more developed features than the plants of this variant from China, Taiwan, and Japan. The stem of the Himalayan plants is up to 3.0(–3.9) cm tall. The leaves of the Himalayan plants have generally longer serrations, which project 15–55(–80) µm. The leaf costa is more distinct and somewhat longer, and the amphigastrium costa somewhat longer. The Sino Japanese plants have stems up to 2.1(–4.3) cm tall, and the serrations at the leaf margin project 4–40 µm.

Notes:

Typification and nomenclature — 1. The typification of *Neckera hookeriana* is problematic and the history and origin of Griffith's collections of *Cyathophorum hookerianum* is poorly known.

Griffith himself (1849a) referred to the type of *Neckera hookeriana* with "*It. Ass. 577*", but none of the collections he made, or is presumed to have made, have such a label. Presumably, the type material must be found among other material of this species that was collected by Griffith.

Mitten (1859) cited material of *Cyathophorum hookerianum* collected by Griffith in the Khasi Hills, but gave neither collection numbers nor any other information.

I found four candidates for types in BM and NY, viz. *Griffith 171 (508)* (Hooker's herbarium, BM) from Moosmai, Khasi Hills, in agreement with Mitten (1859), *Griffith 187* (Mitten's herbarium, NY), of unknown origin, and *Griffith? 187* (Griffith's herbarium, BM), also of unknown origin. Although the label of the last lacks a collector's name and is only provided with the number *187*, the specimen was probably collected by Griffith. The fourth candidate is a collection labelled "Fruct. *Neckera hookeriana* Griff!" in Mitten's herbarium (NY), without any indication of collector or place of origin.

Mohamed & Robinson (1991) cited the collection from Griffith's herbarium (BM), labelled *187*, as the type of *Cyathophorella hookeriana*, but without stating what kind of type. As stated above, this collection lacks a collector's name but Mohamed & Robinson (1991), who did not leave their own label, called it *Griffith 187*. It is referred to as *Griffith? 187* in the present work.

In my opinion, Mohamed & Robinson's choice for the typification of *Neckera hookeriana* cannot be right, as it is not in accordance with Griffith's (1849b) illustrations. He depicted a plant with a creeping stem base, a gemmiferous stem apex, amphigastria with nearly recurved apices, two immature perichaetia, and a single sporophyte. *Griffith? 187* has a fruiting stem with two sporophytes and a non-fruiting one. The other two plausible candidates, *Griffith 187*, and *Griffith 171*, do not resemble this either.

However, the collection in Mitten's herbarium, labelled "Fruct. *Neckera hookeriana* Griff!" contains a stem strongly resembling Griffith's (1849b) illustrations. In fact, it contains two fruiting stems: a stem with five sporophytes – two in a single perichaetium – and a stem with a single sporophyte. The latter matches Griffith's illustrations in all respects, though in mirror image.

Mitten's collection contains two variants of *Cyathophorum hookerianum* in which the widely distributed monsoon variant is mixed with the local variant known from Sikkim and E Nepal. The fruiting plants belong to the monsoon variant while plants that belong to the local variant are sterile.

The occurrence of these two variants in the same collection strongly suggests that Mitten's "Fruct. *Neckera hookeriana* Griff!" shares a common history with *Griffith 171*, *Griffith 187*, and

Griffith? 187 since, among the nineteenth century material examined, these are the only other collections where the two variants of *C. hookerianum* are mixed. Likewise, the fruiting plants of the latter three collections belong to the monsoon variant and the non-fruiting and principally sterile ones belong to the local variant (among plants of the local variant a single perigonium was observed in *Griffith? 187*). Presumably, 1) the four mixed collections are parts of a single master collection in which plants of both variants grew together; 2) fruiting stems of one, or more, collections, from the same or different locations, were combined with non-fruiting ones, from other collections, in order to form representative samples of *C. hookerianum*.

Mitten (1859) remarked that he had received collections of mosses that originally came from Griffith, and had been accompanied with descriptions corresponding to those in Griffith (1849a). However, although Mitten cited material of *Cyathophorum hookerianum* collected by Griffith, Hooker, and Hooker & Thompson, Mitten did not say that he actually had seen the material, which suggests that he had not examined it at the time. Material of *C. hookerianum* is present in his herbarium, but he may have received it later.

The labelling of specimens in Mitten's herbarium in NY is often incomplete. But, because it contains no other collection that is potential type material of *Cyathophorum hookerianum*, and because *Griffith 187* is not depicted in Griffith (1849b), it is virtually certain that the collection labelled "Fruct. *Neckera hookeriana* Griff!" contains the plant that Griffith (1849b) chose for his illustration. Therefore, the stem with the single sporophyte in this collection is designated here as the lectotype of *Cyathophorum hookerianum* and designated *Griffith s.n.* (NY, labelled "Fruct. *Neckera hookeriana* Griff!").

Griffith 171 (BM) and *Griffith 187* (NY) contain plants of *Cyathophorum hookerianum* mixed with *C. adiantum*. They are also numbered *508*. This is probably the specimen's number in the herbarium of the East Indian Company, or the number under which the Royal Botanic Gardens in Kew distributed these collections in 1895. The numbers *171* and *187* may be equivalent to collection numbers.

There are two other collections that may have been gathered by Griffith. These are the ones numbered 1441, in pencil, preserved in the herbaria of Hooker and Wilson (BM). While neither the collector nor the exact locality of these collections is indicated, the collection in Wilson's herbarium came from the E Indies and an annotation states that it came from the herbarium of Griffith & Harvey. These collections contain only sterile plants of the local variant of the species, and are, therefore, not important for the lectotypification of *Cyathophorum hookerianum*.

2. *Strachey & Winterbottom 70*, preserved in Mitten's herbarium (NY) is regarded as the holotype of *Cyathophorum intermedium*.

When Mitten (1859) described *Cyathophorum intermedium*, he cited only a single collection that had been collected by Strachey and Winterbottom and gave no collection number. But in Mitten's herbarium there are two such specimens, annotated with different numbers. The specimen that is numbered "*70*" comes from "Kumaon". The other one, numbered "*101*", is labelled "Hookeria, Dwali, Kumaon, 8,500 ft". Neither of these specimens fits Mitten's description precisely. While he had written that a border is absent in the apical half of the leaf, "foliis lateralibus ... margine ventrali a basi ad medium et ultra anguste tenuiter limbatis caeterum immarginatis ...", the leaf border frequently reaches the acumen on each side of the leaf in both plants, although it is often interrupted or very faint.

However, attached to *Strachey & Winterbottom 70* there is an illustration of a leaf and an amphigastrium that was made by Mitten. It bears the text "margin faint" [= border faint], which points to the postical side of the leaf at a point one third above base, and it bears the text "no marg" [= no border], which points to the entire margin of the amphigastrium. Mitten's illustration, published in mirror image by Gangulee (1977, f. 772 1), agrees perfectly with Mitten's description. Thus *Strachey & Winterbottom 70*, in Mitten's herbarium, must be the holotype of *C. intermedium*.

A few collections made by *Strachey & Winterbottom* are also preserved in BM. They are provided with the number "*70*" or with the number "*101*"; one specimen is provided with both numbers. Three collections in BM are numbered "*70*", two of them labelled "E. Indies", whereas for the third no origin is indicated. They resemble the holotype very closely, and are almost certainly isotypes. One specimen in BM is provided with the numbers "*70*" in black ink, and "*101*" in red ink. Another specimen in BM that is not provided with a collector's name, is provided with the number "*101*" in red ink. Both specimens are labelled "Hookeria, Dwali, Kumaon, 8,500 ft". The specimen provided with the single number very closely resembles *Strachey & Winterbottom 101* in Mitten's herbarium – where the number is written in black ink – and they are probably duplicates. The specimen provided with the numbers "*70*" and "*101*" contains two plants. These plants may come from different collections, viz. *Strachey & Winterbottom 70* and *Strachey & Winterbottom 101*, but this is difficult to prove, because the material of these two collections shows great similarity.

3. Basing his decision on a collection from Taiwan, Herzog in Herzog & Noguchi (1955) erroneously transferred *Cyathophorella intermedia* to *Dendrocyathophorum* Dixon. Herzog misinterpreted *Cyathophorum intermedium*, the type of which has simple stems, no stem cavities, and belongs clearly to *Cyathophorella* (= *Cyathophorum*); see also: Chopra (1975), Gangulee (1977), Kruijer (1996b).

The type of *Cyathophorella intermedia* was correctly excluded from *Dendrocyathophorum* by Chopra (1975), but he erroneously used the combination *D. intermedium* for the *Dendrocyathophorum* species.

4. In the type of *Cyathophorum burkillii* male and female plants are mixed. Male and female plants are very similar. Dixon's (1914: f. 1a) illustration of the habitus of the gametophore is based on the male plant. His illustrations of a portion of the stem, leaves, leaf cells, and amphigastria are probably also based on the male plant (1914: f. 1b–e).

Synonymy — 5. *Cyathophorum intermedium* has dorsiventrally compressed stems and abruptly acuminate lateral leaves, which are weakly to coarsely serrate in the distal part, especially at the antical side of the leaf. The leaf border is faint near the leaf base, but distinct in the middle part of the leaf, where it is 2–4 cells wide, and absent or faint and up to 2 cells wide in the distal part of the leaf. The amphigastria are abruptly acuminate, and entire to crenulate or coarsely serrate. These features are within the variation range of *C. hookerianum*, with which *C. intermedium* is conspecific.

6. Brotherus (1909) compared his new species *Cyathophorum philippinense* only with *Cyathophorum parvifolium* Bosch & Sande Lac., and may have overlooked other related species. Bartram (1939) reduced *Cyathophorum philippinense* to *Cyathophorella hookeriana*, because he considered the plants of the former to agree perfectly with *Cyathophorella hookeriana*, except for the occurrence of ecostate amphigastria in *Cyathophorum philippinense*. Brotherus (1909) observed only ecostate amphigastria in the latter, but Bartram (1939) found occasionally costate amphigastria with a well-developed costa in its type.

However, truly ecostate amphigastria are absent from *Cyathophorum philippinense*. In its type the amphigastrium costa is faint or distinct and reaches 1/5–1/3 of the length of the amphigastrium. The variation in length and extent of the amphigastrium costa in *C. philippinense* is within the variability range of the present species *C. hookerianum*.

In addition, the type specimens of *Cyathophorum philippinense* and *C. hookerianum* have serrate and gradually acuminate leaves, which are continuously bordered. The leaf border is distinct and 2–4 cells wide above the leaf base. These features separate *C. philippinense* from *C. parvifolium*, and there is no doubt that the former is conspecific with *C. hookerianum*.

7. *Cyathophorum burkillii* shows a clear resemblance to *C. hookerianum* by having dorsiventrally compressed stems and leaves being weakly to coarsely serrate in the distal part. Some leaves are gradually acuminate, others are abruptly acuminate. The leaf border is distinct in the basal part of the leaf and faint in the distal half to third. Dixon (1914) considered *C. parvifolium* most related to *C. burkillii* and separated the latter from the Indo Malayan species by its perfectly orbicular amphigastria with a shorter, cuspidate point. The amphigastria in *C. burkillii* are, in fact, orbicular to ovate, elliptic, or obovate, and the shape of the amphigastria as well as the shape and length of the amphigastrium apex are within the variability range in *C. hookerianum*.

Dixon (1914) noticed also that *Cyathophorum burkillii* has comparatively broadly margined leaves and a fine denticulation in the distal half of amphigastria and leaves, but neither feature separates *C. burkillii* from *Cyathophorum hookerianum*. Despite Dixon's claim, that *C. hookerianum* has a less developed peristome than *C. burkillii*, substantial differences in the extent of the peristome do not exist. All features in the type of *C. burkillii* are within the variability range of those of *C. hookerianum*.

8. According to Horikawa's (1934a) original description the type of *Cyathophorella densifolia* shows a close resemblance *Cyathophorum hookerianum*, with which it is almost certainly conspecific. The leaves of *Cyathophorella densifolia* are serrate, and have a distinct and continuous border of 2–4 cells wide. Its amphigastria are abruptly acuminate. Noguchi's (1952) reduction of *Cyathophorella densifolia* to *Cyathophorella hookeriana* is supported by the examination of non-type specimens in S that had been identified by Horikawa as *Cyathophorella densifolia* (*Horikawa 623*, *Horikawa, BAJM 25*).

9. *Cyathophorella kyusyuensis* and *Cyathophorella grandistipulacea* represent small to medium sized forms of *Cyathophorum hookerianum.* Their types are very similar, and Noguchi (1952) already considered *Cyathophorella grandistipulacea* a variety of *Cyathophorella kyusyuensis.*

10. Both syntypes of *Cyathophorella anisodon* have dorsiventrally compressed stems with imbricate to closely set leaves that are weakly serrate in the distal part. Each syntype has continuously bordered leaves. The leaf border is distinct and 1–4 cells wide in the lectotype, and 2–5 cells wide in *Troll 91* (JE). Therefore, *Cyathophorella anisodon* is evidently conspecific with *Cyathophorum hookerianum.*

Both syntypes of *Cyathophorella anisodon* have gradually acuminate leaves, with only a few abruptly acuminate leaves. The syntypes are intermediate between the monsoon and the warm-temperate variants of the present species, but both resemble the former variant more closely.

11. The type of *Cyathophorella taiwaniana* could not be examined, but based on Lai's (1976) clear original description and illustrations, it is almost certainly conspecific with *Cyathophorum hookerianum.*

12. The original material of *Cyathophorum subpiliferum* is a small plant of *C. hookerianum.*

13. The original material of *Cyathophorella rigidula*, nom. nud., certainly belongs to *Cyathophorum hookerianum*, because it has entire to weakly serrate acuminate leaves with a very faint to distinct leaf border, 1–3 cells wide in the apical part of the leaf.

Description — 14. The ornamentation of the dorsal plates of the exostome teeth could be observed in only a few plants (see note 15). The observations suggest that the ornamentation may range from weakly developed in the Himalayas to strongly developed in Luzon, Philippines. The dorsal plates of *Norkett 7398* (Nepal) are moderately to coarsely papillose in the basal fourth of the teeth, and weakly to coarsely papillose in the distal part. The papillae are high and slender in the basal fourth and become low and broad in the distal part of the teeth (Plate 4f, p. 51). In the plants from Luzon the dorsal plates in the basal fourth of the teeth are occasionally weakly reticulate or even weakly striate. They are very coarsely papillose in the distal part having high and slender papillae, which are branched or simple (Plate 4e, p. 51). *Burkill 37737* (Arunachal Pradesh, India) and the fruiting plants in the collections made, or presumed to have been made, by Griffith (see note 1) were not examined with the SEM. What is known about the features of the papillae at their dorsal plates suggests that they are intermediates in this aspect between the collection from Nepal and the collections from Luzon. Their exostome teeth have moderately to coarsely papillose dorsal plates.

The length of the trabeculae also ranges from very short in the entire exostome in the plant from Nepal (*Norkett 7398*; Plate 4f, p. 51) to very short in the basal fourth of the exostome teeth and short to pronounced in the distal part in Luzon (*Williams 1671*; Plate 4e, p. 51).

The ornamentation of the endostome is weak in Nepal (*Norkett 7398*), but very pronounced in the fruiting material from Luzon (see note 15), especially at the innerside of the endostome. The ornamentation of the endostome is insufficiently known for *Burkill 37737* and the *Griffith* collections (see above).

Reproduction — 15. Only a few collections contain fruiting plants. There are four collections with fruiting plants made, or presumed to have been made, by Griffith (see note 1) and the origin is given only for *Griffith 171 (508)*, viz. Khasi Hills (Meghalaya, India). The other collections are: *Kanai et al. s.n.*, labelled "Nov. 15, 1963" (Nepal; only immature capsules), *Norkett 7398* (Nepal), *Burkill 37737* (Arunachal Pradesh, India), *Hu 0857* (Sichuan, China; only immature sporophytes), *Boeken 81.03.2586* (Luzon, Philippines), *Elmer 8544* (Luzon), and *Williams 1671* (Luzon). Fruiting specimens are not known from SE Asia or Japan.

Distribution — 16. *Cyathophorum hookerianum* was not previously known from Borneo. A specimen from Sarawak, which was collected by an unknown collector, is preserved among unidentified Hypopterygiaceae in Mitten's herbarium (NY). The collection evidently consists of *Cyathophorum hookerianum.*

17. There are two clearly labelled specimens in Mitten's herbarium (NY) that claim to be *Cyathophorum hookerianum* from Java collected by Motley. For the most part they have entirely dorsiventrally compressed stems, though a few stems are partly dorsiventrally compressed and have a weak lateral compression near the stem base (the plant for which an origin in Mt Pangerango is claimed) or a distinct lateral compression near the stem base (the plant for which an origin in Mt Megamendong is claimed). Their leaves are continuously bordered. In the 'Mt Pangerango' plant the border is distinct and 2–4 cells wide. In the 'Mt Megamendong' plant the border is faint or distinct and 1 or 2 cells wide. Hence, unquestionably, they belong to *C. hookerianum.*

However, their origin in Java must be questioned. Fleischer (1908) did not treat *Cyathophorella hookeriana* as a Javan species, but reported it from the Himalayas and the Khasi Hills on the Indian subcontinent. The species was not included in the survey of mosses of Java by Van den Bosch & Van der Sande Lacoste (1861), although they examined material collected by Motley and were acquainted with the species, as is demonstrated by a specimen preserved in their herbarium (L). This specimen (without annotations presented as *Cyathophorella hookeriana,* sub herbarium no. *HLB 910.88-134*) has entire or weakly serrate leaves which in their continuous and distinct border are characteristic for *Cyathophorum hookerianum.*

All specimens of *Cyathophorum* from Java with entire or weakly serrate leaves belong to *Cyathophorum parvifolium,* making Motley's specimens unique, if, indeed, they originated there. But Motley's 'Mt Megamendong' collection is a mixed collection, in which *Cyathophorum hookerianum* is combined with *Cyathophorum adiantum.* Since the latter species is not known from Malesia, it is almost certain that the 'Mt Megamendong' collection came from elsewhere. This makes it plausible that Motley's other specimen is also mislabelled. The conclusion is, therefore, most likely that both collections come from localities outside Malesia, presumably from continental SE Asia.

Identification — 18. The differences between *Cyathophorum hookerianum* and *C. parvifolium* are given below the latter species, note 11, p. 356.

Other — 19. The lectotype of *Cyathophorum hookerianum* and the types of *Cyathophorum philippinense* evidently belong to the monsoon variant of *Cyathophorum hookerianum.* The type of *Cyathophorella taiwaniana,* which was not examined, may also resemble this monsoon variant. The type of *Cyathophorum intermedium,* however, for the most part resembles the warm-temperate variant, although the few stems of the type grew probably in a rather open group, and its leaves possess a distinct border that reaches occasionally into the acumen. The original material of *Cyathophorella rigidula* also resembles the warm-temperate variant overall, because its stems are closely set with abruptly acuminate leaves, its gemmaphores are 3 or 4 cells long, and its leaf border is occasionally faint in the apical part of the leaves.

The types of *Cyathophorum burkillii, Cyathophorella kyusyuensis, Cyathophorella grandistipulacea,* the syntypes of *Cyathophorella anisodon,* and the original material of *Cyathophorum subpiliferum* are intermediates between the two variants of the present species.

The type of *Cyathophorum burkillii* resembles the monsoon variant in its size, its long and continuously bordered leaves, and the large terminal cells of its axillary hairs, which are 40–46 µm long and 25–34 µm wide. The type resembles the warm-temperate variant in its closely set leaves, and its gregarious stems and it has abruptly acuminate leaves with a faint border.

The type of *Cyathophorella kyusyuensis* resembles for the most part the monsoon variant. The stems of the type are scattered. The leaves are imbricate or closely set, and most are gradually acuminate. A few leaves are abruptly acuminate. The leaf border is continuous and distinct or partly very faint in the apical half of the leaf, and 2 or 3 cells wide.

The type of *Cyathophorella grandistipulacea* resembles for the most part the warm temperate variant. Most stems are placed in a dense group. The leaves are closely set and gradually to abruptly acuminate. The leaf border is continuous and faint or distinct, but very faint in the distal part of the leaf. The border is 1–3 cells wide.

The syntypes of *Cyathophorella anisodon* have usually gradually acuminate leaves, and occasionally abruptly acuminate leaves, which are continuously bordered with a distinct border. In most respects, they resemble the monsoon variant, but they resemble the warm-temperate variant in their imbricate to closely set leaves. The original material of *Cyathophorum subpiliferum* resembles the warm-temperate variant in its entirely dorsiventrally compressed stems and its closely set leaves. It resembles the monsoon variant in the well pronounced leaf border.

According to the description by Horikawa (1934a) the type of *Cyathophorella densifolia* is an intermediate between the two variants of *Cyathophorum hookerianum*. Its stems with closely set and abruptly acuminate leaves resemble the warm-temperate variant, whereas its size, and its long and continuously bordered leaves resemble the monsoon variant.

20. The two specimens from Laos found in Dixon's herbarium kept at BM (*Kerr 481*, *491b*) were incorrectly presented as *Dendrocyathophorum*. Dixon (1936) identified them as *Cyathophorum intermedium*, which was incorrectly transferred by Herzog (in Herzog & Noguchi, 1955) to *Dendrocyathophorum*. The two specimens evidently belong to *Cyathophorum*.

The plants from Laos resemble the type of *Cyathophorum burkillii*, and may be regarded as intermediates between the warm-temperate and the monsoon variant of *Cyathophorum hookerianum*. Their long stems are partly or entirely laterally compressed. The foliate stems are rather narrow, especially when compared with the monsoon variant of *Cyathophorum hookerianum*. The plants have weakly to moderately serrate leaves, which are relatively short and closely set, especially in *Kerr 481*, and occasionally imbricate in *Kerr 491b*. The leaf border is faint or distinct in the basal part of the leaf, but is frequently interrupted in the basal part of the leaf on the antical side, and absent or interrupted near the leaf apex on each side. The border is 2(–4) cells wide at most. In the plants, particularly in *Kerr 491b*, several innovations were observed, which sprout on the lateral side of the stem.

21. *Okamura s.n.* (JE p.p.) is a collection of *Cyathophorum adiantum* from Mt Hônokawa, Shikoku, Japan, which contains a few very tiny stems of *Cyathophorum hookerianum*.

Selected specimens (260 specimens examined):

E INDIES: *unknown collector s.n. (1441)* (BM, see note 1). — NEPAL: Bagmati: *Long 22123* (E), Langtang Khola, Syabru; *Long 22273* (E p.p.), Sheopuri Lake–Mulkharka. – Kosi: *Long 20363* (E), Arun Valley; *Norkett 7398* (BM), Milke Danda Forest; *Norkett 9356* (BM), *9424a* (BM), Mewa Khola Gorge. – Mechi: *Kanai et al. s.n.* (NICH, 'Nov. 15, 1963'), Hellok–Baroya Khimty; *Long 17302b* (E), Dobala Danda. — BHUTAN: Mongar Distr.: *Long 8659* (E), Namning. — INDIA: Uttar Pradesh ('Kumaun'): *Strachey & Winterbottom 70* (BM, NY; s.loc.); *Strachey & Winterbottom 70/101* (BM), *101* (NY), Dwali. – Tihri Garhwal: *Bahadru (6334)* (BM, S), Kidarkanta. – Sikkim: *Troll s.n.* (JE), Gangtok–Natu La; *Hooker f. 702* (BM), *unknown collector [Hooker f. 702?]* (NY), Singalila Ra. ('Singalelah'); *Long 22942* (E), Yoksam. – Bengal Jalpaiguri. Darjeeling ('Sikkim'): *Decoly & Schaul, Bryoth. Levier 2571* (NY p.p.), *s.n.* (FH), Karsiyang ('Kurseong'); *Kerstan 13a* (BM; JE, sub *no. 13/c*), *29/2* (JE), Darjeeling; *Hooker f. 704* (BM, NY p.p.), Mt Tonglu ('Tonglo'); *Long 22401* (E), Lebong. – Arunachal Pradesh: *Bor 50b* (BM), Kameng Frontier Div., Aka Hills; *Burkill 37737* (BM), Siang Frontier Div. ('Abor Distr.'). – Meghalaya. Khasi Hills: *Hooker f. & Thomson 701* (BM p.p., GRO, NY p.p.), Nongkhlao ('Nunklow'); *Hooker f. 704b* (BM, NY p.p.), Moflong; *Griffith 171 (508)* (BM p.p., see note 1), Moosmai.

CHINA: Sichuan: *Touw 23898* (L), Mt Emei ('Omei'); *Chen 1575* (PE), *Hu 0857* (PE p.p.), Nan Chung, Mt Jinfu. – Yunnan: *Touw 23567* (L), Xishuangbanna. – Guizhou: *Ysiang 4341d* (PE), Cheng-Ling. – Anhui: *Chen et al. 7188* (NICH), Hwangshan. — JAPAN: Honshu. Ishikawa Pref.?: *Toyama 6179* (S), Yamashiro. – Shizuoka Pref.: *Takaki, MJ 613* (L), Misakubo. – Aichi Pref.: *Iwatsuki, MJE 462* (B, BM, BR, EGR, JE, L, NY, S), Miwa. – Shiga Pref.: *Nakajima, MJE 1215* (L), Otsu-shi. – Mie Pref.: *Iwatsuki, MJE 1457* (L), Kumano. – Wakayama Pref.: *Nakajima, MJE 1310* (L), Mt Nachi. – Tottori Pref.: *Ochi 8705* (L), Nichinan-cho. – Shimane Pref.: *Horikawa BAJM 25* (S), Matsue; *Ando s.n.* (S), Oki Is. – Yamaguchi Pref.: *Iwatsuki & Shiomi 12166* (NICH), Mitô-chô. – Shikoku. Tokushima Pref. ('Awa'): *Okamura 317* (FH p.p., S p.p.), Karei. – Kochi Pref. ('Tosa'): *Gôno 242* (FH p.p., s.loc.); *Okamura s.n.* (JE p.p.), Mt Hônokawa; *Kamimura 5000* (NICH p.p., KUMAMOTO p.p.), Mt Yokogura. – Kyushu. Fukuoka Pref.: *Osada, MJ 675* (L), Nogochi Valley. – Kumamoto Pref. ('Higo Prov.'): *Kaneda 7025* (BM, MAKINO), Mt Ichibusa. – Miyazaki Pref. ('Hyûga Prov.'): *Iwatsuki, MJE 1361* (L), Makinokuchi; *Noguchi 236* (NICH, KUMAMOTO, HIRO), Mt Aoidake; *Noguchi & Hattori, MJ 4* (L p.p.), Minaminaka-gun, Sakatani. – Kagoshima Pref. ('Oksumi Prov.'): *Mizutani (M 30912)* (NICH), Mt Hoyoshi; *Takaki & Mizutani*

855 (NICH), Yakushima Is. — TAIWAN ('FORMOSA'): Pingtung Co.: *Lai 9890* (NY, FH), Mt Peitawushan. – Chiayi Co.: *Lin, BTE 210* (NICH,L), Fenchihu. – Nantou Co.: *Lin, BTE 61* (NICH, L), Tsuifeng; *Noguchi (1958)* (NICH), Numanoshira, Mt Arisan. – Taipei Co. ('Taihoku Prov.'): *Noguchi (5917c)* (NICH), Doba.

MYANMAR (BURMA): Karen State: *unknown collector s.n.* (BM), Mt Nattaung ('Nattoung'). — THAILAND: Payap (Chiang Mai): *Touw 9704* (L), Doi (Mt) Inthanon. – Rachasima (Nakhon Ratchasima): *Kerr 123* (BM), 'Kavat' (= Korat?), Kao Laem ('Lem'). – Surat (Surat Thani): *Kerr 223* (BM), Kao Nawng. — CAMBODIA (KAMPUCHEA): Kâmpôt: *Tixier 2989* (HIRO), Bokor, Kam Chay. LAOS. Xiangkhoang: *Kerr 481* (BM), Muang Awn; *Kerr 491b* (BM), Pu Muten. — VIETNAM: Hoang Liên So'n: *Pócs 2579/2* (EGR), Sa-Pâ.

PHILIPPINES: Luzon. Benguet Prov.: *Elmer 8544* (BM, FH, GRO, L, S), *Williams 1671* (FH, NY), *1672* (NY p.p.), Baguio; *Del Rosario 7181* (GRO), Irisan; *Del Rosario 7172A* (GRO), *7127D* (GRO), La Trinidad; *Del Rosario 11100B* (GRO), *12133B* (GRO), *Del Rosario et al. 12126A* (GRO), Mt Pulog; *Tixier 1823* (EGR), *Van Zanten 68.3915c* (GRO p.p.), Mt Sto. Tomas; *Del Rosario 140031* (GRO), Mt Tabayoc; *Van Zanten 68.4036g* (GRO), Mt Polis. – Mountain Prov.: *Boeken 81.03.2321d* (GRO), *81.03.2497c* (GRO), *81.03.2586* (GRO), *Del Rosario 15063 B* (GRO p.p.), Mt Data. – Quezon Prov.: *Tan 84-128* (NICH p.p.), Mt Banahao. — MALAYSIA: Peninsular Malaysia. Perak: *Sheffield 12e* (BM), Gunong Biah. – Pahang: *Wood 1654* (GRO), Fraser's Hills. – Borneo. Sarawak: *Everett s.n.* (NY, s.loc.), *unknown collector s.n.* (NY, s.loc.).

?: INDONESIA: Java. W Java (Jawa Barat): *Motley s.n.* (NY), Mt Pangerango; *Motley s.n.* (NY p.p.), Mt Megamendong.

ORIGIN NOT GIVEN: *Griffith 187* (NY p.p., also sub no. *508*; see note 1), *s.n.* (NY, labelled "Fruct. *Neckera hookeriana* Griff!"; see note 1), *Griffith? 187* (BM, see note 1), and 2 collections of *Cyathophorum adiantum* made by Griffith intermingled with *C. hookerianum*: *Griffith 262* (BM p.p., also sub no. *29/125*), *179* (BM p.p.).

7.7. **Cyathophorum parvifolium** Bosch & Sande Lac. — Fig. 57, 58A, 59A; Map 26; Plate 4c, d

Cyathophorum parvifolium Bosch & Sande Lac., Bryol. Jav. 2 (1861) 5, t. 135. — *Cyathophorella parvifolia* (Bosch & Sande Lac.) M. Fleisch., Musc. Buitenzorg 3 (1908) 1094. — Syntypes: *Motley s.n.* (L lecto, designated here; NY), Java, W Java (Jawa Barat), Mt Megamendong, alt. 4–6000 ft; *Teijsmann s.n.* (L, ?NY), Java, W Java (Jawa Barat), Mt Gedé. — See note 1.

Cyathophorum tenerum Bosch & Sande Lac., Bryol. Jav. 2 (1861) 6, t. 136, syn. nov. — *Cyathophorella tenera* (Bosch & Sande Lac.) M. Fleisch., Musc. Buitenzorg 3 (1908) 1095. — *Hookeria spinosa* auct. non Müll.Hal.: Dozy & Molk. in Zoll., Syst. Verz. (1854) 26; see note 2. — Syntypes: *Zollinger s.n.* (L lecto, designated here, sub no. *HLB 98,291-53*, wrongly labelled "Java"; see note 2), Sumbawa, ["insulam Bima in m. Padjo altit. 4–6000'"]; *Teijsmann s.n.* (L, S), Sumatra, ["ad litus occidentale insulae Sumatra"]. — See note 3.

Cyathophorella aristifolia E.B. Bartram, Philipp. J. Sci. 68 (1939) 281, pl. 21, f. 359, syn. nov. Type: *Bartlett 13851* (FH holo), Mindoro, vicinity of Puerto Galera, distal slopes & summit of Mt Malasimbo, on tree trunk, hepatic, May 5, 1935. — See note 4.

Illustrations: Van den Bosch & Van der Sande Lacoste, Bryol. Jav. 2 (1861) t. 135–136. — Bartram, Philipp. J. Sci. 68 (1939) pl. 21, f. 359. — Akiyama in Kato, Taxon. Studies of the Plants of Seram I (1988) 57, f. 4. — Akiyama, Acta Phytotax. Geobot. 43 (1992) 113, f. 1a–h.

Plants in groups of fans or in colonies growing intermingled with other (epiphytic) bryophytes, small to large and slender, frequently gemmiferous. *Stems* up to 7.0 (–11.5) cm tall, terete, usually entirely dorsiventrally compressed, occasionally not compressed in basal part, dark brown to greenish brown (at base) to brown to pale green (at top), dull (see note 5). *Primordia* naked. *Epidermis cells and cortical cells of stem* equally narrow or cortical ones wider (inner cortex) or narrower (outer cortex); walls thin or incrassate, colourless to brown; inclusions absent. *Central strand* present;

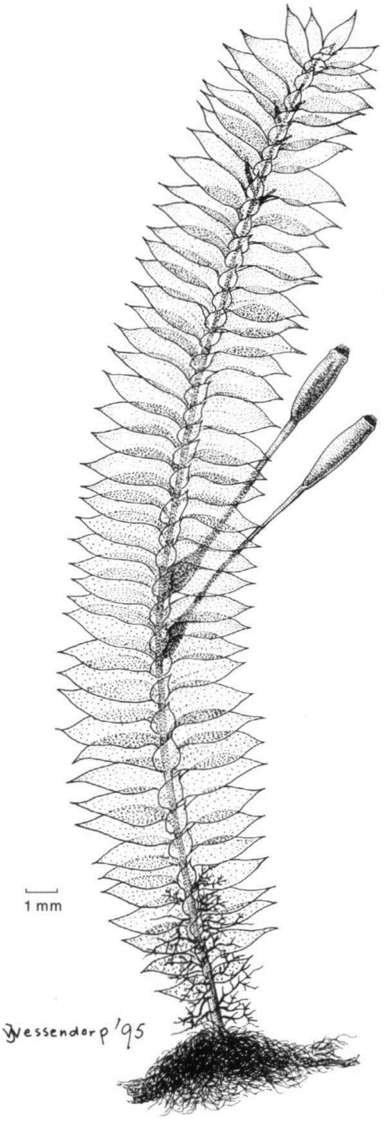


Fig. 57. *Cyathophorum parvifolium* Bosch & Sande Lac. Habit (ventral view, *Meijer B9095*, L).

cells narrow, walls colourless to brown, inclusions absent. *Axial cavities* absent. *Axillary hairs* (0–)2–3 per leaf, 2- or 3-celled, simple; basal cells 1 or 2, usually pale brown to brown, rarely colourless; intermediate cells absent; terminal cell circular to elliptic, 14–30(–35) µm long and 10–20(–30) µm wide, colourless to very pale brown, smooth to strongly verrucose (see note 6). *Leaves* distant to closely set colourless to green, occasionally tinged with brownish red. *Lateral leaves and amphigastria* discolourous or concolourous; lateral leaves pale yellowish green to green; amphigastria colourless (hyaline) to pale green. *Basal leaves* short-elliptic to ovate-oblong; apex acute or gradually to abruptly acuminate. *Distal leaves* generally much smaller at gemmiferous stem parts than in non-gemmiferous stem parts; margin usually serrate, occasionally entire; *teeth* unicellular, up to 80 µm long, projecting up to 2/3 of cell length; border faint or distinct in basal third of leaf at most, absent, faint and interrupted, or in lateral leaves occasionally distinct and interrupted above, in amphigastria less pronounced than in lateral leaves, up to 2 (or 3) cells wide; laminal cells 30–100 µm long and 15–30 µm wide; generally longer and wider in amphigastria than in lateral leaves. *Distal lateral leaves* usually ovate to ovate-oblong, occasionally elliptic or short-lanceolate, 1.0–3.0 mm long and 0.4–1.2 mm wide, oblong to lanceolate in gemmiferous parts; apex gradually or abruptly acuminate; acumen (0.1–)0.2–0.8 mm long; costa obsolete to distinct, reaching up to 1/2 of leaf length. *Distal amphigastria* appressed to patent, usually ovate to elliptic, occasionally obovate, rarely suborbicular or oblong, 0.4–1.3 mm long and 0.2–0.9 mm wide, erect to erecto-patent, elliptic to linear; basal part ± flat or smoothly curved; insertion weakly concave, straight, or convex; apex usually gradually or abruptly acuminate, occasionally acute; acumen up to 0.7(–0.8) mm long; costa usually absent or obsolete, occasionally faint, single and simple or forked, occasionally nearly double when short, reaching up to 1/3(–1/2) of amphigastrium length. *Gemmae clusters*

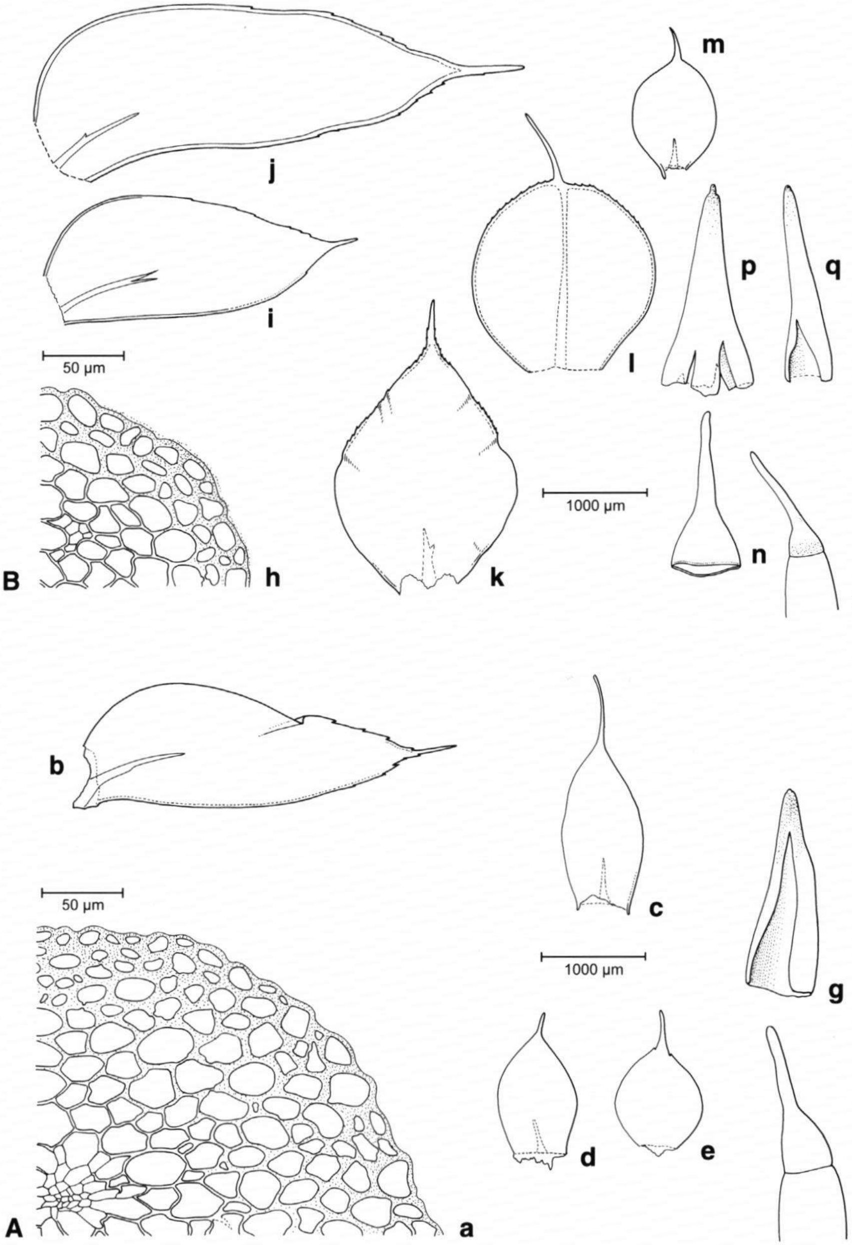
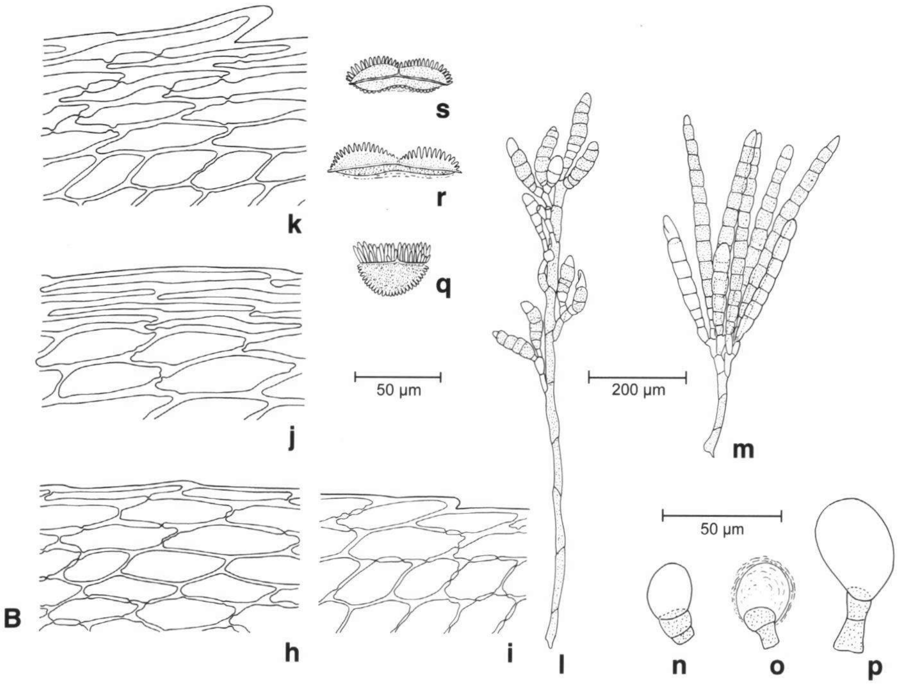


Fig. 58. — A. *Cyathophorum parvifolium* Bosch & Sande Lac. a. Rachis (dorsal quadrant, tissue of central strand partly compressed); b–e. leaves (b. lateral, c–e. amphigastria); f. operculum; g. calyptra. — B. *C. hookerianum* (Griff.) Mitt. h. Rachis (cross section dorsal quadrant); i–m. leaves (i, j. lateral, k–m. amphigastria); n, o. operculae; p, q. calyptrae (A. a–c, f, g: *Meijer B9095*, L; d–e: *Schiffner 12941*, S; B. h: *Williams 1671*, NY; i, m: *Norkett 7398*, BM; j: "Fruct. *Neckera hookeriana* Griff!", NY; k, l, n, p: *Burkill 37737*, BM; o, q: *Kanai et al. s.n.*, 'Nov. 15, 1963', NICH).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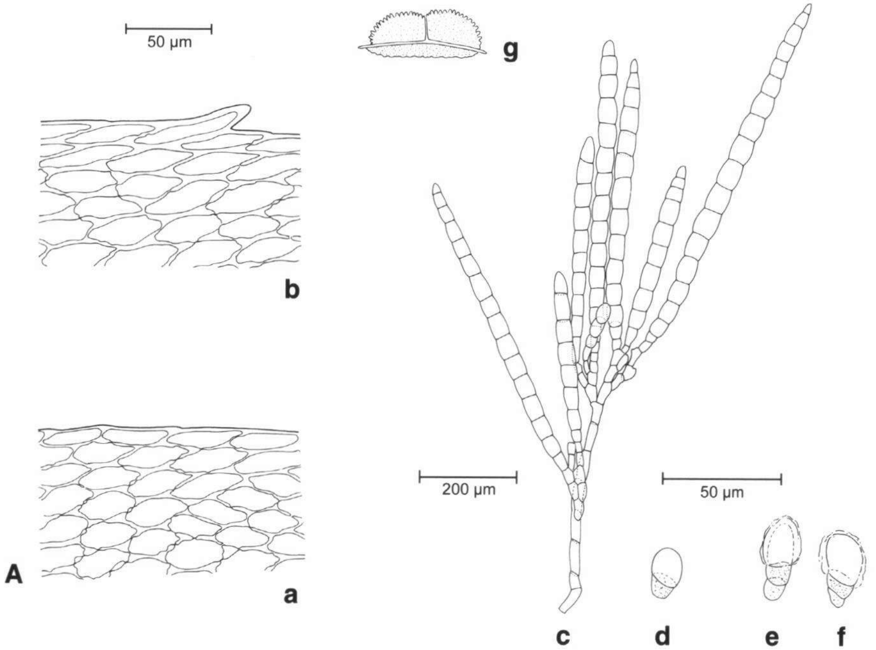
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located in distal fourth of stem, placed in axils of leaves and amphigastria, reaching usually 1/2 of length of associated lateral leaves to ± equally long, rarely much shorter and reaching 1/4 of length of associated leaves (see note 7). *Gemmaphores* penicillate, (1–)4–10 cells long, colourless to brown. *Gemmae* simple, up to 25 cells long; cells 25–50 µm long and 30–40 µm wide.

Dioicous. *Gametoecia* in middle or distal part of stem (see note 8). *Leaves* ovate to elliptic or ovate-lanceolate, occasionally slightly lingulate; margin entire; border faint or distinct, continuous or interrupted in distal part of leaf, up to 3 cells wide; costa absent or faint in perigonial leaves, reaching 1/3 of leaf length. *Inner leaves*: of perigonia up to 1.4 mm long and 0.6 mm wide, acumen up to 0.7 mm long; of perichaetia prior to sporophyte development up to 0.8 mm long and 0.5 mm wide, acumen up to 0.8 mm long; of full-grown perichaetia up to 1.5 mm long and 1.0 mm wide, acumen up to 1.1 mm long. *Antheridia* 0.5–0.6 mm long. *Stalk in full-grown perichaetia* 0.3–0.8 mm long. *Archegonia* 0.4–0.6 mm long. *Vaginula* 0.8–2.0 mm long. *Gametoecial axillary hairs* (0?–)1–3 per gametoecial leaf, 2- or 3-celled, simple; basal cells 1 or 2, colourless to brown; intermediate cells absent; terminal cell broad-elliptic to elliptic, 15–22 µm long and 14–25 µm wide, smooth or verrucose. *Paraphyses* absent.

Sporophytes up to 4 per stem. *Seta* 4.0–8.0 mm long, white to ochraceous (to brown when old), smooth. *Capsule* usually cylindrical to cylindrical-ellipsoid, occasionally cylindrical-ovoid or somewhat turbinate, 1.7–3.2 mm long and 0.3–1.0 mm wide, ochraceous; annulus absent. *Peristomial formula OPL:PPL:IPL* = 4:2:4–6c. *Exostome* pale yellow to dark brown; teeth 375–560 µm long and 35–70 µm wide; dorsal side coarsely papillose; median line not furrowed; dorsal plates narrower than or equally wide as ventral ones, 12–15 µm; papillae high, simple or branched; lamellae not projecting or distinctly projected near base of teeth; ventral plates 8–9 µm thick, moderately to coarsely papillose; papillae (low to) high, simple or branched; trabeculae very short or short. *Endostome* colourless or very pale yellow, weakly to moderately papillose at inner face, (smooth or) weakly to coarsely papillose at outer face; papillae low to high, simple; basal membrane reaching 1/8–1/4 of length of exostome teeth; processes 310–400 µm long beyond orifice and 25–30 µm wide at base, distinctly keeled, somewhat nodulose or not, appendiculate or not with a few very small lateral appendages; cilia absent or rudimentary and consisting of parts of 1 or 2 cells, 1 or 2 cell plates wide. *Operculum* long-rostrate, 1.0–1.5 mm long, reddish brown to brown; *rostrum* oblique. *Calyptra* cucullate, completely covering operculum, 1.6(–3.0?) mm long, very pale ochraceous, membraneous (see notes 9 and 10); margin entire or nearly so. *Spores*: 15–23 µm.

Fig. 59. — A. *Cyathophorum parvifolium* Bosch & Sande Lac. a, b. Leaf cells of lateral leaf (a. basal part of antical side, b. distal part of antical side); c. gemmaphore with gemmae; d–f. axillary hairs; g. exostome tooth (cross section). — B. *C. hookerianum* (Griff.) Mitt. h–k. Leaf cells of lateral leaves (h, j. basal part of antical side, i, k. distal part of antical side); l, m. gemmaphores with gemmae; n–p. axillary hairs; q–s. exostome teeth (cross section) (A. a, b, e–g: *Meijer B9095*, L; c: *Schiffner 12934*, S; d: *Touw 18479*, L; B. h, i, m, o: *Norkett 7398*, BM; j, k: "Fruct. *Neckera hookeriana* Griff!", NY; l: *Norkett 9424a*, BM; n, r: *Williams 1671*, NY; p, s: *Elmer 8544*, S; q: *Boele & Boeken 81.03.2586*, GRO).

Distribution — Philippines (Luzon, Mindoro, Mindanao), Indonesia (Sumatra, Java; Moluccas: Seram; Sumbawa, Flores, Sulawesi, West Papua), Papua New Guinea.

Habitat & Ecology — In the undergrowth of evergreen forests. On tree trunks, and branches of shrubs and trees. Also on rotten logs. Once found on leaves, on soil, and a dripping slope. In New Guinea once above the timberline in the shady underside of a non-calcareous boulder in an alpine tussock. Altitude: 1200–2300(–2980) m; in New Guinea 1000–3400(–4000) m.

Variability — Small plants often show minor differences in various morphological features.

Geographical variation — The plants reach their maximum sizes in the western and eastern part of the distribution area of the species. Their stems are up to 6.6(–11.5) cm, 3.7(–8.0) cm, and 6.9 cm tall in, respectively, Java, Sumatra, and New Guinea. The maximum length of the stems in the central part of the distribution area is 3.0 cm.

In the central and eastern part of the distribution area the axillary hairs are 2- or 3-celled, but in the western part only 3-celled axillary hairs were observed. The terminal cells of the axillary hairs are smooth to strongly verrucose in the central and eastern part of the distribution area, but verrucose in the western part. Small terminal cells, up to 17 µm long and 15 µm wide, were observed, especially, in New Guinea. In plants from the central part of the distribution area small terminal cells were observed as well as taller ones. In the western part the terminal cells of the axillary hairs are generally larger, and at least 17 µm long and wide.

The insertion of the amphigastrium in the plants from the Philippines and the Moluccas is straight to convex. In the plants from New Guinea the amphigastrium insertion is usually convex, and occasionally straight, whereas further west the amphigastrium insertion is straight, or weakly concave, and only sporadically slightly convex.

The leaf acumina in the plants from the western part of the distribution area are nearly always longer than 0.2 mm, and may be up to 0.8 mm long. In the plants from the central and eastern part of the distribution area the leaf acumina are slightly shorter. They are 0.1–0.5 mm long, but frequently shorter than 0.3 mm, in the central part of the distribution area, and usually up to 0.2 mm long, but occasionally up to 0.4 mm long, in New Guinea.

All plants from Mindoro and Luzon, Philippines, have entire to weakly serrate leaves, which are set with only a few, short serrations. Such entire to weakly serrate leaves are also found in the plants from Seram and, to a lesser extent, in those from Mindanao, but the leaves of plants from elsewhere are more coarsely serrate and set with more and longer serrations. The number and length of the serrations at the leaf margin are very variable, and some overlap in these features occurs between the plants from the various regions.

Ecological variation — Not found (insufficient data). However, the size of the plant might be affected by climatic conditions. The plants reach their maximum sizes in the western and eastern part of the distribution area of the species (see 'Geographical variation'), and grow under more constant, humid conditions than plants from the central part, where the climate is more influenced by monsoon conditions.

Notes:

Typification and nomenclature — 1. The lectotype of *Cyathophorum parvifolium*, preserved in Van der Sande Lacoste's herbarium (L), was used by Van den Bosch & Van der Sande Lacoste

(1861) in describing their species and at least for drawing t. 135, f. 2 in their Bryologia Javanica 2. The lectotype is a duplicate from Mitten's specimen, and its label is provided with a herbarium name given by Mitten. The master specimen of the lectotype is preserved in Mitten's herbarium (NY).

Figure 1 of t. 135 in the Bryologia Javanica 2 depicts a well-developed plant with many stems, and does not correspond with the lectotype, or the specimens that were, or appear to have been collected, by Teijsmann in Van der Sande Lacoste's herbarium. Teijsmann's plants have fewer stems. The only plant in this herbarium that matches t. 135, f. 1 lacks a collector's name, but comes from Java, and is labelled "*Cyathophorum parvifolium* n. sp.". A specimen in Mitten's herbarium is labelled identically and is presumably a duplicate. It is almost certain that both specimens belong to the set of syntypes and were collected by Teijsmann at Mt Gedé.

These two specimens labelled "*Cyathophorum parvifolium* n. sp." (L, sub no. *HLB 910, 88-144*; NY) and another part of the syntype collected by Teijsmann (L, sub no. *HLB 910, 88-139*) contain a few fertilised archegonia with embryonic sporophytes as depicted in t. 135, f. 29 of the Bryologia Javanica 2.

Two other specimens in the herbarium of Van der Sande Lacoste contain only a few leaves and a single perichaetium and neither their origin nor their collectors are indicated. However, one of them is labelled "*Cyathophorum parvifolium* n. sp.", and the label of the other specimen bears the herbarium name that was used for the lectotype by Mitten. Although it is possible that they are duplicate specimens of, respectively, the syntype collected by Teijsmann, which is identically labelled "*Cyathophorum parvifolium* n. sp.", and the lectotype, they are further left out of consideration.

2. The label of the lectotype of *Cyathophorum tenerum* bears the initial identification "*Hookeria spinosa*" by Dozy & Molkenboer, and the correction to "*Cyathophorum tenerum* n. sp." by Van den Bosch & Van der Sande Lacoste (1861). The lectotype is labelled "Java", but Zollinger (1854) and Van den Bosch & Van der Sande Lacoste (1861) indicated that it originates from Sumbawa ('Bima').

The perichaetial leaves, the seta, the vaginula, and the calyptra of *Cyathophorella tenera* were first described by Van Zanten (1964), based on *Van Zanten 501b*.

Synonymy — 3. Van den Bosch & Van der Sande Lacoste (1861) distinguished *Cyathophorum tenerum* from *Cyathophorum parvifolium* by its low, that is presumably smaller, size and more slender habitus: "Differe visum est a C. parvifolio: statura humili, habitu multo teniore et graciliore, ..." and the shape of the leaves with smaller, elongate laminal cells: "... foliorum forma et contextu e cellulis manifeste minoribus elongatis ...". In his key Fleischer (1908) distinguished *Cyathophorella parvifolia* from *Cyathophorella tenera* by its dichotomously branched innovations, and its long-acuminate leaves. Fleischer (1908), furthermore, prudently remarked that *Cyathophorella tenera* may differ from *Cyathophorella parvifolia* by its habitus, and its narrower leaves, but declared that the original material was too scanty to give a conclusive opinion on the differences between these two. Van Zanten (1964) stated that *Cyathophorella parvifolia* and *Cyathophorella tenera* differ only slightly or not at all, but did not reduce them to a single species. Van Zanten (1964) remarked that his plants from New Guinea resembled *Cyathophorella parvifolia* in the shape of their leaves, but referred to them as *Cyathophorella tenera*, because of their simple stems.

The syntypes of *Cyathophorum tenerum* are small plants of *C. parvifolium*. Features such as the shape of the leaves, the length of the acumen, and the size of the laminal cells are within the range of variability of the present species *C. parvifolium*. The syntypes of *C. tenerum* have simple stems, but most plants that belong to *C. parvifolium* have also simple stems, and many stems are simple, even in the syntypes of *C. parvifolium*. The syntypes of *C. parvifolium*, therefore, do not differ substantially from those of *C. tenerum*. Both species names have equal priority, but *Cyathophorum tenerum* is reduced to *Cyathophorum parvifolium*, because the type material of the latter is much better developed than the type material of the former.

4. In the type of *Cyathophorella aristifolia* leaves are entire to weakly serrate. The type is a small plant, and resembles weakly developed plants of *Cyathophorum hookerianum*, but, more closely, weakly developed plants of *Cyathophorum parvifolium*. The stems, however, are entirely laterally compressed. The leaf border is up to 2 cells wide on each side of the leaf, but is very faint in the distal third of the postical side of the leaf and absent to faint in the distal half to third on the

antical side. The costa of the lateral leaves is obsolete, and shorter than 1/5 of the length of the leaf. The amphigastria are ecostate. The lateral leaves and amphigastria are concolourous, which occurs more often in *Cyathophorum hookerianum* than in *Cyathophorum parvifolium.* On the other hand, the amphigastria are very narrow and, in this respect, resemble those of *Cyathophorum parvifolium.* Such narrow amphigastria occur only sporadically in *Cyathophorum hookerianum.* In my opinion, the type of *Cyathophorella aristifolia* does not belong to *Cyathophorum hookerianum.*

Bartram (1939) already suggested that his new species *Cyathophorella aristifolia* might be close to *Cyathophorella tenera*, but that the former appeared to be distinct on account of the long-aristate leaves and the more entire leaf margins. However, the shape of the leaf apex and the length of the acumen in the type of *Cyathophorella aristifolia* are within the variability range of these features in the present species *Cyathophorum parvifolium*, which includes *Cyathophorella tenera.*

Furthermore, the type of *Cyathophorella aristifolia* resembles small plants of *Cyathophorum parvifolium* from the Lesser Sunda Islands, and especially those from Flores. The occasional weakly serrate leaves with a few, short serrations, however, resembles those of the Philippine and Molluccan plants of *Cyathophorum parvifolium.*

Description — 5. Fleischer (1908) remarked that the stems of *Cyathophorella parvifolia* are dichotomously innovated, but this is not correct. In *Cyathophorum* the innovations sprout from primordia that are tristichously arranged in the ranks of lateral leaves and amphigastria. Most innovations sprout from the primordia between the lateral leaves, and some from the primordia between the amphigastria.

6. Rather large terminal cells of the axillary hairs were observed in *Akiyama C-15215* (Seram). They were up to 31 µm long and 26 µm wide.

7. Remarkably short gemmae and gemmaphores were found in *Tan 75-292* (Luzon). Its gemmae clusters reach approximately 1/4–1/3(–1/2) of the length of the covering lateral leaves.

8. Perigonia were rarely observed between amphigastria and then at damaged stems only.

9. According to Van Zanten (1964) the calyptra of *Cyathophorella tenera* is narrowly mitriform and short-fringed at base. This description is based upon the examination of a young calyptra. I have observed only cucullate calyptrae in the present species *Cyathophorum parvifolium*, which includes *C. tenera*, and never found a calyptra with a fringed base.

The specimen of *Van Zanten 501b* (see note 2) in GRO bears only a fragment of a seta and the specimen in L bears only a few setae, while neither specimen now contains a calyptra. Thus Van Zanten's (1964) observation could not be verified.

10. *Akiyama C-15316* (KYO) consists of a fruiting plant that belongs to *Cyathophorum parvifolium*, and a detached calyptra 3.0 mm long. This calyptra is exceptionally long for *C. parvifolium*, has a more regular areolation with narrower cells, and a more entire base than the calyptrae of other fruiting plants of *C. parvifolium* (*Akiyama C-14980, Meijer B9095*).

Furthermore, the only operculum in this collection, which is still attached to the sporophyte, differs somewhat from other operculae in *Cyathophorum parvifolium* and in a way which matches the exceptional character of the calyptra. Here the basal part of the operculum is high-conical, whereas it is low-conical and more attenuate towards the rostrum in other fruiting plants of *C. parvifolium.*

This agreement in exceptional character between the calyptra and the operculum taken with the absence of a fruiting plant of another moss in *Akiyama C-15316*, strongly suggests that the calyptra does derive from the plant of *Cyathophorum parvifolium.* Nonetheless, some doubt remains and the possibility that the calyptra belongs to another moss species cannot be ruled out.

Identification — 11. *Cyathophorum parvifolium* differs from *C. hookerianum* in habit of the gametophore, compression of the stem, colour of the lateral leaves and amphigastria, and extent and width of the leaf border.

In *Cyathophorum parvifolium*, the foliate stems are slender. The plants may become taller than those of *C. hookerianum*, but are less robust. The stems are never laterally compressed: they are usually dorsiventrally compressed and occasionally not compressed in the basal part, in particular near the stem base. *Cyathophorum parvifolium* has often discolourous leaves and amphigastria. A leaf border may be absent, faint, or distinct. When present, it is 2 (or 3) cells wide at most. It is usually absent from the antical side of the leaf and it is always interrupted in the distal part of the leaf.

Cyathophorum hookerianum has more robust plants with broader foliate stems than *C. parvifolium*. The stems are partly or entirely laterally compressed or entirely dorsiventrally compressed. The leaves and amphigastria of *C. hookerianum* are always concolourous. Most leaves of *C. hookerianum* are continuously bordered. The border is up to 4 cells wide. It is faint or distinct at both sides of the entire leaf. A border is occasionally absent from the apical third of the leaf, but it is sometimes completely absent in very tiny plants.

The robust plants, the green to dark green colour of the leaves, and the usually partly or entirely lateral stem compression in the monsoon variant of *Cyathophorum hookerianum* (see the latter species under 'Ecological variation', p. 341) prevents confusion with *C. parvifolium*. In the variant, very acuminate leaves may occasionally show resemblance with leaves of *C. parvifolium*, because of their faint and interrupted border.

The extent and width of the leaf border (see above), habit, and foliation prevents confusion between *Cyathophorum parvifolium* and the warm-temperate variant of *C. hookerianum* (see the latter species under 'Ecological variation', p. 341). Stem compression of this variant resembles that of *C. parvifolium*, because it is usually entirely dorsiventral and only occasionally partly lateral. The stem of the variant is, however, always abaxially curved and closely set with leaves, whereas the stem of *C. parvifolium* is usually straight and only occasionally abaxially curved and usually distantly set and occasionally closely set with leaves.

12. Several authors, e.g. Fleischer (1908), incorrectly considered the possession of innovations a distinctive feature for *Cyathophorum parvifolium*, because innovations were frequently found in its syntypes. Plants of *Cyathophorum* species frequently have a few innovations when they are damaged or fully outgrown and the syntypes of *C. parvifolium* are not exceptional. In the syntypes several stems were found having a few innovations, because they had been damaged or fully outgrown. Stems in *C. parvifolium* are rather slender, and accordingly can be very long and sensitive to damages. Therefore, innovations may occur more frequently in *C. parvifolium* than in other *Cyathophorum* species.

Reproduction — 13. Only a few collections contain sporophytes. Mature sporophytes were observed in 6 collections: *Meijer B9095* (Sumatra), *Eddy 5066* (Sulawesi), *Akiyama C-14976* (p.p.), *C-14980*, *C-15316*, and *C-15391b* (all from Seram). Immature sporophytes were observed in 3 collections from Java: *Teijsmann s.n.* (L, sub no. *HLB 910, 88-139*; see also note 1), *unknown collector [Teijsmann?] s.n.*, (L, sub no. *HLB 910, 88-144*; NY; see also note 1), and *unknown collector s.n.* (S).

Distribution — 14. Tixier (1971b) reported *Cyathophorella tenera* from Fraser's Hill in Pahang, Malaysia. I have not seen the specimen concerned, but Tixier's record is probably not correct. I have found a few specimens of *Cyathophorum hookerianum* from the Peninsular Malaysia, but I have not seen any specimen *Cyathophorum parvifolium* from this region. Since *Cyathophorum hookerianum* shows a close resemblance to *Cyathophorum parvifolium*, misidentification of Tixier's specimens cannot be ruled out.

Selected specimens (97 specimens examined):

PHILIPPINES: Luzon. Benguet Prov.: *Del Rosario et al. 14218* (GRO), Kabayan, Mt Tabayoc. – Mountain Prov.: *Boeken 81.03.2340b* (GRO), Mt Data. – Quezon Prov.: *Tan 75-292* (NICH p.p.), Mt Banahao. – Mindoro: *Bartlett 13851* (FH), Mt Malasimbo. – Mindanao: *Van Zanten 81.02.1486a* (GRO), *81.02.1673* (GRO p.p.), Mt Talamo. — INDONESIA: Sumatra: *Teijsmann* (L, S; s.loc.). – Atjeh: *Dransfield 1965* (L), Mt Kemiri. – W Sumatra (Sumatera Barat): *Schiffner 12936* (S), Mt Singalang. – Jambi(?):*Meijer B9095* (L), Mt Tudjuh. – Java. W Java (Jawa Barat): *Teijsmann s.n.* (L), Mt Gedé; *Motley s.n.* (NY, L), Mt Megamendong; *Schiffner 12932* (S), *12941* (S), Mt Pangerango. – E Java (Jawa Timur): *Verdoorn 26 (1770)* (NY), Mt Ajek-Ajek. – Moluccas (Maluku). Seram: *Akiyama C-14980* (KYO), *C-15316* (KYO), *C-15391b* (KYO), Manusela National Park. – Sumbawa: *Zollinger s.n.* (L), Mt Padjo. – Flores: *Schmutz SVD 6933* (L), Ruteng; *Touw & Snoek 22939* (L), Golo Lusang; *Touw & Snoek 23210*, Ngando Napu. – Sulawesi. S Sulawesi (Sulawesi Selatan): *Eddy 5066* (BM), Mt Rantemario. – West Papua (Papua, Irian Jaya). Jayawijaya: *Hiepko & Schultze-Motel 2011* (B), Eipomek Valley. – Merauke: *Van Zanten 300e* (L p.p.), Pegunungan Sterren ('Star Mts'), Ariemkop; *Van Zanten 501b* (GRO, L), Antares. — PAPUA NEW GUINEA:

West Sepik: *Touw 18479* (L), Star Mts, Folongonom. – Western Highlands: *Van Zanten 682969* (GRO), Mt Hagen. – Southern Highlands: *Streimann 23388* (CBG), NW of Erave, Batteri. – Morobe: *Touw 14796* (L), Mt Kaisinik.

DUBIOUS NAMES FOR THE HYPOPTERYGIACEAE

Hypopterygium penniforme auct. non (Thunb. ex Brid.) Brid.: Hornschuch, Linnaea 15 (1841) 143, according to Kindberg, Hedwigia 40 (1901) 297. — Based on: *Drège* (not found), "Zwischen Omsamwubo and Omsamcaba, an schattigen Waldplätzen auf Felsen, 800 F. H., den 14. Mai 1832". — Treated as an insuffiently known species by Müller, Syn. Musc. Frond. 2 (1850) 10. — Excluded from the Hypopterygiaceae Mitt. by Kindberg, Hedwigia 40 (1901) 297, who did not give a new identification.

Hypnum tamariscifolium Sw. ex Brid., Bryol. Univ. 2 (1827) 713, nom. nud. in syn. (*Hypopterygium rotulatum* (Hedw.) Brid.), err. pro *Hypopterygium tamarisci* (Sw.) Brid. ex Müll.Hal.? — Original material: not indicated, not found.

Hypopterygium fuscolimbatum K.I. Goebel, Organogr. Pfl. 1 (1898) 87, nom. nud. — Original material: not indicated, not found.

TAXA EXCLUDED FROM THE HYPOPTERYGIACEAE

Cyathophorella Müll.Hal. in Paris, Index Bryol. Suppl. (1900) 106, nom. nud. = **Calyptrochaeta** Desv. — Based on: *Cyathophorella mniopsidea* Müll.Hal. in Paris, nom. nud. — Excluded here.

Cyathophorella mniopsidea Müll.Hal. in Paris, Index Bryol. Suppl. (1900) 106, nom. nud. — Original material: *Loria (Bryoth. Levier 1608)* (BM, FH, S), New Guinea, SE Papua New Guinea ["Nov. Guin. britann."], Moresby Distr., Mt Moroko ('Mo-roka'), alt. 1300 m, Jul./Aug., 1893. = **Calyptrochaeta** spec. — Excluded here.

Cyathophorella (*'Cyatophorella'*) *nakazimae* E. Ihsiba, Trans. Sapporo Nat. Hist. Soc. 13 (1934) 396. — Type: *Nakazima s.n.* (n.v.), Japan, Honshu, Idzumi Prov., Mt Usitaki, 1934. ≡ **Neckera nakazimae** (E. Ihsiba) Nog., J. Jap. Bot. 8 (1937) 86; fide Noguchi l.c., p. 87.

Cyathophorella (*'Cyatophorella'*) *nakazimae* E. Ihsiba var. *brevinerve* E. Ihsiba, Trans. Sapporo Nat. Hist. Soc. 13 (1934) 396. — *Cyathophorella nakazimae* E. Ihsiba var. *longinerve* E. Ihsiba ex Nog., J. Hattori Bot. Lab. 4 (1950) 5, nom. inval., err. pro *Cyathophorella nakazimae* E. Ihsiba var. *brevinerve* E. Ihsiba. — Type: *Nakazima s.n.* (n.v.), Japan, Honshu, Idzumi Prov., Mt Usitaki, 1933. = **Neckera nakazimae** (E. Ihsiba) Nog.; fide Noguchi, J. Jap. Bot. 8 (1937) 87.

Cyathophorella pacifica (Besch.) Müll.Hal. ex M. Fleisch., Hedwigia 63 (1922) 212, nom. inval. in syn. (*Eriopus pacificus* (Besch.) M. Fleisch.). — *Epipterygium pacificum* Besch., Bull. Soc. Bot. France 45 (1898) 66. ≡ *Eriopus pacificus* (Besch.) M. Fleisch., Hedwigia 63 (1922) 212; fide Fleischer l.c. = **Calyptrochaeta** spec.

Cyathophorella urniopsidea Müll.Hal. ex M. Fleisch., Hedwigia 63 (1922) 212, nom. nud. in syn. (*Eriopus urniopsideus* M. Fleisch.). — Original material: New Guinea (n.v.) ≡ *Eriopus urniopsideus* M. Fleisch. nom. nud., Hedwigia 63 (1922) 212; fide Fleischer l.c. = **Calyptrochaeta** spec.

Cyathophorum bulbosum (Hedw.) Müll.Hal. var. *tahitense* Nadeaud, Enum. Pl. Indig. Tahiti (1873) 14. — *Cyathophorum pennatum* (Labill.) Brid. var. *taitense* Nad. ex M. Fleisch., Musc. Buitenzorg 3 (1908) 1096; Nadeaud ex H. Whittier, Mosses of the Society Islands: Preliminary Studies (1968) 393 pl. 61–62; Mosses of the Society Islands (1976) 296 f. 82, nom. inval., err. pro *Cya-*

thophorum bulbosum (Hedw.) Müll.Hal. var. *tahitense* Nadeaud; corr. by H.O. & B.A. Whittier, Bryologist 77 (1974) 439.— Type: *Nadeaud (67?)* (BM lecto, FH; both n.v.), Tahiti, ['dans les valées humides sur les écorces']. ≡? *Garovaglia tahitensis* Besch., Ann. Sci. Nat. Bot. 7, 20 (1895) 34; fide Bescherelle l.c., p. 8–9, 35. ≡ **Garovaglia powellii** Mitt. var. **tahitensis** (Besch.) During, Bryophyt. Bibl. 12 (1977) 122, '*taitensis*'. — Synonymised to *Cyathophorella tahitensis* (Besch.) M. Fleisch. by Fleischer, Musc. Buitenzorg 3 (1908) 1096. — Merged with *Garovaglia plicata* (Brid.) Bosch & Lac. by Miller et al., Bryophyt. Bibl. 16 (1978) 95. — See also '*Cyathophorum tahitense*', notes 2 and 3, p. 310.

Note — Nadeaud (1873) described *Cyathophorum bulbosum* var. *tahitense* as a new variety and listed *C. b.* var. *bulbosum* and *C. b.* var. *tahitense* as two varieties of *C. bulbosum*, below species number *67*, in his enumeration of Tahitian mosses. It is almost certain that Nadeaud's *C. bulbosum* var. *bulbosum* represent *C. tahitense*, whereas his variety *C. b.* var. *tahitense* belongs to *Garovaglia* Endl. (see also '*Cyathophorum tahitense*', note 2, p. 310).

When Bescherelle (1895) received a collection of *Cyathophorum bulbosum* from Tahiti (*Nadeaud 67*), he re-identified this moss. Based on this collection, he described his new species *Garovaglia tahitensis* and he cited this material as one of the syntypes of his new species. It is almost certain, that only Nadeaud's *Cyathophorum bulbosum* var. *tahitense* is of concern here (see also '*Cyathophorum tahitense*', note 2, p. 310), and it is beyond doubt that Bescherelle's material is type material of this variety.

Later, a specimen of this collection has been designated as the lectotype of this taxon by During (1977), who changed the rank of this taxon into that of a variety of *Garovaglia powellii*.

Cyathophorum dupuisii Renauld & Cardot, Bull. Soc. Roy. Bot. Belgique 38 (1899) 42. — Type: *Dupuis s.n.* (n.v.), tropical Africa, Democratic Republic of Congo (Zaire), upper basin, 300 km W of northern point of Tanganyika Lake, near Nyangoué, Narega Forest, 4° S. ≡ *Rhacopilopsis dupuisii* (Renauld & Cardot) Renauld & Cardot, Rev. Bryol. Lichénol. 27 (1900) 47. = **Rhacopilopsis trinitensis** (Müll.Hal. p.p.) E. Britton & Dixon, J. Bot. 60 (1922) 86; fide Britton & Dixon l.c., p. 88.

Cyathophorum limbatulum Renauld & Cardot, Rev. Bryol. Lichénol. 23 (1896) 108. — *Cyathophorum limbatum* Renauld & Cardot ex Broth. ex Wijk, Margad. & Florsch., Regnum Veg. 17 (1959) 528, nom. inval., err. pro *Cyathophorum limbatum* Renauld & Cardot ex Cardot ['Ren. et Card'] ex Wijk, Margad. & Florsch., Regnum Veg. 65 (1969) 508, nom. inval., err. pro *Cyathophorum limbatulum* Renauld & Cardot; see note 1. — Type: *Massart 1586* (n.v.), Indonesia, Java, Forest of Tjibodas. ≡ *Epipterygium limbatulum* (Renauld & Cardot) Besch.; fide Bescherelle, Bull. Soc. Bot. France 45 (1898) 66. ≡ *Eriopus limbatulus* (Renauld & Cardot) M. Fleisch. in Paris, Index Bryol. ed. 2, 2 (1904) 154; fide Fleischer in Paris l.c.; fide Fleischer, Musc. Buitenzorg 3 (1908) 1010. = **Calyptrochaeta ramosa** (M. Fleisch.) B.C. Tan & H. Rob., Smithsonian Contrib. Bot. 75 (1990) 10; fide Tan & Robinson l.c.

Notes — 1. Van der Wijk et al. (1959, 1969) erronously treated *Cyathophorum limbatum* Renauld & Cardot in Cardot (1901), which was given in a note below *Eriopus remotifolius* Müll.Hal., as an error for *C. limbatulum* Renauld & Cardot. Presumably, Van der Wijk et al. (1959, 1969) were confused by Cardot's (1901) remark on *C. limbatulum* Renauld & Cardot at the end of the note on *C. limbatum*, because this remark is textually only weakly separated from the note. Van der Wijk et al. (1959, 1969) were probably also confused by the similarity between the two epithets. In addition, they must also have overlooked that Renauld & Cardot (1896) and Cardot (1897) gave *Cyathophorum limbatum* and *C. limbatulum* as two separate species.

Van der Wijk et al. (1959) stated that Fleischer (1908) reduced *Cyathophorum limbatulum* to *Eriopus remotifolius* Müll.Hal., but corrected this in 1969. Although Fleischer remarked that *C. limbatulum* may represent a small form of *E. remotifolius*, he still treated it as a separate species when he transferred it to *Eriopus*.

2. The description and illustrations given by Cardot (1897) remind of a *Calyptrochaeta* species and show that *Cyathophorum limbatulum* does not belong to *Cyathophorum*.

Cyathophorum limbatum Renauld & Cardot, Rev. Bryol. Lichénol. 23 (1896) 107. — Syntypes: *Massart 1175 ex parte, 1270 ex parte, 1395 ex parte* (n.v.), Indonesia, Java, Forest of Tjibodas. = *Eriopus remotifolius* Müll.Hal.; fide Cardot, Rev. Bryol. Lichénol. 28 (1901) 118.; fide Fleischer, Musc. Buitenzorg 3 (1908) 1002, 1006. ≡ **Calyptrochaeta remotifolia** (Müll.Hal.) Z. Iwats., B.C. Tan & Touw, J. Hattori Bot. Lab. 44 (1978) 150.

Note — The description and illustrations given by Cardot (1897) clearly show that *Cyathophorum limbatum* does not belong to *Cyathophorum*, and very much resemble those of a *Calyptrochaeta* species.

Cyathophorum (*'Cyatophorum'*) *splendidissimum* (Mont.) Hampe & Lorentz in Lorentz, Bot. Zeit. (Berlin) 24 (1866) 188. — *Hookeria splendidissima* Mont., Ann. Sci. Nat. Bot. 2, 4 (1835) 97. = *Lamprophyllum splendidissimum* (Mont.) Schimp. ex Broth., Nat. Pflanzenfam. ed. 1, 3 (1907) 963, 964, f. 702., nom. gen. illeg. ≡ **Schimperobryum splendidissimum** (Mont.) Margad., Acta Bot. Neerl. 8 (1959) 275.

Hypopterygium arcuatum (Hedw.) Müll.Hal., Syn. Musc. Frond. 2 (1850) 13. — *Hypnum arcuatum* Hedw, Sp. Musc. Frond. (1801) 245, t. 62, f. 1–7. — Type: "Insulae australes", (material absent from Hedwig's herbarium, fide Touw, Blumea 19, 2 (1971) 269); lectotype: Hedwig, Sp. Musc. Frond. (1801) t. 62 f. 1–7, designated by Touw l.c. ≡ **Hypnodendron arcuatum** (Hedw.) Lindb. ex Mitt., fide Touw l.c.

Hypopterygium flaccidum Colenso, Trans. & Proc. New Zealand Inst. 21 (1889) 44, hom. illeg., [non Mitt. in Seem., Fl. Vit. (1873) 390, (= *Hypopterygium tamarisci* (Sw.) Brid. ex Müll.Hal.); nec Sull., U.S. Expl. Exped., Musc. (1860) 27 (102), nom. nud. in syn. (= *Hypopterygium flavescens* Hampe = *Hypopterygium tamarisci* (Sw.) Brid. ex Müll.Hal.)]. — *Hypopterygium colensoi* Paris, Index Bryol. (1896) 699. — Type: *Colenso s.n.* (WELT holo, sub no. *M 4016*), New Zealand, North Island, Hawke's Bay Land District, Dannevirke, humile Creek ("1 Spn. hum. Ck."), "w. [= with] *Symphyogyna*" ["Dry sides of watercourses among small Hepaticae, woods, Dannevirke, County of Waipawa, 1888"]. = **Hypnodendron arcuatum** (Hedw.) Lindb. ex Mitt.

Note — The holotype has correctly been identified by Sainsbury; Sainsbury's identification has recently been verified by Touw.

Although the specimen that is cited here is not indicated as the type of *Hypopterygium flaccidum* Colenso, it is presented with this name, and almost certainly represents the holotype. The annotations by Colenso that are attached to this specimen agree rather well with Colenso's (1889) protologue. According to Pitt (in litt., 1994) there is no other Colenso material so designated in WELT, and I have not seen such material in BM or any other herbaria.

According to Sainsbury in annotations dated 21-9-1947 that are attached to the holotype of *Hypopterygium vulcanicum* Colenso, the type of *H. flaccidum* had been preserved with a few other mosses that were also newly described by Colenso (1889). Among them were the types of *H. vulcanicum* and *H. marginatum* Colenso A later, but undated, anonymous note attached to the type of *H. vulcanicum* stated that since these specimens have been separately preserved in WELT under their correct names, among which *Hypnodendron arcuatum* (Hedw.) Lindb. ex Mitt., which can only be linked with *Hypopterygium flaccidum*.

Hypopterygium lutescens Hornsch., Linnaea 15 (1841) 144. — Type: *Drège s.n.* (B holo, destroyed; S), South Africa, Cape of Good Hope, ["Auf dem Vorgebirge der guten Hoffnung ohne nähere Angabe des Standortes."]. — Already excluded from the Hypopterygiaceae Mitt. by Kindberg, Hedwigia 40 (1901) 297. — Treated by Sim, Trans. Roy. Soc. South Africa 15 (1926) 447, as an *Hypopterygium* species, but because of its narrow cells the suggestion was made, that the moss perhaps belongs to *Porothamnium* M. Fleisch. = **Porothamnium** species, fide Magill & Schelpe, Mem. Bot. Surv. S. Africa 43 (1979) 23.

Notes — 1. The collection in S contains a few leaves only, but they show that the moss beyond any doubt belong to a *Porothamnium* species.

2. Van der Wijk et al. (1969: 739) overlooked Hornschuch's (1841) earlier name, and incorrectly considered *Hypopterygium lutescens* a nomen nudum that was published by Hornschuch in Shaw (1878: 380).

Hypopterygium marginatum W. Frey & Beever, Nova Hedwigia 61 (1995) 336, [non Colenso, Trans. & Proc. New Zealand Inst. 21 (1889) 44]; nom. inval., err. pro **Hypnodendron marginatum** (Hook.f. & Wilson) Lindb. ex A. Jaeger.

Müller (1850) changed the rank of Palisot de Beauvois's (1805) genus *Racopilum* to that of a section of *Hypopterygium* Brid. However, Müller's classification of *Racopilum* as a section of *Hypopterygium* has neither been followed by other authors nor by Müller himself after the fifties of the nineteenth century. Müller's classification has minor nomenclatural consequences for the following taxa:

Hypopterygium Brid. sect. *Racopilum* (P. Beauv.) Müll.Hal., Syn. Musc. Frond. 2 (1850) 11, '*Rhacopilum*'. — *Racopilum* P. Beauv., Prodr. (1805) 36. — Lectotype: *Racopilum mnioides* P. Beauv., designated by Bridel in Léman, Dict. Sci. Nat. 44 (1826) 341. ≡ **Racopilum** P. Beauv.

Hypopterygium convolutaceum Müll.Hal., Syn. Musc. Frond. 2 (1850) 13. — *Racopilum convolutaceum* (Müll.Hal.) Reichardt in Fenzl, Reise Novara, Bot., 1(3) (1870) 194. — Type: *Preiss* (B holo destroyed), Australia, King Island ["Nova Hollandia: Preiss. Ex Isle de King Novae Hollandiae habuit Hb. Reg. Berol."]; neotype: *Von Mueller* (BM n.v.), Australia, Victoria, East Gippsland; designated by Van Zanten & Hofman, Fragm. Florist. Geobot. 40 (1) (1995) 411. ≡ **Racopilum cuspidigerum** (Schwägr.) Ångstr. var. **convolutaceum** (Müll.Hal.) Zanten & L.J. Dijkstra, fide Van Zanten & Dijkstra in Van Zanten & Hofman l.c.

Hypopterygium schmidii Müll.Hal., Bot. Zeitung (Berlin) 12 (1854) 558. — *Racopilum schmidii* (Müll.Hal.) Mitt., J. Proc. Linn. Soc., Bot., Suppl. 1 (1859)136. — Type: *Perrottet & Schmid s.n.* (n.v., B holo presumably destroyed), India, Tamil Nadu, Nilgiri Hills ['Neilgherri Mts'], near Ootacamund. ≡ **Racopilum schmidii** (Müll.Hal.) Mitt., fide Mitten l.c.

Hypopterygium spectabile (Reinw. & Hornsch.) Müll.Hal., Syn. Musc. Frond. 2 (1850) 13. — *Racopilum spectabile* Reinw. & Hornsch., Nova Acta Phys.-Med. Acad. Caes. Leop.-Carol. Nat. Cur. 14(2) (1829) 721, t. 40 f. c 1–5. — Type: 'Java'; presumably collected by Reinwardt (not seen with certainty in L). ≡ **Racopilum spectabile** Reinw. & Hornsch., fide Van den Bosch & Van der Sande Lacoste, Bryol. Jav. 2 (1861) 16.

Hypopterygium strumiferum Müll.Hal., Bot. Zeitung (Berlin) 9 (1851) 563. — *Racopilum strumiferum* (Müll.Hal.) Mitt., J. Proc. Linn. Soc., Bot. 4 (1859, '1860') 93. — Type: *Mossman 732* (n.v., B holo presumably destroyed), New Zealand, North Island, North Auckland L.D., Kiapara Harbour, "supra saxa et truncos arborum prostatum, in sylvis prope Kaipara". ≡ **Racopilum strumiferum** (Müll.Hal.) Mitt., fide Mitten l.c.

Hypopterygium tomentosum (Hedw.) Müll.Hal., Syn. Musc. Frond. 2 (1850) 12. — *Hypnum tomentosum* Sw. ex Hedw., Sp. Musc. Frond. (1801) 240. — *Racopilum tomentosum* (Hedw.) Brid., Muscol. Recent. Suppl. 4 (1818, '1819') 152. — Type: 'Hispaniola'; presumably collected by Swartz (G n.v.). ≡ **Racopilum tomentosum** (Hedw.) Brid., fide Van den Bosch & Van der Sande Lacoste, Bryol. Jav. 2 (1861) 19.

REFERENCES

Akiyama, H. 1988. Bryophyta. In: M. Kato (ed.), Taxonomic studies of the plants of Seram Island: 13–59. Tokyo.

Akiyama, H. 1992. Taxonomic studies of mosses of Seram and Ambon (Moluccas, East Malesia) collected by Indonesian-Japanese Botanical Expeditions, V Hypopterygiaceae. Acta Phytotax. Geobot. 43: 111–120.

Akiyama, H. & N. Nishimura. 1993. Further studies on branch buds in mosses; "pseudoparaphyllia" and "scaly leaves". J. Plant. Res. 106: 101–108

Allison, K.W. & J. Child. 1971. The mosses of New Zealand. Dunedin.

Allorge, V. 1974. La Bryoflore de la Forêt de Bussaco (Portugal). Rev. Bryol. Lichénol. 40: 307–452.

Anderson, L.E. 1963. III. Modern species concepts: mosses. Bryologist 66: 107–119.

Ångström, J. 1876. Primae linae muscorum cognoscendorum, qui ad Caldas Brasiliae sunt collecti. 1. Musci frondosi et Sphagna. Öfvers. Förh. Kongl. Svenska Vetensk.-Akad. 4: 3–50.

Argent, G.C.G. 1973. A taxonomic study of African Pterobryaceae and Meteoriaceae. I. Pterobryaceae. J. Bryol. 7: 353–378.

Arnott, G.A.W. 1825. Disposition Méthodique des Espèces de Mousses. Paris.

Arnott, G.A.W. 1826. Nouvelle Disposition Méthodique des Espèces de Mousses, Mém. Soc. Hist. Nat. Paris 2, 2: 249–320, 412–414.

Bartram, E.B. 1931. Mosses of Raiatea, Society Islands. B.P. Bishop Mus. Occ. Papers 9: 3–14.

Bartram, E.B. 1933. Manual of Hawaiian mosses. Bishop Mus. Bull. 101: 1–275.

Bartram, E.B. 1939. Mosses of the Philippines. Philipp. J. Sci. 68: 1–437, pl. 1–29.

Bastow, R.A. 1887. Tasmanian mosses. Pap. & Proc. Roy. Soc. Tasmania 1886: 38–102.

Bates, J.W. 1998. Is 'life-form' a useful concept in bryophyte ecology? Oikos 82: 223–237.

Beever, J.E. 1984. Moss epiphytes of tree-ferns in a warm-temperate forest, New Zealand. J. Hattori Bot. Lab. 56: 89–95.

Beever, J.E. 1990. Report on the 7th John Child Bryophyte Workshop, Fiordland, New Zealand, 15–20 November, 1990. Australasian Bryological Newsletter 23: 1–3.

Beever, J.E., K.W. Allison & J. Child. 1992. The mosses of New Zealand. Dunedin.

Berthier, J. 1972. Recherches sur la structure et le développement de l'apex du gamétophyte feuillé des Mousses. Rev. Bryol. Lichénol. 38: 421–550, pl. 1–30.

Bescherelle, E. 1873. Florule bryologique de la Nouvelle-Calédonie. Ann. Sci. Nat. Bot. 5, 18: 184–245.

Bescherelle, E. 1877. Note sur les mousses du Paraguay récoltées par M. Balansa. Mém. Soc. Nat. Sci. Nat. Cherbourg 21: 257–272.

Bescherelle, E. 1880. Florule bryologique de la Réunion et des autres Îles Austro-Africaines de l'Ocean Indien. 2. Ann. Sci. Nat. Bot. 6, 10: 233–332.

Bescherelle, E. 1893. Nouveaux documents pour la florule bryologique du Japon. Ann. Sci. Nat. Bot. 7, 17: 327–393.

Bescherelle, E. 1894. Cryptogamae Centrali-Americanae in Guatemala, Costa-Rica, Columbia & Ecuador a cl. F. Lehmann lectae. Musci. Bull. Herb. Boissier 2, 6: 389–400.

Bescherelle, E. 1895. Florule bryologique de Tahiti et des Iles de Nukahiva et Mangareva. Ann. Sci. Nat. Bot. 7, 20: 1–62.

Bescherelle, E. 1898a. Florule bryologique de Tahiti (Supplément). Bull. Soc. Bot. France 45: 52–67.

Bescherelle, E. 1898b. Florule bryologique de Tahiti (Supplément); Deuxième partie. Bull. Soc. Bot. France 45: 116–128.

Bizot, M. & T. Pócs. 1982. East African bryophytes. 5. Acta Bot. Acad. Sci. Hung 28: 15–64.

Breen, R.S. 1953. Tropical mosses on limestone. Bryologist 56: 1–7.

Breen, R.S. 1963. Mosses of Florida. Gainesville.

Bremer, K. 1988. The limits of amino-acid sequence data in angiosperm phylogenetic reconstruction. Evolution 42: 795–803.

Bridel, S.E. 1797. Muscologiae recentiorum. 1. Gotha, Paris.

Bridel, S.E. 1798–1803. Muscologiae recentiorum. 2. Gotha, Paris.

Bridel, S.E. ['a Bridel']. 1806. Muscologiae recentiorum supplementum seu species muscorum. 1 Gotha.

Bridel, S.E. ['a Bridel']. 1812. Muscologiae recentiorum supplementum seu species muscorum. 2. Gotha.

Bridel, S.E. ['a Bridel']. 1817. Muscologiae recentiorum supplementum seu species muscorum. 3. Gotha.

Bridel, S.E. ['a Bridel']. 1819. Muscologiae recentiorum supplementum. 4. Mantissa generum specierumque muscorum frondosorum universa. Methodus nova muscorum. Gotha.

Bridel, S.E. ['a Bridel-Brideri']. 1827. Bryologia universa. 2. Leipzig.

Bridson, G.D.R. & E.R. Smith. 1991. Botanico-Periodicum-Huntianum / Supplementum. Hunt Institue for Botanical Documentation, Carnegie Mellon University, Pittsburgh.

Briggs, J.C. 1989. The historic biogeography of India: isolation or contact? Syst. Zool. 38: 322–332.

Britton, E.G. 1913. West Indian mosses. 1. Bull. Torr. Bot. Cl. 40: 653–676, pl. 25.

Brizi, U. 1893. Sopra alcune particolarità morfologiche, istologiche e biologiche dei Cyathophorum. Atti Reale Accad. Lincei, Rendiconti Cl. Sci. Fis., ser. 5, 2: 102–109.

Brizi, U. 1897. Contributio allo studio morfologico, biologico e sistematico delle Muscinee. Annuario Reale Ist. Bot. Roma 6: 275–369, tab. 22–30.

Brotherus, V.F. 1890. Musci Novi Insularum Guineensium. Bol. Soc. Brot. 8: 173–190.

Brotherus, V.F. 1893. Some new species of Australian mosses, II. Oefvers. Förh. Finska Vetensk.-Soc. 35: 34–56.

Brotherus, V.F. 1894. Musci africani. 1. Bot. Jahrb. Syst. 20: 176–218.

Brotherus, V.F. 1901. Musci. In: K. Schuman & K. Lauterbach (eds.), Fl. Deutsch. Schutzgeb. Südsee. Leipzig. p. 79–104.

Brotherus, V.F. 1907. Hypopterygiaceae. In: A. Engler & K. Prantl. (A. Engler) (eds.), Die natürlichen Pflanzenfamilien. Ed. 1, T. 1, Abt. 3, H. 1, 2: 964–972.

Brotherus, V.F. 1909. Musci novi Philippinensis. Leafl. Philipp. Bot. 2: 651–658.

Brotherus, V.F. 1910. Musci. In: G.W.J. Mildbraed, Wissenschaftliche Ergebnisse der Deutschen Zentral-Afrika-Expedition 1907–1908 unter Führung Adolf Friedrichs, Herzogs zu Mecklenburg, Bd. 2 (Botanik): 136–176.

Brotherus, V.F. 1913. Contributions to the bryological flora of the Philippines, IV. Philipp. J. Sci. 8C: 65–98.

Brotherus, V.F. 1920a. Contribution à la flore bryologique de l'Ecuador. Rev. Bryol. 47: 35–46.

Brotherus, V.F. 1920b. Musci novi Japonici. Oefvers. Förh. Finska Vetensk.-Soc. 62A: 1–55.

Brotherus, V.F. 1925. Hypopterygiaceae. In: A. Engler, A. & K. Prantl. (A. Engler) (eds.), Die natürlichen Pflanzenfamilien. Ed. 2, Bd. 11: 270–278.

Brotherus, V.F. 1927. Hawaiian mosses. Bishop Mus. Bull. 40: 1–37. 1927.

Brotherus, V.F. & W.W. Watts. 1915. The mosses of the New Hebrides. J. & Proc. Roy. Soc. New South Wales 49: 127–157.

Brummitt, R.K. & C.E. Powell. 1992. Authors of Plant Names. Royal Botanic Gardens, Kew.

Buck, W.R. 1987. Taxonomical and nomenclatural arrangement in the Hookeriales with notes on West Indian taxa. Brittonia 39: 210–224.

Buck, W.R. 1988. Another view of familial delimitation in the Hookeriales. J. Hattori Bot. Lab. 64: 29–36.

Buck, W.R., B. Goffinet & A.J. Shaw. 2000a. Testing morphological concepts of orders of pleurocarpous mosses (Bryophyta) using phylogeny reconstructions based on trnL–trnF and rps4 sequences. Mol. Phylogenet. Evol. 16: 180–198.

Buck, W.R., B. Goffinet & A.J. Shaw. 2000b. Novel relationships in pleurocarpous mosses as revealed by cpDNA sequences. Bryologist 103: 774–789.

Buck, W.R. & D.H. Vitt. 1986. Suggestions for a new familial classification of pleurocarpous mosses. Taxon 35: 21–60.

Burges, A. 1935. Notes on the mosses of New South Wales. 2. Proc. Linn. Soc. New South Wales 60: 83–83. 1935.

Burr, I.L. 1938. The development of the antheridium, archegonium, and sporogonium of Cyathophorum bulbosum (Hedw.) C.M. Trans. & Proc. Roy. Soc. New Zealand 68: 437–456, pl. 44–51.

Burrett, C., N. Duhig, R. Berry & R. Varne. 1991. Asian and South-western Pacific continental terranes derived from Gondwana, and their biogeographic significance. Aust. Syst. Bot. 4: 13–24.

Campbell, H.J., P.B. Andrews, A.G. Beu, P.A. Maxwell, A.R. Edwards, M.G. Laird, N. deB Hornibrook, D.C. Mildenhall, W.A. Watters, J.S. Buckeridge, D.E. Lee, C.P. Strong, G.J. Wilson, B.W. Hayward. 1993. Cretaceous-Cenozoic geology and biostratigraphy of the Chatham Islands. New Zealand. Inst. Geol. Nucl. Sci. Monogr. 2: 1–269.

Cande, S.C., J.M. Stock, R.D. Müller & T. Ishihara. 2000. Cenozoic motion between East and West Antarctica. Nature 404: 145–150.

Cardot, J. 1897. Contribution à la flore bryologique de Java. Mousses récoltées par M.J. Massart. Ann. Jard. Bot. Buitenzorg, Suppl. 1: 1–31, pl. 1–7.

Cardot, J. 1901. Note sur deux collections de mousses de l'Archipel Indien. Rev. Bryol. 28: 112–118.

Cardot, J. 1911. Mousses nouvelles du Japon et de Corée. Bull. Soc. Bot. Genève, Sér. 2, 3: 275–294.

Cardot, J. 1912. Mousses nouvelles du Japon et de Corée. Bull. Soc. Bot. Genève, Sér. 2, 4: 378–387.

Catcheside, D.G. 1980. Mosses of South Australia. Adelaide.

Cech, T.R. 1988. Conserved sequences and structures of group I introns: building an active site for RNA catalysis – a review. Gene 73: 259–271.

Chen, P.C. 1955. Bryophyta nova Sinica. Feddes Repert. Spec. Nov. Regni Veg. 58: 23–52.

Chen, P.C., J.S. Lou, M.S. Guo & W.Q. Shi. 1978. Genera muscorum Sinicorum. 2. Beijing. (In Chinese).

Chopra, R.S. 1975. Taxonomy of Indian mosses. Bot. Monogr. Council Sci. Industr. Res., India 10: i–xi, 1–631.

Churchill, S.P. & E.L. Linares. 1995. Prodromus Bryologiae Novo-Granatensis. Bibliotheca Jose Jeronimo Triana 12, 1: 1–454 + i–xxvi.

Colenso, W. 1886. A description of some newly-discovered cryptogamic plants, being a further contribution towards the making known the botany of New Zealand. Trans. & Proc. New Zealand Inst. 18: 219–255.

Colenso, W. 1887. A Description of some newly-discovered Cryptogamic Plants, being a further Contribution towards the making known the Botany of New Zealand. Trans. & Proc. New Zealand Inst. 19: 271–301.

Colenso, W. 1889. A Description of some newly-discovered Cryptogamic Plants; being a further Contribution towards the making known the Botany of New Zealand. Trans. & Proc. New Zealand Inst. 21: 43–80.

Correns, C. 1899. Untersuchungen über die Vermehrung der Laubmoose durch Brutorgane und Stecklinge. Jena.

Cox, C.J., B. Goffinet, A.E. Newton, A.J. Shaw & T.A.J. Hedderson. 2000. Phylogenetic relationships among the diplolepideous-alternate mosses (Bryidea) inferred from nuclear and chloroplast DNA sequences. Bryologist 103: 224–241.

Crosby, M.R. 1974. Toward a revised classification of the Hookeriaceae (Musci). J. Hattori Bot. Lab. 38: 129–141.

Crosby, M.R. & C.R. Bauer. 1987. Index muscorum supplementum: 1984–1985. Taxon 36: 502–527.

Crum, H.A. 1972. The geographic origin of the mosses of North America's eastern deciduous forest. J. Hattori Bot. Lab. 35: 269–298.

Cufodontis, G. 1951. Vorläufige Aufzählung der Laubmoose Aethiopiens. Oesterr. Bot. Zeit. 98: 217–244.

Dalton, P.J., R.D. Seppelt & A.M. Buchanan. 1991. An annotated checklist of Tasmanian mosses. In: M.R. Banks et al. (eds.), Aspects of Tasmanian Botany – a tribute to Winifred Curtis: 15–32. Hobart.

Daly, M.C, M.A. Cooper, I. Wilson, D.G. Smith, & B.G.D. Hooper. 1991. Cenozoic plate tectonics and basin evolution in Indonesia. Marine and Petroleum Geology 8: 2–21.

Dalziel, I.W.D. & D.H. Elliot. 1982. West Antarctica: problem child of Gondwanaland. Tectonics 1: 3–19.

De Jong, Y.S.D.M., G.M. Lokhorst & J.D. Kruijer. 2000. Genealogy in Microspora Thuret (Chlorophyceae). Blumea 45: 477–484.

De Labillardière, J.J.H. 1800. Relation du voyage à la recherche de la Pérouse.1. Paris.

De Labillardière, J.J.H. 1806. Novae Hollandiae plantarum specimen. Bd. 2 (pl. 143–265). Paris.

De Luna, E., W.R. Buck, H. Akiyama, T. Arikawa, H. Tsubota, D. González, A.E. Newton & A.J. Shaw. 2000. Ordinal phylogeny within the hypnobryalean pleurocarpous mosses inferred from cladistic analyses of three chloroplast DNA sequence data sets: trnL–F, rps4, and rbcL. Bryologist 103: 242–256.

De Luna, E., A. Newton, A. Withey, D. Gonzalez & B. Mishler. 1999. The transition to pleurocarpy: a phylogenetic analysis of the main diplolepidous lineages based on rbcL sequences and morphology. Bryologist 102: 634–650.

De Sloover, J.L. 1994. Les mousses de Mooréa (Polynésie Française). Cryptogamie, Bryol. Lichénol. 15: 291–310.

De Vries, A., J.P.J. Bramer, B.O. van Zanten, A. Hofman & R. Bijlsma. 1989. Allozyme variation in populations of four Racopilum species, including the polyploid R. tomentosum. Lindbergia 15: 47–59.

Deckart, K., G. Féraud, L.S. Marques & H. Bertrand. 1998. New time constraints on dyke swarms related to the Paraná–Etendeka magmatic province, and subsequent South Atlantic opening, southeastern Brazil. J. Volcanol. Geoth. Res. 80: 67–83.

Deguchi, H. & T. Kariyasaki. 1991. Preliminary list of mosses of Tanegashima Island, Southern Japan. Mem. Fac. Sci. Kochi Univ., D 12: 11–15.

Diddell, M.W. & E.M. Shields. 1943. A moss new to Florida. Bryologist 46: 22–23.

DiVenere, V. & D.V. Kent. 1999. Are the Pacific and Indo-Atlantic hotspots fixed? Testing the plate circuit through Antarctica. Earth Planet. Sci. Lett. 170: 105–117.

Dixon, H.N. 1914. Report on the mosses of the Abor Expedition 1911–1912. Rec. Bot. Surv. India 6: 56–73, pl. 1–2.

Dixon, H.N. 1918. Uganda mosses collected by R. Dümmer and others. Smith. Misc. Collect. 69(8): 1–10, pl. 1.

Dixon, H.N. 1922. The mosses of the Wollaston Expedition to Dutch New Guinea, 1912–1913; with some additional mosses from British New Guinea. J. Linn. Soc., Bot. 45: 477–510.

Dixon, H.N. 1926. A list of the mosses of the Malay Peninsula. Gard. Bull. Straits Settlem. 15: 1–46.

Dixon, H.N. 1927. Studies in the bryology of New Zealand with special reference to the herbarium of Robert Brown. New Zealand Inst. Bull. 3, 5: 239–298.

Dixon, H.N. 1929. Index of Families, Genera and Synonyms (Studies in the bryology of New Zealand). New Zealand Inst. Bull. 3, 6: v–xviii.

Dixon, H.N. 1932. On the moss flora of Siam. J. Siam Soc., Nat. Hist. Suppl. 9: 1–51

Dixon, H.N. 1935. A contribution to the moss flora of Borneo. J. Linn. Soc., Bot. 50: 57–140, pl. 1–4.

Dixon, H.N. 1936. Decas generum novorum muscorum. J. Bot. 74: 1–10 + pl. 610.

Dixon, H.N. 1937. Notulae bryologicae 1. J. Bot. 75: 121–129.

Dixon, H.N. 1941. Additions to the Mosses of North Queensland. Proc. Roy. Soc. Queensland 53: 23–40.

Dixon, H.N. 1942. Some new Japanese Mosses. Rev. Bryol. Lichénol. 13: 10–19.

Dixon, H.N. & W. Greenwood. 1930. The mosses of Fiji. Proc. Linn. Soc. New South Wales 55: 261–302.

Docters van Leeuwen, W.M. 1936. Krakatau 1883–1933. A. Botany. Ann. Jard. Bot. Buitenzorg 46–47: 1–506.

Downing, A.J., P.M. Selkirk & R.J. Oldfield. 1997. The mosses of the Yarrangobilly Caves District, New South Wales, Australia. A review of the mosses collected by the reverend W.W. Watts in 1906. J. Hattori Bot. Lab. 82: 105–121.

Drinnan, A.N. & P.R. Crane. 1990. Cretaceous paleobotany and its bearing on the biogeography of austral angiosperms. In: T.N. & E.L. Taylor (eds.), Antarctic paleobiology: 192–219. New York.

Duarte Bello, P.P. 1997. Musgos de Cuba. Fontqueria 47: 1–717.

During, H.J. 1977. A taxonomical revision of the Garovaglioideae (Pterobryaceae, Musci). Bryophyt. Biblioth. 12: 1–244, f. 1–80.

Edwards, S.R. 1979. Taxonomic Implications of Cell Patterns in Haplolepideous Moss Peristomes. In: G.C.S. Clarke & J.G. Duckett (eds.), Bryophyte Systematics: 317–346. London, New York.

Enroth, J. 1993. Taxonomic results of the BRYOTROP Expedition to Zaire and Rwanda. 23 Neckeraceae, Pterobryaceae, Hypopterygiaceae. Trop. Bryol. 6: 193–198.

Enroth, J. 1994. A taxonomic monograph of the genus Pinnatella (Neckeraceae, Bryopsida). Acta Bot. Fennica 151: 1–90.

Erdtman, G. 1965. An Introduction to Palynology. 3. Pollen and Spore Morphology / Plant Taxonomy. Gymnospermae, Bryophyta. Stockholm.

Eriksson, T. 1998. AutoDecay version 4.0. Dept. of Botany, Stockholm University, Stockholm.

Ernst, A. 1908. The New Flora of the Volcanic Island of Krakatau, (translated by A.C. Seward), Cambridge.

Felsenstein, J. 1985. Confidence limits on phylogenies: an approach using the bootstrap. Evolution 39: 783–791.

Fife, A.J. ['A.']. 1993. Bryological studies at British Museum. Australasian Bryological Newsletter 28: 1–2.

Fife, A.J. 1996. Lectotypification of Weissia radians Hedw., a neglected name for a widespread Australasian moss species, with notes on the status of Funaria glabra Tayl. and the typification of some other Hedwigian names. J. Bryol. 19: 39–48.

Fleischer, M. 1902. Die Musci der Flora von Buitenzorg (zugleich Laubmoosflora von Java). Bd. 1. Flore de Buitenzorg V, 1, Leiden.

Fleischer, M. 1908. Die Musci der Flora von Buitenzorg (zugleich Laubmoosflora von Java). Bd. 3. Flore de Buitenzorg V, 3. Leiden.

Fleischer, M. 1923a. Die Musci der Flora von Buitenzorg (zugleich Laubmoosflora von Java). Bd. 4. Flore de Buitenzorg V, 5. Leiden.

Fleischer, M. 1923b. Beitrag der Laubmoosflora der Vulkaninsel Krakatau. Ann. Jard. Bot. Buitenzorg 23: 105–109.

Forster, R.M. 1982. A study of the Spatial Distribution of Bryophytes on Rakata. In: J.R. Flenley & K. Richards (eds.), The Krakatoa Centenary Expedition. Final Report, Depart. of Geography, University of Hull, Miscellaneous Series 25: 103–126.

Frahm, J.-P. 1975. Conspectus der mittel- und südamerikanischen Campylopus-Arten (Dicranaceae). Vaduz.

Frey, W. 1981. Morphologie und Anatomie der Laubmoose. Advances in Bryology 1: 399–478.

Frey, W. & J.E. Beever. 1995. Dendroid bryophyte communities of New Zealand. Nova Hedwigia 61: 323–354.

Frey, W., H.H. Hilger & U. Richter. 1983. Kanalsysteme in den Stämmchen des Bäumchenmooses Hypopterygium commutatum C. Müll. (Hypopterygiaceae, Musci), J. Hattori Bot. Lab. 54: 307–319.

Frey, W. & U. Richter. 1982. Perforierte Hydroiden bei Laubmoosen? J. Hattori Bot. Lab 51: 51–60.

Frey, W. & A. Schaepe. 1989. Canalohypopterygium gen. nov. (Hypopterygiaceae, Musci). Ein Beitrag zur Systematischen Stellung von Canalohypopterygium commutatum (Hypopterygium commutatum) und Catharomnium ciliatum. J. Hattori Bot. Lab. 66: 263–270.

Frey, W., M. Stech & K. Meissner. 1999. Chloroplast DNA-relationship in palaeoaustral Lopidium concinnum (Hypopterygiaceae, Musci). An example of stenoevolution in mosses. Studies in austral temperate rain forest bryophytes 2. Plant. Syst. Evol. 218: 67–75.

Frey-Wyssling, A. 1935. Die Stoffausscheidung der höheren Pflanzen. Berlin.

Froehlich, J. 1953. Die von Prof. Dr. Viktor Schiffner in den Jahren 1893/94 in Ceylon, Penang, Singapore, Sumatra und Java gesammelten Laub- und Torfmoose. Ann. Naturhist. Mus. Wien 59: 66–116.

Gangulee, H.C. 1977. Mosses of Eastern India and Adjacent Regions. 6. Hookeriales. H.C. Gangulee, Calcutta.

Gaume, R. 1963. René Henry (1884–1960). Rev. Bryol. Lichénol. 32: 293–295.

Gibbs, L.S. 1909. A contribution to the montane Flora of Fiji (including Cryptogams), with ecological notes, J. Linn. Soc., Bot. 39: 130–212, pl. 11–16.

Gnos, E., A. Immenhauser & T. Peters. 1997. Late Cretaceous / early Tertiary convergence between the Indian and Arabian plates recorded in ophiolites and related sediments. Tectonophysics 271: 1–19.

Goebel, K. 1906. Archegoniatenstudien. X. Beiträge zur Kenntnis australischer und neuseeländischer Bryophyten. Flora 96: 1–202.

Good, R. 1974. The geography of the flowering plants. Ed. 4. London

Griffith, W. 1849a. Notulae ad plantas Asiaticas. 2. Calcutta.

Griffith, W. 1849b. Icones plantarum Asiaticarum. 2. Calcutta.

Grout, A.J. 1943. Note on Hypopterygium. Bryologist 46: 24.

Grunow, A.M. 1999. Gondwana events and palaeography: a palaeomagnetic review. J. African Earth Sci. 28: 53–69.

Hall, R. 1998. The plate tectonics of Cenozoic SE Asia and the distribution of land and sea. In: R. Hall & J.D. Holloway (eds.), Biogeography and Geological Evolution of SE Asia: 99–131. Leiden.

Hampe, E. 1847. Ein Referat über die Columbischen Moose, welche von Herrn Moritz gesammelt wurden. Linnaea 20: 65–98.

Hampe, E. 1856. Plantae Muellerianae: Musci frondosi in Australasia felici lecti. Linnaea 28: 203–215.

Hampe, E. 1874a. Species muscorum novas ex Herbario Melbourneo Australiae. Linnaea 38: 661–672.

Hampe, E. 1874b. Musci frondosi a clar. Dr. A. Glaziou in vicinia urbis Rio de Janeiro lecti. In: E. Warming, Symbolae ad floram Brasiliae centralis cognosendam, 11. Vidensk. Meddel. Dansk. Naturhistor. Foren. Kjøbenhavn 3, 6: 129–178.

Hampe, E. 1880. Musci frondosi Australiae continentalis praesertim e Baronis de Mueller collectionibus. In: F.J.H. von Mueller (ed.), Fragmenta phytographiae Australiae 11, Suppl.: 45–52. Melbourne.

Heads, M. 1998. Biogeographic disjunction along the Alpine fault, New Zealand. Biol. J. Linn. Soc. 63: 161–176.

Hébant, C. 1977. The conducting tissue of bryophytes. Bryophyt. Biblioth. 10: i–xi, 1–157 + pl. 1–80. Vaduz.

Hedenäs, L. 1989. Axillary hairs in pleurocarpous mosses – a comparitive study. Lindbergia 15: 160–180.

Hedenäs, L. 1994. The basal pleurocarpous diplolepidous mosses – a cladistic approach. Bryologist 97: 225–243.

Hedenäs, L. 1995. Higher taxonomic level relationships among diplolepidous pleurocarpous mosses – a cladistic overview. J. Bryol. 18: 723–781.

Hedenäs, L. 1996a. A cladistic evaluation of relationships between the Hookeriales, the Sematophyllaceae and some other taxa. Lindbergia 21: 49–82.

Hedenäs, L. 1996b. A cladistic overview of the "Hookeriales". Lindbergia 21: 107–143.

Hedwig, J. 1784. Theoria generationis et fructificationis. St. Petersburg.

Hedwig, J. 1785–1787. Descriptio et adumbratio microscopico-analytica muscorum frondosorum. 1. Leipzig.

Hedwig, J. 1789. Descriptio et adumbratio microscopico-analytica muscorum frondosorum. 2. Leipzig.

Hedwig, J. 1791–1792. Descriptio et adumbratio microscopico-analytica muscorum frondosorum. 3. Leipzig.

Hedwig, J. 1797. Descriptio et adumbratio microscopico-analytica muscorum frondosorum. 4. Leipzig.

Hedwig, J. 1801. Species muscorum frondosorum. Leipzig.

Henry, R. 1928. Mousses d'Extrême-Orient. Rev. Bryol. Lichénol. 1: 41–48.

Herzog, T. 1910. Beiträge zur Laubmoosflora von Bolivia. Beih. Bot. Centralbl. 26: 45–102.

Herzog, T. & A. Noguchi. 1955. Beitrag zur Kenntnis der Bryophytenflora von Formosa und den benachbarten Inseln Botel Tobago und Kwashyoto. J. Hattori Bot. Lab. 14: 29–70.

Hill, R.S. & L.J. Scriven. 1995. The angiosperm-dominated woody vegetation of Antarctica: a review. Rev. Palaeobot. Palynol. 86: 175–198.

Hodgetts, N.G., H.W. Matcham & J.G. Duckett. 1999. Bryophytes collected in Lesotho, the Natal Drakensberg and Orange Free State, southern Africa. J. Bryol. 21: 133–155.

Hohenacker, R.F. 1859. Verkäufliche Pflanzensammlungen. Flora 42: 574–576.

Holmgren, P.K., N.H. Holmgren & L.C. Barnett. 1990. Index Herbariorum. Part I: The Herbaria of the World. (8th ed.). Regnum Veg. 120: i–x, 1–693.

Hooker, J.D. 1845. Summary of the voyage. In: J.D. Hooker, The botany of the Antarctic voyage. 1. Flora Antarctica. Part 1. Botany of Lord's Auckland Group and Campbell's Island: i–xii. London.

Hooker, J.D. 1857. On the botany of Raoul Island, one of the Kermadec Group in the South Pacific Ocean, J. Proc. Linn. Soc., Bot. 1: 125–129.

Hooker, J.D. 1867. Handbook of the New Zealand Flora: a systematic description of the native plants of New Zealand and the Chatam, Kermadec's, Lord Auckland's, Campbell's, and Macquarrie's Islands. London.

Hooker, J.D. & T. Thomson. 1855. Flora Indica. 1. London.

Hooker, W.J. 1818–1820. Musci Exotici, containing figures and descriptions of new or little known foreign mosses and other cryptogamic subjects. Vol. 1 & 2 . London.

Hooker, W.J. & R.K. Greville. 1825. On the genus Hookeria of Smith, of the order Musci, Edinburgh J. Sci. 2: 221–236.

Horikawa, Y. 1934a. Symbolae florae Bryophytae Orientali-Asiae 1, Bot. Mag. (Tokyo) 48: 452–462, f. 3.

Horikawa, Y. 1934b. Symbolae florae Bryophytae Orientali-Asiae 2, Bot. Mag. (Tokyo) 48: 599–609.

Horikawa, Y. 1955. The range of Cyathophorella tonkinensis (Broth. et Par.) Broth. Mitt. Thür. Bot. Ges. 1: 107–112.

Hornschuch, C.F. ['Fr.']. 1841. Muscorum frondosorum novorum, quos in Africa australiori collegerunt Ecklon, Drège, Mundt et Maire, descriptiones. Linnaea 15: 113–157.

Hu Renliang & Wang Youfang. 1987. A review of the moss flora of East China, Mem. New York Bot. Gard. 45: 455–465.

Inoue, H. 1987. Index of Type Specimens of Bryophyta in National Science Museum, Tokyo. Tokyo.

Inoue, S. 1979. A preliminary report on moss chromosome numbers. Misc. Bryol. Lichenol. 8: 109–113.

Inoue, S. & A. Uchino. 1969. Karyological studies on mosses VI. Karyotypes of fourteen species including some species with the intraspecific euploid and aneuploid. Bot. Mag. (Tokyo) 82: 359–367.

Iwatsuki, Z. & A. Noguchi. 1973. Index Muscorum Japonicarum. J. Hattori Bot. Lab. 37: 299–418.

Jaeger, A. 1876. Genera et species muscorum systematice disposita seu Adumbratio florae muscorum totius orbis terrarum. Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1874–75: 85–188.

Källersjö, M., J.S. Farris, A. Kluge & C. Bult. 1992. Skewness and permutation. Cladistics 8: 275–287.

Kim, Y.H., Y.R. Ri, H.D. Hoang, S. Huneck & R. Grolle. 1995. Bryophytes and lichens of Mts. Kumgang (DPR of Korea). Feddes Repert. 106: 291–301.

Kindberg, N.C. 1898. Studien über die Systematik der pleurokarpischen Laubmoose, Bot. Centralbl. 76: 84–87.

Kindberg, N.C. 1901. Grundzüge einer Monographie über die Laubmoos-Familie Hypopterygiaceae, Hedwigia 40: 275–303.

Koponen, T., J. Enroth, Y.-M. Fang, S. Huttunen, J. Hyvönen, M. Ignatov, A. Juslén, M.J. Lai, S. Piippo, A. Potemkin & P. Rao. 2000. Bryophyte flora of Hunan Province, China. 1. Bryophytes from Mangshan Nature Reserve and Wulingyuan Global Cultural Heritage Area, Ann. Bot. Fennici 37: 11–39.

Kruijer, J.D. 1995a. Systematics of the moss family Hypopterygiaceae Mitt. Acta Bot. Neerl. 44: 492.

Kruijer, J.D. ['H']. 1995b. Systematiek van de Hypopterygiaceae. Buxbaumiella 38: 26–32.

Kruijer, J.D. ['H']. 1996a ['1995–1996']. Canalohypopterygium tamariscinum (Hedw.) Kruijer: typfication and synonymy of a new combination. Lindbergia 20: 85–88.

Kruijer, J.D. ['H']. 1996b ['1995–1996']. Dendrocyathophorum decolyi (Fleisch.) Kruijer: a new combination. Lindbergia 20: 89–90.

Kruijer, J.D. ['H']. 1996c. Phylogeny of the Hypopterygiaceae Mitt. The British Bryological Society Centenary Symposium, 4–8 August 1996, University of Glasgow, Glasgow (abstract poster).

Kruijer, J.D. 1997a. British Bryological Society Expedition to Mulanje Mountain, Malawi 6. Hypopterygiaceae. J. Bryol. 19: 515–520.

Kruijer, J.D. 1997b. The origin of Hypopterygium-populations in some European Botanic Gardens, with special reference to Hypopterygium atrotheca Dix. Glasgow Naturalist 23, 2: 11–17.

La Farge-England, C. 1996. Growth form, branching pattern, and perichaetial position in mosses: cladocarpy and pleurocarpy redefined. Bryologist 99: 170–186.

Lai, M.J. 1976. The Hypopterygiaceae (Musci) of Taiwan. Taiwania 21: 150–158, pl. 1

Lamy, D. 1989. A.M.F.J. Palisot de Beauvois et la classification des mousses. 114^{e} Congrès National des Sociétés Savantes, Paris, 1989, Scientifiques et Sociétés. Résumés des communications: 259–273.

Lawrence, G.H.M., A.F.G. Günther Buchheim, G.S. Daniels & A. Dolezal. 1968. Botanico-Periodicum-Huntianum. Pittsburgh.

Lett, HW. 1904. Notes on Hypopterygium. J. Bot. 42: 249–252.

Lin Pan-juan & Li Zhi-hua(?). 1985. Hypopterygiaceae. In: Li Xing-jiang et al. (eds.), Bryoflora of Xizang: 290–294. (In Chinese).

Longton, R.E. 1976. Reproductive biology and evolutionary potential in bryophytes. J. Hattori Bot. Lab. 41: 205–223.

Lorch, W. 1931. Anatomie der Laubmoose. In: K. Linsbauer, Handbuch der Pflanzenanatomie 2, Bryophyten 7(1). Berlin.

Mabberley, D.J. 1985. Jupiter Botanicus. London.

Macoun, J.M. (& N.C. Kindberg?). 1902. Addendum to part VI. In: J.M. Macoun, Catalogue of Canadian Plants. 7. Geological survey of Canada: 181–318. Ottawa.

Maddison, W.P. & D.R. Maddison. 1992. A user manual for Macclade (Analysis of Phylogeny and Character Evolution), xi + 398 pp. Sinauer Associates, Inc., Sunderland, Massachusetts.

Magill, R.E. & R.E. Stotler. 1990. English bryological glossary. In: R.E. Magill, Glossarium Polyglottum Bryologiae. Monographs in Systematic Botany 33: 1–297. St. Louis.

Magill, R.E. & J. Van Rooy. 1998. Bryophyta. Part 1. Musci. 3. Erpodiaceae–Hookeriacea. In: O.A. Leistner & E. du Plessis (eds.), Flora of Southern Africa. Pretoria.

Malcolm, B. & N. 1989. The Forest Carpet. Nelson.

Margadant, W.D. 1968. Early bryological literature. PhD Thesis, Pittsburgh, Pennsylvania, USA.

Martelli, U. 1921. Odoardo Beccari. Webbia 5: 295–343.

Marticorena, C. 1995. Historia de la exploracion botanica de Chile. In:. C. Marticorena & R. Rodriguez. 1. Pteridophyta–Gymnospermae: 1–62.

Martin, W. 1949. The Bryophytes of Stewart Island. Part 1. Trans. Roy. Soc. New Zealand 77: 257–277.

Martin, W. 1950. The Bryophytes of Stewart Island. Part 2. Trans. Roy. Soc. New Zealand 78: 485–501.

Matteri, C.M. 1973. Revision de las Hypopterygiaceae (Musci) Austrosudamericanas. Bol. Soc. Argent. Bot. 15: 229–250.

Matteri, C.M. 1975. Bryophyta, Musci. Hookeriales. In: S.A. Guarrera, I. Gamundi de Amos & D. Rabinovich de Halperin, Flora Criptogámica de Tierra del Fuego 14 (9): 1–60. Buenos Aires.

Matteri, C.M. 1976. Proposal for the typification of the genus Hypopterygium Brid. 1827. Taxon 25: 189.

McGillivray, J. 1855. The voyage of H.M.S. Herald. Hooker's J. Bot. Kew Gard. Misc. 7: 303–306.

McQueen, C.B. 1985. Spatial pattern and gene flow distance in Sphagnum subtile. Bryologist 88: 333–336.

Meesters, K.A. & B.O. van Zanten. 1988. Methods in experimental biogeography. In: J.M. Glime (ed.), Methods in bryology: 307–310. Nichinan.

Menzel, M. 1988. Nomenklatur, Taxonomie und Geographie von Hypopterygium arbuscula (Hypopterygiaceae, Bryopsida). Willdenowia 18: 301–309.

Metcalfe, I. 1998. Paleozoic and Mesozoic geological evolution of the SE Asian region: multidisciplinary constraints and implications for biogeography. In: R. Hall & J.D. Holloway (eds.), Biogeography and Geological Evolution of SE Asia: 25–41. Leiden.

Michaux, B. 1989. Generalized tracks and geology. Syst. Zool. 38: 390–398.

Michaux, B. 1994. Land movements and animal distributions in east Wallacea (eastern Indonesia, Papua New Guinea and Melanesia). Palaeogeogr. Palaeocl. 112: 323–343.

Michaux, B. & I.M. White. 1999. Systematics and biogeography of southwest Pacific Bactrocera (Diptera: Tephritidae: Dacini). Palaeogeogr. Palaeocl. 153: 337–351.

Miles, C.J. & R.E. Longton. 1992. Deposition of moss spores in relation to distance from parent gametophytes. J. Bryol. 17: 355–368.

Miller, H.A. 1971. An overview of the Hookeriales. Phytologia 21: 243–252.

Miller, H.A., H.O. Whittier & B.A. Whittier. 1978. Prodromus florae muscorum Polynesiae, with a key to genera. Bryophyt. Bibl. 16: 1–334.

Miller, N.G. & M.G. Manuel. 1982. Trachyloma (Bryophytina, Pterobryaceae): a taxonomic monograph. J. Hattori Bot. Lab. 51: 273–321.

Milne, W.G. 1855. The voyage of H.M.S. Herald. Hooker's J. Bot. Kew Gard. Misc. 7: 151–155.

Mishler, B.D. & E.F. De Luna. 1991, The Use of Ontogenetic Data in Phylogenetic Analyses of Mosses. Advances in Bryology 4: 121–167.

Mitten, W. 1851. Catalogue of cryptogamic plants collected by Professor W. Jameson in the vicinity of Quito. Hooker's J. Bot. Kew Gard. Misc. 3: 49–57, 351–361.

Mitten, W. 1859. Musci Indiae Orientalis; an enumeration of the mosses of the East Indies. J. Proc. Linn. Soc., Bot., Suppl. 1: 1–171.

Mitten, W. 1860. On the mosses of New Zealand, Tasmania, etc. J. Proc. Linn. Soc., Bot. 4: 64–100.

Mitten, W. 1864. On the Musci and Hepaticae from the Cameroons Mountain and from the River Niger. J. Proc. Linn. Soc., Bot. 7: 147–169.

Mitten, W. ['G.']. 1869. Musci Austro-Americani, sive Enumeratio Muscorum omnium Austro-Americanorum mihi hucusque cognitorum, eorum praecipe in terris Amazonicis Andinisque Ricardo Spruce lectorum. J. Linn. Soc., Bot. 12: 1–659.

Mitten, W. 1873. New species of Musci collected in Ceylon by Dr. Thwaites. J. Linn. Soc., Bot. 13: 293–326, pl. 5.

Mitten, W. 1882. Australian mosses. Trans. & Proc. Roy. Soc. Victoria 18: 49–96.

Mitten, W. 1891. An Enumeration of all the Species of Musci and Hepaticae recorded from Japan. Trans. Linn. Soc. Bot. London, Ser. 2, 3: 153–206.

Mohamed, H. & H. Robinson. 1991. A taxonomic revision of the moss families Hookeriaceae and Hypopterygiaceae in Malaya. Smithsonian Contr. Bot. 80: 1–44, f. 1–168.

Montagne, C.1845. De Plantes cellulaires exotiques nouvelles. 5. Ann. Sci. Nat. Bot. 3, 4: 86–123.

Morley, R.J. 1998. Palynological evidence for Tertiary plant dispersal in the SE Asian region in relation to plate tectonics and climate. In: R. Hall & J.D. Holloway (eds.), Biogeography and Geological Evolution of SE Asia: 211–231. Leiden.

Mueller, D.M.J. & A.J. Neumann. 1988. Peristome Structure and the Regulation of Spore Release in Arthrodontous Mosses. Advances in Bryology 3: 135–158.

Mueller-Dombois, D. & F.R. Fosberg. 1998. Vegetation of the tropical Pacific islands. Ecological Studies 132: i–xxvii, 1–733. New York.

Müller, C. 1850–1851. Synopsis muscorum frondosorum. 2. Berlin. [published in 5 fasicles, 2 (6): 1–160. 1850; 2(7–10): 161–772. 1851]

Müller, C. 1854. Musci Neilgherrenses. Bot. Zeit. 12: 556–559.

Müller, C. ['K']. 1868. Beiträge zur ostaustralischen Moosflora. Linnaea 35: 613–626.

Müller, C. 1869. De muscorum Ceylonensium collectione. Linnaea 36: 1–40.

Müller, C. 1874. Musci polynesiaci praesertim Vitiani et Somoani Graeffeani. J. Mus. Godeffroy 3: 51–90.

Müller, C. 1876. Musci Hildebrandtiani in Archipelago Comorensi et in Somalia littoris Africani anno 1875 ab I.M. Hildebrandt lecti. Linnaea 40: 225–300.

Müller, C. ['K']. 1886. Beiträge zu einer Bryologie West-Afrikas. Flora 69: 499–525.

Müller, C. 1896. Bryologia Hawaiica adjectis nonnullis muscis novis oceanicis. Flora 82: 434–479.

Müller, C. 1897. Prodromus Bryologiae Argentinicae. 1. Linnaea 42: 217–460.

Nadeaud, J. 1873. Énumération des plantes Indigènes de l'île de Tahiti. Paris.

Nelson, P.P. 1973. Leptodon smithii (Musci, Neckeraceae), a genus new to North America. Bryologist 76: 434–437.

Newton, A.E. & E. De Luna. 1999. A survey of morphological characters for phylogenetic study of the transition to pleurocarpy. Bryologist 102: 651–682.

Newton, M.E. 1973. Chromosome studies in some New Zealand and Jamaican mosses. J. Bryol. 7: 399–403.

Noguchi, A. 1936a. Contributions to the moss flora of Formosa. 4. Trans. Nat. Hist. Soc. Formosa 26 (148): 34–43.

Noguchi, A. 1936b. Studies on the Japanese mosses of the orders Isobryales and Hookeriales I. J. Sci. Hiroshima Univ., Ser. B, Div. 2, Bot. 3: 11–26, pl. 1–2.

Noguchi, A. 1947. Notulae bryologiae, 1. J. Hattori Bot. Lab. 2: 6–82.

Noguchi, A. 1951. Musci Japonici (1) Hypopterygiaceae. J. Hattori Bot. Lab6: 24–32. (In Japanese).

Noguchi, A. 1952. Musci Japonici (1). Hypopterygiaceae (2). J. Hattori Bot. Lab. 7: 1–22. (In Japanese).

Noguchi, A. 1954. Notes on Japanese Musci (16). J. Japanese Bot. 29, 3: 83–86.

Noguchi, A. 1966. Musci. In: H. Hara (ed.), The Flora of Eastern Himalaya: 537–591. University of Tokyo, Tokyo.

Noguchi, A. 1973. Contributions to the bryology of Thailand. J. Hattori Bot. Lab. 37: 235–250.

Noguchi, A. 1991. Illustrated Moss Flora of Japan 4. Hattori Botanical Laboratory, Nichinan.

Noguchi, A. & Z. Iwatsuki, 1972. Mosses of North Borneo. I. J. Hattori Bot. Lab. 36: 455–486.

Norris, R.J. 1999. Dynamic landscapes: the fall and rise of a small continent. Inaugural Professorial Lecture no. 7, University of Otago, Dunedin.

Ochyra, R., H. Bednarek-Ochyra, T. Pócs & M.R. Crosby. 1992. The moss Adelothecium bogotense in continental Africa, with a review of its world range. Bryologist 95: 287–295.

Okamura, S. 1915. Contributiones novae ad Floram Bryophyton Japonicam 1. J. Coll. Sci. Imp. Univ. Tokyo 36, 7: 25. 1915.

O'Sullivan, P.B., M.M. Mitchell, A.J. O'Sullivan, B.P. Kohn, & A.J.W. Gleadow. 2000. Thermotectonic history of the Bassian Rise, Australia: implications for the breakup of eastern Gondwana along Australia's southeastern margins. Earth Planet. Sci. Lett. 182: 31–47.

Palisot de Beauvois, A.M.F.J. 1804. Prodrome de l' Aethéogamie, ou d'un Traité sur les familles de plantes don't la frutification est extraordinaire. Mag. Encycl., 9e Année 5: 289–330.

Palisot de Beauvois, A.M.F.J. 1805. Prodrome des Cinquième et Sixième Familles de l' Aethéogamie. Les Mousses. Les Lycopods. Paris.

Palisot de Beauvois, A.M.F.J. 1822. Muscologie, ou traité sur les Mousses. Mém. Soc. Linn. Paris 1: 388–472.

Paris, E.G. 1894–1898. Index Bryologicus. Paris.

Paris, E.G. 1904. Index bryologicus, ed. 2, 1. Paris.

Paris, E.G. 1905. Index bryologicus, ed. 2, 3. Paris.

Paris, E.G. 1908. Muscinées de l'Asie Orientale (7). Rev. Bryol. 35: 40–55.

Paris, E.G. 1910. Florule bryologique et hépaticologique de l'Île des Pins (Kunié). Rev. Bryol. 37: 34–42.

Patterson, C. & H.G. Owen. 1991. Indian isolation or contact? A response to Briggs. Syst. Zool. 40: 96–100.

Pelser, P.B., H. (J.D.) Kruijer, R. Verpoorte. Accepted. What is the function of oil containing rudimentary branches in the moss Canalohypopterygium tamariscinum? New Zealand J. Bot. 40.

Pfeiffer, T. 2000. Relationships and divergence patterns in Hypopterygium „rotulatum" s.l. (Hypopterygiaceae, Bryosida) inferred from trnL intron sequences. Studies in austral temperate rain forest bryophytes 7. Edinburgh J. Bot. 57: 291–307.

Pfeiffer, T., H. (J.D.) Kruijer, W. Frey & M. Stech. 2000. Systematics of the Hypopterygium tamarisci complex (Hypopterygiaceae, Bryopsida): implications from morphological and molecular data. Studies in austral temperate rain forest bryophytes 9. J. Hattori Bot. Lab. 89: 55–70.

Piippo, S. 1992. On the phytogeographic affinities of temperate and tropical Asiatic and Australasian hepatics. J. Hattori Bot. Lab. 71: 1–35.

Piippo, S. & T. Koponen. 1997. On the phytogeographic biodiversity of Western Melanesian mosses. J. Hattori Bot. Lab. 82: 191–201.

Pócs, T. 1966. Contribution à la Bryoflore du Nord Vietnam. Rev. Bryol. Lichénol. 34: 799–806.

Polhill, D. 1970. Flora of Tropical East Africa. Index of Collecting Localities. Royal Botanic Gardens, Kew.

Porley, R.D, B.J. O'Shea, M.J. Wigginton, H.W. Matcham, N.G. Hodgetts & C.R. Stevenson, 1999. Bryophytes of Uganda. 2. New and interesting records. Tropical Bryology 16: 179–193.

Pryzwara, L. & E. Kuta. 1995. Karyology of Bryophytes. Polish Bot. Stud. 9: 1–83.

Pursell, R.A. & W.D. Reese. 1982. The mosses reported from New Caledonia. J. Hattori Bot. Lab. 53: 449–482.

Rage, J.-C. 1988. Gondwana, Tethys, and terrestrial vertebrates during Mesozoic and Cainozoic. In: M.G. Audley-Charles & A. Hallam (eds.), Gondwana and Tethys. Geological Society Special Publication 37: 255–273.

Ramsay, H.P. 1967a. Intraspecific polyploidie in Hypopterygium rotulatum (Hedw.) Brid. Proc. Linn. Soc. New South Wales 91: 220–230, pl. 6–9.

Ramsay, H.P. 1967b. In: A. Löve, IOPB chromosome number reports XIV, Taxon 16: 552–571

Ramsay, H.P. 1974. Cytological studies of Australian mosses. Austral. J. Bot. 22: 293–348.

Ramsay, H.P. 1983. Cytology of mosses. In: R.M. Schuster (ed.), New Manual of Bryology 1: 149–221. Nichinan.

Ramsay, H.P. 1987. Cytological and other studies on the Hypnodendraceae. Mem. New York Bot. Garden 45: 135–153.

Ramsay, H.P. & G.K. Berrie. 1982. Sex determination in bryophytes. J. Hattori Bot. Lab. 52: 255–274.

Raven, P.H. & T.E. Raven, 1976. The genus Epilobium (Onagraceae) in Australasia: a systematic and evolutionary study. New Zealand Dept. of Scientific and Industrial Research Bulletin 216. Christchurch.

Reichardt, H.W. 1868. Diagnosen der neuen Arten von Laubmoosen welche die Novara-Expedition mitbrachte. Verh. Zool. Bot. Ges. Wien 18: 197–198.

Reichardt, H.W. 1870. Fungi, Hepaticae et Musci frondosi. In: E. Fenzl (ed.), Reise der österreichischen Fregatte Novara um die Erde in den Jahren 1857, 1858, 1859 unter den befehlen des Commodore B. von Wüllerstorf-Urbair. Botanischer Theil, Bd. 1. Sporenpflanzen: 131–196, pl. 20–36. Wien .

Reimers, H. 1953. Über die "dimorphen" Amphigastrien von Hypopterygium setigerum. Ber. Deutsch. Bot. Ges. 66: 409–420.

Renauld, F. 1889. Notice sur une collection de mousses de l'île Maurice (Suite). Rev. Bryol. Lichénol. 16: 81–87.

Renauld, F. 1891. Documents nouveaux sur les Muscinées des îles Austro-Africaines de lÓcean indien. 2. Rev. Bot. (Toulouse) 9: 393–401.

Renauld, F. 1897. Prodrome de la Flore Bryologique de Madagascar. Monaco.

Renauld, F. & J. Cardot. 1893. Musci exotici novi vel minus cogniti, adjectis Hepaticis, quas elaboravit F. Stephani. 4. Bull. Soc. Roy. Bot. Belgique 32: 8–40.
Renauld, F. & J. Cardot. 1896. Mousses récoltées à Java par M.J. Massart. Rev. Bryol. 23: 97–108.
Renauld, F. & J. Cardot. 1915. Mousses. In: A. & G. Grandidier (eds.), Histoire, physique, naturelle et politique de Madagascar. Histoire naturelle des plantes. Vol. 39. Paris.
Rodway, L. 1913. Tasmanian bryophyta. 3. Pap. & Proc. Roy. Soc. Tasmania 1913: 177–263.
Sainsbury, G.O.K. 1955. A handbook of the New Zealand mosses. Roy. Soc. New Zealand Bull. 5: 1–490, pl. 1–76.
Sainsbury, G.O.K. 1956. Notes on Tasmanian mosses from Rodway's herbarium. 7. Pap. & Proc. Roy. Soc. Tasmania 90: 35–39.
Salmon, E.S. 1900. Mosses from China and Japan. J. Linn. Soc., Bot. 35: 449–474, pl. 17.
Sanderson, M.J. 1989. Confidence limits on phylogenies, the bootstrap revised. Cladistics 5: 113–129.
Sanderson, M.J. & M.J. Donoghue. 1989. Patterns of variation in levels of homoplasy. Evolution 43: 1781–1795.
Sastre-De Jésus, I. 1987. Revision of the Cyrtopodaceae and Transfer of Cyrtopodendron to the Pterobryaceae, Memoirs of the N.Y. Botanical Garden 45: 709–721.
Sayre, G. 1975. Cryptogamae exsiccatae – An annotated bibliography of exsiccatae of Algae, Lichenes, Hepaticae, and Musci. V. Unpublished exsiccatae I. Collectors. Mem. New York Bot. Gard. 19: 277–423.
Schnepf, E. 1969. Sekretion and Exkretion bei Pflanzen. Wien, New York.
Schofield, W.B. & C. Hébant. 1984. The morphology and anatomy of the moss gametophore. In: R.M. Schuster (ed.), New Manual of Bryology. 2: 627–657. The Hattori Botanical Laboratory, Nichinan.
Schuster, R.M. 1982. Generic and and familial endemism in the hepatic flora of Gondwanaland: origins and causes. J. Hattori Bot. Lab. 52: 3–35.
Schuster, R.M. 1983. Phytogeography of the Bryophyta. In: R.M. Schuster (ed.), New Manual of Bryology 1: 464–626. Nichinan.
Schwägrichen, C.F. 1811. Species muscorum supplementum. 1, 1 (Tab. 1–49). Leipzig.
Schwägrichen, C.F. 1816. Species muscorum supplementum. 1, 2 (Tab. 50–100). Leipzig.
Schwägrichen, C.F. 1829. Species muscorum frondosorum, supplementum 3, 2 (1, Tab. 251–275). Leipzig.
Schwägrichen, C.F. 1830. Species muscorum frondosorum, supplementum 3, 2 (2, Tab. 276–300). Leipzig.
Scotese, C.R., A.J. Boucot & W.S. Kerrow.1999. Gondwanan palaeography and palaeoclimatology. J. African Earth Sci. 28: 99–114.
Scott, G.A.M. 1977. Bryology in Australia. Bull. Brit. Bryol. Soc. 29: 6–8.
Scott, G.A.M. & I.G. Stone. 1976. The mosses of southern Australia. Academic Press, London, New York, San Francisco.
Sehnem, A. 1969. Musgos Sul-Brasileiros. Pesquisas, Bot. 27: 1–36 + 5 plates.
Sharp, A.J., H. Crum & P.M. Eckel. 1994. The Moss Flora of Mexico. 2. Orthotrichales to Polytrichales. Mem. New York Bot. Gard. 69: i–viii, 581–1113, I–XVII.
Shaw, J. 1878. Catalogue of the mosses of the Cape Colony. Cape Monthly Mag. 17: 376–383. 1878.
Shimotomai, N. & Y. Koyama. 1932a. Geslechtschromosomen bei Pogonatum inflexum Lindb. und Chromosomenzahlen bei einigen anderen Laubmoosen. Bot. Mag. (Tokyo) 46: 385–391. (In Japanese).
Shimotomai, N. & Y. Koyama. 1932b. Geslechtschromosomen bei Pogonatum inflexum Lindb. und Chromosomenzahlen bei einigen anderen Laubmoosen. J. Sci. Hiroshima Univ., Ser. B., Div. 2, Bot. 1: 95–101.
Sim, T.R. 1918. Geographical distribution of the South African Bryophyta. S. African J. Sci. 15: 385–404.
Sim, T.R. 1926. The Bryophyta of South Africa. Trans. Roy. Soc. South Africa 15: i–iii, 1–475.

Smith, J.E. 1808. Characters of Hookeria, a new genus of mosses, with descriptions of ten species. Trans. Linn. Soc. London 9: 272–282.

Song, T. & P.A. Cawood. 2000. Structural styles in the Perth Basin associated with the Mesozoic break-up of Greater India and Australia. Tectonophysics 317: 55–72.

Sprengel, K. 1820. Neue Entdeckungen im ganzen Umfang der Pflanzenkunde. Bd. 1. Leipzig.

Stafleu, F.A. & R.S. Cowan. 1976–1988. Taxonomic literature 1–7, (2nd ed.): 1 (A–G), Regnum Veg. 94: i–xl, 1–1136. 1976; 2 (H–Le), Regnum Veg. 98: i–xviii, 1–991. 1979; 3 (Lh–O), Regnum Veg. 105: i–xii, 1–980. 1981; 4 (P–Sak), Regnum Veg. 110: i–ix,1–1214. 1983; 5 (Sal–Ste), Regnum Veg. 112: 1–1066. 1985; 6 (Sti–Vuy), Regnum Veg. 115: 1–926. 1986; 7 (W–Z), Regnum Veg. 116: i–lvi,1–653. 1988. The Hague / Boston.

Stech, M., T. Pfeiffer & W. Frey. 1999. Molecular systematic relationships of temperate austral Hypopterygiaceae (Bryopsida): implications for taxonomy and biogeography. Studies in austral temperate rain forest bryophytes 3. Hausknechtia Beih. 9: 359–367.

Stilwell, J.D. 1997. Tectonic and palaeographic significance of the Chatham Islands, South Pacific, Late Cretaceous fauna. Palaeogeogr. Palaeocl. 136: 97–119.

Stoneburner, A., D.M. Lane & L.E. Anderson. 1992. Spore dispersal distances in Atrichum angustatum (Polytrichaceae). Bryologist 95: 324–328.

Storey, B.C., P.T. Leat, S.D. Weaver, R.J. Pankhurst, J.D. Bradshaw & S. Kelley. 1999. Mantle plumes and Antarctica-New Zealand rifting: evidence from mid-Cretaceous mafic dykes. J. Geol. Soc. London 156: 659–671.

Streimann, H. 1997. Taxonomic studies on Australian Hookeriaceae (Musci). 1. Introduction, and the genera Achrophyllum, Callicostella, Chaetomitrium, and Cyclodictyon. J. Hattori Bot. Lab. 82: 281–304.

Streimann, H. & J. Curnow. 1989. Catalogue of mosses of Australia, Austral. Flor. Fauna Ser. 10: i–viii, 1–479.

Sullivant, W.S. 1855. Notices of some New Mosses in the Collection of the United States Exploring Expedition under Captain Wilkes. 2. Proc. Am. Ac. Arts. Sci. 3: 181–185.

Sullivant, W.S. 1874. United States Exploring Expedition during the years 1838–1842, under the command of Charles Wilkes, U.S.N. Vol. 17. Botany. 1. Lower Cryptogamia. Musci. Philadelphia.

Swartz, O. 1788. Nova genera et species plantarum. Stockholm, Uppsala.

Swartz, O. 1806. Flora Indiae occidentalis. 3. Erlanga.

Swofford, D.L. 1998. PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods). Version 4.0, 130 pp. Sinauer Associates, Inc., Sunderland, Mass., USA.

Tan, B.C. & H. Robinson. 1990. A review of Philippine Hookeriaceous taxa (Musci). Smithsonian Contr. Bot. 75: 1–41.

Tan, B.C., Q.W. Lin, M.R. Crosby & P.C. Wu. 1994. A report on the 1991 Sino-American Bryological Expedition to Guizhou Province, China: New and noteworthy additions of Chinese moss taxa. Bryologist 97: 127–137.

Tangley, R.S. 1997. A taxonomic revision of the genus Camptochaete Reichdt., Lembophyllaceae (Musci). J. Hattori Bot. Lab. 81: 53–121.

Taylor, T. 1847. Description of New Musci and Hepaticae, collected by Profesor William Jameson on Pichincha, near Quito. London J. Bot. 6: 328–342.

Thewissen, J.G.M. & M.C. McKenna. 1992. Paleobiogeography of Indo-Pakistan: a response to Briggs, Patterson, and Owen. Syst. Biol. 41: 248–251.

Thornton, I. 1996. Krakatau. The Destruction and Reassembly of an Island Ecosystem. Cambridge Ma., London.

Thunberg, C.P. 1800. Prodromus plantarum capensium. 2. Upsaliae.

Thunberg, C.P. 1823. Flora capensis, ed. 2. Stuttgart, Amsterdam, London, Paris.

Tixier, P. 1966. Bryophytes du Vietnam. Récoltes de A. Pételot et V. Demange au Nord Vietnam (Relictae Henryanae). Rev. Bryol. Lichénol. 34: 127–181.

Tixier, P. 1970. Bryophytae Indosinicae. Mousses du Massif Sud Annamitique (Vietnam) - 3e article. Rev. Bryol. Lichénol. 37: 723–761.

Tixier, P. 1971a. Bryophytae Indosinicae, Mousses de Thailande. Ann. Fac. Sci. Phnom Penh 4: 91–166.

Tixier, P. 1971b. A contribution to the bryological knowledge of Fraser's Hill Station (Malaysia). Gard. Bull. Straits Settlem. 25: 335–353.

Tixier, P. 1974. Bryophytes exotiques: Bryophytes des Nouvelles-Hébrides (expédition de la Royal Society). Bull. Mus. Natl. Hist. Nat., Sér 3, Bot. 16 (269): 33–45.

Tixier, P. 1979. Bryogéographie du Mont Bokor (Cambodge). Bryophyt. Bibl. 18: 1–121, f. 1–11, pl. 1–7.

Touw, A. 1968. Miscellaneous notes on Thai Mosses. Nat. Hist. Bull. Siam Soc. 22: 217–244.

Touw, A. 1971. A taxonomic revision of the Hypnodendraceae (Musci). Blumea 19: 211–354.

Touw, A. 1979. Bryology and bryophytes at the Rijksherbarium. Blumea 25: 93–99.

Touw, A. 1982. Notes on the use of infraspecific categories by bryologists. Beih. Nova Hedwigia 71: 1–6.

Touw, A. 1992a. A survey of the mosses of the Lesser Sunda Islands (Nusa Tenggara), Indonesia. J. Hattori Bot. Lab. 71: 289–366.

Touw, A. 1992b. Biogeographical notes on the Musci of South Malesia, and of the Lesser Sunda Islands in particular. Bryobrothera 1: 143–155.

Touw, A. & W.V. Rubers. 1989. De Nederlandse Bladmossen. Utrecht.

Treub, M. 1888. Notice sur la Nouvelle Flore de Krakatau,. Ann. Jard. Bot. Buitenzorg 7: 213–223.

Turner, H. 1995. Cladistic and biogeographic analyses of Arytera Blume and Mischarytera gen. nov. (Sapindaceae), with notes on methodology and a full taxonomic revision. Blumea Suppl. 9: 1–230.

Van Balgooy, M.M.J. 1971. Plant-geography of the Pacific. Blumea Suppl. 6: 1–222.

Van den Bosch, R.B. & C.M. van der Sande Lacoste. 1861. Bryologia Javanica. 2. Leiden.

Van der Sande Lacoste, C.M. 1866. Musci frondosi. Ann. Mus. Lugd.-Bat. 2, 10: 292–300.

Van der Wijk, R., W.D. Margadant, & P.A. Florschütz. 1959–1969. Index Muscorum 1–5: Index Muscorum 1 (A–C), Regnum Veg. 17: i–xxviii, 1–548. 1959; 2 (D–Hypno), Regnum Veg. 26: 1–534. 1962; 3 (Hypnum–O), Regnum Veg. 33: 1–528. 1964; 4 (P–S), Regnum Veg. 48: 1–604. 1967; 5 (T–Z, Addenda), Regnum Veg. 65: i–xii, 1–922. 1969. Utrecht.

Van Steenis, C.G.G.J. 1957. Specific and infraspecific delimitation. Flora Malesiana I, 5: clxvii–ccxxxiv.

Van Steenis-Kruseman, M.J. 1950. Malaysian plant collectors and collections. Flora Malesiana I, 1.

Van Zanten, B.O. 1976. Preliminary report on germination experiments designed to estimate the survival changes of moss spores. J. Hattori Bot. Lab. 41: 133–140.

Van Zanten, B.O. 1978. Experimental studies on trans-oceanic long-range dispersal of moss spores in the Southern Hemisphere. J. Hattori Bot. Lab. 44: 455–482.

Van Zanten, B.O. 1983. Possibilities of long-range dispersal in bryophytes with special reference to the Southern Hemisphere. Sonderbd. naturwiss. Hamburg 7: 49–64.

Van Zanten, B.O. 1992. Historisch overzicht van het onderzoek naar mogelijkheden voor lange-afstand-verspreiding bij mossen. Buxbaumiella 27: 31–34.

Van Zanten, B.O. 1964. Mosses of the Star Mountains Expedition. Nova Guinea, Bot. 16: 263–368.

Van Zanten, B.O. & S.R. Gradstein, 1988. Experimental dispersal geography of Neotropical liverworts. Beih. Nova Hedwigia 90: 41–94.

Van Zanten, B.O. & T. Pócs. 1981. Distribution and dispersal of bryophytes. Advances in Bryology 1: 479–562.

Vitt, D.H. 1979. The moss flora of the Auckland Islands, New Zealand, with a consideration of habitats, origins, and adaptations. Canad. J. Bot. 57: 2226–2263.

Vitt, D.H. 1984. Classification of the Bryopsida. In: R.M. Schuster (ed.), New manual of bryology 2: 696–759, f. 1–110. Nichinan.

Vitt, D.H., B. Goffinet & T.A.J. Hedderson. 1998. Ordinal level classification of the mosses: question and answers for the 1990's. In: J.W. Bates, N.W. Ashton & J.G. Duckett (eds.), Bryology for the Twenty-First Century: 113–123. Leeds.

Wallich, N. 1830. Plantae asiaticae rariores. 1. London, Paris, Strasburgh.

Weijermars, R. 1989. Global tectonics since the breakup of Pangea 180 million years ago: evolution maps and lithosphere budget. Earth-Sci. Rev. 26: 113–162.

Welch, W. 1966. The Hookeriaceae of Mexico. Bryologist 69: 1–68.

Whittaker, R.J. 1982. Aspects of the vegetation of Rakata. In: J.R. Flenley & K. Richards (eds.), The Krakatoa Centenary Expedition. Final Report, Depart. of Geography, University of Hull, Miscellaneous Series 25: 55–82.

Whittemore, A. & B. Allen. 1989. The systematic position of Adelothecium Mitt. and the familial classification of the Hookeriales (Musci). Bryologist 92: 261–271.

Whittier, H.O. 1968. Mosses of the Society Islands: Preliminary Studies on their Taxonomy, Ecology and Geographie. Ph.D. Thesis, New York.

Whittier, H.O. 1973. Mosses of the Marquesas Islands, French Polynesia. Bryologist 76: 174–177.

Whittier, H.O. 1975. A preliminary list of Fijian Mosses. Florida Sci. 38: 85–106.

Whittier, H.O. 1976. Mosses of the Society Islands. Gainesville.

Whittier, H.O. & B.A. Whittier, 1974. List of mosses of Southeastern Polynesia. Bryologist 77: 427–446.

Wigginton, M.J., R.D. Porley & N.G. Hodgetts. 1999. Bryophytes of Uganda. 1. BBS Tropical Bryology Group expeditions. 1996–1998. Introduction and collecting sites. Tropical Bryology 16: 165–177.

Wilson, W. 1855. Musci. In: J.D. Hooker, The botany of the Antarctic voyage. 2. Flora Novae-Zelandiae. Part 2. Flowerless Plants: 57–125. London.

Wilson, W. 1860. Musci. In: J.D. Hooker, The botany of the Antarctic voyage. 3. Flora Tasmaniae. Part 2. Monocotyledones and Acotyledones: 160–221. London.

Wilson, W. & J.D. Hooker. 1845. Musci. In: J.D. Hooker, The botany of the Antarctic voyage. 1. Flora Antarctica. Part 1. Botany of Lord's Auckland Group and Campbell's Island: 117–143. London.

Wolf, J.H.D. 1993a. Epiphyte communities of tropical montane rain forests in the northern Andes. 1. Lower montane communities. Phytocoenologia 22: 1–52.

Wolf, J.H.D. 1993b. Epiphyte communities of tropical montane rain forests in the northern Andes. 2. Upper montane communities. Phytocoenologia 22: 53–103.

Wolf, J.H.D. 1993c. Diversity patterns and biomass of epiphytic bryophytes and lichens along an altitudinal gradient in the northern Andes. Ann. Missouri Bot. Gard. 80: 928–960.

Yamaguchi, T. 2001. Sporophytes of Cyathophorella tonkinensis (Broth. et Par.) Broth. Bryological Research 7: 392–394.

Zollinger, H. 1854. Systematischen Verzeigniss der im indischen Archipel in den Jahren 1842–1846 gesammelten sowie der aus Japan empfangen Pflanzen. Heft 1 & 2. Zurich.

INDEX TO SCIENTIFIC NAMES

Only names of taxa used in the taxonomic treatment are included in this list. The number after the pagenumber(s) is the number of the genus or species in the text. New names are in **bold**, accepted names in roman, and synonyms and dubious names in *italics*.

CURRICULUM VITAE

Johannes Derk (Hans) Kruijer werd geboren op 11 september 1960 te Hoogezand-Sappemeer. In 1978 behaalde hij in deze plaats aan de Dr. Aletta Jacobsscholengemeenschap het HAVO-diploma, in 1979 gevolgd door het VWO-diploma. In datzelfde jaar begon hij met de studie biologie aan de Rijksuniversiteit Groningen. Op 26 augustus 1982 legde hij het kandidaatsexamen af (richting B5b). De doctoraalfase van zijn biologie studie omvatte ondermeer vijf doctoraal onderzoeken op het gebied van de plantenoecologie, de bodemkunde, de bloembiologie en de bryologie:

- Inventarisatie van de Hortus 'de Wolf' te Haren (1983; o.l.v. Dr. B.O. van Zanten)
- Over de populatiebiologie van *Agrostis stolonifera* L. 1. Strategie en polyploïdie (1983; o.l.v. Drs. C. Kik en Dr. L.P. Pijnacker)
- Slib en veraarding van veen in het Hunzedal (1984; o.l.v. Ir. B. van Heuveln)
- Some aspects of the distribution and the morphology on light-microscopic level of odorous cells on corollas (1985; o.l.v. Prof. dr. B.M. Moeliono)
- Experimentele plantengeografie aan mossen: soorten van zuidelijk Zuid Amerika (1986; o.l.v. Dr. B.O. van Zanten).

In het kader van het laatste onderzoek nam hij met zijn begeleider deel aan een bryologische verzamelreis naar zuidelijk Chili en vertoefde hij enige tijd in Davos, Zwitserland, om op de top van de Weissfluh (2844 m) de UV resistentie van mossporen onder natuurlijke condities te onderzoeken. Tijdens de doctoraal fase assisteerde hij bij de practica van het onderdeel 'Overzicht plantenrijk' voor biochemie-studenten (1983), de 'Botanische biologie voor farmaceuten' (1984, 1985), het onderdeel plantenoecologie van de cursus 'Algemene oecologie' (1984, 1985) en de 'Floracursus' (1985) voor biologie-studenten. Het doctoraalexamen biologie met als specialisatie bryologie en als bijvakken plantenoecologie en bodemkunde werd door hem afgelegd op 26 juni 1986.

Na zijn afstuderen werd er vanuit de Subfaculteit Biologie aan de Rijksuniversiteit Groningen verschillende keren beroep op hem gedaan om tijdelijk assistentie te verlenen bij onderwijs en onderzoek. Hij was assistent-cursusleider bij het Laboratorium voor Plantenoecologie voor het practicum van het onderdeel plantenoecologie van de cursus 'Algemene oecologie' (1986), onderwijsmedewerker bij het Laboratorium voor Plantenfysiologie voor het geven van de cursus plantenanatomie voor biologie-studenten (1987, 1988), en onderzoeksmedewerker bij het Laboratorium voor Plantensystematiek voor bloembiologisch onderzoek (1986, 1987).

In februari 1989 ging hij naar Leiden, om in maart aangesteld te worden als Assistent in Opleiding (AIO) aan de Universiteit Leiden bij het voormalige Rijksherbarium met als onderzoeksopdracht een systematische bewerking van de Hypopterygiaceae Mitt. van, in eerste instantie, Zuidoost-Azië, Australazië en Oceanië. Hij vervulde deze functie tot maart 1993. Hierna continueerde hij zijn onderzoek als gastmedewerker van het onderzoekinstituut Rijksherbarium / Hortus Botanicus (RHHB), nu de Leidse vestiging van het Nationaal Herbarium Nederland (NHN/L). De resultaten van dit onderzoek zijn beschreven in dit proefschrift.

Tijdens en na zijn aanstelling als AIO assisteerde hij zeven keer het onderdeel 'Diversiteit en Overzicht van het Plantenrijk' van de cursus Plantkunde voor eerstejaars biologiestudenten in de perioden 1989–1991 en 1997–2000. Vanaf medio 1994 tot eind 1996 verzamelde hij tentoonstellingsmateriaal (planten) voor het Nationaal Natuurhistorisch Museum (nu Naturalis). In 1997 was hij één van de initiatiefnemers en uitbaters van het eerste koffie- en theehuis in de Leidse Hortus Botanicus (Koffie- en theeschenkerij '*De Oranjerie*'). In 1998 was hij betrokken bij de organisatie van de RHHB-cursus 'Tropical Plant Families of Southeast Asia'. Van 1996 tot en met 2001 was hij op het RHHB, nu NHN/L, gastdocent voor het onderdeel bryologie van de cursus 'Biology and Systematics of Cryptogams'. Daarnaast gaf hij in deze periode nog mossencursussen voor (semi-)overheidsdiensten. Vanaf juli 2000 is hij werkzaam als studieadviseur bij de Opleiding Bio-Farmaceutische Wetenschappen aan de Universiteit Leiden.

Publikaties:

Kruijer, J.D., J.P.J. Bramer & B.O. van Zanten. 1987. Mossen in de Hortus. Vereniging tot behoud van de Hortus Henr. Munting, Haren. 47 p.

Kruijer, H. & B.O. van Zanten. 1987. Mossen, een vergeten plantengroep. Noorderbreedte 11: 84–87.

Kruijer, J.D. 1987. The ecological function of the retention of withered, non-rewarding flowers in Echium plantagineum L. Acta Bot. Neerl. 36: 139–140. (samenvatting voordracht).

Kruijer, J.D. & B.M. Moeliono. 1989. A competition for pollinators: differences in attractiveness between Echium vulgare L. and Echium plantagineum L. Acta Bot. Neerl. 38: 100–101. (samenvatting voordracht).

Wallert, A., B.M. Moeliono & J.D. Kruijer. 1989. Mikroskopische Untersuchung von Papyrus und Plinius, Historia Naturalis XIII, 74–83. Eine morphologisch-anatomische Studie. Zeitschrift für Papyrologie und Epigraphik 76: 39–44.

Huizenga, A., J.D. Kruijer & B.M. Moeliono. 1989. Effects of the physical environment on the foraging behaviour of three bumblebee-species visiting fresh and senescent inflorescences of Lupinus polyphyllus Lindley. Acta Bot. Neerl. 38: 507. (Samenvatting voordracht).

Kruijer, J.D. 1990. A revision of the Hypopterygiaceae Mitt. s.l.: relationships between the genera. In: T. Koponen & J. Mänttäri (eds.), Congress of East Asiatic Bryology, Helsinki, August 12–19, 1990. Programme and abstracts: 21. Dept. of Botany, University of Helsinki / Finnish Bryological Society, Helsinki. (Samenvatting poster).

Kruijer, H. 1993. De systematiek van de Cyathophoroideae: een introduktie. Buxbaumiella 31: 31–37. (Samenvatting voordracht).

Kruijer, J.D. & N. Klazenga. 1994. A simple method for clearing up slides of mosses for observation with the light microscope. Bryol. Times 79: 3.

Kruijer, H. 1995. Een korte introduktie tot de mossen. Microwereld 1: 5–14. (Samenvatting voordracht).

Keßler, P.J.A., L.W. Jessup & J.D. Kruijer. 1995. Provisory checklist of the Asiatic-Australian species of Annonaceae. The Herbarium Department of Biology, University Pertanian Malaysia, Serdang, Malesia / Unesco–Botany 2000 Asia. 89 p. (in 1994 verschenen bij RHHB / Unesco–Botany 2000 Asia, Leiden, 516 p.).

Kruijer, J.D. 1995. Systematics of the Moss Family Hypopterygiaceae Mitt. Acta Bot. Neerl. 44: 492. (Samenvatting voordracht).

Kruijer, H. 1995. Systematiek van de Hypopterygiaceae. Buxbaumiella 38: 26–32. (Samenvatting voordracht).

Kruijer, H. 1996 ['1995–1996']. Canalohypopterygium tamariscinum (Hedw.) Kruijer: typification and synonymy of a new combination. Lindbergia 20: 85–88.

Kruijer, H. 1996 ['1995–1996']. Dendrocyathophorum decolyi (Broth.) Kruijer: a new combination. Lindbergia 20: 89–90.

Kruijer. H. 1996. Tegenstroomse voortplanting. Intermediair 32 (24): 37.

Kruijer, H. 1996. Phylogeny of the Hypopterygiaceae Mitt. The British Bryological Society Centenary Symposium, Glasgow (4–8 Augustus). (Samenvatting poster).

Kruijer, H. 1996. Boekbespreking: S.R. Gradstein & H.M.H. van Melick, De Nederlandse Levermossen & Hauwmossen. Flora en verspreidingsatlas van de Nederlandse Hepaticae en Anthocerotae. Gorteria 22: 172.

Kruijer, J.D. 1997a. British Bryological Society Expedition to Mulanje Mountain, Malawi 6. Hypopterygiaceae (Musci). Journal of Bryology 19: 515–520.

Kruijer, J.D. 1997b. The origin of Hypopterygium-populations in some European Botanic Gardens, with special reference to Hypopterygium atrotheca Dix. Glasgow Naturalist 23: 11–17.

Kruijer, H. 1997. Lichtverschijnselen in zee. Daucallium 3: 12–13.

Kruijer, H. 2000. Archeologisch mos uit Leiden. Renus 2000 (1): 7–10.

Kruijer, H., K. Koops, M. Edelenbos, R. Ubels, D. Lutterop, G. Kasemir & B. Corté. 2000. De mossen van de Groninger waddeneilanden. Buxbaumiella 52: 17–31.

De Jong, Y.S.D.M., G.M. Lokhorst & J.D. Kruijer. 2000. Genealogy in Microspora Thuret (Chlorophyceae). Blumea 45: 477–484.

Pfeiffer, T., H. [J.D.] Kruijer, W. Frey & M. Stech. 2000. Systematics of the Hypopterygium tamarisci complex (Hypopterygiaceae, Bryopsida): implications from molecular and morphological data. Studies in austral temperate rain forest bryophytes 9. J. Hattori Bot. Lab. 89: 55–70.

Kruijer, J.D. & C.G. Koops. 2001. Mossen. In: D. Lutterop & G. Kasemir, Vogelwachtersverslag Rottumerplaat Broedseizoen 1999: 47–52. Staatsbosbeheer Regio Groningen-Drenthe, Assen.

Koops, C.G. & J.D. Kruijer. 2001. Korstmossen. In: D. Lutterop & G. Kasemir, Vogelwachtersverslag Rottumerplaat, Broedseizoen 1999: 57–58. Staatsbosbeheer Regio Groningen-Drenthe, Assen.

Kruijer, J.D. & C.G. Koops. 2001. Mossen. In: M. Edelenbos & R. Ubels, Vogelwachtersverslag Rottumeroog Broedseizoen 1999: 61–62. Staatsbosbeheer Regio Groningen-Drenthe, Assen.

Koops, C.G. & J.D. Kruijer. 2001. Korstmossen. In: M. Edelenbos & R. Ubels, Vogelwachtersverslag Rottumeroog Broedseizoen 1999: 63. Staatsbosbeheer Regio Groningen-Drenthe, Assen.

Pelser, P.B., H. [J.D.] Kruijer, R. Verpoorte. Accepted. What is the function of oil containing rudimentary branches in the moss Canalohypopterygium tamariscinum? New Zealand J. Bot. 40.

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