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Reed C. Rollins | STUDIES ON MEXICAN CRUCIFERAE

Rolla Tryon | A REVISION OF THE GENUS CYATHEA

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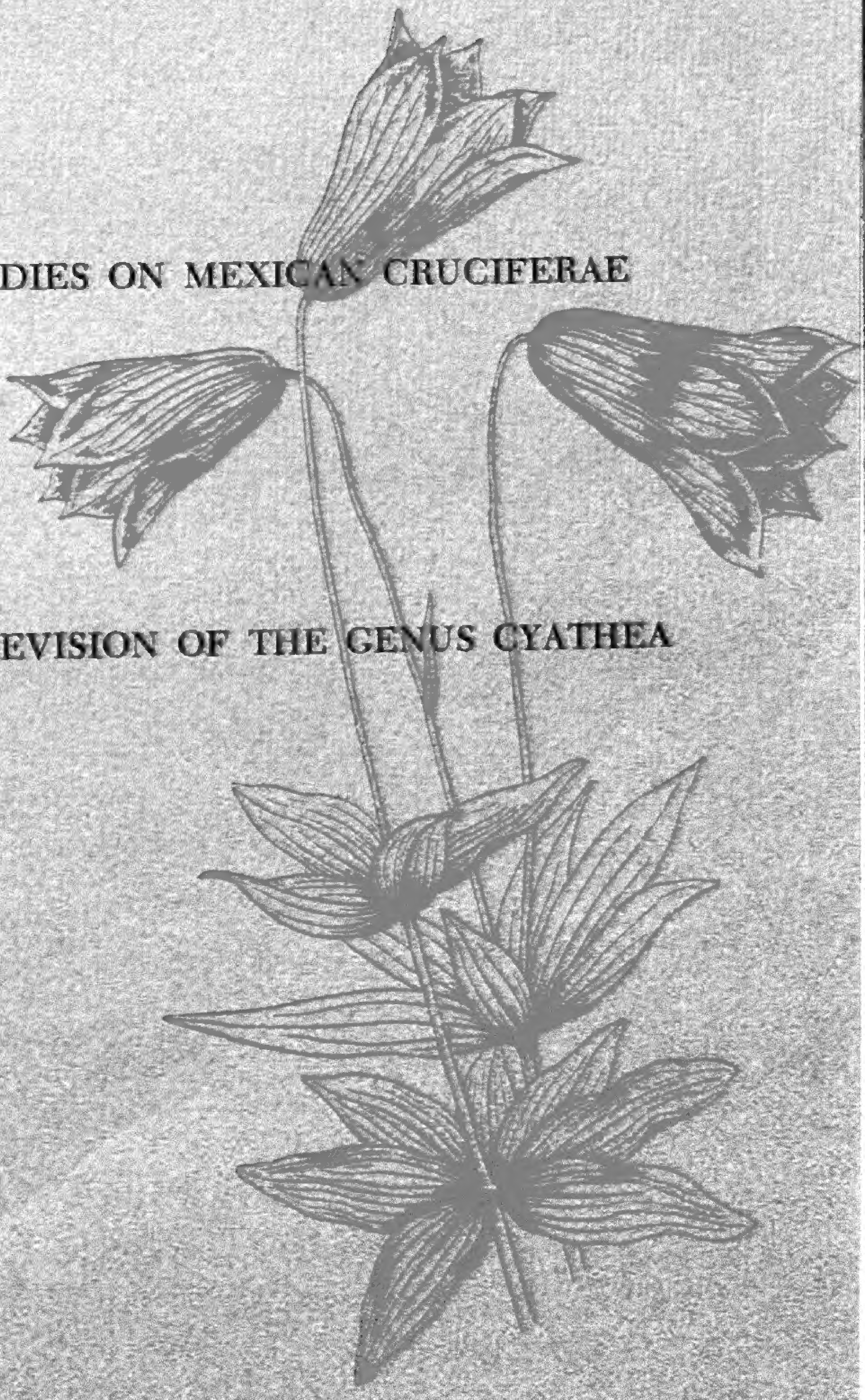

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STUDIES ON MEXICAN CRUCIFERAE[1]

REED C. ROLLINS

In preparing treatments of certain genera of the Cruciferae for Johnston's projected Flora of the Chihuahuan Desert, it has been necessary to study material both within the desert region and often considerably outside of it. In the case of *Mancoa* and *Thelypodiopsis* I have covered the species now known to occur in Mexico. Otherwise, notes and pertinent comments are given concerning a number of species. A new genus, *Raphanorhyncha,* is described and new taxa are presented in *Halimolobos.*

HALIMOLOBOS

My former study of *Halimolobos* (Rollins, 1943) is now quite out of date because of the considerable new material that has been collected since then. However, there are still too few specimens of some species to provide a satisfactory understanding of the variation present and the extent of their geographical distribution.

At the time of my earlier treatment of *Halimolobos,* it was not possible to verify the typification of the genus. Recently, I have seen two specimens in the herbarium of the Komorov Botanical Institute in Leningrad which bear on the matter. One specimen is labeled, "Sisymbrium lasiolobum Lk. Cult. in horto bot. Imp. Petropol 1834." The other specimen is labeled "Sisymbr. lasiolobum Lk., Herb. Fischer." The initials CAM also appear on the label. Thus it is probable C. A. Meyer was the one who annotated the label in the Fischer herbarium. Both of the specimens are *Halimolobos lasioloba* and could easily be from the same seed source as the type which was grown in the Berlin Botanical Garden. Although this does not constitute an adequate verification of the type, it does provide evidence that the proper typification of *Halimolobos* was made by O. E. Schulz (1924).

The following new taxa or taxonomic rearrangements stem from a reexamination of the genus.

Halimolobos minutiflora Rollins, sp. nov.

Low leafy herbs with stems branched above base, 1-2 dm. tall, densely pubescent throughout with dendritic or otherwise highly branched trichomes; cauline leaves shallowly dentate, oblong, prominently one-nerved toward base, (1.5-)2-4(-5) cm. long, 4-9 mm. wide; lower leaves narrowed toward base, non-auriculate; middle and upper cauline leaves widened toward base, auriculate and clasping the stem; sepals oblong, marginate, ca. 1.5 mm. long; petals white, spatulate with a slender claw, ca. 2

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[1] Field research for some of the results reported in this paper was supported by Grant GB-30720 from the National Science Foundation.

mm. long; stamens slightly exserted, spreading, all six similar in length; anthers oval, small, purplish; fruiting pedicels widely spreading, horizontal to slightly ascending, straight, 1.5-3 mm. long; siliques widely spreading, slightly ascending, linear, straight, weakly flattened contrary to septum or nearly terete, densely pubescent, 8-15 mm. long, 1.2-1.5 mm. wide; valves pubescent on interior; styles less than 0.5 mm. long; ovules 15-30 in each loculus; seeds plump, marginless, oblong, ca. 0.75 mm. long; cotyledons incumbent.

Herba 1-2 dm. alta dense pubescens, foliis caulinis oblongis dentatis auriculatis (1.5)2-4(-5) cm. longis, 4-9 mm. latis, sepalis pubescentibus oblongis marginatis ca. 1.5 mm. longis, petalis albis spathulatis ca. 2 mm. longis, infructescentiis 5-10 cm. longis, pedicellis recte horizontalibus vel plus minusve ascendentibus 1.5-3 mm. longis, siliquis recte oblongis divaricatis 8-15 mm. longis, stylis ca. 0.5 mm. longis capitatis, seminibus alatis ca. 0.75 mm. longis.

Holotype in the Gray Herbarium, collected in a rocky area near Mexican Highway 49, between the cities of San Luis Potosí and Zacatecas, 49 miles west of San Luis Potosí, S. L. P., Mexico, Oct. 7, 1974, *Reed C. Rollins and K. W. Roby 74127*. Isotypes to be distributed.

OTHER SPECIMEN STUDIED. **Mexico. Zacatecas:** limestone chip, near Mex. Hwy. 49, 62 miles west of San Luis Potosí, just inside Zacatecas state line, Oct. 7, 1974, *Rollins and Roby 74129* (GH).

Aside from its much smaller stature, *Halimolobos minutiflora* resembles *H. parryi* more than any other species of the genus. It differs in having densely pubescent instead of glabrous siliques and shorter styles than in *H. parryi*. The latter species tends to be leafy with relatively large basal and lower cauline leaves. We have not seen any truly basal leaves of *H. minutiflora* but all indications from the lower cauline leaves are that the basal leaves are either small or a truly basal rosette is not formed. It is interesting that in some specimens of *H. parryi* and in *H. minutiflora* the inner surface of the silique valves are pubescent. All specimens of *H. parryi* do not show this feature.

Halimolobos rigida Rollins, sp. nov.

Plants densely pubescent with dendritic trichomes, ca. 6 dm. tall, highly branched beginning near base, branches ascending; basal leaves not seen; lower cauline leaves shortly petiolate, upper cauline sessile, cuneate at base, leaves coarsely dentate, oblong to linear-oblong, 2-5 cm. long, 4-8 mm. wide; sepals oblong, non-saccate, densely pubescent, ca. 1.5 mm. long; petals white, narrowly spatulate, ca. 2 mm. long; infructescence elongated, 2-3 dm. long; fruiting pedicels rigid, spreading at right angles to rachis, 6-10 mm. long; siliques terete, widely spreading, slightly curved upward, 1.5-2 cm. long, ca. 1 mm. wide, densely pubescent with two size-classes of trichomes, the larger trichomes stalked; styles 0.5-0.75 mm.

long; seeds about 25 per loculus, oblong, plump, angular, radicle evident, ca. 1 mm. long, ca. 0.5 mm. wide; cotyledons incumbent to obliquely incumbent.

Herba ramosa ca. 6 dm. alta dense pubescens, foliis dentatis inferne petiolatis superne cuneatis, sepalis pubescentibus ca. 1.5 mm. longis, petalis albis lineari-spathulatis ca. 2 mm. longis, infructescentiis 2-3 dm. longis, pedicellis rectis horizontalibus 6-10 mm. longis, siliquis teretibus dense pubescentibus 1.5-2 cm. longis, ca. 1 mm. latis, stylis 0.5-0.75 mm. longis, seminibus alatis oblongis ca. 1 mm. longis, ca. 0.5 mm. latis.

Holotype in the Gray Herbarium, collected on coarse crystalline loam derived from basic igneous rock, 12 km. north of El Cubo, 43 km. north of Charcas on road to Catorce, San Luis Potosí, Mexico, lat. 23°26′ N, long. 101°00′ W, at 1700 m. altitude, 3 July 1972, *F. Chiang, T. Wendt and M. C. Johnston 8321.*

Known only from the type collection.

The striking aspects of *Halimolobos rigida* are the many branches beginning near the base of the main stem and extending to some distance up the stem, the rigid widely spreading pedicels and the equally rigid widely spreading but slightly upcurved siliques. The nearest related species, *H. pedicellata,* has divaricately ascending pedicels and the straight siliques are also divaricately ascending. Plants of these two species have quite a different aspect and the flowers of *H. pedicellata* are considerably larger than those of *H. rigida.*

Unfortunately, we have only the one collection of *Halimolobos rigida* which precludes making any statements about range of variation or other such matters. The species was said by the collectors to be infrequent and they listed *Flourensia cernua, Prosopis laevigata, Yucca decipiens,* and *Forestiera angustifolia* as associated species.

Halimolobos pedicellata Rollins, stat. nov., based on *H. lasioloba* var. *pedicellata* Rollins. Contrib. Dudley Herb. 3:260. 1943.

Holotype in the Gray Herbarium, collected at Tejamén, Durango, Mexico, Aug. 21-27, 1906, *Edward Palmer 491.* Isotypes: F,NY,UC,US.

With more and better material available, particularly of *Halimolobos lasioloba,* it is clear that two taxa on the specific level are represented rather than a single species with two infraspecific taxa. The much longer pedicels of *H. pedicellata* are divaricately ascending instead of being at right angles to the rachis or slightly deflexed as in *H. lasioloba.* The position of the siliques is different also. In *H. pedicellata,* the siliques are divaricately ascending whereas in *H. lasioloba,* they are somewhat deflexed or at least widely spreading. The two species occupy different geographic areas, *H. lasioloba* is more easterly in San Luis Potosí and Zacatecas while *H. pedicellata* is more westerly extending from Chihuahua to Morelia.

MANCOA

Specimens of *Mancoa* not seen when my former treatment (1941) was prepared require the addition of two species. One of these, *Mancoa henricksonii,* was collected in a remote area of Zacatecas and to my knowledge has not been seen before. The other, *M. stylosa* from Durango, was collected in 1898 but the specimen had not been associated with its congeners and therefore has been overlooked. A key to the presently known species of Mexico is presented together with brief notes on the taxa other than the new species.

KEY TO THE SPECIES

Siliques glabrous; plants sparsely pubescent or glabrous; leaves pinnatifid to bipinnatifid.
  Pedicels 3-4 mm. long, divaricately ascending; infructescences not congested. .... 1. *M. laxa.*
  Pedicels 5-8 mm. long, widely spreading at right angles to rachis; infructescences congested. .... 2. *M. bracteata.*
Siliques densely pubescent; plants densely pubescent; leaves entire to sinuate dentate except for *M. mexicana* where they are pinnatifid to bipinnatifid.
  Fruiting pedicels 1-2(-3) mm. long; infructescences 2-4 cm. long; siliques flattened contrary to septum. .... 3. *M. mexicana.*
  Fruiting pedicels (4-)5-15 mm. long; infructescences 1-5 dm. long; siliques somewhat inflated, only slightly compressed contrary to septum.
    Apex of siliques rounded; pedicels 8-15 mm. long; siliques more than 3 mm. wide; middle and upper cauline leaves scarcely auriculate.
      Styles less than 1 mm. long; seeds 0.5 mm. or less long. .... 4. *M. pubens.*
      Styles 2.5-3.5 mm. long; seeds about 1 mm. long. .... 5. *M. stylosa.*
    Apex of siliques definitely notched; pedicels 4-6 mm. long; siliques less than 2.5 mm. wide; middle and upper cauline leaves auriculate. ...... 6. *M. henricksonii.*

1. **Mancoa laxa** Roll., Rhodora 59:68. 1957.

Holotype in the United States National Herbarium, collected on wet loam of prairie, Rosario, east of La Junta, Chihuahua, Mexico, Sept. 14-15, 1934, *F. W. Pennell 18767.*

Mancoa laxa is known only from the type collection. It is most nearly related to *M. bracteata.*

2. **Mancoa bracteata** (Wats.) Roll., Contrib. Dudley Herb. 3:193, 1941, based on *Nasturtium bracteatum* Wats., Proc. Amer. Acad. 26:131. 1891. *Hartwegiella nasturtioides* Schulz, Fedde Rep. Spec. Nov. 33:187. 1933.

Holotype in the Gray Herbarium, collected at Aguas Calientes, Mexico, 1937, *T. Hartweg 39.* Known from Aguas Calientes and Durango.

3. **Mancoa mexicana** Gilg and Muschler, Bot. Jahrb. 42:463. 1909. *Capsella mexicana* Hemsl. Diag. Pl. Nov. Mex. 19. 1879.

Type collected in the vicinity of San Luis Potosí, Mexico, 1876, *J. G. Schaffner 147.* Isotype: GH. Known from San Luis Potosí and Zacatecas.

4. **Mancoa pubens** (Gray) Roll., Contrib. Dudley Herb. 3:192, based

on *Hymenolobus pubens* Gray, Smiths. Contr. (Pl. Wright.) 3:9. 1852. *Capsella pubens* (Gray) Wats., Bibl. Index 52. 1878. *Poliophyton pubens* (Gray) O. E. Schulz, Bot. Jahrb. 66: 93. 1933.

Holotype in the Gray Herbarium, collected in a valley about eighty miles beyond the Pecos, Texas, U.S.A., *C. Wright 12*. Isotypes: GH,US. Known in Mexico from the states of Chihuahua and Coahuila.

5. Mancoa stylosa Roll. sp. nov.

Annual or biennial, branched beginning just above base, up to 4 dm. tall, uniformly covered with branching trichomes, cauline leaves sessile, not auriculate, oblong to narrowly oblanceolate, dentate, 1-4 cm. long, 3-8 mm. wide, infructescences terminating each branch, up to 1.5 dm. long, dense; fruiting pedicels almost straight, spreading at right angles to rachis to slightly ascending, 1-1.5 cm. long; sepals broadly oblong, densely pubescent, scarious margined, ca. 2 mm. long; petals white, strongly differentiated into blade and claw, ca. 2.5 mm. long, stamens exserted; filaments spreading, nearly equal, ca. 3 mm. long, anthers ca. 1 mm. long; glandular tissue subtending petals and filaments in a continuous mold with erect lobes; siliques oval in outline, slightly compressed contrary to septum, 8-10 mm. long, 4-5 mm. wide, densely pubescent with two size-classes of trichomes, the smaller numerous and covering most of the surface, the larger scattered; styles 2.5-3.5 mm. long, often pubescent toward base; lower portion of replum pubescent; seeds 20-30 in each loculus, plump, marginless, ca. 1 mm. long; funiculi free, slender, longer than seeds; cotyledons incumbent.

Herba annua vel biennis, caulibus ramosis, foliis caulinis sessilibus dentatis 1-4 cm. longis, 3-8 mm. latis, infructescentiis elongatis 1-1.5 dm. longis, pedicellis fructiferis divaricatis rectis 1-1.5 cm. longis, petalis albis, siliquis ovalis 8-10 mm. longis, pubescentibus, stylis 2.5-3.5 mm. longis, seminibus exalatis oblongis non compressis ca. 1 mm. longis, cotyledonibus incumbentibus.

Holotype in the United States National Herbarium, collected at Carcaria, Durango, Mexico, August 5, 1898. *E. W. Nelson 4657*.

Mancoa stylosa is similar in many respects to *M. pubens* although it is not as strict or tall as that species. The principal, easily seen differences between these species are the much longer styles, larger seeds and longer pedicels of *M. stylosa* as compared to these same structures of *M. pubens*. The petals of *M. stylosa* are strongly differentiated into blade and claw while those of *M. pubens* are spatulate. Another difference is in the size of the flowers which are larger in *M. stylosa* than in *M. pubens*. The latter species is well-known from Trans Pecos, Texas, and from a few localities in Chihuahua and Coahuila. Unfortunately, *M. stylosa* is known only from the single specimen cited above.

6. Mancoa henricksonii Roll. sp. nov.

Erect annual or biennial, branched above, 8-12 dm. tall, densely pubescent with intricately branched trichomes; lower leaves petiolate, sinuate dentate, up to 10 cm. long, middle and upper cauline leaves sessile, auriculate, unevenly dentate; sepals densely pubescent, oblong, nonsaccate, ca. 2 mm. long; petals white, obovate, differentiated into blade and claw, ca. 3 mm. long; stamens slightly exserted; infructescences elongated, narrow, 1.5-3 dm. long; fruiting pedicels densely pubescent, widely spreading, rigid, nearly straight, 4-7 mm. long; siliques oblong, 5-6 mm. long, 1.5-2 mm. wide, sessile, slightly compressed contrary to septum, narrowly notched at apex with the valves projecting above the style-base, densely pubescent with two size-classes of trichomes, smaller trichomes covering entire silique, larger trichomes scattered; styles 1-1.25 mm. long; seeds 15-25 in each loculus, pump, marginless, oblong, 0.75-1 mm. long; cotyledons incumbent.

Herba annua vel biennis ramosa 8-12 dm. alta dense pubescens, foliis caulinis supra auriculatis dentatis, sepalis oblongis non saccatis pubescentibus ca. 2 mm. longis, petalis albis obovatis ca. 3 mm. longis, infructescentiis elongatis 1.5-3 dm. longis, pedicellis fructiferis divaricatis rectis dense pubescentibus 4-7 mm. longis, siliquis oblongis 5-6 mm. longis, 1.5-2 mm. latis, sessilibus 30-50 ovulatis, stylis 1-1.25 mm. longis, seminibus exalatis oblongis non compressis 0.75-1 mm. longis, cotyledonibus incumbentibus.

Holotype in the Gray Herbarium, collected in an open grassland area on upper northwest slopes, near granite summit of Pico de Teyra, 15 miles northeast of Estacion Camacho, Zacatecas, Mexico, near 24°33′ N, 102°10′ W, 8,200 ft., Sept. 23, 1973, *James Henrickson 13471.*

PENNELLIA

When Nieuwland (1918) substituted the name *Pennellia* for the later homonym *Heterothrix* of Rydberg (1907), he made only one combination, *P. micrantha* (Gray) Nieuwl., citing *Thelypodium micranthum* (Gray) without the combining author or reference. However, it is clear from Rydberg's paper that the full author citation should have given Watson (1882) as the author of the combination and that the species is in reality based on *Streptanthus micranthus* Gray (1849). *Heterothrix* Rydberg was based on *Thelypodium* sect. *Heterothrix* of Robinson (1895) which included two species, *T. micranthum* and *T. longifolium,* both now considered to belong to *Pennellia.* Since Nieuwland referred only to *P. micrantha* in establishing *Pennellia,* he in effect selected that species as the type of the genus. Our present concern with *Pennellia* in connection with the Chihuahuan Desert study is to provide a properly constituted name for an infraspecific taxon.

Pennellia micrantha (Gray) Nieuwl. var. **lasiocalycina** (Schulz) Roll., comb. nov., based on *Heterothrix micrantha* var. *lasiocalycina* O. E. Schulz, Das Pflanzenr. 86 (IV, 105):296. 1924.

Type collected in the Sierra de Parras, 8-9,000 ft., Coahuila, Mexico, July 1910, *C. A. Purpus 4604.* Isotype: GH.

OTHER SPECIMENS STUDIED. **Mexico. Coahuila:** Sierra Madre, 40 miles south of Saltillo, July 1880, *Palmer 37* (GH). **Nuevo Leon:** near Ajo de Agua at foot of Cerro de Potosi, 14 July 1945, *Sharp 45732* (GH).

Variety *lasiocalycina* is similar to var. *micrantha* except the buds and pedicels are pubescent instead of glabrous and the lower pedicels of the infructescences are longer than in the Mexican material of var. *micrantha.*

RAPHANORHYNCHA

The presence of an indehiscent beak on the silique is a rather rare and distinctive feature among genera of the Cruciferae of the Western Hemisphere. For example, a beaked silique is found in *Streptanthella longirostris, Thelypodiopsis incisa* and species of *Cakile,* although the fruit of the latter genus is of a distinctive type (Rodman, 1974). On the other hand, beaked siliques are characteristic of a fairly large number of genera of the Eastern Hemisphere, particularly those centered in the Mediterranean regions of Africa and the Middle East. Evidently, the sterile beak, which is usually more slender than the main body of the silique, serves to elevate the stigma in about the same way as does an elongated style in many genera of the Cruciferae. The role of stigma level in relation to pollination is usually both plant species and pollinator specific and, therefore, it can only be assessed by a narrowly directed study. Here, we only call attention to the rarity of beak presence among native American Cruciferae, and to the fact that an undescribed genus with beaked siliques has recently been discovered in Mexico. This is described below as *Raphanorhyncha crassa.*

Although one is tempted to associate *Raphanorhyncha* with such genera as *Eruca* or *Raphanus* because of its indehiscent beak, large flowers and relative succulence, it seems probable that the real relationship of the genus lies elsewhere. The silique is shaped somewhat like that of *Raphanus* but there the similarity ends. The silique of *Raphanorhyncha* has no spongy tissue within, the septum is nearly lacking and the valves are definitely dehiscent, all features distinct from *Raphanus.* It is probable that *Raphanorhyncha* arose evolutionally from a crucifer stock in which the valves of the silique fully dehisce. The characteristic beak is thought to have originated as an independent parallel evolutionary event completely unrelated to Old World genera that possess a beak.

According to the collectors, *Raphanorhyncha crassa* was locally abundant and the flowers possessed a heavy fragrance. The foliage and stems were said to be fleshy and glaucous although the glaucous appearance has been lost in the herbarium specimens we have seen, probably due to the use of heat in the drying process.

Raphanorhyncha crassa Roll. gen. et sp. nov.

Biennial or perennial glabrous fleshy herb up to 8 dm. tall; stems erect, branched, leafy, robust; lower leaves petiolate, oblong with a strong central vein, lobed to pinnatifid, 1-2 dm. long, 2-4 cm. wide, petioles on lower cauline leaves winged, middle and upper cauline leaves auriculate, dentate, becoming more entire upward, overlapping on the stems; inflorescence racemose, dense, elongating in fruit; flowers fragrant; sepals oblong, lavender with age, outer slightly saccate, inner plane, 4-5 mm. long, ca. 2 mm. wide; petals whitish, broadly obovate with a short claw, 7-10 mm. long, 5-7 mm. wide, blade nearly orbicular; glandular tissue in a continuous mold around base of single stamen filaments, poorly developed, otherwise nearly obsolete; stamens erect, included, 4-5 mm. long, paired and single nearly same length; filaments straight, slightly dilated toward base, 2-3 mm. long, anthers 2-2.5 mm. long; stigma deeply cleft, lobes over replum margins; fruiting pedicels widely spreading to gently recurved, 1.5-2 cm. long, scarcely swollen below torus; siliques spindle-shaped with a prominent indehiscent beak, compressed contrary to "septum," 1.5-3 cm. long, valves slightly keeled but not appearing so in dried material; septum obsolete with only remnants along the replum margin; ovules 15-30 per ovary; immature seeds oblong, plump, wingless; ca. 2 mm. long, ca. 1.25 mm. across; cotyledon position not observable.

Herba crassa biennis vel perennis 2-8 dm. alta, caulibus robustis glabris ramosis, foliis inferne lobatis vel pinnatifidis petiolatis, 1-2 dm. longis, 2-4 cm. latis, foliis superne auriculatis dentatis vel integris, sepalis oblongis 4-5 mm. longis, ca. 2 mm. latis, petalis late obovatis 7-10 mm. longis, 5-7 mm. latis, staminibus erectis 4-5 mm. longis, pedicellis fructiferis patentibus vel recurvatis 1.5-2 cm. longis, siliquis patentibus fusiformibus rostratis 1.5-3 cm. longis; seminibus immaturis oblongis exalatis ca. 2 mm. longis.

Holotype in the Lundell Herbarium, University of Texas, collected in fine textured alluvium of a tobosa flat, 25.5 km. north of the Camargo-Jimenez highway on the road to La Perla, 11.5 km. south of Restaurante El Herradero, lat. 26°48′ N, long. 104°51′30″ W, Chihuahua, Mexico, 2 April 1973, *M. C. Johnston, T. L. Wendt and F. Chiang 10536.* Isotypes to be distributed.

SCOLIAXON

When Payson (1924) erected the genus *Scoliaxon,* based on *Cochlearia mexicana* Wats., there were only two collections of the species known. One of these was from the state of Nuevo Leon, the other from Coahuila. Now there are ten additional collections in the Gray Herbarium, all taken within the past three years. This material extends our knowledge of *Scoliaxon mexicanus* considerably. For example, we now know that the species definitely is a perennial, not an annual as Watson suggested, and Payson was in no position to disprove. The petals are white without any question although Payson allowed for the possibility of the petals being yellowish.

Instead of being an exceedingly rare plant and very limited in its distribution as had been supposed, *Scoliaxon mexicanus* turns out to be fairly widespread within the north central region of Mexico and reasonably abundant in some places. Specimens have been seen from the states of Chihuahua, Coahuila, Nuevo Leon, San Luis Potosí and Zacatecas. It grows mostly on calcareous rocky steep slopes, canyon walls, cliffs and gravelly alluvial fans in limestone areas.

THELYPODIOPSIS

The placement of *Thelypodium linearifolium (Sisymbrium linearifolia)* in the genus *Thelypodiopsis* by Al-Shehbaz (1973) has cleared the way for a reassessment of the affinities of several species, mostly placed previously in *Sisymbrium.* Al-Shehbaz has presented convincing evidence that *Thelypodiopsis* should be maintained as a genus distinct from *Thelypodium* and *Sisymbrium.* Following this lead, it is now necessary to assemble those species recognized as being related to *Thelypodiopsis linearifolia* into the genus *Thelypodiopsis.* This is done below by presenting a key to the species followed by their listing with citations of literature and referable specimens. Payson (1922) recognized the pivotal position of species of Mexico in the general alliance represented by the widespread *Thelypodiopsis linearifolia* (as a *Sisymbrium*) and pointed to the need for their detailed study. The number of species and the amount of Mexican material available have increased dramatically since Payson's paper.

KEY TO THE SPECIES

Cauline leaves auriculate, clasping the stem.
Siliques erect or ascending; leaves entire; dentate or lobed.
Lower cauline leaves entire or at most denticulate.
Pedicels 1.5-2.5 cm. long; petals white; inflorescence dense, 2-3 cm. across; plants rhizomatous. .... 1. *T. wootonii.*
Pedicels less than 1.5 cm. long, mostly about 1 cm. long; petals lavender or white; inflorescence open, 1-1.5 cm. across; plants not rhizomatous.
Siliques 1.5-3 cm. long; pedicels erect, mostly appressed to rachis. 2. *T. versicolor.*
Siliques 4-7 cm. long; pedicels spreading to divaricately ascending.
Cauline leaves narrowly oblong, attenuated to a sharp point; petals lavender. .... 3. *T. alpina.*
Cauline leaves ovate to panduriform, obtuse; petals white. .... 4. *T. shinnersii.*
Lower cauline leaves lobed to pinnatifid.
Siliques beaked, torulose; petals 8-10 mm. long; lower leaves and stems hirsute. .... 5. *T. incisa.*
Siliques rounded at apex, not beaked, plane; petals 4-6 mm. long; lower leaves and stems glabrous. .... 6. *T. purpusii.*
Siliques arcuate; pedicels widely spreading to arching downward .... 7. *T. arcuata.*
Cauline leaves narrowed to base, cuneate or short-petioled, not auriculate.
Siliques strongly reflexed. .... 8. *T. retrofracta.*
Siliques widely spreading to ascending. .... 9. *T. linearifolia.*

NOTE: Only the Mexican and Guatemalan species are handled in the key. However, a new combination for the New Mexican species presently known as *Sisymbrium vaseyi* is required to place this species where it belongs. This is provided as follows: *Thelypodiopsis vaseyi* (Wats. ex Robins.) Roll., comb. nov., based on *Sisymbrium vaseyi* Wats. ex Robins. in Gray, Syn. Fl. N. Am. 1:138. 1895.

Lectoholotype in the Gray Herbarium, collected at Las Vegas, New Mexico, 1881, *G. R. Vasey s.n.*

SPECIMENS STUDIED. **New Mexico:** mts. west of Las Vegas, 1881, *Vasey 41* (GH); Lyon Head Trail above Cowles, upper Pecos Valley, Sangre de Cristo Mts., Aug. 3, 1934, *Goodwin 942* (GH); Cloudcroft, Otero Co., Aug. 19, 1968, *Correll and Correll 36129* (GH,TEX-LL); Windsor's Ranch, Pecos River Nat. Forest, Aug. 3, 1908, *Standley 4741* (GH); James Canyon, Sacramento Mts., Aug. 5, 1905, *Wooton s.n.* (NMC); Mescalero Reservation, July 21, 1905, *Wooton s.n.* (NMC).

1. **Thelypodiopsis wootonii** (Robins.) Roll., comb. nov., based on *Sisymbrium wootonii* Robinson, Bot. Gaz. 30:60. 1900.

Holotype in the Gray Herbarium, collected near Colonia Garcia in the Sierra Madres, Chihuahua, Mexico, alt. 7,600 ft., July 27, 1899, *C. H. T. Townsend and C. M. Barber 176.* Isotype: GH.

OTHER SPECIMENS KNOWN. **Mexico. Chihuahua:** Gonogochic, open flat of pine-oak forest, east of Creel, mncpo. de Bacoyna, 19 July 1973, 24 Aug. 1973, 19 Oct. 1973, 16 Oct. 1975, *Robert A. Bye, Jr. 4287, 4775, 5479, 7128* (GH).

2. **Thelypodiopsis versicolor** (Brandeg.) Roll., comb. nov., based on *Thelypodium versicolor* Brandegee, Univ. Calif. Publ. Bot. 4:178. 1911. *Sisymbrium versicolor* (Brandeg.) Schulz, Pflanzenreich 86 (IV, 104) 57. 1924.

Type collected in the Sierra de Parras, Coahuila, Mexico, alt. 9-10,000 ft., Oct., 1910, *C. A. Purpus 4978.* Isotype: GH.

REPRESENTATIVE SPECIMENS. **Mexico. Coahuila:** 9 km. south of Parras on Sierra Negras, scrubby woodland association of pine, juniper and oaks, July 3, 1941, *Stanford, Retherford and Northcraft 216* (ARIZ,GH,NY); 26 km. northwest of Fraile, on top of mountain covered with *Abies, Pseudotzuga,* and *Pinus,* July 16, 1941, *Stanford, Retherford and Northcraft 438* (ARIZ,GH,NY); summit of Mt. Jimulco, 13 km. east of Jimulco, woodland association of oak, pine, and juniper, June 29, 1941, *Stanford, Retherford and Northcraft 98* (ARIZ,GH); ca. 26 (air) miles southwest of Torreon in Sierra de Jimulco, ca. 6 (air) miles south southwest of La Rosita, open limestone ridge between two canyons, just below oak forest, Sept. 18, 1973, *Henrickson 13173* (GH); higher part and north slope of Sierra de la Madera, southeast and south southeast of Rancho Cerro de la Madera, Sept. 20, 1972, *Chiang, Wendt and Johnston 9420* (GH). **San Luis Potosí:** 12 km. al w. de Estacion Bernardo, Municipio de Charcas, Sept. 11, 1955, *Rzedowski 6590* (GH,ENCB).

3. **Thelypodiopsis alpina** (Standley & Steyermark) Roll., comb. nov.,

based on *Romanschulzia alpina* Standley & Steyermark, Fieldiana, Bot. 24:377. 1946. *Sisymbrium standleyi* Roll., Rhodora 58:156. 1956.

Holotype in the Field Museum of Natural History, collected between Tojquiá and Caxín Bluff, summit of Sierra de los Chuchumatanes, Dept. of Huehuetenango, Guatemala, August 6, 1942, *Julian A. Steyermark 50144.*

OTHER SPECIMENS STUDIED. **Guatemala. Huehuetenango:** near Tunima, Sierra de los Chuchumatanes, July 6, 1942, *Steyermark 48923* (F); **Quezaltenango:** Volcán Santa María, July 27, 1934, *A. F. Skutch 864* (GH).

4. **Thelypodiopsis shinnersii** (M. Johnst.) Roll., comb. nov., based on *Sisymbrium shinnersii* Johnston, Southw. Nat. 2:129, 1957, which in turn was based on *Thelypodium vaseyi* Coulter, Contrib. U.S. Nat. Herb. 1:30. 1890.

Holotype in the United States National Herbarium, collected near Rio Grande City, Texas, 1887, *G. C. Neally 188* (12). Tracing of holotype: GH.

This species occurs in the lower Rio Grande Valley of Texas and in Mexico. The Mexican specimens I have studied are as follows, all in the state of Tamaulipas: region of Rancho Las Yucas, ca. 40 km. north northwest of Aldama, Municipio de Aldama, July 25, 1957, *R. L. Dressler 2014* (GH); same locality, Oct. 16, 1957, *R. L. Dressler 2427* (GH); dry bank of small creek, 9 miles south of Ciudad Victoria, Feb. 9, 1961, *Ronald L. McGregor 16296* (GH); mts. along route 70, ca. 6 miles south of Ciudad Victoria, 6 April 1961, *King 4510* (US).

5. **Thelypodiopsis incisa** Rollins sp. nov.

Annual or biennial, sparsely pubescent with spreading trichomes below, glabrous above; stems erect, one to several from base, branched, 4-6 dm. tall, strictly basal rosette of leaves unknown, lower cauline leaves with erect, simple trichomes, deeply pinnatifid, incised, up to 1 dm. long, terminal lobe larger than lateral, petioles winged, lobed and those of lowermost leaves with small auricles at base; lower middle, middle, and upper cauline leaves strongly auricled and clasping stem, incised or uppermost entire, glabrous, ovate to broadly oblong, acute, 3-5 cm. long, with a strong central nerve; inflorescences racemose, terminating each branch; sepals turning lavender, oblong, 4-5 mm. long, ca. 1-5 mm. wide, outer pair saccate, boat-shaped, narrowed above, inner pair flat, blunt at apex; petals lavender, narrowly lingulate, 8-10 mm. long, 3-4 mm. wide, not differentiated into blade and claw; stamens strongly tetradynamous, paired stamens erect, 6-7 mm. long, single stamens curved upward, 4-5 mm. long; anthers ca. 1.5 mm. long, straight; fruiting pedicels 6-9 mm. long, divaricate, not expanded toward apex, straight; siliques erect to divaricate nearly terete to slightly flattened parallel to septum, not nerved, tapering above and below, somewhat torulose, 3.5-5 cm. long; styles ca.

2 mm. long; stigma rarely cleft, very slightly lobed over replum margin; immature seeds wingless, oblong, occupying full width of silique, 1.75-2 mm. long.

Herba annua vel biennis, caulibus erectis ramosis 4-6 dm. altis, foliis pinnatifidis vel incisis inferne lobatis superne auriculatis ovatis vel late oblongis 3-5 cm. longis, sepalis oblongis purpureis 4-5 mm. longis, petalis purpureis anguste lingulatis 8-10 mm. longis, pedicellis fructiferis divaricatis 6-9 mm. longis, siliquis erectis vel divaricatis plus minusve teretibus torulosis 3.5-5 cm. longis, ca. 1.25 mm. latis, stylis ca. 2 mm. longis; seminibus immaturis oblongis immarginatis 1.75-2 mm. longis.

Holotype in the West Texas State University Herbarium, collected on a rocky hillside in a mixed shrub community, ca. 80 miles north of Saltillo along highway 57, Coahuila, Mexico, March 23, 1970, *Larry C. Higgins 2717*. Isotype: ENCB.

One of the most distinctive features of *Thelypodiopsis incisa* is the definite, sterile beak narrowing to the apex of the silique. In this respect, the species is different from all other Mexican species of the genus. It is nearest in its relationship to *T. purpusii* but differs from that species in having much larger flowers, torulose instead of plane siliques, a beak tipped with a prominent style about 2 mm. long instead of no beak and a style about 1 mm. long as in *T. purpusii*. The latter also has narrower, nearly terete instead of flattened siliques and usually white instead of the lavender petals that are characteristic of *T. incisa*.

6. **Thelypodiopsis purpusii** (Brandeg.) Roll., comb. nov., based on *Thelypodium purpusii* Brandegee, Zoe 5:232. 1906. *Sisymbrium purpusii* (Brandeg.), O. E. Schulz, Pflanzenr. 86 (IV, 105) 58. 1924.

Isotype: Sierra de Parras, Coahuila, Mexico, March, 1905, *C. A. Purpus 1329* (GH).

SPECIMENS STUDIED. **Mexico. Coahuila:** Sierra Pata Galana, Feb., 1905, *Purpus 1329A* (GH). **U.S.A. Texas:** head of Fresno Canyon, Big Bend Ranch, about 50 miles east of Presidio, Presidio Co., April 20, 1961, *Rollins 61174 and Correll* (GH); McCormick Ranch, near Fresno Canyon, Presidio Co., March 1, 1959, *M. C. Johnston 3736 and Warnock* (GH). **New Mexico:** about half-way up the North Sister, Tres Hermanas Mts., Luna Co., April 13, 1973, *Spellenberg 3002* (GH,NMC,NY,WTS).

7. **Thelypodiopsis arcuata** (Roll.) Roll., comb. nov., based on *Sisymbrium arcuatum* Rollins, Rhodora 62:58. 1960.

Holotype in the Gray Herbarium, collected 1–2 miles southwest of Pablillo, Nuevo Leon, Mexico, July 21, 1958, *D. S. Correll and I. M. Johnston 19941*. Isotype: TEX–LL.

SPECIMEN STUDIED. **Mexico. San Luis Potosí:** Sierra de Alvarez, cerco del Punta Huerta, Oct. 27, 1954, *Rzedowski 5211* (GH).

8. **Thelypodiopsis retrofracta** (Roll.) Roll., comb. nov., based on *Sisymbrium retrofractum* Rollins, Rhodora 59:66. 1957.

Holotype in the Gray Herbarium, collected on mountain, 18 km. west of Concepcion del Oro, Coahuila, Mexico, July 22, 1941, *Stanford, Retherford and Northcraft 570.*

SPECIMEN STUDIED. **Mexico. Zacatecas:** limestone rocks below Aranzazu, Sierra Madre Oriental, July 19, 1934, *Pennell 17443* (GH).

9. **Thelypodiopsis linearifolia** (Gray) Al-Shehbaz, Contrib. Gray Herb. no. 204, p. 140, 1973, based on *Streptanthus linearifolius* Gray, Mem. Am. Acad. 4:7. 1849. *Pachypodium linearifolium* Gray, Proc. Am. Acad. 6:188. 1866. *Thelypodium linearifolium* (Gray) Wats., Bot. King's Exped. 25. 1871. *Hesperidanthus linearifolius* (Gray) Rydb., Bull. Torr. Bot. Club 34: 434. 1907. *Sisymbrium linearifolium* (Gray) Payson, Univ. Wyo. Publ. Sci. 1:19. 1922.

Holotype in the Gray Herbarium, collected between Santa Fe and Las Vegas, New Mexico, July, Aug., 1847, *Fendler 24.* Isotype: GH.

REPRESENTATIVE SPECIMENS FROM MEXICO ONLY. **Chihuahua:** 3 km. north of Rancho Las Vacas on road to Rio Grande (Cajones), east of Sierra San Martin de Borracho, June 15, 1973, *Johnston, Wendt and Chiang 11334A* (TEX–LL); northwestern end of the Sierra del Diablo, ca. lat. 27°20′ N, July 30, 1941, *Stewart 988* (GH); near Colonia Garcia in the Sierra Madres, July 19, 1899, *Townsend and Barber 147* (ENCB,GH,NMC); Sierra del Pulpito, 11.5 km. north of Rancho La Virgen, Oct. 25, 1972, *Wendt, Chiang and Johnston 9887a* (TEX); off Mex. Hwy. 45, 14.4 mi. north of Chihuahua, Oct. 19, 1974, *Rollins and Roby 74188* (GH); Canon de la Madera, southeastern flank of Sierra Rica, Sept. 25, 1942, *Stewart 2518* (GH). **Coahuila:** Canyon de Tinaja Blanca, west of Santa Elena Mines, Aug. 14, 1940, *Johnston and Muller 255* (GH,TEX); vicinity of La Noria, Sierra del Pino, Aug. 20–26, 1940, *Johnston and Muller 626* (GH,TEX–LL); Canon de Sentenela, Hacienda Piedra Blanca, Villa Acuna, July 7, 1936, *Wynd and Mueller 581* (ARIZ,GH); along Coahuila Hwy. 53, ca. 2 miles east of El Puesto Tres Caminos, northwest of Muzquiz, Aug. 3, 1971, *Reveal 2573, Hess and Kiger* (MEXU,US). **Sonora:** Rancho de la Nacha, region of the Rio de Bavispe, Aug. 15, 1941, *White 3938* (ARIZ,GH); Puerto de los Aserraderos, Aug. 4–9, 1940, *White 3140* (ARIZ,GH); Guadaloupe Canon, Aug. 1852, *Thurber 767* (GH). **Durango:** northwest third of Sierra del Rosario, June 25, 1973, *Johnston, Wendt and Chiang 11459A* (TEX–LL); Penon de Covadonga, cerca de Yerbanis, Municipio de Penon Blanco, Nov. 1, 1960, *Paray 3122* (MEXU); Santiago Papasquiaro, April and Aug., 1896, *Palmer 432* (GH); Tejamén, Aug. 21–27, 1906, *Palmer 487* (GH); 18 miles west of Durango, Mex. Hwy. 41, Sept. 9, 1966, *Breedlove 15495* (GH). **Zacatecas:** 15 miles northeast of Estacion Camacho on northwest slopes near granitic summit of Pico de Teyra, Sept. 23, 1973, *Henrickson*

13462 (GH). **San Luis Potosí:** ca. 23 miles north of Charcas, Sept. 5, 1971, *Henrickson B6396* (GH).

THELYPODIUM

In the recent monograph of *Thelypodium* by Al-Shehbaz (1973), two species, *T. wrightii* and *T. paysonii*, were listed as occurring in Mexico. Our study shows that a third species, formerly treated as *Sisymbrium longipes*, really belongs in *Thelypodium*. This determination has been made possible by the availability of several new collections and others not previously available for study. When *S. longipes* was originally described (1957), I was convinced it was somewhat related to the species now being called *Thelypodiopsis linearifolia* and therefore should follow whatever generic disposition was made of that species. However, on further study of really good flowering material, which was not available earlier, the nearly equal spreading stamens with horizontally spreading anthers make the flower more like that of *Thelypodium* than *Thelypodiopsis*. Also, the stigma is scarcely lobed which is another *Thelypodium* feature.

Following is a key to the species of *Thelypodium* presently known from Mexico.

Leaf-blades ovate, abruptly narrowed to a naked petiole; leaves entire or at most with slightly wavy margins. . . . . 1. *T. longipes*.
Leaf-blades elongated, gradually narrowed to a winged petiole or deeply pinnatifid; leaves dentate to pinnatifid.
  Leaf-blades narrowly lanceolate, narrowed above and below, entire, remotely dentate or simply lobed; filaments and petal claws glabrous. . . . . 2. *T. wrightii*.
  Leaf-blades broadly oblong in outline, deeply lobed; lobes dentate; filaments and petal claws papillose. . . . . 3. *T. paysonii*.

1. **Thelypodium longipes** (Roll.) Roll., comb. nov., based on *Sisymbrium longipes* Rollins, Rhodora 59:65–66. 1957.

Holotype in the Gray Herbarium, collected above La Mina, Sierra Madre Mts., near Monterrey, Nuevo Leon, Mexico, July 23, 1933, *C. H. and M. T. Mueller 548*. Isotype: F.

OTHER SPECIMENS STUDIED. **Mexico. Nuevo Leon:** Sierra Madre Mts., *C. H. and M. T. Mueller* 549 (MEXU). **Coahuila:** Sierra de Jimulco and up to 3 km north of Mina San Jose which is 8 km northeast of Estacion Otto, lat. 25°8′30″ N, long. 103°13′30″ W, 27 Sept. 1972, *Chiang, Wendt and Johnston 9548e, 9552j* (TEX); mid-canyon in disturbed area near the old first lumber campsite, Canyon de la Hacienda, Sierra de la Madera, ca. 35 (air) miles west of Cuatro Cienegas, near 27°04′N, 102°25′ W, Aug. 6, 1973, *Henrickson 11985 and Wendt* (GH); Canon los Almos, west fork just above junction with east fork, Sierra de la Madera, mnpos. Cuatro Cienegas and Ocampo, Aug. 17, 1975, *Wendt and Lott 1185* (ASU).

2. **Thelypodium wrightii** Gray, Smithson. Contrib. (Pl. Wright.) 3:7.

1852. *Stanleyella wrightii* (Gray) Rydb., Bull. Torr. Bot. Club 34:435. 1907.

Holotype in the Gray Herbarium, collected at the Pass of the Limpia, Jeff Davis Co., Texas, August, 1849, *C. Wright 7.*

SELECTED SPECIMENS STUDIED. **Mexico. Chihuahua:** Canon de la Madera, southeastern flank of Sierra Rica, Sept. 25, 1942, *Stewart 2500* (GH,TEX–LL); Poza de Villa, 3 miles west of Coahuila line, road from Castillon to Mula, via S. Salvador and Piramide, Sept. 21–22, 1940, *Johnston and Muller 1387* (GH,TEX–LL); near Chihuahua, Oct. 1885, *Pringle 294* (GH). **Coahuila:** Hacienda Piedra Blanca, Canyon de Sentenela, Sierra del Carmen, Villa Acuna, July 9, 1936, *Wynd and Mueller 621* (ARIZ,GH,MO,US); 2–10 miles north of camp at La Noria, Sierra del Pino, Aug. 22, 1940, *Johnston and Muller 594* (GH,TEX–LL); Cañon de la Barrica, Sierra de la Madera, mnpos. Cuatro Cienegas and Ocampo, Aug. 29, 1975, *Wendt and Lott* (ASU); canyon at San Antonio de los Alamos, Sierra de San Antonio, Sept. 2–3, 1940, *Johnston and Muller 886* (GH,TEX–LL). **Baja California Norte:** Cantillas Mts., Sept. 13, 1884, *Orcutt 945* (GH); road north of Corral de Sam, Sierra San Pedro Martir, near 31°04′ N, 115°34′ W, 30 July 1970, *Moran 18050* (GH). **Hidalgo:** Cerro Grande, al SE de Epazoyucan, 10 Sept. 1972, *Rzedowski 29325* (GH).

3. **Thelypodium paysonii** Roll., Rhodora 59:61–64. 1957.

Holotype in the Gray Herbarium, collected at Cañon de Jara, east of Socorro, about 30 km. west of Cuatro Cienegas, Coahuila, Mexico, Feb. 1–15, 1941, *Schroeder 12.*

OTHER SPECIMENS STUDIED. **Mexico. Coahuila:** canyon, east side of Sierra de las Margaritas, about 13 km. north of Las Margaritas, 13 March 1973, *Johnston, Wendt and Chiang 10349C, 10361A* (TEX–LL); Torreon, 1903, *Purpus 130* (GH); 44 miles east of Torreon, Nov. 27, 1958, *Rollins and Tryon 58296* (GH); Sierra de Parras, March 1905, *Purpus 1028* (GH). **Durango:** 48 miles southwest of Torreon, Nov. 26, 1958, *Rollins and Tryon 58291* (GH); 5 miles along road from Hidalgo del Parral, Durango, toward El Palmito, Nov. 18, 1967, *Kimnach and Brandt 1104* (US).

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A REVISION OF THE GENUS CYATHEA

ROLLA TRYON

Cyathea is a genus of forty neotropical species primarily found in the mountains of the Greater Antilles, Central America, and tropical South America. It is the dominant element in the tree fern flora of cloud forests and is the most frequent genus of Cyatheaceae occurring at higher altitudes. Two species grow at 4200 m in the Andes, the highest altitude recorded for the family.

The genus is here defined in a restricted sense, following my earlier study of the generic classification of the Cyatheaceae (Tryon, 1970). The primitive species of *Cyathea,* with a complex leaf architecture and hemitelioid indusium, are related to *Trichipteris* and to *Cnemidaria.* Recent intensive studies, including species revisions of all three genera, have served to strengthen the earlier generic proposals. *Trichipteris* (Barrington, 1974), *Cyathea,* and *Cnemidaria* (Stolze, 1974) have emerged more clearly as separate evolutionary lines with truly intermediate species few or lacking.

Trichipteris is technically separated from *Cyathea* by the absence of an indusium, while *Cyathea* has a well-developed or at least small (hemitelioid) indusium. Some species of *Trichipteris* have lamina scales regularly associated with the sorus and these scales may be mistaken for indusia. They are, however, thin and clearly cellular, narrowed basally and attached at one point, attenuate at the apex, and often erect. The smallest indusia in *Cyathea* are somewhat thickened, with the cells obscured, broadly attached at the base, rounded at the apex, and appressed to the leaf tissue. The closest relation between *Cyathea* and *Trichipteris* is seen in *Cyathea multiflora* and *Trichipteris nigra* and (or) *T. Schiedeana.*

Stolze (1974) has clarified the definition of *Cnemidaria* and *Cyathea* by removing from *Cnemidaria* a few species that I had earlier placed there which lack large-porate spores. These and some other related species are now seen to represent an independent line of lamina reduction in *Cyathea.* The closest relationship with *Cnemidaria* is evidently represented by *Cyathea* species with a more complex lamina.

KEY TO SCALY GENERA OF CYATHEACEAE

a. Petiole scales structurally conform, the cells of the body similar in orientation, shape, and (usually) in size and color, or a single row of cells at the edge may be differentiated as cilia or denticulations. . . . . *Sphaeropteris.*

a. Petiole scales structurally marginate, with a narrow multicellular marginal band to a broad margin of cells different in orientation, size, and (usually) in shape and color from those of the central portion. . . . . b.

  b. Petiole scales with a dark, opaque apical seta; spores 16 in a sporangium, rarely 64. . . . . c.

    c. Petiole lacking spines, or with corticinate spines, each bearing (when young) a scale at the apex, croziers lacking spines. . . . . *Alsophila.*

    c. Petiole with squaminate spines, many large and black, with a slender apex, these

also present on the croziers, petiole scales borne on the petiole surface. . *Nephelea.*
b. Petiole scales lacking an apical seta, the apex rounded to filamentous; spores 64 in a sporangium, rarely 16 or 32. . . . . d.
d. Indusium absent. . . . . *Trichipteris.*
d. Indusium present. . . . . e.
  e. Spore exine lacking apertures or with variously distributed small pits or pores; costae and costules with adaxial trichomes; veins free, or in two species sometimes areolate, in two species the lamina 1-pinnate-pinnatifid and the petiole either alate or densely long-pubescent . . . . *Cyathea.*
  e. Spore exine with three large equatorial pores, often also with smaller pits or pores; costae and costules lacking trichomes on the adaxial side, or rarely present; basal veins usually forming areolate, or if free then connivent to the sinus, or in one species running to the margin above the sinus and the lamina 1-pinnate-pinnatifid, the petiole nearly glabrous and non-alate. . . . . *Cnemidaria.*

ECOLOGY AND GEOGRAPHY

Cyathea is predominently a genus of the cloud forest, although it is also well-represented in wet montane forests. The cloud forest environment, usually developed on steep mountain slopes, provides nearly constant high humidity and considerable light since the tree fern crowns occupy part of the relatively open canopy. Several species, such as *C. pallescens, C. suprastrigosa,* and *C. caracasana* also grow at higher altitudes in *Chusquea* thickets and in subparamo scrub. Other species grow in lowland rain forest below 500 m, but only five of these, including *C. conformis, C. decorata* and *C. parva* are wholly lowland species. The lowland forest habitat is different from the cloud forest in providing a significant dry season or dense shade, as well as higher temperatures. Some species occasionally grow in other, specialized habitats, for example, *C. parvula* in wet savannahs, *C. Harrissii* in wet pinelands, *C. platylepis* among sandstone rocks, and *C. Delgadii* in gallery forest. Among the 15 species that grow at altitudes of 500 m or less, 11 of them have hemitelioid indusia. The significance of this correlation is not clear since these 11 species are morphologically quite diverse and might be expected to have considerable ecological differences.

Cyathea arborea is a pioneer species, invading landslides where it frequently establishes handsome colonies. It also invades artificial barren sites, such as road cuts and road fills. Since the many cloud forest species usually grow on steep mountain slopes, they probably also grow in landslide areas. However, little is known about their successional position. Some may be pioneers, as *C. arborea,* while others may enter the new community later.

The distribution of the genus (Map 1) correlates closely with the mountains of tropical America. *Cyathea* is notably absent from the Yucatan Peninsula, from the Llanos region of Colombia and Venezuela, the Orinoco Basin, most of the Amazon Basin, and from the Bolivian–Paraguayan lowlands. Table 1 and Map 2 provide information on the occurrence of species, varieties and endemics in countries and regions. The center of diversity is in Venezuela and Colombia, south to Peru. In this region there are 31 taxa and 19 endemics. Colombia is the country with the most diverse *Cyathea* flora, with 22 taxa and 6 endemics. Ecuador seems to be underrepresented. It is usually rich in species of cloud forest groups; for example, in *Hymenophyllum* section *Sphaerocionium* (Morton, 1947), there are 19 species in Colombia, 16 in Ecuador and 22 in Peru. It is expected that additional collecting of tree ferns in Eucador will increase the number to 15 or more.

In southeastern Brazil there is a single species, *Cyathea Delgadii*, and only three species occur in Mexico and Guatemala. The paucity of species in these regions is peculiar for there are considerable areas of wet montane

MAPS 1–2. 1, Distribution of Cyathea (occurrence on isolated islands on Map 2); 2. Numbers of species and varieties, and number of endemics in countries and regions (see Table 1), the left or single bar is the number of taxa (1–22), the right bar is the number of endemics (1–6).

forest and also smaller ones of cloud forest; previous adverse climates may account for the limited number. The situation is probably similar to that in west tropical Africa, where a history of vegetational and climatic change evidently occurred and where there are only three species of Cyatheaceae (Alston, 1959).

There are seven species having wide ranges of 3000 miles (4800 km) or more in extent. They are frequent species with rather broad altitudinal ranges. Successful migration of species is perhaps most dependent on their broad ecological tolerance, as may be seen in those which are the source for populations occurring on isolated islands. These insular species are related to the three most widely distributed continental species: the Cocos Island endemics, *Cyathea Alphonsiana* and *C. notabilis* to *C. multiflora;* the Galapagos endemic, *C. Weatherbyana* to *C. andina;* and *C. Delgadii* of Ilha Trinidade is widespread in South America.

TABLE 1. GEOGRAPHIC OCCURRENCE OF TAXA AND **endemics** OF CYATHEA

Mexico to Nicaragua: 3 taxa, 1 endemic. 1. multiflora, 20b. divergens var. **Tuerckheimii,** 29. fulva.

Costa Rica and Panama: 10 taxa, 3 endemics. 1. multiflora, 9. petiolata, 10. **impar,** 12. conformis, 20a. divergens var. divergens, 29. fulva, 32. **suprastrigosa,** 33. Delgadii, 36e. caracasana var. **Maxonii,** 38. gracilis.

Cocos Island: 2 endemic species. 4. **Alphonsiana,** 5. **notabilis.**

Greater Antilles: 8 taxa, 4 endemic. 2. andina, 6. **parvula,** 17. arborea, 30. **Harrisii,** 31. **furfuracea,** 35. **dissoluta,** 36c. caracasana var. caracasana, 38. gracilis.

Lesser Antilles, Trinidad and Margarita: 2 species, 1 endemic. 17. arborea, 34. **tenera.**

French Guiana, Surinam and British Guiana: 3 taxa, no endemics. 2. andina, 20a. divergens var. divergens, 33. Delgadii.

Venezuela: 14 taxa, 2 endemic. 2. andina, 7. platylepis, 11. **Steyermarkii,** 15. speciosa, 20a. divergens var. divergens, 22. **simplex,** 29. fulva, 33. Delgadii, 36. caracasana vars. a, b, c, d. 37. Lechleri, 39. ebenina.

Colombia: 22 taxa, 6 endemic. 1. multiflora, 2. andina, 7. platylepis, 9. petiolata, 12. conformis, 13. **decorata,** 14. **parva,** 15. speciosa, 16. **Haughtii,** 18. **Alstonii,** 19. **peladensis,** 20a. divergens var. divergens, 21. pallescens, 25. **straminea,** 29. fulva, 33. Delgadii, 36. caracasana vars. a, b, c, d, 38. gracilis, 39. ebenina.

Ecuador: 9 taxa, 1 endemic. 1. multiflora, 2. andina, 20a. divergens var. divergens, 21. pallescens, 23. **corallifera,** 36. caracasana vars. a, b, c, d.

Galapagos Islands: 1 endemic species. 3. **Weatherbyana.**

Peru: 13 taxa, 5 endemic. 1. multiflora, 2. andina, 8. **Vilhelmii,** 20a. divergens var. divergens, 21. pallescens, 26. **Ruiziana,** 27. **microphylla,** 28. **multisegmenta,** 33. Delgadii, 36a. caracasana var. boliviensis, 37. Lechleri, 39. ebenina, 40. **Dudleyi.**

Bolivia: 7 taxa, 1 endemic. 1. multiflora, 2. andina, 21. pallescens, 24. **boliviana,** 33. Delgadii, 36a. caracasana var. boliviensis, 37. Lechleri.

Argentina, Paraguay and Brazil: 3 species, no endemics. 1. multiflora, 2. andina, 33. Delgadii.

Ilha Trinidade: 1 species, not endemic. 33. Delgadii.

SPECIATION

In the scaly Cyatheaceae, speciation is based mainly on eco-geographic isolation and on evolutionary migration (Tryon, 1971, 1972). There are examples of speciation by geographic isolation in the island endemics: *Cyathea Alphonsiana, C. notabilis* and *C. Weatherbyana.* Others involve geographic isolation, possibly preceded by evolution during migration: *C. divergens* var. *Tuerckheimii* in Guatemala and Mexico, from var. *divergens* in Costa Rica; *C. caracasana* var. *Maxonii* of Costa Rica from the *C. caracasana* complex in Colombia; and probably *C. tenera* of the Lesser Antilles, and *C. furfuracea* of the Greater Antilles, from *C. Delgadii* of South America. The relatively uniform collections of *C. multiflora* from Nicaragua to British Honduras possibly indicate a migration from the more diverse populations of the species in Costa Rica.

There are 13 local endemics in Colombia south to Bolivia where the continuity of habitats suggests that geographic isolation is not a factor in their endemism. Tryon and Gastony (1975) have proposed the hypothesis that such local endemics have become ecologically specialized to the extent that other suitable environments are either absent or exist only as small areas distant to the present range.

Most species of *Cyathea* are morphologically and eco-geographically distinct, thus their classification is relatively clear. This is especially apparent in the species having hemitelioid and cyatheoid indusia. These distinctive species probably represent relatively early speciation, which would be consistent with their primitive position in the genus. Among the more advanced species, with sphaeropteroid indusia, there are two groups in which speciation appears to be more recent. There are 12 taxa within these groups (species 29–34, 35–36) that are not clearly differentiated due to intergrading variation. Pleistocene climatic changes may have been instrumental in generating migrations and disjunctions leading to the evolution of these taxa.

Amphiploid speciation does not seem to be a recent phenomenon in *Cyathea,* although several putative hybrids (see below) suggest that it might be present. The four species that have been determined cytologically all have a chromosome number of n=69: *Cyathea arborea, C. furfuracea, C. Harrisii,* and *C. parvula* (Walker, 1966). Considerably more cytological sampling is needed before the status of polyploidy in *Cyathea* can be known. The relatively high number of n=69 also suggests polyploidy, but this probably occurred very early in the evolution of the family since all of the scaly genera of Cyatheaceae share this number.

HYBRIDS

Two hybrids have been recently recognized by Conant (1975) in the Cyatheaceae on the basis of an analysis of several characters and field observations on the hybrids and parental species in the same site. He also discusses five other putative hybrids in *Alsophila* and *Nephelea.* These proposals provide a new perspective on some of the described species in the family. In addition to the hybrid, proposed by Conant, involving

Cyathea arborea and *Cnemidaria horrida (Hemitelia Wilsonii)*, I am recognizing nine others, with varying degrees of confidence. On the basis of the evidence, an interpretation of them as hybrids seems more realistic than treating them as variants of a species or recognizing them as endemics. Putative hybrids present special problems that require careful field study. Hybrids have not been suggested involving parental species that are similar in their indusium and laminar structure. However, such hybrids may also exist, perhaps with some frequency, but they cannot be identified from herbarium materials at hand. Discriminating field study and collecting will be required before the frequency of hybridization in the genus is known.

MORPHOLOGY

The petiole always bears large scales at the apex of spines, where they are usually caducous, or they may be on smaller emergences. In addition to these large *petiole scales*, there is usually also a covering of small to minute scales on the petiole surface, especially on the abaxial side. The large scales, which have characters of systematic importance, are on the abaxial side of the petiole. Other large scales are borne on the adaxial side. The basal scales, especially, are longer and narrower than those on the abaxial side. They tend to be similar in many species, and often lack the differentiated margin characteristic of the genus.

The *body* of the petiole scale includes the whole structure except for *peripheral processes* such as cilia, teeth or setae. The *edge* of the scale is the outer row of cells which bears the peripheral processes. The *margin* of the scale is the cellularly differentiated part of the body on each side of the rather uniformly elongate-celled *central portion*. Scales that are uniformly colored are *concolorous* (Fig. 1). They are usually whitish. Light brown scales may be *nearly concolorous* (Fig. 2), the margins being only slightly lighter than the central portion. Scales that have the margins definitely lighter in color than all or part of the central portion are *bicolorous*. If the central portion is dark and the margins are light, the scale is *concordantly bicolorous* (Fig. 3), while if the light color of the margin extends into the central portion, the scale is *discordantly bicolorous* (Fig. 4).

The large petiole scales are best examined on a crozier because all details of the cellular construction are present at this young state. The base of a recently expanded leaf will also usually have scales in good condition. However, the scales on older leaves are more or less eroded, especially the more delicate margins, or they may have been lost.

The small scaly indument on the petiole surface is called *scurf*, and when it is composed of definite, although small, scales these are referred to as *large scales of the scurf* (Figs. 5, 6). The minute scales of the scurf are referred to as *squamellae* (Figs. 7, 8). Either kind may be *crested* (Fig. 6) and the squamellae may be strongly dissected and *trichomoid* (Fig. 8).

The petiole scurf is best examined in recently expanded leaves. It is usually not fully developed in croziers, and it often becomes abraded in older leaves.

The pinnae and pinnules vary from sessile to very long-stalked. In some species the length of the stalk relative to the width of the basal segment is a useful character. If the stalk is shorter than the width of the basal segment of the pinnule, the pinnule is referred to as *short-stalked*. It is *long-stalked* when the stalk is definitely longer than the width of the basal segment. Short- and long-stalked pinnae are defined in a similar manner.

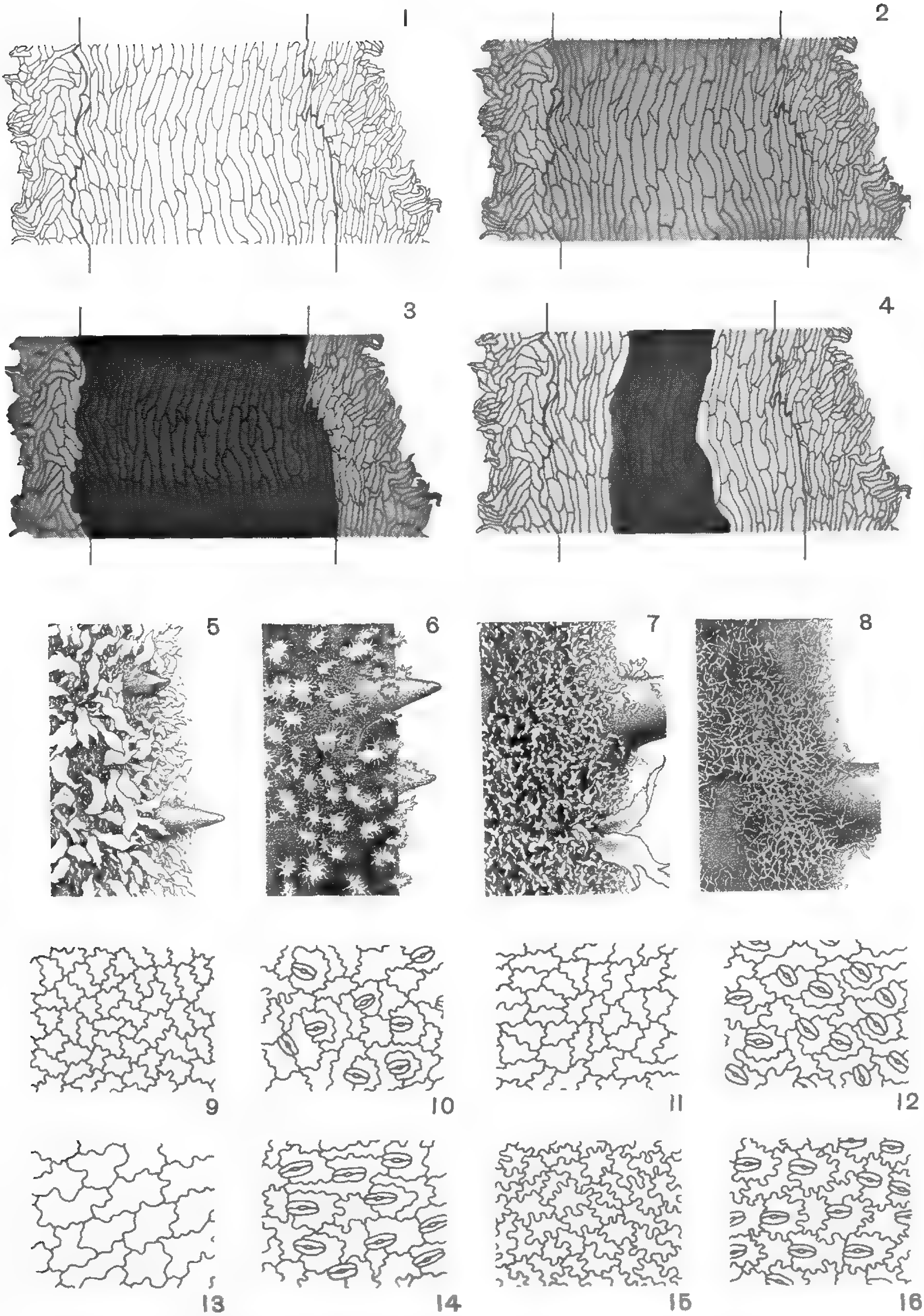
The term *pubescence* or *pubescent* is applied in reference to the under surface (abaxial side) of segments or axes, such as the costa and pinna-rachis, when there is a sufficient number of trichomes to form a uniformly distributed indument. This may be dense to somewhat sparse. If the trichomes are scattered, reference is made to their individual characteristics.

The terminology applied to the scales on the under surface of the pinnae is used in a manner similar to that for the petiole scales.

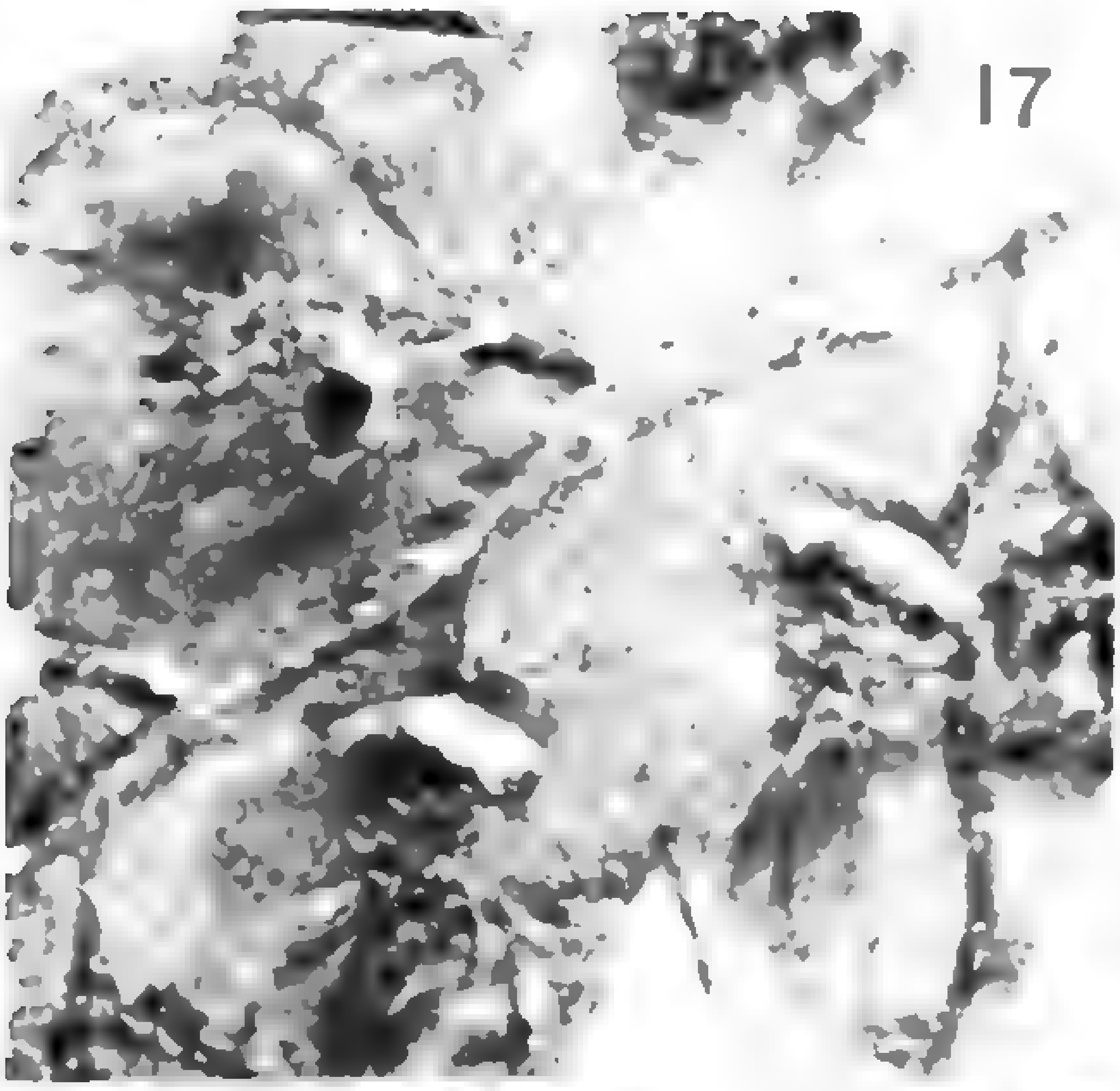
The lower epidermis in *Cyathea* is basically of a uniform type (Figs. 10, 12, 14, 16). The stomates are nearly surrounded by a subsidiary cell with strongly undulating walls. They conform to the polocytic pattern of Van Cotthem (1970). The upper epidermis (Figs. 9, 11, 13, 15) usually shows greater differences in the size of cells and in the undulations of the walls.

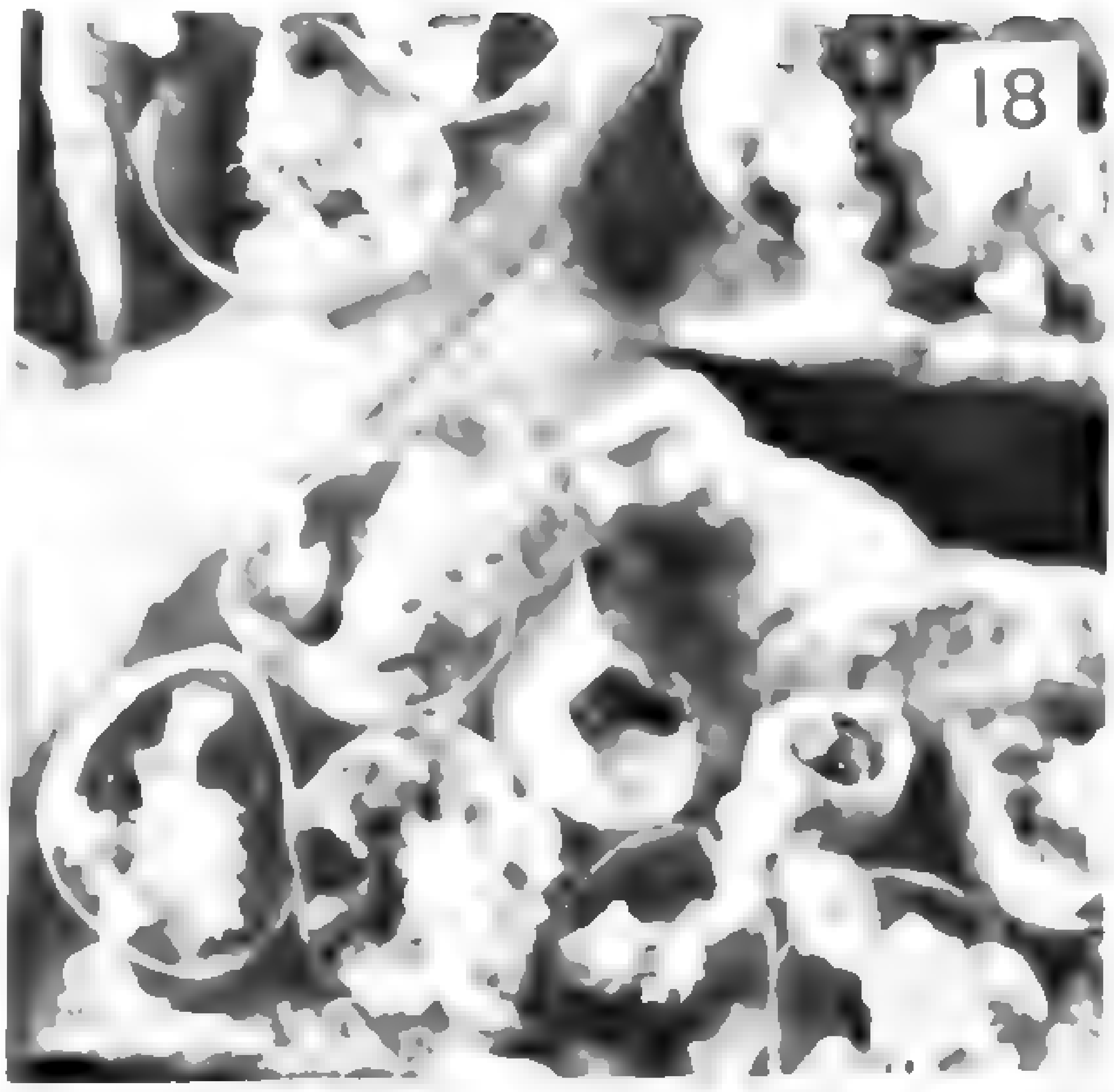
The position of the sorus is sometimes an important character, especially in species with hemitelioid indusia. The following terms are applied: the *costal* position is very near the costa; *subcostal* is slightly removed; *medial* is about half the distance between the costa and the segment margin; *supramedial* is somewhat beyond this; and *submarginal* sori are close to the margin.

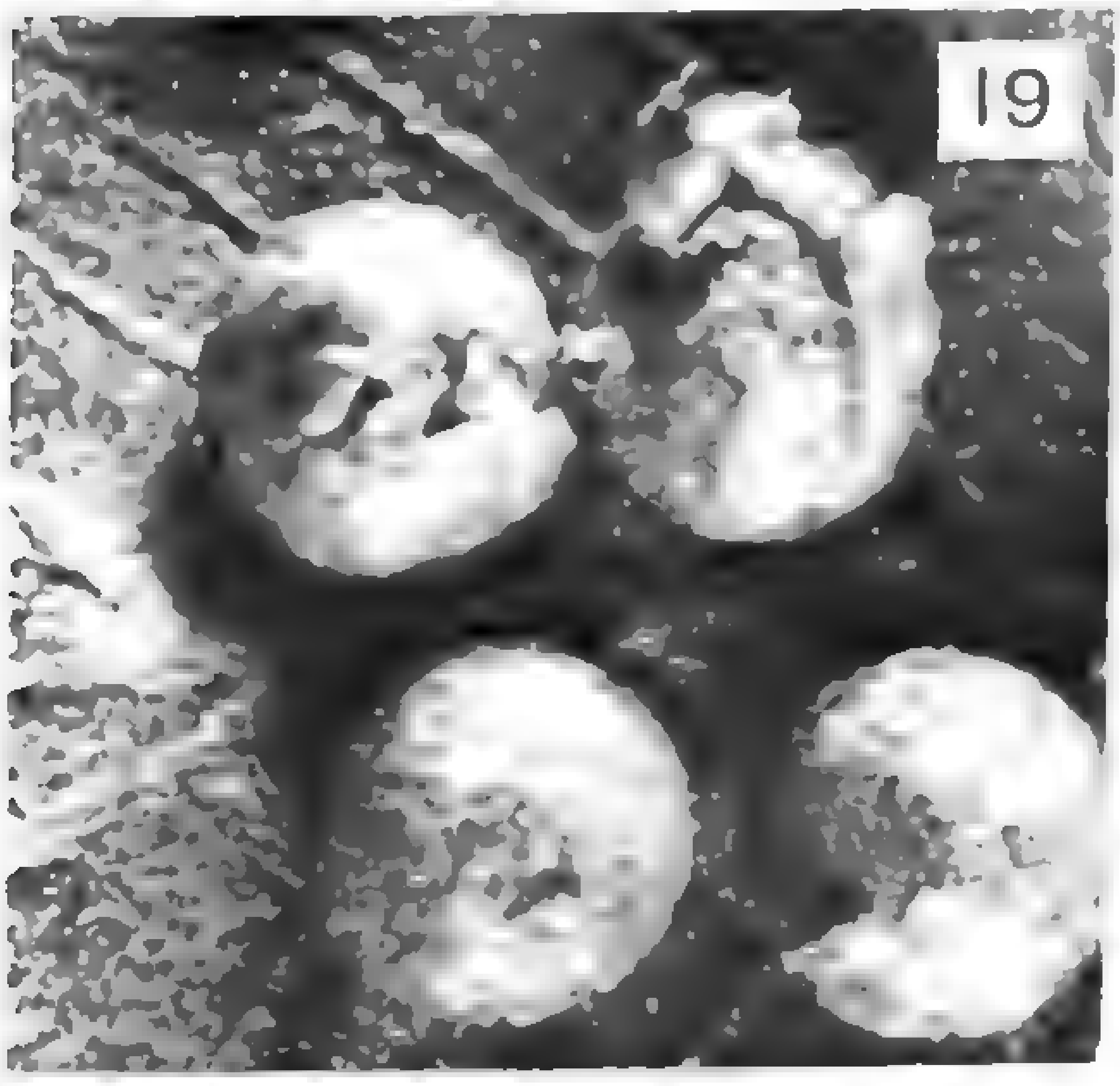
The indusium is considered to be *hemitelioid* (Fig. 17) if it partially surrounds the base of the receptacle. Small hemitelioid indusia are referred to as *minute*. This term seems preferable to the more descriptive one, "scale-like," previously proposed (Tryon, 1970). That term may cause some confusion with the true laminar scales in *Trichipteris* which may be mistaken for indusia. *Cyatheoid* indusia completely surround the base of the receptacle, but do not completely envelop the sorus. Four types of cyatheoid indusia are recognized: *discoid*, if nearly flat; *meniscoid*, if lens-shaped with somewhat raised edges (a shallow saucer); *cyathiform*, if a cup (Fig. 18), usually enveloping about half of the sorus; and *urceolate*, if taller, open, and somewhat contracted at the apex. *Sphaeropteroid* indusia are globose, completely envelop the sorus (Fig. 19) and often have an apical umbo. In some species of *Cyathea* the sphaeropteroid indusium is very fragile and ephemeral, for example, in *C. straminea*, *C. pallescens*, and *C. caracasana* var. *caracasana*. In them the mature indusium breaks into fragments that fall away, leaving only an irregular basal portion of the indusium, if any, attached to the receptacle. Relatively young sori are required to observe the presence of the indusium in these species.

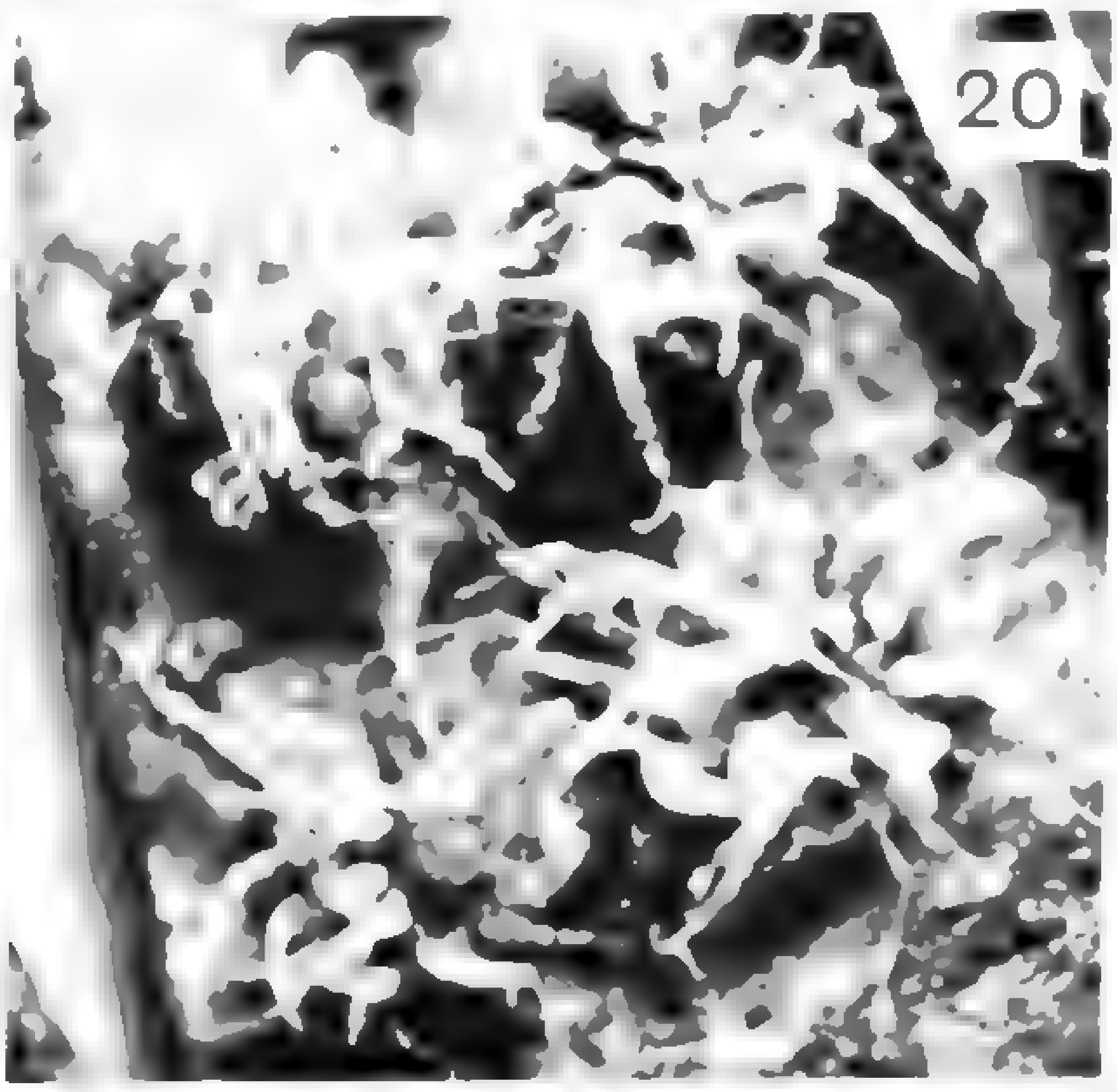


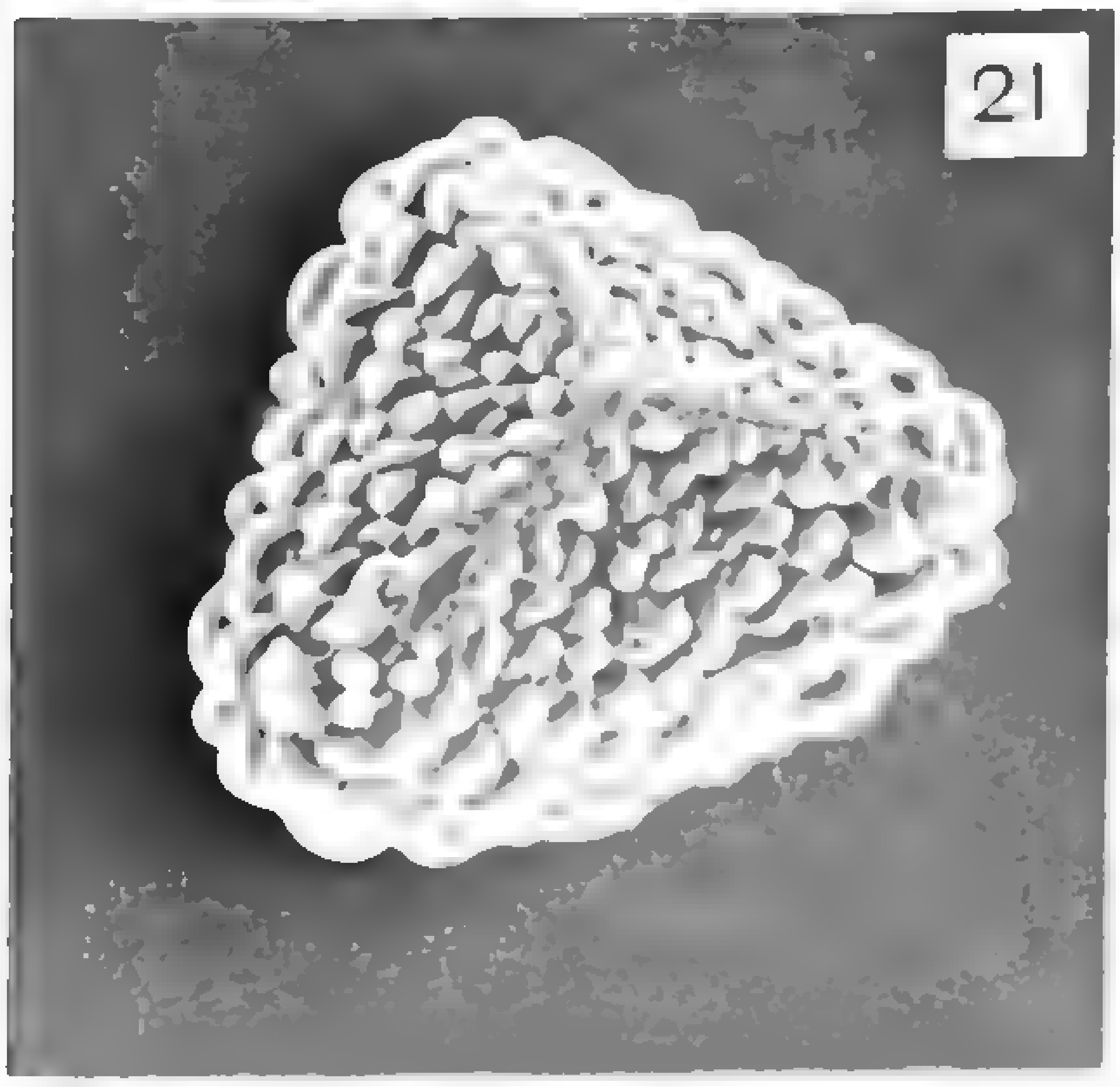
FIGS. 1–16. 1–8. Petiole scales and scurf of *Cyathea*. 1–4, Petiole scale types, enlarged and diagrammatic (see text): 1, Concolorous (whitish); 2, Nearly concolorous (light brown); 3, Concordantly bicolorous; 4, Discordantly bicolorous. 5–8, Petiole scurf types, enlarged; 5, Large scales of scurf, *C. divergens* var. *divergens*, Venezuela, *Steyermark et al. 103580* (GH); 6, Crested large scales of scurf, *C. pallescens*, Ecuador, *Sparre 16946* (GH); 7, Squamellae, source as in 5; 8, Trichomoid squamellae, *C. boliviana*, Bolivia, *Steinbach 9512* (GH). 9–16. Upper and lower lamina epidermis of *Cyathea*, × 90. 9–10, *Cyathea andina*, Peru, *Killip & Smith 23995* (GH): 9, upper; 10, lower; 11–12, *C. speciosa*, Venezuela, *Steyermark 61970* (US): 11, upper; 12, lower; 13–14, *C. divergens* var. *divergens*, Colombia, *Killip 11392* (GH): 13, upper; 14, lower; 15–16, *C. Delgadii*, Peru, *Spruce 4729* (GH): 15, upper; 16, lower.

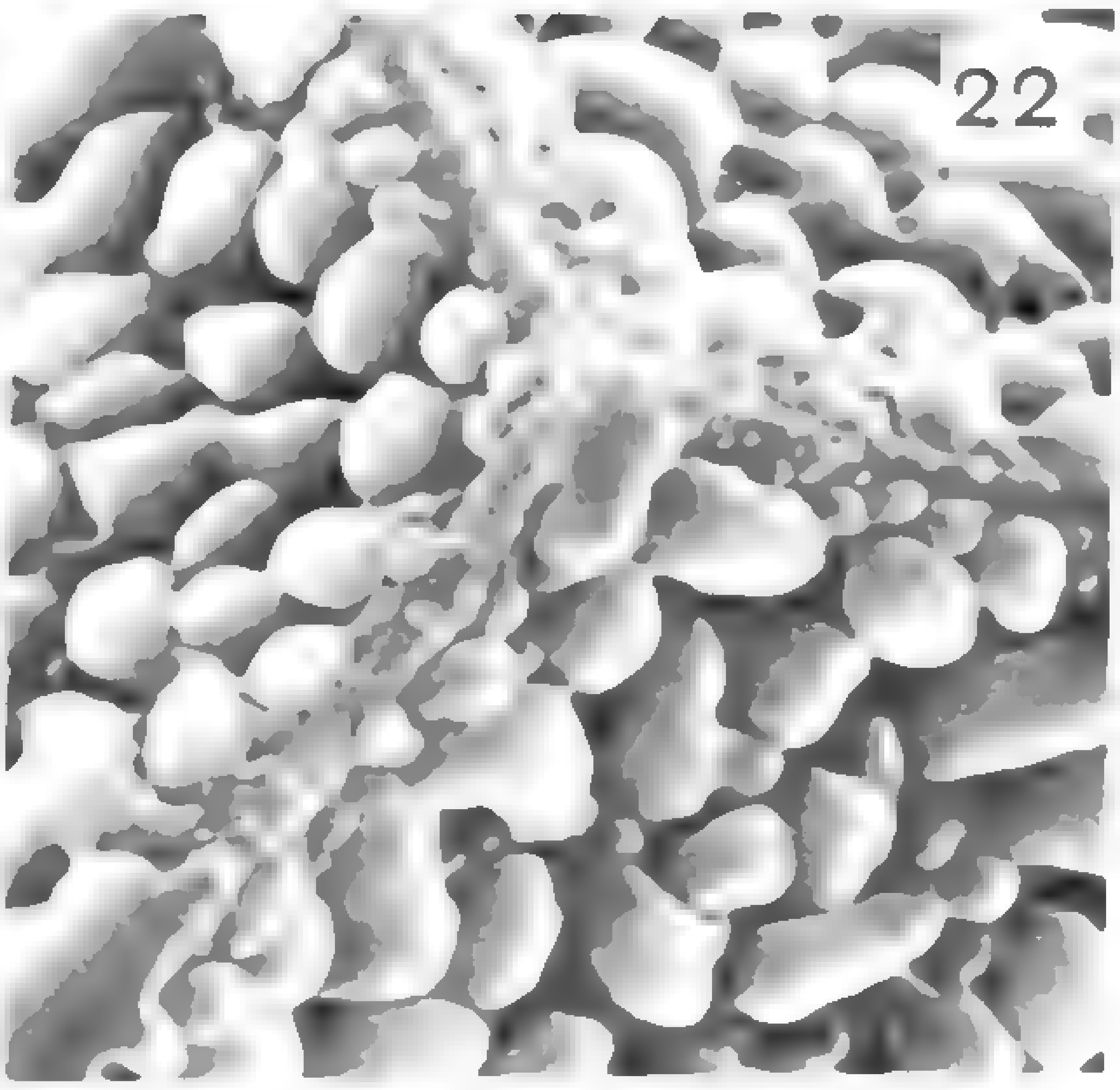












FIGS. 17–22. 17–19. Photographs of indusium types of Cyathea, × 20. 17, Hemitelioid indusium, *C. multiflora*, Honduras, *Yuncker 4745* (F). 18, Cyatheoid indusium, *C. arborea*, Grenada, *Proctor 17270* (A). 19, Sphaeropteroid indusium, *C. lechleri*, Venezuela, *Steyermark 75444* (GH). 20, Large paraphyses in sori of *C. notabilis*, Cocos Island, *Holdridge 5161* (GH), × 20. 21–22. Scanning electron micrographs, spores of *Cyathea furfuracea*, Cuba, *Eggers 5211* (GH): 21, × 1200; 22, × 5000.

Paraphyses are borne on the elevated receptacle among the sporangia. They are usually moderately long and slender, but in *Cyathea notabilis* (Fig. 20) they are much enlarged.

The spores of *Cyathea* have not been treated here in detail because of the current research of Gerald J. Gastony on the palynology of the Cyatheaceae (Gastony, 1974; Gastony & Tryon, 1976). The scanning electron micrographs included here provide some information on the exine and perine layers in *Cyathea*. The exine may be verrucate, as in *C. furfuracea* (Figs. 21, 22), or minutely pitted as in *C. arborea* (Fig. 23). Spores of the latter are usually without perine, as in Fig. 23, but in a few collections some spores were partially covered by a matrix, including large spherical bodies (Fig. 24) that appear to represent perine. In other species the perine consists of a fairly dense network of slender rods superimposed on a relatively smooth surface as in *C. caracasana* var. *Maxonii* (Fig. 25, 26), or on a coarsely tuberculate surface as in *C. divergens* var. *divergens* (Fig. 27), and *C. Delgadii* (Figs. 28, 29). The surface of the slender rods, when examined at high magnification, is seen to consist of fused pelleted material (Figs. 26, 29).

ILLUSTRATIONS

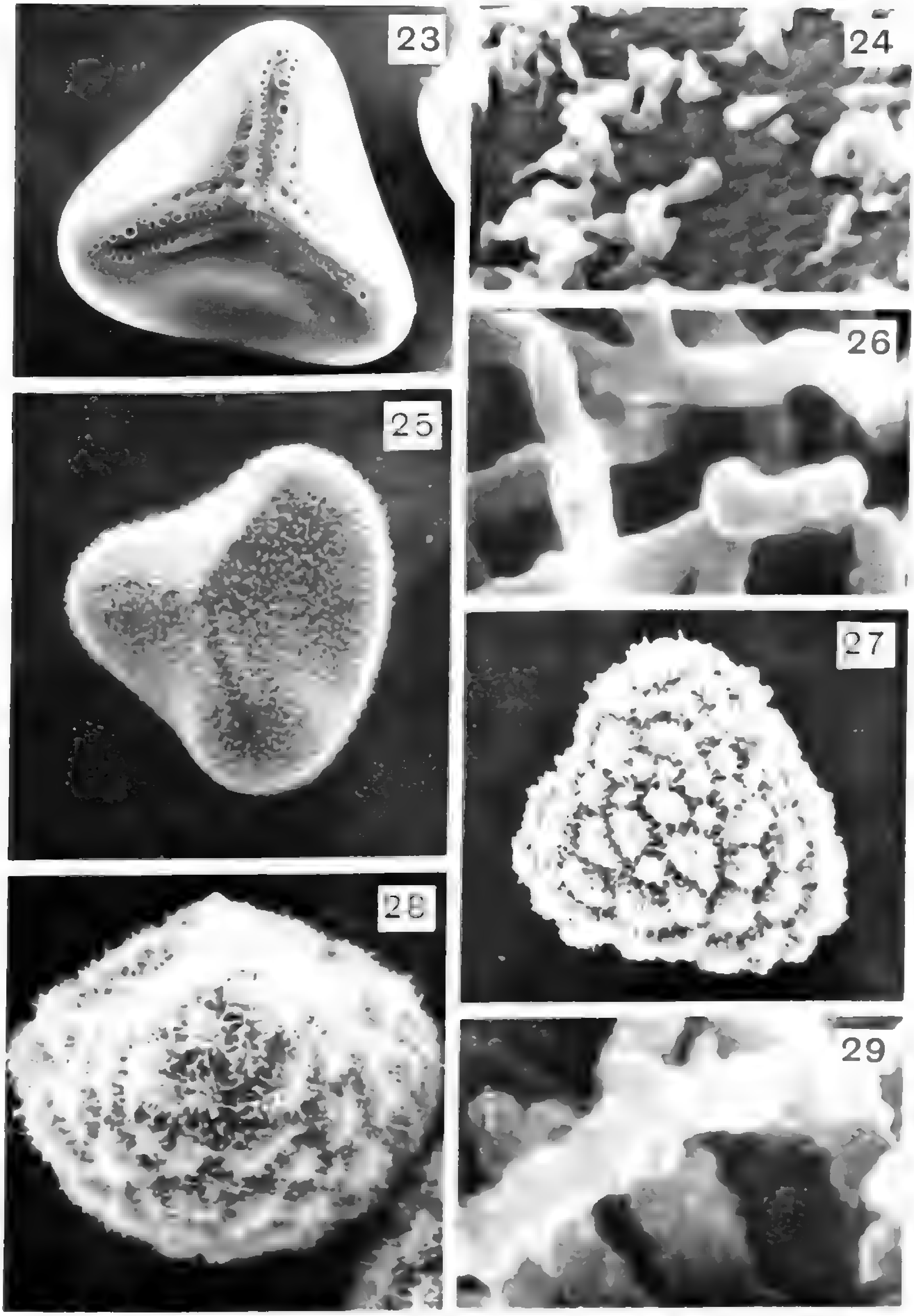
Drawings of the leafy parts: pinnae, pinnules and segments, have been taken, unless otherwise indicated, from central pinnae, from their central pinnules, and from the central portion of a central pinnule. The drawings of enlarged portions of fertile pinnules have the venation and position of the receptacle shown on some of the segments, and the indusia and indument (if any) are shown on others.

ACKNOWLEDGEMENTS

The support of the National Science Foundation through Grants GB4184 to Rolla M. Tryon and GB31170 to Rolla M. Tryon and Alice F. Tryon is gratefully acknowledged.

I am indebted to Dr. Alice F. Tryon for aid in many aspects of the research, and for the photographs of indusia and SEM micrographs of the spores. Dr. Gerald J. Gastony has provided help in a number of technical matters. The drawings have been prepared by Sarah Landry, Lydia Wunsch and Mary Robbins.

The officers and staff of the following herbaria have been generous in the loan of specimens for study and have extended courtesies during visits to their institutions: Botanische Garten und Museum, Berlin-Dahlem; British Museum (Natural History); Botanical Museum and Herbarium, Copenhagen; Field Museum of Natural History; Royal Botanic Gardens, Kew; Missouri Botanical Garden; New York Botanical Garden; Muséum National d'Histoire Naturelle, Paris; Naturhistoriska Riksmuseet, Stockholm; and United States National Herbarium, Smithsonian Institution.



FIGS. 23–29. Scanning electron micrographs, spores of Cyathea. 23–24. C. arborea. 23. Dominican Republic, *Gastony et al. 702* (GH), × 1200. 24. Puerto Rico, *Conant & Conant 51* (GH), × 10000. 25–26. C. *caracasana* var. *Maxonii*, Costa Rica, *Wilbur & Stone 10622* (GH), 25, × 1200, 26, × 60000. 27. C. *divergens* var. *divergens*, Costa Rica, *White & Lucansky* [illegible] (GH), × 1200. 28–29. C. *Delgadii*, Brazil, *Tryon & Tryon 6658* (GH), 28, × 1200, 29, × 35000.

SYSTEMATIC TREATMENT

Cyathea J. E. Smith

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. (no combination by R. Br.).

Disphenia Presl, Tent. Pterid. 55. 1836, *nom. superfl.* TYPE: the same as that of *Cyathea.*

Cormophyllum Newm. Phytol. **5**: 237. 1856, *nom. superfl.* TYPE: the same as that of *Cyathea.*

Cyathea is an American genus of 40 species with its principal development in mountain forests of the Andes from Venezuela and Colombia to Bolivia. Some species of *Trichipteris* have a scale associated with the sorus that may be mistaken for an indusium, and some species of *Cyathea* have a thin, fragile, and ephemeral indusium. Problems of identification of the two genera are discussed in the introduction. The generic characters are also given there, in the key to the American scaly genera. Ten indusiate putative hybrids of *Cnemidaria, Cyathea* and *Trichipteris* species are treated in a section at the end of the Systematic Treatment.

KEY TO SPECIES GROUPS OF CYATHEA

a. Indusium hemitelioid, variously developed, usually not completely surrounding the base of the receptacle (rarely surrounding it and then asymmetrical), or discoid to deeply cyathiform. . . . . b.
  b. Indusium hemitelioid (rarely surrounding the receptacle as an asymmetrical disk), when large often splitting at maturity into 2–3 segments. c.
    c. Pinnae 1-pinnate or more complex. . . . . d.
      d. Pinnules pinnatifid to 1-pinnate, the ultimate segments predominantly less than half-joined, or completely separated, lamina with a gradually to abruptly reduced apex. . . . . Group of *Cyathea multiflora,* species 1–8.
      d. Pinnules entire to lobed, or rarely a few segments less than half-joined, rarely deeply lobed and then the lamina with a strictly conform apical pinna. . . . . Group of *Cyathea petiolata,* species 9–12.
    c. Pinnae entire to pinnatifid. . . . . Group of *Cyathea speciosa,* species 13–16.
  b. Indusium cyatheoid (discoid to deeply cyathiform) not splitting at maturity. . . . . Group of *Cyathea arborea,* species 17–19.
a. Indusium sphaeropteroid, completely enclosing the immature sorus and usually with an apical umbo (rarely very delicate, especially in *C. caracasana, C. pallescens, C. straminea* and *C. tenera,* evanescent and persisting if at all only as an irregular basal disk or portion), very rarely less developed and open on the distal side. . . . . e.
  e. Petiole scales whitish to light brownish, concolorous or nearly so, or discordantly bicolorous with the whitish to brownish color of the differentiated margins extending into part of the otherwise dark colored, elongate-celled central portion of the body; petiole scurf whitish to light brownish, or rarely brown at the base of the petiole. . . . . f.
    f. Lamina wholly bipinnate-pinnatifid, or tripinnate only at the base of the pinnae. . . . . g.
      g. Flattish scales absent on the pinnules beneath, or if present, then lacking peripheral processes of strongly contrasting color to the body. . . . . Group of *Cyathea pallescens,* species 20–22.
      g. Some flattish scales on the pinnules beneath with dark, opaque peripheral processes, or apical processes, of strongly contrasting color to the body, or with brown cilia the same color as the central portion of the bicolorous body. . . . . Group of *Cyathea straminea,* species 23–26.

f. Lamina tripinnate to quadripinnate nearly throughout. .... Group of *Cyathea microphylla*, species 27–28.
e. Petiole scales brown and nearly concolorous, or slightly to definitely concordantly bicolorous with light brown to brown margins; petiole scurf brown or absent. . . . h.
h. Petiole scales light brown to brown, concolorous to slightly bicolorous. .... Group of *Cyathea fulva*, species 29–34.
h. Petiole scales (usually all to rarely several) with a reddish-brown to usually dark reddish-brown or atropurpureous central body, or with dark areas or streaks, bicolorous with definitely lighter colored (sometimes narrow) margins. .... i.
i. Petiole usually aculeate, to abundantly tuberculate, with abundant (sometimes caducous) scaly scurf; petiole tan to brown or sometimes darker. .... Group of *Cyathea caracasana*, species 35–36.
i. Petiole lacking spines, nearly or quite smooth or with some scattered tubercules, scaly scurf absent or rarely sparsely present; petiole dark reddish-brown to usually atropurpureous, at least basally. .... Group of *Cyathea Lechleri*, species 37–40.

GROUP OF CYATHEA MULTIFLORA

KEY TO SPECIES 1–8

a. Paraphyses long, much enlarged; Cocos Island. .... 5. *C. notabilis.*
a. Paraphyses short, to long and slender. .... b.
b. Indusium partly to completely arching over the sorus, or (rarely) concealed by the sorus and curving erect. .... c.
c. Ultimate segments with simple fertile veins and then usually entire, or with forked fertile veins and coarsely dentate; Central America, Colombia to Bolivia, northern Brazil. .... 1. *C. multiflora.*
c. Ultimate segments with forked fertile veins, entire, finely dentate, crenate to crenately lobed to deeply lobed. .... d.
d. Sori supramedial to submarginal. .... e.
e. Basal pinnules of the lower pinnae long-stalked or nearly so; Greater Antilles, French Guiana to Colombia and adjacent Brazil, south to Bolivia. . . 2. *C. andina.*
e. Basal pinnules of the pinnae sessile or nearly so; Galapagos Islands. .... 3. *C. Weatherbyana.*
d. Sori costal to medial. .... f.
f. Sori subcostal to medial, pinnules up to ca 1.5–2 cm broad and 6–8 cm long; Venezuela and Colombia. .... 7. *C. platylepis.*
f. Sori strictly costal, pinnules ca 3–4 cm broad and 10–14 cm long; Peru. .... 8. *C. Vilhelmii.*
b. Indusium appressed or subappressed to the segment surface, nearly or quite concealed by the sorus. .... g.
g. Petiole smooth or slightly muricate; Cocos Island. .... 4. *C. Alphonsiana.*
g. Petiole aculeate, especially toward the base and usually abundantly so; Greater Antilles. .... 6. *C. parvula.*

The first five species of this group, including two continental species and three insular endemics, are clearly related. *Cyathea multiflora* and *C. andina* are not wholly distinctive species; however, it is in the areas where they are allopatric that variations occur which approach intermediate specimens. In the range of sympatry, from Colombia to Bolivia, there is little or no evidence of intergradation.

Cyathea Weatherbyana of the Galapagos Islands is most closely related to *C. andina*. *Cyathea Alphonsiana* and *C. notabilis* of Cocos Island are both closest to *C. multiflora*. It is remarkable to have two endemics on an island, both derived from the same source species. The most divergent of these, *C. notabilis*, has unusual enlarged paraphyses (Fig. 44). It perhaps is the older, while the less distinctive *C. Alphonsiana* may be a younger endemic. It is also possible that each was derived from a different variation of *C. multiflora*. The other three species, *C. parvula, C. platylepis* and *C. Vilhelmii* are all distinctive but are probably related to *C. multiflora* and *C. andina*. Among this group of primitive species, *Cyathea parvula* appears to be closest to *C. arborea* and other derived species.

1. **Cyathea multiflora** Sm.

Figs. 30–34. Map 3.

Cyathea multiflora Sm. Mém. Acad. Turin **5**: 416. 1793. Holotype: Amer. Merid., *Shakespeare*, Herb. Banks, BM! photo GH,NY,US, fragm. US! The locality was erroneously published as Jamaica, see Maxon, Bull. Torrey Bot. Cl. **38**: 545–550, t. 35. 1911.

Hemitelia multiflora (Sm.) Spreng. Syst. Veg. **4**: 126. 1827. Not by R. Br. Fl. Nov. Holl. 158. 1810, as often cited.

Alsophila multiflora (Sm.) Presl, Tent. Pterid. **61**. 1836.

Amphicosmia multiflora (Sm.) Gardner, Lond. Jour. Bot. **1**: 441. 1842.

Hemitelia nigricans Presl, Epim. Bot. **31**. 1849. Holotype: "Guatemala," ad ripas fluvii S. Juan, (Nicaragua), *Friedrichsthal*, W. See Maxon, Bull. Torrey Bot. Cl. **38**: 545–550. 1911.

Amphicosmia nigricans (Presl) Moore, Ind. Fil. **61**. 1857.

Hemitelia obscura Mett. Ann. Sci. Nat. V, **2**: 264. 1864. Holotype: Prov. de Barbacoas, via de Tuquerres, (Colombia), 1600 m, *Triana*. Isotype: P! fragm. ex COL, GH! fragm. ex K,NY!

Hemitelia denticulata Hook. Syn. Fil. **31**. 1865. Holotype: "Elizabeth Island, Pacific, near Pitcairn," *Cuming 1360*, K! This is clearly *Cyathea multiflora* and probably from Panama. Holttum, Blumea **12**: 274. 1965 excludes it from Pacific species of Cyatheaceae.

Hemitelia Lindigii Baker, Syn. Fil. **454**. 1874. Holotype: Alto del Trigo, Andes of Bogotá, (Colombia), *Lindig 310*, K. Isotype: P! photo GH.

Hemitelia Hartii Baker, Jour. Bot. **24** (n.s. 15): 243. 1886. Holotype: Chiriqui Lagoon, Panama, *Hart 43*, K! photo GH. Isotypes: NY! P! photo GH,US!

Alsophila decussata Christ, Pittier, Prim. Fl. Costaric. **3** (1) (Filices 2nd Mém.): 41. 1901. Holotype: Vallé de Diquis, Costa Rica, *Pittier 12027*. Isotypes: NY! P! US!

Alsophila leucolepis var. *pubescens* Christ, Pittier, Prim. Fl. Costaric. **3**(1) (Filices 2nd Mém.): 42. 1901. Syntypes: Cañas Gordas, Costa Rica, *Pittier 10981*, US!, *10989* (not seen), *10992*, P! US!

Alsophila acutidens Christ, Bull. Herb. Boiss. II, **6**: 186. 1906, based on *C. leucolepis* var. *pubescens* Christ.

Hemitelia squarrosa Rosenst. Fedde, Rep. Spec. Nov. **22**: 2. 1925. Holotype: Finca Gebr. Hundriesser, Costa Rica, *Brade & Brade 405*, Herb. S. Birger, S–PA! Isotypes: B! US!

Cyathea acutidens (Christ) Domin, Pterid. 262. 1929.

Cyathea austroamericana Domin, Pterid. 263. 1929, *nom. nov.* for *Hemitelia nigricans* Presl, not *Cyathea nigricans* Mett.

Cyathea columbiana Domin, Pterid. 263. 1929, *nom. nov.* for *Hemitelia obscura* Mett., not *Cyathea obscura* (Mett.) Copel.

Cyathea Hartii (Baker) Domin, Pterid. 264. 1929.

Cyathea Lindigii (Baker) Domin, Pterid. 264. 1929.

Cyathea squarrosa (Rosenst.) Domin, Acta Bot. Bohem. **9**: 161. 1930.

Hemitelia squamulosa Losch, Mitteil. Bot. Staatssaml. München **1**: 20. 1950, *ex char.* Holotype: Orosi, Costa Rica, *Kupper 798*, M, photo BM!

Cyathea leucolepismata Alston, Jour. Wash. Acad. Sci. **48**: 231. 1958. Holotype: near San Diego de Colorado, between Umbria and Puerto Asis, Putumayo, Colombia, *Ewan 16748*, BM. Isotype: US!

Cyathea multiflora is a variable species, especially in its pinnule indument, petiole scales, segment margins, and paraphyses. In British Honduras and Guatemala to Nicaragua the pinnules have few trichomes beneath and mostly few, brown scales. To the south in Costa Rica to Bolivia, the pinnules are often pubescent beneath with long whitish trichomes and often have whitish scales. The petiole scales are usually relatively small, brown and nearly concolorous, while in Ecuador and Colombia especially, they may be large (*Sparre 18482*, GH, Fig. 30) or large and bicolorous (*Cuatrecasas 13918*, F), or they may be mixed with whitish nearly concolorous scales. The segments vary from entire to coarsely toothed. The specimens that have a long pubescence on the pinnules beneath often have long, slender, whitish paraphyses in the sorus, while those with only a few trichomes beneath usually have short and brownish paraphyses.

The variation in these several characters shows some correlations with geography, and with each other. However, they are weak and do not provide a basis for the recognition of other taxa. The more uniform extreme, especially in Central America north of Costa Rica, is interpreted as resulting from a geographic differentiation from the more variable southern populations.

British Honduras and Guatemala to Panama, Colombia south to Bolivia, northern Brazil. In dense forest on steep mountain slopes, along creek banks and in ravines, also in open forest or cloud forest, from near sea level, mostly below 500 m, to 1500 m in Central America and up to 2300 m in Colombia, mostly 500–2000 m in South America. Stem often ca 1 m tall, to 5 m, leaves to 2.5 m long.

SELECTED SPECIMENS. **British Honduras** (Belize). Tomash River, *Schipp S923* (GH); Camp 34, *Schipp S774* (GH). **Guatemala. Alta Verapaz:** near Chirriacté on Petén highway, *Standley 91674* (US). **Izabal:** Livingston, *Deam 483* (F,GH,MO,NY); Rio Frio, Cerro San Gil, *Steyermark 39965* (F,GH,US). **Honduras. Atlántida:** above Lancetilla, *Yuncker 4745* (F,MO); near Tela, *Standley 53132, 53945* (F,GH). **Nicaragua. Cabo Gracias á Dios:** Laimos Creek, southwest of Waspan, *Bunting & Licht 396* (GH). **Zelaya** ("Bluefields"): Río Escondido, Bahia de Bluefields, *Molina 1964, 2013* (F); Río Rama, Río Escondido, Cerro San Isidro, *Proctor, Jones & Facey 26954, 27102* (NY). **Costa Rica. Alajuela:** Quebrada Marin, 7 km east of Ciudad Quesada, *Burger & Stolze 4941* (GH,NY), *4982* (GH). **Heredia:** Finca La Selva, Río Puerto Viejo, *Burger & Stolze 5828, 5876* (GH); Cariblanco, *Nisman 112* (GH). **Limon:** near Río Madre de Dios, *Scamman 6998* (GH). **San José:** vicinity of El General, *Skutch 2161* (F,GH,MO,NY); along Río Hermosa, *Williams, Molina, Williams & Gibson 28434* (F). **Cartago:** Río Grande del Orosi, *Tryon & Tryon 7023* (GH), *Burger & Stolze 6094* (GH); vicinity of Pejivalle, *Standley & Valerio 47189* (GH). **Puntarenas:** San Vito, *McAlpin 2257* (GH); Canton Golfito, *Nisman 139* (GH); Osa, near Rincón, *Nisman 88* (GH). **Panama. Bocas del Toro:** vicinity of Chiriqui Lagoon, *Wedel 2858* (MO). **Herrera:** vicinity of Las Minas, *Stern, Eyde & Ayensu 1755* (GH). **Colon:** Porto Bello, *Maxon 5776* (GH,MO,NY). **Panamá:** La Campana, *Welch 19613* (MO); Cerro Campana, *Madison 779* (GH). **Canal Zone:** Quebrada Salamanca, *Steyermark & Allen 17141* (MO). **Colombia. Bolivar:** Cascade Chorron, south of Antizales, *Pennell 4408* (F,GH,MO,NY,US). **Antioquia:** 8 km west of Valdivia, *Madison 805* (GH); Porcesito, valle del Río Medellin, *Hodge 6872, 6873* (GH,US). **El Valle:** La Cumbre, *Killip 5701* (GH,US); Monte La Guarida, *Cuatrecasas 22161* (F,US); El Cairo, *Cuatrecasas 13918* (F,GH,US). **Cauca:** Río Ortega, north of Tambo, *Pennell & Killip 8058* (GH,NY,US); Cauca valley, Río Sucio, *Pennell & Killip 7230* (US). **Nariño:** Río Guabo, *Ewan 16809* (GH,US). **Caquetá:** Quebrada del Río Hacha, *Cuatrecasas 8779* (F,US). **Putumayo:** San Diego del Colorado, *Ewan 16784* (US). **Ecuador. Pichincha:** Mindo, *Sydow 299* (US); Toáchi, *Sparre 18482* (GH). **Napo-Pastaza:** near Archidona, *Mexia 7318* (US). **Los Ríos:** Cerro Mombre, Río Pita, *Asplund 5557* (NY,US). **Chimborazo:** Chimborazo, *Spruce 5741* (NY,US). **Cañar:** east of El Triunfo, Guayaquil-Cuenca road, *Madison 913* (GH). **Santiago-Zamora:** Bombaiza, south of Gualaquiza, *Sparre 19099* (GH). **Peru. Amazonas:** Laguna Pomacocha, *Soukup 5260b* (GH). **Loreto:** Gamitanacocha, Río Mazán, *Schunke 117* (GH,MO,NY,USM); San Antonio, Río Itaya, *Killip & Smith 29379* (F,NY,US). **Junin:** near La Merced, *Killip & Smith 23930* (F,US), *23979* (F,NY,US). **Cuzco:** near San Lorenzo, Prov. Quispicanchis, *Vargas 16069* (GH); Atalaya, Prov. Paucartambo, *Vargas 16274* (GH). **Bolivia. La Paz:** Mapiri, *Williams 1272* (GH,NY,US). **Brazil.** Upper Amazonas, *Traill 1382* (GH,NY,US).

2. **Cyathea andina** (Karst.) Domin

FIGS. 35–37. MAP 4.

Cyathea andina (Karst.) Domin, Pterid. 263. 1929.

Hemitelia andina Karst. Linnaea **28**: 452. 1856. Holotype: Santa Martha, (Colombia), 2500 m, *Karsten.* Fragment of type collection: Sierra Nevada de Santa Martha, (San Miguel), 6000 ft. *Karsten,* Herb. Mett. B! photo GH. Chosen over *Hemitelia servitensis* Karst. because figured in Karst. Fl. Columb. **2**: t. 197, f. I.

Hemitelia servitensis Karst. Linnaea **28**: 451. 1856. Holotype: Prov. Cundinamarca Novo-Granatae 2000 m, *Karsten.* Isotypes: Servita, Bogotá, (Colombia), *Karsten,* Herb. Mett. B! P! photo GH.

Hemitelia Boryana Mett. ex Kuhn, Linnaea **36**: 161. 1869. Lectotype: French Guiana, *Leprieur 265a,* P! det. Mett. Isolectotype: *Leprieur 265,* US! Isolectoparatype: French Guiana, *Poiteau,* K! photo GH. The "a" was evidently added to the number, perhaps by Mettenius to distinguish the specimen from others under the same number. The sheet at US, however, is also this species.

Hemitelia escuquensis Karst. Fl. Columb. **2**: 181, t. 196. 1869. Holotype: Sinus Maracaibensis prope Escuque, 100 m, *Karsten.* Isotype: *Hemitelia Escuquensis* spec. nov. Escuque, Venezuela, *Karsten 28,* Herb. Mett. B!

Hemitelia Joadii Baker, Ann. Bot. **5**: 187. 1891. Holotype: Santa Marta, (Colombia), Dec. 1863, *Joad,* K!

Hemitelia Leprieurii Jenm. W. Ind. Guiana Ferns 47. 1898. Holotype: Cayenne, French Guiana, *Leprieur,* Herb. Jenman, NY, photo GH.

Cyathea Boryana (Kuhn) Domin, Pterid. 263. 1929.

Cyathea escuquensis (Karst.) Domin, Pterid. 264. 1929.

Cyathea Joadii (Baker) Domin, Pterid. 264. 1929.

Cyathea circumdentata Kramer, Acta Bot. Neerland. **3**: 491. 1954, *nom. nov.* for *Hemitelia Leprieurii* Jenm., not Kze. 1844, not *Cyathea Leprieurii* (Kze.) Domin.

The indusium of *Cyathea andina* is usually larger than that of *C. multiflora* and often splits into two persistent parts at maturity. The sori are borne at the fork of a vein that is simple basally and forks toward, or sometimes very close to, the margin of the segments. The few collections from French Guiana, British Guiana and adjacent Brazil are not typical of the species. They are interpreted as geographically peripheral variations somewhat comparable to those of *Cyathea multiflora* in Nicaragua and Guatemala.

Hispaniola and Puerto Rico, French and British Guiana to Colombia, south to Bolivia, northern Brazil. In montane forest, occasionally in open places in forests, 250–900 m in the Greater Antilles, and 50–2500 m, usually 1000–1500 m in South America. Stem to 8 m tall, leaves to 4 m long.

SELECTED SPECIMENS. **Haiti.** Vicinity of Plaisance, *Leonard 9308* (GH,NY,US). **Dominican Republic.** Distr. Sabaneta, Monte Cristi, *Valeur 566* (GH); La Cumbre, Santo Domingo, *Ekman H11499* (NY,US). **Puerto Rico.** Maricao Forest, *Little 21704* (GH); Maricao, *Hioram 808* (US); near Adjuntas, *Stevens 5950* (NY); Adjuntas, *Sintenis 4102* (MO). **French Guiana.** Near Saul Village, near Crique Cochow, *Bierhorst FG87, FG110* (GH). **British Guiana** (Guyana). Basin of Shodikar Creek, Essequibo tributary, *A. C. Smith 2873* (F,GH,MO,NY,US). **Brazil. Roraima:** Serra Tepequem, *Prance, Forero, Pena & Ramos 4470* (NY,US). **Venezuela. Bolivar:** Auyantepuí, *Schnee 1487* (VEN). **Zulia:** Sierra de Perijá, between Río Negro and Río Apón, *Vareschi 3183* (VEN). **Colombia. Magdalena:** Santa Marta, *H. H. Smith 1017, 2641* (F,GH,MO,NY,US). **Santander:** vicinity of Barranca Bermaja, Magdalena valley, *Haught 1358* (GH,US). **Cundinamarca:** Fusagasuga, *André 2375* (NY). **Meta:** Cordillera La Macarena, *Idrobo & Schultes 748* (A,GH,US). **Putumayo:** Mocoa, *Cuatrecasas 11325* (US). **Ecuador.** Chugiriraja, *André 1134* (NY). **Peru. San Martin:** La Divisoria, *Ferreyra 1694* (US). **Junín:** east of Quimiri Bridge, near La Merced, *Killip & Smith 23995* (GH,NY,US); Prov. Tarma, *Esposto 659* (USM); Chanchamayo valley, *Schunke 53* (F). **Puno:** Prov. Carasaya, *Vargas 17536* (GH). **Bolivia.** La Paz: Tajlini, northeast of La Paz, *Quesada 3* (US).

3. **Cyathea Weatherbyana** (Morton) Morton

FIGS. 38–39. MAP 5.

Cyathea Weatherbyana (Morton) Morton, Amer. Fern Jour. **59**: 65. 1969.

Hemitelia Weatherbyana Morton, Leafl. West. Bot. **8**: 188. 1957. Holotype: Indefatigable Island, Galapagos Islands, *Howell 9227*, US! Isotype: CAS. Paratypes (all Galapagos Islands): Villamil, Albemarle Island, *Stewart 894*, CAS,US; James Bay, James Island, *Stewart 896, 897*, CAS,US; Wreck Bay, Cahtham Island, *Stewart 895*, CAS,US. Isoparatypes: *Stewart 894*, GH! MO!; *895, 896, 897*, F! GH! MO! NY!

The whitish, strongly dissected scales on the pinna-rachises and costae are a distinctive character of *Cyathea Weatherbyana.* The indusium is moderately large and membranous. This endemic species is clearly related to the continental *C. andina.*

Galapagos Islands, in the fern-sedge zone and the *Miconia* zone on mountain sides at 450–800 m. Stem to 6 m tall.

ADDITIONAL SPECIMENS. **Galapagos Islands. Santa Cruz** (Indefatigable): Mt. Crocker, *Wiggins 18561* (GH,US); *Colinvaux 357* (GH); above Fortuna, *Harling 5084* (GH).

4. **Cyathea Alphonsiana** Gómez

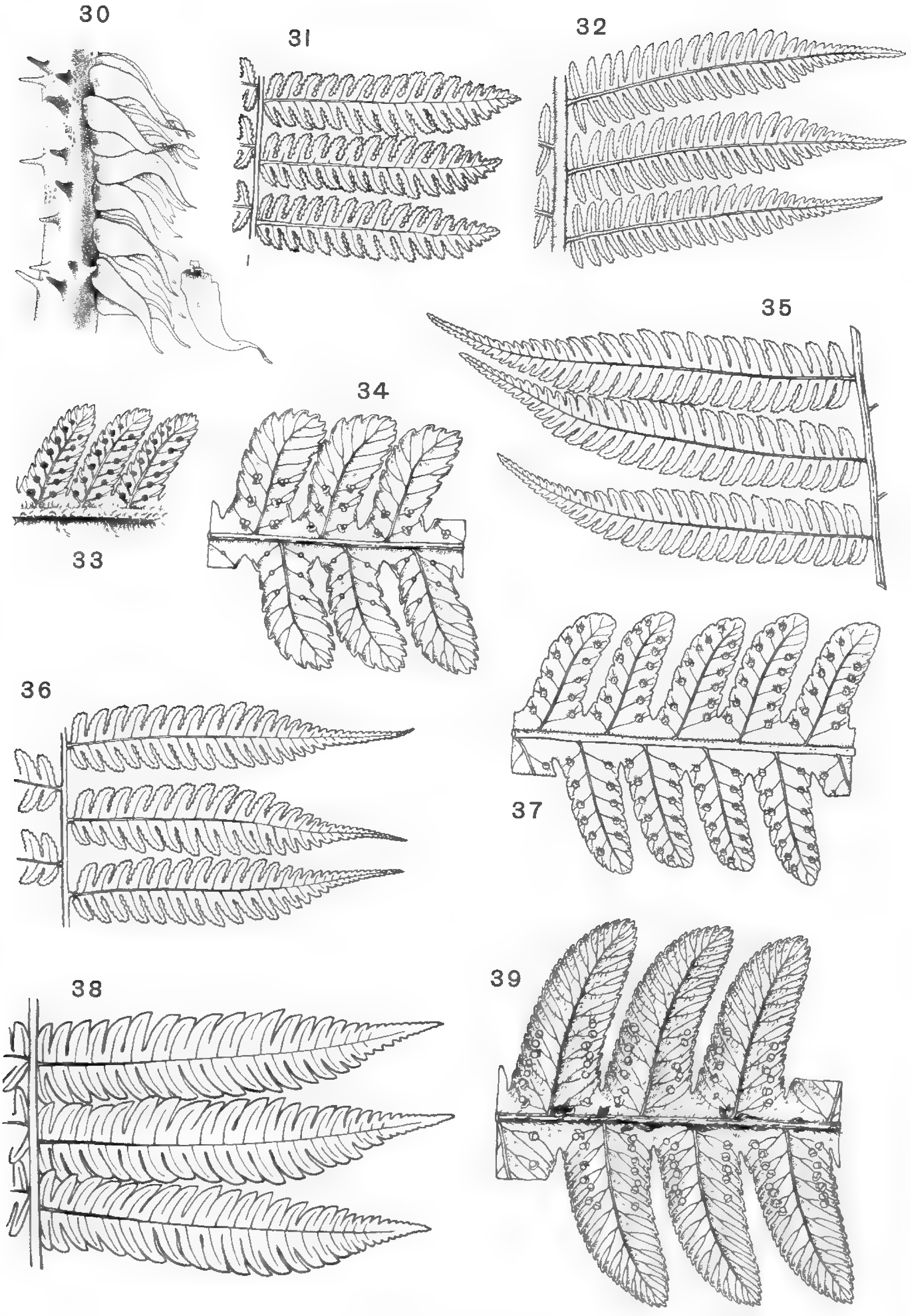
FIGS. 40–41. MAP 6.

Cyathea Alphonsiana Gómez, Amer. Fern. Jour. **61**: 166, f. 1, 2. 1971. Holotype: Twin Mountains, upper Wafer Valley, Cocos Island, Costa Rica, *Gómez 3394*, CR. Isotypes: GH! US!

Cyathea Alphonsiana is most closely related to *C. multiflora,* from which it differs especially in its minute, appressed indusium and usually entire segments with forked veins. The specimens cited below were also indicated as paratypes by Gómez, although not seen by him.

Cocos Island, in dense forest, 450 m. Stem to 4 m tall.

ADDITIONAL SPECIMENS. **Cocos Island.** *Holdridge 5160* (GH); *W. L. Schmitt 129, 130, 131* (US).



FIGS. 30–39. 30–34, *Cyathea multiflora:* 30, Petiole scales, Ecuador, *Sparre 18482* (GH), × ½; 31, Pinnules, Costa Rica, *Scamman 6998* (GH), × ½; 32, Pinnules, source as in 30, × ½; 33, Portion of fertile pinnule, source as in 30, × 2; 34, Portion of fertile pinnule, source as in 31, × 2. 35–37, *C. andina:* 35, Pinnules, Colombia, *Mutis 3291* (US), × ½; 36, Pinnules, British Guiana, *A. C. Smith 2873* (GH), × ½; 37, Portion of fertile pinnule, Puerto Rico, *Little 21704* (GH), × ½. 38–39, *C. Weatherbyana,* Galapagos Islands: 38, Pinnules, *Stewart 897* (MO), × ½; 39, Portion of fertile pinnule, *Wiggins 18561* (GH), × 2.

5. **Cyathea notabilis** Domin

FIGS. 42–44. MAP 7.

Cyathea notabilis Domin, Acta Bot. Bohem. **9**: 141. 1930, nom. nov. for *Alsophila notabilis* Maxon, not Saporta, Mém. Soc. Géol. France II, **8**: 329. 1868.

Alsophila notabilis Maxon, Contrib. U.S. Nat. Herb. **24**: 39, t. 12. 1922. Holotype: Wafer Bay, Cocos Island, Costa Rica, *Pittier 12355,* US! Paratype: same locality, *Pittier 16228,* US! Isoparatype: GH!

Cyathea notabilis is a unique species with its much enlarged paraphyses, many of them forming a conspicuous tuft at the apex of the receptacle. There are ten or fewer sporangia in a sorus, in the materials I have seen, while other *Cyathea* species with smaller paraphyses have more sporangia. Gastony (1974) reports five species of *Cyathea* with 44 up to 106 sporangia per sorus. The apparent reduction of reproductive capacity in *C. notabilis* may be interpreted as the development of precinctiveness (Carlquist, 1966) in this insular endemic. Among the ferns, it is perhaps the only example of this phenomenon.

Cyathea notabilis also differs from *C. Alphonsiana* of Cocos Island in its predominently simple fertile veins and in its minute indusia.

Cocos Island, in forested ravines, 50 m. Stem to 2 m tall.

ADDITIONAL SPECIMENS. **Cocos Island.** *Jiménez 3146* (GH); *Holdridge 5161* (GH); *Schmitt 128* (GH,US).

6. **Cyathea parvula** (Jenm.) Domin

FIGS. 45–47. MAP 8.

Cyathea parvula (Jenm.) Domin, Pterid. 264. 1929.

Alsophila parvula Jenm. Jour. Bot. **17** (n.s.8): 258. 1879. Holotype: Jamaica, *Jenman 97,* K, photo GH,NY,US, fragm. US! One sheet (of four) in the Jenman Herbarium, NY! lacks data but is very similar to the holotype and may be considered authentic.

Hemitelia microsepala Jenm. Jour. Bot. **24** (n.s.15): 266. 1886. Holotype: Bull Head, Clarendon Parish, Jamaica. *Sherring* ?. Three sheets without data in the Jenman Herbarium, NY! are probably authentic.

Hemitelia parvula (Jenm.) Baker, Ann. Bot. **5**: 188. 1891.

Alsophila aquilina Christ, Engl. Bot. Jahrb. **24**: 83. 1897, "1898." Holotype: Monteverde, Cuba, *Eggers 5117,* fragm. ex Christ, US! Isotypes: F! P! photo GH, fragm. ex K, NY!

Alsophila gracilis Underw. & Maxon, Bull. Torrey Bot. Cl. 29. 577. 1902. Holotype: Baracoa, Prov. Santiago, Cuba, *Pollard, Palmer & Palmer 255,* US! Isotypes: F! GH! MO! Paratypes: Monteverde, Cuba, *Wright 951,* NY! US. Isoparatypes: GH! MO! NY!

Alsophila aquilina var. *Maxonii* Rosenst. Fedde, Rep. Spec. Nov. **6**: 179. 1908. Holotype: valley of Río Bayamita, Sierra Maestra, Cuba, *Maxon 3910.* Isotypes: GH! NY! US!

Hemitelia miniuscula Maxon, Jour. Wash. Acad. Sci. **18**: 316. 1928. Holotype: Anse-à-Toleur, Morne Colombeau, Massif de Nord, Haiti, *Ekman H4365,* C. Isotype: US!

Cyathea aquilina (Christ) Domin, Pterid. 262. 1929.

Cyathea gracilescens Domin, Pterid. 262. 1929, *nom. nov.* for *Alsophila gracilis* Underw. & Maxon, not *Cyathea gracilis* Griseb.

Cyathea parvula var. *microsepala* (Jenm.) Domin, Acta Bot. Bohem. **9**: 145. 1930.

The petiole scales of *Cyathea parvula* are often concolorous and whitish; they vary to bicolorous with a darker center. The pinnules often have light to dark brown bullate scales and (or) flattish scales beneath. There is considerable variation in the leaf texture between plants growing in the open sun and those growing in the forest. Although the indusium is usually small, it is especially well-developed in *Conant & Hodgdon 646*, Puerto Rico (GH), in which it may extend about halfway around the receptacle and arch over the lower portion of the sorus. These variations, among others, are found scattered through the Greater Antilles and are not correlated with each other nor with their geography.

A notable feature of *Cyathea parvula*, at least in the Maricao Mountains of western Puerto Rico, is that the stems may produce positively geotrophic branches, some of which extend to the ground and take root. A similar phenomenon has been reported in *Alsophila Manniana* of Africa by Halle (1966, as *Cyathea Manniana*).

Cuba, Jamaica, Hispaniola and Puerto Rico. In rain forest, shaded ravines, and mountain valleys, or more often in open woods, along streams, at the edge of woods, in thickets or savannahs, and along roadsides and in secondary growth, from sea level to 2000 m. Stem to 9 m tall, frequently ca 1-2 m, leaves to 2 m long, usually less.

SELECTED SPECIMENS. **Cuba. Oriente:** northern spur of Sierra Maestra, west of Río Yao, *Morton & Acuna 3487* (GH,MO,NY); Sierra Nipe, near Woodfred, *Shafer 3059* (GH,NY); Sierra de Moa, *Howard 5859, 5963* (GH,MO,NY); *Wright 889* (GH,MO,NY). **Jamaica.** Mount Diabolo, Portland, *Maxon & Killip 441* (F,GH,NY); Tweedside, St. Andrew, *Proctor 4460* (MO); Corn Puss Gap, St. Thomas, *Proctor 5513* (GH); Mason River Field Station, Clarendon, *Riba 209* (GH). **Haiti.** Vicinity of Port de Paix, *Leonard & Leonard 12316* (MO); vicinity of Plaisance, *Leonard 9350* (US); vicinity of Marmelade, *Leonard 8227* (F,GH,MO); Bayeux, Morne Brigand, *Ekman H2873* (NY). **Dominican Republic.** Vicinity of San Francisco de Macoris, Duarte (Pacificador), *Abbott 2067* (GH,NY); Pilón de Azúcar, vicinity of Laguna, Samaná Peninsula, *Abbott 294, 445* (GH); Distr. San José de las Matas, Santiago, *Valeur 317* (F,MO,NY); Seibo, from Miches to Higuey, *Gastony, Jones & Norris 656, 659, 660* (GH,NY). **Puerto Rico.** Río Maricao, *Britton, Stevens & Hess 2482* (F,MO,NY); Maricao State Forest, *Tryon & Tryon 7083* (GH); Espino, *Sintenis 5960* (A,F,MO,NY); near Mayaguez, *Heller 4595* (F,GH,MO,NY).

7. **Cyathea platylepis** (Hook.) Domin

FIGS. 48–51. MAP 9.

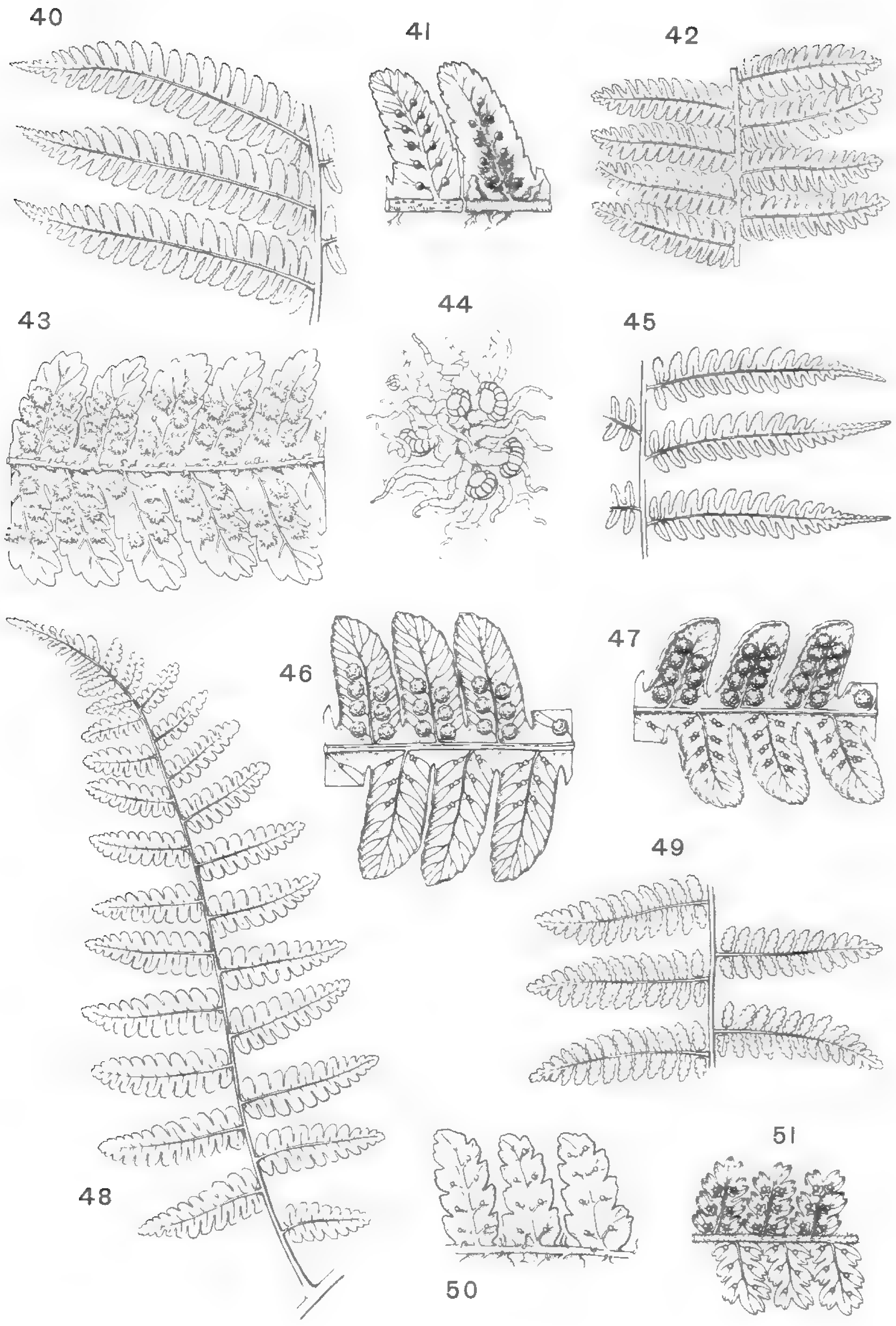
Cyathea platylepis (Hook.) Domin. Pterid. 264. 1929.

Hemitelia platylepis Hook. Second Cent. Ferns t. 100. 1861. Holotype: near San Carlos, Rio Negro, "Brazil," (Venezuela), *Spruce 3127* (not *3027* as published), K! photo GH. Isotypes: GH! P! fragm. ex Christ, NY!

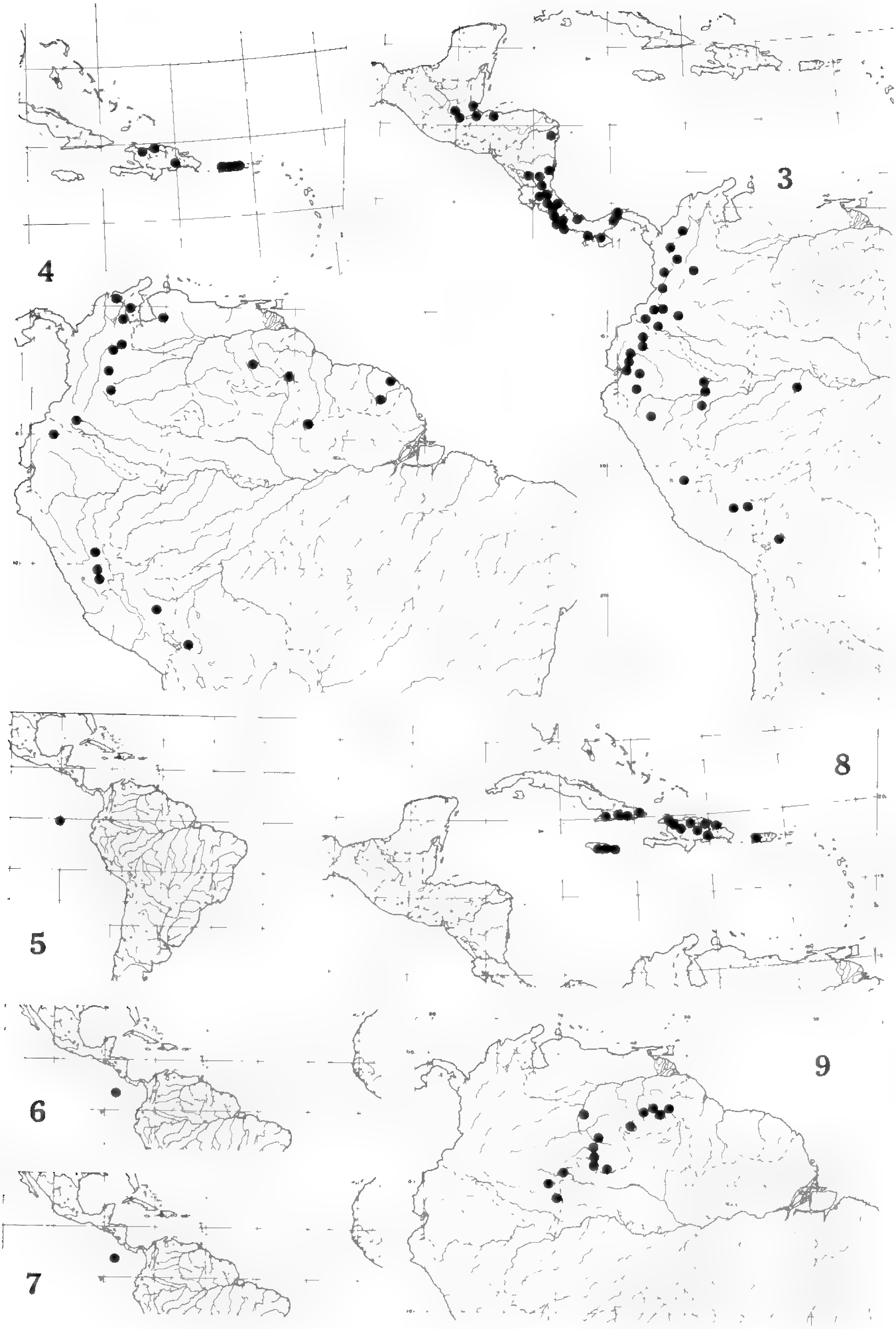
Hemitelia minima Morton, Fieldiana: Bot. **28**: 9. 1951. Holotype: Ptari-tepuí, Bolivar, Venezuela, *Steyermark 59481*, F!

Cyathea platylepis is a distinctive species of the Roraima sandstone and derived soils of the Guayana region of Venezuela and Colombia. The fertile pinnae are characteristically dimorphic. The large indusium is usually half-globose or nearly so; or it sometimes is about ⅓ of a deep cup.

Venezuela and Colombia. In rocky woods, bamboo thickets, mossy forest, moist scrubby woods and boggy savannahs, 125–2200 m. Stem usually short, ca 1 m tall, to 3.5 m, leaves usually 1–1.5 m long, or less.



Figs. 40–51. 40–41, *Cyathea Alphonsiana*, Cocos Island, *Schmitt 131* (US): 40, Pinnules, × ½; 41, Portion of fertile pinnule, × 2. 42–44, *C. notabilis*, Cocos Island, *Pittier 16228* (GH): 42, Pinnules, × ½; 43, Portion of fertile pinnule, × 2½; 44, Sorus with few sporangia and many enlarged paraphyses, × 15. 45–47, *C. parvula:* 45, Pinnules, Cuba, *Maxon 3910* (US), × ½; 46, Portion of fertile pinnule, Jamaica, *Proctor 5060* (MO), × 2; 47, Portion of fertile pinnule, Haiti, *Leonard & Leonard 14535* (US), × 2. 48–51, *C. platylepis:* 48, Sterile pinna, Venezuela, *Maguire 33083* (US), × ½; 49, Fertile pinnules, source as in 48, × ½; 50, Portion of fertile pinnule, source as in 48, × 2; 51, Portion of fertile pinnule, Colombia, *Schultes & Cabrera 15079* (GH), × 2.



MAPS 3–9. 3, Cyathea multiflora; 4, C. andina; 5, C. Weatherbyana; 6, C. Alphonsiana; 7, C. notabilis; 8, C. parvula; 9. C. platylepis.

SELECTED SPECIMENS. **Venezuela. Bolivar:** Cerro Venamo, *Steyermark & Nilsson 122* (US,VEN); Chimatá Massif, *Steyermark 74905, 75451* (NY,US,VEN); Auyan-tepuí, *Steyermark 93922* (GH,US,VEN); **Amazonas:** Cerro de la Neblina, *Maguire, Wurdack & Bunting 37261* (GH,NY,US); Maroa, Río Guainía, *Ll. Williams 14328* (F); Cerro Yapacana, *Steyermark & Bunting 103084* (GH,NY); Cerro Autana, *Steyermark 105183* (VEN). **Colombia. Vaupés:** Río Vaupés, Mitú, *Schultes, Raffauf & Soejarto 24221* (GH); Río Apaporis, Cachivera de Jirijirimo, *Schultes & Cabrera 12469* (GH,US); Cerro Isibukuri, *Schultes & Cabrera 15079* (GH). **Amazonas:** Río Caquetá, vicinity of La Pedrera, *Schultes 5857* (GH).

8. **Cyathea Vilhelmii** Domin

Figs. 52–53. Map 10.

Cyathea Vilhelmii Domin, Pterid. 264. 1929, *nom. nov.* for *Hemitelia Lechleri* Mett., not *Cyathea Lechleri* Mett.

Hemitelia Lechleri Mett. Fil. Lechl. **2**: 28. 1859. Lectotype: Tatánara, (Puno), Peru, *Lechler 2654,* Herb. Mett. B! Isolectotype: Fragm. ex Rosenst. US! Lectoparatype: Tatanara, Peru, *Lechler 2650,* Herb. Mett. B!

Hemitelia Lechleriana Diels, Nat. Pflanz. **1**(4): 131. 1899, *nom. superfl.* Syntypes: *Lechler 2650, 2654,* Herb. Mett. B!

The correct name of this species depends on the nomenclatural status of *Hemitelia Lechleriana* Diels, which, if legitimate, would provide the earliest epithet under *Cyathea.* Diels' name is not obviously superfluous since Mettenius did not cite Lechler collection numbers, and since the specimens in Mettenius' herbarium may have been duplicates, with the original sheets at Leipzig. However, since it is now impossible to resolve the status of these specimens with respect to Leipzig, I believe it is better to consider them as the type collections, which they may have been, and therefore *Hemitelia Lechleriana* becomes superfluous.

The costal sori and tripinnate-pinnatifid lamina are distinctive characters of *Cyathea Vilhelmii.* It is probably closely related to the previous species, *Cyathea platylepis.*

GROUP OF CYATHEA PETIOLATA

KEY TO SPECIES 9-12

a. Lamina with a gradually to abruptly reduced apex, sori submarginal; Panama, Colombia. .... 9. *C. petiolata.*
a. Lamina with a conform apical pinna. .... b.
  b. Stalk of apical pinna not articulate, sori about medial. .... c.
    c. Pinnules subcordate at base, those of the upper pinnae and the conform apical pinna regularly lobed; Panama. .... 10. *C. impar.*
    c. Pinnules mostly cuneate to subcuneate at base, those of the upper pinnae and the conform apical pinnae entire; Venezuela. .... 11. *C. Steyermarkii.*
  b. Apical pinna articulate, sori submarginal; Panama, Colombia. .. 12. *C. conformis.*

The species of this group are all quite distinctive and, with the exception of *Cyathea petiolata,* are known from only one or a few collections. They form a natural group with reduced lamina architecture that appears to be the modern representative of a line leading toward *Cnemidaria. Cyathea petiolata* and *C. conformis,* especially, show affinities to *Cnemidaria* in their pinnules which sometimes have areolate venation. However, *Cnemidaria amabilis,* the most primitive species of the genus (Stolze, 1974) has pinnatifid pinnae and large-porate spores and there is no species of *Cyathea* that is really close to it. Considerable evolution has probably occurred since the origin of *Cnemidaria* from hemitelioid indusiate cyatheas.

9. **Cyathea petiolata** (Hook.) Tryon, comb. nov.
Figs. 54–58. Map 11.

Hemitelia petiolata Hook. Sp. Fil. 1: 31, t. 16. 1844. Holotype: Isthmus of Panama, *Dr. Sinclair,* K (t. 16).

Hemistegia marginalis Presl, Gefässb. Stipes der Farrn 47. 1847 (preprint from Abh. Böhem. Ges. Wiss. V, **5**: 355. 1848), *nom. superfl.*

Cyathea panamensis Domin, Pterid. 264. 1929, *nom. superfl.* An intended *nom. nov.* for *Hemitelia petiolata* Hook., not *Cyathea petiolata* J. Sm. Hook. Jour. Bot. **3**: 419. 1841, but the latter is a *nom. nud.*

Hemitelia Woronovii Maxon & Morton, Amer. Fern Jour. **36**: 91. 1946. Holotype: Peñas Blancas, Antioquia, Colombia, *Woronow & Juzepczuk 4549,* LE. Isotype: US. Paratypes: Peñas Blancas, Antioquia Colombia, *Woronow & Juzepczuk 4584,* LE, US; Norosi-Tiquisio Trail, Lands of Loba, Bolivar, Colombia, *Curran 136,* US!; Barranca Bermeja, Magdalena Valley, between Sogamoso and Colorado Rivers, Santander, Colombia, *Haught 1337,* US. Isoparatypes: *Haught 1337,* F! GH! NY!

Cnemidaria petiolata (Hook.) Copel. Gen. Fil. 97. 1947.

Cyathea Woronovii (Maxon & Morton) Stolze, Fieldiana: Bot. **37**: 81. 1974.

Cyathea petiolata is variable in its leaf architecture. The material described as *Hemitelia Woronovii* is especially different with its large ultimate segments, but in the absence of other characters, this and other variations do not seem to have taxonomic significance.

Two collections from Peru, *Dudley 10616* (GH) and *13214* (US), are sterile but probably represent a new species allied to *Cyathea petiolata.*

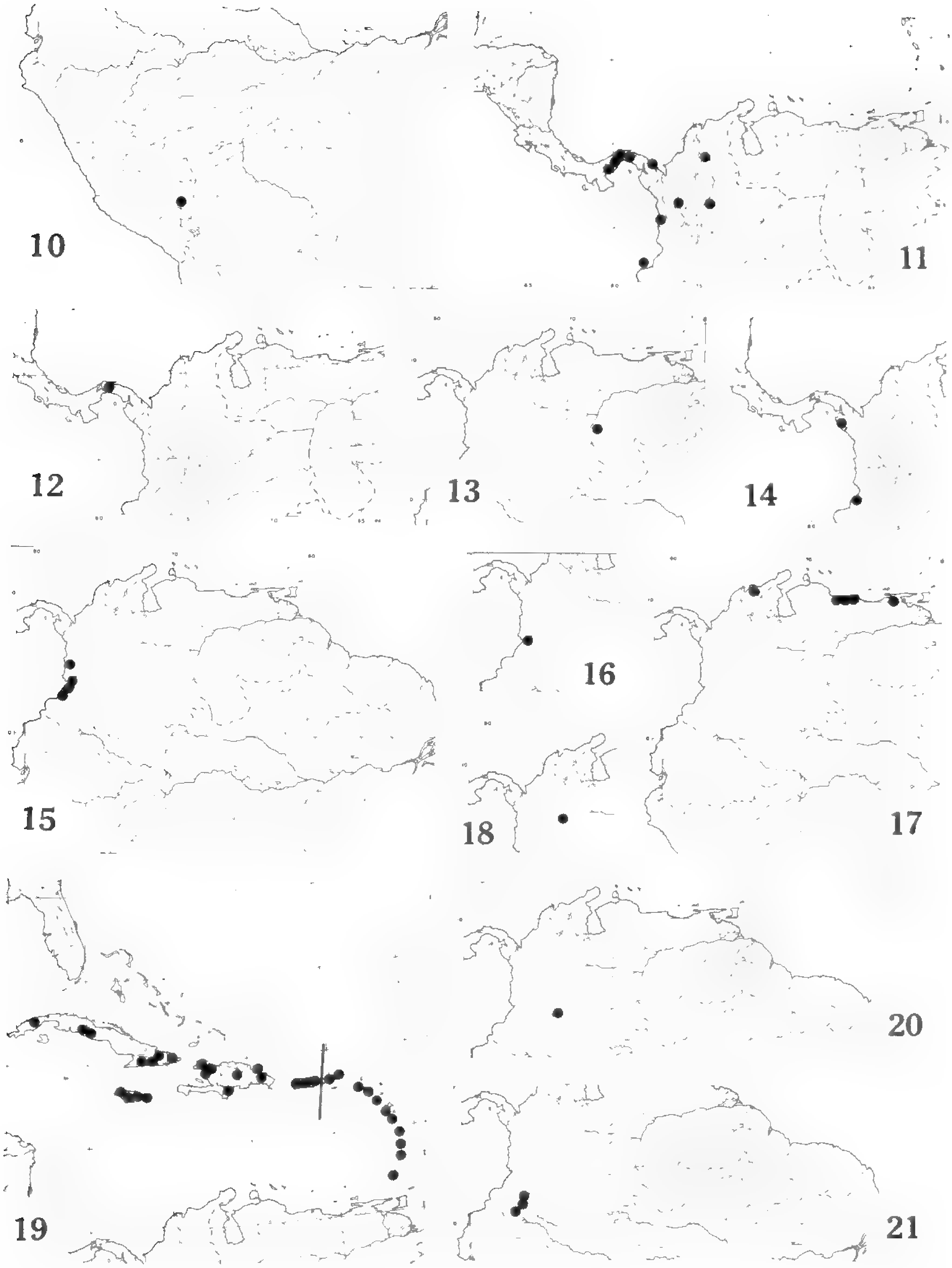
Panama and Colombia. In wet forest, along streams and on hillsides, 30–700 m. Stem to 5 m tall, leaves to 1.5 m long.

SELECTED SPECIMENS. **Panama. Panamá:** near Cerro Azu, road to Cerro Jefe, *Blum, Godfrey & Tyson 1700, 1701* (FLAS). **Canal Zone:** Frijoles, *Killip 2802* (GH,MO); Caño Quebrada, *Pittier 6820* (GH,US); near Gatun, *Maxon 4645* (GH); Chagres, *Fendler 417* (GH,MO), *421* (MO). **San Blas:** Hills of Siridi, near Puerto Obaldia, *Pittier 4412* (GH). **Colombia. Chocó:** Bahi Solano, near Ciudad Mutis, *Killip & Garcia 33624* (NY). **Santander:** 25 km east of Puerto Wilches, Magdalena Valley, *Elias 4* (US). **Nariño:** Gorgona Island, *Killip & Garcia 33173* (GH,NY), *Barclay 908* (GH).

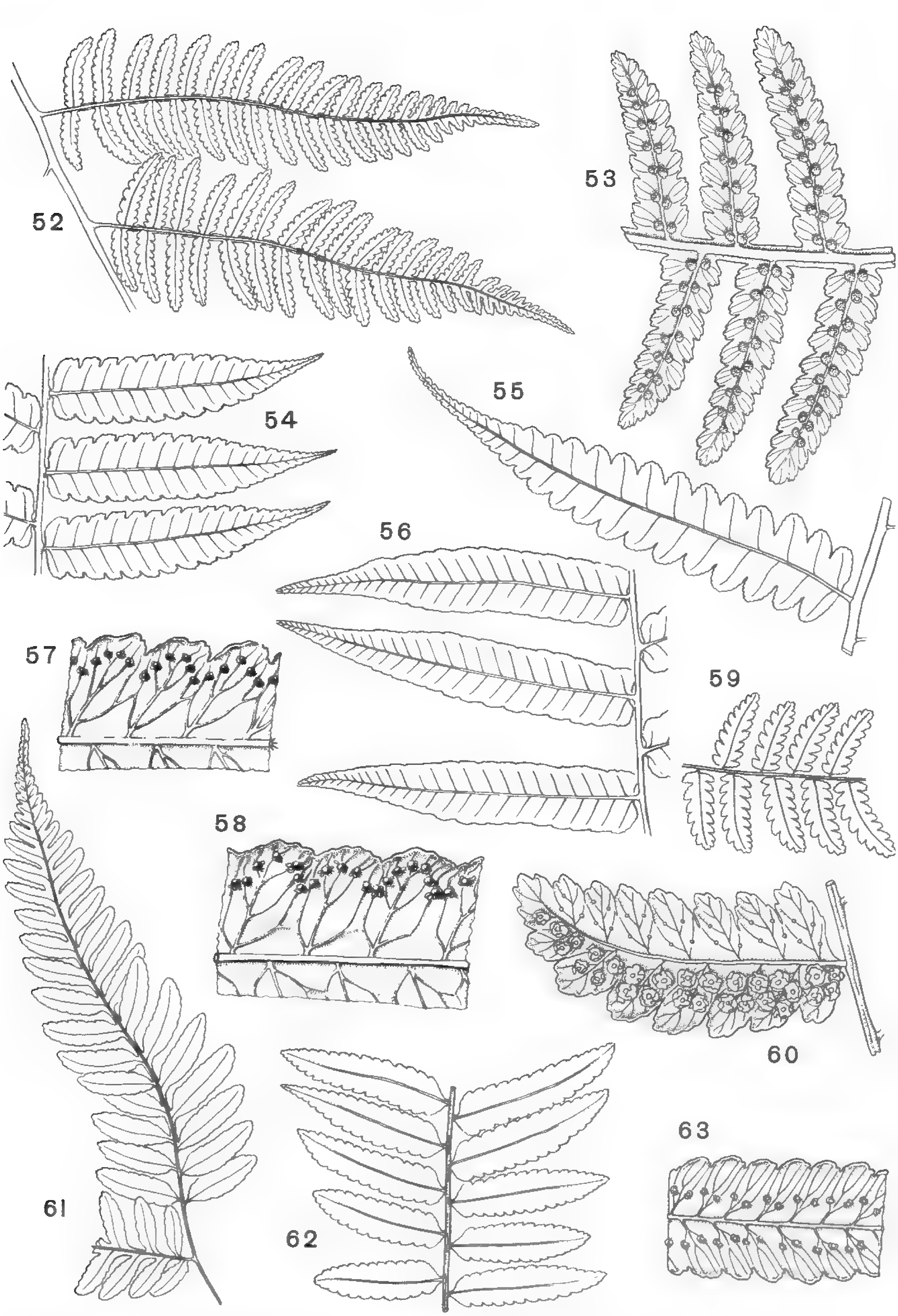
10. **Cyathea impar** Tryon, spec. nov.
Figs. 59–60. Map 12.

Folium 1 m longum; petiolus squamis structura marginata discordanter bicoloribus vel concoloribus pallide brunneis; lamina obovata bipinnato-lobata, pinna apicali conformi 1-pinnato-lobata non articulata; pinnae ad 20 cm longae apice sensim acuminato; pinnulae pagina inferiore breviter pubescenti; sori mediales in venis simplicibus; indusium hemitelioideum semicyathiforme vel fere cyatheoideum. Holotype: northeast slope of Cerro Jefe, on road to Buenos Aires, Prov. Panamá, Panamá, 2600 ft, 27 January 1966, *Tyson, Dwyer & Blum 3264,* MO.

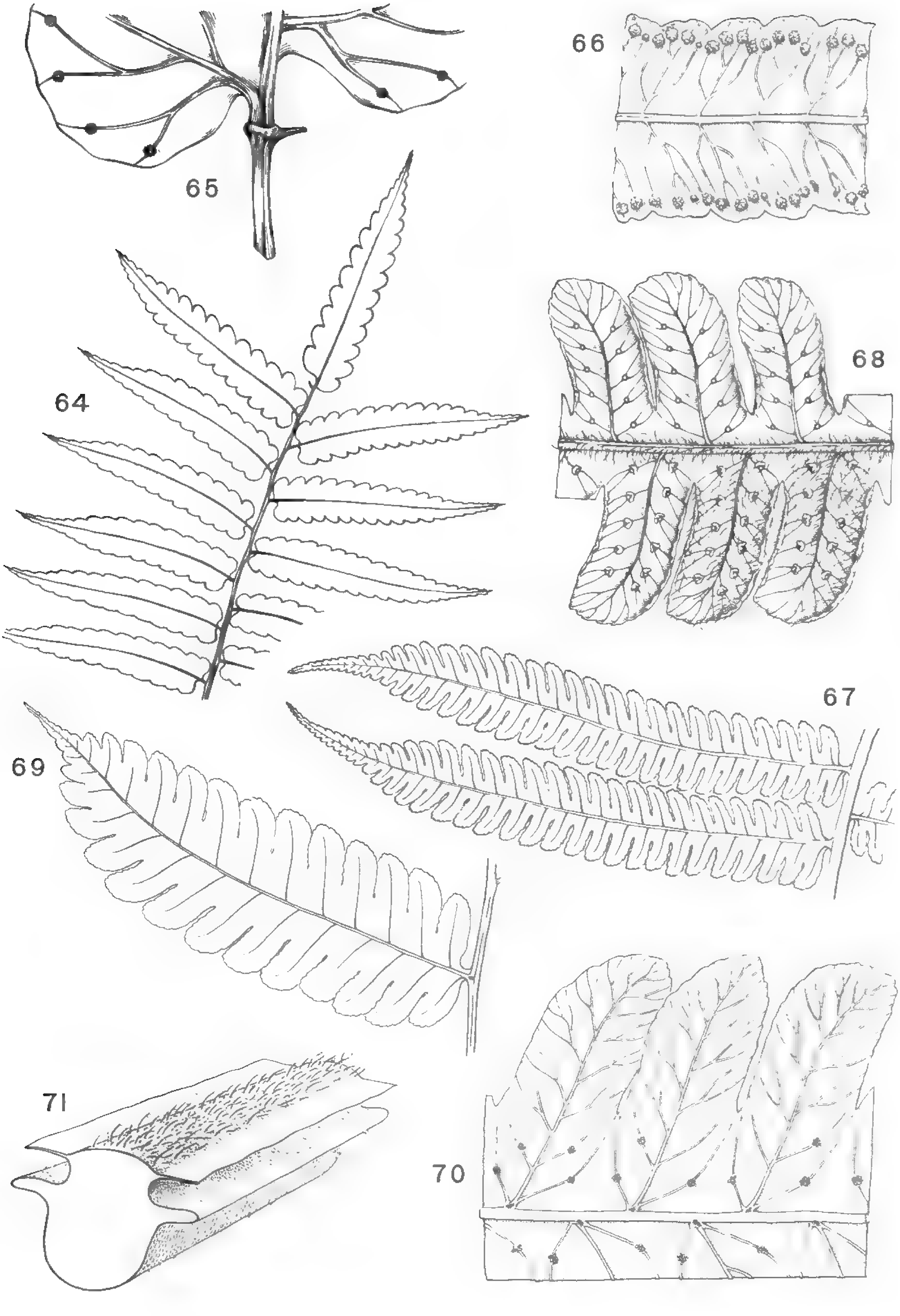
A distinctive species from Cerro Jefe which is considered by Lewis (1971) to be a center of local endemism.



MAPS 10–21. 10, Cyathea Vilhelmii; 11, C. petiolata; 12, C. impar; 13, C. Steyermarkii; 14, C. conformis; 15, C. decorata; 16, C. parva; 17, C. speciosa; 18, C. Haughtii; 19, C. arborea, the line between Puerto Rico and Tortola indicates the geographic break in indusium variation (see text); 20, C. Alstonii; 21, C. peladensis.



FIGS. 52–63. 52–53, *Cyathea Vilhelmii*, Peru, *Lechler 2654* (B): 52, Pinnules, × ½; 53, Portion of fertile pinnule, × 1½. 54–58, *C. petiolata:* 54, Pinnules, Panama, *Maxon 5769* (GH), × ½; 55, Pinnules, Colombia, *Killip & Garcia 33173* (GH), × ½; 56, Pinnules, Colombia, *Haught 1337* (GH), × ½; 57, Portion of fertile pinnule with areolate venation, source as in 54, × 1½; 58, Portion of fertile pinnule with free venation, source as in 56, × 1½. 59–60, *C. impar*, Panama, *Tyson et al. 3264* (MO): 59, Pinnules, × ½; 60, Fertile pinnule, × 2. 61–63, *C. Steyermarkii*, Venezuela, *Steyermark 105194* (GH): 61, Apex of lamina, × ½; 62, Pinnules, × ½; 63, Portion of fertile pinnule, × 1½.



FIGS. 64–71. 64–66, *Cyathea conformis*, Panama, *Stern & Chambers 188* (GH): 64, Apex of pinna, × ½; 65, Base of apical segment of pinna, enlarged; 66, Portion of fertile pinnule, × 2. 67–68, *C. decorata*, Colombia, *Killip 5257* (GH): 67, Pinnae, × ½; 68, Portion of fertile pinna, × 2. 69–71, *C. parva*, Colombia, *Killip 5254* (NY): 69, Pinna, × ½; 70, Portion of fertile pinna, × 1½; Portion of alate petiole, diagrammatic, enlarged.

11. **Cyathea Steyermarkii** Tryon
Figs. 61–63. Map 13.

Cyathea Steyermarkii Tryon, Rhodora **74**: 449. 1972. Holotype: Cumbre del Cerro Autana, Amazonas, Venezuela, *Steyermark 105194,* GH!

This species is known only from the small summit of Cerro Autana, which is a single massive projection rising some 1000 m above the surrounding land (Steyermark, 1974).

Venezuela. In woods, ca 1250 m. Stem 1 m tall, leaves ca 1.5 m long.

12. **Cyathea conformis** (Tryon) Stolze
Figs. 64–66. Map 14.

Cyathea conformis (Tryon) Stolze, Fieldiana: Bot. **37**: 80. 1974.

Hemitelia conformis Tryon, Rhodora **62**: 1, f. 1. 1960. Holotype: Piñas Bay, Prov. Darien, Panamá, *Stern & Chambers 188,* GH! Isotypes: A! MO! US!

Cnemidaria conformis (Tryon) Tryon, Contrib. Gray Herb. **200**: 51. 1970.

The articulate apical pinna of the lamina is unique in the genus, and the articulate apical pinnule of the pinnae is (Fig. 65) unique in the family. This species evidently illustrates the evolution of reduced lamina architecture by abortion of the apical portion of the lamina and of the pinnae. However, the process may be based on a different type of leaf modification in other species.

Panama and Colombia.

ADDITIONAL SPECIMENS. *Seeman 990* (BM). **Panamá.** *Seeman* (K). **Colombia. Valle or Cauca:** Bay of Chocó, 1848, *Seeman* (BM).

Group of the Cyathea speciosa
KEY TO SPECIES 13-16

a. Pinnae deeply lobed to pinnatifid. . . . . b.
  b. Petiole not alate, densely and usually persistently scaly; rachis abundantly long pubescent. . . . . 13. *C. decorata.*
  b. Petiole prominently green alate, sparingly scaly; rachis lacking long trichomes. . . . . 14. *C. parva.*
a. Pinnae entire to shallowly lobed. . . . . c.
  c. Larger pinnae ca 20 cm or more long, stalked pinnae acute to caudate, rarely some subobtuse. . . . . 15. *C. speciosa.*
  c. Larger pinnae ca 2-4 cm long, all pinnae obtuse. . . . . 16. *C. Haughtii.*

A group of distinctive and probably not closely related species. They all represent a continuation of the trend in reduction of lamina architecture evident in the previous group. The most reduced is *Cyathea Haughtii* with a small 1-pinnate lamina. Although these species of *Cyathea* have their lamina architecture comparable to that of *Cnemidaria,* they are evidently convergent in this character. A closer relationship with *Cnemidaria* is seen in the previous *Cyathea petiolata* group.

13. **Cyathea decorata** (Maxon) Tryon, comb. nov.
Figs. 67–68. Map 15.

Hemitelia decorata Maxon, Jour. Arn. Arb. **27**: 439, t. 1. 1946. Holotype: Río Yurumangui, El Valle, Colombia, *Cuatrecasas 15737*, US. Isotype: F! Paratypes (all US): El Valle: Córdoba, Dagua Valley, *Killip 5257;* Costa del Pacifico, Río Cajambre, *Cuatrecasas 17429;* Agua Clara, Buenaventura to Cali, *Killip & Cuatrecasas 38914.* Chocó: Río Condoto, between Quebrada Guarapo and Mandinga, *Killip 35192;* Corcovada Region, upper San Juan, *Killip 35334.* Isoparatypes: *Killip 5257*, GH! NY!, *Cuatrecasas 17429*, F!, *Killip 35192*, GH!

The segments of *Cyathea decorata* are long pubescent on both surfaces and the petiole may be densely and persistently scaly throughout.

Colombia, in wet forest, 5–200 m. Stem to 1 m tall, leaves to ca 1.25 m long.

ADDITIONAL SPECIMEN. **Colombia. Valle:** 22 km. from Buenaventura on road to Río Calima, *Barrington 504* (GH).

14. **Cyathea parva** (Maxon) Tryon, comb. nov.
Figs. 69–71. Map 16.

Alsophila parva Maxon, Jour. Wash. Acad. Sci. **34**: 48, f. 1. 1944. Holotype: near Córdoba, Dagua Valley, El Valle, Colombia, *Killip 5254*, US! Isotypes: GH! NY!

The petiole and rachis are broadly, membraneously green alate (Fig. 71), a character unique in the genus. Other species may have the rachis green alate only toward the apex of the lamina. The indusium is small and appressed.

Colombia. In forest, ca 90 m. Stem a few cm tall, leaves to 75 cm long.

15. **Cyathea speciosa** Willd.
Figs. 72–74. Map 17.

Cyathea speciosa Willd. Sp. Pl. **5**: 490. 1810. Holotype: Caripe (Venezuela), *Humboldt*, Herb. Willd. 20179, B! photo GH. Isotype: Fragm. ex Herb. Kaulf, Herb. Luerssen, P!, photo GH.

Hemitelia speciosa (Willd.) Kaulf. Enum. Fil. 252. 1824.

Hemitelia integrifolia Kl. Linnaea **18**: 539. 1844. Syntypes: Caracas (Venezuela), *Otto 671, Moritz 107*. Lectotype: *Otto 671*, B!

Hemitelia Lindenii Hook. Icones Pl. t. 706. 1848. Holotype: Caracas (Venezuela), *Linden 663*, K!

Cyathea integrifolia (Kl.) Domin, Pterid. 264. 1929.

Cnemidaria integrifolia (Kl.) Tryon, Contrib. Gray Herb. **200**: 52. 1970.

Cnemidaria Lindenii (Hook.) Tryon, Contrib. Gray Herb. **200**: 52. 1970.

The shape of the apex of the pinnae close to the apex of the lamina varies from usually obtuse to rarely attenuate. The lamina apex is sometimes gradually reduced, or it may be abruptly reduced; rarely it is a nearly conform apical pinna.

There is a correlated pattern of variation in the position of the sori and the lobing of the margin of the pinnae. When the margin is quite entire, the sori are submarginal or nearly so (Fig. 74), but when the margin is lobed, the sori are nearly medial, especially those on the basal veins

(Fig. 73). The extremes have often been recognized as distinct species but they clearly represent variations within a single species. Hooker (Species Filicum t. XIIIB) illustrated the variation with entire pinnae as *Hemitelia speciosa.* Klotsch pointed out that this was not the species of Willdenow, and named it *Hemitelia integrifolia.* Hooker did not respond to this suggestion because he later described the lobed variation as a new species, *Hemitelia Lindenii,* a second name for *Hemitelia speciosa sens. str.* This confusion is only of historical interest since it now involves a single species.

Venezuela and Colombia. In dense wet forest, cloud forest, in ravines and gorges, 1000–1700 m. Stem to 2 m tall, leaves to 2 m long.

SELECTED SPECIMENS. **Venezuela. Monagas:** southwest of Caripe, *Steyermark 61970* (MO,NY,US,VEN). **Distrito Federal:** Cerro Naiguatá, *Steyermark 92132* (GH,VEN); cerca de Agua Negra, *Pittier 13740, 13741* (VEN). **Aragua:** Parque Nacional Henry Pittier, *Steyermark 89750* (GH,NY,VEN); Parque Nacional, *Pittier 14997* (VEN); Colonia Tovar, *Fendler 46* (GH,MO). **Colombia. Magdalena:** Sierra Nevada de Santa Marta, *Martin 3395* (MO,US); Santa Marta, *H. H. Smith 1124* (GH,MO).

16. **Cyathea Haughtii** (Maxon) Tryon, comb. nov.

FIGS. 75–76. MAP 18.

Alsophila Haughtii Maxon, Jour. Wash. Acad. Sci. **34**: 46. 1944. Holotype: Cerro Armas, Santander, Colombia, *Haught 1957*, US! Isotype: US!

Cyathea Haughtii, with a very small stem and leaves 20-30 cm (to 40 cm) long, is one of the smallest species in the family.

Colombia. Sandstone cliffs, ca 1400 m.

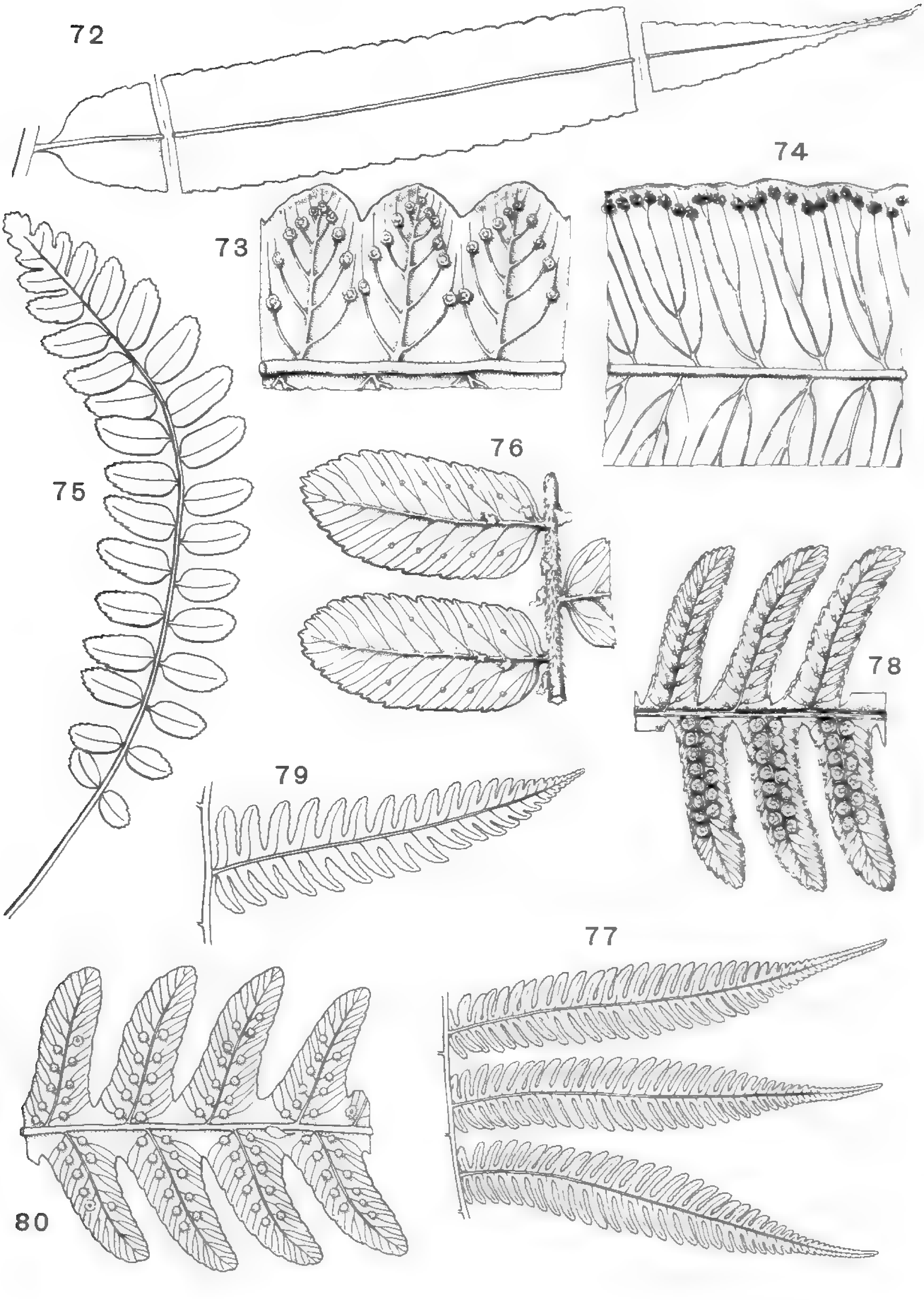
GROUP OF CYATHEA ARBOREA

KEY TO SPECIES 17-19

a. Lamina bipinnate-pinnatifid, to partly tripinnate; indusium with entire margin; West Indies. . . . . 17. *C. arborea.*
a. Lamina pinnate-pinnatifid; Colombia. . . . . b.
  b. Ultimate segments not pubescent above or beneath, a few long trichomes may be present and almost confined to the costules; indusium with the margin irregular, sparingly short dentate-ciliate. . . . . 18. *C. Alstonii.*
  b. Ultimate segments pubescent above and beneath; indusium with the margin long-ciliate with trichomes similar to those on the adjacent leaf surface. 19. *C. peladensis.*

The complete indusium of *Cyathea arborea* with an entire margin is a unique character in the genus. The few collections of *C. Alstonii* and of *C. peladensis* have several differences which may prove to be species characters. The petiole scales of *C. Alstonii* are bicolorous, the lamina is herbaceous in texture, there are very few brownish bullate scales with obtuse to acuminate apex on the costules beneath, and the indusium is cyathiform to deeply cyathiform. The petiole scales of *C. peladensis* are concolorous, the lamina is rigidly coriaceous, there are many light brown to brown bullate scales with a long-attenuate apex on the costules beneath, and the indusium is meniscoid to cyathiform (Fig. 84).

These three species are distinctive but evidently form a natural group, probably derived from a species such as *Cyathea parvula.*



Figs. 72–80. 72–74, *Cyathea speciosa:* 72, Pinna, Colombia, *H. H. Smith 1124* (MO), × ½; 73, Portion of fertile pinna with nearly lobed margin, Venezuela, *Steyermark 61970* (NY), × 1½; 74, Portion of fertile pinna with nearly entire margin, Venezuela, *Fendler 46* (GH), × 1½. 75–76, *C. Haughtii*, Colombia, *Haught 1957* (US): 75, Leaf, × ½; 76, Fertile pinnae, × 1½. 77–78, *C. arborea*, Cuba, *Maxon 3909* (GH): 77, Pinnules, × ½; 78, Portion of fertile pinnule, × 2. 79–80, *C. Alstonii*, Colombia, *Idrobo & Schultes 1130* (US): 79, Pinna, × ½; 80, Portion of fertile pinna, × 1½.

17. Cyathea arborea (L.) Sm.

FIGS. 77–78. MAP 19.

Cyathea arborea (L.) Sm. Mém. Acad. Turin **5**: 417. 1793.

Polypodium arboreum L. Sp. Pl. **2**: 1092. 1753. Holotype: Morne de la Calebasse, Martinique. Filix arborescens, pinnulis dentatis Plumier, Fil. Amer. (Traité Foug.) 1, t. 1; Descr. Pl. Amer. 1, t. 1, 2. Plum. Fil. Amer. t. 2, which Linnaeus did not cite is the same as Descr. Pl. t. 2, except that the sorus and indusium are shown.

Cyathea serra Willd. Sp. Pl. **5**: 491. 1810. Holotype: "Caracas," *Bredemeyer,* Herb. Willd. 20169, B! photo GH, fragm. US! A variation with narrow and lobed fertile pinnules. The species is not known from Venezuela. The specimen may have been obtained from a cultivated plant, or more likely from Puerto Rico where Bredemeyer visited before going to Venezuela.

Cyathea guadalupensis Spreng. Acad. Caes. Leopold. Nova Acta **10**: 233. 1821, *ex char.* In Guadalupa, *Bertier, Perrin.*

Hemitelia serra (Willd.) Desv. Mém. Soc. Linn. Paris **6**: 321. 1827.

Disphenia arborea (L.) Presl, Tent. Pterid. 56. 1836.

Cyathea arborea var. *nigrescens* Hook. Sp. Fil. **1**: 17. 1844. Type: The same as that of *Polypodium arboreum* L.

Hemitelia arborea (L.) Fée, Mém. Fam. Foug. **5** (Gen. Fil.): 350. 1852. Although there is reference neither to Linnaeus, nor to *Polypodium arboreum,* the basionym can be readily traced through the reference to Presl.

Cormophyllum arboreum (L.) Newm. Phytol. **5**: 238. 1854.

Cyathea nigrescens (Hook.) J. Sm. Ferns Brit. For. 242. 1866.

Cyathea barbata Kuhn, Linnaea **36**: 164. 1869. Holotype: Guadaloupe, *L'Herminier 3,* B! fragm. NY! Isotype: P! photo GH, fragm. ex K, NY!

The petiole scales are usually whitish and concolorous, or they may have tinges of very light brown centrally or basally. They vary to rarely also tinged with brown along the edges (*Hodge 7,* Dominica, GH) or brown at the base (*Proctor 21785,* Martinique, GH). Sterile leaves usually have a white scale at the base of the costule beneath.

The indusium is always complete and surrounds the receptacle. It varies in its development from discoid or meniscoid with an only slightly, if at all, elevated margin, to deeply cyathiform. A geographic analysis of this variation (Table 2) indicates that the moderately well-developed indusia (deeply meniscoid) are rather equally distributed throughout the range, while the better developed indusia form 77% of the sample from the Greater Antilles, and the least developed ones form 51% of the sample from the Lesser Antilles. The variation is not clinal, but exhibits a sharp break between the two regions (Table 1, Map 19).

Juvenile plants of *Cyathea arborea* have, among other characters, a narrower lamina than adult leaves. A specimen from Dominica (*Lellinger 642,* GH) has some plants with leaves 9 cm long, the lamina narrowly ovate-acuminate and pinnate-pinnatifid. Another from Puerto Rico (*Jones 10995,* GH) has a stem about 1 cm long and erect, with roots to 25 cm long, the larger leaves are 30 cm long with the lamina 13 cm long, pinnate-pinnatisect and broadly ovate-acuminate. Specimens of leaves with the lamina about 30 cm long essentially have the adult characters of an ovate, bipinnate-pinnatifid lamina.

Greater Antilles and Lesser Antilles south to Grenada. *Cyathea arborea* typically grows in montane forests, in humid ravines, along water courses and on mountain slopes, from sea level to 1200 m, usually from 500–800 m. It frequently persists in cutover land, along forest borders and in forest clearings. It is successful as a pioneer species, often becoming established in disturbed habitats such as landslides, road cuts and spills and on abandoned land. Stem to 10 m tall; leaves to 4 m long.

SELECTED SPECIMENS. **Cuba. Pinar del Rio:** Rangel, upper Taco-Taco River, *León 12721* (NY). **Las Villas** (Santa Clara): Loma Ventana, Trinidad Mountains, *Howard 5221* (GH,MO,NY); Mina Carlotta, Sierra de San Juan, *Senn 386* (F,GH,MO). **Oriente:** Rio Bayamito, Sierra Maestra, *Maxon 3906* (GH,NY), *3909* (GH,NY,US); Rio Navas, *Shafer 4379* (GH,MO,NY); Firmeza to Gran Piedra, *Shafer 8957* (GH,MO,NY); Sierra de Nipe, *Ekman 1805, 3368* (NY); Baracoa, *Pollard, et al. 45* (F,GH,MO,NY). **Jamaica.** Valley of Rio Grande, 7 miles s. of Port Antonio, *Gastony 38* (GH); Bloxburgh, Port Royal mountains, *Maxon 8757* (GH,NY); between House Hill and Cuna Cuna Gap, *Maxon 8886* (GH,NY); above Bowden Pen, to Bath via Cuna Cuna Pass, *Crosby & Anderson 1044* (F,GH,NY); Crooks Bottom, n. of Ipswich, *Maxon & Killip 1449* (F,GH, NY); Quashiba Mountain, 1 mile w. of Georges Plain, *Wilson & Webster 518* (A,US); Hermitage Dam, St. Andrew Parish, *Proctor 3914* (MO); near Cambridge, *Chrysler 1850* (MO). **Haiti.** Vicinity of Plaisance, *Leonard 9365* (GH,NY); vicinity of St. Louis du Nord, *Leonard & Leonard 14256* (GH,NY); vicinity of Port de Paix, *Leonard & Leonard 15707* (MO); Bayeux, Morne Brigand, *Eckman H2954* (NY); Petit Borgne, *Nash 470* (NY). **Dominican Republic.** Sonadór, Prov. La Vega, *Valeur 396* (F,MO); near Barahona, *Türckheim 2716* (F,GH,MO,NY); Laguna, Samaná Peninsula, chiefly on the Pilón de Azúcar, *Abbott 410* (GH,NY); Río Cataline, Las Cañitas, *Abbott 2710* (GH), *2712* (NY); Liali, *Abbott 2612* (GH) between Miches and El Seibo, *Gastony, Jones & Norris 702* (GH,NY). **Puerto Rico.** Sierra de Luquillo, *Sintenis 1375* (A,MO,NY); Adjuntas, *Sintenis 4242* (A,GH); El Verde Experiment Station, *Little 13071* (A,F,NY); vicinity of Barranquitas, *Britton et al. 6622* (F,NY); Fajardo and vicinity, Rio Aribe, *Britton & Shafer 1693* (F,GH,MO,NY); 14 miles ne. of Mayaguez, *Heller 4467* (F,GH,MO,NY); between Caguas and Cayey, *Underwood & Griggs 287* (NY); Sierra de Naguabo, Rio Icaco and adjacent hills, *Shafer 3518* (F,GH,MO,NY). **St. Thomas.** Hopedale, Crown, *Britton & Marble 1422* (F,NY). **Tortola.** Sage Mountain, *Fishlock 381* (NY), *D'Arcy 48D* (GH). **Saba.** *Boldingh 2170* (GH). **St. Kitts.** *Britton & Cowell 165, 286, 331* (NY); *Box 377* (F). **Nevis.** *Proctor 19481* (A). **Montserrat.** *Shafer 175, 343* (F,NY); *Howard 11905* (GH); *Proctor 19169* (A).

TABLE 2. GEOGRAPHIC VARIATION IN THE DEVELOPMENT OF THE INDUSIUM OF *Cyathea arborea*. (Based on three mature indusia from each of 140 collections, see Map 19.)

	Deeply Cyathiform	Cyathiform	Deeply Meniscoid	Meniscoid	Discoid
Greater Antilles					
88 collections	15	53	18	2	0
% of collections	17	60	20	3	0
Puerto Rico					
25 collections	3	14	6	2	0
% of collections	12	56	24	8	0
Lesser Antilles					
52 collections	0	10	15	20	7
% of collections	0	19	29	38	13
Tortola to Nevis					
11 collections	0	2	2	6	1
% of collections	0	18	18	54	9

Guadeloupe. Matouba, *Scamman 8142* (GH); Bois de Bains, *Duss 4322* in 1896 (NY); Morne Papaye, *Duss 4322* in 1892 (NY); south of La Citerne, *Proctor 20135* (A). **Dominica.** *Hodge 6* (GH,MO), *7* (GH); *Hodge & Hodge 2444, 2880* (GH); *Lloyd 333, 653* (NY); *Lellinger 354, 642* (GH); *Wilbur 8055, 8288* (NY). **Martinique.** *Duss 1604* (F,GH,MO,NY); *Sieber, Syn. Fil. 194* (MO,NY-fragm.); *Stehlé 3309* (F), *6081* (MO); *Bailey & Bailey 279* (GH,NY). **St. Lucia.** *Howard 11353* (NY); *Proctor 17829* (GH). **St. Vincent.** *Eggers 6610* (F,GH), *6921* (F), *6996a* (F,GH); *Morton 5193* (GH). **Grenada.** *Eggers 6083* (F,GH,US); *Broadway* (F,GH); *Sherring* (NY).

18. **Cyathea Alstonii** Tryon, spec. nov.

Figs. 79–80. Map 20.

Folia ad 75 cm longa; petiolus ca 25 cm longus squamis structura marginata discordanter valde bicoloribus vel fere concoloribus; lamina 1-pinnato-pinnatifida; pinnae ad 12 cm longae sessiles, pagina inferiore glabra vel squamis paucis bullatis brunneis; sori plerumque subcostales ad furcam venarum; indusium cyatheoideum vel profunde cyatheoideum margine irregulari breviter dentato-ciliato. Holotypus: Pico Renjifo, Central Mountains, Sierra de la Macarena, Intend. Meta, Colombia, *Philipson, Idrobo & Jaramillo 2157* (BM, photo GH). Paratypus: Macizo Renjifo, Cordillera La Macarena, Meta, Colombia. *Idrobo & Schultes 1130* (US).

An endemic of the Macarena, growing on sandstone rocks at 1300-1900 m.

19. **Cyathea peladensis** (Hieron.) Domin

Figs. 81–84. Map 21.

Cyathea peladensis (Hieron.) Domin, Pterid. 263. 1929.

Alsophila peladensis Hieron. Hedwigia **45**: 233, t. 13. 1900. Holotype: Cerro Pelado (upper Magdalena Valley), Colombia, *Stübel 1259*, B!, photo GH.

All leaves of the holotype of *Alsophila peladensis* at Berlin are sterile, in spite of the fact that Hieronymus described sori as ". . . soris in bifurcatione venarum medio inter marginem et costam sitis usque 8-jugis." The "fertile" pinna illustrated in t. 13, f. 3a shows numerous small bullate scales, rather than sori. More recent collections of this species are fertile and are very similar in other characters to the sterile Stübel collection.

Colombia, 2300–2400 m. Stem to 3 m tall, leaves to 1 m long.

ADDITIONAL SPECIMENS. **Colombia. Huila-Cauca boundary:** Head of Río Villa-lobos, southwest of Pitalito, Cordillara Central, *Fosberg 19950* (US). **Huila:** Comisaría del Caquetá, *Cuatrecasas 8507* (F). **Putumayo:** Cerro Portachuelo, Sibundoy to Pepino, *Soejarto 1569* (GH).

GROUP OF CYATHEA PALLESCENS

KEY TO SPECIES 20-22

a. Fertile veins regularly forked, rarely a few simple. . . . . b.
  b. Large scales of the petiole scurf flattish, elongate to sometimes ovate; Mexico to Panama, British Guiana to Colombia and south to Peru. . . . . . . 20. *C. divergens*.
  b. Large scales of the petiole scurf mostly (or many of them) crested, expanded into two or more planes above the base and usually dissected, at least apically, or rarely larger scales absent and only squamellae present; Colombia to Bolivia. . . . . 21. *C. pallescens*.
a. Fertile veins all simple; Venezuela. . . . . 22. *C. simplex*.

The single collection of *Cyathea simplex* is unique among species with large ultimate segments in its simple fertile veins. *Cyathea divergens* and *C. pallescens* are both highly variable species. Within the range of *C. pallescens,* the two can nearly always be separated, in addition to the petiole scurf characters mentioned in the key, by the long-stalked pinnules of *C. divergens* and the sessile to short-stalked pinnules of *C. pallescens.* Only rarely does *C. pallescens* have some of the pinnules long-stalked.

The three species are probably a natural group. A species similar to *Cyathea pallescens* was probably ancestral to the four local endemics of the next group, and perhaps to *C. fulva* of the following group.

22

Map 22. Geography of variation in pinnule characters of Cyathea divergens: Left series, top to bottom: *Hernandez & Sharp X472* (us), *Johnson 966* (gh), *Stone & Stone 2700* (gh), *Johnson 967* (gh), *Pennell 9311* (ny), *Cuatrecasas 13919* (gh), *Ewan 16031* (gh), *Harling et al. 10178* (gh). Right series, top to bottom: *Tonduz 11789* (ny), *Ulloa 102* (gh), *Wilbur et al. 11077* (ny), *Steyermark et al. 105688* (gh), *Steyermark & Wurdack 717* (ven), *Steyermark 93918* (us), *Poeppig* (p).

20. **Cyathea divergens** Kze.

MAP 22.

Cyathea divergens is a highly variable species, for example, the pinnules may be glabrous beneath or there may be indument of trichomes, flattish scales, or bullate scales. The size of the pinnae and pinnules varies, and also their shape and the length of their stalks. The variation is highest in Colombia and Venezuela. A selection of the variation in pinnule characters is presented in Map 22, where a weak correlation with geography may be observed.

It is not possible to recognize two species, but the Mexican and Guatemalan element, var. *Tuerckheimii*, is sufficiently distinctive to merit infraspecific rank. The geography reinforces the characters of the variety and there is a relatively strong break in the variation between Mexico-Guatemala and Costa Rica-Panama. Table 3 provides the principal differences between var. *divergens* and var. *Tuerckheimii.*

Mexico and Guatemala, Costa Rica and Panama, British Guiana to Colombia and south to Peru.

20a. **Cyathea divergens** var. **divergens**

FIGS. 85–87. MAP 23.

Cyathea divergens Kze. Linnaea **9**: 100. 1834. Holotype: Pampayaco, Peru, Jul. 1829, *Poeppig* (Diar. *1163*), LZ, destroyed. Authentic specimens: *Poeppig 219* (Diar. *1152*), B! P! *photo* GH, fragm. ex B,NY!, ex K,NY!

Cyathea equestris Kze. Linnaea **9**: 100. 1834. Holotype: Cerro de Cristobal, Pampayaco, Peru, Jul. 1829. *Poeppig*, LZ, destroyed (Kze. Frarnkr. 1: t. 76), fragm. K! det. Kze., photo GH. In synonomy of *Cyathea divergens* by Mett. Ann. Sci. Nat. V, **2**: 265. 1864.

Cyathea globularis Presl, Epim. Bot. 30. 1849, *ex char.* Holotype: Nova Granada, *Linden.*

Cyathea equestris var. *boconensis* Karst. Linnaea **28**: 456, 1856, *ex char.* and Karst. Fl. Columb. **2**: t. 185, f. 7. Holotype: Páramo de Bocono, Sierra de Merida, (Venezuela), *Karsten.*

Cyathea calva Karst. Fl. Columb. **2**: 175, t. 192. 1869. Holotype: Sierra de Merida, Escuque, 1000 m, Venezuela, *Karsten.* Type collection: Escuque, 1000 m, *Karsten 127*, B! fragm. ex B,NY!, ex Rosenst. US!

Cyathea petiolulata Karst. Fl. Columb. **2**: 163, t. 185. 1869. Holotype: Merida, Venezuela, 2000-2500 m, *Karsten.* Authentic specimen: Merida, *Karsten 135*, B!

Cyathea petiolulata var. *boconensis* (Karst.) Karst. Fl. Columb. **2**: 164. 1869, based on *C. equestris* var. *boconensis,* not *Cyathea boconensis* Karst.

Cyathea firma Kuhn, Linnaea **36**: 163. 1869. Holotype: Merida, Venezuela, *Funck & Schlim 1228.* Fragm. US!

Alsophila subaspera Christ, Pittier, Prim. Fl. Costaric. **3** (1) (Filices 2nd Mém.): 43. 1901. Syntypes: forêts du Copey, Costa Rica, *Tonduz 11787*, A! GH! NY! P! US!, *11802* P! fragm. ex B,NY!, ex BR,NY!, *12183*, NY!

Cyathea petiolulata var. *pastoensis* Hieron. Engl. Bot. Jahrb. **34**: 437. 1904, *ex char.* Holotype: prope Altaquer et San Pablo, Cordillera de Pasto, Colombia, *Lehmann 81.*

Cyathea pelliculosa Christ, Bull. Herb. Boiss. II, **4**: 946. 1904. Syntypes: Costa Rica, *Werklé 45*, P!, *Werklé 50.*

Cyathea divergens var. *minor* Rosenst. Fedde, Rep. Spec. Nov. **22**: 2. 1925. Lectotype: La Palma, Costa Rica, *Brade & Brade 108.* Isolectotype: NY! *(Brade & Brade 853* is excluded as a type, it is *Cyathea gracilis.)*

Cyathea subaspera (Christ) Domin, Pterid. 263. 1929.

Cyathea calva var. *firma* (Kuhn) Domin, Acta Bot. Bohem. **9**: 102. 1930.

Cyathea divergens var. *hirta* Losch, Mittl. Bot. Staatssaml. München **1**: 20. 1950, *ex char.* Holotype: Chirripó Grande, Costa Rica, *Kupper 1265*, M.

A collection from the Chimantá Massif in the Guayana region of Venezuela, *Steyermark & Wurdack 717*, has very coriaceous, narrow leaves, the pinnae ca 35–40 cm long, rather few long-stalked pinnules and an acute lamina apex. This may represent a local Tepuí endemic but the evidence is insufficient to recognize it as a separate variety. Another collection from Auyan-tepuí, Guayana, (*Steyermark 93918*) is rather intermediate between the above collection and typical var. *divergens* in Venezuela. A specimen from Colombia (*Killip 11392*) has a more or less cyatheoid indusium which is very thin, breaking into segments at maturity.

Differences from the superficially similar *Cyathea corallifera* are mentioned under that species.

Costa Rica and Panama, British Guiana west to Colombia and south to Peru. In humid mountain forests, often cloud forests and often persisting in cutover land. In Central America at elevations of 900–2600 m, usually at 1400–1800 m; in South America from 1300–2500 m, usually at 1600–2200 m. Stem to 15 m tall, the leaves to 6 m long.

SELECTED SPECIMENS. **Costa Rica. Heredia:** Isla Bonita, Vallé du Sarapiqui, *Pittier 14160* (MO,NY); Cinchona, upper Sarapiqui valley, *Scamman 7862* (GH). **Guanacaste:** northern (Salazar) slopes of Volcán Orosi, *White & Lucansky 1968–74* (GH). **San Jose:** vicinity of El General, *Skutch 2964* (GH,MO,NY); 25 km. n. of San Isidro del General, toward Cerro de la Muerte, *Gastony & Gastony 755, 759* (GH). **Cartago:** El Cedral near Naranjo river, *Nisman 124* (GH); Pacayas, foot of Volcán Turrialba, *Scamman 7005* (GH). **Puntarenas:** Cantón Golfito, *Nisman 138, 140* (GH); Monteverde, *Nisman 156* (GH). **Panama. Chiriquí:** Casita Alta, Volcán de Chiriqui, *Woodson, Allen & Seibert 922* (GH,MO,NY); Cerro Punta, *Allen 3529* (MO); above El Boquete, *Maxon 5691* (GH,NY); Río Piedra Candela, road to Las Mellisas, *McAlpin 2192* (GH); Cerro Horqueta northwest of Boquete, *Burch 548* (GH,NY). **British Guiana** (Guyana). Mount Roraima, *Tate 428* (NY), *479* (NY). **Venezuela. Bolivar:** Ptari-tepuí, *Steyermark 59588, 59811* (GH,MO,NY,US); Cerro Venamo, *Steyermark, et al. 92701* (GH,VEN); Auyan-tepuí, *Steyermark 93918* (GH,NY,VEN); Meseta de Jauá, *Steyermark 98097* (GH); Sarvén-tepuí, *Wurdack 34115* (GH,NY,US); Churi-tepuí (Muru-tepuí), *Wurdack 34285* (GH,NY,US); Chimantá Massif, headwaters of Río Tirica, *Steyermark & Wurdack 717* (GH,NY,US,VEN). **Amazonas:** Sierra Parima, *Steyermark 105973* (GH). **Lara:** 10 km. ne. de El Blanquito, Dist. Jiménez, *Steyermark et al. 103580* (GH,NY). **Merida:** Loma de San Jacinto, *Bernardi 1868* (NY). **Colombia. Magdalena:** Cincinati region, *Espina & Giacometto A134* (G); Sierra Nevada de Santa Marta, *H. H. Smith 2225* (F,GH,NO,NY,US). **Bolivar:** Antizales, *Pennell 4455* (F,GH,MO,NY). **Norte de Santander:** Loso, north of Toledo, *Killip & Smith 20407* (GH,NY). **Antioquia:** San Antonio del Prado, *Daniel 3017* (GH). **Caldas:** above Salento, *Pennell 9311* (GH,NY) south of Salento, *Hazen 9693* (GH,NY,US). **Cundinamarca:** Fusagasuga, *Lindig 282* (GH); Bogotá, *Lindig 309* (NY); 20 km. south of Bogotá, *Barrington 464* (GH). **Valle** (Valle del Cauca): La Cumbre, *Killip 5684* (GH), *11392* (GH,NY,US); Monte Frio, Yanaconas, *Killip & Garcia 33711* (F,GH,NY); El Cairo, entre Darién y Mediacanoa, *Cuatrecasas 13919* (F,GH). **Cauca:** km. 19, Cali to Buenaventura, *Barrington 500* (GH). **Huila:** 30 km. east-southeast of Baraya, *Little 8846* (US); Hacienda Balsillitas, Meta to El Cedral, *Little 8040, 8044* (GH,US); Rio Sauza, sw. of Alajandría, *Little 8535* (GH,US). **Nariño:** 2 km. above San Juan, *Ewan 16031* (US). **Ecuador. Tungurahua:** Río Verde, *Harling et al. 10178* (GB,GH). **Peru. Huánuco:** Cushi, *Macbride 4819* (F); Pampayacu, *Kanehira 120* (GH). **Cuzco:** Sahuayacu, Chaupiorcco, *Bües 840* (US).

TABLE 3. DISTINGUISHING CHARACTERS OF *Cyathea divergens* var. *divergens* AND var. *Tuerckheimii*.

	var. *divergens*	var. *Tuerckheimii*
Pinna stalk	Usually long-stalked (the stalk longer than the width of the basal pinnule), especially the basal pinnae and those toward the base.	Usually short-stalked (the stalk shorter than the width of the basal pinnule).
Pinnule stalk	Usually long-stalked (the stalk longer than the width of the basal segment of the pinnule), often twice as long, especially on basal pinnules.	Usually short-stalked (the stalk shorter than the width of the basal segment), or all except a few basal pinnules so, or pinnules sessile.
Pinnule shape	Often long-triangular, or tapering to the apex from just above the base.	Usually tapering to the apex from about the middle.
Apex of lamina	Long acuminate.	Acute to acuminate.
Orientation of the lamina	Drooping from beyond the middle.	No data.
Distribution	Costa Rica and Panama, British Guiana west to Colombia and south to Peru.	Mexico and Guatemala.

20b. **Cyathea divergens** var. **Tuerckheimii** (Maxon) Tryon, comb. nov.

FIGS. 88–90. MAP 24.

Cyathea Tuerckheimii Maxon, Contrib. U.S. Nat. Herb. **13**: 4. 1909. Holotype: near Cobán, Alta Verapaz, Guatemala, Feb. and Nov. 1907, *Türckheim II 1645,* US! Isotypes: F! GH! MO! NY! Paratypes: between Cobán and Tactic, Guatemala, Dec. 1907, *Türckheim II 2031,* US!; near Cobán, Guatemala, April, 1887, *Türckheim (J. D. Smith no. 1238),* US! Isoparatypes: *Türckheim II 2031,* GH! MO! NY!, *Smith 1238,* GH! NY!

Cyathea Sartorii Salomon, Nomencl. Gefässkrypt. 144. 1883, *nom. nud.* Mirador, Mexico, *Sartorius,* fragm. ex B,NY! bears this name.

The more abrupt, rather than elongate, lamina apex of *Cyathea divergens* var. *Tuerckheimii* suggests that the leaf probably does not have the pronounced drooping habit of var. *divergens*. However, field observations are needed to confirm this character. *Skutch 1162,* Guatemala, is a variation with a cyatheoid indusium.

Veracruz and southern Mexico to Guatemala. Predominantly in cloud forests, especially those of *Quercus* and *Liquidambar* at elevations of 750–3100 m, usually at 1500–2500 m. Stem to 10 m tall, the leaves to 3 m long.

SELECTED SPECIMENS. **México. Veracruz:** Cerro de San Cristobal, *H. Xolocotzi & Sharp X–1163, 1164* (US); Cordoba, *Farlow* (GH); Orizaba, *Pringle 6088* (GH); Mirador, *Purpus 15312a* (F). **Chiapas:** Laguna Ocotal Grande, Municip. de Ocosingo, *Dressler 1688* (GH,NY,US); Sierra de Soconusco, *H. Xolocotzi & Sharp X–472* (US). **Guatemala. Huehuetenango:** San Juan Atitlán, *Skutch 1162* (GH); Cerro Negro, 2 miles e. of Las Palmas, *Steyermark 51677* (F,GH,US); between San Mateo Ixtatán and Nuća, *Steyermark 49787* (F,GH,US). **San Marcos:** southeast portion of Volcán Tacaná, *Steyermark 36394* (F,US). **El Quiche:** Nebaj, *Skutch 1698* (GH). **Chimaltenango:** Chichavac, *Skutch 743* (US). **Alta Verapaz:** Samac, *Johnson 960, 961* (F,GH,NY);

Chihob, *Johnson 966* (GH,MO). **Baja Verapaz:** 10 km. north of Pantin, *Hellwig & Whitaker 1433* (GH). **Zacapa:** Sierra de las Minas, *Steyermark 29801* (F), *30057* (F,US). **Jalapa:** Volcán Jumay, *Steyermark 32466* (F,US).

21. Cyathea pallescens (Sod.) Domin

FIGS. 91–92. MAP 25.

Cyathea pallescens (Sod.) Domin, Pterid. 263. 1929. Chosen over *Cyathea cystolepis* Sod. because of the more certain typification.

Alsophila pallescens Sod. Rec. Crypt. Vasc. Prov. Quit. 20. 1883. Holotype: bosques de Nanegal, Ecuador, *Sodiro*. Type collection: P! photo GH.

Cyathea cystolepis Sod. Rec. Crypt. Vasc. Prov. Quit. 15. 1883. Syntypes: Crecen en la pendiente occidental del Atacazo y del Corzón, 1600, 2000 m, Ecuador, *Sodiro*. Authentic specimen: in sylv. apud Niebly, Ecuador, 1/1883, *Sodiro*, P! fragm. ex Rosenst. US!

Hemitelia cystolepis (Sod.) Baker, Ann. Bot. **5**: 187. 1891.

Cyathea Borjae Sod. Crypt. Vasc. Quit. 504. 1893, *ex char.* Holotype: en la parroguia de Santo Domingo, Ecuador, *Sodiro*.

Hemitelia subcaesia Sod. Crypt. Vasc. Quit. 522. 1893. Holotype: bosques subandinos de la cordillera occidental hasta 2,800 m, Ecuador, *Sodiro*. Specimens seen: Niebly, *Sodiro*, NY!; Canzacoto, 5/1882, *Sodiro*, P! photo GH; Ecuador, 4/1874, *Sodiro*, US!

Cyathea asperata Sod. Sert. Fl. Ecuad. **2**: 9. 1908. Holotype: Pichincha, Ecuador, 3/1906, *Sodiro*. Type collection: NY! US!

Cyathea asperata var. *brevipes* Sod. Sert. Fl. Ecuad. **2**: 10. 1908, *ex char.* No specimen cited.

Cyathea brachypoda Sod. Sert. Fl. Ecuad. **2**: 8. 1908. Holotype: Sylv. subandin. vulc. Atacazo, Ecuador, *Sodiro*. Specimens seen: Atacazo, 7/1906, *Sodiro*, GH! MO!; Atacazo, 7/1907, *Sodiro*, NY! US!

Cyathea muricatula Sod. Sert. Fl. Ecuad. **2**: 10. 1908. Holotype: Corazón, Ecuador, 12/1907, *Sodiro*. Type collection: MO! P! US!

Cyathea nitens Sod. Sert. Fl. Ecuad. **2**: 3. 1908. Holotype: Silv. sub-andin. occid. vulc. Corazón, Ecuador, *Sodiro*. Type collection: Corazón, 12/1907, *Sodiro*, MO! P! US!

Cyathea ochroleuca Sod. Sert. Fl. Ecuad. **2**: 11. 1908. Holotype: Silvis subandin. occid. vulc. Atacazo, Ecuador, 7/1907, *Sodiro*. Type collection: Atacazo, Julio 8/1907, *Sodiro*, P! photo GH; Atacazo, 7/1907, *Sodiro*, NY! US!

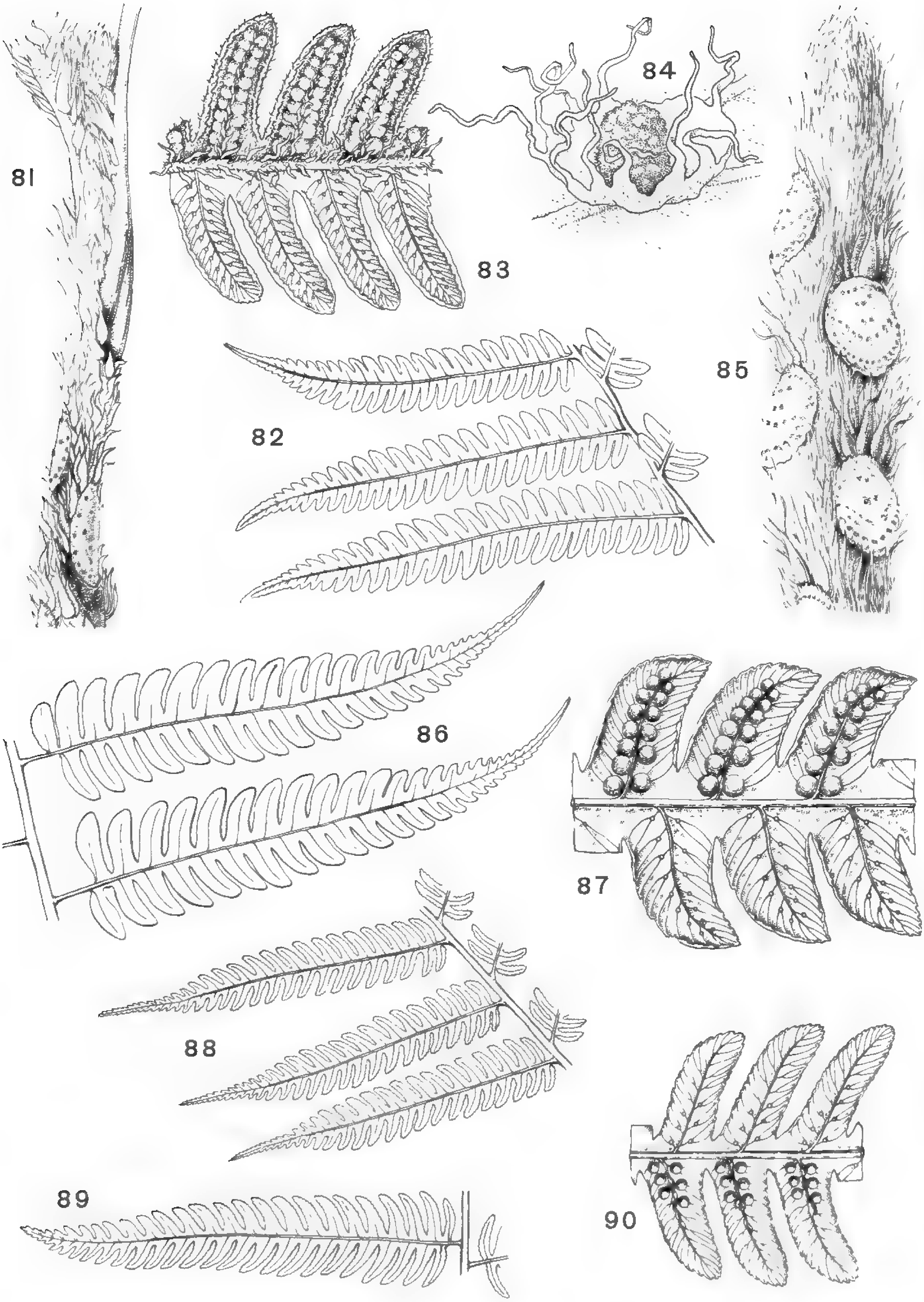
Cyathea subinermis Sod. Sert. Fl. Ecuad. **2**: 10. 1908. Holotype: Silvis subandinis vulcani Atacazo, Ecuador, 7/1907, *Sodiro*. Specimens seen: Pichincha et Atacazo, 1906-1907, *Sodiro*, GH! MO! P! photo GH.

Cyathea tungurahuae Sod. Sert. Fl. Ecuad. **2**: 12. 1908. Holotype: Silvis subandin. vulc. Tungurahuae, Ecuador, *Sodiro*. Type collection: Tungurahua, 8/1901, *Sodiro*, P! photo GH,US!

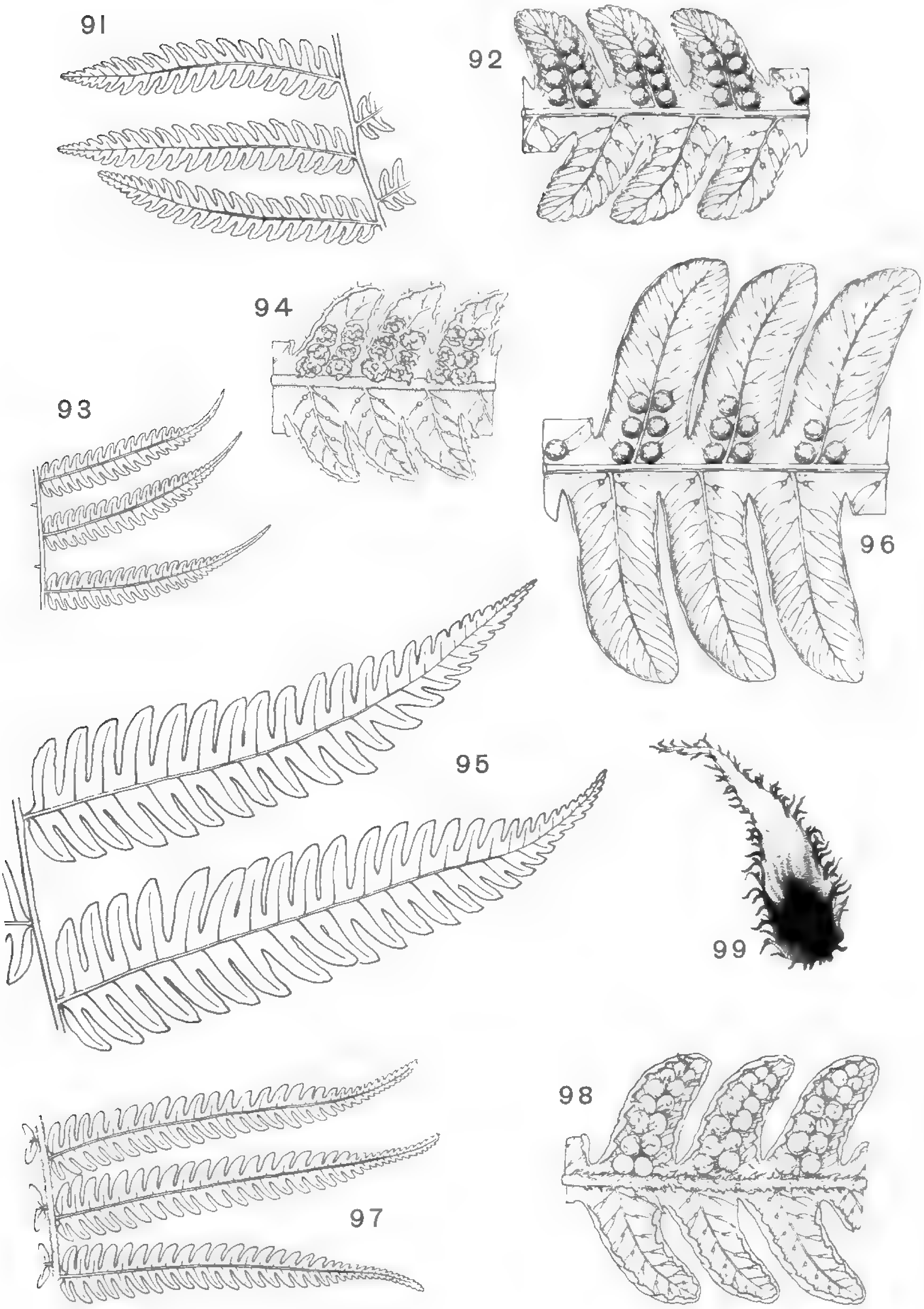
Cyathea subcaesia (Sod.) Domin, Pterid. 264. 1929.

The accurate typification of many of Sodiro's names is difficult because (a) he did not use collection numbers; (b) he often did not cite collection data fully, or he combined two or more collections in one citation; and (c) there is no catalogue of the Sodiro herbarium that remains in Ecuador. I believe that the most complete set of Sodiro's ferns is at Paris, but because of doubt I often hesitate to designate them as holotypes or lectotypes. These do not include, of course, the new species described by Baker from some 200 specimens sent earlier by Sodiro to Kew.

Cyathea pallescens is a highly variable species in several of its characters. The petiole scales are usually not long persistent, although they are in some specimens from Colombia (*Madison 861*). The petiole scales



FIGS. 81–90. 81–84, *Cyathea peladensis*, Colombia, *Soejarto 1569* (GH): 81, Apical portion of stem, × ½; 82, Pinnae, × ½; 83, Portion of fertile pinna, × 2; 84, Receptacle and indusium, enlarged. 85–90, *C. divergens:* 85–87, var. *divergens:* 85, Apical portion of stem, Venezuela, *Steyermark & Wurdack 717* (NY), × ½; 86, Pinnules, Costa Rica, *Scamman 5884* (GH), × ½; 87, Portion of fertile pinnule, source as in 86, × 2. 88–90, var. *Tuerckheimii:* 88, Pinnules with short stalks, Guatemala, *Skutch 1162* (GH), × ½; 89, Pinnule with longer stalk, Guatemala, *Johnson 961* (GH), × ½; 90, Portion of fertile pinnule, source as in 88, × 2.



FIGS. 91–99. 91–92, *Cyathea pallescens*, Ecuador, *Mexia 7600:* 91, Pinnules, (GH), × ½; 92, Portion of fertile pinnule, (US), × 2. 93–94, *C. simplex*, Venezuela, *Maguire 35194* (GH): 93, Pinnules, × ½; 94, Portion of fertile pinnule, × 2½. 95–96, *C. corallifera*, Ecuador, 1874, *Sodiro* (MO): 95, Pinnules, × ½; 96, Portion of fertile pinnule, × 1½. 97–99, *C. boliviana*, Bolivia, *Steinbach 9512* (GH): 97, Pinnules, × ½; 98, Portion of fertile pinnule, × 2½; 99, Scale from costa, enlarged.

are usually strongly bicolorous, but in some collections they may be whitish, tinged with brown or with brown streaks as in *Dudley 11149,* from Peru, or they may be more irregularly tinged with brown. The petiole scurf may consist only of the characteristic crested squamellae, or it may be of appressed and strongly flattened, more or less entire to crested, squamellae at the base of the petiole. The pinnules are sometimes finely pubescent above. They may be essentially glabrous beneath or they may have one or more of the following types of indument, which may be sparse to abundant: narrow, elongate, flattish, whitish scales, whitish to brown bullate scales, with a short or long tip, large trichomes, and strongly dissected small, whitish scales. *Spruce 5367* from Ecuador, has at least some of the indusia urceolate, or partially open on one side.

Colombia to Bolivia. Usually in cloud forests, but sometimes above in paramillo woods or thickets, and sometimes below in montane forest, at elevations of 1200–3500 m, most often at 2500–3000 m. Stem to 10 m tall, leaves to 4.5 m long.

SELECTED SPECIMENS. **Colombia. Cundinamarca:** below Alto de Cuchuco, 7 km southwest of Sibate, *Tryon & Tryon 6113* (GH,NY); Manzanos, Cordillera de Bogotá, *Lindig 289* (GH,US). **Tolima:** 30 km west of Cajamarca, *Madison 861* (GH). **Cauca:** región de Moscopán, *Cuatrecasas 23486* (F). **Huila:** Commis. del Caqueta, *Cuatrecasas 8418, 8438* (F); 20 km southeast of Garzón, *Little 9391* (US). **Nariño:** 3 km north of Victoria, Río Chingual drainage, *Ewan 16182* (GH,US). **Ecuador. Carachi:** Canton Tulcan, near Pun, *Mexia 7600* (F,GH,MO,US). **Pichincha:** vicinity of Huigra, *Rose & Rose 22508* (GH,NY,US), *22605* (GH,NY); between Nono and Tandayápi (Tandayapa), *Sparre 16753* (GH), *Lockwood 800* (GH). **Peru. Cuzco:** Cordillera Vilcabamba, Prov. Convencion, *Dudley 10864, 10950B* (GH), *11149* (GH,US); Camino Panticolla, Prov. Convencion, *Vargas 19857* (GH). **Bolivia. Cochabamba:** Sailapata, *Cardenas 3150* (GH); between Pojo and Comarapa, on the Cochabamba–Santa Cruz road, *Ugent & Ugent 5111* (GH,US).

22. **Cyathea simplex** Tryon, spec. nov.

FIGS. 93–94. MAP 26.

Folia ca 1.5 m longa; petiolus ca 50 cm longus squamis structura marginata discordanter valde bicoloribus marginibus ciliatis; lamina bipinnato-pinnatifida; pinnulae pagina inferiore fere glabra; sori inframediales in venis simplicibus; indusium sphaeropteroideum. Holotypus: Cerro Yutaje, Serranía Yutaje, Río Manapiare, Terr. Amazonas, Venezuela, *Maguire & Maguire 35194,* NY. Isotype: GH,US.

A very distinctive species, with simple fertile veins in relative large ultimate segments.

Venezuela, 1250 m.

GROUP OF CYATHEA STRAMINEA

KEY TO SPECIES 23-26

a. Flattish scales on the costa, and sometimes on the costules, beneath ca 1-2 mm long, and some with dark, opaque peripheral or apical processes (Fig. 99). . . . . . . b.
 b. Squamellae of the petiole scurf nearly entire to slightly dissected. . . . . c.
  c. Larger pinnules 3-5 cm broad, short-stalked, whitish scales and trichomes on the segments beneath; Ecuador. . . . . 23. *C. corallifera.*
  c. Larger pinnules 1-2 cm broad, sessile to subsessile; brownish scales and few trichomes on the segments beneath; Colombia. . . . . 25. *C. straminea.*
 b. Squamellae of the petiole scurf strongly dissected into trichome-like arms, larger pinnules 1-2 cm broad, sessile to subsessile, Bolivia. . . . . 24. *C. boliviana.*

a. Flattish scales on the costa, and sometimes on the costules, beneath up to 3.5 mm long, with the marginal cilia the same color as the brown central portion of the body; Peru. .... 26. *C. Ruiziana.*

A group of four apparently quite distinctive species, although further collections of them will certainly demonstrate variation in some of the characters. The characters of the petiole scurf are evidently important; they are presented in Table 4 to provide additional information to that given in the key. The species represent a radiation from an ancestral type similar to *Cyathea pallescens.*

23. **Cyathea corallifera** Sod.

Figs. 95–96. Map 27.

Cyathea corallifera Sod. Rec. Crypt. Vasc. Prov. Quit. 11. 1883. Syntypes: Crece en los declives del Corazón y del Atacazo (Miligallí-S. Florencio), 1500-2000 m, Ecuador, *Sodiro.* Authentic specimens: Corazón, 1882, *Sodiro,* P! photo GH; Atacazo, prop. Canzacoto, 5/1882, *Sodiro,* NY!

Cyathea aspidioides Sod. Rec. Crypt. Vasc. Prov. Quit. 14. 1883, not (Bl.) Moritz, Syst. Verz. Java 108. 1845. Syntypes: Crece en los bosques del Corazón y del Atacazo, 1800-2000 m, Ecuador, *Sodiro.* Authentic specimens: Corazón, prop. Miligally, 10/1896, *Sodiro,* NY!; Corazón, 10/1891, *Sodiro,* NY!; 1874, *Sodiro,* MO!

Cyathea corallifera var. *alsophilacea* Sod. Rec. Crypt. Vasc. Prov. Quit. 12. 1883, *ex char.* No specimen cited.

Cyathea corallifera var. *firma* Sod. Rec. Crypt. Vasc. Prov. Quit. 12. 1883. No specimen cited. Specimen seen: Ecuador, *Sodiro,* fragm. ex K,NY!

Cyathea corallifera var. *ortholoba* Sod. Rec. Crypt. Vasc. Prov. Quit. 12. 1883. No specimen cited. Authentic specimen: Corazón, 1800 m, 5/1882, Ecuador, *Sodiro,* NY!

Cyathea aspidiiformis Domin, Acta Bot. Bohem. 9: 94. 1930, *nom. nov.* for *Cyathea aspidioides* Sod., not (Bl.) Moritz.

Cyathea corallifera is similar to some forms of *C. divergens* in its large pinnae, pinnules and ultimate segments. It differs, in addition to the characters of pinnule indument provided in the key, in having the large pinnules sessile to short-stalked. Large pinnules, when sometimes found in *C. divergens,* are always long-stalked.

Ecuador, montane forests, 1400–2000 m. Stem to 5 m tall, leaves to 5 m long.

ADDITIONAL SPECIMENS. **Ecuador.** 1897, *Sodiro* (A); Corazón, *Sodiro* (NY); valley of "Tallatanga" (Pallatanga), *Rimbach 67* (US).

24. **Cyathea boliviana** Tryon, spec. nov.

Figs. 97–99. Map 28.

Petiolus squamis structura marginata discordanter valde bicoloribus, furfure squamulis bicoloribus valde dissectis et squamis subplanis albidis elongatis setis peripheralibus fuscatis opacis; lamina bipinnato-pinnatisecta; pinnae ad 50 cm longae sessiles vel subsessiles; pinnulae longe acuminatae, pagina inferiore squamis paucis vel multis subplanis albidis vel brunneis setis peripheralibus fuscatis opacis; sori inframediales ad furcam venarum; indusium sphaeropteroideum. Holotype: Incachaca, Prov. Chapare, Dept. Cochabamba, Bolivia, *Steinbach 9512,* GH. Isotypes: F,GH,MO,NY,US. Paratype: Camarapa, Dept. Santa Cruz, Bolivia, *Steinbach 8572,* GH.

Cyathea boliviana grows in forests at 2000–2200 m. Stem up to 15 m tall.

25. **Cyathea straminea** Karst.
Figs. 100–101. Map 29.

Cyathea straminea Karst. Linnaea **28**: 457. 1856. Holotype: Cresit cum C. Quindiuensi in declivitate montes glacialis vulcaniei Tolima, Colombia, *Karsten,* (Fl. Columb. **2**: t. 182, t. 183, f. III.) Isotype: Quindiu, *Karsten,* fragm. B!

The nearly concolorous, straw-colored petiole scales are the most distinctive character of *Cyathea straminea.*

Colombia, montane forest, ca 2000–2500 m.

ADDITIONAL SPECIMENS. **Colombia. Caldas:** above Salento, *Pennell 9695* (GH,NY,US). **Cauca:** Km 55 on road from Torotó to Inza, *Barrington 481, 482* (GH). **Putumayo:** Laguna de la Cocha, Páramo de Santa Lucia, *Cuatrecasas 11856* (F,US). **Nariño:** 5 km southwest of La Graja Botana, Pasto, *Barrington 505* (GH).

26. **Cyathea Ruiziana** Kl.
Figs. 102–104. Map 30.

Cyathea Ruiziana Kl. Linnaea **20**: 439. 1847. Holotype: In Peruviae Andium nemoribus, *Ruiz 72,* B! The label also bears the name Panatahuas, formerly a province west of Huanúco. Isotype: US!

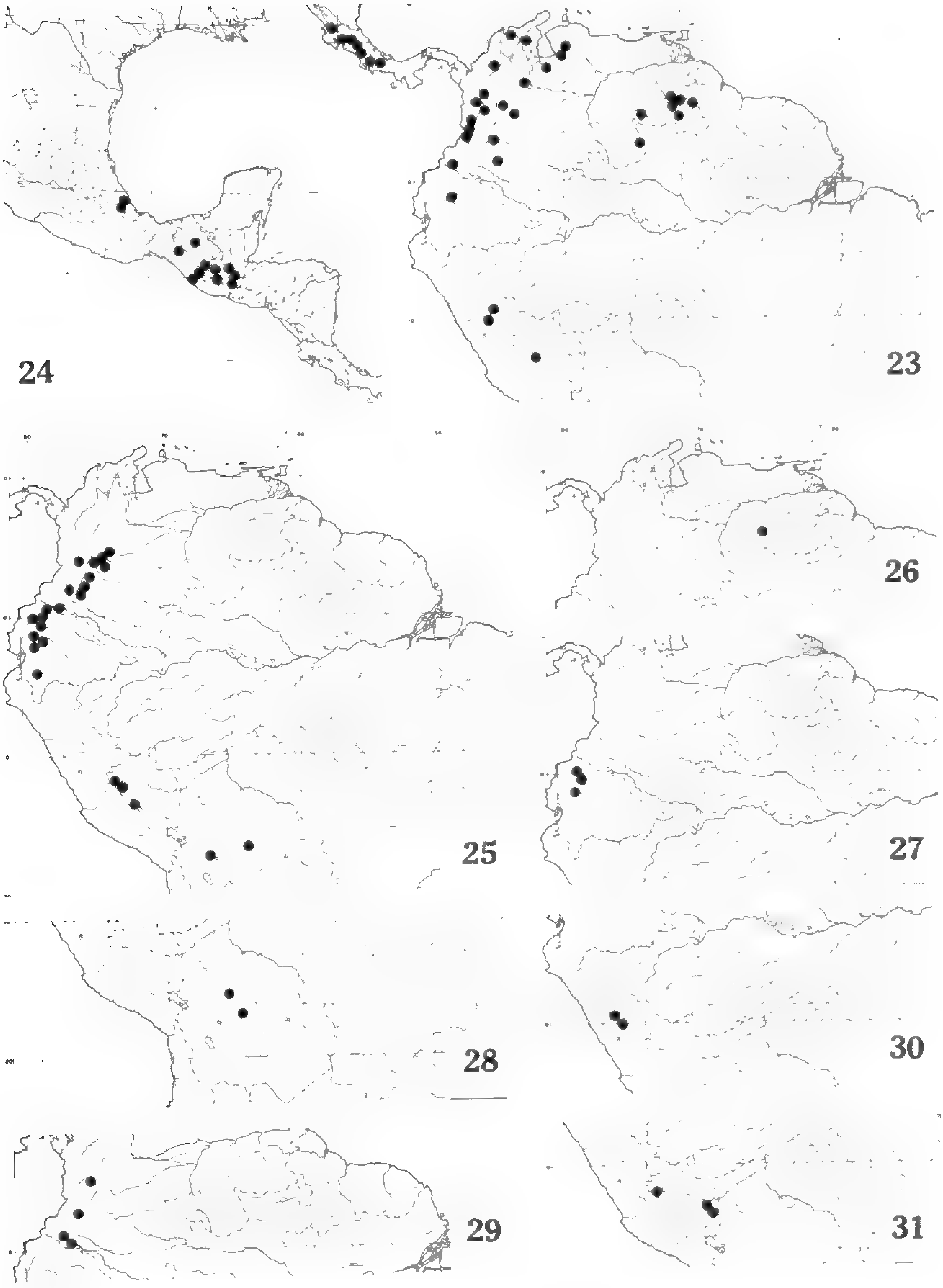
The holotype is a single pinna. Further characters are present in the Macbride collection cited below and especially notable among them are the very long large scales of the scurf (see Table 4), which densely invest the lower portion of the petiole.

Huanúco, central Peru. In montane forest at about 2000 m, stem to 9 m tall.

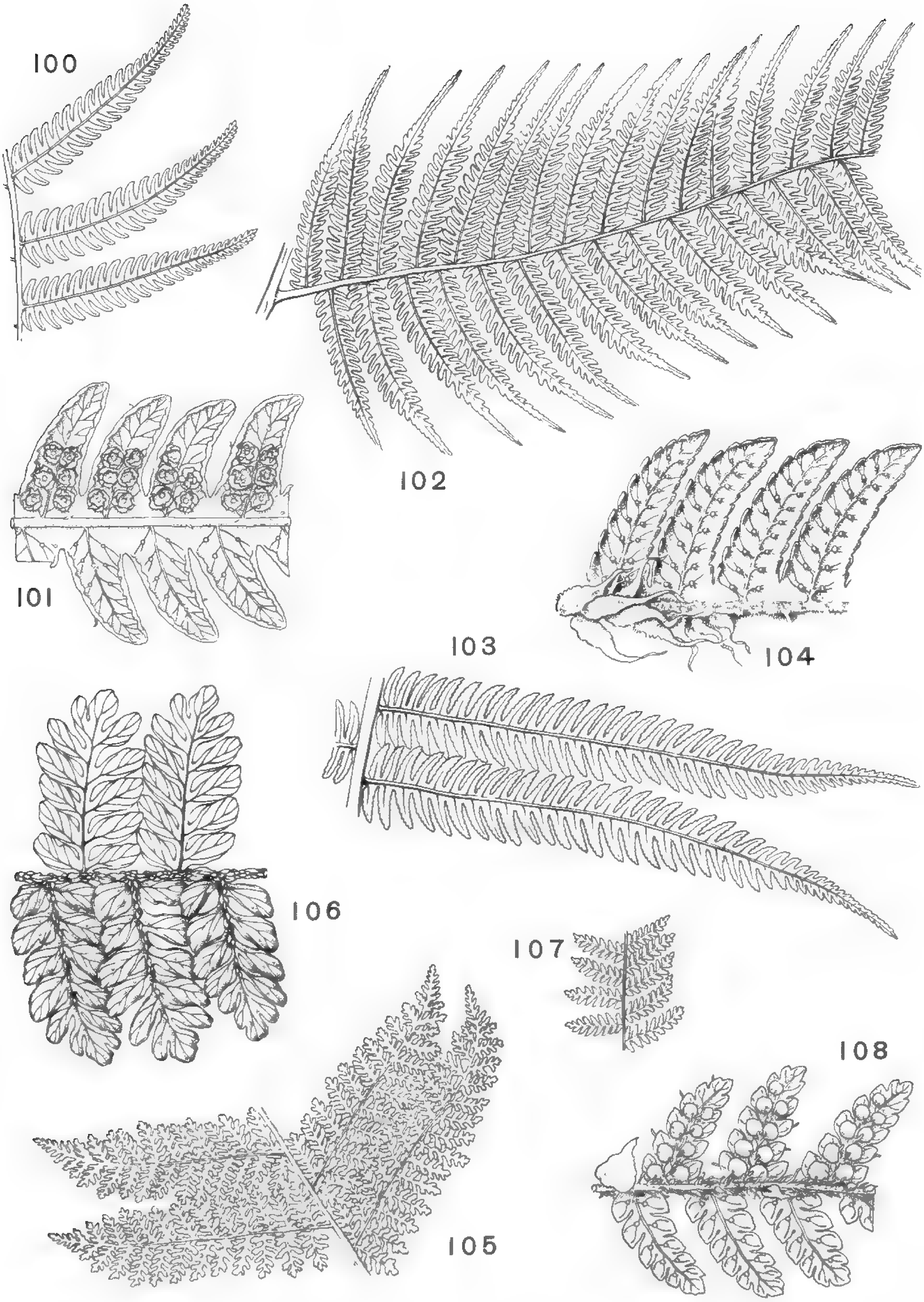
ADDITIONAL SPECIMENS. **Peru. Huanúco:** Huacachi, near Muña, *Macbride 4135* (F,US).

TABLE 4. PETIOLE SCURF CHARACTERS OF SPECIES 23-26.

	Large scales	Squamellae
23. *Cyathea corallifera*	Mostly entire or very nearly so, mostly bicolorous.	Slightly to moderately dissected, whitish to very light brown, mostly concolorous.
24. *Cyathea boliviana*	Elongate, mostly whitish, with dark, opaque peripheral processes.	Strongly dissected into trichome-like arms, bicolorous.
25. *Cyathea straminea*	Mostly entire or nearly so, some bicolorous.	Slightly to strongly dissected, mostly concolorous.
26. *Cyathea Ruiziana*	Borne toward the base of the petiole: elongate, 3-4 mm long, whitish, mostly concolorous.	Elongate, nearly entire, or somewhat dissected toward the apex, mostly concolorous toward the base of the petiole, mostly bicolorous beyond.



MAPS 23–31. 23–24, Cyathea divergens: 23, var. divergens; 24, var. Tuerckheimii; 25, C. pallescens; 26, C. simplex; 27, C. corallifera; 28, C. boliviana; 29, C. straminea, 30, C. Ruiziana; 31, C. microphylla.



Figs. 100–108. 100–101, *Cyathea straminea,* Colombia, *Barrington 482* (GH): 100, Pinnules, × ½; 101, Portion of fertile pinnule, × 2½. 102–104, *C. Ruiziana,* Peru, *Macbride 4135* (F): 102, Basal ⅔rds of pinna toward apex of lamina, × ½; 103, Pinnules, × ½; 104, Portion of fertile pinnule, × 2. 105–106, *C. microphylla,* Peru, *Vargas 11858* (GH): 105, Pinnae, × ½; 106. Sterile pinnules, × 2. 107–108, *C. multisegmenta,* Peru, *Dudley 11326* (GH): 107, Pinnules, × ½; 108, Portion of fertile pinnule, × 4½.

GROUP OF CYATHEA MICROPHYLLA

KEY TO SPECIES 27-28

a. Tertiary segments entire to basally 2-lobed; many small, dark brown, bullate scales on the pinnule-rachis beneath. .... 27. *C. microphylla.*

a. Tertiary segments usually with 5 or more segments or lobes, some with fewer; light brown, bullate scales and trichomes on the pinnule-rachis beneath. .... 28. *C. multisegmenta.*

These two Peruvian species share unusual characters: the highly complex lamina, with small ultimate segments, and the unusually broad petiole scales. From the available data, the two species differ widely in their leaf size. *Cyathea microphylla* has small leaves up to about 75 cm long, while *C. multisegmenta* has large leaves to at least 4 m long.

27. **Cyathea microphylla** Mett.

FIGS. 105–106. MAP 31.

Cyathea microphylla Mett. Fil. Lechl. **1**: 23, t. 3, f. 1-6. 1856. Holotype: St. Gavan, (San Gavan, Puno), Peru, *Lechler 2160*, LZ, destroyed.

Diacalpe microphylla (Mett.) Moore, Ind. Fil. c. 1857.

There is obvious confusion in the Lechler collection (or collections) of this species. Mettenius cites only *Lechler 2160* from St. Gavan but he also cites the same number and locality under *Cyathea Schanschin*. There is a sheet of *Lechler 2160* at Paris, correctly identified as *Cyathea Schanschin* (=*C. Delgadii*). Hooker (Second Century of Ferns, t. 99) also cites *Lechler 2160* but from Tatanara (also in Puno, Peru). In the Mettenius Herbarium at Berlin, there is *Cyathea microphylla* (*Lechler 2569*) from Tatanara, and the same collection at Paris. I have not been able to determine if the different combinations of number and locality represent three collections, or if there was confusion in the labeling of a single collection. In any event, *Cyathea microphylla* is a very distinctive species and the original illustrations and the specimen at Berlin authentically represent the name.

Southern Peru, in thickets and forests at elevations of 2100–2800 m. Stem to 1.25 m tall, with a diameter of 1.5–2.5 cm.

ADDITIONAL SPECIMENS. **Peru. Cuzco:** Prov. Convencion, 73°22'W, 12°37'S, *Dudley 10943* (GH). **Puno:** Valle Grande, Sandia, *Vargas 11858* (GH); Tatanara, *Lechler 2569* (B,P, photo GH, fragms. F,US).

28. **Cyathea multisegmenta** Tryon, spec. nov.

FIGS. 107–108. MAP 32.

Petiolus 1-2 m longus squamis structura marginata fere concoloribus pallide brunneis vel albidis, furfure squamulis albidis dissectis; lamina 1.25-3 m longa plerumque quadripinnata; pinnae sessiles vel subsessiles; pinnulae pagina inferiore squamis subplanis pallide brunneis et squamis bullatis albidis vel pallide brunneis necnon trichomatibus; sori subcostales in venis simplicibus vel ad furcam venarum; indusium sphaeropteroideum. Holotype: 73°37'W, 12°38'S, Prov. Convención, Dept. Cuzco, Peru, *Dudley 11326*, NA. Isotypes: GH,US,NA.

The single collection was made in very dense cloud forest at about 1800 m, the stem was 2.5 m tall, and the leaves to 4 (or more) m long.

GROUP OF CYATHEA FULVA
KEY TO SPECIES 29-34

a. Pinnules with few or no scales beneath and abundantly to moderately long-pubescent, or in Brazil sometimes with few long trichomes or with several scales; petiole scales usually light brown, the scurf of early caducous squamellae, or sometimes with larger scales also present; Costa Rica and Panama, British Guiana to Colombia south to Bolivia, Brazil, Ilha Trindade. . . . . 33. *C. Delgadii.*

a. Pinnules with few or no scales beneath and with few or no long trichomes, or with several to many scales and then sometimes short-pubescent to moderately long-pubescent; petiole scales often brown to dark brown, the scurf of usually persistent squamellae and larger scales. . . . . b.

b. Squamellae of the petiole scurf strongly flattened and appressed, or erect and many crested (in South America rarely also ciliate-dissected); continental North and South America. . . . . c.

c. Upper surface of the ultimate segments glabrous or with a few large trichomes, especially toward the apex; base of the petiole lacking reduced pinnae; Mexico to Panama, Venezuela and Colombia. . . . . 29. *C. fulva.*

c. Upper surface of the ultimate segments pubescent, usually some of the trichomes long, slender, whitish and tortuous; base of the petiole usually with subaphlebioid pinnae; Costa Rica. . . . . 32. *C. suprastrigosa.*

b. Squamellae of the petiole scurf erect, entire, ciliate or branched, rarely some crested; Antilles, Trinidad and Margarita. . . . . d.

d. Segments pubescent above, pinnules usually long-triangular, short-stalked, especially on the central pinnae; Jamaica and Dominican Republic. . . . . 30. *C. harrisii.*

d. Segments with a few long trichomes above or none, pinnules with parallel sides, tapering to an acute to acuminate apex, sessile to subsessile or rarely a few short-stalked. . . . . e.

e. Indument of rachis of (often caducous) scaly scurf beneath, rarely trichomes may also be present; costa with large, flat, usually brownish scales beneath; costules with usually brownish bullate scales beneath; Greater Antilles. . . . . 31. *C. furfuracea.*

e. Indument of rachis of trichomes beneath, these (or their bases) persistent, very rarely also with some scaly scurf; costa lacking large, flat scales beneath, or if present these usually wholly or partly whitish; costules with whitish bullate scales beneath; Lesser Antilles, Trinidad, Margarita. . . . . 34. *C. tenera.*

This is a natural group of not wholly distinctive species. Their relation among the previous species is to *Cyathea pallescens. Cyathea fulva* is rather close to the next group, especially to *C. caracasana* var. *Maxonii.*

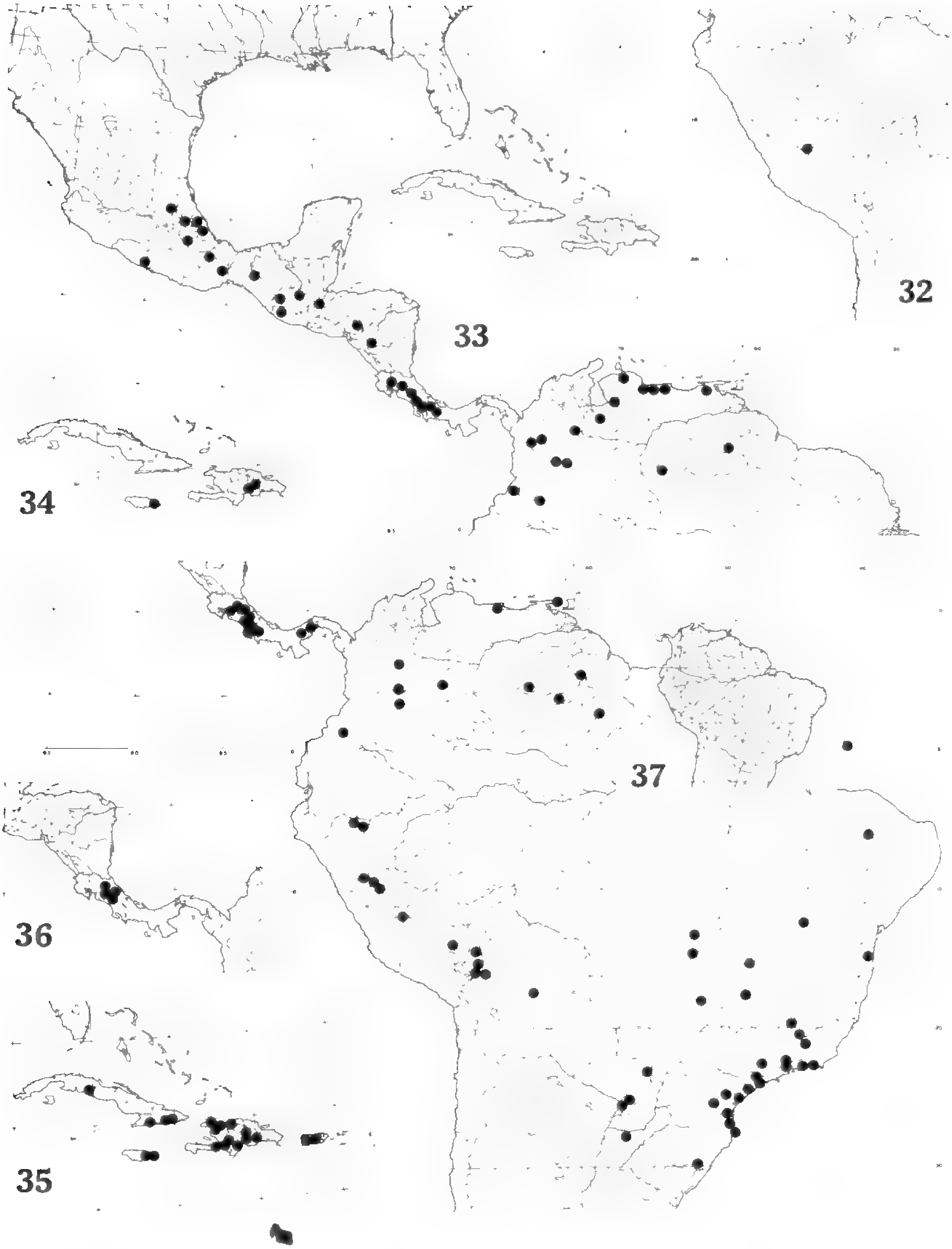
29. **Cyathea fulva** (Mart. & Gal.) Fée
FIGS. 109–113. MAP 33.

Cyathea fulva (Mart. & Gal.) Fée, Mém. Fam. Foug. **9**: 34. 1857.

Alsophila fulva Mart. & Gal. Mém. Acad. Brux. **15**: 78, t. 23. 1842. Holotype: Talea, Cordillère Orientale d'Oaxaca, México, *Galeotti 6346*, BR, photo GH, fragm. ex BR,US! Isotype: P! photo GH.

Cyathea Schlechtendalii Kze. Bot. Zeit. **1845**: 288, *ex char.* Herb. Schlechtendal. A specimen in Herb. Kuhn, B! bears this name.

Cyathea aurea Kl. Allg. Gartenzeit. **24**: 105. 1856. *Karsten.* In Fl. Columb. **2**: 149, t. 178, Karsten cites this species from Caracas, between Petaquire and Colonia Tovar, Venezuela. Fragments: Herb. Schlechtendal, *Karsten 7*, B! and *Karsten 7* ex B,NY! are authentic.



Maps 32–37. 32, Cyathea multisegmenta; 33, C. fulva; 34, C. Harrisii; 35, C. furfuracea; 36, C. suprastrigosa; 37, C. Delgadii.

Cyathea aurea var. *squamosa* Karst. Linnaea **28**: 459. 1857. Holotype: vicinity of Caracas, between Petaquire and Colonia Tovar, Venezuela, *Karsten*. Isotype: B!

Cyathea flaccida Mett. Ann. Sci. Nat. V, **2**: 265. 1864, *nom. nud.* Nova Granada, Prov. Carabobo, *Funck & Schlim 413* was cited; L, photo NY,P! fragm. US!

Cyathea furfuracea Christ, Bull. Herb. Boiss. II, **4**: 950. 1904, not Baker, 1874. Holotype: Costa Rica, 1903, *Wercklé*, Herb. Christ, P! fragm. ex Christ, US! Isotype: NY!

Cyathea onusta Christ, Bull. Herb. Boiss. II, **4**: 950. 1904. Holotype: Costa Rica, *Wercklé 41*, Herb. Christ, P!

Cyathea papyracea Christ, Bull. Herb. Boiss. II, **4**: 946. 1904. Holotype: Costa Rica, *Wercklé 52*, Herb. Christ, P! (2ème feuille). Gastony, Contrib. Gray Herb. **203**: 147. 1973, indicates that this sheet should represent the name; the lère feuille, lacking the number, is *Nephelea mexicana*.

Cyathea conspersa Christ, Bull. Herb. Boiss. II, **5**: 260. 1905, *nom. nov.* for *Cyathea furfuracea* Christ, not Baker.

Cyathea Underwoodii Christ, Bull. Herb. Boiss. II, **6**: 183. 1906. Syntypes: Navarro, Costa Rica, 1903, *Wercklé*, Herb. Christ, P! NY! fragm. ex Christ, NY!; 1901-1905, *Wercklé*, NY! US!; 1905, *Wercklé*, Herb. Christ, P!

Cyathea delicatula Maxon, Contrib. U.S. Nat. Herb. **13**: 4. 1909. Holotype: between Tactic and Cobán, Alta Verapaz, Guatemala, *Türckheim II 1629*, US! Isotype: GH!

Cyathea mollis Rosenst. Fedde, Rep. Spec. Nov. **22**: 2. 1925, not Copel. 1917. Lectotype: La Palma, Costa Rica, *Brade & Brade 631*, Herb. S. Birger, S-PA! Isolectotype: B! Lectoparatype: La Palma, Costa Rica, *Brade & Brade 630*, Herb. S. Birger, S-PA! Isolectoparatypes: B! NY! A sheet with the label indicating "*630* and *631*," US!

Cyathea molliuscula Domin, Acta Bot. Bohem. **9**: 138. 1930, *nom. nov.* for *Cyathea mollis* Rosenst. not Copel.

Cyathea fulva usually has whitish to very light brown bullate scales on the under surface of the costae and costules. It often grows at lower elevations in Central America than other species with a sphaeropteroid indusium, and it is the only species among them that occurs in Nicaragua and Honduras.

In Costa Rica *Cyathea fulva* is sometimes close to specimens of *C. caracasana* var. *Maxonii* that have only some of the petiole scales partly reddish-brown to atropurpureous, the others being brown as in *C. fulva*. These two taxa often grow at different elevations, for example, about 25% of the 24 localities for *C. fulva* are below 2000 m, while over 50% of 18 localities for var. *Maxonii* are above that altitude.

Southern Mexico to Panama, Colombia and Venezuela. In Mexico and Central America in Liquidambar forest, *Podocarpus* forest and oak forest, humid forest to cloud forest, persisting in cleared land, at 800–2600 m, in Costa Rica usually below 2000 m. In Venezuela and Colombia in dense woods, cloud forests, on steep slopes and sandstone escarpments, 1300–4200 m, the highest in Colombia in subparamo forest. Stem up to 10 m tall and 25 cm in diameter, leaves to 3 m long.

SELECTED SPECIMENS. **México. Hidalgo:** near Zacualtipan, *Martinez 1* (GH), *26* (MO,US). **Puebla:** between Zacapoaxtla and Xalacapa, *Sharp 45960* (GH). **Veracruz:** Cuantlancillo (Orizaba), *Copeland 15* (GH); 12 km south of Misantla, *Lockwood 706* (GH). **Guererro:** Teotepec, Dist. Galeana, *Hinton 14274* (GH,NY). **Oaxaca:** 35 km from Huatla, on road to Teotitlan, *Madison 618* (GH). **Chiapas:** Colonia Ach'lun, Municip. Tenejapa, *Ton 892* (NY). **Guatemala. San Marcos:** between San Rafael Pie de la Cuesta and Palo Verde, *Williams, Molina & Williams 25670* (F). **Quezaltenango:** El Pocito, south of San Martin Chile Verde, on road to Colomba, *Standley 85050* (F).

Alta Verapaz: Sacomum, *Johnson 964* (F,GH,US). **Zacapa:** between El Picacho and Cerro de Monos, *Steyermark 42791* (F,GH,US). **Honduras. Morazán:** Montaña del Tigre, *Molina 10255* (F); Mt. Uyuca, *Williams & Molina 11093* (F). **Nicaragua. Matagalpa:** road to La Funadora, north of Sta. María de Ostuma, *Williams, Molina & Williams 24972* (F). **Costa Rica. Alajuela:** La Paña de Zarcero, Canton Alfaro Ruiz, *A. Smith 1538* (NY); 19 km north of San Ramón, *Wilbur & Stone 10109* (GH,US). **Heredia:** Cinchona, upper Sarapaqui valley, *Scamman 7584* (GH); Cariblanco, *Nisman 113, 160* (GH). **San José:** La Palma, *Maxon 417* (NY); above La Hondura, *Gastony & Gastony 774* (GH). **Cartago:** 7 km south of Tapanti, *Tryon & Tryon 6988, 6989, 7123, 7124* (GH); 10 km south of Tapanti, *Burger & Stolze 5667* (GH), *5683* (GH,NY). **Puntarenas:** Monteverde, *Palmer 76* (NY); San Vito, *McAlpin 2259* (GH). **Panamá. Chiriqui:** vicinity El Boquete, *Maxon 5046* (GH,NY); vicinity of Cerro Punta, *Allen 1522* (F,GH,MO,NY). **Venezuela. Sucre:** Cerro Turumuquire, *Steyermark 62467* (GH, MO,NY,US,VEN). **Distrito Federal:** El Junquito, *Pittier 13946* (F,NY,US,VEN). **Aragua:** Colonia Tovar, *Fendler 52* (F,GH,MO). **Carabobo:** east of Los Tanques, south of Borburata, *Steyermark & Steyermark 95396* (NY,VEN). **Falcon:** Sierra de San Luis, *Steyermark 98914* (GH). **Merida:** Carbonerro, *White & Lucansky 1969–237* (NY,US); Cerro El Toro, *Bernardi 1876* (NY). **Bolivar:** Amurí-tepuí, Chimantá Massif, *Steyermark & Wurdack 1328* (GH,NY,US,VEN). **Amazonas:** Cerro Parú, *Cowan & Wurdack 31390* (GH,NY,US). **Colombia. Antioquia:** 10 km east of Sonsón, *Scolnik, López & Barkley 19An214* (MO). **Santander:** Pamplona to Toledo, *Killip & Smith 19962* (GH,NY,US). **Cundinamarca:** Tena, Laguna de Pedro Palo, *Fernandéz & Mora 1451* (US). **Cauca:** El Tambo, Munchique, *Agredo 431* (F,US). **Tolima:** above Anaime, on road south of Cajamarca, *Barrington 474* (GH). **Huila:** inter La Resina et Andaluzia, *Juzepczuk 6595* (US).

30. **Cyathea Harrisii** Maxon

FIGS. 114–115. MAP 34.

Cyathea Harrisii Maxon, No. Amer. Fl. **16**: 81. 1909. Holotype: Blue Mountain Peak, Jamaica, *Underwood 2502*, NY. Isotype: *Maxon 1371, "=Underwood 2502,"* US!

Cyathea Harrisii is characterized, among the Jamaican species of the genus, by its usually long-triangular pinnules that are pubescent on the upper surface of the segments. *Cyathea suprastrigosa* of Costa Rica is its closest relative, rather than species of the Greater Antilles.

Jamaica and Hispaniola. Blue Mountain Peak, Jamaica, in rain forest, 2100–2200 m; and Sierra de Ocoa, Dominican Republic, in mossy forest and wet pinelands, persisting after clearing, 2300–2500 m. Stem to 3.5 m tall, leaves to 2 m long.

ADDITIONAL SPECIMENS. **Jamaica.** Blue Mountain Peak, St. Thomas, *Proctor 4378* (MO), *Faull 12582* (MO), *Chrysler 2049* (GH,MO), *Maxon 9866* (GH,MO,NY), *9889* (GH,NY). **Dominican Republic.** 13 km from Valle Nuevo on road to San José de Ocoa, La Vega, *Gastony, Jones & Norris 720, 730* (GH,NY); Sierra de Ocoa, Azua, *Ekman H11678* (F,GH,NY).

31. **Cyathea furfuracea** Baker

FIGS. 116–118. MAP 35.

Cyathea furfuracea Baker, Syn. Fil. **450**. 1874. Lectotype: Portland Gap, Jamaica, July, 1843, *Purdie*, K! fragm. NY! Isolectotype: BM! photo GH. Lectoparatype: Jamaica, *Bancroft*, K! fragm. NY!

Cyathea monstrabila Jenm. Jour. Bot. **19** (n.s. 10): 275. 1881. Holotype: Portland Gap, Jamaica, *Nock*, Herb. Jenm., NY! fragm. US! (A monstrous form).

Cyathea asperula Maxon, Contrib. U.S. Nat. Herb. **17**: 179. 1913. Holotype: near Constanza, Santo Domingo, *Türckheim 3056,* US! Isotypes: F! GH! MO!

Cyathea Brittoniana Maxon, Jour. Wash. Acad. Sci. **14**: 139. 1924. Holotype: Mt. Alegrillo, Puerto Rico, *Britton, Stevens & Hess 2620,* US! Isotype: F! Paratypes: Monte de la Prenda, Oriente, Cuba, *Eggers 5211,* US; Pinal de Santa Ana, Oriente, Cuba, *Eggers 5031,* US; Paradis, Barahona, Dominican Republic, *Abbott 1590,* US; Maricao, Puerto Rico, *Hioram 809,* US. Isoparatypes: *Eggers 5031,* F! fragm. ex K,NY!; *Eggers 5211,* GH! fragm. ex K,NY! (Trinidad: *Fendler 80,* and *Britton, Hazen & Mendelson 1351* are excluded as paratypes; they are *Cyathea tenera*).

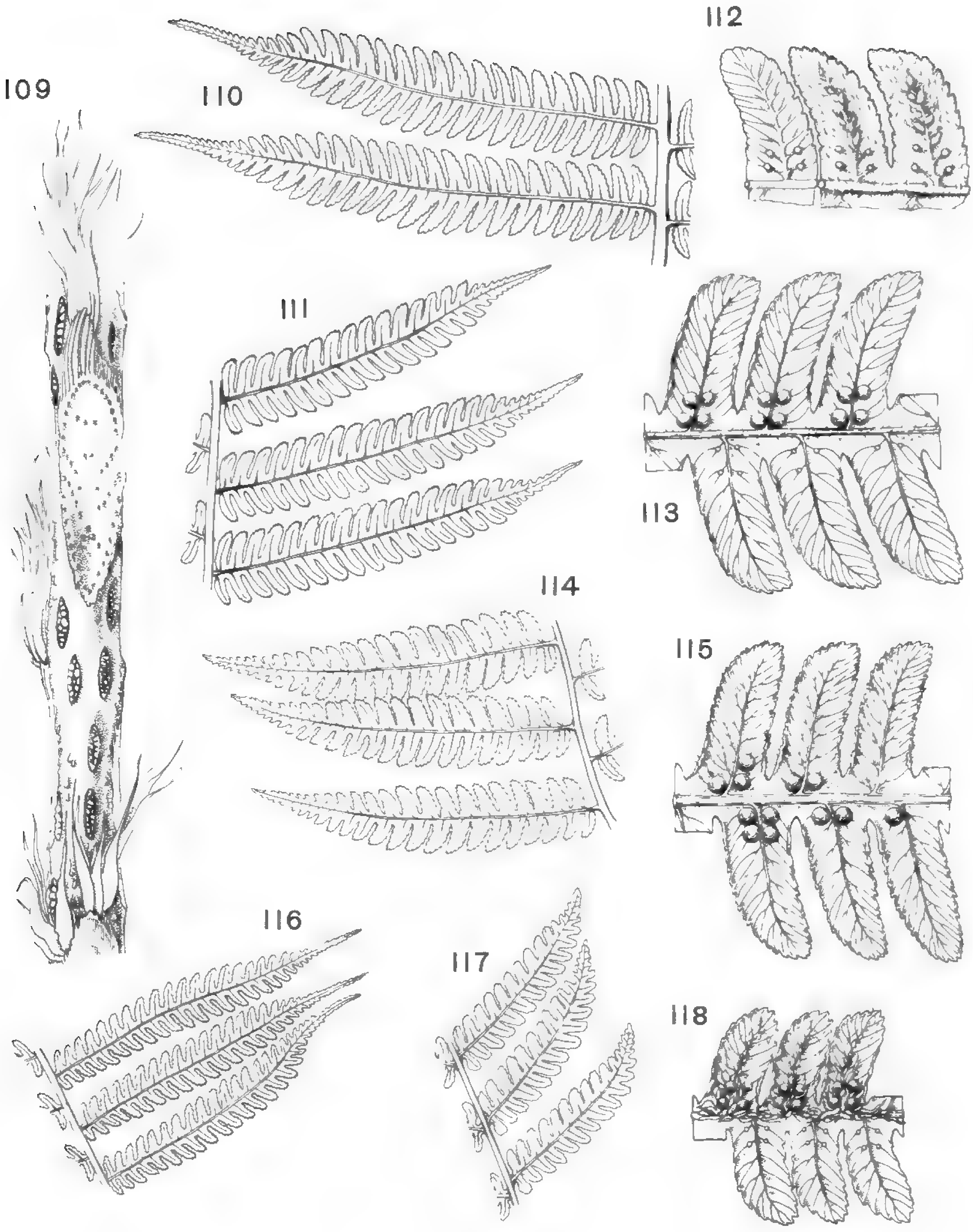
There is considerable variation in the indument on the under surface of the pinnules in *Cyathea furfuracea.* While this shows some correlation with geography, it is not sufficiently strong to suggest the recognition of varieties. Specimens from Cuba often have numerous long trichomes beneath and some have few scales. Jamaica specimens usually have several to numerous trichomes and many scales, while in those of Hispaniola there is usually a moderate investment of both trichomes and scales. The few collections from Puerto Rico include most of this range of variation.

Most of the collections cited by Maxon as *Cyathea Brittoniana* are the relatively pubescent and slightly scaly variation of *C. furfuracea.* They could be interpreted as intermediates with *Cyathea tenera,* which also has variations approaching *C. furfuracea.* However, considering the gap between the range of the two taxa, from Puerto Rico to Montserrate, it seems best to interpret this variation as local infraspecific variation within two closely related species.

Maxon's *Cyathea Brittoniana* is a source of confusion because he included in it Trinidad collections of *Cyathea tenera,* while including in *C. tenera* Greater Antillean collections which are *C. furfuracea.*

Cuba, Jamaica, Hispaniola and Puerto Rico. On steep slopes of montane forest, in wet ravines, *Podocarpus* cloud forest and elfin woodland, rarely 300 to 900–2200 m. Stem to 8 m tall, and 25 cm in diameter, leaves to 3 m long.

SELECTED SPECIMENS. **Cuba. Santa Clara:** Buenos Aires, Trinidad Hills, *Jack 7273* (F,GH,NY). **Oriente:** La Bayamesa, Sierra Maestra, *Ekman 7070* (NY); Gran Piedra, *Maxon 4070* (F,GH,NY); Pico Turquino, *Leon 11154* (NY), *Ekman 5430* (NY). **Jamaica.** Mt. Horeb trail, St. Andrew, *Crosby, Hespenheide & Anderson 308* (F,GH, MO,NY); Morce's Gap, St. Andrew, *Maxon & Killip 660* (F,GH,NY); Sugar Loaf Peak, Portland, *Proctor 4360* (MO); Hardwar Gap, Portland, *Tryon & Tryon 6982, 6983* (GH); Corn Puss Gap, St. Thomas, *Proctor 3996* (GH,MO,US); Blue Mountain Peak, St. Thomas, *Maxon & Killip 1146* (F,GH,NY). **Haiti.** Vicinity of Furcy, *Leonard 4670, 5355* (GH,NY); Morne Haut Piton, vicinity of Bassin Bleu, *Leonard & Leonard 15165* (GH,MO,NY); Morne Tranchant, Massif de la Selle, *Ekman H3217* (NY). **Dominican Republic.** Vicinity of Paradis, Barahona, *Abbott 1664* (GH); La Ciénega, La Vega, *Gastony & Norris 173, 197, 213* (GH); La Cumbre, Santo Domingo, *Ekman H11496* (NY); Monción, Lagunas de Cenobí, Monte Cristi, *Ekman H12865* (F,GH); Sierra de Neiba, near Haitian border, *Gastony, Jones & Norris 431* (GH,NY), *469* (GH). **Puerto Rico.** Monte del Estado, Maricao Forest, *Little 21702* (GH); Cerro de La Punta, km 18.5, road 143, *Conant 596, 603, 685* (GH).



Figs. 109–118. 109–113, *Cyathea fulva:* 109, Apical portion of stem, Venezuela, *Steyermark & Steyermark 95396* (VEN), × ¼; 110, Pinnules, source as in 109, × ½; 111, Pinnules, Mexico, *Martinez 1* (GH), × ½; 112, Portion of fertile pinnule, source as in 109, × 1½; 113, Portion of fertile pinnule, source as in 111, × 2. 114–115, *C. Harrisii*, Jamaica, *Maxon 9866* (GH): 114, Pinnules, × ½; 115, Portion of fertile pinnule, × 2. 116–118, *C. furfuracea:* 116, Pinnules, Dominican Republic, *Ekman H12865* (GH), × ½; 117, Pinnules, Haiti, *Leonard & Leonard 15165* (GH), × ½; 118, Portion of fertile pinnule, Jamaica, *Maxon & Killip 660* (GH), × 2.

32. **Cyathea suprastrigosa** (Christ) Maxon
FIGS. 119–120. MAP 36.

Cyathea suprastrigosa (Christ) Maxon, No. Amer. Fl. **16**: 83. 1909.

Hemitelia suprastrigosa Christ, Pittier, Prim. Fl. Costaric. 3 (1) (Filices, 2nd Mém.): 44. 1901. Holotype: forêts de l'Achiote, Volcán de Poas, Costa Rica, 2000 m, *Tonduz 10701,* fragm. ex Christ, NY! Isotypes: Herb. Bonap. P! photo GH,US! fragm. ex US,NY!

Cyathea conspicua Christ, Bull. Herb. Boiss. II, **6**: 178. 1906. Holotype: Volcán Turrialba, Costa Rica, 1905, *Wercklé,* P! Isotype: US!

Cyathea suprastrigosa is usually characterized, in addition to the characters mentioned in the key, by a strongly outward and downward bent petiole base and by auriculate basal inferior segments, especially on the larger pinnules. The distinctive delicate trichomes on the upper surface of the segments may be lacking in older leaves.

Costa Rica. Montane forest, cloud forest and subparamo woodland, on slopes or in poorly drained sites, 2000 to usually 2400–2800 to 3000 m. Stem to 5 m tall and 10 cm in diameter, leaves to 1 m long.

SELECTED SPECIMENS. **Costa Rica. Alajuela:** Volcán Poás, *Nisman 100, 102* (GH), *Jiminez 1022* (GH,NY). **San José-Cartago:** near El Trinidad, *Burger & Stolze 5238, 5964* (GH); 3 km from El Empalme, toward Cerro de la Muerte, *Gastony & Gastony 747, 748* (GH). **Cartago:** vicinity of Millsville, Pan-American Highway, *Holm & Iltis 533, 601* (A,F,MO), *605* (A,MO); 10 miles southeast of El Empalme, *Wilbur & Stone 9972* (GH).

33. **Cyathea Delgadii** Sternb.
FIGS. 121–123. MAP 37.

Cyathea Delgadii Sternb. Flor. der Vorwelt **1**: 47, t. B. 1820 (also Flor. Monde Prim. **4**: 51, t. B. 1826). Holotype: Gancho do Generale Delgado in via ad Caldas Novas, Goyaz, Brazil, *Pohl,* PRC, fragm. ex PRC,GH! A fragm. ex L,US! is probably from the same collection.

Cyathea vestita Mart. Denkschr. Bot. Ges. Regensberg **2**: 146. 1822. (Icon. Pl. Crypt. Bras. 75, t. 52). Holotype: uncertain without an examination of the original materials. Minas Geraes, *Pohl 663,* W, photo and fragm. BM! may be authentic.

Cyathea oligocarpa Kze. Linnaea **9**: 101. 1834. Holotype: Pampayaco, Peru, *Poeppig* (Diar. *1101*), LZ, destroyed. Isotypes: *Poeppig 218,* B! MO! P!

Cyathea hirtula Mart. Icon. Pl. Crypt. Bras. 76, t. 53. 1834. Holotype: Uncertain without an examination of the original materials, Almada, Serra do Mar, Bahia, Brazil, *Max. Neuwied,* BR photo and fragm. BM! is authentic.

Cyathea schanschin Mart. Icon. Pl. Crypt. Bras. 77, t. 54. 1834. Holotype: Uncertain without an examination of the original materials, São Paulo, Brazil, *Martius,* BM! photo GH, and Curibiba, São Paulo, Brazil, *Martius,* M, photo BM are probably authentic.

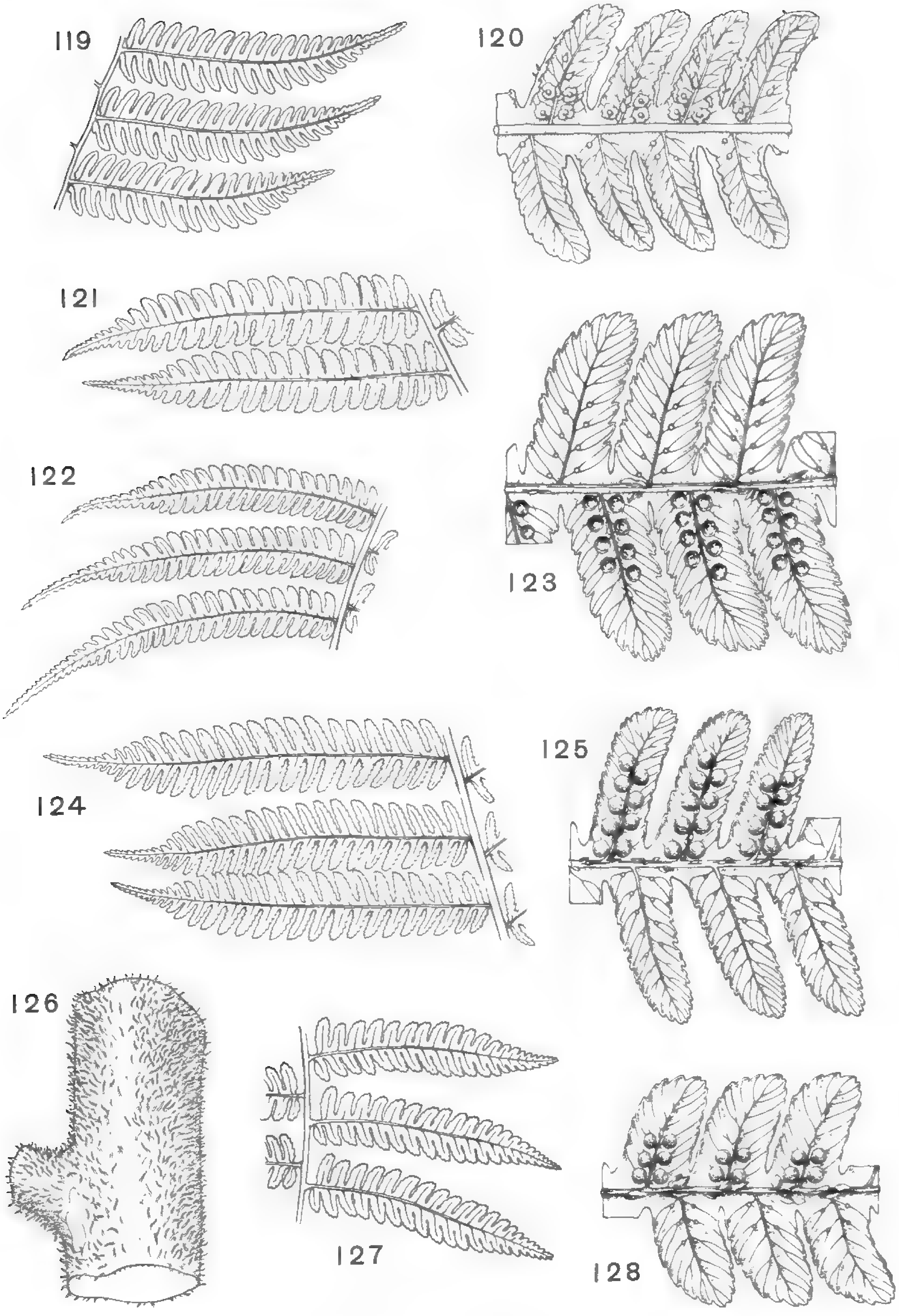
Cyathea denticulata Goldm. Nova Acta Acad. Caesar. Leopold.-Carol. 19, Suppl. **1**: 466. 1843, *ex char.*

Cyathea abruptecaudata Fée, Crypt. Vasc. Brésil **1**: 183, t. 62, f. 2. 1869. Holotype: Rio de Janeiro, Brazil, *Glaziou 2284,* Herb. Fée-Herb. Cosson, P! photo GH, fragm. ex Fée, NY! Isotype: US!

Cyathea Feei Fée, Crypt. Vasc. Brésil **1**: 179, t. 66, f. 2. 1869. Lectotype: Rio de Janeiro, Brazil, *Glaziou 2286,* Herb. Fée-Herb. Cosson, P! photo GH, fragm. ex Fée, NY! Isolectoparatype: Brazil, *Claussen 114,* P!

Cyathea sphaerocarpa Fée, Crypt. Vasc. Brésil. **1**: 180, t. 53, f. 2. 1869. Holotype: Rio de Janeiro, Brazil, *Glaziou 2283,* Herb. Fée-Herb. Cosson P! photo GH.

Cyathea pilosa Baker, Syn. Fil. 19. 1874. Holotype: Andes of east Peru, (Tarapoto),



FIGS. 119–128. 119–120, *Cyathea suprastrigosa*, Costa Rica, *Gastony & Gastony 747* (GH): 119, Pinnules, × ½; 120, Portion of fertile pinnule, × 2. 121–123, *C. Delgadii:* 121, Pinnules, Brazil, *Dusén 11781* (GH), × ½; 122, Pinnules, Bolivia, *Williams 1334* (GH), × ½; 123, Portion of fertile pinnule, Costa Rica, *Nisman 122* (GH), × 2. 124–126, *C. tenera:* 124, Pinnules, Guadeloupe, *Proctor 20134* (A), × ½; 125, Portion of fertile pinnule, source as in 124, × 2; 126, Pubescent rachis, Grenada, *Proctor 16995* (A), enlarged. 127–128, *C. dissoluta*, Jamaica, *Proctor 5819* (MO): 127, Pinnules, × ½; 128, Portion of fertile pinnule, × 2.

Spruce 4729. K. Isotypes: GH! P! photo GH, fragm. (probably ex P) F! fragm. ex Rosenst. US! fragm. ex BM,US!

Cyathea Copelandii Kuhn & Luerrsen, Abhandl. Naturw. Ver. Bremen **7**: 278. 1882. Holotype: Trinidad (Ilha da Trindade, Brazil), *Ralph Copeland,* fragm. Herb. Luerssen, P! photo GH.

Cyathea hypotricha Christ, Bull. Herb. Boiss. II, **4**: 947. 1904. Holotype: Costa Rica, *Wercklé,* Herb. Christ, P! fragm. NY!

Cyathea schanschin var. *oligocarpa* (Kze.) Hieron. Hedwigia **45**: 230. 1906.

Cyathea bahiensis Rosenst. Fedde, Rep. Spec. Nov. **20**: 90. 1924. Holotype: São Gomala, gebiet des Rio Femmeas, Bahia, Brazil, *Luetzelburg 534,* M, photo BM.

Cyathea micromera Rosenst. Fedde, Rept. Spec. Nov. **20**: 90. 1924. Holotype: Apertada-hora, Goyaz, Brazil, *Luetzelburg 12841,* M, photo BM.

Cyathea trindadensis Brade, Archiv. Instit. Biol. Veg. Rio Janeiro **3**: 1, t. 1, f. 1. 1936. Holotype: Ilha de Trindade, Brazil, *Campos Porto 579,* RB. Isotype: F!

Brazilian specimens have considerable variation in the lamina indument but there is relatively little variation in other parts of the range. In Brazil the sterile leaves, especially, may have few trichomes on the under surface and there are also sometimes some scales beneath. This latter variation, for example, in *Tryon & Tryon 6659* and in *Sehnem 4213,* is a very close match to the material from Ihla Trindade, previously considered to be an endemic species.

While the characters employed in the key are all variable, they form a combination that serves to distinguish the species. In addition, the pinna-rachis is usually pubescent, a character otherwise usually seen only in *Cyathea tenera.*

Costa Rica and Panama, around the Amazon Basin in British Guiana to Colombia, south to Bolivia, to southeast Brazil and northeastward to Ceará, Brazil. In primary forest, cloud forest, persisting in partially cleared forest, (in central Brazil) in gallery forest, along streams, usually 500–1200 m, sometimes lower to 100 m, or in Costa Rica and Colombia to 2000 m, and in Peru to 2700 m. Stem to 10 m tall, and 15 cm in diameter, leaves to 3 m long.

SELECTED SPECIMENS. **Costa Rica. Alajuela:** Carrizal toward Cariblanco, *Gastony & Gastony 790, 794* (GH); La Marina, *Nisman 78* (GH); above Los Angeles, north of San Ramón, *Stone 2752* (GH,US). **Heredia:** Cariblanco, *Nisman 110, 115* (GH). **Limón:** La Trocha, Guápiles, *Nisman 133, 135* (GH). **Cartago:** east of Tuis, on road to San Joaquin, *White & Lucansky 1968–182, –184, –191* (GH). **Puntarenas:** Rincón, Osa Peninsula, *Lent 459* (GH); between San Vito de Java and Villa Neilly, *Nisman 144* (GH). **Panamá. Coclé:** crater of El Valle de Antón, *Wilbur, Weaver & Correa 11121* (GH,NY). **Panamá:** Cerro Campana, *McDaniel 6888* (MO). **British Guiana** (Guyana). Makubere Savanna, Kanuku Mountains, *For. Dept. Brit. Guian. WB401* (NY); Roraima Range, *McConnell & Quelch 605* (NY); Mount Roraima, *Im Thurn 92* (US). **Venezuela. Sucre:** Cerro Espejo, Peninsula de Paria, *Steyermark & Rabe 96085* (GH). **Miranda:** Quebrada Humboldt, Guayabitos, *Vareschi 5819* (VEN). **Bolivar:** Meseta de Jaua, Río Kanarakuni, *Steyermark 98224* (GH). **Colombia. Santander:** Mesa de los Santos, *Killip & Smith 15338* (GH,NY,US). **Cundinamarca:** Fosca, Río Sáname, *Garcia-Barriga 17581* (NY). **Vichada:** Northwest of San Jose de Ocune, *Haught 2813* (GH). **Meta:** north end of Cordillera de Macarena, *Smith & Idrobo 1539* (GH,MO,NY,US). **Nariño:** Junin to Altaquer, Municip. Altaquer, *Soejarto 1451* (GH). **Peru. San Martin:** Rioja, northwest of San Martin, *Soukup 5223* (GH). **Huánuco:** Tingo Maria, *Tryon & Tryon 5219* (F,GH). **Cuzco:** Cordillera Vilcabamba, *Dudley 10058, 10268, 11258* (GH). **Puno:** *Lechler 2160* (P). **Bolivia. Santa Cruz:** Buena

Vista, Prov. Sara, *Steinbach 5310* (F,GH,MO,NY). **La Paz:** Polo-Polo bei Coroico, X, XI, 1912, *Buchtien* (F,GH,MO,NY); Apolo, *Williams 1333* (US). **Argentina. Corrientes:** Estancia El Plata, Dept. Ituzaingó, *Meyer 6278* (A,US). **Paraguay.** Tobatis, *Hassler 4004* (GH,NY); Sierra de Amaambay, *Hassler 10442* (MO,NY,US); Carapegua, *Rojas 3010* (GH,P). **Brazil. Roraima:** Serra Tepequem, *Prance, Forero, Pena & Ramos 4499* (NY). **Ceará:** Serra do Araripe, *Duarte 1346* (NY). **Mato Grosso:** Serra do Roncador, 86 km north of Xavantina, *Irwin, Grear, Souza & Santos 16305* (GH,NY). **Goias:** Riberon Grande, Municip. Jatai, *Macedo 2161, 2173* (US). **Distrito Federal:** Parque Municipal do Gama, 25 km south of Brasilia, *Irwin, Souza & Santos 10138* (NY). **Minas Gerais:** Itacolumi, *Sehnem 4213* (A), *Macedo 2825* (US); Viçosa, *Mexia 4582* (F,GH,MO,NY). **Rio de Janeiro:** Monte Serrat, Mt. Itatiaya, *Smith 1593* (F,GH,NY); Riberão Campo Belo, Mt. Itatiaya, *Tryon & Tryon 6658, 6659, 6661, 6671* (GH). **Guanabara:** Foresta de Tijuca, *Martins 262* (GH). **São Paulo:** Morro das Pedras, Iguape, *Brade 8220* (GH,NY); Monte Alegre do Sul, *Kuhlman 1792* (GH); 27 km northwest of Moji-Mirim, *Eiten, Eiten & Sota 2127* (GH,NY,US). **Paraná:** Porto de Cima, *Dusén 623a* (GH,MO,US), *11781* (F,GH,MO); Valhinas, *Dusén 10760* (F,GH,MO, NY). **Santa Catarina:** Blumenau, *Haerchen* (Ros. Fil. Austrobras. 50a) (F,MO). **Ilha Trinidade** (South Trinidad). Pico Desejado, *Mello Filho 961 (Segadas-Viana 2058)* (US); "Discovery," 13 Sept. 1901 (US).

34. **Cyathea tenera** (Hook.) Moore

FIGS. 124–126. MAP 38.

Cyathea tenera (Hook.) Moore, Ind. Fil. 274. 1861.

Alsophila tenera Hook. Sp. Fil. **1**: 49. 1844. Holotype: St. Vincent, *Caley*, K! fragm. ex K,NY! Isotype: BM! photo GH, fragm. ex BM,US!

Cyathea tenera is close to both *C. furfuracea* and to *C. Delgadii.* It is maintained as a species especially on the basis of its geography and the lack of a clinal relationship of intermediates. A few collections of *C. tenera* have large, brown, flattish scales beneath and some have bullate scales on the costules beneath.

Cyathea tenera appears to represent the initial element in a migration accompanied by evolution from *C. Delgadii* in South America. The migration evidently continued to the Greater Antilles with the further speciation which resulted in *C. furfuracea.*

Lesser Antilles, Montserrat to Grenada, Trinidad and Isla Margarita. In rain forest and montane woods and in thickets, 400–1000 m. Stem to 9 m tall, leaves to 3 m long, usually less.

SELECTED SPECIMENS. **Montserrat.** *Howard 11906* (GH). **Guadeloupe.** 1840, *L'Herminier 62* (GH); *Proctor 20134* (A). **Dominica.** *Hodge & Hodge 1973* (GH,NY); *Lloyd 170, 391* (NY). **Martinique.** *Sieber Exsicc. 374* (MO,NY). **St. Lucia.** *Proctor 17781* (GH). **St. Vincent.** *Eggers 6859* (F,GH), *6868* (F); *Morton 5492* (NY), *6213* (GH). **Grenada.** *Howard 10638* (GH); Nov. 1904, *Broadway* (F,GH). **Trinidad.** *Fendler 80* (GH,NO,NY); *Broadway 5514* (F,GH,MO), *7408* (F,MO), *9968* (GH,NY). **Venezuela. Isla Margarita:** *Johnston 143* (F,GH,NY,US).

GROUP OF CYATHEA CARACASANA

KEY TO SPECIES 35–36

a. Jamaica: pinnules with a few to several long trichomes and a few brown bullate scales beneath, sometimes also a few brown flattish scales on the costa, indusium firm, when over-mature the segments persistent. .... 35. *C. dissoluta.*

a. South America, Costa Rica: pinnules usually with different indument beneath, or none; Cuba, and Hispaniola: (var. *caracasana*) ultimate segments short, whitish pubescent beneath, and indusium delicate, evanescent. .... 36. *C. caracasana.*

This group shows its closest relationship with *Cyathea fulva.* The complex and variable *C. caracasana* is the most common species of the Andes. *Cyathea dissoluta* is a rare and questionable endemic of Jamaica. While technically close to *C. caracasana,* it does not seem to fall within the variation of that species.

35. **Cyathea dissoluta** Jenm.

FIGS. 127–128. MAP 39.

Cyathea dissoluta Jenm. Jour. Bot. **19** (n.s. 10): 52. 1881. Holotype: woods near the Cinchona Plantation, Jamaica, 5000 ft., *Jenman 1,* K! Isotypes: Herb. Jenm. NY! fragm. and photo ex NY,US!

Cyathea dissoluta is a rare, variable species of Jamaica. It is quite possibly a hybrid, or a series of hybrids, but field study is required to provide a basis for a better evaluation of its status.

Jamaica. Montane rain forest, ca. 1200 m.

ADDITIONAL SPECIMENS. **Jamaica.** *Jenman* (NY); *Campbell 7731* (F,NY); *Hart* (P); Morce's Gap, St. Andrew, *Sherring 6* (US); near Cinchona, St. Andrew, *Harris 7731* (US); above Murdock's Gap, Portland, *Proctor 5819* (MO); Arntully Gap, St. Thomas, *Sabonabière* (GH).

36. **Cyathea caracasana** (Kl.) Domin

Cyathea caracasana is a complex and highly variable species. The principal variation is in the squamellae of the petiole scurf, which may be crested, strongly dissected or entire, in the length of the pinnule stalk, the shape of the pinnules, the abundance and kinds of trichomes and scales on the segments, costae and pinna-rachises beneath, and in the texture and corresponding persistence of the segments of the indusium. Considerable study has not resulted in the morphological-geographical correlations and group distinctions to be expected of either species or geographic varieties. However, groups can be formed that may have evolutionary validity and I have chosen to recognize them in a formal classification.

Greater Antilles, Costa Rica, Venezuela to Colombia and south to Bolivia.

KEY TO VARIETIES OF CYATHEA CARACASANA.

a. Ultimate segments glabrous, or with 1 to few large trichomes or rarely pubescent above. . . . . b.
  b. Pinnules sessile to short-stalked or rarely long-stalked and the pinnule broadly long-triangular. . . . . c.
    c. Ultimate segments lacking trichomes beneath, or long-pubescent, or rarely short-pubescent; indusium firm to thin, when over-mature, the segments persistent, at least in part. . . . . d.
      d. Pinnules usually tapering to the apex from beyond the middle, to very narrowly long-triangular, sessile to short-stalked; indument beneath usually rather abundant, of various kinds of trichomes and scales; Venezuela and Colombia to Bolivia. . . . . 36a. var. *boliviensis.*
      d. Pinnules, especially toward the base of the central and basal pinnae, broadly long-triangular or nearly so, short-stalked to rarely long-stalked; indument beneath sparse or absent; Venezuela, Colombia and Ecuador. . . 36b. var. *meridensis.*
    c. Ultimate segments short-whitish pubescent beneath; indusium delicate, more or

less evanescent and often persisting, if at all, as an irregular basal disk or parts (segments dull beneath); Cuba, Jamaica, Hispaniola, Venezuela, Colombia and Ecuador. .... 36c. var. *caracasana.*

b. Pinnules, especially basal ones of the central and basal pinnae, long-stalked, indument beneath sparse or absent; very narrowly long-triangular to tapering to the apex from beyond the middle; Colombia and adjacent Venezuela (Zulia), Ecuador. .... 36d. var. *chimborazensis.*

a. Ultimate segments short-pubescent above, at least at the margin, sometimes sparingly so, usually short-pubescent beneath; Costa Rica. ...... 36e. var. *Maxonii.*

36a. **Cyathea caracasana** var. **boliviensis** (Rosenst.) Tryon, comb. nov. FIGS. 129–130. MAP 40.

Cyathea mexicana var. *boliviensis* Rosenst. Fedde, Rep. Spec. Nov. **25**:56. 1928. Holotype: Hacienda Simaco supra Tipuani, Bolivia, *Buchtien 5140.* Isotypes: F! GH! NY! US!

Cyathea grenadensis Trevis. Atti Instit. Venat. II, **2**: 164. 1851, *nom. nud. Linden 1022* is cited.

Cyathea Lindeniana Presl, Epim. Bot. 30. 1852. Holotype: Nova Granada, Prov. Maraquita, (Colombia), *Linden 1022.* Isotypes: fragm. Herb. Mett. B! fragm. ex BM, US!, BR photo GH, K photo GH.

Cyathea boconensis Karst. Linnaea **28**: 458. 1856. Holotype: none cited, but probably: Monte glacialis Meridensis, 1000 m, cited in Fl. Columb. **2**: 171, t. 190. Isotype: Páramo de Bocono, Serrania de Mérida (Venezuela), *Karsten,* fragm. Herb. Mett. B!

Cyathea frondosa Karst. Fl. Columb. **1**: 149, t. 74. 1860. Holotype: Andes of Bogotá, (Colombia), 2700 m, *Karsten.* Isotype: *Karsten 196,* B! (*Lindig 196* is indicated by another label on the same B sheet, P!).

Cyathea Mettenii Karst. Fl. Columb. **1**: 113, t. 56. 1860. Holotype: Andes of Bogotá, (Colombia), 2700 m, *Karsten.* Isotype: Bogotá, 9000 ft., *Karsten,* B!

Cyathea squamipes Karst. Fl. Columb. **1**: 199, t. 99. 1861. Holotype: Mérida, (Venezuela), 1000–1500 m, *Karsten,* W photo and fragm. BM!

Cyathea patens Karst. Fl. Columb. **2**: 173, t. 191. 1869; not Hort. 1851, *nom. nud.* Holotype: Guadelupe, Bogotá, (Colombia), 2900 m, *Karsten.* Isotype: Colombia, *Karsten,* B! is similar to t. 191, f. 1.

Cyathea lepidopoda C. Chr. Ind. Fil. 193. 1905, *nom. superfl.* An intended *nom. nov.* for "Cyathea squamipes Sod." not Karst, but Sodiro uses *C. squamipes* Karst, with reference to the Fl. Columb.

Cyathea Herzogii Rosenst. Meded. Rijks. Herb. Leiden **19**: 7. 1913. Holotype: Yungas de San Mateo, Bolivia, *Herzog 1990,* L photo GH. Isotypes: S! US!

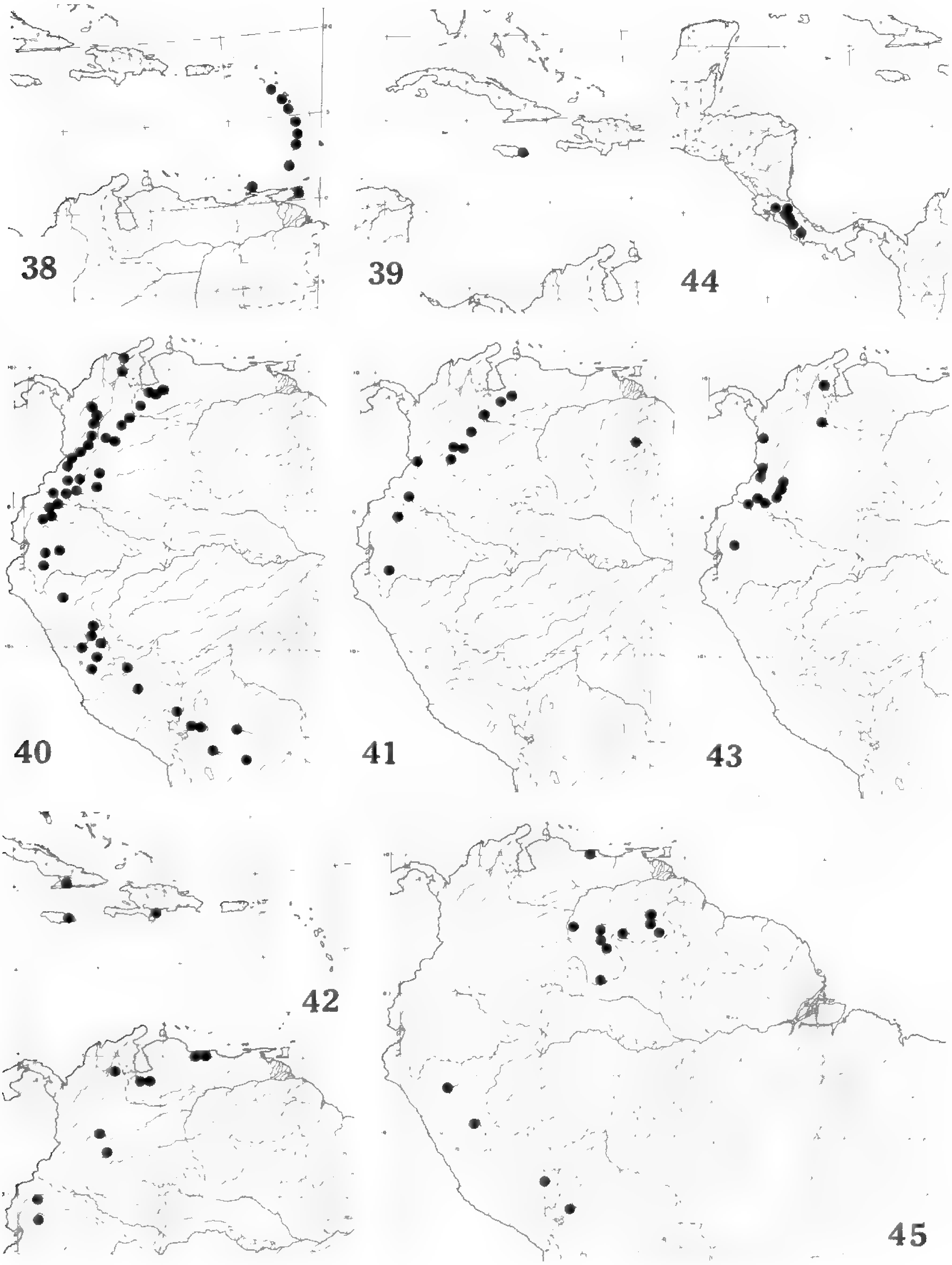
Cyathea catacampta Alston, Jour. Wash. Acad. Sci. **48**: 231. 1958. Holotype: between Río Miraflores and Río San Martin, Volcán de Cumbal region, Nariño, Colombia, *Ewan 16153,* BM. Isotype: US!

This is the most common and widely distributed of the varieties. In its variation it tends toward other sympatric varieties, especially var. *meridensis* and var. *chimborazensis.* In Bolivia there is a variation with the segments slightly pubescent above *(Cardenas 3059)* or strongly so, *(Herzog 1990)* that is similar in this character to var. *Maxonii* of Costa Rica.

Venezuela and Colombia, south to Bolivia. Montane forest, cloud forest, subparamo forest and *Chusquea* thickets, persisting after clearing, 1000 to usually 2200–3000 to 4200 m. Stem to 15 m tall, leaves to 3 m long.

SELECTED SPECIMENS. **Venezuela. Trujillo:** cerca La Puerta, *Vareschi 7492* (VEN). Mérida, (Venezuela), 2000 m, *Karsten.*
Chuchilla, 20 km west of Mérida on road to La Azulita, *Tryon & Tryon 5773* (GH). **Tachira:** south of San Vincente de la Revancha, *Steyermark, Dunsterville & Dunsterville 100748* (GH); debajo de Páramo de La Negra, *Steyermark & Rabe 96956* (GH).

Colombia. Magdalena: Sierra de Perijá, 23 km east of Codazzi, *Grant 10948* (GH,US); Sierra Nevada de Santa Marta, *Smith 1020* (F,GH,MO,NY,US). **Norte de Santander:** Pamplona to Toledo, *Killip & Smith 19835, 19857, 19861* (GH,NY,US). **Antioquia:** Santa Elena, *Archer 1251* (US); 8 km west of Valdivia, *Madison 804* (GH). **Santander:** Mesa de los Santos, *Killip & Smith 15088* (GH). **Cundinamarca:** Páramo San Miguel, *Gutierrez & Jaramillo 279* (GH,NY); Fusugasuga, *Cuatrecasas 8035* (F,US), *8037* (F,GH,US). **Valle:** Piedra de Moler, Río Dagua, *Cuatrecasas 15095* (F,GH,US); Los



MAPS 38–45. 38, Cyathea tenera; 39, C. dissoluta; 40–44, C. caracasana; 40, var. boliviensis; 41, var meridensis; 42, var. caracasana; 43, var. chimborazensis; 44, var. Maxonii; 45, C. Lechleri.

Farallones, Alto del Buey, *Cuatrecasas 17886, 18043* (F,US). **Tolima:** above Anaime, on road south of Cajamarca, *Barrington 477* (GH). **Cauca:** Cerro Munchique, *Tryon & Tryon 6009* (GH,NY). **Huila:** Río Villalobos, vicinity of Río Suazita, *Schultes & Villareal 5185* (GH,MO,NY,US). **Putumayo:** Valle de Sibundoy, *Cuatrecasas 11675* (F,US). **Nariño:** Volcán de Chiles, *Ewan 16012* (GH,US). **Ecuador. Carchi:** Río Chingual drainage, *Ewan 16307* (GH,US). **Pichincha:** confluence Río Tandápi and Río Pilatón, Aloag to Santo Domingo, *Sparre 14049* (GH). **Loja:** 45 km north of Loja on road to Cuenca, *Madison 918* (GH). **Zamora-Chinchipe:** km 18, road to Loja-Zamora, *Sparre 16310, 16312, 16313, 16488* (GH). **Peru. Amazonas:** entre Ingenio y Pomacocha, *López, Sagástegui & Collante 4312* (GH). **Huánuco:** Carpish, *Tryon & Tryon 5326* (F,GH,NY). **Loreto:** Divisoria, Prov. Cornel Portillo, *Ferreyra 1074* (GH), *1696* (US, USM). **Junin:** Oxapampa, *Soukup 2335* (F,GH). **Cuzco:** Machu Picchu, *Iltis, Iltis & Ugent 1025* (GH,US). **Puno:** San Juan del Oro, valle del Alto Tambopata, *Ferreyra 16684* (GH). **Bolivia. La Paz:** Yungas, *Bang 562* (GH,MO,NY); Sailapata, Prov. Ayopaya, *Cardenas 3059* (GH,US). **Cochabamba:** Prov. Chapare, *Steinbach 9046* (F,GH, MO,US), *9425* (F,GH,MO,NY,US), *9449* (F,GH,MO,NY).

36b. **Cyathea caracasana** var. **meridensis** (Karst.) Tryon, comb. nov.
Figs. 131–132. Map 41.

Cyathea meridensis Karst. Fl. Columb. **2**: 161, t. 184. 1869, *ex char.* Holotype: Mérida, (Venezuela), 2000 m, *Karsten.*

Alsophila petiolulata Mett. Ann. Sci. Nat. V, **2**: 263. 1864, *nom. nud.* The epithet is credited to Karsten (=*Cyathea petiolulata* Karst.?), although *Lindig* 285, cited, GH! is *Cyathea caracasana* var. *meridensis.*

Cyathea parvifolia Sod. Sert. Fl. Ecuad. **2**: 7. 1908. Holotype: Silv. subandin. occ. Pichincha, *Sodiro.* Isotypes: 3/1901, *Sodiro,* A! P! photo GH,US!

This variety is rather uniform in its pinnule shape and indument, although it does grade into var. *boliviensis* in these characters. Some specimens approach other varieties, for example, *Barrington 455* has a few of the long-stalked pinnules characteristic of var. *chimborazensis,* and *Cuatrecasas 6710, Killip & Smith 17821* are pubescent on the upper surface of the segments as in var. *Maxonii.*

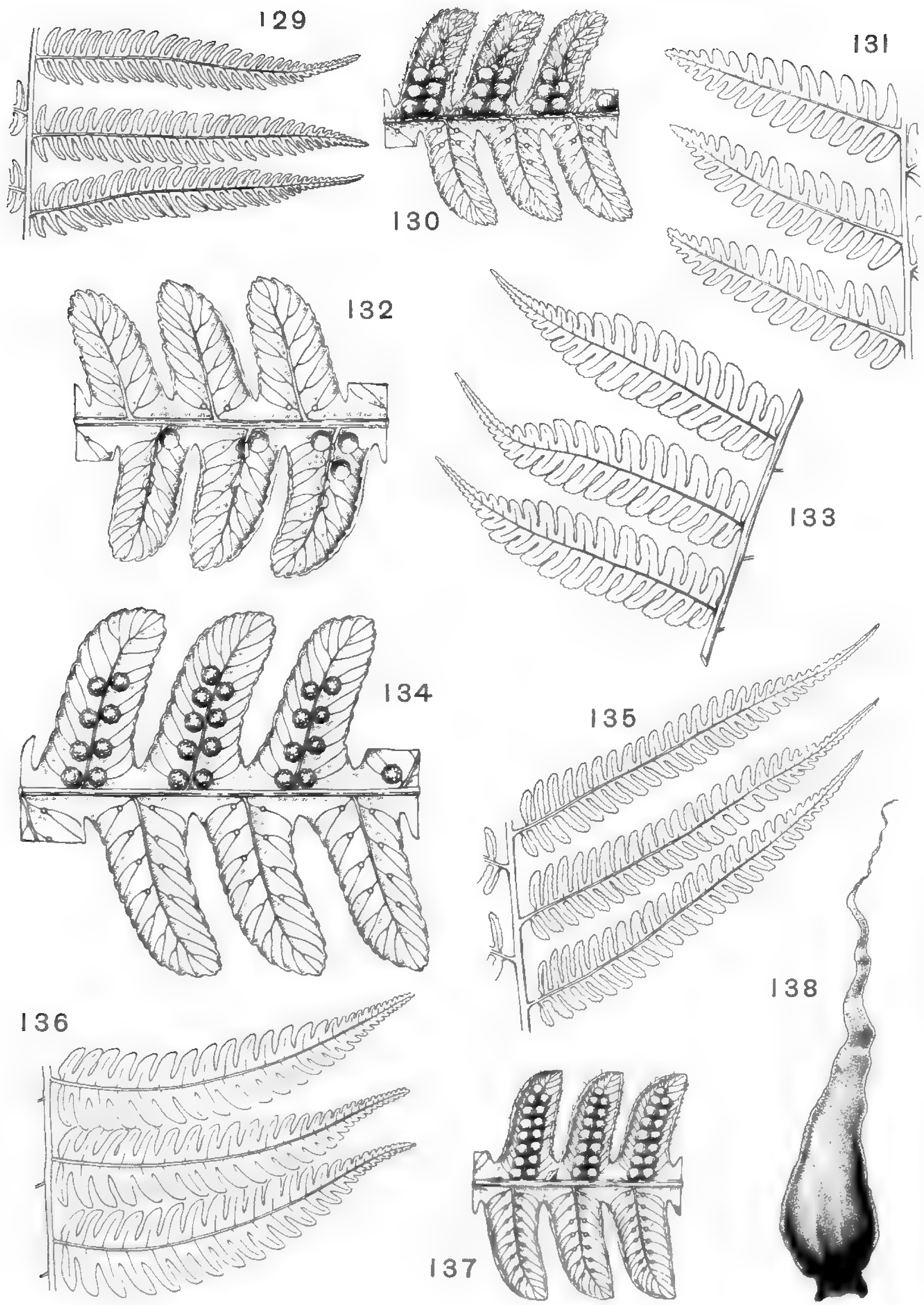
Venezuela, Colombia and Ecuador. In wet forests and woodlands, cloud forest and thickets, 1800 to usually 2400–2800 to 3400 m. Stem 8 m tall.

SELECTED SPECIMENS. **Venezuela. Trujillo:** between Boconó and Guaramacal, *Steyermark 104864* (GH). **Mérida:** Laguna Coromoto, *Vareschi & Vareschi 5822* (VEN). **Tachira:** 20 km south of San Vincente de la Revancha, *Steyermark, Dunsterville & Dunsterville 100967* (GH). **Bolivar:** Ilu-tepuí, Gran Sabana, *Maguire 33530* (NY,US). **Colombia. Santander:** Páramo Rico, *Killip & Smith 17821* (GH,NY,US). **Cundinamarca:** San Miguel, *Cuatrecasas 6710* (F,GH,NY); Bogotá to Fusugasuga, *Barrington 455* (GH). **Valle:** La Cumbre, *Killip 11404* (GH,NY,US). **Tolima:** above Volcancitos, old Quindio Trail, *Killip & Hazen 9496* (GH,NY). **Nariño:** La Granja Botana, Pasto, *Barrington 506* (GH). **Ecuador. Loja:** 5 miles north of San Lucas, *Wiggins 10999* (NY,US).

36c. **Cyathea caracasana** var. **caracasana**
Figs. 133–134. Map 42.

Cyathea caracasana (Kl.) Domin, Pterid. 262. 1929.

Alsophila caracasana Kl. Linnaea **18**: 541. 1844. Holotype: Caracas, (Venezuela), *Moritz 117.* Isotypes: GH! P! (Domin, Pterid. Dominica, t. 10, f. 8 and t. 18, f. 1, figures *Moritz 117*). *Moritz 394* (GH) is nearly identical and Domin cites a sheet bearing both numbers.



FIGS. 129–138. *Cyathea caracasana*. 129–130, var. *boliviensis:* 129, Pinnules, Colombia, *Ewan 16012* (GH), × ½; 130, Portion of fertile pinnules, Bolivia, *Herzog 1990* (US), × 2. 131–132, var. *meridensis*, Colombia, *Killip & Hazen 9496* (GH): 131, Pinnules, × ½; 132, Portion of fertile pinnule, × 2. 133–134, var. *caracasana:* 133, Pinnules, Jamaica, *Proctor 22547* (GH), × ½; 134, Portion of fertile pinnule, Venezuela, *Fendler 56* (MO), × 2. 135, var. *chimborazensis:* Pinnules, Colombia, *Cuatrecasas 18186* (US), × ½. 136–138, var. *Maxonii:* Pinnules, Costa Rica, *Nisman 63* (GH), × ½; 137, Portion of fertile pinnule, Costa Rica, *Scamman 5885* (GH), × 2; 138, Petiole scale, Costa Rica, *Nisman 108* (GH), × 4.

Hemitelia crenata Sod. Rec. Crypt. Vasc. Prov. Quit. 18. 1883. Syntypes: Ecuador, Volcán Atacazo: Canzacoto, Boloña, *Sodiro.* Lectotype: Hacienda Boloña, 1550 m, 1882, *Sodiro,* P! photo GH.

Cyathea fulva Sod. Rec. Crypt. Vasc. Prov. Quit. 13. 1883, not (Mart. & Gal.) Fée, 1857. Lectotype: Tambo-loma, Prov. Ríobamba, Ecuador, 10/1882, *Sodiro,* P! photo GH. Isolectotypes: fragm. ex B,NY!, fragm. ex K,NY! The petiole of this collection agrees with the description. An excluded element, under the same label, is *Cyathea pallescens* (NY).

Hemitelia Sherringii Jenm. Jour. Bot. **24** (n.s. 15): 266. 1886. Holotype: Rose Hill, Jamaica, 11/1886, *Sherring,* K! Isotypes: US! and a series of sheets NY! mostly without data. Baker, Ann. Bot. **5**: 8. 1891 says "only one plant seen."

Cyathea ocanensis Baker, Ann. Bot. **5**: 184. 1891. Holotype: Ocaña, Colombia, *Kalbreyer 608,* K. Dept. Santander, Nuga, *Kalbreyer 608,* B! is evidently an isotype.

Cyathea crenata (Sod.) Christ, Farnkr. 323. 1897.

Cyathea Sodiroi C. Chr. Ind. Fil. 195. 1905, *nom. nov.* for *Cyathea fulva* Sod., not (Mart. and Gal.) Fée.

Cyathea producta Maxon, Jour. Wash. Acad. Sci. **12**: 438. 1922. Holotype: Palma Mocha Peak, Sierra Maestra, Oriente, Cuba, *Léon 11181,* US! Isotype: NY!

Alsophila caracasana var. *petiolularis* Domin, Mem. Roy. Czech Soc. Sci. n.s. **2** (Pterid. Dominica): 95. 1929, *ex char.* Syntypes: Venezuela, Caracas, *Buschel;* Colonia Tovar, *Pittier 10011;* Caracas, *Buschel.*

Cyathea subindusiata Domin, Mem. Roy. Czech Soc. Sci. n.s. **2** (Pterid. Dominica): 67, t. 8, f. 4–6, t. 9, f. 2. 1929. Holotype: Caracas, (Venezuela), *Buschel.* Venezuela, 1855, *Buschel,* BM! photo GH, is probably an isotype.

Cyathea Sherringii (Jenm.) Domin, Pterid. 264. 1929.

Cyathea caracasana var. *petiolularis* (Domin) Domin, Acta Bot. Bohem. **9**: 103. 1930.

Trichipteris caracasana (Kl.) Tryon, Contrib. Gray Herb. 200: 45. 1970.

The disjunct distribution of var. *caracasana* has probably been a major reason for its extensive synonomy. However, the characters of indument and indusium, mentioned in the key, are quite uniform throughout its range. The continental-Greater Antilles distribution is similar to that of *Cyathea andina* and *C. gracilis.*

Cuba, Jamaica and Hispaniola, Venezuela, Colombia and Ecuador. Montane rain forest, 1200–2000 m. Stem to 8 m tall.

SELECTED SPECIMENS. **Cuba. Oriente:** between Río Yara and Río Palmamocha, Sierra Maestra, *Ekman 14362* (US). **Jamaica.** Port Royal Mountains, *Jenman* (NY); Hardwar Gap, Portland, *Proctor 16503* (MO), *22547* (GH). **Dominican Republic.** Above Gros Figuier, Sierra de los Comisarios, Prov. Barahona, *Ekman 6769* (US). **Venezuela. Distrito Federal:** near Avila, *Delgado 3* (GH,US). **Aragua:** Colonia Tovar, *Fendler 56* (GH,MO). **Mérida:** southwest of Canaguá, *Steyermark 56432* (F,GH,MO,NY). **Colombia. Cundinamarca:** Tequedama, *Holton 69* (NY). **Meta:** Macizo Renjifo, Cordillera La Macarena, *Idrobo & Schultes 1105* (US). **Ecuador. Chimborazo:** Chimborazo, *Sodiro* (NY).

36d. **Cyathea caracasana** var. **chimborazensis** (Hook.) Tryon, comb. nov.

FIG. 135. MAP 43.

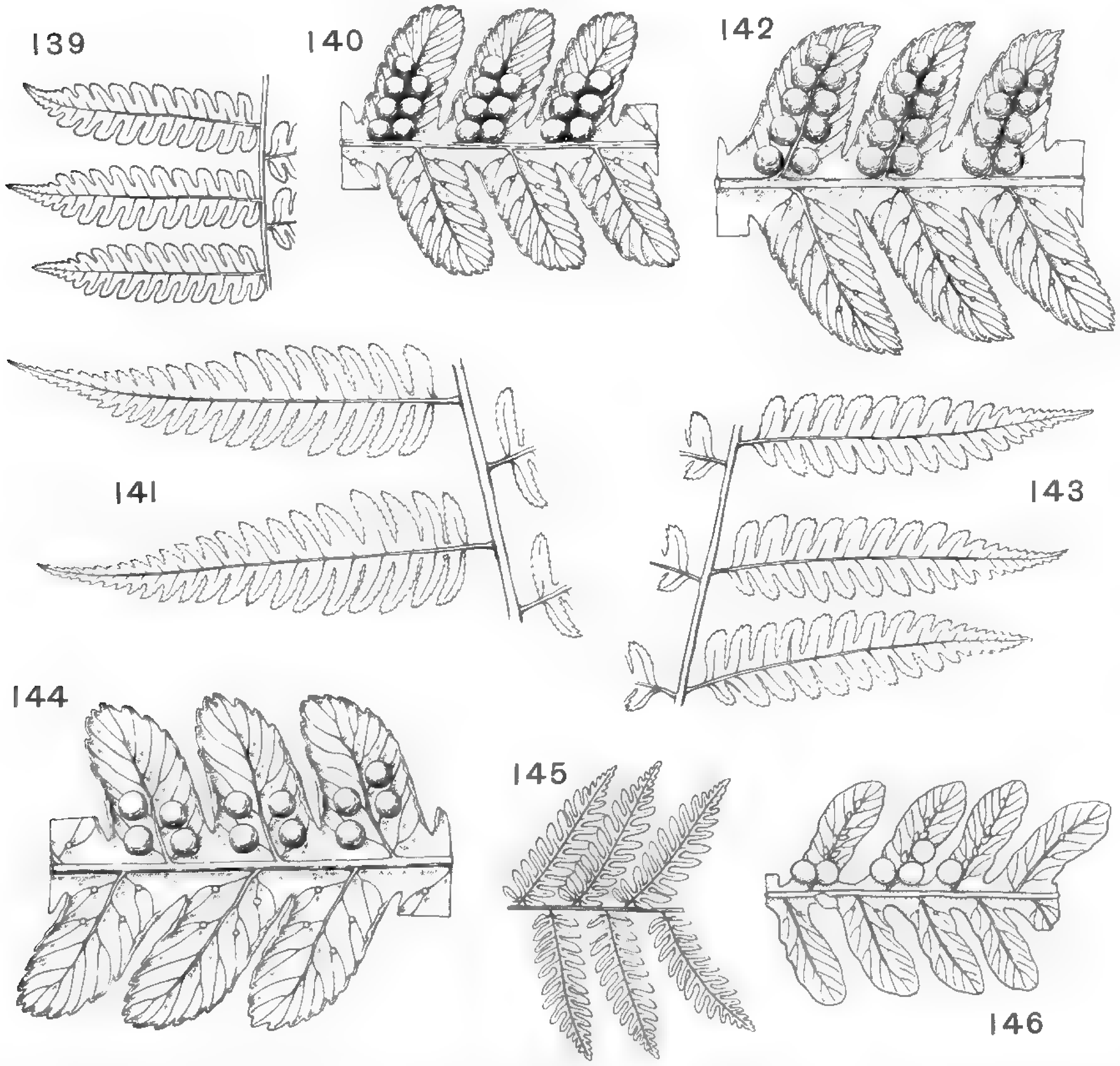
Alsophila chimborazensis Hook. Syn. Fil. 37. 1866. Holotype: Chimborazo, Ecuador, 3000–4000 ft., *Spruce 5743,* K. Isotype: P! fragm. ex. Rosenst. US!

Cyathea chimborazensis (Hook.) Hieron. Hedwigia **45**: 230. 1906.

The characteristic long-stalked pinnules of var. *chimborazensis* rarely occur in var. *boliviensis* also, to the south of their area of sympatry. The pinnule indument is variable: for example, *Little 8906* has rather numerous trichomes beneath, *Cuatrecasas 8674* has bullate and flat scales beneath, and *Bristol 384* is slightly pubescent on the upper surface of the segments.

Colombia and adjacent Venezuela, Ecuador. Wet montane forest, persisting in clearings, 1000 to usually 1600–2300 to 3000 m. Stem to 8 m tall, leaves to 3 m long.

SELECTED SPECIMENS. **Venezuela. Zulia:** Sierra de Perija, southwest of Pishikakao and Iria, *Steyermark, Dunsterville & Dunsterville 105693* (GH). **Colombia.** Chocó: 5°55′ N, 76°10′ W, *Madison 821* (GH). **Norte de Santander:** Vicinity of Toledo, *Killip & Smith 20100* (GH,NY,US). **Santander:** east of Las Vegas, *Killip & Smith 15861* (NY,US). **Valle:** La Cumbre, *Killip 11363, 11364* (GH,NY,US); Piedra de Moler, Río Dagua, *Cuatrecasas 15191* (F,US). **Cauca:** km 19 from Cali to Buenaventura, *Barrington 498, 502* (GH). **Huila:** between Gabinete and Andalucia, *Cuatrecasas 8674* (F,US); near Resina, Guadalupe to Florencia, *Little 9083* (GH,US); 25 km eastsoutheast of Baraya, *Little 8906* (GH,US). **Putumayo:** Valle de Sibundoy, *Bristol 384* (GH,US). **Nariño:** above San Juan, *Ewan 16031* (GH).



FIGS. 139–146. 139–140. *Cyathea Lechleri*, Peru, *Spruce 4723:* 139, Pinnules, (MO), × ½; 140, Portion of fertile pinnule, (GH), × 2. 141–142, *C. gracilis*, Jamaica, *Maxon & Killip 944:* 141, Pinnules, (GH), × ½; 142, Portion of fertile pinnule, (F), × 2. 143–144, *C. ebenina*, Venezuela, *Fendler 50* (GH): 143, Pinnules, × ½; 144, Portion of fertile pinnule, × 2. 145–146, *C. Dudleyi*, Peru, *Dudley 10867B* (GH): 145, Pinnules, × ½; 146, Portion of fertile pinnule, × 2½.

36'e. **Cyathea caracasana** var. **Maxonii** (Maxon) Tryon, comb. nov.

Figs. 136–138. Map 44.

Cyathea Maxonii Maxon, No. Amer. Fl. **16**: 82. 1909. Holotype: 5 miles south of Cartago, Costa Rica, *Maxon 524*, NY. Isotype: US!

Cyathea membranulosa Christ, Bull. Herb. Boiss. II, **7**: 271. 1907. Syntypes: San Pascon, Costa Rica, 1500 m, *Wercklé* (Herb. Instit. Nat. Costaric. 17024), Herb. Christ, P!; La Palma, Costa Rica, 1500 m, *Wercklé* (Herb. Instit. Nat. Costaric. 17082), Herb. Christ, P!

The pinnules of var. *Maxonii* are often long-triangular, although they sometimes taper to the apex from about the middle; they are usually short-stalked, but rarely sessile. The petiole scale often has dark streaks, or areas (Fig. 138), rather than a dark central portion. In some collections the scales are mostly dark brown and rather few of them have the typical dark central portion. While var. *Maxonii* is not as well-defined as the other varieties, it is the only one that is completely allopatric.

Costa Rica. Montane forest and cloud forest, 915–2800 m, usually above 2000 m. Stem to 9 m tall and 30 cm in diameter, leaves to 4 m long.

SELECTED SPECIMENS. **Costa Rica. Alajuela:** 31 km from Carrizal toward Cariblanco, *Gastony & Gastony 789* (GH); 19 km north of San Ramón, *White & Lucansky 1968–26* (GH). **Heredia:** Volcán Barba, near Porrosati, *Burger & Stolze 6007* (GH,NY); Volcán Barba, *Scamman & Holdridge 7868* (F,GH,NY). **San José:** 22 km north of San Isidro del General toward Cerro de la Muerte, *Gastony & Gastony 760* (GH). **Cartago:** 7 km south of Tapanti, *Tryon & Tryon 7022, 7025* (GH); La Chonta, km 55 Pan-American Highway, *Nisman 105, 107, 108, 177* (GH). **Puntarenas:** San Vito, *McAlpin 2263* (GH).

GROUP OF CYATHEA LECHLERI

KEY TO SPECIES 37–40

a. Lamina bipinnate-pinnatifid throughout or tripinnate only at the base of central to basal pinnae; larger ultimate segments usually ca 10 mm long or more. . . . . b.
  b. Pinnules short-stalked, or when long-stalked the basal segments not decurrent on the pinnule stalk which is only somewhat lighter, concolorous, or darker beneath than the pinna-rachis. . . . . c.
    c. Pinnules with nearly parallel sides, tapering to an acute to acuminate apex, sessile to short-stalked throughout the lamina; Venezuela, Peru, Bolivia. 37. *C. Lechleri.*
    c. Pinnules broadly long-triangular and long-stalked, especially toward the base of central to basal pinnae, usually long-acuminate; Jamaica, Costa Rica, Colombia. . . . . 38. *C. gracilis.*
  b. Pinnules long-stalked and the basal segments decurrent onto the pinnule stalk which is of strongly contrasting lighter color beneath to the dark pinna-rachis; Venezuela, Colombia, Peru. . . . . 39. *C. ebenina.*
a. Lamina tripinnate nearly throughout; larger ultimate segments small, ca. 5 mm long; Peru. . . . . 40. *C. Dudleyi.*

A very natural group of distinctive, mostly Andean species. *Cyathea Lechleri* relates the group to either *C. caracasana*, or perhaps to *C. platylepis.* All of the other species are clearly specialized in the pinnule and lamina complexity characters mentioned in the key.

37. **Cyathea Lechleri** Mett.

Figs. 139–140. Map 45.

Cyathea Lechleri Mett. Fil. Lechl. **2**: 32. 1859. Holotype: St. Gavan, (San Gavan, Puno), Peru, *Lechler*, LZ, destroyed, fragm. probably ex LZ: *Lechler 2309*, Herb. Mett. B!

Cyathea castanea Baker, Syn. Fil. 451. 1874. Holotype: Andes of Peru, (Tarapoto), *Spruce 4723*, K. Isotypes: GH! MO! P! US!

Cyathea purpurea Morton, Fieldiana: Bot. 28: 7. 1951. Holotype: between Agüita and summit of Cerro Duida, Amazonas, Venezuela, *Steyermark 58395*, F. Isotype: US!

The Venezuelan materials of *Cyathea Lechleri* are somewhat variable. The petiole and rachis may be pubescent or with only scattered trichomes, and the petiole color varies from atropurpureous to reddish-brown.

Venezuela, Peru and Bolivia. Montane forest, dense cloud forest and bamboo thickets, 1600–2200 m in Venezuela, 800–1500 m in Peru and Bolivia. Stem to 9 m tall, leaves to 2.5 m, or 6 m in one collection.

SELECTED SPECIMENS. **Venezuela. Aragua:** to Los Carayaca from Colonia Tovar, *White & White 1970–31* (NY). **Bolivar:** Auyan-tepuí, *Vareschi 4782* (US,VEN); Churi-tepuí (Muru-tepuí), *Wurdack 34257* (GH,NY,US); Chimantá-tepuí (Torono-tepuí), Chimantá Massif, *Steyermark 75444* (F,GH,NY,VEN). **Amazonas:** Cerro de la Neblina, *Maguire, Wurdack & Maguire 42369, 42370* (US); Cerro Sipapo (Paráque), *Maguire & Politi 28557* (GH,NY,US); Serranía Parú, *Cowan & Wurdack 31365* (GH,NY,US). **Peru. Huánuco:** Cerros del Sira, Río Lulla-Pichis watershed, *Dudley 13007, 13213, 13262* (GH). **Bolivia. La Paz:** San Carlos, Mapiri region, *Buchtien 291* (GH,NY); San José, Mapiri, *Cardenas 1009* (GH).

38. **Cyathea gracilis** Griseb.

FIGS. 141–142. MAP 46.

Cyathea gracilis Griseb. Fl. Brit. W. Indies 704. 1864. Holotype: Fox Gap, Jamaica, *Purdie*, K!

Cyathea gracilis, in Jamaica, Costa Rica, and Colombia, expresses the relatively strong biogeographic affinity between those countries. In addition to the characters mentioned in the key, the species has very long, gradually acuminate pinnules (especially the larger ones) and a very firm, dull indusium.

Jamaica, Costa Rica and Colombia. Montane forest and cloud forest, 900–1600 m in Jamaica, ca 1500 m in Costa Rica, 1700 m in Colombia. Stem to 2 m (probably more) tall, leaves to 3 m long.

SELECTED SPECIMENS. **Jamaica.** Morce's Gap, St. Andrew, *Underwood 1536* (NY); Mt. Horeb Trail, St. Andrew, *Crosby, Hespenheide & Anderson 316* (F,GH,NY); below New Haven Gap, St. Andrew, *Maxon & Killip 944* (F,GH,NY); east slope of John Crow Mountains, 2½ miles southwest of Ecclesdown, *Proctor 5711* (MO); Crown Peak, John Crow Mountains, *Proctor 4583* (MO). **Costa Rica. San José:** La Palma, *Brade & Brade, 853* (US); above La Hondura, *Gastony & Gastony 772, 773* (GH); Las Nubes, *Scamman 7004* (GH). **Colombia. Antioquia:** 8 km west of Valdivia, *Madison 803* (GH).

39. **Cyathea ebenina** Karst.

FIGS. 143–144. MAP 47.

Cyathea ebenina Karst. Linnaea 28: 461. 1856. Holotype: between Caracas and Puerto Cabello, Venezuela, *Karsten*. Isotype: Caracas, *Karsten*, B!

A very distinctive species with long-stalked pinnules with the basal segments decurrent onto the upper part of the pinnule stalk.

Venezuela, Colombia and Peru. Montane forest, 2100–2500 m. Stem to 3 m tall, leaves to 1.5 m long.

SELECTED SPECIMENS. **Venezuela. Aragua:** Colonia Tovar, *Fendler 50* (GH), *Moritz 393* (F,GH,P). **Colombia. Valle:** La Cumbre, *Killip 11386* (GH,NY,US); Gibralter, north of Las Brisas, *Cuatrecasas 22525* (F,US). **Huila:** 25 km eastsoutheast of Baraya, *Little 8905* (GH,US). **Peru. Amazonas:** 3 km north of Lake Pomacocha, Prov. Bongara, *Hutchison & Wright 6814* (GH,NY).

40. **Cyathea Dudleyi** Tryon, spec. nov.

FIGS. 145–146. MAP 48.

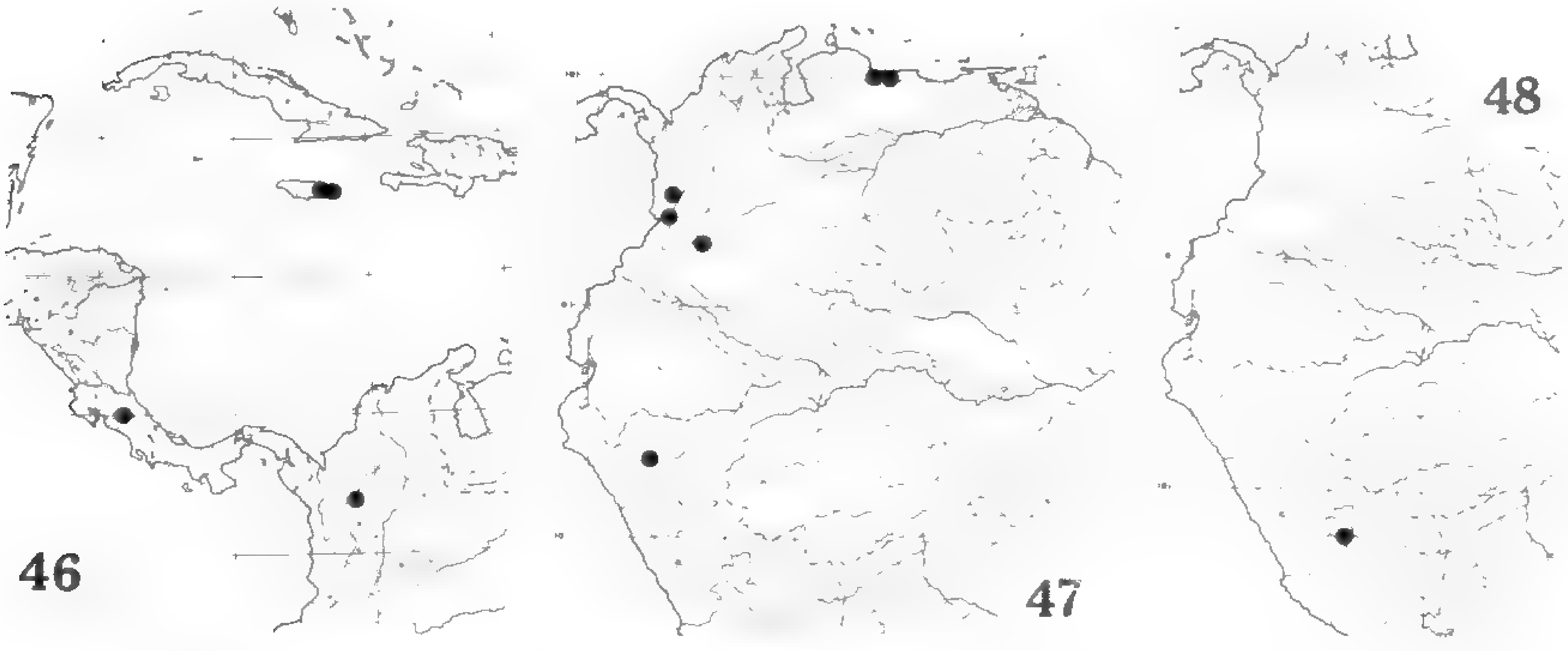
Folia ad 1.25 m longa; petiolus atrovinosus vel atropurpureus fere laevis squamis structura marginata caducis fere concoloribus fuscis; lamina tripinnata; pinnae ad 30 cm longae; pinnulae pagina inferiore squamis bullatis brunneis; segmenta ultima ad 5 mm longa; sori subcostales in venis simplicibus; indusium sphaeropteroideum. Holotypus: 77°33′ W, 12°37′ S, Prov. Convencion, Dept. Cuzco, Peru, *Dudley 10867B*, GH. Paratypes: same locality, *Dudley 10738, 10867*, GH.

Except in its lamina complexity, *Cyathea Dudleyi* appears close to *C. Lechleri*. It is very similar to *C. microphylla* in its lamina architecture, but that species has very different petiole scales. The species is named for Dr. T. R. Dudley, who has added greatly to our knowledge of Peruvian ferns through his extensive collections, especially those from the Cordillera Vilcabamba.

Cordillera Vilcabamba, Peru. Very wet, dense cloud forest, 2600–2700 m. Stem 0.6–1.2 m tall, leaves to ca 1 m long.

PUTATIVE HYBRIDS

The following hybrids are proposed with varying degrees of confidence. The first two, 41 and 42, are certainly hybrids. Conant (1975) has presented a detailed discussion of 41, *Cnemidaria horrida* × *Cyathea arborea*, including observations of its occurrence with both parents. *Cnemidaria horrida* × *Cyathea parvula* is rather similar to 41 and *Cnemidaria horrida* is certainly one parent. The *Cyathea* species involved needs to be con-



MAPS 46–48. 46, Cyathea gracilis; 47, C. ebenina; 48, C. Dudleyi.

firmed by field study. The other, less certain, hybrids have each been assessed individually. In some, the lamina architecture is suggestive of a hybrid, especially those involving a species of *Cnemidaria*. Others are rarely collected and are intermediate between common species. In all cases, the interpretation as a hybrid seems more probable than that of a variation of a species or as an endemic species.

41. Cnemidaria horrida × Cyathea arborea

Fig. 147.

Hemitelia Wilsonii Hook. Syn. Fil. 30. 1865. Holotype: Mansfield near Bath, Jamaica, 1000 ft., *Wilson 731,* K! Isotype (probable): GH!
Cyathea Wilsonii (Hook.) Domin, Pterid. 264. 1929.

This hybrid will key out to species 1–8, 9–12 or usually 17–19. It may be readily distinguished from the species of *Cyathea* in the Greater Antilles, *C. andina, C. parvula* and *C. arborea,* by its predominantly adnate pinnules. The spores are abortive. The relatively well-developed indusium varies from about half cyathiform to fully cyathiform. Conant (1975) has presented a full discussion of the hybrid status of *Hemitelia Wilsonii.*

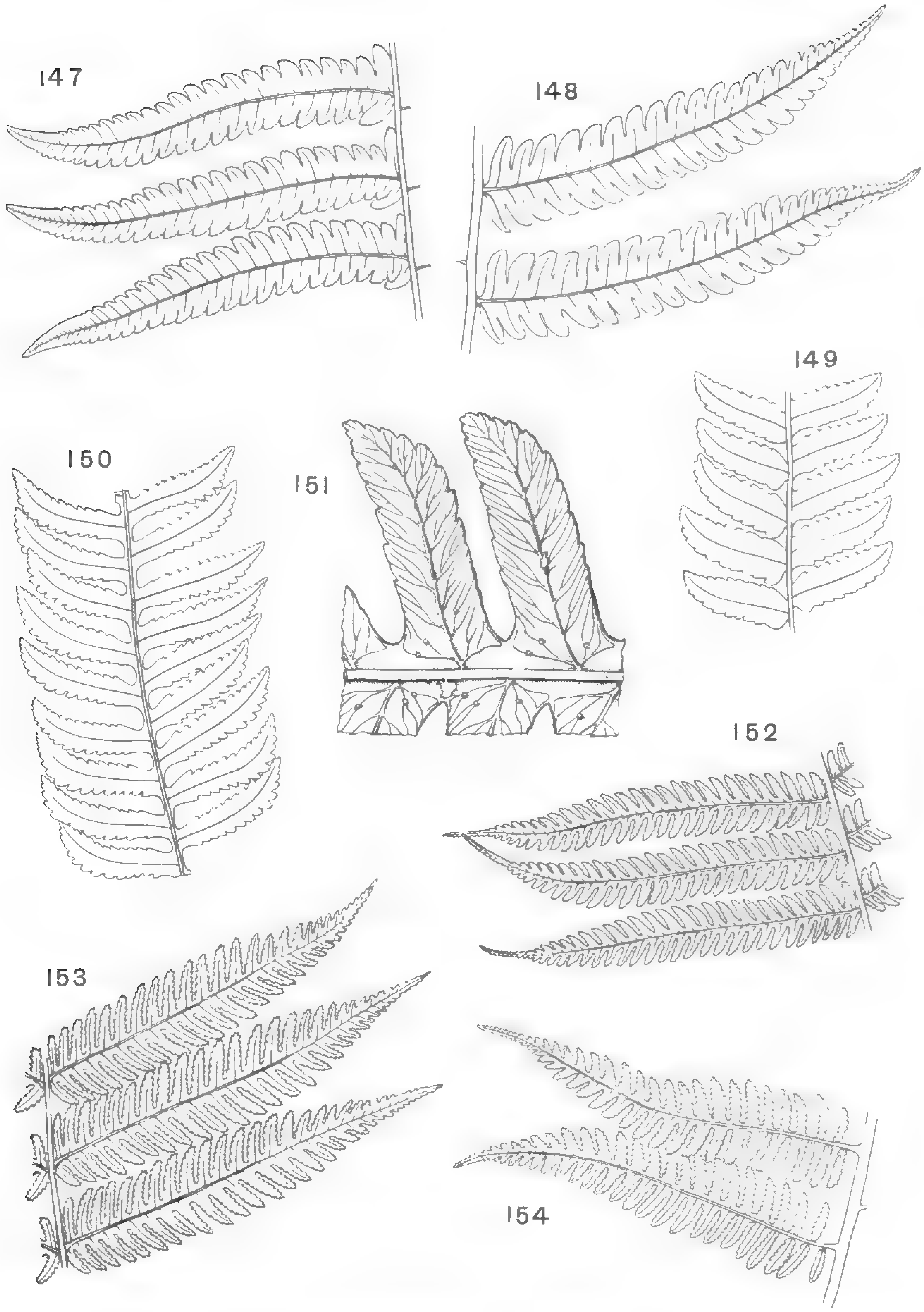
ADDITIONAL SPECIMENS. **Jamaica.** Claverty Cottage, Herb. Jenman (NY); vicinity of Castleton Gardens, St. Mary, *Proctor 18419* (A). **Haiti.** Morne Chapelet, Massif du Nord, *Ekman H4835* (NY,S); Poste Marie Congo, Massif du Nord, *Ekman H4846* (S,US). **Dominican Republic.** Laguna, Península de Samaná, *Ekman H15014* (GH,NY); Sanchez, Península de Samaná, *Ekman H14752* (NY); Liali, *Abbott 2660* (GH,NY,US); Miches to Higuey, Seibo, *Gastony, Jones & Norris 654* (GH,NY). **Puerto Rico.** Sabana Road, Luquillo National Forest, Municip. Río Grande, 5 March, 1970, *Kepler* (El Verde Field Station, Puerto Rico Nuclear Center), *Conant 626, 627* (GH); El Verde, Municip. Río Grande, *Conant 546* (GH); Maricao, *Hess 371* (fragm. ex US,NY), *Hioram 804* (fragm. ex US,NY); Quebradilles, *Hioram 182* (fragm. ex US,NY); El Yunque Road, Luquillo National Forest, Municip. Río Grande, 5 March, 1970, *Kepler* (El Verde Field Station, Puerto Rico Nuclear Center).

42. Cnemidaria horrida × Cyathea parvula

Fig. 148.

Alsophila sessilifolia Jenm. Jour. Bot. **20** (n.s. 11): 325. 1882. Lectotype: Mansfield, near Bath, Jamaica, *Wilson 520,* K! Isotype: BM! photo GH,MO! (an exact match of the lectotype), fragm. ex BM,US!, photo US. Lectoparatypes: *Wilson 513,* BM, *Wilson A1,* BM. Isolectoparatype: *Wilson 513,* NY!
Hemitelia sessilifolia (Jenm.) Jenm. West Ind. Guiana Ferns 44. 1898.
Cyathea sessilifolia (Jenm.) Domin, Pterid. 263. 1929.

This hybrid will key to species 1–8, or to species 9–12. The only Greater Antillean species in these groups are *Cyathea andina* and *C. parvula.* The hybrid differs from both of them in its large, entire, acuminate pinnule-segments near the apex of the pinnae. The spores are evidently abortive. The leaf architecture indicates one parent to be *Cnemidaria horrida;* the other is probably *Cyathea parvula,* which also occurs in Cuba, Jamaica, and Puerto Rico. This hybrid may be distinguished from the previous one, *Cnemidaria horrida × Cyathea arborea,* by its mostly sessile or very short-



FIGS. 147–154. Hybrids. 147, *Cnemidaria horrida* × *Cyathea arborea*, pinnules, Dominican Republic, *Ekman H15014* (GH), × ½; 148, *Cnemidaria horrida* × *Cyathea parvula*, pinnules, Puerto Rico, *Conant 612* (GH), × ½; 149, *Cnemidaria grandifolia* var. *obtusa* × *Trichipteris aspera*, Portion of lower pinna, Grenada, *Sherring* (K), × ½; 150–151, *Cnemidaria spectabilis* var. *spectabilis* × *Cyathea tenera:* 150, Portion of pinna, Trinidad, *Broadway & Hombersley* (US), × ½; 151, Portion of fertile pinna, Trinidad, *Broadway 5719* (MO), × 1½; 152, *Cyathea arborea* × *Trichipteris aspera*, pinnules, Jamaica, *Proctor 4000* (MO), × ½; 153, *Cyathea arborea* × *Trichipteris* sp., pinnules, Cuba, *Wright 950* (GH), × ½; 154, *Cyathea divergens* var. *divergens* × *Trichipteris stipularis*, pinnules, Costa Rica, *White & Lucansky 1972–067* (GH), × ½.

stalked pinnules, the brown rather than white scales on the abaxial surface of the pinnules, and its small, rather than well-developed, indusium. Except for the small indusium, the *Cyathea* parent could as well be *C. furfuracea.*

ADDITIONAL SPECIMENS. **Cuba.** Rancho Mundito, Pinar del Río, Jan. 18, 1953, *Acuña* (US). **Puerto Rico.** Road 143, Municip. Río Grande, *Conant 612* (GH); El Toro Negro, Jan. 14, 1966, *Woodbury* (El Verde Field Station, Puerto Rico Nuclear Center).

43. **Cnemidaria grandifolia** var. **obtusa** × **Trichipteris aspera**

FIG. 149.

Alsophila Elliottii Baker, Ann. Bot. **6**: 96. 1892. Lectotype: St. Catherine's Peak, Pyrenees, Grenada, *Sherring*, K! Lectoparatype: Antoine, Bellevue, Grenada, *Elliott*, K.
Hemitelia Elliottii (Baker) Maxon, Contrib. U.S. Nat. Herb. **17**: 415. 1914.
Cyathea Elliottii (Baker) Domin, Acta Bot. Bohem. **9**: 113. 1930.

This hybrid will key to species 9–12 of Central America and northern South America. The leaf architecture suggests a hybrid with a species of *Cnemidaria*, and the small indusium an exindusiate species as the other parent. The proposed parents are both relatively common in Grenada. *Trichipteris aspera* is an Antillean species, including *Cyathea muricata.*

ADDITIONAL SPECIMEN. **Grenada.** Herb. Jenman (NY).

44. **Cnemidaria spectabilis** var. **spectabilis** × **Cyathea tenera**

FIGS. 150–151.

Hemitelia Hombersleyi Maxon, Jour. Wash. Acad. Sci. **25**: 528, f. 1. 1935. Holotype: Aripo Road, via Arima, Trinidad, June 12, 1925, *Broadway & Hombersley*, US! Paratypes (all Trinidad); Blanchisseuse Road, *Broadway 6118*, US; Las Lapas Road, *Broadway 5913*, US, *Hombersley 208* US! Isoparatypes: *Broadway 5913*, MO! *Hombersley 208*, GH! NY!
Cyathea Hombersleyi (Maxon) Stolze, Fieldiana: Bot. **37**: 81. 1974.

This hybrid will key to species 9–12, 13–16, or often to 17–19, none of them growing in Trinidad. The relatively simple lamina architecture suggests a species of *Cnemidaria*, while the relatively well-developed indusium indicates another parent with a large indusium. *Cyathea tenera* is the only species in Trinidad with a large (sphaeropteroid) indusium. None of the material seen is suitable to assess the degree of development of the spores.

Apparently known from three plants: (a) *Broadway 6118;* (b) *Broadway 5913* and *Hombersley 208;* (c) June 12, 1925, *Broadway & Hombersley, Broadway 5719*, and 1925, *Hombersley.*

ADDITIONAL SPECIMENS. **Trinidad.** Aripo Road, via Arima, 1925, *Hombersley* (GH, NY), and also *Broadway 5719* (MO), are from the same plant as the type.

45. **Cyathea arborea** × **Trichipteris armata**

This hybrid has generally been identified as *Hemitelia calolepis* (see 47), but the type of that name is from Cuba, where *Trichipteris armata* does not grow. It will key to species 1–8 and of these, only *Cyathea parvula*, with a small indusium, is in Jamaica. Most of the sporangia appear to be poorly developed and well-developed spores have not been observed. The pinna architecture and whitish petiole scales suggest *Cyathea arborea* as one parent, and the long trichomes on the pinna-rachis and pinnules beneath as well as the toothed segments suggest *Trichipteris armata* as the other. The large hemitelioid indusium is consistent with this parentage.

SPECIMENS SEEN. **Jamaica.** *Wilson 681* (NY); **St. Thomas:** between House Hill and Cuna Cuna Gap, *Maxon 8968* (NY,US); Corn Puss Gap, *Proctor 4001* (MO,US); Moody's Gap, *Underwood 1550* (NY,US); Bath, 1895, *Gilbert* (GH,MO,NY).

46. **Cyathea arborea × Trichipteris aspera**

Fig. 152.

Hemitelia Lewisii Morton & Proctor, Amer. Fern Jour. **41**: 49. 1951. Holotype: Corn Puss Gap, St. Thomas, Jamaica, *Proctor 4000*, US. Isotypes: IJ,MO! PH.

Cyathea Lewisii (Morton & Proctor) Proctor, Bull. Inst. Jam. Sci. Ser. **5**: 21. 1953.

The collections will key to species 1–8. Among these only *Cyathea parvula*, with an aculeate petiole and usually smaller indusium is in Jamaica. This hybrid has a tuberculate petiole and the indusium is attached about halfway around the receptacle. The material is too mature to allow assessment of the spore development. Eight other tree ferns were listed by Morton and Proctor as occurring in the same locality as *Hemitelia Lewisii*. Among these, the brownish scales on the costules and the moderately developed indusium suggest the indicated parentage.

47. **Cyathea arborea × Trichipteris sp.**

Fig. 153.

Hemitelia calolepis Hook. Syn. Fil. 29. 1865. Holotype: Monte Verde, Cuba, *Wright 950*, K. Isotypes: F! GH! MO! US!

Cyathea calolepis (Hook.) Domin, Pterid. 263. 1929.

This hybrid will key to species 1–8 and among them only *Cyathea parvula* occurs in Cuba. The hybrid may be distinguished by its tuberculate petiole and the pinna architecture that is similar to *C. arborea*. *Cyathea parvula* has an aculeate petiole and different pinna architecture. The sporangia are often not well-developed and the spores appear to be abortive. The whitish scales of the petiole and whitish bullate scales on the under surface of the lamina, as well as the pinna architecture suggest *C. arborea* as one parent. The relatively small indusium, attached from about ¼ to ½ around the receptacle suggests an exindusiate species as the other. However, there is no information on which *Trichipteris* species were growing in the same place as the hybrid.

ADDITIONAL SPECIMENS. **Cuba.** *Wright 891* (GH,NY).

48. **Cyathea divergens** var. **divergens** × **Trichipteris stipularis**

FIG. 154.

Cyathea Holdridgeana Nisman & Gomez, Amer. Fern Jour. **61**: 168, f. 3, 4. 1971. Holotype: La Chonta, km 55 Interamerican Highway, Prov. Cartago, Costa Rica, *Nisman 104*, CR. Isotypes: F,GH! Paratypes: (all La Chonta, Herb. Gómez); *Gómez 2542, 2560, 2577; Goldgewicht & Gómez 2675;* km 54 Interamerican Highway, *J. A. Saenz.*

This hybrid will key to species 1–8, and among these only *Cyathea multiflora* grows in Costa Rica. It has sessile to short-stalked basal pinnules on the pinnae, rather than long-stalked ones as in the hybrid. These long-stalked pinnules suggest *C. divergens* var. *divergens* as one parent, and the small indusium, minute to about ¼ around the receptacle, indicates an exindusiate species as the other. *Trichipteris stipularis* is a common species in the Cordillera de Talamanca and may be the other parent. The spores are unusual in lacking perine and many of them have the outer layer of the exine peculiarly irregular.

Cyathea Holdridgeana is possibly a local endemic species of Costa Rica. Luis D. Gómez (pers. comm.) informs me that neither of the proposed parents were growing in the two localities where he has seen it. However, its characters are suggestive of a hybrid and I prefer to treat it as one until further field studies indicate that it is an endemic species.

ADDITIONAL SPECIMENS. **Costa Rica.** 16 km south of El Empalme, *White, Norris & Soeder 1972–067* (GH).

49. **Cyathea divergens** var. **Tuerckheimii** × **Cyathea fulva**

The long-stalked pinnules, especially the basal ones, suggest *Cyathea divergens* var. *Tuerckheimii* as one parent, and the brown petiole scales suggest *Cyathea fulva* as the other. The petiole scurf is consistent with the parentage; it is brown as in *C. fulva,* although not crested, and there are some whitish small scales, as in *C. divergens*. The indusium is sphaeropteroid, but the sori are too young to assess the development of the sporangia or spores.

SPECIMENS SEEN. **México.** 20 km antes Huatusco, carretera Puente Nacional a Huatusco, Veracruz, *Nevling & Gomez-Pompa 2443* (GH).

50. **Cyathea tenera** × **Trichipteris sp.**

Hemitelia trinitensis Jenm. West Ind. Guiana Ferns 46. 1898. Trinidad. A specimen in TRIN, fragm. BM!, photo BM,GH, is probably the holotype.

Cyathea trinitensis (Jenm.) Domin, Pterid. 264. 1929.

This hybrid will key to species 1–8, or to 17–19, none of which occur in Trinidad. The indusium varies from hemitelioid to discoid, which is suggestive of a hybrid. More adequate material is required.

NAMES OF UNCERTAIN IDENTITY AND EXCLUDED NAMES

The following list includes (a) those names that apply to species of *Cyathea* that I have been unable to place more precisely, (b) those names that cannot be accurately identified to genus without an examination of the original materials, and (c) a few names to be referred to other genera. No attempt has been made to include the much larger number of names placed in *Cyathea* by Domin and others. These are dealt with under other revisions, *Nephelea* (Gastony, 1973), *Cnemidaria* (Stolze, 1974), *Trichipteris* (Barrington, 1974), *Alsophila* (Conant, MS) and *Sphaeropteris* (Windisch, MS).

Cyathea aphlebioides Christ, Bull. Herb. Boiss. II, **6**: 179. 1906. There are three sheets under this name in Herb. Christ, P! One, with two petiole bases and the lower portion of a rachis with basal pinnae has the abortive (subaphlebioid) pinnae emphasized by Christ in the name. The epithet *aphlebioides* was substituted for the original "decrescens." Lectotype: Navarro, 1400 m, *Wercklé,* C. Rica, 1905. Another sheet: Navarro, Costa Rica, *Wercklé,* 1905, is *Cyathea Delgadii* and the third: C. Rica, Navarro, 1400 m, *Wercklé,* 1905, is *Cyathea fulva* (fragm. ex Christ, US).

Cyathea arborea var. *pusilla* Bosco, Nuov. Giorn. Bot. Ital. n.s. **45**: 141. 1938. Páramos de Portrerillos, 3200 m, and Plan de Sapote, 1800–2100 m, Ecuador, *Crespi.*

Cyathea azuayensis Sod. Crypt. Vasc. Quit. 644. 1893. Prov. Azuay, Ecuador, 3000 m, *Rimbach* 23. Sodiro indicated a close comparison with *Cyathea incana,* which suggests that this is a species of *Nephelea* and perhaps *N. incana.*

Cyathea caduca Christ, Bull. Herb. Boiss. II, **7**: 271. 1907. San José, Costa Rica, Jardin de Camiol *Wercklé,* 1906. The spiny trunk indicates that this name refers to a species of *Nephelea.*

Cyathea denudans Kze. Linnaea **18**: 349. 1844. Mexico, *Leibold,* Herb. Roemer, LZ, destroyed.

Cyathea Dyeri Sod. Crypt. Vasc. Quit. 515. 1893. Chimborazo, cerca Saltuco, Ecuador, 300–600 m, *Sodiro.* A portion of a rachis with three pinnae: Saltuco, Prov. Bolivar, 9/1872, *Sodiro,* P! is a species of *Cyathea.*

Cyathea Eggersii Hieron. Engl. Bot. Jahrb. **34**: 438. 1904. El Recreo, Río Puntilla, Prov. Manabi, Ecuador, *Eggers 15320.* Isotypes: F! GH! A species of *Cyathea* but not identifiable from the pinna material seen.

Cyathea fulva var. *minor* Sod. Rec. Crypt. Vasc. Quit. 14. 1883. Holotype: Chimborazo cerca de S. Pablo de Atenas, Prov. de Riobamba, Ecuador, *Sodiro.*

Cyathea furfuracea Sod. Sert. Fl. Ecuad. **2**: 7. 1908, not Baker, 1874. Pichincha, Ecuador, *Sodiro. Cyathea pichinchae* C. Chr. Ind. Fil. Suppl. 21. 1913, *nom. nov.* for *Cyathea furfuracea* Sod., not Baker.

Cyathea hexagona Fée, Mém. Fam. Foug. 8: 111. 1857. Huatusco, Mexico, *Schaffner 237.* A sheet at K! photo GH, is a mixture of a *Cyathea* species and *Nephelea mexicana.* Gastony (Contrib. Gray Herb. 203: 147. 1973), excluded the *Nephelea* material as inconsistent with the description. The *Cyathea* is either *C. fulva* or *C. divergens* var. *Tuerckheimii.*

Cyathea hirtula var. *multisorosa* Karst. Linnaea **28**: 462. 1856. Montalban and Cuirgua, Venezuela, *Karsten.*

Cyathea Jurgensenii Fourn. Mex. Pl. **1**: 135. 1872. *Jurgensen 874,* P! photo GH is a large pinnae which could be either *Cyathea fulva* or *C. divergens* var. *Tuerckheimii;* fragm. ex NY,US!

Cyathea Mettenii var. *caucana* Hieron. Engl. Bot. Jahrb. **34**: 437. 1904. Supra Paletará, Cauca, Colombia, *Lehmann 3482.*

Cyathea patens Houlst. & Moore, Gard. Mag. Bot. **3**: 330. 1851, *nom. nud.* Hort. from Jamaica, the meager description is not sufficient to effect valid publication.

Cyathea pilosa Sampaio, Bol. Mus. Nac. Rio **1**: 13. 1923, *nom. nud.*

Cyathea puberula Sod. Rec. Crypt. Vasc. Prov. Quit. 16. 1883. Río Peripe, cerca San Miguel de los Colorados, Ecuador, *Sodiro.* A small specimen: Peripe, 8/1875, *Sodiro,* P! is a species of *Cyathea.*

Cyathea pygmaea Hort. Gard. Chron. III, **15**: 663. 1894, *nom. nud.*

Cyathea subindusiata var. *chontilla* Domin, Mem. Roy. Czech Soc. Sci. n.s. **2** (Pterid. Dominica): 68. 1929. Andes of Ecuador, 11,000 ft., *Spruce.*

Cyathea Schottiana Kze. Linnaea **23**: 246. 1850, *nom. nud.*, Mexico.

Cyathea Trejoi Christ, Bull. Herb. Boiss. II, **5**: 733. 1905. San Pablo, Chiapas, Mexico, 1500 m, 1903, *Munch.* The spiny trunk, a fragment ex Christ, NY! and the provenence refer this name to *Nephelea mexicana.*

Cyathea venosa (Kuhn) Domin, Pterid. 264. 1929. *Hemitelia venosa* Kuhn, Linnaea 36. 161. 1869. Caracas, *Appun*, fragm. B! photo GH, fragm. ex K,NY! The fragmentary material is not adequate for determination of the genus. Stolze (Fieldiana: Bot. **37**: 81. 1974) came to the same conclusion.

Hemitelia Lindenii Hort. Gard. Chron. III, **15**: 663. 1894, *nom. nud.*

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TAXA, PUTATIVE HYBRIDS AND DISTRIBUTION OF CYATHEA

1. Cyathea multiflora Sm.: British Honduras, Guatemala, Honduras, Nicaragua, Costa Rica, Panama, Colombia, Ecuador, Peru, Bolivia, Brazil.
2. Cyathea andina (Karst.) Domin: Hispaniola, Puerto Rico, French Guiana, British Guiana, Venezuela, Colombia, Ecuador, Peru, Bolivia, Brazil.
3. Cyathea Weatherbyana (Morton) Morton: Galapagos Islands.
4. Cyathea Alphonsiana Gómez: Cocos Island.
5. Cyathea notabilis Domin: Cocos Island.
6. Cyathea parvula (Jenm.) Domin: Cuba, Jamaica, Hispaniola, Puerto Rico.

7. Cyathea platylepis (Hook.) Domin: Venezuela, Colombia.
8. Cyathea Vilhelmii Domin: Peru.
9. Cyathea petiolata (Hook.) Tryon: Panama, Colombia.
10. Cyathea impar Tryon: Panama.
11. Cyathea Steyermarkii Tryon: Venezuela.
12. Cyathea conformis (Tryon) Stolze: Panama, Colombia.
13. Cyathea decorata (Maxon) Tryon: Colombia.
14. Cyathea parva (Maxon) Tryon: Colombia.
15. Cyathea speciosa Willd.: Venezuela, Colombia.
16. Cyathea Haughtii (Maxon) Tryon: Colombia.
17. Cyathea arborea (L.) Sm.: Cuba, Jamaica, Hispaniola, Puerto Rico, Lesser Antilles south to Grenada.
18. Cyathea Alstonii Tryon: Colombia.
19. Cyathea peladensis (Hieron.) Domin: Colombia.
20. Cyathea divergens Kze.
    20a. var. divergens: Costa Rica, Panama, British Guiana, Venezuela, Colombia, Ecuador, Peru.
    20b. var. Tuerckheimii (Maxon) Tryon: Mexico, Guatemala.
21. Cyathea pallescens (Sod.) Domin: Colombia, Ecuador, Peru, Bolivia.
22. Cyathea simplex Tryon: Venezuela.
23. Cyathea corallifera Sod.: Ecuador.
24. Cyathea boliviana Tryon: Bolivia.
25. Cyathea straminea Karst.: Colombia.
26. Cyathea Ruiziana Kl.: Peru.
27. Cyathea microphylla Mett.: Peru.
28. Cyathea multisegmenta Tryon: Peru.
29. Cyathea fulva (Mart. & Gal.) Fée: Mexico, Guatemala, Honduras, Nicaragua, Costa Rica, Panama, Venezuela, Colombia.
30. Cyathea Harrisii Maxon: Jamaica, Hispaniola.
31. Cyathea furfuracea Baker: Cuba, Jamaica, Hispaniola, Puerto Rico.
32. Cyathea suprastrigosa (Christ) Maxon: Costa Rica.
33. Cyathea Delgadii Sternb.: Costa Rica, Panama, British Guiana, Venezuela, Colombia, Peru, Bolivia, Argentina, Paraguay, Brazil, Ilha Trindade.
34. Cyathea tenera (Hook.) Moore: Lesser Antilles, Trinidad, Margarita.
35. Cyathea dissoluta Jenm.: Jamaica.
36. Cyathea caracasana (Kl.) Domin.
    36a. var. boliviensis (Rosenst.) Tryon: Venezuela, Colombia, Ecuador, Peru, Bolivia.
    36b. var. meridensis (Karst.) Tryon: Venezuela, Colombia, Ecuador.
    36c. var. caracasana: Cuba, Jamaica, Hispaniola, Venezuela, Colombia, Ecuador.
    36d. var. chimborazensis (Hook.) Tryon: Venezuela, Colombia, Ecuador.
    36e. var. Maxonii (Maxon) Tryon: Costa Rica.
37. Cyathea Lechleri Mett.: Venezuela, Peru, Bolivia.
38. Cyathea gracilis Griseb.: Costa Rica, Jamaica, Colombia.
39. Cyathea ebenina Karst.: Venezuela, Colombia, Peru.
40. Cyathea Dudleyi Tryon: Peru.
41. Cnemidaria horrida × Cyathea arborea: Jamaica, Hispaniola, Puerto Rico.
42. Cnemidaria horrida × Cyathea parvula: Cuba, Jamaica, Puerto Rico.
43. Cnemidaria grandifolia var. obtusa × Trichipteris aspera: Grenada.
44. Cnemidaria spectabilis var. spectabilis × Cyathea tenera: Trinidad.
45. Cyathea arborea × Trichipteris armata: Jamaica.
46. Cyathea arborea × Trichipteris aspera: Jamaica.
47. Cyathea arborea × Trichipteris sp.: Cuba.
48. Cyathea divergens var. divergens × Trichipteris stipularis: Costa Rica.
49. Cyathea divergens var. Tuerckheimii × Cyathea fulva: Mexico.
50. Cyathea tenera × Trichipteris sp.: Trinidad.

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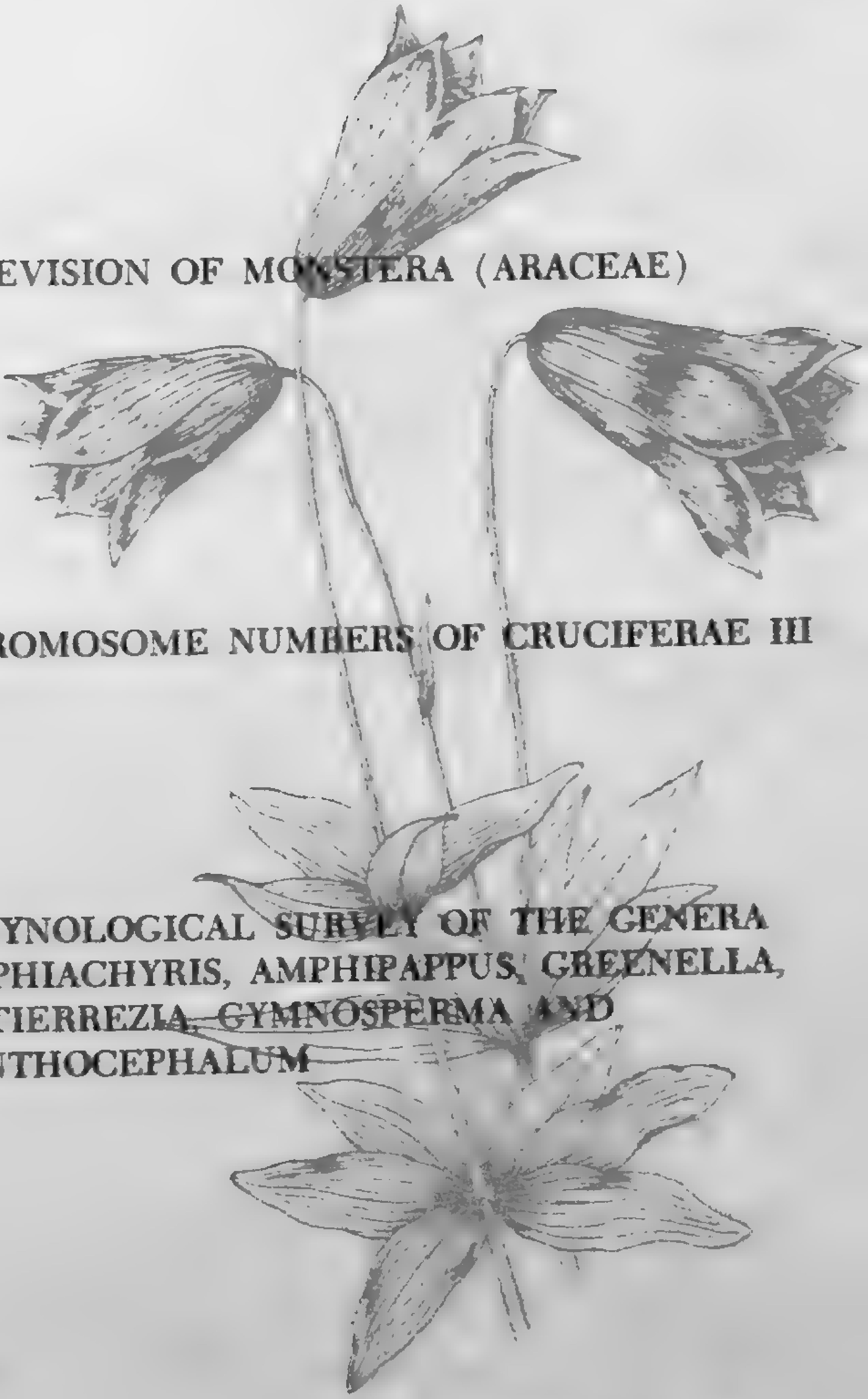

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A REVISION OF MONSTERA (ARACEAE)

Michael Madison[1]

The genus *Monstera*, as here interpreted, comprises 22 species and 3 varieties of scandent epiphytes, including some of the most magnificent and conspicuous climbers of the neotropics, easily recognized by their huge, perforated leaves. Though common and abundant in the wild, *Monstera* species are poorly represented in herbaria, principally because the large fleshy parts are too big for plant presses, difficult to dry, and because the plants usually flower out of reach.

This study had its genesis in an unsuccessful attempt to identify some Mexican monsteras, which revealed the lack of a useful monograph of the genus and the chaotic application of names to specimens in herbaria. Although *Monstera* was monographed by Engler and Krause in 1908, neither author was able to study the plants in the wild and their treatment reflects the inadequacy of herbarium specimens in studies of Araceae. The revision here presented is based on 18 months of field work in Central and South America, encompassing study of about 400 populations representing 17 species. In addition, over 3000 herbarium specimens were examined.

ACKNOWLEDGEMENTS

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History of the Genus

In 1693, *Monstera* first appeared in western literature in an account of the vegetation of Martinique by the French botanist, Charles Plumier. Plumier provided a generous illustration of a plant (as *Arum hederaceum, amplis foliis perforatis*) which is clearly *Monstera adansonii*. The accompanying text included observations on the dimorphism of roots, the structure of the leaves and inflorescence, and the use of the plant by natives as a snake-bite remedy. Plumier's description and illustrations were cited by Linnaeus (1753) as the basis for *Dracontium pertusum* L. The Linnaean genus *Dracontium* included aroids with perfect flowers, numerous seeds, and five perianth parts. His placement of Plumier's plant in this genus suggests that Linnaeus erroneously considered it to have flowers with a perianth, as Plumier supplied no observations on this point.

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[1] Present address: The Marie Selby Botanical Gardens, Sarasota, Fla. 33577.

During the decade following the publication of *Dracontium pertusum,* the species was illustrated and described in several works by Philip Miller (1754, 1760, 1763). It was said to be cultivated in England and Holland as a stove plant and Miller described the method of sending cuttings from the West Indies embedded in bales of damp hay. He also provided a good illustration of its flowers from cultivated material and was the first to note the absence of a perianth.

In 1763 the name *Monstera* was first used by Adanson in his *Familles des Plantes.* It is not clear what concept he intended by *Monstera;* the combination of characters associated in his description represents no known species of plant. Apparently he was attempting to redescribe the genus *Dracontium* L. giving it a new name. In the text, he mentioned a *Monstera* with a tuberous root and spiny petioles, evidently referring to *Dracontium spinosum* L. He also mentioned a *Monstera* with perforated leaves, and it is undoubtedly this single characteristic which later led authors to use the name *Monstera* in its present sense, which otherwise disagrees with Adanson's description in several respects: perianth absent (vs. "calice-5 feuilles"), stamens 4 (vs. "7"), and seeds one, rarely two (vs. "plusieurs"). In his publication, Adanson listed *Dracontium* L. as a synonym, thereby rendering the name *Monstera* superfluous. The conservation of the name is discussed below.

Monstera was next taken up by Aublet (1775). In describing an *Anthurium* from French Guiana (as *Dracontium pentaphyllum*), he gave as a common name "la Monstère de la Guiane." There is no indication that Aublet was using the name *Monstera* in relation to Adanson's use of it; most likely he was using it simply as a variant of the names dragon, draco, etc., as part of a general practice of referring to aroids as snakes, serpents, dragons, and monsters. This is an association which is found in many cultures, and even in ancient Greece *dracunculus,* "little dragon," is given by Theophrastus as the name for a Mediterranean aroid. This association is apparently most commonly based on the snake-like appearance of the mottled petioles and peduncles. It seems most probable that *Monstera,* as used by Adanson, is a latinized French equivalent of *Dracontium,* and is not, as Schott (1858) suggested, based on the apparent monstrosity of the holes in the leaves.

During the 70 years following Adanson's publication of *Monstera,* the West Indian species spread in cultivation to botanical gardens and conservatories throughout Europe, where it was duly noted in seed catalogues and plant lists as *Dracontium pertusum* L.

A new phase in aroid classification began in 1830 with the publication of the first of a series of monographic works on the family by H. W. Schott of Vienna. Schott laid the foundation of the generic classification of the Araceae, based largely on floral morphology, and his studies culminated in the *Genera Aroidiarum* (1858) and *Prodromus Systematis Aroidiarum* (1860) which included descriptions of 104 genera and

972 species. In addition, he commissioned the preparation of more than 3000 illustrations of aroids which rank among the finest botanical illustrations known. They are housed in the Museum of Natural History in Vienna and many serve to typify the Schott species.

Schott (1830) revived the name *Monstera* Adans., though the concept delimited by Schott was quite different from that of Adanson, which was essentially identical to Linnaeus' *Dracontium*. The only *Dracontium* included was *D. pertusum* L. and the other ten *Monstera* species were transferred from *Pothos* L. They represent plants now considered to belong to *Rhaphidophora, Epipremnum,* and *Scindapsus* (all Asian) as well as two species of *Philodendron*. The generic description mentioned a persistent spathe, a two-locular ovary with two basal ovules per loculus, and the operculate fruit characteristic of the group. Since the new combination *Monstera pertusa* (Roxb.) Schott was made based on *Pothos pertusus* Roxb., *Dracontium pertusum* L. was given the new name *Monstera adansonii* Schott.

Two years later, Schott (1832) subdivided *Monstera,* separating the Asian species as the genus *Scindapsus,* with the technical distinction of a unilocular ovary in *Scindapsus* and a bilocular ovary in *Monstera*. The description of the spathe in both genera was changed from *persistens* to *decidua*. This left only three species in *Monstera: M. adansonii* Schott, *M. lingulata* (L.) Schott, and *M. cannaefolia* (Rudg.) Schott, the latter two being philodendrons.

By 1840, *Monstera* had been in the European literature for 150 years, and its known range extended from the West Indies to Brazil, but only the one species, *M. adansonii,* was recognized. (The juvenile of *Monstera dubia* was in cultivation as *Marcgravia dubia* but had not yet been identified as an aroid.) In the 1840's *M. deliciosa* was discovered independently by Liebmann in Mexico and Warszewicz in Guatemala, who brought live material to Copenhagen and Berlin respectively. The introduction of this species was a horticultural triumph, and its cultivation quickly spread throughout Europe. It remains today one of the most extensively cultivated plants in both tropical and temperate countries.

Following the introduction of *Monstera deliciosa* into Europe, there was a rush to discover and describe other new species, and by 1860, when Schott produced the first monograph of *Monstera,* he included 35 species. Six of these were placed in a separate genus, *Tornelia,* on the basis of their having pinnatisect leaves.

Schott's concept of species was a narrow one. Faced with an influx of new collections, he attempted to record the diversity he encountered by giving each variant specific status. Thus many of his species are distinguished by slight differences in leaf shape and texture and later authors have placed the names in synonymy. Nonetheless, Schott's monograph serves as an important record of the early collections of *Monstera,* and the plates at Vienna illustrating the Schott species remain a valuable reference.

Following Schott's death in 1865, Adolf Engler of the Berlin Botanic Garden succeeded him as the world specialist on the Araceae. Engler twice monographed the family in its entirety: first, in 1879 as volume two of DeCandolle's *Monographiae Phanerogamarum,* and second, from 1905 to 1920 as a series of volumes of *Das Pflanzenreich.* Engler's first treatment of *Monstera* was in the *Flora Brasiliensis* (1878) where he provided a key to all the species. This was the first key written for the genus (Schott had not produced any) and the number of recognized species was reduced from Schott's 35 to 12.

In 1882, Hemsley revised the Central American species of *Monstera,* synonymizing some species distinguished by Engler. Hemsley was the first to recognize that several species described in the genus *Marcgravia* were really juvenile plants of *Monstera.*

Engler's studies of *Monstera* culminated in a monograph written with K. Krause and published in *Das Pflanzenreich* (1908), a treatment representing considerable progress over earlier efforts. Twenty-seven species were recognized, and 33 others listed in synonomy. The descriptions are ample and a number of collections are cited. However, the key is inconsistent and unworkable. Specimens are very difficult, if not impossible, to determine by using it. While a number of the distinctive species were, by this time, well demarcated, the complex of species centering on *M. adansonii* remained confused.

In the last fifty years, various accounts of *Monstera* have appeared in floristic works. For the most part, these are simply extracts from the Engler and Krause monograph, but two exceptions are: the *Flora of Suriname* (Jonker-Verhoef & Jonker, 1952); and *Commentary on Mexican Araceae* (Bunting, 1965). They include a number of new observations and emphasize the need for a revision of the genus. However, both are hampered by their geographically limited outlook.

As mentioned earlier, the name *Monstera* was superfluous at publication since *Dracontium* L. was cited as a synonym. Bunting (1962b) proposed the conservation of *Monstera* Schott against *Monstera* Adans., but this proposal was rejected (McVaugh, 1967). Subsequently, Nicolson (1968a) proposed the conservation of *Monstera* Adans. with the designation of *M. adansonii* Schott as the lectotype species; this was accepted by the Committee for the Conservation of Generic Names (McVaugh, 1970).

GENERIC RELATIONSHIPS

The tribe Monstereae of the Araceae is a well-defined and easily recognized group of about 200 species which have a number of features in common. All are scandent or subscandent epiphytes of wet tropical forests and contain in their vegetative and flowering parts numerous needle-like or H-shaped trichosclereids. The leaves have two pulvini, one at each end of the petiole, and the lamina often exhibits natural perforations. The spadix consists of perfect flowers, each with four stamens and lacking a perianth, and the spathe is deciduous after anthesis. The Monstereae are unique among the aroids in having meridiosulcate foveolate pollen (Thanikaimoni, 1969) and, for the few species studied, chromosome numbers of $2n$-60 or $2n$-120 (Marchant, 1970).

The present-day distribution of the Monstereae is Indomalaysian and neotropical, with two species in West Africa. The tribe is represented by fossil seeds in a number of tertiary deposits and was apparently a common element of a Paleogene Boreotropical flora (Madison & Tiffney, 1976).

The apportioning of the extant species into genera has been disputed for more than 100 years (e.g., Koch, 1856; Schott, 1858; MacBride, 1936; Steyermark, 1957; Bakhuizen van den Brink, 1958; Bunting, 1962a; Nicolson, 1968b; Hotta, 1970). Extreme positions are the recognition of 12 genera (Schott, 1860) or the inclusion of all of the species in one or two large genera (Koch, 1856; Bakhuizen van den Brink, 1958). The differences among these treatments reflect differences in philosophies of classification rather than in the kinds of characters used. All of these authors refer to the same few generic characters: placentation (axile, parietal, or basal); septation of the ovary (unilocular or bilocular); and geography (Asian or neotropical). Seed morphology, a character overlooked previously, was investigated by Madison and Tiffney (1976) and proves useful in generic classification. Seeds of the Monstereae are of several distinct types, the extremes of which are fusiform seeds 1 mm. long with abundant endosperm, and highly curved seeds 20 mm. long and lacking an endosperm.

In revising this group, I have tried to delimit the genera in a manner consistent with the generic classification of the rest of the family, and at the same time to provide a treatment which reflects the occurrence of groups of species which in their geography, morphology, and ecology show affinities and appear to be closely related. Seven genera are recognized which are defined by a combination of character states of placentation, septation of the ovary, and seed morphology. The genera are either neotropical or paleotropical in distribution except for *Scindapsus,* which is primarily Asian but has one species in South America. Several of the genera have definitive vegetative characters, but I have found no character to consistently separate *Epipremnum, Rhaphidophora,* and *Monstera* other than floral and seed morphology. Nonetheless, these genera are readily distinguished if the relevant features are examined.

Placentation, septation of the ovary, and seed morphology are interrelated factors of which the evolutionarily significant aspect is probably the number and size of seeds produced in the fruit. Seed size and number are subject to selective forces related to dispersal, seedling ecology, intraspecific competition, weediness, and rate of fruit maturation (Harper *et al.*, 1970). The mode of action of these forces in the evolution of the Monstereae is not altogether clear, though several aspects of it may be noted. The genus *Stenospermation* consists of true epiphytes, the seeds of which normally germinate on the surfaces of trees. Species of this genus have apparently entered a new adaptive zone (the other Monstereae germinate terrestrially) where small seed size is a critical factor for germination and establishment (Madison, 1977). It is noted elsewhere in this paper that in *Monstera* there has been selection favoring an increase in seed size related to host tree location by stoloniferous seedlings. The fossil seeds of Monstereae, mostly described in the genus *Epipremnum*, are intermediate in size, and it seems likely that evolution of seed size in the tribe has been simultaneously toward smaller seeds (in *Stenospermation* and *Rhaphidophora*) and larger seeds (in *Monstera* and *Scindapsus*).

MORPHOLOGY

Stem. Phillip Miller, in 1760, described the stem of *Monstera adansonii* as varying from "the thickness of a goose quill to that of a man's thumb." If all of the species are considered, the diameter of mature stems ranges from about 2 mm. in *M. obliqua* to 8 cm. in *M. deliciosa*. The most notable features of the older stems are the leaf scars, the axillary buds, and the adventitious roots.

Vegetative shoots of *Monstera* are normally unbranched, though lateral buds may be released in very old portions of a stem or in injured stems. Flowering is always accompanied by cryptic sympodial branching; the inflorescence is terminal and the continuation shoot arises in the axil of the leaf preceding the leaf which subtends the inflorescence. During development of the continuation shoot, the inflorescence is displaced to the side and appears axillary as illustrated for *M. dubia* in Figure 1.

The stems of *Monstera* have a distinct dorsiventrality and are usually flattened front to back. The portion facing the trunk produces adventitious roots, and the leaves are borne distichously on the opposite face. In some species the two ranks of leaves are nearly opposite (e.g., *M. lechleriana, M. dilacerata*), but in species of section Marcgraviopsis the angle of divergence of the two ranks (measured from the widest point of the leaf scar) is closer to 120°, and in *M. membranacea* and *M. gracilis* it approaches 90°.

In *Monstera lechleriana* and *M. dilacerata* the leaves are borne in a tight cluster at the top of the stem with the leaf bases overlapping. In other species the leaves are spread further apart on the stems, as is true of all species in section Marcgraviopsis. The length of the internodes is fairly constant within a species and is a reliable taxonomic character.

Also constant and taxonomically useful are the shapes of the leaf scars and the axillary buds. The axillary bud is located in a depression which may extend along the internode as a sulcus.

In all species the young stems are green and presumably photosynthetic; with time they may turn brown. The internodes of species in sections Monstera and Tornelia are smooth, whereas the species of sections Marcgraviopsis and Echinospadix usually have the stem roughened by the presence of numerous hard papillae about 1 mm. across and 0.5 mm. high. In these latter two sections the cuticle is quite thick and

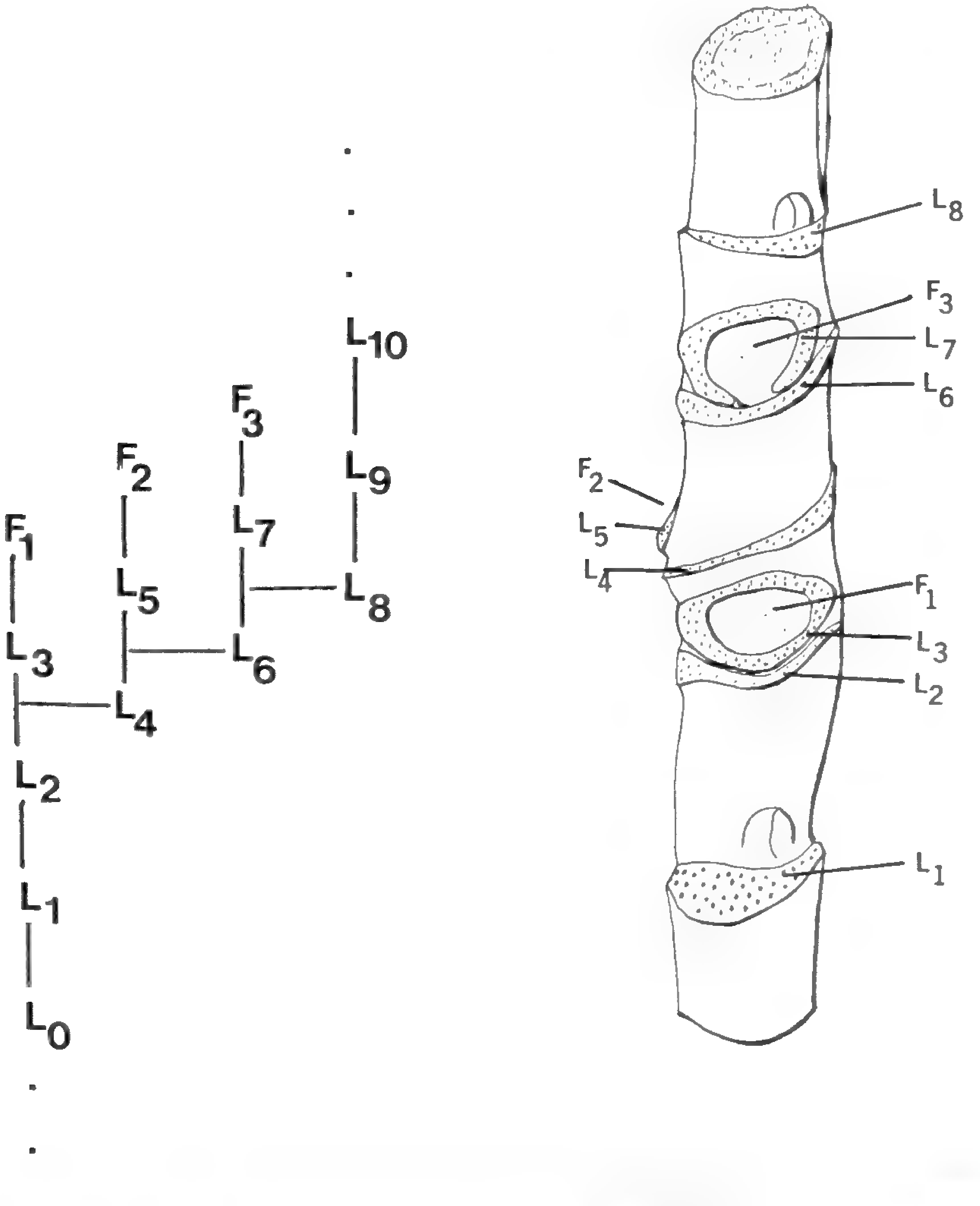


FIG. 1. Sympodial branching accompanying flowering in *Monstera dubia* (L = leaf, F = inflorescence).

yellow-brown in color; with a twisting of the stem it is shed in large flakes.

Roots. In many climbing plants the functions of anchorage, and water absorption and conduction have been divided between different kinds of roots. This root dimorphism has been observed in many lianescent species of dicots, monocots, and ferns (Went, 1895; Schenk, 1892; Lieurau, 1888). Its occurrence in *Monstera* has been discussed by Van Tieghem (1866), Lieurau (1888), and Engler and Krause (1908).

In *Monstera* the radicle elongates to a length of several centimeters at germination, but forms only a limited root system which is apparently short-lived. Most of the plant's root system is adventitious. The terrestrial seedling stages produce roots only at the nodes of the stem; these early roots are usually about 1 mm. thick and rarely exceed 20 cm. in length. The dimorphism of adventitious roots appears only after the plant has begun to climb, and usually when it is more than 1 m. above the ground and the stem is 7–10 mm. thick.

Went (1895) refers to the two kinds of adventitious roots as feeder roots and anchor roots ("Nährwurzeln" and "Haftwurzeln"). The feeder roots arise only at the nodes, generally one per node and more or less opposite the center of insertion of the leaf. These roots are positively geotropic and may either hang in the air or grow attached to the substrate. They are generally unbranched until they reach the ground, which may be a distance of 20–30 meters. But once they penetrate the soil, they branch profusely. Engler and Krause (1908) hypothesized that these roots are the major water-conducting organ of the plant rather than the stem. This seems likely because in older plants the stem may lose all connection with the ground through decay or mechanical injury without the plant wilting or showing other signs of water stress.

The anchor roots which serve to attach the plant to its substrate are produced along the internodes, though they may arise at the nodes as well. They are not positively geotropic, but grow in any direction over the substrate, often following the course of a fissure or irregularity in the surface. Where I have seen *Monstera* growing on a very smooth trunk or sheer rock, the anchor roots grew perpendicular to the stem. They may be 2–50 cm. long, but are usually 10–20 cm. long. The anchor roots adhere to the substrate by means of root hairs which terminate in a sort of suctorial disc (Went, 1895).

The anchor roots seem to require substrate contact for their continued growth after they have been initiated. When a climbing stem loses contact with its substrate, for instance by reaching the top of a stump, the production of roots in the subsequent internodes is decreased in number, and those that are elaborated become hard and cease growing when only about 1 cm. in length. Hanging stolons as well as pendent fertile shoots of those species which normally hang lack feeder roots altogether and bear only a small tuft of aborted anchor roots at each node.

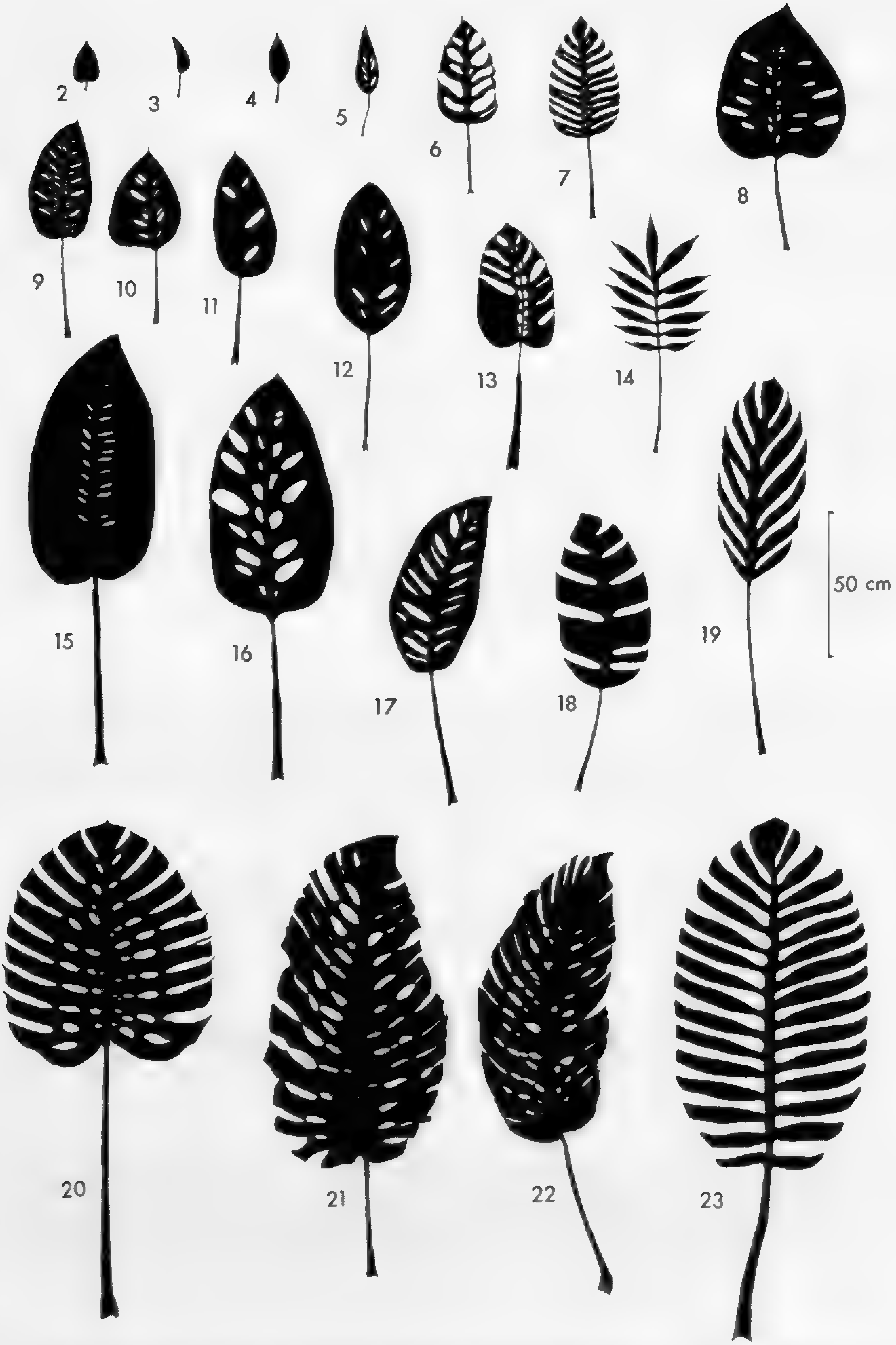
Leaf. The leaves of monocotyledons are normally described as consisting of a sheath, petiole, and lamina, but in the Araceae a different terminology is used (Schott, 1860; Engler & Krause, 1908 and others). The sheath and petiole together are called the petiole, which is described as being vaginate, winged, or canaliculate, or having a sheathing base or portion. For the sake of consistency this terminology is used in the present treatment, and the term petiole thus encompasses all of the leaf from its articulation at the stem to the lamina base.

The nature of the sheathing portion of the petiole, which protects the next developing leaf and terminal bud, is taxonomically useful in *Monstera.* The sheath may be restricted to the lower part of the petiole, or it may extend to the lamina base. At its upper end it terminates bluntly or is widely auriculate or is extended into a ligule. In *M. tuberculata* the ligule is about equal in length to the petiole. After the next leaf has expanded, the sheath may remain green and persist, or it may be marcescent or deciduous. The petioles of *Monstera* leaves have a swollen portion or pulvinus at each end; the upper one, located at the base of the lamina, is called the geniculum and is often conspicuously curved.

Although *Monstera* leaves arise distichously, their insertion is often not readily apparent because they may move to a different position subsequent to unfolding. The result of this movement is that the leaves are fanned out rather than placed one above the other, which is perhaps an adaptation to avoid the shading of the lower leaves by the upper ones. Observation of a large *M. deliciosa* growing in cultivation supports the assumption that this arrangement is a response to variation of light incidence. The plant, which was receiving approximately unilateral light from a window, was rotated 180°. There followed an extensive rearrangement of the leaves, occurring over a period of about two weeks and apparently resulting in less shading than immediately after rotation of the pot. This rearrangement was accompanied by a considerable flexion in the region of the pulvini, even in leaves more than two years old.

The leaf laminae of many species of *Monstera* exhibit perforations, one of the most characteristic features of the genus. Naturally fenestrate leaves also occur in *Epipremnum, Amydrium,* and *Rhaphidophora* in the Monstereae; *Cyrtosperma, Dracontium,* and *Rhektophyllum* in the subfamily Lasioideae (Araceae); and in *Aponogeton fenestralis* (Aponogetonaceae) and *Pentagonia* (Rubiaceae). This phenomenon early attracted the attention of various botanists. A. P. DeCandolle (1827) considered the holes to represent a failure of development and signify a weakness of the plant. August de St. Hilaire (1840), on the other hand, took them as an expression of "une plus grande energie vitale."

The ontogeny of the perforations was first elucidated by Trecul (1854). He observed that early in the development of the lamina, small patches



FIGS. 2–23. Adult leaves of *Monstera* species (to the same scale): 2. M. tuberculata; 3. M. pittieri; 4. M. obliqua; 5. M. xanthospatha; 6. M. gracilis; 7. M. epipremnoides; 8. M. oreophila; 9. M. siltepecana; 10. M. adansonii var. laniata; 11. M. adansonii var. adansonii; 12. M. adansonii var. klotzschiana; 13. M. membranaceae; 14. M. subpinnata; 15. M. lechleriana; 16. M. acacoyaguensis; 17. M. acuminata; 18. M. spruceana; 19. M. dilacerata; 20. M. deliciosa; 21. M. punctulata; 22. M. dubia; 23. M. tenuis.

of cells became discolored and died, and the part of the lamina that they would have developed into failed to develop. The death of these cells began in the mesophyll, and if it started very late in development, an area of mesophyll might be destroyed, but not the epidermis. This situation would result in windows in the leaf, similar to those found in species of *Zantedischia,* with the upper and lower epidermis covering an empty space.

The ontogeny of the fenestrations in *Monstera* leaves was subsequently studied by Schwartz (1878) and Melville and Wrigley (1969), and in *Epipremnum* by Webber (1960), but these authors did not add any substantial observations beyond those of Trecul. Melville and Wrigley (1969) proposed an interpretation of the formation of the holes in terms of Turing's diffusion reaction theory of morphogenesis, but this is so abstract as to be unverifiable.

The significance of the holes is obscure. King (1892) suggested that they allow water to drip through to the roots; otherwise the leaves would act like umbrellas and the roots would be left dry. This is a fanciful interpretation with no basis in reality. It seems possible that the holes may act to break up a still air layer adjacent to the leaf and thereby increase convection and prevent the leaf from overheating when exposed to heavy insolation. Lacerated leaves of *Musa* were shown to have consistently lower temperatures in full sun than equivalent entire leaves (Taylor & Sexton, 1972), and the holes in *Monstera* leaves might well function in the same way as the tears in *Musa* leaves.

If the holes begin to form early enough in development, they may extend to the margin, resulting in a pinnatifid leaf. Subsequent initiation of a second series of holes may lead to a leaf which is both perforate and pinnatifid. Variations in the shape of adult *Monstera* leaves resulting from these phenomena are illustrated in Figure 2–23.

Reproductive structures. There does not seem to be a pronounced seasonality in the reproductive behavior of *Monstera.* In all species for which more than a few collections are known from a region, flowering individuals may be found in any month of the year. When plants do flower, several inflorescences are usually produced sequentially, each shoot of the sympodium bearing two cataphylls and the inflorescence. The usual number is two to four spadices in a cluster, though six to eight is normal in *M. obliqua* while the inflorescences are usually solitary in *M. lechleriana.*

The spadices of *Monstera* are borne on erect peduncles except in *M. tuberculata* where the peduncle and spadix are pendent. The peduncle is terete or flattened, 5–45 cm. long and 0.2–4.0 cm. thick; it continues to grow after flowering and may increase 50% in length and thickness between anthesis and fruit maturity.

The developing spathe is green and tightly wrapped around the spadix, exceeding it in length. At the time of flowering, the spathe unfurls and becomes colored; depending on the species, it may be white to deep yellow to rose. The spathe often shows a constriction about ⅔ of the way up its length which represents the region where it was closed over the top of the spadix in the bud. When fully expanded the spathe may be nearly globose with only a slit-like opening or it may be hemispherical with the spadix fully in view. The spathe persists for two or three days after opening and then falls off following the formation of an abscission layer at the base. Sometimes the spathe is enmeshed in a cluster of inflorescences and may persist *in situ* for a considerable time after abscission.

The spadix goes through a variety of color changes in development. It may be green or white in the bud, and is usually white to yellow at anthesis. Following anthesis it turns green, and at maturity it may remain green or become white, yellow, or orange. During development of the fruit the spadix may double in thickness and length. The use of spadix size as a character in the taxonomy of the genus has been unsatisfactory because authors give dimensions of 'the spadix' without specifying the stage of development.

The axis of the flowering spadix bears numerous, spirally arranged, perfect flowers, each with four stamens and lacking a perianth. The flowers at the base of the spadix are usually sterile. The flowers are protogynous by one or two days, and maturation of the inflorescence is acropetal. Production of stigmatic drops has ceased by the beginning of anthesis, and thus self-fertilization is not possible within an inflorescence.

The stamens have a broad filament 1.0–1.5 mm. wide with an adaxial ridge. The anthers are not visible until just before anthesis, when they emerge from adjacent pistils by elongation of the filament. The pollen, which is shed through slits in the anthers, is aggregated into sticky threads.

The ovary is bilocular with a perforation at the base of the septum. There are two anatropous basal ovules in each loculus borne to either side of the perforation. The slit-like stylar canal opens into an elongate stigma usually surrounded by a slight ridge. The stylar region contains numerous needle-like trichosclereids, 2–3 mm. long, which are oriented along the axis of the pistil.

Bunting (1965) has suggested that *Monstera* may be wind pollinated, but its syndrome of floral characters definitely suggests insect pollination. At the time of flowering, the spathe turns from green to white, rose, or yellow as does the spadix. These inflorescences are conspicuous in a dark forest, and apparently attract visually-oriented pollinators. I have not observed any odor produced by inflorescences of *Monstera* except a faint, sweet smell in a few cases. The flowers at the base of the spadix are sterile, but produce a large stigmatic drop. These may be functioning as nectaries, as there are no nectaries in the fertile flowers.

A pollination phenomenon, known for many of the Araceae, is an increase in temperature of the spadix. Leick (1915) reported for *Monstera deliciosa* an increase of 15°C over ambient temperature at anthesis. This may attract a heat-seeking insect, or may serve to volatilize a relatively non-volatile scent.

Insect visitors to *Monstera* spadices are varied and numerous. In a single inflorescence I have observed several species of beetles, hemiptera, flies, and bees. Of these, the bees are the most mobile and are perhaps the effective pollinators. C. H. Dodson (personal communication) has observed trigonid bees to be the chief pollinators of *M. lechleriana* and *M. dilacerata* in Ecuador. The failure of seed set in isolated plants and in a number of species in cultivation underscores the necessity for a proper pollinating agent and suggests that *Monstera* may be free of the agamospermy which bedevils classification of other aroids, notably *Anthurium.*

Following pollination the spathe abscises and the spadix turns green, apparently becoming photosynthetic and also providing a cryptic coloration to protect the developing seeds. Probably more effective in this regard are the numerous trichosclereids in the stylar region of the pistils, which represent a considerable mechanical barrier around the developing seeds. I have never observed predation of developing *Monstera* fruits.

The fruits mature in a period of 2–15 months, depending on the species, and the protective stylar portion of the pistil is shed, revealing the seeds in a sweet pulp which is usually gray, but may be brightly colored. The seeds are eaten by birds according to observations recorded on herbarium specimens, but I have not observed birds at ripe fruits. It is not uncommon to find, attached to the plant, the axis of an old spadix with all of the seeds gone, suggesting that they may have been picked off and eaten. However, one also frequently finds a large number of seedlings originating in a single spot on the ground below a *Monstera* plant, indicating that either a ripe spadix has fallen or a large number of seeds have fallen or washed off at one time.

Seeds. Although the ovaries of *Monstera* flowers contain four ovules, three usually abort and the fruits are one-seeded; rarely are two-seeded berries encountered. During the development of the seed, the ovule curves and becomes reflexed about the raphe so that the path of the vascular bundle in the raphe is S-shaped. This unusual morphology is illustrated by Madison and Tiffney (1976).

Abundant endosperm is produced early in the development of the seed but is consumed by the growing embryo. In the mature seed, endosperm is absent and the principal storage organ is the swollen hypocotyl of the embryo. Cut, fresh seeds are green or bluish in color within.

In contrast to other Monstereae, the seeds of *Monstera* have a soft seed coat. Seeds of *M. adansonii* and *M. deliciosa,* and probably other species as well, rapidly lost viability if allowed to dry out, but if kept moist may be stored for several months.

Seed shape and size are quite variable in the genus and provide useful taxonomic characters at the specific level. Seeds of a number of species are illustrated by Madison and Tiffney (1976).

Sclereids and Raphides. As with most Araceae, *Monstera* has cells containing bundles of calcium oxalate raphides distributed throughout the tissues of the plant; these are particularly abundant in the fruit and seed coat. In addition, monsteras contain the needle-like trichosclereids characteristic of the subfamily, but these are much less regularly distributed. In most species, they are absent from the roots (except in *M. deliciosa*); they are absent from the leaf lamina in *M. punctulata* and from the stylar portion of the ovary in *M. obliqua*. They are always present in the spathe. Nicolson (1960) found them most consistently in stems and petioles.

The sclereids are usually unbranched as they occur in the ovary, but in the rest of the plant they are often H-shaped and occasionally stellate. Hanstein (1864) considered the H-shaped forms to be the result of 'copulation' of two adjacent fibers, but ontogenetic studies by Van Tieghem (1886), Block (1946), and others have not supported this hypothesis.

In the earlier literature the trichosclereids were sometimes referred to as 'raphides,' initiating a confusion which has persisted to the present. For instance, the scratchy and acrid nature of unripe *Monstera* fruits has been widely attributed to raphides of calcium oxalate, but the stylar portion of the fruit is abundantly supplied with trichosclereids which visibly penetrate the skin when the fruit is handled. This portion of the ovary is deciduous and is not normally eaten, so it remains unclear whether the reported prickly nature of the unripe fruits is due to raphides or trichosclereids.

GROWTH HABITS

Species of *Monstera* are hemi-epiphytes adapted to growing on the lower to middle trunks of trees below the canopy. Germination is terrestrial and the young plants creep along the ground until they encounter a tree and begin to climb. Eventually, as the older portions of the stem die and decay, the plant may lose connection with the ground by its stem although retaining a terrestrial connection by long adventitious roots.

Plants of this habitat and habit have been referred to as 'shade epiphytes' (Walter, 1971) or 'small climbers' (Richards, 1952). They are mostly monocotyledons and ferns and in the neotropics the majority of them belong to a relatively few genera of the families Araceae, Cyclanthaceae, and Polypodiaceae.

The principal advantage of this habit of growth is usually considered to be the interception of a greater amount of sunlight without the necessity of building a self-supporting structure to reach the light. The data of Schulz (1970) show an approximate doubling of total incident light per day between 15 cm. above ground and 2.5 m. above ground in a rain forest in Surinam. Other possible advantages to these species are the evasion of strictly terrestrial predators and the placement of flowers and fruits in a conspicuous situation.

The principal adaptive radiation in *Monstera* has been a diversification of growth habits within the shade epiphyte habitat, involving differences in the kinds of trees on which species grow and the way they grow on them. This combination is so distinctive that most species can be recognized from a distance. In addition, specialization of growth habits has occurred in the seedling and juvenile stages, and in some species evolutionary divergence of the juvenile and adult phases has resulted in marked heterophylly.

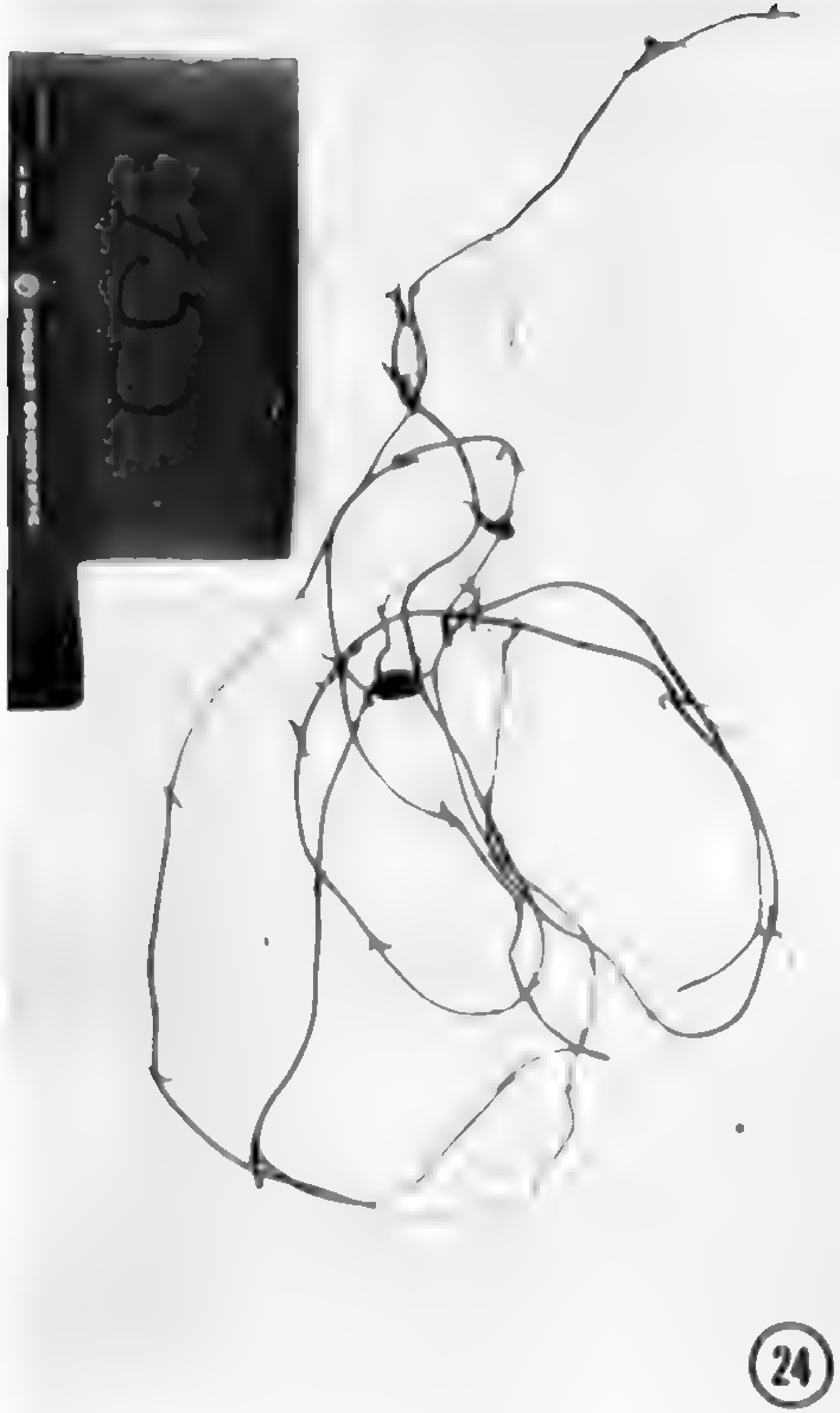
The discussion that follows will consider separately the growth habits of the seedling, juvenile, and adult phases. The term seedling here refers to the portion of the plant which grows, at least in part, on the resources stored in the seed, generally for the first several months of growth. The juvenile is the post-seedling stage before the production of adult foliage, and includes the earliest stages of climbing. The adult phase is that which has leaves typical of flowering individuals. In species where development is by a gradual increase in size, this division is somewhat artificial, but in other species it is clearly marked by well-defined changes in morphology.

In field and geenhouse studies of *Monstera,* I have observed no deviation from the seedling and juvenile type characteristic of each species. The growth habits of adults are more variable, and the types here described represent the modal habits of species rather than definitive categories.

Seedlings. *Monstera* seeds are apparently dispersed by birds, and germinate on the ground. The seedlings and juveniles grow as terrestrial plants until they encounter a tree and begin to climb. Field observations indicate that, where *Monstera* seedlings are found growing on a slope, they almost always grow uphill. This tropism may be fairly effective in locating a tree, since the microrelief of the forest floor generally includes slopes toward the bases of trees because of the accumulation of litter.

Strong and Ray (1975) studied, in the wild, seedlings of a species they refer to by the ambiguous name *Monstera gigantea,* which is probably *M. tenuis* or *M. dubia.* According to their observations the seedlings grow directly toward darkness, a phenomenon which they term 'skototropism.' Since potential host trees represent a dark sector of the horizon, growth toward darkness could be an effective mechanism for tree location by the seedling.

In plants of section Monstera the first two leaves of the seedling are cataphylls, followed by foliage leaves. The plant shows a gradual increase



Figs. 24–25. 24. Stolon-like seedling of *Monstera acuminata (Madison 1755,* gh*)*; 25. Shingle plant, *M. dubia.*

in size of the leaves and diameter of the stems throughout its development. In the subsequent discussion I refer to this type of growth as unspecialized.

In plants of sections Marcgraviopsis and Echinospadix the germinating seed produces a green stolon about 1 mm. in diameter with internodes 4–10 cm. long (Fig. 24). Cataphylls or minute scale leaves are borne at the nodes. This stolon grows along the surface of the ground for a distance of up to two meters without increase in diameter. The seedling normally begins to produce foliage leaves only after it has begun to climb. In the subsequent discussion I refer to this type of growth as specialized.

Seedlings of species in section Monstera, the unspecialized type, are difficult to find in the field. Even in very small and probably young plants the seed coat is not evident. However, I have encountered seedlings of *M. lechleriana* and *M. adansonii* in the wild; in these the seed coat was empty and shriveled and its resources apparently exhausted by the time the third foliage leaf was produced. A similar situation was found in seedlings of *M. adansonii* grown in cultivation, where the seed coats were empty and shriveled by the time the stem had elongated 3–8 cm. from the place of germination.

In contrast, the stolon-like seedlings of species in sections Marcgraviopsis and Echinospadix are fairly commonly encountered in the wild, and are always found attached to the plump seed. Seedlings of this type can elongate for a distance of 1–2 m. on the resources stored in the seed. They are green and photosynthetic where exposed to light, but often they grow under leaf litter and are white in color. These stolon-like seedlings seem to be an adaptation for rapid location of a tree. The species which grow in this way are evading competition as terrestrial plants by reaching an epiphytic habitat as seedlings.

The probability that a stolon-like seedling will successfully reach a tree is a function of the length it can grow, which in turn depends on the energy stored in the seed. This situation would favor an evolutionary increase in seed size for species with stolon-like seedlings, offset by an increased energetic cost per seed, usually resulting in fewer seeds produced per plant. In the size range of *Monstera* seeds (6–22 mm.) increased size also probably involves a decrease in dispersibility. The mean seed weight of FAA-preserved seeds of species with stolon-like seedlings is 255 mg. compared to 140 mg. for species with unspecialized seedlings ($p < .05$).

Juvenile Plants. The *Monstera* species with unspecialized seedlings also have unspecialized juveniles. The terrestrial and climbing plant shows a gradual increase in leaf size and stem diameter toward the adult condition.

The species with stolon-like seedlings, however, have a highly modified juvenile. When the plant begins climbing a tree, it produces asymmetric foliage leaves which are flattened against the tree so as to overlap one another and completely cover the stem (Fig. 25). The petiole is very short and the sheathing portion, which protects the next developing leaf, is extended into a ligular outgrowth. This tightly appressed type of shoot with overlapping leaves is known in the horticultural literature as a 'shingle plant.' The shingle plant grows up the trunk producing successively larger leaves until it reaches a critical size, when in the course of a few nodes it changes abruptly to the adult form with large exserted leaves.

The shingle plant habit appears in several unrelated genera of climbers, e.g., *Marcgravia, Ficus, Metrosideros, Drynaria, Hoya, Scindapsus, Conchophyllum, Teratophyllum.* Goebel (1900) and Karsten (1925) suggest that in *Monstera* it is an adaptation to protect the young adventitious roots from dessication, as they are covered by the appressed leaves. It would also seem that transpirational water loss would be decreased by this habit, since the stomata, which are limited to the abaxial surface, are in contact with a still layer of moist air against the trunk of the tree, and are protected from drying winds.

It is plausible that the shingle plant is an adaptation to water stress when one considers the nature of the seedling. In section Monstera with unspecialized juveniles, a plant which is beginning to climb a trunk has a stem 5–10 mm. in diameter which in its horizontal terrestrial portion has numerous nodes, each with adventitious roots. The shingle plant, which is beginning to climb, is attached to a horizontal stem only 1–2 mm. in diameter, with relatively few nodes and few adventitious roots. Consequently, the young shingle plant has a much smaller terrestrial water-gathering system than those with an unspecialized climbing shoot of section Monstera, and it is more likely to be subject to water stress.

The stem of the growing shingle plant increases in diameter with each successive node, to the point where it can elaborate adventitious roots. These roots range from 4–10 mm. in diameter and usually extend to the ground. The adventitious roots increase the water-gathering capacity of the individual to the extent that it can undergo a phase change to the adult condition.

Thus the stolon-like seedling and the shingle plant juvenile combine to form a complex in which the shingle plant is an adaptation to water stress related to the small root system of the stolon-like seedling, which in turn is an adaptation for rapid location of a suitable substrate.

Adult Plants. The seedlings and juveniles of *Monstera* show two contrasting morphologies, the unspecialized gradual increase in size of plants of section Monstera and the stolon-like seedlings and shingle plant juvenile of sections Marcgraviopsis and Echinospadix. In the adult phase there has been a much greater diversification of growth habits, involving differences in the size of trees on which species grow, as well as the way they grow on them.

There is a correlation in *Monstera* between size of the mature plant and size of the tree on which it grows. The largest species (*M. tenuis, M. acuminata, M. punctulata,* and *M. lechleriana*) are found as reproductive individuals only on the largest forest trees. Smaller trees either do not provide a sufficient length of clear bole for these climbers to mature on, or else lack the strength to support a massive epiphyte. These *Monstera* species sometimes become established on small trees, but on reaching the first few branches, the stem grows away from its support and the pendant tip grows back to the ground.

Smaller species of *Monstera* can grow to maturity on smaller trees though they also colonize larger trees where they mostly grow among buttress roots and on the lower trunk, seldom climbing above 5 meters. *Monstera obliqua, M. xanthospatha,* and *M. minima* are the smallest species of the genus, with stems 2–10 mm. thick and leaves 10–25 cm. long. They can grow to maturity on nearly any woody substrate from the largest trees to twigs of shrubs or small saplings. Compared to the large monsteras, the small species occupy a more abundant but ephemeral habitat.

The size of *Monstera* species is correlated with growth rate and life span as well. Plants of several species were tagged in the field and inspected 12–18 months later. The small *M. obliqua* showed an annual stem elongation of 2–5 m., representing 30–70 new leaves with a total area of 0.2–0.4 m^2. Applying this rate of growth to plants which could be traced back to an apparent germination site suggested that individuals may flower within 1½ years after germination. At the other extreme, adult plants of *Monstera lechleriana* showed an annual rate of stem elongation of 12–20 cm. and a production of 4–8 leaves with a total area of 1.2–2.0 m^2. Individuals of this species apparently do not flower until about 6–8 years of age.

Considering the genus as a whole, the species of *Monstera* show a continuum ranging from small, rapidly elongating and early maturing species which occupy abundant but ephemeral habitats (twigs and small branches) to massive species with a slow rate of stem elongation and late maturation which occupy rare but stable habitats (boles of large forest trees).

Related to differences in elongation rate and host tree size preference, other differences of *Monstera* species are in which might be called the general aspect or attitude of the plants. *Monstera lechleriana* and *M. dilacerata* elaborate a tight head or cluster of 10–15 spreading leaves at the top of the stem. *Monstera punctulata* and *M. tenuis* have a more open habit of growth, with the arching leaves separated by long internodes. *Monstera acuminata* and *M. dubia* have long internodes and the leaf laminae are pendent from the petioles, and hang parallel to the trunk of the host tree. Individuals of the last two species often clothe the entire bole of a large tree to a height of 25 meters.

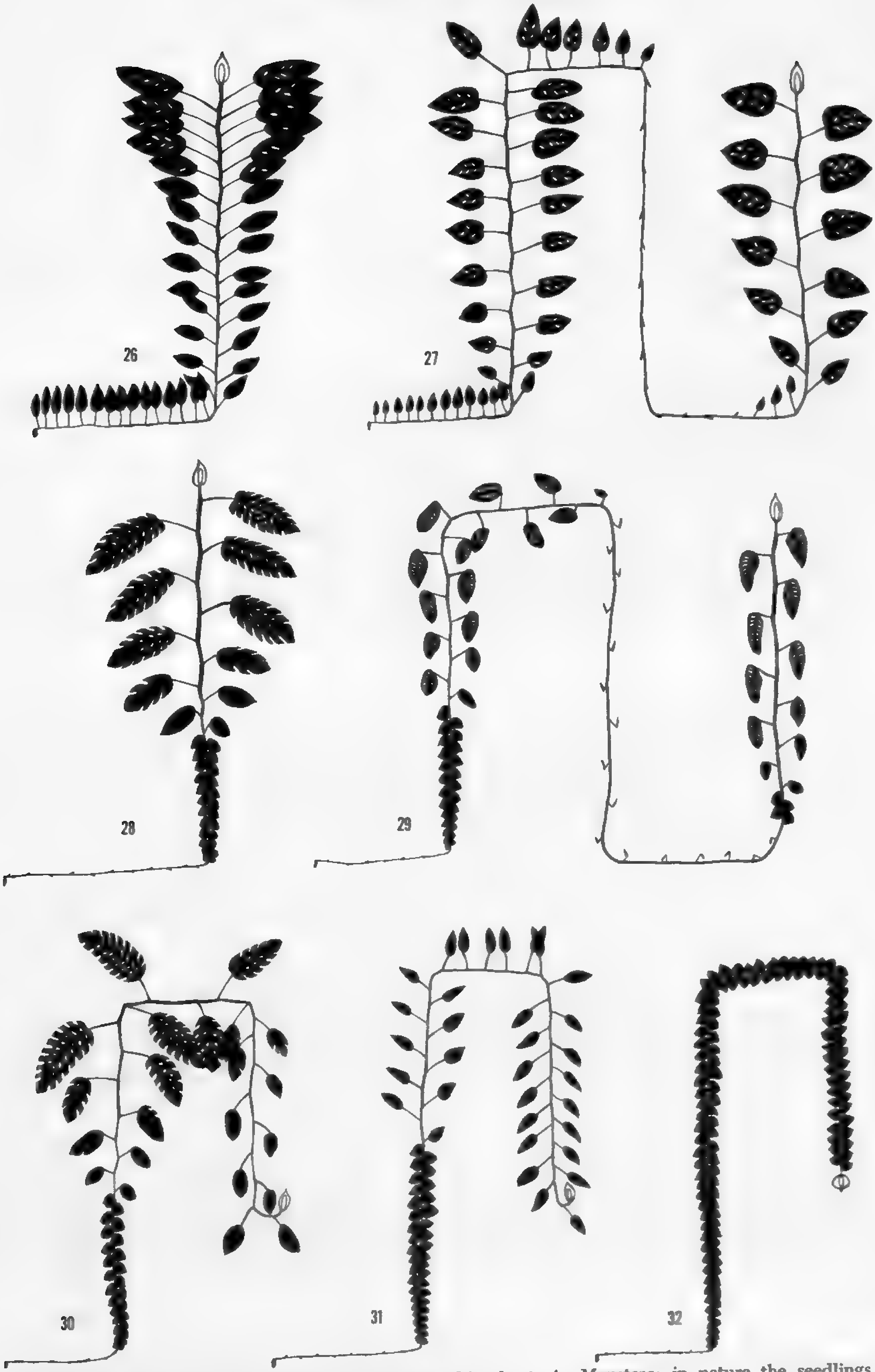
In species having long internodes, the leaves are spaced well apart and the shading of a leaf by the one above is diminished, but fewer leaves can be produced on a trunk before reaching the canopy. When a plant of *Monstera acuminata* reaches branches above the bole of the host tree, the stem is altered into a hanging stolon. This stolon has internodes to 30 cm. long and bears only cataphylls or highly reduced sickle-shaped foliage leaves at the nodes. It drops to the ground and grows horizontally, often for a distance of 10–20 m. until it encounters a tree and begins to climb. This represents a second type of tree searching activity in addition to that of the seedlings. While these stolons ('flagelliform shoots' of Engler and Krause, 1908) are encountered occasionally in most species, they are especially common in *M. acuminata, M. siltepecana,* and *M. obliqua.*

A second type of hanging shoot is found in *Monstera dubia,* a species having internodes 6–12 cm. long and large semi-pendent leaves. When the shoot reaches the first or second forking of branches in a tree, it turns 180° and begins growing downward as a hanging shoot. Unlike the hanging stolons described above, the hanging shoots of *M. dubia* produce full size stems and leaves, just as do the climbing shoots, except in this case the adventitious roots mostly abort. This manner of growth doubles the useful length of the bole of the host tree. When the hanging shoot eventually reaches the ground, it may root and grow up the trunk again as a climbing shoot. Flowering occurs in either ascending or hanging shoots.

Several species *(Monstera luteynii, M. pittieri* and *M. tuberculata)* always produce hanging shoots and flower only in the pendent portions. They all have small coriaceous leaves and thick cuticles, apparently xeromorphic adaptations to the greater water stress of free-hanging rootless shoots as compared to attached shoots with numerous adventitious roots. The hypothetical neotonous origin of *M. tuberculata* from an *M. dubia*-like ancestor is shown in Figures 26–32.

Monstera acuminata, with four radically different kinds of shoots, represents an extreme of heteroblastic development (Fig. 29). The seedling is a thread-like creeper which elongates rapidly while locating a host tree. The second stage is a shingle plant with xeromorphic features encompassing the transition from terrestrial growth to the more xeric epiphytic habitat. Several meters above the ground, an abrupt change to the adult form takes place. This results in a massive sub-canopy epiphyte with exserted leaves, which is the major energy-gathering phase of the life cycle. In addition to the abundant production of fruits and seeds, the adult elaborates shoots of a fourth type—hanging and creeping leafless stolons—which colonize additional trees or serve the individual as a means of recovery after establishment on an unsuitable host.

The elaboration of several different kinds of shoots by a single species has been a source of confusion in the classification and identification of monsteras, and the shingle plant juveniles of section Marcgraviopsis have even been described as new species of the dicotyledonous genus *Marcgravia.* Yet once the life cycles are understood, they furnish an insight



Figs. 26–32. Schematic diagrams of heteromorphic shoots in *Monstera;* in nature the seedlings and juveniles have died and decayed by the time the adult is flowering: 26. *M. lechleriana,* showing unspecialized development; 27. *M. siltepecana,* with a hanging stolon; 28. *M. punctulata,* with a stolon-like seedling, shingle plant, and adult; 29. *M. acuminata,* like *M. punctulata* with the addition of hanging and creeping stolons; 30. *M. dubia;* 31. *M. pittieri;* 32. *M. tuberculata.* Figs. 30, 31, and 32 illustrate a hypothetical reduction series leading to *M. tuberculata,* a vegetatively neotonous form flowering on a shoot which is morphologically a shingle plant.

into the systematic relationships of the species and in this revision provide the basis for the subgeneric classification.

GEOGRAPHY

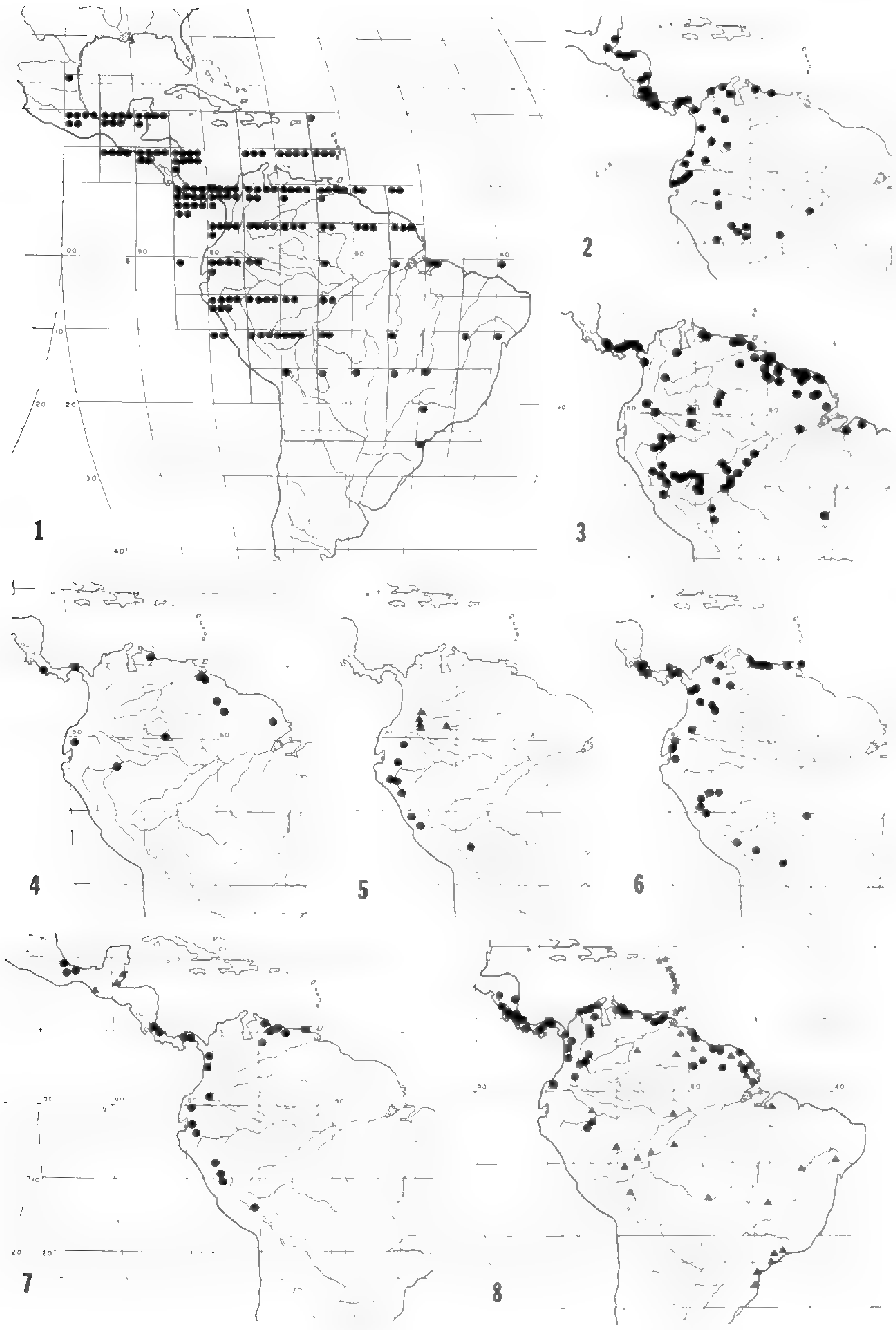
The center of species diversity in *Monstera* is in Costa Rica and Panama, with secondary centers in Mexico and the northern Andes (Map 1). Only a single weedy species, *M. adansonii*, has colonized the Caribbean Islands and coastal Brazil. The absence of endemic species in the Guiana highlands and southern Brazil emphasizes the essentially north-Andean distribution of the genus in South America.

The genus most closely related to *Monstera* and, considered by several authors to be congeneric, is *Epipremnum*, which is found at present in Indomalaya and the Pacific. *Epipremnum* is represented in the Tertiary by fossil seeds first appearing in Eocene deposits, although more common and diverse in Oligocene deposits. These fossils are found from England to western Siberia and occur as far north as 55° latitude (Madison & Tiffney, 1976). The Paleogene boreotropical flora, with which the fossils are associated, was fairly uniform in the eastern and western hemispheres, largely due to the availability of migration routes across the north Atlantic and Beringia (Wolfe, 1975). A possible interpretation of the present distribution of *Epipremnum* and *Monstera* is that they are both derivatives of an ancestral complex in the Paleogene boreotropical flora and have subsequently diverged in geographic isolation.

Wolfe (1975) and Raven and Axelrod (1974) suggest that the North American portion of the Eocene tropical flora was largely extinguished following the onset of climatic deterioration in the late Oligocene; surviving elements are seen in some of the dry Caribbean flora and mesothermal montane floras of Central America.

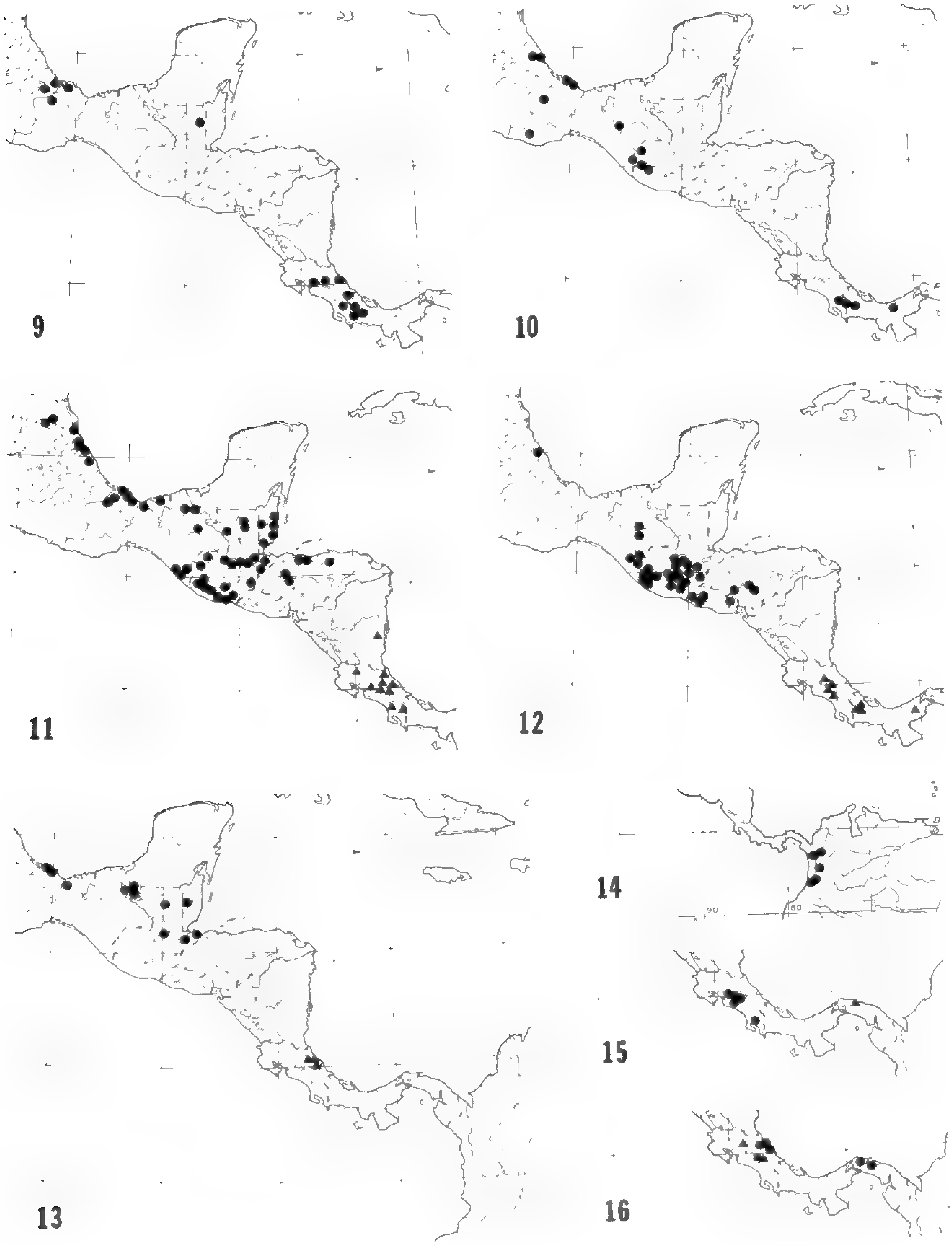
Several lines of evidence suggest that *Monstera* may represent a remnant of this Paleogene tropical flora which has persisted in North America, subsequently spreading into South America in Neogene times. One is the distribution of isolated or relict taxa in the genus. All four sections are represented in Mexico, but only two in South America. The species found in South America all either occur in Central America or show close affinities to Central American species. On the other hand, *M. membranacea* and *M. deliciosa*, which are morphologically isolated and show no close affinities to other species, are confined to Central America and Mexico.

A second is the distribution of species in relation to seed size. The size of *Monstera* seeds spans a critical range for dispersal by birds, the apparent mechanism of dispersal in this genus. The smallest seeds are about 5 mm. long and are probably easily dispersed by most frugivorous birds. However, the largest seeds (20–22 mm. across) have a much more restricted pool of potential dispersal vectors. The largest-seeded species



Maps 1–8. 1. Density distribution of *Monstera* species; for each square of 5° latitude by 5° longitude the number of dots equals the number of species of *Monstera* occurring in that region. 2–8. Distribution of *Monstera* species: 2. *M. dilacerta;* 3. *M. obliqua;* 4. *M. spruceana;* 5. *M. subpinnata* (dots) and *M. gracilis* (triangles); 6. *M. dubia;* 7. *M. lechleriana* (dots) and *M. acacoyaguensis* (triangles); 8. *M. adansonii* var. *adansonii* (stars), var. *laniata* (dots), and var. *klotzschiana* (triangles).

occur in Mexico, and there is a cline of decreasing seed size both within and between species toward South America. All of the South American species have seeds less than 10 mm. long, and one could argue that the species in South America are simply the most disperable



MAPS 9–16. Distribution of *Monstera* species: 9. *M. punctulata;* 10. *M. deliciosa;* 11. *M. acuminata* (dots) and *M. tenuis* (triangles); 12. *M. siltepecana* (dots) and *M. oreophila* (triangles); 13. *M. tuberculata* var. *tuberculata* (dots) and var. *brevinodum* (triangles); 14. *M. xanthospatha;* 15. *M. membranacea* (dots) and *M. minima* (triangles); 16. *M. pittieri* (dots) and *M. luteynii* (triangles).

(and dispersed), assuming the genus to have had a North American origin.

An additional relevant line of evidence is the range of climatic tolerance in *Monstera*. Although strictly tropical in natural distribution, *M. deliciosa*, *M. adansonii*, and *Epipremnum aureum* grow vigorously, flower, and set fruit in central Florida where they are annually exposed to frost. This moderate cold-hardiness, coupled with a degree of drought tolerance, suggests that *Monstera* species could have survived periods of unfavorable climate in the late Paleogene followed by diversification and dispersal into South America in the Neogene.

Distributions of individual *Monstera* species are shown in Maps 2–16. A pattern found in several species is that of a disjunct distribution of Mexico-Guatemala and Costa Rica-Panama. Three species of montane habitats show this distribution: *M. punctulata* (Map 9), *M. deliciosa* (Map 10), and *M. lechleriana* (Map 7). The latter two exhibit morphological differentiation between the southern and northern populations, indicating that this disjunction has persisted long enough to allow some evolutionary divergence. *Monstera siltepecana* and *M. oreophila* are two closely related montane species which may represent geographical speciation based on this disjunction. The barrier between these two regions for montane species seems to be the absence of high and wet mountains in the region of Nicaragua and Honduras, where the mountain ranges are lower than those to the north and south. The mountains of this intervening area are covered with mesic oak-pine forest.

A similar disjunction is found in *Monstera tuberculata* (Map 13), a lowland species of the Atlantic coastal plain not known to occur above 200 m. elevation. The Mexican and Costa Rican populations are separate taxonomic varieties, well differentiated by the morphology of their fruits. At present, a wet tropical forest is continuous along the Atlantic coast from Costa Rica to Mexico. The absence of *M. tuberculata* from Nicaragua and Honduras may represent the extermination of these species in the middle region of a once continuous distribution because of periods of drier climate in the Pleistocene, as suggested by the Raven and Axelrod (1974). The only *Monstera* species distributed continuously through this region, *M. dilacerata* (Map 2), has seeds about one-half the size of the disjunct species. This feature may increase its rate of dispersal to the point that it is the first species to have reinvaded the area after a period of dry climate.

In South America, *Monstera* is distributed primarily in a broad arc extending from Peru to the Guianas, thus reflecting the distribution of the lower montane slopes which are the chief habitat of most species. The only *Monstera* species which is abundant in the Amazon Basin is *M. obliqua*, a tiny creeper inhabiting the margins of waterways. The massive monsteras which form such a characteristic element of wet Central American vegetation are mostly absent from the Amazon region.

SPECIES CONCEPT

In considering the overall pattern of speciation in *Monstera*, two distinct elements may be separated. The species of sections Marcgraviopsis, Tornelia, and Echinospadix are clearly demarcated in terms of their morphology, growth habits, and habitat preferences, and intermediates between species are absent. Thus, even though *M. acuminata* and *M. dubia* are quite variable, they are easily recognized and it is not difficult to distinguish them from other species. This pattern suggests an early speciation followed by the extinction of intermediates.

In contrast, the species of section *Monstera* are connected by numerous intermediates and the delimitation of species is difficult. Quite diverse elements may be joined by a series of intergrading forms, and nearly all of the species intergrade with *M. adansonii*, which is itself polymorphic. In addition, there are broad geographic clines found with respect to several characters, among them fruit color, style length and seed size.

In Mexico, species of section Monstera have white fruits; further south the same or related species have pale yellow fruits, in Colombia medium yellow, and deep yellow or orange in the Guianas and Amazonia. A second cline is in the shape of the style, which is prismatic in Mexico. It is more conical and attenuate to the south, resulting in rather spiny appearing spadices in Brazil in contrast to the smooth spadices found in Mexico. Seed size is greatest in Mexico and decreases to the south and east. Each cline is found within and between species in section Monstera.

The existence of these clines and of large numbers of intermediates suggests that barriers to genetic exchange between these species are weak and that hybridization and introgression are correspondingly common. Thus, for example, the genes for yellow fruit color have spread through the South American populations of all species in section Monstera but are absent from the Mexican populations. This results in the confusing situation where fruit color in populations of *Monstera lechleriana* of Venezuela more closely resemble *M. adansonii* in Venezuela than they do populations of *M. lechleriana* in Mexico.

A number of the species of section Monstera have broad geographic ranges. They are species found at forest margins, along waterways, and in clearings rather than in deep forests. Apparently they have adapted readily to the great increase in habitats resulting from disturbances by man, and *Monstera adansonii* has become a common neotropical weed on fence posts and telephone poles. This has perhaps contributed to the breakdown of ecological or geographic barriers that formerly separated species of this section and accounts in part for the numerous intermediates between species.

The application of binomial nomenclature to this situation is not straightforward. In this revision, I am treating as species groups of individuals which are ecologically and morphologically similar. The degree of similarity requisite for the inclusion of two individuals in a species depends on the amount of variability known to occur within populations and individuals, and on the relative abundance of intermediates between unlike forms. The resulting classification is a broad one and emphasizes similarities rather than differences, though in the description of each species I have tried to indicate the extent of its variability. I am sympathetic to the possibility that a taxonomist of different temperament, using the same data and approach, might accept 40 or 45 species where I recognize 22. It is likely that some of the species recognized in section Monstera are in reality groups of sibling species, but while suspecting this I have been unable, with the information available, to recognize additional taxonomic entities. In addition, there are specimens which, while not fitting any of the known species, are insufficient as the basis for the description of new taxa. I predict that further species of *Monstera* are most likely to be found in section Monstera and to come from Costa Rica and Panama, particularly the mountainous regions.

Several previous authors have recognized infrageneric taxa in *Monstera.* Miquel (1844) divided the genus into two sections: section Monstera, with the flowers at the base of the spadix imperfect and carpelate; and section Heteropsis, with all the flowers perfect. Carl Koch (1857) included the genera *Scindapsus, Alloschemone,* and *Rhaphidophora* in Monstera which he divided into six subgenera. Three of his subgenera include species of *Monstera* as here delimited. These were distinguished on the basis of leaf shape: one included species with entire margins; a second with the leaves pinnatifid but not perforate; and a third with the leaves pinnatifid and perforate. Schott (1860) separated the pinnatifid-leaved species of *Monstera* as a separate genus, *Tornelia.*

I consider these subdivisions of the genus to be artificial, and propose a new classification in which the genus is divided into four sections. The majority of the species are placed into two sections on the basis of their patterns of development. In section Monstera the seedlings have exserted foliage leaves and develop to the adult stage by a gradual increase in size. In section Marcgraviopsis, the species exhibit heteroblastic development with three distinct phases: the seedling is a stolon-like creeper, the juvenile is a shingle plant, and the adult has large exserted leaves. Two unusual species are relegated to monotypic sections on the basis of characters discussed in the description of those sections.

This treatment separates into different sections species which as adults may be rather similar, but have very different developmental histories (e.g., *Monstera dilacerata* and *M. tenuis*). On the other hand, species which show a very similar heteroblastic development in early stages, but differing morphologies as adults, are included in the same section.

TAXONOMIC TREATMENT

TRIBE MONSTEREAE ENGLER

Monstereae Engler, Nov. Act. Akad. Leopold. 39:143 (1876).
Anepsideae Engler, Nov. Act. Akad. Leopold. 39:143 (1876).
Rhaphidophoreae Engler, Nov. Act. Akad. Leopold. 39:143 (1876).
Scindapseae Nakai, Ordines Familia 216 (1943).
Stenospermationeae Nakai, Ordines Familia 216 (1943).
Rhodospatheae Nakai, Ordines Familia 216 (1943).
Callae Schott subtribus Monsterinae Schott, Prod. Syst. Aroid. 346 (1860).

Scandent epiphytes lacking laticiferous elements; trichosclereids usually present in spathe and spadix; the leaves entire, pinnatifid, or foraminate, the latter two conditions resulting from the death of small groups of laminar cells early in development; the petiole geniculate; the primary lateral veins of the lamina parallel, the secondary lateral veins parallel or reticulate. Spathe naviculiform, deciduous after flowering (rarely persistent in *Rhaphidophora*); spadix cylindric, without an appendix; flowers perfect, sometimes sterile near the base of the spadix; stamens 4, extrorse; perianth lacking; ovary 1–2(–6) locular, ovules 1–∞, anatropous or amphitropous; fruit a berry, usually with the stylar portion deciduous; pollen meridiosulcate, foveolate.

TYPE: *Monstera* Adans.

KEY TO GENERA OF THE TRIBE MONSTEREAE

A. Needle-like trichosclereids present in the spathe and spadix.
  B. Ovary unilocular or incompletely bilocular, paleotropical (1 species Brazil).
    C. Ovule amphitropous, solitary, basal; seeds lacking endosperm. . . 1. *Scindapsus.*
    C. Ovules anatropous, more than one; seeds with endosperm.
      D. Ovules 2–4(–6) at the base of a single intrusive parietal placenta; seeds curved, 3–7 mm. long, 1.5–4 mm. wide. . . . . 2. *Epipremnum.*
      D. Ovules numerous, superposed on two (rarely three) parietal placentae; seeds fusiform, straight, 1.3–3.2 mm. long, 0.6–1.0 mm. wide. . . . . 3. *Rhaphidophora.*
  B. Ovary 2–6 locular, neotropical.
    E. Seeds globose to oblong, 6–22 mm. long, the raphe S-shaped, endosperm absent; ovules 2 per loculus; leaves pinnatifid, foraminate, or entire. . . . . . . 4. *Monstera.*
    E. Seeds fusiform, claviform, or lenticular, less than 3 mm. long, endosperm present; ovules (2–)3–∞ per loculus, leaves entire.
      F. Placentation basal, seeds fusiform to claviform, 2.0–2.5 mm. long; leaves thickly coriaceous. . . . . 5. *Stenospermation.*
      F. Placentation axile, seeds lenticular and flattened, curved 180°, 1.0–1.6 mm. across; leaves not coriaceous. . . . . 6. *Rhodospatha.*
A. Needle-like trichosclereids absent from the spathe and spadix; ovary unilocular with one intrusive placenta bearing two ovules near the base, seeds lacking endosperm, Malaysia. . . . . 7. *Amydrium.*

1. **Scindapsus** Schott, Melet. I:21 (1832). TYPE: *S. officinalis* (Roxb.) Schott (*Pothos officinalis* Roxb.).
Cuscuaria Schott, Bonplandia 5:45 (1857). TYPE: *C. marantifolia* Schott (*Pothos cuscuaria* Aublet).
Alloschemone Schott, Genera Aroid. App. (1858). TYPE: *A. poeppigiana* Schott, *nom. illegit.* (*Scindapsus occidentalis* Poepp., *A. occidentalis* (Poepp.) Engler & Krause).

Leaves entire in the Asian species, pinnatifid in the Brazilian species, never perforate. Secondary lateral veins running parallel to the primary lateral veins. Spadix sessile; ovary unilocular, ovule amphitropous, basal, solitary; seed strongly curved, somewhat flattened, 3–9 mm. long, 3–7 mm. wide, 2.0–4.5 mm. thick, testa smooth, hard; endosperm absent.

About 25 species, India and Sikkim to the Solomon Islands, one species in Amazonian Brazil. For a discussion of the Brazilian species see Madison 1976.

2. **Epipremnum** Schott, Bonplandia **5**:45 (1857). TYPE: *E. mirabile* Schott.

Leaves entire or pinnatifid, coriaceous; secondary lateral veins parallel or reticulate. Spadix sessile; ovary unilocular with a single intrusive placenta bearing 2–4(–6) ovules at its base; seeds strongly curved, asymmetric, 3–7 mm. long, 1.6–5.0 mm. wide; testa hard, smooth, pitted or rugose; endosperm present, embryo curved.

About 15 species, Burma to Samoa and the Marshall Islands.

This genus has been merged with *Rhaphidophora* by several authors, but in its seed morphology and vegetative characters it is much closer to *Monstera*.

3. **Rhaphidophora** Hassk. Flora **25** (Beibl. 1):11 (1842). TYPE: *R. lacera* Hasskarl, *nom. illegit. (Pothos pertusus* Roxb., *R. pertusa* (Roxb.) Schott).
Afroraphidophora Engler, Natur. Pflanzenfam. **II**:31 (1906). LECTOTYPE: *A. africana* (N. E. Brown) Engler (*Rhaphidophora africana* N. E. Brown).

Leaves entire, pinnatifid or perforate; secondary lateral veins parallel to primary. Spadix sessile or stipitate; ovary unilocular, divided by 2 (rarely 3) intrusive parietal placentae bearing numerous superposed ovules; seeds elongate, fusiform or flattened, straight or very slightly curved, 1.3–3.2 mm. long, 0.6–1.0 mm. wide, smooth; endosperm present, embryo axile, straight or slightly curved.

About 60 species, West Africa, India and Ceylon, Nepal to Samoa, Formosa.

4. **Monstera** Adans., Fam. des Plantes **II**:470 (1763). LECTOTYPE: *M. adansonii* Schott (*Dracontium pertusum* L.).
Tornelia Guttierez ex Linnaea, Linnaeae **26**:282 (1853). TYPE: *T. fragrans* Guttierez ex Linnaea.
Serangium W. Wood, Salisb. Gen. Pl. Frag., p. 5 (1866). TYPE: *Dracontium pertusum* L.

Leaves entire, pinnatifid, or perforate; secondary lateral veins usually reticulate. Spadix sessile; ovary bilocular, the septum perforate at its base, two basal ovules per loculus; berries mostly one-seeded, seeds sub-globose to oblong, 6–22 mm. long, 4–12 mm. wide, the funiculus S-shaped, testa soft; endosperm absent.

Twenty-two species, Mexico to Brazil, Lesser Antilles.

5. **Stenospermation** Schott, General Aroid. t. 70 (1858). LECTOTYPE: *S. mathewsii* Schott.

Leaves entire, ovate to lanceolate, thickly coriaceous. Stem terete, usually less than 1 m. in length and not closely attached to the substrate. Spadix white, often stipitate; ovary bilocular, ovules numerous and basal; seeds elongate, fusiform to claviform, 2.0–2.5 mm. long, 1.0 mm. wide, long raphe present; abundant endosperm, embryo axile, straight or slightly curved.

About 20 species, western neotropics from Nicaragua to Bolivia.

6. **Rhodospatha** Poepp., Poepp. & Endlicher Nov. Gen. et Spec. **III**:91 (1845). LECTOTYPE: *R. latifolia* Poepp.

Atimeta Schott, Genera Aroid. t. 71 (1858). TYPE: *A. videniana* Schott.
Anespsias Schott, Genera Aroid. t. 73 (1858). TYPE: *A. moritzianus* Schott.

Leaves entire; secondary lateral veins closely parallel to primary; lamina membranaceous, developing leaves red or pink. Spadix sessile or stipitate, fruiting spadix often red; ovary bilocular, rarely 3–6 locular, ovules numerous, superposed in several series on the septum; seeds reniform to lenticular, strongly compressed, 1.0–1.6 mm. across, 0.5 mm. thick; endosperm present.

About 15 species, Mexico to Brazil.

7. **Amydrium** Schott, Ann. Mus. Lugd. Bat. **I**:127 (1863). TYPE: *A. humile* Schott.
Epipremnopsis Engler, Das Pflanzenreich IV 23(B):1 (1908). TYPE: *E. media* (Zoll. & Mor.) Engler (*Scindapsis medius* Zoll. & Mor.).

Trichosclereids lacking. Leaves entire, pinnatifid, or foraminate; secondary lateral veins reticulate. Spathe yellow; spadix stipitate or sessile; ovary unilocular with a deeply intrusive parietal placenta bearing two ovules; seeds reniform, about 9 mm. wide, 7 mm. long; endosperm absent.

Four species, Malaysia.

EXCLUDED GENERA

Anadendrum and *Heteropsis* are intermediate in character between the subfamilies Monsteroideae and Pothoideae. They were included in the Monstereae by Hutchinson (1959) but placed in the Pothoideae by Engler and Krause (1908).

Anadendrum has a perianth of connate tepals in contrast to the naked flowers of the Monstereae. It lacks the characteristic trichosclereids and has inaperturate pollen rather than the meridiosulcate pollen of the Monstereae (Thanikaimoni, 1969). Engler and Krause (1908) mention perforate and pinnate leaves in the generic descriptions of *Anadendrum*, but all the species they describe have entire leaves. If perforate leaves do occur in *Anadendrum* this would suggest a greater affinity to the Monstereae; on the other hand, this condition is also found in *Rhektophyllum* and *Cyrtosperma* of the Lasiodeae, and thus is not definitive. This genus seems best retained in the Pothoideae.

Heteropsis differs from the typical Monstereae in several respects. It has entire, subsessile leaves which apparently lack a geniculum. Trichosclereids are absent. Species of *Heteropsis* exhibit monopodial growth, in contrast to the strictly sympodial growth of the Monstereae. I follow Engler and Krause (1908) in relegating this genus to a separate tribe of the Pothoideae.

MONSTERA ADANS., NOM. CONSERV.

Monstera Adans., Fam. des Plantes **II**:470 (1763). LECTOTYPE: *M. adansonii* Schott (*Dracontium pertusum* L.) see Nicolson (1968a) on typification.
Tornelia Guttierez ex Linnaea, Linnaea **26**:282 (1853). TYPE: *T. fragrans* Guttierez ex. Linnaea.
Serangium W. Wood, Salisb. Gen. Pl. Frag., p. 5 (1866). TYPE: *Dracontium pertusum* L.

Scandent epiphytes of wet tropical forests, climbing by adventitious roots. *Seedling:*

germination hypogeal, the seedling producing two cataphylls and then exserted foliage leaves, or producing a green stolon-like shoot 1–2 mm. in diameter with internodes 4–10 cm. long, bearing scale leaves at the nodes, this stolon to 2 m. long. *Juvenile:* a terrestrial or climbing creeper with exserted leaves, or a climber with a flattened stem and ovate to orbicular leaves tightly appressed against the substrate, overlapping one another and covering the stem, these leaves with a petiole less than one-half the length of the lamina and the sheath extended into a ligular outgrowth about the length of the petiole. *Adult stem:* green or brown, smooth or tuberculate to warty, 2–80 mm. thick, with internodes 1–12 cm. long (to 30 cm. long in stolons), leaves produced distichously, the angle of divergence between the two ranks from about 90° to 180°. *Adventitious roots:* of two types, positively geotropic feeder roots produced at the nodes and extending to the ground, and ageotropic clasping roots produced along the internodes and attaching the plant to the stem. *Petiole:* 4–110 cm. long with a pulvinus at each end, vaginate for 1/6 to all its length, the sheath wings deciduous or persistent. *Lamina:* membranaceous to coriaceous, ovate to lanceolate, 10–120 cm. long, 4–75 cm. wide, the base cordate to acute or cuneate, often oblique, the apex various, usually acute; margins entire or pinnatifid, the lamina perforate or not, the perforations in 1–4 series per side; primary lateral veins indistinct or distinct and 6–40 in number per side, usually white and prominent abaxially, the secondary lateral veins parallel to the primary or reticulate. *Peduncle:* terete or flattened, 2–40 mm. thick, 1–40 cm. long. *Spathe:* white, cream, yellow to deep yellow, or rose at maturity, coriaceous, hemispherical to naviculiform, 5–35 cm. tall, 3–15 cm. across when open, opening widely or only by a narrow slit, deciduous after anthesis. *Flowering spadix:* sessile, white to yellow, cylindric, 5–30 mm. thick, 4–33 cm. long, sterile near the base, the fertile flowers perfect, with four stamens opening extrorsely, ovary bilocular with two basal anatropous ovules per loculus, the pistils prismatic, truncate at the apex or with a curved or straight conical style. *Fruiting spadix:* green, white, or yellow to orange, cylindric, 1.0–9.5 cm. thick, 5–42 cm. long, the stylar portion of the berries deciduous to expose the seeds in a gray or orange pulp, or the berries indehiscent. *Seeds:* globose to oblong, 5–22 mm. long, 3–12 mm. across, the raphe S-shaped by curvature of the seed in development; the testa brown and soft, the embryo macropodial and green or blue.

KEY TO SECTIONS OF MONSTERA

A. Plants in the earliest climbing phase with exserted leaves, the petioles more than ⅔ the lamina length.
  B. Pistils 10–18 mm. across in fruit, seeds 16–22 mm. long. ..... Section *Tornelia.*
  B. Pistils 5–8 mm. across in fruit, seeds 5–13 mm. long. .... Section *Monstera.*
A. Plants in the earliest climbing phase with leaves tightly appressed to the substrate, the petioles less than ½ the lamina length.
  C. Flowering spadix erect, adult leaf with a short ligule or ligule lacking. .... Section *Marcgraviopsis.*
  C. Flowering spadix pendent, adult leaf with a ligule about equal in length to the petiole. .... Section *Echinospadix.*

KEY TO SPECIES OF MONSTERA

A. Lamina regularly pinnatifid (rarely on one side only).
  B. Lamina lacking perforations.
    C. Pinnae 15–30 in number per side, flowering spadix 3.5–5.0 cm. thick (Nicaragua to Panama). .... 18. *M. tenuis.*
    C. Pinnae 4–12 per side, flowering spadix 1–3 cm. thick.
      D. Lamina broadly cordate at the base, secondary lateral veins reticulate, pistils 10–18 mm. across in fruit. .... 22. *M. deliciosa.*
      D. Lamina truncate to acute at the base, secondary lateral veins parallel, pistils 5–8 mm. across in fruit.
        E. Peduncle equal to or shorter than the spadix.
          F. Pistils truncate, flowering spadix 12–25 cm. long, lamina pinnae not constricted at the base. .... 17. *M. spruceana.*

F. Pistils with a conical style, flowering spadix 8–12 cm. long, pinnae usually constricted at the base. . . . . 8. *M. subpinnata.*

E. Peduncle more than 4 cm. longer than the spadix.

G. Flowering spadix 4–6 cm. long, 1.0–1.2 cm. thick, stem 5–10 mm. thick, peduncle 5–8 mm. thick (Colombia). . . . . 9. *M. gracilis.*

G. Flowering spadix 7–16 cm. long, 1.5–2.5 cm. thick, stem 15–40 mm. thick, peduncle 10–16 mm. thick. . . . . 7. *M. dilacerata.*

B. Lamina with perforations.

H. Secondary lateral veins parallel.

I. Pinnae 8–12 per side, petiole sheath deciduous, flowering spadix 4–6 cm. long, peduncle 8–18 cm. long, below 1000 m. (Colombia). . . . . 9. *M. gracilis.*

I. Pinnae 12–20 per side, petiole sheath persistent, flowering spadix 9–12 cm. long, peduncle 20–30 cm., above 1600 m. (Costa Rica). . . . . . . 10. *M. epipremnoides.*

H. Secondary lateral veins reticulate.

J. Petiole sheath green and persistent, lamina membranaceous, spathe decurrent on the peduncle for 3–8 cm. (Costa Rica). . . . . 6. *M. membranacea.*

J. Petiole sheath deciduous or at least marcescent, lamina coriaceous to subcoriaceous, spathe not decurrent on the peduncle.

K. Lamina shorter than the petiole, less than 1⅓ times longer than broad, pistils in fruit 10–18 mm. across. . . . . 22. *M. deliciosa.*

K. Lamina exceeding the petiole, more than 1⅓ times longer than broad, pistils in fruit 5–8 mm. across.

L. Petiole white-spotted, lamina bright green, peduncle more than 12 cm. long, dried pistils with a golden-colored cap. . . . . 16. *M. punctulata.*

L. Petiole and lamina dull green, peduncle less than 11 cm. long, dried pistils brown or black, not capitate. . . . . 15. *M. dubia.*

A. Lamina with the margins entire, or with a few lacerations but not regularly pinnatifid.

M. Lamina with perforations.

N. Petiole 5–18 cm. long, peduncle more than twice the length of the spadix, stems 2–10 mm. thick, spathe deep yellow abaxially.

O. Flowering spadix 5–10 mm. thick, mature berries globose, below 1000 m. elev. . . . . 12. *M. obliqua.*

O. Flowering spadix about 20 mm. thick, mature berries prismatic, above 1400 m. (Colombia). . . . . 11. *M. xanthospatha.*

N. Petiole longer than 18 cm., peduncle less than twice the length of the flowering spadix, stem 10–60 mm. thick, spathe not deep yellow abaxially.

P. Secondary lateral veins reticulate.

Q. Petiole sheath persistent, lamina thinly membranaceous, peduncle 13–17 cm. long (Costa Rica). . . . . 6. *M. membranacea.*

Q. Petiole sheath deciduous, lamina subcoriaceous to coriaceous, peduncle 5–12 cm. long.

R. Spathe 16–25 cm. tall, flowering spadix 10–13 cm. long, fruiting spadix green (Mexico to Honduras). . . . . 4. *M. siltepecana.*

R. Spathe 6–12 cm. tall, flowering spadix 5–10 cm. long, fruiting spadix pale yellow (Costa Rica to South America). 15. *M. dubia.*

P. Secondary lateral veins parallel (rarely reticulate near the margin).

S. Peduncle 4–10 cm. shorter than the spadix, juvenile a shingle plant (Mexico to Honduras). . . . . 14. *M. acuminata.*

S. Peduncle equal to or exceeding the spadix, juvenile with exserted leaves.

T. Primary lateral veins 5–10 mm. apart, above 1600 m. elev. (Panama and Costa Rica). . . . . 5. *M. oreophila.*

T. Primary lateral veins more than 15 mm. apart.

U. Flowering spadix less than 13 cm. long, fruiting spadix less than 17 cm. long. . . . . 1. *M. adansonii.*

U. Flowering spadix more than 15 cm. long, fruiting spadix more than 20 cm. long.

V. Leaf base abruptly truncate or subcordate (16–)20–40 primary lateral veins per side, flowering spadix 2.5–3.5 cm. thick. . . . . . 2. *M. lechleriana.*

V. Leaf lamina with a broadly cuneate portion at the base, 12–16 primary lateral veins per side, flowering spadix 1.5–2.0 cm. thick (Mexico and Guatemala). .... 3. *M. acacoyaguensis.*
M. Lamina entire, without perforations.
W. Lamina 13–120 cm. long, peduncle 1–4 cm. thick.
X. Fruiting spadix 2–4 cm. thick, seeds 5–8 mm. long, petiole sheath deciduous. .... 1. *M. adansonii.*
X. Fruiting spadix 4.0–6.5 cm. thick, seeds 10–20 mm. long, petiole sheath persistent.
Y. Lamina 35–65 cm. long, peduncle 7–13 cm. long, seeds 16–20 mm. long, internodes 6–12 cm. (Mexico to Honduras). .... 14. *M. acuminata.*
Y. Lamina 70–120 cm. long, peduncle 20–40 cm. long, seeds 10–13 mm. long, internodes 4–6 cm. .... 2. *M. lechleriana.*
W. Lamina less than 35 cm. long, peduncle 2–9 mm. thick.
Z. Peduncle equal to or shorter than the spadix, pendent epiphyte flowering on hanging stems, stems with a thick tan cuticle, often flaking off in dried specimens.
AA. Lamina more than 20 cm. long and 15 cm. wide. .... 15. *M. dubia.*
AA. Lamina less than 20 cm. long and 15 cm. wide.
BB. Petiole less than 4 cm. long, spadix pendent. .... 21. *M. tuberculata.*
BB. Petiole more than 7 cm. long, spadix erect.
CC. Lamina 2–5 times longer than broad, veins obscure (Costa Rica and Panama). .... 19. *M. pittieri.*
CC. Lamina 1–2 times longer than broad, veins prominent in dried leaves (Costa Rica). .... 20. *M. luteynii.*
Z. Peduncle longer than the spadix, attached epiphyte flowering in the climbing portion, stems green, lacking a thick flaky cuticle.
DD. Peduncle 1½–2 times the length of the leaves (lamina and petiole) (Panama). .... 13. *M. minima.*
DD. Peduncle shorter than the leaves.
EE. Spathe deep yellow abaxially, flowering spadix less than 8 cm. long, petioles 5–18 cm. long, stem 2–10 mm. thick.
FF. Flowering spadix 5–10 mm. thick, mature berries globose, below 1000 m. elevation. .... 12. *M. obliqua.*
FF. Flowering spadix about 20 mm. thick, mature berries prismatic, above 1400 m. (Colombia). .... 11. *M. xanthospatha.*
EE. Spathe pale yellow or cream abaxially, flowering spadix more than 10 cm. long, petioles more than 20 cm. long, stems 10–30 cm. thick. . . 1. *M. adansonii.*

MONSTERA section MONSTERA

TYPE SPECIES: *Monstera adansonii* Schott
SYNONYM: *Monstera* section Heteropsis Miq., Linnaea 18:79 (1844)
TYPE SPECIES: *Monstera obliqua* Miq.

The species of section Monstera have seedlings with exserted foliage leaves, and development to the adult stage is by a gradual increase in the size of successive leaves without pronounced heterophylly. The peduncle is longer than the spadix in these species except for *M. siltepecana* and *M. subpinnata.*

The species in this section are connected by many intergrading forms, making their delimitation difficult. Most of the species intergrade with *Monstera adansonii,* which is itself polymorphic. *Monstera membranacea* is rather isolated in the section, showing no close relationship to other species.

1. **Monstera adansonii** Schott

Scandent epiphyte 2–4(–6) m. tall. *Juvenile:* terrestrial creeper, stem smooth, green, terete, internodes 1–6 cm. long; petiole vaginate for $\frac{1}{3}$ to $\frac{5}{6}$ its length, the lamina widely ovate to narrowly elliptic, entire or perforated at a very early stage when only 5–10 cm. long. *Adult stem:* subterete, green, smooth, 1.5–3.0 cm. thick, the internodes 3–10 cm. long; leaf scars shallow, 3–10 mm. wide at the widest point, the ends of each leaf scar overlapping for 3–6 mm.; axillary buds longer than wide, located in a depression which is not extended into a sulcus. *Petiole:* smooth, 20–60 cm. long, somewhat shorter than the lamina, vaginate to the geniculum, the wings of the sheath deciduous or persistent, the geniculum 3–5 cm. long. *Lamina:* subcoriaceous, glossy adaxially, very widely ovate to elliptic, 25–70 cm. long, 15–45 cm. wide, the base cuneate to broadly truncate, sometimes oblique and unequal, being cuneate on one side and truncate to subcordate on the other side, the tip acute or shortly mucronate; margin entire, rarely irregularly laciniate, perforations absent to numerous in several series on each side of the midrib; primary lateral veins parallel, 8–16 in number, secondary lateral veins parallel to the primary. *Peduncle:* smooth, green, subterete to flattened, 9–22 cm. long, 1.0–1.4 cm. thick, 1.1–2.0 cm. wide. *Spathe:* cream to pale yellow, coriaceous, 12–28 cm. tall, 10–25 cm. around, acuminate, opening widely at maturity. *Flowering spadix:* cream to yellow, cylindric, 8–13 cm. long, 1.1–2.6 cm. thick, the pistils 4–7 mm. long, truncate or acute at the apex, the lower 6–8 rows of flowers sterile. *Fruiting spadix:* green, becoming yellow to deep yellow at maturity, 10–17 cm. long, 2–4 cm. thick, the stylar portion of the pistil containing trichosclereids, deciduous, revealing the seeds in a gray pulp. Berries mostly one-seeded, the seeds brown or black, 5–7 mm. long, 4–6 mm. wide, 2–3 mm. thick.

KEY TO VARIETIES

Petiole sheath with wings deciduous; leaf base unequal with one side truncate to subcordate and the other side cuneate to acute, the lamina less than twice as long as wide; lateral veins on at least one side arising from the midrib at an angle greater than 60°; Nicaragua to Peru, Venezuela, the Guianas, and Brazil (Amapá). .... 1 b. var. *laniata.*

Petiole sheath with wings persistent; leaf base subequal, cuneate to bluntly acute, the lamina more than twice as long as wide; lateral veins on both sides arising at an angle less than 60°.

  Pistils truncate at the apex, cream to pale yellow in flower; Lesser Antilles. .... 1 a. var. *adansonii.*

  Pistils acute at the apex, medium yellow in flower; Venezuela, the Guianas, Brazil, Peru. .... 1 c. var. ***klotzschiana.***

1 a. **Monstera adansonii** Schott var. **adansonii**

FIG. 33, MAP 8

Monstera adansonii Schott, Wiener Zeitschrift fur Kunst, Literatur & Mode 4:1028 (1830) based on *Dracontium pertusum* L., Species Plantarum p. 967 (1753) non *Monstera pertusa* (Roxb.) Schott, Wiener Zeitschrift fur Kunst, Lit. & Mode 4:1028 (1830). *Calla dracontium* Meyer, Prim. Flor. Essequebo p. 197 (1818). *Calla pertusa* (L.) Kunth, Synopsis 1:129 (1822). *Monstera pertusa* (L.) deVriese, Hort. Sparm. Bergens p. 40 (1839). TYPE: Martinique, Fort St. Pierre, May: R. P. Charles Plumier, Description des Plantes de l'Amerique, t. LVI, LVII (1693). REPRESENTATIVE COLLECTION: Martinique, Fort St. Pierre, May 1820, *Plee* 687 (BH,P,US).

Monstera jaquinii Schott, Oest. Bot. Woch. **IV**:66 (1854). *Monstera pertusa* (L.) deVriese var. *jacquinii* (Schott) Engler, in Martius, Flora Brasiliensis **III** (2):113 (1878). TYPE: cultivated, Hortus Schoenbrun.: Jacquin, Plant Rar. Hort. Schoenbr. **II**: t. 184, 185 (1797). REPRESENTATIVE COLLECTION: habitat in America meridionalis, Herbarium Jacquin, 1778 (s).

Monstera imrayana Schott, Oest. Bot. Zeit. **9**:40 (1859). TYPE: Dominica, *Imray 330*

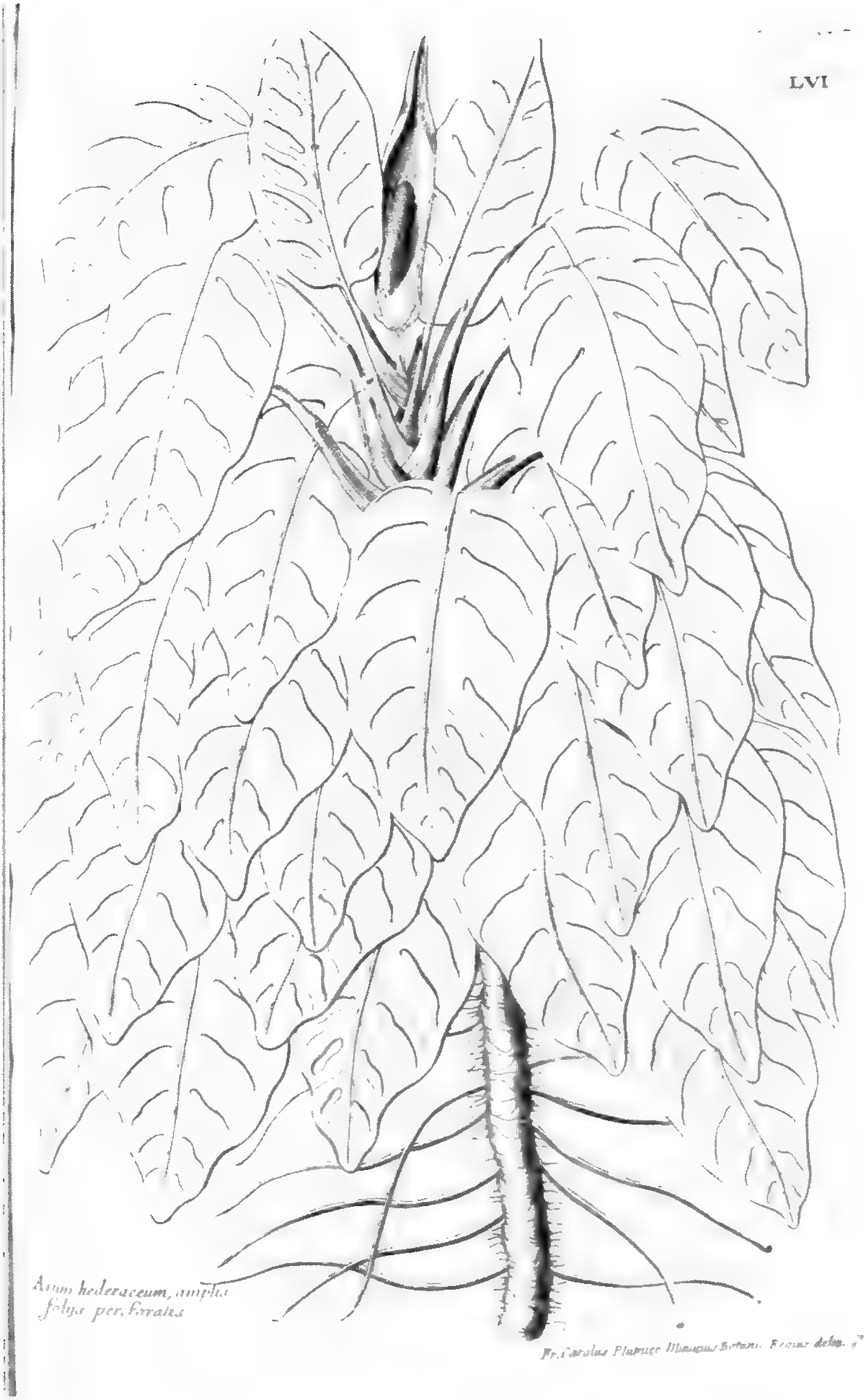


FIG. 33. *Monstera adansonii* var. *adansonii*. From Plumier, Descriptions des Plantes de l'Amerique, pl. LVI. Paris, 1693.

(holotype K; drawing of holotype = Schott Aroideae No. 2269, W, *non vidi,* photo BR,C,GH,NY,S,US).

Monstera macrophylla Schott, Prodr. Syst. Aroid. p. 362 (1868). TYPE: Guadeloupe, *Perotet* (W, destroyed; drawing of holotype = Schott Aroideae No. 2275, W, *non vidi,* photo BH,BR,C,GH,NY,S,US). REPRESENTATIVE COLLECTION: Guadeloupe, 1843, *L'Herminier s.n.* (P).

Juvenile: leaves falcate, the lamina 3–4 times longer than broad. *Adult stem:* 1.5–2.5 cm. thick, internodes 2–3 cm. long. *Petiole:* 25–40 cm. long, the sheath wings persistent. *Lamina:* ovate to elliptic, 14–20 cm. wide, 35–50 cm. long, the length more than twice the width, midrib somewhat falcate, lateral veins mostly arising at an angle less than 60° with the midrib, the leaf base cuneate to bluntly acute; the margin entire; perforations 1 to 5 in number on each side, ovate to elliptic, 2.0–3.5 cm. wide, 5–8 cm. long. *Peduncle:* subterete, about 1.1 cm. thick, 15–22 cm. long. *Spathe:* pale yellow, 16–23 cm. long, twice the length of the spadix or more. *Flowering spadix:* cream to pale yellow, 1.1–1.5 cm. thick, 8–11 cm. long; pistils prismatic, truncate at the apex, 4.0–4.5 mm. long. *Fruiting spadix:* pale yellow, 1.8–2.2 cm. thick, 10–13 cm. long.

ETYMOLOGY. After Michael Adanson (1727–1806), French botanist and author of the name *Monstera.*

COMMON NAMES. Bois de couleuvre, Caracol, Siguini (Guadeloupe).

DISTRIBUTION. Lesser Antilles, Saba to Trinidad.

REPRESENTATIVE SPECIMENS. **Saba:** mountain, 800 m., 16 July 1906, *Boldingh 1811* (U). **St. Kitts:** Buckley Estate, September 1901, *Britton & Cowell 204* (NY). **Antigua:** Wallings, Sept. 1938, *Box 1530* (BM,US). **Guadeloupe:** Basse Terre, Ravine de Belost, 20 m., June 1935, *Stehle 1973* (US); Basse Terre, Dec. 1938, *Quentin 1072* (US); Marne Gommier, 1896, *Duss 3304* (NY,US); Route Gourbeyre, 200 m., Oct. 1937, *Questal 405*(P,US); 1843, *L'Herminier s.n.* (P); Rivières Gourbeyre, 1893, *Duss 3297* (US). **Dominica:** 1843, *McPhail s.n.* (BM); Laiou Valley, June 1888, *Ramage s.n.* (K); Rivière, Sept. 1936, *Stehle 3048* (P); Roseau Valley, 1903, *Lloyd 563* (NY); Hatton Garden Estate, near bridge over St. Mary's River, April 1940, *Hodge & Hodge 3006* (GH); 1903, *Othmer s.n.* (M). **Martinique:** Case Pilote, 1871, *Hahn 1020* (BM,GH,K, P,US); Fort St. Pierre, May 1820, *Plee 687* (BH,P,US); Absalon, 1880, *Duss 522* (NY). **St. Vincent:** damp forest, 500–2000 ft., May–July 1890, *H. H. & G. W. Smith 37* (K); Botanic Gardens, Feb. 1932, *Fairchild 2754* (UC,US). **Tobago:** Mason Hall Bridge, April 1914, *Broadway 4835* (S,US); Castara road, Jan. 1953, *Hunnewell 19920* (GH). **Trinidad:** Mayaro, March 1922, *Bailey 668* (BH).

1 b. **Monstera adansonii** Schott var. **laniata** (Schott) Madison, *comb. nov.*

Tornelia laniata Schott, Oest. Bot. Zeit. 8:179 (1858). *Monstera pertusa* (L.) deVriese var. *laniata* (Schott) Engler, in Martius, Flora Brasiliensis **III** (2):113 (1878). TYPE: Costa Rica, Candelarta, *Orsted 15795* (C; isotype B, *non vidi*).

Heteropsis ovata Miq., Hort. Amstelod. Delect. Sem. (1853). *Monstera ovata* (Miq.) Schott, Oest. Bot. Zeit. 8:387 (1858). TYPE: Surinam, Wildparkstation, cultivated material from this locality given to Koch by Miquel, *Carl Koch s.n.* (holotype B, *non vidi,* fragment of holotype at K).

Monstera holtoniana Schott, Oest. Bot. Zeit. 9:40 (1859). TYPE: Colombia, La Paila, 17 February 1853, *I. F. Holton 217* (holotype K, photo SEL; isotypes PH no. 610479, NY; drawing of holotype = Schott Aroideae no. 2318, W, *non vidi,* photo BR,C,GH,NY,S,SEL,US).

Monstera friedrichsthalli Schott, Oest. Bot. Wochen. 4:65 (1854). TYPE: Nicaragua, Niquinohomo, *Friedrichsthal 1206* (W, destroyed; drawing of holotype = Schott Aroideae No. 2245, W *non vidi,* photo BR,C,GH,NY,S,SEL,US). REPRESENTATIVE COLLECTION: Nicaragua, Dept. Matagalpa, 6–10 km. northeast of Matagalpa on road to El Tuma, 1000 m., 14–16 Jan. 1963, *Williams, Molina & Williams 24033* (F).

Juvenile: leaves ovate, the lamina 1½–2 times longer than wide, entire or perforate with 1–4 elliptic perforations per side. *Adult stem:* elliptic in cross section, 1.5–2.5 cm. across, 1.2–1.6 cm. thick, internodes 2.5–8.0 cm. long. *Petiole:* 20–45 cm. long, the sheath wings neatly deciduous. *Lamina:* ovate to broadly ovate, 15–40 cm. wide, 22–55 cm. long, the length less than twice the width; the base unequal, one side truncate to subcordate, the other side cuneate to acute; primary lateral veins at least on one side arising at an angle greater than 60° with the midrib; perforations absent to numerous in several series, elliptic to elongate, smaller than in the other varieties. *Peduncle:* subterete, 1.0–1.6 cm. thick, 10–18 cm. long. *Spathe:* cream to pale yellow, 12–28 cm. tall, 10–25 cm. around, 1½–2 times longer than the spadix. *Flowering spadix:* pale yellow, 1.4–2.5 cm. thick, 8–13 cm. long; pistils prismatic, truncate at the apex. *Fruiting spadix:* 2.0–3.6 cm. thick, 10–16 cm. long, pale yellow.

COMMON NAMES. Chirrivaca (Costa Rica); Halloquaballa (Arawak, Guyana); Hierba de puerco, Pasmo (Panama); Patquina (Peru); Piñanona (Costa Rica); Sacafrío (Venezuela); Sipó tracuá, Tracuá (Brazil); Ventanillo (Costa Rica, Nicaragua).

DISTRIBUTION. Nicaragua to northeastern Peru, Curacao, Tobago, Venezuela, the Guianas, and Brazil (Amapá and Pará).

REPRESENTATIVE SPECIMENS. **Nicaragua. Jinotega:** Cerro Sialci, 1200–1400 m., July 1947, *Standley 10476* (F). **Zelaya:** vicinity of El Recreo, on Río Mico, 30 m., May 1949, *Standley 19528* (F); vicinity of Rama, 50 m., Sept. 1972, *Madison 716* (GH). **Chinandega:** Ameya, near sea level, June 1923, *Maxon, Harvey & Valentine 7131* (US); vicinity of Chichigalpa, 90 m., July 1947, *Standley 11513* (F). **Managua:** Managua, May 1926, *Chaves 204* (US); Sierra de Managua, 600–900 m., April, *Garnier 768* (US); Casa Colorada & vicinity, 850 m., June 1923, *Maxon, Harvey & Valentine 7370* (US). **Matagalpa:** 6–10 km. northeast of Matagalpa, road to El Tuma, Jan. 1963, *Williams, Molina & Williams 24033* (F). **Granada:** Volcán Mombacho, Feb. 1903, *Baker 2335* (K). **Without locality:** 1853–56, US north Pacific Exploring Expedition, *Wright s.n.* (GH,US). **Costa Rica. Guanacaste:** vicinity of Tilaran, 500–650 m., Jan. 1926, *Standley & Valerio 46587a* (US); vicinity of Santa Rosa, 280–600 m., Sept. 1972, *Madison 721* (CR,GH); vicinity of Cañas, June 1970, *Daubenmire 814* (F); near La Cruz, 200 m., May 1968, *Burger & Stolze 4841* (F); Punta Mala, March 1892, *Tonduz 6807* (CR). **Alajuela:** Zarcero, 5500 ft., Jan. 1938, *Smith H 161* (F); vicinity of Atenas, June 1971, *Gentry 780b* (MO); vicinity of Los Chiles, Río Frío, 30–40 m., Aug. 1949, *Holm & Iltis 780a* (A,BM). **Heredia:** Río Puerto Viejo, 2 km. upstream from confluence with Río Sarapiqui, 100 m., Jan. 1968, *Burger & Stolze 5780* (CR,NY); 10°27′N × 84°07′W, 110 m., May 1973, *Madison 1522* (GH). **Puntarenas:** lower end of road to Monteverde, Jan. 1972, *Wilbur, Almeda & Luteyn 15862* (DUKE); Cabo Blanco Reserve, 9°35′N × 85°56′W, 0–200 m., Dec. 1969, *Burger & Liesner 6614* (F); 8 km. north of Dominical, 10 m., Oct. 1972, *Madison 759* (GH). **San José:** Río Paquita, 1–3 m., Aug. 1936, *Dodge & Goerger 9763* (CR,F,MO); La Verbena, near Alajuelita, 1000 m., Aug. 1894, *Tonduz 8837* (CR,US); San José, 1135 m., April 1890, *Pittier 2839* (CR); basin of El General, 675–900 m., Mar. 1940, *Skutch 4824* (CR,F,US); Las Pavas, 1070 m., Feb. 1924, *Standley 36071* (US); Cerro de las Mercedes, near Desamparados, Sept. 1941, *Alfaro 10* (CR,F); vicinity of El General, 850 m., July 1936, *Skutch 2664* (MICH,US); Las Vueltas, Tucurrique, 635 m., Nov. 1898, *Tonduz 12789* (US). **Cartago:** La Estrella, March 1924, *Standley 39516* (US); Turrialba, July 1965, *Croat 257* (MO). **Panama. Chiriqui:** Quebrada Punta de Piedra, 2 mi. SW of Puerto Armuelles, 0–100 m., Mar. 1973, *Croat 22458* (MO); Puerto Armuelles, 0–75 m., July 1940, *Woodson & Scherry 903* (MO); 16 km. from David on road to Boquete, 400 m., Oct. 1972, *Madison 761* (GH); Guabalá, 50 m., Oct. 1972, *Madison 762* (GH). **Bocas del Toro:** Shepherd Island, Aug. 1964, *McDaniel 5165* (MO); Water Valley, Oct. 1940, *vonWedel 984* (GH, MO,US). **Veraguas:** 5 mi. west of Santa Fé, 800–1200 m., Mar. 1973, *Croat 23053* (MO). **Los Santos:** Guaniquito, 10 mi. north of Tonosi, 100–200 m., July 1970, *Luteyn & Foster 1359* (DUKE); several miles south of Pedasi, July 1967, *Stimson 5303* (DUKE,NY). **Coclé:** 6 mi. north of El Valle, Aug. 1970, *Luteyn & Kennedy 1635* (DUKE); Penonome, 50–1000 ft., Feb.–Mar. 1908, *Williams 571* (NY). **Colon:** Fato, near sea level, July–Aug. 1911, *Pittier 3841* (US); Maria Chiquita on road to Porto Bello, July 1970, *Croat 11359* (MO); near Guasimo, April 1970, *Croat 9986* (MO). **Panama:** Río Pita, 1–3 mi. above Río Maestra, Oct. 1961, *Duke 4748* (BH,GH,NO,US); Perlas Archipelago, San José Island, Fald Hill, April 1945, *Johnston 806* (GH,US); near Arraijan, 15 m., July 1938, *Woodson, Allen & Seibert 1339* (F,GH,MO); Río

Tapia, Dec. 1923, *Standley 28133* (US); 5 mi. west of Chepo, Sept. 1972, *Tyson 6720* (MO). **Canal Zone:** Ancon, 20–80 m., Feb. 1911, *Pittier 3954* (US). **Darien:** Puerto St. Catherine, July 1962, *Dwyer 2299* (MO); 1–4 mi. N of Pucro, June 1967, *Duke 13051* (MO); road from El Real to Pinogana, July 1962, *Duke 5135* (GH,MO, US). **Curacao:** woods of Trinidad, June 1963, *Arnoldo 3025* (US). **Colombia. Atlantico:** region of Baranquilla, Megua, July 1934, *Elias 1217* (F,US); Tubara, 200–250 m., Jan. 1946, *Dugand & Jaramillo 4055* (US). **Magdalena:** Santa Marta, Don Amo Viejo, 2000 ft., June 1899, *Smith 2308* (F,GH,K,MICH,MO,NY,P,PH,US,VT); near Las Nubes, NW slope of Sierra Nevada de Santa Marta, 800 m., Mar. 1973, *Madison 1247* (GH); Parque Tayrona, Canaveral, 45 m., May 1974, *Plowman & Davis 3733* (GH). **Cesar:** Rincon Honda, Aug. 1924, *Allen 258* (F,MO). **Guajira:** Serrania La Macuira, cerro Manzano, 1500–2300 ft., Mar. 1963, *Saravia 2418* (US); 12 km. south of Carraipia, 450 m., July 1944, *Haught 4279* (US). **Cordoba:** near Planeta Rica, 100 m., Nov. 1972, *Madison 787* (GH). **Bolivar:** vicinity of Turbaco, 200–300 m., Nov. 1926, *Killip & Smith 14304* (GH,NY,US). **Chocó:** Río Truando at junction Q. Buche, 40 m., April 1968, *Duke 15752(3)* (US). **Antioquia:** Puerto Berrio, 250 m., May 1949, *Scolnik, Molina & Barkely 19An534* (US); Zaragoza, between Tirana Creek and the hydroelectric plant, 500 m., Feb. 1971, *Soejarto & Villa 2731* (GH); 10 km. W of Venecia, 800 m., Nov. 1972, *Madison 819* (GH). **Cundinamarca:** La Vega, camino a Nocaima, 950–1200 m., Jan. 1942, *Barriga 10651* (US). **El Valle:** Hacienda Valparaiso, Zarzal, 1020 m., July 1939, *Arvelaez & Cuatrecasas 6411* (US); Río Bugalagrande, 1400 m., June 1930, *Dryander 442* (US). **Meta:** Sierrana Macarena, northern end, 600 m., Nov. 1972, *Madison 856* (GH); Río Meta, Cabuyaro, 235 m., Oct. 1938, *Cuatrecasas 3601* (US). **Caqueta:** Morelia, 150 m., Nov. 1941, *von Sneidern s.n.* (S). **Putumayo:** region of Mocoa, 430 m., Dec. 1972, *Madison 874* (GH). **Ecuador. Esmeraldas:** San Lorenzo, Aug. 1967, *Sparre 18076* (S); Hacienda Timbre, April 1967, *Sparre 15446* (S). **Peru. Loreto:** Iquitos and vicinity, July 1967, *Martin, Plowman & Lau-Cam 1629* (ECON); Leticia, Sept. 1929, *Williams 3044* (F). **Venezuela. Zulia:** Dtto. Colon, Caña Dulce, July 1963, *Lescarboura 30* (VEN); El Palmar, 150 m., Aug. 1957, *Medina 910* (VEN). **Lara:** La Miel, Dec. 1966, *Smith V427* (VEN). **Yaracuy:** E of Nirgua, 650 m., Nov. 1967, *Steyermark, Bunting & Wessels-Boer 100329* (VEN). **Miranda:** vicinity of Caucagua, June 1967, *Aristiguieta 2862* (VEN). **Aragua:** Los Cantaños, *Fernandez 110* (VEN). **Anzoátegui:** Río Neveri, 800–1200 m., Mar. 1945, *Steyermark 61388* (F,S). **Monagas:** La Hormiga area, E of Maturin, 14–50 m., Sept. 1955, *Wurdack & Monachina 39402* (NY,S). **Delta Amacura:** between La Margarita and Puerto Miranda, Río Acure, 80–100 m., Nov. 1960, *Steyermark 87816* (NY,VEN). **Apuré:** Reserva Forestal San Camilo, El Nula, 280–300 m., March 1968, *Steyermark, Bunting & Blanco 94966* (VEN). **Bolivar:** Cerro Pichaco, 45 km. N of Tumeremo, 100–300 m., Feb. 1961, *Steyermark 89207* (NY,VEN). **Guyana:** Rupununi River, Sept. 1948, *WB 48* (NY); Waini River, 8°20′N × 59°40′W, April 1923, *De La Cruz 3764* (F,GH,MO,NY,PH,US); Assakatta, 7°45′N × 59°05′W, Sept. 1923, *De La Cruz 4327* (F,GH,MO,NY,PH,US). **Surinam:** lower slopes of Juliana Top, 500–600 m., Aug. 1963, *Irwin et al. 54777* (NY); vicinity of Paramaribo, Peperpot, Jan. 1961, *Kramer & Hekking 2631* (C,K,U); Jagtlust, Aug. 1844, *Focke 830* (U). **French Guiana:** Cayenne, June 1914, *Benoist 21* (P); Iles du Salut, Aug. 1854, *Sagot s.n.* (P); Toukouchipann, 500 m., Aug. 1972, *deGranville 1307* (US). **Brazil. Amapá:** 1°45′N × 50°58′W, Aug. 1962, *Pires & Cavalcante 52495* (MG,NY). **Pará:** Monte Alegre, region of Formosa, Sept. 1953, *Froes 30455* (NY).

1 c. **Monstera adansonii** Schott var. **klotzschiana** (Schott) Madison, *comb. nov.*

Monstera klotzschiana Schott, Oest. Bot. Woch. **4**:419 (1854). *Monstera pertusa* (L.) deVriese var. *klotzschiana* (Schott) Engler, in Martius, Flora Brasiliensis **III** (2):113 (1878). TYPE: Brazil, Rio de Janeiro, *Luschnath s.n.* (holotype B, *non vidi;* isotype LE).

Monstera velloziana Schott, Oest. Bot. Woch. **4**:66 (1854). *Arum pertusum* Vellozo, Flora Fluminense IX, t. 117 (1835). TYPE: Brazil, *Vellozo,* Flora Fluminense IX t. 117 (1835).

Monstera modesta Schott, Genera Aroidiarum: 75 (1858). *Monstera pertusa* (L.) deVriese var. *modesta* (Schott) Engler, in Martius, Flora Brasiliensis **III** (2):113 (1878). TYPE: *Schott,* Genera Aroidiarum t. 75 (1858). In the *Prodr. Syst. Aroid.* (1860) p. 360, Schott amplifies this as "v.v. cult. ex Mexico australis," but this is probably an incorrect location.

Monstera oblongifolia Schott, Prod. Syst. Aroid. p. 369 (1860). TYPE: Brazil, Rio de Janeiro, a cultivated specimen illustrated by Schott Aroideae No. 2305 (W, *non vidi,* photo BR,C,GH,NY,S,US).

Monstera gaudichaudii Schott, Prod. Syst. Aroid. p. 368 (1860). TYPE: Brazil, Rio de Janeiro, 1834, *Gaudichaud 351* (holotype G, *non vidi;* drawing of holotype = Schott Aroideae No. 2268, W, *non vidi;* photo BR,C,GH,NY,S,US; isotypes B, *non vidi,* L,P).

Monstera lanceaefolia Schott, Prod. Syst. Aroid. p. 368 (1860). TYPE: Brazil, Rio de Janeiro, "v.v. cult." the description is the type.

Monstera maximiliana Engler, in Martius, Flora Brasiliensis **III** (2):113 (1878). TYPE: Brazil, Bahia, *Expeditio archiducis Maximiliana* (W, destroyed, the description is now the type).

Monstera brownii Moore, Trans. Linn. Soc. London, 2nd Ser. **IV**:502 (1895). TYPE: Brazil, Mato Grosso, near Santa Cruz, September, *Moore 351* (holotype BM, photo BH,SEL; isotype B, *non vidi,* photo BH,GH,US).

Monstera coriacea Engler, Bot. Jahrb. 37:118 (1905). TYPE: Brazil, Acre, Jurua Miry, August 1901, *Ule 5730* (B, *non vidi,* photo BH,US).

Monstera peckoltii Krause, Engler Bot. Jahrb. 54, Beibl. **118**:124 (1916). TYPE: Brazil, Rio de Janeiro, *Peckolt 37* (B, *non vidi,* photo BH,GH,US).

Juvenile: leaves ovate to elliptic, 2–4 times longer than broad, entire, rarely with 1-2 elliptic perforations. *Adult stem:* internodes short, 1–4 cm. long, sometimes the petiole bases overlapping and hiding the stem. *Petiole:* 25–50 cm. long, the sheath wings persistent. *Lamina:* coriaceous ovate to elliptic, 18–30 cm. wide, 35–65 cm. long, about twice as long as wide; the base cuneate to bluntly acute; primary lateral veins arising at an angle less than 60° with the midrib; perforations 1 to 8 per side in a single series on each side, ovate to narrowly elliptic, 1–2 cm. wide, 5–12 cm. long. *Peduncle:* subterete to flattened, 14–22 cm. long, 1¼–2 times longer than the spadix. *Flowering spadix:* pale to medium yellow, 2.0–2.6 cm. thick, 8–13 cm. long; the pistils turbinate to acuminate at the apex. *Fruiting spadix:* yellow to orange, 3–4 cm. thick, 12–17 cm. long.

ETYMOLOGY. Named for the botanist Johann Friedrich Klotzsch (1805–1860).

COMMON NAMES. Corcamilla, Picatón (Venezuela); Imbe, Palma de S. Sebastião (Brazil).

DISTRIBUTION. Amazonian Peru and Bolivia, southern Venezuela, the Guianas, and Brazil south to Paraná.

REPRESENTATIVE SPECIMENS. **Peru. Loreto:** Mishuyacu, near Iquitos, 100 m., May–June 1930, *Klug 1532* (F). **Bolivia.** Isapuri, 1500 ft., October 1901, *Williams 676* (in part) (NY). **Venezuela. Bolivar:** Cerro Marimarota, Cerro Le Puerta, 100–250 m., Jan. 1956, *Wurdack & Monachina 41385* (F,NY,VEN); Chimanta Massif, near Río Tirica, 1000 m., May 1953, *Steyermark 75581* (F,NY). **Amazonas:** upper Río Yaciba, 120–150 m., Jan. 1954, *Maguire, Wurdack & Bunting 37444* (NY,VEN). **Guyana.** Upper Mazaruni River, Kurupung, Nov. 1922, *Leng 139* (NY); Kaieteur Falls, Potaro River, Oct.–Nov. 1923, *De La Cruz 4485* (NY). **Surinam.** Savanna I, Zanderij, Oct. 1944, *Maguire & Stahel 25505* (F,NY,US,VEN); Emmaketen 800 m., Sept. 1959, *Daniels & Jonker 1153* (U). **French Guiana.** Grand Inini, Saut. Emerillon, Aug. 1970, *deGranville 661* (US). **Brazil. Rio Branco:** Walde des Quellgebietes, von Mniam, Feb. 1910, *Ule 8484* (MG). **Amapá:** Rio Araguari, Serra do Navio, Sept. 1961, *Pires, Rodrigues & Irvine 51214* (NY). **Amazonas:** Rio Livramento, Humayta, Nov. 1934, *Krukoff 6769* (NY); Alto Purus, Ponto Alegre, April 1904, *Huber 4520* (MG); Manaus, km. 3 da Estrada BR–17, Sept. 1955, *Francisco, RB no.* 99990 (RB). **Pará:** BR–22, km. 98, vicinity of Cachoeira, Aug. 1964, *Prance & Silva 58797* (F,GH,MO, NY,S,U,US,W); Belém, Conceição do Aura, May 1952, *Smith 7124* (R,US). **Acre:** Rio

Acre, San Francisco, April 1911, *Ule 9242* (MG); 9°20'S × 69°W, Aug. 1933, *Krukoff 5646* (A,NY). **Ceará:** without locality, *Allemão & deCysneiros 1578* (R); Serra de Baturite, Sept. 1910, *Ule 9002* (L). **Mato Grosso:** near Santa Cruz, *Moore 351* (B,BM, *non vidi*). **Minas Gerais:** without locality, 1816–1821, *Saint-Hilaire 1039* (P). **Bahia:** Rio Preto, 1913, *v. Lutzelburg 361* (M); Rio Sergy, bei S. Bento des Lages, Aug. 1912, *v. Lutzelburg 15102* (M,NY,R). **Rio de Janeiro:** Lidice, July 1969, *Braga 55* (RB); Tres Irmãos, May 1920, *Lampaio 3292* (R). **Guanabara:** Jurujuba, July 1888, *Schwacke 6299* (RB); Sumare, Serra da Carioca, 200–400 m., Nov. 1928, *Smith & Vieira 1297* (F,GH,S,US,). **São Paulo:** Ilha de Sto. Amaro, May 1932, *Hoehne 29667* (NY); Maresias, betw. São Sebastião and Santos, 100 m., July 1967, *Lindeman & de Haas 5626* (US). **Paraná:** Rio do Cedro, 50–100 m., Feb. 1969, *Hatschbach 21184* (C,S,US); Guaratuba, 3 m., Feb. 1952, *Reitz 4372* (US). **Santa Catarina:** S. Francisco do Sul, 100 m., Dec. 1950, *Reitz 3677* (UC).

Synonyms of *Monstera adansonii* Schott of uncertain varietal affinity:

Heteropsis surinamensis Miq., Hort. Amstelod. Delect. Sem. p. 3 (1853).

Monstera surinamensis (Miq.) Schott, Oest. Bot. Zeit. 8:386 (1858). TYPE: Surinam, material cultivated by Miquel, illustrated by Schott Aroideae No. 2326, 2327 (W, *non vidi,* photo BR,GH,NY,S,US).

Monstera fenestrata Schott, Oest. Bot. Woch. 5:290 (1855). TYPE: Venezuela, "Appun. v.v. cult." illustrated by Schott Aroideae No. 2244 (W, *non vidi,* photo BH,BR,C,S).

Monstera milleriana Schott, Oest. Bot. Zeit. 8:386 (1858). TYPE: Surinam, *Hostmann 845* (K).

Monstera crassifolia Schott, Oest. Bot. Zeit. 9:40(1859). TYPE: Venezuela "v.v. cult." illustrated by Schott Aroideae No. 558, 2230, 2233, 2234, 2235 (W, *non vidi,* photo BH,BR,C,GH,NY,S). REPRESENTATIVE COLLECTION: Venezuela, Tovar, 1854–55, *Fendler 1351* (GH,K,NO,NY), determined by Schott.

Monstera seemanii Schott, Oest. Bot. Zeit. 9:40 (1859). TYPE: Taboga, Jan. 1849, *Seeman 1568* (K, isotype BM).

Monstera parkeriana Schott, Oest. Bot. Zeit. 9:41 (1859). TYPE: Guyana, Demerara, *Parker s.n.* (K, photo BH,F,SEL).

Monstera blanchetti Schott, Prodr. Syst. Aroid. p. 367 (1860). TYPE: Brazil, Bahia, *Blanchet s.n.* (holotype G, *non vidi;* drawing of holotype = Schott Aroideae No. 1226, W, *non vidi,* photo BH,BR,C,GH,NY,S,US; possible isotype BM).

Monstera poeppigii Schott, Prodr. Syst. Aroid., p. 365 (1860). TYPE: Peru, Pampayacu, *Poeppig,* illustrated by Schott Aroideae no. 2319; W, *non vidi,* photo SEL.

Monstera ecuadorensis Engler & Krause, Das Pflanzenreich IV 23B:107 (1908). TYPE: Ecuador, in dem Regenwaldern am Fuss der Westcordillere, *Lehman 185* (B, *non vidi,* photo BH,GH,SEL,US).

REPRESENTATIVE SPECIMENS OF UNCERTAIN VARIETAL AFFINITY. **Trinidad.** Coastal hillsides, Maqueripe, March 1920, *Britton, Britton & Hazen 215* (NY,US).**Tobago.** Nov. 1889, *Eggers 5608* (P). **Colombia. Caqueta:** 4 km. south of Florencia, Fan. 1969, *Plowman & Kennedy 2251* (GH). **Peru. Ayacucho:** Río Apurimac Valley, near Kimpitiriki, 400 m., May 1929, *Killip & Smith 22865* (NY,US). **Venezuela. Delta Amacuro:** Río Cuyubini, Sierra Imataca, 100–200 m., Nov. 1960, *Steyermark 87662* (NY,VEN). **Apuré:** Reserva Forestal San Camilo, 280–300 m., March 1968, *Steyermark, Bunting & Blanco 101397* (VEN). **Guyana.** Kanuku Mountains, drainage of Takutu River, 200 m., March 1938, *Smith 3329* (GH,K,NY). **Surinam.** Lucie River, 2–10 km. below confluence of Oost River, 225 m., Sept. 1963, *Irwin et al. 55562* (NY,U). **French Guiana.** Vicinity of Cayenne, July 1921, *Broadway 974* (GH,NY,US). **Brazil. Amazonas:** Serpa, Feb. 1875, *Traill 1132* (P). **Pernambuco:** Tapera, April 1936, *Pickel 4139* (US).

Monstera adansonii was the first species of *Monstera* to be described. Linnaeus named it *Dracontium pertusum* in his Species Plantarum (1753). In 1830 Schott used the generic name *Monstera* Adans. and transferred a number of species previously described in Linnaean genera to it. Among them was *Pothos pertusus* Roxb. which became *Monstera pertusa* (Roxb.) Schott; the epithet *pertusa* was thus preoccupied, and a new name had to be given in *Monstera* for *Dracontium pertusum* L. This nomen novum was *M. adansonii* Schott. Eventually, as generic concepts came to be more clearly defined, *Pothos pertusus* Roxb. was transferred to the genus *Rhaphidophora* Hassk.

Adolf Engler (1878) adopted the name *Monstera pertusa* (L.) deVriese ignoring the fact that this is a later homonym of *M. pertusa* (Roxb.) Schott. The name *M. pertusa* (L.) deVriese thus came to be widely used in floristic and taxonomic works, but it is illegitimate and the correct name for the species is *M. adansonii* Schott.

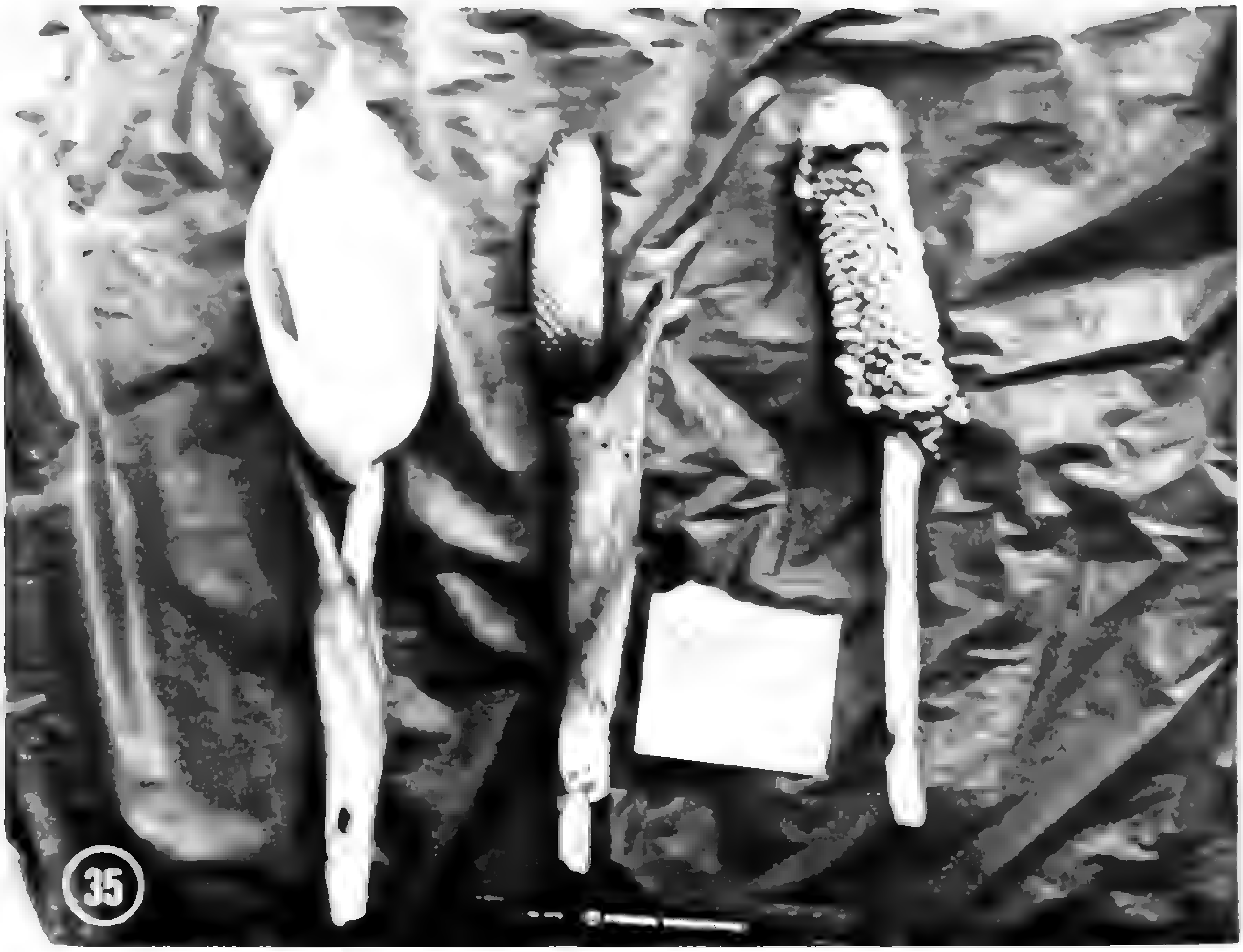
Monstera adansonii is central in a complex of species making up the greater part of section Monstera. These species are extremely variable morphologically and are connected by intermediate forms. Most species of the complex represent morphological and ecological specializations which show connecting links to *M. adansonii;* in addition, transitional forms are found between various combinations of species independent of *M. adansonii.*

Monstera adansonii is the most widespread, most common, most abundant, and most variable species of the complex. Indeed, the range of variation within *M. adansonii* is greater than that existing between some of the other species. Schott, who had very little material to work with, was not presented with the problem of continuous variation between fairly distinct forms; consequently he managed to distinguish 21 species within *M. adansonii* as here delimited. However, a number of his determinations on herbarium specimens are followed by a question mark, suggesting that he recognized some of the problems in his treatment.

Engler and Krause (1908) synonymized most of Schott's species into a "typus polymorphus" *Monstera pertusa* (L.) deVriese, which they subdivided into four varieties. Their varietal division, based largely on the leaf base and the petiole sheath, is rather arbitrary; its artificiality is suggested by the fact that three of the varieties have the same geographical range as the species.

Study of nearly 1,000 specimens of *Monstera adansonii* has led to the recognition of three varieties in the present treatment. These varieties are morphologically and geographically distinct, but in their regions of sympatry they appear to hybridize freely, so that in these areas varietal determinations are difficult or impossible. Thus, much of the material from Venezuela and the Guianas, the main area of sympatry, can only be determined to species.

Monstera adansonii var. *laniata* extends from Nicaragua to northern Peru and across Venezuela and the Guianas to Territoria Amapá in northernmost Brazil. Its most distinctive feature is the very unequal leaf base which is truncate on one side and cuneate to acute on the other. In addition, the petiole sheath is deciduous and the pistils truncate. This



FIGS. [illegible] Monstera [illegible] Madison [illegible] fruiting spadix, and mature fruiting spadix in which most of the berries have already shed the stylar portion (*Madison 871*, [illegible] variety mostly occurs in open situations: along river banks, in clearings, at forest margins, and in disturbed areas. It has a weedy tendency and is found commonly on fenceposts and roadside trees. I have never encountered it in a deep forest.

Monstera adansonii var. *adansonii* is limited in distribution to the Lesser Antilles. It represents a distinct form which apparently originated in northern South America and invaded the Antillean chain along which it has dispersed as far as Saba. It is intermediate between the other two varieties, combining the floral characteristics of var. *laniata* with the vegetative characteristics of var. *klotzschiana*.

Monstera adansonii var. *klotzschiana* is distributed throughout the Amazon Basin as well as along the southeastern coast of Brazil. In this variety, the leaf bases are cuneate to acute on both sides and the petiole sheath is persistent. The pistils are turbinate to acute and the flowers and fruits are medium yellow or orange, in contrast to the cream or pale yellow color found in the other varieties.

2. **Monstera lechleriana** Schott

FIGS. 34–35, MAP 7

Monstera lechleriana Schott, Prodr. Syst. Aroid. p. 366 (1860). TYPE: Peru, Gavan, August 1854, *Lechler 267a* (K, photo BH).

Monstera egregia Schott, Seeman Journ. of Botany **2**:53 (1864). TYPE: cultivated, of Mexican origin. Schott Aroideae No. 2238, 2239 apparently represent type material. (W, *non vidi*, photo C,BR,GH,NY,S,US). REPRESENTATIVE COLLECTION: Mexico, Vera Cruz, 8 km. south of Misantla, Lauraceae Forest, 750 m., 26 December 1971, *Madison 597* (GH).

Monstera maxima Engler and Krause, Das Pflanzenreich IV **23B**:107 (1908). SYNTYPES: Ecuador, Balao, *Eggers 14651* (B, *non vidi*, photo BH,F,GH,US); Ecuador, Gualea, *Sodiro s.n.* (B, *non vidi*, photo BH,SEL). Peru, Prov. Sandia, Chunchusmayo, 900 m., June 1902, *Weberbauer 1182* (B, *non vidi*); Peru, Prov. Huamiles, Río Monzón zwischen Monzón und dem Huallaga, 600–700 m., August 1903, *Weberbauer 3602* (B, *non vidi*).

Monstera standleyana Bunting, Baileya **14**:133 (1966). TYPE: cultivated in conservatory of Cornell University, from material of unknown commercial source. November 1964, *Bunting 1534* (holotype BH no. 100111–6; isotypes K,US no. 2521082–4, UC no. 1327778–9, NY). PARATYPES: Costa Rica, Prov. Cartago, vicinity of Pejivalle, 900 m., 7–8 February 1926, epiphytic vine in wet forest, *P. C. Standley & J. Valerio 47245* (US); Prov. Guanacaste, La Tejona, N of Tilaran, 600–700 m., on tree, acaulescent or with short stems, 25 January 1926, *P. C. Standley & J. Valerio 46054* (US).

Epiphyte on the lower trunks of large trees, to 7 m. tall. *Juvenile:* terrestrial creeper, internodes 1–6 cm. long, leaves exserted and erect, petiole vaginate for $\frac{1}{2}$ to $\frac{5}{6}$ its length, the wings persistent; lamina ovate to lanceolate, cuneate at the base, the tip acute to acuminate, coriaceous, glossy adaxially, pale abaxially, slightly unequal. *Adult stem:* subterete, green, smooth, 4.5–6.0 cm. thick, internodes 4–6 cm. long; leaf scars 3.4 cm. across at widest point, the ends of each scar overlapping for 1–2 cm., the lower part terminating behind the axillary bud of the preceding leaf; axillary bud about 1 cm. wide, half as tall, flat, in a depression on the stem. *Petiole:* smooth, 55–120 cm. long, about equal in length or somewhat shorter than the lamina, widely vaginate nearly to the lamina base, on the largest leaves vaginate to within 15 cm. of the lamina base, the sheath wings persistent, their apices blunt or auriculate; the geniculum curved, (5–)7–10 cm. long. *Lamina:* coriaceous, glossy adaxially, ovate, about twice as long as wide, 75–120 cm. long, 35–70 cm. wide, the base somewhat oblique, broadly truncate to slightly cordate, the tip acute; margin entire, perforations lacking or in a single series on each side of the midrib, the perforation elliptic to narrowly elliptic, 1–8 cm. long; primary lateral veins parallel, (16–)20–40 in number, 1–3 cm. distant, the secondary lateral veins parallel to the primary. *Peduncle:* smooth, green toward the apex, white at the base, flattened, 1.5–2.5 cm. thick, 2–4 cm. wide, (16–)20–40 cm. long. *Spathe:* white or pale yellow, thickly coriaceous, 18–44 cm. tall, 15–34 cm. around, constricted above the spadix, i.e., ⅔ to ¾ of the way up, when fully open only exposing the spadix through a narrow slit 1–6 cm. across; tip acute to acuminate. *Flowering spadix:* cream to pale yellow, stigmatic drop orange, (12–)15–20 cm. long, 2.5–4.5 cm. thick, cylindric or slightly tapering, the flowers near the base sterile, the fertile pistils prismatic, truncate at the apex in Mexican specimens, mostly rounded to acute at the apex in material from Central and South America; pistils 8–11 mm. long, 4 mm. across. *Fruiting spadix:* cream to medium yellow (18–) 20–28 cm. long, 4.5–5.5 cm. thick, the berries 16–20 mm. long, 7–9 mm. across, mostly one-seeded; seeds brown, oblong, 10–13 mm. long, 4–6 mm. wide, 3.4 mm. thick.

ETYMOLOGY. After Wilibald Lechler (1814–1856), collector of the type specimen.

COMMON NAMES. Boa Huasca (Peru); Mamurillo, Pantano, Picaton (Venezuela).

DISTRIBUTION. Mexico, Costa Rica to Peru, and Venezuela, mostly at elevations of 800–2100 meters.

REPRESENTATIVE SPECIMENS. **Mexico. Vera Cruz:** 19 km. E. of Catemaco, Bosque Tropical, March 1965, *Quintero 2243* (MICH,US); Zongolica, El Palmar, Campo Experimental de Hule, Nov. 1944, *Santos 3635* (MICH); km. 45 on road Conejo-Huatusco, Barranca de Santa Maria across from Hda. El Mirador, Sept. 1961, *Moore & Bunting 8858* (BH); 8 km. south of Misantla on road to Jalapa, 750 m., Dec. 1971, *Madison 597* (GH). **Oaxaca:** 12–15 mi. from Valle Nacional on road to Oaxaca, 600–1200 m., Aug. 1972, *Madison 634* (GH). **Costa Rica. Alajuela:** Alto Paloma, 1900 m., Jan. 1970, *Lent 1846* (F); S slope of Volcán Arenal, 550 m., Sept. 1972, *Madison 730* (GH). **Panama. Panama:** Cerro Campana, very top of the peak, 1000 m., May 1973, *Madison 1505* (GH); Cerro Jefe, Jan. 1972, *Gentry, Dwyer & Tyson 3499* (MO). **Colombia. Chocó:** 5°55′N × 76°10′W, 2100 m., Nov. 1972, *Madison 823* (GH). **El Valle:** Timba, 1100 m., March 1937, *von Sneidern 1133* (S). **Putumayo:** 40 km. south of Mocoa, 480 m., Nov. 1972, *Madison 871* (GH). **Ecuador. Pichincha:** road Aloag-Santo Domingo, Tandapi, 1500 m., Jan. 1967, *Sparre 14011* (S). **Canar:** 40 km. east of El Triunfo on road to Cuenca, 610 m., Dec. 1972, *Madison 912* (GH). **Loja:** 49 km. from Loja on road to Zamora, 1550 m., Dec. 1972, *Madison 920* (GH). **Peru. San Martín:** Tocache Nuevo, Fundo Consuelo, 5 km. abajo Puerto Pizana, April 1971, *Schunke V. 4826* (F,US). **Huanuco:** Río Monzón, 10 km. above Tingo Maria, 960 m., Dec. 1972, *Madison 944* (GH); Tingo Maria, Aug. 1940, *Asplund 12937* (S). **Pasco:** Río Paucartambo, 30 km. SW of Oxapampa, 1800 m., Dec. 1972, *Madison 951* (GH). **Cuzco:** Río Marcapato, 20 km. above Quincemil, 780 m., Jan. 1973, *Madison 990* (GH). **Venezuela. Yaracuy:** Cerro La Chapa, N of Nirgua, 1200–1400 m., Nov. 1967, *Steyermark, Bunting & Wessels-Boer 100324* (US,VEN); El Amparo, 7–10 km. N of Salom, 1200–1300 m., Dec. 1972, *Steyermark, Espinoza & Diederichs 106752* (VEN). **Distrito Federál:** between Portachuelo and Peñita, 6–8 mi. below junction of Junquito-Col. Tov. Road, 1300–1500 m., Feb. 1966, *Steyermark 94777* (US,VEN); between Petaquire and the sea, 3500 ft., Feb. 1857, *Fendler 2122* (GH). **Aragua:** Rancho Grande, 1100 m., Aug. 1946, *Pittier 15230* (VEN). **Anzoátegui:** tributaries of Río Neveri, NE of Bergantin, 800–1200 m., March 1945, *Steyermark 61388* (F,NY,VEN). **Sucre:** Peninsula de Paria, Cerro de Humo, 800–1000 m., March 1966, *Steyermark 95099* (US,VEN). **Apuré:** Reserva Forestal San Camilo, Cerro Nulita, 250–280 m., April 1968, *Steyermark, Bunting & Blanco 101860* (VEN).

This species was first collected by Lechler in Peru in 1854. His specimen, consisting of a single leaf, was sent to Hooker and was subsequently seen by Schott who described it as a new species in 1860. A few years later Schott observed a live individual of *Monstera lechleriana* cultivated from a propagule of Mexican origin. He described this as a separate species, *M. egregia*, although he did not clarify its distinctness from *M. lechleriana.*

Engler (1879) treated *Monstera lechleriana* as a synonym of *M. pertusa*, but he was uncertain as to its varietal affinities. He maintained the leading synonym, *M. egregia*, noting its apparent similarity to *M. karwinskyi.* In 1908, Engler and Krause went a step further and reduced *M. egregia* to synonymy under *M. karwinskyi.* These two names have been applied primarily to Mexican material, and somewhat inconsistently so, although the two species in question are quite distinct and are referrable to different sections of the genus. Bunting (1965) finally clarified the situation and revived the name *M. egregia.*

Engler and Krause (1908), having subjugated the names *Monstera lechleriana* and *M. egregia* to synonymy under other species, described a new species, *M. maxima*, to accommodate specimens here considered to be *M. lechleriana.* Their new name was based on material from Ecuador and Peru, and the description is adequate except that the leaves are described as irregularly laciniate, which is presumed to be a result of rough treatment of the specimens.

In 1966 Bunting described *Monstera standleyana* from material cultivated under the names *Philodendron guttiferum* Hort. and *Monstera guttifera* Hort., said to be from Costa Rica. Bunting's type has leaves usually without perforations, as do some collections from the wild, e.g., *Madison* 772. The material called *M. standleyana* also has only 14–18 primary lateral veins, in contrast to the 20–40 typical of *M. lechleriana.* However, in all other respects it conforms to *M. lechleriana.* The evidence does not seem to warrant the recognition of a separate taxon, at least on the basis of the single adult specimen known.

Monstera lechleriana characteristically grows on the lower trunks of large trees below the branches. The internodes are short and the leaves are borne in a tight head of ten to fifteen leaves at the top of the stem, which in the foliated part is completely hidden by the overlapping petiole bases. It is this habit of growth, together with its larger size in every respect, that distinguishes *M. lechleriana* from *M. adansonii.* Ecologically the two species are separated by the fact that *M. lechleriana* generally occurs at higher elevations than *M. adansonii.* In the Mexican material of *M. lechleriana*, the spadix is cream and the pistils are truncate; but collections from Central and South America have a yellowish spadix, and the upper portion of the pistil is conical. In Venezuela some plants intermediate between this species and *M. adansonii* var. *klotzschiana* are found, and the shorter spadices with conical pistils of a yellow color in the Venezuelan specimens suggest introgression from *M. adansonii.*

In Mexico, *Monstera lechleriana* is close to *M. acacoyaguensis*, the latter species being distinguished by its numerous large leaf perforations in several series and by the much narrower spadix on which the ovaries are only half as long as those of *M. lechleriana.* In addition, *M. acacoyaguensis* has longer internodes and the leaves are not borne in a tight head. The specimens examined of *M. lechleriana* are somewhat heterogeneous, and it is possible that several sibling species are included. However, the available material is so inadequate that there is at present no basis for recognizing other taxa.

3. **Monstera acacoyaguensis** Matuda

FIG. 36, MAP 7

Monstera acacoyaguensis Matuda, Madroño **10**:48 (1949). *Monstera magnispatha* Matuda var. *acacoyaguensis* (Matuda) Matuda, Ann. Inst. Biol. Mex. **25**:172 (1954). TYPE: Mexico, Chiapas, shaded woods or forest along the Rio Grande, Acacoyagua, near Escuintla, 100 m., 25 May 1948, *Matuda 17853* (holotype Matuda Herbarium, *non vidi;* isotypes F no. 1330971, MEXU).

Monstera magnispatha Matuda, Rev. Soc. Mex. Hist. Nat. **11**:97 (1950). LECTOTYPE (here designated): Mexico, Chiapas, en orilla de arroyo, bosque alto, Esperanza, Escuintla, 160 m., 28 Sept. 1947, *Matuda 17015* (Matuda Herbarium, *non vidi;* isolectotypes F no. 1273057, 1273060, MEXU,NY). LECTOPARATYPES OF UNCERTAIN AFFINITY: same locality, 11 July 1947, *Matuda 17797* (Matuda Herbarium, *non vidi*); Chiapas, Esperanza, orilla de un arroyo, 5 August 1948, *Matuda 19503* (Matuda Herbarium, *non vidi*). EXCLUDED SYNTYPES: Mexico, Chiapas, bosque claro, Cruz de Piedra, July 1947, *Matuda 17795* (Matuda Herbarium, *non vidi,* MEXU) = *Monstera acuminata* C. Koch; Mexico, Chiapas, Esperanza, 160 m., 11 July 1947, *Matuda 17796* (Matuda Herbarium, *non vidi,* MEXU) = *M. acuminata* C. Koch.

Epiphytic on the lower trunks of large trees to 5 m. tall. *Juvenile:* terrestrial creeper, stem smooth, green, internodes 2–4 cm. long, leaves exserted and erect, petiole vaginate for ⅓ to ⅚ its length, the sheath wings persistent; the petiole about equal in length to the lamina, the lamina subcoriaceous, glossy adaxially, entire, ovate, cuneate at the base, acute at the tip, slightly unequal. *Adult stem:* subterete, smooth, green, 3–5 cm. thick, internodes 3–8 cm. long; leaf scars 1–2 cm. across at the widest point, the ends of each scar overlapping for 0.5–1.0 cm.; axillary buds flat, semicircular, 0.5–1.0 cm. wide, half as tall, in a slight depression on the stem. *Petiole:* smooth, 40–65 cm. long, about ⅔ the length of the lamina, vaginate to the base of the geniculum, the sheath wings persistent, the geniculum 5–6 cm. long. *Lamina:* subcoriaceous, glossy adaxially, paler below, ovate, about twice as long as wide, 60–85 cm. long, 35–45 cm. wide, the base truncate, where it joins the petiole contracted into a cuneate portion about 6 cm. wide and 6 cm. long, the tip acute; margin entire, perforations in one or usually two series on each side of the midrib, the perforations ovate to elliptic, 2–5 cm. wide, 4–12 cm. long, the margin of the perforations often curled adaxially; primary lateral veins parallel, 12–16 in number, 3–5 cm. distant, secondary lateral veins parallel to the primary. *Peduncle:* smooth, terete, about 2 cm. thick, 25–30 cm. long. *Spathe:* light yellow to cream, thickly coriaceous, 25–35 cm. tall, 18–25 cm. around, acuminate, at maturity widest about 5 cm. from the tip. *Flowering spadix:* yellowish, cylindric, not tapered, 18–22 cm. long, 1.5–2.0 cm. thick, the pistils prismatic, truncate at the apex, 4–6 mm. long, 2.5–4.0 mm. across. Fruit and seeds unknown.

ETYMOLOGY. After Acacoyagua, Chiapas, the type locality.

COMMON NAMES. Mimbre, Conte arpón, Bejuco arpón (Mexico, Chiapas).

DISTRIBUTION. Mexico (Western Chiapas), and Belize, at elevations of 0-200 meters.

REPRESENTATIVE SPECIMENS. **Mexico. Chiapas:** Esperanza, Escuintla, 150 m., Dec. 1949, *Matuda 18716* (MEXU,NY,US); El Triunfo, 100 m., Aug. 1974, *Madison 1783* (GH); Acacoyagua, 100 m., 25 May 1948, *Matuda 17853* (F, MEXU). **Guatemala.**

FIG. 36. *Monstera acacoyaguensis:* habit (*Madison 1783*, GH).

Izabal: Modesto Mendez, Río Sarstun, 10 m., June 1970, *Harmon 2562* (MO). **Belize.** Gracie Rock, Sibun River, May 1935, *Gentle 1649* (MICH,MO).

In his original description of this species, Matuda cited five collections. Two of these he later separated as paratypes of *Monstera viridispatha* Matuda, here considered referrable to *M. acuminata* C. Koch. Mixed collections may be involved, as *Matuda 17795* was collected on 25 July

FIG. 37. *Monstera siltepecana:* variation in adult leaf shape, from different individuals (to the same scale).

1947 and the next number, *17796*, on 11 July; *17015* is dated 28 Sept. on some sheets and 15 Sept. on others.

Monstera acacoyaguensis, although known only from a few collections, represents a distinct element in section Monstera. It is most closely allied to *M. lechleriana,* from which it differs in the following respects: the flowering spadix is 1.5–2.0 cm. thick *vs.* 2.5–4.5 cm. thick in *M. lechleriana;* the base of the lamina is contracted into a cuneate portion about 6 cm. long *vs.* the lamina base is abruptly truncate; the lamina having large perforations in several series *vs.* the lamina entire or with a single series of small perforations; and occurrence at elevations of 0–200 m. *vs.* occurrence at elevations mostly above 800 m. in *M. lechleriana. Monstera acacoyaguensis* also has longer internodes and the leaves are not borne in a tight head as in *M. lechleriana. Monstera acacoyaguensis* is readily distinguished from *M. adansonii* by its much longer peduncle, spathe, and spadix.

According to notes on Matuda's specimens, *Monstera acacoyaguensis* occurs in very open situations either along streams or in clearings; I encountered it in Chiapas growing in full sunlight. Matuda (1950) describes the spathes as persisting at maturity for 15–20 days. If this is so, it is distinguished by this feature from other monsteras for which the period of flowering is only two to three days.

4. Monstera siltepecana Matuda

FIGS. 37–38, MAP 12

Monstera siltepecana Matuda, Rev. Soc. Mex. Hist. Nat. **11**:97 (1950). TYPE: Mexico, Chiapas, Orillo de Río Naranjo, Cascada, Siltepec, 1200 m., 11 April 1949, *Matuda 18642* (holotype Matuda Herbarium, *non vidi;* isotype MEXU). PARATYPES: Mexico, Chiapas, Col. San Juan Panama, 1830 m., 23 July 1948, *Matuda 18168* (MEXU); Mexico, Chiapas, Río Naranjo, Cascada, Siltepec, 1600 m., 2 June 1949, *Matuda 18792* (photo BH,MEXU,UC); Mexico, Chiapas, Cascada, Siltepec, 1700 m., 21 April 1950, *Matuda 19657* (MEXU).

Juvenile: terrestrial creeper, internodes 1–3 cm. long, leaves exserted and erect, lamina ovate to widely ovate, cordate at the base, acuminate or acute, membranaceous, unequal with one side 1.1 to 2.0 times wider than the other. *Adult stem:* subterete, smooth, in climbing shoots 2.0–3.5 cm. thick, internodes 4–8 cm. long; in stolons 1–2 cm. thick with internodes 20–30 cm. long; leaf scars narrow, the ends of each scar joining in the back of the stem; axillary buds lanceolate to ovate, acuminate, in a depression in the stem not extended into a sulcus. *Petiole:* 30–45 cm. long, about equal in length to the lamina, vaginate to the geniculum, the wings neatly deciduous, the geniculum 3.0–4.5 cm. long. *Lamina:* subcoriaceous, ovate, unequal, sometimes falcate or the midrib curved, 30–60 cm. long, 20–35 cm. wide, broadly cordate at the base, the tip acuminate; margins entire, perforations mostly numerous in 2 to 4 series on each side of the midrib, round near the midrib, elongate near the margin (rarely perforations only one or two); the primary lateral veins parallel, 8 to 12 in number, secondary lateral veins reticulate. *Peduncle:* smooth, green, terete, 8–20 mm. thick, 5–12 cm. long. *Spathe:* thickly coriaceous, greenish-white outside, rose-colored within, 18–25 cm. long, 15–20 cm. around, cuspidate. *Flowering spadix:* white, cylindric, 10–13 cm. long, 3.0–3.5 cm. thick; flowers near the base sterile, the fertile pistils prismatic; stigma round, sessile. *Fruiting spadix:* deep green, cylindric, 12–17 cm. long, 4.5–6.0

cm. thick, the berries mostly one-seeded; seeds light brown, 6–7 mm. long, 3–5 mm. wide, 2–3 mm. thick.

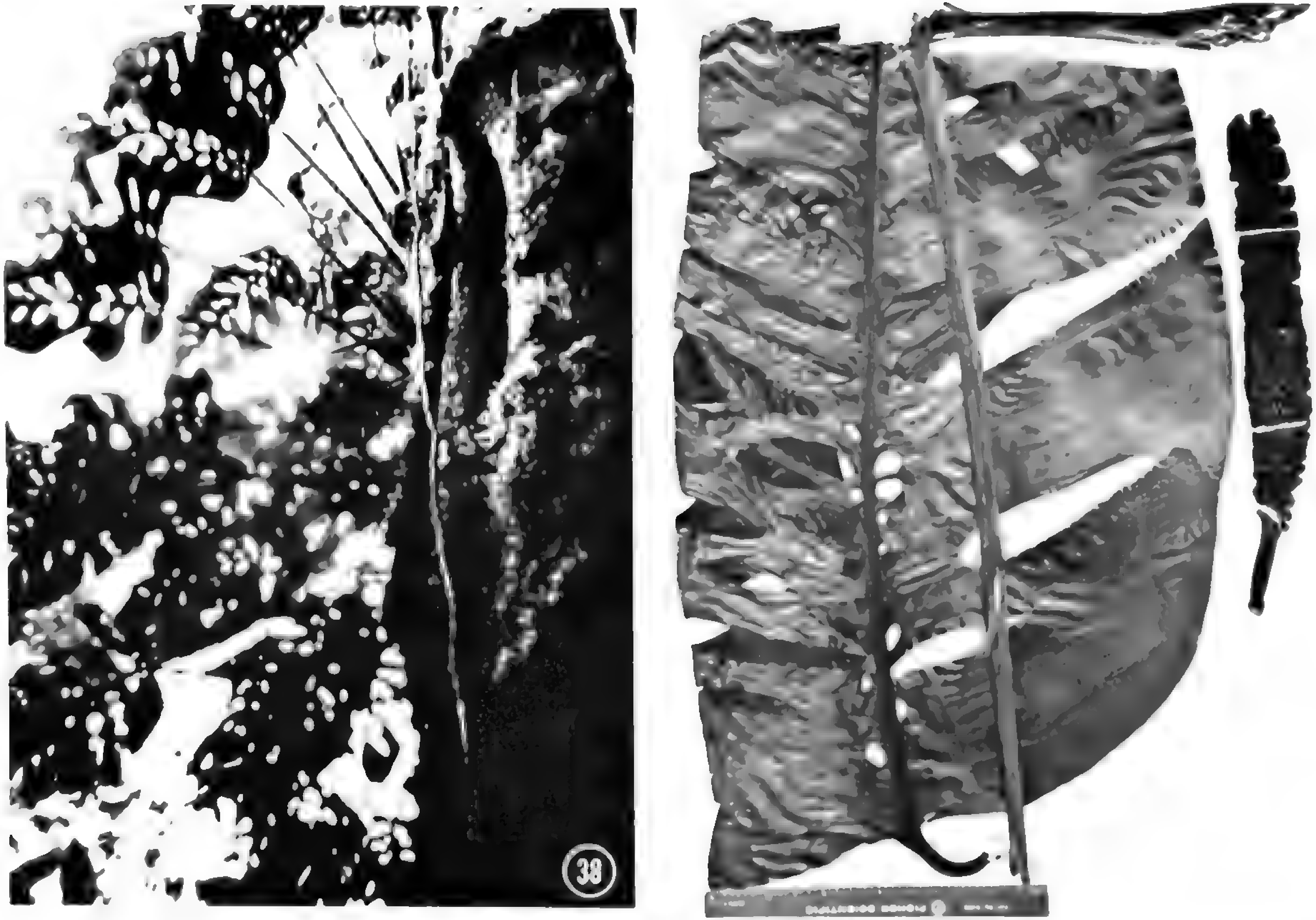
ETYMOLOGY. After Siltepec, Chiapas, the type locality.

COMMON NAMES. Arpón, Hoja de calador (Guatemala); Conte (Mexico); Pico de Zope, Piña anona (El Salvador).

DISTRIBUTION. Mexico (Chiapas and Vera Cruz), Guatemala, El Salvador, and Honduras, in cloud forest at elevations of 1200–2500 meters.

REPRESENTATIVE SPECIMENS. **Mexico. Vera Cruz:** Km. 52 on Jalapa-Misantla road, 1350 m., Dec. 1971, *Madison 598* (GH,MEXU). **Chiapas:** Tenejapa, 8400 ft., Jan. 1966, *Ton 588* (MICH,NY); 52 km. from Huixtla on road to Siltepec, 1850 m., Aug. 1972, *Madison 647* (GH). **Guatemala. Alta Verapaz:** Camche, 6000 ft., April 1889, *J. D. Smith 1538* (US); swamp E of Tactic, 1450 m., April 1941, *Standley 92343* (F). **San Marcos:** between San Rafael Pie de la Cuesta and Palo Gordo, 1800–2400 m., Dec. 1963, *Williams, Molina & Williams 25655* (F,NY); 15 km. from San Marcos on road to Tapachula, 2200 m., Oct. 1974, *Madison 1780* (GH). **Quezaltenango:** between Quebrada Chicharro and Montaña Chicharro, SE facing slopes of Volcán Santa Maria, 1300–1400 m., Jan. 1940, *Steyermark 34358* (F); Los Positos, SW of San Martín Chile Verde, 1500 m., March 1939, *Standley 67904* (F). **Chimaltenango:** between Chimaltenango and San Martin Jilotepeque, 1500–1700 m., Dec. 1940, *Standley 80918* (F); 8 km. S of Acatenango, 2350 m., Sept. 1972, *Madison 673* (GH). **Sacatepequez:** barranco above Dueñas, 1590–1800 m., Jan. 1939, *Standley 63164* (F); Volcán Acatenango, 9000 ft., Feb. 1905, *Kellerman 5253* (US). **Guatemala:** Volcán de Pacaya, 1800–2300 m., Dec. 1940, *Standley 80460* (F). **Baja Verapaz:** region of Patal, 1600 m., March 1939, *Standley 69588* (F). **El Progresso:** slopes SE of Finca Piamonte, 2400–2500 m., Feb. 1942, *Steyermark 43398* (F,NY). **Jalapa:** Volcán Jumay, 1300–2200 m., Dec. 1939, *Steyermark 32362* (F). **Zacapa:** upper Rio Sitio Nuevo, 1500–1800 m., Jan. 1942, *Steyermark 43232* (F,MO,US). **Chiquimula:** Amatillo, 900–1510 m., Oct. 1939, *Steyermark 30527* (F,US). **Escuintla:** Santa Lucia Cotz., Feb. 1927, *Morales 669* (US). **Santa Rosa:** Volcán Jumaytepeque, 6000 ft., Dec. 1892, *Heyde & Lux 4279* (GH,M,NY,US). **El Salvador. Ahuachapan:** Sierra de Apaneca in the region of Finca Colima, Jan. 1922, *Standley 20209* (GH,NY,US). **La Libertad:** Comasagua, Dec. 1922, *Calderon 1358* (GH,US). **Morazan:** Montes de Cacaguatique, 13°46′N × 88°13′W, 1500 m., Dec. 1941, *Tucker 652* (BH,F,K,MICH,NY,PH,UC,US). **Honduras. La Paz:** km. 110 carratera Marcala, 1600 m., April 1956, *Molina 6505* (GH,US). **Distrito Central:** between Cofridia and Rancho Quemada, May 1970, *Barkley & Errazuriz 40313* (GH). **Morazan:** above San Juancito, 1800 m., March 1951, *Williams 17554* (F,GH); Cerro de Uyuca, 1530–1600 m., Feb. 1947, *Standley & Molina 4271* (F).

Monstera siltepecana was first collected in 1889 in Guatemala by John Donnell Smith. The specimen, consisting of a spathe, a flowering spadix, and a leaf, was determined by Engler as *Monstera pertusa* var. *jacquinii*. Apparently Engler considered this material as merely representing a range extension of a polymorphic species already known from southern Central America. In 1922 *M. siltepecana* was collected in El Salvador by Calderon, whose specimen was determined as *M. friedrichsthalii*. This identification was followed by later collectors, and the species became generally known as *M. friedrichsthalii*. In the 1930's and the 1940's Standley and Steyermark made extensive collections of plants in Guatemala, including numerous gatherings of this species. The results of their floristic studies were published in the *Flora of Guatemala* (1958), where they applied the name *M. friedrichsthalii* to this taxon and listed *M. siltepecana* in synonymy. In the meantime, other collections had extended the known range of the species to Mexico and Honduras.



FIGS. 38–39. 38. *Monstera siltepecana*, habit. 39. (right) *Monstera oreophila*, holotype (*Stern, Chambers, Dwyer & Ebinger 1104*, MO).

Apparently the name *Monstera friedrichsthalii* came to be applied to this species in part through a misunderstanding of the type locality. *Monstera friedrichsthalii* Schott is typified by Schott Aroideae No. 2245 based on Friedrichsthal No. 1206, a specimen which was in the herbarium at Vienna, but no longer exists. Schott gave the locality of this collection as Niquimono, Guatemala; however, this is probably not in Guatemala but it does correspond to the present day Niquinohomo in the Departamento of Masaya, Nicaragua. Although superficially resembling *M. siltepecana,* the type of *M. friedrichsthalii* clearly is referrable to *M. adansonii* var. *laniata,* which occurs in Nicaragua and not in Guatemala. Thus, the earliest name for the distinct species occurring in Guatemala is *M. siltepecana* Matuda. In his description of this species, Matuda compares it to *M. pertusa,* from which he distinguished it because of the smaller leaves with numerous perforations and by its occurrence at high elevations. He makes no mention of *M. friedrichsthalii,* of which he was apparently unaware, or else he did not consider it to be closely related.

Monstera siltepecana is a distinctive species. Its outstanding features are the numerous leaf perforations in several series, the reticulate secondary venation, the spathe which is rose-colored within, and the thick, dark green, fruiting spadices. It is most closely allied to *M. oreophila* and *M. adansonii* var. *laniata* of southern Central America.

Monstera siltepecana occurs in cloud forests at elevations of 1200–2500 meters. Characteristically it produces numerous droppers and stolons, and where it is abundant the forest is filled with its climbing and hanging shoots and the ground is criss-crossed with stolons. Because trees in cloud forests are mostly small, *M. siltepecana* often becomes established in trees too weak or too short to allow the individual to grow to maturity; the production of dropper shoots and stolons allows for recovery from this situation.

5. **Monstera oreophila** Madison, *sp. nov.*

FIG. 39, MAP 12

Caudex epiphyticus scandens, 1.5–2.5 cm. crassus, internodiis 2–3 cm. longis. *Foliorum petiolus* lamina paulo longior, 35–55 cm. longus, vagina membranacea marcescens instructus; lamina ovata, 35–50 cm. longa, 17–30 cm. lata, basi late truncata, apice breviter mucronata, integra vel foraminata foraminibus utrinque unserialibus vel biserialibus; nervis lateralibus I. numerosis, patentibus, utrinque 25–50, parallelis, 5–10 mm. inter se remotis; nervis lateralibus II. subparallelis. *Pedunculus* 20–30 cm. longus. *Spatha* salmonea, 15–22 cm. longa. *Spadix fructifer* albus, 15–20 cm. longus, 3–4 cm. crassus, sessilis, cylindricus, obtusus.

TYPE. Panama: Chiriqui, vicinity of Boquete, Finca Collins, 5500 ft., oak-laurel cloud forest, 24 July 1959, *Stern, Chambers, Dwyer & Ebinger 1104* (holotype MO no. 1757942, 1758219; isotypes GH,LE,US no. 2396875).

ETYMOLOGY. From Greek, *oreophilus,* "mountain-loving," referring to the habitat of the species.

COMMON NAME. Comida de Culebras (Costa Rica).

DISTRIBUTION. Costa Rica and Panama, cloud forests, 1600–2500 m. elevation.

REPRESENTATIVE SPECIMENS. **Costa Rica. Alajuela:** road out of Sucre towards Laguna Pozo Verde, 2000 m., Dec. 1974, *Luteyn, Wilbur & Utley 4504* (DUKE).

Heredia: Cerro de Gallito, 1800 m., Nov. 1940, *Leon 326* (CR); vicinity of Vara Blanca, Río Sarapiqui, 1800 m., May 1972, *Luteyn 3026* (DUKE). **San José:** vicinity of Santa Maria de Dota, 1500–1800 m., Dec. 1925, *Standley 41688* (US); Forêts de Santa Rosa du Copey, 1800 m., Feb. 1898, *Tonduz 11932* (CR,US); Asseri, Feb. 1946, *Echeverria 237* (CR). **Cartago:** near Maria del Socorro Power Plant, 5 km. NW of Tres Ríos, 1700 m., May 1967, *Lent 1006* (CR,F). **Panama. Chiriqui:** SW slopes of Cerro Horqueta, 6 km. NW of Boquete, 1700–1800 m., Dec. 1971, *Wilbur, Almeda & Luteyn 15459* (DUKE); Casita Alta, Volcán de Chiriqui, 1500–2000 m., June-July 1938, *Woodson, Allen & Seibert 985* (GH,MO); Audubon Camp, Cerro Punta, 5400 ft., *Tyson 6601* (MO); between Bajo Grande and Paso de Respingo, 2100–2400 m., Dec. 1971, *Wilbur, Almeda & Utley 15172* (DUKE); Cerro Horqueta, 7000 ft., July 1966, *Blum & Dwyer 2673* (MO). **Coclé:** hills north of El Valle, Jan. 1942, *Allen 2950* (F); Cerro Pilon, April 1971, *Croat 14337* (MO).

Monstera oreophila is one of the three Central American species of section Monstera inhabiting cloud forests at elevations of 1600–2500 meters. Included are *M. siltepecana* and *M. epipremoides* to which it is closely related. Like *M. siltepecana,* it has a salmon- or rose-colored spathe and deciduous petiole sheath wings; it differs in having a peduncle twice as long, yellowish white instead of dark green fruit and leaves with numerous parallel veins rather than a few reticulated ones. *Monstera epipremnoides* is separated by its pale yellow spathe and leaves regularly pinnatifid rather than with entire margins. The most distinctive feature of *M. oreophila* is the large number (25–50) of parallel primary lateral veins only 5–10 mm. apart.

Monstera oreophila was recognized as new by H. H. Bartlett, who annotated specimens but did not publish a name.

6. **Monstera membranacea** Madison, *sp. nov.*

FIG. 40, MAP 15

Caudex epiphyticus scandens, internodiis teretibus, 1–2 cm. longis, 1–2 cm. crassis. *Foliorum stirpis juvenculae* lamina exserta, ovata, basi cordata, apice acuminata, foraminibus destituta. *Foliorum stirpis adultae petiolus* 40–50 cm. longus, lamina paulo longior, ad $\frac{2}{3}$ vel $\frac{5}{6}$ longitudinus usque vagina lata persistente instructus; *geniculum* 3–4 cm. logum; *lamina* membranacea, ovata, basi cordata, apice breviter, mucronata, 40–50 cm. longa, 25–32 cm. lata, integra vel irregulariter pinnatifida, foraminibus rotundis uniserialibus juxta costam instructa, nervis lateralibus I. utrinque 6–9, subparallelis, nervis lateralibus II. inter se reticulatis. *Pedunculus* 13–17 cm. longus, cicatricibus spathae 3–8 cm. decurrens notati. *Spadix fructifer* 10–18 cm. longus, 2.5–3.5 cm. crassus. *Baccae virides,* partibus supernis deciduis semina in pulpa aurantiaca praebentibus. *Semina* globosa, 6 mm. longa.

TYPE. Costa Rica: Prov. San José, western slope of Cerro Tufares, 800 m., 2 October 1972, deep woods, *Madison 738* (holotype GH; isotypes to be distributed CR,MO).

ETYMOLOGY. Latin *membranacea,* "membranaceous," referring to the very thin texture of the lamina, unique in the genus.

DISTRIBUTION. Costa Rica, wet forests, 50–800 meters.

REPRESENTATIVE SPECIMENS. **Costa Rica. Alajuela:** vicinity of Capulin, on the Río Grande de Tarcoles, 80 m., April 1924, *Standley 40148* (US). **Puntarenas:** 8°42'N × 83°31'W, 5 km. W of Rincon de Osa, 50–200 m., Jan. 1970, *Burger & Liesner 7212* (F); same locality, March 1973, *Burger & Gentry 8865* (F); Curridabat, April 1932, *Kupper 951* (M). **San José:** road from Santiago to Parrita, 600 m., Sept. 1967, *Lent 1319* (CR,NY,US).

This is a very distinctive, easily recognized species. It possesses at

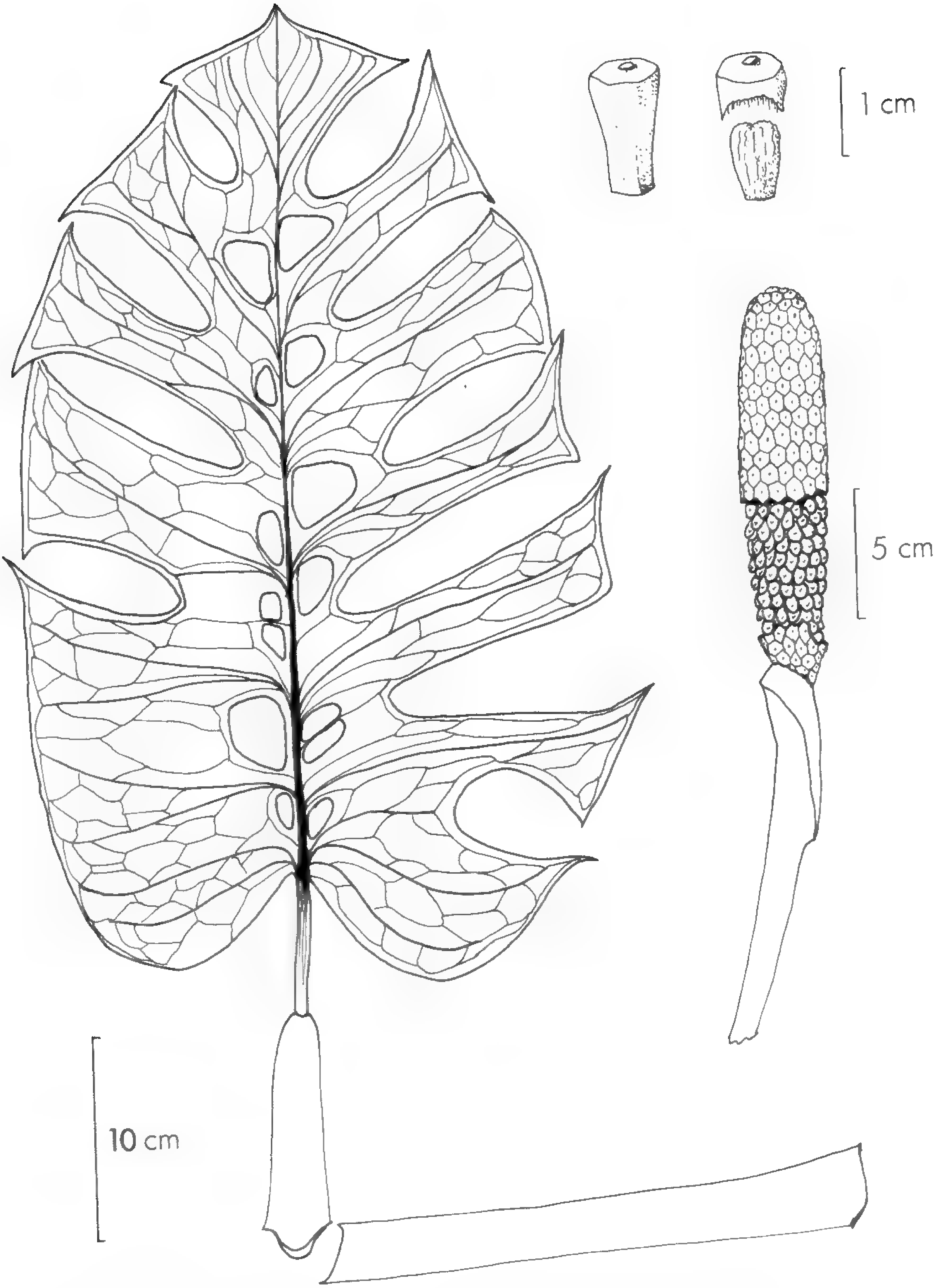


FIG. 40. *Monstera membranacea:* with a fruiting spadix, showing the abscission of the upper portion of berries to reveal the seeds in a colored pulp (based on *Madison 738*, GH).

least four characters unique in the genus: the lamina is very thin and membranaceous, somewhat bullate in live material; the spathe is decurrent on the peduncle for 3–8 cm.; the fruit is green with the stylar portion deciduous to expose the seeds in a bright orange pulp; and the seeds are spherical, with the S-shaped raphe forming a bump on the surface.

The juvenile of *Monstera membranacea* is similar to that of *M. siltepecana,* but many features of the adults separate the two species. Other than this, *M. membranacea* does not appear to be closely allied to any other species, although it clearly belongs in section Monstera.

7. **Monstera dilacerata** (Koch & Sello) Koch

FIGS. 41–42, MAP 2

Monstera dilacerata (Koch & Sello) Koch, Ind. Sem. Hort. Bot. Berol. App. 5 (1855). *Scindapsus dilaceratus* Koch & Sello, Ind. Sem. Hort. Bot. Berol. (1853). *Tornelia dilacerata* (Koch & Sello) Schott, Prodr. Syst. Aroid. p. 356 (1860). TYPE: cultivated, Berlin, *Carl Koch s.n.* (B, *non vidi,* photo NY,US).

Monstera pinnatipartita Schott, Oest. Bot. Woch. 7:197 (1857). TYPE: Venezuela, Caracas, *Reichenbach f. s.n.* (location unknown, *non vidi*).

Monstera peruviana Engler, Bot. Jahrb. 37:117 (1905). TYPE: Peru, Dept. Huanuco, Prov. Huamalies, in Ufergeholzen am Monzon, 1000 m., August 1903, *Weberbauer 3575* (B, *non vidi,* BH, photo GH,SEL,US).

Monstera longipedunculata Matuda, Soc. Bot. de Mexico, Bol. 14:22 (1952). TYPE: Belize, Stann Creek District, Middlesex, epiphyte in high ridge on hilltop, 25 May 1939, *Percy H. Gentle 2796* (MICH).

Tornelia dissecta Schott, Oest. Bot. Zeit. 8:179 (1858). TYPE: Costa Rica, Volcán de Turrialba, *Herb. Wendland* (location unknown, drawing of holotype = Schott Aroideae No. 2237, W, *non vidi,* BR, photo C,GH,NY,S,US).

Epiphyte to 10 m. tall, the leaves borne in a cluster at the top of the stem. *Juvenile:* terrestrial creeper, internodes 1–6 cm. long, leaves exserted and erect, petiole vaginate for ½ to ⅝ its length, the sheath wings persistent; lamina ovate to lanceolate, 3–5 times longer than broad, falcate, coriaceous, the base acute, the tip acute, glossy adaxially, slightly unequal; earliest leaves entire, rarely followed by several leaves with 1–4 perforations before the elaboration of pinnatifid leaves, more commonly going from entire to pinnatifid leaves without bearing perforate leaves. *Adult stem:* elliptic in cross section, green or brown, smooth to slightly papillose, 1.5–3.0 cm. thick, 2.0–4.0 cm. across, the internodes 1.0–3.5 cm. long; the leaves borne in a cluster at the apex of the stem, leaf scars shallow, less than 2.0 cm. wide at the widest point, encircling the stem with the ends of each scar overlapping for 0.5–1.0 cm., the lower part terminating behind the axillary bud of the preceding leaf; axillary bud 6–8 mm. wide, about half as tall, in a depression on the stem. *Petiole:* smooth, 35–75 cm. long, about equal in length to or somewhat shorter than the lamina, vaginate nearly to the lamina base or on the largest leaves to within 7 cm. of the lamina base, the wings persistent; the geniculum 3–5 cm. long. *Lamina:* coriaceous, glossy adaxially, ovate, about twice as long as wide, 40–70 cm. long, 20–40 cm. wide, pinnatifid, the pinnae 4–12 in number on each side, with 1–4 primary lateral veins per pinna, the total number of primary lateral veins 10–20, arising at an angle of about 80° with the midrib near the leaf base, arising at an angle of 30–60° above the base (rarely 60–80°), the pinnae acuminate; the base of the lamina acute to truncate, unequal, the apex acuminate. *Peduncle:* smooth, green toward the apex, white at the base, elliptic in cross section, 1.0–1.6 cm. thick, 1.3–2.5 cm. across, 12–27 cm. long, at least 1 cm. longer than the spadix. *Spathe:* white, 15–25 cm. tall, constricted 5–8 cm. below the apex, acuminate, when fully open the margins 4–8 cm. distant. *Flowering spadix:* white, 1.8–2.0 cm. thick, 7–16 cm. long, cylindric or slightly tapering, the flowers near the base sterile, the fertile pistils prismatic, truncate at the apex. *Fruiting* *spadix:* green, becoming pale yellow at maturity, 10–18 cm. long, 3.5–4.5 cm. thick, berries about 1 cm. across. *Seeds:* brown, 8–10 mm. long, 4–5 mm. wide, 3–4 mm. thick.

ETYMOLOGY. Latin *dilacerata,* "cut" or "torn," referring to the cut or pinnatifid condition of the leaf lamina.

COMMON NAMES. Bejuco de murcielago (Panama); Campanillia (Honduras).

DISTRIBUTION. Guatemala and Belize to Peru, Venezuela, and Amazonian Brazil.

REPRESENTATIVE SPECIMENS. **Guatemala. Alta Verapaz:** 6–8 miles NW of Cubilguitz, 210–250 m., March 1942, *Steyermark 45022* (F,MO). **Belize:** Stann Creek District, Middlesex, May 1939, *Gentle 2796* (MICH). **Honduras. Cortes:** Nacimiento del Río Lindo, 600 m., April 1951, *Williams & Molina 18267* (F). **Atlantida:** Lancetilla Valley, near Tela, 20–600 m., Dec. 1927–March 1928, *Standley 54465* (F,US). **Nicaragua. Zelaya:** vicinity of Rama, 50–100 m., Sept. 1972, *Madison 718* (GH). **Costa Rica. Guanacaste:** near Tilaran, El Silencio, 750 m., Jan. 1926, *Standley & Valerio 44814* (US). **Alajuela:** 5 mi. from La Fortuna on road to Chachagua, 250 m., Sept. 1972, *Madison 726* (GH). **Puntarenas:** Forêts de Santo Domingo de Golfo Dulce, March 1890, *Tonduz 9896* (CR,US). **San José:** Candelarta, 800 m., Oct. 1972, *Madison 746* (CR, GH). **Cartago:** vicinity of Santiago, 1050 m., April 1906, *Maxon 97* (NY). **Limón:** Zent, 50–100 m., Oct. 1972, *Madison 753* (GH). **Panama. Chiriqui:** Burica Peninsula, San Bartolo Limite, 400–500 m., Feb. 1973, *Liesner 204a* (MO). **Coclé:** N rim of El Valle de Anton, near Cerro Turega, 650–700 m., June 1940, *Woodson & Schery 185* (MO). **Panama:** 1 mile below Cerro Azul, 900–1000 m., June 1972, *Luteyn 3212* (DUKE). **Canal Zone:** Barro Colorado Island, Feb. 1969, *Croat 7906* (MO,US). **San Blas:** 2–5 miles S of Mandinga Airport, Oct. 1967, *Duke 14820* (US). **Darien:** Río Balsa between Nanene and Guayabo, Nov. 1967, *Duke & Nickerson 14956* (US). **Colombia. Magdalena:** NW slope of Sierra Nevada de Santa Marta, near Las Nubes, 800 m., March 1973, *Madison 1246* (GH). **Bolivar:** Quimari, 500 m., March 1949, *von Sneidern 5721* (S); Torrecilla, near Turbaco, 150–300 m., Nov. 1926, *Killip & Smith 14417* (GH). **Meta:** 2°77'N × 73°35'W, 300 m., March 1973, *Madison 1213* (GH). **Huila:** La Jagua, Sept. 1924, *Allen 587* (MO). **Nariño:** S end of Gorgona Island, near sea level, Feb. 1939, *Killip & Garcia 33110* (US). **Caqueta:** 20 km. S of Montañita, 300 m., Feb. 1973, *Madison 1184* (GH). **Ecuador. Esmeraldas:** Río San Antonio, Finca El Horizonte, Aug. 1967, *Sparre 18298* (S). **Pichincha:** road from Santo Domingo de los Colorados to Quevedo, Km. 38, 500 m., Oct. 1971, *Dodson & Thien 1131* (MO). **Guayas:** vicinity of Guayaquil, Cerro Azul, Sept. 1955, *Asplund 17592* (S). **Los Ríos:** Hacienda Clementina, between Babahoyo & Montalve, 20 m., Feb. 1967, *Sparre 14555* (S). **Peru. Loreto:** Prov. Maynas, Dtto. Alto Nanay, NW of Santa Maria de Nanay, 130 m., March 1968, *Schunke 2464* (F,US). **Huanuco:** Río Monzón, 10 km. above Tingo Maria, Dec. 1972, *Madison 945* (GH). **Venezuela. Zulia:** Sierra de Perija, SW of Machiques, 550 m., Aug. 1967, *Steyermark & Fernandez 99823* (NY,VEN). **Miranda:** 5.5 km. W of Aricagua, 50 m., March 1973, *Steyermark & Espinoza 106897* (VEN). **Brazil. Amazonas:** Rio Purus–Rio Itaxi, Rio Curuquete, 30 km. above mouth of Rio Coti, July 1971, *Prance et al., 14458* (NY,US). **Acre:** 15 km. below Tarauaca, Sept. 1968, *Prance, Ramos & Farias 7437* (NY).

As with many species of *Monstera,* the type of *M. dilacerata* is an inferior specimen consisting of a few leaves from an immature cultivated plant of uncertain geographic origin. Engler and Krause (1908) applied the name to later unambiguous collections (e.g., *Tonduz 13320*) and it has thus come to be widely used as in its present interpretation.

The Peruvian material of this species generally has only 4–6 pinnae per side, whereas Central American *Monstera dilacerata* has 7–12 pinnae; this has been the basis for the separation of *M. peruviana.* However, material from the two areas agree in all other respects and as the extremes of pinna condition are connected by many intermediates there appears

Figs. 41–42. *Monstera dilacerata:* 41. habit (*Madison 1184,* GH); 42. flowering shoot with overlapping leaf bases, a juvenile shoot to the right (*Madison 1246,* GH).

to be little or no basis for maintaining *M. peruviana* as a separate taxon.

The lengths of the peduncle and the spadix are quite variable in *Monstera dilacerata,* the former ranging from 12–27 cm. However, these characters are quite variable, even within an individual plant, and appear to have no taxonomic significance.

Monstera dilacerata is most easily recognized by its regularly pinnatifid leaves borne in a tight head at the apex of the stem. It occurs either in dark forests or exposed situations. It is readily distinguished from *M. tenuis* and *M. spruceana* by the exserted juvenile leaves, the peduncle exceeding the flowering spadix, the leaves borne in a tight head, and the petiole nearly equaling the lamina. In addition, these two other species have pinnae arising nearly at right angles to the costa, whereas in *M. dilacerata* the pinnae generally arise at an angle of 30–70°.

Monstera subpinnata is distinguished from *M. dilacerata* by the pinnae being constricted at the base and arising at a wide angle, and by the pistil that is prolonged into a conical, rather than truncate, style.

8. **Monstera subpinnata** (Schott) Engler

FIG. 43, MAP 5

Monstera subpinnata (Schott) Engler, D. C. Monog. Phan. **2**:267 (1879). *Tornelia subpinnata* Schott, Prodr. Syst. Aroid. p. 357 (1860). TYPE: Peru, Pompayacu, *Poeppig 1557* (W, destroyed; isotype P, photo BH,US).

Monstera uleana Engler, Bot. Jahrb. **37**:118 (1905). TYPE: Peru, Pampas de Ponasa, 1100 m., *E. Ule 3p* (B, *non vidi,* photo BH,GH,NY,US).

Monstera latiloba Krause, Notizbl. Bot. Gart. Berlin **11**:615 (1932). LECTOTYPE (here designated): Peru, Loreto, Balsapuerto (Lower Rio Huallaga Basin), 150–350 m., dense forest. Epiphyte, spike orange, 28–30 August 1929, *E. P. Killip & A. C. Smith 28421* (B, *non vidi,* photo BH; isolectotypes NY,US no. 1462005, 1462006). LECTOPARATYPE: same locality and date, *E. P. Killip & A. C. Smith 28620* (B, *non vidi,* NY,US no. 1462152).

Scandent epiphyte to 12 m. tall. *Juvenile:* unknown. *Adult stem:* 1.5–2.5 cm. thick, internodes 3–8 cm. long, covered by a thick, light brown cuticle which flakes off in dried material. *Petiole:* 25–38 cm. long, about equaling the lamina, vaginate to within 5 cm. of the blade base, the sheath wings deciduous. *Lamina:* 25–40 cm. long, 18–30 cm. wide, deeply pinnatifid, the pinnae 3–12 in number per side, usually contracted into a narrowly cuneate portion at the base, rarely the pinnae 4–7 cm. wide and then narrowed to 2–4 cm. wide at the base, acuminate at the tip, the terminal portion of the lamina about equaling in size and shape the lateral pinnae; primary lateral veins 8–14 in number, the secondary lateral veins parallel to the primary, arising at an angle of 70–90° with the costa. *Peduncle:* terete, 5–10 mm. thick, 8–12 cm. long, equaling or somewhat shorter than the flowering spadix. *Spathe:* white, cream, or yellowish-pink, 12–18 cm. tall. *Flowering spadix:* pale yellow to yellow, 8-12 cm. long, 1.5–2.0 cm. thick, cylindric or slightly tapering, the pistils prolonged into a pronounced conical or acute style 2–4 mm. long. *Fruiting spadix:* green, becoming yellow or orange at maturity, 12–17 cm. long, 2.0–3.5 cm. thick; seeds about 7 mm. long, 5.5 mm. wide, 3 mm. thick.

ETYMOLOGY. The epithet refers to the pinnatifid condition of the lamina.

COMMON NAMES. Costilla de Adan, katipas, magkamak (Peru).

DISTRIBUTION. Ecuador, Peru and Bolivia, 300–1100 m., elevation.

REPRESENTATIVE SPECIMENS. **Ecuador. Napo-Pastaza:** Mera, 1100 m. 21 Nov. 1955, *Asplund 18540* (S); Mera, March 1940, *Lugo 155* (S). **Morona-Santiago:** Gualaquiza, Mision Bomboiza, 700–800 m., Sept. 1967, *Sparre 19081* (S). **Zamora-Chinchipe:**

5 km. N of Cumbaraza, 900 m., April 1974, *Harling & Anderson 13788* (GB). **Peru. Amazonas:** Yuwientsa, 1700–2000 ft., March 1973, *Ancuash 97* (MO); Río Cenepa, 800–900 ft., December 1972, *Berlin 665* (MO). **Loreto:** Balsapuerto, 150–350 m., Aug. 1929, *Killip & Smith 28241* (B,NY,US); Yurimaguas, 155–210 m., June 1929, *Williams 4694* (F,NY,US). **San Martin:** Prov. Mariscal Caceres, Dtto. Tocache Nuevo, Jan. 1970, *Schunke V. 3724* (F); Alto Río Huallaga, 360–900 m., Dec. 1929, *Williams 6582* (F,US). **Junin:** Río Pinedo, N of La Merced, 700–900 m., May 1929, *Killip & Smith 23639* (NY,US). **Ayacucho:** Río Apurimac Valley, near Kimpitiriki, 400 m., May 1929, *Killip & Smith 22949* (NY,US). **Bolivia. La Paz:** San Buenaventura, 1500 ft., Nov. 1921, *Cardenas 1853* (NY,US).

Monstera subpinnata inhabits the forested western slopes of the Andes.

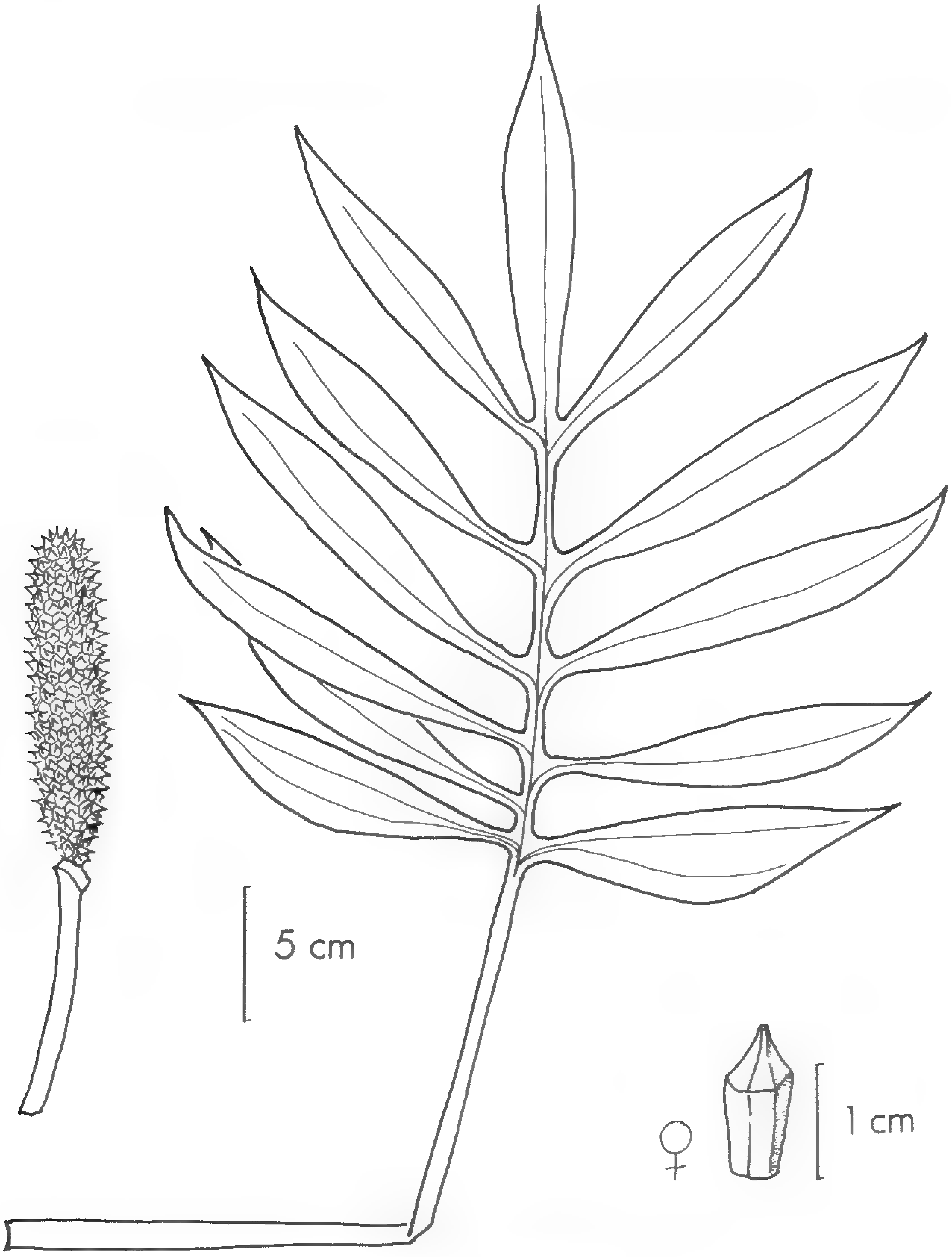


FIG. 43. *Monstera subpinnata:* with the spiny spadix characteristic of the species.

It is distinct among the pinnatifid monsteras by having the pinnae constricted into a narrowly cuneate portion at the base. In a few specimens the pinnae are 4–7 cm. wide rather than the usual 1–3 cm., and though narrowing to 2–4 cm. wide at the base, they are not narrowly cuneate. Plants with the wider pinnae have been separated previously as *M. latiloba,* but they seem to represent only a slight and unimportant variation within *M. subpinnata,* with which they agree in other respects. An additional diagnostic feature of *M. subpinnata* is the prolongation of the pistil into an attenuate conical style. This allows for ready identification of both living and dried material.

9. **Monstera gracilis** Engler

FIG. 44, MAP 5

Monstera gracilis Engler, D. C. Monog. Phan. **II**:258 (1879). TYPE: Colombia, Meta, Villavicentia, Llano de St. Martin, *Karsten* (W, destroyed, the description is now the type). REPRESENTATIVE COLLECTION: Colombia, Meta, 20 km. southeast of Villavicencio, 500 m., 17 March 1939, *E. P. Killip 34288* (F,US).

Slender root-climbing epiphyte, 2–3 m. tall. *Juvenile:* terrestrial creeper, the leaves exserted and erect, the lamina ovate, acute at the apex, membranaceous, perforate even among the earliest leaves. *Adult stem:* subterete, smooth, green, 0.5–1.0 cm. thick, the internodes 1–3 cm. long. *Petiole:* 18–35 cm. long, slightly shorter than the lamina, vaginate to the base of the geniculum, the sheath wings deciduous, the geniculum 1.0–2.5 cm. long. *Lamina:* ovate, 20–30 cm. wide, 25–38 cm. long, membranaceous, truncate to broadly acute at the base, the apex acute; perforate and pinnatifid or pinnatifid only, the perforations small and near the midrib, the pinnae irregularly shaped, 4–10 per side in number, mostly long acuminate at the apex; primary lateral veins 1–2 per pinna, 8–12 in number per side, arising at an angle of 70–90° with the midrib, secondary lateral veins parallel to the primary. *Peduncle:* slender, 5–8 mm. thick, 8–15 cm. long, to 18 cm. long in fruit. *Spathe:* cream to pale yellow, 5–8 cm. tall. *Flowering spadix:* pale yellow, 4–6 cm. long, 1.0–1.2 cm. thick, the pistils truncate, the upper portion of the pistil containing numerous trichosclereids. *Fruiting spadix:* green, becoming yellow at maturity, 6–8 cm. long, 1.5–2.0 cm. thick, the berries prismatic.

ETYMOLOGY. Latin *gracilis,* "thin" or "slender," in reference to the diminutive stature of the plant and its parts.

DISTRIBUTION. Colombia, Meta to Putumayo.

REPRESENTATIVE SPECIMENS. **Colombia. Meta:** 20 km. SE of Villavicencio, 500 m., March 1939, *Killip 34288* (F,US); Villavicencio, 450 m., Aug. 1917, *Pennell 1398* (NY); Sierra de la Macarena, North Ridge, 1400 m., Dec. 1949, *Philipson & Idrobo 1989* (BM,US); Río Guapaya, 500 m., Jan. 1950, *Philipson, Idrobo & Jaramillo 2198* (BM); Llanos de San Martín, 450 m., Nov. 1972, *Madison 843* (GH). **Vaupes:** Río Inirida, 70°50′W, near Santa Rosa, 220 m., Jan. 1953, *Fernandez 1966* (US). **Caqueta:** Montañita, July 1926, *Juzepczuk 6027* (LE). **Putumayo:** Puerto Porvenir, Río Putumayo, 230–250 m., Nov. 1940, *Cuatrecasas 10664* (US).

Monstera gracilis is a rare species confined to a limited geographic area in eastern Colombia, and is known from only a few collections. The population of this species which I observed consisted of half a dozen individuals growing in a riparian forest in the llanos. None climbed above 2 m. without the terminal shoot converting to a stolon and returning to the ground; apparently this is not a high-climbing species, but none of the other collections give any data on this point.

Monstera gracilia differs from *M. dilacerata* in having a membranaceous (*vs.* coriaceous) lamina, deciduous (*vs.* persistent) petiole sheath wings, and much smaller spadices and slenderer stems. It is distinguished from *M. adansonii* by the smaller spathe and spadix and the pinnatifid leaves.

Some of the larger, perforated forms of *Monstera obliqua* approach *M. gracilis* vegetatively, but the fruits of the two species are quite distinct. In *M. gracilis* the yellow berries are prismatic and armed with numerous trichosclereids in the upper portion, whereas *M. obliqua* has orange-colored globose berries lacking trichosclereids in the stylar portion.

As with many aroids, typification of this species is problematical. The holotype collection by Karsten was in the herbarium at Vienna and has been lost. In their 1908 treatment of *Monstera gracilis,* Engler and Krause cite two specimens—the Karsten collection and *Triana 690* (deposited in BM) from the type locality. They provide an illustration of the species based on one of these two specimens. However, the Triana collection was not included in a loan of *Monstera* from the British Museum, and its existence is thus uncertain. The Juzepczuk collection at Leningrad, cited above, was determined by Krause, and this at least provides some basis for my interpretation and a measure of continuity in the identification of the species.

10. **Monstera epipremnoides** Engler

FIG. 45

Monstera epipremnoides Engler, Bot. Jahrb. 37:118 (1905). LECTOTYPE (here designated): Costa Rica, Prov. San José, Santa Maria de Dota, 1300 m., 4 April 1890, *H. Pittier 2486* (B, *non vidi,* photo BH,SEL, as *Biolley 2846;* isolectotype CR as *Biolley 2846,* BR as *Pittier 2486*). EXCLUDED SYNTYPE: Costa Rica, Prov. San José, La Uruca, 1100 m., July 1890, *Biolley 2846* (CR in part; specimens at B and BR under this number are actually *Pittier 2486*).

Epiphytic climber in cloud forest. *Juvenile:* unknown. *Adult stem:* 2–3 cm. thick. *Petiole:* 35–50 cm. long, vaginate to within 5 cm. of the lamina base, the sheath wings persistent. *Lamina:* ovate, subcoriaceous, 35–55 cm. long, 22–35 cm. wide, pinnatifid and perforate, the pinnae 12–20 in number on each side, 1.0–2.5 cm. wide, the sinuses extending to the midrib, primary lateral veins 1 or 2 per pinna, secondary lateral veins parallel to the primary; the perforations mostly small, 0.5–2.0 cm. across, round to elliptic, located along the midrib, other perforations very elongate and extending from the midrib nearly to the margin. *Peduncle:* about 1 cm. thick, 20–30 cm. long. *Spathe:* 15–22 cm. long. *Flowering spadix:* cylindric, 9–12 cm. long, about 2 cm. thick, the pistils truncate. *Fruit:* unknown.

ETYMOLOGY. *Epipremnoides* refers to the similarity in the appearance of the leaf to *Epipremnum pinnatum* (L.) Engler of Malesia.

DISTRIBUTION. Costa Rica, Prov. Cartago and San José.

REPRESENTATIVE SPECIMENS. **Costa Rica. Cartago:** without locality or date, *Orsted 15795* (C). **San José:** Santa Maria de Dota, 1300 m., April 1890, *Pittier 2486* (B, photo BH,BR,CR,SEL); 5 km. S of Santa Maria de Dota, 6000 ft., July 1972, *Primack & Stone 337* (DUKE).

CULTIVATED SPECIMENS. **Venezuela. Caracas:** cultivated in the garden of Mr. Wendlinger, plants originally from Costa Rica, 1960, *Steyermark s.n.* (VEN).

Figs. 44–45. 44. (left) *Monstera gracilis* (*Killip 34288*, F); 45. (right) *M. epipremnoides*: isolectotype (labelled *Biolley 2846*, is probably *Pittier 2486*, CR).

In his description of this species Engler cites two specimens: *Pittier 2486* and *Biolley 2846,* both collected in Costa Rica in 1890. The Biolley specimen at CR is a mixed collection, consisting of one sheet of *Monstera epipremnoides* and one sheet of *M. adansonii* var. *laniata.* La Uruca, the locality of the Biolley collection, is known as a locality for *M. adansonii* var. *laniata* by other collections (e.g., *Pittier 2839*) of the same year. In my opinion, the only collection of *M. epipremnoides* involved here is *Pittier 2486,* and because of the similarity of the two numbers and because both men were working at the same institution at the same time, I think that some of Pittier's specimens accidentally came to be labeled with Biolley's collection data. Engler's description and illustration clearly fit the Pittier collection, which is here designated as the lectotype.

Monstera epipremnoides is very close to *M. dilacerata,* from which it differs morphologically principally in the appearance of the leaves, which have narrower pinnae, as well as perforations which are not found in the leaves of *M. dilacerata.* It is further separated by its habitat. *Monstera epipremnoides* occurs in cloud forests at 1300–1800 m., while *M. dilacerata* mostly occurs below 1000 meters.

Jonker-Verhoef and Jonker (1966) included *Monstera epipremnoides* in the flora of Surinam, based on the collection *Wessels-Boer 872,* housed at Utrecht. However, I consider this specimen to be *M. adansonii* var. *laniata. Monstera epipremnoides* should be excluded from consideration as a taxon in the flora of Surinam.

11. **Monstera xanthospatha** Madison, *sp. nov.*

FIG. 46, MAP 14

Planta epiphytica scandens. *Caulis* teres 5–10 mm. crassus, internodiis 3–6 cm. longis. *Foliorum petiolus* 12–18 cm. longus, ad geniculum usque vaginatus, vagina decidua; *lamina* oblique lanceolata, 16–25 cm. longa, 5–8 cm. lata, inequilatera, basi cuneato-angustata, apice acuminata, integra vel pauciforaminata foraminibus inter nervos primarios solitariis anguste ellipticis ad 5 cm. longis. *Pedunculus* 15–26 cm. longus, petiolo paulo longior. *Spatha* extus aurea, intus alba, circ. 9 cm. longa. *Spadix florifer* flavus, 6–8 cm. longus, 2 cm. crassus, inferne sterilis. *Spadix fructifer* nutans, aurantiacus vel ruber. *Baccae* subprismaticae.

TYPE. Colombia: Dept. El Valle, Cordillera Occidental, La Cumbre, 1600–1800 m. Climbing herb. 14–19 May 1922, *Killip 5668* (holotype GH; isotypes NY, US no. 1142004, PH no. 612990).

ETYMOLOGY. Greek *xanthospatha,* "yellow spathe," referring to the deep yellow color of the abaxial surface of the spathe.

DISTRIBUTION. Colombia, Cordillera Occidental and Cordillera Central.

REPRESENTATIVE SPECIMENS. **Colombia. Antioquia:** Angelópolis, 2000 m., Aug. 1910, *Mayor 169* (Z); Boqueron, between Medellín and Palmitas, 2300–2500 m., Jan. 1948, *Barkely & Klevens 52* (US); Salgar, near Medellín, July 1928, *Toro 1304* (NY). **Caldas:** Canaan, S of Salento, 1400–1700 m., July 1922, *Pennell 9055* (GH,US). **El Valle:** La Cumbre, 1600–1800 m., May 1922, *Killip 5668* (GH,NY,PH,US); 1 km. E of Bitaco, 4500 ft., Nov. 1963, *Hutchison & Idrobo 3038* (US); Hoya del Río Cali, 1580–1650 m., Nov. 1944, *Cuatrecasas 18765* (F); Baga de la Tulia, 1850–2000 m., Oct. 1944, *Cuatrecasas 18382* (F); Dagua, Buenaventura, 600 m., *Lehmann 5312* (K); La Cumbre, 1700–2200 m., Sept. 1922, *Killip 11408* (GH,NY,PH).

FIGS. 46–47. 46. (left) *Monstera xanthospatha*: holotype (*Killip 5668*, GH). 47. (right) *Monstera minima*: holotype (*Duke 14758* (3), MO).

CULTIVATED SPECIMENS. **Colombia.** July 1959, *Kyburz 11* (US); Medellín Jardin Botanico, *Plowman s.n.* (photograph only, to be deposited GH).

Monstera xanthospatha shows close affinities to *M. obliqua* from which it differs by its larger size in every respect and by the subprismatic berries which contain trichosclereids in the stylar portion. The berries of *M. obliqua* are globose and lack trichosclereids in the stylar portion. In addition, the two species are ecologically quite distinct. *Monstera obliqua* occurs mostly near sea level, while *M. xanthospatha* ranges from elevations of 1400 to 2500 meters. *Monstera xanthospatha* is distinguished from the remaining species of the section in various ways, and always by the deep yellow abaxial surface of the spathe.

The three Central American species of *Monstera* with a similar elevational range do not show a close alliance to *M. xanthospatha,* which apparently has not arisen from a high-altitude species complex, but has evolved from some lowland ancestor.

In all but one of the fruiting specimens examined the spadix is nodding from the erect peduncle, a character not known in other *Monstera* species.

12. **Monstera obliqua** Miquel

FIG. 48, MAP 3

Monstera obliqua Miq., Linnaea **18**:79 (1844). TYPE: Surinam, Vredenburger-Zandrits, October 1842, *Focke 719* (U, photo BH,SEL).

Monstera microstachya Schott, Oest. Bot. Woch. **5**:274 (1855). TYPE: Brazil, *Hoffmannsegg s.n.* (Willdenow Herb. No. 7140, B, *non vidi,* photo BH, microfiche IDC 7440. 493:III. 2).

Monstera expilata Schott, Prodr. Syst. Aroid. p. 367 (1860). *Monstera obliqua* Miq. var. *expilata* (Schott) Engler, in Martius, Flora Brasiliensis **III** (2):113 (1878). TYPE: Brazil, Amazonas, Rio Negro, Japura et Rio Solimões, in aboribus sylvarum, *Martius 1196* (M, photo BH; drawing of holotype = Schott Aroideae No. 2243, W, *non vidi,* photo BR,C,GH,S,US).

Monstera falcifolia Engler, Bot. Jahrb. **37**:117 (1905). TYPE: Brazil, Amazonas, Jurua Miry, July 1901, *Ule 5622* (holotype B, *non vidi,* photo BH,GH,US; isotypes K,L,MG, photo BH).

Monstera fendleri Engler, Bot. Jahrb. **37**:117 (1905). TYPE: Trinidad, 1877–1880, *Fendler 736* (holotype K; isotypes NY,P).

Monstera sagotiana Engler, Bot. Jahrb. **37**:117 (1905). TYPE: French Guiana, Karouany, *Sagot 609* (BM, photo BH).

Monstera unilatera Rusby, Bull. New York Bot. Gard. **6**:494 (1910). TYPE: Bolivia, Dept. La Paz, San Buena Ventura, 1400 ft., 25 November 1901, *Williams 526* (NY).

Monstera boliviana Rusby, Bull. New York Bot. Gard. **6**:494 (1910). TYPE: Bolivia, Isapuri, common on trees, 1500 ft., 10 October 1901, *Williams 676* (holotype NY; isotypes US no. 1312955, BM,K, photo BH,SEL). Type is a mixed collection with *M. adansonii* var. *klotzschiana*).

Monstera snethlagei Krause, Notizbl. Bot. Gart. Ber. **9**:272 (1925). TYPE: Brazil, Maranhão, Jury-assu, Mta. de Allegria, Ketterpflanze im Igapowald, gelb, Hullblatt ebenfalls gelb, 14 November 1923, *Snethlage 327* (B, *non vidi,* photo BH,GH,US).

Monstera killipii Krause, Notizbl. Bot. Gart. Berlin **11**:614 (1932). TYPE: Peru, Dept. Loreto, Iquitos, 100 m., epiphyte, spathe and spadix light yellow, woods, 2–8 August 1929, *Killip & Smith 27372* (holotype B, *non vidi,* photo BH,SEL; isotypes F no. 616009, NY, US no. 1461136).

Monstera falcifolia Engler var. *latifolia* Krause, Notizbl. Bot. Gart. Berlin **11**:614 (1932). TYPE: Peru, Dept. Loreto, Puerto Arturo, Lower Río Huallaga below Yurimaguas, 135 m., 24–25 August 1929, *Killip & Smith 27795* (holotype B, *non vidi*, photo BH,SEL; isotypes NY, US no. 1461494).

Slender climbing epiphyte on trees, saplings, or shrubs. *Juvenile:* terrestrial creeper, the leaves entire, exserted and erect, the lamina membranaceous, ovate to lanceolate. *Adult stem:* green, smooth, terete, 2–7 mm. thick, the internodes 1–6 cm. long, occasionally producing hanging and creeping stolons with internodes 10–30 cm. long. *Petiole:* 5–15 cm. long, vaginate for most of its length, the sheath wings deciduous; geniculum 5–15 mm. long. *Lamina:* membranaceous, quite variable in shape, ranging from lanceolate 35 cm. long and 4 cm. wide with an acute base to broadly ovate, 14 cm. long and 12 cm. wide with a truncate to subcordate base; mostly ovate, somewhat falcate, 8–15 cm. long and 4–6 cm. wide, the base oblique, unequal, with one side about twice as wide as the other; usually entire but sometimes perforated, the holes one to many in a single series on each side of the midrib; primary lateral veins not prominent. *Inflorescences:* produced sympodially in groups of six to eight, rarely fewer. *Peduncle:* terete, 1–2 mm. thick, 7–15 cm. long, elongating throughout the development of the fruit. *Spathe:* green to white when immature, becoming a bright yellow at maturity, 4–7 cm. long, 3–5 cm. across when fully open, acuminate or mucronate for 3–8 mm. at the tip. *Flowering spadix:* deep yellow, 5–10 mm. thick, 2.5–6.0 cm. long. *Fruiting spadix:* green to olive-green tinged with orange when immature, becoming lighter and finally deep orange at maturity, 10–15 mm. thick, 4–8 cm. long; the berries globose, 5–8 mm. in diameter, capped by the persistent stylar region, lacking trichosclereids, or if trichosclereides present confined to the walls, very rarely present in the stylar region; the berries free from one another.

ETYMOLOGY. Latin *obliqua,* "oblique," referring to the oblique leaf bases.

COMMON NAMES. Timbo titica (Brazil, Para); mamurillo (Venezuela).

DISTRIBUTION. Panama, Colombia, Peru, Bolivia, Venezuela, Trinidad, Tobago and the Guianas, and Amazonian Brazil.

REPRESENTATIVE SPECIMENS. **Panama. Bocas del Toro:** forest above RR stop at mile 7.5, July 1971, *Croat & Porter 16277* (MO); vicinity of Chiriqui Lagoon, Oct. 1940, *von Wedel 1091* (MO). **Veraguas:** 5 miles NW of Santa Fé, 700–1200 m., March 1973, *Liesner 801* (MO). **Coclé:** mountains beyond La Pintada, 400–600 m., Feb. 1935, *Hunter & Allen 544* (MO,NY,US); Cerro Pilon near El Valle, 700–900 m., June 1967, *Duke 12155* (MO). **Panama:** foot of Loma Larga, E of Cerro Azul, April 1973, *Dressler 4319* (MO). **San Blas:** Río Mulatupo, Aug. 1967, *Kirkbride 229* (MO). **Darien:** Cativo Swamp, Río Chucunaque, ½ hr. below Morti, May 1967, *Duke 11749* (MO,US). **Colombia. Chocó:** Río Nercua, near Camp Curiche, 10–294 m., May 1967, *Duke 11486* (US); Bahia Solano, near Ciudad Mutis, 75 m., Feb. 1939, *Killip & Garcia 33580* (COL,US). **Meta:** 22 km. W of Villavicencio, Aug. 1944, *Grant 9963* (US). **Vaupes:** 1°50′N × 67°W, Oct. 1952, *Schultes, Baker & Cabrera 18051* (BM, GH,NY,U,US); Río Apaporis, Soratama, 900 ft., Feb. 1952, *Schultes & Cabrera 15159* (US). **Putumayo:** Río Gineo, 8 km. W of Villagarzon, Nov. 1968, *Plowman 2047* (GH); Puerto Ospina and vicinity, March 1953, *Schultes & Cabrera 18978* (US). **Amazonas:** Río Loretoyacu, 100 m., March 1946, *Schultes 7177* (US); Puerto Narino, Jan.–Feb. 1969, *Plowman et al. 2344* (GH). **Peru. Loreto:** Río Ucayali near Iparia, 250 m., Sept. 1968, *Schunke 2803* (F,US); between Yurimaguas and Balsapuerto, 135–150 m., Aug. 1929, *Killip & Smith 28258* (NY,US). **San Martín:** Tocache Nuevo, Río Huallaga, Feb. 1970, *Schunke 3815* (F,GH,US). **Huanuco:** Río Pachitea, 20 km. above confluence with Río Ucayali, 300–400 m., July 1967, *Schunke 2126* (F). **Junin:** Río Richis, between Puerto Bermudez and Cahuapanas, 340–375 m., July 1929, *Killip & Smith 26706* (NY,US). **Cuzco:** Atalaya, 700 m., Oct. 1960, *Vargas 13431* (US). **Bolivia. La Paz:** basin of Río Bopi, Asunta, near Evenay, 690–750 m., July 1939, *Krukoff 10662* (F,GH,MICH,MO,NY,S,U,US); Rurrenabaque, 1000 ft., Oct. 1921, *Rusby 771* (NY). **Pando:** Río Madiera, 12 km. above Abuña, July 1968, *Prance et al. 6211* (NY,US). **Venezuela. Tachira:** 15 km. W of Santo Domingo, 420 m., March 1974, *Gentry, Morillo & Morillo 11094* (MO). **Yaracuy:** lower Yaracuy, Feb. 1926, *Pittier*

FIG. 48. *Monstera obliqua:* variation in adult leaf shape from different individuals (to the same scale).

12098 (US). **Carabobo:** between Urama and San Felipe, sea level, Jan. 1939, *Alston 6077* (VEN). **Anzoátegui:** near Carmelita, NE of Bergantin, 800–1100 m., Feb. 1945, *Steyermark 60987* (F,VEN). **Monagas:** Montaña de Aguacate, 600–900 m., April 1945, *Steyermark 62172* (F). **Delta Amacuro:** Río Acure, between La Margarita and Puerto Miranda, 80–100 m., Nov. 1960, *Steyermark 87766* (NY,US,VEN). **Bolivar:** 4°18′N × 63°06′W, 510–525 m., Jan. 1962, *Steyermark 90541* (BH,US,VEN). **Amazonas:** Brazo Casiquiare, Feb. 1931, *Holt & Blake 671* (US). **Trinidad.** Mts. of Aripo, Naranje Valley, L'Orange Est., 800 ft., Feb. 1947, *Simmonds 64* (K,TRIN); vicinity of Tabaquite, March 1921, *Britton, Freeman & Nowell 2603* (GH,NY,TRIN,US). **Tobago.** Black Hill, above Charlotteville, Oct. 1937, *Sandwith 1797* (K). **Guyana.** Demerara River, Oct. 1890, *Jenman 6243* (K,NY); Northwest District, Wanama River, 7°45′N × 60°15′W, May 1923, *De La Cruz 3946* (F,GH,MO,NY,PH,US); Pakaraima Mountains, Paruima Falls, Nov. 1951, *Maguire & Fanshawe 32455* (NY). **Surinam.** Pauluskreek, Oct. 1954, *Mennega 239*(NY,U); Marowijne District, Moengo, bank of Cottica River, Nov. 1961, *Hekking 1046* (A,U); Zuid River, 3°20′N × 56°49′W, 270 m., Sept. 1963, *Irwin et al. 55993* (NY). **French Guiana.** Maroni, 1856, *Sagot 614* (P); Rivière petite Ouaqui, July 1973, *Granville 1846* (US). **Brazil. Amazonas:** near mouth of Rio Embira, 7°30′S × 70°15′W, June 1933, *Krukoff 5890* (GH,NY); Rio Purus, 5 km. above Labrea, Oct. 1968, *Prance, Ramos & Farias 8119* (INPA,NY,US). **Pará:** banks of Rio Piria, S of Curapati, Nov. 1965, *Prance & Pennington 2056* (F,GH,NY,S,U,US); Planalto de Santarem, Estrada Mojui, June 1954, *Froes 30837* (RB). **Amapá:** Serro do Navio, Rio Amapari, above Igarape Sentinela, 70–300 m., Nov. 1954, *Cowan 38194* (NY). **Acre:** mouth of Rio Macauhan, 9°20′S × 69°W, Sept. 1933, *Krukoff 5774* (F,GH,M,MICH,MO,NY,S,U,US); Rio Moa, 15 km. NW of Cruzeiro do Sul, Oct. 1966, *Prance, Pena & Ramos 2772* (MG,NY,US). **Rondonia:** island in Rio Madeira at mouth of Rio Jaciparana, June 1968, *Prance et al. 5339* (INPA,NY,US); Santa Barbara, 15 km. E of km. 117, Aug. 1968, *Prance & Ramos 7010* (INPA,NY). **Mato Grosso:** 14°38′S × 52°14′W, Nov. 1968, *Harley et al. 11018* (K).

Various authors, including Engler and Krause (1908), cite this species as *Monstera obliqua* (Miq.) Walp., based on *Heteropsis obliqua* Miquel. In the publication describing this species, Miquel divided *Monstera* into two sections, section Monstera and section Heteropsis Miq., and indicated this species as "*Monstera* (Heteropsis) *obliqua.*" It is clear from examination of other examples in the same work that Miquel used this procedure to indicate the section of a genus to which a species belongs, and that he was undoubtedly describing *M. obliqua* in section Heteropsis, and not *H. obliqua*. Thus, the species is correctly called *M. obliqua* Miq. and not *M. obliqua* (Miq.) Walp.

Monstera obliqua has been divided into a number of putative species, principally on the basis of differences in leaf shape, but these variations are of little taxonomic significance. For example, about 80% of the specimens of this species that I have examined have entire leaves; the rest have leaves which are slightly to profusely perforated. The material with perforated leaves has been separated as *M. expilata,* but this variation shows no ecological or geographic pattern except that the perforated forms are absent from Panama. Furthermore, some individuals have mostly entire but occasionally perforated leaves.

There is also great variation in the relative width of the leaves, which is correlated with the shape of the leaf base. The shape ranges from narrow, lanceolate leaves with acute bases to broadly ovate leaves with truncate or subcordate bases. The narrowest have been separated as

Monstera falcifolia and the widest as *M. sagotiana,* but again this variation shows no ecological or geographic correlation, and it is impossible to draw a line separating the plants into two or more meaningful groups on this basis.

Jonker-Verhoef and Jonker, in the *Flora of Surinam* (1952), separated *Monstera sagotiana* and *M. expilata* from *M. obliqua* on the basis of leaf shape. They also described differences in the fruits, *M. sagotiana* supposedly having a white to yellowish-green spadix and *M. obliqua* white berries with orange styles. These apparently represent differences in maturity rather than taxonomic differences. In *M. obliqua* the spathe and spadix are green initially, becoming greenish-white and finally bright yellow. After anthesis the color of the spadix changes from yellow to green, in some cases to olive-green, later becoming pale and finally turning a deep orange at maturity.

In terms of its growth habit and floral and fruit morphology the species is a very coherent one, despite the variability in leaf shape. The deep yellow spathes, the flowering spadices and the orange fruits are equalled in the genus only by *Monstera xanthospatha* of the Colombian Andes. The fruits of *M. obliqua* are unique in several respects. The berries are globose and free from one another rather than prismatic and closely pressed together as in the other species. This is probably, in part, a consequence of the small size of the spadix and in particular its very narrow axis. With the exception of a few Panamanian specimens, trichosclereids are absent from the stylar region, though they may be present in the ovary walls. This is clearly related to the failure of the fruits of *M. obliqua* to break in two at maturity and the consequent loss of the ability to get rid of stylar trichosclereids which protect the developing seeds but would deter a dispersing agent when the seeds are mature. In this respect *M. obliqua* seems to have lost an adaptation shared by other *Monstera* species.

Another feature unique to *Monstera obliqua* is that the inflorescences are usually produced sympodially in groups of six to eight, rather than in groups of one to four.

The small size of *Monstera obliqua* enables it to exploit substrates unavailable to other monsteras. It can grow to maturity on saplings, in shrubs and on small twigs of trees; it may even be epiphytic on other aroids. These habitats are more ephemeral than the trunks of large trees, and it seems likely that *M. obliqua* may grow faster and mature more rapidly than other species. Plants of *M. obliqua* tagged in the wild showed an annual growth rate of 30–70 new leaves *vs.* 5–12 new leaves in large-leaved species.

Some of the larger, perforated individuals of *Monstera obliqua* approach *M. gracilis* vegetatively, but the latter species is separated by its lighter colored spathes and spadices and its prismatic berries with trichosclereids in the stylar region.

The distribution of *Monstera obliqua* is disjunct between Panama-Chocó and Amazonia-northern South America, with a gap of 700 km. between the closest collections. This gap may reflect the present-day aridity of the region of northern Colombia which could provide a low-elevation pathway between these two centers. However, the region is not well-known, and it is also possible that further collecting may reveal intervening populations. The Panamanian material of this species is much less variable than that from Amazonia, suggesting that the Panamanian populations may be descended from a limited immigrant line from South America, with a consequent decrease in genetic variability.

13. **Monstera minima** Madison, *sp. nov.*

FIG. 47, MAP 15

Planta exigua epiphytica scandens. *Caulis* teres, 3–4 mm. crassus, internodiis 1–2 cm. longis. *Foliorum petiolus* 2.0–3.5 cm. longus, ad laminam usque vaginatus, vagina decidua; *lamina* integra, lanceolata, 9–12 cm. longa, 2.0–2.8 cm. lata, basi angustate, apice acuta. *Pedunculus* 18 cm. longus, 2 mm. crassus, folium superans. *Spatha* ignota. *Spadix fructifer immaturus* viridis, 5 cm. longus, 1.8 cm. crassus. *Baccae* subprismaticae, 4–5 mm. longae, 6–7 mm. latae, apices truncati.

TYPE. Panama: Comarca de San Blas, trail east of Cangandi-Mandinga airport road, 2–5 miles south of Mandinga airport. Scandant epiphyte, spadix green, 27 October 1967, *J. A. Duke 14758*(3) (MO, sheet no. 2051569).

ETYMOLOGY. Latin *minima*, "very small," this being the smallest known species of *Monstera.*

This species, known only from the type collection, has a peduncle which is 1½ times longer than the leaves; this readily distinguishes it from all other monsteras, since they have peduncles shorter than the leaves. *Monstera minima* is closely related to *M. obliqua*, from which it differs by the much shorter petioles and by the subprismatic and truncate rather than globose berries.

MONSTERA section MARCGRAVIOPSIS Madison, *sect. nov.*

Plantula stoloniformis, 1–2 mm. crassa, 30–200 cm. longa. Folia stirpium juvenilium breviter petiolata, ad truncis arborum adpressae. Pistillum maturum 5–8 mm. latum. Spadix erectus; penduncu1i spadices aequantes vel eis breviores.

TYPE SPECIES. ***Monstera acuminata*** C. Koch.

The species of this section show a heteroblastic development with three distinct phases. The seedling is stolon-like, 1–2 mm. in diameter and 30–200 cm. long. The earliest climbing plant has asymmetric ovate leaves that are cordate at the base, and are tightly appressed to the substrate and overlap one another on the stem. These leaves have a short petiole less than ½ the lamina length, with the sheath extended into a ligule about equal in length to the petiole. The adults have exserted leaves lacking a ligular extension of the sheath. In this section the peduncle is shorter than or equal to the spadix.

The species of section Marcgraviopsis are quite distinct from each other and are without intermediates, though *Monstera dubia, M. pittieri,* and *M. luteynii* are closely related.

14. Monstera acuminata C. Koch

FIGS. 49–51, MAP 11

Monstera acuminata C. Koch, Ind. Sem. Hort. Bot. Berol. App.:5 (1855). TYPE: Central America, live plant collected by Warszewicz cultivated at Berlin, *C. Koch s.n.* (B, *non vidi*). *Engler 45* (C,BM,GH,L,M,P,US) cultivated at Berlin, may represent later specimens of the type collection.

Monstera karwinskyi Schott, Oest. Bot. Woch. 9:99 (1859). TYPE: Mexico, Vera Cruz, Colipa, April 1841, *Karwinsky s.n.* (C, photo BH). PARATYPE: Mexico, Vera Cruz, Papantla to Colipa, 1841–42, *Karwinsky 838* (LE).

Monstera belizensis Lundell, Lloydia 2:76 (1939). TYPE: Belize, El Cayo District, 23 June 1936, *Lundell 6198* (MICH).

Monstera grandifolia Standl. & Steyerm., Pub. Field Mus. Nat. Hist., Botany 23:212 (1947). TYPE: Guatemala, Petén, low forest between Finca Yalpemech and Chinaja, 28 March 1942, *Steyermark 45423* (holotype F no. 1129317–9; isotype US no. 1864956).

Monstera chiapensis Matuda, Madroño 10:48 (1949). SYNTYPES: Mexico, Chiapas, Finca California, Col. Turquia, Escuintla, 150 m., 29 August 1947, *Matuda 17789* (Matuda Herbarium, *non vidi*); Finca Esperanza, 10 km. NE of Escuintla, 200 m., *Matuda 17786* (Matuda Herbarium, *non vidi*).

Monstera viridispatha Matuda, Rev. Soc. Mex. Hist. Nat. 11:98 (1950). TYPE: Mexico, Chiapas, Esperanza, Escuintla, 150–250 m., 7 Dec. 1949, *Matuda 18717* (holotype Matuda Herbarium, *non vidi;* isotypes NY, UC no. 903869, photo BH). PARATYPES: holotype locality, 14 Oct. 1949, *Matuda 17796* (Matuda Herbarium, *non vidi*); 5 Aug. 1948, *Matuda 18318* (Matuda Herbarium, *non vidi*); 23 April 1948, *Matuda 17774* (Matuda Herbarium, *non vidi,* MEXU,NY); Cruz de Piedra, 4 km. N of Acacoyagua, 25 July 1947, *Matuda 17795* (MEXU).

Robust scandent epiphyte to 30 m. tall. *Seedling:* stem terete, 0.5–2.0 m. long, 1–2 mm. thick, internodes 3–10 cm. long, bearing cataphylls but not foliage leaves. *Juvenile:* a shingle plant, stem elliptic in cross section, internodes 1–5 cm. long, leaves highly asymmetric, tightly appressed to the substrate, the petiole 0.5–1.5 cm. long, the sheath extended into a ligule about equal in length to the petiole; the lamina subcoriaceous, slightly longer than wide, midrib curved, the base unequal, rarely peltate, the apex short acuminate. *Adult stem:* smooth or papillose, 2.0–3.5 cm. thick, internodes 6–11 cm. long, axillary buds located in a depression extending as a sulcus for most of the length of the internode. *Petiole:* shorter than the lamina, 25–45 cm. long, vaginate to the base of the blade, the sheath wings persistent, the geniculum 3.5–5.0 cm. long. *Lamina:* usually pendent from the erect petiole, coriaceous, dull green adaxially, paler abaxially, ovate, 15–35 cm. wide, 35–65 cm. long, the base unequal, truncate to acute, the midrib curved; primary lateral veins 10–22 in number, prominent and white abaxially, secondary lateral veins parallel to the primary. *Peduncle:* stout, terete, 1.5–2.5 cm. thick, 7–11(–13) cm. long, smooth or papillose. *Spathe:* greenish-white externally, cream within, 14–22 cm. long, exceeding the spadix by 3–5 cm., terminating in a 0.5–1.0 cm. long acumen. *Flowering spadix:* cream to yellow, cylindric, 2.5–4.0 cm. thick, (12–)15–20 cm. long, the lower 3–4 rows of flowers sterile. *Fruiting spadix:* 4.0–6.5 cm. thick, 15–23 cm. long, yellow at maturity, the stylar portion of the pistils deciduous to reveal the seeds in a gray pulp. *Seeds:* oblong, 16–20 mm. long, 5–8 mm. thick.

ETYMOLOGY. The epithet refers to the acuminate leaves.

COMMON NAMES. Bejuca de Tuza, Conte tuza, Conte arpón, Conte de mimbre (Mexico); Hoka de sereno (Honduras); Madre de harpón, se wan en, kolkuk (Guatemala).

DISTRIBUTION. Mexico, Guatemala, Belize, and Honduras, mostly at elevations of 0–600 meters.

REPRESENTATIVE SPECIMENS. **Mexico. San Luis Potosí:** road to Xilitla 2 km. from junction with Road 85, 300 m., Aug. 1972, *Madison 601* (GH); N of Tamazunchale, July 1935, *Clark 7407* (MO). **Puebla:** Bosque Ajenjibre, March 1951, *Bravo 151* (MEXU). **Vera Cruz:** Coatzacoalcos, April 1895, *Smith 1069* (US); Barranca de Santa Maria at Hda. El Mirador, Sept. 1961, *Moore & Bunting 8859* (BH); Papantla, 100 m., Feb. 1968, *Gutierrez 75* (US). **Oaxaca:** cerro W of Sebastopol, Tuxtepec, March 1968, 200 m., *Rzedowski 25484* (MICH,US). **Chiapas:** Cascada Mizolá, 250 m., Oct. 1974, *Madison 1755* (GH); El Triunfo, 200 m., Oct. 1974, *Madison 1782* (GH); Turquia, Escuintla, August 1957, *Matuda 17785* (NY). **Tabasco:** Comalcalco, Aug. 1962, *Barlow s.n.* (US). **Guatemala. Petén:** Monte Polol, June 1933, *Lundell 3609* (MICH,NY); Uaxactun, April 1931, *Bartlett 12745* (MICH). **Huehuetenango:** Sierra de los Chuchumatanes, 150–200 m., Ixcan, July 1942, *Steyermark 49312* (F,US). **Alta Verapaz:** Teleman, 6000 ft., April 1889, *Smith 1531* (K,US); Pancajche, 360 m., April 1939, *Standley 70803* (F). **Izabal:** between Bananera and La Presa in Montaña del Mico, 40–300 m., March 1940, *Steyermark 38142* (F). **Retalhuleu:** Río Talculan, 5 km. W of Retalhuleu, 300 m., Feb. 1941, *Standley 87368* (F). **Suchiteqequez:** vicinity of Tiquisate, 100 m., June 1942, *Steyermark 47651* (F,MO). **Escuintla:** Escuintla, 1100 ft., March 1890, *Smith 2242* (US). **Santa Rosa:** Guazacaoan, 220 m., Dec. 1940, *Standley 78610* (F). **Belize:** Swasey Branch, Monkey River, March 1942, *Gentle 3956* (GH,MICH,MO,NY); Mile 28.5 on Hummingbird Highway, S of Belmopan, 200–300 ft., June 1973, *Croat 24558* (MO). **Honduras. Cortes:** Lake Yojoa, 600 m., *Williams & Molina 18268* (F). **Comayagua:** El Achote, 1350 m., June-Aug. 1936, *Yuncker, Dawson & Youse 6300* (A,F,GH). **Atlantida:** 35 km. S of La Ceiba, 980 m., Sept. 1972, *Madison 710* (GH); Tela, 20–600 m., Mar. 1928, *Standley 53214* (F,US). **Olancho:** between Catacamas and La Presa, 500–600 m., Mar. 1949, *Standley 18697* (F).

Monstera acuminata was first collected in Central America by Warszewicz who brought it to Europe as a live plant. It was cultivated at the Berlin Botanic Garden where Carl Koch recognized it as a new species. Too impatient to await its maturity, he described *M. acuminata* on the basis of the juvenile form and made a specimen of two leaves for the type.

Engler and Krause (1908) redescribed *Monstera acuminata,* basing their expanded description in part on a further collection from Guatemala *(J. D. Smith 1533).* Unfortunately, this is a specimen of *M. tuberculata,* and Engler and Krause's description combines characters of both species. Apparently they did not understand Koch's concept, for mature material of *M. acuminata* examined by Engler was determined as *M. pertusa* var. *jacquinii* (e.g., *J. D. Smith 1531, 2234*). To further confuse the issue, Engler made a number of specimens of a plant cultivated in Berlin which he distributed as Engler Exsiccatae No. 45 under the name *M. pertusa.* These specimens are actually of *M. acuminata* and are quite probably from the original plant brought from Guatemala by Warszewicz!

The name *Monstera acuminata* emerged from this confusion with a peculiar status—it came to be used for any sterile specimen of a *Monstera* juvenile shingle plant. Thus, *M. acuminata* is cited in the *Flora of Peru* (1936), referring to juveniles of *M. dubia.*

In the meantime, the actual *Monstera acuminata* of Guatemala and Mexico came to be known as *M. karwinskyi*. Various species were segregated from this on the basis of differences in leaf size and presence or absence of perforations, but these are unimportant variations occurring

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FIGS. 49–50. *Monstera acuminata:* 49. seedling and shingle plant; 50. mature shoot (both *Madison 1755,* GH).

FIG. 51. *Monstera acuminata:* habit (*Madison 1782*, GH).

sporadically throughout the range of the species, and I do not consider them taxonomically significant.

Monstera acuminata is readily distinguished from other species of section Marcgraviopsis by its large leaves with entire margins. The habit is also distinctive, with the somewhat falcate laminae pendent from the erect petioles.

The majority of collections of this species are sterile, probably because it flowers more than 15 meters above the ground. Individuals may grow to 30 m. tall, thoroughly covering the trunk of the host tree but without spreading into the branches.

Monstera acuminata is abundant in the central Petén, and may be found growing on the Mayan ruins at Tikal and Uaxactun. Its range extends north to San Luis Potosí, making it the northernmost of the species of *Monstera.*

15. **Monstera dubia** (HBK.) Engler & Krause

FIGS. 52–53, MAP 6

Monstera dubia (HBK.) Engler & Krause, Das Pflanzenreich IV **23B**:112 (1908). *Marcgravia dubia* HBK., Nov. Gen. et Spec. Plant. 7:169 (1825). TYPE: Venezuela, Crescit ad arbores Novae Andalusiae, prope Cocollar et Caripense, alt. 400 hex. *Humboldt and Bonpland* (B, *non vidi*).

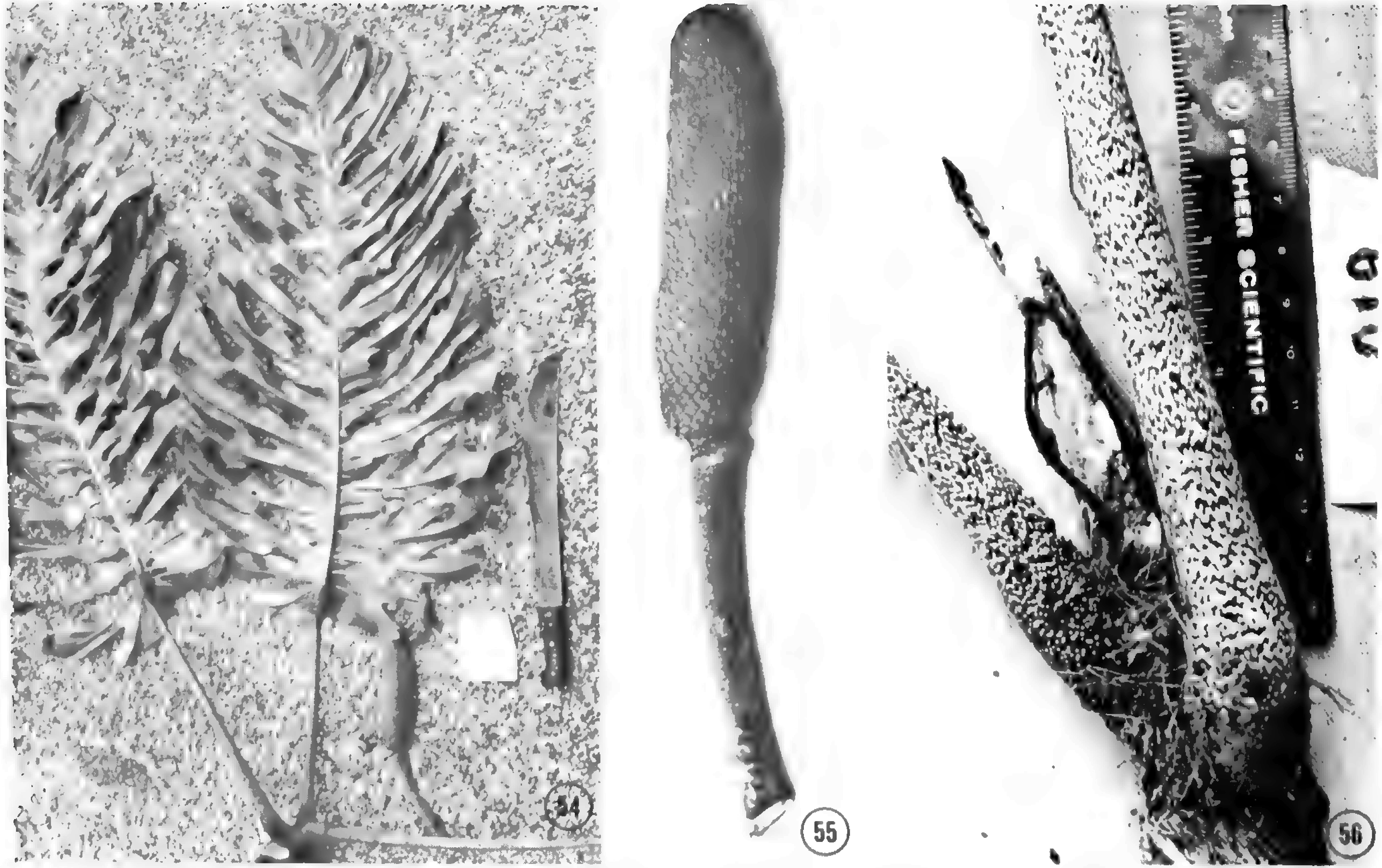
Monstera acreana Krause, Notizbl. Bot. Gart. Berlin 6:114 (1914). TYPE: Brazil, Acre, São Francisco am Alto Acre, August 1911, *Ule 9212* (B, *non vidi,* photo GH,BH,US).

Monstera irritans Simmonds, Kew Bull.:398 (1950). TYPE: Trinidad, Cap de Ville, Feb. 1948, *Simmonds 296* (TRIN, *non vidi;* isotype K).

Stout climber to 25 m., often with fertile hanging shoots; the adult leaves drooping. *Seedling:* a stolon-like creeper, 1–2 mm. in diameter, to 2 m. long. *Juvenile:* shingle plant, the lamina cordate, the sinus 5–10 mm. deep, the apex mucronate; often variegated with silver flecks. *Adult stem:* elliptic in cross section, roughly warty or tuberculate, rarely smooth, dark green to tan, with a thick cuticle; internodes 3–10 cm. long, 1–2 cm. thick and 1.5–3.0 cm. wide; axillary bud in a depression which is extended into a sulcus the length of the internode. *Petiole:* warty or tuberculate at the base or along its length, 20–55 cm. long, vaginate to the geniculum, the sheath wings neatly deciduous, the geniculum 4–7 cm. long. *Lamina:* oblong-ovate, falcate and oblique, coriaceous, dull dark green above, paler below, 20–100 cm. long, 13–50 cm. wide, 1½–2 times longer than wide; the earliest adult leaves entire and some individuals mature in this state, later leaves pinnatifid, the larger pinnatifid and with 1–3 rows of elliptic perforations per side, the perforations 2–8 cm. long, the pinnae truncate; the leaf base rounded to subcordate with a sinus 1–2 cm. deep, never broadly cordate, the apex acute; primary lateral veins 9–18 in number, cream-colored and prominent abaxially, furrowed adaxially, the secondary lateral veins reticulate. *Peduncle:* tuberculate, 0.8–1.4 cm. thick, terete, 5–9 cm. long. *Spathe:* thickly coriaceous, pink abaxially, white adaxially, obovate, 6–12 cm. tall, 4–6 cm. across, shortly mucronate or blunt at the apex, sometimes becoming curled-reflexed and splitting longitudinally before abscission. *Flowering spadix:* white, 5–10 cm. long, 1.5–2.5 cm. thick, the pistils bluntly truncate. *Fruiting spadix:* 7–14 cm. long, 3.5–5.5 cm. thick, pale yellow, the stylar portion of the pistils peeling off individually or in loosely fused groups to reveal the seeds in a gray pulp. *Seeds:* brown, oblong, 6–8 mm. long, 4–5 mm. wide, 2.0–3.5 mm. thick, the embryo turquoise blue in color.

ETYMOLOGY. Latin *dubia,* "dubious," because the authors were not certain that the sterile type specimen was really a *Marcgravia.*

Figs. 52–53. *Monstera dubia:* 52. habit, with pendent flowering shoot; 53. inflorescence (both *Madison 826*, GH).



Figs. 54–56. *Monstera punctulata:* 54. leaf; machete in the photo is 64 cm. long (*Madison 633*, GH); 55. fruiting spadix, 18 cm. long (*Madison 633*, GH); 56. petiole showing punctulate markings characteristic of the species (*Madison 610*, GH).

COMMON NAMES. Chalde (Ecuador); Malanga, Mamurillo, Pantano, Oreja de Tigre (Venezuela).

DISTRIBUTION. Costa Rica to Bolivia, Venezuela, Trinidad, and western Brazil, mostly below 1000 m., but reaching 1800 meters.

REPRESENTATIVE SPECIMENS. **Costa Rica. San José:** Candelarita, 800 m., Oct. 1972, *Madison 745* (GH); Río Paquita, 1–3 m., Aug. 1936, *Dodge & Goerger 9764* (CR,F, MO). **Puntarenas:** 12 km. E of Palmar Sur, Oct. 1973, *Madison 760* (GH); 1 mile S of Río Claro, Aug. 1972, *Vaughan et al. 621* (MO). **Panama. Chirqui:** 1.6 mi. W of Puerto Armuelles, 50 m., Feb. 1973, *Croat 21918* (MO). **Canal Zone:** Barro Colorado Island, May 1968, *Croat 5338* (MO). **Panama:** 34 km. E of Chepo, 100 m., Oct. 1972, *Madison 767* (GH). **Colombia. Magdalena:** Piojo, 400 m., Jan. 1929, *Elias 743* (US). **Norte de Santander:** 45 km. from Cucuta on road to Ocaña, 300 m., March 1973, *Madison 1243* (GH). **Chocó:** 30 km. from Quibdó on Medellín road, 140 m., Nov. 1972, *Madison 826* (GH). **Antioquia:** Villa Arteaga, 100 m., April 1948, *Soto & Barkley 18C543* (US). **Meta:** Sierra de la Macarena, Río Guapaya, 450 m., Dec. 1949, *Philipson, Idrobo & Fernandez 1661* (BM,UC,US); Llanos de San Martín, 500 m., Nov. 1972, *Madison 857* (GH). **Putumayo:** Puerto Asís, 300 m., Dec. 1968, *Plowman 2140* (GH). **Ecuador. Pichincha:** Santo Domingo, 300 m., Sept. 1949, *Acosta Solis 13940* (F). **Los Rios:** 30 km. N of Quevedo, 160 m., Dec. 1972, *Madison 905* (GH). **Guayas:** Balao, Jan. 1892, *Eggers 14229* (LE,US). **Peru. San Martin:** Tarapoto, Alto Río Huallaga, 300–900 m., Dec. 1929, *Williams 5673* (F). **Huanuco:** 10 km. above Tingo Maria on Río Monzón, 960 m., Dec. 1972, *Madison 946* (GH). **Pasco:** Río Paucartambo, 30 km. SW of Oxabamba, 1600 m., Dec. 1972, *Madison 952* (GH). **Junin:** La Merced, 2000 ft., Aug. 1923, *Macbride 5403* (F,US). **Cuzco:** Piliopata, 800 m., Aug. 1960, *Vargas 13377* (US). **Madre de Dios:** Río Tahuamanu, 180 m., Nov. 1973, *Alfaro 1723* (MO). **Bolivia. La Paz:** 10 km. N of Caranavi, 800 m., Jan. 1973, *Madison 1069* (GH). **Venezuela. Zulia:** Sierra de Parija, SE of Machiques, 350–500 m., Aug. 1967, *Steyermark & Fernandez 94972* (VEN). **Falcon:** Tocuyo de la Costa, 100 m., Jan. 1966, *Steyermark & Braun 94494* (US,VEN). **Yaracuy:** Aroa, July 1953, *Aristiguieta & Pannier 1900* (VEN); Selvas de Yumare, 100 m., Feb. 1959, *Bernardi 6971* (VEN). **Distrito Federal:** Cerro Naiguata, 1390–1500 m., Nov. 1963, *Steyermark 91917* (K,US,VEN). **Miranda:** El Guapo, 100 m., July 1957, *Aristiguieta 2876* (VEN). **Anzoátegui:** Río Maravilla, Fila Grande, 900–1400 m., March 1945, *Steyermark 61739* (F,NY,VEN). **Barinas:** Reserva Forestal Caparo, E of El Canton, 100 m., April 1968, *Steyermark, Bunting & Blanco 102010*. **Apure:** Reserva San Camilo, 2 km. SE of San Camilo, 250 m., March 1968, *Steyermark, Bunting & Blanco 101450* (VEN). **Trinidad.** Brazil-Arena Road, March 1959, *Cowan & Simmonds 1406* (US,NY); Tabaquite, Dec. 1955, *Simmonds, Herb Trin No. 15367* (TRIN). **Brazil. Acre:** Rio Moa at Serra da Moa village, April 1971, *Prance et al. 12502* (NY,US). São Francisco, Alto Acre, Aug. 1911, *Ule 9212* (B). **Rondonia:** 4 km. S of Nova Vida, Aug. 1968, *Forero & Wrigley 7077* (INPA,NY,US).

Though a common and abundant species, *Monstera dubia* is represented in the world's herbaria by fewer than 80 collections, more than one quarter of them from Barro Colorado Island. This reflects in part the lack of field botanists working in the Andean countries, as well as the nature of the species, which flowers well out of reach.

Only two collections of *Monstera dubia* are known before the twentieth century. A juvenile shingle plant was collected by Humboldt and Bonpland and described as *Marcgravia dubia* in 1825. While their type specimen itself does not admit to identification beyond inclusion in section Marcgraviopsis, the type locality in the state of Sucre in Venezuela dictates the specific identity. Only a single species of *Monstera* with a shingle plant juvenile is known to occur within 500 km. of this area, and this is the basis on which the name is applied in its present sense.

The first collection of flowering material of *Monstera dubia* was that of Eggers from Ecuador in 1892, which was identified as a *Philodendron.* Later collections were determined to be various different species of *Monstera,* but the name *M. dubia* was not used for any of them.

Hemsley (1885) was the first to recognize that several species described in *Marcgravia* really belong in *Monstera.* Engler and Krause (1908) implemented this and made the new combination *Monstera dubia* (HBK.) Engler & Krause. They provided a description and illustrations based on two specimens: the Humboldt and Bonpland type, and a flowering Seeman collection from Nicaragua. The latter, unfortunately, represents *M. tenuis* C. Koch, and thus the name *M. dubia* came to be generally applied to this Central American species. Further confusion was engendered at this time by Engler and Krause misrepresenting Humboldt and Bonpland's locality as Mexico rather than Venezuela.

Because the name *Monstera dubia* was used for what is in reality *M. tenuis,* the species *M. dubia* was considered to be without a name. Thus Krause gave it the new name, *M. acreana,* but he also inconsistently determined specimens of it as *M. pertusa* and *M. maxima.* This is typical of the history of this section, in which the widespread misapplication of names has led to considerable confusion of what are biologically very distinct and easily recognizable species.

Monstera dubia is a handsome plant which grows at low elevations and it characteristically climbs and hangs on large trees. The vegetative adult stage is variable, relating in part to the type of tree in which it grows. The earliest adult leaves are entire, and if the individual is growing on an inadequate support it may flower at this stage. However, with a large tree to grow on it will produce first entire leaves, then pinnatifid ones, and finally pinnatifid-perforate leaves. These may have a drooping, falcate lamina to 1 meter in length and about half as wide. The species may flower as a climbing plant attached to the trunk; this is most common in Costa Rica and Panama. However, it often flowers at the ends of hanging shoots which may be several times branched, and this is the way it usually grows in South America.

The inflorescences of *Monstera dubia* are very distinctive. The spathe is obovate and blunt, rose to salmon-colored outside and white within. The common name, *oreja de tigre* (tiger's ear), refers to the shape of the intact spathe. It often splits longitudinally and curls up around the abaxial side before abscising. The spadices are white in flower, becoming green in early fruit and pale yellow at maturity. There is a geographic cline in spadix size, the largest ones being found in Costa Rica and smaller ones to the south and east.

The only other species with which *Monstera dubia* might be confused is *M. punctulata,* which is distinguished in flower by its large white spathes, and in fruit by its dark green or golden-green spadices. The petiole of *M. punctulata* is densely marked with white flecks, in contrast to the solid green petioles of *M. dubia.* A further distinction is in the lamina, which in *M. punctulata* is bright green and of a soft texture, and in *M. dubia* is dull dark green and thickly coriaceous.

16. Monstera punctulata (Schott) Engler

FIGS. 54–56, MAP 9

Monstera punctulata (Schott) Engler, D. C. Monog. Phan. **II**:259 (1879). *Anadendrum punctulatum* Schott, Prodr. Syst. Aroid. 393 (1860). TYPE: Mexico, locality and collector unknown, plant cultivated at Vienna and illustrated by Schott Aroideae No. 2281, 3276, and 3279 (W, *non vidi,* photo SEL).

A robust climber on large trees, to 15 m. tall. *Juvenile:* a shingle plant, the stem strongly flattened. *Adult stem:* brown, roughly tuberculate, subterete, 3–4 cm. thick, internodes 3–6 cm. long, the stem often covered with the fibrous remains of petiole sheath wings; axillary bud in a depression extended into a sulcus; adventitious anchor roots numerous, feeder roots rare or absent. *Petiole:* smooth or tuberculate, densely flecked with white spots, 30–55 cm. long, vaginate to the geniculum, the sheath wings deciduous, sometimes persisting as fibrous remains at the base of the petiole, geniculum 3–4 cm. long, often of a rough texture and dark brown. *Lamina:* bright green, often remaining so in dried specimens, of a soft texture, not glossy, trichosclereids absent; 60–120 cm. long, 35–60 cm. wide, ovate to oblong-ovate, cordate at the base, the tip acute, pinnatifid and perforate, the perforations elliptic, 3–6 cm. long, in 1–3 series per side; primary lateral veins 12–18 in number, prominent below and above, milky white, secondary lateral veins reticulate. *Peduncle:* terete, 1.5–2.5 cm. thick, 14–18 cm. long, tuberculate. *Spathe:* white, obovate, 15–18 cm. tall, blunt or shortly mucronate. *Flowering spadix:* deep green to greenish gold, 14–19 cm. long, 3.5–5.5 cm. thick, in dried specimens a golden color, the apical surface of the pistils underlain by a layer of sclereids which form a sharp-edged papery cap in dried specimens.

ETYMOLOGY. Latin *punctulata,* "spotted," in reference to the numerous white spots on the petiole.

DISTRIBUTION. Mexico, Guatemala, Costa Rica, and Panama.

REPRESENTATIVE SPECIMENS. **Mexico. Vera Cruz:** Barranca de Santa Maria, km. 45 on road from Conejo to Jautusco, Sept. 1961, *Moore & Bunting 8861* (BH); 6 miles from Catemaco on road to Sontecomapan, 380 m., Sept. 1961, *Moore & Bunting 8939* (BH). **Oaxaca:** between Chipiltepec and Valle Nacional, 110 m., Aug. 1972, *Madison 633* (GH); 6 km. from Acatlan along road to La Capilla, 100 m., Aug. 1972, *Madison 610* (MEXU). **Guatemala. Petén:** 16°37′N × 89°31′W, 100 m., June 1973, *Madison 1537* (GH). **Costa Rica. Alajuela:** Quebrada La Calera, San Ramón, Feb. 1938, *Brenes 22643* (F). **Cartago:** Rio Virilla, San Juan, Nov. 1913, *Jiminez 922* (US). **Puntarenas:** 1 m. SW of Cañas Gordas, 1170 m., Feb. 1973, *Croat 22280* (MO); Río Coton, 1400–1500 m., 8°55′N × 82°55′W, Jan. 1967, *Burger & Matta 4559* (CR,F,GH,US). **Limón:** Hamburg Finca, Río Reventazon below Cairo, 55 m., Feb. 1925, *Standley & Valerio 48874* (US). **Panama. Chiriqui:** Palo Santo, 3 mi. N of Volcan, Feb. 1971, *Croat 13574* (MO); El Boquete, 1000–1300 m., March 1911, *Pittier 3151* (US). **Darien:** headwaters of Rio Tuquesa, Aug. 1974, *Croat 27179* (MO).

Monstera punctulata is easily recognized by a number of features, among them its brilliant green leaves of a soft texture. These leaves lack trichosclereids, and this is the only species in which I have observed damage to the leaves by leaf-cutter ants, suggesting that the abundant trichosclereids in the leaves of other *Monstera* species may be a defense against such predation. Other features of note are the densely white-spotted petiole with a brown tuberculate geniculum, the prominent white lateral veins of the lamina, and the dark green fruits which dry a golden color.

Monstera punctulata is a rare species in most of its range and is known from a relatively few collections. It is not uncommon in the limestone areas of the central Petén; I collected only a single specimen there as it was not in flower. Later I discovered that this was the first collection of the species from Guatemala.

17. **Monstera spruceana** (Schott) Engler

FIG. 57, MAP 4

Monstera spruceana (Schott) Engler, Flora Brasiliensis **III** (2):115 (1878). *Tornelia spruceana* Schott, Oest. Bot. Zeit. 9:40 (1859). TYPE: Brazil, Amazonas, São Gabriel, March 1852, *Spruce 2293* (K, photo BH,SEL; drawing of holotype = Schott Aroideae No. 2323, W, *non vidi,* photo BH,BR,GH,NY,S).

Climber to 5 m. tall. *Juvenile:* a shingle plant. *Adult stem:* smooth or slightly tuberculate near the nodes, subterete, 2–3 cm. thick, 3–4 cm. wide, internodes 4–10 cm. long, the stem slightly sulcate above the axillary bud. *Petiole:* 25–40 cm. long, the sheath wings disintegrating into fibers, geniculum 5–8 cm. long. *Lamina:* dull dark green, coriaceous, oblong-ovate, somewhat falcate, 50–70 cm. long, 25–40 cm. wide; pinnatifid, the pinnae 5–12 cm. wide with 2–4 primary lateral veins per pinna, pinnae 4–10 per side in number, some leaves pinnatifid on one side only, the lamina base acute to subtruncate, the apex acute; primary lateral veins 12–20 in number, arising at an angle of 70–90° with the costa, the secondary lateral veins subparallel to the primary. *Peduncle:* stout, terete, smooth, shorter than the spadix, 8–13 cm. long, 1.5–2.5 cm. thick. *Spathe:* white, blunt at the apex, 3–4 cm. longer than the flowering spadix. *Flowering spadix:* white, cylindric, tapering gradually toward the apex, 12–25 cm. long, 2.5–3.0 cm. thick, the pistils truncate. *Fruiting spadix:* white, 16–36 cm. long, 4–6 cm. thick.

ETYMOLOGY. After Richard Spruce (1817–1893), British botanist and botanical explorer, collector of the type specimen.

DISTRIBUTION. Costa Rica, Panama, Colombia, Ecuador, Peru, Venezuela, Guyana, and Brazil.

REPRESENTATIVE SPECIMENS. **Costa Rica. Puntarenas:** Golfo Dulce and Río Terraba, 30 m., Dec. 1947, *Skutch 5320* (US). **Panama. Panama:** Cerro Campana, below the summit, 900 m., Oct. 1972, *Madison 763* (GH). **Colombia. Magdalena** (?): Boca de Laino, am Río Magdalena, 100 m., July 1898, *von Bayern 46* (M). **Ecuador. Pichincha:** Road Aloag-Santo Domingo, Toachi, 850 m., Sept. 1967, *Sparre 18446* (S); Alluriquin, 600 m., March 1967, *Sparre 14796* (S). **Los Rios:** Río Palenque Biological Station, 220 m., Sept. 1973, *Dodson & Tan 5303* (US); 20 km. E of Santo Domingo, 680 m., Dec. 1972, *Madison 902* (GH). **Azuay:** Sanaguin, 850 m., May 1943, *Steyermark 52722* (NY). **Peru. Loreto:** Alto Río Itaya, 145 m., Oct. 1929, *Williams 3316* (F,US); Soledad, Río Itaya, 110 m., Sept. 1929, *Killip & Smith 29604* (NY,US). **Venezuela. Yaracuy:** El Guayabito Playon, 15 km. N of Marin, 150–250 m., Nov. 1971, *Steyermark & Bunting 105290* (VEN). **Bolivar:** Sierra Imataca, Río Toro, 200–250 m., Dec. 1960, *Steyermark 88145* (NY,VEN); Cerro Pichacho, 45 km. N of Tumerero, 100–300 m., Feb. 1961, *Steyermark 89207* (VEN). **Guyana.** Pakaraima Mountains, Parima Falls, 600 m., Nov. 1951, *Maguire & Fanshaw 32582* (NY,US, VEN); Minatta, Rupununi River, Oct. 1889, *Jenman 5765* (K). **Brazil. Amapá:** Rio Iaue, 2°53′N × 52°22′W, Aug. 1960, *Irwin, Pires & Westra 47776* (NY). **Amazonas:** São Gabriel, March 1852, *Spruce 2293* (K).

This is one of the few species in section Marcgraviopsis with an

FIG. 57. *Monstera spruceana:* holotype (*Spruce 2293*, K).

adequate, available type specimen, yet its characters remain obscure. Its known wide distribution in eight countries of Central and South America is based on a total of only 18 collections, which are all fairly different from one another. I am of the opinion that at least two species are included in the species as here described, but the paucity of specimens presently available does not permit a meaningful interpretation of the variation among them.

The major morphological features of the species are a pinnatifid leaf with broad pinnae arising at a wide angle from the costa, the petioles one-third to two-thirds the length of the lamina, and the peduncle terete and shorter than the spadix, which is tapered and 16–36 cm. long in fruit. In some specimens, however, the leaf is pinnatifid on only one side, and in *Skutch 5320* it is entire.

That the juvenile of this species is a shingle plant is verified by at least two collections, *Madison 763* and *Killip & Smith 29604*. However, in specimens from western Ecuador, the shingle plant stage is confined to less than a dozen leaves with the transition to the adult form occurring close to the ground.

A further complication for herbarium studies derives from the resemblance of the adult stage of this species to *Monstera dilacerata* and *M. subpinnata* in section Monstera. Though adequate specimens should be easily identifiable, the typical herbarium sheet consisting of a leaf lamina and spadix minus the peduncle makes determination difficult or impossible.

18. Monstera tenuis C. Koch

FIGS. 58–60, MAP 11

Monstera tenuis C. Koch, Ind. Sem. Hort. Bot. Berol. App. 5 (1855). TYPE: Central America, cultivated at Berlin, *Warszewicz* (B?, *non vidi*).

Monstera gigantea Engler, Bot. Jahrb. 37:118 (1905) not *M. gigantea* (Roxb.) Schott. TYPE: Costa Rica, Cartago, Tucurrique, 635 m., Jan. 1899, *Tonduz 13311* (B, *non vidi*, photo BH,GH,US; isotypes P,US).

A robust climber on large trees, to 30 m. tall, with an open habit of growth and exserted arching leaves. *Juvenile:* a shingle plant, the laminae nearly round, mucronate at the apex. *Adult stem:* smooth, 6–8 cm. wide, 4–6 cm. thick, the internodes 8–12 cm. long; leaf scars shallow, less than 2 cm. wide at the widest point, axillary bud in a depression not extended into a sulcus. *Petiole:* ⅓ to ½ the length of the lamina, 30–60 cm. long, vaginate to the lamina base, the sheath wings persistent, to 6 cm. broad near the base, geniculum 3–5 cm. long, 2–3 cm. thick. *Lamina:* bright green, not glossy, oblong ovate, truncate at the base, the apex acute, 60–125 cm. long, 45–70 cm. wide, deeply and regularly pinnatifid, the sinuses extending to the midrib, 12–30 pinnae per side, the pinnae nearly perpendicular to the midrib, 2–5 cm. wide, constricted near the base; primary lateral veins one per pinna, prominent and white abaxially, the secondary lateral veins parallel to the primary. *Peduncle:* subterete, 10–15 cm. long, 3–4 cm. thick. *Spathe:* white, 20–25 cm. tall. *Flowering spadix:* white, cylindric, tapering to the apex, 18–24 cm. long, 3.5–5.0 cm. thick, the pistils truncate. *Fruiting spadix:* green, becoming yellow at maturity, 22–35 cm. long, 5.5–9.5 cm. thick, the seeds oblong, 10–12 mm. long, pistachio green within.

FIGS. 58–60. *Monstera tenuis:* 58. flowering shoot (photo by Timothy Plowman); 59. habit; 60. fruiting spadix, 32 cm. in length.

ETYMOLOGY. Latin *tenuis,* "thin," referring to the membranaceous texture of the juvenile leaf lamina.

DISTRIBUTION. Nicaragua, Costa Rica, Panama, below 1600 meters.

REPRESENTATIVE SPECIMENS. **Nicaragua. Zelaya:** vicinity of Rama, 50 m., Sept. 1972, *Madison 717* (GH). **Costa Rica. Guanacaste:** between Santa Rosa and H. Tenorio, 300–600 m., Sept. 1972, *Madison 722* (GH). **Alajuela:** Forêts de San Ramón, 1500–1600 m., May 1913, *Tonduz 17722* (P). **Heredia:** Río El Angel, between Vara Blanca and Cariblanco, 900–1000 m., March 1953, *Moore 6623* (BH); 10°27′N × 84°07′W, 110 m., May 1973, *Madison 1527* (CR). **Puntarenas:** Finca las Cruces, 4.5 mi. from San Vito de Java, 5000 ft., March 1969, *Stevens 233* (US). **Cartago:** Río Naranjo, 3 km. E of Cachi, 1300 m., April 1969, *Lent 1589* (CR,F,US); Río Sombrero, El Muñeco, 1300 m., June 1972, *Luteyn 3240* (DUKE,MO). **Limón:** 10°5′N × 83°29′W, 50–100 m., Dec. 1969, *Burger & Liesner 6955* (CR,F,MO); 10 km. S of Limón, 0–10 m., Oct. 1972, *Madison 751* (GH); Siquierres, Feb. 1932, *Kupper 582* (M). **Panama. Chiriqui:** 12 km. from Escuela San Benito in Volcán on road to Río Serano, 1200 m., Aug. 1974, *Croat 26495* (MO).

Carl Koch originally described *Monstera tenuis* based on the juvenile stage of a cultivated plant at Berlin, obtained somewhere in Central America by Warszewicz. Koch's specimen was studied by N. E. Brown, who subsequently determined a plant growing at Kew as *M. tenuis.* Whether or not the propagule of the Kew plant was obtained from Berlin is not known. At any rate, the Kew specimen includes both the juvenile and adult leaves, and I am taking it as the basis for interpreting the name *M. tenuis.*

The only other name available for this species, *Monstera gigantea* Engler, is a later homonym of *M. gigantea* (Roxb.) Schott, and is thus illegitimate. Engler and Krause mistakenly applied the name *M. dubia* to this species, and it is illustrated in *Das Pflanzenreich* under that name.

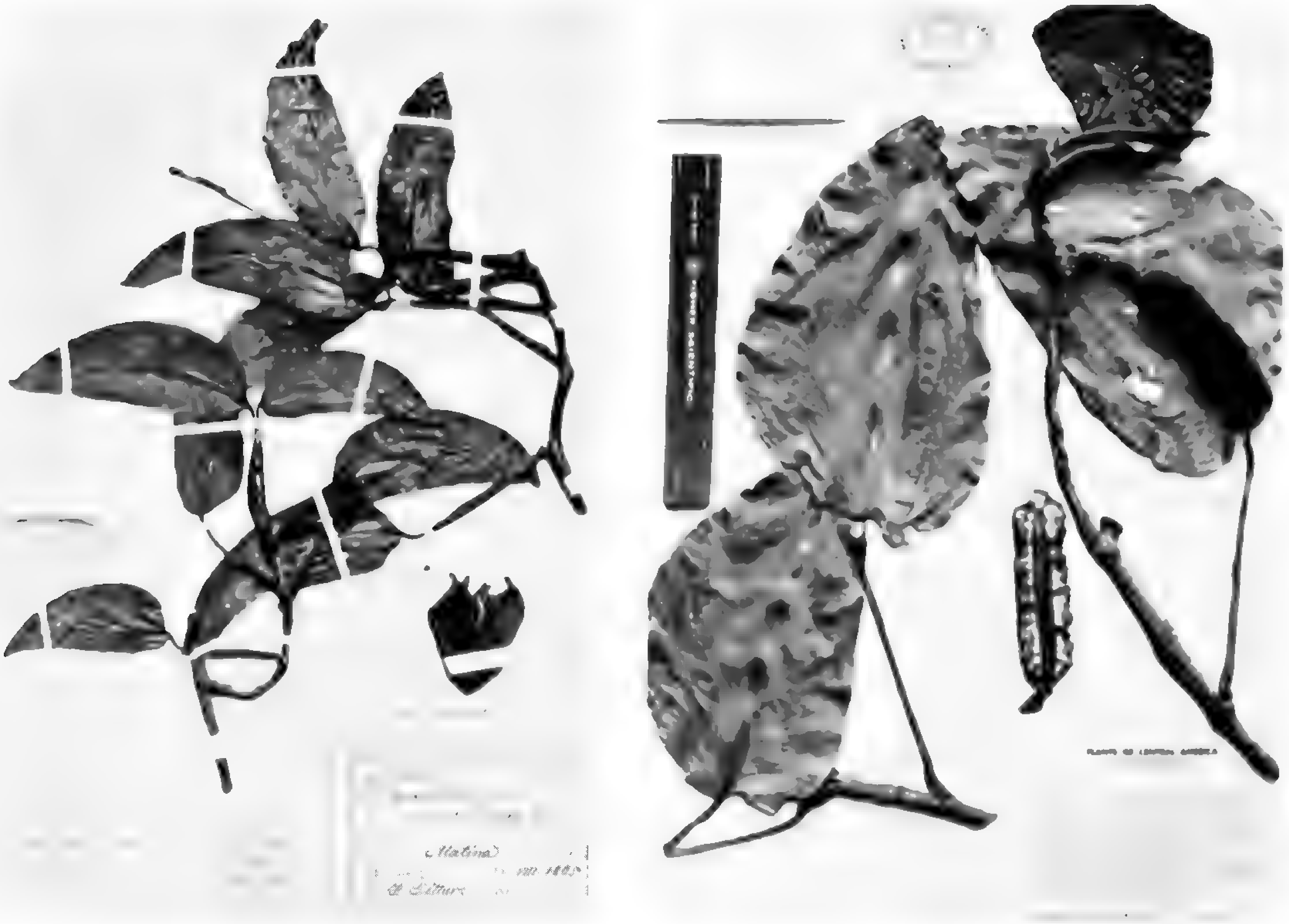
Monstera tenuis is one of the most elegant species of *Monstera,* and is worthy of cultivation. It abounds on the Atlantic coastal plain of Nicaragua and Costa Rica, and ascends the mountains to 1500 meters. It is easily recognized by the regularly pinnatifid leaves with 15–30 pinnae per side, the internodes 8–12 cm. long, and the massive fruiting spadices the dimensions of a man's forearm. At maturity the fruits are often pendent; apparently they are so heavy that the peduncle cannot support them in an erect position.

19. **Monstera pittieri** Engler

FIG. 61, MAP 16

Monstera pittieri Engler, Bot. Jahrb. 37:116 (1905). LECTOTYPE (here designated): Costa Rica, Limón, Matina, Aug. 1895, *Pittier 9766* (B, *non vidi,* photo BH, SEL; isolectotypes CR, BR, US no. 936670). LECTOPARATYPE: Costa Rica, Limón, La Concepción, Llanuras de Santa Clara, 250 m., Feb. 1896, *J. D. Smith 6809* (K, US no. 936671).

Slender climber with pendent shoots from tree branches, the fruit held erect. *Juvenile:* a shingle plant. *Adult stem:* subterete or flattened, 5–10 mm. thick, the internodes 4–9 cm. long, with a thick, tan-colored cuticle which may flake off in dried specimens; adventitious roots lacking in the pendent portions of the stem. *Petiole:* 8–20 cm. long, vaginate nearly to the blade base, the sheath wings ultimately deciduous, sometimes disintegrating into fibres. *Lamina:* coriaceous, dull green, entire,



FIGS. 61–62. 61. (left) *Monstera pittieri*, isolectotype (*Pittier* 9766, US). 62. (right) *Monstera luteynii*, holotype (*Luteyn* 3227, MO).

ovate to lanceolate, 2–5 times longer than wide, strongly falcate and unequal, the base obliquely acute, the apex acute; the veins obscure and not prominent on either surface. *Peduncle:* terete, 2.5–4.0 mm. thick, 2–6 cm. long. *Flowering spadix:* 1.2–1.6 cm. thick, 3–6 cm. long, the pistils truncate at the apex. *Fruiting spadix:* 5–9 cm. long, 2.0–3.5 cm. thick, tapered to either end, the stylar portions of the pistils well separated from one another, giving the fruiting spadix a spiny aspect.

ETYMOLOGY. After Henry Pittier (1857–1950), collector of the type specimen.

DISTRIBUTION. Atlantic Costa Rica, and Panama, below 400 meters.

REPRESENTATIVE SPECIMENS. **Costa Rica. Limón:** Matina, Aug. 1895, *Pittier 9766* (BR,CR,US); La Concepción, 250 m., Feb. 1896, *Smith 6809* (K,US); Río Destierro, Santa Clara, 200 m., June 1899, *Pittier 13398* (US); Guapiles, 250 m., Aug. 1951, *Carpenter 421* (US); Jamburg Finca, Río Reventazon below Cairo, 55 m., Feb. 1926, *Standley & Valerio 48899* (US). **Panama. Colon:** East Ridge, Feb. 1968, *Duke 15280* (US). **Panama:** El Llano-Carti Road, 7–12 km. from Interamerican Highway, 360–400 m., July 1974, *Croat 25175* (MO).

Monstera pittieri is a diminutive climbing and hanging species of Costa Rica and Panama. The Panamanian material is more robust, with larger and more strongly falcate leaves than the Costa Rican plants, but they are clearly the same species.

Monstera pittieri is in appearance like a small version of one of the entire-leaved manifestations of *M. dubia,* and illustrates a possible line of reduction which I hypothesize led to the origin of *M. tuberculata.*

Engler's illustrations of this species in *Das Pflanzenreich* (IV 23B p. 100), are misleading in two respects. He illustrates a flower (fig. H) with six stamens, when the normal number in this species, as in all species of *Monstera,* is four. His drawing of a fruiting spadix (fig. G) shows the pistils tightly crowded together and the spadix with a continuous surface, whereas in the fruiting material I have seen, the stylar portions of the pistils are separate and the surface of the spadix thus irregular and with a spiny aspect. It is this spiny fruit, together with the much narrower leaves, that distinguish *M. pittieri* from *M. luteynii.*

Some specimens of *Monstera pittieri* have been misidentified as *M. falcifolia* (= *M. obliqua*), but the much shorter peduncles and stouter spadices of the former readily distinguish these two species.

20. **Monstera luteynii** Madison, *sp. nov.*

FIG. 62, MAP 16

Planta epiphytica scandens et dependens; rami pendentes floriferi. *Caulis* teres, 5–10 mm. crassus, internodiis 5–9 mm. longis. *Foliorum petiolus* 8–12 cm. longus, ad geniculum usque vaginatus, vagina decidua; *lamina* integra, coriacea, oblique ovata, 12–18 cm. longa, 9–13 cm. lata, basi truncata vel subcordata, apice acuta. *Pedunculus* teres, 5–8 mm. crassus, 1–6 cm. longus. Spatha ignota. *Spadix fructifer* circ. 8 cm. longus, 2 cm. crassus. *Baccae* subprismaticae et truncatae.

TYPE: Costa Rica: Alajuela, along road to and around the edge of Laguna Hule, NE of Cerro Congo, and about 8 km. NW of the village of Cariblanco, 20 km. N of Vara Blanca. Alt. 740–900 m. Vine with stems hanging from trees to 7 m. Spadix olive-green with white dots over surface. Pedicel warty, also stems. Abundant on one tree seen. June 1972. *Luteyn 3227* (holotype MO no. 2180600; isotypes US no. 2684199. DUKE no. 230028).

ETYMOLOGY. Named for James L. Luteyn, ardent collector of Costa Rican Araceae.
DISTRIBUTION. Costa Rica, Provinces of Cartago and Alajuela.
REPRESENTATIVE SPECIMENS. **Costa Rica. Cartago:** Forêts des Tuis, 650 m., Nov. 1897, *Pittier 11370* (BR,US); Forêts de La Vueltas, Tuqurrique, 635–700 m., Jan. 1899, *Tonduz 13312* (US); Las Vueltas, Tuqurrique, 635 m., Dec. 1898, *Tonduz 12841* (GH,K,US).

Monstera luteynii is one of several species of *Monstera* which characteristically flower on pendent shoots. It is perhaps closest to *M. dubia,* from which it differs by its much smaller and entire leaves, narrower stems, and very short peduncles.

Monstera luteynii resembles two other pendent species with entire leaves, *M. pittieri* and *M. tuberculata.* However, both of these have the stylar portions of the pistils separate in the fruiting spadix, giving the spadix a spiny aspect. This is in contrast to the smooth fruiting spadix of *M. luteynii. Monstera pittieri* may be distinguished vegetatively by its lanceolate leaves, 2–5 times longer than wide, whereas in *M. luteynii* the leaves are ovate and less than two times longer than wide. *Monstera tuberculata* has petioles less than 4 cm. long with the sheath extended into a ligule equalling the petiole, in contrast to the petioles of *M. luteynii* which are 8–12 cm. long with a very short ligule.

MONSTERA section ECHINOSPADIX Madison, *sect. nov.*

Plantula stoloniformis. Folia stirpium juvenilium ad truncis arborum adpressae. Vagina petioli foliorum omnium ligulata, ligula petiolum aequans. Pistillum maturum 6–7 mm. latum. Spadix pendens.
TYPE SPECIES: *Monstera tuberculata* Lundell.

Monstera tuberculata, while showing close affinity to section Marcgraviopsis, is placed in a separate section because of two specializations. The third (adult) phase of heteroblastic development as seen in section Marcgraviopsis is not represented here; *Monstera tuberculata* flowers on what is morphologically a juvenile (second phase) shoot in section Marcgraviopsis. *Monstera tuberculata* is the only species with pendent spadices; in all others the spadices are held erect, even if produced on hanging shoots.

21. **Monstera tuberculata** Lundell

FIGS. 63–66, MAP 13

Climbing and hanging epiphyte, flowering in the pendent portions, the juvenile and adult not distinct. *Adult stem:* terete, verruculose, with a thick tan cuticle which flakes off if the stem is twisted, 1.0–1.5 cm. thick, the internodes 6–12 cm. long, a tuft of adventitious roots borne near each node. *Petiole:* 1–4 cm. long, canaliculate to within 6 mm. of the blade base, the sheath wings extended into a ligular outgrowth as long as or exceeding the petiole, 2–6 cm. long, this and the sheath wings deciduous. *Lamina:* entire, coriaceous, smooth or papillose, obliquely ovate, cordate at the base, mucronate or acute at the apex, 8–18 cm. long, 5–11 cm. wide, the lateral veins subparallel, not separable into primary and secondary laterals. *Peduncle:* smooth, terete, 2–6 mm. thick, 4–8 cm. long, the inflorescence pendent. *Spathe:* white, when open

FIGS. 63–66. 63. *Monstera tuberculata* var. *tuberculata*, habit (*Madison 631*, SEL); 64–66. *Monstera tuberculata* var. *brevinoda*: 64. leaf, showing ligule; 65. fruit; 66. inflorescence (all *Madison 752*, cu).

about as wide as tall, 5–9 cm. tall, 5–10 cm. across when open, acuminate, the acumen 1.0–1.5 cm. long. *Flowering spadix:* white, 2–3 cm. thick, 6–9 cm. long, the pistils extended into a conical acuminate style 4–8 mm. long, curved toward the apex of the spadix. *Fruiting spadix:* green, 7–11 cm. long, 4.5–5.5 cm. thick, the berries 7–9 mm. across, the curved stylar region ultimately deciduous to reveal the seeds in a slimy gray pulp. *Seeds:* brown, oblong, 9–12 mm. long, 4–5 mm. across.

KEY TO VARIETIES

Outer surface of the pistil smooth, with no clear demarcation of the style and ovary. .... var. *tuberculata.*

Style arising from a depression on the apex of the ovary, resulting in a pronounced ridge around the pistil at the junction of the style and ovary. .... var. *brevinodum.*

21a. **Monstera tuberculata** Lundell var. **tuberculata**

Monstera tuberculata Lundell, Lloydia **2**:78 (1939). TYPE: Belize, El Cayo District, Valentin, on trees in high advanced forest, June 1936, *C. L. Lundell 6238* (MICH, *non vidi;* isotype GH).

As described in the key, the distinctive feature of this variety is the smooth surface of the pistils with the ovary not demarcated from the style.

ETYMOLOGY. Latin *tuberculata,* "tuberculate," in reference to the spiny aspect of the spadix.

COMMON NAMES. Chile montaña, trepepoyo (Mexico).

DISTRIBUTION. Mexico, Guatemala, Belize, at low elevations.

REPRESENTATIVE SPECIMENS. **Mexico. Oaxaca:** Mogoñe, March 1953, *MacDougall* MEXU *no. 76682* (MEXU); Ubero, 30–90 m., June 1937, *L. Williams 9454* (F). **Vera Cruz:** Playa Escondida, 28 km. NE of Catemaco, 50 m., Aug. 1972, *Madison 631* (SEL); 4 km. NE of Minatitlan, 50 m., Aug. 1958, *King 1114* (MICH,US). **Tabasco:** Estapilla, Tenosique, June 1939, *Matuda 3495* (MEXU,MICH). **Guatemala. Alta Verapaz:** Río Sebol, downstream from Carrizal, 150–200 m., April 1942, *Steyermark 45788* (F,US). **Petén:** 5 mi. S of entrance to Tikal National Park, June 1973, *Croat 24747* (MO). **Izabal:** Bay of Santo Tomas, 2 m., April 1940, *Steyermark 39246* (F). **Livingston:** Río Dulce, 0 m., March 1889, *J. D. Smith 1533* (GH,US). **Belize. El Cayo District:** Valentin, June 1936, *Lundell 6238* (GH,MICH).

21b. **Monstera tuberculata** Lundell var. **brevinodum**
(Standl. & L. O. Wms.) Madison, *stat. et comb. nov.*

Philodendron brevinodum Standl. & L. O. Wms., Ceiba **1**:231 (1951). TYPE: Costa Rica, Cartago, Turrialba, Moravia, 1100 m., June 1950, *Jorge Leon 2548* (photo NY, US no. 2215909).

In this variety there is a sharp ridge around the pistil demarcating the junction of the style and ovary.

ETYMOLOGY. Latin *brevinodum,* "short nodes," as the species was considered to have short internodes (?) for a *Philodendron.*

DISTRIBUTION. Costa Rica.

REPRESENTATIVE SPECIMENS. **Costa Rica. Alajuela:** W slope of Volcán Arenal, 300 m., Sept. 1972, *Madison 725* (CR). **Cartago:** Turrialba, Moravia, 1100 m., June 1950, *Leon 2548* (US). **Limón:** Zent, 50 m., Oct. 1972, *Madison 752* (CR,GH,MO); Río Santa Clara, 1.6 km. E of Guapiles, 200 m., July 1949, *Holm & Iltis 409* (A,F,P,U).

Monstera tuberculata was first collected in 1889 in Guatemala by J. Donnell-Smith. Engler erroneously identified this specimen as *M. acuminata* Koch, and redefined the species to include Donnell-Smith's specimen. Subsequent collections of *M. tuberculata* have mostly been determined as *M. acuminata.* In his original description of *M. tuberculata,* Lundell remarked that it seemed close to *M. acuminata* Koch, but since the application of the latter name has been quite chaotic to the present, it is not clear what relationship he intended to indicate by that statement.

Monstera tuberculata shows a disjunction between Guatemala-Mexico and Costa Rica, although in the intervening area there is continuous wet lowland forest which appears to be a suitable habitat for the species. The northern and southern populations have diverged strikingly in the morphology of the gynoecium, though they are indistinguishable in other respects. I have separated these two gynoecial types as varieties. It is possible that botanical exploration in Nicaragua and Honduras will turn up intermediate forms.

Monstera tuberculata seems most closely related to the pendent species of section Marcgraviopsis—*M. pittier, M. luteynii,* and *M. dubia*—all of which are distinguished from it by their erect fruits and long-petiolate leaves. The adult leaves of *M. tuberculata* have the asymmetric lamina with a short petiole and long ligule typical of the juvenile (shingle plant) stage of these species, and in my opinion *M. tuberculata* is vegetatively a neotonous derivative of section Marcgraviopsis. In its floral morphology, however, the species is highly specialized. It is the only species with pendent spadices, and the curvature and attenuation of the styles are probably related to the pendent orientation of the spadix, although the mechanism of the relationship is not known. In other species of *Monstera* the sterile flowers at the base of the spadix often have long curved styles, suggesting that the genetic capability for producing this kind of flower is present throughout the genus.

A specimen of *Monstera tuberculata* from Tabasco (*Matuda 3380*) is annotated "comestibile;" presumably it is the ripe spadix which is edible. A peasant living near the locality of *Madison 752* (Zent, Prov. Limón, Costa Rica) showed me rough baskets used for storing maize made from the pendent stems of this species.

MONSTERA section TORNELIA Madison, *stat. nov.*

Tornelia Guttierez, Linnaea 26:382 (1853).

Folia plantulae et stirpis juvenilis exserti. Pistillum maturum 10–18 mm. latum; semina 16–22 mm. longa. Spadix erectus.

TYPE SPECIES: *Monstera deliciosa* Liebm.

Monstera deliciosa does not show the heteroblastic development of section Marcgraviopsis, but neither is it similar to the species of section Monstera. A number of features distinguish it: (1) in large-leaved individuals the petiole is vaginate for only $\frac{1}{6}$ its length, as opposed to at least $\frac{5}{6}$ the length in other species; (2) the juvenile leaf has a petiole 2–4 times the lamina length, as opposed to less than or equalling the lamina length in other species; (3) axillary buds are represented only by a swollen region on the stem rather than being distinct and prominent; (4) anatomically, of 16 species I have investigated it is the only one to have asterosclereids in the leaf lamina, and the only one to have trichosclereids in the roots; (5) the berries are about twice the width and the seeds twice the weight of those of other species; and (6) *M. deliciosa* often grows to maturity as a terrestrial or rupestral plant, whereas other *Monstera* species flower only as epiphytes, or very rarely on rocky cliffs.

22. **Monstera deliciosa** Liebmann

FIG. 67, MAP 10

Monstera deliciosa Liebmann, Kjoeb. Vidensk. Meddel. **19**:9 (1849). *Tornelia fragarans* Guttierez, Linnaea **26**:382 (1853). TYPE: Mexico, Oaxaca, Western Cordillera, 5000–7000 ft., Dec. 1842, *Liebmann s.n.* (C).

Monstera borsigiana Engler, D. C. Monog. Phan. **II**:266 (1879). *Monstera deliciosa* Liebm. var. *borsigiana* (Engler) Engler and Krause, Das Pflanzenreich IV **23B**:111 (1908). TYPE: Mexico, Valle de Cordoba, Jan. 1866, *Bourgeau 1904* (holotype B, *non vidi;* isotypes BR,C,GH,L,LEP,S,US).

Monstera tacanaensis Matuda, Ann. Inst. Biol. Univ. Nat. Aut. Mex. **43**: Ser. Bot. (1)55 (1972, published 1974). TYPE: Mexico, Chiapas, Unión Juarez, W slope of Volcán Tacana, 850 m., Feb. 1969, *Matuda 37584* (MEXU).

Monstera deliciosa Liebm. var. *sierrana* Bunting, Gentes Herbarum **9**:320 (1965). TYPE: Mexico, Oaxaca, Sierra de Juarez, 15 mi. S of Valle Nacional on road to Oaxaca, 1220 m., Sept. 1961, *Moore & Bunting 8918* (holotype BH no. 100023; isotypes UC no. 1327227, K, US no. 2578977).

Philodendron pertusum Kunth & Bouché, Ind. Sem. Hort. Berol.:11 (1848). *Monstera lennea* C. Koch, Bot. Zeit. **10**:277 (1852) based on the same type as *P. pertusum.* TYPE: cultivated at Berlin, propagule collected in Guatemala by Warscewicz, C. Koch (B, destroyed? *non vidi*).

Stout sprawling plant, rupestral or epiphytic. *Juvenile:* a terrestrial creeper, the leaves with erect petioles about twice the length of the lamina, the lamina thickly coriaceous, glossy deep green adaxially, pale abaxially, ovate, cordate at the base, acuminate at the tip. *Adult stem:* smooth, green, 2–8 cm. thick, the internodes 4–10 cm. long, the axillary buds not distinct but represented by a swollen region of the stem above the node. *Petiole:* 30–100 cm. long, tuberculate or smooth, vaginate for ⅙ to 9/10 its length, the sheath wings marcescent or deciduous, geniculum 2.0–3.5 cm. long, sometimes with a crispate margin. *Lamina:* coriaceous, glossy adaxially, pale green abaxially, ovate, 25–90 cm. long, 25–75 cm. wide, shorter than the petiole, cordate at the base, acute or mucronate at the apex; regularly pinnatifid, perforate or not, the perforations in 1–5 series per side, elliptic, 0.5–8.0 cm. long; primary lateral veins prominent abaxially, 6–14 in number per side, the secondary lateral veins reticulate. *Peduncle:* tuberculate or smooth, terete, 1.0–1.8 cm. thick, 10–18 cm. long. *Spathe:* white or cream to yellow, thickly coriaceous, 16–25 cm. long. *Flowering spadix:* white or green, 10–18 cm. long, 2.5–3.0 cm. thick, the pistils truncate, 6–11 mm. across. *Fruiting spadix:* green or bluish-green, 15–22 cm. long, 4.5–6.0 cm. thick, the berries 10–18 mm. across. *Seeds:* spheroidal, 16–22 mm. long, 10–13 mm. across, green within.

ETYMOLOGY. Latin *deliciosa,* "delicious," in reference to the sweet edible fruits.

COMMON NAMES. Harpón (Guatemala); Piñanona (Mexico).

DISTRIBUTION. Mexico, Guatemala, Costa Rica, Panama.

REPRESENTATIVE SPECIMENS. **Mexico. Oaxaca:** western Cordilliera, 5000–7000 ft., Dec. 1842, *Liebmann, s.n.* (C); 15 mi. S of Valle Nacional, 1200 m., Sept. 1961, *Moore & Bunting 8918* (BH,K,UC,US); 40 km. above Pochutla on road to Oaxaca, 950 m., Oct. 1974, *Madison 1803* (MEXU). **Vera Cruz:** Laguna Encantada near San Andrés

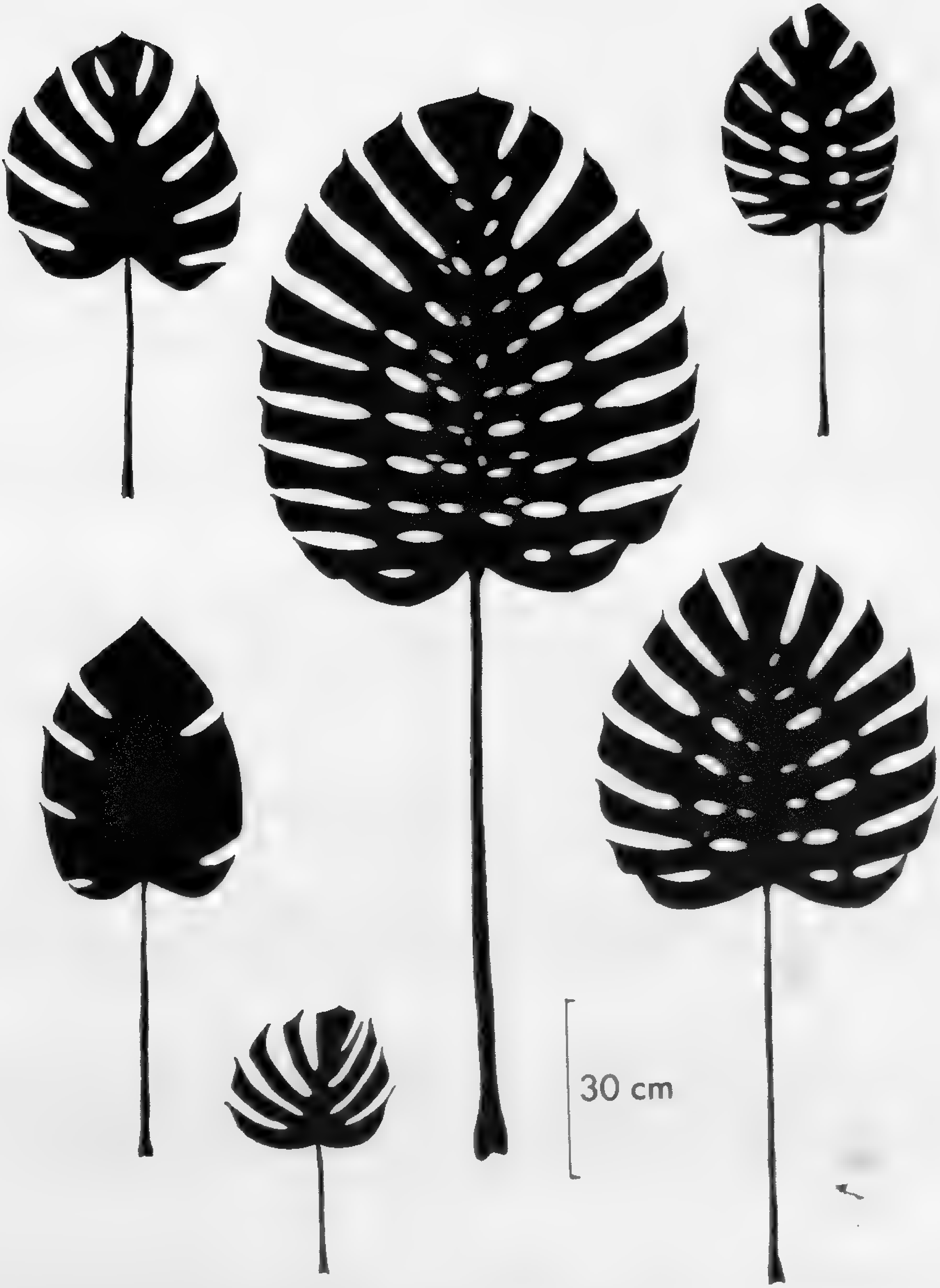


Fig. 67. *Monstera deliciosa:* variation in adult leaf shape, from different individuals (to the same scale).

Tuxtla, April 1952, *Moore & Cetto 6231* (BH,MEXU); Barranca de Santa Maria, km. 45 on Conejo-Huatusco road, Sept. 1961, *Moore & Bunting 8860* (BH). **Chiapas:** canyon N of Chacona NW of Tuxtla G., Dec. 1949, *Miranda 5842* (MEXU); Unión Juarez, W slope of Volcán Tacana, 850 m., Feb. 1969, *Matuda 37584* (MEXU). **Guatemala. Huehuetenango:** Paso del Boqueron, below La Libertad, 1200–1300 m., Aug. 1942, *Steyermark 51186* (F,US); above Democracia on trail towards Jutal, 1000 m., Aug. 1952, *Steyermark 51060* (F,MO). **Quezaltenango:** 10 miles from Colomba on road to San Juan, 1850 m., Aug. 1972, *Madison 657* (GH). **San Marcos:** S facing slopes of Volcán Tajumulco, 1300–1500 m., March 1940, *Steyermark 37200* (F); Finca Vergel, near Rodeo, 900 m., March 1939, *Standley 68917* (F). **Costa Rica. Alajuela:** 8 km. from La Fortuna on road to Chachagua, 250 m., Sept. 1972, *Madison 727* (CR). **Puntarenas:** 6 km. S of San Vito de Java, 5000 ft., Aug. 1967, *Raven 21860* (CR,GH). **San José:** 9°29′N × 83°37′W, 1600 m., Dec. 1969, *Burger & Liesner 7103* (CR,F). **Panama. Chiriqui:** Bajo Chorro, 1900 m., July 1940, *Woodson & Schery 634* (F,GH,MO); roadside S of Cerro Punta, May 1970, *Croat 10434* (MO, UC). **Veraguas:** 5 mi. W of Santa Fé on Pacific side of divide, 800–1200 m., March 1973, *Liesner 909* (MO).

Monstera deliciosa is one of the most widely cultivated of ornamental plants. Its handsome dark leaves, slow rate of growth, and tolerance of shade and low humidity make it an excellent house plant for temperate regions. In the tropics it is widely grown both indoors and as a garden and patio plant.

Monstera deliciosa was first collected in Mexico by Karwinsky in 1832, but his specimen attracted no attention at Munich where it was sent. The species was next collected by Liebmann in 1842, who introduced it into cultivation by bringing cuttings from Mexico to Copenhagen. A second introduction was made in 1846 by Warscewicz, who sent cuttings to Berlin from Guatemala. The subsequent cloning of these two introductions is probably responsible for much of the *M. deliciosa* in cultivation today, as the species is rare in the wild and not often collected.

The species was first given a name by Kunth and Bouché who, in 1848, described the cultivated plant at Berlin as *Philodendron pertusum*. The following year Liebmann described his collection as *Monstera deliciosa*. Kunth and Bouché's name is older and has priority, but the epithet *pertusum* in *Monstera* is preoccupied by *Monstera pertusa* (Roxb.) Schott (1830). Thus, the earliest available legitimate name is *M. deliciosa* Liebm. In his description of the species, Liebmann makes no reference to Warscewicz's collection or to the name *Philodendron pertusum* Kunth and Bouché; clearly he is describing a new species rather than giving a *nomen novum* to *Philodendron pertusum* Kunth and Bouché, and *Monstera deliciosa* is thus typified by Liebmann's specimen and not by the type of *Philodendron pertusum*.

Guttierez (1853) proposed the new name *Tornelia fragrans* for *Monstera deliciosa*; the epithet is superfluous. The genus *Tornelia* was accepted by Schott but by no other authors. Carl Koch (1852) redescribed the Warscewicz plant at Berlin as *Monstera lennea*, considering it to be a different species from *M. deliciosa* (Koch, 1857).

Several species and varieties have been segregated from *Monstera* *deliciosa* on the basis of characters which are primarily related to differences in size. The largest clones at maturity have leaves four times the size of the smallest mature clones. The smallest ones have smooth petioles vaginate most of their length whereas the largest ones have tuberculate petioles vaginate for only $\frac{1}{6}$ their length. Although these differences are considerable, they represent extremes of a continuum in which numerous intermediate conditions are to be found. Under these circumstances I consider it most useful to recognize *M. deliciosa* as a polymorphic species without separating its different forms as varieties.

Monstera deliciosa is either rupestral or epiphytic, and the data accompanying about half of the specimens I have seen describe it as terrestrial. The large population at the type locality of var. *sierrana* grows almost entirely sprawling on the ground, rarely climbing the lower 1–2 m. of tree trunks. On the other hand, I have several times observed the species as an epiphyte climbing to 20 meters *(Madison 727, 1803).*

A chromosome count of $2n=60$ was made for this species by Pfitzer (1957). This was interpreted by Marchant (1970) as a hexaploid based on $x=10$.

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SYNOPSIS OF MONSTERA SPECIES

SECTION MONSTERA

SECTION MARCGRAVIOPSIS MADISON

SECTION ECHINOSPADIX MADISON

SECTION TORNELIA MADISON

INCLUDED NAMES

EXCLUDED NAMES AND NOMINA NUDA

Monstera amomifolia Poepp. & Endl. = Stenospermation amomifolium (Poepp. & Endl.) Schott
M. cannaefolia (Rudge) Schott = Philodendron cannifolium (Rudge) Engler
M. cannaefolia Kunth = Spathiphyllum cannaefolium (Dryand) Schott
M. cuspidata Gard. = Philodendron propinquum Schott
M. decursiva (Roxb.) Schott = Rhaphidophora decursiva (Roxb.) Schott
M. gigantea (Roxb.) Schott = Epipremnum giganteum (Roxb.) Schott
M. latevaginata Engler & Krause = Scindapsus sp. ?
M. lingulata (L.) Schott = Philodendron lingulatum (L.) C. Koch
M. moritziana (Schott) Steyerm. = Rhodospatha sp.
M. occidentalis (Poepp.) Koch ex Ender = Scindapsus occidentalis Poepp.
M. officinalis (Roxb.) Schott = Scindapsus officinalis (Roxb.) Schott
M. peepla (Roxb.) Schott = Rhaphidophora peepla (Roxb.) Schott
M. pinnata (L.) Schott = Epipremnum pinnatum (L.) Engler
M. roseospadix Matuda = Rhodospatha roseospadix (Matuda) Matuda

NOMINA NUDA:

Monstera calloides Mortiz ex Ender, Index Aroidiarum 53 (1804).
M. glauca C. Koch ex Ender, Index Aroid. 54 (1804).
M. guatemalensis Bartlett, Carnegie Inst. Wash. Pub. 461:17 (1935).
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M. inaequilatera Pr. ex Ender, Index Aroid. 54 (1804).
M. multijuga C. Koch ex Ender, Index Aroid. 54 (1804).
M. protensa Schott ex Engler, Flora Brasiliensis III (2):114 (1878).
M. trijuga C. Koch ex Ender, Index Aroid. 55 (1804).

CHROMOSOME NUMBERS OF CRUCIFERAE III[1]

REED C. ROLLINS AND LILY RÜDENBERG

The chromosomes of the Cruciferae in general are hard to work with being both small and often resistant to the usual cytological techniques. There are exceptions to this and the chromosomes of such genera as *Physaria* and *Lesquerella* are not only larger than those of most other cruciferous genera but they are relatively easy to handle. The monotypic genus *Asta* from Mexico, which we have examined cytologically for the first time, has chromosomes much like those of *Physaria* and thus joins a select small group of genera of the Cruciferae with relatively large chromosomes that are reasonably easy to handle.

The following chromosome counts are based on two types of material: fixations of buds in the field, in which case the count was obtained from pollen mother cells (PMC) or immature pollen grains, the count given as *n;* or plants grown from seeds of wild plants where either root-tips were used with the count reported as $2n$ or, if buds were used in determining the latter type of material, the report follows the pattern of bud fixations from wild sources. The herbaria in which voucher specimens are deposited are indicated by the usual designations for herbaria (Holmgren and Keuken, 1974).

Arabis

A. aculeolata Greene

$2n = 32$: plants from seeds of *K. L. Chambers 3188* with Duane Isely, Rough and Ready Botanical Wayside, 5 miles south of Cave Junction on Hwy. 199, Josephine Co., Oregon, OSC.

This is an important count as far as North American *Arabis* is concerned because it helps establish that the two base numbers $x = 7$ and $x = 8$ are both present in strictly North American species. By far the largest number of species that have been counted from North America are based on $x = 7$. However, *A. alpina, A. hirsuta,* and *A. lyrata* are based on $x = 8$ both in Europe or Asia and in North America if the full taxonomic extent of each species is taken into account. Another species, *A. arenicola* (Richardson) Gelert, has been counted from West Greenland, $n = 8$ and $2n = 16$, by Böcher (1966) and from Ungava, Quebec, Canada, $2n = 16$, by Hedberg (1967). This is an exclusively North American species.

The situation now seems clear, as it was not earlier (Rollins, 1966), that those species of North America most closely related to *Arabis* of Eurasia have the same basic chromosome number pattern, i.e., $x = 8$, whereas

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[1] The first two papers in this series were published in Contrib. Gray Herb. no. CXCVII:43–65, 1966, and Contrib. Gray Herb. no. 201:117–133, 1971. Some of the field work involved in this research was supported by funds from National Science Foundation Grant GB-30720 to the senior author.

those species with a somewhat different circle of close affinity are based on $x = 7$. Löve and Löve (1975) have seized this situation as a basis for erecting the new genus *Boechera* to accommodate species with $x = 7$. They did not give any reasons of consequence for doing this and I cannot agree that a different basic chromosome number alone is sufficient evidence to warrant making the kind of separation they proposed. In studying *Arabis* as it occurs in western North America some years ago (Rollins, 1941a), I concluded that truly natural subdivisions of the genus were not present and I have not seen clear evidence since then that dictates a splitting up of *Arabis* or a formal taxonomic ordering of it on an infrageneric basis. In my view, their describing a new genus to accommodate perfectly ordinary species of *Arabis* has no merit and should not be followed.

A. *drummondii* Gray

$n = 7$, $2n = 14$: plants from *Twisselmann et al. 19172,* Tulare Co., California, GH. This count is consistent with others we have of the species (Rollins, 1966).

A. *fendleri* (Wats.) Greene var. *fendleri*

$2n = 21$: plants from seeds of *Beatley and Reveal 10788,* Nye Co., Nevada, GH. Three plants were analyzed in detail. Two of the three were consistently $2n = 21$. In a tapetal cell of the third plant, the number $2n = 22$ was found. Random counts in other plants convinced us that $2n = 21$ is the most frequent and regular number of the population sampled.

Previous counts of $n = 7$, $n = 14$, $n = 21$ and $2n = 14$ have been found in A. *fendleri* including var. *spatifolia* (Rollins 1941, 1966).

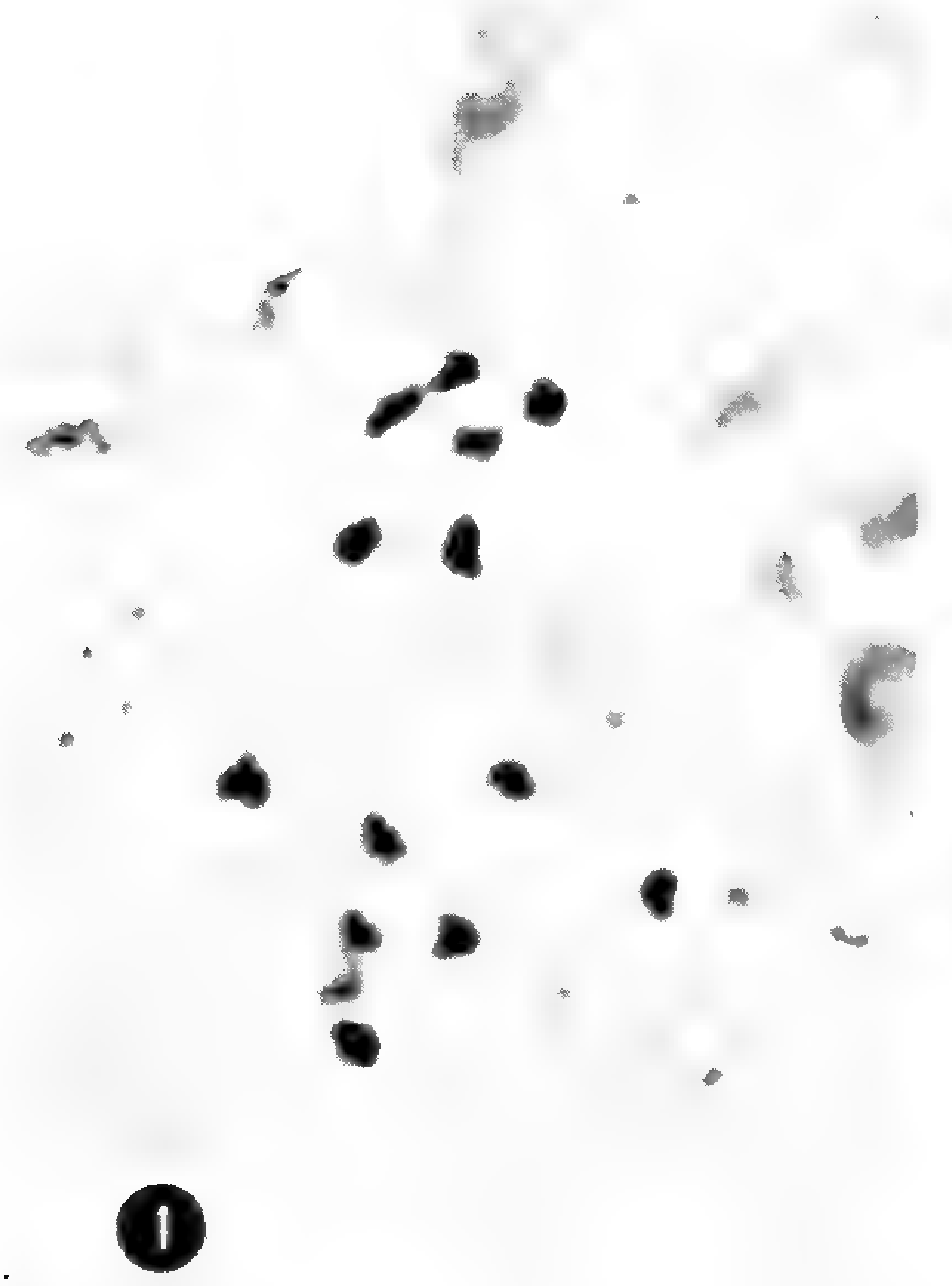
A. *petiolaris* (Gray) Gray

$n = 14$, $2n =$ ca. 28: plants from seeds of *Barclay 3102,* Llano Co., Texas, GH. Somatic cells with reasonably good figures of chromosomes could not be read with complete accuracy. The haploid count in PMC's of $n = 14$ establishes the count for *Arabis petiolaris* but it does nothing to help clarify further the relationship of this apparently anomalous species. Gray (1849) originally described it as *Streptanthus petiolaris* probably reflecting the resemblance of the fruits and seeds to such species of *Streptanthus* as S. *platycarpus* and S. *carinatus.* The chromosome number fits with *Streptanthus* but it is also consistent with most North American species of *Arabis* which have a base number of $x = 7$. Certainly the flowers are not streptanthoid and it would be difficult if not impossible sensibly to admit *Arabis petiolaris* into the genus *Streptanthus.*

We have not seen any previous chromosome counts of *Arabis petiolaris.*

A. *holboellii* Hornem. var. *retrofracta* (Grah.) Rydb.

$n = 7$: plants from seeds of *Walter Knight et al. 2437,* Plumas Co., Calif., GH. Figures in a few cells seem to show $n = 8$ which could easily be the



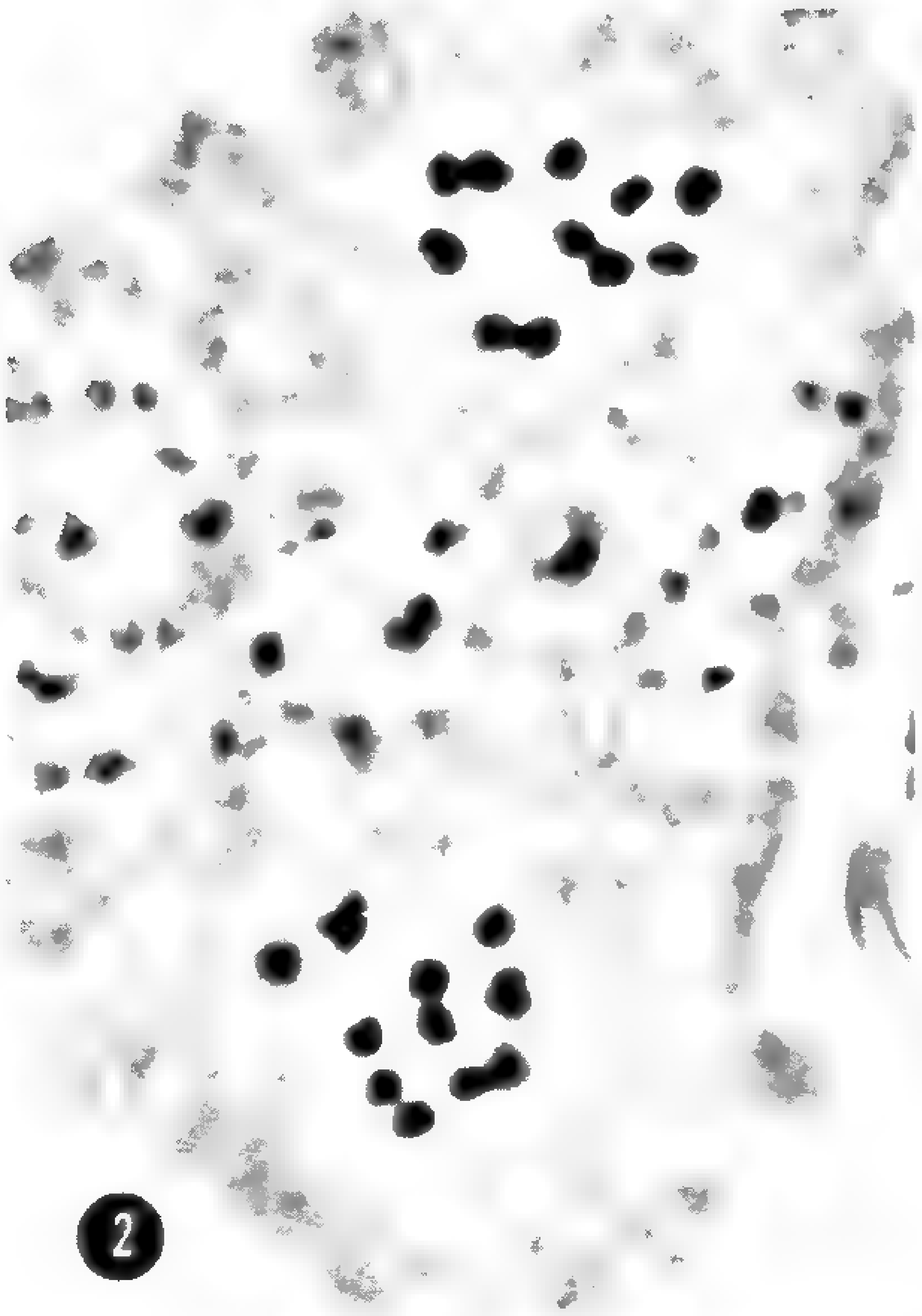


PLATE 1. FIG. 1, *Arabis petiolaris*, $n = 14$, Barclay 3102. FIG. 2, *Leavenworthia alabamica* var. *alabamica*, $n = 11$, Rollins 7163. FIG. 3, *Lesquerella fendleri*, $n = 6$, Rollins 7151. FIG. 4, *Lesquerella schaffneri*, $n = 6$, Rollins and Roby 74123.

case if the plants were members of an apomictic population. Apomixis is known to occur in *A. holboellii* var. *retrofracta.*

A. selbyi Rydb.

$2n$ = ca. 21: field fixed material, Montezuma Co., Colorado, *Rollins and Stafleu 7135,* GH. The fixation was not ideal and we could not be certain of the count. However, it does appear that a triploid is represented by this material and this suggests the possibility of apomixis being present. *Arabis selbyi* is a member of the *A. holboellii* complex where apomixis is known to occur.

A. subpinnatifida Wats.

$n = 7$: count by Kenton L. Chambers, Josephine Co., Oregon, *Chambers 2479* with George York, OSU.

$n = 7$: plants from seeds of *Ground and Muth 1788,* Josephine Co., Oregon, GH.

We have not seen any previously published counts for *Arabis subpinnatifida.*

Asta

A. schaffneri (Wats.) Schulz var. *pringlei* (Schulz) Roll.

$n = 10$: field fixed material, 29 miles south of Saltillo, Coahuila, Mexico, *Rollins and Roby 7491,* GH.

As far as we know, this is the first chromosome count for the monotypic genus *Asta.* The chromosome number $n = 10$ is sufficiently different from $n = 8$, which seems to characterize *Cibotarium,* to support the continuation of *A. schaffneri* as a unique genus (see Rollins, 1941b). Species of *Cibotarium* and *Asta schaffneri* were at one time placed in *Capsella* but they have only a remote relationship to that genus.

Cardamine

C. curvisiliqua Shuttl. ex Chapman

$n = 16$: plants transplanted to the greenhouse from Lake County, Florida, *Rollins and Roby 7311,* GH. This tetraploid count is consistent with a base number $x = 8$, which characterizes most species of *Cardamine* (see Mulligan, 1965, for counts and references).

C. hirsuta L.

$2n = 16$: plants from seeds of *Rüdenberg 7305,* Madison Co., Alabama, GH. Agrees with previous counts.

Caulanthus

C. divaricatus Roll.

$n = 11$: plants from seeds of *Al-Shehbaz 6906,* Emory Co., Utah, GH.

Cibotarium

C. macropetalum Roll.

$n = 8$: 29 miles south of Saltillo, Coahuila, Mexico, *Rollins and Roby 7489*, GH.

$n = 8$: 9.6 miles west of Concepcion del Oro, Zacatecas, Mexico, *Rollins and Roby 74137*, GH.

C. stellatum (Wats.) Schulz

$n = 8$: 29 miles south of Saltillo, Coahuila, Mexico, *Rollins and Roby 7490*, GH.

These are the first known counts for the genus *Cibotarium*. By happenstance, the two species that grow together are the first to be studied cytologically. There was no evident hybridization between *C. macropetalum* and *C. stellatum* at the Coahuila site. It is assumed these species are genetically as well as morphologically distinct.

Coronopus

C. didymus (L.) Sm.

$n = 16$: Galveston Co., Texas, *Rüdenberg s.n.*, GH. This is in accord with several previous counts on Old World plants. The species is widely distributed as a weed. It is not native to the western hemisphere.

Descurainia

D. californica (Gray) Schulz

$n = 7$, $2n = 14$: plants from seeds of *J. Beatley et al. 11484*, Nye Co., Nevada, GH. As far as we can determine, this is the first count for *D. californica*.

D. pinnata (Walt.) Britt.

$n = 7$: Sarasota Co., Florida, *Rüdenberg 7301*, GH.

D. pinnata subsp. *halictorum* (Cockerell) Detling

$n = 7$: plants from seeds of *Beatley and Reveal 11247*, Nye Co., Nevada, GH.

$n = 7$: Quay Co., New Mexico, *Rollins and Stafleu 7155*, GH.

D. virletii (Fourn.) Schulz

$n = 14$: plants from seeds of *Rollins and Tryon 58210*, San Luis Potosí, Mexico, GH. First count for this species.

The chromosome number in *Descurainia* shows polyploidy but so far, no aneuploidy.

Dithyrea

D. wislizenii Engelm.

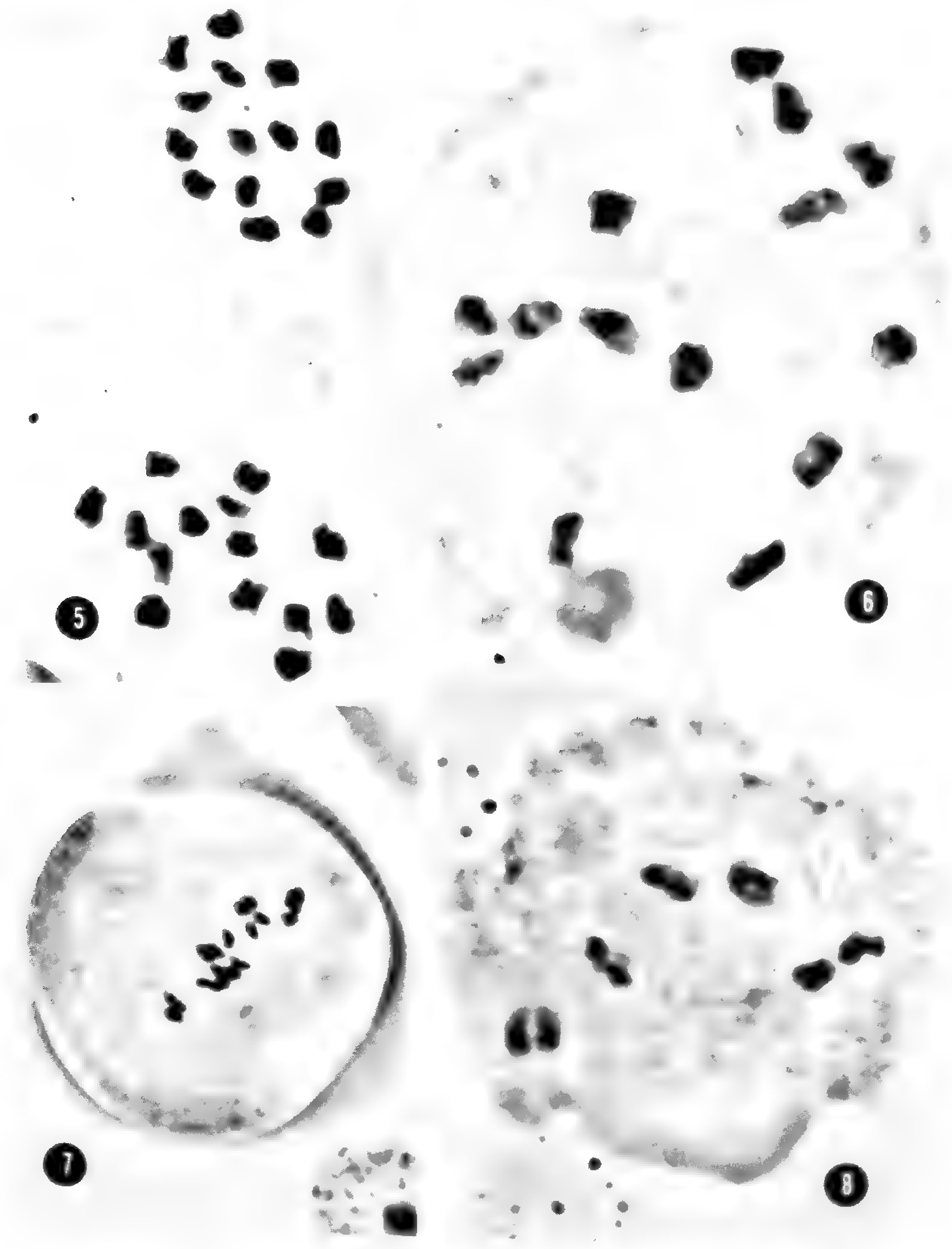


PLATE 2. FIG. 5, *Stanleya pinnata* var. *pinnata*, $n = 14$, Rollins and Stafleu 7129. FIG. 6, *Streptanthella longirostris*, $n = 14$, Rollins and Stafleu 7149. FIG. 7, *Halimolobos parryi*, $n = 16$, Rollins and Tryon 58204. FIG. 8, *Hutchinsia procumbens*, $n = 6$, Beatley 12903.

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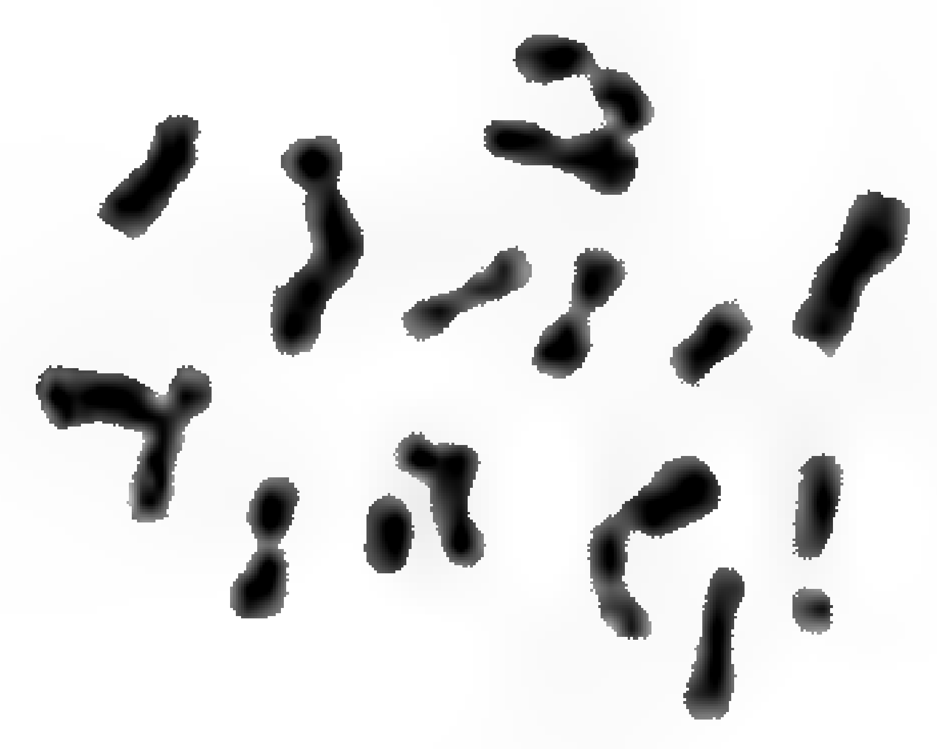

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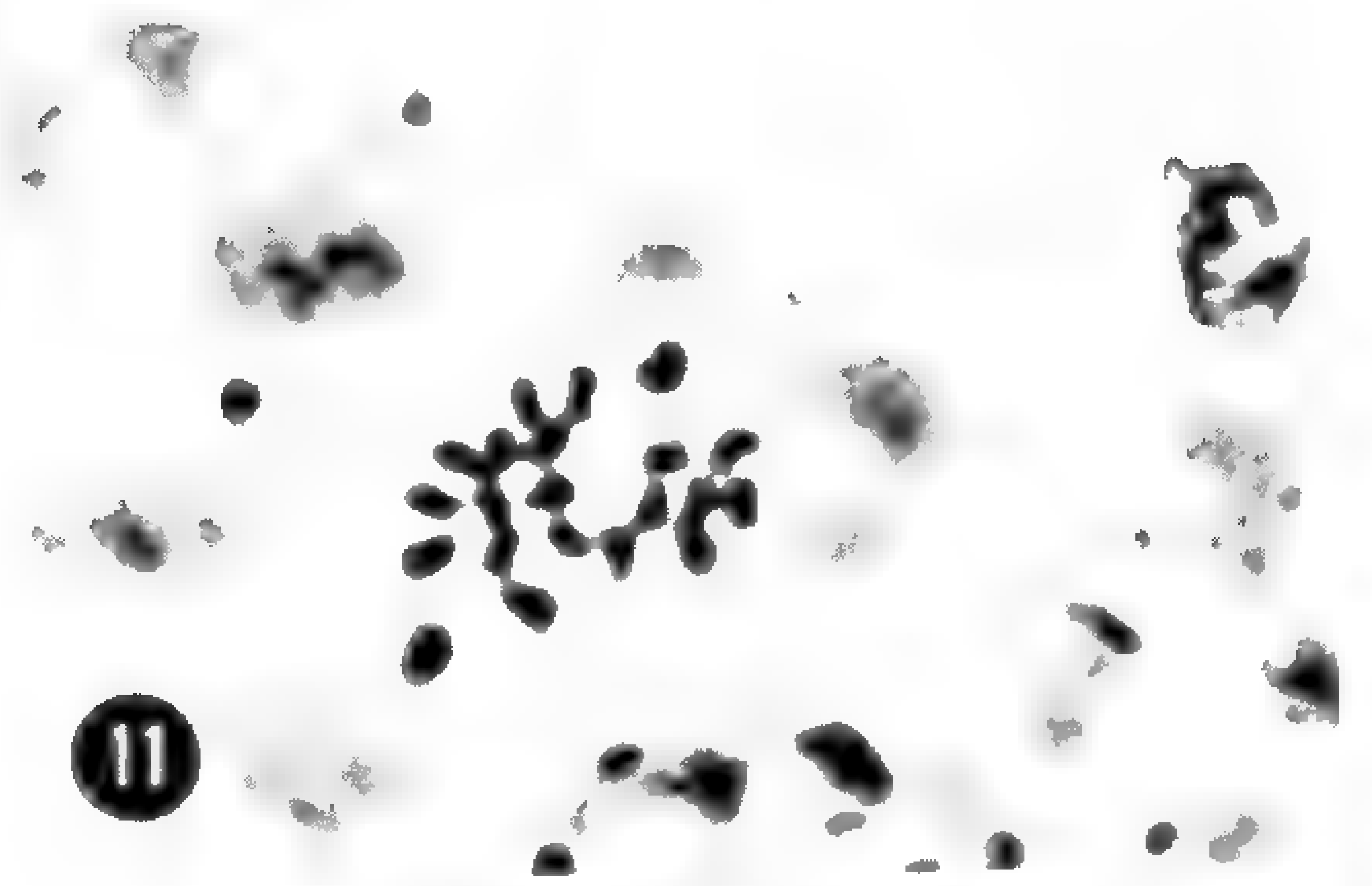

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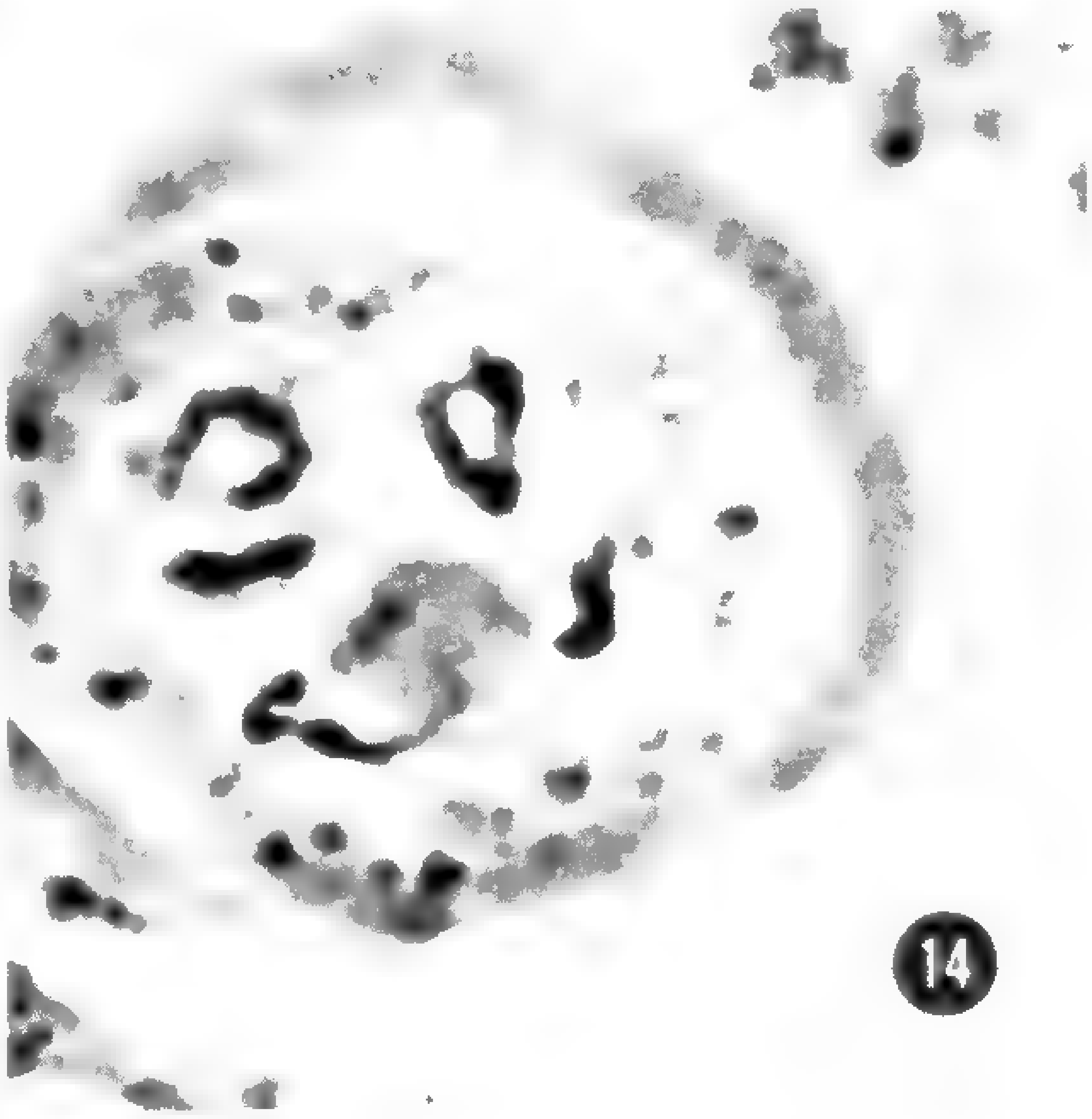

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PLATE 3. FIG. 9, *Physaria acutifolia*, $n = 5$, Rollins and Stafleu 7130. FIG. 10, *Lesquerella grandiflora*, $2n = 18$, Barclay 3086. FIG. 11, *Arabis fendleri*, $2n = 21$, Beatley and Reveal 10788. FIG. 12, *Lepidium virginicum* var. *medium*, $n = 16$, Correll and Correll 38577. FIG. 13, *Synthlipsis greggii*, $n = 10$, Rollins and Tryon 58311. FIG. 14, *Lesquerella kingii* subsp. *latifolia*, $n = 5$, Beatley et al. 13056.

n = 9: Bernalillo Co., New Mexico, *Rollins and Stafleu 7127,* GH. Previous counts for this species are the same (Rollins, 1966; Rollins and Rüdenberg, 1971).

Erysimum

E. asperum Nutt.
n = 18: Pueblo Co., Colorado, *Rollins and Stafleu 7122,* GH.
n = 18: Guadalupe Co., New Mexico, *Rollins 7152,* GH.

E. cheiranthoides L.
2*n* = 16: Hancock Co., Maine, *Rüdenberg 7307,* GH.

Halimolobos

H. lasioloba (Link) Schulz
n = 8: plants from seeds of *Rollins and Tryon 58255,* near Fresnillo, Zacatecas, Mexico, GH.

H. minutiflora Roll.
n = 16: between the cities of San Luis Potosí and Zacatecas, San Luis Potosí, Mexico, *Rollins and Roby 74127,* GH.

H. parryi (Hemsl.) Roll.
n = 8, *n* = 16: plants from seeds of *Rollins and Tryon 58204,* northeast of San Luis Potosí, S. L. P., Mexico, GH. Apparently polyploidy is present in the population sampled.

Together with *Halimolobos mollis,* which has a reported 2*n* = 16 (see Mulligan, 1964), the three species given above show a consistent base number of *x* = 8. *Halimolobos minutiflora* is a polyploid and *H. parryi* has at least some polyploid plants present in its populations but the other two species are diploid.

Hutchinsia

H. procumbens (L.) Desv.
n = 6: plants from seeds of *Beatley 12903,* Nye Co., Nevada, GH. This count accords with those previously given for the species (Bolkhovskikh, 1969).

Leavenworthia

L. alabamica Roll. var. *alabamica*
n = 11: Lawrence Co., Alabama, *Rollins 7163,* GH.

L. alabamica var. *brachystyla* Roll.
n = 11: Morgan Co., Alabama, *Rollins 7202,* GH.
n = 11: " " " *Rollins 7219,* GH.

L. crassa Roll. var. *crassa*
$n = 11$: Morgan Co., Alabama, *Rollins 7206*, GH.

L. crassa var. *elongata* Roll.
$n = 11$: Morgan Co., Alabama, *Rollins 7208*, GH.

L. exigua Roll. var. *exigua*
$n = 11$: Decatur Co., Tennessee, *Rollins 7222*, GH.
$n = 11$: Rutherford Co., Tennessee, *Rollins 7168*, GH.

L. exigua var. *laciniata* Roll.
$n = 11$: Bullitt Co., Kentucky, *Rollins 7231*, GH.

L. exigua var. *lutea* Roll.
$n = 11$: Jefferson Co., Alabama, *Rollins 7201*, GH.

There are no surprises in the above counts on *Leavenworthia*. These confirm earlier chromosome number reports (Rollins, 1963).

Lepidium

L. austrinum Small
$n = 16$: Hidalgo Co., Texas, *Rüdenberg 7502*, GH.
$n = 16$: plants from seeds of *Barclay 3076*, Webb Co., Texas, GH.

L. lasiocarpum Nutt. var. *wrightii* (Gray) Hitchc.
$2n = 32$: plants from seeds of *Correll and Correll 38576*, El Paso Co., Texas, GH.

L. montanum Nutt. var. *alyssoides* (Gray) Jones
$n = 16$: San Juan Co., New Mexico, *Rollins and Stafleu 7128*, GH.

L. montanum Nutt. var. *jonesii* (Rydb.) Hitchc.
$n = 16$: Montezuma Co., Colorado, *Rollins and Stafleu 7142*, GH.
$n = 16$: " " " *Rollins and Stafleu 7143*, GH.

L. virginicum L. var. *medium* (Greene) Hitchc.
$n = 16$: plants from seeds of *Correll and Correll 38577*, El Paso Co., Texas, GH.

The base number $x = 8$ is well established in *Lepidium* and there are both diploid and polyploid species (Manton, 1932; Mulligan, 1961). The counts given above are all of tetraploid plants.

Lesquerella

L. argyraea (Gray) Wats. subsp. *argyraea*
$2n = 30$: Zapata Co., Texas, *Barclay 3072*, GH.

L. argyraea subsp. *diffusa* (Roll.) Roll. and Shaw

$n = 7$: one mile southwest of Pinos, Zacatecas, Mexico, *Rollins and Roby 74106*, GH.

$n = 8$, $2n = 16$: 36 miles west of San Luis Potosí, S.L.P., Mexico, *Rollins and Roby 74125*, GH.

L. fendleri (Gray) Wats.

$n = 6$: Guadalupe Co., New Mexico, *Rollins 7151*, GH.

$n = 6$, $2n = 12$: 51 miles north of Monclova, Coahuila, Mexico, *Rollins and Roby 74207*, GH.

$n = 6$: 23 miles west of Saltillo, Coahuila, Mexico, *Rollins and Roby 7483*, GH.

$n = 6$: Val Verde Co., Texas, *Rollins and Roby 74205*, GH.

L. grandiflora (Hook.) Wats.

$2n = 18$: Atasco Co., Texas, *Barclay 3086*, GH.

L. kingii Wats. subsp. *latifolia* (Nels.) Roll. and Shaw

$n = 5$, $2n = 10$: plants from seeds of *Beatley, Ackerman and Bamberg 13056*, Clark Co., Nevada, GH.

L. lasiocarpa (Hook. ex Gray) Wats. subsp. *lasiocarpa*

$2n = 14$: Hidalgo Co., Texas, *Rüdenberg 7504*, GH.

L. schaffneri Wats.

$n = 6$: 10 miles west of San Lorenzo, San Luis Potosí, Mexico, *Rollins and Roby 74123*, GH.

Lesquerella argyraea continues to be something of an enigma as far as chromosome numbers are concerned. A given population appears to be relatively uniform as to number but different populations frequently show different numbers. Even subspecies *diffusa* now proves to have aneuploidy present whereas earlier the aneuploid series was known only in subspecies *argyraea*. The species as a whole is quite variable morphologically and there are recognizable trends usually correlated with geographic areas. However, in a careful study of a hundred or more herbarium collections, we could not discern distinct taxa that could reasonably be considered separate species (Rollins and Shaw, 1973). The gradual grading from one form to another was too consistent for us to do other than retain the species as a polymorphic one consisting of two subspecies. The cytological picture is unusual for a species and the problem should be studied, probably in an intensified way with an experimental design that would reveal whether apomixis is present or not.

The counts for the other species of *Lesquerella* are the same as those made previously except that the count for *L. schaffneri* is the first for that species. With the three counts given for *L. fendleri* the general distribution of $n = 6$ is strengthened. The only aneuploid population ($n = 7$) so far discovered is the one from New Mexico reported by Rollins and Shaw (1973).

Mancoa

M. henricksonii Roll.

$2n = 16$: plants from seeds of *James Henrickson 13471*, collected 15 miles northeast of Estacion Comacho, Zacatecas, Mexico, GH.

This is the first chromosome count for any species of *Mancoa*. The young seedlings used for the purpose were produced from seeds of the type number and the species was only recently described (Rollins, 1976).

Nerisyrenia

In the course of our present chromosome survey of Cruciferae, we have sampled twenty-two populations of *Nerisyrenia* from New Mexico, Texas, and mostly Mexico. In these materials we have found chromosome numbers of $n = 9$, $n = 10$, $n = 18$, and $n = 20$. At this point, the identities of the collections have not been fully worked out. We await the publication of his thesis research on *Nerisyrenia* by John D. Bacon (1975) who has developed a substantially more complex classification than the one in current use.

Pennellia

P. longifolia (Benth.) Roll.

$2n = 16$: plants from seeds of *Robert Bye*, Sept. 20, 1972, northwest of San Ignacio, about 5 miles east of Creel, Chihuahua, Mexico, GH.

$n = 8$, $2n = 16$: 26 miles east of El Salto, Durango, Mexico, *Rollins and Roby 7423*, GH.

Material of *Pennellia* has not been available previously for the purpose of obtaining chromosome counts. The species of this genus have until recently usually been treated in *Thelypodium*. However, the chromosome number of $n = 13$ most frequently found in *Thelypodium* (Al-Shehbaz, 1973) is sharply different from that of *P. longifolia*. Thus, the cytological picture supports a status of independence from *Thelypodium* of at least one species now placed in *Pennellia*.

Physaria

P. acutifolia Rydb.

$n = 5$: San Juan Co., New Mexico, *Rollins and Stafleu 7130*, GH.

$2n = 10$: Montezuma Co., Colorado, *Rollins and Stafleu 7137*, GH.

These counts agree with those of Mulligan (1967) and apply to his revised interpretation of the species. Earlier counts of $n = 4$ and $2n = 8$ (Rollins 1939, 1966) refer to populations now interpreted to be *Physaria rollinsii* Mulligan. The cytological situation in *P. acutifolia* is complex according to Mulligan's presentation and it appears that interspecific hybridization with *P. chambersii* may be one source of instability. The presence of several different chromosome races, $2n = 8$, $2n = 10$, $2n = 16$, and $2n = 24$, suggests the presence of an agamic complex. Such a possibility should be looked for when appropriate materials and circumstances permit it.

Rorippa

R. sylvestris (L.) Bess.

$2n = 48$: weed in experimental garden, Middlesex Co., Mass., *Rüdenberg 7229*, GH.

Selenia

S. aurea Nutt.

$n = 23$, $n = 69$: greenhouse grown plants from *Barclay 3087*, Muskogee Co., Oklahoma, GH. Three plants were $n = 23$; one was $n = 69$.

$n = 23$?: Montgomery Co., Arkansas, *Rollins 7120*, GH.

Bivalent chromosome associations were most frequent in the observed configurations but there were always some univalents, trivalents and quadrivalents present. That *Selenia aurea* is a natural polyploid seems quite certain from this evidence. The fact that one of the four plants examined turned out to have a very high ploidy level demonstrates this tendency in the species. *Selenia grandis* with $n = 12$ and *S. dissecta* with $n = 7$ are the other species of *Selenia* with known chromosome counts. Although, by comparison, it seems clear that *S. aurea* is a polyploid species, the $n = 23$ count is from only three populations in Arkansas and Oklahoma and does not represent an adequate sampling of the species throughout its natural range.

Sibara

S. virginica (L.) Roll.

$n = 8$: Madison Co., Alabama, *Rüdenberg 7010*, GH.

A previous count of $2n = 16$ from a population in Tennessee is consistent with the present one. *Sibara virginica* is mainly southeastern United States in its distribution and jumps the arid southwest to southern California where it occurs around vernal pools. A chromosome count from the extreme western populations would be of unusual interest.

Sisymbrium

S. altissimum L.

$n = 7$: Montezuma Co., Colorado, *Rollins and Stafleu 7144*, GH.

S. irio L.

$n = 7$: Hidalgo Co., Texas, *Rüdenberg 7503*, GH.

S. officinale L.

n = 7: Madison Co., Alabama, *Rüdenberg 7226,* GH.

These three species of introduced weeds have been counted many times, especially in Europe. The count of *n* = 7 is remarkably consistent.

Stanleya

S. pinnata (Pursh) Britt. var. *pinnata*

n = 14: San Juan Co., New Mexico, *Rollins and Stafleu 7129,* GH.

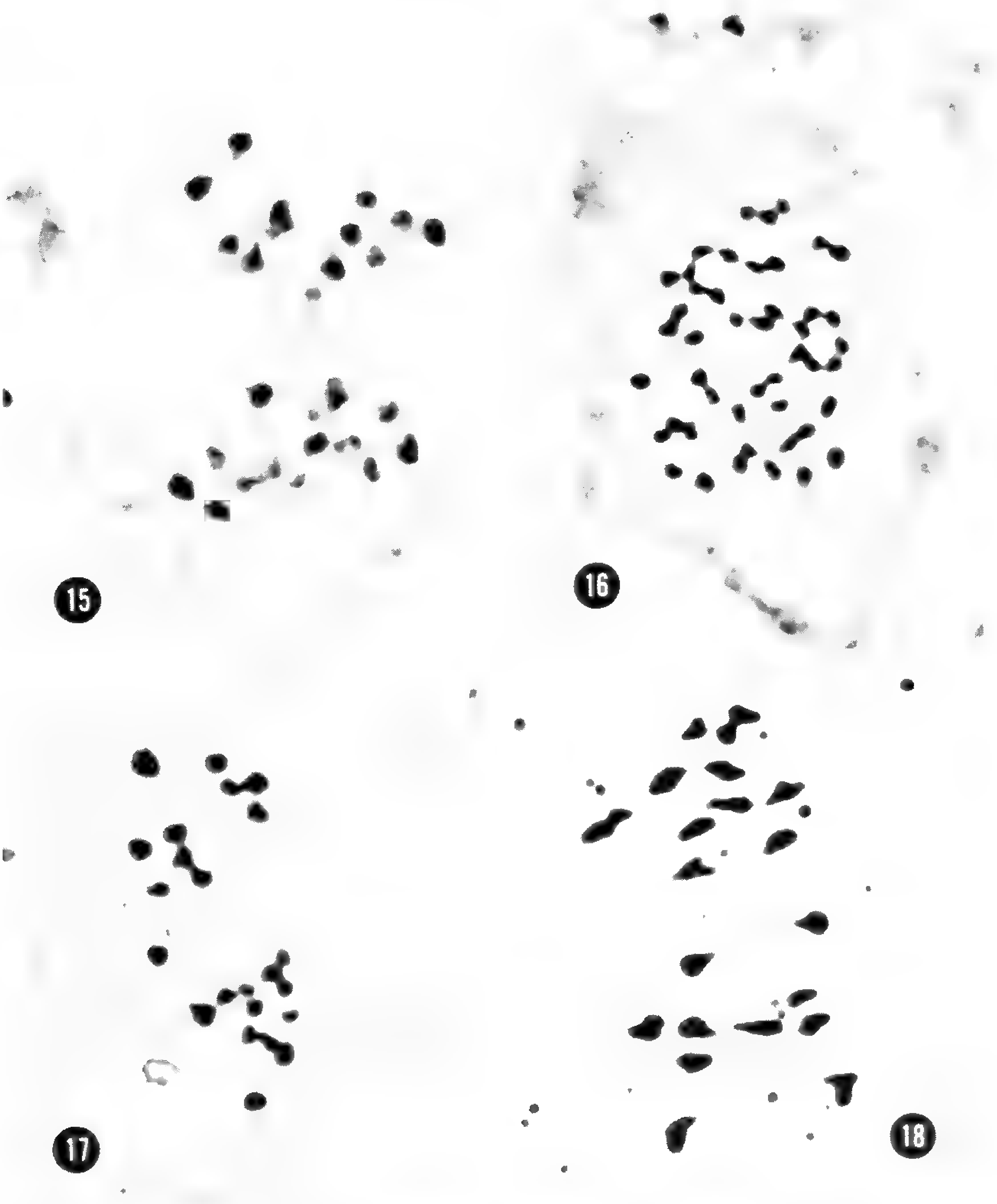

Plate 4. Fig. 15, *Streptanthus arizonicus, n* = 14, Moran and Reveal 20210. Fig. 16, *Selenia aurea,* 2*n* = 46, Barclay 3087. Fig. 17, *Selenia aurea, n* = 23, Barclay 3087. Fig. 18, *Synthlipsis greggii,* 2*n* = 20, Rollins and Correll 5948.

Streptanthella

S. longirostris (Wats.) Rydb.

$n = 7$: Montezuma Co., Colorado, *Rollins and Stafleu 7145*, GH.

$n = 14$: " " " *Rollins and Stafleu 7149*, GH.

Previous counts on this species were at the tetraploid level. With the above information, it is now clear that both diploid and tetraploid populations exist in the wild. The species is widespread and abundant in the arid regions of southwestern United States. It is found in very diverse sites but usually requires some shade. There is no evidence that chromosome number differences are correlated with any other type of diversity in the species.

Streptanthus

S. arizonicus Wats.

$n = 14$: Cerro Azufre, Baja California del Norte, Mexico, *Moran and Reveal 20155, 20171*, SD, GH.

$n = 14$: Volcán las Tres Vírgenes, Baja California del Sur, Mexico, *Moran and Reveal 20210*, SD, GH.

$n = 14$, $2n = 28$: same locality, plants from seeds of *Henrickson 9022*, voucher at CSLA.

S. cordatus Nutt.

$n = 14$: Montezuma Co., Colorado, *Rollins and Stafleu 7138*, GH.

S. sparsiflorus Roll.

$2n = 28$: plants from seeds of *Burgess 1852*, Culberson Co., Texas, TTC.

The count of $n = 14$ for *S. cordatus* is in accord with nearly all other counts for species of *Streptanthus* but not with the previous count of $n = 12$ for *S. cordatus* itself. It is possible that the earlier count is in error or more likely, *S. cordatus* has more than one chromosome race. This species shows a wider range of morphological variation than most species of *Streptanthus*, a situation that could relate to variation in chromosome number.

Synthlipsis

S. greggii Gray

$n = 10$, $2n = 20$: plants from seeds of *Rollins and Correll 5948*, Zapata Co., Texas, GH.

$n = 10$: plants from seeds of *Rollins and Tryon 58311*, Nuevo Leon, Mexico, GH.

$n = 10$: 10 miles southeast of Parras, Coahuila, Mexico, *Rollins and Roby 7459*, GH.

$n = 10$: 8 miles east of Nieves on road to Estacion Comacho, Zacatecas, Mexico, *Rollins and Roby 74133*, GH.

The chromosome number of *Synthlipsis greggii* is now well established and appears to be unvarying throughout its range.

Thelypodiopsis

T. aurea (Eastw.) Rydb.
$n = 11$: Montezuma Co., Colorado, *Rollins and Stafleu 7148,* GH.
$n = 11$: San Juan Co., New Mexico, *Rollins and Stafleu 7133,* GH.

T. linearifolia (Gray) Al-Shehbaz
$n = 20+$: Cochise Co., Arizona, *Rollins and Roby 74196,* GH.

Two species belonging to *Thelypodiopsis* have previously been reported under the genus name *Sisymbrium* (Rollins, 1966; Rollins and Rüdenberg, 1971) both with a count of $n = 11$. Al-Shehbaz (1973) has transferred both of these species, *T. ambigua* and *T. linearifolia,* from *Sisymbrium* to *Thelypodiopsis.* If the chromosome number $n = 11$ stands up as characterizing *Thelypodiopsis,* it will bolster the recognition of this genus as distinct from *Sisymbrium* or *Thelypodium.*

The plant of *Thelypodiopsis linearifolia (Rollins and Roby 74196)* from which buds were fixed was unusual in having very large flowers and in being robust compared to other plants of the species found about one-half mile away. This was a lone plant, somewhat later in flowering compared to the others and because of greater overall size, appeared to be an individual polyploid. The uncertain count given, although not precise, still strongly indicates that the plant indeed is a polyploid. Other than size, differences from other plants of the species could not be detected.

Thelypodium

T. paysonii Roll.
$n = 10$: plants from seeds of *Johnston et al. 10349C,* Sierra de los Margaritas, Coahuila, Mexico, TEX.
$n = 10$, $2n = 20$: plants from seeds of *Johnston et al. 10361A,* locality as above, TEX.

A consistent number of $n = 13$ in nine taxa of *Thelypodium* was reported by Al-Shehbaz (1971). The failure of *T. paysonii* to continue this pattern is not easily explainable. Al-Shehbaz suggested that *T. paysonii* possessed certain anomalous features as far as the genus is concerned but he did not indicate there was a solid basis for removing it from *Thelypodium.* The unusual chromosome number suggests a closer look at the affinities of *T. paysonii.*

Thlaspi

T. montanum L. var. *montanum*
$n = 7$: Pueblo Co., Colorado, *Rollins and Stafleu 7125,* GH.

Previous counts of *Thlaspi fendleri* and *T. glaucum* are now to be referred to one or another variety of *T. montanum* according to the publication of P. Holmgren (1971).

Warea

W. carteri Small

$n = 12, 2n = 24$: plants from seeds of *Rollins and Roby 7305*, GH.

To our knowledge, this is the first count for the genus *Warea*. It is interesting that the number falls nicely into line with other genera of the *Thelypodieae* as interpreted by Al-Shehbaz (*loc. cit.*).

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PALYNOLOGICAL SURVEY OF THE GENERA AMPHIACHYRIS, AMPHIPAPPUS, GREENELLA, GUTIERREZIA, GYMNOSPERMA AND XANTHOCEPHALUM

JOHN RUFFIN[1]

ABSTRACT

This study is concerned with the determination of the pollen characteristics of the members of the genera *Amphiachyris, Amphipappus, Greenella, Gutierrezia, Gymnosperma* and *Xanthocephalum* (Astereae-Compositae). Pollen grains were assessed for both qualitative and quantitative differences. Differences were observed both between species of different genera and between species of the same genera. The principal differences in pollen among the various species were in size and subtle variations in exine surface patterns. Using both palynological and biosystematic evidence, the data seem to support the distinctiveness of *Amphiachyris, Amphipappus* and *Gymnosperma* and support the transfer of species of the previously recognized genera *Gutierrezia* and *Greenella* to the genus *Xanthocephalum.*

INTRODUCTION

The ambiguity concerning the proper relationship of the genera *Amphiachyris, Amphipappus, Greenella, Gutierrezia, Gymnosperma* and *Xanthocephalum* (Compositae) as well as a complete history of the genera have been reviewed by Shinners (1950), Solbrig (1960), and Ruffin (1974a, 1974b). Some confusion as to the generic limits of these genera still exists. Pappus characteristics chiefly were used by earlier botanists in delimiting these genera, and less emphasis was placed on other morphological features. According to Shinners (1950) the taxonomy of the Compositae has suffered greatly from excessive reliance on the nature of the pappus, and its presence or absence, as a character of generic value. Thus, to Shinners, variable pappus features as well as other superficial morphological characters were not adequate for maintaining separate genera; he merged *Amphiachyris, Amphipappus, Greenella, Gutierrezia* and *Gymnosperma* all under *Xanthocephalum.* Solbrig (1960), in attempting to treat the problem in a more objective fashion, showed the chromosome numbers for *Amphiachyris, Amphipappus, Gutierrezia, Gymnosperma* and *Xanthocephalum.* Each genus studied showed a different basic chromosome number. Although cytological data appeared to be distinctive, only one species of *Xanthocephalum, X. gymnospermoides,* and none of *Greenella,* were counted at that time. Chromosome counts for *Greenella* and four more of the eight species of *Xanthocephalum* are now

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[1] Alabama A & M University, Department of Biology, Normal, AL 35762 U.S.A.

available, each with a basic chromosome number of four. This is consistent with counts reported for other species in the genus *Gutierrezia* (Solbrig, 1961; Turner *et al.*, 1962; DeJong and Longpre, 1963; Solbrig *et al.*, 1964). These findings show that there are no real chromosome number differences between *Xanthocephalum, Gutierrezia* and *Greenella.*

To further elucidate the relationship of the genera, comparative studies on gross morphology and anatomy were undertaken (Ruffin 1974a, 1974b). Anatomical and morphological evidence indicate that *Greenella* and *Gutierrezia* should not be maintained as distinct, and they show enough unifying characters to justify the transference of their species to *Xanthocephalum.*

Plant taxonomists tend to think of pollen as a relatively stable feature by which species, genera, and even higher taxonomic categories of plants may be recognized (King and Robinson, 1967). According to Stebbins (1950), few pollen variations within a single species are known and most of these involve size differences that are correlated with polyploidy. Several notable studies have been conducted proving the value of the morphological features of pollen in determining the taxonomic and phylogenetic relationships of species and genera (Oldfield, 1959; Carlquist, 1961; Raj, 1961; Wodehouse, 1965; Jones, 1970; Erdtman, 1972). Because of its reliability and because pollen morphology of these genera has been relatively neglected, detailed palynological evidence is presented as part of a series of studies presently underway in an attempt to unravel the taxonomic position of the groups.

Materials and Methods

All of the pollen examined was taken from the anthers of specimens mounted on herbarium sheets, and an effort was made to sample each genus completely. Pollen was prepared for light microscope observations and measurements and for scanning electron microscopy as well. Both acetolized and nonacetolized grains were used. Acetolized grains were prepared using the standard acetolysis method devised by Erdtman (1969). The pollen grains were mounted in glycerin jelly, cover glass was applied and sealed using clear fingernail polish. According to Reitsma (1969), the glycerin jelly mounting procedure is the most effective because the spores are less apt to expand upon storage if this method is used. A Zeiss microscope, with a calibrated ocular micrometer at a magnification of ca. 1200×, was used to measure the pollen grains. Measurements of spine length and pollen grain diameter were taken from five samples for each of the species studied with the exception of *Gutierrezia californica,* where only one sample was used due to limited material. Each sample represented a different population. Slides were prepared for each taxon, 30 measurements were made per slide for each character, and averages were ascertained. In all, 3960 measurements were made. For scanning, anthers were removed from each specimen, and acetolized as

TABLE 1. SOURCE OF MATERIAL USED IN POLLEN SURVEY.*

Taxon	Collection and herbarium	Location
Amphiachyris dracunculoides (DC.) Nutt.	Ruffin 70361	Kansas: Geary Co., 9 mi. W of Junction City along hwy. 77.
	Ruffin 70372	Kansas: Riley Co., 13 mi. S of Manhattan along hwy. 177.
	Ruffin 70383	Kansas: Chase Co., 25 mi. NE of El Dorado.
	Ruffin 70394	Texas: Brewster Co., along hwy. 118 S of Alpine.
	Solbrig 3275 (GH)	Texas: hwy. 118, 5 mi. S of Kent ($n = 5$).
Amphipappus fremontii Torr. & Gray	Clokey 5962 (KSU)	Nevada: Clark Co., Glendale Jct., rocky hills, Larrea belt.
	Raven 12038 (GH)	California: Inyo Co., Grapevine Mts., Death Valley National Monument ($n = 9$).
	Raven 12003 (GH)	California: Inyo Co., 3.2 mi. S of Mesquite Spring.
	Cronquist 8904 (GH)	Nevada: Clark Co., Larrea community, 4 mi. NE of desert game range station.
	Solbrig 2261 (GH)	California: Inyo Co., 10 mi. N of Darwin near Darwin Falls ($n = 9$).
Greenella arizonica Gray	Peebles 3842 (US)	Arizona: Pima Co., Papago reservation.
	Raven 17378 (GH)	Arizona: Pima Co., west of Robles Jct. ($n = 4$).
	Wiegand 2523 (GH)	Arizona: Pima Co., 15 mi. SW of Tucson.
	Peebles 11356 (GH)	Arizona: Pima Co., Tucson to Vail.
	Nelson 1527 (GH)	Arizona: Pima Co., vacant land about Tucson.
Gutierrezia bracteata Abrams	Solbrig 3440 (GH)	California: Los Angeles Co., south rim of Valley of Tujungo wash, next to Wentworth Street ($n = 8$).
	Solbrig 2743 (GH)	California: Stanislaus Co., 7.2 mi. W of Patterson on Arroyo del Puerto Road ($n = 8$).
	Solbrig 2167 (GH)	California: Ventura Co., 9½ mi. W of Santa Barbara Co. line ($n = 12$).
	Solbrig 3439 (GH)	California: Alameda Co., upper Cuyama Valley, 28 mi. WSW of Maricopa on hwy. 166 ($n = 12$).
	Solbrig 2775 (GH)	California: Riverside Co., 1 mi. from Palm Spring–Palm Desert hwy. ($n = 12$).
Gutierrezia californica DC.	Solbrig 3431 (GH)	California: Marin Co., Point Bonita, left side of road coming out of tunnel to Fort Barry.
Gutierrezia microcephala DC.	Solbrig 2789 (GH)	Arizona: hwy. 80 and city limits of the town of Douglas ($n = 16$).
	Solbrig 3272 (GH)	Texas: 23 mi. S of White City, New Mexico on hwy. 62 ($n = 12$).
	Solbrig 2790 (GH)	Arizona: 3.5 mi. S of St. David on road to Douglas.
	Ruffin 70051, 70062	New Mexico: Grant Co., 15 mi. N of Silver City off hwy. 25, 6600 ft. (70051); 8800 ft. (70062).

Taxon	Collection and herbarium	Location
Gutierrezia sarothrae Pursh	Solbrig 2794 (GH)	Arizona: 5 mi. N of Payson ($n = 8$).
	Solbrig 2805 (GH)	Arizona: east of Hyde Park, 0.8 mi. on hwy. 66 ($n = 4$).
	Solbrig 2768 (GH)	California: San Diego Co., 6.2 mi. E of Chula Vista on road to Dulzura ($n = 4$).
	Solbrig 2773 (GH)	California: Riverside Co., 11.1 mi. E of Keen Kamp on hwy. 74 ($n = 4$).
	Solbrig 2760 (GH)	California: San Diego Co., 12.3 mi. W of Aguanga on hwy. 79 ($n = 4$).
Gutierrezia texana DC.	Ruffin 70071	Texas: Brewster Co., along hwy. 118 to Alpine.
	Ruffin 70082	Texas: Burleson Co., along hwy. 290 S of Giddings.
	Ruffin 70093	Texas: Washington Co., 1 mi. NE of Burton along hwy. 390.
	Tolstead 5829 (GH)	Texas: Taylor Co., at Camp Barkeley.
	Anderson 3028 (KSC)	Texas: Brewster Co., along hwy. 118 S to Alpine.
Gymnosperma glutinosum (Spreng.) Less.	Ruffin 70101	New Mexico: Grant Co., 5 mi. N of Silver City on Cottage Sand Road.
	Ruffin 70112	New Mexico: Hidalgo Co., 1 mi. W of Cloverdale on hwy. 77.
	Ruffin 70123	Texas: Brewster Co., 21 mi. S of Marathon on road to Big Bend National Park.
	Ruffin 70134	Texas: Brewster Co., along hwy. 118 of Alpine.
	Solbrig 4546 (GH)	Mexico: 10 mi. W of Dolores Hidalgo.
Xanthocephalum gymnospermoides (Gray) Benth. & Hook.	Ruffin 70241, 70252, 70263	Arizona: Cochise Co., Garden Canyon, Huachuca Mts.: 6000 ft. (70241); 5500 ft. (70252); 6200 ft. (70263).
	Solbrig 2779 (GH)	Arizona: Cochise Co., 4.1 mi. W from junction of Ramsey Canyon Road and hwy. 92 ($n = 6$).
	Johnston 7935 (GH)	Mexico: 31 mi. NE of Camargo.
Xanthocephalum humile (HBK) Sch. Bip.	Pringle 7422 (US)	Mexico: Distrito Federal, Valle de Mexico.
	Pringle 4220 (US)	Mexico: Distrito Federal.
	Pringle 3202 (GH)	Mexico: Distrito Federal, low meadows, Valley of Mexico.
	Parry 1878 (GH)	Mexico: chiefly in the region of San Luis Potosí.
	Weaver 865 (GH)	Mexico: Puebla, marshy sand of lake shore near Lago Salado, 253 km. E of Mexico City.
Xanthocephalum linearifolium (DC.) Greenman	Pringle 11613 (GH)	Mexico: Distrito Federal, Serrania de Ajusco near Cima Station.

Taxon	Collection and herbarium	Location
	Pringle 4195 (GH)	Mexico: Distrito Federal, Serrania de Ajusco near Cima Station.
	Orcutt (GH)	Mexico: Distrito Federal, Cima Station.
	Moore 19470 (GH)	Mexico: Distrito Federal, La Cima, on road to Cuernavaca.
	Manning 531040 (GH)	Mexico: 12 mi. S of Tlalpan.
Xanthocephalum sericocarpum Gray	Palmer 143 (US)	Mexico: City of Durango and vicinity.
	Mueller 3380 (GH)	Mexico: 12 mi. W of San Antonio.
	Pringle 1278 (GH)	Mexico: pine plains, base of the Sierra Madre.
	Pringle 1150 (GH)	Mexico: state of Chihuahua.
	Palmer 412 (GH)	Mexico: southwestern Chihuahua.
Xanthocephalum wrightii (Gray) Gray	Ruffin 70201	New Mexico: Catron Co., 18 mi. NE of Mogollon on hwy. 78.
	Ruffin 70212	New Mexico: Grant Co., 11 mi. NE of Silver City at bottom of Cherry Creek Canyon.
	Ruffin 70223, 70234	Arizona: Cochise Co., Garden Canyon, Huachuca Mts., 6000 ft. (70223); 5500 ft. (70234).
	Solbrig 3218 (GH)	Arizona: Buffalo Jct., 11 mi. S of Big Bear Lake, 12 mi. W of US 666 and 17 mi. S of Alpine ($n = 4$).

*Voucher specimens are in Alabama A & M University local herbarium unless otherwise indicated.

well as nonacetolized pollen grains were placed on double stick tape mounted on a specimen holder. All samples were then placed in a vacuum chamber and coated with gold-palladium. Observations were made on an AMR "1000" Scanning Electron Microscope. Table 1 lists plants, and their respective sources, used in this pollen morphological survey. A deliberate attempt was made to use authoritatively annotated herbarium sheets. Some sheets also provided original chromosome numbers which appear in the table following locality data. A set of slides of acetolized grains for each genus is on deposit in the palynological collections of Harvard University.

OBSERVATIONS

Tables 2 and 3 list the average measurements for selected pollen features of all the species studied. Figures 1 through 15 depict the surface features of the grains of the species used in this study.

Pollen grains of all of the genera here studied are tricolporate and spheroidal, and of the type described for the Astereae by Wodehouse (1965). The surface of the textum (sexine) bears what appears to be uniformly distributed spines which form the most noteworthy feature of the grain surface. The spines of all the species are frequently crooked or show a strong tendency to curve upward. According to Wodehouse (1965), the length of the spines as well as various other spine features may be used to distinguish some of the genera of the Astereae.

All of the figures show that the spines of all the species studied possess basal perforations. These perforations, or lacunae areas, were also noted by Carlquist (1957) in the genera *Fitchia* and *Helianthus*. In many instances using the nonacetolized grains, the micrographs reveal these spaces to be filled with an extraneous material, thus obscuring the presence of the pores. When some of these same grains (Figs. 3 and 14) are

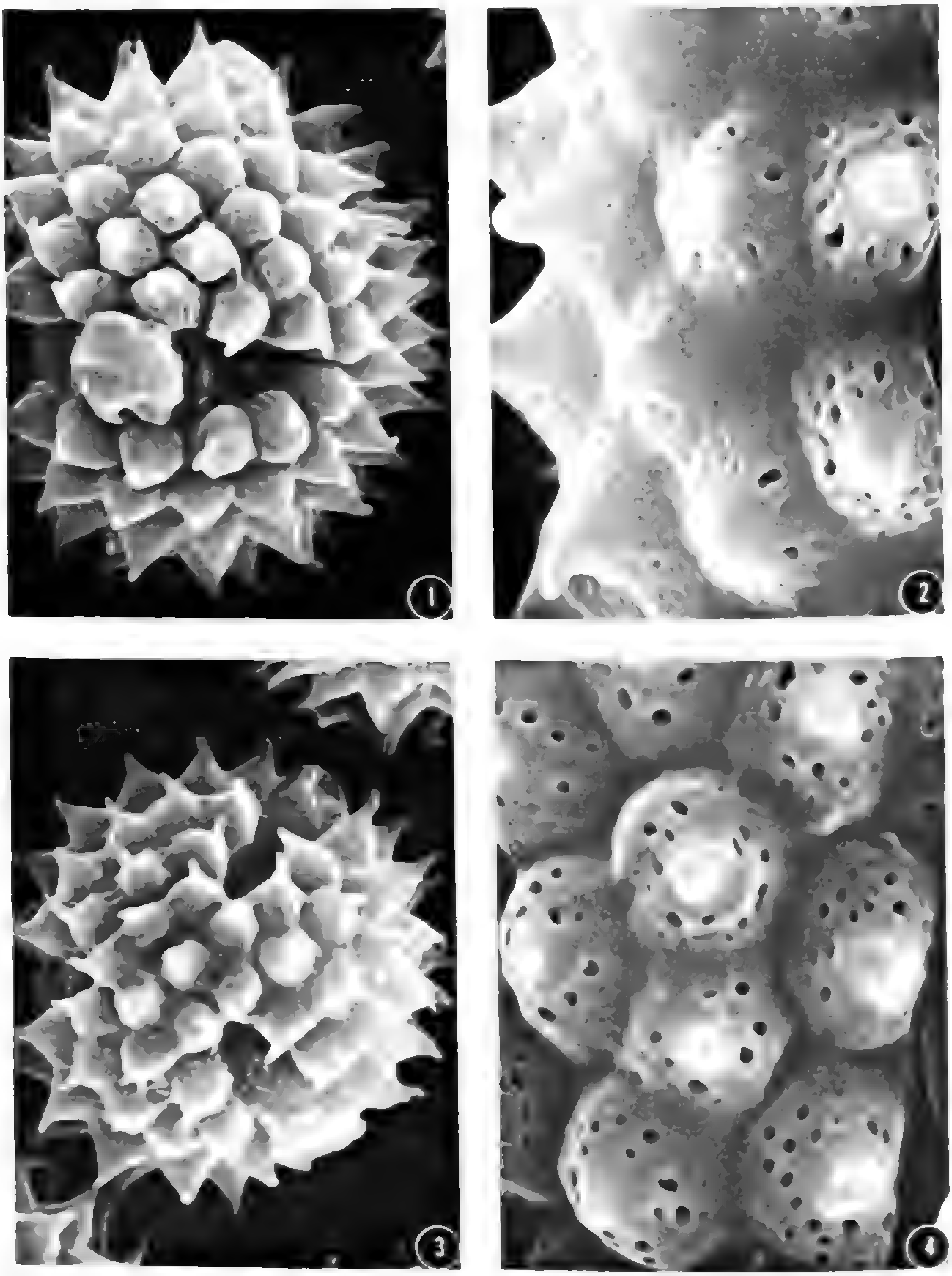
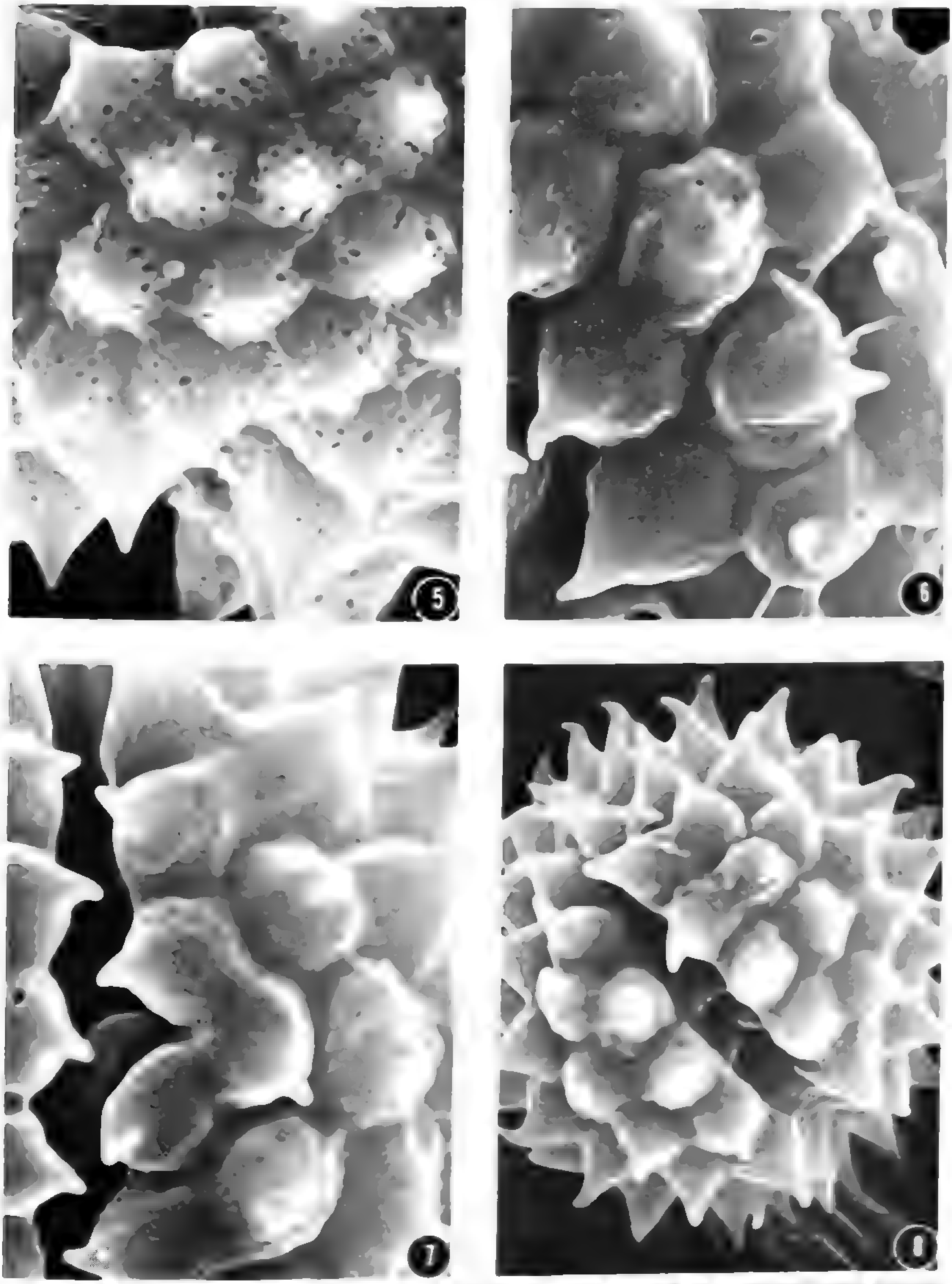


FIG. 1–4. Pollen grains.—1. *Greenella arizonica:* polar view of surface details, 5000 ×.—2. *Gymnosperma glutinosum:* equatorial view showing spinal and interspinal lacunae, 10000 ×.—3. *Amphiachyris dracunculoides:* polar view of surface details, 5000 ×.—4. *Amphipappus fremontii:* equatorial view showing surface details of spinal and interspinal lacunae, 10000 ×.

acetolized, the pores are then free of the material. Due to the investigations of J. Heslop-Harrison (1975), J. Heslop-Harrison *et al.* (1973), and B. J. Howlett *et al.* (1973), it is now known that much of this material is proteinaceous and that in the Compositae, with its complex tectate exine and its invasive tapetum, the protein component passes into the cavities of the baculate sexine through the surface micropores and also into the



FIGS. 5–8. Pollen grains of [illegible] —5. G. [illegible] [illegible] as inconspicuous and filled with extraneous material, 10000 ×.—7. *G. texana:* equatorial view showing spinal [illegible] 10000 ×.—8. G. [illegible]

TABLE 2. POLLEN GRAIN DIAMETER MEASUREMENTS.

Taxon	Diameter Range	Mean Diameter	Diameter S.D.
Amphiachyris dracunculoides	17.0–20.2*	18.750	0.693
Amphipappus fremontii	19.0–28.5	22.449	2.097
Greenella arizonica	13.0–18.1	14.751	0.786
Gutierrezia bracteata	11.0–20.2	16.561	2.050
G. californica	12.0–20.0	16.864	1.723
G. microcephala	11.0–19.5	15.768	1.709
G. sarothrae	10.6–18.9	13.887	1.706
G. texana	13.0–16.0	14.744	0.689
Gymnosperma glutinosum	13.0–20.8	17.011	1.913
Xanthocephalum gymnospermoides	19.0–28.8	22.771	2.830
X. humile	13.0–18.1	15.350	1.051
X. linearifolium	14.0–18.0	15.261	0.929
X. sericocarpum	13.8–19.9	15.588	1.044
X. wrightii	14.0–19.5	16.105	1.486

*All measurements are given in μm.

TABLE 3. POLLEN GRAIN SPINE LENGTH MEASUREMENTS.

Taxon	Length Range	Mean Length	Length S.D.
Amphiachyris dracunculoides	1.7–2.8*	2.406	0.263
Amphipappus fremontii	1.6–2.6	2.184	0.258
Greenella arizonica	1.7–3.1	2.301	0.260
Gutierrezia bracteata	2.0–4.5	3.399	0.488
G. californica	1.9–4.1	3.469	0.396
G. microcephala	1.5–4.4	2.652	0.507
G. sarothrae	1.5–2.8	2.004	0.278
G. texana	1.5–2.8	2.183	0.354
Gymnosperma glutinosum	2.0–3.0	2.518	0.367
Xanthocephalum gymnospermoides	2.9–5.4	3.816	0.367
X. humile	1.6–3.0	2.339	0.253
X. linearifolium	1.9–3.1	2.322	0.237
X. sericocarpum	1.9–3.2	2.335	0.269
X. wrightii	2.0–2.8	2.424	0.183

*All measurements are given in μm.

TABLE 4. COMPARISON OF POLLEN GRAIN DIAMETER TO SPINE LENGTH IN GUTIERREZIA AND XANTHOCEPHALUM.

Species	Average Diameter	Average Spine Length	Average Ratio
Gutierrezia californica	16.8*	3.4	0.20
G. bracteata	16.5	3.3	0.20
G. microcephala	15.7	2.6	0.16
G. texana	14.7	2.1	0.14
G. sarothrae	13.8	2.0	0.14
Xanthocephalum gymnospermoides	22.7	3.8	0.17
X. wrightii	16.1	2.4	0.15
X. humile	15.3	2.3	0.15
X. linearifolium	15.2	2.3	0.15
X. sericocarpum	15.5	2.3	0.15

*All measurements are given in μm.

cavea between sexine and nexine through pores at the bases of the supratectate spines. Here the lipid fractions are left on the surface to form the visible adhesive which clogs the spinal pores. Even though the width of the spines was not measured, the spines of *Amphipappus* appear to be broadest at the base with fewer spines in a given area than in the other species. In addition, in *Amphipappus* the lacunae appear to be more concentrated in the wider portion of the spines. Lacunae in the apical parts of the spines were not observed in any of the species studied. Lacunae are very infrequent in areas between the spines, but a few were noted in pollens of *Amphipappus* and *Gymnosperma* (Figs. 4 and 2 respectively). It is also noteworthy that the diameter of the external apertures in *Amphipappus* appears to be much larger and the pores more numerous than in the other genera studied.

When variations in grain size are correlated with variations in chromosome number at the generic level, there are some clear distinctions worthy of mention. In the case of *Gutierrezia* (with a base chromosome number of four) all individuals representing different ploidy levels were considered as one sample mean. The pollen of *Gutierrezia* has a diameter range of 10.6–20.2 μm, and a mean diameter of 15.5 μm. The pollen of *Greenella,* which has a chromosome count of $n = 4$, is within the diameter range of 13.0–18.1 μm and has a mean diameter of 14.7 μm. Pollen of *Xanthocephalum,* which also has a count of $n = 4$ (with the exception of $n = 6$ for *X. gymnospermoides*) falls within the diameter range of 13.0–28.8 μm. The extended range, as well as the large mean diameter of *Xanthocephalum* (see Table 5), is due solely to the inclusion of *X. gymnospermoides*. If *X. gymnospermoides* is excluded, the mean pollen diameter of the genus (15.5 μm) has a closer relationship with the genera *Gutierrezia* and *Greenella.*

Amphiachyris has a chromosome number of $n = 5$, a diameter range of 17.0–20.2 μm, and a mean diameter of 18.7 μm. With a chromosome number of $n = 7$, the diameter of *Gymnosperma* pollen ranges from 13.0–20.8 μm, with a mean diameter of 17.0 μm. The last genus, *Amphipappus,* is characterized by a chromosome number of $n = 9$. Pollen of this genus has the largest mean diameter of all the genera represented (22.4 μm) and a range of 19.0–28.5 μm.

In plant groups where polyploidy is suspected but cannot be documented, pollen samples acquired from several populations can indicate a suspected polyploidy series. Studies by Rangasamy, Sree and Ramon (1973) clearly indicate what had been suspected all along—that pollen size increases with increased ploidy. As far as is known, among the genera here studied, *Gutierrezia* is the only genus in which there is a polyploid complex. Solbrig (1965) showed the pollen diameters of populations of *G. sarothrae*, *G. bracteata* and *G. californica,* all of which have known chromosome numbers and the statistical results demonstrated a correlation between chromosome number and pollen diameter. As shown in

Table 1. a series of original chromosome counts, taken from herbarium sheets, were available for *Gutierrezia bracteata* ($n = 8$; $n = 12$), *G. microcephala* ($n = 12$, $n = 16$), and *G. sarothrae* ($n = 4$, $n = 8$). When

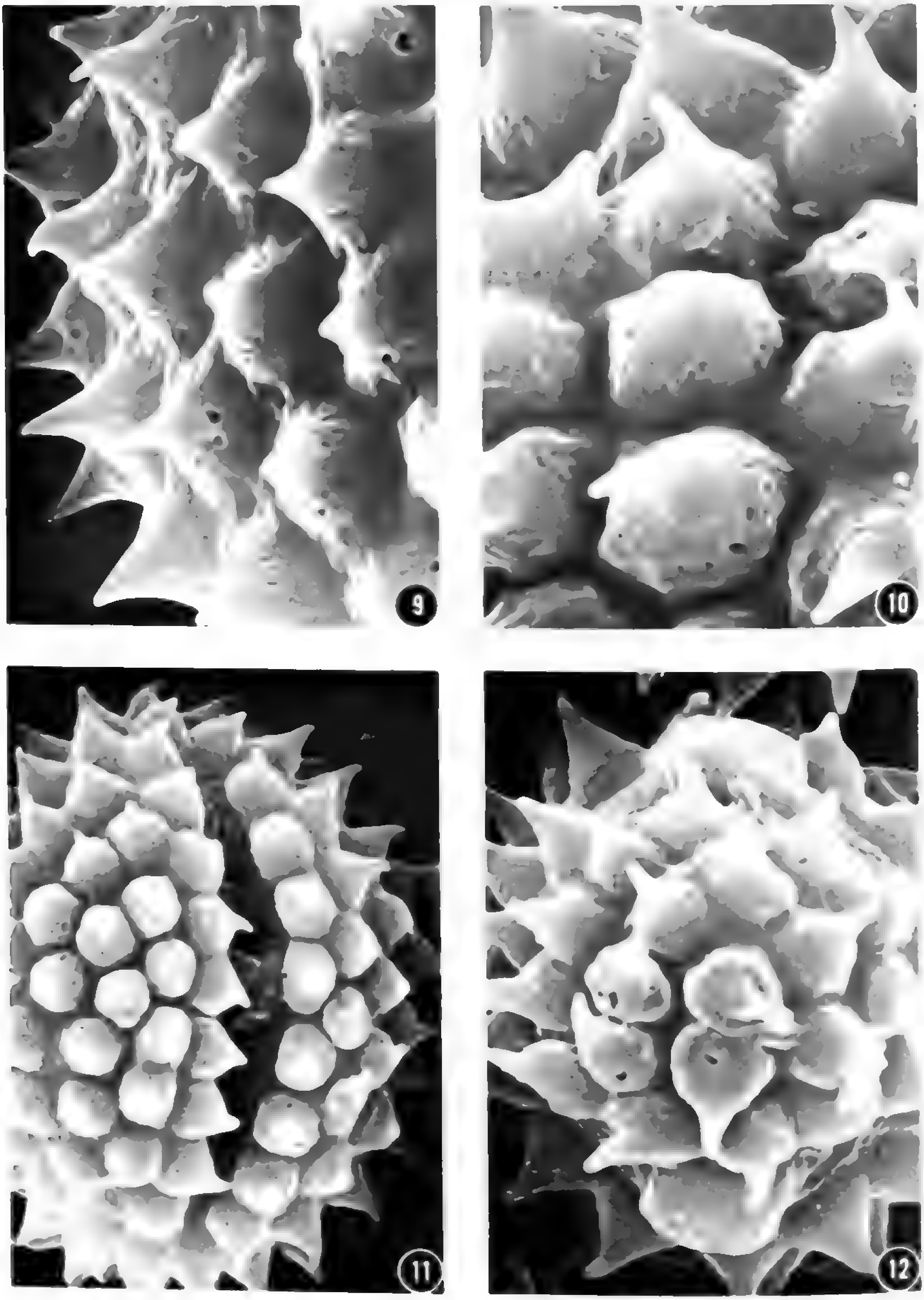


FIG. 9–12. Pollen grains of *Gutierrezia* and *Xanthocephalum*.—9. *Gutierrezia bracteata:* equatorial view of surface details, 10000 ×.–10. *Xanthocephalum linearifolium:* polar view, 10000 ×.—11. *Gutierrezia californica:* equatorial view, 5000 ×.—12. *Xanthocephalum humile:* polar view of surface detail. The cracks noted in the spines are caused by vacuum treatment during processing, 5000 ×.

pollen grain diameter and chromosome number are compared within these known polyploid series, the results confirm the conclusion that it is possible to recognize ploidy levels by a comparison of pollen grain size.

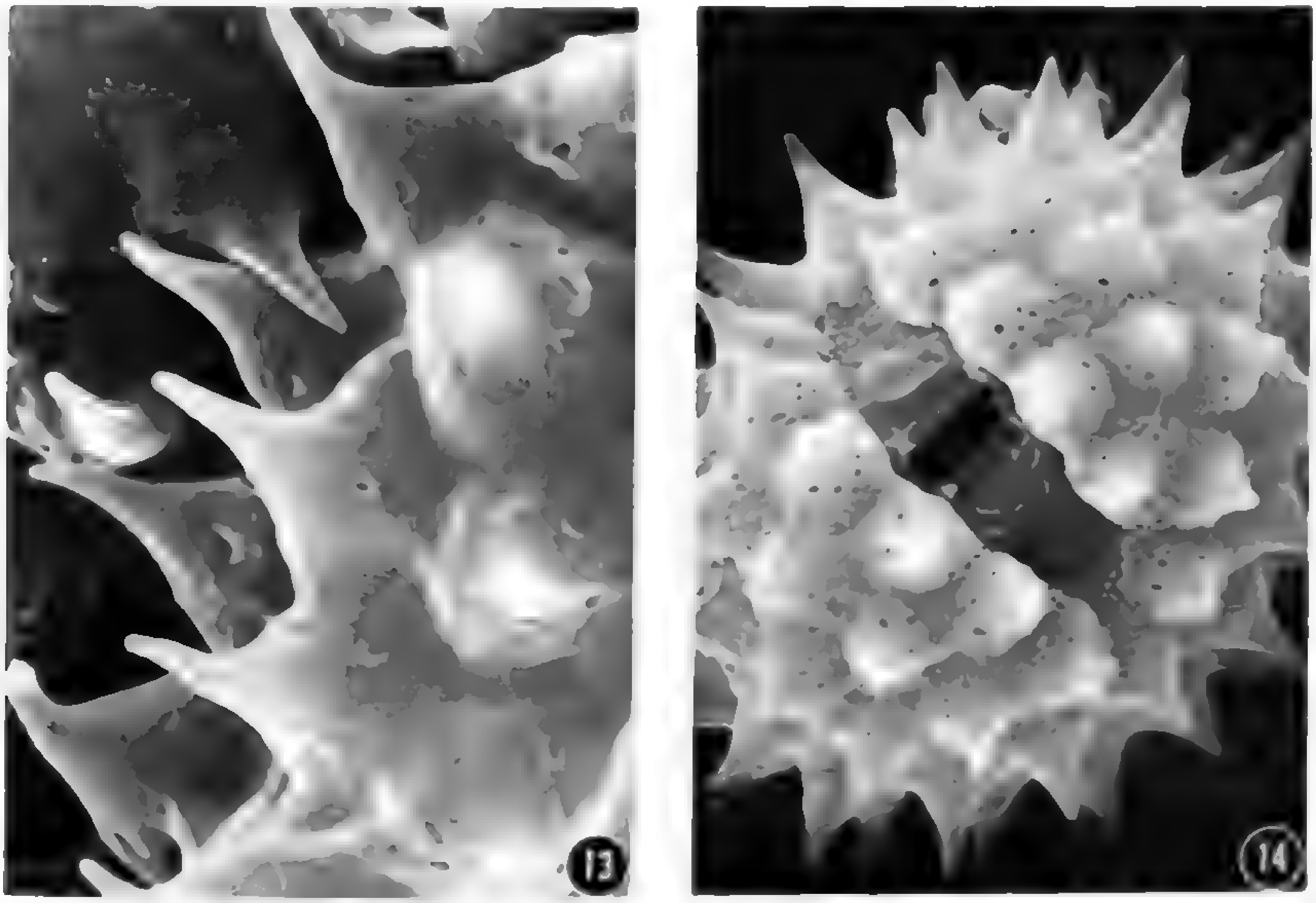


FIG. 13–15. Pollen grains of *Xanthocephalum*.—13. *X. gymnospermoides:* equatorial view of nonacetolized grain depicting long spines (fewer spines are crooked), 10000 ×.—14. *X. gymnospermoides:* acetolized grain showing abundant spinal lacunae, 10000 ×.—15. *X.* [illegible] showing crooked-tip spines, 10000 ×.

TABLE 5. COMPARISON OF POLLEN GRAIN SIZE AND SPINE LENGTH.

Taxon	Mean Spine Length	Mean Diameter of Pollen Grain
Amphiachyris	2.406*	18.750
Amphipappus	2.184	22.449
Greenella	2.301	14.751
Gutierrezia	2.741	15.565
Gymnosperma	2.518	17.011
Xanthocephalum	2.647** (2.346)	17.016** (15.575)

*All measurements are given in μm.
**Averages for Xanthocephalum excluding *X. gymnospermoides.*

DISCUSSION AND CONCLUSIONS

Pollen grains of the genera here studied were assessed for both qualitative and quantitative differences. In both instances, differences were observed between species of different genera and between species of the same genera.

Measuring from the surface of the tectum, the height of the spines ranges from 1.5 μm in *Gutierrezia microcephala, G. sarothrae* and *G. texana* to 5.4 μm in *Xanthocephalum gymnospermoides* (Table 3). According to Wodehouse (1965), a comparison of several different grain types that occur in the Astereae revealed that the length of the spines bore no relation to the size of the grain; that is, small grains do not, as a consequence of their size, have reduced spines and the giant grains do not have giant spines. However, spine size does correspond to pollen grain size in the genera *Gutierrezia* and *Xanthocephalum* (Table 4). It is clear that the longer spines are associated with the grains having higher mean diameters. In this regard, it is noteworthy that the results indicate the reverse trend in the genus *Amphipappus* (Table 5). The pollen grain size of *Amphipappus* is larger than any of the other genera studied, yet spines ornamenting the exine are short and somewhat stubby.

According to Wodehouse (1965), the pollen grains of the Astereae range from ca. 16.5 to ca. 32 μm in diameter. The combined grain sizes for the genera *Gutierrezia, Greenella* and *Xanthocephalum* average only 15.2 μm. These pollens have extremely small diameter sizes for the Astereae. The pollen grains of *Amphipappus*, on the other hand, are distinctly larger with shorter and fewer spines in a given area than those of the other genera. Also, in *Amphipappus* the spines are broader at the base with seemingly larger, more numerous, spinal pores. A more thorough survey of the size, number, and arrangement of the lacunae of the pollen grains should be pursued in order to assess the usefulness of these characters. The Astereae, so far as known, are insect pollinated; thus the compatibility of these characters with the entomophilous habit of the tribe needs further study. Information of this kind is often of considerable taxonomic and evolutionary interest. At present, no systematic studies and observations of pollinators for the genera here studied have been recorded.

Table 6. generic characteristics.

	Amphiachyris	Amphipappus	Gutierrezia	Greenella	Gymnosperma	Xanthocephalum
Basic chromosome number	5	9	4	4	7	4 (6 in *X. gymnospermoides*)
Head with hooklike receptacular glandular trichomes	Absent	Absent	Present	Present	Absent	Present
Pappus disc flowers	Long well-developed setae	Long well-developed setae	Scaly or reduced	Scaly or reduced	Scaly or reduced	Scaly or reduced
Pappus ray flowers	Scaly or reduced	Long well-developed setae	Scaly or reduced	Scaly or reduced	Scaly or reduced	Scaly or reduced
Leaves with glandular cavities	Present	Absent	Present	Present	Present	Present
Leaf shape	Linear-lanceolate	Obovate-lanceolate	Linear-lanceolate	Linear-lanceolate	Linear-lanceolate	Linear-lanceolate
Pollen	Grains medium; spines medium; interspinal lacunae infrequent	Grains large; spines small; interspinal lacunae frequent	Grains small; spines medium; interspinal lacunae infrequent	Grains small; spines medium; interspinal lacunae infrequent	Grains medium; spines medium; interspinal lacunae frequent	Grains small; but large in *X. gymnospermoides;* spines medium; but long in *X. gymnospermoides;* interspinal lacunae infrequent
Wood Vessel	No helical sculpturing of vessel wall	Helical sculpturing in form of coarse bands	Helical thickening consists of grooves connecting the aperatures of pits	No processes	Helical thickening consists of grooves connecting the aperatures of pits	Helical thickening consists of grooves connecting the aperatures of pits
Wood fibers	Fiber dimorphism present	Fiber dimorphism absent	Fiber dimorphism absent	Fiber dimorphism absent	Fiber dimorphism absent	Fiber dimorphism absent

Table 5 shows that, when the averages for pollen characters in *Xanthocephalum gymnospermoides* are omitted, *Xanthocephalum* is hardly different from *Greenella* and *Gutierrezia.* Pollen features in *Xanthocephalum gymnospermoides,* when compared with anatomical studies of the genus (Ruffin, 1974a), correlate with the size of other features, such as chromosome number, size of heads, leaves, involucral bracts, wood features, etc. Because of this, I am of the opinion that *Xanthocephalum gymnospermoides* qualifies as the most primitive species in the genus; however, a complete reassessment of this species may be warranted. Table 6 assembles the pollen data along with previously expressed distinctions gleaned from gross morphology, anatomy, and cytology. On the basis of these unifying data, these characters permit easily recognized taxonomic patterns.

As for *Gutierrezia, Greenella* and *Xanthocephalum,* recognition of a single genus still seems to be the most satisfactory treatment because solid differences between them are negligible.

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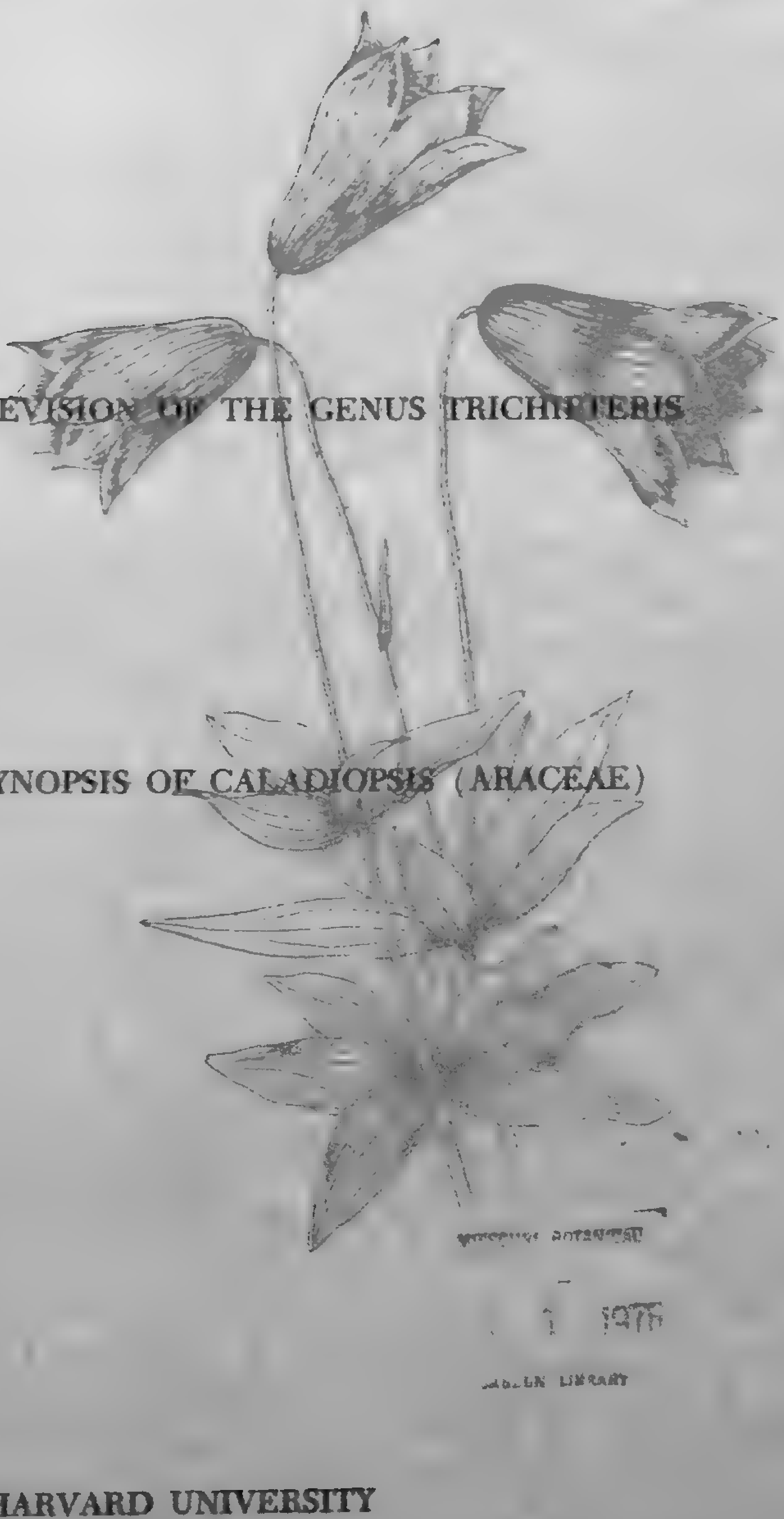

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A REVISION OF THE GENUS TRICHIPTERIS

David S. Barrington[1]

Introduction

The present work is one of a series of revisions of tree fern genera conducted under the aegis of Rolla M. Tryon, Jr. The basis for these studies is Tryon's work on the classification of the family (1970). According to his interpretation, the Cyatheaceae consists of six genera that have petiole scales and two non-scaly genera having only multicellular trichomes. The genus *Sphaeropteris,* the subject of subgeneric revisions by Tryon (1971) and Windisch (1977, 1978), has petiole scales of the unspecialized "conform" type, made up of uniform cells which are all oriented along the long axis of the scales. Two lines of specialization are recognized in *Sphaeropteris:* one in which the petiole scales have dark apical setae and a second with the petiole scales lacking setae. The remainder of the genera with scales have "marginate" petiole scales, made up of a central portion and a specialized margin of cells different in size and orientation, and usually in shape and color. Two of these genera *(Alsophila* and *Nephelea)* have setate petiole scales, and three *(Trichipteris, Cyathea,* and *Cnemidaria)* have asetate petiole scales. Gastony's data on sporangium size and spore number per sporangium (1974) supports Tryon's view that the setate and asetate groups are natural. *Trichipteris* is interpreted by Tryon (1970) as the least specialized of the asetate group of genera, since it has neither an indusium nor anastomosing veins. *Trichipteris* differs from *Cnemidaria* in stem habit, venation, leaf architecture, and spore morphology. Recognition of the exindusiate *Trichipteris* and the indusiate *Cyathea* as distinct genera is based on evidence that each is an independent evolutionary line.

History

"Differt hoc genus ab affini Polypodio praesentia indusii, ab affini Aspidio indusio e pilis copiosis implexis constante et persistente. Nomen derivatum a τριχος et πτερος."

With these words, Presl distinguished the new genus *Trichipteris* in his *Deliciae Pragensis,* published in 1822. Presl speaks of the genus as indusiate, the indusium consisting of copious, persistent, interwoven hairs. In the modern sense, Presl's genus is exindusiate. The paraphyses, prominent in the Brazilian plants that constitute the type species of the genus, remain an important morphological and taxonomic feature, although they are no longer considered to be indusia. Martius (1834) treated *Trichipteris* with *Chnoöphora* Kaulfuss as part of the genus *Alsophila.* Hooker

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[1] Present address: Pringle Herbarium, Department of Botany, University of Vermont, Burlington, VT 05401.

(1844) recognized *Trichipteris* as a subgenus of *Alsophila* but did not treat *Chnoöphora.* Copeland (1947) recognized *Trichipteris* as a genus. Tryon (1970) redefined the genus *Trichipteris* on the basis of characters of the petiole scales to include the majority of the New World species previously ascribed to *Alsophila.*

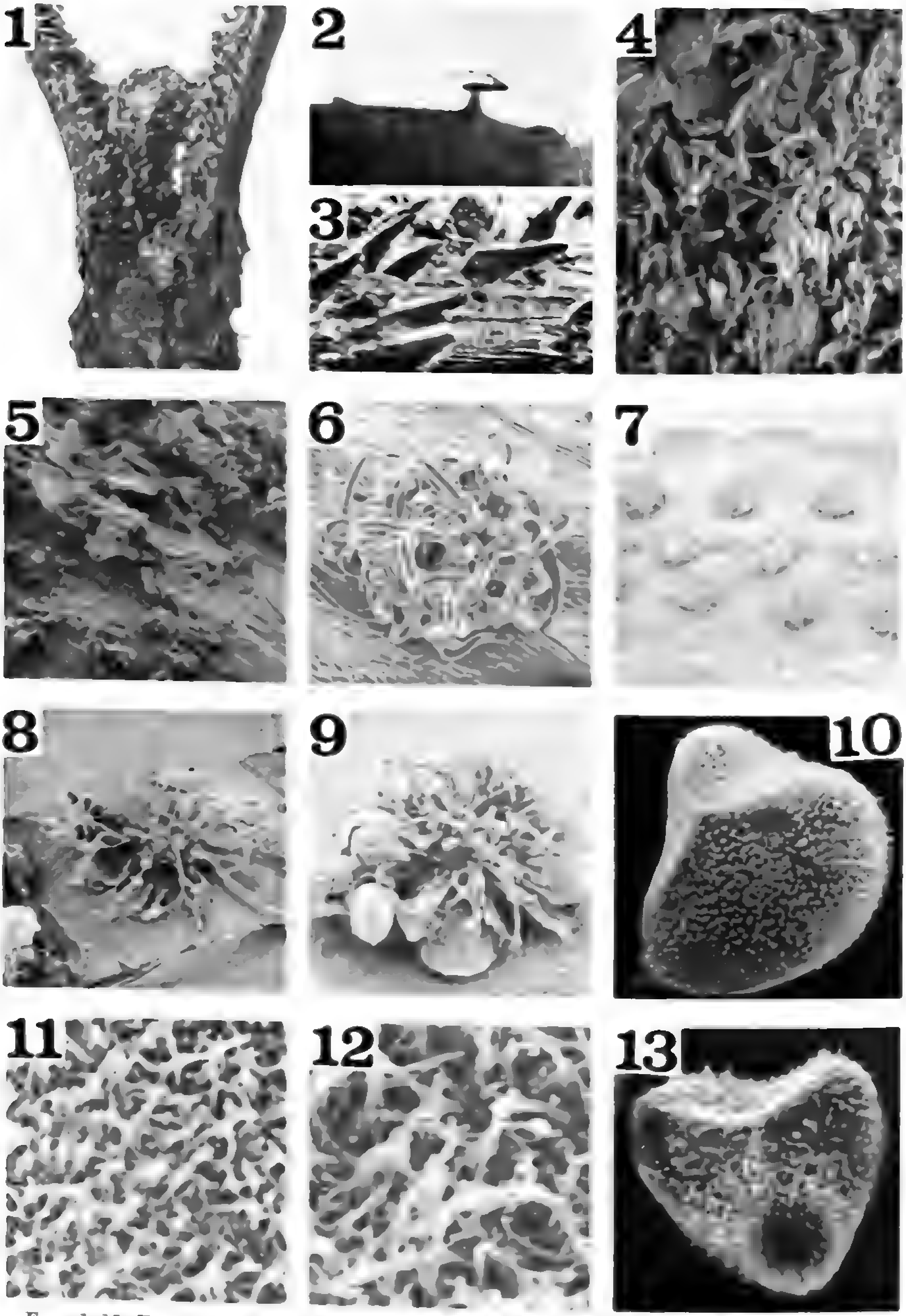
The genus *Alsophila* was recognized as such by Robert Brown in 1810. Until Tryon's reclassification, *Alsophila* included all exindusiate species of the Cyatheaceae with petiole scales. The indusiate species were included in *Hemitelia* and *Cyathea.* Martius (1834), on the basis of his observations on exindusiate Cyatheaceae in Brazil, produced an essentially sound subgeneric classification for the neotropical species of *Alsophila.* The first of his three subgenera is *Chnoöphora,* a name first used by Kaulfuss (1824). *Chnoöphora* Kaulfuss was set up as a genus of one species, now called *Trichipteris villosa* (Willd.) Tryon. The distinctive tomentum of contorted trichomidia characteristic of the species probably inspired the generic name (*χνοös*, tangled hair or cotton; *φορα*, bearing). Martius used the name *Chnoöphora* for a subgenus of three species. Two of those are included here in *Trichipteris corcovadensis* (Raddi) Copel and the third is now recognized as *Metaxya rostrata* (HBK) Presl. Martius described the two remaining subgenera on the basis of venation. Subgenus *Haplophlebia,* including what is now *T. procera* and *T. atrovirens,* was characterized by simple veins. Subgenus *Dicranophlebia,* characterized by veins forking at the sori, included eight of the species of *Trichipteris* recognized in this treatment and one species now included in *Sphaeropteris.* Maxon (1922) associated 13 species of *Alsophila* including *Alsophila armata* on the basis of the structure of the petiole scales, and provided a systematic treatment of the 13 species that he recognized. Tryon (1970) segregated the American species of *Alsophila* into three groups, based on characters of the petiole scales: species with conform petiole scales are included in *Sphaeropteris;* species with marginate scales bearing dark, apical setae are maintained in the genus *Alsophila;* and species with marginate petiole scales but lacking the dark, apical setae he has associated with *Trichipteris corcovadensis* (Raddi) Copel.

Trichipteris includes species and species groups that demonstrate modern concepts in the evolution of ferns. The biogeographical evidence for their integrity is most convincing. However, it would be unwise to interpret the evolutionary history of the genus based only on the information fully worked out in this study. Ten of the 55 species are based on one or two collections. The Guayana Highlands will probably yield several species that are presently unknown. The Brazilian species, which appear to be a group of morphologically variable populations only partially isolated evolutionarily, present taxonomic problems that must await work in the field to be resolved. The present monograph serves as a basis for further investigation of the biology and evolution of *Trichipteris.*

MORPHOLOGY

Stem. The stem morphology of *Trichipteris* is variable. Diminutive species, such as *T. falcata,* have a small, fasciculate rhizome similar to that of many species of *Thelypteris*. Other species, such as *T. Williamsii* and *T. borinquena,* have more substantial rhizomes measuring from three to five centimeters in diameter. The stems of a number of species are ascendant: *T. procera, T. sagittifolia,* and *T. frigida* have ascendant stems reaching a maximum of about one meter in height. Among the arborescent species, *T. pubescens* is the least well-developed and although the stem reaches a height of three meters, it is at most three centimeters in diameter. The branches produced by *T. pubescens* are adventitious, ascendant, and bear leaves reduced in size and amount of dissection. The majority of the species in the genus have an arborescent stem (Fig. 1) up to twelve meters in height. A number of arborescent species, for example *T. Schiedeana* of Central America, have stems of small girth, ranging from three to five centimeters in diameter. A stem of five to ten centimeters in diameter and over three meters in height is typical of most species of the genus. *Trichipteris microdonta* and *T. pubescens* have well-developed lateral branches. The stems have a dictyostelic siphonostele with abundant sclerenchyma characteristic of the entire scaly Cyatheaceae. The corrugated meristeles, surrounded by sclerenchyma sheaths, are apparent in any stem cross section. Medullary bundles were present in all species examined. Lucansky (1974) reports cortical vascular systems in the two species of *Trichipteris* he examined. The stem anatomy of the diminutive species is little known. However, *T. borinquena* has been examined and shows a less condensed form of the dictyostelic siphonostele typical of the family. Meristeles are typically limited to three per cross section, and the vasculature of the petiole is less ramified.

Adventitious roots arise from the base of the petiole. They grow outward and downward as the stem increases in height. The entangled mass of dark, lignified roots near ground level provides a portion of the stem's support. Characters of the mature stem surface are of limited taxonomic importance for *Trichipteris*. The pattern of scars, abraded scales, and pneumatodes (small, hollow cavities in the stem surface), typical of the family Cyatheaceae, does not prove useful in discerning species relations. Stem habit is variable within species and is often the result of environment rather than genetic or ecotypic segregation. The anatomy of the petiole, and consequently the pattern of vasculature observed in any petiole scar, becomes more complex with size, but no pattern of variation that correlates with characters of established evolutionary significance is discernable. By contrast, the indument (epidermal structures) of the petiole, including spines, trichomes, scales, and scurf, is crucial to the taxonomy of *Trichipteris*. This indument is nonfunctional when the leaf is fully expanded. The petiole scales and scurf are a protective coating



FIGS. 1–13. FIG. 1, Stem apex, *Trichipteris* [illegible] (*Maguire* & [illegible]), × [illegible]. 2, Scale subtended by spine, *T.* [illegible] (Harvard University, propagated by C. J. [illegible]) [illegible]. [illegible] 5, [illegible] scale, × 28 [illegible] 6, [illegible] with [illegible] 7, [illegible] 8, Scale [illegible] 10, Spore, × [illegible] *T.* [illegible] (*Barrington 469*, [illegible]). 11, Detail of Fig. 10, × 4000. 12, Detail of Fig. 13, × 4000. 13, Spore, × [illegible], *T. villosa* (*Duarte 10683*, HB).

for the crozier from the time it is differentiated from the stem apex through vernation.

Petiole spines. Petiole spines are undeveloped in the croziers of all *Trichipteris* species. They are variously developed on mature petioles, and are of the corticinate type described by Tryon (1970). I have used four terms to describe the development of spines on mature petioles. Petioles may be inermous: without any spines. Petioles with blunt protuberances, morphologically homologous to spines, are tuberculate. Muricate petioles bear short, conical protuberances with sharp tips. Petioles with any sort of long, fully developed spines are aculeate. In all cases the protuberances of the petioles are the points of attachment of petiole scales (Fig. 2). Species of *Trichipteris* vary considerably with respect to the size and density of spines. Young plants and plants of diminutive species usually have inermous petioles. The best development of spines is among species related to *T. corcovadensis.* However, closely allied species such as *T. villosa* have tuberculate or inermous petioles. Species allied to *T. armata* have unusually long, sharp spines. There is a tendency toward muricate and tuberculate petioles in the Andean species, but they cannot be distinguished as a group on the basis of petiole spines. Spines are noticeably altered when pressed and long, thin spines are especially susceptible to breakage. The color of the spines may differ from that of the petiole as a result of differential drying.

Petiole Scales. The petiole scales of *Trichipteris* lack the apical setae characteristic of *Nephelea, Alsophila,* and some species of *Sphaeropteris.* These scales are of the structurally marginate type (Tryon, 1970), with the central portion consisting of elongated cells appearing on the long axis of the scale. The margin consists of shorter, broader cells oriented more nearly transverse to the axis of the scale (Fig. 3). The development of the scale margin is highly variable. *Trichipteris borinquena* is characterized by petiole scales with a few rows of slightly differentiated cells forming an indistinct margin. *Trichipteris mexicana* has a broad margin of cells which differ from those of the central portion of the scale in shape and orientation. The scale margin in all species is fragile and easily abraded once the leaf has expanded. Collections of *T. phalerata* from Brazil often appear to have emarginate scales, but close examination of intact scales reveals a well-developed margin. Scales of the adaxial part of the base of the petiole commonly lack margins. Emarginate scales have been found in this particular part of the petiole in all species of marginate Cyatheaceae so far examined.

The color of the petiole scales on croziers and mature leaves of *Trichipteris* is of taxonomic importance. Cretaceous petiole-scale borders characterize the species related to *T. procera,* although they are present in species such as *T. costaricensis* as well. Some species related to *T. armata* also have cretaceous petiole-scale borders. The cretaceous border may extend into the structural central portion of the scale. In *T. Dombeyi* some of the cells of the cretaceous border are darkened. In numerous species allied to *T. armata,* dark setae line the edges of the scales. A number of species have concolorous or nearly concolorous scales (the borders may be slightly lighter in color). The coloration of the petiole scales is sometimes highly variable within a species. *Trichipteris dichromatolepis,* of southern Brazil, has petiole scales ranging from bicolorous with a cretaceous border to concolorous. Two species of *Trichipteris* (*T. villosa* and *T. atrovirens*) have petiole scales that are contorted helically when dried.

Petiole Scurf. In many species of *Trichipteris,* the petiole scurf forms a dense, appressed indument covering the surface of the petiole (Figs. 4 & 5). The structural components are trichomidia (small trichomes) and squamulae (small scales), as defined by Tryon (1970). The petiole scurf is useful as a taxonomic character. Large squamulae characterize species such as *T. microphylla* and *T. decomposita.* A scurf consisting of persistent squamulae is characteristic of species such as *T. procera* and *T. aspera.* Most Brazilian species lack a persistent, well-developed petiole scurf, but *T. Gardneri,* a species of the Campo Limpo area of Brazil, has a scurf of persistent squamulae. Petiole scurf becomes abraded with maturity, so that species with scurfy croziers may have glabrous petioles. Diminutive species of *Trichipteris,* even those allied to more robust species with dense, well-developed petiole scurf, usually lack it completely.

Trichomes. The petioles of some species of *Trichipteris,* especially those allied to *T. armata,* are pubescent with long, stiff trichomes. *Trichipteris Gardneri,* a species of Brazil related to *T. phalerata,* has pubescent petioles. Species with stiff, multicellular trichomes on the petioles were considered primitive by Riba (1969) in his work on the species related to *T. armata.*

Lamina Indument. The indument of the petiole often extends upward along the abaxial surface of the lamina axes, and its composition and distribution is taxonomically important. Scales are often present along the rachis. They may differ in color and in the development of the margin from the scales of the petiole base. The scurf along the axes of the lamina is often different from the petiole scurf in both composition and development. In most species, the indument found on the abaxial surface of the costae and costules is considerably different from that of the major axes and the petiole. Flattish to bullate squamulae are often prominent along the costae and costules. The two types of squamulae are usually found on the same costae, in which case the flattish squamulae are proximal and the bullate squamulae are distal along the axes. Trichomes and trichomidia are common on the abaxial surface of the lamina, especially in the species allied to *T. armata.* In a few species *(T. frigida, T. Schlimii,* and *T. Hodgeana)* the axes are covered abaxially with a scurfy tomentum similar in composition to that of the petiole scurf. The basal parts of the pinna-rachises and costae in many species bear a close-packed group of squamulae similar to those scattered along the remainder of the axes. Large, filiform squamulae are borne near the bases of the axes of many species.

The adaxial surface of the axes in *Trichipteris* is glabrous or has stiff, multicellular, arcing trichomes. Squamulae, trichomidia, and scales are not found on the adaxial surface. Because the adaxial indument is so uniform, I have limited my descriptions and discussions of lamina indument to that of the abaxial surface.

The indument of the axes, like that of the petioles, is functional only during the vernation of the leaf. The structures remaining on mature leaves represent only a portion of the original indument. The rest is lost in maturation.

The following terms, which I have used to describe the color of the leaf axes and indument, are based on Stearn's color terms (Stearn, 1966): *atropurpureous*-dark purple; *castaneous*-dark, reddish brown; *cretaceous*-the color of chalk (white with a faint, yellowish tinge); *diaphanous*-translucent; *ferruginous*-reddish brown; *fulvous*-golden brown or light brown; *fuscous*-dark brown; *nigrescent*-blackish.

Lamina. The lamina of *Trichipteris* species varies considerably in degree of dissection. Species with 1-pinnate leaves have evolved at least twice in the genus, and there is a 3-pinnate-pinnatifid species from Venezuela. In *T. demissa* and *T. borinquena,* fertile leaves can be either 1-pinnate-pinnatifid or 2-pinnate-pinnatifid. *Trichipteris corcovadensis,* of southern Brazil, includes both 2-pinnate plants with large, oblong-lanceolate, entire pinnules and 2-pinnate-pinnatifid plants with diminutive, linear-lanceolate, deeply lobed pinnules. I have not considered differences in leaf dissection alone to be evidence of speciation in *Trichipteris.* However, a number of cases exist in which speciation has included a change in the dissection of the lamina. Incipient speciation in *T. demissa* is recognizable in *T. demissa* var. *thysanolepis,* based on plants differing from the putative parent population in both petiole scale morphology and leaf dissection. *Trichipteris decomposita* differs from *T. procera* in its petiole scurf as well as in the dissection of the lamina.

There are young plants which produce fertile leaves less dissected than those typical of older plants of the same species. They occasionally have been recognized as species (*Alsophila Gleasoni,* a synonym of *Trichipteris procera*). Occasionally, damaged plants continue to grow, producing foliage that is reduced in complexity. Unusually small plants and damaged plants have the indument and soral characteristics of more typical plants.

The leaf texture of *Trichipteris* plants often varies with insolation. Those species (e.g., *T. Gardneri* and *T. villosa*) of drier, sunnier areas have revolute, coriaceous leaves, while most of the forest species have flattish, papyraceous to chartaceous leaves. The leaves of the forest species found growing in open areas, for example *T. pauciflora* from the páramo areas of Venezuela, are revolute and coriaceous. Although I have included the texture of the leaves in the species descriptions, it varies enough to be a character of only limited value.

The shape of the leaf apex is often of taxonomic value in *Trichipteris*. In a few species, the apex of the leaf is an articulated pinna conforming in shape and size to the medial pinnae of the lamina. In other species, the width of the leaf near its apex is abruptly reduced. Gradually reduced and acute apices are characteristic of a number of species. The remainder have a gradually reduced and acuminate leaf apex, which I interpret as intermediate between leaves with abruptly reduced apices and those with gradually reduced acute apices. In the intermediates, the apex is drawn out into a long tip, as in the pinna-like leaves, but there is no abrupt reduction in the size of the pinnae. *Trichipteris Schiedeana* and *T. nigripes* are species with a gradually reduced acuminate apex. There is some variation in the leaf apex within species.

Pinnules. The length of the petiolules of the pinnules is of some taxonomic importance in *Trichipteris*. In species such as *T. Kalbreyeri*, the petiolules are unusually long. By contrast, species related to *T. procera* commonly have sessile pinnules. In *T. nigripes* there is considerable variation in petiolule length. For example, although the pinnules of *T. nigripes* var. *nigripes* are petiolulate, those of *T. nigripes* var. *brunnescens* are sessile. In the taxonomic section, the described length of the petiolules is relative to the width of a single ultimate segment in pinnatifid species. Short-petiolulate describes petiolules shorter than the width of one lobe; petiolulate describes petiolules of about the same length; and long-petiolulate describes petiolules longer than the width of one lobe.

The shape of the pinnules (pinnae of 1-pinnate species) is not a reliable taxonomic character. Both attenuate and obtuse pinnules are common in some species, such as *T. procera, T. Schiedeana*, and *T. atrovirens*. Also, there is a tendency for the pinnules of the basal pinnae of most species to be obtuse, though those of more apical parts of the lamina may be acuminate or attenuate. Unfortunately, the shape of the pinnules imparts a characteristic appearance to specimens, and numerous species have been described based on variations in shape alone.

However, the dissection of the pinnules is often a useful taxonomic character. In my descriptions, the depth to which the penultimate segments are dissected is relative. Shallowly pinnatifid pinnules are dissected about one-quarter the distance to the costae. Pinnatifid pinnules are dissected about one-half the distance to the costae. Deeply pinnatifid pinnules are dissected about three-quarters of the distance to the costae. I have defined the tip of the pinnules as distinct from the apex. The shape of the apex is ordinarily useful as a taxonomic character. In some cases, the dissection of the tips of the pinnules (pinnae of 1-pinnate species) is also helpful. The shape and dissection of the lobes (ultimate segments) has been included in my descriptions. Occasionally, distinctive cutting of the lobes is diagnostic, as in *T. Kalbreyeri*.

Veins. Venation is closely correlated with dissection of the penultimate segments. In typical 2-pinnate-pinnatifid species of *Trichipteris,* the pinnules are deeply lobed, and each lobe is supplied with a costule bearing several simple or forked free veins. Venation of 1-pinnate-pinnatifid species is similar. Two-pinnate-pinnatifid species of *Trichipteris* with crenate or entire pinnules have veins that arise from an indistinct costule and are concurrent to the leaf margin. In several 1-pinnate-pinnatifid species with entire pinnae, the concurrent veins are casually anastomosing. Although venation varies from simple to forked in *T. procera, T. dichromatolepis, T. nigripes,* and others, most species are characterized by one, but not both, venation states. Simple veins can be found distally on leaves of many *Trichipteris* species characterized by forked veins, so description and analysis of venation must be from the more typical medial parts of the leaves. Damaged plants often have aberrant veins. Venation states are of taxonomic value in *Trichipteris.* Martius (1832) established two subgenera of *Alsophila* (substantially modern-day *Trichipteris*) based on venation states. Simple venation characterizes the closely related group of species including *T. procera.* Forked veins are characteristic of all but a few scattered species in the remainder of the genus.

Sori. The sori are borne on the veins of the abaxial leaf surface and not on the margin. *Trichipteris praecincta* and *T. nanna* have submarginal sori. *Trichipteris procera* has sori that vary in position from submarginal to subcostal. In the remaining species of the genus, the sori are near the middle of the veins on which they are borne. In 2-pinnate specimens of *T. corcovadensis,* the sori are in a single row along each side of the costae. In *T. Williamsii* and *T. Cyclodium* they are in two or three rows along each side of the costae. The unusual distribution of sori in these species can be related to the dissection of the lamina.

The sorus (Fig. 7) consists of an expanded receptacle on which paraphyses and sporangia are borne. No indusium of tissue derived from the proximal part of the receptacle and adjacent vein is present. The length of the paraphyses has been measured relative to the length of the sporangium and its stalk. *Trichipteris procera* and its relatives have paraphyses that are shorter, if not much shorter, than the sporangia. The remaining species have paraphyses normally as long as, or longer than, the sporangia. The mass of paraphyses gives the receptacle a specific appearance dependent on their length. The receptacle may be described as puberulent, hirsute, pilose, or villous. Variation in the structure of the paraphyses has not proved to be an important character. Uniseriate, multicellular paraphyses are typical of the genus. In species such as *T. dichromatolepis,* some specimens have multiseriate paraphyses. *Trichipteris nesiotica,* endemic to Cocos Island, has unusually short, thick paraphyses. They are, like the petiole scales and scurf, functional only during vernation (Fig. 6). The structures seen on specimens of mature leaves are remnants, which become more and more abraded in older material. Since the length of the paraphyses is of major diagnostic importance, newly mature specimens with intact paraphyses are necessary for critical determination.

The genus *Trichipteris* is by definition exindusiate. The sori are more or less enveloped by soral squamulae in six of the species (Fig. 8). The soral squamulae differ from hemitelioid (partial) indusia in their structure and attachment. Soral squamulae are translucent and attached at the base of the receptacle by a narrow base and may be attached all around the receptacle. In contrast, indusia are opaque, thickened structures attached by a broad base to the proximal side, if not the entire perimeter, of the receptacle. *Trichipteris sagittifolia* and *T. Steyermarkii* have a number of broad, dark squamulae surrounding the sori, forming a complete covering. *Trichipteris costaricensis* has several pale squamulae nearly enveloping the sori; *Trichipteris gibbosa* has one or more associated with the sori; in *T. aspera* the soral squamulae vary from numerous, broad and dark to single, biseriate, and nearly diaphanous. Four of the six species with soral squamulae are found in the area of Golfo de Paría, Venezuela. Soral squamulae constitute a useful character in *Trichipteris*.

Sporangia and spores. The sporangia in *Trichipteris* are borne on a short stalk of four cells (Fig. 9). The sporangium has an oblique, complete annulus that is interrupted laterally by a stomium of thin-walled cells. The sporangia are relatively large, and contain either 32 or 64 spores (Gastony, 1974), having a perine, the surface features of which are nearly uniform throughout the genus (Figs. 10–13). The typical perine bears numerous minute cilia more or less developed into a dense tomentum. The exine is psilate in the species I have examined. Preliminary work on the perine morphology of *Cyathea* and work on the spore morphology in *Cnemidaria* (Stolze, 1974) indicate that spore morphology could be a useful generic character for the Cyatheaceae with asetate, marginate scales. Species relations in *Trichipteris* are not corroborated by variation in surface features of the spores. Walker (1966) reported a chromosome number of $n = 69$ for *Trichipteris armata.*

GEOGRAPHY AND ECOLOGY

Geographic data have often been the basis for initial interpretation of little known and biologically unstudied groups of ferns such as *Trichipteris*. Recent revisionary work in the Cyatheaceae (Gastony, 1973; Stolze, 1974; Tryon, 1971 & 1976) includes geographic distributions that substantiate conclusions drawn from morphological data. The small size of wind-borne spores results in frequent long-distance dispersal of ferns. Uniformity in geographically widely separated populations of a species is common, e.g., the large number of arctic ferns occurring on all the northern continents (Hultén, 1964). At the same time, it is geographic isolation that is often the most significant in the evolution of the pteridophytes. Interference with regular long-distance dispersal results in genetic isolation and morphological discontinuity of geographically isolated populations.

The center of distribution for the genus *Trichipteris* is the Andes, a mountain range presenting diverse barriers to long-distance dispersal. Of the 55 species in the genus, 23 are found in the continental South American Andes. Another 19 are from mountain ranges continuous geographically, if not geologically, with the Andes (the mountains of Central America and the Antilles). These regions include altogether about 75% of the species in the genus.

All of the genera of the Cyatheaceae with petiole scales are represented in the Andes. Four of the six genera with scales are restricted to the New World, and are most diversified in the mountains of the New World tropics. The stem anatomy of the known species of the scaly Cyatheaceae is surprisingly uniform (Lucansky, 1974). Other structures uniform throughout the group, such as sporangia, suggest that it is monophyletic. The typical cyatheaceous stem anatomy is to be seen in fossils from the Jurassic (Ogura, 1927) to the late Tertiary (Bancroft, 1932). Apparently plants of the Cyatheaceae have been in existence since the Mesozoic and have moved into the Andes as the mountains were uplifted. Present diversity may be the result of successful exploitation of habitats created during the Andean uplift.

Trichipteris is interpreted as a relatively unspecialized genus in the family Cyatheaceae (Tryon, 1970). Although it is well-represented in wet forests at high altitudes, 11 of the 42 species, or 26.2%, are restricted to low elevations (below 1000 m.), with another 18 extending below 1000 meters. Thus, two thirds of the genus is found growing below 1000 meters. The montane or cloud forest habitat typical of the vast majority of cyatheaceous species does not extend down to 1000 meters. The adaptation of *Trichipteris* to low altitudes is reflected in the unusual Amazonian distribution of two species and the diversification of the genus in southern

TABLE 1. ALTITUDINAL RANGE*

Altitude	No. of species	% of total species (42)
0–1000 m.	11	26.2
0–2000 m.	13	31.0
0–3000 m.	4	9.5
0–4000 m.	1	2.4
1000–2000 m.	6	14.3
1000–3000 m.	3	7.1
1000–4000 m.	0	0
2000–3000 m.	1	2.4
2000–4000 m.	1	2.4
3000–4000 m.	0	0
Unknown	1	2.4

*Excluding *T. armata* and allies

TABLE 2. HABITATS*

Habitat	No. of species	% of total species (42)
Original forest	28	66.2
Secondary forest	1	2.4
Open situations	1	2.4
Páramo	0	0
Original & secondary forest	3	7.1
Original & secondary forest, open situations	2	4.7
Original forest & páramo	2	4.7
Secondary forest & open situations	3	7.1
Unknown	2	4.7

*Excluding *T. armata* and allies

Brazil. The possibility exists that the Cyatheaceae in modern times have undergone adaptive radiation primarily in the wet forests at higher altitudes, and that evolutionarily older groups such as *Sphaeropteris* and *Trichipteris* are the only genera diversified at lower altitudes.

The genus *Trichipteris* is unique among the genera of the family in its adaptation to mesic and subxeric environments and its tolerance to full sun (Table 2). Maxon (1914) describes the ecology of *Trichipteris costaricensis* as follows:

> "The original specimens . . . have the appearance of being decidedly xerophilous for a tree fern; and it is interesting to note that the Guatemalan specimens cited below are all from the drier, western part of that country, and that the Santa Rosa specimens in particular, which in their lesser size perfectly match the original, are from a region which, in fact, may even be called semiarid. Few tree ferns are able to exist in such surroundings."

Trichipteris villosa has a similar ecology and consequently a distinctive geographical distribution. It is characterized by a tomentum of small, contorted trichomes, which is found to be more dense with increased exposure to sunlight. There is a tendency toward revolute, coriaceous segments. It has been collected in dry washes, open savannas and grasslands throughout South America, commonly in full sun. Several other species *(T. atrovirens, T. corcovadensis, T. dichromatolepis, T. Gardneri,* and *T. phalerata)* are adapted to drier areas with greater insolation.

Two, and possibly three, species of *Trichipteris* occur in the alpine areas (páramos) of South America. They are characterized by many of the same specialized features as the "xeric" species. *Trichipteris frigida* of the northern Andes is largely confined to the páramos. It has segments that are revolute and coriaceous, the axes of the lamina are covered with a dense tomentum of pale trichomidia, and the costae bear finely laciniate squamulae. *Trichipteris demissa,* a species with rigidly coriaceous leaves, is found on open summits of tepuís in the Guayana Highlands. The adaptation of species of *Trichipteris* to alpine areas is unique in the family. Although *Trichipteris* is a relatively unspecialized and theoretically old genus of the Cyatheaceae, it has the broadest tolerance for reduced

TABLE 3. REGIONALISM AND ENDEMISM*†

Geographic Region	Species Numbers	Number (%)	No. endemic (% for region)
Mexico and Central America	*8*,10,*12*,*18*,26,*28*,*39*,40,*42*, *44*,45,*47*,*53*,*54*,55	15 (27.3)	11 (73.4)
Andes, Pacific	*7*,*9*,15,26,40,*45*,*46*	7 (12.7)	4 (57.2)
Andes, Atlantic	1,*2*,*3*,*4*,*6*,*11*,*14*,15,*16*, 17,*20*,*21*,*22*,*23*,*27*,28, 40,45,46,52	20 (36.4)	12 (60.0)
Caribbean	1,*5*,*13*,*25*,26,*35*,*43*,*48*,*49*	9 (16.4)	7 (77.8)
Guayana Highlands	1,10,17,22,27,28,*36*,*37*,*38*	9 (16.4)	3 (33.3)
Amazon Basin	1,*19*,26	3 (5.5)	1 (33.3)
Brazil, Campo Limpo	1,28,30,*31*,50	5 (9.1)	1 (20.0)
Brazil, Serro do Mar	26,*29*,30,*32*,*33*,*34*,*41*,50,*51*	9 (16.4)	6 (66.7)

*Including *T. armata* and allies

†Numbers refer to species numbers used in this revision, endemic species in italics.

moisture and increased sunlight, including the exposure inherent in alpine habitats, of any genus in the family.

There are a number of distinctive geographic relationships involving regionalism and endemism in the genus *Trichipteris* (Table 3). I have discussed the unique presence of *Trichipteris* in the Amazon Basin, indicating the adaptation of the genus to low altitudes. Although each genus of the scaly Cyatheaceae is found in southern Brazil, *Trichipteris* is the only one represented by a large, confusing group of species suggesting adaptive radiation. Eleven species in the genus are found in Brazil; of these, nine are endemic. The majority of these species are polymorphic (a situation fostering a plethora of specific epithets). The success of *Trichipteris* in Brazil can, in part, be correlated with its adaptation to the drier climate of the Campo Limpo area in the states of Goyas, Minas Gerais, and Matto Grosso. Species of *Trichipteris* are also found in secondary forests, shrubby situations, and original forests in the Serra do Mar. One species, *T. phalerata*, occurs in both the Campo Limpo and the Serra do Mar regions. The complex variability found in the Brazilian species may have resulted in part from modern fluctuations in the climates of the Campo Limpo and Serra do Mar, and the episodic isolation of populations in secondary forest and open situations.

The Guyana Highlands are a geologically old formation of isolated tepuís (mesas) with a highly endemic angiosperm flora. The endemism among the ferns is not as common as in the angiosperms: only *Pterozonium* (Lellinger, 1967) and *Hymenophyllopsis* (Lellinger, pers. comm.) have a significant number of endemic species there and are essentially limited to that area. *Trichipteris* is one of the smaller number of genera with species endemic to the region. Three of the nine species found in the Guyana Highlands are endemic. The polymorphic *T. demissa* and the related *T. Cyclodium* are evidence that endemic species in the Guayana Highlands are presently evolving, although they are highly isolated in the genus. Another species, *T. villosa,* occurs in the open savanna areas of the Guayana region, not in association with the tepuís: it is not endemic.

In the Caribbean, the genus *Trichipteris* is characterized by broadly distributed, as well as locally endemic, species. *Trichipteris aspera, T. microdonta,* and *T. procera* are widespread. In contrast, three species are endemic to single islands in the West Indies. *Trichipteris borinquena* of Puerto Rico and *T. Hodgeana* of Dominica have no close relatives in the genus. *Trichipteris sagittifolia,* endemic to Trinidad, is a member of a close-knit group of three species (including *T. Steyermarkii* and *T. cordata*).

The distribution of most *Trichipteris* species in the Andes conforms to one of two patterns: Pacific or Atlantic drainage. Species with distributions along the Atlantic drainage commonly reach the Sierra de Perija and consequently are included in early collections from Colonia Tovar in the Venezuelan Andes. The Atlantic drainage species, *T. pubescens* and *T. Lechleri,* also grow in the Guayana Highlands. The Amazonian *T. nigra* is related to *T. Schlimii,* a species of the Atlantic slopes of the Andes. Endemism among species of this geographic alliance is the most common in Venezuela. In the Andes of Venezuela, the Península de Paria, and in Trinidad there are five species of *Trichipteris* with ranges of less than 300 miles. Species of the Atlantic drainage of the Andes extend southward as far as Bolivia. Species 11 to 26 form a morphologically cohesive group almost entirely confined to the Atlantic drainage.

The Pacific drainage association of species is much smaller. Most important are two 1-pinnate-pinnatifid species *(T. falcata* and *T. phalaenolepis)* endemic to the Dagua Valley of Colombia, growing at altitudes below 1000 meters. *Trichipteris ursina,* a Central American species closely related to *T. phalaenolepis,* is similar in habitat but has a more extensive geographic range. *Trichipteris microdonta,* a broad-ranging species of low altitudes, is also present in the Dagua Valley. There are no species found in the more southern parts of the Andean Pacific drainage because of the extreme aridity.

Among the species of *Trichipteris* (excluding the group of *T. armata,* revised by Riba in 1967) only *T. nigripes* and *T. pilosissima* occur on both the Atlantic and Pacific slopes of the Andes. In *T. nigripes,* the plants from the Pacific drainage are morphologically distinct, especially at lower altitudes, from those of the Atlantic drainage. No vicarious species pairs have been found that are from the opposite slopes of the Andes. The mountain range is apparently a significant barrier to migration. A seemingly impossible disjunct distribution between the mountains of Panama and the Guayana Highlands is reported for *T. Williamsii.* This disjunction is recorded for a number of angiosperms, for example the Chrysobalanaceae (Prance, 1974) and Myristicaceae (Gentry, 1975). The isolated position of *T. Williamsii* in the genus suggests that its distribution is a relict of a formerly continuous range more recently disrupted by the Andean uplift.

The ranges of the species in *Trichipteris* are generally limited. Over 35% have a range of less than 300 miles, while in contrast, only about one-third have ranges exceeding 750 miles (Table 4).

Geographic ranges, when correlated with morphological data, provide insight into the evolution of *Trichipteris* species. The number, their morphological similarity, and divergent populations suggest that there has been substantial evolution in the genus within the recent past. Speciation via peripheral isolation (Tryon, 1972b) is best seen in *T. aspera* and *T. gibbosa. Trichipteris gibbosa* is a continental species, which apparently has become isolated in the recent past from the closely allied Antillean species *T. aspera. Trichipteris gibbosa* has undergone enough modification of the indument of the costae, costules, and paraphyses to suggest that it is isolated genetically from *T. aspera.* The vicarious species pair, *T. sagittifolia* (endemic to Trinidad) and *T. Steyermarkii* (from Sucre and Monagás, Venezuela), also suggests that species on the Caribbean islands can become isolated from those on the adjacent mainland. Incipient speciation resulting from peripheral isolation is apparent in Pacific coastal populations of *T. nigripes. Trichipteris atrovirens* has apparently been derived from Brazilian elements of *T. villosa* through isolation at the southern periphery of *T. villosa*'s range. A change in environmental adaptation toward a secondary forest niche has accompanied this evolution.

Long-distance dispersal, as a precursor to speciation, can be seen in *T. ursina* and *T. phalaenolepis.* The two are morphologically close, differing only in the coloration and distribution of the petiole scales. They are separated geographically by the distance between Costa Rica and southern Colombia. One species apparently has been derived from the other after successful long-distance dispersal. Two varieties of a single species endemic to the Guayana Highlands provide an excellent example of

TABLE 4. RANGE EXTENT*

Range extent	No. of species	% of total species (42)
0–100 mi.	16	29.2
100–300 mi.	5	9.1
300–750 mi.	12	21.8
750–1500 mi.	12	21.8
1500–3000 mi.	8	14.5
3000–5000 mi.	2	3.6

*Including *T. armata* and allies

long-distance dispersal. *Trichipteris demissa,* a variable species, includes an atypical population from the isolated Cerro Duida. In at least one case, isolation of disjunct populations has not resulted in morphological differentiation. The range of *T. villosa* consists of four isolated populations (Guyana Highlands, Atlantic drainage of the northern Andes, Bolivian Andes, and the Brazilian Campo Limpo). Reduction in the geographic extent of the dry, open habitat in which *T. Villosa* is found may have been the cause. Lack of change in the environment of the isolated populations may have made lack of morphological change possible.

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NOMENCLATURE

Format of the nomenclature follows Tryon (1970, 1976) and Gastony (1973). The citation of type collections in this treatment includes only the information in the original descriptive literature for the species. Any additional information from materials of the type collection or other literature sources is included in parentheses.

SYSTEMATIC TREATMENT

TRICHIPTERIS PRESL

Trichipteris Presl, Delic. Prag. 1:172. 1822. (Altered to *Trichopteris* by Schott, Gen. Fil., t. 5. 1834, and others, but Art. 73, Internat. Code Bot. Nomencl., XIIth Internat. Bot. Congress removes all reasons for accepting the altered spelling.) TYPE SPECIES: *Trichipteris excelsa* Presl = *Trichipteris corcovadensis* (Raddi) Copeland.

Chnoöphora Kaulfuss, Enum. Fil. 250. 1824. TYPE SPECIES: *Chnoöphora Humboldtii* Kaulf. *nom. superfl.* for *Cyathea villosa* Willd. = *Trichipteris villosa* (Willd.) Tryon.

Alsophila pro parte auct. pl., e.g., Martius, Icon. Plant. Crypt. Brasil, 62–75. 1834.

Hemitelia pro parte Kuhn, Linnaea 36:159. 1865.

Cyathea pro parte Domin, Pteridophyta 262–263. 1929.

Stem creeping to erect, unbranched or rarely with adventitious branches, to ca. 10 cm. in diameter and 12 m. in height; externally with numerous close-set, oblong to rotund leaf scars composed of numerous bundle scars, subtended by one or more pneumatodes; the intercalary stem surface with the remains of epidermal scales and heavily lignified roots; the roots developed downward in arborescent species into a buttress-like system supporting the base of the stem; the remains of the petioles variously persistent toward the upper portion of the stem; internally with a simple to condensed dictyostelic siphonostele separated by the leaf gaps into corrugated meristeles, more or less enclosed in a sheath of schlerenchyma, the stele often accompanied by series of medullary and cortical bundles. *Croziers* arising from the stem apex in a tight spiral; without well-developed spines; with densely matted, brownish or white to green and photosynthetic scales, the cells of the marginal part of the scales different in orientation, size and usually in shape from those of the central portion; trichomes present in some species; often with a well-developed, closely appressed and usually dark-colored scurf of large to small squamulae and trichomidia; segments of developing leaves revolute, enclosed by scales and scurf, the developing sori more or less enclosed in a layer of paraphyses, and in some species also enclosed in a layer of soral squamulae. *Fully expanded leaves* petiolate, petiole up to 2 m. long, inermous to aculeate; the marginate petiole scales concolorous, or with a paler border more or less corresponding to the structural margin of the scale, lacking dark terminal setae, but sometimes with dark denticulae along the edges; petiole sometimes pubescent with stiff trichomes; persistent petiole scurf variously composed of large to small squamulae and trichomidia, or absent. *Lamina* simply 1-pinnate- to 3-pinnate-pinnatifid; axes with trichomes adaxially; abaxially glabrous or with an indument of trichomidia, trichomes, squamulae, and scales. *Sori* with mature sporangia round, exindusiate, borne on the abaxial surface of the lamina on forking or simple, free or rarely anastomosing veins; sori with short to long paraphyses; receptacle puberulent to villous, occasionally with one or more soral squamulae.

KEY TO THE SPECIES

A. Typical leaves of adult, fertile plants no more than 1-pinnate-pinnatifid. . . Part 1.

A. Typical leaves of adult, fertile plants at least 2-pinnate (fertile specimens from extreme environments rarely dwarfed). . . . . B.

B. Leaf axes with stiff, multicellular trichomes, petiole scurf absent, sinuses between segments often polygonal to subquadrate, petiole scales often with dark denticulae, plants of open habitats with pale green foliage. . . . . Part 2.

B. Leaf axes lacking stiff, multicellular trichomes (except in *Trichipteris Gardneri* and *T. pilosissima*), petiole scurf absent or variously developed, sinuses between segments acute, petiole scales without dark denticulae, plants of diverse habitats. . . . . C.

C. Petiole scales bicolorous, with a darker central portion and a cretaceous border, fertile veins simple, paraphyses shorter than the sporangia. . . . . Part 3.

C. Petiole scales concolorous or bicolorous, rarely with a cretaceous border, fertile veins usually forked at the sori, paraphyses usually as long or longer than the sporangia. .... Part 4.

PART 1

1. Petiole scales fuscous with a cretaceous border, fertile veins simple. .... 2.
 2. Pinnae entire to crenate, the conform apical pinna articulated to the rachis, abaxial surface of the lamina with prominent veins. .... 3.
  3. Pinnae acute, tips of the pinnae entire. .... 37. *T. Cyclodium* (p. 75).
  3. Pinnae acuminate, tips of pinnae serrate. .... 10. *T. Williamsii* (p. 35).
 2. Pinnae crenate to deeply pinnatifid, apex of blade gradually reduced, without a conform apical pinna articulated to the axis, abaxial surface of the lamina with immersed veins. .... 4.
  4. Pinnae deeply pinnatifid, truncate at the base. .... 5.
   5. Axes of pinnae nearly glabrous (with only a few diaphanous squamulae), sori submarginal. .... 38. *T. nanna* (p. 75).
   5. Axes of pinnae with trichomidia and squamulae, sori medial. .... 6.
    6. Scales of rachis crowded, fuscous (Central America). .... 8. *T. ursina* (p. 34).
    6. Scales of rachis scattered, cretaceous (Colombian Andes). .... 9. *T. phalaenolepis* (p. 35).
  4. Pinnae crenate to pinnatifid, cordate-hastate at the base (Colombia). .... 7. *T. falcata* (p. 33).
1. Petiole scales nearly concolorous, the border fulvous or darker, fertile veins forked at the sori. .... 7.
 7. Abaxial surface of the lamina glabrous, pinnae sessile or long-petiolulate. ..... 8.
  8. Pinnae long-petiolulate (Colombia). .... 24. *T. latevagans* (p. 54).
  8. Pinna sessile (Guayana Highlands). . . 36b. *T. demissa* var. *thysanolepis* (p. 74).
 7. Abaxial surface of the lamina with trichomes, pinnae sessile. .... 9.
  9. Rachis densely coated with fuscous scales, petiole aculeolate. .... 23. *T. phegopteroides* (p. 53).
  9. Rachis without scales, petiole inermous. .... 22. *T. pubescens* (p. 52).

PART 2

1. The bicolorous petiole scales without dark denticulae, sinuses acute (Panama to Ecuador). .... 40. *T. pilosissima* (p. 76).
1. The variously pigmented scales with or without dark denticulae, sinuses polygonal (tropical America). .... 2.
 2. Veins of the fertile segments simple or once-forked near the border of the segment, sori borne proximal to the fork in the vein (Jamaica). .... 43. *T. Estelae* (p. 80).
 2. Veins of the fertile segments medially forked at least once, sori borne on the fork in the vein. .... 3.
  3. Petiole abundantly pubescent, the trichomes sometimes deciduous and then leaving a hard, elevated base and a scabrous surface (smooth in *T. Swartziana* of the Greater Antilles). .... 4.
   4. Paraphyses turgid, persistent, dark red, shorter than the sporangia (Cocos Island). .... 44. *T. nesiotica* (p. 80).
   4. Paraphyses slender, deciduous or persistent, longer than the sporangia. .... 5.
    5. Adaxial surface of the segments with abundant trichomes on the costules, veins, and lamina surface. .... 6.
     6. Margin of the petiole scales with dark denticulae throughout, apex of pinnules long-attenuate, often falcate, axes of lamina with or without appressed trichomidia (Costa Rica to Ecuador). .... 45. *T. trichiata* (p. 80).
     6. Margin of the petiole scales inermous or with a few dark denticulae apically, apex of the pinnules acuminate, nearly straight, axes of lamina with appressed trichomidia (Venezuela and Colombia to Bolivia). 46. *T. Tryonorum* (p. 81).
    5. Adaxial surface of the segments glabrous or with trichomes only on the costules and veins. .... 7.
     7. Adaxial surface of the veins with trichomes (when deciduous the bases

evident), mature pinnules with few or no bullate squamulae along the costae abaxially (Mexico to Honduras). . . . . 47. *T. scabriuscula* (p. 81).

7. Adaxial surfaces of veins without trichomes (or rarely with only a few trichomes), mature pinnules with abundant bullate squamulae along the costae abaxially (a flattish squamule nearly always present between the costule and the fork in the vein) (Jamaica and Hispaniola). . . . . . . 48. *T. armata* (p. 81).

3. Petiole glabrous or sparsely pubescent, the trichomes sometimes deciduous and then leaving a prominent scar and a nearly smooth surface. . . . . 8.

8. Pubescence of the abaxial surface of the costae and costules only of abundant flexuous, catenate, ferruginous trichomes (eastern Cuba). 49. *T. strigillosa* (p. 81).

8. Pubescence of the abaxial surface of the costae and costules principally of abundant stiff, terete trichomes. . . . . 9.

9. Petiole scales cretaceous, or cretaceous with a darkened basal streak. . . . . 10.

10. Petiole scales without dark denticulae, rachis and pinna-rachises with flabellate, cretaceous scales (Mexico and Central America). . . . . 42. *T. mexicana* (p. 79).

10. Petiole scales with dark denticulae, rachis and pinna-rachises without scales (southeastern Brazil). . . . . 11.

11. Rachis glabrous, aculeate with sparse, slender spines; slightly hirsute at apex, segments lanceolate and acute, fertile and sterile veins once-forked. . . . . 50. *T. hirsuta* (p. 81).

11. Rachis pubescent or subglabrous, inermous, segments linear, rotund to acute, fertile and sterile veins with one or two pinnate pairs of veinlets. . . . . 51. *T. rufa* (p. 81).

9. Petiole scales, or most of them, cretaceous with a narrow to broad dark central streak. . . . . 12.

12. Edge of the petiole scales smooth or with a few dark denticulae apically, or with a few marginal cells slightly darker than the others, veins impressed above (Colombia to Bolivia). . . . . 52. *T. conjugata* (p. 81).

12. Edge of the petiole scales with dark denticulae throughout. . . . . 13.

13. Rachis inermous or barely muricate, abaxial surface of costules with flexuous trichomes, adaxial surface of costules and veins with thin and flexuous trichomes (Costa Rica and Panama). . . . . 53. *T. stipularis* (p. 81).

13. Rachis aculeolate, abaxial surface of costules with stiff trichomes, adaxial surface of costules and veins glabrous or glabrescent. . . . . 14.

14. Petiole scales with continuous dark denticulae along the margin and a broad, dark central streak (Guatemala). . . . . . 54. *T. pansamalana* (p. 81).

14. Petiole scales with cretaceous cells between the dark denticulae along the margin and a narrow, dark, central streak; at least at the base (Mexico). . . . . 55. *T. bicrenata* (p. 81).

PART 3

1. Pinnules cordate-hastate, crenate to shallowly pinnatifid. . . . . 2.

2. Sori lacking subtending soral squamulae (Venezuela). . . . 4. *T. cordata* (p. 30).

2. Sori with several fuscous soral squamulae investing the sporangia. . . . . 3.

3. Stem erect, to 4 m. tall, petiole aculeate, costae with flattish and bullate squamulae (Trinidad). . . . . 5. *T. sagittifolia* (p. 30).

3. Stem ascendant, to ca. 0.5 m. tall, petiole inermous to muricate, costae with flattish squamulae only (Venezuela). . . . . 6. *T. Steyermarkii* (p. 32).

1. Pinnules truncate, pinnatifid to pinnatisect. . . . . 4.

4. Lamina 3-pinnate-pinnatifid, scurf of large cretaceous squamulae. . . . . 3. *T. decomposita* (p. 28).

4. Lamina 2-pinnate-pinnatifid, scurf variable. . . . . 5.

5. Petiole scurf bicolorous (fuscous and cretaceous) cretaceous border of petiole scales with occasional darkened cells. . . . . 2. *T. Dombeyi* (p. 27).

5. Petiole scurf concolorous, petiole scale border without darkened cells. . . . . . 6.

6. Petiole scurf of large cretaceous squamulae (Colombia and Venezuela). . . . . 11. *T. microphylla* (p. 37).

6. Petiole scurf of fuscous squamulae (widespread species). 1. *T. procera* (p. 23).

PART 4

1. Pinnules entire to pinnatifid, the conform apical pinnules often articulated to the pinna-rachis (southern Brazil). . . . . 33. *T. corcovadensis* (p. 68).
1. Pinnules mostly pinnatifid to pinnatisect, no conform apical pinnules present. . . 2.
2. Sori subtended by squamulae (multiseriate processes attached at or near the base of the receptacle). . . . . 3.
3. Petiole scales fuscous with a cretaceous border, petiole scurf absent. . . . . 39. *T. costaricensis* (p. 76).
3. Petiole scales fuscous, border fuscous to fulvous (not cretaceous), petiole scurf variously developed. . . . . 4.
4. Costae farinose with cretaceous trichomidia, paraphyses longer than the sporangia (Venezuela). . . . . 14. *T. gibbosa* (p. 40).
4. Costae usually lacking cretaceous trichomidia, paraphyses shorter than or equalling the sporangia (West Indies). . . . . 13. *T. aspera* (p. 39).
2. Sori without subtending squamulae. . . . . 5.
5. Petiole scurf developed into a close-fitting persistent indument of trichomidia and/or squamulae. . . . . 6.
6. Axes of lamina covered by a dense, matted tomentum more or less similar to the petiole scurf. . . . . 7.
7. Indument cretaceous, costal squamulae fimbriate. . . . . . . 21. *T. frigida* (p. 51).
7. Indument fulvous or fuscous, costal squamulae entire. . . . . 8.
8. Squamulae fuscous, pinnules sessile, paraphyses longer than the sporangia (Venezuela). . . . . 17. *T. Schlimii* (p. 46).
8. Squamulae fulvous, pinnules petiolulate, paraphyses shorter than the sporangia (Dominica only). . . . . 25. *T. Hodgeana* (p. 56).
6. Axes of lamina without a dense, matted tomentum. . . . . 9.
9. Petiole scales fuscous or nigrescent, leaf apex abruptly reduced and pinna-like to gradually reduced and long-acuminate. . . . . 10.
10. Paraphyses longer than the sporangia, receptacle villous. . . . . 11.
11. Pinna-rachises with a scurf of squamulae and trichomes, costae and costules without trichomes (Costa Rica and Panama). . . . . 18. *T. Wendlandii* (p. 46).
11. Pinna-rachises without appreciable scurf, costae and costules with fulvous trichomes (Amazon River Basin). . . . . 19. *T. nigra* (p. 47).
10. Paraphyses shorter than the sporangia, receptacle pilose to hirsute. . . . . 12.
12. Pinnules very long-petiolulate, lobes acute to acuminate, serrate (Colombia to Bolivia). . . . . 16. *T. Kalbreyeri* (p. 44).
12. Pinnules sessile to petiolulate, lobes rotund, entire to crenulate. . . . . . . 13.
13. Costal squamulae flattish and sparse, petiole tuberculate to aculeate, petiole scurf including squamulae, apex gradually reduced and long-acuminate (Costa Rica to Peru). . . . . 15. *T. nigripes* (p. 41).
13. Costal squamulae bullate and dense, petiole aculeate, petiole scurf lacking squamulae, apex abruptly reduced and pinna-like to gradually reduced and long-acuminate (Mexico to Panama). . . . . 12. *T. Schiedeana* (p. 38).
9. Petiole scales fulvous or lighter, leaf apex gradually reduced and acute to acuminate. . . . . 14.
14. Pinnules sessile or subsessile (broad-ranging species). . . . . 15.
15. Petiole with abundant trichomes, petiole scurf of squamulae, lobes revolute and pubescent (Campo Limpo area of Brazil). . . . . 31. *T. Gardneri* (p. 66).
15. Petiole without trichomes, petiole scurf of trichomidia and squamulae, lobes flattish to revolute and variously hirsute, not pubescent. . . . . 16.
16. Trichomes on surface of lamina minute, costal squamulae entire and more or less appressed (Amazon Basin and coastal regions of tropical America). . . . . 26. *T. microdonta* (p. 56).
16. Trichomes on surface of lamina stiff, costal squamulae erose and more or less erect (Andes of Venezuela and Colombia). . . . 20. *T. pauciflora* (p. 50).
5. Petiole scurf scattered, inconspicuous, deciduous, or absent. . . . . 17.
17. Petiole scales bicolorous with a cretaceous border or uniformly cretaceous. 18.
18. Sori submarginal (known only from Brazil). . . . . 34. *T. praecincta* (p. 71).
18. Sori medial. . . . . 19.

19. Lamina coriaceous, essentially glabrous, pinnules (or lobes of pinnatifid pinnae) obtuse (Guyana Highlands). . . 36a. *T. demissa* var. *demissa* (p. 74).
19. Lamina papyraceous to chartaceous, with an indument, pinnules acuminate to attenuate (southeastern Brazil). . . . . 20.
 20. Scales entirely cretaceous, lobes of pinnules serrate. . . . . 41. *T. leucolepis* (p. 77).
 20. Scales bicolorous, lobes of pinnules entire. . . . . 32. *T. dichromatolepis* (p. 66).
17. Petiole scales concolorous and fulvous or bicolorous and the border fulvous. . . . . 21.
21. Petiole inermous to muricate, abaxial surface of the lamina glabrous (Andes, Guayana Highlands, Puerto Rico). . . . . 22.
22. Veins simple, paraphyses longer than the sporangia (Andes and Guayana Highlands). . . . . 27. *T. Lechleri* (p. 59).
22. Veins forked, paraphyses shorter than the sporangia. . . . . 23.
 23. Petiole scales barely marginate, lobes of pinnules coriaceous and flattish (Puerto Rico). . . . . 35. *T. borinquena* (p. 72).
 23. Petiole scales broadly flabellate, lobes of pinnules rigidly coriaceous and revolute (Guayana Highlands). . . . . . . 36a. *T. demissa* var. *demissa* (p. 74).
21. Petiole aculeate, abaxial surface of lamina glabrous or more often with a well-developed indument of trichomes, trichomidia and squamulae. . . . . 24.
24. Petiole scales helically twisted, abaxial surface of lamina more or less villous with minute, contorted trichomes, veins forked at the sori (Panama to Brazil). . . . . 28. *T. villosa* (p. 60).
24. Petiole scales usually flat, abaxial surface of lamina without minute, contorted trichomes, veins simple or forked at the sori (southern Brazil, Paraguay, Argentina). . . . . 25.
 25. Petiole scales often bicolorous, large cretaceous squamulae common on the abaxial surface of the costae and costules, paraphyses often multiseriate at least at tip. . . . . 32. *T. dichromatolepis* (p. 66).
 25. Petiole scales uniformly fulvous, indument of lamina axes variable, paraphyses uniseriate. . . . . 26.
  26. Veins simple, pinnae inserted at an acute angle on the rachis. . . . . 29. *T. atrovirens* (p. 62).
  26. Veins forked at the sori, pinnae inserted at a right angle on the axis. . . . . 30. *T. phalerata* (p. 63).

1. **Trichipteris procera** (Willd.) Tryon

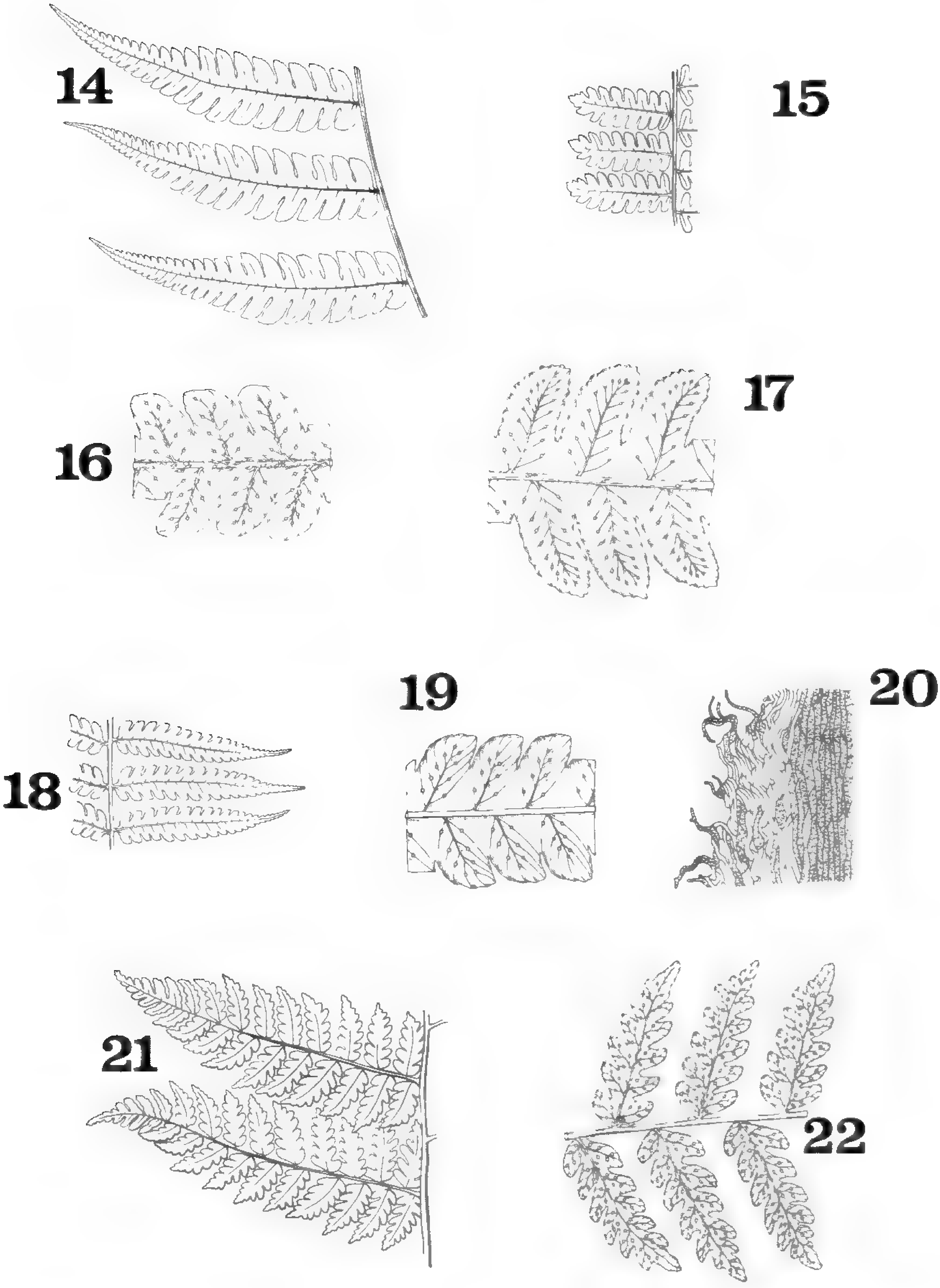
FIGS. 14–17. MAP 1.

Trichipteris procera (Willd.) Tryon, Contrib. Gray Herb. 200:46. 1970.
Polypodium procerum Willd., Sp. Pl. ed. 4. **5**(1):206. 1810. HOLOTYPE: Brasilia, *Hoffmannsegg*, fragment ex B, NY! (Herb. Willd. No. 19717).
Alsophila procera (Willd.) Desv., Mém. Soc. Linn. Paris **6**:319. 1827.
Alsophila procera (Willd.) Presl, Tent. Pterid. 61. 1836.
Polypodium pungens Willd., Sp. Pl. ed. 4. **5**(1):206. 1810. HOLOTYPE: Brasilia, *Hoffmannsegg*, fragment ex B, NY! fragment B, US! (Herb. Willd. No. 19716).
Alsophila pungens (Willd.) Presl, Tent. Pterid. 61. 1836.
Cyathea pungens (Willd.) Domin, Pteridophyta 263. 1929.
Trichipteris pungens (Willd.) Tryon, Contrib. Gray Herb. 200:46. 1970.
Alsophila infesta Kze., Linnaea **9**:98. 1834. HOLOTYPE: Peruviae ad Miss. Tocache fluv. Huallagae vicinam, *Poeppig*, LZ presumably destroyed. ISOTYPES: B! fragment ex B, BM!
Cyathea infesta (Kze.) Domin, Acta Bot. Bohem. **9**:125. 1930.
Trichipteris infesta (Kze.) Tryon, Contrib. Gray Herb. 200:45. 1970.
Alsophila subaculeata Splitgerber, Tijdschr. Nat. Gesch. (Leiden) **4**:430. 1840. HOLOTYPE: Canawappibo, Surinam, *Splitgerber*, L not seen. ISOTYPES: NY! fragment ex P, NY! fragment ex P, US!
Alsophila oblonga Kl., Linnaea **18**:540. 1844. LECTOTYPE (chosen herewith): British

Guiana, *Schomburgk 1125,* B not seen. ISOLECTOTYPE: P!
Cyathea oblonga (Kl.) Domin, Pteridophyta 263. 1929.
Trichipteris oblonga (Kl.) Tryon, Contrib. Gray Herb. 200:46. 1970.
Alsophila platyphylla Presl, Epimel. Bot. 29. 1851. HOLOTYPE: in Gujana gallica, *Perrotet,* PR not seen, fragment ex PR, NY!
Alsophila obtusa Kl., Allgem. Gartenzeit 20(6):41. 1852. HOLOTYPE: Venezuela, *Wagener,* B!
Trichipteris obtusa (Kl.) Tryon, Contrib. Gray Herb. 200:46. 1970.
Alsophila pterorachis Baker, Syn. Fil. ed. 2. 456. 1874. HOLOTYPE: Tarapoto, Peru, *Spruce 4717,* K! fragment ex K, NY!
Cyathea pterorachis (Baker) Domin, Pteridophyta 263. 1929.
Alsophila Eatoni Jenm., Journ. Bot. Brit. & For. **25**:98. 1887, ex. char. HOLOTYPE: Maraccus, Trinidad, *Sherring.*
Cyathea Eatoni (Jenm.) Domin, Acta Bot. Bohem. **9**:112. 1930.
Trichipteris Eatoni (Jenm.) Tryon, Contrib. Gray Herb. 200:44. 1970.
Alsophila pastazensis Hieron., Hedwigia **45**:232., t 12. f. 4. 1906. SYNTYPES: between Baños and Jivaría de Píntuc, Río Pastaza Valley, Cañelos, etc. Ecuador (all numbers), *Stübel 876a,* B not seen. *Stübel 975,* B not seen. *Stübel 988,* B! *Stübel 995a,* B!
Cyathea pastazensis (Hieron.) Domin, Pteridophyta 263. 1929.
Trichipteris pastazensis (Hieron.) Tryon, Contrib. Gray Herb. 200:46. 1970.
Alsophila Gleasoni Maxon, Am. Fern Journ. **15**:55. 1925. HOLOTYPE: near Rockstone, British Guiana, *Gleason 830,* US 1059473!
Cyathea Gleasoni (Maxon) Domin, Acta Bot. Bohem. **9**:119. 1930.
Alsophila bulligera Rosenst., Fedde Repert. Spec. Nov. **25**:57. 1928. TYPE COLLECTION: Bolivia, Mapiri, San Carlos, *Buchtien 288,* B! GH! S!
Cyathea bulligera (Rosenst.) Domin, Acta Bot. Bohem. **9**:101. 1930.
Trichipteris bulligera (Rosenst.) Tryon, Contrib. Gray Herb. 200:45. 1970.
Cyathea obtusata Domin, Pteridophyta 263. 1929. *nom. nov.* for *Alsophila obtusa* Kl., not *Cyathea obtusa* Domin, Pteridophyta 264. 1929.
Cyathea Klotzschiana Domin, Acta Bot. Bohem. **9**:128. 1930. *nom. nov.* for *Cyathea obtusata* Domin, 1929, not *Cyathea obtusata* Rosenst., 1917.
Cyathea Willdenowiana Domin, Acta Bot. Bohem. **9**:171. 1930. *nom. nov.* for *Polypodium procerum* Willd. not *Cyathea procera* Brause, Engl. Jahrb. 56:50. 1920.

Stem decumbent to erect, 0.3–7.5 m. tall. *Petiole* 0.5–1.5 m. long; fuscous, aculeate; scales fuscous with a cretaceous border or occasionally uniformly fuscous; scurf of dense fuscous squamulae; indument of leaf axes of stramineous to fuscous squamulae, trichomes, and trichomidia. *Lamina* 0.9–2.0 m. long, 2-pinnate-pinnatifid, papyraceous to chartaceous, apex abruptly reduced and pinna-like; pinnae sessile to stalked; pinnules sessile, pinnatifid, base truncate to cuneate, apex obtuse to acuminate; lobes rotund to acute, entire; fertile veins simple or rarely forked at the sori, sterile veins simple or rarely forked. *Sori* marginal to supramedial or varying along a single costule; paraphyses much shorter than the sporangia, receptacle pilose.

Although the shape of the leaf segments in *Trichipteris procera* is variable, the species is characterized throughout its range by the cretaceous petiole-scale border, pinna-like leaf apex, and short paraphyses. The foliage has a dusky look. Variability in this species is extreme: most apparent is the shape of the pinnule apices, which varies from obtuse to acuminate. Collections of *T. procera* with obtuse pinnules are found throughout the range of the species. The indument of the pinna-rachises and costae varies according to location. Pale costal squamulae are characteristic of plants from the area of Santa Marta, Colombia. Fuscous, bullate squamulae are characteristic of the Trinidad plants, and there is variation in the angle of insertion of the lobes on the pinnules of plants from Venezuela and the Guianas. The Willdenow epithet "pungens" has been applied to specimens with acute insertion of segments.



FIGS. 14–22. FIGS. 14–17, *Trichipteris procera:* 14, central pinnules of a central pinna (acuminate form), × 1/3 (*Britton, Britton & Freeman 2140*, GH); 15, central pinnules of a central pinna (obtuse form), × 1/3 (*Maguire 24543*, A); 16, central part of a typical pinnule, × 4/3 (*Broadway 5818*, GH); 17, central part of a pinnule, robust specimen, × 4/3 (*Wurdack 1825*, GH). FIGS. 18–20, *T. Dombeyi:* 18, central pinnules of a central pinna, × 1/3; 19, central part of a typical pinnule, × 4/3 (both *Killip & Smith 24541*, GH); 20, petiole scale border with darkened cells, × 16 (*Mexia 8293*, MO). FIGS. 21 & 22, *T. decomposita:* 21, two pinnules from a central pinna, × 1/3; 22, central part of a pinnule, × 1 (both *Vareschi & Pannier 1132*, VEN).

Trichipteris procera is found in Hispaniola, Puerto Rico, occasionally in the Lesser Antilles, the Guayana Highlands, throughout the Andes as far as Bolivia, and in the Brazilian Highlands. It is relatively common in wet, shaded sites in rain forests at relatively low altitudes (100–1400 m.), especially along watercourses. *Polypodium pungens*, a Willdenow species published at the same time and in the same publication as *P. procerum*, was early reduced to synonymy with the latter. I have followed this precedent. The description of *Alsophila bulligera* by Rosenstock probably represents his one contact with an essentially northern species. I have interpreted *Alsophila Gleasoni* Maxon as a precociously fertile form of this species. It agrees well in all characters with the 2-pinnate-pinnatifid material except for the dissection of the lamina and its venation. Two aberrant collections from the Dominican Republic (Samaná, Sanchez, *Ekman 14752 & 14824*) have alate pinna-rachises and a considerably paler look to the foliage. This plant may represent a hybrid between *T. procera* and a species of *Cnemidaria*.

SELECTED COLLECTIONS. **Dominican Republic. Samaná:** vicinity of Laguna, chiefly on the Pilón de Azúcar, *Abbott 424* (GH); Old Heart River (Jato Viejo), *Abbott 1409* (GH); Sanchez, *Ekman 14688* (GH). **Pacificador.** Villa Riva (Almacén), *Abbott 611* (GH); vicinity of San Francisco de Macorís, *Abbott 2030* (GH). **Puerto Rico.** Sabana Road, 0.5 km. E of junction with Rte. 191, *Conant 628*(GH); Rte. 191, km. 5.2, *Conant 634* (GH); Luquillo National Forest, km. 6 on Rte. 191, *Gastony 9* (GH). **Guadeloupe.** *Duss 3882* (F). **Martinique.** *Duss 4600* (F,GH,MO,NY). **Tobago.** *Broadway 3007* (MO); *Broadway 4222* (F,GH,MO); *Webster & Walker 9869* (A). **Trinidad.** *Broadway 5818* (GH,MO); *Fendler 112* (GH,MO,NY). **French Guiana.** May, 1836, *Leprieur* (GH); Karouany, *Sagot 726* p.p. (NY) (remainder of collection is *Sphaeropteris cyatheoides*). **Surinam.** Wilhelmina Gebergte, middle slopes of Frederik Top, 3 km. SSE of Juliana Top, *Irwin, Prance, Soderstrom & Holmgren 55005* (GH,NY); 1.5 km. SE of Juliana Top, headwaters of West Riviere, *Irwin, Prance, Soderstrom & Holmgren 55075* (GH,NY); Tafelberg, SE ridge, *Maguire 24543* (A,NY). **Guyana (British Guiana).** Kamuni Creek, Groete Creek, Essequibo River, *Maguire & Fanshawe 22854* (A,NY); Atkinson Field, *Wagner* (US). **Venezuela. Falcón:** south side of Cerro Santa Ana, *Steyermark & Braun 94663* (GH,VEN); Cerro Santa Ana, Paraguaná, *Famayo 107* (US,VEN). **Yaracuy:** Quebrada Honda, 17.3 km. from Aroa, *Steyermark 105395* (GH); Sierra de Aroa, Cerro Negro, *Steyermark & Wessels-Boer 100438* (GH,NY). **Aragua:** near Colonia Tovar, *Fendler 55* (GH,MO,NY); Rancho Grande, *Pittier 13876* (F,NY,US,VEN). **Distrito Federal:** 6–8 mi. below junction of Junquito-Colonia Tovar Road, *Steyermark 94779* (GH,VEN). **Miranda:** Cárdenas, Siquire Valley, *Pittier 7090* (GH,US); Quebrada de Turumo, near Guarenas, *Pittier 11272* (GH,NY,US). **Sucre:** Cerro Patao, N of Puerto de Hierro, NE of Guiria, Pen. de Paria, *Steyermark & Agostini 91000* (VEN); Cerro do Río Arriba, near "Los Positos," N slope, W of Cerro Humo, *Steyermark & Rabe 96290, 96406* (GH). **Delta Amacuro:** between Amacuro and mouth of Deadwater Creek Moat (Agua Muerto), *Steyermark 87399* (VEN). **Bolívar:** Chimantá Massif, W slopes of Chimantáentepuí (Torono-tepuí), *Steyermark 75598* (F,GH,NY,VEN); Cerro Venamo, SW part, *Steyermark & Dunsterville 92753* (GH,VEN); Cerro Uananapan, S of Uei-tepuí, between Luepa & Cerro Venamo, *Steyermark & Nilsson 754* (US,VEN). **Amazonas:** Cerro Huachamacari, Río Cunucunuma, *Maguire, Cowan & Wurdack 29929* (GH,NY,US). **Colombia. Magdalena:** Santa Marta, *H. H. Smith 2224* (F,GH,MO,NY,US); *H. H. Smith 2229* (F,GH,NY,US). **Antióquia:** Barbosa, Medellín, *Henri-Stanislas 1708* (US). **Norte de Santander:** region of Sarare, valley of the Río Margua, Quebrada del Río Negro, *Cuatrecasas 12921* (F,US). **Santander:** vicinity of Barranca Bermeja, Magdalena Valley, between Sogamoso & Colorado Rivers, *Haught 1422* (GH,US). **Valle:** Valley of the Río Sanguinini, left side, La Laguna, *Cuatrecasas 15608* (F,US). **Tolima:** El Fresno, *Cuatrecasas 9379* (F,US). **Meta:** ridge between Río Manzanares & Quebrada Playón, 30 km. W of La Esperanza, 52 km. W of Villavicencio, *Grant 10126* (US). **Vaupés:** Río Vaupés, Mitú & vicinity, *Schultes, Raffauf & Soejarto 24400, 24401, 24404* (GH). **Putumayo:** at Puerto Ospina, *Cuatrecasas 10578* (F). **Amazonas:** Río Caraparaná, between the outlets & El Encanto, *Schultes 3835* (GH,US); Río Apoporis, between the Río Pacoa and the Río Kananarí, Sorotama, *Schultes & Cabrera 12805* (GH,US). **Ecuador. Santiago-Zamora:** Yunguaza, *Crespi* (US). **Peru. Amazonas:** Valley of the Río Marañón, above Cascadas de Mayasi, near Campamento Ste. Montenegro, *Wurdack 1825* (GH). **Loreto:** Balsapuerto, lower Río Huallaga basin, *Killip & Smith 28522* (F,GH,US); trail to San Juan, upper streamlet of San Juan, Distrito de Iquitos, *Mexia 6497* (F,GH,MO, US); Gamitanacocha, Río Mazán, *Schunke 269* (F,GH,NY); Río Itaya, 10 km. S of Iquitos, *Tryon & Tryon 5173* (GH); *Tryon & Tryon 5182* (F,GH). **San Martín:** E of Tingo María, *Allard 21426* (GH); below English Evangelical Mission, Lamas, *Belshaw 3437* (GH); near Tarapoto, *Spruce 4323* (GH). **Huánuco:** SW slope of Río Llulla-Pichis watershed, on the ascent of Cerros del Sira, *Dudley 13280* (GH); Tingo María, *Tryon & Tryon 5220* (GH). **Junín:** Puerto Yessup, *Killip & Smith 26238* (GH); Cahuapanas on the Río Pichis, *Killip & Smith 26746* (GH). **Cuzco:** Cordillera Vilcabamba, *Dudley 10063, 10105B* (GH); Cosñipata-Pilcopata, Santa Inés, *Vargas 11318* (GH). **Puno:** Hacienda Palmora, *Vargas 16145* (GH). **Brazil. Amazonas:** Rio Negro, near São Gabriel da Cachoeira, *Spruce 2115* (US); Rio Negro, São Gabriel, *Tate 140* (NY). **Matto Grosso:** 12.49° S, 51.46° W, *Harley et al. 10768* (US); *H. Smith 111* (US); *H. Smith 1336* (NY). **Goiás:** Mun. Jataí, *Macedo 1518* (US); Queixada, Mun. Jataí, *Macedo 2184* (US).

2. **Trichipteris Dombeyi** (Desv.) Barr.

FIGS. 18–20. MAP 2.

Trichipteris Dombeyi (Desv.) Barr., Rhodora **78**(813):3. 1976.
Alsophila Dombeyi Desv., Mém. Soc. Linn. Paris **6**:320. 1827 (as *A. Dombei*). HOLOTYPE: in Peruvia, *Dombey*, (Cochero, Herb. Desv.) P! ISOTYPE: P!
Alsophila armigera Kze., Linnaea **9**:98. 1834. HOLOTYPE: mountains of Peru, Ventanilla de Cassapi, July 1829, *Poeppig*, LZ presumably destroyed. ISOTYPES: MO! P!
Alsophila pycnocarpa Kze., Linnaea **9**:97. 1834. HOLOTYPE: Pampayacu, Peru, July 1829, *Poeppig*, LZ presumably destroyed. ISOTYPE: (*Poeppig 201*) B!
Cyathea pycnocarpa (Kze.) Domin, Pteridophyta 263. 1929.
Alsophila peruviana Kl., Linnaea **20**:441. 1847. HOLOTYPE: ad Tarma Peruviae, *Ruiz Herb. 66*, fragment ex B, GH! fragment ex B, NY!
Alsophila floribunda Hook. & Baker, Syn. Fil. ed. 2. 458. 1874. HOLOTYPE: Mt. Campana, Peru, *Spruce 4715*, K not seen. ISOTYPE: P!
Cyathea floribunda (Hook. & Baker) Domin, Pteridophyta 262. 1929.
Trichipteris floribunda (Hook. & Baker) Tryon, Contrib. Gray Herb. 200:45. 1970.

Stem decumbent to erect, 0.1–2.4 m. tall. *Petiole* 0.3–0.6 m. long; fuscous to fulvous, muricate to aculeate; scales fuscous with a cretaceous border, the border with a few to many darkened cells; scurf of cretaceous to fuscous trichomidia and bicolorous squamulae; axes of lamina with an indument similar to the petiole scurf, costae and costules with flattish, bicolorous or bullate, cretaceous squamulae. *Lamina* 1.0–2.5 m. long, 2-pinnate-pinnatifid, papyraceous, apex abruptly reduced and pinna-like; pinnae sessile; pinnules sessile or sub-sessile, crenate to deeply pinnatifid, base truncate to cuneate, apex acute to acuminate; lobes rotund, entire; fertile veins simple, sterile veins simple or forked. *Sori* apically subcostal to basally medial; paraphyses as long as the sporangia, receptacle hirsute.

Trichipteris Dombeyi is allied to *T. procera* but differs in having bicolorous squamulae on the petiole. The darkened cells or groups of cells along the edge of the cretaceous border are unusual for the genus. The number of darkened cells in the petiole scale border is variable. In addition, the costal and costular squamulae vary in color. The costules are much more prominent than the adjacent veins, and the distal sori of a lobe are closer to the costule. *Trichipteris Dombeyi* could be interpreted as part of the widespread and variable *T. procera.* I have chosen to maintain *T. Dombeyi* as a species because of its distinctive indument and peripheral geographic range. *Trichipteris Dombeyi* is confined to the eastern slopes of the Andes in Peru, where it is found in dense rain forests at low to middle altitudes (650–1700 meters). The choice of the Dombey collection and its basionym for this species is tentative, because it lacks material of the petioles. The type collection of *Alsophila floribunda* Baker, *Spruce 4715* (P), is mixed, containing material of *T. Dombeyi* and *T. procera.* Christensen considered this species a synonym for *T. procera* in his *Index Filicum.*

SELECTED COLLECTIONS. **Peru. Loreto:** Pampayacu, *Kanehira 177* (GH,US). **Huánuco:** near confluence of Río Cayumba with Huallaga, *Mexia 8293* (F,GH,MO,NY,US); Tingo María, *Tryon & Tryon 5256* (F,GH). **Junín:** Río Pinedo, N of La Merced, *Killip & Smith 23640* (F,NY,US); Schunke Hacienda, above San Ramón, *Killip & Smith 24541* (F,GH,NY,US); *Killip & Smith 24645* (F,NY). **Cuzco:** Cordillera Vilcabamba, *Dudley 11436* (GH).

3. **Trichipteris decomposita** (Karst.) Tryon

FIGS. 21, 22. MAP 3.

Trichipteris decomposita (Karst.) Tryon, Contrib. Gray Herb. 200:45. 1970.

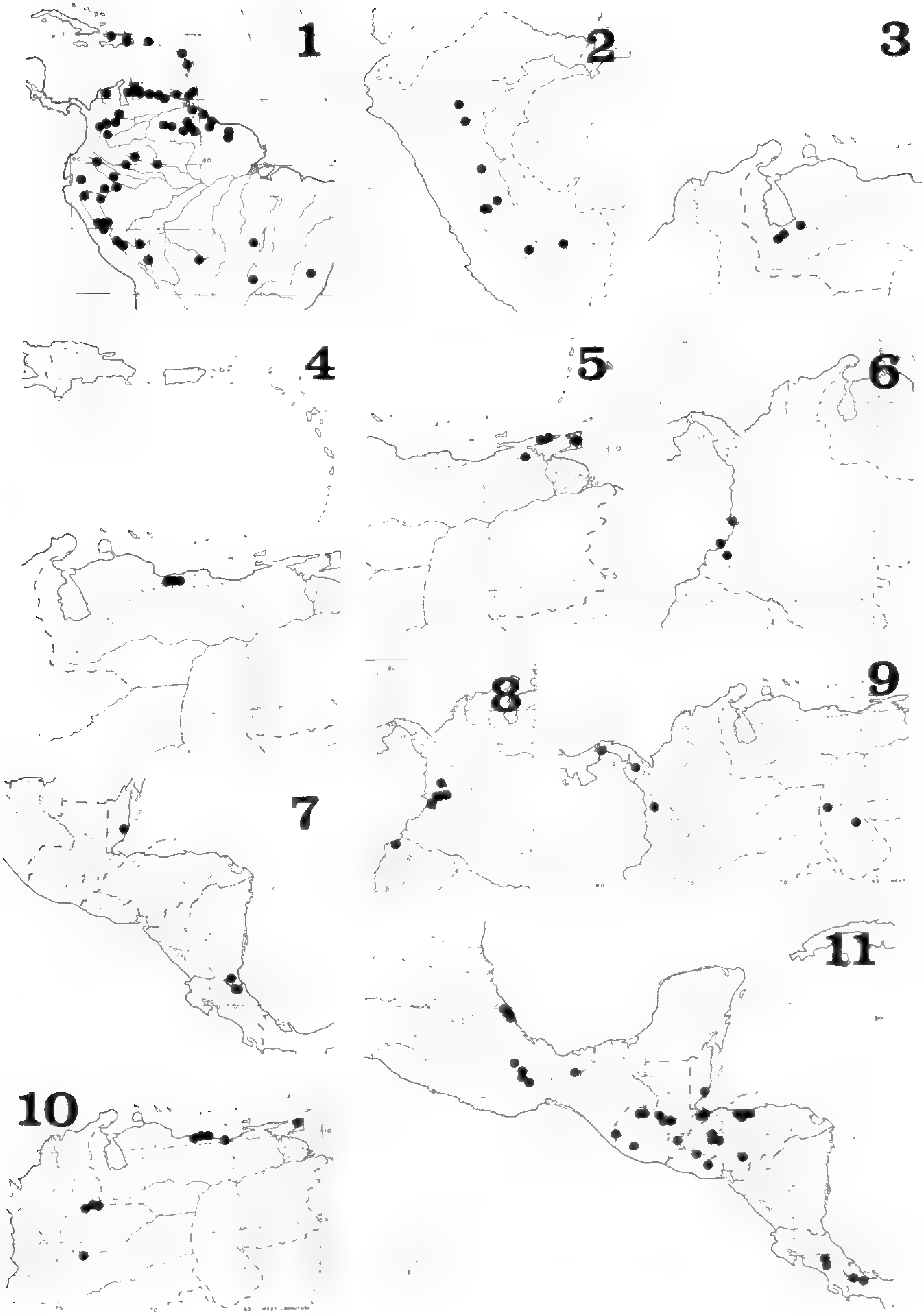
Alsophila decomposita Karst., Fl. Columb. **2**:185, t. 198. 1869. HOLOTYPE: from Cordillera Meridensis, Colombia, 1500 m., (*Engel 129*) fragment ex B, GH!

Cyathea decomposita (Karst.) Domin, Pteridophyta 262. 1929.

Alsophila oligocarpa Fée, Mém. Fam. Foug. **5** (Genera Filicum):346. 1852. *nom. nud.* COLLECTION CITED: Venezuela, *Funck & Schlim 1002,* P not seen. *Funck & Schlim 978,* fragment ex P, NY! is this species.

Stem erect, 1–3 m. tall. *Petiole* ca. 1 m. long, cretaceous to stramineous, aculeate; scales fulvous with a cretaceous border, scurf of large, cretaceous squamulae; rachis and pinna-rachises glabrous or with a few squamulae especially toward the base; costae and costules with trichomidia and fuscous, flattish and erose to bullate squamulae. *Lamina* 2.0–3.0 m. long, 3-pinnate-pinnatifid, papyraceous, apex gradually reduced, acuminate; pinnae stalked; pinnules subsessile, fully pinnate; penultimate segments sessile, pinnatifid, base truncate, apex obtuse to acute, lobes rotund and entire; fertile and sterile veins simple. *Sori* medial, paraphyses shorter than the sporangia, receptacle pilose.

Trichipteris decomposita is the only species with a 3-pinnate-pinnatifid lamina in the genus. The large, cretaceous petiole squamulae separate this species from all others of *Trichipteris* except *T. microphylla.* It can be confused with species of the genus *Ctenitis,* which is characterized by narrow, transparent-celled, and often toothed scales on the leaf axes and polypodiaceous sporangia. *Trichipteris decomposita* is morphologically similar to the other species of the group of *T. procera.* It is less specialized than related species in having relatively undifferentiated petiole scurf. *Trichipteris decomposita* is geographically confined to the Venezuelan Andes in the area of Lake Maracaibo, where it is found in undisturbed rain forest and cloud forest from 1300–2800 meters.



MAPS 1–11: 1, Trichipteris procera; 2, T. Dombeyi; 3, T. decomposita; 4, T. cordata; 5, T. sagittifolia (diamond) and T. Steyermarkii (dots); 6, T. falcata; 7, T. ursina; 8, T. phalaenolepis; 9, T. Williamsii; 10, T. microphylla; 11, T. Schiedeana.

SELECTED COLLECTIONS. **Venezuela. Mérida:** forêts humides, 5500′, 1842, *Linden 517* (P); Cerro San Isidro, above La Carbonera, *Steyermark 56029* (F,GH,MO,US); Río Capaz, above La Azulita, *Steyermark & Rabe 97120* (GH); 22 km. W of Mérida on road to La Azulita, San Euselia, *Tryon & Tryon 5767* (GH); La Carbonera, *Vareschi & Pannier 1132* (US,VEN). **Trujillo:** above Escuque, between Escuque and Mesa de San Pedro, *Steyermark 104676* (GH).

4. Trichipteris cordata (Kl.) Tryon

FIGS. 23, 24. MAP 4.

Trichipteris cordata (Kl.) Tryon, Contrib. Gray Herb. 200:45. 1970.
Alsophila cordata Kl., Linnaea **20**:441. 1847, *ex. char.* (Bot. Zeit. **4**(7):104. 1846 *nom. nud.*) HOLOTYPE: Puerto Cabello, Colombia, *Karsten 168* B, not seen.

Stem decumbent to erect, 0.1–1.0 m. tall, occasionally to 2.5 m. *Petiole* ca. 0.3 m. long, fuscous to atropurpureous, tuberculate to muricate; scales uniformly fuscous or with the border slightly lighter in color, scurf of fuscous trichomidia and a few large squamulae; rachis and pinna-rachises with cretaceous trichomes, base of pinna-rachises with bullate, fuscous squamulae. *Lamina* 0.5–1.5 m. long, 2-pinnate-pinnatifid, chartaceous, apex abruptly reduced and pinna-like; pinnae sessile; pinnules short-petiolulate, entire or crenulate to pinnatifid, base cordate-hastate, apex acute to acuminate; lobes rotund, entire; fertile and sterile veins simple. *Sori* medial to supramedial, lacking soral squamulae; paraphyses much shorter than the sporangia, receptacle puberulous.

The absence of soral squamulae is the most significant diagnostic character for *Trichipteris cordata.* Geographically and morphologically it is closely related to *T. sagittifolia* and *T. Steyermarkii,* and it cannot be consistently separated from them except by the absence of soral squamulae. On the basis of the leaf apex, petiole scurf, venation, and paraphyses length, *T. cordata* and the associated species are allied to *T. procera.* Deeply lobed specimens of *T. cordata* can be confused with *T. procera.* However, in *T. cordata* and its two closest allies, the petiole scales are uniformly fuscous. These three species are a distinct line of evolution among Andean *Trichipteris* with simple veins and short paraphyses.

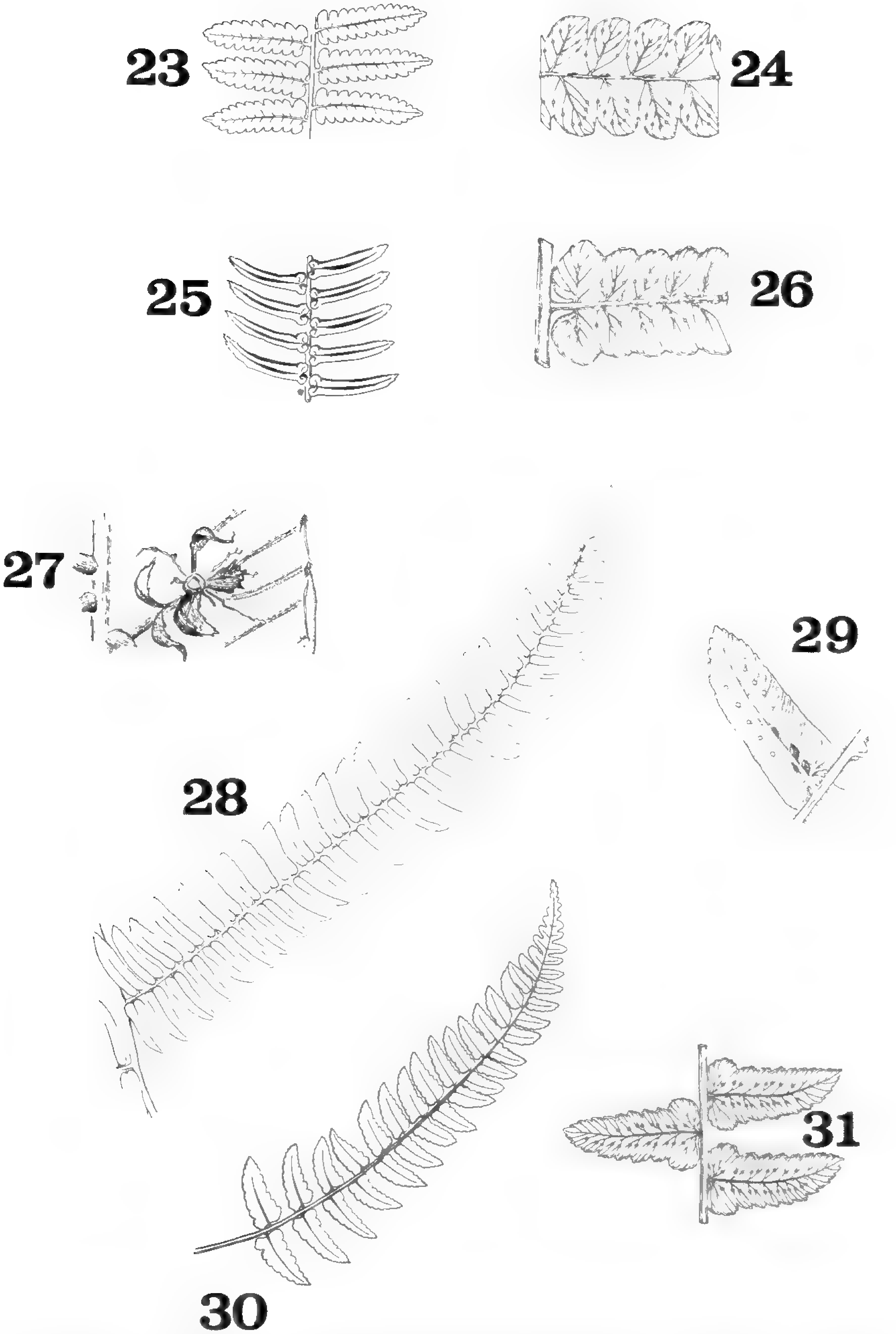
Trichipteris cordata is an uncommon species from the cloud forests of coastal Venezuela at altitudes from 1500–1700 meters. It is a diminutive species with relatively small leaves and a stem averaging under 0.5 meters in height. This sort of reduction in stature is common in the genus and extreme in such species as *T. falcata.*

SELECTED COLLECTIONS. **Venezuela. Carababo:** Hacienda Marturé, *Williams 11014* (F,VEN). **Aragua:** Parque Nacional "H. Pittier," bosque de Rancho Grande, *Agostini & Fariñas 92* (US,VEN); Parque Nacional "H. Pittier," *Sermolli 161* (VEN); Parque Nacional "H. Pittier," above Rancho Grande Biological Station, toward Pico Guacamayo, *Steyermark 89785* (GH,VEN); Parque Nacional "H. Pittier," Rancho Grande, *Tschudi 90* (US,VEN); Rancho Grande, *White & Lucansky 1970126* (US).

5. Trichipteris sagittifolia (Hook.) Tryon

FIGS. 25–27. MAP 5.

Trichipteris sagittifolia (Hook.) Tryon, Contrib. Gray Herb. 200:46. 1970.
Alsophila sagittifolia Hook., Syn. Fil. ed. 1. 37. 1866. HOLOTYPE: Trinidad? (possibly



FIGS. 23–31. **FIGS.** 23 & 24, ***Trichipteris cordata:*** 23, central pinnules of a central pinna, × 1/3; 24, central part of a pinnule, × 4/3 (both *Agostini & Fariñas 92,* VEN). FIGS. 25–27, *T. sagittifolia:* 25, central pinnules of a central pinna, × 1/3 (*Britton et al. 1355,* GH); 26, base of a pinnule, × 4/3 (*Broadway 5810,* F); 27, soral squamulae, sporangia removed, × 10 (*Fendler 142,* GH). FIGS. 28 & 29, *T. Steyermarkii:* 28, central pinna, × 1/3; 29, central pinnule, × 1 (both *Steyermark 94923,* VEN). FIGS. 30 & 31, *T. falcata:* 30, apical portion of a leaf, × 1/3; 31, three central pinnae, × 1 (both *Lehmann 16,* US).

the opposite coast of Venezuela), *Cruger,* (Trinidad! see Tryon, 1972a) seen by Tryon at K.

Hemitelia sagittifolia (Hook.) Jenm., Ferns & Fern Allies of Br. West Indies & Guiana 43. 1898.

Cyathea sagittifolia (Hook.) Domin, Pteridophyta 163. 1929.

Stem erect, 1.0–4.0 m. tall. *Petiole* ca. 0.5 m. long, atropurpureous, aculeate; scales uniformly fulvous or the border slightly lighter in color; scurf of trichomidia and fuscous squamulae; rachis, pinna-rachises, and costae with cretaceous trichomidia, base of pinna-rachises, costae and costules with bullate, fuscous squamulae. *Lamina* 1.5–2.3 m. long, 2-pinnate to 2-pinnate-pinnatifid, coriaceous, apex abruptly reduced and pinna-like; pinnae sessile to barely stalked; pinnules short-petiolulate, barely crenulate to shallowly pinnatifid, base cordate-hastate, apex acute to acuminate; lobes rotund, entire; fertile veins forked at the sori or simple, sterile veins forked, costule indistinct, veins all concurrent to the margin. *Sori* submedial to medial, subtended by several fuscous soral squamulae; paraphyses shorter than the sporangia, receptacle pilose.

The greatest development of soral squamulae in *Trichipteris* is found in two species, *T. sagittifolia* and *T. Steyermarkii.* The several broad, fuscous squamulae form a membranous layer completely covering the sori, which superficially resembles a sphaeropteroid indusium. The foliage of these two species, at least in many collections, has the aspect of species of New World *Alsophila sensu stricto* (i.e., simply 2-pinnate with narrow, revolute pinnules). *Trichipteris sagittifolia* and *T. Steyermarkii* are a vicarious species pair. Close-set, long, thin spines and bullate costal squamulae characterize *T. sagittifolia.* Most collections of *T. Steyermarkii* have poorly developed petiole spines and flattish costal squamulae. Both species are related to the slightly more western *T. cordata,* which lacks soral squamulae. The pinna-like leaf apex is especially well-developed in *T. sagittifolia* and its allies.

Variability in the dissection of the pinnule lobes, perhaps correlated with exposure, is characteristic of this species and of *T. Steyermarkii. Trichipteris sagittifolia* is endemic to Trinidad, one of the few species of *Trichipteris* endemic to a single island. It is found in wet montane forests, especially in reduced or "elfin" forests along mountain ridges from 500–750 meters. Tryon noted that the Cruger collection in Hooker's herbarium has the bullate costal squamulae of the modern Trinidad collections. The Cruger material, which is the type collection of *T. sagittifolia,* must have come from Trinidad. For further discussion of the typification of this species see Tryon (1972a). Jenman's transfer of this species of *Hemitelia* was logical in light of the ambiguous definition of the cyatheaceous indusium at the time.

SELECTED COLLECTIONS. **Trinidad:** *Broadway 5294, 5810* (F,MO); *Fendler 142* (GH, MO,NY,US,VT); *A. C. Smith 10027* (US).

6. **Trichipteris Steyermarkii** Tryon

FIGS. 28, 29. MAP 5.

Trichipteris Steyermarkii Tryon, Rhodora **74**:446, f. 11, 12. 1972. HOLOTYPE: Cerro de Humo, Península de Paria, Estado Sucre, Venezuela, *Steyermark & Agostini*

94923, VEN! ISOTYPE: GH! PARATYPE: Cerro Patao, Península de Paria, Estado Sucre, Venezuela, *Steyermark & Agostini 91048,* VEN! ISOPARATYPE: US!

Stem ca. 0.5 m. tall. *Petiole* ca. 0.5 m. long; fulvous, tuberculate to muricate, scales uniformly fuscous or with a border slightly lighter in color; scurf of trichomidia and minute, fulvous squamulae; rachis, pinna-rachises and costae with fulvous trichomidia; costae and sometimes the costules with a few flattish fulvous squamulae. *Lamina* 1.0–1.5 m. long, 2-pinnate, chartaceous to coriaceous, apex abruptly reduced and pinna-like; pinnae sessile; pinnules petiolulate, serrate to crenulate (shallowly pinnatifid in one collection), base cordate-hastate, apex acute; costules often indistinct and veins all concurrent to the pinnule margin, fertile and sterile veins forked or simple. *Sori* inframedial to medial, subtended by several fuscous soral squamulae; paraphyses shorter than the sporangia, receptacle pilose.

Variation in the dissection of the pinnule segments similar to that in *Trichipteris sagittifolia* is common. *Trichipteris Steyermarkii* is limited to mountain ridges in the wet forests of the Península de Paria and adjacent Monagas, from 1000–1650 meters (higher than the corresponding habitats for *T. sagittifolia* in Trinidad).

SELECTED COLLECTIONS. **Venezuela. Monagas:** Cerro Guácharo, above Guácharo Cave, near Guácharo, *Steyermark 62332* (NY,US).

7. **Trichipteris falcata** (Kuhn) Barr.

FIGS. 30, 31. MAP 6.

Trichipteris falcata (Kuhn) Barr., Rhodora 78:3. 1976.
Alsophila falcata Kuhn, Linnaea 36:155. 1869. HOLOTYPE: Panama, (Gorgona Island, Seeman) B! ISOTYPES: K! fragment ex K, NY! fragment ex K, US!
Cyathea falcata (Kuhn) Domin, Pteridophyta 262. 1929.
Nephrodium Kuhnii Hieron., Engl. Bot. Jahrb. 34:440. 1904. HOLOTYPE: Cordillera de Pasto, Colombia, 1000 m., *Lehmann 16,* K not seen. ISOTYPE: US!
Dryopteris Kuhnii (Hieron.) C. Chr., Ind. Fil. 273. 1905.
Alsophila Kuhnii (Hieron.) C. Chr., Fedde Repert. Spec. Nov. 10:213. 1911.
Cyathea Kuhnii (Hieron.) Domin, Pteridophyta 262. 1929.
Trichipteris Kuhnii (Hieron.) Tryon, Contrib. Gray Herb. 200:45. 1970.

Stem diminutive, fasciculate, 1.0–3.0 m. long. *Petiole* 8–18 cm. long, fulvous, tuberculate; scales fulvous with a cretaceous border; scurf absent or of minute trichomidia (adaxial trichomes of lamina axes extending down the petiole); rachis with bicolorous scales similar to those of the petiole and flattish, fimbriate, fulvous squamulae; pinna-rachises glabrous or with occasional minute, fulvous trichomidia and squamulae. *Lamina* 10–50 cm. long, 1-pinnate to 1-pinnate-pinnatifid, papyraceous, apex gradually reduced, acuminate; pinnae adjacent, sessile or short-petiolulate, crenate to pinnatifid, base cordate-hastate, apex acute to acuminate; costules indistinct and the veins all concurrent to the margin, fertile and sterile veins forked or simple. *Sori* inframedial to medial; paraphyses much shorter than the sporangia, receptacle puberulous to pilose.

Trichipteris falcata is the only 1-pinnate species of *Trichipteris* with shallowly lobed, cordate pinnules. Complete material is unmistakable. Although *T. falcata* belongs in the group of *T. procera,* it is not closely related to any single species. Perhaps it is a more southern representative of the line that gave rise to the three species including *T. sagittifolia.* Variability in *T. falcata* is most pronounced in the size of the plant.

Trichipteris falcata is confined to southern Colombia. All of the three known collections are from the Pacific coast and adjacent islands from sea level to 1000 meters. Interpretation of the type is based wholly on the Haught collection from Buenaventura. The type from Berlin (according to Hooker and Baker (1874)), collected by Seeman on Gorgona Island, represents the upper part of a 1-pinnate leaf. However, without the Haught collection, interpretation of the portion as a part of a pinna was entirely plausible. The third collection of this species, *Lehmann 16*, has been placed in five genera. Nevertheless, it is a *Trichipteris* with marginate, asetate cyatheaceous scales, cyatheaceous sporangia, paraphyses, and no indusium.

SELECTED COLLECTIONS. **Colombia. Valle:** Punta Magdalena, near sea level, *Haught 5585* (US).

8. **Trichipteris ursina** (Maxon) Tryon

FIGS. 32, 33. MAP 7.

Trichipteris ursina (Maxon) Tryon, Contrib. Gray Herb. 200:44. 1970.
Alsophila ursina Maxon, Journ. Washington Acad. Sci. 34:48. 1944. HOLOTYPE: Antelope Ridge, Stann Creek Valley, British Honduras (Belize), *Gentle 3197*, US 1791403! 1791404!

Stem diminutive, fasciculate, to 5 cm. long. *Petiole* ca. 15 cm. long, fuscous, tuberculate; scales fuscous with a narrow cretaceous border; scurf absent; rachis and pinna-rachises tuberculate, scales similar to those of the petiole or uniformly fuscous; scurf of minute trichomidia cretaceous on the rachis and darker on the pinna-rachises. *Lamina* ca. 1 m. long, 1-pinnate-pinnatifid, chartaceous, apex gradually reduced, acuminate; pinnae adjacent, sessile, pinnatifid to pinnatisect, base truncate to cuneate, apex obtuse to acute; lobes rotund, tip crenulate or the entire lobe crenulate; fertile veins simple, sterile veins forked or simple. *Sori* medial to supramedial, paraphyses much shorter than the sporangia, receptacle puberulous.

Among the species of *Trichipteris* with cretaceous petiole scale borders, only this species and *T. phalaenolepis* are characterized by 1-pinnate leaves with scaly rachises and obtuse, deeply dissected pinnae. *Trichipteris ursina* is distinguished from *T. phalaenolepis* on the basis of rachis scales. *Trichipteris ursina* has fuscous scales crowded along the lower part of the rachis, but *T. phalaenolepis* has fewer, paler scales. The two are a vicarious species pair isolated through long-distance dispersal. In *T. ursina* there is variability in the dissection and size of the pinna lobes. Robust specimens approach 1-pinnate-pinnatisect with the lobes of the pinnae pinnatisect. *Trichipteris ursina* occurs from Belize to Costa Rica, where it is found in wet places in tall lowland forests from sea level to 100 meters in altitude.

SELECTED COLLECTIONS. **Nicaragua.** Río San Juan at "El Relos," halfway between El Castillo and Delta de San Juan, *Bunting & Licht 788* (F,GH). **Costa Rica. Heredia:** Río Puerto Viejo, 2 km. upstream from confluence of the Río Sarapiquí, (Finca La Selva of L. R. Holdridge), *Burger & Stolze 5877* (GH,US); Finca of L. R. Holdridge, on the Río Puerto Viejo, near the junction with Río Sarapiquí, *Scamman 7438* (GH).

9. **Trichipteris phalaenolepis** (C. Chr.) Tryon

FIGS. 34, 35. MAP 8.

Trichipteris phalaenolepis (C. Chr.) Tryon, Contrib. Gray Herb. 200:46. 1970.
Alsophila phalaenolepis C. Chr., Fedde Repert. Spec. Nov. **10**:213. 1911. HOLOTYPE: Prov. Esmeraldas, Ecuador, *Sodiro* in 1904, Herb. Sodiro not seen. ISOTYPE: P!
Cyathea phalaenolepis (C. Chr.) Domin, Pteridophyta 263. 1929.

Stem creeping to erect, reaching ca. 10 cm. *Petiole* 20–40 cm. long, fuscous to fulvous, tuberculate; scales fuscous with a cretaceous border or uniformly cretaceous distally along the petiole; scurf of cretaceous squamulae; trichomes present; all axes with trichomidia; rachis and pinna-rachises with cretaceous trichomes; rachis with cretaceous scales similar to those of the upper part of the petiole, pinna-rachises with a few flattish, cretaceous squamulae. *Lamina* 0.5–1.2 m. long, 1-pinnate-pinnatifid, papyraceous to chartaceous, apex gradually reduced and acuminate; pinnae adjacent, sessile to short-petiolulate, deeply pinnatifid, base cordate to truncate, apex obtuse to acute; lobes rotund, serrate at the tip; fertile veins simple or rarely forked at the sori, sterile veins forked or simple. *Sori* basally medial to apically inframedial; paraphyses much shorter than the sporangia, receptacle puberulous.

The close-set, obtuse pinnae are characteristic of *Trichipteris phalaenolepis* and the closely allied *T. ursina.* The occasional cretaceous scales on the rachis serve to distinguish *T. phalaenolepis* from *T. ursina. Trichipteris phalaenolepis* is a species of the Pacific coastal plain of northern South America from Colombia to Ecuador. Ecologically similar to *T. ursina,* it is found in dense forests and swamps near sea level (5–300 meters).

SELECTED COLLECTIONS. **Colombia. Valle:** Río Yurumangui, Veneral, *Cuatrecasas 15877* (F); Córdoba, *Killip 5103* (GH,NY); Santa Rosa, *Killip 11528, 11566* (GH,NY); Córdoba, *Killip & Garcia 33430* (GH); Río Calima, Quebrada de La Bréa, *Schultes & Villarreal 7355* (GH).

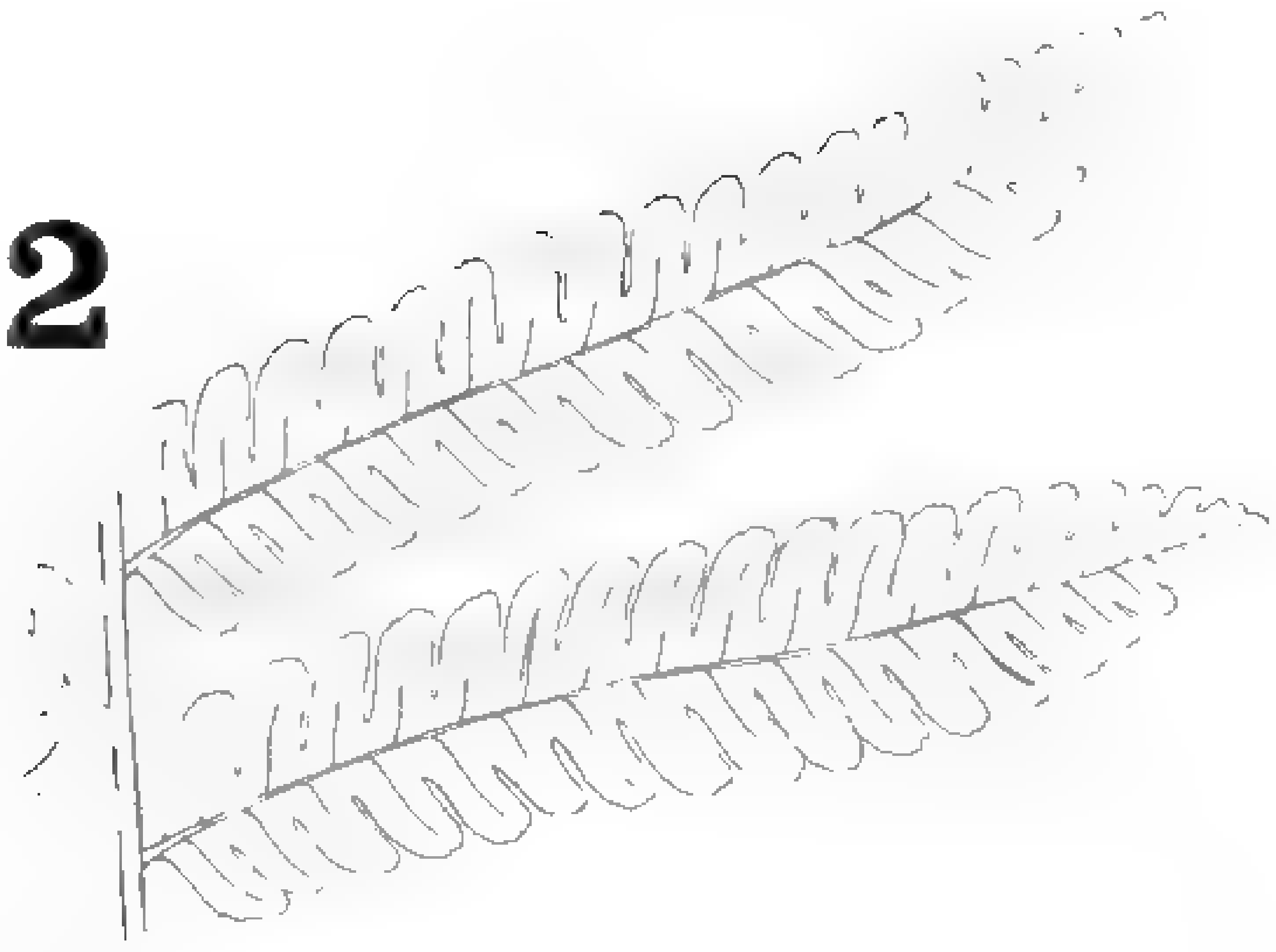
10. **Trichipteris Williamsii** (Maxon) Tryon

FIGS. 36, 37. MAP 9.

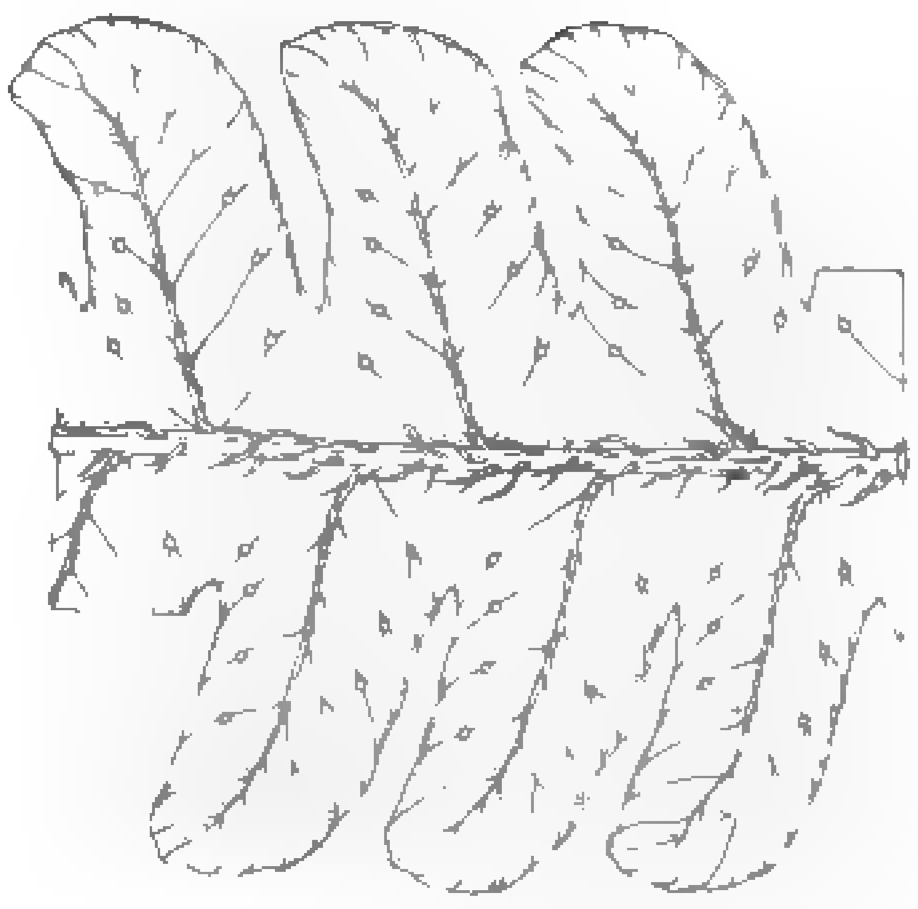
Trichipteris Williamsii (Maxon) Tryon, Contrib. Gray Herb. 200:44. 1970.
Alsophila Williamsii Maxon, Contrib. U.S. Nat. Herb. **24**(2):46 t. 17. 1922. HOLOTYPE: mountains above Cana, Panama, *Williams 850,* US! ISOTYPE: NY! PARATYPE: east slope of Mt. Pirri, Prov. of Panama, Panama, *Goldman 1968,* US!
Cyathea Williamsii (Maxon) Domin, Acta Bot. Bohem. 9:171. 1930.
Trichipteris Maguirei Tryon, Rhodora 74:447, f. 15 & 16. 1972. HOLOTYPE: Cerro Sipapo (Paráque), Terr. Amazonas, Venezuela, 1948, *Maguire & Politi 27597,* NY! ISOTYPES: GH! US! PARATYPES: *Maguire & Politi 27752,* NY! *Maguire & Politi 28493,* NY! *Maguire, Cowan & Wurdack 30188,* NY!

Stem creeping to erect, 0.1–1.5 m. tall. *Petiole* 15–50 cm. long, castaneous to fulvous, inermous to muricate; scales uniformly cretaceous or fulvous with a cretaceous border; scurf absent or of fulvous trichomidia; axes of lamina and leaf surface with minute, fulvous trichomidia. *Lamina* 0.4–1.0 m. long, 1-pinnate, coriaceous, apex abruptly reduced to an articulate apical pinna; pinnae remote, long-petiolulate, entire to serrate, sterile pinnae sometimes irregularly crenate, base long-cuneate, apex attenuate, tip serrate; costules indistinct, veins all concurrent to the margin, fertile and sterile veins anastomosing, often forming one if not two rows of areolae, fertile veins undivided at the sori. *Sori* in one to three medial rows, subtended by evanescent soral squamulae; paraphyses shorter than the sporangia, receptacle pilose.

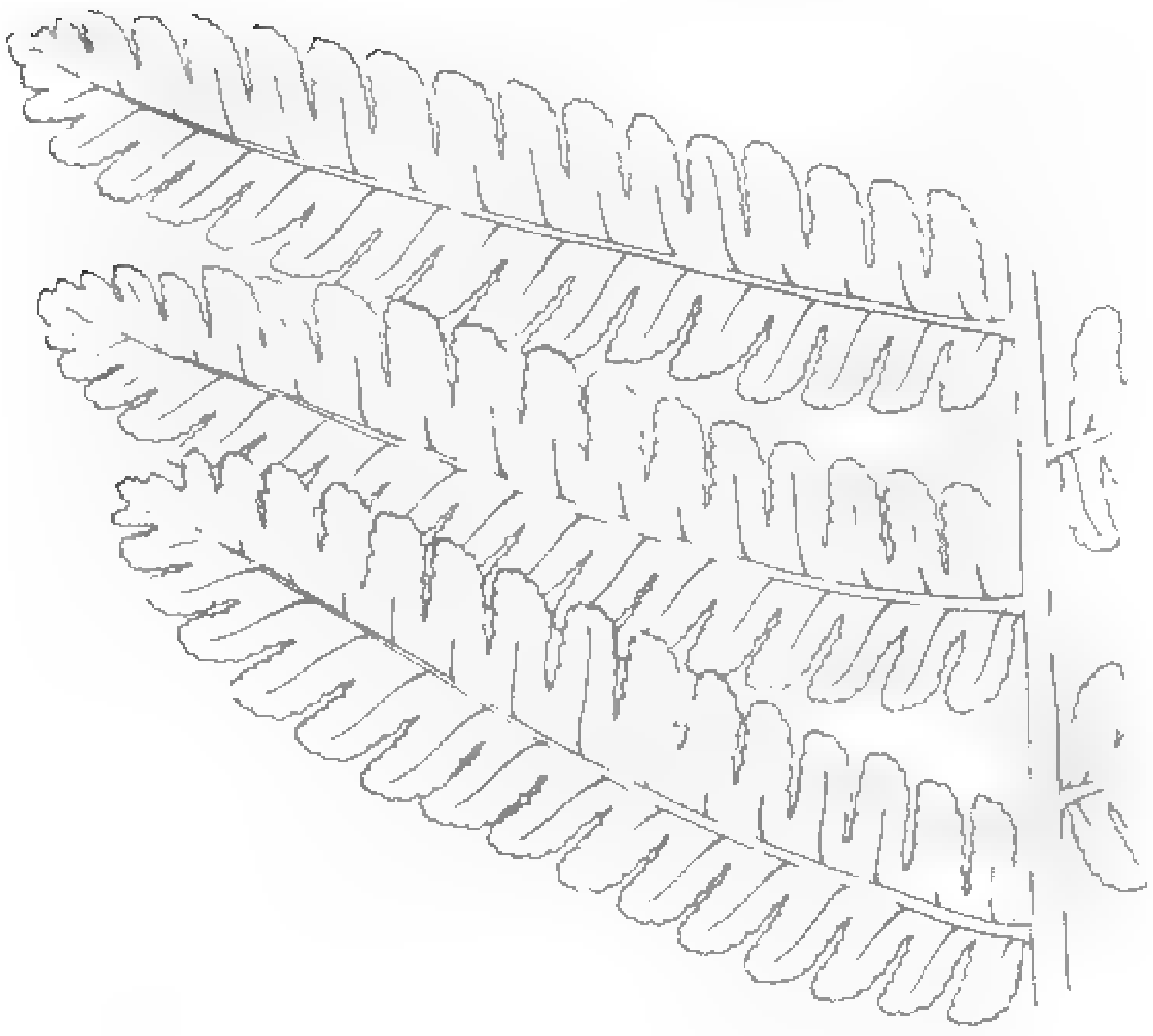
32



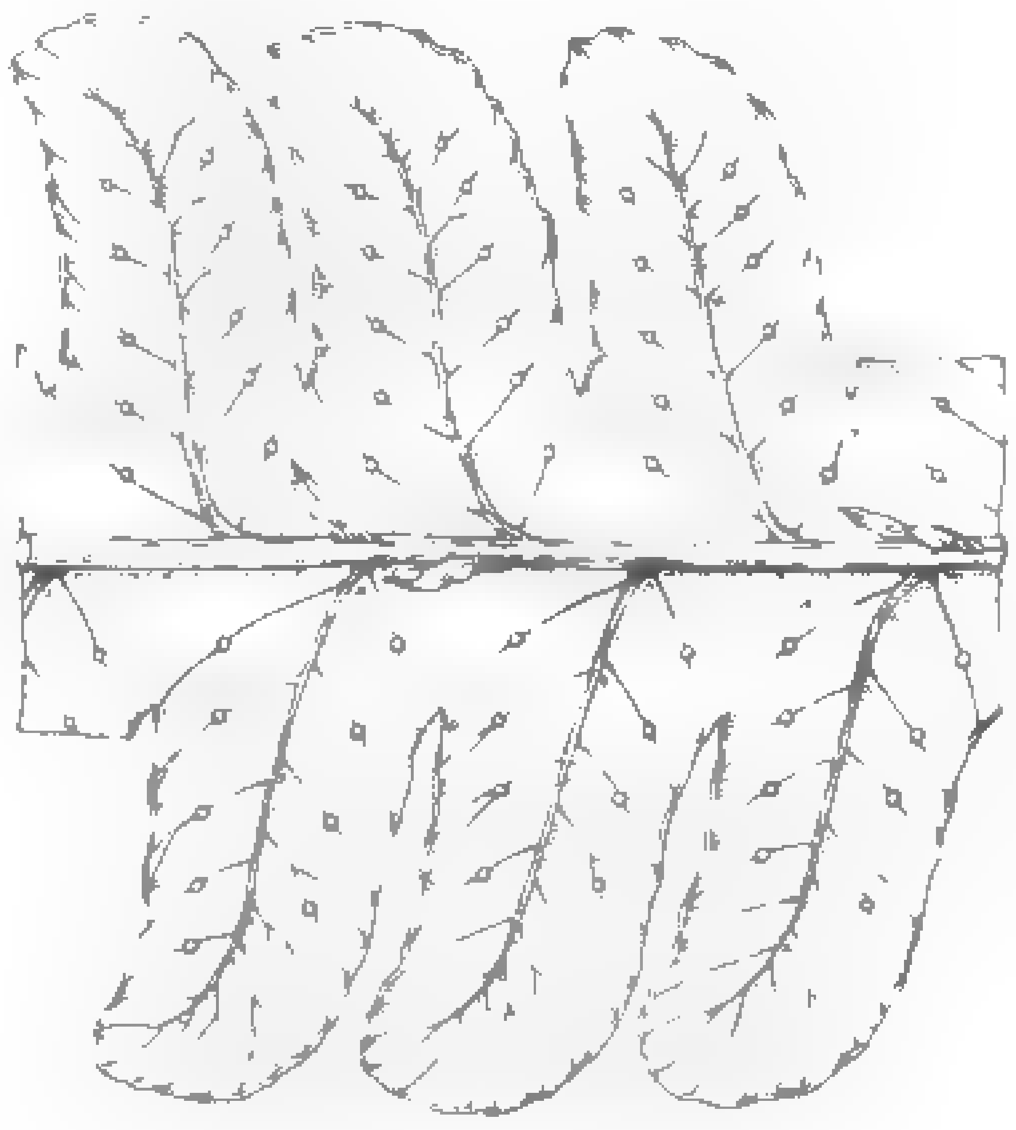
33



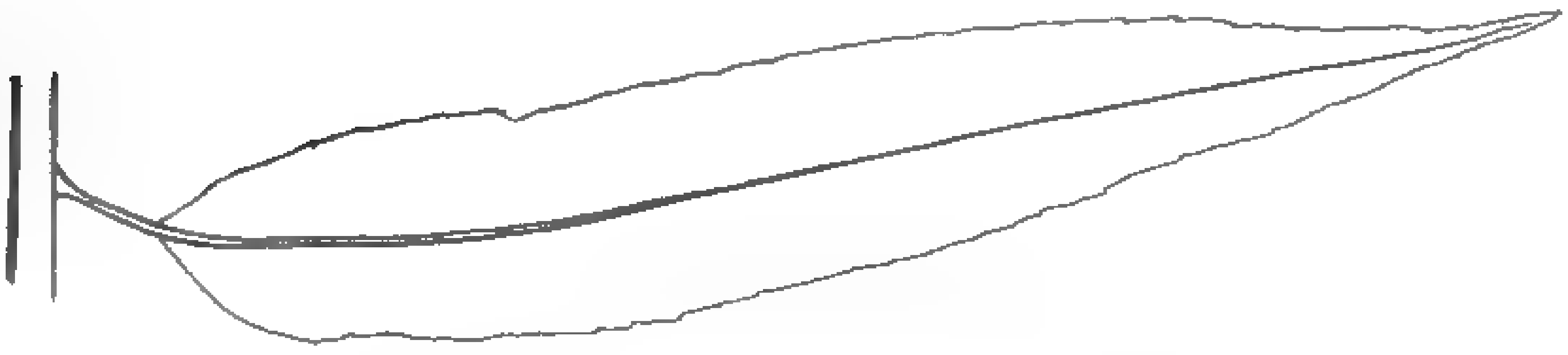
34



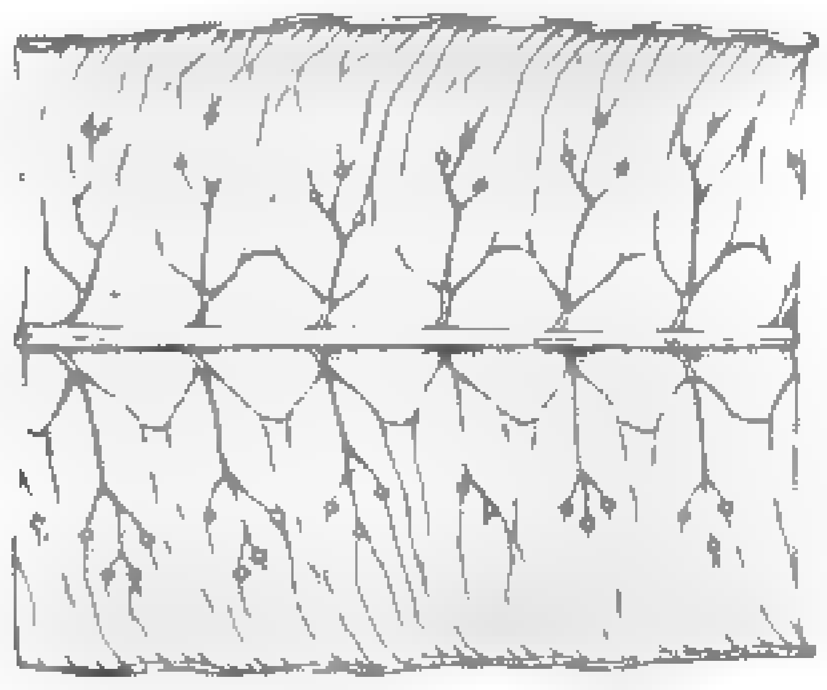
35



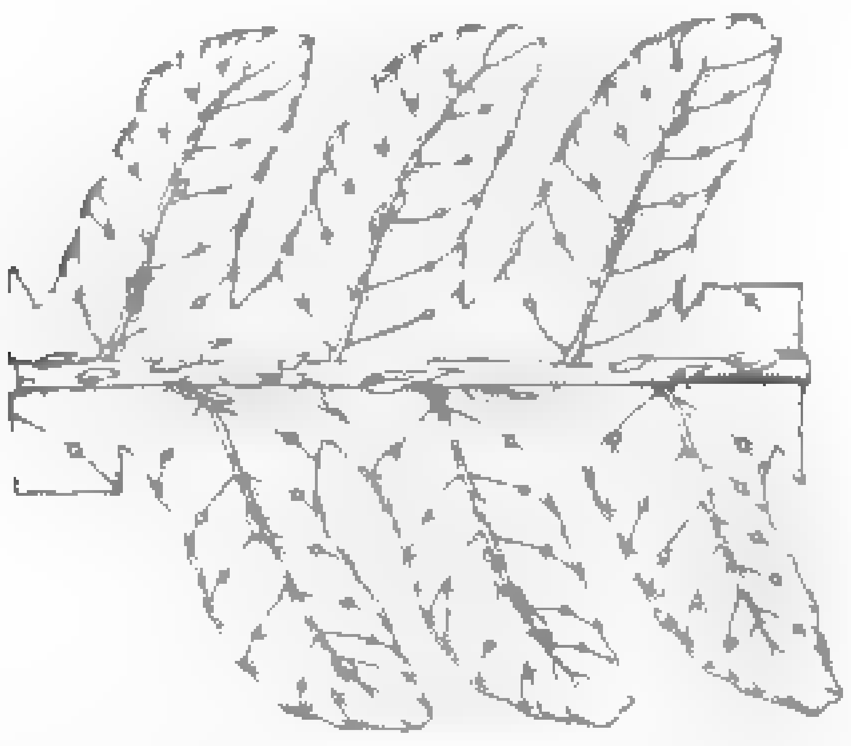
36



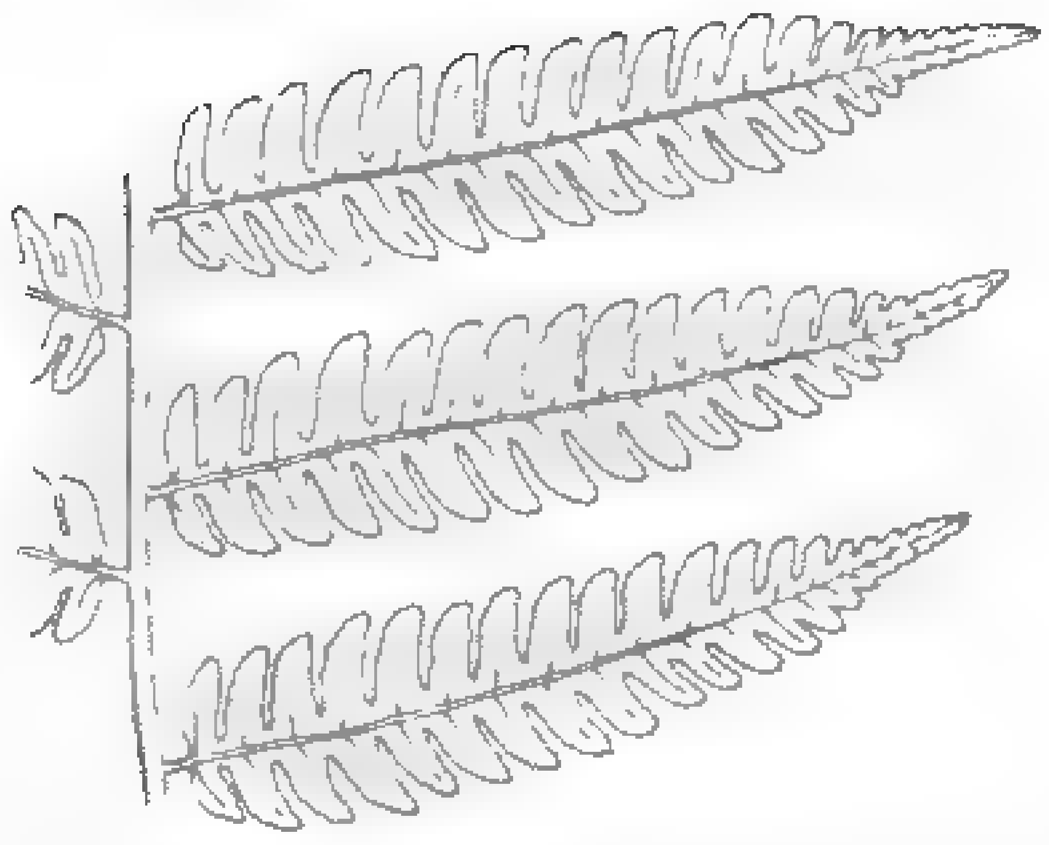
37



39



38



FIGS. 32–39. FIGS. 32 & 33, *Trichipteris ursina:* 32, two central pinnae, × 1/3; 33, central part of a pinna, × 1 (both *Scamman 7438*, GH). FIGS. 34 & 35, *T. phalaenolepis:* 34, three central pinnae, × 1/3; 35, central part of a pinna, × 1 (both *Killip & Garcia 33430*, GH). FIGS. 36 & 37, *T. Williamsii:* 36, a central pinna, × 1/3 (*Williams 850*, US); 37, central part of a pinna, × 2/3 (*Lellinger & de la Sota 258*, US). FIGS. 38 & 39, *T. microphylla:* 38, three central pinnules from a central pinna, × 1/3; 39, basal part of a pinnule, × 4/3 (both *Fendler 53*, GH).

Trichipteris Williamsii is one of two species in the genus with simply 1-pinnate leaves. It has attenuate, serrate pinna tips in contrast to *T. Cyclodium,* which has blunt, entire pinna tips. There is some variation within *T. Williamsii* in size of the plant and coloration of the petiole scales. Geographically *T. Williamsii* comprises two disjunct populations: one in Panama and the other in the Guayana Highlands of Venezuela (including Cerro Autana; Steyermark, 1974). In both areas it is found in wet forests at middle elevations (1350–1900 meters). Similar disjunct distributions are known for *Trichipteris villosa,* the Chrysobalanaceae (Prance, 1974), and the Myristicaceae (Gentry, 1975).

SELECTED COLLECTIONS. **Panama. Canal Zone:** 6 mi. above Goofy Lake on the road to Cerro Jefe, *Croat 15211* (NY); summit of Cerro Jefe, *Dwyer, Durkee & Castillon 5043* (NY). **Colombia. Chocó:** trail along ridge from the confluence of the Río Mutatá and the Río Dos Bocas to the top of Alto de Buey, *Lellinger & de la Sota 258* (US). **Venezuela. Amazonas:** Cerro Huachamacari, Río Cunucunuma, *Maguire, Cowan & Wurdack 30200* (US).

11. **Trichipteris microphylla** (Kl.) Tryon

FIGS. 38, 39. MAP 10.

Trichipteris microphylla (Kl.) Tryon, Contrib. Gray Herb. 200:46. 1970.

Alsophila microphylla Kl., Linnaea **18**:541. 1844. HOLOTYPE: Caracas, *Moritz 281b,* B.

Alsophila squamata Kl., Linnaea **18**:541. 1844. HOLOTYPE: Caracas, *Moritz 110* B! (Tryon noted in 1969 that *Moritz 110* and *Moritz 281b* at B were the same species.)

Alsophila caracasana Kl. var. *Fendleriana* Domin, Pterid. Dominica 95. 1929. HOLOTYPE: Venezuela, near Colonia Tovar, *Fendler 53* annotated *A. leucolepis,* K not seen. ISOTYPES: F! GH! MO! NY!

Cyathea microphyllodes Domin, Pteridophyta 263. 1929, *nom. nov.* for *Alsophila microphylla* Kl., Linnaea **18**:541. 1844, not *Cyathea microphylla* Mett., Fil. Lechl. **1**:23 t. 3 f. 1–6. 1856.

Stem 0.5–3.0 m. tall. *Petiole* 0.4–1.2 m. long fulvous to stramineous, tuberculate to muricate; scales fuscous with a cretaceous margin; scurf of large, cretaceous squamulae; axes of lamina with minute trichomidia, large flattish fulvous squamulae and bullate cretaceous squamulae. *Lamina* 1.0–2.0 m. long, 2-pinnate-pinnatifid, papyraceous, apex gradually reduced and acute; pinnae stalked; pinnules short-petiolulate, pinnatisect, base truncate to cordate, apex acuminate; lobes rotund, entire to crenate; fertile veins forked at the sori, sterile veins forked or simple. *Sori* medial; paraphyses much shorter than the sporangia, receptacle puberulous.

Large cretaceous squamulae distinguish *Trichipteris microphylla* from the remainder of the 2-pinnate-pinnatifid species of the genus. *Trichipteris microphylla* is most easily confused with exindusiate species of *Sphaeropteris,* which lack marginate petiole scales. It is an unspecialized species, judging from the petiole scurf. Geographically *T. microphylla* is confined to the Atlantic slopes of the Cordillera Oriental in northern Colombia and the coastal ranges in Venezuela and perhaps Trinidad. It is a forest species, occurring between 1800 and 3000 meters in altitude.

SELECTED COLLECTIONS. **Trinidad.** Port of Spain, *Anonymous* in 1874 (NY). **Venezuela. Distrito Federal:** Colonia Tovar & vicinity, *Moritz* (possibly isotype material) (NY); between Agua Negra & El Junquito, *Pittier 13807, 13825* (F,NY,VEN). **Miranda:**

Galipan, near crest of Cerro de Avila, *Pittier 6212* (NY,VEN). **Colombia. Norte de Santander:** region of Sarare, between Alto del Loro & Alto de Santa Ines, 1800–2200 m, *Cuatrecasas, Schultes & Smith 12513* (F,GH,US). **Santander:** vicinity of Las Vegas, 2600–3000 m, *Killip & Smith 15968* (GH,US); southern slope of Mt. San Martin near Charta, 2000–2500 m, *Killip & Smith 19173* (GH,US); *Killip & Smith 19188* (GH,NY,US). **Cundinamarca:** La Palma, Cordillera de Helicona, 10 km SE of Gachala, *Grant 10322* (GH,US).

12. **Trichipteris Schiedeana** (Presl) Tryon

FIGS. 40, 41. MAP 11.

Trichipteris Schiedeana (Presl) Tryon, Contrib. Gray Herb. 200:46. 1970.

Alsophila Schiedeana Presl, Tent. Pterid. 62. 1836, based on a description of a *Polypodium* without binomial in Schlecht. & Chamisso, Linnaea **5**:609. 1830. HOLOTYPE: inter Huitamalco et Cuapa regionis calidae. Mex., *Schiede*, fragment ex B, *(Schiede 757)* GH! fragment ex B,US! ISOTYPE: fragment probably ex P,F!

Cyathea Schiedeana (Presl) Domin, Pteridophyta 263. 1929.

Alsophila chnoödes Christ, Bull. Herb. Boiss. II. **4**:958. 1904. HOLOTYPE: Costa Rica, *Wercklé*, (Herb. Christ) P! ISOTYPES: A! NY! US!

Cyathea chnoödes (Christ) Domin, Pteridophyta 262. 1929.

Trichipteris chnoödes (Christ) Tryon, Contrib. Gray Herb. 200:44. 1970.

Alsophila crassifolia Christ, Bull. Herb. Boiss. II. **6**:184. 1906. HOLOTYPE: Luna, Pulanca Quebrada, Costa Rica, *Wercklé*, (Herb. Christ) P! ISOTYPE: US!

Cyathea crassifolia (Christ) Domin, Pteridophyta 262. 1929.

Trichipteris crassifolia (Christ) Gastony, Am. Journ. Bot. **61**(6):673. 1974.

Stem to 7.0 m. tall. *Petiole* 0.3–0.7 m. long, fuscous to stramineous, aculeate; scales fuscous; scurf of congested, fuscous to cretaceous trichomidia; indument of lamina axes of trichomidia, trichomes, and flattish to bullate, fuscous squamulae. *Lamina* 1.0–2.0 m. long, 2-pinnate-pinnatifid, papyraceous, apex abruptly reduced and pinna-like to gradually reduced and acuminate; pinnae sessile; pinnules sessile, deeply pinnatifid to pinnatisect, base truncate to cuneate, apex obtuse to attenuate; lobes rotund, entire to crenulate; fertile veins simple or forked at the sori, sterile veins simple or forked. *Sori* medial, paraphyses shorter than the sporangia, receptacle pilose.

Trichipteris Schiedeana is best determined on the basis of its lustrous, fuscous petiole scales, petiole scurf of fuscous, contorted trichomidia, and bullate costal squamulae. It may be confused with *T. nigripes*, which has a petiole scurf consisting predominantly of squamulae, petiolulate pinnules, and often flattish rather than bullate costal squamulae. *Trichipteris Schiedeana* is a highly variable species. In the southern part of the range the leaf apex is often acuminate, and the veins undivided. A few specimens have petiole scales with narrow cretaceous borders. There is also some variation in the composition of the petiole scurf in plants from Costa Rica and Panama.

Trichipteris Schiedeana is found from Mexico to Panama. It grows in wet forests (especially along streams), in dwarfed forests along mountain crests, and as a weedy plant of wet, secondary forests. At least in Mexico it is an abundant species.

SELECTED COLLECTIONS. **Mexico. Veracruz:** 8 km. S of Misantla, *Barrington 405* (GH); Córdoba, *Bourgeau 1834, 1835, 1836* (GH,MO,NY). **Oaxaca:** between Puerto Eligio & Comaltepec, km. 149 from Tuxtepec to Oaxaca San Juaréz, *Calderón 423* (F,GH,US); Distrito Choapam, Yaveo, above Arroyo de Culebras, *Mexia 9185* (F,GH, MO,NY). **Chiapas:** Cacahuatan, *Fisher 35390* (F,MO,NY); Finca Mexiquito, *Purpus 6713* (GH). **Guerrero:** Río Petetlán, *Langlassé 663* (GH). **Guatemala. Huehuetenango:** between Ixcan and Río Ixcan, Sierra de los Cuchumatanes, *Steyermark 49282, 49287* (F,GH). **Quiché:** Finca Chailá Zona Reyna, *Skutch 1790* (GH). **Alta Verapaz:** S of Cubilquitz, *Steyermark 44537* (F,US); Cerro de Agua Tortuga, vicinity of Cubilquitz, *Steyermark 44601* (F,US). **Izabal:** quebradas, *Pittier 8578* (NY); Cerro San Gil, along Río Frío, *Steyermark 39973* (F,GH,US). **Quezaltenango:** between Finca Pirineos & Finca Soledad, S slopes of Volcán Santa María, *Steyermark 33544* (US). **Belize (British Honduras).** Hummingbird Highway, Stann Creek District, *Gentle 8257* (F,NY); Temash River, *Schipp S–922* (GH). **El Salvador. Chalatenango:** E slope of Los Esesmiles, *Tucker 1129* (F,GH,MO,US). **Morazán:** Finca Gen. J. T. Calderón, Montes de Cacaguatique, *Tucker 788* (F,US). **Honduras. Atlántida:** Lancetilla Valley, near Tela, *Standley 52722* (F,GH); slopes of Mt. Cangrejal, vicinity of La Ceiba, *Yuncker, Koepper & Wagner 8815* (MO,NY). **Comayagua:** Barranco Trincheras, 20 km. N of Siguatepeque, *Morton 7588, 7591* (US); Trincheras, N of Siguatepeque, *Steves & Ray 480* (GH). **Cortés:** mountains, N side of Lake Yojoa, *Morton 7618* (US); N of Lake Yojoa, *Ray 2122* (A,GH). **Costa Rica. Alajuela:** near Zapote on the road to Villa Quesada, *Scamman 7589* (F,GH). **Limón:** 35 km. NE of Turrialba toward Siquirres, *Gastony & Gastony 782* (GH); above Siquirres, *Ulloa 4* (GH). **San José:** vicinity of El General, *Skutch 2891* (GH,MO). **Cartago:** Finca Navarro, *Maxon 631, 634* (NY); San Juan del Norte, *Scamman 7588* (GH). **Puntarenas:** 5 km. S of San Vito de Java, *Wilson & Wilson 69–332* (NY). **Panama. Chiriquí:** valley of the Río Caldera, from El Boquete to the Cordillera, *Killip 5476* (F,US). **Bocas del Toro:** hills behind Fish Creek, vicinity of Chiriquí Lagoon, *von Wedel 2211* (GH,MO).

13. Trichipteris aspera (L.) Tryon

FIGS. 42, 43. MAP 12.

Trichipteris aspera (L.) Tryon, Contrib. Gray Herb. **200**:44. 1970.

Polypodium asperum L., Sp. Pl. **2**:1093. 1753, based on Petiver, Pterigraphia Amer. 47, t. 4 f. 7, *ex icone,* based on a specimen collected by Plumier in Haiti.

Cyathea aspera (L.) Sw., Schrad. Journ. **1800**:93. 1800.

Alsophila aspera (L.) Sprengel, Systema Vegetab. ed. 16. **4**:124. 1827.

Disphenia aspera (L.) Presl, Abh. Bohm. Ges. **5**(5):349. 1848.

Hemitelia aspera (L.) Fée, Mém. Fam. Foug. **5** (Genera Filicum):350. 1852.

Cyathea muricata Willd., Sp. Pl. ed. 4. **5**:497. 1810, based on Plumier, Tractatus 5 t. 4 and Petiver, Pterigraphia Amer. 48, t. 4 f. 8.

Alsophila muricata (Willd.) Desv., Mém. Soc. Linn. Paris **6**:319. 1827.

Disphenia muricata (Willd.) Presl, Abh. Bohm. Ges. **5**(5):349. 1848.

Hemitelia muricata (Willd.) Fée, Mém. Fam. Foug. **5** (Genera Filicum):350. 1852.

Polypodium alsophilum Link, Hort. Berol. **2**:106. 1833, *ex char.* HOLOTYPE: hort. Berlin, originally from Jamaica.

Cyathea alsophilum (Link) Domin, Pteridophyta 262. 1929.

Alsophila nitida Kze. in Ettingsh., Farnkr. 222, t. 154 f. 4, 8 t. 155 f. 1, 7. 1865. HOLOTYPE: Martinique, (*Perrotet* in 1851, orig. Herb. Vindob.) W not seen. ISOTYPE: B!

Stem erect, 1.0–9.0 m. tall. *Petiole* 0.4–0.9 m. long, atropurpureous to fulvous, tuberculate to aculeate, scales uniformly fuscous to fulvous or with a slightly lighter border; scurf of cretaceous to fulvous congested trichomidia and appressed to erect squamulae; rachis, pinna-rachises, and costae tuberculate to muricate, axes of lamina often with cretaceous trichomidia, costae and sometimes pinna-rachises with flattish, erose, fuscous squamulae and bullate, cretaceous squamulae. *Lamina* 1.5–2.5 m. long, 2-pinnate-pinnatifid, papyraceous to coriaceous, apex gradually reduced and long-acuminate; pinnae stalked; pinnules short-petiolulate, pinnatifid to pinnatisect, base cordate to truncate, apex acuminate to a crenulate tip; lobes acute, entire to crenate; fertile veins forked at the sori or simple, sterile veins usually forked. *Sori* medial to supramedial, subtended by evanescent, biseriate to persistent, multiseriate fuscous soral squamulae; paraphyses shorter than to as long as the sporangia, receptacle hirsute.

Trichipteris aspera usually lacks the minute, cretaceous trichomidia on the costae and costules that are characteristic of *T. gibbosa,* and it has shorter paraphyses. Further collections may reveal that the two species are part of one morphological continuum.

Maxon notes on a collection of *Trichipteris aspera* from Martinique *(Dusen 1603),* "This is *A. aspera,* but the locality is certainly to be doubted!" *Alsophila aspera* has traditionally been interpreted as a species of the Greater Antilles, and *Alsophila muricata* as a species of the Lesser Antilles. However, plants with several fuscous soral squamulae, traditionally *A. muricata,* and plants with one cretaceous squamule, traditionally *A. aspera,* can be found throughout the range of *T. aspera* from Cuba to Grenada. A variety of intermediates have been collected. The mosaic distribution of both intermediates and extremes leads me to interpret these plants as members of a single, polymorphic species. *Trichipteris aspera* occurs in rain forests and cloud forests, often along watercourses, and along mountain crests in "elfin" forests. It is also found in secondary vegetation persisting after cutting of the original forest. The species occurs at up to 1500 meters in Jamaica, but generally grows at about 750 meters in the rest of the Antilles (150–1500 meters). It is common throughout its range, but has not been collected from Puerto Rico.

SELECTED COLLECTIONS. **Cuba. Las Villas (Sta. Clara):** SE of Cumanayagua, Sierra de San Juan, *Senn 229* (GH,MO); Trinidad Mts., El Provenir, *Britton & Wilson 5324* (NY). **Oriente:** Santa Ana, ca. 6 mi. N of Jaguey, Yateras, *Maxon 4181* (GH,NY). **Jamaica. Trelawney:** Troy (or Tyre), Cockpit Country, *Underwood 3306* (NY). **St. Ann:** NE slope of Mt. Diablo, *Howard & Proctor 15161* (A). **St. Mary:** valley of the Flint River, 1 mi E of cascade, *Proctor 4914* (MO). **Portland:** Seamen's Valley, *Maxon & Killip 11* (F,GH,NY); trail from Morces Gap to Vinegar Hill, *Maxon & Killip 680* (F,GH,NY). **St. Thomas:** Mansfield, near Bath, *Maxon 2405* (GH,US). **St. Andrew:** Cooper's Hill, Red Hills, *Proctor 9901* (MO). **Manchester:** Blue Mt., *Gilbert* (MO,NY). **St. Elizabeth:** Wallenford, *Harris 7280* (NY). **Haiti. Dept. du Sud:** Massif de la Hotte, Tiburon, western group, Morne Citadelle, *Ekman 10544* (NY); Massif de la Hotte, western group, N slope of Morne Vandervelde, *Ekman 5215* (F). **St. Kitts.** *Proctor 19642* (A). **Nevis.** *Proctor 19477* (A). **Montserrat.** *Proctor 18869* (A). **Guadeloupe.** *Proctor 19997* (A); *Proctor 20348* (A). **Dominica.** *Wilbur 7549* (GH,NY). **Martinique.** *Duss 1602* (F,NY). **St. Lucia.** *Howard 11690* (A,GH,NY). **St. Vincents.** *H. H. Smith 696* (NY). **Grenada.** *Sherring 25* (NY).

14. **Trichipteris gibbosa** (Kl.) Barr.

Figs. 44, 45. Map 13.

Trichipteris gibbosa (Kl.) Barr., Rhodora 78(813):3. 1976.

Alsophila gibbosa Kl., Linnaea 18:542. 1844. HOLOTYPE: in British Guiana, *Schomburgk 1124,* fragment ex B, GH! fragment ex B, NY! ISOTYPE: P!

Cyathea gibbosa (Kl.) Domin, Pteridophyta 262. 1929.

Sphaeropteris gibbosa (Kl.) Tryon, Contrib. Gray Herb. 200:20. 1970.

Alsophila farinosa Mett., Ann. Sci. Nat. Bot. V. 2:262. 1864. *nom. nud.*

Alsophila farinosa Karst., Fl. Columb. 2:163 t. 186. 1869. HOLOTYPE: prope Colonia Tovar, Caracas, Venezuela, 1500 m, 1849, *Karsten,* fragment ex B, GH!

Cyathea farinosa (Karst.) Domin, Pteridophyta 262. 1929.

Stem to 5 m. tall. *Petiole* ca. 0.5 m. long, fulvous, muricate; scales fulvous with a lighter border; scurf of a few trichomidia and a dense covering of fulvous squamulae; costae and costules with cretaceous trichomidia and flattish to bullate, fulvous squamulae. *Lamina* ca. 1.0 m. long, 2-pinnate-pinnatifid, chartaceous to coriaceous, apex gradually reduced and acuminate; pinnae stalked; pinnules petiolulate, pinnatifid to deeply pinnatifid, base truncate, apex acuminate, tip crenulate; lobes rotund to acute, entire; fertile veins forked at the sori or simple especially at the base of the segments, sterile veins forked or simple. *Sori* medial, with large, fuscous soral squamulae (sometimes abraded in older material); paraphyses longer than the sporangia, receptacle villous.

Trichipteris gibbosa is closely related to *T. aspera,* from which it differs in several respects noted under the former species. It is found in Venezuela and Guyana (British Guiana) from 2100 to 2200 meters.

SELECTED COLLECTIONS. **Venezuela. Aragua:** prope coloniam Tovar, *Fendler 54* (GH,MO,US); *Pittier 9995* (GH,US). **Distrito Federal:** mountains near Galipan, *Pittier 111* (NY,US,VEN); between El Junquito & Colonia Tovar, *Steyermark 91731* (GH,VEN).

15. **Trichipteris nigripes** (C. Chr.) Barr.

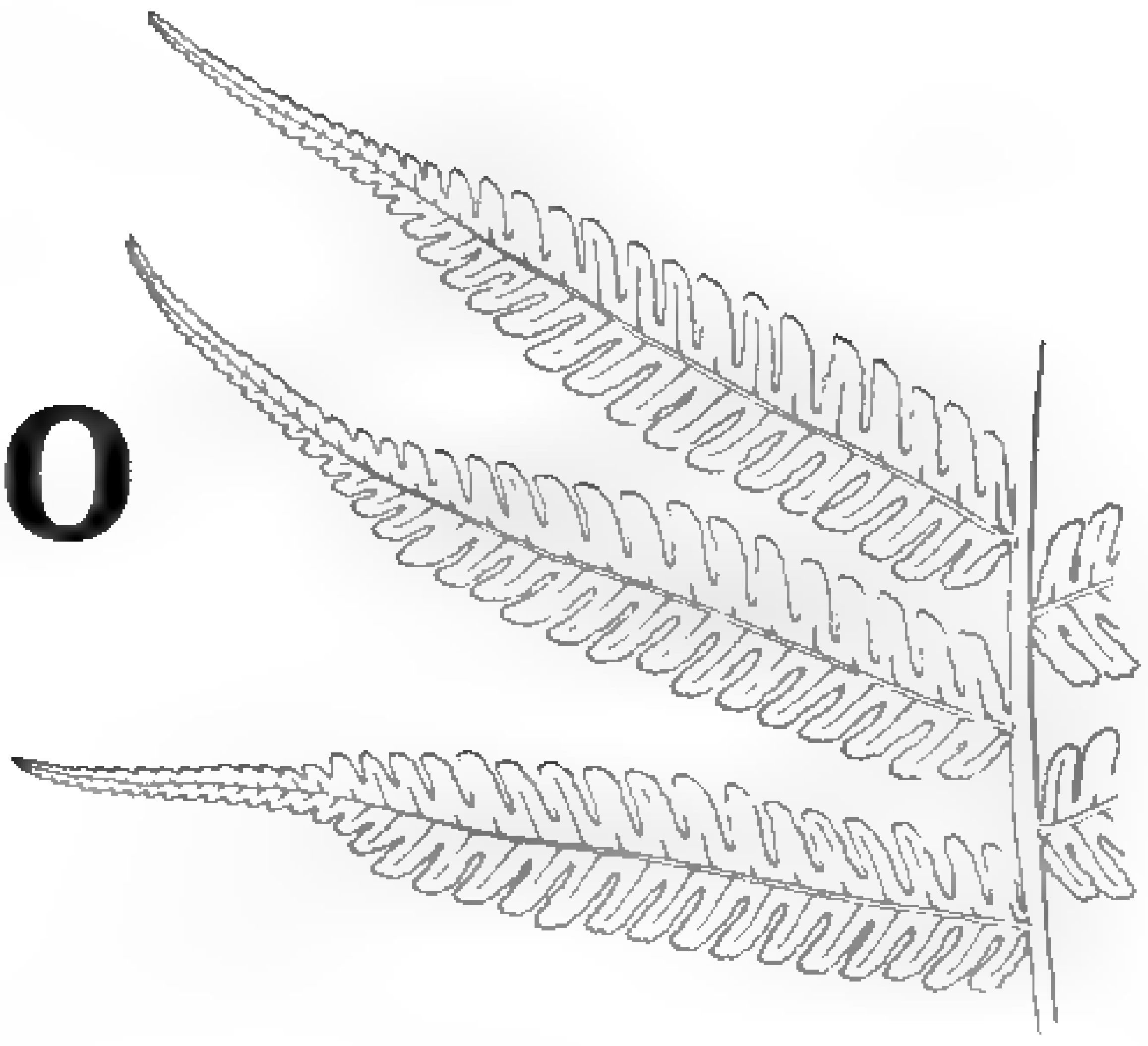
Both varieties of this species have a dark aspect, a composite of the atropurpureous petioles and petiole scales and the dark green foliage. In Costa Rica and Panama, *Trichipteris nigripes* can be confused with *T. Wendlandii,* a species in which the pinna-rachises are clothed with bullate, fuscous squamulae and the paraphyses are longer than the sporangia. *Trichipteris Schiedeana,* a central American species, has close-set, bullate and not remote, flattish costal squamulae. There is some variation in the costal indument and in the development of the petiole spines in *T. nigripes.* In addition, the fertile veins vary from simple to forked on plants throughout the range of *T. nigripes.* Some pinnae have almost no forked fertile veins. The species is found in rain forests and cloud forests (especially on slopes and crests) from sea level to 2200 meters. The two varieties of *T. nigripes* make up a single variable species ranging from Costa Rica to Peru. The combination *Alsophila furcata* Christ, which pertains to *Nephelea mexicana* (Schlecht. & Cham.) Tryon, is occasionally applied to specimens of *T. nigripes* from Costa Rica.

15a. **Trichipteris nigripes** (C. Chr.) Barr. var. **nigripes**

FIGS. 46, 47. MAP 14.

Trichipteris nigripes (C. Chr.) Barr., Rhodora 78(813):4. 1976.
Alsophila nigripes C. Chr., Ind. Fil. 45. 1905, *nom. nov.* for *Alsophila melanopus* Hook., Syn. Fil. ed. 1. 37. 1866, not *A. melanopus* Hassk., Journ. Bot. (Hooker's) 7:325. 1855.
Cyathea nigripes (C. Chr.) Domin, Pteridophyta 263. 1929.
Alsophila melanopus Hook., Syn. Fil. ed. 1:37. 1866, not Hassk., 1855. LECTOTYPE (chosen herewith): Chimborazo, Ecuador, *Spruce 5742,* K! ISOLECTOTYPE: P! LECTOPARATYPE: Mt. Canelos, Ecuador, *Spruce,* K not seen.

Stem 2.0–8.0 m. tall. *Petiole* 0.3–1.5 m. long, nigrescent to fuscous or rarely stra-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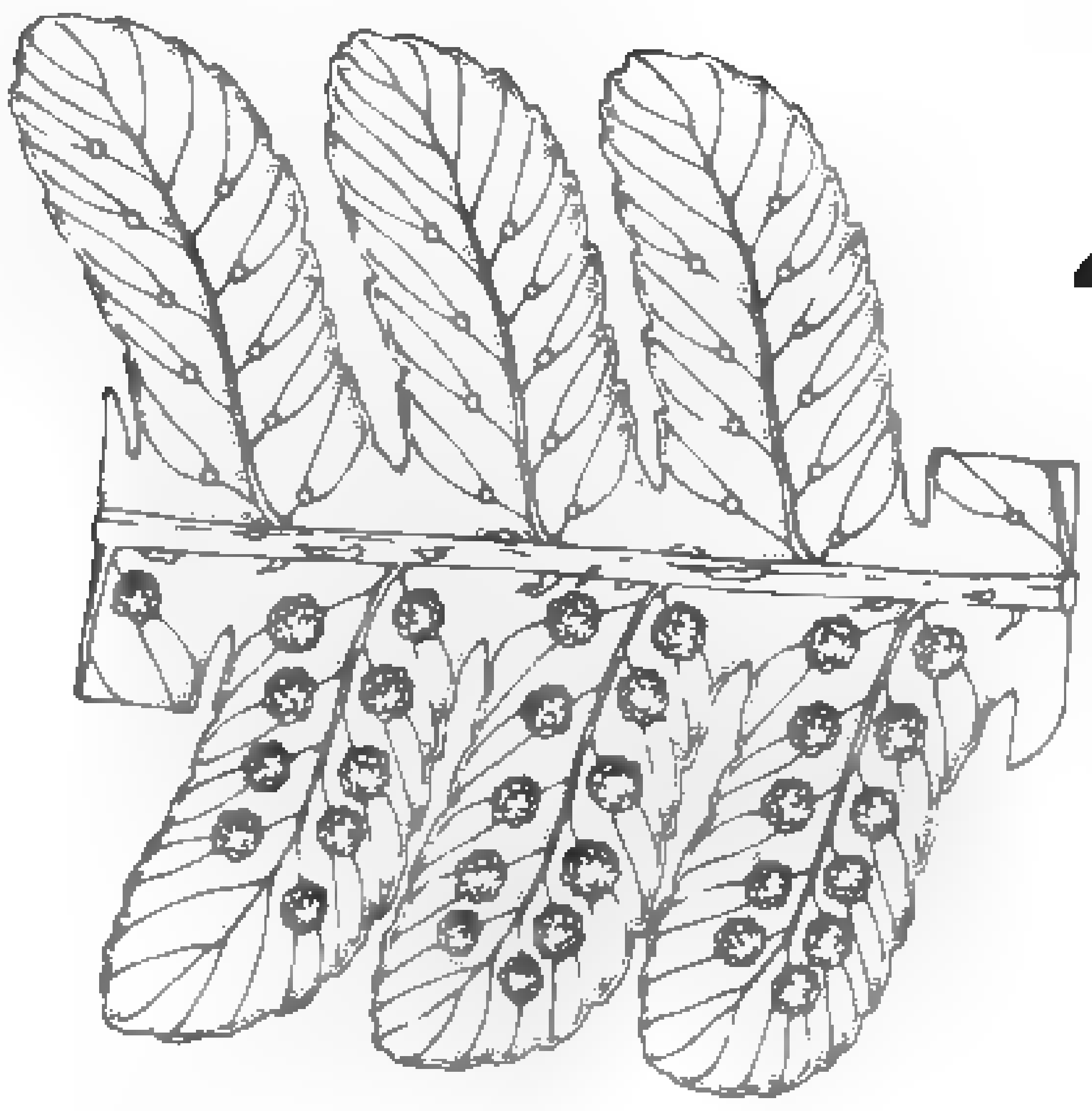
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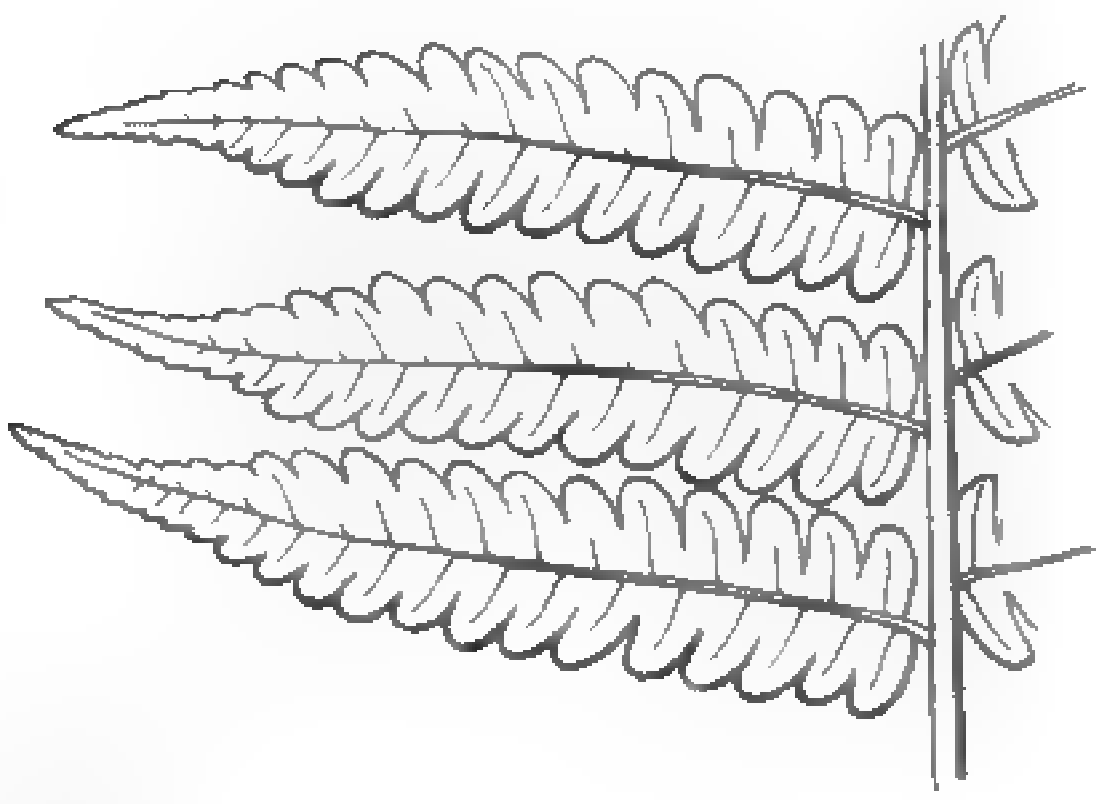
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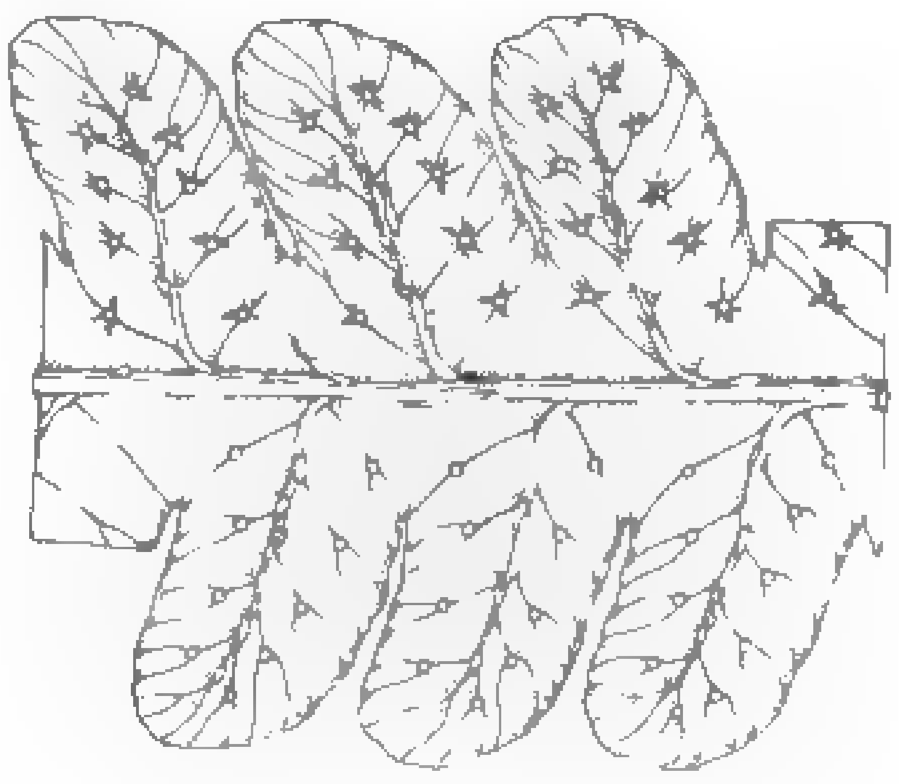
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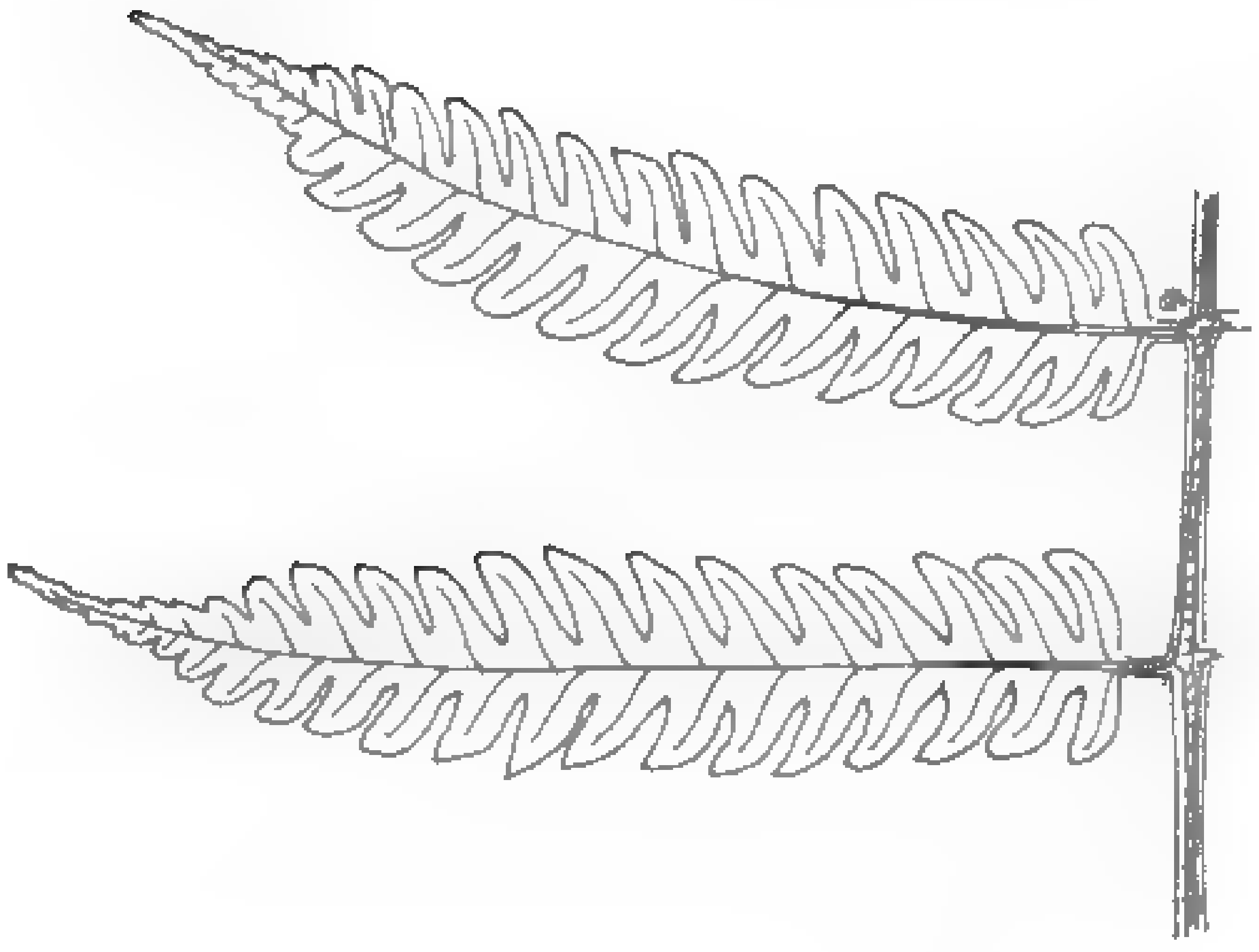
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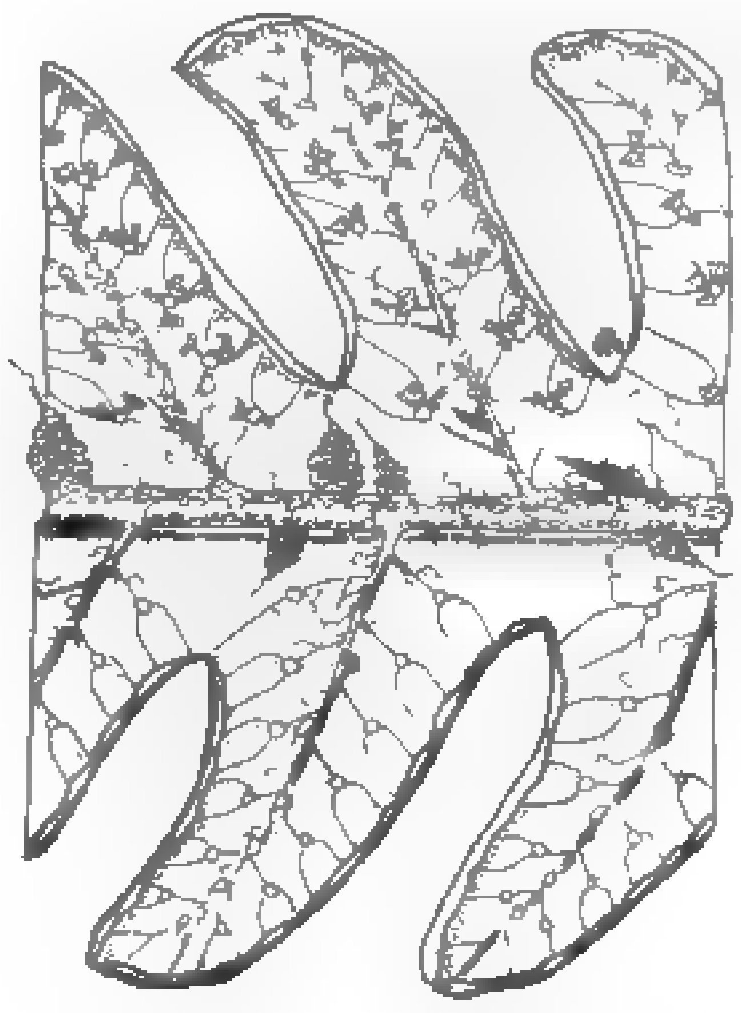
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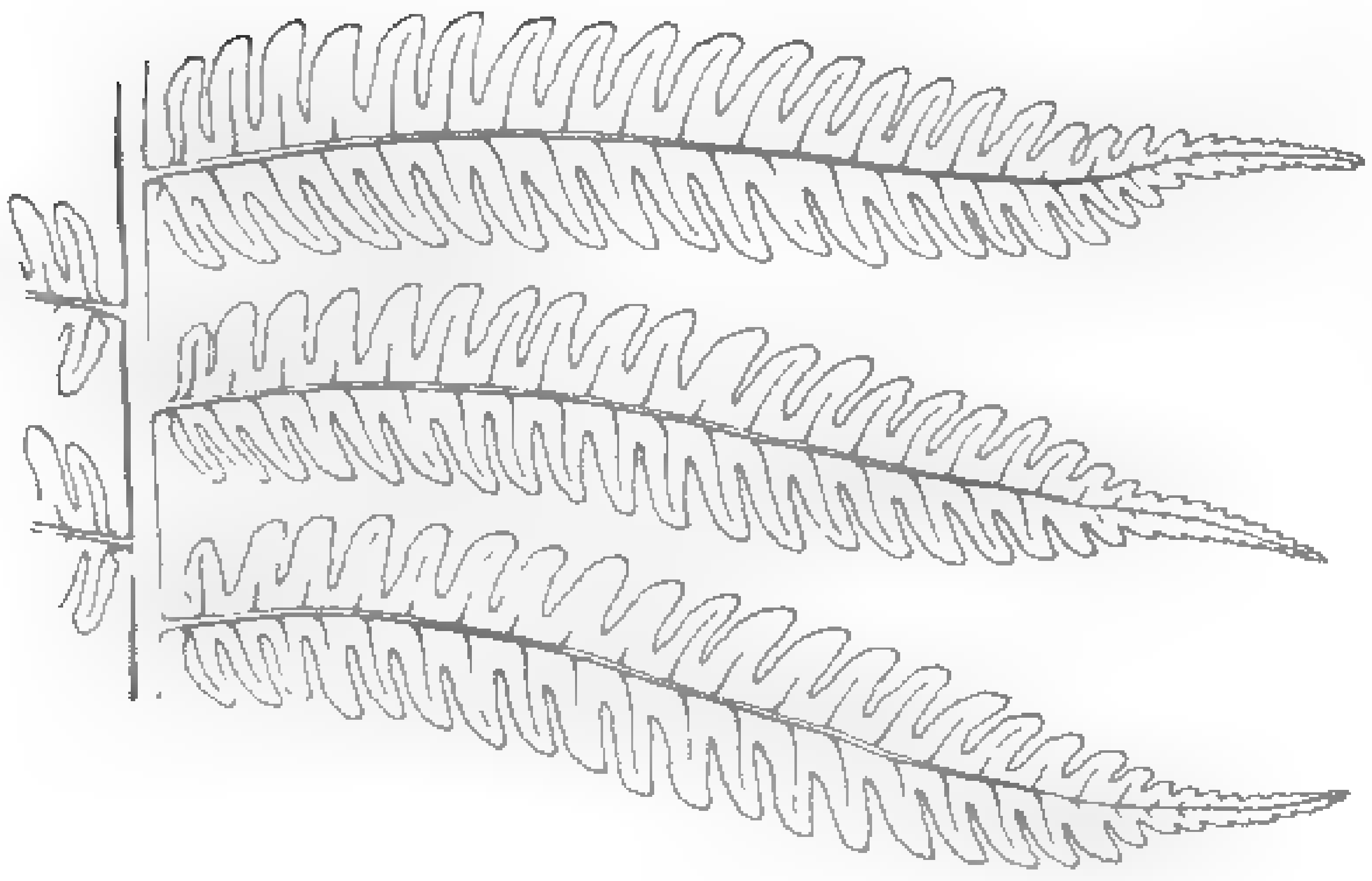
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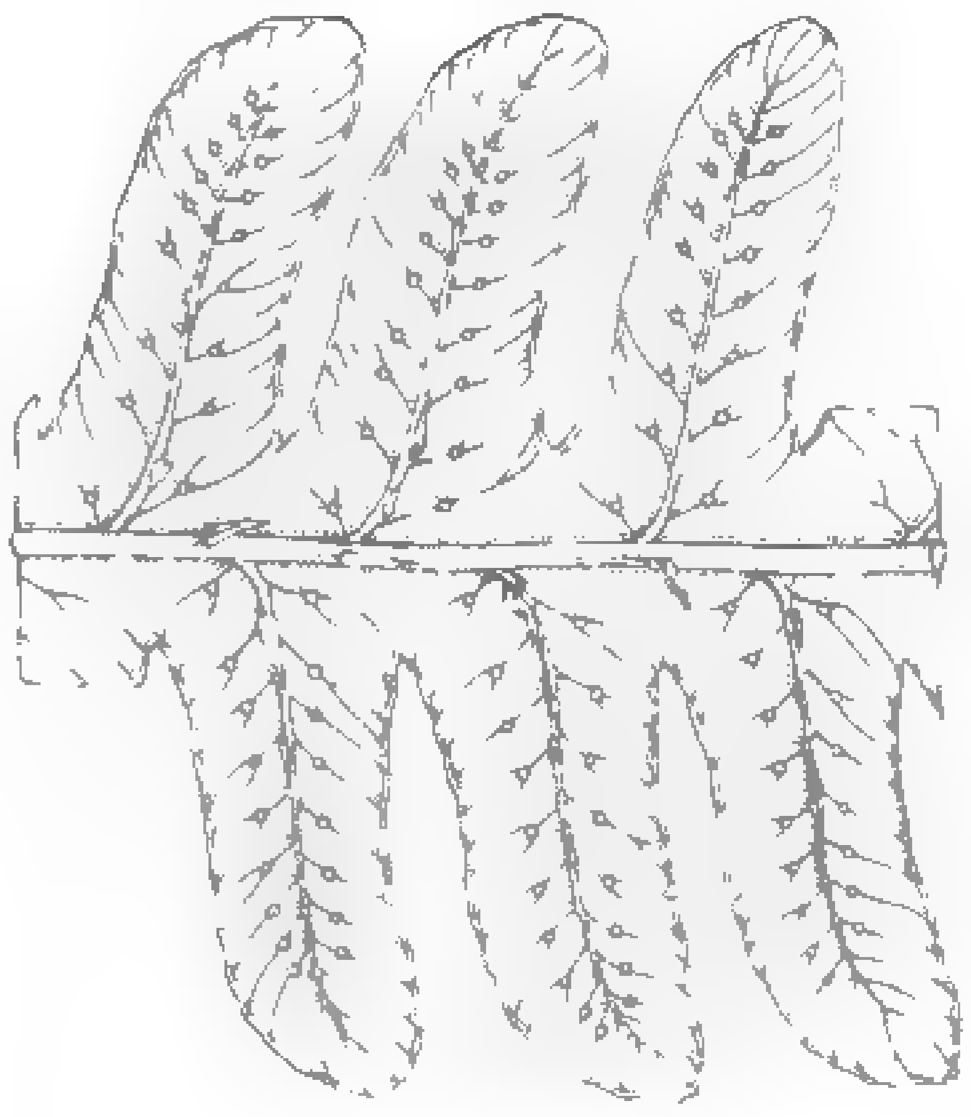
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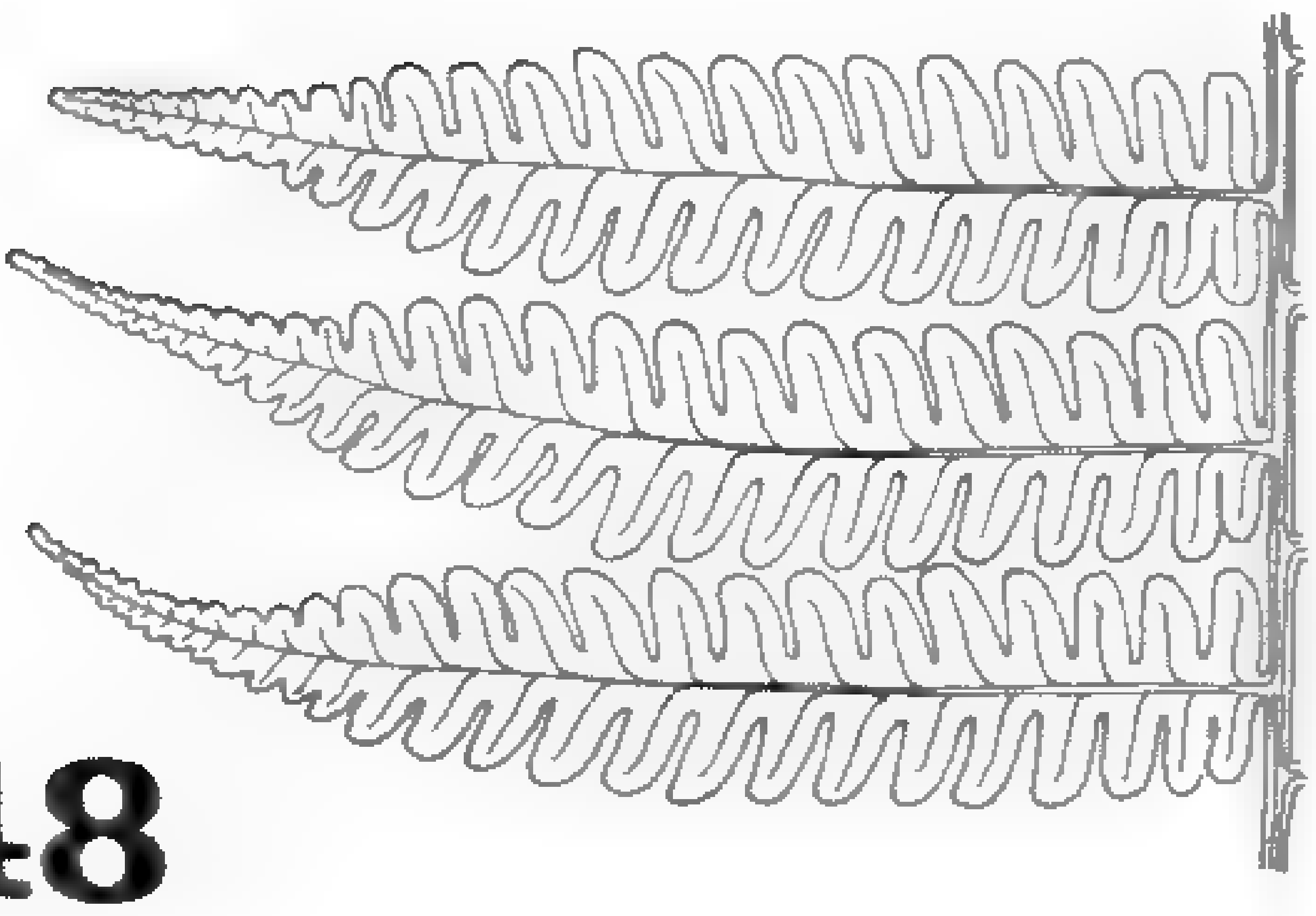
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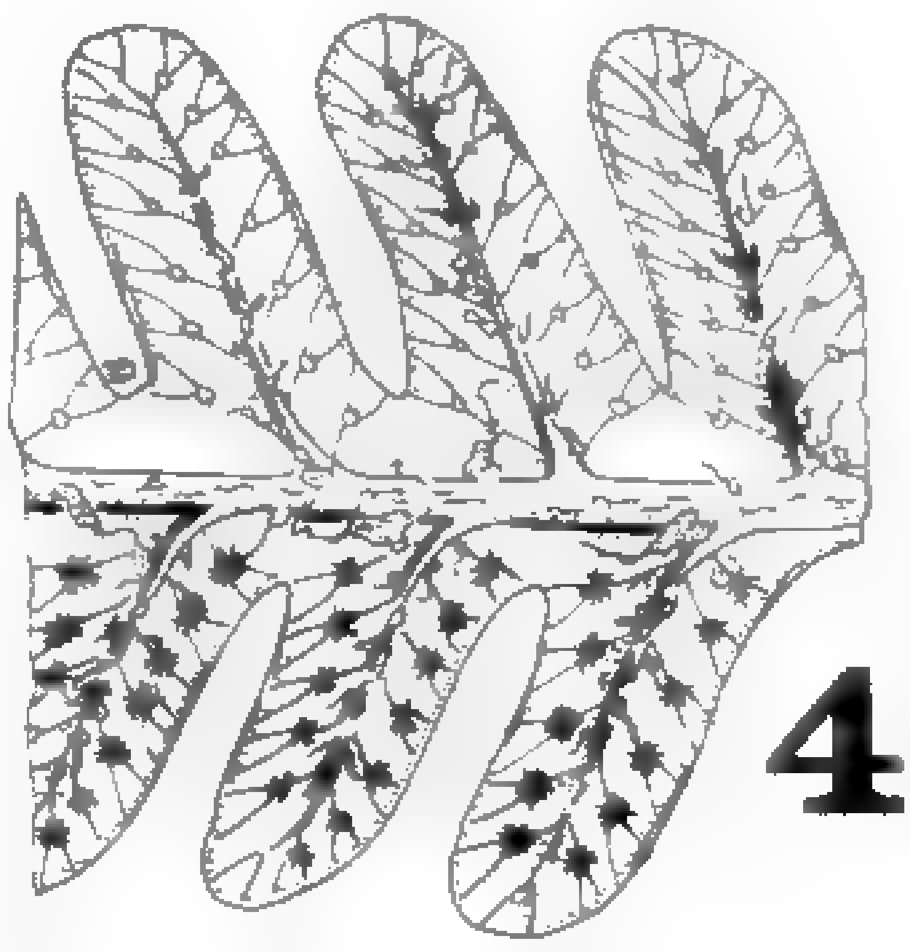
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mineous, tuberculate to aculeate; scales uniformly fuscous; scurf usually of congested, fuscous trichomidia and squamulae; rachis and pinna rachises often tuberculate to muricate, with trichomidia and trichomes; costae with a few cretaceous trichomidia and flattish, deltoid, fuscous squamulae. *Lamina* 1.5–3.0 m. long, 2-pinnate-pinnatifid, chartaceous, apex gradually reduced and long-acuminate; pinnae sessile to stalked; pinnules petiolulate to long-petiolulate, deeply pinnatifid to pinnatisect, base subcordate to truncate, apex acuminate to attenuate, tip crenulate; lobes rotund to acute, entire to crenulate; fertile veins forked at the sori or simple, sterile veins forked or occasionally simple. *Sori* subcostal to medial, paraphyses shorter than the sporangia, receptacle pilose.

SELECTED COLLECTIONS. **Costa Rica. Alajuela:** near Zapote, road to Villa Quesada, *Scamman 7594* (GH). **San José:** 17 km. N of San Isidro el General, *Gastony 754* (GH); La Palma & vicinity, 15 km. NE of San José, *Gastony 769* (GH). **Cartago:** valley of the Río Grande del Orosi, 20 km. S of Cartago, *Tryon & Tryon 7026* (GH); 4.5 km. from bridge at Tapantí, *White & Lucansky 1968120* (GH,US). **Province indet:** *Werckle* (some of the specimens det. *Alsophila furcata,* i.e., US *1903366, 1316805*). **Panama. Darién:** Cerro de Garagará, Sambú Basin, *Pittier 5641* (US). **Colombia. Valle:** km. 19 on road from Cali to Buenaventura, *Barrington 499, 501* (GH); El Cairo, between Darién & Mediacanoa, Río Calima valley, *Cuatrecasas 13930* (F,GH,US). **Nariño:** Mun. Ricaurte, El Palmar, bank of the Quiza River, *Soejarto 1445* (GH). **Ecuador. Pichincha:** Santo Domingo de los Colorados, Rancho Brahman, on the road to Esmeraldas, *Sparre 14072* (GH); Toáchi, confluence of Río Pilatón & Río Toáchi, road from Aloag to Sto. Domingo, *Sparre 18484* (GH). **Cotopaxi:** Cacaoal, *Bell 918* (GH); 5 km. S of Palmar, road from Quevado to Latacunga, *Lockwood 835* (GH).

15b. **Trichipteris nigripes** (C. Chr.) Barr. var. **brunnescens** Barr.

FIGS. 48, 49. MAP 15.

Trichipteris nigripes (C. Chr.) Barr. var. *brunnescens* Barr., Rhodora 78(813):4 t. 1 f. 6. 1976. HOLOTYPE: Río Yurumanguí, Veneral, 5–50 m., Valle, Colombia, 1944, *Cuatrecasas 16155–C,* U.S. Nat. Herb. 1853473–6, US! ISOTYPE: GH! PARATYPE: Agua Clara, highway from Buenaventura to Cali, 100 m., Valle, Colombia, 1944, *Killip & Cuatrecasas 38884,* F! ISOPARATYPES: GH! US!

Stem 1.5–6.0 m. tall. *Petiole* ca. 0.3 m. long, fuscous, tuberculate to aculeate; scales uniformly fuscous; scurf of congested fuscous to fulvous trichomidia or squamulae; axes of lamina with trichomidia, cretaceous trichomes and flattish to bullate squamulae. *Lamina* 1.0–1.3 m. long, 2-pinnate-pinnatifid, chartaceous to coriaceous, apex gradually reduced and long acuminate; pinnae sessile to stalked; pinnules sessile to petiolulate, pinnatisect, base truncate to cuneate, apex obtuse to acuminate, tip crenulate; lobes rotund to truncate, entire to crenulate; fertile veins forked at the sori, sterile veins forked or simple. *Sori* subcostal to supramedial; paraphyses shorter than the sporangia, receptacle hirsute.

Trichipteris nigripes var. *brunnescens* differs from typical plants of the species in having well-developed spines, sessile pinnules, and trichomes on the abaxial surface of the leaf axes. *Trichipteris nigripes* var.

←

FIGS. 40–49. FIGS. 40 & 41, *Trichipteris Schiedeana:* 40, three central pinnules from a central pinna, × 1/3; 41, central part of a pinnule, × 4/3 (both *Standley 52722,* F). FIGS. 42 & 43, *T. aspera:* 42, three central pinnules from a central pinna, × 1/3; 43, central part of a pinnule, × 4/3 (both *Howard & Proctor 15161,* A). FIGS. 44 & 45, *T. gibbosa:* 44, two central pinnules from a central pinna, × 1/3; 45, central part of a pinnule, × 4/3 (both *Steyermark 91731,* GH). FIGS. 46–49, *T. nigripes:* 46, var. *nigripes,* three central pinnules from a central pinna, × 1/3; 47, var. *nigripes,* central part of a pinnule, × 4/3 (both *Sodiro* in 9/1892, NY). 48, var. *brunnescens,* three central pinnules from a central pinna, × 1/3; 49, var. *brunnescens,* central part of a pinnule, × 4/3 (both *Cuatrecasas 16155–C,* US).

brunnescens is in general a Pacific coast population from Colombia. A few plants of this variety have been collected at higher altitudes and on Atlantic slopes in Ecuador.

SELECTED COLLECTIONS. **Colombia. Chocó:** Río Negro, between Quibdó & Tutunendo, *Cuatrecasas & Llano 24215* (GH,US); near Istmina, road to Cértegui, *Garcia-Barriga 11180* (US). **Valle:** Río Cajambre, San Isidro, *Cuatrecasas 17297* (F,GH,US). **Nariño:** Quebrada La Toma, Río Telembi, between Río Pimbi & Río Cuembi, above Barbacoas, *Ewan 16860* (US). **Putumayo:** Río San Miguel, between Quebrada de Sipenae & Quebrada de Churruyaco, *Cuatrecasas 10953* (US); Uchupayaco, plain between Urcusique & Umbria, banks of the Río Uchupayaco, *Schultes 3299, 3365* (GH,US). **Ecuador. Napo:** Cerro Antisana, between Río Napo & Tena, 8 km. SE of Tena, *Grubb et al. 1657* (GH,NY). **Zamora-Chinchipe:** between Yacuambi & Supaca, near confluence of Río Yacuambi & Río Zamora, *Sparre 16426* (GH).

16. **Trichipteris Kalbreyeri** (Baker) Tryon

FIGS. 50, 51. MAP 16.

Trichipteris Kalbreyeri (Baker) Tryon, Contrib. Gray Herb. 200:45. 1970.

Alsophila Kalbreyeri Baker, Summary New Ferns 9. 1892, *nom. nov.* for *Alsophila podophylla* Baker, Journ. Bot. Brit. & For. 19:202. 1881, not *A. podophylla* Hook., Journ. Bot. 9:334. 1857.

Alsophila Kalbreyeri C. Chr., Ind. Fil. 44, 1905, *nom. nov.* for *Alsophila podophylla* Baker, Journ. Bot. Brit. & For. 19:202. 1881, not *A. podophylla* Hook., Journ. Bot. 9:334. 1857. (Christensen was apparently unaware of Baker's earlier and identical *nom. nov.* Tryon (1970) published the combination *Trichipteris Kalbreyeri* (C. Chr.) Tryon based on Christensen's *nom. nov.* and not Baker's. I have corrected this bibliographic error in accordance with the argument of Nicolson, 1975.

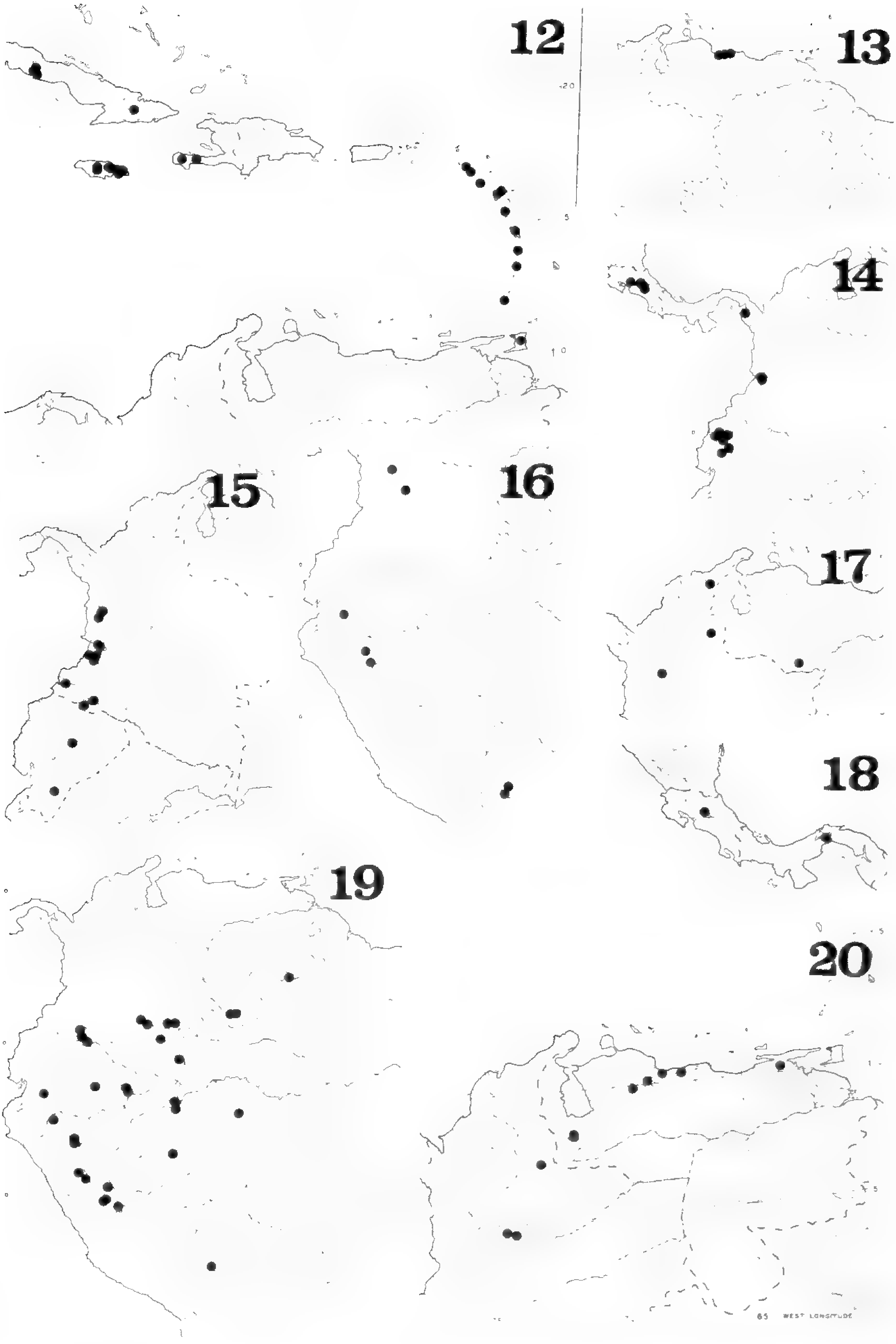
Cyathea Kalbreyeri (Baker) Domin, Pteridophyta 262. 1929.

Alsophila podophylla Baker, Journ. Bot. Brit. & For. 19:202. 1881, not *A. podophylla* Hook., Journ. Bot. 9:334. 1857. HOLOTYPE: forests, 500 ft., Colombia, *Kalbreyer 1375*, K not seen. ISOTYPE: (Antioquia) fragment ex B, GH!

Stem 3.5–4.0 m. or more tall. *Petiole* more than 0.3 m. long, atropurpureous, tuberculate to aculeate; scales atropurpureous with a fuscous border; scurf of occasional trichomidia and fulvous squamulae, large squamulae and small scales; axes of lamina with occasional trichomidia and small, flattish, fulvous squamulae. *Lamina* ca. 4.0 m. long, 2-pinnate-pinnatifid, coriaceous, apex gradually reduced and acuminate; pinnae long-stalked; pinnules long-petiolulate, pinnatisect to deeply pinnatifid, base truncate and inequalateral, apex acute to attenuate, tip serrate; lobes acute to acuminate, serrate at least at the tip; fertile veins forked at the sori, sterile veins forked. *Sori* inframedial to medial; paraphyses shorter than the sporangia, receptacle hirsute.

Trichipteris Kalbreyeri is nearly glabrous and has long petiolules and acuminate, serrate lobes. Although difficult to confuse with any other species of *Trichipteris, T. Kalbreyeri* is very close in leaf architecture to *Cyathea divergens* Kze. var. *divergens.* A careful check of the sori is necessary for critical determination. The size and dissection of the pinnules varies without relation to geography. *Trichipteris Kalbreyeri* is found in rain forests from 500 to 1400 meters in the eastern cordillera of the Andes in Colombia, and on the eastern slopes of the Andes from Ecuador to Bolivia.

SELECTED COLLECTIONS. **Colombia. Cundinamarca:** near Muzo, *Stübel 535* (B,NY).



MAPS 12–20: 12, Trichipteris aspera; 13, T. gibbosa; 14, T. nigripes var. nigripes; 15, T. nigripes var. brunnescens; 16, T. Kalbreyeri; 17, T. Schlimii; 18, T. Wendlandii; 19, T. nigra; 20, T. pauciflora.

Ecuador. Zamora-Santiago: Bomboiza, S of Gualaquiza, Misión Salesiana, *Sparre 19269* (GH). **Peru. San Martín:** Mt. Campana, near Tarapoto, *Spruce 4330* (NY). **Bolivia. La Paz:** region of San Carlos, Mapiri, *Buchtien 289* (GH,MO,NY,US); Tipuani, *Cárdenas 1283* (US).

17. **Trichipteris Schlimii** (Kuhn) Barr.

FIGS. 52, 53. MAP 17.

Trichipteris Schlimii (Kuhn) Barr., Rhodora 78(813):5. 1976.
Alsophila Schlimii Kuhn, Linnaea **36**:157. 1869. (Mett., Ann. Sci. Nat. Bot. V **2**:263. 1864. *nom. nud.*). LECTOTYPE (chosen herewith): Nova Grenada, Ocaña, (Norte de Santander). *Schlim 223,* B not seen. ISOLECTOTYPE: P! LECTOPARATYPE: Minas, Muzo, Colombia, *Lindig 254,* B not seen. ISOLECTOPARATYPE: P!
Cyathea Schlimii (Kuhn) Domin, Pteridophyta 263. 1929.

Stem 3.5 m. tall. *Petiole* more than 0.3 m. long, fulvous, tuberculate to aculeate; scales fulvous with a stramineous border; scurf of fuscous, densely congested trichomidia; rachis, pinna-rachises and costae with congested, fuscous trichomidia; pinna-rachises, costae and often costules with cretaceous trichomes and flattish to bullate, fuscous squamulae. *Lamina* ca. 3.0 m. long, 2-pinnate-pinnatifid, chartaceous, apex abruptly reduced and pinna-like; pinnae sessile; pinnules sessile, pinnatisect, base truncate, apex acuminate to attenuate, tip crenulate; lobes acute, entire; fertile veins forked at the sori, sterile veins presumably forked. *Sori* medial to subcostal, paraphyses longer than the sporangia, receptacle villous.

Although little known, *Trichipteris Schlimii* is a distinctive species, characterized by a dense tomentum of trichomidia and squamulae on all axes of the lamina. Closely allied species such as *T. nigra* and *T. Wendlandii* lack this tomentum. The alliance of *T. Schlimii* with these two species is based on the long, flexuous paraphyses present in all three. *Trichipteris Schlimii* is a mid-altitude rain forest species of the eastern cordillera in Colombia and the Pantepuí area of Venezuela.

SELECTED COLLECTIONS. **Venezuela. Bolívar:** Río Huacawa-kú, drainage of the Río Cuyuní, 139 km. S of El Dorado, *Steyermark & Dunsterville 104380* (GH).

18. **Trichipteris Wendlandii** (Kuhn) Tryon

FIGS. 54, 55. MAP 18.

Trichipteris Wendlandii (Kuhn) Tryon, Contrib. Gray Herb. **200**:46. 1970.
Alsophila Wendlandii Kuhn, Linnaea **36**:158. 1869. HOLOTYPE: San Miguel, Costa Rica, *Wendland 761,* fragment ex B, US!
Cyathea Wendlandii (Kuhn) Domin, Pteridophyta 263. 1929.

Stem 3.0–4.0 m. tall. *Petiole* ca. 0.7 m. long, fuscous, tuberculate to muricate; scales uniformly fulvous; scurf of congested trichomidia and squamulae; trichomidia occasional throughout axes of lamina; rachis and pinna-rachises sometimes with fulvous trichomes; pinna-rachises usually with abundant, fulvous squamulae; costae with flattish to bullate, fulvous squamulae. *Lamina* ca. 1.5–2.0 m. long; 2-pinnate-pinnatifid, papyraceous, apex not seen; pinnae stalked; pinnules sessile to short-petiolulate, pinnatisect, base truncate, apex acuminate, tip crenulate; lobes rotund or acute, tip serrate or crenulate; fertile veins forked at the sori, sterile veins forked. *Sori* subcostal; paraphyses longer than the sporangia, receptacle villous.

The adequate definition of *Trichipteris Wendlandii* as a species must await new, complete collections. No complete petioles are available, and no leaf apex has been collected. *Trichipteris Wendlandii* is a species found in rain forests in Costa Rica and Panama, where it occurs between 500 and 1000 meters. Since most of the intensive collecting of tree ferns in Central America has been above these altitudes, *T. Wendlandii* may grow at too low an altitude to have been collected often. Pinna-rachises with squamulae and long paraphyses separate *T. Wendlandii* from closely allied species *(T. nigra* and *T. Schlimii)* and from *T. nigripes.*

SELECTED COLLECTIONS. **Costa Rica. Alajuela:** La Marina, *Nisman 73, 75, 77* (GH). **Panama. Coclé:** N of El Valle de Anton, vicinity of La Mesa, *Allen 2873* (GH,US).

19. **Trichipteris nigra** (Mart.) Tryon

FIGS. 56, 57. MAP 19.

Trichipteris nigra (Mart.) Tryon, Contrib. Gray Herb. 200:46. 1970.

Alsophila nigra Mart., Icon. Plant. Crypt. Bras. 71 t. 30 f. 5, 6, t. 47. 1834. HOLOTYPE: flumen Japurá in provincia a Rio Negro dicta, *Martius,* M not seen. ISOTYPES: B! fragments ex B and K, NY!

Alsophila lasiosora Kuhn, Linnaea 36:157. 1869. HOLOTYPE: Peruviae orientale, *Spruce 4349,* B not seen. ISOTYPES: GH! P! US!

Cyathea lasiosora (Kuhn) Domin, Pteridophyta 262. 1929.

Trichipteris lasiosora (Kuhn) Tryon, Contrib. Gray Herb. 200:45. 1970.

Alsophila tarapotensis Rosenst., Fedde Repert. Spec. Nov. 7:291. 1909. HOLOTYPE: near Tarapoto, Peru, *Spruce 4349 (an 4249),* S not seen. ISOTYPES: GH! P! US! PARATYPE: same locality, *Spruce 4249* var. *videtur,* S not seen. ISOPARATYPE: P! (Herb. Christ). Since both type collections at P were annotated by Rosenstock in 1909 exactly as cited in Fedde Repert., it may be that the Paris materials are the originals from which Rosenstock described this species.

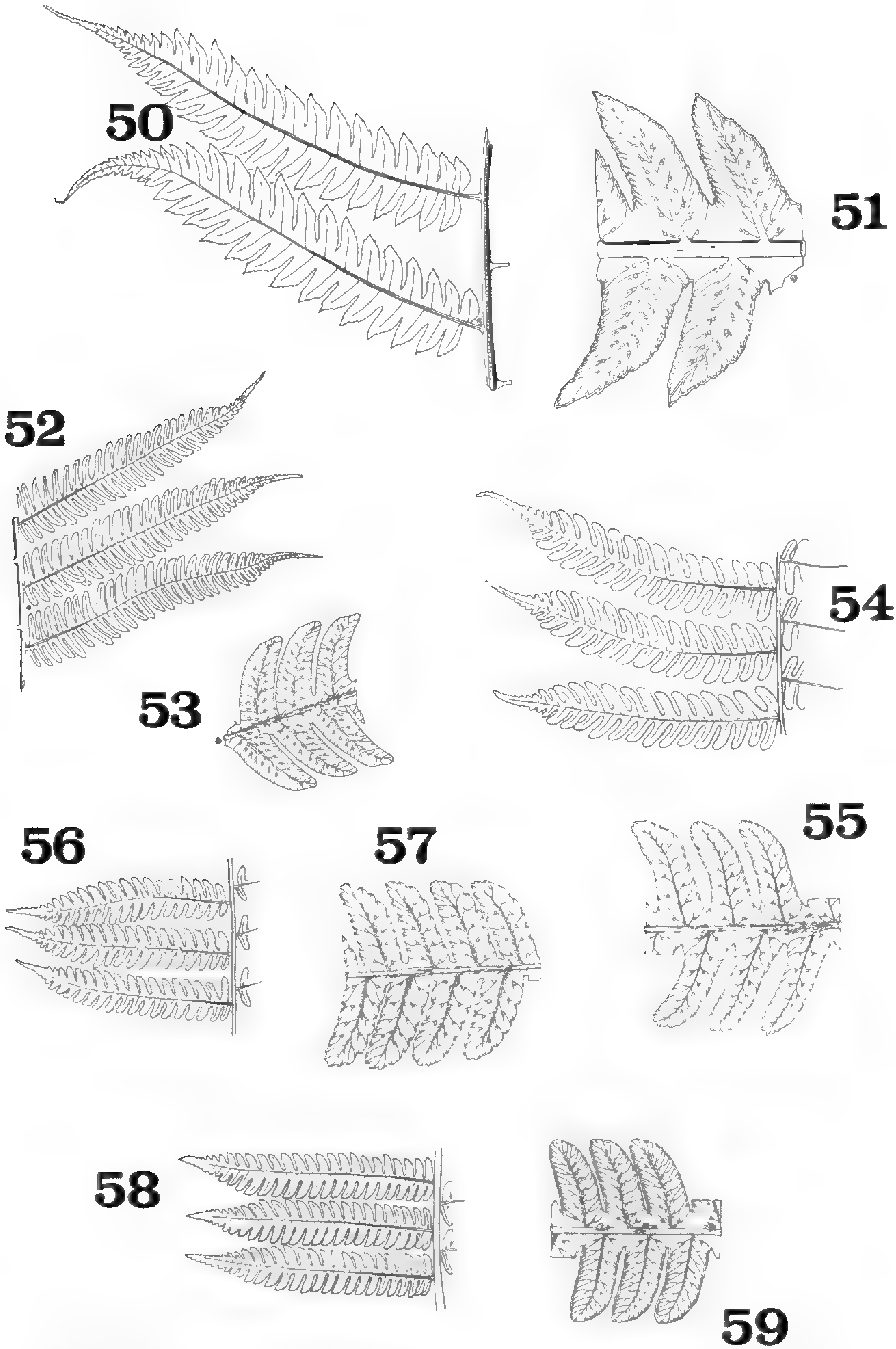
Alsophila mapiriensis Rosenst., Fedde Repert. Spec. Nov. 25:57. 1928. HOLOTYPE: San Carlos, region of Mapiri, Bolivia, *Buchtien 292,* S!

Cyathea mapiriensis (Rosenst.) Domin, Acta Bot. Bohem. 9:134. 1930.

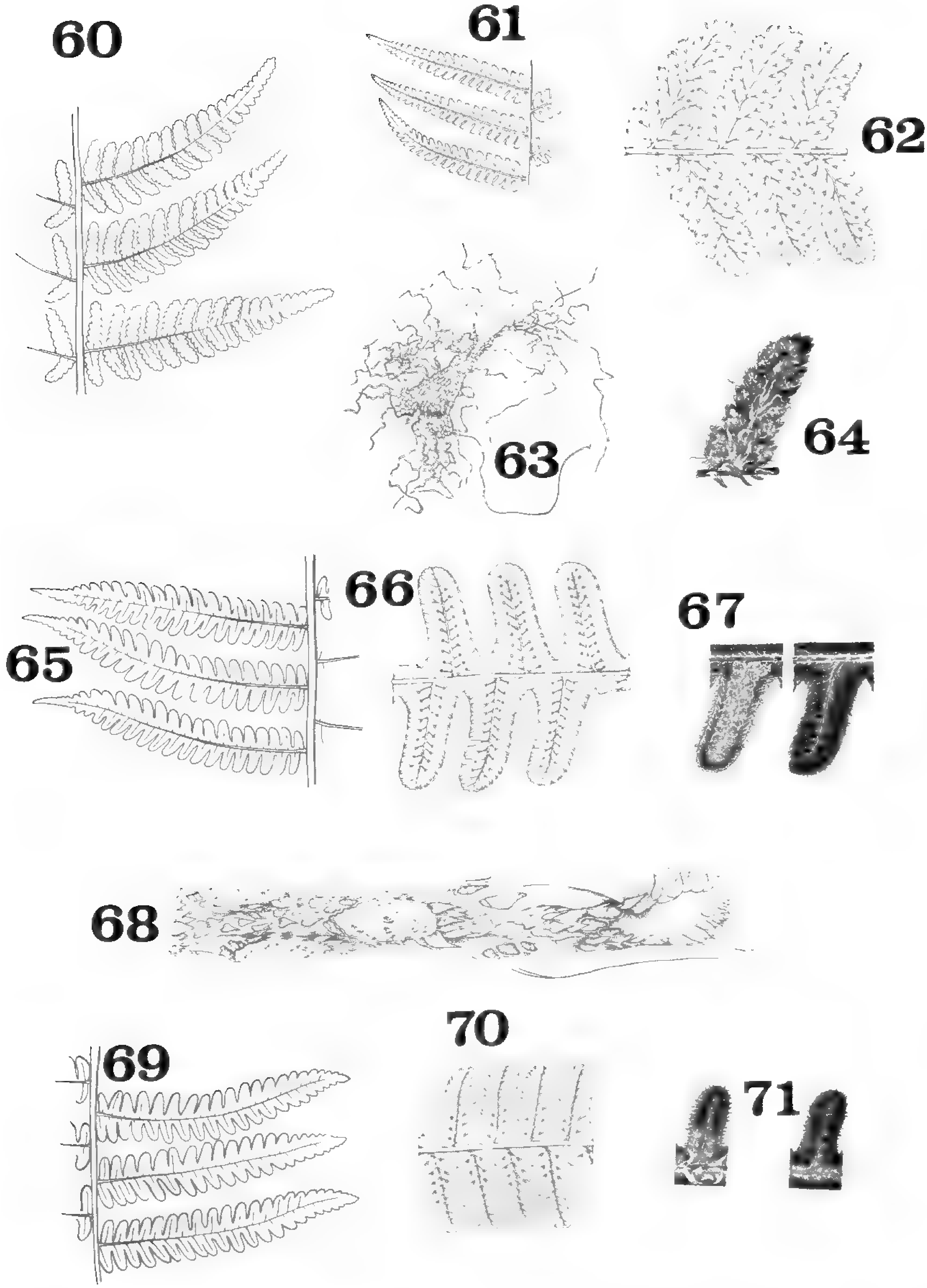
Alsophila Killipii Maxon, Am. Fern Journ. 32(2):58. 1942. HOLOTYPE: between Yurimaguas and Balsapuerto, Dept. Loreto, Peru, 1929, *Killip & Smith 28133,* US Nat. Herb. Nos. 1480024; 1480025; 1480026, US! ISOTYPE: F! PARATYPES: *Killip & Smith 26944,* F! US! *Killip & Smith 26989,* US! *Killip & Smith 28781,* F! US! *Klug 177,* F! US! *Williams 2918,* F! US! *Williams 4848,* F! US! *Krukoff 4937,* US! *Krukoff 7527 in part,* US! ISOPARATYPE: *Krukoff 4937,* F! GH! MO!

Stem diminutive to 6.0 m. tall. *Petiole* 0.3–0.6 m. long, fuscous to stramineous, tuberculate to aculeate; scales fuscous with a lighter margin or uniformly fulvous; scurf absent or of fulvous trichomidia or minute squamulae; rachis and pinna-rachises with occasional trichomidia and prominent fulvous trichomes; costae and costules with trichomes and fuscous to cretaceous, flattish to bullate squamulae. *Lamina* 1.2–2.5 m. long, 2-pinnate-pinnatifid, papyraceous, apex abruptly reduced and pinna-like; pinnae stalked to long-stalked; pinnules sessile to petiolulate, deeply pinnatifid to pinnatisect, base truncate, apex acuminate to attenuate, tip crenulate; lobes acute, crenulate; fertile veins forked at the sori, sterile veins forked. *Sori* medial; paraphyses longer than the sporangia, receptacle villous.

Trichipteris microdonta is similar to *T. nigra* in superficial appearance and geographical distribution. However, *T. nigra* lacks the sharp spines found on the pinna-rachises of *T. microdonta. Trichipteris microdonta* also lacks the pinna-like leaf apex characteristic of *T. nigra. Trichip-*



FIGS. 50–59. FIGS. 50 & 51, *Trichipteris Kalbreyeri:* 50, two central pinnules from a central pinna, × 1/3; 51, central part of a pinnule, × 1 (both *Sparre 19269,* GH). FIGS. 52 & 53, *T. Schlimii:* 52, three central pinnules from a central pinna, × 1/3; 53, central part of a pinnule, × 4/3 (both *Steyermark & Dunsterville 104380,* GH). FIGS. 54 & 55, *T. Wendlandii:* 54, three central pinnules from a central pinna, × 1/3; 55, central part of a pinnule, × 4/3 (both *Nisman 77,* GH). FIGS. 56 & 57, *T. nigra:* 56, three central pinnules from a central pinna, × 1/3; 57, central part of a pinnule, × 4/3 (both *Schultes & Cabrera 12798,* GH). FIGS. 58 & 59, *T. pauciflora:* 58, three central pinnules from a central pinna, × 1/3; 59, central part of a pinna, × 4/3 (both *Tschudi 169,* VEN).



FIGS. 60–71. FIGS. 60–64, *Trichipteris frigida*: 60, three central pinnules from a central pinna, × 1/3 (*Tryon & Tryon 5914*, GH); 61, three central pinnules from a central pinna typical of plants from lower altitudes, × 1/3 (*Weberbauer 2272*, USM); 62, central part of a pinnule, × 4/3 (same as 60); 63, a costal squamule, × 12 (*Cuatrecasas 5604*, F); 64, a single lobe of a pinnule, × 4/3 (same as 60). FIGS. 65–68, *T. pubescens*: 65, three central pinnae, × 1/3 (*Buchtien 5304*, GH); 66, central part of a pinnule, × 4/3 (*Ferreyra 16678*, GH); 67, abaxial and adaxial surfaces of a single lobe, × 4/3 (same as 66); 68, stem apex, × 2/3 (*Maguire 27729*, NY). FIGS. 69–71, *T. phegopteroides*: 69, three central pinnae, × 1/3 (*Spruce 4020*, US); 70, central part of a pinna, × 4/3 (*Spruce 4028*, GH); 71, abaxial and adaxial surfaces of a single lobe, × 4/3 (same as 70).

teris nigra is most closely allied to *T. Wendlandii* and *T. Schlimii.* It is conceivable that *T. Wendlandii* and *T. nigra* arose through isolation of peripheral populations of a previously continuous species. Variation in the serration of the lobes as well as in the coloring of the petiole scales and the density of the petiole scurf is typical of *T. nigra.* It is a species of the Amazon Basin, ranging from northern Brazil and Venezuela to Bolivia, from 100 to 1000 meters in altitude. It is one of three tree ferns (including *T. microdonta* and *T. procera*) that are found in the moist lowland forests of the Amazon Basin.

The typification of two synonyms of *Trichipteris nigra* is complicated by the not unexpected confusion of the Spruce collections. Although Rosenstock was working with *Spruce 4249* and *4349* when he was describing *Alsophila tarapotensis,* it is apparently possible that *Spruce 4349* is in reality a mislabeled *Spruce 4249.* According to a letter at US (Lellinger, pers. comm.) Bentham's list of Spruce's collections indicates that *Spruce 4349* is a "Cornidia." The homonym *Alsophila nigra* Jenman pertains to another genus. It is *Nephelea Imrayana* var. *Imrayana.*

SELECTED COLLECTIONS. **Venezuela. Bolívar:** frontier with Brazil, NE of the Serranía Piasoi (Pia-shauhy, Pia-Savi), *Steyermark 90662* (GH,NY,VEN). **Colombia. Caquetá:** 20 km. S of Montanita, *Madison 1185* (GH); Hetuchá, on the Río Orteguaza, *Woronow & Juzepczuk 6129* (US). **Vaupés:** Mitú, on the Río Vaupés, *Arbeláez & Cuatrecasas 6776* (GH,US); Río Vaupés to Cerro Mitú, *Lockwood 610* (GH). **Putumayo:** Río Putumayo, Puerto Ospina, *Cuatrecasas 10579* (F); 13 km. S of Umbria, near Finca Santa Marta, *Plowman 2073* (GH). **Amazonas:** mouth of Río Pacoa, Río Apoporis, *Schultes & Cabrera 13091* (GH,US); vicinity of Letícia, Río Amazonas, *Schultes, Raffauf, & Soejarto 24025, 24062* (GH). **Ecuador. Napo:** Río Napo, Panacocha, *Harling, Storm & Ström 7566* (GH). **Peru. Amazonas:** Quebrada Chuivi, valley of Río Marañón near Cascadas de Mayasi, *Wurdack 1927* (GH,US). **Loreto:** Iquitos, *Killip & Smith 26944* (F,US); Santa Rosa, lower Río Huallaga below Yurimaguas, *Killip & Smith 28781* (F,US). **San Martin:** Tingo María, *Allard 20607* (GH,US); SE of Nuevo Progresso, Dtto. Uchiza, *Schunke 3152* (GH). **Junín:** Pichis trail, Santa Rosa, *Killip & Smith 26169* (GH,NY); Puerto Yessup, *Killip & Smith 26374* (F,NY). **Bolivia. La Paz:** Charopampa, *R. S. Williams 1336* (GH). **Brazil. Amazonas:** near mouth of Rio Embira, tributary of Rio Tarauccá, basin of the Rio Jurua, *Krukoff 4937* (F,GH,MO,US); Mun. São Paulo de Olivenca, near Esperança, basin of the Rio Javary, *Krukoff 7527* in part (US); Tefé, *Piers 1299* (US).

20. **Trichipteris pauciflora** (Kuhn) Tryon

FIGS. 58, 59. MAP 20.

Trichipteris pauciflora (Kuhn) Tryon, Contrib. Gray Herb. **200**:46. 1970.
Cyathea pauciflora Kze., Bot. Zeit. **4**(6):101. 1846. *nom. nud.*
Alsophila pauciflora Presl, Gefässbündel Stipes der Farrn 35. 1847. (preprint from Abh. Bohm. Ges. **5**(5):343. 1848) *nom. nud.* COLLECTION CITED: Pl. Columb. Exsiccatae, *Karsten,* B!
Alsophila pauciflora Kuhn, Linnaea **36**:156. 1869. HOLOTYPE: Puerto Cabellos, *Karsten 185,* B! ISOTYPE: fragment ex PR, NY!
Alsophila hypolampra Kuhn, Linnaea **36**:158. 1869. SYNTYPES: Merida, *Funck & Schlim 1571,* B! Río Tocarema, Nova Grenada, *Lindig 243,* B!
Cyathea hypolampra (Kuhn) Domin, Pteridophyta 262. 1929.
Alsophila novagranadensis Domin, Pterid. Dominica 97 t. 10 f. 13–15. 1929. HOLO-

TYPE: in New Grenada, Tocarema, Andes of Bogotá, alt. 2200 m, *Lindig 243,* K not seen. ISOTYPE: B!

Stem 1.2–9.0 m. tall. *Petiole* to 0.7 m. long, stramineous to fulvous, inermous to muricate; scales fulvous; scurf of fulvous trichomidia and small to large squamulae; rachis, pinna-rachises, and costae with sparse trichomes and spreading, erect, more or less erose, fulvous squamulae; costules with bullate, fulvous squamulae; veins with trichomes and occasionally bullate squamulae. *Lamina* 1.0–3.5 m. long, 2-pinnate-pinnatifid, papyraceous to rigidly coriaceous, apex gradually reduced and acute; pinnae sessile; pinnules sessile to short-petiolulate, pinnatisect, base cordate to truncate, apex attenuate, tip crenulate to serrate; lobes rotund to acute, entire to crenulate; fertile veins forked at the sori, sterile veins forked. *Sori* inframedial, often confined to the basal portion of the lobe, paraphyses as long as the sporangia, receptacle hirsute.

The sori are in many cases limited to the basal third of the segments, perhaps explaining the species epithet. *Trichipteris pauciflora* lacks the laciniate squamulae of the related *T. frigida* and it has trichomes on the lamina axes. High altitude specimens of *T. pauciflora* are extremely coriaceous and have revolute segments. The two syntypes of *Alsophila hypolampra* Kuhn represent the two morphological extremes to be found in *T. pauciflora. Funck & Schlim 1571* is the basal portion of a medial pinna from a vigorous specimen with coriaceous leaves, probably found in full sun. *Lindig 243* is a nearly complete pinna from near the apex of a leaf of a more typical plant for the species, probably growing in a shadier area than the last. The range of the species includes the Andes of Venezuela from Aragua to Tachira, and a single collection from the area of Bogotá, Colombia. It is found in cloud forests and "elfin" forests along mountain crests from 750 to 3350 meters. Poeppig collections from Peru determined as *Cyathea pauciflora* Kze. are *Cyathea Delgadii* Sternberg.

SELECTED COLLECTIONS. **Venezuela. Lara:** Distrito Palavecino, S of Terepaima, 20 km. S of Cabudare, *Steyermark, Delascio & Dunsterville 103334* (GH,NY). **Yaracuy:** El Amparo to Candelaria, 7 km. N of Salom, *Steyermark 106209, 106780* (GH). **Carababo:** Río San Gián, E of Los Tanques, S of Borburata, *Steyermark 95396* (GH). **Aragua:** Rancho Grande, Parque Nacional "H. Pittier," *Tschudi 135* (fragment US, VEN); *Tschudi 169* (fragment US,VEN). **Táchira:** Po. El Batallon, *Vareschi 5386* (VEN); about 5 km. down road to Queniquea from road intersection at Zumbador, *White & White 197068* (US). **Colombia. Cundinamarca:** Bogotá, 2700 m., *Lindig 240* (GH).

21. **Trichipteris frigida** (Karst.) Tryon

FIGS. 60–64. MAP 21.

Trichipteris frigida (Karst.) Tryon, Contrib. Gray Herb. 200:45. 1970.
Alsophila frigida Karst., Fl. Columb. 1:61 t. 30. 1859. HOLOTYPE: Andes of Bogotá, Colombia, 2600 m., *Karsten,* fragment ex B, NY!
Cyathea frigida (Karst.) Domin, Pteridophyta 262. 1929.

Stem creeping or ascending, to 4 m. tall. *Petiole* ca. 0.8 m. long, fuscous to atropurpureous, tuberculate; scales fuscous with a fulvous border, or rarely fulvous with a cretaceous border; scurf of long, contorted, cretaceous trichomidia and squamulae; axes of lamina covered with a dense tomentum of contorted, cretaceous trichomidia and a few scales similar to those of the petiole, or the tomentum of trichomidia sparse to absent on the costae and costules and the scales and squamulae deeply fimbriate and contorted into a tomentum. *Lamina* ca. 0.5–2.0 m. long, 2-pinnate-pinnatifid, coriaceous, apex gradually reduced and acute; pinnae sessile to stalked; pinnules sessile to short-petiolulate, pinnatisect to pinnatisect and deeply divided, base truncate, apex attenuate, tip entire and obtuse; lobes rotund, entire to deeply crenate, revolute; fertile veins forked at the sori, sterile veins forked. *Sori* inframedial to medial; paraphyses shorter than the sporangia or the same length, receptacle pilose to hirsute.

Trichipteris frigida is a species that varies considerably with altitude and exposure, but can be distinguished throughout its range by the light-colored tomentum of contorted trichomidia (occasionally replaced entirely by fimbriate squamulae on the costae and costules). In addition, it lacks the trichomes typical of *T. pauciflora*, its nearest ally. The color of the petiole-scale border, the development of the tomentum, the dissection of the squamulae, and the coriaceousness and revoluteness of the segments are all variable. The size and dissection of the segments is also variable. *Trichipteris frigida* occurs in the Venezuelan Andes, the eastern cordillera of Colombia, the Andes of Ecuador, and the Atlantic slopes of the Andes in Peru, always at extremely high altitudes (2500–3500 meters). It is found occasionally in cloud forests, but more often in shrubby situations, "paramillo," and shrubby páramo. An herbarium name honoring Weberbauer has been applied to less coriaceous, less revolute leaves from lower altitudes. No other species of *Trichipteris* is commonly found in the páramos.

SELECTED COLLECTIONS. **Venezeula. Tachira:** just below Páramo de Tama, near the Colombian-Venezuelan border, *Steyermark & Dunsterville 98617* (GH). **Colombia. Cundinamarca:** Macizo de Bogotá, Quebrada de las Delicias, *Cuatrecasas 5604* (F, GH); Montserrate, above Valle de Bogotá, *Ewan 16898* (GH,US). **Valle:** Cordillera Occidental, Los Farallones, extremo N, vertiente NW, entre Alto del Buey y Quebrada de los Ramos, *Cuatrecasas 18032* (F,US). **Ecuador. Azuay:** between Huagrarancha & Loma de Galápagos, *Steyermark 53461* (F). **Peru. Huánuco:** Cerros al Sudoeste de Monzón, *Weberbauer 3389* (USM). **Junín:** cerros al oeste de Huacapistana, entre Tarma y San Ramón, *Weberbauer 2272* (P,USM).

22. **Trichipteris pubescens** (Baker) Tryon

FIGS. 65–68. MAP 22.

Trichipteris pubescens (Baker) Tryon, Contrib. Gray Herb. 200:46. 1970.

Alsophila pubescens Baker, Syn. Fil. ed. 1. 449. 1868. LECTOTYPE (chosen herewith): Peru, *Spruce 4712*, fragment ex K, NY! ISOLECTOTYPES: GH! NY! P! LECTOPARATYPES: Peru, *Lechler 2190*, fragment ex K, NY! New Grenada, *Purdie*, fragment ex K, NY! ISOLECTOPARATYPES: *Lechler 2190*, fragments ex B & P, NY!

Alsophila bipinnatifida Baker, Syn. Fil. ed. 2. 456. 1874. HOLOTYPE: British Guiana, *Appun 1032*, fragment ex K, NY! ISOTYPE: P! (with *Glaziou 12375*).

Polypodium bipinnatifidum (Baker) Jenm. Ferns Brit. W. Ind. Guiana 281. 1908, not Baker 1890.

Cyathea bipinnatifida (Baker) Domin, Pteridophyta 262. 1929.

Cyathea pubens Domin, Pteridophyta 263. 1929. *nom. nov.* for *Alsophila pubescens* Baker, not *Cyathea pubescens* Kuhn, Linnaea 36:164. 1869.

Stem 0.6–4.0 m. tall. *Petiole* 20–30 cm. long, stramineous to fulvous, inermous;

scales fulvous with a lighter border; scurf of cretaceous trichomidia and squamulae; rachis and pinna-rachises with cretaceous trichomidia, trichomes, and minute fulvous squamulae; costae and costules with cretaceous trichomidia and bullate, fulvous squamulae; veins and leaf surface with trichomes. *Lamina* to 1.0 m. long, 1-pinnate-pinnatifid, papyraceous to chartaceous, apex gradually reduced and acute to acuminate; pinnae adjacent, sessile to petiolulate, base truncate, apex acuminate to attenuate, tip entire; lobes rotund, serrulate to entire; fertile veins forked at the sori or simple, sterile veins forked or simple. *Sori* inframedial to subcostal; paraphyses as long as the sporangia, receptacle hirsute.

Trichipteris pubescens is an unusually broad-ranging diminutive species. It is the only species in which adventitious buds develop into branches. The stems, which are approximately 3 cm. in diameter, are thin in relation to their height. This species is most closely related to the little-known *T. phegopteroides* of eastern Peru. It is tentatively possible to associate *T. pubescens* with *T. nigripes* and similar species on the basis of venation, paraphyses and geography. The pubescence of the lamina is highly variable within the species. In the area of Puno, Peru, the plants collected are densely pubescent. Nearly glabrous plants have been found in the northern part of the range and in Bolivia. Hieronymus established a variety, named in honor of Spruce, for specimens of *Alsophila pubescens* Baker with scant pubescence. However, variation in pubescence is not correlated with geography sufficiently to merit the recognition of infraspecific taxa. *Trichipteris pubescens* occurs in the Guayana Highlands and the Atlantic slopes of the Andes from Colombia to Bolivia. It is found in talus slope forests, cloud forests, and mossy, wet montane, or "elfin" forests from 1200 to 2500 meters.

SELECTED COLLECTIONS. **Venezuela. Bolívar:** Cerro Venamo, SW part, frontier of Guyana, *Steyermark 92720* (GH,VEN); Chimantá Massif, Toronótepuí, *Steyermark & Wurdack 1078, 1242* (GH,NY,US,VEN). **Amazonas:** Serranía Parú, Río Parú, Caño Asisa, Río Ventauri, *Cowan & Wurdack 31391* (GH,NY,US); Serranía Yutaje, Río Manapiare, *Maguire & Maguire 35297* (GH,NY,US); Cerro Sipapo (Paráque), *Maguire & Politi 27729* (NY,US). **Colombia. Huila:** SW of Alejandría at Río Sauza, *Little 8496* (US). **Ecuador. Napo-Pastaza:** between Baños & Jivaría de Píntuc, valley of the Río Pastaza, *Stübel 996* (fragment NY, B). **Peru. Loreto:** near La Divisoria, between Tingo María & Pucallpa, *Ferreyra 1071* (GH,USM). **Huánuco:** SW slope of Río Llulla Pichis watershed, on the ascent of Cerros del Sira, *Dudley 13019, 13026, 13046, 13371, 13413* (GH). **Junín:** Schunke Hacienda, above San Ramón, *Killip & Smith 24871* (F,US); Pichis Trail, Yapas, *Killip & Smith 25554* (US). **Cuzco:** Cordillera Vilcabamba, *Dudley 10452, 10455* (GH). **Ayachucho:** E massif of Cordillera Central, opposite Cordillera Vilcabamba, *Dudley 11941* (GH). **Puno:** valle del Alto Tambopata, near San Juan del Oro, *Ferreyra 16678, 16701, 16704* (GH). **Bolivia. La Paz:** Hacienda Simaco, on the trail to Tipuani, *Buchtien 5304* (F,GH,MO); *Buchtien 5305* (NY,US). **Cochabamba:** Yungas, *Bang 563* (GH,NY); Kuriloma, near San Onofre, *Steinbach 9331* (F,GH,MO,NY,US).

23. **Trichipteris phegopteroides** (Hook.) Tryon

FIGS. 69–71. MAP 23.

Trichipteris phegopteroides (Hook.) Tryon, Contrib. Gray Herb. 200:46. 1970.
Alsophila phegopteroides Hook., Syn. Fil. ed. 1. 32. 1865. HOLOTYPE: Peru, Tarapoto, *Spruce 4020*, K not seen. ISOTYPES: P! US!
Cyathea phegopteroides (Hook.) Domin, Pteridophyta 263. 1929.

Stem unknown. *Petiole* 3–6 cm. long, fuscous to atropurpureous, tuberculate to muricate; scales fuscous with a fulvous border; scurf of cretaceous trichomes (absent from the petiole base); axes of lamina with a dense indument of cretaceous trichomes, rachis and pinna-rachises with small scales and large, flattish squamulae similar in color to the petiole scales. *Lamina* ca. 0.5 m. long, 1-pinnate-pinnatifid, chartaceous, apex gradually reduced and acute; pinnae adjacent, sessile, deeply pinnatifid to pinnatisect, base truncate, apex attenuate; lobes rotund and entire; fertile veins forked at the sori, sterile veins forked. *Sori* medial; paraphyses shorter than the sporangia, receptacle pilose.

Trichipteris phegopteroides differs from *T. pubescens* in having spines on the petiole and numerous fuscous scales on the rachis. The two can be associated with the group of *T. nigripes* on the basis of petiole scale coloration, paraphyses length, and geography. The type collection and the other known collection were both made by Spruce at about 350 meters on the eastern slopes of the Andes in northern Peru.

SELECTED COLLECTIONS. **Peru. San Martín:** Mt. Guayrapurima, near Tarapoto, *Spruce 4028* (GH,NY). **Province unknown:** *Lechler* (F).

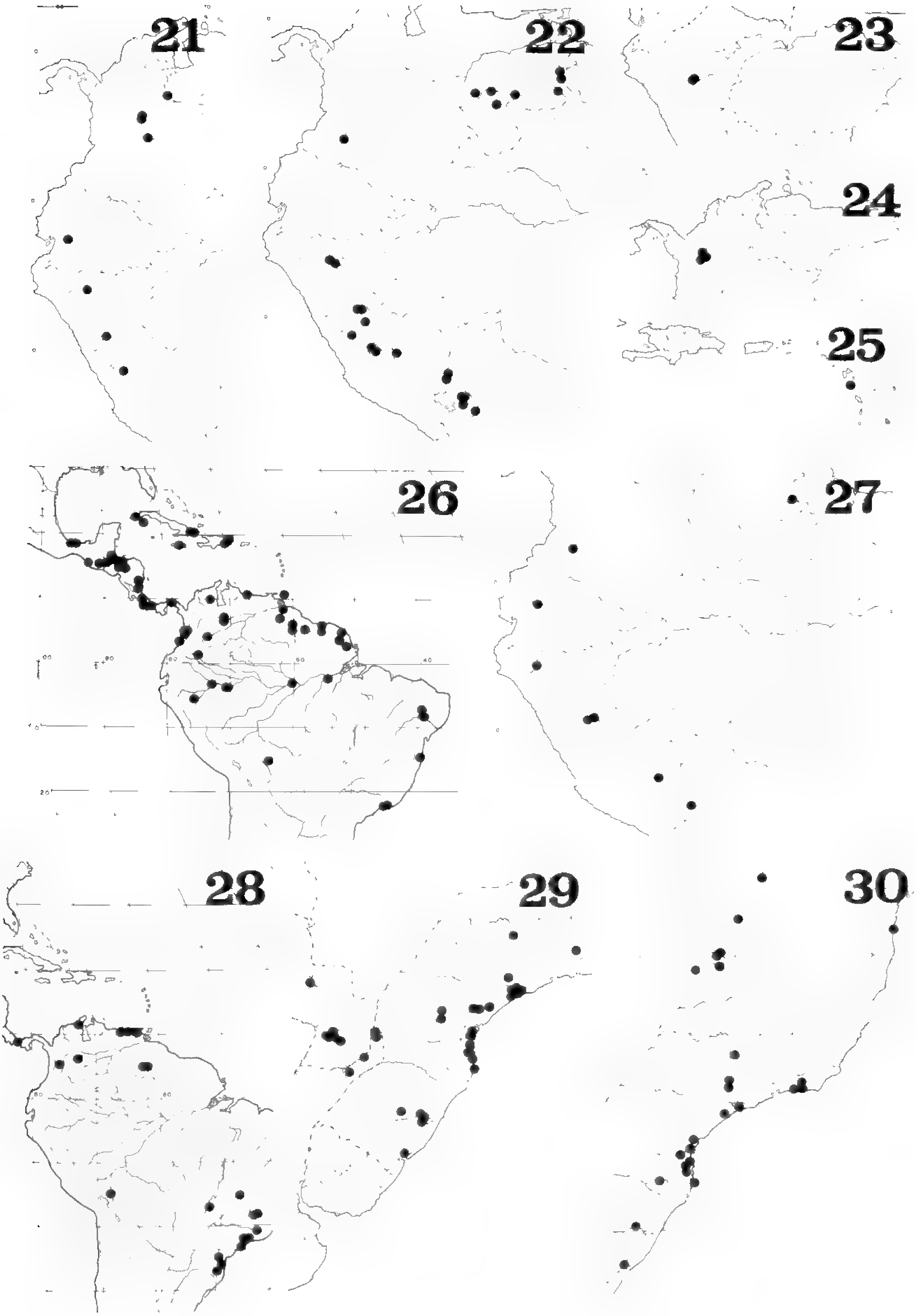
24. **Trichipteris latevagans** (Baker) Tryon

FIGS. 72, 73. MAP 24.

Trichipteris latevagans (Baker) Tryon, Contrib. Gray Herb. **200**:45. 1970.
Alsophila latevagans Baker, Journ. Brit. & For. **19**:203. 1881, *ex char.* HOLOTYPE: open forests, 6700′, Antioquia, Colombia, *Kalbreyer 1327,* K not seen.
Cyathea latevagans (Baker) Domin, Pteridophyta 262. 1929.

Stem fasciculate, to 10 cm. tall, often creeping. *Petiole* 20–35 cm. long, atropurpureous, inermous to tuberculate; scales fuscous with a fulvous border; scurf absent; pinna-rachises occasionally with flattish or bullate fulvous squamulae, axes of lamina normally glabrous. *Lamina* to 1.0 m. long, 1-pinnate-pinnatifid, chartaceous to coriaceous, apex gradually reduced and long-acuminate; pinnae remote, long-petiolulate, pinnatisect, base truncate or subcordate, apex acuminate, tip entire; lobes acute, entire or serrulate; fertile veins forked at the sori, sterile veins forked. *Sori* inframedial to subcostal; paraphyses shorter than the sporangia, receptacle pilose.

Trichipteris latevagans is distinguished by its atropurpureous axes and long-stalked, deeply pinnatifid pinnae with entire lobes. I have tentatively placed this species with the group of *T. nigripes,* based on venation and paraphyses characters. There is some variation in the size of the pinna segments. *Trichipteris latevagans* is interesting because of its endemic and atypical distribution. It is found in cloud forests and pastures cleared from cloud forest, only in the upper part of the Río Cauca valley, between the Cordillera Central and the Cordillera Occidental, in Colombia (from 1800 to 2000 meters). *Trichipteris* in Colombia is represented by species with either Pacific coastal or eastern cordilleran distributions. The intermontane valley distribution of *T. latevagans* is as unusual as its morphology. Baker included a question mark before "latevagans" in his description of the species, apparently because the species was so atypical of the Alsophilas known to him.



Maps 21–30: 21, Trichipteris frigida; 22, T. pubescens; 23, T. phegopteroides; 24, T. latevagans; 25, T. Hodgeana; 26, T. microdonta; 27, T. Lechleri; 28, T. villosa; 29, T. atrovirens; 30, T. phalerata var. phalerata.

SELECTED COLLECTIONS. **Antioquia:** Ventanas (Camino a Valdivia), *Bro. Daniel* 3398 (US); near Amalfi, *Lehmann* 35 (GH,NY,US); 19 km. N of Yaramul, *Madison* 816 (GH); Tolima? *Schmidtchen* (US).

25. **Trichipteris Hodgeana** (Proctor) Tryon

FIGS. 74, 75. MAP 25.

Trichipteris Hodgeana (Proctor) Tryon, Contrib. Gray Herb. 200:44. 1970.
Cyathea Hodgeana Proctor, Rhodora 63:31. 1961. HOLOTYPE: Dominica, Pegoua River, *Hodge & Hodge 3420*, GH! ISOTYPE: US!

Stem 4.5 m. tall. *Petiole* more than 0.3 m. long, fulvous, barely tuberculate; scales uniformly fulvous; scurf of contorted fulvous trichomidia and squamulae; all axes of lamina with a scurfy tomentum similar to that of the petiole; costal squamulae flattish, lanceolate; costular squamulae bullate. *Lamina* ca. 1.0 m. long, 2-pinnate-pinnatifid, papyraceous, apex gradually reduced and acute; pinnae stalked; pinnules petiolulate, deeply pinnatifid, base truncate, apex acuminate; lobes truncate, entire to barely crenulate; fertile veins usually forked at the sori, sterile veins forked or simple. *Sori* medial to supramedial; paraphyses as long as the sporangia, receptacle hirsute.

In addition to the characters included in the key, *Trichipteris Hodgeana* is characterized by tuberculate petioles and small pinnules (ca. 6 cm. long). Based on the petiole scales, scurf, venation, and the length of the paraphyses, *T. Hodgeana* is allied to *T. nigripes* and associated species. However, the species has no close allies in the group. The absence of well-developed spines and the development of a tomentum of trichomidia distinguish *T. Hodgeana* from related species. *Trichipteris Hodgeana* is one of the few species in the genus that is endemic to a single island. Its habitat is described as moist forests along rivers.

26. **Trichipteris microdonta** (Desv.) Tryon

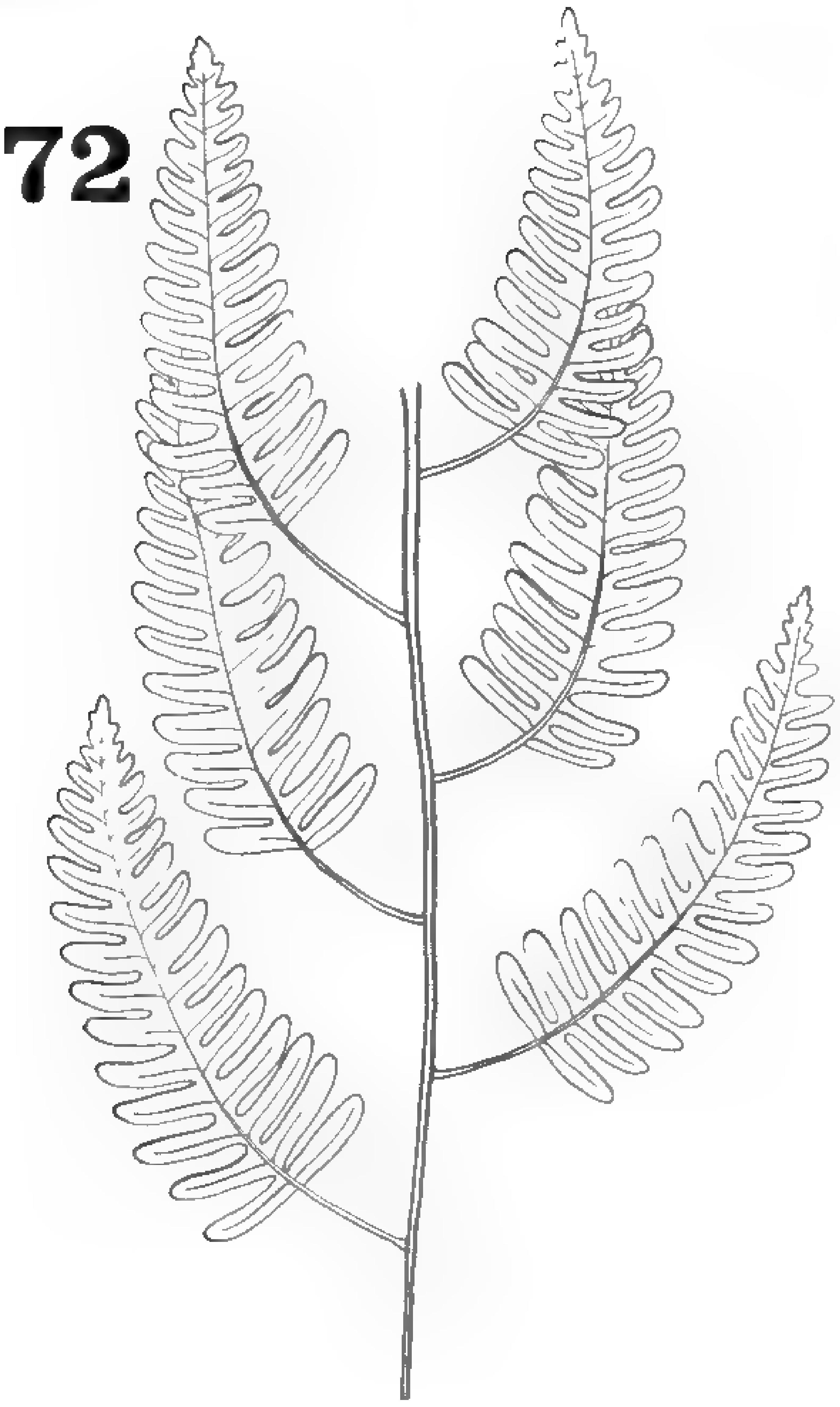
FIGS. 76–78. MAP 26.

Trichipteris microdonta (Desv.) Tryon, Contrib. Gray Herb. 200:46. 1970.
Polypodium microdonton Desv., Ges. Naturf. Freunde Berl. Mag. 5:319. 1811. HOLOTYPE: America australi, *Desvaux*, P! (Herb. Desv.).
Alsophila microdonta (Desv.) Desv., Mém. Soc. Linn. Paris 6:319. 1827.
Cyathea microdonta (Desv.) Domin, Pteridophyta 263. 1929.
Polypodium aculeatum Raddi, Opusc. Sci. Bologna 3:288. 1819 and Pl. Bras. 1:27 t. 42. 1825, *ex icone*. HOLOTYPE: mountains of Rio de Janeiro, *Raddi*, FI not seen.
Alsophila aculeata (Raddi) J. Sm., London Journ. Bot. 1:667. 1842.
Alsophila armata Mart., Icon. Plant. Crypt. Bras. 72 t. 28, 48. 1834 *nom. nov.* for *Polypodium aculeatum* Raddi, Pl. Bras. 1:27 t. 42. 1825, not *Polypodium aculeatum* L., Sp. Pl. 2:1090. 1753, not *Alsophila armata* (Sw.) Presl, Tent. Pterid. 62. 1836.
Alsophila ferox Presl, Tent. Pterid. 62. 1836, *nom. illegit.* a renaming of *Alsophila armata* Mart.

Stem to 6.0 m. tall. *Petiole* 0.6–1.8 m. long, fulvous to atropurpureous, aculeate or rarely tuberculate; scales uniformly fuscous to fulvous; scurf absent or of fulvous trichomidia; rachis and pinna-rachises aculeolate, rachis glabrous or with trichomidia; pinna-rachises, costae, and costules with flattish to bullate, cretaceous to fuscous squamulae; veins glabrous or with a few trichomidia. *Lamina* 1.0–2.5 m. long, 2-pinnate-pinnatifid, papyraceous, apex gradually reduced, acute to acuminate; pinnae short-stalked; pinnules short-petiolulate, deeply pinnatifid to pinnatisect, base truncate, apex attenuate, tip serrate to crenulate; lobes acute, serrate to crenulate; fertile veins forked at the sori, sterile veins forked. *Sori* medial; paraphyses the same length as the sporangia or longer, receptacle villous.

Trichipteris microdonta is the most widely distributed species in the genus. The pinna-rachis spines are distinctive. *Trichipteris nigra,* though superficially similar to *T. microdonta,* lacks these spines. Similar species among the group of *T. armata* also lack pinna-rachis spines and are generally hairy with stiff, multiseriate trichomes. *Trichipteris microdonta* is nearly uniform in leaf architecture and indument throughout its range. Specimens from Brazil are substantially the same as specimens from Mexico. Widespread uniformity is unusual in *Trichipteris,* a genus of highly variable species. *Trichipteris microdonta* ranges from the coastal regions of Central America and the Greater Antilles along the northern and eastern coasts of South America, including the Amazon Basin, as far south as Rio de Janeiro. It is found from sea level to 1700 meters in swamps and bogs, along riverbanks, and in standing fresh or brackish water. The unusual ecology of *T. microdonta* may be, in part, the reason for its peculiar homogeneity, since lowland and coastal forests extend in an almost unbroken band from Mexico to Brazil.

SELECTED COLLECTIONS. **Mexico. Veracruz:** Chinameca, *Orcutt 3194* (MO); Coatzacoalcos, isthmus of Tehuantepec, *C. L. Smith 2095* (F,GH,MO). **Chiapas:** Acacoyagua, *Matuda 17434* (F,GH); Santo Domingo de Palenqué, *Seler 5515* (GH). **Guatemala. Alta Verapaz:** Chama, *Johnson 953* (F,GH). **Izabal:** vicinity of Quiriguá, *Standley 23785* (F,GH,MO); between Virginia & Lago Izabal, Montaña de Mico, *Steyermark 38785* (F). **Honduras. Atlántida:** vicinity of Tela, *Standley 54722* (F,GH); near Salado, vicinity of La Ceiba, *Yuncker, Koepper & Wagner 8347* (F,MO). **Cortés:** Agua Azul, on the shores of Lake Yojoa, *Morton 7602* (US). **Morazán:** above Zamorano Valley, *Barkley & Hourcade 39641* (GH); El Quebracho, above El Zamorano, *Standley 343* (F); along Quebrada El Gallo above El Jicarito, *Standley 22464* (F). **Nicaragua. Bluefields:** area of Bahía de Bluefields, Río Escondido, *Molina R. 1809* (F,GH); along Caño Hendy (a branch estuary of Río Escondido, NNW of Bluefields), *Proctor, Jones & Facey 27179* (NY). **San Juan del Norte (Greytown):** *C. L. Smith 2034* (GH). **Costa Rica. Herédia:** La Virgen, E side of Río Sarapiqui, *Stone 2076* (GH). **Limón:** Los Diamantes, USDA rubber plant station, *Scamman 5889, 7008* (GH). **San José:** San Isidro del General, *Nisman 176* (GH). **Cartago:** San Juan del Norte, *Scamman 7590* (GH). **Panama. Bocas del Toro:** Almirante, N of Dos Millas, *McDaniel 5134* (MO). **Panama:** 2 mi. E of Juan Díaz, *Killip 2540* (GH). **Canal Zone:** 5 mi. NW of Cocoli, *Tyson 1618* (GH,MO). **Cuba. Habana:** Isle of Pines, near San Pedro, *Britton, Wilson & Selby 14329* (F,GH). **Pinar del Río:** Herradura, *Barser & Dinnoch 4849* (F); S of Viñales, *Eiten 1024* (NY). **Oriente:** *Wright 1062* (MO). **Jamaica:** *Smith* (GH ex K). **Dominican Republic. Samaná:** Las Cañitas, *Abbott 2683* (GH). **Santo Domingo:** La Cumbre, Cordillera Central, *Ekman 11497* (F,GH). **Trinidad.** Toco Road, Valencia, *Britton, Coker & Rowland 1774* (F,GH,NY); *Fendler 60* (F,GH,MO,NY). **French Guiana.** Near Saül Village, along trail to Carbet Mais, near Crique Cochow, *Bierhorst FG105* (GH); near Rochambeau Airport, *Bierhorst FG124* (GH). **Surinam.** Along railway, km. 68, vicinity of sectie 0, *Maguire & Stahel 24992* (A,F,NY); near Waneweg, 25 km. S of Paramaribo, *Tryon & Kramer 5597* (GH,NY). **Guyana (British Guiana).** Penal settlement, *Hitchcock 17157* (GH,NY); Kurupung, *Lang & Persaud 187* (F). **Venezuela. Zulia:** Sierra de Perijá, vicinity of Quebrada Koshida, S. of Misión de Los Angeles de Tokuku, SW of Machiques, *Steyermark 99928* (GH). **Delta Amacuro:** Ibaruma, *Tamayo 3618* (VEN). **Barinas:** 32 km. SW of Santa Barbara, 15 km. NE of Punta de



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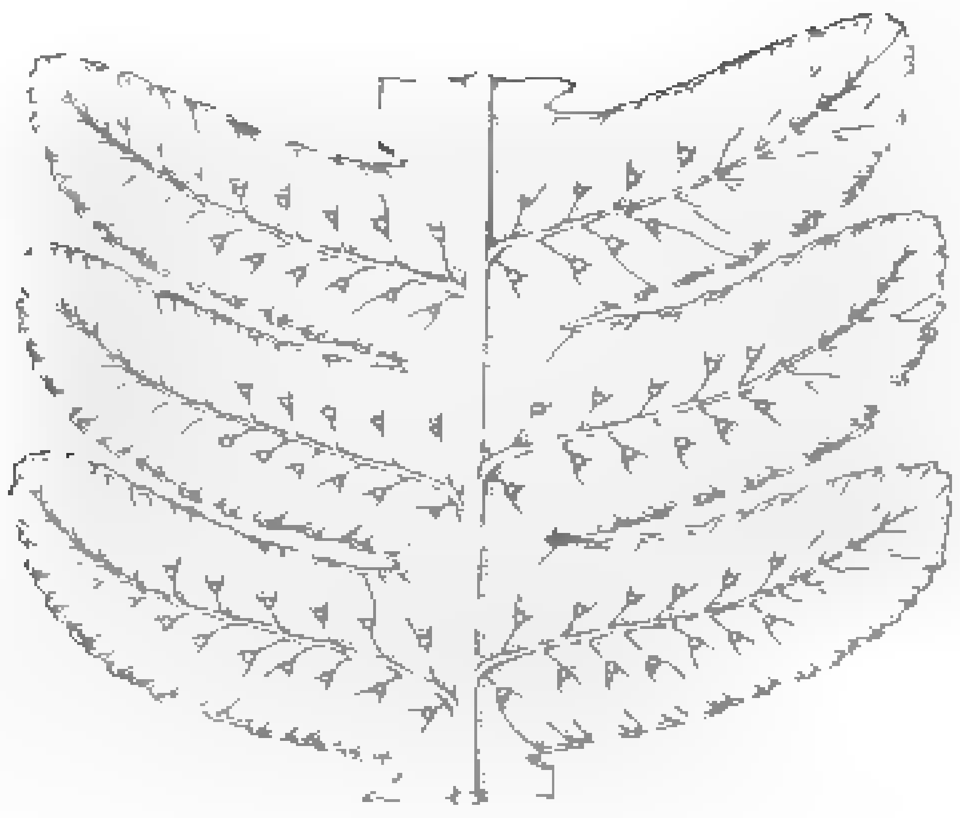

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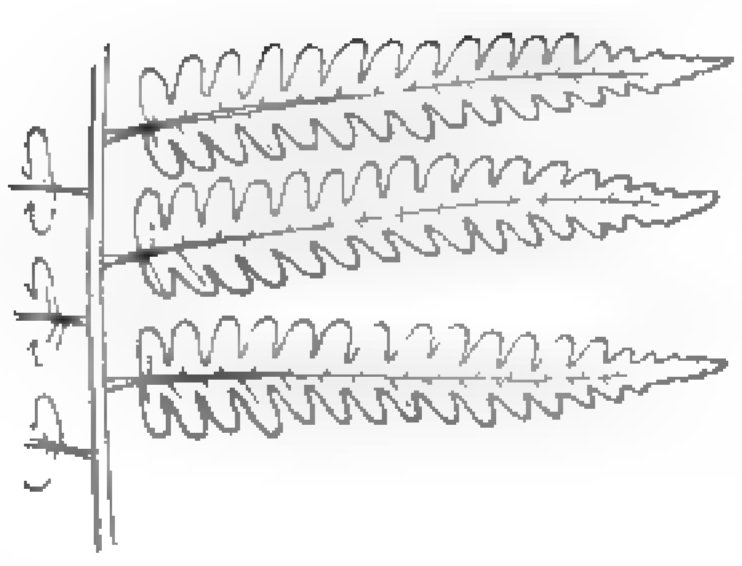

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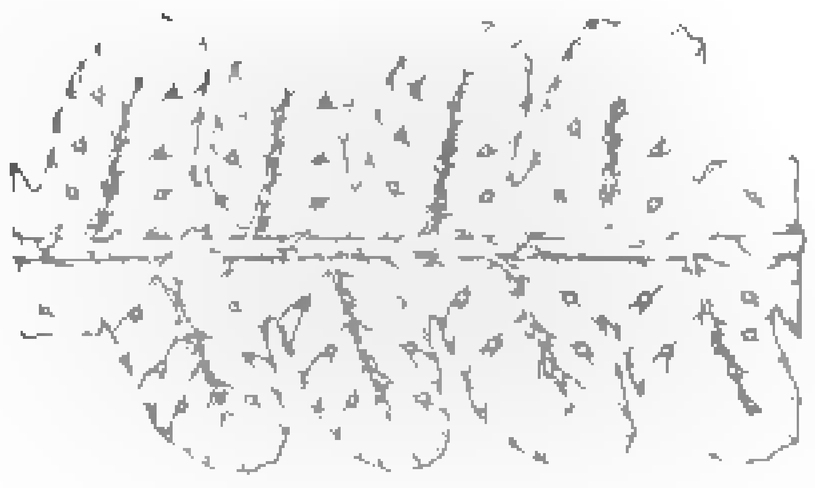

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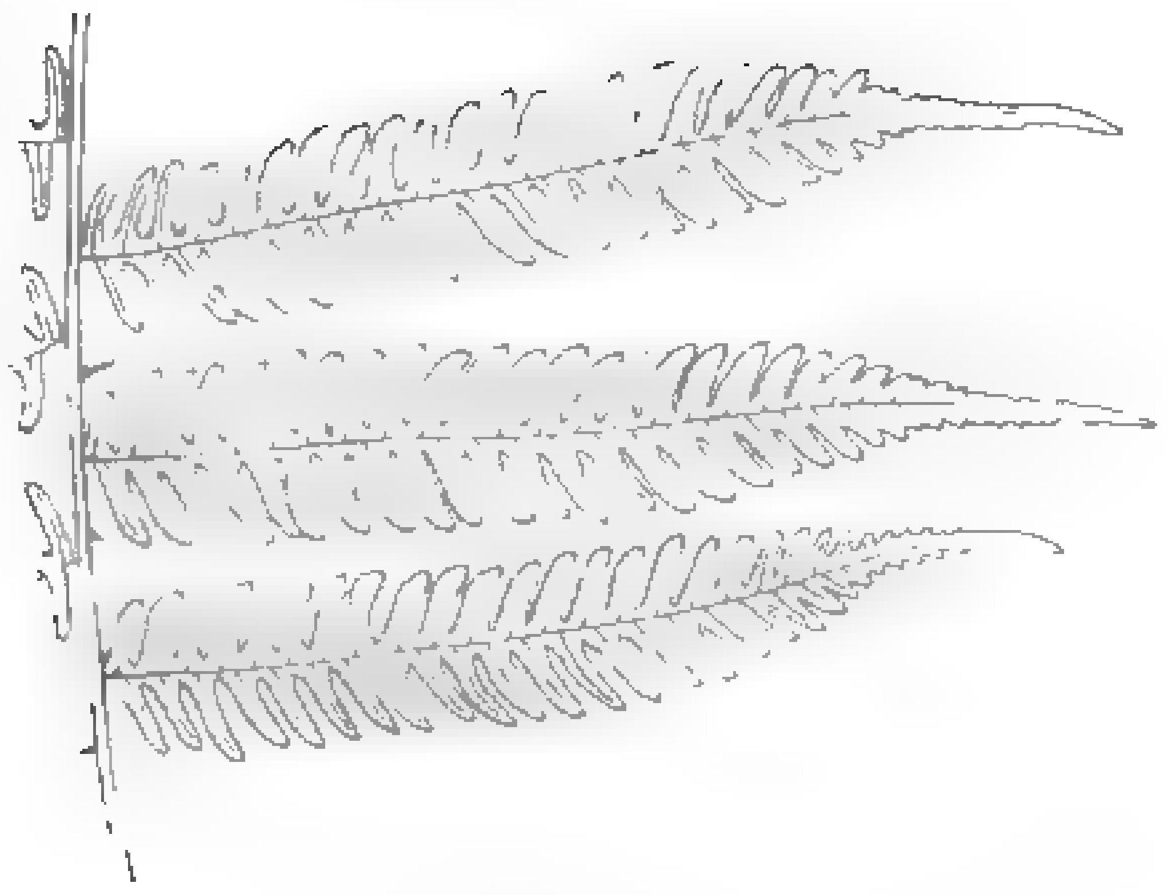

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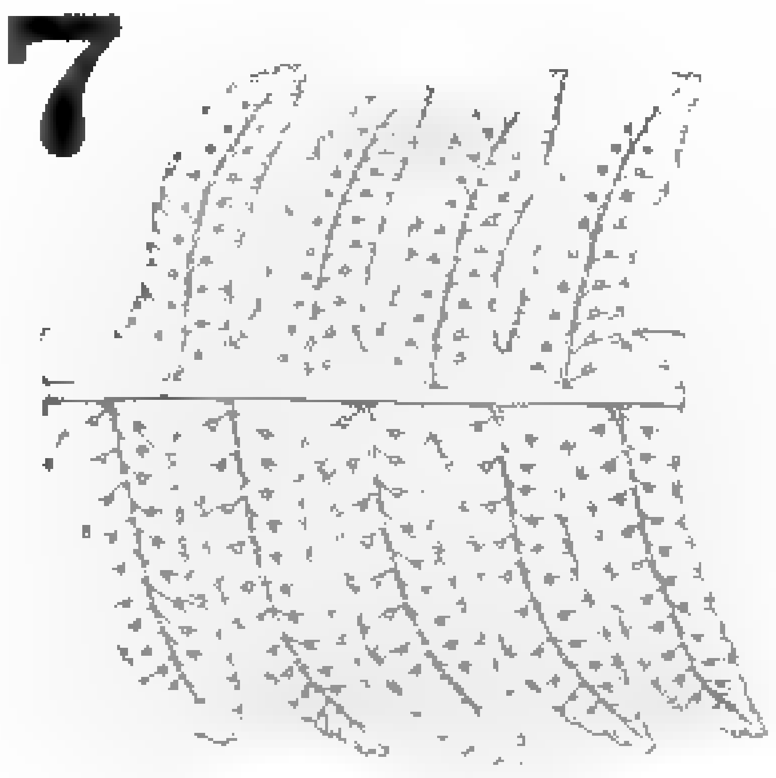

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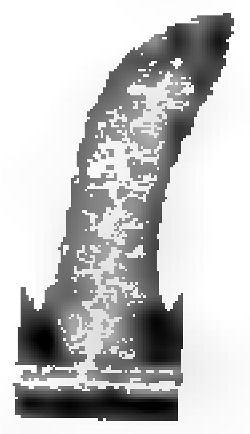

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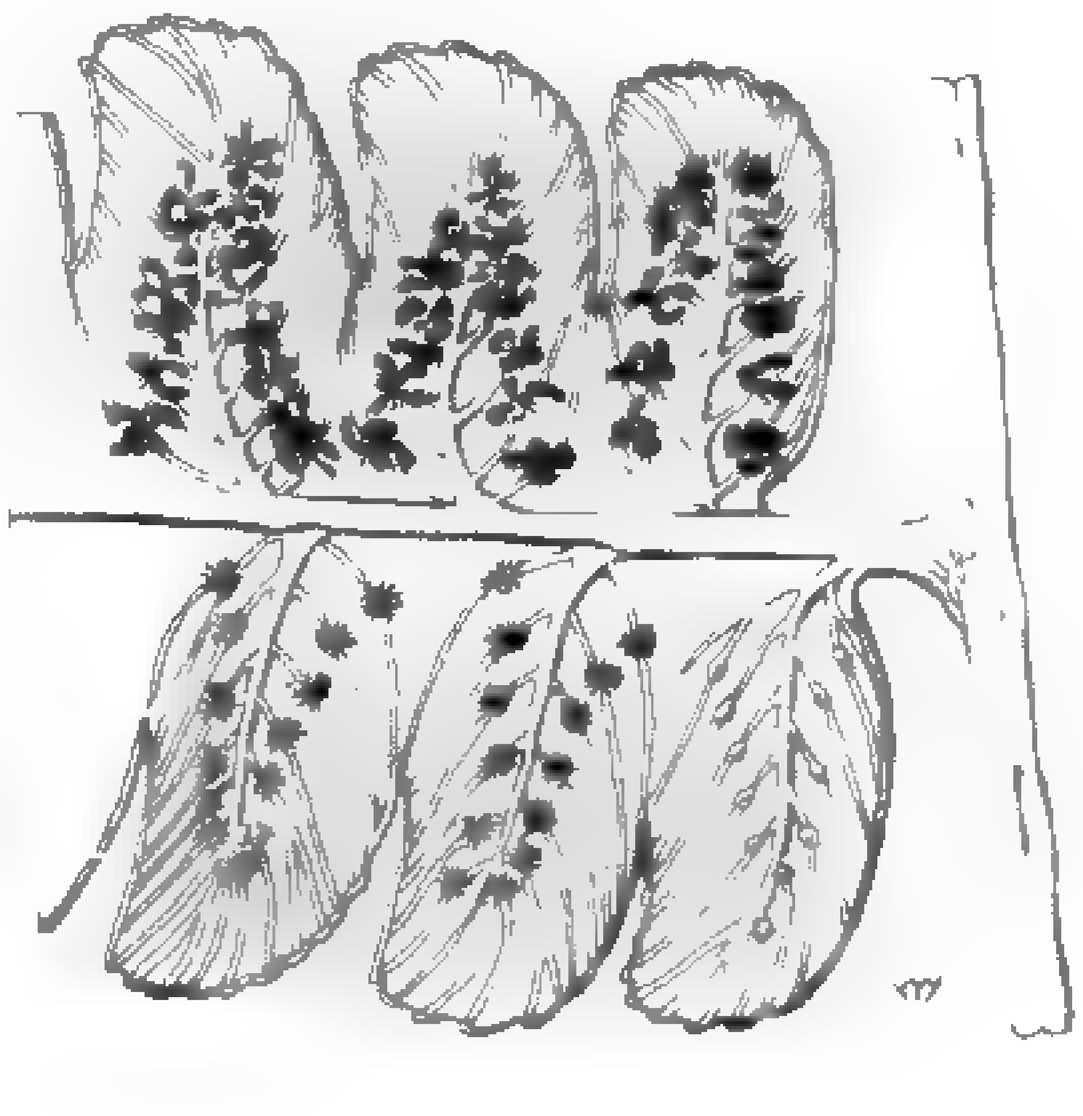

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Figs. 72–80. Figs. 72 & 73, *Trichipteris latevagans:* 72, central part of the lamina, × 1/3; 73, central part of a pinna, × 1 (both *Daniel 3398*, us). Figs. 74 & 75, *T. Hodgeana:* 74, three central pinnules from a central pinna, × 1/3; 75, central part of a pinnule, × 4/3 (both *Hodge 3420*, gh). Figs. 76–78, *T. microdonta:* 76, three central pinnules from a central pinna, × 1/3 (*Ekman 11497*, gh); 77, central part of a pinnule, × 4/3; 78, abaxial surface of a single lobe, × 4/3 (both *Tryon & Tryon 5162*, gh). Figs. 79 & 80, *T. Lechleri:* 79, two central pinnules from a central pinna, × 1/3; 80, basal part of a pinnule, × 4/3 (both *Harling, Storm & Ström 10217*, gh).

Piedra, *Steyermark & Rabe 96257, 96587* (GH). **Apure:** reserva forestal San Camilo, Río Nulita, N of San Camilo (El Nula), *Steyermark, Bunting & Blanco 101334, 101806* (GH). **Bolívar:** 5 km. from Hato de Nuria, E of Miamo, Altiplanacie de Nuria, *Steyermark 88351* (VEN). **Colombia. Valle:** road from Buenaventura road to Río Calima, *Barrington 503* (GH); Buenaventura, Quebrada de Santa Ana, El Tambo, *Cuatrecasas 21050* (F). **Meta:** along stream near Villavicencio, *Barkley & Mullen 38C026* (GH); Los Llanos, Villavicencio, *Cuatrecasas 4534* (F). **Caquetá:** 20 km. S of Montañita, *Madison 1188* (GH–sheets 2 & 3 of 3: Sheet 1 = *Trichipteris nigra* (Mart.) Tryon, probably mixed from *Madison 1185*). **Nariño:** Gorgonilla Island, *Killip & Garcia 33066* (US). **Amazonas:** Río Amazonas, vicinity of Letícia, *Schultes, Raffauf & Soejarto 24094* (GH). **Peru. Loreto:** Mishuyacu, near Iquitos, *Killip & Smith 29876* (F,GH,NY); near Iquitos, *Tryon & Tryon 5162, 5172, 5183* (F,GH). **San Martín:** near Tarapoto, *Spruce 4726* (NY). **Cuzco:** 15 mi. from Río Negro, *Vargas 15340* (GH). **Brazil. Amapá:** Rio Oiapoque area, Rio Pontanari, *Irwin, Egler & Pires 47263* (GH,NY,VEN). **Amazonas:** Manáos, *Killip & Smith 30062* (NY). **Ceará:** base of Serra do Araripe, *Duarte 1345* (MO,NY). **Pará:** Taperinha, near Santarem, *Ginzberger 486* (F); Flores, *Lützelburg 21328* (NY). **Goiás:** Mun. Puerto Nacional, *Macedo 3918* (MO). **Bahia:** São Bento, *Lützelburg 342* (F); Ilheos, *Martius* (GH,NY). **Rio de Janeiro:** *Burchell 950* (NY); Maná, in restinga, *Dusén 1938* (F,GH,NY).

27. Trichipteris Lechleri (Mett.) Tryon

FIGS. 79, 80. MAP 27.

Trichipteris Lechleri (Mett.) Tryon, Contrib. Gray Herb. 200:45. 1970.

Alsophila Lechleri Mett., Fil. Lechl. 2:28. 1859, not *Cyathea Lechleri* Mett., Fil. Lechl. 2:32. 1859. HOLOTYPE: Tatanara, Peru, *Lechler (2532)*, B! (Herb. Mett.)

Alsophila Ulei Christ, Hedwigia **44**:367. 1905. HOLOTYPE: Cerro de Ponasa, Amazonas, Peru, 1300 m., 1903, *Ule 6901*, P not seen. ISOTYPE: B!

Cyathea Ulei (Christ) Domin, Acta Bot. Bohem. 9:168. 1930.

Trichipteris Ulei (Christ) Tryon, Contrib. Gray Herb. 200:46. 1970.

Cyathea subtropica Domin, Pteridophyta 263. 1929. *nom. nov.* for *Alsophila Lechleri* Mett., Fil. Lechl. 2:28. 1859, not *Cyathea Lechleri* Mett., Fil. Lechl. 2:32. 1859.

Stem to 12 m. tall. *Petiole* to 2 m. long, atropurpureous, tuberculate to muricate; scales fuscous with a broad, flabellate, fulvous border; scurf absent; leaf axes stramineous to atropurpureous, glabrous or with a few trichomidia and bullate, fulvous squamulae. *Lamina* 0.5–1.5 m. long, 2-pinnate-pinnatifid, chartaceous, apex abruptly reduced and pinna-like; pinnae stalked; pinnules petiolulate, crenate to pinnatifid, base cuneate to truncate, apex acuminate to attenuate; lobes truncate, tip serrate; fertile veins simple, basal veins of the lobes connivent at the sinuses, sterile veins simple (the basal veins of the lobes sometimes dividing and rejoining at the sinuses). *Sori* apically subcostal to basally medial; paraphyses longer than the sporangia, receptacle villous.

Trichipteris Lechleri is best characterized as a species of Brazilian affinities with an Andean distribution. In addition to the characters of the key, *T. Lechleri* is best distinguished by the basal veins of the segments which are connivent at the sinuses. The species lacks any abaxial indument. The pinnules vary from crenate to shallowly pinnatifid and from papyraceous to coriaceous. *Trichipteris Dombeyi* is superficially similar, but it has an indument of squamulae on the costae and petiole scales with cretaceous borders. *Trichipteris Lechleri* has been collected in the Guayana Highlands and on the eastern slopes of the Andes in Colombia, Ecuador, Peru, and Bolivia. Its habitat is rain forests, especially near watercourses and lakes, from 450 to 1450 meters.

SELECTED COLLECTIONS. **Venezuela. Bolívar:** Cerro Venamo, ca. British Guiana, *Steyermark & Dunsterville 92700* (GH,US,VEN). **Colombia. Huila:** SW of Alejandría at Río Sauza, *Little 8498* (GH,US). **Ecuador. Pastaza:** Mera, *Harling, Storm & Ström 10217* (GH). **Peru. Amazonas:** valley of the Río Marañon above Cascadas de Mayasi, *Wurdack 1868* (GH). **Huánuco:** SW slope of Río Llulla Richis watershed, on the ascent of Cerros del Sira, *Dudley 13047, 13214, 13220* (GH). **Bolivia. La Paz:** Hacienda Simaco, on the road to Tipuani, *Buchtien 5298* (GH); *Buchtien 5300* (F,GH); *Buchtien 5301* (MO).

28. **Trichipteris villosa** (Willd.) Tryon

FIGS. 81–83. MAP 28.

Trichipteris villosa (Willd.) Tryon, Contrib. Gray Herb. 200:46. 1970.

Cyathea villosa Willd., Sp. Pl. ed. 4. **5**(1):495. 1810. HOLOTYPE: America meridionale, ad St. Crucem & ad Caracas (Sucre, Venezuela), *Humboldt 436*, B (Herb. Willd. No. 20175–2) not seen, Tryon photo GH! ISOTYPES: F! P!

Alsophila villosa (Willd.) Desv., Mém. Soc. Linn. Paris **6**:319. 1827.

Chnoöphora villosa (Willd.) Link, Erkenn. Gew. 3:35. 1833.

Chnoöphora Humboldtii Klf., Enum. Fil. 250. 1824, *illegit. nom. superfl.* for *Cyathea villosa* Willd., 1810.

Alsophila Humboldtii (Klf.) Kze., Linnaea **23**:220. 1850.

Alsophila rigidula Mart., Icon. Crypt. Vasc. Bras. 74, t. 51. 1834, *ex icone.* HOLOTYPE: crescit in sylvis provinciae S. Pauli, *Martius*, M not seen.

Alsophila vernicosa Kuhn, Linnaea **36**:155. 1869. HOLOTYPE: Venezuela, *Fendler 344*, B not seen. ISOTYPES: GH! MO! fragment ex K, NY!

Cyathea vernicosa (Kuhn) Domin, Pteridophyta 263. 1929.

Trichipteris vernicosa (Kuhn) Tryon, Contrib. Gray Herb. **200**:46. 1970.

Stem to 1.5 m. tall. *Petiole* ca. 0.2–0.5 m. long, fulvous to ferruginous, tuberculate to aculeate; scales helically twisted, uniformly fulvous to fulvous with a narrow, diaphanous border; scurf absent; pinna-rachises, costae, and often costules attached at acute angles; rachis glabrous; pinna-rachises, costae, costules, veins, and leaf surfaces villous with scarce to abundant, minute, contorted trichomidia; costae and costules with flattish to bullate, cretaceous squamulae. *Lamina* ca. 1 m. long, 2-pinnate-pinnatifid, chartaceous to coriaceous, apex gradually reduced and acute; pinnae sessile to stalked; pinnules sessile to short-petiolulate, pinnatisect, base cordate, apex attenuate, tip crenulate to entire, obtuse; lobes truncate to acute, entire to crenulate; fertile veins forked at the sori or rarely simple, sterile veins forked or simple. *Sori* medial; paraphyses contorted, larger than the sporangia, receptacle villous.

The minute, contorted trichomes found on the costae, costules and veins of this species distinguish it from the rest of the genus. In addition, the attachment of the lamina axes and the usually short, revolute segments of the pinnules are diagnostic. The petiole spines are poorly developed, and the petiole scales are helically twisted. *Trichipteris atrovirens*, the closest species, usually lacks minute, contorted trichomes and has simple veins. *Trichipteris villosa* is one of a group of species centered in the Serra do Mar and Campo Limpo areas of southern Brazil. The petiole scales of some collections of *T. villosa* have narrow, diaphanous borders. The density of the contorted trichomes varies, apparently with exposure to direct sunlight. The veins are occasionally forked at the sori. *Trichipteris villosa* has a remarkably discontinuous distribution. It has been found in Panama and the Andes of Colombia and Venezuela. It occurs as

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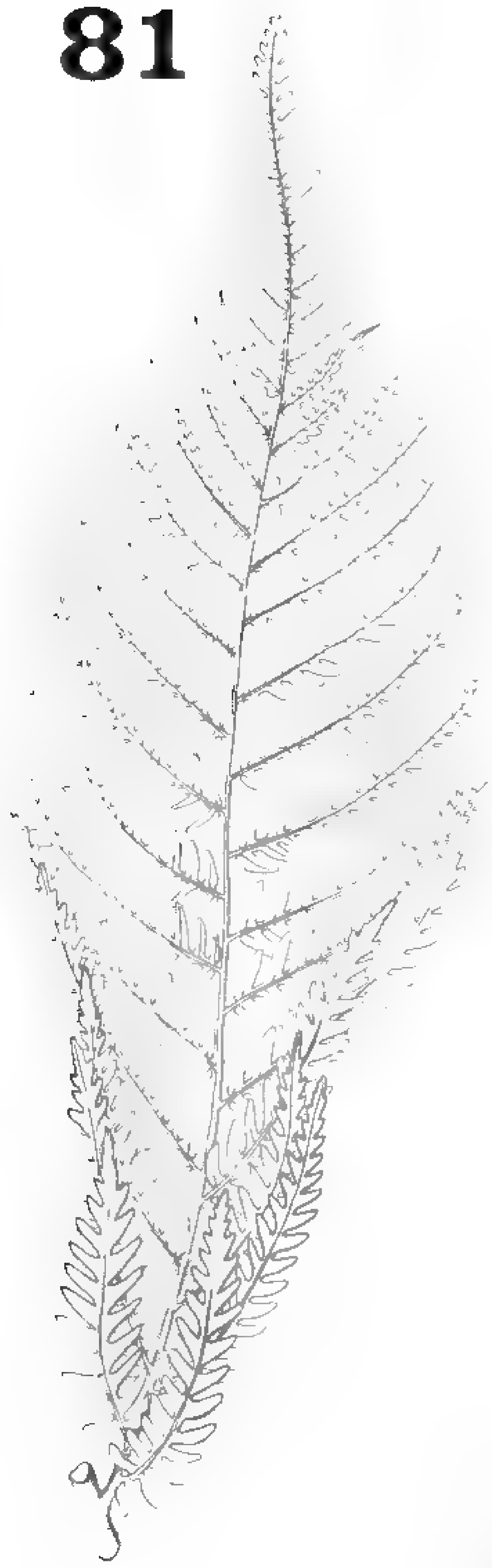

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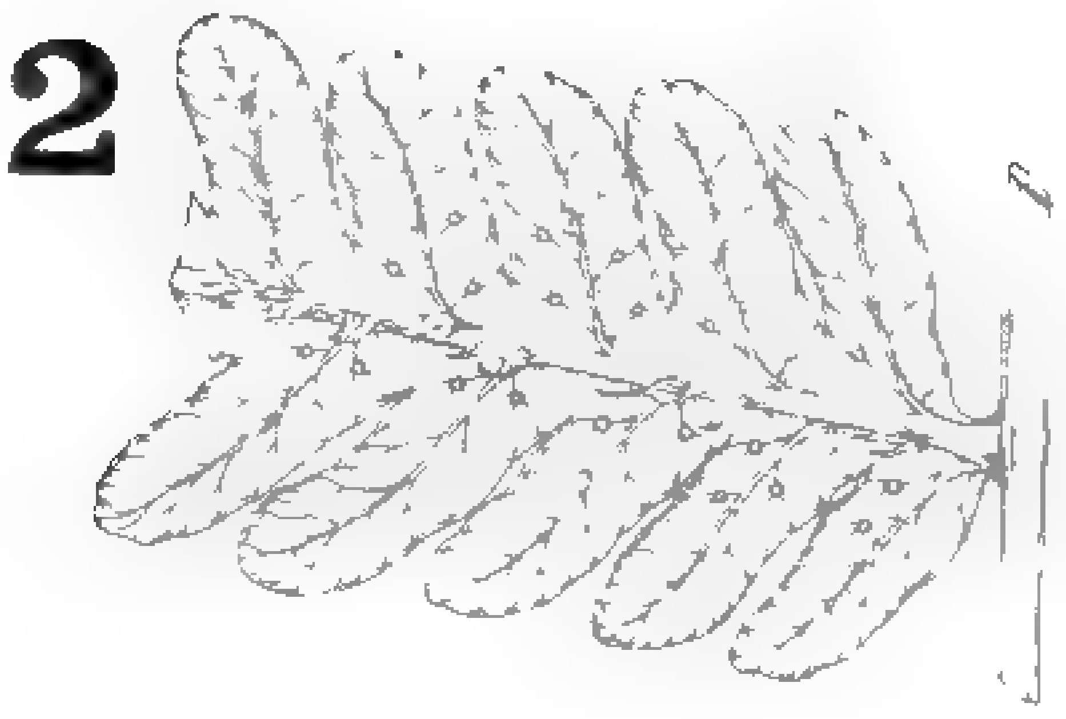

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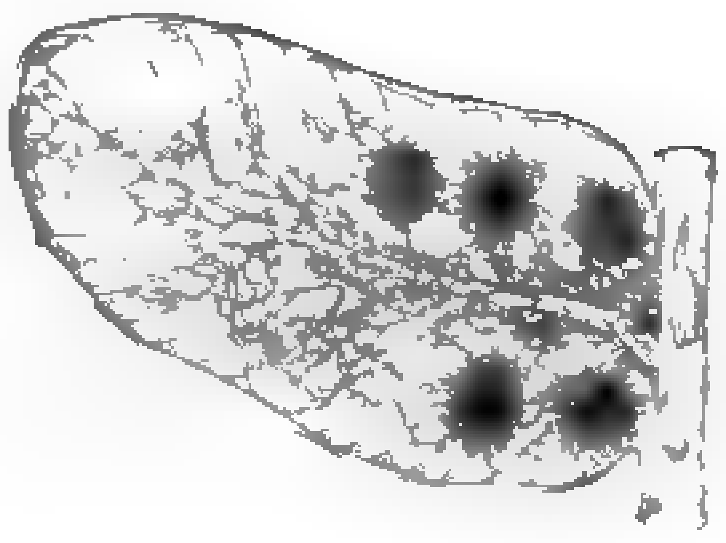

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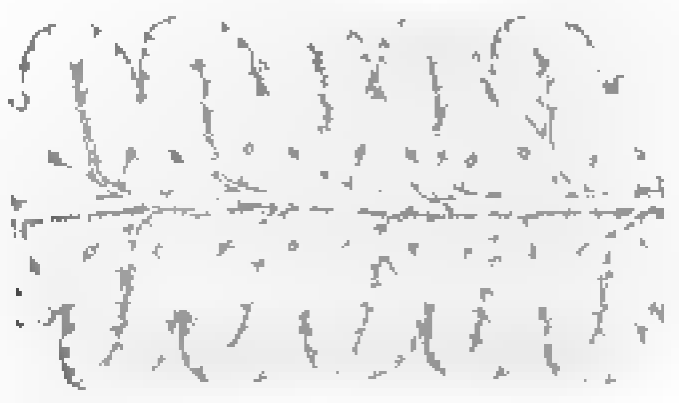

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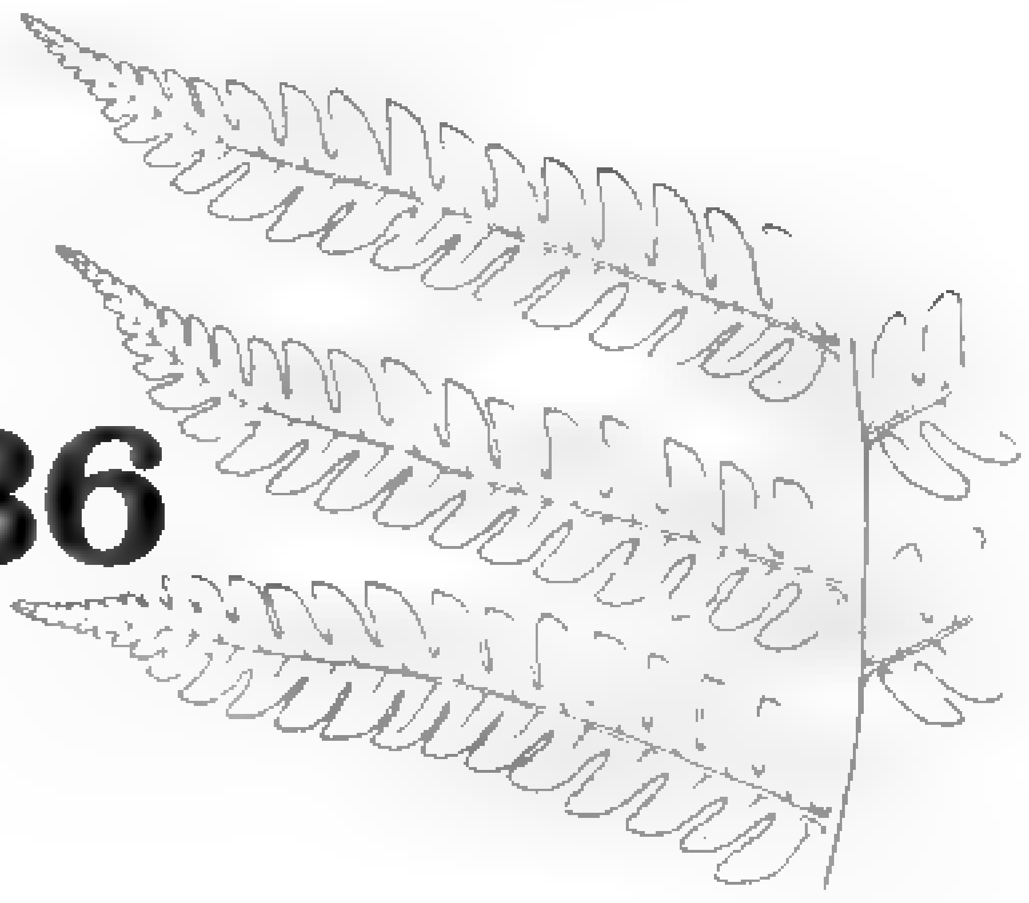

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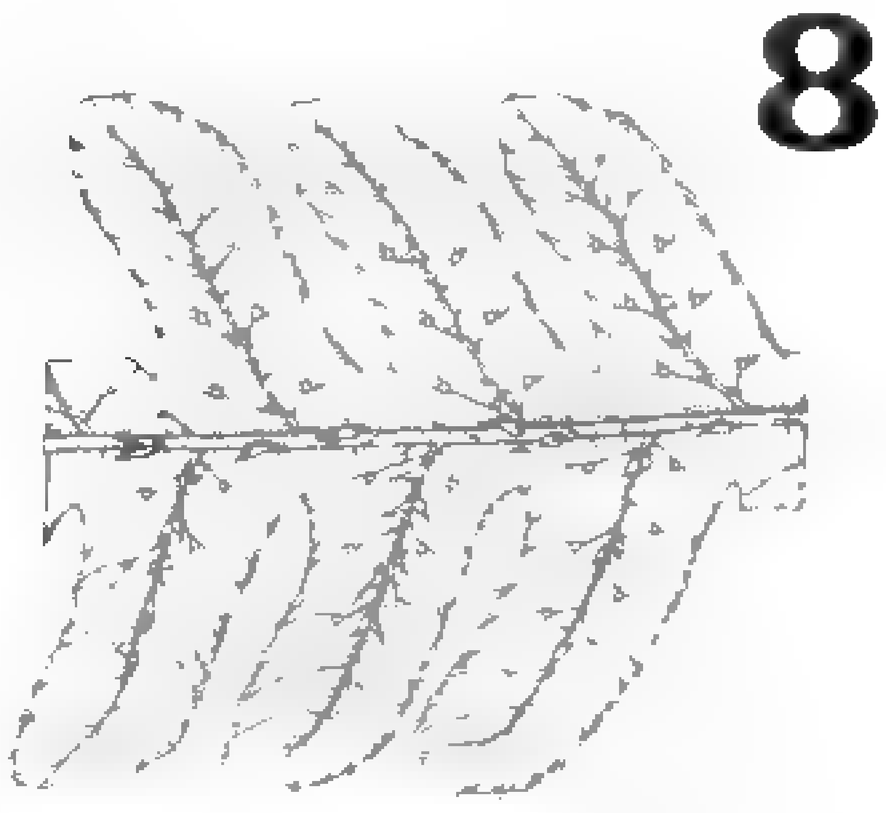

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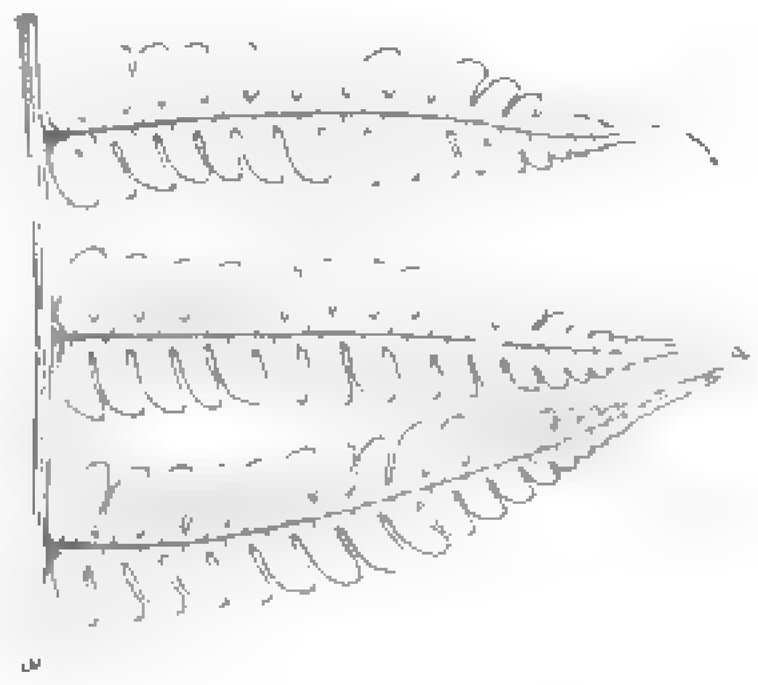

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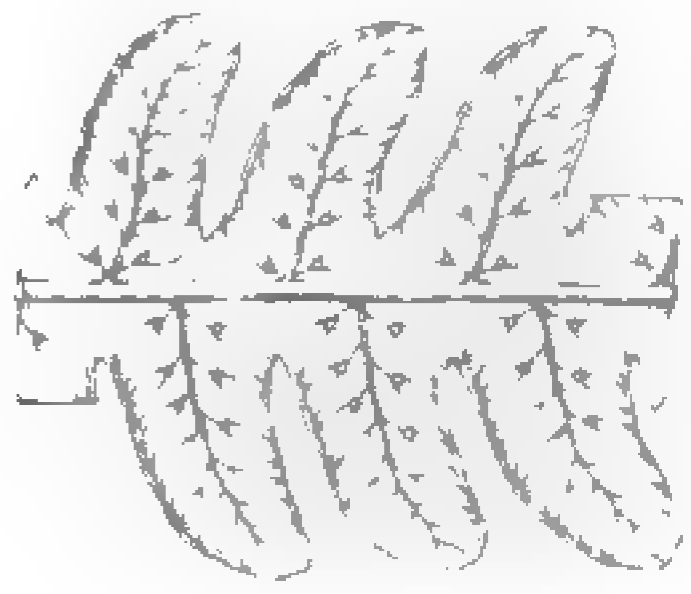

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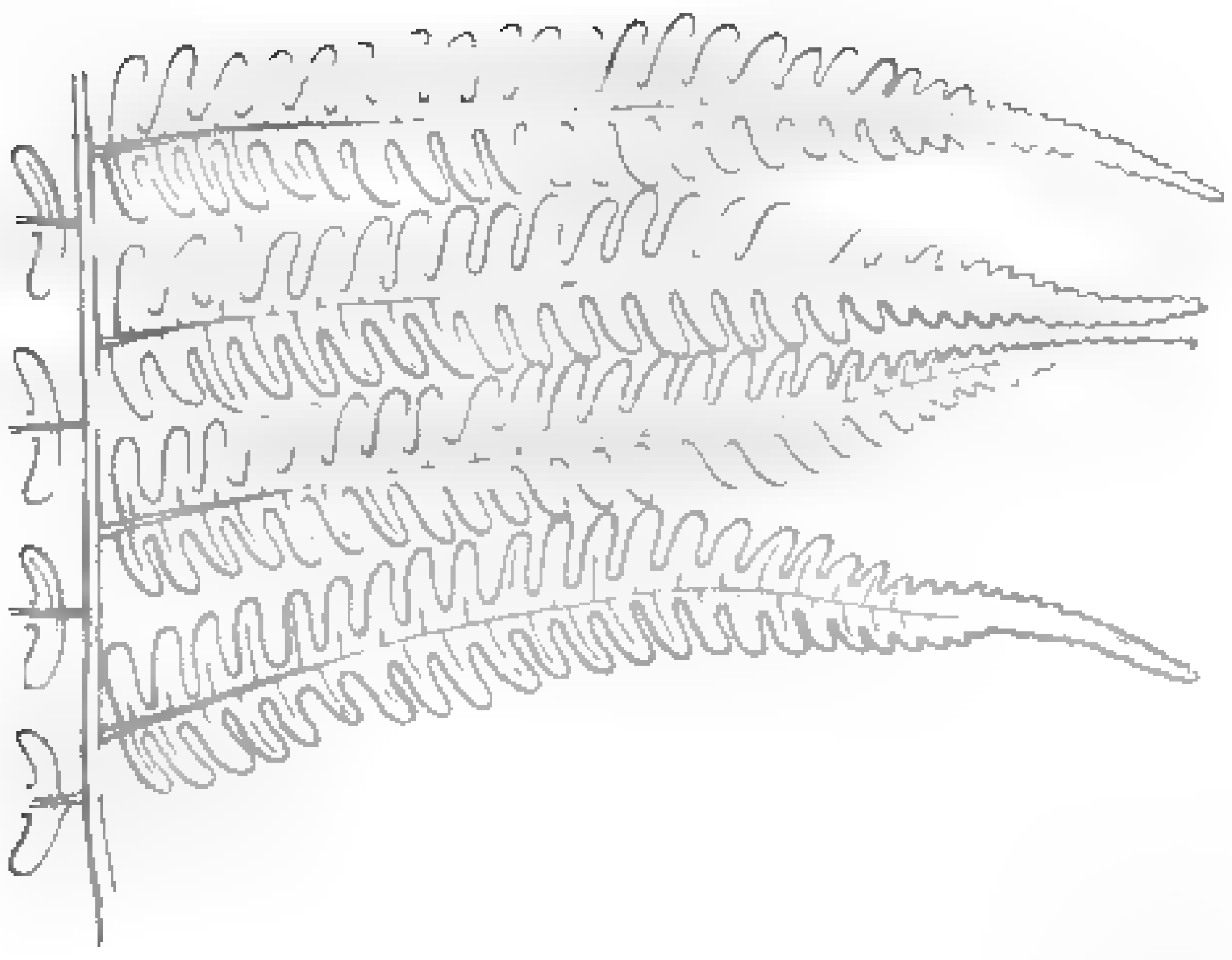

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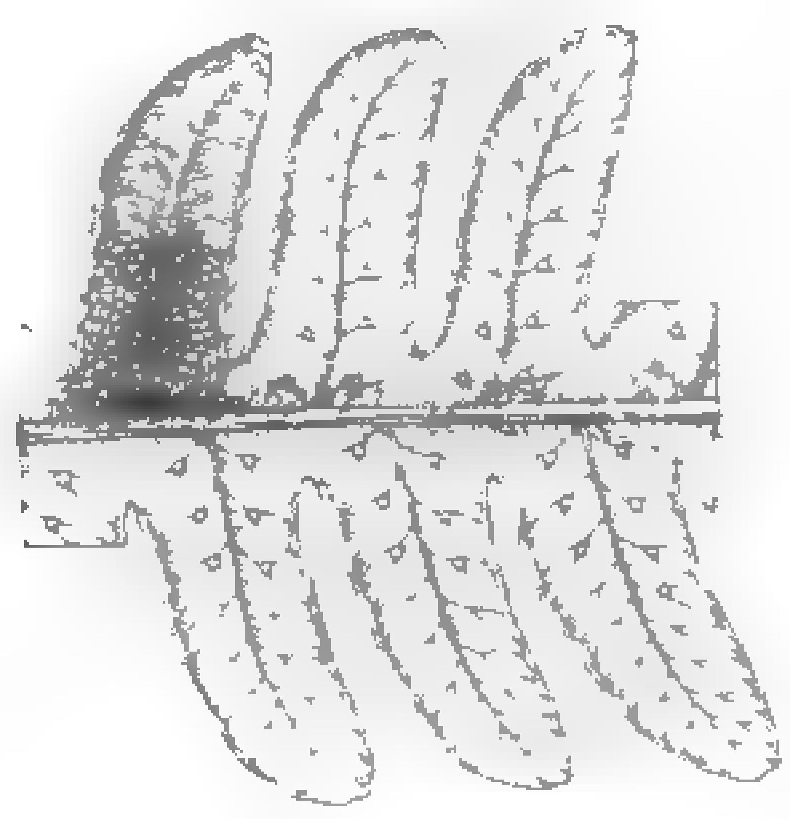


FIGS. 81–91. FIGS. 81–83, *Trichipteris villosa:* 81, central pinna, × 1/3 (*Maguire & Wurdack* 33783, US); 82, base of pinnule, × 4/3 (*Fendler 344*, GH); 83, a single pinnatisect lobe, × 8/3 (*Fendler 47*, GH). FIGS. 84 & 85, *T. atrovirens:* 84, part of a medial pinnule, × 4/3 (*Tryon & Tryon 6576*, GH); 85, abaxial surface of a single lobe, × 8/3 (*Brade 35015*, MO). FIGS. 86–89, *T. phalerata:* 86, var. *phalerata,* three central pinnules from a central pinna, × 1/3; 87, var. *phalerata,* central part of a pinnule, the trichomes omitted above, × 4/3 (both *Smith & Brade 2234*, GH); 88, var. *Iheringii,* three central pinnules from a central pinna, × 1/3; 89, var. *Iheringii,* central part of a pinnule, × 4/3 (both *Brade 10853*, F). FIGS. 90 & 91, *T. Gardneri:* 90, four central pinnules from a central pinna, × 1/3; 91, central part of a pinnule, × 4/3 (both *Mexia 4882*, F).

a disjunct population in the Gran Sabana area of the Guayana Highlands. It occurs in the Bolivian Andes. It is best represented in herbaria by collections from the Campo Limpo area of Minas Gerais, Brazil. These four basic populations show minor variations, which are the result of local variation in ecology. The discontinuous distribution of *T. villosa* may be the result of latter-day geographic restriction of the environment favorable to its growth. *Trichipteris villosa* is a species of open areas, savannas, shrubby vegetation, and gullies in pastures. It almost always grows in full sun, often in poor soil. The species ranges from 780 to 1800 meters in altitude.

SELECTED COLLECTIONS. **Panama. Chiriquí:** trail from San Felix to Cerro Flor, *Allen 1940* (F,GH,US). **Venezuela. Aragua:** near Colonia Tovar, *Fendler 492* (GH); sabanas altas de Guayabitos, *Pittier 12136* (NY,VEN). **Distrito Federal:** Turmerito, *Killip 37724* (GH). **Monagas:** vicinity of La Cuchilla, between Guanaguana & Guacharo, *Steyermark 62274* (VEN). **Bolívar:** vicinity of Misión Santa Teresita de Kavanayén to base of Sororopan-tepuí, *Maguire & Wurdack 33783* (NY,US); Sta. Elena de Uairen, Gran Sabana, *Tamayo 2813, 2968* (VEN). **Colombia. Magdalena:** trail from "Africa" (Sierra Perijá) to Villanueva, *Haught 4531* (NY). **Antioquia:** vicinity of Medellín, *Charetier 14* (US). **Santander:** Mesa de los Santos, *Killip & Smith 15309* (GH). **Bolivia. La Paz:** near Apolo, *R. S. Williams 1290* (GH,US). **Brazil. Goiás:** Chapada de Veadeiros, *Duarte 10683* (HB); Serra do Caiapó, 50 km. S of Caiaponia on road to Jataí, *Irwin & Soderstrom 7375* (NY). **Minas Geraís:** near Caxambú, *Pabst 4047* (F); Cerro de Cipó, *Pires & Black 2715* (US). **São Paulo:** Ypiranga, *Lüderwaldt 900, 22137* (NY). **Paraná:** Serrinha, *Dusén 3437* (GH); Capao Grande, *Dusén 9466* (NY). **Santa Catarina:** Lages, *Sehnem 5503* (A).

29. **Trichipteris atrovirens** (Langsd. & Fisch.) Tryon

FIGS. 84, 85. MAP 29.

Trichipteris atrovirens (Langsd. & Fisch.) Tryon, Contrib. Gray Herb. 200:45. 1970.

Polypodium atrovirens Langsd. & Fisch., Icon. Filic. 12, t. 14. 1810. HOLOTYPE: Isla Sta. Catharina, Brazil, *(Langsdorff)*, LE not seen. ISOTYPE: BM!

Alsophila atrovirens (Langsd. & Fisch.) Presl, Tent. Pterid. 61. 1836.

Cyathea atrovirens (Langsd. & Fisch.) Domin, Pteridophyta 262. 1929.

Cyathea compta Mart., Denkschr. Bot. Ges. Regensb. 2:146, t. 2 f. 1. 1822. HOLOTYPE: Brazil, *Martius*, M not seen. I have taken the plant illustrated by Martius in Icon. Plant. Crypt. Bras. t. 41. 1834, as the type collection of *Cyathea compta* Mart. and placed the name accordingly.

Alsophila compta (Mart.) Mart., Icon. Plant. Crypt. Bras. 1:66, t. 41. 1834, *ex icone*. SPECIMENS CITED: vicinity of Ipanema & Sorocaba, (Rio de Janeiro), São Paulo, Brasil, *Martius*, M not seen.

Trichipteris compta (Mart.) Tryon, Contrib. Gray Herb. 200:45. 1970.

Alsophila radens Klf., Enum. Fil. 248. 1824. HOLOTYPE: *Chamisso*, LE not seen. ISOTYPES: B! P!

Cyathea radens (Klf.) Domin, Pteridophyta 263. 1929.

Alsophila Hookeriana Hook., Sp. Fil. 1:39. 1844. HOLOTYPE: south Brazil, *Sellow*, fragment ex K, NY! ISOTYPE: B! *(Sellow 727)*. PARATYPE: Sta. Catarina, Brazil, *Lay & Collie*, K not seen.

Alsophila leptocladia Fée, Crypt. Vasc. Brés. 1:161, t. 55 f. 1. 1869. HOLOTYPE: Brasilia fluminensi, *Glaziou* 2299, P! (Herb. Cosson).

Cyathea leptocladia (Fée) Domin, Pteridophyta 262. 1929.

Alsophila trichophlebia Baker, Ann. Bot. 5:189. 1891. HOLOTYPE: Paraguay, *Balansa 306*, Herb. de Candolle, P not seen. ISOTYPE: P! (E of Cordillera de Villa Rica).

Cyathea trichophlebia (Baker) Domin, Pteridophyta 263. 1929.

Alsophila verruculosa Rosenst., Hedwigia **46**:66. 1906. TYPE COLLECTION: São Paulo, Campinas, 1904, orig. det. *A. radens* Mett., *Ulbricht*, B!

Cyathea verruculosa (Rosenst.) Domin, Pteridophyta 263. 1929.

Alsophila proceroides Rosenst., Hedwigia **56**:356. 1915. HOLOTYPE: São Paulo, Ribeira, *Brade 5106*, S not seen. ISOTYPE: NY!

Alsophila dryopteridoides Domin var. *fallacina* Domin, Mem. Roy. Czech. Soc. Sci. II, **2**:89, t. 9 f. 11, 12. 1929. HOLOTYPE: in Brasilia, Rio Grande do Sul, *Reineck & Czermak 36*, PR not seen. ISOTYPE: P!

Alsophila fallacina (Domin) Domin, Mem. Roy. Czech. Soc. Sci. II, **2**:85. 1929.

Cyathea fallacina (Domin) Domin, Acta Bot. Bohem. **9**:115. 1930.

Stem 1.0–6.0 m. tall. *Petiole* ca. 0.3 m. long, atropurpureous at the base, fulvous above, aculeate; scales helically twisted, uniformly fulvous or fuscous with a fulvous margin; scurf absent or of scattered trichomidia; axes often attached at an acute angle; pinna-rachises with a few minute, fulvous trichomidia or glabrous; indument of costae and costules absent, or of trichomidia, or of trichomidia and flattish to bullate squamulae; costae, costules, and veins sometimes with trichomes. *Lamina* 1.0–2.0 m. long, 2-pinnate-pinnatifid, papyraceous to coriaceous, apex gradually reduced and acute; pinnae short-stalked; pinnules sessile to short-petiolulate, crenulate to pinnatifid, base truncate to cuneate, apex acuminate to attenuate, tip serrate to crenulate; lobes truncate, entire or serrate at the tip; fertile veins simple, sterile veins simple. *Sori* medial; paraphyses as long as the sporangia or longer, receptacle hirsute to villous.

Simple veins distinguish *Trichipteris atrovirens* from other Brazilian species of *Trichipteris*. The helically twisted petiole scales and acutely attached lamina axes characteristic of *T. villosa* are occasionally seen in *T. atrovirens*. However, *T. villosa* has a tomentum of contorted trichomes and veins forking at the sori. *Trichipteris atrovirens* is found along the Serra do Mar in the states of Rio de Janiero, São Paulo, and Bahía, and southward to the states of Paraná, Sta. Catarina, and Rio Grande do Sul. It also occurs in Paraguay and Argentina. It is the most southern species in the genus. *Trichipteris atrovirens* is a plant of the campo, secondary and scrub forests, and taller forests, between 35 and 900 meters in altitude. "*Alsophila microptera* Baker" is apparently an herbarium name included by Salomon in his Nom. Gefässkrypt. 29. 1883, but never validly published. Material of *T. atrovirens* identified as "*A. microptera*," is at NY, with the erroneous provenance "von Venezuela."

SELECTED COLLECTIONS. **Brazil. Bahía:** *Blanchet 2286* (F). **Minas Gerais:** Juiz de Fóra, *Brade 15902* (F,MO,US). **São Paulo:** Santos, *Ball* (GH); Villa Ema, *Brade 16052* (MO,NY). **Rio de Janeiro:** Mana, *Glaziou 2–7945* (NY). **Paraná:** Parque Nacional do Iguacú, Palmital, *Duarte & Pereira 1693* (F,US); Rio São João, *Duarte & Pereira 1772* (MO,NY). **Sta. Catarina:** Blumenau, *Gooden* (NY); Joinville, *Schmalz 64* (F,MO,NY). **Rio Grande do Sul:** Rio Pardo, Estevão Reseada, *Jürgens* (MO); Villa Manresa, Porto Alegre, *Leite (2456)217* (A,US).

30. **Trichipteris phalerata** (Mart.) Barr.

Trichipteris phalerata is a highly variable species without consistently useful diagnostic features. The Brazilian *Trichipteris* with flat, concolorous petiole scales, little development of petiole scurf, forked veins, and long paraphyses is in general assignable to *T. phalerata*. Similar species include *T. dichromatolepis,* in which specimens with uniformly fulvous petiole scales are occasional. Long, attenuate pinnules with a dusky aspect and tendencies toward multiseriate paraphyses and unforked fertile veins distinguish *T. dichromatolepis. Trichipteris Gardneri,* a species of the Campo Limpo, has petioles with trichomes and squamulae and long, attenuate pinnules with revolute segments. *Trichipteris villosa* has a lamina indument of minute, contorted trichomes, and *T. atrovirens* has simple veins. I have recognized two extreme variants of *T. phalerata* as varieties. *Trichipteris phalerata* var. *Iheringii* includes a series of plants from the Serra do Mar having nearly glabrous, cordate pinnules and paraphyses about as long as the sporangia. *Trichipteris phalerata* var. *phalerata* comprises a series of plants from interior, more northern areas, with an abaxial indument of trichomes and squamulae, truncate pinnules, and paraphyses longer than the sporangia.

The overall range of the species includes the states of Matto Grosso and Bahía south to Rio Grande do Sul. The species is found in advanced, secondary forest and wet, scrubby campo, especially along creek banks. The range of altitude for the species is from 35 to 1300 meters. In some specimens the differentiated scale margin is abraded early so that the scales appear emarginate as in *Sphaeropteris.* Exindusiate *Sphaeropteris* from Brazil has short paraphyses and long, flexuous trichomes borne at the base of the receptacle.

30a. **Trichipteris phalerata** (Mart.) Barr. var. **phalerata**

FIGS. 86, 87. MAP 30.

Trichipteris phalerata (Mart.) Barr., Rhodora 78(813):5. 1976.

Cyathea phalerata Mart., Denkschr. Bot. Ges. Regensb. **2**:146, t. 2, f. 3. 1822. HOLOTYPE: Brazil, *Martius,* M not seen. ISOTYPES: B! BM! NY! fragment ex NY, US! (*Martius* 392).

Alsophila phalerata (Mart.) Mart., Icon. Plant. Crypt. Bras. 67, t. 30 f. 1, t. 42. 1834.

Alsophila paleolata Mart., Icon. Plant. Crypt. Bras. 68, t. 43. 1834. SYNTYPES: Prov. S. Pauli, *Martius,* M not seen. Sebastionopolis (Paraná), *Martius,* M not seen. Bahía, *Martius,* M not seen. ISOSYNTYPE: Bahía, *Martius,* B!

Cyathea paleolata (Mart.) Copel., Univ. Calif. Publ. Bot. **17**:30. 1932.

Trichipteris paleolata (Mart.) Tryon, Contrib. Gray Herb. 200:46. 1970.

Alsophila Blanchetiana Presl, Epimel. Bot. 28. 1849. HOLOTYPE: Bahía, *Blanchet 77,* PR not seen. ISOTYPE: BM!

Cyathea Blanchetiana (Presl) Domin, Acta Bot. Bohem. **9**:98. 1930.

Alsophila Blancheti Trevisan, Atti Ist. Veneto II, **2**:165. 1851, *nom. nud.* COLLECTION CITED: *Blanchet 77,* BM!

Alsophila contracta Fée, Crypt. Vasc. Brés. **1**:167, t. 59 f. 2. 1869. SYNTYPES: Brasilia fluminensi (both numbers), *Glaziou 2288,* P! (Herb. Cosson); *Glaziou 2296,* P! (Herb. Cosson).

Cyathea contracta (Fée) Domin, Pteridophyta 262. 1929.

Alsophila eriocarpa Fée, Crypt. Vasc. Brés. **1**:162, t. 56 f. 1. 1869. SYNTYPES: Corcovado, Brazil (both numbers), *Glaziou 987,* P! (Herb. Cosson) fragment ex P, NY! *Glaziou 1706,* P! (Herb. Cosson) fragment ex P, NY! ISOSYNTYPE: *Glaziou 1706,* US!

Alsophila ludoviciana Fée, Crypt. Vasc. Brés. **1**:169, t. 60 f. 2. 1869. HOLOTYPE: Saint Louis, Brazil, Serra do Orgãos, *Glaziou 1785,* P! (Herb. Cosson).

Alsophila scrobiculata Fée, Crypt. Vasc. Brés. **1**:157, t. 53 f. 1. 1869. SYNTYPES: Brasilia fluminensi (all numbers), *Glaziou 378*, P! (Herb. Cosson) *Glaziou 2293*, P! (Herb. Cosson) fragment ex P (Herb. Cosson) NY! *Glaziou 2294*, P (Herb. Cosson) not seen. *Glaziou 2295*, P! (Herb. Cosson). ISOSYNTYPES: *Glaziou 2294*, A! fragment NY!
Alsophila unguis-cati Fée, Crypt. Vasc. Brés. **1**:165, t. 58 f. 2. 1869. HOLOTYPE: San Ludovico, Brazil, *Glaziou 2297*, P! (Herb. Cosson) fragment ex P (Herb. Cosson) NY!
Alsophila goyazensis Christ, in Schwacke Plant. Nov. Mineiras **2**:33. 1900. HOLOTYPE: plateau de Goyaz, *Glaziou 22630*, P not seen. ISOTYPE: NY!
Alsophila paulistana Rosenst., Hedwigia **46**:67. 1906. HOLOTYPE: Campinas, Est. São Paulo, *Ulbricht 141*, S!
Cyathea paulistana (Rosenst.) Domin, Pteridophyta 263. 1929.

Stem 0.5–10.0 m. tall. *Petiole* 0.4–ca. 1.0 m. long; scales uniformly fulvous; scurf absent or of occasional, minute, fulvous trichomidia; indument of lamina axes consisting of trichomes, trichomidia, and squamulae. *Lamina* to ca. 2.0 m. long, 2-pinnate-pinnatifid; pinnae stalked; pinnules short-petiolulate, deeply pinnatifid to pinnatisect, base truncate, apex acute to attenuate; lobes entire to crenulate, acute to rotund; fertile veins forked at the sori, sterile veins forked. *Sori* medial; paraphyses as long as or longer than the sporangia, receptacle hirsute to villous.

SELECTED COLLECTIONS. **Brazil. Matto Grosso:** *H. Smith 10618* (US). **Goiás:** Goiania, *Brade 15347* (F,MO,NY); Planalto, Chapada dos Veadeiros, ca. 20 km. W of Veadeiros, *Irwin, Grear et al. 12485* (GH). **Minas Gerais:** Caldas, *Regnell 648* (GH); São Tomas de Aquinho, Fazenda Fortaleza do Dr. Luiz Pimenta Neves, *Teodoro 910* (F); *Teodoro 912* (GH). **São Paulo:** Mun. Moji-Guaçu, Campos das Sete Lagôas, N of Rio Moji-Guaçu. 6 km. NW of Moji-Mirim, *Eiten & Eiten 2128* (GH); Campinas, *Ulbricht* (US). **Rio de Janeiro:** Serra dos Orgãos, Corrego Beija-flôr, *Brade 16644* (F,MO); Tijuca, *Smith & Brade 2234* (F,GH). **Paraná:** Porto de Cima, *Dusén 7021* (GH). **Santa Catarina:** Blumenau, Passo Mansa, *Haerchen* (MO); Mun. Florianópolis, Morro Itacorubí, Ilha de Santa Catarina, *Smith & Reitz 6156* (GH,MO,US). **Rio Grande do Sul:** Pelotas, *Brauner 22* (F).

30b. **Trichipteris phalerata** (Mart.) Barr. var. **Iheringii** (Rosenst.) Barr.

FIGS. 88, 89. MAP 31.

Trichipteris phalerata (Mart.) Barr. var. *Iheringii* (Rosenst.) Barr., Rhodora **78**(813):5. 1976.
Alsophila Iheringii Rosenst., Hedwigia **56**:358. 1915. LECTOTYPE (chosen herewith): Serra do Mar, Alto da Serra, *Lüderwaldt 1036*, S or SP not seen. ISOLECTOTYPES: B! NY! LECTOPARATYPES: *Brade 5828* not seen; *Brade 5829* not seen; *Edwall 4972* not seen.
Cyathea Iheringii (Rosenst.) Domin, Pteridophyta 262. 1929.
Alsophila Guinleorum Brade & Rosenst., Bol. Mus. Nac. Rio Janeiro **7**:140, t. 2 f. 3, t. 4 f. 1, t. 6 f. 1. 1931. HOLOTYPE: Serra do Cavalo, vicinity of Teresopolis, Rio de Janeiro, Brazil, *Brade 9842*, HB not seen. ISOTYPE: NY!
Alsophila Roquettei Brade & Rosenst., Bol. Mus. Nac. Rio Janeiro **7**:139 t. 2 f. 2, t. 3 f. 2, t. 5 f. 1. 1931. SYNTYPES: Serra do Cavalo, vicinity of Teresopolis, Rio de Janeiro, Brazil (both numbers). *Brade 9569*, HB not seen; *Brade 9836*, HB not seen. ISOSYNTYPE: *Brade 9569*, B!
Alsophila Portoana Brade, Arch. Inst. Biol. Veg. Rio de Janeiro **1**:223, t. 1 f. 1, 1935, *ex icones*. HOLOTYPE: Itatiaia, *Brade 10235*, HB not seen.
Trichipteris Portoana (Brade) Tryon, Contrib. Gray Herb. 200:46. 1970.
Alsophila Pabstii Brade, Arquiv. Jard. Bot. Rio de Janeiro **18**:26, t. 1 f. 1. 1965, *ex icone*. HOLOTYPE: Brasil, Região da nova Capital, Brasília, *Pabst 4935 & Pereira 4608* (HB 7223) HB not seen.

Stem 1.0–2.0 m. tall. *Petiole* 0.4–0.5 m. long; scales fulvous with a slightly lighter border; scurf absent; axes of lamina nearly or quite glabrous. *Lamina* 0.6–1.2 m. long, 2-pinnate-pinnatifid; pinnae stalked; pinnules deeply pinnatifid to pinnatisect, base cordate, apex acute to attenuate; lobes entire, acute; fertile veins forked at the sori, sterile veins forked. *Sori* medial; paraphyses shorter than the sporangia, receptacle pilose.

SELECTED COLLECTIONS. **Brazil. Bahía:** *Blanchet 2286* (F); São Bento, *Lützelburg 101* (US). **São Paulo:** Paranapiacaba, linha São Paulo-Santos, *Handro 2210* (GH); near Alto da Serra, *Tryon & Tryon 6587* (GH). **Rio de Janeiro:** Itatiaia, *Brade 14009* (MO); Itatiaia, Rio Bonito, 3 picos, *Brade 15887* (MO,NY). **Sta. Catarina:** *Haerchen 234* (MO).

31. **Trichipteris Gardneri** (Hook.) Tryon

FIGS. 90, 91. MAP 32.

Trichipteris Gardneri (Hook.) Tryon, Contrib. Gray Herb. 200:45. 1970.

Alsophila Gardneri Hook., Sp. Fil. 1:40. 1844. LECTOTYPE (chosen herewith): San Gaetano, Brazil, *Gardner 5330,* K not seen. ISOLECTOTYPES: BM! fragment ex P, F! P! US! LECTOPARATYPE: south Brazil, *Sellow,* not seen. ISOLECTOPARATYPE: fragment ex B, NY!

Cyathea Mexiae Copel., Univ. Calif. Publ. Bot. 17(2):30, t. 4. 1932. HOLOTYPE: Viçosa, SE of the Agricultural College, *Mexia 4882,* UC 466093–466096 not seen. ISOTYPES: F! GH! MO!

Alsophila Mexiae (Copel.) C. Chr., Ind. Fil. Suppl. 3:22. 1934.

Trichipteris Mexiae (Copel.) Tryon, Contrib. Gray Herb. 200:45. 1970.

Stem 1.0–4.0 m. tall. *Petiole* 0.6–1.0 m. long, stramineous to fuscous, aculeate; scales uniformly stramineous to fulvous; trichomes long, cretaceous; scurf of a few fulvous squamulae; all axes of lamina pubescent with long, multicellular, cretaceous trichomes; rachis, pinna-rachises and costae with minute, cretaceous trichomidia; costae and costules with long-lanceolate, flattish, fulvous squamulae and bullate, cretaceous squamulae; lamina surface with long, cretaceous trichomes. *Lamina* ca. 2.0–3.0 m. long, 2-pinnate-pinnatifid, chartaceous, apex gradually reduced and acute; pinnae stalked, often long-stalked; pinnules sessile to short-petiolulate, deeply pinnatifid to pinnatisect, base truncate to subcordate, apex attenuate; lobes rotund, entire, revolute; fertile veins forked at the sori, sterile veins forked. *Sori* medial; paraphyses longer than the sporangia, villous.

The petiole is critical to the determination of *Trichipteris Gardneri,* since the foliage appears similar to some of the more densely indumented plants of *T. phalerata. Trichipteris Gardneri* is a species of the Campo Limpo of Minas Gerais and surrounding states. It is related to *T. phalerata* and perhaps derived from it. *Trichipteris Gardneri* varies in the degree of pubescence and the revoluteness of the lobes. It is known from secondary forests and drainage ditches, from 700 to 1000 meters, in the states of Matto Grosso, Rio de Janeiro, São Paulo, and Minas Gerais, Brazil.

SELECTED COLLECTIONS. **Brazil. Matto Grosso:** *Smith 109* (US). **Minas Gerais:** Viçosa, Agricultural College, *Mexia 4902* (F,GH,MO,NY); *Mexia 5175* (F,GH,MO,NY). **São Paulo:** Bananal, Serra da Bocaina, *Brade 15180* (MO,NY). **Rio de Janeiro:** Mt. Itatiaia, *Brade 15043* (F,MO,NY); Nova-Friburgo, *Leite 4231* (MO).

32. **Trichipteris dichromatolepis** (Fée) Tryon

FIGS. 92, 93. MAP 33.

Trichipteris dichromatolepis (Fée) Tryon, Contrib. Gray Herb. 200:45. 1970.

Alsophila dichromatolepis Fée, Crypt. Vasc. Brés **1**:164, t. 57 f. 2. 1869. HOLOTYPE: Serra do Orgãos, Brasil, *Glaziou 1786,* P! (Herb. Cosson).

Cyathea dichromatolepis (Fée) Domin, Pteridophyta 262. 1929.

Alsophila arbuscula Baker, Fl. Bras. **1**(2):322. 1870. SYNTYPES: Rio, Orgaos, Tijuca, etc. (all numbers), *Gardner 114, Gardner 5673, Sellow, Glaziou 981, Glaziou 2155, Glaziou 2300, Glaziou 2301,* all K not seen. ISOSYNTYPES: *Gardner 114,* fragment F! P! *Sellow,* P! *Glaziou 981,* P! *Glaziou 2155,* P! *Glaziou 2301,* P!

Cyathea arbuscula (Baker) Domin, Pteridophyta 262. 1929.

Trichipteris arbuscula (Baker) Tryon, Contrib. Gray Herb. **200**:45. 1970.

Alsophila aperta Fée, Crypt. Vasc. Brés. **1**:158, t. 54 f. 2. 1869. HOLOTYPE: Brasilia fluminensi, *Glaziou 2301,* P! (Herb. Cosson).

Cyathea aperta (Fée) Domin, Pteridophyta 262. 1929.

Alsophila Ceropteris Fée, Crypt. Vasc. Brés. **1**:163, t. 57 f. 1. 1869. SYNTYPES: Brasilia fluminensi, *Glaziou 981,* P! (Herb. Cosson) Serra do Couto, *Glaziou 3169,* P! (Herb. Cosson).

Alsophila corcovadensis Fée, Crypt. Vasc. Brés. **1**:163, t. 56 f. 2. 1869, not *Alsophila corcovadensis* (Raddi) C. Chr., Ind. Fil. 41. 1905. SYNTYPES: Brasilia fluminensi ad montem Corcovado (both numbers), *Glaziou 985,* P! (Herb. Cosson), *Glaziou 1710,* P! (Herb. Cosson).

Alsophila Glaziovii Fée, Crypt. Vasc. Brés. **1**:160, t. 55 f. 2. 1869, not Baker, 1870. SYNTYPES: Serra do Couto (both numbers), *Glaziou 2155,* P! (Herb. Cosson), *Glaziou 3167,* P! (Herb. Cosson).

Cyathea Glaziovii (Fée) Domin, Pteridophyta 262. 1929.

Trichipteris Glaziovii (Fée) Tryon, Contrib. Gray Herb. **200**:45. 1970.

Alsophila guimariensis Fée, Crypt. Vasc. Brés. **2**:81, t. 103 f. 2. 1872–1873. HOLOTYPE: Brasilia fluminensi, *Glaziou 5252,* P! (Herb. Cosson).

Cyathea guimariensis (Fée) Domin, Pteridophyta 262. 1929.

Alsophila pallida Rosenst., Hedwigia **56**:356. 1915. TYPE COLLECTION: São Paulo, Rais da Serra, 1909, *Wacket 225,* B!

Cyathea pallida (Rosenst.) Domin, Pteridophyta 263. 1929.

Alsophila dryopteridoides Domin, Kew Bull. **1929**:218. 1929. HOLOTYPE: Minas Gerais, *Gardner 5331,* K!

Cyathea mesocarpa Domin, Acta Bot. Bohem. **9**:136. 1930, *nom. nov.* for *Alsophila dryopteridoides* Domin, 1929, not *Cyathea dryopteridoides* Maxon, 1925 (as *dryopteroides*).

Alsophila mesocarpa (Domin) C. Chr., Ind. Fil. Suppl. 3:22. 1934.

Stem 1.0–4.0 m. tall. *Petiole* ca. 0.3–0.4 m. long, stramineous to fuscous, aculeate; scales fulvous to fuscous with a cretaceous border or uniformly fulvous; scurf absent or of minute, fulvous trichomidia; trichomidia occasional on lamina axes; costae and costules with bullate, cretaceous squamulae; lamina otherwise glabrous. *Lamina* ca. 1.3 m. long, 2-pinnate to 2-pinnate-pinnatifid, papyraceous, apex gradually reduced and acute; pinnae short-stalked; pinnules short-petiolulate, entire to pinnatifid, base truncate, cuneate, or subcordate, apex attenuate, tip entire; lobes acute, entire; fertile veins forked at the sori or simple, sterile veins forked or simple. *Sori* inframedial to supramedial; paraphyses shorter than the sporangia, receptacle pilose.

The species epithet refers to the broad, cretaceous petiole-scale border present in most collections of this species. Petiole scales of some specimens have darkened borders. In a few cases the scales are uniform in color. Long-attenuate pinnules of a dark green color, bullate cretaceous costal squamulae, and a tendency toward multiseriate paraphyses also characterize *Trichipteris dichromatolepis.* Noticeable variability in the dissection of the pinnules, especially toward the apex of the leaf, and variation in the venation are characteristic of the species. *Trichipteris dichromatolepis* is found in wet, secondary forests in the coastal ranges of southern Brazil, at altitudes from 800 to 2000 meters.

SELECTED COLLECTIONS. **Brazil. Minas Gerais.** Serra do Caparão, *Brade 16939* (GH). **São Paulo:** Serro do Itatius, Mun. Iguape, *Brade 8255* (US); Paranapiacaba, Estação Biológica, *Handro 1231*(GH,US). **Rio de Janeiro:** Estrada Redentor, km. 11, *Brade 16831* (F,MO,NY,US); SE side of Mt. Itatiaia, Riberão Campo Belo, km. 8 beyond Maromba, *Tryon & Tryon 6662* (GH).

33. **Trichipteris corcovadensis** (Raddi) Copel.

FIGS. 94–99. MAP 34.

Trichipteris corcovadensis (Raddi) Copel., Gen. Fil. 97. 1947.

Polypodium corcovadense Raddi, Opusc. Sci. Bol. 3:288. 1819. HOLOTYPE: Brazil, *Raddi*, FI not seen. ISOTYPE: P! (in vertiu montis Corcovado).

Alsophila corcovadensis (Raddi) C. Chr., Ind. Fil. 41. 1905.

Cyathea corcovadensis (Raddi) Domin, Pteridophyta 262. 1929.

Polypodium Taenitis Roth, Nov. Pl. Spec. pr. Ind. Orient. 394. 1821, *ex char.* HOLOTYPE: E Rio Janeiro . . . communicavit . . . Mertens, not seen.

Alsophila Taenitis (Roth) Kze., Linnaea 9:90. 1834.

Trichopteris Taenitis (Roth) Hook., Sp. Fil. 1:35. 1844.

Trichipteris excelsa Presl, Del. Prag. 1:172. 1822. HOLOTYPE: in monte Corcovado ad Rio-Janeiro Brasiliae, *Raddi*, FI not seen. ISOTYPE: P!

Alsophila excelsa (Presl) Mart., Icon. Plant. Crypt. Bras. 63, t. 29 f. 1, 2 t. 37. 1834.

Chnoöphora excelsa (Presl) Mart., Icon. Plant. Crypt. Bras. t. 27. 1834. This combination appears only in t. 27.

Alsophila elegans Mart., Icon. Plant. Crypt. Bras. 63, t. 38. 1834, *ex icone*, not *Cyathea elegans* Hew., 1838. SYNTYPES: crescit in Prov. S. Pauli et Minarum Generalium sylvis, *Martius*, not seen.

Trichipteris elegans (Mart.) Presl. Tent. Pterid. 59. 1836.

Alsophila Miersii Hook., Sp. Fil. 1:38. 1844. SYNTYPES: Rio de Janeiro, Organ Mts., Brazil, *Gardner 117*, K not seen. Tejuco (Tijuca), *Miers*, K not seen. ISOSYNTYPES: *Gardner 117*, P! *Miers* (Rio de Janeiro), P!

Cyathea Miersii (Hook.) Domin, Pteridophyta 263. 1929.

Trichipteris Miersii (Hook.) Tryon, Contrib. Gray Herb. 200:46. 1970.

Alsophila Glaziovii Baker, Fl. Bras. 1(2):592. 1870, not *A. Glaziovii* Fée, 1869. HOLOTYPE: Orgãos, Brazil, *Glaziou 3582*, K not seen. ISOTYPE: B!

Alsophila decipiens Fée, Crypt. Vasc. Brés. 2:81, t. 103 f. 1. 1872–1873. SYNTYPES: Itatiaia, *Glaziou 7032*, P! (Herb. Cosson) *Glaziou 5244*, P! (Herb. Cosson).

Alsophila Feeana C. Chr., Ind. Fil. 42. 1905, *nom. nov.* for *Alsophila Glaziovii* Baker, 1870, not *A. Glaziovii* Fée, 1869.

Cyathea Feeana (C. Chr.) Domin, Pteridophyta 262. 1929.

Trichipteris Feeana (C. Chr.) Copel., Gen. Fil. 97. 1947.

Cyathea Sternbergii Domin, Pteridophyta 263. 1929, *nom. nov.* for *Alsophila elegans* Mart., not *Cyathea elegans* Hew. 1838, not *Cyathea Sternbergii* Sternb., 1820.

Cyathea elegantula Domin, Acta Bot. Bohem. 9:113. 1930, *nom. nov.* for *Alsophila elegans* Mart., 1834, not *Cyathea elegans* Hew., 1838.

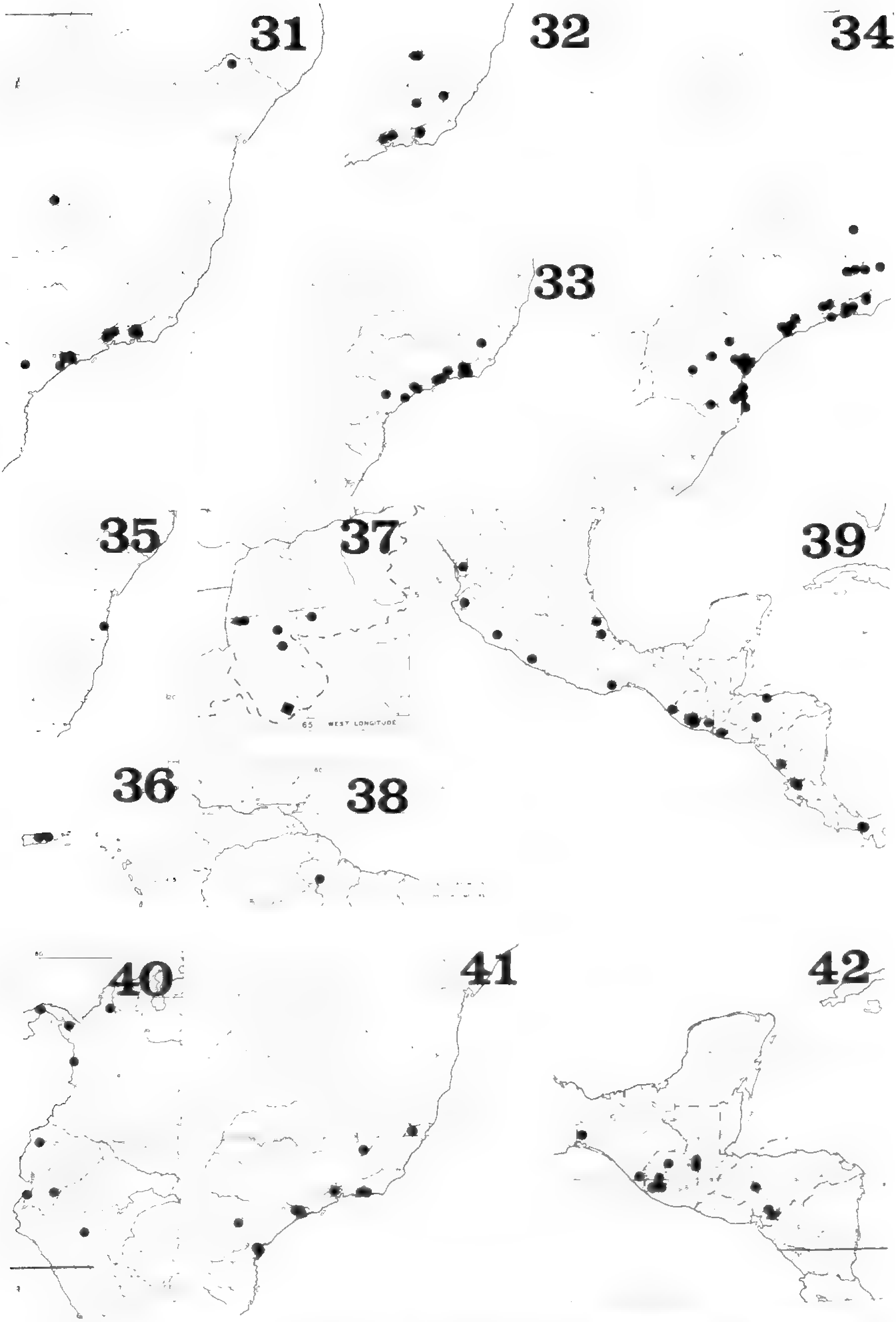
Alsophila Damazioi Brade, Arquiv. Jard. Bot. Rio Janeiro 11:23, t. 3 t. 6 f. 11. 1951. HOLOTYPE: Serra de Sacramento, *Damazio*, HB!

Alsophila Hoehneana Brade, Arquiv. Jard. Bot. Rio Janeiro 11:24, t. 4 t. 6 f. 6. 1951. HOLOTYPE: São Paulo, Parque do Estado, *Hoehne*, HB! ISOTYPE: NY!

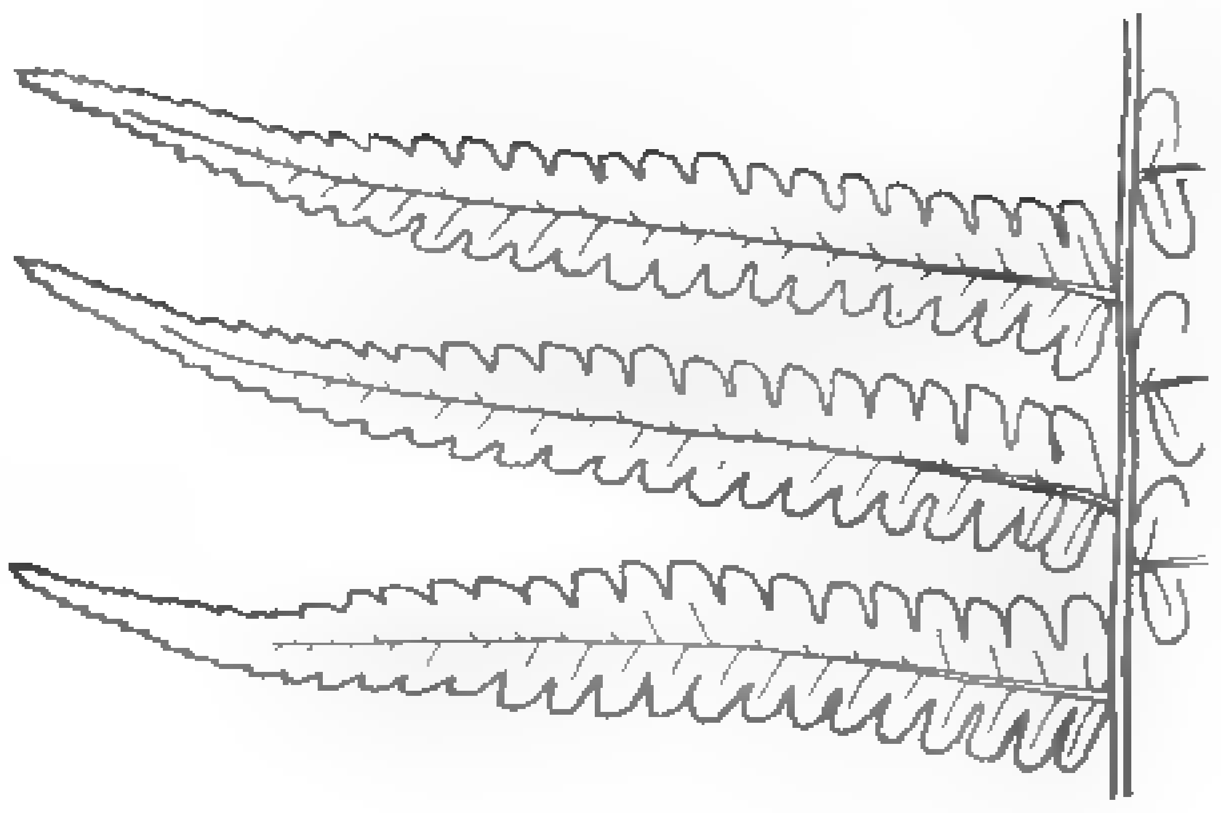
Alsophila Mello-barretoi Brade, Arquiv. Jard. Bot. Rio Janeiro 11:22, t. 2 t. 5 f. 4. 1951. HOLOTYPE: Serro do Cipó, *Mello-Barreto 512*, HB not seen. PARATYPE: *Barreto & Brade 14389*, HB not seen. ISOPARATYPE: MO!

Trichipteris Mello-barretoi (Brade) Tryon, Contrib. Gray Herb. 200:45. 1970.

Stem 0.3–0.6 m. tall. *Petiole* 0.4–0.8 m. long, stramineous to atropurpureous, tuberculate to aculeate; scales uniformly fulvous to fuscous; scurf absent or of fulvous trichomidia; axes of lamina glabrous or with cretaceous to fulvous trichomidia; costae with cretaceous to fulvous, flattish to bullate squamulae. *Lamina* 1.3–2.5 m. long,



MAPS 31–42: 31, Trichipteris phalerata var. Iheringii; 32, T. Gardneri; 33, T. dichromatolepis; 34, T. corcovadensis; 35, T. praecincta; 36, T. borinquena; 37, T. demissa var. demissa (dots), T. demissa var. thysanolepis (diamond) and T. Cyclodium (triangle); 38, T. nanna; 39, T. costaricensis; 40, T. pilosissima; 41, T. leucolepis; 42, T. mexicana.



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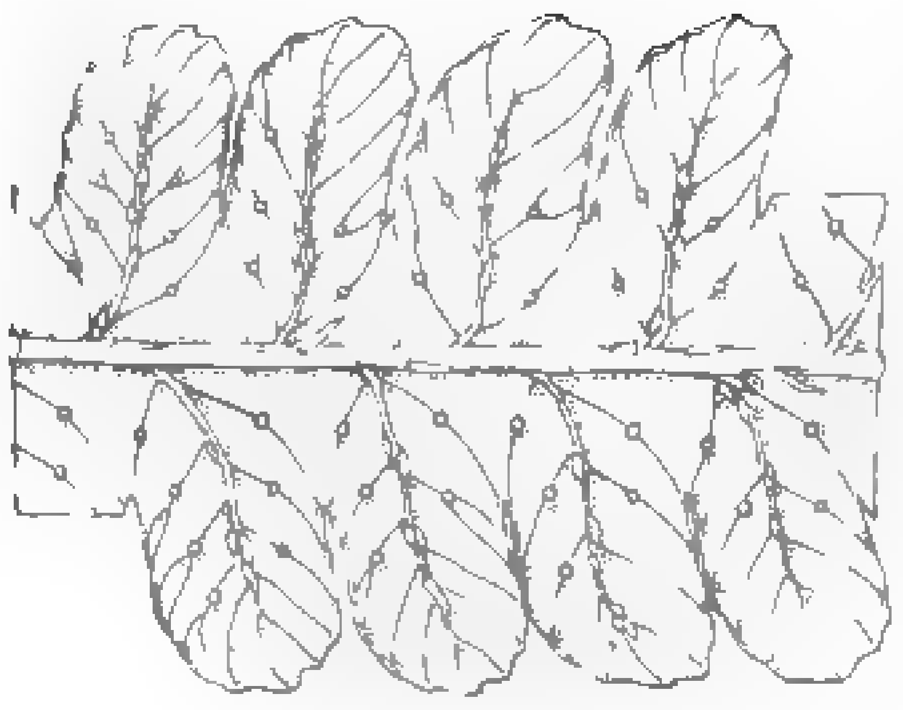

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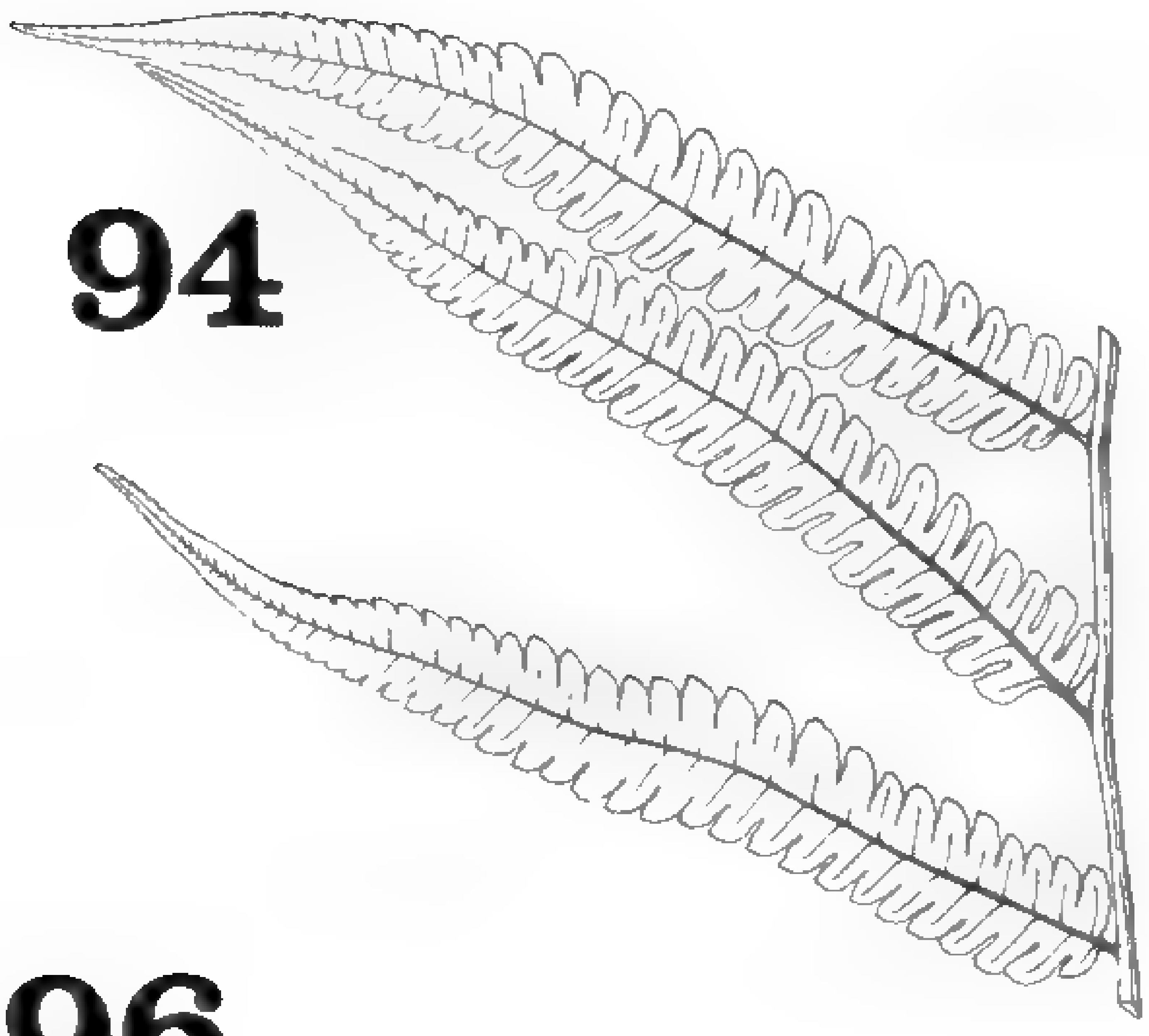

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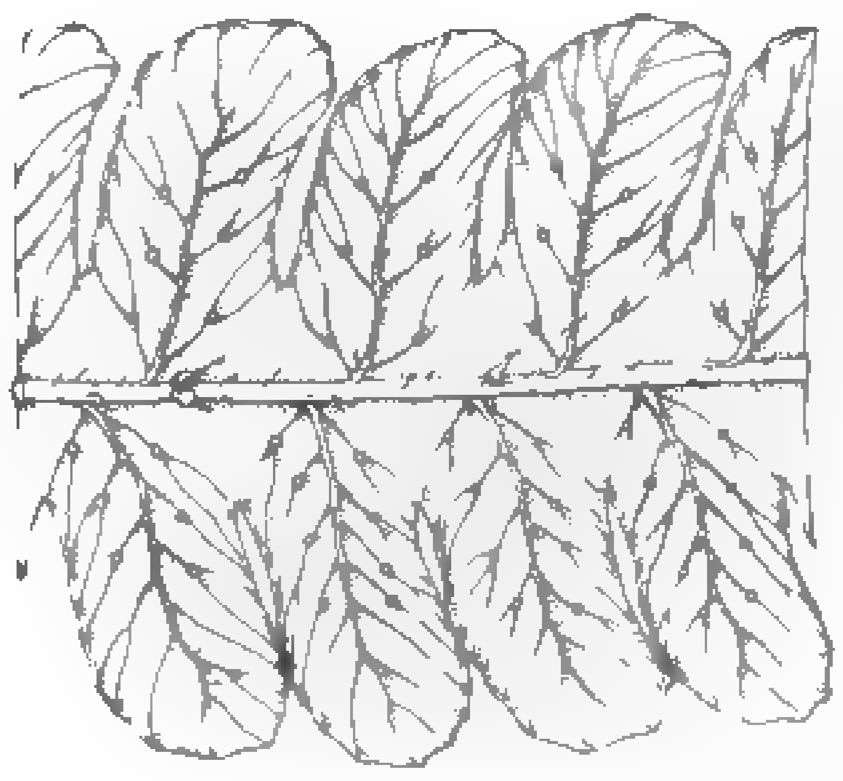

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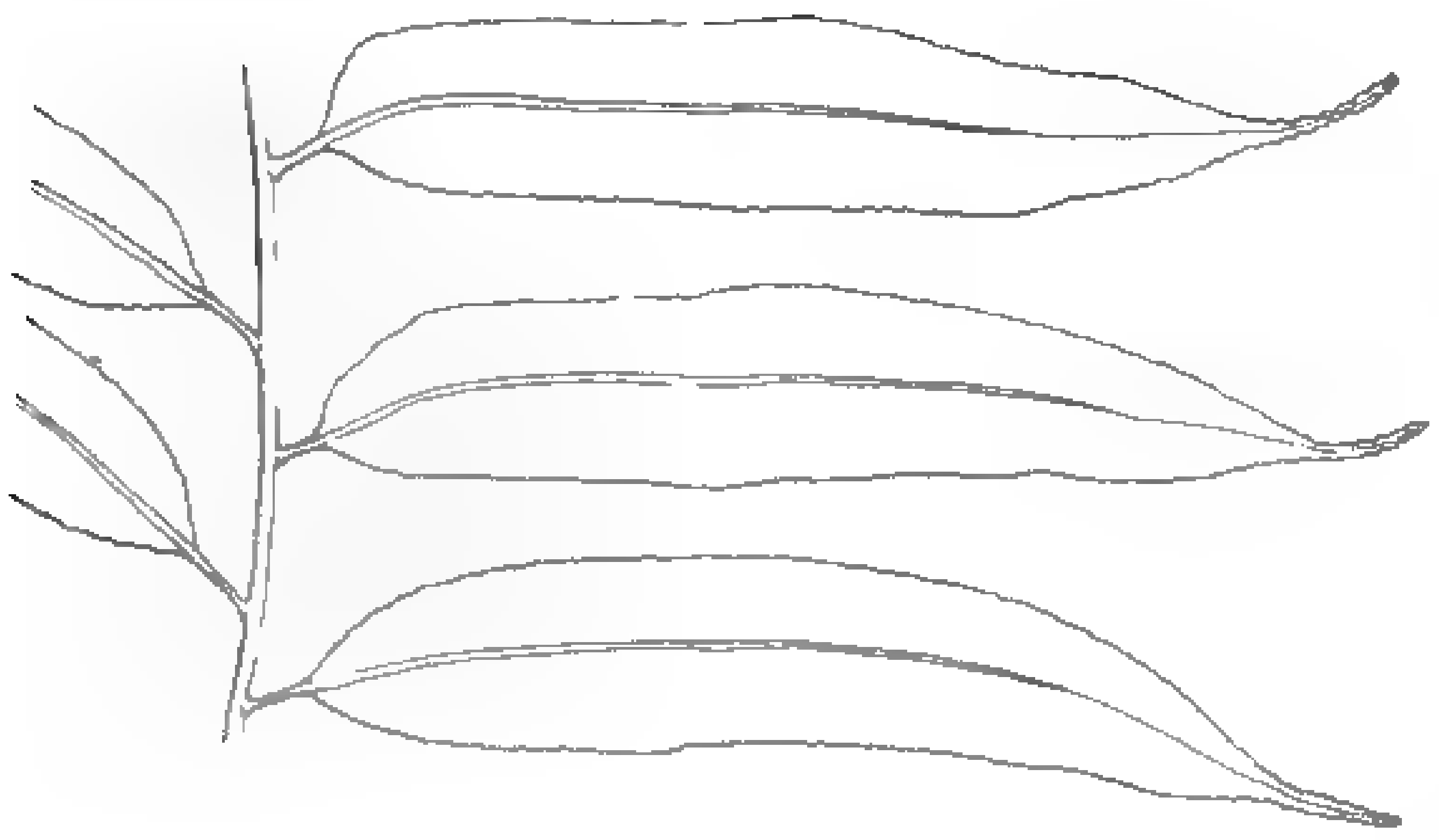

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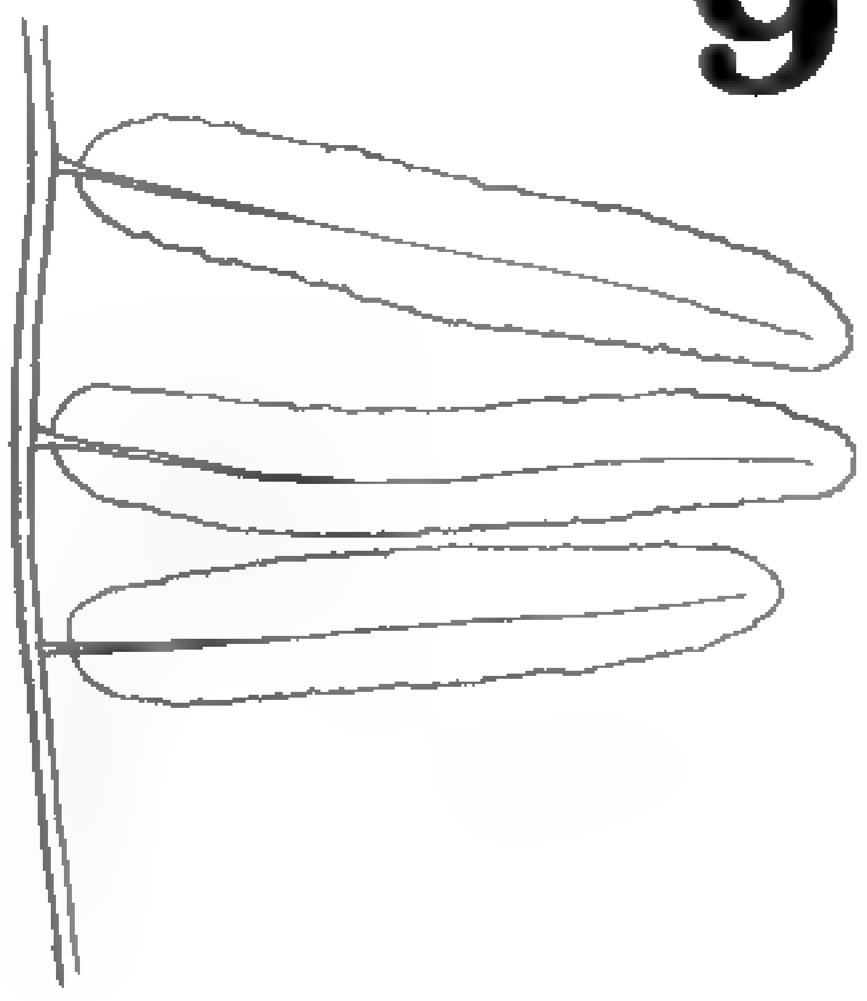

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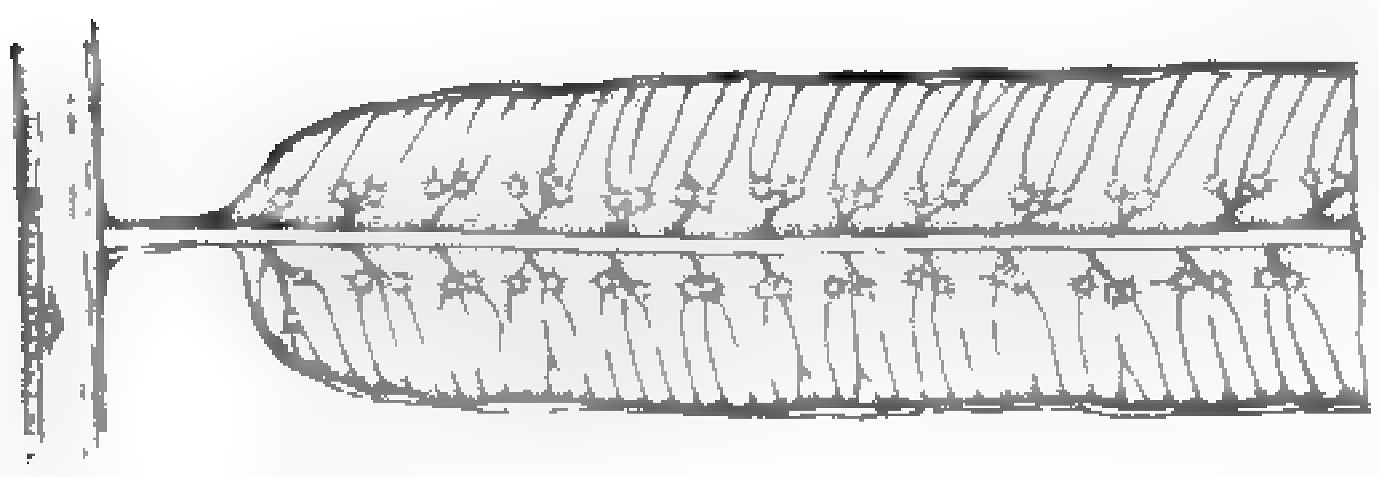

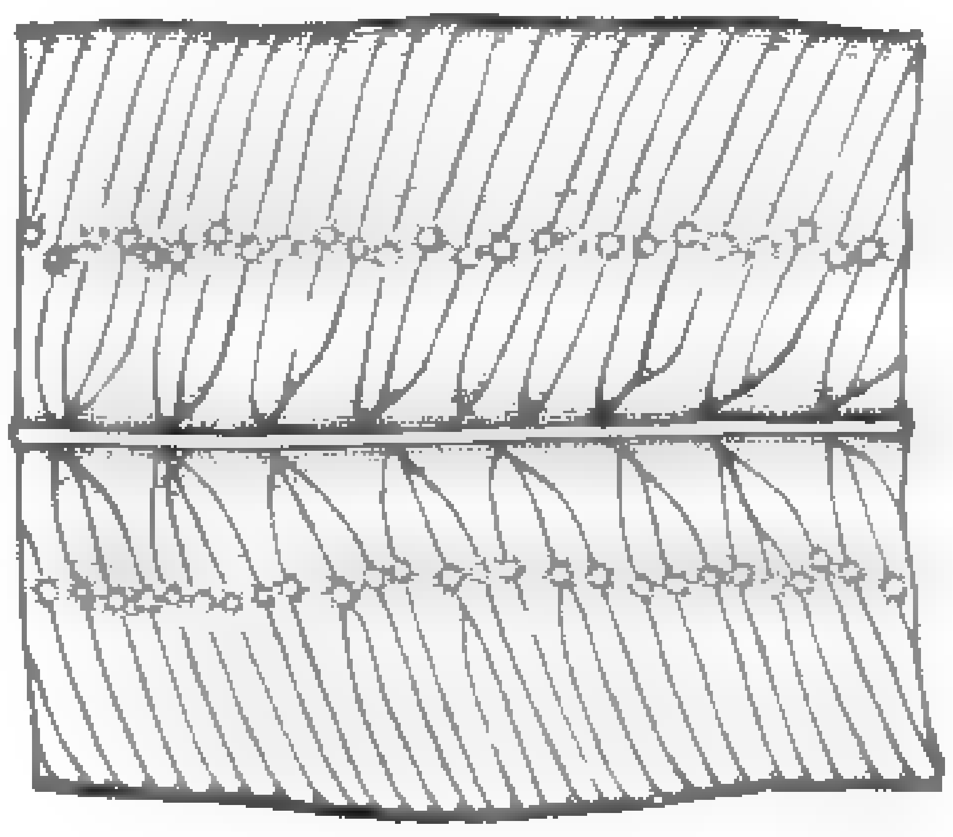

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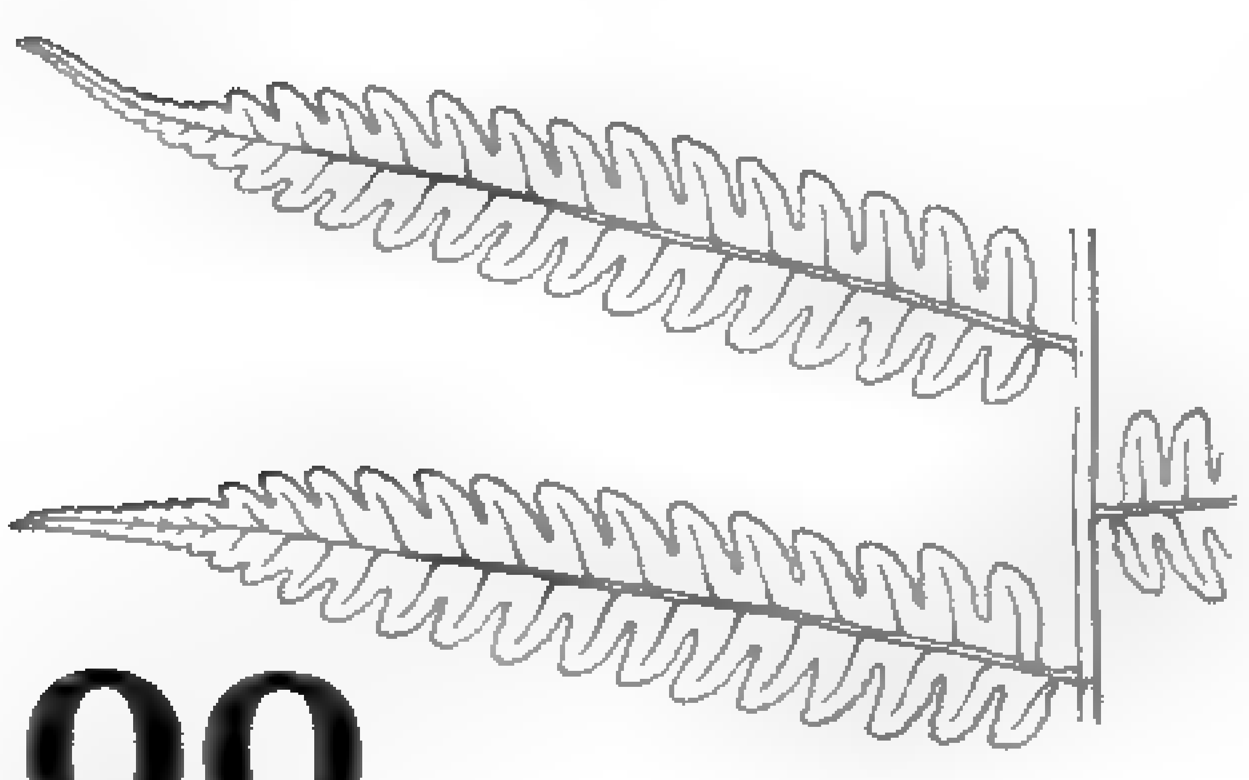

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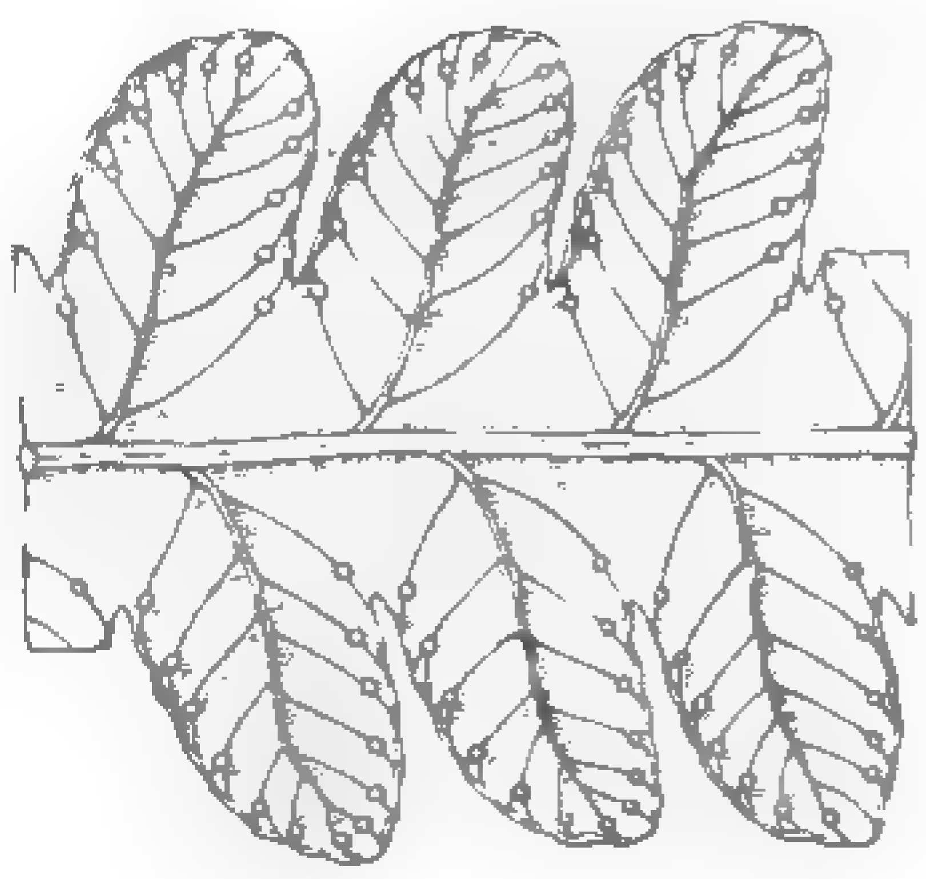

101

2-pinnate to 2-pinnate-pinnatifid, papyraceous to coriaceous, apex gradually reduced, acute to long-acuminate; pinnae stalked, apex abruptly reduced and pinna-like, often articulated to the pinna-rachis; pinnules petiolulate to long-petiolulate, entire to pinnatifid, base cordate to cuneate, apex rotund to attenuate, tip entire to crenulate; lobes rotund, entire; costae often indistinct, the veins all concurrent to the margin; fertile veins simple, sterile veins simple or forked. *Sori* subcostal to supramedial, often in a single medial line; paraphyses longer than the sporangia; receptacle villous.

Trichipteris corcovadensis is the only species in the genus with pinnule-like (conform) pinna apices. There is extreme variation in pinnule shape and dissection. Pinnatifid specimens resemble species associated with *T. phalerata,* and it is probable that *T. corcovadensis* is allied with these species. The type collection is of a plant with simple 2-pinnate leaves and conform, articulate apical pinnules. Some careful collecting and observation by Paulo Windisch indicates that there is some correlation of pinnule dissection with exposure to sunlight and other environmental factors. *Trichipteris corcovadensis* is found in secondary forests, primary forests, and scrubby campos in the Serra do Mar area of southern Brazil, at altitudes of from 250 to 2100 meters.

SELECTED COLLECTIONS. **Brazil. Minas Gerais:** Serra do Cipó, km. 131–Palacio–1100 m., *Duarte 2087* (F,MO,NY); Viçosa, road to São Miguel, near km. 4, *Mexia 4634* (F,GH,MO,NY). **Rio de Janeiro:** Itatiaia, *Brade 15556* (F,GH,NY); Serra dos Orgãos, *Brade 16445* (F,GH,NY). **São Paulo:** São Paulo, Agua Funda, nativa no Jardim Botanico, *Handro 2203* (GH); Sitio São José, Campos do Jordão, *Leite 3572* (A,GH,US). **Paraná:** Jaguariahyva, *Dusén 15148* (GH,MO); Serra da Prata, *Dusén 15300* (F,GH,MO). **Sta. Catarina:** Joinville, 300 m., *Schmalz 51* (F,MO); Mun. Ibirima, Ibirima, alt. 250–350 m., *Smith & Klein 7580* (US).

34. Trichipteris praecincta (Kze.) Tryon

FIGS. 100, 101. MAP 35.

Trichipteris praecincta (Kze.) Tryon, Contrib. Gray Herb. 200:46. 1970.

Alsophila praecincta Kze., Flora 1839 Beiblatt:53. LECTOTYPE (chosen herewith): Ilheus, Prov. Bahía, *Martius 391*, B! ISOLECTOTYPES: MO! NY! LECTOPARATYPE: *Luschnath,* not seen. Presumably the original specimen of *Martius 391* was at LZ and destroyed.

Cyathea praecincta (Kze.) Domin, Pteridophyta 263. 1929.

Alsophila submarginalis Domin, Kew Bull. **1929**:217. 1929, & Mem. Roy. Czech. Soc. Sci. II, **2**:88, t. 9 f. 4–8, t. 17 f. 2. 1929. HOLOTYPE: *Martius 391*, Herbar. Florae Brazil, det. "A. praecincta Kze." not seen. ISOTYPES: B! MO! NY!

Cyathea submarginalis (Domin) Domin, Acta Bot. Bohem. 9:163. 1930.

Trichipteris submarginalis (Domin) Tryon, Contrib. Gray Herb. 200:46. 1970.

Stem unknown. *Petiole* ca. 35 cm. long, fuscous, muricate; scales fulvous with a

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FIGS. 92–101. FIGS. 92 & 93, *Trichipteris dichromatolepis:* 92, three pinnules from a central pinna, × 1/3; 93, central part of a pinnule, × 4/3 (both *Brade 14384*, MO). FIGS. 94–99, *T. corcovadensis:* 94, three central pinnules from a central pinna (pinnatifid form), × 1/3; 95, central part of a pinnule (pinnatifid form, × 4/3 (both *Smith & Brade 2233*, GH); 96, three pinnules of a central pinna (typical form), × 1/3 (*L. B. Smith 5676*, GH); 97, three central pinnules from a central pinna (obtuse form), × 1/3 (*Duarte 2087*, F); 98, basal part of an entire pinnule, × 4/3 (*Brade 16445*, GH); 99, part of an entire pinnule, × 1, (*Glaziou*, GH). FIGS. 100 & 101, *T. praecincta:* 100, two central pinnules from a central pinna, × 1/3; 101, central part of a pinnule, × 4/3 (both *Martius 391*, NY).

cretaceous border; scurf absent; costae and costules with flattish to bullate, cretaceous to fulvous squamulae; axes of lamina otherwise glabrous. *Lamina* length unknown, 2-pinnate-pinnatifid, papyraceous, apex unknown; pinnae stalked; pinnules petiolulate, pinnatifid to deeply pinnatifid, base subcordate to cuneate, apex acuminate to attenuate, tip serrate; lobes rotund to acute, entire; fertile veins forked at the sori or simple. *Sori* submarginal; paraphyses much shorter than the sporangia, receptacle puberulous.

There is not enough material to adequately define *Trichipteris praecincta* as a species. There are no modern collections, and the extant collections include only scanty material of petiole scales. This species is the only one in the genus with acuminate pinnules and submarginal sori. Because of the lack of material, affinities are unclear. I have tentatively placed *T. praecincta* with the Brazilian species group. It is possible, however, that *T. praecincta* represents a coastal species derived from ancestors resembling *T. procera,* which is basically Andean in distribution. The known collections are all from the coastal part of Bahía.

SELECTED COLLECTIONS. **Brazil. Bahía:** *Hohenacker* (GH). **State undetermined:** *Riedel* (GH,US).

35. **Trichipteris borinquena** (Maxon) Tryon

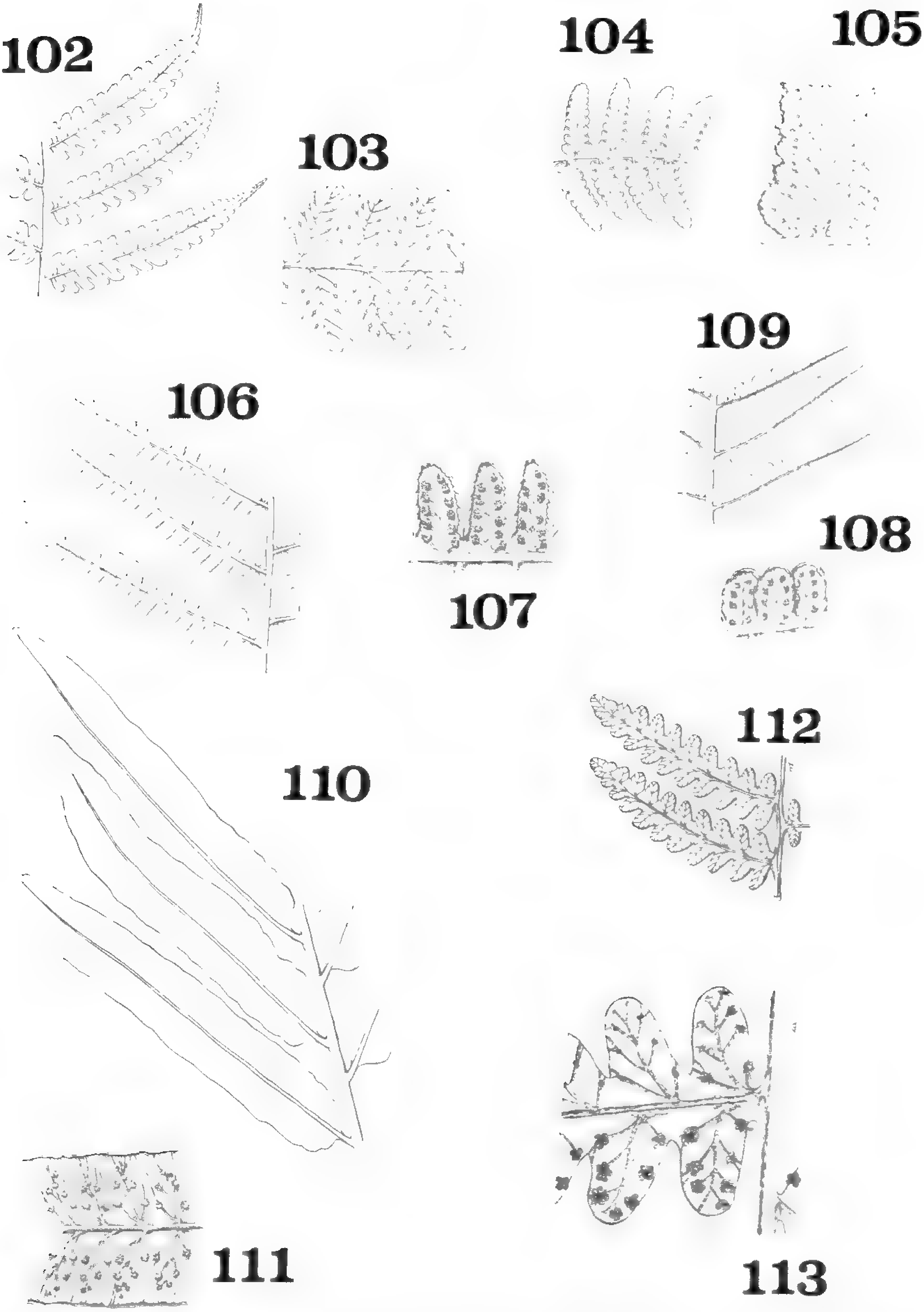
FIGS. 102, 103. MAP 36.

Trichipteris borinquena (Maxon) Tryon, Contrib. Gray Herb. 200:44. 1970.
Alsophila borinquena Maxon, Am. Fern Journ. **15**(2):56. 1925. HOLOTYPE: Luquillo Mts., Puerto Rico, *Britton & Brauner 7571,* US 1145551!
Cyathea borinquena (Maxon) Domin, Acta Bot. Bohem. 8:99. 1930.

Stem creeping to ascendant, to ca. 1 m. long. *Petiole* 0.3–0.8 m. long, fulvous, tuberculate to aculeate; scales uniformly fulvous, the structural margin indistinct; scurf absent; costae and costules with flattish to bullate, fulvous squamulae; axes of lamina otherwise glabrous. *Lamina* to ca. 2.0 m. long, 1-pinnate-pinnatifid or 2-pinnate-pinnatifid, coriaceous, apex gradually reduced and long-acuminate; pinnae stalked, remote in 1-pinnate-pinnatifid plants; pinnules short-petiolulate to petiolulate, deeply pinnatifid (pinnae of 1-pinnate specimens often pinnatisect and approaching 2-pinnate), base cordate to cuneate, apex acuminate, tip entire; lobes rotund to truncate, entire to serrulate (lobes of 1-pinnate plants often acute and crenulate); fertile veins usually forked at the sori or occasionally simple, sterile veins forked or simple. *Sori* medial; paraphyses shorter than the sporangia, sometimes multiseriate, receptacle pilose.

Trichipteris borinquena lacks both soral squamulae and petiole scurf. The lack of petiole scurf and the uniformly pigmented petiole scales suggest that this highly isolated species of the West Indies is allied to Brazilian species such as *T. phalerata. Trichipteris borinquena* varies in the dissection of the lamina and the habit of the stem. It is endemic to Puerto Rico, where it is found in wet, montane forests from 500 to 1000 meters. The margin of the petiole scale is poorly differentiated, suggesting that this species may be one of the least differentiated in the genus.

SELECTED COLLECTIONS. **Puerto Rico.** Monte Cerrote, near Adjuntas, *Britton & Brown 5441* (F,NY); Sierra de Luquillo, in monte Jimenes, *Sintenis 1754* (F,GH,NY).



FIGS. 102–113. FIGS. 102 & 103, *Trichipteris borinquena:* 102, three central pinnules from a central pinna, × 1/3; 103, central part of a pinnule, × 4/3 (both *Scamman 6515*, GH). FIGS. 104–109, *T. demissa:* 104, var. *demissa*, central pinnules from a central pinna, × 1/3; 105, var. *demissa*, basal part of a pinnule, × 4/3 (both *Maguire & Politi 27779*, GH); 106, var. *thysanolepis*, three central pinnae, × 1/3; 107, var. *thysanolepis*, three lobes of a pinna, × 1 (both *Maguire, Wurdack & Bunting 37291*, GH); 108, var. *thysanolepis*, three lobes of a pinna, × 1; 109, var. *thysanolepis*, three pinnae, × 1/3 (both *Maguire, Wurdack & Bunting 37100*, US). FIGS. 110 & 111, *T. Cyclodium:* 110, three central pinnae, × 1/3; 111, part of a fertile pinna, × 2/3 (both *Maguire & Politi 27541*, NY). FIGS. 112 & 113, *T. nanna:* 112, two central pinnae, × 1/3; 113, basal part of a pinna, × 4/3 (both *Tillet, Tillet & Boyan 45119*, US).

36. **Trichipteris demissa** (Morton) Tryon

The genus *Trichipteris* is notable for two species endemic to the Guayana Highlands. *Trichipteris demissa* and the related *T. Cyclodium* differ principally in the architecture of the lamina. Both have nearly to entirely glabrous leaves (excluding the petiole scales). Both have obtuse ultimate segments and paraphyses about as long as the sporangia. Their placement in the genus is uncertain. The two have apparently been isolated from the rest of the genus for some time. Variability in *T. demissa* is extreme in leaf dissection. The species includes both 1-pinnate-pinnatifid and 2-pinnate-pinnatifid plants. *Trichipteris demissa* var. *thysanolepis* is a 1-pinnate-pinnatifid population confined to Cerro de la Neblina. It is characterized by long, multicellular trichomes borne on the edges of the petiole scales. Geographic isolation of this partially differentiated population emphasizes the importance of the Guayana Highlands topography to the evolution in this group. *Trichipteris demissa* is found on five tepuís in the Guayana Highlands. Open slopes, sheltered niches in rock, and tepuí summit scrub forests constitute its habitat. In altitude *T. demissa* ranges from 1500 to 2100 meters.

36a. **Trichipteris demissa** (Morton) Tryon var. **demissa**

FIGS. 104, 105. MAP 37.

Trichipteris demissa (Morton) Tryon, Contrib. Gray Herb. 200:46. 1970.
Alsophila demissa Morton, Fieldiana Bot. **28**(1):7. 1851. HOLOTYPE: summit Cerro Duida, Amazonas, Venezuela, *Tate 402,* US 1498535! ISOTYPE: NY! PARATYPES: same locality, *Tate 626,* US! *Steyermark 58308,* US! ISOPARATYPE: *Tate 626,* NY!

Stem ascendant, ca. 0.3 m. long. *Petiole* 0.3–0.5 m. long, atropurpureous, inermous to tuberculate; scales uniformly fulvous to fulvous with a cretaceous border; scurf absent; axes glabrous. *Lamina* 0.4–0.8 m. long, 2-pinnate to 2-pinnate-pinnatifid, rigidly coriaceous, apex abruptly reduced and pinna-like to gradually reduced and long-acuminate; pinnae stalked; pinnules petiolulate, crenulate to pinnatisect, base cordate or rarely truncate, apex obtuse; lobes rotund, often crenulate; fertile veins forked at the sori, sterile veins forked or simple. *Sori* medial to supramedial; paraphyses shorter than the sporangia, receptacle pilose.

SELECTED COLLECTIONS. **Venezuela. Bolívar:** Meseta de Jaua; Cerro Jaua, Cumbre de la porción Central-Occidental de la Meseta, *Steyermark 97989* (GH), *Steyermark 97900* (GH,NY). **Amazonas:** Serranía Parú, Río Parú, Caño Asísa, Río Ventauri, *Cowan & Wurdack 31126* (GH,NY,US); *Phelps & Hitchcock 519* (US); Cerro Sipapo (Paráque), SE ridge, *Maguire & Politi 27779* (GH,NY,US).

36b. **Trichipteris demissa** (Morton) Tryon var. **thysanolepis** Barr.

FIGS. 106–109. MAP 37.

Trichipteris demissa (Morton) Tryon var. *thysanolepis* Barr., Rhodora **78**(813): 1 t. 1 f. 1, 2. 1976. HOLOTYPE: Venezuela, Territorio de Amazonas, summit, Cerro de la Neblina, Río Yatua, January 15, 1954, *Maguire, Wurdack & Bunting 37291,* NY! ISOTYPES: GH! US! PARATYPES: Venezuela, Territorio de Amazonas, Cerro de la Neblina, Río Yatua, *Maguire, Wurdack & Maguire 42346,* US!; *Maguire, Wurdack & Bunting 37100,* US!

Stem unknown. Petiole 0.2–0.4 m. long, atropurpureous, inermous to tuberculate; scales uniformly fulvous, bearing trichomidia along the edges; petiole with a few trichomes; scurf of large, fimbriate, fulvous squamulae; rachis and pinna-rachises with a few long trichomes and squamulae. *Lamina* 0.3–0.6 m. long, 1-pinnate-pinnatifid, rigidly coriaceous, apex gradually reduced and long-acuminate; pinnae adjacent, sessile, deeply pinnatifid to pinnatisect, base cordate to truncate, apex attenuate, tip crenulate; lobes acute to rotund, entire; fertile veins forked at the sori, sterile veins forked or simple. *Sori* medial to supramedial; paraphyses as long as the sporangia, receptacle hirsute.

37. **Trichipteris Cyclodium** Tryon

FIGS. 110, 111. MAP 37.

Trichipteris Cyclodium Tryon, Rhodora **74**:446. 1972. HOLOTYPE: Cerro Sipapo (Paráque), Amazonas, Venezuela, 1948, *Maguire & Politi 27451*, NY! ISOTYPES: GH! US!

Stem erect, 5–15 cm. tall. *Petiole* ca. 80 cm. long, atropurpureous, barely tuberculate; scales fuscous with a cretaceous border; scurf of a few minute trichomidia; rachis and pinna-rachises with some bicolorous scales similar to those of the petiole and cretaceous squamulae. *Lamina* ca. 0.7 m. long, 1-pinnate, rigidly coriaceous, apex abruptly reduced to an articulate apical pinna; pinnae adjacent, petiolulate, entire to crenate, base cuneate, apex acuminate, tip obtuse, entire; costules indistinct, veins all concurrent to the margin, fertile and sterile veins sometimes anastomosing, fertile veins undivided at the sori, sterile veins simple. *Sori* in three to four inframedial to supramedial rows; paraphyses as long as the sporangia, receptacle hirsute.

Trichipteris Cyclodium is the only 1-pinnate species with entire, blunt-tipped pinnae. It resembles *T. demissa* in indument and texture of the leaves. The species is known only from the type collection.

38. **Trichipteris nanna** Barr.

FIGS. 112, 113. MAP 38.

Trichipteris nanna Barr., Rhodora **78**(813):3, t. 1 f. 3, 4. 1976. HOLOTYPE: upper Mazaruni River Basin, Mt. Ayanganna, on shoulder of E flank, about Thompson Camp, 1418 m., 12 August 1960, *Tillet, Tillet & Boyan 45119*, US!

Stem 1.0 m. tall. *Petiole* 13 cm. long, atropurpureous, tuberculate; scales fulvous with a broad, cretaceous border; scurf absent; rachis with scales similar to those of the petiole; the costae sometimes with trichomidia and flattish, cretaceous squamulae; axes of lamina otherwise glabrous. *Lamina* 40 cm. long, 1-pinnate-pinnatifid, coriaceous, apex gradually reduced and acuminate; pinnae sessile, pinnatifid, base cuneate to truncate, apex acuminate, tip obtuse and entire; lobes rotund, entire; fertile veins forked at the sori or the basal sori of a segment borne on simple veins, sterile veins forked or simple. *Sori* submarginal; paraphyses as long as the sporangia, receptacle hirsute.

Trichipteris nanna superficially resembles *T. phalaenolepis* and *T. ursina*. It differs from those two species in having submarginal sori and normally dichotomous veins. *Trichipteris nanna* is a morphologically derived species, possibly related to *T. demissa*, which has similar petiole scales, ultimate segments, lamina indument, and paraphyses. The one collection is from a mid-elevation crest forest.

39. **Trichipteris costaricensis** (Kuhn) Barr.

FIGS. 114, 115. MAP 39.

Trichipteris costaricensis (Kuhn) Barr., Rhodora 78(813):1. 1976.
Hemitelia costaricensis Mett., Ann. Sci. Nat. V. 2:265. 1864, *nom. nud.*
Hemitelia costaricensis Kuhn, Linnaea 36:159. 1869. LECTOTYPE (chosen herewith): Costa Rica et Varagua, *Warscewicz 36,* B! fragment ex B, NY! fragment ex B, US! LECTOPARATYPE: Panama, *Sutton-Hayes,* fragment ex B, NY! ISOLECTOPARATYPE: P!
Cyathea costaricensis (Kuhn) Domin, Acta Bot. Bohem. 9:107. 1930.

Stem 0.5–7.5 m. tall. *Petiole* ca. 0.5 m. long, fuscous to fulvous, inermous to tuberculate; scales fulvous with a cretaceous border; scurf absent or consisting of a few fulvous trichomidia and cretaceous squamulae; rachis and pinna-rachises glabrous; costae and costules glabrous or with cretaceous trichomidia and cretaceous to fuscous squamulae; veins with cretaceous trichomidia. *Lamina* ca. 2.5 m. long, 2-pinnate-pinnatisect, papyraceous, apex gradually reduced and acute; pinnae short-stalked; pinnules short-petiolulate, pinnatisect, base truncate, apex attenuate, tip crenulate; lobes acute, serrate to crenulate; fertile veins forked at the sori, sterile veins forked. *Sori* inframedial to medial, subtended by several cretaceous soral squamulae; paraphyses shorter than the sporangia, receptacle pilose.

Trichipteris costaricensis is the only Central American species with soral squamulae. It has no close relatives in the genus. The development of the trichomidia on the costae and costules is variable. The soral squamulae closely resemble an indusium, but consist of several closely appressed, bullate squamulae extending over the sorus. *Trichipteris costaricensis* is found in arroyos, canyons, and grassy slopes in Mexico. The more southerly collections are from stream banks, deep quebradas, and cool, moist canyon floors. The species extends as far south as Chiriquí Province in Panama. It grows from 400 to 1400 meters in altitude.

SELECTED COLLECTIONS. **Mexico. Nayarit:** Rancho Cora, Sierra San Juan, *Gentry, Barclay & Arguelles 19480* (GH). **Jalisco:** Arroyo de la Cordoncillera, a little S of Puerto Vallarta, *Philipps* (F,GH,MO). **Michoacán:** Aquila-Coahuayana, Coalcoman, *Hinton et al. 16262* (F,MO). **Guerrero:** Pasion, Montes de Oca, *Hinton et al. 10793* (GH,MO,NY). **Veracruz:** Vallée de Cordova, *Bourgeau 1454* (GH,NY); near Tlapocoyan, on road from Tezuitlan, *Riba, Tryon & Tryon 309* (GH,NY). **Oaxaca:** Pluma Hidalgo, 1200 m., *Hernandez X. 3320* (US). **Chiapas:** Cacahuatan, 1800′, *Fisher 35396* (F,MO, NY,US); Finca Mexiquito, *Purpus 6712* (F,MO,NY). **Guatemala. Quezaltenango:** Colomba, *Skutch 1340* (GH). **Retalhuleu:** San Felipe, *Donnell Smith 2718* (GH,MO, NY); vicinity of San Felipe, *Maxon & Hay 3532* (NY). **Esquintla:** Panaleon, *Tonduz & Rojas 1* (GH,MO,NY); San Andres Osuna, *Seler & Seler 2548* (GH). **Santa Rosa:** Santa Rosa, *Donnell Smith 3219* (GH,MO,NY); Aguacaliente, *Kellerman 7793* (F). **El Salvador. San Salvador:** Tonacatepeque, *Calderón 212* (GH,NY); vicinity of Tonacatepeque, *Standley 19434* (F,GH,MO,NY). **Honduras. Atlántida:** vicinity of La Ceiba, *Yuncker, Koepper & Wagner 8750* (F,GH,MO,NY). **Comayagua:** vicinity of Siguatepeque, *Standley 56189* (GH); hills E of Siguatepeque, *Yuncker, Dawson & Youse 6352* (GH,MO,NY). **Nicaragua.** Managua, *Garnier A–1223, 1414* (GH). **Costa Rica. Alajuela:** entre Liberia y Guachipelín, *Brenes 15514* (F,NY). **Panama. Chiriquí:** near Remedios, *Allen 2683* (GH).

40. **Trichipteris pilosissima** (Baker) Barr., comb. nov.

FIGS. 116, 117. MAP 40.

Alsophila pilosissima Baker, Syn. Fil. ed. 2. 457. 1874. HOLOTYPE: Mt. Campana, East Peru, *Spruce 4322*, K!
Cyathea pilosissima (Baker) Domin, Pteridophyta 262. 1929.

Stem 0.5–2.0 m. tall. *Petiole* 0.5 m. long, fulvous, muricate to aculeate; scales fuscous with a cretaceous border (the border often abrading with age); scurf of minute, appressed trichomidia and sometimes cretaceous squamulae; trichomes when present cretaceous; long, cretaceous to fulvous trichomes present on all axes; pinna-rachises, costae, and costules with cretaceous to fulvous, flattish to bullate squamulae. *Lamina* ca. 1.5 m. long, 2-pinnate-pinnatifid, chartaceous, apex gradually reduced and long-acuminate to abruptly reduced and somewhat pinna-like; pinnae sessile; pinnules sessile to short-petiolulate, pinnatifid to pinnatisect, base truncate, apex obtuse to attenuate; lobes rotund, serrate; fertile and sterile veins forked or less commonly simple. *Sori* medial to supramedial; paraphyses longer than the sporangia, villous; one or two soral squamulae sometimes associated with the sorus.

Trichipteris pilosissima is a species of uncertain affinity within the genus. The variability in development of the scurf and in the venation makes certain placement impossible. A possible relation may be to *T. costaricensis* of Central America, which has similar petiole scales and a similar association of squamulae with the sorus (although poorly developed in *T. pilosissima.*) Interpretation of this species as allied to *T. Gardneri*, on the basis of the long, cretaceous trichomes, is not supported by any correlation with other characters. *Trichipteris pilosissima* can be confused with *Sphaeropteris senilis* (Kl.) Tryon, which has emarginate petiole scales. Species such as *T. hirsuta* and *T. rufa* are characterized by a lighter aspect to the foliage and the dark marginal setae of the petiole scales. *Trichipteris pilosissima* is a species of Panama and the Pacific coast of South America. It is found in rain forests, especially along watercourses, from sea level to 800 meters. A few of the collections from Peru apparently come from regions with Atlantic drainage.

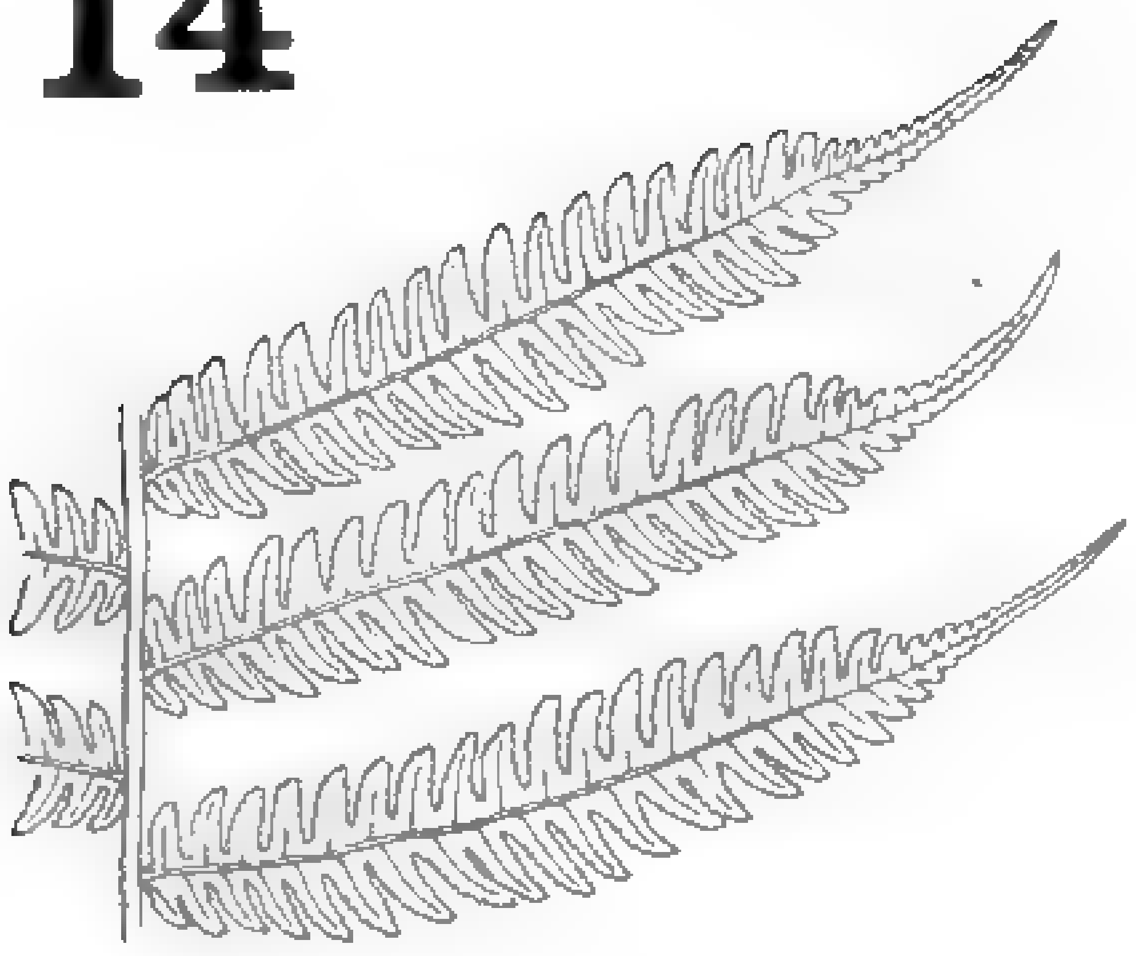
SELECTED COLLECTIONS. **Panama. Canal Zone:** plain of Sperdi, near Puerto Obaldía, San Blas coast, near sea level, *Pittier 4356* (US). **Darién:** summit of knoll above Cana, alt. 2500′, *Stern et al. 529* (GH,MO,US). **Colombia. Chocó:** Acandí, along the Río Monomacho (tributary of the Río Guale) in the foothills of the Serranía de Darién ca. 10 km. W of Acandí, moist, muddy, and rocky riverbank, ca. 150 m. elev., *Lellinger 698* (US); Río Truando, between La Nueva and La Esperanza, *Duke 9906(2)*. **Bolívar:** Norosi-Tiquisio trail, Lands of Loba, altitude 150–600 m., *Curran 126* (F,GH,US). **Ecuador. Manabi-Esmeraldas:** vicinity of Quininde, altitude 100 m., *Holdridge 1677* (US). **Morona-Santiago:** Bomboiza, S of Gualaquiza, Misión Salesiana, 700–800 m., *Sparre 19105* (GH). **Peru. Tumbes:** Ciro Alegría, *Canchaya 5169* (GH).

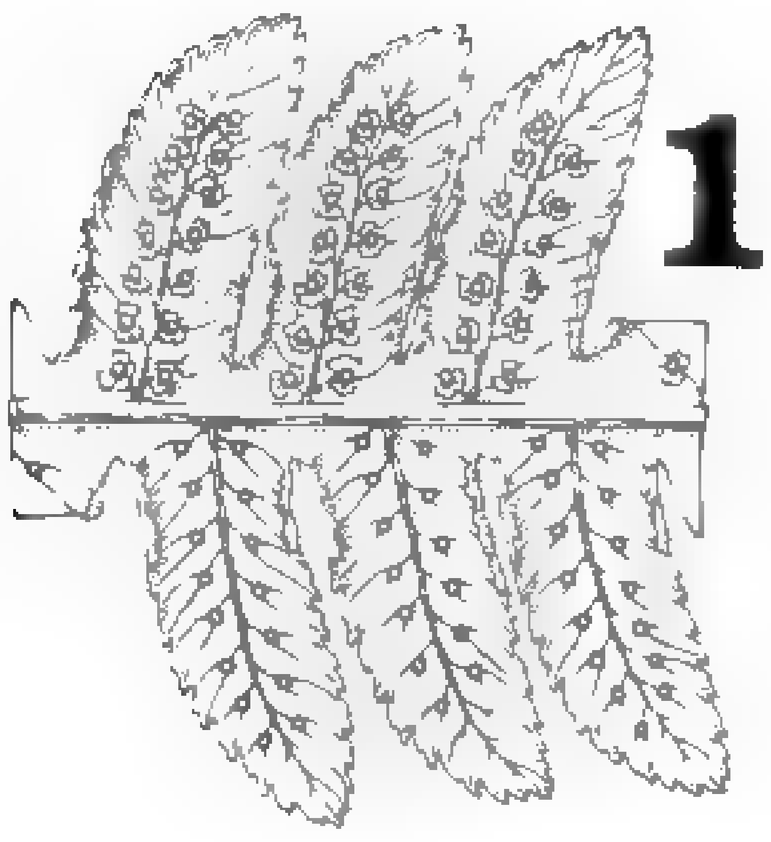
41. Trichipteris leucolepis (Mart.) Tryon

FIGS. 118, 119. MAP 41.

Trichipteris leucolepis (Mart.) Tryon, Contrib. Gray Herb. 200:45. 1970.
Alsophila leucolepis Mart., Icon. Plant. Crypt. Bras. 70 t. 46. 1834, *ex icone.* HOLOTYPE: ad Mariana & alibi in Prov. Minarum Generalium, Brazil, *Martius*, not seen.
Polypodium axillare Raddi, Opusc. Sci. Bol. 3:288. 1819 & Pl. Bras. 1:27 t. 41. 1825, not *P. axillare* Aiton, 1789. HOLOTYPE: in montibus, Rio de Janeiro, Brazil, *Raddi*, FI not seen. ISOTYPES: B! P!
Alsophila axillaris (Raddi) Moore, Ind. Fil. 48. 1857.

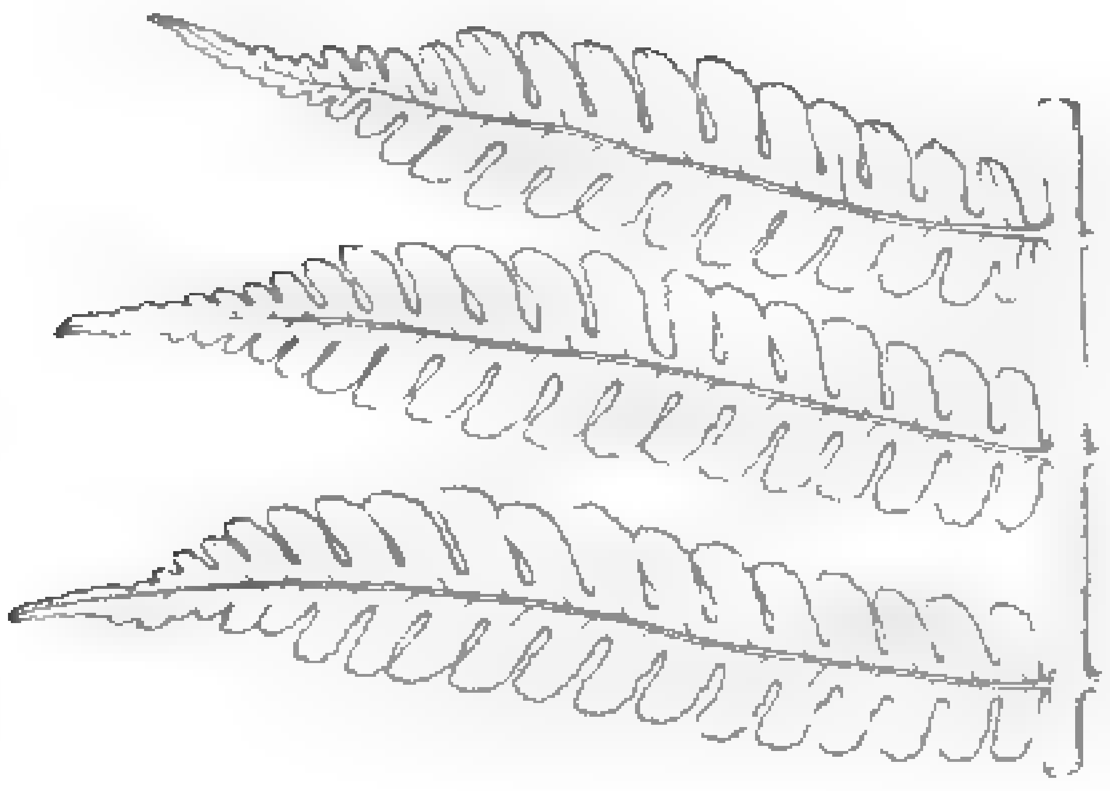
114



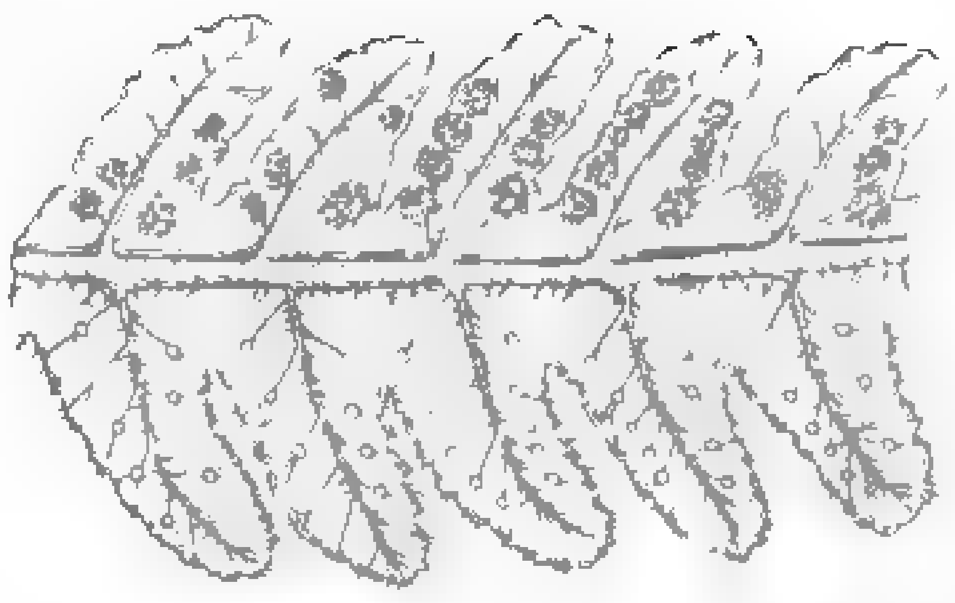


115

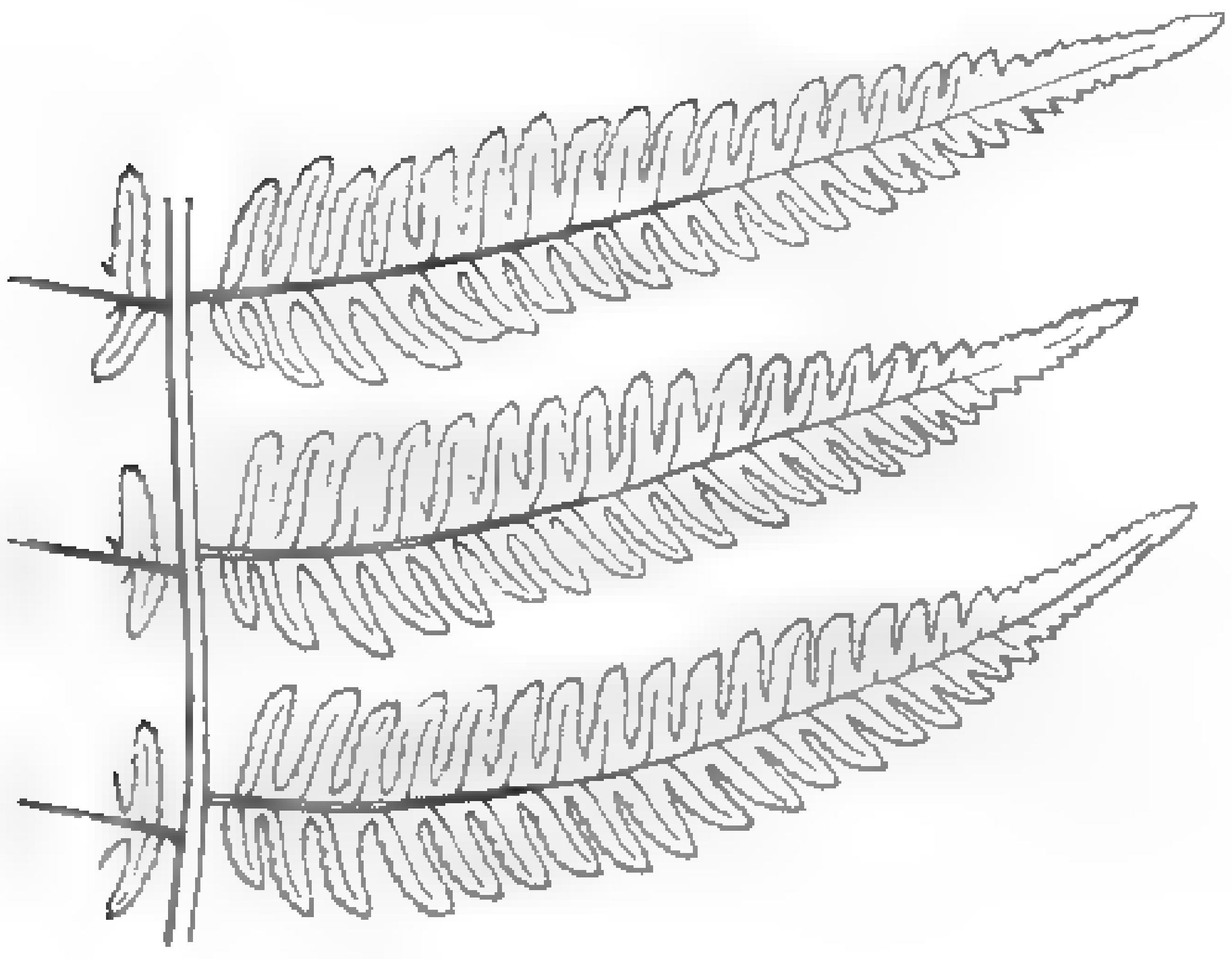
116



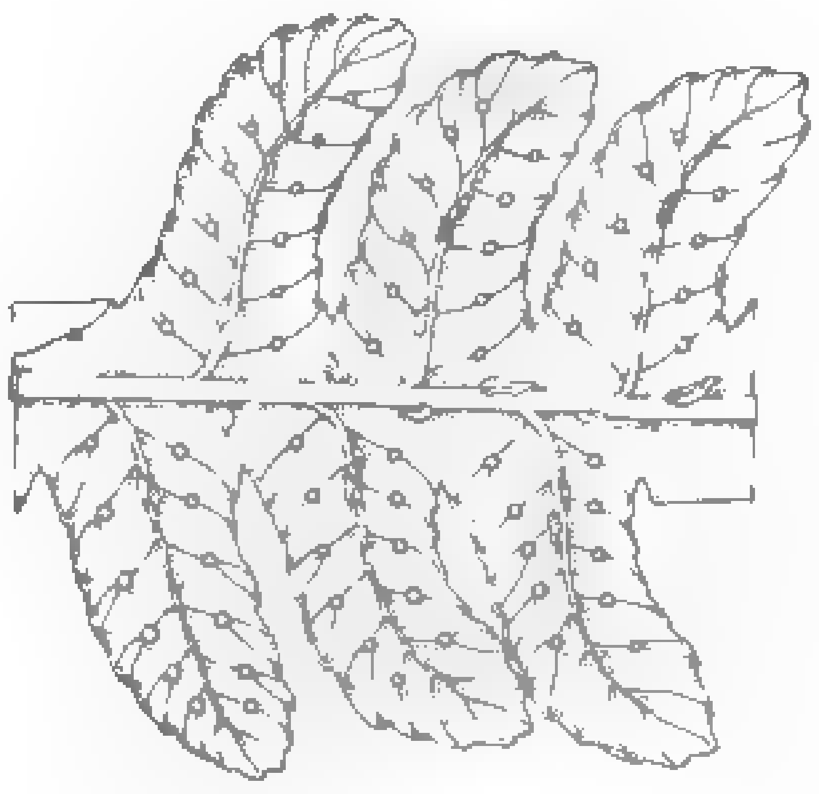
117

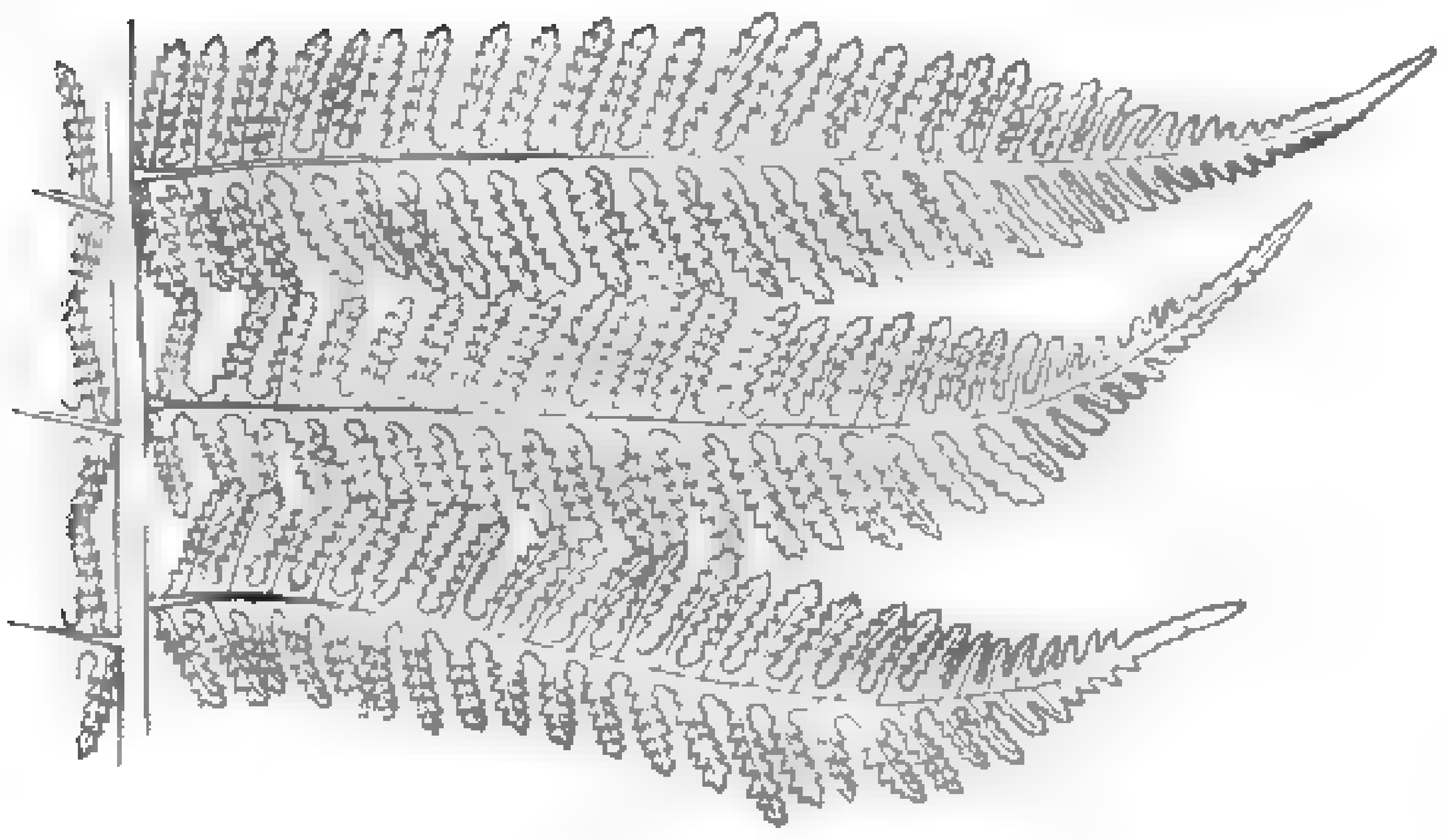


118

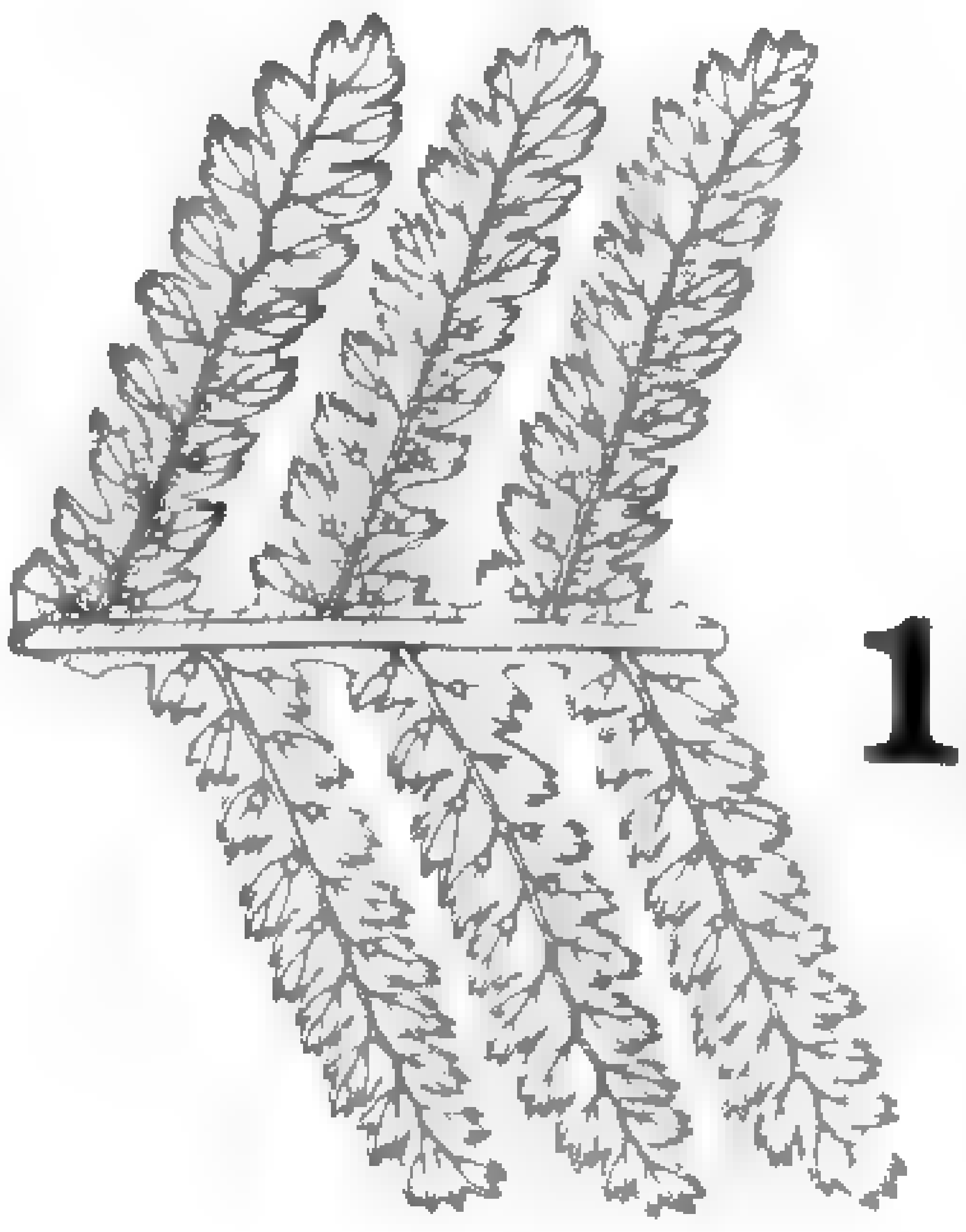


119





120



121

Alsophila glumacea Fée, Crypt. Vasc. Brés. **1**:170, t. 61 f. 2. 1869. HOLOTYPE: Brasilia fluminensi, *Glaziou 2290,* P! (Herb. Cosson).
Alsophila nigrescens Fée, Crypt. Vasc. Brés. **1**:170, t. 54 f. 1. 1869. HOLOTYPE: Brasilia fluminensi, *Glaziou 2289,* P! (Herb. Cosson). ISOTYPE: P!
Alsophila pectinata Fée, Crypt. Vasc. Brés. **1**:168, t. 60 f. 1. 1869. HOLOTYPE: circa Tijuca, *Glaziou 1704,* P! (Herb. Cosson). ISOTYPE: P!
Alsophila fumata Hook., Sp. Fil. **1**:42. 1844. *nom. nud.* in syn.
Alsophila fumata Salomon, Nom. Gefässkrypt. 28. 1883. *nom. nud.*
Cyathea leucofolis Domin, Pteridophyta 262. 1929, *nom. nov.* for *Alsophila leucolepis* Mart., 1834, not *Cyathea leucolepis* Mett., 1863.
Cyathea albidopaleata Copel., Univ. Calif. Publ. Bot. **17**:25 t. 2. 1932. HOLOTYPE: Viçosa, Corriga Reberró, *Mexia 4868,* MICH or UC not seen. ISOTYPES: F! GH! MO! PARATYPE: same locality, *Mexia 4893,* MICH or UC not seen. ISOPARATYPES: F! GH! MO! US!
Alsophila albidopaleata (Copel.) C. Chr., Ind. Fil. Suppl. **3**:20. 1934.
Trichipteris albidopaleata (Copel.) Tryon, Contrib. Gray Herb. 200:44. 1970.

Stem ca. 1.0 m. tall. *Petiole* to 1.0 m. long, fuscous to stramineous, aculeate; scales uniformly cretaceous to fulvous or cretaceous with a central, fuscous streak; scurf of sparse trichomidia or absent; all axes of lamina with trichomidia; costae and costules with flattish to bullate, cretaceous squamulae; pinna-rachises with cretaceous scales. *Lamina* to 2 m. long, 2-pinnate-pinnatifid, chartaceous, apex gradually reduced and acute to long-acuminate; pinnae stalked to long-stalked; pinnules short-petiolulate, deeply pinnatifid to pinnatisect, base truncate, apex attenuate, tip crenulate; lobes rotund to acute, serrate at least at the tip to crenulate; fertile veins forked at the sori or simple, sterile veins forked or simple. *Sori* medial; paraphyses much shorter than the sporangia, receptacle puberulent.

Trichipteris leucolepis is a Brazilian species characterized by cretaceous petiole scales and serrate pinnule lobes. The costae bear cretaceous, bullate squamulae. Morphologically the species is isolated in the genus. The combination of short paraphyses and cretaceous petiole scales is unique. *Trichipteris leucolepis* occasionally has petiole scales with an indistinct, fulvous streak, but the scales are predominantly cretaceous. There is some variation in the serration of the segments as well. *Trichipteris leucolepis* grows in original forests along the Serra do Mar in southern Brazil from 40 to 1000 meters in altitude.

SELECTED COLLECTIONS. **Brazil. Espírito Santo:** Santo Jatiboca, Mun. de Itaguassú, *Brade & Apparicio 18244* (MO,NY). **São Paulo:** Morro das Pedras, Iguape, *Brade 7722* (NY); Serra do Mar, 1000 m., 1908, *Wacket* (MO,NY). **Rio de Janeiro:** *Regnell 2154* (NY); *Glaziou 3583* (US). **Paraná:** Serra da Prata, *Dusén 15331* (GH); Tacarehý, *Dusén 17115* (F,GH,MO,NY).

42. **Trichipteris mexicana** (Mart.) Tryon

FIGS. 120, 121. MAP 42.

Trichipteris mexicana (Mart.) Tryon, Contrib. Gray Herb. 200:44. 1970.
Alsophila mexicana Mart., Icon. Plant. Crypt. Bras. 70 t. 45. 1834. HOLOTYPE: San

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FIGS. 114–121. FIGS. 114 & 115, *Trichipteris costaricensis:* 114, three central pinnules from a central pinna, × 1/3; 115, central part of a pinnule, × 4/3 (both *Skutch 1340,* GH). FIGS. 116 & 117, *T. pilosissima:* 116, three pinnules from a central pinna, × 1/3 (*Canchaya 5169,* GH); 117, central part of a pinnule, × 1 (*Curran 126,* GH). FIGS. 118 & 119, *T. leucolepis:* 118, three central pinnules from a central pinna, × 1/3; 119, central part of a pinnule, × 4/3 (both *Mexia 4893,* GH). FIGS. 120 & 121, *T. mexicana:* 120, three central pinnules from a central pinna, × 1/3; 121, central part of a pinnule, × 4/3 (both *von Türchkheim 1655,* GH).

Pablo de Teoxomulco, Oaxaca, Mexico, *Karwinski,* not seen. ISOTYPE: fragment ex P (Herb. Jeanpert), F!

Alsophila Godmani Hook., Syn. Fil. 1:36. 1866. HOLOTYPE: Cobán, Guatemala, *Salvin & Godman,* seen by Tryon at K and said to be synonymous with *T. mexicana.*

Cyathea valdecrenata Domin, Pteridophyta 263. 1929. *nom. nov.* for *Alsophila mexicana* Mart., 1834, not *Cyathea mexicana* Schlecht. & Cham., 1930.

Stem to 10 m. tall. *Petiole* ca. 1.0 m. long, fuscous or more commonly fulvous to stramineous, tuberculate to muricate; scales uniformly cretaceous or with a darker central streak; scurf of cretaceous trichomidia and fulvous squamulae; trichomes present; axes of lamina with similar indument, the scales lacking from the costae, costules, and veins; costules and veins sometimes glabrous. *Lamina* 1.0–2.0 m. long, 2-pinnate-pinnatifid, chartaceous, apex gradually reduced and acuminate; pinnae sessile to stalked; pinnules sessile, pinnatisect, base truncate, apex attenuate, tip crenulate; lobes acute, crenulate to pinnatisect; fertile veins forked at the sori or the basal veins of a fertile lobe simple, sterile veins forked. *Sori* inframedial; paraphyses longer than the sporangia, receptacle villous.

Trichipteris mexicana has distinctive, broad, flabellate, cretaceous petiole scales that extend upward along the rachis. The petiole and leaf-blade bear stiff trichomes throughout. On the basis of the petiole scales, trichomes, and leaf architecture *T. mexicana* is closely related to species of the group of *T. armata. Trichipteris mexicana* varies in the dissection of the pinnules and in the color of the petiole scales. The variation typical of the species is often visible in a single collection. *Trichipteris mexicana* has been found from Mexico to Honduras in wet forests and cloud forests, especially along watercourses, from 800 to 3000 meters.

SELECTED COLLECTIONS. **Mexico. Chiapas:** Sierra de Soconusco, from El Triunfo to Finca Liquidambar, *Hernandez X. & Sharp X–462* (US); Acacoyagua, *Matuda 17435* (F). **Guatemala. Alta Verapaz:** Quebradas Secas, *Johnson 956* (F,GH,NY); Pansamalaná, *Tuerckheim 1007* (GH,NY, fragment ex K,NY,US). **Huehuetenango:** vicinity of Maxbal, 17 mi. N of Barillas, Sierra de los Cuchumatanes, *Steyermark 48857* (F,GH,US). **Quezaltenango:** El Pocito, S of San Martín Chile Verde, road to Colomba, *Standley 84971* (F,US). **San Marcos:** Barranco Eminencia, road between San Marcos & San Rafael Pie de la Cuesta, *Standley 86460* (F,US); between San Rafael at NE portion of Volcán Tacaná and Guatemala–Mexico line, Río Vega, *Steyermark 36295* (F,US). **Honduras. Comayagua:** above El Achote and the plains of Siguatepeque, *Yuncker, Dawson & Youse 6015* (F,GH,MO,NY,US). **Morazán:** region of Agua Amarilla, above El Zamorano, *Standley, Molina & Chacon 5053* (F); above San Juancito, San Juancito Mts., *L. O. Williams 17553* (F,GH,MO,US).

The following species, which I refer to as the group of *Trichipteris armata,* are the subject of careful revisionary studies by Riba (1967 and 1969). Complete treatment of these species, then included in *Alsophila,* should be sought in these works.

43. **Trichipteris Estelae** (Riba) Tryon, Contrib. Gray Herb. 200:44. 1970. *Alsophila Estelae* Riba, Rhodora 69:67. 1967. Portland and St. Thomas Parishes, Jamaica.

44. **Trichipteris nesiotica** (Maxon) Tryon, Contrib. Gray Herb. 200:44. 1970. *Alsophila nesiotica* Maxon, Contrib. U.S. Nat. Herb. 24:43. 1922. Cocos Island, Costa Rica.

45. **Trichipteris trichiata** (Maxon) Tryon, Contrib. Gray Herb. 200:44. 1970. *Alsophila trichiata* Maxon, Contrib. U.S. Nat. Herb. 24:44. 1922.

From sea level in Costa Rica, through Panama and northern Venezuela, to 100 meters in Ecuador.

46. **Trichipteris Tryonorum** (Riba) Tryon, Contrib. Gray Herb. 200:46. 1970. *Alsophila Tryonorum* Riba, Rhodora 69:66. 1967. High mountain forests of northern Venezuela and the Andes of Colombia and Ecuador, from sea level to 2800 meters.

47. **Trichipteris scabriuscula** (Maxon) Tryon, Contrib. Gray Herb. 200:44. 1970. *Alsophila scabriuscula* Maxon, Proc. Biol. Wash. **23**:125. 1919. Mexico, Guatemala, and Honduras; in the shade of humid tropical forests.

48. **Trichipteris armata** (Sw.) Tryon, Contrib. Gray Herb. 200:44. 1970. *Polypodium armatum* Sw. Prod. Veg. Ind. Occ. 134. 1788. *Alsophila Swartziana* Mart. Icon. Pl. Crypt. Brasil. 73. 1834. Jamaica and Hispaniola.

49. **Trichipteris strigillosa** (Maxon) Tryon, Contrib. Gray Herb. 200: 44. 1970. *Alsophila strigillosa* Maxon, Contrib. U.S. Nat. Herb. **24**:37. 1922. Eastern Cuba.

50. **Trichipteris hirsuta** (Presl) Tryon, Contrib. Gray Herb. 200:45. 1970. *Cyathea hirsuta* Presl, Delic. Prag. 190. 1822. *Alsophila hirsuta* (Presl) Kze. Linnaea **9**:98. 1834. Minas Gerais, Rio de Janeiro, and São Paulo, Brazil.

51. **Trichipteris rufa** (Fée) Tryon, Contrib. Gray Herb. 200:46. 1970. *Alsophila rufa* Fée, Crypt. Vasc. Brés. **1**:165. 1869. Minas Gerais, Rio de Janeiro, and São Paulo, Brazil.

52. **Trichipteris conjugata** (Hook.) Tryon, Contrib. Gray Herb. 200:45. 1970. *Alsophila conjugata* Hook., Syn. Fil. 37. 1866. Damp forests, ravines, creeks, and along streams; 650–2800 meters. Colombia to Bolivia.

53. **Trichipteris stipularis** (Christ) Tryon, Contrib. Gray Herb. 200:44. 1970. *Alsophila stipularis* Christ, Bull. Herb. Boiss. II, **4**:958. 1904. Mountainous regions of Costa Rica and Panama, between 1000 and 2000 meters.

54. **Trichipteris pansamalana** (Maxon) Tryon, Contrib. Gray Herb. 200:44. 1970. *Alsophila pansamalana* Maxon, Contrib. U.S. Nat. Herb. **24**:40. 1922. Guatemala, 1000–2000 meters.

55. **Trichipteris bicrenata** (Liebm.) Tryon, Contrib. Gray Herb. 200: 44. 1970. *Cyathea bicrenata* Liebm. Vid. Selsk. Skr. V, **1**:289. 1849. *Alsophila bicrenata* (Liebm.) Fourn. Mex. Pl. Crypt. 134. 1872. In the shade of humid tropical forest, 1000–2000 m; Mexico from Veracruz and Guerrero south to Chiapas.

NOMINA INCERTAE SEDIS

A number of names, although apparently representing species of *Trichipteris*, are based on material inadequate for critical determination and taxonomic decision.

Alsophila crassa Karst., Flora Columb. **2**:187 t. 199. 1869. TYPE COLLECTION: wet, cold, montane forests, Mérida, 1859, *Engel (136)*, B! The lamina portions included in the type resemble species of *Trichipteris*. There are no modern collections that I can associate with the Engel type, which lacks petiole material.

Alsophila pinnula Christ, Prim. Flor. Costaric. 3:43. 1901. No type was cited in the original publication. Authentic material, probably that which Christ used to describe the species, is from Río La Matina (Limón), *Pittier 10267*, P! fragment ex P, NY! US! The lamina axes of this material have a distinctive tomentum of erose squamulae. Though *Pittier 10267* may represent a *Trichipteris*, lack of petiole material and modern collections makes certain assignment treacherous.

Alsophila Sodiroi Baker, Ann. Bot. **5**:149. 1891, *nom. nov.* for *Alsophila alata* Sodiro, Recensio 19. 1883, not *Alsophila alata* Fourn., Ann. Sci. Nat. V. **18**:349. 1873. SYNTYPES: Volcán Cotacachi and the forests of Los Colorados, (Prov. Pichincha) Ecuador, *Sodiro*, Herb. Sodiro not seen. AUTHENTIC MATERIAL: *Sodiro*, fragment ex K, NY! The Sodiro fragment appears to be a *Trichipteris*.

Alsophila Stübelii Hieron., Hedwigia **45**:235, t. 15 f. 7. 1906. HOLOTYPE: inter Baños & Jivaría de Pintúc in valle Río Pastaza, *Stübel 995*, B! The holotype lacks petioles and leaf apices. I have seen no additional collections comparable to the type. A small soral squamula is associated with most of the sori. The indument and lamina form are those of *Trichipteris*.

The following names may represent species of *Trichipteris*. I have not seen the types and am unable to make inferences from illustrations or text.

Cyathea chamaedendron Copel., Univ. Calif. Publ. Bot. **17**:31 t. 5. 1932. TYPE COLLECTION: Brasil, *Mexia 5855a*.

Cyathea furcinervia Domin, Acta Bot. Bohem. **9**:117. 1930, *nom. nov.* for *Alsophila polyphlebia* Domin, Kew Bull. **1929**:218. 1929 & Mem. Roy. Czech. Soc. Sci. II. **2**:96 t. 10, f. 9, 10. 1929, not *Alsophila polyphlebia* Baker, 1876. TYPE COLLECTION: Ilhios, Brasiliae, Moricand.

Alsophila flexuosa Fée, Crypt. Vasc. Brés. **1**:159. 1869. TYPE COLLECTION: circa Saint-Paul, Brasil, without collector.

Alsophila latisecta Christ, Bull. Boiss. II. **6**:185. 1906. TYPE COLLECTION: valle del Río Navarro, (Prov. Cartago) Costa Rica, *Wercklé 16767*. (Described from sterile material.)

Alsophila monosticha Christ, Bull. Soc. Bot. Belg. **33**(**2**):94. 1894. TYPE COLLECTION: British Guiana, 1889, *Goebel*.

Alsophila mucronata Christ, Bull. Soc. Bot. Belg. **35**:178. 1896. TYPE COLLECTION: Costa Rica, *Pittier 7484*. A specimen of *Pittier 7484* at US is *Nephelea polystichoides* (Christ) Tryon according to Lellinger (pers. comm.).

Alsophila ramisora Domin, Mem. Roy. Czech. Soc. Sci. II, **2**:97, t. 10. f. 11, 12. 1929. TYPE COLLECTION: Demerara, Guyana, *Parker*.

Alsophila Sprengeliana Mart., Icon. Plant. Crypt. Bras. 75. 1834. TYPE COLLECTION: in Dominicae & Guadeloupe insulis, *Bertero*.

The following names of uncertain identity include *nomina nuda* and names, mostly from the horticultural literature, impossible to associate with a type collection.

Trichipteris Aberti Anon., Hort. Rev. Belg. **1905**:275, *nom. hort.*

Disphenia aculeata Presl, Tent. Pterid. 56. 1836, *nom. nud.*

Alsophila aculeata Hook., Sp. Fil. **1**:49. 1844, *nom. nud.*

Alsophila acuminata J. Sm., Journ. Bot. (Hook.) **1**:667. 1842, *nom. nud.*

Alsophila adspersa Kze., Bot. Zeit. **1844**:314, *nom. nud.*

Alsophila alata Fée, Mém. Fam. Foug. **5** (Genera Filicum):346. 1850–1852, *nom. nud.*

Alsophila alutacea Kze., Bot. Zeit. **1844**:327, *nom. nud.*

Alsophila amazonica Linden, Cat. 1871, *nom. hort.*

Alsophila arbuscula Presl, Tent. Pterid. 61. 1836, *nom. nud.* applied to some collections of *Trichipteris dichromatolepis* (Fée) Tryon.

Alsophila articulata Moore & Houlst., Gard. Mag. Bot. **3**:332, f. 81. 1852, *nom. hort.*

Hemitelia atrovirens Trevisan, Atti Ist. Veneto II, **2**:164. 1851, *nom. nud.*

Alsophila brevis J. Sm., Journ. Bot. (Hook.) **1**:667. 1842, *nom. nud.*

Alsophila crenata Kze., Bot. Zeit. **1844**:312, *nom. nud.* in syn. applied to some collections of *T. corcovadensis* (Raddi) Copel.

Alsophila crenata Fée, Crypt. Vasc. Brés. **1**:175. 1869, *nom. nud.* applied to some collections of *T. corcovadensis* (Raddi) Copel.

Trichipteris denticulata Presl, Tent. Pterid. 59. 1836, *nom. nud.*

Alsophila echinata Moore, Ind. Fil. cv. 1857, *nom. nud.* applied to some collections of *T. procera* (Willd.) Tryon.
Alsophila humilis J. Sm., Journ. Bot. (Hook.) **1**:667. 1842, *nom. nud.*
Alsophila latebrosa J. Sm., Journ. Bot. (Hook.) **1**:667. 1842, *nom. nud.*
Alsophila lepifera J. Sm., Journ. Bot. (Hook.) **1**:667. 1842, *nom. nud.*
Alsophila Marshalliana Linden, Gard. Chron. III, **15**:663. 1894, *nom. hort.*
Alsophila mollissima Kze., Bot. Zeit. **1844**:328, *nom. nud.*
Alsophila munita Presl, Tent. Pterid. 62. 1836, *nom. nud.*
Alsophila nitens J. Sm., Journ. Bot. (Hook.) **1**:667. 1842, *nom. nud.* applied to older collections of *T. procera* (Willd.) Tryon.
Alsophila serrata J. Sm., Journ. Bot. (Hook.) **1**:667. 1842, *nom. nud.*
Alsophila tomentosa Presl, Tent. Pterid. 62. 1836, *nom. nud.*

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LIST OF SPECIES

1. Trichipteris procera (Willd.) Tryon; **2.** T. Dombeyi (Desv.) Barr.; **3.** T. decomposita (Karst.) Tryon; **4.** T. cordata (Kl.) Tryon; **5.** T. sagittifolia (Hook.) Tryon; **6.** T. Steyermarkii Tryon; **7.** T. falcata (Kuhn) Barr.; **8.** T. ursina (Maxon) Tryon; **9.** T. phalaenolepis (C. Chr.) Tryon; **10.** T. Williamsii (Maxon) Tryon; **11.** T. microphylla (Kl.) Tryon; **12.** Trichipteris Schiedeana (Presl) Tryon; **13.** T. aspera (L.) Tryon; **14.** T. gibbosa (Kl.) Barr.; **15.** T. nigripes (C. Chr.) Barr.; **15a.** var. nigripes; **15b.** var. brunnescens Barr.; **16.** T. Kalbreyeri (Baker) Tryon; **17.** T. Schlimii (Kuhn) Barr.; **18.** T. Wendlandii (Kuhn) Tryon; **19.** T. nigra (Mart.) Tryon; **20.** T. pauciflora (Kuhn) Tryon; **21.** T. frigida (Karst.) Tryon; **22.** T. pubescens (Baker) Tryon; **23.** T. phegopteroides (Hook.) Tryon; **24.** T. latevagans (Baker) Tryon; **25.** T. Hodgeana (Proctor) Tryon; **26.** T. microdonta (Desv.) Tryon; **27.** T. Lechleri (Mett.) Tryon; **28.** T. villosa (Willd.) Tryon; **29.** T. atrovirens (Langsd. & Fisch.) Tryon; **30.** T. phalerata (Mart.) Barr.; **30a.** var. phalerata; **30b.** var. Iheringii (Rosenst.) Barr.; **31.** T. Gardneri (Hook.) Tryon; **32.** T. dichromatolepis (Fée) Tryon; **33.** T. corcovadensis (Raddi) Copel.; **34.** T. praecincta (Kze.) Tryon; **35.** T. borinquena (Maxon) Tryon; **36.** T. demissa (Morton) Tryon; **36a.** var. demissa; **36b.** var. thysanolepis Barr.; **37.** T. Cyclodium Tryon; **38.** T. nanna Barr.; **39.** T. costaricensis (Kuhn) Barr.; **40.** T. pilosissima (Baker) Barr.; **41.** T. leucolepis (Mart.) Tryon; **42.** T. mexicana (Mart.) Tryon; **43.** T. Estelae (Riba) Tryon; **44.** T. nesiotica (Maxon) Tryon; **45.** T. trichiata (Maxon) Tryon; **46.** T. Tryonorum (Riba) Tryon; **47.** T. scabriuscula (Maxon) Tryon; **48.** Trichipteris armata (Sw.) Tryon; **49.** T. strigillosa (Maxon) Tryon; **50.** T. hirsuta (Presl) Tryon; **51.** T. rufa (Fée) Tryon; **52.** T. conjugata (Hook.) Tryon; **53.** T. stipularis (Christ) Tryon; **54.** T. pansamalana (Maxon) Tryon; **55.** T. bicrenata (Liebm.) Tryon.

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INDEX TO NAMES

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A SYNOPSIS OF CALADIOPSIS (ARACEAE)

MICHAEL MADISON[1]

The tribe Colocasieae Engl. (araceae) in the neotropics comprises five genera of terrestrial herbs, with the majority of the species pertaining to *Xanthosoma* Schott (about 50 species) and *Caladium* Vent. (about 20 species). The technical distinctions among these genera are based on the structure of the carpellate flowers; these floral differences coincide with differences in vegetative morphology, growth habit, and habitat preference, supporting the idea that the genera are phylogenetically natural groups (Madison, 1976).

Although *Caladium* and *Xanthosoma* are widespread and common, the three smaller genera of the tribe, *Chlorospatha* Engl., *Aphyllarum* Sp. Moore, and *Caladiopsis Engler* are rare and known from only a few collections. Recently several new collections of *Caladiopsis* have been made and three species brought into cultivation, allowing for a clarification of this previously obscure genus.

Engler established *Caladiopsis* in 1905 to accommodate a Lehmann collection from southwestern Colombia. The diagnostic generic characters were the adnation of the carpellate portion of the spadix to the spathe and the presence of a narrow, elongate style, in contrast to the broad discoid styles of *Xanthosoma* and the absence of a style in *Caladium*. Study of the new material indicates that neither of these characters holds up throughout the genus; yet *Caladiopsis* is distinct and readily defined by several characters overlooked by Engler.

The species of *Caladiopsis* are terrestrial herbs with fleshy, erect stems to 60 cm. tall and 2–3 cm. thick; these are similar to the stems of some of the 'arborescent' *Xanthosoma* species, e.g., *X. daguense* Engler. The inflorescences of *Caladiopsis* are terminal and produced sympodially in groups of three to six. The slender, flexible penduncles are nearly as long as the petioles and only 1–2 mm. thick. The peduncles are too weak in themselves to support the spadices, and are held erect by the tightly overlapping flanges of the leaf sheath. The narrow spadix is divided into approximately equal portions of carpellate, sterile, and staminate flowers. The carpellate and sterile flowers are widely spaced, in contrast to the densely crowded flowers of *Caladium* and *Xanthosoma*. The sterile flowers are fungiform with a concave disc elevated on a stalk. The pistils may have an attenuate style (*C. lehmannii* Engler, *C. dodsonii* Bunting) or sessile stigma, and the carpellate portion of the spadix may be free from the spathe (*C. atropurpurea* Madison) or adnate to it.

The most striking feature of *Caladiopsis* is the presence of a mantle-like structure between the ovary and the stigma, possibly homologous to the discoid styles of *Xanthosoma*. In *C. castula* this mantle is three times

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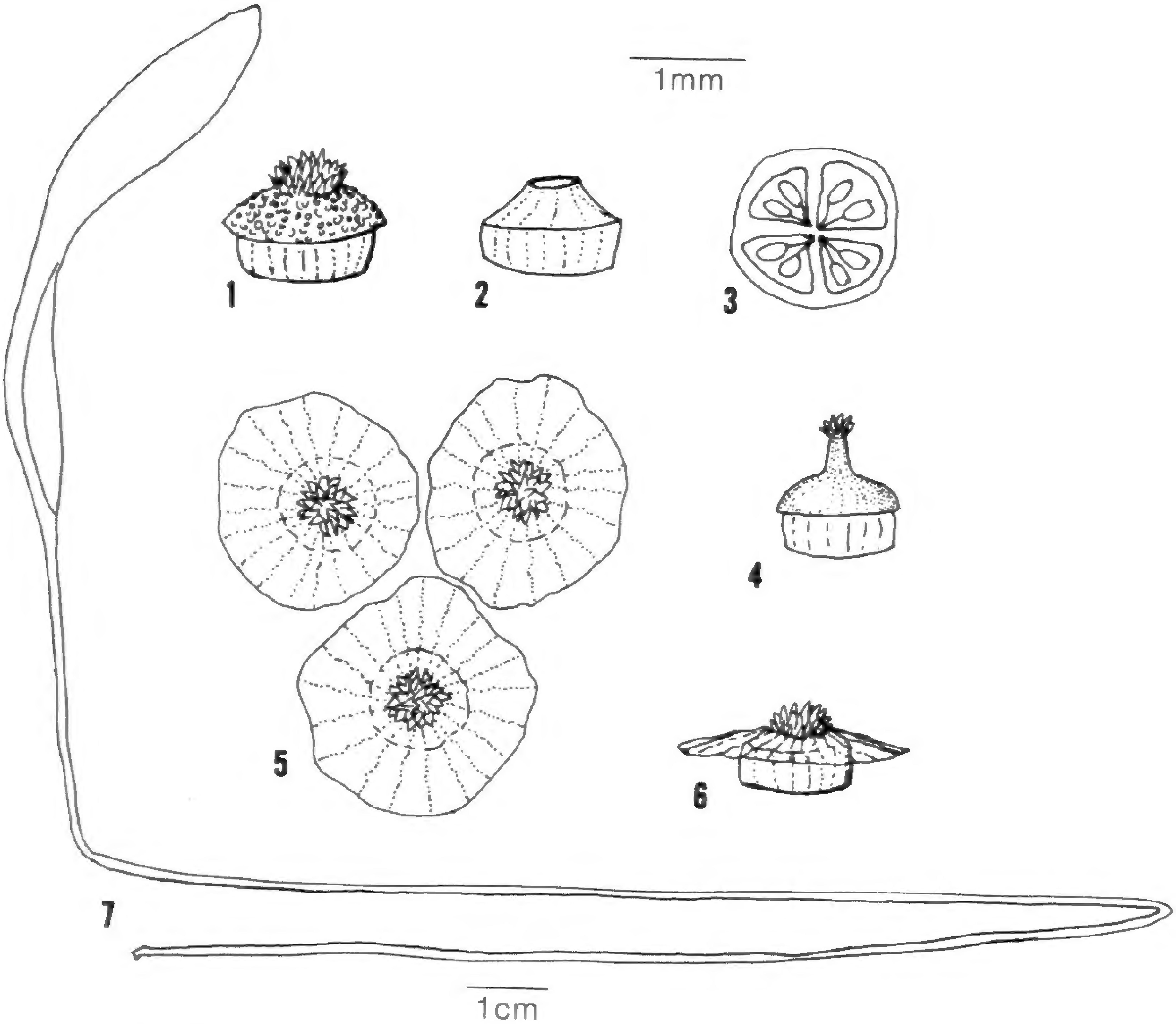
[1] The Marie Selby Botanical Gardens, 800 S. Palm Ave., Sarasota, FL 33577



FIGS. 1–7. Inflorescence and flowers of *Caladiopsis*. (1–3) *C. atropurpurea*, carpellate flowers: 1. lateral view; 2. lateral view with stigma and mantle removed; 3. cross section near the base of the ovary. (4) *C. dodsonii*, carpellate flower. (5–7) *C. castula*: 5. carpellate flowers, apical view; 6. carpellate flower, lateral view; 7. spathe and peduncle. All drawn from live material.

the width of the ovary and is broadly spreading (figs. 5, 6); in *C. dodsonii* and *C. atropurpurea* the mantle is smaller and appressed to the ovary, though it is not adnate and in fresh material can be lifted with a forceps. The mantle is composed of a monolayer or two layers of hyaline or colored sub-spherical cells. The role of this structure in pollination biology remains unknown; possibly it is functioning as an osmophore. Receptive carpellate flowers of *Caladiopsis atropurpurea* produce a strong fruity odor, very similar to that of fruits of *Averrhoa carambola* L.

Caladiopsis as here emended includes four species, all native to wet forests of the western slopes of the Andes in Colombia and Ecuador. The diagnostic features of the genus are the flexible, slender, elongate peduncles held erect by the leaf sheaths; the wide spacing of the carpellate and sterile flowers on the spadix; the concave-fungiform shape of the sterile flowers; and the occurrence of a thin, spreading, mantle-like structure borne at the apex of the ovary.

KEY TO THE SPECIES

A. Leaf hastate, staminate flowers orange. .... 1. *C. dodsonii.*
A. Leaf sagittate, staminate flowers cream. .... B.
  B. Spadix fully free from the spathe. .... 2. *C. atropurpurea.*
  B. Carpellate portion of the spadix mostly or entirely adnate to the spathe. ...... C.
    C. Lower part of the spathe purple, stigma sessile. .... 3. *C. castula.*
    C. Lower part of the spathe green, stigma elevated on a short, narrow style. ......
    .... 4. *C. lehmannii.*

1. **Caladiopsis dodsonii** Bunting

Caladiopsis dodsonii Bunting, Ann. Missouri Bot. Gard. **50**:28. (1963)

Terrestrial herb, sometimes leaning against tree trunks. The stem fleshy, unbranched, 2–3 cm. thick, to 60 cm. tall. Petioles 40–50 cm. long, vaginate for ¼ to ½ the length. Leaf lamina dull green, the veins furrowed above and prominent below, hastate, the central lobe ovate, widest at the middle, 15–25 cm. long, 12–16 cm. broad. Peduncle 25–40 cm. long. Spathe cream, ca. 13 cm. long. Carpellate portion of the spadix cream, adnate to the spathe, 5 cm. long, the pistils with narrow cylindric styles equal in length to the ovary. Staminate flowers bright orange.

TYPE: Ecuador, Prov. Pichincha, Santo Domingo de los Colorados, along Rio Babe 28 km. S of Santo Domingo, elev. 350 m. Nov. 1961, *Dodson & Thueb 1190* (MO!).

This species has recently been collected in a sterile condition near the type locality by Madison (*s.n.*, cultivated at SEL) and by Dodson (*6755*, SEL). These collections flowered in cultivation in December, 1977. The most striking aspect of the fresh inflorescences is the bright orange color of the staminate flowers. The coloring of the spadix is just reversed from *Caladiopsis atropurpurea* in which the carpellate flowers are bright orange.

2. **Caladiopsis atropurpurea** Madison, sp. nov.

Herba terrestris. Caudex erectus, carnosus, 3–4 cm. crassus, ad 50 cm. altus, interdum bulbilliferus. Cataphylla triangularia, 10–15 cm. longa, marcescentia. Petiolus folii 50–80 cm. longus, 1–3 cm. crassus, teres, erectus atropurpureus, vagina 40–50 cm. longa instructus. Lamina glabra, 35–40 cm. longa, 18–25 cm. lata, sagittata, lobo antico 25–30 cm. longo, 12–18 cm. lato, lobis posticis 15–18 cm. longis, costis 3 cm. denudatis, supra saturate viridis, subtus atropurpureus. Pedunculus gracilis, debilis, teres, 1–2 mm. crassus, 25–55 cm. longus. Spatha cucullata, 10–12 cm. longa, tubo pallide viridi 5 cm. longo, lamina cremea 5–6 cm. longa, vix aperienti. Spadicis pars carpellata 2.5 cm. longa, pistilis armeniacis; pars sterilis 2 cm. longa, synandriis fungiformibus, purpureis; pars staminata cremea, 1.8 cm. longa. Fructus ignotus.

TYPE: Ecuador, Prov. Los Rios, Rio Palenque Science Center, km. 56 Quevado-Sto. Domingo, elev. 150–220 m., August, 1975, *Dodson 5911* (SEL!).

ETYMOLOGY: Latin *atropurpurea,* 'dark purple,' referring to the abaxial surface of the leaves.

Earlier, I tentatively identified specimens of this as *Xanthosoma eggersii* (Engler) Engler and published an illustration of it under that name (Madison, 1976), indicating its aberrant status in the genus *Xanthosoma.* Because no authentic material of *X. eggersii* is known to exist, interpretation of the name must be based on the written description which is unfortunately brief. Having further studied the matter, I now consider that the name *Xanthosoma eggersii* does not apply to these specimens, which instead represent a new species of *Caladiopsis.*

Transections of the ovaries of *Caladiopsis atropurpurea* show a three or four locular ovary near the base becoming unilocular near the apex, reflecting the situation that the parietal placentae are more deeply intrusive at the base of the ovary where they are axially connate. A similar situation was found in flowers of *Xanthosoma sagittifolium* (L.) Schott by Eyde et al. (1967). The normally 3–4 locular ovaries of *Xanthosoma* and unilocular ovaries of *Caladium* may evidently be connected by intermediate conditions, of which this is one.

3. **Caladiopsis castula** Madison, sp. nov.

Herba terrestris. Caudex erectus, carnosus, 2–4 cm. crassus, ad 50 cm. altus, interdum bulbilliferus. Cataphylla triangularia, 8–11 cm. longa, marcescentia. Petiolus folii 35–50 cm. longus, 6–10 mm. crassus, teres, erectus, purpureopunctatus, vagina 20–35 cm. longa instructus. Lamina glabra, 25–35 cm. longa, 7–11 cm. lata, sagittata, lobo antico 18–20 cm. longo, lobis posticis 12–15 cm. longis, costis 1–1.5 cm. denudatis, supra saturate viridis, subtus viridis venis prominentibus atropurpureis. Pedunculus teres, gracilis, debilis, 1–2 mm. crassus, 25–35 cm. longus. Spatha cucullata, 7–8 cm. longa, tubo atropurpureo 2.5 cm. longo, lamina cremea circa 5 cm. longa, vix aperienti. Spadicis pars carpellata ad spatham adnata, 1.7 cm. longa, alba, stigmatibus castuliformibus; pars sterilis 1 cm. longa, synandriis fungiformibus, cremeis, marginibus purpureis; pars staminata cremea, 2.2 cm. longa. Fructus ignotus.

TYPE: Ecuador, Prov. Pichincha, vicinity of Chiriboga, wet montane forest, elev. 1200 m. Propagule collected 1975, flowered in cultivation at SEL September, 1977, *Madison 4141* (SEL!).

ETYMOLOGY: Latin *castula,* 'petticoat,' referring to the spreading mantle which covers the ovary (figs. 5, 6).

Development of the mantle in this species is quite extraordinary; it is fully three times the diameter of the ovary. The true stigma is a hemispherical clump of glandular hairs located at the center of the mantle.

4. **Caladiopsis lehmannii** Engler

Caladiopsis lehmannii Engler, Bot. Jahrb. **37**:140. (1905)

Terrestrial herb to 0.5 m. tall. Petiole 35 cm. long, vaginate for 1/4 to 1/3 the length; the lamina elegantly sagittate, the posterior lobes 7–8 cm. long and 1.5–1.8 cm. wide, the central lobe 12–14 cm. long and 4 cm. wide. Peduncle about 20 cm. long. Spathe 10 cm. long, the tube green, the lamina cream. Carpellate portion of the spadix 3–5 cm. long, adnate to the spathe. Ovaries subglobose, contracted to a narrow style bearing a capitate stigma. Staminate portion of the spadix 3.5 cm. long, 5 mm. thick.

TYPE: Colombia, thick rain forest west of Popayan, elev. 1500–1800 m., *Lehmann 5315* (B? non vidi; isotype K, non vidi; photo, SEL!).

ADDITIONAL COLLECTION: Ecuador, Prov. Carchi, vicinity of Maldonado, wet montane forest, elev. 1600 m., April, 1977, *Madison 3988* (SEL, US).

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