

THE PYRROSIA SPECIES FORMERLY REFERRED
TO DRYMOGLOSSUM AND SAXIGLOSSUM
(Filicales, Polypodiaceae)

BY

W.J. RAVENSBERG AND E. HENNIPMAN

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SUMMARY

The taxa formerly referred to *Drymoglossum* and *Saxiglossum* are part of *Pyrrosia*. Of these 6 species the taxonomy is given and the phylogenetic relationships discussed. One monophyletic group could be recognized consisting of *Pyrrosia heterophylla*, *P. niphoboloides* and *P. piloselloides* (*Drymoglossum p.p.*).

GENERAL PART

1. INTRODUCTION

The present study deals with the systematic and taxonomic problems of the *Pyrrosia* species formerly referred to *Drymoglossum* and *Saxiglossum*. Starting point for this revision is Christensen's monograph of the genus *Drymoglossum* (Christensen, 1929), in which six species are enumerated. Christensen was unable to draw generic lines between *Drymoglossum* and *Pyrrosia*, and regarded his classification as 'purely artificial'. In his circumscription the genus *Drymoglossum* is heterogeneous, including also two species of doubtful generic position.

In recent years *Drymoglossum* and *Saxiglossum* have been treated variously. As far as *Drymoglossum* is concerned most authors, e.g., Copeland (1947) and Holt-tum (1954) followed Christensen, whereas Price (1974) accommodated all species in *Pyrrosia*. *Saxiglossum* was created by Ching (1933) for *Cyclophorus taenioides* C. Chr., a species Christensen (1929) and Copeland (1947) referred to *Pyrrosia*. Pichi Sermolli (1977) 'confidently' regarded both *Drymoglossum* and *Saxiglossum* as independent genera. This illustrates the ambiguous position of these genera.

The present study is part of the *Polypodiaceae* Project (Hennipman, 1984): the systematics of the platyceroid *Polypodiaceae*; the genus *Platycerium* was dealt with by Hennipman and Roos (1982) and the genus *Pyrrosia* proper by Hovenkamp (1986). For details of the methodology see Hennipman and Roos (1983).

2. ACKNOWLEDGEMENTS

The study was for the greater part executed at the Rijksherbarium, Leiden. The authors express their gratitude to the Directors of the herbaria from which material was received on loan. The interest of Mr. G. J. de Joncheere as well as the critical remarks of Mr. P. Hovenkamp are greatly appreciated. The scanning micrographs of the spores and the indument were obtained thanks to the cooperation with the authorities of the former Geology Department of Leiden University. The cooperation of Miss. W. Sloot (typing of the MS) and of Mr. H. Rypkema (illustrations), Utrecht, is much appreciated.

3. MATERIAL AND METHODS

Herbarium material was studied from the following herbaria (abbreviations according to Index Herbariorum): A, B, BR, BM, G, GH, K, L, MICH, P, PRC, TI, UC, US, and W.

Anatomical preparations of rhizome, stipe and scales followed routine procedures. The venation pattern was studied from cleared material using projection photography (Hennipman, 1977), or a binocular microscope with transmitted light. Stomata were studied from macerated fronds according to Sen & Hennipman (1981). Spores and paraphyses were studied with a light microscope from preparations in glycerine jelly as well as with a Cambridge scanning electron microscope.

4. TAXONOMIC HISTORY

The genus *Drymoglossum* was established by Presl (1836) to accommodate *Pteris piloselloides* L. and *Drymoglossum spathulatum* (*nom. nud.*). In 1841, J. Smith added *Drymoglossum carnosum* Cunn. ex J. Smith (*nom. nud., non D. carnosum* Hooker) and *D. lanceolatum* (L.) J. Smith (= *Neurodium lanceolatum* (L.) Féé). Hooker (1842) described a heterotypic *Drymoglossum carnosum* from a plant inhabiting Nepal. Presl (1851) added *Drymoglossum rotundifolium* Presl (= *Pyrrosia (D.) piloselloides*) and transferred *D. spathulatum* and *D. carnosum* to his new genus *Lemmaphyllum*, the latter genus including both *D. carnosum* Cunn. ex J. Smith *nom. nud.* (= *Pyrrosia confluens* (R. Br.) Ching), and *D. carnosum* Hooker (= *Pycnoloma rigidum* (Hooker) C. Chr.). Féé (1852) broadly defined *Drymoglossum*, recognizing subgenus *Eudrymoglossum*, and subgenus *Lemmaphyllum*. He newly described *D. subcordatum* (Féé, 1852) and *D. abbreviatum* (Féé, 1857). Féé's generic concept was followed by J. Smith (1875), who did not regard the differences between the types of indument of the fronds of the different species (stellate hairs and scales respectively) 'of sufficient importance to warrant its (*Lemmaphyllum*) adoption as a genus'. Moore (1857) added to the confusion by incorporating another three species, viz. *D. acrostichoides* (Hooker & Grev.) Moore (= *Elaphoglossum conforme* (Hooker & Grev.) Schelpe), *D. cunninghamii* Moore (new name for *D. carnosum* Cunn. ex J. Smith, *nom. nud.*; *non* Hooker = *P. confluens*), and *D. ellipticum* (= *Pyrrosia (D.) heterophylla* (L.) Price).

Other species with scaly fronds were subsequently described in *Drymoglossum* by later workers, and transferred to the genus *Lemmaphyllum* afterwards. For details see: Excluded species (p. 305). In the Index Filicum (1906) Christensen recognized a broadly defined genus *Drymoglossum* including *Lemmaphyllum*.

Christensen (1929) regarded *Drymoglossum* (excluding *Lemmaphyllum*) and *Cyclophorus* (= *Pyrrosia*) 'in reality so near each other that it would be quite natural to unite them, inasmuch as the only character by which they should be distinguished, round sori in one, linear sori in the other genus, here too is an unstable one'. However, Christensen regarded the soral condition of *Drymoglossum*—an only rarely interrupted coenosorus—as consistent. The unstableness of the soral condition in *Cyclophorus* (= *Pyrrosia*) he illustrated by mentioning the transition states between punctiform and linear receptacles as

found in *Cyclophorus* (= *Pyrrosia*) *confluens* and *Cyclophorus* (= *P.*) *taenioides* C. Chr., (syn.: *Saxiglossum taenioides* (C. Chr.) Ching = *P. angustissima* (Diels) Tagawa & Iwatsuki). Apart from the soral condition, Christensen regarded the frond dimorphy as the second character of importance. As frond dimorphy is not rarely found in *Pyrrosia* species as well, Christensen formally restricted the genus 'to include those species only which show the two characters (linear sori and leaf dimorphy) combined'.

Although *Drymoglossum crassifolium* and *D. novo-guineae*, both representing *Pyrrosia novo-guineae*, easily fit the genus thus defined, Christensen preferred to rank these species as 'Species of doubtful position' because 'other characters such as scales and texture show that they come very near to *Cyclophorus*'. Thus within the genus *Drymoglossum* as construed by Christensen (1929), two different elements should be recognized, one of which with a close affinity to a certain group of *Pyrrosia*. Although Christensen himself thought his classification 'purely artificial', his study, nevertheless, can be regarded as a significant contribution to a better understanding of the formerly much confused group of *Polypodiaceae* with coenosori.

Ching (1933) created the genus *Saxiglossum* for *Cyclophorus taenioides* C. Chr. (*nom. illeg.* = *P. angustissima* (Baker) Tagawa & Iwatsuki). A second species was accommodated in this genus by Tagawa (1936). The classification of Christensen dealt with above was followed by all other authors (e.g., Copeland, 1947; Holtum, 1954; Pichi Sermolli, 1977) except Price (1974). It should be noted that Copeland (1947) expressed doubts as regards the polyphyly of *Drymoglossum* ('*Pteropsis*') as delineated by Christensen. On the other hand he reduced Ching's genus *Saxiglossum*: 'It is an aberrant *Pyrrosia*, and I do not see that its generic separation is called for: however, that is a matter of opinion' (op. cit., p. 194). Pichi Sermolli (1977) recognized both *Drymoglossum* and *Saxiglossum*.

5. MORPHOLOGY AND ANATOMY

Morphological studies on parts of the genus *Pyrrosia* include Giesenhangen (1901), Goebel (1926), Nayar (1957, 1961), Nayar & Chandra (1967), and Kim Nah et al. (1973).

Rhizome

Fig. 1a-e

In the drymoglossoid *Pyrrosia*'s and in *P. (Saxiglossum) angustissima* the rhizome is long-creeping, slender (up to 1.5 mm diam.), much branched, cylindrical to dorsoventrally flattened or ventrally furrowed (in older parts), densely set with scales, dorsally bearing spaced articulate fronds in two rows. Cross sections display, apart from the epidermis, a subepidermal sclerenchyma sheath, and a parenchymatous ground tissue with three to five meristoles (vascular strands). In

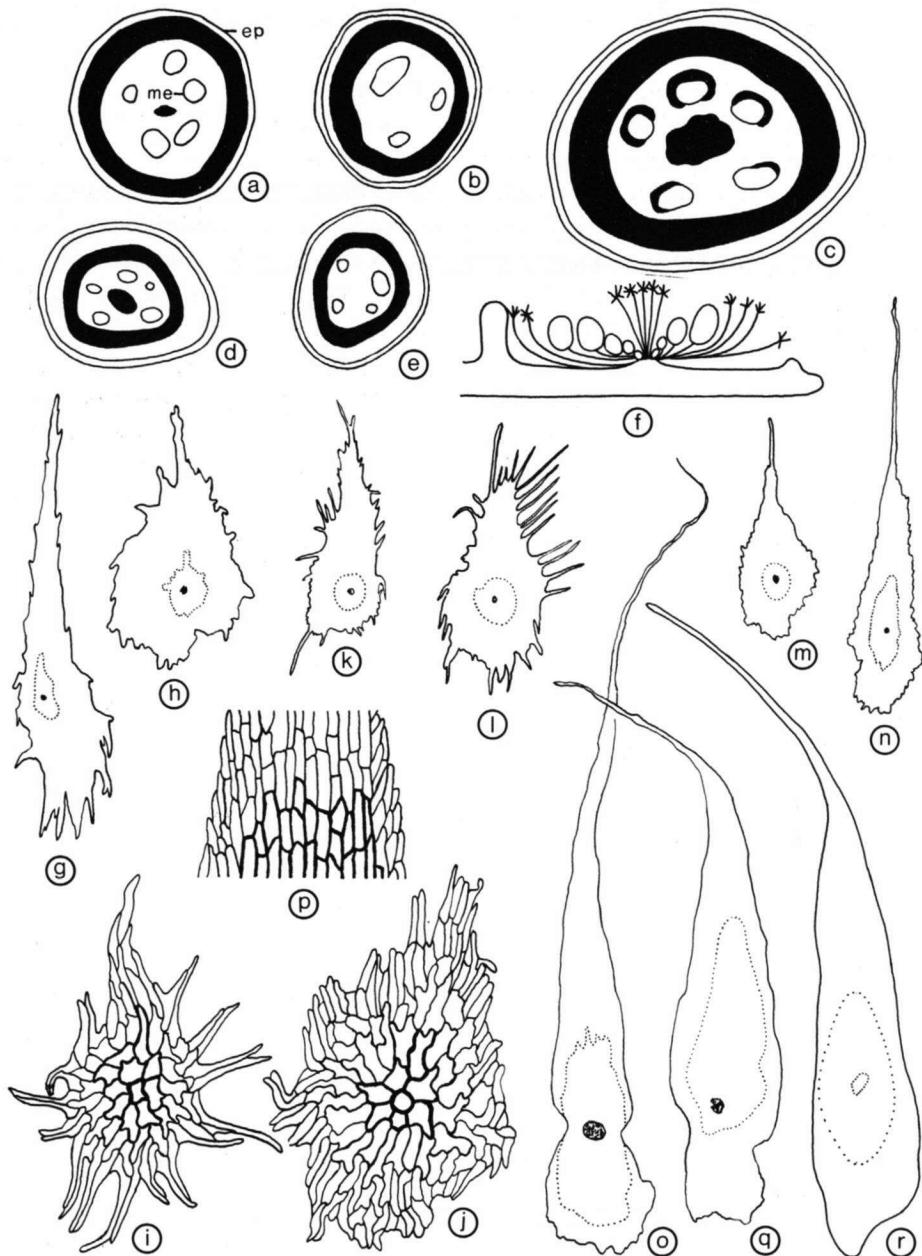


Fig. 1. a-e. Cross sections of rhizome, $\times 17$. a. *Pyrrosia (Saxiglossum) angustissima*; b. *P. (Drymoglossum) heterophylla*; c. *P. (D.) novo-guineae*; d. *P. (D.) fallax*; e. *P. (D.) piloselloides*.—ep = epidermis; me = meristele; sclerenchyma in solid black.—f. Schematic cross section of a coenosorus of *P. (D.) fallax*, $\times 14$.—g-r. Rhizome scales; outlines $\times 17$, details $\times 44$. g-i. *P. (D.) heterophylla*; j. *P. (D.) piloselloides*; k, l. *P. (D.) niphoboloides*; m, n. *P. (D.) fallax*; o, p. *P. (D.) novo-guineae*; q, r. *P. (S.) angustissima*—(a, q, r. *Cavalerie* 1883; b, g, h. *Beddome* 15; c, o, p. *Brass* 23611; d, f, m, n. *Brass* 27363; e. *Nooteboom* 1283; i. *Kew Distr.* No. 1107; j. *BKF* 12345; k, l. *Humbert* 5831).

P. (Drymoglossum) fallax and *P. (D.) novo-guineae* also a solid centrally situated sclerenchyma strand is present. For anatomical details see Nayar (1957) and Kim Nah et al. (1973: *P. ('Drymoglossum') piloselloides*).

The rhizome features of *Pyrrosia* proper show variation, but fully match the characteristics given above. Apart from species with a short-creeping rhizome with many meristoles (e.g., *P. africana*, *P. costata*) many species of *Pyrrosia* likewise have a long-creeping slender rhizome associated with a subepidermal sclerenchyma sheath of varying thickness, with a limited number of meristoles. A centrally situated sclerenchyma core is present in for instance *P. lanceolata*, *P. foveolata* and *P. nummulariifolia*, but absent in *P. rupestris* and other species. Sclerenchyma organizations somewhat different from those just mentioned, also occur in *Pyrrosia* proper, e.g. such with additional relatively small-sized strands scattered in the ground tissue amongst the meristoles (*P. angustata*, *P. samarensis*, and *P. porosa*).

The studies of Giesenhangen (1901), Nayar (1957, 1961), and Nayar & Chandra (1967) convincingly demonstrated that the vascular organization of frond- and root-traces of the drymoglossoid *Pyrrosia*'s is similar—though often anatomically less complex—to that found in *Pyrrosia* proper. The same holds for *P. (Saxiglossum) angustissima*.

Scales

Fig. 1g-r

Scales show much variation in the *Pyrrosia* species studied. The scales of *P. (Drymoglossum) heterophylla*, *P. (D.) niphoboloides*, and *P. (D.) piloselloides* are ± round to elongated, index 1-4(-6), margin irregularly shaped because of the presence of variously large outgrowths of marginal cells, central cells brownish, marginal cells hyaline to whitish (-brown). The scales of *P. (D.) fallax* are ± triangular, margin irregularly toothed or ciliate near the base, entire or ciliate in the upper part.

The scales of *P. (Saxiglossum) angustissima*, *P. (Drymoglossum) novo-guineae* are narrowly triangular, (index 8-12), being generally constricted at the place of insertion of the stalk, margin entire, without cilia or hairs, central cells brownish, marginal cells brownish, whitish, or hyaline.

The scales occurring in the drymoglossoid *Pyrrosia*'s, *P. heterophylla*, *P. niphoboloides*, and *P. piloselloides* are unique in the genus in being equally strongly ciliate at the base and the apex. The scales of *P. fallax* are similar, but usually less strongly ciliate at the apex than at the base. The scales of the other species are similar to those found in *Pyrrosia* proper.

Anatomy of the stipe

The stipes of the sterile and fertile fronds of the drymoglossoid *Pyrrosia*'s have the same anatomy.

In *P. (Saxiglossum) angustissima*, *P. (Drymoglossum) fallax*, *P. (D.) heterophylla*, *P. (D.) niphoboloides* and *P. (D.) piloselloides* two vascular strands are invariably found in the ground tissue of both the phylloodia and the stipe base of small- as well as larger-sized fronds.

The much wider stipes of *P. novo-guineae* have four vascular bundles. It is noted that conspicuous spherical completely lignified cells are also present in the ground tissue of this species.

The number of vascular bundles present in the stipes of species of *Pyrrosia* proper shows much variation in the species studied. For instance, two such bundles are present in the stipes of *P. nummulariifolia*, whereas nine such bundles were found in *P. flocculosa*.

Shape of the fronds

The species under study have dimorphic fronds except *P. (Saxiglossum) angustissima*. The sterile fronds of the drymoglossoid Pyrrosia's are similar to those occurring in species of *Pyrrosia* proper; the fertile fronds, however, have linear coenosori strikingly different from the ± round sori found in most other species of the genus. Exceptions are *P. samarensis* and *P. confluens*.

Soral arrangement

Fig. 1f, fig. 2a-g

The coenosoroid arrangement of the sporangia is not always consistent. In *P. (Saxiglossum) angustissima* fronds with linear sori and fronds with round sori, as well as the intermediate condition can be found. With regard to round sori a comparable inconsistency is found in true *Pyrrosia* species. For instance, the sori as occurring in the lower soriferous part of the fertile frond of *P. samarensis* are sometimes round, those in the upper part are often linear. Transitional stages between sori and coenosori are also found in *P. confluens*. The linear sori of *P. (Drymoglossum) niphoboloides* are characteristically interrupted. Nevertheless, exclusively linear sori are a consistent characteristic of this species, *P. (Drymoglossum) fallax*, *P. (D.) heterophylla*, *P. (D.) piloselloides*, and *P. (D.) novo-guineae*.

The receptacle is variously situated on the veins (fig. 2a-g). In *P. (Drymoglossum) niphoboloides* and *P. (D.) piloselloides* the coenosori are inserted on the veins nearest to the margin, in the other species on the veins nearest to the rhachis. The fertile fronds of *P. (D.) heterophylla* have a venation pattern usually showing but a single vein between rhachis and margin. However, occasionally found broader fertile fronds with a more complex venation have at least part of the receptacle situated on the marginal veins (fig. 2c).

The maturation of the sori has been studied by Kim Nah et al. (1973) for *P. (Drymoglossum) piloselloides*. These authors showed that the sporangia develop without a definite sequence. This seems to be the case in many leptosporangiate ferns.

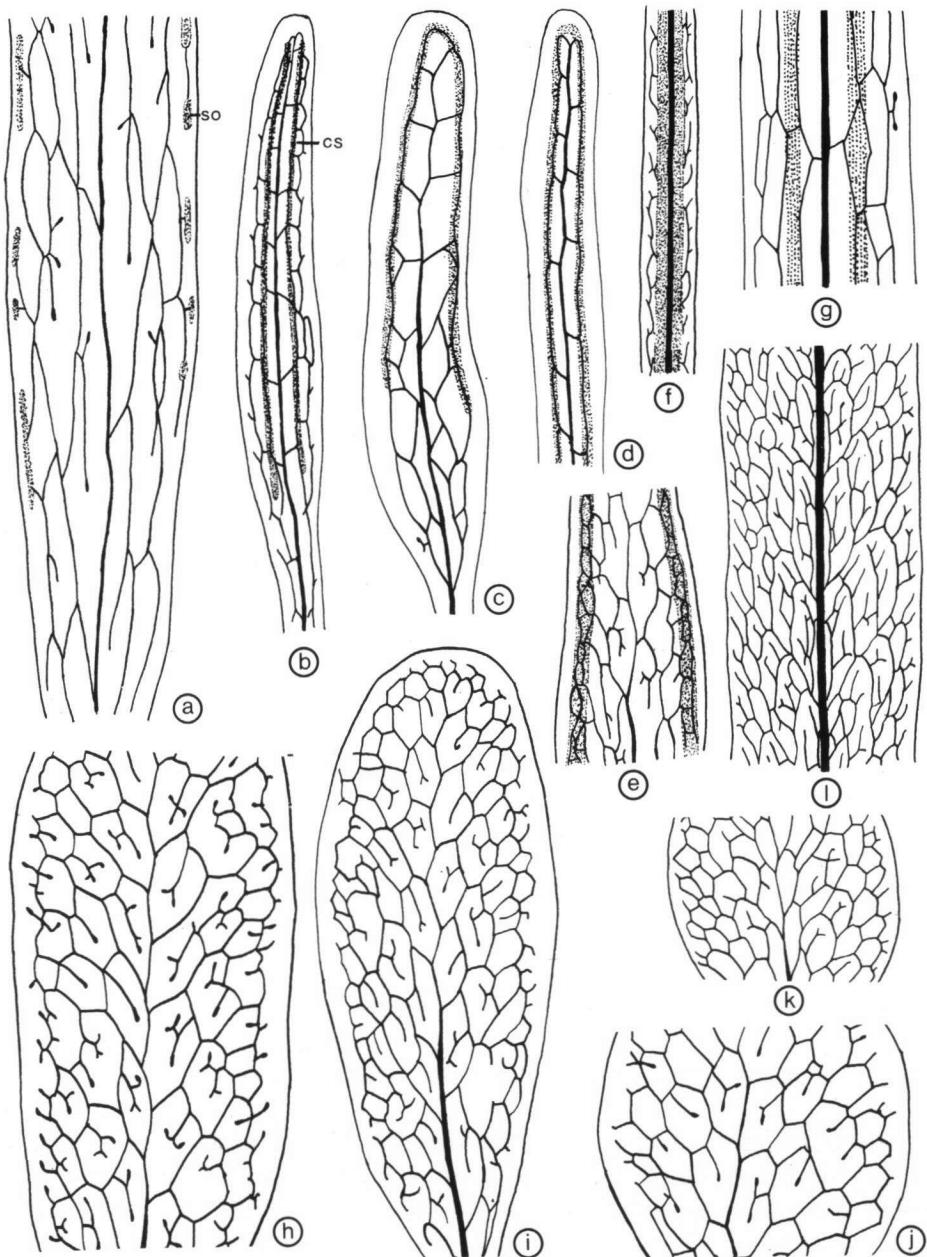


Fig. 2. a-g. Venation pattern and soral insertion of fertile fronds, $\times 1.4$. a. *Pyrosia (Drymoglossum) niphoboloides*; b. *P. (D.) fallax*; c, d. *P. (D.) heterophylla*; e. *P. (D.) piloselloides*; f. *P. (D.) novo-guineae*; g. *P. (Saxiglossum) angustissima*.—cs = coenosorus; so = sorus.—h-m. Venation pattern of sterile fronds, $\times 1.4$. h. *P. (D.) niphoboloides*; i. *P. (D.) piloselloides*; j. *P. (D.) heterophylla*; k. *P. (D.) fallax*; l. *P. (D.) novo-guineae*—(a Webb 177; b, k. Dissing et al. 1927; c. Thwaites 3076; d, j. Beddome 15; e. Balansa 159; f, l. Brass 23611; g. Steward & Cheo 432; h. Scott Elliot 2739; i. Van Beusekom & Phengkhrai 105).

However, in *P. (Drymoglossum) fallax* it was found that the sporangia, situated in two opposite rows on the receptacle, mature centripetally (fig. 1f). This situation is basically similar to the centripetal development of the sporangia occurring in the round sori of some other *Pyrrosia* species, for instance in *P. longifolia*.

Stellate hairs

The stellate hairs are basically similar in all *Pyrrosia* species studied. But one type of stellate hair occurs in the drymoglossoid species and in part of *Pyrrosia* proper, whereas in *P. (Saxiglossum) angustissima* and other true *Pyrrosia* species (e.g. *P. floculosa*, *P. lingua* var. *heteractis*) two or more types of stellate hairs may occur.

Venation pattern

Fig. 2h-1

The venation pattern as found in the sterile fronds of *P. (Drymoglossum) heterophylla*, *P. (D.) niphoboloides* and *P. (D.) piloselloides* (fig. 2h-j) is basically similar. It was first nicely illustrated by Von Ettingshausen (1865) for *P. (D.) piloselloides*. The venation is anastomosed, the areoles provided with characteristic, usually branched, recurrent, free veins. The pattern of *P. (D.) fallax* (fig. 2k) is similar as to the areoles differing in the presence of included excurrent free veins.

The pattern of *P. (Drymoglossum) novo-guinea* (fig. 2l) is much different from that mentioned above, being similar to that found in e.g. *P. angustata*, *P. samarensis*, and *P. lingua* (Nayar & Chandra, 1967: 623, fig. 29). The venation pattern of *P. (Saxiglossum) angustissima* is less complex than that of the species mentioned above and likely to represent a type also found in *Pyrrosia* proper.

Stomata

Peritic stomata in *Pyrrosia* (including *Drymoglossum*) were earlier reported by Giesenagen (1901), Kondo (1929), Van Cotthem (1968) and Sen & Hennipman (1981). They were found in all species studied here. Those of *P. (Drymoglossum) piloselloides*, *P. (D.) heterophylla* and *P. (D.) niphoboloides* are phaneroporic, i.e., situated in the same plane as the remaining epidermis. Those of other species investigated are cryptoporic, i.e., sunken below the surface of the epidermis.

Spores

The spores of the species studied are uniformly provided with a monolete bean-shaped exospore of the microsoroid type (Hennipman & Roos, 1982). However, they show an amazing variation in perispore differentiation. The spores of *P. (Drymoglossum) piloselloides* were first described by Fée (1852) and several authors

since (e.g., Hannig, 1911; Nayar & Devi, 1964). Those of *P. (D.) heterophylla* were excellently figured by Erdtman (1957). The first S.E.M. micrograph was produced by Wagner (1974). Already Goebel (1926) noticed that the spores of *P. (Drymoglossum) piloselloides* conform to those of *P. adnascens* 'nur sind die farblosen Fortsätze des Episporus spitzer'. Using characteristics of the perispore, the following spore types are represented in the species studied.

The outer surface ornamentation of the spores of a great number of *Pyrrosia* species is variously warty, e.g. *P. (Drymoglossum) piloselloides*, *P. (D.) heterophylla*, *P. (D.) fallax*, *P. (D.) niphoboloides*, *P. confluens*, *P. lanceolata*, *P. longifolia* and *P. rupestris*. In *P. (D.) piloselloides* and *P. (D.) heterophylla* conical spine-like protuberances 5-20 µm long, situated 5-15 µm apart are present.

A basically cristate or winged perispore is found in for instance, *P. (Drymoglossum) novo-guineae*, *P. angustata*, *P. samarensis*, *P. nummulariifolia*, *P. rasamalae* and *P. sphaerosticha*.

In *P. (Saxiglossum) angustissima*, *P. lingua*, *P. flocculosa*, and *P. manii*, the perispore consists of a thin, usually wrinkled layer in which a large number of conspicuous globular bodies are embedded.

The above shows that the species attributed formerly to *Drymoglossum* and *Saxiglossum* show a number of different perispore types which also occur in species of *Pyrrosia* proper. A detailed description of the morphology of the spores of *Pyrrosia* species is in preparation (Van Uffelen & Hennipman, 1985; Hennipman & Sen, in prep.).

6. DISCUSSION AND CONCLUSIONS

As pointed out in chapter 4, a great many character states of the features of the species formerly attributed to *Drymoglossum* and *Saxiglossum* are similar in all species studied. The differentiating character states are given in Table 1 which shows that there is no single character state or unique combination of character states that justifies the taxonomic recognition of a genus *Drymoglossum sensu lato* and /or a genus *Saxiglossum* separate from *Pyrrosia*.

Scanning the partial monothetic sets given in Table 2, which is a technical translation of the datamatrix (Table 1) (Zandee, 1985), it appears that the set consisting of species nos. (3 + 4 + 6) is supported by three unique character states (char. nos. 4, 9, 17), this set being congruent with all other sets except (3 + 5). The latter is supported only by character no. 7 which is not a structural character ('acrostichoid appearance') and therefore rejected. Also, as the character states that corroborate (3 + 4 + 6) are lacking in 1, 2, 5, all other *Pyrrosia* species, and in all *Platycerium* species, the monophyly of (3 + 4 + 6) seems unquestioned. *P. heterophylla* (3) and *P. piloselloides* (6) share conical verrucae of the perispore (present in part of *P. heterophylla* only) and might be sister species, whereas *P. niphoboloides*—a tetraploid, Hovenkamp, 1986—(4) has interrupted coenosori as

TABLE 1

TAXON	character state	species no.	'Drymoglossum'						Pyrrosia proper
			3	4	6	2	5	1	-51
1.	Rhizome with a central sclerenchyma strand in the ground tissue		0	0	0	1	1	1	0
2.	Stipe with 2 vascular strands		1	1	1	1	0	1	0
3.	Stipe with 4 vascular strands		0	0	0	0	1	0	1
4.	Scales; margin with cilia		1	1	1	0	0	0	0
5.	Fronds monomorphic		0	0	0	0	0	1	1
6.	Fronds dimorphic		1	1	1	1	1	0	1
7.	Fertile fronds in appearance acrostichoid		1	0	0	0	1	0	1
8.	Coenosori interrupted		0	1	0	0	0	0	1
9.	Receptacles situated on veins nearest to the margin		1	1	1	0	0	0	0
10.	Id. on veins nearest to the rachis		0	0	0	1	1	1	1
11.	Fertile frond with incurved marginal zone		0	0	0	0	0	1	0
12.	Id. with recurved marginal zone		0	0	0	0	1	0	0
13.	Coenosori consisting of 2 rows of 'opposite' sporangia		0	0	0	1	0	0	0
14.	Maturation of sporangia centripetally		0	0	0	1	0	0	1
15.	Stellate hairs; one type present		1	1	1	1	1	0	1
16.	Id.; two types present		0	0	0	0	0	1	1
17.	Type of venation pattern		1	1	1	0	0	0	0
18.	"		0	0	0	1	0	0	1
19.	"		0	0	0	0	1	0	1
20.	"		0	0	0	0	0	1	1
21.	Type of spore		1	0	1	0	0	0	0
22.	"		1	1	1	1	0	0	1
23.	"		0	0	0	0	1	0	1
24.	"		0	0	0	0	0	1	0

an autapomorphy. Assuming the monophyly of this group, its geographical distribution (fig. 3) is striking as it covers a wide range, the distribution of the species being distinctly allopatric. This group is likely to receive taxonomic recognition within the genus.

Regarding *P. (Drymoglossum) fallax*, part of its characters states remind somewhat of those of the group of *P. (D.) piloselloides*. It shares a unique insertion of the spores with some true *Pyrrosia* species. *P. (Drymoglossum) novo-guineae* shares its spore type, anatomy of the stipe, and venation pattern with several species of

TABLE II. Partial monothetic sets drawn from Table I.

partial mon. set	character state
1,2,3,4,6	2
5	3,12,19,23
3,4,6	4,9,17
1	5,11,16,20,24
2,3,4,5,6	6,15
3,5	7
4	8
1,2,5	1,10
2	13,14,18
3,6	21
2,3,4,6	22

Pyrrosia proper. When scanning these *Pyrrosia* species, especially *P. angustata* and *P. samarensis* show similarities with *P. (D.) novo-guineae* regarding frond shape and soral distribution. The fronds of *P. angustata* are dimorphic; the sterile fronds are similar to those of *P. (D.) novo-guineae*, the fertile ones are much narrower with the sori located in the upper part of the frond. Generally the sori are far more closely set in the upper part. The monomorphic fronds of *P. samarensis* are similar in shape to so-called intermediate fronds as sometimes occurring in *P. angustata*. At

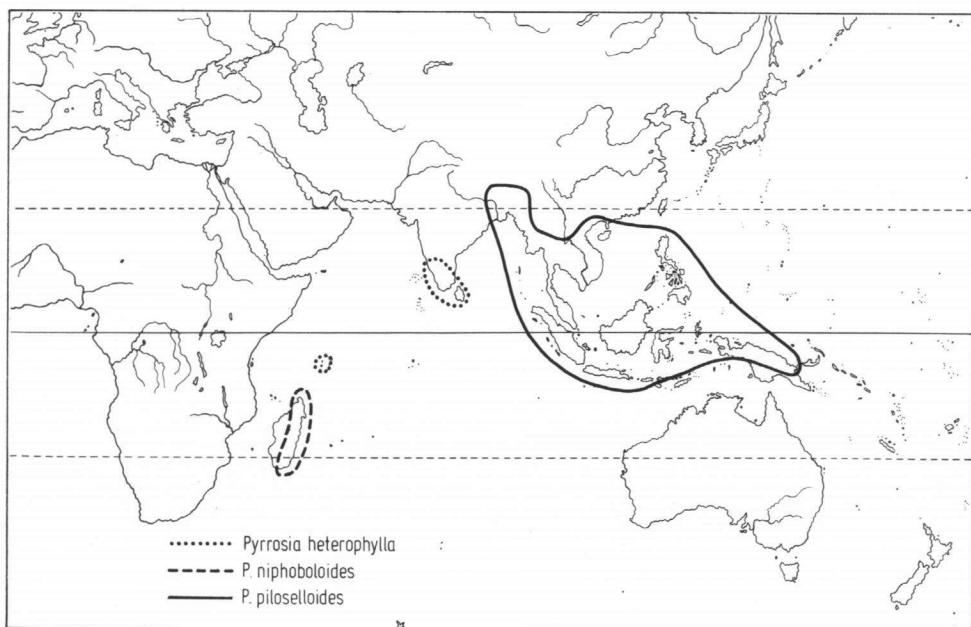


Fig. 3. Geographical distribution of the monophyletic group consisting of *Pyrrosia* (*Drymoglossum*) *heterophylla*, *P. (D.) niphoboloides*, and *P. (D.) piloselloides*.

the base of the fertile part the sori are sometimes ± round, terminally the fronds bear conspicuous coenosori like those present in *P. (D.) novo-guineae*. The sorus shapes discussed above are likely to be the result of parallel development of coenosori in *P. (D.) novo-guineae*, separate from that found in other drymoglossoid *Pyrrosia*'s.

The relationship of the *Pyrrosia* species formerly referred to *Drymoglossum* and *Saxiglossum* to the other platyceriod *Polypodiaceae* is illustrated in a cladogram (fig. 4). The monophyly of the platyceriod *Polypodiaceae* is supported by the presence of uniquely shaped stellate hairs on the frond, that of the genus *Platycerium* (15 species, see Hennipman & Roos, 1982) by the unique frond dimorphism. Character states unique for *Pyrrosia* s.l. (51 species, see Hovenkamp, 1986) are not obvious to the present authors. The monophyly of the group formed by *Pyrrosia* (*Drymoglossum*) *heterophylla*, *P. (D.) niphoboloides* and *P. (D.) piloselloides* is dealt with above.

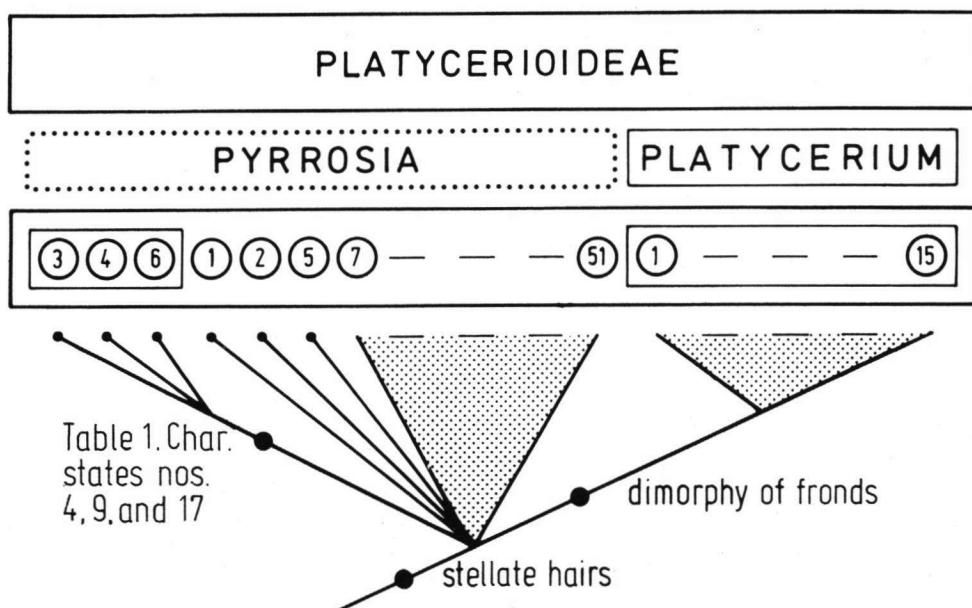


Fig. 4. Cladogram of the platyceriod *Polypodiaceae*. Monophyletic groups are the *Platycerioideae*, *Platycerium* (15 species), and part of *Pyrrosia* (*Drymoglossum*, p.p.); species nos. 3, 4, and 6. The monophyly of *Pyrrosia* s.l. (51 species) needs to be demonstrated. The *Pyrrosia* species no. 1-6 refer to the species formerly treated as *Drymoglossum* and *Saxiglossum*; for details see Table 1 and the Taxonomic part.

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TAXONOMIC PART

The species are arranged alphabetically; their synonymy is listed in full. Basionyms and their homotypic synonyms are listed chronologically. Only relevant additional literature is included. The names of authors are abbreviated according to the Kew Index of author's abbreviations; abbreviations of periodicals follow the World List of Scientific Periodicals. Descriptions of the characters of the fertile fronds are given only if different from those of the sterile fronds.

PYRROSIA

Full synonymy and description of the genus is given in the monograph by Hovenkamp (1986).

Drymoglossum Presl, Tent. Pteridogr. (1836) 227; J. Smith, J. Bot. 4 (1842) 66, *nom. cons.*; Fée, Mém. Fougères 3 (1852) 94; T. Moore, Ind. Fil. (1857) 31; Beddome, Ferns S. Ind. (1863) 6, 18; Hook., Gen. Fil. (1864) pl. 78A; J. Smith, Hist. Fil. (1875) 117; Christ, Farnkr. Erde (1897) 131; Diels in Engl. & Prantl, Nat. Pfl. Fam. I, 4 (1902) 302; C. Chr., Ind. Fil. (1906) xlvi, 246; Nakai, Bot. Mag. Tokio 40 (1926) 387; Goebel, Annls. Jard. bot. Buitenz. 36 (1926) 140; Copel., Univ. Calif. Publs. Bot. 16,2(1929) 103, C. Chr., Dansk bot. Ark. 6 (1929) 83; Ind. Fil. Suppl. 3 (1934) 78; Humbert, Fl. Madagascar (1951) 104; Pichi Sermolli, Webbia 9 (1953) 400; Holttum, Ferns Malaya (1954) 149, Nayar, J. Ind. bot. Soc. 26 (1957) 169.—*Oetosia* O. Kuntze, Rev. Gen. Pl. 2 (1891) 817 (V) *non* Neck.—Type species: *Drymoglossum piloselloides* (L.) Presl = *Pyrrosia piloselloides* (L.) Price.

Pteropsis Desvaux, Mém. Soc. Linn. Paris 6 (1827) 218; Maxon, Contr. U. S. Nat. Herb. 10 (1903) 486; Copel., Gen. Fil. (1947) 194, *nom. rej.*—Lectotype species: (Pichi Sermolli, 1969) *Acrostichum heterophyllum* L. = *Pyrrosia heterophylla* (L.) Price.

Saxiglossum Ching, Contr. Inst. Bot. Acad. Peiping 2 (1933) 1.—Type species: *Saxiglossum angustissimum* (Diels) Ching = *Pyrrosia angustissima* (Diels) Tagawa & Iwatsuki.

Usually epiphytic, sometimes terrestrial, usually small, rarely medium-sized ferns. Rhizome variously creeping, scaly, with tufted or spaced fronds; dictyostelic, usually with a subepidermal sclerenchyma sheath. Scales usually peltate, sometimes basally attached, round to variously triangular. Fronds simple, usually entire, sometimes incised, articulated to the phyllospodia, mono- or dimorphic, coriaceous with 2-many vascular bundles in the stipe. Venation of sterile fronds anastomosed into various patterns, usually with included free veins. Stomata pericytic, hypostomatic. Indument: fronds variously densely covered with stellate hairs, densely tomentose when young. Sori round, sometimes arranged in coenosori. Sporangia with a stalk of 3 rows, with 14–22 indurated capsular cells. Spores monolete with a variously developed perispore.

Distribution. Africa, Asia, New Zealand, Australia, Polynesia.

Habitat. In evergreen or seasonally dry (monsoon) primary and secondary vegetations; lowlands and middle elevations.

Note: A genus of 51 species (Hovenkamp, 1986) which together with the genus *Platycerium* forms a monophyletic group within the *Polypodiaceae* because of the presence of stellate hairs, an inferred synapomorphy.

1. *Pyrrosia angustissima* (Diels) Tagawa & Iwatsuki —Fig. 1a, q, r; 2g, m

Pyrrosia angustissima (Diels) Tagawa & Iwatsuki, Acta Phytotax. Geobot. Kyoto 26 (1975) 171.—

Polypodium angustissimum Baker, Ann. Bot. 5 (1891) 472, nom. illeg. (*non* Féé, 1869).—*Niphobolus angustissimus* Giesenagen ex Diels in Engl. & Prantl, Nat. Pfl. Fam. I, 4 (1902), 326; Diels, Bot. Jahrb. 29 (1900) 207; Giesenagen, FarnGattung Niphobolus 183; Christ, Bull. Acad. Géogr. Bot. (1902) 219–221. — *Cyclophorus taenioides* C. Chr., Ind. Fil. (1906) 201, nom. illeg.; C. Chr., Acta Horti Gothob. 1 (1924) 106. — *Saxiglossum taenioides* (C. Chr.) Ching, Contr. Inst. Bot. Nat. Acad. Peiping 2 (1933) 2, pl. 2, nom. illeg.; C. Chr., Ind. Fil. Suppl. 3 (1934) 170; Ching, Ic. Fil. Sin. 3 (1935) pl. 146; Fu, Ill. Handb. Imp. Chin. Pl. Pterid. (1957) 240, f. 323. — *Saxiglossum angustissimum* (Diels) Ching, Acta Phytotax. Sin. 10 (1965) 301; Tagawa, Acta Phytotax. Geobot. Kyoto 25 (1972) 96 ('*S. angustissimum* (Giesen. ex Diels) Tagawa'); DeVol. et al., Flora of Taiwan 1 (1975) 208, pl. 72; Nakaike, Enum. Pterid. Jap. Filic. (1975) 355. — Type: *Henry 5137* (K), China, Patung.

Niphobolus cavalierianus Christ, Bull. Acad. Géogr. Bot. (1904) 107. — *Cyclophorus cavalierianus* (Christ) C. Chr., Ind. Fil. (1906) 198. — Type: *Cavalerie 1209*, (P), China, Tsin-gai, Tchao-se, -07-1903.

Cyclophorus sasakii Hayata, Ic. Pl. Formosa 6 (1916) 158, f. 61. — *Saxiglossum sasakii* (Hayata) Tagawa, Journ. Jap. Bot. 12 (1936) 753. — *Saxiglossum taenioides* var. *sasakii* (Hayata) Massamune ex Satomi, J. Geobot. 9 (1960) 3, nom. illeg. — Type: *Sasaki s.n.*, -01-1916 (KYO?, TI?), Formosa, Shintiku, Karizenzan.

Rhizome long-creeping, branched, terete, up to 50 by \pm 0.1 cm, phylloodia 0.7–1.5 cm apart. Anatomy: with a subepidermal sclerenchyma sheath usually with a central sclerenchyma strand, with 2–5 meristeles. Scales peltate, linear-triangular, index 8–12, up to 8.5 × 0.5–0.8 mm, base irregularly lobed to rounded, sometimes constricted at the place of attachment to the stalk, margin entire, apex attenuating into a long, filiform, deciduous tip, central part with elongate, parallel cells, brown to shiny black (when old, marginal part lightbrown-transparent). Fronds monomorphic, 2.5–15 cm long; stipe up to 1.5 cm long, with two vascular bundles; lamina index 6–25, widest at the middle, 2–14 × 0.15–0.4 cm, variously incurved when mature, involute and \pm round in cross section when young, base long-attenuate, margin entire, apex acute to rounded. Venation: rhachis prominent beneath, otherwise veins immersed, veins anastomosing into a regular pattern consisting of a costal areole and 2–3 smaller lateral ones, ultimate veins usually anastomosed, sometimes free, excurrent, without hydathodes. Indument: fronds with scattered, \pm sessile, deciduous stellate hairs with 6–10 rays, hyaline except for the brownish central part; on the ventral side in the soral groove also with hairs with strongly wrinkled rays. Coenosori linear, usually not interrupted, rarely with \pm round sori, situated submedially

between rhachis and margin in the upper 1/2–4/5 of the lamina, when mature covered by a variously developed, flap-like, incurved lamina margin, when young completely covered, receptacle situated on the connecting vein of the costal areole. Sporangia irregularly maturing, persistent, with 19–22 indurated cells; paraphyses with 9–12 rays. Spores c. 75–85 × c. 60 µm, yellowish-brown, laesura c. 50 µm, perispore thin, slightly wrinkled, with numerous half spherical globules 3–5 µm across.

Distribution. Warm, humid parts of China and Taiwan.

Habitat. Epiphytic or epilithic in evergreen or monsoon forests; 500–1500 m alt.

2. *Pyrrosia fallax* (v.A.v.R.) Price — Fig. 1d, f, m, n; 2b, k

Pyrrosia fallax (v.A.v.R.) Price, Kalikasan 3 (1974) 177. — *Drymoglossum fallax* v.A.v.R., Philipp. J. Sci. 11 (1916) 111, f. 6, v.A.v.R. Mal. Ferns Suppl. 1 (1917) 419; C. Chr., Ind. Fil. Suppl. 2 (1917) 13; Dansk bot. Ark. 6 (1929) 85, pl. 12 f. 7, pl. 13 f. 5; Ind. Fil. Suppl. 3 (1934) 79.— Type: Robinson 1952 (BO, n.v.).

Drymoglossum schlechteri Hieron. & Brause, Bot. Jahrb. 56 (1920) 117.—Syntypes: Schlechter 16340 (B, BM, K, L), 18950 ('18750') (B, K, L); Ledermann 7639 (B), 8104 ('8184') (B).

Drymoglossum subcordatum auct. non Fée: Fée, Mém. Fougères 3 (1852) 29, p.p., ibid. 5 (1852) pl. 9A f.i.

Rhizome long-creeping, branched, dorsoventrally flattened, sometimes ventrally grooved, up to 80 by 0.1 cm, phylloodia 1.0–1.5 cm apart. Anatomy: with a subepidermal sclerenchyma sheath apart from a central sclerenchyma strand, with 5 meristoles. Scales peltate, triangular, index (2–)5–7, up to 2.5 × 0.4 mm, base rounded, margin especially near the base ciliate, sometimes irregularly toothed, apex attenuating into a long, filiform, deciduous tip, central part (dark-)brown, marginal and apical part lightbrown-transparent. Fronds dimorphic. Sterile fronds: 1.0–4.5 cm long; stipe up to 0.4 cm long with 2 vascular bundles; lamina index 1–5, widest at the middle, 1–4 × 0.5–1.5 cm, base attenuate, margin slightly incurved, apex obtuse to rounded. Venation: rhachis prominent beneath, grooved above, otherwise veins immersed, veins anastomosing into a regular pattern consisting of a costal areole and a regular pattern of angulate areoles part of which with excurrent, simple or forked free veins, without hydathodes. Fertile fronds: (2.5–)4–10 cm long; stipe 1–1.5 cm long; lamina index 7–25, (2.0–)2.5–8.5 × 0.2–0.4 cm. slightly recurved. Indument: fronds with scattered, ± sessile, deciduous, stellate hairs with 8–12 rays, hyaline apart from the brownish central part. Coenosori linear, only rarely interrupted, situated submedially between rhachis and margin, on the upper 4/5 or throughout the lamina, not covered by a marginal outgrowth; receptacle situated on the connecting vein of the costal areole. Sporangia maturing in 2 distinct rows separated by and lined with paraphyses, centripetally, persistent, with 16–19 indurated cells; paraphyses with ± 10 rays. Spores 55–65 × 35–45 µm, lightbrown, laesura c. 20 µm, perispore variously warty.

Distribution. Ambon eastwards to the Solomon Is.

Habitat. Climbing on branches and trunks of tree (sometimes on dead wood) in primary or secondary rainforest, often along rivers or forest margins. Locally very common; 0–400 m alt.

Note. A clearcut species with somewhat variable fronds. So-called intermediate fertile fronds are known from *Carr 16248* (BM), *Hicks & Wamah s.n.* (L), and *Streimann NGF 44355* (L).

3. *Pyrrosia heterophylla* (L.) Price. — Fig. 1b, g-i; 2c, d, j

Pyrrosia heterophylla (L.) Price, Kalikasan 3 (1973) 177.—*Acrostichum heterophyllum* L. Amoen. Acad. 1 (1745) 268, pl. 12 f. 1, Fl. Zeyl. (1749) 378, Spec. Pl. 2 (1753) 1067 (excl. Afric. specim.), Spec. Pl. ed. II, 2 (1763) 1523 (excl. Afric. specim.), Syst. Nat. ed. 13, II (1770) 685; Burman, Fl. Indica (1768) 228; Lamarck, Encyc. Meth. I, 1 (1783) 34 (excl. Afric. specim.)—*Drymoglossum heterophyllum* (L.) Trimen, J. Linn. Soc. 24 (1887) 152; C. Chr., Ind. Fil. (1906) 246 (excl. syn. p.p.); v.A.v.R. Mal. Ferns (1908) 703 (excl. syn. p.p.); Copel. in Elmer, Leafl. Philip. Bot. III, 45 (1910) 847 (excl. specim.); Sarawak Mus. J. 2 (1917) 410 (excl. specim.); Goebel, Annls. Jard. bot. Buitenz. 36 (1926) 140 (excl. specim.); C. Chr., Dansk bot. Ark. 6 (1929) 84, pl. 12 f. 1, 2, 6, pl. 13 f. 3, C. Chr., Ind. Fil. Suppl. 3 (1934) 79; Sledge, Bull. Brit. Mus. Nat. Hist. Bot. 2, 5 (1960) 135.—Type: *P. Hermann s.n.* (BM, Herb. Hermann, photo in L), Ceylon.

Pteris elliptica Willd., Sp. Pl. 5 (1810) 356, nom. illeg. (non Poiret, 1840).—*Pteris ceilanica* Wikström, K. svenska Vetensk.-Akad. Handl. (1826) 447. —*Pteropsis elliptica* (Willd.) Desvaux, Mém. Soc. Linn. Paris 6 (1827) 218.—*Drymoglossum ellipticum* (Willd.) T. Moore, Ind. Fil. (1857) 31, 343. —Type: *Houttuyn*, Nat. Hist. II, 14 (1873) pl. 86 f. 1.

Drymoglossum beddomei Clarke, Trans. Linn. Soc. Lond. 2 (1880) 575, nom. nud.—*Drymoglossum piloselloides* var. *beddomei*, Beddome, Handb. Ferns Br. Ind. (1883) 413, nom. inval. art. 34 ICBN. —*Drymoglossum heterophyllum* var. *beddomei* C. Chr., Dansk bot. Ark. 6 (1929) 85, pl. 12 f. 2a-c. —Type: *Beddome* 15 (K), S. India, Nilgiri.

Pteris piloselloides auct. non L.: Houttuyn, Nat. Hist. II, 14 (1783) p.p., Swartz, Syn. Fil. (1806) 94, 286, p.p.; Schkuhr, Krypt. Gew. (1809) 82 (excl. pl. 87).

Notochlaena piloselloides auct. non (L.) Kaulf.: Kaulf., Enum. Fil. (1824) 133 p.p.

Drymoglossum piloselloides auct. non (L.) Presl: Thwaites, Enum. Pl. Zeyl. 1864) 381.

Niphobolus nummularifolius auct. non (Swartz) J. Sm.: Beddome, Ferns S. Ind. (1863) 62, pl. 186, p.p.

Rhizome long-creeping, branched, terete, up to 70 by 0.1 cm, phylloodia 0.8–3.0 cm apart. Anatomy: with a subepidermal sclerenchyma sheath, without a central sclerenchyma strand, with 3–4 meristeles. Scales peltate, round to triangular, index 1–6, up to 2.0 × 0.7 mm, base rounded, sometimes constricted at the place of attachment to the stalk, margin with up to 0.4 mm long cilia, apex attenuating into a long, filiform, deciduous tip, central part dull brown to shiny black, marginal part lighter coloured. Fronds dimorphic. Sterile fronds: 1.0–4.5 cm long, sessile to shortly stipitate; stipe up to 0.1(–0.4) cm long with 2 vascular bundles; lamina index 1–4.5, widest at the middle, (0.6–)1–4.5 × 0.8–1.8 cm, base rounded to short attenuate, margin entire, slightly incurved, apex rounded. Venation: rhachis prominent on either side, otherwise veins immersed, veins anastomosing into a regular pattern consisting of a costal areole and smaller distal ones, with included, simple or forked, recurrent, free veins without hydathodes.

Fertile fronds: (1.5-)2.5-10 cm long; stipe up to 0.4 cm long; lamina index 10-30, $2.5-9.5 \times 0.3-0.9$ cm, slightly recurved. *Indument*: fronds with scattered, \pm sessile, deciduous, stellate hairs with 4-7 sometimes sinuous rays, hyaline apart from the brownish central part. *Coenosori* linear, all along the lamina, not or rarely interrupted, situated submarginally between rhachis and the somewhat recurved margin; receptacle situated on the outermost connecting vein. Sporangia irregularly maturing, persistent, with 16-20 indurated cells mixed with paraphyses. *Spores* $55-65 \times 35-45 \mu\text{m}$, lightbrown, perispore variously warty in part with conical spines.

Distribution. S. India, Ceylon, Seychelles (*Schlieben 11665*, K).

Habitat. Climbing on trees and rocks in rainforest and mangroves; locally common, lower and middle altitudes.

Notes. 1. A distinct species though similar to *P. (Drymoglossum) piloselloides* from which it is distinguished mainly by its acrostichoid-like fertile fronds.

2. *Beddome 15* from Kerala (*p.p.* from Anamalais, *p.p.* from the Nilgiris) is deviating from all other specimens by its scales (dull brown vs. shiny black), index of fertile fronds (± 10 vs. 10-30), stellate hairs (rays in part sinuous vs. all rays equal), and spore size ($70-80 \times 40-55$ vs $55-60 \times 30-40 \mu\text{m}$). The relative size of spores and stomata is suggestive of a polyploid nature. It was first recognized as a species by Clarke; Christensen gave it varietal rank as *Drymoglossum heterophyllum* var. *beddomei*. C. Chr.

4. *Pyrrosia niphoboloides* (Luerssen) Price.—Fig. 1k, 1; 2a, n.

Pyrrosia niphoboloides (Luerssen) Price, Kalikasan 3 (1974) 177.—*Taenitis niphoboloides* Luerssen, Abh. naturw. Ver. Bremen 7 (1882) pl. 1 f. 3-5, *nom. illeg. non* (Kunze) Moore.—*Drymoglossum niphoboloides* (Luerssen) Baker in Hook., Ic. Pl. 17 (1887) pl. 1686; Christ, Farnkr. Erde (1897) 131; Diels in Engl. & Prantl, Nat. Pfl. Fam. I, 4 (1902) 303; C. Chr., Ind. Fil. (1906) 246; Bonaparte, Not. Pterid. 16 (1925) 113, C. Chr., Dansk bot. Ark. 6 (1929) 88, pl. 12 f. 8, pl. 13 f. 1, 2; ibid. 7 (1932) 162, Ind. Fil. Suppl. 3 (1934) 79; Humbert, Fl. Madagascar (1951) 106.—Type: *Rutenberg s.n.*, herb. Luerssen 9673 (P), Alabé, 06-1878.

Rhizome long-creeping, branched, terete or ventrally flattened (or furrowed), up to 50 by 0.15 cm, phylloodia 0.6-2.5 cm apart. Anatomy: with a subepidermal sclerenchyma sheath without a central sclerenchyma strand, with 4 meristoles. *Scales* peltate, round to triangular, index 1-4, up to $2.5 \times$ up to 0.5 mm, base irregularly lobed to rounded, sometimes constricted at the place of attachment to the stalk, margin usually with cilia up to 0.7(-1.2) mm long, sometimes \pm entire, acute, central part opaque, brown, marginal part lightbrown transparant, whitish when old. *Fronds* dimorphic. Sterile fronds: 1.0-6.5 cm long; stipe up to 0.3 cm long with 2 vascular bundles; lamina index 1-4(-5), widest at the middle, $1-6 \times 1-2$ cm, base rounded to short attenuate, margin entire, slightly incurved, apex rounded. Venation: rhachis prominent in the

lower half, otherwise veins immersed, veins anastomosing into a regular pattern of angulate areoles, the upper half without distinct costal areoles, the greater part of the areoles with simple or forked, recurrent veins, without hydathodes. Fertile fronds: 5-23 cm long; stipe 0.2-0.5 cm long; lamina index 7-20, $7-22.5 \times 0.5-1.0$ cm, slightly recurved. *Indument*: fronds with scattered, \pm sessile, deciduous, stellate hairs with 8-13 rays, hyaline apart from the brownish central part. *Coenosori* interrupted, marginal, situated in the upper 4/5 of the lamina, marginal flap absent, receptacle situated \pm marginally on the ultimate marginal veins or vein endings. Sporangia irregularly maturing, persistent, with 17-20 indurated cells; paraphyses with \pm 10 rays. *Spores* $65-70 \times 40-45 \mu\text{m}$, lightbrown, laesura $22-25 \mu\text{m}$, perispore variously warty including conical spine-like protuberances.

Distribution. N.W. and E. Madagascar.

Habitat. Epiphytic or epilithic in tropical rainforest. In the lowlands to up to 1200 m.

Note. Specimens kept in cultivation (e.g., Kew acc. no. 048-68-04807, Bogner leg.) are dull green, the rachis completely immersed.

5. *Pyrrosia novo-guineae* (Christ) Price.—Fig. 1c, o, p; 2f, 1.

Pyrrosia novo-guineae (Christ) Price, Kalikasan 3 (1974) 177.—*Drymoglossum novo-guineae* Christ in Schum. & Lauterb., Fl. Schutzgeb. (1901) 137; C. Chr., Ind. Fil. (1906) 246; v.A.v.R. Mal. Ferns (1908) 703; C. Chr., Dansk bot. Ark. 6 (1929) 89, pl. 11 f. 2.—*Cyclophorus novo-guineense* Nakai, Bot. Mag. Tokyo (1926) 386. —Type: *Lauterbach* 570 (B?, n.v.).

Cyclophorus bamlerii Rosenst., Reprint. nov. Spec. Regni veg. 10 (1912) 339.—Type: *Rosenstock* Fil. novoguin. exsicc. 107 'Bamler S75' (L, iso in A, B, BM, MICH, P), K. Wilhelmsland, Sat-telberg, -1-1909, 900 m. See note 3.

Drymoglossum crassifolium Brause, Bot. Jahrb. 49 (1912) 35, C. Chr., Ind. Fil. Suppl. 1 (1913) 28; v.A.v.R., Mal. Ferns suppl. 1 (1917) 419; Brause, Bot. Jahrb. 56 (1921) 177; C. Chr., Dansk bot. Ark. 6 (1929) 88, pl. 12 f. 3; Ind. Fil. Suppl. 3 (1934) 79.—Type: *Schlechter* 19874 (B; phot. in BM).

Cyclophorus ledermannii Brause in Lauterb., Bot. Jahrb. 56 (1920) 206.—Type: *Ledermann* 8840 (B, phot. in BM).

Rhizome long-creeping, branched, terete to ventrally flattened or furrowed, up to 70 by 0.15 cm, phyllopodia 1.5-4.0 cm apart. Anatomy: with a subepidermal sclerenchyma sheath apart from a central sclerenchyma strand, with 5 meristoles. Scales peltate, index 8-10, up to 4×0.4 mm, base irregularly shaped, to rounded, sometimes constricted at the place of attachment to the stalk, margin entire, apex attenuating into a long, filiform, deciduous tip, central part brown or black, marginal and upper part lightbrown-transparent to whitish when old. Fronds dimorphic. Sterile fronds: (3-)6-16(-25) cm long; stipe up to 2.5(-5.0) cm long with 4 vascular bundles; lamina index (2-)3-7(-20), widest at the middle, $(3-)5-14.5(-20) \times 1.2-3.5$ cm, base short attenuate, margin entire (to somewhat undulate), straight, apex long-acuminate to obtuse. Venation: rhachis prominent on either side, otherwise veins immersed, veins anastomosing into a regular pat-

tern of \pm elongate primary areoles parallel to the costal areole, primary areoles in part with smaller areoles, always provided with a rather irregular pattern, included free veins usually simple, sometimes forked, without hydathodes. Fertile fronds: (4-)9-28 cm long; stipe 0.8-5.0 cm long; lamina index (10-)20-50, 8-22 \times 0.25-0.4(-0.6) cm, recurved. *Indument*: fronds with scattered, \pm sessile, deciduous, stellate hairs with 8-12 rays, hyaline apart from the brownish central part. *Coenosori* linear, not interrupted, situated closely to the rachis, throughout lined with paraphyses, receptacle situated on the veins closest to the rachis. Sporangia maturing centripetally, deciduous, with 18-20 indurated cells; paraphyses with \pm 10 rays. Spores 60-80 \times 40-55 μm , lightbrown, laesura \pm 25 μm , perispore cristate with low folds, otherwise smooth or somewhat wrinkled.

Distribution. New Guinea.

Habitat. Epiphytic on trunks or branches in rainforest; lowlands to 1000(-1200) m alt. Obviously not common.

Notes. 1. A distinct species although showing variation in shape, size, and texture of its fronds.

2. The identity of *Drymoglossum crassifolium* Brause. The type specimen is aberrant in having sterile fronds far longer than the fertile ones. It puzzled both Brause 'Steht keiner der bekannten *Drymoglossum* Arten nahe' and Christensen, who regarded its systematic position doubtful, mentioning a possible relationship to *P. (Drymoglossum) heterophylla*. The relatively stiff-coriaceous texture of the type specimen is probably due to its occurrence in a rather exposed habitat at a relatively high altitude (1200 m, the highest altitude recorded for the species).

3. In the original description of *Cyclophorus bamlerii* Rosenst., the type is cited as 'Nova Guinea: in mte Sattelberg dicto, 1910, l. G. Bamler no. S 75'. However, the holotype specimen annotated by Rosenstock as '*Cyclophorus Bamlerii* Rosenst. n. sp.' does not show Bamler's collection number S (Sattelberg) 75!.

4. Brass 23611 rather differs in the shape and texture of the fronds: sterile fronds strongly stipitate, (-5 cm), lamina with an acute apex; fertile fronds with a \pm subcoriaceous texture.

Pyrrosia piloselloides (L.) Price.—Fig. 1e, j. 2e, i

Pyrrosia piloselloides (L.) Price. Kalikasan 3 (1974) 176.—*Pteris piloselloides* L., Spec. Pl. ed. II, 2 (1763) 1530; Burman, Fl. Ind. (1768) 229, Syst. Nat., ed. 13, II (1770) 687; Roxb., Calcutta J. Nat. Hist. 4 (1846) 503; Houttuyn, Nat. Hist. II, 14 (1783) 88, p.p.; Thunb., Fl. Japon. (1784) 331, p.p.; Swartz, Syn. Fil. (1806) 94, p.p., 286; Schkuhr, Krypt. Gew. (1809) 82, p.p.; Blanco, Fl. Filip. (1837) 830, p.p.—*Taenitis piloselloides* (L.) R. Brown, Prod. Fl. Novae-Hollandiae (1810) 154; Mettenius, Fil. hort. Lips. (1865) 28, pl. 10 f. 6-8.—*Notochaena piloselloides* Kaulf., Enum. Fil. (1824) 133 (excl. syn. p.p., excl. specim.); Blume, Enum. Pl. Java (1828) 108 (excl. syn. p.p.); Fil. Java (1829) 67 (excl. syn. p.p.); Wallich, Cat. (1829) 139, nom. nud.; Kunze, Bot. Ztg. 4 (1846) 441, ibid. 6 (1848) 506 (excl. Japon. specim.).—*Pteropsis piloselloides* (L.) Desvaux, Mém. Soc. Linn. Paris 6 (1827) 218 (excl. syn. p.p.); Copel., Gen. Fil. (1947) X, Fern Fl. Philipp. 1 (1958) 475.—*Drymoglossum piloselloides* (L.) Presl, Tent. Pterid.

(1836) 227, pl. 10 f. 5, 6, Epim. Bot. (1851) 157 (excl. syn. *p.p.*, excl. S. Indian specim.); Fée, Mém. Fougères 3 (1852) 28, *p.p.*; Mém. Fougères 5 (1851-52) 94, pl. 9 f. 2; T. Moore, Ind. Fil. (1857) 31, 343, *p.p.*; Hook., Garden Ferns (1862) 46, *p.p.*; Beddome, Ferns S. Ind. (1863) 19, pl. 55, *p.p.*; Hook., Sp. Fil. 5 (1864) 190, *p.p.*; J. Sm., Ferns Brit. & Foreign (186) 89 (excl. specim.); Cesati, Atti R. Acad. Sci. M. & F. Napoli 8 (1876) 31; Clarke, Trans. Linn. Soc. Lond. 2 (1880) 575, *p.p.*; Beddome, Handb. Ferns Br. India (1883) 441, *p.p.*; Christ, Farnkr. Erde (1897) 131; Racib., Pteridoph. Fl. Buitenz. (1898) 61; K. Schum. & Hollrung, Fl. Kais. Wilhelmsl. (1889); K. Schum. & Lauterb., Fl. Schutzgeb. (1901) 137; Diels in Engl. & Prantl, Nat. Pfl. Fam. I, 4 (1902) 303; Copel., Dep. int. Bur. Govern. 28 (1905) 112; Ridley, J. Straits Brch. R. Asiat. Soc. 50 (1908) 52; Nakai, Bot. Mag. Tokyo 40 (1926) 389, *p.p.*; C. Chr., Dansk bot. Ark. 6 (1929) 86, pl. 12, 13, C. Chr., Ind. Fil. Suppl. 3 (1934) 79; Backer & Posthumus, Varenfl. Java (1939) 243 (excl. syn. *p.p.*); Holttum, Ferns Malaya (1954) 149; Nayar, J. Ind. Bot. Soc. 26 (1957) 169, *p.p.*; Kim Nah et al., J. Singapore nat. Acad. Sci. 3 (1973) 253.—*Elaphoglossum piloselloides* (L.) Keyserling, Polypod. Cyath. Bungeani (1873) 36.—*Lemmaphyllum piloselloides* (L.) Luerssen, Bot. Zbl. 11 (1882) 78.—*Oetosia piloselloides* (L.) Kuntze, Rev. Gen. Pl. 2 (1891) 817.—Lectotype: *Burman s.n.*, Herb. Delesserti (G), Java 1759 *p.p.* See note 2.

Drymoglossum rotundifolium Presl, Epim. Bot. (1851) 157; Fée, Mém. Fougères 3 (1852) 29; Nakai, Bot. Mag. Tokyo 40 (1926) 388, excl. syn.—Type: *Anonymous s.n.* (PRC), Punjab ('Pendschab').

Drymoglossum piloselloides var. *platyceroides* Teruya, Acta Phytotax. Geobot. Kyoto 1 (1932) 198.—Syntypes: *Teruya s.n.* (KYO?), Johore, Num. Heng, Kota Tinggi distr. Id., (KYO?), Singapore, Upper Serangoon Road.

Drymoglossum heterophyllum auct. non (L.) Trimen, *p.p.*
Drymoglossum maschahense Fée, in Kuhn, Fil. Afric. (1868) 58 as a synonym of *Taenitis microphylla*, nom. inval.—Type: *Anonymous s.n.* (P.).

Rhizome long-creeping, branched, dorsoventrally flattened, ventrally furrowed, up to 80 by 0.1 cm, phylloodia 0.8-2.5 cm apart. Anatomy: with a subepidermal sclerenchyma sheath, apart from a central sclerenchyma strand, with 3-4 meristoles. Scales peltate, round to triangular, index 1-3, up to 1.0 × 0.8 mm, base irregularly lobed to rounded, sometimes constricted at the place of attachment to the stalk, margin with cilia up to 0.5 mm long, apex attenuating into a long, filiform, deciduous tip, central part dark brown, marginal part light brown transparent, whitish when old. Fronds dimorphic. Sterile fronds: 1-7 cm long, sessile to shortly stipitate; stipe with 2 vascular bundles; lamina index 1-6, widest at (or above) the middle, 1-7 × 1-2 cm, base rounded to attenuate, margin entire, slightly recurved, apex rounded or obtuse. Venation: rhachis prominent in the lower half, otherwise veins immersed, veins anastomosing into a regular pattern of angular areoles, the upper half without distinct costal areole; the greater part of the areoles with simple or forked, recurrent, free veins without hydathodes. Fertile fronds: (2.5-)4-16(-25) cm long; stipe 0.1-0.5(-1.0) cm long; lamina index 10-20(-30), (2.5-)4-16(-24) × ± 0.3-1.5 cm, margin slightly recurved. Indument: fronds with scattered, ± sessile, deciduous, stellate hairs with 10-14 rays, hyaline apart from the brownish central part. Coenosori linear, not interrupted, situated submarginally; marginal tiap absent, receptacle situated submarginally on the ultimate marginal veins. Sporangia irregularly maturing, persistent, with 19-21 indurated cells; paraphyses with ± 12 rays. Spores 45-60 × 25-40 µm, light brown, laesura 10 µm, perispore variously warty including conical spine-like protuberances.

Distribution. N. E. India eastwards to Hainan, throughout Malesia (Marianas?; *Haenke s.n.*). Common.

Habitat. Usually epiphytic, sometimes epilithic in all types of primary and secondary vegetations; in the lowlands to up to 1000 m alt.

Notes. 1. A common epiphyte showing much variation in shape and size of its fronds; usually growing luxuriously with rhizomes reported on field labels to measure 3 m in length. The sterile fronds may be confused with those of *Pyrrosia nummulariifolia* which are densely set with permanent stellate hairs and provided with a different venation pattern with excurrent free veins.

2. The typification of *Pteris piloselloides*. A type specimen was not indicated by Linnaeus (1763) in the original description of *Pteris piloselloides*, nor by any author since, including Christensen (1929). No original material is present in the Linnean Herbarium, London, or Stockholm (IDC Microfiches; Jackson 1912). When tracing the type material of *Pteris piloselloides* it was noted that Burman (1768) was the first author after Linnaeus who enumerated both *Acrostichum heterophyllum* ('Ceylon and India') and *Pteris piloselloides* ('India'). According to Merrill (1921) Burman visited Linnaeus in Uppsala in 1760. Afterwards they regularly corresponded and exchanged specimens. According to the Preface of Linnaeus, Spec. Pl. ed. 2 (1763) a number of the species listed is based on specimina from other herbaria including that of Burman; see also Jackson (1912). The specimen in Burman's herbarium (in Herb. Delessert, Geneva) with '*Pteris piloselloides*' (and 'Ex Java, 1759') written on it in Burman's handwriting is a mixture of two species, i.e. *P. piloselloides* and *P. spec.* (the two longest fronds). Other annotations by Burman on the sheet refer to the latter species. The backside of the sheet bears a description of *Pteris piloselloides* (*Pteris 'heterophylla'*, *sphalm*) which is almost similar to that given by Linnaeus (1763). The discrepancy between the locality records in the publications of Linnaeus ('India orientalis') and Burman ('India'), and the locality record on the type sheet ('Ex Java') is insignificant in view of Merrill (1921) who demonstrated that Burman used 'India' in a very broad sense, frequently applying it to material collected from Java.

3. Under the name *Pteris piloselloides* or its homotypic synonyms a mixture of different species was erroneously included by many authors. For instance, Houttuyn (1783) copied the description of Linnaeus citing material from Ceylon (= *P. heterophylla*) and from Japan (= *Lemmaphyllum microphyllum* Presl). Thunberg's description (1784) is based on material from Japan where *P. piloselloides* does not occur; it represents *Lemmaphyllum mirophillum*. Contrary to Linnaeus (1763) many authors, including Beddome (1863), combined the present species with *P. (Drymoglossum) heterophylla*. Christensen (1929) rightfully kept the two species separated.

4. The type specimen of *Drymoglossum rotundifolium* should be from Punjab, India. As no other collections are known from that part of India this locality record is doubted.

5. Deviating frond shapes are not rare. Teruya (*op. cit.*, 1932) described the var. *platyceroides* to accomodate furcated fronds. So-called intermediate fronds have usually only the upper part of the lamina fertile. However, a frond of *Cuming s.n.* (G, herb. Delessert) has the upper part sterile and the basal part fertile.

6. See also "Excluded or dubious names" below: *Drymoglossum martinicense*.

7. Nakai, Bot. Mag. Tokyo 40 (1926) 386 erroneously regarded *Drymoglossum rigidum* (= *Pycnoloma rigida*) 'a well-grown *Drymoglossum piloselloides* Presl'.

EXCLUDED OR DUBIOUS NAMES

E 1. *Drymoglossum abbreviatum* Féé, Mém. Fougères 7 (1857) 26, pl. 10, f. 2; — *Hymenolepis abbreviata* Féé, Mém. Fougères 10 (1865) 12. — *Polypodium abbreviatum* (Féé) C. Chr., Ind. Fil. Suppl. 2 (1917) 25, nom. illeg.: non Mettenius, Fil. Hort. Lips. (1856) 33, nom. nud., Farngatt. 2, I (1856) 130. — *Lemmaphyllum abbreviatum* (Féé) C. Chr., Dansk bot. Ark. 6 (1929) 50, pl. 6 f. 2. — *Macrolethus abbreviatus* (Féé) Tagawa, Acta Phytotax. Geobot. Kyoto 11 (1942) 234. — Type: *Gaudichaud s.n.* Voy. de la Bonite (P) = *Lemmaphyllum abbreviatum* (Féé) C. Chr.

E 2. *Drymoglossum acrostichoides* (Hook. & Greville) T. Moore, Ind. Fil. (1857) 31, 343. — *Vittaria acrostichoides* Hook & Greville, Ic. Fil. (1830) pl. 186. — *Elaphoglossum acrostichoides* (Hook. & Greville) Schelpe, Journ. S. Afr. Bot. 30 (1964) 196. — Type: *D. Thom* (*n.v.*), South Africa, = *Elaphoglossum acrostichoides* (Hook. & Greville) Schelpe.

E 3. *Drymoglossum assamense* Gandoger, Bull. Soc. bot. Fr. 66 (1919) 303. — Type: *Watt 10477*, Assam (*n.v.*) = spec. dub.

E 4. *Drymoglossum brooksi* v.A.v.R., Bull. Jard. bot. Buitenz., II, 28 (1918) 21. — *Grammatopteris brooksi* (v.A.v.R.) v.A.v.R., Bull. Jard. bot. Buitenz., IV, 2 (1922) 318, pl. 15 f. 1a-b. — *Grammatopteridium brooksi* (v.A.v.R.) v.A.v.R., Nova Guinea 14 (1924) 24. — *Grammatopteridium costulatum* (Cesati) C. Chr. var. *brooksi* (v.A.v.R.) C. Chr., Dansk bot. Ark. 6 (1929) 81. — Type: *Brooks 361/S* (BO) = *Grammatopteridium brooksi* (v.A.v.R.) v.A.v.R.

E 5. *Drymoglossum carnosum* [*Notholaena carnosia* Wallich, Cat. (1828) 138, nom. nud.] Hook., Gen. Fil. (1842) pl 78A, Spec. Fil. 5 (1864) 189 (var. *major*). — *Lemmaphyllum carnosum* Presl, Epim. Bot. (1851) 158. — *Taenitis carnosia* Mettenius, Fil. hort. Lips. (1856) 28. — *Asteroglossum carnosum* J. Smith ex T. Moore, Ind. Fil. (1857) 179, nom. nud.. — *Elaphoglossum carnosum* Keyserling, Polypod. Cyath. Bungeani (1873) 36. — Type: *Wallich 138* (iso in BM, US '139'), Nepal, = *Lemmaphyllum carnosum* Presl.

E 6. *Drymoglossum confertum* Copel. in Perkins, Fragm. Fl. Philip. (1905) 187. — *Loxogramma conferta* (Copel.) Copel., Dep. int. Bur. Govern. 28 (1905) 68. — Type: *Copeland 942* (P) = *Loxogramma conferta* (Copel.) Copel.

E 7. *Drymoglossum cordatum* Christ, Not. Syst. 1 (1911) 375. — *Myropteris cordata* (Christ) C. Chr., Dansk bot. Ark. 6 (1929) 73. — *Leptochilus cordatus* (Christ) Ching, Bull. Fan meml. Inst. Biol. 4 (1933) 343. — Type: *Cadière 158* (P) = *Dendroglossa cantoniensis* (Baker) Copel.

E 8. *Drymoglossum crassinerve* Gilli, Ann. Naturhist. Mus. Wien 81 (1978) 23. — Type: *Dosedla 211B* (W), Papua New Guinea, Mt. Hagen = *Crypsinus* spec..

E 9. *Drymoglossum cunninghamii* T. Moore, Ind. Fil. (1857) 31, 343; J. Smith, Hist. Fil. (1875) 118. Type: *Anonymus s.n.*, Norfolk Island (*n.v.*) = *Pyrrosia confluens* (R. Brown) Ching.

E 10. *Drymoglossum lanceolatum* (L.) J. Sm., J. Bot. 4 (1842) 66, *nom. nud.*; T. Moore, Ind. Fil. (1857) 31, 343, pl. 18B.—*Pteris lanceolata* L., Spec. Pl. 2 (1753) 1067. — *Paltonium lanceolatum* (L.) Presl, Epim. Bot. (1851) 156.—*Neurodium lanceolatum* (L.) Fée, Mém. Fougeres 3 (1852) 28.—Type: Plumier, Fil. Amer. (1705) pl. 132 = *Neurodium lanceolatum* (L.) Fée.

E 11. *Drymoglossum martinicense* Christ, Bot. Jahrb. 24 (1897) 137.—*Pteropsis martinicense* (Christ) Maxon, Contr. U. S. natn. Herb. 16 (1912) 51.—Lectotype: Duss 250b (B), in Herb. Krug et Urban, Vauclin, Martinique = *Pyrrosia lanceolata* (L.) Farwell.

Note. A second specimen annotated by Christ as '*Drymoglossum martinicense* Christ n. sp.' and representing a different species, *Pyrrosia* (*Drymoglossum*) *piloselloides*, is present on a sheet in Paris labelled 'Herb. Le Jolis - *Drymoglossum martinicense* Christ, St. Pierre (Martinique) - mai 1870 sur les arbres. The collector of this specimen cannot be Duss as he collected on Martinique not before 1882.

Still it is surprising the *P. piloselloides* and/or *P. lanceolata* -both confined to Asia- are collected from Martinique, lesser Antilles. Christensen (1929) presumed that both specimens were collected as escapes from gardens. This seems possible in view of Duss (Annls. Inst. Col. Marseille 3 (1897) 20): "many of the now-naturalized species are once introduced by 'Chambre d'Agriculture' and by botanical gardens from Trinidad, Guadeloupe and Martinique (St. Pierre) and others by all kinds of men". The director of the Botanical Garden in St. Pierre during 1853–1881 was Bélanger, who earlier established a botanical garden in Pondicherry, India, for which he had obtained many plants from Java. Father Duss corresponded with Bélanger (Urban, Symb. Ant. 3 (1902) 20). No other collections of either two species from Martinique are known to the present authors.

E 12. *Drymoglossum metacoelum* v.A.v.R., Bull. Jard. bot. Buitenz. II, 28 (1908) 21, pl. 2.—*Pycnoloma metacoelum* (v.A.v.R.) C. Chr., Dansk bot. Ark. 6 (1929) 77, pl. 8–10.—Type: Hallier 2942 (L, P) = *Pycnoloma metacoelum* (v.A.v.R.) C. Chr.

E 13. *Drymoglossum microphyllum* (Presl) C. Chr., Ind. Fil. (1906) 246. — *Lemmaphyllum microphyllum* Presl, Epim. Bot. (1851) 263. — *Taenitis microphylla* (Presl) Mettenius ex Kuhn, Fil. Afric. (1868) 58, excl. syn., p.p.—*Drymoglossum carnosum* var. *microphyllum* (Presl) Nakai, J. Coll. Sci. imp. Univ. Tokyo 31 (1911) 413.—Type: Von Siebold s.n., (L), Japan = *Lemmaphyllum microphyllum* Presl.

Note. Presl cited Thunberg and Von Siebold, specimens of which are located in the Rijksherbarium, Leiden. On the Von Siebold specimen is written in Japanese writing 'Mame tsuda' and 'Mame goke', almost similar to Presl's citation of 'Mame dsuta vel Mame goke Japon' in the original description.

E 14. *Drymoglossum nobukoanum* Makino, J. Jap. Bot. 7 (1934) 8. — *Lemmaphyllum nobukoanum* (Makino) Ching, Ic. Fil. Sinicarum (1934) pl. 80.—Type: Ogata s.n., 26-12-1925 (n.v. = *Lemmaphyllum* spec.).

E 15. *Drymoglossum obovatum* (Harrington) Christ, J. Bot. Paris 19 (1905) 73.—*Drymoglossum carnosum* var. *obovatum* Harrington, J. Linn. Soc. 16 (1877) 33.—*Lemmaphyllum microphyllum* var. *obovatum* (Harrington) C. Chr., Dansk bot. Ark. 6 (1929) 47. — Type: Steere 487 (iso in US) = *Lemmaphyllum microphyllum* Presl.

- E 16. *Drymoglossum rigidum* Hook., Ic. Pl. (1854) pl. 996. — *Schizolepton rigidum* (Hook.) T. Moore, Ind. Fil. (1857) 30. — *Oetosis rigidum* (Hook.) O. Kuntze, Rev. Gen. Pl. 2 (1891) 817. — *Taenitis rigidula* (Hook) Copel., Sarawak Mus. J. 2 (1917) 329. — *Pycnoloma rigida* (Hook.) C. Chr., Dansk bot. Ark. 6 (1929) 76, pl. 8 f. 1, 2, pl. 10 f. 1.—Type: *Lobb s.n.* (K), Borneo, near Sarawak.
= *Pycnoloma rigida* (Hook.) C. Chr.
- E 17. *Drymoglossum subcordatum* Féée, Mém. Fougères 3 (1852) 29, ibid. 5 (1852) pl. 9A f. 1. — Lectotype: *Gaudichaud s.n.* (P) = *Lemmaphyllum microphyllum* Presl.
- E 18. *Drymoglossum tetragonum* v.A.v.R., Bull. Jard. bot. Buitenz. II, 28 (1918) 21, pl. 3.—Type: *Teuscher s.n.* (Herb. BO 525) (n.v.) = *Pycnoloma rigida* (Hook.) C. Chr.
- E 19. *Drymoglossum underwoodianum* (Maxon) C. Chr., Ind. Fil., Suppl. 1 (1919) 28. — *Pteropsis underwoodiana* Maxon, Contr. U.S. natn. Herb. 16 (1912) 51, pl. 28.—Type: *Donnell Smith 6941* (BM, P) = *Pleopeltis wiesbaurii* (Sodiro) Lell.
- E 20. *Drymoglossum wiesbaurii* Sodiro, Crypt. Vasc. Quit. (1893) 419. — *Pteropsis wiesbaurii* Maxon, Contr. U.S. natn. Herb. 16 (1912) 51.—*Marginariopsis wiesbaurii* C. Chr., Dansk bot. Ark. 6 (1929) 43, pl. 6 f. 3.—Type: *Sodiro s.n.* (n.v.) = *Pleopeltis wiesbaurii* (Sodiro) Lell.

INDEX OF COLLECTIONS

Collections are referred to the number of the species in the Taxonomic Part as follows:

1: *Pyrrosia angustissima*; 2: *P. fallax*; 3: *P. heterophylla*; 4: *P. niphoboloides*; 5: *P. novo-guineae*; 6: *P. piloselloides*.

For these and other *Pyrrosia* species see also the identification-list in Hovenkamp (1986).

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