STUDIES IN THE FAMILY THELYPTERIDACEAE III. A NEW SYSTEM OF GENERA IN THE OLD WORLD.

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The new scheme of classification presented in this paper is based on the examination of all species in the family *Thelypteridaceae* which I have been able to trace in the Old World. I have gradually compiled a list of about 700 names (basionyms) and have examined type or other authentic material of all but a small proportion; and in the course of study of specimens in many herbaria I have noted about another 50 species which appear to be undescribed. I have attempted to re-describe all the previously-named species, noting characters not mentioned in existing descriptions, especially the detailed distribution of hairs and glands, including those on the body and stalk of sporangia, and characters of spores. It is probable that there remain some published names, not yet detected by me, which refer to species of the family, but I think there are not many.

I have also made a study of all generic and infrageneric names which are typifiable by species of *Thelypteridaceae*, and in doubtful cases I have tried to clarify and fix the typification. As already reported in the second paper of this series (Blumea 18: 195—215), I have had the help of Dr. U. Sen and Miss N. Mittra in examining anatomical and other microscopic characters of some type species, and hope to present further information of this kind later.

As a beginning, I adopted the generic arrangement of Ching (Acta Phytotax. Sinica 8: 289—335. 1963) with the exclusion of *Hypodematium* (which I am sure does not belong to the family) and the addition of *Sphaerostephanos* and *Haplodictyum* (which Ching wrongly excluded in 1940 and did not mention in 1963). It was soon apparent to me that the type species of *Cyclosorus* had little relationship to most of the species included in it by Ching and Copeland (Genera Filicum, 1947), and this led me to ask Dr. Sen to examine it in detail and to compare it with the type species of *Thelypteris*. As a result of this investigation, I concluded that *Cyclosorus s. str.* is a small and rather isolated group, in many ways a tropical counterpart of *Thelypteris s. str.* Apart from *Cyclosorus*, it appears to me that Ching's genera of 1963 are mostly natural groups, but that he did not characterize them clearly. Naturally he omitted consideration of a large number of Malesian species; these complicate the problem more than he realized, and the species falling within his concept of *Cyclosorus* must be subdivided, even after removing the type species.

The other author who has recently devoted a considerable study to this family in Asia is Iwatsuki (Mem. Coll. Sci. Univ. Kyoto B, 30: 21—51. 1963; 31: 1—40. 1964 and 125—197. 1965); his work includes the most comprehensive study to date of comparative morphology within the family. He made some modifications in Ching's scheme of classification, but these do not seem to me an improvement. Like Ching, he had little acquaintance with the Malesian species which form the major part of the family in the Old World. Morton's conspectus of the family (Amer. Fern. J. 53: 153—154. 1963) has little reference to species of the Old World.

Most African species appear to have no close relatives in Asia and Malesia, and it seems to me possible that at least some of them have a relationship to species-groups in the Americas. Apart from these, it looks probable that the only species-groups common to the Old and New Worlds are the small groups of *Thelypteris*, *Oreopteris*, *Phegopteris*, *Stegnogramma*, and *Cyclosorus* (as limited in the present paper) and the larger group named *Thelypteris* subg. *Cyclosoriopsis* by Iwatsuki; the latter has more species in the Old World than in the New. Thus it seems to me possible to present an analysis of the Old World species (omitting some in Africa) without the likelihood that it will upset or be upset by study of New World species. I hope the time is not far distant when the latter will receive a new analysis. I realize that the present attempt is only tentative, and it will probably raise many new problems. At least I hope it will throw some light on aspects of the subject which have hitherto been little considered. Nearly all species already have names in *Thelypteris*, so that authors who prefer to regard my genera as subgenera or sections of *Thelypteris* can easily do so.

In generic diagnoses I give what appear to me to be the assemblages of characters which are distinctive of each, and then cite the type species. In most cases I have not indicated all the older generic synonyms; nearly all species were included in *Dryopteris* by Christensen (*Index Filicum*, 1905, and three Supplements) and variously in other genera by earlier authors. Copeland (Gen. Fil. 1947; Fern Fl. Philip. 1960) included nearly all in *Lastrea* and *Cyclosorus*. I do not here propose transfer of specific epithets except in the case of type species. I intend to publish the necessary new combinations when I have made monographic studies of the various genera; but I give here a fairly complete list of basionyms which I believe belong to each genus. Some of these will later have to be reduced to synonymy, and there will be new species to be added.

Major subdivisions in the family are not easy to discern. The present great diversity within it is probably a rather recent development. Fossils with anastomosis of veins of the Thelypteroid type have been found in lower Tertiary rocks in both Europe and America (see note under *Haplodictyum*) but they lack the kind of diagnostic detail now seen to be necessary to distinguish species-groups within the family. In the Old World the main generalization possible is that the genera here numbered 16—21, which include 55 % of all Old World species, form a natural group (see discussion under *Pronephrium*); so far as known, all have the base chromosome number 36. If all these were included in one genus, its name would have to be *Stegnogramma* Bl. The rest of the genera constitute a number of smaller rather isolated groups. It looks to me as if *Mesophlebion*, *Chingia*, and *Glaphyropteridopsis* may be inter-related. *Coryphopteris* and *Parathelypteris* form an isolated group of free-veined species with small fronds, the majority (*Coryphopteris*) with short erect caudex; many have some septate hairs. They may preserve some of the primitive characters of the family, but do not look like a stock from which the remaining Old World genera can have arisen.

Prof. T. M. Harris has described a Jurassic fossil fern *Aspidistes thomasii* (The Yorkshire Jurassic Flora I: 181. 1961) which has spherical glands on the lower surface of the lamina, much as in *Coryphopteris*, with sporangia and sori of comparable size and form; the frond may, however, have been tripinnate and the leaflets are more like those of *Pseudophegopteris*. The spores are trilete, much as in *Trigonospora* of the present arrangement. These facts may indicate that evolution in the family has resulted in primitive characters being dispersed among different species-groups of today.

The family *Thelypteridaceae* shows many resemblances to the genus *Cyathea* and I believe these to be significant. They may be summarized as follows.

Shape of leaflets (pinnae in most Thelypteroids, pinnules in *Cyathea*). These have an

almost symmetrical base, sides parallel for most of their length, edges lobed with almost symmetric pinnate venation in each lobe.

Shape of fronds. Many pinnae are of similar length, changes near base and apex of frond being relatively abrupt in most cases.

Base of fronds. In some species the lower pinnae are progressively smaller almost down to the caudex, so that the true stipe is short; in others the lowest pinnae are at most slightly reduced, the stipe being elongate. In *Cyathea* closely related species may have one character or the other; in *Thelypteridaceae* each species-group (or genus) has its own character of this kind.

Hairs on upper surface of rachis and costae. These are non-glandular and they are antrorsely curved. In *Cyathea* they consist of several cells, in *Thelypteridaceae* usually of one cell, but in a few species-groups septate hairs occur (*Coryphopteris, Stegnogramma*).

Hairs on lower surface of rachis, costae, and other parts are more varied and more distinctive of individual species.

Aerating tissue. There is a line of aerating tissue (with stomata in the epidermis) down each side of the rachis. This connects the decurrent base of the lamina of one pinna with the edge of the pinna below it. In addition there is a patch of aerating tissue at the base of each pinna on the abaxial side. This patch is always conspicuous on young fronds and is slightly prominent in some species of *Cyathea;* in some Thelypteroids it becomes much swollen or elongate (see note below on aerophore characters).

Indusiate round sori seated on a vein, with vascular tissue passing from the vein into the base of the sorus.

Cyathea species have somewhat less specialized sori and sporangia, and a much more complex vascular system than Thelypteroids; they are likely to be an older group (though there is little evidence from fossils) but they are still a very active one. *Thelypteridaceae* look like somewhat simplified, more efficient, and more diversified relatives of *Cyathea,* and they are certainly in a very active state of development. If one looks to cytology for evidence of relationships, one finds that all species of *Cyathea* so far examined have a chromosome number 69. This is about double the numbers found in *Thelypteridaceae.* It would seem possible that both spring from ancestors with about 35 chromosomes.

CHARACTERS USED IN CLASSIFICATION

As indicated in the second paper in this series, each species-group which can be recognized in the family is characterized by a combination of characters. Few groups can be distinguished by one single character, and in some cases characters (e.g. anastomosis of veins) which are constant in almost all members of a natural group may be lacking in some species. In different groups, different kinds of characters may be of greatest significance or constancy, but there are almost always exceptions. Negative characters may be as important as positive ones; for example, I believe that the complete absence of sessile spherical glands in *Christella* and *Pneumatopteris* is significant. I have found that a binocular microscope with magnification × 25 is essential for examination of hairs and glands, and × 50 is better; the latter is necessary as a minimum when examining sporangia. Though most species, when known, at least in one area, may be recognizable by macroscopic characters, the small characters of hairs and glands must be used for the precise description of many species and for distinction between genera or other species-groups.

Caudex. This may be erect, suberect, short-creeping, or long-creeping; only in the last-named case is it properly a rhizome. Though in a few cases all species in a genus

(as here recognized) may have an erect caudex or a long-creeping rhizome, in most genera there is no constancy in this character. The rhizome is never dorsiventral in structure. In some species of *Sphaerostephanos* the caudex is a slender trunk 100 cm or more tall; in a few others, in New Guinea, it is scandent on tree-trunks; the wide-ranging species of open country originally named *Polypodium unitum* L. has a long and branching rhizome.

Scales. The young parts of the caudex and the bases of fronds are protected by conspicuous scales. The more distal parts of a frond usually bear progressively smaller scales, those on the pinnae being often reduced to a short hair-like single row of cells with glandular apex (such a single row of cells is part of the early development of all scales). In most *Thelypteridaceae* the scales on the leafy parts of fronds are small and soon shrivelled and shed, but in others (e.g. *Mesophlebion*) scales on pinnae are well developed, persistent and diagnostically important. Scale-bases are usually rather thick, and a stipe-scale appears like an outgrowth from the surface of the stipe, carrying on its surface and edges unicellular hairs of the same type as those on the surface of the stipe; thus a majority of scales have superficial unicellular acicular or glandular hairs (these are usually outgrowths from the cells of the scale, not separate cells), but in some genera the scales are broad, thin and lack syperficial hairs. The edges of scales often bear outgrowths which are multicellular and gland-tipped; these should not be confused with the unicellular hairs. Scales on young fronds of some species have long septate marginal hairs ending in large mucilage cells; such occur in various genera.

Frond-form. The principal distinction in frond-form is between species having reduced basal pinnae and those in which the lowest pinnae are largest or little reduced. Among species lacking reduced basal pinnae one may distinguish those in which the frond-apex is pinna-like from those in which it is composed by gradual transition from smaller upper pinnae, but this distinction is not always a sharp one. Whether the lower pinnae are reduced or not, the lowest large pinnae often differ from upper ones in being gradually narrowed towards their bases, and this may be an important character. In some species the transition between large and reduced pinnae is not abrupt, and in a minority it is quite gradual; such cases are often difficult to classify.

Pinnae and venation. The approximate number of pinnae on a mature plant is distinctive, and their shape and size; one takes the largest middle pinnae as standard for comparison. Depth of lobing and shape of pinna-apex are fairly constant characters in fronds of mature plants of a species. The costule of each lobe bears veins in a pinnate pattern, and where the lobing is not deep veins from adjacent costules anastomose, forming an excurrent vein which runs to the ttanslucent membrane filling the base of a sinus between two lobes (the membrane may be folded, the fold prominent on the lower surface); the next veins may run to the sides of the membrane. Where the lobing is shallow more than one pair of veins may anastomose, and the joint excurrent vein is then usually zig-zag; in some cases some individual excurrent veins may be free, as occurs invariably in the tropical American genus *Meniscium*. In the case of deep lobing, basal veins are usually free, and the position at the margin of the ends of these veins is important. In a few species-groups the veins do not reach the margin. The margin usually consists of at least one row of hyaline cells, sometimes more than one row. The sinus-membrane has the structure of two margins joined together, indicating an origin from a condition in which lobing was deeper. Even in the most deeply-lobed species there is some indi-

cation of a membrane, often obliquely decurrent from the sinus base (*Mesophlebion*).

The distinction veins free against veins anastomosing had been used as an important diagnostic one in the family (it is the sole distinction between *Lastrea* and *Cyclosorus* in Copeland's sense); but when delimiting genera on an assemblage of characters I have found that in several genera species with both free and anastomosing veins had to be admitted, though in other genera all species have free veins.

Aerophores. There is usually a line of aerating tissue down each side of the stipe and rachis; on the rachis this line joins the edges of the lamina of successive pinnae. In addition, at the base of each pinna on the abaxial side is a small patch of aerating tissue (which may be crescent-shaped or triangular), variously developed. In some species this patch of tissue becomes much enlarged and may elongate to 2 mm or more; it then serves as an aerating organ while the frond is unfolding and usually in such cases the young frond is covered with mucilage through which the aerophore projects. The occurrence of swollen aerophores has been regarded as a significant generic character (some Asiatic species have been placed in a genus *Glaphyropteris*, based on a species of tropical America, solely because they had this character in common); but I am sure that closely allied species may have or lack swollen aerophores. In a few cases there is also a distinct swelling at the base of each costule. Most species lacking reduced basal pinnae lack also swollen aerophores, but a few have them.

Pubescence. The upper surface of rachis and costae invariably carries unicellular acicular hairs (in a few species they are sparse); on the costae, usually also on the rachis, these hairs are curved antrorsely. In some genera some of these hairs may be septate (perhaps more cases of this are still to be observed). The hairs on other parts of rachis and pinnae are always of diagnostic significance and need to be described carefully for each surface separately. There are almost always some acicular hairs; there may also be short capitate hairs (the head of such hairs in some cases distinctly covered with a waxy or resinous substance) and sessile spherical glands, usually yellow. In *Christella* unicellular, thick, cylindric or club-shaped, reddish, glandular hairs may be present. The presence of glands is always significant, and in many cases has not hitherto been recorded.

Pustular surface of lamina. Dried fronds of most species of *Pronephrium*, *Pneumatopteris*, and *Mesophlebion* subg. *Plesioneuron* have more or less abundant irregular, small, pustular swellings on the surface of the lamina between veins. These pustules are presumably due to some hard substance which does not shrink on drying; the nature of the substance has not been investigated.

Fertile fronds. In many species fertile fronds have longer stipes than sterile ones, and may stand erect above the latter. In such cases fertile pinnae are often smaller than sterile, sometimes much smaller (especially narrower). The sori may then cover the lower surface, and indusia if present are not easy to see distinctly, so that sometimes they have wrongly been reported lacking. In a few cases the pubescence of the lower surface of fertile pinnae, even if not much different in size from sterile ones, may be different. In some species sori, indusiate or not, spread along the veins. In *Coryphopteris* indusia are often *Athyrium*-like.

Sporangia. The presence of acicular or glandular hairs near the annulus of sporangia is always diagnostic; hairs have often been reported, but glands rarely (they may not

occur on every sporangium). On the stalks of sporangia are often hairs of varying length. The presence of these hairs and especially of glandular cells at their tips is important. I have found that in *Christella* the elongate unicellular hairs are always present on sporangium-stalks, but in some species are lacking from the lower surface of veins (presence or absence on veins may even be only a varietal character).

Spores. Spores are certainly important, and special techniques are needed to observe them adequately. My observations are crude and tentative, but I think they have some significance. The spores of *Christella* are certainly distinct from those of *Sphaerostephanos* and *Pneumatopteris*.

Chromosomes. Basic numbers from 27 to 36 (except 33) have been recorded for species of this family; the great majority have 36. So far as present evidence goes, species which on grounds of general morphology appear to form a natural group all have the same base number; but not all species with the same number belong to the same natural group. There is a small group in Asia and Malesia, here named *Metathelypteris* Ching, which is certainly not closely related to *Thelypteris palustris*, but both have a chromosome number 35.

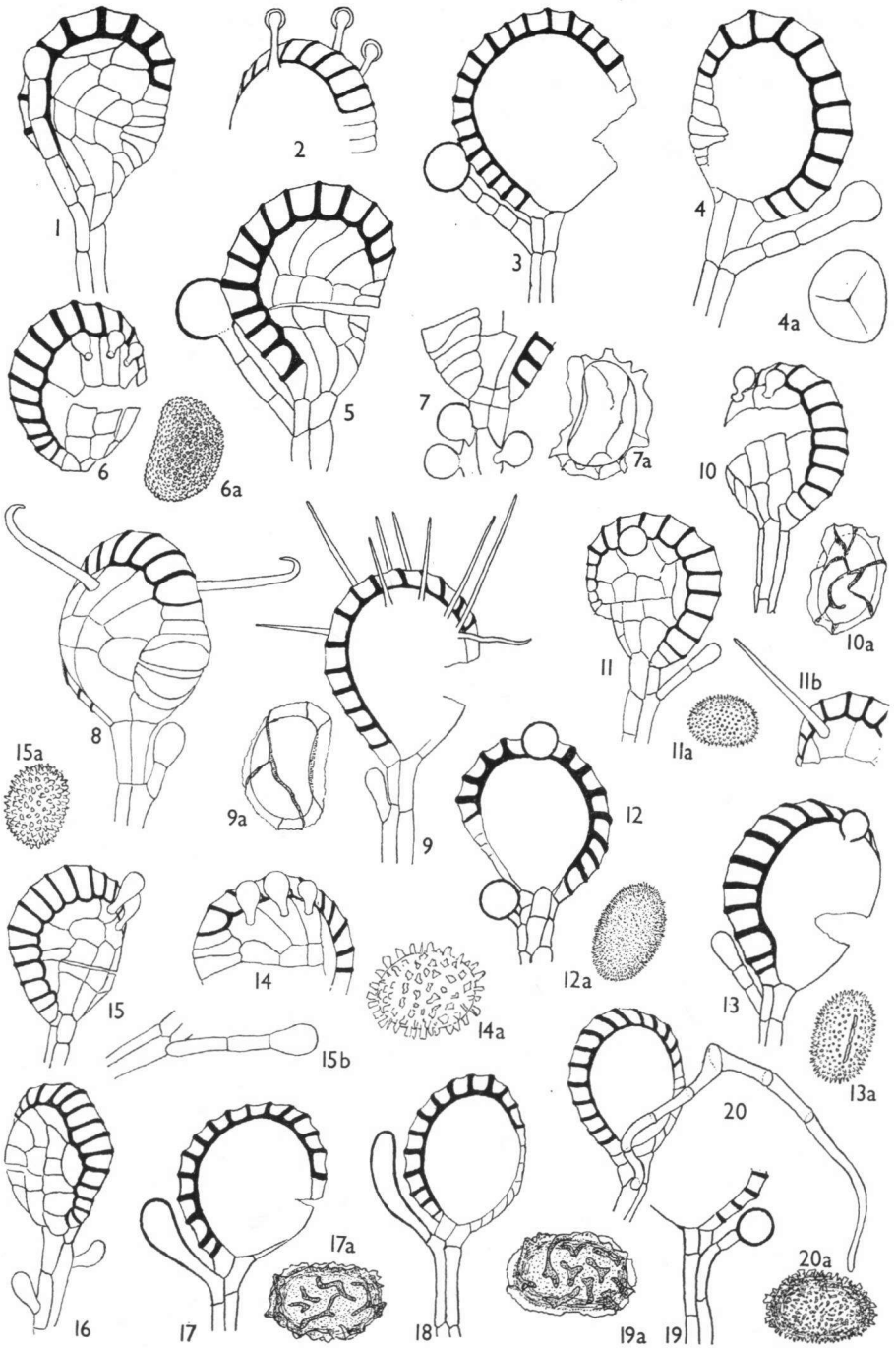
Anatomical characters. Some which appear to be significant have been recorded in the second paper of this series. I have not included them in the generic diagnoses; but such characters may prove helpful as further evidence of generic status in doubtful cases. Much more observation of all characters is needed before one can be confident which are significant.

Gametophytes. I have not mentioned these in the present paper. I have little first-hand knowledge of them, and I believe that primary classification needs to be based on characters which are observable in the sporophyte. But a comparison of gametophyte characters will certainly be of great interest, and may well prove helpful in making a critical revision of the present arrangement.

KEY TO THE GENERA

1. Many buds present on rachis, giving rise to new plants while still attached to the old; some unicellular hairs on rachis forked or branched . . . . . **1. Ampelopteris**
1. At most 1 or 2 buds on rachis, never much proliferating; no forked hairs.
   2. Midribs of pinnae not grooved on upper surface; veins mostly forked, their tips not reaching the margin (except sometimes distal ones).
      3. Stipe-scales with marginal acicular hairs, none on surface; pinnae connected by a wing along rachis, the wing forming semicircular lobes between pinnae . . . . . **2. Phegopteris**
      3. Stipe-scales bearing hairs on surface; rachis-wing, if present, narrow and of even width.
         4. Scales on axes of fronds usually sparse, smaller ones reduced to a row of short cells with brown cross-walls, not ending in a slender hair.
            5. Fronds mostly bipinnate, with pinnae adnate to pinna-rachis; sori exindusiate; spores with a slightly raised surface reticulum . . . . . **3. Pseudophegopteris**
            5. Fronds mostly simply pinnate; sori indusiate; spores otherwise . . . **4. Metathelypteris**
         4. Scales on axes of fronds otherwise, ending in an acicular hair, usually with transitions to long slender septate hairs . . . . . **5. Macrothelypteris**
   2. Midribs of pinnae grooved on upper surface except at junction with rachis; veins mostly simple, their tips reaching the margin or joining other veins.
      6. Lower pinnae not or little reduced; cylindric glandular hairs lacking on lower surface of veins and absent from sporangium-stalks.

7. Rhizome long-creeping; flat thin scales lacking superficial hairs present on lower surface of costae.
   8. Veins anastomosing; large spherical glands at ends of hairs on sporangium-stalks **6. Cyclosorus**
   8. Veins free, mostly forked; such glands lacking . . . . . **7. Thelypteris**
7. Rhizome mostly short-creeping or erect; if long-creeping, such scales lacking on costae.
   9. Veins all free.
      10. Hooked hairs present on lower surfaces . . . . . **8. Cyclogramma**
      10. Hooked hairs lacking.
         11. Spores trilete. . . . . **9. Trigonospora**
         11. Spores monolete.
            12. Basal basiscopic vein of each group arising from costa, at least towards apex of a pinna.
               13. Capitate hairs lacking on lower surface and on sporangia **10. Mesophlebion**
               13. Capitate hairs present on lower surface and on sporangia . **12. Chingia**
            12. Basal veins always from costule.
               14. Sori running almost all along veins; no indusia; sporangia with slender setae **19. Stegnogramma**
               14. Sori not or little running along veins; indusia in most cases present.
                  15. Fronds large, drying red-brown; basal scales broad, thin, not hairy; sori small, close to costules; indusia none or very small **11. Glaphyropteridopsis**
                  15. Fronds rarely large, drying greenish or dark olivaceous; scales mostly narrow and hairy; sori various, rarely very close to costules.
                     16. Fronds with 20—35 pairs of pinnae *c.* 2 cm long; glands present on sporangia . . . . . **18. Nannothelypteris**
                     16. Fronds usually with fewer and larger pinnae; no glands on sporangia.
                        17. Rather small plants of mountains; spores with translucent wing.
                           18. Rhizome slender . . . . . **14. Parathelypteris**
                           18. Rhizome erect, bearing many roots **15. Coryphopteris**
                        17. Large plants of low country; spores with numerous broad dark irregular warts or ridges . . . . . **23. Amphineuron**
   9. Veins anastomosing (at least the basal ones of adjacent costules).
      19. Rigid spine-like scales present on stipe and usually on lower part of rachis; sori near costules, indusium small or lacking; basal basiscopic vein of each group from costa near base of costule. . . . . **12. Chingia**
      19. Such scales lacking; sori rarely very close to costules; basal basiscopic vein arising from costule above base of costule.
         20. Sori running almost all along veins including basal excurrent vein, exindusiate; sporangia setose; spores spinulose . . . . . **19. Stegnogramma**
         20. Sori rarely running along veins, in many cases indusiate; sporangia not always setose; spores usually not spinulose.
            21. Frond consisting of a narrow, parallel-sided, apical lamina with 0—4 pairs of small pinnae, with or without 1 or 2 pairs of very small ones below them; some veins of apical lamina usually forked, forming additional areoles along costules; sori indusiate. . . . . **17. Haplodictyum**
            21. Fronds with many pairs of pinnae, or if with few small ones the apical lamina elliptic; venation normal; sori indusiate or not.
               22. Pinnae always deeply lobed; spores dark, irregularly tuberculate **23. Amphineuron**
               22. Pinnae lobed less than half way to costa; spores pale, winged or minutely papillose.
                  23. Spores trilete . . . . . **9. Trigonospora**
                  23. Spores monolete. . . . . **16. Pronephrium**
6. Lower pinnae gradually or abruptly reduced, lowest much smaller than middle ones; or cylindrical unicellular hairs present on stalks of sporangia.
   24. Cylindric unicellular hairs present on sporangium-stalks, sometimes also on lower surface of veins; sessile spherical glands lacking; sporangia never setose; lower pinnae in almost all cases gradually reduced, lowest never minute . . . . . **22. Christella**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24. Cylindric glandular hairs lacking; sessile spherical glands present in many species; lowest reduced pinnae often very small.
    25. Basal stipe-scales broad and thin; acicular hairs on frond never long nor abundant; surface of lamina ± pustular; short capitate hairs often present on frond or sporangia but not spherical glands . . . . . **21. Pneumatopteris**
    25. Basal stipe-scales usually narrow and hairy; acicular hairs always rather abundant; surface of lamina rarely pustular; spherical glands often present.
        26. Veins free.
            27. Hooked hairs present on lower surface . . . . . **8. Cyclogramma**
            27. Hooked hairs lacking.
                28. Sporangia short-stalked, no glands near annulus.
                    29. Rhizome slender, long-creeping. . . . . **14. Parathelypteris**
                    29. Rhizome erect . . . . . **15. Coryphopteris**
                28. Sporangia with slender stalks, often with glands or setae near annulus.
                    30. Large glands present on lower surface; sori submarginal **13. Oreopteris**
                    30. Small spherical glands or none; sori not always submarginal.
                        31. Reduced pinnae always sharply distinct and very few; spores dark, irregularly tuberculate . . . . . **23. Amphineuron**
                        31. Basal pinnae sometimes gradually reduced, sometimes a sharp transition to small ones; spores pale, usually spinulose, rarely with a thin wing. . . . . **20. Sphaerostephanos**
        26. Veins anastomosing, at least in apical lamina of frond.
            32. Apical lamina long and narrow; veins at least near base forming costular areoles; pinnae few and small . . . . . **17. Haplodictyum**
            32. Additional areoles along costules absent, or present only in fronds with large pinnae.
                33. Reduced pinnae very few; at most basal pair of veins anastomosing; spores dark, irregularly tuberculate . . . . . **23. Amphineuron**
                33. Reduced pinnae usually many; often more than one pair of veins anastomosing; spores light brown, spinulose. . . . . **20. Sphaerostephanos**

1. AMPELOPTERIS

Kunze, Bot. Zeit. 6 (1848) 114; Copel., Gen. Fil. (1947) 143; Holttum, Rev. Fl. Mal. 2 (1954) 298; Ching, Acta Phytotax. Sinica 8 (1963) 330; Holtt., Sen & Mittra, Blumea 18 (1970) 196, 214. — *Dryopteris* subg. *Goniopteris* (Pr.) C. Chr., Dansk Vidensk. Selsk. Skr. 7 Afd., X, no. 2 (1912) 146, *p.p.* — *Meniscium* sect. *Goniopteridopsis* H. Ito in Nakai & Honda, Nov. Fl. Jap. no. 4 (1939) 186. — *Meniscium* sect. *Ampelopteris* K. Iwats., Mem. Coll. Sci. Univ. Kyoto B, 31 (1964) 39. — *Thelypteris* subg. *Meniscium* sect. *Ampelopteris* Reed, Phytologia 17 (1968) 255.

Fronds of indefinite apical growth, bearing many buds on rachis which form new plants freely; forked unicellular hairs present on rachis; pinnae subentire; veins almost all anastomosing with few residual free ones running to the margin; sori exindusiate; hairs on stalks of sporangia bearing terminal glandular cell.

Type and sole species: *A. elegans* Kze = *A. prolifera* (Retz.) Copel.

Distribution: throughout tropics of Old World.

Chromosome number: 36.

Sporangia (×50) and spores (×350) of Malesian *Thelypteridaceae. Metathelypteris*, fig. 1 *(singalanensis). Macrothelypteris*, fig. 2 *(torresiana). Cyclosorus*, fig. 3 *(gongylodes). Trigonospora*, fig. 4, 4a *(ciliata). Mesophlebion*, fig. 5 *(chlamydophora). Chingia*, fig. 6, 6a *(ferox*, Malay Peninsula*). Coryphopteris*, fig. 7 (n. sp. near *viscosa*) 7a *(pectiniformis). Pronephrium* sect. *Grypothrix*, fig. 8 *(triphyllum)*; sect. *Pronephrium*, fig. 9, 9a *(urophyllum)*; sect. *Dimorphopteris*, fig. 10, 10a *(glandulosum). Sphaerostephanos*, fig. 11, 11a, 11b *(stipellata)*, fig. 12, 12a *(unita)*, fig. 13, 13a *(megaphylla)*, fig. 20, 20a *(larutensis). Pneumatopteris*, fig. 14, 14a *(callosa)*, fig. 15, 15b *(ecallosa). Christella*, fig. 16 *(contigua)*, fig. 17, 17a *(sumatrana)*, fig. 18 *(arida). Amphineuron*, fig. 19, 19a *(opulentum)*.

2. PHEGOPTERIS

Fée, Gen. Fil. (1852) 242, *emend.* Ching, Acta Phytotax. Sinica 8 (1963) 312; Holtt., Blumea 17 (1969) 9. — *Polypodium* § *Phegopteris* Presl, Tent. Pterid. (1836) 179, *p.p.* — *Thelypteris* subg. *Phegopteris* sect. *Phegopteris* K. Iwats., Mem. Coll. Sci. Univ. Kyoto B, 31 (1964) 25. — *Thelypteris* subg. *Phegopteris* sect. *Lastrella* K. Iwats. l.c., *spec. typ. tantum.*

Fronds bipinnatifid with adnate pinnae which are connected along the rachis by a wing which forms semicircular lobes between them, the lobes with separate venation; veins free, lower ones not reaching margin; scales on rachis and costae bearing slender, spreading, unicellular, marginal hairs and an elongate unicellular tip; sori subterminal on veins, exindusiate or with very small indusia; sporangia bearing short acicular or capitate hairs.

Type species: *Polypodium phegopteris* L. = *Phegopteris polypodioides* Fée = *Phegopteris connectilis* (Michx) Watt.

Distribution: North temperate regions; one species in SE. Asia.

Species 3 (see Holttum l.c.)

Chromosome number: 30 (*connectilis* triploid; *hexagonoptera* diploid; *decursive-pinnata* diploid and tetraploid.)

3. PSEUDOPHEGOPTERIS

Ching, Acta Phytotax. Sinica 8 (1963) 313; Holtt., Blumea 17 (1969) 12. — *Phegopteris* sect. *Lastrella* H. Ito in Nakai & Honda, Nov. Fl. Jap. no. 4 (1939) 152 *excl. P. decursive-pinnata.* — *Thelypteris* subg. *Phegopteris* sect. *Lastrella* K. Iwats., Mem. Coll. Sci. Univ. Kyoto B 31 (1964) 25, (1965) 137—142, *excl. T. decursive-pinnata.* — *Toppingia* Deg. & Deg., Fl. Hawaii (1968) Fam. 17b. — *Macrothelypteris sensu* Pichi Sermolli, Webbia 24 (1970) 715—717, *p.p.*

Stipe and rachis glossy, ± flushed red-brown, scales (usually near base only) thin, red-brown, lacking conspicuous marginal hairs; scales on frond in most cases sparse, appressed, often reduced to a single row of short cells with dark red-brown walls, never thick and spreading; fronds usually large, bipinnate with adnate pinnules, lower pinnae in most cases ± reduced; veins free, usually branched, not running to margin; hairs on frond acicular or short-capitate, never conspicuously gland-like; sori exindusiate, often spread a little along veins; sporangia sometimes bearing acicular hairs; spores pale, with a slightly raised surface reticulum (size of mesh varying greatly).

Type species: *Polypodium pyrrhorhachis* Kze = *Pseudophegopteris pyrrhorhachis* (Kze) Ching.

Distribution: Islands of St. Helena & S. Thomé; wetter parts of tropical and subtropical Africa, Asia, Malesia, Polynesia, Hawaii.

Species 20 (see Holttum l.c.)

Chromosome number: 31 (*P. aurita* diploid & tetraploid; *P. pyrrhorhachis* tetraploid and hexaploid; *P. cyclocarpa* tetraploid).

4. METATHELYPTERIS

(H. Ito) Ching, Acta Phytotax. Sinica 8 (1963) 305. — *Thelypteris* sect. *Metathelypteris* H. Ito in Nakai & Honda, Nov. Fl. Jap. no. 4 (1939) 137; K. Iwats., Acta Phytotax. Geobot. 18 (1960) 147; Mem. Coll. Sci. Univ. Kyoto B, 31 (1964) 27, (1965) 145, *p.p.* (*excl. T. torresiana, T. ogasawarensis, T. viridifrons, T. ornata*). — **Fig. 1.**

Fronds pinnate with deeply lobed pinnae (in *M. hattorii* bipinnate with adnate pinnules); veins in pinna-lobes free, often forked, always ending short of the margin; costae prominent, not grooved, on upper surface; acicular and/or short capitate hairs present on lower surface, spherical sessile glands absent or rare; reduced scales on lower surface of costae about as in *Pseudophegopteris;* sori with thin indusia; sporangia sometimes with a hair on the stalk, no glands near annulus; spores dark, opaque, with thick wings or raised bands.

Type species: *Aspidium gracilescens* Bl. = *Metathelypteris gracilescens* (Bl.) Ching.

Distribution: India & Ceylon; S. China to Japan; Malesia, Solomon Isl.

Species about 12. *Thelypteris adscendens* Ching, *Dryopteris aureoviridis* Rosenst., *D. calva* Copel., *Thelypteris decipiens* Ching, *Dryopteris diversivenosa* v. A. v. R., *Aspidium flaccidum* Bl., *Dryopteris flavo-virens* Rosenst., *D. hattorii* H. Ito, *Aspidium laxum* Fr. & Sav., *Dryopteris media* v. A. v. R., *Nephrodium singalanense* Bak., *Dryopteris uraiensis* Rosenst., *Nephrodium vulcanicum* Bak.

Chromosome number: 35 (*flaccida* diploid and tetraploid in Ceylon, *singalanensis* tetraploid in Malaya).

5. MACROTHELYPTERIS

(H. Ito) Ching, Acta Phytotax. Sinica 8 (1963) 308; Holtt., Blumea 17 (1969) 25; Pichi Sermolli, Webbia 24 (1970) 715—717, *p.p.* — *Thelypteris* sect. *Macrothelypteris* H. Ito in Nakai & Honda, Nov. Fl. Jap. no. 4 (1939) 141; K. Iwats., Mem. Coll. Sci. Univ. Kyoto B, 31 (1965) 145, *p.p.* — **Fig. 2.**

Caudex short; scales at base of stipe narrow, thickened near bases, with acicular or capitate marginal and superficial hairs; fronds bipinnate-tripinnatifid with adnate pinnules; scales on rachis often with thickened bases, sometimes with marginal hairs, always with an acicular hair-tip; long, slender, septate hairs always present (few in type species); veins usually branched, not reaching margin; sori small, with small indusia (lacking in *M. ornata*); sporangia bearing capitate hairs near annulus; spores ± winged, not as in *Pseudophegopteris.*

Type species (specified by Ito, accepted by Ching): *Nephrodium oligophlebium* Bak. (doubtfully = *M. torresiana* var. *calvata*).

Distribution: Mascarene Islands, warmer parts of mainland Asia, Malesia, NE. Australia, islands of the Pacific (including Hawaii).

Species 9 (see Holttum l.c., with possible addition of *Thelypteris banaensis* Tard. & C. Chr.)

Chromosome number: 31 (*M. torresiana* tetraploid and hexaploid).

Pichi Sermolli has included here all species of *Pseudophegopteris,* stating that there is no clear distinction between the two genera. I believe that there is a clear distinction, both in scales on the frond and in spores. The small frond-scales of *Pseudophegopteris* are always like those of *Metathelypteris,* not of *Macrothelypteris.*

6. CYCLOSORUS

Link, Hort. Berol. 2 (1833) 128; Holtt., Sen & Mittra, Blumea 18 (1970) 200, 212; of all other authors *p.p.min.* — **Fig. 3.**

Rhizome long-creeping; fronds bipinnatifid, basal pinnae not reduced; thin flat scales present on lower surface of costae; spherical glandular cells present on lower surface of veins and at ends of hairs on stalks of sporangia, not on body of sporangia; spores with densely and irregularly spinulose exine and no perine.

Type species: *Aspidium gongylodes* Schkuhr (1809) = *Polypodium tottum* Thunb. (1800).

Distribution: throughout tropics and subtropics.

Species 2: the type and *Aspidium striatum* Schum. (Africa).

Chromosome number: 36 (*gongylodes* tetraploid in Jamaica, diploid in Africa and Asia, *striatum* diploid).

The type species is a complex, and specimens from all parts of its range have never been adequately compared. Morton (Contr. U.S. Nat. Herb. 38, 1967, 73) implies that there are two forms of the species, hairy and glabrous. I cannot distinguish two such forms clearly, and believe that other characters (e.g. distribution of glands) need to be taken into account. A discussion leading to the present restricted use of the generic name is given in Holttum, Sen & Mittra l.c.

7. THELYPTERIS

Schmidel, Icon. Plant. ed. J. C. Keller (1763) 45, t. 11, 13; Fernald & Weatherby, Rhodora 21 (1919) 21—36; Pichi Sermolli, Webbia 9 (1954) 409—417; Ching, Acta Phytotax. Sinica 8 (1963) 297; Rauschert, Taxon 15 (1966) 180; Morton, Contr. U.S. Nat. Herb. 38 (1967) 71; Holtt., Taxon 17 (1968) 330; Holtt., Sen & Mittra, Blumea 18 (1970) 205, 211.

Rhizome slender, long-creeping; fronds simply pinnate with deeply lobed pinnae, basal pinnae not reduced; veins all free, often forked, all running to margin; small, flat, thin scales present on lower surface of costae (also filamentous smaller ones); acicular and short capitate hairs present on lamina but not sessile spherical glands; sori indusiate; short capitate glandular hairs present on sporangia near annulus; spores with spinulose exine and no perine.

Type species: *Thelypteris palustris* Schott.

Distribution: north temperate regions, southern tropical and south Africa, Madagascar, S. India, Sumatra, New Guinea, New Zealand.

Species (see Fernald & Weatherby): probably 4 should be recognized, *T. palustris* being confined to temperate Europe and Asia; but if all are regarded as subspecies the oldest binomial is *Pteris confluens* Thunb. (1800) = *Thelypteris confluens* (Thunb.) Morton.

Chromosome number: 35.

8. CYCLOGRAMMA

Tagawa, Acta Phytotax. Geobot. 7 (1938) 52; Ching, Acta Phytotax. Sinica 8 (1963) 316. — *Glaphyropteris* sect. *Cyclogramma* H. Ito in Nakai & Honda, Nov. Fl. Jap. no. 4 (1939) 148. — *Thelypteris* subg. *Cyclogramma* K. Iwats., Mem. Coll. Sci. Univ. Kyoto B, 31 (1964) 26.

Rhizome short- to long-creeping; scales on stipe bearing acicular or hooked hairs on their surface; fronds drying dark olivaceous, bearing short hooked hairs on lower surface of all axes and usually also on sporangia; lower pinnae reduced or not; aerophores at bases at pinnae at least swollen, in most species elongate; pinnae deeply lobed; veins spreading at a wide angle to costule, basal ones from adjacent costules running to edge close to or just above sinus-membrane, never united; sori exindusiate, not elongate along veins, no glandular hairs on sporangium-stalks; spores pale with a translucent wing or finely spinulose.

Type species: *Thelypteris simulans* Ching = *C. simulans* (Ching) Tagawa (considered by Ching in 1963 to be a local form of *C. auriculata* (J. Sm.) Ching).

Species 7 or 8 (see Tagawa).

Distribution: Northern India (from Mussourie eastwards) to W. and S. China, Formosa, Luzon (*Jacobs 7299*, Mt. Pulog).

Chromosome number not recorded.

9. TRIGONOSPORA Holttum, *gen. nov.*

Pseudocyclosorus Ching, Acta Phytotax. Sinica 8 (1963) 322, *p.p.* — **Fig. 4, 4a.**

Filices praecipue ripariae. Caudex brevis erectus, radices multas tenaces gerens; frondes bipinnatifidae, pinnis imfimis non reductis; aerophorae non vel paulo dilatatae; venae simplices, liberae, vel venae infimae raro anastomosantes; vena infima acroscopica in membrana sinus terminata, vena infima basiscopica marginem supra basin sinus attingens; sori mediales vel inframediales, indusiati; sporangia non setis nec glandulis prope annulum praedita; stipites sporangiorum pilis pluricellularibus, cellulis ultimis globosis, saepe ornati; sporae triletae, minute papillosae.

Species typica: *Aspidium ciliatum* Benth., Fl. Hongkong. (1861) 455 (*Lastrea ciliata* Hook., 1857, *non* Liebm. *nec* Presl) = **Trigonospora ciliata** (Benth.) Holttum, *comb. nov.*

Distribution: India & Ceylon, S. China (including Hainan), Malaya, Sumatra, Java.

Species: probably about 8; some remain to be distinguished. *Aspidium calcaratum* Bl. (*s. str.*, *non sensu* Bedd.), *Thelypteris caudipinna* Ching, *Dryopteris pinnata* Copel., *Lastrea sericea* Scott *ex* Bedd., *Thelypteris zeylanica* Ching.

Chromosome number: 36 (*ciliata* diploid in Ceylon, tetraploid in Malaya).

Bentham attributed his species to Wallich, whose name he adopted; but Wallich's name was *nomen nudum* and Bentham's description applied to the Hong Kong ferns he cited; of these I select *Bowring 25* (K) as lectotype. Bentham (and Hooker before him) wrongly printed Bowman instead of Bowring, but the specimen, in Hooker's herbarium, can be identified from particulars of locality.

If, as I believe, *Thelypteridaceae* have a relationship to *Cyathea*, trilete spores must have been primitive in the family. So far as I know (certainly in the Old World) they only occur in *Trigonospora*, which in other respects is not evidently primitive. Ching included *T. ciliata* and *T. caudipinna* in his genus *Pseudocyclosorus*, because of the similarity in arrangement of the basal veins; but they differ from the type of *Pseudocyclosorus* (*Aspidium xylodes* Kze) in lacking reduced pinnae and in spores. One specimen from Burma in Kew herbarium represents, I believe, a species of this genus with basal veins anastomosing.

10. MESOPHLEBION

Holtt., *nom. nov.* — *Mesoneuron* Ching, Acta Phytotax. Sinica 8 (1963) 325, excl. *M. attenuatum* (orthographic variant of *Mezonevron* Desf., *Leguminosae*). — *Thelypteris* subg. *Glaphyropteridopsis* sect. *Mesoneuron* K. Iwats., Mem. Coll. Sci. Univ. Kyoto B, 31 (1964) 30 *p.p.*, excl. *Pseudocyclosorus* Ching. See also C. Chr., Gard. Bull. Str. Settl. 4 (1929) 381—388; Holttum, Rev. Fl. Malaya 2 (1954) 245—249, fig. 139—141.

Caudex creeping or erect; scales narrow, rather rigid, bearing short acicular hairs throughout; stipe and rachis in some species bearing persistent scales (or spine-like scale-bases) throughout, but persistent scales usually confined to base of stipe; frond simply pinnate (in one species simple), pinnae in most cases deeply lobed; basal pinnae not reduced, always narrowed towards their bases; aerophores sometimes swollen, rarely elongate; veins free (except in species with simple fronds), unbranched, basal acroscopic vein running to side of sinus-membrane, basal basiscopic vein arising from costa at a varied distance from the costule to which it belongs and passing to side of sinus-membrane or to edge just above it; lower surface variously hairy and scaly, rarely with sessile

spherical glands; sori usually indusiate, indusia often dark and firm; sporangia either with a gland-bearing hair on the stalk or glands or setae near annulus; spores with a wing or spinulose.

Type species: *Aspidium crassifolium* Bl. = **Mesophlebion crassifolium** (Bl.) Holtt., *comb. nov.*

Subgenus **Mesophlebion.** Rhizoma repens, interdum elongatum; lamina subtus non pustulosa; costae costulae venaeque subtus semper paleis parvis multis praeditae; sporangia prope annulum non setifera nec glandulosa; stipites sporangiorum pilis pluricellularibus glanduliferis praediti; sporae alatae. — **Fig. 5.**

Distribution: Peninsular Thailand & Burma; throughout Malesia except East Java and Lesser Sunda Islands.

Species at least 15. *Dryopteris auriculifera* v. A. v. R., *Nephrodium beccarianum* Cesati, *Dryopteris chlamydophora* Rosenst., *D. divergens* Rosenst., *Aspidium echinatum* Mett., *Dryopteris endertii* C. Chr., *Aspidium hallieri* Chr., *Nephrodium motleyanum* Hook., *Acrostichum oligodictyum* Bak., *Dryopteris paleata* Copel., *D. pallescens* Brause, *D. persquamulifera* v. A. v. R., *D. subdimorpha* Copel., *D. teuscheri* v. A. v. R., *D. trichopoda* C. Chr., *D. vinosicarpa* v. A. v. R.

Chromosome number: 36 (*crassifolium*, *paleata*, both tetraploid in Malaya).

Acrostichum oligodictyum Bak. (placed successively in *Leptochilus*, *Dryopteris*, *Syngramma*, and *Cyclosorus*) has dimorphous simple fronds with occasional anastomosis of the outer veins of adjacent groups; the basal veins of each group spring from the midrib of the frond. Hairs on the stalks of sporangia have large terminal glands as in this subgenus.

Subgenus **Plesioneuron** Holttum, *subg. nov.* Caudex brevis, repens vel erectum; aerophorae interdum ± dilatatae; vena infima basiscopica interdum e basi costulae orta, vel e costa prope apicem pinnae; costae costulaeque subtus paleis nullis vel paucis praeditae; sporangia plerumque setis rectis vel glandulis globosis vel leviter stipitatis prope annulum ornata; pili stipitum sporangiorum numquam glanduliferi; sporae plerumque spinulosae (vel alis permultis parvis vestitae).

Species typica: *Nephrodium tuberculatum* Cesati = **Mesophlebion tuberculatum** (Cesati) Holttum, *comb. nov.*

Distribution: Philippines (2 spp), New Guinea to Tahiti.

Species at least 30. *Dryopteris alta* Brause, *Lastrea archboldiae* Copel., *Dryopteris belensis* Copel., *D. bipinnata* Copel., *Aspidium brackenridgei* Mett., *Lastrea costulisora* Copel., *D. crassa* Copel., *Alsophila dryopteroidea* Brause, *Dryopteris ensipinna* Brause, *D. falcatipinnula* Copel., *D. fulgens* Brause, *Nephrodium hopeanum* Bak., *D. hunsteiniana* Brause, *Cyclosorus irayensis* Copel., *Aspidium koordersii* Chr., *Dryopteris marattioides* Alston, *D. myriosora* Copel., *D. notabilis* Brause, *D. ophiura* Copel., *Nephrodium phanerophlebium* Bak., *Lastrea prenticei* Carr., *Dryopteris quadriaurita* Chr., *D. quadriquetra* v. A. v. R., *Nephrodium savaiense* Bak., *Dryopteris septempedalis* Alston, *Lastrea varievestita* Copel., *Dryopteris wantotensis* Copel., *D. wariensis* Copel., *Cyathea woodlarkensis* Copel.

Chromosome number: 36 (*wantotensis sensu* Holttum & Roy, Blumea 13: 134 = *fulgens*).

Some members of this subgenus are strikingly similar to those of subg. *Mesophlebion* (most of which can be recognized generically at a glance) but they differ constantly in the characters mentioned. It appears to me that they may be related to *Chingia*. The basal scales of *Dryopteris marattioides* Alston are very similar to those of *Cyclosorus malodorus* Copel., which I place in *Chingia*.

Ching stated that the relationship of *Mesoneuron* to *Pseudocyclosorus* was 'without doubt', and Iwatsuki united the two as one section of subg. *Glaphyropteridopsis;* but I am placing *Pseudocyclorosus* as part of *Pneumatopteris.* I think Ching was unduly influenced by the arrangement of the basal veins; this arrangement occurs also in some species of tropical America (e.g. *Polypodium patens* Sw.) placed by Christensen in *Dryopteris* subg. *Cyclosorus* (here in *Christella*), and these do not seem to me at all nearly related to the species of *Pseudocyclosorus* Ching.

11. GLAPHYROPTERIDOPSIS

Ching, Acta Phytotax. Sinica 8 (1963) 320. — *Glaphyropteris* Fée, Crypt. Vasc. Brésil II (1873) 40 *p.p.* (*G. erubescens tantum*). — *Thelypteris* group 7, Ching, Bull. Fan. Mem. Inst. Biol. Bot. 6 (1936) 250. — *Glaphyropteris* sect. *Euglaphyropteris* H. Ito in Nakai & Honda, Nov. Fl. Jap. no. 4 (1939) 146. — *Thelypteris* subg. *Glaphyropteridopsis* sect. *Glaphyropteridopsis* K. Iwats., Mem. Coll. Sci. Univ. Kyoto B, 31 (1964) 29.

Caudex massive, short-creeping or erect; stipes scaly at base only, scales broad, thin, apparently not hairy; fronds moderate to large, drying brownish, not dark olivaceous; basal pinnae not reduced but deflexed and narrowed to their bases; pinnae lobed to 1—2 mm from costae; veins numerous, close, free, simple, basal veins from adjacent costules passing to sides of short sinus-membrane; lower surfaces variously acicular-hairy, not glandular; sori close to costules, exindusiate or with very small indusia; sporangia sometimes bearing setae near annulus; spores dark with many irregular, small, dark wings.

Type species: *Polypodium erubescens* Hook. = *Glaphyropteridopsis erubescens* (Hook.) Ching.

Distribution: NE. India, China.

Species 4. *G. eriocarpa* Ching, *Aspidium rufostramineum* Chr., *G. splendens* Ching.

Chromosome number: 36 (*erubescens*).

The form of fronds in this genus, their colour when dry, and the position of sori with absence or extreme reduction of indusia, show marked resemblances to the genus *Chingia.* Most species of *Chingia* differ in having anastomosing veins (though a Philippine species is now known to have free veins) and the two genera differ strikingly in the basal scales on caudex and stipes. It think it possible that the two genera are related.

12. CHINGIA Holttum, *gen. nov.*

Caudex erectus, validus, usque ad 30 cm vel ultra altus; stipes vel omnino vel basin versus solum dense paleatus, paleis rigidis, fragilibus, ubi fractis basibus earum persistentibus spiniformibus; frons ampla, in sicco saepe rufo-brunnea (haud atro-olivacea); pinnae lobatae, infimae non reductae; venae valde obliquae, paribus 1 vel 2 anastomosantibus (raro omnibus liberis); membrana sinus longa, subtus prominens; pagina inferior varie-vestita, pilis unicellularibus acicularibus vel capitatis vel minutis sessilibus glandiformibus; sori prope costulas, interdum (praecipue basales) leviter oblongi vel elliptici, exindusiati vel indusiis minutis praediti; sporangia interdum pilis brevibus capitatis prope annulum ornata; sporae fere nigrae, alis permultis minutis vestitae. — **Fig. 6, 6a.**

Species typica: *Aspidium ferox* Bl., Enum. Pl. Jav. (1828) 153 = **Chingia ferox** (Bl.) Holttum, *comb. nov.*

Distribution: Malesia, Solomon Isl., Caroline Isl., Tahiti.

Species 12—15 (including one undescribed from the Philippines having free veins). *Dryopteris armata* Rosenst., *D. atrospinosa* C. Chr., *Cyclosorus christii* Copel., *Dryopteris*

horridipes v. A. v. R., *Polypodium imponens* Cesati, *Dryopteris kusaiana* Hosok., *Goniopteris longissima* Brack., *Dryopteris malodora* Copel., *D. muricata* Brause, *Phegopteris perrigida* v. A. v. R., *Dryopteris supraspinigera* Rosenst.

Chromosome number not known.

This seems to me a very distinct group of species; see note under *Glaphyropteridopsis* above. The basal basiscopic vein usually springs from the costa, not from the costule to which it belongs, in the manner of *Mesophlebion*; the sporangia and spores are also somewhat like those of *Mesophlebion* subg. *Plesioneuron*.

13. OREOPTERIS

Holub, Folia Geobot. Phytotax. 4 (1969) 46. — *Lastrea* Bory, Dict. Class. Hist. Nat. 6 (1824) 588, *p.p.*; Ching, Acta Phytotax. Sinica 8 (1963) 299. — *Thelypteris* subg. *Lastrea* sect. *Lastrea* Morton, Amer. Fern J. 53 (1963) 153. — *Thelypteris* subg. *Thelypteris* sect. *Thelypteris* K. Iwats., Mem. Coll. Sci. Univ. Kyoto B, 31 (1965) 157, *p.p.*

Caudex erect; scales thin, many cells bearing short spherical outgrowths, acicular hairs lacking; frond gradually narrowed to base, lowest pinnae very short; pinnae deeply lobed; veins free, simple or forked, distal ones running to margin, lower ones not; sessile spherical glands usually present on lower surface; sori usually near margin; indusium often bearing glands; sporangia sometimes bearing glands near annulus and also on stalk.

Type species: *Lastrea oreopteris* Bory = *Oreopteris limbosperma* (All.) Holub.

Distribution: N. Temperate regions; further south in Africa?

Species: number uncertain; in Asia *Nephrodium elwesii* Bak., *Dryopteris quelpartensis* Chr.

Chromosome number: 34 (in all three species above mentioned).

Ching did not mention any clearly distinctive features; he wrongly stated that the scales are of Dryopteroid type, and that acicular hairs are absent from upper surface of rachis and costae. A new study of the genus is much needed, to establish its peculiar combination of characters (the spores need careful examination). Species placed in *Dryopteris* subg. *Lastrea* by Christensen in his Monograph of *Dryopteris* in America appear to be from another distinct group, and T. G. Walker has recently shown that several of them have a chromosome number 29 (Trans. R. Soc. Edinb. 66: 179. 1966); but this group also needs to be characterized more clearly. Some African species look as if they might belong to *Oreopteris* (e.g. *Aspidium strigosum* Willd.) but they need comparison also with the West Indian species which have chromosome number 29.

14. PARATHELYPTERIS

(H. Ito) Ching, Acta Phytotax. Sinica 8 (1963) 300, *p.p.* — *Thelypteris* sect. *Parathelypteris* H. Ito in Nakai & Honda, Nov. Fl. Jap. no. 4 (1939) 127. — *Thelypteris* subg. *Thelypteris* sect. *Thelypteris* K. Iwats., Mem. Coll. Sci. Univ. Kyoto B, 31 (1965) 157, *p.p.* (groups of *T. glanduligera* and *T. japonica*).

Rather small ferns; rhizome creeping, slender, sometimes much elongate; scales bearing superficial unicellular hairs, either spherical, acicular, or capitate; basal pinnae in most species not or little reduced, in a few species several pairs of lower pinnae progressively smaller; pinnae deeply lobed (basal one or more lobes sometimes free); basal acroscopic lobe or leaflet often somewhat enlarged and ± toothed; veins free, basal ones both reaching edge above base of sinus; acicular hairs on lower surface of costae in a few species some times septate, on upper surface always unicellular; reduced scales on lower surface of costa never large nor abundant; sessile glands almost always present on lower surface; sori indusiate; sporangia short-stalked, never bearing glands nor setae near annulus; a sessile

glandular cell sometimes on stalk of sporangium; spores often rather opaque, with narrow wing.

Type species: *Aspidium glanduligerum* Kze = *Parathelypteris glanduligera* (Kze) Ching.

Distribution: NE. India, S. China, Philippines, Japan; *P. beddomei* (Bak.) Ching also in Ceylon and throughout Malesia, locally on mountains.

Species about 10. *Aspidium angustifrons* Miq., *Nephrodium beddomei* Bak., *Dryopteris brassii* C. Chr., *Thelypteris calvata* Ching, *Dryopteris castanea* Tagawa, *Thelypteris chinensis* Ching, *Athyrium cystopteroides* Eaton, *Aspidium grammitoides* Chr., *Nephrodium japonicum* Bak., *Aspidium nipponicum* Fr. & Sav., *Aspidium parathelypteris* Chr.

Chromosome number: 31 (*beddomei*).

I here restrict this genus to part of Ching's sect *Parathelypteris*, with a few additions; see commentary under *Coryphopteris*.

15. CORYPHOPTERIS Holttum, *gen. nov.*

Parathelypteris sect. *Melanostipes* Ching, Acta Phytotax. Sinica 8 (1963) 301, *p.p.*

Generi Parathelypteridi Ching affinis, differt: caudice semper erecto, radices multas gerenti; pinnis infimis semper medio dilatatis, basin versus angustatis; costis subtus semper paleis reductis (interdum latis et conspicuis) praeditis; stipitibus basin versus interdum pilis longis pallidis septatis vestitis, pilis brevioribus etiam septatis interdum cum pilis unicellularibus costarum utrinque commixtis; glandulis sessilibus saepe carentibus; soris saepe asymmetricis, interdum symmetricis et elongatis; sporis late alatis, alis translucentibus. — **Fig. 7, 7a.**

Species typica: *Nephrodium viscosum* Bak., Syn. Fil. (1867) 264 = **Coryphopteris viscosa** (Bak.) Holtt., *comb. nov.*

Distribution: NE. India to S. China; throughout Malesia except Java and Lesser Sunda Isl.; in the Pacific to New Caledonia, Samoa, Marquesas.

Species at least 30. *Thelypteris angulariloba* Ching, *Dryopteris badia* v. A. v. R., *D. coriacea* Brause, *D. diaphana* Brause, *Thelypteris didymochlaenoides* Ching, *Dryopteris diversisora* Copel., *D. dura* Copel., *D. engleriana* Brause, *Aspidium fasciculatum* Fourn., *Dryopteris habbemensis* Copel., *Thelypteris herbacea* Holtt., *Lastrea hirsutipes* Bedd., *Athyrium horizontale* Rosenst., *D. indochinensis* Chr., *Lastrea klossii* Ridl., *Dryopteris lauterbachii* Brause, *D. linearis* Copel., *Nephrodium macgregorii* Bak., *Dryopteris megalocarpa* v. A. v. R., *D. multisora* C. Chr., *D. obtusata* v. A. v. R., *D. oligolepia* v. A. v. R., *D. pectiniformis* C. Chr., *Thelypteris petelotii* Ching, *Dryopteris platyptera* Copel., *D. plumosa C.* Chr., *D. propria* v. A. v. R., *Nephrodium pubirachis* Bak., *Dryopteris qualei* E. Brown, *Lastrea ridleyi* Bedd., *Dryopteris rigidifolia* v. A. v. R., *Lastrea robinsonii* Ridl., *Thelypteris simozawae* Tagawa, *Dryopteris squamipes* Copel., *D. stereophylla* v. A. v. R., *D. subnigra* Brause, *D. subviscosa* v. A. v. R., *D. supravillosa* C. Chr., *Lastrea unidentata* Bedd., *Dryopteris villosipes* Gepp.

Chromosome number: 32 (*pectiniformis*).

I am sure this is a natural group of species. In Malesia I have myself seen several species at many localities in Malaya, Borneo, and New Guinea; they always occur in peaty soil near the crests of mountain ridges, usually in the shade of ± dwarfed and ± mossy forest in the cloud zone. The volcanic mountains of Java do not appear to provide suitable conditions. The greatest diversification of species occurs in New Guinea. In the islands of the Pacific species only occur where there are mountains of adequate height.

I maintain this species-group as a separate genus distinct from *Parathelypteris* because the type species of the latter, *P. glanduligera*, has a slender creeping rhizome, whereas an

erect caudex is universal in *Coryphopteris*. The species left in *Parathelypteris* are more diverse; they are mostly not Malesian, and they appear to need a new comparative study. Ching divided *Parathelypteris*, including seven species here placed in *Coryphopteris*, into two sections, each divided into two series. I restrict *Parathelypteris* to sect. *Parathelypteris* Ching, with the omission of *Aspidium immersum* Bl. and *Thelypteris subimmersa* Ching (transferred to *Amphineuron*), adding to it the species *japonica* and *castanea* from sect. *Melanostipes*. Ching has transferred *Polypodium noveboracense* Linn. to *Parathelypteris* on account of its resemblance to the species *beddomei* and *nipponica*, and he may be right; more observations are needed. My new genus *Coryphopteris* corresponds approximately to sect. *Melanostipes* Ching, but I do not think that the distinctions he specifies between this and sect. *Parathelypteris* are valid, even for the species with which he deals. They are quite unacceptable when the many Malesian species are included; most of these he never saw.

16. PRONEPHRIUM

Presl, Epim. Bot. (1851) 258; Holtt., Novit. Bot. Inst. Bot. Univ. Carol. Prag. (1968) 48. — *Abacopteris* Fée. Gen. Fil. (1852) 309; Ching, Bull. Fan Mem. Inst. Biol. Bot. 8 (1938) 230; Acta Phytotax. Sinica 8 (1963) 331; Holtt., Rev. Fl. Mal. 2 (1954) 285. — *Dryopteris* § *Cyclosorus p.p.*, C. Chr., Ind. Fil. (1905) xxi. — *Dryopteris* subg. *Abacopteris* C. Chr., Gard. Bull. Str. Settl. 7 (1934) 247. — *Meniscium* sect. *Goniopteridopsis* H. Ito in Nakai & Honda, Nov. Fl. Jap. no. 4 (1939) 184 *p.p.* — *Thelypteris* subg. *Abacopteris* K. Iwats., Mem. Coll. Sci. Univ. Kyoto B, 31 (1964) 34. — *Dimorphopteris* Tagawa & K. Iwats., Acta Phytotax. Geobot. 19 (1961) 8. — *Thelypteris* subg. *Dimorphopteris* K. Iwats., l.c. (1964).

Caudex suberect to long-creeping; fronds simply pinnate (in a few cases simple), basal pinnae not or little reduced but often with narrowed bases; much-reduced basal pinnae quite lacking; apical lamina pinna-like or widened towards its base and merging with upper pinnae; pinnae crenate to entire, rarely conspicuously lobed; veins several pairs (except in cases of very small or narrow pinnae), almost all anastomosing, their united excurrent veins sometimes free, more usually joining to form zig-zag composite veins alternating with costules; sinus-membrane short or lacking; surfaces usually pustular when dried; acicular hairs (in some cases hooked) frequent on both surfaces, capitate hairs and/or sessile glands also present in some species; sori in some species exindusiate and then spreading ± along veins, never on to excurrent veins; indusia often hairy, sometimes also with glands; sporangia often bearing acicular hairs (hooked where those on lamina are so) near annulus, in some species sessile spherical glands, rarely both hairs and glands; spores with a continuous translucent wing and a few cross-wings.

Type species: *Aspidium lineatum* Bl. = *Pronephrium lineatum* (Bl.) Presl.

Distribution: India & Ceylon; from S. China southwards throughout Malesia, N.E. Australia, in the Pacific to Fiji.

The name *Abacopteris* Fée was published in 1843 in a report of a communication to a Congress, without description. The first publication accompanied by description was in 1852, and the name is thus antedated by *Pronephrium* Presl. Christensen and Ching both cited the date 1843 and *Aspidium lineatum* Bl. as type species, but that species was not cited by Fée. The type species is clearly *A. philippinarum* Fée = *Goniopteris aspera* Presl (see Holttum 1968, p. 18).

The name *Aspidium lineatum* Bl., type of *Pronephrium*, has been misinterpreted since Mettenius (Farngatt. 4, no. 264, 1858) whose description was copied by Hooker (Spec. Fil. 4: 75). Mettenius cited several synonyms (representing, in my judgement, at least

three distinct species), and Hooker felt so baffled that he expressed his inability to judge. The first part of Mettenius's description fits Blume's description of *A. affine* (cited as a synonym by Mettenius) but not Blume's description of *A. lineatum*. There are two specimens from Leiden in Hooker's herbarium labelled *A. lineatum* Bl. but not in Blume's handwriting (Hooker wrote 'Miquel' on both sheets); both agree with *A. affine* Bl. All subsequent descriptions of *A. lineatum* which I have found apply also to *A. affine*, my own description also (Rev. Fl. Mal. 2: 292. 1954) and recorded cytological observations. Christensen listed the name *A. affine* as a synonym of *Dryopteris lineata* (Bl.) C. Chr. in Ind. Fil. (1905).

I recently found the type of *A. lineatum* Bl. in the Rijksherbarium at Leiden; it bears the number 909, 27—60. It is labelled in Blume's hand, but lacks the type locality (island of Nusa Kambangan). It agrees with the important phrase in Blume's description '*pinnis (paucis) sessilibus elliptico-oblongis basi obliquis*' which is quite inapplicable to *A. affine*. A sterile specimen at Paris, received from Blume as *A. lineatum* in 1836, is closely similar. So also is *Zollinger 1019*, type of *Alsophila fragilis* Zoll., from the Tjikoya, River, which Kunze identified with *A. lineatum* (Bot. Zeit. 6: 259. 1848) and also Presl (Epim. Bot. 258) who perhaps copied Kunze. All these specimens are quite different from the type of *A. affine*. Rosenstock, studying specimens at Leiden, must have understood this situation when he gave the new name *Dryopteris oxyotis* (Meded. Rijksherb. no. 31: 5. 1917) to *Gymnogramme macrotis* Kze (not *Dryopteris macrotis* (Hk.) O. Ktze). Kunze's name, placed as a synonym of *D. lineata* (Bl.) C. Chr. in Index Filicum, was based on *Zollinger 324*, of which Rosenstock wrote '= *Aspidium lineatum auct. (non* Bl.).' I have examined this specimen of Zollinger and find it to agree with *A. affine*. (The binomial *Dryopteris affinis* applies to another species, so that in the genus *Dryopteris* the name *D. oxyotis* must be used for *A. affine* Bl.)

The type of *A. lineatum* has two pairs of pinnae; the Paris specimens and *Zollinger 1019* have three pairs. Fertile fronds have longer stipes and smaller pinnae than sterile (this was an important character in Presl's diagnosis of *Pronephrium* and applies also to *A. affine*). The largest sterile pinnae are *c.* 10 × 3 cm; the fertile frond on the type is not fully expanded and its pinnae of 3 × 1.5 cm would probably have grown larger. The pinnae are not auricled at the base, as are the much more numerous pinnae of *A. affine*. The sori have small indusia (not seen by Kunze) which bear both hairs and glands; some sporangia also bear both short hairs and glands.

Copeland (Gen. Fil. 141) stated that a genus *Abacopteris*, as defined by Ching, was not clearly distinguishable as it intergraded with other groups of species included in Copeland's *Cyclosorus*. I have attempted to subdivide the latter as follows:

1. I restrict *Cyclosorus* to *C. gongylodes* and *C. striatus* (see above).
2. From the remainder of Copeland's *Cyclosorus* I remove the genera *Chingia*, *Christella*, and *Amphineuron*, which seem to me alien elements.
3. I remove two small groups of Philippine species as *Haplodictyum* and *Nannothelypteris;* these are not alien elements but make difficult the clear definition of other natural groups.
4. The remaining species are divisible into two groups on the character of presence or absence of much-reduced basal pinnae; those with such reduced pinnae, with the addition of some free-veined species, are divisible into two genera *Sphaerostephanos* and *Pneumatopteris* (both re-defined); the species without much-reduced basal pinnae constitute *Pronephrium*.

Within the genus *Pronephrium* as thus defined, the most distinct species group is here distinguished as sect. *Grypothrix*. The remainder comprises two groups which are not so clearly distinct from each other, though the majority of species in each are distinct enough; I rank them also as separate sections. *Aspidium affine* Bl. belongs to sect. *Dimorphopteris*.

Two African species might be included in *Pronephrium*, as here delimited, namely *Cyclosorus blastophorus* Alston and *Meniscium pauciflorum* Hook. (*Menisorus* Alston). I believe that these two species are allied, and think it probable that they are not closely related to the Asiatic species of *Pronephrium*. They need further study.

Iwatsuki (1964, p. 35) stated that *Thelypteris* subg. *Abacopteris* could be distinguished from subg. *Pneumatopteris* only by the absence in the former of a sinus-membrane. But very few species wholly lack such a membrane, and I cannot see that its presence or absence provides a clear-cut character usable for distinguishing two groups of species.

Sect. **Pronephrium.** Terminal lamina pinna-like; margins of pinnae crenate or subentire; sessile glands on lamina-surface or sporangia rare; hairs on lamina straight, not hooked. — **Fig. 9, 9a.**

Species 20—25. *Dryopteris acanthocarpa* Copel., *Cyclosorus angustipinnatus* C. Chr. & Tard., *Dryopteris aquatiloides* Copel., *Goniopteris aspera* Pr., *Meniscium beccarianum* Cesati, *Dryopteris diminuta* Copel., *D. euryphylla* Rosenst., *D. gymnopteridifrons* Hayata, *Polypodium holophyllum* Bak., *Cyclosorus jacobsii* Holtt., *Meniscium kennedyi* F. Muell., *Dryopteris lakhimpurensis* Rosenst., *Nephrodium latifolium* Pr., *Dryopteris melanophlebia* Copel., *Aspidium menisciicarpum* Bl., *Polypodium multilineatum* Wall. *ex* Hk., *P. penangianum* Hk., *Dryopteris pentaphylla* Rosenst., *Cyclosorus pustulosus* Copel,. *Polypodium rubidum* J. Sm. *ex* Hk., *Dryopteris rubra* Ching, *Phegopteris rubrinervis* Mett., *Phegopteris urophylla* Mett., *Dryopteris verruculosa* v. A. v. R.

Chromosome number: 36 (*aspera, multilineatum, rubra, urophyllum*, all diploid).

Sect. **Grypothrix** Holttum, *sect. nov.* — Lamina terminalis pinniformis; pili plurimi paginae inferioris costarum et pili prope annulum sporangiorum hamati; sori exindusiati, saepe elongati. — **Fig. 8.**

Species typica: *Meniscium cuspidatum* Bl., Enum. Pl. Jav. (1828) 114.

Species about 12. *Meniscium cuspidatum* Bl., *Abacopteris insularis* K. Iwats. *Meniscium liukiuense* Chr., *Abacopteris longipetiolata* K. Iwats., *Polypodium megacuspe* Bak., *Meniscium parishii* Bedd., *Phegopteris rubicunda* v. A. v. R., *Meniscium salicifolium* Wall. *ex* Hk., *Polypodium sampsonii* Bak.,*M. simplex* Hk., *M. thwaitesii* Hk., *M. triphyllum* Sw.

Chromosome number: 36 (*triphyllum* tetraploid; *rubicunda, salicifolium* diploid).

Meniscium thwaitesii has apical lamina widened at the base and pinnae distinctly lobed; it is placed here on account of its hooked hairs and evident relationship to *M. triphyllum*. Its pinnae are rather irregular, and it looks like a hybrid. One parent must be *triphyllum;* the other must have lobed pinnae and basal pinnae unreduced, and I suggest *Trigonospora ciliata* as a possibility. All specimens of *thwaitesii* seen by me have young sporangia, and I have thus not seen spores.

Sect. **Dimorphopteris** (Tagawa & K. Iwats.) Holtt., *stat. nov.* — *Dimorphopteris* Tagawa & K. Iwats., l.c. — Fronds often dimorphous, the fertile pinnae in some cases very narrow; apical lamina widened and ± deeply lobed towards its base, grading into upper pinnae; sessile spherical glands often present on lower surface of lamina and on sporangia. — **Fig. 10, 10a.**

Type species: *Dimorphopteris moniliformis* Tagawa & Iwats., l.c. = **Pronephrium moniliforme** (Tagawa & K. Iwats.) Holtt., *comb. nov.*

Species at least 30. *Dryopteris acrostichoides* v. A. v. R., *Aspidium affine* Bl., *A. amboinense* Willd., *Dryopteris bartlettii* Copel., *Polypodium borneense* Hk., *Acrostichum celebicum* Bak., *Dryopteris clemensiae* Copel., *D. compacta* Copel., *Nephrodium debile* Bak., *N. diversifolium* Pr., *Cyclosorus edanyoi* Copel., *Dryopteris elmerorum* Copel., *Acrostichum exsculptum* Bak.,

Polypodium firmulum Bak., *Aspidium glandulosum* Bl., *Polypodium granulosum* Pr., *Meniscium hosei* Bak., *Dryopteris indica* v. A. v. R., *D. lanceola* Copel., *Dryopteris maquilingensis* Copel., *D. merrillii* Chr., *Meniscium palauense* Hosok., *Dryopteris peltata* v. A. v. R., *Nephrodium pilosiusculum* Zipp. *ex* Racib., *Dryopteris rhombea* Copel., *Cyclosorus samarensis* Copel., *Stegnogramma sandwicensis* Brack., *Dryopteris simillima* C. Chr., *Meniscium stenophyllum* Bak., *Dryopteris subconformis* C. Chr., *Cyclosorus subdimorphus* Copel., *Dryopteris tenompokensis* C. Chr., *D. tibangensis* C. Chr., *D. toppingii* Copel., *D. xiphioides* Chr.

Chromosome number: 36 (*Cyclosorus lineatus sensu* Manton in Holttum, Rev. Fl. Mal. 2: 625 = *Aspidium affine* Bl., tetraploid).

Dimorphopteris moniliformis from Halmahera (Moluccas) is so very like *Acrostichum celebicum* Bak. in every way that I believe the former must be a reduced relative of the latter. The difference in width of fertile pinnae in the two is not great. *A. celebicum* has very small indusia (not seen by Baker) and very crowded sori which even spread on to the upper surface, but I cannot see any sporangia attached to the surface between veins, as reported for *moniliformis;* the venation of the two is quite similar. These two species represent an extreme form of reduction of pinnae; a number of other species show some degree of reduction. *Aspidium affine*, which shows considerable degree of reduction, is variable, and I think it likely that a diploid may occur. It also indicates the possibility that there are hybrids in this assemblage of species, a possibility also indicated by variability in some Philippine species.

17. HAPLODICTYUM

Presl, Epim. Bot. (1851) 50; Ching, Sunyatsenia 5 (1940) 251; Copel., Gen. Fil. (1947) 144; Fern. Fl. Philip. (1960) 377. — *Thelypteris* subg. *Haplodictyum* K. Iwats., Mem. Coll. Sci. Univ. Kyoto B, 31 (1964) 32.

Caudex short-creeping or suberect; scales small, bearing short acicular superficial hairs; fronds dimorphous, sterile with shorter stipe and somewhat larger lamina than fertile; terminal lamina narrowly oblong, ± deeply lobed, much longer than pinnae; pinnae 0—4 pairs, small, lower ones gradually smaller or not; 1 or 2 pairs much-reduced pinnae also present, or lacking; veins anastomosing, at least in the terminal lamina (in pinnae also where not very small); at least in basal part of terminal lamina (except in *bakeri*) veins forked, branches of adjacent veins anastomosing to form a series of areoles along each side of a costule, sometimes with additional areoles also below a sinus; sessile spherical glands present on lower surface and on sporangia; long spreading hairs on lower surface of rachis, shorter ones on costae and costules; sori indusiate, indusia hairy and/or glandular; spores with a single translucent wing and a few cross-wings.

Type species: *Haplodictyum heterophyllum* Presl.

Distribution: Philippines (Luzon, Panay).

Species 5 (one undescribed). *Nephrodium bakeri* Harr., *Cyclosorus dimorphus* Copel., 1954 (not 1951) = *Thelypteris copelandii* Reed, *Haplodictyum majus* Copel.

Chromosome number not known.

Christensen (Ind. Fil. 1905) placed *H. heterophyllum* as one variety among several of *Dryopteris canescens* (Bl.) C. Chr., following Christ (Farnkr. der Erde 244) who also later added others. Ching (l.c., 1940) recognized *Haplodictyum* as a genus but placed it in *Aspidiaceae* on account of its venation; he transferred *canescens* to it, and some of the varieties of Christ and Christensen, as species. Copeland correctly concluded that *Haplodictyum* is closely related to species which he placed in *Cyclosorus*, but maintanined it as a separate genus of two species. A similar type of venation, simulating *Pleocnemia*,

has occurred in three other Thelypteroid ferns known to me: *Dictyocline* (see *Stegnogramma*); *Proferea excellens* (Bl.) Presl (see *Sphaerostephanos*); and *Pleocnemia clarkei* Bedd., an aberrant form of an Indian species of *Christella*. It is interesting to note that the North American fossil *Goniopteris claiborniana* Berry (Bull. Torr. Bot. Cl. 44: 331, t. 22. 1917) has both the *Haplodictyum* type of venation as well as the normal *Goniopteris* type; I think there is little doubt that this fossil represents a Thelypteroid fern.

The species *Aspidium canescens* Bl., known from Java (unlocalized so far as herbarium specimens seen by me are concerned), Halmahera, Amboina, and N. Celebes, is poorly represented in herbaria. It differs from *Haplodictyum* in being exindusiate and in lacking spherical glands; the sporangia are setose. It is also much larger than the species here placed in *Haplodictyum*, with a less distinct apical lamina, larger and more numerous normal pinnae, and about five pairs of much-reduced pinnae. I place it in *Sphaerostephanos*.

18. NANNOTHELYPTERIS Holttum, *gen. nov.*

Physematium Kaulf. *p.p. quoad* Presl. Epim. Bot. (1851) 34; Holttum, Novit. Bot. Inst. Bot. Univ. Carol. Prag. (1968) 44. — Caudex brevis, repens; frondes leviter dimorphae, steriles quam fertiles stipitibus brevioribus pinnisque majoribus praeditae; pinnae parvae (1.2—2.5 cm longae), 20—35-jugatae, inferiores non vel paulo reductae sed sensim leviter remotiores; venae liberae vel in pinnis majoribus paulo anastomosantes; pagina inferior laminae non glandulifera; sori indusiati vel exindusiati; sporangia glandulis prope annulum ornata; sporae alatae.

Species typica: *Polypodium aoristisorum* Harr., J. Linn. Soc. Bot. 16 (1877) 30 = **Nannothelypteris aoristisora** (Harr.) Holttum, *comb. nov.*

Distribution: Philippines (Luzon, Lanay, Mindanao).

Species 3. *Physematium philippinum* Pr. = **Nannothelypteris philippina** (Pr.) Holttum, *comb. nov.* (syn *Dryopteris confusa* Copel.), *Phegopteris nervosa* Fée = **Nannothelypteris nervosa** (Fée) Holttum, *comb. nov.*

Chromosome number not known.

These three species, having basal pinnae hardly reduced, would come under *Pronephrium* but they differ so much from all other species here placed in that genus that I think it best to separate them (Presl was wrong in placing *N. philippina* in *Physematium* Kaulf. which = *Woodsia*). They are undoubtedly closely allied, and Copeland (Fern Flora Philip. 323, 324, 355) failed to understand the distinctions between them. In my discussion of *Physematium philippinum* (l.c. 1968) I also failed to distinguish clearly between that species and *Phegopteris nervosa* Fée. Copeland recognized this distinction, but misidentified plants of *N. aoristisora* occurring on Mt. Makiling, naming them *nervosa*. The following key gives the essential distinctions.

1. Sori exindusiate; some veins anastomosing in larger pinnae . . . . . **aoristisora**
1. Sori indusiate; veins all free.
2. Sterile pinnae to 20 × 6 mm, more deeply lobed on acroscopic than on basiscopic side; indusia glandular **nervosa**
2. Sterile pinnae to 25 × 10 mm, lobed equally on both sides; indusia setose . . . . . **philippina**

19. STEGNOGRAMMA

Blume, Enum. Pl. Jav. (1928) 172; Ching, Sinensia 7 (1936) 90; Acta Phytotax. Sinica 8 (1963) 329; Copel., Gen. Fil. (1947) 144; K. Iwats., Acta Phytotax. Geobot. 19 (1963) 112—116; Mem. Coll. Sci. Univ. Kyoto B, 31 (1964) 18—21; Amer. Fern Journ. 54 (1964) 141. — *Leptogramma* J. Sm. in Hook. J. Bot. 4 (1841) 51; Hist. Fil. (1875) 231; Ching, Sinensia 7 (1936) 96; K. Iwats., l.c. — *Dryopteris* subg. *Leptogramma* C. Chr., Dansk

Vidensk. Selsk. Skr. 7 Afd., X, no. 2 (1913) 196. — *Dictyocline* Moore, Gard. Chron. (1855) 854; J. Sm., Hist. Fil. (1875) 149; Ching, Sunyatsenia 5 (1940) 240; Acta Phytotax. Sinica 8 (1963) 333; Copel., Gen. Fil. (1947) 145; K. Iwats. l.c. — *Lastrea p.p. quoad* Copel., Gen. Fil. (1947) 135.

Caudex short-creeping or erect; stipes densely hairy, hairs unicellular or septate; scales bearing acicular unicellular hairs on edges and surface; fronds simply pinnate, pinnae subentire to deeply pinnatifid, basal pinna not or little reduced; upper pinnae merging with apical lamina; spherical glands lacking; veins free or with goniopteroid anastomosis or forming a more complex network (*Dictyocline*); sori exindusiate, running along the veins, sometimes on excurrent veins; sporangia copiously setiferous; spores finely spinulose or with many small wings.

Type species: *Stegnogramma aspidioides* Bl.

Distribution: warmer parts of the Old World; a few spp. in tropical America.

Species about 15; see Iwatsuki (1963) for full conspectus of Old World species.

Chromosome number: 36 (sect. *Leptogramma*, 2 spp., diploid and tetraploid).

Iwatsuki's arrangement of 1963, including *Leptogramma* and *Dictyocline* as subgenera of *Stegnogramma* (with addition of a fourth subgenus) is acceptable to me, and is the best and most complete to date for the Old World. Ching, however, in 1963, after seeing Iwatsuki's paper, still doubted a close relationship between *Leptogramma* and *Stegnogramma*, though admitting that *Dictyocline* is allied to the latter; he believed that *Leptogramma* is allied more nearly to *Cyclogramma*, but I see no evidence for this. The species of subg. *Leptogramma* in Malesia are uncommon mountain plants, have been little collected, and need a new comparative study. Those in the New World also need re-examination; see Iwatsuki's comments in the American Fern Journal (1964).

If the genera here numbered 16—21 were united, which would be a quite natural arrangement, the correct name for the whole assemblage would be *Stegnogramma*.

20. SPHAEROSTEPHANOS

J. Sm. in Hook. Gen. Fil. (1839) t. 24; Copel., Univ. Cal. Publ. Bot. 16 (1929) 60; Gen. Fil. (1947) 144; Ching, Sunyatsenia 5 (1940) 240. — *Thelypteris* subg. *Sphaerostephanos* K. Iwats., Mem. Coll. Sci. Univ. Kyoto B, 31 (1964) 32. — *Polypodium* § *Mesochlaena* R. Br. in Bennett & Brown, Pl. Jav. Rar. (1838) 5. — *Mesochlaena* (R. Br.) J. Sm. in Hook. J. Bot. 3 (1840) 18; C. Chr., Ind. Fil. (1905) xxii. — *Proferea* Presl, Epim. Bot. (1851) 259; Holttum, Novit. Bot. Inst. Bot. Univ. Carol. Prag. (1968) 48. — *Pronephrium* Presl, Epim. Bot. (1851) 259, *p.p.* — *Cyclosorus quoad* Copel., Gen. Fil. (1947) 140, *p.p.*; Holttum, Rev. Fl. Mal. 2 (1954) 255—285, *p.p.* — *Lastrea quoad* Copel., l.c. 135, *p.p.* — *Thelypteris* subg. *Glaphyropteridopsis* sect. *Neocyclosorus* K. Iwats., Mem. Coll. Sci. Univ. Kyoto B, 31 (1964) 30. — *Thelypteris* subg. *Pneumatopteris* sect. *Macrocyclosorus* K. Iwats., l.c. 34. — **Fig. 11, 11a, 11b, 12, 12a, 13, 13a, 20, 20a.**

Caudex various, rarely long-creeping, in some species arborescent, in a few scandent; scales usually narrow, always bearing acicular hairs on edge and surface; fronds always with much-reduced basal pinnae, the transition from normal pinnae usually abrupt but in some species gradual; aerophores at pinna-bases often swollen, in some species elongate (very young fronds then covered with mucilage); apex of frond rarely pinna-like; pinnae almost always lobed, sometimes deeply, rarely subentire; sinus-membrane almost always distinct; veins anastomosing or in a few species free or just meeting at the sinus; sessile spherical glands often present on lower or both surfaces but lacking in some species; acicular hairs almost always present on both surfaces of costae and costules, often on lamina between veins, these hairs usually antrorse on upper surface, variously directed

on lower, sometimes septate (though not conspicuously); surface rarely pustular when dry; sori usually round, in some species (indusiate or not) ± elongate; indusia usually present, rather thin, often hairy and/or glandular, sometimes small and inconspicuous; sporangia usually bearing either spherical glands or setae near annulus and on the stalk a hair of several cells, apical one ± swollen and sometimes glandular; spores almost always light brown, spinulose or bearing many small translucent wings.

Type species: *Sphaerostephanos asplenioides* J. Sm. = *Aspidium polycarpum* Bl. = *S. polycarpa* (Bl.) Copel.

Distribution: Africa ?; Mascarene Islands, S. India & Ceylon; Burma and Thailand to S. China (including Hainan and Taiwan); throughout Malesia, to Guam, New Caledonia, Fiji, Tonga, Samoa, Tahiti.

Species more than 120. *Dryopteris adenophora* C. Chr., *D. adenostegia* Copel.,? *D. afra* Chr., *Nephrodium alatellum* Chr., *Dryopteris albosetosa* Copel., *D. angusta* Copel., *Nephrodium angustifolium* Pr., *Dryopteris angustipes* Copel., *Gymnogramma appendiculata* Bl., *Dryopteris aquatilis* Copel., *Aspidium arbuscula* Willd., *Dryopteris archboldii* C. Chr., *Polypodium arfakianum* Bak., *Dryopteris atasripii* Rosenst., *D. austera* Brause, *D. austrophilippina* Copel., *D. baramensis* C. Chr., *D. batacorum* Rosenst., *D. batjanensis* Rosenst., *Cyclosorus boholensis* Copel., *Dryopteris bordenii* Chr., *D. brunnescens* C. Chr., *D. calcicola* C. Chr., *Gymnogramma canescens* Bl., *Dryopteris carolinensis* Hosok., *Cyclosorus cataractorum* Wagn. & Greth., *Dryopteris christophersenii* C. Chr., *D. conferta* Brause, *D. cyrtocaulos* v. A. v. R., *Phegopteris debilis* Mett., *Nephrodium decadens* Bak., *Cyclosorus degeneri* Copel., *Dryopteris deltiptera* Copel., *Cyclosorus deminuens* Holtt., *D. dichrotricha* Copel., *Dryopteris dichrotrichoides* v. A. v. R., *D. dimorpha* Brause, *D. doodioides* Copel., *Cyclosorus duplosetosus* Copel., *Dryopteris echinospora* v. A. v. R., *D. elliptica* Rosenst., *Nephrodium eminens* Bak., *D. epaleata* C. Chr., *Cyclosorus erectus* Copel., *Aspidium excellens* Bl., *Dryopteris farinosa* Brause, *D. finisterrae* Brause, *D. glaucescens* Brause, *Nephrodium glaucostipes* Bedd., *Lastrea globulifera* Brack., *Dryopteris grantii* Copel., *Cyclosorus gregarius* Copel., *C. halconensis* Copel., *Dryopteris hamifera* v. A. v. R., *D. hastato-pinnata* Brause, *Aspidium heterocarpum* Bl., ? *Dryopteris hirticarpa* Ching, ? *D. hirtisora* C. Chr., *D. hispidifolia* v. A. v. R., *D. hispiduliformis* C. Chr., *D. hochreutineri* Chr., ? *Cyclosorus houii* Ching, *Dryopteris inconspicua* Copel., ? *Polypodium invisum* Forst., *Dryopteris kotoensis* Hayata, *Nephrodium larutense* Bedd., *Pronephrium lastreoides* Pr., *Aspidium latebrosum* Kze *ex* Mett., *Cyclosorus leucadenius* Copel., *Dryopteris lithophylla* Copel., *D. lobangensis* C. Chr., *Cyclosorus lobatus* Copel., *Aspidium loherianum* Chr., *Cyclosorus maemonensis* Wagn. & Greth., *C. magnus* Copel., *Dryopteris margaretae* E. Brown, ? *Nephrodium mauritianum* Fée, *D. matutumensis* Copel., *Dryopteris megaphylloides* Rosenst., *Aspidium megaphyllum* Mett., *Polypodium metcalfei* Bak., *Dryopteris micans* Brause, *D. mixta* Rosenst., *D. morobensis* Copel., *D. multiauriculata* Copel., *D. munda* Rosenst., *D. mutabilis* Brause, *D. norrisii* Rosenst., *D. novoguineensis* Brause, *D. nuna* J. W. Moore, *D. oblonga* Brause, *D. obtusifolia* Rosenst., *Nephrodium oosorum* Bak., ? *Polypodium oppositifolium* Hook., *Cyclosorus orthocaulis* K. Iwats., *Dryopteris paraphysata* Copel., *D. paripinnata* Copel., *D. parksii* Ballard, *D. peltochlamys* C. Chr., *D. perglandulifera* v. A. v. R., *D. perpilifera* v. A. v. R., *D. perpubescens* Alston, *Nephrodium philippinense* Bak., *Dryopteris pilososquamata* v. A. v. R., *D. plurifolia* v. A. v. R., *Aspidium polycarpum* Bl., *Dryopteris polyotis* C. Chr., *Cyclosorus polypterus* Copel., *Dryopteris porphyricola* Copel., *Aspidium productum* Kaulf., *Dryopteris protecta* Copel., *D. pseudoarbuscula* v. A. v. R., *Phegopteris pseudoarfakiana* Hosok., *D. pseudohirsuta* Rosenst., *D. pseudomegaphylla* v. A. v. R., *D. pterospora* v. A. v. R., *D. pycnosora* C. Chr., *Cyclosorus reederi* Copel., *Dryopteris reineckei* C. Chr., *Nephrodium richardsii* Bak., *Goniopteris rigida* Ridl., *Dryopteris riparia* Copel., *D. roemeriana* Rosenst.,

D. rosenburgii C. Chr., *Goniopteris rudis* Ridl., *Dryopteris rurutensis* Copel., *Cyclosorus sagittifolioides* Copel., *Aspidium sagittifolium* Bl., *Nephrodium sakayense* Zeill., *Dryopteris sepikensis* Brause, *Cyclosorus serratus* Copel., *Dryopteris sessilipinna* Copel., *Aspidium simplicifolium* J. Sm. *ex* Hook., *Nephrodium smithianum* Presl, *Dryopteris spenceri* Chr., *Cyclosorus stenodontus* Copel., *Aspidium stipellatum* Bl., *Dryopteris strigosissima* Copel., *Dryopteris subalpina* v. A. v. R., *D. subappendiculata* Copel., *D. subfalcinella* v. A. v. R., *D. subhispidula* Rosenst., *Nephrodium subjunctum* Bak., *Dryopteris subpectinata* Copel., *Polypodium subtruncatum* Bory, *Dryopteris subulifolia* v. A. v. R., *Mesochlaena sumatrensis* v. A. v. R., *Dryopteris superba* Brause, *D. suprastrigosa* Rosenst., *D. taiwanensis* C. Chr., *Mesochlaena talamauensis* v. A. v. R., *Dryopteris tamiensis* Brause, *D. tandikatensis* v. A. v. R., *D. tannensis* C. Chr., *D. tephrophylla* Copel., *D. terrestris* Copel., *D. todayensis* Chr., *Mesochlaena toppingii* Copel., *Dryopteris uniauriculata* Copel., *Sphaerostephanos unijuga* Copel., *Polypodium unitum* Linn., *Dryopteris urdanetensis* Copel., *D. valida* Chr., *D. vestigiata* Copel., *Aspidium warburgii* Kuhn & Chr., *Cyclosorus weberi* Copel., *Dryopteris williamsii* Copel.

Chromosome number: 36 (*afra*, tetraploid; *arbuscula*, *heterocarpum*, *megaphyllum*, *unitum*, *deminuens*, *conferta*, *invisum*, diploid).

Hitherto six species have been included in *Sphaerostephanos* as defined by an elongate indusiate sorus; they fall into two distinct groups, one group (including the type species) with deeply lobed normal pinnae and very numerous reduced ones, the other with fewer broader less deeply lobed normal pinnae and few reduced ones. These two groups appear to be related to different species-groups which have round sori; further, the degree of elongation of the sorus varies in both. There are a few other species with somewhat elongate sori which have escaped the notice of those who thought this a generic character. It seems to me very clear that this character alone does not provide a generic distinction. Ching removed the genus to a separate family, because he thought the type species had trilete spores. Iwatsuki (1964, p. 32) states that long septate hairs on the fronds are an additional character, but I believe he only observed them in the type species. I have looked for them but have found them infrequent, or at least very inconspicuous even when viewed with a binocular microscope of magnification × 60 (with which the septate hairs of some species of *Coryphopteris* are very distinct). Dr. P. Chandra of Lucknow recently observed them in the hitherto little-known Indian species originally named *Polypodium subtruncatum* Bory, but again they are inconspicuous. Nobody has examined the very numerous other species here included in *Sphaerostephanos* to discover which (if any) have septate hairs. In making my own examination of these ferns I have not noticed septate hairs, but I cannot assert that they are absent.

Thus in the present account, as in my book on the ferns of Malaya, I have merged the species hitherto called *Sphaerostephanos* with those having round sori. But as the earliest generic name applying to a species in this enlarged assemblage is *Sphaerostephanos*, I now use that name in a much wider sense than any previous author, and have modified the generic description.

Presl founded his genus *Proferea* on part of the type material of *Aspidium excellens* Bl., a species closely allied to *A. megaphyllum* Mett., in which the veins are forked and form costular areoles much as in *Haplodictyum*. This condition only occurs in the very large lower pinnae (much broader than in *megaphyllum* and with long acuminate lobes); the apical part of the same frond, preserved at Leiden, is indistinguishable from *megaphyllum*.

The great majority of species here placed most certainly form a natural group. The aberrant species are (1) a few which have very few and very small reduced basal pinnae (e.g. *norrisii* = Malayan specimens ascribed to *Cyclosorus toppingii* in my book of 1954,

p. 280); (2) a few which have lower pinnae gradually reduced, the lowest not very small, and setose sporangia (e.g. *Polypodium invisum* Forst.). The former represent a transition to *Pronephrium*, and some may be hybrids; the latter resemble *Christella* in frond-form but lack the characteristic glandular hairs on sporangium stalks and possess setae on their sporangia, where no setae occur in undoubted species of *Christella*. I include these species in *Sphaerostephanos* with some doubt, not knowing where else to place them, and I will attempt to deal with them more adequately when I come to monograph this very complex genus.

21. PNEUMATOPTERIS

Nakai, Bot. Mag. Tokyo 47 (1933) 179. — *Thelypteris* subg. *Pneumatopteris* K. Iwats., Mem. Coll. Sci. Univ. Kyoto B, 31 (1964) 33, *p.p.* excl. sect. *Macrocyclosorus*. — *Pseudocyclosorus* Ching, Acta Phytotax. Sinica 8 (1963) 322, excl. *P. ciliatus* and *P. caudipinnus*. — *Glaphyropteris* sect. *Euglaphyropteris* H. Ito in Nakai & Honda, Nov. Fl. Jap. no. 4 (1939) 146, excl. *G. erubescens*. — *Thelypteris* subg. *Glaphyropteridopsis* sect. *Mesoneuron* K. Iwats. l.c. 29 *p.p.* excl. *Mesoneuron* Ching. — *Cyclosorus p.p.* and *Lastrea p.p. quoad* Copel., Gen. Fil. (1947) 140, 135; *Cyclosorus p.p. quoad* Holttum, Rev. Fl. Mal. 2 (1954) 255—285. — **Fig. 14, 14a, 15, 15a.**

Caudex usually erect or suberect (long-creeping in 2 spp.); stipes never conspicuously hairy, in a few species bearing short dark spines which are the bases of scales; scales broad, thin, often with slender acicular hairs on edges, sometimes also septate hairs ending in mucilage-cells, superficial hairs lacking or rare; fronds usually large with many pinnae; at least one pair of basal pinnae much reduced, usually several to many pairs, transition from normal to reduced pinnae abrupt or rarely quite gradual; lamina of reduced pinnae in most species distinct, in the type and a few other species greatly reduced; aerophores on reduced and lower normal pinnae ± swollen, in a few species elongate and then small aerophores present at bases of costules; pinnae always lobed, edges of lobes distinctly cartilaginous; veins free in a few species with deeply lobed pinnae, in most species at least the basal veins from adjacent costules anastomosing to form an excurrent vein running to a sinus-membrane; lamina between veins always ± pustular when dried; lower surface of rachis, costae, and other parts never densely or long-hairy, sometimes with short acicular or capitate hairs; sessile glands absent; sori usually indusiate; sporangia often bearing short club-shaped glandular hairs, rarely setae; on stalk of sporangia a hair of 3 or 4 cells, terminal cell enlarged but not glandular; spores light brown with many small ± quadrate wings of irregular shape, thus spinulose in aspect.

Type species: *Aspidium callosum* Bl. = *Pneumatopteris callosa* (Bl.) Nakai.

Distribution: Fernando Po & S. Thomé; SE. Africa, Mascarene Islands, India and Ceylon to S. China, southwards throughout Malesia; Australia and New Zealand, Islands of the Pacific to Hawaii.

Species about 50. *Aspidium abortivum* Bl., *A. abruptum* Bl., *Dryopteris berastagiensis* C. Chr., *D. brooksii* Copel., *D. bryanii* C. Chr., *Pseudocyclosorus caudatus* Holtt., *Lastrea cavitensis* Copel., *Goniopteris costata* Brack., *Dryopteris dicranogramma* v. A. v. R., *D. duclouxii* Chr., *D. eberhardtii* Chr., *Cyclosorus ecallosus* Holtt., *Aspidium elatum* Mett., *Dryopteris esquirolii* Chr., *Pseudocyclosorus excisus* Holtt., *Lastrea falciloba* Hook., *Dryopteris foxii* Chr., *Cyclosorus glaber* Copel., *Aspidium glaberrimum* Richard, *Goniopteris glandulifera* Brack., *Nephrodium hudsonianum* Brack., *Dryopteris inclusa* Copel., *D. keysseriana* Rosenst. *Aspidium laeve* Mett., *Thelypteris latiloba* Ching, *Cyclosorus lepidopodus* C. Chr., *Lastrea ligulata* J. Sm. *ex.* Pr., *Aspidium longipes* Bl., *Nephrodium lucidum* Bak., *Dryopteris luzonica* Chr., *D. macroptera* Copel., *Goniopteris madagascariensis* Fée, *Dryopteris magnifica* Copel.,

D. mesocarpa Copel., *D. microloncha* Chr., *D. nephrolepioides* C. Chr., *Nephrodium nitidulum* Pr., *Dryopteris obstructa* Copel., *Aspidium ochthodes* Kze, *Dryopteris oxyoura* Copel., *Polypodium pennigerum* Forst., *Dryopteris petrophila* Copel., *Nephrodium prismaticum* Desv., *Dryopteris regis* Copel., *Nephrodium repens* Hope, *N. rodrigasianum* Moore, *Cyclosorus rotumaensis* St John, *Dryopteris sambiranensis* C. Chr., *D. sogerensis* Gepp, *D. stokesii* E. Brown, *Thelypteris subochthodes* Ching, *D. subpennigera* C. Chr., *D. sumbawensis* C. Chr., *Nephrodium transversarium* Brack., *Polystichum truncata* Gaud., *Polypodium truncatum* Poir., *Dryopteris tuberculifera* C. Chr., *D. vaupelii* C. Chr., *Cyclosorus viridis* Copel., *Aspidium xylodes* Kze.

Chromosome number: 36 (*pennigerum* tetraploid; '*truncatum*' diploid and tetraploid; *xylodes, subochthodes, caudatus, petrophila,* diploid); 35 (*esquirolii, repens, diploid*).

The species of this genus have the same frond-form as in *Sphaerostephanos,* but I believe they are a quite distinct group, characterized by broad thin rhizome-scales, very slight hairiness on the frond, complete absence of sessile spherical glands, and ± pustular surface of dried lamina. The spores are not different from those of *Sphaerostephanos.* I have admitted one species (*oxyoura*) with setose sporangia.

Certainly some species with free veins belong to the genus. Of these *xylodes* shows a very striking resemblance to *Aspidium callosum* (Nakai's type and only original species) apart from its free veins; the extremely reduced basal pinnae, which consist of little more than a swollen aerophore, are closely similar in both (see Goebel, Ann. Jard. Bot. Btzg 36: 84—96. 1926; and Hennipman, Blumea 16: 97—102. 1968). Ching made *xylodes* type species of his genus *Pseudocyclosorus* and associated with it some other species of India and China; the latter are, however, more hairy and the surface of the dried lamina is not pustular, though the basal scales are similar. Two of these Indian species are also reported to have 35 chromosomes. I therefore include them with some doubt. The Malesian species which have free veins (*caudatus, excisus, keysseriana, ligulata,* and others) are much less hairy and are pustular; two have been reported as having 36 chromosomes. One Philippine species (*cavitensis*) was first described from a small but fertile specimen with free veins; later collections show that on well-grown plants the larger fronds have anastomosing veins.

The specific epithet *truncatum* was used independently by Poiret (1804) and Gaudichaud (1827), and references to these authors have subsequently been confused. Poiret's type was labelled '*Brésil*', but no species of this genus occur in the New World. The type consists of the lower-middle part of a frond, without the basal or reduced pinnae which are of critical importance in the diagnosis of species, and I am thus very uncertain how to apply the name. Gaudichaud's specimens (and figure) show the base of the frond, and his species is thus much better characterized; I believe it to be distinct from Poiret's. In many ways the species of *Pneumatopteris* are difficult to discriminate, and if a specimen lacks the base of a frond it may not be nameable with certainty. Several species have been described from island-groups in the Pacific, and I am sure some names are redundant. Exindusiate species are rare. One such is *pennigerum* in New Zealand and SE. Australia; it appears to show relationship to *madagascariensis.* The species *elata* in Fernando Po and San Thomé is more like some Malesian species than any in Africa.

22. CHRISTELLA

Léveillé, Flore de Kouy-tchéou (1915) 472; Holttum, Taxon 20 (1971). — *Thelypteris* subg. *Cyclosoriopsis* K. Iwats., Mem. Coll. Sci. Univ. Kyoto B, 31 (1964) 28, (1965) 170—176. — *Cyclosorus quoad* Ching, Copel. *et al., p.p.* — **Fig. 16, 17, 17a, 18.**

Caudex erectus, suberectus vel late-repens; paleae stipitis angustae, setiferae; pinnae inferiores sensim reductae (infimis haud minutis) raro deflexae et vix reductae; pinnae lobatae vel crenatae; aerophorae non dilatatae; venae plerumque anastomosantes; costae costulae venae laminaque subtus pilis rectis acicularibus vel pilis brevibus capitatis varievestitae, interdum pilis crassis obtusis aurantiacis praeditae, glandulis orbicularibus carentibus; sori semper indusiati; sporangia prope annulum non setifera nec glandulifera; stipites sporangiorum pilis unicellularibus cylindricis glanduliformibus semper praediti; sporae grosse et irregulariter tuberculatae.

Species typica: *Polypodium parasiticum* Linn., Sp. Plant. (1753) 1090 = *Christella parasitica* (L.) Lév.

Distribution: tropics and subtropics.

Old World species about 40. *Dryopteris acuminata* Rosenst., *Polypodium acuminatum* Houtt., *Dryopteris albociliata* Copel., *Aspidium aridum* Don, *Dryopteris assamica* Rosenst., *Cyclosorus assamicus* Ching, *C. balansae* Ching, *C. benguetense* Copel., *Polystichum benoiteanum* Gaud., *Nephrodium biauritum* Bedd., *Dryopteris boninensis* Kodama, *Cyclosorus burmanicus* Ching, *C. calvescens* Ching, *Pleocnemia clarkei* Bedd., *Dryopteris contigua* Rosenst., *Nephrodium crinipes* Hook., *Aspidium cyatheoides* Kaulf., *Dryopteris cylindrothrix* Rosenst., *Nephrodium didymosorum* Par. *ex* Bedd., *Nephrodium distans* Hook., *Dryopteris ensifera* Tagawa, *D. euaensis* Copel., *Cyclosorus euphlebius* Ching, *Nephrodium eurostotrichum* Bak., *N. evolutum* Bedd., *Cyclosorus falcatulus* Copel., *C. fukienensis* Ching, *Nephrodium gustavii* Bedd., *Aspidium harveyi* Mett., *Dryopteris hirtopilosa* Rosenst., *Aspidium hispidulum* Dcne, *Cyclosorus hokouensis* Ching, *Aspidium jaculosum* Chr., *Cyclosorus jerdonii* Ching, *Nephrodium latipinna* Hook., *Polypodium leboefii* Bak., *Dryopteris meeboldii* Rosenst., *D. mindanaensis* Chr., *Aspidium molliusculum* Kuhn, *Nephrodium namburense* Bedd., *Thelypteris novae-hiberniae* Holtt., *Polypodium nymphale* Forst., *Aspidium obliquatum* Mett., *Cyclosorus omeigensis* Ching, *Nephrodium papilio* Hope, *N. papyraceum* Bedd., *Polypodium parasiticum* Linn., *Dryopteris peekelii* v. A. v. R., *Aspidium procurrens* Mett., *Dryopteris pseudoamboinensis* Rosenst., *Nephrodium quadrangulare* Fée, *N. remotum* Heward, *Dryopteris repandula* v. A. v. R., *Cyclosorus scaberulus* Ching, *Polypodium semisagittatum* Roxb., *Cyclosorus subaridus* Tatew. & Tagawa, *Nephrodium subelatum* Bedd., *Dryopteris submollis* v. A. v. R., *Aspidium subpubescens* Bl., *Dryopteris sumatrana* v. A v. R., *Nephrodium zeylanicum* Fée.

Chromosome number: 36 (*dentatum, parasiticum*, tetraploid; *papilio*, diploid and tetraploid; *quadrangulare, acuminatum* Houtt., *aridum, crinipes, cylindrothrix, molliusculum*, diploid.)

The genus *Christella* Lév. was established to include species with the following characters: pinnae lobed, with unbranched veins pinnately arranged in the lobes; sori with reniform indusia seated on the veins in a row on each side of the costule. These characters apply to most *Thelypteridaceae*, and of twenty-two species listed only two certainly do not belong to the family. Six names are for various reasons of doubtful application, leaving fourteen identifiable, but of these five are exindusiate and so do not conform to the generic diagnosis. The remaining eight species belong to four genera in the present treatment. The present genus, according to my understanding of it, includes three of these species; and as the genus has no other name I typify *Christella* so that Léveillé's name may serve for it. It is pleasing to have the name of Hermann Christ commemorated in this way. His '*Farnkräuter der Erde*' (1897) was the first attempt to present the ferns of the whole world in a natural classification, breaking away from the artificial system of Hooker which had persisted for half a century, and was the fore-runner of much work in the present century.

This genus has its main diversification in the region from Burma to southern China.

As above defined, it comprises fewer species than the 150 estimated by Iwatsuki for his subgenus; he only cited the type species in 1964 and seven others in 1965. In the Pacific there are two free-veined species, *harveyi* and *obliquatum*, but none are known in Malesia. The tetraploid variable species *dentatum* is now quite cosmopolitan, but its introduction into the New World is probably recent; it grows in open places and is a follower of man's destruction of natural vegetation. The only known wide-ranging diploid has been called *contigua* in Malesia and Ceylon, *quadrangulare* in West Africa and tropical America; there are minor local differences in pubescence which may serve to distinguish subspecies. In tropical America the species *Polypodium patens* Sw. and *Dryopteris normalis* C. Chr., with free veins, and some allied species, appear also to belong to this genus. Owing to the position of their basal veins Ching thought these two species to be related to his genus *Pseudocyclosorus* (here included in *Pneumatopteris*) but noted that in other ways they differed. I cannot attempt to deal with them and their allies in the New World; they form the main part of *Dryopteris* subg. *Cyclosorus* in Christensen's monograph of *Dryopteris*, which is now receiving re-appraisal by students of tropical American ferns.

According to my observations, the presence of an elongate, unicellular, thick, blunt hair on the stalks of sporangia is universal in this genus; such hairs may or may not also be present on the lower surface of veins, and I believe that such occurrence may be no more than a varietal character in some cases.

23. AMPHINEURON Holttum, *gen. nov.*

Caudex suberectus vel breviter vel longe repens; frondes mediocrae vel magnae; pinnae 20—30-jugatae, plerumque profunde lobatae, infimae non reductae (in speciebus duabus pinnae multo minores 1—2-jugatae, irregulariter dispositae, adsunt); aerophorae non dilatatae; venae infimae (saepe in eodem fronde) vel liberae vel conniventes et venam brevem ad membranam sinus emittentes, venae ceterae liberae; pagina inferior laminae vel venarum glandulis majoribus sessilibus vel minoribus brevistipitatis saepe ornata; pagina superior interdum pilis brevissimis capitatis praedita; sori indusiati vel exindusiati, venis inferioribus interdum soris destitutis; indusia saepe glandulifera; sporangia stipitibus tenuibus sustenta, prope annulum non setifera nec glanduligera; stipites sporangiorum saepe pilo longo glandulifero praediti; sporae fere nigrae, irregulariter grosse tuberculatae. — **Fig. 19, 19a.**

Species typica: *Aspidium opulentum* Kaulf., Enum. Fil. Chamisso (1824) 238 = **Amphineuron opulentum** (Kaulf.) Holttum, *comb. nov.*

Distribution: type species from East Africa to Polynesia; *interruptum* from India to NE. Australia; the rest in Malesia and the Pacific, especially in New Guinea.

Species 12—15. *Dryopteris attenuata* O. Ktze, *Dryopteris besukiensis* v. A. v. R., *Lastrea caudiculata* Presl, *Phegopteris ceramica* v. A. v. R., *Dryopteris decora* Domin, D. *distincta* Copel., *D. diversifolia* v. A. v. R., *Aspidium extensum* Bl., *Lastrea gretheri* Wagn., *Aspidium immersum* Bl., *Dryopteris incerta* Domin, *Pteris interrupta* Willd., *Dryopteris kiauensis* C. Chr., *D. logavensis* Rosenst., *Phegopteris mamberamensis* v. A. v. R., *Dryopteris moluccana* C. Chr., *D. orbicularis* C. Chr., *D. paraphysophora* v. A. v. R., *D. pseudostenobasis* Copel., *D. rupicola* Hosok., *Thelypteris subimmersa* Ching, *Dryopteris sulfurea* E. Brown, *D. superficialis* v. A. v. R., ? *D. tonkinensis* C. Chr.

Chromosome number: 36 (*extensum* = *opulentum*, *interrupta*, both tetraploid).

This group of species is less clearly characterized than most others here recognized as genera, but I cannot associate them closely with any other group. The spores are most like those of *Christella*, but vegatative features are very different. The most aberreant species

listed is *D. tonkinensis* C. Chr., the pinnae of which are not deeply lobed; its basal veins appear to anastomose but careful examination shows that they pass to the sides of a rather long sinus-membrane. Another doubtful species, not included in the above list, is *Dryopteris subattenuata* Rosenst. from New Guinea; this has spores more like *Pneumatopteris*, three pairs of reduced pinnae, and elongate glands near annulus of sporangia, but it has narrow hairy stipe-scales and no perceptible pustules on dried pinnae, its pinnae shaped much as in *Amphineuron*.

POSTSCRIPT

Key to Genera, head 9, veins all free. Here is included the species of *Nannothelypteris* which has some anastomosis of veins near bases of pinnae.

Mesoneuron Ching (genus no. 10). This name must certainly be regarded as a homonym of *Mesonevron* Unger (1856) which appears as *Mesoneuron* in Engler & Prantl, Nat. Pflanzenfam. I, Abt. 4 (1900) 510.

The following names included in *Sphaerostephanos* should be transferred to *Pneumatopteris: Dryopteris deltiptera* Copel., *D. superba* Brause. These belong to a small group of species in New Guinea (two undescribed) which have brown hairs on lower surface of rachis and costae. I now also think that the African. *D. afra* Chr. and *Polypodium oppositifolium* Hook. are better placed in *Pneumatopteris*, but they do not conform well to either genus.

March 1971.

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