AN ACCOUNT OF THE MALAY-PACIFIC SPECIES OF SELLIGUEA (POLYPODIACEAE)

P. HOVENKAMP

Rijksherbarium / Hortus Botanicus, P. O. Box 9514, 2300 RA Leiden, The Netherlands

SUMMARY

The morphology and taxonomy is discussed of the Polypodiaceous genera *Selliguea*, *Crypsinus*, *Holcosorus*, *Phymatopsis*, *Grammatopteris*, *Pycnoloma*, *Oleandropsis* and *Crypsinopsis*, based on a revision of species from Malesia and the Pacific. All these genera are merged in *Selliguea*. Fifty-two species are revised, 32 new combinations are made. See also the description of a new species on p. 108, added after the proof stage.

TAXONOMIC HISTORY AND GENERIC DELIMITATION

Early views

In the beginning was *Polypodium*. The first authors to describe any of the species included here in *Selliguea* did so in this Linnean genus (Swartz, 1801: *P. taeniatum*; Cavanilles, 1802: *P. enerve*; Poiret, 1804: *P. latifolium* = *Selliguea platyphylla*).

The genus Selliguea was erected by Bory (1824), who characterised it by the transverse coenosori, for his new species S. feei. He commemorated in this name both the innovative early 19th-century French microscopist Selligues and the systematist Fée (who provided him with the specimen, or rather, specimens, see note under S. feei). Not much later, Blume (1828, addenda et emendanda to the Enumeratio Filicum) adopted and expanded this genus, adding three coenosoroid species that he had already, in the main part of the work, described under Grammitis sect. Diagramma. Two of these four species are now included in Microsorum or Colysis (Bosman, 1991). Blume retained the species with separate sori in Polypodium.

Presl (1836) distributed the species he knew, now included in *Selliguea*, over a large number of genera. He retained *Polypodium palmatum* Blume (= *Selliguea taeniata*) in *Polypodium*. He included small, strongly dimorphic species in *Marginaria* (*Marginaria nummularifolia* = *Selliguea pyrolifolia*). He transferred *Polypodium albidosquamatum* Blume to *Pleopeltis*, on the basis of the venation pattern, which shows a row of relatively large areolae on both sides of the midrib of the pinnae. He included the species with a more finely reticulated venation pattern in *Phymatodes*, in the sections *Euphymatodes* and *Pleuridium*. He retained and expanded the genus *Selliguea*, maintaining Blume's circumscription.

Hooker (1842) adopted the name *Selliguea*, but redefined it so as to include only those species later referred to as *Colysis*. In 1864 he combined *Selliguea* with numerous other elements in *Gymnogramme*, and he retained the other selligueoid ferns in *Polypodium*.

John Smith (1841) united Presl's *Phymatodes* with *Drynaria*, distributing the species of *Selliguea* over his sections *Phymatodes* and *Dipteris*. In 1842 he adopted *Selliguea* Bory in Blume's circumscription, but noted that some of the species in this genus agreed in habit and venation with those in *Drynaria*.

Presl subsequently (1851) erected the genera Crypsinus (to accommodate Crypsinus nummularius = Selliguea pyrolifolia) and Microterus for Polypodium neglectum Blume. Microterus, however, is based on a mixture of Polypodium neglectum (Blume, first specimen cited) and Lemmaphyllum microphyllum (Meyen, PRC, second specimen cited). He transferred part of Selliguea to Colysis, but he still left Selliguea a mixture with microsoroid elements included.

Fée (?1853) largely accepted Presl's classification. He transferred Loxogramme C. Presl to Selliguea, thereby substantially increasing its heterogeneity, reduced Crypsinus again to Marginaria, raised Presl's Phymatodes section Pleuridium to generic rank, but retained most species in Drynaria. With regard to one species, Polypodium neglectum Blume, he added to the confusion already caused by Presl (1851), by transferring it to Niphobolus and at the same time redescribing it under Craspedaria as C. calva.

John Smith (1866) followed Fée and retained *Pleuridium* at the rank of genus but redefined it, leaving it a mixture of *Selliguea* and *Niphidium* in the modern sense. In 1875 he erected *Phymatopsis* to accommodate a number of species which he distinguished on basis of well-defined veins and a thickened and notched margin. In *Phymatopsis* he included mainly species of *Selliguea*, but also two species now included in *Lemmaphyllum* (Donk, 1954). He combined *Polypodium stenophyllum* with *Paragramma*.

Diels (1899) reduced most genera mentioned above to *Polypodium* section *Pleopeltis*, in a much wider sense than it had been used before. Christensen (1906) accepted this arrangement but gave *Pleopeltis* the rank of subgenus. He also recognised *Selliguea* as a separate subgenus. *Pleopeltis*, in Christensen's circumscription, was raised to generic rank by Alderwerelt (1909).

Phymatopsis J. Sm., containing mostly species here considered as *Selliguea*, was transferred wholesale to *Microsorum* by Copeland (1929), who fortunately refrained from making all the necessary combinations, and to *Phymatodes* (as a section) by Ching (1933), who did not show such restraint.

Meanwhile, various authors had described a number of strongly dimorphic species with elongated coenosori in different genera. Some small genera had been erected to accommodate a few aberrant species.

Drymoglossum rigidum Hooker (1854) was transferred to Schizolepton by Moore (1857), and to Taenitis by Copeland (1917), all on the basis of an "incorrect and misleading" (Christensen, 1929) illustration, showing a venation without included veinlets; D. brooksii Alderwerelt (1918) was later transferred by Alderwerelt himself to Grammatopteridium. This genus was described by Alderwerelt (1922, as Grammatopteris nom. illeg. non Ren.), to accommodate two more species with longitudinally elongated coenosori.

Holcosorus was established by Moore (1857) for one species with very narrow setaceous fronds (*Grammitis bisulcata* Hook.).

Finally, *Oleandropsis* was erected by Copeland (1942, 1947) to accommodate *Polypodium ferreum* Brause, on the basis of the unique radial rhizome structure of this species.

Recent views

Much of the confusion surrounding the species of *Selliguea* is caused by the failure of all 19th century authors to observe that the scales of the rhizome provide an excellent character to subdivide much of the Polypodiaceae into apparently very natural groups. Excessive reliance on the shape and position of the sori and often on fine details of the venation made them distribute the species of *Selliguea* over at least six genera, in which they were usually combined with a few unrelated species superficially similar in appearance. However, the aspect of the cell walls of the rhizome scales provides a striking diagnostic character. The distinction between 'isotoechous' (Pichi Sermolli, 1972) and 'clathrate' scales can distinguish true *Selliguea* and the microsoroid species often combined with it, as well as the elements of *Pleuridium* which belong to *Selliguea* and those which are now *Niphidium*. *Selliguea stenophylla* and *Paragramma longifolia*, *Selliguea rigida* and *Drymoglossum carnosum*, represent two other pairs of unrelated species which have been put in the same genus, but easily can be distinguished by this character.

Christensen (1929) was the first to distinguish the drymoglossoid species of Selliguea from all other species included in Drymoglossum. He distributed them between two genera, Pycnoloma and Grammatopteridium. In the first he included the species from Borneo and Malaya, in the second all species from New Guinea and the Moluccas, but also Drymoglossum brooksii from Sumatra. He could not distinguish the latter sufficiently sharply from G. costulatum. He noted that the two genera probably had quite different origins, Pycnoloma being derived from Crypsinus or Phymatopsis, Grammatopteridium from Pleuridium.

Currently accepted circumscriptions of the genera under discussion owe most of their definition to Christensen. He suggested (1929) that some of the species of *Phymatopsis* J.Sm. should be transferred to *Crypsinus* (a genus that until then had been almost universally ignored). Later (Christensen & Holttum, 1934), he distinguished a number of subgenera in *Polypodium*. These correspond to a large extent to current generic circumscriptions. He used the subgenus *Crypsinus* for the species with a single row of sori between midrib and margin; and *Leptoselliguea* to distinguish the microsoroid elements formerly included in *Selliguea*, which accordingly was left a much more natural group; he used *Phymatopsis* for the pinnately divided species. However, his subgenus *Pleuridium* still included species of *Selliguea* as well as some microsoroid species, all with separate sori in several rows between midrib and margin.

Ching (1940) raised subgenus *Selliguea* in this circumscription to generic rank. Shortly afterwards (1941) he expanded this concept of *Selliguea* by including species with one or two rows of separate sori between the lateral veins (e.g., *Polypodium platyphyllum* Sw., *P. triquetrum* Blume and *P. enerve* Cav.). Copeland (1947) did the same with *Crypsinus*, including the species formerly included in *Phymatopsis* and the selligueoid elements of *Pleuridium*. He retained *Selliguea* in Bory's original circumscription, excluding all discordant elements. He noted, however, that there existed a number of species which could not be confidently assigned to either *Crypsinus* or *Selliguea* in his circumscription. He retained only a few aberrant species in the genera *Pycnoloma*, *Grammatopteridium*, *Holcosorus* and *Oleandropsis*.

Ching (1964) transferred a large part of Copeland's *Crypsinus* to *Phymatopsis*. In *Crypsinus*, he retained "a small group of ferns." These were all small plants with only a single row of immersed sori between midrib and margin on contracted fertile leaves or on the contracted fertile upper part of the lamina. Judging by this description, this would not only include most dimorphic small species, but also *C. stenophyllus* and *C. soridens*. However, the only species Ching actually mentioned as belonging to it, other than the type (*C. pyrolifolius*), is *C. wrayi*. The remainder of Copeland's *Crypsinus* he considered to form a "very natural group", closely related to *Selliguea*, but which he did not name. Most of the species he cited here he actually had included in *Selliguea* in 1941. They comprise such diverse elements as *C. platyphyllus* and *C. oodes*.

In 1977, Pichi Sermolli emended Ching's name *Phymatopsis* to *Phymatopteris* (*Phymatopsis* J.Sm. 1875 is a later homonym of *Phymatopsis* Trevisan 1857, an ascomycete), adding no new species to it at the time. Ching's unnamed group was formally named *Crypsinopsis* by Pichi Sermolli (1977). He included six species, but noted that another five or six might belong to the genus. It is not quite clear whether these five or six unnamed species would include *C. platyphyllus* and *C. oodes*, the two most obviously discordant elements in Ching's unnamed group. They are more or less left in limbo.

As a result of all this confusion, most species of *Selliguea* not only have names in *Polypodium*, but also in *Pleopeltis* (Alderwerelt, 1909–1922), *Phymatodes* (Ching, 1933), *Crypsinus* (Copeland, 1947), *Phymatopsis* (Ching, 1964), and *Phymatopteris* (Pichi Sermolli, 1973). They have narrowly escaped being named under *Microsorum* (Copeland, 1929), and most still require names in *Selliguea*.

Current generic circumscriptions leave us with the following genera which should be accounted for:

Crypsinus: fronds simple, small, sori separate, in a single row on both sides of the midrib, main veins indistinct (Pichi Sermolli, 1977).

In this circumscription, Crypsinus contains a number of species that can easily be interpreted as reduced forms of one of the other genera. Many of the distinguishing characters between the genera are lost when the fertile fronds are reduced, as in the type species of this genus, C. pyrolifolius. It is, in fact, as easy to connect this species through a series of intermediates to an undisputed species of Crypsinopsis (C. pyrolifolius, Fig. 23 – C. whitfordii, Fig. 24 – C. hellwigii, Fig. 38 – C. enervis, Fig. 34) as it is to link it to species of Phymatopteris (via C. whitfordii – C. simplicissimus, Fig. 25 – C. rhynchophyllus – C. griffithianus). It is ironic that Ching used exactly this species to contrast Phymatopsis and Crypsinus. Apart from C. pyrolifolius, Crypsinus in this circumscription would contain dimorphic and/or reduced forms evidently allied to Crypsinopsis (C. hellwigii, C. neglecta, C. gracilipes, C. bakeri), as well as similar forms allied to Selliguea s.s. (S. lauterbachii, S. dekockii). Apart from these species, it would contain very few other species (C. soridens and C. stenophylla, possibly C. banaensis), and these are possibly allied to elements in Selliguea (e.g., to S. heterocarpa, small forms of which have frequently been mistaken for C. stenophylla).

Crypsinopsis: fronds simple, large, sori separate, in two rows between the adjacent veins, main veins distinct or not (Pichi Sermolli, 1977).

Pichi Sermolli (l. c.) stated that Crypsinopsis "in some ways may be considered as intermediate" between Selliguea and Crypsinus. It mainly contains the C. enervis-aggregate (at least the unreduced forms), C. triquetrus, C. albido-paleata and C. oodes. Ching's statement that C. platyphyllus, with sori in single rows, should also be included must be an error, as he expressly stated that the sori in this group occur in a double row between the main veins.

Selliguea: fronds simple, large, sori separate or confluent, in one row between the adjacent veins, main veins distinct (Pichi Sermolli, 1977).

This genus contains the assemblage around *S. feei* (excluding the reduced, dimorphic forms, which are included in *Crypsinus*), *S. heterocarpa* and *S. lateritia*. By the definition of Pichi Sermollis, it would also include *C. platyphylla*, but it is not clear whether either Ching or Pichi Sermolli really intended that.

Phymatopteris: fronds simple or divided, sori separate, in one row between midrib and margin, singly between adjacent veins, main veins distinct (Ching, 1964).

At first sight, this is a rather natural and homogeneous group, although there is some uncertainty about which small, simple-fronded species should be included. Some of these have traditionally been regarded as belonging to *Crypsinus* (*C. whitfordii*, *C. pyrolifolius*), some as belonging to *Selliguea* (*S. lanceola*), and some are firmly embedded in *Phymatopteris* (*P. simplicissima*, *P. rhynchophylla*). Nevertheless, there are few differences between these species (compare Fig. 23–26), and none that would justify them being distributed between three or four genera. Apart from that uncertainty, on close inspection this genus turns out to be much more heterogeneous than possibly any of the other, smaller genera. There are many more points of difference between *Phymatopteris taeniatus* and *P. albidosquamata* than there are between any two species of *Crypsinopsis*, between *Crypsinopsis triquetrus* and *Selliguea plantaginea*, or between any two species from *Pycnoloma* and *Grammatopteridium*.

Moreover, there are possibly fundamental differences in frond shape between *Phymatopteris hastata* (and a few closely related species) and most other species of the genus. *Phymatopteris hastata* is exclusively hastately divided (by the way, reduced simple forms are again almost indistinguishable from *Crypsinus*), *Phymatopteris* species are usually pinnately divided, sometimes bipinnate.

There are also several striking similarities between some representatives of *Phymatopteris* and *Selliguea*. *Phymatopteris albidosquamata* shares a number of unique characters with *Selliguea platyphylla*; *P. triloba* shares some distinctive characters with several other species of *Selliguea*, most notably *S. heterocarpa* (the character-istically sunken sori), and *S. feei* (the scales of the rhizome and the texture and anatomy of the sterile lamina).

Pycnoloma: dimorphic, small fronds, sorus longitudinal, coenosor, venation relatively simple (Christensen, 1929).

Christensen noted that *Pycnoloma* is probably an heterogeneous assemblage derived from several origins in either *Crypsinus* or *Phymatopsis*. All species included in *Pycnoloma* are small and reduced, and characters reflecting their affinity may easily have been lost.

Grammatopteridium: fronds larger and venation more complicated than in Pycnoloma, otherwise similar (Christensen, 1929).

According to Christensen (l. c.), the species of *Grammatopteridium* have a different origin from those of *Pycnoloma*. When his var. *brooksii* (which is here regarded as a species in its own right, probably allied to the *Selliguea enervis*-aggregate) is removed, all remaining species of *Grammatopteridium* are distinctly allied to *Selliguea*. The evidence for this is the sclerenchyma sheath around the vascular bundle, the very distinct hypodermises on both sides of the lamina, as well as the series of intermediates formed by *S. dekockii* and *S. lauterbachii* (Fig. 10, 11). However, due to the extreme reduction of the fertile lamina it is hardly possible to distinguish clearly between the drymoglossoid derivatives of *S. feei* and those of *S. enervis*.

Holcosorus: fronds setaceous (Copeland, 1947).

The extremely narrow fronds are the only defining character for this genus. There are several other species with similarly narrow fronds, and arguably related to quite different species of *Selliguea* (see below).

Oleandropsis: fronds dimorphic, rhizome radial, coenosorus longitudinal (Copeland, 1947).

The only distinguishing character of the one species composing this genus is the radially organised rhizome, but this is not a constant feature. In one single plant, creeping, dorsiventrally organised pieces of rhizome may be connected to erect, radially organised parts. Otherwise, this species is similar to the dimorphic representatives of the *Selliguea feei*-aggregate (*S. lauterbachii*) and to *S. (Grammatopteridium) costulata*. Similarly radially organised rhizomes occur occasionally as side shoots in another species from New Guinea (*S. tafana*).

Current view

Hennipman et al. (1990), based on a new analysis of numerous characters and species, have combined all the genera mentioned above in *Selliguea* (their omission of *Phymatopteris* from the list of synonyms was not intentional). Considering the difficulties encountered in applying any of the generic circumscriptions, this seems the best course. However, in this circumscription, the genus *Selliguea* can only with great difficulty be distinguished from *Polypodium* s.s. Hennipman et al. (l.c.) have to rely on spore characters best visible with electron microscopy (their key character, spore colour yellow in *Polypodium* vs. brown in *Selliguea*, is the best macroscopical manifestation of these differences) to distinguish the two genera. It is not clear in how far this character also can distinguish some of the more dubious species which

have not been studied here (e.g., *Polypodium erythrocarpum*, which has been placed in *Crypsinus* by Rödl-Linder, 1990, but which, in many aspects, resembles *Polypodium* closely). The distinction between *Selliguea* and *Polypodium* may improve when the discordant elements still remaining in *Polypodium* are removed.

INFRAGENERIC AND SPECIFIC DISTINCTIONS

The genus *Selliguea* in this wide sense presents a complicated picture with a large number of paralellisms and a wide variability in some species. As a consequence, it is not possible to present a phylogenetic analysis. Parsimony analysis using Hennig 86 (Farris, 1988) of a datamatrix constructed on the basis of all available morphological data resulted in large numbers of equally parsimonious cladograms, with consistency indices of approximately 0.15. Such cladograms have very little use (Hovenkamp, 1996), and are accordingly not presented here.

On the species level, I have tried to adopt a middle way between recognizing all more or less distinct forms, which would raise the number of species to over 80, and lumping all forms between which intermediates can be found, in which case the currently accepted 52 species would be reduced to less than 30. In doing so, I adopted the rank of species for all units which I want to distinguish. I have deliberately not adopted a system of infraspecific categories to reflect the close similarities within some groups of species and the various forms and variants of many species. My reasons for not using infraspecific ranks are both practical and theoretical.

A practical reason is that the names of infraspecific taxa are not indexed in any reference database, and therefore much less accessible than the names used for species. At the same time, the rules governing the nomenclature of infraspecific ranks are as rigid as, and even more complicated than, those governing the naming of species. Any infraspecific nomenclature is therefore bound to be unstable, and easily unsettled by the discovery of older names (and their corresponding autonyms) in hitherto unseen publications.

A theoretical reason is that the formal system for naming infraspecific categories uses a rigidly hierarchical system of ranks, similar in structure to that used above the species level. At the same time, it is the very essence of subspecific categories that they do not necessarily form a hierarchical system. It is implicit in nearly all species definitions that units below the species rank may exchange genes (hybridise) or merge completely, and therefore are not exclusively connected by common ancestry. The adoption of a strictly hierarchical system for units which may be connected in a much more complicated, reticulate pattern can only result in an artificial system.

Patterns of variability

There are some recurrent patterns of variability which are noteworthy.

Disjunct look-alikes

There are some strikingly parallel developments in East and West Malesia, leading to nearly indistinguishable, widely disjunct species-pairs.

The species of these pairs are, as far as can be ascertained, not closely related.

West Malesia	East Malesia
S. bakeri	S. lauterbachii
S. brooksii	S. costulata
S. neglecta	S. gracilipes

Specific distinctions breaking down in New Guinea

There are two species-pairs composed of similar, mainly sympatric, species in which the species distinctions are clear and constant over their common range, but breaking down in New Guinea, where both are rare.

One of these is the pair composed of *S. soridens* and *S. stenophylla*. The distinction between these is blurred by the occurrence of specimens sometimes considered as a separate species, *S. cyathisora*. The other pair is formed by *S. heterocarpa* and *S. lateritia*. Although formerly often confused, they can be clearly distinguished over their entire range. In New Guinea, however, the distinctions are blurred by only a few collections from widely scattered locations.

Convergence towards gramineous fronds

In several areas, gramineous forms occur which are difficult to distinguish from each other. A close comparison, involving sometimes intangible characters (such as frond texture, colour, texture of the rhizome scales), have led me to believe that many of these forms have widely different origins.

Crypsinus subfasciatus is here included in S. ceratophylla, mainly on the basis of similarities in the rhizome scales.

Polypodium taeniophyllum is here included in *S. lateritia*, with which it is joined by a series of intermediates.

Pleopeltis renifera is, both by its characters and through intermediates, obviously related to *S. enervis*, and is here included in that species.

The remaining gramineous species are retained as species.

Selliguea setacea may be be allied to S. lateritia, but it has enough constant differences to keep it apart.

The affinities of S. bisulcata are not clear. Traditionally, it was joined with S. setacea in the genus Holcosorus, but the uniting characters may all be direct consequences of the reduction in lamina width.

MORPHOLOGY AND CHARACTERS

Rhizome

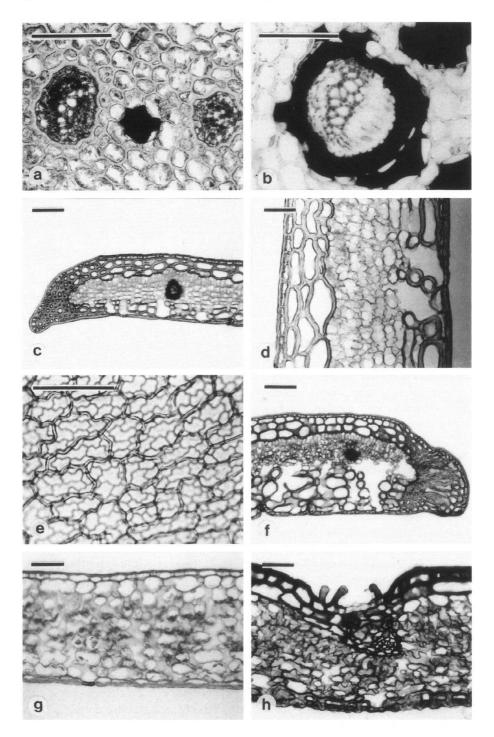
Organisation and stelar structure — In the great majority of species the rhizome conforms to the general polypodiaceous type (Hovenkamp, 1990), with a stele composed of 3-18 (more or less depending on the thickness of the rhizome) vascular strands in a single cylinder. Fronds are inserted in two alternating rows on the dorsal side, on more or less elevated phyllopodia, and roots are inserted in an irregular pattern on those parts of the rhizome that are in contact with the substrate. A differently organised rhizome occurs in *Selliguea ferrea* and in *S. tafana*. In both species parts of the rhizome are organised radially, with fronds inserted all around the rhizome, and without any roots. Both cases may represent a differentiation of the rhizome into terrestrial and aerial parts. This is most clearly demonstrated in a recently collected, sterile specimen (*Mangen 2185*). In this specimen, plants consist of leafless, horizontal rhizomes gradually turning into erect, leaf-bearing shoots. The horizontal parts are dorsiventral, with irregularly distributed buds and branches originating laterally, and roots scattered over the ventral side. The erect parts are densely leafy and rootless. The fronds are set close together, irregularly scattered all around the rhizome. They appear to develop in flushes and leave distinct but barely elevated scars. The transition from leafless to leafy parts is not abrupt: the first frond scar is often present below the last lateral bud or root.

The vascular system of the leafless parts is composed of 5–7 vascular strands, the dorsal 1–3 of which are distinctly larger than the ventral ones. Branches have a two-stranded trace, originating from two laterally placed rhizome strands. One, apparently abortive, frond trace was observed composed of three strands, originating from two rhizome strands. Roots are innervated from a single rhizome strand. The vascular system of the leafy parts has 5–7 main strands, which are all approximately equally large. Frond traces are two-stranded and innervated from two rhizome strands, but soon becoming three-stranded. Fronds may originate from any pair of adjacent rhizome strands, and are thus truly inserted on all sides of the rhizome. This arrangement of the fronds was the main character by which Copeland (1947) distinguished the monotypic genus *Oleandropsis*.

In the remaining species of *Selliguea* there is much variation in overall aspect of the rhizome, which ranges from very thin, filiform (1 mm diameter or less) to stout (1 cm or thicker), and from short, with phyllopodia contiguous, to long-trailing, with internodes up to 6 cm long. Most of the Malesian species, at least, can be assigned to one of two more or less distinct groups. One group, containing *S. enervis* and related species, has relatively thin rhizomes (up to 4 mm thick), and short internodes (up to 3 cm). The other group, containing *S. feei* and related species, has thicker rhizomes (4-12 mm) and longer internodes (2.5-6 cm).

Anatomy — Sclerenchyma occurs mostly in the form of separate strands, rarely in the form of a continuous sheath. The presence or absence of sclerenchyma strands is diagnostic for some species, but very variable in most. Usually the strands occur scattered throughout the ground tissue, but occasionally they are located in a distinct zone. This may be the area within the vascular cylinder, between the vascular strands, or a peripheral zone near the epidermis. Often the strands are smaller towards the periphery, and often the peripheral ones are distinctly periclinally flattened. The systematic value of this variation is small.

Sclerenchyma also occurs in the form of a sheath around the vascular strands (Plate 1a, b). In many species this sheath is very strongly developed and sometimes two cells thick (Plate 1b). These strongly thickened sheaths are clearly visible with the naked eye on cross sections of the rhizome. This character is often correlated with the presence of fairly thick rhizomes with long internodes in the group of *S. feei*. Outside this group, the sclerenchyma round the vascular strands is usually more weakly



developed, with the sheaths incompletely or not at all sclerified and invisible to the naked eye (Plate 1a).

Glaucescence — In many species a distinct, glaucous, waxy layer is present on the rhizome. In some species this layer is thin or indistinct but never completely absent. The most distinctly glaucous rhizomes occur in *S.archboldii*, *S.albicaula* and *S. plantaginea*, especially in specimens where the scales are sparse, and most notably in *S. glauca*, which has often very thick, waxy deposits between the rhizome scales.

Rhizome scales

Rhizome scales are highly variable in the following characters:

Margin — The margin may be entire, flabelloid, dentate, or ciliate. Scales with an entire or flabelloid margin are often thin-textured and relatively wide. This type of scales occurs in widely divergent species such as S. triquetra, S. triloba, S. feei and S. albidopaleata. In some species (S. bellisquamata. S. dekockii) they are strongly overlapping, with the flabelloid margins 'glued' together, forming a distinct hollow cylinder around the rhizome. It has been suggested (Tryon, 1985) that the hollow space below the scales may harbour ants. However, ant remains are rarely found in such places; there are no other indications that they use these spaces, and the presence of ants has never been noted by collectors. Moreover, the impression that the scales form a hollow cylinder around the rhizome may be due merely to the shrinkage of the rhizome when dry, and the hollow space may not be there at all in living plants.

Texture — The texture ranges from thin and translucent to thickened, dark, and sclerified. Particularly thick, dark scales occur in *S. albido-squamata*, *S. platyphylla* and *S. glauca*. In *S. heterocarpa*, the scales are thickened medially, but without any sclerification, resulting in a spongy texture.

Colour — The colour varies from whitish through brown to blackish. Although most scales are darkest near the point of attachment, in some species additional dark colouring may develop in other places in the form of a distinct mottling or a darker spot near the apex. Differences in colour between light to dark brown may be very striking, but are rarely of systematic significance.

Shape, size — All scales are widest near the point of attachment. In several species, the scales are very suddenly contracted into a long, subulate, squarrosely recurved acumen. In others, the acumen is relatively short and wide, with a rounded apex.

Plate 1. Rhizome and lamina anatomy; all scale bars = 1 mm. — a & b. *Rhizome anatomy.* – a: *Selliguea enervis (Iwatsuki P 1206)*, vascular strands without sclerified bundle sheath. – b: *S. triquetra (de Wilde c.s. 15281)*, vascular strand with strongly sclerified bundle sheath. — c-h. *Lamina anatomy.* – c & d: *S. plantaginea (Grant 3805)*; c: cartilaginous margin; d: strongly developed upper and lower hypodermis. – e: *S. plantaginea (Docters van Leeuwen 10945)*, upper epidermis and hypodermis in surface view. – f: *S. bellisquamata (Rau 513)*, cross section through margin notch. – g: *S. subsparsa (de Wilde c. s. 13224)*, mesophyll without distinct hypodermises. – h: *S. platyphylla (Chai S 39822)*, hydathode with ring of papillae.

In most species, however, the acumen is gradually narrowed into a narrow, but not needle-like apex. A subulate acumen is most likely a parallel development within several distinct groups: it occurs in *S. archboldii* and *S. albicaula* (related to *S. plantaginea*), in *S. stenosquamis* (related to *S. enervis*) and in *S. lateritia* and the possibly related species *S. craspedosora* and *S. bisulcata*.

Fronds

Frond dissection — Most species of Selliguea have simple fronds. A small number of species have pinnately dissected fronds, which may be lobed to 1-2 cm from the costa or less, to fully pinnate. Bipinnate fronds rarely occur, as in S. triloba, and there only in fertile fronds, which may have basal pinnae with a number of basiscopic lobes.

Shape of lamina — The majority of species have a more or less narrowly ovate to lanceolate lamina, with a length/width index ranging from three to ten, and the greatest width in the basal half. Both the base and the apex are usually variously narrowed, sometimes truncate or obtuse. Wider, orbicular to ovate shapes, with truncate to cordate bases and obtuse to rounded apices also occur, mostly in sterile fronds of strongly dimorphic species (Fig. 44–49). Occasionally (in *S. oodes, S. neglecta*) fertile fronds may also be ovate to orbicular. Narrow, gramineous fronds are the other extreme, occurring independently in several species. Other lamina shapes occur in few species. *Selliguea ceratophylla* and *S. pampolycarpa* are distinct in the very gradually narrowed lamina base, and a lamina that is widest in the upper half.

Frond dimorphism — Most simple-fronded species show some degree of fertilesterile dimorphism, with fertile parts distinctly narrower than sterile parts. In most species, this dimorphism is expressed as frond dimorphism, with different sterile and fertile fronds. In these cases, the fertile fronds, apart from being narrower than the sterile ones, are also longer and/or with longer stipes. In extreme cases this is very distinct (as in, e.g., S. lauterbachii, Fig. 11; S. pyrolifolia, Fig. 23; S. bakeri, Fig. 44; S. brooksii, Fig. 47). However, even in these strongly dimorphic species, intermediate fronds may occasionally be found in which the base is sterile and wide, and the apex forms a narrow, fertile spike. In most species, the differences between fertile and sterile fronds are less pronounced, and intermediate fronds, with a wide base narrowing to a fertile apex, are more common. This situation gradually merges into one in which all fronds are similar, with a sterile base and a often narrower fertile apex (e.g., S. whitfordii, Fig. 24). When the difference between sterile and fertile parts is pronounced (as in S. soridens), the fronds may be said to be 'internally dimorphic'. However, in these species, the degree of internal dimorphism often merely depends on the length of the sterile basal part, as the dimorphism can only be expressed when this part is long enough to be widened at all. Very short, sterile basal sections are not widened. When the apical, fertile, section of the lamina is little or not narrower than the sterile basal part, this situation merges into one in which the fronds are fully monomorphic (as in S. stenophylla).

When, on the other hand, the fertile fronds are fully fertile from the base upwards, the situation merges again into a complete dimorphism.

A complete transition between all the previous forms of frond dimorphism can be encountered in S. enervis and related species (e.g., S. subsparsa, Fig. 37, S. hellwigii, Fig. 38); and in the group of species around S. plantaginea (e.g., S. lauterbachii, Fig. 11; S. costulata, Fig. 12). When, as is frequently the case in these species, all or nearly all fronds of a collection are fertile, it is not possible to classify that specimen with regard to its type of frond dimorphism.

In the pinnately divided species (Fig. 14–22) the frond dimorphism is more or less similar, with the difference that here not frond width, but pinna width is variable, and that completely sterile fronds are relatively rare. There is only one fully dimorphic pinnate species, *S. triloba* (Fig. 22), with simple sterile fronds frequently present alongside pinnately divided fertile fronds. All other species fall in the category of monomorphic to internally dimorphic species, with a clear internal dimorphism only expressed in *S. lagunensis* (Fig. 20).

Lamina anatomy — Fronds of Selliguea usually have a peculiar, stiff-leathery texture. This is caused by two factors: an epidermis of which the cell walls are often strongly thickened, and the presence of a hypodermis. The cell walls of the hypodermis may be strongly thickened as well. It occurs usually below the upper surface, but in many species a hypodermis is also present below the lower surface (Platec, d). The hypodermis cells are usually larger than the epidermis cells. Otherwise they are similar, with a similar pattern of sinuose or straight anticlinal walls (Plate 1e). In some species, the hypodermis below the upper surface may be composed of two or three cell-layers, and each layer may have thickened cell walls (Plate 1d). As a result of these variously thickened layers, the fronds of many species are very stiff and brittle.

In many species the veins end in distinct hydathodes on the upper surface. Sometimes these are covered by a calcareous accretion. This calcareous scale is particularly large and distinct in *S. albido-squamata* and *S. platyphylla*. After the calcareous accretion has been dissolved in acid, it can be seen that in these species it was attached by epidermal papillae, around which it was deposited (Plate 1h). In other species such papillae were never found and the calcareous scales are accordingly much less persistent.

Lamina margin (Plate 1c, f) — A cartilaginous margin with 'notches' is often seen as the main diagnostic character for Selliguea. In fact, the margin may be variously developed and notches are absent from many species. In one species (S. albidopaleata), the margin is composed of a wide, flat, cartilaginous wing, which is brittle and fragile, and in many specimens eroded. There are no notches in this species near the base of the lamina, but near the apex notches are regularly present. A similar cartilaginous wing, but then totally uninterrupted by notches, is characteristic for the closely related genus Arthromeris. In several species (e.g., S. platyphylla), the margin is clearly cartilaginous and strongly thickened. In most species, the margin has a less distinct cartilaginous zone and differs from the lamina mainly in a more glossy colour, due to the absence of stomata. Almost always cross sections show a more or less strongly developed band of collenchymatous cells.

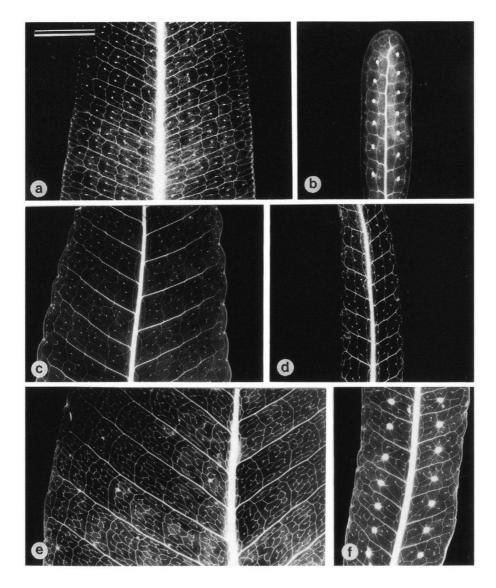


Plate 2. Venation; scale bar (for a-f) = 1 cm. — a: Selliguea albidosquamata, sterile (Lörzing 7808), predominantly excurrent veins, also in a marginal row. – b: S. neglecta, fertile (van Borssum Waalkes 2209), simple pattern with sori singly in areoles. – c: S. taeniata, sterile (Lörzing 14733), excurrent and recurrent veins more or less regularly alternating, no marginal row of excurrent veins. – d: S. albidosquamata, sterile (Meijer 612), narrow form, compare a. –e: S. triloba, sterile (Surbeck 1176), complex reticulating pattern. – f: S. taeniata, fertile (Lörzing 14733), complex pattern with sori singly between main veins.

The term 'notches' is often used (as it is here) to indicate the marginal crenulations which occur regularly in many species of *Selliguea*. In some species with very tough, brittle fronds (e.g., *S. gracilipes*), the notches extend over the lamina in the form of a short groove; in most species, however, they are only narrow restrictions on the margin, which are not structurally different from other parts of the margin (Plate 1f). I can see no clear difference between these 'notches' and the crenulations that are found on the margin of, e.g., some *Polypodium*-species.

Marginal notches occur with varying frequency. In many species they occur regularly, singly between each pair of veins. A larger number of notches, where each single one is not related to the venation, occurs among the species treated here only in *S. simplicissima*. Similarly large numbers of notches occur in *Crypsinus malacophyllus* and related species from northern India. They are there transformed into distinct marginal teeth which have no parallel in the species studied here.

Indument

Baayen & Hennipman (1987a, b) studied the laminar and receptacular indument of a small sample of species of *Selliguea*. They reported small, uniseriate, multicellular hairs on the lamina of all species studied of *Selliguea*. To the naked eye, most species are glabrous. The hairs seem to be of little systematic value in the species studied here. A distinct glandular indument is characteristic for *S. brooksii*. Small laminar scales are characteristic for *S. cretifera*. They are most frequent and persistent in the sori. In other species similar scales may be present on developing fronds, but disappear as the fronds expand.

Some species from mainland Asia are characterised by a denser cover of longer, non-glandular hairs (*Polypodium ebenipes*, *P. trisectum*), but such distinct hairs are absent from the species studied here, although they have been found in a few specimens of *S. enervis* (e.g., *Brass 13360*).

Venation (Plate 2)

Terminology — In a group where both simple and pinnately dissected species occur, the description of the venation may be confusing if the veins are numbered as usual, using the terms 'primary', 'secondary' etc. When this numbering 'from the inside outwards' is applied, veins of an apparently equivalent order are not named similarly in pinnate and in simple fronds (which may occur on a single specimen). I will use the following descriptive terms to facilitate comparison between equivalent elements. These terms are equally applicable to simple and simply pinnate fronds, and designate presumably equivalent veins in both.

Rachis — Continuation of the stipe (so named in pinnate or pinnatifid fronds only). Costa, midrib — Single central main vein of a lamina element (be it an entire lami-

na or a pinna), running parallel to the margin.

Veins, main veins — Veins running from the costa to the margin.

Connecting veins — veins connecting the main veins, thus enclosing the primary areoles.

Veinlets — Veins branching from the connecting veins, be they simple, forked or anastomosing.

Free veinlets — Ultimate, free branches of the venation pattern; in simple venation patterns these may be the same as the veinlets, in more complicated patterns they may be of a higher order.

Description — In Selliguea venation patterns are usually rather complex, but show little significant variation. In the basic pattern (Plate 2a, c-f) the veins are distinct in all but the most reduced, narrow fronds, running straight from costa to the margin. Before they reach the margin they bifurcate to form connecting veins delimiting the outer row of areoles. The other connecting veins delimitate series of mostly regular areoles, the number of which depends on the width of the lamina. Included veinlets in the areoles are simple, variously forked, or anastomosing. In some species with large fronds (Plate 2a, c, e) they form a complex net. The number of veinlets branching from the connecting veins varies from one to several. One aspect of the pattern that appears to be more or less characteristic for the genus is that if recurrent veinlets occur, they are distinctly alternating with the excurrent ones (Plate 2c). Excurrent veinlets predominate, sometimes strongly (Plate 2a), but almost exclusively recurrent veinlets occur in S. simplicissima (and in the very similar, but widely disjunct species Crypsinus rhynchophyllus). Near the margin, variable numbers of excurrent veins branch from the outer connecting vein. Sometimes they fork and anastomose to form a row of outer empty areolae (Plate 2f), in other cases (notably so in S. albido-squamata, Plate 2a) they are all free.

Depending mainly on the width of the lamina, the basic pattern is well-developed or more or less strongly simplified. In simplified patterns the veins tend to loose their distinctness, and the veinlets are fewer and less frequently anastomosing (Plate 2b). In fertile fronds, the pattern may be regular or more or less modified. Usually, the presence of sori disrupts the regularity of the connecting veins, which loose their distinct identity in a mesh of anastomosing veins (Plate 2f). Only rarely in sterile fronds are the veins not distinct but form a mesh of anastomosing veins (as in *S. soridens*).

Sori

Disposition — The disposition of the sori in Selliguea is extremely variable. Round sori, located singly between the veins and in a single row between costa and margin, characterise the pinnately divided species (Fig. 14-22) and a number of reduced simple forms (mainly belonging to the former genus *Phymatopteris*). Within Selliguea there are no transitions from this state leading to other ones. In the genus Arthromeris a similar pattern occurs in many species, but here some species show a multiplication of the number of sori leading to a state in which several rows of sori are irregularly spread between costa and margin, in irregular rows between the pairs of veins.

The remainder of the species with round sori have one to several rows between costa and margin (depending on the width of the lamina), and two rows between each pair of veins (Fig. 34, 40). There are very few species in which the sori occur in more than two rows between each pair of veins. In *S. ceratophylla* some specimens have irregular numbers of rows, in *S. albido-paleata* most specimens are characterised by a larger number of rows (Fig. 27).

Elongated coenosori occur in many species, and can be longitudinal or transverse.

Longitudinal coenosori occur in species with very narrow fertile fronds, and are always single between costa and margin (Fig. 45-48). In some species or speciesgroups (e.g., *S. murudensis-S. pseudoacrostichum*, and in *S. costulata*) intermediate fronds may have interrupted coenosori.

Transverse coenosori run from costa to margin. They always occur in large numbers on each side of the lamina, but never more than one between each pair of veins. Within the group of *S. feei* (Fig. 1–7) intermediates link transverse coenosori to a single row of separate sori. This state, in turn, can in some fronds clearly be seen to be connected to the state with two rows between each pair of veins. Especially near the lamina base, longitudinally enlarged sori are often present and sometimes replaced by two separate sori. From these transitions a distinct hierarchy can be derived, related to the hierarchy of the venation pattern. Before the sori can become confluent transversally, they must have coalesced within a single areola. Before a longitudinal coenosorus is formed, the transverse coenosori must first be condensed to a single row of sori on a narrowed lamina.

Other species with transverse coenosori are not clearly linked to species with separate sori (e.g., S. heterocarpa).

Selliguea platyphylla shows an exceptional state: it has strictly single rows of sori between each pair of veins, but no visible links to a state with two rows of sori.

Paraphyses — Baayen & Hennipman (1987a, b) studied the receptacular indument of a small sample of species of Selliguea. They report uniseriate, multicellular hairs ('paraphyses') in the sorus. From their work it appears that these hairs are of no systematic importance in the genus, and I have not studied their morphology and variability. The density of hairs within the sori varies greatly. Kato & Price (1990) suggest that, within S. enervis, the presence of paraphyses may be due to exposure and altitudinal effects. I have not seen sufficient specimens along a single altitudinal gradient to confirm or refute that observation.

Sporangia — Sporangia are stalked and glabrous, and do not seem to offer any characters of systematic value.

Spores (Plate 3)

The spores have been studied with SEM in a sample of approximately 20 from the 53 species here treated. The observed variability mainly concerns the perispore. This is composed of a thick basal layer, usually closely appressed to the exospore. It may be sculptured ('colliculate', sometimes 'rugulate') with a finer or coarser pattern. Spines or globular structures, often accreting into spines or irregular structures, are attached to the basal layer. Such spines or globules occur in very different sizes and densities. The density is often higher near the ends of the spore or at the laesura. In some cases there are visible transitions between globules and the sculpture elements of the basal layer.

Because of the scarcity of ripe spores in many species a full survey of spore sculpture was not attempted. The systematic value of these characters could therefore not be exhaustively evaluated, but it seems to be limited. Roughly, three groups of species can be recognised. A group consisting of species close to *S. enervis* is character-

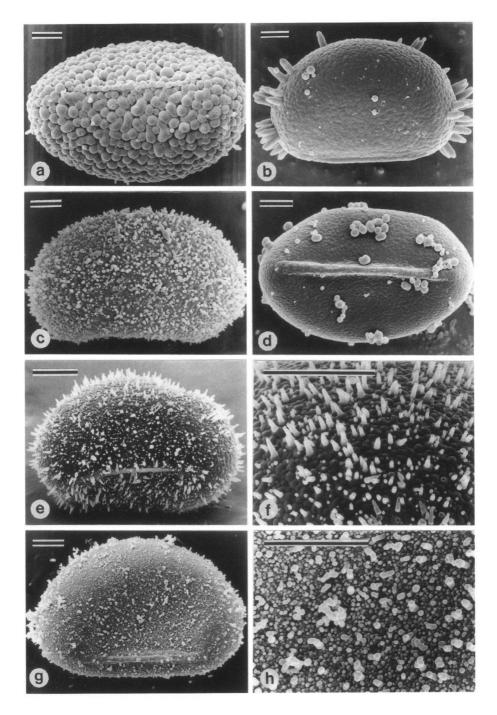


Plate 3. Spores; all scale bars = $10 \mu m$. — a: S. soridens (Hennipman 5294), strongly sculpted spore wall with very few globules. – b: S. simplicissima (van Balgooy 1484), with large perisporal spines concentrated at the narrow ends. – c: S. plantaginea (Croft 1406), perisporal spines and globules dense, all over the surface. – d: S. costulata (Croft 1963), perisporal globules sparse, agglomerating. – e & f. S. lateritia (de Vogel 8496); e: perisporal spines dense, all over the surface; f: detail. – g & h: S. pseudoacrostichum (Surbeck 683); g: perisporal globules dense, small, all over the surface; h: detail, showing aggregated and single globules.

ised by the presence of a large number of small elements on the perispore. A second group, consisting of species around *S. plantaginea* and the species formerly included in *Phymatopteris*, has fewer, but distinctly larger elements. A third, small group of species around *S. soridens* appears to have very few, large elements. However, within these groups there appears to be a considerable variability, and they probably will not stand closer scrutiny.

TAXONOMIC TREATMENT

SELLIGUEA

- Selliguea Bory, Dict. Class. d'Hist. Nat. 17 (1825) pl. 41; Blume, Enum. Pl. Javae (1827), Addenda et emendanda; C. Presl, Epim. Bot. (1851) 145; T.Moore, Index Filic. (1857) lxvi; J.Sm., Hist. Fil. (1875) 101; Ching, Sunyatsenia 5 (1940) 260; Copel., Gen. Fil. (1947) 209; Holttum, Revis. Fl. Malaya 2, sec. ed. (1954) 156; Copel., Fern Fl. Philipp. (1960) 507; Hennipman et al. in Kramer & Green, Fam. & Genera of Vasc. Pl. (1990) 214. Type: Selliguea feei.
- Crypsinus C. Presl, Epim. Bot. (1851) 123; Copel., Gen. Fil. (1947) 205; Holttum, Revis. Fl. Malaya 2, sec. ed. (1954) 193, f. 96-103; Copel., Fern Fl. Philipp. (1960) 500; Ching, Acta Phytotax. Sin. 9 (1964) 181. Type: Crypsinus nummularius (nom. superfl. for Polypodium pyrolaefolium Goldm. = Selliguea pyrolifolia).
- Holcosorus T. Moore, Index Filic. (1857) xxix; Ching, Sunyatsenia 5 (1940) 265; Copel., Gen. Fil. (1947) 208. Type: Grammitis bisulcata (= Selliguea bisulcata).
- Phymatopsis J. Sm., Hist. Fil. (1875) 104; H. Ito, J. Jap. Bot. 9 (1935) 98; Ching, Acta Phytotax. Sin. 9 (1964) 181, nom. illeg., non Trevisan. — Phymatopteris Pichi Serm., Webbia 28 (1973) 460. — Type: Polypodium palmatum (= Selliguea taeniata).
- Grammatopteris Alderw., Bull. Jard. Bot. Buitenzorg III, 5 (1922) 317, pl. 15, nom. illeg., non Renault (1892), fossil. — Grammatopteridium Alderw., Nova Guinea 16 (1924) 24; C. Chr., Dansk Bot. Ark. 6 (3) (1929) 80, pl. 8, f. 7; 11, f. 1; Ching, Sunyatsenia 5 (1940) 261; Copel., Gen. Fil. (1947) 208. — Lectotype (Christensen, 1929): Grammatopteridium brooksii (= Selliguea brooksii).
- Pycnoloma subg. Eupycnoloma C.Chr., Dansk Bot. Ark. 6 (3) (1929) 75, pl. 8, f. 1, 2; pl. 9, f. 2; pl. 10, f. 1, 1. Pycnoloma, Holttum, Revis. Fl. Malaya 2, sec. ed. (1954) 207, f. 109; Ching, Sunyatsenia 5 (1940) 261; Copel., Gen. Fil. (1947) 207. Type: Pycnoloma rigidum (= Selliguea rigida).
- Pycnoloma subg. Pleuripteris C. Chr., Dansk Bot. Ark. 6 (3) (1929) 76, pl. 8, f. 4–6, pl. 10, f. 4. Type: Pycnoloma murudense (= Selliguea murudensis).
- Oleandropsis Copel., Univ. Calif. Publ. Bot. 18 (1942) 226; Gen. Fil. (1947) 208. Type: Oleandropsis ferrea (= Selliguea ferrea).
- Crypsinopsis Pichi Serm., Webbia 31 (1977) 240. Type: Polypodium triquetrum (= Selliguea triquetra).

Epiphytic, epilithic, or terrestrial small to medium-sized ferns. Rhizome creeping, short to long-trailing, dorsiventral, with two alternating dorsal rows of phyllopodia, slightly to strongly glaucous, densely set with persistent or occasionally deciduous scales. Anatomy: ground tissue parenchymatous, often with black sclerenchymatous strands, rarely peripherally sclerified, vascular strands with an unsclerified to very strongly sclerified, sometimes two cells thick, sheath. Rhizome scales basifixed, pseudopeltate to peltate, appressed to squarrose, very variable in shape and texture, margin entire to long-ciliate. Fronds monomorphic or dimorphic, more or less distinctly differentiated in stipe and lamina. Lamina simple, pinnatifid to pinnate, the fertile parts usually narrowed, texture thin- to thick-leathery, sparsely set with inconspicuous short glandular hairs on both sides, upper surface often with hydathodes, margin often with a thickened, cartilaginous border, rarely with a flat, wide, cartilaginous border, with or without notches. Venation: at least one row of closed areolas present, usually with excurrent and recurrent included free veinlets, free veinlets rarely only excurrent, or absent, margin with few to many excurrent free veinlets. Anatomy: stomata on abaxial surface only, polo- and copolocytic, usually flush with the epidermis or very slightly sunken; epidermis both adaxially and abaxially with not to very strongly thickened cell walls; mesophyll usually differentiated in palisade and spongy parenchyma, rarely consisting of spongy parenchyma only, often with a distinct hypodermis on adaxial side, frequently with a distinct hypodermis-like layer on abaxial side as well. Sori 1-5 mm across in smallest diameter, round or elongated, superficial to deeply sunken in pits forming distinct pustules on the adaxial surface, 1 or 2 (rarely more) in each areole, in 1-many rows between midrib and margin, in the latter case forming distinct single or double rows between the adjacent veins, sometimes forming many transverse coenosori, sometimes single longitudinal coenosori. Sporangia of the normal Polypodiaceous type, stalked, glabrous, intermixed with highly variable numbers of uniseriate paraphyses. Spores brown, monolete, bilateral, smooth to colliculate, dotted with spines or globules in varying densities.

Distribution – India to Japan, throughout Malesia, in the Pacific extending to Fiji and Australia (Queensland). See also the note below.

Note – There is one record of *Selliguea* from Madagascar, described by Baker as *Polypodium melleri*. It is based on a single, detached frond (K) purportedly collected by Meller in Anamalazoatra Forest. As far as can be seen, it is identical to forms of *Crypsinus hastatus* from Japan. On the basis of this single specimen, the presence of *Selliguea* on Madagascar cannot be taken as established.

KEY TO THE MALAY-PACIFIC SPECIES OF SELLIGUEA

Notes -1. In the following keys and descriptions, the number of vascular strands and sclerenchyma strands given always refer to the strands in the rhizome. In mounted specimens, these can usually be observed by making an oblique cut through a piece of rhizome with a sharp razor.

2. To observe the attachment of rhizome scales, a few scales should carefully be prized off and observed with a binocular microscope. When the scales are very brittle they may break off above the point of attachment. To avoid this, a light wetting with a strong detergent is usually sufficient to reduce the brittleness.

3. Hydathodes should be looked for on the upper (adaxial) surface of the lamina, with good illumination. In poor light, they may easily be confused with fungal or other infections, which are very common in many fronds.

4. Except for size measurements, all characters of the lamina are described for sterile fronds or parts of fronds, for fertile fronds only if they are distinctly different. Index values refer to length/width proportions.

5. Venation. Veins of a certain order are stated to be 'distinct' if their course is visible in the pattern of the upper epidermis cells. In all cases, it is implicit that veins of a lower order are also distinct, and veins of a higher order are not.

	Sterile or fertile fronds simple or trilobed 2
	Sterile or fertile fronds pinnately divided
2a.	Fertile fronds or portions of the lamina very narrow, strongly contracted, sterile
	fronds wider
b.	Fertile fronds or portions of the lamina similar to sterile or somewhat narrower,
	or all fronds equally narrow, gramineous
	Coenosori present 4
	Sori round, elongate or confluent, not forming continuous coenosori 11
4a.	Coenosori transverse (sori confluent across tertiary veins)
	31. S. heterocarpa
	Coenosori longitudinal (sori confluent across veins) 5
5a.	Rhizome scales contracted to a narrow acumen; coenosori deeply sunken
_	49. S. rigida
	Rhizome scales acute; coenosori superficial
6a.	Rhizome scales pseudopeltate; margin of sterile fronds without notches
_	48. S. metacoela
b.	Rhizome scales peltate; margin of sterile fronds with notches sporadically pres-
_	ent, or notches regularly present
	Vascular strands without fully sclerified bundle sheath
	Vascular strands with fully sclerified bundle sheath, sometimes 2 cells thick 9
8a.	Sclerenchyma strands mainly central; hydathodes infrequent or frequent
·.	51. S. murudensis
	Sclerenchyma strands scattered; hydathodes absent 50. S. brooksii
9a.	Rhizome radial (at least in parts); sclerenchyma strands absent to many; sterile
	fronds narrow, index 6–18 14. S. ferrea
b.	Rhizome dorsiventral; sclerenchyma strands numerous; sterile fronds mostly
• •	wider, index 2–7
10a.	Rhizome with subperipheral sclerified sheath; rhizome scales broad, 1.8-3 mm
	wide, with a flabelloid, irregular margin 11. S. dekockii
b.	Rhizome lacking a subperipheral sclerified sheath; rhizome scales narrow, 1–1.5
	mm wide, remotely and weakly to strongly dentate
	(3) Sori deeply sunken
	Sori superficial or slightly sunken
12a.	Rhizome with 11-14 vascular strands; rhizome scales with a lighter margin;
-	stipe of fertile fronds 14-50 cm long; at least the main veins distinct; walls of
	epidermis strongly thickened 22. S. triloba (simple forms)

b.	Rhizome with 4 vascular strands; rhizome scales evenly coloured; stipe of fer-
	tile fronds 0.5-6 cm long; primary vein only distinct; walls of epidermis weakly
	thickened 29. S. soridens
13a.	Vascular strands with fully sclerified bundle sheath, sometimes 2 cells thick 14
	Vascular strands without fully sclerified bundle sheath
14a.	Sori in 2-4 rows between costa and margin (type, Celebes) . 4. S. caudiformis
b.	Sori in one row between costa and margin 15
15a.	Rhizome scales broad, 1.8-3 mm wide, entire, irregularly flabelloid; rhizome
	with subperipheral sclerified sheath 11. S. dekockii
b.	Rhizome scales narrower, to 1.5 mm wide, dentate; rhizome lacking a subpe-
	ripheral sclerified sheath 16
16a.	Fertile fronds shorter than sterile ones; sori large, spreading over the areole,
	covered with persistent scales; rhizome scales short-dentate 6. S. tafana
b.	Fertile fronds usually longer than sterile ones; sori smaller, not spreading over
	the entire areole, without persistent scales; rhizome scales strongly dentate or
	long-ciliate
17a.	Notches in fertile fronds regularly present; rhizome elongated, internodes 2.5-3
	cm long 12. S. lauterbachii
b.	Notches in fertile fronds absent; rhizome little elongated, internodes 0.5-2 cm
	long 47. S. bakeri
18a.	Sclerenchyma strands few 19
b.	Sclerenchyma strands many to numerous
	Sori in two or more rows between costa and margin, in two rows between ad-
	jacent veins (some forms, New Guinea, Milne Bay Prov.) 37. S. enervis
b.	Sori in one row between costa and margin, sori single between adjacent veins
	23. S. pyrolifolia
	Sori often elongate or confluent 21
b.	Sori round, not elongate or confluent 23
21a.	Rhizome scales strongly dentate; sclerenchyma strands scattered in the rhizome;
	sori large, elongate, all separate 47. S. bakeri
b.	Rhizome scales remotely and weakly dentate to short-dentate; sclerenchyma
	strands mainly central in the rhizome; sori small, separate, confluent or forming
	an interrupted coenosorus 22
22a.	Lamina of fertile fronds 3-6 mm wide; sori separate or elongate, but not con-
	fluent across the veins
b.	Lamina of fertile fronds 2–3 mm wide; sori often crossing the veins
	51. S. murudensis
	Hydathodes absent; rhizome scales strongly dentate 39. S. subsparsa
b.	Hydathodes frequent; rhizome scales remotely and weakly to short-dentate (Bor-
.	neo: 'kamborangana') 37. S. enervis
	(2) Hydathodes frequent
	Hydathodes absent or infrequent
	Margin of sterile fronds with notches frequent
	Margin of sterile fronds with notches absent or infrequent
	Vascular strands 3 or 4
b.	Vascular strands 5 to many29

27a.	Fertile parts similar to sterile part; rhizome lacking sclerenchyma strands
b.	Fertile parts narrowed; rhizome with few sclerenchyma strands
28a.	Sori in 2-many rows between costa and margin, in two rows between adjacent
	veins (New Guinea: form from Milne Bay Prov.) 37. S. enervis
b.	Sori in one row between costa and margin, singly between adjacent veins (sori
0.	2 between adjacent veins: see 40. S. hellwigii)
202	Sori in two, sometimes more rows between adjacent veins
	Sori in one row between adjacent veins
	Sori in 5 or more rows between costa and margin, with a slight but distinct rim
50 a .	around the receptacle; rhizome with fully sclerified, rarely 2 cells thick, bundle
	sheaths around the vascular strands, lacking sclerenchyma strands
	27. S. albidopaleata
D.	Sori in one to 4 rows between costa and margin, without a rim around the re-
	ceptacle; rhizome without fully sclerified bundle sheaths around the vascular
	strands, with many sclerenchyma strands
31a.	Rhizome scales entire; lamina with flat, somewhat recurved margin
b.	Rhizome scales remotely and weakly dentate to short-dentate; lamina with thick
	margin, usually not recurved (unusual forms, New Guinea, Celebes)
32a.	Rhizome scales obtuse (form from Flores, often trilobed) 1. S. feei
b.	Rhizome scales acute or contracted to a narrow acumen
33a.	Sori in 5 or more rows between costa and margin; hypodermis below upper sur-
	face distinct, consisting of a single or double layer
b.	Sori in one row between costa and margin; hypodermis below upper surface ab-
	sent or indistinct
34a.	Sori deeply sunken; hydathodes with conspicuous, persistent calcareous scales;
-	rhizome scales contracted to a narrow, ciliate acumen; lamina margin very strong-
	ly thickened; notches in fertile fronds regularly present 8. S. platyphylla
b.	Sori superficial or slightly sunken; hydathodes without persistent scales; rhizome
0.	scales acute, entire or remotely and weakly dentate; lamina margin not very
	strongly thickened; notches in fertile fronds absent or sporadically present (form
	from Ceram)
250	Rhizome scales pseudopeltate; rhizome short, over 5 mm thick, with 10 or more
JJa.	vascular strands
۲	Rhizome scales peltate; rhizome more slender, 1–3 mm thick, vascular strands
0.	-
~	5-8
36a.	Free veinlets mainly recurrent; veins on upper surface not raised; rhizome $2-3$
	mm thick (Australia) 25. S. simplicissima
b.	Free veinlets mainly excurrent; veins on upper surface raised; rhizome 1-1.5 mm
	thick (Philippines) 24. S. whitfordii
	(25) Sori in two, rarely more, rows between adjacent veins
	Sori in one row between adjacent veins
38a.	Rhizome scales usually appressed, broad, 2-3 mm wide, entire

b.	Rhizome scales usually spreading, narrow, to 1 mm wide, dentate
	37. S. enervis
39a.	Vascular strands without fully sclerified bundle sheath
	Vascular strands with fully sclerified bundle sheath, sometimes 2 cells thick 41
	Rhizome scales strongly dentate or long-ciliate; sori round; hydathodes with per-
1041	sistent calcareous scales 15. S. albidosquamata (simple forms)
h	Rhizome scales remotely and weakly dentate; sori confluent or forming some-
0.	times interrupted coenosori; hydathodes without persistent calcareous scales
41 a	Rhizome scales contracted to a narrow acumen
	Rhizome scales obtuse or acute
	Sclerenchyma strands absent
	Sclerenchyma strands present, few to very many
	Sori occasionally confluent or in short coenosori; epidermis on lower surface with
ч .у ц .	strongly to very strongly thickened cell walls (Philippines, Ternate)
	4. S. caudiformis
h	Coenosori usually long, sometimes interrupted; epidermis on lower surface with
υ.	weakly thickened cell walls 1. S. feei (typical form)
110	Rhizome with mainly peripheral sclerenchyma strands (form from Flores, often
44 a.	trilobed)
Ь	Rhizome with scattered, or mainly central sclerenchyma strands
	Coenosori interrupted or continuous, characteristically spaced and not com-
4Ja.	pletely covering the lamina when old (Fiji)
Ь	Sori separate or confluent, usually in 5 or more rows between costa and margin,
υ.	often a single row of sori along the costa slightly separate from the others, sori
	often contiguous across veins when old (Philippines, Moluccas)
160	(24) Sori singly or in one row between adjacent veins (if unclear follow this
40a.	lead)
Ь	Sori distinctly in two or more rows between adjacent veins
	Rhizome scales obtuse, usually appressed
	Rhizome scales obtuse, usually appressed
40a.	Rhizome scales concolorous or nearly so, strongly overlapping and completely
	covering the rhizome, often with the margins strongly adhering to each other (forms from Celebes and the Moluccas) 10. S. bellisquamata
L	
D.	Rhizome scales bicolorous, with a central or apical dark spot, usually separate,
40.	not adhering to each other
49a.	Lamina narrow, index 4–18; sori usually distinctly costal, not reaching the mar-
	gin; rhizome scales persistent, covering the rhizome, flat or with slightly cucul-
	late apex (New Caledonia) 26. S. lanceola
D.	Lamina usually broader, index 1.6-6.4; sori extending to the margin; rhizome
	scales sparsely set (most conspicuously on older parts of the rhizome), with dis-
5 0-	tinctly cucultate apex (New Guinea) 5. S. plantaginea
	Sori deeply sunken
D.	Sori superficial or slightly sunken

51a.	Sori in 2 or more rows between costa and margin; main veins distinct
	Sori in one row between costa and margin; primary vein only distinct 52 Fertile parts similar to sterile part; notches absent or sporadically present
b.	Fertile parts narrowed; notches in fertile fronds regularly present
53a.	Fronds gramineous, less than 2 mm wide (gramineous form from New Guinea)
	Fronds not gramineous, over 3 mm wide 54
54a.	Rhizome without fully sclerified bundle sheath around the vascular strands 55
b.	Rhizome with fully sclerified, often 2 cells thick bundle sheath around the vas- cular strands
559	Rhizome scales contracted to a narrow subulate acumen; notches absent 56
	Rhizome scales acute; notches sporadically or regularly present
	Sori in one row between costa and margin, close to the margin; primary vein
204	only distinct
b.	Sori in 2 or more rows between costa and margin, or in usually interrupted coe-
	nosori; main veins distinct
57a.	Medium-sized plants, lamina of fertile fronds 14-22 cm long; main veins dis-
	tinct; sori in 2–4 rows between costa and margin; rhizome scales pseudopeltate
	32. S. sri-ratu
b.	Small plants, lamina of fertile fronds 2.5-7 cm long; primary vein only distinct;
	sori in one row between costa and margin; rhizome scales peltate
58a.	Rhizome scales appressed (Luzon) 2. S. elmeri
b.	Rhizome scales spreading or squarrose 59
59a.	Stipe of fertile fronds 10-26 cm long 60
	Stipe of fertile fronds 2–10 cm long 61
	Hydathodes infrequent (Fiji) 3. S. feeoides
	Hydathodes absent 5. S. plantaginea
61a.	Fertile fronds narrow, index 13.4-14.0; rhizome scales squarrose, sparsely set
	and not fully covering the glaucous rhizome
b.	Fertile fronds wider, index 3.3-10.0; rhizome scales densely set, fully cover-
	ing the glaucous rhizome
	Sori in 2 or more rows between costa and margin
	Sori in one row between costa and margin
	Sclerenchyma strands absent (form from Tahiti) 5. S. plantaginea
b.	Sclerenchyma strands present to numerous
64a.	Rhizome scales with a narrow, subulate acumen and a lighter margin; coenosori
	always continuous
b.	Rhizome scales with a wide acumen, often with irregular dark spots; coenosori
	often interrupted or sori separate (form from New Guinea) 5. S. plantaginea
	Sclerenchyma strands absent (form from Tahiti) 5. S. plantaginea
b.	Sclerenchyma strands present to numerous

66a.	Rhizome scales contracted to a subulate acumen with a light margin; margin of sterile fronds with sporadically to regularly present notches
b.	Rhizome scales with a wide acumen, evenly coloured or with irregular dark
0.	spots; margin of sterile fronds without notches
67.	(46) Sori in one row between costa and margin
	Sori in 2 or more rows between costa and margin
68a.	Margin of fronds without notches; rhizome scales contracted to a subulate
	apex
b.	Margin of fronds with notches sporadically to regularly present; rhizome scales
	acute, apex not subulate
69a.	Rhizome scales pseudopeltate 35. S. setacea
b.	Rhizome scales peltate
70a.	Sterile fronds 0.6-1 cm wide, fertile fronds or portions of lamina narrowed;
	rhizome scales evenly coloured 34. S. craspedosora
b.	All fronds 0.1–0.2 cm wide, fertile fronds or portions of lamina similar to ster-
0.	ile; rhizome scales with a lighter margin
710	Rhizome scales pseudopeltate; internodes not elongated ('subfasciata')
/1a.	
1.	Rhizome scales peltate; internodes distinctly elongated
	Margin cartilaginous, strongly thickened (New Guinea) 41. S. gracilipes
	Margin not differentiated to cartilaginous, but not strongly thickened 73
73a.	Rhizome scales strongly dentate; sclerenchyma strands mainly central in rhi-
	zome
b.	Rhizome scales remotely and weakly or short-dentate; sclerenchyma strands
	scattered in rhizome
74a.	(67) Lamina very gradually narrowed to the stipe, more or less spathulate, wid-
	est at or above the middle
b.	Lamina distinct from the stipe, mostly lanceolate, widest at or below the mid-
	dle
759	Rhizome scales pseudopeltate; costa flat or with low ridges on upper surface
75a.	43. S. ceratophylla
L	Rhizome scales peltate; costa with two distinct, narrow ridges on upper surface
U.	44. S. pampolycarpa
-	
76a.	Rhizome scales strongly dentate (Sumatra; some forms of 37. S. enervis from
	New Guinea may also key out here) 39. S. subsparsa
	Rhizome scales entire to short-dentate
77a.	Rhizome scales squarrose, contracted to a narrow acumen
b.	Rhizome scales not squarrose, acute
78a.	(1) Fertile fronds or portions of lamina strongly contracted
	Fertile fronds or portions of lamina similar to sterile or slightly narrowed 80
	Sori superficial; fronds pinnate; sterile fronds normally absent; hydathodes fre-
	quent
b	Sori deeply sunken; fronds pinnatifid; sterile fronds regularly present, simple or
0.	pinnatifid; hydathodes absent or infrequent
	r

Taxonomic arrangement

The species are arranged according to their morphological affinities. This linear arrangement is purely for convenience, to facilitate comparison of species that may easily be confused. It can in no way be interpreted as an infrageneric classification showing affinities.

1. Selliguea feei Bory — Fig. 1

- Selliguea feei Bory, Dict. class. d'Hist. Natur. (1825) pl. 41 (see note 2 for dating of this plate); Blume, Enum. Pl. Javae (1828) Addenda; Fl. Javae Filic. (1829) 123; C.Presl, Epim. Bot. (1851) 145; T. Moore, Index Filic. (1857) lxvi; J. Sm., Hist. Fil. (1875) 102; Copel., Gen. Fil. (1947) 209; Fern Fl. Philipp. (1960) 507. — Polypodium feei Mett., Farngatt. I. Polypodium (1857) 110; Alderw., Malayan Ferns (1908) 675; Backer & Posth., Varenfl. Java (1939) 199. — Pleopeltis feei Alderw., Bull. Dép. Agric. Indes Néerl. 27 (1909) 12; Malayan Ferns, Suppl. 1 (1916) 405. — Type: Leschenault s. n., s. d. (P), Java.
- Grammitis vulcanica Blume, Enum. Pl. Javae (1828) 118 (corrected in Addenda to Selliguea feei).
 Polypodium feei (Bory) Mett. var. vulcanicum Alderw., Malayan Ferns (1908) 676. Pleopeltis feei var. vulcanica Alderw., Bull. Dép. Agric. Indes Néerl. 27 (1909) 12. Type: Blume s. n. (L), Java, Gedeh.

Rhizome. Diameter 3–8 mm, internodes to 4.5 cm long. Vascular strands 10–13, bundle sheath fully sclerified. Sclerenchyma strands absent. Ground tissue not sclerified. *Rhizome scales:* peltate (rarely pseudopeltate); appressed to spreading (more



Fig. 1–4. The Selliguea feei-complex in Malesia. – 1. S. feei Bory. – 2. S. elmeri (Copel.) Ching. – 3: S. feeoides Copel. – 4. S. caudiformis (Blume) J. Sm. – Scale bars = 1 cm.

often); $5-6.5 \times 1.5-2.5$ mm; obtuse to acute (mostly); brown; evenly coloured; entire to (rarely) remotely and weakly dentate. *Frond dimorphy.* Sterile fronds regularly present. Fertile parts narrowed. *Fertile fronds.* Simple. Stipe 4-30(-55) cm long. Lamina $7-25 \times 2-7$ cm, index 3.1-7.7, widest at 0.3-0.5 from base. *Sterile fronds.* Simple. Stipe 2.5-45 cm long. Lamina $5-31 \times 2-10$ cm, index 2.2-2.8, widest at 0.2-0.4 from base. Main veins on upper surface raised or not, distinct; veinlets free and anastomosing; free veinlets excurrent and recurrent. Hydathodes frequent, calcareous scales not persistent. Margin cartilaginous, thickened; without notches or notches sporadically present. *Anatomy.* Upper surface: walls of epidermis weakly thickened; hypodermis a double layer, cell walls not thickened. Lower surface: walls of epidermis weakly thickened; hypodermis distinct. *Sori:* Mostly confluent across connecting veins into interrupted transverse coenosori; in one row between adjacent main veins; 3-5 mm across; superficial. Selected illustrations — Blume (1829): pl. 51, 56 (as *Polypodium vulcanicum*). Distribution — Sumatra, Java, Lesser Sunda Islands.

Ecology — Epiphytic or epilithic, in forest, in open heath or between rocks, on cliffs, roadsides etc. Especially abundant near craters, where it is one of the few plants resistant to volcanic fumes. Altitude 900–3150 m.

Notes on variability — Several specimens from Flores have regularly trilobed fronds, a regularly notched margin and sclerenchyma strands in the rhizome. Similarly trilobed forms occur sporadically in Java, but are much more rare, and with a much lower proportion of trilobed fronds per collection.

The sori are rarely interrupted, and very rarely do fertile fronds have a distinct row of costal sori, as in *S. caudiformis*.

Notes — 1. Selliguea feei is the type of the genus.

2. Date of publication. The exact date of publication is usually given as 1824. However, the combination *Selliguea feei* was not made by Bory in 1824, but probably in 1825. In 1824 (Dictionnaire Classique d'Histoire Naturelle 6: 587–588), Bory gives the following text: "Nous proposons encore aux dépens des Polypodes les trois genres suivants: (...) 3. *Selliguea*, ... sores solitaires disposées en une seule ligne, épaisse, oblongues et parallèle ... deux nervures placeés ... une égale distance l'une de l'autre. C'est au sagace inventeur du meilleur des microscopes que nous dédions (...) Nous n'en connaissons qu'une espèce ... feuilles simples; elle nous a été communiquée par Fée, qui pense l'avoir reçue de Java." The combination S. *feei* appears validly only in Vol. 17, which is dated 1831 on the title page.

However, in 1828 Blume (Enumeratio Pl. Javae, addenda et emendanda) refers not only to Bory's text in Vol. 6, but also to his illustration: "Dict. Class. VI, p. 588. Fasc. VII. fig. 10." Apparently, then, this particular illustration was distributed together with Fasc. VII. In the introductions to Vol. XVI (final text volume) and Vol. XVII (illustrations), Bory explains that he distributed the plates unnumbered, in order to allow the reader to have them bound in their proper order afterwards. In Vol. XVII, the plate of *S. feei* was finally given the number 42. The text on the plate itself gives the name *Selliguea feei* Bory. Thus, although in Vol. VI the combination is not published, it is validly published on the unnumbered plate, which probably accompanied Vol. VII, dated 1825.

3. Typification. The left-hand sterile frond on the plate on which *S. feei* is first validly published (see note 1) is *S. platyphylla*, as is the illustrated rhizome scale. The type specimen (*herb. Bory 5829*, P) is annotated: "Donnée par Fée, comme de Java." It consists of 2 fronds. The left-hand frond has a small piece of rhizome attached, it obviously is a sterile frond (not quite fully expanded) of *S. platyphylla*. The right-hand frond has no rhizome, and the observable characters are consistent with *S. feei* from Java.

There is another specimen in P marked "Selliguea feei Bory, Type" in Fée's hand. It was collected by Leschenault (658) in Java. It is a complete specimen of S. feei (Java form), and corresponds exactly with the right-hand frond of the type specimen. This confirms that the collector of the type specimen was Leschenault, and the location was indeed Java.

4. Selliguea feei is here taken in a restricted sense. It is part of an close-knit aggregate of mainly allopatric species: Selliguea feei: Sumatra to Flores. – S. elmeri: Luzon. – S. caudiformis: Philippines, Celebes, Moluccas. – S. feeoides: Vanuatu to Pacific. – S. plantaginea and related species (see under S. plantaginea): New Guinea to Pacific. – Intermediate forms may be found between any two of these species.

The differences between S. feei and each of these species are discussed under the separate species.

2. Selliguea elmeri (Copel.) Ching - Fig. 2

Selliguea elmeri Ching, Sunyatsenia 5 (1940) 260; Copel., Fern Fl. Philipp. (1960) 508. — Polypodium elmeri Copel. in Perkins, Fragm. Fl. Philipp. 3 (1905) 191; Alderw., Malayan Ferns (1908) 675. — Pleopeltis elmeri Alderw., Bull. Dép. Agric. Indes Néerl. 27 (1909) 12; Malayan Ferns, Suppl. 1 (1916) 405. — Selliguea feei var. elmeri Tagawa, Acta Phytotax. Geobot. 16 (1956) 78. — Type: Elmer 6547 (B, UC), Philippines, Luzon, Santo Tomas.

Rhizome. Diameter 4-6 mm, internodes to 1.5-3.5 cm long. Vascular strands 8-11, bundle sheath fully sclerified. Sclerenchyma strands few to many; mainly around the vascular cylinder; isodiametric; massive or (rarely) hollow. Ground tissue not sclerified. *Rhizome scales:* peltate; appressed; $3.5-6 \times 1.6-3.4$ mm; acute; brown (with a large dark spot at the attachment); evenly coloured or with a lighter margin; entire to remotely and weakly dentate (sometimes irregularly lacerate). Frond dimorphy. Sterile fronds regularly present. Fertile parts narrowed. Fertile fronds. Simple. Stipe 14-30 cm long. Lamina $7-13 \times 1.9-3.5$ cm, index 2-4.7, widest at 0.2-0.4 from the base. Sterile fronds. Simple. Stipe 3.5-27 cm long. Lamina $5.5-14 \times 4-12.3$ cm, index 1.4-2.3, widest at 0.3-0.4 from base. Base mostly truncate, apex rounded, rarely acute. Main veins on upper surface not raised, distinct. Hydathodes absent. Margin cartilaginous, thickened; notches regularly present, in fertile fronds absent to sporadically present. Anatomy. Upper surface: walls of epidermis weakly thickened; hypodermis a double layer, cell walls thickened. Lower surface: walls of epidermis weakly thickened; hypodermis distinct. Sori: in transverse coenosori; confluent across connecting veins; singly between adjacent main veins; 3 mm across; superficial.

Distribution — Philippines: northern Luzon.

Ecology - Epiphytic or epilithic, in pine forests. Altitude 1500-2250 m.

Note — A fairly distinct segregate of the *Selliguea feei*-complex, with a restricted distribution. The shape of the lamina is characteristic, with an abruptly contracted base and a rounded apex.

3. Selliguea feeoides Copel. — Fig. 3

Selliguea feeoides Copel., Bernice P. Bishop Mus. Bull. 59 (1929) 17; Ching, Sunyatsenia 5 (1940) 260; Brownlie, Pteridophyte Flora of Fiji (1977) 370. — Type: Gillespie 3811 (UC), Fiji, Mt Loma laga.

Rhizome. Diameter 3–7.5 mm, the internodes to 1.5–2.5 cm long. Vascular strands 4–11, bundle sheath fully sclerified. Sclerenchyma strands few to many; scattered, or mainly central (sometimes); isodiametric; massive, hollow or perforated. Ground tissue not sclerified, or with peripheral sclerified sheath. *Rhizome scales:* peltate; spreading to squarrose; $5-10 \times 1-1.4$ mm; acute or contracted to a narrow acumen;

brown; evenly coloured or with a lighter margin; remotely and weakly dentate to short-dentate. Frond dimorphy. Sterile fronds regularly present. Fertile parts narrowed. Fertile fronds. Simple. Stipe 17–26 cm long. Lamina 16–20 \times 2.4–3.6 cm (or longer), index 5–7.4, widest at 0.2–0.4 from base. Sterile fronds. Simple. Stipe 9–15.5 cm long. Lamina 11.5–23 \times 3.7–9 cm, index 1.9–3.5, widest at 0.3–0.4 from base. Main veins on upper surface not or occasionally raised, distinct; connecting veins often also raised; veinlets free and anastomosing; free veinlets excurrent and recurrent. Hydathodes mostly frequent, calcareous scales not persistent. Margin cartilaginous, thickened; without notches or notches sporadically present. Anatomy. Upper surface: walls of epidermis strongly thickened; hypodermis a single to double layer, cell walls very strongly thickened. Lower surface: walls of epidermis very strongly thickened; hypodermis distinct, multilayered, with strongly thickened walls. Sori: confluent across connecting veins to an interrupted transverse coenosorus; in one row between adjacent main veins; 3 mm across (not contiguous when ripe); slightly sunken.

Selected illustrations — Brownlie (1977): pl. 44 fig. 4, 5.

Distribution — Vanuatu, Fiji, Samoa.

Ecology — Epiphytic, in forest or on exposed trees. Altitude 600–1250 m.

Notes on variability — The name *Selliguea feeoides* has been applied rather indiscriminately to all forms occurring on the Pacific Islands. In fact, several more or less distinct forms are present, which I consider to represent two distinct species (*S. feeoides* and *S. plantaginea*), with more or less constant forms on five island groups. The main differential characters are: sclerification in the rhizome; size, shape and dentation of the scales; the degree of confluence of the sori. These differences are reinforced by less clearly circumscribed differences in size and shape of the fronds.

Two distinct forms of *S. feeoides* occur. The typical form is from Fiji and Samoa, an aberrant form occurs in Vanuatu. The latter is characterised by rhizome scales which are strongly contracted to an almost entire, thick, dullish acumen, sparsely set on and not fully covering the rhizome. There is a considerable variability in width of the rhizome scales of Fijian material, and the Vanuatu specimens fall only just outside this range of variability. The sparse scales give the rhizome a distinct appearance, which is retained in cultivation (as can be seen at Kew).

On Samoa, where S. feeoides occurs together with S. plantaginea, some intermediate specimens have been found. They differ from typical S. feeoides mainly in the absence of hydathodes.

All other forms which have been identified as *S. feeoides* belong to *S. plantaginea*. *Selliguea feeoides* has the fertile lamina characteristically ovate-lanceolate, gradually tapering to the apex, with sori in mainly uninterrupted coenosori, not covering the lamina when ripe; *S. plantaginea* has a more widely ovate lamina nearly always without hydathodes, and sori ranging from round, separate to fully coenosoroid.

4. Selliguea caudiformis (Blume) J. Sm. - Fig. 4

Selliguea caudiformis J. Sm., Ferns Brit. For. (1866) 97; Carruth. in Seem., Flora Vitiensis (1873) 370; J. Sm., Hist. Fil. (1875) 102. — Polypodium caudiforme Blume, Enum. Pl. Javae (1828) 122; Fl. Javae Filic. (1829) 146. — Polypodium feei (Bory) Mett. var. caudiforme Alderw.,

Malayan Ferns (1908) 676. — Pleopeltis feei var. caudiformis Alderw., Bull. Dép. Agric. Indes Néerl. 27 (1909) 12. — Pleopeltis caudiformis Alderw., Malayan Ferns, Suppl. 1 (1916) 383. — Type: Reinwardt s.n., s.d. (L, BO), Celebes.

- Polypodium phlebiscopum Baker, J. Linn. Soc., Bot. 15 (1876) 110; Alderw., Malayan Ferns (1908) 648. Pleopeltis phlebiscopa Alderw., Malayan Ferns, Suppl. 1 (1916) 386. Selliguea plebiscopa Pichi Serm., Webbia 31 (1977) 249. Type: Moseley, Challenger exp. s.n. (BM, K, L), Moluccas, Ternate.
- Polypodium calophlebium Copel., Philipp. J. Sci. 2, Bot. (1907) 140; Alderw., Malayan Ferns (1908) 676. Pleopeltis calophlebia Alderw., Bull. Dép. Agric. Indes Néerl. 27 (1909) 12; Malayan Ferns, Suppl. 1 (1916) 406. Selliguea calophlebia Copel., Fern Fl. Philipp. (1960) 508. Type: Merrill 5989 (GH, P), Philippines, Mindoro, Mt Halcon.
- Selliguea feei auct. non Bory: Kato & Price, Acta Phytotax. Geobot. 41 (1990) 72 (most specimens cited).

Rhizome. Diameter 2–5 mm, internodes to 2–4.5 cm long. Vascular strands 7–9, bundle sheath fully sclerified, rarely 2 cells thick. Sclerenchyma strands absent. Ground tissue not or lightly sclerified. Rhizome scales: peltate; appressed to spreading (mostly); 4.5–6.5 \times 1–2 mm; acute; brown; evenly coloured or with a lighter margin; entire to remotely and weakly dentate, rarely short-dentate, often with irregular protuberances. Frond dimorphy. Sterile fronds regularly present. Fertile parts narrowed. Fertile fronds. Simple. Stipe 5.5–24 cm long. Lamina 6–21 × 1.7–6 cm, index 2.8-5.2, widest at 0.2-0.4 from base. Sterile fronds. Simple. Stipe 2-19 cm long. Lamina $6-22 \times 2-9.5$ cm, index 1.7-3.4, widest at 0.2-0.4 from base. Base cuneate, apex obtuse, acute, to acuminate/caudate. Main veins on upper surface raised, distinct. Hydathodes frequent, calcareous scales not persistent. Margin cartilaginous, thickened; without notches or notches sporadically present. Anatomy. Upper surface: walls of epidermis not to strongly thickened; hypodermis a single or double layer, cell walls thickened or not. Lower surface: walls of epidermis strongly to very strongly thickened; hypodermis indistinct to distinct. Sori: round to elongate, occasionally confluent across the connecting veins to transverse coenosori; in one row between adjacent main veins (rarely in two rows); in 5 or more rows between costa and margin (rarely less); 3-4 mm across; superficial to slightly sunken.

Selected illustrations — Blume (1829): pl. 54 fig. 2; Copeland (1907): pl. 3 fig. A (as *Polypodium calophlebium*).

Distribution — S Philippines, Celebes, Moluccas.

Ecology — Epiphytic, predominantly on tree trunks, terrestrial, and on rocks, mostly in open or mossy forest, on summits or ridges. Altitude 980–2500, possibly higher.

Vernacular names — Mano-mano, koki (Ternate).

Notes on variability — The description refers to the most common form occurring in Celebes. Some specimens from Celebes (including the type) and the Moluccas have a different aspect, most striking in the more strongly contracted fertile fronds, with fewer sori between costa and margin:

Rhizome. Sclerenchyma strands absent to many; scattered to mainly central. *Frond dimorphy.* Fertile parts strongly contracted. *Fertile fronds.* Stipe 15–19 cm long. Lamina $20-33 \times 0.5-4.1$ cm, index (9–)18–40, widest at 0.3–0.5 from base. Margin notches sporadically to regularly present. *Sterile fronds.* Index 3–20. *Sori* in 2–4 rows between costa and margin.

Notes — 1. A characteristic difference between this species and the closely related *Selliguea feei* is the disposition of the sori, which in *S. caudiformis* are usually separate, with a distinct and well-developed costal row, often clearly distinct from the other sori which are closer to the margin. *Selliguea caudiformis* differs from *S. feei* moreover in the more distinctly acuminate lamina, and from *S. plantaginea* and related species mainly in the usually somewhat wider rhizome scales and the presence of hydathodes. However, the distinctions are not completely sharp. One specimen from Leyte (*Wenzel 1211*, BM) has no hydathodes and uninterrupted coenosori. It is here regarded as an aberrant specimen of *S. caudiformis*, but only by the rather wide, entire scales it can be distinguished from *S. plantaginea*.

2. Polypodium phlebiscopum. This name has usually been applied to specimens from New Guinea (here included in S. plantaginea). However, the type, although consisting of poor material, clearly shows separate, sometimes confluent sori, frequent hydathodes, and a regularly notched margin. These points agree better with S. caudiformis than with any species from New Guinea, especially in the presence of hydathodes. On the other hand, apart from the hydathodes, there is little to distinguish these specimens from S. plantaginea. Intermediates between this form and the more typical S. caudiformis occur in the form of specimens with both caudate fronds with separate sori and rounded fronds with coenosori, e.g. Sarasin 1169.

5. Selliguea plantaginea Brack. — Fig. 5

- Selliguea plantaginea Brack., U. S. Expl. Exped. Filic. (1854) 58. Type: U.S. Expl. Exped. Filic. s. n. (K), Tahiti.
- Polypodium werneri Rosenst., Feddes Rep. Spec. Nov. Regni Veg. 5 (1908) 43; Alderw., Malayan Ferns (1908) 649. Pleopeltis werneri Alderw., Bull. Dép. Agric. Indes Néerl. 27 (1909) 7; Malayan Ferns, Suppl. 1 (1916) 386. Polypodium werneri C. Chr., Brittonia 2 (1937) 312. Selliguea werneri Pichi Serm., Webbia 31 (1977) 249. Type: Werner 75 (B, UC), New Guinea, Gelu.
- Polypodium alloiosorum Brause, Bot. Jahrb. Syst. 56 (1920) 202. Selliguea alloiosora Ching, Sunyatsenia 5 (1940) 260. — Type: Ledermann 12575 (B), New Guinea, Felsspitze.
- Polypodium mafuluense C. Chr., Brittonia 2 (1937) 313. Type: Brass 5204 (BM, NY), New Guinea, Mafulu.
- Crypsinus caudaefolius Gilli, Ann. Naturhist. Mus. Wien 81 (1978) 21. Type: Gilli 334 (W), New Guinea, Mt Wilhelm (W).

Rhizome. Diameter 1.5–8 mm, internodes 1–6 cm long. Vascular strands 6–14, bundle sheath sclerified, to 2 cells thick. Sclerenchyma strands absent, many or very many; scattered or mainly peripheral; isodiametric to periclinally flattened; massive or perforated. Ground tissue not sclerified. *Rhizome scales:* peltate; appressed to spreading; $2-8.5 \times 1-2.6$ mm; obtuse, acute or contracted to a narrow acumen; apex flat or distinctly cucullate, straw-coloured to brown; evenly coloured, mottled or with a darkened apex; entire to strongly dentate (often coarsely and irregularly). *Frond dimorphy.* Sterile fronds regularly present. Fertile parts narrowed. *Fertile fronds.* Simple. Stipe 1.5–23 cm long. Lamina 4–28 × 0.8–5.3 cm, index 2.7–10, widest at 0.2–0.5 from base. *Sterile fronds.* Simple. Stipe 1–20 cm long. Lamina 3–30 × 0.9–10 cm, index 1.6–6.4, widest at 0.2–0.5 from base. Main veins on upper surface not raised, indistinct, or raised, distinct; veinlets free and anastomosing; free veinlets excurrent and recurrent. Hydathodes absent. Margin not or hardly differentiated,



Fig. 5-13. The Selliguea feei-complex in New Guinea. - 5. S. plantaginea Brack. - 6. S. tafana (C. Chr.) Hovenkamp. - 7. S. albicaula (Copel.) Kato & M.G. Price. - 8. S. archboldii Copel. -9. S. bellisquamata (C. Chr.) Hovenkamp. - 10. S. dekockii (Alderw.) Hovenkamp. - 11. S. lauterbachii (Brause) Hovenkamp. - 12. S. costulata (Ces.) Wagner & Grether. - 13. S. ferrea (Brause) Hovenkamp. - Scale bars = 1 cm.

without notches or notches sometimes regularly present. Anatomy. Upper surface: walls of epidermis weakly to strongly thickened; hypodermis a single or double layer, cell walls thickened to strongly thickened. Lower surface: walls of epidermis weakly to very strongly thickened; hypodermis distinct (usually multilayered). Sori: round, elongate or confluent across connecting veins to coenosori; in one row between adjacent main veins (rarely two, near the costa at the base of the lamina); in 2-many rows between costa and margin; 3-4 mm across; superficial to slightly sunken.

Distribution - Celebes, New Guinea, Pacific Islands.

Ecology — Usually epiphytic, mostly in summit forest, occasionally terrestrial, in swamps or on banks, also in alpine grasslands. Altitude 180–3840 m.

Vernacular names --- Port, pot, ak'por (Mendi).

Notes on variability — The degree to which the sori are confluent varies strongly. Forms with uninterrupted coenosori are predominant on the Pacific Islands, in most other localities all transitions between uninterrupted coenosori and regular rows of round sori may be found. Frond size is also very variable. The smaller forms are restricted to the mountain ranges of New Guinea, the larger forms are the dominant form at lower altitudes in New Guinea and on the Pacific Islands. In some localities they occur mixed with smaller forms.

Intermediates between *S. plantaginea* and *S. feeoides* occur on Samoa, where both species occur together. These specimens are similar to *S. feeoides* in the shape of the fertile fronds and the sori, and to *S. plantaginea* in the presence of sclerenchyma in the rhizome and the absence of hydathodes on the fronds.

Throughout the mountain ranges of New Guinea two forms occur, which differ strikingly in the aspect of the rhizome. One form has fairly thick rhizomes (3-8 mm), densely set with spreading, elongated, acute scales which are dark near the point of attachment, and lighter-coloured in the acumen. This form is indistinguishable from the lowland form, and is usually found at altitudes up to 2700 m. The other form has usually thinner rhizomes (1.5-3 mm), which are more strongly glaucous, and are sparsely set with deciduous scales. These scales are nearly always appressed, with an obtuse, distinctly cucullate apex which is usually dark-coloured and thickened. This form has frequently been identified as Selliguea plebiscopa (the type of which is discussed under S. caudiformis). It is almost exclusively restricted to heights of over 3000 m. However, apart from the rhizomes, the two forms are indistinguishable in many locations, exhibiting the same variation in frond shape, size and in soral disposition. Moreover, over a fairly wide altitudinal range (2400-3400 m), specimens are occasionally found which combine characters of the two forms, often on different parts of the same rhizome (e.g., Vink 17580, Hoogland & Schodde 7208, McVean & Wade ANU 7051, Croft 83, Werner 75). This situation is perhaps best explained by assuming that the distinguishing characters of rhizome and rhizome scales are to a large extent governed by external circumstances. Variation in circumstances has, of course, a distinct altitudinal component. At the same time, due to very local effects (such as clumps of moss, or even fallen leaves) conditions may vary strongly over a few centimetres, influencing different parts of a single rhizome in different ways. This microvariation may not be constant enough to influence other aspects of the morphology, but it may have a decisive effect on development during the relatively short time that scales on the the rhizome apex mature.

Note — Selliguea plantaginea is the most widely spread New Guinean/Pacific representative of the complex of mainly allopatric species around S. feei (Fig. 1-4), to which also belong S. elmeri (Philippines), S. caudiformis (East Malesia) and S. feeoides (Pacific). Within this complex, species boundaries are rarely sharp. Selliguea plantaginea differs from S. feei, S. caudiformis and S. feeoides mainly in the absence of hydathodes. Two specimens from Palawan (Edaño PNH 471 & 478, both MICH), in the absence of fertile fronds, cannot be identified with any certainty, but have nothing to distinguish them from S. plantaginea.

At the same time, S. plantaginea is the central species in a complex of mainly sympatric species (Fig. 5–13), in which the specific boundaries are occasionally even less clear. Difficult as it is to draw lines between some of these species, it is even more difficult to draw a line between those distinctions which I confidently regard as specific (e.g., between S. dekockii and S. bellisquamata, or between S. costulata and S. ferrea), and those which could perhaps better be regarded as subspecific (e.g., between S. lauterbachii and either S. costulata or S. tafana). As a practical solution, all members of this complex are here treated as separate species under the following names:

Selliguea albicaula, S. archboldii, S. bellisquamata, S. costulata, S. cretifera, S. dekockii, S. ferrea (Oleandropsis ferrea), S. lauterbachii (used to be called 'gibbsiae'), and S. tafana (often identified as 'squamisora'). The variability within and between these species shows distinct altitudinal effects.

Selliguea plantaginea has a wide altitudinal range, over which it is divided into two more or less distinct altitudinal forms (see above, under variability). Selliguea cretifera, restricted to the higher altitudes, is quite distinct from the high-altitude form of S. plantaginea, but it may be difficult to distinguish from some low-altitude forms.

Selliguea lauterbachii and S. tafana are rather similar, dimorphic species, with S. tafana occurring at higher altitudes, S. lauterbachii mainly at lower altitudes.

The two coenosoroid species (S. costulata and S. ferrea) are distinctly separated, S. costulata being restricted to lower, S. ferrea to high altitudes.

6. Selliguea tafana (C. Chr.) Hovenkamp, comb. nov. — Fig. 6

Polypodium tafanum C. Chr., Brittonia 2 (1937) 311. — Type: Brass 5028 (BM, NY), New Guinea, Mt Tafa.

Polypodium squamisorum C.Chr., Bull. Misc. Inform. 1 (1939) 29. — Type: MacGregor 15 (BM), New Guinea, Musgrave Range.

Rhizome. Diameter 3–4 mm, the internodes to 1–2.5 cm long. Vascular strands 5–11, bundle sheath fully sclerified, to 2 cells thick. Sclerenchyma strands many to very many; scattered; isodiametric; massive. Ground tissue not sclerified. *Rhizome scales:* peltate; spreading to squarrose; 4–6.5 × 1–1.5; acute; brown to blackish; evenly coloured, with a lighter margin, or with irregular dark spots; short-dentate. *Frond dimorphy.* Sterile fronds regularly present. Fertile parts strongly contracted. *Fertile fronds.* Simple. Stipe 0.5–4 cm long. Lamina 4–10 × 0.5–1.2 cm, index 7.5–12.5, widest at 2–5.5 from base, or linear. *Sterile fronds.* Simple. Stipe 1–7.5 cm long. Lamina 6–17.5 × 1.3–3 cm, index 3.3–7.3, widest at 0.3–0.5 from base. Costa only distinct or main veins distinct also. Main veins on upper surface not raised or

raised. Hydathodes absent. Margin not differentiated to cartilaginous, thickened; without notches. *Anatomy*. Upper surface: walls of epidermis weakly to strongly thickened; hypodermis a double layer, cell walls thickened. Lower surface: walls of epidermis weakly to strongly thickened; hypodermis distinct. *Sori:* round to elongate; single between adjacent veins; in one row between costa and margin; 4–5 mm across (receptacle usually covering most of the areole); superficial.

Distribution — Scattered throughout the mountain ranges of Papua New Guinea. Not known from Irian Jaya.

Ecology — Epiphytic, often pendent, or epilithic, in montane to subalpine forest, shrubbery, or in alpine grasslands. Altitude 2400–3600 m.

Notes on variability — The description and illustration apply to the most common form of this species, which was described as *Polypodium squamisorum*. This form is compact, and several specimens of this form have many persistent scales on the lamina and especially in the sori, giving them a highly characteristic appearance. However, this is only one extreme of a variable character; other specimens have few or very few persistent scales.

Selliguea tafana was described on the basis of a more lax form, with few persistent scales. This form differs from the description above in the following characters:

Rhizome. Internodes to 3 cm long. *Rhizome scales* 7.5×2 mm wide, more often appressed than squarrose. *Fertile fronds.* Stipe 6–9 cm long. Lamina $11-19 \times 0.6$ cm or longer, linear. *Sterile fronds.* Stipe 4–10 cm long. Lamina $25-27.5 \times 1.1-1.3$ cm, index 3.4–25, widest at or above the middle, or linear. Margin notches sporadically present. *Sori* remote, not nearly covering the entire areole.

Representative specimens for this form are *Croft 1454* and *Brass 10822*. It is connected to the typical form by a number of intermediates.

Notes — 1. Most easily recognised (if the characteristically persistent soral scales are absent) by the narrowly ovate-elliptic sterile fronds, and the fertile fronds being nearly always not only narrower but also shorter than the sterile ones. All this, and often also a distinct light-green colour (in dried plants) usually easily distinguish *S. tafana* from *S. plantaginea*. On the other hand, *S. tafana* is not always distinct from *S. lauterbachii*, with which it co-occurs at the lower end of its altitudinal range.

2. A few specimens of this species have the rhizome partly radially organised, a feature that is more common in *S. ferrea*.

7. Selliguea cretifera (Alderw.) Ching

Pleopeltis cretifera Alderw., Nova Guinea 16, 1 (1924) 40. — Selliguea cretifera Ching, Sunyatsenia 5 (1940) 260. — Type: Lam 1809 (BO, L, SING, UC), New Guinea, Mt Doorman summit.

Polypodium crassisorum C. Chr., Brittonia 2 (1937) 313. — Type: Brass 4201 (BM, BO, NY, P), New Guinea, Mt Albert Edward.

Rhizome. Diameter 3–6.5 mm, internodes to 2.5–3 cm long. Vascular strands 8–10, bundle sheath fully sclerified, to 2 cells thick. Sclerenchyma strands many to very many; scattered, or mainly peripheral; isodiametric to periclinally flattened. Ground tissue not sclerified, or with a subperipheral lightly sclerified sheath. *Rhizome scales:* peltate; spreading to squarrose; $4-4.5 \times 1-1.3$; acute; brown to blackish; evenly coloured or with irregular dark spots; remotely and weakly dentate to short-dentate.

Frond dimorphy. Sterile fronds regularly present. Fertile parts narrowed, rarely strongly so. Fertile fronds. Simple. Stipe 8.5-9.5 cm long. Lamina $11-14 \times 1.4-2.2$ cm, or longer, index 5-10, widest at 0.3 from base. Sterile fronds. Simple. Stipe 3-8.5 cm long. Lamina $14-18 \times 4.1-6.6$ cm, index 2.3-3.6, widest at 0.2-0.4 from base. Main veins on upper surface raised, distinct. Hydathodes absent. Margin not differentiated to cartilaginous, flat; notches absent or (rarely) present. Sori: elongate to transverse coenosori; singly between adjacent veins; 4-5 mm across; superficial.

Distribution — Throughout the mountain ranges of New Guinea.

Ecology — Usually epiphytic, often pendent, also terrestrial, in montane to subalpine forest. Altitude 1650–3800 m.

Note — These are mainly high-altitude plants, intermediate between *S. plantaginea* and *S. tafana* and difficult to distinguish from either. However, the high-altitude form of *S. plantaginea* ('*plebiscopa*') is quite distinct from *S. cretifera*. The latter is best recognisable by the relatively thick coenosori. A few persistent scales may be found on the lamina. Conceivably it contains a number of intermediate specimens of hybrid origin. The variability in spore size in some samples of this species is notably large.

8. Selliguea albicaula (Copel.) Kato & Price - Fig. 7

Selliguea albicaula Kato & Price, Acta Phytotax. Geobot. 41 (1990) 72. — Polypodium albicaulum Copel., Philipp. J. Sci. 6, Bot. (1911) 90. — Pleopeltis albicaula Alderw., Malayan Ferns, Suppl. 1 (1916) 383. — Type: King 327 (P), New Guinea, Lakekamu.

Polypodium albarium A. Gepp, J. Bot. Suppl. (1923) 61. — Selliguea albaria ('albara') Ching, Sunyatsenia 5 (1940) 260. — Type: Forbes 290 (BM), New Guinea, Sogere.

Rhizome. Diameter 4 mm, internodes to 3.5 cm long. Vascular strands 9, bundle sheath fully sclerified. Sclerenchyma strands many; mainly peripheral; isodiametric. Ground tissue not sclerified. *Rhizome scales:* peltate; squarrose; 5.5×0.7 mm wide (at base); contracted to a narrow acumen with pseudocosta; brown to blackish (cells in pseudocosta almost clathrate); with a very narrow lighter margin; entire to remotely and weakly dentate. *Frond dimorphy.* Sterile fronds regularly present. Fertile parts narrowed. *Fertile fronds.* Simple. Stipe 2–5.5 cm long. Lamina 11–14 × 0.8–1 cm, index 13.4–14, widest at 0.3–0.4 from base. *Sterile fronds.* Simple. Stipe 1.5–4.5 cm long. Lamina 13–18 × 2.5–4.5 cm, index 3.1–6.9, widest at 0.2–0.3 from base. Main veins on upper surface raised, distinct. Hydathodes absent. Margin not differentiated or cartilaginous, flat; notches sporadically present, in fertile fronds absent. *Sori:* forming transverse coenosori; 2 mm across; superficial.

Distribution — New Guinea (3 specimens).

Ecology — Epiphytic in lightly disturbed forest (few data). Altitude 820 m. Vernacular name — Iburi (Kutubu).

Note — Very similar to *S. archboldii*, but the whitish rhizome with sparsely set, distinctly bicolorous scales give this species a distinct appearance.

9. Selliguea archboldii Copel. — Fig. 8

Selliguea archboldii Copel., J. Arnold Arbor. 24 (1943) 442. — Type: Brass 6836 (BM, GH, UC), New Guinea, 528-mile Camp, Fly River. *Rhizome.* Diameter 2–3 mm, internodes to 1.5–3 cm long. Vascular strands 8, bundle sheath fully sclerified. Sclerenchyma strands many to very many; scattered; isodiametric. Ground tissue not sclerified. *Rhizome scales:* peltate; spreading to squarrose; $6.5 \times 1-1.3$ mm (width at base); acute or contracted to a narrow acumen; acumen brown to blackish with a very narrow lighter margin; entire to remotely and weakly dentate. *Frond dimorphy.* Sterile fronds regularly present. Fertile parts narrowed. *Fertile fronds.* Simple. Stipe 6–8 cm long. Lamina 10.5–14.5 × 1.1–1.4 cm, index 9.6–10, widest at 0.3–0.5 from base. *Sterile fronds.* Simple. Stipe 4.5–6 cm long. Lamina 15–17 × 3.3–4.8 cm, index 3.3–4.9, widest at 0.3–0.4 from base. Main veins on upper surface raised, distinct. Hydathodes absent. Margin not differentiated or cartilaginous, flat or slightly thickened; notches sporadically to regularly present, in fertile fronds absent to regularly present. *Anatomy.* Upper surface: walls of epidermis strongly thickened; hypodermis a single to double layer, cell walls strongly thickened. Lower surface: walls of epidermis strongly thickened; hypodermis distinct, multilayered. *Sori:* in transverse coenosori; 2 mm across; superficial.

Distribution — New Guinea (7 collections).

Ecology - Epiphytic. Altitude 600-1220 m.

Notes — A distinct segregate of the *S. plantaginea*-complex, identifiable by the very narrow scales and consistently continuous coenosori. *Selliguea albicaula* is similar, but differs in having the scales much more sparsely set on a distinctly whitewaxy rhizome, and in the almost clathrate structure of the thick costa of the scales. However, there are some intermediate specimens, and it is possible that the specific distinction can no longer be upheld as more material becomes available.

Somewhat similar specimens from Vanuatu differ in the presence of hydathodes, and are discussed under S. feeoides.

10. Selliguea bellisquamata (C. Chr.) Hovenkamp, comb. nov. -- Fig. 9

Polypodium bellisquamatum C. Chr., Brittonia 2 (1937) 313. — Type: Brass 4053 (BM, BO, GH, NY), New Guinea, Tafa Mt.

Selliguea brachylepidota Copel., Univ. Calif. Publ. Bot. 18 (1942) 226. — Type: Clemens 41008 (UC), New Guinea, Matap.

Rhizome. Diameter 4–5 mm, internodes to 1.5–4 cm long. Vascular strands 10–11. Bundle sheath fully sclerified to sclerified, 2 cells thick. Sclerenchyma strands very many; scattered; isodiametric or periclinally flattened; massive. Ground tissue not sclerified. *Rhizome scales:* peltate; appressed; 5–9.5 × 2.3–3 mm; obtuse; straw-coloured to brown, with a lighter flabelloid margin; entire. *Frond dimorphy.* Sterile fronds regularly present. Fertile parts narrowed. *Fertile fronds.* Simple. Stipe 1–12 cm long. Lamina 9–21 × 1.4–3.1 cm, index 3–7.9, widest at 0.2–0.5 from base. *Sterile fronds.* Simple. Stipe 2–8.5 cm long. Lamina 12–21 × 2.4–4.7 cm, index 1.8–5.2, widest at 0.3–0.5 from base. Main veins on upper surface raised, distinct. Hydathodes absent. Margin not differentiated to cartilaginous, flat to thickened; notches sporadically to regularly present. *Anatomy.* Upper surface: walls of epidermis strongly thickened; hypodermis a double layer, cell walls strongly thickened. Lower surface: walls of epidermis strongly thickened; hypodermis distinct. *Sori:* round, elongate or confluent to coenosorus; confluent across connecting veins (occasionally confluent within one areole); in one row between adjacent main veins (occasionally in 2 rows); in 5 or more rows between costa and margin; 2–4 mm across; slightly sunken.

Distribution - East Malesia, Celebes to New Guinea.

Ecology — Epiphytic in mid-montane or mossy mountain forest, occasionally terrestrial on cliffs, road banks or in rock crevices. Altitude 1300-2700 m.

Notes on variability — The description above is based on material from New Guinea. Material from Celebes and the Moluccas differs in the following aspects:

Rhizome thinner, diameter 2–3 mm, with few (4–6) vascular strands and no or few, mainly central, sclerenchyma strands. Ground tissue lightly sclerified with a peripheral sclerified sheath. *Rhizome scales* $3-7 \times 1.5-3$ mm, whitish. *Sori* confluent to transverse coenosori.

Notes — 1. Selliguea bellisquamata differs from the other species in the S. plantaginea-complex mainly but strikingly in the wide, flaccid scales with flabelloid margin.

2. It has been suggested that this species habitually is associated with ants (Tryon 1985), the loosely fitting rhizome scales at the base of the stipes providing cover for the ants. The presence of ants between the scales certainly does not seem to be a frequent phenomenon.

3. The duplicate of van Balgooy 3210 in BO is evidently S. plantaginea.

11. Selliguea dekockii (Alderw.) Hovenkamp, comb. nov. — Fig. 10

Pleopeltis dekockii Alderw., Bull. Jard. Bot. Buitenzorg (1911) Appendix; Malayan Ferns, Suppl. 1 (1916) 382; Nova Guinea 1 (1924) 39. — Crypsinus dekockii Copel., Gen. Fil. (1947) 206. — Type: de Kock 44 (BO), New Guinea, Mt Goliath.

Polypodium prolixum Rosenst., Nova Guinea (1912) 727. — Syntypes: von Römer 717 (L), 1035 (L), New Guinea, Mt Hellwig.

Polypodium argyropus Ridl., Trans. Linn. Soc. London 1 (1916) 262. — Type: Boden Kloss s.n. (BM, K), New Guinea, Nassau Mts, Camp VIb.

Rhizome. Diameter 4-5 mm, internodes to 1.5-3.5 cm long. Vascular strands 8-10, bundle sheath fully sclerified, to 2 cells thick. Sclerenchyma strands very many; scattered or mainly peripheral; isodiametric; massive or perforated. Ground tissue with a distinct subperipheral sclerified sheath. Rhizome scales: peltate; appressed to spreading; $7-9.5 \times 1.8-3$ mm; acute (apex often wrinkled); whitish to brown; evenly coloured or with a lighter margin, rarely with irregular dark spots; entire, with a very irregular flabelloid margin. Frond dimorphy. Sterile fronds regularly present (intermediate fronds sometimes present). Fertile parts strongly contracted. Fertile fronds. Simple. Stipe indistinct, 2-8 cm long. Lamina $12-22.5 \times 0.2-0.4$ cm (-1.3 cm wide in intermediate fronds), linear. Sterile fronds. Simple. Stipe 0.5-5 cm long. Lamina $5-14.5 \times 1.5-3.5$ cm, index 2.9-7.2, widest at 0.2-0.4 from base. Main veins on upper surface not raised or raised, distinct. Hydathodes absent. Margin cartilaginous or concolorous, flat to thickened; notches sporadically to (mostly) regularly present, in fertile fronds sometimes absent. Anatomy. Upper surface: walls of epidermis strongly thickened; hypodermis a double layer, cell walls thickened to strongly thickened. Lower surface: walls of epidermis strongly thickened; hypodermis distinct. Sori: longitudinally elongate or forming short, transverse coenosori (in transitional fronds); in one row between adjacent veins; in one row between costa and margin; 3-4 mm across; superficial.

Selected illustration — Alderwerelt (1924): fig. B.

Distribution — Restricted to the main island of New Guinea.

Ecology - Epiphyte in primary or secondary forest. Altitude 1250-2400 m.

Vernacular name — Iedawieda (Kapaukoe).

Notes -1. In the occasional transitional fronds the basal sterile part is wide, the apical fertile part gradually narrowed into a fertile spike. Transitional sori are elongated, in a single line between each pair of veins (*Pulle 846*).

2. Selliguea dekockii is close to S. bellisquamata, and might be regarded as merely a dimorphic variant of the latter, were it not for the constant differences in rhizome structure (the distinct sclerenchyma sheath), and rhizome scales (acute, with a wrinkled apex).

12. Selliguea lauterbachii (Brause) Hovenkamp, comb. nov. - Fig. 11

Polypodium lauterbachii Brause, Bot. Jahrb. Syst. 49 (1912) 52. — Pleopeltis lauterbachii Alderw., Malayan Ferns, Suppl. 1 (1916) 383. — Type: Schlechter 18688 (B, K, P, UC), New Guinea, Bismarck Mts.

Pleopeltis gibbsiae Alderw., Bull. Jard. Bot. Buitenzorg II, 28 (1918) 37. — Polypodium gibbsiae C. Chr., Ind. Fil. Suppl. 3 (1934) 149. — Type: Gibbs 5689 (BM, P), New Guinea, Arfak.

Rhizome. Diameter 2.5–3 mm, internodes to 2.5–3 cm long. Vascular strands 8 or 9, bundle sheath fully sclerified. Sclerenchyma strands many; scattered or mainly peripheral; isodiametric or periclinally flattened; massive. Ground tissue not sclerified. *Rhizome scales:* peltate; usually squarrose, sometimes spreading; $3-5.5 \times 0.7-1$ mm; acute; brown, with a lighter margin; strongly dentate, occasionally long-ciliate. *Frond dimorphy.* Sterile fronds regularly present. Fertile parts strongly contracted. *Fertile fronds.* Simple. Stipe 4–10 cm long. Lamina 7–9 × 0.2–0.4 cm, linear. *Sterile fronds.* Simple. Stipe 1–7 cm long. Lamina 5–14.5 × 1–4 cm, index 2.6–9, widest at 0.3–0.4 from the base. Main veins on upper surface raised, distinct. Hydathodes absent. Margin cartilaginous, thickened; notches regularly present. *Anatomy.* Upper surface: walls of epidermis weakly to strongly thickened; hypodermis a single to double layer, cell walls not thickened. Lower surface: walls of epidermis weakly to strongly thickened; in one row between adjacent veins and between costa and margin; 2–3 mm across; superficial.

Distribution — Celebes (Rantemario), Moluccas (Tidore), New Guinea (many specimens).

Ecology — Low to high epiphyte, sometimes on rocks, in forest or open places, often in secondary forest or disturbed places. Altitude (390-)1500-2500(-3200) m.

Vernacular names — Me bingga (Kuman, Chimbu), bilmabil (Masul, Chimbu), binga morumere (Mt Wilhelm), dzalosi (Kefamo, Asaro), kumbelan (Minj, Wahgi), kumbiang (Togoba, Hagen).

Notes on variability — In very narrow fronds the coenosori are elongated longitudinally, in somewhat wider fronds they are distinctly oblique, directed towards the margin, forming a transition to *S. plantaginea*.

Note — Selliguea lauterbachii is usually easily recognisable by the narrow fertile fronds with separate sori and the usually squarrose, strongly dentate, brown rhizome scales. It can be similar to forms of S. plantaginea, S. costulata, and S. tafana.

Selliguea plantaginea can be recognised by the wide fertile fronds. However, some specimens have fronds that are intermediate between S. lauterbachii and S. plantaginea, being gradually narrowed from a wide, sterile base to a narrow, fertile apex. In other specimens, the width of the fertile frond varies, with the widest fronds approaching S. plantaginea (e.g., Stevens LAE 51010).

Selliguea costulata has fertile fronds with longitudinal coenosori, but these are frequently interrupted, thus blurring the distinction to S. lauterbachii. In this circumscription S. costulata may contain some specimens with coenosori which have originated independently in local populations of S. lauterbachii. In a single population (compare Brass 11871, 11872, from Bernhard Camp, Irian Jaya) forms with separate sori and one with continuous coenosori occur which are otherwise completely similar. There can be no doubt, however, about the distinctiveness of the typical, low-altitude form of S. costulata.

Selliguea tafana can be distinguished by the blackish rhizome scales which are less strongly dentate, the relatively short fertile fronds, and the frequent occurrence of small scales on the fronds. It usually occurs at higher altitudes than S. lauter-bachii, but sterile specimens, especially from intermediate altitudes cannot always be identified.

13. Selliguea costulata (Ces.) Wagner & Grether — Fig. 12

Acrostichum costulatum Ces., Rend. Reale Accad. Sci. Fis. Napoli 16 (1877) 30. — Polypodium costulatum Baker, J. Bot. n.s. 9 (1880) 215; Alderw., Malayan Ferns (1908) 644. — Pleopeltis costulata Alderw., Bull. Dép. Agric. Indes Néerl. 27 (1909) 6. — Grammatopteridium costulatum C. Chr., Dansk Bot. Ark. 6 (3) (1929) 80. — Selliguea costulata Wagner & Grether, Univ. Calif. Publ. Bot. 23 (1948) 60; Kato & Price, Acta Phytotax. Geobot. 41 (1990) 72. — Type: Beccari s. n. (FI, not seen), New Guinea, Ansus I. (FI, not seen).

Polypodium iboense Brause, Bot. Jahrb. Syst. 49 (1912) 50. — Pleopeltis iboensis Alderw., Malayan Ferns, Suppl. 1 (1916) 386. — Syntypes: Schlechter 17106 (B, BM), 19017 (B, L, UC), Kaiser Wilhelmsland, New Guinea.

- Grammatopteris pseudodrymoglossum Alderw., Bull. Jard. Bot. Buitenzorg III, 5 (1922) 318. Grammatopteridium pseudodrymoglossum C. Chr., Dansk Bot. Ark. 6 (3) (1929) 82. — Type: Lam 826(L), New Guinea, Prauwenbivak.
- Grammatopteris brooksii Alderw. var. beguinii Alderw., Bull. Jard. Bot. Buitenzorg III, 5 (1922)
 318. Grammatopteridium costulatum var. beguinii C. Chr., Dansk Bot. Ark. 6 (3) (1929) 81.
 Type: Beguin 1095, Moluccas, Ternate, Foramadiahi, not traced.

Rhizome. Diameter 2.5–5 mm, internodes to 1–5 cm long. Vascular strands 8–11, bundle sheath fully sclerified. Sclerenchyma strands very many; scattered; isodiametric (smaller and periclinally flattened at periphery); massive. Ground tissue not sclerified. *Rhizome scales:* peltate; spreading to (rarely) squarrose; $3-7 \times 1-1.5$ mm; acute; straw-coloured to brown; evenly coloured (rarely), or with a lighter margin; remotely and weakly to strongly dentate. *Frond dimorphy.* Sterile fronds regularly present. Fertile parts strongly contracted. *Fertile fronds.* Simple. Stipe 2–19 cm long. Lamina $3.5-32 \times 0.2-0.3(-0.8)$ cm, linear. *Sterile fronds.* Simple. Stipe 0.5–18 cm long. Lamina $4.5-20 \times 0.7-6.8(-10)$ cm, index 2.1–6.5, widest at 0.2–0.5 from the base. Apex rounded to long-acuminate. Main veins on upper surface raised, distinct; veinlets anastomosing; free veinlets excurrent and recurrent. Hydathodes absent. Margin cartilaginous, flat (rarely) or thickened; notches sporadically to regu

larly present, in fertile fronds absent. *Anatomy*. Upper surface: walls of epidermis strongly thickened; hypodermis a single or double layer, cell walls thickened. Lower surface: walls of epidermis very strongly thickened; hypodermis distinct. *Sori*: in a longitudinal coenosorus (often interrupted), or (rarely, in transitional fronds) transversally elongated, singly between costa and margin; 2–4 mm across; superficial.

Selected illustrations — Alderwerelt (1922): pl. 15, fig. 2 (as Grammatopteris brooksii var. beguinii): Lauterbach (1920): fig. 3B (as Polypodium iboense).

Distribution - Moluccas to New Guinea.

Ecology — Epiphytic, low down on trunks to high up in crowns. Altitude sea level to 1600 m.

Notes — 1. Usually strongly dimorphic, with very narrow fertile fronds which are almost completely covered with longitudinal coenosori. Transitional fronds (e.g., *Grether & Wagner 4184*) show that in relatively wide fertile fronds (c. 1 cm wide) the sori are fused across the connecting veins to a very oblique transverse coenosorus, and only in narrower parts of the lamina the transverse sori fuse into a completely longitudinal coenosorus.

Small forms with separate sori from the mainland of New Guinea are assigned to *S. lauterbachii*. In some populations, however, it is virtually impossible to find any other differences between *S. lauterbachii* and *S. costulata* (compare *Brass 11872* and *11871*, both from Bernhard Camp). It is possible that in these populations the specimens assigned to *S. costulata* are merely an extreme form of *S. lauterbachii*. In more peripheral localities *S. costulata* is more clearly distinct from co-occurring species.

2. Selliguea costulata has been confused with S. brooksii from Sumatra [Christensen, Dansk Bot. Ark. 6 (3) (1929): 80]. See under S. brooksii for a discussion of these two species.

14. Selliguea ferrea (Brause) Hovenkamp, comb. nov. — Fig. 13

Polypodium ferreum Brause, Bot. Jahrb. Syst. 56 (1920) 197. — Grammatopteridium ferreum C. Chr., Dansk Bot. Ark. 6 (3) (1929) 81. — Oleandropsis ferrea Copel., Univ. Calif. Publ. Bot. 18 (1942) 226; Gen. Fil. (1947) 208. — Lectotype (here selected): Ledermann 8881 (B), New Guinea, Etappenberg.

Rhizome. Diameter 3.5–4 mm, internodes variable (see note 1). Vascular strands 7–10, bundle sheath sclerified, 2 cells thick. Sclerenchyma strands absent to many; scattered or mainly around the vascular cylinder; isodiametric; perforated. Ground tissue with peripheral or subperipheral sclerified sheath. *Rhizome scales:* peltate; appressed to spreading; $5.5-6.5 \times 1-1.7$ mm, acute; brown to blackish at base; upwards lighter, with irregular dark spots; entire or sometimes irregularly, coarsely dentate. *Frond dimorphy.* Sterile fronds regularly present. Fertile parts strongly contracted. *Fertile fronds.* Simple. Stipe 1–5 cm long, or virtually absent. Lamina $4.5-12 \times 0.1-0.3$ cm or longer, linear. *Sterile fronds.* Simple. Stipe 0.5–1 cm long, usually indistinct, often virtually absent. Lamina $5.5-14 \times 0.6-1.3$ cm, index 6.7-18, widest at 0.5–0.8 from base. Main veins on upper surface not raised to raised, distinct. Hydathodes absent. Margin not differentiated to thickened, hardly cartilaginous; notches regularly present, in fertile fronds absent to sporadically present. *Anatomy.* Upper surface: walls of epidermis strongly thickened; hypodermis a double

layer, cell walls strongly thickened (typically more strongly so than the epidermis). Lower surface: walls of epidermis strongly thickened; hypodermis distinct, very strongly developed. Mesophyll with scattered sclerenchyma cells. *Sori:* in a longitudinal coenosorus; singly between costa and margin; 2 mm across; superficial.

Selected illustration — Copeland (1947): pl. 9.

Distribution — New Guinea (5 specimens).

Ecology — High epiphyte or terrestrial in moss. Altitude 600-1200 m.

Notes — 1. Rhizome organisation. This species has been separated into a monotypic genus *Oleandropsis* on the basis of the radial organisation of the rhizome. However, a single rhizome may in part show a creeping, dorsiventral aspect but a more compact, radial organisation in other parts (see under Rhizome organisation, p. 8). Radially organised shoots have also been found in *S. tafana*.

2. The narrow shape of the sterile fronds in combination with the longitudinal coenosorus is distinctive for the species.

3. The BO specimen of *Brass 12795* shows interrupted coenosori, thus coming very close to *S. tafana*.

15. Selliguea albidosquamata (Blume) Parris - Fig. 14

- Selliguea albidosquamata Parris in Parris, Beaman & Beaman, Plants of Mt Kinabalu. I. Ferns and fern allies (1991) 152. Polypodium albido-squamatum Blume, Enum. Pl. Javae (1828) 132;
 Fl. Javae Filic. (1829) 137; Mett., Farngatt. I. Polypodium (1857) 107; Hook., Gard. Ferns (1862) pl. 47; Sp. Fil. (1864) 92 ('albo-squamatum'); Baker, Syn. Fil. (1868) 369 ('albo-squamatum'); Alderw., Malayan Ferns (1908) 668 ('albidosquamatum'); Backer & Posth., Varenfl. Java (1939) 217. Phymatodes albido-squamata J. Sm., Fern Brit. For. (1866) 94 ('albo-squamata'). Pleopeltis albido-squamata Alderw., Bull. Dép. Agric. Indes Néerl. 27 (1909) 10; Malayan Ferns, Suppl. 1 (1916) 401 ('albidosquamata'). Crypsinus albido-squamatus Copel., Gen. Fil. (1947) 207 ('albidosquamatus'); Holttum, Revis. Fl. Malaya 2, sec. ed. (1954) 195; Copel., Fern Fl. Philipp. (1960) 501 ('albidosquamata'); Kato & Price, Acta Phytotax. Geobot. 41 (1990) 70. Phymatopteris albido-squamata Ching, Acta Phytotax. Sin. 9 (1964) 191 ('albidosquamata'). Phymatopteris albido-squamata Pichi Serm., Webbia 28 (1973) 461. Type: Reinwardt s. n. (L), Celebes.
- Polypodium varians Blume, Enum. Pl. Javae (1828) 132; Fl. Javae Filic. (1829) 138. Pleopeltis varians T. Moore, Index Filic. (1862) 344. Polypodium albidosquamatum Blume var. varians Alderw., Malayan Ferns (1908) 668. Pleopeltis albidosquamatus Blume var. varians Alderw., Bull. Dép. Agric. Indes Néerl. 27 (1909) 10. Type: Blume s.n. (L), Java, Salak.
- Polypodium subaquatile H. Christ, Ann. Jard. Bot. Buitenzorg II, 5 (1905) 124; Alderw., Malayan Ferns (1908) 668. Pleopeltis subaquatilis Alderw., Malayan Ferns, Suppl. 1 (1916) 401. Type: Jaheri 214 (BO, BM, L, P), Borneo, Tadjoek.
- Polypodium longicuspe C. Chr., Leafl. Philipp. Bot. 9 (1933) 3167; Copel., Fern Fl. Philipp. (1960) 501 (tentatively under P. albidosquamatum). Type: Elmer 22107 (B, BM, K, UC), Philippines, Luzon, Mt Pinatubo.
- Polypodium bellivenosum C. Chr., Brittonia 2 (1937) 312. Crypsinus bellivenosus Copel., Gen.
 Fil. (1947) 207. Phymatopteris bellivenosa Pichi Serm., Webbia 31 (1977) 249. Type: Brass 4860(BM, BO, NY), New Guinea, Mt Tafa.

Rhizome. Diameter 5–10 mm. Internodes to 1–4 cm long. Vascular strands 12–20. Bundle sheath absent to hyaline. Sclerenchyma strands very many; scattered or mainly peripheral; isodiametric or periclinally flattened; massive or hollow. Ground tissue not sclerified. *Rhizome scales:* peltate; spreading to squarrose; 7–23 mm long; 1–2.5

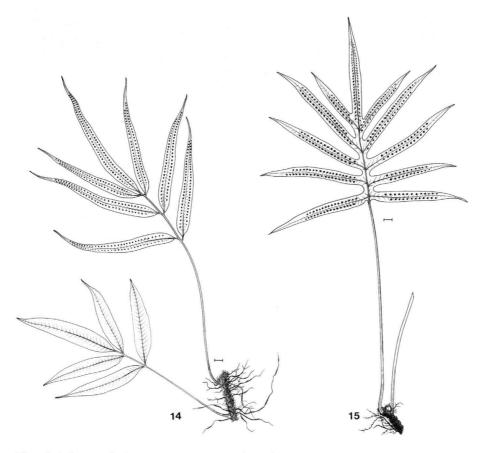


Fig. 14. Selliguea albidosquamata (Blume) Parris. — Fig. 15. S. laciniata (Bedd.) Hovenkamp. — Scale bars = 1 cm.

mm wide; acute to contracted to a narrow, often recurved, acumen; brown, evenly coloured to blackish, with a dark central pseudocosta and a lighter margin (margin often absent in the subulate acumen); margin strongly dentate to long-ciliate; cilia often also present on the exposed parts of the surface. *Frond dimorphy.* Sterile fronds regularly present (sometimes only apical portion fertile). Fertile parts similar to sterile part to narrowed (sometimes narrowed). *Fertile fronds.* Fully pinnate, with 2–18 pairs of pinnae and a conform terminal pinna. Stipe 10–51 cm long. Lamina 26–83 cm long. Largest fertile pinna is 1st or 2nd from base; stalk 0.3–1 cm; blade 11–31 × 0.4–2.5(–7) cm ; cusp 1.3–7 cm; widest at 3.5–11 cm; with 1–7 rows of closed areoles. *Sterile fronds.* Fully pinnate, with 1–9 pairs of pinnae. Stipe 10–39 cm long. Lamina 19–40 cm long (or longer). Largest sterile pinna: stalk 0.2–0.5 cm; blade 9.5–2.2 × 0.3–4.3 cm; cusp 1.5–5.5 cm; widest at 3–8 cm; with 1–6 rows of closed areoles. Main veins on upper surface raised, distinct, often veinlets distinct as well; veinlets free or anastomosing; free veinlets in the areoles excurrent and recurrent, and

forming a distinct row of excurrent marginal veinlets. Hydathodes frequent (especially on the marginal veinlets), with persistent calcareous scales. Margin cartilaginous, flat to (sometimes) thickened; without notches, but sometimes crenate. *Anatomy*. Upper surface: walls of epidermis not to weakly thickened (sometimes strongly contrasting with the thickened hypodermis); hypodermis a single layer, patchily present or complete, cell walls not to strongly thickened. Lower surface: walls of epidermis weakly to strongly thickened; hypodermis indistinct to distinct (sometimes very distinct). *Sori:* round (sometimes slightly elongated towards margin); in one row between adjacent veins; in one row between costa and margin; at 1-6(-13) mm from costa; 1.5-4 mm across; superficial to slightly sunken.

Selected illustrations — Blume (1829): pl. 57 & pl. 58 (as *Polypodium varians*); Hooker (1862): pl. 47.

Distribution — Throughout Malesia, but apparently very local or absent on Java, Malay Peninsula and the Lesser Sunda Islands.

Ecology — In primary forest, secondary forest, scrubland, on disturbed sites etc., often near streams. Low to high epiphyte, epilithic and terrestrial, common in most localities. Altitude sea level to 3500 m.

Vernacular names — New Guinea: howeraree (Dani); klopambugl bamba, kaulgi, tirikandekande (Iaro); ororl (Mendi); pork-tan (Wabag). Philippines: kigayin (Ifugao).

Notes on variability — This is a variable species. The variability has a strong geographic component and mainly concerns the rhizome (thickness, elongation) and rhizome scales (the degree to which a dark costa has developed, and the density of the marginal and superficial indument). The extremes may look very different. In West Malesia (Java, Sumatra, Borneo) the rhizomes are mostly short and thick, set with very long, dark-coloured rhizome scales with a recurved, subular, ciliate acumen. In East Malesia most specimens have thinner, more widely creeping rhizomes with brown, dentate-ciliate scales. I cannot draw any clear lines separating these two extremes, but I cannot exclude the possibility that in this circumscription a number of cryptic, small species are included. However, among these, the following forms almost certainly do not find a place:

Polypodium bellivenosum, a form with a conspicuously goniophleboid venation, described from New Guinea; *P. longicuspe*, a form with longly attenuated pinnae; *P. subaquatile*, an apparently rheophytic form with narrow, long pinnae $(22 \times 0.5 \text{ cm})$.

As in other pinnate species, juvenile fronds may be fertile. These may be simple, or tri- or pentaphyllous. One rather distinct form from New Guinea has the pinnae distinctly decurrent or connected on the rachis. It is connected to the normal form through specimens which are normally pinnate and have the pinnae adnate to the rachis.

Notes — 1. Although very similar in frond shape to S. taeniata (and often been confused), there is a surprisingly large set of characters in which these species differ:

alhidosauamata

	awayaamaa
Rhizome scales	peltate, often rigid, thickened, ciliate
Costa upper surface	rounded
Marginal notches	always absent
Excurrent veins	in marginal row
Calcareous scales	persistent

taeniata

pseudopeltate, soft, flaccid, entire to dentate grooved constantly present not in marginal row absent It is probably a coincidence that two of the most striking characters of *S. albido-squamata*, viz., the rigid rhizome scales with long cilia, and the persistent calcareous deposits on the hydathodes, are duplicated in the otherwise very dissimilar *S. platy-phylla*.

2. The persistence of the calcareous scales is due to the presence of epidermal papillae, protruding from the cells just bordering the hydathode. The calcareous scale appears to develop around the protruding papillae, and is thus fixed to the epidermis.

3. The marginal row of hydathodes is sometimes nearly or just confluent with the cartilaginous margin, which is then conspicuously crenate. These crenations are not notches as seen in other species of *Selliguea*; notches are situated between veins, not connected to them.

16. Selliguea laciniata (Bedd.) Hovenkamp, comb. nov. - Fig. 15

- Polypodium laciniatum Blume, Enum. Pl. Javae (1828) 131, nom. illeg., non Burman (1768); Lam. (1778); Gmelin (1791). Phymatopsis laciniatum J. Sm., Hist. Fil. (1875) 105; Ching, Acta Phytotax. Sin. 9 (1964) 192. Pleopeltis laciniata Bedd., Suppl. Ferns Brit. India (1892) 97; Alderw., Bull. Dép. Agric. Indes Néerl. 27 (1909) 10; Malayan Ferns, Suppl. 1 (1916) 399. Crypsinus laciniatus Holttum, Revis. Fl. Malaya 2, sec. ed. (1954) 198. Type: van Hasselt s.n. (L), Java.
- Polypodium macrochasmum Baker, J. Bot. NS 9 (1880) 216; Alderw., Malayan Ferns (1908) 664;
 Backer & Posth., Varenfl. Java (1939) 219. Phymatodes macrochasma Ching, Bull. Fan Mem.
 Inst. Biol. 10 (1941) 239. Crypsinus macrochasmus Copel., Gen. Fil. (1947) 206. Phymatopteris macrochasma Pichi Serm., Webbia 28 (1973) 463. Type: Beccari 468 (BM, BO, K, P), Sumatra, Mt Singalan.

Rhizome. Diameter 8–13 mm, internodes to 1.5–2 cm long. Vascular strands 10–11, bundle sheath absent or present. Sclerenchyma strands very many; mainly peripheral (occasionally scattered). Ground tissue not sclerified. Rhizome scales: pseudopeltate to peltate; spreading (rarely squarrose); $5-9 \times 1-2$ mm wide; acute; brown; evenly coloured or with a lighter margin (usually not hyaline); strongly to ciliate. Frond dimorphy. Monomorphic. Sterile fronds regularly present. Fertile parts similar to sterile parts. Fertile fronds. Stipe 18-40 cm long. Lamina 28-48 cm long, pinnatifid, rarely pinnate, pinnae 5-11 pairs, width of connecting strip 0.2-0.5 cm. Largest pinna is 2nd-6th from base; $1.7-2.7 \times 1.4-2.5$ cm wide; widest at 5-10 cm; with a cusp 1-5 cm long. Sterile fronds. Stipe 22–27 cm long. Lamina 23–31 cm long, pinnatifid, pinnae 5 or 6 pairs, width of connecting strip 0.1–0.4 cm. Largest sterile pinna: blade 13–19 \times 1.4–2 cm wide; widest at 5–6 cm; with a cusp 1–3 cm long. Lamina base cordate, lowest pinnae narrowed on basiscopic base or cut away to costa. Main veins on upper surface raised; connecting veins distinct or veinlets also distinct; veinlets free and anastomosing; free veinlets excurrent and recurrent. Hydathodes frequent, calcareous scales not persistent (rarely persistent). Margin cartilaginous, thickened; notches sporadically to regularly present (mostly). Sori: round; singly between adjacent veins; in one row between costa and margin; at 2-4 mm from costa; 3-4 mm across; slightly to deeply sunken.

Selected illustrations — Blume (1829): pl. 63; Holttum (1954): fig. 98; Piggott & Piggott, Ferns of Malaya in colour (1988): fig. 432–435.

Distribution — Malesia: Sumatra, Malay Pensinsula (extending into S Thailand), Java, Lesser Sunda Islands, Moluccas? (Ceram, one doubtful record). Distribution outside Malesia unknown (see note 2).

Ecology — Epiphytic on trunks or branches, epilithic, and on earth banks. In forest or more open situations. Altitude 100–2500 m.

Vernacular name — Wassánke (Alor).

Notes on variability — There is a distinct variability with a strong geographical component:

Java, Lesser Sunda Islands: Rhizome shortly creeping, internodes to 2 cm, with many sclerenchyma strands, aggregated to form a peripheral sheath (strands sometimes absent in specimens from Timor). Vascular strands without sclerified sheath. Scales pseudopeltate, densely ciliate. Base of frond usually cordate. Sori distinctly to deeply sunken.

Sumatra: Rhizome more or less widely creeping, internodes to 3 cm. Rhizome with scattered sclerenchyma strands, not concentrated in a peripheral sheath. Vascular strands with a sclerified sheath. Scales peltate, less densely ciliate. Base of frond more or less decurrent, margin more strongly thickened, with more distinct notches. Sori never deeply sunken.

The type of *Polypodium macrochasmum* Baker is intermediate between this and the 'Java' form: the scales are dentate, not ciliate, the lamina base is widely cordate and the sori are deeply sunken.

Malay Peninsula, S Thailand: Rhizome more or less widely creeping, internodes to 2.5 cm, mostly without sclerenchyma strands. Vascular strands with a sclerified sheath. Scales peltate, mainly short-dentate. Base of frond cordate but not deeply, more or less decurrent, margin strongly thickened, with distinct notches. Sori never deeply sunken.

The three forms are not sharply distinct. Specimens from the Malay Peninsula sometimes have a rhizome with scattered sclerenchyma strands, sometimes conform to the 'Sumatra' form, but with an indistinct peripheral sheath. Specimens from Java sometimes have a decurrent lamina base.

Notes — 1. Smells of coumarin when dry. The lower surface of the lamina is often noted to be distinctly glaucous in fresh material.

2. I cannot distinguish between Selliguea laciniata and Crypsinus quasidivaricatus or C. echinosporus from Taiwan. The identity of C. quasidivaricatus in particular needs further elucidation: what is often identified as quasidivaricatus from other localities (e.g. a large set collected by Iwatsuki et al. in Yunnan) is certainly not identical with the Taiwan specimens, but constitutes a mixture of several forms from the aggregate of species around C. glaucopsis.

17. Selliguea taeniata (Sw.) Parris — Fig. 16, 17

Selliguea taeniata Parris in Parris, Beaman & Beaman, Plants of Mt Kinabalu. I. Ferns and fern allies (1991) 152. — Polypodium taeniatum Sw., J. Bot. (Schrader) 1800 (1801) 26; Syn. Fil. (1806) 38, 232; C.Chr., Arkiv f. Bot. 9 (1910) 32; Mitt. Inst. Allg. Bot. Hamburg 7, 2 (1928) 161; Backer & Posth., Varenfl. Java (1939) 221. — Pleopeltis taeniata Alderw., Bull. Jard. Bot. Buitenzorg II, 16 (1914) 30; Malayan Ferns, Suppl. 1 (1916) 401. — Phymatodes taeniata Ching, Bull. Fan Mem. Inst. Biol. 10 (1941) 239. — Crypsinus taeniatus Copel., Gen. Fil. (1947) 206;



Holttum, Revis. Fl. Malaya 2, sec. ed. (1954) 195; Tagawa, Acta Phytotax. Geobot. 15 (1954) 143; Copel., Fern Fl. Philipp. (1960) 502; De Vol & Kuo, Flora of Taiwan (1975) 175; Kato & M.G. Price, Acta Phytotax. Geobot. 41 (1990) 70. — *Phymatopsis taeniata* Ching, Acta Phytotax. Sin. 9 (1964) 193. — *Phymatopteris taeniata* Pichi Serm., Webbia 28 (1973) 465. — Type: *Thunberg s.n.* (BM, fragm.), Java.

- Polypodium angustatum Blume, Enum. Pl. Javae (1828) 133, nom. illeg., non Swartz (1806); Fl. Javae Filic. (1829) 148; Mett., Farngatt. I. Polypodium (1857) 107. Pleuridium angustatum J. Sm., Ferns Brit. For. (1866) 96. Polypodium palmatum Blume var. angustatum Alderw., Malayan Ferns (1908) 670. Pleopeltis palmata (Blume) T. Moore var. angustata Alderw., Bull. Dép. Agric. Indes Néerl. 27 (1909) 11. Polypodium taeniatum Sw. var. angustatum C. Chr, Mitt. Inst. Allg. Bot. Hamburg 7, 2 (1928) 161. Type: van Hasselt s. n. (L), Java, Bantam, Sariak.
- Polypodium palmatum Blume, Enum. Pl. Javae (1828) 131; Fl. Javae Filic. (1829) 150; Mett., Farngatt. I. Polypodium (1857) 107; Hook., Sp. Fil. (1864) 88; Baker, Syn. Fil. (1868) 368; Alderw., Malayan Ferns (1908) 66. — Pleopeltis palmata T. Moore, Index Filic. (1862) 347; Alderw., Bull. Dép. Agric. Indes Néerl. 27 (1909) 11. — Pleuridium palmatum J. Sm., Ferns Brit. For. (1866) 96. — Phymatopsis palmatum J. Sm., Hist. Fil. (1875) 105. — Crypsinus taeniatus (Sw.) Copel. var. palmatus C. Chr., Ind. Fil. Suppl. 1 (1913) 126; Holttum, Revis. Fl. Malaya 2, sec. ed. (1954) 197. — Polypodium taeniatum Sw. var. palmatum C. Chr., Gard. Bull. Straits Settlem. 7 (1934) 310. — Phymatopteris palmata Pichi Serm., Webbia 28 (1973) 464. — Phymatopteris taeniata Pichi Serm. var. palmata Parris in Parris, Beaman & Beaman, Plants of Mt Kinabalu. I. Ferns and fern allies (1991) 108. — Selliguea taeniata (Sw.) Parris var. palmata Parris in Parris, Beaman & Beaman, Plants of Mt Kinabalu. I. Ferns and fern allies (1991) 152. — Type: Reinwardt s.n. (L), Moluccas, Tidore.
- Polypodium moseleyi Baker, J. Linn. Soc., Bot. 15 (1876) 110; Alderw., Malayan Ferns (1908) 669. Pleopeltis moseleyi Alderw., Bull. Dép. Agric. Indes Néerl. 27 (1909) 10; Malayan Ferns, Suppl. 1 (1916) 401. Crypsinus moseleyi Copel., Gen. Fil. (1947) 206. Type: Moseley s. n. (K), Moluccas, Ternate.
- Polypodium quinquefidum Baker, J. Bot. NS 9 (1880) 216; Alderw., Malayan Ferns (1908) 660. —
 Pleopeltis quinquefida Alderw., Bull. Dép. Agric. Indes Néerl. 27 (1909) 9; Malayan Ferns, Suppl. 1 (1916) 395. Type: Beccari s. n. (K), Sumatra, Mt Singalan.
- Polypodium griffithianum Hook. var. borneense H. Christ, Ann. Jard. Bot. Buitenzorg II, 5 (1905) 122; Alderw., Malayan Ferns (1908) 646. Pleopeltis griffithiana var. borneensis Alderw., Bull. Dép. Agric. Indes Néerl. 27 (1909) 6. Polypodium taeniatum Sw. var. borneense C. Chr., Mitt. Inst. Allg. Bot. Hamburg 7, 2 (1928) 161; Gard. Bull. Straits Settlem. 7 (1934) 310. Crypsinus taeniatus (Sw.) Copel. var. borneense Tagawa, Acta Phytotax. Geobot. 22 (1967) 189. Syntypes: Hallier 684, 3286 (BO), Borneo.
- Pleopeltis taenifrons Alderw., Bull. Jard. Bot. Buitenzorg II, 16 (1914) 31; Malayan Ferns, Suppl. 1 (1916) 402. — Polypodium taenifrons C. Chr., Ind. Fil. Suppl. prél. (1917) 28. — Type: Rachmat 896 (BO), Celebes, Sinadji.
- Pleopeltis crenulata [C. Presl, Tent. Pterid. (1836) 197, nom. nud. Polypodium crenulatum Mett., Farngatt. I. Polypodium (1857) 110, nom. nud.] Alderw., Bull. Jard. Bot. Buitenzorg II, 16 (1914) 59. — Polypodium crenulatum, C. Chr., Gard. Bull. Straits Settlem. 7 (1934) 310, nom. illeg., non Gmelin (1791). — Type: Rachmat 485 (BO), Celebes, Mt Klabat.
- Pleopeltis taenitidis Alderw., Bull. Jard. Bot. Buitenzorg II, 16 (1914) 31; Malayan Ferns, Suppl. 1 (1916) 402. — Polypodium taenitidis C. Chr., Ind. Fil. Suppl. prél. (1917) 28. — Type: Matthew 658 (BO, K, L), Sumatra, Indrapoera.
- Polypodium lepidosorum C. Chr., Leafl. Philipp. Bot. 9 (1933) 3166. Type: Elmer 22208 (B, BM, BO, K, P, SING, UC), Philippines, Luzon, Mt Pinatubo.
- Polypodium stenurum C. Chr., Bot. Jahrb. 66 (1933) 64. Syntypes: Kjellberg 1460, 2894, 3510 (all S), 3669 (BM, S), Celebes.
- Polypodium pakkaense C. Chr., Gard. Bull. Straits Settlem. 7 (1934) 310. Phymatopteris pakkaensis Parris in Parris, Beaman & Beaman, The plants of Mount Kinabalu. I. Ferns and fern allies

(1991) 107. — Selliguea pakkaensis Parris in Parris, Beaman & Beaman, Plants of Mt Kinabalu. I. Ferns and fern allies (1991) 152. — Type: Holttum 25515 (BM, BO, UC), Borneo, Mt Kinabalu.

- Polypodium mjöbergii C.Chr., Dansk Bot. Ark. 9 (3) (1937) 70. Type: Mjöberg 6 (BM), Borneo, Mt Murud.
- Crypsinus ramosii Copel., Fern Fl. Philipp. (1960) 506. Type: Ramos BS 14825 (MICH, UC), Philippines, Camiguin de Mindanao.

Rhizome. Diameter 5–9 mm, the internodes to 0.5–3 cm long. Vascular strands 13, bundle sheath incompletely to fully sclerified. Sclerenchyma strands many to very many; scattered or mainly around the vascular cylinder; isodiametric or periclinally flattened; massive or hollow. Ground tissue not sclerified. Rhizome scales: pseudopeltate; spreading; $9-12 \times 2.5-4.5$ mm wide; acute; dull brown; evenly coloured, often with an indistinct pseudocosta; entire or short-dentate, often with irregular, coarse protrusions. Frond dimorphy. Sterile fronds regularly present. Fertile parts narrowed. Fertile fronds. Stipe 24-36 cm long. Lamina 22-40(-110) cm long, fully pinnate, pinnae 5-12 (35) pairs, the lowest pinnae of well-developed fronds often free, others adnate. Largest fertile pinna is 1-4; blade $12-20 \times 0.8-3.5$ cm; widest at 4-7 cm; with a cusp 1.5-4 cm long. Sterile fronds. Stipe 19-39 cm long. Lamina 20-41 cm long, fully pinnate, pinnae 3–12 pairs, basal pinnae often fertile near apex. Largest sterile pinna: blade $12-17 \times 1.5-3.1(-4.5)$ cm; widest at 4-6.5 cm; with a cusp 1.5-3.5 cm long; with 4-6 rows of closed areoles. Rachis and costae on upper surface grooved. Connecting veins distinct to veinlets distinct; veinlets free and anastomosing; free veinlets excurrent and recurrent. Hydathodes frequent, calcareous scales not persistent. Margin cartilaginous, flat or thickened; notches regularly present. Anatomy. Upper surface: walls of epidermis weakly thickened; hypodermis absent. Lower surface: walls of epidermis weakly thickened; hypodermis absent. Sori: round, occasionally slightly elongate towards margin; single between adjacent veins; in one row between costa and margin; at 2-7 mm from costa; 2-3 mm across; superficial.

Selected illustrations — Blume (1829): pl. 62 (as *Polypodium angustatum*); Holttum (1954): fig. 96.

Distribution — Throughout Malesia, common, but rare in New Guinea.

Ecology — Low trunk epiphyte, epilithic or terrestrial, in forest, streambeds, roadsides etc. Sometimes in deep shade. Altitude sea level to 3400 m.

Notes on variability — The above description refers to the typical form (Fig. 17). Several more or less distinctly diverging forms can be distinguished, some of which have been described as species. However, the distinctions between these forms are gradual and, in my opinion, insufficient to keep them apart.

Polypodium palmatum — Smaller plants, with markedly dimorphic fronds. The pinnae are generally fewer, and are not or only slightly narrowed at the base, often connected along the costa by a 1-2 mm wide band. Sori are more often closer to the costa than to the margin. The margin is inconstantly notched (particularly in specimens from the Philippines).

This form differs from small plants of normal *Selliguea taeniata* mainly in the broadly adnate pinnae: even small plants of *S. taeniata* with few, connected pinnae have these distinctly narrowed at the base. On the other hand, larger specimens of

'palmatum' may show a taeniata-morphology. It may be merely a smaller form of S. taeniata, restricted to the eastern part of the distribution range (Malay Peninsula, Borneo, Philippines, Moluccas), and the predominant form in the Philippines. Crypsinus ramosii is a simple-fronded form entirely without marginal notches.

Polypodium quinquefidum — As '*palmatum*', but the rhizome scales shining and the pinnae long, narrow, with a long cusp. Few specimens only, in mossy forest in Borneo and Celebes.

Polypodium pakkaense — As 'palmatum', but the fronds pinnatifid, all pinnae connected along the rachis, not or hardly dimorphic, texture more coriaceous, venation more prominent, margin very distinctly notched, almost toothed, the rhizome usually with fewer sclerenchyma strands. Restricted to Mt Kinabalu, at the upper end of the altitudinal range (1500-3400 m) of *Selliguea taeniata*. In this region, otherwise ordinary specimens of *S. taeniata* have often also a markedly thicker texture, more prominent veins, fewer sclerenchyma strands, distinct notches and costal sori, differing from true *P. pakkaense* only in the separate pinnae. There is, however, a continuous transition in frond shape and dissection, with fully fertile pinnae more strongly narrowed at the base than partially fertile or sterile pinnae.

Polypodium stenurum — A slender form, at first sight very different. It has long fronds (to over 1 m incl. stipe) with a large number of narrow pinnae (to 35 or more), a thin texture, and an indistinctly cartilaginous, but very distinctly notched margin. The rhizome scales of one of the syntype specimens (*Kjellberg 3669*, marked as type in S) are scabrid with many distinct papillae on the surfaces and margins. However, such scabrid scales occur in this specimen only. In all other characters it is either not clearly distinct from *Selliguea taeniata*, or connected to it by intermediates.

An unnamed form has rhizome scales which are more strongly contracted to a narrow acumen, and pinnae with a strongly narrowed, often abruptly cuneate base, and a short stipe. It is represented by few specimens from Borneo (*Mjöberg 1, 8; Native collector 112; Clemens 28153*).

Juvenile plants sometimes have simple fronds, which nevertheless may be fertile (*Loher 882, Parris 5719, Matthew s. n.*, 1-3-1907, all K). Such plants have been separated as var. *borneense*. Intermediates have the pinnae connected along the costa.

Notes -1. Polypodium griffithianum var. borneense was based on forms with simple fronds, which are superficially similar to Crypsinus griffithianus (from mainland Asia). Later, pinnate forms with relatively wide pinnae have also been assigned to var. borneense. There is, however, no justification to separate either the simple, or these pinnate forms.

2. Both *Polypodium palmatum* and *P. pakkaense* are superficially similar to *Selliguea laciniata*. They can be distinguished from that species easily by the characteristically dull, entire scales. There are, however, sometimes intermediates between *S. taeniata* and *S. laciniata* which suggest that, occasionally, the two species may hybridise.

18. Selliguea subtaeniata (Alderw.) Hovenkamp, comb. nov. - Fig. 18

Pleopeltis subtaeniata Alderw., Bull. Jard. Bot. Buitenzorg II, 16 (1914) 30; Malayan Ferns, Suppl. 1 (1916) 402. — Polypodium subtaeniatum C. Chr., Ind. Fil. Suppl. prél. (1917) 28; Gard. Bull. Straits Settlem. 7 (1934) 309. — Lectotype (here selected) Forbes 2061 (BM, BO), Sumatra, Berastagi.

- Pleopeltis matthewi Alderw., Bull. Jard. Bot. Buitenzorg II, 16 (1914) 30; Malayan Ferns, Suppl. 1 (1916) 401. Polypodium matthewi C.Chr., Ind. Fil. Suppl. prél. (1917) 27, nom. illeg., non Tutcher (1905). Type: Matthew 503 (BM, BO, K), Sumatra, Merapi.
- Pleopeltis pseudo-laciniata Alderw., Bull. Jard. Bot. Buitenzorg II, 28 (1918) 38. Polypodium pseudo-laciniata C.Chr., Ind. Fil. Suppl. 3 (1934) 156. Syntypes: Bünnemeijer 1275 (L), Sumatra, Merapi; Bünnemeijer 889 (L), Sumatra, Talamau.

Rhizome. Diameter 6–8 mm, the internodes to 0.5–1 cm long. Vascular strands 8–12, bundle sheath absent. Sclerenchyma strands very many; scattered or mainly peripheral; isodiametric or periclinally flattened; massive. Ground tissue lightly sclerified or with peripheral sclerified sheath. Rhizome scales: pseudopeltate; spreading to squarrose; $5-10 \times 2-2.5$ mm; acute or contracted to a narrow acumen; brown to blackish (often mottled); evenly coloured or with a lighter margin (sometimes very narrow); strongly dentate, or sometimes with an entire acumen. Frond dimorphy. Sterile fronds rarely present. Fertile parts similar to sterile part. Fertile fronds. Stipe 20-48 cm long. Lamina 19-36 cm long, pinnatifid to fully pinnate, pinnae 1-5 pairs, width of connecting strip 0–0.2 cm (mostly absent). Largest fertile pinna is 1–4; blade $15-22 \times$ 1-1.5 cm wide; widest at 4-9 cm; with a cusp 2-4 cm long. Sterile fronds. Stipe 29 cm long. Lamina 18 cm long or longer, fully pinnate, pinnae 2 pairs. Largest sterile pinna: blade 13 × 1.6 cm; widest at 5 cm; with a cusp 1 cm long. Basal pinnae unequally broadly adnate, lamina cut to costa on basiscopic side. Main veins distinct, on upper surface raised; connecting veins also distinct; veinlets free and anastomosing; free veinlets excurrent and recurrent. Hydathodes frequent, calcareous scales not persistent. Margin cartilaginous, thickened; notches regularly present. Anatomy. Upper surface: walls of epidermis strongly thickened; hypodermis a single layer, cell walls thickened to strongly thickened. Lower surface: walls of epidermis strongly thickened; hypodermis indistinct or distinct. Sori: round; single between adjacent veins; in one row between costa and margin; at 2-3 mm from costa; 2-4 mm across; superficial.

Distribution — Sumatra.

Ecology — Epiphytic or terrestrial, in forest. Altitude 900-2400 m.

Note — Selliguea subtaeniata combines characters of S. laciniata and S. taeniata, but within its range it is sufficiently distinct from either species to be retained as a separate species. In the deeply dissected lamina it is like S. taeniata, but in the characters of the rhizome and rhizome scales it resembles S. laciniata. With S. laciniata it also shares the shape of the basis of the pinnae, which is unequal and narrowed at the basiscopic side, often to the midrib. The pinna-base in S. taeniata, if unequal, is nearly always narrowed at the acroscopic side.

19. Selliguea violascens (Mett.) Hovenkamp, comb. nov. — Fig. 19

Polypodium violascens Mett. in Miq., Ann. Mus. Bot. Lugd.-Bat. 2 (1866) 227; Baker, Syn. Fil. (1868) 365; Alderw., Malayan Ferns (1908) 665; Backer & Posth., Varenfl. Java (1939) 220. — Pleopeltis violascens Alderw., Bull. Dép. Agric. Indes Néerl. 27 (1909) 10; Malayan Ferns, Suppl. 1 (1916) 400. — Type: Wichura s.n. (B), Java.

Rhizome. Diameter 4-8 mm, internodes to 1-2.5 cm long. Vascular strands 10-11, bundle sheath fully sclerified, 1 or 2 cells thick. Sclerenchyma strands few, incon-



Fig. 19-22. – 19: Selliguea violascens (Mett.) Hovenkamp. – 20: S. lagunensis (H. Christ) Hovenkamp. – 21: S. glauca (J. Sm. ex T. Moore) Hovenkamp. – 22: S. triloba (Houtt.) M.G. Price. — Scale bars = 1 cm.

spicuous; mainly peripheral, or around the vascular cylinder; isodiametric; massive. Ground tissue not or lightly sclerified. *Rhizome scales:* pseudopeltate or peltate; spreading; $6.5-11 \times 2-2.2$ mm; acute or contracted to a narrow acumen; shiny brown; evenly coloured; short-dentate to strongly dentate, more strongly dentate towards apex. Frond dimorphy. Fully sterile fronds normally absent. Fertile parts narrowed. Fertile fronds. Stipe 13.5–21 cm long. Lamina 23–32 cm long (or longer), fully pinnate. Pinnae 10 or 11 pairs, close, inserted more or less transversally to the rachis, sometimes overlapping. Largest fertile pinna is 2-4, blade 13-15 × 1.1-1.5 cm; narrowed at base, widest at 6-8 cm, with a cusp to 1 cm long. Narrow scales often persistent on costa and veins. Rachis and costae on upper surface grooved, main veins on upper surface distinct, not raised or raised, connecting veins also distinct; veinlets free and anastomosing; free veinlets excurrent and recurrent. Hydathodes frequent, calcareous scales not persistent. Margin cartilaginous, thickened; notches regularly present. Anatomy. Upper surface: walls of epidermis weakly thickened; hypodermis a single layer, patchily present, cell walls not thickened. Lower surface: walls of epidermis strongly thickened; hypodermis absent. Sori: round; single between adjacent veins; in one row between costa and margin; at 2.5 mm from costa; 3 mm across; superficial to deeply sunken.

Distribution — Java, Sumatra.

Ecology - Epiphytic in forests. Altitude 1300-2700 m.

Notes on variability — Variable mainly in the sori, which may be sunken (sometimes very deeply, forming high papillae on the upper surface) to completely superficial.

Note — A neglected but not particularly rare species, easily recognisable by the rhizome which has distinct sclerenchyma except around the vascular strands, the distinctive, shiny, dentate rhizome scales and the closely spaced, strongly transversely set pinnae. *Selliguea taeniata* may occasionally have the lower pinnae similarly inserted transversally, but always has dull brown, entire scales.

20. Selliguea lagunensis (H.Christ) Hovenkamp, comb. nov. - Fig. 20

Polypodium lagunense H. Christ, Bull. Herb. Boissier 6 (1898) 201; Alderw., Malayan Ferns (1908) 667. — Pleopeltis lagunense Alderw., Bull. Dép. Agric. Indes Néerl. 27 (1909) 10; Malayan Ferns, Suppl. 1 (1916) 400. — Crypsinus lagunensis Copel., Gen. Fil. (1947) 206; Fern Fl. Philipp. (1960) 503. — Phymatopteris lagunense Pichi Serm., Webbia 28 (1973) 463. — Type: Loher 90 (K, P), Philippines, Luzon.

Rhizome. Diameter 3.5–4 mm, the internodes to 1–1.5 cm long. Vascular strands 10, bundle sheath hyaline, or partially sclerified. Sclerenchyma strands many to very many; scattered; isodiametric; massive to hollow. Ground tissue not sclerified. *Rhizome scales:* peltate; spreading; $4-4.5 \times 1-1.3$ mm; acute; straw-coloured to brown with a lighter margin; remotely and weakly to short-dentate. *Frond dimorphy.* Fully sterile fronds rarely present. Fertile parts strongly contracted. *Fertile fronds.* Stipe 6.5–25 cm long. Lamina 13.5–26 cm long, fully pinnate, pinnae 5–10 (the lower pairs often wholly or partly sterile). Largest fully fertile pinna, stalk 0–0.2 cm; blade 4.5–13.5 × 0.3–0.5(–1.2) cm. *Sterile fronds.* Stipe 4.5 cm long. Lamina 8 cm long, fully pinnate. Largest sterile pinna is 1 (usually); stalk 0.2–0.5 cm; blade 6–11 × 1.2–

2.2 cm; widest at 2.5–3.5 cm; with a cusp 0.5–2.5 cm long. Main veins on the upper surface not raised, connecting veins distinct. Hydathodes frequent, calcareous scales not persistent. Margin cartilaginous, thickened; notches regularly present, in fertile fronds sporadically to regularly present, fainter than in sterile parts. *Anatomy*. Upper surface: walls of epidermis weakly thickened; hypodermis a single layer, patchily present, cell walls not thickened. Lower surface: walls of epidermis weakly thickened; in one row between adjacent veins; in one row between costa and margin; at 1 mm from costa; 1–2 mm across; superficial.

Selected illustration — H. Christ (1898): pl. 3, fig 4 a-d.

Distribution — Philippines.

Ecology — Epiphytic (few data available). Altitude 1050-1850 m.

Note — The internally strongly dimorphic fronds make this an easily recognisable species. Both fully sterile and fully fertile fronds are rare, usually at least the apical part of the apical segment is fertile, or the basal part of the basal pinnae sterile.

21. Selliguea glauca (J.Sm. ex T. Moore) Hovenkamp, comb. nov. - Fig. 21

- Drynaria glauca Brack., U. S. Expl. Exped. Filic. 16, Bot. (1854) 54. Polypodium glaucum Hook., Sp. Fil. 5 (1864) 88; Alderw., Malayan Ferns (1908) 660, nom. illeg., non Thunberg (1784), Swartz (1788), Raddi (1825), Mettenius (1857). Crypsinus glaucus Copel., Gen. Fil. (1947) 206; Fern Fl. Philipp. (1960) 501. Type: U.S. Expl. Exped. Filic. s.n., Philippines, Luzon, Mt Maijaijai, not seen.
- Drynaria glauca J. Sm., J. Bot. (Hooker) 1 (1841) 397, nom. nud. Polypodium glaucum Mett., Farngatt. I. Polypodium (1857) 102, nom. illeg., non Thunberg (1784), Swartz (1788), Raddi (1825). — Pleopeltis glauca T. Moore, Index Filic. (1857) lxxviii; (1862) 346; Alderw., Bull. Dép. Agric. Indes Néerl. 27 (1909) 9. — Polypodium glauco-pruinatum C. Chr., Ind. Fil. (1906) 248. — Type: Cuming 124 (B, BM, G, K, L, P, SING), Philippines, Luzon.

Rhizome. Diameter 4-6 mm, the internodes to 2.5 cm long. Vascular strands 10-11, bundle sheath hyaline to fully sclerified. Sclerenchyma strands many; central or around the vascular cylinder; isodiametric to periclinally flattened; massive. Ground tissue not sclerified. *Rhizome scales:* peltate; spreading; $9-17 \times 1.5-2.2$ mm; acute; brown to blackish, thick, shining, brittle; evenly coloured; entire. Frond dimorphy. Sterile fronds usually absent. Fertile parts similar to sterile part. Fertile fronds. Stipe 5.5-27 cm long. Lamina 20-40 cm long, pinnatifid (rarely simple or trilobed); pinnae in 2-11 pairs, connected by a 0.2-0.4 cm wide strip; at least upper pinnae, often also basal pinae ascending at 45°, apical segment conspicuous, long, often the only segment to be fertile. Largest fertile pinna is 2nd to 4th from base; blade $10-19.5 \times$ 0.9-1.5 cm; widest at 2-6 cm from base (often tapering from near pinna-base). Sterile fronds. Largest sterile pinna blade 13.5×1.5 cm; widest at 2 cm from base (often tapering from near base). Main veins on upper surface not raised (rarely raised), distinct. Hydathodes frequent, calcareous scales not persistent. Margin cartilaginous, thickened to strongly thickened; notches sporadically to regularly present. Anatomy. Upper surface: walls of epidermis weakly to strongly thickened; hypodermis a single layer, cell walls not thickened. Lower surface: walls of epidermis not or weakly thickened; hypodermis absent or indistinct. Sori: round; in one row between adjacent veins; in one row between costa and margin; at 1.5-3 mm from costa; 3 mm across; superficial.

Distribution — Philippines.

Ecology — Epiphytic. Altitude 1050–1700 m.

Notes -1. A very characteristic species, easily recognisable by the thick, black, brittle rhizome scales and the glaucous fronds.

2. The heavy waxy deposit on the rhizome is composed of fine needles up to 2 mm long. They are often also deposited on debris on the surface of the lamina, which suggests that deposition may continue after the plant has been collected.

3. Nomenclature: In some cases there is no indication at all on which of the two types a particular combination is based. Fortunately, it is totally irrelevant, as all combinations are fully homonymous synonyms.

22. Selliguea triloba (Houtt.) M.G. Price - Fig. 22

- Selliguea triloba M.G. Price, Contr. Univ. Mich. Herb. 17 (1990) 276; Parris in Parris, Beaman & Beaman, Plants of Mt Kinabalu. I. Ferns and fern allies (1991) 108, 152. Polypodium trilobum Houtt., Nat. Hist. (1783) 148; Backer & Posth., Varenfl. Java (1939) 221. Phymatodes triloba Ching, Bull. Fan Mem. Inst. Biol. 1 (1941) 239. Crypsinus trilobus Copel., Gen. Fil. (1947) 206; Holttum, Revis. Fl. Malaya 2, sec. ed. (1954) 196; Copel., Fern Fl. Philipp. (1960) 503. Phymatopsis triloba Ching, Acta Phytotax. Sin. 9 (1964) 194. Phymatopteris triloba Pichi Serm., Webbia 2 (1973) 465. Type: Thunberg s. n., Java, not traced.
- Polypodium triphyllum Jacq., Coll. (1788) 126. Phymatodes triphylla C. Chr. & Tardieu, Not. Syst. VIII (1939) 284; Tardieu & C. Chr., Fl. Indo-Chine 7 (1941) 470. — Type: Jacquin, pl. 22 fig. 1 (see note).
- Polypodium incurvatum Blume, Enum. Pl. Javae (1828) 126; Fl. Javae Filic. (1829) 151; Hook., Sp. Fil. (1864) 77; Baker, Syn. Fil. (1868) 363; Alderw., Malayan Ferns (1908) 663. — Pleopeltis incurvata T.Moore, Gard. Chron. (1860) 1105; Bedd., Handb. Ferns Brit. Ind. (1883) 364; Alderw., Bull. Dép. Agric. Indes Néerl. 27 (1909) 10; Malayan Ferns, Suppl. 1 (1916) 399; Ibid., Corrections (1917) 58. — Phymatopsis incurvatum J.Sm., Hist. Fil. (1875) 105. — Type: Blume s.n. (L, P), Java.
- Selliguea matutumensis Copel., Philipp. J. Sci. 81 (1952) 44; Fern Fl. Philipp. (1960) 509. Type: Copel. s. n. (UC), Philippines, Mindanao, Mt Matutum.

Rhizome. Diameter 4-6.5 mm, internodes to 1.5-4 cm long. Vascular strands 11-14, bundle sheath partially sclerified. Sclerenchyma strands very many; scattered; isodiametric to periclinally flattened (flattened and small at periphery); hollow or perforated. Ground tissue not sclerified. Rhizome scales: peltate; appressed or spreading; $3.8-4 \times 1.2-1.8$ mm; obtuse to acute (often apiculate); whitish to brown; with a lighter margin; entire to short-dentate, also irregularly lacerate. Frond dimorphy. Sterile fronds regularly present. Fertile parts strongly contracted. Fertile fronds. Stipe 14-50 cm long. Lamina simple, pinnatifid or fully pinnate, rarely bipinnatifid, 13-27 cm long. Simple fronds 1-1.3 cm wide, widest at 3-12 cm from base. Pinnatifid/ pinnate fronds with 3–7 pairs of pinnae, width of connecting strip 0.1 cm (or less). Largest fertile pinna is 1; blade $11-18 \times 0.7-1.3$ cm; with a cusp 0-2 cm long. Sterile fronds. Stipe 7-40 cm long. Lamina simple, trilobed or pinnatifid, 6-33 cm long. Simple fronds (or end lobes of trilobed fronds) 4.1-8.8 cm wide, simple fronds widest at 2 cm from base. Pinnae 1-4(-7) pairs, width of connecting strip 0.4-2 cm. Largest sterile pinna: blade $4.5-15(-21) \times 2.3-5.5$ cm; widest at 0.2-0.5 from the base; acute or cuspidate with a cusp to 2 cm long. Main veins on upper surface not raised, distinct, rarely veinlets also distinct; veinlets free and anastomosing; free veinlets excurrent and recurrent. Hydathodes absent or present. Margin cartilaginous, thickened; notches sporadically or regularly present, in fertile fronds sometimes absent. *Anatomy*. Upper surface: walls of epidermis strongly thickened; hypodermis a single layer, cell walls thickened. Lower surface: walls of epidermis strongly to very strongly thickened; hypodermis distinct. *Sori:* round; single between adjacent veins; in one row between costa and margin; at 1.5-3 mm from costa; 4 mm across; deeply sunken.

Selected illustrations — Blume (1829): pl. 65 (as *Polypodium incurvatum*); Diels in Engler & Prantl, Nat. Pflanzenfam. 1, 4 (1899): fig. 165 (as *Polypodium incurvatum*); Tardieu & C.Christensen (1951): fig. 55 4, 5 (as *Pleopeltis triphylla*); Holttum (1954): fig. 97; Piggott & Piggott, Ferns of Malaya in colour (1988): fig. 428–431.

Distribution — Malesia: Sumatra, Malay Peninsula, Java, Borneo, Philippines, Moluccas. Outside Malesia: Indochina, Hainan.

Ecology — Epiphytic, epilithic or terrestrial, in forest, also in more exposed situations. Altitude 540–3200 m.

Notes on variability — Variation mainly concerns the number of lateral lobes, the presence of hydathodes, and the degree to which the margin is notched. In specimens from Java and Sumatra hydathodes are absent, and fertile fronds are less distinctly notched than sterile fronds. In specimens from the Malay Peninsula, Borneo and the Philippines, hydathodes may be present in both sterile and fertile fronds, occasionally they are present in fertile fronds only. Specimens from these latter areas have also more regularly notched fertile fronds.

Depauperate forms have simple fertile and sterile fronds (Borneo: Nooteboom & Chai 1803, Philippines: Copeland s. n., type of Selliguea matutumensis). These can be distinguished from S. heterocarpa by the distinctive rhizome scales.

Note — Polypodium triphyllum Jacq.: the identification of Jacquin's plate as Selliguea triloba by Christensen & Tardieu is open to doubt. Jacquin cites material from Java and Ceylon. There are no species of Selliguea in common between Java and Ceylon, and it is therefore equally likely that the plate refers to S. triloba from Java or to Crypsinus montanus Sledge, which is the only species of Selliguea on Ceylon. It should however also be noted that Kunze (Farrnkräuter 1847: 117) was convinced that P. triphyllum Jacq. is identical to P. ensiforme Thunb., and that the name P. triphyllum Jacq. appears as a synonym to a specimen of P. ensiforme in PRC (collected by Drège). Polypodium ensiforme is a Cape endemic with some superficial similarities to a pinnatifid Selliguea. Both Ceylon and the Cape were regular stops on the journey to Java, and a mix-up may very well have occurred. Judging from the plate itself, its identification with P. ensiforme or C. montanus is more likely than with S. triloba.

23. Selliguea pyrolifolia (Goldm.) Hovenkamp, comb. nov. - Fig. 23

Polypodium pyrolaefolium Goldm., Nov. Actorum Acad. Caes. Leop. Nat. Cur. (1843) 453. — Crypsinus pyrolifolius Copel., Gen. Fil. (1947) 206; Fern Fl. Philipp. (1960) 503. — Type: Meyen s.n., Philippnes, Luzon, Manila, not seen.

Marginaria nummularia C. Presl, Tent. Pterid. (1836) 188, nom. nud. — Crypsinus nummularius C. Presl, Epim. Bot. (1851) 123, nom. superfl. — Craspedaria nummularia Fée, Gen. Filic. (?1853) 264. — Polypodium nummularium Mett., Farngatt. I. Polypodium (1857) 105, nom superfl.. — Goniophlebium nummularium T. Moore, Index Filic. (1857) lxxiv; (1861) 262. — Pleopeltis nummularia Alderw., Bull. Dép. Agric. Indes Néerl. 27 (1909) 4. — Type: Meyen s.n. (B), Philippines, Luzon.

Polypodium hammatisorum Harr., J. Linn. Soc., Bot. 16 (1877) 32; Alderw., Malayan Ferns (1908) 634. — Pleopeltis hammatisora Alderw., Bull. Dép. Agric. Indes Néerl. 27 (1909) 4. — Type: Steere s. n. (K), Luzon, Mt Mahayhay.

Rhizome. Diameter 1 mm, internodes to 0.9–1.5 cm long. Vascular strands 4, bundle sheath hyaline. Sclerenchyma strands few; scattered; isodiametric; massive. Ground tissue not sclerified. *Rhizome scales:* peltate; spreading; $3-5 \times 0.6-0.8$ mm; acute; straw-coloured (rarely), or brown; evenly coloured; remotely and weakly dentate or short-dentate. *Frond dimorphy.* Sterile fronds regularly present. Fertile parts strongly contracted. *Fertile fronds.* Simple. Stipe 1–7 cm long. Lamina 1.5–10 × 0.2–0.3 cm, index 1.4–linear. *Sterile fronds.* Simple. Stipe 0.2–4 cm long. Lamina 1.4–4 × 1–1.7 cm, index 0.9–2.4, widest at 0.3–0.5 from base. Base cuneate to cordate,

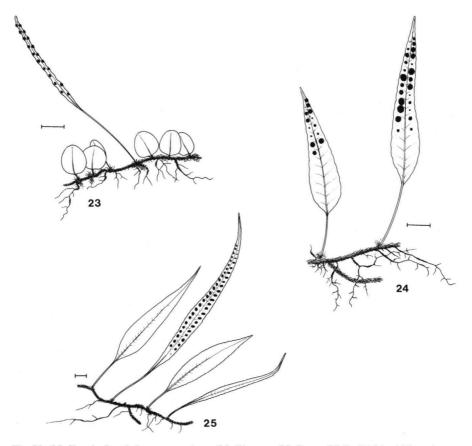


Fig. 23–25. Simple-fronded representatives of *Selliguea*. – 23: *S. pyrolifolia* (Goldm.) Hovenkamp. – 24: *S. whitfordii* (Copel.) Hovenkamp. – 25: *S. simplicissima* (F. Muell.) Hovenkamp. – Scale bar = 1 cm.

apex round to acuminate. Costa only distinct; veinlets free or anastomosing; free veinlets excurrent, rarely recurrent. Hydathodes frequent, calcareous scales not persistent. Margin cartilaginous, flat to thickened; notches regularly present, in fertile fronds absent or irregularly present. *Anatomy*. Upper surface: walls of epidermis strongly thickened; hypodermis absent or a single layer, patchily present, cell walls not thickened. Lower surface: walls of epidermis strongly thickened; hypodermis absent. *Sori:* round; single between adjacent veins; in one row between costa and margin; 2–3 mm across; slightly sunken.

Selected illustrations — Copeland (1947): pl. 8, fig. 1a, b; Alderwerelt, Bull. Dép. Agric. Indes Néerl. 27 (1909): pl. 2.

Distribution — Philippines.

Ecology - No data. Altitude: few data, one record from 900 m.

Note — *Selliguea whitfordii* is similar, differing only in its less strongly dimorphic fronds, the fertile fronds wider, regularly with notches.

24. Selliguea whitfordii (Copel.) Hovenkamp, comb. nov. --- Fig. 24

Polypodium whitfordii Copel., Philipp. J. Sci. 1, Suppl. (1906) 256; Alderw., Malayan Ferns (1908) 646. — Pleopeltis whitfordii Alderw., Bull. Dép. Agric. Indes Néerl. 27 (1909) 6; Malayan Ferns, Suppl. 1 (1916) 384. — Crypsinus whitfordii Copel., Gen. Fil. (1947) 206; Fern Fl. Philipp. (1960) 504. — Type: Copeland 2032 (B, P), Philippines, Luzon, Mt Mariveles.

Crypsinus subdimorphus Copel., Fern Fl. Philipp. (1960) 505. — Type: Copeland s. n. (UC), Philippines, Luzon, Mt Maquiling.

Rhizome. Diameter 1-1.5 mm, internodes to 1-3 cm long. Vascular strands 4 or 5, bundle sheath partially or fully sclerified. Sclerenchyma strands few; scattered; isodiametric; massive. Ground tissue not sclerified. Rhizome scales: peltate; spreading; $4-5 \times 0.5-0.9$ mm; acute; brown; evenly coloured; remotely and weakly dentate to short-dentate, or irregularly strongly dentate. Frond dimorphy. Sterile fronds regularly present. Fertile parts narrowed. Fertile fronds. Stipe 1.5-6.5(-9) cm long. Lamina simple, $2.2-10(-13) \times 0.6-1.6$ cm, index 2.4-11, widest at 0.2-0.4 from base. Sterile fronds. Stipe 1.3-5.5(-7.5) cm long. Lamina simple, $1.5-5(-9.5) \times$ 0.8-2.8 cm, index 1.3-3.3, widest at 0.2-0.6 from base. Main veins on upper surface raised, distinct; veinlets free (rarely), or anastomosing; free veinlets excurrent and recurrent. Hydathodes frequent, calcareous scales not persistent. Margin cartilaginous, thickened; notches regularly present. Anatomy. Upper surface: walls of epidermis strongly thickened; hypodermis a single layer, patchily present, cell walls not thickened. Lower surface: walls of epidermis strongly thickened; hypodermis absent. Sori: round; single between adjacent veins (rarely a few areoles with 2 sori); in one row between costa and margin (rarely a few in a second row); 2.5-4 mm across; slightly sunken.

Distribution — Philippines (9 specimens).

Ecology — Epiphytic or epilithic. Altitude 1000–1600 m.

Notes on variability - Crypsinus subdimorphus is a large form.

Notes -1. Closely allied to *Selliguea pyrolifolia*, which is more strongly dimorphic, with a more obscure venation, fertile fronds with a sinuose margin, often without notches.

2. Selliguea whitfordii has been confused with Crypsinus rhynchophyllus, from Asia, which has fronds with a rounded apex, sori often in a fertile spike on a sterile frond, free veinlets mostly recurrent and a thicker, more distinctly cartilaginous margin.

3. Phymatopsis philippinensis was described by Ching [Acta Phytotax. Sin. 9 (1964) 186], based on one specimen from northern Luzon (Williams 1577). He stated that it is related to, but smaller than Phymatopteris yakushimensis, in my opinion a small form of P. hastata. According to Price [Philipp. J. Biol. 1 (1972) 46] it is possibly identical with Selliguea whitfordii. As Ching's description is rather vague, neither possibility can be excluded. It would not be wholly surprising to find a member of an otherwise continental group on northern Luzon. The type could not be located.

25. Selliguea simplicissima (F. Muell.) Hovenkamp, comb. nov. - Fig. 25

Polypodium simplicissimum F. Muell., Fragm. Phyt. Austral. (1871) 156 (see note 2); F.M. Bailey, Queensl. Fl. (1902) 1985. — Crypsinus simplicissimus S.B. Andrews, Austrobaileya 1 (1977) 12; Ferns of Queensland (1990) 272. — Phymatopteris simplicissima Pichi Serm., Webbia 45 (2) (1991) 332. — Type: Dallachy s.n. (K. P), Australia, Rockingham Bay.
Polypodium simplicissimum var. wurunuran Domin, Bibl. Bot. 85 (1913) 175. — Type not found.

Rhizome. Diameter 2-3 mm, internodes to 2.5 cm long. Vascular strands 6-8, bundle sheath fully sclerified. Sclerenchyma strands absent to many; scattered; isodiametric; massive. Ground tissue not sclerified. Rhizome scales: peltate; spreading; 3.5 \times 0.8–1.5 mm; acute or contracted to a narrow acumen; straw-coloured to brown; evenly coloured or with a lighter margin; remotely and weakly dentate. Frond dimorphy. Sterile fronds regularly present. Fertile parts narrowed. Fertile fronds. Simple. Stipe 1–4.5 cm long. Lamina 6–16.5 \times 0.9–1.2 cm, index 6–16, widest at 0.2–0.4 from base. Sterile fronds. Simple. Stipe 1-4 cm long. Lamina $4.5-11.5 \times 1.2-2.1$ cm, index 3-6, widest at 0.3-0.5 from base. Main veins on upper surface not raised, distinct, sometimes connecting veins also distinct; veinlets free and anastomosing; free veinlets mostly recurrent, some excurrent. Hydathodes frequent, calcareous scales not persistent. Margin cartilaginous, thickened; notches regularly present or abundant, in fertile fronds regularly present. Anatomy. Upper surface: walls of epidermis strongly thickened; the hypodermis absent. Lower surface: walls of epidermis weakly to strongly thickened; hypodermis absent. Sori: round; in one row between adjacent veins; in one row between costa and margin; 3-4 mm across; superficial.

Selected illustrations — Andrews (1990): fig. 28. 2.

Distribution — Australia: Queensland.

Ecology — Epiphytic or epilithic, usually in rain forest. Altitude 1000-1600 m. Notes — 1. An extremely local species, restricted to the Atherton Tablelands in Queensland, where it appears to be quite common.

2. A collection from Rockingham Bay was distributed by Mueller as *Polypodium* simplicissimum, but when he described it in 1870 (F.Mueller, 1871: 120) he considered it as identical with *P. lanceola*, without having validated the name *P. simplicissimum*. The latter name was validated in an addendum in 1871.

26. Selliguea lanceola (Mett.) E. Fourn. - Fig. 26

- Selliguea lanceola E. Fourn., Ann. Sc. Nat. Bot. 18 (1873) 280; Ching, Sunyatsenia 5 (1940) 260;
 Brownlie, Fl. Nouv.-Caléd. 3. Ptérid. (1969) 288. Polypodium lanceola Mett., Ann. Sci. Nat
 Bot. 4 (1861) 78. Type: Vieillard 1595 (P), New Caledonia.
- Selliguea peltatisquama E. Fourn., Bull. Soc. Bot. France 16 (1869). Type: Balansa 860 (P). New Caledonia.

Polypodium selligueoides Baker, Syn. Fil. ed. 2 (1874) 513. — Syntypes: Deplanche s.n. (B, K, P), Pancher s.n. (not found), Richard s.n. (not found), New Caledonia.

Selliguea heterocarpoides Copel., Univ. Calif. Publ. Bot. 14 (16) (1929) 367. — Type: Franc s.n. (UC), New Caledonia, Nouméa.

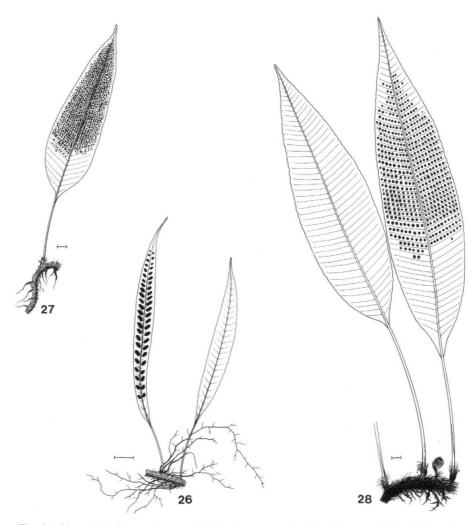


Fig. 26–28. – 26: Selliguea lanceola (Mett.) E. Fourn. – 27: S. albidopaleata (Copel.) Parris. – 28: S. platyphylla (Sw.) Ching. — Scale bars = 1 cm.

Rhizome. Diameter 2-4 mm, internodes to 1-2 cm long. Vascular strands 7, bundle sheath fully sclerified. Sclerenchyma strands many; scattered; isodiametric or periclinally flattened; massive or hollow. Ground tissue not sclerified. Rhizome scales: peltate; appressed to spreading; $2.5-3 \times 1.5-3$ mm; obtuse, apex mostly rounded, often slightly cucullate; brown; with a lighter, flabelloid margin; entire. Frond dimorphy. Sterile fronds absent or present. Fertile parts similar to sterile part or slightly narrowed. Fertile fronds. Simple. Stipe 2.5–7 cm long. Lamina 9–23 \times 0.8–2 (-3.5) cm, index 4.1-18, widest at 0.4-0.6 from base, sometimes linear. Sterile fronds. Simple. Stipe 3-7 cm long. Lamina $10-15 \times 1.7-2.9$ cm, index 4.5-7.2, widest at 0.4-0.6 from base. Costa only distinct or veins also distinct, raised on upper surface. Hydathodes absent. Margin cartilaginous, thickened; without notches. Anatomy. Upper surface: walls of epidermis strongly thickened; hypodermis a single layer, patchily present, cell walls not thickened. Lower surface: walls of epidermis strongly thickened; hypodermis absent or indistinct. Sori: round to elongate or confluent across connecting veins into short transverse coenosori, usually reaching to well within the margin; in one row between adjacent main veins; in 1-4 rows between costa and margin; 2-4 mm across; superficial.

Selected illustration — Brownlie (1969): pl. 39, fig. 4, 5.

Distribution — New Caledonia.

Ecology — Epiphytic or epiplithic. Altitude 450–1200 m.

Notes on variability — Some specimens have wide fronds (up to 5 cm), with irregularly interrupted sori.

Note — Easily recognisable by the short, often distinctly costal sori and the short, ovate scales.

27. Selliguea albidopaleata (Copel.) Parris- Fig. 27

Selliguea albidopaleata Parris in Parris, Beaman & Beaman, Plants of Mt Kinabalu. I. Ferns and fern allies (1991) 151. — Polypodium albidopaleatum Copel., Philipp. J. Sci. 12, Bot. (1917) 63. — Crypsinus albidopaleatus Copel., Gen. Fil. (1947) 207. — Crypsinopsis albido-paleata Pichi Serm., Webbia 31 (1977) 241. — Type: Topping 1749 (B, GH, S, SING), Borneo, Mt Kinabalu.

Rhizome. Diameter 3–8 mm. Internodes to 3–5.5 cm long. Vascular strands 7–10. Bundle sheath fully sclerified, rarely to 2 cells thick. Sclerenchyma strands absent. Ground tissue not sclerified. *Rhizome scales:* peltate; spreading; 6–8.5 mm long; 2–3 mm wide; acute; straw-coloured to brown; evenly coloured; remotely and weakly dentate. *Frond dimorphy.* Sterile fronds absent or present (most fronds fertile in upper part). Fertile parts similar to sterile part. *Fertile fronds.* Simple. Stipe 3.5–18 cm long. Lamina $11-29 \times 4.1-8.9$ cm, index 2.2–4.8, widest at 0.2–0.4 from the base. *Sterile fronds.* Simple. Stipe 4–5.5 cm long. Lamina 10–21 × 3.8–7.7 cm, index 2.6–3.8, widest at 0.2–0.4 from base. Main veins on upper surface raised, distinct. Hydathodes frequent, calcareous scales not persistent. Margin cartilaginous, flat (to c. 1 mm wide, translucent, fragile); notches regularly present (only near the apex). *Anatomy.* Upper surface: walls of epidermis very strongly thickened; hypodermis a single or double layer, cell walls thickened. Lower surface: walls of epidermis very strongly thickened; hypodermis indistinct to distinct. *Sori:* round, or (sometimes) confluent within one areole; in two or more rows between adjacent veins (usually not in regular rows); in 5 or more rows between costa and margin; 2 mm across (or less); slightly sunken (with a slightly raised ridge around the receptacle).

Distribution — Restricted to northern Borneo.

Ecology — Epiphytic or terrestrial. Altitude 1250-2850 m.

Notes on variability — Some specimens are aberrant in having obtuse to rounded scales with a flabelloid margin, quite similar to those of *S. bellisquamata*. They differ in no other character except (in some) an indistinct peripheral sclerenchyma sheath in the rhizome.

Note — The flat, wide, cartilaginous margin of the lamina is a curious feature within *Selliguea*; it does not occur in any other species, but is characteristic of the related genus *Arthromeris*. The small sori, in 2 or 3 irregular rows between the veins, and with a slightly raised rim around the receptacle, readily distinguish this species from all others.

28. Selliguea platyphylla (Sw.) Ching --- Fig. 28

- Selliguea platyphylla Ching, Bull. Fan Mem. Inst. Biol. 1 (1941) 238; Parris in Parris, Beaman & Beaman, Plants of Mt Kinabalu. I. Ferns and fern allies (1991) 151. Polypodium latifolium Poir., Encycl. (1804) 512, nom. illeg., non Forster (1786). Polypodium platyphyllum Sw., Syn. Fil. (1806) 27; Baker, Syn. Fil. (1868) 359; Alderw., Malayan Ferns (1908) 647; Backer & Posth., Varenfl. Java (1939) 197. Pleopeltis platyphylla Bedd., Suppl. Ferns Brit. India (1892) 94; Alderw., Bull. Dép. Agric. Indes Néerl. 27 (1909) 7; Malayan Ferns, Suppl. 1 (1916) 386. Crypsinus platyphyllus Copel., Gen. Fil. (1947) 207; Holttum, Revis. Fl. Malaya 2, sec. ed. (1954) 198. Type: Commerson s.n. (P, US), Java.
- Polypodium crassinervium Blume, Enum. Pl. Javae (1828) 125; Fl. Javae Filic. (1829) 145 (non P. crassinerve Schumacher, 1827 = Microsorum punctatum). Pleopeltis crassinervium T. Moore, Index Filic. (1857) 1xxviii. Pleuridium crassinervium J. Sm., Ferns Brit. For. (1866) 95; Hist. Fil. (1875) 95. Type: Reinwardt s. n. (L), Moluccas.

Rhizome. Diameter 3-10 mm, internodes to 1-2.5 cm long. Vascular strands 17-18, bundle sheath hyaline. Sclerenchyma strands very many; scattered; isodiametric (sometimes very irregularly shaped); hollow. Ground tissue not sclerified. Rhizome scales: peltate; spreading to squarrose, recurved from an appressed base; $7.5-10 \times 1.2-2.1$ mm (width at base); contracted to a narrow acumen; brown to blackish, very stiff, brittle; with a lighter margin; long-ciliate on margin and exposed surfaces, cilia often absent from older scales. Frond dimorphy. Monomorphic. Sterile fronds regularly present. Fertile parts similar to sterile part. Fertile fronds. Simple. Stipe 5-23 cm long. Lamina $11-60 \times 2-12$ cm, index 3.3-6.5, widest at 0.4-0.5 from base. Sterile fronds. Simple. Stipe 2-30 cm long. Lamina 6.5-47 × 1.7-11 cm, index 3-5.4, widest at 0.3-0.5 from base. Main veins on upper surface very distinct, not raised or raised. Hydathodes frequent, calcareous scales persistent, large, conspicuous. Margin cartilaginous, strongly thickened; notches regularly present. Anatomy. Upper surface: walls of epidermis strongly thickened; hypodermis a single or double layer, cell walls not thickened or thickened. Lower surface: walls of epidermis very strongly thickened (surface more or less papillose); hypodermis absent. Sori: round; in one row between adjacent veins; in 5-11 rows between costa and margin; 2 mm across; deeply sunken.

Selected illustrations — Blume (1829): pl. 61 (as *Polypodium crassinervium*); Holttum (1954): fig. 99; Piggott & Piggott, Ferns of Malaya in colour (1988): fig. 436, 437.

Distribution — Sumatra, Malay Peninsula, Java, Borneo. One early collection from the Moluccas (*Reinwardt s.n.*, type of *Polypodium crassinervium*) has not been confirmed by more recent collections.

Ecology — Epiphytic, epilithic or terrestrial, in forest, plantations, roadsides etc. Sea level to 1500 m.

Note on variability — An unmistakable species, surprisingly constant in its characters. It varies in the density of the indument on the rhizome scales and in the size of all parts, but not in any significant characters. Only occasionally the dull monotony with which the sori are arranged is broken when a few sori are lacking from some of the rows.

29. Selliguea soridens (Hook.) Hovenkamp, comb. nov. - Fig. 29

- Polypodium soridens Hook., Sp. Fil. (1864) 61; Baker, Syn. Fil. (1868) 355; Alderw., Malayan Ferns (1908) 635. Pleopeltis soridens Alderw., Bull. Dép. Agric. Indes Néerl. 27 (1909) 4; Malayan Ferns, Suppl. 1 (1916) 377. Crypsinus soridens Copel., Gen. Fil. (1947) 206. Lectotype: Wallace s.n. (B, K), Borneo, Sarawak.
- Polypodium stenopteris Baker, J. Bot. (1879) 43; Alderw., Malayan Ferns (1908) 635. Pleopeltis stenopteris Alderw., Bull. Dép. Agric. Indes Néerl. 27 (1909) 4; Malayan Ferns, Suppl. 1 (1916) 377. Selliguea stenopteris Parris in Parris, Beaman & Beaman, Plants of Mt Kinabalu. I. Ferns and fern allies (1991) 152. Type: Burbidge 297 (K), Borneo.
- Pleopeltis smithii Alderw., Bull. Jard. Bot. Buitenzorg II, 16 (1914) 29; Malayan Ferns, Suppl. 1 (1916) 379. Polypodium smithii C. Chr., Ind. Fil. Suppl. prél. (1917) 28. Type: Rachmat 603 (BO, not found), Celebes, Boesoe.

Rhizome. Diameter 2-3 mm, internodes to 1-1.5 cm long. Vascular strands 4 (remarkably constant!), bundle sheath hyaline to fully sclerified. Sclerenchyma strands many to very many; scattered; isodiametric, or periclinally flattened (occasionally); massive. Ground tissue not sclerified or with peripheral sclerified sheath. Rhizome scales: peltate; spreading; $4.8-9 \times 1-1.5$ mm; acute or contracted to a narrow acumen; brown; evenly coloured; usually entire, rarely remotely and weakly dentate, sometimes also coarsely dentate at base. Frond dimorphy. Sterile fronds usually absent, if present, much shorter than sterile parts of fertile fronds, apex rounded. Fer-tile parts narrowed to strongly contracted, often forming a distinct apical spike. Fertile fronds. Simple. Stipe 0.5-6 cm long (usually not very distinct). Lamina 5.5-49 × 0.1-0.4 cm (fertile part). Index 9-98. Sterile fronds. Simple. Stipe 1-2 cm long. Lamina $3-8 \times 0.7-1.9$, index 2.5-9, widest at 0.5-0.7 from base. Fertile area 0.4-2.5 cm wide. Costa only distinct, main veins indistinct, on upper surface not raised or raised; veinlets mostly anastomosing; free veinlets scarce. Hydathodes absent. Margin not differentiated or cartilaginous, thickened; notches regularly present. Anatomy. Upper surface: walls of epidermis weakly thickened; hypodermis a single or double layer, cell walls thickened. Lower surface: walls of epidermis strongly thickened; hypodermis absent to distinct. Sori: round or longitudinally slightly elongate; in one row between adjacent veins; marginal, in one row between costa and margin; 3 mm across; deeply sunken, forming pustules to 1-1.5 mm high on upper surface.

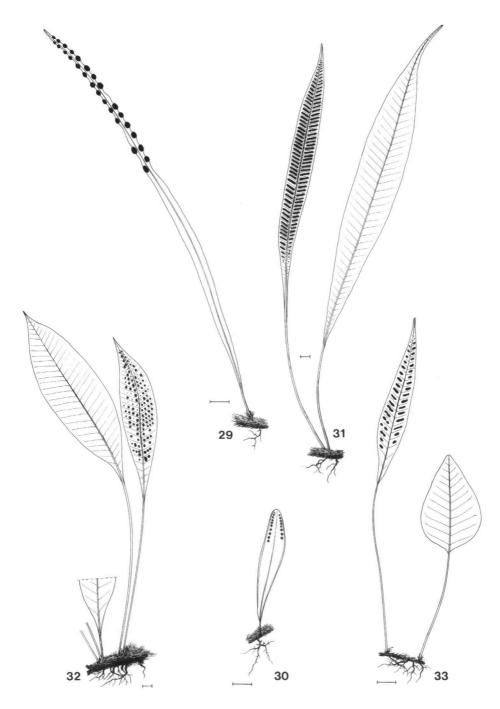


Fig. 29-33. – 29: Selliguea soridens (Hook.) Hovenkamp. – 30: S. stenophylla (Blume) Parris. – 31: S. heterocarpa (Blume) Blume. – 32: S. sri-ratu Hovenkamp. – 33: S. lateritia (Baker) Hovenkamp. – Scale bars = 1 cm.

Selected illustrations — Baker (1868): pl. 283B, Alderwerelt (1909): pl. 3 (aberrant form corresponding to *Polypodium stenopteris*).

Distribution — Borneo, Celebes, Moluccas.

Ecology — Usually epiphytic, occasionally epilithic or terrestrial, in mountain or mossy forest, often in moss cushions. Altitude 750–3150 m.

Notes on variability — *Polypodium stenopteris* was described on the basis of some aberrant specimens with a wide fertile area and sori located on protruding marginal teeth.

A few specimens show some intergradation to *Selliguea stenophylla*. These are discussed below and under that species.

Note — Selliguea soridens can be confused with S. stenophylla, which is obviously closely related. The following characters most easily distinguish the two species:

	stenophylla	soridens
scales	bicolorous, dentate	concolorous, entire
margin	not notched	notched
fertile spike	narrowed	not narrowed
sori	well within margin	close to margin
mouth of soral cup	rimmed	wide

A few specimens from Borneo are more or less intermediate (*Chew et al. 854, 1157*): they have monomorphic fronds and sori with a distinctly rimmed mouth, in these characters corresponding to *S. stenophylla*, but to *S. soridens* in other characters. From either species they differ in the rhizome without sclerenchyma strands. Possibly, these specimens are the result of occasional hybridisation between the two closely related species. Intermediate plants have also been found in New Guinea, where they have been named *Polypodium cyathisorum* (these are discussed under *S. stenophylla*).

30. Selliguea stenophylla (Blume) Parris — Fig. 30

- Selliguea stenophylla Parris in Parris, Beaman & Beaman, The plants of Mount Kinabalu. I. Ferns and fern allies (1991) 151. Polypodium stenophyllum Blume, Enum. Pl. Javae (1828) 124;
 Fl. Javae Filic. (1829) 134; Mett., Farngatt. I. Polypodium (1857) 99; Hook., Sp. Fil. (1864) 65; Baker, Syn. Fil. (1868) 354; Alderw., Malayan Ferns (1908) 638; Backer & Posth., Varenfl. Java (1939) 196. Pleopeltis stenophylla T. Moore, Index Filic. (1862) 348; Bedd., Handb. Ferns Brit. India (1883) 348; Alderw., Bull. Dép. Agric. Indes Néerl. 27 (1909) 5; Malayan Ferns, Suppl. 1 (1916) 379. Paragramma stenophylla J. Sm., Hist. Fil. (1875) 115. Crypsinus stenophyllus Holttum, Revis. Fl. Malaya 2, sec. ed. (1954) 199; Copel., Fern Fl. Philipp. (1960) 505; Kato & Price, Acta Phytotax. Geobot. 41 (1990) 71. Type: van Hasselt s.n. (L), Java, Buitenzorg, Pasar Ipis.
- Polypodium batacorum Rosenst., Feddes Repert. Spec. Nov. Regni Veg. 13 (1914) 220. Pleopeltis batacorum Alderw., Malayan Ferns, Suppl. 1 (1916) 385. — Type: J. Winkler 28a (UC), Sumatra, 'in terra Batacorum'.
- Polypodium cyathisorum Brause, Bot. Jahrb. Syst. 5 (1920) 198. Type: Schlechter 19650 (B, BM, K, P, UC), New Guinea, Kaiser Wilhelmsland.

Rhizome. Diameter 1.5-3 mm, internodes to 1-1.5 cm long. Vascular strands 4 or 5, bundle sheath hyaline. Sclerenchyma strands few to many; scattered to mainly cen-

tral; isodiametric; massive. Ground tissue not sclerified. Rhizome scales: peltate; spreading; $5.5-8 \times 0.9-1.5$ mm; acute; whitish, straw-coloured, or brown; evenly coloured or (mostly) with a lighter margin; remotely and weakly dentate to short-dentate (sometimes irregularly). Frond dimorphy. Sterile fronds absent or present (transitional fronds sometimes present with only 1 or 2 sori). Fertile parts similar to sterile part. Fertile fronds. Simple. Stipe 0.2–3.5 cm long (always indistinct, sometimes virtually absent). Lamina 2-26.5 × 0.7-1.6(-2) cm, index 1.4-23, widest at 0.2-0.7 from base. Sterile fronds. Simple. Stipe 0.2-2.5 cm long (or virtually absent). Lamina 1.5-22 × 0.8-1.6 cm, index 1.6-16. Widest at 0.4-0.8 from base. Apex usually rounded or obtuse. Costa only distinct, main veins indistinct, on upper surface rarely raised; veinlets anastomosing (free veinlets scarce). Hydathodes absent. Margin not differentiated; without notches or notches rarely sporadically present. Anatomy. Upper surface: walls of epidermis strongly thickened; hypodermis a single to double layer, cell walls strongly thickened. Lower surface: walls of the epidermis strongly thickened; hypodermis absent. Sori: round; in one row between adjacent veins; in one row approximately medially between costa and margin; 2 mm across; deeply sunken, with a slightly raised rim around the mouth, forming high narrow pustules on upper surface.

Selected illustrations — Blume (1829): pl. 55 fig. 1; Piggott & Piggott, Ferns of Malaya in colour (1988): fig. 443-445.

Distribution — Throughout Malesia.

Ecology — Usually epiphytic, on trunks or branches, rarely terrestrial, on earth banks. Altitude 100-2550 m.

Notes on variability — The specimens from New Guinea (where Selliguea stenophylla is obviously not a common species) have been described as Polypodium cyathisorum. They share some characters with S. soridens: nearly or completely concolorous, entire scales, and a notched lamina margin. Their narrow, submarginal sori with a raised rim are more typical of S. stenophylla, where notches are also present in some specimens from Celebes (Sarasin 1201).

Note — Selliguea stenophylla can be confused with S. soridens. See under S. soridens for a discussion of the distinction between the two.

31. Selliguea heterocarpa (Blume) Blume. — Fig. 31

- Selliguea heterocarpa Blume, Enum. Pl. Javae (1828) Addenda (correction); Fl. Javae Filic. (1829) 125; J. Sm., J. Bot. (Hooker) 4 (1842) 65; C.Presl, Epim. Bot. (1851) 146; J.Sm., Hist. Fil. (1875) 102; Ching, Bull. Fan Mem. Inst. Biol. 10 (1941) 239; Copel., Fern Fl. Philipp. (1960) 509; Kato & Price, Acta Phytotax. Geobot. 41 (1990) 72. Grammitis heterocarpa Blume, Enum. Pl. Javae (1828) 118 (corrected in Addenda to Selliguea). Polypodium heterocarpum Mett., Farngatt. I. Polypodium (1857) 110; Alderw., Malayan Ferns (1908) 676, nom. illeg., non Blume (1829) = Microsorum. Polypodium mettenianum Ces., Rendiconti Reale Accad. Sci. Fis. Napoli (1876) 27; Backer & Posth., Varenfl. Java (1939) 198. Pleopeltis heterocarpa Alderw., Bull. Dép. Agric. Indes Néerl. 27 (1909) 12; Malayan Ferns, Suppl. 1 (1916) 406, nom. illeg., non (Blume) T. Moore = Microsorum. Selliguea metteniana Ching, Sunyatsenia 5 (1940) 260; Tardieu & C. Chr., Fl. Indo-Chine 7 (1941) 490, nom. superfl. Type: Reinwardt s.n. (L), Java, Pondok Tenga.
- Polypodium morgani Zeiller, Bull. Soc. Bot. France (1885) 76. Type: Morgan s. n. (K, P), Malay Peninsula, Tchangkat Simpah.

- Polypodium heterocarpum var. abbreviatum Alderw., Malayan Ferns (1908) 676. Pleopeltis subcaudiformis Alderw., Malayan Ferns Suppl. (1916) 384. — Type not indicated (see note 2).
- Pleopeltis schouteni Alderw., Bull. Jard. Bot. Buitenzorg II, 7 (1912) 24; Malayan Ferns, Suppl. 1 (1916) 384. Type: Schouten s.n. (BO, not found), Java, Preanger.
- Polypodium papilligerum Rosenst., Feddes Repert. Spec. Nov. Regni Veg. 13 (1914) 220. Pleopeltis papilligera Alderw., Malayan Ferns, Suppl. 1 (1916) 385. Type: J. Winkler 67a (UC), Sumatra, 'in terra Batacorum'.
- Pleopeltis lima Alderw., Bull. Jard. Bot. Buitenzorg II, 28 (1918) 38. Polypodium mettenianum Ces. var. lima C. Chr., Mitt. Inst. Allg. Bot. Hamburg 7 (1928) 161. — Selliguea lima Holttum, Revis. Fl. Malaya 2, sec. ed. (1954) 156. — Type: Brooks 313/S (BM, BO), Sumatra, Bengkoelen.

Rhizome. Diameter 2–4 mm, phyllopodia contiguous or internodes to 0.5 cm long. Vascular strands 10–13, bundle sheath hyaline. Sclerenchyma strands very many; scattered; isodiametric; massive. Ground tissue not sclerified. Rhizome scales: peltate; spreading; $5-8.5 \times 1-1.4$ mm; acute or contracted into a narrower acumen; straw-coloured to dull brown; at the base consisting of a thick, spongy costa with a fragile, thin, narrow, translucent margin; remotely and weakly dentate at base, entire towards the apex. Frond dimorphy. Sterile fronds regularly present. Fertile parts narrowed or sometimes strongly contracted. Fertile fronds. Simple. Stipe 2-20 cm long. Lamina $12-52 \times 0.6-4$ cm, index 6.9-32, widest at 0.4-0.6 from the base or linear. Sterile fronds. Simple. Stipe 0.5–14 cm long (-28). Lamina $23-37 \times 0.8-$ 6.3(-8.5) cm, index 2.9-11, widest at 0.3-0.8 from base. Base and apex acuminate. Main veins distinct, on the upper surface not raised or raised. Hydathodes frequent, calcareous scales not persistent. Margin cartilaginous, slightly thickened; without notches. Anatomy. Upper surface: walls of epidermis strongly thickened; hypodermis absent. Lower surface: walls of epidermis strongly thickened; hypodermis absent (mesophyll hardly differentiated). Sori: forming transverse coenosori (slightly elongate or round in narrow fronds) across connecting veins; single between adjacent main veins; 2–4 mm across; slightly to (usually) deeply sunken.

Selected illustrations — Blume (1829): pl. 52 fig. 2; Holttum (1954): fig. 70 (narrow form, as *Selliguea lima*); Piggott & Piggott, Ferns of Malaya in colour (1988): fig. 352–354.

Distribution — Throughout Malesia, but very rare in East Malesia.

Ecology — Epiphytic in various types of forest, often growing in moss, rarely on rocks or terrestrial. Mostly between 1200 and 2000 m, much less frequent at lower or higher altitudes (200–3500 m).

Notes on variability — Plants from Sumatra have more deeply sunken sori, on the upper surface forming broadly flat-topped ridges with steep sides sharply set off from the flat top. This form has been described as *Selliguea lima*.

Small forms occur with almost rounded, deeply sunken sori, often on almost linear fertile fronds (mainly in Sumatra and the Malay Peninsula). These have been described under the names *Polypodium papilligerum* and *P. morgani*; they also have been confused with *Selliguea stenophylla*.

In plants from Flores the rhizome scales are often wider (to 2 mm), with a barely thickened costa, and often distinctly pseudopeltate. In plants from the Malay Peninsula the rhizome is often somewhat more slender than in typical forms.

Possibly atavistic forms occur which have irregularly interrupted sori, sometimes in two rows between veins, sometimes irregularly confluent. Similarly irregular sori occur also in *S. lateritia*, and may (rarely) lead to confusion between the two species.

Notes -1. Selliguea heterocarpa has very often been confused with S. lateritia, with some consequential nomenclatural confusion. However, the two species are clearly distinct and differ in the following aspects:

	heterocarpa	lateritia
rhizome	short-creeping	elongated
rhizome scales	light dull brown,	dark, often reddish,
	acumen wide, marginate	subulate, not marginate
frond base	tapering	not tapering
frond colour (dry)	dull brown	often tinged with red
coenosori	uninterrupted,	often interrupted,
	deeply sunken,	shallowly sunken

The shape of the lamina base is in most cases characteristically tapering in S. heterocarpa, with a wedge-shaped part more or less sharply set off as some sort of bottleneck.

Holttum (1954) correctly distinguished S. heterocarpa and S. lateritia, but erroneously applied the name 'heterocarpa' to S. lateritia, and used S. lima for the present species.

2. Pleopeltis subcaudiformis Alderw.: no type is indicated for Polypodium heterocarpum var. abbreviatum, on which Pleopeltis subcaudiformis is based. In BO there are many specimens, identified as Pleopeltis subcaudiformis by Alderwerelt, which all clearly belong to Selliguea heterocarpa (as Alderwerelt, 1916, noted: "United with Pleopeltis heterocarpa by intermediates").

32. Selliguea sri-ratu Hovenkamp — Fig. 32

Selliguea sri-ratu Hovenkamp, Blumea 41 (1996) 19. — Type: Iwatsuki c.s. B 2497 (holo L; iso BO), Borneo, G. Mendam.

Rhizome. Diameter 4–8 mm, phyllopodia contiguous or internodes to 0.8 cm long. Vascular strands 7, bundle sheath hyaline. Sclerenchyma strands many; scattered; isodiametric; massive. Ground tissue not sclerified. *Rhizome scales:* pseudopeltate; spreading; 7–13 × 1.2–2.5 mm; acute; brown; evenly coloured (often with a weak pseudocosta); strongly dentate. *Frond dimorphy.* Sterile fronds absent or present. Fertile parts similar to sterile part or narrowed. *Fertile fronds.* Simple. Stipe 7–16 cm long. Lamina 14–22 × 2.8–5.5 cm or longer, index 4.2–6.1, widest at 0.3–0.6 from base. *Sterile fronds.* Simple. Stipe 7.5–18 cm long. Lamina 16.5–22 × 3.4–5.9 cm, index 3.7–5.5, widest at 0.3–0.5 from base. Main veins on upper surface raised, distinct; veinlets free and anastomosing; free veinlets excurrent and recurrent. Hydathodes absent, or infrequent (see note 2), calcareous scales not persistent. Margin cartilaginous, flat or thickened; notches regularly present. *Sori:* round, elongated or confluent across connecting veins to a transverse coenosorus; in one row, or occasionally in 2 irregular rows between adjacent main veins; in 2–4 rows between costa and margin; 2–3 mm across; superficial.

Distribution — Borneo (6 specimens).

Ecology — Epiphytic, in forest. Altitude 660–960 m.

Notes — 1. At first sight similar to *Selliguea heterocarpa*, but easily distinguished by the strongly dentate, pseudopeltate rhizome scales and the only occasionally confluent sori.

2. Apparently hydathodes are present in sterile fronds only. However, the number of sterile fronds in the specimens seen is very small.

33. Selliguea lateritia (Baker) Hovenkamp, comb. nov. - Fig. 33

- Polypodium lateritium Baker, Ann. Bot. (London) 5 (1891) 93. Selliguea metteniana var. lateritium Tardieu & C. Chr., Not. Syst. 8 (1939) 197; Fl. Indo-Chine 7 (1941) 490. — Type: Godefroy-Lebeuf 862 (K), Cambodia.
- Polypodium treubii H. Christ, Ann. Jard. Bot. Buitenzorg II, 5 (1905) 121; Alderw., Malayan Ferns (1908) 646. Pleopeltis treubii Alderw., Bull. Dép. Agric. Indes Néerl. 27 (1909) 6; Malayan Ferns, Suppl. 1 (1916) 384. Polypodium mettenianum Ces. forma treubii C.Chr., Mitt. Inst. Allg. Bot. Hamburg 7 (1928) 161. Selliguea treubii Ching, Sunyatsenia 5 (1940) 260. Lectotype (here selected): Hallier 3438 (K, L), Borneo, Amai Ambit.
- Polypodium taeniophyllum Copel., Philipp. J. Sci. 6, Bot. (1912) 65. Pleopeltis taeniophylla Alderw., Malayan Ferns, Suppl. 1 (1916) 378. Crypsinus taeniophyllus Copel., Gen. Fil. (1947) 207. Selliguea taeniophylla Parris in Parris, Beaman & Beaman, Plants of Mt Kinabalu.
 I. Ferns and fern allies (1991) 152. Type: Native Collector BS 769 (MICH), Borneo, Sarawak.

Rhizome. Diameter 1-3 mm, internodes to 0.5-1 cm long. Vascular strands 5-9, bundle sheath hyaline. Sclerenchyma strands many to very many; scattered, mainly central or around the vascular cylinder; isodiametric or periclinally flattened; massive or hollow. Ground tissue not sclerified. Rhizome scales: rarely pseudopeltate, usually peltate; spreading or squarrose; $5.5-12 \times 0.4-1$ mm (width at base); from the wide base abruptly contracted to a narrow, subulate, brown acumen; at base with a lighter, irregularly lacerate/dentate margin, acumen entire. Frond dimorphy. Sterile fronds regularly present. Fertile parts narrowed. Fertile fronds. Simple. Stipe 3.2-25.5 cm long. Lamina $5.7-21.5 \times 0.7-5.1$ cm, index 3-15, widest at 0.2-0.4 from the base (sometimes linear). Sterile fronds. Simple. Stipe 2–15.5 cm long. Lamina $4.5-14 \times$ 1-7 cm, index 1.5-6, widest at 0.2-0.6 from base. Main veins on upper surface raised, distinct. Hydathodes absent. Margin cartilaginous, thickened; without notches. Anatomy. Upper surface: walls of epidermis strongly thickened; hypodermis absent. Lower surface: walls of epidermis strongly thickened; hypodermis absent. Sori: elongate or confluent across connecting veins to transverse coenosori; in one row between adjacent main veins; in 2-5, sometimes more, rows between costa and margin; 1-4 mm across; slightly to deeply sunken (upper surface never strongly pustulose).

Selected illustrations — Holttum, Revis. Fl. Malaya 2, sec. ed. (1954): fig. 69 (as Selliguea heterocarpa).

Distribution — Malesia. Common: Sumatra, Malay Peninsula, Peninsular Thailand, Borneo (very common); sporadically: Philippines, Celebes, New Guinea. Outside Malesia: Indochina (Thailand, Cambodia, southern Vietnam).

Ecology — Trunk or branch epiphyte, epilithic or terrestrial, in a wide variety of forest types, often in riverbeds. Sea level to 1200 m, occasionally reaching higher, to 2000 m.

Notes on variability — *Polypodium taeniophyllum* represents an extremely narrow form, which is, however, connected to the typical form through a series of intermediates: *Mjöberg s.n.*, Matang Road (P, BM); *Hose s.n.* (SING), *1893* (K); *Moulton's Native collectors 53* (BM); *Brooke 9769* (L, sterile).

Specimens from New Guinea have scales which are slightly thicker and more appressed than the acicular, squarrose scales of the typical form; they are more or less intermediate to *S. heterocarpa*, which, however, is absent from New Guinea.

Notes — 1. Selliguea lateritia has been extensively confused with S. heterocarpa, from which it can be distinguished by the following characters: *Rhizome* usually more slender, scales dark, often reddish brown, with a dark, shining, subulate, often squarrose acumen. *Fronds* often tinged red (after drying), evenly narrowed at base, usually lacking the characteristic 'bottleneck'. *Sori* often separate or in interrupted coenosori, impressed but not deeply sunken in pits, with a narrowly linear receptacle, forming narrow protruding ridges on the upper surface.

2. *Selliguea lateritia* is very well represented in collections from Borneo, especially recent ones. This suggests that it may be increasing in frequency there.

34. Selliguea craspedosora (Copel.) Hovenkamp, comb. nov.

 Polypodium craspedosorum Copel., Philipp. J. Sci. 9, Bot. (1914) 233. — Pleopeltis craspedosora Alderw., Malayan Ferns, Suppl. 1 (1916) 378. — Crypsinus craspedosorus Copel., Gen. Fil. (1947) 206. — Type: Brooks 134 (BM, P), Sumatra, Lebong Tandai.

Rhizome. Diameter 1 mm, the internodes to 1 cm long. Vascular strands 5, bundle sheath absent to hyaline. Sclerenchyma strands many; scattered; isodiametric; massive. Ground tissue not sclerified. *Rhizome scales:* peltate; squarrose; 6×1 mm wide; contracted to a narrow acumen; brown; evenly coloured; entire (dentate at the base). *Frond dimorphy.* Sterile fronds regularly present. Fertile parts narrowed. *Fertile fronds.* Simple. Stipe 2.5–4.5 cm long. Lamina 27–29 × 0.4–0.5 cm, linear. *Sterile fronds.* Simple. Stipe 0.5–3.5 cm long. Lamina 4–12 × 0.6–1 cm, index 4.5–20, widest at 0.5–0.7 from base. Costa only distinct. Hydathodes absent. Margin cartilaginous, thick-ened; without notches. *Sori:* round to elongate; confluent within one areole and across connecting veins; in one row between the costa and margin; 2 mm across; superficial to slightly sunken.

Distribution — Sumatra (1 specimen).

Ecology — On trunk. Altitude not indicated.

Notes — 1. Known from the type specimen only, represented in BM by several good sheets.

2. At first sight similar to *Selliguea subsparsa*, but differs most strikingly in the scales: these are dull brown, suddenly contracted from a broad base to a narrow, entire acumen. The sori are distinctly closer to the margin than to the costa. Especially striking are the very long fertile fronds. The scales point to affinity with *S. lateritia*, which is not contradicted by any other character.

35. Selliguea setacea (Copel.) Hovenkamp, comb. nov.

Polypodium setaceum Copel., Philipp. J. Sci. 5, Bot. (1911) 139. — Holcosorus setaceus Copel., Gen. Fil. (1947) 208. — Type: Brooks 6 (BM), Borneo, Sarawak, Tringos. *Rhizome.* Diameter 2–3 mm, internodes not elongated. Vascular strands 7, bundle sheath hyaline. Sclerenchyma strands many; scattered; isodiametric; massive. Ground tissue not or lightly sclerified. *Rhizome scales:* pseudopeltate; spreading; $2.9-3 \times 0.7-0.8$ mm; contracted to a narrow acumen; brown; with a lighter margin and a central pseudo-costa; base dentate, acumen entire or remotely and weakly dentate. *Frond dimorphy.* Sterile fronds regularly present. Fertile parts similar to sterile part. *Fertile fronds.* Simple. Stipe not distinct from the lamina, 1-1.5 cm long. Lamina $25-50 \times 0.1-0.2$ cm (in dry state), gramineous. *Sterile fronds.* Simple. Stipe not distinct from lamina, 0.5-1 cm long. Lamina $46-54 \times 0.1-0.2$ cm, gramineous. Costa only distinct; venation highly simplified. Hydathodes absent. Margin not differentiated; without notches. *Anatomy.* Upper surface: walls of epidermis strongly to very strongly thickened; hypodermis indistinct. *Sori:* round; two between adjacent veins; in one row between costa and margin; 1 mm across; superficial.

Selected illustration - Copeland (1911): pl. 14.

Distribution — Borneo (7 specimens).

Ecology — Epiphytic. The few available data indicate that this species may be mainly restricted to stunted summit or heath forests. Altitude 150–900 m.

Note — Often confused with a number of other gramineous forms and species; see under S. ceratophylla, S. bisulcata, S. enervis (gramineous forms), S. subsparsa, S. lateritia.

36. Selliguea bisulcata (Hook.) Hovenkamp, comb. nov.

Grammitis bisulcata Hook., Cent. Ferns (1854) tab. 98. — Holcosorus pentagonus T. Moore, Index Filic. (1857) xxx. — Holcosorus bisulcatus Copel., Gen. Fil. (1947) 208. — Type: Lobb s.n. (K), Borneo, Sarawak.

Rhizome. Diameter 1.5 mm, internodes to 0.5 cm long. Vascular strands 6. Bundle sheath hyaline. Sclerenchyma strands many; scattered; isodiametric; massive. Ground tissue not sclerified, or lightly sclerified. *Rhizome scales:* peltate, spreading; $5.5 \times$ 0.9 mm, contracted to a narrow acumen; brown; with a central pseudo-costa and a lighter margin, base dentate, acumen entire. Frond dimorphy. Monomorphic. Sterile fronds regularly present. Fertile parts similar to sterile part. Fertile fronds. Simple. Stipe 0.5–1 cm long (distinction from lamina often not clear). Lamina $8.5-18 \times 0.1$ cm, gramineous. Sterile fronds. Simple. Stipe 0.5–1.5 cm long. Lamina $5-30 \times$ 0.1-0.2 cm, or longer, gramineous. Main veins on upper surface not raised. Venation strongly reduced, costa only distinct. Hydathodes absent. Margin not differentiated; without notches. Anatomy. Upper surface: walls of epidermis strongly thickened; hypodermis a single layer, patchily present (or replaced by collenchyma), cell walls thickened. Lower surface: walls of epidermis very strongly thickened; hypodermis absent. Sori: elongate (sometimes a coenosorus is apparently present); in two rows between adjacent veins; in one row between costa and margin; 1 mm across; in a deep laminar groove.

Selected illustration — Hooker (1854): pl. 98.

Distribution — Borneo. Obviously rare (3 specimens). Outside Malesia once reported from India (see note 3).

Ecology — Epiphytic or terrestrial, in forest. Altitude 100-850 m.

Notes — 1. This has been confused with other species or forms with gramineous fronds. All of these can be distinguished by the wider lamina, which is flat or slightly incurved in cross section. True *S. bisulcata* has an almost quadrangular cross section of the lamina, and a rhizome with the fronds distinctly spaced. Of the other gramineous species, *Selliguea setacea* (Borneo) and the gramineous form of *S. enervis* (*S. renifera*) from New Guinea are the most common ones. The former has the fronds placed closely together on the rhizome and a wider, flat lamina which clearly shows the separate sori; the latter has a similarly flat lamina and a short-creeping rhizome with usually straw-coloured scales. Another similar form from Borneo was described as *Polypodium taeniophyllum* Copel. It represents an extremely narrow form of *S. laterititia*.

2. There is no reason to distinguish both *S. setacea* and *S. bisulcata* as a separate genus *Holcosorus*. These two species merely share the gramineous habit, which they also share with a number of forms of other species (see above).

3. This species has been reported from Arunachal Pradesh, India, by Dixit and Nair [Proc. Indian Acad. Sci. 86 B (1977) 385–387]. The occurrence of this rare species so far from the other location (Borneo) is surprising.

37. Selliguea enervis (Cav.) Ching - Fig. 34, 35

- Selliguea enervis Ching, Bull. Fan Mem. Inst. Biol. 10 (1941) 239; Parris in Parris, Beaman & Beaman, Plants of Mt Kinabalu. I. Ferns and fern allies (1991) 151. Polypodium enerve Cav., Descr. Pl. (1802) 245; Sw., Syn. Fil. (1806) 28; C. Chr., Dansk Bot. Ark. 9 (1937) 12, pl. I fig. 4; Backer & Posth., Varenfl. Java (1939) 200. Crypsinus enervis Copel., Gen. Fil. (1947) 207; Holttum, Revis. Fl. Malaya 2, sec. ed. (1954) 199; Copel., Fern Fl. Philipp. (1960) 506; Kato & Price, Acta Phytotax. Geobot. 41 (1990) 71. Crypsinopsis enervis Pichi Serm., Webbia 31 (1977) 242. Type: Née s.n., Luzon ('Marianas', MA, teste C. Chr., Ic.).
- Polypodium rupestre Blume, Enum. Pl. Javae (1828) 124, nom. illeg., non R. Br. (1810) = Pyrrosia; Fl. Javae Filic. (1829) 142; Baker, Syn. Fil. (1868) 359; Alderw., Malayan Ferns (1908) 650. Pleuridium rupestre Fée, Gen. Fil. (?1853) 274; J. Sm., Ferns Brit. For. (1866) 95. Polypodium saxatile Mett., Farngatt. I. Polypodium (1857) 116; Hook., Sp. Fil. (1864) 63, nom. illeg., non Klotsch (1847). Pleopeltis rupestris Bedd., Suppl. Ferns Brit. India (1892) 94. Polypodium subtriquetrum H. Christ, J. Bot. (Morot) II, 1 (1908) 267, nom. superfl. Pleopeltis rupestris T. Moore, Index Filic. (1857) lxxviii; Alderw., Malayan Ferns, Suppl. 1 (1916) 387. Type: Blume s.n. (L), Java.
- Polypodium induratum Baker, Ann. Bot. (London) 5 (1891) 92; Alderw., Malayan Ferns (1908) 637. Pleopeltis indurata Alderw., Bull. Dép. Agric. Indes Néerl. 27 (1909) 5; Malayan Ferns, Suppl. 1 (1916) 379. Type: Mueller s.n. (BM, K), New Guinea, Mt Yule.
- Polypodium taeniopsis H. Christ, Verh. Naturf. Ges. Basel 11 (1896) 443. Polypodium rupestre Blume var. taeniopsis Alderw., Malayan Ferns (1908) 651. — Pleopeltis rupestris var. taeniopsis Alderw., Bull. Dép. Agric. Indes Néerl. 27 (1909) 7. — Type: Sarasin 1346, Celebes, Lompobattang, not found.
- Polypodium lagopodioides H. Christ, Ann. Jard. Bot. Buitenzorg II, 4 (1904) 37, nom. illeg., non Desv. (1811). Polypodium albulum H. Christ in C.Chr., Ind. Fil. (1906) 508. Pleopeltis albula Alderw., Bull. Dép. Agric. Indes Néerl. 27 (1909) 7. Type: Sarasin 2041 (P), Celebes, Mt Poanaa.
- Polypodium rupestre Blume var. leucolepis Rosenst., Feddes Repert. Spec. Nov. Regni Veg. 5 (1908)
 43; Alderw., Malayan Ferns (1908) 651. Pleopeltis rupestris var. leucolepis Alderw., Bull.
 Dép. Agric. Indes Néerl. 27 (1909) 7. Polypodium leucolepis Rosenst., Feddes Repert.

Spec. Nov. Regni Veg. 12 (1913) 180, nom. illeg., non Gilbert (1897). — Type: Werner 39 (BM, L, UC), New Guinea, Gelu.

- Polypodium holosericeum Rosenst., Feddes Repert. Spec. Nov. Regni Veg. 5 (1908) 375. Type: Werner ROS 32 (L), New Guinea, Gelu.
- Polypodium senescens Copel., Philipp. J. Sci. 6, Bot. (1911) 88. Pleopeltis senescens Alderw., Malayan Ferns, Suppl. 1 (1916) 376. — Crypsinus senescens Copel., Gen. Fil. (1947) 207. — Type: King 274 (B), New Guinea.
- Polypodium cochleare Brause, Bot. Jahrb. Syst. 49 (1912) 48. Pleopeltis cochlearis Alderw., Malayan Ferns, Suppl. 1 (1916) 387. — Type: Schultze (33) 14 (B), New Guinea, Tami.
- Polypodium limaeforme Brause, Bot. Jahrb. Syst. 49 (1912) 49. Pleopeltis limaeformis Alderw., Malayan Ferns, Suppl. 1 (1916) 389. — Type: Schultze (33) 17 (B), New Guinea, Tami.
- Polypodium rhomboideum Brause, Bot. Jahrb. Syst. 49 (1912) 46, nom. illeg., non Blume (1828).
 Pleopeltis rhomboidea Alderw., Malayan Ferns, Suppl. 1 (1916) 389. Type: Schlechter 19090 (B, BM, P), New Guinea, Finisterre Mts.
- Polypodium undulato-sinuatum Rosenst., Feddes Repert. Spec. Nov. Regni Veg. 12 (1913) 179. —
 Pleopeltis undulato-sinuata Alderw., Malayan Ferns, Suppl. 1 (1916) 388. Crypsinus undulato-sinuatus Copel., Gen. Fil. (1947) 207. Type: Keysser B 28 (B, BM), New Guinea, Mt Bolan.
- Polypodium subundulatum Rosenst., Feddes Repert. Spec. Nov. Regni Veg. 12 (1913) 180. Pleopeltis subundulata Alderw., Malayan Ferns, Suppl. 1 (1916) 379. — Crypsinus subundulatus Copel., Gen. Fil. (1947) 207. — Type: Keysser 82 (B), New Guinea, Mt Bolan.
- Polypodium petiolatum Ridl., Trans. Linn. Soc. London 9 (1916) 260, nom. illeg., non Dav. (1894). — Type: Boden Kloss s.n. (BM), New Guinea, Nassau Mts.
- Pleopeltis renifera Ridl., Trans. Linn. Soc. London 9 (1916) 263; Alderw., Malayan Ferns, Suppl. 1 (1916) 525; A. Gepp in Gibbs, Arfak Flora (1917) 75 ('remigerum', see note 3); Alderw., Nova Guinea 16 (1924) 38 ('remigera'). Type: Boden Kloss s.n. (K), New Guinea, Nassau Mts.
- Pleopeltis rupestris T. Moore var. subalbula Alderw., Malayan Ferns, Suppl. 1 (1916) 387. Type: J. J. Smith & Rant 37 (BO), Java.
- Polypodium kamboranganum C. Chr., Gard. Bull. Straits Settlem. 7 (1934) 306. Selliguea kamborangana M.G. Price, Contr. Univ. Michigan Herb. 16 (1987) 198. — Type: Holttum 25543 (BM, SING), Borneo, Kinabalu.
- Polypodium lamprophyllum C. Chr., Brittonia 2 (1937) 311. Crypsinus lamprohyllus Copel., Gen. Fil. (1947) 207. — Type: Brass 4558 (BM, BO, NY), New Guinea, Murray Pass.
- Crypsinus spathulatus Gilli, Ann. Naturhist. Mus. Wien 81 (1978) 21. Type: Gilli 375 (W), New Guinea, Fatima.

Rhizome. Diameter 2–4 mm, internodes to 1 cm long or slightly longer. Vascular strands 9 or 10, bundle sheath hyaline or partially sclerified. Sclerenchyma strands very many; scattered; isodiametric to periclinally flattened; massive to hollow. Ground tissue not sclerified to lightly sclerified. *Rhizome scales:* peltate; spreading; $2.5-5 \times 0.5-1$ mm wide; acute; brown; evenly coloured or with a slightly lighter margin; short-dentate to strongly dentate. *Frond dimorphy.* Sterile fronds absent or present. Fertile parts similar to sterile part. *Fertile fronds.* Simple. Stipe 3.5–25 cm long. Lamina 9–30 × 1–8 cm or longer, index 3.7–10, widest at 0.2–0.4 from base. *Sterile fronds.* Simple. Stipe 2–15 cm long. Lamina 4–18 × 1.2–5.5 cm or longer, index 3–4.7, widest at 0.3–0.5 from base. Main veins on upper surface raised, distinct; veinlets anastomosing; free veinlets excurrent and recurrent. Hydathodes mostly frequent, calcareous scales not persistent, or rarely persistent. Margin cartilaginous, thickened; notches absent or rarely sporadically present. *Anatomy.* Upper surface: walls of epidermis strongly to very strongly thickened; hypodermis a single layer, cell walls not thickened. Lower surface: walls of epidermis strongly to very strongly

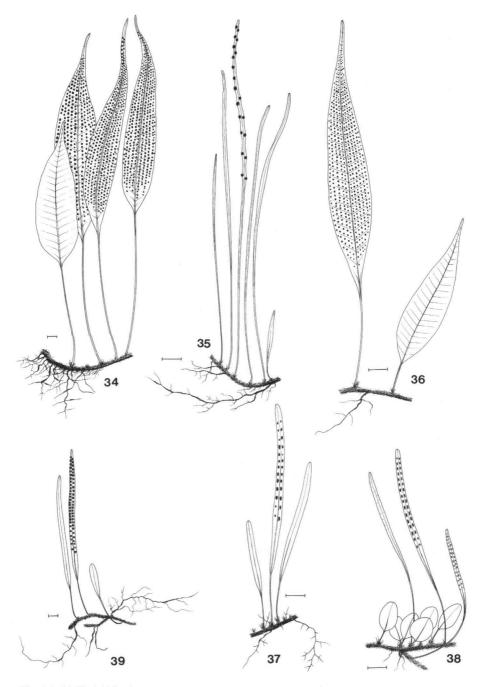


Fig. 34-39. Variability in and around *Selliguea enervis* (Cav.) Ching. - 34: *S. enervis*, typical form from Java. - 35: *S. enervis*, gramineous form from New Guinea. - 36: *S. stenosquamis* Hovenkamp. - 37: *S. subsparsa* (Baker) Hovenkamp. - 38: *S. hellwigii* (Diels) Hovenkamp. - 39. *S. gracillipes* (Alderw.) Hovenkamp. -- Scale bars = 1 cm.

thickened; hypodermis indistinct. *Sori:* round or occasionally confluent within one areole; in two, or occasionally in 3 or more irregular rows between adjacent veins; in 5 or more rows between costa and margin; 2(-3) mm across; superficial.

Selected illustrations — Blume (1829): pl. 55 fig 2, pl 60 fig. 1–3 (as *Polypodium rupestre*); Piggott & Piggott, Ferns of Malaya in colour (1988): fig. 438–440.

Distribution — Throughout Malesia.

Ecology — Trunk or branch epiphyte, rarely terrestrial or on rocks, in a variety of forest types. Altitude 280–3500 m.

Vernacular names — Sumatra: pahoe ngil-ngil. Flores: lukup (Manggarai). New Guinea: jalosi (Dunantina), aiptoinbil (Hagen: Togobe), pfot'pfot (Mendi), balim'bali (Enga, Poio); for the gramineous form: goebie (Kapaukoe, Wissel Lakes); pisawi (Wandammen).

Notes on variability — In order not to clutter the description with too many indications of variability, the description above is based on material from Java.

Selliguea enervis is here conceived as a single, highly variable species, presenting a different aspect and a different pattern of variability in different areas. In addition, in several areas closely related 'satellite' species are found, which are not always sharply distinct from S. enervis. I have distinguished these extremes in variation only when they are represented by a sufficient number of specimens and when they are at least locally distinct. As a result, while these local satellite species are sufficiently distinct for recognition in their area, the distinctions may be blurred when they are contrasted with the entire range of variability in S. enervis.

This rather unsatisfactory arrangement, with a number of locally distinguishable species and a number of sometimes similar, but locally not distinguishable forms, probably reflects an intricate pattern of active speciation and/or hybridisation.

Java, Sumatra, Malay Peninsula, Lesser Sunda Islands (Fig. 34) — Usually large plants. Rhizome thick, scales dentate. Fronds virtually monomorphic, usually wide, ovate. Hydathodes mostly present, without persistent calcareous scales, sometimes very obscure or absent, margin not or only sporadically notched. Sori in 2 or 3 rows between veins, usually in many rows between costa and margin.

A form with a highly irregular disposition of the sori is well represented by a number of sheets collected in 1884 on Maxwell's Hill by Scortechini (SING).

Most specimens from Java in BO are identified as var. *subalbula*. I cannot see any differences between these specimens and other ones.

Related species in this area: S. subsparsa, S. neglecta.

Philippines — Plants more slender generally, rhizome 1.5-2.5 mm thick, rhizome scales $3-4.5 \times 0.5-0.7$ mm; remotely and weakly dentate to short-dentate, fronds weakly dimorphic. Fertile fronds: stipe 2.5-10 cm long; lamina $7-12 \times 1.1-2.3$ cm, index 0.9-11. Sterile fronds: stipe 0.5-5.5(-21) cm long; lamina $3-8(-18.5) \times 1.6-2.8(-4.8)$ cm, index 1.5-4.4. Hydathodes absent. Margin notches regularly present. The type belongs to this form, which is only known from a few localities in northern Luzon.

Borneo — Rhizomes more widely creeping, 2.5-3 mm thick, internodes 1-5 cm long. Rhizome scales $5.5-6 \times 1.2-1.3$ mm; short-dentate. Fertile fronds: stipe 3-24

cm long, lamina $7-23 \times 1.8-5.8$ cm, index 2.7-5.6, widest at 0.3-0.6 from base. Sterile fronds: stipe 2-13 cm long, lamina $7.5-13 \times 2.6-4.6$ cm, index 2.5-3.7. Hydathodes absent. Margin without notches or notches sporadically present, rarely notches regularly present.

Surprisingly few collections are known from Borneo for this otherwise very common species. A few specimens from Mt Kinabalu are aberrant, with sometimes pseudopeltate scales, distinctly dimorphic fronds with hydathodes regularly present.

Polypodium kamboranganum was described on the basis of a single collection from the Kinabalu area. Despite the relatively high collecting density in this area, no other specimens have come to light with the same combination of characters: fronds strongly dimorphic, the fertile ones with a single row of sori between costa and margin, hydathodes and marginal notches regularly present. This specimen is very similar to S. subsparsa (Sumatra and Borneo) and can be distinguished from some forms of the latter (e.g., de Wilde 13224), only by the clearly present hydathodes. Recent reports of S. kamborangana from the Philippines (Price, 1987) are based on misidentifications of two sterile specimens (Edaño PNH 471, 478), here discussed under S. plantaginea.

Celebes — Several more or less distinct forms occur in Celebes, often represented by few specimens or by a single aberrant specimen. There is relatively much variation in the rhizome scales, some of which may perhaps be explained by incidental hybridisation with *S. stenosquamis*.

Some of the more constant forms are:

1) Rhizome 1.5–2 mm thick, long-creeping, internodes to 1.5–3.5 cm long. Rhizome scales peltate, $3.5-5.5 \times 0.4-1$ mm; straw-coloured to brown (often mottled); remotely and weakly dentate to short-dentate. Hydathodes absent or sometimes present. Margin notches sporadically to regularly present.

2) Rhizome 1.5–2 mm thick, short-creeping, internodes to 0.7–1 cm long. Rhizome scales pseudopeltate or peltate, $5-7 \times 1-1.5$ mm, acute to contracted to a narrow acumen; whitish to straw-coloured (sometimes brown); evenly coloured, often with a dull, thickened pseudocosta; remotely and weakly to short-dentate, acumen almost entire. Hydathodes absent. Margin notches regularly present. This is the form described as *Polypodium lagopodioides* Christ.

3) Rhizome 2.5–4 mm thick, short-creeping, internodes to 0.5–0.8 cm long. Rhizome scales pseudopeltate to peltate; spreading to squarrose; $4.5-7 \times 0.5-0.8$ mm; acute or contracted to a narrow acumen; straw-coloured to brown; remotely and weakly dentate to short-dentate. Hydathodes absent. Margin notches sporadically to regularly present.

Related species in this area: S. stenosquamis

New Guinea — In New Guinea and the neighbouring islands there is an almost continuous range from large plants with a wide lamina to narrow, gramineous forms. In virtually all intermediates the presence of hydathodes and marginal notches is variable. As a consequence, forms that are distinguishable as species in other areas here form part of a continuum which I cannot divide. Transitional specimens with fronds of two different forms on a single rhizome sometimes occur. The following names are most widely encountered for forms in this area.

The name *Pleopeltis renifera* (and, erroneously, *Polypodium taeniophyllum*) has been applied to forms with long, gramineous leaves mostly less than 2 mm wide (Fig. 35). (*Polypodium taeniophyllum* properly is a superficially similar gramineous form from Borneo, here considered as a gramineous form of *S. lateritia*.) These gramineous forms are not sharply distinct from the long, narrow forms discussed below, and are connected through the latter to the other forms of *S. enervis* in New Guinea.

The name *Polypodium induratum* has been applied to forms with long, narrow (sometimes very narrow) fronds with a single row of sori between costa and margin, usually without hydathodes. More distinctly dimorphic forms have often been identified as *Crypsinus senescens*, but the type of that is barely dimorphic. The name *C. spathulatus* applies better to these dimorphic forms.

The names Crypsinus subundulatus, C. undulato-sinuatus and C. lamprophyllus have been used for somewhat wider forms, with 1 or 2 rows of sori between the costa and the margin, and an often strongly but irregularly sinuate lamina margin. The differences between these forms and those called C. senescens are gradual.

The name *Polypodium petiolatum* refers to specimens with a wider lamina, not or slightly dimorphic fronds, with 4 or 5 rows of sori between costa and margin. Hydathodes are frequent. This form is more or less a transition to *S. hellwigii*, which, however, differs in the constantly strongly dimorphic fronds.

The name *Polypodium rhomboideum* Brause (non Blume) has been applied to small, barely dimorphic specimens. They are superficially similar to *Selliguea oodes*, from the Philippines, and sometimes difficult to distinguish from true *S. oodes*. However, *S. oodes* is a rheophyte with a very characteristic, spongy mesophyll; the lamina is sharply distinct from the stipe and usually stands at a distinct angle to it.

A few specimens have been found with densely hairy fronds, but in no other way distinct from typical *Selliguea enervis*. Within *Selliguea*, hairiness is a exceptional character, occurring regularly only in a few species from continental Asia.

Related species in this area: S. hellwigii, S. gracilipes.

Notes — 1. Related species: S. subsparsa (Sumatra) has strongly dentate scales, narrow, variably dimorphic fronds without hydathodes, and 1 to several rows of sori. — S. stenosquamis (Celebes) can be distinguished by the somewhat more elongated internodes and the squarrose, acicular acumen of rhizome scales. — S. hell-wigii (New Guinea) can be distinguished by the small, dimorphic fronds, which constantly bear hydathodes and have a distinctly flat, slightly recurved margin. — S. gracilipes (New Guinea) consists of small plants with fronds that have a very thick, coriaceous texture and a rounded apex. — S. neglecta (Sumatra, Java) consists of small to very small plants, fronds usually weakly dimorphic, often with spathulate lamina and rounded apex.

2. Probably unrelated species. The following two species are similar to *S. enervis* and have often been confused with it, but are not nearly as closely related as the species listed above. There is no intergradation between these species or with *S. enervis*. — *S. ceratophylla* can be distinguished by the short rhizome and pseudopeltate, small scales. — *S. pampolycarpa* can be distinguished by the more closely set, long, spathulate fronds with two distinct ridges running along the upper surface of the costa.

3. Pleopeltis renifera. The specific epithet chosen by Ridley was 'remigera', the name occurring on his original specimens. He chose this name to convey the impression of a boat with raised oars, corresponding to the rhizome with erect fronds set in two rows. However, in the process of typesetting and 'correcting' this was corrupted to 'renifera' (kidney-bearing). This name was recognised as fully inappropriate to these plants by Gepp (1917), who accordingly corrected it to the original 'remigera'.

4. Type locality. The type of *Polypodium enerve* Cav. is indicated by Cavanilles himself as originating from the Marianas. However, no other specimens from the Marianas have come to light. Christensen (1937) states "it is not improbable that this fern was collected in Luzon", and, indeed, the type, as illustrated by Christensen, looks like the Philippine form of *S. enervis*. I have no reason to believe that *S. enervis* occurs on the Marianas.

38. Selliguea stenosquamis Hovenkamp — Fig. 36

Selliguea stenosquamis Hovenkamp, Blumea 33 (1988) 396. — Type: Hennipman 5259 (L), Celebes, Roroka Timbu.

Rhizome. Diameter 1.5–2.5 mm, internodes to 1.7–3 cm long. Vascular strands 8–11, bundle sheath absent to hyaline. Sclerenchyma strands few to many; scattered; isodiametric; massive and hollow. Ground tissue not sclerified. *Rhizome scales:* peltate; squarrose; $3.5-6 \times 0.3-0.6$ mm, contracted to a narrow acumen; brown, evenly coloured; the base irregularly dentate/lacerate, acumen entire. *Frond dimorphy.* Sterile fronds regularly present. Fertile parts similar to sterile part or slightly narrowed. *Fertile fronds.* Simple. Stipe 2–16 cm long. Lamina 8–18(–31) × 1.3–4(–9.5) cm, index 5–6.4, widest at 0.3 from base. *Sterile fronds.* Simple. Stipe 1.5–10.5 cm long. Lamina 2–14 × 1.4–4.5 cm, index 2.7–3.5, widest at 0.3 from base. Main veins distinct, raised on upper surface; veinlets free, anastomosing; free veinlets excurrent and recurrent. Hydathodes absent. Margin not differentiated or cartilaginous, thickened; notches regularly present. *Anatomy.* Upper surface: walls of epidermis not or weakly thickened; hypodermis a single layer, patchily present. Lower surface: walls of epidermis not or weakly thickened; hypodermis absent. *Sori:* round; in 2 rows between adjacent veins; in 5 or more rows between costa and margin; 1 mm across; superficial.

Distribution — Celebes.

Ecology — Epiphytic in mountain forest, on trunks and in crowns; also epilithic. Altitude 1000–2250 m.

Note — Not a very variable species, distinct from *Selliguea enervis* mainly in the constantly subulate and strongly squarrose rhizome scales, but also in this lack of variability. In the rhizome scales it is very similar to *S. lateritia*, and my earlier citation of a specimen from Borneo (Hovenkamp & De Joncheere, 1988) actually concerns a misidentified sterile specimen of *S. lateritia*.

39. Selliguea subsparsa (Baker) Hovenkamp, comb. nov. — Fig. 37

Polypodium subsparsum Baker, J. Bot. 18 (1880) 215; Alderw., Malayan Ferns (1908) 630; C. Chr., Gard. Bull. Straits Settlem. 7 (1934) 307. — Pleopeltis subsparsa Alderw., Bull. Dép. Agric. Indes Néerl. 27 (1909) 3. — Crypsinus subsparsus Copel., Gen. Fil. (1947) 207. — Type: Beccari s. n. (K), Sumatra, Singalan.

- Polypodium wrayi Baker, J. Bot. 2 (1887) 206; Ann. Bot. (London) 5 (1891) 90; Alderw., Malayan Ferns (1908) 633. Pleopeltis wrayi Bedd., Suppl. Ferns Brit. India (1892) 93; Alderw., Bull. Dép. Agric. Indes Néerl. 27 (1909) 4. Crypsinus wrayi Holttum, Revis. Fl. Malaya 2, sec. ed. (1954) 200. Type: Wray 573 (K), Malay Pensinsula, Gunong Hijau.
- Polypodium beccarii Alderw., Bull. Dép. Agric. Indes Néerl. 18 (1908) 22; Malayan Ferns (1908) 633; C. Chr., Gard. Bull. Straits Settlem. 7 (1934) 307. Pleopeltis beccarii Alderw., Bull. Dép. Agric. Indes Néerl. 17 (1909) 4; Bull. Jard. Bot. Buitenzorg II, 28 (1918) 37. Type: Beccari 449, Sumatra (BO, not seen; see note 2).
- Pleopeltis insperata Alderw., Bull. Jard. Bot. Buitenzorg II, 16 (1914) 28; Malayan Ferns, Suppl. 1 (1916) 380. Polypodium insperatum C. Chr., Ind. Fil. Suppl. prél. (1917) 26. Type: Matthew 692 (BM, BO, K), Sumatra, Sago.

Rhizome. Diameter 1-2 mm, internodes to 0.5-1 cm long. Vascular strands 5-8, bundle sheath hyaline. Sclerenchyma strands few to many; scattered; isodiametric and periclinally flattened; massive, rarely hollow. Ground tissue not sclerified. Rhizome scales: peltate; appressed (occasionally), or spreading; $2-4 \times 0.5-1$ mm wide; acute or rarely contracted to a narrow acumen; straw-coloured (rarely), or brown; evenly coloured or with a lighter margin; strongly dentate, rarely short-dentate. Frond dimorphy. Sterile fronds regularly present. Fertile parts similar to sterile part to distinctly narrowed. Fertile fronds. Simple. Stipe 1.5–11 cm long. Lamina $5-28 \times 0.2$ – 1.2 cm, widest at 0.3-0.6 from base or linear. Sterile fronds. Simple. Stipe 0.5-7 cm long. Lamina 5.5-19 × 0.4-1.3 cm, index 1.5-20 or more, widest at 0.3-0.6 from base. Costa only distinct; veinlets anastomosing; free veinlets excurrent and recurrent. Hydathodes absent. Margin not differentiated or cartilaginous, flat or thickened; notches regularly present, in fertile fronds sporadically to regularly present. Anatomy. Upper surface: walls of epidermis weakly to strongly thickened; hypodermis a single layer, patchily present or a double layer, cell walls thickened or not. Lower surface: walls of epidermis strongly thickened; hypodermis absent to distinct. Sori: round; in two rows between adjacent veins; in 1–5 rows between costa and margin; 1.5-3 mm across; superficial.

Selected illustrations — Holttum (1954): fig. 102 (as *C. wrayi*); Piggott & Piggott, Ferns of Malaya in colour (1988): fig. 446–449 (as *C. wrayi*).

Distribution — Sumatra, Malay Peninsula, Borneo, Celebes.

Ecology — Epiphytic, often as high epiphyte, rarely epilithic, in forest, often in mountain or summit forest. Altitude 1200–2500 m.

Notes on variability — Selliguea subsparsa is variably dimorphic, with some geographic differentiation. In Sumatra, fairly large forms occur (described as Polypodium subsparsum and Pleopeltis insperata), which vary from distinctly to hardly dimorphic, and have one to several rows of sori between costa and margin. In the Malay Peninsula, a more consistently smaller, dimorphic, form has been called Polypodium wrayi. One specimen from Borneo, described as Polypodium kamboranganum, could fit very well within this species, but for the presence of hydathodes, which argues for its inclusion in S. enervis.

A monomorphic form occurs that has uniformly narrow, mostly fertile fronds. This form could easily be confused with *Selliguea setacea* and with narrow forms of *S. enervis* and *S. ceratophylla*.

Notes — 1. In western Malesia Selliguea subsparsa is sufficiently distinct from S. enervis to recognise it as a separate species. It can be recognised by the narrow

fronds without hydathodes, the thin rhizome, and the usually strongly dentate rhizome scales. Towards the East, however, most notably on Celebes and in New Guinea, narrow forms occur which are similar to *S. subsparsa* but are linked to *S. enervis* by intermediates. Kato & Price [Acta Phytotax. Geobot. 41 (1990) 71] suggest that such narrow fronds may be an altitudinal effect in *S. enervis*. In the relatively few collections I have seen from Celebes and the Moluccas such an effect is not evident; however, it is clearly present in New Guinea. In Sumatra, on the other hand, largefronded specimens of *S. enervis* are found at altitudes of 1300–1900 m, which is the same range as that of *S. subsparsa*. Here, therefore, it seems more likely that the two forms represent two different species. The narrow specimens Kato & Price refer to from Ceram and other similar forms from Celebes and New Guinea are here included in *S. enervis*.

2. The identity of *Polypodium beccarii*. In the original description, Alderwerelt (1908) cited *Beccari 449*, and stated that it was identified by Baker as *Polypodium congener* Hooker (= *Grammitis congener* Blume). In Alderwerelt's Handbook, the type cited is *Beccari 442*. Later, Christensen (Christensen & Holttum, 1934: 307) suggests that *P. beccarii* may be based on the same unnumbered collection as *P. subsparsum* Baker, and is a synonym of *P. clemensiae* (= *S. ceratophylla*). In view of the superficial resemblance between *S. subsparsa* and *Grammitis congener* it is possible that Baker first identified a specimen of *S. subsparsa* as *P. congener* and later described it as a new species. It is also possible that collections of Beccari have become mixed up. I could not trace either *Beccari 442* or *449* in BO. Coming from West Sumatra, it is much more likely to be conspecific with *S. subsparsa* than with *S. ceratophylla*(*P. clemensiae*).

40. Selliguea hellwigii (Diels) Hovenkamp, comb. nov. - Fig. 38

Polypodium hellwigii Diels in K. Schum. & Lauterb., Fl. Schutzgeb. Südsee (1901) 140; Alderw., Malayan Ferns (1908) 645. — Pleopeltis hellwigii Alderw., Bull. Dép. Agric. Indes Néerl. 27 (1909) 6; Malayan Ferns, Suppl. 1 (1916) 383. — Crypsinus hellwigii Copel., Gen. Fil. (1947) 206. — Type: Hellwig 325a (B), New Guinea, Finisterre Mts.

Pleopeltis obolophylla Alderw., Nova Guinea 16 (1924) 38. — Polypodium obolophyllum C. Chr., Ind. Fil. Suppl. 3 (1934) 154. — Type: Lam 1476 (BO, L), New Guinea, Doorman.

Rhizome. Diameter 1 mm (or less), internodes to 0.5-1.2 cm long. Vascular strands 5-7, bundle sheath hyaline or partially sclerified. Sclerenchyma strands many; scattered or mainly central; isodiametric; massive. Ground tissue not sclerified or with a peripheral sclerified sheath. *Rhizome scales:* peltate; spreading; $3-5 \times 0.3-1$ mm; acute; straw-coloured to brown; evenly coloured; entire. *Frond dimorphy.* Sterile fronds regularly present. Fertile parts narrowed. *Fertile fronds.* Simple. Stipe 0.3-4 cm long. Lamina $1.5-7 \times 0.3-1.2$ cm, index 2.1-8.8, widest at 0.3-0.5 from the base (sometimes linear); base narrowed, apex acute or sometimes acuminate. *Sterile fronds.* Simple. Stipe 0.1-3.5 cm long. Lamina $0.6-2.7 \times 0.5-1.5$ cm, index 0.9-4, widest at 0.2-0.5 from base; base often truncate, apex obtuse or rounded. Costa only distinct (or occasionally veins distinct, raised on upper surface); veinlets nearly all free, excurrent and recurrent. Hydathodes frequent (rarely absent in small specimens), calcareous scales not persistent. Margin cartilaginous, flat, usually somewhat

incurved; notches regularly present. *Anatomy*. Upper surface: walls of epidermis not or weakly thickened; hypodermis absent. Lower surface: walls of epidermis weakly to strongly thickened; hypodermis absent. *Sori*: round; two between adjacent veins (often one in small fronds); in one row between costa and margin (sometimes a few in a second row in large fronds); 2 mm across; slightly sunken.

Selected illustration — Diels (1901): pl. 3, fig. A, B.

Distribution — Main island of New Guinea.

Ecology — Low or high epiphyte, rarely epilithic or terrestrial, in forest. Altitude 100–2900 m, mostly at high altitudes.

Vernacular names — New Guinea: warongo (Wapi, Miwaute); pieabo (Kapaukoe, Wissel Lakes).

Notes on variability — The dimorphism is somewhat variable. A few specimens have transitional, wider fertile fronds (e.g., *Brass 29658; Croft 1504; Schlechter 18778*), while some (*Brass 14132; van Valkenburg 247; Womersley & Millar NGF 7625*) are here included which are monomorphic or nearly so, but in all other aspects similar to *S. hellwigii* (small stature, flat, incurved margin, presence of hydathodes).

Note — This is one of the more easily recognisable segregates from the *S. enervis*complex. It can be distinguished by the usually strong dimorphism, the nearly constant presence of hydathodes (rare in the New Guinean representatives of the *S. enervis*-complex), and the flat, incurved lamina margin (usually thickened, not incurved in the *S. enervis*-complex).

41. Selliguea gracilipes (Alderw.) Hovenkamp, comb. nov. — Fig. 39

Pleopeltis gracilipes Alderw., Nova Guinea 16 (1924) 37. — Polypodium gracilipes C. Chr., Ind. Fil. Suppl. 3 (1934) 149. — Crypsinus gracilipes Copel., Gen. Fil. (1947) 207. — Type: Lam 1798 (BO, L, UC), New Guinea, Doorman.

Polypodium crassimarginatum Copel., Univ. Calif. Publ. Bot. 18 (10) (1942) 226. — Crypsinus crassimarginatum Copel., Gen. Fil. (1947) 207. — Type: Brass 13225, New Guinea, not found.

Rhizome. Diameter 2-4 mm, internodes to 0.7-1.2 cm long. Vascular strands 5-7, bundle sheath incompletely or fully sclerified. Sclerenchyma strands 10-many (often a little more than 10); scattered to mainly central; isodiametric; massive or hollow. Ground tissue not sclerified or with peripheral sclerified sheath. *Rhizome scales:* peltate; spreading; $5-6.5 \times 1.2-1.5$ mm; acute; straw-coloured to brown; evenly coloured; remotely and weakly dentate to short-dentate. Frond dimorphy. Sterile fronds usually present. Fertile parts similar to sterile part or very slightly narrowed. Fertile fronds. Simple. Stipe 1.5–9 cm long. Lamina $1.4-23 \times 0.4-0.7$ cm, index 2–46, widest at 0.5–0.7 from base or linear. Sterile fronds. Simple. Stipe 4–9 cm long. Lamina $1.5-4 \times 0.5-0.7$ cm, index 3-6, widest at 0.5-0.7 from base, base narrowly cuneate, apex broadly rounded. Main veins on upper surface not raised, indistinct. Hydathodes absent. Margin cartilaginous, strongly thickened; notches regularly to (rarely) abundantly present, in fertile fronds regularly present. Anatomy. Upper surface: walls of the epidermis weakly to very strongly thickened; hypodermis a single or double layer (rarely), cell walls not thickened to thickened. Lower surface: walls of epidermis weakly to very strongly thickened; hypodermis absent. Sori: round; in two rows between adjacent veins; in one row between costa and margin; 2–3 mm across; slightly sunken.

Distribution — New Guinea (7 specimens).

Ecology — Terrestrial or epiphytic, often in moss cushions. Altitude 1740–3225 m. Notes on variability — The type has characteristic long slender stipes, but in many other specimens these do not occur. Some have notably short stipes.

Notes -1. Distinct from most small species of *Selliguea* in the very thick texture and the thick cartilaginous margin, the regular presence of distinct notches, the absence of hydathodes, the rounded, not acute apex of the lamina, in which the costa ends well below the apex. The species is almost indistinguishable from *S. neglecta* (Sumatra, Java).

2. In MICH, Brass 9030 is marked as a type.

42. Selliguea triquetra (Blume) Ching — Fig. 40

- Selliguea triquetra Ching, Bull. Fan Mem. Inst. Biol. 10 (1941) 238. Polypodium triquetrum Blume, Enum. Pl. Javae (1828) 124; Fl. Javae Filic. (1829) 141; Mett., Farngatt. I. Polypodium (1857) 115; Hook., Sp. Fil. (1864) 63; Baker, Syn. Fil. (1868) 359; Alderw., Malayan Ferns (1908) 650; Backer & Posth., Varenfl. Java (1939) 201. Pleuridium triquetrum J. Sm., Ferns Brit. For. (1866) 95; Hist. Fil. (1875) 95. Pleopeltis triquetra Alderw., Bull. Dép. Agric. Indes Néerl. 27 (1909) 7; Malayan Ferns, Suppl. 1 (1916) 387. Crypsinus triquetrus Copel., Gen. Fil. (1947) 207. Crypsinopsis triquetra Pichi Serm., Webbia 31 (1977) 242. Type: Blume s.n. (L), Java.
- Polypodium vulcanicum Blume, Enum. Pl. Javae (1828) 122, Fl. Javae Filic. (1829) 144; Mett., Farngatt. I. Polypodium (1857) 111. — Pleuridium vulcanicum J. Sm., Hist. Fil. (1875) 95. — Type: Reinwardt s. n. (L), Ternate (see note).
- Polypodium rhomboideum Blume, Enum. Pl. Javae (1828) 124. Type: Blume s.n., Moluccas, not found.

Rhizome. Diameter 3-7 mm (or more), internodes to 1-2.5 cm long. Vascular strands 11-13, bundle sheath partially sclerified. Sclerenchyma strands very many (sometimes less); scattered; isodiametric; massive. Ground tissue not sclerified, very soft. *Rhizome scales:* peltate; appressed to spreading; $5-9 \times 2-3$ mm; obtuse to mostly rounded, somewhat concave, sometimes acute; straw-coloured; with a lighter flabelloid margin; entire. Frond dimorphy. Sterile fronds regularly present. Fertile parts narrowed. Fertile fronds. Simple. Stipe 11-23 cm long. Lamina 12-30 × 2.3-6.4 cm, index 3.9-6.7, widest at 0.2-0.4 from base. Sterile fronds. Simple. Stipe 4.5-12 cm long. Lamina $11-28 \times 4.1-8.5$ cm, index 2.2-3.3, widest at 0.3-0.4 from base. Main veins distinct, on upper surface not raised or raised. Hydathodes frquent, the calcareous scales not persistent. Margin cartilaginous, flat or thickened; notches absent, rarely regularly present, in fertile fronds absent. Anatomy. Upper surface: walls of epidermis strongly thickened; hypodermis a single layer, cell walls thickened or not. Lower surface: walls of epidermis strongly to very strongly thickened; hypodermis absent to distinct. Sori: round, rarely confluent within one areole; in two rows between adjacent veins; in 5 or more rows between costa and margin; 2-3 mm across; superficial, but clearly marked on upper surface.

Selected illustration — Blume (1829): pl. 59.

Distribution — Sumatra, Java, Lesser Sunda Islands, Celebes, Moluccas? (see note 1).

Ecology — Epiphytic, epilithic or terrestrial, in forest, scrub or open places, often in summit vegetation. Altitude 1200-3300 m.

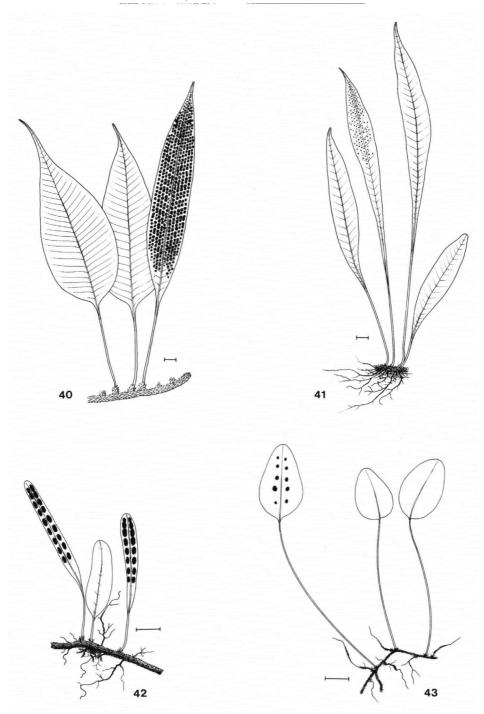


Fig. 40-43. – 40: Selliguea triquetra (Blume) Ching. – 41: S. ceratophylla (Copel.) Hovenkamp. – 42: S. neglecta (Blume) Hovenkamp. – 43. S. oodes (Kunze) Hovenkamp. – Scale bars = 1 cm.

Notes — 1. Most of the type material of *Polypodium vulcanicum* Blume (collected by Reinwardt on Ternate) is *Selliguea triquetra*. Some parts are possibly *S. feei* or *S. caudiformis*. *Polypodium vulcanicum* is not to be confused with *Grammitis vulcanica*, which was transferred by Blume himself to *S. feei*. Considering the confusion between these two species, it cannot be taken for granted that this specimen actually was collected on Ternate, which is outside the known range of *S. triquetra*.

2. Specimens collected without rhizome cannot be distinguished from *S. enervis* with certainty. *Selliguea triquetra* differs from *S. enervis* in the distinctly elongated rhizome, with internodes up to 2.5 cm in well-developed specimens, and with wide, obtuse to rounded scales. If the scales fall off, they usually do so completely in *S. triquetra*, whereas in *S. enervis* usually the base remains tightly fixed to the rhizome, and only the acumen disappears. The sori in *S. triquetra* are usually slightly larger than in *S. enervis*, and more often tend to become elongated or confluent.

Sterile specimens, on the other hand, are very difficult to distinguish from S. feei or related species. The best distinction here is that S. feei usually lacks sclerenchyma stands in the rhizome. However, this cannot distinguish S. triquetra from, e.g., S. caudiformis or some forms of S. bellisquamata.

43. Selliguea ceratophylla (Copel.) Hovenkamp, comb. nov. — Fig. 41

- Polypodium ceratophyllum Copel., Philipp. J. Sci. 3, Bot. (1909) 348. Pleopeltis ceratophylla Alderw., Malayan Ferns, Suppl. 1 (1916) 395. — Type: Foxworthy 205 (MICH), Borneo, Mt Poë.
- Polypodium angustato-decurrens Rosenst., Feddes Repert. Spec. Nov. Regni Veg. 13 (1914) 221
 Type: J. Winkler 79a (UC), Sumatra, Batakerland.
- Pleopeltis lucidula Alderw., Bull. Jard. Bot. Buitenzorg II, 16 (1914) 58; Malayan Ferns, Suppl. 1 (1916) 389. Polypodium lucidulum C. Chr., Ind. Fil. Suppl. prél. (1917) 26. Type: Matthew 706A (BO, K, US), Sumatra, Santubong.
- Polypodium occultivenium Copel., Philipp. J. Sci. 12, Bot. (1917) 63. Crypsinus occultivenius Copel., Gen. Fil. (1947) 207. Crypsinopsis occultivenia Pichi Serm., Webbia 31 (1977) 242. Type: Brooks s.n. (MICH), Borneo, Bidi.
- Polypodium clemensiae Copel., Brittonia 1 (2) (1931) 76. Type: Clemens 20449 (NY, UC), Borneo, Mt Poi.
- Crypsinus subfasciatus Holttum, Revis. Fl. Malaya 2, sec. ed. (1954) 202. Type: Holttum SFN 21559 (BM, K, SING), Malay Peninsula, Fraser's Hill.

Rhizome. Diameter 2–6 mm, internodes to 0.2–1 cm long. Vascular strands 8–10, bundle sheath hyaline. Sclerenchyma strands very many; scattered; isodiametric to periclinally flattened, smaller towards periphery; massive, hollow or perforated. Ground tissue not sclerified. *Rhizome scales:* pseudopeltate, or rarely peltate; spreading; 2–3.5 × 0.6–1.3 mm; acute; brown; evenly coloured; short-dentate to strongly dentate. *Frond dimorphy.* Sterile fronds regularly present. Fertile parts narrowed. *Fertile fronds.* Simple. Stipe 2–12 cm long. Lamina 5–29 × 0.9–4.1 cm, index 5.8–10, widest at 0.5–0.7 from base. *Sterile fronds.* Simple. Stipe 1–7 cm long. Lamina 5–22 × 1–4.3 cm, index 3.1–5.6, widest at (0.4–)0.5–0.6 from the base. Base very gradually narrowed. Apex acuminate in fertile, rounded in sterile fronds. Costa only distinct, or main veins also distinct, raised on upper surface; veinlets anastomosing; free veinlets excurrent and recurrent. Hydathodes absent. Margin cartilaginous, thickened;

without notches (rarely), or notches regularly present. Anatomy. Upper surface: walls of epidermis strongly to very strongly thickened; hypodermis a single or double layer, cell walls not thickened. Lower surface: walls of epidermis strongly to very strongly thickened; hypodermis absent. Sori: round, rarely elongate, confluent within one areole; in 2(-4) rows between adjacent veins; in (2-)5 rows between costa and margin; (0.5-)1.5-2 mm across; superficial or very slightly sunken.

Selected illustrations — Holttum (1954): fig. 103 (narrow form, as *Crypsinus sub-fasciatus*); Piggott & Piggott, Ferns of Malaya in colour (1988): fig. 441-442 (narrow form, as *Crypsinus subfasciatus*).

Distribution — Sumatra, Malay Peninsula, Borneo.

Ecology — Trunk or branch epiphyte, occasionally terrestrial, in forest. Altitude 650–1900 m.

Notes on variability — *Polypodium ceratophyllum* was described on the basis of a plant with irregularly furcate fronds. Some other collections, partly from the type locality, share this aberration (*Anderson 25*, Matang; *Brooks s.n.*, Mt Poë, 3000 ft).

Crypsinus subfasciatus is a very narrow form, with fertile fronds narrowly linear, to $28 \times 0.7-1$ cm. It is easily confused with S. setacea, which differs in the still narrower fronds without notches, and the hypodermis with thickened cell walls.

One specimen (K.M. Wong 1525, K) has very small sori, in four or more rows irregularly scattered between the main veins. Although at first sight a highly aberrant condition, this is linked to normal forms through a few specimens with an irregular third row of sori occasionally present. Apart from this, the specimen is also slightly aberrant in the almost entire margin, and the large size of the fronds (lamina at least 30 cm long in damaged fronds).

Note — Selliguea ceratophylla has often been confused with S. enervis, but can be distinguished by the short rhizome, with the phyllopodia not or hardly spaced; the pseudopeltate scales, which are usually more strongly dentate and have a somewhat coarser cell-net than in C. enervis, and the spathulate fronds, which are more gradually narrowed at the base than in S. enervis.

44. Selliguea pampolycarpa (Alderw.) Hovenkamp, comb. nov.

Pleopeltis pampolycarpa Alderw., Nova Guinea 16 (1924) 37. — Polypodium pampolycarpum C. Chr., Ind. Fil. Suppl. 3 (1934) 155. — Type: Lam 1254 (BO, L), New Guinea, Doorman R.

Rhizome. Diameter 1.5–2.5 mm, internodes to 0.2–0.5 cm long. Vascular strands 8–14, bundle sheath hyaline or partially sclerified. Sclerenchyma strands many; scattered; isodiametric; massive or hollow. Ground tissue not sclerified. *Rhizome scales:* peltate; spreading to slightly squarrose; $7.5-8.5 \times 1$ mm; acute or slightly contracted to a narrow acumen; brown; evenly coloured; entire or remotely and weakly dentate. *Frond dimorphy.* Sterile fronds regularly present. Fertile parts similar to sterile part, or narrowed. Fertile fronds. Simple. Stipe 2–10 cm long. Lamina 17–34 × 0.7–1.3 cm, widest at 0.5–0.8 from base. Sterile fronds. Simple. Stipe 1.5–5 cm long. Lamina 10–21 × 1.6–2.2 cm, index 5.5–8.1, widest at 0.5–0.8 from base. Base very gradually narrowed. Costa distinct, with two very distinct ridges on upper surface, main veins sometimes distinct, not raised on upper surface. Hydathodes absent. Margin not differentiated or cartilaginous, thickened; notches sporadically to regularly present.

Anatomy. Upper surface: walls of epidermis strongly thickened; hypodermis absent or a single layer, patchily present, cell walls not thickened. Lower surface: walls of epidermis strongly thickened; hypodermis absent. Sori: round; in two rows between adjacent veins; in 2–4 rows between costa and margin; 1.5–3 mm across; superficial to slightly sunken.

Distribution - New Guinea (7 specimens).

Ecology - Trunk or branch epiphyte in forest. Altitude 100-820 m.

Note — Apparently a rare species, but easily overlooked and confused with narrow forms of *Selliguea enervis*. The short internodes, the long, spathulate fronds which are very gradually narrowed into usually a short indistinct stipe, but particularly the distinct ridges on the upper side of the costa, are characteristic. In many collections, the apex of the long fronds is missing.

45. Selliguea neglecta (Blume) Hovenkamp, comb. nov. - Fig. 42

- Polypodium neglectum Blume, Enum. Pl. Javae (1828) 121; Fl. Javae Filic. (1829) 133. Drynaria neglecta J. Sm., J. Bot. (Hooker) 3 (1841) 397. Microterus neglectus C. Presl, Epim. Bot. (1851) 124. Niphobolus neglectus Fée, Gen. Filic. (?1853) 264. Craspedaria calva Fée, Gen. Filic. (?1853) 265, nom. illeg. Pleopeltis neglecta Alderw., Bull. Dép. Agric. Indes Néerl. 27 (1909) 4. Type: Kuhl & van Hasselt s. n. (BO), Java, Bantam.
- Pleopeltis parvifrons Alderw., Bull. Jard. Bot. Buitenzorg III, 2 (1920) 165; Bull. Jard. Bot.
 Buitenzorg III, 5 (1922) 216. Polypodium parvifrons C. Chr., Ind. Fil. Suppl. 3 (1934) 155.
 Type: Bünnemeijer 4707 (BO, L), Sumatra, Merapi.

Rhizome. Diameter 1-2 mm, internodes to 0.4-0.7 cm long. Vascular strands 5 or 6, bundle sheath hyaline. Sclerenchyma strands few; scattered; isodiametric; massive. Ground tissue not or lightly sclerified, or with a peripheral sclerified sheath. Rhizome scales: peltate; spreading; $1.4-2.8 \times 0.4-0.6$ mm; acute; brown; evenly coloured; strongly dentate. Frond dimorphy. Sterile fronds regularly present. Fertile parts similar to sterile part (occasionally), or narrowed (usually). Fertile fronds. Simple. Stipe (1-)2.5-3.5(-6.5) cm long. Lamina $2-7 \times 0.3-0.8$ cm, index 4-17, widest at 0.4-0.9 from base or linear. Sterile fronds. Simple. Stipe 0.5–3.5 cm long. Lamina $1.3-4 \times$ 0.7-1.7 cm, index 1.6-5, widest at 0.4-0.7 from base or linear. Apex rounded. Costa only distinct; veinlets anastomosing; free veinlets excurrent and recurrent. Hydathodes absent. Margin cartilaginous, flat to thickened; notches regularly present, in fertile fronds sporadically present (occasionally), to regularly present (usually). Anatomy. Upper surface: walls of epidermis strongly thickened; hypodermis a single or double layer, cell walls not thickened. Lower surface: walls of epidermis very strongly thickened; hypodermis absent or indistinct. Sori: round; in one row between adjacent veins; in one row between costa and margin; 2-3 mm across; superficial.

Selected illustration — Blume (1829): pl. 54 fig. 1.

Distribution — Sumatra (8 specimens), Java (1 specimen).

Ecology — Epiphytic in forest. Altitude 1440–2560 m.

Note — Selliguea neglecta may be confused with forms of S. subsparsa, from which it can be distinguished only with difficulty: S. neglecta has the sori singly between the veins, S. subsparsa usually has two sori between each pair of veins. As the venation is rarely visible, the position of the veins is best inferred from the position of the marginal notches.

46. Selliguea oodes (Kunze) Hovenkamp, comb. nov. - Fig. 43

- Polypodium oodes Kunze, Bot. Zeitung (Berlin) 4 (1846) 421; Mett., Farngatt. I. Polypodium (1857) 115; Hook., Sp. Fil. (1864) 71; Baker, Syn. Fil. (1868) 354; Alderw., Malayan Ferns (1908) 652. Pleopeltis oodes T. Moore, Index Filic. (1857) lxvii; (1862) 347; Alderw., Bull. Dép. Agric. Indes Néerl. 27 (1909) 7; Malayan Ferns, Suppl. 1 (1916) 390. Phymatopsis oodes J. Sm., Hist. Fil. (1875) 105. Crypsinus oodes Copel., Gen. Fil. (1947) 207; Fern Fl. Philipp. (1960) 506. Type: Cuming 58 (BM, BO, K, L, P, PRC), Philippines, Luzon.
- Polypodium dulitense Baker, Kew Bull. (1893) 211; Alderw., Malayan Ferns (1908) 652.
 Pleopeltis dulitensis Alderw., Bull. Dép. Agric. Indes Néerl. 27 (1909) 7; Malayan Ferns, Suppl. 1 (1916) 390.
 Type: C. Hose 300 (K, SING), Borneo, Mt Dulit.
- Polypodium rudimentum Copel. in Perkins, Fragm. Fl. Philipp. 1 (1905) 190. Pleopeltis rudimenta Alderw., Bull. Dép. Agric. Indes Néerl. 27 (1909) 5. — Type: Elmer 6022 (B, K, P), Philippines, Luzon.

Rhizome. Diameter 0.5-1 mm, internodes to 0.7-2 cm long. Vascular strands 3 or 4, bundle sheath hyaline. Sclerenchyma strands absent. Ground tissue not sclerified. *Rhizome scales:* peltate; spreading; $2.5-4.5 \times 0.5$ mm; acute; straw-coloured or brown, thin, translucent, evenly coloured; entire or remotely and weakly dentate, usually more strongly lacerate-dentate at the base. Frond dimorphy. Monomorphic or slightly dimorphic. Sterile fronds regularly present (usually few). Fertile parts similar to sterile part. Fertile fronds. Simple. Stipe 1-10 cm long, usually very thin. Lamina $1.5-8 \times 1-2.5(-3.6)$ cm, index 1.1-3.5, widest at 0.2-0.5 from the base. Sterile fronds. Simple. Stipe 0.4–3.5 cm long. Lamina $1-2.5 \times 1-1.7$ cm, index 0.7–1.2, widest at 0.2–0.6 from base. Base rounded to cordate, occasionally cuneate, apex rounded to acuminate. Costa only distinct; veinlets free or anastomosing; free veinlets excurrent and recurrent. Hydathodes frequent, calcareous scales not persistent. Margin cartilaginous, thickened; notches regularly present. Anatomy. Upper surface: walls of epidermis weakly to very strongly thickened; hypodermis absent or a single layer, patchily present, cell walls not thickened. Lower surface: walls of epidermis weakly to very strongly thickened; hypodermis absent. Sori: round, elongate, or confluent; confluent within one areole or across connecting veins; in one or two rows between adjacent veins; in 1-4 rows between costa and margin; 1-2 mm across; slightly sunken to deeply sunken.

Selected illustration --- Copeland (1947): pl. 8 fig. 3a, b.

Distribution - Borneo, Celebes, Philippines.

Ecology — Epilithic, mostly in riverbeds, rarely epiphytic, on trunks. Altitude 600-1500 m.

Notes on variability — The typical form occurs mainly in the Philippines, and has small, ovate, entire fronds. *Polypodium dulitense*, from Borneo, represents a form with lobed or sinuose margins and an acuminate apex.

Notes — 1. Selliguea oodes can be confused with small forms of the S. enervis complex ('Polypodium rhomboideum'). The distinctly sunken sori, the soft, succulent texture, the presence of hydathodes and the angle between lamina and stipe will usually distinguish S. oodes.

2. *Selliguea oodes* often occurs as a rheophyte, but has none of the rheophytic characters found in other rheophytic ferns [Kato & Imaichi, Can. J. Bot. 70 (1992) 166].

47. Selliguea bakeri (Luerss.) Hovenkamp, comb. nov. — Fig. 44

- Polypodium torulosum Baker, J. Bot. NS 9 (1880) 215, nom. illeg., non Baker (1877), type from Madagascar. Polypodium bakeri Luerss., Abh. Nat. Ver. Bremen 7 (1882) 48; Alderw., Malayan Ferns (1908) 632. Pleopeltis bakeri Alderw., Bull. Dép. Agric. Indes Néerl. 27 (1909) 4. Crypsinus bakeri Tagawa, Acta Phytotax. Geobot. 25 (1973) 180. Type: Beccari 445 (BM, BO, K), Sumatra, Mt Singalan.
- Pleopeltis pseudo-lateralis Alderw., Bull. Jard. Bot. Buitenzorg II, 28 (1918) 36. Type: Bünnemeijer 772 (L), Sumatra, Mt Talamau.

Rhizome. Diameter 2–3 mm. Internodes to 0.5–2 cm long. Vascular strands 6–8. Bundle sheath hyaline or fully sclerified. Sclerenchyma strands many, scattered, isodiametric or periclinally flattened, massive. Ground tissue not sclerified. Rhizome scales: peltate, spreading, $4-8 \times 1-1.5$ mm, acute, brown, evenly coloured or (rarely) with a lighter margin, strongly dentate. Frond dimorphy. Sterile fronds regularly present. Fertile parts strongly contracted. Fertile fronds. Simple. Stipe 8-19 cm long. Lamina linear, 12–19×0.2–0.4 cm. Sterile fronds. Simple. Stipe 2–11 cm long. Lamina $5-12 \times 5-4$ cm, index 1.7-4.5, widest at 0.3-0.5 from base. Main veins on the upper surface not raised or raised, distinct. Hydathodes absent or (occasionally) present, calcareous scales not persistent. Margin cartilaginous, thickened; without notches (sometimes), or notches regularly present, in fertile fronds absent. Anatomy. Upper surface: walls of epidermis strongly to very strongly thickened; hypodermis a single layer, cell walls not thickened. Lower surface: walls of epidermis strongly to very strongly thickened; hypodermis absent. Sori: elongate; in one row between adjacent veins; in one row between costa and margin; 2-4 mm across; superficial to (rarely) slightly sunken.

Selected illustration — Alderwerelt (1918): pl. 6 (as *Pleopeltis pseudo-lateralis*). Distribution — Sumatra.

Ecology — Epiphytic, often in moss-cushions, occasionally on thin twigs or trunks. In open scrub, mossy forest, or in tree crowns. Altitude 1500–3300 m.

Notes on variability — In some specimens there is a tendency towards the formation of longitudinal coenosori (Alston 15057, BM).

Note — Selliguea bakeri has a strong superficial resemblance to the New Guinean S. lauterbachii. The latter can be distinguished from S. bakeri by the more elongated internodes, the squarrose rhizome scales, often with a hyaline margin, the lamina with more distinct hypodermis layers on both sides and the notched fertile fronds.

48. Selliguea metacoela (Alderw.) Parris — Fig. 45

Selliguea metacoela Parris in Parris, Beaman & Beaman, The plants of Mount Kinabalu. I. Ferns and fern allies (1991) 152. — Drymoglossum metacoelum Alderw., Bull. Jard. Bot. Buitenzorg II, 28 (1918) 21. — Pycnoloma metacoelum C. Chr., Dansk Bot. Ark. 6 (3) (1929) 77. — Type: Hallier 2942 (L), Borneo, Liang Gagang.

Rhizome. Diameter 2 mm,the internodes to 0.4–0.8 cm long. Vascular strands 5–8, bundle sheath hyaline. Sclerenchyma strands few; scattered; isodiametric; massive. Ground tissue not sclerified. *Rhizome scales:* pseudopeltate; spreading; $4-5.5 \times 0.6$ mm; acute; straw-coloured, or brown, acumen dull light-brown, base darker; remotely and weakly dentate at base, acumen entire. *Frond dimorphy.* Sterile fronds regularly

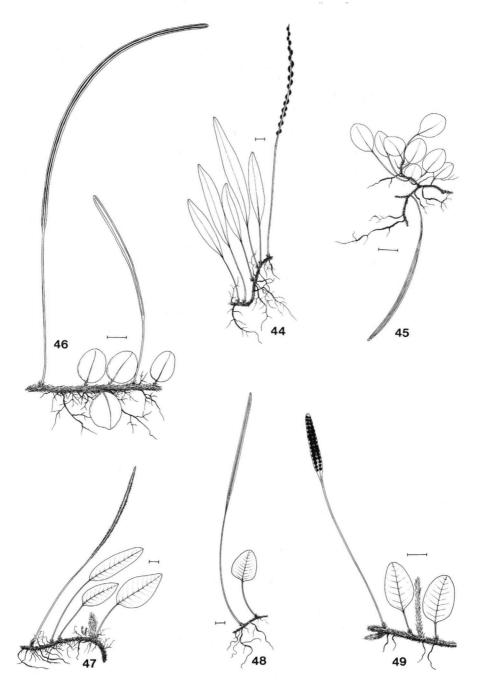


Fig. 44-49. Strongly dimorphic species. - 44: Selliguea bakeri (Luerss.) Hovenkamp. - 45: S. metacoela (Alderw.) Parris. - 46: S. rigida (Hook.) Hovenkamp. - 47: S. brooksii (Alderw.) Hovenkamp. - 48. S. murudense (C. Chr.) Parris. - 49. S. pseudoacrostichum (Alderw.) Hovenkamp. - Scale bars = 1 cm.

present. Fertile parts strongly contracted. *Fertile fronds*. Simple. Stipe 5.5-11 cm long. Lamina $3-8 \times 0.2-0.3$ cm, linear. *Sterile fronds*. Simple. Stipe 0.3-2 cm long. Lamina $1-2.5 \times 1-1.7$ cm, index 1-2.1, widest at 0.3-0.5 from base. Costa only distinct; veinlets anastomosing; free veinlets excurrent and recurrent. Hydathodes absent. Margin cartilaginous, thickened to strongly thickened; without notches. *Anatomy*. Upper surface: walls of epidermis strongly thickened; hypodermis absent. Lower surface: walls of epidermis strongly thickened; hypodermis absent. *Sori:* confluent across veins into a longitudinally elongated coenosorus; a single one between costa and margin; superficial.

Selected illustrations — Alderwerelt (1918): pl. 2 (as *Drymoglossum metacoelum*); C. Christensen (1929): pl. 8 fig. 3, pl. 9 fig. 2; pl. 10 fig. 2.

Distribution — Sumatra (1 specimen), Malay Peninsula (2), Borneo (4).

Ecology — Epiphytic. Altitude 150-800 m.

Note — An easily recognised species, which can only be confused with *Selliguea rigida*. The latter is generally more stiff, with stiff, thick rhizome scales, an extremely thick, coriaceous lamina, and distinctly sunken coenosori.

49. Selliguea rigida (Hook.) Hovenkamp, comb. nov. - Fig. 46

Drymoglossum rigidum Hook., Cent. Ferns (1854) t. 96. — Schizolepton rigidum T. Moore, Index Filic. (1857) xxx; (1862) 344. — Pycnoloma rigidum, C. Chr., Dansk Bot. Ark. 6 (3) (1929) 76; Copel., Gen. Fil. (1947) 207. — Type: Lobb s. n. (K), Sarawak.

Drymoglossum tetragonum Alderw., Bull. Jard. Bot. Buitenzorg II, 28 (1918) 21. — Type: Teuscher s. n. (BO, not found), Borneo.

Rhizome. Diameter 1 mm, the internodes to 0.5 cm long. Vascular strands 5, bundle sheath fully sclerified. Sclerenchyma strands many; scattered; isodiametric, smaller periclinally flattened strands present at periphery; massive. Ground tissue not sclerified. *Rhizome scales:* pseudopeltate or peltate; stiffly spreading; 6×0.6 mm; contracted to a narrow acumen with a dark pseudocosta; brown to blackish with a lighter hyaline margin; strongly dentate. Frond dimorphy. Sterile fronds regularly present. Fertile parts strongly contracted. Fertile fronds. Simple. Stipe 1.7-6.5 cm long. Lamina 4-10 × 0.2 cm, linear. Sterile fronds. Simple. Stipe 0.1–6.5 cm long. Lamina $1-2.8 \times 0.9-1.7$ cm, index 1-2, widest at c. 0.5 from base. Costa only distinct; veinlets anastomosing; free veinlets excurrent and recurrent. Hydathodes absent. Margin cartilaginous, strongly thickened; notches indistinct, sporadically present, in fertile fronds absent. Anatomy. Upper surface: walls of epidermis very strongly thickened; hypodermis a single layer, cell walls strongly thickened, filling lumen entirely. Lower surface: walls of epidermis very strongly thickened; hypodermis indistinct. Sori: confluent across main veins, forming longitudinal coenosori; single between costa and margin; deeply sunken (not raised on upper surface).

Selected illustrations — Alderwerelt (1918): pl. 3 (as *Drymoglossum tetragonum*); C. Christensen (1929): pl. 8 fig. 1a-b & 2, pl. 10 fig. 1; Hooker (1854): pl. 96 fig. 2 (not his fig. 1, which is incorrect).

Distribution — Borneo (5 specimens).

Ecology — Epiphytic, in kerangas, also in lowland dipterocarp forest. Sea level to 380 m altitude.

Note — A rare species. Easily recognised by the rigid stiffness of all its parts. It can only be confused with *S. metacoela*, which is less stiff generally, has scales with a dull brown, entire acumen, and has coenosori which are not sunken.

50. Selliguea brooksii (Alderw.) Hovenkamp, comb. nov. — Fig. 47

Drymoglossum brooksii Alderw., Bull. Jard. Bot. Buitenzorg II, 28 (1918) 21. — Grammatopteris brooksii Alderw., Bull. Jard. Bot. Buitenzorg III, 5 (1922) 318. — Grammatopteridium costulatum var. brooksii C. Chr., Dansk Bot. Ark. 6 (3) (1929) 81. — Grammatopteridium brooksii Copel., Gen. Fil. (1947) 208. — Type: Brooks 361/S (BM), Sumatra, Bengkoelen.

Rhizome. Diameter 2–3 mm, internodes to 1 cm long. Vascular strands 6–9, bundle sheath hyaline. Sclerenchyma strands many to very many; scattered; isodiametric or periclinally flattened, often smaller towards periphery; massive, or hollow. Ground tissue not sclerified or with a lightly sclerified peripheral sheath. Rhizome scales: peltate; spreading; $3.5-5 \times 0.5-1$ mm; acute; straw-coloured to brown; evenly coloured or with a lighter margin; short-dentate (occasionally) to strongly dentate. Frond dimorphy. Strongly dimorphic. Sterile fronds regularly present. Fertile parts strongly contracted. Fertile fronds. Simple. Stipe 6-24 cm long. Lamina 4-18 × 0.1-0.2 cm, linear. Sterile fronds. Simple. Stipe 2-8 cm long. Lamina 3.5-9.5 × 1.7-5.5 cm, index 1.2-3.6, widest at 0.2-0.5 from base; base truncate to cordate, apex rounded. Main veins on upper surface not raised or raised, distinct; veinlets anastomosing; free veinlets excurrent and recurrent. Hydathodes on fertile fronds present, calcareous scales not persistent, absent on sterile fronds. Both surfaces distinctly dotted with conspicuous glands in small depressions. Margin cartilaginous, thickened; notches sporadically to (more often) regularly present, in fertile fronds absent. Anatomy. Upper surface: walls of the epidermis very strongly thickened; hypodermis absent to a double layer, cell walls thickened. Lower surface: walls of epidermis very strongly thickened; hypodermis absent to distinct. Sori: forming a single, longitudinally elongated coenosorus between costa and margin; 1-3 mm across; superficial.

Selected illustration - C. Christensen (1929): pl. 11, fig. 1.

Distribution - Restricted to Sumatra.

Ecology — Epiphytic or epilithic, in mossy forest or exposed. Altitude 1440-1850 m.

Notes — 1. Selliguea brooksii is highly similar to S. murudensis (Borneo) and S. costulata (New Guinea). These two species can be distinguished as follows:

Selliguea murudensis: plants usually smaller, more slender. Fronds thinner, less coriaceous. Lamina-base usually more narrowly cuneate. Surfaces not distinctly glandular (inconspicuous glands may be present). Hydathodes always present (at least a few), also on sterile fronds.

Selliguea costulata: Often large plants. Rhizome widely creeping, bundle sheaths of the vascular strands heavily sclerified. Hydathodes never present on fertile or sterile fronds. Surface not distinctly glandular.

2. Selliguea brooksii can also be confused with S. pseudo-acrostichum (they have occasionally been collected in a mixture), which can be recognised by the more gradually cuneate lamina base and the separate sori.

51. Selliguea murudensis (C. Chr.) Parris - Fig. 48

Selliguea murudensis Parris in Parris, Beaman & Beaman, The plants of Mount Kinabalu. I. Ferns and fern allies (1991) 152. — Pycnoloma murudense C. Chr., Dansk Bot. Ark. 6 (3) (1929) 78; Gard. Bull. Straits Settlem. 7 (1934) 310. — Type: Mjöberg 1923 (BM), Borneo, Mt Murud.

Rhizome. Diameter 1-2 mm, internodes to 0.5-1 cm long. Vascular strands 4 or 5, bundle sheath hyaline. Sclerenchyma strands many; mainly central; isodiametric; massive. Ground tissue not sclerified, or with a lightly sclerified peripheral sheath. *Rhizome scales:* peltate; spreading; $2.9-4.5 \times 0.7-1$ mm; acute; brown; evenly coloured or with a slightly lighter margin; remotely and weakly to short-dentate. Frond dimorphy. Sterile fronds regularly present. Fertile parts strongly contracted. Fertile fronds. Simple. Stipe 6.5–18 cm long. Lamina 9–15.5 \times 0.2–0.25 cm, linear. Sterile fronds. Simple. Stipe 2–7 cm long. Lamina 2–5.5 \times 1.6–2.5 cm, index 1.2–3.4, widest at 0.1-0.5 from base. Base cuneate to truncate, apex rounded. Main veins on upper surface raised, distinct; veinlets anastomosing; free veinlets excurrent and recurrent. Hydathodes sometimes present to frequent, calcareous scales not persistent. Margin cartilaginous, thickened to strongly thickened; notches regularly present, absent in fertile fronds. Anatomy, Upper surface: walls of epidermis weakly to strongly thickened; hypodermis a single layer, patchily present, cell walls not thickened. Lower surface: walls of epidermis weakly to strongly thickened; hypodermis absent. Sori: longitudinally elongate or confluent across veins, forming a longitudinal coenosorus; a single one between costa and margin; 1 mm across; superficial.

Selected illustrations - C. Christensen (1929): pl. 8, fig. 4-6, pl. 10, fig. 4.

Distribution — North Borneo.

Ecology — Epiphytic on trunks or branches, or epilithic. Altitude 150-1700 m.

Notes on variability — The coenosori are usually continuous, but occasionally they may be interrupted.

Note — Selliguea murudensis can be confused with S. brooksii and S. pseudoacrostichum. It differs from S. brooksii in its usually smaller, more slender stature, the lamina-base usually more narrowly cuneate, lamina surfaces not distinctly glandular (inconspicuous glands may be present), with always at least a few conspicuous hydathodes present. From S. pseudo-acrostichum it differs in having mostly shorter internodes, narrower fertile fronds and continuous, or nearly continuous, coenosori.

52. Selliguea pseudoacrostichum (Alderw.) Hovenkamp, comb. nov. - Fig. 49

- Pleopeltis pseudo-acrostichum Alderw., Bull. Jard. Bot. Buitenzorg II, 28 (1918) 36. Polypodium pseudo-acrostichum C. Chr., Ind. Fil. Suppl. 3 (1934) 156. Type: Bünnemeijer 830 (BO), Sumatra, Talamau Mt.
- Polypodium pyrolifolium Goldm. var. sumatrana Rosenst., Feddes Repert. Spec. Nov. Regni Veg. 13 (1914) 220. — Type: Winkler 125 (K, UC), Sumatra.

Rhizome. Diameter 2 mm (dorsoventrally flattened), internodes to 1.5–2 cm long. Vascular strands 6–10, bundle sheath hyaline or partially sclerified. Sclerenchyma strands many; scattered or mainly around the vascular cylinder; isodiametric; massive. Ground tissue with subperipheral sclerified sheath. *Rhizome scales:* peltate, appressed to spreading, $4-5.5 \times 1$ mm; acute; straw-coloured or brown with a lighter

margin, sometimes with irregular dark spots; remotely and weakly dentate. Frond dimorphy. Sterile fronds regularly present. Fertile parts strongly contracted. Fertile fronds. Simple. Stipe 8–14 cm long. Lamina $3.5-10 \times 0.3-0.6$ cm, index 9–12, widest at 0.4–0.5 from the base or linear. Sterile fronds. Simple. Stipe 0.8–6.5 cm long. Lamina $2.5-5 \times 0.9-2.7$ cm, index 1.4–3.7, widest at 0.2–0.5 from base. Main veins on upper surface raised, distinct; veinlets anastomosing; free veinlets excurrent and recurrent. Hydathodes frequent, relatively large and conspicuous, calcareous scales not persistent. Margin cartilaginous, thickened; notches regularly present. Anatomy. Upper surface: walls of epidermis weakly thickened; hypodermis a single layer, cell walls not thickened. Lower surface: walls of epidermis weakly to strongly thickened; hypodermis absent or indistinct. Sori: round; in two rows between adjacent veins, often confluent to a longitudinally elongated sorus; in one row between the costa and margin (occasionally a few sori in a second row); 1.5–2 mm across; superficial.

Selected illustration — Alderwerelt (1918): pl. 5.

Distribution — Sumatra.

Ecology - Epiphytic, in mossy forest. Altitude 1200-2000 m.

Note on variability — Some specimens have light coloured, appressed rhizome scales with a finely dentate, scarious margin; others have more brownish, spreading scales.

Notes — 1. Very similar to Selliguea murudensis from Borneo, from which it differs in the fertile lamina being usually over 3 mm wide with a distinct sterile margin, and in the sori, which may be longitudinally elongated but usually are not confluent across the veins (*Robinson & Boden Kloss 148*, BM, is an exception in that it has continuous coenosori). Selliguea murudensis is more pronouncedly drymoglossoid, with narrower fertile fronds (mostly 2 mm wide) and coenosori which are often uninterrupted for most of their length.

2. Crypsinus hagerupii differs in a much more coriaceous texture, and a lack of hydathodes. It is insufficiently known; no specimens other than the type specimen (Hagerup s. n., 1916–17, Lake Toba, BM) could be found.

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IDENTIFICATION LIST

Demgaca			
1. feei	14. ferrea	27. albidopaleata	40. hellwigii
2. elmeri	15. albidosquamata	28. platyphylla	41. gracilipes
3. feeoides	16. laciniata	29. soridens	42. triquetra
4. caudiformis	17. taeniata	30. stenophylla	43. ceratophylla
5. plantaginea	18. subtaeniata	31. heterocarpa	44. pampolycarpa
6. tafana	19. violascens	32. sri-ratu	45. neglecta
7. cretifera	20. lagunensis	33. lateritia	46. <i>oodes</i>
8. albicaula	21. glauca	34. craspedosora	47. bakeri
9. archboldii	22. triloba	35. setacea	48. metacoela
10. bellisquamata	23. pyrolifolia	36. bisulcata	49. rigida
11. dekockii	24. whitfordii	37. enervis	50. brooksii
12. lauterbachii	25. simplicissima	38. stenosquamis	51. murudensis
13. costulata	26. lanceola	39. subsparsa	52. pseudo-acrostichum

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INDEX OF SYNONYMS

This index lists all epithets that are not simply forms of the epithet of the accepted name with a different ending. The level and form here listed is that of the first publication or of the basionym.

abbreviatum (var.) = 31. heterocarpum albara = 8, albicaulaalbarium = 8. albicaulaalbo-squamatum = 15. albidosquamata albulum = 37. enervis alloiosorum = 5. plantaginea angustato-decurrens = 43. ceratophylla angustatum = 17. taeniata argyropus = 11. dekockii batacorum = 30. stenophylla beccarii = 39. subsparsa beguinii (var.) = 13. costulatum bellivenosum = 15. albidosquamata borneense (var.) = 17. taeniata brachylepidota = 10. bellisquamata calophlebium = 4. caudiformis calva = 45. neglecta caudaefolius = 5. plantaginea clemensiae = 43. ceratophylla cochleare = 37, enervis crassimarginatum = 41. gracilipes crassinervium = 28. platyphylla crassisorum = 7, cretifera crenulata = 17. taenjata cyathisorum = 30. stenophylla dulitense = 46. oodes gibbsiae = 12. lauterbachii glauco-pruinatum = 21. glauca griffithianum (var. borneense) = 17. taeniata hagerupi = 52. pseudo-acrostichum (note 2) hammatisorum = 23. pyrolifolia heterocarpoides = 26. lanceola holosericeum = 37. enervis iboense = 13. costulatumincurvatum = 22. triloba induratum = 37. enervis insperata = 39. subsparsa kamboranganum = 37. enervis lagopodioides = 37. enervis lamprophyllum = 37, enervis latifolium = 28. platyphylla

lepidosorum = 17. taeniata leucolepis (var.) = 37. enervis lima = 31. heterocarpa limaeforme = 37. enervis longicuspe = 15. albidosquamata lucidula = 43. ceratophylla macrochasmum = 16. laciniata mafuluense = 5. plantagineamatthewii = 18. subtaeniata matutumensis = 22. triloba metteniana = 31. heterocarpa mjöbergii = 17. taeniata morgani = 31. heterocarpa moselvi = 17. taeniata nummularia = 23. pyrolifolia obolophylla = 40. hellwigii occultivenium = 43. ceratophylla pakkaense = 17. taeniata palmatum = 17. taeniata papilligerum = 31. heterocarpa parvifrons = 45. neglecta peltatisquama = 26. lanceola pentagonus = 36. bisulcata petiolatum = 37. enervisphilippinensis = 24. whitfordii (note 3) phlebiscopum = 4. caudiformis plebiscopa = 4. caudiformisprolixum = 11. dekockii pseudo-laciniata = 18. subtaeniata pseudo-lateralis = 47. bakeri pseudodrymoglossum = 13. costulatum quinquefidum = 17. taeniata ramosii = 17. taeniata remigerum = 37. enervis renifera = 37. enervis rhomboideum = 37. enervis rhomboideum = 42. triquetra rudimentum = 46. oodes rupestre = 37, enervis saxatile = 37. enervis schouteni = 31. heterocarpa

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taeniophyllum = 33. lateritia taeniopsis = 37. enervis taeniopsis (var.) = 37. enervis taenitidis = 17. taeniata tetragonum = 49. rigida torulosum = 47. bakeri treubii = 33. lateritia treubii (forma) = 33. lateritia triphyllum = 22. triloba undulato-sinuatum = 37. enervis varians = 15. albido-squamata vulcanica (var.) = 1. feei vulcanicum (Polypodium) = 42. triquetra werneri = 5. plantaginea wrayi = 39. subsparsa wurunuran (var.) = 25. simplicissimus

ALPHABETICAL LIST OF ACCEPTED NAMES

The numbers refer to the pages with the descriptions of the concerned species. **Bold-type** names refer to new combinations.

Selliguea Bory albicaula (Copel.) Kato & Price 38 albidopaleata (Copel.) Parris 63 albidosquamata (Blume) Parris 44 archboldii Copel. 38 bakeri (Luerss.) Hovenkamp 90 bellisquamata (C. Chr.) Hovenkamp 39 bisulcata (Hook.) Hovenkamp 73 brooksii (Alderw.) Hovenkamp 93 caudiformis (Blume) J. Sm. 31 ceratophylla (Copel.) Hovenkamp 86 costulata (Ces.) Wagner & Grether 42 craspedosora (Copel.) Hovenkamp 72 cretifera (Alderw.) Ching 37 dekockii (Alderw.) Hovenkamp 40 elmeri (Copel.) Ching 30 enervis (Cav.) Ching 74 feei Bory 27 feeoides Copel. 30 ferrea (Brause) Hovenkamp 43 glauca (J. Sm. ex T. Moore) Hovenkamp 56 gracilipes (Alderw.) Hovenkamp 83 hellwigii (Diels) Hovenkamp 82 heterocarpa (Blume) Blume 68 laciniata (Bedd.) Hovenkamp 47 lagunensis (H. Christ) Hovenkamp 55 lanceola (Mett.) E. Fourn. 62

(Selliguea) lateritia (Baker) Hovenkamp 71 lauterbachii (Brause) Hovenkamp 41 metacoela (Alderw.) Parris 90 murudensis (C. Chr.) Parris 94 neglecta (Blume) Hovenkamp 88 oodes (Kunze) Hovenkamp 89 pampolycarpa (Alderw.) Hovenkamp 87 plantaginea Brack. 33 platyphylla (Sw.) Ching 64 pseudo-acrostichum (Alderw.) Hovenkamp 94 pyrolifolia (Goldm.) Hovenkamp 58 rigida (Hook.) Hovenkamp 92 setacea (Copel.) Hovenkamp 72 simplicissima (F. Muell.) Hovenkamp 61 soridens (Hook.) Hovenkamp 65 sri-ratu Hovenkamp 70 stenophylla (Blume) Parris 67 stenosquamis Hovenkamp 80 subsparsa (Baker) Hovenkamp 80 subtaeniata (Alderw.) Hovenkamp 52 taeniata (Sw.) Parris 48 tafana (C. Chr.) Hovenkamp 36 triloba (Houtt.) M.G. Price 57 triquetra (Blume) Ching 84 violascens (Mett.) Hovenkamp 53 whitfordii (Copel.) Hovenkamp 60

New species added in proof:

Selliguea balbi Hovenkamp, spec. nov.

Rhizoma 5 mm crassum; internodiis ad 8 cm longis; paleis pseudopeltatis vel peltatis, 6–8 mm longis, 0.7–1 mm latis vestitum. Frondes fertiles 14–19 cm stipitatae, laminis ovato-lanceolatis, 14–22 longis, 3–5.3 cm latis, 2–3 cm caudatis; margine late cartilagineo, apicem verso 2–3 crenatis. Sori rotundati, 1.5–2 mm diametro, uniseriatim inter venas, 6–7-seriatim inter costam et marginem. — Typus: *Gideon et al. LAE 78566* (L, holo; iso LAE, NSW), Solomon Islands, Wakunai, Mt Balbi, 8/5/1988.

Rhizome. Diameter 5 mm, internodes to 8 cm long, blackish when dry. Vascular strands 12, bundle sheath fully sclerified, 1 cell thick. Sclerenchyma strands c. 25; central and peripheral; isodiametric. Ground tissue not sclerified. Rhizome scales pseudopeltate or peltate; appressed to squarrose; $6-8 \times 0.7-1$ mm wide (at base); gradually contracted to a narrow acumen and a long acicular apex; brown, concolorous; entire. Frond dimorphy. Sterile fronds not observed. Fertile parts not narrowed. Fertile fronds. Simple. Stipe 14–19 cm long. Lamina $14-22 \times 3-5.3$ cm, index 4–4.6, widest at c. 0.3 cm from base, base cuneate, apex contracted to a 2-3 cm long cauda. Main veins on upper surface raised, distinct. Anatomy: lamina c. 0.2 mm thick, upper and lower epidermis with strongly thickened outer cell walls, hypodermis on upper surface consisting of a single layer of large cells with thin walls, on lower surface not distinct. Hydathodes absent. Margin flat or sinuose, often curving downwards, especially in the cauda, very distinctly cartilaginous, c. 1/3 mm wide; a few notches present only near the apex of the lamina, but not on the cauda. Sori singly between the veins, in 6 or 7 rows between midrib and margin, not confluent; 1.4-2 mm across; very slightly impressed.

Distribution — Solomon Islands: Wakunai, Mt Balbi. Known only from the type. Ecology — Trailing on tree trunks in montane forest. Altitude 1900 m.

Note — In the key to the Malay-Pacific species, S. balbi will key out at lead 61, with S. feeoides and S. plantaginea. It can be easily distinguished from S. feeoides by the separate sori, from either species by the very distinct, flat, cartilaginous margin, more reminiscent of S. albidopaleata than of the species of the S. feei-group, with a few notches only just below the cauda. Because of the absence of a multilayered hypodermis, the texture is also distinctly more papyraceous than in the species of this group.