THE CLASSIFICATION OF THE CYATHEACEAE

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The *Cyatheaceae* is a moderate-sized family of about 650 species nearly equally divided between the neotropics and the paleotropics. The greatest number of species is found in the relatively cool and more or less constantly moist zones of tropical mountains. This feature may be seen in Fig. 1, where, within the distribution of the family in America, the areas of high concentrations of species correlate with the principal areas of cloud forest and montane forest.

I am not including the members of the *Dicksoniaceae* within the *Cyatheaceae* as Holttum and Sen (1961) have recently done. While appreciating the characters that they have brought to the classification, I believe that more information is needed before the evolutionary lines in the Dicksonioid-Cyatheoid alliance can clearly be traced, and the family (or families) recognized with assurance. There is, for example, some evidence which suggests that *Lophosoria* and *Metaxya* may be closer to the *Dicksoniaceae* than to the scaly *Cyatheaceae*. It is the classification of the scaly members of the *Cyatheaceae* which is my present concern and I have left in abeyance the problems raised by the Dicksonioid genera. I am tentatively following Christensen (1938) in recognizing the *Cyatheaceae* as including those genera that have a dorsal sorus.

A few years ago I began a systematic study of the American *Cyatheaceae* and this paper is the first report of the work. I recognize eight genera in the family, one of them new and the others, except for the monotypic *Lophosoria* and *Metaxya,* variously enlarged or remodeled and mostly redefined on the basis of new characters. My initial studies were directed toward the evolutionary developments in the family and the recognition of evolutionary groups which could form the basis of a generic classification. This survey indicated that there was greater morphological diversity among the American members of the family than among those of the Old World. For this reason, it was not possible to integrate the American species into the classification of Holttum (1963, 1964, 1965) which was developed principally on the basis of paleotropical species.

The six main groups of the squamate species have been recog-

nized as genera on the basis of the evidence that each is a major evolutionary line. Some of these genera are more distinctive and better defined than others, and some have more evolutionary innovations than others. There is no certain guide for the recognition of a group of species as a genus and I have chosen to admit to generic status only groups with substantial evolutionary qualifications, either in distinctiveness or in extensive speciation. The more distinctive genera need not have a large number of species while those that have many species may be less distinctive.

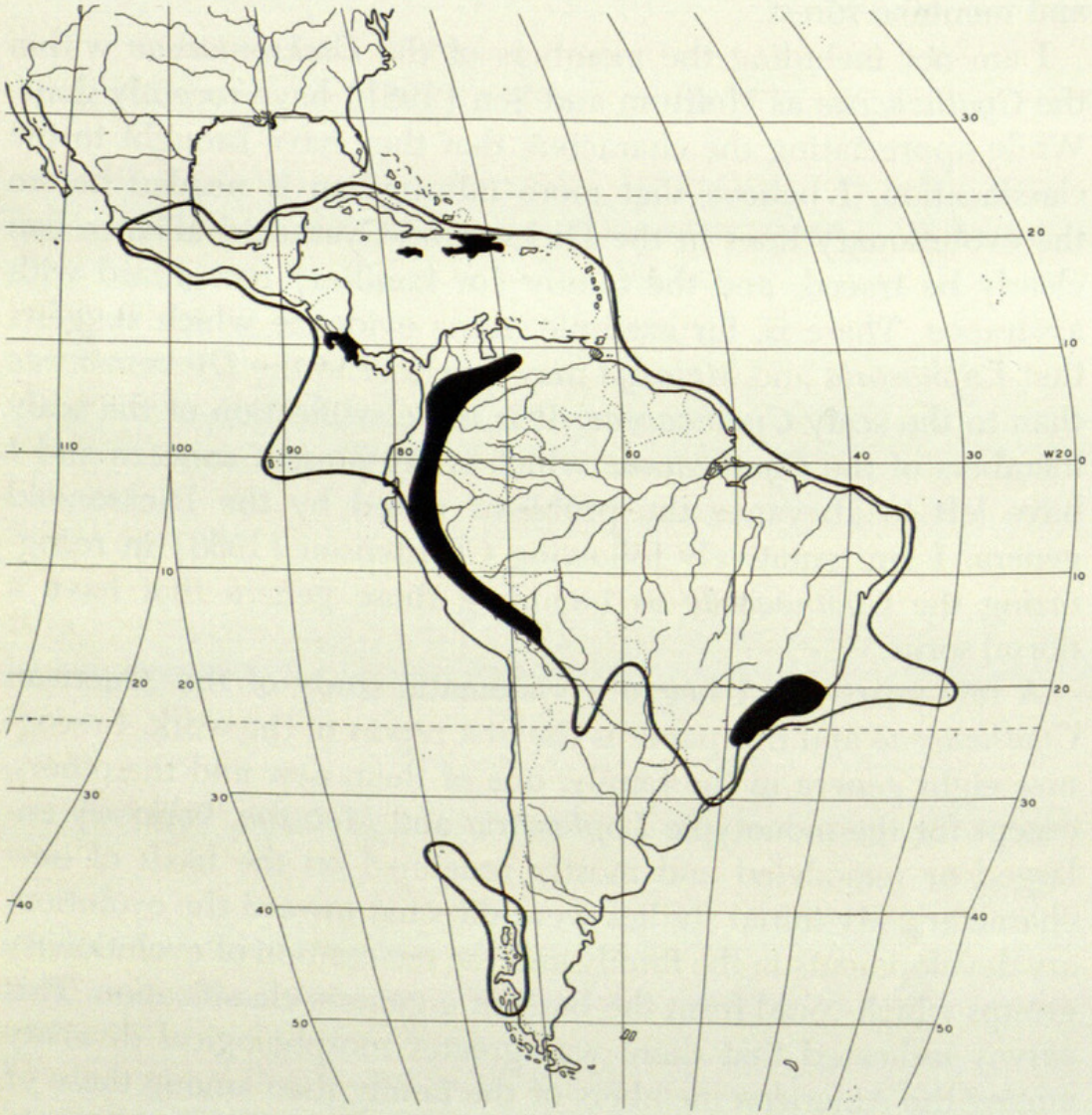


FIG. 1. Map of the distribution of Cyatheaceae in America and (in black) the areas of high concentrations of species: Hispaniola and Jamaica, 40 species; Costa Rica, 45 species; Andes, 125 species; southeastern Brazil, 40 species.

The present classification is based on a study of about 275 American species and about 230 species of the Old World. Approximately 75 per cent of the known species, from all parts of the range of the family and including species of all proposed groups, has been examined. Confidence in the classification has developed since its inception, as it has been brought into ever sharper focus by the incorporation of data from additional species and additional characters.

An unsatisfactory classification has persisted in the *Cyatheaceae* for a longer time than in any other of the large groups of ferns. There is no purpose in a historical discussion of the futile efforts to classify the family. It is sufficient to point out that prior to the work of DeWolf (1953) and of Holttum (1957, 1963), no progress was made toward the development of a realistic classification based on evolutionary developments in the family. It is true that some small segregate genera were proposed earlier that now can be recognized as natural groups, but these proposals (and others that lacked merit) did not improve the classification of the large and heterogeneous assemblage that remained.

The vital clue to the classification of the family was discovered by DeWolf (1953) in his studies of the petiole scales of paleotropical species, where he brought out the difference between "setiferous" (conform) and "flabelloid" (marginate) scale types. These studies were suggested by Holttum, who later (1957, 1963) successfully used the petiole scales over a very wide range of species in developing the classification of his inclusive genus *Cyathea.* In his classification the subgenera *Cyathea* and *Sphaeropteris* were based on the "flabelloid" and the "setiferous" scales respectively. Holttum's several papers (see Literature Cited) have provided the first broad foundation for the modern classification of the family.

My own intensive study of the American species has resulted in some taxonomic and evolutionary conclusions different from those of Holttum; this is probably inevitable as progress is made in the study of a large and complex group. Further attention to the morphology of the petiole scales has added to the diversity of scale types in the family and has provided the basis for the recognition of three principal evolutionary lines. The scale morphology, even when not wholly distinctive (for example, in

Nephelea and *Cnemidaria*) has been an important aid in the recognition of tentative evolutionary groups which have then been confirmed by further study of other characters.

CHARACTERS

A wide range of characters has been studied during the course of this investigation, most of which have not been usable at the generic level. Some are significant for species or species-groups; others, especially those of the stem, have not been represented in a sufficient number of species. Characters of the stem deserve careful attention but many more collections must be made before their significance can be assessed. Among the characters employed in this paper, some require explanation and these are discussed in the following paragraphs.

The petiole is sometimes smooth but more commonly, especially toward its base and on its abaxial side, it is variously roughened or spiny. A petiole that is pubescent sometimes becomes *scabrous* as the trichomes break off and leave a persistent base. In most species the petiole scales are borne on slight to very prominent projections of the petiole and these persist when the scale falls. When these projections are very low, the petiole is *muricate;* when they are larger but rounded and about as tall as broad, the petiole is *tuberculate;* when they are taller and tapering at the apex, they are called *spines*, and the petiole is *aculeate*.

In most of the aculeate species, the spines have evidently evolved by a development of the tissues of the petiole beneath the scale. I call these *corticinate* spines (cortex + natus: born of the cortex of the petiole). These can readily be identified in suitable material because a complete scale is perched on top of the spine (Fig. 22). The scale is sometimes not clearly differentiated from the apex of the spine, suggesting that the apex may be partly formed from the base of the scale. There is a complete transition from species with a smooth petiole to those with large spines of the corticinate type.

In other species the spines (Fig. 31) have evidently evolved by development of the body of the scale and the tissues of the petiole have not been involved in their formation. These are called *squaminate* spines (squama + natus: born of a scale). This kind of spine can be readily identified on suitable material because

some of the smaller spines will bear, on each side, the differentiated margin of the normal scale (Fig. 34). Rarely, an unmodified portion of the scale extends beyond the apex of the spine. There is a transition in *Alsophila* from species with normally developed scales to those with spinelike scales and to one species with squaminate spines. The evidence for the origin of this type of spine from a petiole scale is discussed more fully under the genera *Nephelea* and *Alsophila*.

It is sometimes necessary to refer to different parts of the petiole scales and to different kinds of scales. The *body* of the scale is considered to be the whole scale except for such processes (cilia, teeth, setae) as may be borne on the edge or at the apex. The *edge* of the scale is considered to consist of the single row of ultimate cells, or when cilia, teeth or setae are present, sometimes an additional row of cells that may be related to those processes.

The petiole scales of *Sphaeropteris* have all the cells of the body similar in shape and orientation (elongate with their long axis parallel to that of the scale) and usually in size and color (for example, Figs. 14–17). This kind of scale is called *structurally conform* or simply *conform*. In the other genera, the central cells of the petiole scales are also elongate and parallel to the long axis of the scale, but toward each edge the cells are different in size and orientation, and (usually) in shape and color (for example, Fig. 27). The central area of elongate cells then is called the *central portion* and the differentiated area (on each side) the *margin*. This kind of scale is called *structurally marginate*, or simply *marginate*. The margin may be broad or narrow and it may be well or poorly defined depending on the abruptness of the transition between the elongate cells of the central portion and the differentiated cells near the edge.

In many species there is a *minute indument* on the surface of the petiole that consists of very small scales or trichomes. These are composed of only a few cells. The small scales of this indument are called *squamulae* and the small trichomes *trichomidia*.

The indusium may completely surround the base of the receptacle, or not, and it may be variously developed. Very small indusia that are attached to one part of the base of the receptacle are called *scale-like*. Moderately to well developed indusia that partially surround the base of the receptacle are called *hemitelioid*.

Well developed indusia that completely surround the base of the receptacle are called *cyatheoid* if they are open at their apex, and *sphaeropteroid* if they are closed at their apex.

EVOLUTION

Among the squamate genera the characters of the petiole scales define three groups which I believe reflect the basic evolutionary lines: the genus *Sphaeropteris* with structurally conform petiole scales (Figs. 14–21), the genera *Alsophila* and *Nephelea* with structurally marginate petiole scales having dark apical setae (Figs. 23–30, 35–36), and the genera *Trichipteris, Cyathea* and *Cnemidaria* also with structurally marginate petiole scales but without apical setae (Figs. 39–41, 44–47). These three groups are evident in the phyletic chart (Fig. 2).

Within *Sphaeropteris, Alsophila* and *Nephelea,* further evolutionary developments occur that involve a thickening of the petiole scales. In a number of species of *Sphaeropteris* of Malaysia and Polynesia, the scales are basally thickened and rather fleshy. These species were recognized as *Cyathea* subsection *Sacropholis* by Holttum (1963). A similar development is also evident in some species of *Alsophila* of the West Indies, especially in *Alsophila Urbanii* which has small scales definitely thickened and somewhat fleshy. In other species of *Sphaeropteris* and *Alsophila* and in *Nephelea* the thickened petiole scales are hard and rigid. In *Sphaeropteris procera* of New Guinea some of the scales are quite modified and spine-like; and in *Alsophila auriculata* of Madagascar and in *Nephelea* the thickened and rigid scales form a transition from the normal scales on the petiole to the petiolar spines.

In a general way, it is possible to postulate an adaptive basis for the origin of scales and their structural differentiation. The arborescent habit elevates the apex of the stem with its crown of large leaves far above the root system. This must create problems in water relations that require some compensating adaptations. Any evolutionary development that would aid the roots and tall stem in providing water to the apex would contribute toward the solution of this problem. A dense investment of scaly indument could provide a better means for the absorption of water in the form of fog or rain than an investment of trichomes. The effective-

ness of the scales in water absorption could be improved by different orientations of the scales (Figs. 3, 4) and differences in their cellular construction. This concept provides an evolutionary rationale for the development and differentiation of the petiole scales. It also provides a basis for the conclusion that the developments in the petiole scales have been basic to the establishment of the major evolutionary lines in the squamate group.

I adopt the view that the genera with scales have evolved from ancestors having an indument wholly of trichomes. There are a few species among American *Sphaeropteris* that have petiole scales quite undifferentiated in cellular structure and two of these also have the scales intergrading to trichomes. In these species, *Sphaeropteris macarenensis* and *S. mollicula,* there are long trichomes on the petiole as well as long narrow scales that vary from two to many cells broad (Figs. 5–9). The cells of the scales are similar in size and proportion to those of the trichomes (compare Fig. 5 with 6 and 7). The base of some of the narrow scales is uniseriate (stipitate) (Fig. 6). The structure of these suggests that the first stage in the development of a scale has been a pluriseriate development above the base of a trichome. I consider that *Sphaeropteris macarenensis* and *S. mollicula* are primitive among the scaly species in respect to both their undifferentiated petiole scales and their petiole indument that shows the transition from trichomes to scales.

The origin of the indusium in the *Cyatheaceae,* and its evolutionary significance, has been subject to considerable disagreement. Bower (1926, Chapter 33) considered the exindusiate condition of the sorus to be primitive and the indusium to be a new structure which evolved later. Holttum and Sen (1961) and Sen (1964) interpret the indusium as homologous with that of *Dicksonia,* marginal in origin and the hemitelioid indusium as primitive. I believe that evidence from three sources supports Bower's interpretation that the indusium has originated from a laminar scale attached to the base of the receptacle. In the exindusiate species *Trichipteris armata,* there is usually a small scale closely associated with the receptacle but not attached to it (Riba, 1969). This scale is borne, slightly toward the midvein, on the vein that bears the receptacle. There is a small group of species in Malaysia and Polynesia (*Cyathea* subsection *Fourniera,* Holttum 1963, 1964) that has thin scales investing the sorus,

arising from the base of the receptacle. Finally, there are some species, for example *Cyathea Tuerckheimii,* in which a sphaeropteroid indusium bears an apical squamoid development (Fig. 10). This evidence strongly suggests an intimate relation between a laminar scale and an indusium, which I interpret to mean that the indusium is of squamate origin and that the indusiate sorus has been derived from the exindusiate sorus. The exindusiate condition of *Sphaeropteris macarenensis* and *S. mollicula* is consistent with the conclusion, drawn from their petiole indument, that they are species with primitive characters.

Sphaeropteris macarenensis and *S. mollicula* are different in some characters of the sorus from other scaly species. These characters are their slightly to moderately elevated receptacle, relatively few sporangia in a sorus and nearly globose sporangium capsule. In these soral characters the two species are rather similar to *Lophosoria* as indicated in Table 1. The comparisons presented there include characters of the petiole indument, the sorus and indusium and also the contrasting characters of a scaly indusiate species. It is reasonable to consider the wholly pubescent *Lophosoria* as representing a lower evolutionary level than the scaly genera of the family and the similarities in soral characters between it and *Sphaeropteris macarenensis* and *S. mollicula* suggest that those species are also at a rather low evolutionary level.

These considerations, summarized in Table 1, are all consistent with the conclusion that *Sphaeropteris macarenensis* and *S. mollicula* are species with primitive characters and are the most primitive of the living scaly species. Thus *Sphaeropteris* is taken as the most primitive of the scaly genera.

The phyletic relations of the genera are presented in Fig. 2. *Lophosoria* and *Metaxya* are placed apart in order to avoid the implication that either is directly ancestral to the group of scaly genera. *Sphaeropteris* is considered to have been derived from an ancestral line on an evolutionary level similar to that of *Lophosoria* but not necessarily one that would be congeneric with it. The first development of an indusium occurred in some species of *Sphaeropteris* and in one line setae were developed at the apex (and usually along the edge) of the petiole scales. A major evolutionary line has developed from each of the petiole scale types in *Sphaeropteris.* The setate type has given rise to *Alsophila* by the differentiation of the margin on the petiole scale and then to

TABLE 1

CHARACTERS OF FOUR SPECIES OF CYATHEACEAE

	Lophosoria quadripinnata	*Sphaeropteris macarenensis*	*Sphaeropteris mollicula*	*Cyathea arborea*
Petiole indument	trichomes only	trichomes intergrading to undifferentiated scales		Broad, differentiated scales
Receptacle	low	slightly elevated	moderately elevated	strongly elevated
Number of sporangia in a sorus	ca. 6–12	ca. 8–12	ca. 9–15	ca. 25–50
Sporangium capsule	asymmetrically globose	asymmetrically globose	asymmetrically globose	asymmetrically elongate-compressed
Indusium	none	none	none	cyatheoid

Nephelea by the development of squaminate spines on the petiole. Some species of *Alsophila* are exindusiate, indicating that the indusium evidently originated at least once in this line. An exindusiate group in *Sphaeropteris* with petiole scales lacking dark setae has given rise to the genera *Trichipteris, Cyathea* and *Cnemidaria,* again by a differentiation of the margin on the scale. The exindusiate *Trichipteris* gave rise to *Cyathea* by an independent development of the indusium. *Cnemidaria* has evolved in lamina reduction and vein modification especially; it was probably derived from species of *Cyathea* in which the indusium was only partially developed. This phyletic scheme provides a framework within which other evolutionary developments can be placed and provides an indication of the general evolutionary level of the genera.

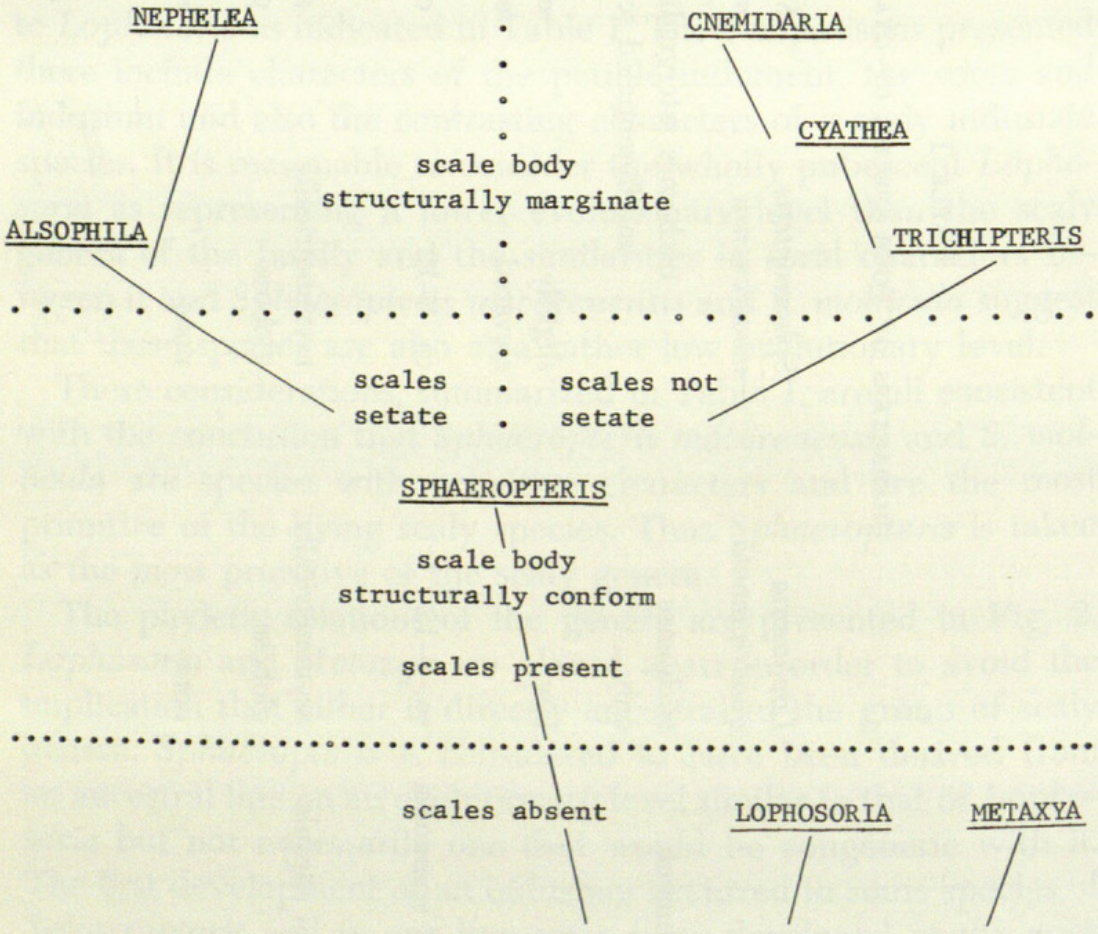
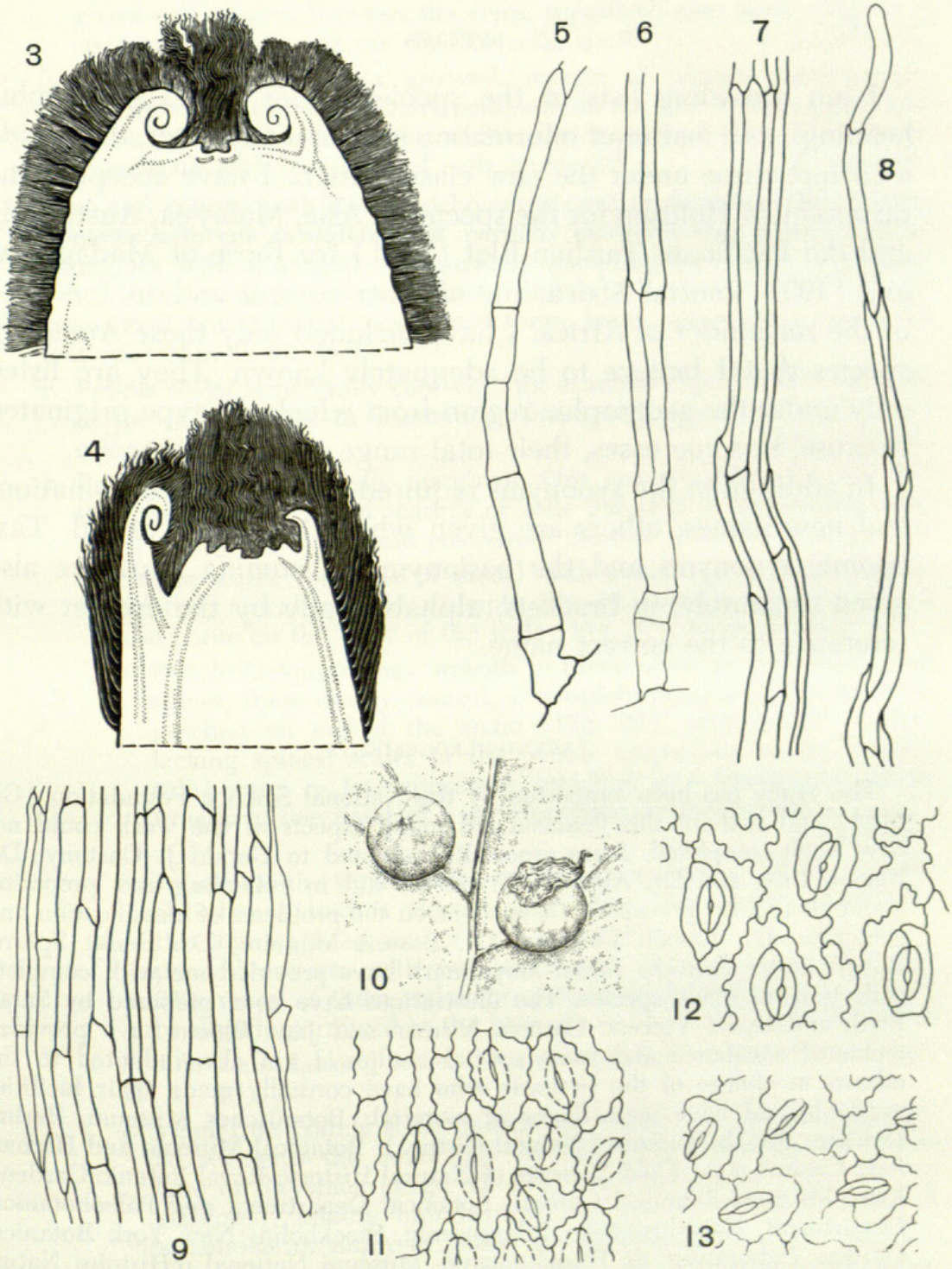


FIG. 2. Phyletic chart of Cyatheaceae.



FIGS. 3–13. CYATHEACEAE. FIGS. 3–4. Longitudinal sections of the stem apex, the older croziers removed, the scales are very tightly packed and the lines indicate only the general orientation and size, not the individual scales: 3, Small, patent scales of *Nephelea aureonitens, Gastony 763,* × 1/2, GH, 4, Larger, imbricate scales of *Cyathea conspersa, Tryon & Tryon 7025,* × 1/2, GH. FIGS. 5–9. Petiole indument of *Sphaeropteris macarenensis, Schultes & Cabrera 13368,* all × 60, A:5, Basal portion of trichome. 6, Basal portion of scale two cells wide. 7, Central portion of narrow scale. 8, Apex of scale in Fig. 7. 9, Central portion of a broad scale. FIG. 10. Indusia of *Cyathea Tuerckheimii,* normal globose indusium (left) and indusium with scale developed apically (right), *Steyermark 46784,* × 8, US. FIGS. 11–13. Lower epidermis with stomata: 11, *Lophosoria quadripinnata,* superficial stomate near vein (left), others are sunken, *Nisman 92,* × 180, GH. 12, *Metaxya rostrata, Kramer et al. 5651,* × 90, GH. 13, *Cnemidaria dissimilis, Wurdack 34154,* × 90, NY.

SPECIES

I am providing lists of the species under broad geographic headings, as a matter of information and, in many cases, to provide a correct name under the new classification. I have accepted the taxonomy of Holttum for the species of Asia, Malaysia, Australasia and the Pacific, of Tardieu-Blot (1951) for those of Madagascar and (1953) central Africa, and of other current authors for those of the remainder of Africa. I have included only those American species that I believe to be adequately known. They are listed only under the geographic region from which the type originated because, in some cases, their total range is uncertain.

In addition to the synonyms required for the new combinations and new names, others are given when they seem useful. Taxonomic synonyms and the basionyms of *nomina nova* are also given separately, in brackets, alphabetically by the epithet with reference to the correct name.

ACKNOWLEDGEMENTS

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KEY TO GENERA

a. Stem and petioles with trichomes, scales absent, receptacle low, capsule of the sporangium large (ca. 0.4–0.5 mm. long). *b.*

b. Lamina decompound, costa raised, margin of the segments scarely modified, stomates with two subsidiary cells, one on the side of each

guard cell, sunken between the veins, superficial near them (Fig. 11), sporangium stalk with six rows of cells, $n=65$ ..... 1. *Lophosoria.*

b. Lamina 1-pinnate, costa grooved, margin of pinnae cartillaginous, stomates with three subsidiary cells, one on the side of each guard cell and a third on the side of the smaller one, superficial (Fig. 12) sporangium stalk with four rows of cells, $n=$ca. 95 ..... 2. *Metaxya.*

a. Stem and petioles with scales, trichomes present or absent on the petioles, stomates with one subsidiary cell, partially enclosing both guard cells, or sometimes with a second one partially enclosing the other, superficial (Fig. 13), receptacle elevated (rarely slightly so), capsule of the sporangium small (ca. 0.15–0.2, rarely to 0.3 mm. long), sporangium stalk with four rows of cells, $n=69$. *c.*

c. Petiole scales structurally conform (for example Figs. 14–17), the cells of the body similar in orientation, shape, and (usually) in size and color. ..... 3. *Sphaeropteris.*

c. Petiole scales structurally marginate (for example Figs. 23, 27, 29) with a narrow to broad margin of cells different in orientation, size, and (usually) in shape and color from those of the central portion. *d.*

d. Petiole scales (or some of them) with a dark (very rarely lighter colored) apical seta (for example, Fig. 24), similar setae sometimes also borne on the body of the scale (Fig. 37), or on its edge. *e.*

e. Petiole lacking spines, smooth to tuberculate, or with corticinate spines, these mostly conical, a complete, usually caducous, scale perched on top of the spine (Fig. 22), unexpanded croziers lacking spines; scales of the petiole (especially on the abaxial side) more or less appressed, attached at a thickened base or usually at one point of a pseudopeltate or peltate base ..... 4. *Alsophila.*

e. Petiole with squaminate spines, many large, black, mostly obturbinate with a slender apex (Fig. 31), small spines bear the differentiated margins of the scales (Fig. 34), the unexpanded croziers with well developed squaminate spines (Fig. 31), many of them caducous; petiole scales patent, fully adnate or slightly narrowed at the base ..... 5. *Nephelea.*

d. Petiole scales lacking setae, the apex rounded to filamentous (Figs. 40, 41, 46). *f.*

f. Veins free (rarely some branch and rejoin), in lobed or pinnatifid segments the basal vein on each side extending above the base of the sinus (Figs. 42–43), costa pubescent above (rarely glabrous), minute indument of the petiole, when present, of squamulae or rarely of patent trichomidia. *g.*

g. Indusium absent ..... 6. *Trichipteris.*

g. Indusium present, rarely scale-like, to sometimes hemitelioid, to usually sphaeropteroid ..... 7. *Cyathea.*

f. Veins forming areolae along the costa (sometimes beyond) (Figs. 49–50), or all free and then in lobed or pinnatifid segments the basal vein on each side connivent to the base of the sinus (Fig. 48) (in parts of the lamina with very deep sinuses sometimes extending above the sinus), costa glabrous above (rarely pubescent), minute indument, when present, of appressed trichomidia, indusium hemitelioid ..... 8. *Cnemidaria.*

1. Lophosoria

Lophosoria Presl, Gefässbündel Stipes der Farrn, 36. 1847 (preprint Abhandl. böhm. Ges. V, **5**:344. 1848). Type: *Lophosoria pruinata* (Sw.) Presl (*Polypodium glaucum* Sw. 1788, not Thunb. 1784, *Polypodium pruinatum* Sw. nom. nov.) = *Lophosoria quadripinnata* (Gmel.) C. Chr.

Trichosorus Liebm. Vid. Selsk. Skr. V, 1:281. 1849. Type: *Alsophila pruinata* (Sw.) Kze. (*Polypodium pruinatum* Sw.) = *Lophosoria quadripinnata* (Gmel.) C. Chr.

I cannot find that the separate publication of Presl's "Gefässbündel" has been accurately dated and therefore accept the date on its title page. Stearn (1954) gives dates for other publications of Presl. Liebmann clearly indicated the type of his genus: "Typus denne Slaegt er *Alsophila pruinata* Kaulf.", although he made no combination for it under *Trichosorus*. At that time a type had not been selected from among the three species originally included in *Lophosoria* by Presl so that although both generic names have the same type, Liebmann's is not superfluous.

An American genus of one species, *Lophosoria quadripinnata* (Gmel.) C. Chr., in the Greater Antilles, Mexico and Central America, Andean South America, south to Bolivia; southern Chile and Juan Fernandez Islands. *Lophosoria* (Fig. 11) is a very distinctive genus and only a selection of its characters is given in the key to genera. Some others are mentioned in the discussion of evolution in the family. A chromosome number of $n=65$ is reported by Walker (1966).

2. Metaxya

Metaxya Presl, Tent. Pterid. 59. 1836. Type: *Metaxya rostrata* (HBK.) Presl (*Polypodium rostratum* Willd. 1810, not Burm. 1768, *Aspidium rostratum* HBK. nom. nov.).

Amphidesmium J. Sm. Ferns Brit. & For. 167. 1866. (Schott, Gen. Fil. sub *Trichopteris*, 1834, nom. nud.; Presl, Tent. Pterid. 246. 1836, nom. nud.; treated as a synonym of *Metaxya* by J. Sm. Lond. Jour. Bot. 1:668. 1842). Type: *Amphidesmium blechnoides* (Hook.) J. Sm. (*Alsophila blechnoides* Hook.) = *Metaxya rostrata* (HBK.) Presl.

Schott's publication of *Amphidesmium* is clearly invalid, although it was generdally accepted by his contemporaries. Presl adopted the genus but supplied so brief a diagnosis that his publication of its name can also be considered to be invalid. If one chooses to accept it as valid, however, then it is important to note that John Smith treated *Amphidesmium* as a synonym of *Metaxya*

a few years later. The name was certainly validly published by John Smith in 1866 and may have been validated earlier.

An American genus of one species, *Metaxya rostrata,* (Fig. 12) in the Lesser Antilles, Central America, northern South America and the Andes south to Bolivia. *Metaxya,* like *Lophosoria,* is a very distinctive genus and only a few of its characters are mentioned in the key to genera. A chromosome number of n=ca. 95 is reported by Roy and Holttum (1965).

3. Sphaeropteris

Sphaeropteris Bernh. Schrad. Jour. Bot. 1800 (2): 122. 1801, not Wall. 1830 (=*Peranema*). Type: *Sphaeropteris medullaris* (Forst.) Bernh. (*Polypodium medullare* Forst).

Schizocaena J. Sm. in Hook. Gen. Fil. t. 2. 1838. Type: *Schizocaena brunonis* J. Sm. = *Sphaeropteris moluccana* (Desv.) Tryon.

Eatoniopteris Bomm. Bull. Soc. Bot. France 20: xix. 1873. Lectotype: *Cyathea insignis* D. C. Eaton (Bommer made no combinations for the names of the 19 species he placed in his new genus) = *Sphaeropteris insignis* (D. C. Eaton) Tryon.

Fourniera Bomm. Bull. Soc. Bot. France 20: xix. 1873. Type: *Fourniera novaecaledoniae* (Mett.) Bomm. (*Alsophila novae-caledoniae* Mett.) = *Sphaeropteris novaecaledoniae* (Mett.) Tryon.

Petiole smooth to tuberculate, or with corticinate spines, sometimes with trichomes; petiole *scales* patent, fully adnate or slightly narrowed at the base, or stipitate, or (especially on the abaxial side) more or less appressed and attached at one point of a somewhat expanded base, structurally conform, the cells of the body all similar in their orientation and shape, and (usually) in their size and color (cilia, teeth or dark setae may be borne on the edge and one or more, usually dark, setae may be borne at the apex); *minute indument* of the petiole, when present, of trichomidia and (or) of squamulae; *costa* pubescent above or rarely glabrous; *veins* free, in lobed or pinnatifid segments the basal vein on each side extending above the base of the sinus; *indusium* absent, or present and hemitelioid to sphaeropteroid, or formed of several closely investing scales.

Sphaeropteris (Figs. 5–9, 14–21) is a genus of about 120 species, some 20 of them American and the remainder distributed from India and southeastern Asia to New Zealand, the Marquesas and Pitcairn Island. In the Old World the genus is exactly *Cyathea* subgenus *Sphaeropteris* of Holttum (1963, 1964, 1965). This subgenus was classified by Holttum as follows: section *Sphaeropteris* with subsection *Sphaeropteris* and subsection *Fourniera,* and section *Schizocaena* with subsection *Schizocaena* and subsection *Sacropholis.* In America there are several species, for example, *Sphaeropteris insignis, S. Brunei* and *S. horrida* (Fig. 19) that have

the petiole scales very like those of *Sphaeropteris medullaris*, *S. concinna* (Figs. 20, 21) and other related species of Holttum's subsection *Sphaeropteris*. Other American species do not exhibit relations outside of the western hemisphere. These are represented by a number of rather isolated species or distinctive species-groups that are sufficiently diverse so that, at this time, I hesitate to accommodate them (perhaps as a coordinate section) in Holttum's classification. A chromosome number of $n=69$ was reported by Brownlie (1961) for *Sphaeropteris medullaris* (as *Cyathea medullaris*).

The genus *Sphaeropteris* is characterized by the petiole scales that are structurally conform (undifferentiated or poorly differentiated) in their cellular construction. In most species the cells of the scale (except for processes such as cilia, teeth or dark setae that may be borne on the edge or apex) are nearly alike in their size, color, thickness of walls, their elongate shape and their orientation parallel to the long axis of the scale. Sometimes the cells near the edge are smaller than those at the center, or have thinner walls, or may be much lighter in color. These variations, as well as the various processes that may be borne on the edge or apex, are illustrated in Figs. 14–17 and 20. They are all developed on a basically uniform cellular pattern of the body of the scale. A few species, such as *Sphaeropteris hirsuta* and *S. marginalis*, have some petiole scales slightly marginate with the margin weakly modified and very narrow; others, such as *Sphaeropteris senilis* and *S. stigmosa*, have areas of slightly modified cells occurring at intervals along the margin. These examples of species with tendencies toward a marginate scale nearly provide a connection with *Trichipteris* in which a few species have slightly marginate scales.

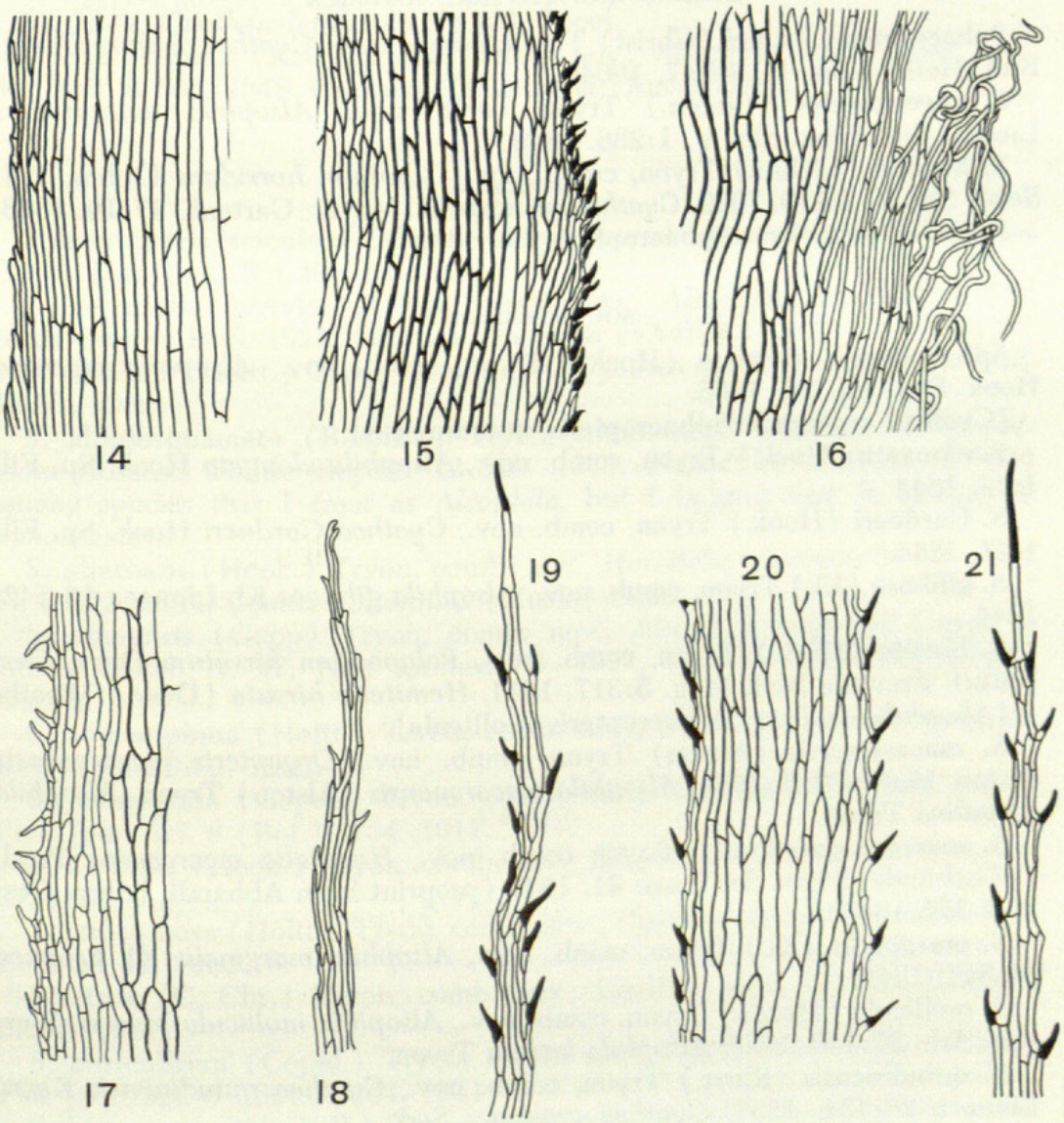
Some species, including the most primitive ones, *Sphaeropteris macarenensis* and *S. mollicula*, lack a dark apical seta on the petiole scale. The others have a dark seta and these include most of the species of *Sphaeropteris* of the paleotropics. However, in *Sphaeropteris albifrons* the seta is nearly concolorous with the brownish scale body; in *S. vittata* it is very small; in *S. discophora* there are two small dark setae at the apex and in *S. agatheti* there are several setulae.

The scales of the species treated by Holttum as subsection *Sacropholis* are much enlarged basally and may be at least 15 cells

thick. The relation to other species of *Sphaeropteris* is clearly indicated by their conform cellular structure, which is most easily seen beyond the thickened basal portion.

Sphaeropteris procera of New Guinea is unique in the genus in having some of the larger scales rather spine-like. These are rigid and subterete basally, while toward the apex the scale body is like that of the smaller scales. They become variously broken with age and are not persistent as definite spines.

The primitive type of indument of the petiole of *Sphaeropteris macarenensis* and *S. mollicula,* which is partly composed of long



FIGS. 14–21. SPHAEROPTERIS, portions of petiole scales, all × 30: 14, *S. mollicula, Schultes & Cabrera 13368a,* GH. 15, *Sphaeropteris sp. nov., Schultes 3389,* GH. 16, *S. marginalis, Maguire 24544,* A. 17, *S. myosuroides, Deam 482,* GH. 18, Apex, *S. senilis, Steyermark 91129,* US. 19, Apex, *S. horrida, Morton & Makrinius 2681,* US. 20, *S. concinna, Brass 3724,* GH. 21, Apex, *S. concinna, Brass 3124,* GH.

trichomes, has been discussed in the remarks on evolution. It would be of interest to know whether similar trichomes occur on the stem of these species. I am not able to determine this in the materials available because the persistent petiole bases are so closely crowded that the small areas of stem surface cannot be distinguished with certainty.

WEST INDIES

Sphaeropteris insignis (D. C. Eaton) Tryon, comb. nov., *Cyathea insignis* D. C. Eaton, Mem. Amer. Acad. n.s. 8:215. 1860.

MEXICO AND CENTRAL AMERICA

Sphaeropteris Brunei (Christ) Tryon, comb. nov., *Cyathea Brunei* Christ, Bull. Herb. Boiss. II, 4:947. 1904.

S. myosuroides (Liebm.) Tryon, comb. nov., *Alsophila myosuroides* Liebm. Vid. Selsk. Skr. V, 1:286. 1849.

S. horrida (Liebm.) Tryon, comb. nov., *Cibotium horridum* Liebm. Vid. Selsk. Skr. V, 1:279. 1849, *Cyathea princeps* E. Mayer, Gartenfl. 17:10. 1868. [*Cyathea princeps*=**Sphaeropteris horrida**].

SOUTH AMERICA

Sphaeropteris aterrima (Hook.) Tryon, comb. nov., *Alsophila aterrima* Hook. Syn. Fil. 38. 1866.

[*Cyathea crassipes*=**Sphaeropteris quindiuensis**].

S. elongata (Hook.) Tryon, comb. nov., *Alsophila elongata* Hook. Sp. Fil. 1:43. 1844.

S. Gardneri (Hook.) Tryon, comb. nov., *Cyathea Gardneri* Hook. Sp. Fil. 1:21. 1844.

S. gibbosa (Kl.) Tryon, comb. nov., *Alsophila gibbosa* Kl. Linnaea 18:542. 1844.

S. hirsuta (Desv.) Tryon, comb. nov., *Polypodium hirsutum* Desv. Ges. Naturf. Freunde Berl. Mag. 5:317. 1811, *Hemitelia hirsuta* (Desv.) Weath. [*Alsophilia lechria*=**Sphaeropteris mollicula**].

S. macarenensis (Alston) Tryon, comb. nov., *Dryopteris macarenensis* Alston, Mutisia 7:5. 1952, *Alsophila macarenensis* (Alston) Tryon, *Alsophila scopulina* Tryon.

S. macrocarpa (Presl) Tryon, comb. nov., *Hemitelia macrocarpa* Presl, Gefässbündel Stipes der Farrn 41. 1847 (preprint from Abhandl. böhm. Ges. V, 5:352. 1848).

S. marginalis (Kl.) Tryon, comb. nov., *Alsophila marginalis* Kl. Linnaea 18:542. 1844.

S. mollicula (Maxon) Tryon, comb. nov., *Alsophila mollicula* Maxon, Jour. Arn. Arb. 27:440. 1946, *Alsophila lechria* Tryon.

S. quindiuensis (Karst.) Tryon, comb. nov., *Cyathea quindiuensis* Karst. Linnaea 28:454. 1857, *Cyathea crassipes* Sod.

[*Alsophila scopulina*=**Sphaeropteris macarenensis**].

S. senilis (Kl.) Tryon, comb. nov., *Alsophila senilis* Kl. Linnaea 20:442. 1847.

S. stigmosa (Desv.) Tryon, comb. nov., *Hemitelia stigmosa* Desv. Mém. Soc. Linn. Paris 6:321. 1827.

ASIA

Sphaeropteris albosetacea (Bedd.) Tryon, comb. nov., *Alsophila albosetacea* Bedd. Suppl. Ferns So. India Brit. India 2. 1876, *Cyathea albosetacea* (Bedd.) Copel.

S. brunoniana (Hook.) Tryon, comb. nov., *Alsophila brunoniana* Hook. Sp. Fil. 1:52. 1844, *Cyathea brunoniana* (Hook.) Clarke & Baker.

[*Cyathea contaminans*=**Sphaeropteris glauca**].

S. crinita (Hook.) Tryon, comb. nov., *Alsophila crinita* Hook. Icon. Pl. 7: t. 671. 1844, and Sp. Fil. 1:54. 1844, *Cyathea crinita* (Hook.) Copel.

S. glauca (Bl.) Tryon, comb. nov., *Chnoophora glauca* Bl. Enum. Pl. Jav. 243. 1828, *Cyathea contaminans* (Hook.) Copel.

S. hainanensis (Ching) Tryon, comb. nov., *Cyathea hainanensis* Ching, Acta Phytotax. Sinica 8:168. 1959.

S. lepifera (Hook.) Tryon, comb. nov., *Alsophila lepifera* Hook. Sp. Fil. 1:54. 1844, *Cyathea lepifera* (Hook.) Copel.

S. Mertensiana (Kze.) Tryon, comb. nov., *Alsophila Mertensiana* Kze. Bot. Zeit. 6:586. 1848, *Cyathea Mertensiana* (Kze.) Copel.

MALAYSIA

Sphaeropteris aciculosa (Copel.) Tryon, comb. nov., *Cyathea aciculosa* Copel. Phil. Jour. Sci. 60:104. 1936.

S. aeneifolia (vAvR.) Tryon, comb. nov., *Alsophila aeneifolia* vAvR. Nova Guinea 14:3. 1924, *Cyathea aeneifolia* (vAvR.) Copel.

S. agatheti (Holtt.) Tryon, comb. nov., *Cyathea agatheti* Holtt. Kew Bull. 16:51. 1962.

S. albidosquamata (Rosenst.) Tryon, comb. nov., *Cyathea albidosquamata* Rosenst. Fedde Repert. 12:525. 1913. Placed by Holttum (1963) among species that I treat as *Alsophila,* but I believe that it belongs in *Sphaeropteris.*

S. alternans (Hook.) Tryon, comb. nov., *Hemitelia alternans* Hook. Icon. Pl. t. 622. 1844, *Cyathea alternans* (Hook.) Bedd.

S. angiensis (Gepp) Tryon, comb. nov., *Alsophila angiensis* Gepp, in Gibbs, Dutch N. W. New Guinea 69. 1917, *Cyathea angiensis* (Gepp) Domin.

S. angustipinna (Holtt.) Tryon, comb. nov., *Cyathea angustipinna* Holtt. Kew Bull. 16:52. 1962.

S. arthropoda (Copel.) Tryon, comb. nov., *Cyathea arthropoda* Copel. Phil. Jour. Sci. 6 (Bot.): 134. 1911.

S. assimilis (Hook.) Tryon, comb. nov., *Cyathea assimilis* Hook. Syn. Fil. 24. 1865.

S. atrospinosa (Holtt.) Tryon, comb. nov., *Cyathea atrospinosa* Holtt. Kew Bull. 16:52. 1962.

S. atrox (C. Chr.) Tryon, comb. nov., *Cyathea atrox* C. Chr. Brittonia 2:275. 1937.

S. auriculifera (Copel.) Tryon, comb. nov., *Cyathea auriculifera* Copel. Phil Jour. Sci. 6 (Bot.): 364. 1911.

S. binuangensis (vAvR.) Tryon, comb nov., *Cyathea binuangensis* vAvR. Bull. Jard. Bot. Buitenz. III, 2:136. 1920.

S. capitata (Copel.) Tryon, comb. nov., *Cyathea capitata* Copel. Phil. Jour. Sci. 12 (Bot.): 49. 1917.

S. Carrii (Holtt.) Tryon, comb. nov., *Cyathea Carrii* Holtt. Kew Bull. 16:53. 1962.

S. celebica (Bl.) Tryon, comb. nov., *Cyathea celebica* Bl. Enum. Pl. Jav. 245. 1828.

S. concinna (Baker) Tryon, comb. nov., *Alsophila concinna* Baker, Syn. Fil. ed. 2, 459. 1874, *Cyathea sangirensis* (Christ) Copel.

[*Cyathea contaminans*=**Sphaeropteris glauca**].

S. Curranii (Copel.) Tryon, comb. nov., *Cyathea Curranii* Copel. Phil. Jour. Sci. 3:356. 1909.

[*Cyathea deminuens*=**Sphaeropteris parvifolia**].

S. discophora (Holtt.) Tryon, comb. nov., *Cyathea discophora* Holtt. Kew Bull. 16:54. 1962.

S. elliptica (Copel.) Tryon, comb. nov., *Cyathea elliptica* Copel. Phil. Jour. Sci. 12 (Bot.): 51. 1917.

S. Elmeri (Copel.) Tryon, comb. nov., *Alsophila Elmeri* Copel. Leafl. Phil. Bot. 2:419. 1908, *Cyathea Elmeri* (Copel.) Copel.

S. fugax (vAvR.) Tryon, comb. nov., *Cyathea fugax* vAvR. Bull. Jard. Bot. Buitenz. II, 7:8. 1912.

S. fusca (Baker) Tryon, comb. nov., *Cyathea fusca* Baker, in Beccari, Malesia 3: 31. 1886.

S. glauca (Bl.) Tryon (supra).

S. inaequalis (Holtt.) Tryon, comb. nov., *Cyathea inaequalis* Holtt. Kew Bull. 16:56. 1962.

S. insularum (Holtt.) Tryon, comb. nov., *Cyathea insularum* Holtt. Kew Bull. 16:57. 1962.

S. integra (J.Sm.) Tryon, comb. nov., *Cyathea integra* J.Sm. Icon. Pl. t. 638. 1844.

S. Ledermannii (Brause) Tryon, comb. nov., *Hemitelia Ledermannii* Brause, Bot. Jahrb. 56:60. 1920, *Cyathea macrophylla* Domin.

S. lepifera (Hook.) Tryon (supra).

S. leucotricha (Christ) Tryon, comb. nov., *Cyathea leucotricha* Christ, Ann. Jard. Bot. Buitenz. 20:135. 1905.

S. lunulata(Forst.) Tryon, comb. nov., *Polypodium lunulatum* Forst. Fl. Ins. Aust. Prod. 83. 1786, *Cyathea lunulata* (Forst.) Copel.

[*Cyathea macrophylla*=**Sphaeropteris Ledermannii**].

S. magna (Copel.) Tryon, comb. nov., *Cyathea magna* Copel. Univ. Calif. Publ. Bot. 18:218. 1942.

S. marginata (Brause) Tryon, comb. nov., *Alsophila marginata* Brause, Bot. Jahrb. 56:63. 1920, *Cyathea marginata* (Brause) Domin.

S. megalosora (Copel) Tryon, comb. nov., *Cyathea megalosora* Copel. Phil. Jour. Sci. 12 (Bot.): 54. 1917.

S. moluccana (Desv.) Tryon, comb., nov., *Cyathea moluccana* Desv. Mém. Soc. Linn. Paris 6:322. 1827.

S. Moseleyi (Baker) Tryon, comb. nov., *Cyathea Moseleyi* Baker, Jour. Linn. Soc. Bot. 15:104. 1876.

S. obliqua (Copel.) Tryon, comb. nov., *Cyathea obliqua* Copel. Leafl. Phil. Bot. 4:1150. 1911.

S. obscura (Bedd.) Tryon, comb. nov., *Alsophila obscura* Bedd. Jour. Bot. 25:321. 1887, *Cyathea obscura* (Bedd.) Copel.

S. papuana (Ridley) Tryon, comb. nov., *Alsophila papuana* Ridley, Trans. Linn. Soc. Lond. II, (Bot.) 9:252. 1916, *Cyathea papuana* (Ridley) vAvR.

S. parvifolia (Holtt.) Tryon, comb. nov., *Alsophila parvifolia* Holtt. Jour. Mal. Br. Roy. As. Soc. 6:19. 1928, *Cyathea deminuens* Holtt.

S. parvipinna (Holtt.) Tryon, comb. nov., *Cyathea parvipinna* Holtt. Kew Bull. 16:60. 1962.

S. persquamulifera (vAvR.) Tryon, comb. nov., *Cyathea contaminans* var. *persquamulifera* vAvR. Bull. Jard. Bot. Buitenz. II, **28**:13. 1918, *Cyathea persquamulifera* (vAvR.) Domin.

S. philippinensis (Baker) Tryon, comb. nov., *Cyathea philippinensis* Baker, Ann. Bot. **5**:186. 1891.

S. pilulifera (Copel.) Tryon, comb. nov., *Cyathea pilulifera* Copel. Univ. Calif. Publ. Bot. **18**:219. 1942.

S. polypoda (Baker) Tryon, comb. nov., *Cyathea polypoda* Baker, Trans. Linn. Soc. Lond. II (Bot.) **4**:250. 1894.

S. procera (Brause) Tryon, comb. nov., *Cyathea procera* Brause, Bot. Jahrb. **56**:50. 1920.

S. pulcherrima (Copel.) Tryon, comb. nov., *Cyathea pulcherrima* Copel. Univ. Calif. Publ. Bot. **18**:219. 1942.

S. Robinsonii (Copel.) Tryon, comb. nov., *Cyathea Robinsonii* Copel. Phil. Jour. Sci. **6** (Bot.): 145. 1911.

S. Rosenstockii (Brause) Tryon, comb. nov., *Cyathea Rosenstockii* Brause, Bot. Jahrb. **56**:49. 1920.

S. runensis (vAvR.) Tryon, comb. nov., *Cyathea runensis* vAvR. Bull. Dépt. Agric. Ind. Néerl. **18**:1. 1908.

[*Cyathea sangirensis*=**Sphaeropteris concinna**].

S. Sarasinorum (Holtt.) Tryon, comb. nov., *Cyathea Sarasinorum* Holtt. Kew Bull. **16**:61. 1962.

S. senex (vAvR.) Tryon, comb. nov., *Cyathea senex* vAvR. Bull. Jard. Bot. Buitenz. II, **16**:4. 1914.

S. setifera (Holtt.) Tryon, comb. nov., *Cyathea setifera* Holtt. Kew Bull. **16**:62. 1962.

S. sibuyanensis (Copel.) Tryon, comb. nov., *Cyathea sibuyanensis* Copel. Leafl. Phil. Bot. **4**:1150. 1911.

S. squamulata (Bl.) Tryon, comb. nov., *Gymnosphaera squamulata* Bl. Enum. Pl. Jav. 243. 1828, *Cyathea squamulata* (Bl.) Copel.

S. stipitipinnula (Holtt.) Tryon, comb. nov., *Cyathea stipitipinnula* Holtt. Kew Bull. **16**:62. 1962.

S. strigosa (Christ) Tryon, comb. nov., *Cyathea strigosa* Christ, Ann. Jard. Bot. Buitenz. **15**:84. 1898.

S. suluensis (Baker) Tryon, comb. nov., *Cyathea suluensis* Baker, Jour. Bot. **17**:65. 1879.

S. tenggerensis (Rosenst.) Tryon, comb. nov., *Alsophila tenggerensis* Rosenst. Medel. Rijksherb. **31**:1. 1917, *Cyathea tenggerensis* (Rosenst.) Domin.

S. Teysmannii (Copel.) Tryon, comb. nov., *Cyathea Teysmannii* Copel. Phil. Jour. Sci. **4** (Bot.): 51. 1909.

S. tomentosa (Bl.) Tryon, comb. nov., *Chnoophora tomentosa* Bl. Enum. Pl. Jav. 244. 1828, *Cyathea tomentosa* (Bl.) Zoll. & Mor.

S. tomentosissima (Copel.) Tryon, comb. nov., *Cyathea tomentosissima* Copel. Univ. Calif. Publ. Bot. **18**:219. 1942.

S. trichodesma (Bedd.) Tryon, comb. nov., *Alsophila trichodesma* Bedd. Jour. Bot. **25**: 321. 1887, *Cyathea trichodesma* (Bedd.) Copel.

S. trichophora (Copel.) Tryon, comb. nov., *Cyathea trichophora* Copel. Phil. Jour. Sci. **6** (Bot.): 363. 1911.

S. tripinnata (Copel.) Tryon, comb. nov., *Cyathea tripinnata* Copel. Phil. Jour. Sci. 1, Suppl. : 251. 1906.

S. tripinnatifida (Roxb.) Tryon, comb. nov., *Cyathea tripinnatifida* Roxb. Calc. Jour. Nat. Hist. **4**:518. 1844.

S. verrucosa (Holtt.) Tryon, comb. nov., *Cyathea verrucosa* Holtt. Kew Bull. **16**:63. 1962.

S. Wallacei (Kuhn) Tryon, comb. nov., *Alsophila Wallacei* Kuhn, Linnaea **36**:153. 1869, *Cyathea Wallacei* (Kuhn) Copel.

S. Werneri (Rosenst.) Tryon, comb. nov., *Cyathea Werneri* Rosenst. Fedde Repert. **5**:34. 1908.

S. Womersleyi (Holtt.) Tryon, comb. nov., *Cyathea Womersleyi* Holtt. Kew Bull. **16**:63. 1962.

S. zamboangana (Copel.) Tryon, comb. nov., *Cyathea zamboangana* Copel. Phil. Jour. Sci. **30**:325. 1926.

AUSTRALIA AND PACIFIC

Sphaeropteris aciculosa (Copel.) Tryon (supra).

S. albifrons (Fourn.) Tryon, comb. nov., *Cyathea albifrons* Fourn. Ann. Sci. Nat. V, **18**:351. 1873.

S. aramaganensis (Kanehira) Tryon, comb. nov., *Cyathea aramaganensis* Kanehira, Bot. Mag. Tokyo **48**:731. 1934.

S. australis (Presl) Tryon, comb. nov., *Hemitelia australis* Presl, Epim. Bot. 33. 1852, *Cyathea Leichardtiana* (F.v.Muell.) Copel.

S. Brackenridgei (Mett.) Tryon, comb. nov., *Cyathea Brackenridgei* Mett. Ann. Mus. Bot. Lugd.-Bat. **1**:56. 1863.

[*Cyathea Brownii*=**Sphaeropteris excelsa**].

S. celebica (Bl.) Tryon (supra).

S. Cooperi (F.v.Muell.) Tryon, comb. nov., *Alsophila Cooperi* F.v.Muell. Fragm. Phyt. Austrl. **5**:117. 1866, *Cyathea Cooperi* (F.v.Muell.) Domin.

S. excelsa (Endl.) Tryon, comb. nov., *Alsophila excelsa* Endl. Prod. Fl. Norf. 16. 1833, *Cyathea Brownii* Domin.

S. feani (E. Brown) Tryon, comb. nov., *Cyathea feani* E. Brown, Bishop Mus. Bull. **89**:14. 1931.

S. intermedia (Mett.) Tryon, comb. nov., *Alsophila intermedia* Mett. Ann. Sci. Nat. IV, **15**:83. 1861, *Cyathea intermedia* (Mett.) Copel.

[*Cyathea Leichardtiana*=**Sphaeropteris australis**].

S. leucolepis (Mett.) Tryon, comb. nov., *Cyathea leucolepis* Mett. Ann. Mus. Bot. Lugd.-Bat. **1**:56. 1863.

S. lunulata (Forst.) Tryon (supra).

S. medullaris (Forst.) Bernh., *Cyathea medullaris* (Forst.) Sw.

S. microlepidota (Copel.) Tryon, comb. nov., *Cyathea microlepidota* Copel. Jour. Arn. Arb. **30**:435. 1949.

S. nigricans (Mett.) Tryon, comb. nov., *Cyathea nigricans* Mett. Ann. Mus. Bot. Lugd.-Bat. **1**:56. 1863.

S. novaecaledoniae (Mett.) Tryon, comb. nov., *Alsophila novae-caledoniae* Mett. Ann. Sci. Nat. IV, **15**:82. 1861, *Cyathea novaecaledoniae* (Mett.) Copel.

S. Parksiae (Copel.) Tryon, comb. nov., *Cyathea Parksiae* Copel. Univ. Calif. Publ. Bot. **12**:377. 1931.

S. propinqua (Mett.) Tryon, comb. nov., *Cyathea propinqua* Mett. Ann. Mus. Bot. Lugd.-Bat. **1**:56. 1863.

S. robusta (Watts) Tryon, comb. nov., *Alsophila robusta* Watts, Proc. Linn. Soc. N. S. Wales **39**:261. 1914 (not de Vriese, in Junghuhn, Java, Gestalt Pflanzend. Bauart. **1**:310, 476. 1852, nomen nudum), *Cyathea robusta* (Watts) Holtt.

S. samoensis (Brack.) Tryon, comb. nov., *Alsophila samoensis* Brack. U.S.Explor. Exped. **16**:287. 1854, *Cyathea Whitmeei* Baker.

S. subsessilis (Copel.) Tryon, comb. nov., *Cyathea subsessilis* Copel. Phil. Jour. Sci. **6** (Bot.): 359. 1911.

S. truncata (Brack.) Tryon, comb. nov., *Alsophila truncata* Brack. U. S. Explor. Exped. **16**:289. 1854, *Cyathea truncata* (Brack.) Copel.

S. Vaupelii (Copel.) Tryon, comb. nov., *Cyathea Vaupelii* Copel. Phil. Jour. Sci. **6** (Bot.): 360. 1911.

S. vittata (Copel.) Tryon, comb. nov., *Cyathea vittata* Copel. Phil. Jour. Sci. **60**:102. 1936.

[*Cyathea Whitmeei*=**Sphaeropteris samoensis**].

4. Alsophila

Alsophila R. Br. Prod. Fl. Nov. Holl. 158. 1810. Type: *Alsophila australis* R. Br.

Gymnosphaera Bl. Enum. Pl. Jav. 242. 1828. Type: *Gymnosphaera glabra* Bl. = *Alsophila glabra* (Bl.) Hook.

Amphicosmia Gardn. Lond. Jour. Bot. **1**:441. 1842. Lectotype: *Amphicosmia riparia* (Willd.) Gardn. (*Cyathea riparia* Willd.) = *Alsophila capensis* (L. f.) J. Sm.

Dichorexia Presl, Gefässbündel Stipes der Farrn, 36. 1847 (preprint from Abhandl. böhm. Ges. V, **5**:344. 1848). Type: *Dichorexia latebrosa* (Hook.) Presl = *Alsophila latebrosa* Hook.

Thysanobotrya vAvR. Bull. Jard. Bot. Buitenz. II, **28**:66. 1918. Type: *Thysanobotrya arfakensis* (Gepp) vAvR. (*Polybotrya arfakensis* Gepp) = *Alsophila biformis* Rosenst.

Petiole smooth to tuberculate, or with corticinate spines (with squaminate spines in one species), lacking trichomes (in species examined); petiole *scales* (especially on the abaxial side) more or less appressed, attached either at one point of a pseudopeltate to peltate base or at a thickened base (rarely patent and adnate at the thickened base), structurally marginate, with a narrow to broad margin of cells different in orientation, size, shape and usually in color from those of the central portion, some or all scales bearing a dark (rarely lighter colored) seta at the apex and often one seta (or more) on the edge or body of the scale; *minute indument* of the petiole, when present, of trichomidia and (or) squamulae; *costa* usually pubescent above, rarely glabrous; *veins* free, in lobed or pinnatifid segments the basal vein on each side extending above the base of the sinus; *indusium* absent, or present and scale-like to sphaeropteroid.

The name *Amphicosmia* might appear to be superfluous because Gardner included *Cyathea multiflora*, the type of *Hemitelia*, in his genus. However, the typification of *Hemitelia* had not been settled at that time and Gardner explicitly considered *Cyathea horrida* to be the type of *Hemitelia*.

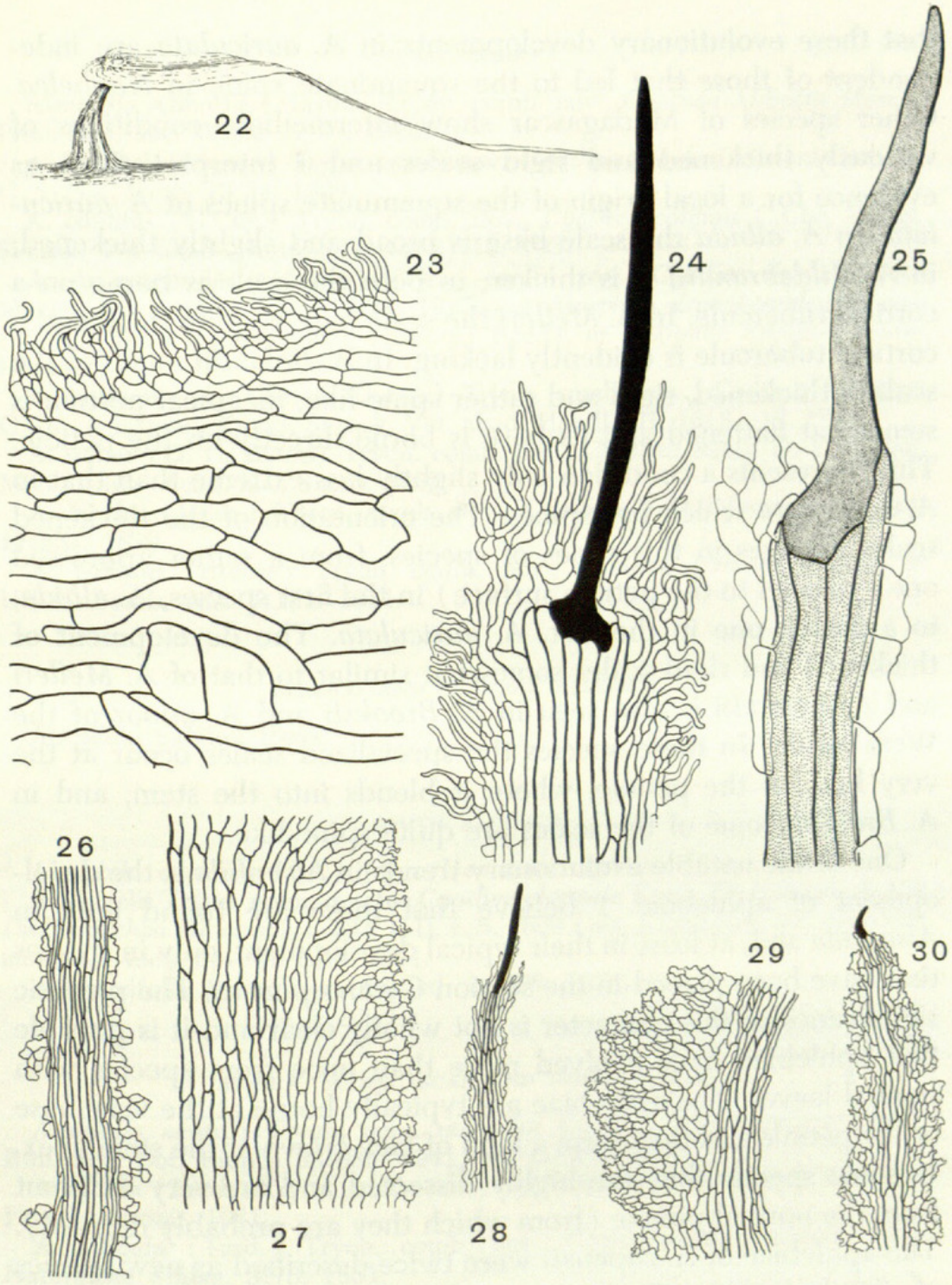
Alsophila (Figs. 22–30) is a pantropic genus of about 230 species, poorly represented in America by about 12 species, well represented in Africa-Madagascar by about 60 species and from India and Ceylon to southern Japan, the Auckland Islands and to the Marquesas by about 160 species. In the paleotropics the

genus is exactly *Cyathea* subgenus *Cyathea* Holttum (1963, 1964, 1965), including section *Cyathea* and section *Gymnosphaera.* Most American species, for example, *A. Brooksii, A. Nockii* and *A. Urbanii,* form a distinct group of indusiate bipinnate species in the Greater Antilles which perhaps has affinities with similar species of Africa and Madagascar. The two other American species, *A. capensis* (also in Africa) and *A. Salvinii,* are evidently related to species of the section *Gymnosphaera.* The size and diversity of *Alsophila* suggest that further studies are desirable to determine the major evolutionary lines within it. A chromosome number of $n=69$ has been reported, for example, in *A. gigantea* (as *Cyathea gigantea*) by Manton and Sledge (1954).

The genus is characterized by its differentiated petiole scales that are marginate and apically setate, and by the petiole spines that (when present) are corticinate (Fig. 22) and arise from the petiole tissue. The cellular differentiation of the petiole scale margin is of two types which are connected by intermediates. One type (Fig. 26), similar to that found in *Nephelea,* has the thin walled marginal cells more or less isodiametric in shape and abruptly distinct from the heavy walled, elongate cells of the central portion of the scale. The other type (Fig. 27) has more elongate marginal cells which gradually differ from the cells of the central portion as they approach the edge of the scale. The scales of *Alsophila Nockii* (Figs. 29, 30) are more or less intermediate between these two types.

All of the species of *Alsophila* that I have seen have an apical seta on some of the petiole scales and, except in a few species of Madagascar, it is dark in color. The seta is more or less concolorous with the brownish scale body in *A. Ballardii, A. bellisquamata, A. Hildebrandtii, A. Hyacinthei* and *A. similis* of Madagascar.

Two further developments in the petiole scales are of interest. One is in *Alsophila Urbanii* of the West Indies, which has small and rather thickened and fleshy petiole scales. They are similar in their texture to some of the species of *Sphaeropteris* having thickened and fleshy scales. The other development is the squaminate spine of *A. auriculata* in Madagascar. The species is similar in this respect to the genus *Nephelea* and, in addition, the stem is spiny as it is in some *Nephelea* species (whether the unexpanded croziers also have spines like *Nephelea* is not known). I believe



FIGS. 22–30. ALSOPHILA. FIG. 22. Corticinate petiole spine bearing a scale, *A. Manniana, Goodwin 5,* × 4, GH. FIGS. 23–30. Portions of petiole scales: 23, *A. Manniana, Tryon & Tryon 5626,* × 90, GH. 24, Apex, *A. Manniana* (as in Fig. 23). 25, Apex, *A. capensis,* Brazil, *Leite 3565,* × 150, A. 26, *A. Foersteri, Brass 23382,* × 30, GH. 27, *A. Salvinii, Hernandez X–336,* × 30, US. 28, Apex, *A. Salvinii* (as in Fig. 27). 29, *A. Nockii, Underwood 1355,* × 30, NY. 30, Apex, *A. Nockii* (as in Fig. 29).

that these evolutionary developments in *A. auriculata* are independent of those that led to the squaminate spine in *Nephelea.* Other species of Madagascar show intermediate conditions of variously thickened and rigid scales and I interpret these as evidence for a local origin of the squaminate spines of *A. auriculata.* In *A. albida* the scale base is broad and slightly thickened; in *A. Hildebrandtii* it is thicker; in both the scale is borne on a cortical tubercule. In *A. Melleri* the scale base is quite thick and a cortical tubercule is evidently lacking. In *A. Rolandii* much of the scale is thickened, rigid and rather spine-like; its apical portion is somewhat flattened and its base is borne directly on the petiole. This represents a condition only slightly less extreme than that in *A. auriculata* which has spines. The orientation of the thickened scales changes in this series of species, from a rather appressed one (parallel to the petiole surface) in the first species, *A. albida,* to a patent one in the last, *A. auriculata.* The development of thickened and rigid scales somewhat similar to that of *A. Melleri* and *A. Rolandii* is also seen in *A. Brooksii* and *A. minor* of the West Indies. In these species the specialized scales occur at the very base of the petiole, where it blends into the stem, and in *A. Brooksii* some of the scales are quite spine-like.

One of the notable evolutionary trends in *Alsophila* is the development of aphlebiae. I believe that these are found only in *Alsophila* and, at least in their typical development, only in species that have been placed in the section *Gymnosphaera.* The phyletic significance of this character is not wholly clear and it is possible that aphlebiae have evolved more than once from species with normal leaves. The aphlebiae are typically borne at the very base of the petiole and they form a kind of lacy crown at the stem apex. In some species they are highly dissected and are very different from the normal pinnae (from which they are probably derived). The aphlebiae of *A. capensis* were twice described as new species of *Trichomanes* (*T. incisum* Thunb. and *T. cormophyllum* Kaulf.). Tardieu-Blot (1941) discusses aphlebiae with special reference to the species of Madagascar and presents the various concepts of their nature and origin.

The current literature on African *Cyatheaceae* does not include all of the proposed species and, because of doubt about their taxonomic status, some of these have not been included in the following list.

WEST INDIES

Alsophila Abbottii (Maxon) Tryon, comb. nov., *Cyathea Abbottii* Maxon, Proc. Biol. Soc. Wash. **37**:98. 1924.

A. Brooksii (Maxon) Tryon, comb. nov., *Cyathea Brooksii* Maxon, Contrib. U. S. Nat. Herb. **13**:24. 1909.

A. confinis (C.Chr.) Tryon, comb. nov., *Cyathea confinis* C.Chr. Kungl. Svensk. Vet.-akad. Handl. III, **16**(2):13. 1937.

A. dryopteroides (Maxon) Tryon, comb. nov., *Cyathea dryopteroides* Maxon, Amer. Fern Jour. **14**:99. 1925, not *Alsophila dryopteroidea* Brause (=*Thelypteris dryopteroidea* (Brause) Reed), or *Alsophila dryopteridoides* Domin.

A. hotteana (C. Chr. & Ekman) Tryon, comb. nov., *Cyathea hotteana* C.Chr. & Ekman, Kungl. Svensk. Vet.-akad. Handl. III, **16**(2):12. 1937.

A. minor (D. C. Eaton) Tryon. comb. nov., *Cyathea minor* D. C. Eaton, Mem. Amer. Acad. n.s., **8**:215. 1860.

A. Nockii (Jenm.) Tryon, comb. nov., *Cyathea Nockii* Jenm. Jour. Bot. **17**:257. 1879.

A. Urbanii (Brause) Tryon, comb. nov., *Cyathea Urbanii* Brause, in Urban, Symb. Ant. **7**:151. 1911.

MEXICO AND CENTRAL AMERICA

5996 **Alsophila Salvinii** Hook.

SOUTH AMERICA

4284 4283 **Alsophila capensis** (L.f.) J.Sm. *Hemitelia capensis* (L.f.) Kaulf.

6634 **A. Engelii** Tryon, nom. nov. for *Cyathea elongata* Karst. Fl. Columb. **2**:159 6632 6635 (sub *Cyathea erinacea*), t. 183, f. II, f. 5. 1869 (leg. Engel B!), not *Alsophila* 6619 *elongata* Hook. Sp. Fil. **1**:43. 1844.

16193 **A. paucifolia** Baker, Syn. Fil. ed. 2, 456. 1874.

AFRICA, MADAGASCAR AND INDIAN OCEAN

Alsophila acutula Tryon, nom. nov., for *Cyathea tsaratananensis* Tard. Bull. Soc. Bot. France **88**:681. 1941, not C.Chr. 1934.

A. albida (Tard.) Tryon, comb. nov., *Cyathea albida* Tard. Bull. Soc. Bot. France **88**:680. 1941.

A. alticola (Tard.) Tryon, comb. nov., *Gymnosphaera alticola* Tard. Naturaliste Malag. **3**:76. 1951.

A. andohahelensis Tard. *Gymnosphaera andohahelensis* (Tard.) Tard.

A. appendiculata (Baker) Tryon, comb. nov.. *Cyathea appendiculata* Baker, Jour. Linn. Soc. **15**:411. 1876.

A. approximata (Bonap.) Tryon, comb. nov., *Cyathea approximata* Bonap. Notes Ptérid. **5**:41. 1917.

A. auriculata (Tard.) Tryon, comb. nov., *Cyathea auriculata* Tard. Naturaliste Malag. **3**:75. 1951.

A. Ballardii (Tard.) Tryon, comb. nov., *Cyathea Ballardii* Tard. Naturaliste Malag. **3**:75. 1951.

A. bellisquamata (Bonap.) Tryon comb. nov., *Cyathea bellisquamata* Bonap. Notes Ptérid. **16**:18. 1925.

A. Boivinii Ettingsh. *Gymnospaera Boivinii* (Ettingsh.) Tard.

[*Cyathea Boivinii*=**Alsophila Hyacinthei**].

A. borbonica (Desv.) Tryon, comb. nov., *Cyathea borbonica* Desv. Ges. Naturf. Freunde Berl. Mag. **5**:328. 1811.

A. camerooniana (Hook.) Tryon, comb. nov., *Cyathea camerooniana* Hook. Syn. Fil. 21. 1865 (not *Alsophila camerunensis* Diels).

A. campanulata Tryon, nom. nov., for *Cyathea Holstii* Hieron. in Engler, Pflanzw. Ost. Afr. C. 88. 1895, not *Alsophila Holstii* Hieron.

A. capensis (L.f.) J.Sm. *Cyathea capensis* (L.f.) Sm.

A. celsa Tryon, nom. nov., for *Cyathea excelsa* Sw. Schrad. Jour. Bot. 1800(2):93. 1801, not *Alsophila excelsa* Endl. 1833.

[*Cyathea costularis*=**Alsophila Rolandii**].

A. Coursii Tard. *Gymnosphaera Coursii* (Tard.) Tard.

A. Deckenii (Kuhn) Tryon, comb. nov., *Cyathea Deckenii* Kuhn, in v. Decken Reis. Ost.-Afr. 3(3)Bot.:57. 1879.

A. decrescens (Kuhn) Tryon, comb. nov., *Cyathea decrescens* Kuhn, Fil. Afr. 164. 1868.

A. Dregei (Kze.) Tryon, comb nov., *Cyathea Dregei* Kze. Linnaea **10**:551. 1836.

[*Cyathea excelsa*=**Alsophila celsa**].

A. glaucifolia Tryon, nom. nov., for *Cyathea glauca* Bory, Voy. Iles Afrique **2**:206. 1804, not *Alsophila glauca* (Bl.) J.Sm. Ferns Brit. & For. 245. 1866.

A. Hildebrandtii (Kuhn) Tryon, comb. nov., *Cyathea Hildebrandtii* Kuhn, Ind. Sem. Hort. Berol. 20. 1875.

[*Cyathea Holstii*=**Alsophila campanulata**].

A. Humbertiana (C.Chr.) Tryon, comb. nov., *Hemitelia Humbertiana* C. Chr. Arch. Bot. (Caen) Bull. Mens. **2**:210. 1928, *Cyathea Humbertiana* (C.Chr.) Diels.

A. Hyacinthei Tryon, nom. nov., for *Cyathea Boivinii* Kuhn, Fil. Afr. 162. 1868, not Ettingsh.. *Cyathea rigidula* Baker, not *Alsophila rigidula* Mart.

A. isaloensis (C.Chr.) Tryon, comb. nov., *Cyathea isaloensis* C.Chr. Dansk. Bot. Ark. **7**:35. 1932.

A. Kirkii (Hook.) Tryon, comb. nov., *Cyathea Kirkii* Hook. Syn. Fil. 22. 1865.

A. Lastii (Baker) Tryon, comb. nov., *Cyathea Lastii* Baker, Jour. Bot. **29**:3. 1891.

A. leptochlamys (Baker) Tryon, comb. nov., *Cyathea leptochlamys* Baker, Jour. Linn. Soc. **22**:535. 1887.

A. ligulata (Baker) Tryon, comb. nov., *Cyathea ligulata* Baker, Jour. Bot. **22**:140. 1884.

A. longipinnata (Bonap.) Tryon, comb. nov., *Cyathea longipinnata* Bonap. Notes Ptérid. **5**:48. 1917.

A. madagascarica Bonap., *Gymnosphaera madagascarica* (Bonap.) Tard.

[*Cyathea madagascarica*=**Alsophila maititanensis**].

A. Manniana (Hook.) Tryon, comb. nov., *Cyathea Manniana* Hook. Syn. Fil. 21. 1865.

A. marattioides (Kaulf.) Tryon, comb. nov.. *Cyathea marattioides* Kaulf. Enum. Fil. 256. 1824.

A. matitanensis Tryon, nom. nov., for *Cyathea madagascarica* Bonap. Notes Ptérid. **5**:49. 1917, not *Alsophila madagascarica* Bonap.

A. melanocaula (Desv.) Tryon, comb. nov., *Cyathea melanocaula* Desv. Mém. Soc. Linn. Paris **6**:322. 1827 (not *Alsophila melanocaulos* vAvR.).

A. melanotricha Tard., *Gymnosphaera melanotricha* (Tard.) Tard.

A. Melleri (Baker) Tryon, comb. nov., *Hemitelia Melleri* Baker, Syn. Fil. ed. 2, 456. 1874, *Gymnosphaera Melleri* (Baker) Tard.

A. Mildbraedii Brause.

A. mossambicensis (Baker) Tryon, comb. nov., *Cyathea mossambicensis* Baker, Ann. Bot. **5**:185. 1891.

A. Nicklesii (Tard. & Ballard) Tryon, comb. nov., *Gymnosphaera Nicklesii* Tard. & Ballard, Not. Syst. **14**:329. 1952.

A. obtusiloba Hook., *Cyathea obtusiloba* (Hook.) Domin.

A. orthogonalis (Bonap.) Tryon, comb. nov.. *Cyathea orthogonalis* Bonap. Notes Ptérid. **5**:32. 1917.

A. Perrieriana (C.Chr.) Tryon, comb. nov., *Cyathea Perrieriana* C.Chr. Dansk Bot. Ark. **7**:19. 1932.

A. pilosula (Tard.) Tryon, comb. nov., *Cyathea pilosula* Tard. Bull. Soc. Bot. France **88**:681. 1941.

A. quadrata (Baker) Tryon, comb. nov., *Cyathea quadrata* Baker, Jour. Linn. Soc. **15**:411. 1876.

[*Cyathea rigidula* Baker=**Alsophila Hyacinthei**].

A. Rolandii Tryon, nom. nov., for *Cyathea costularis* Roland Bonap. Notes Ptérid. **5**:44. 1917, not *Alsophila costularis* Baker.

A. Schliebenii Reim.

[*Cyathea Schliebenii*=**Alsophila tanzaniana**].

A. sechellarum (Mett.) Tryon, comb. nov., *Cyathea sechellarum* Mett. Ann. Mus. Bot. Lugd.-Bat. **1**:58. 1863.

A. serratifolia (Baker) Tryon, comb. nov., *Cyathea serratifolia* Baker, Jour. Bot. **22**:139. 1884.

A. similis (C.Chr.) Tryon, comb. nov., *Cyathea similis* C.Chr. Ind. Fil. 195. 1905, nom. nov. for *Cyathea discolor* Baker, not Bory.

A. Stuhlmannii (Hieron.) Tryon, comb. nov., *Cyathea Stuhlmannii* Hieron. Bot. Jahrb. **28**:340. 1900.

A. tanzaniana Tryon, nom. nov.. for *Cyathea Schliebenii* Reim. Notizbl. Bot. Gart. Berlin **11**:916, 1933, not *Alsophila Schliebenii* Reim.

A. Thomsonii (Baker) Tryon, comb. nov., *Cyathea Thomsonii* Baker, Jour. Bot. **19**:180. 1881.

A. tsaratananensis (C.Chr.) Tryon, comb. nov., *Cyathea tsaratananensis* C.Chr. Ind. Fil. Suppl. **3**:64. 1934, nom. nov. for *Cyathea subincisa* C.Chr., not (Kze.) Domin.

[*Cyathea tsaratananensis* Tard.=**Alsophila acutula**].

A. tsilotsilensis (Tard.) Tryon, comb. nov., *Cyathea tsilotsilensis* Tard. Bull. Soc. Bot. France **88**:682. 1941.

A. Viguieri (Tard.) Tryon, comb. nov., *Cyathea Viguieri* Tard. Bull. Soc. Bot. France **88**: 682. 1941.

A. Welwitschii (Hook.) Tryon, comb. nov., *Cyathea Welwitschii* Hook. Syn. Fil. 21. 1865.

A. zakamenensis (Tard.) Tryon, comb. nov., *Cyathea zakamenensis* Tard. Bull. Soc. Bot. France **88**:683. 1941.

ASIA

Alsophila Andersonii Bedd. *Cyathea Andersonii* (Bedd.) Copel.

A. borneensis (Copel.) Tryon, comb. nov., *Cyathea borneensis* Copel. Phil. Jour. Sci. **6** (Bot.): 135. 1911.

[*Cyathea chinensis*=**Alsophila costularis**].

A. costularis Baker, *Cyathea chinensis* Copel.

A. denticulata Baker, *Cyathea Hancockii* Copel.
A. gigantea Hook. *Cyathea gigantea* (Hook.) Copel.
[*Cyathea Hancockii*=**Alsophila denticulata**].
A. Henryi Baker, *Cyathea Henryi* (Baker) Copel.
A. Hookeri (Thwaites) Tryon, comb. nov., *Cyathea Hookeri* Thwaites, Enum. Pl. Zeylan. 396. 1864.
A. khasyana Kuhn, *Cyathea khasyana* (Kuhn) Diels.
A. latebrosa Hook. *Cyathea latebrosa* (Hook.) Copel.
A. Loheri (Christ) Tryon, comb. nov., *Cyathea Loheri* Christ, Bull. Herb. Boiss. II, **6**:1007. 1906.
A. Metteniana Hance, *Cyathea Metteniana* (Hance), C.Chr. & Tard.
A. nilgirensis (Holtt.) Tryon, comb. nov., *Cyathea nilgirensis* Holtt. Kew Bull. **19**:468. 1965.
A. Ogurae Hayata, *Cyathea Ogurae* (Hayata) Domin.
A. podophylla Hook. *Cyathea podophylla* (Hook.) Copel.
A. Salletii (Tard. & C.Chr.) Tryon, comb. nov., *Cyathea Salletii* Tard. & C.Chr. Bull. Mus. Hist. Nat. Paris. II, **6**:450. 1934.
A. sinuata (Hook. & Grev.) Tryon, comb. nov., *Cyathea sinuata* Hook. & Grev. Icon. Fil. t. 106. 1828.
A. spinulosa (Hook.) Tryon, comb. nov., *Cyathea spinulosa* Hook. Sp. Fil. **1**:25. 1844.
A. Walkerae (Hook.) J.Sm. *Cyathea Walkerae* Hook.

MALAYSIA

Alsophila acanthophora (Holtt.) Tryon, comb. nov., *Cyathea acanthophora* Holtt. Kew Bull. **16**:51. 1962.
A. acrostichoides vAvR., *Cyathea acrostichoides* (vAvR.) Domin.
A. acuminata (Copel) Tryon, comb. nov., *Cyathea acuminata* Copel. Phil. Jour. Sci. **81**:15. 1952, (*Alsophila acuminata* J.Sm. Lond. Jour. Bot. **1**:667. 1842 is a nomen nudum).
A. Alderwereltii (Copel.) Tryon, comb. nov., *Cyathea Alderwereltii* Copel. Phil. Jour. Sci. **4** (Bot): 50. 1909, nom. nov. for *Hemitelia sumatrana* vAvR., not *Cyathea sumatrana*. Baker
A. Alleniae (Holtt.) Tryon, comb. nov., *Cyathea Alleniae* Holtt. Kew Bull. **16**:52. 1962.
A. alpina vAvR., *Cyathea trachypoda* vAvR.
A. amboinensis vAvR., *Cyathea amboinensis* (vAvR.) Merrill.
A. Annae vAvR., *Cyathea Annae* (vAvR.) Domin.
A. apiculata Rosenst., *Cyathea apiculata* (Rosenst.) Domin.
A. apoensis (Copel.) Tryon. comb. nov., *Cyathea apoensis* Copel. Leafl. Phil. Bot. **3**:802. 1910.
A. Archboldii (C.Chr.) Tryon, comb. nov., *Cyathea Archboldii* C.Chr. Brittonia **2**:278. 1937.
A. arfakensis Gepp, *Cyathea Kanehirae* Holtt.
[*Cyathea arfakensis*=**Alsophila Lilianiae**].
[*Cyathea ascendens*=**Alsophila Rosenstockii**].
A. atropurpurea (Copel.) C.Chr., *Cyathea atropurpurea* Copel.
A. batjanensis Christ, *Cyathea batjanensis* (Christ) Copel.
A. biformis Rosenst. *Stenochlaena dubia* vAvR., not *Alsophila dubia* Bedd., *Cyathea biformis* (Rosenst.) Copel.
A. borneensis (Copel.) Tryon (supra).

A. Brausei Tryon, nom. nov., for *Cyathea Hunsteiniana* Brause, Bot. Jahrb. **56**:58. 1920, not *Alsophila Hunsteiniana* Brause.

A. Buennemeijeri (vAvR.) Tryon, comb. nov., *Cyathea Buennemeijeri* vAvR. Bull. Jard. Bot. Buitenz. III, **5**:187. 1922.

A. callosa (Christ) Tryon, comb. nov., *Cyathea callosa* Christ, Bull. Herb. Boiss. II, **6**:1008. 1906.

A. catillifera (Holtt.) Tryon, comb. nov., *Cyathea catillifera* Holtt. Kew Bull. **16**:53. 1962.

A. caudata Hook. *Cyathea caudata* (Hook.) Copel.

[*Cyathea Christii*=**Alsophila Hermannii**].

A. cincinnata (Brause) Tryon, comb. nov., *Cyathea cincinnata* Brause, Bot. Jahrb. **56**:52. 1920.

A. cinerea(Copel.) Tryon, comb. nov., *Cyathea cinerea* Copel. Leafl. Phil. Bot. **5**:1681. 1913.

A. coactilis (Holtt.) Tryon, comb. nov., *Cyathea coactilis* Holtt. Blumea **11**:533. 1962.

A. commutata Mett. *Cyathea recommutata* Copel.

A. costalisora (Copel.) Tryon, comb. nov., *Cyathea costalisora* Copel. Univ. Calif. Publ. Bot. **18**:218. 1942.

[*Cyathea costulisora*=**Alsophila montana**].

A. crassicaula Tryon, nom. nov., for *Cyathea Ledermannii* Brause, Bot. Jahrb. **56**:56. 1920, not *Alsophila Ledermannii* Brause.

A. crenulata (Mett.) Hook. *Cyathea Raciborskii* Copel.

[*Cyathea crenulata*=**Alsophila polycarpa**].

A. cucullifera (Holtt.) Tryon, comb. nov., *Cyathea cucullifera* Holtt. Kew Bull. **16**:54. 1962.

A. dicksonioides (Holtt.) Tryon, comb. nov., *Cyathea dicksonioides* Holtt. Blumea **11**:529. 1962.

A. dimorpha Christ, *Cyathea dimorpha* (Christ) Copel.

A. Doctersii (vAvR.) Tryon, comb. nov., *Cyathea Doctersii* vAvR. Bull. Jard. Bot. Buitenz. III, **2**:136. 1920.

A. Edanoi (Copel.) Tryon, comb. nov., *Cyathea Edanoi* Copel. Phil. Jour. Sci. **46**:211. 1931.

A. eriophora (Holtt.) Tryon, comb. nov., *Cyathea eriophora* Holtt. Kew Bull. **16**:55. 1962.

A. everta (Copel.) Tryon, comb. nov., *Cyathea everta* Copel. Univ. Calif. Publ. Bot. **18**:218. 1942.

A. excavata (Holtt.) Tryon. comb. nov., *Cyathea excavata* Holtt. Gard. Bull. Str. Sett. **8**:306. 1935.

A. Fenicis (Copel.) C.Chr. *Cyathea Fenicis* Copel.

A. ferruginea (Christ) Tryon, comb. nov., *Cyathea ferruginea* Christ, Phil. Jour. Sci. **2** (Bot.): 181. 1907.

A. Foersteri (Rosenst.) Tryon, comb. nov., *Cyathea Foersteri* Rosenst. Fedde Repert. **10**:321. 1912.

A. fuliginosa Christ, *Cyathea fuliginosa* (Christ) Copel.

A. geluensis (Rosenst.) Tryon, comb. nov., *Cyathea geluensis* Rosenst. Fedde Repert. **5**:371. 1908.

A. gigantea Hook. *Cyathea gigantea* (Hook.) Holtt.

A. glabra (Bl.) Hook. *Cyathea glabra* (Bl.) Copel.

A. glaberrima (Holtt.) Tryon, comb. nov., *Cyathea glaberrima* Holtt. Kew Bull. **16**:55. 1962.

A. gleichenioides (C.Chr.) Tryon, comb. nov., *Cyathea gleichenioides* C.Chr. Brittonia **2**:281. 1937.

A. gregaria Brause, *Cyathea gregaria* (Brause) Domin.

A. halconensis (Christ) Tryon, comb. nov., *Cyathea halconensis* Christ, Phil. Jour. Sci. 3 (Bot.): 270. 1908.

A. Havilandii (Baker) Tryon, comb. nov., *Cyathea Havilandii* Baker, Trans. Linn. Soc. Lond. II, (Bot.) 4:249. 1894.

A. Hermannii Tryon, nom. nov., for *Cyathea Christii* Copel. Phil. Jour. Sci. 1, Suppl. II: 144. 1906, not *Alsophila Christii* Sod.

A. heterochlamydea (Copel.) Tryon, comb. nov., *Cyathea heterochlamydea* Copel. Leafl. Phil. Bot. 2:418. 1908.

A. Hooglandii (Holtt.) Tryon, comb. nov., *Cyathea Hooglandii* Holtt. Kew Bull. 16:56. 1962.

A. Hornei Baker, *Cyathea Hornei* (Baker) Copel.

A. horridula (Copel.) Tryon, comb. nov., *Cyathea horridula* Copel. Univ. Calif. Publ. Bot. 18:219. 1942.

[*Cyathea Hunsteiniana*=**Alsophila Brausei**].

A. hymenodes (Mett.) Tryon, comb. nov., *Cyathea hymenodes* Mett. Ann. Mus. Bot. Lugd.-Bat. 1:57. 1863.

A. imbricata (vAvR.) Tryon, comb. nov., *Cyathea imbricata* vAvR. Nova Guinea 14:11. 1924.

A. incisoserrata (Copel) C.Chr. *Cyathea incisoserrata* Copel.

A. inquinans (Christ) Tryon, comb. nov., *Cyathea inquinans* Christ, Verhandl. Naturf. Ges. Basel 11:422. 1896.

A. insulana (Holtt.) Tryon, comb. nov., *Cyathea insulana* Holtt. Kew Bull. 16:56, 1962.

A. javanica (Bl.) Tryon, comb. nov., *Cyathea javanica* Bl. Enum. Pl. Jav. 245. 1828.

A. Junghuhniana Kze. *Cyathea Junghuhniana* (Kze.) Copel.

[*Cyathea Kanehirae*=**Alsophila arfakensis**].

A. Klossii (Ridley) Tryon, comb. nov., *Cyathea Klossii* Ridley, Trans. Linn. Soc. II (Bot.) 9:251. 1916.

A. latebrosa Hook. *Cyathea latebrosa* (Hook.) Copel.

A. latipinnula (Copel.) Tryon, comb. nov., *Cyathea latipinnula* Copel. Leafl. Phil. Bot. 4:1149. 1911.

[*Cyathea Ledermannii*=**Alsophila crassicaula**].

A. lepidoclada Christ, *Cyathea lepidoclada* (Christ) Domin.

A. Lilianiae Tryon, nom. nov., for *Cyathea arfakensis* Gepp, in Lilian S. Gibbs, Dutch N.W. New Guinea 69. 1917, not *Alsophila arfakensis* Gepp.

A. Loerzingii (Holtt.) Tryon, comb. nov., *Cyathea Loerzingii* Holtt. Kew Bull. 16:58. 1962.

A. Loheri (Christ) Tryon (supra).

A. longipes (Copel.) Tryon, comb. nov., *Cyathea longipes* Copel. Phil. Jour. Sci. 12 (Bot.): 54. 1917.

A. lurida (Bl.) Hook. *Cyathea lurida* (Bl.) Copel.

A. Macgillivrayi Baker, *Cyathea Macgillivrayi* (Baker) Diels.

A. Macgregorii (F. v. Muell.) Tryon, comb. nov., *Cyathea Macgregorii* F. v. Muell. Trans. Roy. Soc. Victoria 1(2):40. 1889.

A. macropoda (Domin) Tryon, comb. nov., *Cyathea macropoda* Domin, Acta Bot. Bohem. 9:133, 1930, nom. nov. for *Cyathea longipes* vAvR., not Copel.

A. magnifolia (vAvR.) Tryon, comb. nov., *Cyathea magnifolia* vAvR. Bull. Jard. Bot. Buitenz. III, 2:135. 1920.

A. masapilidensis (Copel.) Tryon, comb. nov., *Cyathea masapilidensis* Copel. Phil. Jour. Sci. 81:17. 1952.

A. media (Wagn. & Greth.) Tryon, comb. nov., *Cyathea media* Wagn. & Greth. Univ. Calif. Publ. Bot. **23**:44. 1948.

A. mesosora (Holtt.) Tryon, comb. nov., *Cyathea mesosora* Holtt. Kew Bull. **16**:57. 1962. Placed by Holttum (1963) among species of *Sphaeropteris,* but I believe that it belongs in *Alsophila.*

A. micra Tryon, nom. nov., for *Cyathea parva* Copel. Univ. Calif. Publ. Bot. **18**:219. 1942, not *Alsophila parva* Maxon.

A. microchlamys (Holtt.) Tryon, comb. nov., *Cyathea microchlamys* Holtt. Kew Bull. **16**:58. 1962.

A. microphylloides (Rosenst.) Tryon, comb. nov., *Cyathea microphylloides* Rosenst. Fedde Repert. **12**:164. 1913.

A. modesta Baker, *Cyathea modesta* (Baker) Copel.

A. montana (vAvR.) Tryon, comb. nov., *Hemitelia montana* vAvR. Bull. Jard. Bot. Buitenz. III, **2**:153. 1920, *Cyathea costulisora* Domin.

A. Muelleri (Baker) Tryon, comb. nov., *Cyathea Muelleri* Baker, Jour. Bot. **28**:104. 1890.

A. negrosiana (Christ) Tryon, comb. nov., *Cyathea negrosiana* Christ, Phil. Jour. Sci. **2** (Bot.): 181. 1907.

A. nigrolineata (Holtt.) Tryon, comb. nov., *Cyathea nigrolineata* Holtt. Kew Bull. **16**:58. 1962.

A. nigropaleata (Holtt.) Tryon. comb. nov., *Cyathea nigropaleata* Holtt. Kew Bull. **16**:59. 1962.

A. oinops (Hassk.) Tryon, comb. nov., *Cyathea oinops* Hassk. Jour. Bot. Hook. Kew Gard. Misc. **7**:322. 1855.

A. oosora (Holtt.) Tryon, comb. nov., *Cyathea oosora* Holtt. Kew Bull. **16**:59. 1962.

A. orientalis (Kze.) Tryon, comb. nov., *Disphenia orientalis* Kze. Bot. Zeit. **6**:283. 1848, *Cyathea orientalis* (Kze.) Moore.

A. pachyrrhachis (Copel.) Tryon, comb. nov., *Cyathea pachyrrhachis* Copel. Univ. Calif. Publ. Bot. **18**:218. 1942.

A. pallidipaleata (Holtt.) Tryon, comb. nov., *Cyathea pallidipaleata* Holtt. Kew Bull. **16**:60. 1962.

[*Cyathea parva*=**Alsophila micra**].

A. patellifera (vAvR.) Tryon, comb. nov., *Cyathea patellifera* vAvR. Bull. Jard. Bot. Buitenz. II, **16**:4. 1914.

A. percrassa (C.Chr.) Tryon, comb. nov., *Cyathea percrassa* C.Chr. Brittonia **2**:279. 1937.

A. perpelvigera (vAvR.) Tryon, comb. nov., *Cyathea perpelvigera* vAvR. Nova Guinea **14**:11. 1924.

A. perpunctulata (vAvR.) Tryon, comb. nov., *Hemitelia perpunctulata* vAvR. Bull. Jard. Bot. Buitenz. II, **28**:25. 1918, *Cyathea perpunctulata* (vAvR.) Domin.

A. physolepidota (Alston) Tryon, comb. nov., *Cyathea physolepidota* Alston, Nova Guinea n.s. **7**:1. 1956.

A. polycarpa (Jungh.) Tryon, comb. nov., *Cyathea polycarpa* Jungh. Nat. Geneesk. Arch. Neerl. Ind. **2**:40. 1845, *Cyathea crenulata* Bl., not *Alsophila crenulata* (Mett.) Hook.

A. pruinosa (Rosenst.) Tryon, comb. nov., *Cyathea pruinosa* Rosenst. Fedde Repert. **12**:163. 1913.

A. pseudomuelleri (Holtt.) Tryon, comb. nov., *Cyathea pseudomuelleri* Holtt. Kew Bull. **16**:61. 1962.

A. punctulata vAvR. *Cyathea punctulata* (vAvR.) vAvR.

A. pycnoneura (Holtt.) Tryon, comb. nov., *Cyathea pycnoneura* Holtt. Blumea **11**:533. 1962.

[*Cyathea Raciborskii*=**Alsophila crenulata**].

A. ramispina Hook. *Cyathea ramispina* (Hook.) Copel.

A. Rebeccae F. v. Muell. *Cyathea Rebeccae* (F. v. Muell.) Domin.

[*Cyathea recommutata*=**Alsophila commutata**].

A. recurvata Brause, *Cyathea recurvata* (Brause) Domin.

A. rigens (Rosenst.) Tryon, comb. nov., *Cyathea rigens* Rosenst. Fedde Repert. **12**:163. 1913.

A. Rosenstockii Brause, *Cyathea ascendens* Domin.

A. rubella (Holtt.) Tryon, comb. nov., *Cyathea rubella* Holtt. Kew Bull. **16**:61. 1962.

A. rubiginosa Brause, *Cyathea rubiginosa* (Brause) Domin.

A. rufopannosa (Christ) Tryon, comb. nov., *Cyathea rufopannosa* Christ, Phil. Jour. Sci. **2** (Bot.): 180. 1907.

A. saccata (Christ) Tryon, comb. nov., *Cyathea saccata* Christ, Ann. Jard. Bot. Buitenz. II, **4**:42. 1904.

A. scandens Brause, *Cyathea scandens* (Brause) Domin.

A. Schlechteri Brause, *Cyathea Schlechteri* (Brause) Domin.

A. semiamplectens (Holtt.) Tryon, comb. nov., *Cyathea semiamplectens* Holtt. Kew Bull. **16**:62. 1962.

A. setulosa (Copel.) Tryon, comb. nov., *Cyathea setulosa* Copel. Phil. Jour. Sci. **81**:14. 1952.

A. subtripinnata (Holtt.) Tryon, comb. nov., *Cyathea subtripinnata* Holtt. Blumea **11**:534. 1962.

A. sumatrana (Baker) Tryon, comb. nov., *Cyathea sumatrana* Baker, Jour. Bot. **18**:209. 1880.

A. tenuis Brause, *Cyathea tenuicaulis* Domin.

A. ternatea (vAvR.) Tryon, comb. nov., *Cyathea ternatea* vAvR. Bull. Jard. Bot. Buitenz. III, **5**:191. 1922.

[*Cyathea trachypoda*=**Alsophila alpina**].

A. Vandeusenii (Holtt.) Tryon, comb. nov., *Cyathea Vandeusenii* Holtt. Blumea **11**:529. 1962.

A. wengiensis Brause, *Cyathea wengiensis* (Brause) Domin.

AUSTRALASIA AND PACIFIC

[*Cyathea affinis*=**Alsophila tahitensis**].

Alsophila alata Fourn. *Cyathea alata* (Fourn.) Copel.

A. alta (Copel.) Tryon, comb. nov., *Cyathea alta* Copel. Phil. Jour. Sci. **60**:104. 1936.

A. aneitensis (Hook.) Tryon, comb. nov., *Cyathea aneitensis* Hook. Syn. Fil. 26. 1865.

A. Archboldii (C.Chr.) Tryon (supra).

A. australis R.Br. *Cyathea australis* (R.Br.) Domin.

A. Baileyana Domin, *Cyathea Baileyana* (Domin) Domin.

A. brevipinna (Benth.) Tryon, comb. nov., *Cyathea brevipinna* Benth. Fl. Austral. **7**:709. 1878.

A. cicatricosa (Holtt.) Tryon, comb. nov., *Cyathea cicatricosa* Holtt. Blumea **12**:274. 1964.

A. Colensoi Hook. f. *Cyathea Colensoi* (Hook. f.) Domin.

A. Cunninghamii (Hook. f.) Tryon, comb. nov., *Cyathea Cunninghamii* Hook. f. Icon. Pl. t. 985. 1854.

[*Cyathea dealbata*=**Alsophila tricolor**].

A. decurrens Hook. *Cyathea decurrens* (Hook.) Copel.

A. Ferdinandii Tryon, nom. nov., for *Hemitelia Macarthurii* F. v. Muell. Fragm. Phyt. Austral. **8**:176. 1874, *Cyathea Macarthurii* (F. v. Muell.) Baker, not *Alsophila Macarthurii Hook. Cyathea Moorei* Baker, not *Alsophila Moorei* J.Sm.

A. Hornei Baker (supra).

A. kermadecensis (Oliver) Tryon, comb. nov., *Cyathea kermadecensis* Oliver, Trans. N. Z. Instit. **42**:158. 1910.

[*Cyathea Macarthurii*=**Alsophila Ferdinandii**].

A. marcescens (N.A.Wakef.) Tryon, comb. nov., *Cyathea marcescens* N.A.Wakef. Victoria Nat. **59**:33. 1942.

A. Milnei (Hook. f.) Tryon, comb. nov., *Cyathea Milnei* Hook. f. Handb. Fl. New Zeal. 349. 1864.

A. plagiostegia (Copel.) Tryon, comb. nov., *Cyathea plagiostegia* Copel. Bishop Mus. Bull. **59**:9. 1929.

A. Rebeccae F. v. Muell. *Cyathea Rebeccae* (F. v. Muell.) Domin.

A. Robertsiana F. v. Muell. *Cyathea Robertsiana* (F. v. Muell.) Domin.

A. Smithii (Hook. f.) Tryon, comb. nov., *Cyathea Smithii* Hook. f. Fl. New Zeal. **2**:8. 1854.

A. solomonensis (Holtt.) Tryon, comb. nov., *Cyathea solomonensis* Holtt. Blumea **12**:252. 1964.

A. stelligera (Holtt.) Tryon, comb. nov., *Cyathea stelligera* Holtt. Blumea **12**:250. 1964.

A. Stokesii (E. Brown) Tryon, comb. nov., *Cyathea Stokesii* E. Brown, Bishop Mus. Bull. **89**:16. 1931.

A. tahitensis Brack. *Cyathea affinis* (Forst.) Sw., not *Alsophila affinis* (Presl) Fée.

A. tricolor (Colenso) Tryon, comb. nov., *Cyathea tricolor* Colenso, Trans. New Zeal. Instit. **15**:304. 1883, *Cyathea dealbata* (Forst.) Sw., not *Alsophila dealbata* Presl.

A. Vieillardii (Mett.) Tryon, comb. nov., *Cyathea Vieillardii* Mett. Ann. Sci. Nat. IV, **15**:82. 1861.

A. Woollsiana F. v. Muell. *Cyathea Woollsiana* (F. v. Muell.) Domin.

5. Nephelea

Nephelea, genus novum Cyatheacearum petiolis crosieribusque spinis squaminatis magnis atris et squamis cellulose marginatis setam atratam apicalem ferentibus. Nomen e *nephele* (Gr.): species generis in silvis nubilis plerumque habitantes. Typus: *Nephelea polystichoides* (Christ) Tryon (*Alsophila polystichoides* Christ), Costaricae.

Petiole with squaminate spines, these large, black, mostly obturbinate, with a slender apex, the unexpanded croziers with well developed squaminate spines, many of them caducous, lacking trichomes; petiole *scales* patent, fully adnate or slightly narrowed at the base, structurally marginate, with a narrow to broad margin of cells different in orientation, size, shape, and usually in color from those of the central portion, bearing a dark seta at the apex and sometimes one or more on the edge or body of the scale; *minute indument* of the petiole, when present, of trichomidia and (or) of squamulae; *costa* pubescent above; *veins* free, in lobed or pinnatifid segments the basal vein on each side extending above the base of the sinus; *indusium* present, hemitelioid to sphaeropteroid.

Nephelea (Figs. 3, 31–38) is an American genus of about 30 species. It is especially distinctive in its squaminate spines that are present on the petiole and are precociously developed on the croziers. Typical petiole spines and the spiny crozier are illustrated in Fig. 31. There is evidence clearly indicating that these spines have evolved from petiole scales. Species of *Nephelea* have some petiole scales thickened basally, some that are spine-like, and some that are small spines with the differentiated margins of the normal scales on each side (Figs. 32–34), as well as the larger spines. These transitional stages are indicative of a squamate origin of the spine proper, as are the caducous spines of the croziers that become detached at their very base. As noted in the discussion under *Alsophila*, the series of species leading to *A. auriculata* illustrates how, in *Nephelea*, the spines may also have evolved by thickening the sclerotic central portion of the scale.

The lamina bears scales similar to those of the petiole, but much smaller, and these are an aid in identifying specimens of *Nephelea* that lack the petiole. However, similar small laminar scales with dark setae also occur on some American species of *Alsophila*. Some characters which show interesting evolutionary developments are not mentioned in the description because they do not occur in all or most of the species. These are the pubescent indusium of species such as *N. portoricensis* and *N. cuspidata*, the spiny stems of species such as *N. polystichoides* and *N. aureonitens* (Fig. 38) and the very small petiole scales of species such as *N. Sternbergii*. The chromosome number of $n=69$ has been reported by Walker (1966) for *N. Tussacii* and *N. Grevilleana* (as *Cyathea Tussacii* and *C. Grevilleana*, respectively).

The following list of species will serve as examples of the genus. It does not include those in which problems of taxonomy or nomenclature are known.

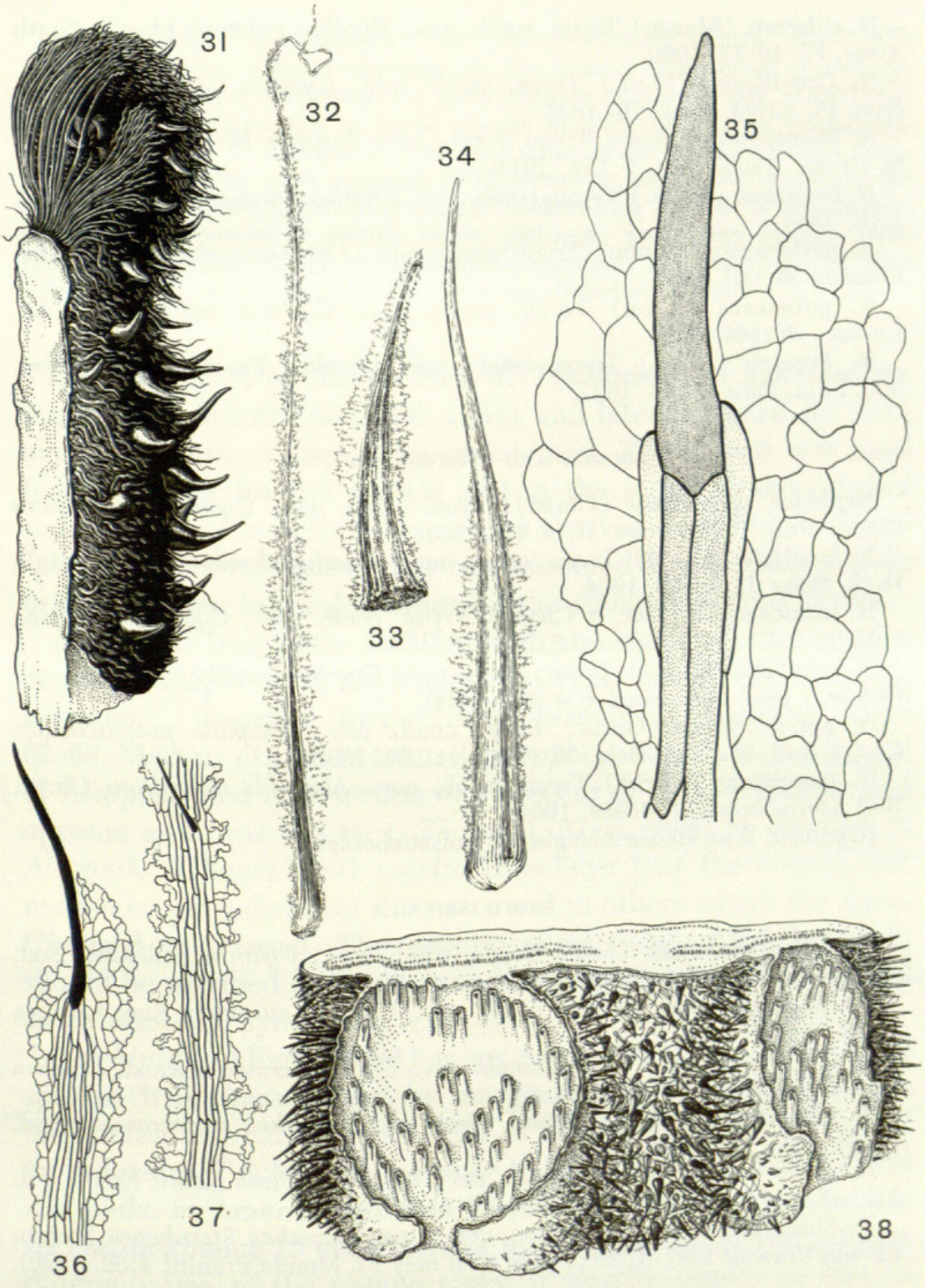
WEST INDIES

Nephelea araneosa (Maxon) Tryon, comb. nov., *Cyathea araneosa* Maxon, North Amer. Fl. 16:74. 1909.

N. balanocarpa (D. C. Eaton) Tryon, comb. nov., *Cyathea balanocarpa* D. C. Eaton, Mem. Amer. Acad. n.s. 8:215. 1860.

N. concinna (Baker) Tryon, comb. nov., *Cyathea arborea* var. *concinna* Baker, Jour. Bot. 19:52. 1881, *Cyathea concinna* (Baker) Jenm.

N. crassa (Maxon) Tryon, comb. nov., *Cyathea crassa* Maxon, Contrib. U. S. Nat. Herb. 13:40. 1909.



FIGS. 31–38. NEPHELEA. FIG. 31. Unexpanded crozier of *N. polystichoides, Gastony 793,* × 1, GH, the apical portion is the unexpanded crozier proper with spines among the scales, the basal portion has been detached from the stem and shows spines typical of the stem and petiole base. FIGS. 32–34. Transitions from petiole scales to squaminate spines, *N. aureonitens, Gastony 763,* all × 8, GH. 32, Petiole scale thickened basally. 33, Spine-like petiole scale. 34, Small squaminate spine. FIGS. 35–37. Portions of petiole scales: 35, Apex, *N. purpurascens, Sodiro,* July 1907, × 150, US. 36, Apex, *N. Sternbergii, Mexia 4650,* × 30, GH. 37, *N. Sternbergii, Dusén 6775,* × 30, GH. FIG. 38. Portion of spiny stem of *N. aureonitens, Gastony 763,* × 1, GH.

N. cubensis (Maxon) Tryon, comb. nov., *Cyathea cubensis* Maxon, North Amer. Fl. **16**:73. 1909.

N. Grevilleana (Mart.) Tryon, comb. nov., *Cyathea Grevilleana* Mart. Icon. Pl. Crypt. Bras. 78. 1834.

N. Hieronymi (Brause) Tryon, comb. nov., *Cyathea Hiermonymi* Brause, in Urban, Symb. Ant. **7**:152. 1911.

N. Imrayana (Hook.) Tryon, comb. nov., *Cyathea Imrayana* Hook. Sp. Fil. **1**:18. 1844.

N. portoricensis (Kuhn) Tryon, comb. nov., *Cyathea portoricensis* Kuhn, Linnaea **36**:163. 1869.

N. pubescens (Kuhn) Tryon, comb. nov., *Cyathea pubescens* Kuhn, Linnaea **36**:164. 1869.

N. Tussacii (Desv.) Tryon, comb. nov., *Cyathea Tussacii* Desv. Mém. Soc. Linn. Paris **6**:323. 1827.

MEXICO AND CENTRAL AMERICA

16726 16725

Nephelea aureonitens (Christ) Tryon, comb. nov., *Cyathea aureonitens* Christ, Bull. Herb. Boiss. II, **4**:948. 1904.

16730 9856

N. basilaris (Christ) Tryon, comb. nov., *Cyathea basilaris* Christ, Bull. Herb. Boiss. II, **4**:949. 1904.

7301 7302

N. mexicana (Schlect. & Cham.) Tryon, comb. nov., *Cyathea mexicana* Schlect. & Cham. Linnaea **5**:616. 1830.

8409 8408

N. patellaris (Christ) Tryon, comb. nov., *Cyathea patellaris* Christ, Ann. Conserv. Jard. Bot. Genève **4**:207. 1900.

16734 16733

N. polystichoides (Christ) Tryon, comb. nov., *Alsophila polystichoides* Christ, Bull. Soc. Bot. Belg. **35** (Mém.): 177. 1896.

8414 8412

N. tenerifrons (Christ) Tryon, comb. nov., *Alsophila tenerifrons* Christ, Bull. Herb. Boiss. II, **4**:959. 1904.

[*Cyathea Werckleana*=**Nephelea polystichoides**].

SOUTH AMERICA

16209 16201

Nephelea canescens (Sod.) Tryon, comb. nov., *Cyathea canescens* Sod. Sert. Fl. Ecuad. **2**:4. 1908.

6643 6640

N. cuspidata (Kze.) Tryon, comb. nov., *Cyathea cuspidata* Kze. Linnaea **9**:101. 1834.

6638 6635

N. erinacea (Karst.) Tryon, comb. nov., *Cyathea erinacea* Karst. Linnaea **28**:453. 1857.

16198 16197

N. purpurascens (Sod.) Tryon, comb. nov., *Cyathea purpurascens* Sod. Crypt. Vasc. Quit. 503. 1893.

21101 21102

N. setosa (Kaulf.) Tryon, comb. nov., *Alsophila setosa* Kaulf. Enum. Fil. 249. 1824, *Hemitelia setosa* (Kaulf.) Mett.

21103 21104

N. Sternbergii (Sternb.) Tryon, comb. nov., *Cyathea Sternbergii* Sternb. Fl. von Vorwelt **1**:47. 1820 (I have seen only Fl. Monde Primitif **4**:52. 1826).

6. TRICHIPTERIS

Trichipteris Presl, Delic. Prag. **1**:172. 1822, often as *Trichopteris*. Type: *Trichipteris excelsa* Presl = *Trichipteris corcovadensis* (Raddi) Copel.

Chnoophora Kaulf. Enum. Fil. 250. 1824. Type: *Chnoophora Humboldtii* Kaulf., nom. superfl. for *Cyathea villosa* Willd. = *Trichipteris villosa* (Willd.) Tryon.

Petiole smooth to tuberculate, or with corticinate spines, often with trichomes; petiole *scales* (especially on the abaxial side) more or less appressed, attached at one point of a pseudopeltate or peltate base, structurally marginate, with a narrow to broad margin of cells different in orientation, size, and usually in shape and color from those of the central portion, lacking dark setae, the apex rounded to filamentous; *minute indument* of the petiole, when present, rarely of patent trichomidia, usually of squamulae; *costa* usually pubescent above, rarely glabrous; *veins* free (rarely some branch and rejoin), in lobed or pinnatifid segments the basal vein on each side extending above the base of the sinus; *indusium* absent.

The alteration of the spelling of *Trichipteris* to *Trichopteris,* initiated by Schott (Gen. Fil. 1834) and later accepted by Presl and other authors, cannot be maintained. *Trichipteris* was used for the genus, for the species and in the index of the original publication. Although the name was derived from "trichos" and "pteros," and *Trichopteris* may be considered as preferable, Presl's original choice in the formation of the compound must stand.

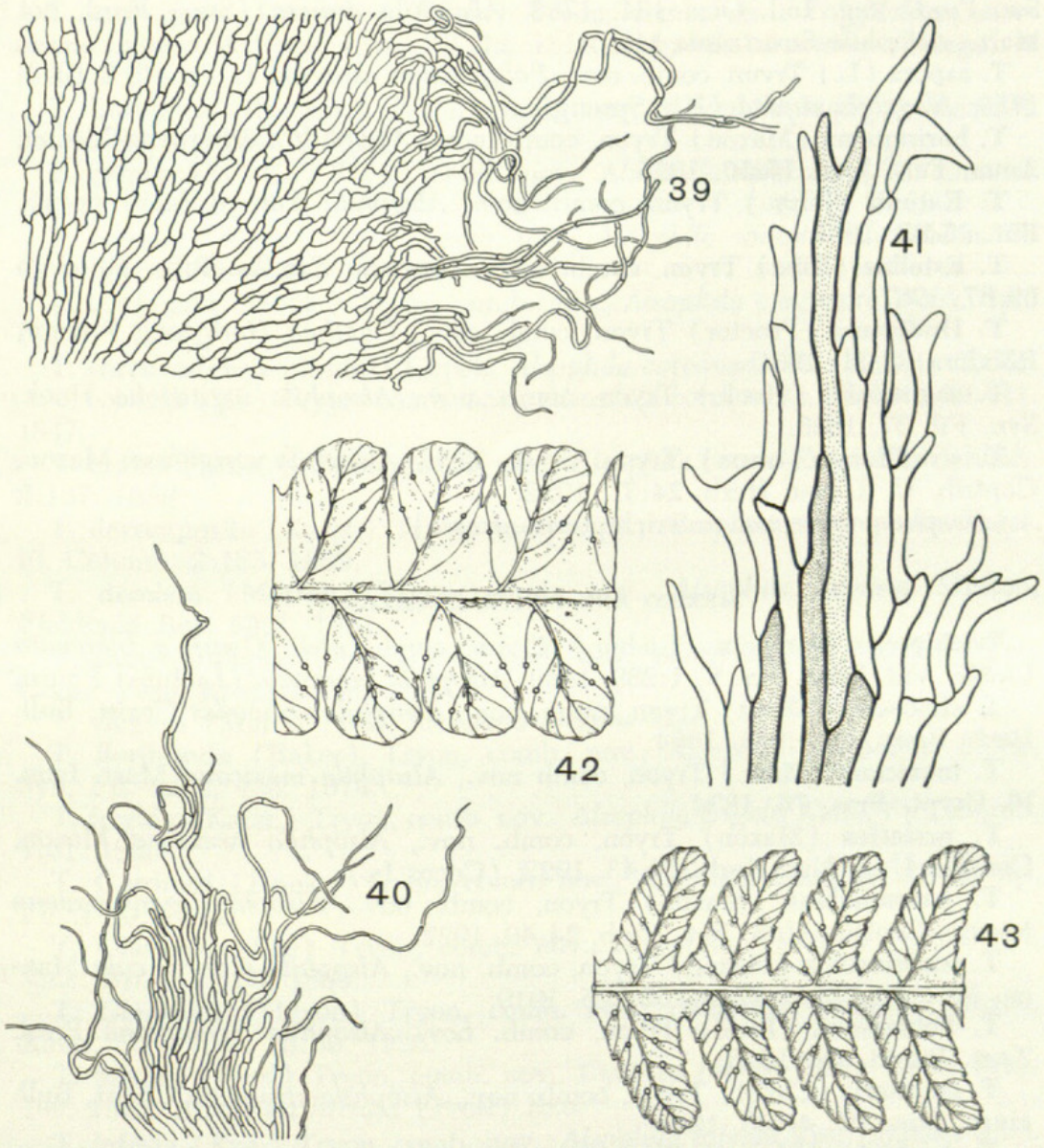
Martius is frequently credited with the valid publication of a genus *Chnoophora,* in his Icones Pl. Crypt. Brasil. 1834, but this is evidently incorrect. In the formal taxonomic treatment, pages 62–63, Martius explicitly treats *Chnoophora* Kaulf. as a synonym of *Alsophila* and as a section or subgenus of it. The species that appears as *C. excelsa* on t. 27 and t. 37 is given in the text as *Alsophila (Chnoophora) excelsa.* I believe that the formal text must take precedence in this case, and in others where the name *Chnoophora* is used. The generic name, when used by itself, should be ascribed to Kaulfuss and new binomials with it treated as published in synonymy.

Trichipteris (Figs. 39–43) is an American genus of about 90 species. It is characterized by marginate petiole scales that lack dark setae, normal, free venation (Figs. 42–43) and absence of an indusium. *Trichipteris* is nearly the equivalent of the classical *Alsophila,* in America, because there are only a few exindusiate species belonging to other genera in the neotropics. The cellular differentiation of the petiole scales is usually similar to that in *Cyathea* and is described in some detail there. In some species, such as *T. albidopaleata* and *T. aspera,* the modified margin is very narrow; in others such as *T. scabriuscula* it is rather broad but poorly developed; in *T. Wendlandii,* although definite, it is both narrow and slightly modified. These examples of species with only slightly marginate scales nearly provide a connection with

Sphaeropteris in which some species have tendencies toward marginate scales. Species of *Trichipteris* often grow at lower altitudes than those of other genera and it the only genus represented in the Amazon basin. The chromosome number of $n=69$ has been reported by Walker (1966) for *T. armata* (as *Cyathea armata*).

Recognition of *Trichipteris* and *Cyathea* as genera is based on evidence that each represents a separate evolutionary line. They are undoubtedly closely related and their evolutionary status and affinities could also be expressed by their classification as subgenera. However, the large numbers of species in each enforces their claim to generic rank. A comparison of the species in these two genera has shown very few cases of close similarity between indusiate species of *Cyathea* and exindusiate *Trichipteris.* Aside from these cases, species groups and distinctive species seem to have closest affinities within their own genus.

There are three groups of species that might indicate an intimate relation between *Trichipteris* and *Cyathea:* (1) *Trichipteris armata* and *T. bicrenata* with *Cyathea acutidens* and *C. leucolepismata;* (2) *Trichipteris obtusa, T. oblonga* and *T. chnoodes* with *Cyathea columbiana;* and (3) *Trichipteris pubescens* and an undescribed allied species with two undescribed species of *Cyathea.* Similarities among the species in these three groups are in characters of the lamina architecture and indument, the venation, the relative length of the petiole and lamina and the habit. These characters may show convergent evolution in species of different genera. This interpretation is especially clear in the species of the third group. These four species all have a short petiole and a pinnate-pinnatifid lamina of similar size and shape which is pubescent on both surfaces. However, the two exindusiate species of *Trichipteris* have similar paraphyses and petiole scales and in these structures they differ from the two similar indusiate species of *Cyathea.* The characters common to the two pairs of species are best interpreted as convergent. Characters of the paraphyses and the details of the petiole scales, in addition to the indusium, are alike in members of other species-groups and they are a more certain guide to evolutionary affinity than the size, architecture and shape of the lamina and its pubescence.



FIGS. 39–43. TRICHIPTERIS. FIGS. 39–41. Portions of petiole scales: 39, *T. mexicana, Yuncker et al. 6015,* × 30, GH. 40, Apex, *T. mexicana* (as in Fig. 39). 41, Apex, *T. albidopaleata, Mexia 4869,* × 150, GH. FIGS. 42–43. Portions of pinnules showing venation and receptacles, all × 2. 42, *T. arbuscula, Brade 8255,* US. 43, *T. compta, L. B. Smith 6579,* US.

The following list of species will serve as examples of the genus. It does not include those in which problems of taxonomy or nomenclature are known.

WEST INDIES

Trichipteris armata (Sw.) Tryon, comb. nov., *Polypodium armatum* Sw. Prod. Veg. Ind. Occ. 134. 1788, *Alsophila armata* (Sw.) Presl, not Mart., *Alsophila Swartziana* Mart.

T. aspera (L.) Tryon, comb. nov., *Polypodium asperum* L. Sp. Pl. **2**:1093. 1753, *Alsophila aspera* (L.) Spreng.

T. borinquena (Maxon) Tryon, comb. nov., *Alsophila borinquena* Maxon, Amer. Fern Jour. **15**:56. 1925.

T. Eatonii (Jenm.) Tryon, comb. nov., *Alsophila Eatonii* Jenm. Journ. Bot. **25**:98. 1887.

T. Estellae (Riba) Tryon, comb. nov., *Alsophila Estellae* Riba, Rhodora **69**:67. 1967.

T. Hodgeana (Proctor) Tryon, comb. nov., *Cyathea Hodgeana* Proctor, Rhodora **63**:31. 1961.

T. sagittifolia (Hook.) Tryon. comb. nov., *Alsophila sagittifolia* Hook. Syn. Fil. 37. 1866.

T. strigillosa (Maxon) Tryon, comb. nov., *Alsophila strigillosa* Maxon, Contrib. U. S. Nat. Herb. **24**:37. 1922.

[*Alsophila Swartziana*=**Trichipteris armata**].

MEXICO AND CENTRAL AMERICA

Trichipteris bicrenata (Liebm.) Tryon, comb. nov., *Cyathea bicrenata* Liebm. Vid. Selsk. Skr. V, **1**:289. 1849, *Alsophila bicrenata* (Liebm.) Fourn.

T. chnoodes (Christ) Tryon, comb. nov., *Alsophila chnoodes* Christ, Bull. Herb. Boiss. II, **4**:958. 1904.

T. mexicana (Mart.) Tryon, comb nov., *Alsophila mexicana* Mart. Icon. Pl. Crypt. Bras. 70. 1834.

T. nesiotica (Maxon) Tryon, comb. nov., *Alsophila nesiotica* Maxon, Contrib. U. S. Nat. Herb. **24**:43. 1922, (Cocos Is.).

T. pansamalana (Maxon) Tryon, comb. nov., *Alsophila pansamalana* Maxon, Contrib. U. S. Nat. Herb. **24**:40. 1922.

T. scabriuscula (Maxon) Tryon, comb. nov., *Alsophila scabriuscula* Maxon, Proc. Biol. Soc. Wash. **32**:125. 1919.

T. Schiediana (Presl) Tryon, comb. nov., *Alsophila Schiediana* Presl, Tent. Pterid. 62. 1836.

T. stipularis (Christ) Tryon, comb. nov., *Alsophila stipularis* Christ, Bull. Herb. Boiss. II, **4**:958. 1904.

T. trichiata (Maxon) Tryon, comb. nov., *Alsophila trichiata* Maxon, Contrib. U. S. Nat. Herb. **24**:44. 1922.

T. ursina (Maxon) Tryon, comb. nov., *Alsophila ursina* Maxon, Jour. Wash. Acad. Sci. **34**:48. 1944.

T. Wendlandii (Kuhn) Tryon, comb. nov., *Alsophila Wendlandii* Kuhn, Linnaea **36**:158. 1869.

T. Williamsii (Maxon) Tryon, comb. nov., *Alsophila Williamsii* Maxon, Contrib. U. S. Nat. Herb. **24**:46. 1922.

SOUTH AMERICA

Trichipteris albidopaleata (Copel.) Tryon, comb. nov., *Cyathea albidopaleata* Copel. Univ. Calif. Publ. Bot. **17**:25. 1932, *Alsophila albidopaleata* (Copel.) C.Chr.

T. anacampta (Alston) Tryon, comb. nov., *Cyathea anacampta* Alston, Jour. Wash. Acad. Sci. **48**:230. 1958.

T. arbuscula (Kze.) Tryon, comb. nov., *Alsophila arbuscula* Kze. Bot. Zeit. **2**:313. 1844.

T. atrovirens (Langsd. & Fisch.) Tryon, comb. nov., *Polypodium atrovirens* Langsd. & Fisch. Icon. Fil. 12. 1810, *Alsophila atrovirens* (Langsd. & Fisch.) Presl.

T. bulligera (Rosenst.) Tryon, comb. nov., *Alsophila bulligera* Rosenst. Fedde Repert. **25**:57. 1928.

T. caracasana (Kl.) Tryon, comb. nov., *Alsophila caracasana* Kl. Linnaea **18**:541. 1844.

T. compta (Mart.) Tryon, comb. nov., *Alsophila compta* Mart. Icon. Pl. Crypt. Bras. 66. 1834.

T. conjugata (Hook.) Tryon, comb. nov., *Alsophila conjugata* Hook. Syn. Fil. 37. 1866.

T. corcovadensis (Raddi) Copel., *Alsophila corcovadensis* (Raddi) C.Chr.

T. cordata (Kl.) Tryon, comb. nov., *Alsophila cordata* Kl. Linnaea **20**:441. 1847.

T. crassa (Karst.) Tryon, comb. nov., *Alsophila crassa* Karst. Fl. Columb. **2**:187. 1869.

T. decomposita (Karst.) Tryon, comb. nov., *Alsophila decomposita* Karst. Fl. Columb. **2**:185. 1869.

T. demissa (Morton) Tryon, comb. nov., *Alsophila demissa* Morton, Fieldiana Bot. **28**:7. 1951.

T. dicromatolepis (Fée) Tryon, comb. nov., *Alsophila dicromatolepis* Fée, Crypt. Vasc. Brésil **1**:164. 1869.

T. elegans (Mart.) Presl, *Alsophila elegans* Mart.

T. floribunda (Baker) Tryon, comb. nov., *Alsophila floribunda* Baker, Syn. Fil. ed 2, 458. 1874.

T. frigida (Karst.) Tryon, comb. nov., *Alsophila frigida* Karst. Fl. Columb. **1**:61. 1860.

T. Gardneri (Hook.) Tryon, comb. nov., *Alsophila Gardneri* Hook. Sp. Fil. **1**:40. 1844.

T. Glaziovii (Fée) Tryon, comb. nov., *Alsophila Glaziovii* Fée, Crypt. Vasc. Brésil **1**:160. 1869.

T. Gleasonii (Maxon) Tryon, comb. nov., *Alsophila Gleasonii* Maxon, Amer. Fern Jour. **15**:55. 1925.

T. hirsuta (Presl) Tryon, comb. nov., *Cyathea hirsuta* Presl, Delic. Prag. 190. 1822. *Alsophila hirsuta* (Presl) Kze.

T. infesta (Kze.) Tryon, comb. nov., *Alsophila infesta* Kze. Linnaea **9**:98. 1834.

T. Kalbreyeri (C.Chr.) Tryon, comb. nov., *Alsophila Kalbreyeri* C.Chr. Ind. Fil. 44. 1905 (nom. nov. for *Alsophila podophylla* Baker, not Hook.).

T. Kuhnii (Hieron.) Tryon, comb. nov., *Nephrodium Kuhnii* Hieron. Engl. Bot. Jahrb. **34**:440. 1904, *Alsophila Kuhnii* (Hieron.) C.Chr.

T. lasiosora (Kuhn) Tryon, comb. nov., *Alsophila lasiosora* Kuhn, Linnaea **36**:157. 1869.

T. latevagans (Baker) Tryon, comb. nov., *Alsophila latevagans* Baker, Jour Bot. **19**:203. 1881.

T. Lechleri (Mett.) Tryon, comb. nov., *Alsophila Lechleri* Mett. Fil. Lechl. **2**:28. 1859.

T. leucolepis (Mart.) Tryon, comb. nov., *Alsophila leucolepis* Mart. Icon. Pl. Crypt. Bras. 70. 1834.

T. Mellobarretoi (Brade) Tryon, comb. nov., *Alsophila Mello-barretoi* Brade, Arq. Jard. Bot. Rio Janeiro **11**:22. 1951.

T. Mexiae (Copel.) Tryon, comb. nov., *Cyathea Mexiae* Copel. Univ. Calif. Publ. Bot. **17**:30. 1932.

T. microdonta (Desv.) Tryon, comb. nov., *Polypodium microdontum* Desv. Ges. Naturf. Freunde Berl. Mag. **5**:319. 1811, *Alsophila microdonta* (Desv.) Desv.

T. microphylla (Kl.) Tryon, comb. nov., *Alsophila microphylla* Kl. Linnaea **18**:541. 1844.

T. Miersii (Hook.) Tryon, comb. nov., *Alsophila Miersii* Hook. Sp. Fil. **1**:38. 1844.

T. nigra (Mart.) Tryon, comb. nov., *Alsophila nigra* Mart. Icon. Pl. Crypt. Bras. 71. 1834.

T. oblonga (Kl.) Tryon, comb. nov., *Alsophila oblonga* Kl. Linnaea **18**:540. 1844.

T. obtusa (Kl.) Tryon, comb. nov., *Alsophila obtusa* Kl. Allgm. Gartenzeit. **30**:41. 1852.

T. pastazensis (Hieron.) Tryon, comb. nov., *Alsophila pastazensis* Hieron. Hedwigia **45**:232. 1906.

T. pauciflora (Presl) Tryon, comb. nov., *Alsophila pauciflora* Presl, Gefässbündel Stipes der Farrn 35. 1847 (preprint from Abhandl. böhm. Ges. V, **5**:343. 1848), (sp. nov. based on taxon sub nom. *Alsophila aculeata* (Kaulf.) Kl. Linnaea **18**:540. 1844).

T. phalaenolepis (C.Chr.) Tryon, comb. nov., *Alsophila phalaenolepis* C.Chr. Fedde Repert. **10**:213. 1911.

T. phegopteroides (Hook.) Tryon, comb. nov., *Alsophila phegopteroides* Hook. Syn. Fil. 32. 1865.

T. Portoana (Brade) Tryon, comb. nov., *Alsophila Portoana* Brade, Arch. Instit. Biol. Veg. Rio Janeiro **1**:223. 1935.

T. praecincta (Kze.) Tryon, comb. nov., *Alsophila praecincta* Kze. Flora 1839 (1): Beibl. 53.

T. procera (Willd.) Tryon, comb. nov., *Polypodium procerum* Willd. Sp. Pl. **5**:206. 1810.

T. pubescens (Baker) Tryon, comb. nov., *Alsophila pubescens* Baker, Syn. Fil. 449. 1868.

T. pungens (Willd.) Tryon, comb. nov., *Polypodium pungens* Willd. Sp. Pl. **5**:206. 1810, *Alsophila pungens* (Willd.) Presl.

T. rufa (Fée) Tryon, comb. nov., *Alsophila rufa* Fée, Crypt. Vasc. Brésil **1**:166. 1869.

T. submarginalis (Domin) Tryon, comb. nov., *Alsophila submarginalis* Domin, Kew Bull. 1929: 217.

T. Tryonorum (Riba) Tryon, comb. nov., *Alsophila Tryonorum* Riba, Rhodora **69**:66. 1967.

T. Ulei (Christ) Tryon, comb. nov., *Alsophila Ulei* Christ, Hedwigia **44**:367. 1905.

T. vernicosa (Kuhn) Tryon, comb. nov., *Alsophila vernicosa* Kuhn, Linnaea **36**:155. 1869.

T. villosa (Willd.) Tryon, comb. nov., *Cyathea villosa* Willd. Sp. Pl. **5**:495. 1810, *Alsophila villosa* (Willd). Desv.

7. Cyathea

Cyathea Sm. Mém. Acad. Turin, **5**:416. 1793. Type: *Cyathea arborea* (L.) Sm. (*Polypodium arboreum* L.).

Hemitelia R. Br. Prod. Fl. Nov. Holl. 158. 1810. Type: *Cyathea multiflora* Sm. (Brown did not make any combinations for the names of the species of his new genus).

Disphenia Presl, Tent. Pterid. 55. 1836, nom. superfl. Type: the same as that of *Cyathea* (all species, except *Cyathea arborea*, that were originally included in *Cyathea* had, prior to Presl's publication, been removed to other genera: two species of the original six to *Cystopteris* and three species to *Hemitelia*).

Cormophyllum Newm. Phytol. 5:237. 1856, nom. superfl. Type: the same as that of *Cyathea* (Newman included *Polypodium arboreum* L. in his genus).

Petiole smooth to tuberculate, or with corticinate spines, sometimes with trichomes; petiole *scales* (especially on the abaxial side) more or less appressed, attached at one point of a pseudopeltate or peltate base, structurally marginate, with a narrow to broad margin of cells different in orientation, size and usually in shape and color from those of the central portion, lacking dark setae, the apex rounded to filamentous; *minute indument* of the petiole, when present, of squamulae and (or) rarely of patent trichomidia; *costa* pubescent above; *veins* free, in lobed or pinnatifid segments the basal vein on each side extending above the base of the sinus; *indusium* present, scale-like to sphaeropteroid.

Cyathea (Figs. 4, 10, 44–46) is an American genus of about 110 species. It is characterized by marginate petiole scales that lack a dark seta, normal, free venation (as in Figs. 42–43) and the presence of an indusium. The separation of exindusiate *Trichipteris* and indusiate *Cyathea* has been discussed under the former genus. The petiole scales of *Trichipteris, Cyathea* and *Cnemidaria* are similar in having a cellular differentiation of the margin (Figs. 39, 44–46). The central portion is of large, elongate cells with their long axis parallel to that of the scale; beyond this center the cells become progressively smaller, often more rectangular, and finally oriented approximately at a right angle to the edge of the scale. There is also usually (but not always) a transition from heavy walled and dark colored central cells to thin walled and light colored marginal cells which often gives the scale a bicolorous appearance. Species of *Cyathea* with a sphaeropteroid indusium are especially numerous in the northern Andes where they seem to form a large group of closely related species. The chromosome number of $n=69$ has been reported by Walker (1966) for *Cyathea arborea*.

The following list of species will serve as examples of the genus. It does not include those in which problems of taxonomy or

nomenclature are known. It includes only a selection of the many closely related and inadequately known species of the northern Andean region, especially of Ecuador and Colombia.

WEST INDIES

Cyathea aquilina (Christ) Domin, *Alsophila aquilina* Christ.
C. arborea (L.) Sm.
C. asperula Maxon.
C. Brittoniana Maxon.
C. calolepis (Hook.) Domin, *Hemitelia calolepis* Hook.
C. dissoluta Jenm.
C. furfuracea Baker.
C. gracilis Griseb.
C. Harrisii Maxon.
C. Lewisii (Morton & Proctor) Proctor, *Hemitelia Lewisii* Morton & Proctor.
C. muricata Willd., *Hemitelia muricata* (Willd.) Fée.
C. parvula (Jenm.) Domin, *Alsophila parvula* Jenm.
C. producta Maxon.
C. Sherringii (Jenm.) Domin, *Hemitelia Sherringii* Jenm.
C. tenera Griseb.

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Cyathea acutidens (Christ) Domin, *Alsophila acutidens* Christ.
C. aphlebioides Christ.
C. conspersa Christ.
C. costaricensis (Kuhn) Domin, *Hemitelia costaricensis* Kuhn.
C. delicatula Maxon.
C. fulva (Mart. & Gal.) Fée, *Alsophila fulva* Mart. & Gal.
C. Jurgensenii Fourn.
C. Maxonii Maxon.
C. multiflora Sm., *Hemitelia multiflora* (Sm.) Spreng.
C. notabilis Domin, *Alsophila notabilis* Maxon, 1922, not Saporta, Mém. Soc. Géol. France II, 8:329. 1868. (Cocos Is.).
C. onusta Christ.
C. pelliculosa Christ.
C. suprastrigosa (Christ) Maxon, *Hemitelia suprastrigosa* Christ.
C. Tuerckheimii Maxon.

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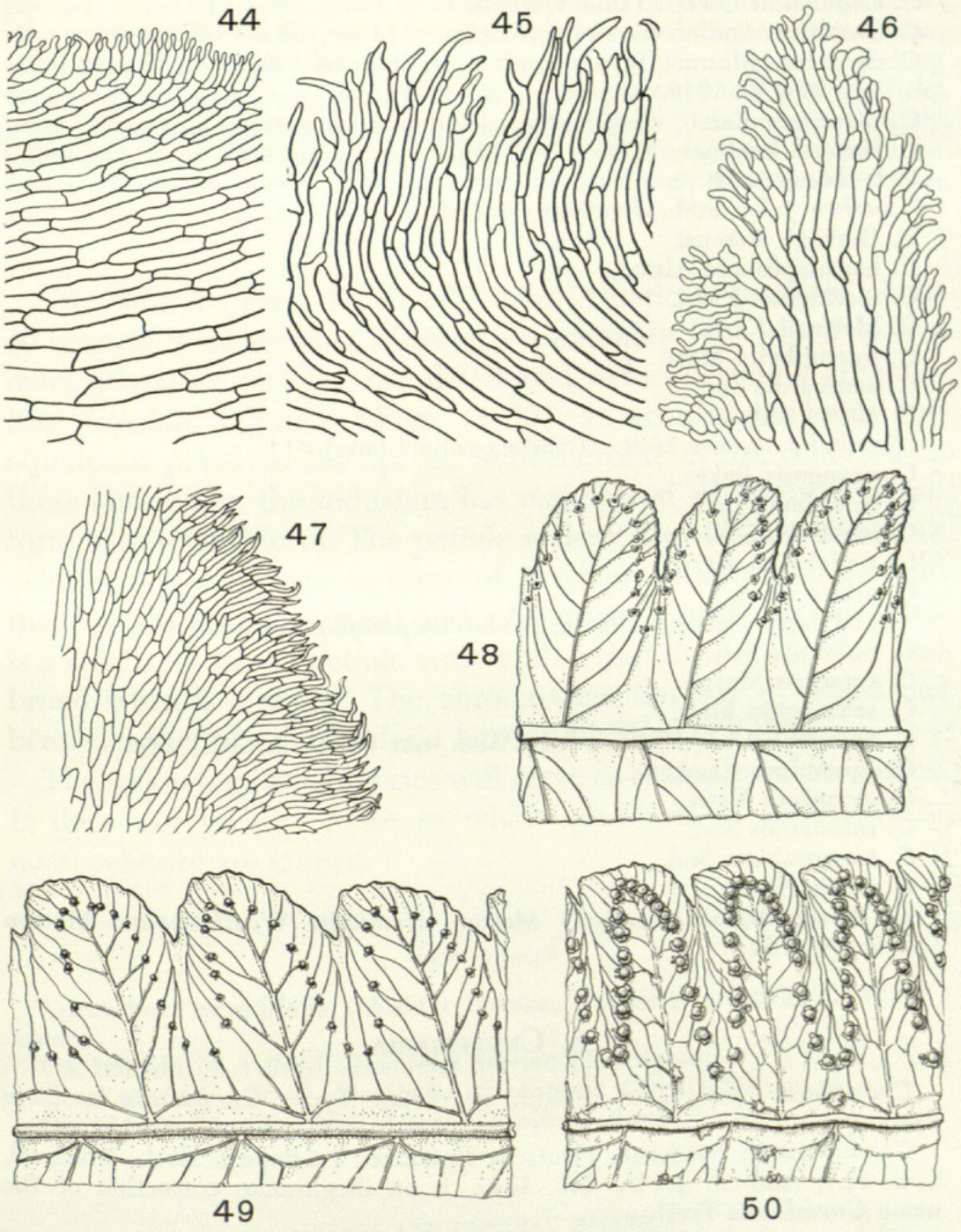
Cyathea asperata Sod.
C. aspidiiformis Domin, *Cyathea aspidioides* Sod., not (Bl.) Moritz.
C. aurea Karst.
C. Boryana (Kuhn) Domin, *Hemitelia Boryana* Kuhn.
C. brachypoda Sod.
C. castanea Baker.
C. catacampta Alston.



FIGS. 44–50. CYATHEA and CNEMIDARIA. FIGS. 44–46. CYATHEA, portions of petiole scales, all × 90: 44, *Cy. puberula, Cuatrecasas 18186,* US. 45, *Cy. platylepis, Schultes & Cabrera 15079,* GH. 46, *Apex, Cy. parvula, Proctor 5513,* GH. FIGS. 47–50. CNEMIDARIA. FIG. 47. Portion of petiole scale, *Cn. spectabilis, Britton et al. 1238,* × 30, NY. FIGS. 48–50. Portions of pinnae showing venation, receptacles and indusia: 48, *Cn. bella, Hort. Lips.* × 1, MO. 49, *Cn. speciosa, Killip & Smith 24536,* × 1–1/2, GH. 50, *Cn. Ewanii, Ewan 16729,* × 1–1/2, US.

C. columbiana Domin, *Hemitelia obscura* Mett., not *Cyathea obscura* (Bedd.) Copel.

C. Copelandii Luerrs. (Ilha Trindade).

C. corallifera Sod.

C. decorata (Maxon) Tryon, comb. nov., *Hemitelia decorata* Maxon, Jour. Arn. Arb. **27**:439. 1946.

C. divergens Kze.

C. ebenina Karst.

C. frondosa Karst.

[*Cyathea fulva* Sod.=**Cyathea Sodiroi**].

C. Herzogii Rosenst.

C. leucolepismata Alston.

C. meridensis Karst.

C. Mettenii Karst.

C. microphylla Mett.

C. muricatula Sod.

C. nitens Sod.

[*Hemitelia obscura* Mett.=**Cyathea columbiana**].

C. ocanensis Baker.

C. ochroleuca Sod.

C. parvifolia Sod.

C. petiolulata Karst.

C. pilosa Baker.

C. platylepis (Hook.) Domin, *Hemitelia platylepis* Hook.

C. puberula Sod.

C. rupestris Maxon.

C. schanschin Mart.

C. Sodiroi C.Chr., *Cyathea fulva* Sod., not (Mart. & Gal.) Fée.

C. squamipes Karst.

C. straminea Karst.

C. subinermis Sod.

C. tungurahuae Sod.

C. vestita Mart.

C. Weatherbyana (Morton) Morton, *Hemitelia Weatherbyana* Morton (Galápagos Isls.).

8. Cnemidaria

Cnemidaria Presl, Tent. Pterid. 56. 1836. Type: *Cnemidaria speciosa* Presl.

Cnemidopteris Reichenb. Deutsche Botaniker 1 (Repert, Herb. Nomencl. Gen. Pl.), Abtheil. **2**:148, 235. 1841, is an illegitimate correction of the name *Cnemidaria* Presl.

Microstegnus Presl, Gefässbündel Stipes der Farrn, 45. 1847 (preprint from Abhandl. böhm. Ges. V, **5**:353. 1848). Type: *Microstegnus grandifolius* (Willd.) Presl (*Cyathea grandifolia* Willd.) = *Cnemidaria grandifolia* (Willd.) Proctor.

Hemistegia Presl, Gefässbündle Stipes der Farrn, 46. 1847 (preprint from Abhandl. böhm. Ges. V, **5**:354. 1848). Lectotype: *Hemistegia Kohautiana* (Presl) Presl = *Cnemidaria Kohautiana* Presl.

Actinophlebia Presl, Gefässbündel Stipes der Farrn, 47. 1847 (preprint from Abhandl. böhm. Gas. V, **5**:355. 1848). Type: *Actinophlebia horrida* (L.) Presl (*Polypodium horridum* L.) = *Cnemidaria horrida* (L.) Presl.

Petiole smooth to tuberculate, or rarely with corticinate spines, lacking trichomes; petiole *scales* (especially on the abaxial side) more or less appressed, attached at one point of a pseudopeltate or peltate base, structurally marginate, with a narrow to broad margin of cells different in orientation, size, shape, and usually in color from those of the central portion, lacking dark setae, the apex rounded to filamentous; *minute indument* of the petiole, when present, of appressed trichomidia; *costa* usually glabrous above, rarely pubescent; *veins* forming areolae along the costa (sometimes beyond), or free and in lobed or pinnatifid segments, the basal vein on each side connivent to the base of the sinus; *indusium* present, hemitelioid.

Cnemidaria (Figs. 13, 47–50) is an American genus of about 40 species. It represents a strong evolutionary line which, in the more advanced species, has developed reduced lamina architecture, areolate venation (Figs. 49–50), an acaulescent habit and equatorial pores on the spores. While evolution has occurred in these characters, the indusium has maintained an essentially uniform hemitelioid form. The petiole scales (Fig. 47) are similar in cellular differentiation to those of *Trichipteris* and *Cyathea* and they are discussed in detail under *Cyathea.* In most species there is a relatively broad petiole scale with a dark central portion and broad whitish margins. The chromosome number of $n=69$ has been reported for *Cnemidaria horrida* by Walker (1966).

The following list of species will serve as examples of the genus. It does not include those in which problems of taxonomy or nomenclature are known.

WEST INDIES

Cnemidaria grandifolia (Willd.) Proctor, *Hemitelia grandifolia* (Willd.) Spreng.

Cn. horrida (L.) Presl, *Hemitelia horrida* (L.) Spreng.

Cn. Kohautiana Presl, *Hemitelia Kohautiana* (Presl) Kze.

Cn. obtusa (Kaulf.) Presl, *Hemitelia obtusa* Kaulf.

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Cnemidaria arachnoidea (Maxon) Tryon, comb. nov., *Hemitelia arachnoidea* Maxon. Contrib. U. S. Nat. Herb. **16**:34. 1912 (*Cnemidaria arachnoidea* Underw., in synon.).

Cn. chiricana (Maxon) Tryon, comb. nov., *Hemitelia chiricana* Maxon, Contrib. U. S. Nat. Herb. **16**:33. 1912.

Cn. choricarpa (Maxon) Tryon, comb. nov., *Hemitelia choricarpa* Maxon, Contrib. U. S. Nat. Herb. **16**:40. 1912.

Cn. conformis (Tryon) Tryon, comb. nov., *Hemitelia conformis* Tryon, Rhodora **62**:1. 1960.

Cn. contigua (Maxon) Tryon, comb. nov., *Hemitelia contigua* Maxon, Contrib. U.S. Nat. Herb. **16**:32. 1912 (*Cnemidaria contigua* Underw., in synon.).

Cn. decurrens (Liebm.) Tryon, comb. nov., *Hemitelia decurrens* Liebm. Vid. Selsk. Skr. V, **1**:286. 1849.

Cn. grandis (Maxon) Tryon, comb. nov., *Hemitelia grandis* Maxon, Contrib. U. S. Nat. Herb. **16**:37. 1912.

Cn. mutica (Christ) Tryon, comb. nov., *Hemitelia mutica* Christ, Bull. Soc. Bot. Genève II, **1**:233. 1909.

Cn. petiolata (Hook.) Copel., *Hemitelia petiolata* Hook.

Cn. rudis (Maxon) Tryon, comb. nov., *Hemitelia rudis* Maxon, Contrib. U. S. Nat. Herb. **17**:413. 1914.

Cn. subglabra (Maxon) Tryon, comb. nov., *Hemitelia subglabra* Maxon, Contrib. U. S. Nat. Herb. **16**:36. 1912 (*Cnemidaria subglabra* Underw., in synon.).

SOUTH AMERICA

Cnemidaria abitaguensis (Domin) Tryon, comb. nov., *Hemitelia abitaguensis* Domin, Kew Bull. 1929: 215.

Cn. amabilis (Morton) Tryon, comb. nov., *Hemitelia amabilis* Morton, Fieldiana Bot. **28**:10. 1951.

Cn. bella (Mett.) Tryon, comb nov., *Hemitelia bella* Mett. Fil. Hort. Bot. Lips. 110. 1856.

Cn. dissimilis (Morton) Tryon, comb. nov., *Hemitelia dissimilis* Morton, Fieldiana Bot. **28**:8. 1951.

Cn. Ewanii (Alston) Tryon, comb. nov., *Cyathea Ewanii* Alston, Jour. Wash. Acad. Sci. **48**:231. 1958.

Cn. integrifolia (Kl.) Tryon, comb. nov., *Hemitelia integrifolia* Kl. Linnaea **18**:539. 1844.

Cn. Karsteniana (Kl.) Tryon, comb. nov., *Hemitelia Karsteniana* Kl. Allgem. Gartenzeit. **20**:42. 1852.

Cn. Lindenii (Hook.) Tryon, comb. nov., *Hemitelia Lindenii* Hook. Icon. Pl. t. 706. 1848, *Cyathea speciosa* Willd. (not *Cnemidaria speciosa* Presl) *Hemitelia speciosa* (Willd.) Kaulf.

Cn. nervosa (Maxon) Tryon, comb. nov., *Hemitelia nervosa* Maxon, Jour. Wash. Acad. Sci. **34**:309. 1944.

Cn. quitensis (Domin) Tryon, comb. nov., *Hemitelia quitensis* Domin, Kew Bull. 1929: 215.

Cn. roraimensis (Domin) Tryon, comb. nov., *Hemitelia roraimensis* Domin, Kew Bull. 1929: 216.

Cn. speciosa Presl, *Hemitelia subincisa* Kze. (nom. nov. for *Cnemidaria speciosa* Presl, not *Hemitelia speciosa* (Willd) Kaulf.).

[*Hemitelia speciosa*=**Cnemidaria Lindenii**].

Cn. spectabilis (Kze.) Tryon, comb. nov., *Hemitelia spectabilis* Kze. Linnaea **21**:233. 1848.

[*Hemitelia subincisa*=**Cnemidaria speciosa**].

Cn. Uleana (Sampaio) Tryon, comb. nov., *Hemitelia Uleana* Sampaio, Bol. Mus. Nac. Rio Janeiro **1**:65. 1923.

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