THE GENUS NERVILIA (ORCHIDACEAE) IN AFRICA
AND THE ARABIAN PENINSULA

BÖRGE PETTERSSON

Department of Systematic Botany, Uppsala University, Uppsala, Sweden

SUMMARY

The orchidaceous genus *Nervilia* Comm. ex Gaud. is revised for Africa, including Madagascar and other islands, and the Arabian peninsula. Sixteen species are recognized, two of which are each subdivided into two varieties. Keys are presented for all taxa. Lectotypes or neotypes are given for all relevant names from Africa. For each species full synonymy, description, distribution map, notes on habitat, flowering time etc., and a line drawing are provided. All species but two are also illustrated by colour photographs. A cladistic analysis of the genus is presented. Phytogeography, morphology, pollination, altitudinal range etc. are briefly discussed.

INTRODUCTION

The genus *Nervilia* includes around 60 species distributed in tropical and (to some extent) subtropical parts of Africa, Asia and Australia.

The present work is a revision of the taxa occurring in Africa (including Madagascar and all other islands) and the Arabian peninsula. Altogether 16 species are recognized, three of which are endemic to Madagascar. All but two species are endemic to Africa in the wide sense. The exceptions are *N. crociformis*, widespread in the warmer parts of Asia, avoiding the drier areas, and also found in Australia, and further *N. bicarinata*, found in Arabia.

When sect. *Linervia* is mentioned in the morphology chapter, it should be understood in the recircumscribed form explained in the phylogeny chapter, i.e. including sect. *Kyimbilaeae*.

MATERIAL AND METHODS

Herbarium material pertaining to African *Nervilia* has been studied (and mostly obtained on loan) from the following 57 herbaria (boldface means that the herbarium has been visited): AMES, B, BM, BOL, BR, C, COI, DS, DSM, E, EA, ETH, FT, G, GC, H, HBG, IEC, JE, K, L, LAU, LD, LE, LG, LISC, LISJC, LISU, LMU, M, MAL, MEL, MO, NH, NHT, NU, NY, O, P, P-LA, PRE, RUH, S, SRGH, TAN, TOGO, U, UC, UCJ, UPS, VBI, W, WAG, WRSL, WU, YA, Z (abbreviations according to Holmgren, Keuken & Schofield 1981 with later additions in Holmgren 1984).


Living material of 11 species has been brought back for cultivation in the greenhouse, permitting various observations of morphology, development, floral biology, cytology etc. Further living material from Africa has been added through travelling colleagues and interested amateurs, while Asian material of *N. crociformis* has been contributed by the Botanical Garden of Gothenburg. The following five species have flowered in cultivation: *N. crociformis* (from Malawi, Moçambique and Thailand), *N. adolphi* (Tanzania and Zambia), *N. gassneri* (Malawi and Tanzania), *N. bicarinata* (Madagascar) and *N. kotschyi* (Moçambique).

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When necessary, dried flowers were softened in boiling water or 25% ammonia solution. Measurements of floral parts of dried specimens (esp. column length) were greatly facilitated by the use of a fiber optic cold light illumination device for ‘x-raying’ the flowers of the herbarium sheets. This method, which considerably reduces the need of softening dry flowers, is described by Pettersson (1984, 1986).

Measurements of width of leaves, flower parts etc., were made on the widest part. Length of the scape (Fig. 1A) was measured from the tip of the leaf bud (or corresponding level if the leaf had started to develop), indicating the approximate soil surface, up to the tip of the uppermost bract (the longest if more than one). Length of the gynostemium (Fig. 1B) was measured the shortest way from the base (excluding ovary) to the top (including the anther in normal position, partly enclosed in the clinandrium). Length of the leaf blade in cordate leaves (Fig. 1C) was measured perpendicularly from the line connecting the lowest part of the basal lobes to the apex. Other measurements should be self-evident. When the number of veins of the leaf is given it refers to the main veins running (radially in most leaves) from the petiole to the rim of the blade. These major veins follow keels of the lower side in pleated leaves. The keels visible on the upper side are supported by much thinner veins.

Chromosome counts were made on actively growing rhizome tips collected in the field and immediately fixed in Navashin-Karpechenko solution. At the laboratory they were embedded in solid paraffin, sectioned and stained with crystal violet.

Scanning electron microscope studies (SEM) were performed on a JEOL JSM35 operating at 25 keV. Fresh leaf material was treated with Karnofsky’s reagent and OsO4 followed by critical point drying (a series of ethanol solutions terminated with Freon TF). Pollinia and seeds were air-dried. Finally the material was coated with gold-palladium for eight minutes.

For the study of stoma development young leafy buds were fixed in FAA after removal of cataphylls so as to expose the leaf base to the fluid. The material was transferred to 70% ethanol, dissected and the epidermis was peeled off with a fine forceps after loosening of the tissue with a razor blade. The peels were stained in acetocarmine, rinsed and mounted in glycerol for temporary mounts.

The flower-visitor insects collected are deposited at the Department of Systematic Botany, Uppsala.

The location of fragrance glands was investigated using the method described by Vogel (1963) and Stern, Curry & Whitten (1986). A 1:1000 solution of neutral red in tap water was allowed to work until sufficient colouring appeared. The UV photographs were taken through a Hoya U-360 filter on 400 ASA black and white film.

The distribution maps are based mainly on voucher specimens seen by the author. In a few cases, also lost types and other reliable literature records have been included. Collection sites closer than 15 (distance) minutes (approximately corresponding to 28 km) are represented by a single dot.

For the phylogenetic analysis the computer programs Hennig86 (Farris 1988) and PAUP (Swofford 1989) were used to construct the trees and to find the different alternative character optimizations. In Hennig86 the Implicit enumerator option was used and in PAUP the Branch and Bound option. MacClade (Maddison & Maddison 1987) was used as a tool for rapid check of character distributions.

The identification of the hand-writings of Blume and Perrier de la Bâthie was done through comparisons with examples in Burdet (1979) and, in the latter case, comparison with herbarium labels of material collected by Perrier himself. The hand-writing of Schlechter was identified through comparisons with determination slips and herbarium labels of his own material. Several lectotypifications and one neotypification were briefly made in Pettersson (1990a). These choices are discussed under the respective species in the present paper.
A morphological species concept has been applied, i.e. groups of morphologically similar specimens have been considered different species unless linked by intermediates.

A complicating factor for the taxonomy of *Nervilia* is its effective vegetative propagation which enables diverging clones to live on for a long time without mixing their genes. One prerequisite to treat a new form as a taxon should be that it is found in more than one locality, thus demonstrating its ability of dispersal.

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**TAXONOMIC CONCEPTS**

The rank variety is chosen within two species, *N. adolphi* and *N. kotschyi*, where there is a major discontinuous difference in leaf morphology that is not accompanied by a consistent difference in the flower characters, nor by separated geographical distribution.

**SYSTEMATIC POSITION**

The species now placed in *Nervilia* were assigned by Lindley (1840) to the tribe *Arethuseae*, which was not part of his *Neottieae*.

Bentham (1881) put them into his tribe *Neottieae*, subtribe *Arethuseae*. For a long time they were kept in essentially the same taxonomic position, but sometimes under different names and ranks. Thus Schlechter (1911) used the tribe name *Polychondreae* with *Neottieae* Pfitz. as a synonym. *Nervilia* was placed in subtribe *Gastrodiinae* together with, among others, *Arethusa*, *Auxopus*, *Didymoplexis* and *Gastrodia*. *Pogonia*, in which *Nervilia* had earlier been included, was separated and included in subtribe *Vanilliinae*. Later (Schlechter 1926), he created the monotypic subtribe *Nerviliinae* (as 'Nervilieae'). (*Arethusa* was moved to *Bletillinae*.) Brieger (1975) placed the genus in subfamily *Epidendroideae*, tribe *Arethuseae*, subtribe *Nerviliinae*. The latter contained the genera *Nervilia* and *Triphora*.

Dressler (1974) placed *Nervilia* among the "Epidendroid tribes" (without formal rank) and reunited it with the *Pogonia* alliance in tribe *Gastrodieae*, subtribe *Pogoniinae*. Later (Dressler 1981), he returned to Schlechter's first arrangement (but with different rank) with *Nervilia* in tribe *Gastrodieae* and *Pogonia* in tribe *Vanilliinae*. According to this classification, *Nervilia* belonged to subfamily *Epidendroideae* Lindl., tribe *Gastrodieae* Lindl., subtribe *Nerviliinae* Schlr. The genus *Arethusa*, to which many of the earliest described species of *Nervilia* were ascribed (see below), was placed in a different tribe. The placing of *Nervilia* in *Gastrodieae* was supported by Rasmussen (1982, 1985) and Burns-Balogh & Funk (1986).

Recently Dressler (1990) revised the gross systematics of *Epidendroideae*, expelling *Nerviliinae* from *Gastrodieae*. The unique and isolated position of *Nervilia* was accentuated through the creation of the new tribe *Nervilieae* Dressler. This tribe was regarded as monotypic, but an unidentified collection of a *Nervilia*-like plant from Sumatra might be a new genus also belonging here (see below under Phylogeny).

**THE HISTORY OF THE GENUS NERVILIA**

*Nervilia* was named and described by Commerson in a manuscript prepared in about 1770. However the publication was delayed for more than 50 years (see below). The name was probably chosen because of the prominent leaf veins of *N. bicornata* and other species.

The first published name of a species now belonging to this genus was *Arethusa petraea* (Afzelius ex Swartz 1800, nom. nud.) from Sierra Leone (see below).

The first validly published name was *Arethusa plicata* described by Andrews (1803) from India. Then followed *Arethusa petraea* (Swartz 1805) from Sierra Leone and *Stellorkis* ('*Stellorchis*') *apostellis* (or *Arethusa? simplex* alternatively) from Mauritius (Thouars 1822, see below).

The first generic name published for the present entity was *Stellorkis* (Thouars 1809), followed by *Cordyla* (Blume 1825), *Nervilia* (Commerson ex Gaudichaud-Beaupré in Freycinet 1827), *Roptrostemon* (Blume 1828) and *Bolborchis* (Zollinger & Moritz in Moritzi 1846). *Cordyla* Blume was illegitimate because of *Cordyla* Loureiro (1790) (*Caesalpiniaeeae*). When Blume realized this he chose *Roptrostemon* to replace it. Eventually *Nervilia* was conserved against *Stellorkis* at the International Botanical Congress in Vienna 1905 (Brieger 1906).
From 1832 and onwards, Lindley and others placed the *Nervilia* species in *Pogonia* Jussieu. In 1840, Lindley created the section *Nervilia for Pogonia* species with solitary, plicate, hysteranthous leaves.

In 1888, Pfitzer reinstalled *Nervilia* as a genus and from 1900 and onwards Schlechter strongly advocated that *Nervilia* was not closely related to *Pogonia* (Schlechter 1900, 1903, 1906, 1911, 1915b, 1921), a view subsequently adopted by all botanists.

A sectional subdivision of *Nervilia* was proposed by Schlechter (1911), who created the sections *Linervia, Vinertia* and *Nervilia* (as 'Eunervilia') based mainly on the number of flowers in the inflorescence. Later he added section *Kyimbilaea* for a species with a spurred lip (Schlechter 1915b).

The only global revision was made by Schlechter in 1911. Local revisions have been made for Thailand – also covering most of Indochina and India (Seidenfaden 1978), Australia (Dockrill 1969) and parts of Africa (see below).

THE HISTORY OF NERVILIA IN AFRICA

1. Collecting and descriptions of new species

The earliest known collections of *Nervilia* from Africa in the wide sense were made by Commerson in 1769, 1770 and 1771 from Mauritius, the Comores and Réunion and include *N. bicarinata*.

The first species to be described was based on material collected by Afzelius in Sierra Leone some time between 1792 and 1796. It was the flowers of *N. petraea*, one of the most inconspicuous species with anthesis often restricted to one day each year, that was found. This taxon was named *Arethusa petraea* by the collector himself and the name was first validly published by Swartz (1805).

Surprisingly enough, the tiny flower of *N. petraea* was the subject also of the second species description from the area. Du Petit-Thouars found it in Mauritius some time between 1793 and 1796 and published it first as *Stelkorkis* without a specific epithet (Thouars 1809) and later (1822) as *Stellorchis aplostellis* or *Arethusa? simplex* (for du Petit-Thouars' proposal on an alternative nomenclature, see Friis & Rasmussen 1975).

Blume (1859) described four new species (including the large and widespread *N. bicarinata*) under *Pogonia*, all originating from the African islands of the Indian Ocean. They were based on collections made by Pervillé, Commerson, Boivin and Thouars. *Pogonia thouarsii* was erroneously considered to be a synonym to *Arethusa simplex* by Durand & Schinz (1894) and several later authors (Rolfe 1897, Schlechter 1911, 1915a, 1924, Pellegrin 1938 and Perrier de la Bâthie 1939). The three other species were neglected by all subsequent workers except Schlechter (1911), who made the combinations in *Nervilia* and called them "nicht genügend bekannte Arten". The reasons for this neglect were discussed by Pettersson (1990b).

Between 1864 and 1885 Reichenbach f. described seven new species (one together with Sonder) on the basis of material originating from the Cape Verde Islands and Sudan in the north to Angola, South Africa and Madagascar in the south, based on collections by Cienkowski, Zeyher, Mann, Welvitsch, Bolle, Hildebrandt, von Mechow [& Teusch] and Humblot. Today three of these are regarded as conspecific with the already described *N. bicarinata*.

Rolfe (1897) described two new species from presentday Malawi, based on material collected by Buchanan.
From Ethiopia, two new species were collected and described by, respectively Chiovenda (1911) and Fiori (1912).

In a precursory paper for Flore de Madagascar, Jumelle & Perrier de la Bâthie (1912) described five new species, all based on collections by the latter.

Schlechter described 11 new species (one together with Perrier de la Bâthie) between 1911 and 1924: one from West Africa (own collection), one from South Africa (Rudatis and Meeser), six from East Africa (Stolz) and three from Madagascar (Perrier de la Bâthie).

Summerhayes (1938) described a new species from the Central African Republic, based on material collected by Le Testu.

During the last 30 years six new species have been described: one from Madagascar (Senghas 1964), one from West Africa (Hallé & Toilliez 1971) and four from the Flora Zambesiaca area (Cribb 1977; Williamson 1980; Pettersson 1990b).

2. Check-lists and revisions

Durand & Schinz (1894) listed seven species from Africa in the wide sense, omitting the ones described by Swartz and Blume and also Reichenbach's Cape Verdean species.

In Flora of Tropical Africa, Rolfe (1897) treated six species.

The diligent orchidologist Schlechter (1911) in his world-wide revision of the Neottieoideae also provided a sectional subdivision of Nervilia (see above), a key for all species (unfortunately containing several "geographical characters") and a list of 37 species, 10 of which were from our area. In a check-list of the orchids of Madagascar, the Mascarenes, the Comores and the Seychelles, he (Schlechter 1915a) mentioned seven species. In the same year (Schlechter 1915b) he gave an account of the orchids collected in the Southern Highlands of presentday Tanzania by the German missionary Stolz, including eight identified Nervilia species and five unnamed ones. A list of orchids collected in Madagascar by Perrier de la Bâthie (Schlechter 1924) contains nine named species of Nervilia.

In Flore de Madagascar, Perrier de la Bâthie (1939) listed 10 species of Nervilia.

In the first edition of Flora of West Tropical Africa, Summerhayes (1936) listed four species and one variety. In the second edition (Summerhayes 1968) the number of species had increased to six. Another local revision for West Africa centered around the Ivory Coast was made by Hallé & Toilliez (1971).

Flore of Tropical East Africa (Cribb 1984) and Flore d' Afrique Centrale (Geerinck 1984) treated 14 species plus one variety and 8 species respectively.

The forthcoming account of Nervilia in Flora Zambesiaca (Pettersson in press) contains 11 species and two varieties.

The present treatment finally recognizes 13 species and two varieties in the African mainland plus three additional endemics in Madagascar.

MORPHOLOGY

Growth habit — The genus Nervilia has an unusual growth habit among the orchids. Firstly, the single, often prostrate leaf of most species is more or less orbicular, reniform or very broadly cordate. Secondly, members of the genus are hysteranthous, i.e. flowers and leaves are normally not found at the same time, a fact which has caused taxonomists many problems and is also the reason for a widespread erroneous opinion that Nervilia is a saprophytic genus. Other unusual traits are the very effective vegetative propagation producing "colonies" (Fig. 34), the low light demand that makes it possible for most species to occupy dark softwood plantations (Figs. 35, 36), the short anthesis (less than a day) of the species in sect. Linertia, and elongation of the scape during fruit maturation in the same group.
Rhizome and tuber — The genus is characterized by a subspherical subterranean rhizomatous tuber of 2–7 contracted and swollen internodes (Figs. 2, 3). It continues in a very short ascending (subterranean) stem (1–15 cm), from which several (normally 2 or 3, sometimes more) horizontal runners (Figs. 55a, 68, 69f) are produced, in the large species reaching up to 50 cm, eventually ending in new tubers. These are the perennial parts of the plant surviving the dry season, but they also constitute a very effective way of vegetative (clonal) propagation. Because of this, individuals of the genus are often found in more or less dense colonies probably built up by a single clone (Fig. 34). It also makes it possible for different aberrant types to live on and spread locally and to conquer pollinator-poor man-made habitats like softwood plantations.

The tubers are storage organs for carbohydrates (starch) and water. The formation of tubers and the rhizome system have been studied by Moreau (1912, 1913), Dietz (1930), Burgeff (1936) and Trouslot (1969, 1973, 1976).

Roots — The runners (Figs. 2, 55a, 68, 69f) are frequently mistaken for roots. The real roots are short and straight and are found on the tuber, ascending stem and sometimes on the runners. Often they are totally lacking. Probably the humidity and other qualities of the soil determine the presence, number and location of roots.

Root hairs appear on all subterranean parts (except perhaps cataphylls), viz. roots, tuber, runners and ascending stem.

Leaf — The solitary, plicate and non-articulate foliar leaf has a shape that is very unusual within the orchid family. They are mostly cordate to reniform or almost circular, but three taxa (*N. kotschyi* var. *purpurata*, *N. ballii* and *N. shirensis*) have more “normal” elliptic or ovate leaves. The size variation within the genus ranges from a diameter of one or two cm up to 20–25 cm (Fig. 4). Many species have strongly prostrate leaves, while in others the blade is held horizontally on a petiole of a few to several centimeters length. The elliptic leaves mentioned are held in a more or less erect position.

The prostrate condition is probably advantageous because it guarantees a more or less horizontal position to the blade. In areas where the sun passes zenith during the growing period this would give a maximum of light to an immobile leaf located among other plants, especially in grassland.

The upper leaf surface is pubescent with vertical, pluricellular hairs in *N. crociformis* (Figs. 6, 7), *N. leguminosarum*, *N. affinis*, *N. stolziana*, *N. pectinata*, and *N. subintegra*. This pubescence is possibly an adaptation to low light intensities. The transparent cylindrical hairs might be able to concentrate the light in a similar way as the cells of the silvery pat-
Figs. 4-11. Leaf morphology of *Nervilia*. 4. Size comparison between the smallest and the largest species. Two leaves of *N. petraea* on a leaf of *N. bicarinata*, Ankarafantsika, Madagascar. 5. Reticulate venation visible on dead leaf of *N. adolphi var. adolphi*. 6 & 7. Developing leaves of *N. crocifera*. Note plicate venation. Arrows denote just opened leaf buds. 8. Young leaf of *N. petraea*. Note granular surface in sectors. 9. Three young leaves of *N. kotschyi var. kotschyi* from the same population (probably a clone) showing different degrees of fringe development. The left one shows very distinct fringes along all keels, the middle one is totally smooth (will become like the one in Fig. 67g when fully developed) and the right one is intermediate between the two. 10. Young leaf of *N. stolzianna*. Note reticulate silvery pattern and short vertical hairs. 11. Leaves of *N. adolphi var. seposita*. Note tessellate silvery pattern.
term (see below) and also to lead it into the leaf as a natural optical fibre (J. Bornman pers. comm.).

Long, thin hairs are sometimes observed in *N. crociformis* on the lower surface during leaf development. Apparently they are shed very quickly.

The young leaves of *N. petraea* have small warts (Fig. 8) that might correspond to the hairs in other species (see below).

Various silvery patterns appear on the upper leaf surface, either obligately (so far as known) as in *N. adolphi* var. *seposita* (the designation seposita as understood here is reserved exclusively for specimens showing such a pattern) and *N. ballii*, or facultatively as in *N. petraea*, *N. stolziana*, *N. fuerstenbergiana* and *N. kotschyi* var. *kotschyi*. This pattern has the form of rays running along or parallel to the main veins in *N. ballii*, *N. petraea* and *N. kotschyi*, while it is reticulate in *N. stolziana* (Fig. 10) and distributed in spots or blotches in *N. adolphi* (Fig. 11) and *N. fuerstenbergiana*. The term "feuilles argentées" for this leaf type was adopted by Rodrigue (1900), who studied *Lamium galeobdolon* and *Tradescantia zebrina*. She found that the silvery areas differed in two respects from the green ones: They contained air (probably between the epidermis and the mesophyll [my comment]) and their epidermal cells were much larger. These large cells are probably advantageous in situations with low light levels. If the photosynthesis of the cells in a normal green leaf is below the compensation point, the epidermis cells of the silvery areas are probably able to act as minute lenses and concentrate the weak light enough to exceed this point and give a positive net assimilation in some of the underlying green cells. The air space would then give the necessary distance between the "lens" and its "focal area". Another possible function of the silvery pattern would be to reflect the light much in the same way as the "tapetum lucidum" does in the cat's eye (J. Bornman pers. comm.), thus giving a light ray a double opportunity to be absorbed inside the leaf.

A similar marble pattern as in these *Nervilia* species is common in leaves of shade-adapted plants like *Oeceoclades maculata*, *Lamium galeobdolon*, several *Disperis*, *Sansevieria*, *Begonia* and *Cyclamen* species etc. Focussing effects from lens-shaped epidermal cells or cell parts have been investigated by, e.g., several workers around the turn of the century (Haberlandt 1909) and recently by Martin, Josserand, Bornman & Vogelmann (1989).

The lower leaf surface and the petiole are often (strongly) purple as a result of the presence of anthocyanin. This is the rule in *N. petraea*, *N. stolziana*, *N. adolphi* var. *seposita*, *N. fuerstenbergiana* and *N. ballii*; it commonly occurs in *N. pectinata*, *N. adolphi* var. *adolphi* and *N. kotschyi* var. *kotschyi*, but is only occasionally encountered in *N. bicarinata*.

Peltate leaves occasionally appear in this genus. A collection of *N. crociformis* from Malawi (la Croix 335) showed a mixture of peltate and normal leaves from the same colony, while another collection (Pettersson, Englund, Kustvall & Ranaivo VJR 104) of the same species from the same country had one peltate leaf. A specimen of *N. adolphi* var. *adolphi* from Malawi (Pettersson 354) and one of *N. petraea* from Tanzania (Pettersson, Hedrán & Kibuwa 422) each produced one peltate leaf when cultivated in the greenhouse in Uppsala.

Two leaves from the same tuber are sometimes found in most species. Very rarely they come from the same shoot but mostly from two adventitious shoots in response to an injury to the ordinary leaf or leaf bud.

The vernation is plicate (Figs. 6, 7).

Scape — The scape is erect, terete and laxly 1–12-flowered, with 2–5 sheathing cattaphylls, of which the uppermost one sometimes is substituted by a sterile bract. The size ranges from almost zero in some cleistogamous forms of *N. gassneri* up to 75–80 cm tall scapes in *N. bicarinata* and *N. renchiana*. 

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Sect. *Linervia* has a single-flowered inflorescence. With one exception, sect. *Nervilia* has members with several-flowered, racemose inflorescences. (One member, *N. ballii*, is normally one-flowered.)

In sect. *Linervia* the scape elongates several times through rapid extension growth during fruit development in a way similar to that known from the pedicel in *Didymoplexis* and *Auxopus*, saprophytic orchid genera belonging to *Gastrodieae* and believed to be close relatives of *Nervilieae* (see above).

**Flower** — The flowers are generally resupinate, but three species, *N. petraea*, *N. crocif. formis* and *N. leguminosarum* have erect flowers, an unusual feature among the orchids.

Within sect. *Nervilia* the flowers are very similar except for size and number. They have a very prominent false nectar guide pattern to the lip, consisting of red to purple (seldom green) veins, especially on the sidelobes (see i.e. Figs. 67c, 69e).

In sect. *Linervia* the flowers are fragrant, while in sect. *Nervilia* only *N. shirensis* is known to have a scent perceptible to the human nose.

Cleistogamy seems to be quite common in *N. gassneri* (Plate 3c) and occasional in *N. pectinata* (Pettersson 1989).

**Petals and sepals** — The tepals (except the labellum) are similar in colouration, shape and size. They are green or brownish green, sometimes with red or purplish venation or short longitudinal streaks of the same colour. They are more or less reflexed in sect. *Linervia* and held rather close to the labellum in sect. *Nervilia* and then often forming a hood over the column and lip.

The spreading tepals in sect. *Linervia* start to close after pollination.

**Lip** — The labellum is spurless or shortly spurred, 3-lobed to almost entire, sometimes papillate or pubescent and variously marked with red or purple.

The reddish or green, false nectar guide pattern (see below under Ecology: Pollination and floral biology) in sect. *Nervilia* is a synapomorphy for the whole section found also in the Asian and Australian species.

The lip in sect. *Linervia* is mainly white, often with a pink or lilac tinge, in *N. petraea*, *N. crocif. formis*, *N. leguminosarum* and *N. subintegra*, and has various distinctly red or purple markings in the other species.

Two species, *N. stolziana* and *N. pectinata*, have a short, nectariferous spur. *N. subintegra* often has trace of a spur, which could be interpreted as a rudiment from a spurred ancestor. *Nervilia crocif. formis* has a small pit-like deepening from the bottom of the flower into the ovary, constituting a very short functional spur.

A yellow area along the midline of the lip, found in *N. petraea*, *N. crocif. formis*, *N. stolziana*, *N. pectinata* and *N. subintegra*, probably constitutes a general pollen or anther mimic to attract insect visitors (see Pettersson 1989).

**Gynostemium** — The gynostemium is long, curved to almost straight, more or less slender towards the base (Figs. 1c–d, 12, 54, 55, 58–62, 64–69). The clinandrium is a deep apical cavity (Fig. 65f) embracing a large part of the incumbent anther which is hinged at the back. The stigma is ventral and elliptic to almost square. The anther in sect. *Nervilia* has two protruding teeth pointing towards the lip (Fig. 69d). This is a synapomorphy for the whole section, found also in the Asian and Australian species. The teeth are advantageous during visits by pollinating insects when they engage with the back rim of the animal's thorax, thus lifting the anther and placing the pollinia on top of the pollen vector. The gynostemium of *N. adolphi*, *N. fuerstenbergiana* and *N. gassneri* is hairy on the ventral
side (Figs. 1c, 61, 62d, 64e), a synapomorphy for this group. It is also found in some Asian and Australian species, which consequently could be expected to be closely related (some possibly even conspecific).

Rostellum — The rostellum (the modified portion) is a lip-shaped to roundish swelling bordering the stigmatic area upwards (Fig. 12). At anthesis the cellular structure dissolves into a mucus and becomes a “glue”, functioning as a diffuse viscidium in the sense of Rasmussen (1982).

Pollinia — The two pollinia are deeply bipartite and sectile (Fig. 13 and Pettersson 1989: Fig. 1), the partition reflecting the two pollen sacs (locules) of each theca. Each pollinium consists of many massulae of different size joined by thin elastoviscin strands (Figs. 14, 15) and each massula is composed of a large number of pollen tetrads. The outer exine sculpturing (as studied by SEM in *N. crociformis*, Figs. 15, 16) is tectate-imperforate (cf. Burns-Balogh 1983) with a laevigate (cf. Dressier 1990) but strongly wrinkled surface. It corresponds to type 1, “± laevigat-skabros” (most similar to that of *Platanthera hyperborea*), of Schill & Pfeiffer (1977). The pollen formation was studied to some extent in *N. crociformis*. The meioses were found to take place as late as only one or two days before the anthesis. It was immediately followed by the division giving rise to the generative and the vegetative nuclei, and the pollen is dispersed in the binucleate state. Voucher material: *N. crociformis*, Malawi, Pettersson 313.

Fruit — The fruit is a capsule, opening while green by means of six slits (Figs. 23–26). In sect. *Nervilia* it is heavily keeled, giving the cross section the appearance of a six-pointed star (or five-pointed; the keel corresponding to the lip is less prominent and often obsolete), while in sect. *Linervia* it is smoother with keels almost absent or very obtuse. As noted by Halld (1986), no elaters are present.

Seed — The seeds are diminutive and dust-like as in most orchids (Figs. 23, 26). Two species have been investigated with SEM, one from each of the recognized sections (see below). *Nervillia crociformis* has elongated and often curved, 0.3–0.4 mm long, seeds (Figs. 17, 18), while in *N. kotschyi* var. *kotschyi* they are 0.2–0.25 mm, with blunter ends (Figs. 20, 21). Both have an orifice at one end, apparently the scar from the attachment of the placenta. An interesting feature found in all investigated seeds from both species is the intercellular space where three (or four) testa cells meet (Figs. 19, 22). Nothing similar has been reported previously from the orchid family. Dressler (1990) stated the seed type to be unique, but without giving any details. Voucher material: *N. crociformis*, Malawi, Pettersson 313; *N. kotschyi* var. *kotschyi*, Moçambique, Pettersson 164.
Chromosome number — No chromosome counts on Nervilia species have previously been reported from African material. However, there are two records on Asian material of N. crociformis. Surprisingly enough they are very different from one another. Chennaiveeraiah & Jorapur (1966) report 2n = 144, while Singh (Löve 1983) found 2n = 20. There are similar conflicting results reported from three other Asian Nervilia species. Thus, in four different investigations, N. plicata has got 2n = 20, 62, 72 and 108.

My own counts were made difficult by the small and aggregated chromosomes. However, 2n = c. 54 was found in N. petraea from Madagascar and Moçambique. Additional
counts made on the collection from Moçambique by a technician gave c. 56 and c. 58. Unfortunately, lack of sufficient flower material from cultivation prevented use of the squash technique on meiotic divisions in anthers. Voucher material: *N. petraea*, Madagascar: Pettersson & Nilsson 79; Moçambique: Pettersson 211.

Chemistry — The most important flower pigment (apart from chlorophyll) is anthocyanin, a substance often present also in other aerial parts, e.g. scape and leaf (see above under Morphology: Leaf). Otherwise nothing is known about the chemistry in African species,
but a couple of Asian species have been thoroughly investigated in this respect by a Japanese-Taiwanese team (Kikushi, Kadota, Suehara & Namba 1981, Kikushi, Kadota, Hanganaki, Suehara, Namba, Lin & Kan 1981, and several later works by these authors). They revealed the presence of various triterpenes and sterols in \textit{N. plicata} (as \textit{N. purpurea}) and \textit{N. aragoana}.

Lüning (1974) reported an alkaloid content exceeding or equal to 0.1\% in four out of 12 investigated species. He was dealing mainly with Asian species.

\textbf{Anatomy} — The leaves of most \textit{Nervilia} species are characterized by a broadly cordate to almost orbicular shape. The blade is supported by radially running main veins (vascular strands) along the pleats of the lower side and thinner veins along the pleats (if any) of the upper side. These major vascular strands are connected through a reticulate system of minor bundles (Fig. 5).

A SEM micrograph of the leaf of \textit{N. shirensis} (Fig. 27) shows a rather distinct differentiation of the mesophyll in a palisade and a spongy layer. Chloroplasts are concentrated near the cell wall. Voucher material: \textit{N. shirensis}, Moçambique, Pettersson 152.
The ontogeny of the stomata has been studied by Hanne Rasmussen (pers. comm.). The development is euperigenous. Before the meristemoids divide to form the guard cells, perigene cells (see Rasmussen 1981) are produced by unequal divisions in surrounding epidermal cells (Fig. 28). These later become subsidiary cells to the stomata. In this phase the epidermal cells are stretched in breadth to eventually become almost isodiametrical (Fig. 29). This is a characteristic of Nervilia and probably a result of the particular leaf shape in the genus. Normally orchids have oblong epidermal cells oriented towards the apex of the leaf. Voucher material: N. crociformis, Thailand, Seidenfaden & Smitinand 3720. The stomata of the investigated species were found to belong to the tetracytic type.

Idioblasts with raphide bundles abound in Nervilia, especially in the rhizome and the perianth parts. These bundles are generally considered to consist of calcium oxalate and being of advantage as protection against grazing by insect larvae (Jonsson 1981: 28f and references therein). Jonsson (loc. cit.) was able to verify the presence of calcium oxalate in the raphides of the orchid Microcoelia exilis. However, the raphides that are believed to be protective against certain insects, might instead be attractive to shell-bearing molluscs as a mineral source (see below under Ecology: Enemies).

The anatomy of the subterranean parts has been investigated by Moreau (1912, 1913) and Dietz (1930). The former also studied the leaves.

**ECOLOGY**

Ecological demands — As Nervilia species grow in shallow soil and have a very rudimentary root system, they depend on a fairly regularly distributed precipitation during the growing period. However, the tubers constitute effective water storage organs, permitting them to bridge shorter dry periods during their active season and to survive a hibernation of several months without rain. The superficial position of the tubers in the soil allows them to benefit also from precipitation coming as dew and mist.

An important property of the species of this genus is their shade-tolerance. This quality consists partly of an ability to utilize low light intensities for photosynthesis, but the capacity for photosynthesizing more efficiently in short-lived sun-flecks is more important (see
Woodward 1990 for review). Leaves growing in deep shade are very dark green and many species also show silvery patterns. This pattern and possibly also the special vertical hairs present in some species are here interpreted as adaptations to low light intensities (see above under Morphology: Leaf). The velvety sheen of the leaf of *N. bicaudata* (see Fig. 4) might also be an optical adaptation. According to Haberlandt (1909), leaves with a velvety surface have an epidermis with strongly focussing qualities and, contrary to other leaves, are able to retain these properties even when wet. As this focussing ability allows perception of the direction of the light and is believed to be connected with foliar movements to achieve optimal position for photosynthesis, it is not surprising that it is found in the species with the longest petiole, a species also often found in quite humid habitats.

The hysteranthous life form is a characteristic of this genus. The advantage of this morphological and ecological trait probably is to be sought in the fact that most species are living in areas with a long dry period. When they start to flower, triggered by the first (often irregular) rains of the season, at a time when the number of pollinating insects are increasing, they still need to economize with water and cannot afford to grow both flowering and vegetative shoots at the same time. On the rare occasions when more or less developed leaves are found together with flowering scapes, it is either among species adapted to more humid habitats, like *N. pectinata* and *N. subintegra*, or the early leaves are restricted to non-flowering individuals, as in *N. gassneri*, which do not have to save water for a flower.

Hysteranthy is known also in other geophytes from tropical Africa. A group of seven acaulescent species of *Monadenium* (*Euphorbiaceae*), occurring in the Zambezian region, show the same phenological profile as *Nervilia* (Malaisse 1989). *Eriospermum abyssinicum*, a liliaceous plant widespread in the savanna of tropical Africa, is another example. The orchid *Eulophia guineensis* is of particular interest as it is hysteranthous when growing in savanna regions or in "dry situations" as in shallow soil on rocks, but not in more humid environments like the forest floor (Cribb 1979). The two types have sometimes been recognized as different varieties or species.

**Habitat** — Most species are found in deciduous and semideciduous forests, woodland (Fig. 32) and wooded savanna including adjacent grassland (Fig. 33) and dambo margins. They constitute a very characteristic floral element in the miombo woodland with *Brachystegia*, *Uapaca*, *Julbernardia*, *Isoberlinia* etc. that is found roughly between 10° and 20°S. According to Hamilton (1974), this vegetation type is "a fire-climax community [...] which is unlikely to have covered extensive areas before man began regularly to burn the plant cover."

The genus also occurs in more moist forest types, like riverine forest (Fig. 31), spray forest, evergreen submontane or montane forest (Fig. 30) and coastal rain forest. Especially *N. pectinata*, *N. subintegra*, *N. fuerstenbergiana* and *N. bicaudata* prefer humid forest types. They are also the species with the most flimsy leaves.

Recently many species have colonized tree plantations, especially those of exotic soft-woods like *Pinus patula* (Figs. 34, 35) and *Cupressus lusitanica* (Fig. 36). Plantations recorded on collector labels include: *Pinus* (38 records), *Cupressus* (13), *Eucalyptus* (5), *Gmelina* (5) (Fig. 37), *Theobroma* (4), *Elaeis* (2), *Acacia/Eucalyptus* (1), and *Cassia* (1). Apparently these plantations are suitable because the more or less naked litter of the floor offers little competition from other plants. The low light demand of the *Nervilia* species gives them a possibility to invade areas otherwise almost devoid of herbaceous plant cover. Their effective vegetative propagation also makes them less susceptible to the relative poverty of pollinating insects in these areas. Furthermore, some species are known to be autogamous or apogamous (see below). The thick layer of litter in softwood plantations conserves the moisture of the soil and is probably of special advantage for mycotrophic plants
Figs. 30–37. Habitats for Nervilia. 30–33. Natural habitats. 30. Evergreen forest on Mt Soche, Malawi. N. pec


tinata was growing in abundance just below the summit outcrop. 31. Riverine forest with Phoenix reclinata close
to tea plantations in Mwalanthunzi near Thyolo, Malawi. Locality for N. bicarinata. 32. Brachystegia-Uapaca


woodland in Malosa near Zomba, Malawi. Locality for N. petraea, N. crociformis, N. stolziana, N. adolphi var.


adolphi, N. kotschyi var. kotschyi and N. ballii. 33. Grassland near river in Kasungu National Park, Malawi. Lo-
cality for N. kotschyi var. purpurata. — 34–37. Plantations. 34. Large and dense colony of N. crociformis in


Pinus patula plantation in Lichinga, Mozambique. 35. Pinus patula plantation in Lichinga, Mozambique. Locality


for N. crociformis, N. adolphi var. adolphi, N. kotschyi var. kotschyi, N. ballii and N. shirensis. 36. Cupressus


lusitanica plantation on Zomba Plateau, Malawi. Locus classicus for N. gassneri. 37. Gmelina arborea plantation


near Zomba, Malawi. Locality for N. kotschyi var. kotschyi, N. ballii and N. shirensis (the latter in foreground).
like orchids. Other genera that have exploited the same man-made habitat include *Cynorkis, Disperis* and to a lesser extent *Habenaria, Liparis, Malaxis* and *Satyrium*. Several of these also possess very evident adaptations to low light intensities.

The fact that most species have the same habitat demands means that when one species is found, others can be expected in their vicinity. In other words, two, three or more species are often found growing together, especially in woodland.

According to Jumelle & Perrier de la Bâthie (1912) and Perrier de la Bâthie (1939), *N. kotschyi* var. *kotschyi* and var. *purpurata* are found in Madagascar almost exclusively below trees of *Sclerocarya caffra* (Anacardiaceae) and *Dalbergia* (Leguminosae), respectively. They also report *N. leguminosarum* as growing only under trees of the family *Leguminosae*, like *Tamarindus* and *Erythrophleum*. Nothing similar has been found elsewhere.

**Enemies** — The leaves and buds are often severely attacked by snails and slugs both in the wild and in the greenhouse. The giant land snail *Achatina* was observed feeding on a leaf of *N. shirensis* in Lichinga, Moçambique. Probably the calcium content of the raphides (see above under Morphology: Anatomy) attracts these animals. Especially in areas where the bedrock and soil are poor in lime (which is the case in Lichinga) the calcium necessary to maintain the shell must be obtained from the food plants.

Also aphids often attack plants in cultivation and seem to prefer them to most other plants. Blister beetles (*Mylabris amplectens* Gerst.) were observed to consume a considerable amount of the flowers of *N. stolziana* in Malosa, Malawi (Fig. 38). On the same occasion, small flea beetles of the genus *Aphthona* (*Chrysomelidae, Halictinae*) also were seen feeding on them.

In Ankarafantsika, Madagascar, weevils of a hitherto undescribed genus (M. Ferragu in litt.) were observed to gnaw the tissue of flowers and developing fruits in *N. bicarinata*. They also pupated superficially in the ripening capsules (Fig. 39), but seemed to cause little harm to the normal seed production of the plant.

Signs of feeding by the bush pig (*Potamochoerus porcus*) are sometimes seen in and near *Nervilia* stands. Probably the pigs consume the tubers. Yellow baboons (*Papio cynocephalus*) have been observed to dig up and eat the tubers (A. Gassner, pers. comm.).

Human consumption and use in traditional medicine or sorcery is reported from several parts of the world. Gaudichaud (1826) said that *N. aragoana* from Guam has edible bulbs. Safford (1905) reported the following from the same island: "The natives of Guam frequently chew the firm, fleshy, juicy tuber as they walk through the woods, to quench their thirst, especially in the northern part of the island, where there are no springs nor streams." Espírito Santo (1969), on the other hand, claimed that the tuber of *N. bicarinata* is poisonous.

N. bicarinata is reported by Exell (1944, 1956) and Silva (1958) to be extensively used by jealous women from São Tomé in witchcraft. A woman puts leaves in the food of a man to make him keep to her alone.

Pollination and floral biology — A type of gregarious flowering triggered by the first rains of the season seems to be the rule within sect. Linervia. Many herbarium labels report anthesis to occur three days after the first heavy rains. The main portion of the flowers within a population seems to flower on the same day and the anthesis is over in less than a full day. In subsequent days there are only occasional flowers, but about two weeks later there might be a new mass flowering in the same population, showing that not all individuals flowered on the first occasion.

The flowering of most species is known to be very irregular. Mrs la Croix (pers. comm.) says, about the genus in general: "In some years, no flowers at all are produced even in large colonies and the proportion of flowers to leaves is always low, e.g., a colony of over 200 plants may produce only 5 inflorescences." King (1987) wrote about N. petraea: "I came across a population of some 50 plants growing in long grass in my compound. Henceforward I cleared the grass before the first rain and after another eight years was rewarded by the sight of two flowers."

The first notion about pollination within Nervilia concerned N. crociformis and was published by Ames (1915), who noted that the flower was nodding after pollination. Dressler (1981) concluded that nothing was known, "but the flowers appear to be adapted to pollination by small bees."

Pettersson (1989) treated pollination and floral biology of several African species and could partly verify Dressler's prediction. Small halictid bees were confirmed to transport pollinia of N. crociformis and N. petraea in Malawi and Madagascar.

A scoliid wasp was found to visit N. stolziana. It corresponded remarkably well both in size and shape to the flower and is probably an important pollinator.

The flowers within the sect. Nervilia are nectar-less and probably adapted to pollination by deceit directed towards solitary true wasps. The floral structure, pattern and colouration in this group are very uniform. The species differ mainly in number and size of the flowers. The colours green, yellow and purple are similar to those found in typical "wasp flowers" (Proctor & Yeo 1973). The lip displays a false nectar guide system of red or purplish veins. A large eumenid wasp was found to visit N. shirensis and transport pollinia. It corresponded well to the lip morphology of the species and can safely be regarded as a pollinator. Less conclusive observations of relations between N. bicarinata and other members of the same insect group need to be confirmed. The uniformity in flower structure and colouration within this section strongly suggests an adaptation to a group of closely related pollinators with a range of species of different sizes fitting the flowers of the different species.

As the determination of pollinators has been further revised by specialists and as there have been some minor additions since publication, the table of flower-visitor first published in Pettersson (1989) is included here again.

Autogamy (and/or apogamy) and cleistogamy were found in N. gassneri (see Plate 3b, c) and N. pectinata.

The site of odour production in N. crociformis and N. petraea was investigated using the neutral red staining method. Parts that take stain have been found to be associated with fragrance-producing tissue. However, a positive reaction is only an indication that fragrance might be formed in that area.

Material of N. crociformis was taken from Malawi and Madagascar, while that of N. petraea came only from Madagascar. Indication was found that scent production takes place
Table 1. Flower-visitors of *Nervilia petraea, crociformis, stolziana, pectinata, bicarinata* and *shirensis*

<table>
<thead>
<tr>
<th>Species</th>
<th>Visitor</th>
<th>Visits observed</th>
<th>Visitors with pollinia</th>
<th>Others with pollinia</th>
<th>Total with pollinia</th>
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<tbody>
<tr>
<td><em>Nervilia petraea</em></td>
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<td><strong>Hymenoptera</strong></td>
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<td>Scoliidae</td>
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<tr>
<td>Halictidae</td>
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<tr>
<td>Lasio glossum emirnense (Ben.)</td>
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<tr>
<td>Ceylalictus alabranus (Cock.)</td>
<td>3 ♀ 2 ♂</td>
<td>1 ♀ 1 ♂</td>
<td>1 ♀</td>
<td>1 ♀ 1 ♂</td>
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<tr>
<td>Anthophoridae</td>
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<td>Braunsapis cf. madecassella Mich.</td>
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<td><strong>Lepidoptera</strong></td>
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<td><strong>Acraeidae</strong></td>
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<td>Pardopsis punctatissima (Boisd.)</td>
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<td><strong>MALAWI:</strong></td>
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<td><strong>Hymenoptera</strong></td>
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<td>Halictidae</td>
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<tr>
<td>Lasio glossum (subg. Ctenonomia) sp.</td>
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<td>?Lasio glossum sp.</td>
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<td>Thrinchostoma sp.</td>
<td>2 ♀</td>
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<td><strong>MALAGASY:</strong></td>
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<td><strong>Hymenoptera</strong></td>
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<td>Halictidae</td>
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<td>Lasio glossum moderatum (Ben.)</td>
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<td>Ceylalictus alabranus (Cockerell)</td>
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<td>Anthophoridae</td>
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<td>Ceratina nyassensis Strand</td>
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<td>Pardopsis punctatissima (Boisd.)</td>
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<td><strong>Nervilia stolziana</strong></td>
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<td><strong>Hymenoptera</strong></td>
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<td>Scoliidae</td>
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<td>Micromeriella rhodesiae Betr.</td>
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<td>Vespidae</td>
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<td>Belonogaster sp.</td>
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<td>Acraeidae</td>
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<td>Pardopsis punctatissima (Boisd.)</td>
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<td><strong>Diptera</strong></td>
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</tbody>
</table>
**Nervilia pectinata**

**Hymenoptera**

?Ichneumonidae  
Apoidea  
1♀  
1♂

**Nervilia bicarinata**

**Hymenoptera**

Eumenidae  
{
*Synagris aestuans* (F.)
?*Delta* sp.
1♀  
1♂

**Lepidoptera**

Amatidae  
?*Euchromia* sp.
1♀  
1♂

**Nervilia shirensis**

**Hymenoptera**

Eumenidae  
*Synagris mirabilis* Guérin  
1♀  
1♂  
2♂

a) 1♀ with only traces of pollinia on thorax.
b) not recorded

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Figs. 40–43. Odour production indication in flowers of *N. crociformis*. 40 & 41. Tepals and lips after submerging in neutral red solution. Note partially stained tepals and staining along midline of lips. An air bubble has prevented the solution from reaching the base of the lips. 40. Material from Madagascar (wild). 41. Material from Malawi (cultivated). 42. Lip from Madagascar before submerging. 43. The same lip after submerging in neutral red solution. Note staining along midline.
both in the projections of the lip, especially along the midline, and in the petals and sepals (Figs. 40 & 41, 42 vs. 43). Essentially the same results were obtained for the two species and from the two different countries. Voucher material: N. crociformis, Malawi: Pettersson 313, N. crociformis, Madagascar: Pettersson & Nilsson 80, N. petraea, Madagascar: Pettersson & Nilsson 79.

The UV reflection was investigated in the same two species in order to find out if there is a colour pattern in the flowers that is invisible to man. The lip proved to have strong UV absorption in the apical part and along the midline (Figs. 44 vs. 45, 46 vs. 47, 48 vs. 49). There was no substantial difference between the two species. Voucher material is the same as for the neutral red staining.

Altitudinal range — The following analysis is based on the portion of herbarium sheets (49%) with the altitude of the collection site recorded on the label. (In a few cases map-readings and reliable literature information have also been included.) It must be strongly emphasized that this selection could be biased in various ways. (For example: collections
from below 500 m seem to lack information about altitude more often than those from higher elevations.) Measuring-errors, transformations between different measuring-units and division in classes for the histograms constitute other sources of uncertainty. However, I still believe that the material can be of some value, especially for comparisons between different species when the sources of error are liable to be of less importance.

The reported altitudes range from sea level to 2300 m, but most collections have been made in the interval 1000–1500 m (38%) followed by 500–1000 m (31%) (see Fig. 50).

According to their altitudinal distribution, African Nervilia species have been subdivided in groups based on the 500 m class in which they have their peak of occurrence. The corresponding graphs are found in Fig. 50. The genus as a whole has, as already mentioned, a peak between 1000 and 1500 m.

0–500 m group — Nervilia fuerstenbergiana, N. bicarinata and N. leguminosarum have a peak in the lowland. Nervilia fuerstenbergiana is known only from the two lowest classes (but there are only six records altogether), whereas N. bicarinata is almost as common in the 500–1000 m interval as below 500 m and extends up to 1500 m. Nervilia leguminosarum, only known from three neighbouring localities, is restricted to the lowermost interval.

500–1000 m group — Nervilia subintegra and N. renschiana both have at least 50% of their records in this interval. The eight collections of N. subintegra from the 1000–1500 m interval are all made between 1000 and 1100 m.

1000–1500 m group — This is the interval where the majority of the species belong: N. petraea, N. crociformis, N. affinis, N. stolziana, N. adolphi, N. kotschyi, N. ballii and N. shirensis. Of these, all but N. petraea and N. stolziana show the same “profile” as the genus as a whole. Nervilia petraea is special in that it is lacking in the two highest intervals and has a quarter of its records in the lowest one between 0 and 500 m. Nervilia stolziana, on the other hand, is lacking in the lowest interval and has a third of its records between 1500 and 2000 m. Probably also N. lilacea belongs here, but as the material is very scarce, no safe conclusions can be drawn. The only collection is from c. 1000 m.

1500–2000 m group — N. pectinata and N. gassneri have a peak in this interval. The former has a quarter of its records above 2000 m, but the latter does not extend beyond that limit.

PHYLOGENY

A phylogenetic analysis of the Orchidaceae has been presented by Burns-Balogh & Funk (1986). A somewhat conflicting cladogram covering the Epidendroideae was made by Dressler (1990). In both cases the genus Nervilia is situated in a basal position within the subfamily Epidendroideae. Apart from a brief summary in Pettersson (1990a) of the analysis presented below, no cladistic investigation has hitherto been made within Nervilia.

Phylogenetic analysis — The genus Nervilia is monophyletic. Synapomorphies for all species are the subspherical rhizomatous tuber, the long subterranean runners, the branching rhizome, the hysteranthous life form and probably the intercellular space between the testa cells of the seeds. The tribe Nervilieae, which probably also includes an undescribed genus (see below), is also characterized by the single leaf.

An investigation comprising all Nervilia species is desirable, but was beyond the scope of the present work. However, the general relationships to the bulk of the Australasian species have been analysed and are shown in Fig. 51.
Fig. 50. Altitudinal distribution of *Nervilia*. For explanation see text.
The 13 species occurring on the African mainland were included in a computer-mediated cladistic analysis, while the three less well-known Malagasy endemics were left out, because of insufficient information about many of the characters.

The characters with their different character states used for the analyses are listed in Table 2 and the matrix is shown in Table 3. Autapomorphies and characters shared by all taxa are excluded. The multistate character 19 (pollinator), however, includes one autapomorphic state (19:1), for *N. stolziana*. This multistate character, the only one, was treated as unordered (non-additive). In the data matrix *N. kotschyi* has been represented by its nominate variety, because it is considered to be the original taxon. The reason for this is that var. *purpurata* is rarer, less widespread and more erratic in appearance (cf. Maps 20–21), suggesting that it might have originated several times within *N. kotschyi* or that it is part of a polymorphism controlled by recessive genes.

As an outgroup for polarization of characters 1–4, 6–15 and 19, an unidentified collection of a *Nervilia*-like plant (de Wilde & de Wilde-Duyfjes 12112) from Sumatra has been used. It has a very primitive non-branching rhizome morphology and probably represents the hitherto unknown, most close sister-group of *Nervilia*, or a very primitive member of the genus itself.

Polarization of character 19 (pollinator) was done as follows. From flower colour and structure it was immediately clear that the *Eumenidae* could be excluded as the primitive state. Small bees were chosen simply because they are more common in most areas.
Table 2. Characters used in the phylogenetic analysis of *Nervilia*.

<table>
<thead>
<tr>
<th>Char. no.</th>
<th>Character</th>
<th>Character states</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Leaf position</td>
<td>raised (0); prostrate (1)</td>
</tr>
<tr>
<td>2</td>
<td>Leaf base</td>
<td>cordate (0); tapering (1)</td>
</tr>
<tr>
<td>3</td>
<td>Leaf outline</td>
<td>even (0); star-shaped (1)</td>
</tr>
<tr>
<td>4</td>
<td>Leaf hairs</td>
<td>absent (0); present (1)</td>
</tr>
<tr>
<td>5</td>
<td>Leaf hairs</td>
<td>scattered (0); along small veins (1)</td>
</tr>
<tr>
<td>6</td>
<td>Leaf silvery pattern</td>
<td>absent (0); present (1)</td>
</tr>
<tr>
<td>7</td>
<td>Flower number</td>
<td>one (0); several (1)</td>
</tr>
<tr>
<td>8</td>
<td>Flower position</td>
<td>horizontal (0); vertical (1)</td>
</tr>
<tr>
<td>9</td>
<td>Spur</td>
<td>absent (0); present (1)</td>
</tr>
<tr>
<td>10</td>
<td>Tepals</td>
<td>reflexed (0); not reflexed (1)</td>
</tr>
<tr>
<td>11</td>
<td>Sepals</td>
<td>greenish (0); reddish (1)</td>
</tr>
<tr>
<td>12</td>
<td>Lip 'nectar guide'</td>
<td>absent (0); present (1)</td>
</tr>
<tr>
<td>13</td>
<td>Lip papillae</td>
<td>absent (0); present (1)</td>
</tr>
<tr>
<td>14</td>
<td>Lip midlobe</td>
<td>straight (0); recurved (1)</td>
</tr>
<tr>
<td>15</td>
<td>Lip sidewalks</td>
<td>not clasping column (0); clasping column (1)</td>
</tr>
<tr>
<td>16</td>
<td>Gynostemium</td>
<td>glabrous (0); hairy (1)</td>
</tr>
<tr>
<td>17</td>
<td>Anther teeth</td>
<td>absent (0); present (1)</td>
</tr>
<tr>
<td>18</td>
<td>Fruiting scape</td>
<td>not elongating (0); elongating (1)</td>
</tr>
<tr>
<td>19</td>
<td>Pollinator</td>
<td>small bees (0); Scoliidae (1); Eumenidae (2)</td>
</tr>
<tr>
<td>20</td>
<td>Breeding system</td>
<td>allogamy (0); autogamy (1)</td>
</tr>
</tbody>
</table>

Table 3. Data matrix for the phylogenetic analysis of *Nervilia*. 0 = plesiomorphic, 1 (2) = apomorphic, – = polymorphic, unknown or inapplicable. Character numbers are explained in Table 2.

<table>
<thead>
<tr>
<th>Species</th>
<th>Character number</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20</td>
</tr>
<tr>
<td>Hypothetical ancestor</td>
<td>0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0</td>
</tr>
<tr>
<td><em>N. petraea</em></td>
<td>1 0 0 0 - - 0 1 0 0 0 0 1 0 0 0 0 0 1 0 0 0 0 0 1 0 0</td>
</tr>
<tr>
<td><em>N. crociformis</em></td>
<td>1 0 0 1 0 0 0 1 0 0 0 0 1 0 0 0 0 0 1 0 0 0 1 0 0 0</td>
</tr>
<tr>
<td><em>N. stoliiana</em></td>
<td>1 0 0 1 0 - 0 0 1 0 0 0 1 0 0 0 0 1 1 0 0 0 0 0 1 0 0</td>
</tr>
<tr>
<td><em>N. pectinata</em></td>
<td>0 0 0 1 1 0 0 0 0 0 0 1 0 0 0 1 0 0 0 0 0 0 0 0 1 0 0</td>
</tr>
<tr>
<td><em>N. subintegra</em></td>
<td>0 0 1 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 1 0 1 0 0 1</td>
</tr>
<tr>
<td><em>N. adolphi</em></td>
<td>- 0 0 0 - - 0 0 0 0 - 0 0 1 1 0 1 0 1 0 0 0 1 0 1 0 0</td>
</tr>
<tr>
<td><em>N. fuerstenbergiana</em></td>
<td>0 0 0 0 - 1 0 0 0 0 0 0 0 0 1 1 0 1 0 1 0 1 0 1 0 2 0</td>
</tr>
<tr>
<td><em>N. gassneri</em></td>
<td>0 0 0 0 - 0 0 0 0 - 0 0 0 0 1 0 1 0 1 - 1 0 0</td>
</tr>
<tr>
<td><em>N. bicarinata</em></td>
<td>0 0 0 0 - 0 1 0 0 1 0 1 0 1 0 0 1 0 1 0 0 0 1 0 1 0 0 2 0</td>
</tr>
<tr>
<td><em>N. renchiana</em></td>
<td>1 0 0 0 - 0 1 0 0 1 0 1 0 1 0 0 1 0 1 0 0 0 1 0 1 0 1</td>
</tr>
<tr>
<td><em>N. kotschyi</em></td>
<td>1 0 0 0 - - 1 0 0 1 0 1 0 1 0 0 1 0 1 0 0 0 1 0 1 0 0 0 0</td>
</tr>
<tr>
<td><em>N. ballii</em></td>
<td>0 1 0 0 - 1 0 0 1 1 1 0 1 0 0 1 0 1 0 1 0 0 0 1 0 1 0 0</td>
</tr>
<tr>
<td><em>N. shirensis</em></td>
<td>0 1 0 0 - 0 1 0 0 1 1 0 1 0 1 0 0 1 0 2 0 1 0 0 1 0 2 0</td>
</tr>
</tbody>
</table>

Besides, an alternative analysis with scoliid wasp pollinators as the plesiomorphic state showed the resulting trees to be the same.

As characters 16–18 were not available for study on the outgroup specimen, another outgroup was needed for the polarization of these. The tribe *Gastrodieae* is generally considered to be the closest relative of *Nervillae* (see above under Systematic position). Within *Gastrodieae* the genera *Didymoplexis*, *Auxopus*, *Gastrodia* and *Epipogium* are the best known, and have been used as a second outgroup for polarization of characters 16–18.
Character 5 was polarized through comparison with other orchid species having pubescent leaves. The character state 5:1 is not known from elsewhere within the orchid family. From these outgroups a hypothetical ancestor has been constructed and used for rooting the cladograms.

Three equally parsimonious cladograms were obtained by the analysis. The length was 28 steps and the consistency index 0.75. From the three trees a single one has been chosen (Fig. 52) as the most probable, taking into account also other available knowledge about the genus than that included in the matrix. This tree was also identical with the strict consensus tree of all three alternative trees.

In one solution *N. bicarinata*, *N. renschiana* and *N. kotschyi* constitute a clade supported only by character 7 (several flowers) as a synapomorphy, appearing as a parallelism also in *N. shirensis*. As all members of sect. *Nervilia* (clade I), except *N. ballii*, both in Africa and Australasia, are several-flowered, a reversal in the latter species for this character is much more likely than parallel evolution of a several-flowered inflorescence from a single-flowered ancestor. This character optimization is strengthened by the fact that two-flowered inflorescences of *N. ballii* occasionally have been found.

In the other alternative solution *N. bicarinata*, *N. ballii* and *N. shirensis* constitute a clade supported solely by character 19:2 (solitary true wasp pollination) as a synapomorphy. This implies that the remaining species of the section have flowers pollinated either by scolid wasps (19:1) or small bees (19:0). However, the African members of sect. *Nervilia* are exceedingly homogeneous as to flower colouration and structure (see above under Ecology: Pollination and floral biology, and Pettersson 1989), and solutions implying different insect groups as pollinators are considered unrealistic. As a result there is no synapomorphy available to support a grouping of *N. bicarinata* with either of the clades J or K. Consequently a trichotomy at node I is favoured.

Even though an arrangement with character 9 (spurred lip) as a parallelism in *N. stolziana* and *N. pectinata* makes the shortest tree (28 steps), I prefer another character optimization which is one step longer for the following reasons: *N. stolziana* (Fig. 58) and *N. pecti-
nata (Fig. 59) are very similar in flower structure. Likewise N. pectinata and N. subintegra (Fig. 60) have almost identical leaves. I find it hard to believe that either of the two striking similarities could have arisen through parallelism, and prefer character 9 as a synapomorphy at node C and as a reversal at node E and in N. subintegra. As a matter of fact, the latter species shows a bulge at the base of the lip which could be interpreted as a rudiment of a spur.

There are two equally parsimonious ways of interpreting character 6 (silvery leaf pattern) in clade H, either as a synapomorphy at node H and a reversal in N. adolphi var. adolphi, or as an autapomorphy for N. fuerstenbergiana and a parallelism in N. adolphi var. seposita (the varieties are not shown in the cladogram). As the leaves are very similar (see Figs. 61j, 62f), I find the first alternative much more likely.

Character 13 (lip papillae) is another example of where two parallelisms (at node D and in N. pectinata) or one synapomorphy and one reversal (at node C and in N. subintegra, respectively) will yield trees of equal length. In this case the latter alternative is preferred, again because a parallelism is less probable as an explanation of the similar flowers of N. stolziana and N. pectinata.

Character 20 (autogamy) can be placed either as a synapomorphy of N. pectinata and N. subintegra at node F or as an autapomorphy of N. pectinata. As it is not known whether N. subintegra is autogamous or not, the most correct alternative must be to place character 20 as an autapomorphy of N. pectinata.

At the varietal level, not shown in the cladogram, N. kotschyi var. purpurata has a reversal in character 1 and a parallelism in character 2.

Some forms of N. petraea, N. stolziana and N. kotschyi var. kotschyi have a parallelism in character 6, while some forms of N. adolphi var. adolphi and all N. adolphi var. seposita have a parallelism in character 1.

Consequences for classification — Traditionally, Nervilia is classified into four sections, three of which occur in Africa. Sect. Nervilia comprises node I in the cladogram in Fig. 52. It is clearly monophyletic and requires no change in circumscription.

Sect. Linervia comprises node B, but excluding the two species N. stolziana and N. pectinata. The latter two are traditionally grouped into a section of their own, sect. Kyimbilaea characterized by a spurred lip. In the cladogram (as well as in the two equally parsimonious alternatives), this section is shown to be polyphyletic. The section cannot be maintained and it is here included in sect. Linervia.

The recircumscribed sect. Linervia is monophyletic, albeit supported only by a single character, the polarization of which was not done with the sister-group but with a more distant outgroup. However, later investigations may reveal synapomorphies for this section that are at present unknown.

PHYTOGEOGRAPHY

According to Dressler (1981), Nervilia belongs to the "Middle-aged hoppers" between Asia and Africa, probably reflecting "long-distance dispersal in mid Tertiary."

Following Dressler's interpretation, that intercontinental distributions are the result of long-distance dispersal, a minimum of three "hops" must have occurred, as there are at least three monophyletic groups involved in this disjunction (see Fig. 51). The first two of the connections, involving sect. Nervilia and the N. adolphi/punctata alliance, were probably "middle-aged", but not necessarily "long-distance" compared with the present situation, as the climate and the position of the continents and subcontinents (India) probably were more favourable at that time. After a separation between Africa and Eurasia in the
Jurassic, the connection was re-established in the Miocene, i.e. about 20 million years ago (Suding 1979). According to Nilsson (1972) there was, at least periodically (and before the appearance of the Red Sea), a broad land connection between Africa and South Asia (Arabia) during the Tertiary and thus relatively good possibilities for exchange. In fact, most of *Nervilia*’s large terrestrial “fellow-genera” from the woodland habitat show the same disjunction: *Eulophia, Habenaria, Liparis, Malaxis, Brachycorythis, Disperis* and *Satyrium*. Of these, the four mentioned first are pantropical and might have a different history. The only large terrestrial genus from open habitats that is missing is *Disa*, which probably evolved in southernmost Africa and spread northwards comparatively recently.

According to Hamilton (1974), “disjunction of two populations of the same species is likely to be due to more recent isolation than disjunction of two different species of the same genus.” Therefore the last “hop”, involving the species in common, should have been fairly recent. It probably corresponds more to Dressler’s “Young hoppers”, “which represent dispersal in the very late Tertiary or Pleistocene, or even after the Pleistocene.” Probably the present “arid barrier” in West Asia was substituted (at least partly) by vegetation types more suitable for *Nervilia* several times during the Pleistocene in connection with wetter periods in Africa. At present, the northern distribution border of *N. crociformis* is roughly the same as that of the hippopotamus. Fossils of the latter have been found as far north as in northern Israel, both from the lower Middle Pleistocene and from the last interglacial period (Nilsson 1972). There is also evidence of late Quaternary lakes in the Arabian Desert (McClure cited in Hamilton 1982). This implies that large parts of the Arabian peninsula probably had savanna vegetation and good habitats for several *Nervilia* species. A humid period in NE Africa contemporary with the last interglacial is also supported by the fact that Lake Abhé, situated at the border between Ethiopia and Djibouti, had a high-lake stand at that time (Hamilton 1982). Later (c. 40,000–20,000 B.P.) there was a second long period with high water level both in Abhé and the Ziway-Shala basin in the Ethiopian Rift Valley. Also the Climatic Optimum of the Holocene (c. 7000 B.P.) was relatively humid in northern Africa, as indicated by crocodiles depicted on rock-carvings and rock-paintings in central Sahara (Nilsson 1972). The Abhé basin had at least three high stands during the Holocene, two of large amplitude, dated 9400–8400 and 7000–4000 B.P., respectively (Hamilton 1982). Exactly the same picture of the last 10,000 years is given from Lake Bosumtwi in Ghana (Talbot 1983), thus showing the continental comprehension of the climatic changes. At least in West Africa the 7000–4000 B.P. period was clearly the wettest during the last 27,500 years.

Even if the circumstances mentioned made dispersal much easier during certain periods of the Quaternary, there is only one “fellow-species” to *N. crociformis* from another terrestrial orchid genus found also in Asia, namely the pantropical *Liparis nervosa*.

To conclude, the conditions for dispersal between Africa and Asia during the Tertiary might not have to be described in terms of long-distance dispersal; i.e. a more or less continuous distribution of *Nervilia* (and other groups with similar ecology) between the continents could have existed for some periods. Even if the conditions during the Quaternary allowed tropical African plants to reach large parts of the Middle East, other barriers apparently prevented a large-scale mixing of the two continental floras at that time. In this case it is still probably suitable to talk about long-distance dispersal, even if the distance to be covered was far less than today.

The greater morphological span between the *Nervilia* species in Asia (presence of sect. *Vinerlia* and the primitive ancestor-like species mentioned above under Phylogeny etc.) points to an origin of the genus in that continent. If this hypothesis holds true the first two dispersals were made from Asia to Africa. The fact that there are more near relatives of *N. crociformis* in Africa than in Asia indicates that the third dispersal went in the other direction.
In Africa the genus is known to occur between 16° 38' N in São Nicolau, Cape Verde Islands and 30° 16' S near Durban in South Africa. The east-west extension goes from Cape Verde Islands (24° 19' W) to Mauritius (57° 30' E).

The following treatment is based mainly on the phytogeographical concepts of White (1983). The distribution of the species between the different phytochoria is given in Table 4.

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**Table 4. Distribution of *Nervilia* species in Africa and the Arabian peninsula. The taxa are numbered as in the taxonomic part. Regional endemics are denoted by asterisks (*).**

<table>
<thead>
<tr>
<th>Region</th>
<th>Taxa</th>
</tr>
</thead>
<tbody>
<tr>
<td>Macaronesian Region</td>
<td>2</td>
</tr>
<tr>
<td>Guineo-Congolian Region</td>
<td>1, 2, 7, 8, 9, 12, 14</td>
</tr>
<tr>
<td>Lake Victoria Regional Mosaic</td>
<td>1, 8, 12, 13, 14</td>
</tr>
<tr>
<td>Sudanian Region</td>
<td>1, 2, 7, 8, (9), 12, 14</td>
</tr>
<tr>
<td>Zambezan Region</td>
<td>1, 2, 5*, 6*, 8, 11*, 12, 13, 14, 15*, 16*</td>
</tr>
<tr>
<td>Zanzibar-Inhambane Regional Mosaic</td>
<td>1, 2, 12, 13, 14</td>
</tr>
<tr>
<td>Tongaland-Pondoland Regional Mosaic</td>
<td>2, 12, 13, 14</td>
</tr>
<tr>
<td>Africomontane Region</td>
<td>(2), 6, 14, 16</td>
</tr>
<tr>
<td>Somalia-Masai Region</td>
<td>2, 12, 14</td>
</tr>
<tr>
<td>East Malagasy Region</td>
<td>2, 4*, 10*, 12, 13</td>
</tr>
<tr>
<td>West Malagasy Region</td>
<td>1, 2, 3*, 12, 13, 14</td>
</tr>
</tbody>
</table>

**DISTRIBUTION TYPES IN AFRICAN NERVILIA**

**Guineo-Congolian group** (Maps 2 & 3). *N. subintegra* and *N. fuerstenbergiana*. The former has two additional occurrences in the Sudanian Region, one in Jabal Kinyeti (Imatong Mts) in southern Sudan and the other near N'délé in northern Central African Republic, while the latter has an outlier on the Jos Plateau in Nigeria, slightly inside the same region. *N. fuerstenbergiana* seems to be restricted to the Upper Guinea subcentre and the northern part of Lower Guinea, avoiding both the Dahomey interval and the Congoia subcentre, while *N. subintegra* is represented both in the southern Lower Guinea subcentre and the Dahomey interval (but also absent from Congolia).

**Zambezan Region endemics** (Maps 4–8). *N. stolziana*, *N. pectinata*, *N. gassneri*, *N. ballii* and *N. shirensis*. Of these *N. pectinata* and *N. gassneri* have a pronounced eastern distribution and only *N. shirensis* is known to occur in Angola. However, the absence of the others in the west might – at least partly – be explained by insufficient botanical exploration. *N. stolziana*, for example, has been collected in Mwinilunga District in Zambia within a few kilometers of the Angolan border. *N. shirensis* and *N. pectinata* extend somewhat into the Afromontane Region.

*Nervilia renshiana* (Map 9) is best placed as a loosely attached satellite to this group. It extends chiefly to Madagascar, but also has outliers in the Ružízi Plain in Burundi (Lake Victoria Regional Mosaic) and near Durban in South Africa (Tongaland-Pondoland Regional Mosaic).

**West Malagasy Region endemics** (Map 10). *N. leguminosarum*.

**East Malagasy Region endemics** (Maps 11 & 12). *N. affinis* and *N. lilacea*. 

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Widespread Sudano-Zambezian group (Maps 13–17). The members of this group have their main distribution in the Sudano-Zambezian Super-Region supplemented chiefly with Guineo-Congolian and/or one or both of the Malagasy Regions. They often extend into most other Regions and Regional mosaics within the same latitudes.

*Nervilia petraea*: Mainly Sudano-Zambezia, Guineo-Congolia and West Malagasy. Also Lake Victoria and Zanzibar-Inhambane Regional Mosaics.
Map 14. *Nervilia crociformis*. Open circles denote aberrant leaf form, see note 2 under species description.

Map 15. *N. adolphi*.
Nervilia crociformis: Mainly Sudano-Zambezia, Guineo-Congolia and Madagascar. Also Macaronesian and Somalia-Masai Regions, Zanzibar-Inhambane and Tongaland-Pondoland Regional Mosaics (and probably the Mascarenes; see Note 3 under the species description). It touches the Afromontane Region. Outside Africa it extends into Indian, Indochinese, Malesian and Northeast Australian Regions (regions according to Takhtajan 1986).

The occurrence in Macaronesia deserves a special note. Leaves were found once in São Nicolau, Cape Verde Islands in 1851. The plant was thought to be endemic and was described as Pogonia bollei. It has never been refound in this area. This region is often included in the Holarctic Kingdom (see e.g. Takhtajan 1986) but the flora of the southern archipelago, the Cape Verde Islands, has much in common also with tropical Africa and thus the Paleotropical Kingdom (see Sunding 1973, 1979). The orchids (two or three species) all also occur in tropical Africa.

Nervilia adolphi: Mainly Sudano-Zambezia and Guineo-Congolia. Also Lake Victoria Regional Mosaic.


Even if the southernmost part of the Arabian peninsula is outside the main area treated by White, this part is often included in the same region as the adjacent African mainland both by him and, e.g., Takhtajan (1986). According to Hepper (1977: 312), the valley in Yemen where N. bicarinata grows “is hot enough to support species with a distinct tropical African affinity”, and it is not uncommon that plants otherwise restricted to tropical Africa extend their occurrence to the southern part of Arabia. Among the orchids such cases are found in 18 species (Cribb 1979; Miller & Morris 1988), of which five show a somewhat wider distribution in Arabia. Thirteen of the 18 species have a fairly restricted occurrence centered in the Somalia-Masai Region, but the remaining eight, Habenaria keayi, H. malacophylla, H. myodes, H. schimperiana, Bonatea steudneri, Eulophia guineensis, E. petersii and E. streptopetala, are widespread and comparable to N. bicarinata.

Nervilia kotschyi: Mainly Sudano-Zambezia and West Malagasy. Also Afromontane and Somalia-Masai Regions, Lake Victoria, Zanzibar-Inhambane and Tongaland-Pondoland Regional Mosaics. One locality is known from Guineo-Congolia.

VICARIOUS SPECIES

There are two examples of species pairs showing vicariance, both geographical as well as ecological.

Nervilia pectinata and N. subintegra (Maps 5 & 2) are centered in the eastern Zambezian region and West Africa, respectively, without any overlapping. They have virtually indistinguishable leaves and share a preference for humid forests, but they prefer quite different altitudes (Fig. 50). While N. pectinata has 92% of its records above 1000 m, N. subintegra always grows below 1100 m.

The other example is N. adolphi and N. fuerstenbergiana (Maps 15 & 3). The former is widespread in the mainland of tropical Africa, preferring woodland and savanna, while the latter is confined to West Africa, preferring wet forest. N. fuerstenbergiana is found in the southern parts of the West African states, while N. adolphi has its West African occurrence north of this area. The division coincides with the borderline between rain forest and savanna and also with White’s borderline between the Guineo-Congolian Region and its transition zone to the Sudanian Region. There are overlaps in two areas, the island of Bioko and the Jos Plateau of Nigeria, where both species occur. Also between these two species
there is a clear difference in altitudinal distribution (Fig. 50), *N. fuerstenbergiana* being a pronounced lowland species and *N. adolphi* preferring intermediate altitudes.

REFERENCES


TAXONOMIC TREATMENT

Note. The species are arranged according to the sequence in the cladogram (see above under Phylogeny) in a way that is reflecting a maximum of phenoetic similarity between adjacent species.

For countries included in any of the large Flora works the geographical subdivision adopted for the Floras have been followed. For Flore d’Afrique Centrale, instead of I, II, III etc. the abbreviations Z1, Z2, Z3 etc. have been used. “n.v.” = not seen.

NERVILIA Commerson ex Gaudichaud


Bolborchis Zoll. & Mor. in Moritz, Syst. Verz. Zoll. PI. (1846) 89. — Type species: Bolborchis crociformis Zoll. & Mor. = Nervilia crociformis (Zoll. & Mor.) Seidenf.

Notes. 1. The genus Nervilia is here considered as validly published when plate 35 appeared in June 1827, in accordance with the opinion of Hallé (Fl. Nouv.-Cal. & Dép., 8 Orchid. (1977) 410), and not in Sept. 1829 as indicated in Index nomen livicorum genericorum (Parr, Leusink & Staffleu 1979) and the list of nomina conservanda (The International Code of Botanical Nomenclature 1988). There can be no doubt that this plate is an “illustration with analysis” as stated in Art. 42.2 of the Code. If the other standpoint is taken, Roptrostemon (Blume, Fl. Jav. Rar. (1828) Praef. p. VI) becomes the oldest name, and hence should be adopted unless Nervilia is conserved also against that name.

2. Synonyms without any connection to African species have been omitted.

Hysteranthous terrestrial herbs; shoot consisting of a subspherical subterranean rhizomatous tuber of 2–7 internodes, sometimes carrying short straight roots and continuing in a very short (subterranean) ascending stem (1–15 cm). Foliar leaf solitary, erect or prostrate, plicate, petiolate, non-articulate, elliptic to reniform, cordate or almost circular, with reticulate venation; upper surface sometimes pubescent and/or with various silvery patterns; lower surface often purple. Inflorescence erect, 1- to many-flowered, racemose, scape 2–80 cm. Flowers resupinate or (in some single-flowered species) erect; tepals except lip similar, greenish or brownish green; lip spurless or shortly spurred, 3-lobed to almost entire, often more or less papillate or pubescent and variously marked with red; gynostemium long, curved or almost straight, more or less slender towards base, clinandrium a deep apical cavity embracing a large part of the anther; stigma ventral, elliptic to almost square, viscidium diffuse; anther incumbent, hinged; pollinia 2, bipartite, sectile.
### Key to the Species of Nervilia Occurring in Africa

Note: All characters used refer to unpollinated flowers in full anthesis (A) and to fully developed and mature leaves (B). Variable species are keyed out in more than one place. The variability of some of the species makes it necessary, in extreme cases, to know both flowering scape and leaf for a certain determination. However, most “single-aspect” specimens (leaf only or flowers only) are easily determinable.

Unfortunately, “geographical characters” have had to be used to separate the leaves of *N. pectinata* and *N. subintegra*. Apart from a difference in mean size they are indistinguishable.

**A — Key to flowering specimens**

<table>
<thead>
<tr>
<th>Step</th>
<th>Description</th>
<th>Key</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Lip with spur</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>Lip without spur</td>
<td>3</td>
</tr>
<tr>
<td>2</td>
<td>Lip white with purple markings; scent of camphor; spur 1.5–3 mm</td>
<td>6. <em>N. pectinata</em></td>
</tr>
<tr>
<td>3</td>
<td>Flower single</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>Flowers 2–several</td>
<td>16</td>
</tr>
<tr>
<td>4</td>
<td>Lip mainly white, without strong markings, often with yellow central line</td>
<td>5</td>
</tr>
<tr>
<td></td>
<td>Lip with distinct red or purple markings</td>
<td>8</td>
</tr>
<tr>
<td>5</td>
<td>Lip ± horizontal, not trumpet-shaped, very obscurely trilobed with entire margin</td>
<td>7. <em>N. subintegra</em></td>
</tr>
<tr>
<td></td>
<td>Lip erect, trumpet-shaped, distinctly trilobed or with fringed margin</td>
<td>6</td>
</tr>
<tr>
<td></td>
<td>Lip above covered by short, inflated, club-shaped hairs, flower large, sepals 25–40 mm long, Madagascar only</td>
<td>3. <em>N. leguminosarum</em></td>
</tr>
<tr>
<td></td>
<td>Lip with much longer, often hairlike outgrowths (seldom glabrous), flower smaller, sepals &lt; 20 mm long</td>
<td>7</td>
</tr>
<tr>
<td>7</td>
<td>Lip with a tuft of spaghetti-like outgrowths, flower very small, sepals mostly less than 13 mm long</td>
<td>1. <em>N. petraea</em></td>
</tr>
<tr>
<td></td>
<td>Lip with thin, hairlike outgrowths (sometimes lacking) and 3 rows of blunt tubercles or elongated, tapering emergences, flower larger, sepals mostly more than 13 mm long</td>
<td>2. <em>N. crociformis</em></td>
</tr>
<tr>
<td>8</td>
<td>Lip side lobes with strong reddish (or greenish) venation, midlobe recurved</td>
<td>9</td>
</tr>
<tr>
<td></td>
<td>Lip side lobes without strong venation, midlobe seldom recurved</td>
<td>11</td>
</tr>
<tr>
<td>9</td>
<td>Column 9–13.5 mm, inflorescence normally 1-flowered, sepals reddish</td>
<td>15. <em>N. ballii</em></td>
</tr>
<tr>
<td></td>
<td>Column 10–25 mm, inflorescence normally several-flowered, sepals reddish or green</td>
<td>10</td>
</tr>
<tr>
<td>10</td>
<td>Column 10–15 mm, inflorescence normally 2–12-flowered, sepals green</td>
<td>12. <em>N. bicarinata</em></td>
</tr>
<tr>
<td></td>
<td>Column 16–25 mm, inflorescence normally 2–3-flowered, sepals reddish</td>
<td>16. <em>N. shirensis</em></td>
</tr>
<tr>
<td>11</td>
<td>Flower cleistogamous</td>
<td>11. <em>N. gassneri</em></td>
</tr>
<tr>
<td></td>
<td>Flower not cleistogamous</td>
<td>12</td>
</tr>
<tr>
<td>12</td>
<td>Lip sidlobes acute, lip glabrous, Madagascar only</td>
<td>10. <em>N. lilacea</em></td>
</tr>
<tr>
<td></td>
<td>Lip sidlobes rounded, lip glabrous or hairy</td>
<td>13</td>
</tr>
<tr>
<td>13</td>
<td>Lip densely or sparsely pubescent, hairs long, Madagascar only</td>
<td>4. <em>N. affinis</em></td>
</tr>
<tr>
<td></td>
<td>Lip glabrous, sometimes with short papillae on coloured parts, African mainland</td>
<td>14</td>
</tr>
<tr>
<td>14</td>
<td>Lip midlobe with erect or rolled-in edges</td>
<td>8. <em>N. adolphi</em></td>
</tr>
<tr>
<td></td>
<td>Lip midlobe almost flat with convex central ridge</td>
<td>15</td>
</tr>
</tbody>
</table>

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15 - Lip midlobe (epichile) much longer and wider than hypochile ... 9. *N. fuerstenbergiana*
- Lip midlobe (epichile) of approximately the same length and width as hypochile

11. *N. gassneri*

16 - Inflorescence 4–12-flowered .............................................. 17
- Inflorescence usually 2–3-flowered, ± secund ............................. 19

17 - Flowers yellow with red veining; column 15–19 mm (lowest flower) 13. *N. renschiana*
- Flowers yellow-green with purple or green veins; column 7–15 mm .......... 18

18 - Column 10–15 mm ......................................................... 12. *N. bicarinata*
- Column 7–11 mm ............................................................ 14. *N. kotschyi*

19 - Flowers small, column 7–11 mm; sepals < 26 mm 14. *N. kotschyi var. purpurata*
- Flowers large, column 16–25 mm; sepals > 25 mm .......................... 16. *N. shirensis*

B — Key to vegetative specimens

1 - Leaf pubescent .............................................................. 2
- Leaf glabrous .................................................................... 7

2 - Leaf distinctly polygonal or star-shaped in outline, thin, held a few cm above ground ... 3
- Leaf reniform to orbicular, often rather thick, mostly prostrate .................. 4

3 - From Malawi, Mozambique, Zambia, Zimbabwe or southern Tanzania ... 6. *N. pectinata*
- From Northern Hemisphere or lower Zaire .................................... 7. *N. subintegra*

4 - A ± wide zone near main veins glabrous, leaf width 4–6 cm, Madagascar only

4. *N. affinis*
- Hairs also on or near main veins ............................................. 5

5 - Leaf small, < 3 cm across, purple below, reticulated with silver above (silvery pattern may be absent) ........................................... 5. *N. stolziana*
- Leaf larger, 4.5–20 cm wide, green on both sides .............................. 6

6 - Leaf 4.5–14 cm wide ......................................................... 2. *N. crociformis*
- Leaf larger, 18–22 cm across, Madagascar only ................................ 3. *N. leguminosarum*

7 - Leaf base attenuate to truncate, leaf blade erect .......................... 8
- Leaf base cordate, leaf blade prostrate or raised ............................ 10

8 - Leaf olive green with silvery veins above, purple below .................. 15. *N. ballii*
- Leaf green on both sides .................................................................. 9

9 - Leaf blade > 4 cm wide ......................................................... 16. *N. shirensis*
- Leaf blade < 4 cm wide .................................................................. 14. *N. kotschyi var. purpurata*

10 - Petiole very long, > 10 cm; leaf held well above ground ............. 12. *N. bicarinata*
- Petiole < 6 cm; leaf often more or less prostrate ............................ 11

11 - Leaf pleated with ragged keels running along the ridges of the pleats

14. *N. kotschyi var. kotschyi*
- Leaf without such keels ................................................................ 12

12 - Leaf large, > 9 cm wide, very pleated ................................. 13. *N. renshchiana*
- Leaf smaller, < 9 cm wide, not pleated .......................................... 13

13 - Leaf very small, not more than 2 cm wide .................................. 14
- Leaf larger .................................................................................. 15

14 - Leaf with silvery rays (silvery pattern may be absent), ± orbicular, purple below

1. *N. petraea*
- Leaf without silvery pattern, broadly cordate, green below, Madagascar only

10. *N. lilacea*

15 - Leaf above marbled or tessellate with silver or light green ........ 16
- Leaf above uniformly green ..................................................... 17
16. Leaf very conspicuously tesselated silver and dark green, reniform, shortly apiculate or with rounded apex. 8. N. adolphi var. seposita
- Leaf marbled in light and dark green, cordate, with prominent, triangular apical part
9. N. fuerstenbergiana

17. Leaf < 5 cm wide. 18.
- Leaf > 5 cm wide. 19.

18. Leaf with apical apex, not strongly prostrate, never dark purple below 11. N. gassneri
- Leaf with more or less rounded apex, often strongly prostrate and dark purple below
8. N. adolphi var. adolphi

19. Leaf spade-shaped, slightly longer than wide, thick. 14. N. kotschyi var. kotschyi
- Leaf reniform, cordate to orbicular, wider than long, ± thin. 20.

20. Leaf broadly heart-shaped with distinct apical point, not strongly prostrate
8. N. adolphi var. adolphi
- Leaf reniform to almost orbicular without distinct apical point, often strongly prostrate
2. N. crociformis

I - Nervilia section Linervia


1. Nervilia petreae (Afz. ex Sw.) Summerh. — Fig. 54; Plate 1a.


Erect terrestrial herb 2–8.5(–10.5) cm tall, glabrous except for lip and subterranean parts. Tuber subspherical or ovoid, 3–8 mm diam., (2–)3(–4)-nodded. Leaf solitary, appearing after flowering, prostrate, cordate to almost orbicular, sometimes obscurely angled, glabrous, dark olive green above, often with silvery rays, purple below, 6–15 by 8–25 mm; veins 7–9(–10); petiole 0–1 cm long, sulcate with 1–2 sheathing cataphylls. Scape erect, terete, 1-flowered, with (1–)2–4 sheathing cataphylls, lengthening to c. 10 cm when fruiting; bract 0–1.5 mm. Flower more or less erect. Sepals and petals spreading, closing again after about 8 hours anthesis or earlier if pollinated, subequal, linear-ligulate, acute, brownish green, lateral sepals oblique, 8–15.5 by 3.5 mm. Lip obovate-cuneate, to 9–15.5 by 8 mm, 3-lobed, white with a yellow centre; lateral lobes oblong-triangular, obtuse; mid-lobe fimbriate, suborbicular, with numerous subulate appendages. Gynostemium clavate, glabrous, 4–9 mm; anther white or purple; pollinia pale yellow or purple, c. 1.5 mm; ovary c. 3 mm; capsule c. 9 mm.

Ecology. Woodland, grassland, dambo and pine plantation; 0–1470 m. Flowering: Northern hemisphere IV–VI; Southern hemisphere X–XII; Uganda both periods.


Notes. 1. Lectotypification of *Arethusa simplex*. As no original plant material seems to have been saved, the plate 'g' from the original publication was indicated as a lectotype.

2. The leaves of this species often are uniformly dark green above, but sometimes they show distinct silvery rays along the main veins. Populations with silvery rays are known mainly from the area around Lake Nyasa, but also from NE Tanzania. The young blade is frequently obscurely angled or slightly polygonal in outline, but when mature it tends to become more or less rounded. When young the upper surface is granular in certain sectors (Fig. 8), a distinguishing feature against certain forms of *N. adolphi*. The granules could be rudimentary hairs. They are seldom visible in dried herbarium specimens.

2. *Nervilia crociformis* (Zoll. & Mor.) Seidenf. — Fig. 55.

(The description below includes African material only.)


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Nervilia baihiei Senghas, Adansonia, ser. 2, 4 (1964) 303, fig. 1; id., Die Orchidee 15 (1964) 217, figs. 1–4; Vóth, Die Orchidee 16 (1965) 68, fig.: Berhaut, Fl. Sénégal, ed. 2 (1967) 305, fig.; Ebel, Sch. und selts. Welt der Orch. (1971) 178, fig. 64; Brieger in Schltr., Die Orchideen, ed. 3 (1975) 390, fig. 237. — Type: Rauh M 1622 (Holo HEID, n.v., cult. 'clonotype' seen), Madagascar, Centre, between Antsirabe and Ambositra, 120 km SSW of Antananarivo, c. 1100 m, dry Uapaca forest, 18 Dec. 1959.

Nervilia eosa Cribb, Kew Bull. 32 (1977) 155, fig. 10. — Type: Williamson & Drummond 1679 (Holo K; iso SRGH), Zambia, North-Western Prov., 75 km S of Mwinilunga, undisturbed Brachystegia woodland, 29 Oct. 1969.


Nervilia francoisi Perr. ex François, Rev. Hort., n.s. 21 (1928) 304 (in adnot.), nom. nud. (see also Anonymus, Bull. Acad. Malg. 11 (1929) xi).


Erect terrestrial herb 1.5–10 cm tall, glabrous except for lip, leaf and subterranean parts. Tuber subshperical or ovoid, 0.5–1.4 cm diam., (2–)3–6-noded. Leaf solitary, appearing after flowering, prostrate or nearly so, reniform to almost orbicular, usually densely pubescent above, but glabrous clones are not uncommon, nor are ones with hairs only near the rim, 1.5–9 by 3.5–14 cm; veins (5–)7–16; petiole 0–6 cm long, sulcate with 1–3 sheathing cataphylls. Scape erect, terete, 1-flowered, with 2–3 sheathing cataphylls, lengthening to c. 20 cm when fruiting. Flower more or less erect, fragrant; bract 1–2 mm long. Sepals and petals spreading, closing again after about 8 hours anthesis or earlier if pollinated, subequal, linear-ligulate, acute, brownish green, lateral sepal oblique, 12–19 by 3.5 mm; petals slightly shorter and narrower. Lip oblong-cuneate, 12–18 by 9–11 mm, 3-lobed, white with a yellow centre and often faint lilac or purple tinge or markings in the apical area; inner surface more or less covered with thin hairs and a few thicker formations more or less arranged in three rows along the centre of the mid-lobe and ranging from low tubercles to long, acute, tapering emergences of different appearance; lateral lobes obtusely triangular or rounded, sometimes less prominent or absent; midlobe ovate-triangular to ovate, subacute to obtuse; margin crenulate-undulate-fimbriate. Gynostemium almost straight, clavate, glabrous, (5.5–)7–9 mm; pollinia yellow with a few purplish massulae at lower end, (0.8–)1.5–2 mm; ovary 4–5 mm long; capsule (7–)10–17 by c. 5 mm; seeds elongated, curved, (0.15–)0.3–0.4 mm long with one end narrower.

Ecology. Woodland, evergreen forest, grassland, riverine forest and pine plantations; 75–2000 m. Flowering: Northern hemisphere II–V; Southern hemisphere X–XII(–I) (Usambara, NE Tanzania III).

Distribution. Cape Verde Is.: São Nicolau (1 coll.), Senegal: Casamance (2). Mali: Sikasso (1). Guinea: "Haut Niger" (1); Dalaba (2); Faranah (1); Kindia (1); Kouroussa (1); Siguiri (1). Sierra Leone: North (1). Ivory Coast: Province unknown (4); Ouest (6); Centre (1); Nord (1). Ghana: (2). Togo: II (2); III (1); IV (1). Nigeria: Benue-Plateau (7); North-Eastern (3); Ogoja (1); Western (2). Cameroun: East (2). Central African Republic: (4). Congo: Pool (1). Zaïre: Ubangi-Uele Z7 (2); Lac Albert Z8 (2); Haut-Katanga Z11 (6). Ethiopia: Arssi AR (1); Bale BA (1); Eritrea EW-EE (1); Shoa SU (1). Tanzania: North T2 (1); Tanga T3 (1); Southern Highlands T7 (30). Zambia: West (13); Central (2); East (1). Zimbabwe: North (1); Central (2); East (7). Malawi: Province unknown (1); North (13); Central (3); South (8). Moçambique: Niassa (8). Swaziland: (1). South Africa: Transvaal (1). Madagascar: Ouest (3); Centre (4). Réunion: (?). Mauritius: (?). Material seen from AMES, B, BM, BOL, BR, C, COI, DSM, EA, FT, G, GC, H, JE, K, L, LD, LMU, M, MAL, MO, NHT, O, P, PRE, S, SRGH, TOGO, U, UCJ, UPS, W, WAG, WU, YA, Z.

Distribution outside Africa: India, Nepal, Thailand, Indo-China, Malaysia, Indonesia, Philippines, New Guinea, Australia (Queensland).

Notes. 1. For full synonymy and literature references in Asia see N. prainiana and N. crociformis in Seidenfaden (1978), p. 149 and 151.

2. There is a wide variation in leaf characters in this species. The leaves are normally quite densely pubescent on the upper surface, but at least around Lake Nyasa totally glabrous forms are not uncommon, nor are intermediate forms with only a few hairs near the rim. The recently discovered populations in Australia are reported to be glabrous. Also several collections from western Madagascar (see Map 14, open circles) have glabrous leaves. In this case also the shape of the blade was aberrant: cordate to broadly reniform, slightly lobed or polygonal; apex triangular with concave sides. Two similar leaves are also found on a Commerson sheet from Mauritius together with N. bicarinata and hairy N.
crociformis-like leaves. The size variation within the species is also considerable. The type material of *N. erosa* has very small leaves with few or no hairs and an erose margin. A small-flowered form from Malawi (specimen Pettersson 317) has leaves with a narrow, purple rim, while a specimen from Madagascar (Barthlott O-12753, slide only) has the central portion of the upper surface purple.

3. This species is (or was) probably also present on Réunion and Mauritius. Thouars' type material of *Pogonia thouarsii* from Mauritius presumably belongs here (see below under Incompletely known species). There are also many Commerson sheets of *N. crociformis*-like leaves stated to come from Réunion and Mauritius. There is, however, some uncertainty about the labelling of those. There are almost identical sheets with one specimen of *N. bicarinata* and one or several specimens of smaller, hairy, *N. crociformis*-like leaves stated to come from Réunion, Mauritius and Madagascar. It seems too much of a coincidence to find the same two species growing together in three different places at great distance from each other, when no other collector has made similar finds.

4. During cultivation in Adiopodoumé in Ivory Coast a specimen with two flowers appeared (S. coll. s.n. pressed 27.III.1970 (UCJ)), showing that the step back from single-floweredness is not as difficult as one would imagine.

3. *Nervilia leguminosarum* Jum. & Perr. — Fig. 56.


Erect, terrestrial herb, 5.5–10 cm tall, glabrous except for lip, leaf and subterranean parts. Tuber spherical. Leaf solitary, prostrate, pubescent on upper surface; blade orbicular, deeply cordate at base, 20–22 by 18–20 cm; veins 5; petiole short, subterranean, sulcate with 3 sheathing cataphylls. Scape erect, terete, 1-flowered, with 2 sheathing cataphylls, lengthening to 14.5–15 cm when fruiting. Flower pure white. Bract straight, 1–12 mm long; sepals and petals oblanceolate, acute, 25–40 by 4–6 mm; lip of same length, 3-lobed, covered above by short, inflated, clavate hairs; sidelobes acutely triangular, 6–8 mm; midlobe obtuse, of same length or slightly shorter. Gynostemium clavate, (7.5–)12–14 mm; capsule 11 by 8.5 mm.

Ecology. On sandy soil under *Tamarindus, Erythrophleum* etc.; below 200 m alt. Flowering: XII–I.

Distribution. Madagascar: Ouest (4 coll.). Material seen from K, P.

Note. Lectotypification of *Nervilia leguminosarum*. Three collections in P made by Perrier de la Bâthie under the numbers 1377 (2 sheets), 1377" (3 sheets) & 1377ter (1 sheet) make up the original material. None of them is mentioned in the protologue, but they are all annotated as types of *N. leguminosarum* in Perrier’s handwriting. Perrier de la Bâthie 1377" is the richest with most duplicates. As the flowering scape, fig. 18/3, in Fl. Mad. 49, 1 (1939) was based on material from sheet II, containing three flowering specimens and two half-developed leaves, it was selected as a lectotype.

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4. *Nervilia affinis* Schltr. — Fig. 57; Plate 1b.


*Nervilia perrieri* Schltr., Fedde, Rep., Beih. 33 (1925) 117; id. 68 (1932) t. 47/186; Perrier in Fl. Mad. 49, 1 (1939) 208. — Type: Perrier de la Bâthie 11335 (Holol P), Madagascar, Centre, Mt Tsaratanana, 1400 m, forest, Nov. 1912.

?*Nervilia pilosa* Schltr. & Perr. in Schltr., Fedde, Rep., Beih. 33 (1925) 118; Perrier in Fl. Mad. 49, 1 (1939) 208. — Type: Perrier de la Bâthie 15716 (Holol P), Madagascar, Centre, Massif de Tsaratanana, c. 1700 m, forest with herbaceous undergrowth, Jan. 1923.

Erect, terrestrial herb, 7–13 cm tall, glabrous except for lip, leaf and subterranean parts. Tuber subspherical, 7–10 mm. Leaf solitary, appearing after flowering, not prostrate, above sparsely covered with short hairs (except a ± wide zone near the main veins); blade suborbicular to reniform, obscurely polygonal to obtusely 7-lobed, (2.7–)4–6 cm wide with cordate base; veins 7–9; petiole 2.5–8 cm long, sulcate with 3 sheathing cataphylls. Scape erect, terete, 1-flowered, with 3 sheathing cataphylls. Bract oblong, apiculate, 0.5–15 mm. Sepals and petals spreading, subequal, yellowish brown or red inside and pink outside; lateral sepals linear-lanceolate, subacute to acute, 3-veined, (12–)18–24 by 3.5–5 mm; petals of same length and slightly broader, oblique, narrowly oblong. Lip (14–)17–20 by 14–16 mm, 3-lobed, sparsely to densely pubescent, purplish red or white with red throat and upper margins. Gynostemium clavate, straight, 7–10 mm. Anther 3 by 2 mm, pollinia yellow. Ovary 4–5 mm.

Ecology. Rather dry to very humid forests; 1000–1600(–1700) m. Flowering: X–XII(–I).

Distribution. Madagascar: Centre (6 coll.); Est (17). Material seen from P, UPS.

Notes. 1. The collection from east Madagascar (see Map 11, open circle) consists of leaves only. Pending flowering material, the determination remains somewhat uncertain.

2. A collection from "Herb. E. Cosson" without collector is stated to be from Réunion. This needs confirmation.

3. Lectotypification of *Nervilia affinis*. There are two syntypes in P, one having a single flowering scape with a half-developed leaf and five mature leaves, and the other having two flowering scapes and two leaves. According to written information the first one was sent on loan to Schlechter in May 1923 and returned to P in Oct. 1928. As there is no proof that Schlechter saw the second sheet, the first one was selected as a lectotype.

4. The holotype sheet of *Nervilia perrieri* has nine flowering scapes with half-developed leaves, details of one dissected flower and four mature leaves. According to written information it was sent on loan to Schlechter in May 1921 and returned to Paris in July 1922. This probably means that there never existed any material in B.

5. The holotype sheet of *Nervilia pilosa* has one flowering scape and seven leaves. It carries the designation "Nervilia pilosa Perr. & Schltr." in Schlechter's hand.

6. The only flower in the type material of *N. pilosa* is considerably smaller than the rest of the material. Because of that its inclusion in *N. affinis* is only tentative. The collection Bogner s.n. (Kew EN 719-67, see Fig. 57d, e, Plate 1b) from northern Madagascar differs in having an apiculate midlobe to the lip. Its inclusion is also somewhat questionable.

5. *Nervilia stoltziana* Schltr. — Fig. 58; Plate 1c.

Erect terrestrial herb 2.7—13.5 cm tall, glabrous except for lip, leaf and subterranean parts. Tuber subspherical or ovoid, 6—9 mm diam., 3—4-noded. Leaf solitary, appearing after flowering, prostrate, reniform to orbicular, obusue, 1.4—3.0(—3.9) by 2.0—3.5 (—4.2) cm, above covered with short stiff hairs and often with silvery reticulate pattern, below usually purple; veins (5—)7—11; petiole 5—7 mm long, sulcate with 1 or 2 sheathing cataphylls. Scape erect, terete, 1-flowered, with 2 or 3 sheathing cataphylls, lengthening to 16—23 cm when fruiting. Flower more or less horizontal; bract 0.5—3 mm. Sepals and petals spreading, closing again after about 8 hours anthesis or when pollinated, subequal, linear-lanceolate, acute, reddish green; lateral sepals slightly oblique, 12—16 by 2 mm; petals slightly shorter to 14 mm. Lip elliptic to elliptic-cuneate, spurred, 14—23 (spur included) by 8—12.5 mm, lilac, mauve or red with white markings and yellow centre, with numerous long papillae on inner surface, veins with several anastomoses; spur straight, short, often slightly bifid, 3—4.2 by 2.6 mm. Gynostemium almost straight, clavate, glabrous, 6—7 mm; pollinia yellow, c. 2.5 mm.

Ecology. Woodland, dense dry mushitu and plantations of pine or Eucalyptus; 900—1800 m. Flowering: X—XII.


Note. This species often has leaves with a reticulate silvery pattern (see Figs. 10, 58f), but forms with uniformly green leaves are also rather common (see Fig. 58g). The pubescence may occasionally be very reduced.

6. Nervilia pectinata Cribb — Fig. 59; Plate 1d.


Nervilia sp. no. 5 Grosvenor, Excelsa 6 (1976) 84. — Specimen: Ball 1010 (SRGH).


Erect terrestrial herb 5—14 cm tall, glabrous except for lip, leaf and subterranean parts. Tuber subspherical or ovoid, 7—10 by 7 mm. Leaf solitary, appearing after flowering (sometimes sterile specimens with fully developed leaves can be seen together with flowering ones), horizontal but not prostrate, more or less polygonal or star-shaped, (1.5—)2.9—5.0 by (1.9—)3.5—5.5 cm, above sparsely covered with short hairs (very occasionally glabrous), hairs avoiding the main veins and a few mm adjacent to them but following the small veins radially, dark green above, pale green or sometimes purple below; veins
5–7; petiole 2–6 cm long, sulcate with 1 or 2 sheathing cataphylls. Scape erect, terete, 1-flowered, with 2 or 3 sheathing cataphylls, lengthening when fruiting to 9–19 cm. Flower more or less horizontal, fragrant; scent of camphor; bract 0.5–13 mm long. Sepals and petals spreading, closing again after about 8 hours anthesis, subequal, lanceolate, acute, pale green lined with purple; lateral sepals slightly oblique, 10.5–22 by 3 mm; petals lanceolate, acute, slightly shorter and 2 mm wide. Lip elliptic, more or less obscurely 3-lobed in middle, spurred, 10–19 (spur included) by 8.5–10 mm, white with purple dots and yellow towards base, shortly papillate on inner surface, veins with no or very few anastomoses, margins plicate in apical half; spur straight, short, rounded, 1.5–3 by 1–2 mm. Gynostemium almost straight, clavate, glabrous, 4.5–6 mm; pollinia 1.5–2 mm; capsule 7–11 by 3–5 mm.

Ecology. Evergreen montane forest and cypress plantation; 1000–2200 m. Flowering: X–XII.


7. Nervilia subintegra Summerh. — Fig. 60; Plate 2a.


Erect, terrestrial herb, 5–13 cm tall, glabrous except for leaf and subterranean parts. Tuber subspherical or ovoid, 4–15 by 9–17 mm. Leaf solitary, appearing after flowering, horizontal but not prostrate, above sparsely covered with short hairs; blade star-shaped, (7–)9(–11)-lobed, (2.5–)4–9(–13) cm broad; veins (7–)9(–11); petiole (2–)3–9 cm long, sulcate with 1 or 2 sheathing cataphylls. Scape erect, terete, 1-flowered, with (2 or) 3 sheathing cataphylls, lengthening to 17–27 cm when fruiting. Flower small, more or less horizontal, 25–40 mm diam. Bract 1 (occasionally 2), linear, 7–15 by 0.7 mm. Sepals and petals spreading, subequal, ligulate, acute, greenish brown with reddish veins; lateral sepals 12–22 by 2–5 mm; petals slightly shorter than sepals. Lip 10–17 by 5–7 mm, very obscurely 3-lobed, mainly pink with yellow midline in proximal half, tightly clasping column; apical part with convex central ridge; sidlobes with radially running furrows and ridges. Gynostemium clavate, glabrous, pale yellow (6–)7–10 mm. Anther pale yellow, c. 2 mm, pollinia yellow. Capsule 14 mm.

Ecology. Dense and humid lowland and submontane forest, forest edge, gallery forest, occasionally secondary forest and tree savanna; 300–1100 m. Flowering: III–IV.


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Notes. 1. Lectotypification of Nervilia subintegra. Summerhayes indicated that the name was based on Le Testu 4634 and added: "type in Herb. Le Testu, Caen". According to Holmgren, Keukcn, & Schofield (Index Herbariorum 1, ed. 7, 1981) and Mme Gayral (in litt.) the phanerogamic part of Le Testu's herbarium has been transferred to P. There are at present two sheets of the type collection, one in BM and one in P. Both, according to labels, have been seen by Summerhayes, which means that the BM sheet must have been transferred from CN after the type designation. As there was no obvious holotype a lectotypification was needed. The sheet in P was selected as a lectotype.

2. Occasionally the leaf can be glabrous as in the specimen Callens 1148 from near Kisantu in Zaire.

8. Nervilia adolphi Schltr. — Fig. 61; Plate 2b, c.

Literature: see under the varieties.

Erect terrestrial herb 2–10(–13) cm tall, glabrous except for subterranean parts. Tuber subspherical or ovoid, 6–15 mm diam., (2–)3(–4)-noded. Leaf solitary, appearing after flowering, prostrate to suberect (blade up to 5 cm above litter surface), glabrous; blade broadly cordate or reniform, subacute, obtuse, or obtuse, 1.5–2 cm long; petiole 0.5–1 cm, sulcate with 1 or 2 sheathing cataphylls. Scape erect, terete, 1-flowered, with 2 sheathing cataphylls, lengthening to 8.6–21 cm when fruiting; bract 1.5–5.5(–10.5) cm. Flower small, more or less horizontal, fragrant (scent lilac-like, fide la Croix). Sepals and petals spreading, closing again after about 8 hours anthesis, subequal, ligulate, acute, brownish green; lateral sepals slightly oblique, 10–22 by 2.5–3.5 mm; petals slightly narrower than sepals. Lip oblong, 9.5–20 by 4–7 mm, 3-lobed, white to faint pink with purple-violet shortly papillate markings; lateral lobes short, obtuse, erect, tightly clasping column; midlobe (= epichile) ovate, with convex central ridge and incurved margin, 3–9.5 mm. Gynostemium almost straight, clavate, pubescent on ventral side, 6–10 mm; pollinia yellow, 2–3 mm; ovary 2–7 mm long; capsule 7.5–10 by 4–5 mm.

Ecology. Woodland, grassland, "virgin forest", riverine fringe-forest and pine plantation; 225–1750 m. Flowering: Northern hemisphere I, IV; Southern hemisphere X–XII(–II).


Notes. 1. As flowering specimens normally are impossible to determine to variety there will always remain many collections without infraspecific name.

2. The leaves of var. seposita have a very distinctive tessellate or marbled pattern to the upper side, where the silver appears in spots, while the dark green between the spots creates a reticulate pattern (see Figs. 11, 61j; Plate 2d). The lower side is more or less purple.

In var. adolphi it is possible to recognize two rather distinctive types. The most common is green on both sides, growing with the blade one or two cm above the ground and rather large (see Fig. 61h). The other is much smaller, strongly prostrate, dark purple below and dark olive green above through a mixture between anthocyanin and chlorophyll (see Fig. 61i). It seems to be restricted to south central Africa. As the delimitation between these
two forms is far less clear-cut than that between the two existing varieties, and as the differences are difficult to study on herbarium material I have refrained from a formal naming of them.

There is a correlation between the variation in leaf morphology and flower morphology in this species. Thus var. seposita as understood here, mostly has a very short midlobe to the lip (see Fig. 61g; Plate 2d), which also is the case in the type material for this variety. Also, forms of var. adolphi with the above-mentioned second leaf type (dark olive green, small, prostrate and purple below) normally has very small flowers with a lip length of 10–14 mm (see Fig. 61f; Plate 2c). However, this correlation is not absolute and most combinations between flower and leaf variants are known.

3. Schlechter described this species as “N. Adolphi”. The spelling “adolphi” has been followed by most later authors, while some (including myself) have been using “adolphii”. However, as Geerinck (pers. comm.) kindly pointed out to me, Schlechter was clearly using the latinized form “Adolphus” of the Christian name of the German missionary Adolf Stolz as a base for the epithet. Thus, in accordance with Recommendation 73C.2. of the International Code of Botanical Nomenclature (Greuter & al. 1988) the genitive becomes “Adolphi”, which as an epithet is commonly written “adolphi” (Recommendation 73F.1.).

KEY TO THE VARIETIES

1 - Leaf uniformly green on upper surface .......................................................... a. var. adolphi
   - Leaf tesselated silver and green above .......................................................... b. var. seposita

a. var. adolphi — Fig. 61; Plate 2b, c.


*Nervilia* sp. no. 1 Grosvenor, Excelsa 6 (1976) 84. — Specimen: Ball 715 (SRGH).

Leaf prostrate or raised, uniformly green or olive green above and green or purple below. Lip mid-lobe usually about half the length of the lip.

Ecology. Woodland, grassland, riverine fringe-forest and pine plantation; 750–1750 m.


Notes. 1. Lectotypification of *Nervilia adolphi*. The type material of Stolz 1870 in B was destroyed during the war. The extant material of the type collection is divided in (at least) 31 sheets distributed in 24 different herbaria: AMES, B, BM, BOL, BR, C, DR, DS, G, JE, K, L, LD, LE, M, NU, O, P, S, U, UPS, W, WAG and Z. (The present sheet in B has been acquired after the war.) Some sheets contain leaves only, but flowers, only one sheet in K has both leaves and flowers. Unfortunately it is quite poor with only two rather bad flowers and two leaves. A sheet in BM with 15 flowers was selected as a lectotype.

2. The colour photo 32.1 in Stewart & al. (1982), representing a flowering scape of *N. adolphi*, is from Zambia (Photo: G. Williamson). The species is not found in South Africa.

b. var. seposita N. Hallé & Toilliez — Fig. 61; Plate 2d.


Chevalier 22169.


Leaf more or less prostrate, tesselated silver and green above, purplish grey below. Lip usually short; mid-lobe about one-third of lip, typically 3–3.5 by 3–3.5 mm.

Ecology. Virgin forest, margins of forests and marshes, woodland and grassland; 1190–1700 m.
Distribution. Senegal; Sire-Saloum (2 coll.). Mali: Sikasso (1). Guinea: (2). Ivory Coast: Nord (2); Centre (4); Est (4). Central African Republic: (1). Equatorial Guinea: Bioko [Fernando Póo] (2). Zaïre: Bas-Congo Z3 (2); Forestier Central Z6 (1); Ubangi-Uele Z7 (1); Lac Albert Z8 (3); Lacs Édouard et Kivu Z9 (1). Uganda: Buganda U4 (1). Zambia: Central (1). Material seen from BM, BR, K, P, UCI.

Notes. 1. Originally Hallé & Toilliez described var. *seposita* as always having a short lip with mid-lobe about one-third of the total length of lip. However, even if most West African specimens combine tesselate leaves with a short lip, there are both short-lipped specimens with green leaves as well as long-lipped ones with tesselate leaves. Also elsewhere occasional specimens with short mid-lobe are found. Because of this, var. *seposita* is here described as based primarily on the leaf of the type.

2. The specimen Pettersson, Hedrén & Kibuwa 429 from the Southern Highlands in Tanzania (see Map 19, open circle) is somewhat intermediate and shows leaves with a longer petiole, much fainter pattern above and without the purplish underside.

9. *Nervilia fuerstenbergiana* Schltr. — Fig. 62; Plate 3a.


Erect terrestrial herb 3–6.5 cm tall, glabrous except for subterranean parts. Tubersubshpherical or ovoid, 7–12 by 10–17 mm. Leaf solitary, appearing after flowering, not prostrate (blade up to 9 cm above litter surface), glabrous; blade broadly cordate, obscurely polygonal, acute to apiculate, apical part triangular with concave sides, 3.5–7.7 by 2.8–8.5 cm, ± clearly marbled in dark and light green above and purple blotched below; veins 7–9; petiole 1–9 cm long, sulcate with 1–3 sheathing cataphylls. Scape erect, terete, 1-flowered, with 2 or 3 sheathing cataphylls, lengthening to 13.5–21.5 cm when flowering. Flower small, ± horizontal, bract lanceolate to triangular, 4.5–7 mm. Sepals and petals spreading, subequal, lanceolate-ligulate, acute, green; lateral sepals slightly oblique, 12–15 by 2.5–3.5 mm; petals slightly narrower than sepals. Lip oblong, 11.5–16 by 4.5–6 mm, 3-lobed, white to faint pink with purple-violet shortly papillate markings; lateral lobes short, obtuse, erect, green, tightly clasping column; midlobe (= epichile) ovate, with convex central ridge, 6.5–10 by 4.5–5.5 mm. Gynostemium relatively short, clavate, pubescent on ventral side, 5.5–6.5 mm; pollinia yellow, 2 mm; ovary 3.5–4 mm long; mature capsule 10–18 by 7 mm.

Ecology. Humid forest types; 150–700 m. Flowering: II–IV.

Distribution. Sierra Leone: (2 coll.). Liberia: (1). Ivory Coast: Province unknown (3); Ouest (3). Ghana: (3). Nigeria: Western (2); Zaria (1); Benue-Plateau (1). Cameroun: West (3) Equatorial Guinea: Bioko [Fernando Póo] (1). Material seen from BR, E, K, MO, P, UCI, UPS.

Note. Neotypification of *Nervilia fuerstenbergiana*. All original material seems to have been lost during World War II. Of the other two collections from Cameroun, one
consists of a single poorly preserved flowering scape in a mixed sheet with *N. subintegra*, and the other, as well as a collection from the neighbouring island of Bioko, contains leaf material only. Therefore a sheet from the Jos Plateau in Nigeria, King 95, containing three flowers and three leaves and preserved in K was selected as a neotype.

10. *Nervilia lilacea* Jum. & Perr. — Fig. 63.


Erect, terrestrial herb, 6–10 cm tall, glabrous except for subterranean parts. Tuber spherical. Leaf solitary, not prostrate, glabrous; blade wider than long, 1.5 by 2 cm; veins 5; petiole c. 3 cm long, sulcate with a sheathing cataphyll. Scape erect, terete, 1-flowered, with 2 sheathing cataphylls, the upper one 1 cm and longer than the lower one and than the bract. Flower small, more or less horizontal. Bract c. 1 mm; sepals and petals greenish white, spreading, linear-lanceolate, slightly attenuate towards the base, 11–12 by 2–2.5 mm; lip slightly shorter, 3-lobed, white with lilac midlobe; side lobes acute, much shorter than the midlobe, which is lanceolate, 3 by 3 mm with a finely toothed front margin. Gynostemium clavate, curved forwards, lilac, c. 5 mm.

Ecology. Altitude 1000 m.

Distribution. Central Madagascar (1 coll.). Material seen from P.

Note. Only known from the single type specimen with one leaf and one flower. Both flower and leaf were obtained from cultivation.

11. *Nervilia gassneri* B. Pettersson — Fig. 64; Plate 3b, c.


*Nervilia* sp. no. 2 Grosvenor, Excelsa 6 (1976) 84. — Specimen: Ball 427 (K, SRGH).


Erect terrestrial herb 2.5–10 cm tall, glabrous except for subterranean parts. Tuber sub-spherical or ovoid, 7–13 by 8–9 by 6–9 mm. Leaf solitary, appearing after flowering (sterile specimens sometimes develop leaves while the fertile ones are flowering), prostrate or nearly so (blade up to 2 cm above litter surface), glabrous; blade cordate, subacute to obtuse, 1.4–5.5 by 1.2–4.5 cm, apical part triangular with sides straight or often slightly concave; veins (5–)7, the middle one often with a more prominent groove on the upper surface; petiole 1–6 cm long, sulcate with 1 or 2 sheathing cataphylls. Scape erect, terete, 1-flowered, with (1 or) 2 sheathing cataphylls, lengthening to (4.5–)6–20 cm when fruiting; bract 1–2.5 by 0.5 mm. Flower small, often cleistogamous (see Fig. 64c, Plate 3c), c. 22 by 18 mm, ± horizontal, faintly scented (scent spicy, reminding of *N. adolphii*).
Sepals and petals spreading, subequal, ligulate, acute, reddish green with maroon longitudinal flecks; lateral sepals ± oblique, 9.5–14 by 2 mm; petals slightly shorter than sepals, narrower towards base and with fainter colours. Lip oblong, 9–13 by 5–6 mm, 3-lobed, divided in the middle by a narrow waist into hypochile and epichile of subequal length, white to faint pink with cerise, shortly papillate markings; lateral lobes short, obtuse, erect, enclosing column; midlobe (= epichile) ovate, flat with convex central ridge, almost as wide as the hypochile. (In the cleistogamous flowers the perianth parts are often very reduced in size.) Gynostemium almost straight, clavate, pubescent on ventral side, 4.5–6 by 1.3 mm; pollinia creamish white to pinkish grey, 1.5 by 0.6 mm, sometimes sticking together, forming a single compound pollinium, massulae scale-like; capsule 9–12 by 4.5 mm.

Ecology. Woodland, riverine forest and cypress plantation; 1150–1900 m. Flowering: XI–XII (–I).

Distribution. Tanzania: Southern Highlands T7 (7 coll.). Zambia: West (1?); Central (1?). Zimbabwe: Without locality (1); East (3). South Africa: Transvaal (3). Material seen from BOL, BR, K, LISC, LMU, MAL, NHT, SRGH, UPS.

Note. The specimens Morze 100A (K) and Williamson & Odgers 181 (K) (Fig. 53) from Zambia differ by having very acute (sometimes horn-like) sidelobes to the lip and tooth-like projections along the centre of the midlobe. This entity was treated as Nervilia sp. (Williamson & Odgers 181) by Williamson (1977), who intended to describe a new species (pers. comm.), but the material turned out to be inadequate; a situation still prevailing. Here it is provisionally put under N. gassneri but may prove to represent a distinct taxon when more material becomes available. Another possibility would be that it is conspecific with the poorly known N. lilacea from Madagascar, which also has acute sidelobes. However, the lip midlobe of the latter species is smooth without any medial projections or irregularities.

Fig. 53. The collection Williamson & Odgers 181 from Zambia. Photo: G. Williamson.

II – Nervilia section Nervilia


12. Nervilia bicarinata (Blume) Schltr. — Fig. 65; Plate 3d.


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(? Pogonia sp. Rchb. f., Ota Bot. Hamb. 1 (1878) 60. — Specimen: Schweinfurth 3787 (B lost, n.v., identity uncertain), Sudan, Tuhamis Seribu (near Yambio), 20 May 1870 (leaf only).


**Nervilia buchananii** auct. non (Rolfe) Schlr.: Schieben, Gartenfl. 86 (1937) 14.


Erect terrestrial herb 17–75 cm tall, glabrous except for lip and subterranean parts. Tubers subspherical or ovoid, 1–2 by 1–3 by 1–4.7 cm, 3–7–noded. Leaf very large, to 22.5 cm long and 26.5 cm wide, solitary, appearing after flowering, orbicular (reniform when flattened) to cordate, always cordate at base, apiculate, glabrous, 10–30–veined, heavily pleated, pleats keeled, keels sometimes white and always somewhat ragged near the margin; blade more or less horizontal, held well above ground; petiole (2–)5–26 cm long, sulcate with 1–2 sheathing cataphylls when young. Scape erect, terete, laxly (1–)2–12-flowered, with 2–5 sheathing cataphylls, the uppermost one often substituted by a sterile bract up to 4 cm long. Flowers 2–4 cm apart, evenly spaced along rachis; bracts foliiform to lanceolate, 10–27 by 0.9–2.5 mm. Sepals and petals greenish, subequal, ligulate-lanceolate, acute; lateral sepals slightly oblique, 17–31 by 0.9–4 mm; petals slightly shorter than sepals. Lip greenish white with purple or green veneration, ovate, 20–31 by 17–25 mm, obscurely 3-lobed, bearing 2 parallel fleshy pubescent ridges running from base of lip to base of midlobe; side lobes short, oblong to shortly triangular, obtuse, erect, enclosing column; midlobe triangular to ovate, acute, recurved. Gynostemium curved, clavate, glabrous, 10–15(–16) mm; anther front rim with two protruding teeth; pollinia yellow, 2.5–3.2 mm; stigmatic surface 4–5 mm diam. Capsule c. 13 mm long.

**Ecology.** Riverine and spray forest, often in *Syzygium* thicket; 0–1500 m. Flowering: Northern hemisphere II–VI(–VII); Southern hemisphere mainly X–XII, near equator also VIII–IX (western side) and XII–I (eastern side).

**Distribution.** Senegal: Casamance (1 coll.). Burkina Faso: (1). Guinea-Bissau: (2). Guinea: Dalaba (1); Kindia (1); Kourossa (1); Mamou (1). Sierra Leone: Northern (1). Ivory Coast: Province unknown (4); Nord (3); Ouest (4); Centre (8). Ghana: (3). Togo: ? (1); II (2); IV (5); V (1). Bénin: Nord-Ouest (1). Nigeria: Benue-Plateau (14); Kano (1); Kwara (2); Niger (1); North-Central (2); Western (4). Cameroun: East (1). Central African Republic: Ouaka (1). Chad: Logone (1). Equatorial Guinea: Pagalu [Annobon] (1). São Tomé & Príncipe: Príncipe (1); São Tomé (12). Congo: Pool (1). Zaïre: Bas-Congo Z3 (3); Kasai Z4 (6); Forestier Central Z6 (3); Lac Albert Z8 (1); Lacs Éduard et Kivu Z9 (1); Haut-Katanga Z11 (3). Ethiopia: Erítreà EE (2); Ilubabor IL (1); Wellega WG (1). Uganda: Bunyoro U2 (1). Tanzania: Tanga T3 (6); North T4 (2); East T6 (2); Southern Highlands T7 (1); Zanzibar Z (6); Pemba P (1). Angola: Malange (1). Zambia: North (1); Central (4); South (2). Zimbabwe: West (1). Malawi: North (1); South (6). South Africa: Transvaal (6); Natal (5). Comoro Is.: Grande Comore (3); Mayotte (1). Madagascar: Without locality (8); Ouest (14); Centre (2); Est (4); Sambirano (4). Réunion: (3). Mauritius: (2). Material seen from AMES, B, BM, BOL, BR, C, COI, DS, EA, ETH, FT, G, GC, H, K, L, LE, LG, LISC, LISJC, LISU, M, MAL, MO, NHT, NU, O, P, PRE, S, SRGH, TAN, TOGO, UCI, UPS, VBI, W, WRSL, WU, YA, Z. Distribution outside Africa: Yemen and Oman.
Note. The leaf is mostly almost orbicular in outline when fresh (reniform when flattened) with green keels on the upper side. However, coriaceous leaves, that often have more a rigid texture and are smaller, are not uncommon in West Africa (see Hallé & Toilliez 1971: Pl. 4/3) and Madagascar. This type is often equipped with wholly or partly white keels on the upper side (Plate 3d).

13. *Nervilia renshiana* (Rchb. f.) Schltr. — Fig. 66; Plate 4a.


Non *Nervilia grandiflora* Schltr., Fedde, Rep. 9 (1910) 85.


*Nervilia* sp. no. 6 Grosvenor, Excursa 6 (1976) 84. — Specimen: Wild 4194 (K, SRGH).


*Pogonia purpurata* auct. non: Bews, An Intr. to the Fl. of Natal and Zululand (1921) 75.


Erect terrestrial herb 25.5–80 cm tall, glabrous except for lip and subterranean parts. Tuber subspherical or ovoid, 3–3.5 cm diam. Leaf large, prostrate, (5–)9–17 cm long and (6–)11–19 cm wide, solitary, appearing after flowering, reniform to almost orbicular, deeply coriaceous at base, apiculate, glabrous, 11–20–veined, heavily pleated (especially when young); lateral veins strongly curved towards leaf margin; petiole 0.1–5.0 (–5) cm long, sulcate with 1–2 sheathing cataphylls when young. Scape erect, thick, yellowish brown to purple, laxly to rather densely 3–5–flowered, with 2–4 sheathing cataphylls, the uppermost one rarely substituted by a sterile bract c. 4 cm long. Flowers large, yellowish tinged with brown, bracts filamentous to lanceolate, 14–35 by 1–4.2 mm. Sepals and petals
subequal, ligulate-lanceolate, acute, light green to yellowish green; lateral sepals slightly oblique, 24–37 by 4–5.5 mm; dorsal sepal 28–40 by 4–6 mm; petals slightly shorter and wider than sepals, 21–33 by 4.5–6 mm. Lip yellowish with reddish veins, ovate, 24–38 by 17.5–26 mm, obscurely 3-lobed, bearing 2 parallel fleshy pubescent ridges from base to base of midlobe; side lobes semicircular to oblong, rounded, erect, enclosing column; midlobe ovate, subacute, recurved. Gymnostemium curved, clavate, glabrous, 13.5–19 mm (in lowest flower 15–19 mm); anther front rim with two protruding teeth.

Ecology. Woodland and riverine forest fringe; c. 100–1760 m. Flowering: IX, XI–XII.


14. Nervilia kotschyi (Rchb. f.) Schltr. — Fig. 67; Plate 4b.


Nervilia sp. Saunders, Soc. Malawi Journ. 33, 2 (1980) 38, 40, p.p. — Specimen: Saunders T21M (MAL) (there are 2 sheets with the same designation; the other = Nervilia shirensis).


The following references concern flowering material of N. kotschyi which cannot be determined to variety and which comes from areas where var. purpurata is not known:


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Erect terrestrial herb 8–42 cm tall, glabrous except for lip and subterranean parts. Tuber subspherical or ovoid, up to 14–32 mm diam., (3–)4–6-noded. Leaf prostrate or erect (var. purpurata), (2.3–)3–17 cm long and (1.6–)2.5–16 cm wide, solitary, appearing after flowering, broadly cordate or sometimes ovate, acute to apiculate, glabrous, 6–25-veined, often dark olive green above and purple below, upper side sometimes with silvery lines along veins, usually heavily pleated, pleats raggedly keeled, keels often purple, sometimes without keels, then not pleated and green on both sides; petiole 0–6 cm long, sulcate with 1–2 sheathing cataphylls when young. Scape erect, terete, (1–)2–8–(12)–flowered, with 2–4 sheathing cataphylls, the uppermost one sometimes substituted by a sterile bract up to 25 mm long. Flowers greenish with purple veins; bracts linear-setose, acuminate, 7–25 by 1–2 mm. Sepals and petals subequal, linear-lanceolate, acute, greenish; lateral sepals slightly oblique, (8–)12–26 by 3–3.5 mm; petals slightly shorter than sepals. Lip greenish white with purple venation, elliptic, 10–19 by 7–12 mm, obscurely 3-lobed, bearing 2 parallel fleshy pubescent ridges running from base of lip to base of midlobe; side lobes shortly triangular, acute or subacute, erect, enclosing column; midlobe ovate-triangular or triangular often with an irregular callus in the middle, acute or subacute, recurved. Gynostemium curved, clavate, glabrous, 7–11.5 mm; anther front rim with two protruding teeth; pollinia yellow, c. 2 mm; ovary c. 4 mm long; capsule 8–13 by c. 10 mm; seeds straight or slightly curved, 0.13–0.2–0.25 mm long, often with rather blunt ends.

Ecology. Altitude 70–2300 m. Flowering: Northern hemisphere (including southern Kenya) II–VII; Southern hemisphere (IX–)X–XII(–I).

Distribution. Material of undetermined varietal status seen from Senegal: Oriental (1 coll.); Casamance (1); Thiès (1). Mali: Sikasso (1). Ghana: (1). Nigeria: (9). Central African Republic: (1). Zaire: Bas-Katanga Z5 (2); Haut-Katanga Z11 (11). Sudan: An Nil al Azraq [Blue Nile] (1); Equatoria (1). Ethiopia: Harergrhe HA (1); Tigray TU (1); Wellega WG (2). Uganda: North U1 (1); West U2 (1) East U3 (1). Kenya: Rift Valley K3 (2); Coast K7 (4). Tanzania: West T4 (4); Southern Highlands T7 (11); South T8 (2); Zanzibar Z (4). Angola: Bié (1). Zambia: Barotse (1); North (4); West (5); Central (9); South (3). Zimbabwe: Province unknown (1); North (4); Central (3); East (2). Malawi: North (3); Central (1); South (8). Moçambique: Niassa (2); Manica e Sofala (1); Maputo (2). South Africa: Transvaal (1). Madagascar: Ouest (5). Material seen from B, BM, BOL, BR, COI, E, EA, ETH, FT, G, HBG, K, LISC, M, MAL, MO, NHT, NY, P, PRE, S, SRGH, UPS, W, WAG, Z.

Notes. 1. From Central African Republic and Angola there is no collection possible to identify to variety.

2. N. kotschyi is extremely variable as to leaf morphology and colouration (see Pettersson 1990). The var. purpurata, which has erect, elliptic leaves without keel fringes, silver pattern or anthocyanin colouring on the blade, is the most distinctive type (see Fig. 67h). However, intermediates have been collected. The var. kotschyi shows all intergrades between heavily pleated types with silver rays, strong, dark purple anthocyanin colouration on both sides (making the lower side pure dark purple and the upper dark olive green through mixing with dark green chlorophyll) and up to four parallel rows of purple fringes along pleats as one extreme (see Fig. 67f; Plate 4b) and all green types with totally smooth upper side (lacking silver pattern, anthocyanin colouration, pleats and keels) as the other (see Fig. 9 middle specimen, 67g). The most common type is a moderately pleated intermediate with one fringed keel to each pleat, pure green colour to the upper side and green or purple to the lower one (see Fig. 9 left specimen).

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KEY TO THE VARIETIES

1 - Leaf cordate, ± prostrate .............................................. a. var. kotschyi
- Leaf elliptic to lanceolate, erect ..................................... b. var. purpurata

a. var. kotschyi — Fig. 67; Plate 4b.


Nervilia petraea auct. non (Afz. ex Sw.) Summerh.: Troupin, Fl. Sp. P. Garamba 1 (1956) 257, fig. 62/B.


Leaf broadly cordate, normally strongly prostrate and often heavily pleated; blade up to 16 cm wide; 10–14-veined; mostly with 1–4 ragged keels or fringes running along pleats; often with irregular interruptions; fringes and underside of leaf often dark purple; upper side sometimes with silvery lines along veins; petiole very short. Inflorescence in Flora Zambesiaca area and adjacent parts of Tanzania normally 2-flowered. Gynostemium 7–9 mm.

Ecology. Woodland, thicket and pine plantation; 300–1800 m.

Distribution. Senegal: Casamance (2 coll.); Oriental (1). Mali: Kayes (2); Sikasso (1). Guinea: Kouroussa (2). Sierra Leone: North (2). Ivory Coast: Nord (4). Ghana: North (1). Togo: II (1); III (1). Bénin: Nord-Ouest (1). Nigeria: Benue-Plateau (4). Chad: (1). Zaïre: Bas-Katanga Z5 (1); Ubangi-Uele Z7 (1); Haut-Katanga Z11 (5). Sudan: Darfur (1). Ethiopia: Eritrea EE (1); Kefa KF (1); Tigray TU (1); Wellelega WG (1). Uganda: West U2 (1); East U3 (1). Kenya: Coast K7 (1). Tanzania: Tanga T3 (2); East T6 (2); Southern Highlands T7 (10). Zambia: West (5); Central (5); East (1); South (1). Zimbabwe: North (7); West (1); Central (3); East (4). Malawi: North (4); South (10). Moçambique: Niassa (3); Zambezia (1); Manica e Sofala (1). Madagascar: Ouest (10). Material seen from AMES, B, BM, BOL, BR, C, DS, DSM, EA, FT, G, GC, JE, K, L, LD, LISC, LMU, M, MAL, MO, NHT, O, P, PRE, S, SRGH, TOGO, U, UC, UCI, UPS, WAG, Z.

Note. The upper leaf surface is sometimes totally smooth without any keels. Such collections are known from Zambia (C), Moçambique (N) and Madagascar (Ouest). ‘N. sakoae’ applies to such plants from Madagascar with leaves nearly devoid of keels and hence almost smooth on upper surface. However, there is a perfectly continuous variation to the heavily keeled ones.

b. var. purpurata (Rchb. f. & Sond.) B. Pettersson — Fig. 67.


Non Pogonia purpurata auct.: Bews, An Intr. to the Fl. of Natal and Zululand (1921) 75 (= Nervilia ren schiana); Brain, Rhod. Agric. Journ. 1939 (1939) 827, t. 65 (= Nervilia shirensis).


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Leaf erect, elliptic to lanceolate, plicate, petiolate; ridge of pleats keeled on both sides; edge of keels smooth; blade 6–13 by 2.5–4 cm; main veins 6–10; petiole 3–6 cm. Inflorescence in Flora Zambesiaca area mostly 3-flowered. Gynostemium 8–11 mm.

**Ecology.** Grassland and dambo; 475–2300 m.


15. **Nervilia ballii** Williamson — Fig. 68; Plate 4c.


*Nervilia* sp. Moriarty, W. Fl. of Malawi (1975) 57, t. 29 fig. 3. — Specimen: Moriarty 761 (MAL).

*Nervilia* sp. no. 3 Grosvenor, Excelsa 6 (1976) 84. — Specimen: Wild 4174 (K, MO, PRE, SRGH).


Erect terrestrial herb 11–30 cm tall, glabrous except for lip and subterranean parts. Tuber subspherical or ovoid, 15–17 by 15 by 10–15 mm diam., (2–)3–5-noded. Leaf erect, 5–6 by 3–4 cm, solitary, appearing after flowering, ovate, acute, glabrous, heavily pleated, dark olive green above with silvery lines along veins, dark purple below; petiole about 6 cm long, sulcate with 1–2 sheathing cataphylls when young. Scape erect, 1–2–flowered, with 3–4 sheathing cataphylls, the uppermost one sometimes substituted by a sterile bract up to 4 cm long. Flower reddish tinged on outside; bracts 1–2, filamentous to lanceolate, 14–23 by 0.6–1.6 mm. Sepals and petals subequal, lanceolate, acute, greenish with red veins and a general reddish tinge to the outside; lateral sepals slightly oblique, 19.5–25 by 3–4.5 mm; petals slightly shorter than sepals. Lip cream or pale yellow with prominent red or purple venation, ovate to oblong-ovate, 18–25 by 14–18 mm, obscurely 3-lobed, bearing 2 parallel fleshy pubescent ridges from base to base of midlobe; side lobes rounded or oblong, obtuse, erect, enclosing column; midlobe ovate, reflexed. Gynostemium curved, clavate, glabrous, 9–13.5 mm; anther front rim with two protruding teeth; anther purple; pollinia yellow, c. 2.5 mm; ovary 4.5–5.5 mm long.

**Ecology.** Woodland, grassland, grassland-scrub, *Syzygium* thicket and plantations of pine or *Gmelina*; 600–1830 m. Flowering: X–XII.

**Distribution.** Tanzania: Southern Highlands T7 (2 coll.); South T8 (1). Zambia: Central (4); East (1); South (2). Zimbabwe: North (8); Central (4); East (3). Malawi: North
(3); South (11). Moçambique: Niassa (4). Material seen from BOL, K, LNU, MAL, MO, PRE, SRGH, UPS.

16. Nervilia shirensis (Rolfe) Schltr. — Fig. 69; Plate 4d.


*Non Nervilia buchananii* auct.: Schlieben, Gartenfl. 86 (1937) 14 (= *Nervilia bicornata*).


Erect terrestrial herb (10–)15–44 cm tall, glabrous except for lip and subterranean parts. Tuber subspherical or ovoid, 1.5–3 by 1.5–2.8 by 0.8–2 cm, 4–7-noded. Leaf large, erect to suberect, ovate to almost round, 6–16 cm long and 3.5–11 cm wide, solitary, appearing after flowering, glabrous, pleated; apex obtuse to acute or slightly acuminate; leaf base attenuate to truncate or slightly cordate; veins 6–10; petiole 5.5–17 cm long, sulcate with 1–2 sheathing cataphylls when young. Scape erect, terete, (1–)2–3-flowered, with 2–4 sheathing cataphylls. Flowers large, more or less secund; bracts linear, setose, acute, to 22–31 mm long. Sepals and petals subequal, linear-lanceolate, acute, greenish-yellow with red veins and a general reddish tinge to the outside; lateral sepals slightly oblique, 25–42(–45) by 5.2–7.5 mm; petals slightly shorter than sepals. Lip cream or pale yellow with prominent red or purple venation, ovate, (19–)24–40 by 22–31 mm, 3-lobed, bearing 2 parallel fleshy pubescent ridges running from base of lip to base of midlobe; side lobes oblong, rounded to obtuse, erect, enclosing column; midlobe ovate, obtuse, reflexed. Gynostemium curved, clavate, glabrous, 16–25 mm; anther front rim with two protruding teeth; pollinia yellow, 3.9–5.2 mm; stigmatic surface 5–8 mm diam. Capsule 14–19 by 12 mm.

Ecology. *Brachystegia* woodland, grassland, plantations of pine, cypress or *Gmelina*, and riverine forest; 480–2150 m. Flowering: X–XII (–I).

Distribution. Zaïre: Haut-Katanga Z11 (4 coll.). Tanzania: North T4 (3); Southern Highlands T7 (17); South T8 (5). Angola: Cuanza Norte (1); Lunda (2); Benguela (2). Zambia: North (10); West (2); Central (3); East (1); South (1). Zimbabwe: North (3); Central (6); East (10). Malawi: North (5); Central (2); South (26). Moçambique: Niassa (9); Zambézia (1). Material seen from AMES, B, BM, BOL, BR, COI, DS, EA, G, K, L, LISC, LISU, LNU, MAL, MO, P, PRE, S, SRGH, UPS, WAG, Z.
INCOMPLETELY KNOWN SPECIES


Notes. 1. Lectotypification of *Pogonia hirsuta*. Two herbarium sheets in L and P can be considered as syntypes, both having four leaves each, a designation in Blume’s handwriting and the number 3087. Only the sheet in P has Boivin’s name. Instead, the sheet in L has “Mayotte 3087”, thus reflecting Blume’s error in believing that Mayotte was a collector and not an island (see Pettersson, Nord. Journ. Bot. 9 (1990) 488). The sheet in L is named “*Pogonia hirsuta* Blume” and the one in P “*Pogonia* (ex Blume)”. The fig. 2B–C of plate 59 in the original description are clearly based on specimens from the sheet in L. As this is also preserved at the institute where Blume worked and is the only one bearing the specific name, it was selected as a lectotype.

2. *Nervilia hirsuta* is probably conspecific with *N. stolziana*, for which it would be an earlier name. However, as the type material has no flowers and no other collections of *N. stolziana* from the Comores are known, I am reluctant to formally propose a change of name.


Notes. 1. Lectotypification of *Pogonia thouarsii*. Two herbarium sheets can be considered as syntypes, both originating from the herbarium of du Petit-Thouars and both also having one leaf each and a designation in Blume’s handwriting. A sheet in L is named “*Pogonia Thouarsii* Blume” and another in P “*Pogonia* (ex Blume)”. Figs. 1A–B of plate 59 in the original description are clearly based on the specimen in L. As this is also preserved at the institute where Blume worked and is the only one bearing the specific name, it was selected as a lectotype.

2. *Pogonia thouarsii* of course belongs to *Nervilia*, but as the name has long been erroneously thought to be a synonym of *N. simplex* [= *N. petraea*], a combination in that genus has not been needed. I believe the name to be synonymous to *N. crociformis*, but as no flowers of this have been found on Mauritius, I refrain from a formal synonymization pending more material.

ENTITIES OF DUBIOUS IDENTITY


Note. Lindley says it was found in soil from the Mauritius. According to Hereman it is about 15 cm tall, flowers in April, is native to Mauritius and was introduced in cultivation in Britain in 1839. He erroneously calls it an epiphyte. No specimen seems to have been preserved.

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Pogonia carinata auct. prob. non (Roxb.) Lindl.: Gilg in Engler, Pflanzenw. O-Afr. 2, c (1895) 154. — Specimen: Peters (B, lost), Moçambique, Sofala Prov. (MS) or Gaza Prov. (SS), Beira-Braga, 1842–1848.

Note. Pogonia carinata (sometimes considered synonymous with Nervilia aragoana Gaudich.) has a leaf that is very similar to that of N. bicarinata. However, no other collection of this species is known from Moçambique.


Pogonia umbrosa Rchb. f., Kränzl. in Mildbraed, Deutsch. Zentr.-Afr.-Exp. 1907–1908, 2 (1914) 73. — Specimen: Mildbraed 2904 (B lost), Zaïre, Bunia or Mambasa zone (VIII or VI), Ituri River, between Irumu and Mawambi, “Hochwald auf der Barra barra”, end of March 1908 (flowering specimen).

Note. Probably = Nervilia bicarinata.

Pogonia thouarsii Blume, Kränzl. in Mildbraed, Deutsch. Zentr.-Afr.-Exp. 1907–1908, 2 (1914) 73. — Specimen: Mildbraed 3035 (B lost, identity uncertain), Zaïre, Mambasa zone (VI), Ituri River, between Irumu and Mawambi, at Kalonda by the road, beginning of April 1908 (leaf only).

Pogonia sp. nov. Kränzl. in Mildbraed, Deutsch. Zentr.-Afr.-Exp. 1907–1908, 2 (1914) 73. — Specimen: Mildbraed 3208 (B lost, identity unknown), Zaïre, Mambasa or Bafwasende zone (VI), Ituri River, between Mawambi and Awakubi, “Hochwald auf der Barra barra”, middle April 1908 (leaf only).

Nervilia nov. sp. Schltr., Fedde, Rep., Beih. 33 (1925) 120. — Specimen: Perrier de la Bâthie 15714 (P), Madagascar, Centre, Mt Tsaratanana, 1400 m, dry places, forest, Oct. 1922 (leaf only).

Nervilia nov. sp. Schltr., Fedde, Rep., Beih. 33 (1925) 121. — Specimen: Perrier de la Bâthie 15715 (P), Madagascar, Centre, Mt Tsaratanana, c. 1600 m, very humid places, forests with herbaceous undergrowth, Dec. 1922 (leaf only).

Nervilia sp. no. 4 Grosvenor, Excelsa 6 (1976) 84. — Specimen: Baker in SRGH 122620 (SRGH), Zimbabwe (C), Goromonzi Distr., 43 km from Harare on the road to Shamva, 11 Feb. 1961 (leaf only).

Note. Probably = Nervilia petraea.
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