

A MONOGRAPH OF THE FERN GENUS *Thylacopteris* (POLYPODIACEAE)

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SUMMARY

This study deals with the systematics of the free-veined Polypodiaceae lacking any soral paraphyses and represented only in the paleotropics. It includes the recognition and description of two species of *Thylacopteris* Kunze ex J. Sm., a full synonymy and a discussion of its systematic position.

INTRODUCTION

This study concentrates on the analysis of two species earlier referred to the genus *Polypodium* L. (sensu lato) with free, once forking veins. John Smith established the genus *Thylacopteris* to accommodate only one species, *T. papillosa*. As the taxonomic history shows, not much attention was given to this genus. Some authors assume an alliance with *Polypodium* L. (sensu stricto) and *Goniophlebium* (Blume) Presl, others declare its systematic position as uncertain.

In order to clarify the identity and to unravel the systematic position of this genus an analysis of characters was undertaken. They concern the morphology of the mature sporophyte, with respect to the rhizome, the rhizome scales, the gross morphology, the venation pattern, the indument, the sori, the sporangia, and the spores. Microscopical and submicroscopical features were included. Several of these characters were studied in detail for this group for the first time. Character states such as the articulation of the pinnae with the rhachis and the absence of any soral paraphyses confirm its generic status and justify the retention of the genus. Within *Thylacopteris* two species are recognised, *T. diaphana* having been neglected by most authors. The results of the character analysis were compared with corresponding detailed information available on *Goniophlebium* (Blume) Presl and *Polypodium* L. (s.s.) (Rödl-Linder, 1990). A number of characters suggest a relation with the genus *Goniophlebium* (Blume) Presl, especially with the (partly) free-veined species of this genus, rather than with any other genera.

Geographical and ecological particularities were investigated. It was attempted to clarify eventual relationships also in correlation with the geographic distribution pattern.

In the taxonomic part an emended description of the genus is given. The species are described in detail and a list of distinguishing characters for identification is provided. A full synonymy of concerned taxa is given and information on the distribution, the habitat and on other relevant observations is added. An index of the specimens studied is included.

MATERIAL AND METHODS

Dried specimens of c. 200 collection numbers, partly with many duplicates, were studied from the following herbaria (the abbreviations follow the Index Herbariorum): A, BM, BO, GH, K, L, MICH, NY, P, PNH, UC, US. Selected specimens were also examined from RO.

For anatomical studies, common methods as described by the present author (1990) have been applied.

TAXONOMIC HISTORY OF THYLACOPTERIS

The genus *Thylacopteris* was created by John Smith (1875) to accommodate *Polypodium papillosum* Blume as the only species. As distinguishing characters from true *Polypodium* he stressed the deeply impressed sori and the articulation of the lateral segments with the rhachis.

Christensen (1934) stressed the resemblance of *Thylacopteris papillosa* to *Polypodium vulgare* L. and the close relationship of these both to *Goniophlebium* (Blume) Presl. Considering *Thylacopteris diaphana* congeneric with *T. papillosa*, Copeland (1947) had difficulties to recognise generic characters. Ching (1978) confirmed Christensen's suggestion of a close relationship between *Thylacopteris*, *Polypodium* L. (sensu stricto) and the free-veined species of *Goniophlebium* (Blume) Presl.

Other authors such as Holttum (1966) and Tryon & Lugardon (1991) preferred to keep *Thylacopteris* within the genus *Polypodium*. Tryon & Tryon (1982) placed *Thylacopteris* into an alliance with *Polypodium* and *Goniophlebium*, however, without accepting it as a genus. Hennipman et al. (1990) recognises a genus *Thylacopteris* "the systematic position of which is still uncertain", within the tribe Polypodieae.

MORPHOLOGY AND ANATOMY OF THE MATURE SPOROPHYTE

Characters and character states

After the recognition of the species, analyses of a total of 65 morphological and anatomical characters were executed. Characters were selected considering their importance for comparison with *Goniophlebium* (Blume) Presl and *Polypodium* L. (s.s.) in order to elucidate systematic relationships.

Thirty-six distinguishing characters were recognised and a certain number of character states were attributed to them. A discussion is given about the comparison between the two species of *Thylacopteris* and the character states recognised in *Goniophlebium* (Blume) Presl, with special reference to the (partly) free-veined species of this genus. These are *G. manmeiense* (Christ) Rödl-Linder and *G. microrhizoma* (Baker) Bedd., two of the nine species building the *Goniophlebium subauriculatum*-group which is considered a monophyletic group. In addition the respective character states in an Asian representative of the *Polypodium vulgare*-complex, *P. vulgare* L. var. *japonicum* Franchet & Savatier (syn. *Polypodium fauriei* Christ) are included in the comparison. (For further details on the descriptions, see Rödl-Linder, 1990.) Characters are based on studies of mature sporophytes. They concern rhizomes, rhi-

zome scales, fronds including gross morphology, venation pattern, laminar indument, sori with sporangia, and spores.

Rhizome

Distance of phyllopodia – The phyllopodia of *Thylacopteris* are situated 3–12 mm apart. This overlaps with the values in *Goniophlebium manmeiense* and *G. micro-rhizoma*, but is more distant than in *Polypodium fauriei*.

Dark bundle sheaths – Dark bundle sheaths are present only in *Thylacopteris papillosa*, while they are absent in *T. diaphana* and the species under comparison from the other genera.

Number of sclerenchyma strands – For *Thylacopteris papillosa* between 12 and 100 sclerenchyma strands have been counted, while sclerenchyma strands are absent in rhizomes of *T. diaphana*. Dark sclerenchyma strands are present in all *Goniophlebium* species, varying in number from 1 to more than 100. Sclerenchyma strands are absent in the species belonging to the *Polypodium vulgare*-complex and in all neotropical species with goniophlebioid venation.

Rhizome scales

Major differences between the species groups have been found concerning the rhizome scales.

Insertion – Rhizome scales of both species of *Thylacopteris* as well as of the (partly) free-veined *Goniophlebium* species are evenly inserted. Those of *Polypodium fauriei* are inserted in an invagination. Both character states are found in other groups of *Goniophlebium*.

Colour – All species of *Thylacopteris* and *Goniophlebium* have brown rhizome scales, whereas in *Polypodium fauriei* they are orange.

Exposition – All rhizome scales are at least basally adpressed to the rhizome. However, in both *Thylacopteris* species they are apically spreading, as they are in most *Goniophlebium* species. In *Polypodium fauriei* the whole scale is firmly adpressed to the rhizome.

Density – The rhizome scales of *Thylacopteris* cover the rhizome less densely than they do in the other species under comparison.

Persistency – Rhizome scales of *Thylacopteris* are deciduous. Respective species of *Goniophlebium* and *Polypodium* have persistent rhizome scales.

Dimorphism and general shape – Dimorphism here refers to the presence of mucronate and deltoid rhizome scales only in *Thylacopteris diaphana*. In *T. papillosa* and the *Goniophlebium* species under study the rhizome scales are always deltoid. The shape of the rhizome scales of *Polypodium fauriei* is broadly deltoid.

Apex shape – The apex of deltoid or mucronate rhizome scales is acute or acuminate (Fig. 1a–d). In *Polypodium fauriei* the apex of the rhizome scales is rounded.

Shape of auricles – Auricles are round except in *Goniophlebium microrrhizoma* where they are pointed.

Attachment – Generally rhizome scales of all species belonging to the genus *Goniophlebium* as well as to *Thylacopteris* are pseudopeltately attached (Fig. 1a–d). Pel-tate attachment is a frequent character state in goniophlebioid species from the neotropics which are retained in *Polypodium*.

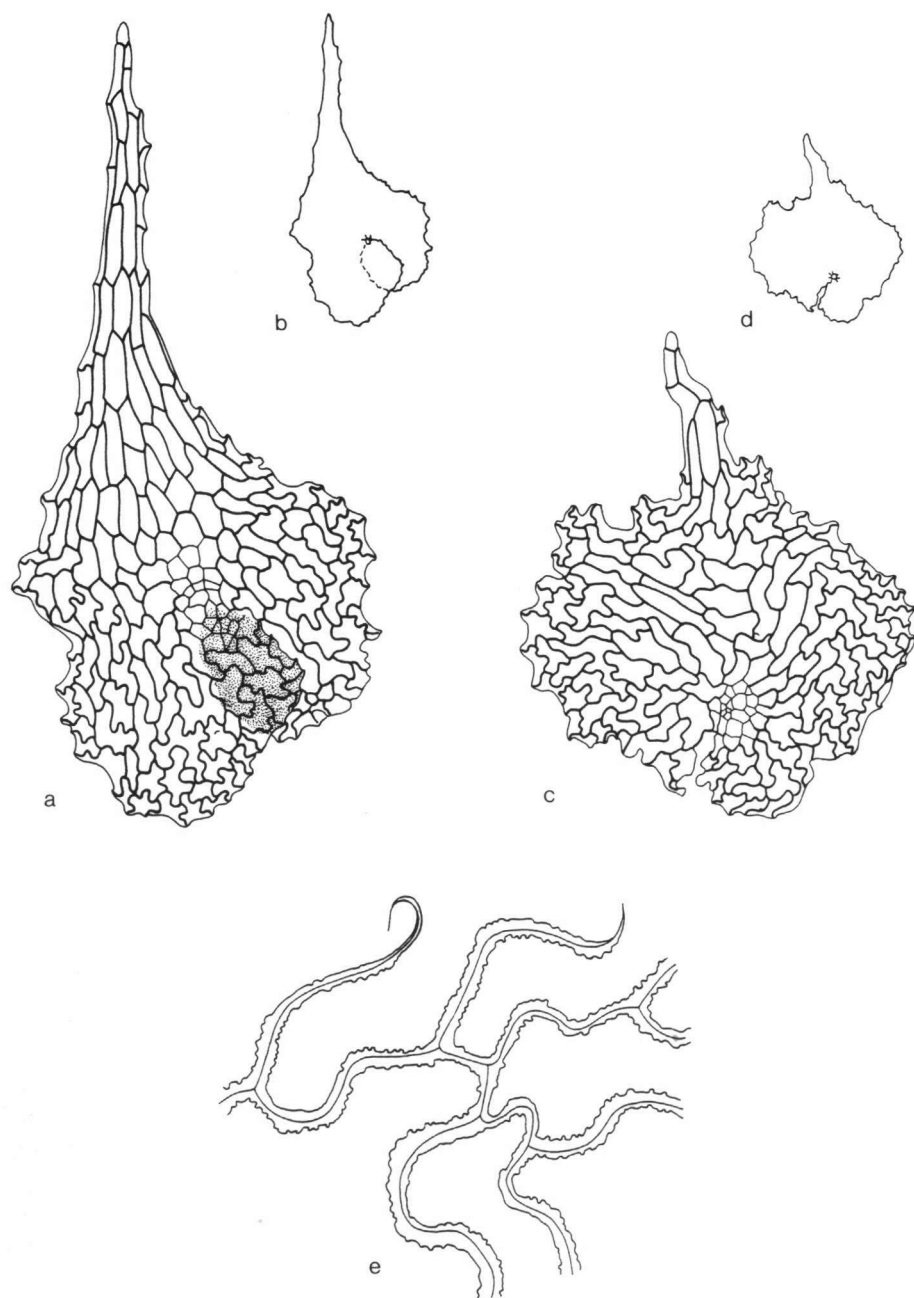


Fig. 1. *Thylacopteris diaphana* (Brause) Copel. (Brass 24996). a. Deltoid rhizome scale detail, $\times 80$: perfoliate, auricles overlapping, basal cells puzzle-shaped; b. deltoid rhizome scale outline; c. mucronate rhizome scale detail, $\times 80$: perfoliate, auricles cordate, marginal cells puzzle-shaped; d. mucronate rhizome scale outline; e. detail of puzzle-shaped cell walls with the inner layer warty, $\times 550$.

Index length/width – The length/width ratio is clearly lower in rhizome scales of *Polypodium fauriei* than it is in the other species under comparison.

Clathration of cell walls – Rhizome scales of *Polypodium fauriei* are completely opaque, while most of their cell walls are thickened in *Thylacopteris* and *Goniophlebium*.

Clathrate cell walls inner layer – Obviously a rare appearance is a warty state of the thickened inner layer (Fig. 1e). It is present in both *Thylacopteris* species, however never in *Goniophlebium* nor in *Polypodium*. It has earlier only been observed in one species of *Microsorium*, viz. *M. spectrum* (Kaulf.) Copel. (Bosman, 1991).

Shape of cells basally – This character of *Thylacopteris* represents an unique state. The cells of the basal part of the scales are clearly jigsaw-puzzle-shaped (Fig. 1a–e). This has not been described from any other species of the family. Some *Microsorium* species have slightly wavy anticlinal cell walls which are, however, not really jigsaw-puzzle-shaped. In *Selliguea feei* Bory a similar cell shape is present, but the scales are otherwise very different.

Clathrate marginal protrusions – The margin of the rhizome scales in *Goniophlebium* is ciliate, i.e. clathrate marginal protrusions are present. Such protrusions are very short in *Thylacopteris* (Fig. 1a, c) and absent in *Polypodium* (s.s.).

Rhizoid-like surface hairs – Rhizoid-like surface hairs on rhizome scales are absent in *Thylacopteris*, but present in *Goniophlebium manmeiense*, *G. microrrhizoma* and in *Polypodium fauriei*.

Fronds

Gross morphology

Texture – The texture of fronds of *Thylacopteris* is transparently membranaceous. In *Goniophlebium* it is generally thin herbaceous and in *Polypodium* (s.s.) firm herbaceous.

Maximum length of blade – With a length of 59 cm, the longest fronds have been encountered in *Thylacopteris*, while fronds of *Polypodium fauriei* do not exceed 32 cm.

Lateral segment articulation – The lateral segments are in all species concerned deeply divided, almost to the rhachis. *Thylacopteris diaphana* and *T. papillosa* show a unique character state here. A rudimentary abscission layer indicates an articulation of the lateral segments with the rhachis (Fig. 2).

Lateral segments distance – Lateral segments are closest to each other in species of *Thylacopteris* and widest apart in *Polypodium fauriei*.

Venation pattern

The species under comparison here have a free venation pattern in common. The veins are usually easily seen, but in *Polypodium fauriei* the venation is sometimes indistinct due to the firm texture of the lamina.

Free veins – In species of *Thylacopteris* the free veins may be simple, but are mostly once-forked. In *Goniophlebium manmeiense* they are once-forked, whereas in *G. microrrhizoma* as well as in *Polypodium fauriei* they are twice-forked.

Areolae – Goniophlebioid areolae with free included veins are sometimes present in *Goniophlebium microrrhizoma* and absent in the other species under study.

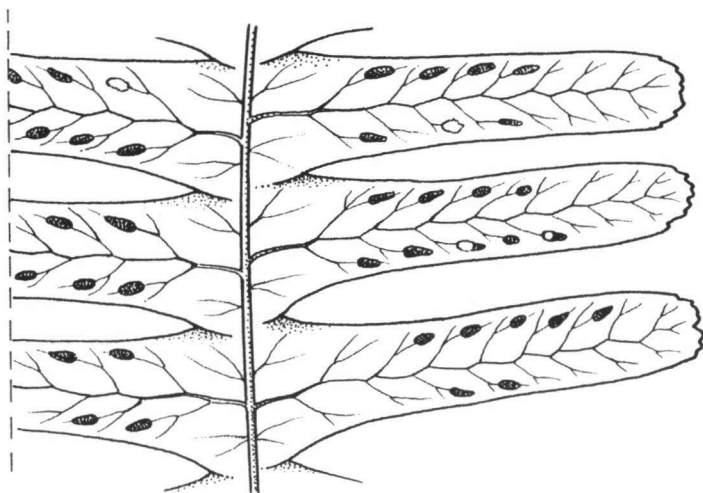


Fig. 2. *Thylacopteris papillosa* (Blume) Kunze ex J. Sm. (Jermy 13985), part of a fertile frond, detail of the upper surface of three middle pinnae, articulation of the pinnae with the rachis indicated; $\times 3.2$.

Laminar indument

Glandular hairs are present on the lamina and petioles of all species of the family Polypodiaceae. However, there are differences in the length and in the number of terminal glands. It seems that *Thylacopteris* has only 2-celled glandular hairs including one terminal gland, whereas in *Goniophlebium* and *Polypodium* longer hairs with sometimes 2 or 3 terminal glands occur.

Laminar/petiolar acicular hairs – Acicular hairs are absent in *Thylacopteris* as well as in the free veined species of *Goniophlebium*. In *Polypodium fauriei* they are present. They may be present or absent in other species of *Goniophlebium*.

Sori, paraphyses and sporangia

Sori are arranged uniserial at either side of the main vein, terminally at a free vein. If the vein is once forked, then the sorus is located at the acroscopic branch. In *Polypodium fauriei* the vein is forked twice. In this case the position of the sorus is at the end of the acroscopic branch situated closer to the main vein.

Relation of the sori to the surface of the lamina – *Thylacopteris diaphana* has superficial sori, as do the species of the other genera under comparison. In *T. papillosa* the sori are deeply sunken. Species of the *Goniophlebium percussum*-group have more or less sunken sori, but differ in many other aspects from *Thylacopteris*.

Shape of the sori – Concerning this character *Goniophlebium microrrhizoma* with slightly oval shaped sori represents an exception. The common state is a round shape.

Receptacular hair-like paraphyses – Receptacular hair-like paraphyses were found in all species of *Goniophlebium* and *Polypodium* (s.s.) but are absent in *Thylacopteris*.

Hair-like paraphyses branching from sporangial stalk – These episporangial structures are absent in *Thylacopteris* and *Polypodium fauriei*, but present in *Goniophlebium manmeiense* and *G. microrrhizoma*.

Total annulus cells of the sporangium – The annulus of sporangial capsules of *Polypodium fauriei* consists of 21–25 cells, while all other species under comparison have a total of only 17–20 annulus cells. However, other *Goniophlebium* species also have higher numbers of annulus cells.

Length of the sporangial capsule – Within the genus *Goniophlebium*, *G. manmeiense* and *G. microrrhizoma* have relatively small capsules. Capsules of *Thylacopteris* with a length of c. 325 μm reach the upper limit of the range found for *Polypodium fauriei*.

Spores

Size of the spores – Corresponding to a smaller size of the sporangial capsule, the spores of the free-veined species of *Goniophlebium* are also smaller than those of *Thylacopteris* and *Polypodium fauriei*.

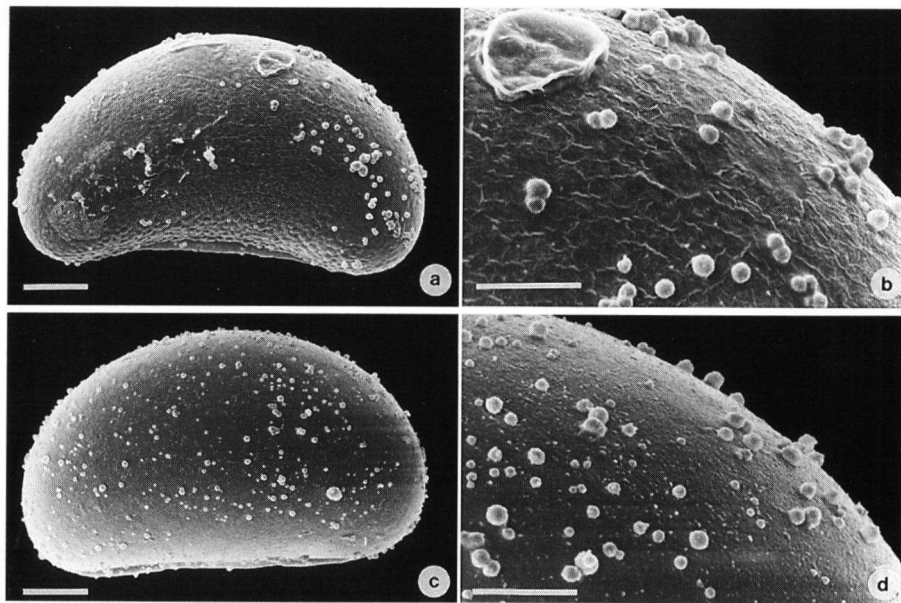


Fig. 3. *Thylacopteris diaphana* (Brause) Copel. (Brass 12838). a. Lateral view: exospore pustulate, laesura $0.5 \times$ length of spore; b. detail: perispore shallowly reticulate, globules many in various sizes. — *Thylacopteris papillosa* (Blume) Kunze ex J. Sm. (Johansson c. s. 84); c. lateral view: exospore smooth, laesura $0.7 \times$ length of spore; d. detail: perispore plain, globules many in various sizes. — Scale bars: a & c = 10 μm ; b & d = 5 μm .

Perispore surface ornamentation seen with the SEM ($\times 5000$) – Whilst the perispore of *Thylacopteris papillosa* is smooth (Fig. 3c, d), the perispore of *T. diaphana* is shallowly reticulate (Fig. 3a, b), the one of *Goniophlebium manmeiense* is granulate, and slightly undulate in *G. microrhizoma* and *Polypodium fauriei*.

Globules on the perispore – Whilst there are always (few to) many globules, i.e. spherical deposits, present on the spores of *Thylacopteris*, these are usually absent in the other species under comparison.

Surface ornamentation of the exospore – The smooth condition, present in *Thylacopteris papillosa*, has been found as well in the *Goniophlebium percussum*-group. The other taxa under comparison show some kind of exospore ornamentation, i.e. slightly pustulate or colliculate and verrucate. The verrucate exospore is quite distinct, showing a decrease in the size of verrucae towards the distal pole.

MONOPHYLY AND SYSTEMATIC POSITION OF THYLACOPTERIS

Delimitation of the genus

One character in the original description (Smith, 1875) has been overlooked by all later authors who commented on this genus. At first it appears confusing to read “fronds ... pinnatifid ..., laciniae articulate with the rachis.” One could imagine these two terms as contradictory. The articulation of the lateral segments with the rachis obviously refers to a rudimentary abscission layer present basally between the pinnae, which breaks and facilitates a separation of the pinnae exactly along the rachis. In fact, this predetermined breaking point is absent in other free-veined Polypodiaceae, e.g. species of the *Polypodium vulgare*-complex and the (partly) free-veined species of *Goniophlebium*.

The deeply impressed receptacles are emphasised in all relevant publications, even though they are present only in one of the two species of *Thylacopteris*. One species of the genus *Goniophlebium*, *G. mehibitense* (C. Chr.) Parris, shares this character state, but is otherwise certainly not closely related to *Thylacopteris papillosa*. Christensen (1934) did not find any character, the free veins excepted, by which *T. papillosa* differs from several Malayan species of *Goniophlebium* with immersed sori. According to him, it stands in relation to such species exactly as *Polypodium vulgare* stands to the Asian species of *Goniophlebium* with superficial sori. Here the degree of immersion of the sori is not considered a useful character to recognise relationships.

The third distinguishing character mentioned by John Smith (1875) is the free, once-forked venation. Holttum (1966) states: “In Malaya we have one species with free veins.” He does not take into account either *Thylacopteris diaphana* or *Goniophlebium manmeiense*.

In addition to the free venation and the articulation of the lateral segments with the rachis, the present study revealed the importance of other characters. In *Thylacopteris* the cell walls at the base of the rhizome scales are jigsaw-puzzle-shaped and their inner, thickened layer is warty (Fig. 1e). Receptacular paraphyses are totally absent. These characters are considered generic and a monophyly of the genus *Thylacopteris* is assumed.

Delimitation of the species

Due to the free venation combined with other characters, as elucidated above, *Thylacopteris papillosa* has always been accepted as a distinct species. Brause stated in his original description of *Polypodium diaphana* the similarity with *P. papillosa*, mentioning the superficial situation of the sori as the only difference. Copeland (1947) in addition stressed the sclerenchyma strands, which he considered as "merely indicated" in *Thylacopteris diaphana*. In this study sclerenchyma strands in the rhizome of *T. diaphana* have not been found. According to Copeland (1947), "this species could be left in *Polypodium*, if it were considered by itself." The present study revealed some more specific characters: dark bundle sheaths are present in the rhizome of *Thylacopteris papillosa*, whilst they are absent in *T. diaphana*. The spores of *T. diaphana* have a shorter laesura and a shallowly reticulate perispore (Fig. 3b), while the perispore of *T. papillosa* is completely smooth (Fig. 3d). Considering the geographic restriction, the specific identity of *T. diaphana* is recognised.

Systematic position of Thylacopteris

After detailed morphological studies, the close relationship between *Thylacopteris* and *Goniophlebium* suggested by Christensen (1934), Ching (1978) and Tryon & Tryon (1982) is confirmed. The (partly) free-veined species of *Goniophlebium* are in gross morphological aspects quite similar to the species under study and therefore often misidentified as such. The main distinguishing character states are the articulate pinnae (Fig. 2), the absence of soral paraphyses and the jigsaw-puzzle-shaped, warty cell walls of the rhizome scales in *Thylacopteris* (Fig. 1).

The geographical distribution and several morphological characters suggest a closer relationship with *Goniophlebium* than with *Polypodium*. These characters are the distance between the phyllopodia, the attachment, shape and clathration of the rhizome scales, the venation pattern, and the surface ornamentation of the exospore.

TAXONOMIC PART

Presentation of data

Since the genus *Thylacopteris* is represented by only two species, the key to the species is replaced by a list of diagnostic characters. A full synonymy is given for each species. Selected literature is included. The description of the species refers to characters recognised only in dry herbarium specimens of adult sporophytes. Living material has not been examined. Information on the habitat has been taken from herbarium labels. Notes are added for special remarks and additional data (e.g. numbers of specimens seen), when necessary. Drawings and photographs illustrate the most important details.

THYLACOPTERIS

Thylacopteris Kunze ex J. Sm., Hist. Fil. (1875) 87; Kunze apud Mett., Farngett. Polypod. (1856) 57, nomen; C. Chr. & Holttum, Gard. Bull. Sing. 7 (1934) 304; Copel., Gen. Fil. (1947) 181; HENNIPMAN in KRAMER et al., Pteridophytes and Gymnosperms 1 (1990) 228. — *Polypodium* subg. *Ctenopteris* (Blume) J. Sm., J. Bot. 3 (1841) 394. — Type species: *Thylacopteris papillosa* (Blume) Kunze (basonym *Polypodium papillosum* Blume).

Moderate-sized. *Rhizome* long creeping, terete, 2–6 mm in diam., light brown, clothed with scales, phyllopodia more or less prominent, 0.5–6(–12) cm apart; anatomy: ground tissue parenchymatous, number of vascular strands 4–14, related to diameter of rhizome, arranged in a regular circle, bundle sheaths present or absent, black sclerenchyma strands longitudinal, scattered in the ground tissue, present or absent. *Rhizome scales* evenly inserted, dull brown, adpressed or apically spreading, quite densely set, deciduous, pseudopeltate, deltoid or mucronate, up to 6.5 mm long, apex acute, rarely acuminate, auricles round, cells light yellow, clathration of cell walls present, close to stalk absent, at basal and central part puzzle-shaped with wavy, anticlinal walls, at apical part rectangular; inner layer of thickened cell walls warty, clathrate marginal protrusions absent or sometimes merely indicated, marginal gland only apical. *Fronde* monomorphic, articulate to rhizome, petiolate, stipe glabrous or sparsely scaly, in cross section near base 0.8–3.5 mm across, index length of stipe/length of blade 0.2–0.6, blade membranous, index length/width 3.6–11.2, equally wide all along blade or somewhat wider above base, pectinate, lateral segments separated from the rhachis by what possibly is an abscission layer, in an angle of (80–)90° towards the rhachis, number relative to length of blade, linear, apically obtuse to acute, margin entire, crenate or serrate, lowermost segments rarely slightly reduced and/or deflexed, apical segments continuously reduced in length, terminal segment adnate conform to lateral segments or caudate. *Laminar indument*: glandular hairs rarely present, 2 cells long with 1 or 2 terminal glands. *Stomata* (co-)polocytic. Veins free, simple or once-forked, excurrent with terminal hydathodes. *Sori* exindusiate, uniserial at each side of costa, situated medially between costa and margin, superficial or deeply sunken, on hydathodes terminal on an acroscopic vein, round, 0.5–1.8 mm in diam., receptacular paraphyses absent; sporangial capsule length c. 325 µm, index length/width 1.1–1.3, annulus vertical, indurated cells (10 or) 11 (or 12), cells in total 18–20, sporangial stalk 2-rowed. *Spores* bilateral, oblong (polar view), plano-convex (lateral view), light yellow, laesura 0.5–0.7 of the length of the spore, exospore smooth or pustulate, perispore thin, surface smooth or shallowly wrinkled, globules few or many in various sizes.

Chromosomes – $n = 35, 36, 37$.

Distribution – Malesia: Sumatra, Peninsular Malaysia, Borneo, Java, Philippines, Celebes, Lesser Sunda Islands, Moluccas, New Guinea.

Habitat & Ecology – Primary forest, creeping, epiphytic, epilithic or terrestrial; shaded; altitude (0–)500–1500(–3500) m.

Note – The name *Thylacopteris* derives from the Greek word 'thylacos', meaning cyst, sack or pouch.

DIAGNOSTIC CHARACTERS OF THE SPECIES

1a. Sori deeply embossed, bundle sheaths in rhizome present, sclerenchyma strands in rhizome 12–100, widespread in Malesia, except New Guinea

2. *T. papillosa*

b. Sori superficial, bundle sheaths in rhizome absent, sclerenchyma strands in rhizome absent, endemic to New Guinea **1. *T. diaphana***

1. *Thylacopteris diaphana* (Brause) Copel.

Thylacopteris diaphana (Brause) Copel., Gen. Fil. (1947) 182. — *Polypodium diaphanum* auct. non Bory (1804): Brause, Bot. Jahrb. 49 (1912) 42. — Type: *Schlechter 18220*, Papua New Guinea, 'Kaiser Wilhelmsland, in den Wäldern des Finisterre-Gebirges', 1100 m, 06-ix-1908 (lecto B; iso B, L).

Epiphytic or epilithic. *Rhizome* 2–3 mm in diam., phyllopodia 3–12 cm apart, brown bundle sheaths absent, sclerenchyma strands absent (note 2). *Rhizome scales* (Fig. 1) clathrate, pseudopeltate, deltoid, continuously narrowing towards apex, then apex spreading, or mucronate, base cordate, overlapping, index 2.3–3.8, 2.3–4.4 by 0.9–1.2 mm, marginal protrusions absent. *Fronde*s: blade index length/width 6.2–11.2 maximal length 45 cm, lateral segments acute, margin crenate to serrate, index length of stipe/length of blade 0.2. Veins free, simple or once-forked (note 3). *Sori* 1–1.8 mm in diam.; sporangial stalk: length c. 0.4 mm. *Spores* (Fig. 3a, b): length 58–63.5 µm, laesura 0.5 times the length of spore, exospore slightly pustulate, perispore shallowly reticulate.

Distribution – Endemic to New Guinea.

Habitat & Ecology – Primary forest; *Elmerillia* and *Pasania* dominant; on mossy rock face; on limestone cliffs; east slopes; in dense forest shade; near creeks; altitude 750–1400 m.

Notes – 1. Nine specimens (plus duplicates) seen.

2. Sclerenchyma strands have not been observed, even though Copeland (1947) mentioned them as merely indicated.

3. It has been observed that very rarely the forking veins unite and form an areole lacking an included free veinlet, e.g. *Henty & Streiman NGF 38924* (BM).

4. Etymology. The epithet 'diaphanus' refers to the transparent rhizome scales: 'paleis fuscis diaphanis' (ex original description).

5. Collector's notes. Leaves pendant; pinnae undulate; dark green; sori brown.

2. *Thylacopteris papillosa* (Blume) Kunze ex J. Sm.

Thylacopteris papillosa (Blume) Kunze ex J. Sm., Hist. Fil. (1875) 87; Copel., Fern Fl. Philipp. 3 (1960) 463. — *Polypodium papillosum* Blume, Enum. Pl. Javae 2 (1828) 131; Benn. et al., Pl. Jav. Rar. (1838) 6, pl. 2; Hook., Cent. Ferns ad pl. 46, Sp. Fil. 4 (1862) 198; Ces., Atti Accad. Sc. Fis. (1876) 25, name only; Bedd., Suppl. Ferns Brit. India (1892) 88; Holttum, Rev. Fl. Malaya 2 (1966) 202. — Type: *Zippelius 89*, Java: 'crescit in silvis montanis ad arbores' (L).

Terrestrial, epiphytic or epilithic. *Rhizome* 1–6 mm in diam., phyllopodia 0.5–6.0 cm apart, bundle sheaths dark or light brown, sclerenchyma strands 12–100. *Rhizome scales* clathrate, pseudopeltate, continuously narrowing towards apex, apex spreading, base cordate, overlapping, index 2.0–3.8, 2.4–3.9 by 1.0–1.9 mm, marginal protrusions absent. *Fronde*s: blade index length/width 3.6–11.0, maximal length 59 cm, lateral segments usually obtuse, margin entire, at apex crenate (note 2), index length of stipe/length of blade 0.3–0.6 (note 3). Veins free, simple or once forked. *Sori* 0.5–1.0 mm in diameter, deeply embossed, depth of papillae 1–2 mm; sporangial stalk: length 0.8–1.7 mm (note 5 & 6). *Spores* (Fig. 3c, d): length 54–63.5 µm, laesura 0.7 times length of spore, exospore smooth, perispore plain.

Distribution – Sumatra, Peninsular Malaysia, Borneo, Java, Philippines, Celebes, Lesser Sunda Islands, Moluccas.

Habitat & Ecology – Primary forest; on moss-covered trunks; on steep flanks of limestone boulders with organic soil in-between; dark brown clayey soil; shaded close to stream; alt.(0–)500–1500(–3500) m.

Notes – 1. Hundred sixty-eight specimens (plus duplicates) seen.

2. The pinnae of a few specimens from Sumatra and Borneo are crenate throughout, e.g. *Robinson & Kloss 1914* (BM), *Clemens 29572* (BM). This form is apparently mentioned in the original description as “Var. B. frondibus brevioribus et laciniis acutiusculis”.

3. Indices as length/width of blade and length stipe/blade are different In juvenile plants, e.g. *Alston 16992* (BM).

4. The present species is described in detail by Bennett & Brown and illustrated by J. & C. Curtis (1838). A feature, not seen in dry material, is the “white, obviously calcareous secretion intermixed with its capsules, and entirely concealing them in their young state ...”

5. The length of stalks of mature sporangia corresponds with the depth of the papillae. Mature sporangial capsules therefore protrude from the papillae.

6. On old fronds papillae sometimes break off and the pinnae appear perforated.

7. Collector’s notes. Fairly erect, bright green or pale bluish green, sori yellowish brown.

ACKNOWLEDGEMENTS

I wish to express my gratitude to Prof. Dr. P. Baas, who invited me to participate in the Flora Malesiana Project as a scientific researcher of the Rijksherbarium Leiden. I am glad I could discuss specific details with Dr. H. Nooteboom and Dr. P. Hovenkamp and I am grateful for their advice. Most valuable technical and artistic assistance was received from B.J. van Heuven and J. Wessendorp. Thanks are also due to the directors and keepers of the herbaria of A, BAS, BM, BO, GH, K, L, MICH, NY, P, PNH, RO, UC and US for facilitating the study of their collections.

REFERENCES

- Baayen, R.P., & E. Hennipman. 1987. The paraphyses of the Polypodiaceae (Filicales). *Biol. Pflanzen* 62: 251–316.
- Beddome, R.H. 1892. Supplement to the ferns of British India, Ceylon and the Malay Peninsula: 88.
- Bennett, J.J., R. Brown & T. Horsfield. 1838. *Plantae javanicae rariores, descriptae iconibus illustratae, ...* : 6. London.
- Blume, C.L. 1828. *Enumeratio plantarum Javae et insularum adjacentium ...* 2: 128, 131. Leiden.
- Blume, C.L. 1829. *Flora Javae nec non insularum adjacentium. Filices*: 181, 191. Brussels.
- Bory de Saint-Vincent, J.B.G.M. 1804. *Voyage dans les quatre principales îles des mers d’Afrique* 1: 382. Paris.
- Bosman, M.T.M. 1991. A monograph of the fern genus *Microsorium* (Polypodiaceae). Thesis, Leiden University.
- Brause, G. 1912. Neue Farne Papuasiens, nebst allgemeinen Bemerkungen über das Vorkommen der Pteridophyten in Neu-Guinea von R. Schlechter. *Bot. Jahrb.* 49: 42.
- Cesati, V. de. 1876. *Felci e specie nei gruppi affini raccolte a Borneo dal Signor Odoardo Beccari. Atti R. Accad. Sc. Fis. Mat. Napoli* 7: 25.

- Christ, K.H.H. 1905. Filices borneenses. Fougères reçues par les expéditions des Messieurs Nieuwenhuis et Hallier etc. Ann. Jard. Bot. Buitenzorg 2, 5: 120.
- Christensen, C. & R.E. Holttum. 1934. The ferns of Mt. Kinabalu. Gard. Bull. Sing. 7: 304.
- Copeland, E.B. 1947. Genera Filicum. Chronica Botanica Co., Waltham, Mass.
- Copeland, E.B. 1960. Fern flora of the Philippines 3: 463.
- Harrington, M.W. 1877. The tropical ferns collected by Professor Steere in the years 1870–1875. J. Linn. Soc. Bot. 16: 31.
- Hennipman, E., K.U. Kramer & P. Veldhoen. 1990. Polypodiaceae. In: K.U. Kramer & P.S. Green (eds.), I. Pteridophytes and Gymnosperms: 228. In: K. Kubitzki (ed.), The families and genera of vascular plants. Springer Verlag, Berlin etc.
- Holttum, R.E. 1966. Flora of Malaya 2. Ferns of Malaya, ed. 2.: 203.
- Hooker, W.J. 1854. Icones plantarum 10: t. 946. London.
- Hooker, W.J. 1854. A century of ferns: t. 46.
- Hooker, W.J. 1862. Species filicum. London.
- Mettenius, G. 1856. Über einige Farngattungen. 1. Polypodium. Abh. Senckenb. Naturforsch. Ges. 2, 1: 49, 56.
- Nelson, G.J., & N. Platnick. 1981. Systematics and biogeography. Columbia University Press, New York.
- Paris, B.S., R.S. Beaman & J.H. Beaman. 1992. The plants of Mt. Kinabalu 1. Ferns and fern allies: 108. Royal Botanic Gardens, Kew.
- Rödl-Linder, G. 1990. A monograph of the fern genus *Goniophlebium* (Polypodiaceae). Blumea 34: 277–423.
- Sen, V., & E. Hennipman. 1981. Structure and ontogeny of stomata in Polypodiaceae. Blumea 27: 175–201.
- Smith, J. 1841. Enumeratio filicum Philippinarum, or ... J. Bot. (Hooker) 3: 394.
- Smith, J. 1875. Historia filicum.
- Sota, E.R. de la. 1973. On the classification and phylogeny of the Polypodiaceae. In: A.C. Jermy et al., The phylogeny and classification of the ferns. J. Linn. Soc. Lond., Bot. 67: 229–244.
- Tryon, A.F., & B. Lugardon. 1991. Spores of the Pteridophyta. Surface, wall structure, and diversity based on electron microscope studies. Springer Verlag, New York etc.

IDENTIFICATION LIST

Collections are referred to the number given to the species in this treatment.

- Alston 16992: 2 — Anderson, E.F. 3896: 2 — Anderson, J.A.R. 8986, S 29900: 2 — Anonymous 41994: 2.
- Backer & Posthumus 604: 2 — Bakhuizen van den Brink 2396, 4192, 4697: 2 — Bartlett 6753b: 2 — Bolster 320: 2 — Brass 12838, 24996, 32210: 1 — Brooke 9132: 2 — Brooks 205s, 423s: 2 — Bünnemeijer 5937: 2.
- Canicosa 9824: 2 — Chai S 27528: 2 — Chew, Corner & Stainton 636, 2859: 2 — Clemens 66: 2; 2356: 1; 10326, 22014, 26092, 26488, 26892, 27290, 27290bis, 29572, 29572bis, 34392: 2; 41787: 1 — Copeland 265, 1533: 2 — Cuming 185, 189: 2.
- Edaño (all PNH) 467, 517, 5180, 5217, 17314, 21263, 21370, 24808, 77947, 77953: 2 — Elmer 6018, 9867, 10769, 13642, 15174, 16883: 2 — Elsener H128: 2 — Endert 3024, 4629: 2.
- Fénix 15750: 2 — Forbes 424: 2.
- Hallier 1824: 2 — Hancock 58: 2 — Haniff 14215: 2 — Henderson 29572: 2 — Hennipman 5063: 2 — Henty & Streiman NGF 38924: 1 — Hirano & Hotta 443, 1520: 2 — Holttum 25143: 2.
- Iwatsuki c.s. B1002, B3263, C649: 2.

- Jermy 13296, 13819, 13985: 2 — Jermy & Rankin 15459, J14900: 2 — Johansson, Nybom & Riebe 84: 2 — de Joncheere 1323: 2.
- Kato c.s. B3761, C1225, C3259, C4156, C4730, C6552, C7471, C11339, C11904, C12023, C12445, C13744: 2 — Kehding 2938: 2 — Keith 8897: 2 — Keyser 222: 1 — bin Kiah 23964, 31916: 2 — King's collector 1994, 7206: 2 — Koorders 15400b: 2 — Korthals 174: 2.
- Lörzing 5583, 5816, 12259: 2.
- Maskuri 705: 2 — Meijer 7480, 9569, 9580: 2 — Mendoza & Convocar 8629: 2 — Merrill 5979, 8284: 2 — Molesworth Allen 3071, 4111: 2 — Mousset 9, 110, 774: 2 — Moysey 33822: 2.
- Native collector 1565, 1580, 2348: 2 — bin Nur 12173: 2.
- Parris 6807, 6999: 2; 7812: 1; 8912, 10679, 11107: 2 — Price 1889, 1941, 2523, 2954, 3306: 2 — Purseglove P5236: 2.
- Rachmat (Exp. van Vuuren) 490: 2 — Ramlanto c.s. 553: 2 — Ramos 1651, 23418, 30277, 41947, 43029, 77199: 2 — Ramos & Edaño 49582: 2 — Richards 2348: 2 — Ridley 14741: 2.
- Sarip 340: 2 — Schlechter 18220: 1 — Schmutz 1655, 5339: 2 — Shim Phyu Soon SAN 81670: 2 — Sinclair & Edaño 9589: 2 — Sulit 8666: 2.
- Topping LeRoy 1588, 1764, 1797: 2.
- Wenzel 532, 932: 2 — de Wilde 13618, 19868: 2 — Williams 2469: 2 — Wray 809: 2.
- Zollinger 2112: 2.