

## GLEICHENIACEAE (R. E. Holttum, Kew)

Rhizome relatively slender, creeping, protostelic (solenostelic only in *Dicranopteris pectinata* (WILLD.) UND. of tropical America), in *Stromatopteris* bearing erect irregularly dichotomous branches which bear the fronds, in all other cases bearing fronds directly; young parts covered with peltate fringed scales (scales otherwise in *Stromatopteris*) or branched hairs. *Fronds* unbranched in *Stromatopteris*, in all other cases branched in fully developed plants, the main rachis bearing a series of pairs of branches, its apex periodically dormant while each successive pair of branches develops; each primary branch often bearing a pair of secondary branches and a permanently dormant apex between them, the process sometimes repeated several times; ultimate branches either bipinnatifid or pinnatifid, the lamina (whether of an ultimate branch, or leaflet of an ultimate branch) cut almost to the costa; veins in lamina-segments pinnate, branches simple or forked, free (in some cases apparently joining a thickened non-vascular margin). *Sori* of 2–15 or more sporangia, attached to a small receptacle on the surface of a vein (except in *Stromatopteris*, where each sorus is spread along part of both branches of a forked vein), never at the end of a vein, all sporangia in one sorus developing simultaneously; branched hairs or scales often present with sporangia but no indusium. *Sporangia* with complete oblique annulus, dehiscing vertically, containing c. 200–800 or more spores. *Spores* monolete or trilete, smooth, translucent, colourless.

*Gametophyte* (not known in *Stromatopteris*) at first cordate, then ribbon-like with heavy midrib, finally branching at apex; rhizoids stiff, abundant, usually reddish-brown; two-celled glandular hairs developed by many species in association with archegonia and also on margin; antheridia comparatively large and complex in structure (some more so than others); archegonia with long necks (longest in *Gleichenia subg. Gleichenia*) directed towards apex of prothallus; no cases of apogamy observed.

*Distribution*. Throughout the wetter parts of the tropics and subtropics, and in south temperate regions. Three genera: *Stromatopteris* (monotypic, in New Caledonia), *Gleichenia* (3 subgenera, c. 150 species, in the tropics mainly on mountains, at lower altitudes in southern temperate regions), and *Dicranopteris* (2 subgenera, c. 10 species, mainly tropical, at low and moderate altitudes). *Dicranopteris* is much more polymorphic in Malaysia than in any other part of the tropics. (The genus *Platyzoa* is excluded from the family; see HOLTTUM in Kew Bulletin no 3, 1956, p. 551).

*Fossils*. The fragmentary nature of the earlier fossils ascribed by various authors to the family makes judgment upon them difficult. The form and arrangement of sporangia is the best criterion; on this basis paleozoic fossils named *Oligocarpia* have been assigned to *Gleicheniaceae*, but they do not always show details of structure of the individual sporangia clearly. Some have been found on fronds of the *Pecopteris* type (not unlike *Gleichenia* of today), some on the rather different *Sphenopteris*, but none show pseudo-dichotomy of the kind now universal in the family. It may be that some of these fossils represent members of the family before periodic growth and pseudo-dichotomy developed.

*Gleichenia gracilis* ZIGNO, from the Jurassic of northern Italy, has been more confidently referred to the family by paleobotanists; but the main branches of the frond are not opposite, and the irregular forking of the smaller branches looks more like true dichotomy than pseudo-dichotomy (judging from ZIGNO's figure); there are no sori.

Wealden fossils from Belgium show anatomical structure of rhizome and petioles as in living *Gleichenia*. In somewhat later Cretaceous rocks of various parts of the world, but especially in West Greenland, are fossils which show every character (except scales, which have not been seen) of existing members of *Gleichenia subg. Diplopterygium* (HEER, Flora Fossilis Arctica, II) and some are very like *subg. Gleichenia*, with more or less transitional stages between the two conditions which are not shown by living members of the family. Some of them show permanent dormancy of a lateral branch of a frond, but none show the condition either of *Gleichenia subg. Mertensia* or of *Dicranopteris*, which have what I regard as the most highly developed forms of branching. Some Greenland fossils show many sporangia in a sorus, a character not shown by any living member of the family having similar leaf-form, and TUTIN (Ann. Bot. Lond. 46, 1932, p. 503–508) has described *Gleicheniopsis* with numerous small

sporangia each containing less than 32 spores; the latter were not attached to any forked axis.

The only fossil known to me which corresponds in leaf-form with *Dicranopteris* is *Gleichenia hantonensis* WANKLYN from Eocene beds at Bournemouth (southern England). This was the subject of a reconstruction, copied by other authors, by GARDNER and ETTINGSHAUSEN (British Eocene Flora, I fig. 28) which (on the same frond as typical *Dicranopteris* ultimate branches) incorporated accessory branches as in living *D. linearis* (not shown in the fossils) and also some curious hook-bearing leaflets which are associated with the *Dicranopteris* fossil leaflets but nowhere attached to them. Disregarding these unwarranted additions, *Gleichenia hantonensis* agrees with *Dicranopteris* in branching, venation and sori (position, shape and number of sporangia); if hairs could be found, agreement with *Dicranopteris* would be complete. The Greenland and Bournemouth fossils offer evidence hard to reconcile with COPELAND's opinion that the family is of antarctic origin (Genera Filicum, p. 26).

**Ecology.** All species are sun-ferns, and most form thickets, to which they are adapted by their creeping rhizomes, and by the indefinite growth in length of the fronds (at least in the wet tropics). Periodic dormancy of the apex of the main rachis permits periodic upward growth of the rachis-apex, unencumbered by branches; it may thus pass between any other leaves or branches which may be above it, and then develop its new pair of leafy branches in a fully exposed position while the apex itself is again dormant. The most efficient members of the family from this standpoint are species of *Dicranopteris* and of *Gleichenia subg. Mertensia*, because by repeated forking their lateral branch-systems produce a spreading fan-shaped arrangement, but it is notable that in *Dicranopteris* a reversion to an effectively pinnate form of branching has occurred, seen at its full development in *D. speciosa* (PR.) HOLTZ.

Most members of the family are pioneer plants, establishing themselves on bare ground, sometimes in fully exposed places, talus, earthslides, precipices, rocks (fig. 3), steep ridges (fig. 2, 10), often on poor rocky or leached soils. Prothalli (which are often very abundant) need a little shelter, but a young sporophyte can quickly spread by means of its rhizome, and *Dicranopteris linearis*, for example, can grow in places where few other plants can establish themselves. A *Dicranopteris* thicket, once formed, can persist for a long time (fig. 11, 13), unless tree seedlings have established themselves in it at an early stage (shade of trees weakens or kills *Dicranopteris* plants unless they can climb); such thickets have been greatly encouraged by man-made clearings of forest. On the edge of forest, some of the larger members of the family can climb to a considerable height.

At high altitudes on mountains, where slower-growing alpine scrub occurs, smaller species of the family are often abundant and form lower thickets. They may grow in association with *Sphagnum*, or in dry rocky places. An important character is that their demands of mineral substances are small.

**Vegetative morphology.** *Stromatopteris* is peculiar in its erect rhizome-branches, in its scales and hairs, and in having sori spread along both branches of a vein. NAKAI (Bull. Nat. Sc. Mus. Tokyo n. 29, 1950) has proposed its separation as a distinct subfamily, and I consider this separation fully justified. The genus does not occur in Malaysia. It is probably to be regarded as a reduced relic of an otherwise extinct group.

As above noted (under Ecology), the fronds of other members of the family are all branched (except in young or stunted plants), the branching being pinnate in plan, with dormancy, either periodic or permanent, of apices of various orders. Fig. 1, 7, 12. The branch-patterns are in some cases complex, and are characteristic in the different genera and subgenera (for a comparative account, see HOLTZUM, Phytomorphology 7, 1957, 168-184). FILARSKY attempted a detailed analysis of these branch-patterns (Ann. Hist.-Nat. Mus. Nat. Hungarici 20, 1923, 1-23; *ibid.* 21, 1924, 163-170) but the results seem to me confused. He did not distinguish clearly between *Dicranopteris* and *Gleichenia subgen. Mertensia* of the present treatment, nor between *Platyzoma* and *Gleichenia subgen. Gleichenia*. The form of branching shown in his fig. 12 and 24 is one I have never seen (shorter branches on the same side at successive unequal forkings).

The major divisions of the family are also distinguished by their dermal appendages. Those of *Stromatopteris* are quite peculiar (scales, only on rhizome, not peltate, and long simple hairs also on rhizome). The rest of the family have either fringed peltate scales and stellate hairs with unicellular rays (*Gleichenia*) or branched hairs of complex structure, true scales being absent (*Dicranopteris*, fig. 14)

The venation in *Gleichenia* is pinnate in each segment of the lamina, lateral veins being forked (fig. 8c) except in *subg. Gleichenia* (where the area of the segment is very small). In *Dicranopteris* the lateral veins are at least twice forked. Fig. 15a, c. The sori are always attached on the surface of a vein, the sporangia attached to a small raised receptacle. In *Gleichenia subg. Gleichenia* the veins are very short, and are not visible unless the lamina is cleared; in many taxonomic works the sori are said to be terminal on the veins in this subgenus, but cleared specimens show that they are not. The arrangement of sporangia in a sorus, in both genera, has been discussed and illustrated by BOWER (The Ferns, vol. 2, 203-206, fig. 476, 486-489). In some species of *Gleichenia subg. Gleichenia* the sori are in depressions in the substance of the lamina (*e.g. G. peltophora* COPEL.); in others they are protected by the reflexed margins of the lamina and by outgrowths of tissue from the costa (*G. vulcanica* BL., fig. 1d-e). NAKAI (*l.c.*), following PRESL, attempted to use these characters to establish separate genera, but the species *G. microphylla* R.Br. is intermediate.

**Sporangia and spores.** The structure of sporangia has been fully described by BOWER (*l.c.*). Both trilete and monolete spores occur in the family. NAKAI (*l.c.*) proposed a basic division of the family

on spore-form, but in so doing he supposed that only trilete spores occur in his restricted genus *Dicranopteris* (*D. linearis* and its near allies); in fact closely related species of this group have spores of different forms, and a division of the family on spore-form is certainly unnatural.

Gametophyte. The most recent and most complete account of gametophytes in the family is by A. G. STOKEY (Bull. Torrey Bot. Club 77, 1950, 323-339) and includes references to earlier accounts. Species of all genera and subgenera here recognized were studied. Dr STOKEY's conclusion is that the gametophyte in all cases shows many primitive characters, but there is little significant difference within the family to indicate that one part is more primitive than the rest. *Gleichenia* subg. *Gleichenia* shows specialized characters (notably the long neck of the archegonium) and on characters of the gametophyte is judged to be further removed from the rest of the family than they are from each other. Two-celled hairs of a peculiar nature have an origin similar to that of the larger hairs on prothalli of *Cyatheaceae*; apart from these hairs, the prothalli of *Gleicheniaceae* most resemble those of *Dipteris*.

Cytology. MANTON & SLEDGE (Phil. Trans. Roy. Soc. B, 238, p. 143, pl. 4) report for *Dicranopteris unearis* from Ceylon both  $n = 39$  and  $n = 78$ ; from Singapore, for what is now recognized as *D. curranii* COPEL.,  $n = 39$ . MANTON reports verbally that a plant of *D. linearis* sent from Singapore and cultivated at Kew is a sterile triploid hybrid. MEHRA & SINGH also report  $n = 39$  for *D. linearis* from Northern India (Curr. Sc. 25, 1956, 168), and  $n = 56$  for *Hicriopteris glauca* (probably *Gleichenia gigantea* WALL., which is the common Himalayan species of this group), a species of *Gleichenia* subg. *Diplopterygium*. BROWNIE (Trans. R. Soc. N.Z. 85, 1958, 213-214) reports  $n = 20$  for *G. (subg. Gleichenia) microphylla* R. BR. and  $n = 34$  for *G. (subg. Mertensia) cunninghamii*. T. G. WALKER reports (personal communication)  $n = 34$  for two species of subg. *Mertensia* from Jamaica.

Anatomy. The rhizome has a simple protostele structure except in *Dicranopteris pectinata* (see BOWER, l.c.). The rachis has a single C-shaped vascular strand; all the outer tissues in the rachis are thick-walled and when mature form a very strong protection for the vascular strand. Such protection is important in fronds which continue to grow in length for a long period.

Economic importance. HEYNE (Nutt. Pl. N.I. 1927, p. 97) records the following uses for parts of plants of this family; the chief species used are *Dicranopteris linearis* and *D. curranii*. The rachises of mature fronds are tied into bundles and the bundles used in making the fences of a certain kind of fish trap; they will last two years when immersed in sea-water. Parts of the rachis of a large frond (the largest are produced by *D. curranii*) when suitably split make excellent pens for writing Arabic characters (I learned of this use also in Singapore). The vascular strands of stipe and rachis are separated and used for special kinds of fine plaited work, being strong and pliable.

*Dicranopteris* thickets may be useful as preventing erosion, but they are troublesome to the forester when they prevent regeneration of tree-seedlings in forest clearings. As the rhizomes are almost or quite superficial, they are exposed when the thicket is cut down, and usually one such cutting is enough to kill almost all of the plants. Fronds are sometimes cut — when in absence of other suitable material — to provide light shade for transplanted seedlings.

Taxonomy. I published a statement on taxonomy, with discussion of the present arrangement, in 1957 (Reinwardtia 4, p. 257-280). COPELAND (Gen. Fil. 1947) divided the Malaysian members into four genera. It seems to me, however, that *Dicranopteris* is so different from the rest that a main division should indicate this difference, and I therefore recognize two genera, *Gleichenia* and *Dicranopteris*, the former with three subgenera which correspond to COPELAND's genera. For one of the latter he used the name *Hicriopteris* PRESL, but the type species of that genus is a *Dicranopteris* (described as *D. speciosa* in the present work). I have therefore adopted the subgeneric name *Diplopterygium*, first proposed (as a sectional name) for this group of ferns by DIELS (in ENGLER & PRANTL, Pfl. Fam. 1, 4, p. 350-356). For the other subgenus the name *Mertensia* is available; it was first used in this rank by HOOKER, though with a larger content. This name was first proposed by WILLDENOW in 1804 as a generic name to cover all known members of the family with larger divisions of the lamina than the original *G. polypodioides* (THUNB.) SMITH; but as a generic name it was antedated by *Mertensia* ROTH (*Boraginaceae*) and so it is illegitimate. In 1806 BERNHARDI published the generic name *Dicranopteris*, citing under it only one species of *Mertensia* WILLD., viz *Polypodium dichotomum* THUNB., which thus becomes the type species of *Dicranopteris*. I have typified *Mertensia* by the species *M. truncata* WILLD. (Reinwardtia 4, 1957, 261). Both *Mertensia* and *Dicranopteris* are used here in a more restricted sense than intended by some earlier authors. COPELAND used the generic name *Sticherus* PRESL for subg. *Mertensia* of the present account. This name was established by PRESL for two species of which he had seen no specimens, with a brief and confused description, and the lapse of the name is not to be regretted.

#### KEY TO THE GENERA

1. Young parts of plants protected by fringed peltate scales and stellate hairs. Sori of 2-5 sporangia. Veins simple or once forked . . . . . 1. *Gleichenia*
1. Young parts of plants protected by branched hairs of various form, scales lacking. Sori of 8-15 or more sporangia. Veins forked at least twice . . . . . 2. *Dicranopteris*

## 1. GLEICHENIA

SMITH, Mem. Ac. Turin 5 (1793) 419, *non* NECK. 1790, *nom. cons.* — *For synonyms see the subgenera.*—Fig. 1–10.

*Rhizome* dichotomously branched, protostelic, near the apex protected by peltate scales. *Fronde*s of mature plants of indefinite growth in length (except sometimes at high altitudes), bearing *primary branches* in pairs, the apex of the main rachis dormant during the development of each pair of primary branches, the dormant apex in some cases protected by a pair of stipule-like leaflets of distinctive form (such *stipular leaflets* less often present in conjunction with dormant apices of lateral branch-systems); primary branches often each bearing a pair of *secondary branches* with a usually dormant apex between them, the process sometimes repeated to produce ultimate branches of fourth or fifth orders; dormant apices protected by peltate scales which (with two exceptions) are fringed by outgrowths from the marginal cells; *ultimate branches* either simply pinnatifid or bipinnatifid; *lamina* in all cases lobed almost to the costa, the veins in each segment pinnately branched; lateral veins simple or once forked; costae, costules and veins when young protected by small fringed peltate *scales* and by stellate hairs, sometimes glabrescent when mature; *sori* one or several to each segment of the lamina, upon the lateral veins, not terminal upon them (on the acroscopic branch of a forked vein), exindusiate, each consisting of 2–5 large *sporangia*; *paraphyses*, in the form of small stellate hairs or small scales with long marginal hairs, often present with the sporangia; annulus complete and oblique, dehiscing dorsally. *Spores* monolete or trilete, smooth and translucent, 256 or more in each sporangium.

## KEY TO THE SPECIES

1. Ultimate branches (branches on each side of an ultimate dormant apex) bipinnatifid.
2. Segments of the lamina not much longer than wide; one sorus on each segment. (*subg.* *Gleichenia*).
3. Fully developed pinnule-lobes not deeply concave beneath (the edges only slightly revolute). Tissues adjacent to costa not swollen. Sporangia when young in a circular depression in the lamina.
4. Edge of depression occupied by sorus distinctly raised. Small scales on lower surface of lamina.
  1. *G. peltophora*
4. Edges of depression occupied by sorus not raised. No small scales on lower surface of lamina.
  2. *G. microphylla*
3. Fully developed pinnule-lobes deeply concave beneath, the distal edges strongly revolute. Tissue adjacent to the costa more or less swollen. Sporangia not in a depression in the lamina.
5. Costae persistently scaly; tissue adjacent to the costa slightly swollen. Sporangia often 3.
  3. *G. vulcanica*
5. Costae of fully developed fronds usually quite glabrous; tissue adjacent to the costa much swollen. Sporangia 2.
  4. *G. dicarpa*
2. Segments of the lamina elongate, the costule bearing several forked veins, each of which may bear a sorus on its acroscopic branch. (*subg.* *Diplopterygium*).
6. Scales on dormant apex of rachis entire, to 10 by 3 mm. Segments of lamina at *c.* 45° to costae.
  5. *G. laevis*
6. Scales on dormant apex of rachis fringed with hairs or setae, or with a broad translucent margin. Segments of lamina almost at right angles to costae.
7. Scales on dormant apex of rachis 1 mm wide or more, edges fringed with spreading hairs to 0.5 mm long, or with translucent edge bearing fine short hairs.
8. Rachis-branches persistently quite covered with scales, or with a mixture of scales and hairs, on lower surface.
9. Rachis-branches covered almost entirely with thin brown scales 4–5 mm long and nearly 1 mm wide, stellate hairs few.
  6. *G. paleacea*
9. Rachis-branches covered with a dense felt of stellate hairs, and also with ± abundant scales.
10. Pinnules commonly 12–16 by 2–2½ cm. Upper surface of the lamina not swollen between the veins. Stipular leaflets present.
  7. *G. volubilis*
10. Pinnules commonly 6–9 by 0.9–1.3 cm. Upper surface of the lamina much swollen between



- the veins. No stipular leaflets . . . . . 8. *G. bullata*
8. Rachis-branches not persistently quite covered with scales nor with a felt of stellate hairs on the lower surface.
11. Very few persistent scales on the lower surface of rachises and costae. Pinnules to 22 by 3.5 cm. 9. *G. longissima*
11. Many persistent dark scales on rachises and costae. Pinnules to 12 by 2 cm 10. *G. clemensiae*
7. Scales on dormant apex of rachis narrower, their edges bearing short stiff oblique setae.
12. Segments of the lamina near base of each pinnule constricted at the base (*i.e.* widening just a little above the constriction), joined together by a very narrow wing of even width along the costa.
13. Many such segments (20 or more pairs) on each pinnule.
14. Lamina rigid; segments of lamina  $2\frac{1}{2}$  mm wide; scales of dormant apex uniformly dark brown . . . . . 11. *G. angustiloba*
14. Lamina thin; segments of lamina  $3\frac{1}{2}$  mm wide; scales of dormant apex pale with dark edges. 13. *G. deflexa*
13. Few (at most 7-8) such segments on each pinnule.
15. Pinna-rachises more or less persistently scaly; costules  $3\frac{1}{2}$ - $4\frac{1}{2}$  mm apart. 14. *G. sordida*
15. Pinna-rachises sparsely scaly, soon glabrous; costules  $5\frac{1}{2}$ -7 mm apart. 12. *G. elmeri*
12. Segments of lamina near base of each pinnule not thus constricted (or not more than one segment on the largest pinnules).
16. Stipular leaflets having lobes similar to pinnule-segments, not narrow and acuminate. Scales on rachis-apex not dark-fringed . . . . . 15. *G. norrisii*
16. Stipular leaflets having very narrow acuminate lobes quite different from normal segments of pinnules. Scales on rachis-apex dark-fringed.
17. Distal half of each rachis-branch strongly zig-zag, the pinnules deflexed so that each is in line with the part of the rachis beyond it . . . . . 16. *G. matthewii*
17. Distal half of each rachis-branch not thus zig-zag.
18. Pinnules c. 10 by 2 cm. . . . . 17. *G. brevipinnula*
18. Pinnules commonly 20 by 3-4 cm.
19. Dark rigid stellate hairs abundantly persistent on the lower surface of veins and lamina. 18. *G. blotiana*
19. Stellate hairs light brown, not abundant nor persistent on the lower surface of veins and lamina . . . . . 19. *G. conversa*
1. Ultimate branches simply pinnatifid. (*subg.* *Mertensia*).
20. Stipule-like leaflets, different from ordinary segments of the lamina, present at the branchings of the main rachis (on fronds of mature size).
21. Segments of lamina at right angles to the costa, or more or less deflexed. Lower surface not conspicuously glaucous.
22. Segments of lamina deflexed (lower ones much so), thick, with edges much revolute when dry. Main rachis-branches once or twice forked . . . . . 20. *G. reflexipinnula*
22. Segments of lamina not or little deflexed. Main rachis-branches often more than twice forked.
23. Forkings of rachis-branches equal or nearly so, not alternately unequal with larger branches at successive forks forming almost a straight line.
24. Scales on costules very abundant, spreading so as almost to cover the lower surface of the lamina. Veins on lower surface strongly raised . . . . . 21. *G. venosa*
24. Scales on costules not persistently covering the lower surface of the lamina. Veins not strongly raised . . . . . 22. *G. truncata*
23. Forkings of rachis-branches unequal, the larger branch at successive forks alternately to left and right, axes of these larger branches in almost straight line. . . . . 23. *G. milnei*
21. Segments of lamina distinctly oblique-ascending. Lower surfaces distinctly glaucous.
25. Primary branch-systems 5 times forked on large fronds, branches of all orders except the first leafy; no stellate hairs on the lower surface of veins . . . . . 24. *G. oceanica*
25. Primary branch-systems twice forked; stellate hairs (or at least their bases) persistent on the lower surface of veins . . . . . 25. *G. erecta*
20. Stipule-like leaflets absent (sometimes present in *G. loheri* var. *major*).
26. Margins of segments of lamina not distinctly toothed.
27. Only the ultimate branches fully leafy (penultimate without lamina or with some scattered segments).
28. Ultimate branches to 20 cm long. . . . . 26. *G. pulchra*
28. Ultimate branches 30-40 cm long.
29. Segments of the lamina to 25 mm long, costules  $5\frac{1}{2}$ -6 mm apart. Primary rachis-branches usually 3 times forked . . . . . 27. *G. pseudoscandens*
29. Segments of lamina to 17 mm long, costules 4 mm apart. Primary rachis-branches usually twice forked . . . . . 28. *G. alstonii*
27. At least the penultimate branches fully leafy, lower ones sometimes also.

30. Lamina-segments rarely more than twice as long as the distance between bases of adjacent costules.
31. Segments 8–12 mm long, costules 4–5 mm apart. Rachis-branches of 1st and 2nd orders 3–4 cm long. Scales on the main rachis-apex brown, more than 1 mm wide at base; scales on the costae rusty brown . . . . . 29. *G. vestita*
31. Segments 3–6 mm long, costules 3 mm apart. Rachis-branches of 1st and 2nd orders 1–2 cm long. Scales on the main rachis-apex very dark, narrower; scales on the costae dark at base, paler distally . . . . . 30. *G. bolanica*
30. Lamina-segments much more than twice as long as the distance between adjacent costules.
32. Scales on the costae only a few cells wide at the base, about half their length consisting of a hair, these hairs crisped and entangled . . . . . 31. *G. hispida*
32. Scales on the costae with short hair-points, their bases wider and their apices not entangled.
33. Costules at 60°–70° to costae . . . . . 25. *G. erecta*
33. Costules at almost a right angle to the costae.
34. Ultimate branches 25–45 cm long, 3–4 $\frac{1}{2}$  cm wide; costules on ultimate branches 4–5 mm apart . . . . . 32. *G. brassii*
34. Ultimate branches smaller, costules on ultimate branches 3–4 mm apart. 33. *G. loheri*
26. Margins of the segments of the lamina distinctly toothed, at least towards the apex.
35. Margins toothed almost to base of segments. Costules at c. 45° to costae. 34. *G. flabellata*
35. Margins toothed only near apex of segments. Costules at wider angle to costae. 35. *G. hirta*

### 1. Subgenus *Gleichenia*

HOLTT. Reinwardtia 4 (1957) 262.—*Calymella* PRESL, Tent. Pterid. (1836) 48; CHING, Sunyatsenia 5 (1940) 287; NAKAI, Bull. Nat. Sc. Mus. Tokyo n. 29 (1950) 40.—*Gleicheniastrum* PRESL, Abh. (K.) Böhm. Ges. Wiss. M.-N. Cl. 5 (1848) 338; NAKAI, l.c. 42.—*Gleichenia* subg. *Eugleichenia* DIELS in E. & P. Pfl. Fam. 1, 4 (1900) 355.—*Gleichenia*; COPEL. Gen. Fil. (1947) 26.—Fig. 1–3.

Young plants first producing determinate bipinnatifid fronds, the largest of these as large as the branches of later fronds and sometimes fertile (plants in exposed places at high altitudes sometimes producing only fronds of this kind); then *fronds* bearing pairs of primary branches like the fronds of the first stage; in some cases the primary branches bearing one or more pairs of determinate bipinnatifid secondary branches, or the secondary branches leafless and bearing pairs of tertiary branches, the ultimate branches always determinate and bipinnatifid. *Leaflets* of bipinnatifid fronds or of ultimate branches lobed almost to the costa, lobes hardly longer than wide; veins in each lobe pinnately branched but without a conspicuous costule, lateral veins simple. One *sorus* on each lobe, upon the basal acroscopic vein, superficial or sunk in the substance of the lamina.

Distr. About 10 spp. in tropical and southern Africa, the Mascarene Islands, Malaysia and Australasia (not in Ceylon and India).

Ecol. In *Malaysia* only on mountains, in exposed places, usually in sandy or acid, peaty soils, sometimes in association with members of the other subgenera.

1. *Gleichenia peltophora* COPEL. Philip. J. Sc. 40 (1929) 292, t. 1.—*G. circinnata* var. *borneensis* BAK. J. Bot. 17 (1879) 37.—*G. borneensis* C. CHR. Gard. Bull. S. S. 7 (1934) 211.—*Calymella borneensis* CHING, Sunyatsenia 5 (1940) 288.

#### var. *peltophora*.

Rhizome-scales ovate, dark, entire. Determinate bipinnatifid *fronds* to 40 cm high (including stipe), often fertile; branched fronds bearing 1 or few pairs of branches; primary branches bipinnatifid-determinate or once forked with a permanently dormant apex in the fork, the primary branch always bearing leaflets (where primary branches are not forked, the main rachis may be leafy below junction with branches); *scales* on resting apex of rachis to 1 $\frac{1}{2}$  by 1 mm, ovate, entire, convex,

shining, very dark brown with narrow pale edge; similar but smaller scales scattered on lower surfaces of rachises and less abundantly on costae; ultimate branches 20–30 cm long, bearing many *leaflets*, costae of adjacent leaflets 4–6 mm apart; leaflets 2–5 cm long, 2 $\frac{1}{2}$ –4 mm wide; lobes c. 1 $\frac{1}{2}$  mm wide at base, gradually narrowed to rounded apex, edges slightly reflexed, lower surface slightly concave, glaucous, bearing scattered circular scales 0.2–0.3 mm diameter. *Sori*, if present, each sunk in a circular depression in the substance of the lamina, the lower surface of the lamina somewhat raised round the edge of the depression which occupies about half the width of the base of a lobe.

Type: Copeland s.n., 1 May 1917, Mt Matutum, Mindanao, 1600 m (H. Copel.).

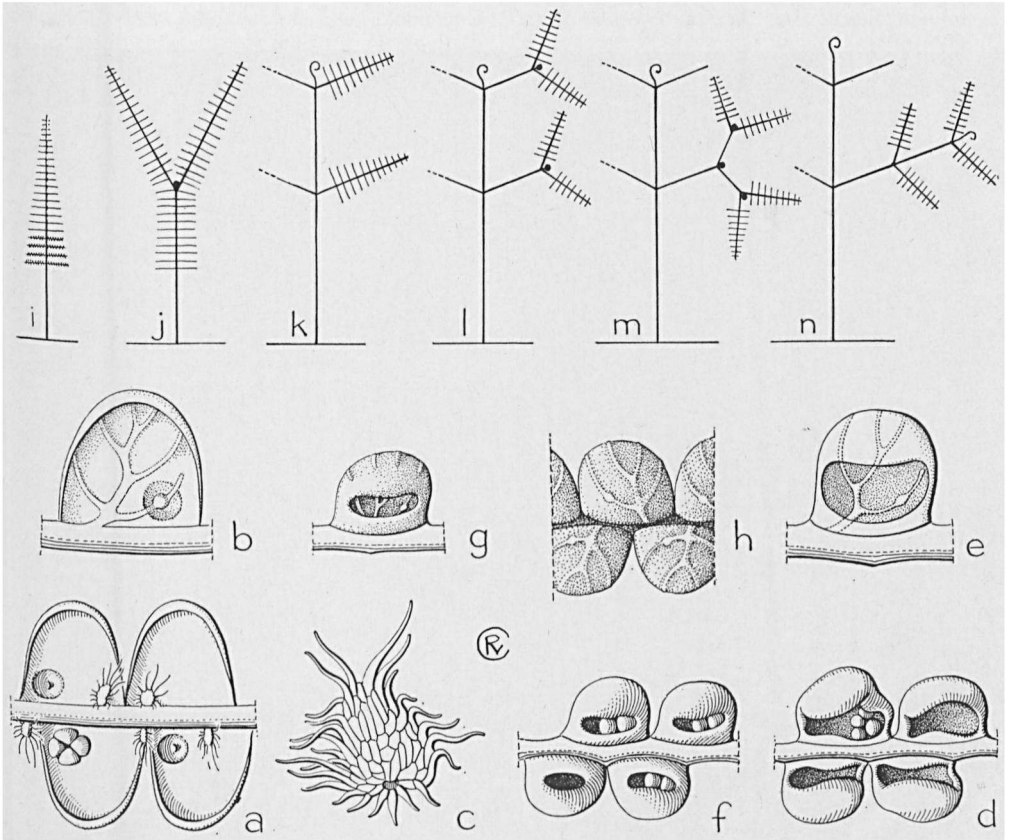


Fig. 1. *Gleichenia microphylla* R. BR. a. Lower surface of part of a pinnule, showing one mature sorus, and two soral depressions from which sporangia have been removed,  $\times 10$ , b. one lobe of lamina, cleared to show veins and position of sorus,  $\times 13$ , c. a scale,  $\times 50$ . — *G. vulcanica* BL. d. Part of pinnule from below (scales removed),  $\times 10$ , e. same cleared to show veins and position of sorus,  $\times 13$ . — *G. dicarpa* R. BR., f. Lower surface of part of pinnule,  $\times 10$ , g. same cleared to show veins,  $\times 13$ , h. upper surface of cleared pinnule showing position of sori. — Diagrams of various stages of branching which may occur during development of a single plant of *G. vulcanica* BL., i. First stage: plants in exposed places or at high altitudes may never develop further, j. transition stage, k. primary branches simple (corresponding to condition of subg. *Diplopterygium*), l. primary branches once forked, m. primary branches twice forked, n. primary branch proliferous beyond the first fork.

Distr. *Malaysia*: N. Borneo (Mt Kinabalu), Philippines (Mindanao), South Central Celebes, West New Guinea (several localities).

Ecol. In open places on mountain summits or high ridges, 1500–2500 m; on Mt Kinabalu in association with *G. vulcanica* and *Dipteris novoguineensis* POSTH.

*var. schizolepis* C. CHR. ex HOLTZ. Reinwardtia 4 (1957) 262.

Scales on rhizome short-fringed; scales on costae bearing a few rigid dark brown marginal hairs; scales on lower surface of lamina replaced by dark red-brown stellate hairs; fronds of the only specimen unbranched, with leaflets  $2\frac{1}{2}$  cm long, sterile.

Distr. Borneo (Sarawak: Mt Murud), 2500 m, once found.

2. *Gleichenia microphylla* R. BR. Prod. (1810) 161; v. A. v. R. Handb. Suppl. (1917) 80, incl. *var. semivestita* v. A. v. R.—*G. semivestita* LABILL. Sert. Austro-Cal. (1824) 8, t. 11.—*Calymella microphylla* PRESL, Tent. Pter. (1836) 49.—*Gleicheniastrum microphyllum* PRESL, Abh. (K.) Böhm. Ges. Wiss. M.-N. Cl. 5 (1848) 338; NAKAI, Bull. Nat. Sc. Mus. Tokyo n. 29 (1950) 45, incl. *var. semivestitum* NAKAI.—*Calymella circinnata* (?*G. circinnata* Sw.) CHING, Sunyatsenia 5 (1940) 288.—*Calymella semivestita* CHING, l.c.—*Gleicheniastrum lowei* NAKAI, Bull. Nat. Sc. Mus. Tokyo n. 29 (1950) 44.—Fig. 1a-c, 2.

Rhizome to 3 mm diameter, the young parts covered with narrow dark brown rigid fringed scales. Fronds on young plants bipinnatifid, determinate, rarely fertile, on old plants usually



Fig. 2. *Gleichenia microphylla* R. BR. on edge of dwarf forest on wet sandy soil near summit of Kedah Peak, Malaya, 1200 m (HOLTUM, 1953).

branched, the primary branches sometimes forked with leaflets below the fork, rarely proliferous beyond the fork and then not bearing leaflets below the fork; secondary branches sometimes also forked. *Scales* on resting apices of rachis narrow, very dark, with pale thin marginal hairs towards the base and rigid dark setae near apex; rachises and costae more or less densely clothed with very small dark scales, their edges bearing rigid concolorous setae. Ultimate branches 12–25 by 4–5 cm; leaflets 7–9 mm apart, 2½–4 mm wide; lobes of lamina 1–1.8 mm long, 0.7–1.5 mm wide at the base, apex rounded, edges usually a little reflexed; lower surface slightly concave, not glaucous. *Sorus* (if present) at first embedded in a circular cavity which occupies half the width of the lobe, edges of cavity not raised; sporangia 3–4 (rarely 5), surrounded by brown hairs not longer than the ripe sporangia.

Type: Robert Brown, Port Jackson, N.S. Wales (BM; dupl. at K).

Distr. From Annam through Malaysia to Australia, New Caledonia, and New Zealand; in Malaysia: Sumatra, Malay Peninsula, Lingga Arch., Borneo, and Moluccas (Ambon).

Ecol. In open places in sandy or thin peaty soil on summits or exposed ridges of mountains at 750–1800 m, especially on sandstone. At Fraser's Hill, Malay Peninsula, 1250 m, this species occurs in open places on a quartzite ridge, not on the neighbouring granite; it occurs on the summits of some isolated granite mountains (Mt Ophir, G. Belumut). It is abundant from 1000 m upwards in open *Leptospermum* forest, with *Sphagnum*, in thin peaty soil on the sandstone mountain G. Jerai or Kedah Peak.

Note. For a note on the type specimen of *G. circinnata*, see note under 4. *G. dicarpa*.

3. *Gleichenia vulcanica* BL. En. Pl. Jav. (1828) 251; RACIB. Fl. Btzig 1 (1898) 10; v. A. v. R. Handb. (1909) 56; BACKER & POSTH. Varenfl. Java (1939) 353.—*Calymella vulcanica* PRESL, Abh. (K.) Böhm. Ges. Wiss. M.-N. Cl. 5 (1848) 338; CHING, Sunyatsenia 5 (1940) 287; NAKAI, Bull. Nat. Sc. Mus. Tokyo n. 29 (1950) 42.—*G. dicarpa* var. *vulcanica* CHRIST, Ann. Jard. Bot. Btzig 15 (1898) 75.—*G. squamosissima* COPEL. Philip. J. Sc. 75 (1941) 348, pl. 1.—*Calymella squamosissima* NAKAI, l.c.—Fig. 1d–e, i–n, 3.

Similar in habit to *G. microphylla*, differing as follows: leaflets commonly 4–5 mm apart; segments of lamina less than 1 mm long and wide; lower surface glaucous, deeply concave, with edges much reflexed and the surface adjacent to the costa also swollen; many small thin scales, with slender crisped marginal hairs, all along costules; sporangia 2 or 3, not in a depression in the lamina. At very high altitudes often only unbranched fronds, very densely scaly, are produced.

Type: Blume, Java (L).

Distr. Malaysia: Sumatra, Malay Peninsula (3 localities), W. Java, Borneo, Philippines (Mindanao, Mindoro), Celebes, and New Guinea.

Ecol. Abundant in open scrub (on both dry

stony and wet ground) on volcanic mountains throughout W. Java and Sumatra, 1800–3600 m, at these altitudes apparently less abundant on granite mountains in Borneo; densely scaly at highest elevations both in N. Sumatra and in New Guinea (*G. squamosissima* COPEL.).

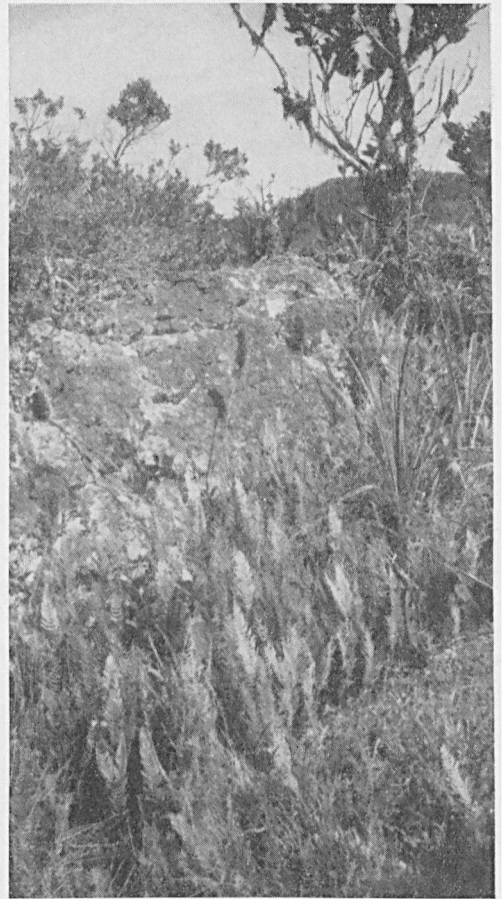


Fig. 3. *Gleichenia vulcanica* BL. in the high mountains of Mt Goh Lembuh, Gajo Lands, N. Sumatra, sheltered in rock crevices, c. 3000 m (1937).

4. *Gleichenia dicarpa* R. BR. Prod. (1810) 161; C. CHR. Ark. Bot. 9<sup>11</sup> (1910) 33.—*Calymella dicarpa* PRESL, Abh. (K.) Böhm. Ges. Wiss. M.-N. Cl. 5 (1848) 338.—*Calymella circinnata* (non *G. circinnata* SW.) CHING, Sunyatsenia 5 (1940) 288.—Fig. 1f–h.

Like *G. vulcanica*, but the leaflets not copiously scaly (costae almost or quite glabrous when mature), the aperture of the concave lower surface of each segment of the lamina reduced to much less than half of the area enclosed by the outline of the segment as seen from below, owing to much swelling of the costal tissue; sporangia 2, filling the aperture.



Type: Robert Brown, Tasmania (BM; dupl. at K).  
 Distr. Australia, New Caledonia, in *Malaysia*: New Guinea, Philippines (Mindanao).  
 Ecol. On Normanby and Rossel Islands, SE.

New Guinea, occurring at 750–850 m, in open forest or rocky places.  
 Note. Though typical specimens of *G. vulcanica* in Java differ markedly from typical specimens of *G. dicarpa* in Australia, some specimens on moun-

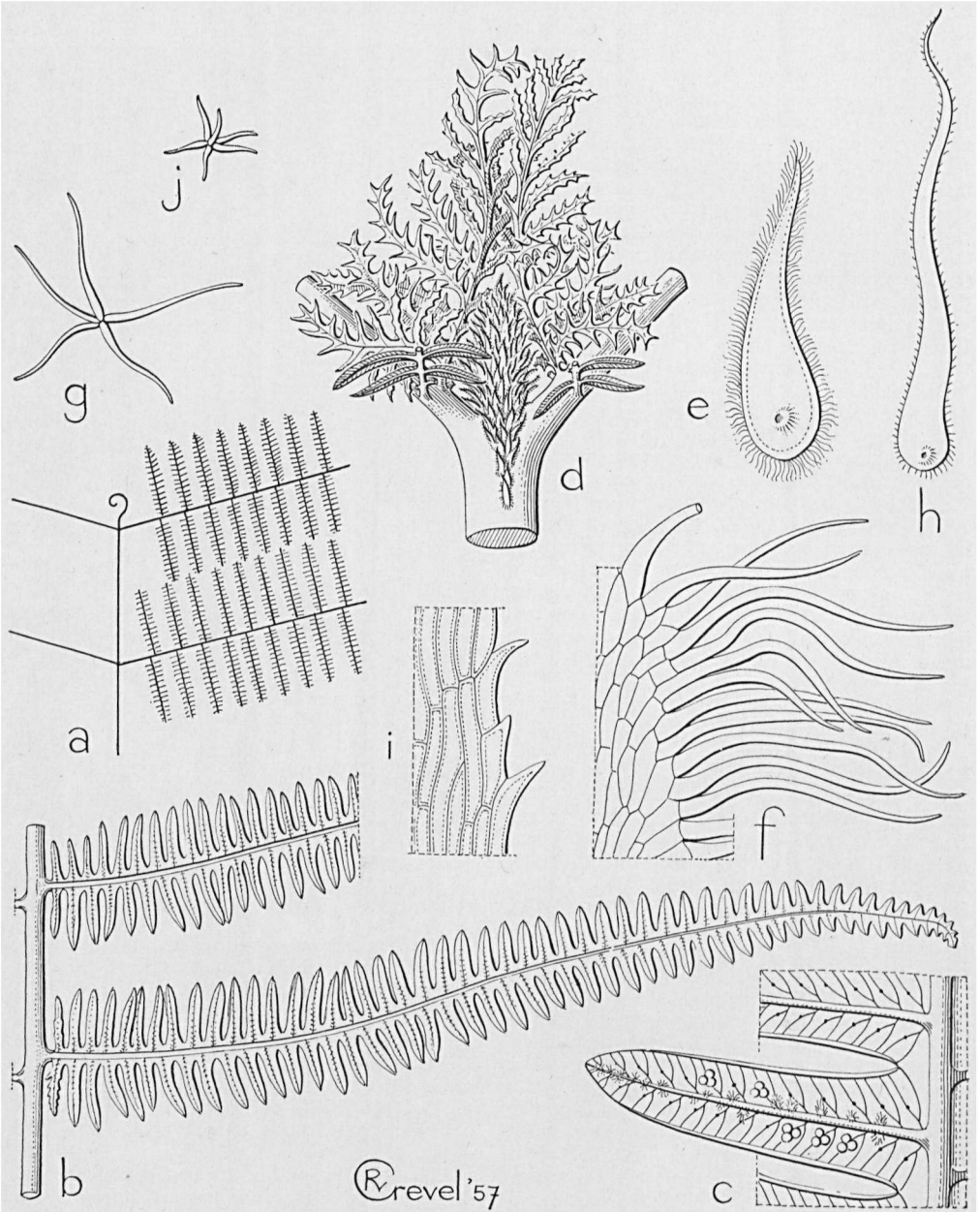


Fig. 4. a. Diagram of branching in *Gleichenia* subg. *Diplopterygium*. — *G. longissima* BL., b. Part of rachis-branch bearing two pinnules,  $\times \frac{2}{3}$ , c. segment of lamina, lower surface, showing veins and sori,  $\times 4$ , d. resting apex of main rachis and bases of branches, with stipular leaflets, nat. size. — Scales and hairs. — *G. longissima* BL., e. A single scale from apex of rachis,  $\times 8$ , f. edge of scale,  $\times 133$ , g. stellate hair,  $\times 33$ . — *G. conversa* v. A. v. R., h. A single scale,  $\times 8$ , i. edge of scale,  $\times 133$ , j. stellate hair,  $\times 33$ .

tains in Mindanao and New Guinea seem somewhat intermediate. Ecological distinctions between the two have not been studied.

CHRISTENSEN, in his notes on specimens in the herbarium of SWARTZ at Stockholm (*l.c.*) stated that the type specimen of *G. circinnata* was identical with *G. dicarpa* R. BR. With his original description SWARTZ gave no precise locality, but in his 'Synopsis Filicum' he stated that the species was from Botany Bay, near Sydney. The only specimen labelled *G. circinnata* in SWARTZ's herbarium from that locality is certainly not *G. dicarpa*, though it has only two sporangia on each lamina-segment; the segments are not pouch-

shaped in the manner of *G. dicarpa*. One can only conclude that CHRISTENSEN did not make a careful examination of the specimen. However, the Botany Bay specimen is not certainly the original on which the species *G. circinnata* was based (furthermore, the original description included the phrase *capsulis quaternis*, not true of the Botany Bay specimen). I therefore refrain from reverting to CHRISTENSEN's earlier identification of *G. microphylla* R. BR. with *G. circinnata* SW.

After the publication of CHRISTENSEN's note, some botanists used the name *G. circinnata* to replace *G. dicarpa*, but it seems clear that this was an error, and I therefore restore R. BROWN's name.

## 2. Subgenus Diplopterygium

HOLT. Reinwardtia 4 (1957) 261.—*Gleichenia subg. Mertensia sect. Diplopterygium*  
 DIELS in E. & P. Pfl. Fam. 1, 4 (1900) 353.—*Gleichenia subg. Mertensia § 1* HOOK.  
 Sp. Fil. 1 (1844) 4.—*Gleichenia subg. Mertensia sect. Dicranopteris v. A. v. R.*  
 Handb. (1909) 57, *p.p.*—*Dicranopteris* UND. Bull. Torr. Bot. Cl. 34 (1907) 249,  
*p.p.*—*Sticherus § Hicriopteris* C. CHR. in Verdoorn, Man. Pterid. (1939) 530.—  
*Hicriopteris (non PRESL)* CHING, Sunyatsenia 5 (1940) 277; COPEL. Gen. Fil.  
 (1947) 28.—*Mesosorus* HASSK. Fil. Jav. 1 (1856) 2, *p.p.*—*Diplopterygium* NAKAI,  
 Bull. Nat. Sc. Mus. Tokyo n. 29 (1950) 47.—Fig. 4-6.

Fronds of a young plant producing pairs of bipinnatifid branches, with periodic dormancy of the apex, from an early stage, the lateral branches of such fronds of immature plants small and sterile; periodic dormancy of the apex of the main rachis, and no other dormancy, occurring on *fronds* of mature plants; lowest leaflets on the branches often deltoid and bipinnatifid (or with deltoid-bipinnatifid lowest branchlets), forming stipule-like structures which protect the dormant apex of the main rachis; remaining leaflets very deeply pinnatifid, segments of the lamina oblong, each with a costa bearing on either side several once-forked veins. *Sori* on the acroscopic branches of the veins, several to each segment of the lamina.

Distr. More than 20  *spp.* in NE. India, Burma and Indo-China, China, Japan, Malaysia, Polynesia, Hawaii, and tropical America (1  *sp.*). This subgenus is far more diversified in Malaysia than elsewhere.

Ecol. All species occur on mountains, some descending to only 600 m. All may form dense thickets on edges of forest or other open places; fronds can climb to a height of 6-7 m, if trees suitable for support are present.

Note. Some fossils of Cretaceous age in West Greenland (lat. 70-71°N) have exactly the characters of this subgenus (habit of branching, venation, position of sori, nature of sporangia).

5. *Gleichenia laevisissima* CHRIST, Bull. Ac. Inst. Geogr. Bot. III, 11 (1902) 268; v. A. v. R. Handb. (1909) 795; Suppl. (1917) 82.—*Hicriopteris laevisissima* CHING, Sunyatsenia 5 (1940) 280.—*Diplopterygium laevisissimum* NAKAI, Bull. Nat. Sc. Mus. Tokyo n. 29 (1950) 52.

Scales on rachis-apex 10 mm long, nearly 3 mm wide, acuminate, entire; rest of *frond* quite glabrous except for very short simple hairs on lower surface of veins and lamina of young fronds and soral hairs. Primary rachis-branches to at least 70 cm long, lowest leaflets not stipule-like; *leaflets* at an angle of about 45° to rachis, largest 17-20 cm long, 2½-3 cm wide, costae 2½-3½ cm

apart; lamina lobed almost to the costa, costules at about 45° to the costa and 3½-4½ mm apart; segments of lamina 2-2½ mm wide above the base, narrowed gradually towards the apex; lower surface not glaucous, veins only slightly raised; upper surface not raised along margins of costae, veins raised only near their bases. *Sporangia* usually 4, pale, with very slender pale hairs.

Type: Bodinier 1295, Kouy-yang (P).

Distr. China (Kweichow, Chekiang, Yunnan, Fukien), Formosa, and Malaysia: Philippines (Luzon).

Ecol. In the mountains of Luzon, c. 2000 m.



Fig. 5. *Gleichenia longissima* BL. on edge of forest, Taiping Hills, Malaya, c. 800 m (HOLTUM, 1952).



6. *Gleichenia paleacea* (COPEL.) HOLTT. Reinwardtia 4 (1957) 265.—*Hicriopteris paleacea* COPEL. Philip. J. Sc. 81 (1952) 3.

Scales on main rachis-apex not seen; scales on primary branches and costae beneath very copious, light brown, larger ones 4–5 mm long and 1 mm wide, those on costae commonly 2 mm long and more than 0.5 mm wide, thin, fringe fine, close, concolorous; smaller scales narrower with long fine fringe and hair-tips; no persistent stellate hairs on veins except in sori. *Primary rachis-branch* more than 100 cm long (collector's note); costae 2½ cm apart, at right angles to rachis; largest pinnules 15–16 cm long, 2½–3 cm wide, lobed almost to the costa, basal lobes slightly reduced and very close to the rachis; costules c. 4 mm apart, very slightly oblique; *lamina-segments* thin but firm, hardly narrowed above the base, edges slightly reflexed when dry so that sinuses between segments are 1–2 mm wide; lower surface glaucous, veins distinct and slightly raised; lamina on each side of the costa on upper surface raised as in *G. gigantea* WALL. and some long hairs persistent in the groove, veins slightly sunk in upper surface of lamina when dry. *Sori* commonly of 3 sporangia, with numerous pale hairs nearly 1 mm long.

Type: Elmer 9902 (Herb. Copel.; dupl. at BM, K, Bo, L, P).

Distr. *Malaysia*: Philippines (Negros: Cuernos Mts), once collected.

Note. This is near to *G. longissima* BL., but differs in persistent abundant scabiness. A collection of *G. longissima* from Canlaon Volcano, Negros (MERRILL 607) shows very scaly young parts of a frond, but the scales are much narrower and the old parts are glabrous.

7. *Gleichenia volubilis* JUNGH. Java 1 (1853) 592, 664; v. A. v. R. Handb. Suppl. (1917) 83, p.p.; BACKER & POSTH. Varenfl. Java (1939) 256.—*Mertensia arachnoides* HASSK. in Hook. J. Bot. Kew Misc. 7 (1855) 332.—*Mesosorus arachnoides* HASSK. Fil. Jav. 1 (1856) 6.—*G. arachnoides* METT. in Miq. Ann. Mus. Bot. Lugd.-Bat. 1 (1863) 47; RACIB. Fl. Btzig 1 (1898) 11; v. A. v. R. Handb. (1909) 58 (*arachnoidea*); non *G. arachnoidea* CUNN. 1844.—*G. glauca* var. *arachnoides* C. CHR. Ind. Fil. (1905) 320.—*Hicriopteris volubilis* CHING, Sunyatsenia 5 (1940) 280.—*Diplopterygium volubile* NAKAI, Bull. Nat. Sc. Mus. Tokyo n. 29 (1950) 55.

var. *volubilis*.

Scales on main rachis-apex nearly black, to at least 6 mm long and 1½ mm wide, gradually narrowed towards apex, edges closely fringed with fine spreading pale hairs (or with a broad, thin translucent border bearing short hairs); similar but smaller scales on lower surfaces of branch-rachises, costae and costules (smallest scales not dark), these surfaces also densely covered with a persistent felt of pale stellate hairs each less than 0.5 mm diameter, old costae showing the raised points of attachment of former scales;

stellate hairs on costules and lower surface of veins rusty brown. *Primary rachis-branches* to at least 150 cm long and 30 cm wide; stipule-like leaflets present and deeply lobed; pinnules 12–16 cm long, 2–3 cm wide, costules 3½–4 mm apart, at right angles to costae; *lamina-segments* firm, slightly narrowed above the base, their edges reflexed when dry, lower surface not (or very slightly?) glaucous, veins strongly raised; upper surface of rachis covered with stellate hairs as lower surface together with very narrow pale ciliate scales; smaller pale scales and hairs at first in groove of upper surface of costae (lamina slightly raised on each side of the groove); veins on upper surface paler than lamina and slightly raised in dried specimens (lamina between veins sometimes slightly raised but not swollen); *sporangia* surrounded by a group of crisped red-brown hairs.

Type: Junghuhn s.n., 1839, G. Gedeh (L).

Distr. *Malaysia*: Java, Sumatra, and Central Celebes (one collection).

Ecol. Forming dense thickets in open places on ridges, and on edges of forest, often very abundant, 1800–3000 m.

Note. The Celebes specimen has smaller pinnules than normal in Java (10–12 cm long, 1½ cm wide), with thinner lamina and veins hardly prominent beneath.

var. *peninsularis* HOLTT. Reinwardtia 4 (1957) 265.

Scales on lower surfaces of rachises and costae rusty brown like the stellate hairs, not black.

Type: F. M. S. Museum s.n., June 1917 (K).

Distr. *Malaysia*: Malay Peninsula (G. Bintang on Kedah-Perak boundary), once collected.

8. *Gleichenia bullata* MOORE, Ind. Fil. (1862) 374; C. CHR. Gard. Bull. S.S. 7 (1934) 212.—*G. volubilis* (non JUNGH.) v. A. v. R. Handb. Suppl. (1917) 83, p.p.—*Hicriopteris bullata* CHING, Sunyatsenia 5 (1940) 279.

Differs from *G. volubilis* JUNGH. as follows: scales on rachises, costae and costules much more abundant, those on costules often pale with a dark base; stipular leaflets lacking; *primary rachis-branches* shorter, pinnules commonly 1.3–1.5 cm apart, 6–9 cm long, 0.9–1.3 cm wide; veins on upper surface of *lamina* (when dry) much sunken, the surface between them swollen.

Type: Low, Mt Kinabalu, 7000 ft (K).

Distr. *Malaysia*: Borneo (Sarawak: Mts Dulit and Tibang; N. Borneo: Mt Kinabalu), New Guinea (Mt Dayman).

Ecol. Forming thickets like *G. volubilis*, 1700–3000 m.

Note. The bullate character of the upper surface of the lamina, and the scabiness, distinguish this from dwarfed specimens of *G. volubilis* which may have pinnules no larger than those normal in *G. bullata*.

9. *Gleichenia longissima* BL. En. Pl. Jav. (1828) 250; RACIB. Fl. Btzig 1 (1898) 10; BACKER &

POSTH. Varenfl. Java (1939) 256; HOLTT. Rev. Fl. Mal. 2 (1955) 67.—*G. excelsa* J. SM. ex HOOK. Sp. Fil. 1 (1844) 5, t. 4B.—*G. glauca* v. A. v. R. Handb. (1908) 58 *et al. p.p.*—*Hicriopteris longissima* CHING, Sunyatsenia 5 (1940) 280.—*Diplpterygium longissimum* NAKAI, Bull. Nat. Sc. Mus. Tokyo n. 29 (1950) 53.—Fig. 4b-g, 5.

*Scales* on resting apex of rachis as in *G. volubilis* JUNGH.; young expanding parts of fronds covered with loose indumentum of narrow rust-coloured scales and lax stellate hairs, a few such scales and hairs sometimes persistent on lower surface of costae and costules, mature rachises quite smooth and glabrous. *Primary rachis-branches* to about 200 cm long and 40 cm wide; largest pinules 15–22 cm long, 2½–3½ cm wide, costae 2.8–3½ cm apart; lamina thin, lobed almost to costa, costules 4–5 mm apart, slightly oblique to costa; *segments of lamina* slightly narrowed above the base, edges slightly reflexed when dry; lower surface glaucous, veins slender and slightly raised; upper surface of rachis and costae glabrous, lamina slightly raised on each side of costae; veins on upper surface slightly raised near base, rarely also distally, very slender; *sori* usually of 3 sporangia, surrounded by crisped brown hairs.

Type: Blume, Java (L; dupl. at K, P).

Distr. Southern China to Indo-China through Malaysia to Melanesia (Fiji, Tahiti), in *Malaysia*: not collected in the Lesser Sunda Islands E of Flores, Celebes, the Moluccas, and New Guinea.

Ecol. Forming thickets in clearings and on edges of forest, more or less persisting in open secondary forest; 750–1800 m. RACIBORSKI states that this species may climb very high on trees.

Note. This is the most widely distributed species in the subgenus. In Java and Sumatra it is replaced at higher altitudes by *G. volubilis*; a comparison of the two species near the transition zone needs to be made.

**10. *Gleichenia clemensiae* (COPEL.) HOLTT. comb. nov.**—*Hicriopteris clemensiae* COPEL. Un. Cal. Publ. Bot. 18 (1942) 217.—*G. papuana* HOLTT. Reinwardtia 4 (1957) 266.

*var. clemensiae.*

*Scales* on resting apex of main rachis dark brown, shining, 4 mm long, more than 1 mm wide, edges bearing spreading hairs to 0.5 mm long; lower surface of rachises and costae bearing numerous persistent scales like those on the resting apex but smaller, dark and shining with pale edges and fringe, those on the costae commonly 1½ mm long and ½ mm wide, old costae minutely warty from the raised bases of former scales; scales on lower surface of costules abundant, very small, laxly fringed; no hairs on veins, apart from *sori*; upper surface of rachis rather persistently covered with very narrow scales and long lax hairs, upper surface of costae hairy near the base only. *Rachis-branches* 120 cm long; pinules spreading at right angles, 2½ cm apart, largest 12 cm long, 2 cm wide; costules 2½–3 mm apart; lamina thin, veins slightly prominent on lower surface, not on

upper; *sori* commonly of 3 sporangia, with crisped paraphyses.

Type: Clemens 41227, Morobe, Matap, 5000–6000 ft (H. Copel.).

Distr. *Malaysia*: SE. New Guinea (Morobe, and Milne Bay Distr.: Mt Dayman).

Ecol. Scrambling to 2–3 m, forming dense tangles on edges of mossy forest, 1600–2250 m.

*var. membranacea* (HOLTT.) comb. nov.—*G. papuana* *var. membranacea* HOLTT. Reinwardtia 4 (1957) 266.

*Scales* on rachis-apex pale and very thin near the edges which are very shortly fringed; scales on rachises and costae more abundant, dark at the base only.

Type: Brass 24763 (BM).

Distr. *Malaysia*: New Guinea (Goodenough I.).

Ecol. Plentiful in openings in forest, 1600 m.

**11. *Gleichenia angustiloba* HOLTT. Reinwardtia 4 (1957) 263.**

Rhizome 7 mm diam., young parts covered with shining dark brown scales 5–7 by 1½ mm, old parts warty from bases of former scales; stipes 6–7 mm diam., the base at first scaly like the rhizome and then warty, upper part covered with small scales like those of the rachises, later asperulous. *Primary rachis-branches* 100 cm long or more; stipular leaflets broadly deltoid, to 4 cm long, pinnatifid, lowest lobes deeply and narrowly lobed again; scales on apex of main rachis dark brown, shining, narrow, 3–4 mm long, the edges bearing concolorous oblique rigid setae; rachises and costae, and lower surfaces of costules more or less persistently covered with smaller scales of various sizes and red-brown stellate hairs. Pinules to 15 cm long and 3–3½ cm wide, 2–3½ cm apart, the distal ones distinctly deflexed, the lower ones at right angles to rachis; all *segments of the lamina* c. 2½ mm wide, separated by wide sinuses, many of the lower segments being constricted at the base and joined laterally by a very narrow wing along the costa (wing about 0.2 mm wide); lowest segments forming distinct separate leaflets; costules 4 mm apart; veins prominent on both surfaces; *sori* of 4 sporangia with long red-brown crisped hairs, no other hairs on the veins of mature fronds.

Type: Brass 4960, Mt Tafa (BM, dupl. at K, Bo, US).

Distr. *Malaysia*: E. New Guinea (Mt Tafa, and on Asaro-Mairi Divide, Goroka Subdistr.).

Ecol. Altitude 2400 m; “Common in native rest clearings in ridge-crest forest; conspicuous, rambling amongst forest fringe bushes and small trees; fronds 4–5 m with 6–8 or more pairs of large spreading pinnae” (BRASS).

**12. *Gleichenia elmeri* COPEL. in Elmer, Leaf. Philip. Bot. 3 (1910) 799.**—*Diplpterygium elmeri* NAKAI, Bull. Nat. Sc. Mus. Tokyo n. 29 (1950) 49.

Scales on rachis-apex not seen; scales on costae sparse; scales on costules at first abundant,

longest 1-1½ mm long, narrow, rusty brown with well-spaced rigid spreading marginal hairs; very small scales and stellate hairs present on veins and with sporangia, hair-branches stiff, c. 0.2 mm long; dark brown short clavate hairs abundant on costules and less so on sides of costae. Pinnae 150 cm long (*vide* COPELAND); largest pinnules 25 cm long, 3½-4 cm wide, 4½-5 cm apart; costules 5½-7 mm apart, at right angles to costa; several segments of lamina constricted at base, widely separated and joined by a wing ½ mm wide along the costa; lower surface pale green, veins slightly raised; upper surface of lamina along sides of costae wrinkled when dry, probably somewhat raised in living fronds; veins not raised on upper surface except near base; sporangia commonly 3-5, less often 6 or 7, not always completely covering lower surface (as reported in original description); numerous pale hairs, longer than sporangia, attached to the receptacle.

Type: Elmer 11423 (H. Copel.; dupl. at K, US, F, L, P).

Distr. *Malaysia*: Philippines (Mindanao: Mt Apo), once collected.

13. *Gleichenia deflexa* HOLTT. Reinwardtia 4 (1957) addendum p. 280.

Scales on apex of main rachis light brown with darker obliquely setose edges; branch rachises and lower parts of costae at first covered on both surfaces with a close felt of small setose scales and stellate hairs and also with numerous narrow scales (those on rachis 5 mm long, 0.2 mm wide), setae of scales and hairs of upper surface all rigid and rather dark, of smaller scales and hairs on lower surface pale and lax; lower surface of costules scaly and hairy near their bases like the costae; lower surface of veins bearing persistent scattered stellate hairs with slender pale rays. *Rachis-branches* 120 cm or more long, fertile ones to 35 cm wide, sterile sometimes only 18 cm wide, all pinnules distinctly deflexed, making angles of about 75° with the rachis; costae on large fertile rachis-branches 4½ cm apart, on smaller sterile branches 2½-3½ cm apart; fertile pinnules 16-20 cm long, widest part 3½-3.8 cm wide, costules 4-5 mm apart; lamina thin, veins raised near their bases on both surfaces when dry; 20 or more pairs of segments on each larger pinnae constricted at the base, connected by a very narrow wing along the costa, c. 3½ mm wide above the base, lowest segment sometimes quite free and shortly stalked; sori of 3-5 sporangia; stipular leaflets to 4 cm long, bipinnatifid, segments c. 1 mm wide, acuminate.

Type: Brass 27171, Ferguson Isl. (L).

Distr. *Malaysia*: SE. New Guinea (Normanby and Fergusson Islands).

Ecol. Scrambling to 7 m high in rather open forest, 800-850 m.

14. *Gleichenia sordida* COPEL. in Elmer, Leaf. Philip. Bot. 3 (1910) 798.—*G. novoguineensis* BRAUSE, Bot. Jahrb. 56 (1920) 210.—*Hicriopteris novoguineensis* COPEL. Philip. J. Sc. 75 (1941) 358.

—*Hicriopteris astrotricha* COPEL. *l.c.*—*Diplopterygium novoguineense* NAKAI, Bull. Nat. Sc. Mus. Tokyo n. 29 (1950) 54.—*G. sumatrana* HOLTT. Reinwardtia 4 (1957) 264.

Scales on dormant apex of rachis 8-10 mm long; 0.5 mm wide, light brown with dark edges bearing oblique setae; rachises and costae more or less persistently covered with a felt of stellate hairs (all dark brown or some rusty brown) and some narrow scales to 4 mm long; lower surfaces of costules and veins more or less persistently covered with stellate hairs. *Rachis-branches* 120-200 cm long, costae 2½-4½ cm apart; largest pinnules 15-20 cm long, 2½-3 cm wide, slightly deflexed or not; costules 3½-4½ mm apart; 2-8 basal segments of lamina on each pinnae constricted at the base and connected by a very narrow wing along the costa, rest separated by narrow sinuses; lamina rather thin, not glaucous beneath; veins raised on lower surface, sometimes not on upper surface; sori of 3-5 sporangia; stipular leaflets broadly deltoid, 2½-4½ cm long, their lobes c. 1 mm wide.

Type: Elmer 11423a, Mt Apo, Mindanao (H. Copel.; dupl. at US, BM).

Distr. *Malaysia*: Sumatra, Malaya, Celebes, Moluccas (Halmahera, Batjan, Morotai), Philippines (Mindanao), New Guinea, and Solomons.

Ecol. High-climbing in open forest and on forest-edge, apparently not forming thickets, 1000-2000 m.

15. *Gleichenia norrisii* METT. in Kuhn, Linnaea 36 (1869) 165; v. A. v. R. Handb. (1908) 58; C. CHR. Gard. Bull. S.S. 7 (1934) 212, *incl. var. floccigera* C. CHR.; HOLTT. Rev. Fl. Mal. 2 (1955) 67.—*Hicriopteris norrisii* CHING, Sunyatsenia 5 (1940) 280.—*Diplopterygium norrisii* NAKAI, Bull. Nat. Sc. Mus. Tokyo n. 29 (1950) 54.—Fig. 6.

Scales on apex of main rachis 2-3 mm long, narrow, medium brown, edges bearing short oblique concolorous setae; costae and costules when mature quite glabrous or bearing a few scales near the base; young rachises, costae and costules bearing scattered very narrow brown scales, small setose scales and stellate hairs with rusty brown rays; stellate hairs at first present on veins but not persistent. *Rachis-branches* 100 cm or more long; largest pinnules to 20 cm long and 3 cm wide, the costae 4-5 cm apart, distinctly deflexed, distal pinnules more acutely deflexed than basal ones; lobes of lowest pinnules usually only slightly enlarged and not stipuliform, but stipule-like leaflets, with broad blunt lobes, sometimes produced; costules 4½-5½ mm apart; lamina light green, drying light olive green without reddish tinge, thin, lower surface more or less glaucous in young plants, often not appreciably so in older ones; segments of lamina only slightly narrowed above the base, separated by sinuses not over 1 mm wide, apices broadly rounded, lowest segments much reduced but not separated from the rest; veins slender, distinctly raised on lower surface, slightly on upper surface; sori



Fig. 6. *Gleichenia norrisii* METT. on edge of forest, Penang, c. 650 m; one pair of rachis-branches showing widely spaced and deflexed pinnules (HOLTUM, 1926).

commonly of 3–5 sporangia, with *paraphyses* consisting of small scales bearing long, pale, marginal hairs.

Type: Norris, Malay Peninsula (B?; dupl. at K, BM, P).

Distr. *Malaysia*: Malay Peninsula, Sumatra (Bencoolen), and N. Borneo.

Ecol. In clearings and on edge of forest, 650–1250 m. On Penang Hill this species is abundant at 650–750 m, below the lower limit of altitude of *G. longissima*; above 750 m the latter, which forms denser thickets because of its closer pinnules, is the common species.

Note. CHRISTENSEN'S *var. floccigera* was based on immature fronds which had not lost their indumentum. The development of stipule-like leaflets varies, but they never have the narrow caudate lobes found in most other species.

16. *Gleichenia matthewii* HOLTT. *Reinwardtia* 4 (1957) 265.

*Scales* of main rachis-apex hardly  $\frac{1}{2}$  mm wide, edges with their setae shining dark brown, middle part paler; costae bearing a few scales near the base, the frond otherwise glabrous. *Rachis-branches* 70 cm or more long, strongly flexuous above the basal part; all pinnules deflexed, the upper ones at an angle to  $45^\circ$  so that each is in line with the portion of the rachis beyond it, the uppermost grading into the spreading lobes of the terminal lamina; largest pinnules 12 cm long and  $2\frac{1}{2}$  cm wide, the costae 4 cm apart; costules  $4\frac{1}{2}$  mm apart; *lamina* firm, glaucous beneath, lobed to  $1-1\frac{1}{2}$  mm from the costa, segments oblong, contiguous, almost truncate at the apex and often slightly retuse; no *sori* seen; *stipular leaflets* deltoid, 2 cm long, narrowly lobed.

Type: Matthew s.n., 31 Jan. 1912, G. Singalang (K).

Distr. *Malaysia*: Central Sumatra (Mt Singalang), twice collected, altitude 1800 m.

17. *Gleichenia brevipinnula* HOLTT. *Reinwardtia* 4 (1957) 264.

*Scales* on apex of rachis c. 5 mm long, hardly  $\frac{1}{2}$  mm wide, brown, with almost black shining edges bearing oblique setae; rachises rather persistently covered with very dark rigid stellate hairs with a few narrow scales; scattered similar hairs on costae and costules beneath, and scattered somewhat paler stellate hairs on lower surface of veins. Main *rachis* 5 mm diameter; branches 70 cm long; costae c. 2 cm apart, pinnules to 10 cm long and 2 cm wide, not or slightly deflexed; costules  $3-3\frac{1}{2}$  mm apart; *lamina* cut down to 1 mm from the costa, very firm, sinuses very narrow, edges of segments slightly toothed near apices at the ends of the veins, lower surface strongly glaucous; veins raised on both surfaces; *stipular leaflets*  $3\frac{1}{2}$  cm long, broadly deltoid, all lobes with very narrow caudate tips, lower lobes deeply and very obliquely lobed again; segments of sub-basal pinnules often with caudate tips like the stipular leaflets; *sori* of 3 or 4 sporangia.

Type: Bell 2042, Pueh Range, Sarawak (BM).

Distr. *Malaysia*: Borneo (Sarawak & N. Borneo).

Ecol. On ridges and summits of mountains, in dwarf forest or scrub, 1250–2500 m. Fronds are reported up to  $2\frac{1}{2}$  m long.

18. *Gleichenia blotiana* C. CHR. Bull. Mus. Hist. Nat. Paris II, 6 (1934) 103.—*Hicriopteris blotiana* CHING, *Sunyatsenia* 5 (1940) 279.—*Diplopterygium blotianum* NAKAI, Bull. Nat. Sc. Mus. Tokyo n. 29 (1950) 49.

*Scales* on dormant apex of rachis nearly black, edges bearing oblique black setae; scales on growing main rachis usually with a paler median band; rachis-branches when young bearing many dark stellate hairs with rigid rays (so close that hairs touch each other but do not completely obscure surface of rachis) and also very narrow ciliate scales 2 mm long and some long lax multicellular hairs; a similar indumentum on upper surface of costae at first, later deciduous; indumentum on lower surface of costae and costules mostly of dark rigid stellate hairs, with a few scales at bases of costae; dark stellate hairs scattered abundantly on veins and lamina beneath, persistent. *Main rachis-branches* c. 150 cm long, the lowest pinnules stipule-like,  $3\frac{1}{2}$  cm long, deltoid, with very narrow deeply pinnatifid basal lobes; pinnules commonly 20 cm long, 3–4 cm wide, the base of the costa distinctly deflexed as in *G. norrisii*; costae 4–5 cm apart, costules c. 5 mm apart; segments of lamina  $3\frac{1}{2}$ –4 mm wide, rather thin, their apices broadly rounded and sometimes retuse; veins distinctly raised on upper surface and slightly so below; *sporangia* 3–4 in each sorus.

Type: Pételot 3900, near Chapa, Indo-China (BM; dupl. at P).

Distr. Indo-China and S. China, in *Malaysia*: Malay Peninsula, once collected.

Ecol. In the Malay Peninsula on edge of forest in a thicket with *G. longissima*, at 1500 m.

19. *Gleichenia conversa* v. A. v. R. Bull. Jard. Bot. Btzg II, n. 20 (1915) 17; Handb. Suppl. (1917) 81; BACKER & POSTH. *Varenfl. Java* (1939) 255.—*Diplopterygium conversum* NAKAI, Bull. Nat. Sc. Mus. Tokyo n. 29 (1950) 49.—Fig. 4h–j.

Differs from *G. norrisii* as follows: *scales* on rachis-apex brown with almost black edges; some rather light brown stellate hairs often persistent on costules and sides of costae; largest pinnules to 25 cm long and 4 cm wide; distal pinnules not appreciably deflexed; *segments of lamina* separated by sinuses about 2 mm wide; lamina and rachises drying rather red-brown, lamina usually thicker than in *G. norrisii*; veins usually not at all raised on upper surface (slightly so in specimens with thin lamina); *stipular leaflets* well developed, the lobes narrow.

Type: Hasskarl, Kandang Badak, G. Gedeh (Bo; dupl. at L).

Distr. *South Malaysia*: Java and Lesser Sunda Islands (Flores).

Ecol. In open places in forest and on forest-edges, 900–2400 m.

3. Subgenus *Mertensia*

HOOK. Sp. Fil. 1 (1844) 6, *pro* § 2; HOLTT. Reinwardtia 4 (1957) 266.—*Mertensia* WILLD. Kongl. Vet. Ak. Nya Handl. 25 (1804) 163, *p.p.*, non ROTH 1797.—*Gleichenia* subg. *Mertensia* sect. *Holopterygium* DIELS in E. & P. Pfl. Fam. 1, 4 (1900) 353.—*Dicranopteris* (non BERNH.) UND. Bull. Torr. Bot. Cl. 34 (1907) 249, *p.p.*—*Gleichenia* subg. *Mertensia* sect. *Dicranopteris* v. A. v. R. Handb. (1908) 56, *p.p.*—*Sticherus* PRESL, Tent. Pterid. (1836) 51; CHING, Sunyatsenia 5 (1940) 281; COPEL. Gen. Fil. (1947) 27; NAKAI, Bull. Nat. Sc. Mus. Tokyo n. 29 (1950) 7.—*Sticherus* § *Eu-Sticherus* C. CHR. in Verdoorn, Man. Pterid. (1938) 530.—*Mesosorus* HASSK. Fil. Jav. 1 (1856) 2, *p.p.*—Fig. 7–10.

Primary rachis-branches each ending in a dormant apex which lies in the angle between a pair of secondary branches; secondary branches behaving similarly, the process usually repeated to produce pseudo-dichotomous branching of several orders; ultimate branches simply deeply pinnatifid, the venation of segments of the lamina and sori as in subg. *Diplopterygium*; penultimate branches (often also

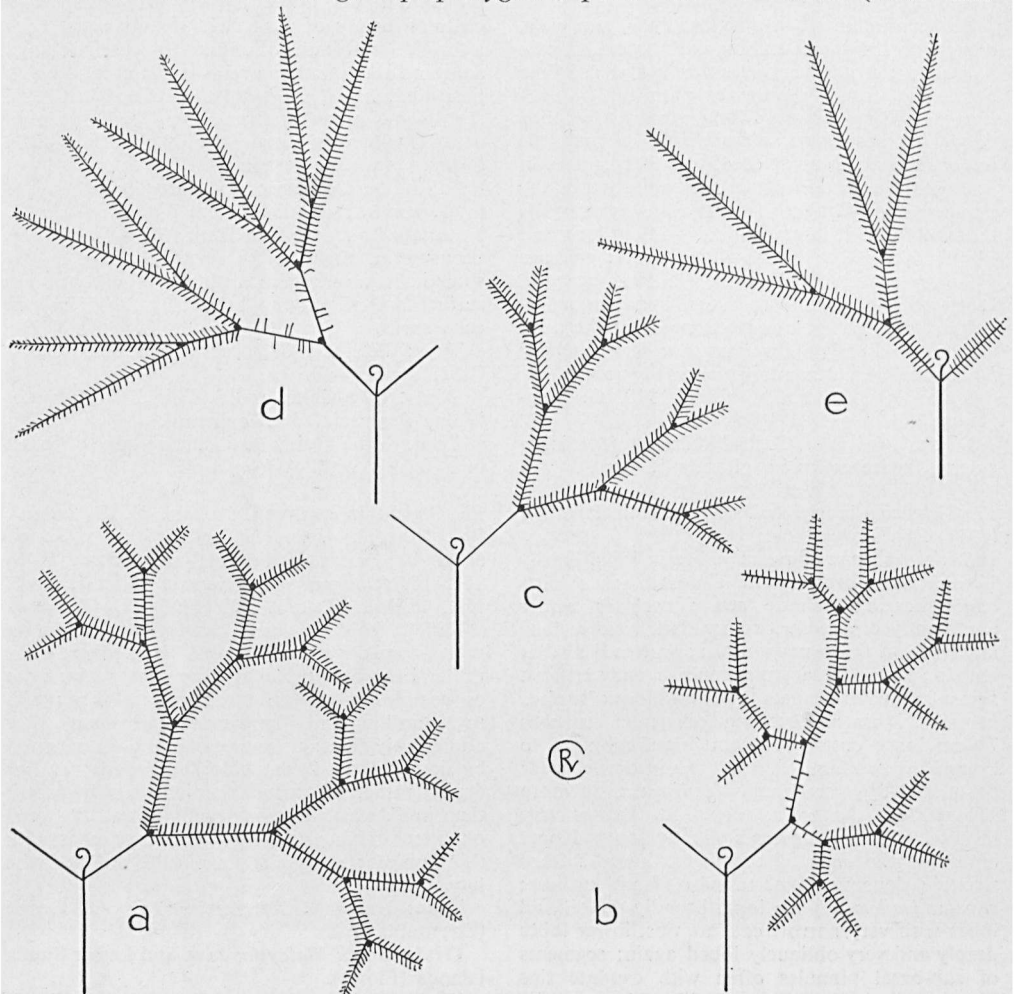


Fig. 7. Diagrams showing branching habit of species of *Gleichenia* subg. *Mertensia*. a. *G. truncata* (WILLD.) SPR., b. *G. milnei* BAK., c. *G. hispida* METT., d. *G. hirta* BL., e. *G. vestita* BL.



branches of lower orders) more or less completely provided with a deeply pinnatifid lamina like that of the ultimate branches.

Notes. This subgenus includes far more species than any other major division of the family, in all continents, and its distribution is mainly south of the equator. Most of the species are rather small in size, as compared with representatives of *subg. Diplopterygium*, and could not compete as thicket-forming ferns either with the latter or with *Dicranopteris*. The only Malaysian species which can so compete is *G. truncata*, and it is also the only species of *subg. Mertensia* which occurs at sea-level in our region. The others are mountain plants occurring in scrub and dwarf forest of high ridges or in open grassy or rocky places, which are comparable with the habitats of related species in south temperate regions.

As in other divisions of the family, the characters and distribution of scales and hairs are important diagnostically in this subgenus. The number of times the lateral branch-systems are forked (the number of orders of forking) is probably important, but shows considerable variation within a species according to the age of the plant and to environmental conditions, and these cannot be fully judged from dried specimens. A more important kind of character is the relative length of branches of the first and ultimate orders. But in some species one frond will have branch-systems forked to 2 orders with long ultimate branches, other fronds (even part of the same frond) may be forked to 3 orders with much shorter ultimate branches. The glaucous character of the lower surface of the lamina may be significant, but is easily destroyed by heat in drying. In all these characters, and in all species, more field study is needed to establish distinctions between species more clearly.

Judging from anatomical characters, CHRYSLER (Am. J. Bot. 31, 1944, 483-491) has argued that *subg.*

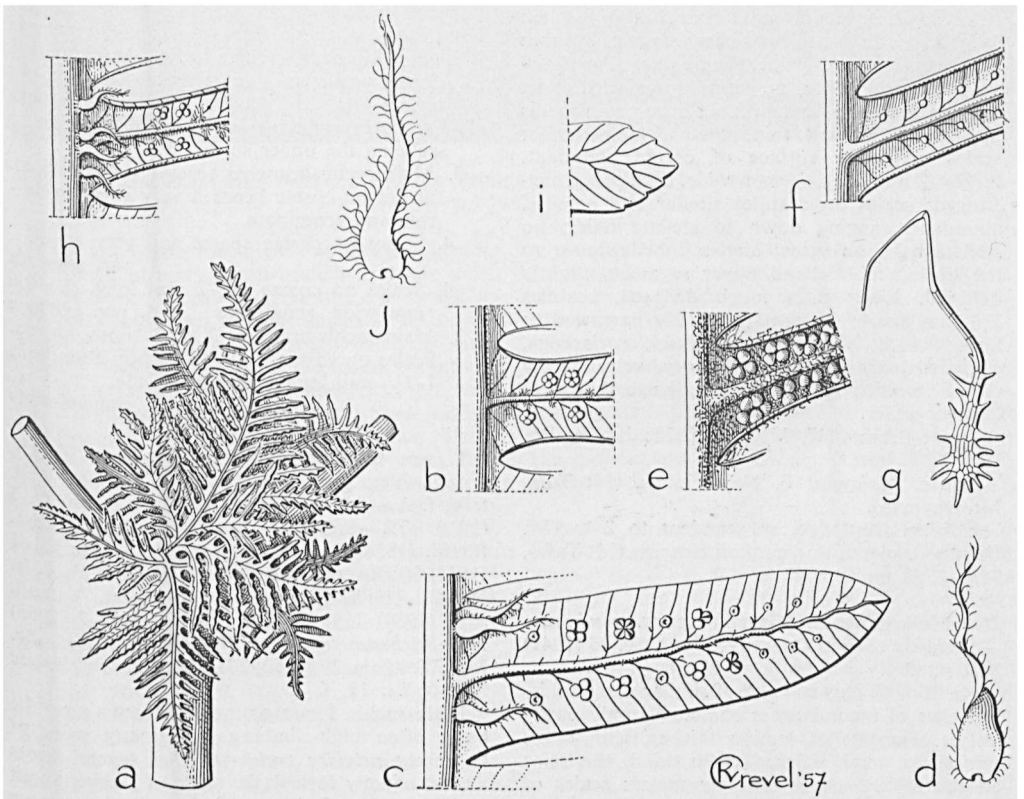


Fig. 8. *Gleichenia truncata* (WILLD.) SPR. a. Stipular leaflets at main branching, nat. size, b. lower surface of part of frond,  $\times 4$ . - *G. vestita* BL., c. Lower surface of a large segment of lamina,  $\times 4$ , d. a single scale from costa,  $\times 8$ . - *G. hispida* METT., e. Lower surface of part of frond, showing sori and hair-pointed scales,  $\times 8$ , f. same with scales and sporangia removed, g. a single scale from costa,  $\times 22$ . - *G. hirta* BL. h. Lower surface of part of frond,  $\times 4$ , i. tip of a segment of the lamina, showing toothed edge, j. a scale from the costa,  $\times 20$ .

*Mertensia* is the most primitive division of the genus. But from the point of view of sporangia and sori it is exactly in equality with *subg. Diplopterygium*, and in leaf-form it is clearly more highly organized (in having a branching-pattern dependent on a series of permanently dormant apices). It seems to me significant that among fossils none are clearly referable to this subgenus, whereas there are abundant fossils having a close resemblance to *subg. Diplopterygium*. An apparent exception is *Gleichenites gracilis* ZIGNO. But the branching-pattern of this fossil is very irregular and there is no clear evidence of pseudo-dichotomy; I think that its resemblance to *subg. Mertensia* is superficial.

20. *Gleichenia reflexipinnula* C. CHR. Brittonia 2 (1937) 27.—*Sticherus reflexipinnula* COPEL. Philip. J. Sc. 75 (1941) 355.

Rhizome 5 mm diameter, covered when young with dark brown shining acuminate scales hardly 1 mm wide at the base, when old closely warty; stipe 30 cm or more long, scaly and then warty like the rhizome near the base; main *rachis* bearing 2 or more pairs of primary branches, with deeply pinnatifid stipular leaflets 2–4 cm long at bases of branches; primary branches once or twice forked, leafy down to the junction with the main *rachis*, not proliferous beyond the first fork; angle of ultimate forks rather less than a right angle; ultimate branches to *c.* 20 cm long and 3½–4 cm wide (shorter if primary branch is twice forked), penultimate branches 3½–9 cm long; *scales* on resting apex of main *rachis* 3½ mm long, less than 1 mm wide, acuminate but not hair-pointed, rather thin, medium brown with short sparse fringe of paler hairs; *scales* on main *rachis* persistent, abundant, thin, pale and long-fringed; *scales* on lower surface of costae abundant, largest 2 mm long, ½ mm wide, thin, pale, long-fringed; *scales* on costules similar and smaller, abundant, ranging down to stellate hairs; no stellate hairs on veins; *lamina* lobed almost to the costa, middle and upper segments slightly deflexed, lower ones much deflexed, costules 3½ mm apart; segments gradually narrowed to apex (which is sometimes retuse), coriaceous, edges strongly revolute when dry, veins hardly raised on either surface; *sporangia* usually 4, sori close together.

Type: Brass 4847, Mt Tafa (BM; dupl. at Bo, US).

Distr. *Malaysia*: E. New Guinea (Mt Tafa, Mt Dayman).

Ecol. Forest-edge, subsucculent to 2 m (Mt Dayman), plentiful in summit clearing (Mt Tafa), 2230–2700 m.

21. *Gleichenia venosa* (COPEL.) HOLTZ., *comb. nov.*—*Sticherus venosus* COPEL. Philip. J. Sc. 75 (1941) 356, pl. 5.

Habit of *G. truncata* and of similar size (*rachis*-branches of second order sometimes only partly leafy); segments of *lamina* thicker, with edges sometimes much reflexed when dried, the veins on the lower surface strongly raised; *scales* of apex of main *rachis* similar to those of *G. truncata*; *scales* on costae abundant and persistent, dark rusty-brown, to 1½ mm long and more than ½ mm wide, fringed; *scales* on costules similar but smaller, very abundant, spreading and closely overlapping so as completely to cover lower surface of *lamina*; smaller *scales* also present

throughout on *rachises*, persistent as a continuous rusty covering at and just below the forks.

Type: Brass 12348, Idenburg River (H. Copel.; dupl. at Bo, BM, L).

Distr. *Malaysia*: New Guinea.

Ecol. Thickets in open places, scrambling to 2–3 m, 1600–2700 m.

22. *Gleichenia truncata* (WILLD.) SPR. Syst. Veg. ed. 16, 4 (1827) 25; HOLTZ. Reinwardtia 4 (1957) 271.—See for further synonyms under the varieties.—Fig. 7a, 8a–b, 9.

#### KEY TO THE VARIETIES

1. Additional stipular leaflets present about 1 cm below main and first lateral forks of *rachis*, as well as just above forks . . . . . 2. *var. bracteata*
1. Such additional stipular leaflets lacking.
2. Costae persistently densely scaly on the upper surface . . . . . 4. *var. involuta*
2. Costae at most sparingly and not persistently scaly on the upper surface.
3. Main *rachis*-branches several times forked. Scales on costae beneath very small or narrow and acuminate.
4. Scales on costae sparse and very small. . . . . 1. *var. truncata*
4. Scales on costae 1½–2 mm long, 0.3–0.6 mm wide, acuminate . . . . . 5. *var. celebica*
3. Main *rachis*-branches 2 or 3 times forked. Scales on costae beneath rather abundant, 1–1½ mm long, 0.7–1 mm wide. . . . . 3. *var. plumaeformis*

1. *var. truncata*.—*Mertensia truncata* WILLD. Kongl. Vet. Ak. Nya Handl. 25 (1804) 169, t. V, f. A.—*Mertensia laevigata* WILLD. Sp. Pl. 5 (1810) 75.—*Sticherus laevigatus* PRESL, Tent. Pterid. (1836) 52.—*G. laevigata* HOOK. Sp. Fil. 1 (1844) 10; RACIB. Fl. Btzig 1 (1898) 11; v. A. v. R. Handb. (1908) 59; BACKER & POSTH. Varenfl. Java (1939) 255; HOLTZ. Rev. Fl. Mal. 2 (1955) 71.—*Sticherus truncatus* NAKAI, Bull. Nat. Sc. Mus. Tokyo n. 29 (1950) 20.—*Sticherus myriapoda* NAKAI, l.c. 12, f. 1.

Main *rachis* 8 mm or more diameter near the base, often high-climbing with many pairs of branches; *primary rachis*-branches several times almost equally forked, the angle of forking about a right angle, of ultimate forks sometimes more than 90°; basal segment of primary *rachis*-branch leafless (apart from stipular leaflets), branches of second and later orders usually all leafy, length of each branch from one fork to the next commonly 10–15(–20) cm; *stipular leaflets* usually present at base of primary branch and at its first fork,



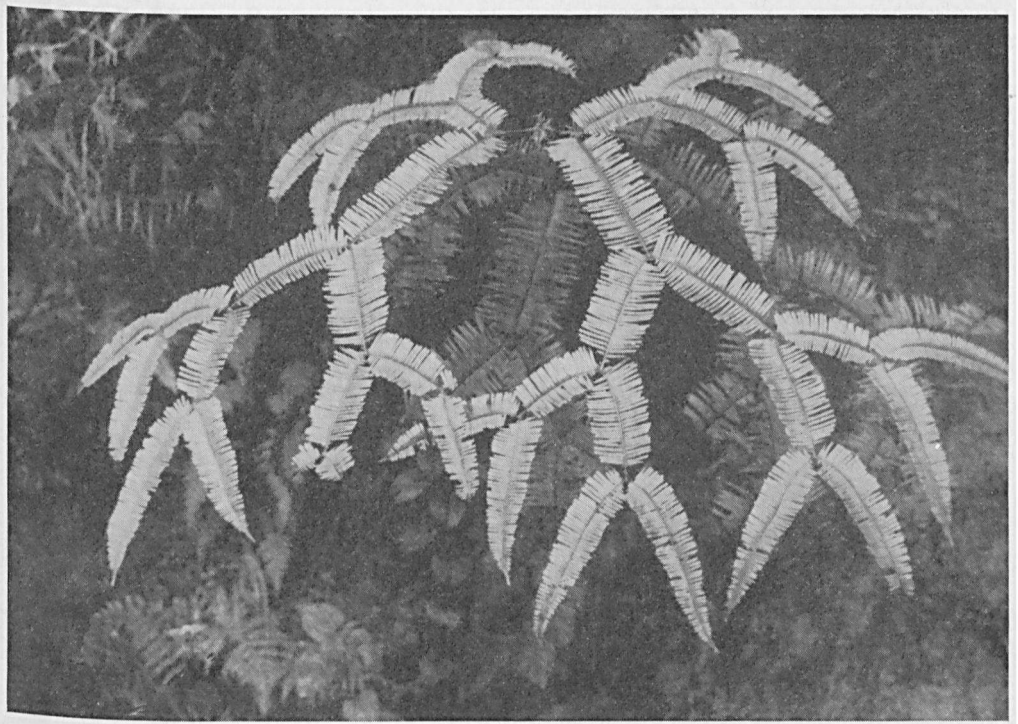


Fig. 9. *Gleichenia truncata* (WILLD.) SPR. on Taiping Hills, Malaya, by roadside, c. 1200 m (HOLTUM, 1952).

deltoid and deeply lobed (basal lobes again lobed), at base of primary rachis-branch to 3 cm long, at next fork  $1\frac{1}{2}$  cm long; lamina cut almost to the costa into lobes at right angles to the costa; lobes rather irregular in length even on same branch, longest on lowest branches, commonly  $2-3\frac{1}{2}$  cm long (to 5 cm) and about  $2\frac{1}{2}$  mm wide (to 3 mm), costules 3-4 mm apart; lower surface not glaucous, veins dark when dry, slightly raised; veins on upper surface not raised when dry, concolorous; sori of 3-5 sporangia, surrounded by pale hairs. Scales on smaller dormant apices mostly very small, often not more than 1 mm long, rusty brown, of varying shape, fringed; on larger apices also some very narrow scales; scales on costae very small, long-fringed, at first rather abundant; very short simple hairs, often shrivelled and black when old, present on lower surface of costules, veins and lamina.

Type: Herb. Willd. (B).

Distr. Throughout *Malaysia*, apparently most abundant in the west.

Ecol. On edges of forest, often climbing to a considerable height, 0-1600 m, growing with varieties of *Dicranopteris linearis*, also in thickets at higher altitudes.

Note. The original specimen of *Mertensia truncata* WILLD. had incompletely expanded lamina-lobes, which thus appeared to be truncate.

*Sticherus myriapoda* NAKAI was described from

a plant in the Riouw Archipelago differing only from typical *var. truncata* in having a twining main rachis. Such a condition has also been observed in one plant in Johore, but is not general in this variety. Experimental culture is desirable to decide whether the twining condition is genetically controlled. The Johore plant had rachises twining both to the left and to right, and the length of rachis making one complete turn round the support was about 20 cm. NAKAI described a closer spiral.

2. *var. bracteata* (BL. ex HOOK. & BAKER) HOLTUM. *Reinwardtia* 4 (1957) 271.—*G. bracteata* BL. ex HOOK. & BAKER, *Syn. Fil.* (1865) 14 (as synonym but with descr.)—*G. laevigata var. bracteata* v. A. v. R. *Handb. Suppl.* (1917) 85.

Lamina-segments commonly less than 2 mm wide, 10-18 mm long; additional *stipular leaflets* present about 1 cm below main and first lateral forks of rachis, on the outside.

Type: Blume, Java (L; dupl. at K).

Distr. *Malaysia*: Java, Flores, S. Celebes.

Ecol. On edges of forest, apparently abundant at 1000-1600 m; extremes of altitude recorded 600 and 2000 m.

3. *var. plumaeformis* (PRESL) HOLTUM. *Reinwardtia* 4 (1957) 272.—*Mertensia plumaeformis* PRESL, *Abh. (K.) Böhm. Ges. Wiss. M.-N. Cl. V.*

5 (1848) 338; Epim. Bot. (1851) 24, t. 15.—*Sticherus plumaeformis* NAKAI, Bull. Nat. Soc. Mus. Tokyo n. 29 (1950) 25.

*Primary rachis-branches* once or twice forked, 3–6 cm to first fork (this part almost or quite leafless), ultimate branches up to 25–35 cm long; costae usually bearing rather numerous, thin, broad, almost entire *scales* 1–1½ mm long, 0.7–1 mm wide, on lower surface.

Type: Cuming 377, Malacca (PRC; dupl. at K, BM, P, L, F).

Distr. *Malaysia*: Sumatra, Malay Peninsula, Borneo (?).

Ecol. In open places on mountains, 1200–1800 m. As seen by me in W. Sumatra this variety does not form long climbing fronds.

**4. var. involuta** HOLTT. Reinwardtia 4 (1957) 272.

*Primary rachis-branches* 3 times forked; ultimate branches sometimes much longer than lower ones; ultimate forks forming an angle of rather less than 90°; upper surfaces of costae densely scaly, scales persistent, 1 mm long, pale-fringed; lower surfaces of costae bearing *scales* ½ mm long; edges of dried lamina-lobes much revolute.

Type: J. Winkler; Rosenst. Fil. Sum. Exsic. 182 (L; dupl. at BM, P).

Distr. *Malaysia*: N. Sumatra (Karo Plateau).

**5. var. celebica** HOLTT., var. nov.

*Primary rachis-branches* 3 times equally forked, ultimate and penultimate branches leafy, angle of ultimate forks less than a right angle, segments of lamina c. 2 cm long; *scales* on lower surface of costae copious, acuminate, fringed, c. 1½–2 mm long, 0.3–0.6 mm wide.

Distr. *Malaysia*: Central Celebes, altitude 2600–3000 m (once collected).

**23. *Gleichenia milnei*** BAKER, Syn. Fil. (1874) 449; Hook. Ic. Pl. t. 1602; HOLTT. Reinwardtia 4 (1957) 270.—*G. kajewskii* COPEL. Philip. J. Sc. 60 (1936) 102, pl. 6.—*Sticherus milnei* CHING, Sunyatsenia 5 (1940) 284.—*Sticherus kajewskii* COPEL. Gen. Fil. (1947) 27.—Fig. 7b.

General aspect of *frond* as in *G. truncata* (in its wide forkings and narrow lamina-segments at right angles to the costa), but at each fork (apart from forks of main rachis) one branch larger than the other, larger branches alternately to left and right and successive larger branches almost in line with each other; ultimate branches, and branches of 2–3 lower orders leafy; leafy branches in general 2½–3½ cm wide (lower ones to 4½ cm), lamina-segments 2–3 mm wide, costules 3–5 mm apart; *scales* as in *G. truncata*; additional *stipular leaflets* often present outside the lower forks, as in *G. truncata* var. *bracteata* but nearer the forks.

Type: Milne 341, New Hebrides (K).

Distr. *Malaysia*: Celebes, ? Philippines (?Luzon), Moluccas, New Guinea, Admiralty Islands, Solomon Islands, New Hebrides.

Ecol. Altitude 100–1400 m.

**24. *Gleichenia oceanica*** KUHN, Verh. K. K. Zool.-Bot. Ges. Wien 19 (1869) 583; non CHRIST, Ann. Jard. Bot. Btzig 15 (1898) 76; v. A. v. R. Handb. (1908) 60; Suppl. (1917) 85, 497; COPEL. Univ. Cal. Publ. Bot. 12 (1931) 388.—*Sticherus oceanicus* ST JOHN, Occ. Pap. Bish. Mus. 17 (1942) 81.

Habit and scaliness of *G. truncata*, but the forkings of the rachis-branches much less than a right angle (ultimate forks often less than 45°), the lamina glaucous beneath, its segments distinctly oblique and commonly less than 2 cm long (often not more than 1½ cm); *primary rachis-branches* of large fronds 5 times forked, with deltoid stipular leaflets at their base, of smaller fronds sometimes only 3 times forked and lacking stipular leaflets.

Type: Herus 66, Aneityum, New Hebrides (B).

Distr. Melanesia (New Hebrides, Fiji, Samoa), may occur in *East Malaysia*.

Note. The SARASIN specimens from Celebes referred to this species by CHRIST (*l.c.*) are *G. hispida* and *G. hirta* var. *paleacea*; I have not seen the WARBURG specimen.

**25. *Gleichenia erecta*** C. CHR. Brittonia 2 (1937) 269; HOLTT. Reinwardtia 4 (1957) 268.—*Sticherus erectus* COPEL. Philip. J. Sc. 75 (1941) 353.—*Sticherus habbemensis* COPEL. *l.c.* 355, pl. 3.

Rhizome 2½–4 mm diameter, young parts covered with thin brown ciliate scales to 3 mm long and 1 mm wide, old parts closely warty; stipe at first scaly, then warty, near the base, like the rhizome, rest smooth, 12–40 cm long; *frond* bearing one or more pairs of primary branches which are simple or once or twice forked, sometimes proliferous beyond the first pair of secondary branches; if twice forked, the first-order branch 2–3 cm long, bearing a stipular lobed leaflet 15 mm long and sometimes 1 or 2 other lamina-segments but not fully leafy, the second-order branch 3–6 cm long, fully leafy; angle of ultimate forks less than 45°; ultimate branches 12–30 cm long, largest *lamina-segments* commonly 15–23 mm long, sometimes to 40 mm, rather coriaceous, entire, edges much reflexed when dry, abruptly narrowed just above the base, the rest 2–2½ mm wide when flattened, tapering to apex, lower surface glaucous; veins not raised on either surface; costules 3–4 mm apart (lowest ones on large fronds to 5 mm apart), basal part at 60–70° to the costa, distal part often falcate when dry; *scales* on resting apices of main rachis like those on base of stipe but more finely fringed; some persistent scales on lower surface of costae, 1½ mm long, ½ mm wide, shortly hair-pointed, edges fringed at least towards the apex (these scales sometimes very pale with a darker base); scales on costules very small and long-fringed; pale-rayed stellate hairs on veins, their red-brown bases sometimes persistent; *sori* of 3–4 sporangia.

Type: Brass 4591, Murray Pass, Wharton Range, Papua (BM; dupl. at K, Bo, US).

Distr. *Malaysia*: New Guinea.

Ecol. In open places, in peaty grassland, and on wet clay-soil of land-slips, 1000–3225 m.

26. *Gleichenia pulchra* (COPEL.) HOLTT. Reinwardtia 4 (1957) 271.—*Sticherus pulcher* COPEL. Philip. J. Sc. 75 (1941) 355, pl. 4.

Main *rachis* slender, bearing several pairs of branches, each primary branch bearing up to at least 3 pairs of secondary branches, each secondary branch simple or once forked; only ultimate branches leafy, except sometimes where a secondary branch is forked, in which case the penultimate branch may bear a few lamina-lobes; ultimate branches to 20 cm long and  $2\frac{1}{2}$  cm wide (to 3 cm wide if a simple secondary branch), *lamina* lobed almost to the costa, segments very slightly oblique, 3 mm wide above the base, costules 4 mm apart; veins slightly raised on lower surface, on upper surface only at the base of each vein; lower surface glaucous when living (not clearly so on dried specimens available); *scales* on main dormant apices small, on lower surface of costae  $\frac{1}{2}$ –1 mm long, firm, dark brown with a pale fringe; scales on lower surface of costules abundant, small, long-fringed; many small rusty-brown stellate hairs on lower surface of veins and on lamina.

Type: Brass 12351, Idenburg River (H. Copel.; dupl. at BM, L).

Distr. *Malaysia*: New Guinea (NW. part, once collected, SE. part, doubtful).

Ecol. Scrambling in mossy forest, 1650 m.

27. *Gleichenia pseudoscandens* v. A. v. R. Nova Guinea 14 (1924) 24.—*Sticherus pseudoscandens* COPEL. Philip. J. Sc. 75 (1941) 356.

Fronds to 4 m long, with several pairs of primary branches; primary branch-systems usually with 3 orders of forking, the *primary branch* sometimes proliferous beyond its first pairs of branches, only the ultimate branches leafy; ultimate branches to 40 cm long, lower ones 10–20 cm long; costules  $5\frac{1}{2}$ –6 mm apart, at right angles to the costa or nearly so; segments of lamina 17–25 mm long, 3 mm wide above the base, *lamina* firm, drying dark, veins not raised on either surface; *scales* on resting apex of main *rachis* 4–5 mm long, rigid, dark, very narrow, with short oblique marginal setae; scales on lower surface of costae dark and small, almost entire, mostly deciduous leaving the surface warty; very short hairs copious on lower surface of lamina and on costules; some hairs with the sporangia.

Type: Lam 1935, Doorman summit (U; dupl. at L, Bo, BM).

Distr. *Malaysia*: NW. New Guinea, once collected.

Ecol. Altitude 2480 m.

28. *Gleichenia alstonii* HOLTT. Reinwardtia 4 (1957) 267.

Main *rachis* 4 mm diameter; primary branch-systems usually with forking of two orders, only the ultimate branches leafy; primary branches rarely proliferous beyond the first fork; branches of first order 4–5 cm long, of second order 6–7 cm long; ultimate branches 30–35 cm long,  $3\frac{1}{2}$  cm wide, the basal 10–15 mm sometimes

bare of lamina; costules 4 mm apart, slightly oblique; segments of *lamina* c. 17 mm long, 3 mm wide above the base, thin, apices entire or nearly so, veins slightly prominent on both surfaces; *sori* of 3–4 sporangia. *Scales* on dormant apex of *rachis* 4 mm long, 0.7 mm wide, narrowly acuminate, brown, with short spreading pale marginal hairs near base, dark oblique sparse setae towards apex; scales on lower surface of costae scattered, dark,  $1\frac{1}{2}$  mm long, 0.2 mm wide, edges with sparse oblique dark hairs; scales on lower surface of costules pale, very narrow; scattered pale lax stellate hairs on lower surface of veins.

Type: Alston 14981, Lae Pandom (BM).

Distr. *Malaysia*: N. Sumatra (Tapanuli), once collected.

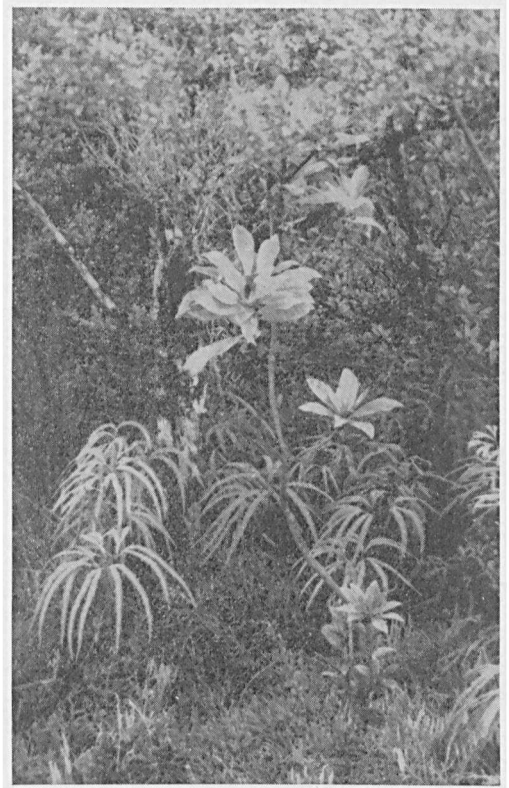


Fig. 10. *Gleichenia vestita* BL. on ridge with ericoid ridge forest from Poka Pindjang to Rante Mario in the Latimodjong Range, Central Celebes, c. 3000 m (1937).

29. *Gleichenia vestita* BL. En. Pl. Jav. (1828) 249; RACIB. Fl. Btzg 1 (1898) 11; v. A. v. R. Handb. (1908) 61; Suppl. (1917) 86; BACKER & POSTH. Varenfl. Java (1939) 255.—*Sticherus vestitus* CHING, Sunyatsenia 5 (1940) 285.—Fig. 7e, 8c–d, 10.

*Rachis* of a well-grown frond bearing several

pairs of primary branches, usually without *stipular leaflets* at their base; primary branch-systems usually forked to 2 orders (rarely 3), primary branch not proliferous beyond its first fork; all branches leafy, down to junction with main rachis; angle of forks about 45°; ultimate branches 15–25 cm long, lower ones 5–7 cm long; *lamina* cut down to within 1 mm of costa, segments distinctly oblique, thin but very rigid, 8–12 mm long, not narrowed immediately above the base but tapering very gradually, then abruptly to broadly pointed or rounded entire apex, edges not usually much reflexed, lower surface glaucous; costules 4–5 mm apart; veins slightly raised on both surfaces; *sori* of 3–5 sporangia, without evident paraphyses. *Scales* on dormant apex of main rachis firm, rusty to rather dark brown, 4–5 mm long, more than 1 mm wide, gradually narrowed to hair point, edges rather sparsely obliquely ciliate towards apex; scales on lower surface of costae abundant and persistent, spreading, rusty brown, 0.6–1.2 mm wide, 2–3 mm long, ciliate towards hair-pointed apex; smaller scales few, stellate hairs quite lacking; very short reddish simple hairs frequent on costules and veins beneath.

Type: Blume, Java (L; dupl. at K).

Distr. *Malaysia*: Sumatra, Java, S. Celebes.

Ecol. In open alpine forest and scrub, 2300–2800 m.

Note. At high elevations and in exposed places, fronds may be smaller than above described, with branches of first and second order only 2–3 cm long.

30. *Gleichenia bolanica* ROSENST. in Fedde, Rep. 12 (1913) 162; v. A. v. R. Handb. Suppl. (1917) 86.—*G. monticola* RIDL. Trans. Linn. Soc. Bot. 9 (1916) 252.—*G. subulata* v. A. v. R. Nova Guinea 14 (1924) 23.—*Sticherus bolanicus* COPEL. Philip. J. Sc. 75 (1941) 352.—*Sticherus monticola* NAKAI, Bull. Nat. Sc. Mus. Tokyo n. 29 (1950) 23.

Lateral branch-systems of well-grown fronds with forks to 4th order; primary branches not normally proliferous beyond first fork nor bearing stipular leaflets at their base; ultimate branches 7–20 cm long, 6–10 mm wide, lower branches 1–2 cm long; usually only ultimate and penultimate branches leafy, but lower ones sometimes partly leafy; *lamina* cut almost down to the costa, segments apparently triangular because of their much-reflexed edges, 3 mm wide at the base, rather thick and very rigid when dry, lower surface glaucous with slightly raised veins; costules slightly oblique; *sori* often very crowded, of 3–6 sporangia. *Scales* on dormant apex of main rachis rigid, dark and shining, 3–4 mm long, to 0.7 mm wide, apex not hair-pointed, marginal hairs short, oblique, rigid; scales on lower surface of costae abundant, to 2 mm long, not hair-pointed, base 0.5–0.7 mm wide, brown at base and pale distally, edges bearing short hairs which are sometimes very rigid and dark brown; small similar scales or stellate hairs on costules and veins.

Type: Keysser B. 14, Mt Bolan, New Guinea (B).

Distr. *Malaysia*: New Guinea.

Ecol. In open scrub or rocky places, fronds to 2 m or more long, 2800–3950 m.

31. *Gleichenia hispida* METT. ex KUHN, Verh. K. K. Zool.-Bot. Ges. Wien 25 (1875) 600; RACIB. Fl. Btzig 1 (1898) 12; v. A. v. R. Handb. (1908) 61; BACKER & POSTH. Varenfl. Java (1939) 255; HOLTZ. Reinwardtia 4 (1957) 270.—*G. koordersii* CHRIST, Ann. Jfrd. Bot. Btzig 15 (1898) 76, pl. 13, f. 1.—*Sticherus caudatus* COPEL. Philip. J. Sc. 75 (1941) 354, pl. 2.—*Sticherus hispidus* COPEL. Gen. Fil. (1947) 27.—*Sticherus pinnatus* COPEL. Philip. J. Sc. 83 (1954) 98, pl. 3.—Fig. 7c, 8e–g.

Well-grown fronds with several pairs of primary branches which are not proliferous beyond their first fork and have no *stipular leaflets*; lateral branch-systems with forks to 2nd or 3rd order; branches of first order leafless or only partly leafy, rest fully leafy; first order branches 2½–6 cm long, second order branches 5–12 cm long; from second-order fork to end of ultimate branches (whether 2 or 3 forks present) 20–30 cm, the third fork (if present) about the middle of this length; *lamina* cut almost down to the costa, the segments slightly oblique, coriaceous, stiff and rigid when dry with much-recurved edges, longest segments on lower branches to 3½ cm long, on ultimate branches sometimes only 1 cm long, effective width when dry 1½–2½ mm, costules 3–4 mm apart; lower surface of lamina more or less glaucous, veins dark and slightly prominent, not raised on upper surface; *sori* of 3 or 4 sporangia with rather long crisped rusty hairs. *Scales* on dormant apex of main rachis rusty brown, 5–7 mm long, 0.5 mm wide, narrowed above the base and for the most part very narrow, hair-pointed; scales on lower surface of costae only a few cells wide at the base, the hair-point forming at least half of the length, hair-points crisped and entangled with those of other scales; scales on costules similar and smaller, grading to stellate hairs on veins and edges.

Type: Jagor 558, G. Galungung (B; not seen). Syntype: De Vries, Ternate (dupl. at U).

Distr. *Malaysia*: Sumatra, Java, Bali, N. Celebes, Ternate, and Philippines (Negros, Luzon).

Ecol. In thickets in open places, 1000–2200 m.

Note. Isolated plants in exposed places may have fertile fronds much smaller and less branched than those described; *Sticherus pinnatus* COPEL. appears to represent a condition of this species with unbranched fertile fronds.

32. *Gleichenia brassii* C. CHR. Brittonia 2 (1937) 271.—*Sticherus brassii* NAKAI, Bull. Nat. Sc. Mus. Tokyo n. 29 (1950) 15.

Rhizome 6 mm diameter, strongly warty from bases of old scales, young parts scaly, scales 5 mm long, 1 mm wide, ciliate; stipes to 100 cm long, persistently scaly throughout but only warty near the base, scales of all sizes with rather copious pale fringe, the longest ones hair-pointed; main rachis to about 200 cm long, bearing several pairs

of primary branches which lack stipular leaflets; lateral branch-systems with forks of 2 orders, ultimate and penultimate branches fully leafy, ultimate forks less than 90°; first and second order branches 12–15 cm long, ultimate branches 30–40 cm long and 4–4½ cm wide; costules about 5 mm apart, at right angles to costae; *segments of lamina* 3 mm wide above the base, firm, edges more or less revolute when dry, lower surface not glaucous when dry; veins slightly prominent on lower surface, not on upper surface except their bases; *sori* of 3–4 sporangia without evident paraphyses. *Scales* on dormant apex of main rachis like those on rhizome but thinner, edge shortly ciliate, apex a short hair; scales on lower surface of costae spreading, 1½–2 mm long, 0.5 mm wide, thin, brown, darker at the base, shortly hair-pointed, closely fringed with spreading pale hairs; scales on lower surface of costules abundant, ½–1 mm long, rusty brown with long pale fringe; upper surface of costae raised and terete, bearing persistent small pale long-fringed scales, rest of upper surface glabrous; lower surface of veins bearing many very short simple hairs.

Type: Brass 4922, Mt Tafa (BM; dupl. at Bo).

Distr. *Malaysia*: New Guinea (Mts Arfak and Iafa).

Ecol. Scrambling in open places in forest, 1550–2400 m.

33. *Gleichenia loheri* CHRIST, Bull. Herb. Boiss. II, 6 (1906) 1009; v. A. v. R. Handb. (1908) 796; HOLTT. Reinwardtia 4 (1957) 272.—*Sticherus loheri* COPEL. Gen. Fil. (1947) 27.—*Sticherus perpaleaceus* COPEL. Philip. J. Sc. 81 (1952) 3.

var. *loheri*.

Lateral branch-systems with forks of 1, 2 or 3 orders, ultimate and penultimate branches fully leafy, angle of ultimate fork much less than a right angle; with forks of 1 or 2 orders, penultimate branches 5–7 cm long, ultimate branches 17–23 cm long; with forks of 3 orders, ultimate and penultimate branches together 17–20 cm long; ultimate branches 1½–2.2 cm wide, costules 3–3½ mm apart, at right angles to costa or very slightly oblique, *lamina* cut almost down to the costa, segments not abruptly narrowed above the base, edges when dry somewhat reflexed, apex rounded and entire, texture firm but not coriaceous, veins distinctly raised on lower surface, slightly so above, lower surface not glaucous when dry; *sori* of 3–4 sporangia. *Scales* on apex of main rachis 5 mm long, 1 mm wide, thin, medium rusty brown, hair-pointed, edges with oblique slender hairs; scales on lower surface of costae copious and spreading, the largest 2 mm long, 0.8 mm wide, shortly hair-pointed; scales on costules very small, long-fringed, pale, mixed with long-armed stellate hairs; upper surface of costae raised and terete, more or less persistently covered with small pale long-fringed interlacing scales; very short simple hairs abundant on lower surface of veins and occasionally also on lamina.

Type: Loher s.n., 7 Feb. 1906, Mt Banaho (P).

Distr. *Malaysia*: Philippines (Luzon).

var. *major* HOLTT. Reinwardtia 4 (1957) 272.

Larger than typical form of species; ultimate branches 20–30 cm long, 2½–3½ cm wide, costules 3–4 mm apart; 3-lobed stipular leaflets 15 mm long sometimes present.

Type: Bünnemeijer 11965, Celebes (Bo; dupl. at L, K).

Distr. *Malaysia*: S. Celebes, N. Borneo, and Philippines (Negros).

Ecol. Altitude 2000–2500 m.

34. *Gleichenia flabellata* R. BR. Prod. (1810) 161; HOOK. Sp. Fil. 1 (1844) 6; DOMIN, Bibl. Bot. 85 (1915) 204; v. A. v. R. Handb. (1908) 60; K. SCH. & LAUT. Fl. Schutzgeb. (1901) 144.—*Sticherus flabellatus* H. ST. JOHN, Occ. Pap. Bish. Mus. 17 (1942) 81.

Stipe to 60 cm long, scaly at the base; main rachis bearing 2 or more pairs of branches; lateral branch-systems compact, forked to 3 orders at short intervals (lower branches commonly 1 cm long, penultimate 2–3 cm long), ultimate and penultimate branches leafy, angle of forks less than 45°; ultimate branches 12–15 cm long, 2–3(–4) cm wide; costules 4 mm apart, at an angle of 45° to the costa; *lamina* cut almost to the costa, segments 2½ mm wide above the base, edges toothed almost to the base, apex broadly pointed, veins very oblique and raised on both surfaces, lower surface not glaucous. *Scales* on apex of main rachis 4 mm long, shining medium brown, acuminate, fringe copious, long, lax; scales on lower surface of costae few and persistent only near base, narrow, hair-pointed and long-fringed; smaller scales or long-armed pale stellate hairs occasional on costules near base of branch, surfaces otherwise glabrous.

Type: Robert Brown, Port Jackson, N. S. Wales (BM; dupl. at K).

Distr. E. & SE. Australia, New Caledonia, New Zealand, in *Malaysia*: E. New Guinea (SCHUMANN & LAUTERBACH l.c.).

35. *Gleichenia hirta* BL. En. Pl. Jav. (1828) 250; v. A. v. R. Handb. (1908) 60; Suppl. (1917) 85; HOLTT. Reinwardtia 4 (1957) 268.

—See for further synonyms under the varieties.—Fig. 7d, 8h–j.

Main rachis bearing several pairs of branches, not high-climbing; lateral branch-systems forked in 2–4 orders (rarely 5), the first-order branches in most varieties not normally proliferous beyond their first fork; ultimate branches always much longer than those of lower order, angle of ultimate forks less than 45°; *lamina* thin, cut almost down to the costa into thin oblique segments, edges distinctly toothed towards apices of segments, lower surface more or less glaucous (glaucous character destroyed by heat in drying). *Scales* on apex of main rachis to 5 mm long, less than 1 mm wide, fringed with short hairs; scales on costae abundant or not, spreading, 1½–2 mm long, less than ½ mm wide, thin and rather pale, not

conspicuously hair-pointed, edges fringed with slender hairs; smaller scales and stellate hairs also present on costae, costules and veins, or quite lacking; *sori* with raised receptacle, conspicuous paraphyses present or not.

## KEY TO THE VARIETIES

1. Lower surface of costae of fully expanded ultimate branches scaly near the base only or more generally, the scales all about equal in size with rather rigid fringing hairs; no scales on costules nor on veins except when young.
2. Scales 3-4 cells wide at the base. Ultimate branches to 40 cm long and 3½ cm wide.
  2. Scales wider. Ultimate branches rarely over 25 by 2½ cm.
  3. Costules 4-4½ mm apart . . . . . 3. *var. paleacea*
  3. Costules 3½-4 mm apart . . . . . 4. *var. candida*
1. Lower surface of costae persistently scaly almost throughout, the scales of various sizes, often with lax fringe; smaller scales also persistent on costules and sometimes scales or hairs on veins.
4. Segments of the lamina not abruptly narrowed above the base, separated by narrow sinuses.
5. Scales on costules abundantly long-fringed.
6. Ultimate branches of well-grown fronds 2-3 cm wide; primary rachis-branches not always proliferous beyond first fork . . . . . 1. *var. hirta*
6. Ultimate branches 1½-2½ cm wide; primary rachis-branches always proliferous beyond first fork . . . . . 5. *var. amboinensis*
5. Scales on costules with very few long marginal hairs . . . . . 6. *var. virescens*
4. Segments of lamina *c.* 2 mm wide except at the very base, separated by sinuses 1-1½ mm wide.
  7. *var. lanuginosa*

1. *var. hirta*.—*Dicranopteris dolosa* COPEL. in Perk. Frag. Fl. Philip. (1905) 193, *t. 4 f.c.*—*G. dolosa* C. CHR. Ind. Fil. (1906) 664; v. A. v. R. Handb. (1908) 62; Suppl. (1917) 85.—*Sticherus hirtus* CHING, Sunyatsenia 5 (1940) 203 (*err. hirsutus*).

Lateral *branch-systems* forked in 3 or 4 orders; ultimate branches 15-22 cm long, 2-2½ cm wide (rarely to 3 cm); penultimate branches fully leafy and often wider than ultimate ones; costules 3 mm apart; *scales* on lower surface of costae copious, persistent, of many sizes together, very long-fringed; pale stellate hairs present on veins.

Type: Reinwardt, Tidore (L; dupl. at BM).

Distr. *Malaysia*: Moluccas and Philippines (Luzon, Mindoro, Mindanao), 1200-1800 m.

2. *var. amoena* (v. A. v. R.) HOLTT. Reinwardtia 4 (1957) 269.—*G. amoena* v. A. v. R. Bull. Jard. Bot. Btzg II, n. 23 (1916) 12; Handb. Suppl. (1917) 497.—*Sticherus amoenus* NAKAI, Bull. Nat. Sc. Mus. Tokyo n. 29 (1950) 13.—*G. peninsularis* COPEL. Un. Cal. Publ. Bot. 12 (1931) 387.—*Sticherus peninsularis* CHING, Sunyatsenia 5 (1940) 284.—*G. hirta*; HOLTT. Rev. Fl. Mal. 2 (1955) 71.

Lateral *branch-systems* forked in 1-3 orders; penultimate branches fully or partly leafy, branches of lower order not leafy; ultimate branches 25-40 cm long, 2½-3½ cm wide; costules 4-4½ mm apart; *lamina-segments* 3-3½ mm wide above the base, strongly glaucous beneath; *scales* on lower surface of costae narrow (fringe of hairs longer than width of scale), very sparse and near base of costae only, mature fronds otherwise glabrous (stellate hairs on veins when young).

Type: Teysmann 16628, Lingga (Bo; dupl. at P).

Distr. *Malaysia*: Sumatra, Lingga Archipelago, Malay Peninsula.

Ecol. Altitude 700-1600 m; scrambling or trailing in lightly shaded places or edge of forest, not forming dense thickets; fronds usually not over 200 cm long.

3. *var. paleacea* (BAK.) C. CHR. Gard. Bull. S. S. 7 (1934) 212; HOLTT. Reinwardtia 4 (1957) 269.—*G. vestita* *var. paleacea* BAK. J. Bot. 17 (1879) 38.—*G. hallieri* CHRIST, Ann. Jard. Bot. Btzg 20 (1905) 138; v. A. v. R. Handb. (1908) 61.—*G. barbula* C. CHR. Dansk Bot. Ark. 9, 3 (1937) 67.—*Sticherus hallieri* NAKAI, Bull. Nat. Sc.-Mus. Tokyo n. 29 (1950) 18.—*Sticherus barbula* NAKAI, l.c. 13.

Lateral *branch-systems* usually forked in 2 or 3 orders (to 5 orders in type specimen of *G. barbula*); if in 2 orders penultimate branches incompletely leafy and ultimate branches to 30 cm long, otherwise ultimate branches 15-24 cm long and 2-2½ cm wide; costules 4-4½ mm apart; *scales* on mature fronds confined to costae and all alike (not mixed with smaller ones) with rather stiff fringing hairs as long as width of scale.

Type: Burbidge, N. Borneo (K).

Distr. *Malaysia*: Borneo, Lesser Sunda Islands (Bali), Celebes (Menado), 1100-3000 m.

Ecol. On Mt Kinabalu on open places in ridge forest.

4. *var. candida* (ROSENST.) HOLTT. Reinwardtia 4 (1957) 269.—*G. candida* ROSENST. in Fedde, Rep. 5 (1908) 33; v. A. v. R. Handb. (1908) 796.—*Sticherus hirtus* *var. candidus* NAKAI, Bull. Nat. Sc. Mus. Tokyo n. 29 (1950) 19.

Similar to *var. paleacea*, but costules 3½-4 mm apart, lamina of firmer texture.

Type: Werner 72, Mt Gelu (B; dupl. at BM, US, L).

Distr. *East Malaysia*: New Guinea, Admiralty Islands, Solomon Islands.

Ecol. On edges of forest and in light shade, sometimes forming dense thickets to 3 m high, 700–2150 m.

5. *var. amboinensis* (v. A. v. R.) HOLTT. Reinwardtia 4 (1957) 269.—*G. amboinensis* v. A. v. R. Bull. Dép. Agr. Ind. Néerl. n. 18 (1908) 3; Handb. (1908) 62; Suppl. (1917) 85 (as a synonym).

Like *var. hirta* in scaliness; ultimate branches  $1\frac{1}{2}$ – $2\frac{1}{2}$  cm wide; primary rachis-branch always proliferous beyond first fork and bearing 2 or more pairs of secondary branches.

Type: Teysmann, Amboyna (Bo; dupl. at L).

Distr. Malaysia: S. Central Celebes, Moluccas (Ambon, Buru, Waigeo Isl.).

Ecol. Climbing to 4 m in open places in mountain forest.

6. *var. virescens* (HIERON.) HOLTT. Reinwardtia 4 (1957) 270.—*G. dolosa var. virescens* HIERON. ex BRAUSE, Bot. Jahrb. 56 (1920) 209.—*Sticherus hirtus var. virescens* NAKAI, Bull. Nat. Sc. Mus. Tokyo n. 29 (1950) 19.

Similar to *var. hirta*, but scales on costules with very few long marginal hairs.

Type: Ledermann 9935 (B).

Distr. Malaysia: E. New Guinea.

Note. Collector of type specimen stated that lower surface of lamina was white (i.e. glaucous) when fresh.

7. *var. lanuginosa* (v. A. v. R.) *comb. nov.*—*G. ornamentalis* ROSENST. Nova Guinea 8 (1912) 715; v. A. v. R. Handb. Suppl. (1917) 85.—*G. ornamentalis var. lanuginosa* v. A. v. R. Nova Guinea 14 (1924) 23.—*Sticherus lamianus* COPEL. Philip. J. Sc. 75 (1941) 356, pl. 6.—*G. hirta var. ornamentalis* (ROSENST.) HOLTT. Reinwardtia 4 (1957) 269.

Lateral branch-systems commonly forked to 4 orders; costae persistently and densely scaly, scales as in *var. hirta*; costules 3–4 mm apart, segments of lamina 2 mm wide, thus separated by rather wide sinuses.

Type: Lam 1945, Doormantop, 3480 m (U; dupl. at Bo, US, L).

Distr. Malaysia: New Guinea.

Ecol. Altitude 800–2500 m; specimens from the higher altitudes are the most densely scaly.

## 2. DICRANOPTERIS

BERNHARDI in Schrad. Neu. J. Bot. 1, 2 (1806) 38; UNDERW. Bull. Torr. Bot. Cl. 34 (1907) 244, *p.p.*; CHING, Sunyatsenia 5 (1940) 272; COPEL. Gen. Fil. (1947) 28; NAKAI, Bull. Nat. Sc. Mus. Tokyo n. 29 (1950) 56; HOLTT. Reinwardtia 4 (1957) 273.—*Mertensia* WILLD. Kongl. Vet. Ak. Nya Handl. 25 (1804) 163, *p.p.*; PRESL, Tent. Pterid. (1836) 50, *p.p.*; non ROTH, 1797 (*Borag.*).—*Gleichenia subg. Mertensia*, § III and § IV, HOOK. Sp. Fil. 1 (1844) 11, 12.—*Hicriopteris* PRESL, Epim. Bot. (1851) 26, non CHING, nec COPEL.—*Gleichenia subg. Mertensia sect. Heteropterygium* DIELS in E. & P. Pfl. Fam. 1, 4 (1900) 355.—*Gleichenia subg. Mertensia sect. Dicranopteris* v. A. v. R. Handb. (1908) 56, *p.p.*—*Mesosorus* HASSK. Fil. Jav. 1 (1856) 2, *p.p.*—Fig. 11–16.

Indumentum on rhizome, dormant apices, and on other parts of fronds consisting of multiseptate hairs which have outgrowths from cells near the base and sometimes also from other cells. Apex of main rachis of fronds resting periodically while each pair of lateral branch-systems develops; primary rachis-branches repeatedly branched pseudo-dichotomously (forked), the apex between each pair of branches usually permanently dormant, the members of a pair equal or unequal; a short stipule-like lobed leaflet usually present at the base of each primary rachis-branch, these leaflets growing upwards and protecting the temporarily dormant apex of the main rachis (smaller stipule-like leaflets sometimes also present at forks of the lateral branch-systems); a pair of accessory branches, bearing a lamina like that of the ultimate branches, present at some of the forks of the lateral branch-systems, on the outside of the fork (usually attached just above it) and deflexed; apart from stipular leaflets and accessory branches, only the ultimate branches leafy. Ultimate branches bearing throughout a deeply pinnatifid lamina, the segments of the lamina usually entire, each with costule bearing lateral veins which are forked at least twice; *sori* one to each vein-group on an acroscopic branch (rarely also on a basisopic branch), each of 8–15 or



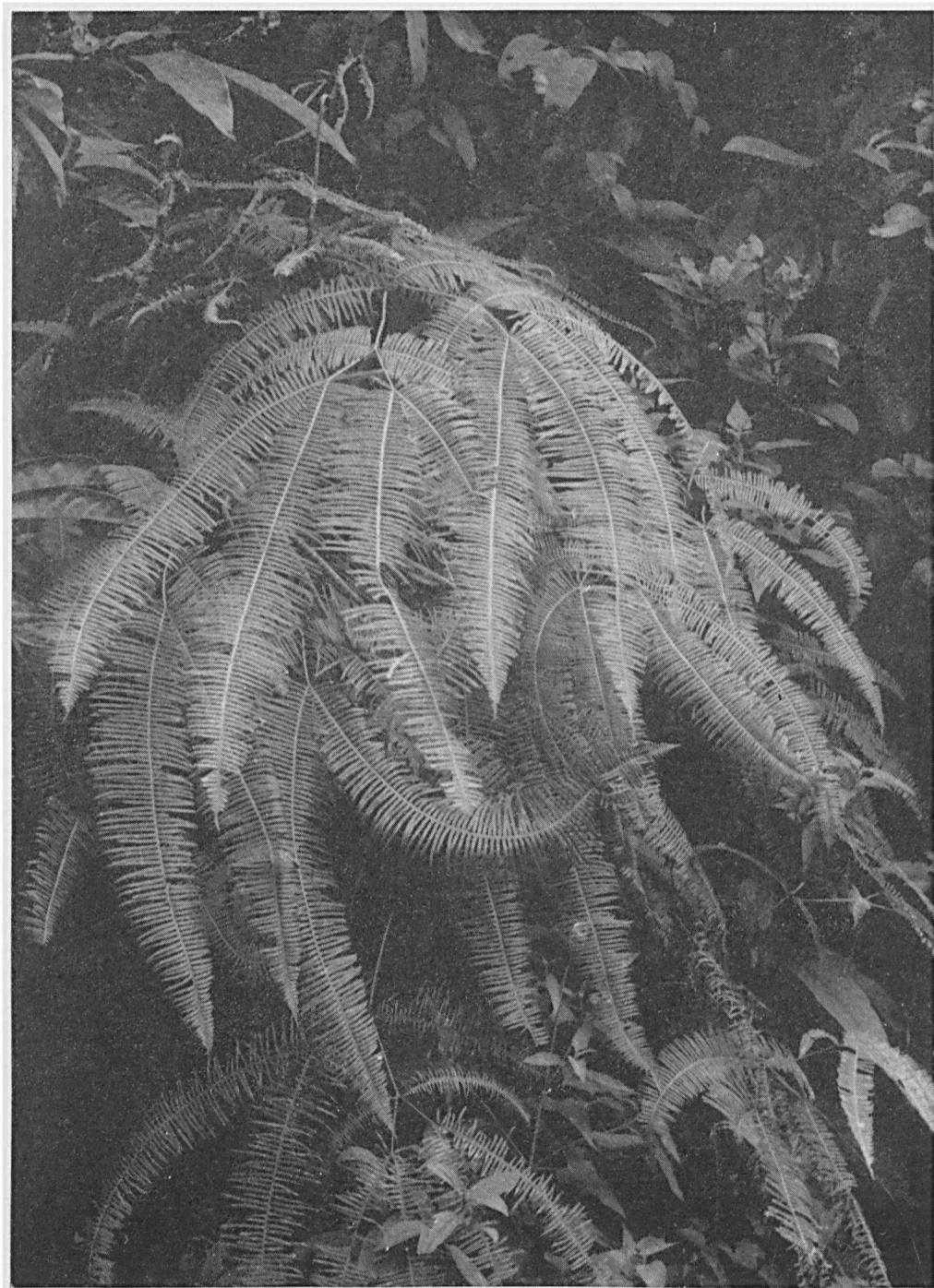


Fig. 11. *Dicranopteris curranii* COPEL. Harau gorge, near Pajakumbuh, W. Sumatra, c. 500 m (MEIJER, Jan. 1958).



more sporangia without paraphyses, the sporangia smaller than in *Gleichenia*; spores monolete or trilete.

Distr. and Ecol. Thicket-forming ferns, abundant in open places throughout the wetter parts of the tropics and subtropics, especially characteristic of equatorial lowlands (the species of *Gleichenia* being almost exclusively mountain plants in Malaysia).

Notes. There are two well-marked subgenera, *Dicranopteris* (pantropic) and *Acropterygium* (one species, in tropical America; no accessory branches, rhizome with solenostele).

The subgenus *Dicranopteris* is much more diversified in Malaysia than in any other part of the world. A small group of species may be clearly distinguished by their monolete spores. Almost all other specimens are at present regarded as belonging to a polymorphic species, *D. linearis*. Some of the varieties of *D. linearis* are more clearly distinct than others, and probably should be recognized as species. They

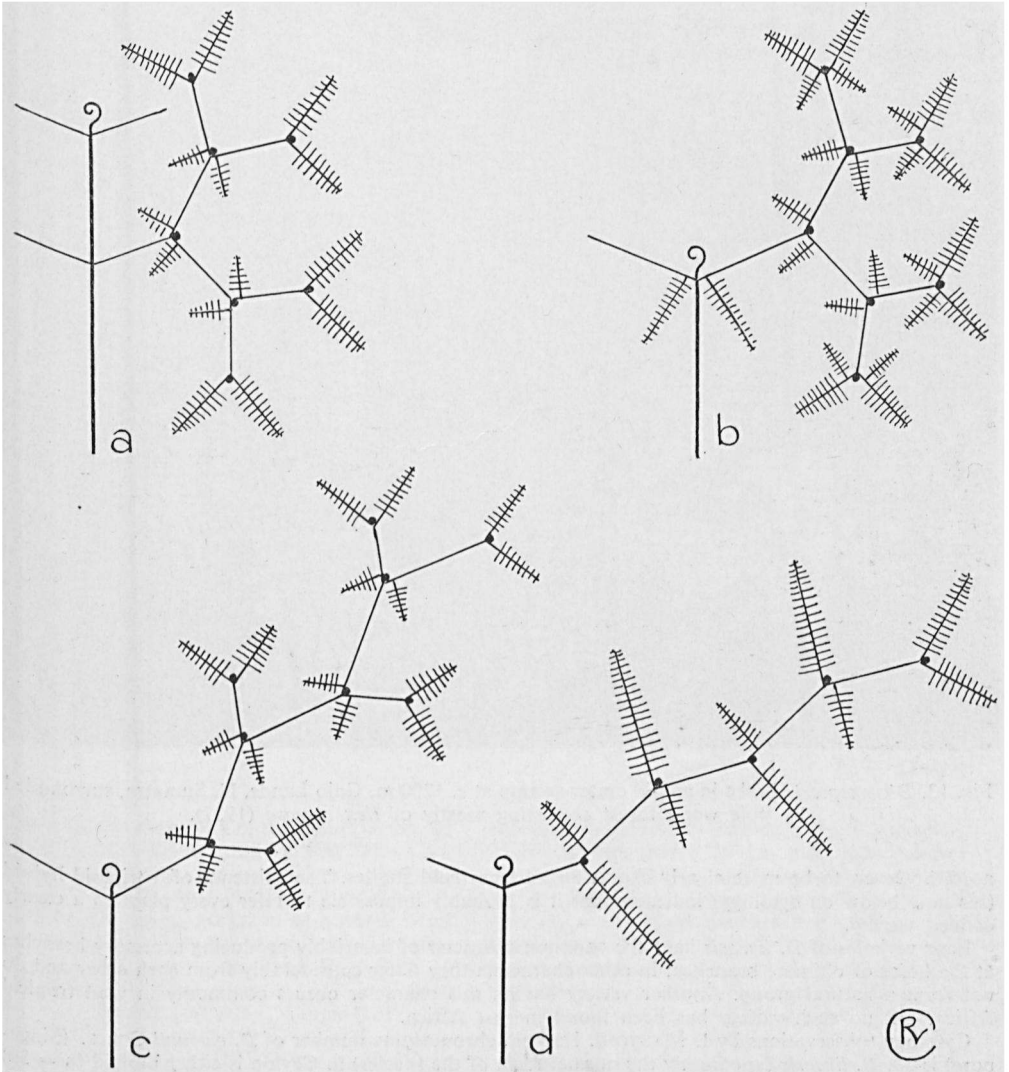


Fig. 12. Diagrams showing variations of branching-habit in *Dicranopteris*. a. Basic habit, found in *D. linearis* (BURM. f.) UND. var. *linearis*, *D. pubigera* (BL.) NAKAI, and *D. curranii* COPEL., b. accessory branches present at ultimate forks, as in *D. linearis* var. *montana* HOLT. and var. *tetraphylla* (ROS.) NAKAI, c. alternate unequal forking, as in *D. linearis* var. *subpectinata* (CHRIST) HOLT., var. *alternans* (METT.) HOLT., and var. *subspeciosa* HOLT., d. special development of c, found only in *D. speciosa* (PRESL) HOLT.

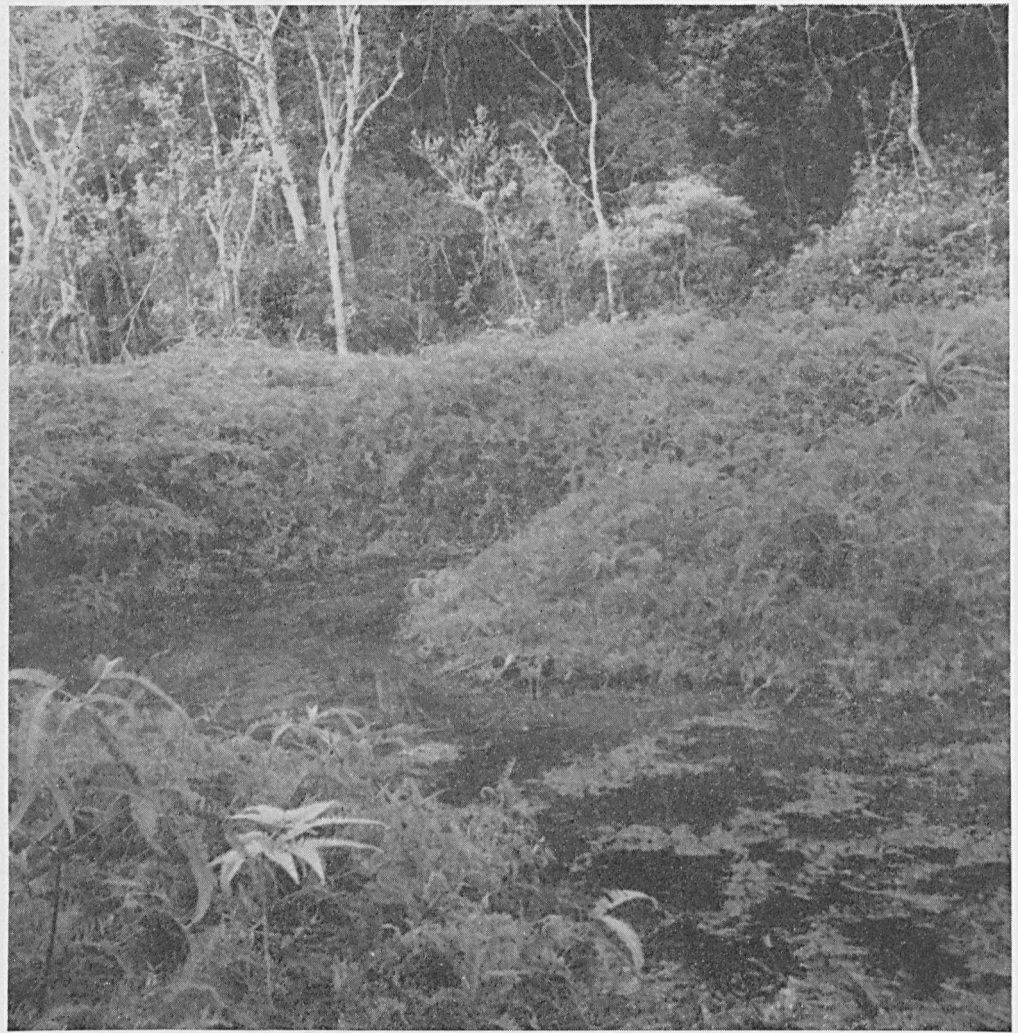


Fig. 13. *Dicranopteris* brake in an old crater swamp at c. 1200 m, Gajo Lands, N. Sumatra, surrounded by pole wood forest consisting mostly of *Ilex cymosa* (1937).

need, however, to be more clearly characterized from field studies. The existence of a triploid hybrid (see note below on cytology) indicates that it is probably impossible to refer every plant to a clearly defined variety.

Four varieties of *D. linearis* have the common character of invariably producing accessory branches at the bases of ultimate branches; in other characters they differ considerably from each other and do not form a natural group. Another variety having this character occurs commonly in west tropical Africa, but no such variety has been found in east Africa.

Cytology (observations by I. MANTON). Haploid chromosome number of *D. curranii* COPEL. (Singapore) is 39. *D. linearis* (apparently the normal form of the species) in Ceylon is either diploid ( $n = 39$ ) or tetraploid ( $n = 78$ ); a plant of *D. linearis* sent to Kew from Singapore is a sterile triploid.

#### KEY TO THE SPECIES

1. Spores monolete. The two branches at each fork equal; either lowland plants with ultimate branches 9–12 cm wide, or mountain plants. First fork of each vein at its very base.
2. Lamina not very thick nor with the veins grooved on the lower surface.

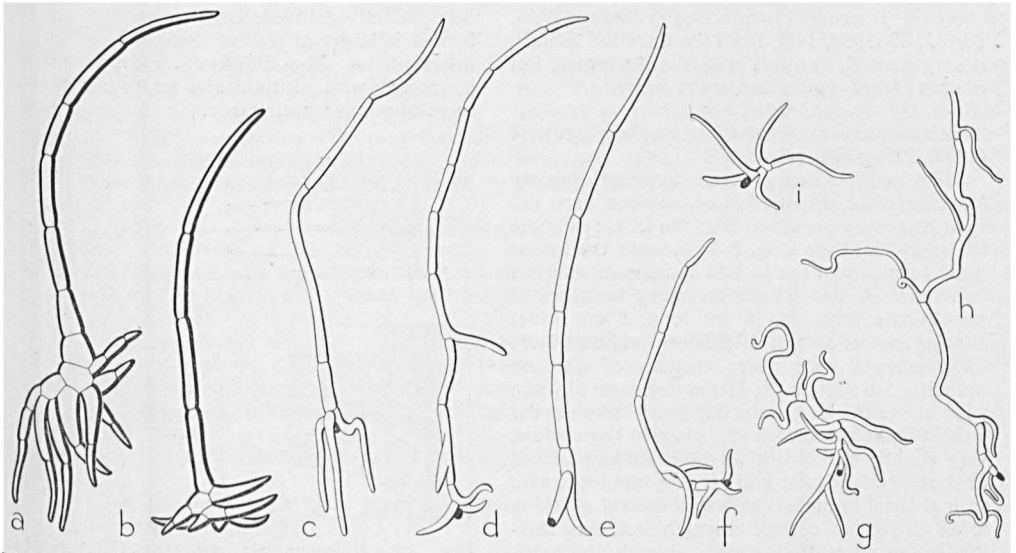


Fig. 14. Hairs of *Dicranopteris*, all  $\times 60$ . Except in fig. a and b the cell of attachment is shown, black.—*D. curranii* COPEL. a. Hair from base of costa. — *D. clemensiae* HOLTT. b. One of the rigid, shining hairs from lower surface of costa, c. thin-walled hair from costule. — *D. pubigera* (BL.) NAKAI. d–e. Hairs from costule, lower surface. — *D. linearis* (BURM. f.) UND., hairs from lower surface of costules: f. var. *subferruginea* (HIERON.) NAKAI, g. var. *linearis*, h. var. *subspeciosa* HOLTT., i. var. *alternans* (METT.) HOLTT.

- 3. Ultimate branches commonly 40 cm long and 9–12 cm wide; lower surface almost glabrous. 1. *D. curranii*
- 3. Ultimate branches not over 7 cm wide; lower surface of costae and costules rather persistently hairy. 2. *D. clemensiae*
- 4. Ultimate branches 30–55 cm long, 5–7 cm wide; costae at first with many shining hairs (1–1½ mm long) throughout . . . . . 3. *D. pubigera*
- 4. Ultimate branches 15–25 cm long, 2.7–5 cm wide; costae with such hairs near base only. 3. *D. pubigera*
- 2. Lamina very thick, the veins grooved on the lower surface . . . . . 3. *D. pubigera*
- 1. Spores trilete. Branches at a fork in many cases unequal; ultimate branches to c. 6 cm wide. Veins never grooved on lower surface; first fork of each vein distinctly above the base. 4. *D. speciosa*
- 5. At each fork, except primary and ultimate ones, one branch leafy and without accessory branch, the other branch not leafy and with an accessory branch . . . . . 4. *D. speciosa*
- 5. At each fork, except (in most cases) an ultimate one, a pair of accessory branches present. 5. *D. linearis*

1. *Dicranopteris curranii* COPEL. Philip. J. Sc. 81 (1952) 4; HOLTT. Reinwardtia 4 (1957) 274.—*Gleichenia hermannii* var. *venosa* BL. incl. also var. *tenera* BL. En. Pl. Jav. (1828) 249.—*Gleichenia dichotoma* var. *tenera* METT. in Miq. Ann. Mus. Bot. Lugd. Bat. 1 (1863) 50.—*Gleichenia dichotoma* var. *malayana* CHRIST, Ann. Jard. Bot. Btzg 15 (1898) 77.—*Gleichenia linearis* var. *malayana* V. A. v. R. Handb. (1908) 59; Suppl. (1917) 84; HOLTT. Rev. Fl. Mal. 2 (1955) 70.—*D. lessonii* NAKAI, Bull. Nat. Sc. Mus. Tokyo n. 29 (1950) 61, *quad. specim., excl. basion. Mertensia lessonii* A. RICH.—Fig. 11, 12a, 14a, 16.  
Fronds large, strongly erect but not greatly elongate nor high-climbing; primary rachis-branches few times equally forked; ultimate branches commonly 40 cm long and 12 cm wide,

accessory branches at penultimate forks commonly 20–30 cm long and 7–10 cm wide; costules 5–7 mm apart; lamina-segments 3½–4½ mm wide above the base, texture firm, lower surface glaucous, usually quite glabrous apart from minute simple hairs on the veins, often pinkish on costae and lower parts of costules; veins slender, slightly prominent on lower surface but not on upper; stipular leaflets to 3 cm long at bases of primary branches; spores monolete.  
Type: Curran, For. Bur. 19265, Laguna Prov., Luzon (H. Copel.; dupl. at US, P).  
Distr. *Malaysia*: Sumatra, Malay Peninsula, W. Java, Lesser Sunda Islands (Flores), Borneo, Celebes, Philippines (Luzon).  
Ecol. In thickets with varieties of *D. linearis*, from sealevel up to 1500 m.

Note. *Gleichenia weatherbyi* FOSBERG (Am. Fern J. 40, 1950, 140), from the Caroline Islands, is very near *D. curranii*, with similar spores, but is even larger, and much more hairy.

2. *Dicranopteris clemensiae* HOLTT. Reinwardtia 4 (1957) 275.—Fig. 14b-c.

Main rachis 7 mm or more diameter; primary branches twice equally forked, copious dark red rigid hairs very persistent near the forks; ultimate branches 30–55 cm long, 5–7 cm wide, the lowest outer segments of the lamina sometimes enlarged and more or less lobed; accessory branches at penultimate forks 16–18 cm long, 5 cm wide; stipular leaflets at base of primary branches 3 cm long, lobes 3 mm wide; costules of ultimate branches 5–6 mm apart; lamina-segments 3½ mm wide above the base, thin but firm; veins usually 3 times forked, first fork very close to the costule, very slightly prominent on both surfaces; stout dark red multicellular hairs (1–1½ mm long, with several basal branches) at first abundant all along lower surface of costae, at length deciduous leaving costae perceptibly rough; thinner and paler, dull rusty-brown, hairs at first abundant on costules, slightly crisped and with short unicellular branches near base only; sori of 10–15 sporangia, often two on a vein-group (on each of the outermost branches); spores monolete, *c.* 32 × 16 μ.

Type: Clemens 28745, Mt Kinabalu (BM; dupl. at Bo, K, L, US).

Distr. *Malaysia*: N. Borneo (once collected, 1600 m).

3. *Dicranopteris pubigera* (BL.) NAKAI, Bull. Nat. Sc. Mus. Tokyo n. 29 (1950) 68; HOLTT. Reinwardtia 4 (1957) 274.—*Gleichenia hermannii* var. *pubigera* BL. En. Pl. Jav. (1828) 249.—*Gleichenia dichotoma* var. *pubigera* METT. in Miq. Ann. Mus. Bot. Lugd. Bat. 1 (1863) 50.—*Gleichenia linearis* var. *pubigera* v. A. v. R. Handb. Suppl. (1917) 85.—*Mertensia spissa* (non FÉE) var. *pubigera* NAKAI, Bot. Mag. Tokyo 39 (1925) 180.—Fig. 12a, 14d-e, 15a-b.

Primary rachis-branches 2–4 times equally or subequally forked; ultimate branches 15–25 cm long, 3–8 cm wide; costules 4½–6 mm apart; lamina-segments *c.* 4 mm wide when flattened, thick and rigid when dry and usually with edges reflexed; lower surface not glaucous, the costules at first covered rather densely with coarse dull rusty flexuous hairs and also some rigid shining hairs; veins grooved on the lower surface when the lamina is very thick, on thinner leaves hardly grooved, pale but not raised on the upper surface; spores monolete.

Type: Blume, Java (L; dupl. at K, P).

Distr. *Malaysia*: Sumatra, Java, and Lesser Sunda Islands (Bali, Lombok, Flores).

Ecol. Abundant in open scrub and in clearings in mountain forest, forming dense thickets, 1100–3000 m.

Note. The extreme forms of this species, one with very thick lamina with veins grooved on the lower surface, the other with thinner lamina and veins

not distinctly grooved, appear very different (the former is larger as well as thicker) but there are intermediates. The differences may in part be connected with altitude and exposure; no observations have been made.

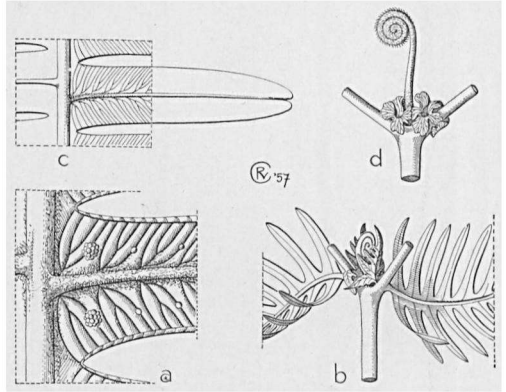


Fig. 15. *Dicranopteris pubigera* (BL.) NAKAI. a. Lower surface of part of frond (veins grooved), × 4, b. a main fork with stipular leaflets and accessory branches, × ½. — *D. speciosa* (PRESL) HOLTT. c. Part of frond to show venation, × 2, d. main fork showing stipular leaflets, × ½.

4. *Dicranopteris speciosa* (PRESL) HOLTT. Reinwardtia 4 (1957) 273.—*Hicriopteris speciosa* PRESL, Epim. Bot. (1851) 27.—*Gleichenia opposita* v. A. v. R. Bull. Jard. Bot. Btzg II, n. 11 (1913) 13; HOLTT. Rev. Fl. Mal. 2 (1955) 70, f. 14 F.—*Gleichenia parallela* RIDL. J. Mal. Br. R. As.: Soc. 4 (1926) 3.—*D. opposita* NAKAI, Bull. Nat. Sc. Mus. Tokyo n. 29 (1950) 68.—Fig. 12d, 15c-d.

Primary rachis-branches several times very unequally forked; at each fork the smaller branch unbranched and leafy throughout, commonly 20–25 cm long and 4–5 cm wide, with no accessory branch, the larger branch continuing almost the same straight line as the larger branch from the previous fork and bearing an accessory branch 12–15 cm long and 3½ cm wide (this accessory branch almost opposite the simple leafy branch of the fork); ultimate fork formed by two normal leafy branches without accessory branches; irregularities from this basic scheme occasionally present; lamina-segments 3½–4 mm wide, flat and rather rigid, separated by very narrow sinuses, apices often retuse; veins distinctly prominent on the upper surface; lower surface more or less glaucous, the costules when young rather densely covered with fine pale entangled woolly hairs, some similar hairs on veins; some dark reddish, rigid, shining hairs, like those on resting apices, also at first present on costae and costules; sori as in *D. linearis*; spores trilete.

Type: collector unknown, "Pendschab" (PRC). Perhaps from Penang.

Distr. *Malaysia*: Sumatra, Malay Peninsula, Moluccas (Sula Isl.: P. Mangoli).

Ecol. Growing with *D. linearis* on the edges of forest, 100–600 m.

Note. The remarkable pseudo-pinnate lateral branch-systems of this species were described in detail by PRESL, but because he compared these branches to *Gleichenia glauca* (THUNB.) HOOK. later authors thought he was describing a species of *Gleichenia* subg. *Diplopterygium* and conse-

quently used the generic name *Hicriopteris* in a wrong sense.

5. *Dicranopteris linearis* (BURM. f.) UNDERW. Bull. Torr. Bot. Cl. 34 (1907) 249; HOLTT. Reinwardtia 4 (1957) 275.—*Polypodium dichotomum* THUNB. Fl. Jap. (1784) 338, t. 37.—*Gleichenia dichotoma* HOOK. Sp. Fil. 1 (1844) 6; RACIB. Fl. Btztg 1 (1898) 13.—Fig. 12, 14f–i.

## KEY TO THE VARIETIES

1. Accessory branches not always present at ultimate forks.
2. Branches at each fork of a lateral branch-system approximately equal; lateral branch-systems forked 1–3 times.
  3. Costules less than 5 mm apart, their lower surface with some persistent hairs.
    4. Hairs not persistent on lower surface of veins . . . . . 1. var. *linearis*
    4. Hairs persistent along lower surface of veins.
      5. Hairs long, very finely woolly and entangled; no distinct separate hairs present.
        2. var. *ferruginea*
        5. Hairs coarse, shorter, more or less entangled on costules, some distinctly separate on veins.
          3. var. *subferruginea*
    3. Costules 5–7 mm apart, their lower surface glabrous.
      6. Lamina thick and rigid . . . . . 4. var. *rigida*
      6. Lamina thin . . . . . 5. var. *latiloba*
  2. Branches at successive forks alternately unequal; lateral branch-systems on well-grown plants forked at least 3 times.
    7. Lower surface quite glabrous and persistently pale glaucous; lamina thin 6. var. *subpectinata*
    7. Lower surface more or less persistently hairy, less strongly glaucous (often losing glaucous character on drying); lamina firm.
      8. Hairs very slender, their long branches much crisped and entangled; no separate short hairs.
        9. Hairs copious, at first covering whole lower surface, persistent along the veins, rusty when dry; edges of lamina strongly reflexed when dry . . . . . 2. var. *ferruginea*
        9. Hairs not covering whole lower surface, persistent only on costules, pale when dry; edges of lamina not much reflexed when dry.
          10. Angle of secondary and later forks not more than a right angle . . . . . 7. var. *subspeciosa*
          10. Angle of secondary and later forks more than a right angle . . . . . 8. var. *inacqualis*
      8. Hairs coarser and shorter, some more or less crisped and entangled but separate short hairs also present.
        11. Hairs confined to bases of some of the costules . . . . . 1. var. *linearis*
        11. Hairs more abundant on costules, and some also on veins.
          12. Hairs persistently rust-coloured, copious all along veins. . . . . 3. var. *subferruginea*
          12. Hairs pale on dried specimens, sparse on the veins; W. Malaysia . . . . . 9. var. *alternans*
  1. Accessory branches always present at ultimate forks.
    13. Accessory branches, especially the lower ones, distinctly below the fork; branches at successive forks alternately somewhat unequal . . . . . 10. var. *demota*
    13. Accessory branches opposite the fork or distinctly above it; branching usually equal at all forks.
      14. Ratio of length to width of branches commonly 2 : 1; costules c. 3 mm apart, segments of lamina 2½–3 mm wide . . . . . 11. var. *tetraphylla*
      14. Ratio of length to width greater; costules more widely separated.
        15. Costules on ultimate branches 5–7 mm apart; texture subcoriaceous; lower surface quite glabrous; accessory branches at ultimate forks almost opposite the fork . . . . . 12. var. *montana*
        15. Costules on ultimate branches 3½–4½ mm apart; texture thin; some rusty hairs often on lower surface; accessory branches at ultimate forks 3–4 mm above the fork . . . . . 13. var. *altissima*

1. var. *linearis*.—*Polypodium lineare* BURM. f. Fl. Ind. (1768) 235, t. 67 f. 2.—*Gleichenia hermannii* R. BR. Prod. (1810) 161.—*Gleichenia dichotoma* var. *normalis* METT. in Miq. Ann. Mus. Bot. Lugd. Bat. 1 (1863) 50; RACIB. Fl. Btztg 1 (1898) 13.—*Mertensia pteridifolia* PRESL, Abh. (K.) Böhm. Ges. Wiss. M.-N. Cl. V, 5 (1848) 339; Epim. Bot. (1851) 23, t. 14.—*Gleichenia linearis* CLARKE, Trans. Linn. Soc. Bot. 1 (1880) 428; v. A. v. R. Handb. (1908) 59 *pro* var. *normalis*; Suppl.

(1917) 84, *ditto*; HOLTT. Rev. Fl. Mal. 2 (1955) 70, *ditto*.—Fig. 12a, 14g, 16.

Primary rachis-branches commonly 2 or 3 times forked, the two branches at all forks equal or nearly so (not regularly alternately unequal); stipular leaflets at bases of primary branches c. 1 cm long, lobed near the base only; ultimate branches 15–25 cm long, 4–6 cm wide; lamina-segments 2½–3 mm wide, separated by rather wide sinuses, texture very firm; lower surface slightly

glaucous; veins slightly prominent on lower surface and bearing very short simple hairs, not prominent on upper surface; some persistent much-branched rusty hairs on costules; *spores* trilete.

Type: Ceylon, Herb. Delessert (G).

Distr. Tropical and subtropical Africa, Asia, *Malaysia*, Australasia, and Polynesia.

Ecol. Thicket-forming but not high-climbing, from sealevel to 1400 m.

Note. *Polypodium dichotomum* THUNB. was described from Japan, and as noted by NAKAI (*l.c.*) is not quite identical with *Polypodium lineare* BURM. (BURMAN's specimens, preserved at Geneva, are from Ceylon). I have therefore ranked it as a *Dicranopteris linearis* var. *dichotoma* (Reinwardtia 4, 1957, 277). The lamina of the fronds is thinner than in var. *linearis* and the veins are prominent on the upper surface. This may be connected with the fact that (at least in part of its range) the fronds of var. *dichotoma* only last for one season, dying in the winter, whereas those of var. *linearis* grow for an indefinite period which is usually not climatically limited. Var. *dichotoma* apparently occurs also in China and probably in the Sikkim region; field studies in these regions are needed to establish clear distinctions between var. *linearis* and var. *dichotoma*.

2. var. *ferruginea* (BL.) HOLTT. Reinwardtia 4 (1957) 278.—*Gleichenia ferruginea* BL. En. Pl. Jav. (1828) 249; METT. Ann. Mus. Bot. Lugd. Bat. 1 (1863) 50.—*Gleichenia dichotoma* var. *ferruginea* RACIB. Fl. Btzg 1 (1898) 13.—*Gleichenia linearis* var. *ferruginea* v. A. v. R. Handb. (1908) 59; Suppl. (1917) 85.—'*Dicranopteris ferruginea*' COPEL. Philip. J. Sc. 75 (1941) 349, not *Mertensia ferruginea* DESV. 1811.

Lateral branch-systems of small plants symmetrically forked twice, on larger plants forked to 3 or more orders, branches at successive forks alternately unequal; ultimate branches 15–20 cm long, 3–5 cm wide; costules 4–5 mm apart; segments of lamina brittle when dry, with recurved edges, when flattened c. 2½ mm wide above the base, lower surface covered with very fine floccose entangled pale rusty hairs (c. 10 μ diam.) which are attached mainly along the veins, the veins thus persistently hairy on old fronds; stiff hairs present on dormant apices only; upper surface smooth, the veins very distinct and slightly raised when dry; accessory branches not normally present at the ultimate forks, but the lowest basiscopic lobes of the ultimate branches usually larger than the rest, their edges more or less lobed.

Type: Blume, Java (L).

Distr. *Malaysia*: Java, Celebes, Moluccas, New Guinea.

Ecol. Altitude 1000–2500 m.

3. var. *subferruginea* (HIERON.) NAKAI, Bull. Nat. Sc. Mus. Tokyo n. 29 (1950) 66.—*Gleichenia linearis* var. *subferruginea* HIERON. ex BRAUSE, Bot. Jahrb. 56 (1920) 209.—Fig. 14f.

Like var. *linearis* but perhaps more often with unequal branches at the more distal forkings,

veins somewhat prominent on upper surface, veins on the lower surface rather persistently hairy, the hairs rusty, rather coarse (diam. c. 25 μ) and much-branched, not finely woolly nor forming a continuous entangled web as in var. *ferruginea*.

Type: Ledermann 6926, New Guinea (B).

Distr. Queensland, Polynesia (Fiji, Samoa), and *East Malaysia*: Celebes, Moluccas, New Guinea.

Ecol. From sealevel to 1200 m.

Note. It is probable that this variety is much more abundant than var. *linearis* in New Guinea and regions further eastwards. The hairs on the lower surface of the veins are of the same general character as those of var. *linearis*, but much more copious; they are more abundant on plants at higher altitudes than near sealevel, and possibly abundance of hairs also depends on degree of exposure.

4. var. *rigida* (BL.) HOLTT. Reinwardtia 4 (1957) 277.—*Gleichenia hermannii* var. *rigida* BL. En. Pl. Jav. (1828) 249.—*Mertensia crassifolia* PRESL, Abh. (K.) Böhm. Ges. Wiss. M.-N. Cl. V, 5 (1848) 339; Epim. Bot. (1851) 23, t. 13.—*Gleichenia dichotoma* var. *rigida* METT. in Miq. Ann. Mus. Bot. Lugd.-Bat. 1 (1863) 50.—*Gleichenia warburgii* CHRIST, Ann. Jard. Bot. Btzg 15 (1898) 78.—*Gleichenia linearis* var. *rigida* v. A. v. R. Handb. (1908) 59; Suppl. (1917) 84.—*Gleichenia crassifolia* COPEL. Philip. J. Sc. 1 (1906) Suppl. I 257.—*D. crassifolia* NAKAI, Bull. Nat. Sc. Mus. Tokyo n. 29 (1950) 57. (*Non Mertensia rigida* KZE 1834, *D. rigida* NAKAI).

Lateral branch-systems once or twice forked, members of all forks equal or nearly so; ultimate branches 15–25 cm long, 3–5½ cm wide; costules 5–6 mm apart; segments of lamina 4–5 mm wide above the base, thick and very rigid when dry with edges slightly reflexed, apices not or slightly retuse; lower surface quite glabrous from an early stage; veins broad, slightly prominent on lower surface, distinctly so on upper surface; *spores* trilete.

Type: Reinwardt, Tidore (L).

Distr. *Malaysia*: Moluccas (type from Tidore), Celebes, and Philippines (Mindanao, Luzon, Negros).

Ecol. Altitude 1500–3000 m.

Note. METTENIUS (and apparently also RACIBORSKI) referred some specimens of *D. pubigera* from Java to this variety of *D. linearis*.

5. var. *latiloba* HOLTT. Reinwardtia 4 (1957) 277.

Lateral branch-systems forked to about 4th order, branches at all forks subequal; stipular leaflets at bases of primary branches to 4 cm long, deeply and broadly lobed; ultimate branches c. 20 cm long, to 9 cm wide, the lowest segments of the lamina somewhat enlarged and deflexed but not pinnately lobed; costules c. 7 mm apart; segments 4–5 mm wide above the base, firm but not very thick, edges slightly sinuous, only reflexed when dry; lower surface quite glabrous apart from minute simple hairs; veins sometimes



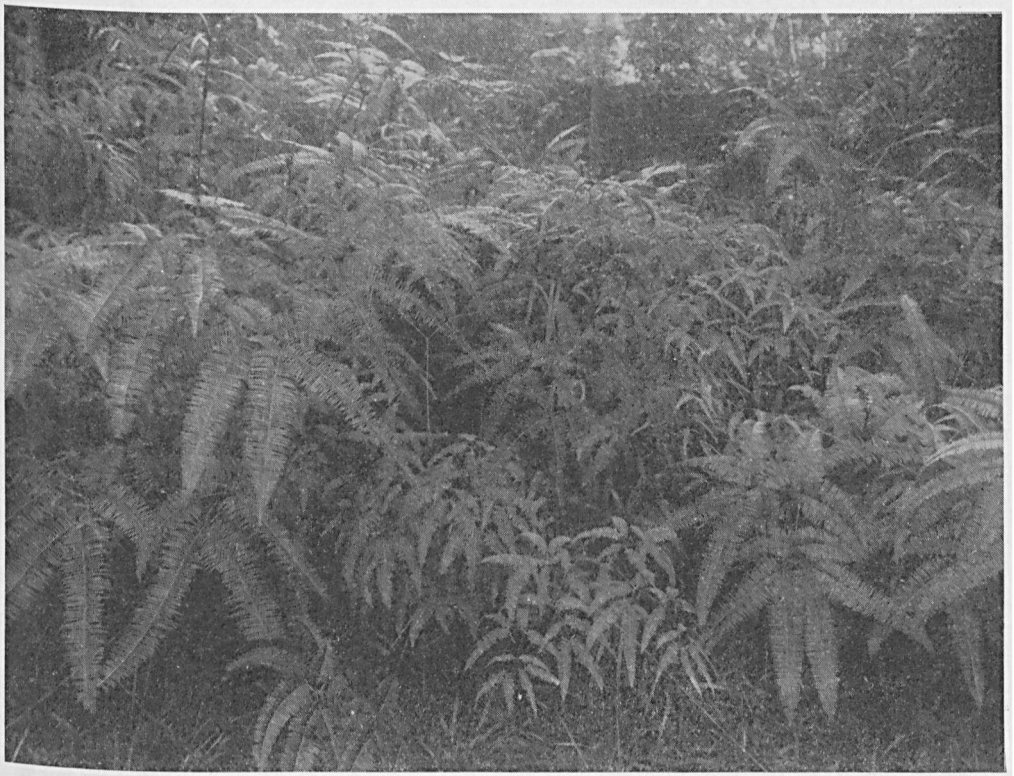


Fig. 16. Thicket of *Dicranopteris* on edge of forest, Singapore. *D. curranii* COPEL. (large fronds) to left and right; *D. linearis* (BURM. f.) UND. var. *linearis* in centre; var. *subpectinata* (CHR.) HOLTUM to right of centre, below (HOLTUM, 1925).

pale and distinctly prominent on the upper surface, concolorous and only slightly prominent on lower surface.

Type: Merrill 975, Luzon (US; dupl. at P, U, F).

Distr. *Malaysia*: Philippines (Luzon, Negros, Mindanao), Celebes (?).

Ecol. Altitude 1000–1600 m.

6. var. *subpectinata* (CHRIST) HOLTUM. Reinwardtia 4 (1957) 277.—*Gleichenia subpectinata* CHRIST, Bot. Tidsskr. 24 (1901) 111.—*Gleichenia pteridifolia* (non *Mertensia pteridifolia* PRESL) RIDL, J. Mal. Br. R. As. Soc. 4 (1926) 4.—*D. warburgii* (non *Gleichenia warburgii* CHRIST) sensu NAKAI, Bull. Nat. Sc. Mus. Tokyo n. 29 (1950) 70.—*Gleichenia linearis* var. *alternans* (non METT.) HOLTUM. Rev. Fl. Mal. 2 (1955) 70 and frontispiece.—Fig. 12c, 16.

Lateral branch-systems several times forked, branches at successive forks alternately unequal, successive larger branches forming almost a straight line; ultimate branches 9–15 cm long, 2–3½ cm wide (sterile ones sometimes to 18 by 6 cm); lamina thin, lower surface pale glaucous and quite glabrous when mature; segments of

lamina gradually and rather evenly tapering from base to apex, the sinuses thus narrowly triangular; costules 4–4½ mm apart; veins slightly raised on both surfaces, concolorous with lamina; the smaller accessory branches usually attached 3–5 mm above the forks (sometimes lacking or reduced at penultimate forks).

Type: Schmidt, Koh Chang Isl. (P).

Distr. Lower Siam (type from Koh Chang Island), and *Malaysia*: Sumatra, Malay Peninsula, Lingga Archipelago, Banka, Borneo.

Ecol. On edges of forest, in thickets with var. *linearis* and other varieties, climbing higher than var. *linearis*, from sealevel up to 700 m.

7. var. *subspeciosa* HOLTUM. Reinwardtia 4 (1957) 278.—Fig. 12c, 14h.

Resembling *D. speciosa* in shape, texture etc. of ultimate branches and in hairiness, but lateral branch-systems branched as in var. *alternans*.

Type: Topping 1516, Mt Kinabalu, Kiau (US; dupl. at SING).

Distr. *Malaysia*: Sumatra, Malay Peninsula, Borneo, and Philippines (Mindanao, Mindoro, Luzon).

Ecol. On edges of forest, in thickets with other varieties, 0–1400 m.

8. *var. inaequalis* (ROSENST.) HOLTT. Reinwardtia 4 (1957) 278. — *Gleichenia linearis var. inaequalis* ROSENST. in Fedde, Rep. 13 (1915) 212; v. A. v. R. Handb. Suppl. (1917) 85.

Shape and venation of *lamina-segments*, and hairiness, as in *var. subspectiosa*, differing as follows in branching: forking in lateral branch-systems alternately very unequal, the angle of the forks much more than a right angle (sometimes nearly 180°), the smaller branch at a fork simple or once forked and sometimes lacking an accessory branch, the accessory branch on the larger branch attached 5–10 mm above the base of that branch.

Type: J. Winkler 114, Batakerland, Sumatra (H. Selim Birger, S).

Distr. *Malaysia*: Sumatra, Malay Peninsula (three collections in all).

Ecol. Altitude c. 1400 m.

9. *var. alternans* (METT.) HOLTT. Reinwardtia 4 (1957) 278.—*Gleichenia dichotoma var. alternans* METT. in Miq. Ann. Mus. Bot. Lugd. Bat. 1 (1863) 51.—*Gleichenia linearis var. alternans* v. A. v. R. Handb. Suppl. (1917) 84.—Fig. 12c, 14i.

Very similar to *var. linearis* in texture, shape, and hairiness of the ultimate branches, but lateral *branch-systems* several times forked, the branches at successive forks alternately unequal about as in *var. subpectinata*, differing from the latter in larger somewhat hairy ultimate branches of much firmer texture.

Type: Korthals, Sumatra (L).

Distr. *Malaysia*: Sumatra, Malay Peninsula, Banka, Borneo.

Ecol. Apparently not common, but needs field study; perhaps only a growth-form of *var. linearis*; from sealevel up to 500 m.

10. *var. demota* HOLTT. Reinwardtia 4 (1957) 275.

Lateral *branch-systems* several times forked, branches at successive forks alternately unequal; accessory branches normally present at all ultimate forks; ultimate branches to 18 cm long, 3–6 (rarely to 7) cm wide; costules 5 mm apart; *lamina* thin, lower surface glabrous and probably glaucous; veins distinctly prominent on upper surface and slightly so on lower surface; accessory branches at the lower forks attached distinctly below the fork.

Type: Clemens 29535, Mt Kinabalu, 5600 ft (K; dupl. at BM, Bo, L, US).

Distr. *Malaysia*: N. Borneo, Ceram (doubtful), New Guinea.

Ecol. Altitude 1600–2250 m.

11. *var. tetraphylla* (ROSENST.) NAKAI, Bull. Nat. Sc. Mus. Tokyo n. 29 (1950) 67.—*Gleichenia*

*linearis var. tetraphylla* ROSENST. in Fedde, Rep. 13 (1914) 213; v. A. v. R. Handb. Suppl. (1917) 84.—Fig. 12b.

Lateral *branch-systems* several times forked, branches at successive forks alternately somewhat unequal; penultimate branches less than 1 mm diam. when dry; accessory branches always present at bases of ultimate branches; ratio of length to width of ultimate and accessory branches about 2 : 1; ultimate branches to 12 cm long and 7 cm wide, costules 3 mm apart, *lamina* very thin and strongly glaucous on the lower surface, quite glabrous; veins very slender, distinctly prominent on both surfaces.

Type: J. Winkler 136, Batakerland, Sumatra (H. Selim Birger, S).

Distr. Indo-China, Hainan, Kwangtung, in *Malaysia*: Sumatra.

Ecol. Altitude 1250 m.

Note. The specimens from China have ultimate branches proportionately rather narrower than those from Sumatra, but are otherwise similar.

12. *var. montana* HOLTT. Reinwardtia 4 (1957) 276.—*Gleichenia linearis var. montana* HOLTT. Rev. Fl. Mal. 2 (1955) 69, descr. angl.—Fig. 12b.

Lateral *branch-systems* several times equally forked; ultimate branches 15–25 cm long, 3½–6 cm wide; costules (5–)6–7 mm apart; *lamina* coriaceous, glabrous and glaucous on the lower surface, veins rather strongly prominent on both surfaces; accessory branches, about half as long as the ultimate branches, always present at the bases of ultimate branches.

Type: Molesworth Allen 2720 (SING).

Distr. Ceylon, S. India, Sikkim, in *Malaysia*: Sumatra, Malay Peninsula, Java, Borneo, and Moluccas (Ternate).

Ecol. On the edges of forest and in clearings, with other varieties of *D. linearis* and with other members of the family; 1000–1600 m.

13. *var. altissima* HOLTT. Reinwardtia 4 (1957) 276.—*Gleichenia linearis var. altissima* HOLTT. Rev. Fl. Mal. 2 (1955) 69, descr. angl.

Sometimes very high-climbing, the main *rachis* to 10 mm diameter; lateral *branch-systems* equally forked 4 or 5 times; ultimate branches to 15 cm long and 3 cm wide; costules 3½–4½ mm apart; *lamina* thin, lower surface glaucous, glabrous apart from scattered rusty hairs on lower surface of costules; veins prominent on upper surface, not on lower surface; accessory branches always present at bases of ultimate branches.

Type: Corner 31447, Johore, Malay Peninsula (SING; dupl. at K, L).

Distr. *Malaysia*: Malay Peninsula, Philippines (Palawan, Luzon), Moluccas (Talaud), New Guinea, and Solomon Islands.

Ecol. At low altitudes, climbing on edges of forest.