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A REVISION OF THE GENUS *ALSOPHILA*
(CYATHEACEAE) IN THE AMERICAS

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THE GENUS *Alsophila* R. Br. is here redefined based on the recent biosystematic studies of Conant (1975, 1976) and Conant and Cooper-Driver (1980). A major contribution to the understanding of the classification of the Cyatheaaceae has been Tryon's (1970) separation of the scaly tree ferns into three natural alliances: *Sphaeropteris* Bernh. (with conform petiole scales; see Tryon, 1970, for definition of scale types); *Alsophila* sensu Tryon and *Nephelea* Tryon (with setate, marginate scales); and *Trichipteris* Presl, *Cyathea* Sm. sensu Tryon, and *Cnemidaria* Presl (with nonsetate, marginate scales). Based on this system, recent revisionary studies of the Cyatheaaceae by Tryon (1971a, 1976), Gastony (1973), Stolze (1974), Windisch (1977, 1978), and Barrington (1978) have provided excellent data against which the present systematic conclusions have been compared.

Holtum (1961) divided the scaly tree ferns into two genera, *Cyathea* sensu lato and *Cnemidaria*. *Cnemidaria* sensu Holtum is equivalent to *Cnemidaria* sensu Tryon, whereas *Cyathea* sensu Holtum includes the rest of Tryon's scaly genera. *Cyathea* sensu lato was divided into subg. SPHAEROPTERIS (with setiferous (conform) petiole scales) and subg. ALSOPHILA (with flabelloid (marginate) scales). Subgenus ALSOPHILA included sects. ALSOPHILA (indusiate, axes greenish, fertile and sterile pinnules monomorphic) and GYMNOSPHAERA (exindusiate, axes dark, chocolate brown, fertile and sterile pinnules dimorphic) (Holtum, 1974).

The present genus *Alsophila* includes Tryon's *Alsophila* and *Nephelea* in the New World and Holtum's *Cyathea* subg. ALSOPHILA in the Old World. (All Old World species with marginate petiole scales also have setae. Species with nonsetate, marginate scales are restricted to the New World.) The extensive hybridization documented by Conant (1975, 1976) and Conant and Cooper-Driver (1980) is evidence that *Alsophila* sensu Tryon and *Nephelea* are more

closely related than they are distinct and separable genera. Furthermore, Conant and Cooper-Driver (1980) have presented evidence that new species have arisen from these "intergeneric" hybrids. These species of hybrid origin can be assigned to a genus only on an arbitrary basis—i.e., whether genes for squamate spines are inherited and expressed or not. Gastony (1973, 1974) has demonstrated that most species of *Alsophila* sensu Tryon and *Nephelea* have 16-spored sporangia, a feature that distinguishes them from other scaly Cyathea-ceae. Gastony (1973) and Gastony and Tryon (1976) have shown that species of *Alsophila* sensu Tryon cannot be distinguished from *Nephelea* by their spores, lending additional support to their inclusion in the single genus *Alsophila*.

Species of *Alsophila* (in the present sense), however, are not known to hybridize with species of the nonsetate, marginate alliance (*Trichipteris*, *Cyathea* sensu stricto, *Cnemidaria*). The setate and nonsetate groups with marginate scales appear to be morphologically distinct and reproductively isolated from each other. Therefore, I cannot accept the conclusion of Holttum (1974) that these groups are elements of the single genus *Cyathea*.

This redefinition of *Alsophila* obviates the need for a reclassification of the family. Such a task is best left until there have been further biosystematic studies of the species with nonsetate, marginate scales and until the relationships of the species with marginate scales to those with conform scales are more fully understood.

DISTRIBUTION AND ECOLOGY

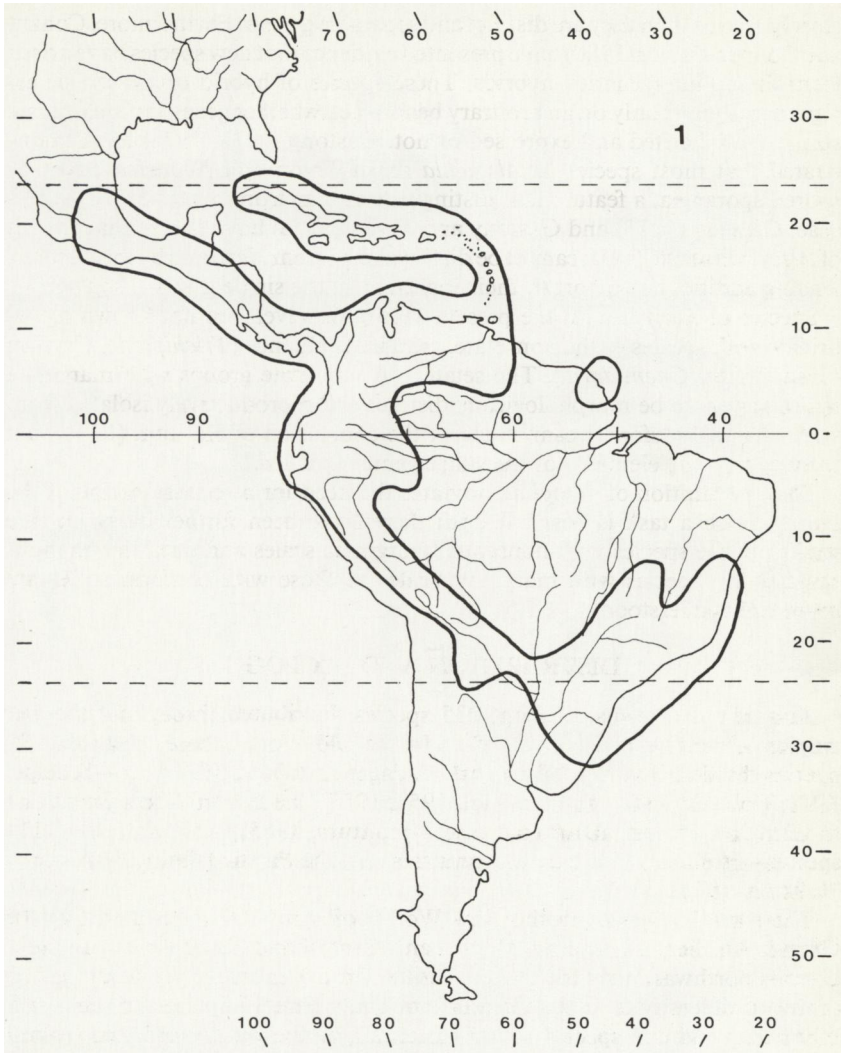
Alsophila is a genus of about 235 species distributed throughout the wet tropics of the Old and New Worlds. In the Old World, there are about 205 species divided between Africa and Madagascar (about 50 species—Schelpe, 1970; Holttum, 1981; Tardieu-Blot, 1951, 1953), the Indian subcontinent east to China and Japan (about 15 species—Holttum, 1965), Malaysia (about 114 species—Holttum, 1963), and Australasia and the Pacific (about 26 species—Holttum, 1964).

There are 30 species in the New World, of which 16 are centered in the Greater Antilles, 14 occur in Mexico and Central and South America, and 1 extends northward into the Lesser Antilles from Venezuela (see MAP 1). The center of diversity is in the Greater Antilles, where 16 species are endemic; Hispaniola, with 8 species and 5 endemics, is the island with the highest diversity.

The American species of *Alsophila* are mostly plants of the cloud forest-elfin forest type of habitat. Exceptions to this are *A. jimeneziana*, *A. cuspidata*, and *A. sternbergii*, which can often be found at lower elevations in gallery forest. *Alsophila* is primarily a genus consisting of understory, shade-loving species. Heliophilic plants like those found in the genera *Sphaeropteris*, *Trichipteris*, and *Cyathea* sensu Tryon are not found in American *Alsophila* and apparently do not occur in eastern Asian *Alsophila* either (Holttum, 1963).

MORPHOLOGY

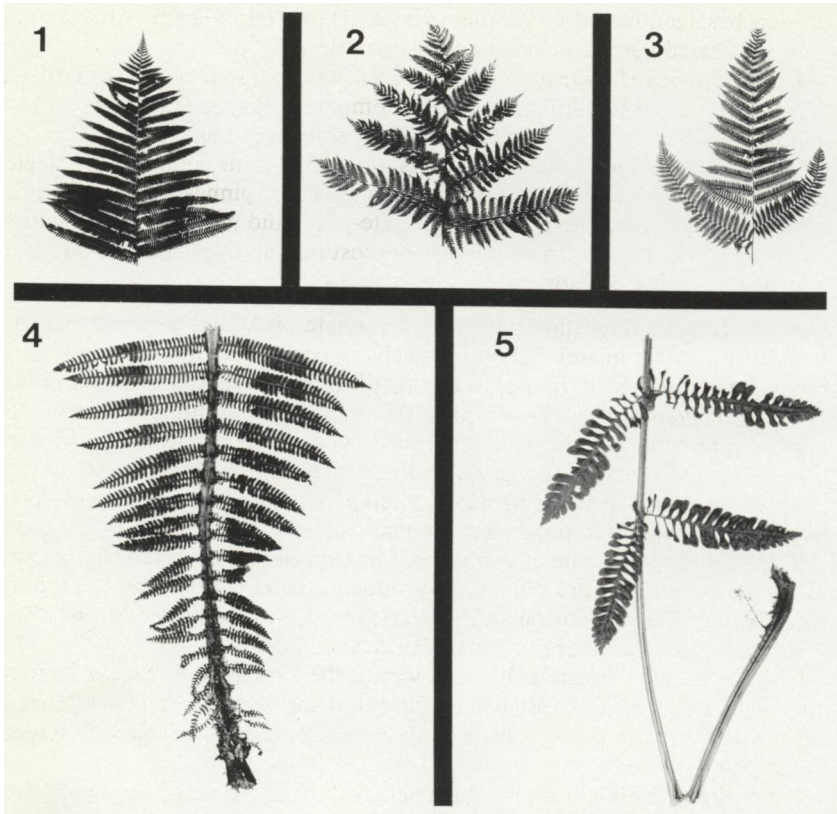
STEM. Stem habit and size provide good diagnostic characters for some species. In *Alsophila nockii* and *A. rupestris* the stem is short, prostrate, and less than



MAP 1. Distribution of the genus *Alsophila* in the Americas.

2 cm in diameter; in *A. brooksii* and *A. urbanii* it is short, prostrate (sometimes decumbent in *A. urbanii*), and to 6.5 cm in diameter. Among species with erect stems, most are greater than 6 cm in diameter and 2 m in length. Exceptions are *A. paucifolia*, which has an unusually slender (less than 2 cm in diameter) stem of unknown length, and *A. amintae* and *A. abbottii*, which generally have stems less than 5 cm in diameter and 1.5 m in length.

Squaminate spines may or may not be present on the stem. In general, spines are restricted to the species with tall, stout stems, although reduced spines are present in *Alsophila brooksii* and in certain hybrids between spiny and spineless species.



FIGURES 1–5. Lamina apices and bases: 1, *Alsophila bryophila* (Conant 2265), gradually tapering apex, $\times .08$; 2, *A. woodwardioides* (Conant 2028), gradually tapering apex, $\times .09$; 3, *A. cuspidata* (Haught 2001), imparipinnate apex, $\times .07$; 4, *A. bryophila* (Conant 2263), gradually tapering base, $\times .18$; 5, *A. urbanii* (Conant 2102), abruptly reduced base, $\times .18$.

Adventitious buds occur in six of the nine species with squamate spines in Mexico and Central and South America, as well as in *Alsophila woodwardioides*, of Jamaica, Hispaniola, and Cuba. *Alsophila sternbergii* is reported to produce stolons at the base of the stem that may facilitate vegetative reproduction in this species (Brade, 1971; as *Cyathea sampaioana*). Stolons are not known elsewhere among American species of the genus but are well documented (Hallé, 1966) in the African *A. manniana*.

The stem apices of all species are protected by deltoid to lanceolate scales with either a single apical seta or both apical and marginal setae.

LEAF. Although the petiole and the lamina are usually described separately, many of the characters of the petiole are present on the rachis in a reduced form, reminding us that the division of the leaf into petiole and lamina is arbitrary. This arbitrariness is also apparent in the treatment of aplebieae and

disjunct basal pinnae. Although these may more properly be parts of the lamina, they are treated here as belonging to the petiole.

The terminology for the parts of the fern leaf has been somewhat standardized (Tryon, 1960), but it is still confusing to compare fern species having complex (bipinnate-pinnatifid) leaves and those having simpler (pinnate-pinnatifid) ones. A factor contributing to the confusion is that some terms connote homologies whereas others relate more to size: petioles, rachises, pinna-rachises, pinnule-rachises, pinnae, and pinnules of bipinnate-pinnatifid and pinnate-pinnatifid leaves are homologous structures; costae, costules, and penultimate and ultimate segments are nonhomologous.

LAMINA. Lamina dissection varies from pinnate-pinnatifid to tripinnate (occasionally quadripinnate). Ten of the twelve species with pinnate-pinnatifid to bipinnate laminae occur in the Greater Antilles. *Alsophila rupestris* (Colombia) and *A. paucifolia* (Ecuador) also have the pinnate-pinnatifid architecture. Bipinnate-pinnatifid lamina dissection occurs in sixteen species distributed throughout the range of the genus in the Americas. Two species, *A. salvinii* (Mexico, Guatemala, Honduras) and *A. polystichoides* (Costa Rica and Panama), have tripinnate to quadripinnate laminae.

The lamina apex is one of two types. Most species have an acuminate apex in which the more distal pinnae are gradually reduced (FIGURES 1, 2). Nine species from Mexico, Central and South America, and the Lesser Antilles have a distinctly pinnalike imparipinnate lamina apex (FIGURE 3).

The lamina may be gradually narrowed at the base as in *Alsophila amintae* and mature leaves of *A. bryophila* (FIGURE 4) or abruptly reduced as in *A. urbanii* (FIGURE 5). Some species (e.g., *A. portoricensis*) are variable with respect to the lamina base.

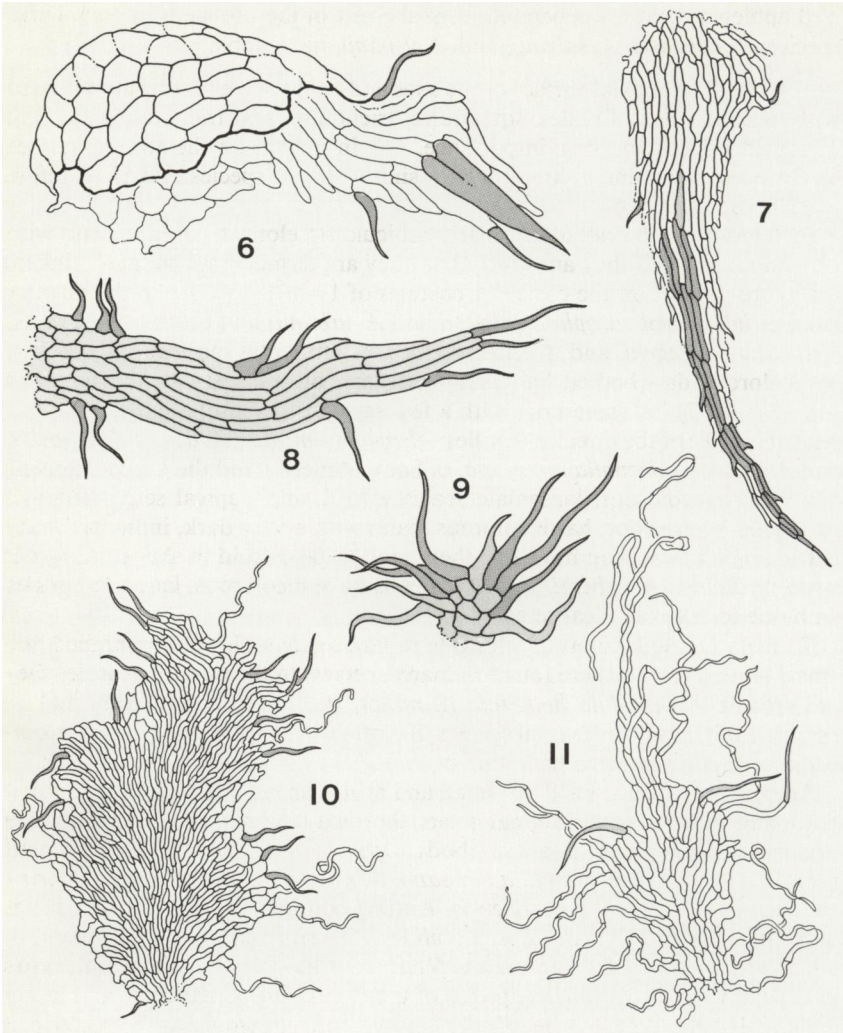
Pinna shape is often a useful character. A measure of pinna shape is width divided by length: long, narrow pinnae will have low width/length quotients; broader ones will have higher quotients.

PETIOLE. Petiole length is generally correlated with lamina base. Species with gradually narrowed lamina bases are usually short petiolate, whereas those with abruptly reduced lamina bases tend to be long petiolate.

Squaminate spines may or may not be present on the petiole. The presence of petiole spines is precisely correlated with the presence of stem spines. Reduced petiole spines may be present in *Alsophila brooksii* and on certain hybrids between spiny and nonspiny species.

Tardieu-Blot (1941) found that the aphlebioid¹ species of Madagascar were of three basic types. The first, including *Alsophila decrescens* (Kuhn) Tryon (as *Cyathea decrescens*), has gradually tapering lamina bases in which pinnae grade into basal subaphlebioid pinnae. American species belonging to this group include *A. amintae*, *A. abbottii*, *A. minor*, *A. auneae*, *A. grevilleana*, and *A. setosa*. (In *A. minor* the basal subaphlebioid pinnae may be disjunct.) The

¹Although the terms aphlebiae and aphlebioid may be technically incorrect, as suggested by Holttum (1981), they are maintained here because these terms have historically been consistently used in describing skeletonized basal pinnae.



FIGURES 6–11. Lamina scales. 6, 7, *Alsophila nockii*: 6, Hart 13, bullate scale, $\times 100$; 7, Underwood 1355, bicolorous, lanceolate scale with single apical seta, $\times 65$. 8, *A. brooksii* (Conant 677), lanceolate scale with marginal and apical setae, $\times 68$. 9, *A. salvinii* (Stone & Broome 2814), acaroid scale, $\times 105$. 10, 11, *A. engelii* (Pennell 9695): 10, setate, flabellate scale, $\times 28$; 11, highly dissected scale, $\times 50$.

second type, including *A. dregei* (Kunze) Tryon (as *C. dregei*), has nonaphlebioid basal pinnae that are separated from the rest of the pinnae by a large gap. Although *A. bryophila* has disjunct basal pinnae of this type in some juvenile plants, its pinnae are pinnatifid and those of *A. dregei* are pinnate-pinnatifid. The third type, including *A. boivinii* Ettingsh., has highly skeleton-

ized aphebiae that are separated from the rest of the pinnae by a gap. Three species, *A. capensis*, *A. salvinii*, and *A. urbanii*, have aphebiae of this type.

INDUMENT. The abaxial surface of the axes and veins of the lamina are invested with various kinds of scales, squamules, trichomes, and trichomidia that are of considerable taxonomic importance. The indument on the adaxial surface of the axes and veins is more or less similar in all species and is therefore usually not described.

Bullate scales (FIGURE 6) are nearly orbicular to elongate, inflated, and with or without setae. If they are nearly flat, they are termed "subbullate." Bullate scales are present on the costae or costules of 14 of 16 species in the Greater Antilles (all except *Alsophila brooksii* and *A. urbanii*) and of 4 (*A. salvinii*, *A. tryoniana*, *A. engelii*, and *A. capensis*) of 14 continental species.

Bicolorous (dark bodied, light margined), lanceolate scales with a single apical seta (FIGURE 7) (or sometimes with a few setae at the base) are found in four related species of the Greater Antilles: *Alsophila amintae*, *A. abbottii*, *A.nockii*, and *A. tussacii*. *Alsophila imrayana*, of South America and the Lesser Antilles, has often concolorous, lanceolate scales with a single apical seta. *Alsophila paucifolia*, of Ecuador, has bicolorous scales with a very dark, indurated body and a single apical seta; however, these tend to be deltoid in shape. *Alsophila woodwardioides*, *A. salvinii*, and *A. capensis* have bicolorous, lanceolate scales with one to several apical setae.

Concolorous to bicolorous, elongate to lanceolate scales with marginal and apical setae (FIGURE 8) are found in many species. In the Greater Antilles they are present in *Alsophila hotteana*, *A. minor*, *A. brooksii*, *A. urbanii*, and *A. portoricensis*. Four continental species, *A. tryoniana*, *A. polystichooides*, *A. sternbergii*, and *A. firma*, also have this type of scale.

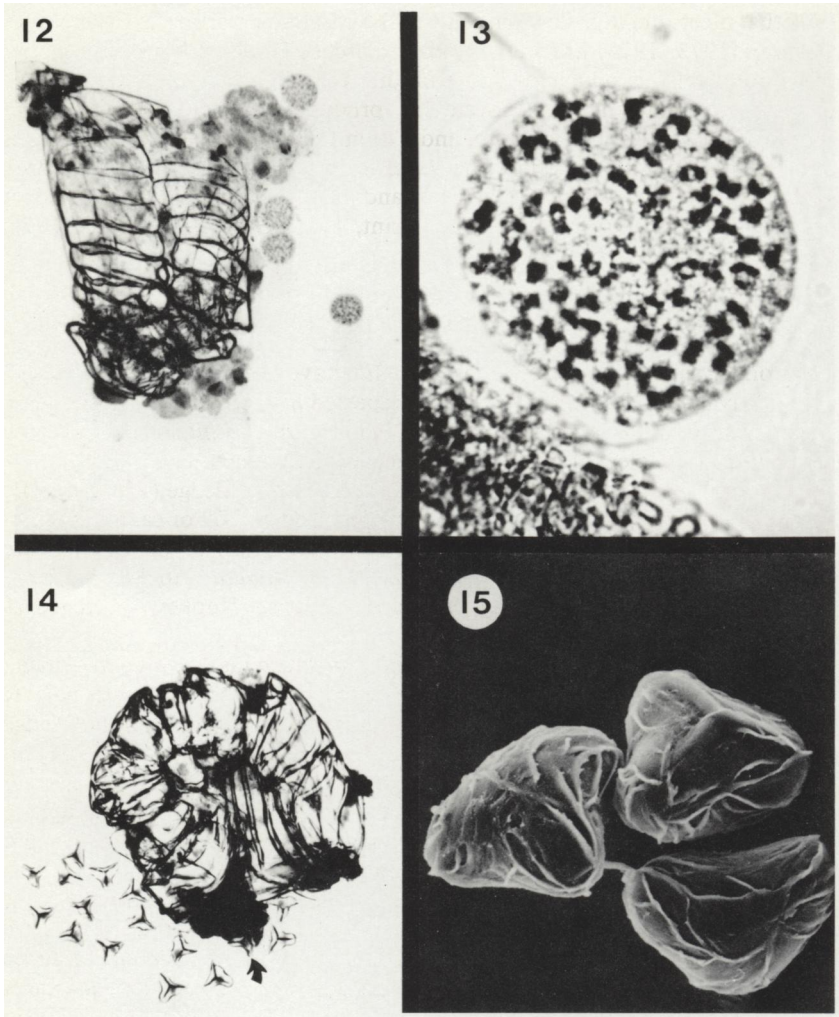
Acaroid scales (FIGURE 9) are small and orbicular, usually with an indurated body and many dark, marginal setae; they may be reduced to tiny, setate squamules nearly without a scale body. Species in the Greater Antilles with acaroid scales include *Alsophila hotteana*, *A. minor*, *A. brooksii*, *A. balanocarpa*, *A. urbanii*, and *A. portoricensis*. Among continental species, such scales occur in *A. salvinii*, *A. setosa*, *A. sternbergii*, *A. cuspidata*, and *A. erinacea*.

Alsophila engelii, of Colombia and Venezuela, has two additional scale types not found in other American species of the genus. One is flabellate and setate (FIGURE 10) (this type may be reduced to tiny, setate squamules with unsclerified bodies). The second is highly dissected and setate (FIGURE 11), giving an axis the appearance of being pubescent.

Young axes may be densely deciduously scurfy with tiny, appressed squamules; this character was not found to be of taxonomic significance, however.

Most species of *Alsophila* have trichomes on the abaxial surface of their smaller axes. *Alsophila bryophila* and *A. auneae* are characterized by a particularly dense pubescence, while *A. amintae*, *A. nockii*, *A. paucifolia*, *A. salvinii*, and *A. capensis* lack trichomes on their axes. *Alsophila cuspidata* and *A. sternbergii* have stellate trichomes on their veins in addition to unbranched ones on their larger axes.

Tiny, antrorse trichomidia may or may not be present on the abaxial surface



FIGURES 12–15. Chromosomes and spores of *Alsophila amintae*. 12–14, *Conant & Kitfield 2274*: 12, sporangium with 4 spore mother cells, $\times 200$; 13, spore mother cell in diakinesis showing $n = \text{ca. } 69$ pairs, $\times 1850$; 14, sporangium with 16 spores (arrow indicates spore partially obscured by sporangium), $\times 200$. 15, *Conant 595*, spores, $\times 1500$.

of the veins. These are usually golden in color, but in *Alsophila engelii* they are whitish.

SORI. The sori are exindusiate or with a hemitelioid (FIGURE 48), menisoid (FIGURE 25), cyatheoid (FIGURE 18), or sphaopteroid (FIGURE 38) indusium. Sporangia are clustered about a usually columnar receptacle, resulting in a semiglobose to nearly globose sorus. They have an oblique annulus and a short

stalk that meets the capsule to one side of the basalmost portion of the annulus. Gastony (1973, 1974) has shown that the archesporial cell typically divides twice mitotically, producing 4 spore mother cells (FIGURE 12), and that each of these undergoes meiosis (FIGURE 13), producing a total of 16 spores per sporangium (FIGURE 14). Gastony and Tryon (1976) reported several species of *Alsophila* (including the American *A. salvinii* and *A. capensis*) with 64-spored sporangia. Spores of *Alsophila* are trilete and have a reticulate pattern of ridges (FIGURE 15) (Gastony, 1973, 1974; Conant, 1975; Gastony & Tryon, 1976; Conant & Cooper-Driver, 1980).

CYTOLOGY

Chromosome counts in the genus *Alsophila* have been $n = 69$ or $n = \text{ca. } 69$ pairs of bivalents. Brownlie (1958, 1965) reported $n = 69$ for four species from Australasia: *A. alata* Fourn., *A. colensoi* Hooker, *A. smithii* (Hooker) Tryon, and *A. tricolor* (Colenso) Tryon (all as species of *Cyathea*).

From the areas of India and Sri Lanka, Manton and Sledge (1954), Mehra and Singh (1955), and Ghatak (1962) have reported $n = 69$ or ca. 69 for eight species: *Alsophila gigantea* Hooker, *A. hookeri* (Thwaites) Tryon, *A. khasiana* Kuhn, *A. latebrosa* Hooker, *A. ornata* Bedd., *A. sinuata* (Hooker & Grev.) Tryon, *A. spinulosa* (Hooker) Tryon, and *A. walkerae* (Hooker) J. Sm. (all as species of *Cyathea*).

Manton (1954) cited $n = 69$ for *Alsophila latebrosa* (as *Cyathea latebrosa*), from Malaysia. Roy and Holttum (1965) cited $n = \text{ca. } 69$ for *A. podophylla* Hooker (as *Cyathea podophylla*), from southern China. Manton and Sledge (1954) reported $n = 70$ for *A. capensis* (L. f.) J. Sm., and Manton (1959) reported $n = \text{ca. } 69$ for *A. camerooniana* (Hooker) Tryon (both from Africa and both as species of *Cyathea*). The report of $n = 70$ for *A. capensis* was from a single plant at Kew Gardens. Since other species in the family have $n = 69$, cytological reexamination of this species in the field is desirable.

Walker (1966) reported $n = 69$ for three Jamaican species, *Alsophila auneae*, *A. grevilleana*, and *A. tussacii* (all as species of *Cyathea*). Gomez-Pignataro (1971) reported $n = 69$ for two Costa Rican species, *A. erinacea* and *A. firma* (both as species of *Cyathea*). Conant (1976) and Conant and Cooper-Driver (1980) cited $n = \text{ca. } 69$ for *A. amintae*, *A. bryophila*, *A. amintae* \times *A. portoricensis*, and *A. bryophila* \times *A. portoricensis*, all from Puerto Rico.

Perhaps the most unusual aspect of the cytology of the genus *Alsophila* is that the two hybrids that have been examined are fertile diploids. Spores are well formed and germinate readily when sown on a nutrient agar medium.

SPECIATION

The genus *Alsophila* apparently originated in the Old World, where 87 percent of the known taxa are found. The American species of *Alsophila* are most closely related to the African and Madagascan elements of the genus (Holttum, 1981), and the presence of *Alsophila* in the New World is undoubtedly the result of long-distance dispersal from the east. Dust from the Sahara Desert

encountered by aerobiologists sampling air in the Caribbean provides evidence that wind patterns favor such long-distance dispersal (Prospero, 1968; Prospero *et al.*, 1970).

At least four separate migrations are believed to have established the basic geographic elements of American *Alsophila*. In some cases migration may have been recent, resulting in little morphological differentiation of the immigrant. Thus, *A. capensis* in southeastern Brazil is only slightly different from that species in southern Africa and was assigned subspecific rank in accordance with the degree of differentiation. *Alsophila salvinii*, of Mexico, Guatemala, and Honduras, is a distinct American species clearly related to species of Holttum's sect. GYMNOSPHAERA (Holttum, 1974, 1981), of Madagascar and Borneo.

In other cases, migrations may have occurred in the more distant past, allowing time for more morphological differentiation and resulting in new American species groups. It is more difficult to determine the relations between American and Old World species groups than it is to relate the above two American taxa to their Old World relatives. This may be a direct result of the diversification process. Although a few characters may still be held in common, shifts in gene frequencies result in a situation where characters that are obscure in the Old World group may become common and predominant in the New World group. Such may have been the case with the development of the squamate spine in the New World.

Holttum (1981) suggests there are about 20 species with complex leaves and squamate spines (excluding *Alsophila setosa*, as *Cyathea setosa*) that form a closely allied group. Gastony (1973) recognized only 15 such species (all as *Nephelea*, and with one suggested as a probable hybrid) and clearly demonstrated that they fall into two distinct groups, which are referred to below as the *A. cuspidata* and the *A. woodwardioides* groups.

The South American species with imparapinnate lamina apices, ovate to elliptic pinnae (width/length quotient (0.23–)0.27–0.31), and sphaeropteroid indusia include *Alsophila cuspidata*, *A. sternbergii*, *A. erinacea*, *A. incana*, *A. imrayana*, and *A. firma* and are hereafter referred to as the *A. cuspidata* group. This appears to be related to the *A. serratifolia* group of Madagascar, which includes *A. serratifolia* (Baker) Tryon, *A. marattioides* (Kaulf.) Tryon, *A. perrieriana* (C. Chr.) Tryon, and *A. tsilotsilensis* (Tardieu-Blot) Tryon (all as species of *Cyathea*) (Tardieu-Blot, 1951) and is characterized by the imparapinnate lamina apex, a similar pinna size and shape, and (usually) a sphaeropteroid indusium. In the *A. cuspidata* group the lamina is slightly more complex (bipinnate-pinnatifid) and the petioles and stems are armed with conspicuous squamate spines, whereas in the *A. serratifolia* group the lamina is bipinnate and the spines are inconspicuous or absent.

The Greater Antillean species with a gradually tapering lamina apex, long, narrow pinnae (width/length quotient 0.12–0.17(–0.24)), and pinnate-pinnatifid to bipinnate lamina dissection (including *Alsophila minor*, *A. bryophila*, *A. hotteana*, *A. aminatae*, *A. abbottii*, *A. nockii*, *A. brooksii*, and *A. urbani*) are hereafter referred to as the *A. minor* group. Holttum (1981) comments that these Antillean species appear to be related to the group of African and Mad-

agascan species (here referred to as the *A. decrescens* group) with a similar lamina apex, pinna shape, and lamina dissection. African species include *A. mossambicensis* (Baker) Tryon, *A. camerooniana* (Hooker) Tryon, and *A. welwitschii* (Hooker) Tryon (all as species of *Cyathea*). Madagascan species with these characters, too numerous to list in their entirety, include *A. madagascarica* Bonap., *A. approximata* (Bonap.) Tryon, *A. zakamenensis* (Tardieu-Blot) Tryon, and *A. decrescens* (Kuhn) Tryon (Tardieu-Blot, 1951; all as species of *Cyathea*). In the *A. minor* group the cyatheoid indusium is predominant, whereas in the *A. decrescens* group the sphaeropteroid indusium is more common among Madagascan species. Both the *A. minor* and the *A. decrescens* groups include several species with aphlebioid to subaphlebioid basal pinnae; *A. urbanii* and *A. zakamenensis* are notably similar in this respect.

Once established, the South American element may have diversified to some extent, forming some or most of the species in the *Alsophila cuspidata* group. The sequence of species from southeastern Brazil north through the Andes to Mexico suggests that a process such as evolutionary migration (Tryon, 1971a, 1971b) may have been involved in forming this species group. Similarly, the Greater Antillean immigrant may have undergone some adaptive radiation, as frequently occurs in island archipelagoes, forming some or most of the species in the *A. minor* group. These geographic processes, however, are thought to account for only half to two-thirds of the species diversity within present-day American *Alsophila*. The remainder is believed to have arisen via allohomoploid speciation. Conant and Cooper-Driver (1980) have discussed the origins via allohomoploidy of *A. setosa*, *A. tryoniana*, *A. polystichoides*, *A. balanocarpa*, and *A. auneae* (as species of *Nephelea*). The six Greater Antillean species with bipinnate-pinnatifid leaf architecture, spines, a gradually tapering lamina apex, and bullate scales (*A. woodwardioides*, *A. jimeneziana*, *A. fulgens*, *A. grevilleana*, *A. portoricensis*, and *A. tussacii*; hereafter referred to as the *A. woodwardioides* group) are interesting to consider in relation to the allohomoploid pathway. Gastony (1973) viewed them as perhaps being derived via divergent geographic speciation from an ancestral plexus similar to the spiny, pinnate-pinnatifid *A. auneae* and *A. balanocarpa* (as *Nephelea pubescens* and *N. balanocarpa*), which presumably were related to the *A. minor* group. *Alsophila tryoniana*, the only spiny continental species with bipinnate-pinnatifid leaf architecture, a gradually tapering lamina apex, and bullate scales, was interpreted as being related to the Antillean *A. woodwardioides* group, and as perhaps being intermediate between the Antillean and the continental *A. cuspidata* groups. Conant and Cooper-Driver (1980) have proposed a different origin for *A. tryoniana* (as *Nephelea tryoniana*), suggesting that the gradually tapering lamina apex and the bullate scales were inherited from *A. salvinii* via allohomoploid speciation.

Reappraisal of the *Alsophila woodwardioides* group in view of the allohomoploid pathway results in an interpretation different from that of Gastony (1973). The numerous instances of hybridization between the *A. minor* and the *A. woodwardioides* groups (Conant, 1975, 1976; Conant & Cooper-Driver, 1980) and the extent to which they share unusual characters indicate an intimate, reticulate relationship of the groups. Characters such as the pubescent indusium

in *A. minor*, *A. brooksii*, and *A. portoricensis*, the bicolorous, lanceolate laminar scales with a single apical seta in *A. abbottii*, *A. amintae*, *A. nockii*, and *A. tussacii*, and the subaphlebioid basal pinnae in *A. amintae*, *A. abbottii*, *A. minor*, and *A. grevilleana* result in a reticulate pattern of species relationships. The only significant differences between the *A. minor* and the *A. woodwardioides* groups are that members of the former tend to be pinnate-pinnatifid and spineless whereas those of the latter are bipinnate-pinnatifid and spiny. The origin of the latter two characters may have been in the *A. cuspidata* group. Migration of a member of this South American group into the Greater Antilles, subsequent hybridization with a member or members of the *A. minor* group, and later allohomoploid speciation could account for the bipinnate-pinnatifid leaf architecture, the spines, and the gradually tapering lamina apex of the *A. woodwardioides* group. This would also explain the sphaeropteroid indusium in *A. fulgens* and the adventitious buds in *A. woodwardioides*, characters otherwise restricted to continental species of the *A. cuspidata* group. Following introduction of Andean characters into the Greater Antilles, allohomoploid speciation could account for all species of the *A. woodwardioides* group and for *A. auneae* and *A. balanocarpa*.

HYBRIDS

Hybrids in the genus *Alsophila* can be divided into two groups. The first comprises species of hybrid origin in which reproduction has been stabilized by allohomoploidy. Conant and Cooper-Driver (1980) have discussed the origins of *A. auneae*, *A. balanocarpa*, *A. tryoniana*, *A. polystichooides*, and *A. setosa* (as species of *Nephelea*), dealt with above in the section on Speciation. Holttun (1981) also suggests that *A. setosa* is the result of hybridization between *A. capensis* and *A. sternbergii* (all as species of *Cyathea*).

The second group consists of hybrids that are not reproductively stable or are too poorly known to be admitted to specific status. Diagnoses of these follow the enumeration of species in the Systematic Treatment. Comments below pertain to this latter group.

The detection of hybrids has been facilitated by the presence of certain morphological markers. Lamina dissection, pinna shape, and presence of squamate spines have been particularly useful. In the Greater Antilles six species (the *Alsophila woodwardioides* group) have bipinnate-pinnatifid laminae, ovate to elliptic pinnae (width/length quotient 0.29 or more), and long, squamate spines. Eight species (the *A. minor* group) have pinnate-pinnatifid to bipinnate laminae, long, narrow pinnae (width/length quotient 0.17 or less, except 0.24 or less in *A. urbanii*) and are without spines. Crosses between the two groups can be recognized in the field by the combination of a bipinnate-lobed to bipinnate-pinnatifid lamina dissection with a longer and narrower (width/length quotient 0.17–0.29) pinna shape than is normally encountered in the more complex leaves. Plants with this intermediate lamina also usually have short spines, an intermediate condition in a cross between long-spined and spineless species. Crosses within groups are difficult to recognize and have been detected only by intensive field or herbarium study.

Field observations have been made on six of the nine hybrids listed at the end of the Systematic Treatment. All were growing in or near ecologically disturbed areas. In some cases the disturbances were due to the activities of man, such as road building or the clearing of land for agricultural purposes. Three of the hybrids were found along the upper reaches of streams remote from any disturbance by man, and two were encountered numerous times in apparently virgin cloud forest. Small landslips are common along stream banks and in the water-soaked soil of the cloud forest; such disturbances provide places where natural hybridizations can occur.

It is difficult to determine whether the hybrid plants encountered in the field are F_1 or later-generation hybrids. Some tend to be rare and intermediate in morphology, suggesting they are the first generation. Others are very close to one parent or the other, indicating either a backcross or F_2 segregate origin. Conant and Cooper-Driver (1980) have demonstrated that *Alsophila amin-tae* \times *A. portoricensis* (as *A. dryopteroides* \times *Nephelea portoricensis*) is more abundant than either of its parents in one population and appears to be re-producing itself. These later-generation plants are morphologically uniform (see fig. 2 in Conant & Cooper-Driver, 1980), suggesting that this hybrid may be an incipient allohomoploid species. Recognition at specific rank, however, will await laboratory analysis of its reproductive stability.

HERBARIA

In addition to the herbaria listed in Lanjouw and Stafleu (1964) and cited by the recommended abbreviations, the following are also mentioned: herbarium of the El Verde Field Station of the Center for Energy and Environmental Research, Río Piedras, Puerto Rico (Herb. EVFS), and the herbarium of the Jardín Botánico Rafael M. Moscoso, in Santo Domingo, Dominican Republic (Herb. JBRMM).

SYSTEMATIC TREATMENT

Alsophila R. Br. Prodr. Fl. Novae Holland. 158. 1810. TYPE: *Alsophila australis* R. Br.

Gymnosphaera Blume, Enum. Pl. Javae, 242. 1828. TYPE: *Gymnosphaera glabra* Blume = *Alsophila glabra* (Blume) Hooker.

Amphicosmia Gardner, London J. Bot. 1: 441. 1842. LECTOTYPE: *Amphicosmia riparia* (Willd.) Gardner (*Cyathea riparia* Willd.) = *Alsophila capensis* (L. f.) J. Sm. (for lectotypification, see R. M. Tryon, Contr. Gray Herb. 200: 25. 1970.)

Dichorexia Presl, Gefäßbündel Stipes der Farnn, 36. 1847 (preprint from Abhandl. Königl. Böhm. Ges. Wiss. V. 5: 344. 1848). TYPE: *Dichorexia latebrosa* (Hooker) Presl = *Alsophila latebrosa* Hooker.

Thysanobotrya Alderw. Bull. Jard. Bot. Buitenzorg, II. 28: 66. 1918. TYPE: *Thysanobotrya arfakensis* (Gepp) Alderw. (*Polybotrya arfakensis* Gepp) = *Alsophila biformis* Rosenstock.

Nephelea Tryon, Contr. Gray Herb. 200: 37. 1970. TYPE: *Nephelea polystichoides* (Christ) Tryon = *Alsophila polystichoides* Christ.

Stem prostrate, decumbent, or erect, to 15 m tall and 15 cm in diameter (excluding adventitious roots), with or without squaminate spines. Leaves to 4.4 by 1.6 m, exstipitate to long-petiolate; petiole brown to black, smooth to tuberculate or with squaminate spines, the base with uniformly tan to bicolorous, deltoid to lanceolate, marginate scales (these fleshy in 1 species) having single (usually dark) apical seta or both apical and marginal setae, with or without aphlebiae or subaphlebioid basal pinnae, occasionally with gap between basal aphlebiae, subaphlebioid basal pinnae, or basal pinnae and next higher pinna pair; lamina pinnate-pinnatifid to rarely quadripinnate, the base gradually tapering or abruptly narrowed, the apex gradually tapering and acute to acuminate or abruptly reduced and imparipinnate, the rachis stramineous to black, invested with various combinations of trichomes, squamules, and/or scales, or glabrous; pinnae sessile to stalked, narrower to broader at base, apex blunt tipped to attenuate, the pinna-rachis with various combinations of trichomes, scales, and/or squamules, the veins free, 6 to 24 pairs, often with tiny, antrorse, golden trichomidia beneath; indusia lacking or hemiteloid, meniscoid, cyatheoid, or sphaeropteroid, glabrous or pubescent; sporangia with oblique annulus uninterrupted by stalk, usually with 16 trilete spores. (Description applies especially to American elements of genus; all variations of nondiagnostic characters of Old World species not included.)

USE OF THE KEY

The following is a key to complete and mature specimens; it includes characters of the lamina apex, middle pinnae, petiole, and basal pinnae, as well as data on size, posture, and armament of the stem, provenance, and ecology. Incomplete specimens can be identified if one has some knowledge of the geography of certain character combinations discussed above in the sections on Morphology and Speciation. Juvenile specimens may be problematic. For example, young plants of *Alsophila bryophila* and *A. minor* may have a conspicuous gap between the basal one to three pairs of pinnae or subaphlebioid pinnae and the main portion of the lamina. If the disjunct basal pinnae are reduced or lost, specimens often appear to have a long petiole, which may cause confusion at couplet 3 in the key.

The descriptions of lamina complexity apply to the mid-portions of the middle pinnae. The user should beware of specimens from the Greater Antilles that are bipinnate-lobed to bipinnate-pinnatifid and have long, narrow pinnae (width/length quotient 0.17–0.29). These may be hybrids and are discussed above in the section entitled Hybrids. They are enumerated at the end of the Systematic Treatment (nos. 31–39).

Descriptions of indument and scales apply to the abaxial surface of axes.

KEY TO SPECIES OF ALSOPHILA

1. Stem and petiole without conspicuous squaminate spines (reduced spines occasionally present in *A. brooksii*).
2. Lamina pinnate-pinnatifid to bipinnate; stem prostrate, decumbent, or erect.

3. Lamina sessile to short-petiolate, gradually narrowed at base (abruptly narrowed in *A. rupestris*).
4. *Indusia cyatheoid*.
 5. Large, erect plants; stem always more than 2.5 cm in diameter.
 6. *Indusia* glabrous; stem less than 6 cm in diameter, less than 2 m tall; scales of pinna-rachis and costule mostly without lateral setae.
 7. Pinna-rachis sparsely to moderately pubescent; basal pinnules often completely overlapping and clasping rachis; petiole and rachis tan to brown. [Hispaniola]. 3. *A. abbottii*.
 7. Pinna-rachis glabrous; basal pinnules not or only partly overlapping rachis; petiole and rachis dark purplish-brown. [Puerto Rico]. 2. *A. amintae*.
 6. *Indusia* pubescent; stem to 11 cm in diameter and 7 m tall; scales of pinna-rachis and costule with many conspicuous lateral setae. [Hispaniola, Cuba]. 6. *A. minor*.
 5. Small, prostrate plants; stem never more than 2.5 cm in diameter.
 8. Petiole and rachis black; pinna-rachis with trichomes only. [Colombia]. 9. *A. rupestris*.
 8. Petiole brown; rachis stramineous; pinna-rachis with whitish to bicolorous, lanceolate scales with single apical seta, and with trichomes and bullate scales. [Jamaica]. 1. *A. nockii*.
4. *Indusia meniscoid*.
 9. Pinna-rachis densely pubescent and with few nonsetate to setate, whitish, bullate scales; petiole and rachis purplish-brown. [Puerto Rico]. 5. *A. bryophila*.
 9. Pinna-rachis sparsely to moderately pubescent and with acaroid scales and dark, ovate scales with apical and lateral setae; petiole brown; rachis tan. [Haiti]. 4. *A. hotteana*.
3. Lamina long-petiolate, abruptly narrowed at base.
 10. Pinnules less than 5 mm wide; petiole never with aphlebiae.
 11. *Indusia* sphaeropteroid, variously rupturing at maturity, glabrous; petiole and rachis black; stem erect. [Ecuador]. . . 10. *A. paucifolia*.
 11. *Indusia* cyatheoid, intact at maturity, pubescent; petiole and rachis brown to stramineous; stem prostrate. [Puerto Rico, Hispaniola, Cuba]. 7. *A. brooksii*.
 10. Pinnules more than 5 mm wide; *indusia* cyatheoid, occasionally with 1 or 2 clefts, glabrous (occasionally slightly pubescent); petiole with or without aphlebiae at base; stem prostrate to decumbent. [Dominican Republic]. 8. *A. urbanii*.
2. Lamina bipinnate-pinnatifid to tripinnate (rarely quadripinnate); stem erect.
 12. Sorus indusiate; lamina bipinnate-pinnatifid; petiole and rachis tan to brown.
 13. *Indusia* hemitelioid; petiole with 1 to few pairs of aphlebiae at base; middle pinnae with width/length quotient ca. 0.36. [SE Brazil]. 13. *A. capensis*.
 13. *Indusia* deeply cyatheoid to sphaeropteroid; petiole without aphlebiae; middle pinnae with width/length quotient ca. 0.27. [Colombia, Venezuela]. 11. *A. engelii*.
 12. Sorus exindusiate; lamina tripinnate (rarely quadripinnate); petiole and rachis shiny black; petiole with several pairs of aphlebiae. [Mexico, Guatemala, Honduras]. 12. *A. salvinii*.
1. Stem and petiole with conspicuous squamate spines.
 14. Lamina pinnate-pinnatifid to bipinnate.
 15. Pinnules sessile and often basally auriculate; basal pinnae reduced but not

- subaphlebioid; middle pinnae with width/length quotient ca. 0.19. [Cuba].
 15. *A. balanocarpa*.
15. Pinnules adnate and without basal auricles; basal pinnae reduced and often subaphlebioid; middle pinnae with width/length quotient ca. 0.12. [Jamaica].
 14. *A. auneae*.
14. Lamina bipinnate-pinnatifid to tripinnate (rarely quadripinnate).
16. Lamina apex gradually tapering. [Greater Antilles, except *A. tryoniana*].
17. Sorus indusiate; scales and trichomes of costae and costules various.
18. Indusia meniscoid to deeply cyatheoid, glabrous or pubescent; leaf tissue papyraceous to subcoriaceous.
19. Veins and indusia glabrous.
20. Basal pinnae reduced or not, not subaphlebioid; scales and trichomes of costae various.
21. Costa usually sparsely squamose, the scales brown to blackish and with apical and lateral setae.
22. Pinna-rachis usually narrowly alate distally, the wings green; costa glabrous to sparsely pubescent; stem spines less than 5 mm long. [Hispaniola].
 17. *A. jimeneziana*.
22. Pinna-rachis not alate distally; costa pubescent, often densely so; stem spines to 15 mm long. [Jamaica, Hispaniola, Cuba].
 20. *A. woodwardioides*.
21. Costa usually densely squamose, the scales tan to bicolorous and with a single apical seta. [Jamaica].
 21. *A. tussacii*.
20. Basal pinnae often highly reduced and subaphlebioid; costa squamose to furfuraceous and with dark-setate, bullate scales; pinna-rachis usually narrowly alate distally, with wings green. [Jamaica]. 16. *A. grevilleana*.
19. Veins and indusia pubescent. [Puerto Rico].
 19. *A. portoricensis*.
18. Indusia sphaeropteroid, glabrous; leaf tissue coriaceous. [Hispaniola].
 18. *A. fulgens*.
17. Sorus exindusiate; costules sparsely pubescent and with bullate to subbullate scales. [Guatemala, Nicaragua, Honduras]. . . 23. *A. tryoniana*.
16. Lamina imparipinnate. [Mexico, Central and South America, Lesser Antilles].
23. Indusia meniscoid to sphaeropteroid; basal pinnae not subaphlebioid.
24. Lamina bipinnate-pinnatifid; indumentum of veins various; indusia various; width/length quotient of middle pinnae 0.23–0.32.
25. Veins with whitish, stellate trichomes or minute, white, stellate squamules.
26. Leaf tissue papyraceous; veins with white, stellate trichomes; petiole scales with apical setae and with or without lateral setae. [Below 1200 m alt.].
27. Veins and indusia with stellate trichomes having 3 or 4 more or less straight (sometimes dark) arms; indusia firm, brown, persistent, mostly subsphaeropteroid. [Nicaragua, Costa Rica, Panama, Colombia, French Guiana, Ecuador, Amazonian Brazil, Peru, Bolivia, Paraguay].
 26. *A. cuspidata*.
27. Veins and indusia with stellate trichomes having irregular arms; indusia firm, brown, and persistent (or

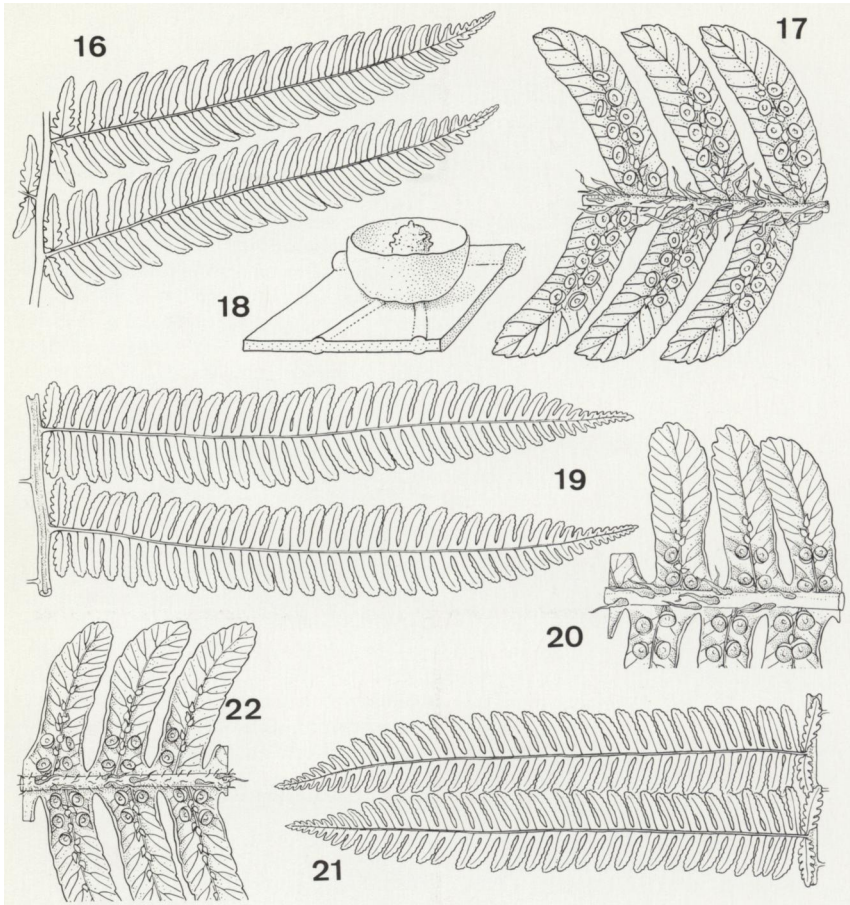
- indument of indusia and veins less conspicuous and indusia fugacious). [Brazil, Paraguay]. 27. *A. sternbergii*.
26. Leaf tissue coriaceous; veins with occasional minute, white, stellate squamules; indusia glabrous to squamulate; petiole scales with single apical seta. [700–2800 m alt.; Costa Rica, Panama, Venezuela, Colombia, Ecuador, Peru, Bolivia]. 24. *A. erinacea*.
25. Veins mostly without trichomes or with unbranched trichomes or with squamules not white or stellate.
28. Indusia subsphaeropteroid to sphaeropteroid, glabrous or with few minute squamules; petiole spines to 14 mm.
29. Petiole scales with single apical seta; basal pinnae not reduced; middle pinnae with width/length quotient ca. 0.30; pinna rachis not alate distally. [Costa Rica, Panama, Venezuela, Lesser Antilles, Colombia, Ecuador]. 25. *A. imrayana*.
29. Petiole scales with apical and numerous lateral setae; basal pinnae reduced; middle pinnae with width/length quotient ca. 0.23; pinna-rachis usually alate distally, with wings green. [Mexico, Guatemala, El Salvador, Honduras, Nicaragua, Panama, Ecuador]. 29. *A. firma*.
28. Indusia meniscoid, cyatheoid, or subsphaeropteroid, the latter type pubescent; petiole scales with single apical seta; petiole spines to 4 mm. [Colombia, Ecuador, Peru, Bolivia, Argentina]. 28. *A. incana*.
24. Lamina tripinnate (rarely quadripinnate); veins glabrous to sparsely squamulose; indusia sphaeropteroid, glabrous; width/length quotient of middle pinnae ca. 0.34. [Costa Rica, Panama]. 30. *A. polystichoides*.
23. Indusia hemiteloid; basal pinnae often subaphlebioid. [SE Brazil, Argentina]. 22. *A. setosa*.

1. *Alsophila nockii* (Jenman) Tryon, Contr. Gray Herb. 200: 29. 1970.

FIGURES 16–18.

Cyathea nockii Jenman, J. Bot. 17: 257. 1879. TYPE: Jamaica, Parish St. Andrew, Cinchona, *Nock 107* (holotype, presumably at K, not seen). POSSIBLE ISOTYPE: Jamaica, *Nock s.n.*, s.d. (us!).

Stem prostrate, to 20 cm long and 2 cm in diameter. Leaves 0.3–1.2 m by 11–26 cm; petiole 1–3 cm long, brown, base with persistent, tan to brown, often light-margined, lance-ovate to lanceolate scales with 1 apical seta; lamina pinnate-pinnatisect to bipinnate, the base gradually tapering, the apex gradually tapering, acuminate, the rachis stramineous, invested with lanceolate, flexuous, whitish to bicolorous scales with 1 apical seta (occasionally few marginal setae) and many rusty-brown trichomes beneath; pinnae 5.5–13.5 by 1–2.4 cm, sessile, conspicuously broader at base, gradually tapering at apex, adjacent ones widely spaced, the pinna-rachis with few stiff, brown trichomes beneath, base with lanceolate, flexuous, whitish to bicolorous scales with 1 apical seta (rarely with few marginal setae), these grading into whitish, setate, bullate scales apically; pinnules 6–15 by 2.5–3.5 mm, margin becoming slightly serrate at apex, the

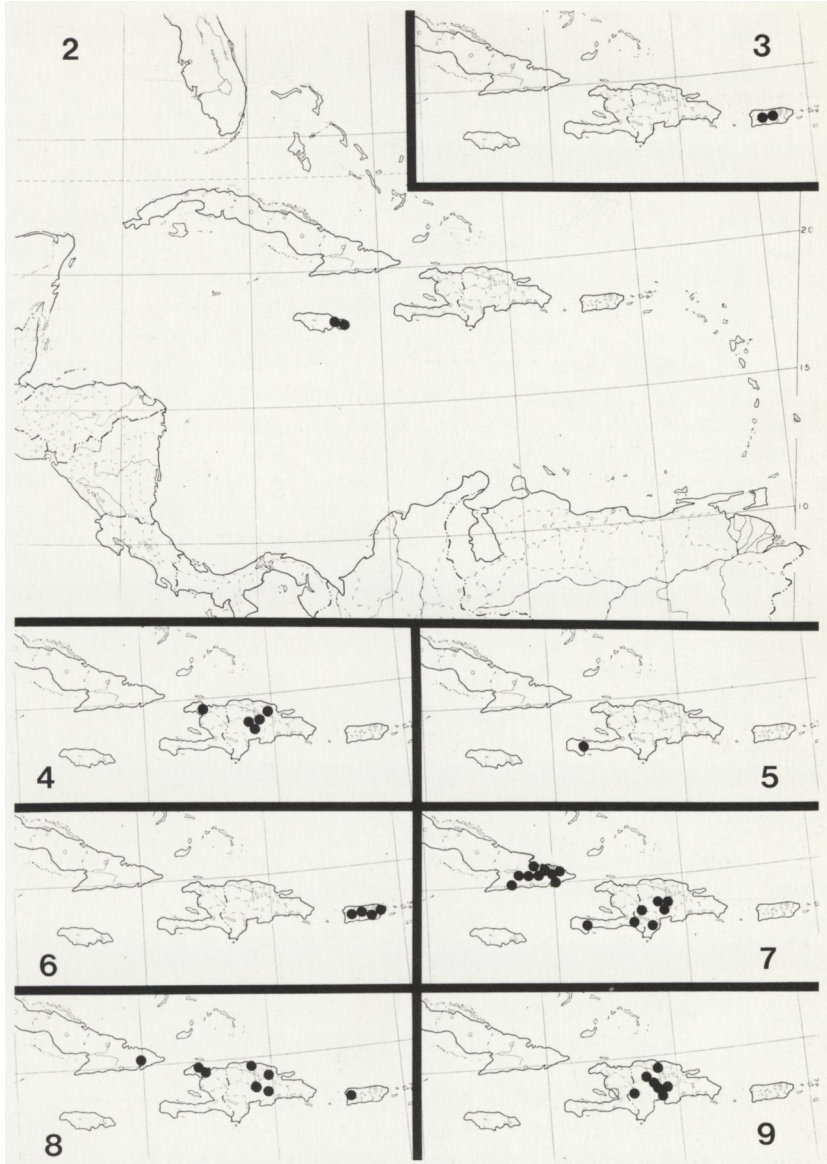


FIGURES 16–22. 16–18, *Alsophila nockii*. 16, 17, *Nock s.n.* (us 1,421,983): 16, central pinnae, $\times .5$; 17, central pinnules of central pinnae, $\times 2$. 18, *Hart 13*, indusium, $\times 15$. 19, 20, *A. amintae* (*Conant 1852*): 19, central pinnae, $\times .5$; 20, central pinnules of central pinnae, $\times 2$. 21, 22, *A. abbottii*: 21, *Conant 2118*, central pinnae, $\times .5$; 22, *Conant 2121*, central pinnules of central pinnae, $\times 2$.

basal ones much larger and more dissected, free to partially overlapping rachis, the pinnule-rachis with indument on undersurface similar to that of pinna-rachis, the veins 6 to 9 pairs, with tiny, antrorse, golden trichomidia beneath; indusia cyatheoid, glabrous.

DISTRIBUTION AND ECOLOGY. Jamaica, Blue Mountains (MAP 2). Steep, forested slopes; 910–1830 m alt.

REPRESENTATIVE SPECIMENS. **Jamaica.** No further locality: *Hart 13* (us), *Hart 2838* (mo), *Jenman s.n.*, September, 1879 (k), *Jenman s.n.*, 1874–79 (ny), *J. P. 42* (us). Blue Mountains: *Moore s.n.*, 1896 (gh). ST. THOMAS: Vinegar Hill, near Bath, *Maxon 2791* (us), *Underwood 1355* (ny). ST. ANDREW: Cinchona, *Harris 7322* (ny).



MAPS 2-9. Distribution of species of *Alsophila* in the Greater Antilles: 2, *A.nockii*; 3, *A.amintae*; 4, *A.abbottii*; 5, *A.hotteana*; 6, *A.bryophila*; 7, *A.minor*; 8, *A.brooksii*; 9, *A.urbanii*.

Alsophila nockii is the smallest and rarest species of *Alsophila* in the Greater Antilles. Jenman (1898, p. 49) reported it as "common on a limited area of the disintegrated acclivous forest near Vinegar Hill," but it has rarely been collected since then.

2. ***Alsophila amintae*** Conant, *Rhodora* **83**: 149. 1981. FIGURES 19, 20.

Cyathea dryopteroides Maxon, *Amer. Fern J.* **14**: 99. 1925. TYPE: Puerto Rico, near Adjuntas, Monte Cerrote, *Britton & Brown 5424* (holotype, US!; isotypes, GH!, MO!). *Alsophila dryopteroides* (Maxon) Tryon, *Contr. Gray Herb.* **200**: 29. 1970, not *Alsophila dryopteroides* Brause (= *Thelypteris dryopteroides* (Brause) Reed), or *Alsophila dryopteroides* Domin (= *Trichipteris dichromatolepis* (Fée) Tryon).

Stem erect, to 1.3 m tall and 5.1 cm in diameter. Leaves 0.5–1.6 m by 16–43 cm; petiole 1.3–3.5 cm long, purplish brown, the base with deciduous, golden-brown, concolorous to occasionally lighter-margined, lanceolate scales with 1 apical seta; lamina pinnate-pinnatifid, the base gradually tapering, the apex gradually tapering and acuminate, the rachis purplish brown, deciduously puberulous beneath; pinnae 8–20 by 1.3–3 cm, sessile or nearly so, broadest at base, gradually tapering at apex, adjacent ones widely spaced, lowermost reduced and subaphlebioid, the pinna-rachis with scales on undersurface bicolorous, lanceolate, with 1 apical seta; pinnules 10–17 by 2.5–5 mm, margin becoming crenate to serrate at apex, the basal ones slightly larger and more dissected, partially overlapping rachis, the pinnule-rachis with scales on undersurface of base few, tan, bullate, with or without apical setae, the veins 7 to 9 pairs, with tiny, antrorse, golden trichomidia beneath; indusia cyatheoid, glabrous.

DISTRIBUTION AND ECOLOGY. Puerto Rico, Cordillera Central (MAP 3). Shaded ravines and cloud forest; 1000–1200 m alt.

REPRESENTATIVE SPECIMENS. **Puerto Rico.** Cordillera Central: Monte Jayuya, near Cerro de Punta, ca. 65 km WSW of San Juan, *Conant 595* (GH, NY, US), *682* (GH, Herb. EVFS, Herb. JBRMM, IJ, K, NY), *683* (F, GH, NY, SV), *689* (GH, Herb. JBRMM), *Conant & Kitfield 2256* (SV), *2301* (GH), *2309* (US), *Sargent 3141* (US); Monte Guilarte, W of Adjuntas, ca. 85 km WSW of San Juan, *Conant 1700* (US), *1852* (K), *1853* (F), *1856* (NY), *1858* (GH).

The name *Alsophila amintae* appears here in its corrected form (with the epithet in the genitive); the error was kindly pointed out by K. U. Kramer (pers. comm.).

The basipetal transition from normal to subaphlebioid pinnae in *Alsophila amintae* is similar to that found in the *A. decrescens* group of Madagascar.

This species hybridizes with *Alsophila bryophila* and *A. portoricensis* on Monte Jayuya and Monte Guilarte, Puerto Rico.

3. ***Alsophila abbottii*** (Maxon) Tryon, *Contr. Gray Herb.* **200**: 29. 1970.

FIGURES 21, 22.

Cyathea abbottii Maxon, *Proc. Biol. Soc. Wash.* **37**: 98. 1924. TYPE: Dominican Republic, Prov. Duarte [Pacifcador], near San Francisco de Macoris, Loma Quita Espuela, *Abbott 2051* (holotype, US (3 sheets)!; isotypes, GH!, NY!).

Stem erect, to 1.6 m tall and 5.1 cm in diameter. Leaves 1.1–1.5 m by 30–42 cm; petiole 1.5–3.8 cm long, brown, base with deciduous, golden-brown, concolorous to occasionally lighter-margined, lanceolate scales with 1 apical seta; lamina pinnate-pinnatifid, the base gradually tapering, the apex gradually tapering, acuminate, the rachis brown, deciduously puberulous beneath; pinnae

14–21 by 2.1–3.2 cm, sessile, broadest at base, gradually tapering at apex, the adjacent ones contiguous, the lowermost ones reduced and subaphlebioid; the undersurface of pinna-rachis having stiff, erect trichomes, bicolorous, lanceolate scales with 1 apical seta, and tiny, brown squamules with or without apical setae; pinnules 10–17 by 3–4.5 mm, margin becoming serrate at apex, the basal ones much larger and more dissected, overlapping rachis, the pinnule-rachis with scales on undersurface of base rusty brown, bullate, with 1 apical seta, the veins 9 to 11 pairs, with tiny, antrorse, golden trichomidia beneath; indusia cyatheoid, glabrous.

DISTRIBUTION AND ECOLOGY. Hispaniola (MAP 4). Shaded montane rainforest; 725–1200 m alt.

REPRESENTATIVE SPECIMENS. **Haiti.** DÉP. DU NORD-OUEST: Haut-Piton, near Port de Paix, *Ekman H3728* (US). **Dominican Republic.** LA VEGA: Loma de la Campana, *Ekman H11515* (NY, US); between Bonao and El Río, *Jiménez & Marcano 3062* (US); Palo Aboqueteado, SW of Bonao, *Liogier 14806* (Herb. JBRMM); Firma de Banilejo, near Piedra Blanca, *Liogier & Liogier 19943* (Herb. JBRMM); Loma de la Sal, 25 km NE of Constanza, *Judd 1386–1389* (GH). DUARTE: Loma Quita Espuela, NE of San Francisco de Macoris, *Abbott 2145* (US), *Conant 2115* (GH), *2117* (US), *2118* (NY), *Ekman H1227* (US).

Alsophila abbottii is most closely related to *A. amintae*, of Puerto Rico. These species are similar in size and appearance, and on the undersurface of the pinna-rachis both have bicolorous, lanceolate scales with one apical seta. A relationship also exists between these species and *A. nockii* and *A. tussacii*, of Jamaica, which are the only other species of *Alsophila* in the Greater Antilles with this type of laminar scale.

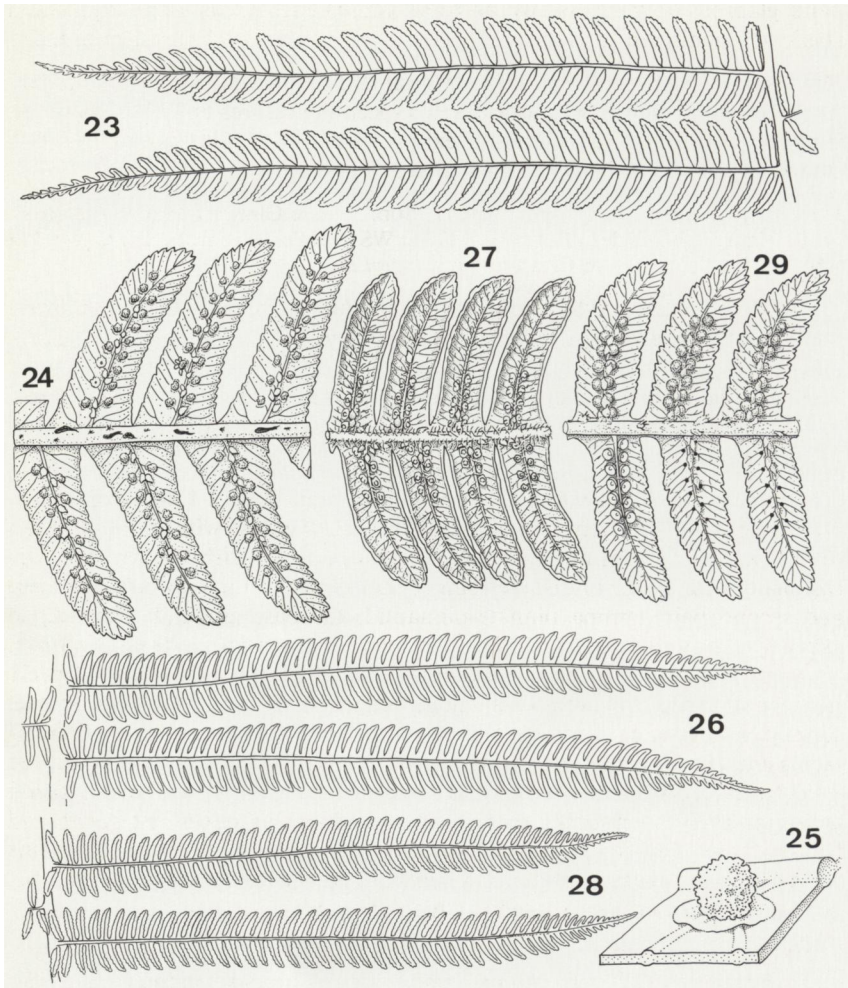
There is a gradual basipetal transition from normal to subaphlebioid pinnae in *Alsophila abbottii*—a trend similar to that found in the *A. decrescens* group of Madagascar.

Several collections from the Dominican Republic, Prov. La Vega, Loma de la Sal (e.g., *Judd 1388*) are unusual in that the pinnae are widely spaced. *Howard & Howard 8545* (A) is unusually pubescent and may represent a hybrid of *Alsophila abbottii* with *A. minor*. *Jiménez & Marcano 3062* has leaves that are more dissected than usual and may be a hybrid involving a species of *Alsophila* with more complex leaves.

4. *Alsophila hotteana* (C. Chr. & Ekman) Tryon, Contr. Gray Herb. **200**: 29. 1970. FIGURES 23–25.

Cyathea hotteana C. Chr. & Ekman, Kongl. Svenska Vetenskapsakad. Handl. III. **16**(2): 12. 1937. TYPE: Haiti, Dép. du Sud, near Camp Perrin, SE of Jérémie, Morne l'Étang, *Ekman H10383* (holotype, presumably in Herb. Ekman, Port-au-Prince, not seen; isotype, us!).

Stem erect, to ca. 2 m tall and 8 cm in diameter. Leaves ca. 2 m by 50 cm; petiole 1–4 cm long, brown, the base with deciduous, brown, lanceolate scales with 1 apical seta; lamina pinnate-pinnatifid to pinnate-pinnatisect, the base gradually tapering, the apex gradually tapering and acuminate, the rachis tan, deciduously puberulous beneath; pinnae to 24 by 3.5 cm, sessile, slightly broad-



FIGURES 23–29. 23–25, *Alsophila hotteana* (Barrington 544): 23, central pinnae, $\times .5$; 24, central pinnules from central pinna, $\times 2$; 25, indusium, $\times 15$. 26, 27, *A. bryophila* (Conant 1727): 26, central pinnae, $\times .5$; 27, central pinnules from central pinna, $\times 2$. 28, 29, *A. minor* (Gastony, G. C. Jones, & Norris 635): 28, central pinnae, $\times .5$; 29, central pinnules from central pinna, $\times 2.5$.

er at base, gradually tapering at apex, the undersurface of pinna-rachis having few trichomes apically, acaroid scales, and dark-bodied, ovate scales with 1 to few apical setae; pinnules to 17 by 4.5 mm, margin becoming serrate at apex, the basal ones only slightly larger and slightly more serrate, not overlapping rachis, the undersurface of pinnule-rachis with acaroid scales and setate, bullate scales toward base and with few stiff trichomes apically, the veins 11 to 13

pairs, glabrous or with few tiny, antrorse, golden trichomidia beneath; indusia shallowly meniscoid to meniscoid, occasionally with 1 or 2 clefts, glabrous.

DISTRIBUTION AND ECOLOGY. Haiti, Massif de la Hotte (MAP 5). Cloud forest. The label on *Ekman H5423* ascribes this species to an area at 700 m; however, it is doubtful that suitable habitat exists below 1000–1200 m today due to extensive clearing of forest for agriculture.

REPRESENTATIVE SPECIMENS. Haiti. DÉP. DU SUD: Rivière Glace, *Holdridge 2175* (NY); Pic de Macaya, Massif de la Hotte, ca. 180 km WSW of Port-au-Prince, *Barrington 544* (GH); Jardins Coutard, near Camp Perrin, *Ekman H5243* (us).

Alsophila hotteana hybridizes with *A. woodwardioides*, producing an intermediate plant known as *A. confinis* (C. Chr.) Tryon (*Cyathea confinis* C. Chr.).

5. *Alsophila bryophila* Tryon, *Rhodora* 74: 443. 1972. TYPE: Puerto Rico, Luquillo National Forest, near West Peak, *Gastony 12* (holotype, GH (4 sheets!)). FIGURES 26, 27.

Stem erect, to 7.3 m tall and 10 cm in diameter. Leaves 1.4–2.6 m by 41–58 cm; petiole 3.2–15 cm long, purplish brown, the base with deciduous, tan to brown, concolorous to bicolorous, lanceolate scales with 1 apical seta, occasionally with 1 pair of disjunct pinnae and gap of 6–15.2 cm between these and second pair; lamina pinnate-pinnatifid, the base gradually tapering to abruptly narrowed in plants with gap between basal and second pairs of pinnae, the apex gradually tapering and acuminate, the rachis purplish brown, densely invested with tan trichomes throughout; pinnae 15–31 by 1.6–3.8 cm, sessile, slightly broader at base, gradually tapering at apex, the undersurface of pinna-rachis densely pubescent, occasionally with few bullate scales at base; pinnules 7–13 by 2–3.5 mm, margin entire to serrulate at apex, the basal ones slightly larger, partially overlapping rachis, the pinnule-rachis pubescent above and beneath, base of undersurface with whitish, nonsetate, bullate scales, the veins 11 to 15 pairs, pubescent above and beneath and with abundant tiny, antrorse, golden trichomidia beneath; indusia meniscoid, glabrous.

DISTRIBUTION AND ECOLOGY. Puerto Rico; Sierra de Luquillo, Sierra de Cayey, Cordillera Central (MAP 6). An understory species in upper montane and elfin forest; 750–1200 m alt. (occasionally below 750 m in protected river valleys).

REPRESENTATIVE SPECIMENS. Puerto Rico. Sierra de Luquillo: no further locality, *Wilson 170* (NY); Pico del Este, *Conant & Kitfield 2325* (GH); Pico del Oeste, *Howard 15722*, *15725*, *16376* (A), *Howard et al. 15645* (A), *Howard & Nevling 15740*, *16004*, *16014* (A), *Schafer 3305* (GH, MO), *3632* (F, NY), *Sintenis 1480* (GH); Mount Britton, *G. N. Jones 10996*, *11009* (GH); El Yunque, *Blomquist 11942* (F), *Conant 1565* (GH), *1647* (κ), *Conant & Kitfield 2335* (GH, NY, US), *Cowles 408* (US), *Hess & Stevens 2951* (NY), *Little 21606* (GH), *Scamman 6519* (GH), *W. H. Wagner s.n.*, 14 May 1944 (GH); La Mina, *Conant 1599* (sv), *1600*, *1602* (hb); El Cacique, *Conant 1587* (GH), *1588* (us), *1589* (NY), *1591* (F); El Toro Trail, *Conant 1754* (GH), *Conant & Kitfield 2338* (κ); El Toro, *Conant 1726*, *1727* (GH). Sierra de Cayey: Cerro la Santa, *Conant 1625* (GH). Cordillera Central: Monte Jayuya, near Cerro de Punta, ca. 65 km WSW of San Juan, *Conant 688* (GH), *1811* (us), *2003* (F, Herb. EVFS, sv), *Conant & Kitfield 2253* (GH), *2255* (us), *2268* (F), *2270* (κ),

2320 (NY); Monte Guilarte, ca. 85 km WSW of San Juan, *Conant 1918* (F, K, NY, US), 1921 (GH, NY, US).

Alsophila bryophila was formerly known as *Cyathea pubescens*. The latter is *A. auneae* and is endemic to Jamaica.

This species is subject to damage by a lepidopteran larva that chews on the sori, making tunnels of a mixture of spores, sporangia, and silk on the under-surface of the leaf and undoubtedly reducing spore output.

Leaves of specimens of *Alsophila bryophila* from the Cordillera Central are more tapered at the base, have shorter petioles, and have more closely spaced pinnae than those of specimens from the Sierra de Luquillo. The few existing specimens from the Sierra de Cayey are similar to plants from the Sierra de Luquillo.

The gap occasionally found between the basal pinnae and the main portion of the lamina in *Alsophila bryophila* isolates the basal pinna-pair, a condition characteristic of the *A. dregei* group in Madagascar. *Alsophila bryophila* has the pinnate-pinnatifid leaf architecture of the *A. decrescens* group of Madagascar.

Alsophila bryophila hybridizes with *A. amintae* in the Cordillera Central, and with *A. portoricensis* in the Cordillera Central and the Sierra de Luquillo. Hybrids between *A. bryophila* and *A. portoricensis* are to be expected in the Sierra de Cayey, where the two species commonly occur together.

6. *Alsophila minor* (D. C. Eaton) Tryon, *Contr. Gray Herb.* **200**: 29. 1970.

FIGURES 28, 29.

Cyathea minor D. C. Eaton, *Mem. Amer. Acad. Arts*, n.s. **8**: 215. 1860. TYPE: Cuba, Prov. Oriente, near Guantánamo, Monte Verde, *Wright 949* (holotype, YU!; isotypes, GH!, MO (2 sheets!), US!).

Cyathea tenuis Brause in Urban, *Symb. Antill.* **7**: 155. 1911. TYPE: Cuba, Prov. Oriente, Pinal de Santa Ana, *Eggers 5171B* (holotype, not seen; isotypes, K! (photos GH!, US!), NY!).

Stem erect, to ca. 7 m tall and 11 cm in diameter. Leaves 1.7–2.5 m by 20–53 cm; petiole 1.5–13 cm long, dark- to purplish-brown, the base having deciduous, uniformly brown, lanceolate scales with 1 apical seta, occasionally having 1 to 3 pairs of disjunct, subaphlebioid pinnae and gap of 11–42 cm between these and first pair of regular pinnae; lamina pinnate-pinnatifid to pinnate-pinnatisect, the base gradually tapering to abruptly narrowed in plants with gap between basal subaphlebioid pinnae and first pair of regular pinnae, the apex gradually tapering and acuminate, the rachis brown to stramineous, deciduously puberulous to persistently pubescent, occasionally with few acaroid scales beneath; pinnae 10–27 by 1.5–3.6 cm, sessile, slightly narrower to slightly broader at base, gradually tapering at apex, the undersurface of pinna-rachis sparsely to densely pubescent and invested with subbullate, setate scales that occasionally grade into acaroid scales, with bicolorous, lanceolate scales having a single apical seta, and often with marginal setae; pinnules 8–20 by 2–5 mm, margin becoming serrate at apex, the basal ones shorter to slightly larger and more dissected, overlapping rachis, the undersurface of pinnule-rachis pubes-

cent and with whitish, setate, bullate scales, the veins 10 to 14 (rarely 16) pairs, pubescent and sometimes with tiny, antrorse, golden trichomidia beneath, glabrous (rarely with few scattered trichomes) above; indusia cyatheoid, pubescent.

DISTRIBUTION AND ECOLOGY. Hispaniola and Cuba (MAP 7). Wet montane forest; 450–2500 m alt.

REPRESENTATIVE SPECIMENS. **Cuba.** ORIENTE: *Eggers 5252* (F), *Wright 893* (GH); Cerro de la Mina, 100 km N of Santiago, *Clément 6732* (US); Sierra de Buena Vista, ca. 80 km WNW of Santiago, *Ekman 3873* (NY, US), *Shafer 4454* (NY); Sierra Maestra, Pico Turquino, ca. 100 km W of Santiago, *Acuña 6731* (NY), *Ekman 14545* (NY), *León & Ekman 11151* (NY); La Bayamesa, near Pico Turquino, *Morton 9346, 9362* (US); Sierra de Nipe, Mayarí, ca. 80 km N of Santiago, *Ekman 4041* (US), *Morton & Acuña 3193* (GH, US); Sierra del Cristal, ca. 80 km NE of Santiago, *Clément 3976* (US), *Ekman 6854* (US); Sierra de Moa, ca. 130 km NE of Santiago, *Acuña 12351* (US), *Alain 3278* (US), *Shafer 8033, 8224* (NY); Cuchillas de Toa, Finca la Prenda, ca. 10 km N of Guantánamo, *Hioram 4107*, on Dec. 29 in part (GH), on Dec. 30 in part (US), *5009* (US), *Maxon 4134* (GH, NY, US), *Shafer 4154* (NY, US). **Haiti.** DÉP. DU SUD: Torbec, Massif de la Hotte, ca. 180 km WSW of Port-au-Prince, *Ekman H5334* (s). DÉP. DE L'OUEST: Morne la Visite, Massif de la Selle, SE of Port-au-Prince, *Ekman H1440* (s). **Dominican Republic.** SAN RAFAEL-INDEPENDENCIA: Sierra de Neiba, along Carretera Internacional, *Gastony, G. C. Jones, & Norris 426, 629, 630* (GH), *631* (GH, NY), *632* (GH), *633* (GH, NY), *634* (GH), *635* (GH, NY), *636* (GH). BARAHONA: Mingo, *Fuertes 1547* (F, NY, US); Montiada Nueva, *Howard & Howard 8563* (GH), *Judd, Liogier, & Liogier 1087* (GH). AZUA: between Valle Nuevo and Azua, *G. C. Jones & Norris 1129* (NY). PERAVIA: Loma Lucia, near San José de Ocoa, *Ekman H12009* (s). LA VEGA: between Valle Nuevo and La Horma, *Conant 2047* (κ), *2049* (GH, NY, US), *Gastony, G. C. Jones, & Norris 728, 736* (GH, NY), *Judd 1223* (GH); between Constanza and Valle Nuevo, *Conant 2024* (GH, κ), *Türkheim 3115* (GH, MO, NY); Ciénaga, N of Constanza, *Liogier 17067* (Herb. JBRMM); Los Tablones, NW of Constanza, *Gastony, G. C. Jones, & Norris 321* (GH, NY); Loma de la Sal, 25 km NE of Constanza, *Judd 1390* (GH).

Alsophila minor is most closely related to *A. bryophila*, of Puerto Rico. These are the only species of *Alsophila* in the Greater Antilles known to have the unusual "droop-tip" type of leaf vernation and occasionally to have a gap between the basal 1 to 3 pairs of pinnae (or subaphlebioid pinnae) and the next higher pinna-pair. These species may also be related to *A. hotteana*, which has scales like those of *A. minor* and an indusium resembling that of *A. bryophila*, and which is similar in size and appearance to both species.

Cuban material of *Alsophila minor* generally has smaller, less aphlebioid basal pinnae and a somewhat more slender stem than specimens from Hispaniola; however, a few Cuban specimens do show moderately well developed subaphlebioid basal pinnae, and a few from Hispaniola have basal pinnae that are hardly subaphlebioid.

The undersurface of the rachis of Cuban specimens is pubescent and is generally without acaroid scales. With the exception of *Morton 9346*, material with acaroid scales on the undersurface of the rachis is usually *Alsophila balanocarpa*. The Morton specimen is not *A. balanocarpa* by virtue of its nonspiny petiole, but it may represent a hybrid between this species and *A. minor*. *Acuña 6731* is unusual in having segments that are quite pubescent above—as in *A. bryophila*.

Some collections of this species are mixed. For example, *Eggers 5252* at us is *Alsophila woodwardioides*, while *Eggers 5252* (F) is *A. minor*.

There is usually a gradual basipetal transition from pinnae to subaphlebioid pinnae in *Alsophila minor*—a trend similar to that found in the *A. decrescens* group of Madagascar.

Alsophila minor hybridizes with *A. woodwardioides*, producing an intermediate plant known as *Cyathea irregularis* Brause. A specimen (*Howard & Howard 8545*) with pinna shape and leaf texture more like those of *A. abbotii* suggests that it may also hybridize with *A. abbotii* of Montaña Nueva, Prov. Barahona, Dominican Republic. An unusual series of collections by *Gastony, G. C. Jones, & Norris* (nos. 629 to 636) from the Sierra de Neiba, between San Rafael and Independencia provinces, Dominican Republic (near the Haitian border), includes specimens with truly aphlebioid basal pinnae and with larger than usual middle pinnae. This suggests that the specimens might represent hybrids with *A. urbanii*, which was also growing in the vicinity.

7. *Alsophila brooksii* (Maxon) Tryon, Contr. Gray Herb. 200: 29. 1970.

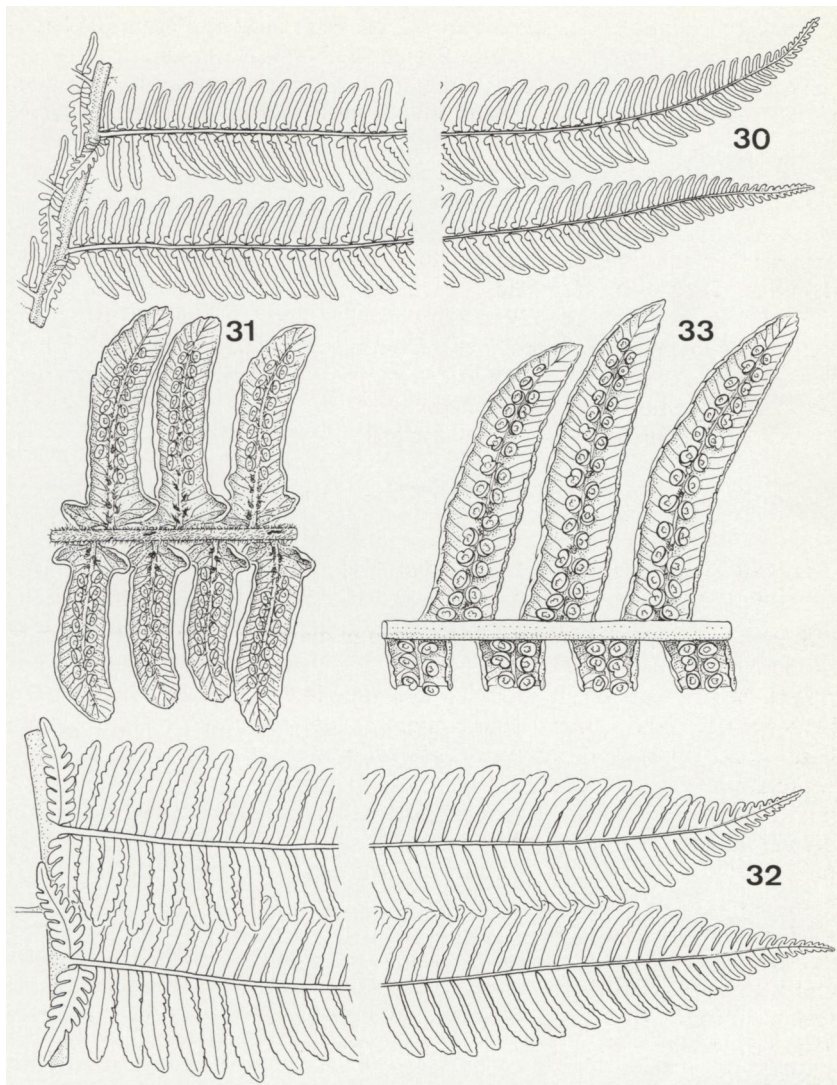
FIGURES 30, 31.

Cyathea brooksii Maxon, Contr. U.S. Natl. Herb. 13: 24. 1909. TYPE: Cuba, Prov. Oriente, Yateras, Finca las Gracias, *Maxon 4474* (holotype, US!; isotype, NY!).

Stem prostrate, to 43 cm long and 6.3 cm in diameter. Leaves 0.9–2.1 m by 24–62 cm; petiole 35–78 cm long, brown, the base having deciduous to persistent, heavily indurated, short- to long-deltoid scales with blackish body, lighter margin, and 1 apical seta; lamina pinnate-pinnatifid to bipinnate, the base abruptly narrowed, the apex gradually tapering and long-acuminate, occasionally nearly acute, the rachis brown to stramineous, pubescent beneath; pinnae 13–21 by 1.6–4 cm, sessile to short-stalked, slightly narrower to slightly broader at base, gradually tapering at apex, the undersurface of pinna-rachis pubescent and having acaroid scales and short to long, lanceolate scales with marginal and apical setae; pinnules 11–20 by 3–4 mm, margin entire to crenulate at apex, the basal ones slightly shorter to longer and more dissected, occasionally overlapping rachis, the undersurface of pinnule-rachis pubescent and with abundant acaroid scales, occasionally with dark, setate, lanceolate scales, the veins 12 to 18 pairs, undersurface with or without few trichomes, and with abundant tiny, antrorse, golden trichomidia; indusia cyatheoid, pubescent.

DISTRIBUTION AND ECOLOGY. Puerto Rico, Hispaniola, and Cuba (MAP 8). Shaded ravines along streams and forested slopes; 250–950 m alt. Usually on serpentine soils in Puerto Rico and Hispaniola, and to be expected in Cuba wherever such soils occur in wet mountains.

REPRESENTATIVE SPECIMENS. **Haiti.** DÉP. DU NORD-OUEST: Morne Baron, near St. Louis du Nord, *Ekman H3864* (US), *H3864a* (GH, NY), *H3864b* (F). DÉP. DU NORD: Morne Brigand, W of Port Margot, *Ekman H2874* (US). **Dominican Republic.** PUERTO PLATA: Pico Isabel de Torres, *Liogier, Liogier, & Melo 23490* (Herb. JBRMM). DUARTE: Loma Quita Espuela, NE of San Francisco de Macoris, *Abbott 2052, 2148* (GH, US), *2054* (US), *Conant 2141, 2142* (GH), *Ekman H12278* (US). LA VEGA: La Manaclita, 16 km S of La



FIGURES 30–33. 30, 31, *Alsophila brooksii*: 30, Conant 2142, central pinnae (22 cm long), $\times .5$; 31, Britton & Cowell 4223, central pinnules of central pinna, $\times 2$. 32, 33, *A. urbanii*: 32, Conant 2017, central pinnae, $\times .5$; 33, Gastony, G. C. Jones, & Norris 384, central pinnules from central pinna, $\times 1.5$.

Vega, Liogier 11482 (Herb. JBRMM). SAN CRISTÓBAL: Río Isabel, near Altagracia, Ekman H11195 (US). Puerto Rico. Vic. of Maricao: Britton & Cowell 4223 (F, GH, MO, NY, US), Conant 676, 677 (GH), 1656 (K), 1681 (US), 1923, 1924 (NY), Hess 182, 349 (US), 7008 (NY), Sargent 404, 636 (US).

Alsophila brooksii hybridizes with *A. portoricensis* in Puerto Rico and with *A. fulgens* in the Dominican Republic.

8. *Alsophila urbanii* (Brause) Tryon, Contr. Gray Herb. 200: 29. 1970.

FIGURES 32, 33.

Cyathea urbanii Brause in Urban, Symb. Antill. 7: 151. 1911. TYPE: Dominican Republic, Prov. La Vega, near Constanza, *Türckheim 3076* (holotype, b, photo and fragment us!).

Cyathea urbanii var. *conferta* Brause in Urban, Symb. Antill. 7: 152. 1911. TYPE: Dominican Republic, Prov. La Vega, near Constanza, *Türckheim 3076b* (holotype presumably at b, not seen; isotypes, GH!, us!).

Stem prostrate to decumbent, to 40 cm long and 6.5 cm in diameter. Leaves 1.4–3 m by 39–63 cm; petiole 14–58 cm long, stramineous, the base occasionally with aphlebiae and with deciduous, fleshy, brown, lanceolate scales, these grading into more typical dry, brown, lanceolate scales with 1 apical seta; lamina pinnate-pinnatifid to pinnate-pinnatisect, the base abruptly narrowed, the apex gradually tapering and acuminate, the rachis stramineous, deciduously invested with tiny, setate squamules; pinnae 19–33 by 4–8 cm, sessile or nearly so, broadest at base, gradually tapering at apex, undersurface of pinna-rachis with acaroid scurf, acaroid scales, and marginally setate, ovate scales; pinnules 21–40 by 5–8 mm, margin entire to crenate, the basal ones larger and more dissected, often overlapping rachis, the undersurface of pinnule-rachis with setate squamules and acaroid scales at base, and with golden squamules throughout, the veins 13 to 24 pairs, glabrous to sparsely pubescent and with abundant tiny, antrorse, golden trichomidia beneath; indusia subcyatheoid to deeply cyatheoid, occasionally with 1 or 2 clefts, sometimes slightly pubescent.

DISTRIBUTION AND ECOLOGY. Dominican Republic (MAP 9). In shaded ravines along streams at lower elevations and in cloud forest at higher altitudes; 800–2000 m alt.

REPRESENTATIVE SPECIMENS. **Dominican Republic.** AZUA: Sierra de Ocoa, N of Azua, *Ekman H11815* (us), *H11628* (s). LA VEGA: Loma Culo de Maco, SW of Constanza, *Ekman H6339* (s, us); Loma de la Sal, 25 km NE of Constanza, *Judd 1400* (A); Loma del Campanario, N of Constanza, *Conant 2014* (NY), *2015* (us), *2016* (GH), *2017* (K), *Liogier 16071* (Herb. JBRMM); Loma de la Vieja, near Constanza, *Ekman H14057* (s); La Ciénaga, N of Constanza, *Jiménez 3968, 4013* (us); Constanza, *Seifriz 5* (us); between Constanza and Valle Nuevo, *Conant 2075* (GH); between Valle Nuevo and La Horma, *Conant 2050* (GH); along road from Bonao to Constanza, *Lavastre 2016* (NY), *2041* (A); Palo Aboqueteado, SW of Bonao, *Liogier 14807* (Herb. JBRMM). SAN RAFAEL-INDEPENDENCIA: Sierra de Neiba, along Carretera Internacional, *Gastony, G. C. Jones, & Norris 577* (GH, NY). SANTIAGO: Pico Diego de Ocampo, N of Santiago, *Conant 2102* (GH), *2103* (us), *2104* (K), *Ekman H13211* (NY), *Jiménez 4551* (us), *Judd 1521, 1523, 1524* (GH). SANTIAGO-SAN JUAN: *Gastony, G. C. Jones, & Norris 384* (GH, NY).

The relationship of *Alsophila urbanii* to other species of *Alsophila* in the Greater Antilles is not clear. The prostrate stem and long petiole suggest a link with *A. brooksii*, while its aphlebiae may indicate a relation to *A. minor*. The closest relative of *A. urbanii* appears to be *A. zakamenensis*, of Madagascar, which has similarly large pinnules and well-developed aphlebiae.

There is nothing distinctive about Brause's var. *conferta*. With more material now available, it is clear that both original collections (*Türckheim 3076* and *3076b*) fit well within the normal variation of the species.

This species may hybridize with *Alsophila minor* in the Sierra de Neiba, between Prov. San Rafael and Prov. Independencia near the Haitian border.

9. ***Alsophila rupestris*** (Maxon) Gastony & Tryon, Amer. J. Bot. **63**: 743. 1976. FIGURES 34, 35.

Cyathea rupestris Maxon, J. Arnold Arbor. **27**: 438. 1946. TYPE: Colombia, Dept. Norte de Santander, region of Sarare, between Junín and Córdoba, Río Margua, *Cuatrecasas 13396* (holotype, us!; isotypes, f!, us!).

Stem presumably erect, length unknown, to 1.5 cm in diameter. Leaves 41–47 by 10–11.5 cm; petiole 4–6 cm long, black, the base with persistent, heavily indurated, deltoid scales with blackish body, lighter margin, and 1 apical seta; lamina pinnate-pinnatifid, the base abruptly narrowed, the apex gradually tapering and long-acute, the rachis black, glabrous toward base, pubescent with stiff, brown trichomes toward apex; pinnae 5–5.8 by 1.2–1.3 cm, sessile, slightly narrower to equal at base, tapering to rather blunt tip at apex, undersurface of pinna-rachis with stiff, brown trichomes; pinnules 6–7 by 3 mm, margin entire, the basal ones equal to or slightly smaller than middle ones, the inferior basal ones with auricle overlapping rachis, the indument on undersurface of pinnule-rachis similar to that of pinna-rachis, the veins 5 to 7 pairs, with tiny, antrorse, golden trichomidia beneath; indusia cyatheoid, glabrous.

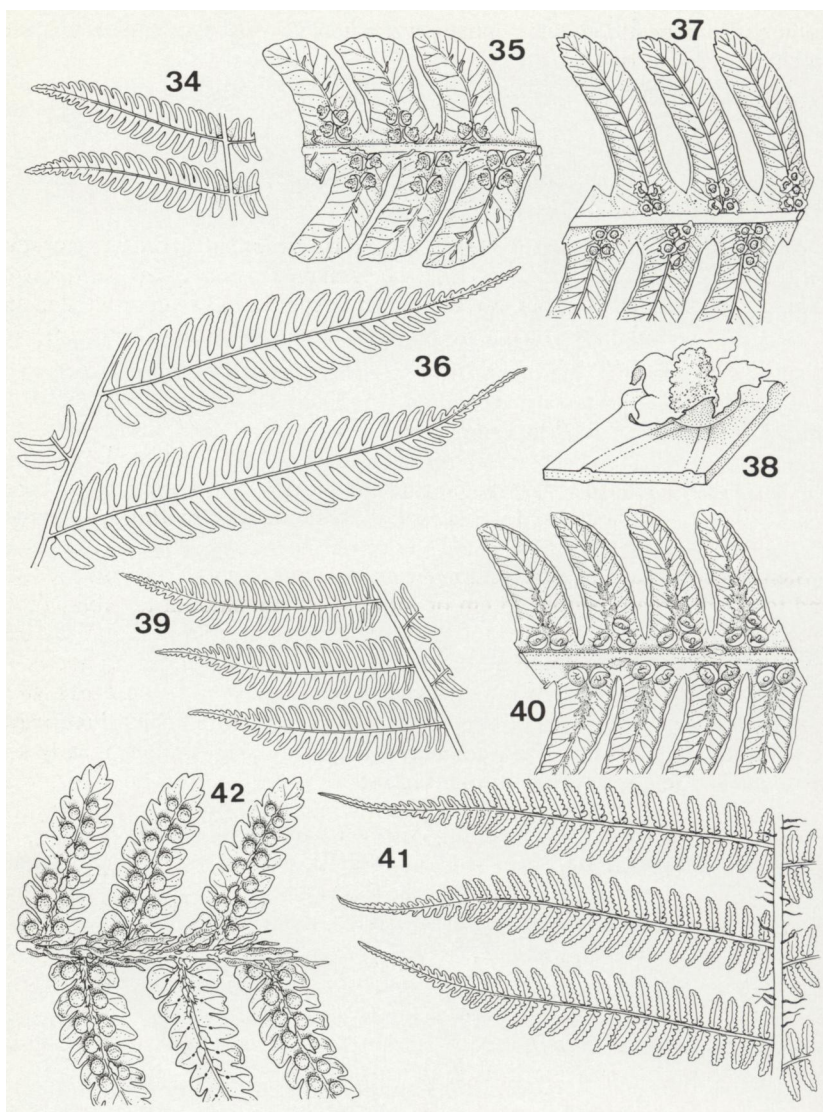
DISTRIBUTION AND ECOLOGY. Colombia, Dept. Norte de Santander, Río Margua, near Sarare (MAP 10). Known only from the type collection, 920–1240 m alt.

Alsophila rupestris is the smallest species of American *Alsophila*. Although it is similar in leaf architecture to species in the Greater Antilles, it does not have the laminar scales present in all of those species.

10. ***Alsophila paucifolia*** Baker in Hooker & Baker, Synopsis Fil. ed. 2. 546. 1874. TYPE: Ecuador, Montana de Canelos, *Spruce s.n.*, Oct. 1857 (holotype, κ!, US (fragment)!). POSSIBLE ISOTYPES: Ecuador, *Spruce s.n.*, 1857–59 (κ!); Ecuador, Canelos, *Spruce 5363* (P!). FIGURES 36–38.

Cyathea stübelii Hieron. Hedwigia **45**: 229. t. 12, fig. 2. 1906. TYPE: Ecuador, Prov. Tungurahua, between Baños and Jívaría de Pintuc, in valley of Río Pastaza, *Stübel 1007* (holotype, v!, photo GH!).

Stem erect, length unknown, to 1.8 cm in diameter. Leaves to ca. 1.5 m by ca. 40 cm; petiole 12–25 cm long, black, the base with persistent, heavily indurated, lanceolate scales with blackish body, lighter margin, and 1 apical seta; lamina pinnate-pinnatifid, the base abruptly narrowed, the apex gradually tapering and long-acuminate, the rachis black, glabrous; pinnae 15–18.5 by 2.9–4 cm, sessile, slightly narrower to equal at base, tapering to long-attenuate tip at apex, base of undersurface of pinna-rachis sparsely scurfy and with few deciduous, dark, indurated, deltoid scales with 1 apical seta; pinnules 18–22 mm by 4–4.5 mm, margin becoming serrulate at apex, the basal ones equal to or smaller than middle ones, not overlapping rachis, the undersurface of pin-



FIGURES 34–42. 34, 35, *Alsophila rupestris* (Cuatrecasas 13396): 34, central pinnae, $\times .5$; 35, central pinnules from central pinna, $\times 2.5$. 36–38, *A. paucifolia* (Spruce 5363): 36, central pinnae, $\times .5$; 37, central pinnules from central pinna, $\times 2$; 38, indusium, $\times 15$. 39, 40, *A. engelii* (White 1969240): 39, central pinnules from central pinna, $\times .5$; 40, central ultimate segments from central pinnule, $\times 2.5$. 41, 42, *A. salvinii* (Williams & Molina 10730): 41, central pinnules from central pinna, $\times .5$; 42, central tertiary segments from central pinnule, $\times 2.5$.

nule-rachis sparsely scurfy, the veins 12 to 15 pairs, with tiny, antrorse, golden trichomidia beneath; indusia sphaeropteroid, variously ruptured in mature specimens, glabrous.

DISTRIBUTION AND ECOLOGY. Ecuador (MAP 11). Border of montane forest; ca. 1700 m alt.

REPRESENTATIVE SPECIMEN. **Ecuador.** PUTUMAYO: Río Mocoa between Sachamate and San Antonio, *Ewan 16695* (US).

Although the thin, sphaeropteroid indusia, rupturing at maturity, resemble those often found in *Alsophila engelii*, the closest relation of *A. paucifolia* seems to be *A. rupestris* of Colombia. Both of the latter species have unusually slender stems, black petioles and rachises, and dark, indurated scales at the apex of the stem and the base of the petiole.

11. *Alsophila engelii* Tryon, Contr. Gray Herb. 200: 29. 1970.

FIGURES 39, 40.

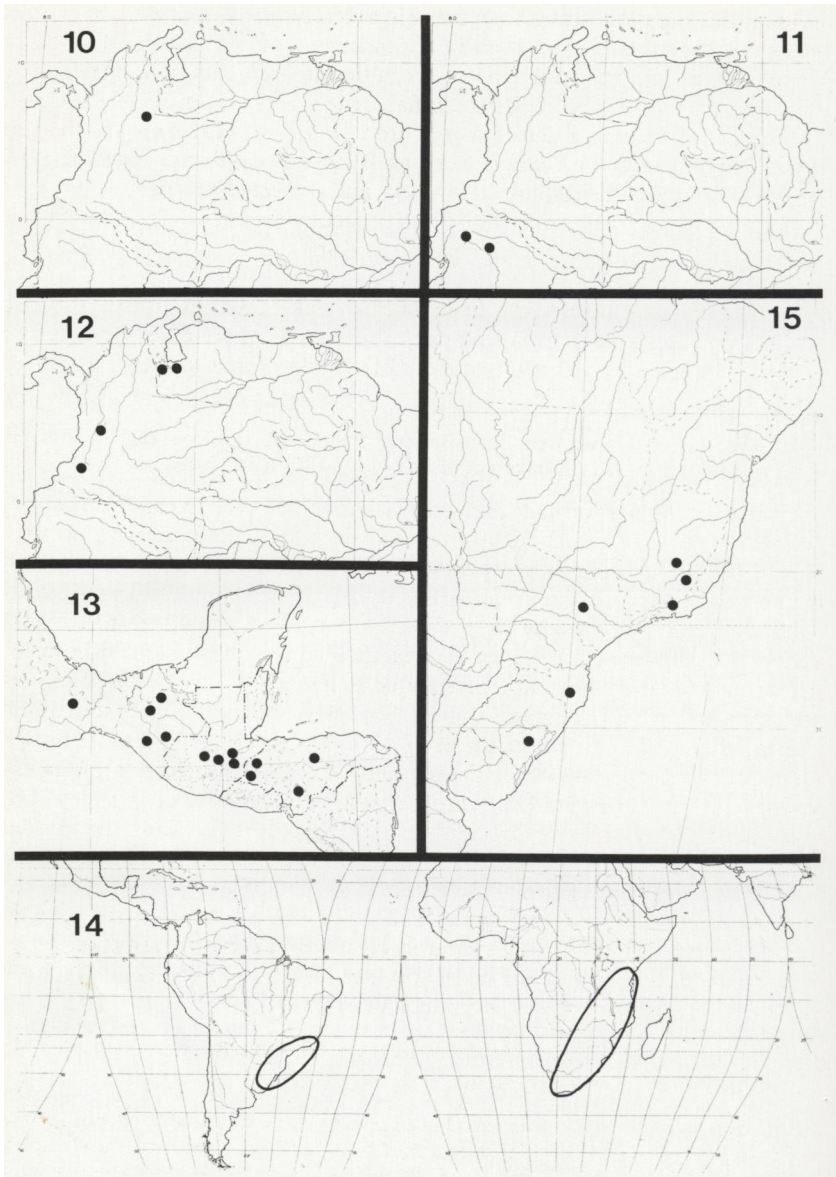
Cyathea elongata Karsten, Fl. Columb. 2: 159 (sub *Cyathea erinacea*). t. 183, figs. 15, II. 1869. TYPE: Venezuela, Mérida, *Engel 138* (holotype, v!). Not *Alsophila elongata* Hooker, Sp. Fil. 1: 43. 1844.

Stem erect, to ca. 11 m tall, diameter unknown. Leaves of unknown length and to 1.3 m broad; petiole 25 cm or more in length, smooth to tuberculate, brown, the base with deciduous, tan, lanceolate scales with 1 apical seta; lamina bipinnate-pinnatifid, the base narrowed, the apex gradually tapering and acuminate, the rachis tan to brown, undersurface deciduously invested with highly dissected, setate scales (appearing pubescent) and few tan to brown, lanceolate scales with 1 apical seta; pinnae 50–65 by 10–17.5 cm, sessile or nearly so, broadest at base, abruptly narrowing to long, slender tip at apex, undersurface of pinna-rachis with indument similar to that of rachis; pinnules 7–9.3 by 1–2 cm, pinnatifid, apex abruptly narrowed to long, slender tip, the basal ones equal to or slightly smaller than middle ones, not overlapping rachis, the undersurface of pinnule-rachis with flabellate to lanceolate, tan to brown, often partially indurated, multisetate scales and with highly dissected scales and/or trichomes; ultimate segments 6–10 by 2–3 mm, the margin becoming crenulate to serrulate at apex, the undersurface of midvein with scattered, translucent, brownish, setate, subbullate scales to densely invested with highly dissected scales, the veins 8 to 10 pairs, with whitish to tan trichomidia beneath; indusia deeply cyatheoid to sphaeropteroid, glabrous.

DISTRIBUTION AND ECOLOGY. Colombia and Venezuela (MAP 12). Mountains; 2000–2900 m alt.

REPRESENTATIVE SPECIMENS. **Colombia.** CAUCA: Cordillera Occidental, Cerro de Munchique, *Arbeláez & Cuatrecasas 6256* (US). CALDAS: Cordillera Central, Pinares, above Salento, *Pennell 9695* (GH, NY, US). **Venezuela.** MÉRIDA: *Bernardi 6198* (GH, NY); Carbonera, near Mérida, *White 1969240* (GH), *White & Lucansky 1970143* (US).

The holotype of *Alsophila engelii* (*Engel 138*) is without a petiole; however, recent collections (e.g., *Pennell 9695* and *White 1969240*) similar to that spec-



MAPS 10–15. Distribution of species of *Alsophila* in Mexico and Central and South America: 10, *A. rupestris*; 11, *A. paucifolia*; 12, *A. engelii*; 13, *A. salvinii*; 14, *A. capensis* (Old and New World distribution); 15, *A. capensis* subsp. *polypodioides*.

imen in size, dissection, and indument of the lamina have nonspiny petioles and marginate petiole scales with a single apical seta.

There is considerable variation in the indument on the undersurface of the pinnule-rachis and the midveins of the ultimate segments. Some specimens (e.g., *Pennell 9695*) have multisetate, flabellate scales and dissected scales on the pinnule-rachis and a dense investiture of dissected scales on the midvein of the ultimate segments. Others, such as *White 1969240* and *Bernardi 6198*, are sparsely invested with flabellate scales and dissected scales.

Alsophila engelii was named for Franz Engel, collector and field artist, who contributed to the plates of Cyatheaceae in Karsten's *Flora Columbiae*.

12. ***Alsophila salvinii*** Hooker in Hooker & Baker, Synopsis Fil. 36. 1866.

TYPE: Guatemala, Baja Verapaz, Chilasco, *Salvin & Goodman s.n.*, s.d. (holotype, K). POSSIBLE ISOTYPE: Guatemala, *Salvin s.n.*, s.d. (GH!).

FIGURES 41, 42.

Alsophila munchii Christ, Bull. Herb. Boissier, II. 5: 743. 1905. TYPE: Mexico, Chiapas, San Pablo, *Munch 139* (fragment of holotype, NY!; isotype, US!).

Stem erect, to ca. 9 m tall, diameter unknown. Leaves to ca. 2.5 by 1.4 m; petiole to 0.5 m or more, slightly tuberculate, black, the base with up to 15 pairs of aphyllae, densely invested with deciduous, appressed squamules and with persistent, brown, lanceolate scales having 1 apical seta; lamina tripinnate to rarely quadripinnate, the base abruptly narrowed, the apex gradually tapering and short-acuminate, the rachis black, slightly tuberculate, undersurface deciduously invested with appressed squamules; pinnae 40–77 by 15–34 cm, bipinnate to rarely tripinnate, stalked, slightly narrower at base, acuminate and tapering to long, slender tip at apex, undersurface of pinna-rachis with indument similar to that of rachis; pinnules 7.5–18 by 1.4–3.5 cm, pinnate to rarely bipinnate, apex gradually tapering to long, slender tip, the basal ones equal to or slightly smaller than middle ones, distant from rachis, the pinnule-rachis alate, undersurface with few to many dark brown, lanceolate scales having 1 to few apical setae, these grading into subbullate scales apically, and with acaroid scales; tertiary segments 7–20 by 2.5–5 mm, crenate to nearly pinnate at base, the base of undersurface of midvein with acaroid scales and with brown, setate, subbullate scales, these grading into bullate scales apically, the veins 8 to 12 pairs, glabrous; indusia lacking.

DISTRIBUTION AND ECOLOGY. Southern Mexico, Guatemala, and Honduras (MAP 13). Cloud forest; 910–2600 m alt.

REPRESENTATIVE SPECIMENS. **Mexico.** OAXACA: between Oaxaca and Tuxtepec, *Hellwig 408* (US), *Stone & Broome 2814* (GH, NY, US). CHIAPAS: Sierra de Soconusco, *Hernández & Sharp X336* (US); Cerro del Boquerón, *Purpus 6768* (US), *6769* (F, GH, NY, US); Yerba Buena Mission, *Tillet 636-4* (GH, US); between Canada Honda and Triunfo, *Xolocotzi & Sharp X336* (US). **Guatemala.** Without further locality, *Türkheim s.n.*, s.d. (NY). HUEHUETENANGO: between Xoxlac and Nucapuxlac, Sierra de los Cuchamotones, *Steyermark 48924* (F, US). EL QUICHÉ: *Aguilar 1220* (F). ALTA VERAPAZ: Chihot, *H. Johnson 959* (NY, US); near Tactic, *Stone & Stone 2706* (GH, NY); Cobán, *Türkheim 845* (GH,

NY, US), *II 2027* (F, GH, MO, NY); Sierra de las Minas, *Steyermark 42538* (F, US). ZACAPA: between Loma el Picacho and Cerro de Monos, *Steyermark 42790* (F, GH, US). **HONDURAS.** Without further locality, *Williams & Molina 10730* (F, GH, MO, US). OCOTEPEQUE: Montecristo, Cordillera de Miramundo, *Molina, Burger, & Wallenta 16749* (NY); Cordillera Merendon, 20 km NW of Ocotepeque, *Molina 22104* (NY). FRANCISCO MORAZÁN: above San Juancito, *Williams, Molina, & Merrill 15637* (F, GH, US); La Tigra, S of San Juancito, *Molina 10253* (F, NY, US), *Molina et al. 16974* (NY); Monte San Juancito, near El Rosario, *Molina 23405* (NY); Monte Uyuca, *Molina 10674, 13619* (NY), *Morton 6932, 7173* (US), *Standley 4826* (F, US), *13550* (F, NY, US), *Standley & Williams 735* (F, GH), *738* (F).

Although *Alsophila salvinii* has black axes similar to those found in *A. paucifolia* and *A. rupestris*, it seems to be most closely related to the *A. boivinii* group of aplebioid species in Madagascar and Borneo.

It appears that *Alsophila salvinii* has hybridized with *A. firma*, and that segregates of this cross have become stabilized via allohomoploidy, resulting in two distinct species: *A. tryoniana* and *A. polystichoides* (see Conant & Cooper-Driver, 1980).

13. ***Alsophila capensis*** (L. f.) J. Sm. London J. Bot. 1: 666. 1842.

Stem erect, to ca. 4.5 m tall and ca. 15 cm in diameter. Leaves of unknown length by 64 cm; petiole to 40.5 cm long, smooth to slightly tuberculate, dark brown at base, becoming lighter above, the base with 1 to few pairs of highly dissected aplebiae and with persistent to deciduous, brown, lanceolate scales having 1 apical seta; lamina bipinnate-pinnatifid, the base abruptly narrowed, the apex gradually tapering and short-acuminate, the rachis smooth to slightly tuberculate, with persistent to deciduous, brown, lanceolate scales having 1 apical seta, and occasionally with tan, appressed scurf; pinnae 24–53 by 9.5–19 cm, pinnate-pinnatifid, nearly sessile to conspicuously stalked, slightly narrower at base, acuminate to attenuate at apex, the undersurface of pinna-rachis with bullate scales, with tan to brown or dark brown, indurated, lanceolate scales having 1 apical seta, these sometimes tortuous and having light margin, and occasionally with appressed scurf; pinnules 5–11.5 by 1–2 cm, pinnatifid, sinuses between ultimate segments equilateral or inequilateral and directed toward base of pinnule, apex acuminate to attenuate, the basal ones equal to or slightly smaller than middle ones, not overlapping rachis, the undersurface of pinnule-rachis with bullate scales and with light brown or dark, indurated, lanceolate scales; ultimate segments 6–11 by 1.8–3 mm, the margin serrate, the undersurface of midvein with tan, bullate scales, sometimes also with small, dark, indurated, lanceolate scales, the veins 6 to 9 pairs, occasionally with tiny, antrorse, golden trichomidia beneath; indusia hemitelioid, glabrous.

DISTRIBUTION. Southeastern Africa and southeastern Brazil.

Alsophila capensis is the only species of Cyatheaceae to occur in both the Old and New World tropics (Holtum, 1981, as *Cyathea capensis*). Hooker (1844) and Tardieu-Blot (1941) have attributed this species to Java, but Holtum (1965) did not cite *A. capensis* as occurring there.

This species is differentiated into African and American subspecies that occupy similar latitudinal ranges in southeastern Africa and southeastern Brazil.

Key to Subspecies of *Alsophila capensis*

1. Undersurface of pinna-rachis with tan to brown, nonindurated, lanceolate scales; sinuses between ultimate segments of pinnules inequilateral at base. 13a. subsp. *capensis*.
1. Undersurface of pinna-rachis with dark brown to blackish, indurated, lanceolate scales, these sometimes tortuous and with light margin; sinuses between ultimate segments of pinnules equilateral at base. 13b. subsp. *polypodioides*.

13a. *Alsophila capensis* subsp. *capensis*

FIGURES 43–45.

Polypodium capense L. f. Suppl. Pl. 445. 1781. *Cyathea capensis* (L. f.) J. E. Sm. Mém. Acad. Turin 5: 417. 1793. *Aspidium capense* (L. f.) Sw. Synopsis Fil. 61. 1806. *Hemitelia capensis* (L. f.) Sprengel, Syst. Veg. 4. 126. 1827, not R. Br. Prodr. 158. 1810. *Cormophyllum capense* (L. f.) Newman, Phytologist 5: 238. 1854. *Polystichum capense* (L. f.) Newman, *ibid.* TYPE: Union of South Africa, Cape of Good Hope, *Sparrmann s.n.* (LINN, not seen).

Trichomanes incisum Thunb. Pl. Capens. 173. 1800. TYPE: Union of South Africa, Cape of Good Hope, *Thunberg s.n.* (probably U, not seen).

Cyathea riparia Willd. Sp. Pl. ed. 5. 493. 1810. *Hemitelia riparia* (Willd.) Desv. Mém. Soc. Linn. Paris 6: 322. 1827. *Amphicosmia riparia* (Willd.) Gardner, London J. Bot. 5: 438. 1842. TYPE: Union of South Africa, Cape of Good Hope, *Herb. Willd. 20172* (B, not seen).

Trichomanes cormophyllum Kaulf. Enum. Fil. 266. 1824. TYPE: Union of South Africa, Cape of Good Hope, *Chamisso s.n.* (probably at LE, not seen).

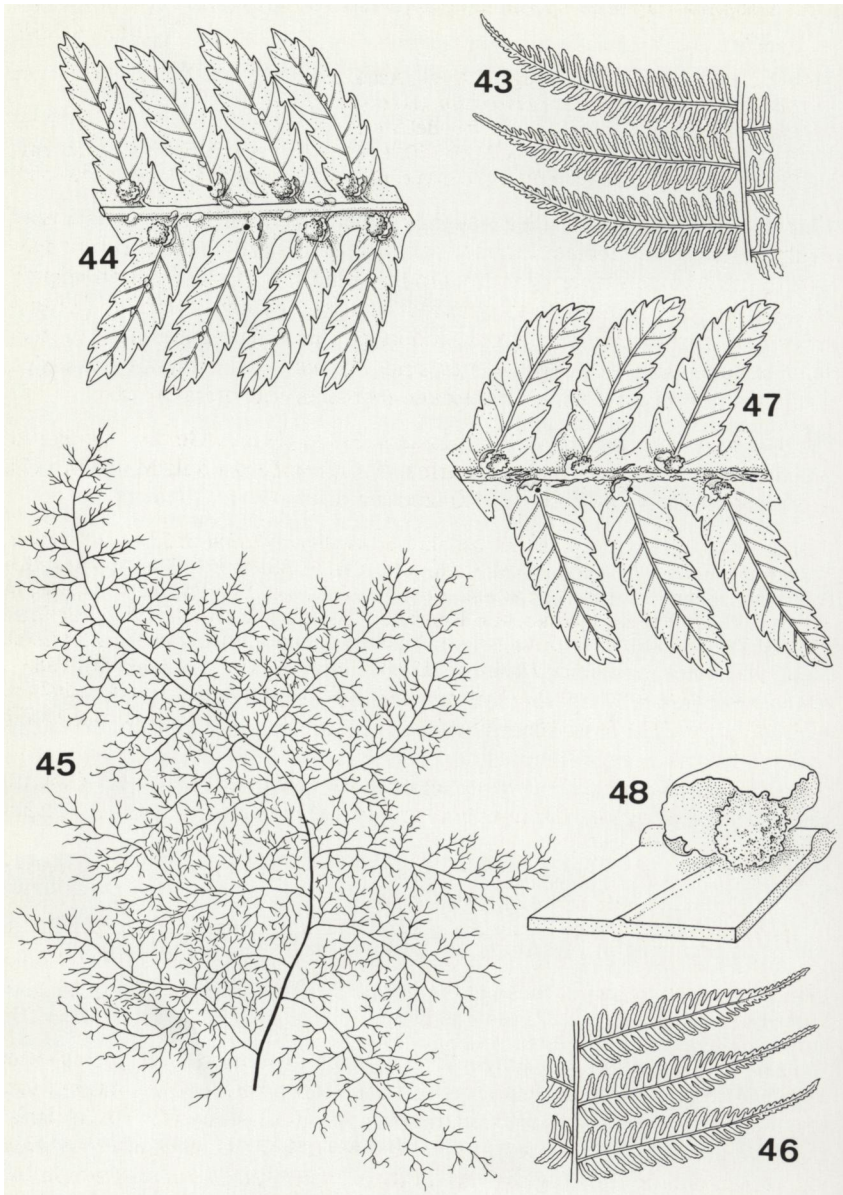
Stem erect. Petiole smooth to slightly tuberculate, with 1 to few pairs of highly dissected aphlebiae; lamina bipinnate-pinnatifid, base abruptly narrowed, apex gradually tapering and short-acuminate; pinnae pinnate-pinnatifid, slightly narrower at base, acuminate at apex, the undersurface of pinna-rachis with tan to brown, nonindurated, lanceolate scales with 1 apical seta; pinnules pinnatifid, sinuses between ultimate segments inequilateral and directed toward base of pinnules.

DISTRIBUTION AND ECOLOGY. Tanzania, Malawi, Zimbabwe, South Africa, and Swaziland (MAP 14). Shaded forests and along rivers, especially near waterfalls; 360–1820 m alt. Holttum (1981) reports *Alsophila capensis* (as *Cyathea capensis*) as occurring in Mozambique; however, he does not cite a specimen.

REPRESENTATIVE SPECIMENS. **Tanzania:** no further locality, *Peter 28018* (US). **Malawi:** Lucheny, *Brass 16600* (US). **Zimbabwe:** Inganga, *Chase 5671* (GH). **South Africa.** No further locality: *Burchell 5862* (GH), *Rogers 17502* (US), *Sim et al. 1573* (GH). NATAL: *Abraham 38* (GH, US), *Buchanan 519* (US), *Fisher & Schweickerdt 48* (US), *Rudatis 1551* (US), *Tidmarsh 2* (GH). CAPE OF GOOD HOPE: *Allen 3553* (US), *Cummings 315* (GH, US), *Dummer 1Dt* (GH), *Flanagan 1531* (US), *Kennedy 1853* (GH), *Rodin 1190* (US), *J. Smith 10* (GH), *Tryon & Tryon 6347, 6381* (GH). **Swaziland:** no further locality, *Schelppe 6181* (US).

Although I have not seen the type of *Polypodium capense*, it is undoubtedly *Alsophila capensis* since this is the only tree fern known to occur on the Cape of Good Hope (Adamson & Slater, 1950).

There is little known about the dimensions of leaves of *Alsophila capensis*; however, Sim (1891, p. 21) described a plant with fronds "six to nine feet long and two to three feet broad."



FIGURES 43–48. 43–45, *Alsophila capensis* subsp. *capensis*. 43, 44, *Tidmarsh* 2: 43, central pinnae from central pinna, $\times .5$; 44, central ultimate segments from central pinnule, $\times 3$. 45, *Fisher & Schweickerdt* 48, *aphlebia*, $\times .33$. 46–48, *A. capensis* subsp. *polypodioides*. 46, *Gardner* 5954, central pinnae from central pinna, $\times .5$. 47, 48, *Brade* 16527: 47, central ultimate segments from central pinnule, $\times 3$; 48, indusium, $\times 15$.

13b. *Alsophila capensis* subsp. *polypodioides* (Sw.) Conant, comb. et stat. nov. FIGURES 46–48.

Cyathea polypodioides Sw. Kongl. Vetensk. Acad. Handl. 78. 1817. TYPE: Brazil, Est. Minas Gerais, Villa Rica, *Freyreis s.n.* (holotype, s!).

Hemitelia gardneriana Presl, Gefässbündel Stipes der Farnn, 42. 1847 (preprint from Abh. Königl. Böhm. Ges. Wiss. V. 5: 350. 1848). TYPE: Brazil, Est. Rio de Janeiro, Serra dos Órgãos, *Gardner 5954* (holotype, not located; isotypes, pl, usl, photo GH!).

Stem erect. Petiole smooth to slightly tuberculate, with 1 to few pairs of highly dissected aphanopodiae; lamina bipinnate-pinnatifid, base abruptly narrowed, apex gradually tapering and acuminate; pinnae pinnate-pinnatifid, slightly narrower at base, acuminate to attenuate at apex, the undersurface of pinna-rachis with dark brown to blackish, indurated, lanceolate scales, these sometimes tortuous and with light margin and 1 apical seta; pinnules pinnatifid, apex attenuate, sinuses between ultimate segments equilateral at base.

DISTRIBUTION AND ECOLOGY. Southeastern Brazil (Minas Gerais, São Paulo, Rio de Janeiro, Paraná, Santa Catarina, Rio Grande do Sul; MAPS 14, 15). Along rivers in montane forest; 900–2000 m alt.

REPRESENTATIVE SPECIMENS. **Brazil.** No further locality: *Glaziou 3583* (NY); Taimbe, *Sehnm 6327* (US). MINAS GERAIS: Serra do Caparão, *Brade 17091* (NY); Villa Rica [Ouro Preto], *Freyreis s.n.* (s); Carassa, *Vainio 33210* (GH). SÃO PAULO: Rio Castilho, *Jürgens 147* (s). RIO DE JANEIRO: Rio Roncador, Theresopolis, *Brade 9871* (NY); Serra dos Órgãos, *Brade 16527* (GH, MO, NY, US), *Glaziou 4440* (NY), *Luetzelburg 211a* (s), *18905* (NY). PARANÁ: Lucana, *Hialewstri 52* (s). SANTA CATARINA: Campo dos Padres, Bom Retiro, *Reitz 2350* (US), *L. B. Smith & Klein 7852* (US); Lages, *Sehnm 5507* (A), *L. B. Smith & Reitz 10101* (US), *Spannagel 108* (s). RIO GRANDE DO SUL: *Jürgens 270* (F, MO, US).

Holttum (1981, p. 471) uses the epithet var. *polypodioides* (Sw.) Conant. However, the suggested combination at varietal rank for the epithet *polypodioides* was never made.

In addition to the diagnostic characters in the key, subsp. *polypodioides* often has the pinnule apices more attenuated and serrated than in subsp. *capensis*.

Alsophila capensis subsp. *polypodioides* has apparently hybridized with *A. sternbergii*. Reproduction of a segregate has become stabilized via allohomoploidy (see Conant & Cooper-Driver, 1980; Holttum, 1981), resulting in *A. setosa*.

Species 14–30 include 17 of the 18 recognized by Gastony (1973; as species of *Nephelea*); full descriptions and illustrations can be found in his revision. Citations of types for new combinations are from Gastony (1973). *Nephelea concinna* has an intermediate leaf architecture similar to that of other hybrids, and its extreme morphological variability indicates that its reproduction has not become stabilized. It is listed with the other hybrids at the end of the Systematic Treatment.

14. *Alsophila auneae* Conant, nom. nov.

Cyathea pubescens Kuhn, Linnaea 36: 164. 1869. *Nephelea pubescens* (Kuhn) Tryon, Contr. Gray Herb. 200: 40. 1970, not *Alsophila pubescens* Baker in Hooker & Baker,

Synopsis Fil. ed. 2. 456 (= *Trichipteris pubescens* (Baker) Tryon). TYPE: Jamaica, collector not named but probably *Purdie* in 1843 (holotype, B; isotype, BM). This species is named for my mother, Aune Lepisto Conant. Jamaica.

15. ***Alsophila balanocarpa*** (D. C. Eaton) Conant, comb. nov.

Cyathea balanocarpa D. C. Eaton, Mem. Amer. Acad. Arts, n.s. 8: 215. 1860. *Nephelea balanocarpa* (D. C. Eaton) Tryon, Contr. Gray Herb. 200: 38. 1970. TYPE: Cuba, Oriente, 1859, 1860, *C. Wright 1063* (holotype, YU; isotypes, GH, MO, NY, US). Cuba.

16. ***Alsophila grevilleana*** (Martius) Conant, comb. nov.

Cyathea grevilleana Martius, Ic. Pl. Crypt. Brasil. 78. 1834. *Nephelea grevilleana* (Martius) Tryon, Contr. Gray Herb. 200: 40. 1970. TYPE: Jamaica, comm. *Greville* in 1832 (holotype, BR, fragment and photo BM, fragment US). Jamaica.

17. ***Alsophila jimeneziana*** Conant, nom. nov.

Cyathea crassa Maxon, Contr. U.S. Natl. Herb. 13: 40. 1909. *Nephelea crassa* (Maxon) Tryon, Contr. Gray Herb. 200: 40. 1970. TYPE: Dominican Republic, Puerto Plata, Pico de Isabel de Torres, 8 July 1887, *Eggers 2735C* (holotype, US; isotype, US). Not *Alsophila crassa* Karsten, Fl. Columb. 2: 187. t. 199. 1869. This species is named in honor of Dr. José de Jesús Jiménez, Santiago, Dominican Republic, in recognition of his contributions to botany in that country. Hispaniola.

18. ***Alsophila fulgens*** (C. Chr.) Conant, comb. nov.

Cyathea fulgens C. Chr. Kongl. Svenska Vetenskapsakad. Handl. III. 16: 14. t. 1 (figs. 9–12). 1937. *Nephelea fulgens* (C. Chr.) Gastony, Contr. Gray Herb. 203: 104. 1973. TYPE: Haiti, Dép. du Nord, St. Louis du Nord, Morne Chavaray, *Ekman H4721* (holotype, S; isotype, US). Hispaniola.

19. ***Alsophila portoricensis*** (Kuhn) Conant, comb. nov.

Cyathea portoricensis Kuhn, Linnaea 36: 163. 1869. *Nephelea portoricensis* (Kuhn) Tryon, Contr. Gray Herb. 200: 40. 1970. TYPE: Puerto Rico, *Balbis s.n.* (holotype, perhaps B; isotypes, B, fragment NY, P). Puerto Rico.

20. ***Alsophila woodwardioides*** (Kaulf.) Conant, comb. nov.

Cyathea woodwardioides Kaulf. Enum. Fil. 255. 1824. *Nephelea woodwardioides* (Kaulf.) Gastony, Contr. Gray Herb. 203: 107. 1973. TYPE: without locality or collector (holotype, LZ, presumably destroyed, fragment “ex Herb. Kaulf. fragm. origin., ohne Standortsangabe,” P). Jamaica, Hispaniola, Cuba.

21. ***Alsophila tussacii*** (Desv.) Conant, comb. nov.

Cyathea tussacii Desv. Mém. Soc. Linn. Paris 6: 323. 1827. *Nephelea tussacii* (Desv.) Tryon, Contr. Gray Herb. 200: 40. 1970. TYPE: Jamaica, *De Tussac s.n.* (holotype, P, photos GH, UC, US). Jamaica.

22. *Alsophila setosa* Kaulf. Enum. Fil. 249. 1824.

Nephelea setosa (Kaulf.) Tryon, Contr. Gray Herb. **200**: 40. 1970. TYPE: Brazil, *Chamisso s.n.* (holotype, LZ, presumably destroyed; isotype, B). Southeastern Brazil, Argentina.

23. *Alsophila tryoniana* (Gastony) Conant, comb. nov.

Nephelea tryoniana Gastony, Contr. Gray Herb. **203**: 118. 1973. *Alsophila tryonorum* Riba is *Trichipteris tryonorum* (Riba) Tryon. TYPE: Guatemala, Dept. Zacapa, Sierra de las Minas, *Steyermark 3009* (holotype, F; isotype, US). Guatemala, Nicaragua, Honduras.

24. *Alsophila erinacea* (Karsten) Conant, comb. nov.

Cyathea erinacea Karsten, *Linnaea* **28**: 453. 1857. *Nephelea erinacea* (Karsten) Tryon, Contr. Gray Herb. **200**: 40. 1970. TYPE: Venezuela, Mérida, *Karsten s.n.* (holotype, probably LE or W; isotype, B). Costa Rica, Panama, Venezuela, Colombia, Ecuador, Peru, Bolivia.

25. *Alsophila imrayana* (Hooker) Conant, comb. nov.

Cyathea imrayana Hooker, Sp. Fil. **1**: 18. t. 9, B. 1844. *Nephelea imrayana* (Hooker) Tryon, Contr. Gray Herb. **200**: 40. 1970. LECTOTYPE: Dominica, Couliaban Mt., *Imray s.n.* (holotype, K, fragments NY). Lesser Antilles, Venezuela, Ecuador, Panama, Costa Rica.

26. *Alsophila cuspidata* (Kunze) Conant, comb. nov.

Cyathea cuspidata Kunze, *Linnaea* **9**: 101. 1834. *Nephelea cuspidata* (Kunze) Tryon, Contr. Gray Herb. **200**: 40. 1970. TYPE: Peru, prov. Maynas, February 1831, *Poeppig 2286* (holotype, LZ, presumably destroyed; isotypes, B, P, NY, US). Nicaragua, Costa Rica, Panama, Colombia, French Guiana, Ecuador, Amazonian Brazil, Peru, Bolivia, Paraguay.

27. *Alsophila sternbergii* (Sternb.) Conant, comb. nov.

Cyathea sternbergii Sternb. Fl. Vorwelt **1**: 47. t. c. 1820. (Essai Monde Prim. **4**: 52. t. c. 1826.) *Nephelea sternbergii* (Sternb.) Tryon, Contr. Gray Herb. **200**: 40. 1970. TYPE: habitat in Brasiliae Capitania Goyaz ad Limoero non procul St. Izidro, *Pohl s.n.* (holotype, PRC or perhaps W; isotypes, BM, BR, PRC). Southeastern Brazil, Paraguay.

28. *Alsophila incana* (Karsten) Conant, comb. nov.

Cyathea incana Karsten, Fl. Columb. **1**: 75. t. 37. 1860. *Nephelea incana* (Karsten) Gastony, Contr. Gray Herb. **203**: 137. 1973. TYPE: Colombia, Cundinamarca, *Lindig s.n.* (authentic material (Villeta, 1900 m), LE, P). Not *Alsophila incana* Geert, Rev. Hort. Belg. Étrangère **32**: 242. 1906; **34**: 172, 179. 1908. Neither the figure facing p. 172 nor the apparent date of publication complies with Article 44 of the *International Code of Botanical Nomenclature*. Colombia, Ecuador, Peru, Bolivia, northern Argentina.

29. *Alsophila firma* (Baker) Conant, comb. nov.

Hemitelia firma Baker, J. Bot. 15: 161. 1877. TYPE: Ecuador, collected in Andes of Quito, August 1875, *Sodiro s.n.* (holotype, K; isotypes, P, US). *Cyathea mexicana* Schlect. & Cham. Linnaea 5: 616. 1830. *Nephelea mexicana* (Schlect. & Cham.) Tryon, Contr. Gray Herb. 200: 40. 1970. TYPE: Mexico, Jalapa, *Schiede s.n.* (holotype, B; isotype, BM). Not *Alsophila mexicana* Martius, Ic. Pl. Crypt. Brasil. 70. t. 45. 1834 (= *Trichipteris mexicana* (Martius) Tryon). Not *Alsophila articulata* Houlston & Moore, Gard. Mag. Bot. 3: 332. fig. 8l. 1852. Mexico, Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, Ecuador.

30. *Alsophila polystichoides* Christ, Bull. Soc. Roy. Bot. Belgique 35(Mém.): 177. 1896.

Nephelea polystichoides (Christ) Tryon, Contr. Gray Herb. 200: 40. 1970. TYPE: Costa Rica, "arborescent" pentes boisées au dessus d'Aragon, 600 m, 20 Oct. 1894, *Pittier 9017* (holotype, BR; isotypes, NY, US). Costa Rica, Panama.

HYBRIDS

The following list of hybrids is in geographic order (Puerto Rico, Hispaniola, Cuba, Jamaica). Conant (1975) made a detailed morphological study of no. 33, *Alsophila amintae* × *A. portoricensis* (as *A. dryopteroides* × *Nephelea portoricensis*) and proposed nos. 34, 36, 37, and 38 as putative hybrids. Since then, field work has supplied further evidence for the hybrid origins of nos. 34, 36, and 37 and has disclosed additional hybrids in Puerto Rico (nos. 31, 32) and the Dominican Republic (no. 35). Conant and Cooper-Driver (1980) presented morphological and chemosystematic evidence for the hybrid origins of nos. 31, 32, and 33 and provided an analysis of their population ecology and fertility.

Puerto Rico

31. *Alsophila amintae* Conant × *Alsophila bryophila* Tryon

DISTRIBUTION AND ECOLOGY. Puerto Rico (Cordillera Central, Monte Jayuya). Disturbed cloud forest; 1150 m alt. This hybrid is to be expected on Monte Guilarte, where plants of the two parent species occur together.

REPRESENTATIVE SPECIMENS. **Puerto Rico:** Cordillera Central, Monte Jayuya, near Cerro de Punta, ca. 65 km WSW of San Juan, *Conant 1964* (GH), *1966* (F, GH, IJ, K, NY, US), *Conant & Kitfield 2282* (GH).

This hybrid has a short stem, which may be quite slender (as in *Alsophila amintae*) or moderately stout (as in *A. bryophila*). It has pinnate-pinnatifid leaves (as in both parents), which are quite pubescent and are gradually narrowed at the base to one to a few pairs of subaphlebioid basal pinnae. Some plants (e.g., *Conant 1964*, *Conant & Kitfield 2282*) have coriaceous leaves similar to those of *A. bryophila*, while others (e.g., *Conant 1966*) have more herbaceous leaves as in *A. amintae*. All have abundant trichomes, a character of *A. bryophila*, and on the undersurface of the pinna-rachis all have bicolorous, lanceolate scales with a single apical seta, a character of *A. amintae*. One

collection from Monte Jayuya, *Conant & Kitfield 2281* (GH), is similar in size to plants of this hybrid, is quite pubescent, and has subaphlebioid basal pinnae, but it lacks the bicolorous, lanceolate scales with a single apical seta.

32. *Alsophila bryophila* Tryon × *Alsophila portoricensis* (Kuhn) Conant

DISTRIBUTION AND ECOLOGY. Puerto Rico (Sierra de Luquillo, Cordillera Central). Along streams and trails in cloud forest; 725–1200 m alt. This hybrid is to be expected in the Sierra de Cayey, where plants of the two parent species frequently occur together.

REPRESENTATIVE SPECIMENS. **Puerto Rico.** Sierra de Luquillo: *Conant 1562* (F, GH, HB, Herb. EVFS, Herb. JBRMM, IJ, NY, SV, US), *1650* (GH), *1652* (F), *1653* (US), *1654* (NY). Cordillera Central: Monte Jayuya, near Cerro de Punta, ca. 65 km WSW of San Juan, *Conant 1759* (GH, NY, US), *1788* (F, GH, Herb. EVFS, Herb. JBRMM, IJ, SV), *1789* (GH, NY, US), *1814* (GH, K, US), *Conant & Kitfield 2288* (GH, Herb. EVFS, Herb. JBRMM, IJ, SV); Monte Guilarte, W of Adjuntas, ca. 85 km WSW of San Juan, *Conant 1907* (GH, NY, US), *1919* (K, NY, SV, US).

Plants of this hybrid are tall and stout stemmed, as are both *Alsophila bryophila* and *A. portoricensis*, and vigorous ones may reach a height of 12 meters. The stem of the hybrid is usually quite spiny. There is a continuous gradation of leaf morphology in hybrids between these species, suggesting that extensive backcrossing and/or F₂ segregation is occurring (see Conant & Cooper-Driver, 1980). Some plants (e.g., *Conant 1698, 1711, 1774, 1780, 1840, and 1907, and Conant & Kitfield 2287 and 2294*) are close to *A. portoricensis*, while others (e.g., *Conant 1789, 1790, 1791, 1792, and 1958, and Conant & Kitfield 2323*) are quite close to *A. bryophila*. Still other plants (e.g., *Conant 1562, 1696, 1716, 1779, 1788, 1814, 1850, and 1919*) are definitely intermediate between the parent species.

In general, leaves of the hybrid tend to be longer and narrower and to have longer, narrower pinnae than leaves of *Alsophila portoricensis*. The pinnae of *A. portoricensis* have a width/length quotient of 0.31–0.48, whereas those of *A. bryophila* have a quotient between 0.09 and 0.13. Plants agreeing with the parental species in other characters and with width/length quotients between these ranges are most likely hybrids.

Other diagnostic characters of this hybrid are pubescent indusia and short spines on the petiole (both as in *Alsophila portoricensis*), and moderate to dense pubescence on the axes and veins and a “droop-tip” type of vernation (as in *A. bryophila*).

A series of juvenile plants collected on the El Toro Trail in the Sierra de Luquillo, *Conant 1742, 1744, 1746, 1747, and 1753*, undoubtedly represent natural F₂ segregates. They closely resemble juvenile plants of *Alsophila bryophila* in leaf shape and dissection, but bear spines on their petioles—a character unmistakably inherited from *A. portoricensis* (see Conant & Cooper-Driver, 1980).

33. *Alsophila amintae* Conant × *Alsophila portoricensis* (Kuhn) Conant

Alsophila dryopteroides (Maxon) Tryon × *Nephelea portoricensis* (Kuhn) Tryon, *Rhodora* 77: 442. 1975.

DISTRIBUTION AND ECOLOGY. Puerto Rico (Cordillera Central). Shaded palm forest; 1000–1200 m alt.

REPRESENTATIVE SPECIMENS. **Puerto Rico.** Cordillera Central: Monte Jayuya, near Cerro de Punta, ca. 65 km WSW of San Juan, *Conant 680* (GH, NY, US), *687* (F, GH, Herb. EVFS, IJ, NY, RPPR, US, USD), *1705* (GH, NY, US), *1954* (sv), *1960* (K), *1961* (US), *1963* (NY), *Conant & Kitfield 2259, 2260, 2316, 2321* (GH); Monte Guilarte, W of Adjuntas, ca. 85 km WSW of San Juan, *Conant 1906* (F, GH, HB), *1915* (GH, K, NY, US).

Plants of this hybrid grow to about 2 meters in height and usually have a slender stem armed with short spines; they are similar in size and overall appearance to *Alsophila amintae*. They can be distinguished from this species by several characteristics inherited from *A. portoricensis*: spiny stems and petioles, bipinnate-lobed to bipinnate-pinnatifid leaves, and presence of marginally setate, acaroid scales on the undersurface of the pinna-rachis. A few vigorous hybrid plants (e.g., *Conant 1915, 1959, 2291, and 2292*) have a rather stout stem and are unusually spiny.

In this hybrid gradation of leaf morphology is not continuous between the parental species. All plants are much more similar to *Alsophila amintae* than to *A. portoricensis*, suggesting either that backcrossing occurs only in the direction of *A. amintae* or that this hybrid has a stable reproduction and is reproducing itself. Population studies by Conant and Cooper-Driver (1980) have shown that in one area this hybrid is more abundant than its parents and appears to be forming small colonies.

34. *Alsophila brooksii* (Maxon) Tryon × *Alsophila portoricensis* (Kuhn) Conant

Alsophila brooksii (Maxon) Tryon × *Nephelea portoricensis* (Kuhn) Tryon, *Rhodora* 77: 451. 1975.

DISTRIBUTION AND ECOLOGY. Puerto Rico (vicinity of Indiera Fria, near Maricao). Shaded ravines along streams; 760–850 m alt.

REPRESENTATIVE SPECIMENS. **Puerto Rico:** Indiera Fria, near Maricao, *Britton, Cowell, & Brown 4520* (NY), *Conant 1677* (GH, Herb. EVFS, Herb. JBRMM, IJ, NY, sv, US), *Conant & Wells 3446, 3447* (GH).

The prostrate stem, long petioles, and long, narrow pinnae of this hybrid are characters of *Alsophila brooksii*, while the stoutness of the stem, the spines on the stem and petioles, and the bipinnate-pinnatifid leaves are derived from *A. portoricensis*. All collections of this plant are from the vicinity of Indiera Fria, near Maricao on the western end of Puerto Rico, where *A. brooksii* and *A. portoricensis*, the only two species of *Alsophila* in this region, commonly occur together.

Hispaniola

35. *Alsophila brooksii* (Maxon) Tryon × *Alsophila fulgens* (C. Chr.) Conant

DISTRIBUTION AND ECOLOGY. Dominican Republic (vicinity of San Francisco de Macoris). Cloud forest; 725 m alt.

REPRESENTATIVE SPECIMENS. **Dominican Republic.** PROV. DUARTE. Vicinity of San Francisco de Macorís: Los Bracitos, *Abbott 2031* (GH (in part), US); Loma Quita Espuela, *Conant 2113* (GH, Herb. EVFS, U, SV, US), *2114* (GH, Herb. JBRMM), *2140* (GH, NY).

This hybrid has a short, prostrate to decumbent stem, long petioles, and long, narrow leaves and pinnae. The dissection of the lamina varies from bipinnate-lobed to bipinnate-pinnatifid—a character that, when combined with the long narrow pinnae, is characteristic of hybrids between pinnate-pinnatifid and bipinnate-pinnatifid species. Plants of this hybrid were growing with *Alsophila brooksii* and *A. fulgens* at Loma Quita Espuela, near San Francisco de Macorís. The short, prostrate stem, long petioles, and long, narrow leaves indicate that *A. brooksii* is one parent. The complexity of the lamina of the hybrid suggests that the second parent is one of the bipinnate-pinnatifid species (*A. fulgens*, *A. jimeneziana*, or *A. woodwardioides*). Although *A. fulgens* was the only bipinnate-pinnatifid species encountered in the immediate vicinity of the hybrid plants and its characters are consistent with the requirements of the second parent, confirmation of the second parent must await further detailed morphological and chemosystematic analyses.

36. ***Alsophila minor*** (D. C. Eaton) Tryon × ***Alsophila woodwardioides*** (Kaulf.) Conant

Cyathea irregularis Brause, pro species, in Urban, Symb. Antill. 7. 155. 1911. TYPE: Dominican Republic, Prov. La Vega, prope Constanza infra Valle Nuevo, *Türkheim 3212* (holotype, B, photos GH! and US!; isotype, NY!).

DISTRIBUTION AND ECOLOGY. Dominican Republic (La Vega and Barahona provinces). Cloud forest; 1650 m alt.

REPRESENTATIVE SPECIMENS. **Dominican Republic.** LA VEGA: between Constanza and Valle Nuevo, ca. 16 km S of Constanza, *Conant 2026* (GH), *2029* (F, GH, NY), *2031* (GH, Herb. EVFS, Herb. JBRMM, U, K, NY, SV, US). BARAHONA: Montiaada Nueva, *Liogier 14251* (Herb. JBRMM).

Plants of this hybrid are tall, stout stemmed, and with adventitious buds at the base and spines on the stem and petioles; in these characters they resemble *Alsophila woodwardioides*. The leaves and pinnae, however, are longer, narrower, and less dissected than in this species and approach the shape of leaves of *A. minor*. The hybrids also have the unusual “droop-tip” type of vernation otherwise found in Hispaniola only in *A. minor*.

Several plants of this hybrid (*Conant 2026, 2029, 2031*) that were growing with *Alsophila minor* and *A. woodwardioides* at the edge of the forest (1650 m alt.; 16 km S of Constanza) are quite similar to Türkheim’s original collection.

37. ***Alsophila hotteana*** (C. Chr. & Ekman) Tryon × ***Alsophila woodwardioides*** (Kaulf.) Conant

Cyathea confinis C. Chr., pro species, Kongl. Svenska Vetenskapsakad. Handl. III. 16(2): 13. 1937. TYPE: Haiti, Dép. du Sud, near Jérémie, Massif de la Hotte, Morne l’Étang, *Ekman H10382* (holotype presumably at s, not seen; isotypes, US (2 sheets)!). *Alsophila confinis* (C. Chr.) Tryon, pro species, Contr. Gray Herb. 200: 29. 1970.

Alsophila hotteana (C. Chr. & Ekman) Tryon \times *Nephelea* sp. in Conant, *Rhodora* 77: 452.

DISTRIBUTION AND ECOLOGY. Haiti (Massif de la Hotte). Cloud forest; 1200 m alt.

REPRESENTATIVE SPECIMEN. **Haiti.** DÉP. DU SUD: Massif de la Hotte, above Sapoti, Pic Macaya, *Barrington* 545 (GH).

This hybrid has been collected only once since Ekman's original collection.

The stem of *Alsophila hotteana* \times *A. woodwardioides* is erect, grows to about 2 m tall, and is rather slender. The small spines on the stem and petioles of this hybrid are characters inherited from *A. woodwardioides*. Characters intermediate between *A. woodwardioides* and *A. hotteana* are the bipinnate-lobed leaves and the subcyatheoid indusium. This hybrid is similar to *A. hotteana* in having either no or few trichomes on the pinna- and pinnule-rachises. Leaves of this hybrid have the typical circinate vernation, as does *A. woodwardioides*. Although the vernation of *A. hotteana* is not known, it is presumably also of this type.

Cuba

38. *Alsophila balanocarpa* (D. C. Eaton) Conant \times *Alsophila woodwardioides* (Kaulf.) Conant

Nephelea balanocarpa (D. C. Eaton) Tryon \times *Nephelea woodwardioides* (Kaulf.) Gastony, *Rhodora* 77: 452. 1975.

DISTRIBUTION AND ECOLOGY. Cuba (Oriente). Presumably in cloud forest.

REPRESENTATIVE SPECIMENS. **Cuba.** ORIENTE: *León, Clément, & Roca 10533* (NY), *Hioram & Clément 6377* (US).

Like other hybrids between pinnate-pinnatifid and bipinnate-pinnatifid species, this hybrid has an intermediate lamina dissection and pinna width/length quotient. *Alsophila woodwardioides* is one parent since it is the only bipinnate-pinnatifid *Alsophila* in Cuba. Three pinnate-pinnatifid to bipinnate species of the genus (*A. brooksii*, *A. balanocarpa*, and *A. minor*) occur in Cuba, but only the latter two are common. *Alsophila balanocarpa* and *A. minor* are readily separable (even with incomplete or fragmentary specimens) due to the presence of abundant conspicuous, tiny, antrorse, golden trichomidia on the veins of *A. balanocarpa*. These trichomidia are inconspicuous or absent in *A. minor* but abundant on the veins of the hybrid, indicating that *A. balanocarpa* is probably the second parent (the veins of *A. woodwardioides* lack these trichomidia).

Jamaica

39. *Alsophila auneae* Conant \times *Alsophila tussacii* (Desv.) Conant

Cyathea arborea var. *concinna* Jenman, *J. Bot.* 19: 52. 1881. TYPE: Jamaica, 1879, *Jenman 2* (holotype, κ , not seen). *Cyathea concinna* (Jenman) Jenman, pro species, *Bull. Bot. Dept.* 26: 4. 1891. *Nephelea concinna* (Jenman) Tryon, pro. species, *Contr. Gray Herb.* 200: 38. 1970.

DISTRIBUTION AND ECOLOGY. Jamaica (Blue Mountains). Cloud forest; 1000–1700 m alt.

REPRESENTATIVE SPECIMENS. **Jamaica.** PORTLAND: *Gastony 24* (GH), *Gastony & Gastony 951* (GH), *Riba 198* (GH). PORTLAND–ST. THOMAS: *Maxon 10039* (GH).

Gastony (1973) questioned the status of *Nephelea concinna* as a species and suggested that the taxon might represent a hybrid between *Alsophila auneae* and *A. tussacii* (as species of *Nephelea*). He noted that it was similar to *A. tussacii* in its stem, croziers, and indument, and that it was separated mainly on the bases of its less complex lamina and its tendency to have reduced basal pinnae (two features attributable to *A. auneae*, which has a pinnate-pinnatifid lamina and subaphlebioid basal pinnae).

The range of lamina dissection seen in specimens of *Nephelea concinna* is similar to that in hybrids between the Puerto Rican species *Alsophila bryophila* and *A. portoricensis* (see Conant & Cooper-Driver, 1980, fig. 3, p. 1277). Gastony (1973, p. 115) noted that the spores and sporangia of *N. concinna* appeared “quite normally developed” (see also Gastony & Tryon, 1976, fig. 116, p. 756 for a scanning electron micrograph of the spore of *N. concinna*), suggesting that it is a fertile hybrid. Morphological variability is to be expected among the segregates and backcrosses of fertile F₁ hybrid plants.

DUBIOUS NAMES

Cyathea conquisita Jenman, J. Bot. 20: 324. 1882. TYPE: Jamaica, *Wilson 134* (holotype, BM!, fragment US!, photo GH!).

Cyathea pendula Jenman, *ibid.* TYPE: Jamaica, *Wilson 16* (holotype, BM!, fragment US!, photo GH!). *Cyathea conquisita* and *C. pendula* probably belong to the same taxon but are known only from single fragmentary specimens inadequate for critical determination.

Cyathea jamaicensis Jenman, *ibid.*: 323. TYPE: Jamaica, *Wilson 686* (holotype, BM, not seen, fragments NY!, US!, photo GH!; isotypes, GH!, κ!). This presumed hybrid (Conant, 1975) is known only from Wilson's type collection at Mansfield, near Bath, Jamaica. Although it is similar in leaf architecture to other hybrids between pinnate-pinnatifid and bipinnate-pinnatifid species, the single fragmentary specimen is inadequate for taxonomic determination and its parentage remains unknown.

Alsophila grevilleana Wallich, Num. List, no. 7075. 1829. Nomen nudum.

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The numbers in parentheses refer to the corresponding species and subspecies in the text. Not all exsiccatae are listed under "Representative Specimens" in the text.

- Abbott* 2031 (35, in part); 2051 (3); 2052, 2054 (7); 2145, 2148 (3).
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- Acuña* 12351 (6).
- Aguilar* 1220 (12).
- Alain* 3278 (6).
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