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ROBERT G. STOLZE

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Custodian, Pteridophyte Herbarium
Field Museum of Natural History

October 28, 1974

Publication 1194

Patricia M. Williams
Managing Editor, Scientific Publications

Library of Congress Catalog Card Number: 74-791 75

US ISSN 0015-0746

PRINTED IN THE UNITED STATES OF AMERICA

INTRODUCTION

Cnemidaria, a genus of tropical American ferns belonging to the tree-fern family, Cyatheaceae, is confined largely to wet habitats, in or at the edges of forests, at elevations ranging from sea level to 2,300 m. (typically 500-2,000 m.). These ferns are mostly subarborescent, with leaves caespitose, their caudices rarely attaining a thickness of more than 7 cm. or a length of more than a meter. Individual leaves, however, may reach great proportions, occasionally up to a length of 3.5 m. in some Antillean species. Within the family the species of *Cnemidaria* are characterized by the generally acaulescent habit, a comparatively simple leaf architecture (never more than pinnate-pinnatisect), the basal veinlets conniving strongly or forming costal areoles, a general lack of trichomes on the axes, and the spores possessing large, regularly disposed pores. A total of 23 species is recognized in this treatment.

In his *Tentamen Pteridographiae* (1836), C. B. Presl proposed the genus *Cnemidaria,* based on five species formerly included within *Cyathea* and *Hemitelia.* These species he considered distinct, basing his decision chiefly on the character of the costal areoles formed by anastomosing basal veins. Later (1847) he created three more genera, *Actinophlebia, Hemistegia,* and *Microstegnus,* into which he placed most of his original species of *Cnemidaria* along with several other taxa. In *Cnemidaria* itself he maintained only one species: *C. speciosa.* Subsequent authors, (Kunze, Fée, William Hooker, *et al.*) chose to treat Presl's original species of *Cnemidaria* under *Hemistegia* and (or) *Hemitelia,* and for over 50 years the genera of Cyatheaceae were separated primarily by the presence, absence or shape of the indusium.

Maxon (1912) considered that a number of species of *Hemitelia* formed a natural group and brought them together under the subgenus *Cnemidaria.* In this subgenus were included all the earlier "genera" of Presl, as well as a number of new species, many of which were based on single collections. They were distinguished from the subgenus *"Euhemitelia"* either by the presence of costal areoles, or by the "scarcely arborescent" habit and less-dissected leafy parts. Maxon's work cleared up much of the earlier confusion in the nomenclature and in the typification of species.

Copeland (1947) concurred with Maxon on the naturalness of the group, and restored *Cnemidaria* to generic rank. This concept was supported by Holttum & Sen (1961), who reinforced the distinctiveness of the genus by pointing out the peculiar character of the spores. They further suggested that some of the free-veined species earlier placed in the genus lacked this type of spore and thus should be excluded. Tryon (1970) included *Cnemidaria* in his classification of the family, refined the generic concept, and pointed out still another pertinent character to further delimit the genus within the Cyatheaceae: that trichomes are rare or lacking on the adaxial side of the costa. Other genera are characterized by the common occurrence of trichomes along most of the axes, particularly on the adaxial side.

Throughout the years, poor or incomplete collecting has contributed to lack of understanding of the generic features of tree ferns. Due to the size of individual plants, collectors either ignore them in the field or are satisfied with a pinna or two. The problem remains a current one. However, enough material (nearly 2,000 specimens) has been gathered for this study to indicate that the group of species as treated here forms perhaps the most natural and distinctive genus in the family. In addition to the characters already noted in this "Introduction," *Cnemidaria* also has whitish or bicolorous petiole scales, rudimentary paraphyses, arachnoid scurf on the axes, hemitelioid indusia, and pinnae never articulated at the base. These characters, however, may also occur in species of other genera.

EVOLUTION AND GEOGRAPHY

The principal characters of *Cnemidaria* rarely, if ever, occur in other genera of Cyatheaceae. Within the family, only *Cnemidaria* has spores with large, regularly disposed, equatorial pores. Furthermore, the basal veins of nearly all of the species either merge to form costal areoles or are at least strongly connivent to the sinus, whereas veins of the species of the other genera are normally free and non-connivent. Minute, terete, recurved trichomes are found on relatively few species of *Cnemidaria,* and then generally on the abaxial side of the axes, although this kind of trichome is characteristically abundant along the axes throughout the other genera. It is important to note that these trichomes are present on the adaxial side of the rachis *only* in the free-veined species of *Cnemidaria,* which thus links two primitive characters together in the same few species. Finally, the leaf architecture in the genus shows less dissection (never fully bipinnate) than in the remainder of the scaly Cyatheaceae, whose leaves are typically twice- to thrice-pinnate.

So it appears that *Cnemidaria* is the most advanced genus of the family, with more complex venation and simpler lamina architecture being the end products of its adaptive development. A majority of the species are highly specialized in these characters. Such evolutionary developments also occur in at least one species of *Trichipteris* and in several species of *Cyathea. T. williamsii* of Panama is not only simply pinnate but has costal areoles as well; and in *Cyathea* there are several species exhibiting costal areoles, e.g., *C. conformis, C. woronovii,* and *C. panamensis,* as well as a few with subentire pinnae, e.g., *C. integrifolia* and *C. speciosa* Humb. & Bonpl. ex Willd. (not *Cnemidaria speciosa* Presl). All of the above species of *Cyathea* have a partially developed (hemitelioid) indusium. This character is common to *Cnemidaria* and, with the other similarities mentioned, indicates that *Cnemidaria* has probably arisen from this particular line of *Cyathea.* Tryon (1970) has also indicated the derivation of *Cnemidaria* from *Cyathea.*

Within the genus, a phylogeny (fig. 1) can be derived from the occurrence of advanced or primitive characters in the species. The most primitive species is *Cnemidaria amabilis,* which has the greatest number of unspecialized features (see discussion under that species) and ex-

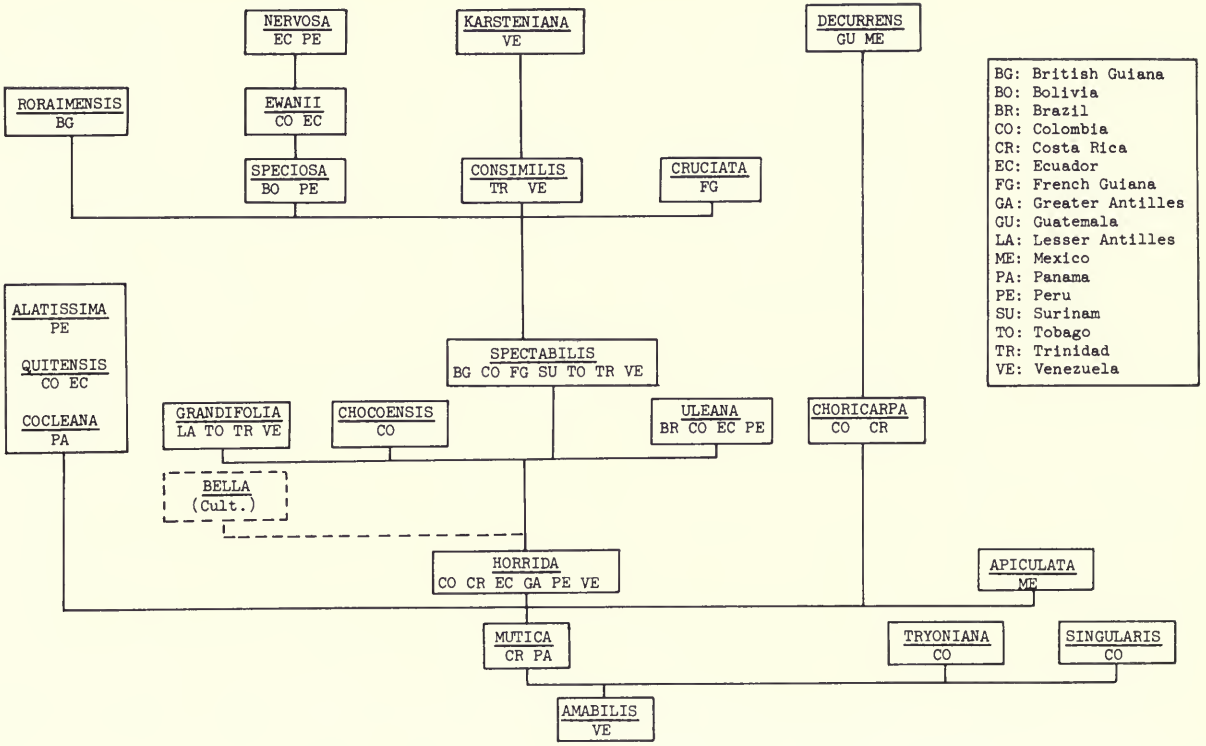


FIG. 1. Distribution and proposed phylogeny of species of *Cnemidaria*.

hibits the closest links with *Cyathea,* especially in venation and indument. Other primitive species are those, such as *Cnemidaria singularis* and *C. tryoniana,* with free veins and deeply dissected pinnae. The free-veined *C. mutica* might represent an ancestral type that gave rise to species with costal areoles, such as *C. horrida,* which is probably the most primitive of the predominately South American areolate group. The most advanced species are *C. karsteniana* and *C. nervosa,* which are strongly areolate, simply pinnate, and virtually glabrous and acaulescent.

The geography of at least one group of species can be seen to correlate with its line of evolution, and this suggests the route of migration along which speciation has occurred. The evolutionary line connects the very primitive *C. amabilis* in Venezuela with the simple-veined but less primitive *C. mutica* in Panama and Costa Rica, with especially strong ties to var. *chiricana.* The line then passes, in Costa Rica, to *C. choricarpa* which has costal areoles and less deeply-cut pinnae, but still closely resembles *C. mutica* var. *mutica* in many respects. Continuing northward into Guatemala and Mexico, the evolutionary line reaches an advanced state in *C. decurrens,* a relative of *C. choricarpa* with subentire pinnae.

Other evolutionary lines may have developed in a similar geographic manner, but their species are now often allopatric. One such line, originating with *C. horrida,* passes from *C. spectabilis* to *C. consimilis,* and finally to *C. karsteniana,* a species endemic in Venezuela. Another line passes from *C. spectabilis* through *C. speciosa* and *C. ewanii,* and thence to *C. nervosa* of Ecuador and Peru. In both lines, the progression is from species with deeply dissected pinnae and considerable indument on the axes, to species nearly lacking in indument and with pinnae entire or subentire.

The greatest number of species, as well as the most primitive ones, are principally near the center of the range, whereas a majority of the highly advanced species are near the borders of the range (fig. 1, map 1). Hence the most likely place of origin of *Cnemidaria* could be construed as that area in which the most primitive species are currently found, and in which there is the greatest present concentration of species. Thus it is likely that the genus originated in the area of Colombia and northern Venezuela, for here are found a total of 11 species, including the three most primitive.

A fossil record is reported by Graham and Jarzen (1969) from an Oligocene formation at San Sebastian, Puerto Rico, and, although positive identification is difficult from the photomicrograph, it strongly resembles a *Cnemidaria* spore not unlike those of *C. horrida,* a species

MAP 1. Generalized range of *Cnemidaria* (outline) and area of highest concentration of species (black): 11 species occur in this area, including the three most primitive ones: *C. amabilis, C. singularis,* and *C. tryoniana.*

found currently in Puerto Rico. Graham and Jarzen also mention similar spores from a Miocene formation in Veracruz, Mexico. There is another report by Hammen and Gonzalez (1960) of fossil spores from Upper Pleistocene and Holocene formations in Colombia, and the excellent photomicrograph shows these to be unquestionably *Cnemidaria.* However, these records are too few at present to be useful in determining the area of origin of the genus.

The distribution of *Cnemidaria* is generally continuous, with species overlapping through most of the range. However, there are two notable regions of disjunction: southeastern Brazil, and an area containing the provinces of Chiapas and Oaxaca in Mexico and Alta Verapaz in Guatemala. There is no record of the genus between *C. decurrens* in Guatemala and *C. choricarpa* in Costa Rica, even though that area has been rather well-collected in recent years, and there is a much larger gap (2,000 km.) between the collections of *C. uleana* in Brazil and *C. speciosa* in Bolivia. Such disjunctions are apparently due to lack of proper growing conditions in the intervening regions. *Cnemidaria* is typi-

cally found on slopes in or at the edges of forests, at middle elevations in wet areas where there are no prolonged dry periods. A lack of any one of these factors will apparently result in an unfavorable habitat.

A list of the distribution of species according to country or area follows:

MEXICO: *apiculata, decurrens.*
GUATEMALA: *decurrens.*
COSTA RICA: *choricarpa, horrida, mutica* vars. *chiricana, contigua, grandis,* and *mutica.*
PANAMA: *cocleana, mutica* vars. *chiricana, grandis,* and *mutica.*
GREATER ANTILLES: *horrida.*
LESSER ANTILLES: *grandifolia* vars. *grandifolia* and *obtusa.*
TRINIDAD: *consimilis, grandifolia* var. *obtusa, spectabilis* var. *spectabilis.*
TOBAGO: *grandifolia* var. *obtusa, spectabilis* var. *spectabilis.*
FRENCH GUIANA: *cruciata, spectabilis* var. *spectabilis.*
SURINAM: *spectabilis* var. *spectabilis.*
BRITISH GUIANA: *roraimensis, spectabilis* var. *spectabilis.*
VENEZUELA: *amabilis, consimilis, grandifolia* var. *obtusa, horrida, karsteniana, spectabilis* var. *spectabilis.*
COLOMBIA: *chocoensis, choricarpa, ewanii, horrida, quitensis, singularis, spectabilis* var. *colombiensis, tryoniana, uleana* var. *abitaguensis.*
ECUADOR: *ewanii, horrida, nervosa, quitensis, uleana* var. *abitaguensis.*
PERU: *alatissima, horrida, nervosa, speciosa, uleana* var. *uleana.*
BOLIVIA: *speciosa.*
BRAZIL: *uleana* var. *uleana.*

MORPHOLOGY

In spite of the large number of specimens examined in this study, some morphological data are still incomplete, especially pertaining to those species represented by only a few collections. Collectors often neglect to gather adequate material for tree fern specimens, either because they feel it is time-consuming or because they fail to appreciate the taxonomic problems involved. Like any other fern, tree ferns can be properly classified only on the basis of characters of the entire plant, and a specimen without petiole or leaf apex may lack the very portion by which it is readily distinguished from related species. Thus a specimen of any large fern, to be of optimum value, should contain leaf apex, a section of rachis with several central pinnae, a few of the lowermost pinnae, and a basal section of petiole. A small portion of the caudex (or perhaps a cross-section of a very thick one) is also desirable. Where this is impractical, adequate label data should be included, noting length, diameter, type of scale, spines, etc. With little extra time and effort, a complete sample of the plant can be adequately collected for mounting on two herbarium sheets.

A discussion of morphological features is presented here, with special emphasis on those characters which are particularly diagnostic in *Cnemidaria*. Explanation is given for terminology used throughout the text and in the key.

Caudex

Among the species, caudices vary in length up to 1.5 m. and in diameter up to 7 cm. However, relatively few collections include this portion of the plant, or even label data describing it. Where such data are available, they appear to be of little taxonomic value at the species level.

Petiole and Rachis

The primary axis of the leaf in species of *Cnemidaria* is terete on the abaxial side, shallowly or deeply sulcate on the adaxial side,[1] with color varying from dark brown to light brown to stramineous on dried speci-

[1] Throughout the descriptions and key, in the interest of brevity, the "adaxial side" will be referred to as "above" and "abaxial side" as "beneath."

mens. Toward the apex the rachis is always light colored, but the shade commonly deepens toward the base of the petiole. Color may vary among plants of a given species. Frequency and color of scales on the

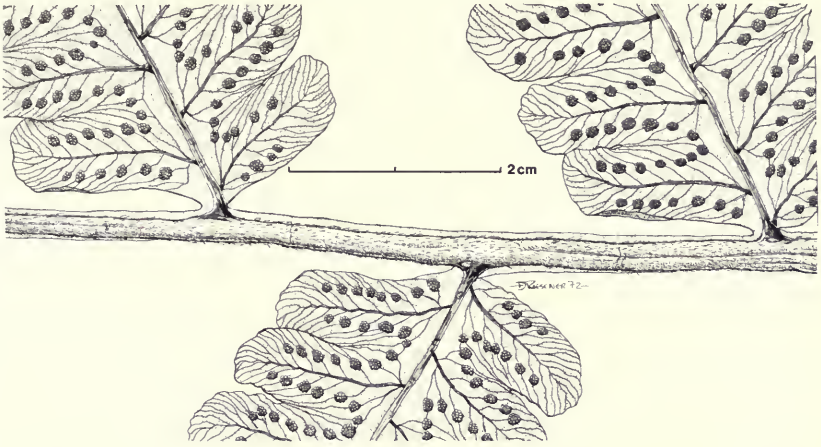


FIG. 2. Portion of leaf showing alate rachis: *Cnemidaria choricarpa, Nisman 35* (GH).

petiole and rachis can be extremely valuable in identifying species, and their importance is discussed under "Indument" below.

The rachis is generally smooth in *Cnemidaria,* but minute spines can be found, particularly toward the base, in *C. consimilis, C. horrida, C. quitensis,* and *C. spectabilis.* The petiole may be smooth or muricate or quite spiny, and this may be inconstant even within a variety (e.g., *C. mutica* var. *mutica*). But presence or lack of spines can be diagnostic in several species, especially when used in conjunction with other characters.

The narrow, green wing of tissue along each side of the rachis (fig. 2) can be a valuable character. Although lacking in most species and occurring sporadically in others, it is particularly prominent in *Cnemidaria alatissima, C. choricarpa,* and *C. decurrens.* In some species, a scarcely observable wing may run downward from the decurrent base of the apical section, and extend as far as the second or third pair of pinnae. In *C. choricarpa* the rachis is generally alate for most of its length, and in *C. alatissima,* the wing is prominent well down the petiole. In *C. decurrens* the wing is often worn away so that in older plants only the remnants, or merely the lines marking the previous points of attachment may be seen. On many mounted specimens, especially those having a considerably thickened rachis, the wing may be difficult to detect from

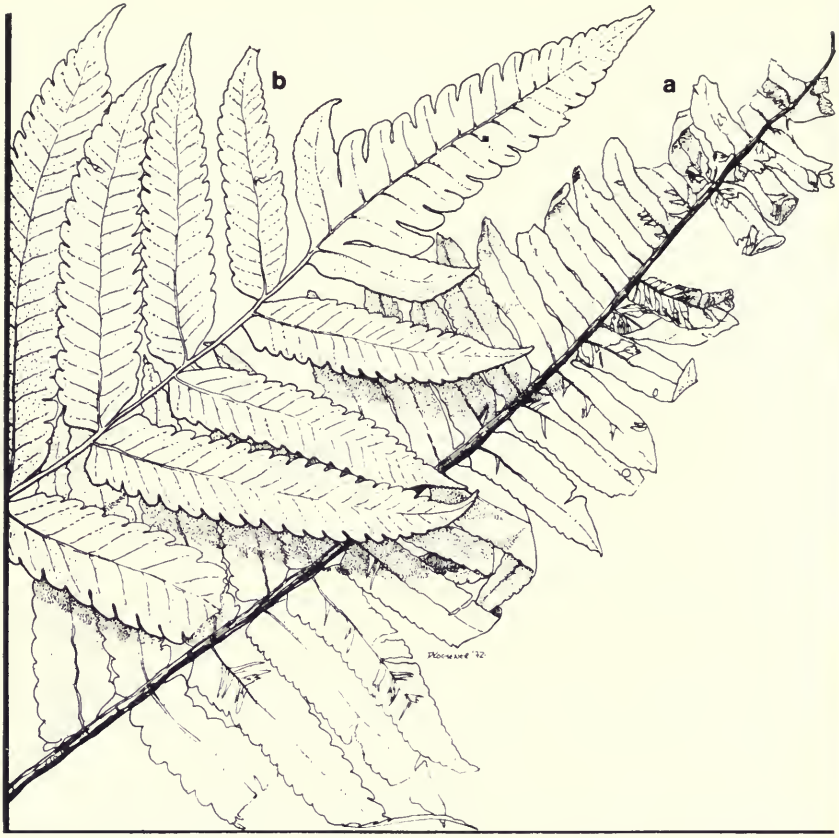


FIG. 3. Types of leaf apex: a, no distinct apical section, *Cnemidaria cruciata, LePrieur s.n.* 1838 (US); b, nonconform apical section, *C. spectabilis* var. *spectabilis, Hombersley 30* (US).

beneath. Therefore in mounted material it is often necessary to view the rachis at an oblique angle to be certain there is a wing present. On specimens mounted with adaxial side up, the wing, if present, will be generally obvious to the naked eye.

One character which merits brief mention is that of the pneumatophores (or pneumathodes), which occur along each side of the petiole. These are areas of soft surface tissue which evidently function in gas exchange with the inner tissues. In fresh material they may be seen as a single (sometimes double) line of linear to lanceolate spindle-shaped areas, pale or light green in color as contrasted with the darker color of the petiole tissue. In dried material these pneumatophores may be difficult or impossible to detect, and hence of questionable taxonomic value at present. However, future study of their size, shape, and spacing,

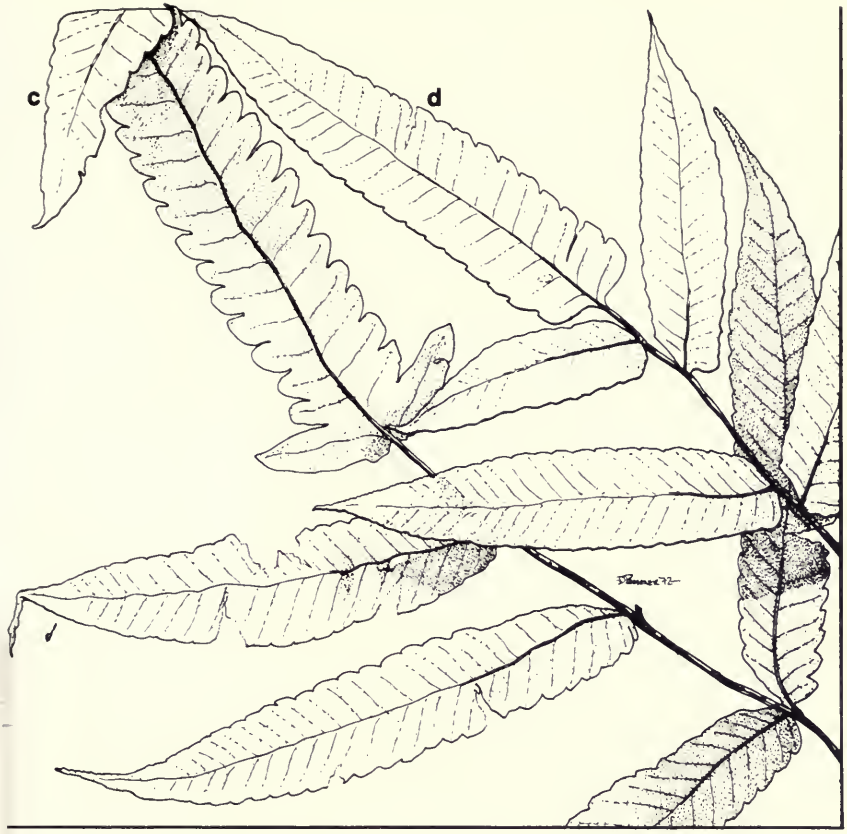


FIG. 3. **c**, subconform terminal pinna, with elongated basal lobes, *C. speciosa, Schunke A-143* (US); **d**, conform terminal pinna, C. *ewanii, Cuatrecasas 9022* (US).

especially in living plants, may provide further clues to the relationship of species.

LAMINA

The lamina in *Cnemidaria* is broadly lanceolate to ovate-oblong, and in larger species may attain a length of more than 2 m. In fully grown specimens the pinnae may number 20 to 30 pairs, rarely less than a dozen. However, one unusual species, *C. singularis,* may be distinguished from all others by its few (three to six pairs) pinnae.

Within the genus the basal pair of pinnae are usually considerably shorter than the penultimate pair, and also somewhat deflexed (sometimes as much as 45°). This feature can vary substantially from plant to plant, but at least one, *C. tryoniana,* can be separated from similar

species partly on the fact that its basal pinnae are scarcely or not at all reduced.

Within other genera of the Cyatheaceae pinnae are commonly long-stalked and articulate to the rachis. Pinnae in *Cnemidaria* are never articulate to the rachis, and are commonly sessile or subsessile. An exception is found in *C. bella* (fig. 16), where the larger pinnae may have stalks to 2 cm. long; hence the character is diagnostic. This unusual character is part of the evidence suggesting that it may be a hybrid (see also discussion of the species), and hence is atypical of *Cnemidaria.*

A high degree of variation may be encountered in depth of dissection of pinnae and in the shape of ultimate segments. Therefore, these characters may not be particularly useful in separating certain species. Indeed, they may be confusing. Where dissection of the pinnae is used as a key character, the basal pair of pinnae and reduced apical ones are excluded. Apical and basal pinnae, due to their marked reduction in size, generally have their segments differing from other pinnae in length and shape of the segments. Thus, in a leaf where central pinnae are cut three-fourths to seven-eighths to the costa, and the segments are acute to acuminate, a reduced apical or basal pinna may be cut less than halfway to the costa and its segments obtuse. However the character, when properly utilized, can be extremely valuable in delimiting certain groups of species, or individual species. In the extremely variable *C. mutica* (see fig. 13), it is useful at varietal rank, and a detailed discussion is presented under that species.

A peculiar feature is present in the pinnae of *C. cruciata, C. spectabilis* var. *colombiensis,* and *C. quitensis* (fig. 18). The segments are commonly enlarged toward the tips and curved in such a way as to cause the margins to crowd or overlap those of adjacent segments. Concomitantly in these species there is such a strong convergence of veins at the sinus that a thickened, cartilaginous mass is formed. In dried specimens of *C. quitensis* and *C. spectabilis* var. *colombiensis* the sinuses, particularly as viewed from above, exhibit a light yellowish or brownish color which contrasts markedly with the adjacent tissue. In other species, the segments commonly diverge at a broader angle, and only a few veins converge at the sinus, where the tissue is uniformly colored.

The apex of the lamina can be especially diagnostic in delimiting groups of species within *Cnemidaria* (fig. 3). Throughout the key reference is made to "conform," "subconform," or "nonconform" apical pinnae. Although it may not be morphologically correct to describe the terminal segment of the lamina as a pinna, I have used this terminology as a matter of convenience and conciseness. A *conform terminal pinna*

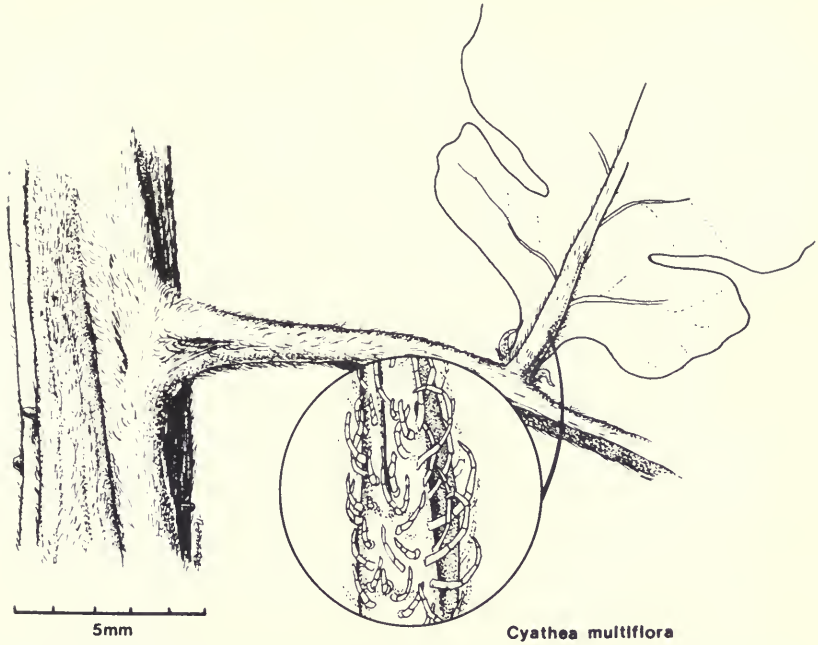


FIG. 4. Trichomes; adaxial side of rachis, costa, and base of costule (insert = 6.5 mm. diam.): *Cyathea multiflora, Burger & Matta 4237* (F).

is an apical section which closely corresponds in size and shape to typical pinnae on the leaf, usually resembling those of the second and third pair. *Subconform* is a term given to an apical section which is otherwise conform but has a pair of elongated or oversized basal lobes. A *nonconform terminal pinna* is a distinct apical section which differs from the typical pinna in shape and width (and often length). Its general outline is broadly triangular, widening gradually from apex to base, and having especially elongated basal lobes.

The most unusual types of leaf apex occur in *C. cruciata* and *C. singularis*. Leaves of the former (fig. 3a) completely lack a distinct apical section, as the pinnae gradually diminish in size all the way to the tip. In *C. singularis* (fig. 15) nearly half the lamina appears to be an apical section, which actually dwarfs each of the main pinnae.

INDUMENT

In *Cnemidaria* the indument is confined to the petiole, rachis, other axes, and veins, whereas the laminar tissue is glabrous. Character and color of the scales may vary on a plant depending upon their location on the leaf, and provide an important means of identifying species. Tri-

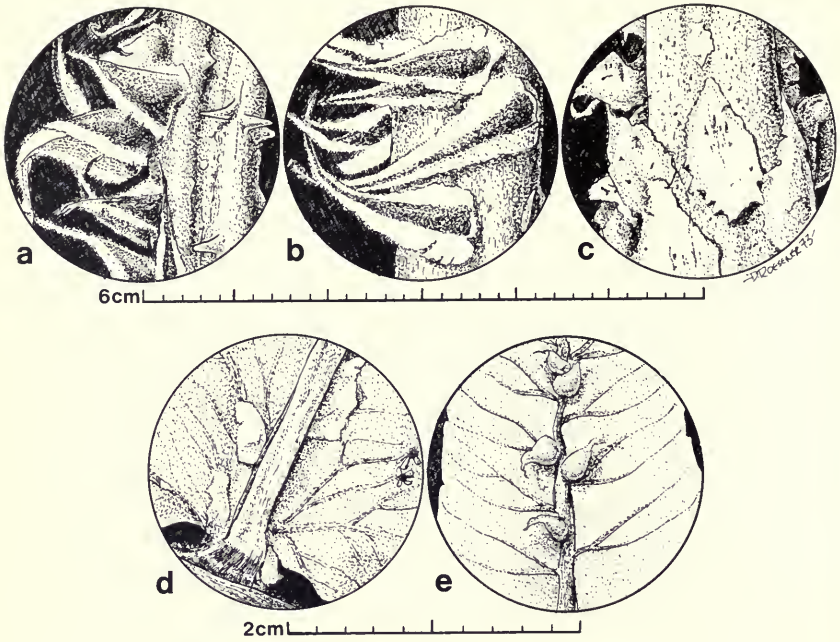


FIG. 5. Scales: bicolorous petiole scales, **a,** *Cnemidaria spectabilis* var. *spectabilis* and **b**, *C. consimilis;* white petiole scales, **c**, *C. amabilis;* **d**, typical amorphous costal scales; bullate costule scales, **e**, *C. grandifolia.*

chomes are of one basic type, and while their value as a diagnostic character applies only to a few species, their relative position on the axes is of great significance in delimiting the genus from others in the Cyatheaceae (see "Evolution and Geography" above). A third type of indument is a whitish, cobwebby tomentum often thickly matted on any of the axes, which has been referred to as "arachnoid scurf." It is of little taxonomic value within the genus, but seems to be confined to species of *Cnemidaria* and to a few rather closely related species in *Cyathea.*

The trichomes are identical with a type that is characteristically found in other genera of the Cyatheaceae (fig. 4). They are minute (±0.3 mm.), stiff, terete, recurved, pluricellular and relatively colorless. In many species of *Cnemidaria* they are virtually absent. On others they may be found scattered sparsely along the rachis and costae beneath. On a few primitive species they are quite abundant on most of the axes beneath, and even on the rachis above. However, they are *always* lacking on costae and costules above—areas where they are most copious in species of other genera. Species on which trichomes may be

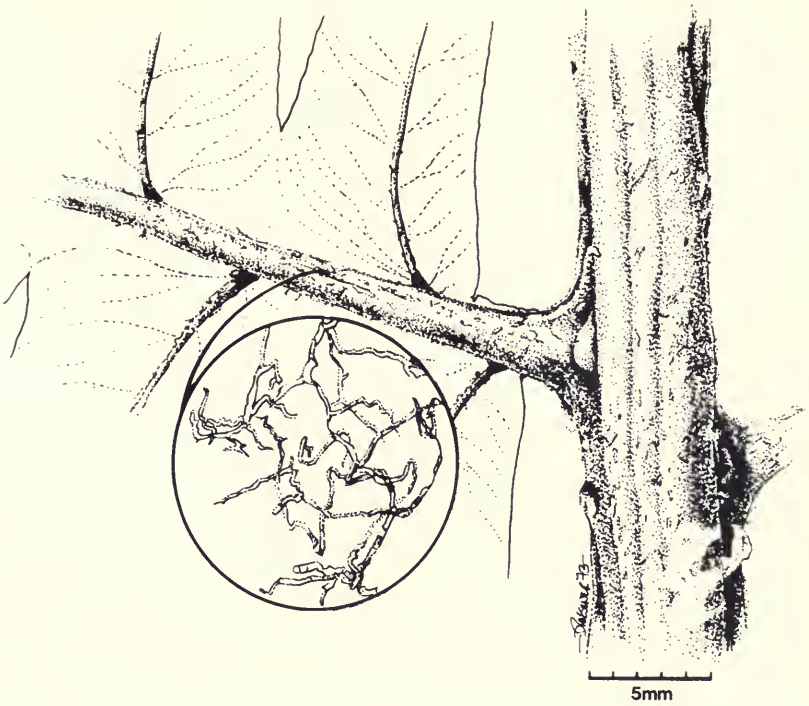


FIG. 6. Arachnoid scurf: abaxial side of rachis and costa (insert = 1.5 mm. diam.); *Cnemidaria mutica* var. *mutica, Nisman 22* (GH).

particularly numerous are *C. amabilis, C. quitensis,* and varieties of *C. mutica* except var. *contigua.*

The color and placement of petiole scales serve to distinguish many species. Those of *C. spectabilis* var. *spectabilis* (fig. 5a), for example, are located at the very base, and are deep brown with narrow whitish margins. This particular pattern in bicolorous petiole scales is characteristic of most species. Bicolorous scales occur along most of the petiole length in *C. consimilis* (fig. 5b), but the brown median stripe is commonly narrower than either of the whitish margins. Petiole scales of this pattern also occur on *C. ewanii, C. quitensis, C. speciosa,* and *C. uleana.* During the course of this study an attempt was made to classify a number of species on the basis of this distinction, i.e., petiole scales; a) concolorous; b) bicolorous, with median stripe much broader than either of the white margins; c) bicolorous, with median stripe much narrower than either margin. On material examined, scale color and pattern seemed constant within each species, but a sufficient number of petioles was not available for the results to be conclusive. The character, how-

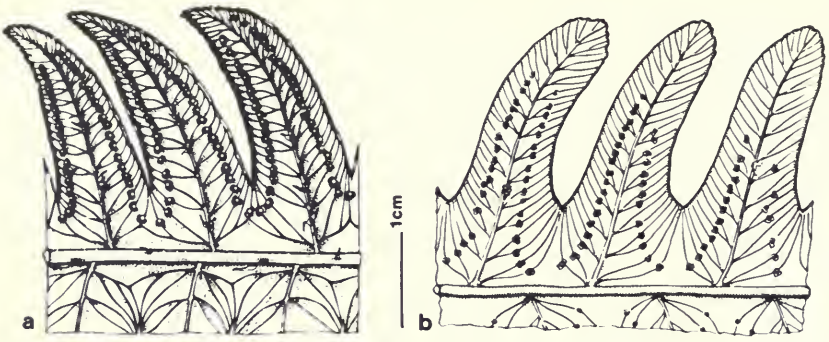


FIG. 7. **a**, Basal veins anastomosing, *Cnemidaria grandifolia* var. *grandifolia, Bailey 274* (GH); **b**, basal veins free, but connivent, *C. mutica* var. *mutica, Nisman 62* (GH).

ever, merits future consideration. Scales on the petioles of *C. amabilis* (fig. 5c) and *C. alatissima* are white (rarely with minute splotches of brown), lacking a brown median stripe. On both species, the color is constant well up onto the rachis, so that even specimens lacking petioles may be distinguished on this basis, and it is a most useful key character.

Shape of scales may be relatively constant on various parts of the plant, e.g., linear, linear-lanceolate, or lance-ovate on the petiole, bullate (in one species) with hair tips on the costule, but the most predominant scale along all the upper axes in *Cnemidaria* is characterized by its lack of definite shape (fig. 5d). Scales scattered along the rachis, costae, and costules of most species are generally broad, with irregular margins, and are appressed to the axis. These may be white, brown, or bicolorous.

The most distinctive of all *Cnemidaria* scales occur only in *C. grandifolia,* along the costules beneath, and are described as "bullate" (fig. 5e). These are blunt or, more frequently, with long-attenuate hairlike tips, and have each margin folded around to touch or overlap the other, which gives them an inflated appearance. This is one of the characters which effectively separate this species from *C. horrida,* whose costular scales, when present, are of the typical flattened, amorphous type. Bullate scales are quite common throughout other genera of Cyatheaceae.

Arachnoid scurf (fig. 6), usually appearing macroscopically as faint patches of whitish powder, can be a variable character in *Cnemidaria* as to position, frequency, and abundance on the axes. It can also be inconstant in its nature: always whitish and only one cell in thickness, but sometimes appearing in thick, scalelike masses, or at other times like filamentous trichomes. Occasionally it may be scalelike at the point of

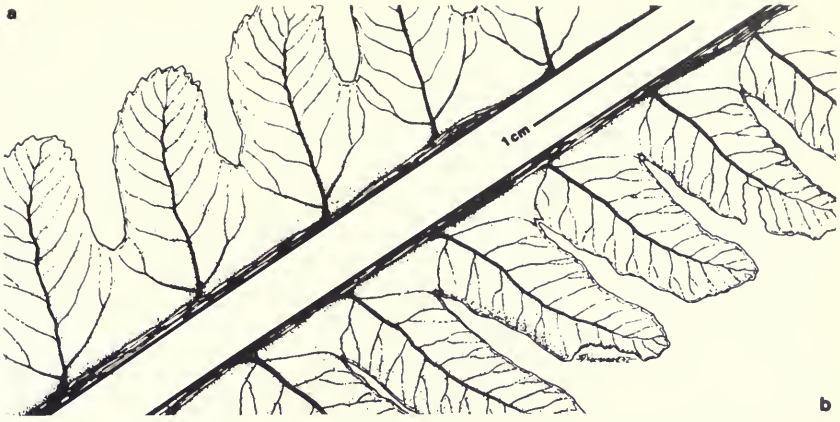


FIG. 8. Branching of basal acroscopic veins: **a**, veins once-forked, *Cnemidaria mutica var. chiricana, Killip 5350,* (US); **b**, veins simple, *C. amabilis, Steyermark 94886* (NY).

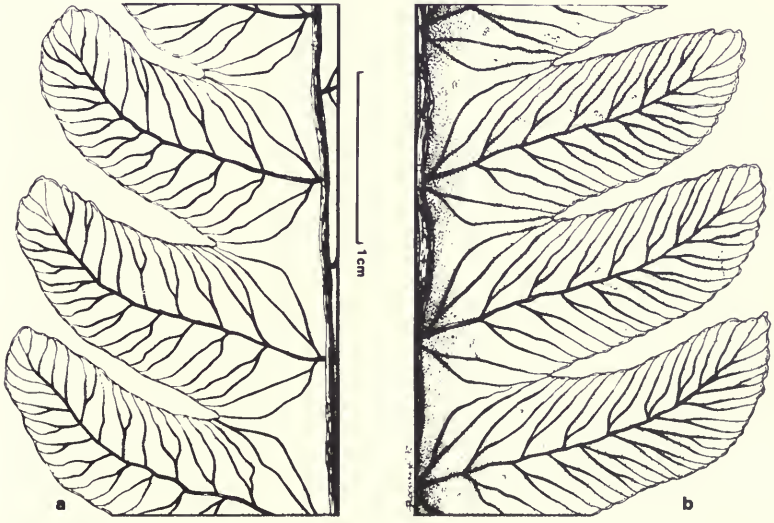


FIG. 9. Position of basal basiscopic veins: **a**, arising from costule, *Cnemidaria mutica var. mutica, Scamman & Holdridge 7881* (GH); **b**, arising from the costa, *C. uleana* var. *uleana, Tryon & Tryon 6871* (GH).

attachment, but tapering to an extremely long hairlike tip, one cell broad, but many cells long. In these instances, it appears to be a modified scale in its origin. When hairlike, they have no similarity to the relatively thickened, terete trichomes discussed above. Instead, they can be long and tortuous, with their cells flattened and extremely elongated. Arachnoid scurf can be quite abundant on the axes of *C. horrida* or *C. mutica,* at times obscuring portions of the rachis or costa, or it may be completely lacking on species such as *C. amabilis* and *C. uleana.* On some specimens it may be confined almost entirely to the point of juncture of two axes. Of little or no apparent taxonomic significance *within* the genus, it may still be considered as a generic characteristic of *Cnemidaria,* and as atypical in other genera of Cyatheaceae.

Veins

A characteristic feature in *Cnemidaria* is the anastomosing of basal veins to form costal areoles. It has been discussed above (see "Evolution and Geography") as one of the important clues to phylogeny within the genus as well as to evolutionary development of *Cnemidaria* within the family. In a majority of the 23 species, the basal vein in each segment forks once or several times, and the lowermost branches of adjacent veins are joined by a transverse veinlet, thus forming an areole along the costa (fig. 7a). Veins of several species lack such a connecting veinlet, and whereas the basal veins are directed toward those of the adjacent segment, they bend rather sharply and are merely connivent to the sinus (fig. 7b), therefore no areoles are formed. In only one species, *C. amabilis,* the veins are scarcely or not at all connivent, and they reach the segment margin at a point just above the sinus (fig. 8b). This condition is typical of the venation of the other genera of Cyatheaceae.

The degree of branching of veins is rather variable within the genus and is usually unreliable as a diagnostic character. Veins in some species may be 0- to 3-forked, or in others 2- to 4-forked. Often this appears correlated with the size of the particular leaf. However, in all but a few species the basal veins are always at least once-forked (fig. 8a). One exception is *C. amabilis,* in which the basal acroscopic veins are always simple, which thus provides a useful means of separating this species from the closely-related *C. mutica* var. *chiricana.* Two other species which might be confused may also be distinguished partly on the basis of venation: *C. karsteniana* has veins mostly once-forked, whereas the veins of *C. nervosa* are always simple.

The position of basal veins on the axes is another character which may be somewhat variable on some species, yet distinctive in others. In

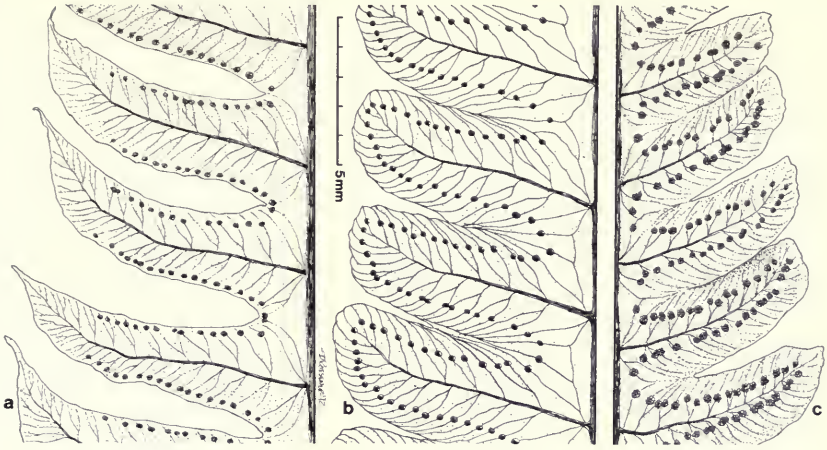


FIG. 10. Position of soral lines: **a**, submarginal, *Cnemidaria apiculata, Hallberg 1557* (NY); **b**, supramedial, *C. spectabilis* var. *spectabilis, Miller & Johnson 164* (F); **c**, inframedial, *C. tryoniana, Metcalf & Cuatrecasas 30122* (GH).

the typical condition the lowermost veins on either side of the segment arise from the costule at or near its base (fig. 9a). However, in several species the basal basiscopic veins commonly arise from the costa (fig. 9b), e.g., *Cnemidaria chocoensis, C. singularis, C. tryoniana,* and *C. uleana*. Where this character is used in the key to separate the latter two from *C. mutica,* the condition is best observed in the basal third or apical third of the pinna. At these points the basal basiscopic veins are constant in their position on the costa, whereas toward the center of the pinna they may assume the more typical position at the base of the costule.

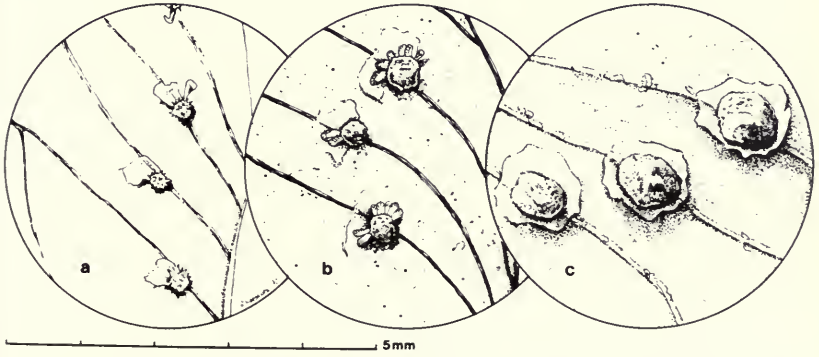


FIG. 11. Shape of indusium: **a**, spathulate, *Cnemidaria apiculata, Jurgensen 873* (NY); **b**, semicircular, *C. horrida, Lopez 143* (US); **c**, circular, *C. cocleana, Tyson et al. 2452,* (FSU).

Sori and Indusia

In *Cnemidaria,* sori are more or less globose and placed on the veins (when branched) generally above the fork. On some larger species the sori may be arranged in several series, but typically they are disposed in a single line between the costule and segment margin (fig. 10). On fully mature plants the soral pattern may be so regular and unbroken as to form a continuous zigzag line along each side of the costa, from base to apex of pinna. On certain species, such as *C. mutica,* the sori may vary in their relative position on the segment—placed nearer the costule on some plants, or nearer the margin on others—so that within the species the soral line may be inframedial, medial, or supramedial. In other species the relative position of the sorus is constant and can be used effectively as a diagnostic character. In *C. bella* and *C. apiculata* (fig. 10a) the soral line is placed so close to the edge of the segment as to appear almost marginal. In *C. spectabilis* var. *spectabilis* the sori are located away from the margin, and yet are nearer the margin than the costule (fig. 10b). With other species, e.g., *C. quitensis* and *C. tryoniana* (fig. 10c), the soral line is inframedial, at times nearly touching the costule; in this case the veins are usually branched at or near the costule, and the sori placed at or just above the forks.

The indusium in *Cnemidaria* is characteristically *hemitelioid,* i.e., it subtends the sorus, partially surrounding the receptacle (fig. 11b). It is roughly semicircular (commonly 120-180°), saucer-shaped, with margins subentire, erose or 2- to 3-lobed. In young plants of *C. horrida* and a few other large species some of the indusia may be *subcyatheoid,* i.e., irregularly cup-shaped to subglobose, thus almost covering the sorus. In respect to the degree the indusium encircles the receptacle, there are a few notable exceptions within the genus. In *C. apiculata* the indusia are very narrow and spathulate (fig. 11a), or in young plants sometimes so strongly cupped as to appear narrowly cucullate. In *C. nervosa* and *C. cocleana,* the indusium completely encircles the sorus (fig. 11c). This character is so unique in these three species that it may be used exclusively in the key to distinguish them from others.

Spores

Cnemidaria spores are unique in the family. Features of size, shape, and surface ornamentation are not particularly significant, but the large pores located on each side constitute an excellent generic character. Mature spores are trilete and have an approximate lateral diameter of 37-52μ. Perine is often lacking or very thin and closely surrounding the exine, and there are no definable surface patterns. However, in all

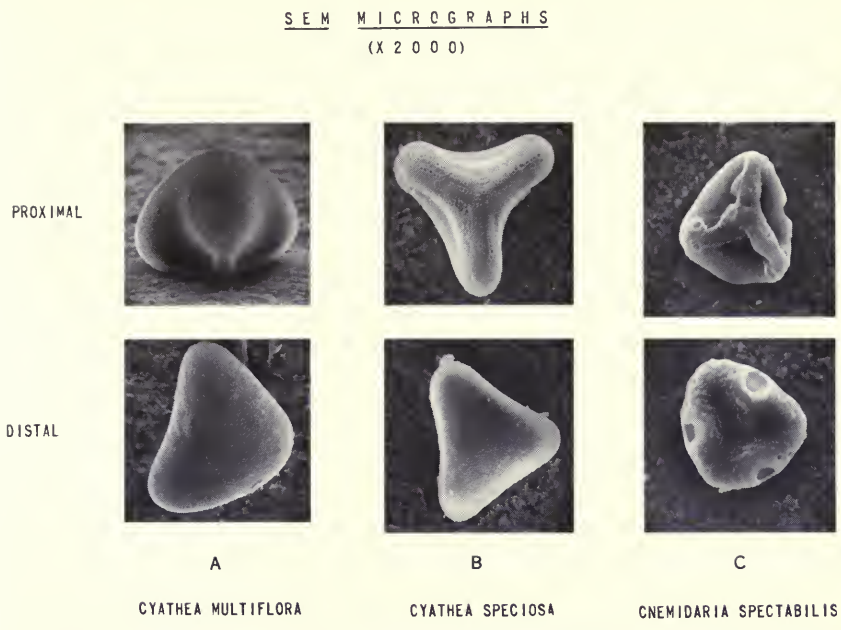


FIG. 12. SEM micrographs (c. 2000 ×) of Cyatheaceae spores: without large equatorial pores, **a**, *Cyathea multiflora*, **b**, *C. speciosa;* with typical large equatorial pores, **c**, *Cnemidaria spectabilis*.

Cnemidaria spores there is one large pore (up to 15 μ in diameter) located near the center of each side, on or near the equator (fig. 12c). In Erdtman and Sorsa (1971) this aperture is referred to as "a conspicuous lenticular hollow or depression in the exine." These are easily visible under a light microscope, but the results are much more dramatic when examined by means of a scanning electron microscope. Such pores are lacking in spores of all other genera of the Cyatheaceae.

Cnemidaria spores may also have small apertures or depressions, quite irregular in size and spacing, scattered along the surface, and this feature is sometimes also seen in the spores of other genera. For example, *Cyathea* spores (figs. 12a, b) may have hundreds of minute apertures covering the surface, arranged at random or in vague patterns, although in this instance they are much more constant in size and shape than those of *Cnemidaria*. A species considered by Maxon (1912) as part of the subgenus *Cnemidaria* was *Hemitelia speciosa* (Willd.) Kaulf. (= *Cyathea speciosa* Willd.). These plants resemble *Cnemidaria* in that their pinnae are subentire, but they do *not* conform in characteristics of venation and indument. Examination of the spores (fig. 12b) confirms the evidence that this species does not belong in *Cnemidaria*.

Scanning electron micrographs are presented on pages 78-79 to illustrate spores of a number of species of *Cnemidaria.* To prepare spores for SEM photography, aluminum stubs were first coated with silver conductive paint and allowed to dry. Sporangia were then crushed in a drop of distilled water on the stubs and bits of sporangial walls removed from the surface. After drying, stubs were vapor coated with 200 Å gold and examined under a Cambridge Stereoscan Mark II-A SEM.

MATERIALS

This revision is based on the study of nearly 2,000 specimens which were either loaned to me by various institutions or made available to me on visits to their herbaria. I also made several visits to Gray Herbarium to examine specimens on loan to Dr. Rolla Tryon from Berlin, Paris, Stockholm, Caracas, and the Missouri Botanical Garden. These herbaria, with the abbreviations of Lanjouw and Stafleu, Index Herbariorum, 1964, are listed here:

B— Botanisches Museum, Berlin, Germany
C— Botanical Museum and Herbarium, Copenhagen, Denmark
CR— Museo Nacional de Costa Rica, San José, Costa Rica
F— Field Museum of Natural History, Chicago, Illinois
FSU— Florida State University Herbarium, Tallahassee, Florida
GH— Gray Herbarium, Harvard University, Cambridge, Massachusetts
IJ— Institute of Jamaica, Kingston, Jamaica
K— Royal Botanic Gardens, Kew, England
MO— Missouri Botanical Garden, St. Louis, Missouri
NA— U. S. National Arboretum, Washington, D.C.
NY— New York Botanical Garden, Bronx, New York
P— Musée National d'Histoire Naturelle, Paris, France
R— Museu Nacional, Rio de Janeiro, Brazil
S-PA— Paleobotanical Department, Naturhistoriska Riksmuseum, Stockholm, Sweden
U— Botanisch Museum, Rijksuniversiteit, Utrecht, Netherlands
US— U. S. National Museum, Washington, D.C.
VEN— Instituto Botienico, Caracas, Venezuela

A number of specimens were collected in Costa Rica in 1968 on a Field Museum trip with Dr. William Burger, the primary purpose of which was continued general collecting for current research on the "Flora Costaricensis."[1] Some important additional collections were

[1] This trip was supported by funds from National Science Foundation Grant GB-7300, L. O. Williams, Principal Investigator.

made at my request, in the critical areas of Oaxaca, Mexico, by Dr. John Mickel, and Chocó, Colombia, by Dr. David Lellinger.

MAPS

Maps showing distribution of species (pages 82-85) were charted on the Goode Series of base maps, published by the University of Chicago Press, Chicago, Illinois. Each symbol represents a specific locality where a particular species has been collected.

ACKNOWLEDGEMENTS

I wish to express my deep appreciation to Dr. Rolla Tryon for his advice and criticism throughout the course of this work, and for so unselfishly granting me hours of his time during my frequent visits to the Gray Herbarium. It was, in large part, his inspiration and guidance that provided the original impetus for this research.

My sincere thanks are also extended to Dorothy Nash for her assistance in the typing and proofreading of manuscript; to Dr. Rolf Singer for criticism and correction of the Latin descriptions; and to Dr. Thomas Taylor (now of Ohio State University) and Mr. Ron Wibel for their help in use of the scanning electron microscope at the University of Illinois, Circle Campus, in Chicago, Illinois. I am indebted to T. R. Dudley, David Lellinger, Terry Lucansky, John Mickel, Timothy Plowman, and Richard White for *Cnemidaria* collections of special importance, and to the many herbarium curators for their generous loans of specimens used in this study. I am especially grateful to Luis D. Gómez and other members of the staff of the Museo Nacional, San José, Costa Rica, for the co-operation and courtesies extended to me while collecting in their country.

Many specimens which I examined at Gray Herbarium had been collected on field trips, or borrowed on visits to European herbaria, by Drs. Rolla and Alice Tryon. These trips were supported by funds from National Science Foundation Grants GB-4184 (Rolla Tryon) and GB-31170 (Rolla and Alice Tryon).

Most of the fine drawings used as illustrations were done by Richard Roesener of Field Museum. Others were done by Sally Babb Landry and Lydia Vickers Wunsch at Gray Harbarium. Useful information about the spores of many species of Cyatheaceae was obtained from dozens of slides prepared and loaned to me by Dr. Gerald Gastony.

Finally, I wish to thank Dr. Louis O. Williams, whose advice and encouragement have been a continual source of strength to me from the inception of this work.

SYSTEMATIC TREATMENT

Cnemidaria Presl, Tent. Pterid. 56. 1836. TYPE SPECIES: *Cnemidaria speciosa* Presl.

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

Hemistegia Presl. Gefässbündel Stipes der Farrn, 46, 1847 (preprint of Abh. Böhm Ges. Wiss. V, 5: 354. 1848). TYPE SPECIES: *Hemistegia kohautiana* (Presl) Presl=*Cnemidaria grandifolia* (Willd.) Proctor.

Microstegnus Presl, Gefässbündel Stipes der Farrn, 45, 1847 (preprint of Abh. Böhm Ges. Wiss. V, 5: 353, 1848). TYPE SPECIES: *Microstegnus grandifolius* (Willd.) Presl=*Cnemidaria grandifolia* (Willd.) Proctor.

Actinophlebia Presl, Gefässbündel Stipes der Farrn, 47, 1847 (preprint of Abh. Böhm Ges. Wiss. V, 5: 355, 1848). TYPE SPECIES: *Actinophlebia horrida* (L.) Presl=*Cnemidaria horrida* (L.) Presl.

Hemitelia pro parte auctt.

Caudex ascending to erect, *rudimentary* to 1.5 m. long, rarely reported up to 7 cm. in diameter at base and 3.5 m. in length, bases often thickly covered with adventitious roots; *leaf* to 3.5 m. long, 1.5 m. wide, broadly lanceolate to ovate-oblong; *lamina* pinnate to pinnate-pinnatisect, *never fully bipinnate,* tissue glabrous; *petiole* smooth to muricate, or provided with stout, conical spines up to 7 mm. long, with pneumatophores 0.5 to 1 cm. long, spaced 4 to 5 cm. apart in a single line (rarely double) along either side of the petiole, spindle-shaped, linear to lanceolate; *petiole scales* generally appressed, linear to ovate, or amorphous, whitish, or more commonly bicolorous with a dark brown median stripe and a whitish margin, *marginal cells differentiated* from those of the central portion also in shape and orientation; *major axes* rounded beneath, sulcate above, often provided with minute, appressed, arachnoid pubescence; *scales* of the rachis and minor axes scattered to rare, or lacking, broad, ovate or amorphous, whitish, pale, brown or bicolorous, flat and appressed (or some species with bullate costal scales); stiff, terete, recurved, pluricellular *trichomes* to 0.4 mm. long copious to sparse to commonly lacking on rachis and costa, but always *lacking on costa and costules above; pinnae* sessile to short-stalked, patent to ascending, or commonly the basal pair reduced and deflexed, apices acute to acuminate, margins entire or crenately to deeply cleft, the segments obtuse to acuminate, rarely apiculate; *veins* pinnately arranged in the segments, the basal veinlet merging with the one opposite to form a *costal areole,* or *strongly connivent to the sinus,* or (only in *C. amabilis*) non-connivent and reaching the margin at a point just above the sinus; *sori* subglobose at maturity, disposed on the veins in a single inframedial to submarginal line between costule and segment margin, or in the most deeply dissected species arranged in several lines; *receptacle* elevated, subglobose, with

paraphyses rudimentary or lacking; *indusia* subtending the sorus, commonly saucer-shaped to semicircular, with margins erose-entire or several-lobed, or rarely fully circular or reduced to one narrow lobe, or in young plants of some species irregularly cup-shaped to subglobose; *spores* trilete, ca. 37-52 μ., provided with *one large pore near the center of each face* on or near the equator, and with numerous smaller apertures of irregular size and shape scattered over the surface.

This description is an emendation of that in Tryon (1970), restricting the genus to those species with the characteristics enumerated here and in the "Introduction." Thus the excluded species previously included under the old generic name, *Hemitelia,* are herewith placed in the genus *Cyathea* (See "Excluded Species").

Therefore I would emend the part of the key which includes the genera *Trichipteris, Cyathea,* and *Cnemidaria,* in Tryon's "The Classification of Cyatheaceae," (1970) as follows:

Spores with or without apertures of various size and shape, but never with a single very large pore near the center of each face on or near the equator; costae and often costules with minute, terete, recurved trichomes abundant on adaxial side; basal veins of segments commonly free (only in rare species merging to form costal areoles), non-connivent, reaching the margin at a point above the sinus; leaves commonly twice-pinnate or more (in rare species once-pinnate).
- Indusium absent ..... *Trichipteris*
- Indusium present, rarely scalelike, to sometimes hemitelioid, to usually sphaeropteroid ..... *Cyathea*

Spores always provided with one very large pore near the center of each face on or near the equator; costae and costules lacking trichomes on adaxial side; basal veins of segments commonly merging to form costal areoles, or, when free, connivent to the sinus (only in *C. amabilis* non-connivent); leaves pinnate to pinnate-pinnatisect, never fully bipinnate ..... *Cnemidaria*

Key to the Species and Varieties of Cnemidaria

a. Basal veins of segments commonly free, rarely (if ever) joining to form costal areoles. b.
- b. Soral line submarginal on segments. c.
  - c. Segments cuspidate; pinnae mostly sessile or subsessile; indusia narrow, usually entire. Mexico. ..... 5. *C. apiculata*
  - c. Segments rounded; pinnae often stalked; indusia broad, semicircular to circular, with 2-3 lobes. .... 8. *C. bella*
- b. Soral line inframedial to supramedial between costule and margin of segment. d.
  - d. Petiole scales commonly concolorous, whitish; basal acroscopic veins of segments simple. Venezuela. ... 1. *C. amabilis*
  - d. Petiole scales commonly bicolorous; basal acroscopic veins of segments branched. e.

e. Minute, terete, recurved trichomes abundant on rachis beneath; segments obtuse. Panama, Costa Rica ..... 2b. *C. mutica* var. *chiricana*

e. Minute, terete, recurved trichomes lacking, or when present the segments acute to acuminate. f.

f. Terminal section of leaf nearly half the total length of lamina; pinnae 6 pairs or less. Colombia. ..... 4. *C. singularis*

f. Terminal section of leaf one-fifth the total length of lamina (or less); pinnae on mature leaves 10 pairs or more. g.

g. Basal basiscopic veins of segments commonly arising from costule or its junction with costa; petiole frequently spiny. Panama, Costa Rica. h.

h. Larger secondary segments crenate to shallowly-lobed, some basal ones with broad, rounded sinuses, or a few segments adnate. 2c. *C. mutica* var. *grandis*

h. Secondary segments subentire (except at serrulate tips), with acute, mostly narrow sinuses, all segments joined. i.

pinnae more than twice as long as broad

i. Secondary segments (or lobes) of larger pinnae more than twice as long as broad beyond the sinus; sinuses extending more than three-fourths to costa ..... 2a. *C. mutica* var. *mutica*

i. Secondary segments (or lobes) of larger pinnae not more than 1½ times as long as broad beyond the sinus; sinuses extending one-half to three-fourths to costa. ..... 2d. *C. mutica* var. *contigua*

g. Basal basiscopic veins of segments (especially in basal one-third or apical one-third of pinna) commonly arising from costa; petiole lacking spines. j.

j. Soral line distinctly inframedial; basal pair of pinnae not conspicuously reduced. Colombia. ..... 3. *C. tryoniana*

j. Soral line medial to mostly supramedial; basal pair of pinnae distinctly reduced. k.

k. Lamina gradually reduced to a non-conform, pinnatifid apex. Peru, Brasil ... 9a. *C. uleana* var. *uleana*

k. Lamina with a conform terminal pinna. Colombia, Ecuador ..... 9b. *C. uleana* var. *abitaguensis*

a. Basal veins commonly joining to form a series of costal areoles, rarely (if ever) free. l.
  l. Pinnae (excluding the basal pair and reduced apical ones) deeply pinnatifid, the sinuses extending more than halfway to costa. m.
    m. Rachis and petiole broadly alate throughout; large creamy-white scales abundant along petiole. Peru. . 12. *C. alatissima*
    m. Rachis and petiole not alate; petiole scales brown, or bicolorous with whitish margins. n.
      n. Indusia circular, completely surrounding receptacle. Panama. ..... 10. *C. cocleana*
      n. Indusia semicircular, positioned on costular side of receptacle. o.
        o. Lamina with a conform terminal pinna; segments of pinnae subimbricate, with sinuses markedly cartilaginous above and contrasting in color with adjacent tissue; soral line inframedial between costule and margin of segment. Colombia, Ecuador. ..... 11. *C. quitensis*
        o. Lamina gradually or abruptly reduced to a nonconform, pinnatifid apex; segments with broader sinuses, these not cartilaginous, tissue uniformly green; soral line medial to mostly supramedial. p.
          p. Scales on costules beneath abundant, bullate. lesser Antilles, northern Venezuela. q.
            q. Segments mostly acute to acuminate; scales on costae and costules beneath white to bicolorous. St. Lucia northward to Saba. . 7a. *C. grandifolia* var. *grandifolia*
            q. Segments mostly obtuse; scales on costae and costules beneath brown. St. Vincent southward to coastal Venezuela ..... 7b. *C. grandifolia* var. *obtusa*
          p. Scales on costae and costules beneath rare or scattered, broad, flat, never bullate. r.
            r. Rachis and petiole muricate to spiny; scales of costae and costules brown. Greater antilles, Costa Rica, Venezuela to Peru .. 6. *C. horrida*
            r. Rachis smooth, petiole smooth to tuberculate; scales of costae and costules pale or whitish. Brazil, Peru ..... 9a. *C. uleana* var. *uleana*

  l. Pinnae (excluding the basal pair and reduced apical ones) entire to shallowly pinnatifid, the sinuses extending halfway or less to costa. s.
    s. Pinnae (excluding the basal pair and reduced apical ones) entire to broadly and shallowly crenate or broadly serrate; 5-9 cm. broad. Venezuela, Peru. t.

t. Veins mostly once-forked; bases of pinnae truncate; indusia semicircular, attached on costular side of receptacle. Venezuela. ..... 22. *C. karsteniana*

t. Veins simple; bases of pinnae rounded to broadly cuneate; indusia circular, completely surrounding receptacle. Ecuador, Peru. ..... 23. *C. nervosa*

s. Pinnae (excluding the basal pair and reduced apical ones) deeply-crenate to shallowly pinnatifid, or if subentire, then never over 4 cm. broad. u.

u. Lamina gradually or abruptly reduced to a pinnatifid apex, or with a non-conform terminal pinna. v.

v. Pinnae (excluding the basal pair and reduced apical ones) shallowly pinnatifid, the sinuses extending one-third to halfway to costa; veins commonly branched. w.

w. Narrow, membranous wing commonly extending well down each side of rachis. Costa Rica, Colombia. ..... 13. *C. choricarpa*

w. Narrow wing lacking on the rachis below the 2 uppermost pairs of pinnae. x.

x. Lamina reduced very gradually to a pinnatifid apex, lacking a distinct apical section; pinna segments often imbricate, with sinuses tending to be cartilaginous; pinnae less than 4.5 cm. wide. Probably only French Guiana. ..... 16. *C. cruciata*

x. Lamina reduced very abruptly into a conspicuous, separate apical section; segments not imbricate, or if so, the larger pinnae 5-7 cm. wide. y.

y. Indusia fully circular, the margins subentire. Panama. ..... 10. *C. cocleana*

y. Indusia more or less semicircular, the margins erose to several-lobed. z.

z. Soral line medial between costule and margin of segment; segments commonly imbricate, with sinuses cartilaginous and brownish colored. Colombia. ..... 15b. *C. spectabilis* var. *colombiensis*

z. Soral line supramedial; segments usually with broader sinuses, these rarely cartilaginous. Trinidad, Tobago, Margarita, Guianas, Venezuela. ..... 15a. *C. spectabilis* var. *spectabilis*

v. Pinnae (excluding the basal pair and reduced apical ones) subentire to deeply crenate, the sinuses extending less than one-third to costa; veins simple. aa.

aa. Trichomes and scales scattered to abundant on rachis beneath; sori inframedial on veins. Mexico, Guatemala. ..... 21. *C. decurrens*

aa. Trichomes and scales lacking on rachis; sori in a V-shaped pattern, supramedial on veins near segment base but inframedial near tip. British Guiana. ..... 20. *C. roraimensis*

u. Lamina with a conform or subconform terminal pinna (this rarely with a pair of longer basal lobes). bb.

bb. Soral line mostly inframedial on the veins between costule and margin of segment. cc.

cc. Petiole and often the lower rachis spiny; minute, terete, recurved trichomes scattered to abundant on rachis and costae beneath. Colombia, Ecuador. ..... 11. *C. quitensis*

cc. Petiole lacking spines; axes lacking terete, recurved trichomes. dd.

dd. Veins from the costule simple to once-forked; scales of costa and rachis commonly whitish or pale; pinnae (excluding the basal pair and reduced apical ones) mostly deeply crenate. Colombia, Ecuador. ..... 19. *C. ewanii*

dd. Veins from the costule 2- or 3-forked; scales when present commonly glossy, dark brown; pinnae (excluding the basal pair and reduced apical ones) pinnatifid, the sinuses extending one-third to halfway to costa. Colombia. ..... 14. *C. chocoensis*

bb. Soral line medial to supramedial between costule and margin of segment. ee.

ee. Petiole spiny or strongly muricate. Trinidad, northern Venezuela ..... 17. *C. consimilis*

ee. Petiole smooth, or rarely tuberculate at base. Peru, Bolivia ..... 18. *C. speciosa*

1. **Cnemidaria amabilis** (Morton) Tryon, Contr. Gray Herb. 200: 52. 1970. Figure 8b, Map 2.

Hemitelia amabilis Morton, Fieldiana Bot. 28: 10. 1951. TYPE COLLECTION: *Steyermark 62042,* northeast of Caripe, Monagas, Venezuela, April. 13, 1945. HOLOTYPE: US! PHOTO: F! GH! ISOTYPES: F! VEN!

Caudex to 1 m. long, 3 to 7.5 cm. in diameter; *leaves* to 1 m. long and 0.5 m. broad, terminating abruptly in a pinnatifid apex; *petiole* to 20 cm. long, with spines to 1.5 mm. long or lacking, the scales commonly concolorous, whitish, occasionally with a dark brown spot at the point of attachment; *rachis* with thin, green, herbaceous (often inconspicuous) wing extending partly to wholly down each side, the scales frequent, white or yellowish to light brown, or rarely bicolorous, the

trichomes minute, terete, recurved, abundant above and beneath; *pinnae* sessile, cut three-fourths to costa, basal pair substantially reduced and deflexed; *costae* and *costules* with whitish or brown scales scattered to frequent beneath, and trichomes scattered to abundant beneath; ultimate *segments* subfalcate, obtuse to rarely subacute, basal pair occasionally overlapping the rachis; *veins* always free, basal ones non-connivent, and reaching the margin at a point above the sinus, commonly once-forked (except basal acroscopic veins simple), basal basiscopic ones arising from the costule; *sori* in a single line, supramedial between costule and segment margin; *indusia* yellow to brown, mostly semicircular, subentire to 2- or 3-lobed.

Cnemidaria amabilis is evidently the most primitive species in the genus. Characters that are common in the other genera of scaly Cyatheaceae—but present in *Cnemidaria* only in *C. amabilis* or a few other primitive species—are the following: the upper side of the rachis is closely invested with recurved, terete trichomes (also in *C. mutica* var. *chiricana*); the pinnae are deeply dissected (ca. three-fourths of the way to the costa); and the axes lack the peculiar arachnoid scurf which is present on most other species of *Cnemidaria*. In addition the venation is similar to that in most Cyatheaceae, not modified as in the other species of *Cnemidaria*. The basal veins are completely free, extending from the costule to the margin at a point above the sinus of the converging segments, the opposing veins having no tendency to incline toward one another. Thus *C. amabilis* has fewer of the specialized characters of *Cnemidaria* than any other species.

Within the genus, *C. amabilis* might be confused with *C. mutica* var. *chiricana* of Panama and Costa Rica; however, the former has whitish petiole scales with rarely a minute spot of brown at point of attachment, and the basal acroscopic veins in each pinna segment are always simple (fig. 8b), whereas the latter has bicolorous petiole scales, pale or whitish with a broad median stripe of dark brown from base to tip, and all basal veins of segments are once-forked.

In mountain forests, northern Venezuela, 850-1,450 m.

Additional specimens examined.—**Venezuela. Sucre:** Peninsula de Paria, Cerro Humo, n.e. de Irapa, *Steyermark 94886* (GH, NY, U, VEN). Peninsula de Paria, Cerro Patao, n.e. de Güiria, *Steyermark & Agostini 91205* (US, VEN).

2. **Cnemidaria mutica** (Christ) Tryon, Contr. Gray Herb. 200: 52. 1970.

Caudex to 0.7 m. long and 6 cm. in diameter; *leaves* to 3 m. long and 1.5 m. broad, terminating in a gradually pinnatifid apical section; *petiole* to 1.5 m. long, with spines to 2.5 mm. long or lacking, the scales commonly bicolorous, dark brown with a narrow, whitish margin; *rachis* with thin, green membranaceous

(often inconspicuous) wing extending partly to wholly down each side, or lacking entirely, the scales scattered to frequent beneath, pale to brownish or bicolorous, the trichomes minute, terete and recurved, abundant to lacking; *pinnae* sessile to short-stalked, cut two-thirds to (rarely) entirely to the costa, basal pair substantially reduced and often deflexed; *costae* and *costules* with pale to brown or bicolorous scales scattered to frequent beneath, and trichomes lacking or scattered beneath; *secondary segments* subfalcate to falcate, obtuse to acuminate, basal pair rarely overlapping the rachis; *veins* free, connivent to the sinus, only rarely merging to form costal areoles, 1- to 4-forked, to pinnately branched, basal basiscopic ones commonly arising from the costule; *sori* in one to several lines, inframedial to supramedial between costule and segment margin; *indusia* pale yellow to brown, more or less semicircular, subentire, erose or 2- to 3-lobed, often irregularly cup-shaped in young material.

C. mutica has the most variable leaf outline of any species in the genus. Of seven species treated by Maxon (1912, 1914), I can recog-

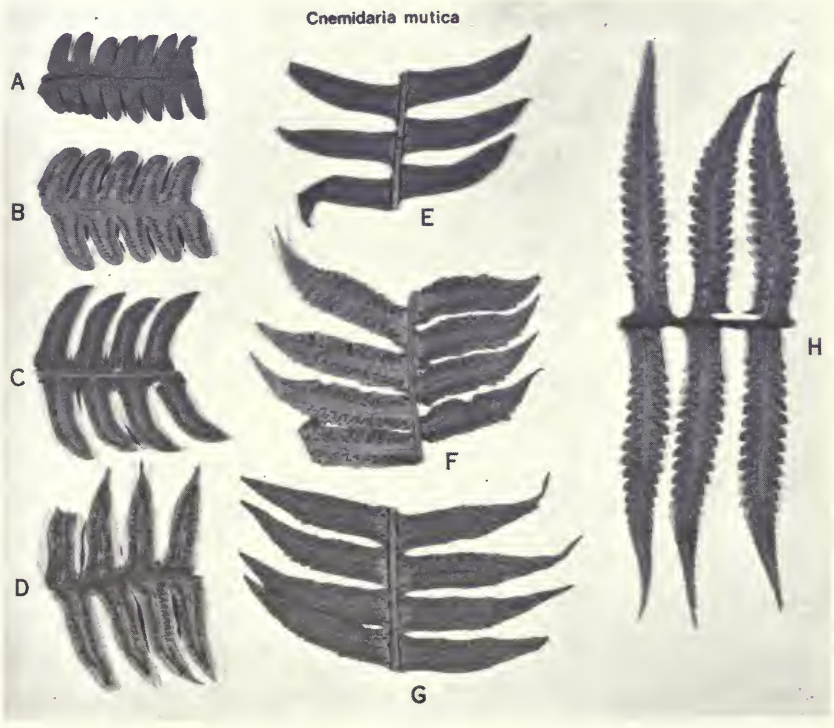


FIG. 13. Variable pinna outline of *Cnemidaria mutica*: **a**, var. *contigua;* **b-e**, var. *mutica;* **f-h**, var. *grandis*.

nize only one, including four varieties. The differences between these are based primarily on segment shape and degree of dissection of the pinnae. Although there is no difficulty in separating the two extremes (var. *contigua* and var. *grandis*), the degree of dissections and relative shape of the segments blend gradually and almost imperceptibly from one variety to the next (fig. 13). Thus the varietal limits I have set are necessarily somewhat arbitrary. The differences between members of the *C. mutica* complex are mostly all quantitative, although var. *chiricana* is set apart from the rest by the presence of the terete, recurved trichomes on the rachis above. There is apparently a correlation between size of the leaf and pinnae and the degree of dissection, shape of segment apices, and number of forks in the veins. Thus the smaller leaf of var. *contigua* has pinnae about 3 cm. broad cut three-fourths to the costa, with rounded segments, and veins only once- to twice-forked, whereas the much larger leaf of var. *grandis* has pinnae often up to 15 cm. broad, sometimes cut entirely to the costa, with mostly acuminate secondary segments, and veins several-forked to pinnately branched. The lack of costal areoles and the deep dissection of pinnae indicate that this species is among the most primitive in the genus. In var. *chiricana,* the presence of trichomes on the rachis above indicates that it is closely related to the Venezuelan *C. amabilis,* which it also resembles in numerous other features. All varieties of *C. mutica* are found growing at middle elevations, encompassing only a narrow geographic range: four Costa Rican provinces, and the neighboring Chiriqui area of Panama. It is presumed that these are incipient species, but that reproductive isolation has been insufficient to result in morphological distinction.

2a. **Cnemidaria mutica** var. **mutica.** Figure 7b, Map 4.

Hemitelia mutica Christ, Bull. Soc. Bot. Genève II. 1: 233. 1909. TYPE COLLECTION: Wercklé s.n., Turrialba, Costa Rica, 850 m. FRAGMENT: US!

Hemitelia arachnoidea Maxon, Contr. U.S. Natl. Herb. 16: 34. 1912. TYPE COLLECTION: *Maxon 453,* vicinity of La Palma, Costa Rica, May 6 to 8, 1906. HOLOTYPE: (2 sheets) US! ISOTYPE: NY!

Hemitelia horrida (L.) R.Br. var. *heterosora* Rosenst., Repert. Spec. Nov. Regni Veg. 10: 275. 1912. TYPE COLLECTION: *Brade 451* Iuan Viñas prope Rio Chis, 20/III/1910. FRAGMENT: US!

Hemitelia pittieri Maxon, Contr. U.S. Natl. Herb. 16: 32. 1912. TYPE COLLECTION: *Pittier 10969 pro parte,* Cañas Gordas, Valle de Agua Buena, Costa Rica, Feb. 1897. HOLOTYPE: US! FRAGMENT: F!

Hemitelia subglabra Maxon *tom. cit.* 36. TYPE COLLECTION: *Maxon 451,* vicinity of La Palma, Costa Rica, May 6 to 8, 1906. HOLOTYPE: US!

Cyathea mutica (Christ) Domin, Pteridophyta 264. 1929.

Cyathea pittieri (Maxon) Domin, *loc. cit.*

Cyathea subarachnoidea Domin, *loc. cit., nom.nov.* for *Hemitelia arachnoidea* Maxon.

Cyathea subglabra (Maxon) Domin, *loc. cit.*

Petiole spines to 2.5 mm. or, rarely, lacking; *rachis* commonly lacking the minute, terete, recurved trichomes; larger *pinnae* cut more than three-fourths to costa; scondary segments subentire (except at serrulate tips), obtuse to acuminate, joined by narrow, acute sinuses, the segments of larger pinnae more than twice as long as broad beyond the sinus; *veins* 1- to 4-forked; *sori* in 1 or 2 series between margin of segment and costule.

In addition to the specimen of *Pittier 10969,* listed above as the holotype of *Hemitelia pittieri,* there is another at Museo Nacional in San José, Costa Rica labeled *Pittier 10969,* also identified as *H. pittieri.* The latter is evidently a mixed collection. With its pinnae incised only one-third of the way to the costa, and its abundant costal areoles, it is obviously *Cnemidaria choricarpa.* Maxon's description (1912) of *H. pittieri* was based solely on the single sheet he saw at U.S. National Herbarium, so he was apparently unaware of the existence of the other similarly labeled collection in San José. Since *Pittier's No. 10966,* also collected at Cañas Gordas, is *C. choricarpa,* it may be assumed that one of the leaves of this plant was somehow mixed with the other collection and therefore received the number *10969* in error.

Larger specimens of var. *mutica* may resemble *Cnemidaria horrida;* comparisons are presented under the discussion of *C. mutica* var. *grandis.*

Forests and edges of forests, 450-2,100 m., Costa Rica (Alajuela, Cartago, Heredia, San José) and Panama (Chiriquí).

Selected specimens examined.—**Costa Rica. Alajuela:** Along Río San Rafael, Aguas Zarcas, *L. O. Williams et al. 29109* (F). **Cartago:** La Estrella, *Standley 39349* (GH, US). Finca El Muñeco, South of Cartago, *Stork 4756* (GH, US). South of Tapantí above Río Grande de Orosi, *Burger & Stolze 5685* (F, GH). **Heredia:** Vara Blanca de Sarapiquí, *Skutch 3262* (GH, US). Roadside waterfall near Vara Blanca, *Burger & Stolze 5936* (F, GH). Cinchona, above Upper Sarapiquí Valley, *Scamman 7575* (GH, US). **San Jose:** La Palma, northeast of San Jerónimo, *Burger & Stolze 5328* (F, GH). Lisiere des paturages a La Palma, *Tonduz 12532* (CR, US). **Panama. Chiriqui:** 5 miles east of El Boquete, *Killip 5156* (GH, MO, US). Vicinity of El Boquete, *Cornman 1285* (US).

2b. **Cnemidaria mutica** var. **chiricana** (Maxon) Stolze, stat. et comb. nov. Figure 8a, Map 5.

Hemitelia chiricana Maxon, Contr. U.S. Natl. Herb. 16: 33. 1912. TYPE COLLECTION: *Maxon 5519* (as "H. chiriquana"), between Alto de la Palmas and

top of Cerro de la Horqueta, Chiriquí, Panama, March 18, 1911. HOLOTYPE: (3 sheets) US!

Cyathea chiricana (Maxon) Domin, Pteridophyta, 263. 1929.

Petiole spines lacking; *rachis* with minute, terete, recurved trichomes abundant beneath, scattered to abundant above; *pinnae* cut two-thirds to four-fifths to costa; *secondary segments* subentire (except at serrulate tips), obtuse to rarely subacute, joined by narrow, acute sinuses, segments of larger pinnae 1½-2 times as long as broad beyond the sinus; *veins* 1- to 2-forked; *sori* in single line between margin of segment and costule.

Var. *chiricana* may be easily confused with *C. amabilis;* the two are compared in the discussion of the latter species.

Forests and wooded slopes, 1,400-2,200 m., Costa Rica (Cartago) and Panama (Chiriquí).

Additional specimens examined.—**Costa Rica. Cartago:** Río Grande de Orosi beyond Tapantí, *White & Lucansky 196840* (GH). **Panama. Chiriqui:** Near the divide, above El Boquete, *Killip 5347 & 5350* (US). Cordillera above El Boquete, *Killip 5297* (GH, US), and *Killip 5294* (US). Between Alto de las Palmas and Cerro de la Horqueta, *Maxon 5474 & 5521* (US) and *Maxon 5517* (GH, US).

2c. **Cnemidaria mutica** var. **grandis** (Maxon) Stolze, stat. et comb. nov. Figure 13, Map 6.

Hemitelia grandis Maxon, Contr. U.S. Natl. Herb. 16: 37. 1912. TYPE COLLECTION: *Maxon 307*, vicinity of Coliblanco, Costa Rica, April 30-May 2, 1906. HOLOTYPE: (2 sheets) US! ISOTYPE: US!

Hemitelia rudis Maxon, *op. cit.* 17: 413, 1914. TYPE COLLECTION: *Maxon 5682*, Holcomb's Trail, above El Boquete, Chiriquí, Panama, March 23, 1911. HOLOTYPE: (4 sheets) US! ISOTYPE: GH!

Cyathea grandis (Maxon) Domin, Pteridophyta, 264. 1929.

Cyathea rudis (Maxon) Domin, *loc.cit.*

Petiole spines to 2.5 mm. or, rarely, lacking; rachis with minute, terete, recurved trichomes lacking above, scattered to lacking beneath; *pinnae* cut nearly to costa (or larger ones fully to costa at base); larger *secondary segments* crenate to shallowly-lobed, some basal ones joined by broad, rounded sinuses, or a few segments adnate, most segments twice to four times as long as broad beyond the sinus; *veins* thrice-forked to pinnately branched; *sori* in 1-4 series between margin of segment and costule.

In general size and pinna architecture, leaves of var. *grandis* and larger leaves of var. *mutica* closely resemble those of *C. horrida* and *C. grandifolia* var. *grandifolia*. Also, although the former two are basically free-veined and the latter two commonly have basal veins merging to form costal areoles, occasional specimens have variation in these char-

acters. For example, rarely a pinna of *C. mutica* may have a number of costal areoles, or occasionally a pinna of *C. horrida* or *C. grandifolia* may have segments with a number of free basal veins. However, in *C. mutica* (except in var. *contigua*) the soral line or lines are roughly equidistant between margin and costule, or, in the largest specimens, nearly fill both sides of the secondary segment. The soral lines of *C. horrida* or *C. grandifolia* extend to very near the margin, a rather distinctive character shared within the genus only by *C. bella* and *C. apiculata*. *Cnemidaria grandifolia* var. *grandifolia* is further distinguished by the costules which bear abundant white, bullate scales often terminating in a hairlike tip, a feature peculiar to this species.

Forest and wooded slopes, 1,250-1,900 m., Costa Rica (Cartago, San José) and Panama (Chiriquí).

Selected specimens examined.—**Costa Rica. Cartago:** Valley of Río Grande de Orosi, *Tryon & Tryon 7036* (GH); Near Tapantí, *Lent 28* (F, GH). El Muñeco, on the Río Navarro, *Standley & Torres 51250* (F, US). El Cedrál, near Naranjo River, *Nisman 123* (GH). South slope of Turrialba Volcano, *L. O. Williams 19647* (US). **San Jose:** La Palma area, northeast of San Jerónimo, *Burger & Stolze 5270* (F, GH). Vicinity of La Palma, *Maxon & Harvey 8023 & 8042* (US). **Panama. Chiriqui:** 10 miles above El Boquete, *Killip 5231 & 5248* (US). Valley of Río Piarnasta, above El Boquete, *Killip 5391* (GH, MO, US).

2d. **Cnemidaria mutica** var. **contigua** (Maxon) Stolze stat. et comb. nov. Underw. ex Maxon Figure 13, Map 7.

Hemitelia contigua Maxon, Contr. U.S. Natl. Herb. 16: 32. 1912. TYPE COLLECTION: *Maxon 523,* 5 mi. south of Cartago, Costa Rica, May 12, 1906. HOLOTYPE: (2 sheets) NY! FRAGMENT: US!

Cyathea contigua (Maxon) Domin, Pteridophyta 263. 1929.

Petiole spines minute or commonly lacking; *rachis* lacking minute, terete, recurved trichomes; *pinnae* cut one-half to three-fourths to costa; *secondary segments* subentire (except at serrulate tips), obtuse to rarely subacute, joined by narrow, acute sinuses, the segments not more than 1½ times as long as broad beyond the sinus; *veins* 1- to 2-forked; *sori* in a single line between margin of segment and costule.

In addition to the differences noted in the key, var. *contigua* may also be distinguished by the V-shaped soral pattern on the segments (the apical sori situated very near the costule, while the basal ones are quite close to the margin), whereas the sori in other varieties of *C. mutica* are relatively constant in their position between margin and costule, whether inframedial, medial, or supramedial. Trichomes are completely lacking in var. *contigua,* and scales on all axes except the petiole are

uniformly brown, whereas scales may be pale to brown, or commonly bicolorous, in other varieties of *C. mutica*.

Mountain forests, 1,250-2,100 m., Costa Rica (Cartago, Heredia).

Additional specimens examined.—**Costa Rica. Cartago:** Santa Clara de Cartago, *Maxon & Harvey 8220* (US). La Sierra, 25 km. south of Cartago, *L. O. Williams et al. 28016* (CR, F). **Heredia:** Socorro de San Ramon, *Brenes 4992* (F). Forests of Río Vueltas, *Gómez 2246* (CR, F, GH, NY, US). Slope of Volcán Barba, *Scamman & Holdridge 7879* (GH, US).

3. **Cnemidaria tryoniana** Stolze, sp. nov. Figures 10c, 14; Map 2.

Caudex brevissimus vel nullus; petiolus inermis; pinnae infimae vix deminutae vel deflexae; costae subtus paleis latis niveis adpressis instructae; venae semel furcatae, liberae; venae infimae haud anastomosantes sed arcuatae et in sinum conniventes; venae infimae basioscopicae e costa egredientes; sori uniseriati, inter costulam et marginem inframediani.

TYPE COLLECTION: *Metcalf & Cuatrecasas 30122*, between Valdivia and Yarumal, Antioquia, Colombia, Feb. 20, 1942. HOLOTYPE: (2 sheets) US! PHOTO: F! ISOTYPES: GH! MO! FRAGMENT: F!

Caudex very short or lacking; *leaves* to 1.8 m. long and 0.5 m. broad, terminating abruptly with a subconform apical pinna; *petiole* to 0.7 m. long, unarmed, the scales sparsely scattered, lanceolate, bicolorous, dark shiny brown with narrow, whitish margins; *rachis* non-alate, the scales scattered, broad, dirty white or occasionally with dark brown centers, trichomes lacking; *pinnae* distant, sessile, cut three-fourths to costa, basal pair scarcely (if at all) reduced or deflexed; *costae* and *costules* with whitish scales scattered to frequent beneath, trichomes lacking; ultimate *segments* subfalcate, subacute to acute, basal pair commonly crowding or overlapping the rachis; *veins* free, once-forked, basal ones conniving at the sinus, basal basiscopic ones arising from the costa; *sori* in a single line, inframedial between costule and segment margin; *indusia* yellow to brownish, mostly semicircular and subentire.

This species is one of the most primitive in the genus, as evidenced by its free venation and deeply dissected pinnae, and is closely related to *C. amabilis* and *C. singularis*. It could perhaps be confused with *C. uleana* (*especially* var. *abitaguensis*), which also has unarmed petioles and basal veins which arise from the costae rather than from the costules. However, in addition to characters noted in the key, *C. tryoniana* can further be distinguished by the abundance of large, whitish scales along the costae beneath, whereas the scales of *C. uleana* are rare or sparse.

It is with great personal satisfaction that I name this species in honor of Dr. Rolla M. Tryon, Jr., who has done excellent work with the ferns of tropical America, and who is currently involved in a comprehensive study of the Cyatheaceae.

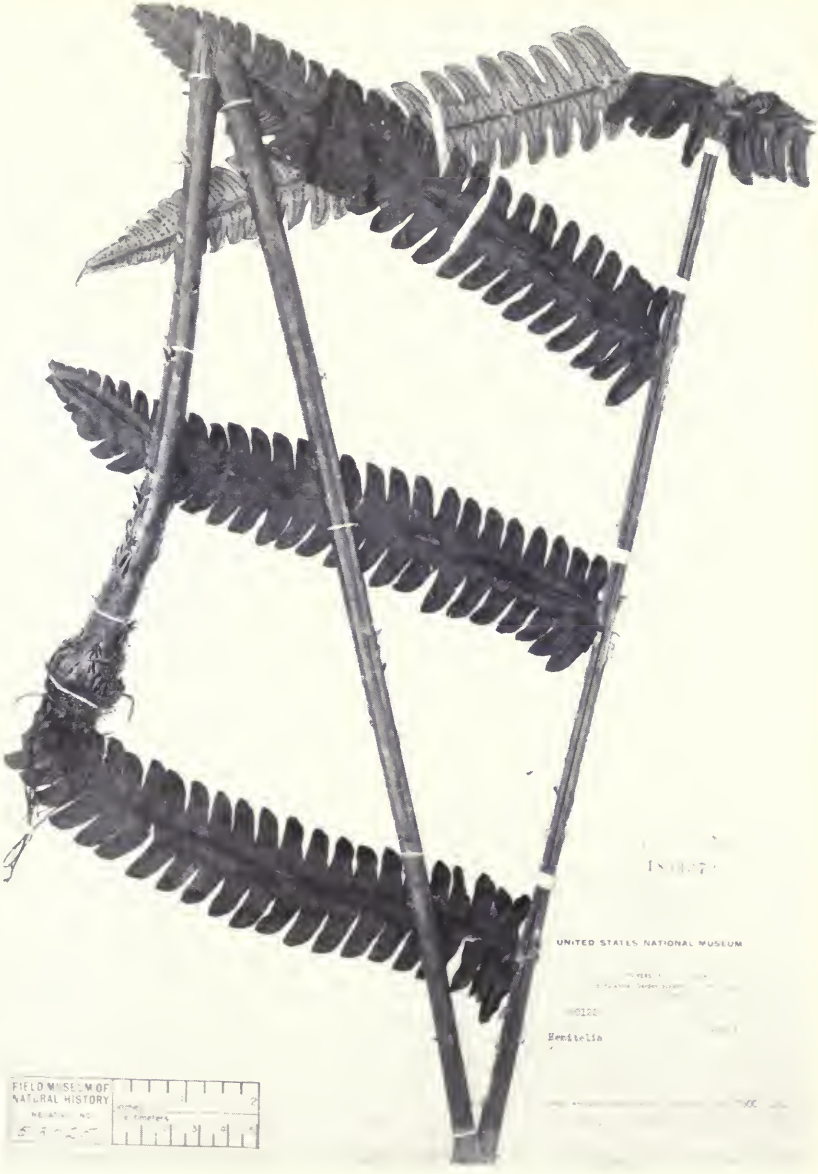


FIG. 14. *Cnemidaria tryoniana, Metcalf & Cuatrecasas 30122* (US, holotype).

The species is known only from the type collection; found at an altitude of 2,200 m.

4. **Cnemidaria singularis** Stolze, sp. nov. Figure 15, Map 8.

Caudex brevissimus vel nullus; petiolus inermis; folii sectio terminalis dimidiae parti longitudinis laminae aequalis; pinnae 3-6-jugatae; costae subtus paleis latis niveis adpressis sparsis instructae; venae furcatae vel bifurcatae, liberae; venae infimae haud anastomosantes sed arcuatae et in sinum conniventes; venae infimae basioscopicae e costa egredientes; sori uniseriati, inter costulam et marginem medii vel supramediani.

TYPE COLLECTION: *Soejarto 1571*, Cerro Portachuelo, Depto. de Putumayo, Colombia, Aug. 27, 1965. HOLOTYPE: GH! PHOTO: F! ISOTYPE: F!, GH!

Caudex very short or lacking; *leaves* to 1.2 m. long and 0.4 m. broad, pinnatifid apical section nearly half the total length of the lamina; *petiole* to 0.6 m. long, unarmed, the scales sparse except at very base, lanceolate to linear-lanceolate, bicolorous, dark shiny-brown with narrow whitish margins; *rachis* non-alate, the scales rare, thin, very pale brown or whitish, trichomes lacking; *pinnae* distant, six pairs or less, sessile, commonly cut a little more than halfway to costa, basal pair slightly reduced and somewhat deflexed; *costae* and *costules* with thin, whitish, amorphous scales rare to scattered beneath, trichomes lacking; ultimate *segments* subfalcate, rounded to subapiculate; *veins* free, once- or twice-forked, basal ones conniving at sinus, basal basiscopic ones arising from the costa; *sori* in a single line, medial to supramedial between costule and segment margin; *indusia* yellowish-brown, mostly semicircular, subentire to deeply two-lobed.

This shares with *C. tryoniana* the more primitive characteristics of the genus. The two species also have in common a number of other morphological features, notably: the rudimentary caudex, the lack of spines of the petiole and trichomes on the axes, the basal basiscopic veins arising from the costa rather than from the costules, and the scales on the axes (when present) thin, translucent, and whitish. However, *C. singularis* is one of the most unique species in the genus, and cannot be confused with others. Its laminar architecture is almost monstrous in that the terminal section measures nearly half the length of the entire lamina, while the remainder is comprised of only 3-6 pairs of pinnae. The leaves therefore present a strange, top-heavy aspect.

The species is known only from the type collection, which was found at 2,300 m. in a wet mountain forest, along the road from Sibundoy to Pepino, Dept. Putumayo, Colombia.

5. **Cnemidaria apiculata** (Hook.) Stolze, comb. nov. Map 3.

Hemitelia apiculata Hook. & Bak., Syn. Fil. 29, 1865. TYPE COLLECTION: *Jurgensen 873*, Sierra San Pedro Nolasco, Talea, etc., Oaxaca, Mexico, 1843-

FIG. 15. *Cnemidaria singularis, Soejarto 1571,* (GH, holotype).

1844. HOLOTYPE: K, FRAGMENTS: NY! US! ISOTYPE: P! PHOTO: F!

Cyathea aristata Domin, Acta Bot. Bohem. 9: 93. 1930, *nom. nov.* for *Hemitelia apiculata* Hook., (*non Cyathea apiculata* Domin, 1929).

Caudex not seen; *leaves* to 1.5 m. long and 0.7 m. broad, terminating in a gradually pinnatifid apical section; *petiole* to 0.7 m. long, spines lacking or, very rarely, minute, scales frequent, bicolorous, dark brown with narrow whitish margins, trichomes lacking; *rachis* non-alate, the scales scattered to abundant, bicolorous, trichomes lacking; *pinnae* rather crowded, sessile, cut three-fourths to seven-eighths to costa; *costae* and *costules* with minute, amorphous, brown or bicolorous scales scattered to lacking beneath, trichomes lacking; ultimate *segments* falcate, sharply cuspidate, basal pair commonly overlapping the rachis; *veins* free, basal ones conniving at the sinus, basal basiscopic ones arising from the costule; *sori* in a single line, submarginal on the segments; *indusia* brown, subentire, narrow, spathulate or cucullate.

Cnemidaria apiculata is the northernmost representative of the species related to *C. amabilis.* It is probably derived from the same ancestral stock as the Central American *C. mutica,* which it resembles in a number of characters. However, *C. apiculata* is unique in two respects: no other species has such sharply cuspidate segments nor such narrow indusia (fig. 11a). It is further distinguished by having a soral line so far from the costule as to usually appear almost marginal (fig. 10a). This characteristic occurs elsewhere only in *C. bella, C. grandifolia,* and *C. horrida.* In the original description of Hooker the number "273" is given for Jurgensen's collection. This was probably a printer's error, for the isotype and fragments I have seen are all clearly marked "Jurgensen No. 873", and Maxon (1912) gives this same number for the holotype at Kew.

In rain forests, 1,200-1,600 m., found only in the State of Oaxaca, Mexico.

Additional specimens examined.—**Mexico. Oaxaca:** Ridge between Yetzelalag & Lovani, Depto. Choapam, *Hallberg 1557* (NY) ca. 20 miles n.e. of Villa Alta, Distr. of Villa Alta, *Mickel 994* (NY) 79 km. west of Ixtlán de Juarez on Rt. 175, Depto. Ixtlan, *Mickel 5676, 5717* (NY) 24 km. south of Valle Nacional, Depto. Tuxtepec, *Mickel 5935* (NY).

6. **Cnemidaria horrida** (L.) Presl, Tent. Pterid. 57. 1836. Map 10.

Polypodium horridum L., Sp. Pl. 1092. 1753. TYPE: Plumier Descr. Pl. Amer. 1693, *t.*4 (Fil. Amer. *t.*8. 1705).

Cyathea horrida (L.) J.E. Sm., Mem. Acad. Roy. Sci. (Turin) 5: 416, 1793. (non Kaulf. 1823).

Cyathea commutata Sprengel, Anleit. Kennt. Gewäsche 3: 146, *fig. 32*, 1804. TYPE COLLECTION: Santo Domingo.

Hemitelia horrida (L.) R.Br., Prod. Fl. Nov. Holl. 158, 1810. (*non H. horrida* var. *imrayana* Hook. in Hook. & Bak. 1865.)

Actinophlebia horrida (L.) Presl, Gefässb. Stipes der Farrn 48: 1847. (preprint of Abh. Böhm Ges. Wiss V. 5: 356. 1848.)

Hemitelia hookeri Presl, *tom. cit.* 350. *nom. nud.*

Hemistegia horrida (L.) Fée, Mem. Fam. Foug. 5 (Gen. Fil.): 351. 1850-52.

Hemistegia repanda Fée, *loc. cit.* TYPE COLLECTION: *Linden, s.n.*, Cuba.

Cormophyllum horridum (L.) Newm., Phytologist 5: 238. 1854.

Hemitelia acuminata Schlecht., Bot. Zeit. 14: 474, 1856. *nom. nud.*

Hemitelia commutata (Sprengel) Schlecht., *loc. cit., nom. nud.*

Hemitelia hookeriana Schlecht., *loc. cit., nom. nud.*

Candex to 4 m. tall and 7 cm. in diameter; *leaves* to 3.5 m. long and 1.5 m. broad, terminating gradually in a nonconform, pinnatifid apex; *petiole* to 1.5 m. long, muricate or, more commonly, with stout spines to 5 mm. long, the scales lanceolate, bicolorous, dark brown with narrow whitish margins, usually found only at base; *rachis* non-alate, often spiny, the scales rare, when present lanceolate to ovate, dark brown or bicolorous, trichomes lacking; *pinnae* sessile to short-stalked, cut seven-eighths to (rarely) entirely to the costa, basal ones slightly reduced and deflexed; *costae* and *costules* with dull brown, amorphous scales rare to scattered beneath, trichomes lacking; secondary *segments* subfalcate or falcate, acute to acuminate, basal pair often overlapping the rachis; *veins* 1- to 5-forked, basal ones commonly merging to form costal areoles, basal basiscopic ones usually arising from the costule; *sori* in one to several lines, supramedial to submarginal between costule and segment margin; *indusia* whitish to yellow, more or less semicircular, subentire to erose, saucer-shaped or sometimes, in young material, irregularly cup-shaped to subglobose.

Because of its huge size and deeply-dissected pinnae, *Cnemidaria horrida* is perhaps more representative of the typical aspect of tree ferns than any other species of the genus. It is evidently the most primitive of the areolate-veined group, and from its ancestral stock was probably derived not only the other Antillean species, *C. grandifolia*, but most of the South American areolate species as well.

Cnemidaria horrida is geographically the most successful species in the genus, enjoying the widest distribution as well as the greatest altitudinal range. It is common in the Greater Antilles, and ranges along the subcoastal regions of northern South America southward down the Andes to southern Peru, and has been found at times in Costa Rica.

Larger specimens of the typical variety of *Cnemidaria grandifolia* var. *grandifolia*, especially those with acuminate segments, may be confused with *C. horrida*. Besides the scale differences noted in the key, however, the latter has whitish or pale yellow indusia and the lamina beneath has some white, arachnoid, scurfy indument. The indusia of *C. grandifolia*

var. *grandifolia* are most often dark- or yellowish-brown, and the lamina lacks arachnoid scurf.

Some specimens of *C. mutica* in Costa Rica exhibit enough costal areoles to be confused with *C. horrida*. However, the leaf texture of *C. horrida* is quite thin, and the lines of sori crowd the margin closely, whereas the leaves of *C. mutica* are much thicker, and the soral line medial to supramedial (never closely approaching the margin). I have found only two collections of *C. horrida* from Costa Rica; several previous determinations were of *C. mutica*. Maxon (1912) cities another Costa Rican collection (*Alfaro 108*) as *C. horrida,* but I have not seen this.

In and at the edges of forests, along stream banks and on mountainsides, from sea level to 2,000 m., Greater Antilles, Costa Rica, and Venezuela to Peru.

Selected specimens examined.—**Puerto Rico:** Alto de La Bandera, near Adjuntas, *N. L. Britton & Shafer 2075* (F, MO, NY, US). Lares, in sylva ad Buenos Aires, *Sintenis 6088* (F, GH, NY, US). **Dominican Republic. Barahona:** Vicinity of Paradis, *Abbott 1618* (GH, NY, US). **Santiago:** San José de las Matas, *Valeur 350* (F, MO, NY, US). **Santo Domingo:** Vicinity of Colonia Ramfis, *Allard 14303* (US). **Haiti:** Massif du Nord, Morne Brigand, *Ekman H-2875* (F, US). Vicinity of Port de Paix, *E. C. Leonard 12275* (GH, NY, US). **Cuba:** Santiago de Cuba, *Linden 1738* (F, US). **Las Villas:** Buenos Aires, Trinidad Mountains, *Morton 4240* (GH, US). **Oriente:** Monteverde, Yateras, *Maxon 4336* (GH, NY, US). **Pinar Del Rio:** Sierra cerca de Taco Taco, *Baker 3835* (F, NY, US). **Jamaica. Portland:** Valley of Trafalgar River, *Maxon & Killip 779* (F, GH, NY, US). **St. Andrew:** Near Heritage Dam, *Proctor 3911* (US). **St. Thomas:** Between House Hill and Cuna Cuna Gap, *Maxon 8879* (F, GH, NY, US). **Costa Rica. Heredia:** Pies de Sta. Barbara, *Pittier 1679*. Along Río Sarapiquí, between Cariblanco and San Miguel, *L. O. Williams 20304* (F, US). **Venezuela. Aragua:** Selvas tropofilas de Guamitas, Parque Nacional, *Delgado 81* (F, US, VEN). **Distrito Federal:** Cortada del Guayabo, *Tamayo 154* (US, VEN). **Lara:** En selvas nubladas, San Isidro, *Tamayo 2543* (US, VEN). **Miranda:** Near Agua Fria, km. 26, road to Carascua, *Pittier 11510* (US, VEN). **Colombia. Antioquia:** Porcecito, *Bro. Daniel 913* (US). **Caldas:** San Bernardino, Cordillera Central, *Killip & Hazen 10159* (GH, NY, US). **Caqueta:** Sucre, *Juzepczuk 6510* (US). **Cundinamarca:** Arriba de Sasaima, *Dugand & Jaramillo 3813* (US). **Magdalena:** Dibulla, Seifriz *277x* (US). **Meta:** Along Rio Guatiquia, Villaviciencio, *Pennell 1577* (F, GH, MO, NY, US). **Putumayo:** Between Umbria & Urcusique,

Ewan 16790 (GH, US). **Santander:** Jordan, 10 km. S.E. of Landazuri, *Ewan 15669* (GH). **Ecuador. Napo-Pastaza:** Tena, *Asplund 9230* (US). Cerro Antisana, trail to Tena, *Grubb et al. 1392* (NY, US). Near Archidona, *Mexia 7320* (F, GH, US). **Santiago-Zamora:** Primary rain forest, Taisha, *Cazalet & Pennington 7711* (NY, US). **Peru. Amazonas:** Valley of Río Marañon, Bagua, *Wurdack 1991* (US). **Cuzco:** Kosñipata-Pilcopata, Prov. Paucartambo, *Vargas 11269* (GH). **Loreto:** Pumayacu, between Balsapuerto & Moyobamba, *Klug 3182* (F, GH, MO, NY, US). **San Martin:** San Roque, *L1. Williams 7156* (F, NY, US).

7. **Cnemidaria grandifolia** (Willd.) Proctor, Rhodora 63: 31. 1961.

Caudex to 1 m. long and 4 cm. in diameter; *leaves* to 3 m. long and 1 m. broad, terminating in a gradually- or abruptly-reduced pinnatifid apical section; *petiole* to 1.3 m. long, muricate, or with spines to 3 mm. long, the scales bicolorous, dark to light brown with a whitish margin, linear to lanceolate, commonly with long attenuate tips; *rachis* non-alate, with scales scattered to abundant, ovate to lanceolate, brown or white or bicolorous, the minute, terete, recurved trichomes scattered to abundant beneath, or lacking; *pinnae* sessile, cut three-fourths to nine-tenths to the costa, basal pair usually somewhat reduced and deflexed; *costae* with broad brown, white or bicolorous scales beneath, *costules* with white or brown bullate scales beneath, trichomes rare or lacking; secondary *segments* falcate, obtuse to acuminate, basal pair often overlapping the rachis; *veins* 1- to 4- (6) times forked, basal ones commonly merging to form costal areoles, basal basiscopic ones usually arising from the costule; *sori* in one or two lines, supramedial to submarginal between costule and segment margin; *indusia* yellow-brown to dark brown, semicircular, subentire to several-lobed.

Cnemidaria grandifolia has traditionally been divided into three species, *Hemitelia grandifolia, H. obtusa,* and *H. kohautiana,* based mainly on the quantitative differences of pinna width and (or) shape of the secondary segments. However, comparison of a large series of collections will demonstrate that such characters blend almost insensibly throughout the species and hence cannot provide a basis for taxonomic delimitation. Pinna width varies from less than 3 cm. to more than 10 cm., while the segment apices vary from broadly rounded to long-acuminate; and in every other morphological character examined I have found no further evidence to warrant distinction at the species level.

"Hemitelia kohautiana," including the type collection and most specimens so determined in herbaria, shares geographic distribution and morphological characters with *H. grandifolia.* However, the plants previously treated as *Hemitelia obtusa* differ sufficiently from the typical *Cnemidaria grandifolia* to warrant varietal distinction. The pinnae are generally much narrower in var. *obtusa,* and the segments are primarily obtuse, although enough specimens can be found with wider pinnae and

at least subacute segments to be confused with similar specimens in the typical variety. In this case, color of the bullate scales along the costules beneath affords a more effective varietal delimitation: those of var. *obtusa* are glossy and deep amber to castaneous, while those of var. *grandifolia* are dull and white. Thus the combination of scale and segment characters affords an adequate basis for recognition of the two varieties, and these are correlated with an interesting disjunction in the Lesser Antilles. Variety *grandifolia* is found from Saba southward to St. Lucia, while the range of var. *obtusa* begins at St. Vincent, the next island south, and continues on to the Island of Margarita and the Paraguana Peninsula in Venezuela. Hence there is a clear disjunction between the varieties at St. Vincent Passage. This is no greater water barrier than others which occur among the Lesser Antilles, so the isolation of the two taxa within *C. grandifolia* presumably has an environmental basis, possibly related to the more recent emergence of the southernmost islands after the Pleistocene.

7a. **Cnemidaria grandifolia** var. **grandifolia.** Figure 7a, Map 10.

Cyathea grandifolia Willd., Sp.Pl. 5: 490. 1810. TYPE COLLECTION: *Herb. Willd. No. 20167,* Habitat in America Calidiore. HOLOTYPE: B; PHOTO: F! GH!; FRAGMENT: US!

Hemitelia grandifolia (Willd.) Sprengel, Syst. Veg. 4: 125. 1827.

Cnemidaria kohautiana Presl, Tent. Pterid. 57. 1836. TYPE COLLECTION: *Sieber (Flora Martin. 375),* Martinique; HOLOTYPE: PR or PRC? ISOTYPES: MO! P!; FRAGMENT: US!

Hemitelia monilifera J.Sm., London J. Bot. 1: 662. 1842. *nom.nud.*

Hemitelia serrata J.Sm., *loc.cit. nom.nud.*

Hemitelia imrayana Hook., Icon. Pl. VII, *t.669.* 1844 (non *Cyathea imrayana* Hk. 1844). TYPE COLLECTION: *Imray 14,* Dominica; ISOTYPE: P!

Hemitelia kohautiana (Presl) Kunze, Bot. Zeit. 2: 298. 1844.

Hemistegia grandifolia Presl, Gefässb. Stipes der Farrn, 47. 1847 (preprint of Abh. Böhm Ges. Wiss. V. 5: 355. 1848). TYPE COLLECTION: *Plumier tab. 26.* (non *Hemitelia grandifolia* (Willd.) Sprengel).

Microstegnus grandifolius (Willd.) Presl., *tom.cit.* 46.

Hemistegia kohautiana (Presl) Presl., *tom.cit.* 47.

Hemistegia willdenowii Fée, Mem. Fam. Foug. 5 (Gen.Fil.): 351. 1850-52 *nom.nov.* for *Cyathea grandifolia* Willd.

Hemitelia horrida var. *imrayana* Hook., in Hook. & Bak., Syn. Fil. 28, 1865.

Hemistegia insignis Fée, Mem. Fam. Foug. 11: 99, 1866 (non *Cyathea insignis* Eat. 1860). TYPE COLLECTION: *Herb. l'Herminier s.n.,* Flore de la Guadeloupe, ISOTYPE: P!

Hemitelia insignis (Fée) C.Chr., Index Fil. 349, 1905.

Cyathea kohautiana (Presl) Domin, Pteridophyta 264. 1929.

Hemitelia obtusa var. *kohautiana* (Presl) Domin, Mem. Roy. Czech. Soc. Sci. 2: 71. 1929.

Cyathea antillana Domin, Acta. Bot. Bohem. 9: 91. 1930. *nom.nov.* for *Hemitelia imrayana* Hk.

Cyathea obtusa var. *kohautiana* (Presl) Domin, *tom.cit.* 142.

Leaves terminating in a gradually pinnatifid apical section; *petioles* muricate to short-spiny; *rachis* and *costae* with white to bicolorous scales; *pinnae* cut four-fifths to nine-tenths to the costa; *costules* with dull white, bullate scales occasional to abundant beneath; secondary *segments* falcate, mostly subacute to acuminate (only rarely obtuse); *veins* 1- to 4- (6-) times forked; *sori* in 1 to 2 lines between costule and segment margin.

In and at edges of forests on stream banks and mountainsides: 300-1,100 m. Saba, St. Kitts, Nevis, Montserrat, Guadeloupe, Dominica, Martinique, St. Lucia.

Selected specimens examined.—**Saba:** Mountain, 800 m., *Boldingh 2221* (= *1427*) (IJ, U). Summit of The Mountain, *Stoffers 4203,* (U, US). **St. Kitts:** Slopes of Mount Misery, *N. L. Britton & Cowell 510* (NY, US). N.W. rim of The Crater, *Proctor 19501* (GH, IJ). **Nevis:** Summit of Nevis Peak, *Proctor 19318* (GH, IJ). Nevis Peak, *A. C. Smith 10516* (IJ, US). **Montserrat:** Chaner's Mountain, *Shafer 283* (F, NY, US). **Guadeloupe:** Bois du Haut Matouba, *Duss 4449* (F, GH, MO, NY, US). **Dominica:** Sylvania Estate, alt. 488 m., *Hodge 10* (GH, NY, US). Parish of St. Paul, *Wilbur et al. 8185* (F. NY). **Martinique:** *Duss 4435* (F, GH, MO, NY, US) and *Duss 1607* (NY, US). Camp de Colson, *M. & H. Stehlé 4605* (US) **St. Lucia:** Milette Bridge, *Box 490* (US). Upper slopes of Piton Flore, *Proctor 18092* (GH, IJ).

7b. **Cnemidaria grandifolia** var. **obtusa** (Kaulf.) Stolze, stat. et comb. nov. Map 10.

Hemitelia obtusa Kaulf., Enum. Fil. 252, 1824. TYPE COLLECTION: *"Habitat in Antillis."* POSSIBLE SYNTYPES: *Ryan s.n.,* Montserrat; *Sieber fl. mixta 331.*

Cyathea munita Kaulf., *tom.cit.* 260. *nom.nud.*

Cnemidaria munita Presl. Tent. Pterid. 57. 1836. *nom.nud.*

Cnemidaria obtusa (Kaulf.) Presl, *l.c.*

Hemitelia munita Hk., Sp. Fil. 1: 32. 1844. *nom.nud.*

Hemistegia munita Presl, Gefässb. Stipes der Farrn 47. 1847. (Preprint of Abh. Böhm. Ges. Wiss. V. 5: 355. 1848.) *nom.nud.*

Hemistegia obtusa (Kaulf.) Presl. l.c.

Hemitelia munita Kuhn, Linnaea 36: 162. 1869. TYPE COLLECTION: *Willd. Herb. No. 20168,* America. ISOTYPE: US!

Hemitelia bullata Christ, Bot. Jahrb. Syst. 24: 81. 1897. TYPE COLLECTION: Eggers 6035, Grenada, 1400'. 28/XI/1889. ISOTYPES: F! P! US! FRAGMENT: NY!

Hemitelia obtusa var. *bullata* (Christ) Domin, Mem. Roy. Czech. Soc. Sci. 2: 71. 1929.

Cyathea obtusa (Kaulf.) Domin, Pteridophyta 264, 1929.

Cyathea obtusa var. *bullata* (Christ) Domin, Acta Bot. Bohem. 9: 142. 1930.

Leaves terminating abruptly in a pinnatifid apical section; *petioles* with stout spines to 3 mm. long; *rachis* and *costae* beneath with brown (or very rarely a few whitish) scales; *pinnae* cut three-fourths to seven-eighths to the costa; *costules* with glossy, amber to castaneous, bullate scales occasional to abundant beneath, or very rarely some whitish or bicolorous scales intermingled; secondary *segments* falcate, obtuse; *veins* once- (rarely twice-) forked; *sori* in a single line between costule and segment margin.

No type was designated by Kaulfuss for *Hemitelia obtusa.* However, Krug (1898) cites a *Ryan* specimen from Montserrat as well as *Sieber fl. mixta No. 331* (no locality) as *H. obtusa* from Kaulfuss' herbarium. It is likely these are the specimens that provided the basis for Kaulfuss' description. Hence these specimens (destroyed at LZ) can be considered as syntypes. I have seen no duplicates of them.

Of hundreds of specimens of *Cnemidaria grandifolia* examined, one juvenile plant collected in 1938 on Morne Gimie, St. Lucia (*Box 1963*) fails to fit the pattern of distribution. Though the leaves are too immature for positive determination, the brown and rather glossy scales of the axes lead to a tentative identification as var. *obtusa.* Furthermore, a few specimens of var. *obtusa* from St. Vincent have been observed with a scattering of very light colored—nearly white—scales interspersed among the brown, so they appear similar to those of var. *grandifolia.* Thus it seems that St. Vincent and St. Lucia, where the ranges of the varieties converge, comprise an "area" where they also tend to intergrade.

In and at edges of forests, on stream banks, and mountainsides, 300-1,050 m. St. Vincent, Grenada, Tobago, Trinidad, Venezuela (Margarita Is., Paraguana Peninsula).

Selected specimens examined.—**St. Vincent:** In glens, about 1,000 ft., *H. H. & G. W. Smith 854* (GH, IJ, MO, US). Rain forest, *Beard 1434* (F, MO). Morne Garou Mountains, *Morton 5072* (GH, MO, NY, US). **Grenada:** Forest borders, Grand Etang, *Beard 1194* (F, GH, US). Above Windsor Forest, St. David Parish, *Proctor 16904* (GH, IJ, U, US). **Tobago:** *Eggers 5859* (F, US). **Trinidad:** *Parker s.n.* (GH). **Venezuela:** San Juan Mountain, Margarita Island, *Johnston 191* (F, GH, NY, US).— some specimens a mixture with *C. spectabilis* var. *spectabilis.* Cerro Santa Ana, Paraguana Peninsula, *Curran & Haman 676 & 736* (GH) and *683* (GH, US).

8. **Cnemidaria bella** (Mett.) Tryon. Contr. Gray Herb. 200: 52. 1970. Figure 16.

Hemitelia bella Mett., Fil. Hort. Lips. 110. 1856. TYPE COLLECTION: *"Hort. Bot. Lips., cult."* AUTHENTIC SPECIMENS: K! P! MO! US!

FIG. 16. *Cnemidaria bella, T. C. Porter s.n.* (U.S. Herb. No. 2204421), cult. Bot. Garden, Leipzig.

Cyathea bella (Mett.) Domin, Pteridophyta 263, 1929.

Caudex, petiole and leaf apex not seen; *leaves* to 1 m. broad; *rachis* non-alate, lacking scales and trichomes; *pinnae* distant, stalked (to 2 cm.), cut one-third to a little more than halfway to the costa; *costae* and *costules* with scales and trichomes lacking, except for rare, dull brown, amorphous scales on the costae beneath; secondary *segments* subfalcate, broadly rounded; *veins* simple to once-forked, commonly free but occasionally some basal ones merging to form costal areoles, basal basiscopic ones usually arising from the costule or, rarely, from the costa; *sori* in a single line, submarginal on the segments; *indusia* dark brown, semicircular, with 2 to 3 lobes.

Hooker's (1865) description mentions "st. aculeated at the base;" i.e., the petiole spiny at the base. Although no petioles were available in material I examined, portions of the rachis were strongly muricate, a condition generally occurring when petioles are spiny.

Cnemidaria bella is a highly distinctive species, not likely to be confused with any other, but it is somewhat questionable that it be included

as a valid species. The original collections were from cultivated material at the Botanical Garden at Leipzig, and apparently the species has never been found in the wild. The sum total of its representation today are the fragments and parts of leaves which have made their way into various herbaria. The few mature spores seen have the three, large, characteristic Cnemidarioid pores, the lamina is completely devoid of trichomes, and the veins, though mostly free, are connivent to the sinus, so the species must definitely be placed in *Cnemidaria*. However, the pinnae are relatively long-stalked, a condition otherwise unknown in the genus, the soral line is submarginal (rare in the genus), and most spores are abortive. All of these characters indicate that the plant at the Leipzig Gardens may have been a hybrid between a species of *Cnemidaria* and one of *Cyathea*. One likely parent would be *Cyathea speciosa* or *C. integrifolia,* both of which have subentire or entire, short-stalked pinnae, submarginal sori, and trichomes thinly scattered on costae and rachis. The *Cnemidaria* parent might be *C. horrida* or *C. spectabilis,* both common species, with supramedial to submarginal sori, costal areoles, and indument rare to lacking.

9. **Cnemidaria uleana** (Samp.) Tryon, Contr. Gray Herb. 200: 52. 1970.

Caudex to 0.5 m. long and 3 cm. in diameter; *leaves* to 2 m. long and 0.7 m. broad, pinnatifid apical section gradually reduced (or conform in var. *abitaguensis*); *petiole* to 0.7 m. long, smooth to slightly muricate, the scales bicolorous, dark brown with broad whitish margins, linear-lanceolate to lance-ovate, trichomes lacking; *rachis* non-alate, scales sparse, pale to bicolorous or lacking, trichomes lacking; *pinnae* sessile, cut two-thirds to seven-eighths to the costa, basal pair distinctly reduced and often deflexed; *costae* and *costules* with broad, amorphous, pale yellowish or whitish scales scattered to rare beneath, trichomes lacking; secondary *segments* falcate to subfalcate, obtuse to acute, basal pair often overlapping the rachis; *veins* once-to thrice-forked, free, or basal ones often merging to form costal areoles, basal basiscopic ones (especially in basal one-third or apical one-third of pinna) arising from the costa; *sori* in one or two lines, medial to supramedial between costule and segment margin; *indusia* pale yellow or yellowish brown, semicircular, subentire to several-lobed.

Cnemidaria uleana appears to have been derived from the same stock as *C. horrida,* which shares the range of var. *uleana* in Peru and that of var. *abitaguensis* in Colombia and Ecuador. The typical variety of *C. uleana* is the sole representative of the genus in Brazil. *C. uleana* var. *uleana* exhibits a condition unique in the genus, in that the degree of anastomosing of basal veins is inconstant, i.e., one leaf may be predominantly free-veined, another mostly areolate along the costa, and

yet another may show an equal mixture of both conditions. Var. *abitaguensis* is always free-veined.

9a. **Cnemidaria uleana** var. **uleana.** Figure 9b, Map 8.

Hemitelia uleana Samp., Bol. Mus. Nac. Río de Janeiro 1: 65. 1923. TYPE COLLECTION: *Ule s.n.,* Perto de Nova Friburgo, Alto da Serra. Est. do Río, Brazil, 1898. HOLOTYPE: R! PHOTO: F! GH!

Hemitelia maxonii Rosenst., Repert. Spec. Nov. Regni Veg. 21: 344. 1925. TYPE COLLECTION: *Brade 6901,* Serra do Mar. Est. São Paulo, Brazil, 26/IV/1914. HOLOTYPE: R! ISOTYPE: S-PA!

Cyathea subarborescens Domin, Acta Bot. Bohem. 9: 162. 1930, *nom.nov.* for *Hemitelia maxonii* Rosenst., not *Cyathea maxonii* Underw. ex Maxon.

Leaves terminating in a gradually reduced, pinnatifid apical section; *rachis* with pale to bicolorous scales scattered beneath; scales of *costae* and *costules* beneath scattered, whitish, sometimes faintly red-margined.

Specimens of *C. uleana* var. *uleana* with costal areoles could be confused with *C. speciosa* in Peru, but the latter has pinnae lobed less than halfway to the costa and leaves terminating in conform or subconform apical sections. *C. tryoniana* and some varieties of *C. mutica* are somewhat similar to free-veined specimens of var. *uleana,* but are distinguished by the characters shown in the key.

Until recently plants of the typical variety of *C. uleana* were known only from Brazil, but some fine collections were made by Dudley in 1968 from Dept. Cuzco, Peru. However, it is unlikely that further collections will be made between these two disjunct regions (except perhaps in the wet, montane areas of Bolivia contiguous with Peru) since the combinations of altitude and climate favorable to the growing habits of *Cnemidaria* are lacking.

Forests, shaded ravines, and hillsides, 580-2,000 m., Brazil, Peru.

Selected specimens examined.—**Peru. Cuzco:** Prov. La Convención, *Dudley 10459, 11312* (GH, NA). **Brazil. Minas Gerais:** 2-3 km. ENE of Ouro Preto, *Tryon & Tryon 6871* (GH). **Parana:** Serra do Mar, *Dusén 17306* (F, GH, MO, NY). **Rio:** Río Bonito, Itatiaia, *Pereira 312* (F, GH, MO, US). **São Paulo:** Serra do Bocania, *Lutz 727* (US). Alto da Serra, *L. B. Smith 2077* (GH, NY, R, US).

9b. **Cnemidaria uleana** var. **abitaguensis** (Domin) Stolze, stat. et comb. nov. Map 8.

Hemitelia abitaguensis Domin. Mem. Roy. Czech. Soc. Sci. 2: 74. 1929. TYPE COLLECTION: *Spruce 5364,* Monte Abitagua, Andibus Ecuadorensibus. HOLOTYPE: K! PHOTO: F! ISOTYPES: GH! NY!

Cyathea abitaguensis (Domin) Domin, Acta Bot. Bohem. 9: 88. 1930.

Leaves terminating in a conform or subconform apical pinna; *rachis* lacking scales; *Costae* and *costules* with pale to light brown scales very rare beneath, or lacking.

Other than the character used in the key, little can be seen to separate *C. uleana* var. *abitaguensis* from the free-veined specimens of the typical variety, except that scales are virtually absent on the axes of the latter, and the rare scales found are pale yellowish or very light brown. Scales of var. *uleana,* though not abundant, can be found scattered along the axes, and are generally whitish, with those of the rachis sometimes possessing a thin, dark brown median stripe, or those of the costae and costules occasionally with a thin, reddish margin. Such subtle differences would not merit even varietal distinction, but they are reinforced by the character of the apical section. Future collections of var. *abitaguensis* will confirm the value of this character or demonstrate intergradation with var. *uleana.*

Forests, 1,900-2,100 m., Colombia and Ecuador

Additional specimen examined.—**Colombia. Huila:** Hondonada del Abra de San Andres, *Cuatrecasas 8640* (F, US).

10. **Cnemidaria cocleana** Stolze sp. nov. Figure 17, Map 12.

Petiolus spinis usque ad 3 mm. longis instructus; pinnae per mediam plus minusve distantiam inter apices pinnularum et costam incisae; pinnae basales aliquantum deminutae et deflexae; venae 1- vel 4-furcatae, venae infimae anastomosantes et areolas costales efformantes; venae infimae basiscopicae e costulis egredientes; sori uniseriati, inter costulam et marginem medii vel inframediani; indusia omnino circularia.

TYPE COLLECTION: La Mesa, 5 miles N. El Valle, Cocle, Panama, Nov. 10, 1965, *Tyson, Godfrey et al. 2452.* HOLOTYPE: (3 sheets) FSU! PHOTO: F! GH!

Caudex not seen; *leaves* to 0.8 m. broad, terminating in an abruptly reduced apical section; *petiole* with spines to 3 mm. long, the scales sparse, bicolorous, dark brown with whitish margins, trichomes lacking; *rachis* non-alate, the scales rare, bicolorous, the minute, recurved trichomes sparse to scattered beneath; *pinnae* sessile, incised more or less halfway to the costa, basal pair somewhat reduced and deflexed; *costae* and *costules* without scales or trichomes; secondary *segments* falcate, obtuse, basal pair commonly overlapping the rachis; *veins* 1- to 4-times forked, basal ones merging to form costal areoles, basal basiscopic ones arising from the costules; *sori* in a single line, medial to scarcely inframedial between costule and segment margin; *indusia* yellowish brown, fully circular, with margins subentire and undulate.

This species bears a resemblance to *C. spectabilis* and *C. choricarpa;* however, both have the pinnae lobed consistently less than halfway to the costa, and their indusia have the conventional semicircular shape, whereas *Cnemidaria cocleana* has at least its larger pinnae cut more

FIG. 17. *Cnemidaria cocleana, Tyson et al. 2452* (FSU, holotype).

than halfway to the costa and the indusia forming an unbroken circle (fig. 11c) around the receptacle. Furthermore, *C. cocleana* does not have the broadly alate rachis of *C. choricarpa.* The completely circular indusium is a rather unique character in the genus, otherwise being found only in *C. nervosa,* the species from Peru and Ecuador with subentire pinnae.

The species has been collected in the deep shade of forests, only in the province of Cocle, Panama, 760-1,000 m.

Additional specimen examined.—**Panama. Cocle:** Crater of El Valle de Anton, La Mesa, *Wilbur et al. 11,111.* (F, NY).

11. **Cnemidaria quitensis** (Domin) Tryon, Contr. Gray Herb. 200: 52. 1970. Figure 18, Map 11.

Hemitelia quitensis Domin, Kew Bull. 215, 1929 (*non Cyathea quitensis* [C.Chr.] Domin, 1929). TYPE COLLECTION: *Sodiro s.n.,* In Ecuador in Andibus Quitensis, 1875. HOLOTYPE: K?

Cyathea andicola Domin, Acta Bot. Bohem. 9: 91, 1930; *nom. nov.* for *Hemitelia quitensis* Domin.

Caudex to 2 m. long and 4 cm. in diameter; *leaves* to 3 m. long and 1 m. broad, terminating in a conform apical pinna; *petiole* to 1.2 m. long, with spines to 3 mm. long, the scales sparse, bicolorous, dark brown with whitish margins, mostly ovate; *rachis* non-alate, scales sparse, pale to bicolorous or lacking, the minute, terete, recurved trichomes abundant beneath; *pinnae* subsessile to sessile, cut one-third to a little more than halfway to the costa, the basal pair somewhat reduced; *costae* and *costules* with broad, amorphous, pale to tawny scales scattered beneath, the trichomes scattered to lacking beneath; secondary *segments* falcate to subfalcate, obtuse, commonly imbricate with their sinuses cartilaginous above and contrasting in color with adjacent tissue, basal segments often overlapping the rachis; *veins* once- to thrice-forked, basal ones commonly merging to form costal areoles, basal basiscopic ones commonly arising from the base of the costule, or

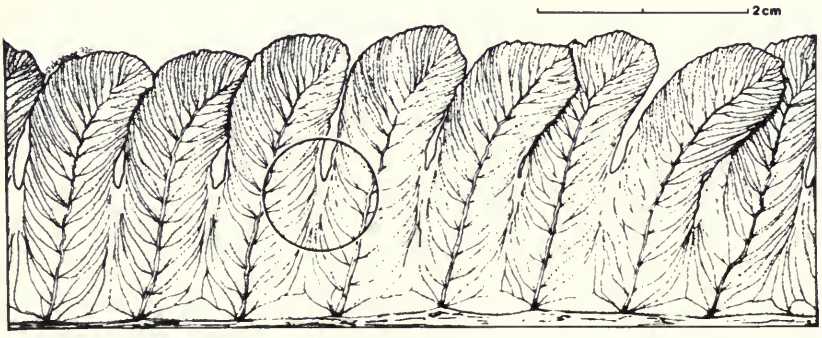


FIG. 18. *Cnemidaria quitensis, Ewan 16812* (US): portion of pinna, adaxial side, showing imbricate segments and cartilaginous sinuses.

infrequently from the costa; *sori* in one or two lines, commonly inframedial between costule and segment margin; *indusia* pale yellow or yellowish-brown, more or less semicircular, subentire to several-lobed.

When a loan for this study was prepared at Kew, the holotype of *H. quitensis* was not located, although it would be expected to be there along with other Domin types.

Pinnae of *Cnemidaria quitensis* are commonly cut halfway or less to the costa, but in some of the larger specimens a number of pinnae may be incised more deeply. The less deeply divided specimens might be confused with *C. spectabilis* var. *colombiensis,* especially when the leaf apex is not available. However, the soral line in *C. quitensis* is consistently nearer to the costule than the margin, the minute, terete, recurved trichomes are scattered to abundant on the rachis beneath, and there are frequent whitish or pale to tawny scales on the costae and costules beneath. In *C. spectabilis* var. *colombiensis,* the soral line is usually situated midway between costule and margin, trichomes are lacking, and the rare scales on the axes beneath are commonly dull and dark brown.

The cartilaginous sinuses of *C. quitensis* afford a good diagnostic character within the genus (fig. 18), since only *C. spectabilis* var. *colombiensis* and, to a lesser degree, *C. cruciata* exhibit this condition. Especially evident on the adaxial side, the veins converge so strongly at the sinuses as to form a cartilaginous mass, yellowish or very light brown in color in dried material, which contrasts markedly with the adjacent tissue.

In forests, Colombia and Ecuador, 100-1,400 m.

Selected specimens examined.—**Colombia. Caldas.** Cordillera Occidental, Santa Cecilia, *von Sneidern 5199,* (F, US). **Cauca:** La Gallera, Micay Valley, *Killip 7774,* (GH, NY, US). **Chocó:** N. of San José del Palmar, *Lellinger and de la Sota 728,* (US). **Nariño:** Near Altiquer, Río Guabo, *Ewan 16812* (GH, US); Barbacoas, Corregimento Santander a Barbacoas, *Garcia-Barriga 13120* (US); Forest, Ricaurte, *von Sneidern A.473* (GH). **Ecuador. Esmeraldas:** Playa Rica, Parroquia de Concepción, *Mexia 8479* (F, GH, US); **El Oro:** Near Moromoro, 21½ miles west of Portovelo, *Wiggins 10930* (MO, US). **Imbabura:** Entre El Pajón y Cachaco, *Acosta Solís 12720* (F).

12. **Cnemidaria alatissima** Stolze sp. nov. Figure 19, Map 11.

Petiolus spinis brevibus et paleis numerosis latis albidis instructus; rachis ex toto alata; pinnae sessiles, per duas tertias vel tres quartas partes distantiae inter apices pinnularum et costam incisae; venae furcatae vel bifurcatae, venae infimae anastomosantes et areolas costales efformantes; venae infimae basiscopicae e costulis egredientes; sori uniseriati, inter costulam et marginem medii.

FIG. 19. *Cnemidaria alatissima, Dudley 13282* (GH, holotype).

TYPE COLLECTION: *Dudley 13282,* Río Llulla Pichis watershed, Dept. Huanuco, Peru, 25 July 1969. HOLOTYPE: (2 sheets) GH! PHOTO: F! ISOTYPE: NA!

Caudex short or lacking; *leaves* to 2 m. long and 0.5 m. broad, terminating in a subconform apical pinna; *petiole* to 1.5 m. long with minute spines, thickly covered near the base with large, ovate, whitish scales; *rachis* provided on either side with a green wing 1 to 2 mm. wide, and broad amorphous, whitish scales scattered beneath, trichomes rare to scattered beneath; *pinnae* sessile, cut two-thirds to three-fourths to the costa, basal pair not seen; *costae* and *costules* lacking scales or trichomes; secondary *segments* falcate, obtuse to acute, the basal pair often overlapping the rachis; *veins* once- to twice-forked, basal ones commonly merging to form costal areoles, basal basiscopic ones usually arising from the costule; *sori* in a single line approximately midway between costule and segment margin; *indusia* brownish, often rudimentary, usually less than semi-circular, subentire.

The broadly alate rachis and the large white scales of the petiole make this species one of the most striking in the genus. Green wings to 2 mm. wide extend along either side of the rachis from apex to base, and even well down the petiole. The lower part of the petiole is nearly obscured by the abundant scales, which measure up to 1.5 cm. long and 0.7 cm. broad. These are commonly creamy-white throughout, but some at the very base of the petiole have a thin, shiny-brown median stripe at their tips. The indusia, also, are rather distinctive. Although characteristically hemitelioid in that they are nearly semicircular in outline, they are so small and thin and so appressed to the leaf tissue that they can be observed only by scraping away most of the sporangia. The only other species of *Cnemidaria* possibly confused with this would be *C. choricarpa* of Costa Rica, especially in that both have strongly alate rachises. But *C. alatissima* can be easily distinguished by its much deeper lobing, as well as by the abundant whitish scales.

Thus far known only from the type collection, and one juvenile plant *(Dudley 13281)* collected with the type; found in large numbers in dark cloud forest, in wet places, especially in spray of waterfall, Huanuco, Peru, ca. 1,540 m.

13. **Cnemidaria choricarpa** (Maxon) Tryon, Contr. Gray Herb. 200: 51, 1970. Figure 2, Map 12.

Hemitelia choricarpa Maxon, Contr. U.S. Natl. Herb. 16: 40. 1912. TYPE COLLECTION: *Pittier 4835,* Buenos Aires, Costa Rica. HOLOTYPE: US! PHOTO: F! GH!

Cyathea choricarpa (Maxon) Domin, Pteridophyta 263, 1929.

Caudex to 0.6 m. long and 2.5 cm. in diameter; *leaves* to 2 m. long and 0.6 m. broad, terminating in an abruptly reduced, pinnatifid apex; *petiole* to 0.8 m. long,

spines to 3 mm. long or, rarely, lacking, the lanceolate scales bicolorous, dark brown with narrow, whitish margins, sparse except at the very base; *rachis* provided on either side with a narrow green wing, up to 1.5 mm. wide above, often vestigial below, the scales dark brown, scattered or lacking, the minute, terete, recurved trichomes scattered to mostly abundant beneath; *pinnae* sessile to subsessile, cut one-third to halfway to the costa, basal ones somewhat reduced and occasionally deflexed; *costae* and *costules* with broad, brown, amorphous scales scattered beneath, and trichomes scattered to lacking beneath; secondary *segments* falcate, obtuse, basal pair crowding or overlapping the rachis; *veins* simple to once-forked, basal ones mostly merging to form costal areoles, basal basiscopic ones arising from the costule; *sori* in a single line, medial to mostly inframedial between costule and segment margin; *indusia* brownish, more or less semicircular, subentire to erose, or slightly lobed.

Cnemidaria choricarpa is closely related to *C. mutica* of Costa Rica and Panama and *C. decurrens* of Mexico and Guatemala, sharing a number of morphological features with both, and intermediate between them in other characters. The winged rachis is common in *C. decurrens* and is frequently found in *C. mutica,* at least in vars. *grandis* and *chiricana.* Furthermore, all three species are similar in the shape of their leaf apices and vestiture. The subentire or shallowly lobed pinnae of *C. decurrens* are commonly areolate along the costae, but those of *C. mutica* are quite deeply lobed and free-veined. Thus *C. choricarpa* lies midway between these species in having pinnae cut one-third to halfway to costa, and although the basal veins generally merge to form costal areoles, many specimens can be found which show occasional tendencies to free venation. In fact, *Scamman 5881* from San Isidro and *L. O. Williams et al. 28785* from Rio Sonador are notable in their almost complete lack of costal areoles.

The range of *C. choricarpa* is basically confined to Costa Rica, but two collections that probably represent the species have been seen from Colombia. A recent collection from Chocó. *Lellinger & de la Sota 277,* matches *C. choricarpa* in every way, except that it lacks petiole spines. If subsequent collections lacking spines are found from this area, then perhaps it will merit varietal distinction. One other collection from Colombia, *Triana s.n.,* is mounted on a sheet at Kew, together with a pinna of *C. quitensis,* and is apparently *C. choricarpa,* but unfortunately no petiole is available to examine. Hence, on the strength of these two collections, the range of the species is provisionally extended to Colombia.

At least two sheets of *Pittier 10969* are extant. I have examined one—the holotype of *Hemitelia pittieri* (US); the other is *Cnemidaria choricarpa* (CR). A discussion of this mixed collection may be found under *C. mutica* var. *mutica.*

Wet, forest slopes, Costa Rica and Colombia, 30-1,700 m.

Selected specimens examined.—**Costa Rica. Puntarenas:** Slopes above Golfito, *Burger & Matta 4756* (F). 4 miles west of Rincón, Osa Peninsula, *Burger & Stolze 5499* (F, GH). Cañas Gordas, *Pittier 10966,* (US) and *10969 p.p.* (CR). **San José:** Vicinity of San Isidro El Generál, *Molina et al 17954* (CR, F, GH, MO). Vicinity of El Generál, *Skutch 2265* (GH, MO, US). **Colombia. Chocó:** N.W. side of Alto del Buey, *Lellinger & de la Sota 277* (COL, CR, F, HUA, LP, US). **Nariño:** Entre Tuquerres et Barbacoas, *Triana s.n.* (K).

14. **Cnemidaria chocoensis** Stolze sp. nov. Figure 20, Map 12.

Petiolus haud spinosus; pinnae sessiles, per unam tertiam vel mediam partem distantiae inter apices pinnularum et costam incisae; pinna apicalis subconformis, segmentis basalibus elongatis; costae et costulae subtus paleis atrobrunneis, nitidis instructae; venae 2- vel 3-furcatae, venae infimae anastomosantes et areolas costales efformantes; venae infimae basiscopicae e costis egredientes; sori uniseriati, inter costulam et marginem manifeste inframediani.

TYPE COLLECTION: *Lellinger & de la Sota 763,* 2 km. east of San José del Palmar, Chocó, Colombia. HOLOTYPE: US! PHOTOS: F! GH! ISOTYPES: COL, CR, F! HUA, LP.

Caudex not seen; *leaves* to 2.3 m. long and 0.4 m. broad, terminating in a subconform apical pinna, this usually with a pair of elongate basal lobes; *petiole* to 1.2 m. long, spines lacking, the scales scattered to frequent, bicolorous, dark brown, shiny, with broad pale to whitish margins, trichomes lacking; *rachis* nonalate, the scales scattered to frequent, dark shiny-brown or rarely with whitish margins, trichomes lacking; *pinnae* sessile, cut one-third to halfway to the costa, basal ones slightly reduced; *costae* and *costules* with broad, dark shiny-brown scales scattered to abundant beneath, trichomes lacking; secondary *segments* subfalcate, obtuse, basal pair crowding or overlapping the rachis; *veins* 2- to 3-times forked, basal ones commonly merging to form costal areoles, basal basiscopic ones (especially in the basal one-third or apical one-third of pinna) arising from the costae; *sori* in a single line, distinctly inframedial between costule and segment margin; *indusia* pale to yellowish brown, more or less semicircular, subentire to shallowly lobed.

This species has the lamina terminated by a subconform, apical pinna, like many specimens of *C. speciosa,* i.e., the terminal section closely resembles the larger pinnae in size and shape except for a pair of rather elongate basal segments. *C. chocoensis* is similar to *C. speciosa* in many other respects, but may be distinguished from the latter by its obviously inframedial sori, the frequent, shiny brown scales along the axes, and the basal basiscopic veins arising mainly from the costa. *C. speciosa* has medial to supramedial sori, the scales along the axes, when present, are dull brown, and the basal basiscopic veins arise

FIG. 20. *Cnemidaria chocoensis, Lellinger & de la Sota 763,* (US, holotype).

from the costules. *C. chocoensis* could also be confused with *C. ewanii,* but may be easily separated by the characters noted in the key.

Another Chocó specimen seen, *Lellinger & de la Sota 853,* is identical with the type in every way except that its pinnae are much thicker in texture and appear rather constricted, i.e., much narrower in relation to their length, and they are a dark brown color when dry instead of olive green. Perhaps it is merely an altitudinal variant, but is at least provisionally determined as *C. chocoensis* along with the other two collections from the area.

Disturbed secondary forests, Chocó, Colombia, 750-1,650 m.

Additional specimens examined.—**Colombia. Chocó:** Along Bolivar-Quibdo road, *Lellinger & de la Sota 895* (COL, CR, F, HUA, LP, US). 8 km. S.W. of El Cairo, *Lellinger & de la Sota 853* (COL, CR, HUA, LP, US).

15. **Cnemidaria spectabilis** (Kunze) Tryon, Contr. Gray Herb. 200: 52. 1970.

Caudex to 0.5 m. long and 5 cm. in diameter; *leaves* to 1.7 m. long and 0.8 m. broad, terminating in an abruptly reduced, pinnatifid apex; *petiole* to 1.2 m. long, spines to 5 mm. long, the scales sparse or lacking except at the very base, lanceolate to linear-lanceolate, bicolorous, dark brown with narrow whitish, often fimbriate margins; *rachis* often spiny toward base of lamina, non-alate, except rarely between the several upper pinnae, scales and trichomes usually lacking; *pinnae* sessile, cut one-third to halfway to the costa, basal ones somewhat reduced and deflexed; *costae* and *costules* with brown, broad, amorphous scales scattered or lacking beneath, trichomes lacking; secondary *segments* subfalcate, obtuse to rarely subapiculate, basal pair crowding or overlapping the rachis; *veins* simple to thrice-forked, basal ones commonly merging to form costal areoles, basal basiscopic ones arising from the costule; *sori* in a single line, medial to supramedial between costule and segment margin; *indusia* pale to yellowish-brown, more or less semicircular (rarely almost fully circular in var. *colombiensis*), subentire to lobed.

Lying approximately midway along the phyletic line, this species ranks next to *C. horrida* as the most widespread species in the genus. Specimens have been collected all along the northern edges of South America, from Colombia through the Guianas, including Trinidad and Tobago. It is likely that seven other species, from northern South America to Bolivia, have been derived from *C. spectabilis* or its ancestral stock (see fig. 1), and all may be considered "typically Cnemidarioid," in that their pinnae are strongly areolate and rather shallowly lobed.

15a. **Cnemidaria spectabilis** var. **spectabilis** Figures 3b, 10b; Map 9.

Hemitelia spectabilis Kunze, Linnaea 21: 233. 1848. TYPE COLLECTION:

Kappler 1771, Surinam, pr. stationem Victoriam, Apr. 1847. ISOTYPES: K! P! PHOTO: F!

Actinophlebia obtusa Presl, Gefässb. Stipes der Farrn 48, 1847 (preprint of Abh. Böhm Ges. Wiss. V. 5: 356. 1848) (non *Hemitelia obtusa* Kaulf. 1824.). Based on Hooker's plate 14, Sp.Fil. 1. 1844.

Hemistegia spectabilis (Kunze) Fée, Mem. Fam. Foug. 5 (Gen.Fil.): 351. 1850-52.

Hemitelia klotzschiana Klotzsch, Allg. Gartenzeitung 20: 42. 1852. TYPE COLLECTION: probably *Karsten 143,* Venezuela, Jan. 1852. PROBABLE ISOTYPE: B! PHOTO: F!

Hemitelia spectabilis var. *trinitensis* Domin, Mem. Roy. Czech. Soc. Sci. 2: 72. 1929. TYPE COLLECTION: *Wakefield s.n.,* La Seiva Valley, Trinidad, 16/I/1921.

Hemitelia spectabilis var. *longipinna* Domin, *tom.cit.* 73. (Domin's "typical variety", based on *H. spectabilis* Kunze.)

Cyathea spectabilis var. *trinitensis* (Domin) Domin, Pteridophyta 264, 1929.

Cyathea spectabilis var. *longipinna* (Domin) Domin, *loc. cit.*

Larger pinnae 3-5 (6) cm. wide and 28-36 (38) cm. long, *secondary segments* approximate or divergent, only rarely subimbricate, the sinuses rarely (if ever) cartilaginous, the tissue more or less uniformly green; *soral* line mostly supramedial between costule and segment margin; *indusia* more or less semicircular.

The typification of *Hemitelia klotzschiana* Kl. is somewhat in doubt. Although no type is designated in the original description, Klotzsch's citation of "Karsten" after the name, implies the type is from a Karsten collection. There is a specimen of *Karsten 143* at Berlin marked *"Hemitelia (Cnemidaria) klotzschiana* Karsten" which could very well be the plant Klotzsch had in mind.

This variety of the species most closely resembles *Cnemidaria consimilis* and *C. cruciata.* From the latter, it may be distinguished by the characters of leaf apex and pinna segments noted in the key. It also differs from *C. consimilis* in shape of leaf apex, but, unfortunately, this feature is often lacking on many herbarium sheets, and in these instances the position and color of the petiole scales furnish the most reliable diagnostic character. In *C. spectabilis* var. *spectabilis* the scales are rare or lacking on the petiole, except at the very base. They are bicolorous, i.e., mostly dark brown with very narrow whitish margins; however, in *C. consimilis* the scales are either completely white or with a very narrow brown median stripe, and are quite abundant throughout the petiole, from lamina to base.

Two Steyermark specimens, *89525* and *92924* from Estado Bolivar, Venezuela, are especially close to *C. consimilis,* because of the somewhat subconform apical pinna. However, the petiole scales are dark brown, with very narrow whitish margins, and are present only at the base, as in typical *C. spectabilis.*

In and at the edges of forests, along stream banks and mountainsides, 100-1,200 m., Venezuela, the Guianas, Trinidad, and Tobago.

Selected specimens examined.—**Trinidad:** Balandra Bay, *E. G. Britton et al. 433* (GH, NY, US). Shaded gully, Dibe Valley, *N. L. Britton et al. 1748* (F, GH, NY, US). 1877-78 (no locality), *Fender 25* (F, GH, MO, NY, US). **Tobago:** Main ridge, *Broadway 3886* (F, GH, MO, NY, U. US). Near Caledonia, *Broadway 4540* (F, GH, MO, NY, U, US). **Venezuela:** Lower Orinoco, Eleanor Creek, *Rusby & Squires 110* (F, GH, MO, NY, US). **Anzoategui:** N.E. of Bergantin, by Sucre boundary, *Steyermark 61207* (F, US, VEN). **Merida:** prope Coloniam Tovar, *Fendler 480* (GH, K, MO). **Miranda:** Cardenas, Siquire Valley, *Pittier 7091,* (GH, US, VEN) and *5945* (F, NY, US). **Nueva Esparta:** Margarita Island, El Valle, *Miller & Johnston 164* (F, GH, MO, US). **Sucre:** Aricagua, vicinity of Cristobal Colon, *Broadway 567* (GH, NY, US). **British Guiana:** Demerara, Region Mt., 1895, *Jenman s.n.* (NY). Demerara, Isorooroo River, 1899, *Jenman s.n.* (NY). **Surinam:** Rikanau, near Moengo, *Lindeman 6124* (K, MO, U. US). Distr. Brokopondo, trail from Bronsweg, *Kramer & Hekking 3195* (U). **French Guiana:** "Guyane," *coll. unknown, F herbarium No. 808351* (F). Guyana, in sylvis humidis, *LePrieur s.n.* (K).

15b. **Cnemidaria spectabilis** var. **colombiensis** Stolze, var. nov. Figure 21, Map 9.

Pinnae maximae 5-7 cm. latae, 34-42 cm. longae; segmenta secundaria plerumque imbricata vel subimbricata, sinibus plerumque cartilagineis et colore suo contrastantibus cum textura adiacente; sori inter costulam et marginem medii; indusia semicircularia vel fere omnino circularia.

Largest pinnae 5-7 cm. wide and 34-42 cm. long; *secondary segments* commonly imbricate or subimbricate (at least near apices), the sinuses mostly cartilaginous above and contrasting in color with adjacent tissue; *soral line* medial between costule and segment margin; *indusia* semicircular to almost fully circular.

TYPE COLLECTION: *Killip 5039,* Cordoba, Dept. El Valle, Colombia, May 6-8, 1922. HOLOTYPE: (3 sheets) US! PHOTO: F! ISOTYPES: GH! NY!

Besides the characters noted in the key, this variety can often be separated from var. *spectabilis* by its wider pinnae. Although some rare specimens of the latter can be found which have occasional pinnae to 6 cm. wide, the largest pinnae normally measure from 3-5 cm. wide, whereas the largest pinnae of var. *colombiensis* commonly measure 6-7 cm. wide.

The indusia of var. *colombiensis* are commonly much more than semicircular in shape, occasionally appearing to be almost fully circular,

FIG. 21. *Cnemidaria spectabilis* var. *colombiensis, Killip 5039,* (US, holotype).

such as in *C. cocleana* and *C. nervosa*. But closer examination will reveal a sinus, which is sometimes partially obscured by the overlapping tissue of the indusium.

Wooded areas, Colombia, 70-500 m.

Additional specimens examined.—**Colombia. Chocó:** Between La Oveja and Quibdo, *Archer 1764* (US). Second growth forest, Andagoya, *Killip 35377* (GH, US). West of Istmina, road to Pie de Pepe, *Lellinger & de la Sota 431* (US).

16. **Cnemidaria cruciata** (Desv.) Stolze. comb. nov. Figure 3a, Map 9.

Hemitelia cruciata Desv., Prodr. 320. 1827. TYPE COLLECTION: *Desvaux s.n.*, "Habitat in America." HOLOTYPE: P! PHOTO: F! GH!

Hemitelia leprieurii Kunze, Bot. Zeit. II: 296. 1844. TYPE COLLECTION: *LePrieur 200*, Fr. Guiana.

Cyathea leprieurii (Kunze) Domin, Pteridophyta 264. 1929.

Caudex not seen; *leaves* to 0.6 m. broad, reduced very gradually to a pinnatifid apex, lacking a distinct apical section; complete *petiole* not seen, spines to 2 mm. long, scales lacking on most of petiole seen; *rachis* often short-spiny toward the base, non-alate, scales and trichomes lacking; *pinnae* sessile, or lower ones sometimes short-stalked, cut one-third to halfway to the costa, basal ones somewhat reduced and deflexed; *costae* and *costules* without scales or trichomes; secondary *segments* subfalcate, obtuse to occasionally subapiculate, commonly imbricate, with their sinuses tending to be cartilaginous above, basal segments often crowding or overlapping the rachis; *veins* simple to twice-forked, basal ones commonly merging to form costal areoles, basal basiscopic ones arising from the costule; *sori* in a single line, supramedial between costule and segment margin; *indusia* pale to yellowish-brown, more or less semicircular, subentire to lobed.

This species is poorly represented in herbaria, and I have not seen a caudex, or even a complete petiole. The type consists only of a rachis with four pairs of pinnae, and most other material is even more fragmentary. Only one specimen shows the leaf apex.

It has been suggested that *Cnemidaria cruciata* is equivalent to *C. spectabilis*. Indeed, they are very closely related; but the aspect of the pinnae, segments, and leaf apices is quite distinct in each species, and if more complete collections are made in the future, perhaps additional differences will be noted. The pinnae of *C. spectabilis* are rather widely separated, while those of *C. cruciata* are approximate and, at least near the leaf apex, often crowded or even overlapping. The leaf apex of *C. cruciata* is like no other in the genus. An excellent specimen (*LePrieur, 1838*) on four sheets at the U.S. National Herbarium reveals a leaf gradually reduced to the tip, so that it lacks a distinct terminal section. This is in marked contrast to all other species of *Cnemidaria*, which have

their leaves abruptly reduced into a conspicuous, separate apical section, or terminating in a conform terminal pinna (see fig. 3).

According to the labels, all specimens of *Cnemidaria cruciata* examined are from French Guiana. Only Desvaux's type is in doubt, for the label is marked simply "Habitat in America." But although the source of his specimen may not be known, there is no evidence to suggest that it was collected anywhere other than French Guiana.

Additional specimens examined.—**French Guiana:** Guyane Francaise, 1838, *LePrieur s.n.* (US). Guyane, Jul. 1824, *Poiteau s.n.* (K). Guiana Francaise, 1824, *Poiteau 139* (B, US). Acarouany, Fr. Guiana, 1856, *Sagot 873* (K).

17. **Cnemidaria consimilis** Stolze, sp. nov. Figure 22, Map 13.

Petiolus spinis usque ad 3 mm. longis instructus, petioli paleae abundantes, albidae, vel stria centrali angustissima brunnea instructae; pinnae per unam quartam vel mediam partem distantiae inter apices pinnularum et costam incisae, sinibus inter segmenta haud cartilagineis; pinnae laterales et terminales consimiles; venae 1- vel 3-furcatae, venae infimae anastomosantes et areolas costales efformantes; venae infimae basiscopicae e costulis plerumque egredientes; sori uniseriati, inter costulam et marginem medii vel supramediani.

TYPE COLLECTION: *Steyermark & Rabe 96260,* Cerro de Río Arriba, Peninsula de Paria, Sucre, Venezuela, 9 Agosto 1966. HOLOTYPE: GH! ISOTYPE: F!

Caudex not seen, reported to 1.5 m. long; *leaves* to 2.5 m. long and 1.2 m. broad, terminating in a conform apical pinna; *petiole* to 1.5 m. long, muricate or with spines to 3 mm. long, the scales abundant, lanceolate, whitish, or with a thin brown to atropurpureus median stripe; *rachis* often spiny towards the base of the lamina, non-alate, the scales sparse, pale to brownish, ovate to lanceolate, trichomes lacking; *pinnae* sessile, cut one-fourth to almost halfway to the costa, basal ones reduced and often deflexed; *costae* and *costules* with brown, amorphous scales rare beneath or lacking, trichomes lacking; secondary *segments* subfalcate, obtuse to rarely subapiculate, basal ones often crowding or overlapping the rachis; *veins* once- to thrice-forked, basal ones commonly merging to form costal areoles, basal basiscopic ones arising from the costule or its base; *sori* in a single line, medial to supramedial between costule and segment margin; *indusia* yellowish- or grayish-brown, more or less semicircular, 2- to 3-lobed, saucer-shaped to deeply cup-shaped.

Although the central portion of the lamina of this species bears a strong resemblance to that of *Cnemidaria spectabilis,* the petiole scales and the shape of the apical section are quite distinct. Whereas the lamina of *C. spectabilis* is abruptly reduced to a non-conform, broadly-triangular apical section, the lamina of *C. consimilis* terminates in an apical section similar in shape and size to one of the upper pinnae. The difference in petiole scales is described fully in the discussion of *C. spectabilis.*

FIG. 22. *Cnemidaria consimilis, Steyermark & Rabe 96260* (GH, holotype).

C. consimilis might be confused also with *C. speciosa,* but the petiole of the latter is smooth or rarely tuberculate, with scales clustered mostly at the base and the brown median stripe quite broad. The petiole of *C. consimilis* is quite spiny, or at least strongly muricate, and thickly beset throughout with scales that are either completely white or with a very narrow brown median stripe, or a brown spot near the point of attachment.

In forests, 600-1,200 m., Trinidad and the Peninsula de Paria, Venezuela.

Additional specimens examined.—**Venezuela: Sucre:** Cerro de Humo, Peninsula de Paria, *Steyermark 94899* (F, GH, NY, U, VEN). **Trinidad:** Mt. Tucuche, below the summit, *Seifriz* 4 (F). Forest, Mt. Tocuche, *N. L. Britton et al. 1238* (GH, NY, US). Mt. Tucuche, *Broadway 5296* (F), *7137* (US).

18. **Cnemidaria speciosa** Presl, Tent. Pterid. *pl. 1, figs. 16, 17,* 1836 (non *Cyathea speciosa* Willd. 1810). Figure 3c, Map 11.

TYPE COLLECTION: *Poeppig 221* (Diar. 1144) Pampayaco, Peru, Juli 1829. HOLOTYPE: PR or PRC. FRAGMENTS: NY! US! ISOTYPES: B! BR, P!

Hemitelia subincisa Kunze, Bot. Zeit. 2: 296. 1844. *nom. nov. quoad Cnemidaria speciosa* Presl, *non Hemitelia speciosa* (Willd.) Kaulf.

Hemistegia speciosa (Presl) Fée, Mem. Fam. Foug. 5 (Gen. Fil.): 351. 1850-52.

Cyathea subincisa (Kunze) Domin, Pteridophyta 264. 1929.

Caudex to 1 m. long and 3.5 cm. broad; *leaves* to 2.2 m. long and 0.7 m. broad, terminating in a conform or subconform apical pinna; *petiole* to 1.2 m. long, smooth or rarely tuberculate at the base, the scales lanceolate to ovate, bicolorous, whitish with brown median stripe; *rachis* non-alate, scales and trichomes lacking; *pinnae* sessile, broadest at or beyond the center, very deeply crenate to lobed less than halfway to the costa, basal ones slightly, if at all, reduced and deflexed; *costae* and *costules* with dull brown, amorphous scales rare beneath or lacking, trichomes lacking; secondary *segments* subfalcate, obtuse to rarely subapiculate, basal ones crowding or overlapping the rachis; *veins* simple to once-forked, basal ones commonly merging to form costal areoles, basal basiscopic ones mostly arising from the costule or its base; *sori* in a single line supramedial between costule and segment margin; *indusia* pale or yellowish, more or less semicircular, saucer-shaped to deeply cup-shaped.

The lamina of *Cnemidaria speciosa* commonly terminates in a conform "apical pinna," the apical section closely resembling most of the pinnae in shape and size. However, on some plants the apical section is "subconform," i.e., it conforms to the shape of the pinnae except for a pair of larger or elongate basal lobes. This is in marked contrast to

the "nonconform pinnatifid apex" of most species of *Cnemidaria,* which are characterized by a very broad base and a triangular outline.

Cnemidaria speciosa resembles *C. consimilis,* especially in the central portion of the lamina; however, in addition to the distinctions listed under the discussion of the latter species, *C. speciosa* exhibits another subtle difference. In most species of *Cnemidaria* (including *C. consimilis*) the pinnae are generally broadest near the base, or at least below the middle. *C. speciosa* is one of a few species having most pinnae slightly broader at or beyond the middle. This may not always be evident upon examination of a single pinna, but it becomes rather apparent on viewing the entire lamina.

Much confusion has existed between this species and *Cyathea speciosa* Willd., and although there was a partial clarification by Kunze (1844) and later by Maxon (1912), further elaboration is desirable especially in reference to typification.

In 1836, Presl established the genus *Cnemidaria,* designating *"Cnemidaria speciosa* (*Hemitelia speciosa* Kaulf. nec Willd.)" and four other taxa as the representatives of the new genus. Although he cited no material for *C. speciosa,* he illustrated it by the figures 16 and 17, which show the anastomosing of the lowest veins and serve to distinguish it from *Cyathea speciosa* Willd. (earlier transferred to *Hemitelia* by Kaulfuss [1824]). Presl's publication made a new species, *Cn. speciosa,* validated by the illustrations presented. The reference to *"H. speciosa* Kaulf. nec Willd." was partly erroneous (it should have been *"H. speciosa* Kaulf. in herb.," not *"Cyathea speciosa* Willd."), and a fuller explanation is to be found in Presl's (1847) later publication. Here the citation of *"Hemitelia speciosa* Kaulf. herb.", of "Mart. ic. crypt. bras. 78 t. 48 f.II," and of "Kunze fil. Poepp. in Linn. IX 99 (excl. syn)" as to specimens, provides the basis for Presl's action. In the same publication he restricts the genus to *Cn. speciosa,* removing the other four species to *Actinophlebia* and *Hemistegia.* The Poeppig specimen at Paris is labelled "No. 221. *Hemitelia speciosa* Kaulf.?," and it is this identification (rather than Kaulfuss' description) that Presl argued correctly did not agree with *Cyathea speciosa* Willd. Kunze's published identification of the Poeppig collection was without question *Hemitelia speciosa* Kaulf. [i.e. (Willd.) Kaulf.]. Maxon notes that "In the Presl herbarium at Prague . . . is a specimen of *'Cnemidaria speciosa'* collected in Peru by Pöppig," and in the "Gefässbündel" Presl cites a specimen as "Pampayaco, Peru (Poeppig)." The fragment obtained by Underwood from the Presl herbarium was from a Poeppig collection. Finally, in the Syn. Fil., Poeppig cites "Diar. 1144" and places *H.*

speciosa Kaulf. as No. 263 in Kunze's enumeration. The Poeppig specimen at Paris is marked "No. 221 *Hemitelia speciosa* Klfs." (with the "1" changed to a "4" in another handwriting and different ink) as well as "Peru Pöppig, Kunze 263." This specimen relates the *Poeppig 221* to Dira. 1144 and clearly establishes the fact that these are different numbers for the same collection.

In and at the edges of forests, along stream banks and mountainsides, 375-1,900 m., Peru, Bolivia.

Selected specimens examined.—**Peru. Cuzco:** San Lorenzo, *Vargas 11714* (GH). Kosñipata-Pilcopata, *Vargas 11294* (GH). Entre Atalaya y Carbón, Prov. Paucartambo, *Vargas 14653* (GH). **Huanuco:** Tingo Maria, *Asplund 12116* (US). Tingo Maria, roadside, *Tryon & Tryon 5260* (F, GH, U). **Junin:** Near La Merced, *Killip & Smith 23889,* (NY, US). Río Paucartambo Valley, *Killip & Smith 25289,* (NY, US). Pichis Trail, Yapas, *Killip & Smith 25563* (GH, NY, US). Chanchamayo Valley, *C. Schunke 52* (F). La Merced-Chanchamayo, *Soukup 1069* (F). **Bolivia. La Paz:** Sobre el camino a Tipuani, *Buchtien 4224* (F, MO, NY, US). Mapiri Region, San Carlos, *Buchtien 42 & 43* (US). Copacabana, Prov. Larecaja, *Krukoff 11297* (F, GH, MO, NY, U, US). Mapiri, *Rusby 149* (GH, NY, US).

19. **Cnemidaria ewanii** (Alston) Tryon, Contr. Gray Herb. 200: 52. 1970. Figure 3d, Map 14.

Cyathea ewanii Alston, J. Wash. Acad. Sci. 48: 231, 1958. TYPE COLLECTION: *Ewan 16729,* between Mocoa & Urcusique, Putumayo, Colombia, 9 Jan. 1945. HOLOTYPE: BM, ISOTYPES: GH! NO, US! PHOTO: F!

Caudex to 0.2 m. long and 3 cm. in diameter; *leaves* to 2.5 m. long and 0.5 m. broad, terminating in a conform to subconform apical pinna; complete *petiole* not seen, smooth to lightly muricate, the scales ovate to lanceolate, bicolorous, whitish with brown median stripe; *rachis* non-alate, scales scattered, whitish to bicolorous, trichomes lacking; *pinnae* sessile, mostly truncate at base, broadest at or beyond the center, deeply crenate or rarely cut one-fourth to the costa, basal ones scarcely reduced or deflexed; *costae* with whitish or pale amorphous scales scattered beneath, trichomes lacking; *costules* with pale or dull brown scales scattered or rare beneath, or lacking, trichomes lacking; secondary *segments* or lobes obtuse to subapiculate; *veins* simple to once-forked, basal ones merging to form costal areoles, basal basiscopic ones arising from the costule; *sori* in a single line inframedial on the veins between costule and segment margin; *indusia* pale to yellowish-brown, semicircular, subentire to several-lobed, saucer-shaped.

Cnemidaria ewanii is one of the more advanced species of the genus, as evidenced by the costal areoles, the shallow lobing of the pinnae, and the lack of trichomes on the axes. It is very closely related to *C.*

speciosa, and it may be that the two merit only varietal distinction, but until more complete collections are made of *C. ewanii* I prefer to treat them as separate species. They are the only species in the genus with pinnae broadest at or above the middle and share most other characters as well. The pinnae of *C. ewanii* are more shallowly lobed, with the upper ones often merely deeply crenate. The sori are inframedial on the veins and the scales along the rachis and costae beneath are whitish or pale in color. The sori of *C. speciosa* are supramedial and the scales of the axes, when present, are dull brown.

Specimens of *C. quitensis* with less deeply dissected pinnae might also be confused with *C. ewanii,* and the two species share the same range. However, the pinnae of the former are slightly broader below the center and there are spines on the petiole, and terete, recurved trichomes on the rachis and costae beneath. The petiole of *C. ewanii* is smooth or lightly muricate, and the axes lack trichomes.

In thickets and forests, 75-1,000 m., Colombia and Ecuador.

Additional specimens examined.—**Colombia. Caqueta:** Florencia, Quebrada de las Perdices, *Cuatrecasas 8854* (US). Sucre, Orillas del Río Hacha, *Cuatrecasas 9022* (US). Sucre, *Juzepczuk 6533* (US). **Chocó:** Istmina, on Río San Juan, *Killip 35454* (US). **Putumayo:** Umbria, alt. 325 m., *Klug 1846* (F, GH, MO, NY, US). Orito, near road at Río Calderas, *Plowman 2133* (COL, F, GH). **Ecuador.** "In sylvis f. Bombonasa," *Spruce 5365* (K, P). **Guayas:** Milagro, *Crespi s.n.* (US).

20. **Cnemidaria roraimensis** (Domin) Tryon, Contr. Gray Herb. 200: 52. 1970. Figure 23, Map 9.

Hemitelia roraimensis Domin, Kew Bull. 216, 1929. TYPE COLLECTION: *Appun 1127,* Roraima, Br. Guiana 1863/64. HOLOTYPE: K! PHOTO: F!
Cyathea roraimensis Domin, Acta Bot. Bohem.9: 154. 1929.

Caudex not seen; *leaves* to ca. 1.2 m. long and 0.4 m. broad, terminating abruptly in a nonconform, pinnatifid apical section; complete *petiole* not seen; *rachis* non-alate, scales and trichomes lacking; *pinnae* sessile, cut one-fourth to one-third to the costa; *costae* and *costules* lacking scales and trichomes; secondary *segments* or lobes rounded, obtuse to subapiculate, basal ones crowding or overlapping the rachis; *veins* simple, basal ones merging to form costal areoles, basal basiscopic ones arising from the costule; *sori* in a single line medial to supramedial on the veins between costule and segment margin, commonly forming a V-shaped pattern on the segments; *indusia* brownish-yellow, semicircular, several-lobed, saucer-shaped.

Cnemidaria roraimensis is known only from a small number of incomplete specimens; future collections, hopefully, will include petioles and sections of the caudex. Its affinities are with *C. spectabilis,* from

FIG. 23. *Cnemidaria roraimensis, Appun 1127* (K, holotype).

which it differs in its more shallowly-lobed pinnae, simple veins, and the V-shaped soral pattern on the segments (formed by the apical sori lying close to the costule while the basal ones are much nearer the margin). The pinnae of *C. spectabilis* are often cut nearly halfway to the costa, the veins are usually branched at least once, and the sori are uniformly arranged in a line supramedial between costule and segment margin.

Although probably not closely related, *C. roraimensis* and *C. decurrens* have at least a superficial resemblance, especially in their shallowly-lobed pinnae. Besides the differences noted in the key, the two are further distinguished by the relatively broad wing running well down the sides of the rachis in most specimens of *C. decurrens,* whereas the rachis is always non-alate in *C. roraimensis.* The shallow lobing of the pinnae and the strongly areolate venation of both species place them among the most highly advanced species in the genus.

Along stream banks and on mountainsides, 1,000-1,500 m., British Guiana.

Selected specimens examined.—**British Guiana:** Quating Creek, 1864, *Appun 1035* (K). Mt. Ayanganna, Pakaraima Mts., *Maguire et al. 40581* (NY). Roraima Range, 3,500 ft. alt., *McConnell & Quelch 620* (K, NY).

21. **Cnemidaria decurrens** (Liebm.) Tryon, Contr. Gray Herb. 200: 52. 1970. Figure 24a, Map 12.

Hemitelia decurrens Liebm., Kongel Danske Vidensk. Selsk. Skr. V. 1: 286 (seors. 134), 1849. TYPE COLLECTION: *Liebmann Pl. Mex. 2089 (No. 912),* Pr. Lobani, Distr. Chinantla, Dep. Oajaca, Mexico, 1842. HOLOTYPE: C! FRAGMENT: US!

Hemitelia mexicana Liebm., *tom. cit.* 287 (seors. 135). TYPE COLLECTION: *Liebmann Pl. Mex. 2105* (3 sheets: *Nos. 909, 910, 911*), Pr. Lacoba, Dist. Chinantla, Oajaca, Mexico, 1842. HOLOTYPE: C! FRAGMENT: US!

Hemistegia lucida Fée, Mem. Fam. Foug. 5 (Gen.Fil.): 351. 1850-52. TYPE COLLECTION: *Galeotti 6537,* Prov. de Oaxaca, Mexico, 1842. HOLOTYPE: BR, ISOTYPE: P! US!

Hemistegia elegantissima Fée, *op. cit.* 8: 110. 1857. TYPE COLLECTION: *Linden s.n.,* Mexico. Nothing of the type is known beyond Fée's reference, "Mexique (Linden)," but according to the description, this plant can be nothing other than *Cnemidaria decurrens.*

Hemistegia decurrens (Liebm.) Fourn., Mex. Pl. 1: 135. 1872.

Hemistegia mexicana (Liebm.) Fourn. *loc. cit.*

Hemitelia guatemalensis Maxon, Contr. U.S. Natl. Herb. 16: 40. 1912. TYPE COLLECTION: *Salvin s.n.,* Alta Verapaz, Guatemala, 1800. HOLOTYPE: US. ISOTYPE: GH! K! US!

Hemitelia lucida (Fée) Maxon, *tom. cit.* 39.

Cyathea guatemalensis (Maxon) Domin, Pteridophyta 264, 1929.

Cyathea liebmanii Domin, *loc. cit.* (*nom. nov.* for *Hemitelia mexicana* Liebm., non *Cyathea mexicana* S. & C. 1830.)

Cyathea lucida (Fée) Domin, *loc.cit.*

Cyathea decurrentiloba Domin, Acta Bot. Bohem. 9: 110. 1930. (*nom. nov.* for *Hemitelia decurrens* Liebm., *non Cyathea decurrens* [Hook.] Copel. 1929.)

Cyathea elegantissima (Fée) Domin, *tom. cit.* 113.

Caudex rudimentary to 0.3 m. long; *leaves* to 2.5 m. long and 0.8 m. broad, terminating in a gradually reduced apical section; *petiole* to 0.5 m. long, with spines to 2 mm. long, the scales scattered to abundant, ovate to lanceolate, whitish or bicolorous; *rachis* with membranous wing to 2 mm. wide running partially to fully down each side or (rarely) lacking, the ovate to lanceolate scales whitish or bicolorous, sparse to abundant beneath, the minute, terete, recurved trichomes scattered to abundant beneath; *pinnae* subsessile, rounded to truncate at base, subentire or crenate or cut one-third to the costa, basal ones scarcely or not at all reduced and deflexed; *costae* with broad, amorphous, pale to whitish or bicolorous scales scattered beneath, trichomes lacking; *costules* with scales and trichomes lacking; secondary *segments* or lobes (when present) obtuse to rarely subapiculate; *veins* simple, basal ones commonly merging to form costal areoles, basal basiscopic ones arising from the costule; *sori* in a single line medial to inframedial on the veins between costule and segment margin; *indusia* pale to yellowish-brown, semicircular to (rarely) almost fully circular, subentire to several-lobed, saucer-shaped.

Cnemidaria decurrens has a variable leaf outline, probably correlated with the age and size of the individual plant. Perhaps due to this variability, four distinct species had been previously recognized, most of these originally represented by single collections. The types of *Hemitelia decurrens* and *H. mexicana* represent the extremes: the pinnae of the former nearly entire and the rachis strongly alate and copiously pubescent and scaly. The type of *H. mexicana* has nearly entire upper pinnae, but the large, central ones are lobed nearly one-third to the costa, a wing is just barely evident along the rachis, and the pubescence and scales sparse. However, examination of more recently collected material shows these characters to be highly variable from one plant to another, and hence there is little significant correlation between them.

Cnemidaria decurrens occurs at one border of the generic range, and, as evidenced by the strongly areolate venation and the subentire to shallowly lobed pinnae, is one of the most highly advanced species in the genus. Its relationship is with *C. choricarpa* of Costa Rica, and was probably derived from the latter's ancestral stock.

Hemitelia decurrens and *H. mexicana* were published at the same time, so a choice of one of the names is necessary. *Hemitelia decurrens* seems most appropriate because the pinnae are strongly decurrent, and the rachis is commonly alate for most of its length. Furthermore,

the majority of specimens more closely resemble the type of *H. decurrens* in that the margins of the pinnae are scarcely lobed. Leaves with the pinnae lobed one-third to the costa as in the type of *H. mexicana* are rather rare.

In the type folder of *H. decurrens,* at Copenhagen are two sheets, both marked "Liebm. Pl. Mex. 2089," each containing a small but complete specimen. However, the labels of each are further designated with different numbers, one "912," the other "913." The holotype is considered to be No. 912, and it is referred to by Fournier as such. The other, numbered "913," is a paratype. In the Copenhagen type folder of *H. mexicana* are three sheets, "Liebm. Pl. Mex. 2105," and they are further numbered "909," "910," and "911." These sheets are presumably from the same plant: obviously the apex, middle, and base of one large lamina. Therefore, all three sheets must be considered parts of the holotype of *H. mexicana.*

Forest slopes, 200-1,100 m., Mexico (Chiapas, Oaxaca) and Guatemala (Alta Verapaz).

Selected specimens examined. **Mexico. Chiapas:** Palenque, *Munch 4* and *s.n.* (U.S. herb. no. *1791748*) (US). **Oaxaca:** Dto. Choapam, Lovani, *Hallberg 1567* (F, NY). Tuxtepec, S. of Valle Nacional, *Mickel 5889, 5890* (NY). Tuxtepec, N. of Campamento Vista Hermosa, *Mickel 5934* (NY). **Guatemala: Alta Verapaz:** Chapultepec Farm, *Contreras 4822* (US). Finca Sepacuite, *Cook & Griggs 107* (US). Finca Seamay, Senehu, *Hatch & Wilson 190* (GH, US). Finca Sepacuite, Senehu, *Wilson 218A* (F).

22. **Cnemidaria karsteniana** (Kl.) Tryon, Contr. Gray Herb. 200: 52, 1970. Figure 24b, Map 13.

Hemitelia karsteniana Kl., Allg. Gartenzeitung 20: 42. 1852. TYPE COLLECTION: possibly *Karsten 142,* "Columbien, Decker 1851 am 31 Debr." HOLOTYPE: B! (?).

Cyathea karsteniana (Kl.) Domin. Pteridophyta 264, 1929.

Caudex to 0.6 m. long and 2.5 cm. in diameter; *leaves* to 2.5 m. long and 0.8 m. broad, terminating in a conform or subconform apical pinna (often with a pair of enlarged basal lobes); *petiole* to 1 m. long, muricate to short-spiny, the scales lanceolate to linear-lanceolate, bicolorous, brown with narrow, whitish margins; *rachis* non-alate, lacking scales and trichomes; *pinnae* subsessile, crenate or shallowly lobed, truncate at base, the tissue sometimes crowding or overlapping the rachis; *costae* and *costules* with scales and trichomes lacking; *veins* mostly once-forked, basal ones merging to form costal areoles, basal basiscopic ones arising from the costule; *sori* in a single line mostly inframedial on the veins between costule and segment margin; *indusia* yellowish-brown, more or less semicircular, subentire to lobed, saucer-shaped.

This and *Cnemidaria nervosa* are the most highly advanced species in the genus. Both have strongly areolate venation along the costae, subentire to shallowly lobed pinnae, and are completely lacking in scales

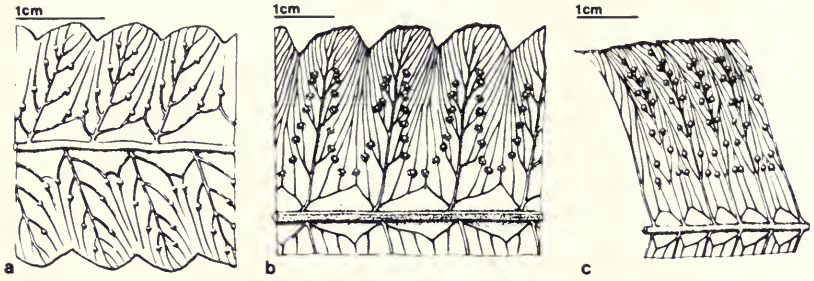


FIG. 24. Portions of pinnae, showing venation; simple, **a**, *Cnemidaria decurrens, Hatch & Wilson 190* (GH), and, **c**, *C. nervosa, Mexia 6291* (GH, isotype); once-forked, **b**, *C. karsteniana, Tschudi 99* (VEN).

or trichomes except on the petiole. They are not, however, closely related and can easily be distinguished by the characters noted in the key. They have apparently arisen along different branches of the phyletic line and have attained their similar advanced characteristics through parallel evolution. It is likely that *C. nervosa* stems from the same line as *C. speciosa* and *C. ewanii,* whereas *C. karsteniana* is more closely related to *C. consimilis.*

There is a specimen of *Hemitelia karsteniana* at Kew, designated as a type, with the label data simply "Hort. Lips. Mett., Herb. Hookeriana," but I find no evidence to indicate this is type material. However, at Berlin, a specimen of *Karsten 142,* marked *"Hemitelia* (*Cnemidaria*) *karsteniana* Klotzsch," bears a handwritten label nearly identical with that of *Karsten 143* which is determined as *"Hemitelia klotzschiana"* (see also discussion under *C. spectabilis* var. *spectabilis*). Both of these were collected in 1851, and both species were described together a year later by Klotzsch, rather strong evidence that these were the specimens on which he had based his original descriptions.

Slopes of cloud forests, 1,000-1,600 m. Apparently confined to northern Venezuela (Aragua, Carabobo, Sucre). *Karsten 142,* cited above, bears no collection locale other than "Columbien," a designation Karsten used for Venezuelan as well as Colombian collections.

Selected specimens examined.—**Venezuela. Aragua:** Alto de Choroni, *Chardon 188* (US, VEN). Highway between Maracay & Choroni,

Lasser 210 (GH, US, VEN). Cloud forests of Rancho Grande, *Pittier 13982* (F, US, VEN). Maracay, 1939, *Vogl s.n.* (F). Parque Nacional, *Ll. Williams 10758, 10786* (F). **Carabobo:** *Funk & Schlim 613* (F). **Sucre:** Cerro Patao, Penin. de Paria, *Steyermark & Agostini 91093* (US, VEN).

23. **Cnemidaria nervosa** (Maxon) Tryon, Contr. Gray Herb. 200: 52, 1970. Figure 24c, Map 14.

Hemitelia nervosa Maxon, J. Wash. Acad. Sci. 34: 309, 1944. TYPE COLLECTION: *Mexia 6291,* mouth of Río Santiago, Loreto, Peru, Dec. 18, 1931. HOLOTYPE: (3 sheets) US! ISOTYPES: F! GH! NY!

Caudex not seen, reported to be less than 1 m. long; *leaves* to 2.5 m. long and 0.7 m. broad, terminating in a conform or subconform apical pinna; *petiole* to 1 m. long, smooth or muricate, the scales mostly near the base, lanceolate to linear-lanceolate, bicolorous, brown with narrow whitish margins; *rachis* non-alate, lacking scales and trichomes; *pinnae* short-stalked, subentire to broadly serrate, rounded to broadly cuneate at base; *costae* and *costules* with scales and trichomes lacking; *veins* simple, basal ones merging to form costal areoles, basal basiscopic ones arising from the costule; *sori* in a single line inframedial on the veins between costule and margin; *indusia* pale or yellowish, commonly circular, completely surrounding the receptacle, entire to lobed, flattened or saucer-shaped.

This is one of the most distinctive species in the genus. Its pinnae are often nearly entire, with rounded bases, and commonly reach a breadth of 9 cm. Probably the most highly advanced species of *Cnemidaria,* it could perhaps be confused only with *C. karsteniana.* (A discussion of both is included under the latter.)

One of the unique characters of *C. nervosa* is the completely circular indusium, which fully surrounds the receptacle. It is flat or slightly concave and looks very much like a saucer. Only *C. cocleana* shares this feature. Other species of *Cnemidaria* have more or less semicircular indusia, positioned on the costular side of the receptacle.

Rain forests, 300-450 m., Peru (Amazonas, Loreto) and Ecuador (Santiago-Zamora).

Additional specimens examined.—**Peru. Amazonas:** Valley of Río Marañon, Prov. de Bagua, *Wurdack 2059* (NY, US). **Ecuador: Santiago-Zamora:** Taisha, banks of Río Guaguayme, *Cazalet & Pennington 7746* (NY).

DUBIOUS NAMES

HEMISTEGIA AMERISTONEURA Fée, Mem. Fam. Foug. VIII: 110. 1857. TYPE COLLECTION: *Poiteau s.n.,* Guayane Francaise.

Hemitelia ameristoneura (Fée) C. Chr., Ind. Fil. 347. 1905.

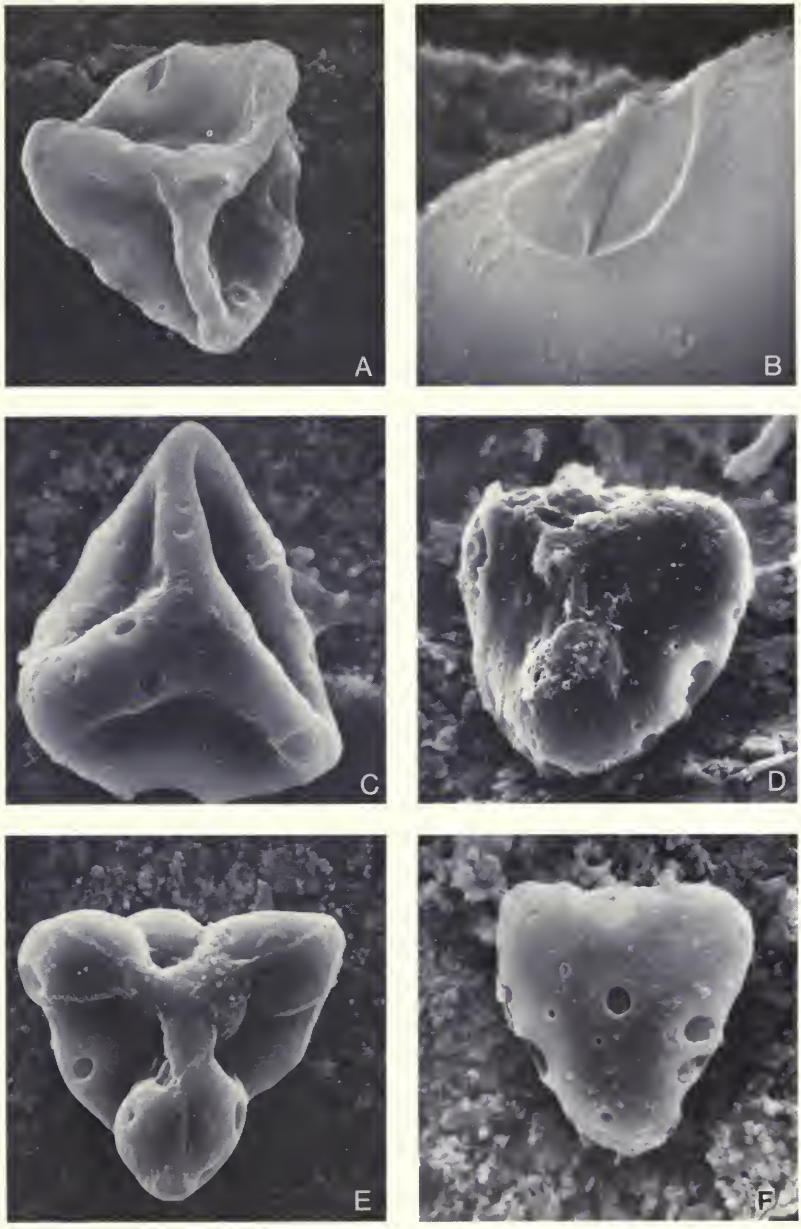


FIG. 25. *Cnemidaria* spores: **a**, *C. chiricana*, proximal view (1260 ×); **b**, *C. chiricana*, fine relief (6300 ×); **c**, *C. mutica* var. *mutica*, proximal view (1350 ×); **d**, *C. choricarpa*, proximal view (1200 ×); **e**, *C. uleana* var. *uleana*, proximal view (1300 ×); **f**, *C. ewauii*, distal view (1250 ×).

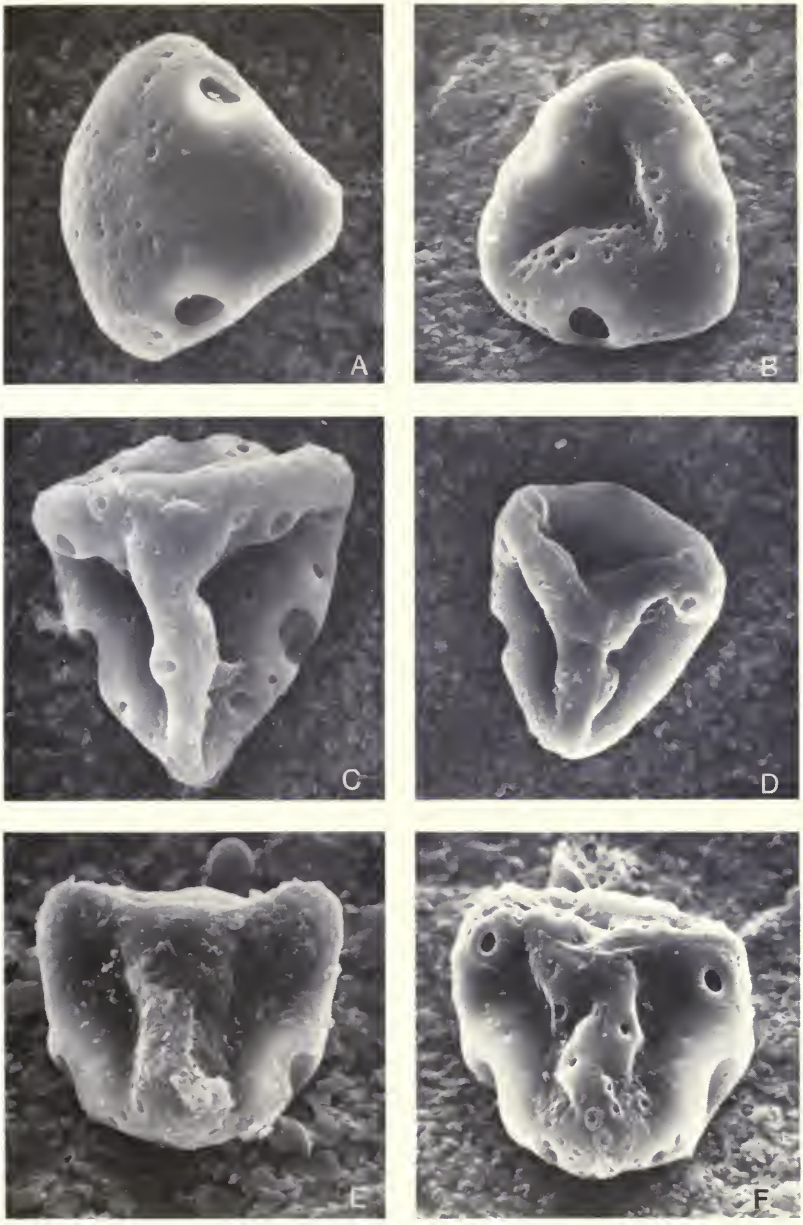


FIG. 26. *Cnemidaria* spores: **a,** *C. horrida,* lateral view (1250 ×); **b,** *C. horrida,* distal view (1270 ×); **c,** *C. grandifolia* var. *grandifolia,* proximal view (1250 ×); **d,** *C. spectabilis* var. *spectabilis,* proximal view (1220 ×); **e,** *C. decurrens,* proximal-lateral view (1300 ×); **f,** *C. karsteniana,* proximal-lateral view (1270 ×).

Cyathea ameristoneura (Fée) Domin, Pteridophyta 263. 1929.

I have not seen the type specimen, and from the description it is difficult to determine with certainty if this is a distinct species or one of the known species of *Cnemidaria*. It could be either *C. cruciata* or *C. spectabilis*, the two representatives of the genus known in French Guiana. The only Poiteau specimens I have seen are those of *C. cruciata*, and Fée's description perhaps matches this species more closely than it does *C. spectabilis*: ". . .longeur des frondules 14-17 centim., sur 3 centim. de largeur." Rarely do larger pinnae of *C. spectabilis* measure less than 4.5 cm. wide. However, too little evidence is currently available to place this name with certainty.

HEMITELIA MONILIFERA J.Sm., London J. Bot. 1: 662. 1848. *nom. nud.*

Hemistegia monilifera Presl, Gefässb. Stipes der Farrn 47. 1847 (preprint of Abh. Böhm Ges. Wis. V. 5: 355. 1848). *nom. nud.*

The name *Hemitelia monilifera* first appears in Smith's "Genera of Ferns," and later is listed by Presl (1847) under *Hemistegia*. I have seen no authentic specimens, therefore I am uncertain whether the plants thus referred are actually *Cnemidaria*. Neither Smith nor Presl included descriptions of any kind, although it may be inferred from the former's general remarks that *H. monilifera* belongs to the ". . .true Hemiteliae of Mr. Brown," in which "the lower venules anastomose." Nothing further may be positively determined at this time.

EXCLUDED SPECIES

On the basis of the evidence presented in this revision, five species included in *Cnemidaria* by Tryon (1970) must now be excluded. These are herewith placed in *Cyathea*, with new combinations where nceessary:

CYATHEA **conformis** (Tryon) Stolze, comb. nov.

Hemitelia conformis Tryon, Rhodora 62: 1. 1960.

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

CYATHEA **dissimilis** (Morton) Stolze, comb. nov.

Hemitelia dissimilis Morton, Fieldiana Bot. 28: 8. 1951.

Cnemidaria dissimilis (Morton) Tryon, Contr. Gray Herb. 200: 52. 1970.

CYATHEA INTEGRIFOLIA (Kl.) Domin, Pteridophyta 264. 1929.

Hemitelia integrifolia Kl., Linnaea 18: 539. 1844.

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

CYATHEA PANAMENSIS Domin, Pteridophyta 264. 1929.

Hemitelia marginalis J. Sm. 1842. *nom. nud.* (*non Cyathea marginalis* Domin 1929.)

Hemitelia petiolata Hook., Spec. Fil. I. 31, *t. 16.* 1844. (*non Cyathea petiolata* J. Sm. 1841).
Hemistegia marginalis Presl, Gefässb. Stipes der Farrn, 47. 1847 (preprint of Abh. Böhm Ges. Wiss V. 5: 355. 1848).
Cnemidaria petiolata (Hook.) Copel., Gen. Fil. 97. 1947.

CYATHEA SPECIOSA Willd., Spec. Pl. V: 490. 1810 (*non Cnemidaria speciosa* Presl 1836).

Hemitelia speciosa (Willd.) Kaulf., Enum. Fil. 252. 1824.
Hemitelia lindenii Hook., Icon. Pl. *t. 706* 1848.
Cnemidaria lindenii (Hook.) Tryon, Contr. Gray Herb. 200: 52. 1970.

Three other species have occasionally been confused with *Cnemidaria,* either because of the anastomosing of some veins, or because the lamina is not highly dissected. These are also excluded from *Cnemidaria* and new combinations are herewith provided as needed:

CYATHEA **hombersleyii** (Maxon) Stolze, comb. nov.
Hemitelia hombersleyi Maxon, J. Wash. Acad. Sci. 25: 528. 1935.

CYATHEA WILSONII (Hook.) Domin, Pteridophyta 264. 1929.
Hemitelia wilsonii Hook. in Hook. & Bak. Syn. Fil. 30. 1865.

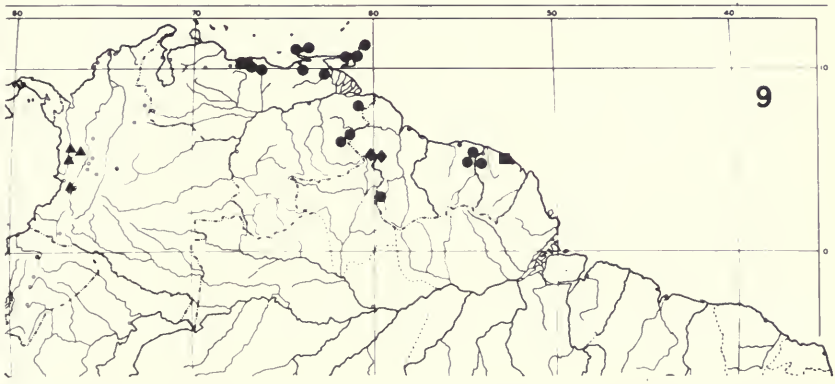
CYATHEA **woronovii** (Maxon & Morton) Stolze, comb. nov.
Hemitelia woronovii Maxon & Morton, Amer. Fern J. 36: 91. 1946.

One other species which bears superficial resemblance to species of *Cnemidaria* was described by Kuhn (1869) as:

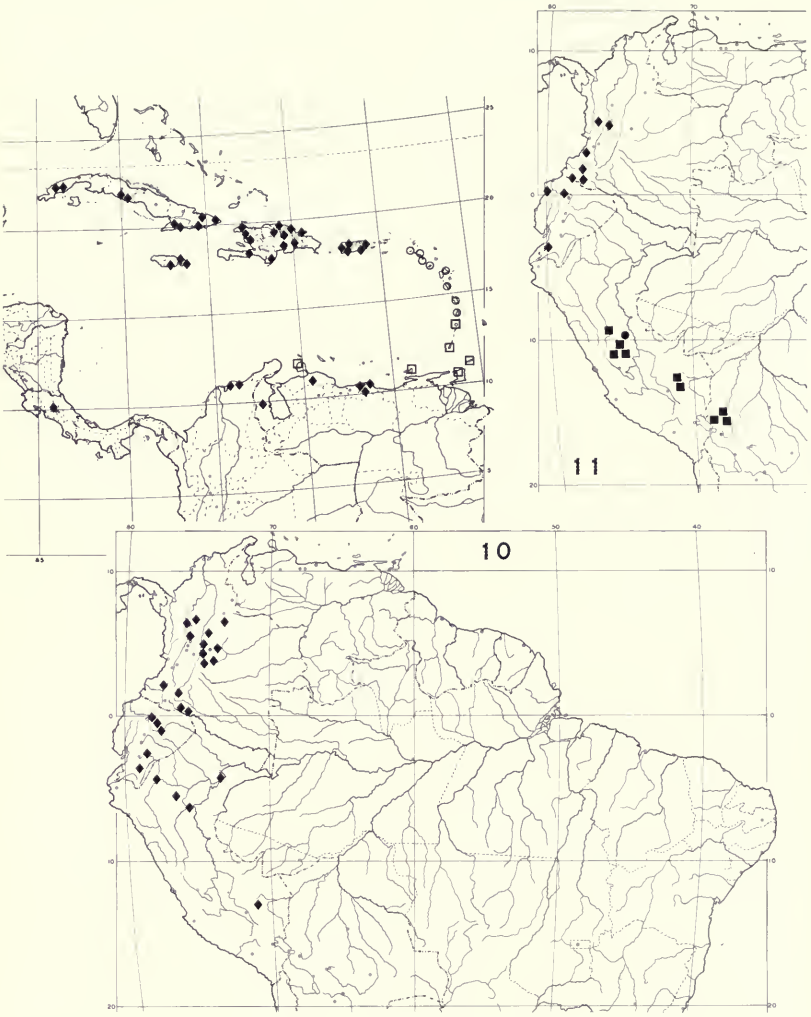
HEMITELIA VENOSA Reichb. Herb. Linnaea 36:161. 1869.

Unfortunately, the only material I have been able to locate is a type fragment at U.S. National Herbarium, consisting of a single pair of segments, and a photograph taken by Drs. Rolla and Alice Tryon of the type collection at Berlin. Little can be determined from the fragment except that the veins are free and somewhat connivent to the sinus, and that the indusia are hemitelioid. The type photograph reveals an unnumbered specimen of Appun, from "Caracas," consisting of what appears to be a rachis with three fragmentary pairs of pinnae. The pinnae bear a few subfalcate, obtuse segments, cut fully (or nearly) to the costa, which is a condition atypical of *Cnemidaria.* Kuhn's description sheds no further light on the plant's generic status. It could therefore be a strange species of *Cnemidaria,* or, more probably, a *Cyathea.* It is of little use to conjecture further.

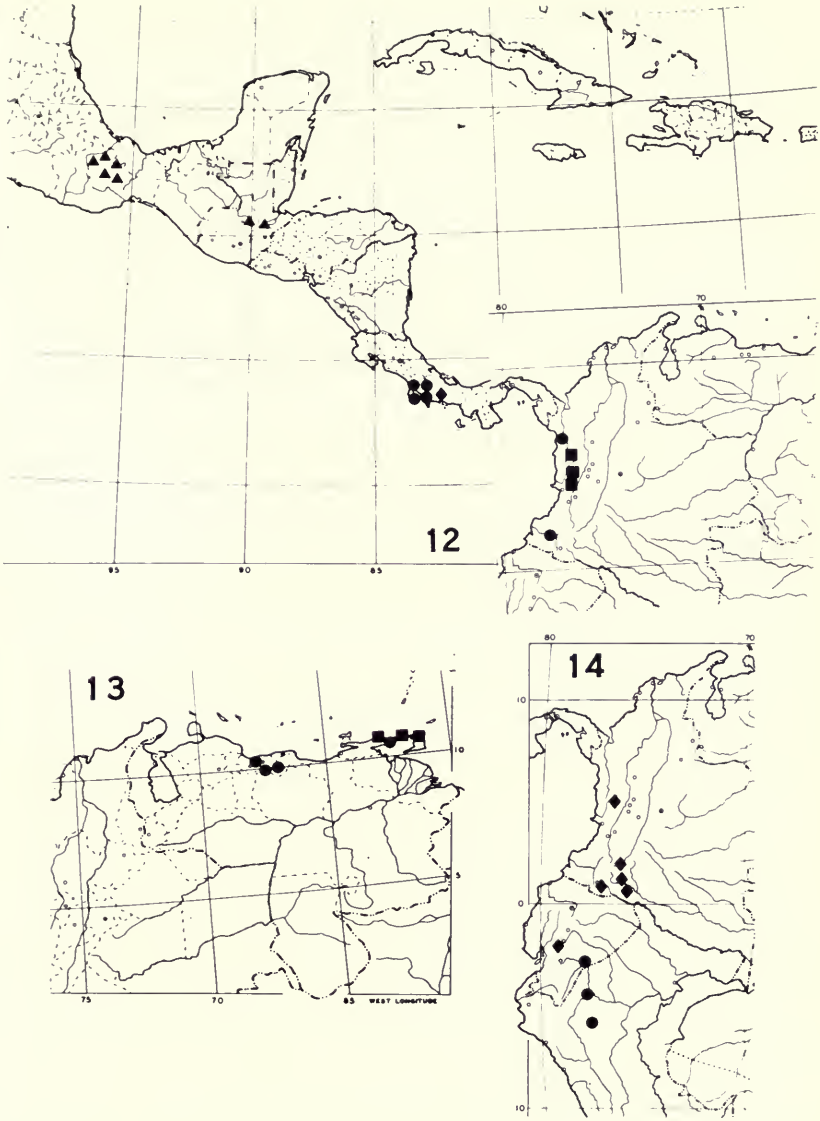
MAPS 2-7. **2**, *Cnemidaria amabilis*, dot; *C. tryoniana*, square. **3**, *C. apiculata*. **4**, *C. mutica* var. *mutica*. **5**, *C. mutica* var. *chiricana*. **6**, *C. mutica* var. *grandis*. **7**, *C. mutica* var. *contigua*.



MAPS 8-9. **8**, *Cnemidaria singularis*, dot; *C. uleana* var. *uleana*, square; *C. uleana var. abitaguensis*, diamond. **9**, *C. spectabilis* var. *spectabilis*, dot; *C. spectabilis* var. *colombiensis*, triangle; *C. cruciata*, square; *C. roraimensis*, diamond.



MAPS 10-11. **10,** *Cnemidaria horrida,* diamond; *C. grandifolia* var. *grandifolia,* circle; *C. grandifolia* var. *obtusa, open square.* **11,** *C. speciosa,* square; *C. alatissima,* dot; *C. quitensis,* diamond.



MAPS 12-14. **12,** *Cnemidaria chocoensis,* square; *C. choricarpa,* dot; *C. cocleana,* diamond; *C. decurrens,* triangle. **13,** *C. consimilis,* square; *C. karsteniana,* dot. **14,** *C. nervosa,* dot; *C. ewanii,* diamond.

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INDEX TO COLLECTORS' NUMBERS

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2726 *horrida*
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AGUILAR, P.
246 *speciosa*
ALLARD, H. A.
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1052 *horrida*
APOLLINAIRE-MARIE, BRO.
12 *horrida*
APPUN, C. F.
1035 *roraimensis*
1127 *roraimensis*
ARCHER, W. A.
1764 *spectabilis* var. *colombiensis*
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HAHN, L.
52 *grandifolia* var. *grandifolia*
HALLBERG, B.
1557 *apiculata*
1567 *decurrens*
HARRIS, W. and N. L. BRITTON
10697 *horrida*
10709 *horrida*
HART, J. H.
174 *horrida*
HATCH, W. R. and C. L. WILSON
190 *decurrens*
HEKKING, W. H. A.
1421 *spectabilis* var. *spectabilis*
1435 *spectabilis* var. *spectabilis*
1441 *spectabilis* var. *spectabilis*
HELLER, A. A.
1043 *horrida*
HENRI-STANISLAUS, Bro.
1644 *horrida*
HIORAM, Bro.
277 *horrida*
HIORAM, Bro. and Bro. CLEMENT
6526 *horrida*
HIORAM, Bro. and C. MAUREL
2473 *horrida*
4695 *horrida*
HODGE, W. H.
8 *grandifolia* var. *grandifolia*
9 *grandifolia* var. *grandifolia*
10 *grandifolia* var. *grandifolia*
1332 *grandifolia* var. *grandifolia*
1711 *grandifolia* var. *grandifolia*
2378 *grandifolia* var. *grandifolia*
3438 *grandifolia* var. *grandifolia*
HODGE, W. H. and B. T.
1814 *grandifolia* var. *grandifolia*
HOLDRIDGE, L. R.
2208 *horrida*

*Indicates collectors for whom I was unable to locate initials or first names.

HOLM, T.
169a *horrida*
HOMBERSLEY, A.
30 *spectabilis* var. *spectabilis*
210 *spectabilis* var. *spectabilis*
HOWARD, R. A.
5222 *horrida*
5376 *horrida*
6427 *horrida*
11964 *grandifolia* var. *grandifolia*
HOWARD, R. A. and L. I. NEVLING
15585 *horrida*
15763 *horrida*
HUMPHREY, J. E.
3340 *horrida*
HUNNEWELL, F. W.
11530 *horrida*
HUSNOT, T.
388 *grandifolia* var. *grandifolia*
IDROBO, J. and R. SCHULTES
735 *horrida*
IMRAY*
14 *grandifolia* var. *grandifolia*
JACK, J. G.
6438 *horrida*
6477 *horrida*
7341 *horrida*
JENMAN, G. S.
124 *spectabilis* var. *spectabilis*
s.n. (1895) *spectabilis* var. *spectabilis*
s.n. (1899) *spectabilis* var. *spectabilis*
JIMÉNEZ, A.
1644 *mutica* var. *mutica*
2015 *mutica* var. *mutica*
JIMÉNEZ, J.
3069 *horrida*
JOHNSTON, J. R.
191 *grandifolia* var. *obtusa* (pro parte)
191 *spectabilis* var. *spectabilis* (pro parte)
JONES, G. C. and D. H. NORRIS
1187 *horrida*
JONES, G. N.
10993 *horrida*
JURGENSEN, C.
"273" *apiculata*
873 *apiculata*
905 *decurrens*
JUZEPCZUK, S.
6510 *horrida*
6533 *ewanii*
KAPPLER, A.
1771 *spectabilis* var. *spectabilis*
KARSTEN, H.
142 *karsteniana*
143 *spectabilis* var. *spectabilis*
s.n. (B) *karsteniana*
s.n. (F) *karsteniana*
KARWINSKY, W. F.
s.n. (F) *decurrens*
KILLIP, E. P.
5039 *spectabilis* var. *colombiensis*
5156 *mutica* var. *mutica*
5162 *mutica* var. *mutica*
5231 *mutica* var. *grandis*
5248 *mutica* var. *grandis*
5294 *mutica* var. *chiricana*
5297 *mutica* var. *chiricana*
5347 *mutica* var. *chiricana*
5350 *mutica* var. *chiricana*
5391 *mutica* var. *grandis*
7774 *quitensis*
34434 *horrida*
35377 *spectabilis* var. *colombiensis*
35454 *ewanii*
KILLIP, E. P. and T. E. HAZEN
10159 *horrida*
KILLIP, E. P. and A. C. SMITH
23889 *speciosa*
24536 *speciosa*
24539 *speciosa*
24548 *speciosa*
25289 *speciosa*
25563 *speciosa*
25737 *speciosa*
26341 *speciosa*
26574 *speciosa*
KLUG, G.
1846 *ewanii*
3182 *horrida*
KRAMER, K. U. and W. H. A. HEKKING
3195 *spectabilis* var. *spectabilis*
KRUKOFF, B. A.
11297 *speciosa*
KUNKEL, G.
596 *speciosa*
KUNTZE, O.
s.n. (NY) *spectabilis* var. *spectabilis*
s.n. (US) *horrida*
LANKESTER, C. H.
726 *mutica* var. *mutica*
732 *mutica* var. *mutica*
LASSER, T.
210 *karsteniana*
2216 *karsteniana*
LASSER, T. and L. ARISTIGUIETA
3413 *grandifolia* var. *obtusa*
LAVASTRE, B. A.
1887 *horrida*
1889 *horrida*
LECHLER, W.
2172 *speciosa*
s.n. (F) *speciosa*
LEHMANN, F. C.
7367 *horrida*
LELLINGER, D. B.
619 *grandifolia* var. *grandifolia*

LELLINGER, D. B. and E. R. de la SOTA
277 *choricarpa*
431 *spectabilis* var. *colombiensis*
728 *quitensis*
763 *chocoensis*
895 *chocoensis*
LENT, R. W.
28 *mutica* var. *grandis*
LEÓN, Bro. and C. MAUREL
3823 *horrida*
LEONARD, E. C.
7863 *horrida*
8209 *horrida*
9189 *horrida*
9191 *horrida*
9193 *horrida*
9373 *horrida*
LEONARD, E. C. and G. M.
12275 *horrida*
14238 *horrida*
14312 *horrida*
LEPRIEUR, M.
s.n. (K) *spectabilis* var. *spectabilis*
LIEBMANN, F.
909 (Pl. Mex. 2105) *decurrens*
910 (Pl. Mex. 2105) *decurrens*
911 (Pl. Mex. 2105) *decurrens*
912 (Pl. Mex. 2089) *decurrens*
913 (Pl. Mex. 2089) *decurrens*
s.n. (US) *decurrens*
LINDEMAN, J. C.
6124 *spectabilis* var. *spectabilis*
LINDEN, J. J.
448 *horrida*
1738 *horrida*
LLOYD, F. E.
263 *grandifolia* var. *grandifolia*
LÓPEZ, M.
143 *horrida*
LORD, M. L.
s.n. (1952) *grandifolia* var. *grandifolia*
LUERSSEN, C.
s.n. (P) ("Hort. Bot. Lips.") *bella*
LUTZ, B.
727 *uleana* var. *uleana*
729 *uleana* var. *uleana*
MÄGDEFRAU, K.
6 *horrida*
MAGUIRE, B. et al.
40581 *roraimensis*
MAXON, W. R.
307 *mutica* var. *grandis*
382 *mutica* var. *mutica*
434 *mutica* var. *mutica*
451 *mutica* var. *mutica*
453 *mutica* var. *mutica*
523 *mutica* var. *contigua*
869 *horrida*
2387 *horrida*
2456 *horrida*
4034 *horrida*
4104 *horrida*
4187 *horrida*
4336 *horrida*
5474 *mutica* var. *chiricana*
5517 *mutica* var. *chiricana*
5519 *mutica* var. *chiricana*
5521 *mutica* var. *chiricana*
5682 *mutica* var. *grandis*
8879 *horrida*
9346 *horrida*
MAXON, W. R. and A. D. HARVEY
8023 *mutica* var. *grandis*
8032 *mutica* var. *mutica*
8042 *mutica* var. *grandis*
8066 *mutica* var. *mutica*
8136 *mutica* var. *contigua*
8220 *mutica* var. *contigua*
MAXON, W. R. and E. P. KILLIP
12 *horrida*
779 *horrida*
1550 *horrida*
MCCONNELL, F. V. and J. J. QUELCH
620 *roraimensis*
METCALF, R. D. and J. CUATRECASAS
30122 *tryoniana*
MEXIA, Y.
6291 *nervosa*
7320 *horrida*
8479 *quitensis*
MICKEL, J. T.
994 *apiculata*
5676 *apiculata*
5717 *apiculata*
5889 *decurrens*
5890 *decurrens*
5934 *decurrens*
5935 *apiculata*
MILLER, G. S.
1180 *horrida*
s.n. (1924) *grandifolia* var. *obtusa*
MILLER, O. O. and J. R. JOHNSTON
164 *spectabilis* var. *spectabilis*
MOLINA, A. et al.
17954 *choricarpa*
MORITZ, J.
290 *horrida*
MORTON, C. V.
4240 *horrida*
4326 *horrida*
5072 *grandifolia* var. *obtusa*
5207 *grandifolia* var. *obtusa*
5717 *grandifolia* var. *obtusa*
MUNCH, G.
4 *decurrens*
s.n. (US) *decurrens*
MURILLO, M. T.
70 *horrida*
NASH, G. V.
239 *horrida*

NISMAN, C.
7 *mutica* var. *grandis*
14 *mutica* var. *mutica*
15 *mutica* var. *mutica*
22 *mutica* var. *mutica*
35 *choricarpa*
62 *mutica* var. *mutica*
87 *choricarpa*
93 *mutica* var. *grandis*
123 *mutica* var. *grandis*
127 *mutica* var. *mutica*
146 *choricarpa*
155 *mutica* var. *mutica*
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OWNBEY, M.
2707 *horrida*
PALMER, C.
64 *mutica* var. *mutica*
PENNELL, F. W.
1577 *horrida*
PEREIRA, E.
312 *uleana* var. *uleana*
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1658 *horrida*
PITTIER, H.
1679 *horrida*
1837 *mutica* var. *mutica*
4835 *choricarpa*
5945 *spectabilis* var. *spectabilis*
7091 *spectabilis* var. *spectabilis*
7794 *spectabilis* var. *spectabilis*
10966 *choricarpa*
10969 p.p. *mutica* var. *mutica*
10969 p.p. *choricarpa*
11510 *horrida*
13906 *karsteniana*
13982 *karsteniana*
PLOWMAN, T.
2133 *ewanii*
POEPPIG, E. F.
"221" *speciosa*
224 *speciosa*
POITEAU, A.
139 *cruciata*
s.n. (1824) *cruciata*
POLLARD, C. L. and W. PALMER
118 *horrida*
154 *horrida*
PORTER, T. C.
s.n. (US) *bella*
PROCTOR, G. R.
3894 *horrida*
3911 *horrida*
5117 *horrida*
16773 *grandifolia* var. *grandifolia*
16904 *grandifolia* var. *obtusa*
17523 *grandifolia* var. *grandifolia*
18092 *grandifolia* var. *grandifolia*
19097 *grandifolia* var. *grandifolia*
19318 *grandifolia* var. *grandifolia*
19501 *grandifolia* var. *grandifolia*
20379 *grandifolia* var. *grandifolia*
21553 *spectabilis* var. *spectabilis*
21699 *grandifolia* var. *grandifolia*
21787 *grandifolia* var. *grandifolia*
25768 *grandifolia* var. *grandifolia*
26107 *grandifolia* var. *obtusa*
QUESTEL, A.
1117 *grandifolia* var. *grandifolia*
2929 *grandifolia* var. *grandifolia*
RAMSAMMY, J. R.
88 *grandifolia* var. *obtusa*
RIDOUTT, C. A.
12975 *speciosa*
RODRIGUEZ, G.
394 *karsteniana*
ROIG, J. and EDWARDS*
6429 *horrida*
ROPER, E. W.
s.n. (GH) *horrida*
RUSBY, H. H.
149 *speciosa*
3020 *speciosa*
RUSBY, H. H. and R. W. SQUIRES
110 *spectabilis* var. *spectabilis*
SAGOT, P.
873 *cruciata*
SALVIN, O.
s.n. (GH) *decurrens*
s.n. (K) *decurrens*
s.n. (US) *decurrens*
SARGENT, F. H.
332 *horrida*
536 *horrida*
SCAMMAN, E.
5881 *choricarpa*
6520 *horrida*
6996 *choricarpa*
7000 *mutica* var. *mutica*
7575 *mutica* var. *mutica*
7576 *mutica* var. *mutica*
7577 *mutica* var. *mutica*
7578 *mutica* var. *mutica*
7579 *mutica* var. *mutica*
8117 *horrida*
8143 *grandifolia* var. *grandifolia*
SCAMMAN, E. and L. R. HOLDRIDGE
7879 *mutica* var. *contigua*
7881 *mutica* var. *mutica*
7882 *mutica* var. *mutica*
SCHULTES, R. E. and B. P. REKO
678 *decurrens*
SCHUNKE, C.
52 *speciosa*
82 *speciosa*
879 *speciosa*
A-143 *speciosa*
SCHUNKE, J.
4744 *speciosa*
SEIFRIZ, W.
3 *spectabilis* var. *spectabilis*
4 *consimilis*
13 *spectabilis* var. *spectabilis*
277 *horrida*

SEIFRIZ, W. *(continued)*
572 *horrida*
SENN, H. A.
230 *horrida*
387 *horrida*
SHAFER, J. A.
283 *grandifolia* var. *grandifolia*
3270 *horrida*
4456 *horrida*
8825 *horrida*
8950 *horrida*
SHERRING, R. V.
74 *grandifolia* var. *obtusa*
163 *grandifolia* var. *obtusa*
164 *grandifolia* var. *obtusa*
174 *grandifolia* var. *obtusa*
SIEBER*
(Fl. Martin 375)
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SINTENIS, P.
417 *horrida*
1507 *horrida*
2490B *horrida*
4168 *horrida*
6088 *horrida*
SKUTCH, A. F.
2265 *choricarpa*
3262 *mutica* var. *mutica*
5307 *choricarpa*
SMITH, A. C.
3584 *spectabilis* var. *spectabilis*
3585 *spectabilis* var. *spectabilis*
10074 *spectabilis* var. *spectabilis*
10516 *grandifolia* var. *grandifolia*
SMITH, H. H.
2596 *horrida*
SMITH, H. H. and G. W.
849 *grandifolia* var. *obtusa*
854 *grandifolia* var. *obtusa*
1715 *grandifolia* var. *obtusa*
SMITH, L. B.
2077 *uleana* var. *uleana*
SNEIDERN, K. VON
5199 *quitensis*
A473 *quitensis*
SODIRO, A.
s.n. (MO) *quitensis*
s.n. (US) *quitensis*
SOEJARTO, D. D.
1571 *singularis*
SOUKUP, J.
1069 *speciosa*
SPRUCE, R.
3943 *horrida*
4730A *horrida*
5364 *uleana* var. *abitaguensis*
5365 *ewanii*
STAHEL and GONGERIJP*
338 *spectabilis* var. *spectabilis*
STANDLEY, P. C.
39349 *mutica* var. *mutica*
STANDLEY, P. C. and R. TORRES
51250 *mutica* var. *grandis*
STANDLEY, P. C. and J. VALERIO
50216 *mutica* var. *mutica*
STEHLÉ, H.
98 *grandifolia* var. *grandifolia*
102 *grandifolia* var. *grandifolia*
1221 *grandifolia* var. *grandifolia*
1774 *grandifolia* var. *grandifolia*
STEHLÉ, H. and M.
3281 *grandifolia* var. *grandifolia*
3294 *grandifolia* var. *grandifolia*
3422 *grandifolia* var. *grandifolia*
4605 *grandifolia* var. *grandifolia*
4703 *grandifolia* var. *grandifolia*
STEYERMARK, J. A.
61207 *spectabilis* var. *spectabilis*
62042 *amabilis*
89525 *spectabilis* var. *spectabilis*
94886 *amabilis*
94899 *consimilis*
STEYERMARK, J. A. and G. AGOSTINI
91093 *karsteniana*
91205 *amabilis*
STEYERMARK, J. A. and S. NILSSON
218 *spectabilis* var. *spectabilis*
STEYERMARK, J. A. and M. RABE
96260 *consimilis*
STEYERMARK, J. A. et al.
92924 *spectabilis* var. *spectabilis*
STOFFERS, A. L.
4203 *grandifolia* var. *grandifolia*
4206 *grandifolia* var. *grandifolia*
4210 *grandifolia* var. *grandifolia*
STORK, H. E.
2580 *mutica* var. *grandis*
2582 *mutica* var. *mutica*
4756 *mutica* var. *mutica*
TAMAYO, F.
154 *horrida*
2543 *horrida*
TATE, G. H. M.
424 *speciosa*
1162 *speciosa*
TONDUZ, A.
12532 *mutica* var. *mutica*
TRIANA, J.
s.n. (1853) *quitensis*
TRYON, R. M. and A. F.
5260 *speciosa*
6871 *uleana* var. *uleana*
6993 *mutica* var. *mutica*
7019 *mutica* var. *mutica*
7036 *mutica* var. *grandis*
TSCHUDY, R. H. and B. D.
42 *horrida*
99 *karsteniana*
132 *karsteniana*
TÜRCKHEIM, H. VON
2707 (2717?) *horrida*

TURNER, F. T.
s.n. (US) *grandifolia* var. *grandifolia*
TYSON, E. L. et al.
2452 *cocleana*
ULE, E.
s.n. (R) *uleana* var. *uleana*
UNDERWOOD, L. M.
86 *horrida*
1548 *horrida*
2024 *horrida*
3479 *horrida*
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1056 *horrida*
UNDERWOOD, L. M. and R. F. GRIGGS
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273 *horrida*
VALEUR, E. J.
350 *horrida*
1018 *horrida*
VARGAS, C.
11269 *horrida*
11294 *speciosa*
11714 *speciosa*
14584 *speciosa*
14653 *speciosa*
16073 *speciosa*
16275 *speciosa*
16502 *speciosa*
17738 *speciosa*
18863 *speciosa*
VAUTHIER*
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WACKET, M.
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303 *uleana* var. *uleana*
WATT, D,
110 *horrida*
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9148 *grandifolia* var. *grandifolia*
WENT, F. A. F. C.
1018 *spectabilis* var. *spectabilis*
WHITE, R. A. and T. W. LUCANSKY
196818 *mutica* var. *mutica*
196840 *mutica* var. *chiricana*
196852 *mutica* var. *mutica*
196854 *mutica* var. *mutica*
196857 *mutica* var. *grandis*
1968108 *mutica* var. *mutica*
1968139 *mutica* var. *mutica*
1968168 *mutica* var. *grandis*
WIGGINS, I. L.
10930 *quitensis*
WILBUR, R. L. et al.
7791 *grandifolia* var. *grandifolia*
8142 *grandifolia* var. *grandifolia*
8185 *grandifolia* var. *grandifolia*
10192 *mutica* var. *grandis*
10492 *mutica* var. *mutica*
10624 *mutica* var. *mutica*
10625 *mutica* var. *grandis*
11111 *cocleana*
WILLDENOW, K. L.
20167 *grandifolia* var. *grandifolia*
20168 *grandifolia* var. *obtusa*
WILLIAMS, LL.
7156 *horrida*
10758 *karsteniana*
10786 *karsteniana*
10985 *horrida*
WILLIAMS, L. O.
19647 *mutica* var. *grandis*
20267 *mutica* var. *mutica*
20304 *horrida*
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28785 *choricarpa*
29109 *mutica* var. *mutica*
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Publication 1194

UNIVERSITY OF ILLINOIS-URBANA
580.5FB C001
FIELDIANA, BOTANY$CHICAGO
37-39 1974-76
3 0112 009379170