Monograph of the Neotropical Fern Genus *Polybotrya* (Dryopteridaceae)

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Volume 34, Article 1
November 1987

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Illinois Natural History Survey Bulletin
Volume 34, Article 1
November 1987

This work is dedicated to my parents, Livia Ann Moran and John Howard Moran.

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Illinois Natural History Survey, Lorin I. Nevling, Chief
A Division of the Illinois Department of Energy and Natural Resources

Printed by Authority of the State of Illinois
(62997—1,200—11-87)

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Citation:
Moran, R.C. 1987. Monograph of the Neotropical Fern Genus *Polybotrya* (Dryopteridaceae). Illinois Natural History Survey Bulletin 34 (1): 1–138.

US ISSN 0073-4918

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Acknowledgments

No one helped me more than the five pteridologists who carefully reviewed every page of this monograph: Dr. David B. Lellinger, Smithsonian Institution, Washington, D.C.; Dr. Alan R. Smith, University of California, Berkeley; Mr. Robert G. Stolze, Field Museum of Natural History, Chicago, Illinois; Dr. Rolla M. Tryon, Harvard University, Cambridge, Massachusetts; and Dr. Warren H. Wagner, Jr., University of Michigan, Ann Arbor. Not only did they spend long hours reading my rough manuscripts, but they also patiently answered my numerous queries about the intricacies of fern taxonomy.

My first field trip—to Costa Rica—was made on funds awarded by the Tinker Foundation. Doctoral Dissertation Improvement Grant # 83-06990 from the National Science Foundation provided most of my financial support, primarily for three additional collecting trips in Latin America and for a semester of study at Harvard University.

Two people were particularly helpful during my fieldwork in Latin America. First, Mr. Luis D. Gómez P. of the Museo Nacional de Costa Rica, San José, gave me lodging in his house and extended numerous other courtesies while I worked in Costa Rica. Second, Professor Francisco Ortega, UNELLEZ, Guanare, Venezuela, gave me the use of his herbarium and plant-drying facilities and took me on collecting trips through the Andes of western Venezuela. I thank them both for their hospitality and for sharing their knowledge of ferns.

During my semester of study at Harvard University, Dr. Alice F. Tryon was extremely helpful in showing me how to obtain high quality scanning electron microscope photographs of spores. Dr. Rolla M. Tryon helped with nomenclatural, systematic, and other matters.

I learned much about pteridophyte biology from two summer field courses with Drs. Warren H. Wagner and Florence S. Wagner, the first at Flathead Lake Biological Station, Montana, and the second at Mountain Lake Biological Field Station, Virginia. I thank them for these memorable summers.

Dr. Kenneth R. Robertson of the Illinois Natural History Survey, Champaign, was my major advisor and provided much help and encouragement. Others who served on my doctoral committee were Dr. J. Leland Crane, Illinois Natural History Survey, Champaign; Drs. Johannes M. J. de Wet, Zane B. Carothers, and Malcolm L. Sargent, University of Illinois at Urbana-Champaign; Dr. Rolla M. Tryon, Harvard University, Cambridge; and Dr. Warren H. Wagner, University of Michigan, Ann Arbor. Dr. Tom L. Phillips, University of Illinois at Urbana-Champaign, provided numerous helpful comments, especially on the Ecology and Geography sections.

I completed most of the work for this monograph in the herbarium at the Illinois Natural History Survey, and I am greatly indebted to that institution for its support and for the use of its facilities. Several biologists at the Survey helped me in various ways. Mr. John Taft and Ms. Mary Kay Solecki provided useful discussion and patiently tested my keys. Dr. David Swofford was helpful with the cladistic analysis. Mr. Bill N. McKnight was a constant friend and critic throughout the study and assisted with the reproduction of the illustrations. I am also indebted to the editorial staff at the Survey, especially Patty Duzan and Eva Steger who typeset the manuscript, Audrey Hodgins who edited it, and Molly Scott who helped with the production.

I am grateful to the directors and curators of the following herbaria for the large quantities of valuable material they made available to me, often for a considerable period of time. The abbreviations used in the text follow the names of the herbaria: Arnold Arboretum, Harvard University (A), Cambridge, Massachusetts; Herbarium Jutlandicum, University of Aarhus (AAU), Risskov, Denmark; Herbarium Amazonense, Universidad Nacional de la Amazonía Peruana (AMAZ), Iquitos, Peru; Botanischer Garten und Botanisches Museum (B), Berlin, Federal Republic of Germany; British Museum of Natural History (BM), London, England; Herbier (CAY), Cayenne Cedex, French Guiana; Herbario Nacional Colombiano, Museo de Historia Natural, Universidad Nacional (COL), Bogotá, Colombia; Herbario Nacional de Costa Rica, Museo Nacional (CR), San José, Costa Rica; John G. Searle Herbarium, Field Museum of Natural History (F), Chicago, Illinois; Conservatoire et Jardin botaniques de la Ville de Genève (G), Switzerland; Gray Herbarium, Harvard University (GH), Cambridge, Massachusetts; Rijksherbarium (L), Leiden, Netherlands; Instituto Miguel Lillo de la Fundación Miguel Lillo (LIL), Tucumán, Argentina; Facultad de Ciencias Naturales y Museo, División Plantas Vasculares, Universidad Nacional de La Plata (LP), La Plata, Argentina; Herbario Nacional de Bolivia, Universidad Mayor de San Andres (LPB), La Paz, Bolivia; Herbarium of the University of Michigan (MICH), Ann Arbor, Michigan; Missouri Botanical Garden (MO), St. Louis, Missouri; New York Botanical Garden (NY), Bronx, New York; Muséum National d'Histoire Naturelle (P), Paris, France; Academy of Natural Sciences of Philadelphia (PH), Philadelphia, Pennsylvania; Herbario Universitario, Universidad Nacional Experimental de los Llanos Occidentales "Ezequiel Zamora" (PORT), Portuguesa, Venezuela; Herbario del Instituto de Ciencias Naturales, Universidad Central (Q), Quito, Ecuador; Instituto de Ciencias, Pontificia Universidad Catolica del Ecuador (QCA), Quito, Ecuador; Jardim Botânico do Rio de Janeiro (RB), Rio de Janeiro, Brazil; Department of Botany, University of California (UC), Berkeley, California; United States National Herbarium, Smithsonian Institution (US), Washington, D.C.; Herbario San Marcos, Museo de Historia Natural, Universidad Nacional Mayor de San Marcos de Lima (USM), Lima, Peru; Instituto Botánico (VEN), Caracas, Venezuela; Pringle Herbarium, University of Vermont (VT), Burlington, Vermont; Institut für systematische Botanik der Universität Zürich (Z), Zürich, Switzerland.

This work was originally part of a dissertation submitted to the Graduate College of the University of Illinois at Urbana-Champaign in partial fulfillment of the requirements for the degree of Doctor of Philosophy in plant biology.

Monograph of the Neotropical Fern Genus *Polybotrya* (Dryopteridaceae)

Robbin C. Moran

Part One: Introduction and Discussion

The need still is for more monographic work on tropical species, which represent the great majority of all ferns.

R.E. Holttum (1982)

The genus *Polybotrya* (Dryopteridaceae) includes 35 species of neotropical ferns. It is distinguished by 1) strongly dimorphic leaves with fertile leaves that resemble skeletons of the sterile, photosynthetic ones; 2) usually high-climbing stems that are covered with scales; and 3) a unique stem anatomy with 5 to 12 circularly arranged meristeles, each surrounded by a black sclerenchymatous sheath, with numerous tiny leaf traces arching between adjacent meristeles. The center of diversity of the genus is the Andes, where 23 species occur, 12 of which are endemic. The coastal mountains of southeastern Brazil are notable because they contain 5 species, all endemic. The range of *Polybotrya* is from Chiapas, Mexico, southward through Central America; the West Indies; northern South America southward along the Andes to Bolivia and Paraguay and eastward to the Guiana Highlands; the Amazon River basin and the Matto Grosso; and southeastern Brazil. Species of the genus typically inhabit wet, shaded, primary tropical forests from sea level to 2500 m, most often occurring at middle altitudes between 500 and 2000 m.

Polybotrya is divided into three subgenera: 1) *Soromanes*, leaves simply pinnate and veins anastomosing; 2) *Sorbifolia*, leaves simply or twice pinnate and veins free, close, and parallel; and 3) *Polybotrya*, leaves decompound and veins free. *Polybotrya cervina*, a species usually included in *Polybotrya*, is removed to the monotypic genus *Olfersia* (Moran 1986). *Polybotrya* is related to dryopteroid genera such as *Arachniodes*, *Cyclodium*, *Maxonia*, *Olfersia*, and *Polystichopsis*. Carl Christensen, the father of modern fern taxonomy, observed (1916) that *Polybotrya* may have arisen from *Maxonia* because both have high-climbing stems and strongly dimorphic leaves. The morphological and anatomical evidence presented here suggests that *Polybotrya* may have evolved instead from a *Cyclodium*-like ancestor.

I chose *Polybotrya* for study because two aspects of the genus immediately intrigued me: its strongly differentiated sterile and fertile leaves and its long, creeping hemiepiphytic stem (Fig. 1). Since these features evolved separately in unrelated fern genera, studying *Polybotrya* might well provide insight into broader questions of fern evolution. *Polybotrya* was suited to monographic study because the number of species (35), all of which are neotropical, was manageable. Finally, no previous monographic work had been done on *Polybotrya* and many problems of nomenclature and identification remained to be solved.

Materials and Methods

This monograph is based on the study of about 2500 herbarium sheets, which represent approximately 800 individual collections from 30 herbaria (see acknowledgments). Unfortunately, *Polybotrya* at Kew could not be examined because their policy precludes loaning specimens for use by graduate students (G.L. Lucas, *in litt.* 1983; pers. comm.). Kew, however, did send color slides of several critical type specimens.

Figure 1. Habit sketches for two species of *Polybotrya*. Above, *P. crassirhizoma*, a climbing species; below, *P. sorbifolia*, a terrestrial species. Note that the fertile leaves are skeletonlike and that their orientation is more erect than that of the spreading sterile leaves.

I spent seven months observing and collecting 18 of the 35 species of *Polybotrya* in Costa Rica, Ecuador, Peru, and Venezuela and was able to make such important observations about the biology of the species as presence of aerophores and mucilage on stems, duration and habit of sterile versus fertile leaves, and variation within and between populations. During field work, herbarium, cytological, and anatomical materials were also collected.

Anatomical cross sections were prepared by freehand sectioning, and staining was rarely needed to determine cell types or tissue layers. Leaf segments were cleared by soaking them in 10 percent NaOH in a warm oven for 5 to 6 days. Several changes of clearing solution were usually needed to replace solution that had become darkly stained by phenolic substances. Since this procedure did not remove all the dark color from the leaf, the segments were placed in full-strength Clorox bleach from 10 to 60 minutes. This treatment usually rendered even the most stubborn leaves translucent for microscopic study.

Taxonomic History of the Genus

Polybotrya was first described by Willdenow in his fourth edition of Linnaeus's *Species Plantarum* (1810), as distinguished by "Capsules sessile, globose, aggregated in naked paniculate spikes. Nonindusiate" [my translation]. *Polybotrya osmundacea*, the sole species described in the new genus, received its specific epithet because of the fancied resemblance of its fertile leaf with the fertile leaf apex of *Osmunda regalis*. Since strongly contracted, nonindusiate fertile leaves were considered the principal feature of the new genus, other species with similar leaves were eventually placed in *Polybotrya*. Since fully differentiated fertile leaves have arisen separately along many phyletic lines, this procedure resulted in a highly unnatural, polyphyletic genus. Species placed in *Polybotrya* at one time and then excluded are represented today in as many as 12 genera (see Excluded Taxa).

Past Generic Concepts

Each of the nineteenth-century pteridologists who wrote about *Polybotrya* had a slightly different concept of the genus (Table 1). Blume (1828) placed many unrelated acrostichoid ferns, including species of *Lomagramma*, *Stenosemia*, and *Bolbitis*, in *Polybotrya*. Schott (1834–1836) later restricted *Polybotrya* to the American species allied to *P. osmundacea*. The subsequent recognition of the Asian acrostichoids as distinct from the American genus *Polybotrya* testifies to Schott's keen perception. Although Schott's classification was not immediately adopted by his colleagues, it was eventually revived by Smith (1875) and Christensen (1934).

Presl (1836) relied heavily on venation patterns and anatomical characters in defining his genera and did not accept Schott's circumscription of *Polybotrya*. He merged species of *Bolbitis* sect. *Egenolfianae* with *Polybotrya* because both had free veins, but he removed the anastomosing-veined species placed in *Polybotrya* by Blume (1828).Smith (1841) largely followed this classification in his arrangement of fern genra.

Fée (1845) was the first pteridologist to try to make sense out of the increasing number and diversity of acrostichoid ferns. He included the species related to *P. osmundacea* in his subgenus *Eupolybotrya* and created two subgenera of *Polybotrya* (see Excluded Taxa) in which he put many species now placed in *Bolbitis*, *Blechnum*, *Lomariopsis*, and *Teratophyllum*. Fée also erected the segregate genus *Soromanes* for species of *Polybotrya* with anastomosing veins and 1-pinnate leaves. In my treatment, *Soromanes* is a subgenus of *Polybotrya*.

The German pteridologist Mettenius had a wide circumscription of *Polybotrya*. He described several new species in the genus, some of which are here retained. The majority, however, have been placed in *Bolbitis*, *Elaphoglossum*, and *Leptochilus*.

Hooker (1864: 194–195) and Baker in Hooker and Baker (1874: 399ff.) subsumed both *Polybotrya* and *Soromanes* as subgenera in their large, eclectic genus *Acrostichum*, which consisted of any fern with acrostichoid sori. This decision was essentially a reversion to Swartz's (1806) concept of *Acrostichum*, and although both genera were recognized as subgenera, *Polybotrya* continued to include unrelated species that have since been placed in *Atalopteris*, *Elaphoglossum*, *Psomiocarpa*, and *Teratophyllum*. Hooker and Baker's classification was accepted by several pteridologists, especially by flora writers, until the hegemony of Hooker's concepts was supplanted by the more natural views of Smith (1875). Smith accorded generic status to *Polybotrya*, restricting it to *P. osmundacea* and its immediate allies; however, he kept *Soromanes* as a distinct genus.

Unfortunately, Smith's views were not immediately accepted by pteridologists. Christ (1897) and Diels (1899) classified many of the acrostichoids with free veins in *Polybotrya*, a decision that again resulted in an amalgamation of unrelated species. Christensen (1905) in *Index Filicum* used *Polybotrya* at the rank of genus, but it had essentially the same circumscription as it had had under Hooker. Unlike the writers cited above, he placed *Olfersia cervina* in *Polybotrya*. His classification was used by Schumann (1915) in her important work on the vascular supply in fertile leaves of acrostichoid ferns. Christensen (1934) later removed the discordant species from *Polybotrya* and placed most of them in the genera where they are found today (*Atalopteris*, *Egenolfia*, *Lomagramma*, and *Psomiocarpa*).

Copeland's *Genera Filicum* (1947) adopted Christensen's earlier (1905) concept. Pichi-Sermolli (1977) treated *Polybotrya*,

TABLE 1. Comparative treatment of *Polybotrya*.

Reference	*Polybotrya* subgenus *Soromanes**	*Polybotrya* subgenus *Sorbifolia**	*Polybotrya* subgenus *Polybotrya**	Genera formerly included in *Polybotrya*
Willdenow (1810)			*Polybotrya*	
Kaulfuss (1824)			*Polybotrya*	*Olfersia*
Blume (1828)			*Polybotrya*	*Bolbitis*, *Lommagramma*, *Stenosemia*
Schott (1834–1836)			*Polybotrya*	
Presl (1836)			*Polybotrya*	*Bolbitis*
Smith (1841)			*Polybotrya*	*Bolbitis*
Fée (1845)	*Soromanes*		*Polybotrya* subgenus *Eupolybotrya*	*Blechnum*, *Bolbitis*, *Lomariopsis*, *Teratophyllum*
Hooker (1864)	*Acrostichum* subgenus *Soromanes*	*Acrostichum* subgenus *Polybotrya*	*Acrostichum* subgenus *Polybotrya*	*Atalopteris*, *Psomiocarpa*, *Teratophyllum*
Smith (1875)	*Soromanes*	*Polybotrya*	*Polybotrya*	
Christensen (1905)	*Polybotrya*	*Polybotrya*	*Polybotrya*	*Atalopteris*, *Bolbitis*, *Olfersia*, *Psomiocarpa*, *Teratophyllum*
Christensen (1934)	*Polybotrya*	*Polybotrya*	*Polybotrya*	
Copeland (1947)	*Polybotrya*	*Polybotrya*	*Polybotrya*	*Olfersia*
Pichi-Sermolli (1977)	*Soromanes*	*Polybotrya*	*Polybotrya*	
Tryon & Tryon (1982)	*Polybotrya*	*Polybotrya*	*Polybotrya*	*Olfersia*

* refers to the treatment of the genus in this work.

Soromanes, and *Olfersia* as distinct genera but placed *Soromanes* and *Polybotrya* on separate branches of his phylogenetic diagram. Tryon and Tryon (1982) are the most recent authors to discuss *Polybotrya* and related genera; their concept is like that used in the present work, except that they include *Olfersia cervina* in *Polybotrya*. In the present monograph, I restrict *Polybotrya* to the species allied closely to *P. osmundacea*, make *Soromanes* a subgenus of *Polybotrya*, and keep *Olfersia cervina*, which has been placed in *Polybotrya* by many recent pteridologists, in its own monotypic genus. I recognize 35 species of *Polybotrya*, all of which are neotropical and 10 of which are new.

Work at the Species Level

The species of *Polybotrya* have received less study over the years than those of most other fern genera. Fée (1845), Hooker (1864), and Hooker and Baker (1874) have been the only monographers of the genus. Although they attempted to identify all of the then-known species of *Polybotrya*, they did not always see types, overlooked several published names, put some species in synonymy without adequate study, and did not make detailed observations on the genus because they were studying hundreds of other ferns at the same time. Despite these shortcomings, the works of these three men have been the best source for identifying specimens of *Polybotrya* in many regions of tropical America.

The difficulty of identifying specimens of *Polybotyra* has been partially alleviated by local or regional floras, but these cover only a limited portion of the geographic range of the genus and are often incomplete. In many of these floras, types were rarely examined and names, therefore, were often applied incorrectly. Only Sodiro's (1897) treatment of the ferns of Ecuador is available for the Andean region; yet he was aware of only 6 of the 23 species that occur in that region. Vareschi's (1969) treatment for Venezuela and Brade's (1971) for Brazil have helpful illustrations, but the names are often misapplied. The best treatment of *Polybotrya* for Mesoamerica is Stolze's (1981) excellent work for the *Flora of Guatemala*, but Guatemala lacks several species found in Mesoamerica. In brief, adequate keys and descriptions are lacking for identifying *Polybotrya* throughout most of its range and, as a result, many specimens have been misidentified.

In this century, most of the research on *Polybotrya* has focused on the specific level. Brade (1935, 1948) described two new species of *Polybotrya* in papers that included other ferns as well. Later, in a series of three papers published in the Brazilian journal *Bradea* (1969a,b,c), he described ten additional new species from Brazil, Costa Rica, and Venezuela. These papers were based on field studies in the American tropics, and most of the types were plants he had collected by himself or with his brother Alfred. Brade (1971) published a synopsis providing keys and illustrations of the Brazilian species of *Polybotrya*. Unfortunately, he died before completing the descriptions, habitats, and distributional information. Only five of Brade's names are accepted in this monograph as representing valid species; the remainder are relegated to synonymy.

More recently, Lellinger (1972, 1977) published two important papers on *Polybotrya*. In the first, he described five new species from South America and offered interesting ecological notes on the genus. In the second, which deals with other ferns as well, he described two new species that are endemic to Colombia. Only three of these seven species are accepted here. About half of the species described by Brade and by Lellinger have, therefore, been relegated to synonymy in the present work, largely because I found older, obscure names during my research. In some cases, these names had not been used since their original publication. The proliferation of names is one of the pitfalls faced by taxonomists when synthetic or revisionary works are unavailable for a group and in this case indicates how much *Polybotrya* has needed a monograph.

Ecology

Polybotrya inhabits wet, shaded, tropical forests. These may be hot, humid, lowland rain forests or cool, cloud forests at high elevations. The genus rarely occurs in disturbed forests, and when it does, it is represented by only a few isolated plants. However, small scale disturbances within mature forest, such as light gaps created when a huge tree dies, appear to be important in establishing young plants (Lellinger 1972). During fieldwork in tropical America, I never observed young sporophytes or their associated gametophytes establishing themselves on roadbanks or on shaded, disturbed slopes adjacent to roads. Furthermore, all herbarium specimens that contained habitat information listed only primary forest as the habitat. The restriction of *Polybotrya* to wet, shaded, primary, tropical forest is reflected by its geographic distribution (Fig. 2a). The genus is absent from such arid regions as central Mexico and the western coast of Peru and from such nonforested regions as the Llanos of Venezuela and Colombia (Figs. 2a & 3). The altitudinal range of *Polybotrya* is from sea level to 2500 m, with most plants collected from 500–2000 m (Fig. 4). This range certainly corresponds to my field observations that *Polybotrya* is most diverse, frequent, and abundant at middle elevations.

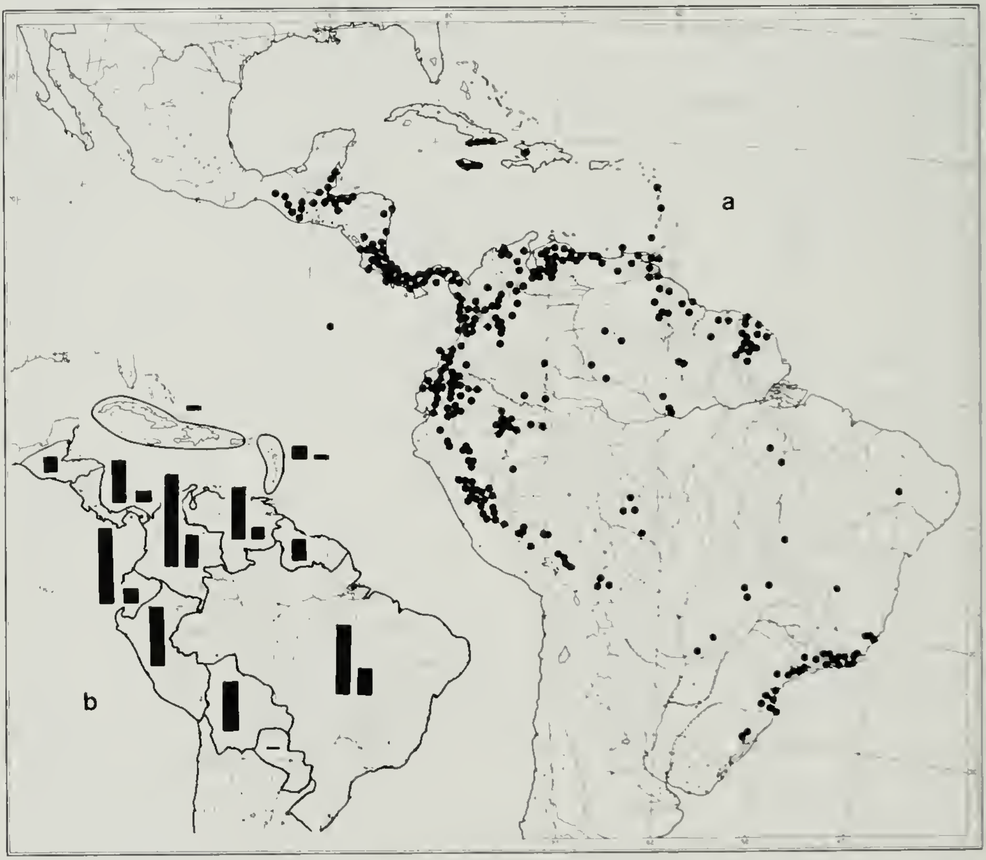

FIGURE 2. Distribution of *Polybotrya*. a. composite of Maps 1–21; b. number of species (left bar), number of endemics (right bar). Countries or areas are outlined; those with only one bar have no endemics. See Table 3 for numbers of taxa in each country.

Geography

In the following discussion, the distribution of *Polybotrya* is given according to the regional centers defined by Tryon (1972). These regional centers, all mountainous, were determined by their high endemism and species richness.

The most important regional center in the diversification of *Polybotrya* is the Andean, from Venezuela and Colombia south to Bolivia (Fig. 2b, Table 2). The Andean Region contains 23 species, 12 of which are endemic, and I suspect that new species of *Polybotrya* will be found there. Within this region, Colombia contains the richest *Polybotrya* flora: 17 species, 6 of which are endemic (Table 3). The coastal mountains of northern Venezuela contain *P. canaliculata* and *P. serratifolia*, both occurring in cloud forests from 1200–2400 m. *Polybotrya canaliculata* has a very limited distribution and is a true endemic to the coastal mountains (Map 19); it occurs outside of the Andean Region as defined by Tryon (1972). *Polybotrya serratifolia* is considered a near-endemic, extending southwest into the Andes around Mérida and eastward to Trinidad (Map 1).

The Serra do Mar Mountains of the Southeastern Brazilian Region contain five species

FIGURE 3. Distribution of *Polybotrya* species within regional centers of diversity and endemism for tropical American ferns defined by Tryon (1972). Primary centers are indicated with dark shading; secondary centers, with light shading. The number on the left is the total number of species; the number in parentheses indicates how many of those species are endemic. See Table 4 for comparisons.

of *Polybotrya*, all of which are endemic (Fig. 3, Tables 2 & 3). I find it remarkable that this region has no species of *Polybotrya* in common with those of the other regional centers (Table 4) or with intervening areas. This distinctiveness of the *Polybotrya* flora is accentuated by its lack of the simply pinnate species, that is, subgenera *Soromanes* and *Sorbifolia*. The biogeography of *Polybotrya* strongly supports data from many other sources that suggest that the isolated Serra do Mar Mountains are a distinctive biogeographic center (Tryon 1972).

Only one species, *P. goyazensis*, occurs in the Matto Grosso and intervening area between the Andean and Brazilian regional centers (Map 6). This species is closely related to the widespread *P. caudata* and is probably an example of the peripheral "budding" of a new species from the southern part of the range of *P. caudata*.

The Amazon basin contains one endemic, *P. glandulosa*, which has been collected only three times (Map 7). Most species of *Polybotrya* in the Amazon basin also grow in the Andean Region. In contrast, the coastal mountains of southeastern Brazil have contributed no species to the Amazonian lowlands. My field experience in the Amazon basin of Ecuador and Peru showed that in forests on wet, sandy soils *P. caudata* was common; forests on lateritic soils, however, had *P. crassirhizoma*, *P. caudata*, *P. osmundacea*, and *P. pubens*. All five species were abundant in the western Amazon basin where I collected, and I suspect that they extend farther eastward into the Amazon basin than is shown on their range maps.

The Guiana Highlands Region does not contain a distinctive *Polybotrya* flora. Only six species occur there and most of these are widespread elsewhere. The region, therefore, has a high floristic affinity with the Andean and Central American regional centers (Table 4). *Polybotrya sessilisora*, which occurs in the Guiana Highlands and in the adjacent Amazon basin (Map 20), is probably more common in the Highlands and its range may be centered there. *Polybotrya* has two notable examples of Andean-Guianan range disjunc-

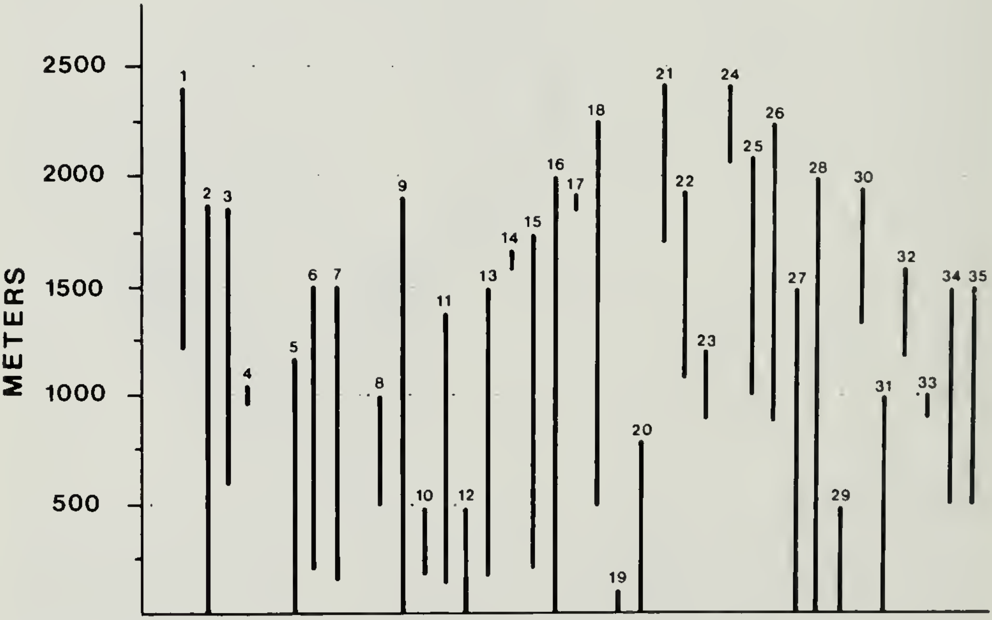

FIGURE 4. Altitudinal ranges of *Polybotrya* species. The numbers above the bars correspond to the species numbers assigned in the taxonomic treatment.

tions. The first example, *P. lechleriana*, is known in the Guianas from a single collection at Mount Roraima in Guyana, 1900 km from its nearest locality in Colombia (Map 7). This disjunction is probably best explained by long-distance spore dispersal from Andean populations. The second example, *P. fractiserialis*, occurs primarily in the foothills of the Andes and is disjunct in the southern Pakaraima Mountains of British Guiana, 2000 km from the nearest Andean population in Ecuador. Unlike *P. lechleriana*, *P. fractiserialis* is common and widespread in the Guianas (Map 3).

The Central American Region contains seven species, including one endemic (Fig. 3, Table 2). All seven species occur in Costa Rica (Table 3). My fieldwork there showed that *P. polybotryoides*, *P. osmundacea*, *P. alfredii* and *P. gomezii* (endemic) were particularly common in the mountains and that *P. caudata* was frequent in the costal lowlands. *Polybotrya alfredii* and *P. gomezii* were particularly abundant in cloud forests, often growing together. In the mountains of central Panama, just outside the Central American Region as defined by Tryon (1972), one endemic occurs, *P. alata*.

The Greater Antilles Region, otherwise quite rich in fern species, has only one *Polybotrya* species, the widespread *P. osmundacea* (Figs. 2 & 3, Table 2). Puerto Rico lacks *Polybotrya* but certainly has suitable forest habitat. In the Lesser Antilles, *P. osmundacea* is found on Grenada. Martinique and Guadeloupe have the closely related endemic *P. cyathifolia*. The Caribbean islands have played a minor role in the diversification of *Polybotrya*.

Polybotrya caudata and *P. osmundacea* clearly have the largest geographical and altitudinal ranges of any species in the genus (Maps 5 & 18). With the exception of southeastern Brazil, these two species extend nearly throughout the entire area covered by all of the other species in the genus.

Polybotrya occurs on only one oceanic island—Cocos Island, about 500 km (310 mi) southwest of Costa Rica in the Pacific Ocean. Three species occur there: *P.*

TABLE 2. The geographic regions shown in Figure 3 and the species of *Polybotrya* that occur in them.

Geographic Region (after Tryon 1972)	Species (numbers correspond to those in the taxonomic treatment)	No. in Region (% of total species in genus)	No. Endemic (% for region)
Greater Antilles	28	1 (3)	0
Lesser Antilles	28, 29	2 (6)	1 (50)
Mexican		0	0
Mexican–Central American	2,9	2 (6)	0
Central American	2, 3, 5, 9, 16, 27, 28	7 (20)	1 (14)
Central American–Andean	2, 3, 9, 16, 23, 28	6 (17)	1 (17)
Andean	1, 2, 3, 4, 5, 6, 7, 9, 11, 12, 13, 14, 15, 16, 17, 18, 19, 21, 22, 24, 25, 26, 28, 30	23 (66)	12 (52)
Andean–Guianan	1, 5, 7, 9, 11, 12, 28, 31, 32	9 (26)	1 (11)
Guianan	5, 6, 9, 13, 28, 31	6 (17)	0
Guianan–Southeast Brazilian	5, 7, 9, 10, 11, 12, 31	7 (20)	0
Southeast Brazilian	10, 20, 33, 34, 35	5 (14)	5 (100)
Southeast Brazilian–Andean	10	1 (3)	0

Table 3. Distribution of *Polybotrya* by country. Endemics are in boldface. Numbers in parentheses refer to the species numbers assigned in the taxonomic treatment.

Mexico: 2 species, no endemics. *polybotryoides* (2), *caudata* (9).

Belize: 2 species, no endemics. *polybotryoides* (2), *caudata* (9).

Guatemala: 3 species, no endemics. *polybotryoides* (2), *caudata* (9), *osmundacea* (28).

Honduras: 3 species, no endemics. *polybotryoides* (2), *caudata* (9), *osmundacea* (28).

Nicaragua: 3 species, no endemics. *caudata* (9), *alfredii* (16), *osmundacea* (28).

Costa Rica: 6 species, 1 endemic. *polybotryoides* (2), *sorbifolia* (5), *caudata* (9), *alfredii* (16), **gomezii** (27), *osmundacea* (28).

Cocos Island: 3 species, no endemics. *polybotryoides* (2), *caudata* (9), *osmundacea* (28).

Panama: 5 species, 1 endemic. *polybotryoides* (2), *caudata* (9), *alfredii* (16), **alata** (23), *osmundacea* (28).

Cuba: 1 species, not endemic. *osmundacea* (28).

Jamaica: 1 species, not endemic. *osmundacea* (28).

Haiti: 1 species, not endemic. *osmundacea* (28).

Guadeloupe & Martinique: 1 endemic. **cyathifolia** (29).

Grenada: 1 species, not endemic. *osmundacea* (28).

Trinidad: 3 species, no endemics. *serratifolia* (1), *caudata* (9), *osmundacea* (28).

French Guiana: 3 species, no endemics. *fractiserialis* (6), *caudata* (9), *osmundacea* (28).

Surinam: 2 species, no endemics. *fractiserialis* (6), *caudata* (9).

Guyana: 4 species, no endemics. *fractiserialis* (6), *caudata* (9), *lechleriana* (13), *osmundacea* (28).

Venezuela: 6 species, 2 endemics. **serratifolia** (1), *sorbifolia* (5), *caudata* (9), *glandulosa* (12), *osmundacea* (28), **canaliculata** (32).

Colombia: 17 species, 6 endemics. *polybotryoides* (2), *suberecta* (3), *sorbifolia* (5), *crassirhizoma* (7), *caudata* (9), *pubens* (11), *lechleriana* (13), **attenuata** (14), **stolzei** (15), **botryoides** (17), **lourteigiana** (18), **pittieri** (19), *hickeyi* (21), *altescandens* (26), *osmundacea* (28), **latisquamosa** (30), *sessilisora* (31).

Ecuador: 14 species, 3 endemics. *polybotryoides* (2), *suberecta* (3), **andina** (4), *fractiserialis* (6), *crassirhizoma* (7), *caudata* (9), *pubens* (11), *lechleriana* (13), *alfredii* (16), **puberulenta** (22), *aequatoriana* (24), **appressa** (25), *altescandens* (26), *osmundacea* (28).

Peru: 11 species, no endemics. *polybotryoides* (2), *suberecta* (3), *fractiserialis* (6), *crassirhizoma* (7), *caudata* (9), *pubens* (11), *glandulosa* (12), *lechleriana* (13), *alfredii* (16), *altescandens* (26), *osmundacea* (28).

Bolivia: 10 species, no endemics. *fractiserialis* (6), *crassirhizoma* (7), *caudata* (9), *pubens* (11), *lechleriana* (13), *alfredii* (16), *hickeyi* (21), *puberulenta* (22), *aequatoriana* (24), *osmundacea* (28).

Paraguay: 1 species, not endemic. *goyazensis* (10).

Brazil: 13 species, 5 endemics. *sorbifolia* (5), *crassirhizoma* (7), **espiritosantensis** (8), *caudata* (9), *goyazensis* (10), *pubens* (11), *glandulosa* (12), **cylindrica** (20), *osmundacea* (28), *sessilisora* (31), **semipinnata** (33), **speciosa** (34), **pilosa** (35).

caudata, *P. osmundacea*, and *P. polybotryoides*. As noted in the previous paragraph, *P. caudata* and *P. osmundacea* have the most extensive range of any species in the genus. Although not as wide ranging, *P. polybotryoides* has a long north-south distribution from Chiapas, Mexico, to Pasco, Peru, and is the most far-ranging species of the subgenus *Soromanes*. This distribution supports Tryon's (1970) findings that the ferns of oceanic islands tend to be those that are widespread beyond the source area for the island (the source area for Cocos Island is defined by Tryon as Central America and Colombia). According to Tryon (1970), widely distributed species have a broader ecological amplitude and therefore establish themselves more often on oceanic islands because of their ability to grow under a wide range of environments.

Morphology and Anatomy

Information on the morphology and anatomy of *Polybotrya* has been extremely useful for assessing affinities of related genera and for understanding functional aspects of the biology of the genus. Every phylogenetic argument made here relies heavily on evidence from stem anatomy (along with other features, of course) in determining how *Polybotrya* relates to other fern genera and families. Anatomical studies have also answered other biological questions about the genus. For example, studies of the diplodesmic venation system showed how the sori are efficiently supplied with water and nutrients. Studies of sterile-fertile transitional leaves established that the diplodesmic veins are homologous with the veinlets of the sterile leaves. In short, anatomical studies of root, stem, and leaf have been valuable in understanding diverse questions about the biology of *Polybotrya*.

Roots

A dense tangle of dark, tough, fibrous, adventitious roots arises from the ventral side of climbing stems and from all sides of terrestrial stems. No positional relationship exists between the leaf bases and the roots; roots are apparently borne at random. Roots arising directly from the stem measure about 1 mm in diameter, but their terminal branches may be only 0.3 mm wide. Roots branch at irregular intervals, increasing the number of tiny supportive rootlets. On climbing plants, these tenacious rootlets penetrate the outer layers of tree bark and firmly anchor the stem. This firm attachment hinders pulling the stem away from the tree. When a stem is forcibly pulled away from a trunk, the large roots of *Polybotrya* remain attached to the stem, clinging to shredded pieces of bark, lichens, and mosses.

I studied the root anatomy of six species—*P. alfredii*, *P. caudata*, *P. gomezii*, *P. osmundacea*, *P. polybotryoides*, and *P. sorbifolia*. All were similar. Figure 5a shows

TABLE 4. Affinities of *Polybotrya* floras between regional centers (see Fig. 3). Floristic affinity is the percent species in common (C) of the total species in the two regions (A + B), i.e., 100C/A + B.

Regional Center (Tryon 1972)	Total Species (A + B)	Species in Common (C)	Floristic Affinity (%)
Andean & Guianan	29	5	17.2
Central American & Andean	30	5	16.6
Andean & Southeast Brazilian	28	0	0
Central American & Guianan	13	3	23.0
Guianan & Southeast Brazilian	11	0	0
Central American & Southeast Brazilian	12	0	0

a root in cross section taken about 0.5 cm from the ventral surface of a scandent stem of *P. osmundacea*. The stele is weakly elliptic, protostelic, and comprises about one-fifth of the root's diameter. Two protoxylem poles occur; each is exarch and consists of four to seven protoxylem elements. The center of the stele contains three to five large metaxylem cells. Surrounding the xylem are phloem elements—minute, angular, thin-walled cells about the same diameter as the protoxylem elements. They are not shown in Figure 5a because they were poorly preserved.

Surrounding the stele is the innermost layer of the cortex—the endodermis. It consists of a single, continuous, light-colored layer composed of thin-walled, rectangular

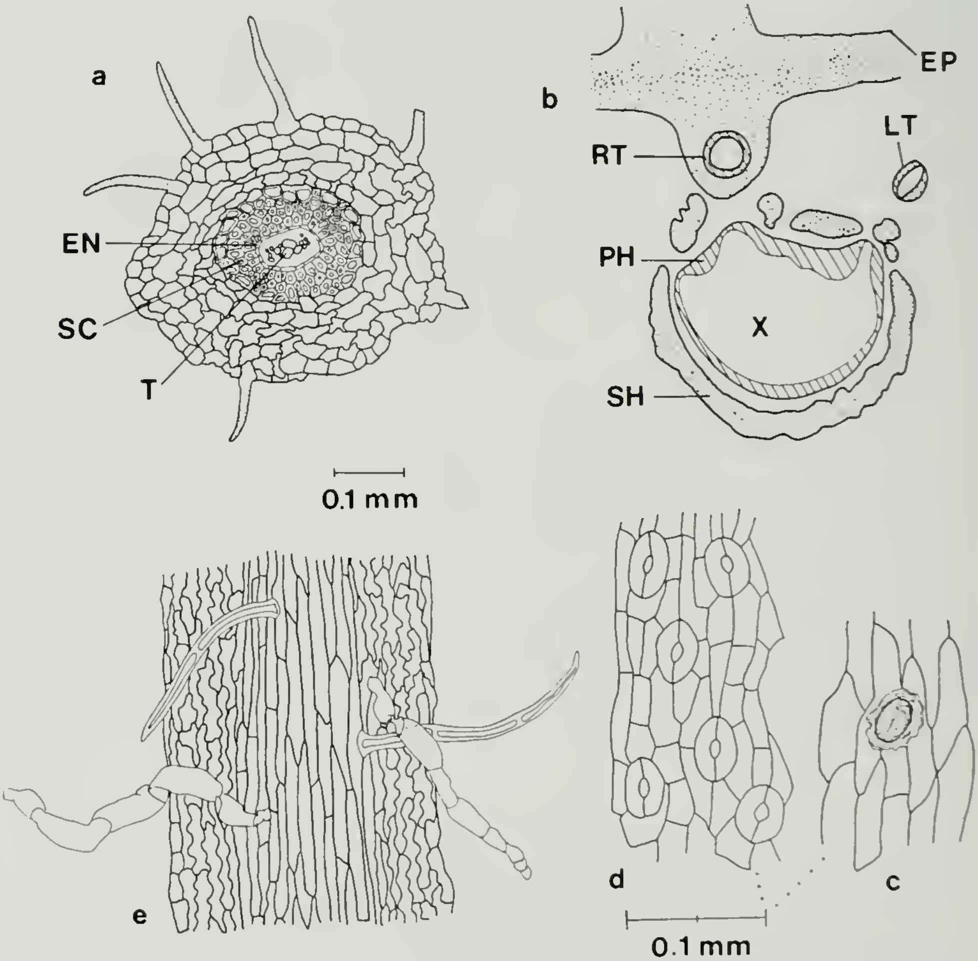

FIGURE 5. Root anatomy and various epidermal features of *Polybotrya*. a,b, and e are the same size. a. root cross section of *P. osmundacea*; b. close-up of a stem meristele in cross section, showing root trace diverging about midway between the laterally diverging leaf traces; c. phloroglucinol-containing gland from the stem epidermis of *P. caudata*; d. stomata on stem aerophore of *P. caudata*; e. fertile segment of *P. stolzei*, adaxial surface. Note different shapes of epidermal cells and the two kinds of hairs; the flaccid hair represents the type that intergrades with scales. EN endodermis; EP epidermis; LT leaf trace; PH phloem; RT root trace; SC sclerenchyma; SH sclerenchyma sheath surrounding a meristele; T tracheid; X xylem.

cells. Although the endodermis is narrow, it contrasts sharply with the dark, thicker-walled cells on either side. The anticlinal walls have casparian strips that are easily visible even in unstained material.

Outside the endodermis is a ring of dark, thick-walled fibers (Fig. 5a). This ring is the most conspicuous feature of *Polybotrya* root anatomy. Unstained, the walls of the fibers appear orangy or reddish and may become so thick that they nearly occlude the entire lumen of the cell. The walls thicken evenly on all sides, unlike many angiosperms and some ferns where the deposition of cell walls occurs centripetally (Bierhorst 1971; Wagner 1952).

Outside the ring of dark fibers, the cortical cells take on a different appearance. In contrast to the cells of the inner ring of fibers, the outer cortical cells are parenchymatous with thin, irregular, dark brown cell walls.

Cells of the epidermis are compact and quadrangular, in contrast to the shape of the cortical cells immediately below. The most conspicuously differentiated cells of the epidermis are the root hairs, generally 0.2–1.0 mm long and straight, narrow, and unicellular. Their color normally varies from brown to amber, but brilliant yellow hairs occur in several species. Unfortunately, the root anatomy of *Polybotrya* cannot be compared with that of other genera of dryopteroid ferns because of inadequate information for those genera.

Stem

Habit. The stem is climbing in all species of *Polybotrya* except for *P. fractiserialis* and *P. sorbifolia*, where it is terrestrial (Fig. 1). Climbing stems grow horizontally about 0.5–2.0 cm beneath the forest floor until they contact a tree. The stem then turns upward, anchoring itself to the tree by adventitious roots produced on the ventral surface. Stems usually climb to a height of 1 to 5 m, but the highest scandent stem I saw was just under 15 m. The longest underground stem that I saw was traced back 8 m from where it entered the soil at the base of its support tree. As a stem begins to climb, it grows wider. The diameter of a climbing stem may reach 3.5 cm; terrestrial stems seldom grow wider than 1 cm. The internode length on climbing stems is generally 10–15 cm.

Stems of the two terrestrial species of *Polybotrya* differ in overall appearance from stems of the climbing species. Stems of terrestrial species are about 15–20 cm long with internodes 1–3 cm long. These short internodes impart a basketlike aspect to the arrangement of leaves instead of the linearly spaced aspect typical of the leaves of climbing species (Fig. 1). The amount of scale cover is another difference. Stems of the terrestrial species are less scaly than stems of climbing species due to the sloughing off or rotting away of scales, presumably because the scales are buried in moist, tropical soils where decay is rapid. Furthermore, the petiole bases hide the few scales that remain in terrestrial species; the best place to find scales is the stem apex, where there is less decay and fewer petiole bases. Despite these differences, both types of stems show affinity by sharing the distinctive anatomy described below.

Branching is rare in stems of *Polybotrya*. I never saw dichotomy of the stem apex, and lateral branching was exceedingly rare in scandent stems, although occasional in terrestrial portions. I did not investigate the relationship, if any, of branching to leaf position, but that examination might provide further evidence for comparisons with other genera of dryopteroid ferns.

Anatomy. The stems of all dryopteroid fern genera have radially symmetric dictyosteles; however, the stems of *Polybotrya* are distinctive (Fig. 6). The most noticeable feature in cross section is the vascular bundles—terete, circularly arranged, each bundle ensheathed by a jet-black ring of sclerenchyma. The 5 to 12 vascular bundles are positioned around the central portion of the stem, their dark outlines contrasting vividly with the matrix of bright white ground parenchyma. Numerous tiny leaf traces emanate from the

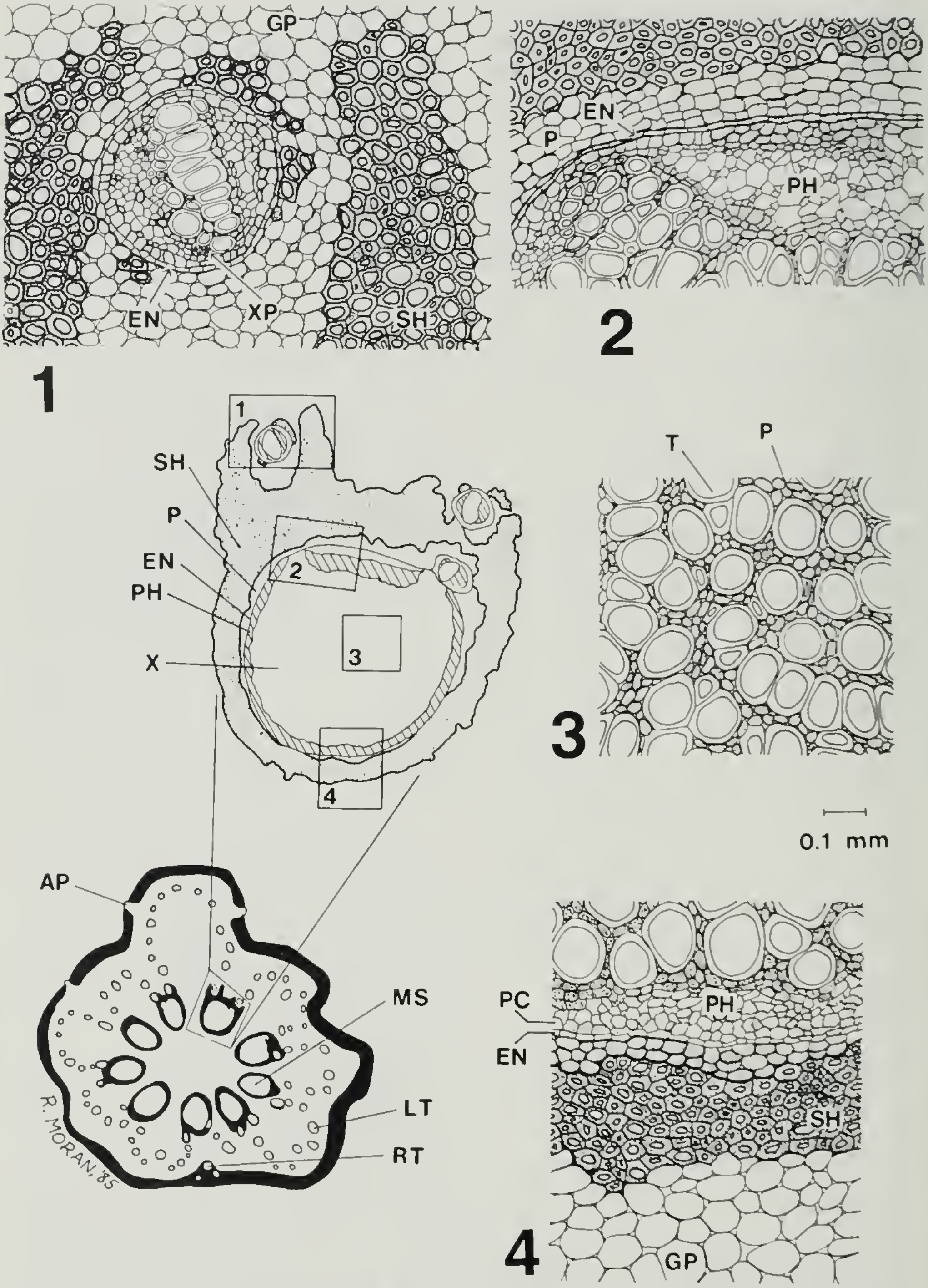

FIGURE 6. Stem anatomy of *Polybotrya osmundacea*, typical of the genus. Lower left is a cross section of the stem with a meristele enlarged above. Note "xylary arm" in 2. AP aerophore; EN endodermis; GP ground parenchyma; LT leaf trace; MS meristele; P parenchyma; PC pericycle; PH phloem; RT root trace; T tracheid; SH sclerenchyma sheath consisting of fibers; X xylem; XP protoxylem.

sides of the bundles, collectively forming a C-shaped line that connects adjacent bundles. This pattern is unmistakable (Fig. 6), and no other fern genus yet studied has this kind of stem anatomy. (For comparison of stem anatomy with closely related groups, see Relationships with Other Groups.)

The epidermis of the stem is darkly sclerotized and one cell layer thick; it produces numerous scales (described separately below). The cell walls of the epidermis are relatively straight compared to the sinuous ones of the leaf epidermis (cf. Figs. 5c & 9).

The stems of *Polybotrya* have minute glandular hairs on the epidermis. These short-stalked hairs have, in relation to their length, exceptionally large, round heads, 54–56 microns in diameter (Fig. 5c). Because these glands are tiny and few, they had been overlooked until found by Widén et al. (1983), who were also the first to report phloroglucinols in *Polybotrya*. The phloroglucinols are apparently produced and stored in these glands. In other dryopteroid ferns, such glands are known to secrete an oleoresin, along with various lipids, between the cuticle and the outer layer of the cell wall. The phloroglucinols are, presumably, located in this secretion (Widén et al. 1983). Using extracts from the stem and petiole bases of *P. caudata*, Widén et al. found that aspidin BB was the principal compound, along with smaller amounts of albaspidin BB, desaspidin BB, and flavaspidic acid BB. Internal glandular hairs, which probably also contain phloroglucinols, occur in the stems and petioles of other dryopteroid ferns (Mehra & Mittal 1961). I did not, however, find internal glands in *Polybotrya*.

Aerophores occur on the stems of most species of *Polybotrya* but are apparently absent in species having a mat of thick, woollike scales, such as in *P. aequatoriana*, *P. altescandens*, and *P. crassirhizoma*. On living stems, aerophores appear as yellowish white lines 1–3 mm wide that connect with aerophores on the petiole (for description of petiolar aerophores, see section below on petioles). Aerophores usually extend 2–6 cm down the stem from the base of the petiole. In cross section, they project about 0.5–1 mm above the surrounding surface and consist of thin-walled parenchyma cells that interrupt the otherwise continuous, thickened epidermis (Figs. 6 & 16g). Stomata abound and can be seen with a binocular microscope (Fig. 5d). Presumably, aerophores allow oxygen into the stem that is otherwise surrounded by compact, oxygen-impermeable, sclerenchyma fibers. Because aerophores shrink and darken upon drying, thereby matching the contour and color of the stem's sclerenchyma, they cannot be seen on herbarium material.

Below the epidermis is a well-developed hypodermis, usually three to eight cells thick and darker than the epidermis that forms a conspicuous ring around the white ground parenchyma. The cells of the hypodermis are thick-walled sclerenchyma fibers that thwart cutting the stem, sometimes even with a hefty machete, and I had problems cutting thin, even, cross sections for microscopic study. A ring of hypodermal sclerenchyma also encircles the stem in closely related genera such as *Arachniodes*, *Cyclodium*, *Maxonia*, *Olfersia*, and *Stigmatopteris* (pers. obs.).

Below the hypodermis lies the cortex, which consists of scattered clusters of brachysclereids (stone cells) in a matrix of whitish parenchyma. The parenchyma cells are generally rounded and contain abundant amyloplasts. In a freshly cut stem, the white color of these cells contrasts vividly with the darkly sclerotized hypodermal and meristelar sheaths. Sclereids never abound, as in *Olfersia* (Fig. 16i), but are scattered in clusters throughout the ground parenchyma. The deposition of secondary walls is extremely uneven; most of the wall is laid down on the side of the cells facing the inside of the sclereid cluster. A small, cuplike lumen can usually be seen on the side of the cell facing away from the center of the sclereid cluster. The thick, dark cell walls contain numerous simple pits and a lesser number of ramiform pits. Many Dryopteridaceae and Lomariopsidaceae also have sclereid clusters in the ground parenchyma of their stems (pers. obs.).

Inside the sclerenchyma sheath that surrounds each meristele lies a band of parenchyma two to four cells wide (Fig. 6). The cells of this layer are more compact and smaller than the cortical parenchyma, but like the cortical parenchyma, they contain amyloplasts. This inner parenchymatous layer stops abruptly at the endodermis, which stands out as a single row of clear, narrow, rectangular cells interrupting the darker parenchyma on either side of it (Fig. 6). The next layer toward the center is the pericycle, which consists of compact, orangy cells that form a continuous band around the xylem and phloem.

The phloem consists mostly of clear, angular, thin-walled sieve cells (Fig. 6.2 & 6.4). Phloem is broadest on the distal side of the stele but forms a thin band elsewhere. This band is broken in two locations by arms of the xylem that extend to the pericycle (Fig. 6.2). Scattered among the clear cells of the phloem are parenchymatous cells.

Inside the ring of phloem is the xylem, which has large, conspicuous metaxylary tracheids (Fig. 6.3). These tracheids occur singly and in clusters within a matrix of dark brown (when unstained) parenchyma. The tracheids are generally rounded or somewhat angular; when adjacent to another tracheid, the walls are straight. Numerous pits occur between all the cells of the xylem. Protoxylem elements occur in the xylary "arms" (Fig. 6.2). Each meristele is, therefore, diarch and exarch.

Root traces arise between the xylary arms of the meristele (Fig. 5b). The roots diverge through the cortex to the ventral surface of the stem. In contrast to the root traces, the leaf traces originate from the xylary arms. Four to six leaf traces are usually produced at each leaf gap from adjacent meristeles. During their passage from the cortex to the petiole, the leaf traces bifurcate and anastomose, forming a reticulum like that in *Maxonia* (Chandra 1975). Each leaf trace is surrounded by a single layer of sclerotized cells (Fig. 5b). The walls of these cells are brownish and slightly thickened on the inner tangential surface. The distance from the inception of a leaf gap to the point where the leaf diverges from the stem is about 10–15 cm.

Stem scales. Many species of *Polybotrya* have distinctive stem scales. Some species, in fact, can be identified solely on the basis of their stem scales (thus the importance of always collecting part of the stem). Color is the easiest feature of the scales to use in identifying the species of *Polybotrya*. Botanists should have no difficulty identifying *P. altescandens*, with its bright golden or yellow scales; *P. crassirhizoma*, with its dull orange or red scales; and *P. latisquamosa*, with its shiny, castaneous scales. Depending on the species, scales range from concolorous to slightly darker in the center to bicolorous with a dark central stripe.

Scale habit is another helpful identification feature. Some species, such as *P. altescandens* and *P. crassirhizoma*, have narrow, densely tangled scales that impart a woolly appearance to the stem. Other species, such as *P. appressa*, *P. caudata*, and *P. cylindrica*, have thick, dark, massive scales that are conspicuously appressed to the stem. Because of their great width and spreading habit, the scales of *P. serratifolia* are distinct from those of other species of the subgenus *Soromanes*. Most species of *Polybotrya* have ascending and slightly spreading scales—a characteristic that is not particularly distinctive because of its prevalence in the genus.

The shape of stem scales is usually not helpful in identification because most species have lanceolate to linear-lanceolate stem scales. Two species, however, *P. alata* and *P. altescandens* (Figs. 42 & 45), have extremely long, attenuate scales that differ strikingly from those of the other species. Petiole scales are generally similar to those of the stem but tend to be shorter and wider. The petiolar scales of *P. latisquamosa* have become, as the specific epithet implies, greatly widened so that this characteristic distinguishes the species from all others in the genus (Fig. 50d).

Despite variation in color, habit, and shape, stem scales are of two general types, here termed simply Type 1 and Type 2. Scales of Type 1 are thin and translucent and have easily visible cell walls (Fig. 7). Most of the scale is one cell layer thick, although the center may be thicker and darker. The margins vary from denticulate to erose, with the teeth formed from the projecting ends of two adjacent cells (Fig. 7). Marginal teeth in

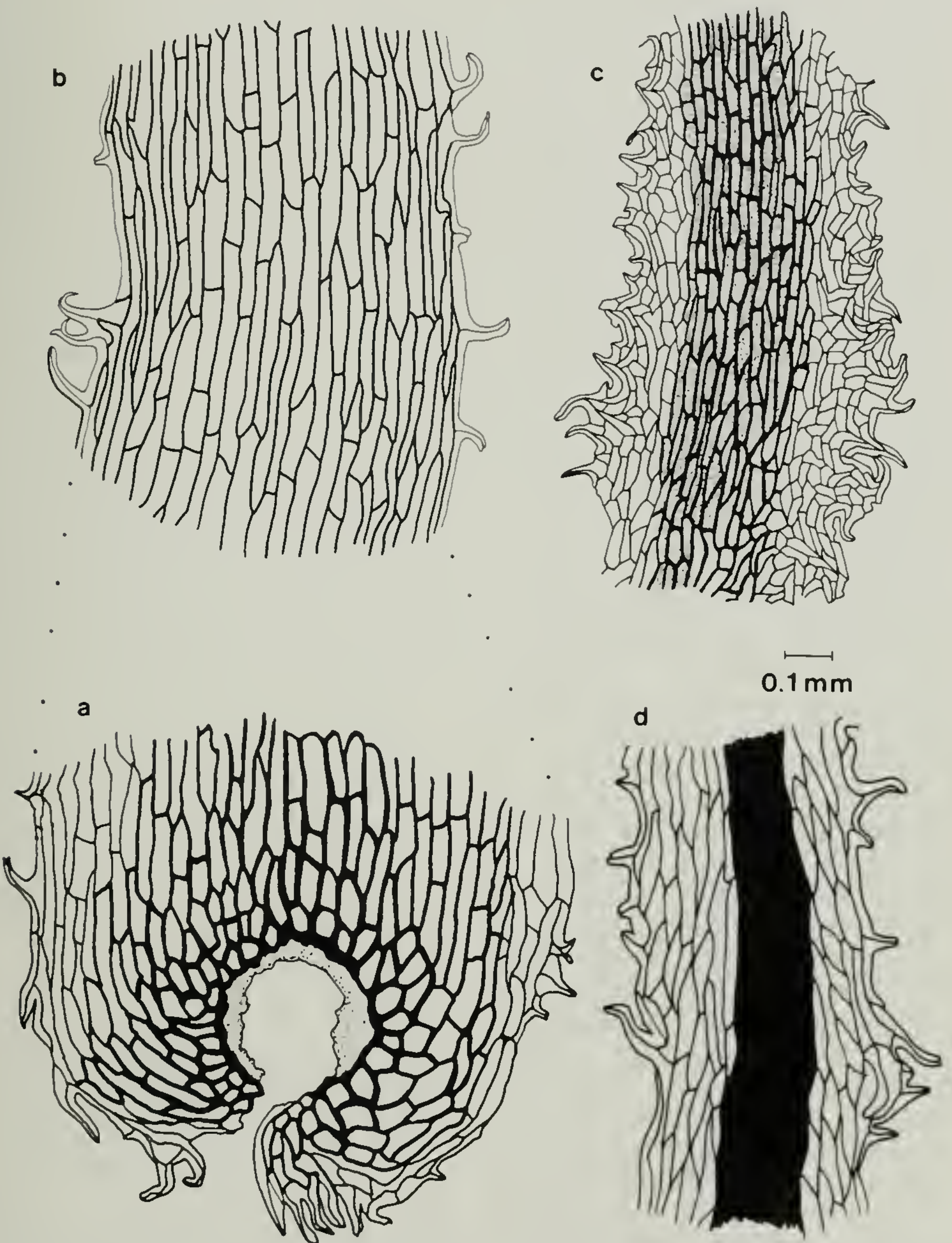

FIGURE 7. Stem scales of various *Polybotrya* species. a, b. *P. altescandens*; c. *P. botryoides*; d. *P. crassirhizoma*.

Polybotrya are never glandular, as in *Bolbitis* (Hennipman 1977) and *Stigmatopteris* (pers. obs.). Scales of Type 1 are attached basally at a single point or, more rarely, across the full length of the base. This point or line of attachment is always darkly sclerotized (Fig. 7a). Representative species with scales of Type 1 include *P. crassirhizoma*, *P. goyazensis*, *P. puberulenta*, and *P. serratifolia* (Figs. 26, 29, 41, & 19).

Scales classified as Type 2 are thick, opaque, and composed of many cell layers. The margins are entire or subentire. The base is greatly thickened, sometimes almost stipelike, and is curved and ascending. When the scale is removed, a circular or oval scar remains on the stem. Scales of this type are usually appressed, but they are squarrose in *P. osmundacea*. Representative species with scales of Type 2 include *P. appressa*, *P. caudata*, and *P. cylindrica* (Figs. 44, 28, & 39). In contrast to scales of Type 1, which show tremendous variety in habit, color, and shape, those of Type 2 are relatively homogeneous.

Evidence suggests that morphological transition occurs easily between the two types of scales. Species such as *P. lechleriana*, *P. lourteigiana*, *P. osmundacea*, and *P. pubens* have both types of scales but on different individuals. Even on a single plant, scales belonging to Type 1 can occur on the climbing portion, with scales of Type 2 and/or intermediates on the terrestrial portion. If morphological transition is easily accomplished, then evolutionary change in scale type could be expected to occur in closely related species pairs. This hypothesis is supported by two closely related species *P. caudata* and *P. goyazensis* (Figs. 28 & 29); the former has scales of Type 2 whereas the latter has scales of Type 1. Clearly, the stem scales of *Polybotrya* have been morphologically and evolutionarily plastic.

The evolutionary advantage of scales in *Polybotrya* is unknown. Their contribution to protecting the stem from mechanical damage is probably minimal since the stem is surrounded by a tough, resistant, sclerenchymatous sheath. Scales seem unnecessary on the older, hardened parts of the stem. During fieldwork in Latin America, I found several plants of *Polybotrya* that had lost all of their scales on the lower, older part of the climbing stem, yet the plants appeared vigorous. Perhaps the scales afford protection to the stem apex, where young tissues have not yet become sclerified.

Another hypothesis is that the scales retain water by capillary action for later use by the roots. Retention would be advantageous to a climbing plant that has the leaves on the scandent portion of the stem separated by several meters from the roots in the soil. Stems collected in the field, however, never seemed to hold water between the scales and plants never appeared water stressed. The bark of the support tree, which is usually covered with water-retaining mosses, lichens, and organic debris, probably could provide most of the water needed by the plant. Further, the retention of capillary water between stem scales might be harmful in a hot, humid, tropical environment that promotes decay. No satisfactory hypothesis, therefore, has been offered to explain the adaptive significance of scales in *Polybotrya*.

Even more difficult to explain is the adaptive advantages of the numerous minor modifications of scales. What could be the function of a dark, central stripe, of reddish color, of an appressed habit, or of a linear shape? How these and other minor modifications of scales are significant in evolution, if indeed they are, is baffling.

Leaves

Petiole. The petiole base in some ferns is specialized to accumulate food and to persist as a storage organ long after the rest of the leaf to which it was attached has withered and decayed. These specialized petiole bases, called "trophopods," are a new source of systematic data in ferns (Wagner & Johnson 1983). *Polybotrya*, however, lacks trophopods, and the food-storing function of the trophopod is performed by the stem in the amyloplast-containing cells of its ground parenchyma.

A cross section of the petiole of *Polybotrya* reveals leaf traces that are arranged in a mushroomlike outline, with the base of the mushroom oriented adaxially (Fig. 8a). This pattern also occurs in *Cyclodium trianae*, a species closely related to *Polybotrya*, and in some species of the similar family Lomariopsidaceae (Hennipman 1977; Holttum 1978). Other closely related dryopteroid genera, however, such as *Cyrtomium*, *Dryopteris*, and *Polystichum*, display a C-shaped arrangement of leaf traces in the petiole (pers. obs.). These genera also have fewer leaf traces than *Polybotrya*, probably as a consequence of their narrower petioles. Further study of petiole anatomy in dryopteroid genera may provide helpful information for assessing their relationships.

In *Polybotrya*, the two vascular bundles closest to the adaxial surface of the petiole differ from the lower vascular bundles in several respects. The most obvious difference is their shape: elongate and slightly curved instead of round (cf. Fig. 8b,d). Inside each of the two adaxial bundles, the xylem is hook-shaped in outline, in contrast to the lenticular shape seen in the lower traces. Only these uppermost vascular bundles, not the lower, yield the lateral traces that supply the pinnae. As they traverse the rhachis and petiole, all traces remain separate; they do not anastomose to form a reticulum within the petiole.

Aerophores run down the sides of the petiole and join below with those on the stem. On living petioles, they appear narrow, linear, and light green. The surface of the aerophores bears stomata, and beneath them is parenchyma that contains intercellular spaces. This parenchyma, when seen in cross section (Fig. 8c), interrupts the otherwise continuous band of collenchyma that encircles the petiole. Upon drying, the aerophores darken and collapse, leaving a sulcus on either side of the central, adaxial sulcus of the petiole. Drying, therefore, makes the petiole trisulcate; in living petioles only a central sulcus is present.

Petiole and stem mucilage. Mucilage has apparently never been reported in *Polybotrya* or any other genus of Dryopteridaceae. During fieldwork in Costa Rica and Ecuador, however, I found that stems and petiole bases of *P. alfredii* usually had a thick coat of translucent mucilage similar to that on the stems and/or petioles of certain *Blechnum* and *Thelypteris* species. Upon drying, the mucilage disappeared completely, although sometimes the scales exhibited a matted or flattened appearance, as if stuck together. Attempts to rehydrate the mucilage failed.

Other species of *Polybotrya* probably have mucilage. Several dried specimens of *P. lechleriana* and *P. lourteigiana* exhibited matted, flattened scales that suggested the earlier presence of mucilage. These two species are closely related to *P. alfredii*, an observation that suggests that mucilage is probably confined to the *P. alfredii* group (species nos. 13–20). I did not see matted, flattened scales in any other species of *Polybotrya*. The mechanism of mucilage secretion and its adaptive significance, if any, is unknown.

Nectaries. Koptur et al. (1982) were the first to report the existence of nectaries in *Polybotrya*. They found them in *P. osmundacea* on the rhachis of unfurling leaves, near the yellowish, lateral, linear aerophores. Several times during fieldwork in Costa Rica, I noticed ants on young leaves, but I never saw them feeding on nectar. The nectar itself would certainly be nutritious because it contains sucrose, glucose, and fructose in concentrations up to 35–75 percent by weight (Koptur et al. 1982). Amino acids also occur in the nectar, and Koptur et al. list those present. Although ants may benefit from the nectaries, additional fieldwork is needed to establish whether or not the plants benefit. Apparently, ants do not defend the plants — at least I was never attacked by ants while collecting *Polybotrya*.

Costa-costule architecture. Costa-costule architecture refers to the morphology of the juncture of these axes. Several kinds of

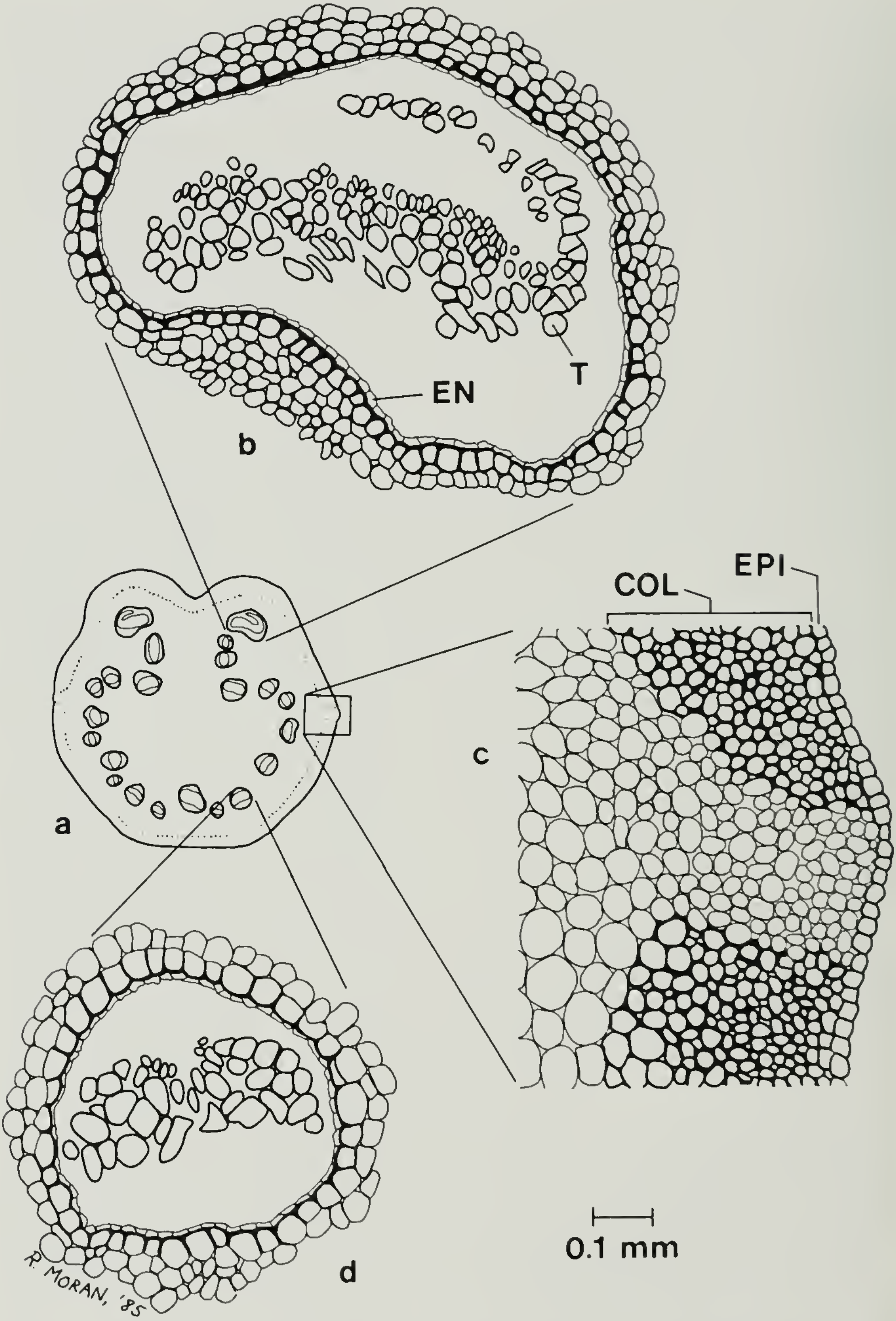

FIGURE 8. Petiole anatomy of *Polybotrya alfredii*. a. cross section of petiole 2 cm above the stem showing the arrangement of vascular bundles in the shape of a mushroom; b. adaxial bundle showing hooked xylem; c. aerophore; d. abaxial bundle. COL collenchyma; EN endodermis; EPI epidermis; T tracheid.

costa-costule architecture occur; the most thorough review of them is by Holttum (1959); more than any other pteridologist, he has shown the importance of this feature in the taxonomy of ferns. According to Holttum (1984), the dryopteroid genera have "midribs of ultimate leaflets grooved, the groove of the rachis bearing the leaflets being open to admit the leaflet-groove, the margin of the lamina of the leaflet being decurrent (but not prominent) down the side of the rachis; hairs of ctenitoid type lacking." This type of architecture is illustrated in Figure 47h. Holttum (1984) describes the tectarioid genera as having "midribs of ultimate leaflets more or less prominent (in *Tectaria* sometimes slightly grooved) and bearing ctenitoid hairs, usually many." In *Polybotrya*, the basic type of architecture is dryopteroid, a finding that supports its classification among the dryopteroid ferns.

Within *Polybotrya*, however, modifications are found in the dryopteroid pattern of costa-costule architecture. Typical dryopteroid costa-costule architecture is shown in the most primitive group in the genus—the group of species related to *P. osmundacea*. In contrast, the most advanced species in the genus—*P. attenuata*, *P. lechleriana*, and *P. stolzei*—always have the costular groove truncated by the ridges of the costa; therefore, the groove is not decurrent (Figs. 33b, 32b, & 34f). This truncated costa-costule architecture is considered to have been derived from the decurrent-grooved condition, as evidenced from outgroup comparison with other dryopteroid ferns. Intermediates, such as *P. aequatoriana* and *P. alfredii*, have costular grooves that gradually fill up near the costa, so that the ridges of the costa are only slightly interrupted by the shallow, weakly decurrent groove of the costule (Fig. 43d). In *P. alfredii* and *P. lourteigiana*, these three types of costa-costule architecture can be found on different parts of the same leaf, although the intermediate type predominates. In summary, most species of *Polybotrya* have dryopteroid costa-costule architecture, but distinctive modifications of this basic type occur.

Anatomy of the lamina. I studied leaf clearings and cross sections for 17 species of *Polybotrya* to determine differences between species or subgenera. Leaf clearings revealed that stomata were absent from the adaxial epidermis but abundant on the abaxial surface between the veins. The long axes of the stomata ran almost parallel to the veins. The mean length of the stomata (for all species) was 56 microns, but means for the species ranged from 48 to 74 microns. Subsidiary cells surrounded the distal one-half to two-thirds of the guard cells. The shape of the subsidiary cells can be like the sinuous epidermal cells or slightly more rounded and circular (Fig. 9d,f).

In face view, the epidermal cell walls fit together like the pieces of a jigsaw puzzle (Fig. 9). This interlocking is best exemplified by the abaxial epidermal cells, which have a more highly irregular outline than the adaxial ones. The cells above and below the veins, however, have straight walls. The slightly elongate axes of the cells are oriented parallel to the veins and point in the direction of the leaf margin.

In cross section, the abaxial epidermis and adaxial epidermis form a single, compact layer of relatively thick-walled cells (Fig. 9g,h). Palisade parenchyma is absent from the mesophyll, which is composed mostly of large intercellular air spaces surrounded by long, cylindrical, parenchymatous cells. An arm of collenchyma extends from the abaxial epidermis to the vein, where it forms a sheath around the vein but does not continue to the adaxial side of the leaf. Leaf anatomy was similar in all species of *Polybotrya*, probably because the entire genus occupies a similar habitat.

Hair types. Two fundamentally different types of hairs occur in *Polybotrya*. One type intergrades with scales, the other does not. The nonintergrading type is erect or spreading, usually cylindrical, and whitish or tawny. The size of hairs of this type varies tremendously, from unicellular hairs that are less than 0.1 mm long and not visible to the naked eye to readily visible acicular hairs that have up to 15 cells and are up to 2 mm long (Fig. 10 a–i,k). The apical cell is pointed, rarely rounded. All but five species of *Polybotrya* have this kind of hair.

Hair of the second type is fundamentally different from hair of the first type because each hair is a tiny, uniseriate scale and, therefore, by definition, a hair. Every intermediate stage exists between these hairs and the scales, as evidenced by studying their change in form from the apex to the base of the costa (Figs. 10j & 36a,b). At the apex of the costa,

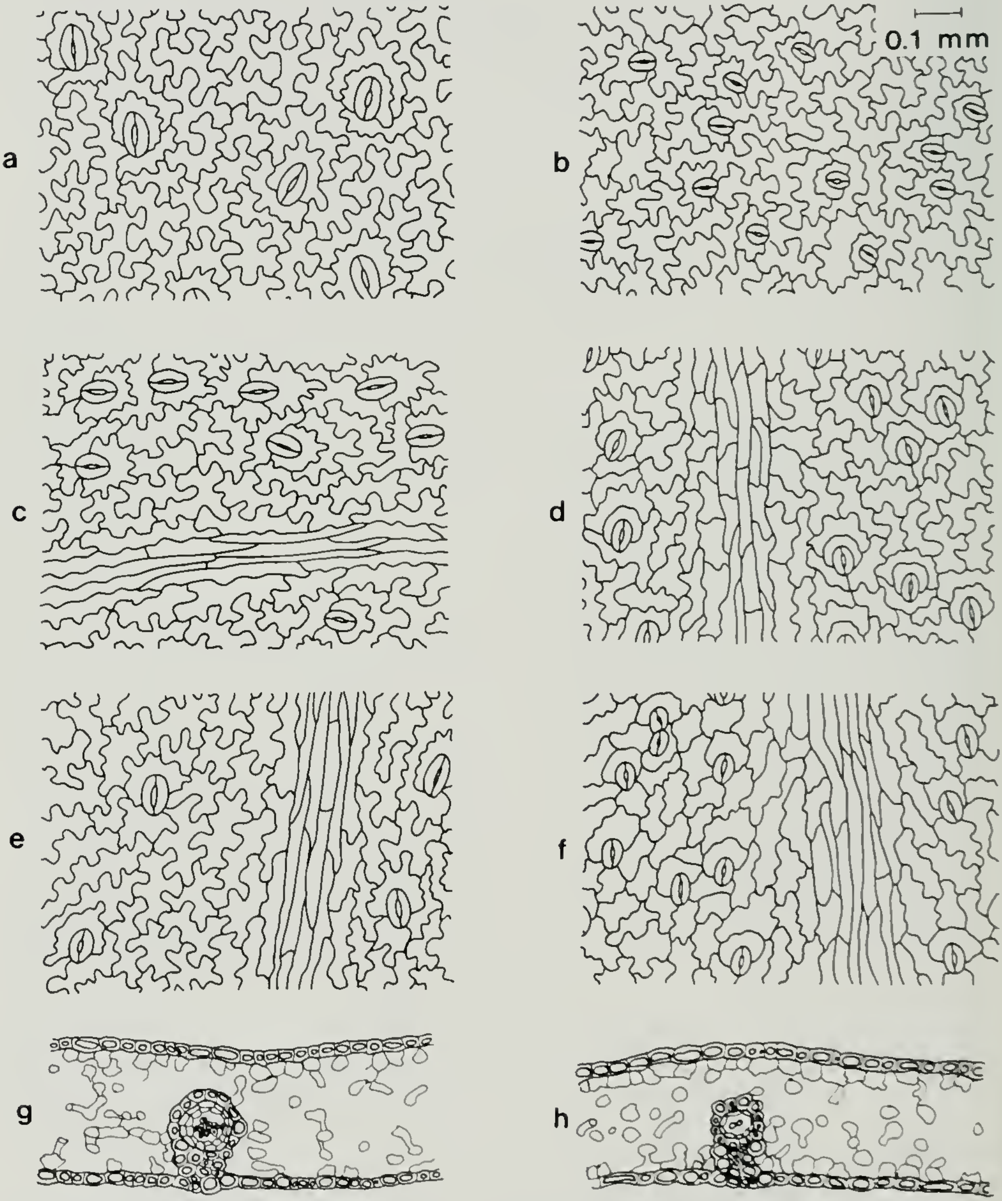

FIGURE 9. Leaf anatomy of *Polybotrya*. a–f. face views of the abaxial leaf epidermis. The elongated cells with straight walls lie above the veins. g, h. cross sections of the leaf. a. *Polybotrya serratifolia*; b. *P. pubens*; c. *P. fractiserialis*; d. *P. canaliculata*; e, g. *P. crassirhizoma*; f, h. *P. speciosa*.

only the tiny uniseriate scales, the "hairs," occur. These are readily distinguished from other hairs by their flattened cells, appressed habit, and darkened transverse walls. Towards the base of the costa, the hairs become longer and are composed of more cells; soon are found "hairs" that are two cells wide near their base, that is, scales. These small scales grade imperceptibly into the larger scales on the rhachis. The scales on the rhachis and costae are, therefore, developmentally homologous with this second kind of hair.

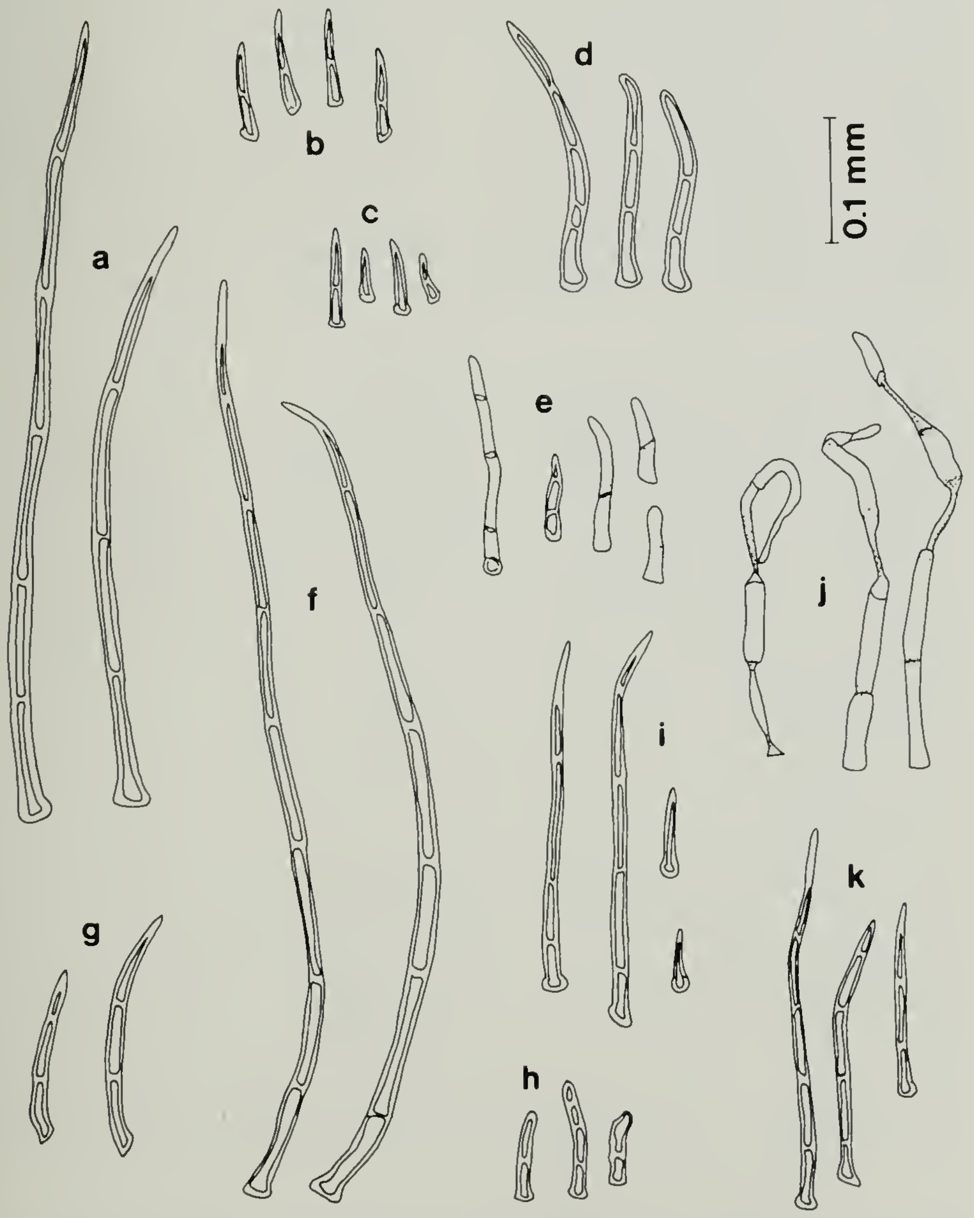

FIGURE 10. Hair types in *Polybotrya* taken from the abaxial surface of the costa. a. *P. pubens*; b. *P. semipinnata*; c. *P. altescandens*; d. *P. pittieri*; e. *P. alfredii*; f. *P. glandulosa*; g. *P. speciosa*; h. *P. osmundacea*; i. *P. caudata*; j. *P. lechleriana* (reduced scale type); k. *P. cylindrica*.

These hairs are called proscales since they are developmentally, and probably evolutionarily, precursors to scales (Moran 1986).

Proscales occur on the lamina and axes of all species of *Polybotrya* and all genera of dryopteroid ferns. Proscales are, however, so minute that pteridologists often overlook them or do not bother to mention them. Proscales are smallest on the distal parts of the lamina (Fig. 49h) and at least 30× is needed to see them. Their flattened cells, often having reddish cross walls, occasionally twist upon drying, imparting the appearance of a *Ctenitis*-hair. These are not true *Ctenitis*-hairs, however, because such hairs never intergrade with scales (Christensen 1913). This nonintergrading feature is rarely mentioned in the definition of *Ctenitis*-hairs.

Fertile Leaves

Moran (1987) has presented a detailed study of the sterile and fertile leaves (trophophylls and sporophylls) of *Polybotrya*. Below is a synopsis of the subject.

The fertile leaves of *Polybotrya* resemble a skeleton of the sterile ones because their green lamina has been reduced to a narrow wing above the veins. This extreme dimorphy, termed "holodimorphy," is distinguished from other types of dimorphy by the nearly total loss of photosynthesis in the fertile leaf (Wagner & Wagner 1977). The reduction of green tissue is the most conspicuous aspect of dimorphy, but differences in seasonality, duration, orientation, insertion on the stem, size, color, texture, and venation are also involved. Thus, sterile-fertile leaf dimorphy is an ensemble of characteristics and not merely a single feature of the leaf. Pteridologists previously described the sori of *Polybotrya* as acrostichoid, but three types of sori occur in the genus: botryoid, coenosoric, and a new type here termed "amphiacrostichoid." Botryoid sori, which are round and discrete, are considered primitive on the basis of outgroup comparison with other dryopteroid ferns (Fig. 38b). The coenosoric type, which are oblong to linear, probably evolved from the botryoid type by basipetal fusion of the sori (Fig. 35h). The amphiacrostichoid type developed from a coenosoric ancestor by the expansion of the margins of the receptacle beyond the original adaxial surface; as a result, the receptacle assumed its own adaxial surface and sporangia appeared on both surfaces of the leaf (Fig. 30g). Coenosoric and amphiacrostichoid sori contain diplodesmic veins that are developmentally homologous with veins of the sterile leaf.

Sporangia. The sporangial stalk of *Polybotrya* is three-celled at its apex, immediately below the capsule. Below the apex, however, only two rows of cells occur, each three to four (rarely 5) cells long (Fig. 11). Where the two rows of the base join the three cells at the apex, a paraphysis occurs; it is always uniseriate, unbranched, and multicellular. About three-fourths of the species of *Polybotrya* have paraphysate sporangial stalks, but paraphyses occur on only 40–80 percent of the stalks from a single sample. In dried or rehydrated material, the apical cell of the paraphysis is smaller and shriveled compared to the cells below. In fresh material, the apical cell appears swollen and glandular. Sporangial stalks of *P. fractiserialis* are unique because they have lightbulb-shaped, glandular cells at the base of the paraphyses (Fig. 11g). The functions of these glandular cells and paraphyses are unknown.

Sporangial capsules of *Polybotrya* are typical of those found in related dryopteroid ferns. The mean number of annular cells for species of *Polybotrya* ranges from 12 to 24, with most species having between 14 and 18. Both the epistomium and hypostomium consist of three or four thin-walled, transversely elongated cells. All species of *Polybotrya* have glabrous sporangial capsules, except *P. pubens*, which has short, subulate hairs at the top of the capsule near the annulus (Fig. 30e,f). Usually two of these hairs occur on either side of the annulus, creating the impression that the capsule has "horns."

Spores. Spore sizes, measured by the longest axis, are given (when available) at the end of each species description. Numbers are for spores measured immediately after being placed in distilled water because this medium is readily available to taxonomists. Fifteen spores were measured per specimen.

Spores of most *Polybotrya* species range from 45–65 microns in length, with extremes of 32 and 80 microns. According to Tryon and Tryon (1982), *Polybotrya* has relatively large spores compared to those of other genera in their tribe Dryopteroideae. The spores appear dark brown when viewed with transmitted light under a compound microscope but deep orange when viewed with reflected light under a dissecting microscope.

Spores of *Polybotrya* are fairly uniform within the genus compared to the variation encountered in other genera of dryopteroid ferns (e.g., *Dryopteris* and *Polystichum*). *Polybotrya* spores are monolete, with the aperture linear and one-third to three-fourths the length of the long axis. The aperture is often obscured by the broad perispore folds and smaller spines. The exospore appears smooth (Fig. 12), as it does in spores of most genera of dryopteroid ferns. The perispore consists of two layers: the lower layer is thin and appressed to the exospore; the upper layer is thicker, with inflated folds and echinate to various degrees (Fig. 12). No constant differences were found between the three subgenera or smaller species groups.

The principal differences between species appear in the prominence and density of perisporal folds and spines. Typically, the in-

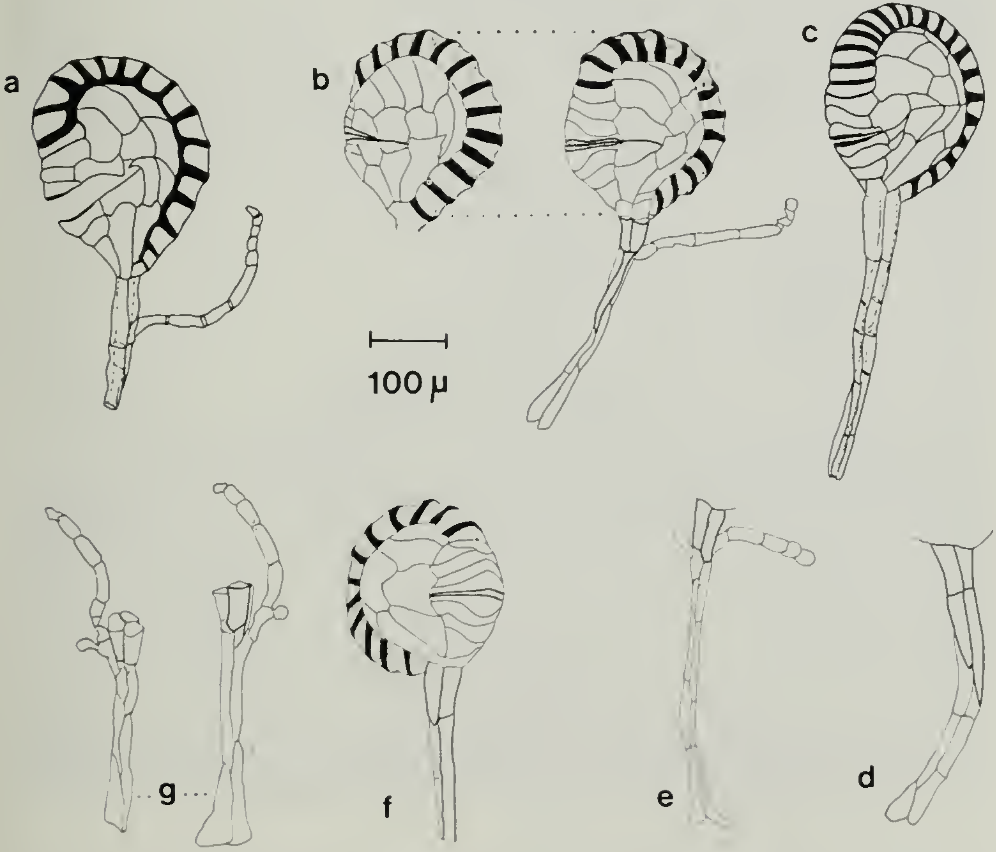

FIGURE 11. Sporangia of various *Polybotrya* species. a. *P. attenuata*; b. *P. sorbifolia*, showing both sides of the same sporangium; c. *P. espiritosantensis*; d. *P. speciosa*; e. *P. osmundacea*; f,g. *P. fractiserialis* (note in g the globose, glandular cell at the base of the paraphysis).

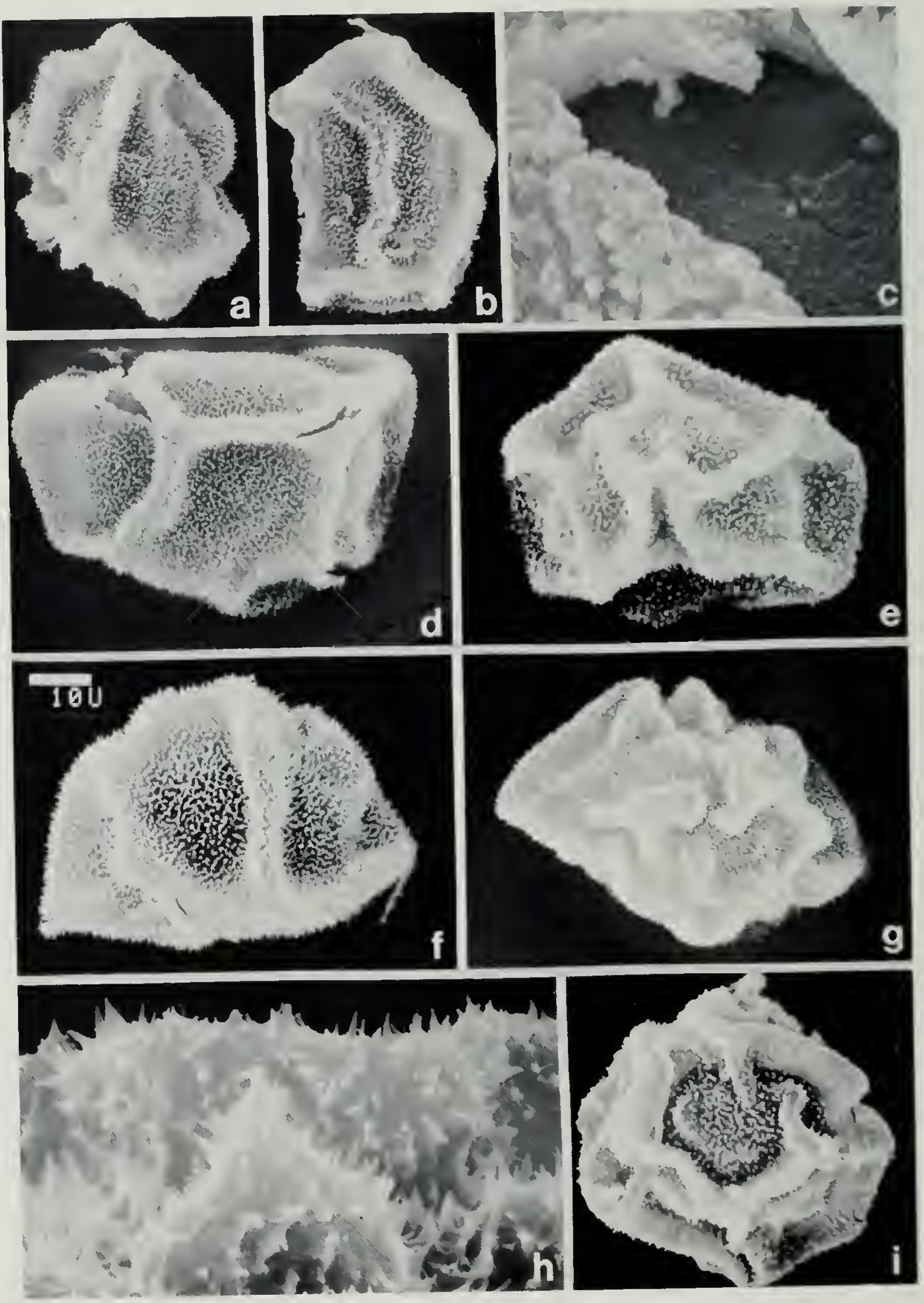

FIGURE 12. Spores of *Polybotrya*. a. *P. semipinnata*; b. *P. osmundacea*; c. *P. serratifolia*; d. *P. pittieri*; e. *P. gomezii*; f. *P. alfredii*; g. *P. crassirhizoma*; h. *P. cylindrica*; i. *P. speciosa*. a: *Duarte et al. 65322* (F). b: *C. Schunke 380* (GH). c: *Fendler 261* (GH). d: *Lellinger & de la Sota 251* (US). e: *Moran 3241* (CR). f: *Moran 3168* (CR). g: *Plowman et al. 4025* (GH). h: *Handro 2228* (GH). i: *Webb 26* (GH). c and h are × 5000, all others are × 1000.

flated folds are well developed and the spines are so numerous that they impart a "fuzzy" appearance. However, the folds may be relatively low, as in *P. goyazensis* and *P. sorbifolia*, or the spines may be reduced in height and/or density, as in *P. speciosa* (Fig. 12i). Species may also differ in spore size. This range is clearly shown by the two terrestrial species in the subgenus *Sorbifolia: P. sorbifolia* and *P. fractiserialis* differ greatly in spore size (40–47 and 52–56 microns long, respectively), a difference that probably reflects different ploidy levels.

Comparison of the spores shown in Figure 12 with the spores of other dryopteroid ferns illustrated by Tryon and Tryon (1982) shows that the spores of *Polybotrya* are most like those of *Maxonia* and *Stigmatopteris* (Tryon and Tryon include *Cyclodium* in *Stigmatopteris*). *Cyclodium*, which is most closely related to *Polybotrya*, has spores similar to those of *Polybotrya* but less spiny (A.R. Smith 1986). This observation supports evidence from external morphology that these genera form a closely related group.

Chromosome Numbers

The only previous reports of chromosome numbers in *Polybotrya* came from two separate counts of *P. osmundacea*, one from Jamaica and the other from Trinidad; both gave a chromosome number of $n=41$ (Walker 1966; Smith & Mickel 1977). To add to the information about chromosome numbers in the genus, I collected meiotic material during fieldwork in Latin America. Young fertile segments were placed for 3–5 hours in distilled water saturated with paradichlorobenzene. The segments were then removed, blotted gently, and placed in a fixative of 3:1 ethyl alcohol to glacial acetic acid. The material was stored in a freezer until it could be examined. Sporangia were squashed in a drop of aceto-carmine and then photographed.

This work recorded new chromosome number counts for four species—*P. alfredii*, *P. altescandens*, *P. polybotryoides*, and *P. serratifolia* (Fig. 13). Each of the four counts had a chromosome number of $n=41$, a finding that argues, along with morphological features, for classifying *Polybotrya* among the dryopteroid ferns, all of which have $n=41$. Chromosome counts are still needed from the other species of *Polybotrya*, especially where polyploidy may be involved in the evolution of one species from another, as in *P. fractiserialis* and *P. sorbifolia*.

Cladistic Analysis of the Species

A cladogram of species relationships was constructed using the PAUP program, version 2.3 (Swofford 1985; PAUP is an acronym for Phylogenetic Analysis Using Parsimony). Table 5 shows the input data used in the analysis, and Table 6 gives the characters and character states used in the input data matrix. The character state trees (hypothesized evolutionary pathways) for the characters (Table 6) are shown in Figure 14. Further information on the characters and justification of their postulated evolutionary pathways is given in the Morphology and Anatomy section.

Because of homoplasy in the data set, PAUP found a large number of equally parsimonious cladograms. Therefore, a consensus cladogram (Fig. 15) was printed for the first 50 trees to determine the branching patterns they all had in common. The 50 trees agreed on the branching patterns for 12 species—about one-third of the genus. The groups that had congruent branching patterns were subgenera *Soromanes* and *Sorbifolia* (Fig. 15, *serratifolia—espiritosantensis*) and the group of species related to *P. caudata* (Fig. 15, *caudata—pubens*). Homoplasy in the remaining species accounted for the numerous, equally parsimonious cladograms. Nevertheless, distinct groups of species are shown on the consensus cladogram, a result that supports the following subdivision of the genus.

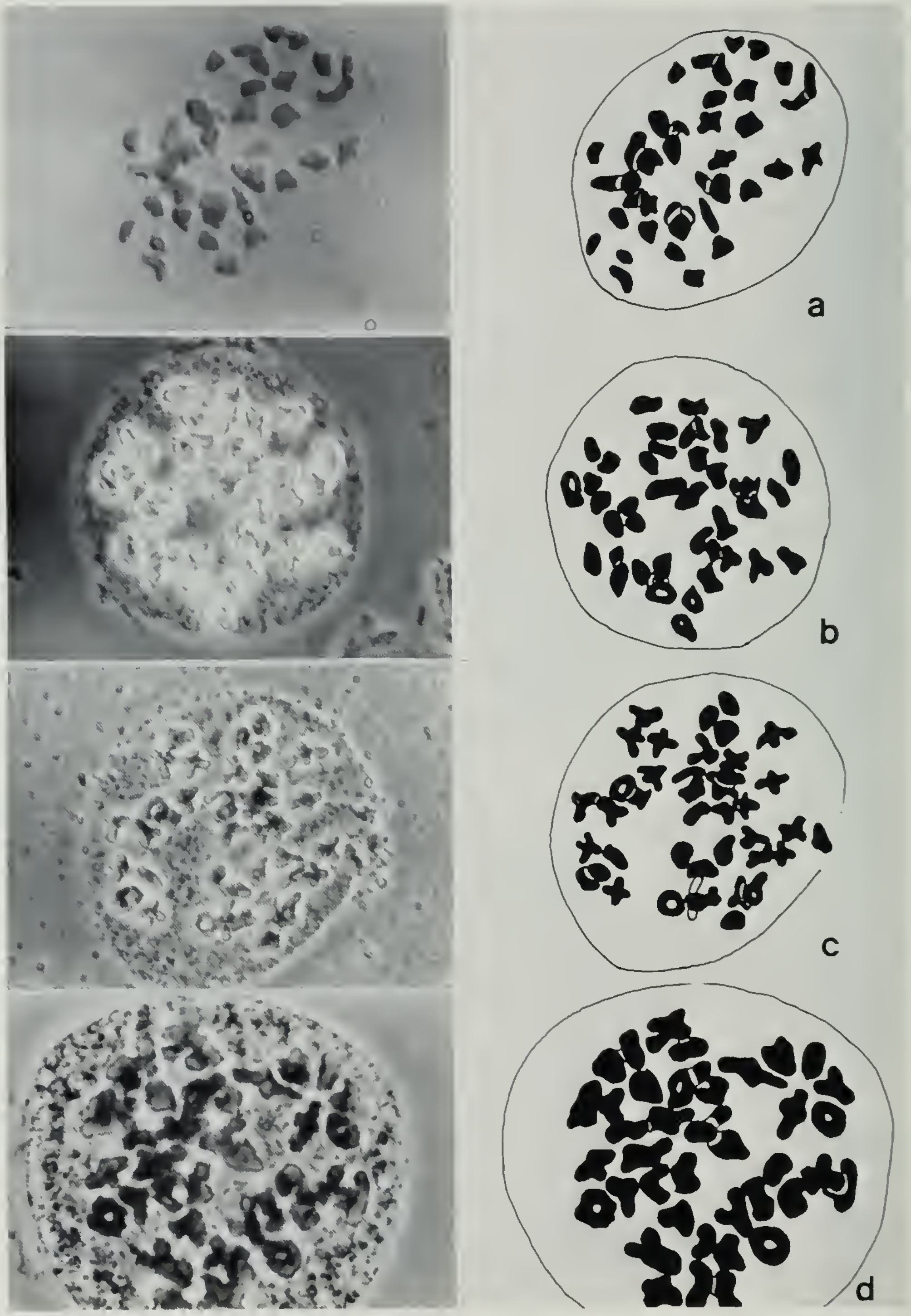

FIGURE 13. Chromosome squashes of four species of *Polybotrya*. All squashes have *n* = 41. My interpretations are at the right. a. *P. altescandens*, Ecuador, Pichincha, *Moran 3559* (GH); b. *P. polybotryoides*, Costa Rica, Cartago, *Moran 2178* (MO); c. *P. serratifolia*, Venezuela, Trujillo, *Moran 3709* (MO); d. *P. alfredii*, Costa Rica, Cartago, *Moran 2442* (CR).

TABLE 5. Data matrix for cladistic analysis of 35 species of *Polybotrya*. See text for discussion of character states and polarity. Ancestor = hypothetical ancestor possessing all primitive character states. ? = unknown character state. NA = not applicable.

	Character States																			
Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
serratifolia	5	2	3	0	NA	0	0	1	1	0	2	1	1	0	0	1	0	0	0	0
polybotryoides	5	2	3	0	NA	2	0	1	1	0	2	1	1	0	0	1	1	0	0	0
suberecta	5	2	3	0	NA	1	0	2	2	0	0	1	1	0	0	1	0	0	0	0
andina	5	2	3	0	NA	1	0	1	2	0	0	1	1	0	1	1	0	0	0	0
sorbifolia	5	0	3	0	NA	0	0	1	1	0	2	1	1	0	0	1	0	1	0	0
fractiserialis	5	0	3	0	NA	0	0	1	1	0	2	1	1	0	0	1	0	1	0	1
crassirhizoma	5	0	3	0	NA	0	0	1	1	0	2	1	2	0	0	1	0	0	0	0
espiritosantensis	4	0	4	0	2	0	0	1	1	0	2	1	2	0	0	3	1	0	0	0
caudata	3	1	4	1	1	0	1	0	2	1	0	1	1	0	0	1	0	0	0	0
goyazensis	3	1	4	1	1	0	0	0	2	1	0	1	2	0	0	1	0	0	0	0
pubens	3	1	4	1	1	0	0	0	0	1	0	1	3	0	0	1	0	0	0	0
glandulosa	3	1	2	1	1	0	1	0	0	1	0	2	1	0	0	1	0	0	0	0
lechleriana	0	1	2	1	0	0	?	1	0	0	0	1	3	0	1	0	0	0	1	0
attenuata	2	1	2	1	0	0	0	1	1	0	0	0	1	0	1	2	0	0	2	0
stolzei	2	1	?	1	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0
alfredii	1	1	3	1	0	0	1	1	1	0	0	1	1	0	0	0	0	0	0	0
botryoides	0	1	2	1	0	0	1	1	1	0	0	1	1	0	0	0	0	0	0	0
lourteigiana	3	1	3	1	0	0	?	1	1	0	0	1	1	0	0	0	0	0	0	0
pittieri	2	1	2	1	0	0	0	1	1	0	0	0	1	0	1	0	0	0	0	0
cylindrica	1	1	3	1	0	0	1	1	1	0	0	1	1	0	0	1	0	1	0	0
hickeyi	1	1	1	1	1	0	1	1	1	0	0	1	1	0	0	1	0	0	0	0
puberulenta	2	1	?	1	1	0	0	1	0	1	0	0	0	0	0	1	0	0	0	0
alata	3	1	?	1	1	0	0	1	2	0	0	1	0	0	0	0	2	0	0	0
aequatoriana	2	1	3	1	1	0	0	1	1	0	0	1	0	0	0	1	0	0	0	0
appressa	3	1	?	1	1	0	1	1	1	0	0	0	1	0	0	1	0	0	0	0
altescandens	3	1	3	1	1	0	0	1	1	0	0	1	0	0	0	1	0	0	0	0
gomezii	3	1	3	1	1	0	0	1	1	0	2	1	1	0	0	3	0	0	0	0
osmundacea	2	1	3	0	1	0	?	1	1	0	1	1	1	0	0	1	0	0	0	0
cyathifolia	2	1	3	0	1	0	0	1	2	0	1	1	1	0	0	1	0	0	0	0
latisquamosa	1	1	?	0	1	0	1	1	1	0	1	1	2	0	0	1	0	0	0	0
sessilisora	2	1	1	0	1	0	0	1	1	0	1	0	1	0	0	2	0	0	0	0
canaliculata	1	1	2	0	1	0	0	1	1	0	2	1	1	0	0	0	0	0	0	0
semipinnata	3	1	3	0	1	0	0	1	1	0	0	1	2	0	0	1	0	0	0	0
speciosa	2	1	3	0	1	0	0	1	0	1	0	1	2	1	0	1	0	0	0	0
pilosa	2	1	3	0	1	0	0	0	0	1	0	1	2	1	0	1	0	0	0	0
ancestor	3	1	1	0	1	0	0	1	1	0	1	1	0	1	0	1	0	0	0	0

TABLE 6. Characters and character states used in the cladistic analysis of 35 species of *Polybotrya*. The numbers given to each character state correspond with those shown on one of the cladograms in Figure 14.

1. Dissection of sterile leaves (Fig. 14a). 0 = 4-pinnate; 1 = 3-pinnate-pinnatifid; 2 = 3-pinnate; 3 = 2-pinnate-pinnatifid; 4 = 2-pinnate; 5 = 1-pinnate.
2. Venation (Fig. 14b). 0 = close and long-parallel; 1 = obliquely ascending; 2 = anastomosing.
3. Type of fertile leaf (Fig. 14c). 1 = botryoid, but with lamina not completely reduced; 2 = fully botryoid; 3 = coenosoric; 4 = caudate.
4. Pinnule arrangement (Fig. 14d). 0 = anadromic; 1 = catadromic.
5. Symmetry of pinnule base (Fig. 14b). 0 = symmetrical and truncate; 1 = prolonged acroscopically and truncate; 2 = symmetrical and cuneate.
6. Submarginal connecting strand (Fig. 14e). 0 = absent; 1 = several connections; 2 = present.
7. Stem scale base (Fig. 14d). 0 = attached by a single point; 1 = attached across the width of the base.
8. Hair type (Fig. 14b). 0 = long, acicular; 1 = small, jointed; 2 = uncinate.
9. Pubescence of laminar surface (Fig. 14b). 0 = both surfaces pubescent; 1 = glabrous; 2 = abaxial surface pubescent.
10. Pubescence of laminar margin (Fig. 14d). 0 = glabrous; 1 = ciliate.
11. Pubescence of costae (Fig. 14b). 0 = uniform and dense pubescence; 1 = moderately pubescent or with scattered hairs; 2 = glabrous.
12. Lamina base (Fig. 14b). 0 = deltate; 1 = reduced; 2 = cuneate.
13. Scale color (Fig. 14f). 0 = golden or yellow; 1 = brown; 2 = reddish or bright castaneous; 3 = cream or whitish.
14. Receptacular hairs (Fig. 14d). 0 = unbranched; 1 = branched.
15. Size of lamina (Fig. 14d). 0 = > 1 meter; 1 = < 1 meter.
16. Costal scale type (Fig. 14f). 0 = flaccid and ovate; 1 = linear to narrowly lanceolate; 2 = linear and tortuous; 3 = caducous.
17. Apex of sterile leaf (Fig. 14d). 0 = pinnatifid; 1 = subconform.
18. Stem habit (Fig. 14d). 0 = hemiepiphytic; 1 = terrestrial.
19. Shape of the tertiary pinnules (Fig. 14b). 0 = ligulate; 1 = oblong or ovate; 2 = obovate.
20. Spore size (Fig. 14d). 0 = 40–50 microns long; 1 = 52–56 microns long.

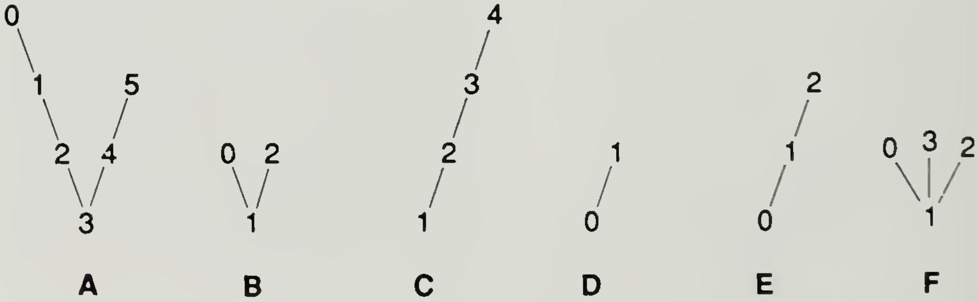

FIGURE 14. Character state trees used in the cladistic analysis of 35 species of *Polybotrya*. Table 6 lists characters and character states. For example, tree B represents the hypothesized evolutionary pathway for character states 2, 11, 12, and 19.

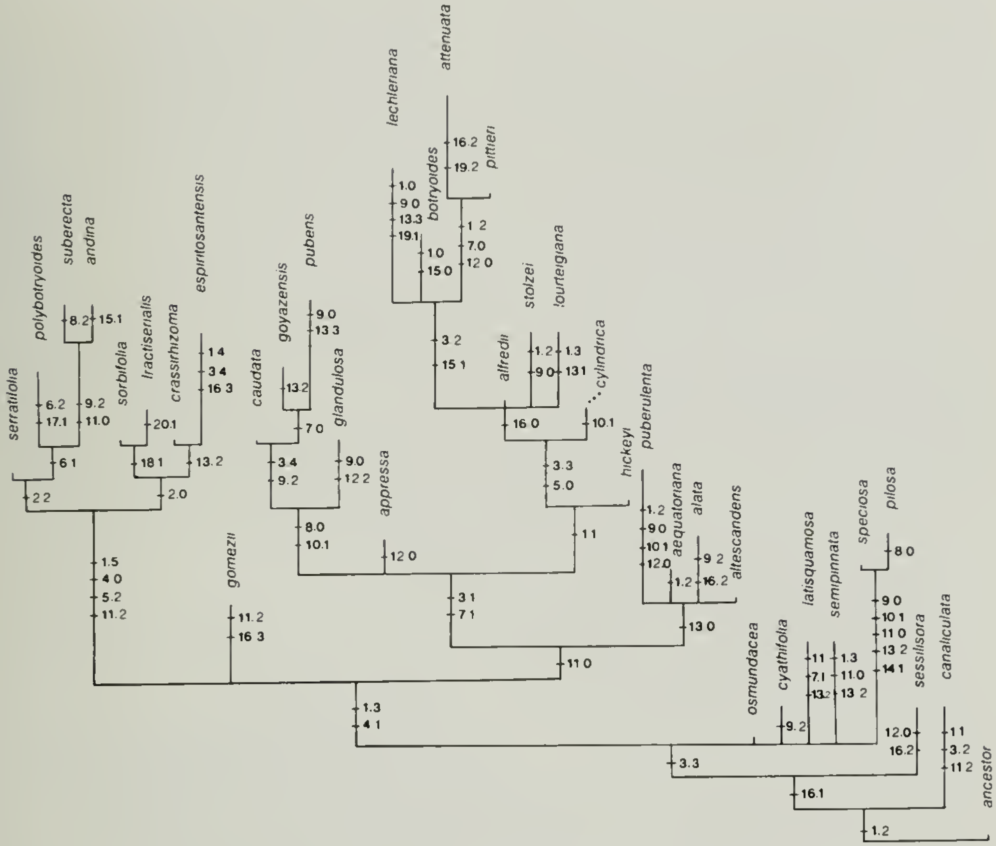

FIGURE 15. Consensus tree for 50 equally parsimonious cladograms of species relationships in *Polybotrya*. The number before the decimal refers to the character; the number after the decimal refers to the character state (Table 6).

Subdivision of the Genus

I subdivide *Polybotrya* into three easily recognized subgenera: 1) *Soromanes*, sterile leaves 1-pinnate, veins anastomosing; 2) *Sorbifolia*, sterile leaves 1-2-pinnate, veins free, close, and parallel; 3) *Polybotrya*, sterile leaves decompound, veins free.

Subgenus *Soromanes* ranges throughout Central America and the Andes, primarily in mountainous areas, but it is conspicuously absent from the Amazon basin and from southeastern Brazil (Maps 1 & 2). This subgenus consists of four well-defined species (species nos. 1–4) that occur in montane forests, primarily from 500–2000 m (Fig. 4).

The only contemporary pteridologist who has maintained *Soromanes* at the generic level is Pichi-Sermolli (1977), who also placed *Soromanes* and *Polybotrya* on separate branches of his phylogenetic diagram, associated with different generic groups. Other pteridologists, such as Christensen (1905), Copeland (1947), and Tryon and Tryon (1982) have subsumed *Soromanes* in *Polybotrya*. My research on both genera has shown that *Soromanes* is the closest genus to *Polybotrya*. Both genera share a unique stem anatomy: a circular grouping of meristeles with each meristele surrounded by a dark, sclerenchymatous sheath (Figs. 6 & 16g). No other fern genus has this unmistak-

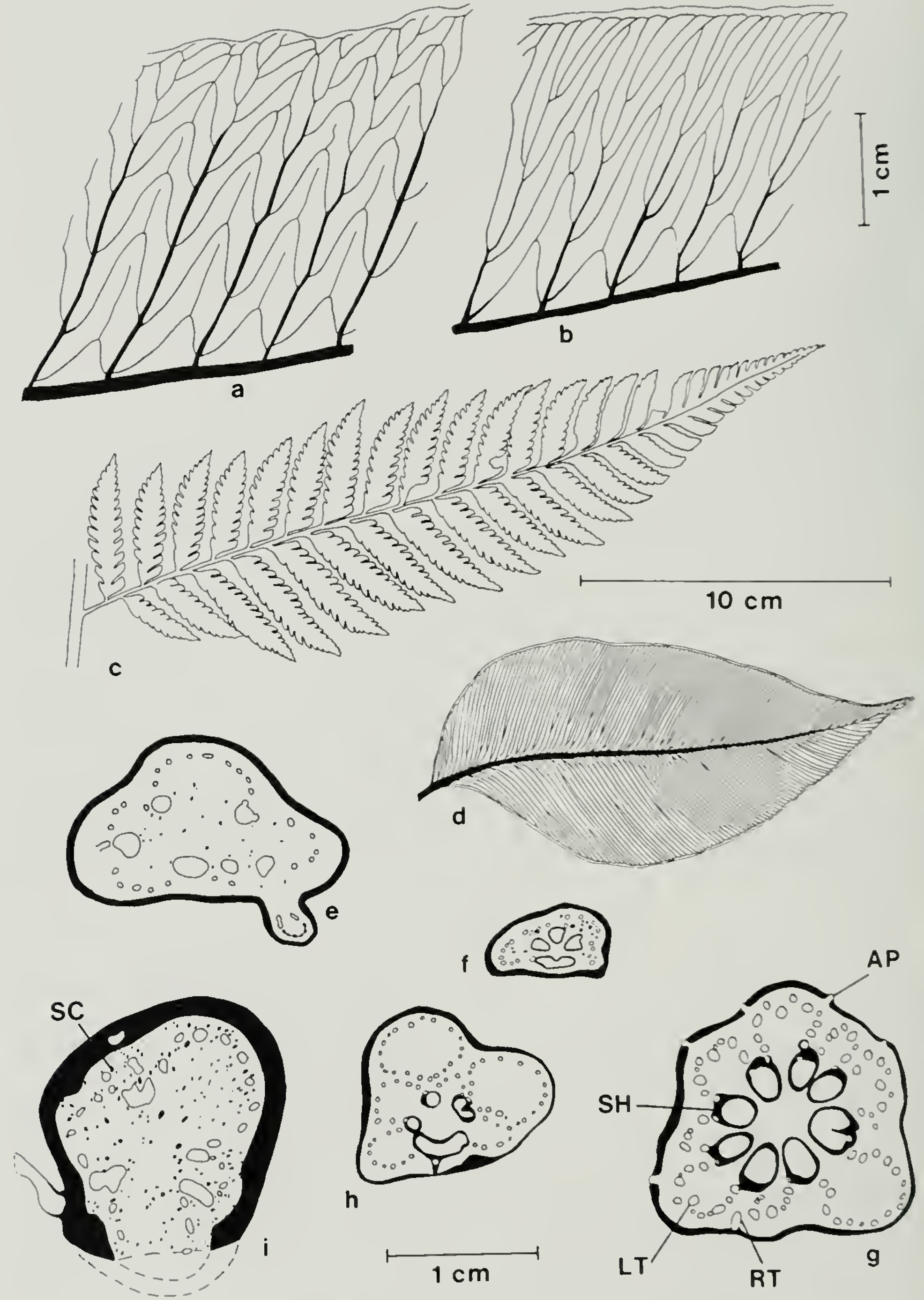

FIGURE 16. *Polybotrya* and closely related genera. a. venation of sterile pinna, *Cyclodium meniscioides*; b. venation of sterile pinna, *Polybotrya polybotryoides*; c. pinna of *Cyclodium trianae* var. *trianae* (compare to *P. sessilisora* and *P. osmundacea*); d. sterile pinna of *Olfersia cervina*, showing venation entirely unlike any *Polybotrya*; e–i. stem cross sections (dorsal surface is up) of e. *Maxonia apiifolia*, f. *Lomariopsis fendleri*, g. *Polybotrya caudata*, h. *Bolbitis lindigii*, i. *Olfersia cervina*. AP aerophore; LT leaf trace; RT root trace; SH sclerenchyma sheath; SC sclereid or stone cell.

able stem anatomy, one of the hallmarks of *Polybotrya*. Other compelling similarities, such as holodimorphic leaves, long-creeping and densely scaly stems, petiole anatomy, and spore morphology, further demonstrate that *Soromanes* and *Polybotrya* are closer genealogically to each other than to any other genus; that is, they are sister groups. In my opinion, these similarities justify including *Soromanes* in *Polybotrya*.

Subgenus *Sorbifolia* is primarily South American (Maps 3 & 4) and consists of four species (species nos. 5–8) that occur in low-elevation forests primarily from 0–1200 (1500) m (Fig. 4). Two species, *P. sorbifolia* and *P. fractiserialis*, are very closely related and contrast sharply with the rest of the genus because of their terrestrial stems. These two species also have distinctive venation: the veins are long, parallel, and sharply ascending (Figs. 24 & 25). The third species, *P. crassirhizoma*, is dissimilar from the others and has dull orange stem scales and slightly more spreading veins (Fig. 26). It is an abundant fern in the western Amazon basin, from Colombia south to Bolivia. *Polybotrya espiritosantensis* is included in this subgenus, even though its leaves are 2-pinnate because its venation (Fig. 27b) is exactly like that of *P. fractiserialis* (Fig. 25e); this similarity suggests a close relationship.

The species having decompound leaves, all free veined (species nos. 9–35), make up the subgenus *Polybotrya*, which is further subdivided into four species groups. Since I see no purpose in giving these groups formal taxonomic names, I informally refer to them with the name of a typical, widespread species for each group, e.g., the "*P. caudata* group." The first three groups described below have catadromic pinnules; the fourth has anadromic pinnules. Pinnule arrangement, however, cannot be used to classify the species groups at a higher level because no other characters correlate with it.

The *P. caudata* group (species nos. 9–12) is the most distinctive because it has peculiar, caudate fertile pinnules that are soriferous on both surfaces, that is, amphiacrostichoid. Actually, what looks like the adaxial soriferous surface is the expanded, thickened margin of the receptacle; the true, phylogenetic, adaxial surface is reduced to a thin green line (see Morphology and Anatomy section). In addition to this diagnostic sorus, the group is further united by the presence of whitish, septate, acicular hairs (Fig. 10a,f,i). *Polybotrya glandulosa* is tentatively assigned to this group because of similarities in leaf cutting and pubescence; however, it has botryoid fertile leaves. This character is constant in *P. pubens*, but both *P. caudata* and *P. goyazensis* can be glabrous. The *P. caudata* group is most frequent and abundant at low elevations from 0–1000 m, although *P. caudata* itself occasionally occurs up to 1900 m (Fig. 4).

The second species assemblage, the *P. alfredii* group, consists of eight primarily Andean species (species nos. 13–20). This group has a characteristic appearance, although it is difficult to describe because few features are constant. In general, the pinnae are short-stalked and crowded near the costa and rhachis. The pinnae bases are more or less equilateral and not acroscopically prolonged as in the rest of the genus. The tertiary segments are often oval or rounded, never narrow or strap-shaped. The grooves of the costules are either truncated by the ridges of the costa or very weakly admitted to the groove of the costa (see Morphology and Anatomy section). Most species in the *P. alfredii* group have botryoid fertile leaves.

The third species group, the *P. altescandens* group, consists of seven species (species nos. 21–27). These species, with the exception of one endemic to the mountains of Costa Rica, grow in the Andes at slightly higher altitudes than the rest of the genus (Fig. 4). This group has pinnule bases slightly to strongly asymmetric, a characteristic that helps to distinguish it from the *P. alfredii* group.

The fourth species group centers on the type of the genus, *P. osmundacea*, and differs from the rest of the genus by having anadromically arranged pinnules. As shown in the illustrations, the species (species nos. 28–35) are very similar in dissection of the leaf. The pinnule base ascends obliquely on the basiscopic side and prolongates conspicuously on the acroscopic side. This asymmetry imparts a distinctive appearance to the pinnule base (Fig. 48).

Relationships with Other Groups

Pteridologists have always classified *Polybotrya* with *Dryopteris* and such closely related genera as *Arachniodes*, *Cyclodium*, *Cyrtomium*, *Maxonia*, *Olfersia*, *Polystichopsis*, *Polystichum*, and *Stigmatopteris*. These genera share the following features with *Polybotrya*: base chromosome number $x = 41$, dryopteroid costa-costule architecture, spores monolete with prominently inflated perisporial folds, more than three vascular bundles in the petiole, and petioles and petiolules not articulate at their bases.

Familial Relationships

The dryopteroid genera are most closely related to the tectarioid ferns, such as *Ctenitis*, *Lastreopsis*, and *Tectaria*. These genera constitute a natural group on the basis of their costa-costule architecture and special "*Ctenitis*-hairs." As noted in the Morphology and Anatomy section of this monograph, *Polybotrya* lacks *Ctenitis*-hairs, and their absence argues strongly against a close relationship with the tectarioid genera. Furthermore, *Polybotrya* has costa-costule architecture of the dryopterioid type rather than the tectarioid type.

Polybotrya might possibly be construed as a member of the Lomariopsidaceae. Three genera of Lomariopsidaceae—*Lomagramma*, *Lomariopsis*, and *Teratophyllum*—closely resemble *Polybotrya* in overall habit because they have densely scaly, high-climbing stems, strongly differentiated sterile and fertile leaves, and nonindusiate, acrostichoid sori. Furthermore, at the anatomical level, the three genera have diplodesmic venation and dark, sclerenchymatous sheaths surrounding each meristele in the stem. Although no pteridologist has ever classified *Polybotrya* with the Lomariopsidaceae, these similarities prompt me to consider the possibility.

Stem anatomy is tremendously important in the taxonomy of *Polybotrya* and the Lomariopsidaceae. The stem anatomy of *Polybotrya* is unique and has been thoroughly described in the Morphology and Anatomy section. The stem anatomy of the Lomariopsidaceae is also unique among ferns because it has a broad, strap-shaped, ventral meristele that differs from the remaining circular or oblong meristeles (Fig. 16f,h). Like *Polybotrya*, each meristele is surrounded by a dark, sclerenchymatous sheath. This elongated ventral meristele creates a dorsiventral dictyostele. Presumably, this ventral meristele was formed during phylogeny by the fusion of two, once-distinct meristeles like the upper ones (Holttum 1978). In fact, the two ventral meristeles have not completely fused in *Lomariopsis*, as evidenced by the shallow indentation in the ventral band (Fig. 16f). The ancestor of the Lomariopsidaceae, therefore, had a radially symmetrical dictyostele of several to many, circularly arranged meristeles with each meristele surrounded by a dark, sclerenchymatous sheath. In other words, the ancestral stem anatomy was like that of *Polybotrya*. If one looks at Figure 16g, a cross section of a *Polybotrya* stem, and imagines what it would look like if the two or three ventral meristeles were fused into a single meristele, the result would be a replica of the stem anatomy of the Lomariopsidaceae. This compelling similarity in stem anatomy suggests that *Polybotrya* and the Lomariopsidaceae arose from a similar ancestral stock among the dryopteroid ferns. The possibility also exists, however, that parallel evolution accounts for these similarities in stems adapted for climbing.

The leaf architecture of the two differs, however, and most species of Lomariopsidaceae have simply pinnate leaves. The leaves of *Polybotrya*, like those of most dryopteroid ferns, are primitively decompound. All Lomariopsidaceae, except *Bolbitis*, have articulate leaves and/or pinnae. In contrast, *Polybotrya* and other dryopteroid genera have nonarticulate leaves and/or pinnae. In the climbing genera *Lomariopsis* and *Teratophyllum*, leaves on the terrestrial portion of the stem (bathyphylls) differ greatly from those on the scandent portion (acrophylls). In *Lomariopsis*, the bathyphylls are less divided (usually simple and entire) than the acrophylls, and in *Teratophyllum* they are more dissected than the acrophylls. In *Polybotrya*, however, the bathyphylls and acrophylls are about the same size and shape.

Venation is yet another difference. Several kinds of venation occur in the three genera of Lomariopsidaceae most similar to *Polybotrya*. *Teratophyllum* has simple or forked veins, as does *Lomariopsis*, except that the veins of the former unite with the cartilaginous margin (Holttum 1978). *Polybotrya* also has free veins, but the pattern is entirely different from that of these two genera, as can be seen by comparing the illustrations in this monograph with those shown by Holttum (1978, Figs. 1–8). The veins of *Lomagramma* differ completely from those of these three genera; its veins form a network of three or more rows of oblique areoles without main veins. Venation, therefore, does not support a relationship between *Polybotrya* and the Lomariopsidaceae.

In summary, *Polybotrya* and some genera of Lomariopsidaceae share the following characteristics: climbing stems, dimorphic sterile and fertile leaves, diplodesmic veins, and dark sclerenchymatous sheaths surrounding each meristele. The two groups, however, contrast sharply in such features of leaf architecture as the amount of dissection, pinnae articulation, acrophylls versus bathyphyll differences, venation patterns, and stem anatomy. This conflicting evidence is difficult to assess. Certainly, the climbing habit, sterile-fertile leaf dimorphy, and diplodesmic veins have arisen many times in ferns, but the similarity in stem anatomy is less easily explained. I suspect, however, that the Lomariopsidaceae may have had a separate origin among the dryopteroid ferns, apart from *Polybotrya*. Strong evidence exists that *Polybotrya* was derived from a *Cyclodium*-like ancestor (see below).

Relation to Similar Dryopteroid Genera

Maxonia. This monotypic genus was first described by Christensen (1916), who observed that his new genus "must stand between *Polybotrya* and certain species of *Dryopteris* grouped with *D. amplissima* [*Arachniodes*]." Copeland (1947) also held that *Maxonia apiifolia* (Swartz) C. Chr. represented a phylogenetic intermediate between *Arachniodes* and *Polybotrya* (Fig. 17), and most later pteridologists have agreed that *Maxonia* is intimately related to *Polybotrya*.

Maxonia and *Polybotrya* appear very similar because both have highly differentiated sterile and fertile leaves and densely scaly, climbing stems. Nevertheless, a comparison of stem anatomy shows some important differences (Fig. 16e,g). The most evident dissimilarity is that each meristele of *Maxonia* is not surrounded by a dark sclerenchymatous sheath as in *Polybotrya*. Also, the dictyostele of *Maxonia* is dorsiventral (Chandra 1975; Walker 1972), unlike that of *Polybotrya*, which is radially symmetrical. Clearly, *Maxonia* lacks the stem anatomy that characterizes *Polybotrya*, thus weakening the hypothesis that these genera are closely related.

Strong evidence exists that *Maxonia* is most closely related to the American species of *Arachniodes*, in particular *A. macrostegia* (Hooker) Tryon and Conant. Indeed, if *Maxonia apiifolia* had monomorphic leaves it would without doubt be placed in *Arachniodes*. The similarities between the two genera are striking and are best seen in the sterile leaves. Both genera have pinnules arranged anadromically, basal pinnae elongated basiscopically, and laminae broadened notably at the base and of similar thickish texture. In addition, the pinnules and smaller segments have cuneate bases and acute apices, thereby imparting a characteristic "streamlined" appearance to the lamina that contrasts sharply with the truncate or acroscopically prolonged bases and rounded apices in *Polybotrya*. Both *Maxonia* and *Arachniodes* have costa-costule architecture of the dryopteroid type (grooves decurrent into each other; Holttum 1984). Finally, both genera have remarkably similar brown, thickish, round-reniform indusia.

The evolution of the climbing stem of *Maxonia* poses no problem if *Arachniodes* is accepted as the ancestor. Since the American species of *Arachniodes* have creeping stems, the potential to evolve a fully hemiepiphytic stem, as in *Maxonia*, was initially present and easily achieved.

In short, *Maxonia* is similar to *Polybotrya* because it arrived at a comparable evolutionary grade or level, but it came from a different source (Fig. 17). *Polybotrya* was probably derived from *Cyclodium* (see below), and *Maxonia* from *Arachniodes*, probably from an ancestor close to *A. macrostegia*. *Maxonia* should not, however, be subsumed with *Arachniodes* because it is derived from it. It is convenient, and certainly in harmony with past taxonomic practice, to distinguish *Maxonia* generically on the basis of its leaf dimorphism and climbing stem.

Olfersia. This genus consists of a single species, *O. cervina* (L.) Kunze, the placement of which has been controversial. Most recently, pteridologists have placed *Olfersia* in *Polybotrya* because both have strongly dimorphic sterile and fertile leaves, nonindusiate sori, similar perispore morphology, and densely scaly, creeping stems. Yet *Olfersia* differs from *Polybotrya* by its venation, conform apical pinna, and stem anatomy. Moran (1986) studied *Olfersia* and concluded that it and *Polybotrya* are sister taxa best maintained in separate genera.

Cyclodium (*sensu* Smith 1986). *Polybotrya* was probably derived from an ancestor which, if it were alive today, would be placed in *Cyclodium*. This genus has two important prerequisites for the evolution of *Polybotrya*. First, the fertile leaves of *Cyclodium* are slightly to strongly dimorphic. Second, the stem is creeping in all species of *Cyclodium*, and in several species it becomes fully hemiepiphytic. *Cyclodium*, therefore, has the genetic capacity to evolve two cardinal features of *Polybotrya*: holodimorphic sterile and fertile leaves and a climbing stem.

Moreover, *Cyclodium* contains species that look remarkably like certain species of *Polybotrya*. The 2-pinnate-pinnatifid leaf of *C. trianae* (Mett.) A.R. Smith var. *trianae* is strikingly like some species of *Polybotrya* with respect to cutting and venation (cf. Fig. 16c to *P. caudata*, *P. osmundacea*, and *P. sessilisora*, Figs. 28, 47, & 51, respectively). In fact, several times during fieldwork in Ecuador, I mistook sterile leaves of *C. trianae* for terrestrial leaves of *P. caudata*. Similarity is also seen in the simply pinnate lamina of *C. meniscioides* (Willd.) Presl, which has anastomosing venation notably like that found in *Polybotrya* subgenus *Soromanes* and is also simply pinnate (Fig. 16a,b). This similarity of venation was noted long ago by Hooker and Baker (1874). I am not suggesting that these two species of *Cyclodium* gave rise to *Polybotrya*, but within both genera, species have evolved with similar characteristics, and this homologous vari-

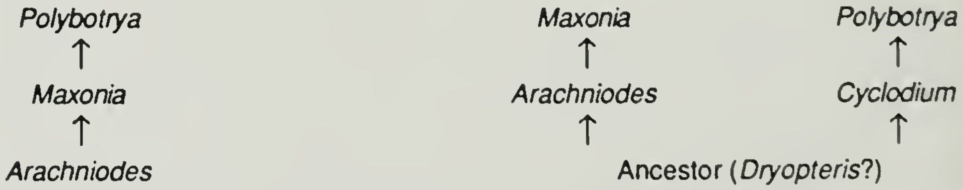

FIGURE 17. Two phylogenetic hypotheses concerning the relationships of *Maxonia* and *Polybotrya*: left, the hypothesis proposed by Christensen (1916); right, the hypothesis proposed here. See text for explanation of characters involved.

ation implies a close genetic relationship. In conclusion, the close relationship between *Cyclodium* and *Polybotrya* is evidenced by their mutual possession of dimorphic leaves, creeping stems, similar evolutionary tendencies, and, at least in some species, remarkably similar leaf dissection and venation.

Part Two: Taxonomic Treatment

In evolutionary biology almost all phenomena and processes are explained through inferences based on comparative studies. These, in turn, are made possible by very careful and detailed descriptive studies. It is sometimes overlooked how essential a component in the methodology of evolutionary biology the underlying descriptive work is.

Ernst Mayr (1982)

Notes on the Presentation of Data

In most cases, the key can be used with specimens lacking fertile leaves. Fertile leaves, however, are often helpful in identification and are given as additional characters in many couplets. The key will generally not work when leaves are less than 45 cm long. To facilitate the comparison of similar species, I have arranged the species phylogenetically rather than alphabetically. The synonymy given for each species is complete. I have kept the descriptions short by not repeating characteristics that are constant for the genus. For example, all species of *Polybotrya* have a pinnatifid leaf apex; this characteristic is mentioned only in the generic description and is not repeated in each species description. The distribution maps (see appendix) were compiled from the specimens listed in the Specimens Examined section in each species treatment. In some cases, I could not find localities despite searching various atlases, indices, and gazetteers.

The terms *basiscopic* and *acroscopic* are used frequently in the key and in descriptions to refer to the sides of pinnules (Fig. 18). The acroscopic side of a pinnule is the side directed toward the apex of the pinna bearing the pinnule. Conversely, the basiscopic side of a pinnule is that side directed toward the pinna base and rhachis. Two other frequently used terms, *catadromic* and *anadromic*, refer to pinnule arrangement. The pinnule arrangement is catadromic when the pinnule closest to the rhachis is basiscopic; when the pinnule closest to the rhachis is acroscopic, the arrangement is anadromic (Fig. 18). I have de-

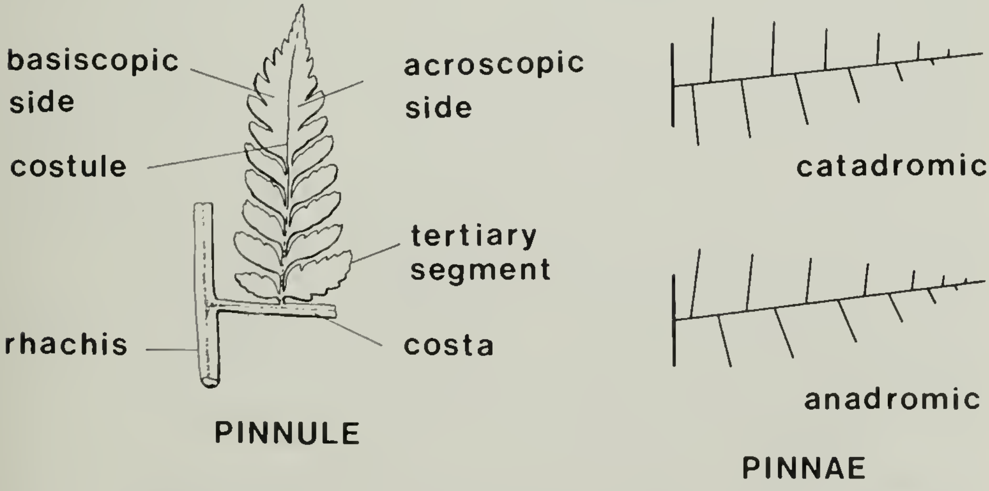

FIGURE 18. Terms frequently used to describe the leaves of *Polybotrya*. See text for further explantions.

fined the specialized terms that refer to the fertile leaves, such terms as *botryoid*, *coenosoric*, and *amphiacrostichoid*, in the Morphology and Anatomy section and in the Description of the Genus section.

Description of the Genus

POLYBOTRYA WILLD.

Polybotrya Willd., Species Plantarum, ed. 4. 5:99. 1810. Type species: *Polybotrya osmundacea* Willd.

Soromanes Fée, Mém. Fam. Foug. 2 (Hist. Acrost.) 16. 1845.Type species: *Soromanes serratifolium* Fée = *Polybotrya serratifolia* (Fée) Klotzsch.

Botryothallus Klotzsch, Bot. Zeit. 4:104. 1846. *nom. nudum*. Type species: *Botryothallus kunzei* Klotzsch *nom. nudum* = *Polybotrya serratifolia* (Fée) Klotzsch.

Stem hemiepiphytic, long-creeping, or (two species) terrestrial and short-creeping, 1.0–3.5 cm wide (excluding scales), the scandent portions unbranched, the terrestrial portions occasionally branched; dictyostelic, in cross section with a characteristic pattern of 4–10 circularly arranged meristeles, each meristele surrounded by a dark sclerenchyma sheath; *aerophores* present in most (all?) species, continuous and decurrent from the lateral aerophores of the petiole, darkening upon drying and not visible in herbarium specimens, in fresh material appearing yellowish, linear, 1–3 mm wide, slightly raised and bearing stomata; *rootlets* produced only on the ventral surface; *scales* numerous, densely covering the stem, spreading or appressed, primarily of two general types: 1) thick, dark brown, opaque, margins entire, attached across the length of the curved, thickened base, and 2) thin, variously colored (ranging from yellow, orange, red to brown), translucent, margins denticulate or highly erose, attached at a central, basal point. **Sterile leaves** up to 2.0 m long, reclining when mature, internodes generally 10–15 cm apart, bulbils lacking; *petiole* with 8–16 vascular bundles arranged in a mushroomlike outline, the base decurrent for a short distance on the stem, scaly, with scales shorter and wider than those on the stem, the aerophores present laterally as thin yellowish green lines, the adaxial surface slightly flattened, trisulcate in dried material; color stramineous, light green or darkened abaxially; *rhachis* trisulcate below becoming unisulcate above, the groove pubescent within: *lamina* papyraceous to subcoriaceous, 1-pinnate (subgenera *Soromanes* and *Sorbifolia*) or 1-pinnate-pinnatifid to 4-pinnate (subgenus *Polybotrya*), usually lanceolate, the base rarely deltate or cuneate, the apex pinnatifid; *pinnae* not articulate to the rhachis, linear, lanceolate or deltate, symmetrical or slightly prolonged acroscopically, a few species having the basal pair slightly prolonged basiscopically; *pinnules* arranged catadromically or anadromically, symmetrical or asymmetrical at the base, if asymmetrical then with the basiscopic side reduced and oblique and the acroscopic side prolonged; *grooves of costules* decurrent into the the grooves of the costa or truncated by the ridges of the costa and therefore not decurrent (intermediates exist); *veins* free or (in subgenus *Soromanes*) anastomosing, ending close to the margin, hydathodes absent; *hairs* of two types: 1) all species have tiny, reddish, appressed, jointed, flattened hairs on the lamina that grade into the scales (these actually represent reduced scales), and 2) most species have hairs that do not intergrade with the scales. these are whitish and cylindrical, ranging from unicellular and less than 0.1 mm long to 15 cells and 2.0 mm long, or uncinate. **Fertile leaves** appearing as a skeletonized version of the sterile, more ephemeral than the sterile, produced only on the scandent portion of the stem in hemiepiphytic species: *sori* nonindusiate and of three types: 1) round, discrete, usually at the tips of pinnately arranged stalks (botryoid type), 2) oblong or linear formed by the fusion of several different sori (coenosoric type), and 3) sori apparently occupying both surfaces of a caudate pinnule (amphiacrostichoid type); *diplodesmic veins* present except in botryoid sori; *sporangia* with 64 spores per capsule, the capsule glabrous except in *P. pubens* which has setose hairs at the apex near the annulus; sporangial stalks with three rows of cells at the apex, two-rowed below, paraphysate in most species by lateral hairs, these multicellular and unbranched (branched only in *P. speciosa*); annulus of 15–22 indurated cells; *spores* (32)45–65(80) microns long, dark brown when viewed with transmitted light under a compound microscope, deep orange when viewed with reflected light under a dissecting microscope, monolete, aperature linear and ⅓–¼ the length of the long axis, exospore smooth, perispore bilayered with inflated folds and echinate to various degrees. $x = 41$.

Key to the Species of Polybotrya

1. Sterile leaf 1-pinnate.

2. Veins of sterile leaf anastomosing (subgenus *Soromanes*).

3. Plants of Mesoamerica; vein tips joined into a faint, continuous, submarginal connecting strand. .... 2. *P. polybotryoides*, p. 80.

3. Plants of South America and Trinidad; vein tips usually, but not always, free.

4. Lamina pubescent abaxially with uncinate hairs. Western cordillera of Ecuador.

5. Hairs on abaxial surface 0.1–0.3 mm long, colorless, erect, 1–3 celled; free pinnae pairs 6–13 below the pinnatifid apex, mostly 15–21 × 4–5 cm. .... 3. *P. suberecta*, p. 50.

5. Hairs on abaxial surface 0.5–1.2 mm long, tawny, spreading, 5–12 celled; free pinnae pairs 4–7 below the pinnatifid apex, mostly 17–33 × 5.7–10 cm. .... 4. *P. andina*, p. 50.

4. Lamina glabrous abaxially.

6. Apex evenly pinnatifid, not similar to the lateral pinnae (Fig. 20a); vein tips free or incompletely anastomosing.

7. Stem scales linear, stiffish, mostly 0.3–1.0 mm wide, usually opaque and concolorous; fertile pinnules more than 2.0 cm long. Colombia, Ecuador, and Peru. .... 3. *P. suberecta*, p. 50.

7. Stem scales lanceolate, flaccid, mostly 1–2 mm wide, often with a dark central stripe and lighter borders; fertile pinnules generally less than 2.0 cm long. Andes of Venezuela; Trinidad. .... 1. *P. serratifolia*, p. 43.

6. Apex subconform, similar to lateral pinnae, or with one or a few small basal lobes (Fig. 20b,c); vein tips joined into a faint continuous submarginal connecting vein (see text for observation of this character). Southern Mexico to Peru. .... 2. *P. polybotryoides*, p. 80.

2. Veins of sterile leaf free (subgenus *Sorbifolia*).

8. Stem terrestrial and short-creeping; scales brown, essentially concolorous; fertile pinnules commonly round or oblong, usually less than 1 cm long.

9. Largest pinnae 7–10 times longer than broad, abaxial surface often with white or light brown, sessile, globose glands; apex of 3–7 pinnalike lobes (Fig. 24a), these with long decurrent bases; stem scales shiny brown, mostly transparent and denticulate; spores 40–47 microns long. .... 5. *P. sorbifolia*, p. 53.

9. Largest pinnae 5–7 times longer than broad, abaxial surface without glands; apex of 2 or 3 lobes, their bases not long decurrent (Fig. 25b,c); stem scales dull brown, mostly opaque with entire or subentire margins; spores mostly 52–56 microns long. .... 6. *P. fractiserialis*, p. 54.

8. Stem hemiepiphytic and long-creeping; scales reddish brown or orange, with a prominent central stripe and lighter borders; fertile pinnules linear and usually more than 1 cm long. .... 7. *P. crassirhizoma*, p. 58.

1. Sterile leaves 1-pinnate-pinnatifid to 4-pinnate (subgenus *Polybotrya*).

10. Pinnules of medial pinnae catadromic (Fig. 18).

11. Rhachis and costae pubescent, hairs 1.0–2.5 mm long. Amazonian lowland forests.

12. Lamina more than 15 cm wide at the base; petiole more than 15 cm long; largest pinna lobes with entire margins; stem scales usually denticulate, translucent, cream to castaneous; fertile pinnules caudate, 3–15 mm wide, sori acrostichoid, apparently covering both surfaces; sporangial capsules setose (Fig. 30e,f). .... 11. *P. pubens*, p. 68.

12. Lamina up to 10 cm wide at the base; petiole up to 4 cm long; largest pinna lobes with serrate margins; stem scales entire, dark, and opaque; fertile pinnules botryoid, sori round, discrete, 1–3 mm wide; sporangial capsules glabrous. .... 12. *P. glandulosa*, p. 71.

11. Rhachis and costae glabrous, or if pubescent, hairs shorter than 1 mm long. Amazonia and elsewhere.

13. Ultimate segments or lobes of sterile leaf 0.5–1.5 mm wide *and* only one-nerved; lamina often pubescent on both surfaces. Andes of Colombia to Bolivia, Guyana. .... 13. *P. lechleriana*, p. 71.

13. Ultimate segments or lobes of sterile leaf more than 1 mm wide and with several nerves; lamina rarely pubescent on both surfaces.

 14. Stem scales bright golden or yellowish *and* the pinnatifid portions of the pinnae or pinnules with a single veinlet running towards the sinus arising directly from the costa or costule between the main lobes or vein groups (Fig. 45d). Andes of Colombia to Peru. .... 26. *P. altescandens*, p. 97.

 14. Plants without the above combination of characters.

  15. Laminar margins sparsely ciliate, hairs minute, less than 0.1 mm long (Fig. 28a) *and* fertile pinnules caudate, sori amphiacrostichoid, covering both surfaces of the leaf.

   16. Stem scales dull brown, opaque, appressed-ascending, margins subentire, base curved and thickened (Fig. 28h). Widespread. .... 9. *P. caudata*, p. 60.

   16. Stem scales shiny reddish to castaneous, membranous, spreading, margins denticulate, base usually cordate at point of attachment (Fig. 29f). Paraguay and Brazil. .... 10. *P. goyazensis*, p. 66.

  15. Laminar margins glabrous, or if sparsely ciliate, fertile pinnules not caudate and sori not amphiacrostichoid.

   17. Abaxial surface of sterile leaf pubescent, hairs fine, erect, whitish, less than 0.1 mm long *and* costae scaly with numerous, golden brown, tortuous scales. Panama. .... 23. *P. alata*, p. 92.

   17. Plants without the above combination of characters. Panama and elsewhere.

    18. Plants nearly glabrous throughout, even within the grooves *and* pinnule margins cut less than ⅔ of the way to the costule. Costa Rica. .... 27. *P. gomezii*, p. 99.

    18. Plants usually pubescent on the major axes and within the grooves; pinnules cut more than ⅔ of the way to the costule.

     19. Lamina margins sparsely ciliate, hairs 0.1 mm long *and* stem scales opaque, appressed, the base curved and thickened. Southeastern Brazil. .... 20. *P. cylindrica*, p. 86.

     19. Lamina margins glabrous; stem scales as above or thin, spreading, and translucent. Plants not from southeastern Brazil.

      20. Pinnule bases more or less symmetrical (Fig. 35); tertiary segments often inserted at about right angles to the costule, ovate to oblong, usually less than 2.5 (3.0) times longer than broad.

       21. Pinnules up to 2.5 × 1.2 cm, with only 5–7 segments and/or lobes; lamina up to 55 × 26 cm, apex long-attenuate; major axes with narrow, dark, tortuous scales. Colombia. .... 14. *P. attenuata*, p. 74.

       21. Pinnules larger than 2.5 × 1.2 cm, with more than 5 segments and/or lobes; lamina often larger than 55 × 26 cm, apex rarely long-attenuate; major axes rarely with narrow, dark, tortuous scales.

        22. Sterile lamina slightly reduced at the base; basal pinnae less than 3.5 times longer than broad, usually elongated basiscopically; fertile leaves coenosoric; sori not stipitate but placed close to the midrib.

         23. Sterile lamina pubescent adaxially. Colombia. .... 15. *P. stolzei*, p. 76.

         23. Sterile lamina glabrous adaxially.

          24. Margins of tertiary segments entire to crenate, serrate or lobed; pinnules of medial pinnae cut more than half way to the costule for most of their length in pinnae 25 cm or longer. Mesoamerica, Ecuador, and Bolivia. .... 16. *P. alfredii*, p. 78.

24. Margins of tertiary segments entire, never crenate, serrate, or lobed; pinnules of medial pinnae cut less than half way to the costule for most of their length. Colombia. .... 18. *P. lourteigiana*, p. 82.

22. Sterile lamina broadest at the base; basal pinnae 3.5–4.0 times longer than broad, not strongly elongated basiscopically; fertile leaves botryoid; sori stipitate, stalks 1–4 mm long. Colombia. .... 19. *P. pittieri*, p. 84.

20. Pinnule bases acroscopically prolonged (Fig. 44); tertiary segments and lobes usually inserted obliquely to the costule, somewhat elongate and falcate, more than 2.5 times longer than broad.

25. Costal scales scattered, dark, ovate to lanceolate, flaccid (Fig. 52b); fertile leaves botryoid (Fig. 52c). Cloud forests of northern Venezuela. .... 32. *P. canaliculata*, p. 111.

25. Costal scales absent, or if present, then linear, tortuous; fertile leaves rarely botryoid.

26. Sterile lamina 3–4-pinnate-pinnatisect, ultimate segments or lobes 1–2 mm wide; major axes on all sides with numerous, narrow (1–3 cells wide), reddish brown, tortuous, spreading scales; fertile leaves botryoid. Colombia. .... 17. *P. botryoides*, p. 80.

26. Sterile lamina to only 3-pinnate-pinnatifid, ultimate segments or lobes more than 1–2 mm wide; major axes lacking numerous scales, or if scales present, then not as above.

27. Lamina puberulent on both surfaces; veins prominulous. Andes of Ecuador and Bolivia. .... 22. *P. puberulenta*, p. 90.

27. Lamina always glabrous adaxially and usually so abaxially; veins not prominulous.

28. Stem scales dull brown, thick and opaque, attached across the length of the curved and thickened base, margins subentire.

29. Tertiary segments lobed, lamina usually 3-pinnate-pinnatifid.

30. Costae evenly pilosulous, hairs less than 0.1 mm long; costular grooves truncated by the ridges of the costae and therefore not decurrent; grooves glabrous or nearly so within. Andes of Colombia and Bolivia. .... 21. *P. hickeyi*, p. 88.

30. Costae glabrous or with only scattered hairs; costular grooves decurrent into the costal grooves; grooves filled with reddish or brownish hairs. Widespread species. .... 28. *P. osmundacea*, p. 101.

29. Tertiary segments entire or only minutely serrate at the apex; lamina mostly 2-pinnate-pinnatifid. Andes of Ecuador. .... 25. *P. appressa*, p. 94.

28. Stem scales reddish brown or golden, thin and translucent, attached at a central point, base not curved or thickened, margins denticulate to erose.

31. Stem scales reddish brown; lamina with punctate, resinous glands; costal grooves packed with protruding hairs 0.3–0.8 mm long. Guadeloupe and Martinique. .... 29. *P. cyathifolia*, p. 106.

31. Stem scales golden; lamina lacking punctate, resinous glands; costal grooves glabrous. Andes of Ecuador. .... 24. *P. aequatoriana*, p. 94.

10. Pinnules of medial pinnae anadromic (Fig. 18).

32. Stem scales yellowish to golden; lamina usually with a single veinlet springing directly from the costa or costule between the main lobes or vein groups (Fig. 45d). Andes of Colombia, Ecuador, and Peru. .... 26. *P. altescandens*, p. 97.

32. Stem scales brown, castaneous, or reddish; lamina lacking a veinlet as described above.

33. Sterile leaves 2-pinnate; pinnules entire, bases symmetrical and cuneate; fertile pinnules cylindrical and entire. Known only from the state of Espírito Santo, southeastern Brazil. .... 8. *P. espiritosantensis*, p. 60.

33. Sterile leaves 2–4-pinnate; pinnules divided, lobed, or serrate, the bases usually prolonged acroscopically; fertile pinnules lobed and/or divided.

34. Scales of the petiole base 5–6 mm wide, broadly ovate, castaneous. Colombia. .... 30. *P. latisquamosa*, p. 108.

34. Scales of the petiole base less than 4 mm wide, usually narrowly lanceolate, brown, castaneous, or reddish.

35. Abaxial surface of lamina evenly pubescent; stem scales reddish. Southeastern Brazil.

36. Costal hairs less than 1 mm long. .... 34. *P. speciosa*, p. 115.

36. Costal hairs 1–2(2.5) mm long. .... 35. *P. pilosa*, p. 117.

35. Abaxial surface of lamina glabrous; stem scales variously colored. Southeastern Brazil and elsewhere.

37. Fertile leaves botryoid, i.e., all ultimate soriferous segments round and discrete, not fusing to form an oblong or linear sorus (Fig. 52c).

38. Sterile lamina to 4-pinnate; stem scales dull to unaided eye, dark brown, with entire or subentire margins; costal scales broadly ovate to lanceolate; costae glabrous or more rarely pubescent; hairs short, reddish, less than 0.1 mm long; sori short-stalked (Fig. 52c). Cloud forests, Andes of Venezuela. .... 32. *P. canaliculata*, p. 111.

38. Sterile lamina to 3-pinnate; stem scales shiny, dark castaneous, with denticulate-erose margins; costal scales narrowly lanceolate to linear; costae often pubescent, hairs 0.5–1.0 mm long, whitish; sori sessile (Fig. 51c). Lowland forests, northern Amazon basin and Guiana Highlands. .... 31. *P. sessilisora*, p. 108.

37. Fertile leaves coenosoric, i.e., some or most of the ultimate soriferous segments, especially those near the apex, fusing to form an oblong to linear sorus (Fig. 47g).

39. Abaxial surface of costules evenly hirsute, hairs less than 0.1 mm long, or if glabrous, stem scales reddish. Southeastern Brazil.

40. Stem scales reddish; margins of tertiary segments or lobes crenate to lobed. .. .. 34. *P. speciosa*, p. 115.

40. Stem scales bright castaneous; margins of tertiary segments or lobes entire. ... . 33. *P. semipinnata*, p. 113.

39. Abaxial surface of costules glabrous or variously pubescent by soft whitish hairs more than 0.1 mm long; stem scales rarely reddish. Plants not of southeastern Brazil.

41. Costal grooves glabrous within; sterile lamina mostly 2-pinnate-pinnatifid. Costa Rica. .... 27. *P. gomezii*, p. 99.

41. Costal grooves pubescent within, hairs reddish to brownish; sterile lamina mostly 3-pinnate-pinnatifid.

42. Basal acroscopic segment of pinnules usually with a slight basal gibbosity on both margins (Fig. 49c); lamina membranaceous, almost always with reddish punctate glands abaxially. Guadeloupe and Martinique. .... 29. *P. cyathifolia*, p. 106.

42. Basal acroscopic segment of pinnules lacking basal gibbosity, usually slightly reduced or oblique (Figs. 47 & 48); lamina thicker, papyraceous to chartaceous, rarely with reddish punctate glands abaxially. Widespread. .... 28. *P. osmundacea*, p. 101.

Species Descriptions

POLYBOTRYA subgenus SOROMANES (Fée) Moran *comb. & stat. nov.*

Soromanes Fée, Mém. Fam. Foug. 2 (Hist. Acrost.) 16. 1845. TYPE SPECIES: *Soromanes serratifolium* Fée = *Polybotrya serratifolia* (Fée) Klotzsch.

Polybotrya section *Soromanes* (Fée) Klotzsch, Linnaea 20:430. 1847.

Polybotrya subgenus *Soromanes* (Fée), attributed incorrectly to Klotzsch by Fée, Genera Filicum 50, invalid.

Acrostichum subgenus *Soromanes* Hooker, Species Filicum 5:256. 1864. TYPE SPECIES: *Acrostichum caenopteris* Hooker = *Polybotrya serratifolia* (Fée) Klotzsch.

Sterile leaves 1-pinnate; *veins* from adjacent costules anastomosing, 4–6 pairs, curved ascending, the basal pair joining ⅓–½ the distance from the margin to the costa, then with an excurrent vein to the base of the above anastomosing pair, the distal veinlets strongly curved towards the apex, vein tips at the margin free or, in *P. polybotryoides*, joined by a submarginal vein. *Fertile pinnae* pectinate.

1. **Polybotrya serratifolia** (Fée) Klotzsch (Fig. 19, Map 1).

Polybotrya serratifolia (Fée) Klotzsch, Linnaea 20:430. 1847.

Soromanes serratifolium Fée, Mém. Fam. Foug. 2 (Hist. Acrost.) 82, tab. 43. 1845. TYPE: P! (3 sheets), in Bory Herbarium, cited by Fée as "*Polybotrya serrata*, Galeotti, in herb. Bory, Habitat in Mexicana republica, Lagunetta (Galeotti). - V.S. in herb. Bory." but probably collected by Linden in Venezuela and later distributed by Galeotti (see text discussion). I have selected as the lectotype that sheet which Fée illustrated for his tab. 43.

Soromanes dentatum Fée, Mém. Fam. Foug. 2 (Hist. Acrost.) tab. 43. 1845. Fée's tab. 43 was erroneously labeled as "*S. dentatum*" instead of *S. serratifolium*. His tab. 43 is a precise illustration of the lectotype of *P. serratifolia*.

Soromanes integrifolium Fée, Mém. Fam. Foug. 2 (Hist. Acrost.) 82, tab. 42. 1845. Fertile leaf only, the sterile one is that of *Cyclodium meniscioides*. TYPE: Alexander Braun Herbarium (B).

Botryothallus kunzei Klotzsch, Bot. Zeit. 104. 1846. *nom. nudum*, cited by Ettingshausen (1864).

Polybotrya kunzei Ettingshausen, Denkschr. Akad. Wien. 22:66, fig. 2. 1864. TYPE: Only "in Colombia" was mentioned.

Acrostichum caenopteris Hooker, Species Filicum. 5:256. 1864. *nom. nov.* for *Soromanes serratifolium* Fée, *non* Kaulf. 1824, with same type.

Polybotrya coenopteris (Hooker) Christ, Farnkr. 44. 1897.

Soromanes coenopteris (Hooker) Christ, Bull. Herb. Boissier, II. 3:613. 1903.

Acrostichum hartii Baker, J. Bot. 371. 1881. TYPE: Trinidad, *Hart 228* (holotype: K, photo at US!; isotype: NY!).

Polybotrya hartii (Baker) C. Chr., Index Filicum. 504. 1906.

Polybotrya crassa Morton, Fieldiana Bot. 28:13. 1951. TYPE: Venezuela. Monagas: south-facing forested slopes above limestone bluffs, northeast of Guacharo, alt. 1300–1400 m, 11 April 1945, *Steyermark 61991* (holotype:US!; isotypes: F!, VEN!).

Stem hemiepiphytic, 1.5–3.0 cm thick; *scales* 0.8–1.5 mm long, 0.5–2 mm wide, narrowly lanceolate, reddish brown to light orange, with or without a prominent dark central stripe, membranous, lustrous, spreading, margins highly erose to merely denticulate at the apex. *Sterile leaves* up to 0.8 m long, dull green adaxially, pale green abaxially, chartaceous to subcoriaceous; *petiole* scaly at base, up to 30 cm long, trisulcate and flattened adaxially; *lamina* up to 50 × 27 cm, 1-pinnate; *pinnae* 6–12 pairs, mostly (7)10–20(23) × (2)3–4.5(5.5) cm wide, lanceolate, base rounded, cuneate to truncate, margins entire to serrate, apex acuminate; *veins* in pinnated groups 3–6 mm apart, the tips arcuate, free; *axes* with a few scattered scales, rarely pubescent, the hairs tiny, less than 0.1 mm long, unicellular, whitish; *grooves* nearly glabrous within. *Fertile leaves* 2-pinnate, often about the same length as the sterile

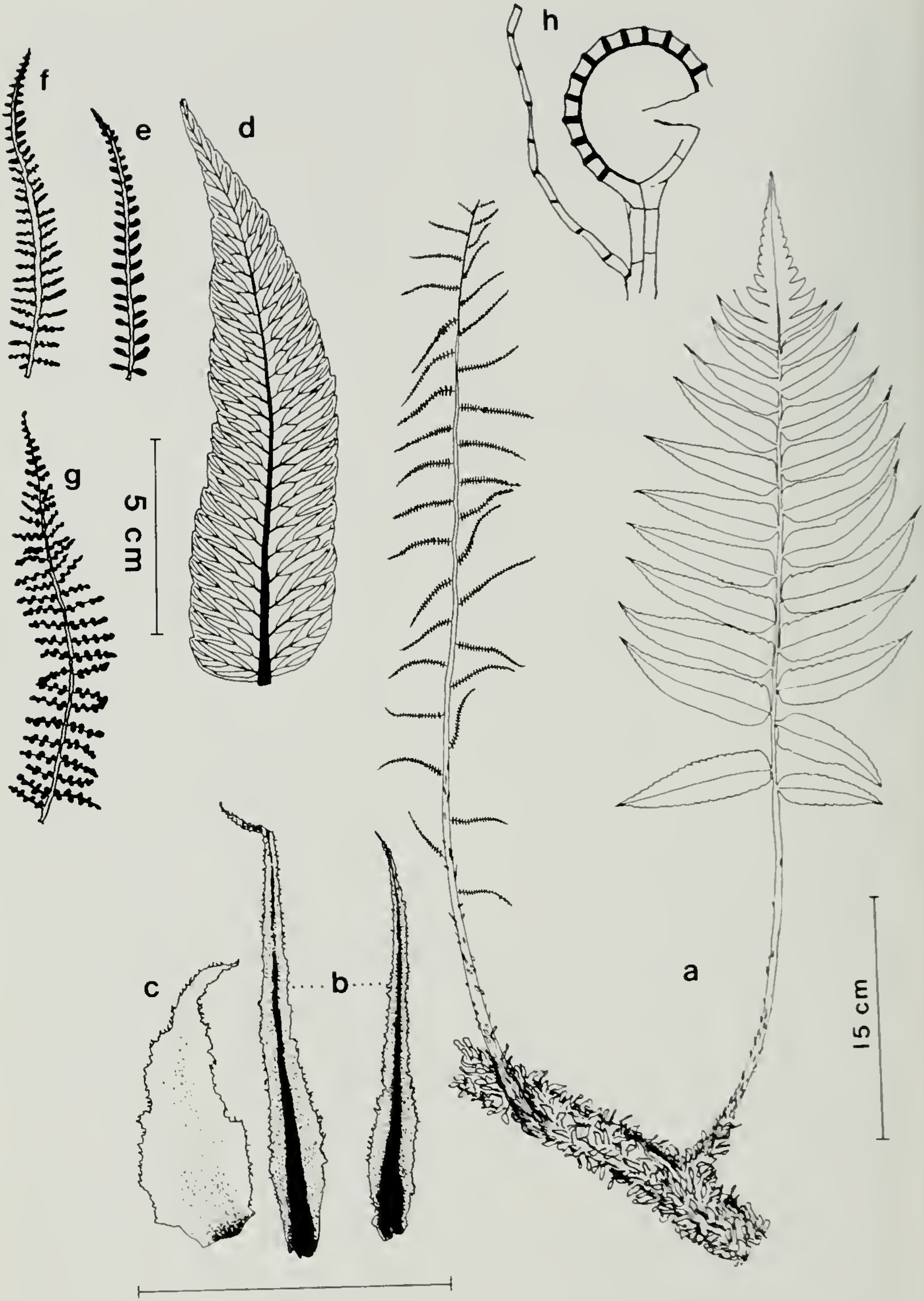

FIGURE 19. *Polybotrya serratifolia* (Fée) Klotzsch. a. habit; b. stem scales (note erose margins and dark central stripes); c. petiole scale; d. sterile pinna; e–g. fertile pinnae showing variation in cutting; h. sporangium with paraphysis. a–c: *van der Werff & Wingfield 3430* (MO). d: *Aristeguieta 3963* (VEN). e: *Fendler 261* (MO). f,h: *Broadway 9947* (GH). g: type, probably *Linden* (P).

leaves; *pinnae* linear to narrowly triangular, evenly long-tapered to apex, up to 14 × 2.5 cm; *pinnules* entire to occasionally slightly lobate, linear, oblong or sometimes clavate, 4–15(20) mm long, 2–3 mm wide, the adaxial margins folding together at maturity, giving the pinnules a cylindrical appearance; *sori* coenosoric, continuously covering the pinnule, occasionally lobed at the base or botryoid; *sporangial stalks* paraphysate; *spores* (44)50–60(63) microns long. $n = 41$.

Other illustrations: Fée's tab. 43 is an excellent, precise illustration of the lectotype; Vareschi, Fl. Venez., Helechos, vol. 1, tab. 71. 1969 (as *P. crassa*).

Polybotrya serratifolia grows in undisturbed, wet, premontane and cloud forests from 1200–2400 m elevation. It is known only from the mountains of northern Venezeula and Trinidad (Map 1). Van der Werff and Smith (1980) report this species (as *Polybotrya* sp., aff. *crassa*) from the state of Falcón, Venezuela, where it grows in wet premontane forest with another Venezuelan endemic, *P. canaliculata*.

The distinctive, wide, flaccid, erose scales of *P. serratifolia* (Fig. 19b,c) distinguish it from the other species in subgenus *Soromanes*. *Polybotrya serratifolia* differs from the similar *P. polybotryoides* by its submarginal connecting vein. This vein, however, is not easily seen because the connecting vein of *P. polybotryoides* is very faint and the vein tips of *P. serratifolia*, though free, are arcuate and simulate a submarginal connecting vein.

Polybotrya hartii and *P. crassa* are placed in synonymy, although at first sight they look different. Both were originally distinguished from *P. serratifolia* by their more dissected (botryoid) fertile leaves. But these botryoid leaves represent a break-up of the coenosorus—a phenomenon that I interpret as atavistic. These highly divided fertile leaves are not uncommon; even the type at Paris contains a sheet with a 3-pinnate fertile leaf (Fig. 19g). As might be expected, intermediates exist between coenosoric and botryoid fertile leaves (Fig. 19f). Still, the most common type of fertile leaf in *P. serratifolia* is 2-pinnate (coenosoric) with relatively short pinnules (Fig. 19a,e).

In addition to its finely divided fertile leaf, *Polybotrya crassa* was distinguished by having an acroscopic auricle and several lobes at the pinna base. This condition represents nothing more than a part-fertile, part-sterile leaf; such transitional forms are commonly found in other species of subgenus *Soromanes* and frequently cause taxonomic confusion. Accordingly, *P. crassa* is here placed in synonymy.

Fée's citation of the type locality and collector ("Mexicana republica, Lagunetta (Galeotti). -V.S. in herb. Bory") seems to be the result of confusion. One of the labels on the type specimen reads (my translation): "Lagunetta, sent from Galeotti, October 1845." The word Lagunetta appears without mention of Mexico. Fée probably thought that Galeotti had collected the specimen in Mexico, the principal American country in which Galeotti collected (Morton 1971:63). Galeotti returned to Europe in 1840, where he sold many duplicates of his own and other collections. Morton (1971) observed: "Galeotti collected only in Mexico and a few specimens in Cuba but is often cited as the collector of plants from Brazil, Venezuela, and Colombia, but these plants were actually collected by Linden, and Galeotti was merely the distributor of the Linden plants." Presumably, Jean Jules Linden collected the type of *P. serratifolia*, which was later distributed by Galeotti. Although Linden collected in Cuba, Mexico, and Guatemala, his last and most profitable trip was to Venezuela and Colombia (1841–1844) where, based on other collections, this species is known to occur. *Polybotrya serratifolia* has not been collected in Mexico. I cannot find a town called "Lagunetta" in Mexico, but a town with that name is located in the state of Lara, Venezuela, and I suspect that is where Linden collected the type.

Specimens examined: Trinidad. *Prestoe 1491* (MO), *1492* (MO); heights of Aripo, *Broadway 9947* (GH, US), *9949* (F, NY, US), *Fay 859* (BM).

Venezuela. **Aragua:** Cordillera Interior, Cerro El Pauji, Topo El Pauji, al sur de El Consejo, *Steyermark & Stoddart 118051* (GH, VEN); cerca Tejerias, *Vareschi 7764* (VEN); Parque Nacional "H. Pittier," bosque de Rancho Grande, *Tschudi 167* (VEN); Colonia Tovar, *Fendler 235* (BM), *261* (GH, K, MO, NY, PH, US); Colonia Tovar, *Moritz 277* (BM). **Falcón:** Curimagua (Coro), *van Cotthem 1327* (UC); Sierra de San Luis, Montaña de Paraguariba, *van der Werff & Wingfield 3430* (MO). **Distrito Federal:** between El Junquito and Colonia Tovar, *Steyermark 91756* (GH, VEN); El Junquito, *Schnee 615* (VEN); off road Caracas–Colonia Tovar, in forest below Club Jundolandia, *Berry 948* (VEN). **Lara:** Lagunetta, *Galeotti s.n.* (P); Dtto. Morán, 8.7 mi SE of Sanare, Parque Nacional Yacambu, *A.R. Smith 1259* (PORT, UC); Dtto. Morán, *Rivero et al. 1608* (PORT); Dtto. Iribarren, Parque Terepaina, *Iriarte 52* (PORT); Dtto. Andres Elroy Blanco, 7 km de Sanare, *Rivero 513A* (PORT); selva arriba de Sanare, *Aristeguieta 3963* (US, VEN); 2200 m sobre los baños de Río Claro, *A.R. Smith 4055*. **Mérida:** vertientes del Río Capaz, arriba de La Azulita, *Steyermark & Rabe 97133* (VEN); rich forest above Hacienda Agua Blanca, above La Azulita, *Steyermark 56114* (F, US). **Monoagas:** south-facing forested slopes above limestone bluffs, northeast of Guacharo, alt. 1300–1400 m, 11 April 1945, *Steyermark 61991* (F, US, VEN). **Portuguesa:** 15 km E of Chabasquen, 67 km NNW of Guanare, *Steyermark et al. 126675* (PORT), *126680* (UC, VEN). **Trujillo:** arriba de Escuque, entre Escuque y La Mesa de San Pedro, *Steyermark 104717* (MO, VEN); Dtto. Bocono, ca. 10 mi SW of Batatal on road to Bocono, Laguna de Aguas Negras, *A.R. Smith et al. 922* (PORT, UC); 2 km NW of Caserío Cerros de Guaramareal, 42 km SE of Bocono, *Moran 3709* (F, MO, PORT, VEN). **Yaracuy:** El Amparo hacia Candelaria, a 7–10 km al Norte de Salom, *Steyermark et al. 106758* (NY, MO, PORT); Distrito Bruzual, Serranía de Aroa, 11–15 km NNE of Urachiche, 3 km NE of Caserío Buenos Aires, *Steyermark et al. 124749* (PORT, UC, VEN); Dtto. Bolívar, entre las Parchitas, Tierra Fria y Ojo de Agua, *Ortega & Smith 2491* (PORT), *2510* (PORT).

2. **Polybotrya polybotryoides** (Baker) Christ (Figs. 20 & 21, Map 2).

Polybotrya polybotryoides (Baker) Christ, Bull. Herb. Boissier, II. 1:70. 1901.

Acrostichum polybotryoides Baker, J. Bot. 207. 1881. Type: Colombia. Norte de Santander: Ocaña, on trees in the forest, 7000 ft., *Kalbreyer 1254* (holotype: K, color slide at MO!; photo GH!, MO!).

Acrostichum juglandifolium Baker, J. Bot. 207. 1881, *nom. illeg.*, *non* Kaulfuss, 1824. Type: Colombia. Antioquia: *Kalbreyer 1798* (holotype: K, color slide at MO!; photo GH!, MO!).

Polybotrya juglandifolia Christ, Bull. Herb. Boissier, II. 4:965. 1904, *nom. nov.* for *Acrostichum juglandifolium* Baker, *non* Kaulfuss, with same type.

Polybotrya juglandifolia Christ var. *lobata* Christ, Bull. Herb. Boissier, II. 6:168. 1906. Type: Costa Rica. Cartago: Río Navarro, Coll. Inst. Costaricensis no. 16769, *Wercklé s.n.* (P?).

Polybotrya kalbreyeri C. Chr., Index Filicum. 504. 1906. *nom. superfl.* for *Polybotrya juglandifolia* Christ; with the same type.

Polybotrya aucuparia Christ, Bull. Herb. Boissier, II. 6:166. 1906. Type: Costa Rica. Cartago: Valley of the Río Navarro, 1400 m, *Wercklé 16770* (P!; photos F!, NY!, UC!).

Stem 0.5–2.0 cm thick, hemiepiphytic; *scales* linear, mostly 9–15 mm long, 0.5–1.0 mm wide, ascending with spreading tips, lustrous, golden yellow when fresh, turning yellow brown to purple brown upon drying, margins denticulate. *Sterile leaves* up to 1.45 m long; *petioles* up to 45 cm long; *lamina* up to 1.0 m, 1-pinnate, but occasionally becoming pinnate-pinnatifid to 2-pinnate in transitional sterile-fertile leaves, subcoriaceous, dark green adaxially, pale green abaxially, nearly glabrous on both surfaces; *pinnae* up to 12 pairs, mostly 12–20(30) × 3–6(8) cm, lanceolate, the base round, cuneate or subtruncate, with the acroscopic side slightly prolonged, the margins entire, crenate or serrate, the apex acuminate; *veins* in pinnate groups 5–12 mm apart, the side branches ascending and anastomosing at acute angles with the adjacent ones (rarely, the veins fail to anastomose locally), the vein tips connected by a faint intramarginal connecting strand; *axes* nearly glabrous or with scattered hairs, these unicellular and colorless. *Fertile leaves* 2-pinnate, 12–28 cm broad; *pinnules* oblong to linear, 0.9–2(2.5) × 1–2 mm; *sori* coenosoric, continuously covering the abaxial surface of the pinnules; *sporangial stalks* paraphysate; *spores* mostly (45)50–65(68) microns long. $n = 41$.

Other illustrations: Ettingshausen, Farnkr. fig. 2. 1864 (as *P. kunzei*, portion of pinnae showing vein); Hooker, Icones Plant. 1877. pl. 1690 (as *Acrostichum polybotryoides*) and pl. 1691 (as *A. juglandifolium*); Rovirosa, Pterid. Sur. Mex. pl. 60. 1909 (as *A. coenopteris*); Smith, Flora of Chiapas, part II. fig. 71. 1981 (as *P. aucuparia*); Stolze, Fieldiana Bot. II. fig. 60d. 1981 (portion of pinna with venation, as *P. aucuparia*).

Polybotrya polybotryoides grows in wet, shaded, tropical forests from sea level to 1400 (1850)m. It has the largest range of any species in subgenus *Soromanes*, even occurring on Cocos Island (Map 2). Gómez (1976) reported this species from Nicaragua, but I have not seen a specimen from that country.

The shape of the leaf apex varies clinally from southern Mexico to Peru (Fig. 21). From southern Mexico to Costa Rica, the apex is pinnatifid, hav-

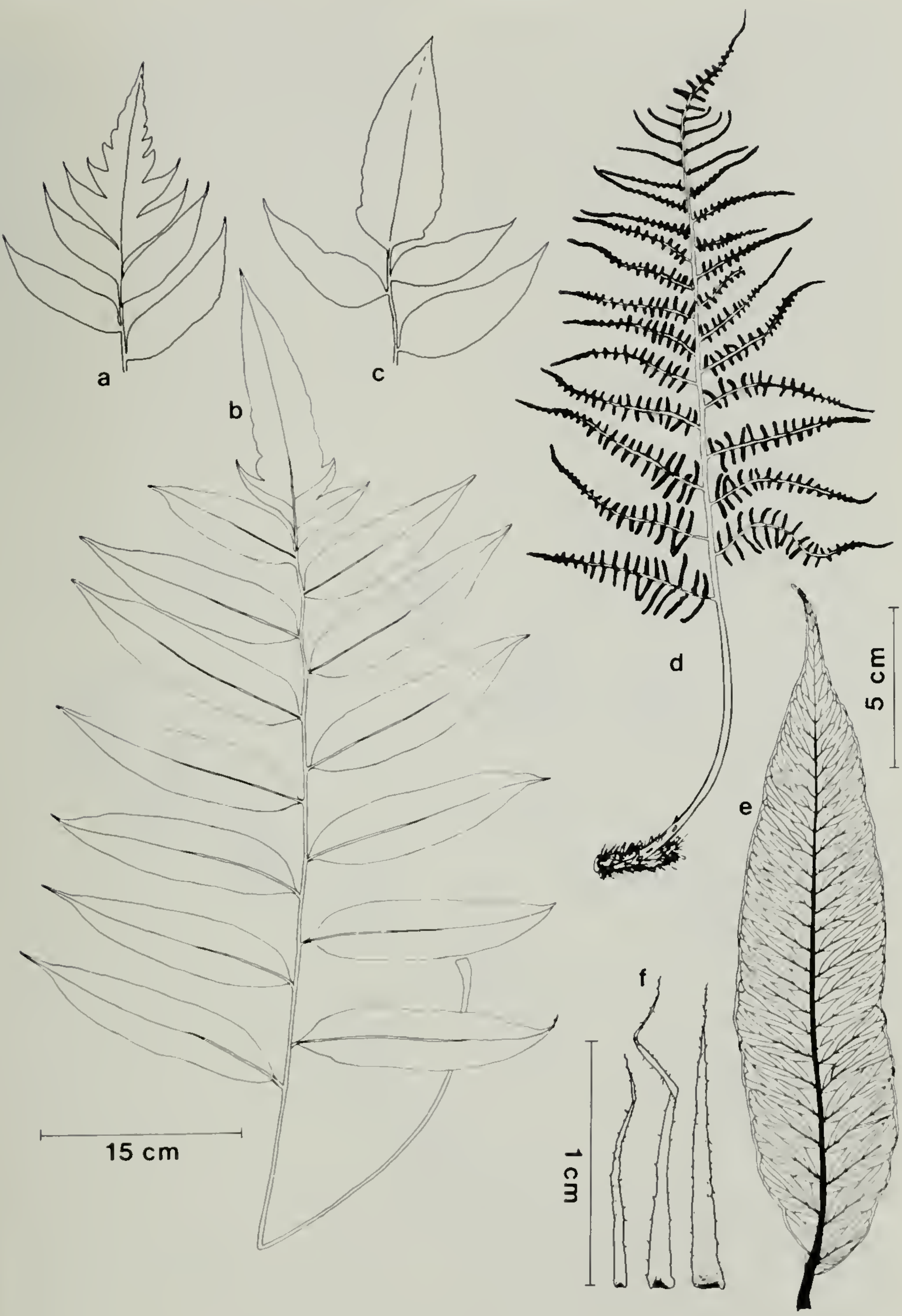

FIGURE 20. *Polybotrya polybotryoides* (Baker) Christ. a. northern apex form, Guatemala; b. sterile leaf with intermediate apex form, Panama; c. southern apex form, Ecuador; d. fertile leaf; e. sterile pinna; f. stem scales. a: *Steyermark 37320* (F). b: *Croat 12143* (MO). c,d: *Moran 3569* (F). e,f: *Moran 2178* (CR).

ing two to four basal lobes; this apex does not resemble the lateral pinnae. South of Costa Rica, the apex resembles the lateral pinnae because it has only one or two basal lobes with the remainder of the apex relatively narrow and the margins entire to crenate. Since apex shape varies clinally and no other characters correlate with it, I interpret the two extreme shapes as geographic variations of the same species and do not believe that these should be named. Plants having an intermediate apex shape do not appear to be hybrids, since they do not have aborted spores. In South America, the nearly conform apex of *P. polybotryoides* is taxonomically useful because the three other species of subgenus *Soromanes*, which might possibly be confused with this species, have strongly and evenly pinnatifid apices. The subconform apex in southern populations of *P. polybotryoides* is derived within the genus, as evidenced by comparison to all other species of *Polybotrya* and to all other genera of dryopteroid ferns.

Polybotrya polybotryoides is most like *P. suberecta*. Another morphological character separating these two, besides apex shape, is the submarginal connecting vein present in *P. polybotryoides* (Fig. 20e) but only partially formed in *P. suberecta* (Fig. 22d). Unfortunately, the connecting vein is faint and difficult to see because of the thick lamina and, in some specimens, margins that have become revolute upon drying and thereby hide the region just inside the margin. The connecting strand is best seen with magnification on the abaxial surface of the pinna or with the unaided eye and the pinna held up to strong light.

Specimens examined: Mexico. **Chiapas:** Tumbala, *Rovirosa 972* (GH, PH); Finca Mexiquito, *Purpus 6761* (BM, F, GH, MO, NY, UC, US), *7245* (BM, GH, US); 18–20 km N of Ocozocoautla de Espinoza, along road to Mal Paso, *Breedlove & Smith 21886* (MICH, NY, UC).

Belize. **Cayn:** Hwy 28.5 mi S of Belmopan, *Croat 24566* (CR, MO); Toledo district, Maya Mts., between Río Caraval and Union Camp, *Boutin & Schlosser 5902* (MO).

Guatemala. **Alta Verapaz:** 7 mi up the road to Oxec along road off Hwy. 7E between Tucuru and El Estor ca. 6 km NE of Panzos, *Croat 41637* (CR, MO). **Izabal:** along Río Bonita, Cerro San Gil, *Steyermark 41698a* (F, US); Cerro San Gil, *Steyermark 41870* (F). **Quezaltenango:** near Calahuache, *Standley 67135* (F); Finca Pireneos, below Santa María de Jesús, *Standley 68203* (F). **San Marcos:** above Finca El Porvenir, Volcán Tajumulco, up Loma Bandera Shac, *Steyermark 37320* (F).

Honduras. **Atlántida:** Lancetilla Valley, near Tela, *Standley 53955* (F, US); Montaña La Manga, 30 km SE de La Ceiba, *Nelson et al. 3296* (MO); Cordillera Nombre de Dios, *Gómez 7027* (CR). **Comayagua:** Quebrada Potrero, Cerro Azul de Meambar, *Gómez 6914* (CR). **Cortés:** mountains on N side of Lake Yojoa, *Morton 7629* (US).

Costa Rica. **Cartago:** Valley of the Río Navarro, 1400 m, *Wercklé 16770* (P, photos F, NY, UC); along Camino Raiz de Hule, SE of Plantanillo, *Croat 36800* (CR, MO); Raiz de Hule, Moravia de Chirripó, *Ocampo 727* (CR); Chitaría, forest near old jailhouse, *Moran 2170, 2171, 2173, 2176, 2178* (CR, F, MO, NY); Chitaría, *Valerio 329* (US), *33133* (CR); Finca Navarro, *Maxon 639* (NY). **Cocos Island:** Wafer Bay, *Gómez 3324* (CR, F, US); Wafer Valley, *Pittier 16232* (CR, US); Wafer Bay river valley, *Holdridge 5153* (GH), *Klawe 1545* (US); trail between Chatham and Wafer bays, *Gómez 18064* (CR); Chatham Bay, *Jiménez M. 3209, 3210* (CR, F, GH, MICH); Chatham Bay, *Fournier 357* (NY). **Puntarenas:** Osa Peninsula, on ridge 9.5 km W of Rincon de Osa, *Mickel 2742* (NY); above San Vito at Finca Wilson, NE of home, *Evans & Bowers 3152* (MO); vicinity of biological field station at Finca Wilson, 5 km S of San Vito de Java, *Mickel 3180* (NY). **San José:** Carrillo, *Brade 372* (UC).

Panama. **Coclé:** Continental divide on road to Coclesito, *Hammel 3503* (CR). **Darién:** El Llano–Cartí road, *Churchill & de Nevers 4993* (MO); Serranía de Pirre, along ascent of Serranía de Pirre above Cana Gold Mine between Río Cana and Río Escucha Ruido, *Croat 37757* (MO), *37794* (MO). **Panamá:** El Llano–Cartí road, 13.7 km N of Pan-American Highway, *Folsom 3590* (MO); Cerro Campana, ca. 10 km SW of Capira, trail to summit, *Mori & Kallunki 3574* (MO, NY); 1 mi upstream from Frizzel's Finca Indio, on slopes of Cerro Jefe, *Foster & Kennedy 1814* (F, MO); Cerro Jefe, *Webster et al. 16467* (UC); along road to Cerro Campana, *Croat 14687* (F, MO, NY); trail to Cerro Campana, *Kirkbride & Hayden 274* (MO, NY); Cerro Campana, FSU Field Station, *Kennedy et al. 2074* (MO); cloud forest on Cerro Campana above Su Lin Motel, *Croat 14742* (MO); Cerro Campana, above Su Lin Motel, *Croat 4266* (MO); Cerro Campana, near FSU building, *Croat 12114* (F, MO), *12143* (MO, US), *14786* (MO); 8–12 km N of El Llano, along new El Llano–Cartí road, *Nee et al. 8768* (MO); Cerro Campana, lower slopes above FSU cabin, *Croat 22789* (MO); Cerro Campana along trail to summit, *Croat 17161* (MO, US); high point of ridges S of Ipeti, 5–6 hr walk from Chocó village, Serranía de Maje, *Knapp et al. 4542* (MO); along trail to top of Cerro Campana, SW slope from road, *Nee & Stockwell 11610* (MO); Cerro Campana, *Armond 298* (MO). **Veraguas:** 5 mi NW of Santa Fé, slope above Río Primero Brazo, below Escuela Agricola Alta Piedra, *Croat 23244* (MO), *Liesner 820* (MO); Valley of Río Dos Bocas along road between Escuela Agricola Alto Piedra and Calovebora, 15.6 km NW of Santa Fé, *Croat 27648* (MO); 0.6 mi beyond Escuela

Agricola Alto Piedra, *Croat & Folsom 34051* (MO); vicinity of Escuela Agricultura Alto Piedra near Santa Fé along trail to top of Cerro Tute, *Antonio 4019* (MO); ridge of Cordillera de Tute, trail to Cerro Tute, above Escuela Agricola Alto de Piedra, just W of Santa Fé, *Knapp & Dressler 5461* (MO).

COLOMBIA. **Antioquia:** *Kalbreyer 1798* (K, color slide at MO; photo GH, MO); vic. Planta Provedencia, 28 km SW of Zaragoza, *Alverson et al. 342* (MO, US); cerca de Porcesito en el valle de Río Medellín, *Hodge 6780* (GH); Barbosa, *Henri-Stanislas 1709* (US). **Chocó:** Trail to Miniquía E of Puerto Mutis, *Lellinger & de la Sota 39* (US); Río Mutatá ca. 3 km above junction with Río El Valle, NW of Alto del Buey, *Lellinger & de la Sota 190* (US). **Norte de Santander:** Ocaña, on trees in the forest, alt. 7000 ft., *Kalbreyer 1254* (K, color slide at MO; photo GH, MO).

ECUADOR. **Bolívar:** Limón, estrivaciones inferiores de la Cordillera Occidental, *Acosta Solis 6358* (F). **Napo:** 73 km al noreste de Baeza, Cascada de San Rafael, *Moran 3593* (Q, QCA), *Foster 85-162* (UC); camino Baeza–Tena, 15 km al norte de Tena, *Moran 3530* (Q, QCA). **Morona-Santiago:** Cordillera de Cutucu, western slopes, trail from Logrono to Yaupi, *Madison et al. 3356* (GH). **Pastaza:** 6.5 km W of Mera, *Moran 3590* (F, Q, QCA). **Pichincha:** Hotel Tinalandia, bosque primario al lado norte del Río Toachi, *Moran 3562* (Q, QCA). **Tungurahua:** 25 km al este de Baños, detras el pueblo Río Negro, *Moran 3569* (F, Q, QCA).

PERU. **Huánuco:** SW slope of Río Lulla Pichis watershed, ascent of Cerros del Sira, *Dudley 13290D* (GH). **Pasco:** Prov. Oxapampa, Abra los Mellizos, 4–8 km from Enanas, *Skog et al. 5036* (US).

FIGURE 21. Clinal variation in apex shape of *Polybotrya polybotryoides* (Baker) Christ. Plants from the northern portions of the range have deeply and evenly pinnatifid apices. Southward, this shape gradually changes into a subconform apex. Intermediates are found primarily in Costa Rica and Panama.

3. Polybotrya suberecta (Baker) C. Chr. (Fig. 22, Map 1).

Polybotrya suberecta (Baker) C. Chr., Index Filicum 506. 1906.

Acrostichum suberectum Baker, J. Bot. 207. 1881. TYPE: Colombia. Antioquia: 4000–4500 ft., *Kalbreyer 1877* (holotype: K, color slide at MO!; photo GH!, US!).

Acrostichum hackelianum Sodiro, Anal. Univ. Quito XII (78):21. 1895. (Crypt. Vasc. Quit. 491. 1893.) TYPE: Ecuador. Pichincha: banks of the Río Pilaton, *Sodiro s.n.* (holotype: Q!).

Stem 1–2 cm thick, hemiepiphytic; *scales* dark brown, narrow, linear, 0.2–0.4(1.0) × 8–15 mm, stiff to spreading. *Sterile leaves* up to 1.6 m long; *petioles* about ½ to ¾ the length of the lamina, scaly at base, becoming less so distally; *lamina* 1-pinnate, mostly 0.5–1.0(1.2) m long, lanceolate; *pinnae* oblong-lanceolate, (10)15–21(25) × (3)4–5(6.5) cm, 6–13 free pairs, glabrous to densely pubescent beneath, the hairs uncinate, multicellular, reddish or clear, 0.1–0.6 mm long, the margins entire, or (more rarely) shallowly and inconspicuously serrate, the base cuneate to broadly rounded, the apex acuminate; *veins* anastomosing, the tips sporadically uniting to form a discontinuous, submarginal connecting strand; *axes* with a few narrow, scattered scales, usually glabrous, rarely pubescent by uncinate hairs, or rarely by short (less than 0.2 mm), subulate, clear hairs. *Fertile leaves* 2-pinnate to 2-pinnate-pinnatifid, 10–30 cm wide, pectinate; moderately scaly, the scales appressed, linear; *pinnules* linear, 25–55 × 1–3 mm; *sori* coenosoric, continuously covering the abaxial surface of the pinnule; *sporangial stalks* paraphysate; *spores* (43) 46–55(58) microns long.

Other illustrations: Hooker, Icones Plant. 17, pl. 1692. 1877 (as *Acrostichum*).

Polybotrya suberecta grows in montane forests from 600 to 1800 m elevation. Most of the specimens are from the western slopes of the Andes (Map 1). These locations correspond to my field experience in Ecuador, where this species was common on the western side of the Andes but absent from the eastern side.

The range of this species overlaps with *P. polybotryoides*, a similar species. The two species are most easily distinguished by the shape of the leaf apex: *P. polybotryoides* has a subconform apex in Colombia and Ecuador, but *P. suberecta* has an evenly tapering, pinnatifid apex. Other distinguishing characters of *P. suberecta* are the uncinate hairs that occur in some specimens (Fig. 22a) and the discontinuous, submarginal connecting vein (Fig. 22d). *Polybotrya serratifolia* also resembles *P. suberecta* but differs by its wide, flaccid stem scales and a distribution that is restricted to high altitude forests in Venezuela and Trinidad (Map 1). *Polybotrya suberecta* looks very much like *P. andina*—a species with which it grows in the western Andes of Ecuador. See *P. andina* for comparison.

Specimens examined: COLOMBIA. **Antioquia:** 4000–4500 ft., *Kalbreyer 1877* (K, color slide at MO; photo GH, US). **Chocó:** hills above Río Capa and Río Mumba, up river from Lloro, *Juncosa 1467* (MO, COL); NW side of Alto del Buey, *Lellinger & de la Sota 248* (COL, LPB, US); 0.3 km E of the Ciudad Bolívar–Quibdó road, across the suspension bridge at km 141, *Lellinger & de la Sota 894* (COL, US). **Cundinamarca:** Ojo de Agua, S side of Río Guavio, 32 km E of Gachala, *Grant 10556* (US). **Magdalena:** below Valparaiso, *H.H. Smith 983* (F, GH, NY); "Cincinnati," lower slopes of Mt. San Lorenzo, near Sta. Marta, 1300 m, *Seifriz 24* (US). **Santander:** along highway between Pamplona and Bucaramanga, Munic. Tona, Corregimento Corcova, Vereda la Marina, *Croat 56510* (MO, UC).

ECUADOR. **Los Ríos:** Patricia Pilar, *Dodson 7380* (COL, MO, US), *Dodson et al. 8679* (MO, US). **Pichincha:** banks of the Río Pilaton, *Sodiro s.n.* (Q); 2.5 km E of Cornejo Astorga, *Moran 3546.5* (F, GH, Q, QCA); 3 km from El Paraiso, road El Paraiso–Saguangal, *Øllgaard et al. 37823* (AAU, Q, QCA); 3 km from La Armenia, road Gualea–La Armenia, *Øllgaard et al. 37859* (AAU); about 40 km WNW of Quito, 3.5 km N of Mindo, *Moran 3565* (F, GH, Q, QCA); Tinalandia Resort, N side of Río Toachi, about 25 km E of Sto. Domingo, *Moran 3561* (F, GH, Q, QCA); ca. 2 km N of Mindo, Hacienda San Vicente, *Foster 85-37* (UC).

PERU. **Junín:** Prov. Tarma, Chanchamayo, *Esposto 10928* (USM).

4. Polybotrya andina C. Chr. (Fig. 23, Map 2).

Polybotrya andina C. Chr., Index Filicum 7. 1905. *nom. nov.* for *Acrostichum insigne* Baker, *non* Fée 1872–73, with same type.

Acrostichum insigne Baker, J. Bot. 167. 1877. *nom. illeg.*, *non* Fée 1872–73. TYPE: Ecuador. Pichincha: "Andes of Quito," *Sodiro* (holotype: K, photo GH!, US!; isotypes: AAU!, GH!, Q!, UC!).

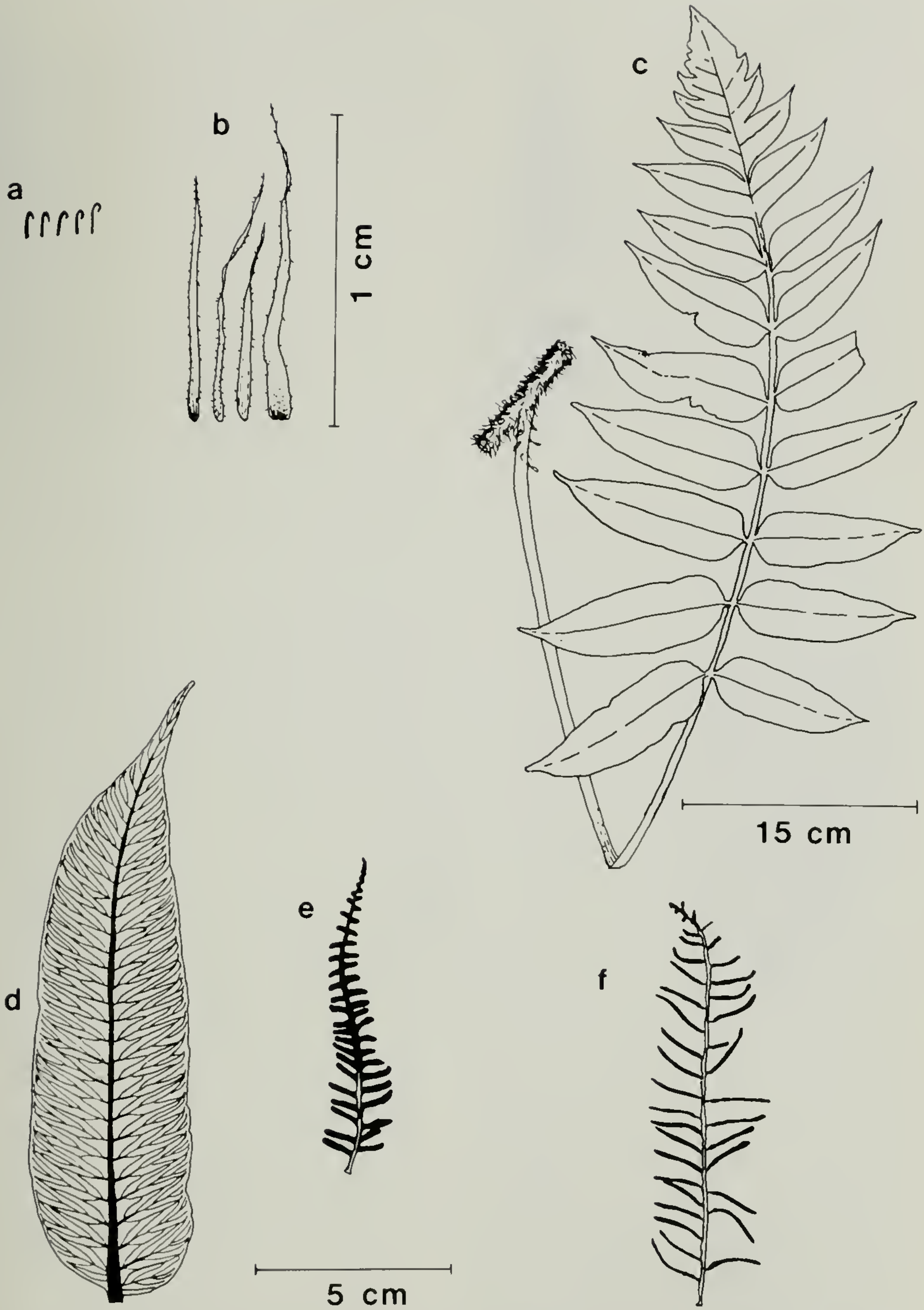

FIGURE 22. *Polybotrya suberecta* (Baker) C. Chr. a. uncinate hairs from abaxial leaf surface; b. stem scales; c. sterile leaf; d. sterile pinna; e,f. fertile pinnae. a: *Øllgaard et al. 37823* (AAU). b–d: *Moran 3546.5* (F). e: *Smith 983* (NY). f: *Dodson 7380* (US).

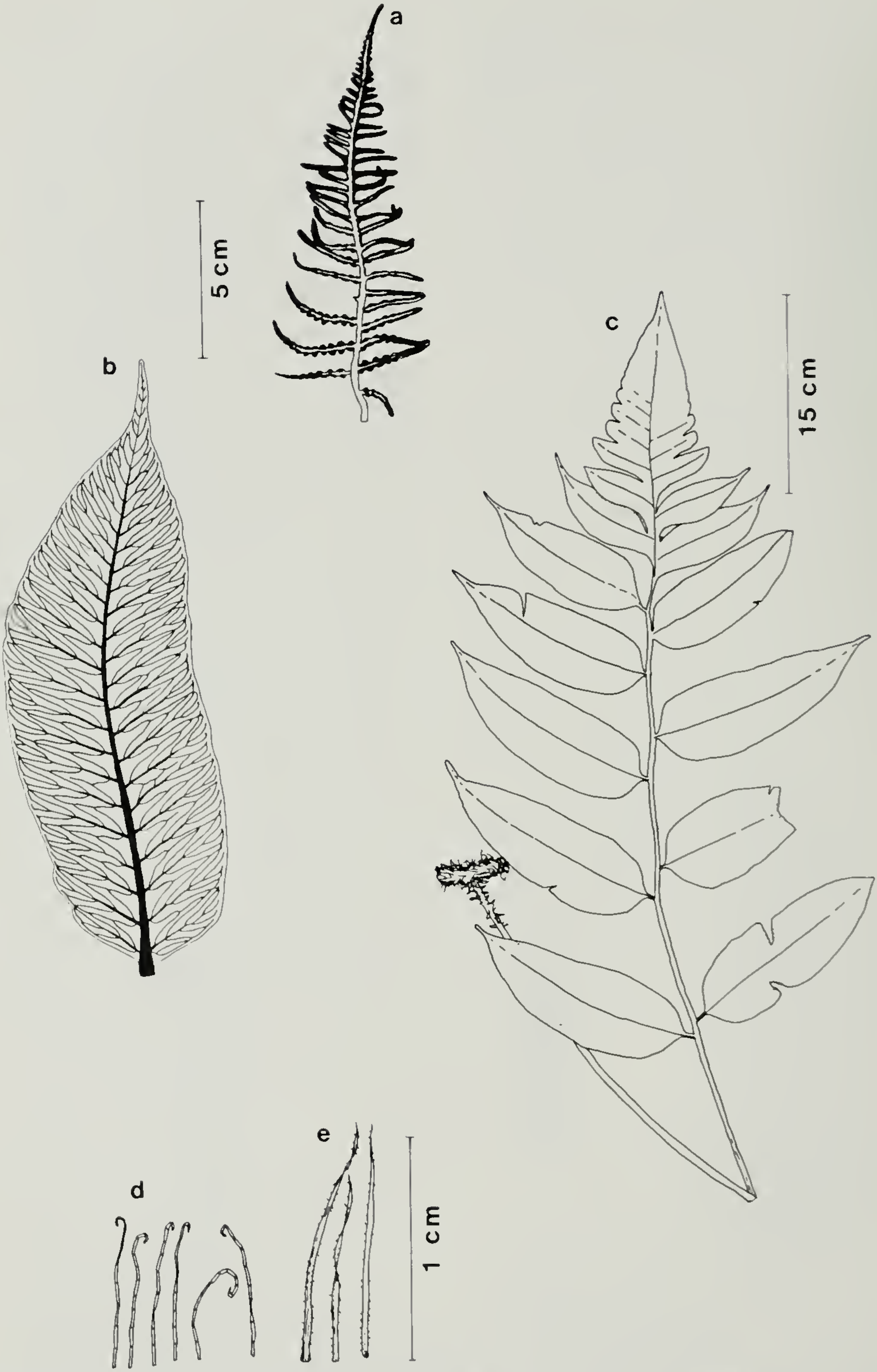

FIGURE 23. *Polybotrya andina* C. Chr. a. fertile pinna; b. sterile pinna; c. sterile leaf; d. multicellular uncinate hairs from abaxial surface of the leaf; e. stem scales. a: *Sodiro s.n.* (AAU). b–e: *Moran 3563* (F).

Stem 1–1.5 cm thick, hemiepiphytic; *scales* mostly 8–13 mm long, dark castaneous, shiny or dull, opaque, margins denticulate. *Sterile leaf* up to 1.0 m long; *petiole* up to 30 cm long, ¾ to as long as the lamina, scaly at base, becoming less so upwards; *lamina* mostly 60–80 × 30–50 cm, deltate or broadly ovate-lanceolate, subcoriaceous, glabrous above, below densely pubescent with spreading, tawny, uncinate, 4-to-10-celled hairs, these 0.5–1.2 mm long; *pinnae* 17–33 × 5.7–10 cm, mostly less than 3.5 times as long as broad, 4–7 pairs below the pinnatifid apex, margins entire, base cuneate-rounded, petiolulate, gradually becoming sessile distally; *veins* anastomosing, the tips uniting discontinuously; *axes* pubescent, the hairs like those on the lamina. *Fertile leaves* slightly smaller, 40–80 × 20–32 cm, pubescent with hairs like those of the sterile lamina; *pinnae* pectinate; *pinnules* proximally lobulate, becoming entire apically, 3–6 mm wide; *sori* coenosoric, covering most of the abaxial surface of the pinnule; spore length unknown.

Sodiro (1897) noted that this species "grows in the tropical and subtropical region up to 1200 m in the forests around Sto. Domingo de los Colorados and in the Nanegal and Mindo valleys" (translation mine). This species is very rare and restricted in range and has been collected only twice from the western cordillera of Ecuador west of Quito (Map 2). I saw only three plants at the Tinalandia site. *Polybotrya suberecta* and *P. polybotryoides* also occurred at this locality and were more abundant.

This species is most closely related to *P. suberecta*, from which it differs by its longer and wider pinnae, fewer (4–7) free pinnae pairs below the apex, and spreading, multicellular, tawny hairs on the abaxial surface (Fig. 23d). Pubescent plants of *P. suberecta* occur in the region of Ecuador where *P. andina* grows. Within this region, the hairs of both species are uncinate, but in *P. suberecta* they are much shorter (0.1–0.3 mm), 1- or 2-celled, erect, and easily overlooked by the naked eye (Fig. 22a). Only these two species of *Polybotrya* have uncinate hairs. Because the fertile leaf of *P. andina*, known only from Sodiro's type collection, had very few spores, I could not make an adequate measurement of spore length.

Specimens examined: ECUADOR. **Pichincha:** Hotel Tinalandia, casi 25 km al este de Sto. Domingo de los Colorados, bosque primario arriba la montaña al lado norte del Río Toachi, 1000 m, *Moran 3563* (F, Q, QCA); "Andes of Quito," *Sodiro s.n.* (K, photo GH, US; AAU, GH, Q, UC).

POLYBOTRYA subgenus SORBIFOLIA

Moran, *subgen. nov.*

TYPE SPECIES: *P. sorbifolia* Kuhn, Linnaea 34:64. 1869.

Folia 1-pinnata, pinnae lineares vel lanceolatae, 6–10 sexies vel decies longiores quam latiores, apice longiacuminato; venae sibi parallelae pinnatae, 3–5 in quoque turmae, liberae.

Stem terrestrial and short-creeping (2 spp.) or hemiepiphytic and long-creeping (1 sp.). *Sterile leaves* 1-pinnate; pinnae linear to lanceolate, 6–10 times as long as broad, apices long-acuminate; veins in pinnate groups of 3–5, strongly ascending, free all the way to the margin. *Fertile leaves* pectinate or more rarely, moniliform.

5. **Polybotrya sorbifolia** Kuhn (Fig. 24, Map 3).

Polybotrya sorbifolia Kuhn, Linnaea 36:64. 1869. Based on var. *salicifolium* Hooker and with same type.

Acrostichum caenopteris Hooker var. *salicifolium* Hooker, Species Filicum 5:257. 1864. TYPE: Brazil. Pernambuco: Serra do Araripe, *Gardner 1901* (holotype: K, photo GH!; fragment NY!).

Polybotrya salicifolia Lellinger, Amer. Fern J. 62:54. 1972. TYPE: Colombia. Santander: vicinity of Puerto Berrio, between Carare and Magdalena River, 100–700 m, 8 June 1935, *Haught 1757* (holotype: US!; isotype: BM!).

Stem terrestrial, 1–2.5 cm thick; *stem scales* shiny brown, linear, 0.4–1 × 10–20 mm, membranaceous, spreading, the margins denticulate. *Sterile leaves* up to 1.3 m; *petiole* 15–50 cm long; *lamina* lanceolate to oblanceolate, 0.3–1.5 × 0.15–0.50 m, chartaceous, with 12–18 pinnae pairs, the apex abruptly acuminate, its lowermost lobes decurrent; *pinnae* lanceolate-acuminate, (7.3)10–22(25.5) × (0.7)1–3(3.5) cm, the base truncate on its acroscopic side, cuneate on the basiscopic side, the margins entire, crenate, usually serrate at the apex, the abaxial surface glabrous or glandular, the glands scattered, round, whitish to reddish, sessile glands; *veins* slender, sharply ascending, long parallel, usually oblique to the costa, the tips free; *axes* with a few scattered, appressed scales. *Fertile leaves* lanceolate, 0.3–1.3 × 15–40 m, pinnate-pinnatifid; *pinnae* linear, 4–15 × 0.7–1.0 cm, moniliform because of the round to oblong pinnules, these 1–3 mm wide;

sori coenosoric, completely covering the abaxial surface of the pinnules; *sporangial stalks* paraphysate; *spores* mostly 40–47 microns long.

Other illustrations: Murillo, Cat. Illustrado de las Plantas de Cundinamarca, 2:103. 1966 (as *P. serratifolia*); Vareschi, Flora Venez., Helechos, vol. I, tab. 73. 1968 (as *P. serratifolia*); Brade, Bradea 1(9):62, fig. 3. 1971 (as *P. serratifolia*); Lellinger, Amer. Fern J. 62, figs. 3, 4, 10. 1972 (as *P. salicifolia*).

The distribution of *P. sorbifolia* is spotty but extensive (Map 3). This species looks like *P. fractiserialis*; see that species for comparison. Unlike all other species in the genus, both *P. sorbifolia* and *P. fractiserialis* are terrestrial—*never* climbing—and it is doubtful that they could climb because their stems are only short-creeping. Both species grow in shaded, rocky habitats along streambanks, from 0–1200 m. I collected *P. sorbifolia* in Costa Rica at the El Rodeo site. It is common at this locality, growing on talus along a stream in the bottom of a humid, limestone ravine that is surrounded by dry uplands.

Unfortunately, the specific epithet "*salicifolia*" cannot be used for this species even though its pinnae bear a strong resemblance to leaves of certain *Salix* species, most notably *S. nigra* and *S. amygdaloides*. This resemblance was noted by Hooker (1864) and Lellinger (1972).

Specimens examined: COSTA RICA. **San José:** Alajuelita, *Alfaro 8073* (US); El Rodeo, *Moran 3145* (CR, F, GH, MO, PORT), *Knight s.n.* (US), *Gómez 7122* (CR), *Hunnewell 16514* (MICH).

VENEZUELA. **Aragua:** Parque Nacional "H. Pittier," Rancho Grande, *Tschudi 162* (VEN), *Steyermark et al. 95827a* (US). **Portuguesa:** Dtto. Araure, Fila San José, al oeste de Sta. Lucía, *Ortega & Grimann 2707* (PORT). **Yaracuy:** "La Enjalma" al sur de Chivacoa, *Vareschi & Pannier 2636* (US, VEN).

COLOMBIA. **Boyaca:** valle del Río Cusiana, entre Pajarito y Guazul, *Murillo 1457* (COL), *1491* (COL). **Cundinamarca:** entre Nilo y la quebrada de Agua de Diosito, *Murillo et al. 289* (COL, US). **Magdalena:** Santa Marta, near Jiracasaca, *H.H. Smith 1052* (F, GH, L, MICH, MO, NY, PH, US). **Meta:** along Cono Rosa Blanca, a small stream outside of Villavicencio, *Kirkbride 404* (MO, NY). **Santander:** vicinity of Puerto Berrio, between Carare and Magdalena River, *Haught 1757* (BM, US).

BRAZIL. **Goiás:** Serra Dourada, 17 km (straight line) S of Goiás Velho, 6 km NE of Mossamedes, *Anderson 10152* (NY). **Pará:** Serra dos Carajás, Serra Norte, near waterfall near AMAZ Exploration Camp, *Silva et al. BG 526* (AAU, F, GH, MICH, NY, UC). **Pernambuco:** Serra de Araripe, *Gardner 1901* (NY, photo of K specimen at GH). **Roraima:** Indian trail from Surucucu to Uaica, Maita Mts. *Prance et al. 10466* (NY).

6. **Polybotrya fractiserialis** (Baker) J. Smith (Fig. 25, Map 3).

Polybotrya fractiserialis (Baker) J. Smith, Hist. Filicum 133. 1875.

Acrostichum fractiseriale Baker, Synopsis Filicum 414. 1868. TYPE: Peru. San Martín: "in sylvis montis campana, terrestre," Dec. 1855, *Spruce 4337* (holotype: K, color slide at MO!; photo GH!, US!).

Acrostichum plumbicaule Baker, Synopsis Filicum 413. 1868. TYPE: Peru. San Martín: Terapoto, Ad rupes secus rivularum, Aug. 1855, *Spruce 4090* (lectotype: K, photo GH!, photo and fragment P!, US!).

Polybotrya plumbicaulis (Baker) J. Smith, Hist. Filicum 133. 1875.

Stem terrestrial, 1–1.5 cm thick, short-creeping with internodes 1–3 cm long, apex scaly, behind the apex usually naked or only sparsely scaly; *scales* dull brown, opaque, 0.3–0.9 × 8–17 mm, ascending, margins entire to more rarely denticulate. *Sterile leaves* to 1.4 m tall; *petiole* about equaling the lamina, stramineous to lead-gray; *lamina* slightly reduced or broadest at the base, chartaceous to subcoriaceous, apex with one or two major basal lobes, merely crenate-lobulate above; *pinnae* mostly 9–15 pairs, linear to oblong, (11)15–25(28) × (2.1)2.5–4.0(4.5) cm, margins serrate, especially towards the acuminate apex, base rounded to cuneate, with the acroscopic margin usually more oblique; *veins* numerous, fine, and in closely parallel pinnate groups, occasionally with a simple vein springing directly from the costa; *axes* usually glabrous or with fine, subulate, 0.1–0.2 mm hairs. *Fertile leaves* erect, 2-pinnate, commonly taller than the sterile, to 1.5 m long; *pinnae* linear, mostly 7–12(17) × 5–10(15) cm; *pinnules* round, oblong, or linear, 1–3 mm wide; *sori* coenosoric, completely covering the abaxial surface of the pinnule; *sporangial stalks* paraphysate, often with a bulbous glandular cell at base of the paraphysis; *spores* (48)52–56(60) microns long.

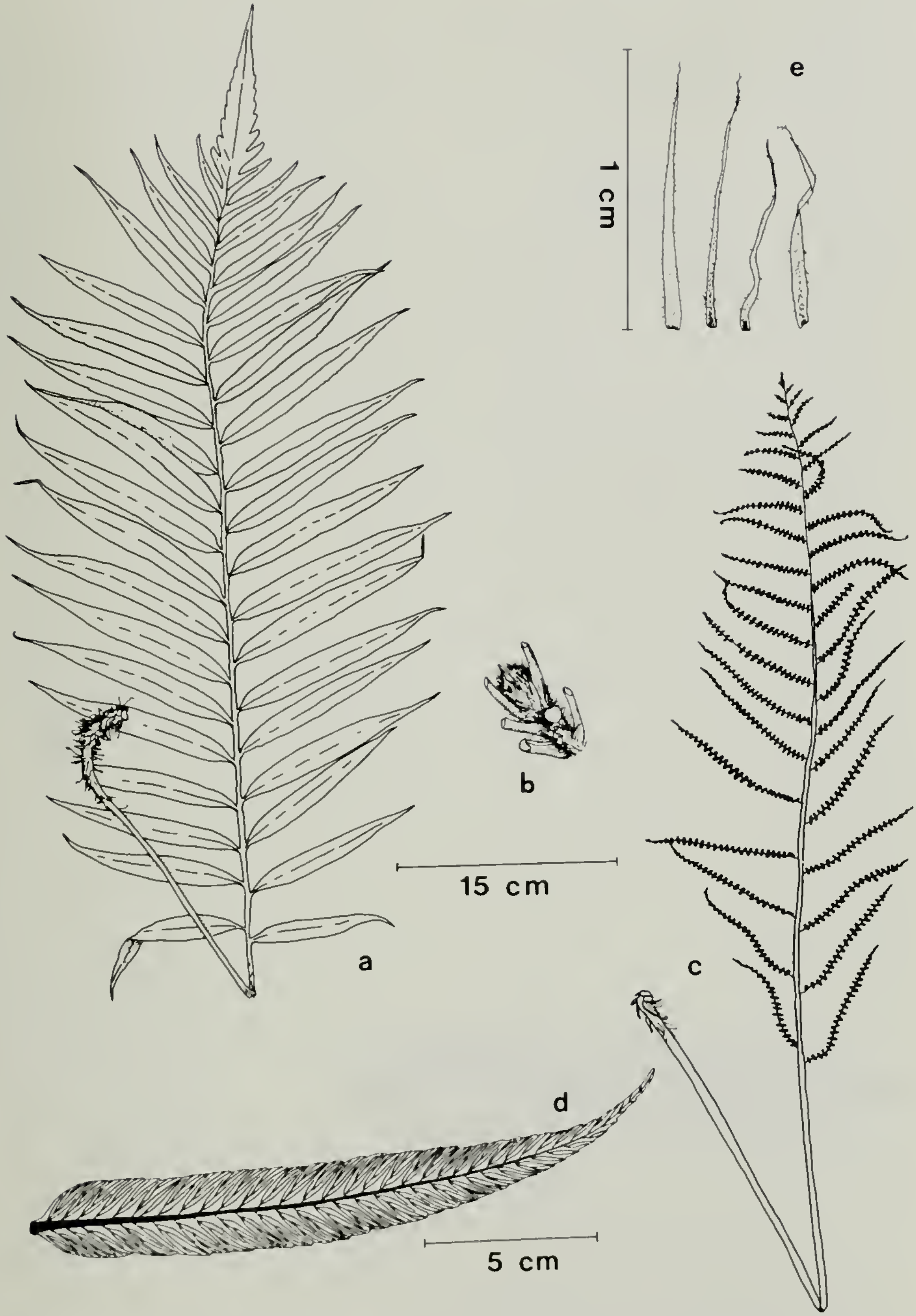

FIGURE 24. *Polybotrya sorbifolia* Kuhn. a. sterile leaf; b. stem; c. fertile leaf; d. sterile pinna; e. stem scales. a–e: *Moran 3145* (F).

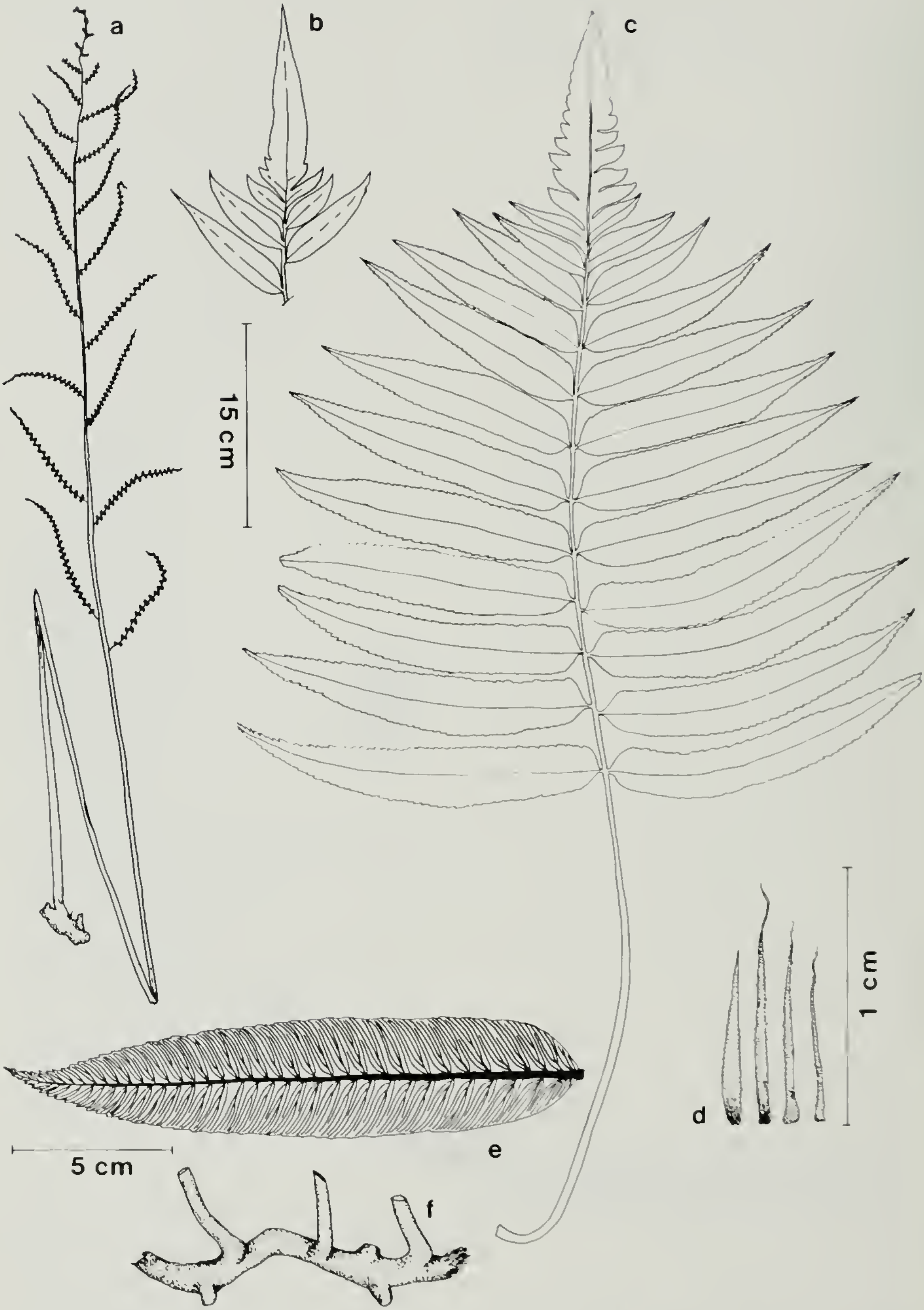

FIGURE 25. *Polybotrya fractiserialis* (Baker) J. Smith. a. fertile leaf; b. apex of sterile leaf; c. sterile leaf; d. stem scales; e. sterile pinna; f. stem. a: *C. Schunke 666* (F). b,d,e: *Moran 3536* (F). c: *Gonggrijp & Stahel 3300* (MO). f: *Tryon & Tryon 5221* (GH).

Other illustrations: Brade, Bradea 1(9):62, fig. 4. 1971 (as *P. polybotryoides*).

This species, like *P. sorbifolia*, is terrestrial and grows in wooded talus slopes, usually along rocky streamsides. The altitudinal range of *P. fractiserialis* is from 200–1500 m, but about 80 percent of the collections come from the 400–800 m range. Although principally a forest species, I have seen vigorous fertile plants growing along sunny streamsides in Ecuador, an observation which suggests that this species has more tolerance to higher light conditions than its cogenerics.

The range of *P. fractiserialis* occupies two discontinuous regions: 1) the Andes from Bolivia to Ecuador, and 2) the Guianas (Map 3). A distance of 900 km separates the northernmost population in Ecuador from the westernmost population in British Guiana. All populations of this species occur on the eastern side of the Andes. Their absence from the western side is probably due to the extreme dryness that characterizes that side of the Andes south of the equator.

Polybotrya fractiserialis and *P. sorbifolia* look very much alike and can be easily confused. Several characters, however, distinguish the two. The easiest feature to recognize is the shape of the medial pinnae: those of *P. fractiserialis* are relatively shorter and broader than those of *P. sorbifolia* (see key and descriptions); this stoutness is accentuated just below the apex (Fig. 25). The apex of *P. sorbifolia* is another difference; it has more numerous, decurrent, narrower pinnae (Fig. 24). Usually, the veins of *P. sorbifolia* are at a more oblique angle to the costa than those of *P. fractiserialis*. Another difference, albeit more recondite, is found in the sporangial stalks of *P. fractiserialis*, which have a lightbulb-shaped gland at the base of the paraphysis (Fig. 11f,g); *P. sorbifolia* lacks such a gland (Fig. 11b). In fact, no other species of *Polybotrya* has a glandular cell on the paraphysis or elsewhere on the sporangium. *Polybotrya sorbifolia*, however, has round, sessile glands on the lamina; such glands are lacking on *P. fractiserialis*.

Spore size is yet another diffence: *P. fractiserialis* has much larger spores than *P. sorbifolia*. This difference suggests that *P. fractiserialis* may be a polyploid, but chromosome counts are still wanting for the two species. Polyploidy has not yet been documented cytologically in *Polybotrya*.

Polybotrya fractiserialis and *P. plumbicaulis* were described at the same time, in the same publication, and were distinguished on the basis of leaf size, number of pinnae pairs, and two versus three or four veinlets in each pinnate group. These characters, however, intergrade completely even on leaves from a single plant. I chose the name *P. fractiserialis*, rather than the simultaneously published name *P. plumbicaulis*, because it was used by Posthumus (1928) in his treatment of Surinam ferns.

Specimens examined: FRENCH GUIANA. **Guyane:** Cayenne, 1847, *Leprieur s.n.* (P). **Inini:** Cocao, La Comte Riv., 1847, *Leprieur s.n.* (P); Tumuc Aumac, Haut Itany, *Hoock s.n.* (P); ca. 45 km SE of Saul, *Granville 3674* (CAY, Z); region de Paul Isnard, Montagne Lucifer, *Granville 5219* (CAY, Z); Saul, Monts du Fumée, *Granville 5121* (CAY, Z).

SURINAM. 3 km S of Juliana Top, 12 km N of Lucie Riv., *Maguire et al. 54384* (MO, NY), *Irwin et al. 54669* (NY), *54784* (F, MO, NY); Brownsberg, *Gonggrijp & Stahel 3300* (MO, US).

GUYANA. **Essequibo:** Southern Pakaraima Mts., Kopinang Falls, *Maguire et al. 46068-A* (NY).

ECUADOR. **Napo:** east 10 km SE de Tena, 3 km E de Puerto Nuevo por camino a Puerto Misahuallí, *Moran 3536* (F, GH, MO, Q, QCA, US). **Pastaza:** Río Capihuari, tributary of Río Pastaza, *Øllgaard et al. 35124* (AAU).

PERU. **Amazonas:** Prov. de Bagua, Valley of Río Marañon above Cascadas de Mayasi near Campamento Sta. Montenegro (kms. 280–284 of Marañon rd.), *Wurdack 1854* (US). **Cuzco:** Prov. Paucartambo, *Vargas 11280* (GH). **Huánuco:** Prov. Huánuco, Tingo María, *Tryon & Tryon 5221* (GH); Tingo María, *Allard 20661* (US), *22305* (GH, US), *22526* (US); Previsto, antes de Aguaitia, *Aguilar 947* (USM); Prov. Leonicio Prado, Distrito Rupa Rupa, al este de Tingo María, cerca al Cerro Quemado, *J. Schunke 10173* (MO); hills E of Tingo María, *Croat 21152* (MO). **Junín:** Prov. Satipo, Pichanaki, *León 226* (USM); Schunke Hacienda, above Ramón, *C. Schunke A214* (US); Chanchamayo Valley, *C. Schunke 165* (F, US), *666* (F), *1396* (F). **Loreto:** above Pongo de Manseriche, *Mexia 6246a* (UC, US); Aguaytia, *Croat 21014* (MO). **Madre de Dios:** Prov. Manu, town of Atalaya, 2–3 km W of village, *Foster 7455* (F, MO, USM); Pantiacolla, serranía across Río Alto Madre de Dios from Shintuya, *Gentry et al. 27365* (MO); prov. Manu, km 139 on road between Cabo de hornas and Shintuya, *Foster 4020* (F, USM); Parque Nacional de Manu, Cocha Cashu Biological Station, *Foster P-84-91* (F); valle de Marcapata, *Herrera 1200* (US). **Oxapampa:** Prov. Pasco, Iscoazin, *Foster 7937* (F, USM). **San Martín:** Mt. Campana, *Spruce 4337* (color slide of K specimen at MO; photo GH, US); Tarapoto, Ad rupes secus rivularum, Aug. 1855, *Spruce 4090* (photo of K specimen at GH; photo and fragment P, US); Prov. de Lamas, beween Tarapoto and Moyobamba, ca. 10 km NW of Tabalosas, *Croat 51154* (MO).

BOLIVIA. **La Paz:** Cordillera Real, Río Chimate, *Tate 502* (NY), *513* (NY); Mapiri, *Williams 1188* (NY, US); Mapiri, *Buchtien 1015* (US), *2138* (US); Mapiri region, San Carlos, *Buchtien 13* (US); Mapiri, Charopampa, *Buchtien 11* (MICH, P). **Prov. unknown:** Challana Riv., *Cardenas 1249* (LIL, US).

7. **Polybotrya crassirhizoma** Lellinger (Fig. 26, Map 4).

Polybotrya crassirhizoma Lellinger, Amer. Fern J. 62:49, figs. 1, 8. 1972. TYPE: Peru. Loreto: Gramitanacocha, Río Mazán, alt. 100–125 m, *J. Schunke 268* (holotype: US!; isotypes: F!, GH!, NY!, UC!).

Polybotrya macbridei Lellinger, Amer. Fern J. 62:51, figs. 2, 9. 1972. TYPE: Peru. Junín: Hacienda Schunke, La Merced, *Macbride 5602* (holotype: US!; isotype: F!).

Stem 1–2 cm thick, hemiepiphytic; *scales* 10–25 × 0.2–1.1 mm, dull orange or reddish brown, rarely shiny and dark brown, with a dark central stripe and lighter borders, rarely concolorous, margins denticulate to erose. *Sterile leaves* up to 1.35 m; *petiole* ½ to ¼ the length of the lamina, scaly at base; *lamina* lanceolate, to 1.0 × 0.44 m; *pinnae* 6–20 pairs, (11)15–20(24) × 2–4 cm, lanceolate to oblong-lanceolate, the base unequal, broadly rounded or truncate on the acroscopic side, slightly excavate or tapering on the basiscopic side, the margins crenate-dentate or more rarely lobate-serrate, apex acuminate, often serrate; *veins* free, often with a single veinlet springing from the costa between the main pinnate groups; *axes* with a few, scattered, narrow, appressed scales, occasionally pubescent, the hairs short, less than 0.1 mm, erect, colorless, subulate, unicellular. *Fertile leaves* 2-pinnate, occasionally 2-pinnate-pinnatifid in large individuals, ½ to ⅓ smaller than the sterile leaves; *axes* similar to those of the sterile leaves but with larger more numerous scales; *sori* coenosoric, completely covering the abaxial surface of the pinnules, occasionally discrete and round at the pinnule base; *sporangia* nonparaphysate; *spores* (48)52–56(61) microns long. $n = 41$.

Other illustrations: See original descriptions of *P. crassirhizoma* and *P. macbridei*, cited above.

Polybotrya crassirhizoma grows primarily in lowland forests of the western Amazon basin and in premontane forests of the eastern Andes (Map 4) from 100 to 1500 m. The cluster of dots in eastern Ecuador reflects recent collecting activity in that area and this species' true abundance there. I saw this species in nearly every forest that I visited in the Amazon basin of Ecuador, and it was one of the most frequent and abundant ferns. This abundance suggests that *P. crassirhizoma* occurs farther east in the Amazon basin than is shown in Map 4. Apparently, *P. crassirhizoma* flourishes on clayey soils and does not grow in sterile, sandy soils.

I chose the name *P. crassirhizoma* over *P. macbridei* because of the more widely distributed type collection. *Polybotrya crassirhizoma* and *P. macbridei* were said to differ by stem thickness, scale luster and color, and the presence versus the absence of lobing at the base of the sterile pinnae (Lellinger 1972). These characters, however, intergrade completely as shown by a series of specimens collected near Coca in the Amazon basin of Ecuador (*Moran 3616*). The most obvious character that supposedly distinguishes *P. macbridei* is the basally lobed pinnae, but this character represents the lobing that typically occurs in transitional sterile-fertile leaves. This example illustrates how part-fertile leaves can cause taxonomic confusion. Accordingly, I placed *P. macbridei* in synonymy.

Specimens examined: COLOMBIA. **Amazonas:** Loreto-Yaco, *Schultes & Black 46-266* (GH).

ECUADOR. **Napo:** 27 km SE of Coca, petroleum well Auca 4, *Moran 3616* (F, GH, NY, Q, QCA, US); 20 km NE of Coca, 5 km N of Joya de las Sachas, *Moran 3615* (F, GH, NY, PORT, Q, QCA, US); about 10 km SE of Tena, 3 km E of Puerto Nuevo on road to Puerto Mishahuallí, *Moran 3535* (F, GH, NY, Q, QCA, US); Bimbino, on the Río Pacuno, 10 hr W of confluence with Río Napo, *Whitmore 752* (BM); Río Cuyabeno, about 2 km upstream from Puerto Bolívar, *Brandbyge et al. 33684* (AAU); San Pablo de los Secoyas, *Brandbyge & Asanza C. 32881* (AAU); San Pablo de los Secoyas, Río Wai si aya, *Brandbyge et al. 32617* (AAU); San Pablo de los Secoyas, on path to Shushufindi, *Brandbyge et al. 32544* (AAU); 50 km NE of Coca, *Lugo S. 3293* (GH); Canton Putumayo, Río Aguarico, town of Dureno, *Plowman et al. 4025* (GH); Anagua, Parque Nacional Yasuni, SEF forest project area, *Øllgaard et al. 38836* (AAU), *39084* (AAU). **Pastaza:** Curaray, Valle de la Muerte, *Holm-Nielsen et al. 22484* (AAU, Q, QCA); basin of Río Pastaza, Pacayacu-Sarayacu region, *Gill 47* (NY); village of Río Chico, 8 km from Puyo, *Shemluck 280* (F); Río Bobonaza, between oil exploration camp Chichirota and Destacamento Cabo Pozo, *Øllgaard et al. 34855* (AAU, Q, QCA); Río Bobonaza, between Cachitama and the outlet of Río Bufeo, *Øllgaard et al. 34748* (AAU); Río Pastaza, near the Peruvian border, around Destacamento Ishpingo,

FIGURE 26. *Polybotrya crassirhizoma* Lellinger. a. fertile leaf; b. sterile leaf; c. fertile pinna; d. sterile pinna; e. stem scales. a: *Øllgaard et al. 34855* (AAU). b–e: *Moran 3615* (F).

Øllgaard et al. 34970 (AAU); 2 km W of Yuralpa, S border of Río Napo, *Holm-Nielsen & Jeppsen 987* (AAU).

PERU. **Huánuco:** Prov. Pachitae, Río Pozouso, *Foster 9284* (F, MO, USM). **Junín:** Chanchamayo Valley, *C. Schunke 157* (F), *158* (F), *661* (F), *812* (F); Schunke Hacienda, above San Ramón, *Killip & Smith 24605* (NY, US); E of Quimiri Bridge, near La Merced, *Killip & Smith 23876* (NY, US); Hacienda Schunke, La Merced, *Macbride 5602* (F, US); La Merced, Chanchamayo, *Soukup 1065* (F). **Loreto:** Prov. Maynas, Quebrada Yanomono, Explorama tourist camp, Río Amazonas above mouth of Río Napo, Transect 6, *Gentry et al. 27880* (MO), *Moran 3640, 3641* (F, Q, QCA); Mishuyacu, near Iquitos, *Klug 1386* (NY, US); Gamitanacocha, Río Mazán, *J. Schunke 268* (F, GH, NY, UC, US), *14285* (US); Veradera de Mazán, *Croat 20763* (MO); Río Napo near Entrada de Isla Inayuga, *Croat 20551* (MO).

BOLIVIA. **Cochabamba:** Prov. Carrasco, confluence of Río Leche with Río Isarsama, *Beck 1635* (LPB).

BRAZIL. **Acre:** Cruzeiro do Sul, vicinity of Serra da Moa, *Prance et al. 12180* (NY).

8. **Polybotrya espiritosantensis** Brade (Fig. 27, Map 21).

Polybotrya espiritosantensis Brade, Rodriguesia 10:28, tab. 3. 1948. TYPE: Brazil. Espírito Santo: Municipality of Itaguaçu, Jatiboca, virgin forest, 700–800 m, *A. C. Brade 18224* (holotype: RB!).

Stem 1–2 cm wide, hemiepiphytic; *scales* mostly 10–15 × 1.0–2.5 cm, bright reddish brown, spreading, membranous, the center often darkened to varying degrees, margins highly erose-denticulate, occasionally fimbriate. *Sterile leaves* up to 1.2 m long; *petiole* to 30 cm long, about half as long as the lamina, scaly at base; *lamina* ovate, 2-pinnate proximally, becoming 1-pinnate distally, 60–90 × 50–70 cm, subcoriaceous, pale green, nearly glabrous on both surfaces, the apex subconform and pinnalike but with one or two basal lobes; *pinnae* alternate, 6–8 pairs, the apex conform, like the lateral pinnules, the upper pinnae simple and resembling the pinnules of the lower; *pinnules* anadromic throughout, 3–4 pairs, elliptic, 10–13 × 2–3 cm, the margins entire, the apex acuminate, the base cuneate, the proximal pinnules with stalks 2–4 mm long, the distal pinnules sessile; *veins* slender, none conspicuously thicker than the others, long, parallel, 1–2 branched, the tips free; *axes* with a few scattered, appressed, narrow scales, otherwise glabrous. *Fertile leaves* 2-pinnate, amphiacrostichoid; *pinnules* caudate, entire, appearing cylindrical when mature; *sporangial stalks* paraphysate; *spores* (52)54–60(62) microns long.

Other illustrations: Brade's original description has an excellent photograph of the type; Brade, Bradea 1:67, tab. 6, fig. 5. 1971 (stem scales only).

Polybotrya espiritosantensis is endemic to the state of Espírito Santo in southeastern Brazil (Map 21). I expect this species will eventually be found in other parts of mountainous coastal Brazil. *Polybotrya espiritosantensis* has the most distinctive laminar cutting of any species in the genus. No other species has the simple, entire pinnules that evenly taper at the base and apex (Fig. 27b). Unlike all other species of *Polybotrya* that have pinnatifid apices, the leaf and pinnae apices of this species are conform or nearly so (Fig. 27a). The numerous, close, long, parallel veins (Fig. 27b) are like those of the 1-pinnate species *P. fractiserialis* and *P. sorbifolia* and probably indicate a close relationship.

Specimens examined: BRAZIL. **Espirito Santo:** Santa Thereza, 900 m, *Foster & Foster 854* (GH, US); Municipality of Itaguaçu, Jatiboca, virgin forest, 700–800 m, *A. C. Brade 18224* (RB).

POLYBOTRYA subgenus POLYBOTRYA

TYPE SPECIES: *P. osmundacea* Willd., Sp. Pl. ed. 4, 5:99. 1810.

Polybotrya subgenus *Eupolybotrya* Fée, Mém. Fam. Foug. (Hist. Acrost.) 2:16. 1845.

Acrostichum section *Polybotrya* Hooker, Species Filicum 5:244. 1864.

Stem hemiepiphytic; *sterile leaves* 1-pinnate-pinnatifid to 4-pinnate; *veins* free.

9. **Polybotrya caudata** Kunze (Fig. 28, Map 5).

Polybotrya caudata Kunze, Linnaea 9:23. 1834. TYPE: Peru. Huánuco: Pampayaco, July 1829, *Poeppig s.n.* (B!).

Polypodium adiantoides Aublet, Hist. Pl. Guiane Françoise 2:962. 1775, *nomen illeg., non* Burm. (1768). TYPE: Guyana. *Aublet s.n.* (holotype: BM!, Morton photo 6626 at B!, F!, GH!).

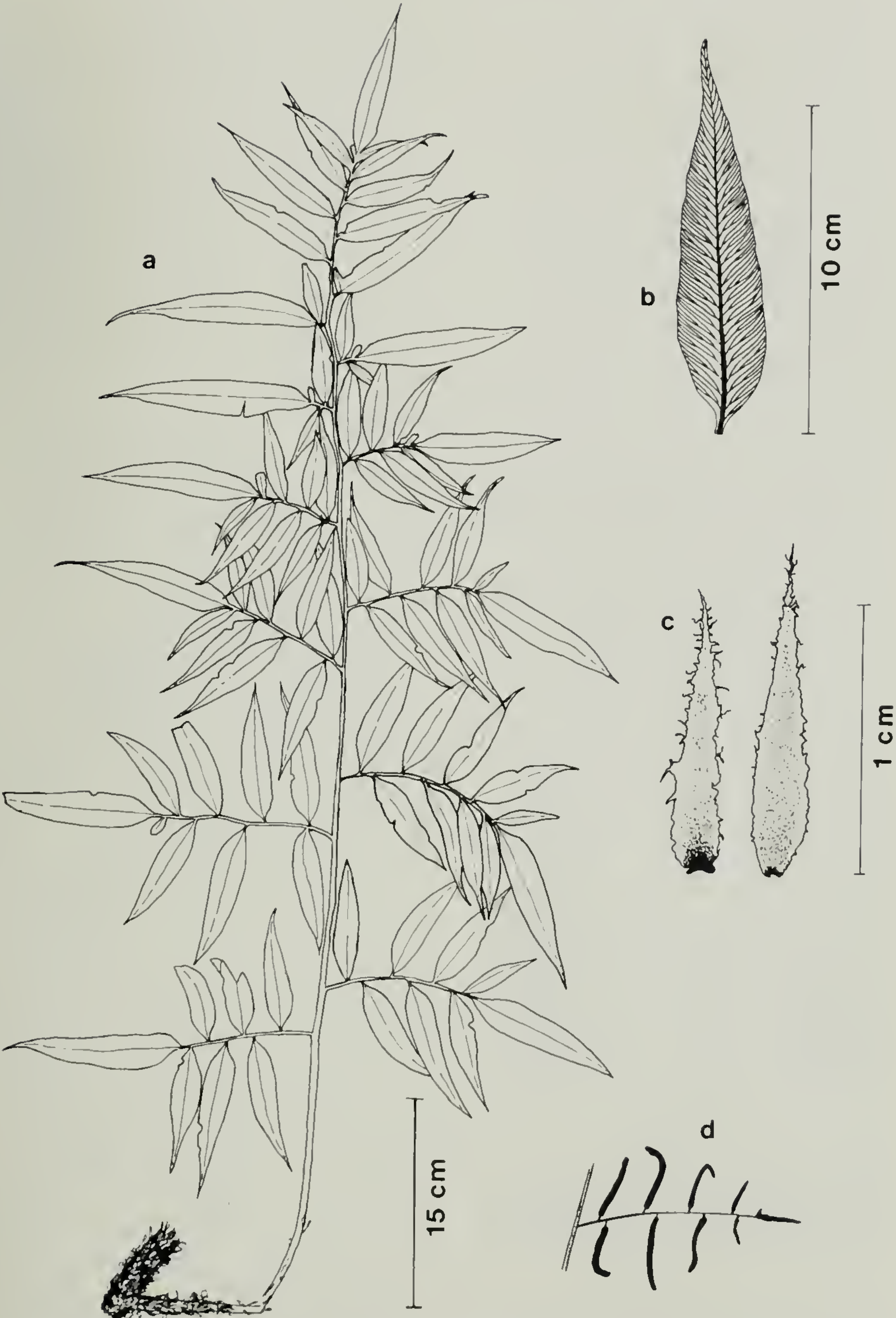

FIGURE 27. *Polybotrya espiritosantensis* Brade. a. sterile leaf; b. sterile pinnule; c. stem scales; d. fertile pinna. a–d: *Brade 18224* (RB).

Olfersia caudata (Kunze) Kunze, Linnaea 21:206. 1848.

Psomiocarpa caudata (Kunze) Presl, Epim. Bot. 162. 1849.

Acrostichum caudatum (Kunze) Hooker, Species Filicum 5:244. 1864. *nomen illeg. non* Hooker (1840).

Polybotrya acuminata Kaulfuss var. *villosa* Christ, Prim. Fl. Costar. 3(1):9. 1901. TYPE: Costa Rica. Limón: Llanuras de Santa Clara, 500 m, *Biolley 10688* (lectotype: US!; isotype: CR!).

Polybotrya villosula Christ, Bull. Herb. Boissier, II. 6:168. 1906. TYPE: Costa Rica. Santa Clara, Las Delicias, 1897, 500 m, *Pittier 10688* (P?).

Polybotrya costaricensis Brade, Bradea 1:11, tab. 1, fig. 1. 1969. TYPE: Costa Rica. Limón: Hundrisser Ranch, Atlantic shore, Sept. 1909, *Brade & Brade 374* (holotype: HB; isotypes: NY!, UC!).

Stem 0.5–2.5 cm thick, hemiepiphytic; *scales* linear-lanceolate to narrowly triangular, 8–20 × 1–2 mm, dull brown, opaque, entire to denticulate, the base elevated, thickened, curved, and appressed. *Sterile leaves* up to 2 × 1 m; *petioles* 30–70 cm long, about ⅓ the length of the lamina; *lamina* mostly 2-pinnate-pinnatifid, rarely 3-pinnate at the base, firm-chartaceous, glabrous to pilose, the hairs 0.2–1.5 mm long, acicular, the margins sparsely ciliate, the hairs minute, less than 0.2 mm long; *pinnae* up to 20–45(60) × 7–20(30) cm, subdeltate, acuminate, subequilateral, slightly more developed on the acroscopic side; *pinnules* slightly prolonged acroscopically, the base truncate to slightly cordate, catadromically arranged in the medial pinnae; *veins* free, sometimes with a single vein springing from the costa between the pinnate groups; *axes* nearly glabrous or pubescent to various degrees, the hairs acicular, whitish; *grooves* usually pubescent within, often densely so at the junctures. *Fertile leaves* similar in size to the sterile, mostly 2-pinnate, but with some of the larger pinnules lobed at base; *pinnae* caudate, 4–8(11) × 0.5–1.5 cm, apparently soriferous on both surfaces; *spores* (43)46–50(53) microns long. $n = 41$.

Other illustrations: Fée, Mém. Fam. Foug. (Hist. Acrost.), Atlas, tab. 34, 1845; Vareschi, Fl. Venez., vol. 1, tab. 73. 1968; Brade, Bradea 1(9):63, fig. 1; p. 67, fig. 6.; Croat, Fl. Barro Colorado Is., figs. 28 & 29. 1978 (as *P. villosula*); Stolze, Fieldiana Bot. n.s. 6, fig. 60a,b. 1981; Tryon & Tryon, Ferns & Allied Plants, figs. 80.8, 80.9, 80.22, 80.23. 1982.

Polybotrya caudata is one of the most widely distributed species in the genus (Map 5). It grows primarily in lowland forests from sea level to 800 m, but specimens from the Andes have occasionally been collected as high as 1900 m. I found this species at many of the sites where I collected in Costa Rica, Ecuador, and Peru, but not in Venezuela. *Polybotrya caudata* is one of only three species in the genus that occur on an oceanic island—Cocos Island, about 500 km (310 mi) southwest of Costa Rica.

Polybotrya villosula was said to differ from *P. caudata* only by its long and villous pubescence, but specimens are usually glabrous or fully pubescent, with few intermediate forms. Since pubescence does not correlate with any other character and I found no difference in geographical range between the two forms, I regard *P. villosula* as a synonym of *P. caudata*.

The juvenile leaves in glabrous plants of this species may be difficult to distinguish from *P. osmundacea*. A good character to separate the two species is the minutely and sparsely ciliate leaf margin of *P. caudata* (Fig. 28a): that of *P. osmundacea* is always glabrous (Fig. 47). The thick, dull brown, curved, and appressed stem scales (Fig. 28b,h) also help distinguish *P. caudata* from many other *Polybotrya* species.

Specimens examined: MEXICO. **Chiapas:** eastern highlands near Guatemalan border, *Breedlove 34101* (CAS).

GUATEMALA. **Alta Verapaz:** near Río Icvolay, near Hacienda Yaxcbnal, 5 mi NW of Cubilquitz, 250–300 m, *Steyermark 44675* (F); Cubilquitz, 350 m, *Tuerckheim 148* (US), *358* (P, Z), *7812* (US), 8040B (US), *8041* (GH, NY). **Izabal:** between Bananera and "La Presa" in Montaña del Mico, *Steyermark 38229* (F), *38271* (F), *39197* (F); Río Chacón, 30 m, *Johnson 1221* (US); between Los Amates and Izabal, Sierra del Mico, *Kellerman 7354* (F, NY); along Río Frío, 65 m, *Steyermark 39895* (F, US); 2.5 mi N of Rio Dulce on gravel road to Petén, *Dunn & LeDoux 22005* (MO, NY); vicinity EXMIBAL Camp 2 (La Gloria), NW of Lake Izabal, 400–500 m, *Jones & Facey 3246* (NY); vicinity of Quirigua, *Standley 24195* (GH); vicinity of Puerto Barrios, *Standley 25085* (GH, US).

BELIZE. **El Cayo:** Vallentin, *Lundell 6416* (GH, US). **Stann Creek:** along road and stream at Dry Creek, near Dist. of Cayo Border, *Croat 24541* (CR, MO); Middlesex, *Gentle 2947* (GH, MICH, US); *Schipp 273* (BM, F, GH, MO, UC, US, Z).

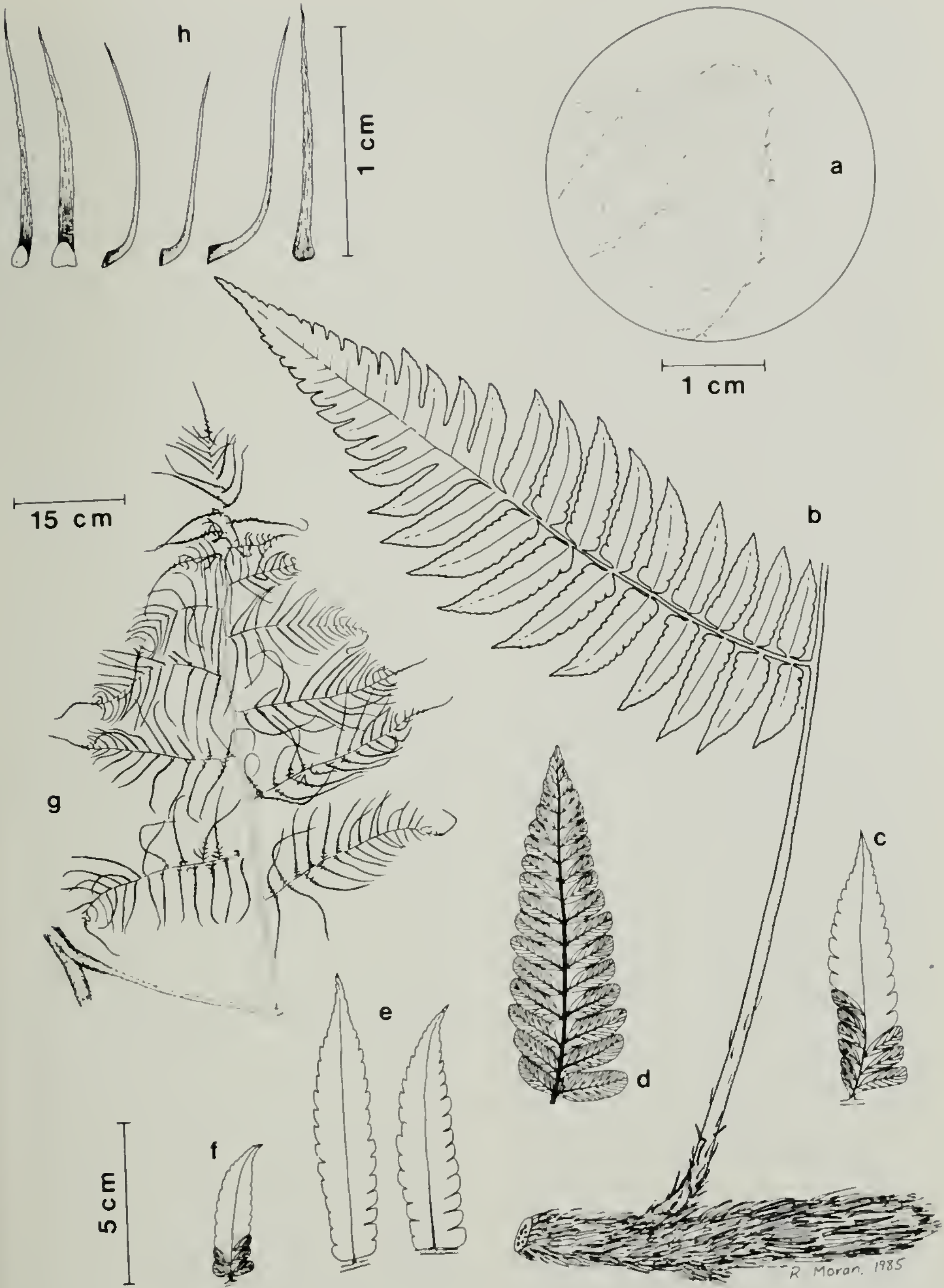

FIGURE 28. *Polybotrya caudata* Kunze. a. leaf margin showing minute cilia; b. stem and basal pinna (note appressed scales—same scale as f); c–f. acroscopic pinnules, pinnae apex toward the right in all; g. fertile leaf; h. stem scales, abaxial view at left, side view in center, adaxial view at right. a,c: Costa Rica, *Scamman 7156* (GH). b: French Guiana, *Cremers 7369* (CAY). d,g,h: Costa Rica, *Moran 2186* (F). e: Bolivia, *Steinbach 7499* (MO). f: Trinidad, *Fendler 105* (GH).

Honduras. **Atlántida:** Lancetilla Valley, near Tela, *Standley 53983* (F, US); near Ceiba, 400 m, *Dyer A225* (US).

Nicaragua. **Chontales:** 4 km al oeste de La Libertad, El Comatillo, *Gómez & Cittar 6731* (CR); vicinity of La Libertad, 500–700 m, *Standley 9047* (F). **Zelaya:** road to Mina Nueva Americana, *Stevens & Krukoff 12666* (CR, MO); along new road from Río Blanco to Río Copalar, *Stevens & Krukoff 12056* (CR, MO); Caño Aamora on Río Rama, *Stevens & Krukoff 8827* (CR, MO); base camp 3.6 km SE Cerro San Isidro, Río Kama, Río Escondido, 0–65 m, *Proctor et al. 27091* (F, NY, VEN); Mosquito Coast, *Schramm s.n.* (US); Bluefields, *Niell 2610* (CR); area de la Bahía de Bluefields, Río Escondido, 0–30 m, *Molina R. 1907* (F, US); near Bluefields, *Danneberger s.n.* (US); Braggman's Bluff, *Englesing 291* (F, US); Mina Nueva Americana, 11.3 km N of main road, *Pipoly 5299* (CR, MO); 13 mi above Kururia, *Pipoly 3824*; Colonia Kururia, *Pipoly 3880* (CR, MO), *3901* (CR, MO); Neptune Mining Co., *Stevens & Krukoff 13005* (CR, MO); near junct. of road to Alimidkanba with road between El Empalme and Limbiaka, *Stevens & Krukoff 12741* (CR, MO); Apz. 5 km de Rama sobre el Río Rama, *Gómez & Cittar 6409* (CR); El Salto along Río Pis Pis, *Pipoly 3542* (CR, MO); 13 mi above Kururia on road to San Jerónimo, *Pipoly 3817* (CR, MO).

Costa Rica. **Cartago:** near Turrialba, slope of the Río Reventazón behind the Instituto Interamericano de Ciencias Agricolas, 600 m, *Mickel 3368* (NY); Valley of Río Reventazón 9 km ENE of Turrialba near Pavones, 650 m, *Holm & Iltis 200* (F, NY). **Cocos Island:** *Barclay 2199* (BM); Wafer Bay, *Gómez 3354* (CR, F, US, Z); *Gòmez 4528* (CR); Chatham Bay, *Jiménez M. 3200* (CR, GH). **Heredia:** Holdridge's Finca La Selva, Río Puerto Viejo at Quebrada El Sura and Q. El Salto, *Rossbach 3710* (GH), *Scamman 7482* (GH), *Scamman & Holdridge 7998* (CR, GH); 2 km upstream from confluence of Río Puerto Viejo with Río Sarapiquí, Finca "La Şelva," *Burger & Stolze 5865* (CR, F, GH, US), *Mickel 3570* (NY). **Limón:** Llanuras de Santa Clara, *Biolley 10688* (CR, US); Hundrisser Ranch, Atlantic slope, *Brade & Brade 374* (NY, UC); 7 km SW of Bribri, 100–250 m, *Gómez et al. 20423* (CR, MO, UC); N end of Tortuguero Natl. Park, *Burger & Antonio 11263* (CR, F, NY); near Guápiles, at bridge over Río Guácimo, 50 m, *Moran 2182, 2185, 2186* (CR, F, P, PORT); near banana plantation and Pandora, near Río Estrella, *Rossbach 3624, 3625* (GH); La Lola, a cacao finca, near Río Madre de Dios, *Scamman 7156* (GH); Finca Montecristo, on the Río Reventazón below Cairo, 25 m, *Standley & Valerio 48622* (US). **Puntarenas:** Osa Peninsula, *Mickel 1944* (CR, NY); hills N of Palmar Norte, along trail to Jalisco, *Croat 35176* (MO); Osa, 40 km W of IA rt. 2, *Gómez 19489* (CR, MO).

Panama. **Bocas del Toro:** in Laguna de Chiriquí and its neighborhood, *Hart 53* (US). **Canal Zone:** "Isthmo Panama," *Hayes 8* (B, GH, Y, US); hills N of Frijoles, *Standley 27597* (MO, US); Cerro Azul, *Tyson 2109* (MO); along hogback ridge S of Fuertes Cove, Pearson Peninsula, *Croat 8153* (MO); headwaters of the Río Chinilla, above Nuevo Limón, *Maxon 6895* (US); ravine near Frijoles, *Killip 2929* (US); along riverbank between Fort Sherman and Fort Lorenzo, *Croat & Porter 15436* (MO); hilly forest around the Agua Clara Reservoir, near Gatun, 20–30 m, *Maxon 4641* (GH, NY, US); Orange River Trail, *Cornman 544* (UC, US); Barro Colorado Island, Gatun Lake, *Maxon et al. 6817* (GH), *Seaverns 56* (F), *Starry 91* (F, GH), *Croat 5114* (MO), *6850* (MO), *7362* (MO), *8025* (MO), *9000* (MO, NY), *9004* (MO, UC), *9103* (COL, MO, UC), *10804* (MO), *15256* (MO), *17367* (F, MO), *Bailey & Bailey 541* (GH), *Chrysler 4836* (UC); 10 mi from main gate, near Río Frijolito, *Croat 15081* (F, MO, US); Allison Armour Trail, *Wetmore & Woodworth 130* (GH). **Chiriquí:** above Río San Felix near town of San Felix, ca. 13 mi N of Río San Felix bridge, 800–1200 m, *Croat 33452* (MO); forest behind Vivero forestal, 12 km N of Los Planes de Hornito, IRHE Fortuna Hydroelectric Project, 1200–1300 m, *Knapp 4966* (MO). **Colón:** Santa Rita Ridge, end of road from Transisthmian Highway, ca. 10 mi from road, *Porter et al. 4763* (MO); Santa Rita Ridge, 2.8 mi from Boyd–Roosevelt Hwy., *Croat & Porter 15342* (F, MO); forest along Portobelo–Nombre de Dios road, 10 km W of Nombre de Dios, *Knapp & Mallet 5402* (MO). **Darién:** vicinity of Cana, summit of knoll above Cana, *Stern et al. 523* (GH). **Panamá:** 2.5 mi N of Goofy Lake on road to Cerro Azul, *Croat 11544* (F, MO); upper Mamoni River, 150–400 m, *Pittier 4492* (US); Orange River Valley, E of Juan Diaz, *Killip 2544* (GH, US); along Río Pirati, foothills of the Serranía de Maji, *Knapp & Mallet 5133* (MO); in high ridges of the Serranía de Maji, S of the Chocó village of Ipeti, *Knapp et al. 4479* (MO); along Juan Diaz River, 4 mi above Juan Diaz, 0–75 m, *Killip 2845* (US). **San José Island:** Perlas archipelago, Gulf of Panama, 55 mi SSE of Balboa, *Johnston 452* (GH, US). **Veraguas:** Isla de Coiba, *Mendez 75* (MO).

Trinidad. Aripo road via Arima, *Broadway 5717* (F, Z); without locality, *Fendler 105* (GH, MICH, MO, NY, P, PH, UC); without locality, *Broadway 5358* (NY); forest, Brazil, *Britton et al. 2144* (GH, NY); Mount Tamana, *Britton et al. 1935* (NY); Oropuche, local road via Valencia, *Broadway 9207* (MO, UC); without locality, *Crueger 139* (B); La Sierra, Maraval, *Hombersley s.n.* (MO); Arima Ward, Guanapo River Valley, ca. 1 mi SE of La Leja village, *Jermy 3122* (BM); Cumaca Road, *Fay 472* (BM); Brickfield's Tea Plantation, 3 mi S of Forestry Rest House, *Jermy 2137* (BM); Valencia Ward, near Valencia, *Jermy 10826* (BM); Hollis Reservoir Road, *Mickel 9472* (UC).

French Guiana. Saint Jean du Mearoni, *Benoist 1271* (P); Central Guyana, *Leprieur s.n.* (P); Sommet Tabulaire, 650–750 m, ca. 45 km SE of Saul, *Cremers 6374* (CAY), *6523* (CAY, Z); Bassin du Haut Inipi, 7 km WSW du Pic Coudreau (Monts Bakra), *Granville 4012* (CAY, Z); Haut Oyaopock, W of Trois Sauts Crique Euleupousing, rive gauche du Saut Cambrouse, *Granville 1143, 1165* (CAY, NY, Z); S of Tampoc: Saut Koumakou Soula, *Cremers 4460* (CAY, Z); Saut Tampoc, *Granville 4841* (CAY); Haute Riv. Mana: Saut Grous Tigre, *Cremers 7552* (CAY, Z); Haute Crique Baboune, affluent de la Riv. Mana, *Cremers 7369* (CAY, Z); Haute Crique Waamahpann, au depart du chemin indien, *Granville 971* (CAY); Frontiere Guyane–Surinam, Tuma Humac, *Granville 991* (CAY, Z); Crique Gabaret, 25 km de l'embouchure, layon N–W, *Oldeman 1933* (CAY, NY); Crique "Roche Fende" (affleunt de la Comte) a 1 km environ de son embouchure, *Granville B.4711* (CAY, Z); W of Saul on trail to Monts Galbao, *Boom & Mori 1856* (CAY, NY); Piste allant de Citron vers le Massíf du Decou Decou, *Billiet & Jadin 1683* (CAY); Región de Paul Massíf du Decou Decou, *Cremers 7951* (CAY, Z).

SURINAM. West Rivier, 2–5 km SW of Juliana Top, 275–300 m, *Irwin et al. 54896* (NY); no locality, *Hostmann s.n.* (NY); 45 km S of Paramaribo, new road to Hanover, N of Zanderij, *Tryon & Kramer 5611* (GH, MICH, NY); about 25 km S of Paramaribo, *Lindeman 4570* (GH), *Kramer 1954* (MO); 3 km S of Juliana Top, 12 km N of Lucie River, 300–325 m, *Irwin 55161* (MO, NY); Para Dist., *Lindeman & Teunissen 15291* (Z); Suriname River, Plantage "Accaribo," *d'Angremond s.n.* (Z).

GUYANA. Kamuni Ck., Groete Ck., Essequibo River, *Maguire & Fanshawe 22855* (GH, NY); Essequibo River, *Persaud 372* (F); Rockstone, *Gleason 582* (GH, NY); Demerara, *Jenman s.n.* (NY); Barima River, *Jenman s.n.* (NY); 3 mi S of Chodikas, *Guppy 462* (BM); Essequibo River, Moraballi Ck., near Bartica, *Richards 803* (BM); lower Cuyuni River, *Sandwith 1561* (BM).

VENEZUELA. **Bolívar:** Dtto. Heres, Campamento Guri, *Fernández 951* (PORT, UC); Roraima, *Schomburgk s.n.* (B, NY); without locality, anno 1843, *Schomburgk 1659* (B); E of Cerro El Picacho, N of Las Nieves and Las Chicharras, 45 km N of Tumeremo, vicinity of Beborah, Altiplanicie de Nuria, 600–650 m, *Steyermark 89120* (NY, VEN); a lo largo de la Quebrada Acarabisí, limites del Estado Bolívar con la zona dereclamación, *Aymard et al. 952* (PORT, UC). **Portuguesa:** Depto. Paez, Pozo Blanco, entre Acarigua y Payara, 190 m, *Ortega 636* (PORT, UC, VEN). **Sucre:** selva del Rectangulo N del Lago de Tuanoco, *Lasser & Vareschi 3926* (VEN); vicinity of Cristóbal Colón, Avicagua, *Broadway 560* (GH, NY, US). **Territorio Federal Delta Amacuro:** Depto. Antonio Diaz, 9°15'N, 60°57'W, upper reaches of riverine forest of Caño Atoiba tributary of Boca Araguao, *Steyermark et al. 115033* (VEN); Depto. Antonio Diaz, vicinity of Caño Jotajana (= tierra alta), tributary of Caño Guiniquina, NW of Epana near boundary with Depto. Tucupita, 9°15'N, 61°10'W, 50 m, *Steyermark et al. 115021* (MO, UC, VEN); Depto. Pedernales (boundary with Depto. Tucupita): Caño Simoina, west of Isla Coucuina, S of Barra de Coucuina, 50 m, *Steyermark et al. 114331* (MO, VEN), *114332* (MO, UC, VEN).

COLOMBIA. **Amazonas:** Trapecio Amazonico, Loretoyacu River, 100 m, *Schultes & Black 8467* (GH, US). **Cauca:** Cali, *Lehmann 2998* (BM); en la orilla opuesta Puerto Limón–Río Caqueta, *Mora 4430* (COL); Gorgona Island, off Nariño, *Taylor 1223* (MICH, NY); Río Timbiqui, *B.T. 443* (GH). **Chocó:** slopes and ridge of Loma del Cuchillo, ca. 15 km WSW of Chigorodó, 150–400 m, *Lellinger & de la Sota 643* (LLP, US); upper Río Truando, 2 km SSW of the confluence of Río Nercua near the MADUREX Camp, 100 m, *Lellinger & de la Sota 589* (COL, LP, US); trail to Miniquia E of Puerto Mutis (Bahía Solano), 20–120 m, *Lellinger & de la Sota 26* (CR, COL, LP, US); Río San Juan, 3.5 km SW of Andagoya, just NE of the mouth of the Río Suruco, 60 m, *Lellinger & de la Sota 496* (COL, LP); Municipio de Río Sucio, Parque Nacional Los Catios, alrededor del Campamento de Tilupo, 250–320 m, *Forero & Jaramillo 1745* (COL, MO). **Cundinamarca:** Cordillera Oriental, Mesa Negra, Gazuguan Valley, 6 km NW of Medina, 580 m, *Grant 10436* (F, US). **El Valle:** La Cumbre, Cordillera Occidental, 1700–2200 m, *Killip 11343* (GH, NY, US); Finca La Pradera ca. 6 km SW of El Cairo on trail to Río Blanco, between El Brillante and Boquerón, *Lellinger & de la Sota 790* (COL, US). **Nariño:** Pambana, between Río Pimbi and Río Cuembi, on Río Telembi, above Barbacoas, 50 m, *Ewan 16846* (BM, GH, UC).

ECUADOR. **Los Ríos:** Río Palenque biological station, km 56 Quevedo–Sto. Domingo road, *Evoy 104* (NY). **Morona-Santiago:** Pachicutza, at "Escuela iscomisional [*sic.*] Cardinal Dofner," km 140 on road Loja Gualaquiza, 900–1000 m, *Holm-Nielsen et al. 4489* (AAU, Q, QCA), *4495* (AAU, Q, QCA); Sucua, *Swingle et al. 70-02-05-2* (UC, US). **Napo:** casi 10 km SE de Tena, 3 km este de Puerto Nuevo por camino a Puerto Misahuallí, 300 m, *Moran 3534* (F, Q, QCA); 10 km al sur de Tena a Puerto Misahuallí, *Moran 3588* (Q, QCA); Anangu, Parque Nacional Yasuni, SEF project, 260–350 m, *Øllgaard et al. 38932* (AAU, Q, QCA); 27 km SE of Coca, *Moran 3617* (MO, C, QCA). **Pastaza:** Río Bufeo, northern tributary of Río Bobonaza, 300 m, *Øllgaard et al. 43798* (AAU, Q, QCA); Río Bobonaza, around houses between Huagracachi and Cachitama, below Montalvo, 300 m, *Øllgaard et al. 34634* (AAU, Q, QCA); oil exploration camp Chichirota, on the Río Bobonaza, 300 m, *Øllgaard et al. 35290* (AAU, Q, QCA). **Sur de Santander:** vicinity of Barran ca Bermeja, *Haught 1325* (MO).

PERU. **Amazonas:** Prov. de Bagua, left bank of Río Marañon opposite Quebrada Mirana (opposite km 277 of Marañon road above Cascadas de Mayasi), 425–450 m, *Wurdack 2011* (GH, US, USM). **Cuzco:** Prov. La Convención, 73°40'W, 12°30'S, at Camp Zero, 710 m, *Dudley 11513* (GH, US); Camp 1, 910–940 m, in J. Knox's quadrate, *Dudley 10168* (GH); Prov. Paucartambo, Mautainiza [?], 800–900 m, *Vargas 17800* (GH). **Huánuco:** Tingo María, 615–1100 m, *Allard 22593* (US); Cuchero, *Poeppig s.n.* (BM); hills

E of Tingo María, *Croat 21191* (MO); 10 km S of Tingo María, *Stork & Horton 9509* (F, UC, US); Pampayaco, *Poeppig 201* (B). **Loreto:** Prov. Maynas, Peter Jensen's Explorama Lodge, 50 mi downriver from Iquitos at Yanamono Ck., *Moran 3663* (AMAZ, USM); Prov. Maynas, about 10 km SW of Iquitos at zoological park, *Moran 3671* (AMAZ, USM); Pebas on the Amazon River, *Williams 1739* (F); Caballo–Cocha on the Amazon River, *Williams 2137* (F); Río Mazan, 100–125 m, *C. Schunke 380* (GH, NY); Prov. Maynas, Río Itaya, 10 km S of Iquitos, *Tryon & Tryon 5204* (GH); lower Río Huallaga, 155–210 m, *Williams 3999* (F, US); Quebrada Nawampa, *Croat 17620* (MO); Puerto Arturo, lower Río Huallaga below Yurimaguas, 135 m, *Killip & Smith 30690* (NY, US); Mishuyacu, near Iquitos, 100 m, *Klug 1166* (F, NY, US); Quebrada Tahuayo above Tamishiyaco, *Croat 19717* (MO); Río Itaya above Iquitos, *Croat 19220* (MO); primary forest 17 km SW of Iquitos on road to Puerto Almendara, *Croat 18388* (MO); 12 km SW of Iquitos, *Croat 18219* (MO). **Madre de Dios:** 12°49′S, 69°17′W, Prov. Tambopata, Tambopata Nature Reserve, ca. 30 air or 70–80 river km SSW of Puerto Maldonado at effluence Río Torre/Río Tambopata, 260 m, *Barbour 4764, 4790* (F, MO); Parque Nacional de Manu, Cocha Casha Biological Station, *Foster P-84-42* (F). **Pasco:** Puerto Bermudez, 375 m, *Killip & Smith 26637* (NY, US). **Puno:** San Gaván, *Lechler 2321, 2329* (B). **San Martín:** San Roque, 1350–1500 m, *Williams 7681* (F, US); Cerro de Campana, *Spruce 4634* (P).

BOLIVIA. **La Paz:** Prov. Sud Yungas, Límite de los Deptos. La Paz/Beni, Río Quiquibey, 320 m, *Beck 8037* (LPB); San Carlos, Mapiri, Mapiri River, *Tate 422* (LPB, NY); Mapiri, *Buchtien 35* (B), *290* (NY, UC). **Santa Cruz:** Prov. Sara, Río Yapaicani, 400 m, *Steinbach 7499* (B, F, GH, MO, Z); bosque del Río Surutú, 400 m, *Steinbach 3032* (US).

BRAZIL. **Acre:** Cruziero do Sul vicinity, Rio Moa between Igarape Ipiranga and Aquidaba, *Prance et al. 12069* (F, LP, NY, UC). **Amazonas:** prope São Gabriel da Cachoeira, ad Rio Negro, *Spruce 2116* (B, BM, P, RB); Larges, on the Amazon River 1 km below mouth of Rio Negro, *Conant 940* (F, GH, NY). **Pará:** Serra dos Carajás, AMAZ camp AZUL, *Sperling 5914* (GH, NY); Belém, *Huber 2599* (BM), *7235* (BM).

10. **Polybotrya goyazensis** Brade (Fig. 29, Map 6).

Polybotrya goyazensis Brade, Bradea 1:24, tab. 1, fig. 1. 1969. TYPE: Brazil. Goiás: Goiania, primary forest, December 1936, *A. C. Brade 15373* (holotype: RB!; isotype: NY!).

Polybotrya macedoi Brade, Bradea 1:24. 1969. TYPE: Brazil. Goiás: Municipio Jataí, Localidad Balsans, 1 November 1950, *Macedo 2682* (holotype: HB; isotypes: HB, MO!, SP, US!; paratypes: Brazil. Goiás: Fazenda Queixado, 8 December 1948, *Macedo 1447* (RB, SP); Fazenda Balsamo, 15 December 1948, *Macedo 1521* (SP).

Stem 1–2.5 cm thick, hemiepiphytic; *scales* spreading, membranaceous, generally 6–12(16) mm long, dark castaneous or dark reddish with lighter borders, margins strongly denticulate to erose, the base cordate to various degrees, often black and sclerified at the point of attachment. *Sterile leaves* up to 1.45 m long; *petiole* ⅓ to ½ as long as the lamina; *lamina* mostly 2-pinnate-pinnatifid, lanceolate to ovate, 1.2 × 0.9 m, the abaxial surface nearly glabrous to densely pubescent, the hairs whitish, acicular, up to 1 mm long, glands occasionally present, these reddish, sessile, resinous; *pinnae* up to 45 × 23 cm, lanceolate to narrowly deltate, the suprabasal ones soon becoming pinnatifid; *pinnules* narrowly deltate, mostly falcate, catadromically arranged above the base, 4–8(10) × 1–2(3) cm, the acroscopic side slightly prolonged, the margins entire to crenate, ciliate, the hairs minute, 4–10 celled; *axes* nearly glabrous abaxially or densely pubescent, by tiny, unicellular hairs, scales very small or lacking, adaxially pubescent in the central groove with reddish hairs, 0.3–0.8 mm long; *grooves* usually ciliate on the ridges. *Fertile leaves* 2-pinnate, amphiacrostichoid; *pinnules* caudate, often lobed or undulate at the base; *sporangial stalks* paraphysate; *spores* (44)48–62(70) microns long.

Other illustrations: See original description of *P. goyazensis*; Sehnem, Fl. Ilust. Catarinense, pl. 18, 1979.

Polybotrya goyazensis occurs in Paraguay—the only species of *Polybotrya* known from that country—and in the southern half of Brazil but not in the coastal mountains (Map 6). This range is unusual because it comprises regions apparently not occupied by other species of *Polybotrya*. I suspect that *P. goyazensis* evolved from southernmost, isolated populations of *P. caudata*.

Polybotrya goyazensis has stem scales that are spreading, shiny, membranaceous, translucent, darkened in the center with lighter borders, margins strongly denticulate to erose, and the base cordate around the darkened point of attachment (Fig. 29f). In contrast, *P. caudata* has stem scales that are curved, appressed, thick, dull brown, concolorous, margins entire, and attached across the length of the thickened base (Fig. 28h). The minute cilia on the margins of the lamina serve to distinguish these two species from almost all other species of *Polybotrya* (Fig. 28a).

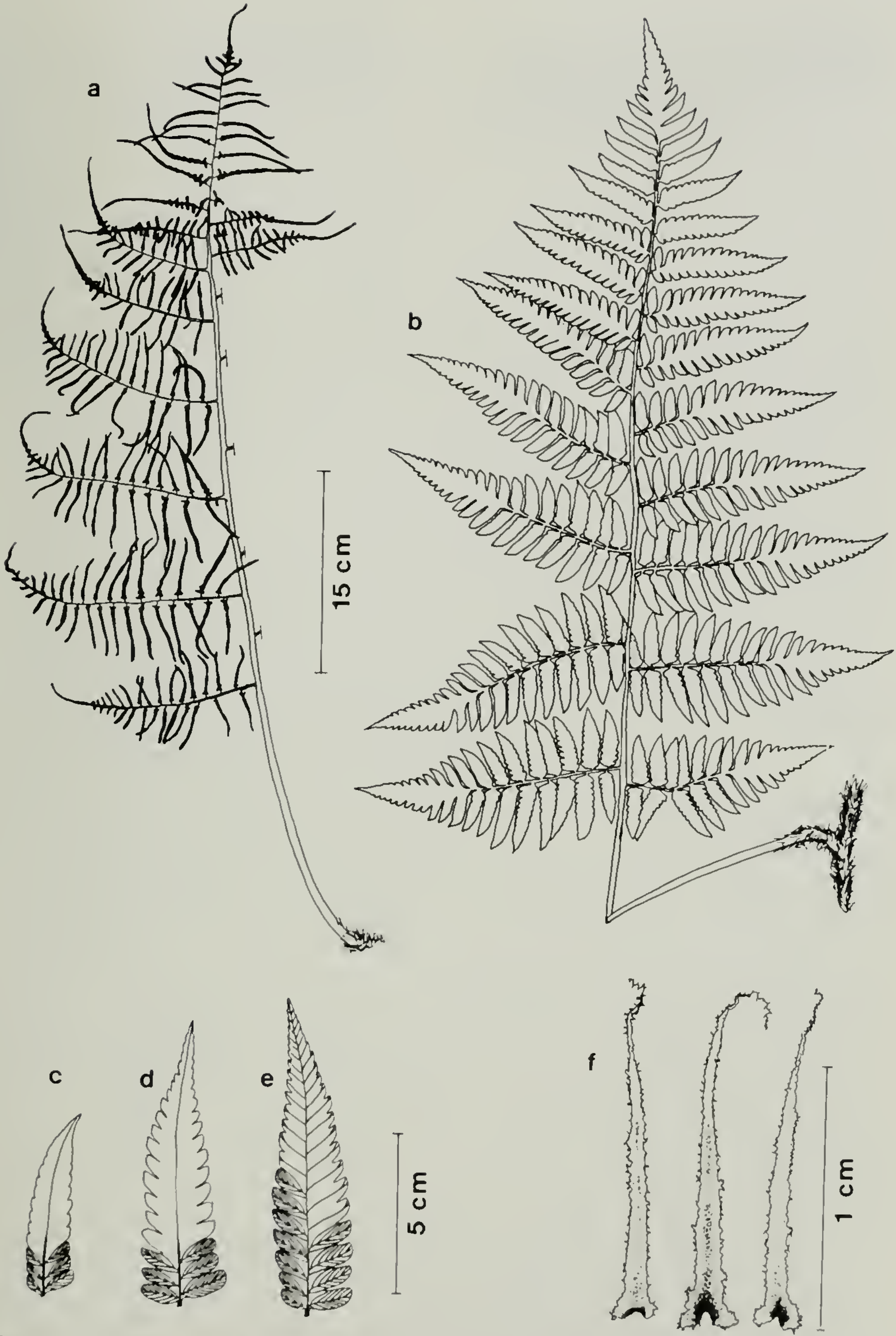

FIGURE 29. *Polybotrya goyazensis* Brade. a. fertile leaf; b. sterile leaf; c–e. proximal acroscopic pinnules; f. stem scales. a,b: *Rojas 10431* (B). c: *Brade 15373* (RB). d: *Prance & Selva 59677* (NY). e,f: *Argent et al. 6336* (UC).

Brade (1969c) distinguished *P. macedoi* from *P. goyazensis* by the former's pilose hairs on the axes and its slightly darker scales with lighter borders and a longer acuminate tip. These differences are not constant. Various degrees of pubescence exist, from densely pilose to nearly glabrous. This intergradation is shown by the type of *P. goyazensis:* the holotype at RB is nearly glabrous but the isotype at NY is densely hirsute. Examination of the stem scales shows a complete gradation of color, sometimes even on a single specimen.

Specimens examined: BRAZIL. **Goiás:** Goiania, primary forest, December 1936, *A. C. Brade 15373* (RB, NY); Serra do Caiapo, 40 km S of Caiaponia, *Prance & Silva 59677* (NY); Municipio Jataí, Localidad Balsans, *Macedo 2682* (MO, US). **Federal District:** "Brasilia," *Glaziou 14456* (B, P). **Mato Grosso:** 270 km N of Xavantina, 12°54′S, 51°52′W, *Ratter et al. 2047* (MO); Municipio Brilhante, Rio Anhanduí, *Hatschbach 25118* (UC); Expedition Base Camp, Brejo, 12°49′S, 51°46′W, *Argent & Richards 6651* (NY); 49.5 km N along road from base camp, *Harley et al. 10922* (NY); Xavantina, ca. 4 km N of ferry, *Argent et al. 6336* (RB, UC). **Pará:** no locality, 1914, *Petelot s.n.* (F).

PARAGUAY. Southern Paraguay, Sierra de Amambay, *Rojas 10182* (B, BM), *10431* (B, L, LIL, M, MICH, P), *10804* (B, BM, L); no locality, *Hassler 11618* (MICH).

11. **Polybotrya pubens** Martius (Fig. 30, Map 6).

Polybotrya pubens Martius, Icon. Plant. Crypt. Brasil. 87, tab. 25. 1834. TYPE: Brazil. ad flum. Amazonas prope Serpa, September, *Martius s.n.* (holotype: M).

Polybotrya pubens Kunze, Linnaea 9:22. 1834. *non* Martius. TYPE: Peru. Loreto: Prov. Maynas, ad Yurimaguas, September 1830, *Poeppig s.n.* (lectotype: P!).

Acrostichum pubens (Kunze) Hooker & Baker, Synopsis Filicum 414. 1868.

Acrostichum caudatum (Martius) Hooker var. *pubens* (Martius) Baker, Fl. Brasil. 1(2):586, tab. 38, figs. 1,2. 1870.

Dryopteris guentheri Rosenstock, Feddes Repert. 25:59. 1928. TYPE: Bolivia. La Paz: region of Mapiri, San Carlos, 15 November 1926, *Buchtien 260* (holotype: UC!).

Polybotrya crespiana Bosco, Nouvo Giorn. Bot. Ital., II. 45:145, tab. 9, fig. 1. 1938. TYPE: Ecuador. Santiago–Zamora: Indanza, *Crespi s.n.* (type not found, known only from Bosco's fig. 1).

Polybotrya decorata Lellinger, Amer. Fern J. 62:54, figs. 5, 6, 11. 1972. TYPE: Peru. Loreto: Iquitos, alt. ca. 100 m, *Killip & Smith 26955* (holotype: US!; isotype: NY!).

Stem 1.0–1.5 cm thick, hemiepiphytic; *scales* of large mature stems mostly 10–15 × 2–5 mm, flaccid, membranaceous, concolorous, whitish to coffee brown or castaneous, spreading or more commonly matted, margins fimbriate, young or terrestrial stems with narrowly lanceolate, castaneous, denticulate scales. *Sterile leaves* up to 1.2 m long; *petiole* up to 21 cm long, about ¼ to ⅓ the length of the lamina; *lamina* to 1 m long, narrowly deltate to elliptic, tapered evenly to the apex, mostly 1-pinnate-pinnatifid, the base occasionally 2-pinnate-pinnatifid, pubescent throughout or rarely glabrous adaxially, rarely with punctate, reddish glands; *pinnae* narrowly triangular, up to 9–19 × 2.5–3.5 cm, serrate to pinnatifid, often with only the lowest pinnae having a few free proximal segments; *pinnules* or *segments* catadromic, slightly falcate, oblong, the basal ones slightly longer than the suprabasal and more deeply cut; *veins* free, 6–9 per segment; *axes* conspicuously pubescent, the hairs 1–2 mm long, unbranched, acicular, whitish, 6–15 celled, the septae often reddish, polyseriate scales lacking, but scales present as reduced, appressed, reddish, flattened, uniseriate "hairs." *Fertile leaves* 2-pinnate, to 0.8 m long, amphiacrostichoid; *axes* pubescent on both surfaces, the hairs ca. 0.1 mm long, colorless, subulate; *proximal pinnae* deeply lobed or fully pinnate, long-caudate; *sporangia* with the capsule walls setose at the apex near the annulus by two hairs, these 1–3 celled; *sporangial stalks* paraphysate; *spores* (44)48–57(63) microns long.

Other illustrations: Martius, Icones Plant. Crypt. Brasil. 87, tab. 25. 1834; von Ettingshausen, Denkschr. Ak. Wien., tab. 7, figs. 3, 10, 11. 1864; Martius, Fl. Brazil, 1(2):586, tab. 38, figs. 1, 2. 1870; Brade, Bradea 1(9): 63, fig. 4; *Ibid.* 67, fig. 7. 1971.

Polybotrya pubens grows primarily in lowland forests of the Amazon basin but occurs in premontane forests up to 1400 m in the Andes (Map 6). During my fieldwork in Ecuador, I found this species in well-drained forest soils that were slightly elevated above the surrounding swamp forest.

This is one of the most distinct species of *Polybotrya*, readily distinguished by its combination of stem scales, lamina shape and cutting,

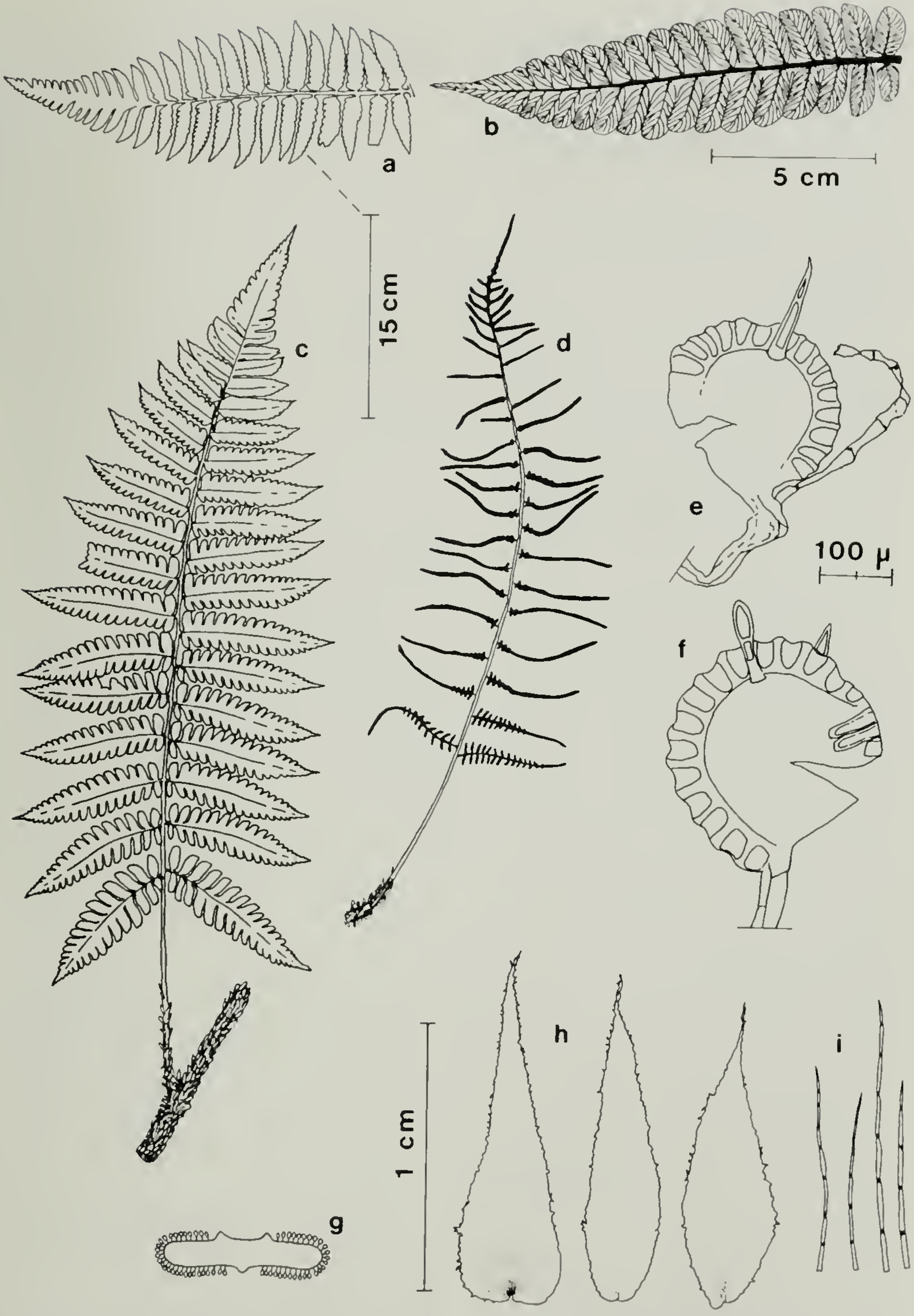

FIGURE 30. *Polybotrya pubens* Martius. a. pinna of a large, highly divided leaf; b. pinna of typically cut leaf; c. sterile leaf; d. fertile leaf; e. setose sporangium with paraphysis on stalk; f. setose sporangium; g. cross section of fertile pinna apex; h. stem scales; i. hairs from sterile lamina. a: *Killip & Smith 26955* (US). b: *Killip & Smith 26543* (NY). c,h,i: *Balslev 4787* (CR). d,g: *Killip & Smith 26194* (NY). e,f: *Holm-Nielsen & Jeppsen 663* (AAU).

pubescence, and long-caudate fertile pinnae. In addition, *P. pubens* has, unlike any other species of *Polybotrya*, setose sporangial capsule walls (Fig. 30e,f). The sterile lamina is usually 1-pinnate-pinnatifid or almost 2-pinnate at the base, but large leaves that are 2-pinnate-pinnatifid for much of their length are occasionally collected (Fig. 30a). These large, more highly divided leaves appear quite distinct but there are intermediate forms between the extremes of lamina cutting. The 2-pinnate-pinnatifid form was named as *P. decorata*.

Polybotrya pubens and *P. glandulosa* might be confused because both have similar laminar cutting, long, acicular hairs, and both grow in lowland forests of the Amazon basin. But the lamina of *P. glandulosa* is, unlike any other species of *Polybotrya*, cuneate and the petiole is extremely short, only 2.5 cm long. Furthermore, its fertile leaf is botryoid instead of amphiacrostichoid, and its sporangial capsules are glabrous instead of setose.

Juvenile stems and thin terrestrial stems have narrow, castaneous, spreading scales that differ from those on the scandent stems. *Dryopteris guentheri* represents a juvenile form of *P. pubens* with this scale type. The transition from juvenile to mature plants and the changes in scale and lamina morphology are shown in an excellent series of specimens collected in Ecuador by Balslev (#4787).

The pubescence of the fertile leaf consists of colorless, subulate hairs about 0.1 mm long—these are much reduced in comparison to the hairs on the sterile leaves. The setae on the sporangial capsule walls are unique in *Polybotrya*. They occur only at the apex of the sporangium near the annulus (Fig. 30e,f); it is odd that these setae are not shown on the sporangia illustrated in 1834 by Martius in his otherwise excellent plate of *P. pubens*. The adaptive value (if any) of the hairs on the capsules is not known.

Unlike all other species of *Polybotrya*, *P. pubens* lacks wide, polyseriate scales on the axes. Rather, scales are present only in their reduced form, that is, as tiny, appressed, reddish, jointed, uniseriate "hairs."

Both Martius and Kunze published the name *P. pubens* in 1834. Kunze's work appeared in the first issue of *Linnaea*, which was published 22–28 June 1834 (Stafleu 1967). Stafleu and Cowan (1981) report that Martius's second fascicle of "*Icones plantarum crytogamicarum*" was published in 1834. Since no month or day is given, I cannot determine which work was published first. I consider Martius the author of *P. pubens* because Kunze clearly attributed this name to Martius.

Specimens examined: COLOMBIA. **Amazonas:** Río Apaporis, Soratama (above mouth Río Kananari) and vicinity, *Schultes & Cabrera 16053* (US).

ECUADOR. **Morona-Santiago:** Taisha, 3–4 km ESE of the military camp, *Brandbyge & Asanza C. 31870* (AAU). **Napo:** Reserva Faunistica Cuyabeno, al lado norte de Laguna Grande, *Balslev 4787* (AAU, CR, Q, QCA), *4802* (AAU, Q, QCA), *Laegaard 51136* (AAU, Q, QCA), *51150* (AAU, Q, QCA), *51224* (AAU, Q, QCA); Parque Nacional Yasuní, in the area of the SEF project, *Øllgaard et al. 38969* (AAU), *39039* (AAU), *39040* (AAU); 6 km along Río Pano, *Halm-Nielsen & Jeppsen 663* (AAU). **Pastaza:** Río Bobonaza, oil exploration camp Chichirota and Destacamento Cabo Pozo, *Øllgaard et al. 34894* (AAU, Q, QCA); Curaray, SE of the airstrip, *Halm-Nielsen et al. 22121* (AAU); oil exploration camp Chichirota, on the Río Bobonaza, *Øllgaard et al. 35350* (AAU); Río Bobonaza, between Cachitama and the outlet of Río Bufeo, *Øllgaard et al. 34703* (AAU). **Santiago-Zamora:** Taisha, *Cazalet & Pennington 7720* (BM, F, K, NY, US).

PERU. **Amazonas:** ridge crest of Quebrada Chuivi (above km 278 of Marañon road), valley of Río Marañon near Cascadas de Mayasi, *Wurdack 1933* (US). **Junín:** E of Quimirí Bridge, near La Merced, *Killip & Smith 23916* (NY, US); Pichis Trail, Santa Rosa, *Killip & Smith 26194* (NY, US); Pichis Trail, San Nicolas, *Killip & Smith 25972* (NY, US); Puerto Bermudez, *Killip & Smith 26543* (NY, US). **Loreto:** above Tamishuyacu, *Croat 19771* (AMAZ, MO); primary forest 17 km SW of Iquitos, *Croat 18508* (MO); Iquitos, ca. 100 m, *Killip & Smith 26955* (NY, US); December 1830, *Poeppig s.n.* (photo of specimen at V, BM); Prov. Maynas, ad Yurimaguas, September 1830, *Poeppig s.n.* (P); La Victoria on the Amazon River, *Williams 3136* (F); lower Río Huallaga, *Williams 4797* (F, US); Yurimaguas, *Spruce 3880* (P, fragment NY); along Quebrada Nawampa, *Croat 17689* (MO); Santa Rosa, lower Río Huallaga below Yurimaguas, *Killip & Smith 28760* (NY, US). **Pasco:** Prov. Oxypampa, Iscoazin, *Foster 7858* (F, USM). **San Martin:** Monte Campana, *Spruce 4740* (photo GH, US); camino a Pushurumbo, 7–8 km al este del Puente de Palo Blanco, Mariscal Caceres, Tocache Nuevo, *J. Schunke 5789* (NY, US); San Roque, *Williams 7620* (F).

BOLIVIA. **La Paz:** Prov. Larecaja, Consata 7 km towards Mapiri, *Beck 4924* (F, LPB); region of Mapiri, San Antonio, *Buchtien 35* (US), *1123* (US), *1124* (NY); region of Mapiri, San Carlos, *Buchtien 260* (UC), *299* (NY); Mapiri, *Rusby 442* (NY).

BRAZIL. **Amazonas:** Rio Negro, 1819, *Martius s.n.* (photo of M specimen at BM). **Pará:** *Martius s.n.* (photo of M specimen at BM).

12. **Polybotrya glandulosa** Kuhn (Fig. 31, Map 7).

Polybotrya glandulosa Kuhn, Linnaea 36:65. 1869. Type: Brazil. Amazonas: San Gabriel, no date, *Spruce s.n.*, not *2116* as indicated on Morton negative, (holotype: B!).

Polybotrya subelliptica Lellinger, Amer. Fern J. 62:56. 1972. Type: Peru. Loreto: Mishuyacu, near Iquitos, 100 m, *Klug 1390* (holotype: US!; isotypes: F!, NY).

Stem 1–2 cm thick, hemiepiphytic; *scales* dull brown, thick, opaque, concolorous to bicolorous, curved-appressed, 8–15 × 1.5–2.5 mm, the margins entire, the base thickened and expanded, slightly elevated, the dorsal surface sometimes with a medial groove. *Sterile leaves* up to 75 cm long; *petiole* very short, up to 2.5 cm long; *lamina* 2-pinnate-pinnatifid, subelliptic, 65–73 × 22–28 cm, the base cuneate, about 8 cm wide, the apex long-attenuate, the abaxial surface with or without sessile, red, resinous, round glands, the margins ciliate with hairs similar to those of the veins and axes; *pinnae* ca. 35 pairs, the medial ones 14–16 × 3–3.5(4) cm, sessile or short-stalked, oblong, the base truncate; *pinnules* catadromic, oblong, falcate at the apex, those of the medial pinnae 15–20 × 5–7 mm, the margin entire, crenate or lobed, generally with 6–10 veins, the basal basiscopic margin decurrent; *axes* and *veins* densely pilose on both surfaces, the hairs tawny, pluricellular, acicular, 1.0–2.5 mm long, the scales few or absent. *Fertile leaves* narrowly elliptic, 45 × 15 cm, 2-pinnate-pinnatifid, botryoid; *medial pinnae* 6–8 × 1.5–2 cm; *axes* sparsely pilose, with scattered, linear, appressed, dark scales; *sporangial stalks* paraphysate.

Polybotrya glandulosa, which has been collected only three times, is one of the rarest species of *Polybotrya*. It is the only species in the genus that is endemic to the Amazon basin (Map 7); however, I suspect it will be found in the adjacent Guiana Highlands as that region becomes better explored. I failed to find this species during my fieldwork in the Iquitos area, in part because the location of "Mishuyacu" is unknown. The elevational range for this species is 100–140 m.

This species is unlikely to be confused with any other *Polybotrya* since, unlike other species in the genus, the lamina tapers gradually to an extremely short petiole (Fig. 31c). The long, acicular hairs on the axes and veins further distinguish this species from most other congenerics. *Polybotrya pubens*, however, has long acicular hairs and leaf cutting similar to *P. glandulosa*; since it grows in Amazonian forests, the two species could be confused. *Polybotrya glandulosa*, however, can be distinguished from *P. pubens* because the former has a botryoid, instead of an amphiacrostichoid, fertile leaf and a short petiole.

The specific epithet refers to the red, sessile, round, resinous glands on the abaxial suface of the type specimen (Fig. 31d). The two other collections, however, lack such glands. This variability is not unusual, since glands are variably present in all gland-bearing species of *Polybotrya*.

Specimens examined: Venezuela. **Territorial Federal Amazonas:** Dept. Río Negro, 0–3 km N of Cerro de Neblina Base Camp, on the Río Mawarinuma, 140 m, *Liesner 16293* (MO, UC).

Peru. **Loreto:** Mishuyacu, near Iquitos, 100 m, *Klug 1390* (F, NY, US).

Brazil. **Amazonas:** São Gabriel, no date, *Spruce s.n.* (B).

13. **Polybotrya lechleriana** Mettenius (Fig. 32, Map 7).

Polybotrya lechleriana Mettenius, Filices Lechler. 1:4, tab. 1, figs. 1-5. 1854. Type: Peru. Puno: San Gavan, *Lechler 2156* (lectotype: B!; isotype: L!; fragments F!, US!; photo GH! of K).

Acrostichum lechlerianum (Mettenius) Hooker, Species Filicum 5:246. 1864, *nom. illeg.*, *non* Mettenius 1856.

Stem to 1.5 cm thick, hemiepiphytic, mucilaginous?; *scales* lanceolate, up to 15 × 3 mm, cream to dull brown, thin, appressed, the margins denticulate to entire. *Sterile leaf* pubescent throughout, the hairs 3–12 celled, 0.3–1.2 mm long, lax, spreading, colorless; *petiole* ⅓–½ as long as the lamina, stramineous; *lamina* finely divided, (4)3-pinnate-pinnatisect, lanceolate, both surfaces pubescent, especially along the axes and veins, eglandular, the apex acute, not long-attenuate; *pinnae* lanceolate to ovate, (7)10–15 × (2)3–7(12) cm, the base truncate, short-stalked, crowding the rhachis; *pinnules* catadromic, oblong with subparallel sides, the base truncate, nearly sessile, crowding the costa, the apex acute to rounded; *ultimate segments* single veined, falcate, 0.5–1 mm wide; *axes* pubescent abaxially, usually with a single scale at the juncture of the costa and

FIGURE 31. *Polybotrya glandulosa* Kuhn. a. stem scales; b. fertile leaf; c. sterile leaf; d. abaxial surface of sterile pinna showing sessile reddish glands (as dots) and acicular hairs; e. medial pinna. a–c,e: *Klug 1390* (US, F). d: *Spruce s.n.* (B).

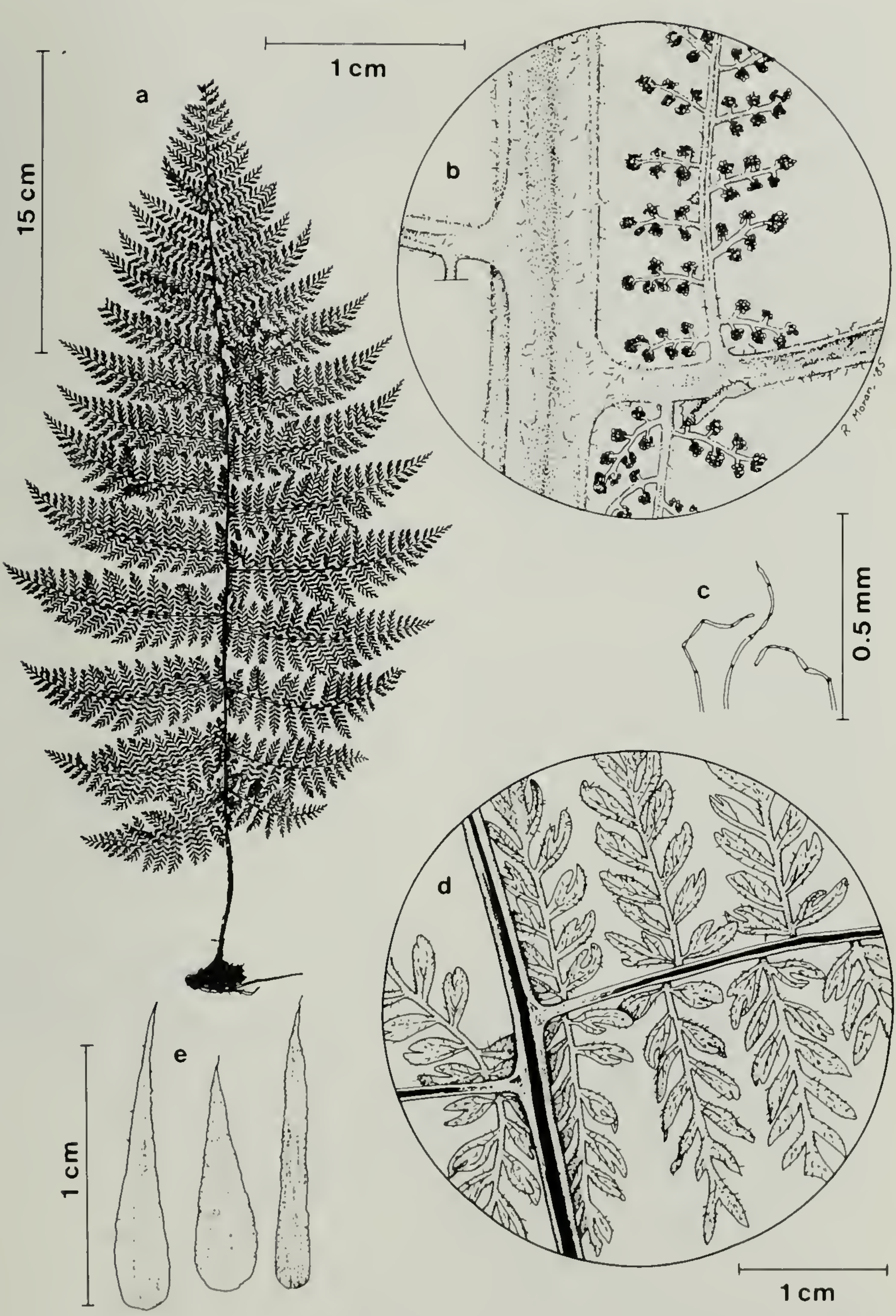

FIGURE 32. *Polybotrya lechleriana* Mettenius. a. sterile leaf; b. rhachis-costa juncture of fertile leaf; c. costal hairs; d. rhachis-costa juncture of sterile leaf; e. stem scales. a,c: *Spruce 4744* (P). b,d: *Stübel 914* (B). e: *Dudley 10325* (GH).

costule, the scale ovate, appressed, thin, brown; *grooves* glabrous or puberulent within, truncated by the ridges of the next lower order, usually becoming shallower near the juncture. *Fertile leaf* 3-4-pinnate, botryoid, pubescent with hairs like those on the sterile leaf; *sori* distinct, round, 0.5–0.8 mm wide, on short stalks, these 1–2 mm long, the receptacle moundlike; *sporangial stalks* paraphysate; *spores* (50)54–60(65) microns long.

Other illustrations: Hooker, Second Century of Ferns, tab. 97. 1861; Mettenius's original description has an excellent illustration of the type at Berlin.

Polybotrya lechleriana occurs in rich montane forests from (100)1000–1500 m. This species is primarily Andean but has a notable range disjunction in the Guiana Highlands at Mt. Roraima in Guyana, 1900 km from the nearest known population in Colombia (Map 7). This disjunction is best explained as an example of long distance spore dispersal. Another significant Andean–Guianan range disjunction occurs in *P. fractiserialis* (Map 3).

This species is easily recognized by its finely divided sterile lamina with very narrow, single-veined segments and lobes (Fig. 32). The finely cut leaves, so unlike others in the genus, are probably what prompted Copeland (1947) to remark that this species "looks out of place here [in *Polybotrya*]." But *P. lechleriana* has all the features of a typical *Polybotrya* including the unique stem anatomy of the genus.

Some forms of this plant resemble *Polybotrya stolzei* an endemic to the Andes of Colombia, but *P. lechleriana* differs by the narrower width of its ultimate segments or lobes, each of which is one-veined (see key). *Polybotrya lechleriana* probably evolved from a less dissected ancestor in the *P. alfredii* group by cessation of the growth of the marginal meristem to produce a more finely divided sterile lamina. This species is named in honor of Wilibald Lechler (1814–1856), a German pharmacist, botanist, and explorer, who sent many of his collections to Mettenius.

Specimens examined: GUYANA. Mt. Roraima, Waruma Trail, *Persaud 114* (NY).

COLOMBIA. **Cauca:** forests of Rio Timbiqui, *Lehmann B.T413* (GH). **Chocó:** alrededores de San José del Palmar, Cerro S de la población, *Forero & Jaramillo 2469* (COL, MO, NY); NW side of Alto del Buey, *Lellinger & de la Sota 281* (COL, US); Río Nuqui, *Haught 5498* (COL, F, NY, US). **Nariño:** Municipio de Altaquer, entre Junín y Buenavista, 650 m, *Mora 4287* (COL).

ECUADOR. **Chimborazo:** Río Palora, eastern cordillera of Riobamba, 1400 m, *Rimbach 31* (GH, PH, US). **Pastaza:** Mera, remnants of primary forest in hills above town, *Plowman & Davis 4542* (GH). **Tungurahua:** along road between Puyo and Baños at second bridge W of Mera, ca. 3 km W of Mera, 1160 m, *Croat 49718* (MO, UC); Baños–Pintuc, *Stübel 913a, 914* (B, BM).

PERU. **Cuzco:** Prov. La Convención, Cordillera Vilcabamba, Camp 2.5, 1760 m, 73°38′W, 12°38′S, *Dudley 10325* (GH); Paucartambo, Valle de Pillahuata, *Gerrera 1624* (US). **Junín:** Prov. Satipo, "Mapiri" ca. 12 km SW of Chequitavo, *A.C. Smith 61713* (MO, USM); Pichis Trail, Porvenir, 1500–1900 m, *Killip & Smith 25921* (NY, US). **Puno:** San Gavan, *Lechler 2156* (B, F, GH, L, US), *2176* (B); La Pampa, Río Tavara, *Watkins s.n.* (US). **San Martín:** in monte Guayrapurima, prope Tarapoto, *Spruce 4744* (L, P; fragment US). **Dept. unknown:** entre Los Ríos Tintiuiguiato del Pachiri y Tapecia del Tocate, 1500 m, *Bues 1743* (US).

BOLIVIA. **La Paz:** Hacienda Simaco sobre el camino a Tipuani–Tale, 1400 m, *Buchtien 5308* (BM, GH, MO, NY, UC, US, Z).

14. **Polybotrya attenuata** Moran, *sp. nov.* (Fig. 33, Map 7).

Polybotrya attenuata Moran, *sp. nov.* TYPE: Colombia. Antioquia: Guatape, forests on slopes above river, 1/77, *McAlpin & Kuhn 77-12* (holotype: NY!). The plant from which the type specimen was taken is cultivated in the fern greenhouse, New York Botanical Garden (accession no. 332/78).

Planta hemiepiphytica; caulis ca. 1 cm diam.; squamulis membranaceis, linearibus, acutis, 9–12 mm longis, 0.3–0.7 mm latis, in margine denticulatis vel integris; laminae steriles lanceolatae vel anguste deltatae, 3-pinnatae, apice longiattenuatae, usque ad 55 cm longae, 26 cm latae, glabrae vel punctatae, glandulis resinaceis, rotundis; pinnulae catadromicae, 2.0–2.5 cm longae, 0.8–1.2 cm latae, apice rotundatae; segmenta tertiaria obovata, ad basim cuneata; costae et rhachides sulcatae pubescentes in sulco, squamis angustis, fuscatis, denticulatis; folia fertilia botryoidea; sori rotundi, ca. 1 mm longi, pedicellati.

Stem about 1 cm wide, hemiepiphytic; *scales* light to dark brown, mostly concolorous or rarely with a narrow hyaline border, thin, linear, 9–12 × 0.3–0.7 mm, the margins subentire to denticulate. *Sterile leaf* up to 0.8 m long; *petiole* ⅓–¼ as long as the lamina; *lamina* to 55 × 26 cm, 3-pinnate, narrowly lanceolate or triangular, the apex long-attenuate, the tissue with or without

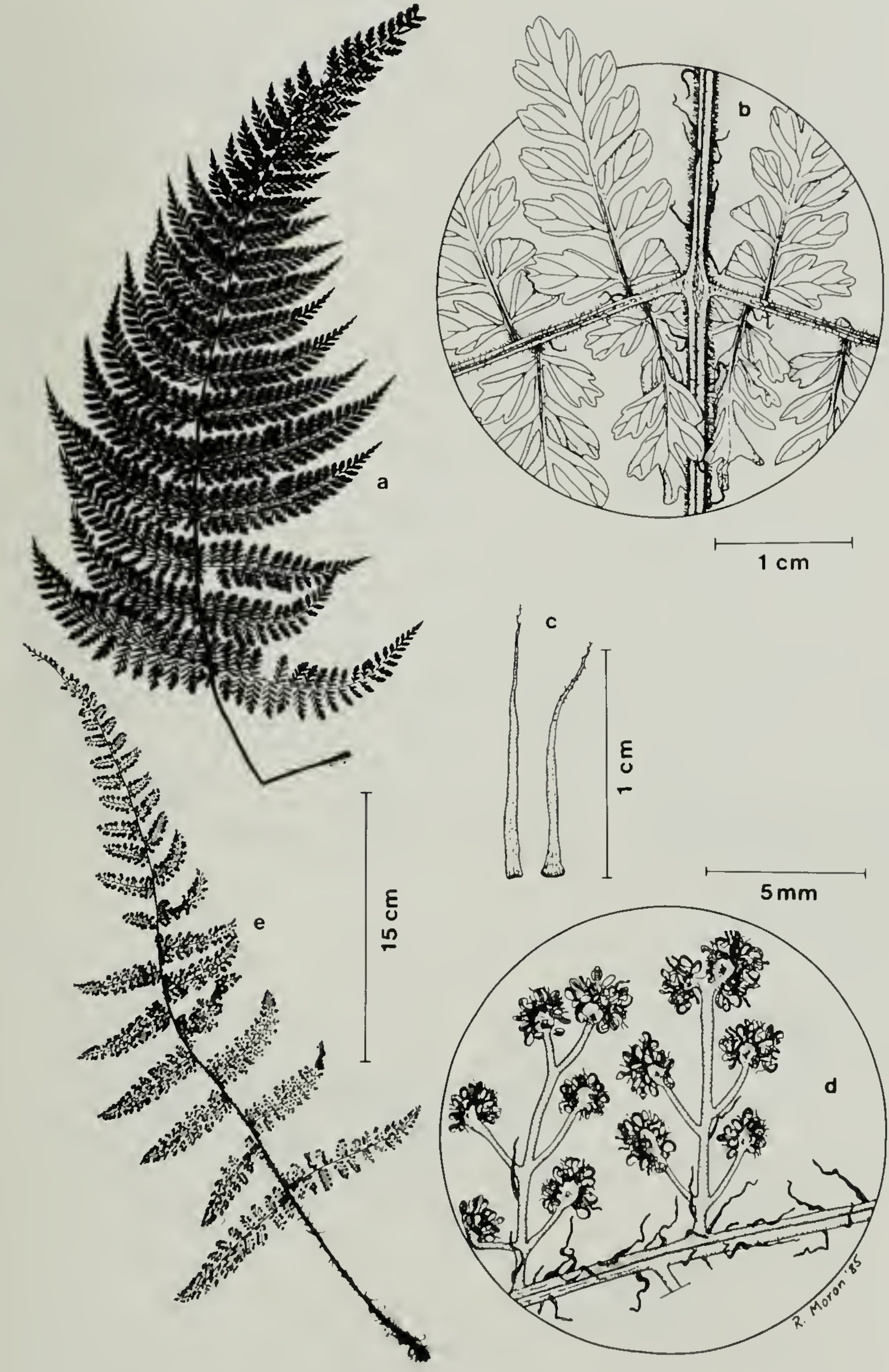

FIGURE 33. *Polybotrya attenuata* Moran. a. sterile leaf; b. pinnules and costa-rhachis juncture (note the abundance of narrow, dark scales on the axes); c. stem scales; d. two pinnules of fertile leaf; e. fertile leaf. a–e: *McAlpin & Kuhn 77-12* (NY).

punctate, resinous, spherical, sessile glands; *pinnae* 10–13 × 3.5–4.0 cm long, lanceolate to oblong, the base truncate, short-stalked, crowding the rhachis; *pinnules* catadromic, 2.0–2.5 × 0.8–1.2 cm, with only 5–7 lobes or segments, the apex acute or rounded, the base truncate, sessile or with a short stalk less than 1 mm long; *tertiary segments* obovate, entire to slightly lobed, containing several vein branches, the base cuneate; *axes* pubescent within grooves and especially abaxially, the hairs 4–12 celled, 0.2–0.3 mm long jointed, with reddish cross-walls; *costal scales* numerous, narrow, dark, denticulate, tortuous, appressed; *grooves* pubescent within, the hairs reddish, multicellular. *Fertile leaves* botryoid, 3-pinnate, densely scaly, the scales grading into jointed hairs (the hairs are actually reduced scales); *sori* stipitate, the stalks 1–3 mm long; *sporangial stalks* paraphysate.

Polybotrya attenuata, named for its distinctive, long-attenuate leaf apices, is endemic to the Andes of Colombia (Map 7). This species differs from *P. lechleriana*, a similar species, by its long-attenuate apex, oval tertiary segments, resinous glands on the lamina, and the darker, narrower scales on the axes. The pinnules, furthermore, are shorter and stubbier, having only 5–7 lobes and/or segments, and these have a cuneate base (Fig. 33a,b).

The presence of glands on the lamina is not constant. The living plant from which the holotype was made has always produced leaves having round, sessile, resinous glands on the undersurface. The Lehmann specimen, however, lacks such glands. Similar glands are also variably present in other species, such as *P. osmundacea* and *P. glandulosa*.

Specimens examined: COLOMBIA. **Antioquia:** Guatape, *McAlpin & Kuhn 77-12* (NY). **Nariño:** along river Pipulquer, west slopes of the western Andes, *Lehmann 500B* (US).

15. **Polybotrya stolzei** Moran, *sp. nov.* (Fig. 34, Map 9).

Polybotrya stolzei Moran, *sp. nov.* TYPE: Colombia. El Valle: Santa Rosa, Dagua Valley, forest along Río Cabellete, 200–300 m, 22 September 1922, *Killip 11549* (holotype: US!; isotypes: GH!, NY!, PH!).

Planta hemiepiphytica; caulis 0.6–1.5 cm diam., (mucilaginus?); squamae fuscatae, opacae, lineares, integrae, usque ad 12 mm longae, 0.4 mm latae; lamina sterilis 3-pinnata, plerumque pubescens in superficiebus ambabus; rhachis et costae pubescentes, squamis ovatis tenuibus aliquot; pinnulae catadromicae, pro parte maxima sessiles, usque ad 33 × 9 cm; segmenta tertiaria ovalia vel oblonga integra, (5)6–8(10) × (2)3–4(5) mm. Folia fertilia ignota.

Stem 0.6–1.5 cm thick, hemiepiphytic, mucilaginous (?); *scales* dull brown, appressed, opaque, linear, 0.4–12.1 × 0.3–1.0 mm, margins subentire. *Sterile leaves* up to 1 m long; *petiole* ¼ to ½ as long as the lamina; *lamina* lanceolate or subdeltate, 30–65(80) × 19–32(60) cm, 3-pinnate, usually pubescent on both surfaces, always so along the veins beneath, the hairs whitish to tawny, articulated, 0.1–0.4 mm long, spreading; *pinnae* to 33 × 9 cm, narrowly triangular to lanceolate, equilateral or, in the basal pair, with the basiscopic side slightly prolonged, the base truncate, short-stalked, crowding the rhachis; *pinnules* catadromic, oblong, the base truncate, nearly sessile, the apex rounded to acute; *tertiary segments* ovate to oblong, (5)6–8(10) × (2)4(5) mm, with several vein branches, the margins entire to slightly lobed; *axes* pubescent abaxially, with a few thin, ovate, brown scales, especially at the pinnule junctures; *grooves* nearly glabrous to moderately puberulent within, never packed with long-protruding hairs, truncated by the ridges of the next lower order. *Fertile leaf* unknown.

This new species is named for Robert G. Stolze, pteridologist at the Field Museum of Natural History, Chicago, Illinois. He originally suggested this genus to me and has given much help and encouragement during the preparation of this monograph.

Polybotrya stolzei is endemic to the western Andes of Colombia (Map 9), occurring in wet, shaded forests from 200–1750 m. The laminar cutting of *P. stolzei* is intermediate between *P. lechleriana* and *P. alfredii*. Extremely large pinnules of *P. stolzei* look like those of *P. alfredii* but are distinguished by the pubescence on both surfaces of the lamina and by the blunter apices of the medial pinnules. Smaller, more delicate forms of *P. stolzei* may look like *P. lechleriana* but are distinguished by their oblong tertiary segments with more than one vein per segment. Un-

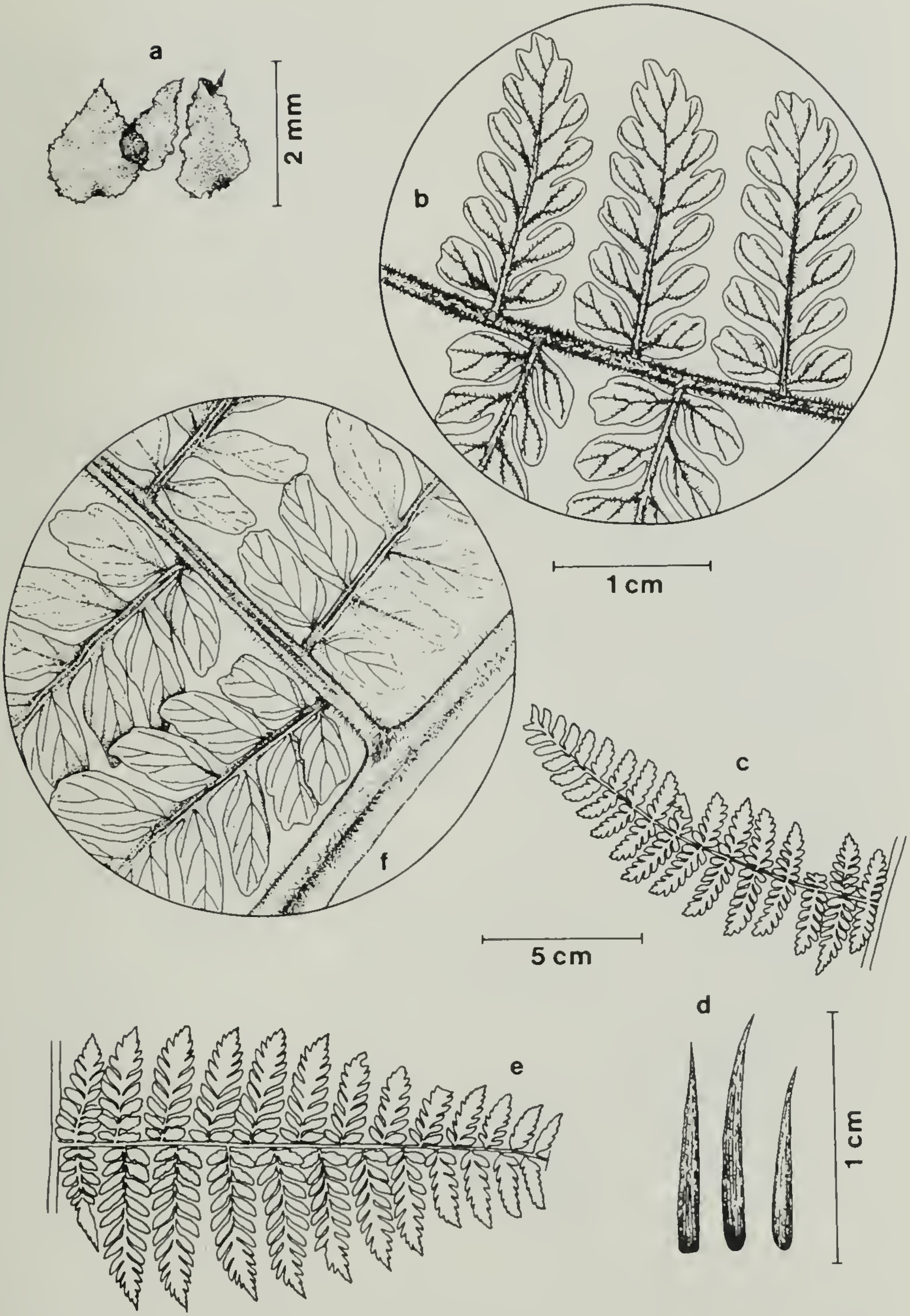

FIGURE 34. *Polybotrya stolzei* Moran. a. costal scales from the pinnule-costa junctures; b. abaxial view of medial pinnules of "c"; c. medial pinna; d. stem scales; e. basal pinna of large leaf; f. adaxial view of rhachis-costa juncture. a-d: *Killip 11549* (GH). e,f: *Lellinger & de la Sota 284* (COL).

fortunately, none of the collections contain fertile leaves and this structure, therefore, cannot be compared to the distinctive botryoid fertile leaf of *P. lechleriana*.

Specimens examined: Colombia. **Chocó:** NW side of Alto del Buey, *Lellinger & de la Sota 280* (COL, US), *284* (COL, US); principal ridge and slopes 2 km E of San José del Palmar, 1550–1600 m, *Lellinger & de la Sota 747* (COL, LP, US), *748* (COL, LP, US). **El Valle:** Santa Rosa, Dagua Valley, forest along Río Caballete, 200–300 m, *Killip 11549* (GH, NY, PH, US).

16. Polybotrya alfredii Brade (Fig. 35, Map 8).

Polybotrya alfredii Brade, Bradea 1:12, tab. 1, fig. 2. 1969. Type: Costa Rica. San José: Tablazo, 1900 m, July 1908, (Brade's original description states August, apparently an error.) *Brade & Brade 98* (holotype: HB; isotype: NY!).

Polybotrya alfredii Brade f. *carpinterae* Brade, Bradea 1:13. 1969. Type: Costa Rica. San José: Carpintera, terrestrial, 1500 m, 25 November 1908, *Brade & Brade s.n.* (holotype: HB).

Polybotrya gracilis Brade, Bradea, 1:14, tab. 1, fig. 3. 1969. Type: Costa Rica. Cartago: Tablazo, 1900 m, 28 August 1908, *Brade 554* (holotype: HB).

Stem 1–2 cm wide, hemiepiphytic, the apex in living plants usually covered by a thick mucilage that disappears upon drying; *scales* dull, dark to light brown, opaque to translucent, 8–16(22) × 1–1.5(2.0) mm wide, narrowly lanceolate, spreading, attached across the width of the slightly thickened base, the margin denticulate or more commonly entire. *Sterile leaves* up to 1.4 m × 0.7 m; *petiole* up to 35 cm long; *lamina* ovate, up to 3-pinnate-pinnatifid, subchartaceous, often drying greyish green, the proximal margins of the pinnule bases often ciliate, the hairs less than 0.1 mm long; *pinnae* up to 45 × 22 cm, apex acuminate; *pinnules* up to 12 × 5 cm, ovate to narrowly triangular, the base truncate and symmetrical, those of the basal pinnae anadromic or subequal, those of the medial pinnae catadromous; *ultimate segments* ovate to oblong, entire, crenulate, serrate or lobed, the apex obtuse or acute; *axes* evenly pilosulous abaxially, the hairs 0.1–0.2 mm long, usually tawny; *grooves* pubescent within, very shallow or even disappearing within about 1 cm of the rhachis so that the costa is almost terete where it joins the rhachis. *Fertile leaves* up to 0.8 × 0.35 m, up to 3-pinnate-pinnatifid, ovate, coenosoric; *axes* pubescent, the hairs short, 0.1–0.2 mm long, usually with ovate to lanceolate, appressed, thin, denticulate to fimbriate scales; *sporangial stalks* paraphysate; *spores* (50)55–62(66) microns long.

Other illustrations: See the original descriptions cited above.

The altitudinal range of *Polybotrya alfredii* is 700–1900 m. In Ecuador, this species grows in rich montane forests in the eastern Andes. In Costa Rica, this species occurs primarily in wet, shaded cloud forests, usually growing alongside *P. gomezii*. *Polybotrya alfredii* produces numerous terrestrial leaves that often predominate the forest floor. Twice in Costa Rica and once in Ecuador, I saw fertile leaves produced from the terrestrial portion of the stem. These are the only instances in which I saw fertile leaves produced terrestrially by a scandent species.

Polybotrya alfredii looks like *P. lourteigiana* but can be distinguished by its more highly cut lamina. Since leaves lower on the stem tend to be smaller and less divided than those higher on the stem, cutting should be compared using pinnae over 25 cm long (see couplet 24 in the key). The two species also differ in the shape of the ultimate segments or lobes; *P. alfredii* has relatively more ovate and shorter segments than *P. lourteigiana* (compare Figs. 35 & 37).

Unlike all other species of *Polybotrya*, *P. alfredii* has the stem apex and the lowermost 5 to 15 cm of the petiole covered with a thick, translucent mucilage. Mucilage is totally lost upon drying and therefore not visible on herbarium specimens. The function of this mucilage is unknown. More fieldwork is needed to determine if this unusual mucilage occurs in two closely related species, *P. lechleriana* and *P. lourteigiana*. Nectaries are another unusual feature of the morphology of *P. alfredii*. During fieldwork in Costa Rica, I saw nectaries on the rhachis of *P. alfredii* like those described by Koptur et al. (1982) for *P. osmundacea*. See the Morphology and Anatomy section of this monograph for further information concerning nectaries.

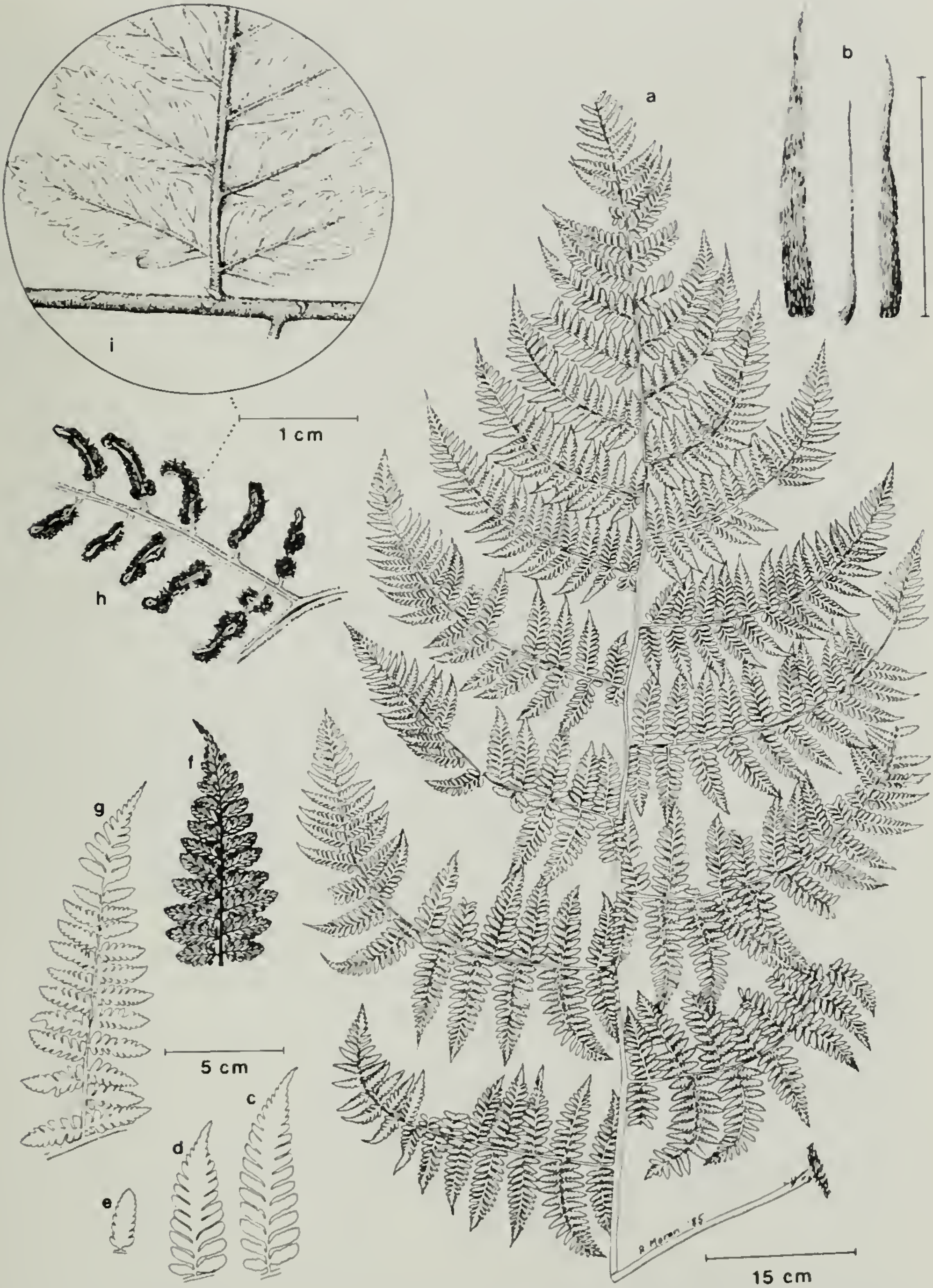

FIGURE 35. *Polybotrya alfredii* Brade. a. sterile leaf; b. stem scales, the middle shown sideways; c–g. pinnules, acroscopic side to the right; h. fertile pinnule, adaxial view; i. adaxial surface of costa and pinnule base. a,b,f,h,i: *Moran 2442* (CR). c: *Moran 3532* (F). d: *Buchtien 5164* (US). e: *Moran 3214* (CR). g: *Dwyer 8337* (MO).

I put *P. gracilis* in synonymy with *P. alfredii*, although the former appears distinct because the leaf is smaller, only 2-pinnate, and has obtuse pinnule apices (Fig. 35e). *Polybotrya gracilis* resembles *P. alfredii*, however, in such characteristics as scales, pubescence, stem mucilage, habitat, and range. Furthermore, at several localities in Costa Rica, I collected plants that exhibited complete intergradation between the typical large leaves of *P. alfredii* and the smaller ones of *P. gracilis*. *Polybotrya gracilis*, therefore, represents a small-leaf form of *P. alfredii* that has well-rounded pinnule apices. I chose the name *P. alfredii* over *P. gracilis* because an isotype has been seen. This species is named in honor of Alexander Brade's brother and field companion, Alfred Brade.

Specimens examined: NICARAGUA. **Rivas:** Isla de Ometepe, NW slope of Volcán Maderas, *Stevens & Krukoff 6518* (CR); Graytown, Camp Murroeal, *Shimek & Smith s.n.* (MICH).

COSTA RICA. **Alajuela:** Univ. of San Ramón biological field station, *Moran 3214* (CR, F, GH, MO); 12 km NNW of San Ramón by road on way to San Lorenzo, 1 km S of Balsa, *Liesner & Judziewicz 14855* (CR, MO); San Jerónimo, *Wercklé 559* (US); Suerre, llanuras de Santa Clara, *Donnell Smith 6939* (US); Santa Clara, *Cooper 10240* (US); NW of Zarcero, ca. 2 km W of Zapote on dirt road to Sta. Elena, *Lellinger & White 1361* (US); San Antonio de Zarcero, *A.C. Smith 48/293* (US); N of San Ramón, ca. 4 km N of Balsa along road to Colonia Palmerena, *Lellinger & White 1244* (US); Santiago de San Ramón, *Brenes 21980* (F), *14248* (GH); Alto de la Palma de San Ramón, *Brenes 11676* (F, NY); 7 miles N of San Ramón square along ridge road, *Evans & Bowers 2944* (MO); Finca La Selva, San Rafael de Vara Blanca, pendiente N del Volcán Barba, *Jiménez 803* (F); vicinity of La Palma, *Maxon 412* (NY); 11 km N of San Ramón, *Mickel 2958* (LP, NY, UC); San Luis de Zarcero, *A.C. Smith 778* (NY). **Cartago:** road between La Suiza and Tuis, *DeWolf 385* (CR); Pacayas, *Lankester 653* (US); along Inter-American Hwy. between Cartago and San Isidro del General, *Scamman 5985* (CR), *5986* (CR); Orosi, Finca del Sr. Valverde, *Brade 16824* (CR); El Muñeco, S of Navarro, *Standley 33648* (US); Santa Clara de Cartago, *Maxon & Harvey 8242* (US); SE of Platanillo, along Camino Raiz de Hule, *Croat 36761* (MO); Platanillo, *de la Sota 5252* (LP, US); foot of Volcán Turrialba, Pacayas, *Scamman 7155* (CR); along road from Moravia to Quebrada Platanillo (Tsipiri), *Croat 36669* (MO); ca. 22 km E of Turrialba, high ridge above Platanillo, *Mickel 3426* (LP, NY); near the town of Estrella, *Moran 2237* (CR), *2241* (CR); near Alto Patillos, *Moran 2442* (CR); Reserva e Tapantí, *Gómez 18906* (CR, MO, UC); Tapantí, *Grayum & Sleeper 3448* (MO); 12–16 km S of Tapantí, along the road above the Río Grande de Orosi, *Stolze 1488* (F, UC). **Heredia:** 7.5 km N of Vara Blanca, in vicinity of Río La Paz Grande, *Croat 36007* (MO); Vara Blanca de Sarapiquí, N slope of Central Cordillera, *Skutch 3236* (GH, US); Santo Domingo de Vara Blanca, *Valerio 2356* (US); Vara Blanca, between Volcán Poas and Barba, *Chrysler & Roever 5095* (US); 4 km N of Vara Blanca, *Croat 35608* (MO); near Río Las Vueltas, NE of Volcán Barba, *Lent 2642* (F); Virgen del Socorro, *Moran 3168* (CR). **Puntarenas:** 5 km NE Finca las Cruces, San Vito de Java, *Burch 4505* (NY); near field station, Rincón de Osa, *Burch 4414* (NY); 5 km S of San Vito de Java, in vicinity of biological field station at Wilson finca, *Mickel 2003* (NY); 5 km S of San Vito de Java, 1–4 km SW of biological station at Finca Wilson, *Mickel 3126* (NY). **San José:** Tablazo, *Valerio 63* (US); *Biolley 73* (US, Z); Tablazo, *Brade & Brade 67* (P), *98* (NY); Alto La Palma, *Moran 2325* (CR).

PANAMA. **Chiriquí:** Palo Alto, just E of Boquete, *Stern et al. 1034* (CR, US); Holcomb trail, *Cornman 927* (MICH, UC, US); vicinity of El Boquete, *Cornman 1178* (US), *1233* (US), *Maurice 699* (US); Río Caldera, from El Boquete to the Cordillera, *Killip 5202* (CR, US); valley of Río Piamasta, about 5 mi E of Boquete, *Killip 5163* (US), *5386* (US), *5429* (CR, MICH, US). **Coclé:** Valle de Antón, *Ocampo 877* (CR); Cerro Pilon, *Dwyer 8337* (MO); cloud forest at La Mesa above El Valle, *Croat 13431* (MO, UC).

ECUADOR. **Napo:** camino Baeza–Tena, 15 km al norte de Tena, 1100 m, *Moran 3532* (F, GH, PORT, Q, QCA). **Pastaza:** village of Río Chico, 8 km from Puyo, *Shemluck 304* (F). **Tungurahua:** casi 25 km al este de Baños, detras el pueblo Río Negro, por Río Topo (malempresado "Río Toro" en el mapa), *Moran 3570* (F, GH, Q, QCA).

PERU. **Huánuco:** SW slope of the Río Llulla Pichis watershed on the ascent of Cerro del Sira, *Dudley 13258* (GH), *18265A* (GH).

BOLIVIA. **La Paz:** Hacienda Simaco sobre el camino a Tipuana, *Buchtien 5164* (GH, US).

17. **Polybotrya botryoides** (Baker) C. Chr. (Fig. 36, Map 8).

Polybotrya botryoides (Baker) C. Chr., Index Filicum 504. 1906.

Acrostichum botryoides Baker, J. Bot. 19:206. 1881. TYPE: Colombia. Antioquia: on trees in the forest, 6000–7000 ft, 22 July 1880, *Kalbreyer 1873* (holotype: K; photo and fragment GH!, US!).

Stem to 2 cm thick, hemiepiphytic; *scales* dull brown, about 1 cm long, with the margins subentire to erose, the base curved and thickened. *Sterile leaves* up to 1.5 m (?); *petiole* densely scaly at

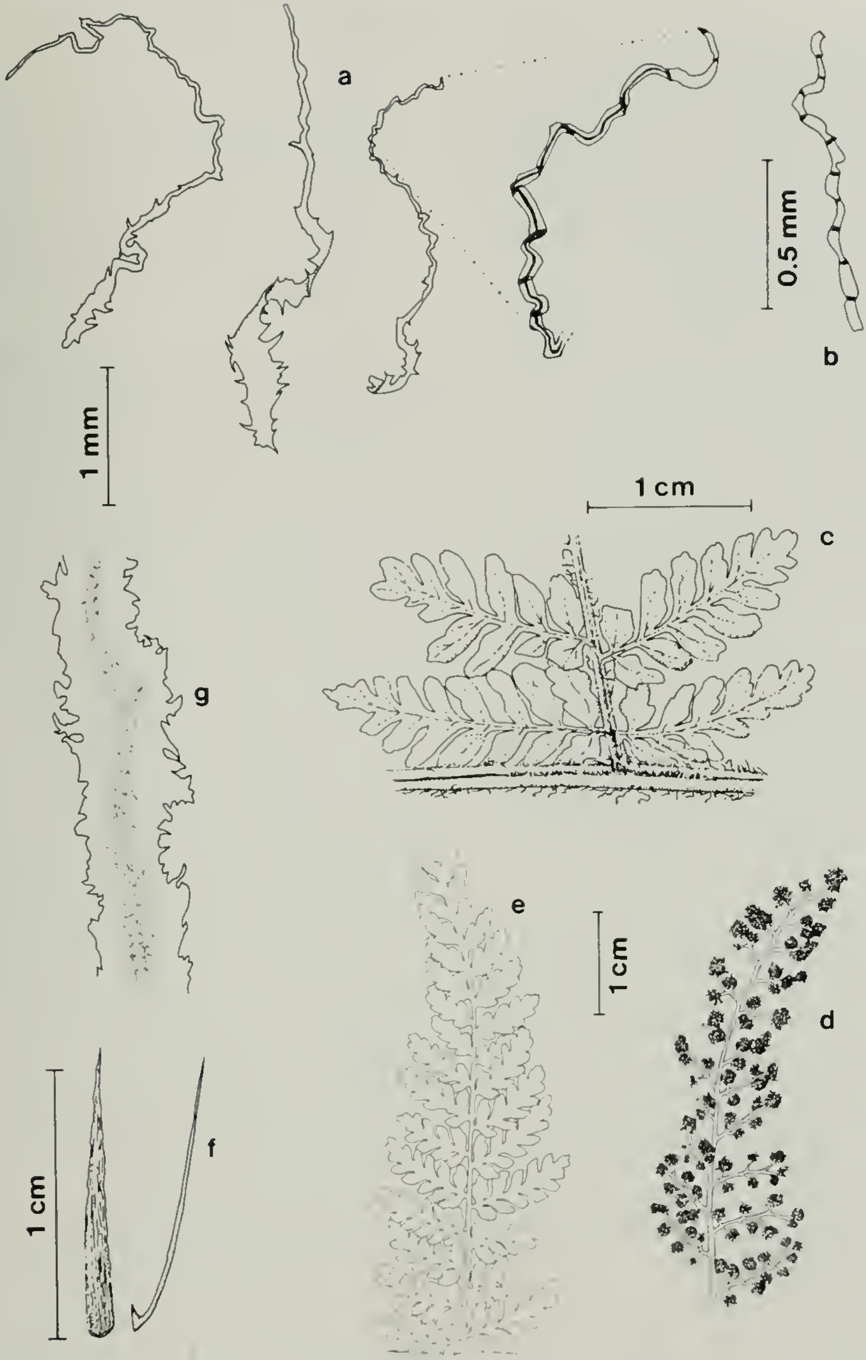

FIGURE 36. *Polybotrya botryoides* (Baker) C. Chr. a. costal scales, the one on the right enlarged to show the biseriate apex; b. uniseriate "hair" from the costa. Such hairs are actually reduced scales as shown by their intergradation with the scales and by their characteristics which differ from those of true hairs; c. sterile pinnule base; d. botryoid fertile pinnule; e. sterile pinnule; f. stem scale, at right is a side view showing the thickened base; g. petiolar scale, medial portion darkened and margins erose. a–g: *Juncosa 1369* (MO).

base, the scales similar to those on the stem, but with wider pale borders and more strongly erose; *lamina* 4-pinnate, nearly glabrous on both surfaces; *pinnae* lanceolate, up to 35 × 20 cm, finely divided all the way to the apex; *pinnules* up to 10 × 3 cm, catadromic or subequal, lanceolate, the base often overlapping the costa, subequilateral, i.e., not prolonged acroscopically, short-stalked (1–2 mm long); *tertiary segments* oblong, sessile, up to 2 × 0.9 cm, apex acute or rounded, base equilateral; *quaternary segments* oblong to ovate, sessile, up to 5 × 3 mm, the margins entire or crenate; *axes* scaly, the scales numerous, tortuous, thin, reddish, most of these only 2–5 cells wide, intergrading with hairs, these articulate, reddish, 4–8 celled, 0.1–0.3 mm long; *grooves* pubescent within by reddish hairs. *Fertile leaves* botryoid, 3-4-pinnate, with the ultimate soriferous segments globose, 1–2 mm diameter; *receptacle* paraphysate by articulate hairs, these often buried among the sporangia; *sporangial stalks* paraphysate; *spore size* unknown.

Polybotrya botryoides is endemic to the Andes of Colombia (Map 8), occurring in forests from 1830–2130 m. The above description is based primarily on the Juncosa collection, which was the only dried specimen I had available for study. I could not find enough spores on this specimen to make an adequate measurement of spore size.

This rare species can be separated from all other species of *Polybotrya* by its distinctive combination of botryoid fertile leaf, 4-pinnate sterile leaf, and axes covered by numerous, linear, tortuous, reddish scales (Fig. 36a). No other species of *Polybotrya* is as finely divided as this one. *Polybotrya botryoides* looks like *P. alfredii* because of its large decompound lamina, catadromically arranged pinnules, subequal pinnule bases, pubescence of the axes, and dull brown stem scales. The Venezuelan endemic *P. canaliculata* also has botryoid fertile leaves, but it lacks hairs on the axes, has very different axial scales, and s less finely cut (Fig. 52).

Specimens examined: COLOMBIA. **Antioquia:** *Kalbreyer 1873* (photo and fragment GH, US); main hwy. Medellín–Puerto Triunfo, Municipality Cocorna, ca. 5 km E of Cocorna Peaje, Quebrada El Biadal, 1830 m, *Juncosa 1369* (MO, UC).

18. Polybotrya lourteigiana Lellinger (Fig. 37, Map 10).

> *Polybotrya lourteigiana* Lellinger, Proc. Biol. Soc. Washington 89:723, fig. 5. 1977. TYPE: Colombia. Chocó: Trail along ridge from the confluence of the forks of the Rio Mutatá above the Río Dos Bocas to the top of Alto del Buey, ca. 1450–1750 m, *Lellinger & de la Sota 251* (holotype: US!; isotypes: COL!, LP!).

Stem to 2 cm thick, hemiepiphytic, mucilaginous (?); *scales* dark brown, concolorous, and entire, or cream-colored with a darker center and ciliate margins, mostly 8–17 × 0.5–2.0 mm. *Sterile leaves* up to 1.6 m long; *petiole* up to ½ as long as the lamina; *lamina* glabrous on both surfaces, up to 3-pinnate but mostly 2-pinnate-pinnatifid throughout, deltate to lanceolate; *lower pinnae* mostly 30–45 × 10–18, elliptic, lanceolate or narrowly triangular; *pinnules* arranged catadromically, subequilateral at base, subsessile, narrowly oblong, generally 10–15 free pairs, 5–8(11) × 1.5–2.0(3.0) cm, the apex slightly falcate; *tertiary segments* 5–12(15) × 2–4(6) mm, arranged catadromically, oblong, the apex rounded to truncate, the margins entire; *axes* pubescent abaxially, the hairs either tawny or reddish, 0.5–1.2 mm long, multicellular, lax, or with the hairs shorter, stiffer, 0.1–0.3 mm long, costal scales present, inconspicuous, often at the junctures with the costules, ovate to orbicular, flaccid, brown; *grooves* pubescent within, especially at the junctures, truncated by the ridges of the next lower order. *Fertile leaves* 4-pinnate, coenosoric, or subbotryoid, if the sori discrete, then not on long stalks; *costa* pubescent, with or without ovate, denticulate scales; *sporangial stalks* paraphysate; *spores* (50)55–67(70) microns long.

Other illustrations: See Lellinger's original description (cited above) which contains a photograph of a portion of the holotype.

This plant occurs in mid-elevation forests from 750 to 2250 m in the western Andes of Colombia (Map 10). See comments under *Polybotrya alfredii* and *P. pittieri* for comparisons with those species. Considerable morphological variation exists in the specimens cited below, but I found

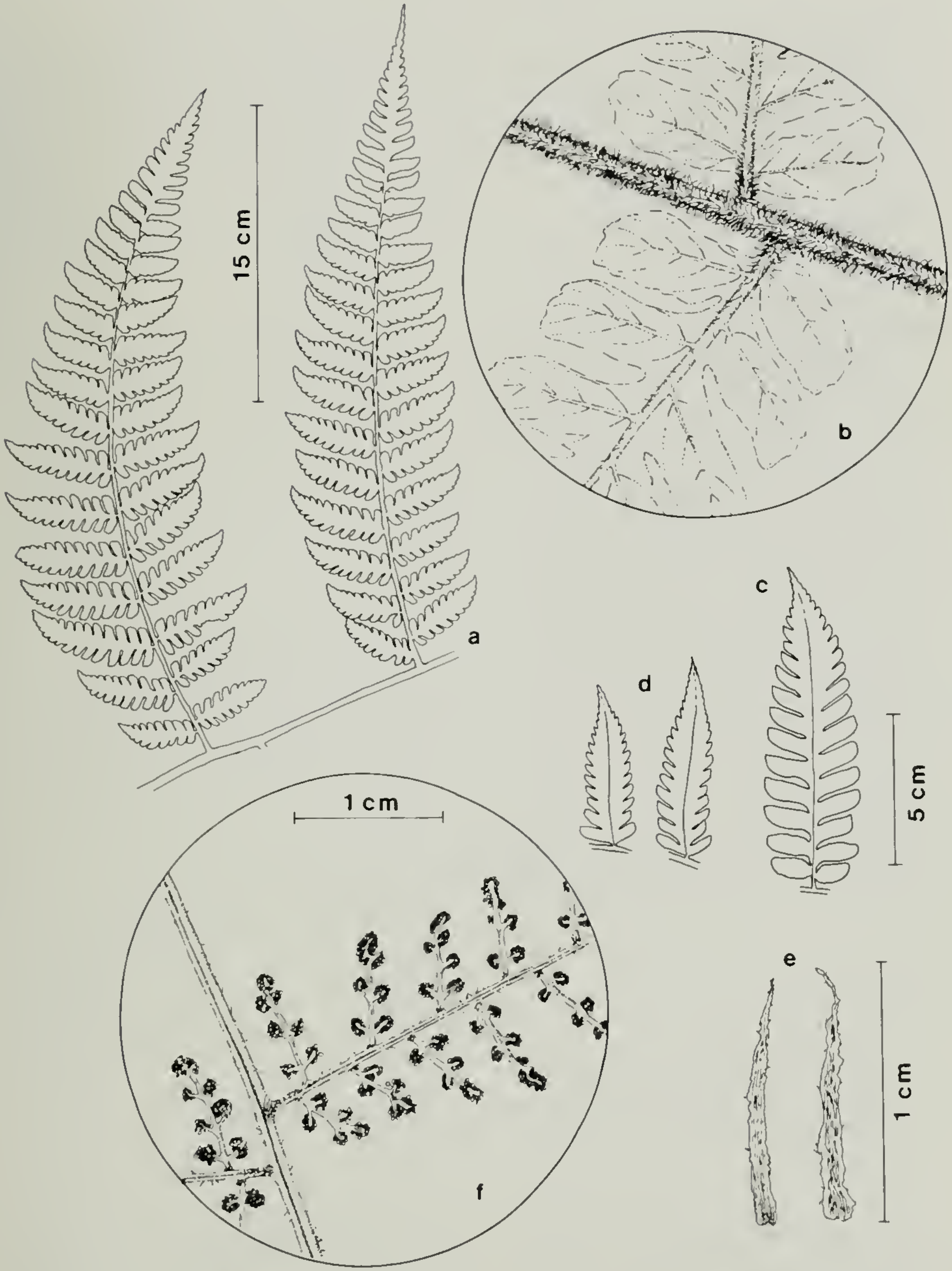

FIGURE 37. *Polybotrya lourteigiana* Lellinger. a. basal pinnae; b. pinnule bases, apex to the left; c,d. sterile pinnules, apex to the left; e. stem scales; f. fertile pinnules. a,b,c,e,f: *Lellinger & de la Sota 251* (US). d: *Cuatrecasas 15527* (US).

no constant characters to separate the extreme forms. Pubescence varies tremendously; the Lellinger and de la Sota specimens are mostly long pilose on the axes whereas the Cuatrecasas specimens have shorter, stiffer hairs. Intermediates exist, and no other characters correlate with pubescence.

The type collection consists of six sheets, of which US #2748016 is here excluded; it actually represents *P. stolzei*.

Specimens examined: COLOMBIA. **Chocó:** Trail along ridge from the confluence of the forks of the Río Mutatá above the Río Dos Bocas to the top of Alto del Buey, ca. 1450–1750 m, *Lellinger & de la Sota 251* (COL, LP, US); principal ridge and slopes 2 km E of San José del Palmar, *Lellinger & de la Sota 768a* (COL, LP, US); 0.3 km E of the Ciudad Bolívar–Quibdó road across the suspension bridge at ca. km 141, *Lellinger & de la Sota 899* (COL, LP, US); Mojarras de Tadó, 8.5 km E of Istmina, *Lellinger & de la Sota 387* (CR, COL, LP, US). **Chocó-Antioquia:** principal ridge W of La Mansa, at ca. km 105.5 of the Ciudad Bolívar–Quibdó road, *Lellinger & de la Sota 948* (COL, LP, US). **Chocó–El Valle:** Serranía de Los Paraguas, along the trail from El Cairo to Río Blanco, ca. 8 km SW of El Cairo, *Lellinger & de la Sota 843* (COL, LP, US). **El Valle del Cauca:** Hoya del Río Cali, La Margarita, *Duque-Jaramillo 1868* (COL); Cordillera Occidental, vertiente occidental, del Río Sanquinini, La Laguna, *Cuatrecasas 15527* (US); Cordillera Occidental, vertiente occidental, monte La Guarida, filo de la cordillera sobre La Carbonera, entre Las Brisas y Albán, *Cuatrecasas 22143* (F, US). **Nariño:** Municip. de Altaquer, Carretera entre Altaquer y Junín, Guyambe, *Mora 4160* (COL).

19. **Polybotrya pittieri** Lellinger (Fig. 38, Map 11).

Polybotrya pittieri Lellinger, Proc. Biol. Soc. Washington 89:725, fig. 6. 1977. TYPE: Colombia. Cauca: Dagua Valley, Córdoba, Pacific Coastal Zone, 30–100 m, *Pittier 587* (holotype: US!).

Stem 1 cm thick, hemiepiphytic; *scales* 9–14 × 1.0–1.4 mm, spreading, reddish, membranaceous, the margin denticulate. *Sterile leaves* up to 1.3 m long; *petiole* to 38 cm long; *lamina* triangular at base, to 60 × 90 cm, 3-pinnate at the base, 2-pinnate-pinnatifid medially, nearly glabrous on both surfaces, the apex long-tapered; *pinnules* arranged catadromically, up to 5 × 2 cm, relatively short and stubby, the base subequilateral, the apex obtuse or slightly acute; *tertiary segments* up to 1.0 × 0.5 cm, oblong; *axes* pubescent on the abaxial surface, the hairs short, stiff, ca. 0.2 mm long; *grooves* truncated by the ridges of the next lower order or only indistinctly admitted to the groove, pubescent within, the hairs reddish or tawny, 0.2–0.5 mm long. *Fertile leaves* subtriangular, 4-pinnate, botryoid, the apex long-attenuate; *pinnules* to 2.1 × 1 cm; *sori* stipitate, round, the stalks 1–4 mm long, arranged pinnately; *sporangial stalks* paraphysate; *spores* (62)65–70(77) microns long.

Other illustrations: Lellinger's original description has a photograph of the type.

Polybotrya pittieri, known from only two collections, is endemic to the western Andes of Colombia (Map 11). This species occurs at low elevations, from 30–100 m, unlike its most closely related species, *P. attenuata* and *P. botryoides*, which occur at higher elevations. It is named after Henry F. Pittier (1857–1950), a Swiss botanist and civil engineer who collected prolifically in the American tropics.

Polybotrya pittieri looks most like *P. lourteigiana*. Lellinger (1977) observed only that *P. pittieri* had a rather stiffly pilose indument on the rhachis and costae, whereas *P. lourteigiana* had a lax, hirtous indument. From the greater number of specimens of *P. lourteigiana* available to me, however, pubescence type does not appear constant. Nevertheless, *P. pittieri* seems to be a distinct species, and the best way to distinguish it is by its botryoid fertile leaves with prominently stipitate sori (Fig. 38b). *P. lourteigiana*, on the other hand, has coenosoric fertile leaves and subsessile sori (Fig. 37f). Another difference, although one that may prove inconsistent when more specimens are known, is the broadly deltate lamina of *P. pittieri*; *P. lourteigiana* is slightly reduced at the base. Using these characters, I find that the paratypes of *P. pittieri* actually belong to *P. lourteigiana*.

Polybotrya pittieri might also be confused with *P. canaliculata* since both have botryoid fertile leaves, but *P. pittieri* differs by its broadly deltate lamina, pinnule cutting, and pubescent axes that lack scales. Its spores are extremely large compared to others in the genus, suggesting that *P. pittieri* is a polyploid.

Specimens examined: COLOMBIA. **Cauca:** Dagua Valley, Córdoba, Pacific Coastal Zone, 30–100 m, *Pittier 587* (US); El Tambo, *von Sneidern 1590* (US)

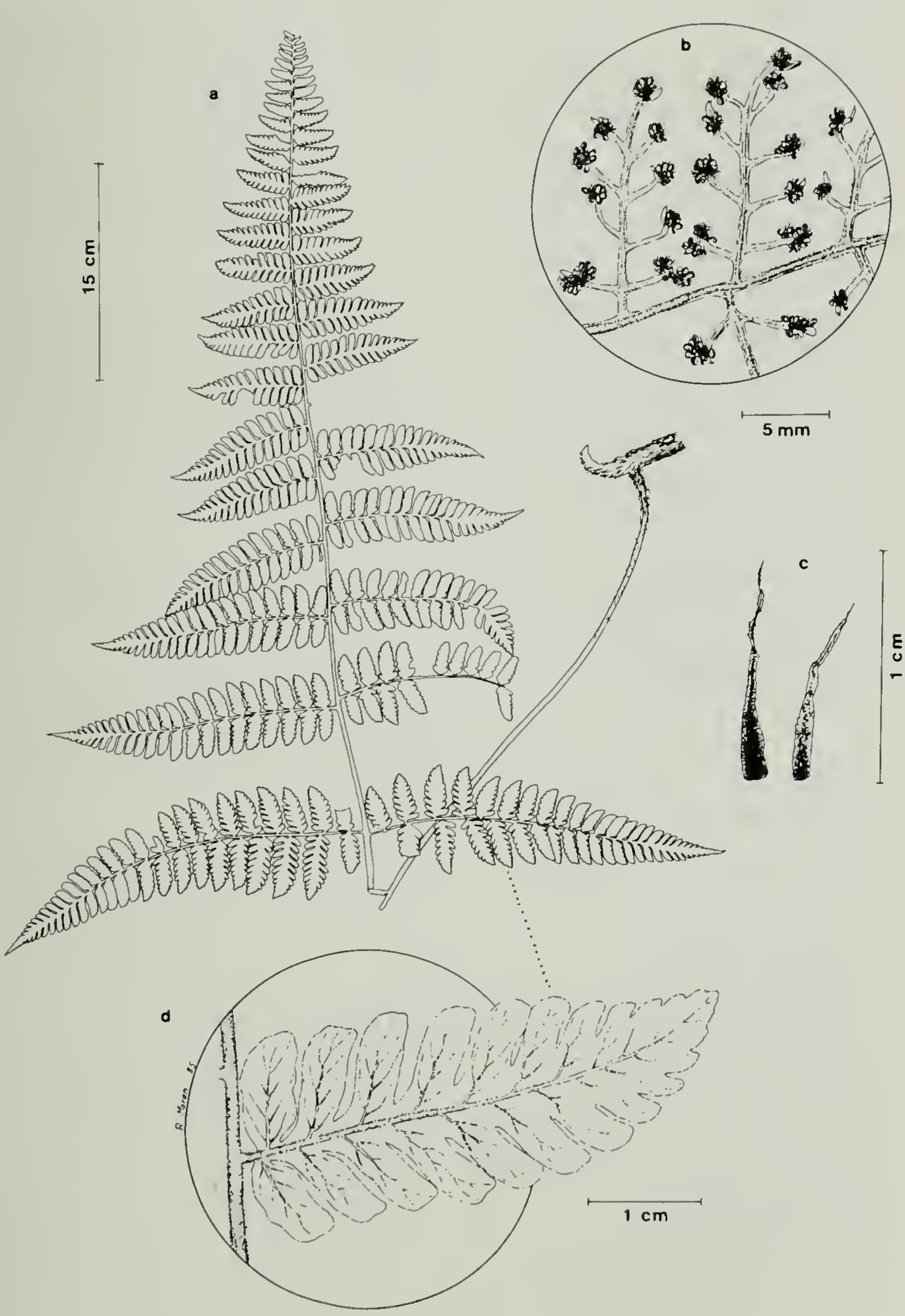

FIGURE 38. *Polybotrya pittieri* Lellinger. a. sterile leaf; b. fertile leaf; c. stem scales; d. sterile basiscopic pinnule from basal pinna. a–d: *Pittier 587* (US).

20. Polybotrya cylindrica Kaulfuss (Fig. 39, Map 16).

Polybotrya cylindrica Kaulfuss, Enum. Filicum 56. 1824. TYPE: Brazil. Santa Catarina: Island of St. Catharina, *Chamisso s.n.* (LE).

Polybotrya incisa Link, Hort. Berol. 2:135. 1833. TYPE: Brazil. No collector or date given (holotype: B!).

Acrostichum incisum (Link) Hooker, Species Filicum 5:245. 1864.

Acrostichum cylindricum (Kaulfuss) Hooker, Species Filicum 5:246. 1864.

Polybotrya frondosa Fée, Crypt. Vasc. Brésil. 1:15. 1869. TYPE: Brazil. No exact locality given, *Glaziou 2428* (holotype: K; photo GH!).

Polybotrya osmundacea var. *cylindrica* (Kaulfuss) Luetzelb. Estudo Bot. Nordeste Brazil 3:245. 1923.

Polybotrya osmundacea var. *frondosa* (Fée) Luetzelb. Estudo Bot. Nordeste Brazil 3:245. 1923.

Polybotrya osmundacea var. *incisa* (Link) Luetzelb. Estudo Bot. Nordeste Brazil 3:245. 1923.

Stem 1–2 cm thick, hemiepiphytic; *scales* dull brown, opaque, concolorous or with a very narrow hyaline border, entire, generally 6–12 mm long, the base thickened, curved, appressed. *Sterile leaves* up to 1.7 m long; *petiole* 30–50 cm long; *lamina* to 1.3 m long, 3-pinnate-pinnatifid, glabrous or pubescent with small, unicellular, whitish hairs, the margins sparsely to moderately ciliate by jointed hairs, these ca. 0.1 mm long; *pinnae* narrowly lanceolate to subdeltate, the lowermost to 52 × 28 cm; *pinnules* generally 9–14 × 3.5 × 5.5 cm, anadromic proximally, becoming catadromic distally, the acroscopic side slightly prolonged, proximal ones with a short 3–5 mm stalk; *tertiary segments* ca. 7–11 per pinnule, ovate to oblong, the largest usually pinnatisect, the apex acute or rounded; *vein tips* slightly clavate and prominulous; *axes* abaxially sparsely to densely pubescent, the hairs colorless, clear, stiff, subulate ca. 0.1–0.3 mm long, with the cross walls not easily visible, mixed with appressed, linear, scraggly, inconspicuous scales; *grooves* filled with reddish hairs. *Fertile leaves* to 90 × 62 cm, 3-4-pinnate; *ultimate segments* often oblong and appearing cylindrical due to folding back of the segment margins; *sporangial stalks* paraphysate; *spores* (55)60–66(70) microns long.

Other illustrations: Fée, Mém. Fam. Foug. 2 (Hist. Acrost.), tab. 36. 1846; *op. cit.* tab. 35 (as *P. incisa*); Brade, Bradea, 1(9):66, figs. 1 & 2; 67, figs. 16 & 17. 1969; Sehnem, Flora Ilustrada Catarinense, plate 19; plate 20 (as *P. cylindrica* var. *frondosa*). 1979.

Polybotrya cylindrica, endemic to the coastal mountains of southeastern Brazil (Map 16), is the largest and most finely divided species of *Polybotrya* in Brazil. It occurs in wet, shaded, primary forests from 0 to 775 m. This species differs further from other *Polybotrya* species in southeastern Brazil by its stem scales that are dull brown with entire margins and the thickened and curved bases. The curved scale base orients the rest of the scale parallel to the surface of the stem, so that the scales are appressed (Fig. 39f,g). Another helpful feature in identification is the laminar margin, which is sparsely ciliate by jointed hairs less than 0.1 mm long.

Brade (1971) distinguished *P. frondosa* from *P. cylindrica* by the amount of lamina dissection. But lamina dissection exhibits complete intergradation from 2-pinnate to 3-pinnate-pinnatifid and no other characterisitcs correlate with it (Fig. 39a-d).

Although I have not seen the type of this species, the original description by Kaulfuss is sufficient to ascertain his plant's identity. He specifically mentions the ciliate margins that distinguish this plant from others in southeastern Brazil. Furthermore, this species is the only *Polybotrya* that grows on the Island of Santa Catarina, where the type was collected. The specific epithet probably refers to the fertile segments which, upon drying, reflex so that the sori appear on all surfaces, thereby imparting a cylindrical shape to the segments.

Specimens examined: BRAZIL. **Espirito Santo:** Municipio de Cachoeira de Itapemirim–Vargem (?), *Brade 19972* (HB, MO, NY). **Paraná:** Mun. Guaratuba, Pedra Branca de Araraquara, *Hatschbach 8141* (US); Pedra Branca de Araraquara, *Hatschbach 7424* (US); no locality, *Hatschbach 10749* (NY); no locality, *Dusén 13658* (GH); Porto Dom Pedro II, *Dusén 4423*(BM);

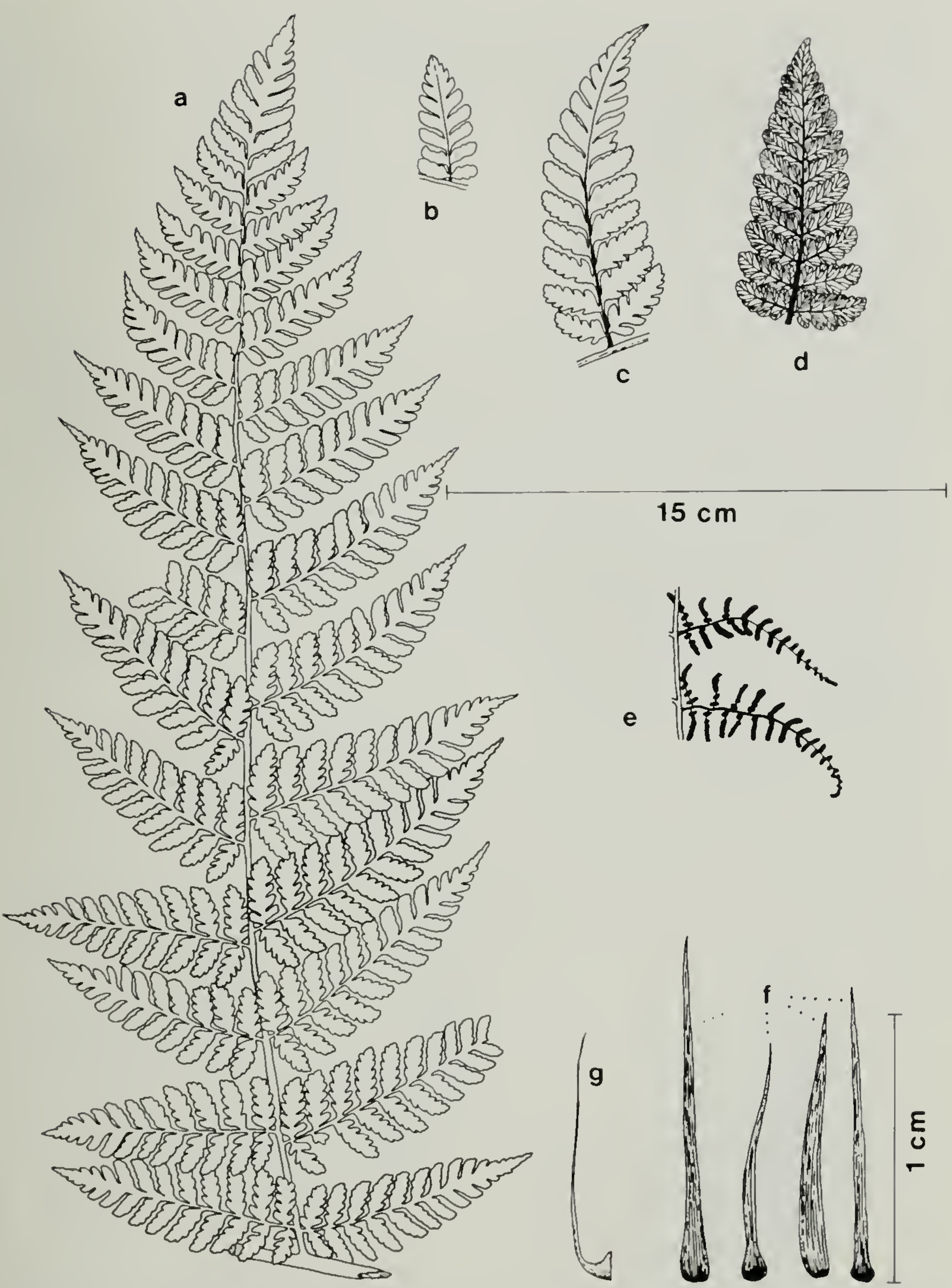

FIGURE 39. *Polybotrya cylindrica* Kaulfuss. a. sterile pinna; b–d. sterile pinnules showing variation in amount of dissection; e. fertile pinnules; f. stem scales, top view; g. stem scale, side view. a,e: *Goedas 217* (NY). b: *Mosen 3050* (B). c,f,g: *Schmalz 158* (UC). d: *Dusén 6926* (F).

Volta Grande, *Dusén 6984* (BM); Porto de Cima, *Dusén 6926* (F, GH, LIL, MO, NY, PH, UC, Z); Tacarehy, *Dusén 15351* (BM, F, PH), *15353* (GH, MO, PH, UC, Z). **Rio de Janeiro:** without locality, *Hunnewell 18511* (MICH); Distrito Federal, Guanabara, Represa Camori, *Brade 12576* (RB); Rezende, 80 mi WNW of Rio, on Paraiba River, Rio Palmital, *Castellanos 25710* (F); Serra de Itatiaia, *Brade 12614* (NY, RB); Brene, *Glaziou 955*(RB); vicinity of Meio da Serra, *Smith & Brade 2286* (GH); Estrada Velha de Barrira a Teresópolis, *Duarte & Pereira 65323* (F, LP); Corcovado, *Miers s.n.* (NY); Teresópolis, *Brade 9365* (NY, UC); Serra da Carioca, *Brade 13982* (RB). **Rio Grande do Sul:** S. Leopoldo, *Lehnun 2562* (LIL); Porto Alegre, *Fargens 251* (UC). **Santa Catarina:** Municip. Ibirama, Horto Florestal, *Smith & Klein 7546* (US); Horto Florestal, I.N.P., Ibirama, *Reitz & Klein 1101* (US), *1102* (US), *2665* (US), *3466* (US); Blumenau, Warnow, *Goedas 217* (NY, UC, US); Itajaí, *Reitz 151* (LIL); Municipality Brusque, Azambruja, *Smith and Reitz 6135* (COL, GH, MO, US); Reserva Florestal, dos Piloes, *Duarte 3179* (LP, NY); Mina Velha, Garuva, São Francisco do Sul, *Reitz & Klein 4635* (US), *4682* (US); Sabia, Vidal Ramos, *Reitz & Klein 5108* (US); Passo Mansa, *Haerchen 124* (NY); Joinville, *Schmalz 78* (MO), *158* (NY, UC); Tres Barras, Garuva, São Francisco do Sul, *Reitz & Klein 5549* (US); Sta. Catherine 1834, *Gaudichaud 73* (P); Azambuja–Brusgui, *Reitz 2825* (LIL, P); Blumenau, *Muller 6039* (MICH). **São Paulo:** São Bento, *Luetzelburg 254* (MICH, US); Serra da Bocaina, *Brade 20931* (LP); Morro das Pedras, Iguape, *Brade s.n.* (US); Paranapicaba, Biological Station, *Handro 1229* (GH, US); Agua funda, *Handro 2228* (GH, US); Serra do Mar, *Wacket 21556* (GH); Campo Grande to Alto da Serra, 40 km SE of São Paulo, *Tryon & Tryon 6591* (GH); Santos, 1874, *Mosen 3050* (B, P). **State unknown:** *Glaziou 2428* (photo of K specimen at GH); no locality, *Claussen s.n.* (P); *Micken s.n.* (NY); Capão do Fradie, *Schneus 3412* (GH); Morro do Antão, *Sehnem 3092* (GH).

21. **Polybotrya hickeyi** Moran, *sp. nov.* (Fig. 40, Map 13).

Polybotrya hickeyi Moran, *sp. nov.* TYPE: Bolivia. Cochabamba: Prov. Chapare, road from Cochabamba to Villa Tunari, in thick rain forest, very heavily shaded, on trunk of *Ficus* 1700 m, 23 March 1980, *Hickey 801* (with Eshbaugh) (holotype: GH!; isotype: MU).

Caulis hemiepiphyticus, 1–2 cm diam.; squamae atrobrunneae, vulgo opacae, leviter nitidae, concolores vel marginibus tenuioribus et pallidioribus ad apicem; lamina usque ad 3-pinnata-pinnatifida, deltata, usque ad 1 m longa, leviter pubens inferne, pilis cylindricis, appressis, usque ad 0.1 mm longis; pinnae usque ad 46 × 25 cm, deltatae, paribus proximalibus acroscopice prolongatis; pinnulae catadromicae supra basin, deltatae, oblongae vel lanceolatae; costae sine sulcis prominentibus; venae prominulae superne, apice leviter incrassatae. Sori discreti, rotundi, oppositi vel subopposititi.

Stem 1–2 cm thick, hemiepiphytic; *scales* dark chocolate brown, mostly opaque, concolorous, or the apex with thinner, lighter borders, the margins denticulate to entire, the base thickened, attached across its full width. *Sterile leaves* up to 1.5 m (?); *petiole* with thin, ovate to lanceolate scales; *lamina* to 3-pinnate-pinnatifid, deltate, to about 1 m long, the abaxial surface slightly puberulent, the hairs cylindrical, appressed, up to 0.1 mm long; *pinnae* up to 46 × 25 cm, deltate, the proximal pair basiscopically prolonged, the distal ones gradually becoming acroscopically prolonged; *pinnules* catadromic above the base, deltate to oblong-lanceolate, the basiscopic margins thickened and decurrent on the costa, the base slightly prolonged acroscopically, the apices acuminate; *tertiary segments* also with a thickened, decurrent, light-colored basiscopic margin; *veins* prominulous adaxially, the tips thickened and ending just behind the margin; *costules* bordered by a raised, erect flap or wing of tissue; *axes* often not prominently grooved, pubescent by ca. 0.1 mm long, colorless, erect hairs, the scales appressed, denticulate, flexuose. *Fertile leaves* botryoid; *sori* with few fusions, arranged mostly oppositely or suboppositely.

Polybotrya hickeyi grows in high elevation forests in the Andes of Colombia and Bolivia; it has not yet been collected from Ecuador or Peru (Map 13). This species looks most like *P. puberulenta*—see that species for comparison. This plant is named for one of the collectors, Dr. R. James Hickey, who has made important contributions to the study of *Isoetes* and *Lycopodium*.

The Colombian specimens look like the Bolivian type specimen except for the stem scales. The Bolivian type has dark, chocolate brown scales with denticulate margins and lighter borders apically (Fig. 40g). The Colombian specimens have merely dull brown, concolorous scales with

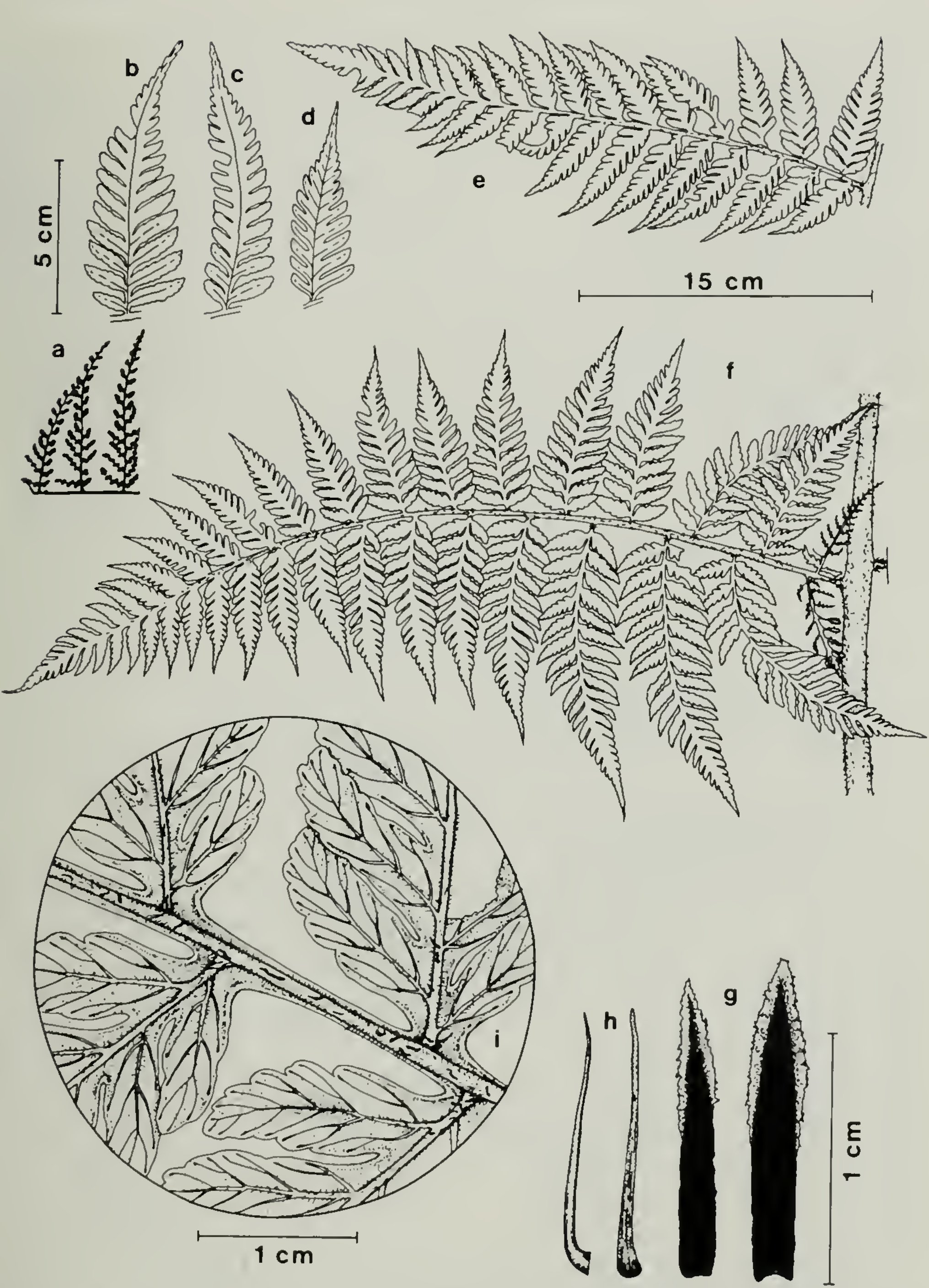

FIGURE 40. *Polybotrya hickeyi* Moran. a. fertile pinnules; b,c,d. sterile pinnules, acroscopic side to the right; e. medial pinna; f. basal pinna (note that the two proximal basal pinnules are fertile); g. stem scales (Bolivia); h. stem scale (Colombia); i. abaxial surface of distal pinnules. a,d: *Ludwig 262* (NY). b,h: *Grant 10283* (F). c: *Killip & Smith 20210* (US). e,f,g,i: holotype, *Hickey 801*, with Eshbaugh (GH).

entire margins and a prominently curved and thickened base; therefore, they appear appressed (Fig. 40h). This thickened and curved scale base appears somewhat elevated, like those of *P. caudata* and *P. cylindrica* . The lamina of *P. hickeyi* turns a peculiar yellowish green upon drying.

Specimens examined: COLOMBIA. **Cauca:** W slope of W Cordillera, above Carpinteria, *Alston 8278* (BM). **Cundinamarca:** Cordillera Oriental, Toquiza, Gazaunta Valley, Cordillera de Helicona, 15 km NW of Medina, 2200 m, *Grant 10283* (F, US); Fusagasugá, *Ludwig 262* (BM, MO, NY). **Norte de Santander:** Pica-Pica Valley, above Tapata (N of Toledo) 2100–2400 m, *Killip & Smith 20210* (GH, NY, US).

BOLIVIA. **Cochabamba:** Prov. Chapare, road from Cochabamba to Villa Tunari, 1700 m, *Hickey 801* with Eshbaugh (GH).

22. **Polybotrya puberulenta** Moran, *sp. nov.* (Fig. 41, Map 13).

Polybotrya puberulenta Moran, *sp. nov.* TYPE: Ecuador. Napo: camino Baeza–Tena, 5 km al sur de Cosanga. Cordillera Oriental, bosque perturbado, 1100 m, 4 de enero 1984, *Moran 3528* (holotype: F!; isotypes: COL!, GH!, LPB!, MO!, NY!, Q!, QCA!, UC!, US!, VEN!).

Caulis hemiepiphyticus; squamae aurantiacae sordidae vel luteae, membranaeae, late patentes, centro leviter fuscatae, marginibus denticulatis vel erosis; lamina 2-pinnata-pinnatisecta perlate ovata, crassa, flavovirentes pallide, pubents utrinque, pilis patentibus, flexuosis, ca. 0.1 mm longis; pinnae usque ad 34 × 18 cm, infimus basiscopice prolongatae; pinnulae catadromicae oblongae, in margine incrassatae et decurrentes; lobi tantum crenati, apice truncati vel rotundati; venae prominulae superne, apice leviter incrassatae. Folia fertilia 4-pinnata, axibus dense pubescentibus, pilis 3–5 mm longis et squamis linearibus, appressis vel leviter patentibus; segmenta opposita vel subopposita, receptaculo pubescenti, pilis 1–2 mm longis, articulatis.

Stems 1–2 cm thick, hemiepiphytic; *scales* yellow to sordid orange, darker in the center with light yellow borders, membranous, spreading, 1–3 mm wide, the margins erose to denticulate, attached across the width of the narrowed base, in fresh material somewhat rugose transversely. *Sterile leaves* up to 1.2 m long; *petiole* up to 27 cm long; *lamina* to 2-pinnate-pinnatisect, broadly ovate, thick and somewhat fleshy in living material, color light yellowish green, puberulent on both surfaces, the hairs spreading, flexuous, ca. 0.1 mm long, intergrading with the scales on the lower surface; *pinnae* up to 34 × 18 cm, the proximal pairs basiscopically prolonged, the distal ones gradually becoming equilateral or slightly acroscopically prolonged; *pinnules* catadromic throughout, oblong, the basiscopic margin thickened, decurrent on the costa, the apices obtuse to acute, base cuneate and slightly prolonged acroscopically; *costules* bordered by a raised flap of lighter colored tissue; *lobes* of the largest pinnules merely crenate, the margins thickened, the apices obtuse or truncate; *veins* prominulous adaxially, the tips slightly thickened and ending just behind the margin; *axes* evenly pubescent abaxially, the hairs 0.1 mm long, tawny, erect, scales caducous, usually lacking; *grooves* pubescent within, becoming shallow and flat at the junctures, not admitted to the groove of the next lower order. *Fertile leaves* 4-pinnate, the axes densely pubescent, the hairs jointed, 3–5 mm long, the scales 5–10 mm long, linear, appressed to slightly spreading; *sori* opposite or subopposite; *sporangial stalks* paraphysate; *receptacle* pubescent by jointed hairs, 1–2 mm long, that protrude beyond the sporangia; *spore size* unknown.

Polybotrya puberulenta grows at high elevations in the Andes of Ecuador, Bolivia, and probably Peru (Map 13). The specific epithet refers to the sterile lamina, which is puberulent on both surfaces. Another distinctive feature of this species is the stem scales, which are relatively wide (1–3 mm), thin, spreading and yellowish when viewed with transmitted light. The lamina is relatively thick and fleshy: the mesophyll cells apparently collapse when dry and the veins become prominulous. The lamina, which is always broadest at the base, has a peculiar light greyish green color when dry.

This species differs from *P. hickeyi* in several characteristics of the stem scales, pinnule arrangement, lamina dissection, pubescence, paraphysis length, and scalyness of the major axes. Both species, however, have thickened, decurrent, basiscopic margins. The medial, less cut pinnules of *P. hickeyi* may approach in outline those of *P. puberulenta*, but the largest pinnules of the basal

FIGURE 41. *Polybotrya puberulenta* Moran. a. pinnules; b. stem scales; c. sterile leaf; d. abaxial surface of costa and pinnules. a–d: *Moran 3528* (F).

pinnae are much more highly divided in *P. hickeyi* (compare Figs. 40f and 41a).

Unfortunately, Rusby's Bolivian collection consists only of the fertile leaf, but I believe it belongs to this species because of its cutting, indument type, and yellowish stem scales. The long, protruding paraphyses are easily seen with a hand lens and offer an excellent character to distinguish this species from *P. hickeyi*.

Specimens examined: ECUADOR. **Napo:** camino Baeza–Tena, 5 km al sur de Cosanga, Cordillera Oriental, bosque perturbado, 1100 m, *Moran 3528* (COL, F, GH, LPB, MO, NY, Q, QCA, UC, US, VEN).

BOLIVIA. **La Paz:** Yungas, 6000 ft, "only the fertile frond collected," *Rusby 443* (NY).

23. **Polybotrya alata** Moran, *sp. nov.* (Fig. 42, Map 14).

Polybotrya alata Moran, *sp. nov.*, TYPE: Panama. Panamá: Campo Tres, 3 mi NE of Altos de Pacora, primary forest, alt 500–800 m, epiphytic, the caudex closely appressed, sterile, 10 March 1973, *Croat 22706* (holotype: MO!; isotype: L!).

Caulis hemiepiphyticus usque ad 2.5 cm diam.; squamae lineares, 15–25 × 0.8–1.2 mm, chrysobrunneae, concolores vel centris leviter fuscatis, appressis, ascendentibus, marginibus denticulatis. Lamina 2-pinnata-pinnatifida, superne glabra, inferne pubens, pilis circa 0.1 mm longis, niveis, subulatis; pinnae usque ad 30 × 8 cm, anguste triangulares, apicibus attenuatis, zonis mediis alatis secus costam; pinnulae catadromicae, usque ad 6 × 2 cm, lobis catadromicis, crenatis; rhachis et costae pubescentes et squamatae. Folia fertilia ignota.

Stem 2.5 cm thick, hemiepiphytic; *scales* linear, 15–25 × 0.8–1.2 mm, membranaceous, golden brown, concolorous or with a slightly darkened central stripe, appressed-ascending, margins denticulate. *Sterile leaves* up to 1.3 m long; *petiole* to 45 cm long, scaly, pubescent with 0.2 mm long, unicellular, colorless hairs; *lamina* 2-pinnate-pinnatifid, the adaxial surface glabrous, the abaxial surface lightly to moderately pubescent, the hairs unicellular, less than 0.1 mm long, whitish, subulate; *pinnae* up to 30 × 8 cm, narrowly triangular with a long tapering apex, 3–4 times as long as broad, the lowest becoming pinnatifid in the apical one-third, the transition zone between pinnate and pinnatifid marked by a narrow, straight, decurrent, green wing parallel to the costa; *pinnules* catadromically arranged in the medial pinnae, lobed almost to the costule, inequilateral at base, up to 6 × 2 cm, the proximal acroscopic ones longer than the proximal basiscopic; *pinnule lobes* catadromically arranged, the margins crenate, the apices rounded; *axes* pubescent abaxially, the hairs 0.1–0.2 mm long, subulate, colorless, often difficult to see on the lamina, intermixed on the costae with long, scraggly, subclathrate, denticulate scales; *groove* usually glabrous, abruptly truncated by the raised ridge of the costal groove, the junctures short-pubescent. *Fertile leaves* unknown.

Polybotrya alata has been collected only twice, both times in the mountains of Panama (Map 14), but I suspect it also occurs in the mountains of southern Costa Rica. Distinctive features of this species are the narrowly triangular pinnae with long attenuate apices and the pinnules that are lobed almost to the costule, thereby making the lamina 2-pinnate-pinnatifid (Fig. 42a). The transition zone from the free pinnules to the pinnatifid apex differs from all other species of *Polybotrya* by the thin, basally decurrent, green wing, which imparts an alate appearance to the costa (Fig. 42c). The stem scales are also distinctive by their long length (15–25 × 0.8–1.2 mm) and shiny, golden brown color.

The short, even pubescence on the abaxial surface of the leaf separates *P. alata* from all other Central American *Polybotrya*, except *P. caudata*, which can also have pubescent leaves. The laminar hairs of *P. caudata*, however, are longer (1–3mm) than those of *P. alata* and are 4–10 celled. The two species also differ sharply by their stem scales. The only other Central American species with which *P. alata* could be confused is *P. osmundacea*, but that species is easily distinguished by its anadromic pinnule arrangement and nonalate costae. Furthermore, the costular groove of *P. alata* is truncated by the ridges of the costa; in contrast, *P. osmundacea* has uninterrupted, decurrent grooves (Fig. 47h).

Specimens examined: PANAMA **Panamá:** Campo Tres, 3 mi NE of Altos de Pacora, *Croat 22706* (MO, L). **Veraguas:** 5 mi W of Santa Fe on road past Escuela Agricola Alto Piedra on Pacific side of divide, 800–1200 m, *Croat 23011* (MO).

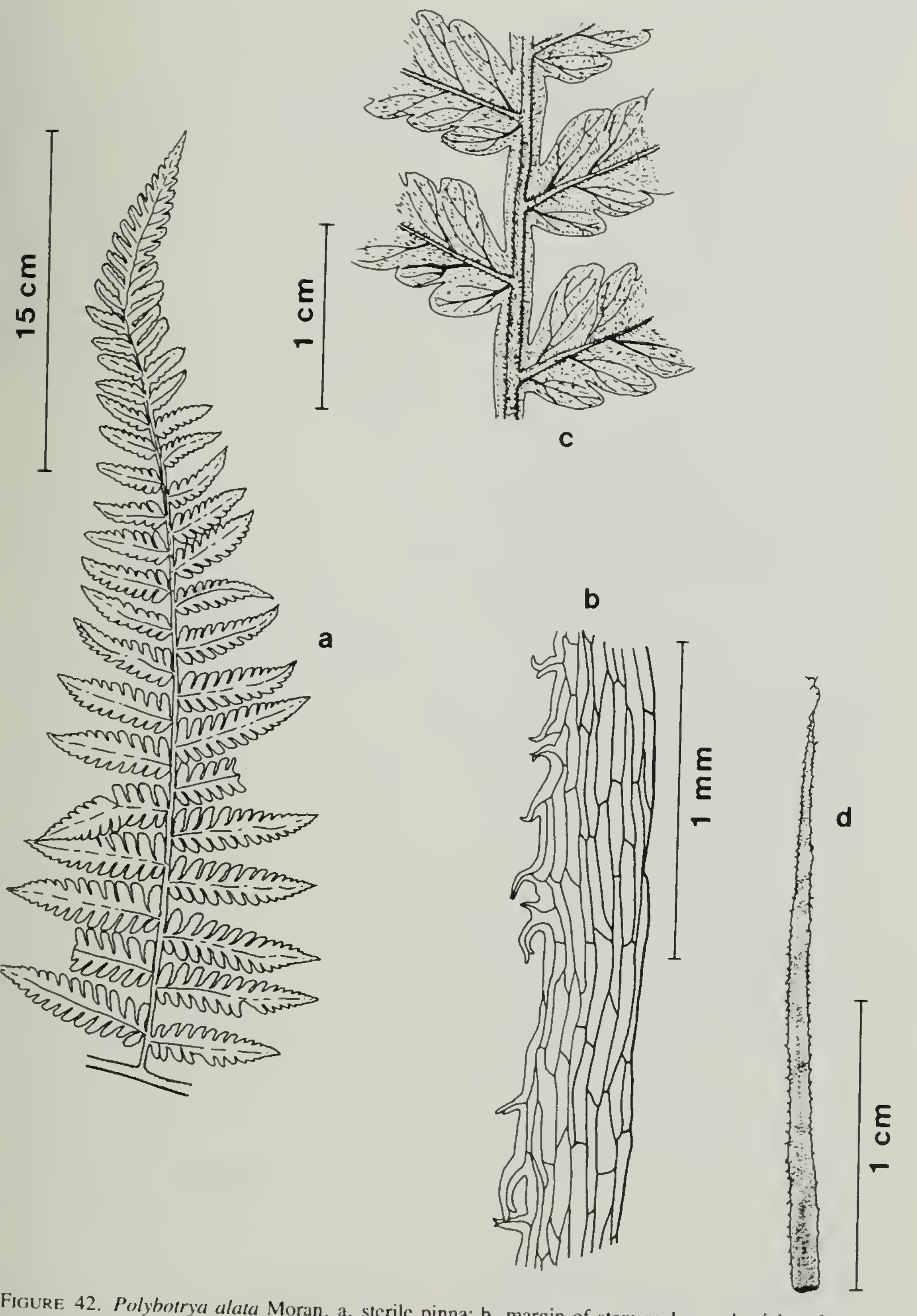

FIGURE 42. *Polybotrya alata* Moran. a. sterile pinna; b. margin of stem scale; c. abaxial surface of distal pinnules (note pubescence and decurrent pinnule bases); d. stem scale. a–d: *Croat 22706* (MO).

24. Polybotrya aequatoriana Moran, *sp. nov.* (Fig. 43, Map 15).

Polybotrya aequatoriana Moran, *sp. nov.* Type: Ecuador. Napo: Cordillera Oriental, camino Baeza–Tena, 34 km al sur de Baeza, 2100 m, 30 de diciembre 1983, *Moran 3512* (holotype: F!; isotypes: AAU!, COL!, GH!, LPB!, MO!, NY!, Q!, QCA!, UC!).

Caulis hemiepiphyticus, 1.5–3.4(4.0) cm diam.; squamis sordide aurantiaco-luteis, nitidis, membranaceis, implexis, lanatis, in margine minute denticulatis, 1–2(3) × 12–20(25) mm; lamina lanceolata, usque ad 1.4 × 0.7 m, 2-pinnata-pinnatifida, modice vel sparse puberula subter, pilis appressis, 0.1–0.3 m longis; pinnae longideltatae, 25–35 × 13–18(20) cm; pinnulae catadromicae, acroscopice prolongatae, basiscopice valde obliquae; lobi integri vel vade crenati; rhachis et costae pubescentes, pilis rigidis albidis, sulcis profundis pubescentibus. Pinnulae fertiles lineares, vulgo 4–6 × 0.5–1.0 cm, segmentis oppositis vel suboppositis circularibus vel oblongis, 3–5 × 1–2 mm.

Stem 1.5–3.5(4) cm thick, hemiepiphytic; *scales* dingy orange yellow, mostly darkening upon drying, shiny, membranous, tangled and woollike, the margins minutely denticulate, 1–2(3) × 12–20(25) mm. *Sterile leaves* up to 1.6 m long; *lamina* lanceolate, to 1.4 × 0.7 m, 2-pinnate-pinnatifid, moderately to lightly pubescent below, the hairs fine, appressed, 0.1–0.3 mm long, grading into scales along the axes, often with a few scattered resinous, circular glands (use at least 30 ×), the margins somewhat thickened and lighter colored, often becoming revolute upon drying; *pinnae* long-triangular, 25–35 × 13–18(20) cm; *pinnules* arranged catadromically above the base, prolonged acroscopically, reduced and very oblique basiscopically; *lobes* entire or rarely shallowly crenate; *axes* pubescent below with unevenly scattered, whitish, erect hairs 0.1–0.2 mm long, scaly by linear, flexuous, darkened, often appressed scales, these most abundant at the junctures; *grooves* deep and distinct, filled with hairs, these sometimes clavate, ca. 0.1 mm long, reddish, the ridges well defined, stramineous, continuous with those of the costules but truncated by the ridges of the rhachis. *Fertile leaves* botryoid; *pinnules* linear, mostly 4–6 × 0.5–1.0 cm; *sori* arranged oppositely or suboppositely, round to oblong; *sporangial stalks* paraphysate; *spore size* unknown.

Polybotrya aequatoriana occurs in the cloud forests of Ecuador and Bolivia (Map 15), from 2100–2410 m, the highest known altitudinal range of any species of *Polybotrya*. *Polybotrya aequatoriana* is named for Ecuador, where I collected the type.

Polybotrya aequatoriana can be easily separated from *P. hickeyi* and *P. appressa* by its stem scales, which are thin, yellowish orange, and membranaceous (Fig. 43b); see *P. appressa* for further comparison with that species. *Polybotrya aequatoriana* has highly reduced basiscopic lobes on the sterile pinnules (Fig. 43c), and the fertile pinnules are much narrower than those of other congenerics.

Specimens examined: Ecuador. **Napo:** Cordillera Oriental, camino Baeza–Tena, 34 km al sur de Baeza, 2100 m, *Moran 3512* (AAU, COL, F, GH, LPB, MO, NY, Q, QCA, UC), *3585* (F, Q, QCA); road Baeza–Lago Agrio, ca. 114 km from Lago Agrio, 1750 m, *Øllgaard et al. 35776* (AAU, QCA).

Bolivia. **La Paz:** Prov. Sud Yungas, Huancane, 7.5 km hacia el sud sobre el camino nuevo, 2410 m, *Beck 3108* (LPB); same locality, but at 6.5 km, 2280 m, *Beck 3060* (LPB, NY).

25. Polybotrya appressa Moran, *sp. nov.* (Fig. 44, Map 17).

Polybotrya appressa Moran, *sp. nov.* Type: Ecuador. Napo: Cordillera Oriental, camino Baeza–Tena, 34 km al sur de Baeza, bosque virgen, 2100 m, 24 de enero 1984, *Moran 3586* (holotype: F!; isotypes: GH!, MO!, NY!, Q!, QCA!, US!).

Caulis hemiepiphyticus, 1–2 cm diam.; squamae concolores, obscure brunneae, integrae, appressae, vulgo 1–2 × 0.1–0.2 cm; lamina ovata vel late deltata, 2-pinnata-pinnatifida, superne glabra, inferne pilosa, pilis dispersis, ca. 0.1 mm longis; pinnae usque ad 37 × 18 cm; pinnulae prolongatae acroscopice, latis basiscopicis reductae; lobis rotundatis vel plusminusve truncatis; rhachis et costae aequaliter pubescentes, pilis usque ad 0.1 mm longis, sulcis glabris. Folia fertilia ignota.

Stem 1–2 cm thick, hemiepiphytic; *scales* concolorous, dull brown, thick, opaque, entire,

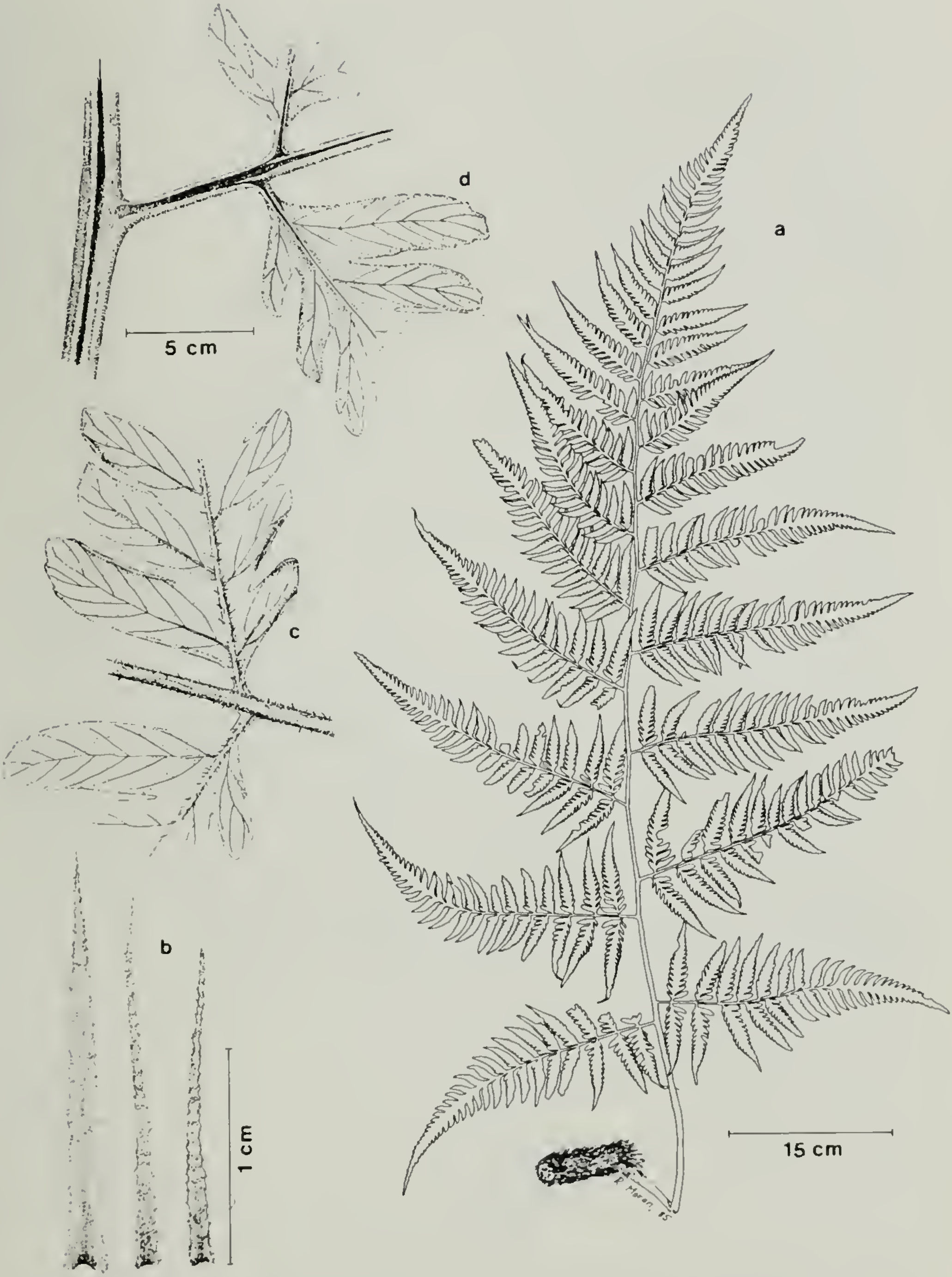

FIGURE 43. *Polybotrya aequatoriana* Moran. a. sterile leaf; b. stem scales; c. costa and pinnule bases, abaxial view (note only scattered hairs); d. rhachis, costa, pinnule bases, adaxial view, groove minutely pubescent, thin. a–d: *Moran 3512* (F).

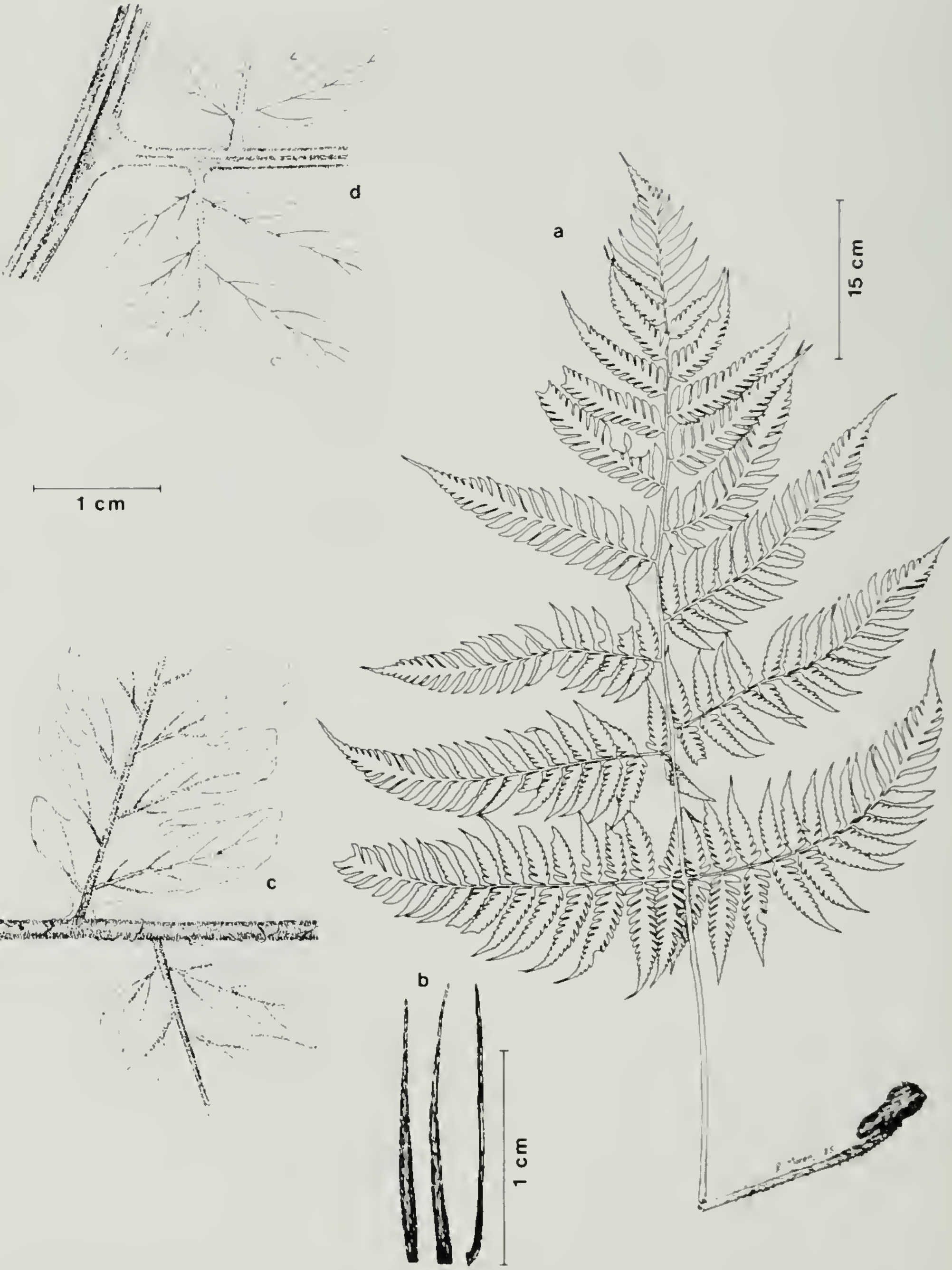

FIGURE 44. *Polybotrya appressa* Moran. a. sterile leaf; b. stem scales; c. costa and pinnule bases, abaxial view; d. costa and pinnule bases, adaxial view. a–d: *Moran 3586* (F).

appressed, mostly 1–2 × 0.1–0.2 cm. *Sterile leaves* up to 1.5 m long; *lamina* ovate to broadly deltate, dark green above, slightly paler below, 2-pinnate-pinnatifid, up to 1.3 × 0.74 m, glabrous adaxially, abaxially with a few scattered, appressed hairs, these less than 0.1 mm long, intergrading with scales on the costae; *pinnae* to 37 × 18 cm, widest at the base, the apex long-tapering, the acroscopic basal pinule usually prolonged beyond the rest; *pinnules* arranged catadromically, prolonged acroscopically and reduced basiscopically at the base, the proximal ones with acuminate apices, the distal ones with falcate and truncate apices; *lobes* rounded to somewhat squarish, entire or rarely minutely serrate at the apex; *axes* evenly pubescent abaxially, the hairs short, less than 0.1 mm long, the costal scales present or caducous and absent, linear to lanceolate, appressed, light brown, thin; *grooves* sparsely pubescent within, not very deep or prominent, bordered by broad, shallow ridges, not admitted to the groove of the next lower order. *Fertile leaf* unknown.

Polybotrya appressa is known only from the eastern Andes of Ecuador (Map 17), where it grows in cloud forests at high elevations. This new species is named for its distinctive, appressed stem scales (Fig. 44b), which help separate it from similar species, many of which have spreading, membranous stem scales. *Polybotrya caudata* has similiar dull, thick, opaque stem scales, but that species does not grow at high elevations.

Polybotrya appressa differs from *P. aequatoriana*, a closely allied Ecuadorian species, by its stem scales, groove architecture and pubescence, and lamina shape. *Polybotyra hickeyi* is also very closely related, especially by its short, even, abaxial, costal pubescence, and the indistinct adaxial grooves that are glabrous within; but it differs primarily by its more finely cut lamina. In addition, the lamina of *P. appressa* is dark green, in contrast to the pale yellowish green laminae of *P. hickeyi* and *P. aequatoriana*.

Specimens examined: ECUADOR. **Napo:** Cordillera Oriental, camino Baeza–Tena, 34 km al sur de Baeza, Bosque virgen, 2100 m, 24 de enero 1984, *Moran 3586* (F, GH, MO, NY, Q, QCA, US); Cordillera Oriental, 5 km al sur de Cosanga, camino Baeza–Tena, 1000 m, 4 de enero 1984, *Maran 3527* (Q, QCA); Cerro Huacamayos, on road Baeza–Tena, ca. 34 km from Baeza, *Øllgaard et al. 53824* (AAU, QCA).

26. **Polybotrya altescandens** C. Chr. (Fig. 45, Map 12).

> *Polybotrya altescandens* C. Chr., Index Filicum 7. 1905. *nom. nov.* for *Acrostichum chrysolepis* Sodiro, *non* Fée 1869.
>
> *Acrostichum chrysolepis* Sodiro, [Anal. Univ. Quito (XI)77:561. 1894.] Crypt. Vasc. Quit. 485. 1893. *nom. illeg.*, *non* Fée 1869. TYPE: Ecuador. Pichincha: selva tropical, de Pilaton-Toachi, septiembre 1892, *Sodiro s.n.* (holotype: P!).

Stem (1)2–3(4) cm thick, hemiepiphytic; *scales* golden to yellowish, mostly concolorous, shiny, tangled and forming a dense "wool" around the stem, linear, 0.6–1.3 × 15–25(32) mm, base cordate and darkened at the point of attachment. *Sterile leaves* up to 2 m long; *lamina* to 1.65 m long, lanceolate, to 2-pinnate-pinnatifid or rarely 3-pinnate, usually moderately pubescent, the hairs fine, appressed, more or less cylindrical, multicellular, 0.2–0.4 mm long, intergrading with scales on the costa; *pinnae* evenly tapering to a truncate base, the acroscopic side slightly prolonged, especially in the distal pinnae, 14–25(35) × 3–10(17) cm, soon becoming pinnatifid in the distal portions; *pinnules* anadromous or subequal proximally, catadromous distally, entire to coarsely serrate, the basal acroscopic one almost always conspicuously prolonged beyond the others; *axes* pubescent abaxially, the hairs subulate, colorless, 0.1–0.2 mm long, unicellular, the scales few, scattered, denticulate; *grooves* slightly pubescent within, those of the costule decurrent into those of the costa, costal groove gradually becoming shallow and expanded before the juncture with the rhachidial groove; *veins* in pinnate groups, in large pinnae and pinnules the lowermost basiscopic veinlet often springing directly from the costa or costule, appearing as a single isolated veinlet between the main pinnate groups. *Fertile leaves* 3-pinnate, pubescent by jointed hairs 0.5–1.0 mm long, these grading into linear, tortuous scales; *sori* obovate or oblong; *sporangial stalks* paraphysate; *spores* (54)59–69(72) microns long. $n = 41$.

This species has an altitudinal range of (800)1200–2500 m. Most of the collections come from the western cordillera of Ecuador, but two apparently disjunct locations occur in Colombia

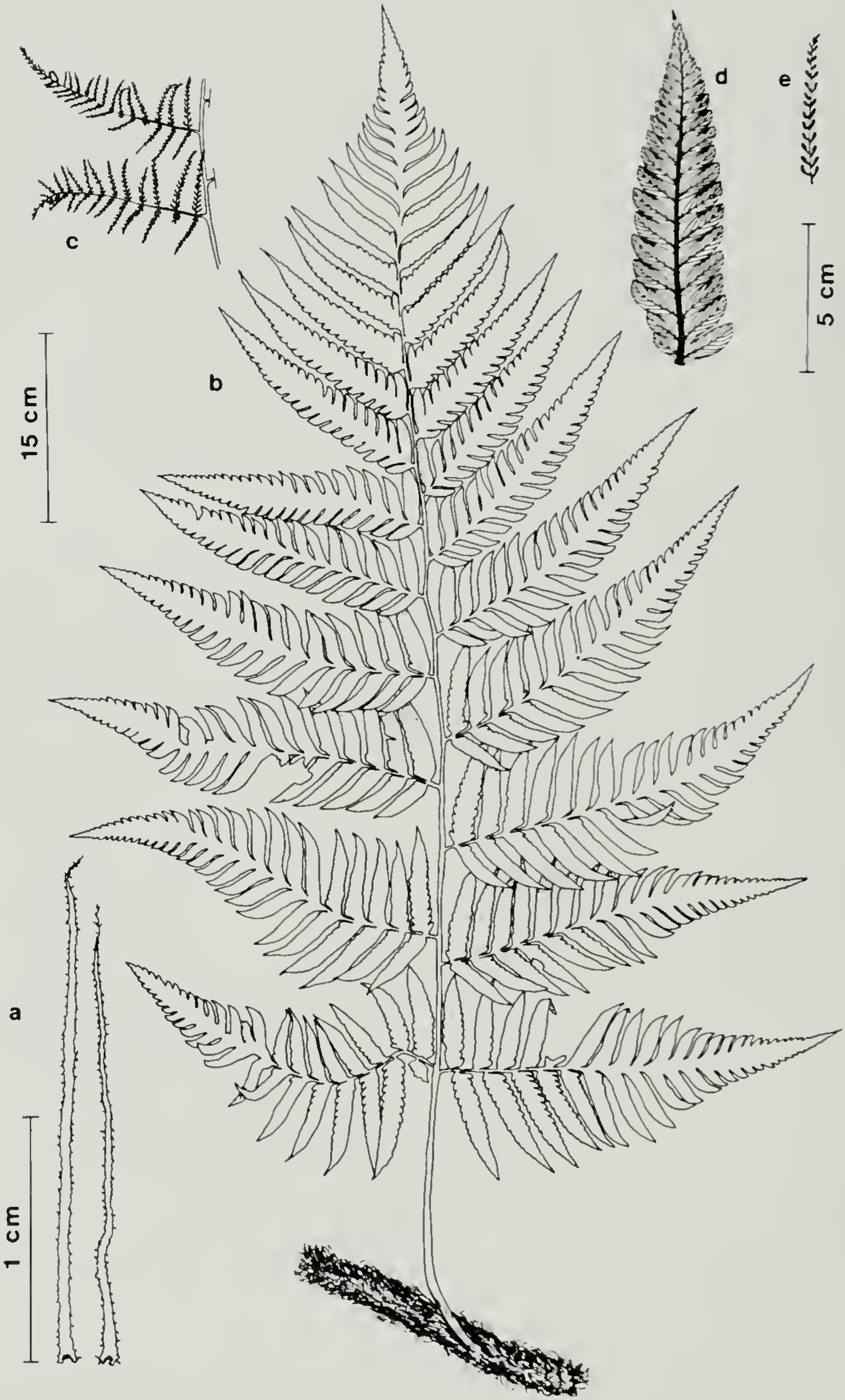

FIGURE 45. *Polybotrya altescandens* C. Chr. a. stem scales; b. fertile leaf; c. fertile pinnae; d. sterile pinnule (note isolated veinlet between the main pinnate groups); e. fertile pinnule (note obovate segments). a,b: *Moran 3559* (CR). c,e: *Rimbach 91* (F). d: *Steyermark 52812* (F).

and Peru (Map 12). I suspect that this species occurs in many other valleys of the Colombian and Peruvian Andes, and that lack of collecting accounts for the apparent disjunctions. My field experience in Ecuador showed this species to be quite common in the western cordillera but absent from the eastern cordillera.

Polybotrya altescandens can be immediately recognized by its bright golden to yellowish scales that thickly cover the stem. These scales are longer and narrower than those of any other species of *Polybotrya* (Fig. 45a). The lamina is less cut than that of similar Andean species, and the pinnae soon become pinnatifid in their distal portions, a characteristic that further accentuates this less-divided look. The sori are usually clavate or short-oblong, in contrast to the more elongated sori of other species (Fig. 45c). An unusual tendency of the venation further distinguishes this species: in large pinnae and pinnules the lowermost basiscopic vein migrates onto the costa or costule and therefore appears as a single isolated veinlet between the main pinnate groups (Fig. 45d).

Specimens examined: COLOMBIA. **Antioquia:** bosque bajo la cumbre cerca de Boquerón, camino entre Medellin y Palmitas, 2300–2500 m, *Hodge 6592* (GH).

ECUADOR. **Azuay:** rich dense jungle between Chacanceo and Río Blanco, on road to Molleturo, between Río Putucay and Río Norcay, 1220 m, *Steyermark 52812* (F). **Carchi:** environs of Maldonado, 1450 m, *Madison et al. 4851* (F). **Chimborazo:** mountains in Sacramento area, *Wiggins 11073* (NY). **Cotopaxi:** road between Quevedo and El Corazón, 6.4 km NW of El Corazón, 67.5 km SE of Quevedo, *Croat 55844* (MO). **Guayas:** valley of Río Chimbo, 800 m, *Rimbach 91* (F, US). **Imababura:** in the vicinity of the Río Verge, ca. 5 km SW from the village of Mani, Río Cachaco, 1300 m, *Sperling & Bleiweiss 5034* (GH, Q, QCA). **Pichincha:** tropical forest de Pilaton-Toachi, September 1892, *Sodiro s.n.* (P); road El Paraiso–Saguangal, 11 km from El Paraiso, *Øllgaard et al. 37702* (AAU), *37867* (AAU); road El Paraiso–Saguangal, 3 km from El Paraiso, 1500 m, *Øllgaard et al. 37820* (AAU); selva topical, Valle de Nanegal, *Sodiro s.n.* (P, US); Mindo, *Sydow 339* (US); road from Sto. Domingo de los Colorados to Aloag, 2.5 km E of Cornejo Astorga, 1200 m, *Moran 3544* (F, GH, Q, QCA); Tinalandia Resort, ca. 25 km E of Sto. Domingo de los Colorados, N side of Río Toachi, 1000 m, *Moran 3559* (CR, F, GH, NY, Q, QCA); ca. 30 km WNW of Quito, 67 km on road to Mindo, 2200 m, *Moran 3564* (F, Q, QCA, US). **Province unknown:** western cordillera, 800 m, forest region, *Rimbach 312* (US); without locality, *Jameson 33* (P).

PERU. **Huánuco:** La Divisoria, ca. 25 km NE of Tingo María, *Moran 3688* (F, GH, MO, USM). **Loreto:** Prov. Coronel Portillos, Dtto. Padre Abad., divisoria cerca al Río Chino, *J. Schunke 10200* (MO).

27. **Polybotrya gomezii** Moran, *sp. nov.* (Fig. 46, Map 14).

> *Polybotrya gomezii* Moran, *sp. nov.* TYPE: Costa Rica. Alajuela: ca. 20 km N of San Ramón, at the Univ. of San Ramón's Biological Field Station, 1100 m, cloud forest, 17 July 1983, *Moran 3241* (holotype: CR!; isotypes: F!, GH!, MO!, NY!, UC!, US!).

Caulis hemiepiphyticus, 1–2 cm diam.; squamae appressae vel ascendentes, brunneae, obscurae, opacae, anguste lanceolatae, vulgo 10–20 × 1–2 mm, marginibus vulgo integris; lamina usque ad 1.5 × 0.75 m, ovata vel deltata, admodum glabra, 2-pinnata-pinnatifida, coriacea, inferne anadromica, superne catadromica; pinnae usque ad 45 × 20 cm, anguste deltatae, apicibus longiacuminatis; pinnulae usque ad 12 × 2.5 cm, acroscopice leviter prolongata. Folia fertilia usque ad 0.75 m, 3-pinnata; sporae (50)54–60(64) micrometralae.

Stem 1–2 cm thick, hemiepiphytic; *scales* appressed to spreading, dull brown, opaque, thickened in the middle, narrowly lanceolate, 10–20 × 1–2 mm, margins entire or with a few apical denticulations. *Sterile leaf* up to 1.5 m long; *lamina* up to 1.2 × 0.75 m, 2-pinnate-pinnatifid or very rarely 3-pinnate, coriaceous, ovate-triangular, nearly glabrous, usually anadromic below, becoming catadromic in the distal one-third, the change from anadromic to catadromic marked by a small, reduced, basiscopic pinnule or segment; *pinnae* up to 45 × 20 cm, narrowly triangular, the apex long acuminate, the lower ones pinnatifid in the apical third, giving a broadened appearance to the pinnae; *pinnules* up to 12 × 2.5 cm, apex of proximal ones acuminate to long acuminate, gradually becoming curved and then truncate in the pinnatifid apex, the base inequilateral with the acroscopic side slightly more developed, the margins serrate to pinnatifid; *axes* usually glabrous abaxially or with unicellular, fine, whitish hairs, scaly, the scales caducous, appressed, up to 2 mm long, light brown, with a long narrow apex; *grooves* mostly glabrous within or nearly so, sometimes

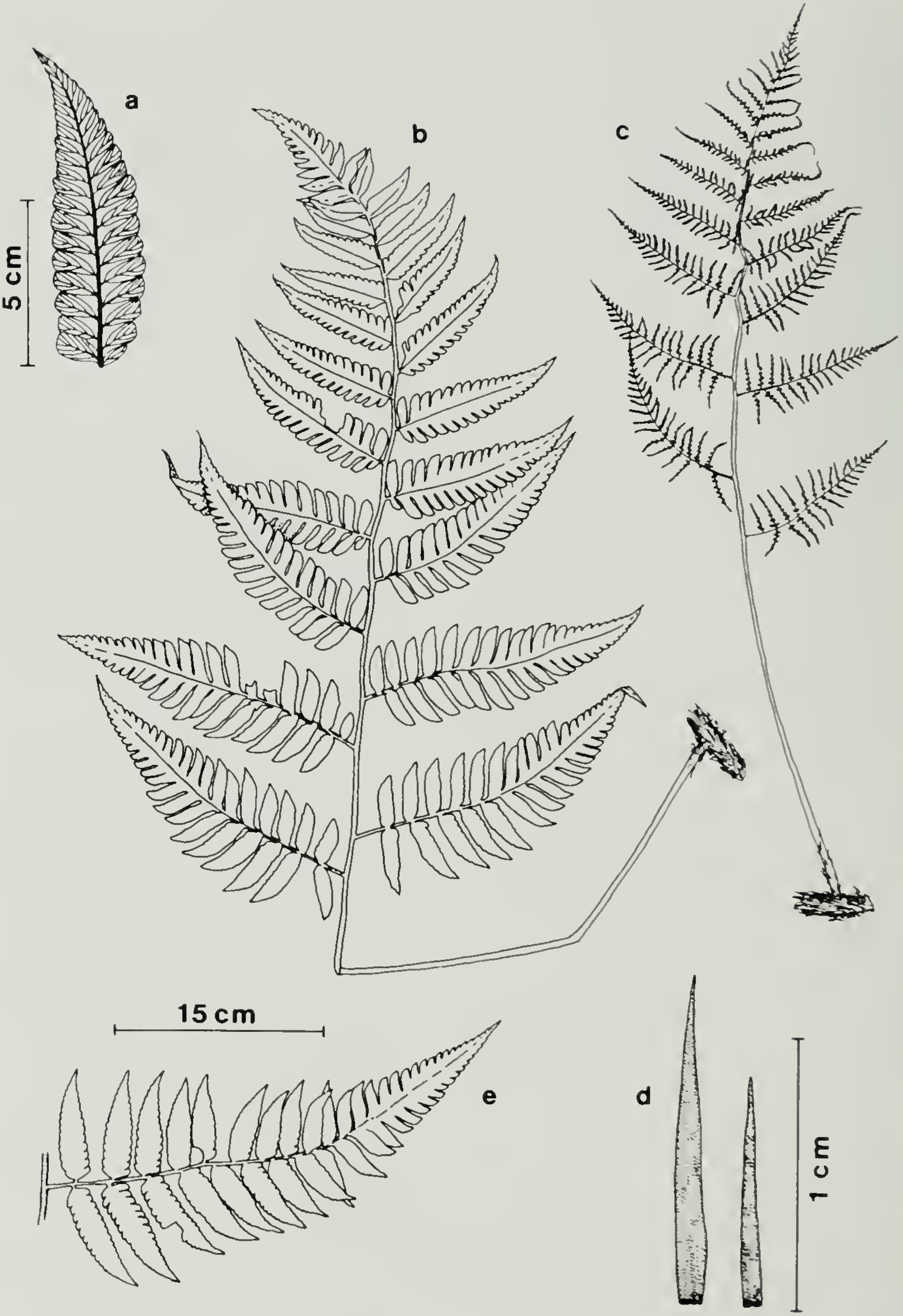

FIGURE 46. *Polybotrya gomezii* Moran. a. acroscopic basal pinnule, pinnae apex toward the left (note catadromous venation); b. sterile leaf (note that the transition zone from anadromic to catadromic is marked by reduced basiscopic pinnules); c. fertile leaf; d. stem scales; e. basal pinna. a,d: *Moran 3241* (CR). b,e: *Moran 2441* (F). c: *Lent 3537* (F).

pubescent at the junctures, the hairs short, less than 0.1 mm long and inconspicuous. *Fertile leaves* up to 0.75 m long, 3-pinnate, coenosoric; *axes* with scattered scales similar to those on the sterile leaf, junctures pubescent, the hairs numerous, short, less than 0.2 mm long; *sporangial stalks* paraphysate; *spores* (50)54–60(64) microns long.

This species is named in honor of Luis D. Gómez P., pteridologist, formerly at the Museo Nacional de Costa Rica, who has encouraged my study of *Polybotrya* and extended much hospitality during my thesis research in Costa Rica. *Polybotrya gomezii* is endemic to Costa Rica (Map 14), where it occurs from sea level up to 1500 m, reaching its greatest frequency and abundance in cloud forests. Most of the specimens were collected in the mountains around San José. I found *P. gomezii* at five localities, always with *P. alfredii*; no hybrids were found.

This species can be distinguished from others in Central America by its nearly glabrous, only 2-pinnate-pinnatifid leaves, and the nearly glabrous axes. The pinnae soon become pinnatifid in the apical half, which also gives a more broad, less finely cut appearance to the leaf (Fig. 46b). The opaque, dull brown stem scales with entire or sparsely denticulate margins (Fig. 46d) also help separate this species from others found in Costa Rica. The veinlets of the pinnules are always arranged catadromically, even in pinnae having the pinnules arranged anadromically. This ordering is unusual because the disposition of the veinlets usually reflects the pinnule arrangement; that is, if the pinnules are anadromic, the veinlets are also anadromic.

Specimens examined: COSTA RICA. **Alajuela:** ca. 20 km N of San Ramón, at the Univ. of San Ramón's Biological Field Station, cloud forest, *Moran 3241* (CR, F, GH, MO, NY, UC, US); forest between Quebrada Quicuyal and Quebrada Arrayanes, Cariblanco, *Lent 3537* (F). **Cartago:** near Alto Patillos, *Moran 2441* (CR, F, GH, MO, NY, US); cloud forest near the entrance to Parque Nacional Tapantí, 1270 m, *Moran 3338* (CR, F, GH, NY, US); 3 km SE of Tapantí, lower slopes of Alto Patillos, *Lent 1084* (F); La Hondura, 1400 m, *Valerio s.n.*, (CR); Navarro, 1400 m, *Wercklé s.n.* (GH, P). **Heredia:** about 10 km on the road towards Virgen de Socorro, 1000 m, *Moran 3160* (CR). **Puntarenas:** Monteverde Cloud Forest Reserve, 1560 m, *Fiedler & Koptur 51* (UC). **San José:** Parque Nacional Braulio Carrillo, ca. 1 km along road from entrance, *Moran 3271* (CR).

28. Polybotrya osmundacea Willd. (Figs. 47 & 48, Map 18).

Polybotrya osmundacea Willd., Species Pl., ed. 4, 5:99. 1810. TYPE: Venezuela. Monagas: Caripe, *Humboldt 459a* (fertile), *459b* (sterile), Herb. Willd. 19507-1, 19507-2 (holotype: B; photos F!, GH!).

Acrostichum osmundaceum (Willd.) Hooker, Species Filicum 5:246. 1864.

Polybotrya aristeguietae Brade, Bradea 1:19, tab. 1. 1969. TYPE: Venezuela. Miranda: Santa Teresa-Altogracia de Orituco, June 1953, *Aristeguieta 1780* (holotype: VEN!).

Polybotrya vareschii Brade, Bradea 1:20, tab. 2. 1969. TYPE: Venezuela. Aragua: Rancho Grande, Dependiente Norte, selva nublada, 800 m, *Vareschi & Gessner 1875* (holotype: VEN!).

Stem 1–2.5(4) cm thick, hemiepiphytic; *scales* extremely variable, with plants from Amazonia tending to have thick, opaque, dark brown, subentire, somewhat squarrose scales and plants from elsewhere tending to have shiny, ascending, spreading, bicolorous scales, often with a dark central stripe and lighter borders, margins highly erose or, less commonly, denticulate, mostly 1.0–2.2 × 0.8–1.9(2.3) cm. *Sterile leaves* up to 1.8 m long; *lamina* deltate, ovate, or lanceolate, to 3-pinnate-pinnatifid, chartaceous, rarely with scattered, round, sessile, resinous glands on the abaxial surface, the margins glabrous; *pinnae* narrowly deltate, equilateral, (7)13–18 pairs; *pinnules* arranged anadromically or rarely catadromically (Peru), up to 14 × 4 cm, the largest deeply cut at the base, apex acuminate; *basal acroscopic tertiary segments* ovate, lanceolate or rhombic, margins entire, crenate or lobed, the apex often serrulate; *axes* glabrous or pubescent abaxially, the hairs whitish, 0.2–0.5 mm long, the scales absent or few and inconspicuous; *grooves* decurrent into those of the next lower order, usually filled with short, less than 0.7 mm long, reddish or brownish hairs. *Fertile leaves* to 3-pinnate-pinnatifid, deltate, coenosoric; *sporangial stalks* paraphysate; *spores* (50)54–62(66) microns long.

Other illustrations: See original descriptions of *P. aristeguietae* and *P. vareschii*; Humboldt et al., Nov. Gen. Sp. Pl., tab. 2. 1815; Proctor, Ferns of Jamaica, fig. 107. 1985.

FIGURE 47. *Polybotrya osmundacea* Willd. a. sterile leaf (Costa Rica); b. stem scale, dark, opaque type (Amazon basin of Ecuador); c. stem scales, thin, transparent type (Andes of Colombia); d. sterile pinnule (northern Venezuela); e. sterile pinnule, same scale as d (Costa Rica); f. basal pinnae of fertile leaf, same scale and plant as a (Costa Rica); g. two basal tertiary segments (Colombia); h. rhachis-costa juncture; note decurrent axial grooves (Ecuador). a,f,e: *Moran 2167* (F). b: *Moran 3547* (F). c,g: *Killip & Smith 15341* (US). d: *Vareschi & Gessner 1875* (VEN). h: *Moran 3592* (F).

Polybotrya osmundacea, the type species of the genus, is one of the most widely distributed species of *Polybotrya* (Map 18). It occurs in wet, shaded forests from sea level to 2100 m. The specific epithet refers to the fancied resemblance of the fertile leaves to the fertile apex of *Osmunda regalis* (Willdenow 1810).

This species varies tremendously in scales, cutting, and pubescence. In plants from Amazonia, the scales are usually thick, dark, opaque, more or less squarrose, and not thickly investing the stem so that the yellowish stem aerophores are easily visible in fresh material (Fig. 47b). Plants from other parts of the range may be similar, but more often the scales are thin, lighter colored, transparent, often bicolorous, and more thickly investing the stem (Fig. 47c). The stem scales, however, do not correlate with any other characteristics.

Laminar cutting is another variable characteristic. The type specimens of *P. aristeguietae* and *P. vareschii*, both collected in northern Ven-

FIGURE 48. Geographical variation in the pinnule cutting of *Polybotrya osmundacea* Willd. The elongated side of the pinnule is always acroscopic. Clockwise, starting from Bolivia: *Buchtien 298* (UC); *Killip & Smith 23991* (F); *Moran 3642* (F); *Moran 3618* (PORT); *Lellinger & de la Sota 213* (COL); *Moran 2167* (CR); *H. Smith 1050* (US); *Vareschi & Pannier 1686* (US); *Killip & Lasser 37756* (US); *Murillo 2580* (F); *Broadway 5589* (F); *Steyermark 107148* (MO); *Granville 3865* (CAY); *Berg et al. P18138* (NY).

ezuela, scarcely differ from each other in cutting. These two specimens, however, seem to differ from *P. osmundacea* elsewhere in its range by their less-cut leaves (Fig. 47d; Fig. 48, pinnules from northern Venezuela). From the greater number of specimens available to me, it appears that these extremes of cutting are connected by intermediates and that no other characters correlate with these extremes. Accordingly, I have placed *P. aristeguietae* and *P. vareschii* in synonymy with *P. osmundacea*.

Specimens examined: Guatemala. **Izabal:** vicinity of Quiriguá, *Standley 24195* (NY, US).

Honduras. **Prov. unknown:** near Lake Yojoa, *Steeves & Ray 504* (GH, US); near Cockscomb Mts., *Schipp 8101* (US); Maya Mounds, *Schipp 8108* (F).

Nicaragua. **Comarca del Cabo:** 40–50 km SW of Waspán, *Atwood 3711* (VT). **Zelaya:** Cerro la Pimienta, no. 1, summit area, *Pipoly 5146* (CR); costado S del Cerro La Pimienta, *Grijalva 300* (CR).

Costa Rica. **Cartago:** forests of Las Vueltas, Tucurrique, *Tonduz 13337* (US), *18879* (US); forests of Tuis, *Pittier 12416* (CR, US); Aragón, *Pittier 9076* (Z); Chitaría, *Valerio 328* (US); Chitaría, forest near old jailhouse, *Moran 2167* (CR, F); Turrialba, Aragon, *Tonduz 9006* (US), *9016* (US); vicinity of Pejivalle, *Skutch 4637* (CR, US); Peralta, *Lankester s.n.* (US); vicinity of Pejivalle, *Standley & Valerio 47127* (US); Turrialba, Instituto Interamericana, Ganadería, *Croat 690* (MO), *738* (MO); Florecia, Turrialba, *Jiménez 3299* (F), *3304* (CR, F); Reventazón below Turrialba, *Hatch 90* (F); Turrialba, *Pittier 9016* (Z); 3 km W of Turrialba, *Mickel 2624* (LP, NY); Turrialba, near the Interamerican Inst., *Scamman 7152* (GH), *7687* (GH); Turrialba, *Lent 299* (GH); valley of Río Reventazón, 3 km SE of Turrialba, *Holm & Iltis 200* (MICH). **Cocos Island:** *Stewart 241* (US); *Fisher s.n.* (US); *Klawe 1474* (US), *1504* (US). **Limón:** SW of Siquirres, on road to Turrialba between Moravia and Guayacán 1 km of Guayacán, *Lellinger & White 1436* (F, US); near banana plantation and Pandora, Río Estrella, *Rossbach 3628* (GH); Los Diamantes, USDA Rubber Plant Station, *Scamman 5987* (GH), *7153* (GH); hills of Atlantic slope, *Tonduz 14568* (P); vicinity of Guápiles, *Standley 37096* (US). **Puntarenas:** Coto, at sea level, *Valerio 333* (F); San Vito, *de la Sota 5181* (LP); Finca Loma Linda 1 mi SW of Cañas Gordas, *Croat 22260* (MO); road to Puerto Jimènez, Osa, 40 km W of I.A. route 2, *Gómez 19489* (CR, UC); Osa Peninsula, 15 km S of Tropical Science Center field station and ca. 20 km S of Rincón de Osa, *Mickel 2803* (NY), *2817* (NY); Finca Las Cruces, San Vito de Java, *Burch 4613* (MO, NY); ca. 10 mi. SE of Rincón de Osa along road to Pacific, *Evans & Bowers 2792* (MO). **San José:** vicinity of El General, *Skutch 3018* (F, MO); San Isidro de El General, *Scamman 5984* (GH).

Panama. **Chiriquí:** 10–11 miles W of Puerto Armuelles in vicinity of San Bartolo Limite, *Croat 21987* (MO); vicinity of Gualaca ca. 10.7 miles from Planes de Hornito, La Fortuna on road to dam site, *Antonio 5133* (MO, UC); 4.5–5.0 km N of dam over Fortuna Lake, *Croat & Grayum 60022* (MO); Fortuna Dam area, Quabrada Bonito to N of reservoir, *Churchill 5776* (MO). **Darién:** vicinity of airstrip at Caña gold mine, *Croat 38047* (MO). **Panamá:** Cerro Jefe, near summit, *Croat 22682 (MO)*.

Cuba. **Oriente:** Sierra Maestra on ascent from Río Yara, *Ekman 14210* (US); Bahía de Taco, on the ridge below Santa María and Río Jiguaní on the path to the "Iberia" mines, *Ekman 3769* (NY); Trail Navas to Camp Buena Vista, *Shafer 4458* (NY); La Perla, *Maurel & Maurel 3816* (NY); La Perla, *Shafer 8889* (NY); near Monte Verde, *Wright 786* (BM, F, GH, MO, NY, PH, UC, US); *Eggers 5324* (F); Finca Guadalupe, Placetas, Las Villas, *Acuña 17531* (US); Sevilla Estate, near Santiago, trail from Magdalena to Sierra Maestra, *Taylor 447* (NY); Loma del Gato and vicinity, Sierra Maestra, *Hioram & Clement 6424* (GH, US); La Prenda, *Hioram 2495* (COL, P, US, UC); Santiago, Loma del Gato-Cobre, *Clement 725* (US).

Jamaica. **Clarendon:** "Second Breakfast Spring" below Tweedside, *Underwood 1612* (NY). **Portland:** Dollwood, *Watt 160* (GH, P, US), *7276* (BM); Mabess River, below Vinegar Hill, *Underwood 1323* (NY); trail from Vinegar Hill to Mabess River, *Underwood 1246* (NY), *1250* (NY); Mabess, *Fisher 132* (NY); Blue Mts., Stony River to Macungo River, *Morely & Whitefoord 655* (BM), *675* (BM); Blue Mts., Stony River Base Camp, *Morely & Whitefoord 695* (BM, MO); John Crow Mts., E slope, 1.5 mi SW of Ecclesdown, *Wilson & Webster 549* (MICH); above Moore Town, *Clute 259* (NY, US); valley of the Río Grande, 8 air miles S of Port Antonio, *Gastony 43* (GH); vicinity of Thomsons Gap, *Maxon & Killip 756* (F, GH, NY, US); Spur of John Crow Mts. opposite Mill Bank, *Maxon 9366* (GH, NY, PH); vicinity of Mill Bank, *Maxon & Killip 148* (F, GH, NY, US); along trail to waterfall N of Hardwar Gap, *Proctor 16506* (MO), *22269* (GH). **St. Andrew:** Blue Mts. near Cinchona, 15 km from Kingston, *Fisher s.n.* (P); Catherine Peak, *Faull 12583* (GH). **St. Ann:** Blue Mts., Trafalgar, *Perkins 1163* (GH). **St. Catharine:** vicinity of Hollymount, Mount Diablo, *Maxon 2293* (NY, US). **St. Thomas:** Mansfield and adjoining properties, near Bath, *Maxon 2470* (NY, US); Manchester Blue Mt., *Day s.n.* (NY); forested ridge E of Cuna Cuna Gap, *Maxon 9464* (NY, US); Bath, *Gilbert s.n.* (GH); upper southern slopes and summit of Maccasucker Bump, *Maxon 9522* (GH, NY, PH); SE slopes of Stone Hole Bump, *Maxon 8978* (GH, NY, PH); Corn Puss Gap and vicinity, trail W over Blue Mts., *Wilson & Murray 564* (BM, GH, MICH); Corn Puss Gap, *Proctor 3969* (PH, US).

Haiti. Massíf du Nord, Chavary, *Ekman 4734* (US); Camp Perrin, *Ekman 5214* (US).

Grenada. Grand Etang, *Beard 1252* (UC, US); no locality, *Fraser s.n.* (P); in Mirabeau Mts., *Broadway*

2520 (Z); St. Georges, Azimas, 1896, *Broadway s.n.* (NY); without locality, *Sherring 13* (BM).

Trinidad. Pass, Arima Valley, *Fleming & Fleming 52* (NY); no locality, *Fendler 69* (BM, F, GH, MICH, MO, NY, P, PH, UC); *Hart 229* (P); Mount Tocuche, *Britton et al. 1267* (GH, NY, US); Tacarigua Ward, El Tocuche, *Walker T10995* (BM); Morne Bleu, *Britton et al. 2276* (GH, NY, US); St. George, Blanchisseuse, Las Lapas trace, *Barnard et al. 411* (BM, MO); Blanchisseuse saddle, *Richardson 2037* (US); Blanchisseuse road, 11-mile post, *Broadway 6902* (F, MO, Z); Blanchisseuse road, 10-mile post, *Broadway 5589* (F, MO); Heights of Aripo, *Broadway 9948* (F, NY, US), *9950* (F, GH, NY, US), *9951* (GH, NY, US); Las Lapas road, *Broadway 6459* (BM); Arima–Blanchisseuse road, 13-mile post, *Jermy 11195* (BM), 9-10-mile post, *Jermy 2368* (BM); Morne Bleu ridge, *Jermy 2846* (BM); Arima–Blanchisseuse road, 10-mile post, *Fay 373* (BM); Maracas Valley, Las Cuevas trail, *Fay 345* (BM); 10.5 mi N of Arima, *Crosby 76* (MICH).

French Guiana. Sommet tabulaire, zone centrale, about 40 km SE of Saul, *Granville 3865* (CAY, Z).

Guyana. Region of Mt. Raywa, *Jenman s.n.* (NY).

Venezuela. **Anzoátegui:** Dtto. Bolívar, Fila El Gácharo, ridge of the fila above Los Chorros and El Cielo, Serranía de Turumiquire, *Davidse & González 19444* (MO). **Apure:** Reserva Forestal San Camilo, SW of caserío San Camilo (El Nula), *Steyermark et al. 101552* (US, VEN). **Aragua:** selva nublada de Rancho Grande, Dependiente Norte, *Vareschi & Gessner 1875* (VEN); Parque Nacional, Dos Ritos, *Killip & Lasser 37756* (US, VEN). **Barinas:** Dtto. Bolívar, along road from Barinitas to Mérida, near one land bridge at San Isidro, 30 km NW of Barinitas, *Moran 3718* (PORT, VEN); Dtto. Bolívar, San Isidro, ca. 5 mi NW of La Soledad along Barinas–Sto. Domingo road, *A.R. Smith et al. 1388* (PORT, UC, Z). **Distrito Federal:** virgin wet forest on slopes along old road between "Portachuelo" and "Penita" (Petaquire) and Carayaca, between Colonia Tovar–Junquito road and Hacienda El Limón, 6–8 mi below junction of Junquito–Colonia Tovar road, *Steyermark & Nevling 95930* (GH, VEN). **Falcón:** Cerro Azul, *Wingfield 6914* (VEN). **Falcón/Lara:** Cerro Socopa, *Liesner et al. 8359* (MO, VEN). **Lara/Yaracuy:** Dtto. Urdaneta y Bolívar, la fila Azul y Hda. El Jaguar, *Ortega & Smith 2387* (PORT); Sierra de Aroa, 10–13 mi NW of Urachiche (Edo. Yaracuy) along dirt road leading NW from Urachiche to Duaca (Edo. Lara), *A.R. Smith et al. 1347* (UC, PORT, Z). **Miranda:** Santa Teresa–Altogracia de Orituco, *Aristeguieta 1780* (VEN); Cerros del Bachiller, near E end of virgin evergreen forest, above Quebrada Corozal, S of Santa Cruz, 10 km (by air) W of Cupira, *Steyermark & Davidse 116499* (MO, UC, VEN). **Monagas:** Caripe, *Humboldt 459a,b* (P, photo F, GH); Cerro de Gáucharo, of Guácharo, *Steyermark 62015* (F). **Nueva Esparta:** Cerro Copey, *Sugden 1151* (UC). **Territorio Federal Amazonas:** Sierra Parima, vecinidades de Simarawochi, Río Matacuni, a unos 6–7 km al oeste de la frontera Venezolana–Brasilera, *Steyermark 107148* (MO, NY, VEN); Depto. Río Negro, 0–2 km E of Cerro La Neblina Base Camp on Río Mawarinuma, *Liesner 16133* (MO, UC); environs of Neblina Base Camp, *Plowman & Thomas 13678* (F, UC). **Sucre:** Península de Paria, Dtto. Mariño, camino Mundo Nuevo–Manacal, 18–20 km N de Irapa, *Dumont et al. 7439* (NY, VEN); alrededore de Manacal, *Murillo 2580* (F, NY, VEN); Península de Paria, Cerro de Humo, NE de Irapa, *Steyermark 94952* (F, GH, VEN); Península de Paria, arriba de Mundo Nuevo, oeste de Cerro de Humo, *Steyermark & Rabe 96145* (GH, VEN); Península de Paria, vicinity of Manacal 15 km (by air) NW of Irapa, *Steyermark & Liesner 120634* (MO, UC, VEN); Península de Paria, arriba de Mundo Nuevo, oeste de Cerro de Humo, *Steyermark & Rabe 71756* (VEN). **Táchira:** Dtto. Uribante, along road from La Siberia to entrance to Las Cuevas Represa, *van der Werff & González 5202* (MO, UC). **Yaracuy:** Dtto. Bruzual, selva siempreverde, Montaña de María Lionoza, Quebrada Quibayo, desde abajo hasta casi la cumbre, *Steyermark et al. 125039* (UC, VEN); Cerro "Chimborazo," Sierra de Aroa, *Vareschi & Pannier 2715* (US, VEN); en la selva que cubre la fila "La Enjalma" al sur de Chivacoa, *Vareschi & Pannier 2660* (VEN). **Zulia:** Parija, *Vareschi 3147* (VEN); Dist. Mara, NW wooded slopes of Cerro Negro, 5.5 km SW of Rancho 505, S of Río Guasare, *Steyermark et al. 122814* (MO, VEN); Dtto. Bolívar, Cuenca del Embalse Burro Negro (Pueblo Viejo), sector entre Quiros–El Pensado y el pie de Cerro Socopo, en el área aprox. 10 km en línea recta al este de Churugauarita, *Bunting 9516* (VEN); 15 km de El Vigía, carretera Panamericana, *Vareschi & Pannier 1686* (US).

Colombia. **Antioquia:** Río Leon, Bendix site, *Cain 74* (MICH); carretera al mar cerca de Villa Arteaga, *Gutiérrez & Barkley 170109* (GH); Municip. Anori, Providencia, *Soejarto 2805* (COL). **Boyacá:** Muzo, *Lindsay 262* (BM). **Cauca:** Agua Clara, along hwy from Buenaventurea to Cali, *Killip & Cuatrecasas 38902* (F, US); Costa del Pacífico, Río Micay, brazo Noanamito, orilla derecha, El Chachajo, *Cuatrecasas 14246* (US). **Chocó:** 0.5–2.5 km N of the INDERENA Camp on Río Truando near Caserío La Teresita, *Lellinger & de la Sota 553* (COL, US); NW side of Alto del Buey, *Lellinger & de la Sota 213* (COL, US), *250* (COL, LP, US); trail from Río Mecana to Alto de Mecana, *Gentry & Juncosa 41021* (MO, UC). **Magdalena:** Sierra Nevada de Santa Marta, región del Campano, *Barkley & Gutiérrez V. 1897* (MICH); Santa Marta, near Las Partidas, 3500 ft, *H.H. Smith 1050* (B, F, NY, MICH, MO, PH, US, VT); Forest Boca Toma, El Recuerdo, 2500 ft, *Bennett 23* (F); Santa Marta Mts., trail beyond falls, El Recuerdo, *Niemeyer 44* (US). **Meta:** Villavicencio, *Alston 7641* (BM). **Santander:** Barbosa, *Henri-Stanislas 1710* (US); Mesa de los Santos, *Killip & Smith 15341* (COL, GH, NY, US); between Lebrija and San Vicente, *Alston 7341*

(BM). **Prov. unknown:** Municip. de Marsella, Vereda La Nona, Finca Palermo, cerca al caserío Caracas, Cordillera Central, vertiente occidental, *Idrobo et al. 10116* (COL).

Ecuador. **Los Ríos:** Río Palenque Biological Station, km marker 56 N of Quevedo, *Moran 3600* (Q, QCA). **Napo:** 27 km SE de Coca, alrededor de pozo de petroleo Auca 4, *Moran 3618* (PORT, Q, QCA); 12 km SW of Coca, por el camino se llama "Los Zorros," *Moran 3612* (Q, QCA); 73 km NE de Baeza, propiedad de Inecel, "Cascada de San Rafael," *Moran 3592* (F, MO, Q, QCA); Puerto Francisco de Orellana (Coca), 17 km SW of the town at road along Río Napo (Los Zorros), *Balslev & Madsen 10649* (AAU, Q, QCA); Río Napo, Pañachocha (Oasis), *Harling et al. 7535* (F, GH); Añangu, Parque Nacional Yasuni, SEF project area, *Øllgaard et al. 38845* (AAU, Q, QCA), *38894* (AAU, Q, QCA), *39086* (AAU, Q, QCA). **Pastaza:** Lorocachi, zone oeste del campamento militar a 3 km del Río Curaray, *Jaramillo et al. 30783* (AAU, Q, QCA). **Pichincha:** Pululahua, *Sodiro s.n.* (US); Chimborazo, *Spruce 5685* (P); Los Colorados, *Sodiro s.n.* (P); 15 km E of Sto. Domingo de los Colorados, road behind Brasilia a Toachi, along Río Toachi, *Moran 3547* (F, Q, QCA). **Santiago-Zamora:** Cordillera Cutucú, ridge just S and W of Río Itzintza, *Camp 1298* (NY), *1359* (NY). **Tungurahua:** Baños-Jivaria de Pintuc, *Stübel 875* (B). **Prov. unknown:** Junganza, *Crespi s.n.* (US); San Miguel, *Sodiro 81* (UC).

Peru. **Huánuco:** SW slope of the Río Llulla Pichis watershed, on the ascent of Cerros del Sira, Camp 3 (Laguna), *Dudley 13005* (GH); Tingo María, *Allard 21609* (US), *21997* (US). **Junín:** Pichis Trail, Yapas, *Killip & Smith 25452* (NY, US); Chanchamayo Valley, *C. Schunke 164* (F), *705* (F), *1341* (F), *1395* (F), *1451* (F); E of Quimiri bridge, near La Merced, *Killip & Smith 23991* (F, NY, US). **Loreto:** Prov. Maynas, Peter Jensen's Explorama Lodge, 50 mi downriver on the Amazon at Yonamono Ck., *Moran 3642* (AMAZ, F, USM); Altura Tuta Pishco on Río Napo, *Croat 20287* (MO); Gamitanacocha, Río Mazán, *J. Schunke 275* (F, GH, NY, UC, US), *380* (F, GH, UC, US); Pumayacu, between Balsapuerto and Moyobamba, *Klug 3208* (F, GH, MO, US); Veradera de Mazàn, *Croat 20786* (MO); 17 km SW of Iquitos, *Croat 18476* (MO); Río Napo near Entrada de Isla Inayuga, *Croat 20543* (MO). **Madre de Dios:** Prov. Manu, *Vargas 17743* (GH). **San Martín:** Camino a Pushurumbo, 7–8 km E del puente de Palo Blanco, Mariscal Caceres, Tocache Nuevo, *J. Schunke 5785* (COL, NY, US). **Ucayali:** Río Aguaytia above mouth of Quebrada Yurac–Yacu, *Croat 20851* (MO).

Bolivia. **La Paz:** Región de Mapiri, *Buchtien 298* (NY, UC, US); Mapiri, San Carlos, *Buchtien 1066* (LP); Yungas, Mururata, 1839, *Pentland s.n.* (P).

Brazil. **Amazonas:** Manaus–Caracarai road, km 148, *Berg et al. P18138* (F, NY, VEN). **Pará:** Serra dos Carajás, AMAZ Camp Azul, *Sperling et al. 5915* (GH, NY).

29. Polybotrya cyathifolia Fée (Fig. 49, Map 19).

Polybotrya cyathifolia Fée, Mém. Fam. Foug. 6. (Hist. Acrost.) tab. 2. 1866. Type: Guadeloupe. "near the house of Mr. Bovie," *L'Herminier s.n.* (holotype: P!; other L'Herminier specimens that are probably types are at GH!, L!, fragment NY!).

Stem 1–2 cm thick, hemiepiphytic; *scales* dull, light reddish brown, concolorous, spreading, the margins subentire to denticulate. *Sterile leaves* up to 1.5 m long; *lamina* to 3-pinnate, ovate to lanceolate, up to 1.2 × 0.8 m, membranaceous, almost always with round, sessile, reddish, punctate glands; *pinnae* up to 40 × 23 cm, narrowly deltate, pinnatifid to the very apex, stalked 5–10 mm; *pinnules* catadromous to anadromous but mostly subequal, narrowly deltate, stalked 1–3 mm, the base subequilateral, slightly prolonged acroscopically but not oblique or cuneate on the basiscopic side; *tertiary segments* serrate to entire, the proximal ones of the largest pinnules oblong, slightly gibbous at the base on both the basiscopic and acroscopic sides; *axes* abaxially sparsely to moderately pilose with hairs similar to those above; *grooves* densely packed with multicellular reddish or tawny hairs, these 0.3–0.8 mm long and conspicuously exserted from the groove, evident to the unaided eye, especially at the pinnae junctures. *Fertile leaves* 3-pinnate-pinnatifid, coenosoric; *sporangial stalks* paraphysate; *spores* (47)50–59(63) microns long.

Other illustrations: See original description; Plumier, Tr. Foug. Amér. tab. 32. 1705.

Polybotrya cyathifolia is endemic to the Caribbean islands of Guadeloupe and Martinique (Map 19). Few collections have been made of this fern, but the original collection by L'Herminier is well prepared and has many duplicates.

Polybotrya cyathifolia is very much like *P. osmundacea*, but it differs by the shape of its tertiary segments, the resinous punctate glands, and by the long-pilose hairs on the axes. The best way to distinguish *P. cyathifolia* is by the costal groove hairs that copiously fill and protrude from the groove, especially at the junctures (Fig. 49c). *Polybotrya osmundacea*, on the other hand, usually has very short hairs (0.1–0.2 mm long) in the groove. An important tendency in lamina cutting is for the basal tertiary segments to be slightly

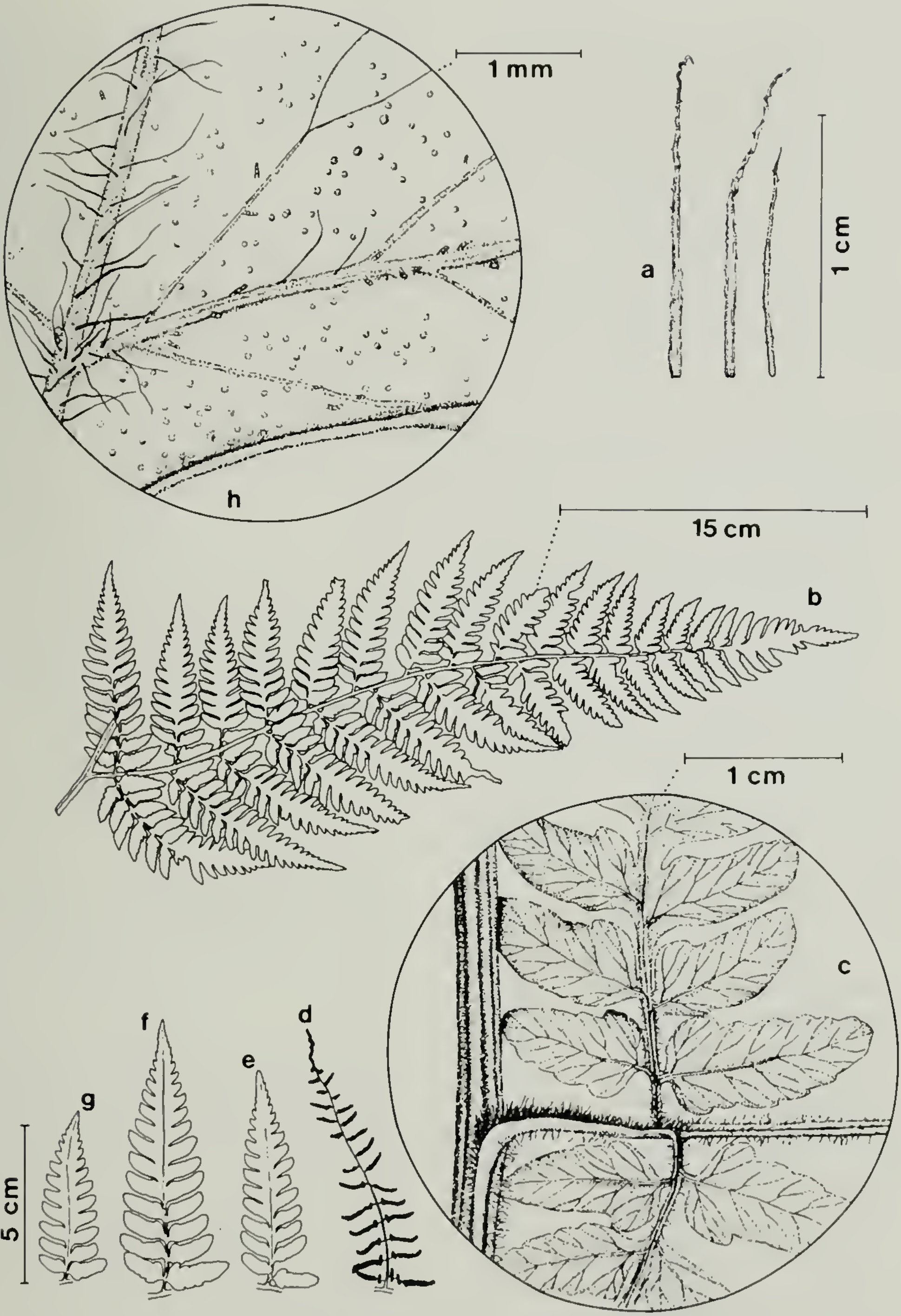

FIGURE 49. *Polybotrya cyathifolia* Fée. a. stem scales; b. basal pinna; c. rhachis-costa-costule junctures; d. fertile pinnule; e–g. sterile pinnules; h. abaxial view of lamina showing resinous glands. a,c,h: *L'Herminier s.n.* (P). b,g: *L'Herminier s.n.* (GH). d: collector unknown (GH). e,f: collector unknown (B).

gibbous at its base on both sides (Fig. 49c). This gives the pinnules a characteristic appearance, although it is somewhat difficult to describe. *Polybotrya osmundacea* rarely has these lobules and, if so, they are developed only on the acroscopic side. Most specimens of *P. cyathifolia* have the abaxial surface of the lamina covered with punctate, resinous glands (Fig. 49h); *P. osmundacea* rarely has such glands.

Specimens examined: GUADELOUPE. "near the house of Mr. Bovie," *L'Herminier s.n.* (P, GH, L, fragment NY).

MARTINIQUE. *Duss 1503* (NY, US), *3897* (NY), *4719* (F, US); *Hahn s.n.* (P); *Belanger s.n.* (F).

30. **Polybotrya latisquamosa** Moran, *sp. nov.* (Fig. 50, Map 19).

Polybotrya latisquamosa Moran, *sp. nov.* TYPE: Colombia. Meta: Cordillera La Macarena (extremo nordeste), macizo Renjifo, alrededores, alt. 1300–1900 m, 6–20 de enero 1951, *Idrobo & Schultes 1106* (holotype: US!; isotype: COL?).

Caulis 2 cm diam.; squamae castaneae, lineares vel anguste lanceolatae, 7–12 × 0.8–2.0 mm; petiolus ad basim squamatus, squamis castaneis, longioribus, 12–16 × 5–6 mm, deltatis vel late ovatis, marginibus pallidis erosis; lamina late deltata, 3-pinnata-pinnatifida, glabra in superficiebus utrinque, usque ad 13.5 × 5 cm, petiolulis usque ad 8 cm; segmenta tertiaria valde ascendentia basiscopice. Folia fertilia ignota.

Stem 2 cm thick, hemiepiphytic; *scales* castaneous, linear to narrowly lanceolate, ascending-spreading, darker and opaque in the center with lighter borders, margins erose, 7–12 × 0.8–2.0 mm. *Sterile leaves* up to 1.5 m (?); *petiole* scaly at the base with scales similar to those of the stem but much larger, 12–16 × 5–6 mm, deltate to broadly ovate; *lamina* broadly deltate (?), 3-pinnate-pinnatifid, glabrous on both surfaces; *pinnae* ca. 10–12 free pairs (?), alternate, the largest 45 × 26 cm; *pinnules* arranged anadromically, the proximal ones with stalks up to 8 mm long, the base strongly prolonged acroscopically, basiscopically shortened and strongly ascending, up to 13.5 × 5 cm; *tertiary segments* up to 3.5 × 1.3 cm, lanceolate, cuneate at the base, pinnatifid, 3–5 free below the pinnatifid apex, the basiscopic side strongly oblique, often with the first proximal 1–3 lobes completely suppressed; *costae* glabrous abaxially or with a few scattered, inconspicuous, less than 0.1 mm long, whitish, subulate hairs; *grooves* filled with reddish, inconspicuous hairs less than 0.1 mm long. *Fertile leaf* unknown.

The type location is a remote area in south-central Colombia, the Cordillera de Macarena, separated from the main Andean chain (Map 19). Since the holotype consists of only a portion of the stem and several incomplete pinnae, additional collections of this species would add greatly to the incomplete description.

Polybotrya latisquamosa resembles *P. osmundacea* because of its large decompound leaves with anadromically arranged pinnules but differs by its exceedingly large, broad, castaneous scales at the base of the petiole (Fig. 50d); thus the specific epithet. The stem scales differ from those of *P. osmundacea* by their deep castaneous color. The holotype is larger and more finely cut than the average *P. osmundacea* specimen, and the basiscopic sides of the pinnules and tertiary segments are extremely reduced and oblique-ascending (Fig. 50a). Finally, the major axes of *P. latisquamosa* are glabrous (Fig. 50e), unlike those of *P. osmundacea*, which are often pubescent.

31. **Polybotrya sessilisora** Moran, *sp. nov.* (Fig. 51, Map 20).

Polybotrya sessilisora Moran. TYPE: Colombia. Vaupés: Río Vaupés, Mitú y alrededores, 250 m, 8 September 1951, *Schultes & Cabrera 13963* (holotype: US!; isotypes: COL!, GH!).

Caulis hemiepiphyticus, 5–10 mm diam.; squamae appressae, ascendentes, lineares, 8–12 mm longae, atrocastaneae, marginibus pallidis et valde vehementer denticulatis; lamina usque ad 3-pinnata-pinnatifida, glabra, coriacea, pallide viridis; pinnae anguste deltatae vulgo 17–36 × 7–16 cm; pinnulae vulgo 3.5–10 × 1.2–3.0 cm, anadromicae, apicibus persaepe obtusis; rhachis et costae sparsim pubescentes, squamis fuscatis, appressis, flexuosis; venae conspicuae et prominulae. Folia fertilia usque ad 3-pinnata; lamina anguste alata viridis, marginibus leviter incrassatis; sori ca. 1 mm longi, discreti, circulares.

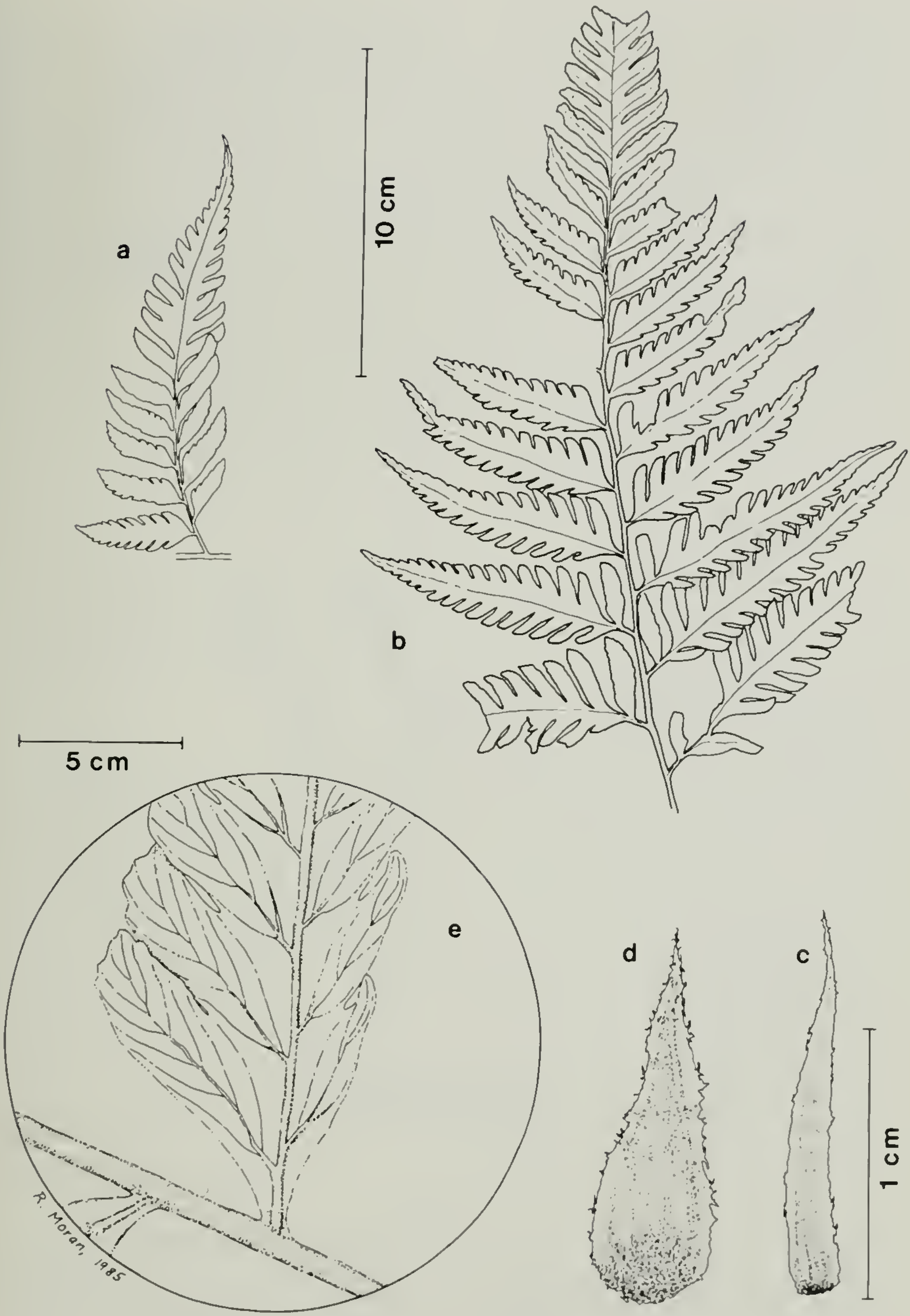

Figure 50. *Polybotrya latisquamosa* Moran. a. sterile pinnule; b. apex of sterile leaf; c. stem scale; d. scale from petiole base; e. pinnule from medial pinna. a–c: *Idrobo & Schultes 1106* (US).

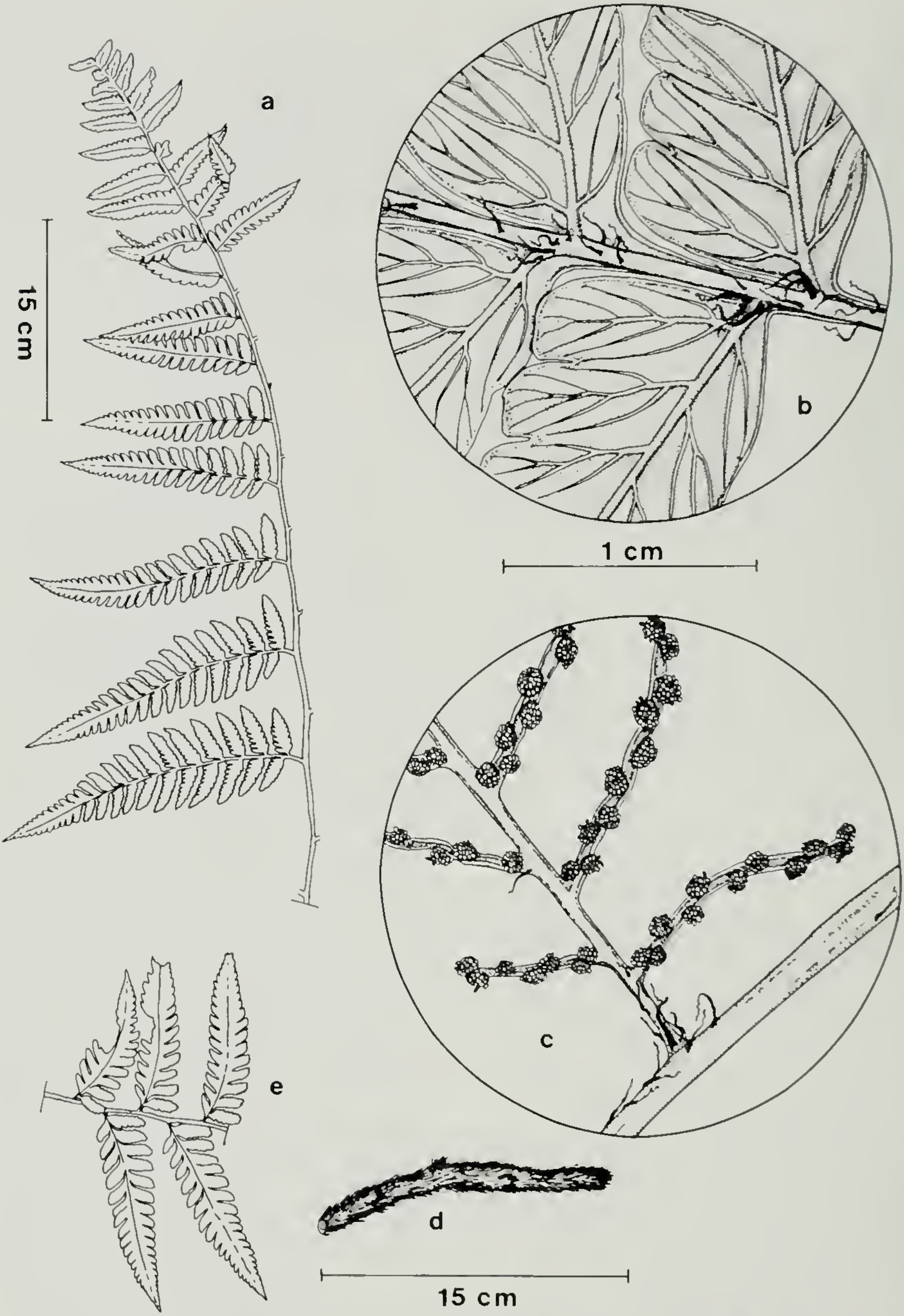

FIGURE 51. *Polybotrya sessilisora* Moran. a. distal half of sterile leaf; b. abaxial surface of costa and pinnules (note the thickened, lighter colored margin and dark tortuous scales); c. fertile pinnule, abaxial view (note the thickened margins and discrete sori); d. stem showing straight, appressed scales; e. medial pinnules of basal pinna, acroscopic side is up. a,c,d,e: *Schultes & Cabrera 13963* (COL). b: *Prance et al. 15332* (NY).

Stems 5–10 mm thick, hemiepiphytic; *scales* appressed, ascending, linear, 8–12 mm long, dark castaneous with lighter narrow borders and strongly denticulate margins. *Sterile leaves* up to 75 cm long; *petiole* ½ to as long as the lamina, scaly with scales similar to those of the stem, but more tortuous and spreading, the base mostly cordate; *lamina* to 40 cm long, up to 3-pinnate-pinnatifid, narrowly deltate, the tissue glabrous, coriaceous, light green, the margins glabrous; *pinnae* narrowly deltate, 17–36 × 7–16 cm, the proximal acroscopic pinnule or segment slightly prolonged above the rest; *pinnules* to 3.5–10 × 1.2–3 cm, arranged anadromically, the basiscopic margin thickened and decurrent on the costa, the apex of the less cut medial pinnules merely acute or obtuse; *veins* conspicuous and prominulous abaxially; *axes* moderately to sparsely pubescent abaxially, the hairs colorless, tawny, 0.5–1.0 mm long; *grooves* of axes decurrent on those of lower order, not interrupted, pubescent within by tiny, less than 0.2 mm long, reddish, jointed hairs, covered with dark, spreading, tortuous, denticulate scales like those of the petiole. *Fertile leaves* 3-pinnate, botryoid, the margins slightly thickened; *sori* sessile, round, about 1 mm long; *spores* (44)46–52(56) microns long.

Polybotrya sessilisora grows in lowland forests of the northern Amazon basin (Map 20). It is probably more common than the number of collections suggests, since the northern Amazon basin is poorly collected. I suspect that this species also occurs in the adjacent Guiana Highlands.

The specific epithet refers to the botryoid sori that are sessile instead of short-stalked as in other species of *Polybotrya*. Moreover, the sori are embedded in the lamina, which is not completely reduced to the axis (Fig. 51c). As evidenced by outgroup comparison to other dryopteroid ferns, the ancestor to *Polybotrya* surely had fertile leaves with discrete, round sori from which the lamina was reduced. Because the lamina of *P. sessilisora* is not fully reduced, I interpret its fertile leaf as the most primitive in the genus. No other species in the genus has this distinct kind of fertile leaf.

Another distinctive feature of *P. sessilisora* is the dark castaneous scales that contrast sharply with the light green lamina. The scales of the axes are spreading and tortuous, whereas those of the stem are appressed and straighter (Fig. 51b,d). These scales become smaller and narrower in the distal parts of the lamina until they become uniseriate, appressed hairs. The lamina is always broadest at the base, in contrast to the closely related *P. osmundacea*, which is usually reduced at the base. *Polybotrya osmundacea* also tends to be much more highly dissected when leaves of equal size are compared.

Specimens examined: COLOMBIA. **Vaupés:** Río Vaupés, Mitú y alrededores, 250 m, *Schultes & Cabrera 13963* (COL, GH, US).

BRAZIL. **Amazonas:** Tapuruquara, beside road to airport, *Prance et al. 15332* (NY); Reserva Experimental, km 60, Manaus–Caracarai road, *Conant 1016* (GH), *1482* (GH); Reserva Ducke, km 26, Manaus–Itacoatiara road, *Conant 1080* (GH).

BRAZIL–GUYANA BOUNDARY: Akarai Mountains, height of land between drainage of Río Mapuera (Trombetas tributary) and Shodikar Creek (Essequibo tributary), dense forest 600–800 m, *A.C. Smith 2984* (GH, NY).

32. **Polybotrya canaliculata** Klotzsch (Fig. 52, Map 19).

Polybotrya canaliculata Klotzsch, Linnaea 20:429. 1847. LECTOTYPE: Venezuela. Aragua: Colonia Tovar, 1846, *Moritz 278* (lectotype: B!; isolectotypes: F!, GH!, L!, NY!, P!, US!; photo GH! of L). LECTOPARATYPE: Colonia Tovar, 1846, *Karsten (Coll. II) no. 13* (B!; isolectoparatypes; BM!, L!; photo of L specimen, NY!).

Acrostichum canaliculatum (Klotzsch) Hooker, Species Filicum 5:247. 1864.

Stems 0.5–2 cm thick, hemiepiphytic; *scales* ascending with spreading tips, 12–20 × 0.7–1.2 mm, dull brown to dark purple brown, concolorous or rarely with a very narrow hyaline border, the margins entire to denticulate, opaque to slightly thickened at the center and base. *Sterile leaves* up to 1.8 m long; *petiole* up to 45 cm long, shorter than the lamina, scaly at the base or throughout, the scales becoming progressively smaller and more ovate-lanceolate and erose-denticulate upwards, with a blackened basal point of attachment; *lamina* glabrous, lanceolate to triangular or subtriangular, 50–80 cm wide, to (4)3-pinnate-pinnatifid, subcoriaceous, the abaxial surface lighter in color than the adaxial; *basal*

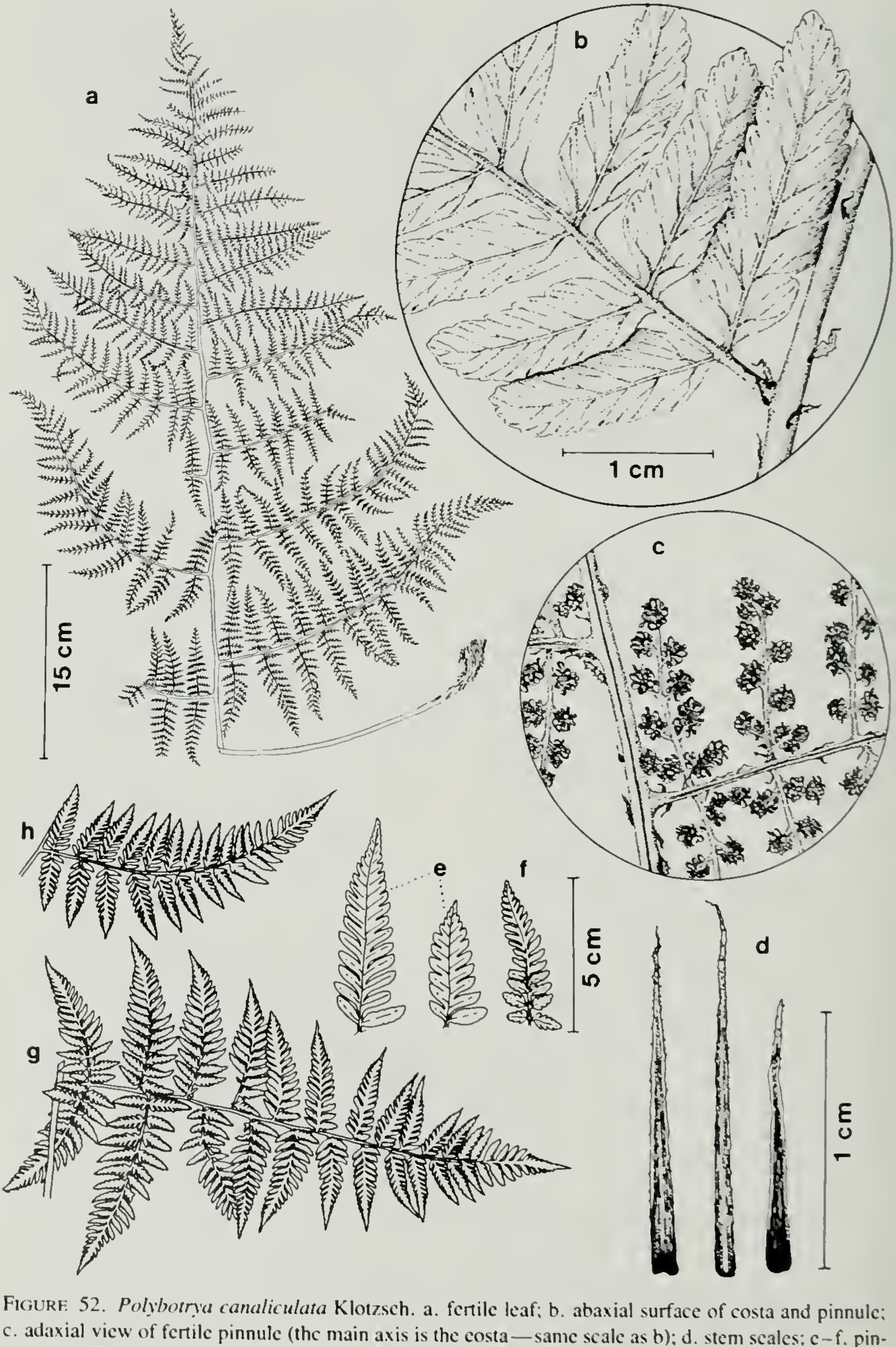

FIGURE 52. *Polybotrya canaliculata* Klotzsch. a. fertile leaf; b. abaxial surface of costa and pinnule; c. adaxial view of fertile pinnule (the main axis is the costa—same scale as b); d. stem scales; e–f. pinnules; g. basal pinna; h. medial pinna, from same leaf as in g. a–d: *Moritz 278* (B). e,f: *Karsten 13*(B). g,h: *van der Werff 3486* (MO).

pinnae triangular to subtriangular, up to 40 × 28 cm, the lowermost pinnate throughout except pinnatifid at the extreme apex; *pinnules* arranged catadromically or anadromically, up to 16 × 6.5 cm, triangular-lanceolate, the acroscopic side usually prolonged; *costules* adaxially deeply grooved and bordered by a raised, erect to spreading flap of tissue; *tertiary segments* entire to pinnatifid (deeply so in large leaves), equilateral at the base with a rounded to acute apex; *axes* scaly, the scales scattered, flaccid, membranaceous, ovate to lanceolate, denticulate, 1–3.5 mm long, the abaxial surface usually glabrous; *grooves* pubescent within, and especially at segment junctures, the hairs tiny, less than 0.2 mm long, reddish. *Fertile leaves* botryoid, 0.8 × 0.6 m, 4-pinnate; *axes* with numerous septate hairs that often grade into narrow scales; *pinnae* up to 30 cm long, subtriangular; *sori* round to obovate, distinctly stalked, the stalk about 1 mm long; *spores* (50)55–66(70) microns long.

This species grows in cloud forests in the Andes of northern Venezuela from 1200 to 1600 m (Map 19). Van der Werff and Smith (1980) state that this species can be abundant locally, but that the plants rarely bear fertile leaves.

The specific epithet refers to the raised flap of tissue that borders the costules and accentuates the depth of the central groove. This character is not diagnostic, since other decompound *Polybotrya* species also have raised costular ridges, although in *P. canaliculata* these ridges tend to be relatively taller and more well developed.

When available, the botryoid fertile leaves (Fig. 52a,c) distinguish this species from *P. osmundacea* and its allies. Distinguishing vegetative characters are the dull brown, concolorous stem scales, and the major axes with prominent, ovate to lanceolate, flaccid scales (Fig. 52b). The pinnule arrangement of *P. canaliculata* may be either anadromic or catadromic. This variation is peculiar because the pinnule arrangement is usually constant within most species of *Polybotrya*. A similarly variable species in this respect is *P. gomezii*, an endemic from Costa Rica. I interpret *P. canaliculata* as a primitive species of *Polybotrya* because of its decompound lamina and botryoid fertile leaf.

I have chosen the Moritz collection as the lectotype because of its wide distribution in herbaria and the excellent quality of the specimens.

Specimens examined: VENEZUELA. **Aragua:** Colonia Tovar, 1846, *Moritz 278* (B, BM, F, GH, L, NY, P, US); Colonia Tovar, 1846, *Karsten 13* (B, BM, L; photo of L specimen, NY); Parque Nacional Henri Pittier, bosque de Rancho Grande, *Tschudi 166* (VEN); Colonia Tovar, 1854–5, *Fendler 262* (GH, MO, NY, P, PH, US). **Falcón:** Sierra de San Luis, arriba de Sta. María, alt. 1200 m, 5 June 1979, *van der Werff 3486* (MO, UC); Sierra de San Luis, selva nublada, entre La Chapa y Uria, *Steyermark 99185* (VEN). **Yaracuy:** Dtto. Bolívar, entre las Parchitas, Tierra Fria y Ojo de Agua, *Ortega & Smith 2498* (PORT), *2511* (PORT). **State unknown:** Andes of Venezuela, 1889, *Goebel s.n.* (P).

33. Polybotrya semipinnata Fée (Fig. 53, Map 18).

Polybotrya semipinnata Fée, Crypt. Vasc. Brésil. 1:16. 1869. TYPE: Brazil. Rio de Janeiro: Yacuacanga, 15 June 1869, *Glaziou 2427* (K, P!, RB!, US!; photo of K specimen at US!).

Aspidium scandens Raddi, Plant. Brasil. 1:34, tab. 49. 1825. TYPE: Brazil. *Raddi s.n.* (FI; isotype: K, photo GH!).

Polybotrya scandens (Raddi) Christ, Bull. Herb. Boissier, II. 4:965. 1904. *nom. illegit.*, *non* Fée 1852.

Stem 1–1.5 cm thick, hemiepiphytic; *scales* membranous, spreading, mostly 9–12 × 0.5–1.2 mm, bright castaneous, concolorous or with a dark central stripe and lighter borders, the margins denticulate to strongly erose. *Sterile leaves* up to 1 m long; *petiole* ⅓ to ½ the length of the lamina; *lamina* ovate to lanceolate to 3-pinnate but mostly 2-pinnate-pinnatifid throughout, generally 45–60(75) × 30–55(64) cm, coriaceous, glabrous except on major axes; *pinnae* broadly triangular to ovate, mostly 15–30 × 11–17 cm, divided at base and soon becoming pinnatifid distally; *pinnules* 5–10(13) × 2–3 cm, lanceolate, anadromic throughout, the bases mostly cuneate, unequal, the basiscopic side more narrowly cuneate and the acroscopic side slightly prolonged, proximal ones with a 3–5 mm long stalk, rarely with the lowermost acroscopic segment cut to the costule; *axes* pubescent abaxially with hairs less than 0.1 mm long, stiff, colorless, subulate, the scales few or absent; *grooves* glabrous or nearly so within, decurrent on those of the next lower order. *Fertile leaves* smaller than the sterile, 3-pinnate (-pinnatifid), coenosoric; *tertiary segments* oblong, generally 3–7 mm long; *sporangial stalk* paraphysate; *spores* (48)50–62(66) microns long.

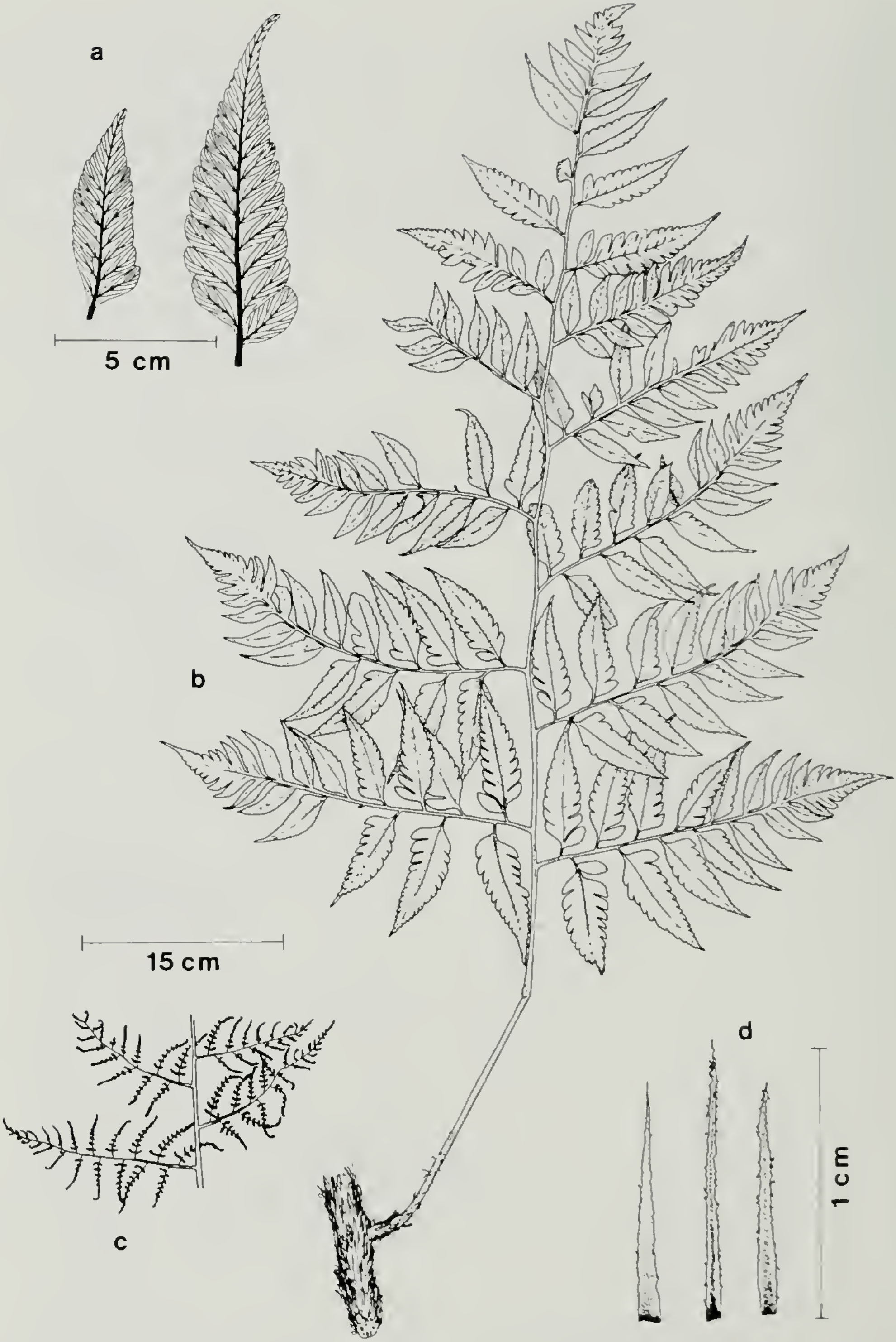

FIGURE 53. *Polybotrya semipinnata* Fée. a. sterile pinnules; b. sterile leaf; c. middle pinnae of fertile leaf; d. stem scales. a–c: *Brade 8061* (PH). d: *Duarte et al. 65322* (F).

Other illustrations: Raddi, Plant. Brasil. tab. 49. 1825; Mettenius, Filices Hort. Lips., 23, tab. 2, figs. 1–6. 1856 (as *P. acuminata*); Brade, Bradea 1:64, fig. 1; 67, fig. 9. 1971 (as *P. scandens*).

Polybotrya semipinnata is one of five *Polybotrya* species that are endemic to the coastal mountains of southeastern Brazil (Map 18, Table 2), a distribution that emphasizes the biogeographic distinctness of the Serra do Mar Mountains. The altitudinal range of *P. semipinnata* is from 800 to 1000 m.

This plant, easily recognized by its lamina cutting, is not readily confused with other species of *Polybotrya*. The pinnule bases are distinctive because they are stalked and more narrowly cuneate on the basiscopic side. The pinnae are stouter and much less divided compared to those of other decompound *Polybotrya* species; the distal portions soon become pinnatifid, a characteristic that accentuates this less-cut appearance.

An earlier published name, *P. acuminata* Link, has often been applied to this species. Since the type specimen cannot be located and I cannot discern from Link's description the species he had in mind, I treat *P. acuminata* as a name of uncertain application.

Specimens examined: BRAZIL. **Rio De Janeiro:** Yacuacanga, *Glaziou 2427* (P, RB, US; photo of K specimen at US); Estrada Velha da Bocaina, Teresópolis, *Duarte et al. 65322* (F, LP); Serra dos Orgãos, Teresópolis can. Quebrafrasco, 1000 m, *Brade 16456* (RB). **São Paulo:** Piruhyba, *Loefgren & Duvall 36217* (RB); prope Rio Grande ad São Paulo Railway, 800 m, *Wettstein & Schiffner s.n.* (P); Alto da Serra, *Luederwaldt s.n.* (BM, NY), *21547* (NY); Iguape, morro das Pedras, Serrinha Peroupara, *Brade 8061* (NY, PH, UC, US); Pilar, *Gerdes 102* (NY, UC). **Sta. Catarina:** without locality, *Schwacke s.n.* (P).

34. **Polybotrya speciosa** Schott (Fig. 54, Map 21).

Polybotrya speciosa Schott, Genera Filicum tab. 7. 1834. NEOTYPE: (here chosen) Schott, Genera Filicum tab. 7, based on material from "Brasiliae provincia Sebastianopolitana."

Polybotrya tomentosa Brade, Arq. Inst. Biol. Veg. Rio de Janeiro 1:224, fig. 2, plates 2 and 3. 1935. TYPE: Brazil. Minas Gerais: Serra do Itatiaia Maromba, 25 June 1930, *Brade 10351* (holotype: RB!).

Polybotrya osmundacea Willd. var. *crispopaleacea* Rosenst., Feddes Repert. 21:349. 1925. TYPE: Brazil. São Paulo: Alto da Serra, 11 February 1925, *Brade 5838* (S; isotype: UC!).

Polybotrya litoralis Brade, Bradea 1:26, tab. 1, fig. 2. 1969. TYPE: Brazil. Rio de Janeiro: Angra dos Reis, Serra do Mar, 29 June 1935, *Brade 14943* (holotype: RB!).

Polybotrya rosenstockiana Brade, Bradea 1:27, tab. 1, fig. 3. 1969. TYPE: Brazil. Rio de Janeiro: Serra dos Orgãos, Corrego Beija-flor, *Brade 16579* (holotype: RB!; isotype: LP!).

Stem 1–3 cm thick; *scales* commonly brick red, rarely dull brown, concolorous or with a dark central stripe, generally 8–20(27) × 0.5–1.5(2.0) mm, spreading, membranous, the margins denticulate to strongly erose. *Sterile leaves* up to 1.4 m long; *petiole* 1/10–1/4 the length of the lamina; *lamina* to 1.2 × 0.8 m, lanceolate to ovate, to 3-pinnate but mostly 2-pinnate-pinnatifid throughout, tomentose to glabrous, the margins sparsely ciliate to glabrous; *pinnae* to 40 × 15 cm, free pinnules usually 5–9; *pinnules* acroscopic, short to long triangular, mostly 4.5–8.0(10.0) × 1.5–3.5 cm, the base stalked, the stalk 2–4 mm long, the acroscopic side prolonged, the basiscopic side oblique; *tertiary segments* generally oblong, the margins entire to crenulate or dentate; *axes* tomentose to glabrous or subglabrous, the hairs usually 0.1–0.5 mm long, the scales few, appressed, tortuous, narrow; *grooves* pubescent within, the hairs reddish. *Fertile leaves* coenosoric, 3-pinnate; *sporangial stalks* paraphysate; *receptacle* glabrous or with multicellular, branched paraphyses, these as long as or slightly longer than the sporangia; *spores* (56)60–75(82) microns long.

Other illustrations: See original descriptions cited above; Brade, Bradea, tab. 3, fig. 4 (as *P. littoralis*); tab. 4, fig. 1 (as *P. rosenstockiana*); tab. 4, fig. 3; tab. 6, figs. 12, 13 & 15. 1971.

Polybotrya speciosa is endemic to the Serra do Mar Mountains along the coast of southeastern Brazil (Map 21). It differs from the four other species of *Polybotrya* there by its combination of strongly denticulate, red stem scales, finely cut lamina, and multicellular, branched paraphyses (Fig. 54). The pubescence of the abaxial surface varies from densely tomentose to nearly glabrous.

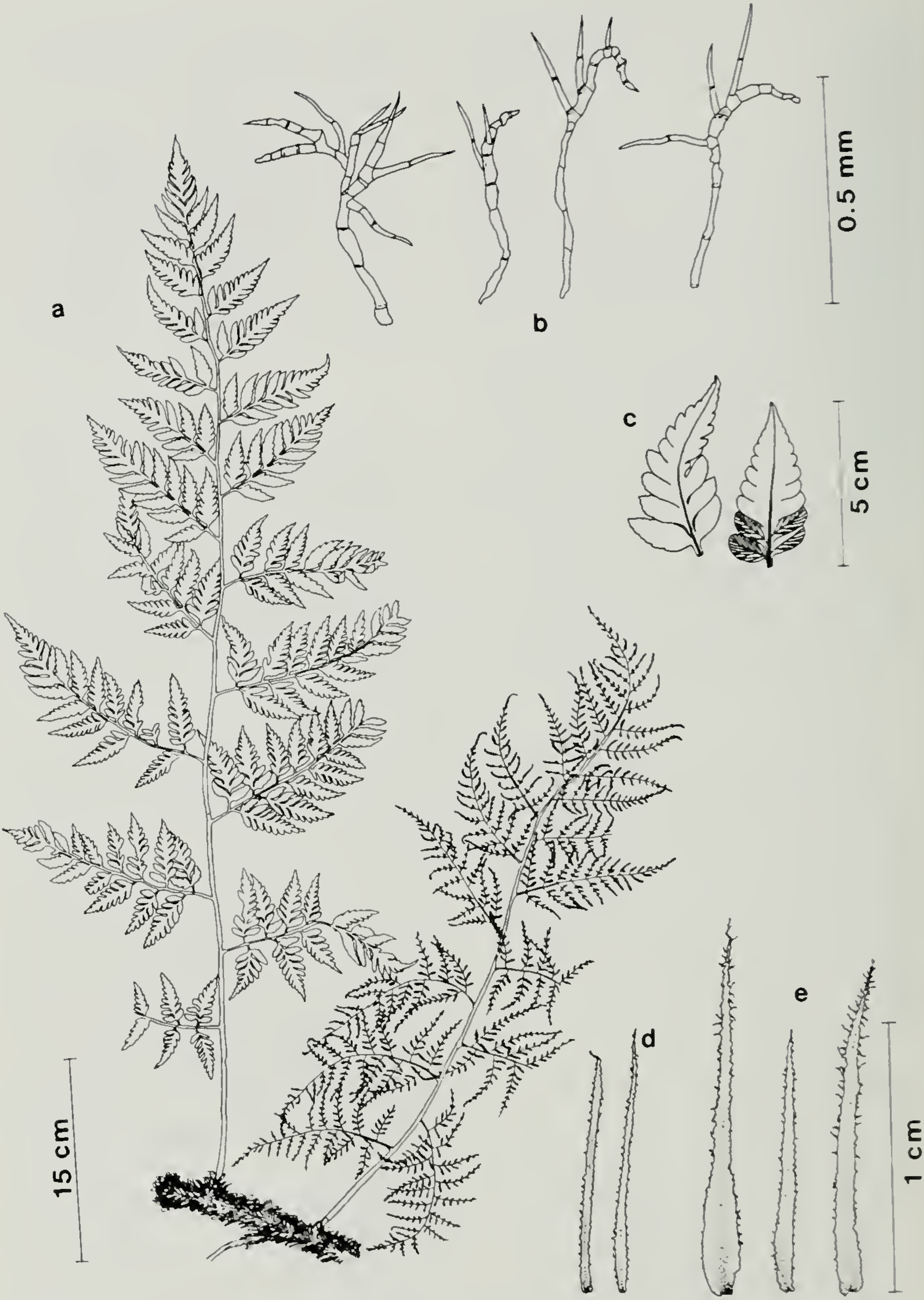

Figure 54. *Polybotrya speciosa* Schott. a. sterile and fertile leaves; b. branched paraphyses; c. pinnules; d,e. stem scales. a,b,e: *Brade 16579* (RB). c,d: *Brade 10351* (RB).

Five of the specimens examined had the adaxial surface slightly pubescent whereas the remaining were completely glabrous. No other species of *Polybotrya*, except *P. pilosa*, has branched paraphyses.

The spore size varies greatly, perhaps reflecting different ploidy levels. The averages from eight collections, with 15 spores measured from each, are as follows (in microns): 56, 57, 57, 58, 69, 69, 79, 82. This problem needs further study of additional collections and cytological samples.

I have been unable to locate Schott's type, but I feel quite certain that Schott's excellent plate represents this species. Schott's specimens became part of the Cardinal Hynald herbarium now located in Budapest, Hungary (BP). The curator of the fern collection at Budapest, Mr. Tibor Szerdahelyi, informed me (in litt.) that much of Schott's type material had been destroyed during World War II and that he could not find the type.

My placement of the three species described by Brade in synonymy with *P. speciosa* requires comment. I find no differences between the types of *P. tomentosa* and *P. litoralis*—the two might well have been collected from the same individual. Given this likeness, I find it odd that Brade (1969c) did not mention *P. tomentosa* in his discussion after the description of *P. litoralis*. I also place *P. rosenstockiana* and *P. osmundacea* var. *crispopaleacea* in synonymy, although they differ slightly from most specimens of *P. speciosa* by their somewhat broader stem scales (Fig. 54, compare d & e). They also differ by their leaves, which are less pubescent, primarily so along the axes and veins. Both these characters, however, intergrade and do not correlate with any others.

Specimens examined: BRAZIL. **Rio de Janeiro:** Serra dos Orgãos, Corrego Beijaflor, *Brade 16579* (LP, RB); Serra do Taquaral, *Brade 17464* (MO, NY); Therezopolis, *Brade 9773* (BM, UC), *9843* (NY); Parque Nacional de Serra dos Orgãos, *de la Sota 2343* (LP); Serra dos Orgãos, Morro Assu, *Luetzelburg 6858* (US); Organ Mts., *Rose & Russell 20790* (US); Corcavado, collected by the U.S. South Pacific Exploring Expedition, 1838–42 (NY, US); Mt. Tijuca, *Cuyler 4796* (US); Angra dos Reis, Serra do Mar, *Brade 14943* (RB); Guanabara, Estrada do Sumaro, *Pabst et al. 6772* (LP). **Minas Gerais:** Serra do Itatiaia, Maromba, *Brade 10351* (RB); Itatiaia, Maromba, *Brade 20214* (F, LP, MO, NY); same locality, *Brade 12616* (BM); Tijuca, *Alston 8991* (BM). **São Paulo:** Alto da Serra, *Brade 5838* (UC). **State unknown:** "Brazil," *Webb 26* (GH).

35. **Polybotrya pilosa** Brade (Fig. 55, Map 20).

> *Polybotrya pilosa* Brade, Bradea 1:27, tab. 1, fig. 4. 1969. TYPE: Brazil. Rio de Janeiro: Teresópolis, Varesea, 1000 m, 27 October 1929, *Brade 9787* (holotype: RB!; isotypes: NY!, UC!).

Differing from *P. tomentosa* only by characteristics of the pubescence; *hairs* 1–2(2.5) mm long, pilose, acicular, pluricellular, whitish or tawny, disposed along the abaxial surface of the veins and major axes, rarely on the intervening laminar tissue between the veins, also occurring on the adaxial surface and protruding from the costal and rhachidial grooves. Paraphyses present, of both branched and unbranched types.

Polybotrya pilosa is endemic to southeastern Brazil (Map 20). This species may be subject to reinterpretation in the future, as it differs from *P. speciosa* only by its pubescence, which shows no intergradation between the two species. The hairs of *P. speciosa* are less than 1 mm long, somewhat tortuous, and occur on the veins and intervening laminar tissue. The hairs of *P. pilosa* are more than 1 mm long, straightish, and acicular; they occur only along the veins, *not* on the intervening laminar tissue (Fig. 55a). These differences are readily apparent to the unaided eye. The reinterpretation of *P. pilosa* will require fieldwork designed to study intra- and interpopulational variation in southeastern Brazil.

Other illustrations: See Brade's original description, cited above.

Specimens examined: BRAZIL. **Rio de Janeiro:** "near Rio de Janeiro," collected by U.S. Exploring Expedition, 1838–42 (US); Tijuca, *Brade 20733* (NY, UC); "Rio Janeiro," 1851, *Andersjon s.n.* (LP); Organ Mts., *Wagner s.n.* (GH); Teresópolis, Varesca, *Brade 9787* (NY, RB, UC); Serra Estrela, *Weddell 952* (P); "Brasilia," *Riedel 81* (GH).

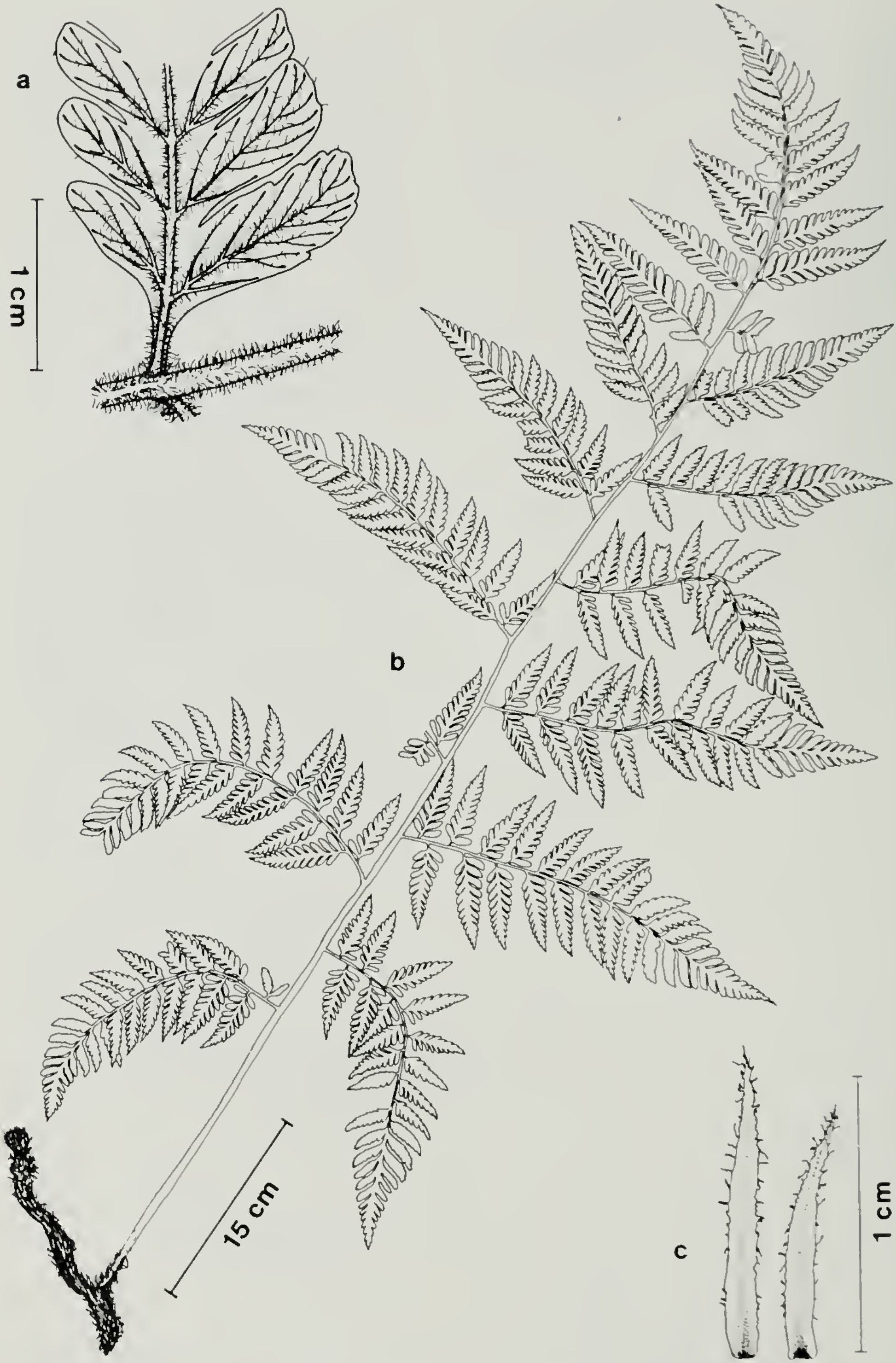

FIGURE 55. *Polybotrya pilosa* Brade. a. costa and pinnule with characteristic long, acicular hairs; b. sterile leaf; c. stem scales. a: *Wagner s.n.* (GH). b,c: *Brade 9787* (RB).

Names of Uncertain Application

Polybotrya acuminata Link, Hort. Berol. 2:135. 1833. *Psomiocarpa acuminata* (Link) Presl, Epim. Bot. 162. 1849. TYPE: Brazil. Collector? I have been unable to locate the type and cannot discern from the original description the taxon to which this name applies. The type specimen may have been lost during World War II; I have, however, Link's other type specimens from Berlin. Mettenius (1856, tab. 2) has an excellent illustration of *P. semipinnata*, which he refers to as *P. acuminata*, but I do not know whether he saw type material.

Polybotrya fulvostrigosa Christ, Bull. Herb. Boissier, II. 1:70. 1901. TYPE: Peru. Loreto: Cerro de Canchahuaya, *Huber 1448*. I cannot find the type and am uncertain from Christ's description to what species this name belongs.

Polybotrya lomarioides Mettenius, Filices Lechler. 2:5. 1858. TYPE: Peru. Puno: San Gaván, *Lechler s.n.*. I have not seen the type and cannot be certain from the description if this name applies to a *Polybotrya* species or to another genus.

Polybotrya nutans Kunze, Linnaea 9:24. 1834. TYPE: Peru. "Sylvae flor. Peruv. ad Pampayaco in cortice arborum vetustarum parasitica, Jul. 1829," *Poeppig s.n.* (B!, P!). The fertile leaf of the type specimen came from a species of *Polybotrya*, but I do not know which one. The sterile leaf of the type specimen is a tree fern, perhaps a species of *Trichipteris*.

Polybotrya scandens Fée, Genera Filicum 47. 1852. TYPE: Venezuela. Lagunetta, *Galeotti*. I have not seen the type and cannot ascertain from Fée's description the species to which this name applies. I suspect it is *P. osmundacea*. Windisch (1982) reported Fée's specimen of *P. scandens* to be at the Botanical Gardens in Rio de Janeiro (RB). Although I received other Fée specimens from RB, *P. scandens* was not among them. Fée gives the location as "Lagunetta, Mexico," but this site is certainly an error; see the discussion under *P. serratifolia*.

Polybotrya trapezoides Link, Filicum Species 164. 1841. TYPE: Cultivated plant at Berlin of unknown origin (B!). I received a specimen from Berlin (B) labelled as species but cannot be sure that this is the type. This specimen, however, is certainly not a species of *Polybotrya*. Because it is so young, I am uncertain what genus it represents.

Excluded Taxa

Excluded Subgenera

Polybotrya subg. *Ectoneura* Fée, Mém. Fam. Foug. (Hist. Acrost.) 75. 1845 (*nomen illegit.*). = *Bolbitis* (*fide* Hennipman 1977).

Polybotrya subg. *Egenolfia* Fée, Mém. Fam. Foug. (Hist. Acrost.) 14. 1845. = *Bolbitis* (*fide* Hennipman 1977).

Excluded Sections

Polybotrya sect. *Arthrobotrya* v.A.v.R., Handb. 725. 1908. = *Lomariopsis* sect. *Polyseriatae* (*fide* Holttum 1978).

Polybotrya sect. *Egenolfia* Diels, E&P Nat. Pfl. Fam. 1:195. 1900. = *Bolbitis* (*fide* Hennipman 1977).

Polybotrya sect. *Lomagramma* Kuhn, Ann. Mus. Bot. Ludg.-Bat. 4:198. 1899. = *Lomagramma* (*fide* Holttum 1978).

Polybotrya sect. *Teratophyllum* Christ, Farnkr. Erde 42. 1897. = *Lomariopsis* sect. *Polyseriatae* (*fide* Holttum 1978).

Excluded Species

Polybotrya acrostichoides Kuhn, Fil. Afr. 52. 1868. = *Bolbitis acrostichoides* (Sw.) Ching (*fide* Hennipman 1977).

Polybotrya apiifolia Kunze, Farnkr. 1:142, tab. 62. 1844. = *Psomiocarpa apiifolia* (Kunze) Presl.

Polybotrya appendiculata (Willd.) J. Smith, Jour. Bot. 4:150. 1841. = *Bolbitis appendiculata* (Willd.) Iwatsuki, (*fide* Hennipman 1977).

Polybotrya arfakensis Gibbs, Arfak 71. 1917. = *Alsophila biformis* Rosenstock (*fide* Holttum 1963).

Polybotrya articulata Fée, Mém. Fam. Foug. (Hist. Acrost.) 74, tab. 37. 1845. = *Teratophyllum articulatum* (Fée) Kuhn (*fide* Holttum 1978).

Polybotrya aspidioides Grisebach, Cat. Pl. Cub. 276. 1866. = *Atalopteris aspidioides* (Grisebach) Maxon & C. Chr.

Polybotrya asplenifolia (Belanger) Presl, Tent. Pterid. 231. 1836. = *Bolbitis appendiculata* (Willd.) Iwatsuki (*fide* Hennipman 1977).

Polybotrya aurita Blume, Fl. Jav. Fil. 15, tab. 1. 1828. = *Stenosemia aurita* (Sw.) Presl (*fide* Christensen 1905).

Polybotrya bifurcata (L.f.) J. Smith, Jour. Bot. 4:150. 1841. = *Elaphoglossum bifurcatum* (Jacq.) Mickel (*fide* Mickel 1980).

Polybotrya blumeana (Fée) Mettenius, Fil. Lips. 24, tab. 2, fig. 10. 1856. = *Leptochilus lomarioides* Blume.

Polybotrya cervina (L.) Kaulf., Enum. Fil. 55. 1824. = *Olfersia cervina* (L.) Kunze, Flora 7:312. 1824.

Polybotrya cicutaria Blume, Enum. Fil. 100. 1828. = *Stenosemia aurita* (Sw.) Presl (*fide* Christensen 1905).

Polybotrya duplicato-serrata Hayata, Ic. Fl. Formosa 5:305, fig. 123. 1915. = *Bolbitis rhizophylla* (Kaulf.) Hennipman (*fide* Hennipman 1977).

Polybotrya exaltata Brackenridge, U.S. Expl. Exp. 16:78. 1854. = *Bolbitis rhizophylla* (Kaulf.) Hennipman (*fide* Hennipman 1977).

Polybotrya filiculifolia (L.) Farw., Amer. Midl. Nat. 12:303. 1931. = *Anemia?*

Polybotrya flabellata (Willd.) Mettenius, Ann. Sci. Nat., Paris, V, 2:206. 1864. = *Peltapteris peltata* (Sw.) Morton.

Polybotrya fraxinifolia (Presl) Mettenius, Fil. Lechler. 2:8. 1959. = *Bolbitis serratifolius* (Kaulf.) Schott (*fide* Hennipman 1977).

Polybotrya furcata (L.f.) Kuhn, Fil. Afr. 52. 1868. = *Elaphoglossum bifurcata* (Jacq.) Mickel (*fide* Mickel 1980).

Polybotrya gaudichaudiana (Gaudich.) Moore, Index Fil. XV. 1857. = *Bolbitis appendiculata* (Willd.) Iwatsuki (*fide* Hennipman 1977).

Polybotrya hamiltoniana (Wallich) Fée, Mém. Fam. Foug. (Hist. Acrost.) 78. 1845. = *Bolbitis appendiculata* (Willd.) Iwatsuki (*fide* Hennipman 1977).

Polybotrya helferiana Kunze, Farnkr. Erde 2:35, tab. 94. 1848. = *Bolbitis appendiculata* (Willd.) Iwatsuki (*fide* Hennipman 1977).

Polybotrya intermedia Fée, Mém. Fam. Foug. (Hist. Acrost.) 76, tab. 40, fig. 1. 1845. = *Bolbitis rhizophylla* (Kaulf.) Hennipman (*fide* Hennipman 1977).

Polybotrya lomarioides (Blume) Kuhn, Ann. Mus. Ludg.-Bat. 4:295. 1869. = *Lomagramma lomarioides* (Blume) J. Smith (*fide* Holttum 1978).

Polybotrya marattioides Brackenridge, U.S. Expl. Exped. 16:79. 1854. = *Asplenium marattioides* (Brackenridge) C. Chr. (*fide* Christensen 1905).

Polybotrya marginata Blume, Enum. Pl. Jav. 100. 1828. = *Bolbitis appendiculata* (Willd.) Iwatsuki (*fide* Hennipman 1977).

Polybotrya montana (Gaudich.) Moore, Index Fil. 350. 1862. = *Bolbitis appendiculata* (Willd.) Iwatsuki (*fide* Hennipman 1977).

Polybotrya nana Fée, Mém. Fam. Foug. (Hist. Acrost.) 75, tab. 38, fig. 1. 1845. = *Blechnum lanceolatum* (R. Br.) Sturm. (*fide* Christensen 1905).

Polybotrya neglecta Fée, Mém. Fam. Foug. (Hist. Acrost.) 75, tab. 39, fig. 2. 1845. = *Bolbitis rhizophylla* (Kaulf.) Hennipman (*fide* Hennipman 1977).

Polybotrya nieuwenhuisenii Raciborski, Bull. Int. Ac. Cracovie 57. 1902. = *Heterogonium stenosemioides* (Baker) Christ (*fide* Holttum 1975).

Polybotrya nodiflora Belanger, Voy. Ind. Or. Bot. 2:17. 1833. = *Bolbitis appendiculata* (Willd.) Iwatsuki (*fide* Hennipman 1977).

Polybotrya orientalis Blume, Enum. Pl. Jav. 99. 1828. = *Stenosemia aurita* (Sw.) Presl (*fide* Christensen 1905).

Polybotrya peltata (Sw.) J. Smith, Jour. Bot. 4:150. 1841. = *Peltapteris peltata* (Sw.) Morton.

Polybotrya plumieri (Fée) Moore, Index Fil. 13. 1857. = *Elaphoglossum plumieri* Moore (*fide* Proctor 1977).

Polybotrya polyphylla (Brackenridge) C. Chr., Index Fil. 505. 1906. = *Lomagramma polyphylla* Brackenridge.

Polybotrya prolifera Mettenius, Fil. Lips. 24, pl. 2, fig. 11. 1856. = *Bolbitis subcrenata* (Hooker & Grev.) Ching (*fide* Hennipman 1977).

Polybotrya pteroides (J. Smith) Kuhn, Ann. Mus. Bot. Lugd.-Bat. 4:295. 1869. = *Lomagramma pteroides* J. Smith (*fide* Holttum 1978).

Polybotrya quercifolia (Retz.) Mettenius, Fil. Lechler. 2:12. 1859. = *Leptochilus zeylandicus* (Houtt.) C. Chr. (*fide* Christensen, 1905).

Polybotrya rhizophylla (Kaulf.) Presl, Tent. Pterid. 231. 1836. = *Bolbitis rhizophylla* (Kaulf.) Hennipman (*fide* Hennipman 1977).

Polybotrya serrulata Fée, Mém. Fam. Foug. (Hist. Acrost.) 76, pl. 39, fig. ii. 1845. = *Bolbitis rhizophylla* (Kaulf.) Hennipman (*fide* Hennipman 1977).

Polybotrya sinensis (Baker) C. Chr., Index Fil. 57. 1913. = *Bolbitis sinensis* (Baker) Iwatsuki (*fide* Hennipman 1977).

Polybotrya sorbifolia (L.) Keyserling, Pol. Cyath. Herb. Bung. 32. 1873. *nomen illegit.* = *Lomariopsis sorbifolia* (L.) Fée (*fide* Proctor 1977).

Polybotrya stenosemioides (Baker) Copel., Polypod. Philipp. 40. 1905. = *Heterogonium stenosemioides* (Baker) C. Chr. (*fide* Holttum 1975).

Polybotrya subquinquefida (Fée) Mettenius, Fil. Lechler. 2:12. 1859. = ?*Leptochilus latifolium* (Meyen) C. Chr. (*fide* Christensen 1905).

Polybotrya taccaefolia (J. Smith) Mettenius, Fil. Lechler. 2:12. 1859. = *Leptochilus latifolius* (Meyen) C. Chr. (*fide* Christensen 1905).

Polybotrya tenuifolia (Desv.) Kuhn, Fil. Afr. 52. 1868. = *Stenochlaena tenuifolia* (Desv.) Moore (*fide* Christensen 1905).

Polybotrya teysmanniana (Baker) Posthumus, Rec. Trav. Bot. Neerl. 33:872. 1930. = *Stenosemia teysmanniana* (Baker) Diels (*fide* Christensen 1905).

Polybotrya trilobata (J. Smith) Mettenius, Fil. Lips. 24. 1856. = *Leptochilus latifolius* (Meyen) C. Chr. (*fide* Christensen 1905).

Polybotrya tripartita (Hooker & Grev.) J. Smith, Jour. Bot. 4:150. 1841. = *Peltapteris tripartita* (Hooker & Grev.) Morton (*fide* Morton 1955).

Polybotrya vivipara Hooker, Exotic Flora, 2: pl. 107. 1825. = *Bolbitis appendiculata* (Willd.) Iwatsuki subsp. *vivipara* (Hooker) Hennipman (*fide* Hennipman 1977).

Polybotrya wilkesiana Brackenridge, U.S. Expl. Exped. 16:80, tab. 10. 1854. = *Teratophyllum wilkesianaum* (Brackenridge) Holttum (*fide* Holttum 1978).

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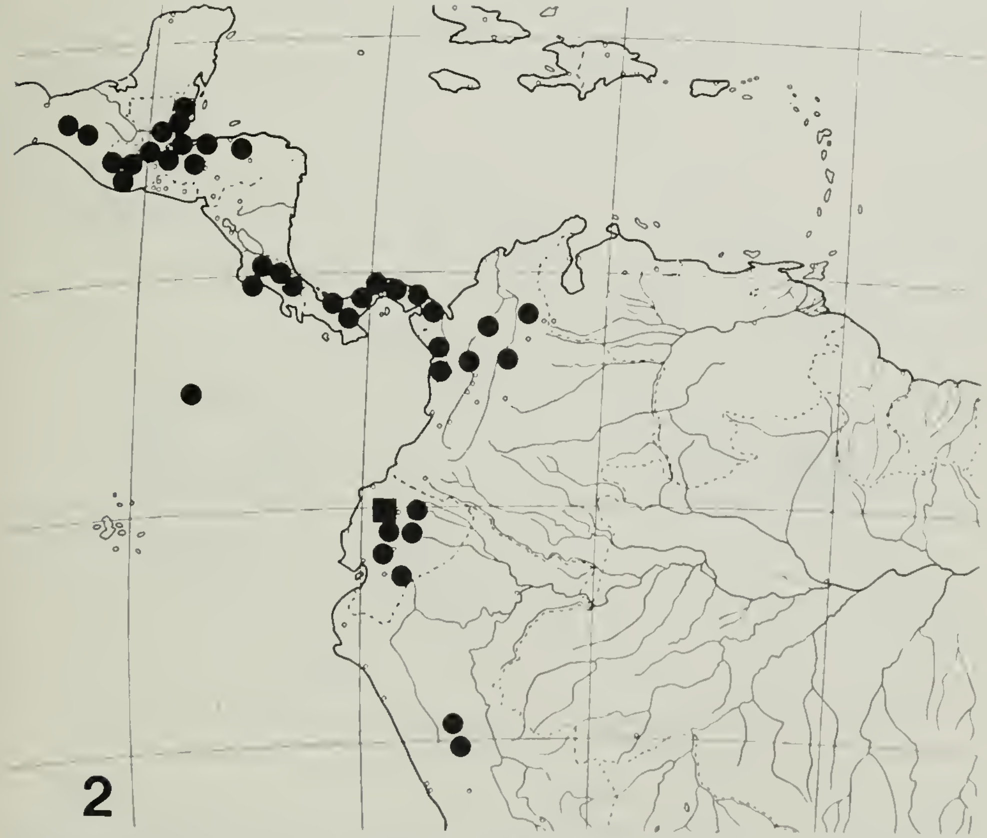
Taxa and Distribution of Polybotrya

Numbers correspond to the species numbers assigned in the taxonomic treatment.

1. *Polybotrya serratifolia* (Fée) Klotzsch: Trinidad, Venezuela.
2. *Polybotrya polybotryoides* (Baker) Christ: Mexico, Belize, Guatemala, Honduras, Costa Rica, Panama, Colombia, Ecuador, Peru.
3. *Polybotrya suberecta* (Baker) C. Chr.: Colombia, Ecuador, Peru.
4. *Polybotrya andina* C. Chr.: Ecuador.
5. *Polybotrya sorbifolia* Kuhn: Costa Rica, Venezuela, Colombia, Brazil.
6. *Polybotrya fractiserialis* (Baker) J. Smith: French Guiana, Surinam, Guyana, Ecuador, Peru, Bolivia.
7. *Polybotrya crassirhizoma* Lellinger: Colombia, Ecuador, Peru, Bolivia, Brazil.
8. *Polybotrya espiritosantensis* Brade: Brazil.
9. *Polybotrya caudata* Kunze: Mexico, Guatemala, Belize, Honduras, Nicaragua, Costa Rica, Panama, Trinidad, French Guiana, Surinam, Guyana, Venezuela, Colombia, Ecuador, Peru, Bolivia, Brazil.
10. *Polybotrya goyazensis* Brade: Brazil, Paraguay.
11. *Polybotrya pubens* Martius: Colombia, Ecuador, Peru, Bolivia, Brazil.
12. *Polybotrya glandulosa* Kuhn: Venezuela, Peru, Brazil.
13. *Polybotrya lechleriana* Mettenius: Guyana, Colombia, Ecuador, Peru, Bolivia.
14. *Polybotrya attenuata* Moran: Colombia.
15. *Polybotrya stolzei* Moran: Colombia.
16. *Polybotrya alfredii* Brade: Nicaragua, Costa Rica, Panama, Ecuador, Peru, Bolivia.
17. *Polybotrya botryoides* (Baker) C. Chr.: Colombia.
18. *Polybotrya lourteigiana* Lellinger: Colombia.
19. *Polybotrya pittieri* Lellinger: Colombia.
20. *Polybotrya cylindrica* Kaulfuss: Brazil.
21. *Polybotrya hickeyi* Moran: Colombia, Bolivia.
22. *Polybotrya puberulenta* Moran: Ecuador, Bolivia.
23. *Polybotrya alata* Moran: Panama.
24. *Polybotrya aequatoriana* Moran: Ecuador, Bolivia.
25. *Polybotrya appressa* Moran: Ecuador.
26. *Polybotrya altescandens* C. Chr.: Colombia, Ecuador, Peru.
27. *Polybotrya gomezii* Moran: Costa Rica.
28. *Polybotrya osmundacea* Willd.: Guatemala, Honduras, Nicaragua, Costa Rica, Panama, Cuba, Jamaica, Haiti, Grenada, Trinidad, French Guiana, Guyana, Venezuela, Colombia, Ecuador, Peru, Bolivia, Brazil.
29. *Polybotrya cyathifolia* Fée: Guadeloupe, Martinique.
30. *Polybotrya latisquamosa* Moran: Colombia.
31. *Polybotrya sessilisora* Moran: Colombia, Brazil.
32. *Polybotrya canaliculata* Klotzsch: Venezuela.
33. *Polybotrya semipinnata* Fée: Brazil.
34. *Polybotrya speciosa* Schott: Brazil.
35. *Polybotrya pilosa* Brade: Brazil.

Distribution Maps

The small open dots on the twenty-one distribution maps that follow indicate towns. Other symbols are explained in the legends.



MAP 1. Distribution of *Polybotrya suberecta* (Baker) C. Chr. (diamond) and *P. serratifolia* (Fée) Klotzsch (circle). MAP 2. Distribution of *Polybotrya polybotryoides* (Baker) Christ (circle) and *P. andina* C. Chr. (square).

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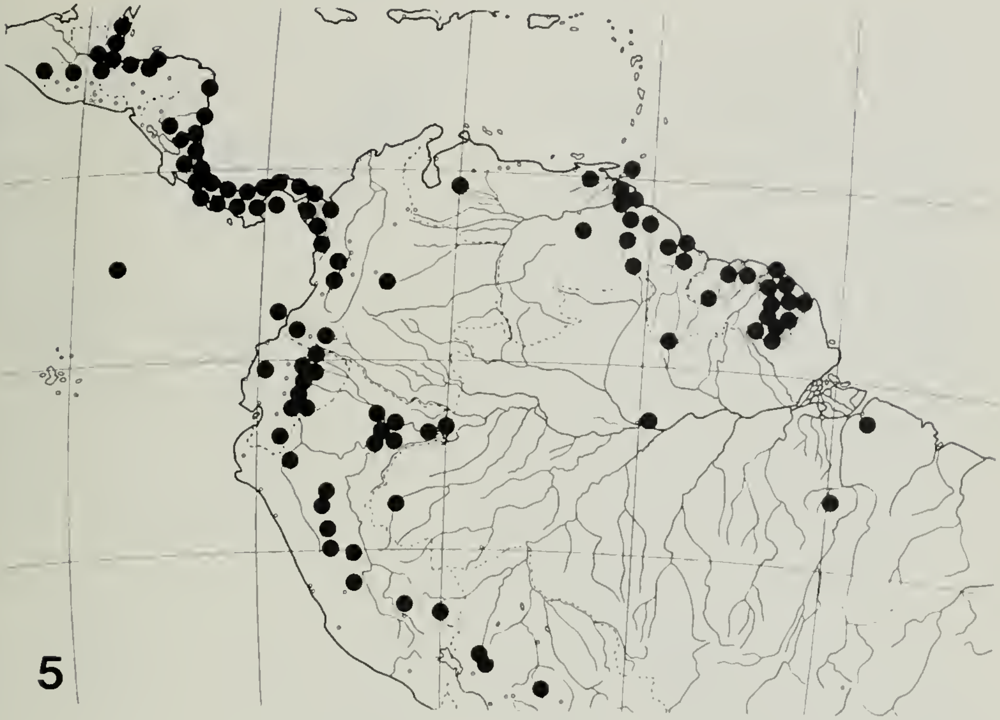
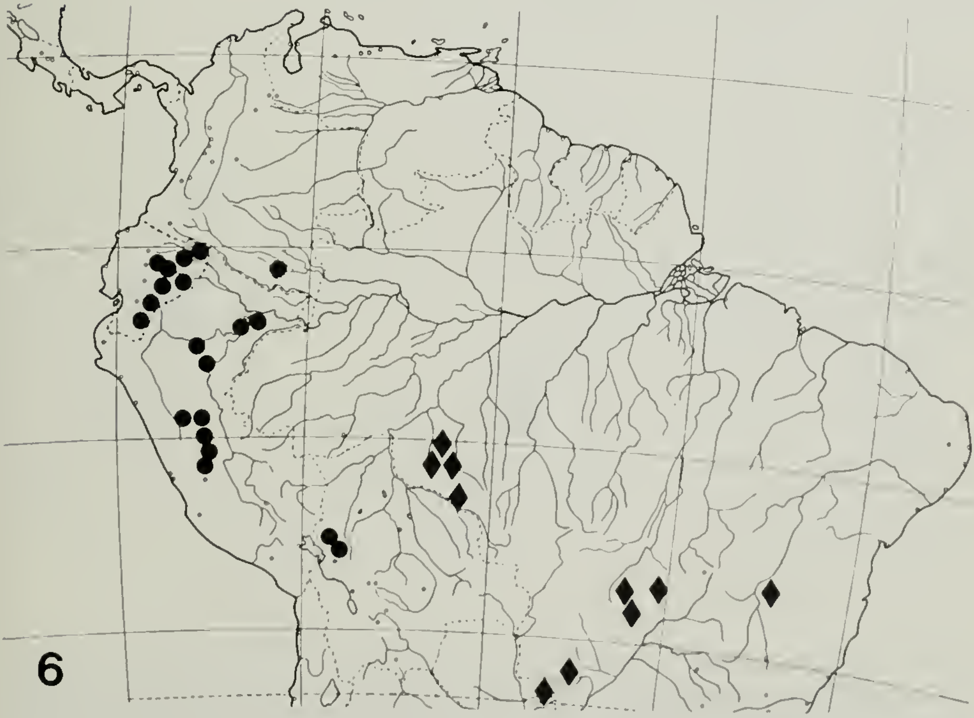
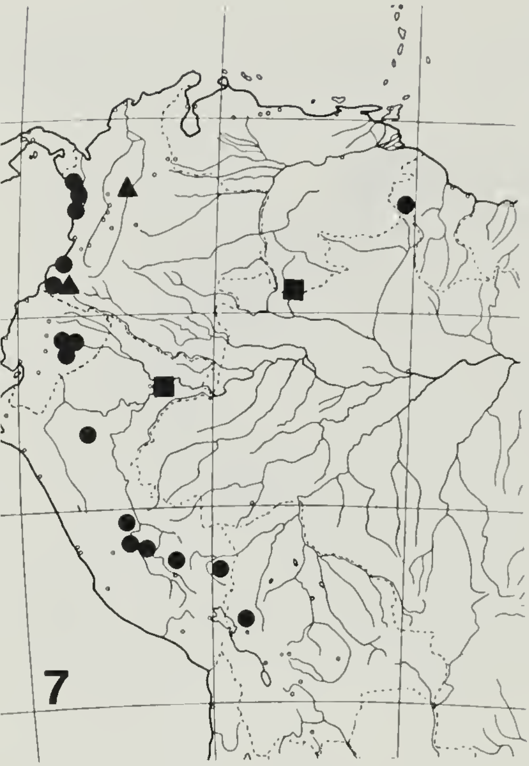
MAP 3. Distribution of *Polybotrya sorbifolia* Kuhn (diamond) and *P. fractiserialis* (Baker) J. Smith (circle). MAP 4. Distribution of *Polybotrya crassirhizoma* Lellinger.





MAP 5. Distribution of *Polybotrya caudata* Kunze. MAP 6. Distribution of *Polybotrya pubens* Martius (circle) and *P. goyazensis* Brade (diamond).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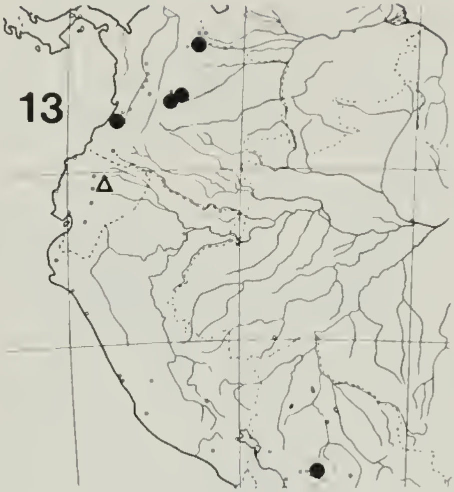
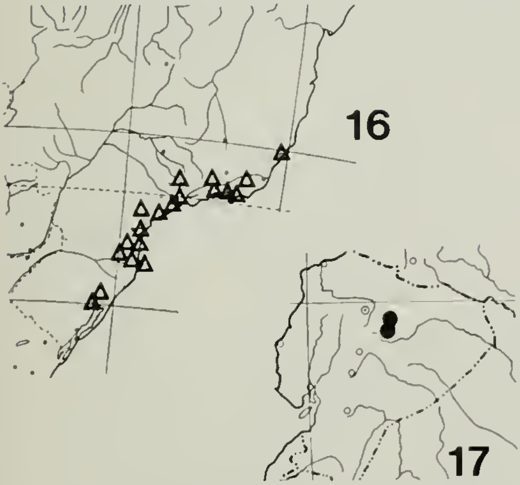
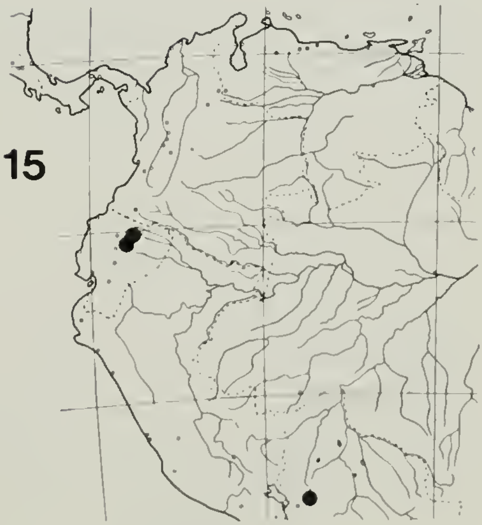
MAP 7. Distribution of *Polybotrya lechleriana* Mettenius (circle), *P. attenuata* Moran (triangle), and *P. glandulosa* Kuhn (square). MAP 8. Distribution of *Polybotrya alfredii* Brade (circle) and *P. botryoides* (Baker) C. Chr. (triangle). MAP 9. Distribution of *Polybotrya stolzei* Moran. MAP 10. Distribution of *Polybotrya lourteigiana* Lellinger. MAP 11. Distribution of *Polybotrya pittieri* Lellinger.







MAP 12. Distribution of *Polybotrya altescandens* C. Chr. MAP 13. Distribution of *Polybotrya hickeyi* Moran (circle) and *P. puberulenta* Moran (triangle). MAP 14. Distribution of *Polybotrya gomezii* Moran (circle) and *P. alata* Moran (triangle). MAP 15. Distribution of *Polybotrya aequatoriana* Moran. MAP 16. Distribution of *Polybotrya cylindrica* Kaulfuss. MAP 17. Distribution of *Polybotrya appressa* Moran.

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MAP 18. Distribution of *Polybotrya osmundacea* Willd. (circle) and *P. semipinnata* Fée (triangle). MAP 19. Distribution of *P. latisquamosa* Moran (solid square), *P. canaliculata* Klotzsch (triangle), and *P. cyathifolia* Fée (open square).

MAP 20. Distribution of *Polybotrya sessilisora* Moran (circle) and *P. pilosa* Brade (triangle).
MAP 21. Distribution of *Polybotrya speciosa* Schott (circle) and *P. espiritosantensis* Brade (triangle).

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