A REVISION OF THE GENUS LINDSAEA IN THE NEW WORLD WITH NOTES ON ALLIED GENERA

K. U. KRAMER
(*Botanical Museum & Herbarium, Utrecht*)

(*received March 21st, 1957*)

A. GENERAL PART

1. INTRODUCTION

The undertaking of the present study suggested itself to the author when, during the identification of ferns from Suriname with POSTHUMUS' treatment (1928), it became evident that the species of the genus *Lindsaea* were particularly poorly understood. As it proved to be impossible to elucidate the status of the species from that region only, without a survey of those from adjacent regions, it was decided that a revision of all New World species was indicated. It was possible to restrict the study largely to the representatives in that part ot the world, as there is not a single species occurring in both hemispheres. This, of course, does not imply that the Old World species have been completely left out of account; as a matter of fact, reference is made to them repeatedly in the present paper, especially where generic limits are concerned; but it would be altogether too big a task to complete a revision of the whole genus. Probably close to 3/4 of all species are restricted to the Asiatic-Oceanic region.

No really complete revision of the genus has ever been given, apart from HOOKER's treatment in the Species Filicum (Vol. I, 1844/46), and HOOKER & BAKER's Synopsis Filicum (1868, 1874). DIELS (1902) gave only a superficial synopsis of the principal species. The situation is by no means better as far as the neotropical species only are concerned; the treatments are unsatisfactory, with ambiguous keys, as BAKER's (1870, in Flora Brasiliensis), and, as stipulated above, in Posthumus' Ferns of Surinam, even, if only a small number of species are involved, e.g. in MAXON's Pteridophyta of Porto Rico (1926).

It is hoped that the present revision helps to clear up the taxonomy of this rather intricate genus. The author realizes that some problems still remain to be solved. To several of them cytotaxonomic studies would presumably contribute most valuable data. This applies particularly to *Lindsaea quadrangularis* and its relatives and to the diverse forms united under *L. stricta.*

Acknowledgements. The author wishes to express his deep gratitude to Dr. Rolla M. Tryon, Jr., and Dr. Alice F. Tryon, under whose guidance and with whose kind help this study was started, to Prof. Dr. J. Lanjouw, at whose institution and under whose supervision it was completed, and to Dr. Warren H. Wagner, Jr., for his constructive criticism of the general part.

2. HISTORY OF THE GENUS.

The genus *Lindsaea* was described in extenso by DRYANDER (1797), although it had been included a few years before in a paper by J. E. SMITH (1793) as "Lindsaea Dryandri (inedit.)" which constitutes valid publication. However, for none of the three species listed the combination under the new genus was actually made; this was left to Dryander's publication, which included a total of 10 species, 7 of which were published as new; the others were transferred to the new genus from *Adiantum*. The similarity in general aspect of many species of *Lindsaea* to species of *Adiantum* is indeed striking (for a more detailed account, see p. 132). Nevertheless, even apart from the fertile structures, there are quite a number of differences to be observed without the aid of a microscope, many of which were overlooked for a long time, so that FÉE still wrote (1865): "Ces fougères ont le port des Adiantum, dont elles ne diffèrent guère que par le mode de déhiscence des sporothèces . . .". It is even more surprising that careful authors like Swartz and Aublet were deceived by the similarity; the latter author, when publishing his "*Adiantum guianense*" (1775), which, as shown by his good plate, is beyond doubt a *Lindsaea*, was so convinced that he was dealing with an *Adiantum* that he described the sorus as "le bord supérieur de chaque portion est membraneux, réplié en dessous pour couvrir les fleurs qui y son placées", apparently without careful study of the actual condition.

Soon after the publication of Dryander's paper, the validity of the genus seems to have been generally accepted, and many authors working in the nineteenth century described new species, particularly Swartz, Desvaux, Klotzsch, G. Kunze, and Fée. However, many of these authors did not understand each other's, or even their own species, and already at that time, with still a comparatively small number of names to be kept in record, many misidentifications occurred. One of the few authors of that time who seems to have had a good understanding of at least the neotropical species was Klotzsch (chiefly in his publication of 1844); rather few of his species had to be cancelled later. Hooker's treatment in the Species Filicum did not do as much injustice to the naturalness of the genus as in many other cases, but his concept of species was also poor. The unsatisfactory condition in such treatments as BAKER's (1870) and POSTHUMUS' (1928) has already been commented on. This condition can be said to have prevailed practically up to present times. During the author's studies, large portions of the material sent to him on loan, sometimes close to 3/4, were incorrectly named, and at least part of the correct identifications were due to the fact that many authors dumped all material they could not readily match in *Lindsaea lancea* (or "*trapeziformis*"), which is, indeed, the commonest species. Furthermore, it seems that apart from usually very inadequate descriptions, the confusion of the species was enhanced by the existence of several suggestive names; thus all specimens with small rigid pinnules were called *L. stricta*, specimens with quadrangular stipe became *L. quadrangularis*, etc., regardless of other characters. Among modern authors who studied the genus, Hieronymus seems to have been one of the few who understood which characters were of importance for distinguishing the species and which were not, as can be seen in his annotations on the specimens in the Berlin herbarium; unfortunately he published very little on the genus (his most important paper was in 1920.) On the other hand, Rosenstock, who wrote on the genus several times, describing new forms and making new combinations (e.g. 1906), and who distributed large numbers of specimens in his fern exsiccatae from South Brazil and Costa Rica, rather helped to increase the confusion.

To convey an impression of the number of species known and recognized in the course of time, the following figures may be given. From Dryander's original publication which included 10 species, 6 of which were from the New World, the number increased to 20 neotropical ones in HOOKER's Species Filicum (1844/46). FÉE (1852) listed 25 species from the Western Hemisphere; BAKER (HOOKER & BAKER, 1874) recognized only 15. DIELS (1902) credited the genus with only 30 species, of which about 1/3 (!) was said to occur in America, although Jenman only three years before had listed 20 from the British West Indies and British Guiana alone. This progressive lumping was somewhat checked by CHRISTENSEN (1906), who recognized in his Index Filicum 27 neotropical species, which number was increased to 37 in the subsequent supplements (until 1934). Of these, 25 are maintained on the species-level in the present treatment; several others listed by him as synonyms are recognized as valid species.

Hitherto, 96 names have been published on the species-level. Of these, 33 are retained in this study, 6 are treated as taxa of lower rank, 36 as synonyms, 13 are excluded from the genus, and the application of 8 remains uncertain, or the species to which they apply are of doubtful validity. In addition, 11 are published as new, and one previously published in a lower rank is raised to species-rank, which brings the total number of species in the New World to 45.

The generic limits have fluctuated comparatively little. Of Dryander's 10 original species, all are still maintained in the genus, although some with different epithets. The highly dissected species which lack the dimidiate pattern of pinnules long considered as typical for the genus were at first put in *Davallia*, where they were retained by some authors until about 80 years ago (e.g. in the second edition of Hooker & Baker's Synopsis Filicum, 1874). Other authors included them in *Odontosoria* or *Sphenomeris* ("*Stenoloma*"), where several of them remained till present times (some of them were transferred to *Odontoloma* and *Schizoloma*, not recognized here). These genera were, however, often associated with *Lindsaea*, either as close relatives within the Davallioid ferns, or as a separate group; certain authors included even all of them in *Lindsaea* (Christ, 1897; Pérez Arbeláez, 1928). Only few authors (e.g. Fée, 1852) grouped the dimidiate and less dissected forms with more or less continuous sori together and placed the highly compound ones in a quite different group, not even close to the Lindsaeoids.

3. The group of Lindsaeoid ferns

Although the name "*Lindsaeaceae*" or "*Lindsaeeae*" appeared considerably earlier (probably for the first time used by Presl, 1836), the group as such can be said to have been established in a truly natural circumscription by Christensen (1938). It had been separated before from the Davallioids, with which *Lindsaea* was most often associated by earlier authors, but was then made to include only *Lindsaea* itself and a few very closely allied genera such as *Isoloma* and *Schizoloma* (e.g. Fée, 1852), which were sometimes united with it. To Christensen goes the merit for recognizing the affinity of *Tapeinidium*, *Sphenomeris* and *Odontosoria* with *Lindsaea* only, not with *Davallia*, with which they had been placed on account of their short sori with more or less pouch-shaped indusia. Christensen did, however, still include a few genera in the group, although with misgivings, that are now considered members of other groups, namely, *Taenitis*, *Platytaenia* (united by Copeland with the former), *Diellia*, and *Dictyoxiphium*. Copeland retained *Taenitis* and the allied genus *Syngramma* in the Linsaeoid group of his *Pteridaceae*, mainly because of supposed relationship between *Taenitis and "Schizoloma" (Schizolepton)*, but Holttum's arguments (1947, p. 156) for inclusion of the two genera in the Gymnogrammoid ferns seem to be much stronger. The Asplenioid affinity of *Diellia*, already suspected by Christensen and assumed by Copeland (1941, p. 161; 1947, p. 168) was firmly established by Wagner (1952b, 1953). *Dictyoxiphium*, for a long time included in the Lindsaeoid ferns as a very aberrant member with "venatio anaxeti", may be safely referred to the Tectarioid group (see Copeland, 1941, p. 160; 1947, p. 135; and Holttum, 1947, p. 153).

The genus *Ormoloma* was described by Maxon in 1933; he only pointed out the differences from *Saccoloma*, where the type-species had usually been placed before, without committing himself as to its place in the system. Christensen (1938), Ching (1940) and Holttum (1947) placed it near *Saccoloma*, but Copeland (1947) correctly pointed out its close alliance to *Lindsaea*.

The following genera should be retained in the Linsaeoids: *Tapeinidium*, *Isoloma*, *) *Schizolepton* (see p. 11), *Odontosoria*, *Ormoloma*, *Sphenomeris*, and *Lindsaea* itself. The three first-named genera are confined to the Eastern Hemisphere, the fourth and fifth to the Western, and

---

*) Dr. M. A. Donk in an unpublished m.s. which he very kindly made available to the writer pointed out that *Isoloma* J. Smith cannot be typified by the Lindsaeoid fern *I. divergens* (Roxb.) J. Sm., but rather by *Lindsaea lanuginosa* Wall., a species of *Nephrolepis*. The genus that comprises *I. divergens* should bear the name *Guerinia* J. Smith. As his discussion has not yet been published and as the name *Isoloma* is currently applied to the Lindsaeoid genus, it is here still used in that sense.

Lindsaea and *Sphenomeris* are represented in both. To these has probably to be added an undescribed monotypic genus based on *Schizoloma stortii* v.A.v.R. which will be discussed elsewhere, and perhaps also an additional genus to accomodate *Lindsaea walkerae* Hooker. Contrary to HOLTTUM's opinion (1947, 1954), and in accordance with CHRISTENSEN (1938) and COPELAND (1947), the genus *Schizoloma* Gaud. (based on *Lindsaea ensifolia* Sw.) is not recognized here, although it is maintained in a restricted sense as a subgenus, with some doubt as to its tenability.

The Lindsaeoid ferns may be characterized as follows: Small to medium-sized ferns, terrestrial, occasionally scandent or epiphytic. Rhizome creeping or climbing, solenostelic or with a special kind of protostele (*Lindsaea*-type), clothed with scales, usually mixed with reduced, ± hair-like, but always flattened scales, sometimes these reduced scales only present; the scales non-peltate, entire, with very few exceptions not clathrate. Petioles non-articulate, with one U- or V-shaped vascular strand (two reported in *Tapeinidium*), ± persistently scaly at the base only. Lamina very variable, simple to decompound, rarely dimorphous, anadromic, in mature condition seemingly glabrous but thinly clothed with microscopic, mostly two- or three- (rarely more) celled hairs (see p. 32). Petiole and rachises with very few exceptions sulcate on the adaxial side, the groove bordered by ridges which are continuous with those on the axes of higher order and with the thickened edge of the ultimate divisions at least on the basiscopic side. Pinnae and pinnules non-articulate (except in *Isoloma*), attached on the margin of the adaxial side of the rachis. Veins dichotomously branched, free, or less often anastomosing, without included veinlets; a midrib mostly absent. Sori indusiate, terminal on the veins (occasionally slightly decurrent along them), inframarginal, the part of the lamina projecting beyond them without veins ("upper indusium"), the receptacle formed by the broadened end of one vein or by a commissure uniting from two to all the veins of an ultimate segment (pinnule) or of half or the whole lamina. Indusium fixed by its base or its base and sides, opening towards the margin, al least the distal half of one layer of cells. Sporangia long-stalked, the stalk at least just below the head consisting of three rows of cells; paraphyses present in some (all?) species, ± similar to the hairs of the vegetative parts. Annulus continuous or mostly interrupted by the stalk, mostly slightly oblique, with 8–22 indurated cells; a stomium of 2–6 cells mostly differentiated; spores smooth or almost so, without a perispore, monolete or trilete.

Nothing seems to be known about the gametophyte (see STOKEY, 1951).

4. COMMENT ON THE GENERA

The monotypic genus *Schizolepton* (*Schizoloma* sensu COPELAND, 1947), *Ormoloma* with two species, and *Odontosoria* (in MAXON's restricted and certainly most natural circumscription, 1913) with ten, seem to be well-defined genera. The same is true for *Isoloma*, from which genus should be excluded *Lindsaea walkerae*, referred to it by Presl, on account of the non-articulate pinnae, and the species sometimes called *Isoloma* *lanuginosum*. This was for a long time included in *Isoloma*, and recently (1952) TARDIEU-BLOT argued that it should be kept there. It is, however, a *Nephrolepis*, and not at all closely allied to the Lindsaeoid ferns, as shown by the ciliate rhizome-scales, the scaly rachis, the distinctly hairy leaf-tissue, the different structure of the rachis, and the very conspicuous hydathodes often covered with small pellets. The only characters shared with *Isoloma* are the articulate pinnae (found throughout *Nephrolepis*), and the sorus; and the latter character alone is not sufficient to warrant inclusion in *Isoloma*, probably not even exclusion from *Nephrolepis*. TARDIEU-BLOT's first group of *Isoloma* consists of aberrant species of *Nephrolepis*, and her second group is true *Isoloma*. The differences between the two groups, stressed by herself (l.c., p. 331) in the writers' opinion show the unnaturalness of *Isoloma* as defined by her. Her opinion that "Le genre *Isoloma* est incontestablement un passage entre les *Lindsaea* et les *Nephrolepis*" is not shared by the writer; *Isoloma* and *Nephrolepis acutifolia* (*Isoloma lanuginosum*) in his opinion both constitute specialized, in certain ways analogous, offshoots of quite different groups of ferns.

The genus *Schizoloma* Gaudichaud has been defined in various ways. It is difficult to understand what GAUDICHAUD had in mind when he described it; his description (1824, p. 507) is: "sori lineares, continui, marginales; indusium duplex exterius dehiscens", and fits several different forms of Lindsaeoid affinity. Of Gaudichaud's three original species, two were subsequently removed to other genera, which justifies the selection of the third, *S. billardieri*, as type-species, rather than *S. cordatum*, maintained as such by COPELAND (1947). ALSTON (1956, p. 23) published *Schizolegnia* as a new name for *Schizoloma* (as currently understood, based on *Lindsaea ensifolia*), arguing that *Schizoloma* in this sense did not contain any of Gaudichaud's original species; but this is not so, as *Schizoloma billardieri* Gaud. is a heterotypic synonym of *Lindsaea ensifolia* Sw. (*Schizoloma ensifolium* (Sw.) J. Sm., and Alston's name is superfluous.

Schizoloma has been made to include several species removed from *Lindsaea*, sometimes also from *Isoloma*, by later authors; it was defined in such a way as to accomodate all forms with equal-sided rather than cuneate (*Odontosoria*) or dimidiate (*Lindsaea*) blades or segments, e.g. by DIELS (1902). In this circumscription it contained quite diverse and not at all closely related elements, a.o. the two well-known simple-leaved species of *Lindsaea*, *L. reniformis* and *L. sagittata*, which, as is shown in this revision, have their natural place among the neotropical Lindsaeas with a large terminal pinnule. HOLTTUM (1954) defined *Schizoloma* as including all species having equal-sided, non-articulate pinnae, or being bipinnate with the primary pinnae gradually decreasing in size and complexity towards the top of the leaf. This, however, makes delimitation towards *Sphenomeris* very difficult, as HOLTTUM himself observed (l.c., p. 341); moreover, there are closely related species (in the New World *L. pendula* and *L. meifolia*) which, by this definition, would go in different genera.

In the present author's opinion, *Schizoloma* can be maintained on the basis of the combination of anastomosing veins with equal-sided pinnae (*L. ensifolia*, *L. vieillardii*, *L. macrophylla*) or with long undivided pinna-apices (*L. heterophylla*); but it is possible that future work on the species from the Indo-Malayan region and New Caledonia, where most representatives of this type are found, will show that even in this reduced sense the group is untenable. Most species referred to *Schizoloma* should be put or put back in *Lindsaea*, except *S. cordatum*, the only species of the monotypic genus *Schizolepton* Fée, all species with articulate pinnae which constitute *Isoloma*, and *S. stortii* (perhaps also *S. walkerae*) as discussed above.

A more intricate problem is the separation of *Lindsaea* and *Sphenomeris*.*) Usually, in floras and handbooks (e.g. DIELS, 1902, BACKER & POSTHUMUS, 1939, TARDIEU-BLOT & CHRISTENSEN, 1939, COPELAND, 1947, etc.) the following kind of key is found;

a. Segments dimidiate . . . . *Lindsaea*
b. Segments cuneate . . . . . *Sphenomeris* (or *Odontosoria*, sens. lat.)

It is evident that such a distinction, based on the shape of the ultimate segments only, does not look very natural, at any rate in a group with such diverse types of leaf-pattern as the Lindsaeoids, and several authors have commented on the difficulty to distinguish the two genera (notably HOLTTUM, 1947, p. 134/135). MAXON's distinction (1926, p. 392):

a. Rhizomes densely hairy . . . . (a.o.) *Sphenomeris*
b. Rhizomes paleaceous . . . . (a.o.) *Lindsaea*

is only true with regard to *S. clavata*, the only species included in his treatment, and even there the flattened structures that clothe the rhizome are occasionally two cells wide at the base; they are certainly not comparable to the true hairs on rhizomes of other fern-genera. Moreover, in most other species of *Sphenomeris* true scales are found. (It seems, however, that in later years Maxon himself became doubtful with regard to the validity of *Sphenomeris*; see p. 153).

During the author's studies of the neotropical species it soon became evident that none of the afore-mentioned distinctions between the two genera is of much value. The south-east Brazilian *Lindsaea virescens*, which has incised, yet clearly dimidiate pinnules, is closely related to the sympatric *L. bifida* which fits perfectly in the description of *Sphenomeris* (*Stenoloma*) of most authors, is keyed out to that genus in their keys and is usually included there (or in *Odontosoria* sens. lat.). Likewise, *L. meifolia*, also currently referred to *Odontosoria* or *Sphenomeris*, is very close to *L. pendula*; an intermediate between the two has been found which is almost certainly of hybrid origin (described in this paper as

---

*) It seems superfluous to discuss again the application of the name *Stenoloma*, sometimes made to replace *Sphenomeris*, as this has already been done at great length. The interested reader may be referred to COPELAND (1947, p. 54) and PICHI-SERMOLLI (1954, p. 445). The necessity to conserve *Sphenomeris* against *Stenoloma*, as was done by the International Botanical Congress at Paris, 1954, is in the present author's opinion at least questionable.

L. × *dissecta*) *), and it seemed quite arbitrary to put the members of these pairs of species into different genera. Moreover, *L. bifida* and *L. meifolia* would be quite isolated among the bulk of species of *Sphenomeris*. Must we then conclude that *Lindsaea* and *Sphenomeris* cannot be seperated? The author was at first inclined to believe that this was the case. In this connection PÉREZ ARBELÁEZ (1928) might be cited who went even further and included *Odontosoria* with *Sphenomeris* and "*Saccoloma*" *imrayanum* (removed by him on good grounds from that genus) all in *Lindsaea*. His taxonomic conclusions are, however, based on anatomical and morphological data taken from a few sample-species only. But he observed correctly that the shape of the ultimate divisions alone cannot be used to divide the Lindsaeoid ferns into satisfactory genera. CHRISTENSEN's suggestion (1932, p. 77) to create a new genus between *Lindsaea* and *Sphenomeris* confronts us with the difficulty to draw two borderlines instead of one and therefore does not simplify the matter at all.

Subsequent studies of morphological details carried out by the present author showed, however, the presence of points of difference that can serve to distinguish the two genera. They may be summed up as follows:

	Sphenomeris	*Lindsaea*
rachis-ridges	continuous on both sides	interrupted on the acroscopic side
indusium	short, attached at the base and at least part of the sides	short, attached only at the base, or elongate
sporangia	large, over 300 μ long (exc. *S. clavata*), > 14 indurated annulus-cells	smaller, rarely slightly over 200 μ long, mostly 9–14 indurated annulus-cells

The importance of the structure of the rachis for the taxonomy of ferns was fully recognized by HOLTTUM (1947). In the Lindsaeoid ferns, the adaxial side of the axes is channelled, the channel bordered by ridges which, at least on the basiscopic side, are continueus with those of the axes of the next higher order and with the thickened edge of the leaflets. (There are a few exceptions to this rule, e.g. in *L. macraeana*, where the adaxial face of the petiole and rachis is raised beyond the point of insertion of the pinnules and not sulcate). In *Sphenomeris* and *Odontosoria* these ridges are continuous on both the acroscopic and the basiscopic side; in *Lindsaea* they are interrupted on the acroscopic side (in the "axil" of the junction.) In some species this interruption is not too well-marked (e.g. in *L. virescens*), but generally it can be observed.

---

*) Hybridization in itself is not quite sufficient to warrant inclusion in one genus; there are a few examples of intergeneric hybrids in ferns, e.g. *Pleuroderris michleriana*, supposed to be *Dictyoxiphium panamense* × *Tectaria* (*rivalis*?). The hybrids *Camptosorus* × *Asplenium* and *Ceterach* × *Phyllitis* should not be taken as examples, as inclusion of all these genera in *Asplenium* is perhaps more natural.

The indusium of *Sphenomeris* (which has uni- to quadrinerval sori) is attached at the base and at least part of the sides; its base, particularly in short sori, tends to be convex, and in most species the sporangia do not strongly protrude at full maturity. In *Lindsaea*, on the other hand, the indusium of species with short (uni- or binerval) sori is attached at the base only, with tendency to be concave, more or less horseshoe-shaped. This is clearly observed in *L. bifida* and its relatives and in short sori of *L. virescens*. In species with long (coeno-) sori it is sometimes more or less attached at the sides, but these differ widely from *Sphenomeris* in other characters.

The sporangia of *Sphenomeris* are large, over 300 μ long and 200 μ wide, with the sole exception of *S. clavata*, where they are about 220 × 170 μ; their number per sorus is mostly small, which is particularly noticeable in uninerval sori. *Lindsaea* has smaller sporangia, most of them between 130 and 165 μ in length, in a few species (nos. 4, 5, 27, 28, 30, 33, 42, 43, 44) slightly over 200 μ long, but all these species are clearly Lindsaeas by the virtue of other characters. The number of sporangia is large in *Lindsaea*, even in uninerval sori. The shape of the spores cannot be used as a differential character, as monolete and trilete spores occur side by side both in *Lindsaea* and *Sphenomeris*.

An additional differentiating character is found in the rhizome scales. Those of *Sphenomeris* are either very long, in some species over 5 mm, and have a very long subulate apex of only one row of cells, or they are shorter, but retain the very long hair-like apex (e.g. in a form from São Tomé called *Stenoloma chinense* var. *divaricatum* (Christ) Alston by ALSTON 1944, p. 73, which probably represents a separate species), or all of them, not only the reduced ones, are of one row of cells throughout or practically throughout (e.g. in *S. clavata*). The scales of *Lindsaea* are ovate to narrowly lanceolate, up to 2 mm long (in a few cases longer, but then without a long subulate apex), the apex of one row of cells is comparatively short or wanting, and only the strongly reduced scales occurring together with the larger ones in many species are of one row of cells throughout (fig. 2, 4, 5).

We see, then, that although the architecture of the leaf and the shape of the ultimate divisions alone are not sufficient to separate *Lindsaea* and *Sphenomeris*, there are other characters that help to place species of doubtful alliance. There is a gap between *Sphenomeris* and *Lindsaea* that separates them clearly; from this, however, we must not conclude that it is easy to define them. Two of the characters mentioned above as typical for *Sphenomeris*—acroscopically not interrupted rachis-ridges and large sporangia—do occasionally occur to a certain extent in *Lindsaea*; and the small scales of some Lindsaeas are approached by those of certain species of *Sphenomeris*. In these cases, however, the combination of all other characters presents sufficient evidence to place these species in one of the two genera.

It has been possible to study most species referred to *Sphenomeris* (or "*Stenoloma*"). In the writer's opinion, the following species have their natural place in this genus:

S. alutacea (Mett.) Copel., New Caledonia.

S. chusana (L.) Copel., widespread in the tropics of the Eastern Hemisphere.

S. deltoidea (C, Chr.) Copel., New Caledonia and adjacent islands.

S. killipii (Maxon), Colombia.

S. melleri (Hook.) C. Chr., Madagascar.

S. retusa (Cav.) Maxon, Philippines, New Guinea, etc. (probably including *Odontosoria decipiens* (Cesati) Christ)

S. spathulata (Maxon), Colombia.

S. veitchii (Baker) C. Chr., North Borneo.

S. clavata (L.) Maxon, Florida, Bahamas, and Greater Antilles, the type species of the genus; it has smaller sporangia than any of the above-named species, and very narrow scales, shared only with *S. chusana.*

Stenoloma bifidum (Klf.) C. Chr., *S. decompositum* (Bak.) C. Chr. and *S. eberhardtii* (Christ) Ching constitute a group of closely related, very primitive species of *Lindsaea,* more fully discussed in connection with the first-named species and on p. 135.

It is not impossible that *Sphenomeris* is not a natural genus, but was developed along several distinct lines. In this connection it may be of interest that two types of sporangia are found in the genus. One possesses an annulus the indurated part of which touches the apex of the stalk of the sporangium and is there slightly oblique, a condition found throughout *Lindsaea* (fig. 21) (except in the section *Tropidolindsaea,* fig. 20) and in *Ormoloma* (fig. 19); in the other, the last indurated cell is separated from the stalk by one non-indurated cell. The first type was found in *S. alutacea, S. chusana* and *S. clavata,* the other in *S. retusa, S. melleri, S. spathulata, S. killipii,* and *S. deltoidea,* (fig. 18), but in some of these species the lowest indurated cell almost reaches the stalk, and the character is probably of comparatively little importance. A revision of *Sphenomeris,* preferably connected with one of the Old-World Lindsaeas, would be necessary to decide whether *Sphenomeris* is a natural entity or not. In such a revision, it would also be necessary to demonstrate in what way the strongly dissected forms of *Tapeinidium* (mostly from New Caledonia) can be separated from *Sphenomeris* in a satisfactory way; at present the writer is unable to suggest in what direction the solution should be sought.

5. THE PLACE IN THE SYSTEM

The first species of *Lindsaea* were described in *Adiantum,* those of *Sphenomeris, Odontosoria,* as well as highly compound forms of *Lindsaea,* mostly in *Davallia.*

As mentioned before, many authors placed *Lindsaea* in the Davallioid (or Dicksonioid) ferns (in an inclusive sense, comprising also the genera centering around *Dennstaedtia,* now considered to form a special group), although sometimes in a group *Lindsaeae* etc. of lower rank; examples are PRESL (1836), HOOKER & BAUER (1842), J. SMITH (1842), METTENIUS (1856), CHRIST (1897), DIELS (1902), VAN ALDERWERELT VAN

ROSENBURGH (1908), SIM (1915), BOWER (1928), and PÉREZ ARBELÁEZ (1928); by others it was classified as a separate tribe etc., all by itself, or associated with closely allied genera, some of which are now united with it, such as *Synaphlebium* J. Smith, *Isoloma* J. Smith and *Schizoloma* Gaud. As examples may be given HOOKER (1844–46). FÉE (1852), MOORE (1857), BAKER (1870, 1874), KUHN (1882). In both cases, *Lindsaea* was usually followed in the system by *Adiantum*, which formed a group of its own or was the first genus of the *Pterideae*. But rarely was *Lindsaea* included in one group with *Adiantum*: KAULFUSS (1827).

CHRISTENSEN (1938) definitely assigned the Lindsaeoid ferns to the rank of a subfamily of the *Polypodiaceae*. Here they appeared in the second place, after the *Dennstaedtioideae* and before the *Davallioideae*, thus in a position that indicated primitiveness. CHING (1940) raised them to family-rank in a similar position. COPELAND (1947) included them in his *Pteridaceae* as a group of probably remote independent origin (p. 79). HOLTTUM (1917, 1949) placed them in his *Dennstaedtiaceae* between the *Dennstaedtioideae* and the *Davallioideae*, which is in close agreement with CHRISTENSEN's ideas. In the second publication cited, HOLTTUM expressed some doubt on the naturalness of inclusion in the *Dennstaedtiaceae* and suggested they might perhaps better be put in a separate family of their own (p. 286), but he kept them in that family in 1954.

It appears to the author that at the present stage of our knowledge it would hardly be justified to recognize a family *Lindsaeaceae*. It is true that the alliance to the Dennstaedtioid ferns is not very close, and that to the Davallioids, which differ markedly by their mostly peltate scales, articulate stipes, and much more complicated vascular system of rhizome and stipe, is even less evident; but as long as we cannot conclude with reasonable certainty whether some supposedly primitive characters of the Lindsaeoids, particularly the very simple stele, are signs of true primitiveness or are due to reduction, it would be rash to remove them from the vicinity of these groups, which, at any rate, seem to be their closest relatives. It seems best to treat them as a subfamily; whether of the *Polypodiaceae* or of the *Dennstaedtiaceae* *) (which, in the author's opinion, are a more natural entity than Copeland's *Pteridaceae*) depends on the more modern or more conservative attitude one assumes in the classification of the leptosporangiate ferns; the author would at present prefer the second alternative.

6. CYTOLOGY

In recent years, cytological data have contributed very materially to clear up the taxonomy of species as well as larger groups of ferns. We owe most contributions in this field to the brilliant work of I. MANTON. Unfortunately, in the case of the *Lindsaeoids*, the chromosome numbers do not furnish much new insight, neither for the delimitation of the genera nor for the establishment of the affinities

---

*) For the name of this family, see Morton in Am. Fern Jo. 46:159 (1956).

of the whole group, although it must be admitted that so far they are known in a very small number of species only.

The following data have been taken from Manton & Sledge (1954) and from Manton's appendix to Holttum (1954). The author is much indebted to Professor Manton for her permission to include some additional unpublished data which she was kind enough to communicate. All are from Old World species.

		origin	n
Lindsaea	caudata	Ceylon	82
	concinna	Australia	47
	cultrata	Ceylon	82
	”	”	± 150
	decomposita	Malaya	± 50
	”	”	± 100
	ensifolia (Schizoloma)	Ceylon	88
	nitida	Malaya	± 47
	parallelogramma	”	47
	pectinata	”	± 50 (47?)
	scandens f. terrestris	”	± 47
Sphenomeris	chusana	Ceylon	± 100
	”	Malaya	± 145–147

Although the majority of the species have about 50 as basic number, with which *Sphenomeris chusana* agrees, several do not seem to fit at all; these are morphologically not particularly distinct, except *L. ensifolia*. It is to be hoped that more data will be available before long, also of species from the Western Hemisphere. The supposed affinity to the Dennstaedtioid and Davallioid ferns has so far not been found to be reflected by the chromosome numbers; Dennstaedtioids: *Microlepia* n = 43, *Hypolepis* n = ca. 104, *Dennstaedtia* n = prob. 32; Davallioids: all n = 40.

7. Morphology and anatomy

The most detailed accounts on the anatomy and morphology of the Lindsaeoid ferns have been given by Bower (1923, 1928), Pérez Arbeláez (1928) and Wagner (1952 b.) The two last-named publications are in the following simply referred to as "Pérez Arbeláez" and "Wagner."

Some aspects of the morphology have already been dealt with in the preceding paragraphs and are not again discussed extensively. For details of the laminal morphology, the reader is referred to the next paragraph.

The observations on anatomical structures reported in this paragraph are based on sections of samples of such material as was readily available or particularly suitable. A complete survey of the anatomy of all species would, of course, fall outside the scope of the present revision. As it is quite possible that the results obtained from one or a few species are not generally applicable, especially as to details,the species from which they were taken are mentioned as a rule.

Most sections were prepared from herbarium specimens, as the author had no access to fresh material, except several wild plants of *L. stricta* which Dr. G. R. Proctor, Kingston, Jamaica, was kind enough to send, and a leaf of the Asiatic *L decomposita* from the greenhouses of Kew Gardens. That so little cultivated material has been available is due to the fact that Lindsaeoid ferns are hardly ever kept alive in greenhouses for a long time, especially species of *Lindsaea*, and their spores refuse to germinate. Herbarium specimens prepared from cultivated plants are exceedingly rare. KUNZE's statement (Linnaea 21: 229, 1848): "Qua ex causa Lindsayae culturae resistant, nescio. Sporae optimae notae.... nunquam germinarunt" still holds good. We do not know the reason.

All sections were prepared by hand, with so-called single-edge razor-blades on a substrate of soft wood. This method proved to yield good results in a very short time. Sections of leaves were mostly stained, either with safranin or with ferrichloride and tannic acid. Fragments of leaves were cleared in dilute KOH or NaClO, stained with the afore-mentioned agents, and mounted in glycerine-jelly. Sections of rhizomes and petioles were mounted in the same way without staining; these organs were softened before sectioning by short immersion in a solution of "Aerosol O.T." (a commercially available detergent) in distilled water and methyl-alcohol. The author is indebted to Dr. F. Meyer, St. Louis, Mo., for drawing his attention to this very useful agent. It also proved invaluable in preparing slides of rhizome-scales and sporangia; the rhizome or sorus was moistened with a few drops of "Aerosol"-solution, and scales or sporangia could be scraped off practically without any loss or breakage. Afterwards they were mounted in lactic acid which apparently did not have a swelling effect but made them somewhat more translucent, and ringed with ringing cement.

The author is very much indebted to Mrs. P. Y. de Leng–Doewes who prepared for him the majority of the sections.

a. The rhizome

The stele of most Lindsaeoid ferns is of a peculiar type, as yet not observed in adult rhizomes of any fern outside this group. It is known as the *Lindsaea*-type and was discovered by TANSLEY & LULHAM (1902). It was later commented on by BOWER (1923, p. 146/47; 1928, p. 31), PÉREZ ARBELÁEZ (p. 55/56), OGURA (1938, p. 52, 373), COPELAND (1947, p. 79), and others. It is essentially a protostele, but inside the xylem a strand of phloem is found (see BOWER, fig. 136 = fig. 600, fig. 137, PÉREZ ARBELÁEZ, fig. 24, etc.). This internal phloem is not accompanied by pith or by an endodermis, as is the case in a solenostele, although a small strand of these two tissues is present inside the internal phloem near the nodes (TANSLEY & LULHAM, l.c.). The internal phloem is usually situated towards the dorsal side of the rhizome (reported by the authors cited above; checked by the writer in *L. lancea*, *virescens*, *protensa*, and *Sphenomeris clavata*), but occasionally approximately central (in both species of *Ormoloma* where it is very large and occupies about one-half of the diameter of the stele). A true solenostele, with internal endodermis and pith, has been reported in some species of *Lindsaea* ("*Odontoloma*", Bower, 1923, p. 147), in *Odontosoria* (id. 1928, p. 31) and in some species of *Sphenomeris* (S. *retusa*, Bower, l.c.; *S. alutacea*, Pérez Arbeláez, p. 56).

The fact that the *Lindsaea*-type of stele is a kind of intermediate between protostele and solenostele and that it has been found in young stages of genera where in mature plants true solenosteles are found ("*Pteris aquilina*", "*Nephrodium molle*" and *Anemia phyllitidis*, Tansley & Lulham, l.c., p. 160) has induced several authors to regard it as a true intermediate, that is, from a phylogenetic viewpoint. These arguments seem to the present author to be by no means conclusive; the possibility that the *Lindsaea*-type is a reduced type of solenostele, already indicated by Copeland (l.c.), should be seriously considered. The relation between diameter and structure of the stele in different species found by Bower (1928, p. 31), i.e. stouter rhizomes having a solenostele, more slender ones a *Lindsaea*-stele, shows how careful we should be before assigning any phylogenetic significance to this character.

The xylem, consisting mainly of tracheids of rather variable diameter with scalariform pitting, is approximately circular in cross-section and is surrounded by a thin layer of phloem, the structure of which has not been examined more closely, as herbarium-material is hardly suitable for this purpose. On the outside of the phloem are the pericycle and the endodermis, which in their turn are surrounded by a few (3–4) layers of thin-walled, parenchymatous cortex-cells filled with starch-grains. These pass to the outside abruptly into a thick strong sheath of highly sclerenchymatous outer cortex consisting of about 10–15 layers of cells of rather variable diameter, the outer ones mostly smaller and somewhat less sclerified. All walls are strongly tinged with brown, and as a rule all cells contain starch-grains. This thickened cortex occupies 1/2 to 3/4 of the diameter of the rhizome, thus rendering it difficult to dissect; the layers between the thickened cortex and the xylem are usually crushed or torn in sectioning. The little differentiated peripheral layer of cells that constitutes the epidermis of the rhizome bears the scales. These are attached to a few cells along a short line which in very broad scales is surpassed by their lateral edges, giving them a subpeltate appearance (see also Pérez Arbeláez, fig. 23 j). The equal thickening of all walls of the scales can be well observed in cross-sections. For further notes on the scales, see pp. 105, 118.

The narrow, reduced scales are most numerous near the apex of the rhizome because they are more readily caducous than the broader ones; relatively few are found on older parts.

b. The root

The roots are attached to the ventral and lateral surfaces of the rhizome, sometimes close to the dorsal side. Pérez Arbeláez described them as arising in pairs below each leaf. Such a regular distribution was not observed by the present author; moreover, their number is often considerably larger than twice that of the leaves or leaf-bases. They are about 1/4–3/4 mm in diameter and ramify freely in their distal part in a non-dichotomous way. Root-hairs are present almost throughout.

In cross-sections (fig. 1) a simple protostele without internal phloem can be observed. The xylem consists of a few large and two groups of small tracheids (diarch), surrounded by phloem, a discontinuous layer of pericycle-cells, and the endodermis. The stele is approximately hexagonal in cross-section, as the innermost layer of cortex consists of six (or a few more) very large cells, the space between them being occupied by the stele; the outer layers of the cortex are formed by smaller and more highly sclerified cells. All cortex-cells contain starch (not indicated in the figure).

c. The petiole

The petioles are attached to the dorsal side of the rhizome. When they are remotely disposed, they are aranged in one row only, but where they are close together they often show a tendency to be more or less distichous. Their length varies with the size of the leaf; in small leaves they are relatively short, much shorter than the laminal part, but in large leaves they are much longer, often considerably longer than the blade. They are continuous with the rhizome, the xylem of which is broken at the nodes where inner and outer phloem come into contact; but true leaf-gaps are absent, as the phloem is unbroken (see Tansley & Lulham, l.c., Bower, l.c., etc.; not checked by the author.) The petiole is terete at the base, otherwise at least the adaxial surface is flattened or mostly sulcate. The abaxial side is terete, angular, or channelled, depending on the species. These angles or channels do not seem to appear as a result of drying as was suggested by Wagner (p. 87), but represent the natural condition, as can be observed in fresh material and also in sections, where no shrivelled or collapsed cells are found adjacent to these structures. The description of the channels, ridges, etc., sometimes given in field-notes, is in close agreement with the condition observed in the dried specimens.

The stele of the petiole is approximately triangular in cross-section, rarely oblong (observed in *L. protensa*). The xylem is arranged in one deeply U- or V-shaped strand with the sinus on the adaxial side. The smallest elements occur at the bottom and on the outer sides of the arms; the xylem is apparently triarch. This kind of petiolar stele is called the *Loxsoma*-type. Pérez Arbeláez figured the stele in the petiole of *Sphenomeris chusana* as consisting of two separate strands of xylem (fig. 24 1, as "*Lindsaya chinensis*"); but according to the present author's observations which were, however, carried out in other species, there is always a strand, sometimes very narrow, of small tracheids that links the two arms together at the base. The sinus of the xylem is filled with parenchymatous tissue. The phloem is most strongly developed towards the ends of the arms; it penetrates into the sinus for some distance and is only very weakly developed at the abaxial side of the bottom. There is a distinct pericycle of 1–3 layers of cells and an unbroken endodermis. The structure of the cortex is essentially the same as in the rhizome, but there are usually more layers of internal non-sclerotized cells, and the transition to the outer heavily thickened layers is mostly more gradual. The thickened walls are stramineous to dark brown, depending on the species, except at the extreme base of the stipe, where the cortex is always very dark. There are no traces of pneumathode-areas with soft, well-aerated tissue which were described from other ferns by BOWER (1923, p. 169), TINDALE (1956, p. 328), and others. The petiole is apparently devoid of stomata.

d. The rachis

There is no fundamental difference in anatomical structure between the petiole and the rachis. In primary and secondary rachises the same adaxial channels are found as on the petiole, and all are continuous with each other. The ridges bordering these channels are, at least in *Lindsaea*, almost always distinctly discontinuous on the acroscopic side of a node, whereas they are continuous on the basiscopic side, as has been described above. This condition prevails practically invariably at the insertion of the pinnules. The channel is continuous to the very apex of the rachis of the highest order where its sides pass into the thickened edges of the terminal segment or pinnule.

The abaxial side is more variable in structure; it may be terete, angular, channelled, or in a few species keeled; but at least in its apical part the rachis of the highest order is almost always grooved on the abaxial side. The ridges bordering this groove fuse towards the apex of the pinna (lamina) to form a keel, approximately at the point where the pinnules are confluent into the terminal segment, or in the base of the terminal pinnule in the species where this is present.

Fig. 1: Cross-section of a root of *Lindsaea stricta* var. *stricta* (Mexía 5486). Fig. 2: Rhizome-scale of *L. stricta* var. *stricta* (Fanshawe M 240). Fig. 3: Scale from very young leaf of the same species (Blanchet 2315). Fig. 4: Rhizome-scale of *L. filipendula* (v. Lützelburg 141). Fig. 5: Rhizome-scale of *L. seemannii* (Haught 5581). Fig. 6: Cross-section of secondary rachis of *L. divaricata*, showing membranous wings on the adaxial side and a pinnule-trace to the left of the main stele (Ll. Williams 14685). Fig. 7: Diagrammatic cross-section of primary rachis of *L. stricta* var. *parvula;* cross-hatched: stele; dotted: chlorophyll-containing inner cortex; vertical lines: sclerified outer cortex. Fig. 8: Cross-section of pinnule of *L. schomburgkii* f. *densa*, showing sclerotic tissue along vein and edge (Steyermark 59474). Fig. 9: Hairs from the dorsal epidermis of pinnule of *Sphenomeris melleri* (Lam & Meeuse 5349). Fig. 10: Dorsal epidermis of pinnule of *Lindsaea arcuata*, showing hair and stomata (Skutch 3737). Fig. 11: Dorsal side of apex of pinnule of *L. virescens*, showing receptacle, indusium, and marginal strand (sporangia omitted) (Hooker s.n.). Fig. 12: Ventral epidermis of segment of *L. bifida*, showing pattern of more elongate cells above the veins and its evanescence towards the distal side ((Mexía 4066). Fig. 13: Cross-section of rachis of *L. stricta* var. *stricta* near junction with secondary rachis, showing patch of dark, sclerified cortex between the steles ("axillary cushion") (Proctor s.n.).

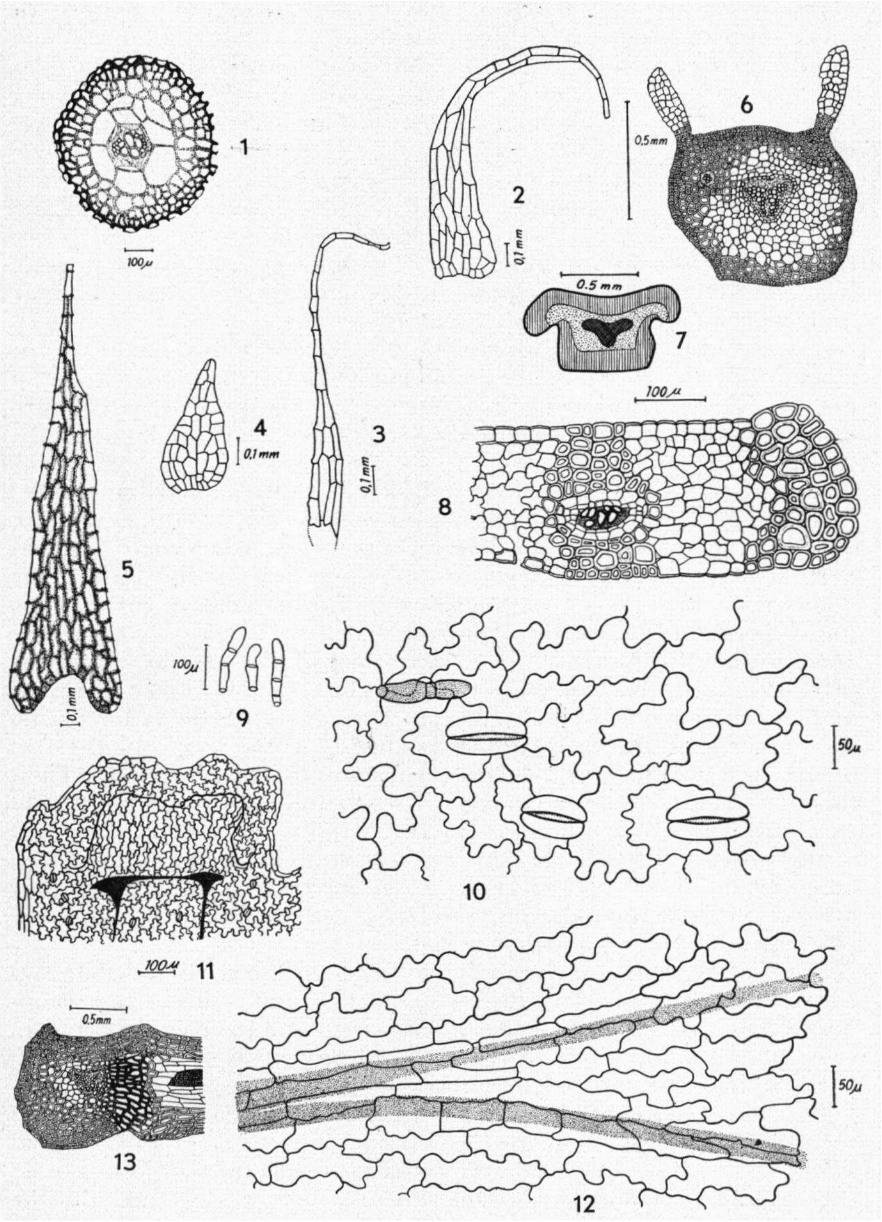

1
100μ
2
0,1 mm
0,5mm
6
0.5 mm
7
5
4
0,1 mm
3
0,1 mm
100μ
8
100μ
9
0,1 mm
10
50μ
11
100μ
0.5mm
13
50μ
12

Fig. 1—13

The vascular bundle of the rachis becomes less deeply lobed as it decreases in size and the two arms of the xylem touch across the sinus, sometimes cutting off small areas of parenchyma. The vascular supply to the secondary rachises and the pinnules is given off from the apex of the arms; the daughter-strands run for a small distance outward under a small angle, then bend sharply to the side and leave the main axis.

The outer layers of the rachis cortex are again heavily sclerified, mostly with a gradual transition to the thin-walled inner layers (see fig. 6, 13). In recently collected specimens these thin-walled layers can be seen to contain chlorophyll; this may be universally present, but probably disappears through discoloration in older material. Starch-grains are often present in addition. The walls of the thickened layers are often tinged with brown; this colour may prevail on the adaxial side (*L. stricta*), on the abaxial side (the Asiatic *L .decomposita*) or may be evenly distributed (e.g. *L. hemiptera*). The presence and distribution of this colouring matter is sometimes characteristic for the species.

On the edges of the rachises (and of the upper part of the petiole) membranous, more or less wing-like outgrowths are sometimes present. They prove to have a taxonomic importance which has thus far hardly been recognized. They are as a rule less sclerified than the rachis itself and are never tinged with brown; consequently, when the rachis itself is dark, they contrast sharply. They are found on the adaxial side of the rachises in *L. hemiptera*, on the adaxial side of the primary and on both sides of the secondary rachises in *L. divaricata*, and on the four sides of all rachises in *L. tetraptera*. In the latter species they are rather thick and taper gradually to the edge; in the two others they are of approximately constant thickness (fig. 6). Their function seems to be unknown. They definitely do not represent aerating tissue; their internal structure is not less compact than that of the cortex, although they are less sclerified. No stomata have been observed on them; moreover, in *L. divaricata* and *L. hemiptera* they are cut off from the loose inner layers of the rachis by a continuous layer of sclerotic tissue at their bases.

A structure which probably serves aerating purposes was found in *L. stricta* var. *parvula*. Here the adaxial side of the primary and secondary rachis, usually also of the upper part of the petiole, is at least in some places considerably broadened and projects beyond the abaxial portion; it is visible from the adaxial side as a ledge. This, incidentally, is the main characteristic feature of var. *parvula*. In cross-section the axis has roughly the shape of a felt hat, with the rim on the adaxial side (fig. 7). The inner layers of the cortex consist of thin-walled cells containing chlorophyll. This zone of green cells extends into the "rim" of the "hat". On the groove that separates the "rim" from the main body the sclerotic tissue that surrounds the green layer in other places is absent, and the latter almost reaches the surface. The epidermis is strongly wrinkled in this place; here one stoma was observed by the writer. It is possible that this structure represents a special adaptation to the swampy habitat with badly aerated subsoil in which *L. stricta* var. *parvula* is usually found.

A structure that to the author's knowledge has not been described so far is found in many (perhaps most or even all) species. On the abaxial side of the primary rachis in at least bipinnate leaves at the junction with a secondary rachis an oblong or cuneate swelling is found which in species with pale rachises is often darker, in species with very dark axes sometimes paler. It is particularly conspicuous in *L. cultriformis* and *L. divaricata*. Under the binocular microscope the epidermal cells can be seen to be larger and approximately round, whereas elsewhere on the axes they are quite elongate. In the taxonomic part of this paper these structures are referred to as "axillary cushions".

Their internal structure could be studied in one instance, namely, in fresh material of *L. stricta* var. *stricta* from Jamaica. In this material in a cross-section of the primary rachis at a node a large group of cortical cells was observed, mostly belonging to the inner layers with larger diameters, which were strongly tinged with brown and appeared to be somewhat more sclerified than the surrounding cells. This tissue extended to the abaxial surface and almost reached the stele of the primary rachis which it surrounded for about one-third of its circumference (fig. 13). The sections did not show whether it also extended to the stele of the secondary rachis. Similar but less extensive structures were found at the point of attachment of the pinnules; they were observed in the same material, and in a fresh leaf of the Asiatic species *L. decomposita*. The large brown cells appeared as a plate in cross-section, situated between the main and the tributary stele, but closer to the latter. From the outside these groups of cells near the base of the pinnules are not visible but it is quite possible that they are found in all species with compound leaves. In cleared material they appear as triangular patches extending from the axil of the junction some distance downwards, keeping clear of both vascular bundles.

We can only make a guess about the function of these cells. It seems likely that they have a mechanical function, possibly strengthening the point of junction in order to prevent splitting off of the divisions of higher order that in most species come off under a rather small angle (at least rachises of higher order). Perhaps the larger lumina of these cells also play a role as aerating tissue, but so far no evidence for permeability to air from the outside has been found.

Externally similar, probably analogous structures can be observed on the axes of *Odontosoria* spp., notably *O. aculeata*.

e. The laminal parts

The lamina is practically always anadromic in the more than once pinnate Lindsaeoid ferns, the only ones where this character can be observed. The basal pinnule or secondary pinna is inserted on the acroscopic side of the secondary rachis. The basal pinnule is often strongly reduced and cuneate, especially if it is inserted very close to the junction with the rachis of next higher order, almost in the axil ("axillary pinnule") (fig. 23, 52). It is occasionally wanting; then the leaf is catadromic, but this is exceptional and never regularly found in any species. In addition to the basal pinnule, a few additional lower ones may be more or less reduced, sometimes only on the acroscopic side. The different types of pinnules and leaves of juvenile plants in terms of their general shape are discussed in the next paragraph.

In spite of their very diverse shape, the anatomy of the ultimate segments is rather uniform. A thickened strand of elongate, sclerotic cells runs along the margin. It is particularly well developed in the basal part of the basiscopic margin where it is continuous with the borders of the adaxial groove of the rachis, but it is present throughout the whole margin, although in some species, especially in those preferring dry or exposed habitats, it is much better developed and more conspicuous than in others; in *Lindsaea virescens*, for instance, it is almost absent, consisting only of one or two marginal rows of elongate, hardly thickened cells. Here the distal (apical) edge of the ultimate segments is minutely and irregularly erose; the smaller irregularities are due to certain cells of the marginal strand which project like papillae beyond the edge (fig. 11). A very obscure marginal strand is, however, uncommon. Comparable strands of sclerified cells extend along the bases of the veins in most species. The strand accompanying the main vein is as a rule united with the marginal strand of the lower edge of the pinnule for a certain distance. In a few species the sclerotic cells run along the greater part of or the whole of the veins which are elevated in dry specimens, as the leaf-tissue between them collapses in desiccation which is impossible for the sclerified tissue around the veins. In fresh material the veins are presumably immersed. Examples are *L. schomburgkii*, *L. semilunata*, *L. rigidiuscula*. The sclerotic tissue is most strongly developed on the dorsal and ventral sides of the bundles, especially the latter; laterally it consists of one layer of but weakly sclerified cells only and therefore hardly deserves to be called a sheath (fig. 8). Where it does not extend along the whole of the veins, it gradually tapers off in their distal part.

Comparable mechanical cells accompanying the veins have been described by WYLIE (1948) from the dorsal epidermis of *Adiantum*.

The epidermis of *Lindsaea*, *Sphenomeris*, and *Ormoloma* consists of cells of very irregular outline that fit into each other like pieces of a jig-saw puzzle (fig. 10, 11, 12). On the ventral (adaxial) side where they overly the veins they are more regular in shape with much less wavy walls, and sometimes also more elongate. This condition gradually disappears in the distal parts of the veins (fig. 12), but reappears above their broadened ends in sterile pinnules. All epidermal cells contain chlorophyll; this is even the case in at least some of the thickened cells of the marginal strand. The cuticle is slightly thickened, more strongly in species from exposed habitats (*L. stricta*, L. *schomburgkii*, etc.). Stomata occur more or less in groups together between the veins, in *Sphenomeris clavata* in a few rows along the veins; in most species they are not at all numerous. The stomatal apparatus is surrounded by 2–6 epidermal cells (fig. 10). The stomata are restricted to the dorsal (abaxial) surface; otherwise no differences between the epidermis of the dorsal and ventral surfaces has been found, except for the cells overlying the veins described above. The author has not investigated possible differences in epidermis-pattern between different species such as have been found, for instance, by WAGNER (1954 a) in *Asplenium*. It seems that such differences are present at least in some cases, but only as slight variations of the same pattern.

Below the epidermis on the ventral (adaxial) side one or two layers of compact tissue analogous to palisade parenchyma but with approximately isodiametric cells are found; these and the ventral epidermis contain more chlorophyll than the rest of the leaf-tissue. This results in a darker shade of green on the adaxial surface of most species. The mesophyll is a very loose tissue of cells which have projecting arms; they appear to be round or oval (or rather irregular in sections prepared from dried material) in cross-section and more or less star-shaped in optical section in entire cleared pinnules. They are in contact with each other at the ends of their branches, leaving large open spaces between them. Small air cavities are found below the stomata.

The veins are evenly forked, but the angles they form with the vein from which they stem are often not quite equal, in connection with the oblique venation, especially towards the apex of the pinnules. They consist mainly of elongate tracheids with scalariform pitting and are enclosed in a sheath of elongate mesophyll cells visible in cleared material, some of which may be sclerified, as described above. In sterile pinnules they end in the tissue, well within the margin, and are broadened at their ends where the number of tracheids lying side by side is considerably increased; these tracheids are short and broad ("storage tracheids"). No hydathodes have been found at the ends of the veins, neither in sections nor in cleared and stained material.

f. Dermal appendages

Formerly the Lindsaeoid ferns were described as glabrous. But WAGNER (1952 b, p. 111/113) drew attention to the presence of two-celled glandular hairs in *Lindsaea*, *Sphenomeris*, and *Isoloma*. The present author is indebted to him for the communication of the best method to render these hairs visible. With the naked eye or a hand-lens they cannot be observed except in a few species of *Odontosoria*. *Notably* in *O. uncinella* and *O. jenmanii*, sometimes also in *O. gymnogrammoides*, a thin cover of hairs can be seen on the primary and secondary rachises near their junction. This was not mentioned by MAXON (1913), but observed in the first-named species by KUNZE (1851). This, however, is quite exceptional, and even under the microscope they are very hard to detect in unstained material, although they sometimes contrast by their yellowish colour. Staining with safranin renders them more readily visible, but the best contrast is obtained when cleared leaf-fragments or sections are stained with ferrichloride and tannic acid. According to WAGNER (in litt.) they are most readily found in young yet fully expanded leaves, especially on the abaxial surface along the veins and proximal to the sori. This can be fully confirmed by the writer. WAGNER (l.c.) reported them from *Sphenomeris clavata*, *Isoloma jamesonioides*, and four species of *Lindsaea* (3 Asiatic ones and *L. stricta*, called by him *L. guianensis*). To these the author can add *Sphenomeris melleri* (Madagascar), *Ormoloma imrayanum*, *O. standleyi*, *Lindsaea arcuata* (fig. 10), *L. bifida*, *L. guianensis ssp. lanceastrum*, *L. klotzschiana*, *L. parkeri*, *L. pendula*, *L. portoricensis*, *L. protensa*, and *L. quadrangularis* ssp. *antillensis*, that is, practically all species where they were sought after, and in species from almost all American sections. In none of the species was the absence of trichomes definitely established; it is quite likely that they occur throughout the group. They are usually two-celled, as stated by Wagner, and about 0.10–0.15 mm long, but three- or even four-celled ones (e.g. in *Sphenomeris melleri*, fig. 9), do occasionally occur.

Very young leaves are clothed with scales similar to those of the rhizome but narrower (fig. 2, 3). They are shed at a very early stage, as soon as the leaf begins to elongate, and are persistent only on the extreme base of the stipe.

g. The sorus and related structures

The sori are borne terminally on the veins the ends of which are considerably broadened, with short, wide tracheids. In species with uninerval sori the sporangia are borne on the broadened apex of the veins; otherwise there is a vascular commissure that also consists of rather short and wide elements (see BOWER, 1928, fig. 602.). This commissure usually extends laterally beyond the outermost veinlets which bear it, especially in species with long sori. In species with short sori and in incompletely fertile pinnules of species with continuous sori the commissures are usually present between the veins stemming from an ultimate or penultimate bifurcation, but this is no absolute rule, and at the base or apex of a pinnule one vein or a pair of veins is not rarely seen to be left out of the sorus (see BOWER, 1928, fig. 601). In species with short sori the sporangia may sometimes not be restricted to the end of a vein but may slightly extend along its distal part. The indusium is then somewhat oblique and approaches the situation found in the Asplenioid genus (or subgenus) *Loxoscaphe*. This condition is regularly observed in *Lindsaea millefolium* and *L. eberhardtii* (see p. 135); a somewhat different condition prevails in *Ormoloma* where the apex of the vein is sometimes extended parallel to the margin of the pinna; the indusium is then, of course, not oblique.

The vascular tissue of the receptacle does not reach the ventral surface (fig. 14, 15). The part of the lamina that extends beyond the receptacle, sometimes called the upper indusium, is similar in structure to the rest of the lamina but is devoid of veins and often also of stomata; these have, however, been found to be present in this part of the pinnule in *L. guianensis* ssp. *lanceastrum*, *L. klotzschiana*, *L. pendula*, *L.*

portoricensis, and *L. stricta*. This "upper indusium" consists in its outer part mostly only of the two epidermal layers which touch at their inner side; stomata, if they are present, are restricted to the proximal part where mesophyll is found between them. This part of the lamina is often set off from the remainder by a shallow groove on the adaxial side along the receptacle which may be visible to the nake eye, e.g. often in *L. portoricensis*. The edge of the "upper indusium" is formed by the sclerotic strand already described.

The indusium is attached along the proximal side of the receptacle (fig. 14). Laterally its attachment exceeds the extension of the receptacle. In species of *Lindsaea* with short sori and in *Ormoloma* it is attached by its base only; in species with longer sori the sides, too, may be more or less adnate, but they often taper considerably and it is then difficult to decide whether only the base or also part of the sides are attached. In *Sphenomeris* at least part of the sides are adnate to the epidermis.

At its base the indusium consists of several layers of cells, in its outer part of one layer only, or the latter condition prevails almost throughout, depending on the species. The outer edge is formed by a thickened strand similar to that of the laminal margin but much less developed. The cells are comparable to the epidermal cells of the lamina but tend to be more regular in shape and more elongate in a direction at right angles to the edge, except the marginal strand (fig. 11). In most species the indusium is reflexed at full maturity, apparently pushed aside by the bulging, dehiscing heads of the sporangia, but it seems that it becomes fixed in this position as it remains reflexed in cross-sections where the heads of the sporangia are almost always lost in sectioning. There is perhaps an active process involved that acts through the epidermal cells at the attachment of the indusium, pushing it back when the sporangia approach maturity.

The sporangia occur in several rows on the receptacle. Bower (1928, p. 32/33) found them to originate in an initially gradate sequence that passed into a mixed state in *L. linearis*. The present author's material was not adequate to furnish additional data on this subject. They are long-stalked, the slender stalk consisting of about 4–7 stories of cells; at the base each story is formed by one or two cells only, in the upper part by three, and the cells of different stories may overlap considerably. The uppermost group of three cells is short and broad and forms a kind of pedestal for the head of the sporangium (fig. 15, 20, etc.). Paraphyses are frequently found intermingled with the sporangia; they resemble the trichomes of the vegetative parts. The autor found them in *L. cultriformis*, *L. dubia* (fig. 15), *L. hemiglossa*, *L. hemiptera*, *L. javitensis*, *L. lancea*, *L. quadrangularis* ssp. *terminalis*, *L. spruceana*, *L. stricta*, and *L. surinamensis*, but it is not unlikely that they are generally present. In ordinary slides prepared by scraping the sporangia off the receptacle with a flattened needle paraphyses are mostly not found; they are best observed when also pieces of the receptacle are scraped off, in sections, or in cleared and stained material. They are usually about 70 μ long and consist of two cells. Wagner (1952 b, fig. 30) figured three-celled paraphyses in

L. stricta (as *guianensis*) and in *Sphenomeris chusana*; but the one figured by him in fig. 30 q may have been a sporangium the development of which was arrested at a young stage. The present author found large, up to 9-celled, paraphyses in *Sphenomeris melleri* (fig. 16), where they are so numerous and conspicuous that they are already visible under a binocular microscope. The strange forked or club-shaped paraphyses found by Kunze in *L. reniformis* (1840, p. 32; t. 16 fig. 2) have not been observed by the writer.

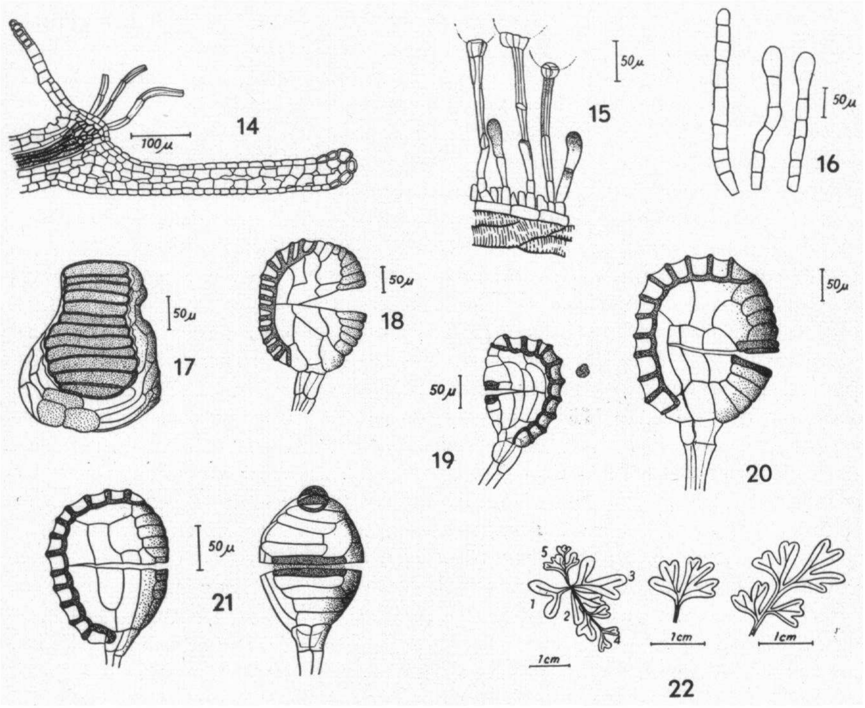


Fig. 14: Cross-section of edge of pinnule with sorus of *Lindsaea lancea* var. *lancea;* heads of sporangia detached (Krukoff 11264). Fig. 15: Receptacle, paraphyses and sporangia (without heads) of *L. dubia* (Steyermark 74684). Fig. 16: Paraphyses of *Sphenomeris melleri* (Lam & Meeuse 5349). Fig. 17: Sporangium of *Odontosoria aculeata*, showing oblique annulus at the point of insertion of the stalk (Valeur 291). Fig. 18: Sporangium of *Sphenomeris deltoidea* (Franc 358). Fig. 19: Sporangium of *Ormoloma standleyi* (Brade s.n.). Fig. 20: Sporangium of *Lindsaea seemannii* (Lehmann 737). Fig. 21: Front and side view of sporangium of *L. stricta* var. *jamesoniiformis* (Maguire & Fanshawe 23159). Fig. 22: Young sporeling and detached leaves of slightly older sporeling of *L. cultrata;* leaves of plant at left numbered in sequence, no. 5 not quite expanded (Kew Gardens).

The head of the sporangium is broadly elliptic, not more than about 1 1/2 × as long as wide, often less. The annulus tends to be slightly oblique, especially towards the base (see fig. 17), but is mostly interrupted at the stalk; it is continuous or almost so in the species of the section *Tropidolindsaea* (fig. 20). The indurated part is always strongly interrupted and never extends along the insertion of the stalk. The number of indurated cells is usually between 9 and 14, the number in one species mostly not varying by more than 4 or 5. A stomium is always present; it consists usually of 2 or 3 narrow transversely elongate cells, but 4-, even 5- or 6-celled stomia are sometimes met with in the same sorus as 2- or 3-celled ones. The slit occurs between the stomial cells but was in a few instances observed to be situated below them. The sporangia are mostly largest in those species of *Lindsaea* which occur in open habitats. This phenomenon is not found in *Sphenomeris* where all species have large or very large sporangia, whether they inhabit open localities (*S. alutacea*, *S. chusana*, *S. clavata*) or forests (*S. killipii*, *S. melleri*). The sporangia of *Ormoloma* (fig. 19) are very similar to the type commonest in *Lindsaea*, but the lowest indurated annulus-cell usually reaches to the middle of the uppermost stalk-cell and the interruption of the annulus is only very short. In *Sphenomeris* the structure of the sporangium is rather variable (see also p. 106); in some species they are very much like those of *Lindsaea*, e.g. in *S. clavata*, in others, especially in *S. alutacea* and *S. deltoidea*, the distinction between the indurated and the non-indurated part of the annulus is rather weak. The stomium-cells in these species are hardly or not more indurated than the adjacent cells, although they are laterally more elongate, and the edge of the sporangium opposite the indurated part of the annulus consists of an almost equal series of flat, elongate, stomium-like cells (see fig. 18). The spores of *Lindsaea* are with few exceptions smooth; they are minutely tuberculate in the Asiatic *L. eberhardtii*, not muricate, as stated by TARDIEU-BLOT & CHRISTENSEN (1939); see also WAGNER's illustration of the spores of *L. ensifolia* (1952 b, pl. 5 b). A perispore is always wanting. In most species of *Lindsaea* the spores are trilete; in most species from exposed habitats they are semiglobose, rather strongly coloured and rather large, whereas forest-inhabiting species mostly have deeply lobed tetrahedral spores which have probably collapsed; they are pale or hyaline and rather small. In *Sphenomeris* monolete and trilete spores are more evenly distributed; they are all large and strongly coloured, not collapsing. In the few American species of *Lindsaea* with monolete spores (*L. cubensis*, *cyclophylla*, *L. macrophylla*, *L. pallida*, *L. quadrangularis* ssp. *quadrangularis*, and the three species of the section *Tropidolindsaea*) these are flattened-elliptic or bean-shaped and hyaline or pale brown.

The taxonomic value of the spore-shape is not high but varies with the groups. In one subspecies of *L. quadrangularis* they are monolete, in the three others trilete; even if the treatment of these forms as subspecies of one species is proved to be unnatural, they are certainly closely related. *L. ensifolia*, rather closely allied to *L. macrophylla* with monolete spores, has trilete ones. *L. cyclophylla* is very close to *L. reniformis*, the spore-shape being one of the few diagnostic characters. On the other hand, the isolated position of the section *Tropidolindsaea* is stressed by the invariably monolete shape of their spores. There are a few other genera of ferns, e.g. *Vittaria*, where spore-shape is likewise not constant.

It has not been possible to make exact counts of the number of spores per sporangium. In some slides unopened, sufficiently translucent sporangia were present to permit close estimates. In some species the number was found to be probably 16, while in others it was definitely higher, but not much more than about 30. In this case it may be assumed that it is essentially 32, although it may be slightly smaller through abortion of one or two sporemothercells. In the special part, spore-numbers that were approximately established in this way are given as 16? and 32? respectively. BOWER (1928) gave the spore-number in *Lindsaea* as 16 or 32.

8. EVOLUTIONARY TRENDS

The Lindsaeoid ferns possess a number of characters that with justification may be considered as primitive, which has been the motive for regarding them as one of the most primitive groups of *Polypodiaceae* sens. lat. or of such families as have been split off from them. The creeping, radially symmetric rhizome of very simple structure and without leaf-gaps, the simple vascular supply of the stipe, the unspecialized scales may be interpreted as such. It is, however, open to doubt whether the Lindsaeoid stele in itself is evidence of primitiveness as opposed to the solenostele found in some representatives of the same group; it was supposed to be a transition between a true protostele and a siphonostele by Tansley & Lulham, Bower, and others. This has been discussed more fully in the preceding paragraph. Another point the author wishes to stress is that in his opinion the reduced rhizome-scales of many Lindsaeoids cannot be interpreted as transitions between hairs and scales as has been done on several occasions. The reduced ramenta called "hairs" or "bristles" are flattened, not cylindrical or moniliform, their cells are exactly like those of the true scales that mostly accompany them, and in species where the "bristles" prevail, undisputable scales with at least two rows of cells at the base are found sparsely intermingled with them (*Sphenomeris clavata* and *chusana*). They are quite different from the trichomes with presumably glandular function found on the foliar parts as was already pointed out by WAGNER (1952 b, p. 80). These hairs are perhaps reduced, and it is not impossible that the Lindsaeoid ferns stem from ancestors which had a more liberal indument of both hairs and scales; they may, at any rate, not be looked upon as a group where the transition from hairs to scales is taking place, so to speak, under our eyes. Generally the importance of the presence of hairs versus scales seems to have been somewhat overstressed in morphological and phylogenetic discourses on leptosporangiate ferns.

The uninerval submarginal sorus borne on the end of the vein present in *Tapeinidium*, *Odontosoria*, *Ormoloma*, and certain species of *Sphenomeris* and *Lindsaea*, is in all probability a primitive structure. But in *Sphenomeris* and—to a much greater extent—in *Lindsaea* we find along with it sori borne on an intramarginal commissure, culminating in the coenosorus with a receptacle uniting all vein-ends of a pinnule. This point is discussed more extensively below.

In this connection BOWER's findings with regard to the development of the sorus in *Lindseae linearis* should be mentioned. He reported (1928, p. 33, fig. 603) that "the receptacle arises from the actual margin of the blade into which the marginal segmentation is directly continuous, the indusial flaps arising as superficial outgrowths. The upper is stronger from the first, and elongates into the false margin of the blade, while the receptacle is tilted slightly towards the more delicate indusium." This is of great importance from a viewpoint of comparative morphology, but as the "false margin" exhibits the same structure as the rest of the blade, apart from the absence of veins and sometimes of stomata, whereas the "lower indusium" is much simpler, the sori may for practical purposes, when the mature condition is described, be called intramarginal and dorsal.

The slightly oblique, sometimes hardly or only shortly interrupted annulus (though always with strongly interrupted indurated part) is further evidence of primitiveness. On the other hand, the small number of spores in the sporangia (in *Lindsaea* probably 16 or 32) and the small number of sporangia per sorus in many species of *Sphenomeris* is an advanced character. Finally the venation, with dichotomous free or less often anastomosing veins (but always without included veinlets) is very probably a primitive feature. A midrib is almost always absent; the main vein, if there is one, is flexuose, suggesting sympodial origin.

The lamina

In few fern-genera such a great diversity of leaf-pattern is found as in *Lindsaea*. Here MARTENS & GALEOTTI's dictum "... cette belle famille des Fougères, où la nature a déployé dans le feuillage un luxe de formes que l'on ne rencontre dans aucune autre famille de plantes d'un ordre plus élevé" (1842, p. 3) is almost equally true within one genus.

As a result of his studies the author arrived at certain conclusions with regard to primitive versus derived types of leaves and the ways in which they are connected. In order to facilitate the understanding of the following pages, these conclusions are summed up in a scheme, where primitive characters appear at the beginning, derived ones at the end of each series.

Lamina: decompound—bipinnate (subtripinnate) *cum impari*—simply pinnate (with reduced confluent upper pinnules)—simply pinnate (with large terminal pinnule)—simple.
Pinnules (segments): cuneate, more or less divaricately furcate—dimidiate, incised—dimidiate, entire—hardly dimidiate, with an equal-sided apex.
Sori: uninerval—bi-plurinerval, discontinuous—continuous.

As far as other characters are concerned, monolete spores are probably derived, trilete ones primitive. The width of the indusium seems to be of little phylogenetic significance, but very narrow indusia are probably more derived.

The highly dissected leaf-type met with in *Odontosoria*, *Sphenomeris*, and some species of *Tapeinidium* and *Lindsaea*, with cuneate or linear ultimate segments and decompound architecture, should be looked upon as the most primitive. This opinion is shared by other Pteridologists, especially by HOLTTUM (1947), who believed this to be true also in other groups of ferns, notably in the Asplenioid, Blechnoid, and Lomariopsidoid ferns. It can hardly be denied that the highly compound leaf-type in the Lindsaeoids, if any, links them with their supposed relatives, the Dennstaedtioid and possibly also the Davallioid group, whereas the more condensed types, especially those with dimidiate pinnules, are not comparable to anything found in those groups, although analogous types are met with in much more remotely related genera (see below). Finally, phytogeographical data are in favour of this view. HOLTTUM (l.c.) regarded *Odontosoria* as the most primitive *Lindsaeoid*, but in the writer's opinion it seems more likely that the scandent, often spiny leaves with indefinite growth and subopposite primary pinnae of that genus arose as a specialization. It is difficult to decide whether *Sphenomeris* or the decompound group in *Lindsaea* is more primitive; *Sphenomeris* is perhaps more diverse, and if it can be shown to be polyphyletic, the evidence would be in favour of *Lindsaea* as the basic genus, a possibility pronounced by COPELAND (1947, p. 54). A further possibility would be the derivation of all these genera from an extinct parental form.

The leaf-type with dimidiate pinnules, the commonest in *Lindsaea*, is apparently derived from the previous type, largely through simplification. If on the penultimate division of a leaf of the first (decompound) type the number of ultimate divisions is strongly reduced, the only that are left are, for instance, a large acroscopic, perhaps forked, basal segment (because of the anadromic pattern of dissection found throughout the Lindsaeoids the first segment is always found on the acroscopic side), a smaller basiscopic and a still smaller apical one, this again more strongly developed on the acroscopic side. This is what is actually observed in the upper, reduced primary pinnae of e.g. *L. bifida* (fig. 36). If we turn to still more reduced pinnae above them, we see the basiscopic segment shift to a terminal position, pushing the apical segment to the acroscopic side. No segments are left on the basiscopic side, and the pinna looks rather like a dimidiate, but dissected pinnule of, e.g., *L. virescens* (fig. 34). Thus, together with the shifting of the basiscopic segment to the apex for which no "explanation" can be offered here, simplification (that is, reduction of the number of segments and also of their complexity) is the only process required to produce a dimidiate leaflet from a more highly dissected, merely anadromic, non-dimidiate one. This, of course, does not mean that simplification in such a case always results in the formation of a dimidiate pinnule. Yet strong arguments in favour of the concept developed above are found in some other genera. In *Odontosoria* there is only one species with ultimate segments that approach the dimidiate type, namely *O. uncinella*, which is the least compound species of the genus. Here, too, we see the transition from more highly dissected segments with approximately cuneate or flabellate lobes to dimidiate leaflets in the apex of the pinnae (fig. 25). The analogy with what is observed in *Adiantum* is discussed more at length in the next paragraph.

Together with the process that leads to dimidiateness we observe a tendency towards fusion of the segments which in turn creates the opportunity for the sori to fuse, as two or more vein-ends are found side by side in one ultimate segment, not separated by an incision. In *L. bifida* the sori are uni- or less often binerval, those of *L. virescens* are mostly bi- to quadrinerval. The process of the fusion is also met with quite independent from that leading to dimidiateness in *Sphenomeris* where certain species have strictly uninerval sori (*S. killipii*, *S. spathulata*) and others have broader segments with bi- to quadrinerval sori (*S. alutacea*, *S. retusa*, etc.).

The next step is taken when the webbing of the segments proceeds further, resulting in but shallowly incised pinnules which are found, for instance, in *L. klotzschiana* (fig. 45) and *L. cultriformis* (fig. 37), generally in the section *Temnolindsaea.* It is significant that in these species the edges of the lobes, and thus the sori, are not lying in one line in each other's prolongation, but are part of different lines intersecting at small angles with their neighbours (fig. 37). This apparently shows that they originated through condensation from more highly dissected types with ± divaricate segments and are not derived from forms with entire pinnules, through secondary occurrence of incisions.

Leaves of sporelings of the Asiatic *L. cultrata* were observed in the greenhouses of Kew Gardens; they are shown in fig. 22 and are somewhat different from those figured by WAGNER (1952 b, fig. 18 a). The webbing of the pinnule-segments observed on the mature plant which has only very shallowly incised pinnules is present here to a much lesser degree, which would be in accordance with the ideas expressed above if it is true that juvenile plants retain certain primitive characters not found in mature plants; but this is questionable.

PÉREZ ARBELÁEZ vaguely indicated a rather similar line of development (l.c., p. 88/89, fig. 34 a—f.) He was, however, inclined to read the sequence conversely as is done here. The assumption of the dimidiate type as basal seems to the present author to be untenable. It is morphologically isolated, and is certainly more specialized than the cuneately dissected type.

An interesting phenomenon is the simplification of the gross leaf-pattern that goes hand in hand with the webbing of the leaflets. The highly incised types, *L. bifida* and *L. virescens*, are decompound, but the species of the section *Temnolindsaea*, their closest relatives outside their own section, *Pseudosphenomeris*, are bipinnate *cum impari* (some of them occasionally even simply pinnate), that is, with a terminal pinna conform to the lateral ones. In some species of *Temnolindsaea*, notably in *L. klotzschiana*, but also in a few others from sections with continuous sori, the basal pinnules of the terminal pinna are sometimes larger, in *L. klotzschiana* often more deeply incised, which has probably to be interpreted as an obscure relict of decompound architecture. Also, the rachis of the terminal pinna shows by its structure that it is a prolongation of the primary rachis and not homologous to the lateral secondary rachises. In almost all species where the secondary rachises are channelled or flattened on the abaxial surface they have a terete portion at their extreme base which forms a discontinuity between the primary and the secondary rachis. This is absent in the terminal pinna whose abaxial channel is continuous with that found in many species in the upper part of the primary rachis.

In the New World there is one species which does not fit into this morphological series, viz. *L. stenomeris* (fig. 46). It has dimidiate, yet deeply incised pinnules with uninerval sori but is bipinnate *cum impari*. This type of leaf is much more common in the Indo-Malayan region; examples are *L. blumeana* (Hook.) Kuhn, *L. schlechteri* Brause, *L. tenuifolia* Bl. and *L. versteegii* (Christ) v.A.v.R.; some of them are even simply pinnate (*L. schlechteri* and sometimes *L. versteegii*). Possibly the fine dissection, leading to capillary divisions in some Malaysian species, is a secondary phenomenon; but it is not impossible that it was retained as a primitive character that did not evolve further than the dimidiate stage of the pinnules whereas the architecture of the divisions of higher order advanced (that is, became simpler) independently.

When the marginal incisions become very shallow to obsolete, the conditions for the development of one uninterrupted sorus per pinnule are developed. This type of pinnule, entire or almost entire, and with a continuous sorus, is found in the majority of the American species. The sorus is found along the upper and outer margin, as it is situated on the commissure between the vein-ends, and in a dimidiate pinnule the veins radiate from the lower margin and end along the upper and outer edge. This type, with continuous sori, is less common among the Asiatic species, but a few of them represent striking parallels to American representatives, such as *L. scandens* resembling *L. lancea* with which it was confused for a long time (see p. 252), *L. borneensis* approaching *L. guianensis* ssp. *guianensis*, etc. Intermediates between continuous and interrupted sori are not common. In the New World examples are found in *L. ovoidea* (fig. 39) and *L. botrychioides* (fig. 47, 48), which in most pinnules have continuous sori but where in large pinnules often two incisions occur that interrupt the sorus, one in the upper and one in the outer margin.

Something quite different are the so-called incompletely fertile pinnules. In many species of *Lindsaea* quite sterile leaves are rare on full-grown rhizomes. One of the few exceptions is L. *guianensis*; besides, *L. cubensis* has somewhat dimorphous leaves (sterile versus fertile); in *L. stricta* the basal part of otherwise fertile leaves is mostly sterile. But this is rather exceptional, and in some species the author has not seen a single wholly sterile leaf, a condition which is just the opposite of what is observed in some other genera, for instance *Elaphoglossum*, where the scarcity of fertile leaves often drives the Pteridologist to despair. The sterile leaves of *Lindsaea*, where they occur, tend to have crenate, sometimes more deeply incised pinnules, whereas fertile ones of the same species may be quite entire. This is particularly true for sterile leaves found on juvenile rhizomes, e.g. in the Old World species *L. macraeana* (see HOLTTUM, 1954, fig. 185, and CHRIST, 1910, fig. 46 and 47). The phenomenon has been interpreted in a phylogenetic sense; juvenile plants were believed to produce leaves of an ancestral type. This kind of explanation, strongly reminiscent of Haeckel's biogenetic base-law, although it has proved to be useful in some cases (for instance the derivation of the pseudopedate leaf-pattern of *Adiantum pedatum* from a bipinnate one, see WAGNER, 1952 a), should be applied with great caution. Sometimes leaves are found that are intermediate between the sterile and fertile condition; sori occur in a part of the lamina only and tend to be interrupted, not rarely uninerval, in species with normally continuous sori. These short sori are most often found at the border of zones with normal fertility; sometimes, for instance, the inner part of a pinnule may bear sori occupying several veins while the outer sori are uninerval. The margin of such incompletely fertile pinnules or portions of pinnules is often crenate in the same way as in sterile pinnules of the same species. These incompletely fertile leaves or pinnules are not of very frequent occurrence but are very confusing as they diverge from the normal pattern of the species; they cannot be keyed out with the key presented in this paper where great value is attached to the structure of the sorus in the normally fertile condition.

It seems likely that the explanation of this phenomenon has to be sought in connection with phytohormones. It does not seem a very daring guess to assume that the production of fertile leaves in ferns is regulated by phytohormones comparable to the flowering hormones demonstrated in many Angiosperms. The incompletely fertile parts may then be supposed to have developed with a supply of this hormone insufficient to induce the formation of complete, normal sori.

In this context a few species must be mentioned that have interrupted, largely uninerval sori but only shallow marginal incisions which cannot be held responsible for the lack of a commissure between the fertile vein-ends. These species have been separated as a genus (or subgenus), *Odontoloma* J. Smith, but certainly not all of them are closely related within the genus *Lindsaea*. But for the constant occurrence of very short sori one would be inclined to take the leaves of these species for incompletely fertile ones. In the New World there is only one representative of this type, *L. parkeri* (fig. 40); the Old World has several of them, the most widespread being *L. macraeana*. We must thus express the relation between not or little incised pinnules and continuous sori in a more cautious way; we can state only that an uninterrupted margin provides the opportunity for the development of a continuous sorus, but that the latter is not a necessary consequence of the former.

A further simplification, rare among species with incised pinnules, but common among forms with entire pinnules and continuous sori, is the occurrence of simply pinnate leaves. In some species the leaves are exclusively or almost exclusively once-pinnate (*L. botrychioides*, *L. dubia*, *L. hemiglossa*, *L. schomburgkii*, *L. semilunata*, *L. ulei*), in many others once pinnate and bipinnate (occasionally even subtripinnate or tripinnate) leaves are regularly found side by side (e.g. *L. arcuata*, *L. lancea*, *L. parkeri*, *L. portoricensis*, *L. stricta*). This shows that the character: pinnate versus bipinnate is generally unreliable for diagnostic purposes, and it has consequently been used very little in the key to the species. This has not always been realized, and bipinnate or subtripinnate specimens of ordinarily less compound species have sometimes been described as new varieties. Moreover, juvenile specimens bear less compound leaves than adult ones; therefore, on rhizomes which are in a transitional stage, simply pinnate leaves may be found together with bipinnate ones, the latter representing the normal pattern. The former are then, however, mostly sterile. Incidentally, this shows that Haeckel's law is not applicable here; simply pinnate leaves appear in the development of a single plant before the bipinnate ones, but in a phylogenetic sense they are very probably more derived.

In all species where once- and twice-pinnate leaves occur side by side the structure of the ultimate divisions is exactly the same. For this reason they are in this paper consistently called pinnules, whether they occur on pinnate, bipinnate, or subtripinnate leaves; it would not have been logical to speak of pinnae in the first, of pinnules or secondary or tertiary pinnae in the second case, as they are all alike in structure and undoubtedly homologous. The term segments has been reserved for divisions that are not completely free, or has occasionally been used in a general sense, including both pinnules and segments in the more restricted meaning.

Another character that shows certain variations where a primitive and a derived pattern can be detected is the structure of the pinna- or (in simply pinnate species) lamina-apex. In all species with incised pinnules and in many with entire ones the upper pinnules gradually decrease in size towards the apex of the pinna or lamina and are finally and often very gradually confluent into a terminal segment (see, e.g., fig. 27, 51, 65). In other forms, such as L. *quadrangularis* ssp. *terminalis* (fig. 49) and *L. surinamensis* (fig. 58), the reduction in size of the upper pinnules is considerably less evident, and one or two only are joined by a wing to the terminal segment which is thus almost free; in these species it has a peculiar shape, ± triangular, asymmetric at the base, with two unequal lobes, the largest and lowest found on the side opposite the uppermost lateral pinnule, but otherwise entire, or sinuate in the lower part. Apart from the two basal lobes the origin of this segment from confluent reduced pinnules is hardly evident. The next step is taken when the terminal segment becomes quite free and may be called a terminal pinnule. It is interesting to note the presence of a correlation between this process of simplification of the architecture of the apex and the overall dissection-pattern of the leaf; all species with a free terminal segment, namely, *L. lancea*, *L. latifrons*, *L. hemiglossa*, *L. semilunata*, *L. schomburgkii*, and *L. ulei*, have simply pinnate leaves, and in all but the two first-named species this is always the case. Here also the upper pinnules decrease often very little in size, and the number of lateral pinnules as a whole is rather small.

In *Lindsaea lancea* the terminal pinnule is of the asymmetric triangular shape described above (fig. 5–7, 79), but in the other species it is rather different. The apex becomes obsolete or is altogether wanting, i.e. the distal margin becomes flattened, the lateral lobes protrude strongly, the pinnule is approximately obtriangular, often transversal and approximately symmetric (see fig. 82). A central main vein (present in L. *lancea*) is apparently absent, but a trace of it can still be found. The keel formed by the junction of the margins bordering the abaxial groove of the rachis shortly enters the terminal pinnule; it lies to one side of the base, the side where the uppermost lateral pinnule is found. This can be explained by the assumption that one-half of the terminal pinnule is apparently formed by the largest, lowest lobe of the terminal segment, whereas the other half consists of the other lobe and the almost obsolete apex. The fact that the distal margin is usually slightly bulging at this side of the terminal pinnule shows that a trace of the apex is still present. The keel, which in *L. lancea* evanesces in the midvein, is thus an indication where the apical shank that contains it should be looked for. Fig. 78, showing the upper part of the lamina of *L. ulei*, gives an illustration of what has been described above. Even if there is no bulging portion of the distal edge, as is sometimes the case, the asymmetry in venation at the base of the terminal pinnule is still there.

These Lindsaeas with large terminal and few lateral pinnules are probably to be regarded as the source whence the simple-leaved species have sprung that are so outstanding among the American representatives and, as a matter of fact, unique in the whole genus. Particularly *L. ulei* agrees with them in such characters as rhizome-scales, dark and (at least in the lower half) terete petioles and strongly intramarginal indusia; furthermore they are approximately sympatric. It seems likely that the species of this group, the section *Haplolindsaea*, originated from a form allied to *L. ulei*, or perhaps from this species itself, through suppression of the lateral pinnules and basipetal expansion of the lateral lobes of the terminal pinnule, resulting in an approximately round lamina. It may be significant that the leaves of juvenile plants of *L. cyclophylla* are bean-shaped or semi-elliptic with very little lateral basipetal expansion (fig. 90), but again, the value of such characters observed in juvenile plants is questionable. The acute basal lobes of the lamina sometimes found in *L. sagittata* (fig. 88) may be a remnant of the lateral horns of the terminal pinnule present in *L. ulei* and some allied species. WAGNER (1952 b, 1954 b) believed the species with a midrib to be the basal type (he called it *L. sagittata*, but his figure (1952 b, fig. 9 I) represents *L. reniformis*, where he apparently mistook the median prolongation of the sclerotic patch at the base of the lamina for a midrib), and the midrib-less species *)

---

*) There may be a short midrib in the sclerotic patch at the base of the lamina which would be only visible in sections.

derived from it through loss of the main vein; but the species grouped around *L. ulei* have no midrib to speak of in their terminal pinnules, whereas that of *L. sagittata* is quite pronounced and long. It seems more likely that the prolongation of an originally obtuse apex, as found in *L. cyclophylla* (fig. 90, 91) and *L. reniformis* (fig. 89), to the long acumen of *L. sagittata* is a secondary phenomenon, which was accompanied by a stronger development of the vein catering to this apex, i.e. to a larger portion of the lamina than the other veins. Then *L. reniformis* or *L. cyclophylla* would represent the basal type of the section. An alternative solution that cannot be completely dismissed is that the simple-leaved species did not arise from a form resembling *L. ulei* but from a hypothetical form with an acute terminal pinnule provided with a median main vein not unlike simply pinnate forms of *L. lancea*.

A structure peculiar to the section *Haplolindsaea* is a patch of black sclerotic tissue on the abaxial side of the lamina above the insertion of the petiole. Its apex is prolonged into a tapering extension overlying the base of a vein in *L. reniformis*, *L. sagittata*, occasionally also in *L. cyclophylla*. The function of this structure is probably mechanical, but no details are known.

From this discussion follows the unnaturalness of DIELS' inclusion of *L. reniformis* and *L. sagittata* in *Schizoloma* (1902). With *L. ensifolia*, *L. walkerae*, *Isoloma*, or *Schizolepton* which constitute the rest of Diels' genus they have little in common, except the lack of dimidiate pinnules. If Diels had been consistent, he would have been obliged in such a species as *L. schomburgkii* to put the terminal pinnule in *Schizoloma* and the lateral ones in *Lindsaea*!

Finally, a few species have to be dealt with that do not fall within the sequence of forms outlined above and are not or only in a vague way connected with the bulk of the American species, or that are outstanding by very peculiar characters.

Firstly *L. meifolia* and *L. pendula*, which together form the section *Crematomeris*. These species (fig. 41–43) are very remarkable by their pendulous pinnules or—in *L. meifolia* in places where the leaves are more than twice pinnate—secondary pinnae. In order to attain this position twisting occurs, strangely enough, in two places. The secondary rachises which depart from the primary rachis at approximately right angles—hardly ever found in other sections—are twisted over 90° at their bases in such a way that the morphologically adaxial side with the groove faces the apex of the leaf, the terete abaxial side the base. The organs inserted on the secondary rachises, pinnules or tertiary rachises, are again bent over 90° at their bases, all to the basiscopic side, which makes them pendulous. To a certain degree this is also observed in the pinnules (of third order) in the basal part of the pinnae in *L. meifolia;* the pinnules in the apical part of the pinnae are thus in the same plane as the secondary rachises in the basal part, as both are of the same (second) order, and the pinnules on the tertiary and in the apical part of the secondary rachises are in planes that are at right angles to each other, although both are pendulous. This is not always clearly observed in herbarium specimens, as all organs are pressed in the plane of the sheet. In *L. pendula* the terminal pinna joins the lateral ones in being bent over to one side and bearing also pendulous pinnules (fig. 42).

It is very tempting to assume that the pendulous position of the pinnules on an erect rachis arose as an adaptation to the open habitats in which *L. pendula* occurs (savannas and bogs), and it is probably of biological importance in this species; *L. stricta*, another species occurring mostly in open habitats, is also reported by collectors to have stiffly erect leaves with almost vertical pinnules. Yet *L. meifolia* has invariably been collected in moist dense forests! The phenomenon originated apparently without connection with a special milieu, but, once it was present, enabled *L. pendula* to colonize an open habitat, or was at least advantageous in the process. Incidentally, the step from incised to entire pinnules linked with that from decompound to bipinnate *cum impari* leaves can be beautifully observed in these two closely related species.

Among the American species there is only one with anastomosing veins and equal-sided pinnae, namely, *L. macrophylla* (fig. 92). The reason for the inclusion of this species in the genus, although tentatively in a separate subgenus, has already been discussed. It may be of interest to note that the occurrence of anastomosing veins in the genus *Lindsaea* is not limited to species with comparatively large, undivided segments. The Asiatic species with anastomosing veins often placed in the subgenus (originally genus) *Synaphlebium* J. Smith have dimidiate pinnules, and in some of them the pinnules are so narrow that only a few anastomoses per pinnule are left, e.g. in *L. sinuato-crenata* v.A.v.R. On the other hand, species with large undivided laminal parts such as *L. taeniata* and the simple-leaved forms have quite free veins. The relation between the degree of dissection and anastomosis: the less dissected, the more anastomoses, reported, for instance, in *Tectaria* (Copeland, 1947, p. 129), and in *Cnemidaria* versus *Cyathea* (id., l.c., p. 98) is not met with in *Lindsaea*.

Almost all neotropical species have laminae that are truncate at the base, i.e. the basal pinnae or pinnules are not or hardly shortened. The only exception is formed by the section *Tropidolindsaea* which occupies a rather isolated position. In the three species forming this section, *L. seemannii*, *L. pratensis*, and *L. protensa*, the lower pinnules are very gradually reduced and farther apart (fig. 32). More about this group is found on p. 136; it is sufficient to point out in this place that *L. seemannii*, with incised pinnules, seems to be the most primitive member of the section, whereas *L. pratensis* with almost always continuous and particularly *L. protensa* with wholly continuous sori and small, very numerous pinnules are apparently more derived.

A peculiar development of an almost equal-sided pinnule from a dimidiate one is observed in *Lindsaea herminieri* and especially in *L. taeniata*. In the first species the apex of many pinnules is protracted into a long, obliqualy ascending point with an approximately median (diagonal) main vein; the sori are borne on both of its sides, as one side is formed by the upper, the other by the outer margin (fig. 60). A similar phenomenon is observed in a caudate form of *L. arcuata.* In *L. taeniata* this is developed in such a way that the protracted apex forms the greater part of the pinnule; the dimidiate portion is quite short, the (morphologically) outer margin is almost a prolongation of the lower margin, which therefore seems to be soriferous in its outer part (fig. 62). Technically *L. taeniata* would answer the diagnosis of the genus *Schizoloma* of most authors, although its closest relative is undoubtedly *L. arcuata*, which has little in common with *L. ensifolia*, the type species of *Schizoloma.*

When the forms of the New World in general are compared with those of the Old World, it springs to the eye that whereas the primitive forms of both regions are comparable and often similar, the derived ones are different. The highly condensed forms with few large lateral and a large free terminal pinnule or even with simple lamina are almost absent in the Old World, the only representative of that type known to the other being a form of *L. scandens* which duplicates *L. lancea.* On the other hand, species with dimidiate but incised, usually rather small pinnules abound in the Indo-Malayan region but are very scarce in the Western Hemisphere (*L. virescens, L. stenomeris*). The same is true for species with entire of almost entire pinnules but interrupted sori (some species of the section *Temnolindsaea* in America).

9. LINDSAEA AND ADIANTUM

As has been pointed out above, the first species of *Lindsaea* were described under *Adiantum*, and still the two genera are not rarely confused by collectors and in preliminary sorting in herbaria. The superficial resemblance of leaf architecture and pinnule structure between the two genera is indeed striking, and so many types in one of them are matched by species in the other that we may speak of parallel development.

In the neotropical Lindsaeas this is even more noticeable than in the paleotropical ones, although, of course, the corresponding types of *Adiantum* do not necessarily occur in the same hemisphere. The common dimidiate type of *Lindsaea* represented by such species as *L. lancea* and *L. quadrangularis* has its counterpart in the forms usually united under *Adiantum tetraphyllum* which is almost equally widespread in the Western Hemisphere. The transition to simply pinnate forms, found in several species of *Lindsaea* (see p. 49/50), is met with in such species as *Adiantum obliquum.* The simple-leaved type, so outstanding among the American Lindsaeas, is duplicated in the well-known *Adiantum reniforme*, but this fern, occurring chiefly in Macaronesia, is a xerophyte, as opposed to the species of *Lindsaea* section *Haplolindsaea*, which, though not infrequently growing on rocks, avoid truly dry or seasonally dry habitats. The species of *Adiantum* with approximately equal-sided, mostly tongue-shaped pinnae or pinnules, with a tendency towards anastomosis of veins, such as *A. dolosum* and *A. adiantoides*, can be compared to the Lindsaeas with similar ultimate divisions that are usually included in *Schizoloma*, *L. macro-*

phylla and *L. ensifolia,* also with reticulate venation; as a matter of fact, the author found several specimens of *Adiantum dolosum* determined as *Lindsaea macrophylla.* But this type of leaf is more common in *Adiantum* than in *Lindsaea. L. stricta,* the species from open habitats with small, rigid erect pinnules resembles to a certain extent *Adiantum serratodentatum* that grows in similar situations. In the forests of eastern Perú the miniature *Lindsaea spruceana* has been found, and in the same region occurs its counterpart *Adiantum humile;* and so on. It is not so easy to find an obvious counterpart to the highly compound species, e.g. *L. bifida;* but it seems reasonable to compare them to the numerous species of *Adiantum* with decompound or bi—tripinnate leaves and cuneate pinnules (*A. raddianum, A. tenerum,* etc.). The author believes these species of *Adiantum* to represent the most primitive type of that genus, the dimidiate and equal-sided forms being more derived, probably along several lines of descent. This derivation did not necessarily and even not probably happen in the same way as in *Lindsaea,* through reduction of segments and their fusion, but the dimidiate and the equal-sided Adiantums are certainly a simplified type as compared with the cuneate ones, as they are (at least the neotropical ones, with which the author is acquainted to a certain extent) bipinnate *cum impari* or simply pinnate, whereas many cuneate ones are decompound. There are, of course, other ways in which the cuneate type specialized and produced simplified types, leading, for instance, to a once-pinnate leaf with cuneate leaflets (*A. deflectens*), a pseudopedate pattern (*A. pedatum*), etc. In this connection it is probably significant that we have a third genus with highly divided and with dimidiate (as well as many other) types of leaves, namely, *Asplenium.* It seems likely that here, too, at least some of the highly divided forms (in the New World for instance those grouped with *A. rutaceum*) represent the more primitive leaf-type, and HOLTTUM (1947) regards them as such. This seems to be corroborated by the fact that in the genus or subgenus *Loxoscaphe* highly dissected leaves are found of a type comparable to, for instance, that of *Lindsaea bifida;* and Holttum believed *Loxoscaphe* to link the Asplenioids with the Davallioids. It should be mentioned, however, that WAGNER (1952 b, p. 140/141) presented anatomical and morphological and MANTON & SLEDGE (1954) cytological evidence against this supposed relationship of *Loxoscaphe* with the Davallioids.

There are, of course, points of difference and cases of peculiar, unmatched types in *Lindsaea* versus *Adiantum.* The highly dissected, yet dimidiate types in *Lindsaea* (*L. stenomeris, L. blumeana,* etc.) have nothing really comparable in *Adiantum,* and the pseudopedate leaf of *Adiantum pedatum* and others has not been developed in *Lindsaea.* But as a whole there are few fern genera showing such a striking parallel development as *Lindsaea* and *Adiantum.*

The genus *Didymochlaena,* the only other instance of a fern genus with dimidiate pinnules known to the author, occupies a rather isolated position among the Dryopteridoid ferns; its derivation is unknown. DICKASON (1946) associated it with the Lindsaeoids, apparently on account of the shape of the pinnules alone, a most unnatural procedure, as all other characters point to Dryopteridoid affinity. Even fragments can be easily distinguished by the scaly rachises and the teeth at the bases of the pinnules.

10. SUBDIVISION OF THE GENUS

After the account of the morphology and the supposed evolutional tendencies of the genus *Lindsaea*, it will be described in the following how these data have been used formerly and are being used in the present study to subdivide the genus into as natural as possible taxa of lower rank, above the rank of species.

The various ways in which older authors have arranged the species in groups according to more or less—mostly less—natural characters need not concern us here, as far as no names were attached to these groups.

HOOKER (1844–46) distinguished two subgenera: *Eulindsaea*, with "simple or forked", i.e. free, veins, and *Schizoloma* (published as a genus by Gaudichaud), with more or less anastomosing veins.

MOORE (1857) based his subdivisions on the shape of the segments; these were isomerous, with a midrib, in his subgenus *Isoloma* (originally a genus of J. Smith), and flabellate or dimidiate, ecostate, in *Eulindsaea*.

BAKER (1868) more or less combined these ideas and recognized four groups: *Eulindsaya*, with unilateral, free-veined pinnae (i.e., pinnules), *Isoloma*, with equilateral, free-veined divisions, *Synaphlebium* (a genus of J. Smith), with dimidiate segments and reticulate venation, and *Schizoloma*, with equilateral pinnae and anastomosing veins. These groups appear also in his treatment in Flora Brasiliensis (1870), except the third, which is not represented in the New World.

KEYSERLING (1873) had five subordinate groups, probably intended as subgenera: *Eulindsaya*, with dimidiate segments and mostly continuous sori, *Odontoloma* (originally a genus, created by J. Smith), with similar segments and interrupted sori, *Paralindsaya*, with cuneate segments and continuous sori, *Stenoloma*, also with cuneate segments but short, bi- to quadrinerval sori and spinose rachises, and *Isoloma*, similar to the previous group, but with unarmed rachises. The latter is a complete misinterpretation of J. Smith's genus of the same name on which it is based; Keyserling listed "*Davallia*" (= *Sphenomeris*) *retusa* as an example. *Paralindsaya*, the only group published as new, is based on incorrect morphological interpretation, as the segments of its only species, *L. linearis*, are no less dimidiate than they are in "*Eulindsaya*", though this is less evident because of their reduced length.

DIELS (1902), who excluded *Isoloma* and *Schizoloma* from *Lindsaea* and put the highly compound species in *Odontosoria*, consequently restricting *Lindsaea* to the dimidiate types, had two sections, *Eulindsaya*, with free veins, and *Synaphlebium*, with reticulate veins. In the first section two subordinate groups appear, presumably intended as series: *Pinnatae*, with simply pinnate leaves, and *Bipinnatae*, with at least partly bipinnate leaves. It has been shown already that this criterium is next to useless; moreover these groups were not typified and can be ignored.

CHRISTENSEN (1906, p. xxx) recognized four subgenera, namely, *Eulindsaya*, based on *L. lancea*, *Hymenotomia* (based on a genus published by Gaudichaud), with *L. microphylla*, *Odontoloma*, typified by *L. repens*, and *Synaphlebium*, with *L. decomposita*. The first subgenus was divided in two sections, *Paralindsaya* Keyserling (see above), and *Lindsaynium*, based on Fée's genus, erected for *L. rigida*. It is not clear in which of these sections Christensen wanted to put *L. lancea*, the type of the subgenus; at any rate, *Lindsaynium* does not deserve recognition. Fée was impressed by the "marginal vein", for which he mistook the thick sclerotic marginal strand of *L. rigida*.

Later authors did not contribute anything new; nothing original appears, for instance, in VAN ALDERWERELT VAN ROSENBURGH's treatment (1908).

The writer has pointed out already (p. 102/103) that he prefers to maintain *Schizoloma*, typified by *Lindsaea ensifolia* Sw., as a subgenus, although with misgivings. As far as the American species are concerned, all but *Lindsaea macrophylla* go then in the other subgenus "*Eulindsaea*", which according to our present rules of nomenclature should bear the name *Lindsaea* unaltered (Art. 22). In this subgenus the following sections are recognized (Latin diagnoses for those which are new are provided in the taxonomic part):

I. *Pseudosphenomeris*

Leaves decompound; ultimate segments not pendulous, cuneate, or rarely dimidiate, incised pinnules. This is the most primitive group; it includes the neotropical *L. bifida*, *L. sphenomeridopsis*, and *L. virescens*. Close relatives, especially of the two first-named species, in the Eastern Hemisphere are *Lindsaea millefolium* Kramer, nom nov. [*Davallia decomposita* Baker, Jo. Bot. 22:141 (1884); *Odontosoria decomposita* (Bak.) C. Chr., Ind. Fil. 465 (1906); *Sphenomeris decomposita* (Bak.) C. Chr., Dansk Bot. Ark. 7:78 (1932); *Stenoloma decompositum* (Bak.) C. Chr., Ind. Fil. Suppl. 3:173 (1934); not *Lindsaea decomposita* Willd., 1810], from Madagascar, and *Lindsaea eberhardtii* (Christ) Kramer, comb. nov. [*Odontosoria eberhardtii* Christ, Journ. de Bot. 21:235 (1908), *Stenoloma eberhardtii* (Christ) Ching, Sinensia 3:338 (1933)] from Annam and Hai-nan. Perhaps eventually also *L. microphylla* from Australia, New Zealand, and New Caledonia will have to be included in the same section.

II. *Crematomeris*

Leaves decompound or bipinnate *cum impari*; secondary rachises patent under an angle of ca. 90°, twisted at their bases, the channelled adaxial side acroscopic, the terete abaxial side basiscopic; segments of the second order pendulous, divided or entire. This section is, through *L. meifolia*, related to the preceding group, but not very closely. The morphological details are discussed on p. 130/131.

III. *Temnolindsaea*

Leaves bipinnate *cum impari*, rarely simply pinnate. Pinnules dimidiate, not pendulous, shallowly or occasionally more deeply incised; sori interrupted, occupying one or mostly a few veins. Here belong the species grouped with *L. klotzschiana; L. parkeri* is doubtfully related. The latter species has been placed in *Odontoloma*, but that genus, reduced to subgeneric rank by Keyserling but perhaps better to be made a section, is quite different in its long-creeping or rather scandent rhizomes, at least if typified by *Dicksonia repens* Bory, not by *Lindsaea tenuifolia* Blume, as was done by Copeland.

IV. *Lindsaea*

This section is discussed at the end.

V. *Haplolindsaea*

This includes the forms with simple lamina and is probably derived from the preceding section; see p. 129.

VI. *Paralindsaea* (Keyserling) C. Chr.

Leaves simply pinnate, or the fertile ones bipinnate, with dimidiate pinnules decreasing in size towards the apex; leaves dimorphous, the sterile ones short, ± spreading, the fertile ones longer, erect. The type species of this section is *L. linearis* from Australia, etc., as indicated by Keyserling. *L. cubensis*, the American species grouped with it in the present study, resembles it in dimorphism and in the shape of the pinnules, but differs by sometimes bipinnate fertile leaves and monolete spores. The alliance of the two species is not entirely certain, and *L. cubensis* is only tentatively placed in the present section; it is, however, isolated among the other American species.

Another species to be placed in this section, but without doubt, is *L. dimorpha* Bailey (*L. heterophylla* Prentice, non Dryander) from north-eastern Australia; it differs from *L. linearis* chiefly in its incised sterile (sometimes also fertile) pinnules. It is probably connected with *L. microphylla* through *L. incisa* Prentice, both last-named species from the same region, which are, however, not dimorphous and should probably be placed in another section.

VII. *Tropidolindsaea*

This is the group of *L. seemannii*, confined to the Caribbean region and the northern Andes. The leaves are simply pinnate, gradually reduced above and below; the rachis is keeled (*L. seemannii*, *L. pratensis*) or narrowly rounded (*L. protensa*) on the abaxial side. The scales are very large and broadly lanceolate or ovate, clathrate in *L. seemannii;* the spores are monolete. The sporangia are of a type slightly different from the other species, as the indurated part of the annulus does not quite reach the stalk. The group of species is quite isolated among the American species, probably even in the whole genus. The only species to which alliance is evident is *L. viridis* Colenso from New Zealand. It has bipinnate or mostly bipinnate + pinnatifid leaves;

otherwise it agrees rather closely with the American group, especially with *L. seemannii*, whose incised pinnules on simply pinnate leaves may be regarded as simplified derivatives of the pattern of *L. viridis*. Characters of agreeance are the abaxially keeled petiole and rachis, upwards and downwards reduced lamina (in *L. viridis* not strongly reduced below), the sudden transition from the dark primary rachis to the pale secondary rachis or base of the pinnules, the sporangia, and the monolete spores. The scales of *L. viridis* are narrowly lanceolate, of a type otherwise found in *Sphenomeris*, but in their apical part they are distinctly clathrate, as in *L. seemannii*. The inclusion of *L. viridis* in *Lindsaea* is perhaps not justified; it may represent a specialized offshoot from *Sphenomeris* that gave independently rise to dimidiate species, or it may be close to the common source of *Lindsaea* and *Sphenomeris*. Perhaps the section *Tropidolindsaea* would better be made a subgenus or even excluded from the genus; but again, this should be decided after thorough study of all species in the Eastern Hemisphere.

Finally the section *Lindsaea* is to be discussed more at length. It includes the bulk of the neotropical species, but probably none from the Old World. The type species of the genus must be included; there has been some controversy as to which species should be selected as type.

JOHN SMITH (1875, p. 267) selected as type *L. trapeziformis*, in which selection he was followed by CHRISTENSEN (1906, p. xxx) and CHING (1940, p. 217). COPELAND (1929, p. 83), on the other hand, argued that this was incorrect, as *L. trapeziformis* was not among the three species listed by J. E. SMITH in his original publication of the genus (1793, p. 413: "Exempl. Gener.: Adiantum guianense Aubl., sagittatum ejusd., stricta Swartz"). He chose (1947, p. 53) *L. guianensis* as type. His argumentation is, however, not conclusive. Plate IX accompanying J. E. Smith's paper shows (fig. 4) a pinnule on a rachis-fragment and a detail of the sorus, said to belong in the "Explicatio Tabulae" to "Lindsaea, forte nova species". Dryander himself stated that this illustration represented his *L. trapeziformis* (apparently a reduced axillary pinnule; the shape is not at all like typical *L. trapeziformis* = *lancea*, nor like Dryander's figure of that species on his pl. 9). *L. trapeziformis* was therefore included in the original material on which the genus was based; moreover, the species cited by J. E. Smith were merely examples and apparently did not claim to constitute the whole genus, and no transfer was made, which was left to Dryander in his paper four years later. Therefore the present author cannot see any objection against the maintenance of *L. trapeziformis* as type-species of the genus.

It is very difficult to arrange the rather numerous species of the section *Lindsaea* in subsections or series. Certain groups of rather closely related species can be distinguished, but generally the morphological similarities are what one might call reticulate, which makes it very difficult to establish clear-cut groups of closer affinity.

Two groups can, however, be segregated from the majority of species. Firstly, *L. ovoidea* and *L. botrychioides*, distinguished by slightly interrupted sori in the largest pinnules, forming together the sub-section *Subinterruptae*. Secondly, the species with a large terminal pinnule which is quite free from the upper lateral pinnules, brought together in the sub-section *Terminales*: *L. ulei*, *L. hemiglossa*, *L. latifrons*, *L. lancea*, *L. semilunata*, and *L. schomburgkii*. It is not quite certain whether all these species represent one phyletic line, and the distinction from the third sub-section *Decrescentes*, comprising all other species of the section, with reduced upper pinnules ± confluent into a terminal segment, is not very sharp, as some forms, e.g. *L. surinamensis* and *L. quadrangularis* ssp. *terminalis*, often have an almost free terminal segment. This element of doubt seems to be adequately expressed by the assignation of subsectional rank to the group.

The section *Lindsaea* and the sub-section *Decrescentes* as well as a few others are not easy to define in such a way that all Old World species are excluded; the author has to leave this to a monographer of those forms, who, after all, may find some species that have to be put side by side with neotropical ones.

11. APPLICATION OF CATEGORIES BELOW THE RANK OF SPECIES

It may be necessary to explain briefly the entities and the rank assigned to them that are recognized in this paper. No comment on the species- concept seems to be required, but below the rank of species three categories have been employed about which some elucidation may not be out of place. These categories are the subspecies, the variety, and the forma, and their use side by side is to a certain extent in disagreement with the custom of many contemporary taxonomists who often have a favorite rank (most commonly the variety) to which all infraspecific taxa are assigned, while others, known as splitters, have a tendency to raise each entity they recognize to full species rank.

In the present revision all those forms that are sufficiently clear-cut but are very close together, i.e. closer than most or all other related species, and show at least some degree of geographic isolation, have been combined under one species as *subspecies*. The author fully realizes that it is more or less a matter of taste whether they are treated as subspecies or species, and he would not strongly object to assign species rank to *L. guianensis* ssp. *lanceastrum* or the subspecies of *L. quadrangularis* described below as new.

As *varieties* those forms are recognized that differ from each other in one or a few characters of rather little relevancy, where intermediates are found, though not very often, and where no geographic isolation is observed. In some cases, e.g. in *L. stricta* var. *parvula* or *L. lancea* var. *remota*, there are indications that some of these forms represent ecotypes, restricted to or preferring peculiar habitats; the fact that these forms occur within the area of the entities to which they are most closely related (though not throughout their area), and that intermediates, compared to the total number of known specimens, are not very rare, seems to justify their treatment as varieties.

Forms that are aberrant in one rather trivial character only, but by virtue of this are outstanding among the bulk of the specimens, or that differ by a combination of a few characters, but show rather numerous intermediates, either by combination of characters, or by intermediate stages, are distinguished as *formae.* If the series of intermediates becomes so large that the localization of the boundary between typical form and intermediate on the one hand, and intermediate and special form on the other hand, becomes quite arbitrary, the aberrant specimens are included in the species without any special name (examples are the simply pinnate, dark-petioled form of *L. lancea* and the thin, lax form of *L. stricta*). It is possible that in these cases cytological investigation will show two (or more) extremes, with a long series of intermediates formed by introgression; but such an assumption can hardly be made on the base of morphological data taken from herbarium-specimens only

The different types of diversity of intraspecific units are, of course, not sharply distinct, and future investigations, particularly study in the field, may show that certain forms have been put here in the wrong category. But with the data available at the present time, and the directions for application of infraspecific ranks described above, the author has been able to assign most forms to a certain rank without too much hesitation.*)

Hybrids. Great caution has been observed in calling intermediate forms hybrids. In a few cases there are strong indications that certain forms (notably *L. dissecta* and a few doubtful ones discussed at the end) are of hybrid origin, because characters of two species and abortive sporangia or spores are combined in them. In other cases of intermediate specimens, where nothing abnormal about the spores could be observed, the assumption of hybrid nature could not be made with reasonable certainty, particularly because in the genus *Lindsaea* where few species possess absolutely dependable differentiating characters or combinations of characters aberrant specimens are found in many species. Here, again, we cannot but hope that, a.o., cytology will help to clear up such problems; as a matter of fact, cytological research has already brought to light the presence of hybrids even among species or species-groups where they had not been expected (MANTON, 1950; MANTON & SLEDGE, 1954).

12. GEOGRAPHICAL DISTRIBUTION

Lindsaea is mainly a tropical genus; the bulk of the species occur between the tropics, especially in the Western Hemisphere and in south-east Asia. Whereas a number of species occur in Madagascar (seven are listed by CHRISTENSEN, 1932, but several referred to *Schizoloma* and *Sphenomeris* have to be included, which brings the total number to about fifteen) and the adjacent islands, continental Africa is remarkably poor in having only the widespread *L. ensifolia* (*Schizoloma ensifolium*), reported from Natal and West Tropical Africa.

*) Here Kunze may be quoted who complained (Linnaea 21:229, 1848): "Antequam Lindsayae . . . locis suis a pteridologo quodam perito studiose observantur, quid sit species, quid varietas aegre dijudicatur."

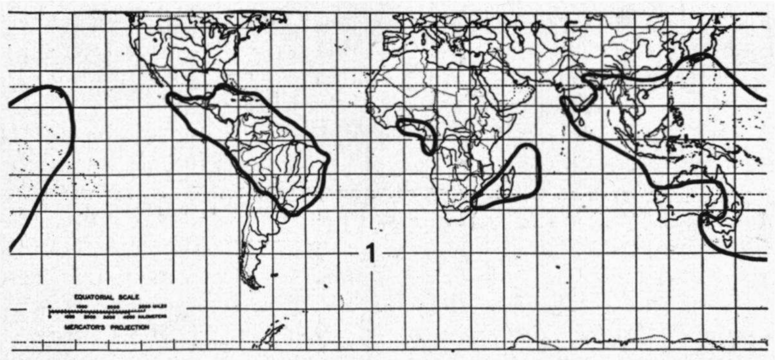
The area of the genus as a whole extends, however, considerably beyond the tropics in certain regions, especially in Japan (ten species, three reaching Honshu, see TAGAWA, 1937), Australia (two species in Victoria, see EWART, 1930, and one in South Australia, according to BLACK, 1922), and New Zealand (three species listed by DOBBIE & CROOKES, 1952). In the Pacific the genus reaches the Marquesas with two (BROWN & BROWN, 1931) and Hawaii with one species (CHRISTENSEN, 1925).

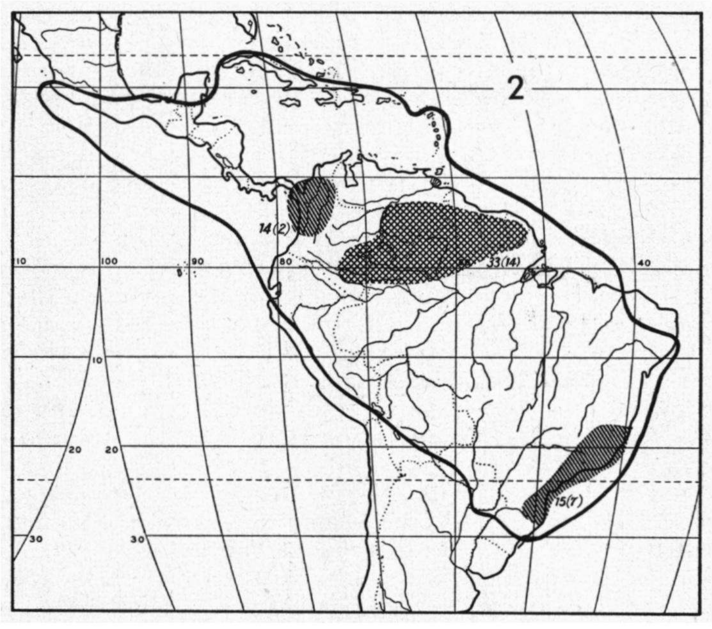
In the New World the genus is distributed from south-western Mexico and Cuba in the north to Bolivia, Paraguay, and Rio Grande do Sul (Brazil) in the south. The reported occurrence of one species in Misiones, north-eastern Argentina, could not be checked by the author (see under *L. lancea*).

Map 1 gives an outline of the area of the whole genus; the limits of the distribution in the Old World shown there are only approximations, especially in China and Africa.

The species occurring in Mexico are mostly confined to the moist tropical South-East in the states of Chiapas, Oaxaca, and Vera Cruz, but one species mostly occurring in open habitats, *L. stricta*, extends to Jalisco (map 32). In the south the two species found in Rio Grande do Sul, *L. lancea* and *L. quadrangularis* ssp. *terminalis*, are forest-dwellers. No Lindsaeas have so far been collected in Florida and the Bahamas (where the allied genus *Sphenomeris* occurs), Yucatán, El Salvador (see STANDLEY & CALDERÓN, 1925, MAXON & STANDLEY, 1930, and LÖTSCHERT, 1954, none of which reports any Lindsaeas), the smallest of the Lesser Antilles (Saba, St. Kitts, Anguilla, etc.), the Galápagos Archipelago, the extreme north-east of Brazil (states of Rio Grande do Norte and Paraiba), the coastal areas of Perú and Bolivia, and the whole of Chile, including Juan Fernández (see map 2). The absence in most of these regions can be explained by their dry climate; but one would certainly except the presence of such species as *L. lancea* and *L. arcuata* in the remnants of forest on the volcanoes of El Salvador; also the complete absence from the moist temperate regions of central Chile is not easy to understand in the light of the presence of several species at approximately the same latitude in Australia and New Zealand. The climate of the latter regions is, however, warmer and/or moister than of central Chile (Cf in New Zealand, Cfa, Cfb or Csa in the temperate parts of Australia where the genus occurs, as opposed to Csb and Cfc in central Chile, in Köppen's classification of climates).

Only four of the species occurring in the New World can be called widespread, namely, *L. lancea*, (maps 37—41), *L. portoricensis* (map 25), *L. stricta* (maps 31—34) and *L. divaricata* (map 27). Most others are more or less restricted in their range, although it is often difficult to say how much, as too little collecting has been done in many regions to get an even approximately reliable picture of the distribution of such species. Species which can be said with some reasonable certainty to be narrow endemics are *L. herminieri* (Guadeloupe), *L. protensa* (Massif de la Hotte, Hispaniola), *L. pratensis* (Costa Rica) and *L.* cubensis (western Cuba and Isla de Pinos).





Map 1: Distribution of *Lindsaea* as a whole. Map 2: Distribution of *Lindsaea* in the New World. (Cross-hatched lines: primary centre of species-concentration; diagonal lines: secondary centres. See also p. 141/142).

The centre of species-concentration (see map 2) is the region of the Guiana-shield, sometimes called "Guayana" (a term used in the taxonomic part of this paper), extending from south-eastern Colombia to French Guiana and northern Brazil. Of 51 taxa in the rank of species, subspecies, or variety, which are sufficiently distinct to be used for phytogeographical analysis, 33 are present in Guayana; 14 of these are endemic, and 9 have their main distribution here. The Brazilian shield or Brasilia possesses 18 taxa, including 8 endemics; of the remaining 10, none occurs mainly but not exclusively in this region *). Brasilia, therefore, may be called a secondary centre. Another, but less pronounced, secondary centre is situated in the Andes, on the slopes of the approximately north-south-running valleys of the western Cordilleras of Colombia, and on the Pacific slope from El Valle (Valle del Cauca), Colombia, to Darien, Panamá. Here 14 forms are found, but only 2 of them are endemic, namely, *L. seemannii* and *L. taeniata*. Moreover, *Sphenomeris killipii* and *S. spathulata* are only known from this region. Of the 12 forms that are not restricted to this centre, 4 have their main distribution in Guayana, 6 occur there but also elsewhere, and only 2, *L. arcuata* (apart from two collections from Suriname referred to the caudate form of *L. arcuata*, but with misgivings) and *L. quadrangularis* ssp. *subalata*, are absent from that area. Almost all localities of these species in the Colombian sub-centre are situated to the west of the Eastern Cordillera, in what is called "Choco" by Schuchert **), i.e. the Pre-Mesozoic massifs of the Colombian borderland, largely composed of plutonic rocks. It seems likely that most of them reached this region from the Guianas before the main upheaval of the Andes *sensu stricto* in middle and late Tertiary times; thus they were more or less cut off from most other regions, but endemics were hardly developed. *L. seemannii*, endemic in the Choco region, is probably a relic species, belonging to a group of three rather closely allied species without obvious relatives in the Western Hemisphere, but with a more distantly allied species in New Zealand. The closest relative of *L. seemannii*, *L. pratensis*, probably reached the volcanoes of Costa Rica from the same massif or was developed as a local endemic. The third species of the group, *L. protensa*, occurs in a very restricted part of south-western Hispaniola, where it was collected on lateritic soil. It is probably of similar origin and its presence in Hispaniola is presumably connected with the fact that the Choco massif formerly extended into the Caribbean sea (SCHUCHERT, p. 638).

The poverty in taxa of the Andes and the West-Indian region is indeed remarkable. Outside the secondary centre in Colombia and adjacent Panamá there is no area that can be said to be rich in forms. Ecuador/Perú has two endemics on the eastern slopes which are very closely allied, and *L. spruceana*, once collected in eastern Perú, which is perhaps not a good species. Even Costa Rica which in other fern genera harbours a wealth of endemics has only one endemic *Lindsaea*, *L. pratensis*, dealt with before, and besides *Ormoloma standleyi*, extending to Chiriquí, Panamá. Otherwise only widespread species are found in the Andes; the only more restricted ones are *L. arcuata* and *L. klotzschiana*, the first occurring also in south-eastern Brazil and the second on the table-mountains of western Guayana. In the West Indies

---

*) On map 2 only the south-eastern part of Brasilia is shown as a secondary centre, where the greatest concentration of species is found and which is floristically best known. The figures are slightly lower for this part of Brasilia than for the whole shield.

**) The geological data used in this paragraph were taken from GERTH (1941), SCHUCHERT (1935), WEEKS (1948), and BEARD (1949).

(exclusive of Trinidad and Tobago) there are but four endemics: *L. cubensis* (western Cuba, Isla de Pinos), *L. protensa* (Hispaniola, discussed above), *L. herminieri* (Guadeloupe) and *L. quadrangularis* ssp. *antillensis* (Puerto Rico to Grenada, but also on the Paraguaná-Peninsula, Venezuela). Even the number of more widespread forms occurring in this area is small; only *L. lancea* var. *lancea* is found almost throughout. *L. stricta* (3 varieties) and *L. portoricensis* are restricted to the Greater Antilles, *L. arcuata* to Cuba and Hispaniola, and *L. quadrangularis* ssp. *subalata* to Cuba. With the possible exception of the latter these forms are probably of South American origin, as the greater parts of their areas and their relatives are found there. They probably reached Central America not earlier than late Miocene times when the mainly volcanic land connection between Colombia and Nicaragua is believed to have come into existence (an earlier, Mesozoic connection is probably of no importance for the species under consideration). In the same period, and well into the Pliocene, Jamaica and Hispaniola were connected with Honduras—Nicaragua. The few continental forms of these islands may be assumed to have reached them in this era. Cuba was already isolated at that time, but it is not very difficult to imagine that the continental species of eastern Cuba arrived there from closely adjacent Hispaniola or Jamaica without the help of a land connection. *L. quadrangularis* ssp. *subalata*, known from eastern Cuba but neither from Hispaniola nor from Jamaica, will perhaps eventually be discovered on the former island or on both. Immediately the question arises why only a few very widespread species occur in Jamaica but none of the Andean or Central American forms found in Hispaniola and/or Cuba, whereas Jamaica must have served as a stepping-stone if a land bridge was of any importance for their dispersion. This is even much more striking when we turn to other ferns. Numerous examples of this type of distribution, i.e. occurring in Hispaniola but nowhere else in the West Indies, were given by CHRISTENSEN (1937, p. 4). Here only the examples of the genera *Phanerophlebia* and *Phyllitis* may be cited, each of which has one species in Hispaniola only, on none of the other islands, but is represented in Central America and/or Mexico. The following solution for this problem is suggested. In Miocene and Pliocene times, when the immigration to these islands may be supposed to have taken place, the mountains of Jamaica are believed to have reached much higher elevations than at present (SCHUCHERT, p. 416), but by subsequent erosion and subsidence became later again considerably lower. Many of the continental (montane) forms must then have disappeared from Jamaica but remained in Hispaniola where to-day the highest elevations of all West Indian islands are found. This explanation does not fit all species with such a gap in their distribution; *L. quadrangularis* ssp. *subalata*, for instance, occurs in Central America at elevations well within the range of the mountains of Jamaica. Besides, it should be pointed out that Jamaica still has a considerable proportion of continental elements in its fern-flora, many of which reach Hispaniola and/or eastern Cuba.

The geological history of western Cuba is quite independent from the East, the general vegetation is quite different, and it is not astonishing that only *L. portoricensis* occurs there (although *L. stricta* might also be expected), besides the strange endemic *L. cubensis*. As the taxonomic position of this fern is not known with sufficient certainty, it is preferable not to speculate about the geological-paleogeographical backgrounds of its distribution; the only species which is probably related is *L. linearis* from Australia, New Zealand, and New Caledonia.

It seems to the author that the distribution of the species discussed above which occur on the Greater Antilles and on the continent can be much better explained by the assumption of a tertiary land-connection between Central America and those islands than by explaining their presence through dispersal of diaspores across the sea (waif-arrivals). This was done by BEARD, who did not believe in any former land-connection in this area.

On the other hand, the poverty in widespread and in endemic species of the Lesser Antilles is in good accordance with their volcanic origin (with few exceptions for islands that are of no interest here), without any land-connection throughout their history. It seems feasible that *L. divaricata* (Guadeloupe), *L. guianensis* ssp. *guianensis* (Guadeloupe, Martinique, Grenada), and *Ormoloma imrayanum* (Guadeloupe, Dominica) came from the adjacent mainland by wind-borne spores; *L. quadrangularis* ssp. *antillensis* may have come from Puerto Rico, or may be a locally developed species. *L. herminieri*, the only endemic of the Lesser Antilles in the genus, is restricted to Guadeloupe, which belongs to the central, probably oldest (Miocene) group of islands.

This demonstrates again that the widespread belief in easy dispersal of viable fern-spores across great distances of lowlands or sea is not generally true. Otherwise it is difficult to explain why at least eight taxa migrated across the land-bridge between Colombia and Nicaragua, whereas at most half that many are distributed over northern South America and the Lesser Antilles. In this connection it is remarkable that Trinidad, which is botanically and geologically part of South America, and is very close to it, possesses but six or possibly seven forms of *Lindsaea*. All of them occur in adjacent Guayana.

The preponderance of Guayana in terms of concentration of species (endemics and non-endemics) is very outstanding. The explorations of the Guayana Highlands, begun by Humboldt & Bonpland, Spruce, the Schomburgk-brothers, Appun, and others, recently resumed by Ll. Williams, Schultes, Cabrera, and especially by Steyermark and by Maguire and his collaborators, have revealed the presence of a wealth of interesting forms, and more may be expected. In the present study, 10 species and varieties are described as new that so far have only been found in that area. This does not mean, of course, that collecting in other regions would not be promising; very little material is extant from the interior of the Brazilian shield (states of Matto Grosso, Goias, western Minas Gerais, etc.); most if it is from von Lützelburg's collections. More or less the same is true for Paraguay, Bolivia, and the Amazonian parts of Ecuador and Perú. Only from the West Indies, most of Central America (except Nicaragua), and the coast of south-eastern Brazil, few new forms or records may be expected.

Exchange of species between the Guiana and the Brazilian shield may have occurred (and still occur) across what is now the mouth of the Amazon river where the gap between them is comparatively narrow. This way may have been followed by *L. pallida* (map 18), *L. stricta* var. *parvula* (map 34), and a number of other ferns which show this type of distribution, such as *Bolbitis macrophylla* and *Doryopteris sagittifolia*. The gap in north-eastern Brazil that cuts the area of some of these species in two more or less separate parts may be due to the drier climate of this area, but it is possible that more intense collecting will reveal the presence of some species, now believed to be discontinuous, in locally suitable habitats. Yet it is unlikely that all floristic discontinuities between Guayana and south-eastern Brazil can be explained in this way. A number of species extend from the Guianas to the South along the eastern slope of the Andes and reappear in south-eastern Brazil, sometimes across Bolivia and Paraguay with hardly any break in their area, others with a considerably discontinuity. TRYON's distribution-maps for the species of *Doryopteris* (1942, 1944) provide excellent examples. While in some instances it may be argued that such species may eventually be found in intermediate localities or may have been present there in former times, this explanation can hardly serve for all these discontinuous patterns of distribution. BRADE (1942), who cited numerous examples of this kind of discontinuity, assumed that the mountains of Matto Grosso and Minas Gerais might have served as stepping-stones; but it is doubtful whether this explanation holds in all cases, particularly for such ferns of higher elevations as *Jamesonia* (Andes from Costa Rica to Bolivia; one endemic species on Mt. Itatiaia, s.e. Brazil). In the author's opinion no satisfactory explanation for this type of distribution has been given. Even more puzzling are the cases where the southern Andes are not included in the area, for example in *Lindsaea quadrangularis* (maps 14—17), and on Tryon's map of *Doryopteris nobilis*.

It is not easy to decide whether both Guayana and Brasilia developed their own more advanced species side by side that later did or did not become more widespread, but this seems quite likely. *L. ovoidea* from south-eastern Brazil, for instance, is probably a local derivative of the section *Pseudosphenomeris*, whereas in Guayana an almost unbroken series from primitive to advanced forms is present, with a gap between the type represented by *L. sphenomeridopsis* and that of the section *Temnolindsaea*, which was probably once bridged by a form analogous to the Brazilian *L. virescens*. It is not possible to ascertain whether *L. filipendula* and the two ssp. of *L. quadrangularis*, endemic in Brasilia, are phyletically connected with autochthonous primitive forms or whether they are derived from more advanced ones that originated elsewhere.

Let us now turn to the distribution of primitive groups and allied genera in order to make an attempt to reconstruct something of the history of the genus and its constituents.

COPELAND (1939, p. 179; 1947, p. 53) was convinced that *Lindsaea* is of Antarctic origin, which he believed to be true for about nine-tenths of the living ferns (1947, p. 7). The writer does not believe that in the case of *Lindsaea* the evidence is conclusive.

The section of this genus regarded at the most primitive by the author, at least in the New World, perhaps in the whole genus, is *Pseudosphenomeris*. It has one species in Annam and Hai-nan, one in Madagascar, two in south-eastern Brazil, and one in Venezuela (map 3). This kind of distribution strongly suggests a relic-group, and there is little evidence for linkage with Antarctic or Subantarctic regions. The presence of one species in Indo-China and one in Venezuela cannot be readily explained by the assumption of Antarctic origin. Notably the presence of *L. sphenomeridopsis* in the Upper Orinoco region is very interesting because it presents evidence for the presence of the most primitive section on both tropical South American shields, whereas formerly it was only known from the southern shield, which might have been interpreted as evidence for a southern centre of distribution. But if this section were of Antarctic origin, one would expect it in Chile, New Zealand, and Tasmania. The presence of several species of *Lindsaea* in New Zealand and Australia has been used as an argument in favour of southern origin; but a larger number is found in Japan, but little closer to the equator, and considerably farther from Antarctica. It must be admitted that some Australian and New Zealand species are probably rather primitive (*L. viridis*, *L. microphylla*, *L. trichomanoides* *)), but in the light of the presence of equally or perhaps more primitive forms in the northern hemisphere this does not appear to be of overwhelming significance.

Sphenomeris is another primitive group, as primitive as or perhaps more primitive than *Lindsaea* sect. *Pseudosphenomeris*. A glance at the list on p. 106 where most species correctly referred to *Sphenomeris* are listed, together with their distribution, conveys again the impression that this is a relic-group. There is only one widespread species, the others are scattered through the tropical and, in the New World, also the subtropical regions. The presence of two endemic or subendemic species in New Caledonia may be significant, as on that island other forms occur which are very likely Antarctic elements, e.g. *Nothofagus;* but again, this evidence is not conclusive, as it may well be explained by the very early isolation of New Caledonia where primitive, perhaps formerly more widespread types survive that were elsewhere replaced by more modern forms. There is nothing in the distribution of the three species of *Sphenomeris* in the Western Hemisphere that points to Antarctic origin.

It is a fact that generally the genus *Lindsaea* extends farther southward

---

*) Attention is drawn to the fact that the name *L. cuneata* (Forst. f.) C. Chr., 1906, for this well-known species from New Zealand and Australia is illegitimate, as it is a later homonym of *L. cuneata* Willd., 1810. The correct name is *L. trichomanoides* Dryand.

than northward from the equator, which is also observed in many other groups of ferns (*Cyatheaceae*, *Dicksoniaceae*, *Gleicheniaceae*, etc.), but this is no unambiguous argument pointing to Antarctic provenience. The climate in South Temperate latitudes is in many regions more equable in terms of temperature and precipitation than the more arid or continental climates prevailing in comparable northern latitudes, and supports a greater number of ferns. But this has not necessarily always been the case, and the presence of single representatives of mainly tropical and southern genera in northern regions where they often appear to be relics, e.g. *Schizaea pusilla* and *Lygodium palmatum* in Atlantic North America, *Culcita macrocarpa* on the Iberian Peninsula and in Macaronesia, *Trichomanes* in Atlantic Europe, eastern North America, and the Russian Far East (see KRYSHTOFOVICH, 1935) suggests that it has been different at one time. Fossil evidence for the past distribution of some groups of ferns pointing in the same direction has been summed up by SEWARD (1922). But even if Antarctica was involved in the migration of many recent ferns, it does not follow that it was the cradle of most or any of them. The author believes that with the evidence available at the present time it is impossible to establish the place of origin of *Lindsaea* and *Sphenomeris*, but it seems likely that they had a wide distribution from very early, possibly Mesozoic, times, and evolved in different directions in their two present-day centres, Malaysia/Polynesia, and Tropical America.

The absence of any endemic and all but one widespread Old World species in continental Africa has probably to be explained by the aridity which is widely believed to have prevailed in most of Africa during geologically rather recent times. Madagascar did not or only partly share this fate and retained an assortment of endemics and widespread, otherwise mainly Asiatic species. It is difficult to say whether *L. ensifolia* reached continental Africa before the arid period and survived locally, or whether it is a more recent immigrant. Its discontinuous distribution and the presence of a related, probably derived species on the other side of the Atlantic (*L. macrophylla*) seems to favour the first assumption; but then the absence of any differences between the West African and the Asiatic specimens of *L. ensifolia* is difficult to understand.

13. ECOLOGY

The great majority of species inhabit moist forests at lower and middle elevations. A few prefer more open habitats: *L. pratensis*, *L. pendula*, *L. schomburgkii*, *L. rigidiuscula*, *L. javitensis*, and *L. stricta*, and two are restricted to forests at middle and higher elevations, above 1000 m, namely, *L. klotzschiana* and *L. arcuata* (the latter not quite throughout its range). The number of euryoecous species is small; the only good example is *L. portoricensis* (p. 221), whereas some forms of *L. stricta* prefer marshes and others forests. None of the neotropical species is essentially epiphytic (some of the Old World representatives have scandent rhizomes), but a few are occasionally reported as growing on moss-covered tree-trunks, notably in western Colombia and south-eastern Brazil. There are few data on the composition of the soil where Lindsaeas grow; specimens that were not collected in the humus of a forest have been reported from sand, igneous or sandstone rocks, swamps, etc. There is little or no relation between habitat and range; two of the most widespread species, *L. lancea* and *L. divaricata*, inhabit forests, the third, *L. stricta*, occurs mostly in exposed situations, and *L. portoricensis* is found in very diverse surroundings.

In *L. stricta* and *L. protensa* the leaf-apex is often absent, and when it is present, it is usually immature, although the rest of the leaf may be fully developed, with mature sori. The leaves seem to develop very slowly, perhaps even intermittently, as in *Jamesonia*. Generally the leaves are probably rather long-lived; epiphyllous Hepatics are often present.

14. Uses

No reference to any use of ferns of the genus *Lindsaea* has been found, except in Seba (1735), who wrote about his "*Adiantum lancea*" (= *Lindsaea L.*): "ses vertus sont pectorales, telles que celles du capillaire de nos climats, dont l'usage si efficace contre la Toux & les autres maladies du poumon, est connu de tout le monde." This may, however, be due to confusion with true species of *Adiantum*. The very small number of vernacular names (recorded in the special part) is probably a reflection of this lack of application of these plants. Santamaria (1942) did not list a single vernacular name for the genus.

B. TAXONOMIC PART

Material

The present revision is based on the study of about 6000 herbarium-sheets, mainly consisting of the material from the following herbaria (standard abbreviations now in general use):

A	The Arnold Arboretum of Harvard University, Cambridge, Mass.
B	Botanisches Museum, Berlin-Dahlem, Germany.
BM	British Museum (Natural History), London, England. (including the herbarium of Carl Christensen cited as C. Chr. in BM)
BR	Jardin Botanique de l'Etat, Bruxelles, Belgium.
C	Botanical Museum & Herbarium, Copenhagen, Denmark.
F	Chicago Natural History Museum, Chicago, Ill.
FI	Herbarium Universitatis Florentinae, Florence, Italy.
G	Conservatoire et Jardin Botaniques, Genève, Switzerland.
GH	The Gray Herbarium of Harvard University, Cambridge, Mass.
GOET	Systematisch-Geobotanisches Institut, Göttingen, Germany.
IA	Department of Botany, State University of Iowa, Iowa City, Ia.
K	The Herbarium, Royal Botanic Gardens, Kew, England.

L	Rijksherbarium, Leiden, Netherlands.
LE	Botanical Institute of the Academy of Sciences, Leningrad, U.S.S.R.
M	Botanische Staatssammlung, München, Germany.
MO	The Missouri Botanical Garden, St. Louis, Mo.
NY	The New York Botanical Garden, New York, N.Y.
PH	The Academy of Natural Sciences, Philadelphia, Pa.
S	Botanical Department, Naturhistoriska Riksmuseum, Stockholm, Sweden.
S-PA	Paleobotaniska Avdelningen, Naturhistoriska Riksmuseum, Stockholm, Sweden.
U	Botanisch Museum & Herbarium, Utrecht, Netherlands.
UC	Herbarium of the University of California, Berkeley, Cal.
UPS	Institute of Systematic Botany, University of Uppsala, Sweden.
US	United States National Herbarium, Smithsonian Institution, Washington, D.C.
W	Naturhistorisches Museum, Wien, Austria.

In addition smaller quantities of material were received for study from the following herbaria:

EAP	Escuela Agricola Panamericana, Tegucigalpa, Honduras.
HBR	Herbario "Barbosa Rodrigues", Itajaí, Santa Catarina, Brazil.
P	Laboratoire de Phanérogamie, Muséum National d'Histoire Naturelle, Paris, France.
PI	Istituto Botanico dell'Università, Pisa, Italy.
Pic.-Ser.	Private herbarium of Prof. Dr. R. E. G. Pichi-Sermolli, Florence, Italy.
RB	Jardim Botânico, Rio de Janeiro, Brazil.
SI	Instituto Botánico "Darwinion", San Isidro, Argentina.
USM	Herbario San Marcos, Museo de Historia Natural, Lima, Perú.

The author wishes to express his deep gratitude to the directors and curators of all these Herbaria who made large quantities of valuable material available to him, often for a considerable time. Furthermore, he is much indebted to Dr D. E. Meyer, Berlin-Dahlem, for sending him photographs of specimens in the Willdenow-Herbarium that could not be sent on loan.

MAPS

The distribution-maps have been compiled from the data on the herbarium-labels or in enumerations of specimens where they are sometimes more extensive. No literature-records alone have been used, mainly because of the general unreliability of identifications published in enumerations and floras. The localities were mainly located with the help of the "Index to Map of Hispanic America" (Washington, 1943–44) published by the American Geographic

Society. The author is highly indebted to this Society for sending him a free copy of this most excellent and useful Index. The spelling of the names is generally in accordance with the Index.

Each dot represents one or several closely adjacent localities; those which could only approximately be located are indicated by open circles. Localities of dubious specimens and those which could not be found in the Index or on any map have not been indicated, except in the latter case when the province or country in which they were situated was comparatively small; then a circle has been used. Species known from only one locality have mostly not been mapped. The maps are from Goode's series of base maps, published by the University of Chicago Press.

KEY AND DESCRIPTIONS

The key to the species of *Lindsaea* offered below is largely artificial, although the sections appear more or less as units. As several species are not constant in characters used in the key which serve to separate others, these forms appear in more than one place. For this reason and because of the fact that in the section *Lindsaea* which contains the bulk of the species the relationships are often not quite clear or appear to be reticulate, it would be practically impossible to construct a key in such a way that each species appears only once and is always closest to its nearest relatives.

It is hoped that perhaps 90 % of the specimens can be keyed out in a satisfactory way. (In most cases it will be difficult or impossible to determine sterile or incompletely fertile and immature specimens, although these can not rarely be named by an expert well acquainted with all species). For the remaining 10 %, where certain characters used in the key will be found to be aberrant, the descriptions and figures will have to be consulted in the first place. For this reason almost every taxon has been figured, and the descriptions are rather detailed, which would be superfluous in a group where one or a combination of a small number of characters serve to separate the species quite unambiguously. The degree of dissection has but rarely been used as a key character, but it is mentioned with all species or species-groups because although it is often unreliable it may sometimes be of importance. In addition the overall distribution has been listed in the key, as this may also help to prevent misidentifications where the characters employed are rather subtle.

Although most characters used in the key can be observed on the abaxial side of the leaves, in some cases the adaxial side should also be accessible for examination. In this connection the author wishes to point out that fern-specimens should never be pasted directly to the sheets, as in most cases, especially in small ferns which are not folded, this renders one of the sides inaccessible. Material mounted in such a way may become quite worthless in extreme cases, and it is most regrettable that in some of the largest herbaria of the world this way of mounting is still in practice.

A few remarks on the terminology have to be made, although for the greater part the terms usually employed in pteridological publications have been used.

The terms "above" and "below" are always used in the sense of distal and proximal with regard to the rhizome. For the upper and lower surfaces of lamina, petiole, etc., the terms "adaxial" (ventral) and "abaxial" (dorsal) have been used consistently. The word pinnule always applies to a free ultimate segment, regardless of whether the leaf is pinnate, bipinnate, or tripinnate (see p. 128), except in *Lindsaea macrophylla* and *Ormoloma*, where the large symmetric ultimate divisions are presumably homologous to primary pinnae. A segment is a more or less, but not completely, free division (sometimes used in a general way to indicate any kind of ultimate division). When describing the dissection of laminae which are once or several times pinnately divided and then incompletely incised, the terms bipinnate + bipinnatifid, etc., have been used, instead of bipinnate-bipinnatifid, as is usually done, because the latter expression might be misunderstood to mean bipinnate passing into bipinnatifid.

Measurements of pinnules etc. apply to the largest specimens found on a single lamina, unless otherwise stated. The width of more than simply pinnate laminae has mostly not been given, as it is often not readily measured, apices of pinnae being frequently lost or bent to fit collectors' presses or small herbarium-sheets. The general shape of more than simply pinnate laminae depends strongly on the number of primary pinnae, which in most species is quite variable, and therefore has likewise not been described in most cases.

The citations of literature with the synonyms have been restricted to the principal and most readily accessible publications. Because of the widespread misinterpretation of many species there would be little use in endeavouring to give an almost complete list of citations.

KEY TO THE NEW WORLD GENERA OF LINDSAEOIDS

1\. a. Leaves scandent, indeterminate, at least tripinnate, the axes often spiny; sori uninerval . . . . 2. *Odontosoria*

b. Leaves not scandent, determinate, variously incised or simple, never spiny; mostly at least some of the sori borne on more than one vein 2

2\. a. Ultimate divisions cuneate, linear, or spathulate; sori uni- or binerval (rarely on more veins); leaves decompound . . 3

b. Ultimate divisions dimidiate or equilateral, in the latter case not cuneate or spathulate; leaves rarely decompound, mostly bipinnate, pinnate, or simple, rarely (sub)tripinnate. 4

3\. a. Indusia attached by the base and part of the sides; scales narrowly lanceolate, the largest in some species over 5 mm long, or, if shorter, of one row of cells throughout or almost throughout; sporangia large, over 200 μ, mostly over 300 μ 1. *Sphenomeris*

b. Indusia attached by their bases only; scales lanceolate, not over 1.5 mm long, the larger ones never of one row of cells only; sporangia with few exceptions below 200 μ in length, never much larger . . . . 3. *Lindsaea*

4\. a. Ultimate divisions dimidiate, or, if equal-sided, with continuous sori . . . . 3. *Lindsaea*

b. Ultimate divisions equal-sided; sori uninerval 4. *Ormoloma*

1. SPENOMERIS

Sphenomeris Maxon, Journ. Wash. Acad. Sci. 3: 144 (1913).

Rhizome creeping, mostly with a Lindsaeoid protostele, in a few species reported to be solenostelic. Scales narrowly lanceolate to linear, either with a long subulate apex consisting of one row of cells only, or of one row of cells throughout or almost throughout. Leaves rather close to close, ± distichous, decompound. Ultimate segments linear, cuneate, or spathulate. Sori terminal on one to four veins; indusium fixed at the base and at least part of the sides, opening outwardly; sporangia over 200 μ, mostly over 300 μ long, often few per sorus, mixed with paraphyses (always?); spores monolete or trilete.

About 10 species in tropical and subtropical regions of both hemispheres.

Type species: *Sphenomeris clavata* (L.) Maxon (*Adiantum clavatum* L.)

Key to the American species:

1″. Sori of larger segments occupying more than one vein; scales linear, consisting of one row of cells throughout or almost throughout . . . . 1. *S. clavata* (Florida, Greater Antilles)

1′. Sori occupying one vein; scales lanceolate, with at least two rows of cells at the base

  2″. Ultimate segments spathulate, $1^1/_2$—2 mm wide near the apex . . . . 2. *S. spathulata* (Colombia)

  2′. Ultimate segments linear or slightly cuneate, not over 1 mm wide . . . . 3. *S. killipii* (Colombia)

1\. **Sphenomeris clavata** (L.) Maxon, Journ. Wash. Acad. Sci. 3:144 (1913).

Basionym: *Adiantum clavatum* L., Spec. Plant. 2:1096 (1753).

Homotypic synonyms: *Davallia clavata* (L.) J. E. Smith, Mém. Acad. Roy. Turin 5:415 (1793).

Stenoloma clavatum (L.) Fée, Gen Fil. 330 (1852).
Odontosoria clavata (L.) J. Smith, Hist. Fil. 264 (1875).

It is not necessary to describe this well-known species here. A good illustration was given by SMALL (1938, p. 318). Its range (map 4) is: Southern Florida, Bahamas, and Greater Antilles. In Florida, it is restricted to the extreme South; for a long time it was only known from the Everglade Keys (Dade County), but it was recently (March 1952) discovered in the Florida Keys (Monroe County): Big Pine Key, Killip 41421, 42001 (US). In Cuba it is apparently uncommon, except in the East, where it seems to be plentiful; also on Isla de Pinos; otherwise Jamaica, Hispaniola (both Haiti and San Domingo), western Puerto Rico, and Bahamas: islands of New Providence, Andros, Eleuthera, Rose, and Great Abaco.

In Florida, this species occurs in lime-sinks, limestone outcrops and walls of sinkholes in pinelands, also, but rarely, in hammocks (see SMALL, 1920, 1938, CORRELL, 1938, BROUN, 1938). In the West Indies, its habitats seem to be more diverse; it has often been collected on precipitous cliffs, in crevices of calcareous or serpentine rocks, along streams, etc.

The rhizome-scales are up to 2½ mm long, rather dark brown, and consist of one or occasionally at the extreme base of two rows of cells. The sporangia are small for the genus, ca. 220—170 μ, the annulus with 15–17 indurated cells that reach the stalk; spores rather dark brown, trilete, subglobose, ca. 50 × 45 μ. For a figure of the spores, see WAGNER (1952 b, pl. 5 c).

2. **Sphenomeris spathulata** (Maxon) Kramer, comb. nov.

Basionym: *Lindsaea* (?) *spathulata* Maxon, Contr. Gray Herb. 165:74 (1947).

There is little to add to Maxon's very complete description. The scales are very narrowly lanceolate and consist of 2 or 3 rows of cells at the base. The head of the sporangium is ca. 320 × 250 μ, with an annulus with 16—18 indurated cells that do not quite reach the stalk; the spores are trilete, subglobose, pale brown, ca. 46 × 37 μ, probably 32 per sporangium. Type: Haught 1960 (US), from Cerro Armas, dept. Santander, Colombia.

3. **Sphenomeris killipii** (Maxon) Kramer, comb. nov.

Basionym: *Lindsaea* (?) *killipii* Maxon, Contr. Gray Herb. 165:74 (1947).

As in the preceding species, the reader is referred to Maxon's description, to which the following data may be added: scales lanceolate, long-acuminate, with up to 7 rows of cells at the base. Sporangia ca. 330 × 250 μ, annulus with 18—20 indurated cells that do not quite reach the stalk; spores trilete, subglobose, medium brown, ca. 46 × 42 μ.

Type: Killip 7947 (US), from La Gallera in the Micay Valley, dept. Cauca, Colombia.

It is difficult to understand why Maxon included these two species in *Lindsaea*, though with a ?. He commented himself on the resemblance to certain species of *Sphenomeris*, but excluded them from that genus because it had "diplanate spores, and the truly marginal sori are endophyllous and urceolate, with both valves of the indusium similar in texture . . ." (l.c.p. 75). The second statement is not generally true and the first one is very strange, as *S. clavata*, chosen by Maxon himself as type species, has trilete spores.

2. ODONTOSORIA

Odontosoria (Presl) Fée, Gen. Fil. 325 (1852).

Type species: *Odontosoria uncinella* (Kze.) Fée (*Davallia uncinella* Kunze).

For this genus, the reader is referred to MAXON's excellent revision (1913), to which little remains to be added. It seems somewhat doubtful whether *O. wrightiana* Maxon is more than a local form of *O. aculeata* (L.) J. Smith; there are several intermediates, some of them duplicates of specimens cited by Maxon with the type.

Otherwise, there are a few range-extensions which will perhaps be dealt with elsewhere.

3. LINDSAEA

Lindsaea Dryander in J. E. Smith, Mém. Acad. Roy. Sci. Turin 5:401 (1793); Dryander, Trans. Linn. Soc. 3:39 (1797); Roem. Arch. 2 (II): 234 (1801); Swartz, Syn. Fil.x, 5 (1806); Schkuhr, Krypt. Gew. I: 105 (1809); Poiret in Lamarck, Encycl. Suppl. I: 133 (1810); Willdenow, Spec. Pl. V:420 (1810); Poiret in Lamarck, Encycl. Suppl. III:447 (1813); Kunth in H.B.K., Nov. Gen. Spec. I:18 (1815); Kaulfuss, Enum. 218 (1824); Sprengel, Syst. Veget. IV: 79 (1827); Desvaux, Prod. 171 (1827); Sprengel, Gen. Pl. 9th ed. 723 (1830); Presl, Tent. Pterid. 131 (1836); J. Smith, Jo. Bot. 25/26: 88 (1841); J. Smith, Lond. Jo. Bot. 1:423 (1842); Hooker & Bauer, Gen. Fil. t. 63 A (1842); Hooker, Spec. Fil. I:203 (1844)*); Kunze, Bot. Zeit. 8:299 (1850); Fée, Gen. Fil. 104 (1852); Mettenius, Fil. Lips 104 (1856); Moore, Ind. Fil. I:39 (1857); Fée, 10e mém. 13 (1865); Ettingshausen, Farnkr. 211 (1865); Fée, 11e mém. 15 (1866); Bommer Monog. Cl. Foug. 69 (1867); Hooker & Baker, Syn. Fil. 1st ed. 104 (1868), 2nd ed. 104, app. 471 (1874); Fée, Crypt. vasc. Brés. I:29 (1869) Baker, Fl. Bras. I^2: 349 (1870); J. Smith, Hist. Fil. 267 (1875); O. Kuntze, Rev. Gen. Pl. 815 (1891); Sodiro, Crypt. Vasc. Quit. 56 (1893); Christ, Farnkr. d. E. 291 (1897); Jenman, W. Ind. Gui. F. 70 (1899); Diels, N. Pfl. I^4: 219 (1902); Duss. Fl. Crypt. Ant. franç. 58 (1904); Maxon, Pter. Port. 488 (1926); Pérez Arbeláez, Bot. Abh. Goebel 14:53 (1928); Posthumus, Fl. Surin. Suppl. 68 (1928); Domin, Pterid. Domin. 242 (1929); Copeland, Univ. Calif. Publ. Bot. 16 (2): 83 (1929); C. Christensen in Verdoorn, Man. Pterid. 538 (1938); Dutra, An. Prim. Reun. Sul-Am. Bot. II:29 (1938); Capurro, ibid., 106 (1938); Copeland, Gen. Fil. 52 (1947); Hodge, Lloydia 17 (2):102 (1954).

Schizoloma Gaudichaud; Presl, Tent. Pterid. 132 (1836), in part; Hooker & Bauer, Gen. Fil. t. 63 B (1842); Fée, Gen. Fil. 108 (1852), in part; Diels, N. Pfl. I^4:218 (1902), in part; and of other authors.

---

*) The year of publication of vol. I of Hooker's Species Filicum is given by Christensen (Ind. Fil.) as 1844 for p. 1–128, for the rest as 1846, probably on the base of Kunze's critical notes in Bot. Zeit. (1844–1850). But Klotzsch in 1844 (Linnaea 18:544) referred already to *Davallia imrayana* as published in Spec. Fil. I: 171, which must have been issued at least up to that page in 1844.

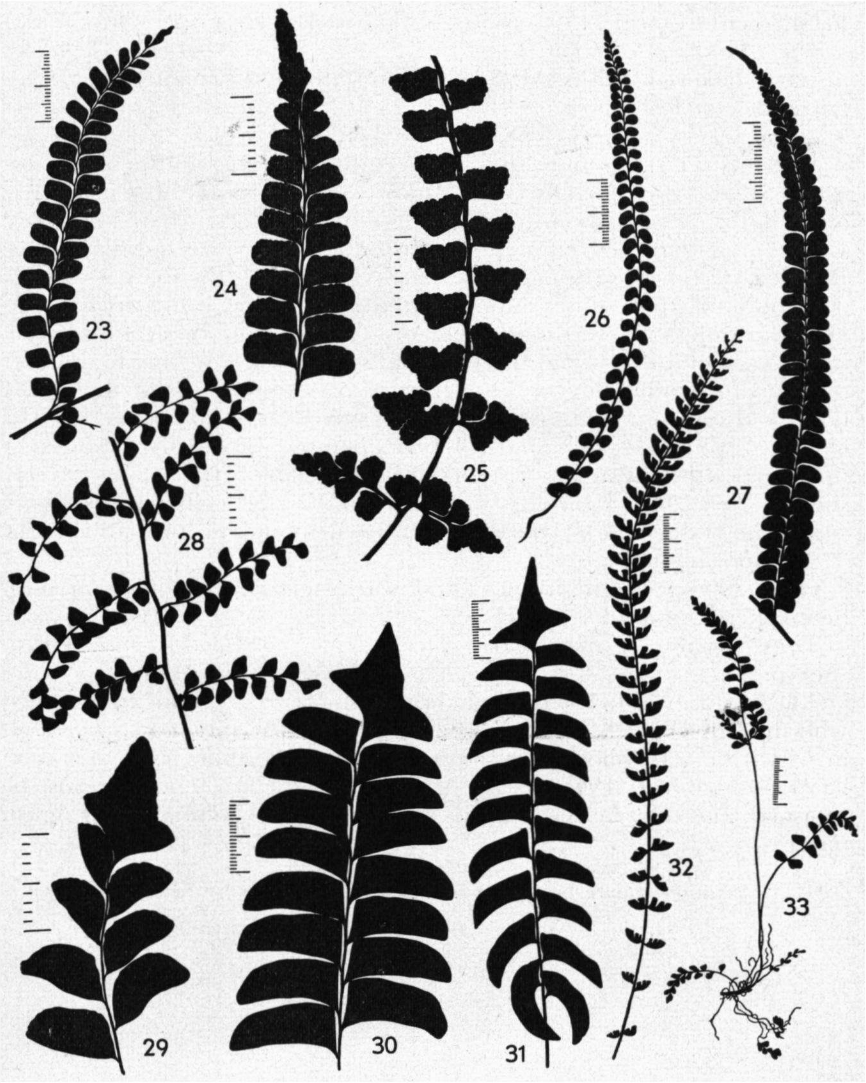


Fig. 23: *Lindsaea ovoidca;* rachis and pinna from middle of lamina (Wacket 167). Fig. 24: *L. portoricensis;* apex of lateral pinna (Focke 913). Fig. 25: *Odontosoria uncinella;* upper part of primary pinna (Howard 6129). Fig. 26: *Lindsaea stricta* var. *stricta;* complete leaf (Glaziou 15722). Fig. 27: *L. guianensis* ssp. *guianensis*; middle pinna (Hostmann & Kappler s.n.). Fig. 28: *L. tenuis;* part of lamina (Schomburgk 1185). Fig. 29: *L. lancea* var. *remota;* apex of simply pinnate lamina (Lanjouw & Lindeman 516). Fig. 30: *L. lancea* var. *falcata;* upper ⅔ of lamina (Sagot 734). Fig. 31: *L. lancea* var. *leprieurii;* lamina (Kappler 1353). Fig. 32: *L. seemannii;* complete lamina (Seemann 976). Fig. 33: *L. cubensis;* complete plant with two fertile leaves (Wright 3947). (Scales in mm).

Davallia J. E. Smith; Sprengel, Syst. Veget. IV: 18 (1827), in part; Presl, Tent. Pterid. 129 (1836), in part; Hooker, Spec. Fil. I: 151 (1844); Hooker & Baker, Syn. Fil. 1st ed. (1868), 2nd ed. (1874) 88, in part; Baker, Fl. Bras. I^2: 343 in part; and of other authors.

Odontosoria Fée; Diels, N. Pfl. I^4: 215 (1902), in part; and of other authors.

*) Rhizome creeping or slightly ascending, with a Lindsaeoid protostele. Scales ovate to lanceolate, mostly evenly dark brown, hardly ever clathrate, mostly intermingled with reduced ± hair-like ones. Leaves close to rather remote, inserted in a single row or subdistichous. Petiole stramineous to blackish, always dark at the base. Lamina decompound, three times to once pinnate or simple; ultimate divisions very variable, mostly dimidiate. Sori terminal on the veins (rarely slightly extending along the vein-ends, oblique) or on a vascular commissure connecting two to all veins of a pinnule or of the whole lamina. Indusium semi-ovate to linear, fixed at its base and, if it is elongate, often at part of its sides, opening outwardly; sporangia numerous, the head mostly between 120 and 200 μ long, rarely slightly over 200 μ; annulus with 7–15 indurated cells which mostly reach the stalk; spores trilete or less often monolete, probably 16 or 32 per sporangium.

Over 200 species in tropical and warm-temperate regions of both hemispheres (map 1).

Type species: *L. trapeziformis* Dryander (= *L. lancea* (L.) Bedd.). (See p. 137).

The genus was named after John Lindsay, a Jamaican botanist who died in 1803. KAULFUSS (1824) changed the spelling to *Lindsaya*, in which he was followed by most subsequent authors, but, as COPELAND pointed out (1947, p. 53), the original spelling *Lindsaea* must be retained, and may be regarded as admissible latinization of an English name.

*) Description chiefly based on the American species.

KEY TO THE SPECIES

(The number of dashes indicates the number of alternatives; for instance, 1″ means that the key is dichotomous, 2‴ that it is trichotomous under that number, etc.).

1″. Ultimate divisions approximately equilateral, oblong, with anastomosing veins; sori continuous; leaves simply pinnate . . 45. *L. macrophylla* (n.e. South America)

1′. Ultimate divisions cuneate or dimidiate, rarely almost equilateral, or leaves simple; veins, apart from the receptacle, free.

2‴. Leaves simple.

3″. Petiole abaxially terete throughout or with short, irregular angles below the apex; spores trilete.

4″. Lamina with an acumen at the apex; a central main vein present, from which lateral veins depart in a not truly dichotomous way . . . . . 38. *L. sagittata* (Guayana)

4′. Apex of the lamina rounded; all veins evenly dichotomous. 39. *L. reniformis* (Guayana)

3′. Petiole abaxially angular above up to the sclerotic patch at the base of the lamina; spores monolete . . . . 40. *L. cyclophylla* (Guayana)

2″. Leaves simply pinnate, the pinnules downwards gradually reduced and more widely spaced; rachis abaxially terete or keeled; spores monolete.

5″. Scales clathrate; pinnules incised, sori interrupted . . 42. *L. seemannii* (Panamá, Colombia)

5′. Scales not clathrate; pinnules mostly entire with continuous sori.

6″. Pinnules small, the middle ones 5–8 × 3–5 mm, 80–100 to a side, herbaceous; abaxial side of the petiole narrowed-rounded. . . . . 44. *L. protensa* (Hispaniola)

6′. Pinnules larger, 8–13 × 5–8 mm, 30–50 to a side, coriaceous; abaxial side of the petiole keeled . . . 43. *L. pratensis* (Costa Rica)

2′. Leaves simply pinnate to tripinnate; when simply pinnate, the lower pinnules never gradually reduced, rarely slightly more apart; spores with few exceptions trilete.

7″. Secondary pinnae or pinnules pendulous.

8‴. Pinnules cleft; leaves often subtripinnate to tripinnate, the upper pinnae gradually reduced, the leaf-apex gradually simpler in structure. . . 4. *L. meifolia* (w. Guayana)

8.″ Pinnules simple; leaves bipinnate with an odd terminal pinna; a few shortened upper pinnae may be present. 5. *L. pendula* (w. Guayana)

8′. Lower pinnules cleft, upper ones simple, as in the preceding species; lamina rather suddenly contracted below the terminal pinna (a hybrid of nrs. 4 and 5) . . . . . . 6. *L.* × *dissecta*

18′. Axes not winged.

19″. Pinnules 3 × as long as wide, narrowed to the subacute apex; axes stramineous to medium brown; bipinnate . . 8. *L. cultriformis* (n.w. S. America)

19′. Pinnules less than 3 × as long as wide, little or not narrowed at the obtuse, truncate, or broadly rounded apex; axes dark reddish-brown to blackish.

20″. Largest (basal) pinnules decurved and flabellate-widened towards the apex, the base of the lower margin sterile, concave; almost always simply pinnate . . . . 13. *L. botrychioides* (s.e. Brazil)

20′. Pinnules not flabellate-widened towards the apex, the lower ones not decurved; the whole lower margin sterile, straight or convex; almost always bipinnate.

21″. Sori, except in strongly reduced pinnules, regularly interrupted . . . . 7. *L. klotzschiana* (C. and n.w. S. America)

21′. Sori only in some of the largest pinnules with one interruption in the outer and one or two in the upper margin . . . . 12. *L. ovoidea* (s.e. Brazil)

13′. Sori continuous (in completely fertile leaves).

22″. Leave smostly simply pinnate, somewhat dimorphous, the fertile ones surpassing the sterile ones which are always present; spores monolete . . . . 41. *L. cubensis* (Cuba, Isla de Pinos)

22′. Leaves pinnate to tripinnate, not dimorphous, but often the sterile ones with slightly incised margins; in most species completely sterile leaves rarely found on mature rhizomes; spores with few exceptions trilete.

23″. Petiole abaxially terete throughout.

24″. Petiole reddish-brown to blackish or atropurpureous.

25″. Petiole very slender, wiry, 0.3–0.6 mm in diam.

26″. Indusium ca. 0.5 mm wide; pinnules 4–6 × 2–3 mm; upper margin minutely erose to subentire in fertile pinnules; bipinnate . . . 31. *L. tenuis* (Guayana)

26′. Indusium 1–1 ½ mm wide; pinnules 6–7 × 4–5 mm; upper margin irregularly erose-lacerate in fertile pinnules; pinnate or bipinnate . . . . 30. *L. filipendula* (c. and s.e. Brazil)

25′. Petiole stouter.

27‴. Primary rachis adaxially and secondary rachises on both sides (rarely only abaxially) with pale lateral wings; pinnules obtuse . . 23. *L. divaricata* (widespread)

7.′ Secondary pinnae or pinnules not pendulous.

9″. Leaves more than once pinnate; upper primary pinnae gradually reduced in size and complexity, no conform terminal pinna present; ultimate divisions cuneate or linear, or, if dimidiate, incised.

10″. Ultimate segments dichotomous-divaricate, cuneate or linear, the largest not over 0.8 mm wide at the base; sori mostly uninerval.

11″. Sori of large, broad segments often oblique; colour dull olivaceous in dry specimens . . . . 2. *L. sphenomeridopsis* (Venezuela)

11′. Sori practically always at right angles with the veins; colour vivid green in dry specimens . . . . 1. *L. bifida* (e. Brazil)

10′. Ultimate segments consisting of dimidiate, incised pinnules, their largest lobes at the base up to 2 mm wide, mostly but little divaricate; most sori bi- to quadrinerval . . . . . 3. *L. virescens* (s.e. Brazil)

9′. Leaves simply pinnate, or, if more dissected, with a conform terminal pinna, the upper pinnae not strongly reduced.

12″. Pinnules only with a short basal dimidiate portion, consisting mainly of an obliquely ascending apex with a diagonal midrib, fertile along both sides, 5–7½ × as long as wide; bipinnate. 22. *L. taeniata* (Colombia)

12′. At least the basal half, mostly the whole pinnule dimidiate, or, if the greater part is non-dimidiate, soriferous only along the upper side.

13″. Sori interrupted, mostly separated by incisions of the margin (beware of incompletely fertile pinnules of species with normally continuous sori!).

14″. Most sori uninerval.

15″. Pinnules cleft into narrow oblique lobes, 1.5–2 cm long . . . . 9. *L. stenomeris* (Venezuela)

15′. Pinnules shallowly lobed or subentire, up to 1 cm long . . . . . 11. *L. parkeri* (Guayana)

14′. Most sori at the ends of two or more veins.

16″. Pinnules linear, ca. 10–20 × as long as wide; simply pinnate . . . . 20. *L. dubia* (Guayana, Colombia)

16′. Pinnules relatively much wider.

17″. Pinnules ca. 7 × 3 mm . . . . 11. *L. parkeri* ssp. *steyermarkiana* (Venezuela)

17′. Pinnules larger.

18″. Upper part of the petiole, primary and secondary rachises with conspicuous pale wings along the four edges; mostly bipinnate . . . . 10. *L. tetraptera* (n.w. S. America)

27″. Primary and secondary rachises adaxially with pale wings; pinnules mostly acute or subacute. 25. *L. hemiptera* (Guayana)

27′. Rachises not winged, or only traces of paler wing-like portions present on the adaxial side of the secondary rachises.

28″. Pinnules coriaceous; veins hidden.

29″. Leaves simply pinnate, or with few (up to 3, rarely 5) pairs of strongly ascending pinnae; margin of pinnules mostly incurved around the sori . . . .
27. *L. stricta* (widespread)

29′. Leaves bipinnate, with 6–15 spreading pinnae to a side; margin of pinnules not incurved around the sori . . .
28. *L. javitensis* (Guayana)

28′. Pinnules thinner in texture, or, if firm, veins evident.

30″. Indusim mostly repand-erose; pinnae strongly ascending; secondary rachises with sharp often paler lateral ridges, these irregularly interrupted towards the base . . . .
27. *L. portoricensis* (widespread).

30′. Indusium entire to minutely erose, rarely more strongly erose; secondary rachises abaxially terete, or with continuous lateral ridges; or leaves simply pinnate.

31″. Upper pinnules gradually reduced, confluent with a small terminal segment.

32″. Spores monolete; bipinnate . . . .
14. *L. quadrangularis* ssp. *quadrangularis* (s.e. Brazil)

32′. Spores trilete; pinnate or bipinnate.

33″. Simply pinnate, the greater part of the rachis abaxially angular. 26. *L. portoricensis* (widespread)

33′. Bipinnate, or, if simply pinnate, the greater part of the rachis abaxially terete.

34‴. Texture coriaceous; secondary rachises abaxially angular almost to the base; bipinnate . .
28. *L. javitensis* (Guayana)

34″. Texture herbaceous; secondary rachises abaxially for a considerable part terete; or simply pinnate . . . .
24. *L. guianensis* ssp. *lanceastrum* (Brazil)

34′. Texture herbaceous; secondary rachises dark, abaxially grooved almost to the base, the borders pale and wing-like; bipinnate . . .
14. *L. quadrangularis* ssp. *subalata*
(Cuba, Mexico to Colombia)

31′. Upper pinnules but little reduced, not less than half as long as the lower ones, not or only by a very narrow wing connected with the terminal segment.

35″. Secondary rachises abaxially terete at the base, then gradually angular or sulcate, or rarely angular almost to the base; bipinnate
14. *L. quadrangularis* ssp. *terminalis*
(s.e. Brazil, Paraguay)

35′. Secondary rachises abaxially terete at the extreme base, then abruptly grooved; or lamina simply pinnate . . . 32. *L. lancea* (widespread)

24′. Petiole stramineous to pale brown.

36″. Texture coriaceous; veins hidden; pinnate or bipinnate 27. *L. stricta* (widespread)

36′. Texture thinner.

37″. Pinnules not more than 1½ × as long as wide, roundish.

38″. Indusium 0.15 mm wide, entire or minutely erose; pinnules often slightly imbricate; bipinnate or pinnate . . . . . . 24. *L. guianensis* (widespread)

38′. Indusium 0.3–0.5 mm wide, more strongly erose; pinnules mostly not imbricate; bipinnate, rarely simply pinnate or subtripinnate . . . . forms of *L. stricta* (no. 27), mainly from s.e. Brazil

37′. Pinnules at least twice as long as wide.

39″. Sterile margin (mostly present in the apex of the pinna) sharply dentate; indusium strongly and irregularly erose-dentate; spores monolete; bipinnate....15. *L. pallida* (Trinidad, S. America)

39′. Sterile margin entire or crenate, or, if with acute teeth, the indusium not strongly erose.

40″. Pinnules 5–9 × 2–2½ mm; pinnate or bipinnate . . . . 17. *L. spruceana* (Perú)

40′. Pinnules longer and wider.

41″. Secondary rachises abaxially at least for a considerable basal part terete, or leaves simply pinnate. 24. *L. guianensis* (widespread)

41′. Secondary rachises abaxially sulcate to the base or mostly with a short terete portion at base.

42″. Pinnules at least 3 × as long as wide . . 16. *L. arcuata* (widespread)

42′. Pinnules not over 2½ × as long as wide 14. *L. quadrangularis* ssp. *antillensis* (e. Caribbean area)

23′. Petiole abaxially at least near the apex flattened or obtusely to sharply angular.

43″. Veins elevated throughout or for the greater part; texture mostly chartaceous or coriaceous.

44″. Leaves bipinnate, with upwards gradually reduced pinnules and a small terminal segment . . . . 29. *L. rigidiuscula* (n. and c. South America)

44′. Leaves simply pinnate, with a large terminal pinnule.

45″. Pinnules 18–35 mm long, up to 2½ × as long as wide . . 33. *L. schomburgkii* (n. and c. South America)

45′. Pinnules 30–45(–70) mm long, 3–3½(–4) × as long as wide 34. *L. semilunata* (Guayana)

43′. Veins raised at their extreme bases only or wholly immersed, obscure or visible as wrinkles in the leaf-tissue.

46″. Petiole delicate, wiry, up to 0.6 mm in diam., mostly quite dark.

47″. Indusium 1–1½ mm wide, grossly erose-dentate; pinnate or bipinnate . . . 30. *L. filipendula* (c. and s.e. Brazil)

47′. Indusium narrower.

48″. Indusium 0.4 mm wide; pinnules trapeziform to dimidiate-ovate, 4–8 mm wide; almost always bipinnate . . . . 12. *L. ovoidea* (s.e. Brazil)

48′. Indusium ca. 0.2 mm wide; pinnules lanceolate, not over 2.5 mm wide; pinnate or bipinnate . . . . . 17. *L. spruceana* (Perú)

46′. Petiole stouter.

49″. Petiole reddish or brown to blackish, sometimes pale-angled.

50″. Pinnules linear, 10–20 × as long as wide; simply pinnate . . 20. *L. dubia* (Guayana, Colombia)

50′. Pinnules relatively wider, not linear.

51‴. Terminal pinnule large, free, without a distinct apex, the distal margin faintly and evenly convex or sinuous; petiole abaxially for the greater part terete; simply pinnate . . . . . 37. *L. ulei* (Venezuela, n. Brazil)

51″. Terminal pinnule free or almost free, with an obtuse or mostly acute apex.

52″. Largest pinnules flabellately widened towards the apex; practically always simply pinnate 13. *L. botrychioides* (s.e. Brazil)

52′. Largest pinnules not flabellately widened towards the apex; once or twice pinnate.

53″. Pinnules narrowed towards the apex, mostly lanceolate; no distinct outer margin developed.

54″. Pinnules lanceolate, 5–6 × as long as wide.

55″. Apex of pinnules acute or shortly acuminate; pinnate, rarely bipinnate 19. *L. surinamensis* (Guayana)

55.′ Apex of pinnules long-acuminate, upturned in the upper ones; bipinnate 18. *L. coarctata* (n.w. S. America, s.e. Brazil)

54′. Pinnules trapeziform to dimidiate-elliptic or oval, ca. 2–2½ × as long as wide: see 53′

53′. Pinnules hardly or not narrowed towards the apex, a distinct outer margin mostly present.

56″. Secondary rachises abaxially gradually passing from a terete into an angular shape or angular close to base; bipinnate . . . .
14. *L. quadrangularis* ssp. *terminalis* (s.e. Brazil, Paraguay)

56′. Secondary rachises abaxially sulcate, the groove abruptly starting just above the base; or leaves simply pinnate . .
32. *L. lancea* (widespread)

51′. Upper pinnules gradually confluent into a small terminal segment.

57″. Largest pinnules 5– more than 6 × as long as wide; bipinnate. 18. *L. coarctata* (n.w. S. America, s.e. Brazil)

57″. Largest pinnules 3–3½ × as long as wide; pinnate or bipinnate . . . . . . 16. *L. arcuata* (widespread)

57′. Largest pinnules up to 2½ × as long as wide.

58″. Texture coriaceous; veins hidden; pinnate or bipinnate . . . . . . 27. *L. stricta* (widespread)

58′. Texture herbaceous to chartaceous; veins evident.

59″. Largest pinnules flabellate-widened towards the apex; almost always pinnate . . . .
13. *L. botrychioides* (s.e. Brazil)

59′. Largest pinnules not widened towards the apex.

60″. Leaves simply pinnate, with reddish petioles, or, if bipinnate, the secondary rachises abaxially angular, the angles irregularly interrupted towards the base . . . .
26. *L. portoricensis* (widespread)

60′. Leaves bipinnate (rarely simply pinnate, with blackish petioles), the secondary rachises without lateral angles irregularly interrupted at the base.

61″. Pinnules not narrowed to the apex, or, if narrowed, there broadly rounded and ± ovoid-elliptic . . 12. *L. ovoidea* (s.e. Brazil)

61′. Pinnules narrowed to the apex, or, if of almost equal width, more elongate . . . .
14. *L. quadrangularis* (widespread)

49′. Petiole stramineous to pale brown, only at the base darker.

62″. Terminal segment large, free or almost so; upper pinnules not strongly reduced, not less than half as large as the lower ones.

63″. Apex of at least some of the pinnules prolonged, pointing obliquely upwards, these pinnules with a diagonal main vein; pinnate or bipinnate.

64″. Inner margin of pinnules divergent from the rachis; upper pinnules but little reduced, terminal segment almost free . . 21. *L. herminieri* (Guadeloupe)

64′. Inner margin of pinnules approximately parallel to the rachis; upper pinnules more strongly reduced, connected with the terminal segment . . . . the caudate form of 16. *L. arcuata*

63′. Apices of pinnules not prolonged, or, if so, without a diagonal main vein.

65″. Pinnules little or not at all narrowed towards the apex which is rounded at the acroscopic, mostly angular at the basiscopic side; pinnate or bipinnate . . . . . . 32. *L. lancea* (widespread)

65′. Pinnules strongly narrowed towards the acute or acuminate, often upturned apex.

66″. Pinnules 3–4 × as long as wide, mostly dark olivaceous to brown in dry specimens; pinnate or rarely bipinnate 35. *L. latifrons* (Perú)

66′. Pinnules 4–6 × as long as wide, usually bright green in dry specimens; simply pinnate . . . . 36. *L. hemiglossa* (Ecuador, Perú)

62′. Terminal segment small, connected by wings with the uppermost of the gradually confluent, strongly reduced upper pinnules.

67″. Apex of pinnules protracted, pointing obliquely upwards . . . . see 64′

67′. Apex of pinnules not protracted.

68″. Pinnules not more than 2½ mm wide; pinnate or bipinnate . . . . 17. *L. spruceana* (Perú)

68′. Pinnules wider.

69″. Spores monolete; indusium strongly and irregularly erose-denticulate; bipinnate . . . . 15. *L. pallida* (Trinidad, S. America)

69′. Spores trilete; indusium mostly not so irregularly erose.

70″. Pinnules 3–3½ × as long as wide; pinnate or bipinnate . . 16. *L. arcuata* (widerspread)

70′. Pinnules less than 3 × as long as wide.

71″. Pinnules not over 8 mm long, roundish-elliptic; veins hidden; pinnate or bipinnate 27. *L. stricta* (widespread)

71′. Pinnules longer, at least 11 mm, more elongate; veins evident.

72″. Apex of pinnules broadly rounded, sometimes narrowed, but not angular at the basiscopic side . . . . 14. *L. quadrangularis* ssp. *antillensis* (e. Caribbean region)

72′. Apex of pinnules angular at the basiscopic side . . . . aberrant forms of 32. *L. lancea*, with strongly reduced upper pinnules and small terminal segment.

Subgenus A. LINDSAEA.

Ultimate segments various, not free and equal-sided with a median main vein; veins free, or, if anastomosing (Asiatic species), pinnules dimidiate, the upper ones gradually reduced.

Type species: *Lindsaea trapeziformis* Dryander (= *L. lancea* (L.) Bedd.).

Sectio I. **Pseudosphenomeris** Kramer, sect. nov.

Lamina decomposita, apice sensim redacta, sine pinna terminali basalibus conformi; segmenta ultima haud pendula, cuneata, sublinearia, vel dimidiata et dissecta; sori uni- vel usque ad quadrinervii, indusio basi solum affixo.

Species typica: *Davallia bifida* Kaulfuss (= *Lindsaea bifida* (Klf.) Mett. ex Kuhn).

This section, the most primitive in the New World and probably in the whole genus, comprises the decompound species with non-pendulous pinnules, with linear or cuneate, ± divaricate segments or with dimidiate, incised pinnules. For the Old World species belonging to this section, see p. 135.

1. **Lindsaea bifida** (Kaulfuss) Mettenius ex Kuhn, Chaetopt. 26 (1882); Schenck, Hedwigia 35:158 (1896); Christ, Farnkr. d. E. 296 (1897). **Fig. 36**

Basionym: *Davallia bifida* Kaulfuss, Enum. 222 (1824); Sprengel, Syst. Veget. IV:121 (1827); Hooker & Greville, Icon. Fil. II t. 238 (1831?); Presl, Tent. Pterid. 129 (1836); Hooker, Spec. Fil. I:188 (1844), incorr. ascribed to Hooker & Greville; Hooker & Baker, Syn. Fil. 1st ed. (1868), 2nd ed. (1874) 101; Baker, Fl. Bras. I^2:346 (1870), t. 41 fig. 3; Rosenstock, Hedwigia 43:216 (1904).

Type: Chamisso s.n., from Santa Catarina, Brazil (prob. P, not seen; Isotype in B!).

Homotypic synonyms: *Odontoloma bifidum* (Klf.) Mettenius, Fil. Hort. Lips. 104 (1852).

Acrophorus bifidus (Klf.) Moore, Ind. Fil. II:1 (1857).

Odontosoria bifida (Klf.) J. Smith, Hist. Fil. 264 (1875); Diels, N. Pfl. I^4:215 (1902), fig. 116 D–F; Rosenstock, Hedwigia 43:216 (1904); Sampaio, Arch. Mus. Nac. Rio de Jan. 32:36 (1930); Wagner, Univ. Calif. Publ. Bot. 26 (1) pl. 18d, fig. 24 f (1952).

Stenoloma bifida (Klf.) Fée, Crypt. vasc. Brés. 1:153 (1869).

Heterotypic synonym: *Stenoloma Glaziovi* Fée, Crypt. vasc. Brés. I:153 (1869), pl. 52 fig. 2. Type: Glaziou 2326 from the state of Rio de Janeiro (P!).

Petioles reddish brown to dark castaneous; lamina decompound, thinly herbaceous; ultimate segments narrowly cuneate, dichotomously divaricate; sori uninerval or rarely binerval; indusium ovate, semi-elliptic or slightly horseshoe-shaped, attached only at the base; spores trilete.

Rhizome short-creeping, often with short ascending branches, ca. 2 mm in diam.; scales narrowly lanceolate, long-acuminate, up to 1½ mm long and 0.25 mm wide, with up to 5 rows of cells at the base. *Petioles* close, 10–30 cm long or less in depauperate specimens, in large leaves roughly as long as the lamina, in small ones often shorter, ± shining, the upper part of the adaxial side with a narrow channel bordered by stramineous ridges which become indistinct towards the base where the channel evanesces rather abruptly, the very base terete, abaxially angular or slightly sulcate above, the angles sometimes paler, becoming gradually obsolete towards the base, the lower ½ or $^1/_3$ obtusely angular or subterete; diameter ½–1 mm at base of lamina. *Lamina* 9–27 cm long, from almost as wide as to half as wide as long, rhombic or ovate in outline, tripinnate + pinnatifid + bifid or tripinnate + bifid, rather dark green on the ventral, paler on the dorsal side. *Primary rachis* similar to the upper part of the petiole, but the dark colour often hardly visible on the adaxial surface where the ridges are quite broad; axillary cushions obsolete or visible as faint swellings near the bases of the lower pinnae. About 5–7 major *primary pinnae* present on each side, the lower ones mostly subopposite, the upper ones alternate and by degrees reduced to form the gradually less compound leaf-top; the finer the dissection of the leaf, the more gradual the transition. The pinnae are short-stalked (1–3 mm), ascending under an angle of ca. 30–50°, the largest 5–13 cm long and 2–8 cm wide, lanceolate, or, when several more highly dissected basal secondary pinnae are present, ovate. Secondary rachises only in basal pinnae of large leaves similar to the primary, otherwise pale, adaxially shallowly grooved, abaxially terete at the base, above flattened, with ± wing-like margins, the upper part often shallowly sulcate. Larger pinnae with 8–15 secondary pinnae to a side, these rather close, often subcontiguous or contiguous, obliquely ascending, alternate, the largest pinnate + pinnatifid + bifid, smaller ones pinnate + bifid, the upper ones bifid and finally simple, denticuliform, connected by a wing with each other and with the often lobed apical segment. Rachises of higher order with more prominent wings and less obvious central strand, gradually passing into the bases of the ultimate segments. *Ultimate segments* ± equally bifid, with divergent lobes and rather broad acute sinuses, narrowest at the bottom of the incision where they are 0.2–0.8 (rarely 0.1) mm wide, broadened to the apex which is 1–1.5 mm wide, outer margin erose in fertile, subentire but often apiculate or emarginate in sterile segments; marginal strand very narrow and inconspicuous, whitish, the basiscopic side of the base adaxially with a short yellowish somewhat revolute thickening that probably represents a trace of dimidiate condition. Length of the ultimate segments varying with the depth of the sinus, commonly about 2–5 mm. Veins simple and median in the segments, (binerval segments rare), somewhat elevated in dry material, their ends in fertile segments adaxially visible as triangular patches below the receptacle. *Sori* with the receptacle surpassing the vein-end in width, mostly convex; indusium pale, subentire or mostly erose-denticulate, 0.5–1.5 mm long, 0.2–0.3 mm wide, not reaching the margin by its own width or less, ± reflexed at full maturity. Sporangia ca. 115–135(–140) × 95–100 μ; annulus with 10–13 indurated cells; spores very pale brown, ca. 20–23 μ.

Distribution: Eastern and south-eastern Brazil (map 5). In moist primary forests, terrestrial or on decaying logs or moss-covered rocks, from 200 to 1400 m.

Representative specimens:

Brazil. Bahia: without loc., Blanchet 310 (L).

Minas Gerais: Caldas, Mosén 4593 (B, BR, K, M, S–PA, UPS); Serra do Cipo, north of Belo Horizonte, M. & R. Foster 608 (GH, US).

Espíritu Santo: Serra da Caparaó, Mexía 4053 (B, BM, C, GH, S, UC, US); ibid., id. 4066 (B, BM, C, F, GH, K, MO, S, U, UC, US).

Rio de Janeiro: Itatiaia, Dusén 677 (S, S–PA, US, W); Serra dos Orgãos, Gardner 155 (BM, FI, K, W); Nova Friburgo, Beyrich s.n. (B, C, GOET, L); near Rio de Janeiro, Miers 131 (B, K); Upper Macahé, Glaziou 2326 (P, Holotype of *Stenoloma glaziovi* Fée: Isotypes in B, BR, C, C. Chr. in BM, K, S); without loc., Glaziou 5254 (B, C, K, S).

São Paulo: Alto da Serra, Estacão Biologica, L. B. Smith 1836 (C, GH, US); Ypiranga, Matta do Governo, Lüderwaldt 1633 (BM, GH); Paranapiacaba, Brade 8373 (UC), Sorocaba, Mosén 3748 (C, S, S–PA, UPS).

PARANÁ: Serra do Mar, Porto de Cima, Dusén 599a (GH); Villa Nova, Annies 146 (S–PA).

SANTA CATARINA: Pilões, Mun. Pelhoça, L. B. Smith 6213 (US); Joinville, Schmalz 136 (F, MO, UC), id. s.n. (Rosenstock-exs. 53) (B, M, S, SI, S–PA, US, W); Blumenau, Ule s.n. (GH); ibid., W. Müller 642 (B); Spitzkopf, Viereck 49 (M); Ilha Santa Catarina, Gaudichaud s.n. (B); ibid., Schenck 31 (B).

Very easily recognized among all species from the New World by the decompound leaves with narrow cuneate ultimate segments and hardly any trace of a dimidiate leaf-pattern; the only species with which it can be confused is *L. sphenomeridopsis* from Venezuela. The differences are discussed under that species. Perhaps even more closely allied is *L. millefolium* (see p. 135) from Madagascar, which differs chiefly by the more extensive atropurpureous colour of the rachis which has more sharply delimited pale wings, especially on the adaxial side. The similarity of these two species was already pointed out by CHRISTENSEN (1932). Less closely allied are *L. eberhardtii* (p. 135) from Annam and Hai-nan and *L. virescens*, particularly the variety *catharinae*, from the same region as *L. bifida*. The differences are discussed under *L. virescens*.

2. **Lindsaea sphenomeridopsis** Kramer, spec nov.

L. bifidae valde affinis; differt statura minore, lamina olivacea, segmentis ultimis linearibus, non ultra circa ½ mm latis, soris maioribus saepe obliquis.

Typus: Spruce 3416, from the Casiquiare R., Amazonas, Venezuela (W).

This species is closely allied to *L. bifida*. As only two specimens have been examined by the writer, the following description has been restricted to the essential points.

Rhizome creeping, ca. 1 mm in diam.; scales small, lanceolate, up to 0.8 mm long and 0.1 mm wide, with up to 3 rows of cells at the base. *Petioles* close, castaneous, 5–11 cm long, adaxially terete below, flattened above, with pale but hardly wing-like borders, abaxially terete or angular above. *Lamina* 6–8 cm long, about as wide, decompound, bipinnate + bipinnatifid or tripinnate + bipinnatifid; primary rachises and secondary rachises at the base castaneous abaxially, otherwise the axes stramineous, abaxially rounded, adaxially with pale, sometimes slightly wing-like borders. *Ultimate segments* 2–5 mm long, ca. ½ mm wide, uni- or less often binerval, unevenly dichotomously joined, one branch stouter, less divergent, and often incised at the apex. Texture thinly herbaceous. Apex of fertile segments crenate-crenulate, less sharply than in *L. bifida*, of sterile segments blunt, entire. *Sori* uni- or binerval, in the latter case often oblique; indusium strongly erose, ca. 0.3 mm wide, attached at the straight or faintly concave base, ± reflexed at full maturity. Sporangia ca. 140 × 115 μ; spores trilete.

Only known from type-collection (see the cross on map 3).

VENEZUELA. AMAZONAS: ad flumina Casiquiari, Vasiva et Pacimoni [= Yatua], Spruce 3416 (W, HOLOTYPE; Isotype in K).

The Kew sheet bears the additional annotation: "These specms were brought by a woman from a Morichal (= Mauritia-grove) a day's journey at the back of Zuirabuena".

The main differences with *L. bifida*, as indicated above, are the olive colour, the linear segments, and the often oblique sori. The smaller, less elongate laminas may prove to be more variable when more material is available. The segments are rather like those of *Sphenomeris clavata*, but much smaller.

The phytogeographic implications of the presence of a member of the section *Pseudosphenomeris* in Guayana are discussed on p. 146.

3. **Lindsaea virescens** Swartz, Kungl. Vet. Akad. Handl. 1817: 53; Kunze, Bot. Zeit. 8:345 (1850); Hooker & Baker, Syn. Fil. 1st ed. (1868), 2nd ed. (1874) 106; Baker, Fl. Bras. I^2:356 (1870); Kuhn, Chaetopt. 26 (1882); Schenck, Hedwigia 35:158 (1896): Diels, N. Pfl. I^4:221 (1902).

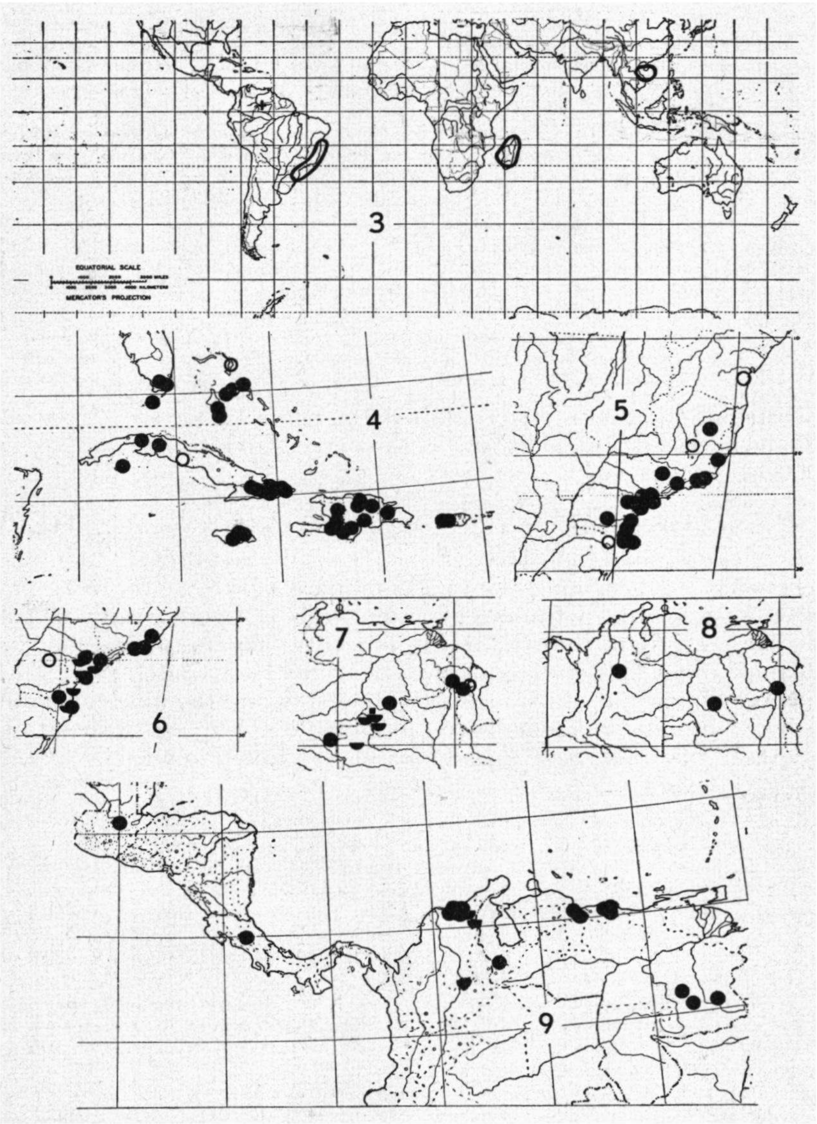
Type: Freyreiss s.n. from Villa Ricca, Brazil (S-PA!).
Homotypic synonyms: *Odontosoria virescens* (Swartz) Rosenstock, Hedwigia 46:79 (1906).
Stenoloma virescens (Swartz) C. Christensen, Ind. Fil. Suppl. III:174 (1934).

Heterotypic synonyms: *Lindsaea genkofolia* St. Hilaire, Voy. Distr. Diam. I:379 (1833). Type: St. Hilaire s.n. from Serra da Piedade, Minas Gerais, Brazil (P!).

Lindsaea Gardneri Hooker, Spec. Fil. I:213 (1844), pl. 65 C; Fée, Crypt. vasc. Brés. I:29 (1869). Type: Gardner s.n. from Serra dos Orgãos, Rio de Janeiro, Brazil (K!).

Petioles reddish brown to dark castaneous; lamina decompound, herbaceous; pinnules dimidiate, ovate to trapeziform, deeply incised; sori mostly bi- to quadrinerval; indusium ovate to linear, attached only at the base; spores trilete.

Rhizome short-creeping, ca. 1–1.5 mm in diam.; scales lanceolate, long-acuminate, up to 1.2 mm long, 0.2 mm wide, with up to ca. 5 rows of cells at the base. *Petioles* very close, about as long as to 1½ × as long as the lamina, ½–1 mm in diam. near the apex, ± shining above, adaxially above with a narrow groove with stramineous lip-like borders, these gradually less distinct below, rather suddenly evanescing near the base which is terete, abaxially angular or slightly sulcate above, the angles paler or concolorous, becoming indistinct downwards, the lower half or one-third bluntly angular, the base, or sometimes also the lower half or third, subterete. *Lamina* 8–ca. 25 cm long, as wide as to $^2/_3$ as wide as long, bipinnate + pinnatifid or bipinnatifid, at the base usually tripinnate + pinnatifid, dark green on the ventral, slightly paler on the dorsal side, dull, rhombic or pentagonal in outline, with 2–5 primary pinnae to a side. *Primary rachis* similar to the upper part of the petiole, adaxially mostly shallowly sulcate with paler margins, abaxially often pale in the upper part. Axillary cushions obsolete or visible as faint swellings at the bases of the lower pinnae. *Primary pinnae* short-stalked (1–3 mm), the upper ones alternate, the lower ones usually subopposite, 7–12 cm long, 1.5–2.5 cm wide, or wider, if pinnate secondary pinnae are present, the upper ones gradually reduced, lower pinnae 1.5–4 cm apart, the upper ones gradually closer, patent under an angle of ca. 30–50°. Secondary rachises adaxially with a green channel bordered by stramineous lips which project laterally and are visible from the abaxial side as narrow green wings continuous with the bases of the pinnules, abaxially mostly stramineous, roundish at the base, flattened or narrowly and shallowly sulcate above; rachises of secondary pinnae similar, with more conspicuous adaxial wing-like margins. Lower primary pinnae with one or two pinnate secondary pinnae on the basiscopic side, rarely also on the acroscopic side, these up to 5 cm long, similar to the upper primary pinnae; sometimes transitions between secondary pinnae and deeply cleft pinnules present. Upper pinnae gradually reduced, the uppermost ones 2–4 cm long, ca. 1 cm wide, finally passing into pinnules, the leaf-top gradually simpler in structure. Ultimate *pinnules* ca. 8–20 to a side in larger pinnae, alternate, subcontiguous to about half their width apart, laxly ascending, the larger ones with a stalk-like base of 1–1½ mm, surprisingly constant in size, 9–12 mm long, 4–6 mm wide, about twice as long as



Map 3: Distribution of *Lindsaea* sect. *Pseudosphenomeris*. Map 4: *Sphenomeris clavata*. Map 5: *Lindsaea bifida*. Map 6: *L. virescens;* complete dots: var. *virescens;* half dots: var. *catharinae*. Map 7: complete dots: *L. pendula;* half dots: *L. meifolia;* square: *L.* × *dissecta*. Map 8: *L. cultriformis*. Map 9: *L. klotzschiana;* complete dots: f. *klotzschiana;* half dots: f. *sublacera*.

wide; transitions between secondary pinnae and pinnules often larger. Lower pinnules hardly or not reduced; axillary pinnule not smaller, but more cuneate in shape. Upper pinnules gradually reduced, more strongly so in the apical part, the uppermost ones denticuliform, 1–2.5 mm long, connected by a wing and confluent with a similar terminal denticule; all lobes up to the extreme apex may be soriferous. Lower margin of pinnules straight or very faintly S-shaped, inner margin straight or ± concave, upper margin in larger pinnules deeply incised, the outer edges of the lobes not in one line, but at small angles with one another. Marginal strand whitish, present throughout, but inconspicuous except at the lower base. Outer margin of pinnules erose-denticulate when fertile, subentire when sterile; quite sterile pinnules rarely observed. Veins immersed but readily visible, (1–)2–4 per lobe, in the latter case the margin often shallowly incised between the members of a pair; main vein not connected with the marginal strand, gradually remote from the lower margin, ca. ½ mm above it near the apex. *Sori* with the receptacle visible adaxially as a fold or wrinkle, laterally extending beyond the vein-ends. Indusium ca. 0.5–3 mm long, 0.2–0.3 mm wide, whitish, subentire to erose-denticulate, not reaching the margin by a distance equalling its width or larger, ± reflexed and conceiled at full maturity. Sporangia ca. 140–160 × 110–120 μ; annulus with 8–13 indurated cells; spores pale brown, ca. 22–28 μ.

Distribution: South-eastern Brazil (map 6). In forests, terrestrial, among rocks, occasionally on moss-covered tree-trunks, up to ca. 1000 m.

a. var. **virescens.** **Fig. 34**

L. catharinae auct. non Hooker; Fée, Crypt. vasc. Brés. I:30 (1869).

Petioles 7–25 cm long; lamina tripinnate mostly at the very base only; lobes of the pinnules close, touching or overlapping; usually one large basal incision in the upper edge, separating a lobe that occupies about half of the pinnule, connected by a wing of ¼–½ mm with the outer lobe which is usually incised again, the inner one often entire. Ultimate lobes of larger pinnules 0.9–1.9 mm wide at the bottom of the sinus. Sori, esp. the basal ones, often quadrinerval.

Representative specimens:

Brazil. Minas Gerais: Serra da Piedade, St. Hilaire s.n. (P, Holotype of *L. genkofolia;* Isotype in B); without loc., Freyreiss s.n. (S–PA).

Rio de Janeiro: Tijuca, L. B. Smith & Brade 2217 (GH, US); ibid., Dusén 2537 (S–PA), s.n. (S, UPS); Serra dos Orgãos, Gardner s.n. (K, Holotype of *L. Gardneri*); ibid., Vauthier 668 in part (B, GH); Gardner 156 (BM, FI, G, Isotypes of *L. Gardneri*?); Nova Friburgo, Beyrich s.n. (L); Mt. Corcovado, Vauthier 658 (B, L); ibid., Langsdorff s.n. (BR); without loc., Glaziou 7959 in part (BR, C, K, LE, US); Dusén s.n. (M, S–PA).

São Paulo: Bosque da Saude, Brade 5175 (UC); Iguape, Brade 8258 in part (UC), s.n. (Rosenstock-exs. II 67) (PH); Rio Grande, Wacket 136 (Rosenstock-exs, 180) (B, BM, L, M, S, SI, S–PA, US, W); Matta do Governo, Ypiranga, Lüderwaldt 1629 in part (BM, GH).

Paraná: Villa Ricca, Freyreiss s.n. (S–PA, Holotype).

Santa Catarina: Flaggenberg near Desterro, Schenck 32 (B); Isla Santa Catarina, Ule 209 (B).

b. var. **catharinae** (Hooker) Baker, Fl. Bras. I^2:356 (1870) **Fig. 35**

Basionym: *Lindsaea Catharinae* Hooker, Spec. Fil. I:212 (1844), t.65 B.

Homotypic synonym: *Odontosoria virescens* (Swartz) Ros. var. *catharinae* (Hooker) Rosenstock, Hedwigia 46:79 (1906). Type: Beechey s.n. from Santa Catarina, Brazil (K!).

Petioles up to 37 cm long; lamina more fully tripinnate; secondary rachises abaxially occasionally dark; sinuses of the incisions of the pinnules wider, the lobes more divergent; largest pinnules often with 6 distinct lobes; ultimate lobes narrower, 0.6–1.5 mm wide at the bottom of the sinus. The great majority of the sori binerval, quadrinerval ones quite rare. A few giant spores, 42 × 32 μ, found together with normal ones.

BRAZIL. SÃO PAULO: Matta do Governo, Ypiranga, Lüderwaldt 1629 in part (GH); Iguape, Brade 8258 in part (BM, GH, S–PA, US); Serra do Itatins, Brade 8258a (UC).

RIO DE JANEIRO: Without loc., Glaziou 2325 (BR, C, K, S).

SANTA CATARINA: Joinville, Schmalz 161 (F); without loc., Beechey s.n. (K, HOLOTYPE).

Although the two varieties occur in the same area and are not rarely collected together, they are usually quite distinct, and intermediates are rare. Very ample material may show in the future that they cannot be maintained, but with the material extant it seems that they can stand as varieties. *L. virescens* can hardly be confused with any other species, except var. *catharinae*, which sometimes approaches *L. bifida*, but that species has mostly uninerval sori, smaller sporangia, and narrower ultimate lobes.

Sectio II. **Crematomeris** Kramer, sect. nov.

Lamina decomposita vel bipinnata, petiolo rhachidibusque abaxialiter teretibus, rhachidibus secundariis angulo fere recto patentibus, basi torquatis, ut facies abaxialis basiscopica, adaxialis acroscopica; segmentis secundariis (pinnulis) deflexis, pendentibus.
Species typica: *Lindsaea pendula* Klotzsch.

This section comprises the two strange species with patent secondary rachises twisted at the base and pendulous secondary segments, *L. pendula* and *L. meifolia*, and their hybrid, described here as new. The morphology of this group is discussed more at length on p. 130/131.

4. **Lindsaea meifolia** (H.B.K.) Mettenius ex Kuhn, Linnaea 36:79 (1869/70); Kuhn, Chaetopt. 26 (1882). **Fig. 41**

Basionym: *Davallia meifolia* H.B.K., Nov. Gen. & Spec. I:19 (1815); Sprengel, Syst. Veget. IV:121 (1827); Presl, Tent. Pterid. 129 (1836); Hooker, Spec. Fil. I:189 (1844); Moore, Ind. Fil. 2:297 (1857); Hooker & Baker, Syn. Fil. 2nd ed. append. 470 (1874); prob. not of Presl, Rel. Haenk. I:67 (1825).

Type: "Near Caracas et Chacao", Venezuela, Humboldt & Bonpland s.n. (not seen; Isotype in B!).

Homotypic synonyms: *Odontosoria meifolia* (H.B.K.) C. Chr., Ind. Fil. (164,) 465 (1906); Knuth, Fedde Rep. Beih. 43 (1):30 (1926); Sampaio, Arch. Mus. Nac. Rio de Jan. 32:36 (1930).
Stenoloma meifolium (H.B.K.) C. Chr., Ind. Fil. Suppl. III:173 (1934).

Homotypic (?) synonyms: *Darea fumarioides* H. & B. in Willd., Spec. Pl. V:299 (1810).
Caenopteris fumarioides (H. & B. in Willd.) Desvaux, Prod. 268 (1827); not *Lindsaea fumarioides* (Swartz) Mettenius, 1864, which is *Odontosoria*

fumarioides (Swartz) J. Smith. Type: "Caracas (v.s.)", Humboldt & Bonpland (?), ubi?

Heterotypic synonyms: *Lindsaea Sprucei* Hooker in Hooker & Baker, Syn. Fil. 1st ed. 108 (1868).

Type: Spruce 2988 from San Carlos, Rio Negro, Venezuela (K!). Homotypic synonyms: *Davallia sprucei* (Hooker) Baker, Fl. Bras. I^2:346 (1870).

Odontosoria sprucei (Hooker) Diels, N. Pfl. 1^4:215 (1902).

Stenoloma gratissima Fée, Crypt. vasc. Brés. I: 152 (1869), pl. 52. fig. 1. Type: Spruce 2988, as above (P!).

Petioles stramineous, abaxially terete; lamina decompound, coriaceous; ultimate segments pendulous, the larger ones once or twice cleft; sori mostly binerval; spores trilete.

Rhizome short-creeping, ca. 1.5 mm in diam.; scales lanceolate, acuminate, up to 0.8 mm long, 0.25 mm wide, with up to 8 rows of cells at the base. *Petioles* close, 6–28 cm long, from slightly longer than to twice as long as the lamina, $^3/_4$ mm in diam. near the apex, dull, adaxially sulcate, the groove flat below, broadly and shallowly concave above. *Lamina* bipinnate + pinnatifid to tripinnate + pinnatifid, ovate to lanceolate in outline, olivaceous to rather dark brown, often ± shining, 5–16 cm long, 3–5.5 cm wide. (Lamina of juvenile plants with secund pinnules, deflexed-pendulous on one side). *Primary rachis* similar to the upper part of the petiole. Axillary cushions not seen. *Primary pinnae* ca. 6–15 to a side, the lower ones subopposite, the upper mostly alternate, subsessile, patent under an angle of ca. 90° or the upper ones slightly ascending, their apex often decurved, 1.5–3 cm long, their width very variable depending on the degree of dissection, in the upper half of the lamina gradually, near the apex more suddenly reduced, rarely (in small leaves) gradually shortened from base to apex of lamina, the lower ones 1–1.5 cm apart, the upper ones slightly closer. Secondary rachises terete abaxially, sulcate adaxially, with a torsion at the extreme base, the adaxial side orientated towards the apex, the abaxial side towards the base of the lamina. Lower primary pinnae with one or two, sometimes with more, pairs of pinnate secondary pinnae at their bases, these up to 0.5–1.5 cm long, prob. those of both sides pointing downwards in the natural condition, but in dried specimens sometimes folded out. Ultimate *pinnules* (which are rarely borne directly on the secondary rachises, except in the apical part of the pinnae) bent over 90° in the stalk-like base, narrowly lanceolate, or almost linear and acute when sterile, the lower ones subopposite, the upper ones alternate, ca. 10–15 to a side, 1–2 mm apart, 2–2.5 mm long, the upper ones shorter, ca. 1 mm long, 0.2–0.8 mm wide, the largest twice deeply cleft, the smaller ones once, those in the apical part of the pinnae and in the apical primary pinnae spathulate, entire but for the erose outer margin, resembling those of the next species, intermediates between these extremes not rare. Basiscopic margin of pinnules thickened, stramineous, the other margins less thickened, pale. Apex of lamina gradually simpler in structure, with transitions from short pinnae through strongly incised pinnules to little or not divided pinnules, these deflexed, and also pendulous, as the primary rachis of the leaf-top is bent over to one side. *Sori* mostly binerval; indusium stramineous, rigid, ca. 0.4 mm wide, irregularly erose-denticulate, as the fertile margin, which it equals, more or less bulging at full maturity. Sporangia ca. 230 × 160 μ; annulus with 13–16 indurated cells; spores medium brown, ca. 32–40 μ.

Distribution: Along the north-western border of the Amazon basin; apparently uncommon (map 7). In most forests, up to 300 m.

COLOMBIA. VAUPÉS: Puerto Colombia (opp. Venezuelan Maroa), Río Guainía, Schultes, Baker & Cabrera 18168 (US).

VENEZUELA. AMAZONAS: San Carlos, R. Negro, Spruce 2988 (K, HOLOTYPE of *L. sprucei;* P, HOLOTYPE of *Stenoloma gratissima;* Isotypes in BM, BR, G, GH, W); Maroa, R. Guainía, Ll. Williams 14279 (F, G, US), "near Caracas and Chacao",

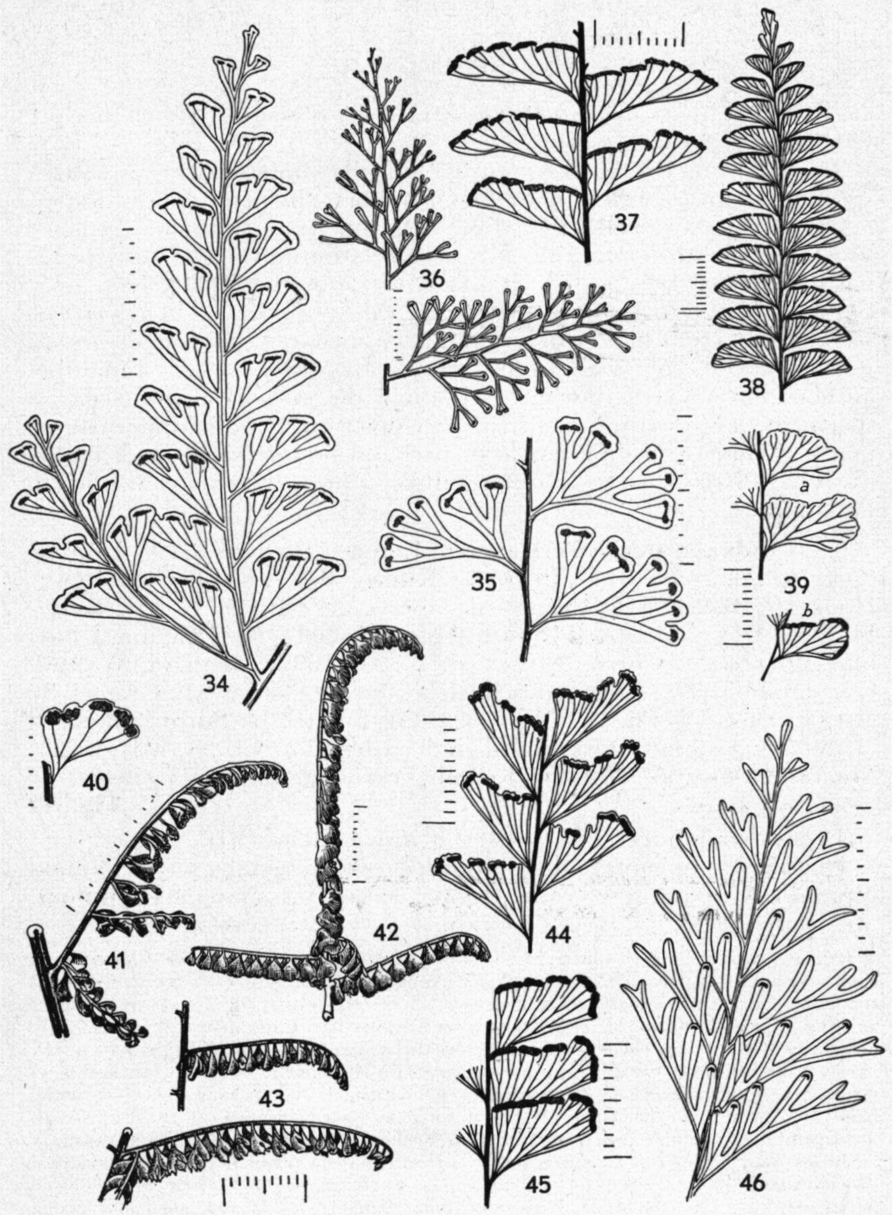


Fig. 34: *Lindsaea virescens* var. *virescens;* middle pinna (Schenck 32). Fig. 35: *L. virescens* var. *catharinae;* pinnules from middle of pinna (Glaziou 2325). Fig. 36: *L. bifida;* apex of lamina (above) and middle pinna (Mendonça 417). Fig. 37: *L. cultriformis;* pinnules from base of terminal pinna (Kalbreyer 1650). Fig. 38: *L. tetraptera;* apex of lateral pinna (Jenman s.n.). Fig. 39: *L. ovoidea;* sterile (a) and fertile (b) pinnules from terminal pinna (Brade 8261). Fig. 40: *L. parkeri* ssp. *parkeri;* pinnule from bipinnate leaf (Sandwith 1391). Fig. 41: *L. meifolia;* middle pinna (v. Lützelburg 23606). Fig. 42: *L. pendula;* apex of lamina (Maguire & Fanshawe 23160). Fig. 43: *L.* × *dissecta;* basal and upper lateral pinna (Ll. Williams 13934). Fig. 44: *L. klotzschiana* f. *sublacera;* pinnules from middle of basal pinna (Haught 3831). Fig. 45: *L. klotzschiana* f. *klotzschiana;* pinnules from base of terminal pinna (H. H. Smith 937). Fig. 46: *L. stenomeris;* apex of pinna (Maguire, Wurdack & Bunting 37365). (Scales in mm).

more probably from southern Venezuela, Humboldt & Bonpland s.n. (B, Isotype). Brazil. Amazonas: Jutica, Rio Uaupés, von Lützelburg 23606 (M, NY, UC).

A very distinctive species, not likely to be confused with any other species, except *L. pendula*, with which it shares the pendulous pinnules; *L. meifolia* is, however, more dissected, and has a gradually reduced leaf-top. It is surprising that the close relationship of the two species has hardly ever been noted; Baker (1870) observed the resemblance, but believed it to be only superficial. Most specimens of *L. meifolia* seen by the writer had been wrongly identified as *L. pendula*. *L. meifolia* was incorrectly reported from Panamá by Presl (1825) and other authors who copied from him; although the author has not seen his specimen, his description "specimen nostrum Humboldtiano duplo majus" points to a different fern, perhaps an *Odontosoria* or a highly dissected *Asplenium*. It is quite unlikely that *L. meifolia* occurs in Panamá.

5. **Lindsaea pendula** Klotzsch, Linnaea 18:548 (1844); Hooker, Spec. Fil. I:213 (1844), pl. 65A; Kunze, Bot. Zeit. 8:346 (1850); Hooker & Baker, Syn. Fil. 1st ed. (1868), 2nd ed. (1874) 108; Baker, Fl. Bras. I^2:352 (1870); J. Smith, Hist. Fil. 268 (1875); Kuhn, Chaetopt. 26 (1882); Christ, Farnkr. d.E. 293 (1897); Jenman, W. Ind. Gui. F. 78 (1899); Christ in Schwacke, Novas Plantas Mineiras II:30 (1900); Diels, N. Pfl. I^4:221 (1902); Posthumus, Fl. Surin. Suppl. 72 (1928); A. C. Smith in Gleason, Bull. Torr. Bot. Cl. 58:303 (1931); Maxon & Morton in Maguire, Bull. Torr. Bot. Cl. 75:73 (1948). **Fig. 42**

Type: Schomburgk 253 in part, British Guiana (B!).

Petioles stramineous to dark reddish brown, abaxially terete; lamina bipinnate with conform terminal pinna, coriaceous; pinnules pendulous, obovate-cuneate, not incised; sori on 3—5 veins; spores trilete.

Rhizome rather long-creeping, 1.5–2 mm in diam.; scales narrowly lanceolate, long-acuminate, up to 1.6 mm long, 0.15 mm wide, with up to 6 rows of cells at the base. *Petioles* moderately close to close, 11–44 cm long, 1½–3 × (rarely more) as long as the lamina, ¾–1¾, mostly ca. 1 mm in diam. near the apex, dull, adaxially flattened in the lower, sulcate in the upper part. *Lamina* bipinnate (very rarely subtripinnate; simply pinnate on juvenile rhizomes), ovate to lanceolate in outline, yellowish-green to olivaceous or brownish, 4–26 cm long, 4–11 cm wide, from as long as to almost four times as long as wide, truncate at the base, with 3–18 pinnae to a side. *Primary rachis* similar to the upper part of the petiole. Axillary cushions not seen. *Pinnae* subopposite or alternate, subsessile or the terminal short-stalked (ca. ½ cm), patent under an angle of ca. 90°, their apices often decurved, (2–)3–6 cm long, the upper ones shorter, 1–2½ cm, terminal pinna about the size of the lower pinnae or slightly larger, curved to one side, lower pinnae ca. 1–3 cm apart, the upper ones closer. Structure and orientation of the secondary rachises as in the preceding species. *Pinnules* bent over 90° at their narrow stalk-like base, ca. 10–25 to a side, alternate or the lower ones subopposite, sometimes contiguous or slightly imbricate, the basal pinnule (not reduced) usually more or less overlying the rachis, the largest 2–5 mm long, 2–3 mm wide, 2- less than 2½ × as long as wide, asymmetrically obovate, the basiscopic margin mostly more convex than the opposite side, long-cuneate at the base, entire, or the distal margin erose-repand, especially in fertile pinnules, in sterile ones sometimes with an approximately median apiculus, otherwise truncate or slightly convex, all margins thickened, the thickening strongest at the basiscopic edge. Upper pinnae somewhat shortened, but not strongly and gradually, the terminal pinna always distinct, with second, pendulous pinnules. Upper pinnules gradually reduced, the uppermost ones about half the size of the lower ones, not confluent, with a distinct terminal pinnule which may be the smallest or the size of one of the larger ones. Veins 3–5 to a segment, forked at the base, somewhat raised adaxially, especially towards their ends. *Sori* continuous along the outer margin, the receptacle clearly visible on the ventral side as a wrinkle; indusium rigid, ca. 0.5 mm wide, repand-erose, almost equalling the margin, bulging, but usually hardly reflexed at full maturity. Sporangia ca. 230 × 185 μ; annulus with 9–12 indurated cells; spores medium brown, ca. 32–40 μ, 32?

Distribution: Sandstone regions of the Guiana Highlands (map 7). In scrub and bogs in savannas, among boulders and in sand, usually in locally moist places, from ca. 300–1400 m.

COLOMBIA. VAUPÉS: Cerro Isibukuri, near summit, Schultes & Cabrera 15046 (US).
VENEZUELA. AMAZONAS: Summit of Mt. Duida, Tate 731 (NY, US); ibid., Steyermark 58247 (F, MO, NY, US).
BRITISH GUIANA: Hooroobea-savanna, Jenman 3739 (BM, K); Kaietuk-savanna, Tutin 682 (BM, K, U, US); savanna near Mt. Roraima, Appun s.n. (B, W); Kaieteur-savanna, Im Thurn s.n. (K); Maguire & Fanshawe 23160 (A, F, K, MO, NY, U, US); Sandwith 1283 (BM, K, NY, U); Jenman s.n. (NY); Jenman 1382 (K); Line 28, right bank of Essequibo R., Guppy 157 (BM); without loc., Schomburgk 253 in part (B, HOLOTYPE; Isotype in BM); id. 146 in part (G, K, W); Appun 93 (B); id. 804 (K); Glaziou 12351 (prob. an Appun-coll.) (B, BR, C, C. Chr. in BM, G, K, LE); Lobscheid s.n. (W); Jenman s.n. (NY, US).

The differences between this species and its closest relative, *L. meifolia*, have been discussed under that species. *L. pendula* has been incorrectly reported from the state of Rio de Janeiro by CHRIST (in Schwacke, l.c., see above, and in Bull. Herb. Boiss. II, 2:637, 1902) on the base of the Glaziou-specimen cited above, which was probably collected by Appun, but provided with an incorrect label by Glaziou when it was added to his herbarium. It has never again been found in south-eastern Brazil, and its occurrence there is most unlikely.

6. **Lindsaea x dissecta** Kramer, hybr. nov. **Fig. 43**

(*Lindsaea meifolia* (H.B.K.) Mett. ex Kuhn × *L. pendula* Klotzsch.)

Inter *L. meifoliam* et *L. pendulam* interjecta; lamina apice minus sensim redacta, pinnulis inferioribus semel vel bis furcatis, superioribus cuneatis, integris, pinnulis *L. pendulae* similibus; sporis obscuris, ut videtur, abortivis.

Typus: Ll. Williams 13934 from Yavita, Amazonas, Venezuela (US.)

Intermediate between the two preceding species. *Petioles* 6–26 cm long, as long as to twice as long as the lamina. *Lamina* bipinnate + pinnatifid or + bipinnatifid, or mostly subtripinnate + pinnatifid or + bipinnatifid, rhombic to broadly lanceolate, 5–20 cm long; primary pinnae 6–15 to a side, the lower ones 2–5 cm long, the upper ones little reduced (in some small leaves the lamina gradually narrowed from base to apex), more abruptly reduced at the apex than in *L. meifolia*, and more gradually than in *L. pendula*, which has none or at most two reduced upper pinnae. Lower pinnae, rarely also higher ones, with 1 or 2 pinnate deflexed secondary pinnae to a side, these rarely quite absent. Ultimate *pinnules* pendulous, 3–4.5 mm long, variously incised; in sterile leaves the larger pinnules are three times bifid, the depth of the incisions decreasing in the lobes of higher order, the lobes lanceolate, acute; otherwise the pinnules mostly bifid, the upper lobe often shallowly cleft again; upper segments of fertile leaves often obovate-cuneate, entire, except for the erose outer margin, resembling those of *L. pendula*. Sori of various width, depending on the degree of dissection of the pinnules;

indusium erose to subentire. Sporangia as in the parent species; spores dark, ± collapsed, with wrinkled wall, apparently not viable.

Distribution: Only known from the type-collection (map 7).

VENEZUELA. AMAZONAS: Yavita, in low, somewhat moist situations, Ll. Williams 13934 (US, HOLOTYPE; Isotypes in F, GH).

The exactly intermediate leaf-pattern points to the hybrid-origin of this form; the abortive spores may be taken as proof for this assumption. Moreover, both *L. pendula* and *L. meifolia* occur in the region where the hybrid has been found. Small leaves may be rather strongly dissected and are closer to those of *L. meifolia*. This is the first hybrid in the genus described from the Western Hemisphere.

Sectio III. **Temnolindsaea** Kramer, sect. nov.

Lamina bipinnata, cum pinna terminali lateralibus conformi, raro simpliciter pinnata, pinnulis dimidiatis, plus minusve incisis, superioribus sensim redactis, soris interruptis.

Species typica: *Lindsaea klotzschiana* Moritz in Ettingshausen.

In this section the species with ± incised pinnules and interrupted sori are united. The lamina is mostly bipinnate *cum impari*, rarely simply pinnate, but never throughout a species. The upper pinnules are always gradually reduced.

7. **Lindsaea klotzschiana** Moritz in Ettingshausen, Farnkr. 212; t. 145 f, 1,2 (1865); Bot. Zeit. 12 (Beil.):855 (1854), *nomen.*

Type: Moritz 238 from Tovar, Venezuela (B!).

Heterotypic synonyms: *L. elegans* Fée, Gen. Fil. 106 (1852); Kuhn, Chaetopt. 26 (1882); non Hooker (1837). Type: Moritz 238 from Tovar, Venezuela (P!).

Homotypic synonym: *L. Feei* C. Christensen, Ind. Fil. 393 (1906); Hieronymus, Hedwigia 62:16 (1920); Knuth, Fedde Rep. Beih. 43 (1):31 (1926).

L. trapeziformis Dryand. var. *γ laxa* Baker, Fl. Bras. I^2:355 (1870), as to synon. and fig. (pl. 22 fig. 1), not as to specimen cited. Type: Moritz s.n., prob. 238, from Venezuela (K!).

Misapplied names: *L. guianensis* auct. non Dryand.; Knuth, Fedde Rep. Beih. 43 (1):31 (1926), in part.

L. quadrangularis auct. non Raddi; Knuth, l.c.

L. crenata auct. non Klotzsch.; A. C. Smith in Gleason & Killip, Brittonia 3:145 (1939).

Petioles brown to blackish, abaxially at least above angular; lamina bipinnate with conform terminal pinna, herbaceous or subcoriaceous; pinnules dimidiate-ovate to subtriangular, 1½—slightly over 2 × as long as wide, upper and outer margin incised; sori interrupted, mostly three per pinnule; spores trilete.

Rhizome creeping, prob. rather long, 1½–2½ mm in diam.; scales narrowly lanceolate, long-acuminate, up to 2.8 mm long, 0.3 mm wide, with up to 7 rows of cells at the base. *Petioles* close or rather close, (5–)10–52 cm long, mostly roughly as long as the lamina, ¾–2, mostly 1 mm in diam. near the apex, dull to shining, adaxially sulcate in the upper part, flattened or subterete below, or sulcate almost to base, abaxially subterete or at base only, the upper part flattened-angular or sulcate above, rarely angular almost to base. *Lamina* bipinnate, very rarely simply pinnate or subtripinnate, ca. 15–45 cm long, dark green on the ventral, paler on the dorsal side, with 1–8, mostly 2–5 primary pinnae to a side and a conform terminal one. *Primary rachis* similar to the upper part of the petiole; axillary cushions very indistinct or obsolete. *Pinnae* rather strongly ascending, angle 20–40°, but often decurved in their upper part, the lower ones subopposite, the upper ones alternate, the lower 3–8 cm apart, 10–15(7–25) cm long, the upper ones closer, two-thirds to half as long, 1.5–2.5 cm wide, the terminal often widest, up to 3 cm, subsessile or with a stalk of 2–3 mm, in the terminal up to 2 cm, widest in the lower third or in the middle, slightly narrowed at the base, especially on the acroscopic side, very gradually narrowed above. Secondary rachises stramineous to reddish brown, adaxially with a deep constricted channel, abaxially subterete at the base, becoming suddenly angular at the level of the second or third pinnule, the upper part mostly sulcate. *Pinnules* ca. 10–30(–40) to a side, mostly alternate throughout, laxly ascending or the lower ones spreading, rarely slightly deflexed, subsessile, more than their width apart, the basal ones often considerably more, sometimes contiguous or even slightly imbricate, 8–14 mm long, 4.5–8 mm wide, a few basal pinnules somewhat reduced, a strongly reduced slightly decurrent axillary pinnule almost invariably present. Inner margin ± straight, mostly parallel to the sec. rachis, upper base shortly rounded, lower base shortly cuneate, hardly stalk-like, lower margin straight or slightly concave at the base, increasingly convex towards the apex, outer margin rounded or sometimes almost truncate, upper/outer margin more or less incised, in addition often minutely erose, in sterile pinnules (rarely found) with incisions ca. 1–1.5 mm deep, the teeth obtuse or acute. Marginal strand stramineous to pale brown, distinct but not conspicuous. Veins immersed or slightly raised abaxially, mostly once forked, their ends ¾–1 mm apart. Main vein hardly united with the marginal strand, ca. 0.4 mm above it near the apex. Upper pinnules very gradually reduced, a few denticuliform upper ones confluent with a linear blunt terminal segment 0.5–1.5 cm long, lobed below, crenate above, sometimes soriferous in the basal lobes. *Sori:* indusium pale, ca. 0.5 mm wide, not reaching the margin by ca. 0.2 mm, less often equalling it, ± reflexed and conceiled at full maturity. Sporangia 147–160 × 115–125 μ; annulus with 10–12 indurated cells; spores pale brown, ca. 26–28 μ, 32?.

Distribution: North-eastern and coastal Andes of Colombia and Venezuela, mountains of Venezuelan Guayana; scattered in Central America (map 9). In moist mountain-forests, from ca. 1000–2200 m, occasionally on trunks of trees; apparently not rare.

Vern.names: mantsána šižé (Colombia, Pittier); sumi-peu (Bolívar, Venezuela, Steyermark).

a. forma **klotzschiana**. **Fig. 45**

Pinnules herbaceous or, esp. in specimens from southern Venezuela, subcoriaceous, the incisions of the upper margin mostly 0.5, up to 1 mm deep; sori not in one line, at slightly different levels and forming small angles with each other, the basal and apical quadrinerval, the middle one binerval, or most of them binerval, occasional quadri-, qui- or sexinerval ones present; indusium subentire to erose or superficially lacerate.

Guatemala. Alta Verapaz: Rubelpec, Finca Seamay, Wilson 187 (F).

Costa Rica: Santiago–Picacho Mondongo, Brenez 16962 (F; very slender).

Colombia. Magdalena: Sierra Nevada de Santa Marta, Las Nubes, H. H. Smith 937 (BM, F, G, GH, K, L, MO, NY, PH, S, S–PA, U, US); ibid., hacienda Cincinnati, Martin 3324 (IA, MO, US); Dos Aguas, Carriker 26 (US); near S. Andrés de la Sierra, w. slope of the Cordillera, Pittier 1640 (GH, US).

Dept.?: S. Cristobal, Engel s.n. (LE).

Without exact loc., Karsten II (B).

Venezuela. Mérida: near Tovar, Moritz 238 (B, Holotype; 7 Isotypes; BM, C, FI, G, GH, GOET, K, Holotype of *L. trapeziformis* var. *laxa*, and Isotype; L, LE; P, Holotype of *L. elegans* Fée and *L. feei;* S–PA, UPS); ibid., id. 164 (BR, C, C. Chr. in BM, NY); ibid., Fendler 63α, β (BR, G, GH, GOET, K, MO, PH, US); Mérida, Engel 208 (B).

Carabobo: Hacienda Marture between La Entrada and Las Trincheras, Ll. Williams 11038 (F).

D.F.: Caracas, Linden 82 (G); Los Venados near Caracas, Allart 107 (NY, US); Cordillera del Avila, los Venados–Papelón, Steyermark 55094 (US).

Miranda: Between Antímano and Aguas Negras, Pittier 6019 (B, US).

Bolívar: Cerro Apacará, Cardona 1530 (US); Cerro Guaiquinima, Upper R. Paragua, Cardona 969 (US); Ptari-tepuí, Steyermark 59739 (F, K, MO, NY, US); ibid., id. 59503 (F, MO, NY, US); Auyan-tepuí, Tate 1247 (NY, US); ibid., id. 1246 (NY).

State?: Cadena de la Silla, Vogl 667 (F, M).

Without exact loc.: Birschell s.n. (BM); van Lansberge 19 (L).

b. forma **sublacera** Kramer, f. nov. **Fig. 44**

Differt a forma typica incisionibus pinnularum valde irregularibus, altioribus, nonnullis usque ad 1 vel 2 mm altis, lobo apicali saepe prominente, soris fere omnibus binerviis, indusio margineque fertili magis erosis.

Typus: Haught 3831, east of Codazzi, Magdalena, Colombia (US).

Pinnules herbaceous; sori more pronouncedly on different levels and at larger angles with one another.

Colombia. Magdalena: Forest 12 km east of Codazzi, Haught 3831 (US, Holotype; Isotypes in BM, GH, US); "Cincinnati", lower slopes of Mt. San Lorenzo, near Santa Marta, Seifriz 37 (GH, US; less typical).

Santander: Las Cruces, Kalbreyer 933 (B, K).

L. klotzschiana is closest to *L. cultriformis*, where the differences are mentioned, also allied to *L. tetraptera*.

Comment on the synonymy: The name *Lindsaea klotzschiana* was published without a description and has been rejected for this reason. However, Ettingshausen's figure is quite good, showing essential characters, and leaves no doubt as to the identity of the depicted species. Therefore, Art. 43 of the Code of Nomenclature applies. Christensen (1906, p. 394) referred it incorrectly to *L. lancea;* as the oldest name for the present species, *L. elegans* Fée, is a later homonym of *L. elegans* Hooker, he created a new name for it, *L. feei*, which is superfluous if *L. klotzschiana* is accepted as validly published. The name *L. laxa* Kunze ex Baker, listed by Christensen (l. c., p. 394), was never validly published; it appears as *L. trapeziformis* var. *β*, *L. laxa* Kunze in *Synopsis Filicum*, p. 107, which is contrary to Art. 24 of the Code. It was, however, validly published in the rank of variety in Fl. Bras. I^2:355, and in this connexion the question of typification arises. The only specimen cited is Spruce 2277 from Brazil (included in *L. tetraptera* in the present study), but this was not definitly designated as type, and in the author's opinion it should not be regarded as such. The synonyms cited by Baker and his figure all apply to *L. klotzschiana*, and two specimens in K bear Baker's name var. *laxa* in his handwriting; *L. klotzschiana* is cited as synonym with the invalid publication of "*β*, *L. laxa* Kunze", and both should therefore be based in the same type, Moritz 238 from Venezuela, which was, of course, not cited in Flora Brasiliensis as it is from outside Brazil. Even if this argumentation is not accepted, *L. tetraptera* has priority on the species-level, as *L. laxa* was never validly published in that rank.

8. **Lindsaea cultriformis** Kramer, spec. nov. **Fig. 37**

Misapplied names: *L. trapeziformis* auct. non Dryand.; Wright, Trans. Linn. Soc. Bot. II, 6:80 (1901). *L. crenata* auct. non Klotzsch; A.C. Smith in Gleason, Bull. Torr. Bot. Cl. 58:303 (1931).

Folia bipinnata; petiolo stramineo vel fuscescente, facie abaxiali tereti; lamina herbacea, laetevirens; pinnulis lanceolatis leviter falcato-decurvatis vel patentibus, latitudine circa partem tertium longitudinis aequante, margine superiore incisa, incisionibus plerumque minus quam 1 mm altis, pinnulis superioribus sensim redactis; soris interruptis, fere in venis duabus insidentibus, 4–6 in quaque pinnula; sporis tetraedriformibus.

Typus: Tate 893 from Mt. Duida, Amazonas, Venezuela (NY).

Rhizome creeping to obliquely ascending, about 3 mm in diam.; scales minute, ovate-lanceolate, acute to shortly acuminate, up to 0.6 mm long and 0.2 mm wide, with up to 7 rows of cells at the base. *Petioles* close, subdistichous, castaneous to atropurpureous at the base, about as long as the lamina, ½–1 mm in diam. near the apex, adaxially channelled. *Lamina* 20–35 cm long, with 3–4 pinnae to a side and a similar terminal one. *Primary rachis* similar to the upper part of the petiole, but the abaxial side in the upper half with a suddenly appearing groove. Axillary cushions conspicuous, dark. *Pinnae* subopposite or alternate, short-stalked (up to 1 cm) to sessile, 2½–5 cm apart, laxly ascending under an angle of about 45°, 8–20 cm long, the upper ones slightly shortened, 2–3 cm wide, slightly narrowed at the base, gradually narrowed above. Secondary rachises abaxially terete at the extreme base, above sulcate, the groove mostly suddenly appearing at the level of about the second pinnule, flattened towards the apex, adaxially with a deep narrow groove with almost touching borders. *Pinnules* 20–40 to a side, subopposite, the upper ones alternate, mostly about 14 mm long and 4–5 mm wide, the basal ones slightly shortened, a strongly reduced axillary pinnule sometimes present. Inner margin straight and more or less parallel to the sec. rachis, lower base hardly stalk-like, upper base rectangular or shortly rounded, upper margin increasingly convex towards the acute or subacute apex, no outer margin developed; lower margin approximately straight or mostly shallowly concave at the base, convex at the apex. Upper margin with shallow incisions, mostly 3–5 per pinnule, these deeper and wider in sterile pinnules. Marginal thickening pale brown, inconspicuous, except at lower base. Veins immersed but readily visible, once or the basal twice forked, ca. 1 mm apart at the margin; main vein hardly united with the marginal strand. Upper pinnules very gradually reduced, the uppermost ones denticuliform, confluent into a lobed or toothed, often caudate, up to 2 cm long apex. *Sori* mostly binerval, or the basal tri- or quadrinerval (rarely occupying up to 6 veins); indusium ca. 0.2 mm wide, firm, entire, fixed at the base and the greater part of the sides, equalling the margin, hardly or not reflexed at full maturity. The receptacle and the indusium laterally surpass the ends of the outer veins bearing the sorus. Sporangia ca. 142–150 × 100 μ; annulus with 9–12 indurated cells; spores hyaline, almost colourless, ca. 22–27 μ.

Distribution: North-western South America (map 8). In forests, from ca. 120–2000 m.

Colombia. Antioquia: Amalfi, La Vivora, Kalbreyer 1650 in part (B, K); ibid., Lehmann XXXIII (BM, G, K, LE, US).

Venezuela. Amazonas: Mt. Duida, Tate 893 (NY, Holotype); Capihuara, Upper Casiquiare, Ll. Williams 15536 in part (GH).

British Guiana: Mt. Roraima, McConnell & Quelch 617 (K, NY); without loc., Appun s.n. (herb. Glaziou 12357) (B, C, LE, NY).

Most closely allied to *L. klotzschiana*, probably also to *L. stenomeris*. In general aspect not unlike *L. decomposita* from the Old World. It is strange that this rather distinctive species, known from a number of collections the first of which of considerable age, has never been recognized.

9. **Lindsaea stenomeris** Kramer, spec. nov. **Fig. 46**

Folia pinnata vel bipinnata, petiolo badio, nitidulo, facie abaxiali inferne obtuse angulata subteretive, superne applanata, angulis pallidis; lamina membranacea; pinnulis laciniatis, laciniis obliquis, linearibus vel sublinearibus, nonnullis furcatis; pinnulis superioiribus sensim redactis; soris uninerviis; sporis tetraedriformibus.

Typus: Maguire, Wurdack & Bunting 37365 from Cerro de la Neblina, Amazonas, Venezuela (US).

Rhizome creeping, ca. 1.5–2 mm in diam.; scales lanceolate, acuminate, up to 0.65 mm long, 0.15 mm wide, with up to 5 rows of cells at the base. *Petioles* close, ca. 5–15 cm long, ⅓–¾ the length of the lamina, ¾–1 mm in diam. at the apex, abaxially bordered by pale ridges which gradually evanesce downwards, obsolete near the middle, the lower part obtusely angular to subterete, adaxially above similar to the abaxial side, but the stramineous borders extending farther downwards, gradually disappearing towards the terete or subterete base. *Lamina* dull dark green, narrowly lanceolate to linear when simply pinnate, ca. 10–20 cm long, when bipinnate with one or two pinnae to a side and a similar terminal one which resemble simply pinnate blades. *Primary rachis* similar to the upper part of the petiole, axillary cushions visible as distinct swellings. Simply pinnate laminae and primary pinnae 2½–3 cm wide, the latter patent under an angle of ca. 50°. *Pinnules* ca. 15–30 to a side, laxly ascending, alternate or the lower ones subopposite, rather close, the upper ones subcontiguous, short-stalked to subsessile, the largest 1½–2 cm long, 4–6 mm wide, approx. lanceolate in outline, ca. 3½–4 × as long as wide, the lower ones not or hardly reduced; a strongly reduced axillary pinnule present. Lower margin straight or faintly concave at the base, more strongly concave towards the apex, inner margin approx. straight, parallel or divergent, blade of the pinnule from the upper margin dissected by deep incisions, the divisions linear or slightly cuneate, obtuse, ca. 4–6 mm long, ¾–1 mm wide, connected by a narrow wing (0.1–0.3 mm), oblique, somewhat divergent, about 5 per pinnule, the largest mostly once forked, otherwise entire; base of pinnules cuneate, with a stalk-like base up to 1 mm long in which the dark colour of the rachis ends rather abruptly. Marginal strand stramineous, present throughout but weak except at the lower base. Main vein marginal at the base only, otherwise at the basiscopic side with a laminal wing ca. 0.2 mm wide. Veins immersed but evident, single in each lobe, in forked ones dichotomous considerably below the bifurcation. Upper pinnules rather suddenly shortened near the pinna-apex, of simpler structure, a few rather abruptly confluent into a pinnatifid apex. *Sori* uninerval (very rarely binerval); indusium usually semi-elliptic, attached at the base only, entire, ca. 0.4 mm wide, its edge 0.2–0.4 mm from the margin, not reflexed at full maturity. Sporangia protruding, 160–165 × 130 μ; annulus with 10–12 indurated cells; spores rather pale brown, 24–27 μ, 32?

Distribution: Only known from type-collection.

VENEZUELA. AMAZONAS: Cerro de la Neblina, Río Yatua; occasional on rocks in forest, 900 m, Maguire, Wurdack & Bunting 37365 (US, HOLOTYPE).

A second dubious specimen may represent a special form or subspecies; it has a simply pinnate lamina with much less incised pinnules with broader lobes, approaching those of *L. cultriformis*, but with many uninerval sori, and in other characters agreeing with *L. stenomeris:*

VENEZUELA. BOLÍVAR: Chimantá-Massif, Toronto-tepuí, in *Clusia*-forest on slopes of Río Tirica below Summit camp, 1760–1880 m, Steyermark & Wurdack 1205 (US).

L. stenomeris is a very remarkable species as it is the only American representative with a type of leaf much more common in the Eastern Hemisphere, with strongly dissected, yet quite dimidiate pinnules (see also p. 126). Its closest relative is probably *L. cultriformis*, which, however, is rather different in freely bipinnate blades with pale axes, much less incised pinnules, and mostly binerval sori. It is at present impossible to say whether the strong dissection of the pinnules is a primitive character or whether it may be of secondary development, being derived from a type comparable to that of *L. cultriformis* or *L. klotzschiana*. It is to be hoped that new collections of this interesting species will show more of its range of variation and distribution.

10. **Lindsaea tetraptera** Kramer, spec. nov. **Fig. 38**

L. trapeziformis Dryand. var. *γ laxa* Baker, Fl. Bras. I^2:355 (1870), as to specimen cited.

Folia pinnata vel vulgo bipinnata, petiolo badio, lucido, superne alis pallidis marginalibus quattuor instructo; lamina olivaceo-pulla vel nigricans, herbacea, rhachidibus secundariis quadrialatis; pinnulis leviter falcato-decurvatis, margine superiore incisa, incisionibus plerumque duabus vel tribus in quaque pinnula, vix ultra 0.8 mm altis; soris venas 2–4 vel ultra occupantibus; sporis tetraedriformibus.

Typus: Schultes & Cabrera 16503 from Cerro de la Gente Chiquita, Río Miritiparaná, Amazonas, Colombia (US).

Rhizome short-creeping, ca. 2 mm in diam.; scales narrowly lanceolate, long-acuminate, up to 1.75 mm long, 0.25 mm wide, with up to 9 rows of cells at the base. *Petioles* close, about as long as the lamina or shorter (often incompletely collected), diam. 1–2 mm near the apex, castaneous, shining, subterete at the very base, adaxially below with small lateral ridges which soon pass into stramineous wings, abaxially similar wings present in the upper part which do not extend so far downwards, sometimes only to the middle; upper part of the petiole therefore four-winged, the surfaces between the wings somewhat convex. *Lamina* ca. 15–30 cm long, with 1–3 pinnae to a side and a conform terminal one. *Primary rachis* similar to the upper part of the petiole, but abaxially often channelled, especially at the base. Axillary cushions distinct, often darker. *Pinnae* mostly subopposite, laxly spreading under an angle of ca. 45–60°, subsessile or short-stalked (up to 5 mm), the terminal often with a longer stalk, 4–7 cm apart, ca. 12–25 cm long, 2–3½ cm wide, widest in the lower third, thence gradually but not strongly narrowed to the apex, slightly narrowed at the base, the upper ones somewhat shortened, the terminal about the size of the basal ones. Secondary rachises dark, with conspicuous spreading wings on the four edges which evanesce in the apical part, those of the adaxial side continuous with the wings of the primary rachis, those of the abaxial side either approaching each other below the lowermost pinnule and evanescing abruptly or sometimes merging into one which may be connected with the abaxial wing on the corresponding side of the primary rachis. *Pinnules* ca. 20–30 to a side, subopposite or mostly alternate, spreading or slightly deflexed, subsessile, separated by spaces equal to about half their width, (9–)12–18 mm long, (4–)5–7 mm wide, 2–2½ × as long as wide, broadest at the base, gradually narrowed to the apex, approximately dimidiate-ovate, ± falcate. Inner margin straight, ± parallel to the secondary rachis, lower base cuneate, hardly stalk-like, upper base shortly rounded, lower margin usually rather strongly concave, upper margin rather evenly convex, incised, with mostly 2 or 3 incisions 0.2–0.8 mm deep, narrow, with acute sinus, the margins otherwise entire; no separate outer margin developed the lower and upper edge meeting at the acute to obtuse apex which may bear a few sterile teeth in incompletely fertile pinnules. Upper edge of sterile pinnules with small crenulations in the basal part which become much larger towards the apex, the teeth obtuse, often more highly connected in pairs. Veins immersed but clearly visible, once or twice forked, their ends rather irregularly spaced, ca. ½–1 mm apart. Main vein not united with the marginal strand, ca. ⅓ mm above it near the apex. Marginal strand present throughout but inconspicuous except at the base of the lower margin. Upper pinnules gradually but not strongly reduced except just below the apex of the pinnae where a few 2–5 mm in length are present (rarely more gradually shortened), one or two connected by a wing with the terminal segment which is lanceolate, lobed at the base, otherwise serrate or crenate, 6–18 mm long, sterile or with small sori in the lobes, lanceolate. *Sori* along the upper/outer margin, interrupted, occupying 2–4 veins, the basal ones sometimes more, mostly 3–4 per pinnule. Indusium greyish, entire, ca. 0.2 mm wide, not reaching the margin by about the same distance, largely reflexed and conceiled at full maturity. Sporangia ca. 150 × 140 μ; annulus with 10–13 indurated cells; spores pale brown, ca. 23–25 μ.

Distribution: North-western South America (map 10). In forests and scrub, occasionally epiphytic, at lower altitudes, ca. 100–500 m.

Colombia. Amazonas: Río Miritiparaná, Cerro de la Gente Chiquita, headwaters of Quebrada Guacayá, epiphytic, Schultes & Cabrera 16503 (US, Holotype).

Venezuela. Bolívar: Cerro Guaiquinima, Upper Río Paragua, Cardona 899 (F, US).

Amazonas: Maroa, R. Guainía, Ll. Williams 14200 (F, US), 14264 (F, US); Capihuara, Upper Casiquiare, Ll. Williams 15533 (US).

British Guiana: Potaro R., Jenman s.n. (NY); Rockstone, Essequibo R., Jenman s.n. (NY); without loc., Jenman s.n. (NY, US); Appun s.n. (Glaziou 12355 in part) (B, G, LE, NY, US).

Brazil. Amazonas: Near São Gabriel da Cachoeiras, Rio Negro, Spruce 2277 (B, BM, BR, G, K, W).

A very clear-cut and distinctive species, characterized by dark four-winged axes and interrupted sori. The closest relative seems to be *L. klotzschiana*. The author's views on the typification of *Lindsaea trapeziformis* Dryand. var. *laxa* Baker are explained under *L. klotzschiana*.

11. **Lindsaea parkeri** (Hooker) Kuhn, Chaetopt. 26 (1882); Posthumus, Fl. Surin. Suppl. 71 (1928); Maxon & Morton in Maguire, Bull. Torr. Bot. Cl. 75:73 (1948).

Basionym: *Davallia Parkeri* Hooker, Spec. Fil. I: 176 (1844), t. 53 C; Hooker & Baker, Syn. Fil. 1st ed. (1868), 2nd ed. (1874) 93; Baker, Fl. Bras. I^2:344 (1870), pl. 41 fig. 1; Jenman, W. Ind. Gui. F. 67 (1899).

Type: Parker s.n. from British Guiana (K!)

Homotypic synonym: *Odontoloma parkeri* (Hooker) Presl, Epimel. Bot. 97 (1849); Fée, Gen. Fil. 329 (1852); J. Smith, Hist. Fil. 269 (1875).

Petioles dark brown to atropurpureous, quadrangular; lamina simply pinnate or bipinnate with conform terminal pinna, thinly herbaceous; pinnules ovate to triangular or subtrapeziform, 2–2½ ×

as long as wide, shallowly incised to subentire; sori interrupted, uninerval or the outer ones bi—quadrinerval; spores trilete.

Rhizome rather short-creeping, ¾–1 mm in diam.; scales lanceolate, acuminate, up to 1 mm long and 0.2 mm wide, with up to 5 rows of cells at the base. *Petioles* rather close, from less than 1 to 16 cm long, much shorter than the lamina in small leaves, slightly longer in large ones, diam. 0.3–1 mm at base of lamina, often shining, quadrangular or terete at the extreme base, the surfaces more or less flat, with sharp, above often paler angles. *Lamina* from about 3 cm in apparently depauperate specimens to about 15 cm long, blackish-green on the ventral, paler on the dorsal side. *Rachis* similar to the stipe, but often paler, and the paler colour of the angles often more distinct, the abaxial and adaxial surfaces concave. *Pinnules* not very close, not contiguous, the basal ones farther apart, about 15–35, mostly 18–20 to a side, the lower ones subopposite, the upper ones usually alternate, subsessile, gradually reduced above, finally confluent into a short, lanceolate, serrate-lobed, subacute terminal segment. Lower margin of pinnules straight or convex, or concave in large leaves, inner margin straight, mostly somewhat divergent, upper edge crenulate or lobed, convex, a separate outer margin hardly developed, apex rounded. Marginal strand hardly developed. Veins immersed, simple or the basal ones once forked, lax, 1–2 mm apart at the margin; main vein departing from the marginal strand near the base, rather divergent from the lower margin and up to 1 mm above it near the apex. *Sori* more or less interrupted; indusium delicate, ca. 0.4–0.6 mm wide, the upper edge erose-denticulate. Sporangia ca. 180 × 140 μ, annulus with 11–15 indurated cells; spores medium brown, ca. 28–32 μ, 32?.

Key to the subspecies:

1. a. All or the great majority of the sori uninerval; upper edge of pinnules mostly lobed; lamina pinnate or bipinnate . . . . . . a. ssp. *parkeri*

b. At least the outer sori bi—quadrinerval; upper edge of pinnules crenate or erose; simply pinnate . . b. ssp. *steyermarkiana*

a. ssp. **parkeri.** **Fig. 40**

Lamina pinnate or less often bipinnate, 10–20, mostly about 14 mm wide and acuminate when once pinnate, with 1–3 primary pinnae to a side and a conform terminal pinna when bipinnate; pinnae 5–12 cm long (the terminal one largest), subsessile, with a reduced axillary pinnule, otherwise similar to once pinnate laminae. Pinnules 5–10 mm long, 2.5–5 mm wide, mostly 2 (up to 2½) × as long as wide, the lower ones spreading, the upper ones ascending, in large leaves the basal ones occasionally somewhat decurved; upper edge lobed with incisions up to ¾ mm deep or sometimes sinuous only, in addition erose-crenulate; in sterile pinnules lobed, not erose. Sori uninerval, rarely binerval, 3–6 per pinnule; indusium semi-elliptic to semi-orbicular or subreniform, attached by its straight or slightly concave base only, not reaching the margin by about its own width, reflexed at full maturity.

Distribution: Guayana; on moist rocks, often along watercourses, sometimes periodically flooded, from 525 to ca. 1000 m. Apparently uncommon (map 11).

VENEZUELA: BOLÍVAR: Chimantá–Massif, Abácapa-tepuí, Steyermark 74809 (US). BRITISH GUIANA: Wismar, Demerara R., Jenman s.n. (NY); Macouria Creek, Essequibo R., Jenman s.n. (NY), Jenman 2284 (BM, K), Fanshawe M 329 (BM, K); Moraballi Creek, Essequibo R., Persaud 18 (K); Arrowye Creek, Essequibo R., Lobscheid s.n. (W); Essequibo R., without exact loc., Appun s.n. (K, W), Appun 30 (B); Amaku, Potaro R., Im Thurn s.n. (K); Sheenabowa, Potaro R., Jenman 1379 (K); Potaro R., above Kaieteur Falls, Sandwith 1391 (BM, K, U); Potaro R. Gorge, Amatuk Portage, Maguire & Fanshawe 23543 (NY, US); Kaieteur Savannas, Maguire & Fanshawe 23413 (K, NY, US);

Demerara and Potaro Rs., Jenman s.n. (NY); without exact loc., C. S. Parker s.n. (K, HOLOTYPE).
SURINAME: Tafelberg, Lower Augustus Creek, Maguire 24731 (A, F, K, NY, U, US).

b. **ssp. steyermarkiana** Kramer, ssp. nov.

Recedit a ssp. typica foliis semper simpliciter pinnatis, pinnulis margine superiore minus lobatis, soris, praecipue exterioribus, bi-quadrinerviis.

Typus: Steyermark 60229 from Bolívar, Venezuela (US).

Resembling in most respects simply pinnate forms of ssp. *parkeri*, but pinnules much less lobed, often hardly at all; sori, especially the outer ones, occupying 2–4 veins, but uninerval ones mostly present besides; indusia firmer, almost reaching the margin.

Distribution (map 11):

VENEZUELA. BOLÍVAR: Salto de Iwaracarú-merú at western end of Sororopán-tepuí, alt. 1615 m, Steyermark 60229 (US, HOLOTYPE; Isotypes in F, MO, NY); Ptari-tepuí, forested slopes along Large Lunch River below Misia Kathy Camp, alt. 1500 m, Steyermark 59454 (F, NY, US, Paratypes).

L. parkeri is easily recognized by the dark axes and small pinnules and particularly by the interrupted sori but hardly incised upper margin. The latter character is not observed in any other neotropical species, but is found in such Old World-species as *L. macraeana*. Its affinity is not clear; it is placed with misgivings in the present section.

Sectio IV. **Lindsaea.**

The bulk of the species belong to this section. The lamina is bipinnate (rarely subtripinnate or tripinnate), with a conform terminal pinna, or simply pinnate; pinnules dimidiate (rarely at the base only), with continuous or (in the largest pinnules) slightly interrupted sori; the upper pinnules are reduced or not.
Type species: the same as that of the subgenus.

Subsectio 1. **Subinterruptae** Kramer, subsect. nov.

Pinnulae maximae semel vel bis incisae, incisionibus soros interrumpentibus, minores integrae, soris continuis.
Species typica: *Lindsaea ovoidea* Fée.
Additional characters are dark petioles and trilete spores.

12. **Lindsaea ovoidea** Fée, Crypt. vasc. Brés. II:21 (1872/73).
Fig. 23, 39

Type: Glaziou 4381 from Serra dos Orgãos, Rio de Janeiro, Brazil (P!).

Heterotypic synonym: *Lindsaea Christii* Rosenstock, Fedde Rep. 4:292 (1907). Type: Wacket s.n. from Serra do Mar, São Paulo, Brazil (M!).

Misapplied name: *L. trapeziformis* Dryand. var. *laxa* auct. non Kunze; Rosenstock, Hedwigia 43:216 (1904).

Petioles dark reddish brown to blackish, at least above sharply quadrangular; lamina bipinnate with conform terminal pinna, herbaceous to chartaceous; pinnules dimidiate-ovate, rhombic, or almost rectangular, ca. 2 × as long as wide, the smaller ones entire, the larger ones often with one incision in the upper and one in the outer margin, the upper ones gradually reduced; margins often slightly revolute; sori continuous or slightly interrupted; spores trilete.

Rhizome short-creeping, ca. 1 mm in diam.; scales lanceolate, long-acuminate, up to 2 mm long and 0.3 mm wide, with up to 7 rows of cells at the base. *Petioles* close, 11–27 cm long, about as long as the lamina, ca. ¾ (½–1¼) mm in diam. near the apex, shining, below obtusely quadrangular apart from the subterete base, above sharply quadrangular, the adaxial side sulcate, the groove with paler margins, abaxially and laterally flattish or shallowly concave. *Lamina* bipinnate, very rarely simply pinnate, 12–25 cm long, ca. 9–17 cm wide, from as long as wide to almost twice as long, often somewhat spongiose, medium green on the ventral, slightly paler on the dorsal side, with 1–6 pinnae to a side and a conform terminal one. *Primary rachis* similar to the upper part of the petiole, rarely paler. Axillary cushions not seen. *Pinnae* alternate or the lower ones subopposite, rather remote, the lower ones 2–5½ cm apart, the upper ones in plurijugate leaves about half as far, spreading at an angle of 40–50° (rarely more), 6–15 cm long, 1–2.5(–3) cm wide, not or hardly narrowed at the base, gradually narrowed in the upper half or two-thirds, subsessile, the terminal short-stalked; upper pinnae of plurijugate leaves about half as long as the lower. Secondary rachises adaxially sulcate, abaxially with a short basal terete portion, above, at the level of the first to third pinnule, with a rather abruptly appearing groove, which may sometimes be virtually absent in the upper pinnae of plurijugate leaves, mostly stramineous, the dark colour of the primary rachis ending rather suddenly in or just above the base of the pinna, rarely extending into it for a greater distance. *Pinnules* ca. 10–20 to a side, 8–17 mm long, 4–8 mm wide, widest at the base or of equal width almost throughout, almost invariably alternate, spreading or somewhat ascending, subsessile to short-stalked (up to 1.5 mm), a flabellate axillary pinnule mostly present, sometimes a few additional basal pinnules somewhat reduced. Lower margin straight or faintly concave, inner margin straight or somewhat convex and then often touching or overlying the secondary rachis, outer margin broadly rounded, rarely subtruncate, entire, or, especially in sterile pinnules, superficially crenate, upper margin irregularly and shallowly crenate in sterile pinnules, otherwise entire or often, esp. in larger pinnules, with one rather deep incision at $^3/_5$ of the distance to the apex, a similar incision not rarely found above the middle of the outer margin, thus the apex of the pinnule on a lobe which may be a little protracted. Marginal thickening very inconspicuous, except at the lower base. Veins immersed, obscure, once or twice forked, rather lax, ¾–1 mm apart at the margin; main vein somewhat elevated at the base, especially on the dorsal side, ca. ½ mm above the margin. Upper pinnules gradually reduced, the uppermost ca. 2.5–5 mm long, joined by a narrow wing, then rather suddenly confluent into an irregularly lobed, lanceolate-caudate terminal segment up to 1 cm long, obtuse or subacute, sometimes soriferous at the base. *Sori* continuous along the upper and outer margin, or, esp. in larger pinnules, often once or twice interrupted by the larger incisions. Indusium pale, greyish, ca. 0.4 mm wide, subentire or faintly erose, not reaching the margin by half its width to almost equalling it, ± reflexed at full maturity. Sporangia ca. 130 × 115 μ; annulus with 9–11 indurated cells; spores medium brown, ca. 23–28 μ, 16?

Distribution: South-eastern Brazil (map 12). Terrestrial in forests, from ca. 250–1200 m.

BRAZIL. MINAS GERAIS: Without loc., Damazio s.n. (RB).

RIO DE JANEIRO: Serra dos Orgãos, Glaziou 4381 *) (P, HOLOTYPE; Isotypes in B, C); id. s.n. (S–PA); near Rio, Glaziou 7957 (B, C, G, K, LE, M); without loc., Glaziou 7892 (B, C, K), 11701 (B, C, FI, K).

SÃO PAULO: Rio Grande, Serra do Mar, Wacket s.n. (Rosenstock-exs. 320) (M, HOLOTYPE of *L. Christii;* Isotypes in NY, S–PA, photogr. in BM); Serra do Itatins, Brade 8261 in part (S–PA, UC); ibid., id. 8260 (BM).

*) On the label and with Fée's citation no. 3481 is given, but the tag attached to the plant and the duplicates bear no. 4381, which may be assumed to be correct.

PARANÁ: Volta Grande, Dusén 3730 (UC); Serra do Mar, Mt. Marumby, Dusén 3733 (BM, G).

SANTA CATARINA: Morro Queimados, Pelhoça, Spannagel 214 (NY, S-PA, UC); São Francisco, Stadtberg, Ule 144 (B, US); Joinville, Schmalz 133 (F, MO), 134 (NY); Pirai, Schmalz s.n. (F); Blumenau, Heins 13 in part (US); Pilões, Pelhoça, Reitz & Klein 2427 (HBR); Spitzkopf, id. 545 (BM); Brusque, Reitz C 1906 (S).

A clear-cut, yet not very distinctive species; the closest relative is *L. botrychioides* which may be derived from it; it is distinguished by almost always simply pinnate leaves and at the apex flabellate-widened lower pinnules. Smaller pinnules of both species are very similar, and the incisions of the margin in larger pinnules—one in the upper, one in the outer margin—are also a common feature.

Two sheets of Glaziou 7959 (B) from Brazil, probably from Rio de Janeiro, are intermediate between *L. ovoidea* and *L. virescens*. The leaves are bipinnate (one with one sec. pinna), the upper pinnae shortened, the basal pinnules of the terminal pinna large and subpinnate, the other pinnules more incised than in *L. ovoidea* and less than in *L. virescens*, but more like those of the former. They may represent a hybrid; the spores are, however, not abortive.

13. **Lindsaea botrychioides** St. Hilaire, Voy. Distr. Diam. 1:379 (1833); Kunze, Bot. Zeit. 8:328 (1850); Hooker & Baker, Syn. Fil. 1st ed. (1868), 2nd ed. (1874) 105; Baker, Fl. Bras. I^2:352 (1870); Kuhn, Chaetopt. 26 (1882); Christ in Schwacke, Plant. Nov. Min. II:30 (1900); Diels, N. Pfl. I^4:221 (1902); Rosenstock, Hedwigia 46:79 (1906); Sampaio, Arch. Mus. Nac. Rio de Jan. 32 pl. 12 f. 6 (1930); Dutra, An. Prim. Reun. S. —Am. Bot. 2:29 (1938); not of Jenman, W. Ind. Gui. F. 75 (1899). **Fig. 47, 48**

Type: St. Hilaire 421bis from the Serra da Piedade, Minas Gerais, Brazil (P!).

Heterotypic synonym: *L. botrychioides* St. Hil. var. *subbipinnata* Rosenstock, Hedwigia 46:79 (1906). Type: Wacket 161 from Rio Grande, São Paulo, Brazil (S-PA!).

Petioles dark reddish brown to atropurpureous, quadrangular almost throughout; lamina simply pinnate, herbaceous to chartaceous; pinnules 1½–2 × as long as wide, the largest asymmetrically flabellate, widened in the outer part, often with two incisions as in the preceding species, smaller pinnules rounded-rectangular to subovate, entire; upper pinnules gradually reduced, the terminal free or almost free; sori continuous or slightly interrupted; spores trilete.

Rhizome short-creeping, 1–1.5 mm in diam.; scales lanceolate, acute-acuminate, very small, not over 0.5 mm long and 0.15 mm wide, with up to 6 rows of cells at the base. *Petioles* very close, ± distichous, (5–)10–24 cm long, usually about as long as the lamina, but sometimes not more than half as long, 0.6–1.2 mm in diam., rather shining, duller at the base, adaxially grooved, the groove rather deep and extending almost to the base, abaxially grooved in the upper part, the groove wide and shallow, becoming flat downwards with evanescing angles, subterete at the extreme base. Borders of the adaxial groove stramineous at least above, those of the abaxial groove sometimes paler above. *Lamina* simply pinnate (very rarely subbipinnate, with one or one pair of lower pinnae cleft or lobed or truly pinnate, with up to 10 pinnules to a side), approximately linear, (9–)14–34 cm long, 2–3½ cm wide, gradually narrowed in the upper half or mostly third to fourth, bright to dark green on the ventral, paler on the dorsal side. *Rachis* similar to the upper part of the petiole, upwards reddish; the abaxial groove narrowed above, its borders joining into a keel which evanesces in the base of the terminal segment. *Pinnules* ca. 15–25 to a side, alternate or the lower sometimes opposite, spreading, the basal wide-spaced, 1.5–4.5 cm apart, the upper ones gradually closer, but not or only the uppermost ones contiguous; largest pinnules with a short stalk up to 3 mm long, smaller ones subsessile; the largest 9–21 mm long, 6–14 mm wide, mostly widest in the outer third; shape rather variable: small pinnules are rounded-rectangular to subovate, large pinnules asymmetrically flabellate, often superficially lobed. Inner margin truncate, often slightly concave, the upper base acute or shortly rounded, sometimes touching or somewhat overlying the rachis, lower margin ± straight, in large pinnules concave, upper margin evenly rounded or almost straight in small pinnules, sinuous-convex in larger ones, usually with a concave portion or a shallow incision near the middle and one in the middle of the outer margin; the apex broadly rounded or almost truncate. Margin hardly thickened, sometimes crispate-undulate and/or minutely erose-repand in fertile pinnules, shallowly crenate, often with two deeper incisions as described above, in addition usually slightly revolute in sterile ones. Lower pinnules not reduced, or a few remote ones occasionally slightly smaller, upper pinnules gradually reduced, the apical ones 3–11 mm long; terminal segment asymmetrically lanceolate, very obtuse, 7–13 mm long, lobed on one or rarely on both sides of the base, mostly free, but sometimes connected by a very narrow wing with one or two upper pinnules, mostly fertile at the side, with a short abaxially keeled midrib. Veins twice or rarely three times forked, rather lax, their ends irregularly spaced at the margin, ca. ¾–1 mm apart, mostly immersed and rather obscure; main vein running ca. ½ mm above the lower margin. *Sori* along the upper/outer margin, continuous or in larger pinnules usually once or twice interrupted by the incisions of the margin; indusium greyish, ca. 0.5 mm wide, not reaching the margin by about the same distance, subentire or usually rather superficially erose-repand, commonly reflexed and conceiled at full maturity. Sporangia ca. 145 × 110–115 μ; annulus with 11–13 indurated cells; spores medium brown, ca. 25 μ, 32?

Distribution: South-eastern Brazil (map 13). Terrestrial in forests, often in moist places, up to 1650 m.

Representative specimens:

BRAZIL. MINAS GERAIS: Serra da Piedade, St. Hilaire 421bis (P, HOLOTYPE); Ouro Preto, Morro São Sebastião, Damazio s.n. (RB 36245).

RIO DE JANEIRO: near Rio, Glaziou 7958 (B, C, C. Chr. in BM, G, K).

SÃO PAULO: Alto da Serra, Estação Biologica, Gehrt 7830 (GH, NY); ibid., L. B. Smith 1904 (C, GH, US); Rio Grande, Wacket 161 (S–PA, HOLOTYPE of var. *subbipinnata* Ros.; Isotypes in NY, UC); Bosque da Saude, Brade 5174 (NY, UC); Serra da Bocaina, Brade 20644 (RB).

PARANÁ: Lucena, Wielewski 78 (Rosenstock-exs. 66) (B, BM, L, M, NY, RB, S, SI, S–PA, UC, US, W); Roça Nova, Dusén 8334 (B, BM, K, NY, S, S–PA, US); Jaguariaiva, Dusén 1411 in part (GH), 18036 (C. Chr. in BM, GH, MO, S–PA).

SANTA CATARINA: São Francisco, Schmalz s.n. (MO).

Reported from Rio Grande do Sul by DUTRA (1938).

The closest relative of this species is *L. ovoidea*, which agrees in dark axes, general shape of the smaller pinnules, revolute sterile margin, and incised larger pinnules with once or twice interrupted pinnules, but can be distinguished by more gradually confluent upper pinnules, never flabellately widened pinnules, and mostly bipinnate leaves. As the latter character is generally unreliable in the genus, the subbipinnate form of *L. botrychioides* described as a variety by Rosenstock does not deserve special recognition. *L. botrychioides* is not closely related to *L. flabellulata*, as was suggested by HOOKER &BAKER (1868, p. 105), nor to *L. guianensis* (id. 1874, p. 105). *L. crenulata* Fée and *L. multifrondulosa* Fée were incorrectly referred *L. botrychioides* in the first-cited publication.

Subsectio 2. **Decrescentes** Kramer, subsect. nov.

Pinnulae fertiles omnes integrae vel subintegrae, superioribus plus minusve decrescentibus, segmento terminali haud libero; soris continuis.

Species typica: *Lindsaea quadrangularis* Raddi.

14. **Lindsaea quadrangularis** Raddi, Opusc. sci. Bol. 3:294 (1819); Fl. Bras. Nov. Gen. Spec. I:55 (1825), t. 74; Hooker, Spec. Fil. I:214 (1844), in part; Ettingshausen, Farnkr. t. 146 fig. 1–3 (1865); Fée, Crypt. vasc. Brés. I:29 (1869), p.p. min.; J. Smith, Hist. Fil. 268 (1875); Kuhn, Chaetopt. 26 (1882); Hassler, Trab. Inst. Bot. Farm. Buenos Aires 45:36 (1928); not of Moore, Ind. Fil. I pl. 22 (1857); Mettenius, Ann. sci. nat. V, 2:217 (1864); Posthumus, Fl. Surin. Suppl. 75 (1928).

Type: Raddi s.n. from the vic. of Rio de Janeiro, Brazil (PI!). Homotypic synonym: *L. lancea* (L.) Bedd. var. *quadrangularis* (Raddi) Rosenstock, Hedwigia 46:80 (1906); Dutra, An. Prim. Reun. S.-Am. Bot. II:29 (1938).

Misapplied names: *L. trapeziformis* auct. non Dryander; Langsdorf & Fischer, Ic. Fil. p. 21, pl. 24 (1810); Baker, Fl. Bras. I^2:354 (1870), p.p. min., excl. syn.; Rosenstock, Hedwigia 43:216 (1904), in part.

L. curvans of Fée, Crypt. vasc. Brés. I:29 (1869), in part, non Fée, 1852.

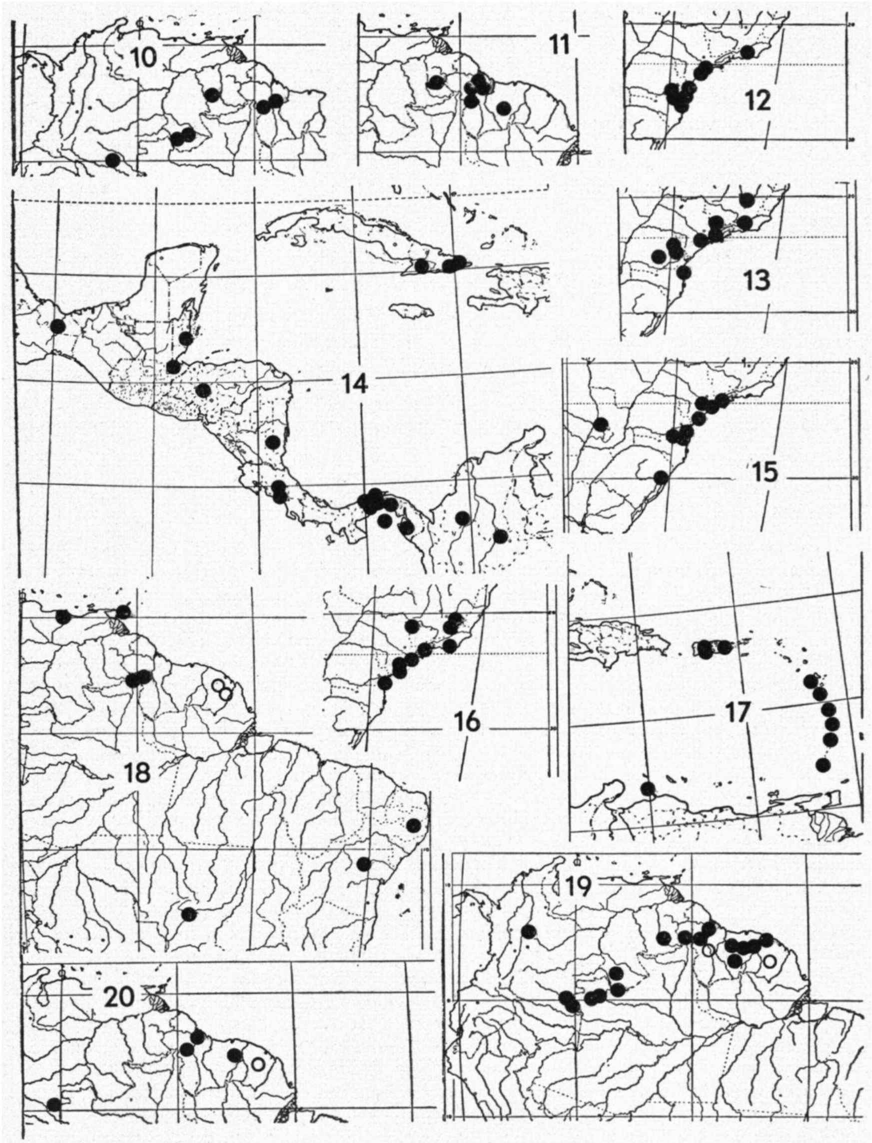
L. guianensis auct. non Dryander; Baker, Fl. Bras. I^2:354 (1870), p.p. min., excl. syn.

L. lancea (L.) Bedd. f. *montana* (Fée) Lindman, Ark. f. Bot. I:198 (1903), as to specimens cited, not as to type.

Rhizome creeping, 1.5–3 mm in diam.; scales lanceolate, acuminate, up to 1.5–2 mm long and 0.3–0.4 mm wide, with up to 8 rows of cells at the base. *Petioles* rather close to close, ca. 10–60, mostly about 15–40 cm long, about as long as to twice as long as the lamina (less often only half as long). *Lamina* bipinnate (very rarely simply pinnate or subtripinnate), herbaceous, medium to dark green or olivaceous on the ventral, paler on the dorsal side, 15–40 (–50) cm long. *Pinnules* rather close but mostly not contiguous, usually dimidiate-ovate or -oblong, sometimes rhombic or trapeziform, 2–2½ × as long as wide, the upper ones ± reduced, ± confluent with the terminal segment. Veins immersed, once or twice (or three times) forked. *Sori* continuous along the upper/outer margin.

This species consists of four clear-cut subspecies which can be distinguished as follows:

1. a. Upper pinnules but little reduced, terminal segment large, almost free . . . . c. ssp. *terminalis*
   b. Upper pinnules gradually and strongly reduced, confluent into a narrow, mostly small terminal segment 2



Map 10: *L. tetraptera.* Map 11: *L. parkeri;* complete dots: ssp. *parkeri;* half dot: ssp. *steyermarkiana.* Map 12: *L. ovoidea.* Map 13: *L. botrychioides.* Maps 14–17: *L. quadrangularis;* map 14: ssp. *subalata;* map 15: ssp. *terminalis;* map 16: ssp. *quadrangularis;* map 17: ssp. *antillensis.* Map 18: *L. pallida.* Map 19: *L. dubia.* Map 20: *L. surinamensis.*

2\. a. Secondary rachises pale, abaxially with a groove starting abruptly above the subterete base . . . d. ssp. *antillensis*
   b. Secondary rachises with pale ± wing-like margins bordering a dark concave or flat central portion . . . a. ssp. *subalata*
   c. Secondary rachises mostly dark, terete at the base, gradually becoming angular, sulcate above, without wing-like margins 3
3\. a. Spores monolete . . . . b. ssp. *quadrangularis*
   b. Spores trilete. . . . . . . atypical specimens of ssp. c.

a. ssp. **subalata** Kramer, ssp. nov. **Fig. 50**

Misapplied name: *L. horizontalis* auct. non Hooker; Standley & Record, Field Mus. Publ. 350:64 (1936).

Petiolus griseo- vel rubro-fuscus vel pullus, facie abaxiali plerumque angulari, raro subtereti; lamina bipinnata, pinnis patentibus, rhachidibus secundariis rubro-fuscis, facie abaxiali marginibus plus minusve aliformibus stramineis limbatis; pinnulis herbaceis, atrovirentibus vel olivaceis, superioribus sensim redactis; indusio pallido, angusto, 0.1–0.2 mm lato, integro, marginem non attingente; sporis tetraedriformibus.

Typus: Skutch 2241 from the vicinity of El General, San José prov., Costa Rica (US).

Rhizome often strongly branched. *Petioles* 1–2 mm in diam. near the apex, ± shining, quadrangular except at the subterete base, less often (especially in Cuban specimens) the abaxial side terete, the surfaces, especially the adaxial one, often sulcate, the angles often more acute and paler in the upper part. *Lamina* with 1–7 pinnae to a side and a conform terminal one. *Primary rachis* reddish to dark brown, adaxially with a broad shallow groove with pale, not wing-like borders, abaxially terete, angular, or sulcate, in the latter case often with paler margins; transitions sometimes found in a single leaf. *Pinnae* alternate or the lower ones mostly subopposite, subsessile, the lower ones 3–5 cm apart, the upper ones little or not closer, laxly ascending under an angle of ca. 30–50°, the largest 12–25 cm long, 1¾–2½ cm wide, slightly narrowed at the base, gradually narrowed from slightly above the base to the apex, the upper ones mostly somewhat shortened. Terminal pinna usually longest and widest (up to 3 cm). Secondary rachises reddish-brown, adaxially with a narrow groove bordered by pale, not wing-like margins, abaxially with pale membranous wings sharply contrasting with the reddish flat or sulcate middle portion, ending rather abruptly at the level of approximately the second pinnule, the extreme base terete. *Pinnules* 20–30(–40) to a side, almost invariably alternate, spreading or slightly ascending, subsessile or shortly stalked (up to 0.5 mm), sometimes subfalcate or truncate-subtriangular, 8–16 mm long, 3.5–7 mm wide, a strongly reduced axillary pinnule present, 1–3 adjacent basal ones often ± reduced. Inner margin straight, parallel or slightly overlying the sec. rachis, lower base cuneate, ± stalk-like, upper base subangular, upper margin straight or sometimes faintly concave at the base, convex towards the apex, sometimes slightly crispate, lower margin straight or mostly faintly S-shaped, slightly concave at the base; apex rounded or subtruncate, in the latter case a distinct outer margin developed; pinnules widest at the base but not rarely hardly narrowed close to the apex. Marginal thickening whitish, inconspicuous except at the base of the lower margin; all margins entire or the upper minutely erose in fertile pinnules, sterile pinnules similar or sometimes with a ± prolonged apex, though never as pronouncedly as sometimes in *L. arcuata*, upper/outer margin shallowly crenate. Vein-ends ca. 1 mm apart, main vein hardly or not united with the marginal strand, but close to it, ca. ¼ mm above it near the apex. Upper pinnules gradually and strongly reduced, the highest 2–5 mm long, confluent with the terminal segment which is rather variable, asymmetrically-triangular or lanceolate, lobed at the base, ¾–1½ cm long, obtuse or subacute, or long-caudate, linear, up to 3 cm long, subacute, sterile or soriferous in the basal lobes. Indusium not reaching the margin by its own width to twice its width, rarely almost equalling it, ± reflexed at full maturity; sporangia ca. 145 × 115 μ; annulus with 11–13 indurated cells; spores ca. 25 μ.

Distribution: Cuba and southern Mexico to Colombia (map 14). In moist forests, sometimes along streams, from sea-level to ca. 1500 m.

Representative specimens:

Cuba. Oriente: Navas-Sierra de Buena Vista, Ekman 3856 (S, US); ibid., Shafer 4432 (GH, NY, US); Taco Bay between Rs. Santa Maria and Jiguaní, Ekman 3770 (K, NY, S, US); Río Yao, Marie-Victorin 21394 (GH, US).
Mexico. Vera Cruz: Coatzacoalcos, Ch. L. Smith 2078 in part (MO).
Oaxaca: Without loc., Buchinger 343 (B).
British Honduras: Mullins River Road, Schipp 200 (B, BM, F, G, GH, K, NY, S, S–PA, UC, US).
Guatemala: Livingston, Deam 489 (GH).
Honduras: El Sauce, Santa Barbara prov., L. O. Williams & Molina 17692 (US).
Nicaragua: Rama, Carhart s.n. (NY).
Costa Rica: Vic. of El General, San José prov., Skutch 2241 (US, Holotype; Isotypes in K, MO, NY, S–PA); San Isidro del General, ibid., Scamman 5911 (GH); ibid., Chrysler & Roever 5216 (MO, UC); Finca los Cusingos near San Isidro del General, Norby & Norby 25 B, 370 (EAP); vic. of Pejivalle, Cartago prov., Standley & Valerio 47056 (US).
Panamá: Chagres, isthmus, Fendler 412 (K, MO, US); Chico Trail, R. Indio, C.Z., Steyermark & Allen 17463 (G, K, MO, S, US); e. of Las Cascadas, C.Z., Maxon 4888 (GH, M, MO, NY, Pic.-Ser., S, US); San José Island, Perlas Archipelago, Johnston 477 (BM, GH, Pic.-Ser., S, U, US); Loma de la Gloria near Fató, Colón prov., Pittier 4080 (GH, NY, US); Cana-Cuapi-trail, Chepigana distr., Darien prov., Terry & Terry 1467a (F, US); Juan Diaz, Killip 2550 (B, S–PA, US).
Colombia. Bolívar: Boca Antizales, R. Esmeralda, Pennell 4473 (F, GH, K, MO, NY, US).
Santander: Vic. of Barranca Bermeja, Magdalena Valley, Haught 1513 (GH), 1519 (F, GH, UC, US).

Usually ssp. *subalata* is easy to distinguish by the character of the secondary rachises, but it is sometimes difficult to separate it from *L. arcuata*, where the differences are discussed. From *L. portoricensis*, the only other species with which it is likely to be confused, it can be distinguished by more patent pinnae, continuous pale margins on the abaxial side of the sec. rachises, abaxially mostly angular petioles and narrower, entire indusia.

b. ssp. **quadrangularis.** **Fig. 51**

Petioles dark reddish brown to blackish, abaxially angular or subterete; secondary rachises stramineous to reddish brown, abaxially terete at the base, above gradually angular and/or sulcate; fertile pinnules subentire to erose-denticulate along the upper/outer margin, sterile ones crenate-dentate; upper pinnules gradually and strongly reduced, confluent; spores monolete.

Petioles 1–2 mm in diam. near the apex, dark reddish-brown to blackish, rather dull, subterete at the extreme base, otherwise quadrangular, with often sulcate surfaces, or the abaxial side obtusely angular to subterete. *Lamina* with 1–9(–11) pinnae to a side and a conform terminal one. *Primary rachis* reddish to dark brown, abaxially angular to subterete, sometimes sulcate above. *Pinnae* subopposite or alternate, short-stalked (a few mm) or mostly subsessile, the lower ones 2–6 cm apart, the upper ones closer, laxly ascending under an angle of 30–50°, the lower ones ca. 10–25 cm long, 1¾–3, mostly 2–2½ cm wide, slightly narrowed at the base, especially on the acroscopic side, gradually and strongly narrowed from the middle to the apex, upper pinnae somewhat shortened, the terminal about the size of the lower ones. Secondary rachises stramineous to (mostly) reddish-brown, abaxially terete at the base, becoming angular (mostly gradually) at the level of the 1st–4th pinnule, mostly sulcate above, the margins not or hardly paler. *Pinnules* ca. 10–35 to a side, almost always alternate, spreading or often somewhat ascending, subsessile, (7–)9–18 mm long, (3–)4–7 mm wide, a strongly reduced axillary pinnule usually present, a few additional basal ones, especially on the acroscopic side, slightly reduced. Inner margin straight, often touching or slightly overlying the sec. rachis, lower base cuneate, hardly stalk-like, upper base subangular or very shortly rounded, upper margin straight in the inner, convex in the outer part, lower margin straight or often slightly concave, apex rounded or narrowed-subacute, or angular at the basiscopic side, a separate outer margin often ± developed, the pinnules mostly distinctly but not very strongly narrowed to the apex, widest at the base. Marginal thickening pale, inconspicuous. Upper/outer margin subentire to erose-denticulate or slightly crispate in fertile pinnules, crenate-dentate, often with acute teeth, in sterile ones. Vein-ends ca. ¾–1½ mm apart; main vein hardly united with the marginal strand, ca. 0.4 mm above it near the apex. Upper pinnules gradually and strongly reduced, the highest denticuliform, 2–4 mm long, several confluent with the terminal segment which is narrowly lanceolate to linear, subacute or obtuse, crenate-lobed at the base, ½–2 cm long, rarely caudate and up to 3 cm long, sterile or soriferous in the basal lobes. Indusium pale, delicate, 0.2–0.3 mm wide, erose-denticulate to subentire, not reaching the margin by a distance of 0.1–0.4 mm, strongly reflexed and conceiled at full maturity. Sporangia ca. 132 × 95 μ; annulus with 11–14 indurated cells; spores monolete, bean-shaped, hyaline, almost colourless, ca. 16 × 25 μ.

Distribution: South-eastern Brazil (map 16). Im moist forests, sometimes along watercourses, at lower altitudes (few data extant).

Representative specimens:

Brazil. Minas Gerais: Viçosa, Cha-Cha-valley, Mexía 4410a (UC, US); São Sebastião do Paraiso, Brade, Altamiro & Teodoro Ba 77 (GH); São João Nepomuco, Lopes s.n. (RB).

Rio de Janeiro: Near Rio, Raddi s.n. (PI, Holotype, 3 sheets; Isotypes in FI, G, K, P); ibid., Forssell 225, 231 (S–PA); Corcovado, Glaziou 1653 (BR); ibid., Lindman A 165 (S, S–PA); Serra dos Orgãos, Miers 135 (NY); Catumby, Mosén 73 (C, K, LE, S).

São Paulo: Campinas, Severin 48 (B, BR, FI, M, S, S–PA, UPS); Alto da Serra, L. B. Smith 1965 (GH); Iguapé, Brade 8226 (BM, US); Cajures, Brade 8262 (S–PA).

Paraná: Serra da Prata, Dusén 15298 (B, S, S–PA, US).

The dark axes, gradually reduced upper pinnules with small terminal segment, and monolete spores characterize this subspecies. It is closely related to ssp. *terminalis*, which has trilete spores and usually less reduced upper pinnules with a larger terminal segment, and to *L. pallida*, where the differences are pointed out.

c. ssp. **terminalis** Kramer, ssp. nov. **Fig. 49**

Petiolus atrofuscus vel atratus, quadrangularis, vel facie abaxiali obtuse angularis vel subteres; lamina bipinnata, rhachidibus obscuris, secundariis facie abaxiali inferne subteretibus, superne angularibus vel sulcatis; pinnulis herbaceis, atrovirentibus vel olivaceis, superioribus plerumque paullum redactis, segmento terminali magno, late lanceolato, pinnulis superioribus vix iuncto; indusio pallido, angusto, 0.15

mm lato, leviter eroso-crenulato, marginem non attingente; sporis tetraedriformibus.

Typus: Lindman A 1757 from Colonia Presidente Gonzalez, Paraguay (S).

Petioles ca. 1 mm in diam. near the apex, ± shining, subterete at the extreme base, otherwise quadrangular, or abaxially mostly obtusely angular to subterete, the adaxial surface, sometimes also the others, sulcate. *Lamina* with 2–7 pinnae to a side and a conform terminal one. *Primary rachis* similar to the upper part of the petiole, mostly obtusely angular on the abaxial side, the edges of the adaxial groove pale, somewhat wing-like, sometimes extending to the upper part of the petiole. *Pinnae* subopposite, the upper alternate, subsessile, the lower ones ca. 3–4 cm apart, laxly ascending under an angle of 30–40°, the largest 12–15 cm long, 2–3(–3½) cm wide, widest just below the base or in the basal one-third or half, slightly narrowed at the base, gradually and more strongly narrowed towards the apex, the upper ones somewhat shortened and closer. Terminal pinna often widest, stalked (1–2 cm). Secondary rachises at least at the base brownish to blackish-brown, adaxially broadly and shallowly grooved, the borders somewhat pale and wing-like, abaxially subterete or terete at the base, gradually obtusely or sharply angular above, mostly not sulcate or near the apex only, occasionally angular almost throughout. *Pinnules* 10–20 to a side, mostly alternate throughout, usually somewhat ascending, subsessile, 11–16 mm long, 5–7 mm wide, a strongly reduced axillary pinnule mostly present, a few additional ones often somewhat reduced. Inner margin straight, approximately parallel to the sec. rachis, lower base cuneate, hardly stalk-like, upper base angular or shortly rounded, lower margin straight or often slightly convex towards the apex, upper margin straight at the base, strongly convex towards the apex which is subacute or shortly rounded; pinnules rather strongly narrowed towards the apex, a separate outer margin hardly developed. Marginal thickening narrow, pale, inconspicuous. Upper margin shallowly crenate to sinuous in sterile pinnules, minutely erose to subentire, sometimes slightly crispate in fertile ones. Vein-ends ca. 1–1½ mm apart; main vein hardly united with the marginal strand, ca. ½ mm above it near the apex. Upper pinnules not strongly reduced, ca. 5–10 cm long, one or two connected by a narrow wing with the terminal segment which is rather large, 1–2 cm long, broadly lanceolate, with two unequal basal, often soriferous lobes, subacute to obtuse, the central shank shallowly sinuate-crenate; rarely the upper pinnules are more strongly reduced and the terminal segment is small. Indusium not reaching the margin by a distance equal to about twice its width, strongly reflexed and conceiled at full maturity. Sporangia ca. 165 × 125 μ; annulus with 7–11 indurated cells; spores very pale brownish-yellow, ca. 25 μ.

Distribution: South-eastern Brazil and Paraguay (map 15). In similar localities as the preceding subspecies, not rarely collected together with it.

Representative specimens:

BRAZIL. RIO DE JANEIRO: Maná, Schreiner 18468 (NY).

SÃO PAULO: Sorocaba, Mosén 3733 (S, S–PA, UPS); Iguapé, Bõa Vista, Brade 7727 (UC); Alto da Serra, Wacket s.n. (Rosenstock-exs. 348) (B, M, NY, S, S–PA, UC, US, W); São José dos Campos, Löfgren 422 (S); Rio Grande, Edwall 4967 (S–PA); Moóca, Brade 5386 (S–PA); Alto da Serra, Wacket 16 (S–PA); Santos, Regnell s.n. (UPS).

PARANÁ: Serra da Prata, Dusén 15298 in part (BR, S); Volta Grande, Dusén 14139 in part (B, S, US), 11439 (S).

SANTA CATARINA: Itajaí, Reitz 3974 (US); Blumenau, Heins 13 in part (US); Joinville, Ule 37 (B); ibid., Schmalz 25 in part (F, MO, S–PA).

RIO GRANDE DO SUL: Porto Alegre, Stier 280 (S–PA); near São Leopoldo, Eugenio 48 (NY).

PARAGUAY: Colonia Presidente Gonzalez, Lindman A 1757 (S, HOLOTYPE; Isotypes in BM, G, GH, K, S, S–PA, UPS, US); Central Cordillera, Upper Río Y-acá, Hassler 6732 (B, BM, G, K, S–PA).

Most closely related to the preceding subspecies: aberrant specimens of ssp. *terminalis* with small upper pinnules and small terminal segment can only safely be distinguished by the spore-shape. Other relatives are *L. divaricata*, which is often very close, especially specimens with less distinctly developed wings on the axes occurring in Paraguay and southern Brazil, *L. lancea*, and *L. guianensis* ssp. *lanceastrum*, to which species the reader is referred.

d. ssp. **antillensis** Kramer, ssp. nov. **Fig. 53, 54**

L. montana Fée, 11e mém. 17 (1866), in part (*nomen confusum*, see p. 343); Duss, Fl. Crypt. Ant. franc. 58 (1904); Hieronymus, Hedwigia 62:15 (1920); Maxon, Pterid. Port. 489 (1926); Domin, Pterid. Domin. 244 (1929); Stehlé, Caribb. For. 4 (2): 92 (1943); Hodge, Lloydia 17 (2):102 (1954). Type: L'Herminier s.n. from Guadeloupe (P!, consisting partly of *L. guianensis* ssp. *guianensis*).

Homotypic synonyms: *L. lancea* (L.) Bedd. f. *montana* (Fée) Lindman, Ark. f. Bot. I:198 (1903), as to type only.

L. lancea (L.) Bedd. var *montana* (Fée) Bonaparte, Notes Ptérid. VII:343 (1918), X:202 (1920).

Misapplied name: *L. trapeziformis* auct. non Dryander; Krug in Urban, Engl. Bot. Jb. 24:91 (1897), p.p. mai.

Petiolus stramineus vel pallide fuscus, facie abaxiali inferne tereti vel subtereti, superne angulari vel interdum etiam subtereti; lamina bipinnata, herbacea, rhachidibus secundariis stramineis, facie abaxiali basi infima tereti, deinde subito canaliculata, marginibus nunquam alatis; pinnulis linguiformibus vel rotundato-subrhomboideis, apice plerumque late rotundatis, pinnulis superioribus sensim redactis; indusio pallido, integro vel subintegro, 0.2–0.3 mm lato, marginem subaequante vel breviore; sporis tetraedriformibus.

Typus: Eggers 647 from Roseau-lagoon, Dominica (B).

Petioles ¾–1¼, mostly 1 mm in diam. near the apex, dark brown at the base, there subterete, otherwise stramineous to pale (rarely medium) brown, adaxially sulcate close to the base or flattened below. *Lamina* with 1–4 primary pinnae to a side and a conform terminal one, very rarely simply pinnate. *Primary rachis* abaxially flattened or sulcate, less often subterete below or throughout. *Pinnae* subopposite, the upper ones mostly alternate, subsessile, the lower ones 2½–7 cm apart, the upper ones gradually closer, laxly ascending under an angle of ca. 30–50°, the largest 9–25 cm long, 1.5–3(–3.5) cm wide, widest somewhat above the base, slightly narrowed towards the base, very gradually narrowed to the apex, the upper ones little or not shortened, the terminal pinna sometimes largest, with a stalk up to 2 cm long. Secondary rachises adaxially narrowly and deeply sulcate, abaxially with a short terete basal portion, from the level of the 1st–3rd pinnule abruptly sulcate. *Pinnules* ca. 15–40, mostly about 25, to a side, alternate or the lower or medium ones subopposite, spreading or slightly ascending, rarely decurved, or subfalcate, the largest 12–18, mostly ca. 13 mm long, 5–8, mostly 6 mm wide, widest at the base, but little narrowed to the broadly rounded apex, less often more strongly narrowed or of equal width throughout. Inner margin straight, parallel or slightly divergent from the rachis, lower base shortly cuneate, hardly stalk-like, upper base subangular or shortly rounded, lower margin straight or faintly concave, convex, or S-shaped, upper margin straight in the inner, convex in the outer part, less often more evenly convex throughout. Marginal thickening stramineous, inconspicuous except along the lower edge. Upper/outer margin entire in fertile pinnules, sinuate or distantly crenate, with incisions up to 1 mm deep and rounded teeth in sterile ones which are not very rare. Vein-ends 1–1½ mm apart; main vein only shortly connected with the marginal strand, ca. 0.5 mm above it near the apex. Upper pinnules gradually reduced, the highest ca. 3–5 mm long, 1–3 connected by a wing with the terminal segment, which is lobed-triangular to narrowly lanceolate, obtuse, ½–3 cm long, sterile except in the basal lobes. Indusium almost equalling the margin or falling short of it by its own width, ± reflexed at full maturity. Sporangia ca. 160 × 125 μ; annulus with 9–12 indurated cells; spores pale brownish-yellow, ca. 28 μ, 16?

Distribution: Puerto Rico and Lesser Antilles, sometimes incorrectly ascribed to other regions (as *L. montana*), apparently commonest in Dominica and Guadeloupe; also on the Paraguaná-Peninsula, Venezuela (map 17). In dense rainforests and elfin woodland, mostly terrestrial, occasionally on tree-trunks, from ca. 300–1100 m (rarely lower).

Representative specimens:

Puerto Rico: Sierra de Naguabo, Barrio de Maizales, Britton & Hess 2290 (F, NY, S, US); Adjuntas, Mt. Andubo, Sintenis 4675 (B); Adjuntas, Las Cruces, Sintenis 4051 (B, BM, G, GH, GOET, L, LE, M, MO, S–PA, US); Peñuelas, Las Cruces, Sintenis 4374 (B, US); Sierra de Luquillo, Blauner 293 (BM, G).

Guadeloupe: Husnot 272 (BM, BR, F, FI, G, K); Questel 1848, 3031, 3273 (US); Duss 4239 (NY), 4243 (NY, US); Stehlé 521 (F, US), 2419 (US); L'Herminier 42, 44 in part (B, BR, G, GOET, K, P, W); id. s.n. in part (P, Holotype of *L. montana*; other authentic specimens in B, BM, G, K, L, LE, MO, NY, P, US).

Dominica: Eggers 647 in part (B, Holotype; Isotypes in B, G, GOET, L, LE, W); Jenman s.n. (NY); Lloyd 213 (NY, US); Hodge 66, 1119 (GH, NY), 1219, 1386, 2281 (GH); Hodge & Hodge 1713, 1914, 2620 (GH).

Martinique: Duss 1707 (F), s.n. (B, F, M, US).

St. Lucia: Box 429 (BM, US), 1705 (BM); Day 390 (B), Murray s.n. (K).

St. Vincent: H. H. & G. W. Smith 1893 (BM); Arnott s.n. (NY).

Grenada: Eggers 6191 (GOET, L, US); Beard 1309 (GH, MO, S, US); Broadway s.n. (F, GH, MO, NY, US); Jenman s.n. (NY); Sherring s.n. (G, NY, US).

Venezuela. Falcón: Paraguaná-Peninsula, Cerro Santa Ana, Curran & Haman 681 (GH, NY).

L. quadrangularis ssp. *antillensis* is not as closely allied to the other subspecies as those are among each other, and deserves perhaps recognition as a species. Otherwise it is rather close to *L. lancea*, but that species differs in almost always much less reduced upper pinnules and larger, free terminal segment, and by the apex of the pinnules wich is angular at the basiscopic side. The reason for rejecting Fée's name *L. montana* is explained on p. 343.

The subspecies of *L. quadrangularis* are clear-cut and rather distinct and there would be hardly any serious objection against treating them as separate species, particularly ssp. *antillensis*.

L. quadrangularis can be said to occupy a central or perhaps rather a basal position in the section *Lindsaea*, as it is related to several, rather diverse species probably representing separate lines of evolution: *L. lancea*, *L. divaricata*, *L. arcuata*, *L. pallida*, *L. guianensis*, possibly also *L. portoricensis*.

15. **Lindsaea pallida** Klotzsch, Linnaea 18:547 (1884); J. Smith, Hist. Fil. 268 (1875); Kuhn, Chaetopt. 26 (1882); Hieronymus, Hedwigia 62:17 (1920). **Fig. 52**

Type: Schomburgk 1205, British Guiana (B!).

Heterotypic synonym: *L. lancea* f. *marginalis* Lindman, Ark. f. Bot. I:199 (1903), pl. 8 fig. 3. Type: Lindman A 3341 ½ from Serra do Itapirapuan, Matto Grosso, Brazil (S!).

Misapplied names: *L. quadrangularis*, *β*, of Hooker, Spec. Fil. I:214 (1844); Kunze, Bot. Zeit. 8:346 (1850).

L. quadrangularis auct. non Raddi; Fée, Crypt. vasc. Brés. I:29 (1869), in part; Posthumus, Fl. Surin. Suppl. 75 (1928).

L. trapeziformis auct. non Dryand.; Baker, Fl. Bras. I^2:355 (1870), in part.

Petioles pale, abaxially obtusely angular to subterete; lamina bipinnate with conform terminal pinna, chartaceous; pinnules rounded-trapezoidal or dimidiate-ovate, ca. 2 × as long as wide, the upper ones gradually reduced; sterile upper/outer margin with small acute teeth; sori continuous; indusium strongly and irregularly erose-denticulate; spores monolete.

Rhizome creeping, 2–2.5 mm in diam.; scales narrowly lanceolate, long-acuminate, up to 1.7 mm long and 0.3 mm wide, with up to 7 rows of cells at the base. *Petioles* rather close, ca. 10–40 cm long, about as long as to 1½ × the length of the lamina, (¾–)1–1.5 mm in diam. at the base of the lamina, ± shining, adaxially in the upper part with a deep narrow groove which often evanesces downwards, the lower half more flattened to subterete. *Lamina* bipinnate (very rarely with a few subbipinnate primary pinnae), ca. 15–30 cm long, rather bright green to olive on the ventral, paler on the dorsal side, with 2–6 pinnae to a side and a conform terminal one. *Primary rachis* similar to the upper part of the petiole, abaxially often sulcate above. Axillary cushions indistinct, hardly ever discoloured. *Pinnae* mostly subopposite, laxly ascending under an angle of ca. 40–60°, subsessile, the lower up to 5 cm apart, the upper closer, 9–18 cm long, the upper ones about ⅔ of the length of the lower, 1.5–3.5, mostly 2–3 cm wide, widest somewhat above the base which is slightly narrowed, the upper part gradually narrowed to the long-acuminate apex. Secondary rachises stramineous, slender, adaxially with a deep narrow groove the thick borders of which often touch, abaxially terete at the base, then becoming gradually angular to shallowly sulcate, the terete part occupying ⅓ or ¼, occasionally less, of the length; rachis of terminal pinna abaxially sulcate throughout. *Pinnules* ca. 15–25 to a side, alternate, spreading or mostly somewhat ascending, 8–20 mm long, 5–10 mm wide, widest at base, the apex but little narrowed, broadly rounded. The pinnules are in shape approximately intermediate between the most common form of *L. lancea* and *L. quadrangularis*, resembling large forms of *L. stricta* f. *moritziana*. Lower base cuneate, hardly or not stalk-like, upper base shortly rounded to almost angular, inner margin approximately straight, parallel or mostly slightly touching to overlying the secondary rachis; upper margin straight or faintly convex at the base, more strongly convex towards the apex, lower margin straight to very faintly S-shaped, convex at the extreme apex; upper edge minutely but distinctly erose-denticulate when fertile, when sterile (in normally fertile leaves the tips of the apical pinnules are usually sterile) with acute uninerval teeth up to ½ mm long. Marginal thickening stramineous, indistinct except at the base of the basiscopic edge. Upper pinnules gradually reduced, the apical ones denticuliform, 1–2 mm long, strongly ascending, confluent into a narrowly lanceolate caudate-acuminate apical segment 1.5–2.5 cm long, acute or subacute, lobed at the base, the lobes mostly sterile and sharply denticulate. Veins immersed, obscure, mostly twice forked, rather close, their ends about ½–¾ mm apart; main vein hardly united with the marginal strand, ca. 0.3 mm above it near the apex. *Sori* along the upper/outer margin; indusium stiff, greyish, 0.4–0.6 mm wide, not reaching the margin by 0.2 mm to almost equalling it, little or not reflexed at full maturity. Sporangia 155–160 × 115–120 μ; annulus with 12–14 indurated cells; spores bean-shaped, very pale brownish, ca. 24 × 36 μ.

Distribution: Venezuela, Trinidad, Guiana, northern, central, and eastern Brazil; apparently uncommon (map 18). Terrestrial, collected in forests and campos; very few ecological data extant.

Venezuela. Miranda: El Hatillo, Br. Ginés 211 (US).

Trinidad: St. Ann's Hill, Trin. Bot. Gard. Herb. 102 in part (US); without loc., id. 103 (US).

British Guiana: Potaro R., Jenman s.n. (NY); Humirida Mts., Appun 1259 (K); prob. the same coll., Glaziou 12356 (B, BR, C, G, LE, NY); without loc. Schomburgk 1205 in part (B, Holotype; Isotypes in B and BM).

French Guiana: Oyapok, Leprieur (?) s.n. (K); without loc., Leprieur 164 in part (B, G, P).

Brazil. Amazonas: Toê-câ, Igarapé, von Lützelburg 21520 (M, UC).

Rio Branco: Igarapé, Rio Quinô, von Lützelburg 21364 (M).

Pernambuco: Catucá, Gardner 1225 (K); near Macacos, Ridley, Lea & Ramage s.n. (BM).

Bahia: Jacobina, Blanchet s.n. (G); without exact loc., Blanchet s.n. (G).

Matto Grosso: Serra do Itapirapuan, Affonso, Lindman A 3341 1/2 (S; Holotype of *L. lancea* f. *marginalis* Lindman).

Colombia?: "New Grenada", Linden 708 (BR, K).

This species is most closely allied to *L. quadrangularis* ssp. *quadrangularis*, from which it differs mainly in pale axes and more strongly erose indusium and fertile margin. The general shape of pinnae and pinnules, the sharply incised sterile margin, and the monolete spores (otherwise not found in the present section) are points of similarity. It is strange that this species, which, though not very outstanding in appearance, can easily be told apart by the above-mentioned characters, has become almost obsolete after its original publication. Specimens in herbaria are generally referred to *L. stricta* (because of pale colour and obscure veins) or *L. quadrangularis*. Its distribution seems to be still very insufficiently known.

16. **Lindsaea arcuata** Kunze, Linnaea 9:86 (1835); Hooker, Spec. Fil. I:215 (1846); Kunze, Farrnkr. II:46; t. 119 (1850); Bot. Zeit. 8:369 (1850); Ettingshausen, Farnkr. 212; t. 146 fig. 23 (1865); Hieronymus, Hedwigia 47:209 (1908); Rosenstock, Fedde Rep. 11:60 (1912); Hieronymus, Hedwigia 62:15 (1920); C. Christensen, Kgl. Sv. Vet.—Akad. Handl. Ser. 3, 16 (2): 46 (1937); not of Jenman, W. Ind. Gui. F. 74 (1899). **Fig. 55**

Type: Poeppig 1133 from Pampayaco, Perú, prob. destroyed in LZ; Isotype (?) in B!

Homotypic synonyms: *L. trapeziformis* Dryand. var. *β arcuata* (Kze.) Baker, Fl. Bras. I^2: 355 (1870), as to part of cited specimens only; t. 21 fig. 20, 21, t. 22 fig. 2.

L. lancea (L.) Bedd. var. *arcuata* (Kze.) Rosenstock, Hedwigia 46:80 (1906).

Heterotypic synonyms: *L. horizontalis* Hooker, Spec. Fil. I:214 (1844), pl. 62 B; Kunze, Bot. Zeit. 8:347 (1850); Kunze, Farrnkr. II:47 (1850); Seemann, Bot. Voy. Herald 239 (1854); Fée, Crypt. vasc. Brés. I:29 (1869); J. Smith, Hist. Fil. 268 (1875). Lectotype: Gardner 157 from Serra dos Orgãos, Rio de Janeiro, Brazil (K!).

Homotypic synonyms: *L. trapeziformis* Dryand. var. *horizontalis* (Hook.) Grisebach, Catal. Plant. Cub. 274 (1866).

L. lancea (L.) Bedd. var. *horizontalis* (Hook.) Losch, Mitt. Bot. Staatss. München 1:23 (1950).

L. dolabra Kunze, Farrnkr. 2:47 (1849); Bot. Zeit. 8:370 (1850). Type: Funck & Schlim 598 from the state of Carabobo, Venezuela, prob. destroyed in LZ; Isotypes in BM, G, M!

L. curvans Fée, Gen. Fil. 106 (1852), Crypt. vasc. Brés. I:30 (1869), II:20 (1872/73). Type: Galeotti 6489 from the state of Oaxaca, Mexico, (P!).

L. Galeottii Fée, Gen. Fil. 107 (1852). Type: Galeotti 6469 from the state of Oaxaca, Mexico (P!).

L. Kunzei Moritz in Ettingshausen, Farnkr. t. 147 fig. 7 (1869). Type: not indicated; a specimen with authentic annotation agreeing very well with Ettingshausen's plate should be regarded as type: Moritz 454 from Tovar, state of Mérida, Venezuela (B!).
Homotypic synonym: *L. trapeziformis* Dryand. f. *kunzei* (Moritz) Kümmerle, Mag. Bot. Lap. 13:37 (1914).

L. lancea (L.) Bedd. var. *angulata* Rosenstock, Fedde Rep. 22:6 (1925). Type: Brade 317 from Carillo, Costa Rica (S-PA!).

Misapplied names: *L. quadrangularis* auct. non Raddi; Mettenius, Ann. sci. nat. V, 2:217 (1864). *L. trapeziformis* auct. non Dryander; Christ in Pittier, Prim. Fl. Costar. 3:38 (1901); probably also of Rovirosa, Pteridogr. Mex. pl. IX (1909).

L. lancea (L.) Bedd. var. *montana* (Fée) Bonaparte of Losch, Mitt. Bot. Staatss. München 1:24 (1950); not *L. montana* Fée.

Petioles stramineous to pale brown; lamina bipinnate with conform terminal pinna or simply pinnate, herbaceous; pinnules very variable in shape, acute or truncate, 3-3½ × as long as wide, the upper ones gradually reduced; sori continuous; indusium narrow, subentire; spores trilete.

Rhizome creeping, often long and with numerous short branches, (1.5–)2–4 mm in diam.; scales lanceolate, acute-acuminate, up to 1 mm long and 0.2 mm wide, with up to 6 rows of cells at the base. *Petioles* rather remote to densely clustered, (7–)12–ca. 40 cm long, from half to twice as long as the lamina, mostly of approximately equal length, ¾–2 mm in diam. near the apex, often considerably stouter at the base, abaxially flattened below, broadly and shallowly grooved above, abaxially angular above, obtusely angular to subterete below, often sharply angular almost to the base, occasionally obtusely angular or subterete throughout. *Lamina* dark to medium green, paler on the dorsal side, ca. 10–45 cm long, with 1–3, occasionally up to 8 pinnae to a side and a conform terminal one when bipinnate. *Primary rachis* adaxially broadly and shallowly sulcate, abaxially sharply angular and often sulcate, less often subterete or terete. Axillary cushions mostly visible as slight swellings. *Pinnae* (if any) subopposite or alternate, mostly subsessile, the terminal distinctly stalked (up to 3 cm), forming a rather variable angle with the primary rachis but mostly ascending (ca. 30°), rather far apart, ca. 3–6 cm, ca. 10–35 cm long, (2.5–)3–7 cm wide, the terminal often largest, especially in paucijugate leaves, mostly widest just above the base, slightly narrowed at the base, from the widest point gradually, close to the apex more strongly narrowed. The same applies mutatis mutandis to simply pinnate laminae. Secondary rachises adaxially with a rather narrow groove, abaxially subterete at the base, from the level of the second or third pinnule angled, the angles not or hardly paler, not wing-like, the surface between them shallowly concave or flat; rachis of terminal

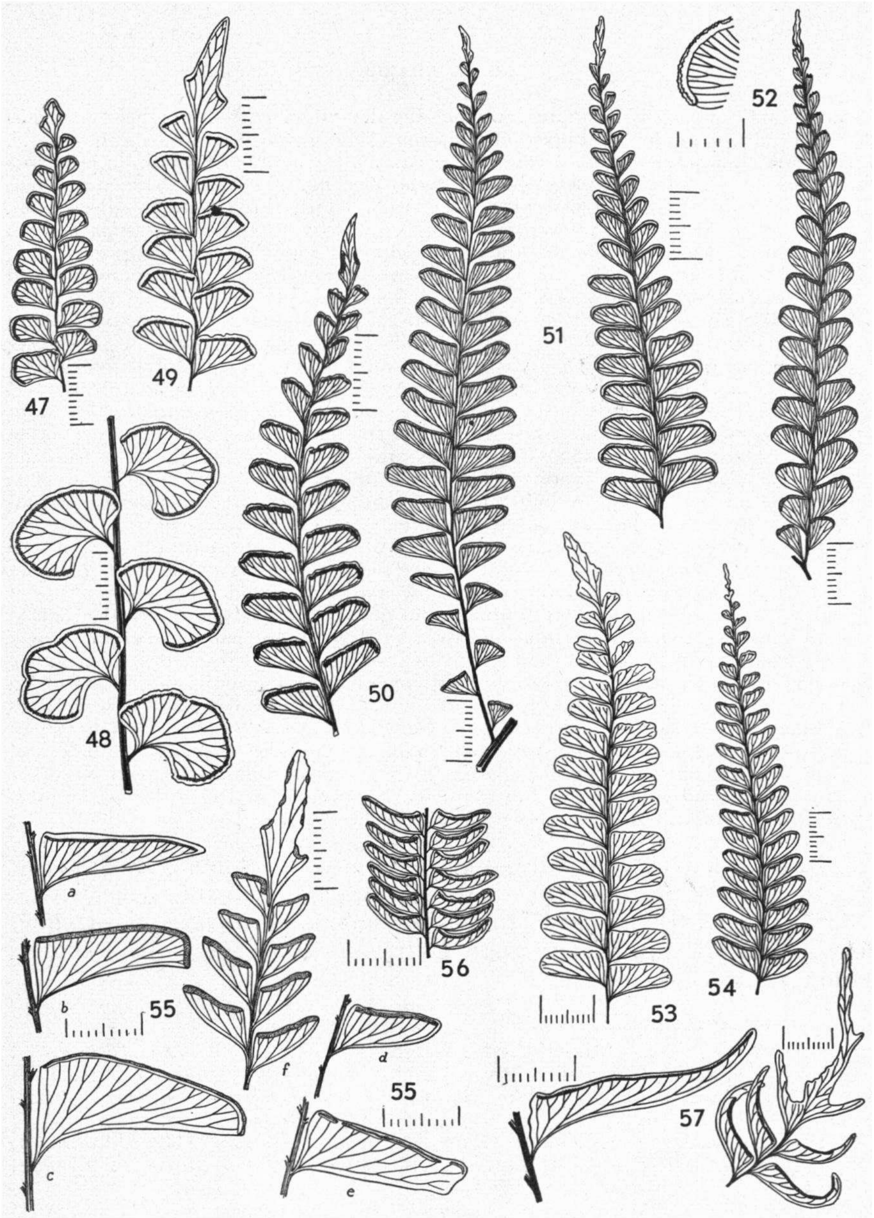


Fig. 47–48: *Lindsaea botrychioides;* fig. 47: apex of lamina; fig. 48: middle pinnules (Dusén 8334). Fig. 49: *L. quadrangularis* ssp. *terminalis;* apex of upper pinna (Mosén 3733). Fig. 50: *L. quadrangularis* ssp. *subalata;* apex of upper pinna (no coll.). Fig. 51: *L. quadrangularis* ssp. *quadrangularis;* middle pinna (left) and upper half of lower pinna (right) (Dusén 15298). Fig. 52: *L. pallida;* upper pinna and apex of pinnule (left) (Appun s.n., Glaziou 12356). Fig. 53–54: *L. quadrangularis* ssp. *antillensis;* fig. 53: apex of sterile terminal pinna (Eggers 647); fig. 54: apex of fertile terminal pinna (Booth s.n.). Fig. 55: *L. arcuata;* a–e pinnules of bipinnate leaves (a: Wallis s.n., b: Donnell Smith 6022, c: Moritz 454, d: Burchell 2457, e: Wright 976); f: apex of basal pinna (Donnell Smith 6022). Fig. 56: *L. spruceana;* basal portion of simply pinnate lamina (Spruce 4023). Fig. 57: *L. coarctata;* left: pinnule from middle pinna; right: apex of middle pinna (Schultes & Cabrera 15308). (Scales in mm).

pinna and of simply pinnate laminae angular or sulcate throughout. *Pinnules* 20–35(–50) to a side, the upper ones alternate, the lower ones mostly subopposite, subsessile, spreading or ± ascending, occasionally slightly deflexed, rather close but not contiguous, very variable in shape (see fig. 55), (12–)15–35 mm long, (4–)5–11 mm wide, of equal or almost equal width throughout or more often rather strongly narrowed towards the apex, and by this character separable in two forms: one with truncate, the other with ± acute, narrowed apex, which, however, are connected by numerous intermediates. Inner margin straight and then parallel, or often convex above and then touching or overlying the rachis, lower base cuneate, hardly stalk-like, upper base angular, rarely subauriculate, lower margin mostly shortly concave at the base, otherwise straight or shortly concave at the apex again (in truncate pinnules which are sometimes hamate at the apex) or there slightly convex, more strongly in pinnules with acute upturned apex (e.g. in the type-specimen, whence the name *arcuata*) upper margin straight or slightly convex throughout and parallel to the lower in truncate pinnules, often shortly convex or concave in acute ones; an outer margin only developed in truncate ones. The acute form is more common than the truncate one; the two are but rarely found together on a single leaf. Marginal thickening stramineous, inconspicuous, except at the base of the lower margin. Upper/outer margin entire or minutely erose in fertile pinnules, shallowly sinuate-crenate in sterile ones which are very rare. Veins immersed, mostly twice forked, lax, their ends ca. 1–1½ mm apart; main vein hardly connected with the marginal strand, ca. ½ mm above it near the apex. Upper pinnules gradually but not very strongly reduced, the highest ca. 5 mm long, one or two connected by a wing with the terminal segment which is lanceolate, cuneate at the base, with two unequal basal teeth or lobes, obtuse or subacute at the apex, ca. 1–2 mm long; sometimes the upper pinnules are much more gradually reduced, several denticuliform ones passing into a sometimes caudate terminal segment (especially in Central American, Cuban, and Brazilian specimens). *Sori* along the upper/outer margin; indusium greenish or pale, ca. 0.2 mm wide, not reaching the margin by a distance equal to its own width or less, reflexed and conceiled at full maturity. Sporangia ca. 160 × 115 μ; annulus with 10–13 indurated cells; spores very pale brown, ca. 22–27 μ.

Distribution: Cuba, Hispaniola, Mexico to Bolivia, and southeastern Brazil (erroneously reported from Grenada by Baker, Ann. Bot. 6:97, 1892) (map. 21) In forests, sometimes in clearings or along streams, from ca. 1000 to 2000 m (rarely lower, near the southern limit of its range).

Representative specimens:

CUBA. ORIENTE: Near Monte Verde, Wright 976 in part (B, BM, BR, F, G, GH, GOET, K, L. NY, PH, S-PA, UC, US); Pinales de Monte Verde to Falls of Río Palenque, Shafer 8861 (NY); Santa Ana, north of Jagüey, Yateras, Maxon 4180 (NY, S-PA, US).

HISPANIOLA. HAÏTI: Massif de la Hotte, w. group, Torbac, Morne Formond, Ekman H 7427 (C. Chr. in BM, K, S, US); ibid., Jérémie, Morne de l'Etang, Ekman H 10380 (B, C, K, S, US).

MEXICO. OAXACA: Without loc., Galeotti 6469 (P, HOLOTYPE of *L. Galeottii*); id., Galeotti 6489 (P, HOLOTYPE of *L. curvans*).

GUATEMALA: Near Finca Sepacuite, Alta Verapaz, Cook & Griggs 857 (US); Pansamalá, ibid., von Türckheim s.n. (Donnell Smith-exs. 830) (B, GH, K, NY, UC, US).

COSTA RICA: Cartago, Cooper s.n. (Donnell Smith-exs. 6023) (B, G, GH, K, M, NY, US); Estrella, Cooper s.n. (Donnell Smith-exs. 6022) (B, F, G, GH, K, MO, NY, US); s. of Cartago, along Pan-American Highwav, Chrysler 5456 (MO, UC); Finca Navarro, Maxon 645 (NY, US); Navarrito, Lankester 751 (S-PA, US).

PANAMÁ: Mt. Pirri, prov. Panamá, Goldman s.n. (US).

COLOMBIA. EL VALLE: La Cumbre, Killip 5914 (GH, NY, US); Monte Frío, Yamacones, Killip & García 33709 (US).

CAUCA: La Gallera, Micay Valley, Killip 7778 (PH, US); w. slopes of Cali-Cordillera, Lehmann 3003 (BM, G).

NORTE DE SANTANDER: Salazar, Engel s.n. (LE).

SANTANDER: Ocaña, Schlim 606 (BR, G, FI, K, L). Las Cruces, Kalbreyer 938 (B, K); Mesa de los Santos, Eastern Cordillera, Killip & A. C. Smith 15129 (NY, US).

ANTIOQUIA: Cineguetas, Kalbreyer 1872 (B, K).

HUILA: E.s.e. of Garzón, Fosberg 19899 (US).

META: W. of Villavicencio, between R. Manzanares and Quebrada Playón, Grant 10101 (US).

VENEZUELA. MÉRIDA: Near Tovar, Moritz 454 (B, HOLOTYPE of *L. Kunzei*; Isotypes in BM, GH, L, UPS).

CARABOBO: Without loc., Funck & Schlim 598 (BM, G, M, Isotypes of *L. dolabra*).

ECUADOR: Without exact loc., e. part of the country, Gardini 78 (Pic.-Ser.).

PERÚ. JUNÍN: Pichis Trail, Yapas, Killip & A. C. Smith 25522 (F, NY, US).

LORETO: Tierra Doble on R. Nanay, Ll. Williams 1071 (F, US).

Dept.?: Pampayaco, Kanehira 177 (GH, US).

BOLIVIA. LA PAZ: Hacienda Simaco above road to Tipuani, Buchtien 5116 (GH, S-PA, UC, US); San Carlos near Mapiri, Buchtien 1098 (S-PA, US); Hacienda Casana, Tipuani-Valley, Buchtien 7028 (G, GH, NY, S-PA).

BRAZIL. MINAS GERAIS: Capão Redondo near Lagoa Santa, Warming 59 (C); Ouro Preto, Morro São Sebastião, Damazio s.n. (RB); without loc., de Moura s.n. (B).

RIO DE JANEIRO: Upper Macahé, Mendonça 414 (B); Serra d'Estrella, near Petropolis, von Lützelburg 13750 (M); ibid., Ohaus s.n. (US); Serra dos Orgãos, Gardner 157 (K, Lectotype of *L. horizontalis;* Isotypes in BM, FI, W); ibid., Burchell 2457 (B, K); Theresopolis, Frazão 2120 (US); ibid., Brade 9368 (NY).

SÃO PAULO: Paranapiacaba, Brade 8412 (UC); Serra do Mar, Lüderwaldt 1426 (S-PA); Alto da Serra, Hoehne 1224 (BM); ibid., L. B. Smith 1965 (GH).

SANTA CATARINA: Piraí, Schmalz s.n. (US); Serra do Quiririm, Schmalz 83b (S-PA).

In spite of the very variably shape, *L. arcuata* can be recognized by the great relative length of the pinnules, a character shared with *L. spruceana* which is perhaps not distinct (see there). Otherwise the closest relative of *L. arcuata* is *L. quadrangularis*. Certain Central American specimens of *L. arcuata* are very close to *L. qu.* ssp. *subalata*, from which they can be distinguished by more elongate pinnules and paler axes, and to ssp. *antillensis*, which has relatively shorter, more rounded pinnules. A few specimens are, however, more or less intermediate between the two species.

Some specimens, notably from Central and northern South America have pinnules with a more or less protracted apex that points obliquely upwards, not unlike those of *L. herminieri*. One of these specimens has been described as *L. lancea* var. *angulata* Rosenstock. Examples of this form are Killip & Garcia 35627 (US) from Buenaventura, El Valle, Colombia, Brade 317 (S-PA, HOLOTYPE of *L. lancea* var. *angulata*, Isotype in NY) from Carillo, Costa Rica, Kalbreyer 1872 (B) from Cineguetas, Antioquia, Colombia, Buchtien 44 (S-PA) from Mapiri, Bolivia, and, the most extreme specimens, with caudate apices up to 3½ cm long, Killip 5276 (NY, PH, US) from Cordoba, El Valle, Colombia. Two specimens from Suriname, where *L. arcuata* has never been found, are referred with misgivings to this form: B.W. 321 and 599 (U) from Brownsberg; they have been included by POSTHUMUS (1928) in *L. herminieri;* the reasons for excluding them from that species have been explained there. Extreme specimens of the caudate form can be distinguished from *L. taeniata* by closer pinnules and by the sterile outer margin (lower margin of the apex), which is soriferous in that species. They are not distinguished here as a separate form, because they gradually pass into the normal form of *L. arcuata* through a series of intermediates, and caudate and non-caudate pinnules are often found together on one leaf.

17. **Lindsaea spruceana** Mettenius ex Kuhn, Linnaea 36:79 (1869); Hooker & Baker, Syn. Fil. 2nd ed. 108 (1874); Kuhn, Chaetopt. 26 (1882); Christ. Farnkr. d. E. 293 (1897); Diels. N. Pfl. I^4:221 (1902). **Fig. 56**

Type: Spruce 4023 from Mt. Guayrapurima near Tarapoto, San Martín, Perú (B!).

Homotypic synonym: *L. tarapotensis* (lapsu: *tarapotense*) C. Christensen, Ind. Fil. 398 (1906).

Similar to the preceding species, but pinnules small, not over 9 mm long and 2.5 mm wide, obtuse.

Rhizome short-creeping, ca. 1 mm in diam.; scales small, yellowish-brown, lanceolate, acuminate, up to 0.7 mm long, 0.15 mm wide, with up to 4 rows of cells at the base. *Petioles* rather close, 2–9 cm long, from ⅕ the length of to about as long as the lamina, ca. 0.5 (0.4–0.6) mm in diam. near the apex, stramineous or pale reddish-brown, rather shining, especially at the dark base, quadrangular (at the apex sharply, otherwise obtusely), or the adaxial side angular at the apex only, for the rest, as the abaxial side, terete or subterete. *Lamina* once or twice pinnate, thinly herbaceous, medium green, 8–16 cm long, when bipinnate with 1–4 pinnae to a side and a conform terminal one. *Primary rachis* of bipinnate leaves adaxially flattened or shallowly sulcate and angular, abaxially terete. Axillary cushions not seen. Pinnae subopposite, ascending under an angle of ca. 40°, subsessile or the terminal shortly stalked (up to 5 mm), ca. ¾–1 cm apart, ca. 6–7 cm long, 7–18 mm wide, the terminal mostly longest, widest just above the base, gradually narrowed in the upper half or two-thirds, slightly narrowed at the base. Secondary rachises adaxially flattened and angular or sulcate, abaxially similar but with a terete basal portion of up to 1 cm; rachis of simply pinnate leaves similar but not terete at the base. *Pinnules* ca. 25–60 to a side, subopposite or alternate, close but hardly or not contiguous, short-stalked (up to 1 mm), spreading, but because of the convex lower margin seemingly ascending, the largest 5–9 mm long, 2–2.5 mm wide, mostly 3–3½ × as long as wide, lanceolate, almost crescent-shaped, a few lower ones usually somewhat shortened and deflexed, a strongly reduced axillary pinnule present in bipinnate leaves. Inner margin slightly convex, parallel to the rachis or divergent, lower base cuneate, in the larger pinnules stalk-like, upper base angular or subauriculate, lower margin evenly convex, upper margin concave, usually somewhat constricted near the middle, subentire or often erose-repand, not rarely somewhat undulate-crispate, apex very obtuse, pointing obliquely upwards. Marginal thickening very inconspicuous except at the base of the lower margin. Veins immersed, obscure, rather irregular, simple or the basal ones once, rarely twice, forked, ½–1 mm apart at the margin, the main vein ca. 0.2 mm above the lower margin. Upper pinnules gradually and strongly reduced, confluent (4–10 connected by a wing), the uppermost ca. 2 mm long, terminal segment lanceolate-linear, lobed-repand, obtuse, sterile or soriferous in the basal lobes, 5–15 mm long. *Sori* continuous along the upper margin, often not quite reaching the apex; indusium pale, greyish or brownish, subentire, 0.15–0.25 mm wide, not reaching the margin by a distance of 0.10–0.15 mm, reflexed or not at full maturity. Sporangia ca. 145 × 100 μ; annulus with 9–14 indurated cells; spores trilete, very pale brown, ca. 24 μ.

Distribution: Only known from the type-collection. No ecological data extant.

PERÚ. SAN MARTÍN: Mt. Guayrapurima near Tarapoto, Spruce 4023 (B, HOLOTYPE; Isotypes in BM, BR, C. Chr. in BM, F, G, K, LE, W).

It is doubtful whether this is more than a very small, perhaps depauperate, form of *L. arcuata.* There are a few small specimens of that species, e.g. Stübel 904 from Ecuador (B) and Lehmann XXXIII from Colombia (B), which approach it rather closely.

Christensen re-named *L. spruceana* because its name was supposed to be a homonym of *L. sprucei* Hooker (which is *L. meifolia*); but Art. 75 (examples) of the Code of Nomenclature states explicitly that such names are not be regarded as homonyms, and Christensen's name is therefore superfluous.

18. **Lindsaea coarctata** Kramer, spec. nov. **Fig. 57**

Folia bipinnata, petiolo stramineo vel rubro-fusco, facie adaxiali angulari, plerumque etiam canaliculata, abaxiali superne adaxiali simili, inferne subtereti vel tereti; lamina herbacea, atrovirens; pinnulis anguste lanceolatis, longitudine latitudinem quinquies vel ultra sexies superante; soris continuis, indusio angustissimo, integro, marginem non attingente; sporis tetraedriformibus.

Typus: Schultes & Cabrera 15308 from Rio Pacoa, Vaupés, Colombia (US).

Rhizome creeping, ca. 2–3 mm in diam.; scales narrowly lanceolate, long-acuminate, up to 2.2 mm long and 0.4 mm wide, with up to 10 rows of cells at the base. *Petioles* close, ca. 15–45 cm long, about as long as to 1½ × as long as the lamina, 1–2 mm in diam. near the apex, dull or ± shining, adaxially with stramineous, in the upper part more or less wing-like angles. *Lamina* ca. 15–30 cm long, dark to blackish green on the ventral, paler on the dorsal surface, with 1–3 pinnae to a side and a conform terminal one. *Primary rachis* stramineous to reddish brown, the angles, especially on the abaxial side, pale, wing-like; axillary cushions visible as faint swellings or obsolete. *Pinnae* subopposite or alternate, or the terminal short-stalked (–1.5 cm), subsessile, spreading under an angle of 45–60°, ca. 15–20 cm long, 4–8 cm wide, suddenly narrowed at the base and at the apex. Secondary rachises abaxially terete at the base, from the level of about the second pinnule sulcate, the groove starting rather suddenly, adaxially shallowly grooved, the margins hardly wing-like. *Pinnules* ca. 15–25 to a side, alternate or the lower ones subopposite, subsessile, spreading or slightly deflexed, as far apart as they are wide or subcontiguous at their bases, 2–5 cm long, 4–8 mm wide, a few lower ones shortened, a cuneate-flabellate axillary pinnule present. Inner margin of pinnules straight, divergent, upper base slightly auricled or angular, the greatest width of the pinnules there, the outer part gradually narrowed, lower base shortly cuneate, lower margin concave throughout or convex towards the apex, upper margin convex, or concave at the apex, the pinnules then gracefully S-shaped; apex blunt or mostly long acuminate and acute, pointing outwards, obliquely downwards or—in the upper pinnules—upwards; no separate outer margin present. All margins entire in fertile pinnules, the upper margin sometimes indistinctly crispate, in sterile pinnules shallowly but distinctly (up to ½ mm) sinuate or crenate; marginal strand stramineous, inconspicuous. Veins immersed or slightly raised at their bases, the basal ones twice, the outer ones once forked, very oblique, the ends ca. 1 mm apart; main vein intramarginal, about ½ mm above the lower margin near the apex. A few upper pinnules suddenly shortened, ca. ½–1 cm long; terminal segment mostly connected by a narrow wing with the uppermost lateral pinnule, hastate, sometimes caudate at apex, 1–4 cm long, with two or rarely more large unequal basal lobes, the rest sinuate to the blunt apex, often more strongly on one side and then distinctly asymmetrical, sterile or with short sori at the base. *Sori* along the upper margin, sometimes not reaching the apex; indusium greyish- or brownish-green, 0.1–0.2 mm wide, not reaching the margin by a distance equal to once or twice its width, reflexed and conceiled at full maturity. Sporangia ca. 142 × 95 μ; annulus with 8–11 indurated cells; spores very pale brownish, ca. 18–21 μ.

Distribution: Western Guayana and south-eastern Brazil; one of the few species with a strongly discontinuous area (map 23). Reported to be terrestrial, prob. in forest, at 300 m; hardly any ecological data extant.

COLOMBIA. VAUPÉS: Río Pacoa, R. Apaporis-trib., 0°20′ N., 71°20′ W., Schultes & Cabrera 15308 (US, HOLOTYPE); R. Piraparaná, R. Apaporis-trib., headwaters of Caño Tumuña, Schultes & Cabrera 17371 (US).

BRAZIL. AMAZONAS: Panuré, R. Uaupés, Spruce 2673 (K; fragm. in B).

RIO DE JANEIRO: Corcovado, Serra d'Estrella, Martius s.n. (M; also bearing the loc. "Japura").

SÃO PAULO: Mt. Arassojava, Martius s.n. (M). Without exact loc., "prov. Paraënsis et Rio Negro, variis locis", Martius s.n. (M; atypical, appr. *L. surinamensis*)

The name *L. coractata* was published by Kunze (Bot. Zeit. 8:326, 1850) for one of the Brazilian specimens, but with hardly any description, and must be considered as a *nomen nudum.*

A remarkable species, most closely related to *L. surinamensis* (where see for the differences), also to *L. arcuata*, which has less elongate and less acuminate pinnules, a different terminal segment, and is not rarely simply pinnate. *L. hemiglossa* is perhaps a more distant relative.

19. **Lindsaea surinamensis** Posthumus, Rec. trav. bot. néerl. 23:401 (1927), fig. 1; Fl. Surin. Suppl. 72 (1928); Alston, Kew Bull. 1932:311. **Fig. 58**

Type: Boschwezen (B.W.; Stahel & Gonggrijp) 641 from Brownsberg, Suriname (U!).

Misapplied names: *L. trapeziformis* of Baker, Fl. Bras. I^2:355 (1870), p.p. min., excl. synon.

L. arcuata auct. non Kunze; Jenman, W. Ind. Gui. F. 74 (1899).

Petioles pale to reddish brown, abaxially terete below, angular above; lamina usually simply pinnate, herbaceous; pinnules lanceolate, ca. 5 × as long as wide, acuminate, the apex obtuse or subacute; upper pinnules somewhat reduced; sori continuous; spores trilete.

Rhizome creeping, 1–2 mm in diam.; scales narrowly lanceolate, very dark brown, up to almost 1 mm long and 0.2 mm wide, with 4–5 rows of cells at the base. *Petioles* close, subdistichous, 5–10 (–20) cm long about half as long as the lamina, ½–¾ mm in diam. at the apex, rather dull, adaxially flattened and bordered by paler margins almost throughout, abaxially angular above, the angles of both sides more or less wing-like. *Lamina* simply pinnate (very rarely bipinnate, with one pair of primary pinnae ca. 12 cm long), 11–20 cm long, 3–5 cm wide, pale to medium green. *Primary rachis* similar to the upper part of the petiole, surfaces flat to channelled (sec. rachises similar, abaxially terete at the extreme base). *Pinnules* 11–21 to a side, slightly falcate, subopposite to alternate, spreading, sessile, 1.5–2.5 cm long, 3.5–5 mm wide, widest at base, thence gradually narrowed to the acute or shortly acuminate apex. Inner margin straight, divergent, meeting the upper margin under an open angle, or the upper base shortly rounded, upper margin rather evenly and feebly convex, or straight to shallowly concave at base, lower margin shallowly concave, no outer margin developed. Margins entire, or in sterile pinnules with a few shallow crenations towards the apex, inconspicuously thickened. Veins slightly elevated on the dorsal surface, at least near the base, otherwise immersed, once or twice forked, not close, ca. 1 mm apart at the margin; main vein ca. 0.4 mm above the margin. Upper pinnules not strongly reduced, ca. ½–1 cm long, mostly one of them connected by a narrow wing with the terminal segment, which is subsessile, 2.5–5 cm long, ca. 1.5 cm wide, lanceolate, with two short unequal basal lobes, the apex caudate, obtuse, with a median almost percurrent main vein, often soriferous at the sides. *Sori* along the upper margin; indusium 0.2–0.3 mm wide, pale greenish-brown, rather rigid, entire or slightly sinuous, ca. ⅔ cm from the margin, bulging to reflexed at full maturity. Sporangia 140–148 × 100–110 μ; annulus with 9–11, mostly 10, indurated cells; spores pale brownish-yellow, 25–28 μ, 32?

Distribution: Northern South America (map 20). Terrestrial in forests and clearings, from sea-level to ca. 300 m.

Colombia. Amazonas–Vaupés: Sorotama, Río Apaporis above mouth of R. Kananarí, Schultes & Cabrera 15972 in part (US).
British Guiana: Moraballi Creek near Bartica, Richards 154 (BM, K); Pacatout below the Kaieteur, Jenman 1384 (K); ibid., Im Thurn s.n. (K); without loc., Appun 729 (K, partly bipinnate); Rawson W. Rawson 3310 (BM).
Suriname: Brownsberg, in forest, Boschwezen (B.W.; Stahel & Gonggrijp) 641 (U, Holotype; fragm. in US).
French Guiana: without loc., Leprieur 159 in part (P, fragm.); Leprieur s.n. (B).

Posthumus compared this species with *L. lancea* var. *falcata* (*L. falcata*), the shape of the pinnules is, however, more like var. *leprieurii*. It is not likely that *L. lancea* is at all closely allied. The closest relative seems to be *L. coarctata*, which differs by always bipinnate leaves and by more acuminate and more strongly curved pinnules. *L. dubia* is probably also allied.

20. **Lindsaea dubia** Sprengel, Syst. Veget. IV:79 (1827); Presl, Tent. Pterid. 131 (1836); Kunze, Anal. 38 (1837), pl. 26; Klotzsch, Linnaea 18:544 (1844); Hooker, Spec. Fil. I:209 (1844), pl. 64 C; Kunze, Linnaea 21:226 (1848); Bot. Zeit. 8:326 (1850); Hooker & Baker, Syn. Fil. 1st ed. (1868), 2nd ed. (1874) 105; J. Smith, Hist. Fil, 268 (1875); Kuhn, Chaetopt. 26 (1882); Jenman, W. Ind. Gui. F. 73 (1899); Wright, Trans. Linn. Soc. Bot. II (6): 80 (1901); Diels, N. Pfl. I^{4}:220 (1902), fig. 119 D, E; Bonaparte, Notes Ptérid. VII:374 (1918); Knuth, Fedde Rep. Beih. 43 (1):31 (1926); Posthumus, Fl. Surin. Suppl. 70 (1928); C. Christensen, Dansk Bot. Ark. 6 (3):97 (1929); Sampaio, Arch. Mus. Nac. Rio de Jan. 32:34 (1930); Alston, Kew Bull. 1932:311; Posthumus, Rec. trav. bot. néerl. 31:469 (1934); Maxon & Morton in Maguire, Bull. Torr. Bot. Cl. 75:73 (1948). **Fig. 61**

Type: Richard s.n., locality unknown (prob. P, not seen; Isotype in C!).

Homotypic synonym: *L. tenera* Kaulfuss, Enum. 219 (1824), non Dryander, 1797.

Prob. homotypic synonym: *Wibelia pectinalis* Fée, Gen. Fil. 331 (1852) (*L. dubia* cited as synonym).

Petioles olivaceous to reddish brown, for the greater part quadrangular; lamina simply pinnate, herbaceous to chartaceous; pinnules linear, 10– over 20 × as long as wide, the outer part of the upper margin in fertile pinnules mostly crenate, in sterile ones crenate throughout; upper pinnules somewhat reduced; terminal segment usually asymmetrical; sori continuous or at the apex mostly strongly interrupted; spores trilete.

Rhizome short-creeping, ca. $^3/_4$–1 mm in diam.; scales narrowly lanceolate, long-acuminate, up to 1 mm long, 0.15 mm wide, with up to 5 rows of cells at the base. *Petioles* close, 3.5–14 cm long, about half as long to as long as the lamina, 0.5–0.7 mm in diam. near the apex, mostly dull, the upper part quadrangular with paler angles and flat or shallowly concave surfaces, the angles gradually evanescing downwards, those of the abaxial side in the lower third or fourth, the adaxial ones just above the base. *Lamina* ovate-lanceolate, 7–17(–25) cm long, 4–8 cm wide, dull, dark bluish-green on the ventral, paler on the dorsal surface, of almost equal width throughout, shortly narrowed at the apex, sometimes also at the base when the lower pinnules are deflexed, with 8–40, mostly 12–25 pinnules to a side. *Rachis* similar to the upper part of the petiole. *Pinnules* opposite or subopposite, the upper ones mostly alternate, spreading or the lower ones deflexed, sometimes upcurved in the outer part, 3–5 mm apart or the basal ones more remote, 15–40 mm long, 1–2 mm wide, windest just above the long-cuneate, not rarely somewhat stalk-like base, thence gradually tapering to the obtuse apex, sometimes slightly decurved at the base. Lower margin entire, upper margin in fertile pinnules entire at the base, the outer part crenate, with acute incisions 0.3–0.5 mm deep, the teeth between them rounded, oblique uninerval; in sterile pinnules the whole upper margin with such incisions. Rarely, small fertile pinnules are quite entire. In large, wide pinnules with upcurved apex there is sometimes a separate outer margin at the lower side of the appical part of the pinnule, often with a few teeth, and a more or less median main vein. Inner margin obliquely divergent, meeting the upper margin under an open angle. Marginal thickening very weak, not discoloured. Veins, especially the distinctly intramarginal main vein (0.3–0.4 mm from the lower edge) somewhat elevated near their bases, otherwise immersed, lateral veins very oblique, lax, springing from the main vein at intervals of 2–3 mm, simple, or the basal ones mostly forked just below the receptacle. One to four upper pinnules somewhat shortened, in addition mostly one or two at a side strongly upcurved and connected by a wing with the terminal segment, which is usually curved to the side of the uppermost confluent lateral pinnule, on the convex side entire or crenate at the base only, on the concave side crenate throughout, in size comparable to the lateral pinnules or a little shorter, sterile, or soriferous in a few of the basal teeth. Aberrant forms are not very rare, e.g. symmetrical terminal segments, or two, facing each other with the convex entire side. *Sori* continuous in the basal part of the upper margin, occupying 3–6 (or, as they are mostly forked below the receptacle 6–12) veins, short and uninerval in the lobes of the outer part, the outermost lobes mostly sterile, rarely the whole upper margin occupied by one continuous sorus; receptacle of uninerval sori considerably longer than the width of a vein-end, ca. 1–2 mm long. Indusium attached at the base only, 0.2 mm wide, entire, almost reaching the margin, somewhat reflexed at full maturity. Sporangia ca. 135 × 115 μ; annulus with 9–13 indurated cells; spores pale brownish-yellow, ca. 22–27 μ.

Distribution: Northern South America (map 19). In forests, terrestrial, on clay banks, and in crevices of rocks, sometimes in clearings of ravines, once reported as epiphytic on a palm (*Attalea*), from sea-level to ca. 1000 m. According to Jenman common in forests near river-banks in Br. Guiana.

COLOMBIA. VAUPÉS: Cerro de Circasia, Cuatrecasas 7189 (GH, US).

AMAZONAS–VAUPÉS: Sorotama, Río Apaporis, Schultes & Cabrera 15972 in part (US), 15975 (US); R. Apaporis, between R. Pacoa and R. Kananarí, Schultes & Cabrera 13002 (US).

SANTANDER: Magdalena valley, near Barranca Bermeja, Haught 1369 (GH, UC, US; atypical, with short, strongly upcurved pinnules, sori mostly quite continuous, also on the outer margin).

VENEZUELA. AMAZONAS: Capihuara, Upper Casiquiare, on palm trunks, Ll. Williams 15818 (US); w. foothills of Serra Imeri, near Salto de Huá, Holt & Blake 491 (NY, US).

BOLÍVAR: Rapids of Río Apácara, w. side of Apácara-tepuí, Chimantá-Massif, Steyermark 74684 (US); ibid., n.-w. part of Abácapa-tepuí, Steyermark 74827 (US); Mt. Roraima, Venezuelan side, Schomburgk s.n. (K).

BRAZIL. AMAZONAS: Near Panuré, Rio Uaupés, Spruce 2599 (B, BM, C, F, G, GH, GOET, K, L, LE, US, W); Rio Uaupés, Taracuá, Igarapé da Chuva, Schultes & Pires 9068 (US); Taracuá, Roman 13 (C. Chr. in BM, S–PA).
BRITISH GUIANA: Moraballi Creek near Bartica, Essequibo R., Sandwith 114 (K); ibid., Richards 148 (BM, K); Mazaruni R., McConnell & Quelch 593 (K); ibid., Appun s.n. (K); Appun 57 (B, W); ibid., Kurupung, Lang 310 (NY); Amutu, Potaro R., Im Thurn s.n. (K); Pacatout, below the Kaieteur, Jenman 1383 (K); Yamakuri, Berbice-Rupununi Cattle Trail, Abraham 225 (NY, US); Macouria Creek, Jenman 2273 (BM, US), s.n. (NY, very large form); Mt. Roraima, Schomburgk 47 in part (B, BM, US); without loc., Lobscheid s.n. (W); Schomburgk 145 (BM, K), 256 (B, BM, K), 1134 (B).
SURINAME: Brownsberg, Boschwezen 3194 (U); ibid., Stahel & Gonggrijp 327 (U, US); Nassau Mts., Lanjouw & Lindeman 2224 (U); Upper Wayombo R., Gonggrijp & Stahel 1095 (Pic.-Ser., U); Suriname R. near Morningstar Creek, Went 509 (U); Wilhelmina Mts., Stahel 484 (U); Saramacca R. headwaters, Maguire 24136 (A, NY, U, US); Tafelberg, Maguire 24345a (NY, U, US); ibid., East Ridge Creek, Maguire 24531 (A, F, K, NY, U, US).
FRENCH GUIANA: "Cayenne", Rawson W. Rawson 2309 (BM); Mt. Oyor, Leprieur 38 (B, C, C. Chr. in BM, GH, K, LE, P, US); 158 (FI, G); s.n. (F); Acarouany, Sagot 949 (B, BM, G, GH, GOET, K, NY, U, W); ibid., Kappler 1757 (B, G, GOET, L, MO, W); Conana & Inini, Richard s.n. (P, perhaps Isotype); without loc., Jelski 33 (LE); Leprieur s.n. (K); Poiteau s.n. (K); Perrottet s.n. (G).

Without any loc., Richard s.n. (French Guiana?) (C, Isotype).

A very clear-cut and outstanding species, unlike any other neotropical species. The linear pinnules, with the upper margin entire at the base, with continuous sori, crenate towards the apex, with short interrupted sori, are very characteristic. The only species somewhat comparable to *L. dubia* known to the author is *L. sinuato-crenata* v.A.v.R. from New Guinea, which, however, belongs to a quite different group, having a downwards gradually reduced lamina and somewhat anastomosing veins.

21. **Lindsaea herminieri** Fée, 11ᵉ mém. 15 (1886), t. 6 fig. 1 (as *L'Herminieri*); Duss, Fl. Crypt. Ant. franç. 59 (1904); Domin, Pterid. Domin. 245 (1929); Stehlé, Caribb. For. 4 (2):92 (1943); not of Posthumus, Fl. Surin. Suppl. 73 (1928). **Fig. 59, 60**

Type: L'Herminier s.n. from Guadeloupe (P!).
Homotypic synonym: *L. trapeziformis* Dryand. var. *L'Herminieri* (Fée) Kuhn ex Krug apud Urban, Engl. Bot. Jb. 24:91 (1897).

Petioles stramineous, quadrangular; lamina bipinnate with conform terminal pinna, rarely simply pinnate, thinly herbaceous; pinnules ± rhombic, with a more or less protracted apex, 2½–3½ × as long as wide, the upper ones hardly or not reduced; terminal segment slightly connected or free; sori continuous but often interrupted at the protracted apex; spores trilete.

Rhizome creeping, 2–2.5 mm in diam.; scales lanceolate, long-acuminate, up to 1.2 mm long, 0.2 mm wide, with up to 5 rows of cells at the base. *Petioles* rather close to close, 20–27 cm long (in simply pinnate leaves ca. 10–20), about as long as the lamina, 1–1.3 mm in diam. near the apex, rather dull, adaxially for the greater part sulcate, abaxially mostly sulcate above. *Lamina* rather pale yellowish-green, especially on the dorsal side, 18–40 (in simply pinnate leaves 14–20) cm long, when bipinnate with 1–3 pinnae to a side and a conform terminal one. *Primary rachis* similar to the upper part of the petiole. Axillary cushions visible as indistinct swellings or obsolete. *Pinnae* subopposite or alternate, 2.5–6(–9) cm apart, laxly spreading under an angle of ca. 60°, short-stalked or mostly sessile, the terminal with a stalk of up to 3 cm, 10–25 cm long, 2.5–5(–7) cm wide, hardly or not narrowed at the base, very slightly narrowed above, abruptly narrowed in the terminal segment. *Secondary rachises* adaxially narrowly and deeply sulcate, abaxially terete at the extreme base, from the level of the first to third pinnule angular, the angles mostly sharp, not or hardly discoloured, not wing-like, the surface between them flattened or shallowly concave; rachis of terminal pinna and of simply pinnate leaves angular throughout. *Pinnules* ca. 10–30 to a side, alternate or the lower ones subopposite, laxly to strongly ascending, sessile, roughly rhombic, with a protracted apex which is rudimentary or up to 2 cm long, 20–35 mm long (measured along the lower margin), 7–12 mm wide. Inner margin straight, at least in the lower pinnules divergent from the rachis, upper base angular, lower base cuneate, not stalk-like, upper margin straight or mostly concave, the bottom of the concavity near the middle of the pinnule, occasionally lobed, lower margin straight or often shallowly concave, outer margin straight or somewhat concave, the protracted apex obtuse or subacute. Upper and outer margin shallowly to distinctly sinuate in fertile pinnules, shallowly to distinctly crenate in sterile ones (which are quite common); marginal thickening indistinct except along the lower margin. Veins immersed, the inner ones once or twice forked, the outer ones simple, their ends 1–1.5 mm apart; at least the outer ⅔ of the pinnule with a slightly flexuose diagonal main vein. Upper pinnules often with upcurved apices. Terminal segment connected with a very narrow wing with the uppermost pinnule or practically free, large, broadly lanceolate, hastate, with several narrow mostly acuminate lobes at the base, the central shank sinuate to crenate, often caudate, the base cuneate, with concave sides, 2.5–5 cm long, sterile or soriferous in the lower lobes. *Sori* along the upper and outer margin; indusium pale, yellowish, entire, ca. 0.2 mm wide, about equally far to twice as far from the margin, somewhat reflexed at full maturity. Sporangia ca. 145 × 120 μ; annulus with 10–12 indurated cells; spores very pale, ca. 23–30 μ, 16?

Distribution: Endemic in Guadeloupe. In forests, ca. 250–500 m.

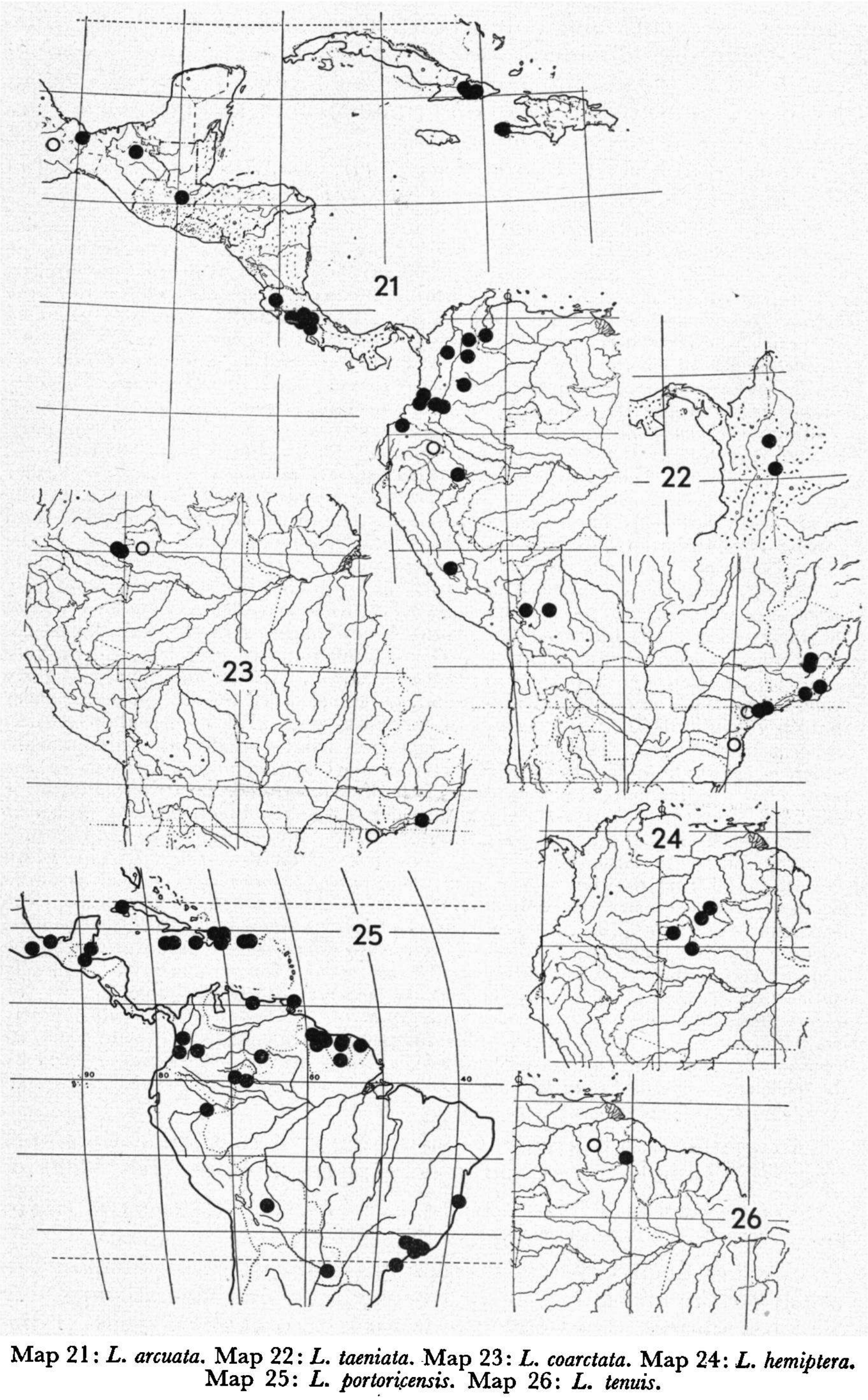
GUADELOUPE: L'Herminier 2 (B), 43 (B, G, K, W), s.n. (P, HOLOTYPE, 2 sh.; Isotypes in BM, C. Chr. in BM, F, G, L, NY); Duss 4237 (NY, US), s.n. (F, NY, US); Questel 2631 (US); Mazé 737 (K); Husnot 273 (BM).

In spite of the variable shape of the pinnules this is a very distinctive species, marked by ascending rhombic, ± caudate pinnules and large, almost free terminal segment. Posthumus included in this species two specimens from Suriname which have somewhat similar pinnules but differ in the non-divergent inner margins, spreading, less constantly caudate pinnules, and smaller, more highly connected terminal segment; they are referred with misgivings to the caudate form of *L. arcuata*. The closest relative of *L. herminieri* is probably *L. quadrangularis* ssp. *antillensis*.

Fée and most subsequent authors spelled the name "L'Herminieri", which stands for "Le Herminieri" and is contrary to Art. 23 of the Code. As it would not be a very desirable solution to hyphenate or unite the two words ("le-herminieri" or "l-herminieri" or "lehermininieri" or "lherminieri"), the name is spelled here "herminieri" (a spelling already adopted by Duss, l.c.), although this change affects the first letter. This spelling is in agreeance with such names as *Elaphoglossum herminieri* and the genus *Herminiera* (= *Aeschynomene*, *Papilionaceae*).

22. **Lindsaea taeniata** Kramer, spec. nov. **Fig. 62**

Folia bipinnata, petiolo stramineo vel pallide fusco, facie abaxiali obscure angulari vel subtereti; lamina herbacea, laetevirens, pinnulis



Map 21: *L. arcuata.* Map 22: *L. taeniata.* Map 23: *L. coarctata.* Map 24: *L. hemiptera.* Map 25: *L. portoricensis.* Map 26: *L. tenuis.*

anguste lanceolatis, longitudine latitudinem 5 usque ad 7½ × superante, basi solo dimidiatis, medio at apice marginibus ambobus fertilibus, apice adscendente, obtuso vel aubacuto, vena mediali flexuosa munito; soris continuis, indusio integro, marginem non attingente; sporis tetraedriformibus.

Typus: Kalbreyer 1345 from Dos Quebradas, Antioquia, Colombia (B).

Rhizome (only small pieces seen) creeping, stout, ca. 3 mm in diam.; scales lanceolate, acuminate, up to more than 2 mm long, 0.4 mm wide, with up to 11 rows of cells at the base. *Petioles* up to 50 cm long, about as long as the lamina, 1–3 mm in diam. near the apex, ± shining, adaxially strongly channelled, the channel broad and almost flat towards the apex, abaxially obtusely angular to subterete (often crushed or incompletely collected in the few specimens extant). *Lamina* ca. 25–50 cm long, with 1–2 pinnae to a side and a conform terminal one. *Primary rachis* similar to the upper part of the petiole, abaxially sometimes shallowly sulcate in the upper part. Axillary cushions present as swellings, not discoloured, or obsolete. *Pinnae* subopposite, ascending under an angle of ca. 45°, 8–9 cm apart, stalked (the lateral 1–3.5 cm, the terminal up to 4.5 cm), ca. 17–40 cm long, (5–)9–10 cm wide, widest in the lower third, slightly narrowed at the base, rather abruptly narrowed in the upper third or fourth. Secondary rachises adaxially broadly and shallowly channelled, abaxially flattened-angular, the flattened portion passing into a channel towards the base which evanesces rather suddenly at the level of the first or second pinnule, the extreme base terete. *Pinnules* 20–30, mostly ca. 25, to a side, usually at least the lower ones subopposite, spreading or slightly ascending, sessile, separated by interstices equal to their width or half their width, the largest 3½–5 cm long, 6–7 mm wide. Inner margin straight, parallel to the sec. rachis or slightly divergent, lower base cuneate, not stalk-like, upper base ± rectangular, upper margin approximately straight in the basal part, slightly concave in the somewhat falcate-ascending apical part of the pinnule, lower margin straight or slightly concave in the basal part (1–1.5 cm), then passing under a more or less developed open angle into what is really the outer margin which is approximately straight. The greater part of the pinnule consists of the protracted apex which is soriferous at both sides, gradually narrowed, obtuse or subacute, sinuate when sterile. Marginal thickening very inconspicuous except at the extreme base of the lower margin, entire. Veins immersed, very oblique, once or twice forked, lax, their ends ca. 1 mm apart along the upper margin. Main vein diagonal from the base to the apex, flexuose in its outer part. Upper pinnules gradually reduced (strongly only in the upper third or fourth of the pinna), the uppermost ca. 4 mm long, a few connected by a very narrow wing with the terminal segment which is narrowly lanceolate, subhastate-lobed at the base, up to 3½ cm long, often caudate, obtuse, soriferous below, sterile and subentire to shallowly sinuate above. *Sori* along the upper and the greater part of the lower (really the outer) margin, absent from the extreme base of the lower margin and mostly from the outer part of the apex; indusium pale, delicate, 0.15–0.20 mm wide, its edge ca. 0.5 mm from the margin, bulging at full maturity, sometimes covered by the reflexed margin. Sporangia ca. 122 × 90 μ; annulus with 10–12 indurated cells; spores very pale, ca. 22 μ.

Distribution: Only known from the dept. of Antioquia, Colombia (map 22). In light forests and in open places in forest, 1000–2000 m.

COLOMBIA. ANTIOQUIA: Dos Quebradas, Kalbreyer 1345 (B, HOLOTYPE; Isotype in K); Amalfi, La Vivora, Kalbreyer 1650 in part (B).

A most distinctive species, outstanding by the very elongate pinnules which are dimidiate only at the extreme base and have a completely diagonal midrib. The tendency towards a protracted apex of the pinnule, found regularly in *L. herminieri*, sometimes in *L. arcuata*, and occasionally in other species, is developed here to an extreme degree;

the pinnules approach those of quite unrelated species usually segregated as *Schizoloma* whose diagnosis would include *L. taeniata.* Its closest relative is undoubtedly *L. arcuata*, the caudate form of which is very close to *L. taeniata* but differs in less elongate, closer pinnules and an always sterile non-dimidiate outer part.

23. **Lindsaea divaricata** Klotzsch, Linnaea 18:547 (1844); Kunze, Bot. Zeit. 8:349 (1850); Kuhn, Chaetopt. 26 (1882); Hieronymus, Hedwigia 62:15 (1920); not *L. divaricata* (Schlecht. & Cham.) Mett. ex Kuhn, Jo. Bot. 15:231 (1877), which is *Odontosoria schlechtendalii* (Presl) C. Chr. **Fig. 63**

Type: Schomburgk 368 from British Guiana (B!).

Heterotypic synonym: *L. trapeziformis* Dryand. var. *erythromera* Kunze, Linnaea 21:227 (1848). Type: Kegel 698 in part, from Oude Rijweg, Suriname (GOET)!.

Misapplied names: *L. trapeziformis* auct. non Dryand.; Baker, Fl. Bras. I^2:355 (1870), in part, excl. syn.; t. 21 fig. 17, prob. also fig. 16.

L. trapeziformis Dryand. var. *β arcuata* (non *L. arcuata* Kunze); Baker, Fl. Bras. I^2:355 (1870), p. p. min., excl. syn.

L. caudata auct. non Hooker; Jenman, W. Ind. Gui. F. 75 (1899)?

L. *quadrangularis* auct. non Raddi; Sampaio, Arch. Mus. Nac. Rio de Jan. 32:35 (1930).

Petioles castaneous to almost black, abaxially terete, adaxially above with pale membranous wings, similar wings on the adaxial side of the primary and on both sides of the secondary rachises; lamina bipinnate with conform terminal pinna, herbaceous: pinnules ca. 2½ × as long as wide, the upper ones reduced; terminal segment rather large, not distinct; sori continuous; indusium very narrow, entire or subentire; spores trilete.

Rhizome creeping, 2–2.5 mm in diam.; scales lanceolate, long-acuminate, up to 1.4 mm long, 0.2 mm wide, with up to 8 rows of cells at the base. *Petioles* close, ca. 10–60 cm long, from about as long as to (in very large leaves) almost twice as long as the lamina, 1–2.5 mm in diam. near the apex, stronger at the base, shining, adaxially near the apex with a flattened portion bordered by pale membranous wings which gradually evanesce downwards, the lower half or two-thirds of the petiole quite terete. *Lamina* dark green, often brownish or blackish, on the ventral side, paler on the dorsal side, with 2–7, mostly 3–5 pinnae to a side and a conform terminal one. *Primary rachis* castaneous to reddish brown, shining, ca. 1–1.5 mm in diam., abaxially terete, adaxially with two lateral spreading pale to brownish wings 0.2–0.3 mm wide. Axillary cushions present as distinct, often discoloured swellings. Pinnae alternate or the lower ones subopposite, laxly spreading under an angle of ca. 45–60°, ca. 2–5 cm apart, subsessile or with a short stalk up to 1.3 cm long, 7–30, mostly 12–25 cm long, the upper ones somewhat shortened, the terminal about the size of the basal, (1.5–)2–4 cm wide, widest ca. $^1/_3$ from the base, thence gradually but not strongly narrowed to the base, with one or mostly several shortened pinnules to a side, a strongly reduced axillary pinnule often present, not strongly narrowed upwards to near the apex, occasionally more gradually so. Secondary rachises adaxially with similar wings as the primary rachis (fig. 6), but these narrower, occasionally almost obsolete, abaxially with similar wings which arise above the base, at the level of the first or second pinnule, and evanesce gradually in the apical part; rarely, they are absent from the entire lower half. *Pinnules* 15–30, mostly about 25, to a side, close, subcontiguous to contiguous, occasionally somewhat overlapping (succubous), spreading or, especially the upper, somewhat ascending, never decurved, 10–20(–23) mm long, 4–8 mm wide, mostly alternate throughout, in shape intermediate between those of *L. lancea* and *L. quadrangularis*, or almost matching one of them. Inner margin ± straight, parallel or somewhat divergent from the sec. rachis, lower margin straight or somewhat concave, mostly convex towards the apex; upper margin slightly convex to almost straight, very gradually passing into the more strongly convex outer margin, entire, or, especially towards the apex, faintly crenulate or erose when fertile, subentire or sinuate at the base, shallowly and bluntly crenate towards the apex in sterile pinnules; lower base shortly cuneate, hardly stalk-like; apex mostly subacute. Marginal strand present throughout, very narrow and inconspicuous, except at the lower base, stramineous. Veins immersed, or, especially adaxially, slightly elevated, mostly twice forked, ca. ½–¾ mm apart at the margin; main vein shortly united with the marginal strand, otherwise 0.1–0.2 mm above it. Uppermost pinnules 3–10 mm long, one or two connected by a narrow wing with the terminal segment which is triangular-lanceolate, acute, ca. 1–1.5 cm long, lobed at the base, serrate-crenate above, quite sterile or sometimes soriferous in the basal lobes. *Sori* along the upper and outer margin; indusium ca. 0.1–0.15 mm wide, not reaching the edge by a distance of ¾–1 mm, soon reflexed and quite conceiled at full maturity. Sporangia ca. 150 × 115 μ; annulus with 9–11 indurated cells; spores pale yellowish, ca. 23–28 μ.

Distribution: Rather widespread, largely in South America (map 27). In rainforests, mostly in very moist situations, sometimes along watercourses, up to ca. 750 m.

Representative or widely distributed specimens:

Guadeloupe: Duss s.n. (F, PH).

Guatemala: Izabal, Bernoulli 861 (B); ibid., Bernoulli & Cario 338 (B).

Panamá: Swamp near Almirante, n.w.-Pan., Rowlee & Stork 991 (NY, US).

Colombia. Vaupés: Río Kuduyarí, R. Vaupés-trib., Schultes & Cabrera 17886 (US).

Venezuela. Amazonas: San Carlos, Río Negro, Ll. Williams 14685 (G, US); Yavita, id. 13998 in part (F).

British Guiana: Rockstone, Essequibo R., Jenman s.n. (NY); Macouria Creek, Essequibo R., Jenman 2268 (BM, K, NY); ibid., Fanshawe M 325 (BM); Oreala, Corantyne R., Jenman 432 in part (M); without loc., Schomburgk 368 (B, Holotype; Isotype in BM).

Suriname: Oude Rijweg, Kegel 698 in part (GOET, Holotype of *L. trapeziformis* var. *ervthromera* Kunze).

French Guiana: Near Saï R., Leprieur 16 (FI, GH, NY, US); without loc., Leprieur 10 (US), 15 (NY), 165 (G, P, U).

Brazil. Amazonas: Near Panuré, Rio Uaupés, Spruce 2325 in part (BR); Tunuy, Rio Içana, von Lützelburg 22405 (M); Barra, Rio Negro, Spruce 1367 (K); Trinidade, Rio Negro, Koch 2a (B).

Goias: Sucuriu on Rio das Femeas, von Lützelburg 1509 in part (M, NY, US).

Matto Grosso: Palmeiras, Lindman A 2385 (US).

São Paulo: Retiro da Lagem near Cajurú, Regnell III 1469 (BR, M, S, UPS, US).

Perú. Loreto: Mishuyacu, near Iquitos, Klug 69 (F, NY, US), 1337 (F, NY, US); above Pongo de Manseriche, mouth of R. Santiago, Mexía 6133b (UC, US).

Huánuco: Near Tingo María, Aguilar 301 in part (UC); ibid., R. M. & A. F. Tryon 5339 (U).

Bolivia. Santa Cruz: Buena Vista, Sara, Steinbach 5309 (GH, US).

Paraguay: Cordillera de Piribebuy, Balansa 4454 (B, BM, G, K, L, LE, S–PA, U, UPS, US); Sierra de Amambay, Hassler 10044 in part (B, W).

Although the character of the wings on the axes is not always readily observed, this species can be recognized without much difficulty by the dark axes, dark leaf-tissue which is often wrinkled with slightly elevated veins, and the broad almost always sterile terminal segment. It is closest to *L. quadrangularis* ssp. *terminalis*, from which it is sometimes difficult to distinguish in the southern part of its range (notably Paraguay); there may be some introgression of the two taxa.

It is surprising that this rather well-marked species almost fell into oblivion after it was published; it was incorrectly referred to *L. lancea* by Christensen (Ind. Fil. p. 393, 1906), and the specimens appear under this name or *L. crenata* (because of the crenate sterile parts of the upper/outer margin) in most herbaria. The only more modern author who apparently understood and recognized it was Hieronymus.

Several specimens from Guiana agree with *L. divaricata* in many characters, but the wings on the abaxial side of the secondary rachises are obsolete or weakly developed in the upper part; all are sterile or incompletely fertile. They are probably merely a depauperate or aberrant form of *L. divaricata*. Some of them were cited as *L. crenata* by Alston (Kew Bull. 1932:311) and by Maxon & Morton (in Maguire, Bull. Torr. Bot. Cl. 75:73, 1948). The specimens are:

BRITISH GUIANA: Potaro River Gorge below the Kaieteur Falls, Maguire & Fanshawe 23427 (US); Moraballi Creek near Bartica, Richards 55 (K); Essequibo R., 35 mi. s. of Rockstone, Guppy 100 (BM).
SURINAME: Tafelberg, Maguire 24325 (A, NY, U, US).

24. **Lindsaea guianensis** (Aublet) Dryander, Trans. Linn. Soc. 3:42 (1797); Roem. Arch. 2 (II):237 (1801); Swartz, Syn. Fil. 119 (1806); Willdenow, Spec. Pl. V:424 (1810); Desvaux, Prod. 313 (1827); Sprengel, Syst. Veget. IV:79 (1827); Presl, Tent. Pterid. 131 (1836); Hooker, Spec. Fil. I:216 (1844), p.p. mai.; Kunze, Linnaea 21:221 (1848); Fée, 11^{e} mém. 15 (1866); Hooker & Baker, Syn. Fil. 1st ed. (1868), 2nd ed. (1874) 107 in part; Fée, Crypt. vasc. Brés.I:31 (1869); Baker, Fl. Bras. I^{2}:354 (1870), in part, excl. syn.; J. Smith, Hist. Fil. 268 (1875); Kuhn, Chaetopt. 26 (1882); Krug in Urban, Engl. Bot. Jb. 24:91 (1897), in part; Christ, Farnkr. d. E. 293 (1897); Duss, Fl. Crypt. Ant. franç. 58 (1904); Posthumus, Fl. Surin. Suppl. 73 (1928), in part; Alston, Kew Bull. 1932; 311; not of Lindman, Ark. f. Bot. 1:199 (1903), nor of Graham, Ann. Carnegie Mus. 22:87 (1934).

Basionym: *Adiantum guianense* Aublet, Hist. Pl. Guian. 2:963, 4, pl. 365 (1775); Lamarck, Encycl. I:43 (1783); J. E. Smith, Mém. Acad. Roy. Sci. Turin 5:413 (1793).

Type: Aublet s.n. from French Guiana (P? not seen).

Heterotypic synonym: *L. guianensis* (Aubl.) Dryand. var. *imbricata* Jenman, W. Ind. Gui. F. 76 (1899). Type: Jenman s.n. (?) from Bartica Grove, British Guiana (not seen).

Misapplied names: *L. trapeziformis* auct. non Dryand.; Baker, Fl. Bras. I^{2}:355 (1870), p.p. min.

L. horizontalis auct. non Hooker; Shimek, Ferns Nicar. 152 (1897), pl. XI fig. 8–11.

Petioles and primary rachises of bipinnate leaves abaxially terete; lamina mostly bipinnate with conform terminal pinna, herbaceous; secondary rachises abaxially terete in the lower part; pinnules close, the upper ones gradually reduced; sori continuous; indusium narrow; spores trilete.

Rhizome creeping, prob. short; scales narrowly lanceolate, with up to 7 rows of cells at the base. *Petioles* close, very variable in length, ca. 10– over 60 cm long, from about half as long as to somewhat longer than, rarely up to 1½ × as long as the lamina, adaxially channelled almost to the base. *Lamina* bright green, sometimes dark green, paler on the dorsal side. Primary rachis (in bipinnate leaves) similar to the upper part of the petiole. Axillary cushions present, sometimes discoloured. *Pinnae* short-stalked to subsessile, laxly spreading under an angle of 40–50°, often more ascending in paucijugate leaves; secondary rachises abaxially terete below, in the upper part gradually angular, sometimes shallowly sulcate towards the apex, rarely terete for only a short part at the base. *Pinnules* subopposite or the upper ones alternate, rarely alternate throughout, close, subsessile, a few lower ones somewhat reduced, those in the upper half or third of the pinna gradually reduced, confluent in the apex. *Sori* along the upper/outer margin; indusium entire or mostly minutely erose-denticulate, distinctly intramarginal, reflexed and conceiled at full maturity. Sporangia ca. 140 × 115 μ; annulus with 9–12 indurated cells; spores very pale yellowish-brown, ca. 18–25 μ, 32?

This species consists of two quite clear-cut subspecies which may be distinguished as follows:

a. Pinnae long-acuminate; uppermost pinnules minute, 1–2 mm long; axes usually pale; almost always bipinnate . . . . a. ssp. *guianensis*

b. Pinnae acute or shortly acuminate; uppermost pinnules not denticuliform, ca. 5 mm long; axes often reddish to dark brown; pinnate or bipinnate . . . . b. ssp. *lanceastrum*

a. ssp. **guianensis.** **Fig. 27, 65**

Rhizome 3–4 mm in diam.; scales long-acuminate, up to 1.2 mm long, 0.2 mm wide. *Petiole* dark brown to blackish at the base, for the rest stramineous, rarely castaneous, rather shining, especially at the base, 1–2(–3) mm in diam. near the apex. *Lamina* bipinnate (simply pinnate almost always in juvenile specimens only), 20–65 cm long, with 1–13, mostly about 4–7 pinnae to a side and a conform terminal one; *pinnae* subopposite to alternate, rather remote, 2–4(–7) cm apart, rarely subcontiguous, ca. 10–25 cm long, the upper pinnae of plurijugate leaves shorter, ca. 2(1½–2½) cm wide, long-acuminate. *Pinnules* ca. 50(30–70) to a side, often strongly overlapping, succubous, dimidiate-ovate, occasionally subfalcate, spreading or sometimes a little deflexed, the upper ones not rarely ascending, the largest (7–)10–12 mm long, (3–)5–7 mm wide, about twice as long as wide, relatively very constant in size and shape, widest at the base or in the whole lower half. Inner margin straight, parallel or somewhat divergent from the sec. rachis, lower base cuneate, hardly stalk-like, upper base shortly rounded, lower margin straight or faintly concave, upper margin convex, but often straight at the base, a more or less separate outer margin often present; apex obtuse or subacute. Upper and outer margin often sinuous in sterile or incompletely fertile pinnules, laxly crenate in juvenile plants, otherwise quite entire. Marginal thickening stramineous, very narrow. Veins immersed but readily visible, once or twice forked, ca. 1 mm apart at the margin. Main vein and basal lateral vein ca. ¾ from the edges. Upper pinnules very gradually reduced, the uppermost pinnules in the long-acuminate or caudate top of the pinna denticuliform, ca. 1–2 mm long, rather suddenly confluent into a lanceolate-linear, often caudate terminal segment, which is obtuse, sinuous below, entire above, 1–1½(½–2½ in extreme cases) cm long, with a flexuose midrib, almost always quite sterile. Indusium ca. 0.15 mm wide, not reaching the margin by a distance equalling 2–4 × its width.

Distribution: Mostly confined to northern South America (map 28). Incorrectly reported by Baker (Jo. Bot. 25:24, 1887) from Costa Rica

Fig. 58: *Lindsaea surinamensis;* upper half of lamina (Boschwezen 641). Fig. 59–60: *L. herminieri;* fig. 59: apex of lateral pinna (above) (L'Herminier 43), sterile pinnuel (L'Herminier s.n.); fig. 60: fertile pinnules from middle of terminal pinne (L'Herminier 2). Fig. 61: *L. dubia;* lateral pinnule (below), apex of lamina (above) (Boschwezen 3194). Fig. 62: *L. taeniata;* apex of lateral pinna (above), lower pinnule of lateral pinna (below) (Kalbreyer 1345). Fig. 63: *L. divaricata;* middle pinna (Leprieur s.n.). Fig. 64: *L. guianensis* ssp. *lanceastrum;* upper part of upper pinna (Dusén 15013). Fig. 65: *L. guianensis* ssp. *guianensis;* upper ⅔ of lateral pinna (Spruce s.n.). Fig. 66–67: *L. javitensis;* fig. 66: portion of lamina below the apex; fig. 67: apex of middle pinna (Schultes & Cabrera 14528). Fig. 68: *L. rigidiuscula;* portion of lamina (Koch 65). Fig. 69: *L. portoricensis;* base of lateral pinna (Fanshawe M 334). Fig. 70: *L. hemiptera;* a: pinnules from simply pinnate sterile lamina (Steyermark 57824); b: fertile pinnules from base of lateral pinna; c: apex of lateral pinna (Ll. Williams 15536). Fig. 71: *L. cubensis;* a: sterile pinnule, b: fertile pinnule (Wright 3947). (Scales in mm).

and by Gardner (London Jo. Bot. 1:548, 1842) from Rio de Janeiro. In forests, sometimes on tree-trunks or even pendulous from branches but mostly terrestrial, from sea-level to ca. 750 m.

Representative specimens:

Nicaragua: Camp Menocal near Greytown, Shimek s.n. (IA).
Guadeloupe: Duss 4239 in part (NY), 4139 (US), 4242 in part (NY, US); L'Herminier s.n. (B, BM, F, G, K, LE, P, US, part of Type-material of *L. montana*).
Grenada: Jenman s.n. (NY); Trinidad Bot. Gard. Herb. (Alexander 6180) (C. C. Chr. in BM, G, S-PA).
Colombia. Santander: Magdalena Valley, vic. of Barranca Bermeja, Haught 1371 (GH, UC, US); vic. of Puerto Berrio, between Carare and Magdalena Rs., Haught 1880 (GH, US); Puerto Wilches-Puerto Santos, Killip & A. C. Smith 14873 (GH, NY, S, US).
El Valle: Buenaventura, Killip 11755 (US).
Chocó: South of R. Condoto, Quebrada Guarapo-Mendinga, Killp 35142 (GH, K, UC, US).
Vaupés: R. Piraparana, trib. of R. Apaporis, Schultes & Cabrera 17399 (US).
Venezuela. Amazonas: Yavita, Ll. Williams 13998 (US); Capihuara, Upper Casiquiare, Ll. Williams 15819 (US); Maroa, R. Guainía, Ll. Williams 14277 (F).
British Guiana: Macouri Creek, Essequibo R., Jenman s.n. (NY); Kangaruma-Potaro Landing, Gleason 229 (GH, NY, US); Moraballi Creek near Bartica, Richards 30, 347, 465 (K); ibid., Fanshawe M 327 (BM); Oreala, Corantyne R., Jenman 431 (K); Berbice, Schomburgk 346 in part (BM, F, K, U, W).
Suriname: Near Blaauwe Berg, Splitgerber 888 (L); Suhoza, Upper Suriname R., Lanjouw & Lindeman 3379 (BM, U); near Jodensavanne, Kegel 1076 (GOET).
French Guiana: Acarouany, Sagot 850 (B, BM, K); Inipi, Leprieur 17 (GH, US); Mana, Perrottet s.n. (G).
Brazil. Amazonas: Panuré, Rio Uaupés, Spruce 2325* (BM); near Manáos, Rio Negro, Ule 5419 (B, G, L); Barra, Rio Negro, Spruce 1768 (B, G); São Gabriel, Rio Negro, Spruce s.n. (B); Santarem near Pará, Spruce 349 (K).
Perú. Huánuco: Near Tingo María, Allard 21502 (US); ibid., R. M. & A. F. Tryon 5275, 5289 (U).

The most conspicuous character of this subspecies is found in the apices of the pinnae, which are long-acuminate or caudate, with a sudden transition from denticuliform pinnules to a lanceolate terminal segment.

b. ssp. **lanceastrum** Kramer, ssp. nov. **Fig. 64**

Petiolo saepe rubro-fusco vel badio, facie abaxiali petioli rhachidiumque primariarum et secundariarum tereti; lamina laete- vel atrovirens, pinnulis approximatis, saepe leviter imbricatis, semi-ovatis vel semi-ellipticis, forma *L. lanceam* imitantibus, superioribus sensim redactis, autem sine apice pinnarum longe caudato ut in subspecie guianensi; soris indusio plerumque minute eroso.

Typus: Dusén 15013 from Jaguariaiva, Paraná, Brazil (F).

Rhizome 2–3 mm in diam.; scales acuminate, up to 1¾ mm long, 0.2 mm wide. *Petioles* often rather shining, 1–1.5 mm in diam. near the apex. *Lamina* mostly bipinnate but sometimes simply pinnate in apparently full-grown plants, 20–45, mostly ca. 30–40 cm long. *Primary pinnae* (if any) 1–4(–7) to a side and a conform terminal one, subopposite or mostly alternate, rather widely spaced, (2–)3–6½ cm apart, 10– over 35 cm long, 2–4, mostly 2.5–3 cm wide, shortly narrowed at the base, gradually and strongly narrowed in the upper ⅓ or ¼; terminal pinna largest in paucijugate leaves, mostly stalked. Secondary rachises stramineous or often reddish (rarely dark) brown. *Pinnules* (15–)20–50 to a side, resembling those of *L. lancea*, spreading or somewhat ascending, the basal ones often somewhat falcate-deflexed, the largest (8–)12–20 mm long, (4.5–)5–10 mm wide, about twice as long as wide, widest at the base or of equal width almost throughout, entire. Inner margin straight, ± parallel to the sec. rachis, lower base cuneate, hardly stalk-like, upper base rounded, sometimes broadly, rarely subangular, lower margin straight or faintly concave, upper margin convex, more strongly so towards the apex, a separate outer margin mostly not present, the lower and upper/outer margin sometimes meeting at almost right angles, otherwise the apex more gradually narrowed, the very top obtuse. Marginal thickening stramineous, not prominent. Veins immersed but not obscure, mostly twice forked, their ends ca. $\frac{1}{2}$–$\frac{3}{4}$ mm apart; main vein shortly united with the marginal strand, ca. $\frac{1}{2}$ mm above it near the apex. Upper pinnules gradually reduced, the uppermost ones ca. 5 mm long, mostly one or two connected by a wing with the terminal segment which is lanceolate, acute or obtuse, shallowly lobed to subentire, with cuneate base and a flexuose midrib, 0.5–2(–2.5) cm long, often soriferous at the base. Indusium 0.2–0.3(–0.4) mm wide, not reaching the margin by a distance equal to its width or twice as wide.

Distribution: Central, eastern, and southern Brazil; Paraguay (map 29). In swampy forests and along watercourses, up to ca. 700 m.

Representative specimens:

BRAZIL. MARANHÃO: West of Riachão, E. N. Shaw s.n. (US).

BAHIA: Pedra Santa near São Bento, von Lützelburg 18934 (M, S–PA).

GOIAS: Sucuriu, Rio das Femeas, von Lützelburg 13749a (M).

MATTO GROSSO: Santa Ana da Chapada, Buriti, Malme s.n. (Regnell II) (S); ibid., id. s.n. (Regnell II 2215a) (UPS); Floriano, Hoehne 5364 (UC).

SÃO PAULO: Campinas, Heiner 537 (S, S–PA); ibid., Severin 74 (UPS), 169 (S, UPS).

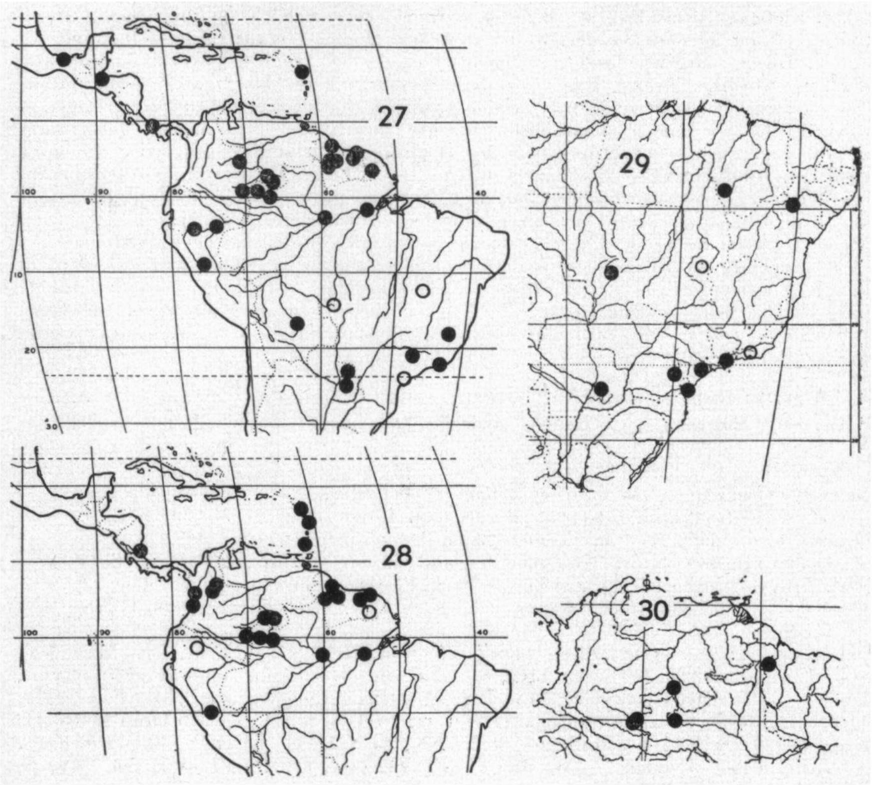
PARANÁ: Jaguariaíva, Dusén 14117 p.p. mai. (BM, G, GH, K, LE, MO, NY, S, US); ibid., id. 13213 (LE, MO, S); ibid., id. 15013 p.p. mai. (F, HOLOTYPE; Isotypes in B, BR, C, G, GH, NY, PH, S, S–PA); ibid., id. s.n. (BR, F, G, GH, MO, PH); Volta Grande, Dusén 14139 in part (B, S, S–PA); Porto Dom Pedro II, Dusén 4424 (B, BM, S); ibid., id. 9872 (BM, G, GH, K, LE, NY, S, S–PA, US).

Without loc., Riedel 17 (B, BR, C, FI, G, GH, GOET, L, LE, M, NY, S, UPS, US, W).

PARAGUAY: Paraguari, Sierra de Amambay, Hassler 10044 in part (B, K); without loc., Fiebrig 6343 in part (K, L, M).

The two subspecies, although very closely allied, are clear-cut, and there would be no fundamental objection against treating them as distinct species. The closest relative seems to be *L. quadrangularis* ssp. *terminalis*, which is quite close to *L. guianensis* ssp. *lanceastrum*, but has smaller, mostly more elongate, more remote pinnules, darker axes, esp. the secondary rachises, which are more slender, and narrower indusia. *L. hemiptera* is perhaps more distantly related.

The author has not examined the type of *Adiantum guianense* Aublet, and there is some uncertainty whether the name is correctly applied. Although Aublet's plate resembles most closely the species described above, there is a possibility that it represents a form of *L. stricta* var. *parvula*. If this would be the case, it would cause very regrettable name-changes, as *L. stricta* would have to be called *L. guianensis*, and the species which used to bear that name would need a new one. Because of this, the name *L. guianensis* is used here as currently applied. It has been widely misapplied for the lax form of *L. stricta* which is most common in south-eastern Brazil (LINDMAN, l.c., WAGNER 1952b, etc.), with which it has nothing to do, however, as this form does not occur in the Guianas.



Map 27: *L. divaricata.* Maps 28–29: *L. guianensis;* map 28: ssp. *guianensis;* map 29 ssp. *lanceastrum.* Map 30: *L. javitensis.*

Jenman's var. *imbricata* probably represents ssp. *guianensis;* the author has seen no specimen in K or NY from the forest opposite Bartica Grove, British Guiana, whence Jenman reported it, but three sheets from the Macouria Creek in NY are annotated "var. *imbricata*" and constitute at least authentic material; therefore, this name may safely be referred to ssp. *guianensis*, with which Jenman's description is in excellent agreement.

L. guianensis was chosen as type-species of the genus by COPELAND (1947); for arguments against this choice, see p. 137.

25. **Lindsaea hemiptera** Kramer, spec. nov. **Fig. 70**

Misapplied name: *L. guianensis* auct. non Dryand.; Baker, Fl. Bras. I^2:354 (1870), in part, excl. syn.

Folia pinnata vel plerumque bipinnata, petiolo pullo vel atropurpureo, facie abaxiali tereti, adaxiali superne lateraliter alata; lamina rigide herbacea vel papyracea, rhachide primaria et rhachidulis secundariis parti superiori petioli similibus, pinnulis dimidiato-ellipticis, longitudine latitudinem bis vel bis et dimidius superante, pinnulis superioribus sensim decrescentibus; soris continuis, indusio rigido, angusto, integro vel subintegro, marginem non attingente; sporis tetraedriformibus.

Typus: Ll. Williams 15536 in part from Capihuara, Upper Casiquiare, Amazonas, Venezuela (US).

Rhizome short(?)creeping, ca. 2 mm in diam.; scales narrowly lanceolate, long-acuminate, up to 1.5 mm long, 0.3 mm wide, with up to 7 rows of cells at the base. *Petioles* close, ca. 8–50 cm long. about as long as the lamina, ⅔–1½ mm in diam. near the apex, shining, adaxially terete at the base, the upper ¾ or more less convex, bordered by ridges which at least in the upper half are distinctly wing-like, pale or reddish, obliquely spreading, attaining a width of ca. ¼ mm at the base of the lamina. *Lamina* medium to dark olivaceous on the ventral side, paler on the dorsal side, 15–40 cm long, with 2–6 pinnae to a side (if any) and a conform terminal one. *Primary rachis* similar to the upper part of the petiole, the adaxial wings shortly interrupted above the insertion of the pinnae. Axillary cushions very indistinct. *Pinnae* alternate or subopposite, sessile or shortly stalked (up to 2 or 3 mm), spreading under an angle of ca. 60°, 1–8, mostly 2–4 cm apart, 10–30 cm long, 1.5–2.5 cm wide, widest in the lower third or half, slightly narrowed at the base, gradually, but not very strongly narrowed in the upper half or two-thirds. Upper pinnae slightly shortened. Secondary rachises similar to the primary, the wings shortly interrupted above the insertion of the pinnules, gradually evanescing above. *Pinnules* 35–50(–70) to a side, the lower ones mostly subopposite, the upper ones alternate, close, subcontiguous to slightly imbricate, very regularly spaced, spreading, sometimes subfalcate, ca. 9 mm long and 4 mm wide; sterile pinnules more elongate, ca. 7–10 × 3–3.5 mm, about 2½–3 × as long as wide. Inner margin straight or slightly convex, parallel or somewhat divergent from the sec. rachis, passing with a short rounded portion into the upper/outer margin which is rather evenly convex, lower margin straight or somewhat concave, lower base shortly cuneate, not stalk-like, apex obtuse or mostly subacute to acute. Fertile pinnules quite entire; sterile pinnules along the outer margin with rather irregular teeth separated by incisions 1–1.5 mm deep, often more highly united in pairs, passing rather abruptly into shallow crenations present along the upper margin; incompletely fertile pinnules with a few large teeth near the apex. Marginal thickening with a very thick stramineous or reddish portion occupying ⅓–¼ of the lower edge, there continuous with the main vein, otherwise less conspicuous but visible throughout, entire. Veins slightly elevated, especially their bases on the dorsal side, once or twice forked, close, their ends ½–⅔ mm apart; main vein 0.2–0.3 mm above the lower margin near the apex. Upper pinnules gradually reduced, more strongly so in the apical part of the pinnae which are therefore shortly acuminate; uppermost pinnules 2–5 mm long, one or a few connected by a wing with the terminal segment which is lanceolate, subacute or acute, 0.5–2 cm long, asymmetrically lobed at the base, the margin dentate-crenate, not or hardly soriferous. *Sori* along the upper/outer margin; indusium stiff, 0.2–0.25 mm wide, not reaching the margin by 0.1–0.2 mm, rarely less; sporangia ca. 150 × 115 μ; annulus with 10–14 indurated cells; spores pale brownish-yellow, ca. 23–28 μ.

Distribution: Adjacent regions of Venezuelan and Brazilian Amazonas (map 24). In moist woods, along watercourses; one record of 120 m alt.

Venezuela. Amazonas: Capihuara, Upper Casiquiare, dense forest, Ll. Williams 15536 in part (US, Holotype; Isotype in GH); between Esmeralda Savanna and base of Mt. Duida, Steyermark 57824 (F, GH, MO, NY, US).

Brazil. Amazonas: Near São Gabriel da Cachoeiras, Rio Negro, Spruce 2326 (B, K, LE); Tunuy, Rio Aiari, von Lützelburg 23658 (M, NY).

A very distinctive species, with dark, shining, abaxially quite terete, adaxially winged axes, small, evenly spaced pinnules and narrow indusia. Its alliance within the section is not quite clear; perhaps related to *L. guianensis*, or to *L. divaricata*.

26. **Lindsaea portoricensis** Desvaux, Berl. Mag. 5:326 (1811); Kuhn, Chaetopt. 26 (1882); Krug in Urban, Engl. Bot. Jb. 24:91 (1897), p.p. mai.; Jenman, W. Ind. Gui. F. 77 (1899); Kuhn in Urban, Symb. Ant. 4:31 (1903), p.p. mai.; Knuth, Fedde Rep. Beih. 43 (1):32 (1926); Maxon, Pterid. Port. 489 (1926); Posthumus, Fl. Surin. Suppl. 74 (1928); Domin, Pterid. Domin. 243 (1929); Weatherby, Contr. Gray. Herb. 114:26 (1936); C. Christensen, Kungl. Sv. Vet.-Akad. Handl. 16 (2):46 (1937). **Fig. 24, 69**

Type: without coll., "in Antillis", apparently from Puerto Rico (P!; the smaller part of the material belonging to *L. lancea*).

Heterotypic synonyms: *Lindsaea crenata* Klotzsch, Linnaea 18:546 (1844); Hooker, Spec. Fil. I:208 (1844); J. Smith, Hist. Fil. 268 (1875); Jenman, W. Ind. Gui. F. 73 (1899); Hieronymus, Hedwigia 62:16 (1920); Posthumus, Fl. Surin. Suppl. 74 (1928); not of most other authors. Type: Schomburgk 274 in part from British Guiana (B!).

Lindsaea rufescens (lapsu: *rubescens*) Kunze, Linnaea 21:227 (1848); J. Smith, Lond. Jo. Bot. 1:200 (1842), nomen; Kunze, Bot. Zeit. 8:385 (1850); Fée, 9ᵉ mém. App. (1856). Type: Schomburgk 346 in part, from British Guiana (B!).

Lindsaea consanguinea Fée var. *β rigida* Fée, Crypt. vasc. Brés. I:30 (1869). Type; Glaziou 2805 from Jacú, Serra dos Orgãos, Rio de Janeiro, Brazil (prob. P, not seen; Isotypes in B, BR, C, K, S).

Misapplied names: *Lindsaea stricta* auct. non Dryand.; Klotzsch, Linnaea 18:546 (1844); Krug in Urban, Engl. Bot. Jb. 24:91 (1897), p.p. min.; Kuhn in Urban, Symb. Ant. 4:31 (1903), in part.

Lindsaea guianensis auct. non Dryand.; Ettingshausen, Farnkr. t. 146 fig. 24, 25 (1865); Baker, Fl. Bras. I²:354 (1870), in part, excl. of most synonyms; Posthumus, Fl. Surin. Suppl. 73 (1928), in part.

Lindsaea quadrangularis auct. non Raddi; Fée, Crypt. vasc. Brés. I:29 (1869), in part.

Lindsaea consanguinea of Fée, ibid. 30 (1869), non 11ᵉ mém. 16 (1866).

Lindsaea trapeziformis auct. non Dryand.; Baker, Fl. Bras. I²:355 (1870), p.p. min., excl. syn.

Petioles brownish red or dark brown, abaxially terete; lamina simply pinnate or bipinnate with conform terminal pinna, firmly herbaceous to chartaceous; secondary rachises abaxially with paler angles which are irregularly interrupted at the base; pinnules subrectangular or mostly tongue-shaped, ca. 2 × as long as wide; veins often visible as wrinkles in the leaf-tissue; upper pinnules gradually reduced; sori continuous; indusium mostly repand-erose; spores trilete.

Rhizome creeping, ca. 1½–2 mm in diam.; scales narrowly lanceolate, long-acuminate, up to 1¾ mm long and 0.2 mm wide, with up to 5 rows of cells at the base. *Petioles* ± close, ca. 5–50 cm long, ratio to length of lamina very variable, ¾–2 mm in diam. near the apex, dull or often shining, adaxially mostly terete below, rarely for the greater part or at the extreme base only, flattened above, with sharp, sometimes paler but never wing-like borders, abaxially terete, or rarely with short lateral angles near the apex. *Lamina* on the ventral side medium or mostly dark olivaceous to brownish-green, on the dorsal side similar or somewhat paler, quite dull, ca. 15–50 cm long, when simply pinnate considerably longer than the petiole, up to six times as long, when bipinnate of comparable size, often not more than two-thirds the length of the petiole, with one odd pinna at one side to 4(–6) on each side and a conform terminal one. *Primary rachis* of bipinnate leaves similar to the upper part of the petiole, abaxially often flattened and laterally angular above, rarely throughout; of simply pinnate leaves as the secondary rachises of bipinnate leaves. Axillary cushions often visible as swellings, not discoloured. *Pinnae* strongly ascending, often almost vertical, touching each other and the terminal pinna, the lower ones 3–5 cm apart, the upper ones gradually closer in plurijugate leaves, subsessile, the terminal mostly stalked (up to 3 cm), the lower ca. 15–25(–40) cm long, 1.5–3 cm wide, the upper ones somewhat shortened, the terminal 1½–2 × the length of the basal pinnae, only in plurijugate leaves of comparable size. Lamina of simply pinnate leaves similar to the primary pinnae of bipinnate ones. Secondary rachises (and primary of once-pinnate laminae) brown or reddish, adaxially flattened, with sharp borders, abaxially with a short terete basal portion, from the level of the first to third pinnule with sharp, paler at the base almost always irregularly interrupted angles which above are mostly somewhat wing-like. Pinnae slightly narrowed at the base, gradually narrowed from somewhat above the base to the apex. *Pinnules* up to ca. 80 to a side, mostly less, subopposite to alternate, subsessile, spreading or the basal ones usually somewhat falcately deflexed, remote, the upper ones gradually closer, contiguous or slightly imbricate, 5–14 mm long, 3–7 mm wide, mostly hardly narrowed to the broadly rounded apex. Inner margin straight, parallel or slightly divergent from the sec. rachis, upper base shortly rounded to almost rectangular, lower base shortly cuneate, hardly stalk-like, lower margin concave in the inner, faintly concave or straight in the outer part, upper margin approximately straight in the inner, convex in the outer part, sometimes almost angularly passing into the outer margin, minutely crenate or subentire in fertile pinnules, shallowly crenate or sinuate, less often dentate or denticulate, in sterile ones, sometimes crispate, occasionally revolute around the sorus. Marginal thickening stramineous, rather conspicuous throughout, sometimes remaining in withered leaves where the leaf-tissue has decayed. Veins elevated and stramineous at their bases on both sides, otherwise immersed but visible as wrinkles in the leaf-tissue in dried specimens, mostly two or three times forked, rather close, their ends ½–¾ mm apart; main vein only shortly continuous with the marginal strand but close to it, ca. ¼ mm above it near the apex. Upper pinnules gradually reduced, 2–4 mm long, one or two connected by a wing with the terminal segment which is lanceolate, subacute, ½–1½ cm long, crenate or lobed at the often soriferous base. *Sori* along the upper and outer margin; indusium thin, pale, ca. 0.3 mm wide, not reaching the margin by a distance of 0.3–0.5 mm, strongly reflexed and ± conceiled at full maturity. Simply pinnate leaves are often sterile in the lower half or third. Sporangia ca. 175–190 × 140 μ; annulus with 8–10 indurated cells; spores medium brown, ca. 27–36 μ.

Distribution: Almost throughout the range of the genus in the New World, but so far not collected in the Lesser Antilles and most of Central America; commonest in the Greater Antilles and the Guianas, including Trinidad (map 25). One of the very few euryoeceous species; in moist forests, in thickets, swamps, among rocks, on banks of roads, on exposed sandy soil, sometimes on laterite, etc., from sea-level to about 1200 m.

Representative specimens:

CUBA: Pinar del Rio, Wright 3948 (B, GH, K, NY, S–PA, US).

HISPANIOLA. SAN DOMINGO: Samaná Penins., Jato Viejo, Abbott 1334 (GH, US); Liali, Abbott 2589 (C, GH, US); Cordillera Septentrional, Matanzas, Sabana de los Gengibres, Ekman H 15869 (C, G, K, S).

JAMAICA: Pedro Morass, near Clarendon, Harris 11165 (BM, C, F, GH, K, MO, NY, US); Tea Gully, near New Market, Harris 9911 (BM, C, F, K, NY, US);

Bluefield Mts., Purdie s.n. (BM, K); Bull Head, Clarendon, Sherring 393 (BM, K).
PUERTO RICO: Near Dorado, Britton, Britton & Brown 6647 (F, G, NY, PH, US); Utuado, Sintenis 6382 (B, BM, MO, US); Aguada, Piedra Blanca, Sintenis 5709 (B, BM, BR, C, F, G, GH, K, L, LE, M, MO, NY, PH, S–PA, US, W); Vega Baja, Heller & Heller 1312 (F, K, NY, US).
MEXICO. VERA CRUZ: Minatitlan, J. G. Smith 57 (MO, US).
OAXACA: Talea, Galeotti 6470 in part (B, BR, W); without loc., Galeotti 6495 in part (FI, W).
BRITISH HONDURAS: Boomtown, O'Neill 8411 (F, GH, NY, S–PA, UC); Cow-Pen near Monkey River, Gentle 4128 (GH, MO, NY, US).
GUATEMALA: Zacapa, Palmilla, Walker s.n. (Donnell Smith 1203) (US).
COLOMBIA. EL VALLE: Buenaventura, Killip 11739 (US).
META: Villavicencio, Hacienda San Carlos, Hermann 11139 (US).
CHOCÓ: La Equis, Molina & Barkley 19 Ch 069 (K); Lloró, south of Quibdó, Archer 2063 (US).
VENEZUELA. D.F.: Caracas, Karsten s.n. (W).
AMAZONAS: La Esmeralda, Croizat * 164 (U).
TRINIDAD: Valencia, Britton, Britton & Hazen 1016 (GH, NY, US); Sangre Grande, Broadway 5381 (F, MO, U, UC, US); Aripo Road, Broadway 8025 (BM, G, MO, S); Long Stretch, Hombersley 73 (K).
BRITISH GUIANA: Kaieteur Savanna, Jenman 1386 (K); Rockstone, Gleason 603 (GH, K, NY, US); Kamakusa, Leng & Persaud 368 (F, NY, US); Parabaru Savanna, A. C. Smith 3056 (F, G, GH, K, NY, U, US); Forest Station, Mazaruni R., Forest Dept. 6896 (K, U); ibid., Fanshawe M 334 (K, U); without loc., Schomburgk 274 in part (B, HOLOTYPE of *L. crenata*); Schomburgk 346 in part (B, HOLOTYPE of *L. rufescens*; Isotypes in BM, FI, G, L).
SURINAME: Near plant. Onoribo, Para R., Focke 913 (K, U); Para Distr., Hostmann & Kappler 1738 (B, G, FI, LE); Paramaribo, plant. Jagtlust, Suringar 6092 (L); Upper Sipaliwini R., Tumuc Humac Range, Rombouts 403 (U).
FRENCH GUIANA: Oyor, Leprieur 18 (B, GH, LE, NY, US); Montsinéry, near Cayenne, Leprieur 67 (G); Cayenne, Sagot 1363 (B, BM, K, S–PA); ibid., Leprieur 168 (FI, NY, P, U), Baduel, near Cayenne, Broadway 909 (GH, K, NY, US).
BRAZIL. AMAZONAS: Near Panuré, Rio Uaupés, Spruce 2325 (BM, G).
BAHIA: Ilheos, Riedel s.n. (L); ibid., Blanchet 2 (G).
MINAS GERAIS: Corrego Fundo, C. Verde, Macedo 3378 (MO, US).
RIO DE JANEIRO: Serra dos Orgãos, Burchell 2663 (B, K, US); Rio Maná, Spannagel 534 (UC); Tijuca, Miers 136 (BM); ibid., L. B. Smith & Brade 2202 (GH, US); Jacú, Glaziou 2805 (B, BR, C, K, S, Isotypes of *L. consanguinea* var. *rigida*).
SÃO PAULO: Serra São João, near Santos, Wettstein & Schiffner s.n. (W).
BOLIVIA. SANTA CRUZ: Buena Vista, prov. del Sara, Steinbach 2200 (B, GH, S–PA, U).

The simply pinnate forms of this species are sometimes difficult to separate from *L. stricta*, probably its closest relative. *L. stricta* has smaller, thicker pinnules with obscure veins and the rachis is abaxially at least for a considerable basal part terete, but there are a few intermediates, e.g. Ekman H 9021 (C. Chr. in BM, K, NY, S, US) from Massif de la Hotte, Haïti, Hispaniola, which are difficult to assign to either of the two species. There is probably some hybridization; they often occur in the same sort of habitat and are frequently collected together.

27. **Lindsaea stricta** (Swartz) Dryander, Trans. Linn. Soc. 3:42 (1797); Roem. Arch. 2 (II): 237 (1801); Swartz, Syn. Fil. 119 (1806); Schkuhr, Krypt. Gew. I:105 (1809), t. 114; Willdenow, Spec. Pl. V:425 (1810); Presl, Rel. Haenk. I:59 (1825); Sprengel,

Syst. Veg. IV: 80 (1827); Desvaux, Prod. 313 (1827); Presl, Tent. Pterid. 131 (1836); Gardner, Lond. Jo. Bot. 1:200 (1842); J. Smith, ibid.: 200 (1842); Hooker, Spec. Fil. I:216 (1844), p.p. mai.; Liebmann, Vid. Selsk. Skr. 5 (1):269 (1849); Kunze, Bot. Zeit. 8:371 (1850); Mettenius, Ann. Sci. Nat. 5ᵉ sér. 2:216 (1864); Ettingshausen, Farnkr. t. 142 fig. 4, 145 fig. 5–8, 14 (as *guianensis*), 146, fig. 8, 19, 20 (1865); Wawra, Bot. Ergebn. Max. Reise Südbras. 192 (1866); Hooker & Baker, Syn. Fil. 1st ed. (1868), 2nd ed. (1874) 108; Fée, Crypt. vasc. Brés. I:30 (1869); Baker, Fl. Bras. I²:353 (1870), t. 21 fig. 22–25; J. Smith, Hist. Fil. 268 (1875); Eaton, Bot. Gaz. 3:91 (1878); Kuhn, Chaetopt. 26 (1882); Jenman, Jo. Bot. 25:98 (1887); O. Kuntze, Rev. Gen. Pl. 815 (1891); Eaton, Mem. Torr. Bot. Cl. 4 (3):272 (1895); Schenck, Hedwigia 35:158 (1896); Christ, Farnkr. d. E. 293 (1897); Krug in Urban, Engl. Bot. Jb. 24:91 (1897), p. p. mai.; Wright, Trans. Linn. Soc. II, 6:80 (1901); Diels, N. Pfl. I⁴:221 (1902); Rosenstock, Hedwigia 46:80 (1906); Hieronymus, Hedwigia 47:209 (1908); Bonaparte, Notes Ptérid. VII:343 (1918); Urban, Symb. Ant. 9:322 (1925); Knuth, Fedde Rep. Beih. 43 (1):32 (1926), p. p. mai.; Posthumus, Fl. Surin. Suppl. 74 (1928); Domin, Pterid. Domin. 242 (1929); Standley & Record, Field Mus. Publ. 350:64 (1936); Weatherby, Contr. Gray Herb. 114:26 (1936).

Basionym: *Adiantum strictum* Swartz, Prodr. 135 (1788); J. E. Smith, Mém. Acad. Roy. Sci. Turin 5:413 (1793); Poiret in Lamarck, Encycl. Suppl. I:140 (1810).

Type: Swartz s.n. from Jamaica (S-PA!).

Homotypic synonym: *L. guianensis* (Aubl.) Dryand. f. *stricta* (Sw.) Lindman, Ark. f. Bot. I:201 (1903), pl. 8 fig. 4 a, b.

Heterotypic synonyms: *L. elongata* Cavanilles, Descr. 265 (1802). Type: "Don Luis Née, Panamá; tambien se cria en Puerto-Rico" (MA? not seen).

L. rigescens Willdenow, Spec. Pl. V:421 (1810); Desvaux, Prod. 313 (1827); Presl, Tent. Pterid. 131 (1836); Klotzsch, Linnaea 48:546 (1844); Fée, Crypt. vasc. Brés. I:29 (1869), in part. Type: Bredemeyer s.n. from Caracas, Venezuela (W!).

L. brasiliensis Desvaux, Berl. Mag. 5:330 (1811); Prod. 313 (1827); Weatherby, Contr. Gray Herb. 114:26 (1936). Type: Unknown coll., "habitat in Brasilia" (P!).

L. elata Desvaux, Berl. Mag. 5:326 (1811); Prod. 313 (1827); Weatherby, Contr. Gray Herb. 114:26 (1936). Type: Unknown coll., "habitat in Caribaeis" (P!).

L. imbricata Desvaux, Berl. Mag. 5:326 (1811); Prod. 313 (1827); Weatherby, Contr. Gray Herb. 114:26 (1936); non Liebmann, 1849. Type: Unknown coll., "habitat in America?" (P!).

L. microphylla Presl, Rel. Haenk. I:59 (1825), non Swartz 1800. Type: Haenke s.n. from Mexico (prob. PR; not seen).

Homotypic synonyms: *L. stricta* (Sw.) Dryand. var. *microphylla* (Pr.) Hassler, Trab. Inst. Farm. Buenos Aires 25:36 (1928).

L. parvifolia Presl, Tent. Pterid. 131 (1836); Hooker, Spec. Fil. I:207 (1844).

L. elegans Hooker, Icon. Plant. t. 98 (1837); Sampaio, Arch. Mus. Nac. Rio de Jan. 32:34 (1930), pl. 12, fig. 3; non Fée, 1852. Type: Cuming 1101 from Colombia (K!).
Homotypic synonyms: *L. guianensis* (Aubl.) Dryand. var. *elegans* (Hook.) von Luetzelburg, Est. Bot. Nordéste Bras. 3:245 (1923).
L. stricta (Sw.) Dryand. var. *elegans* (Hooker) [incorr. attributed to C. Christensen by] Sampaio, Arch. Mus. Nac. Rio de Jan. 32:35 (1930).

L. Raddiana Klotzsch, Linnaea 18:549 (1844); Fée, Crypt. vasc. Brés. I:30 (1869). Type: Schomburgk 253 in part, from British Guiana (B!).

L. stricta (Sw.) Dryand. var. *β tripinnata* Hooker, Spec. Fil. I:216 (1844). Type: Gardner 5323 from Cocaes, Minas Gerais, Brazil (K!).

L. multifrondulosa Fée, Gen. Fil. 105 (1852), t. 28. fig. 1; 11ᵉ mém. 17 (1866). Type: Galeotti 6470 in part, from Oaxaca, Mexico (P!).

L. dentata Fée, Crypt. vasc. Brés. II:20 (1872/73). Type: Glaziou 5357, from Corcovado, Rio de Janeiro, Brazil (P!).

L. portoricensis Desv. var. *brachypoda* Domin, Pterid. Domin. 243 (1929). Type: not indicated; three coll. cited: Sherring s.n. from Bull Head, Jamaica, Fendler 89 from Trinidad, and Kalbreyer 1423 from Antioquia, Colombia. The second coll. is most eligible as type; if there is a specimen in PR, that should be the lectotype; otherwise the specimen in K.

Misapplied names: *L. javitensis* auct. non H. & B. in Willd.; Raddi, Opusc. Sci. Bol. 3:294 (1819); Plant. Bras, nov. gen. spec. 56 (1825).

L. guianensis auct. non Dryand.; Baker, Fl. Bras. I^2:354 (1870), p.p. min., excl. syn.; Christ in Pittier, Prim. Fl. Costar. 3:37 (1901); Rosenstock, Hedwigia 46:80 (1906); Sampaio, Arch. Mus. Nac. Rio de Jan. 32:34 (1930.

Petioles pale or dark, abaxially terete; lamina simply pinnate, bipinnate with conform terminal pinna, or occasionally tripinnate, herbaceous to coriaceous; pinnules close, roundish or oval to rounded-subtrapeziform, as long as to 1½ × as long as wide; veins immersed, mostly obscure; upper pinnules gradually and strongly reduced; sori continuous, often absent from the lower part of the lamina, especially in simply pinnate leaves; indusium mostly strongly erose to lacerate; spores trilete.

Rhizome creeping (often widely), 1–3 mm in diam.; scales narrowly lanceolate, long-acuminate, up to 2 mm long, 0.3 mm wide, with up to 8 rows of cells at the base (relatively narrowest in specimens from exposed habitats) (fig. 2). *Petioles* mostly rather close or close, adaxially flattened or broadly and shallowly sulcate towards the apex. *Primary rachis* of more than once pinnate leaves abaxially terete or slightly flattened. Axillary cushions visible as slightly discoloured spots or obsolete. *Pinnules* rather close to contiguous or slightly overlapping. Veins immersed except at their extreme bases, once or twice forked, their ends ca. ½ mm apart. Upper pinnules gradually reduced, 1–3 mm long, one or a few connected with the small elliptic-lanceolate or roundish terminal segment. *Sori* around the upper/outer margin; indusium stiff, 0.3–0.5 mm wide, not reaching the margin by 0.2–0.4 mm. Spores medium brown, ca. 35 μ.

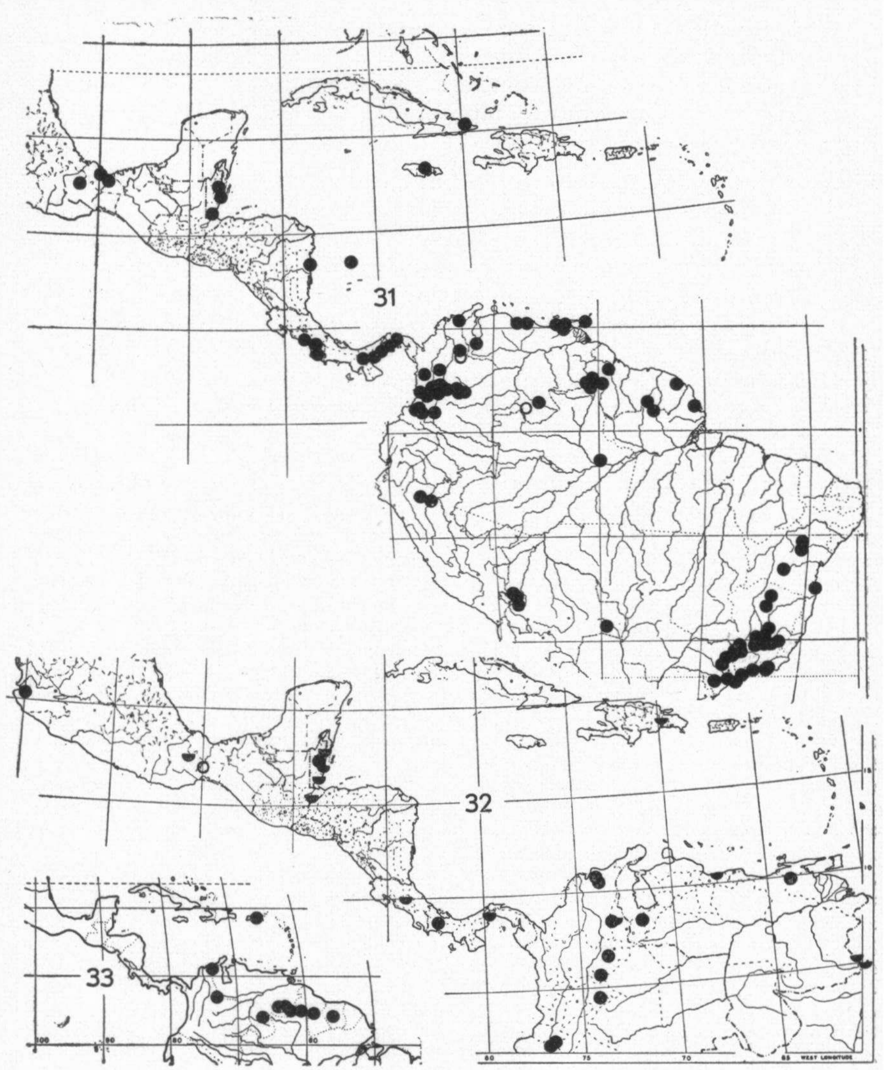
This very widespread species consists of three rather clear-cut varieties which can be distinguished as follows:

1. a. Upper part of the petiole, primary rachis at least near the nodes and secondary rachises at least at the base with thick laterally projecting ridges on the adaxial side, visible from the abaxial side; mostly bipinnate . . . . . b. var. *parvula*
   b. Axes without these ridges 2
2. a. Primary rachis of simply pinnate leaves and secondary rachises of bipinnate leaves abaxially angular to the base or almost to the base, flattened or convex between the angles, red to blackish; leaves very coriaceous, pinnate, or bipinnate with ascending pinnae . . c. var. *jamesoniiformis*
   b. Primary and secondary rachises abaxially at least in a considerable basal portion terete, rarely the greater part angular or sulcate, stramineous or pale brown; leaves herbaceous to coriaceous, once or twice, rarely three times pinnate a. var. *stricta*

a. var. **stricta f. stricta.** **Fig. 26, 73**

Petioles ca. 2–30 cm long, ¾–1.5, mostly 1 mm in diam. near the apex, stramineous to pale brown, or, especially in simply pinnate leaves, tinged with red (mostly less than in *L. portoricensis*), rarely castaneous to blackish, dull or ± shining, abaxially almost always quite terete. Length-ratio petiole : lamina very variable, the petiole from as long as to more than 10 × as long as the lamina. *Lamina* pinnate or bipinnate (very often on the same rhizome), rarely subtripinnate or fully tripinnate, chartaceous to coriaceous (herbaceous in the form discussed below), mostly yellowish green, up to ca. 70 cm long, with one odd up to 6 pinnae to a side when more than once pinnate. *Primary rachis* of more than once pinnate leaves similar to the petiole. *Pinnae* (if any) subopposite or alternate, mostly strongly ascending, parallel to each other or ± contiguous, sometimes spreading in amply bipinnate leaves, the largest ca. 1.5–4 cm apart, the upper ones gradually closer, subsessile or the terminal stalked (up to 2 cm), the lower ones ca. 10–25 cm long, (¾–)1–1.5(–2) cm wide, the upper ones somewhat shorter, the terminal longest in paucijugate leaves. Secondary rachises and rachis of simply pinnate leaves adaxially very shallowly sulcate, the groove hardly concave, abaxially terete in the lower third or often considerably more (rarely less), in the upper part gradually obtusely, then sharply angular, sulcate only near the apex. *Pinnules* ca. 25–70 to a side, the basal ones of simply pinnate laminae and of terminal pinnae, rarely also of lateral pinnae, more remote and/or strongly deflexed, otherwise spreading or slightly deflexed, subsessile, glossy when thick in texture, 4–8 mm long, 3–5½ mm wide; a strongly reduced axillary pinnule present, one or two adjacent pinnules sometimes ± reduced, those in the upper half or one-third of the lamina gradually reduced. Inner margin faintly convex, mostly somewhat divergent from the rachis, lower base hardly cuneate, not stalk-like, upper base shortly rounded or almost rectangular, upper margin convex, more strongly so towards the apex, lower margin straight or, at least in the basal part, concave, apex broadly or shortly rounded, a separate outer margin hardly ever developed. Marginal thickening visible throughout, conspicuous especially along the lower margin, stramineous or pale brown, entire or minutely repand-erose along the soriferous margins, in withering leaves sometimes remaining when the leaf-tissue has dropped out. Sterile pinnules entire or shallowly sinuate or subdentate with small obtuse teeth along the upper/outer margin; fertile pinnules quite entire, apart from the erose marginal strand. Terminal segment 0.4–1 cm long, triangular-lanceolate, obtuse or subacute, soriferous at the base, sometimes also around the apex. Leaf- and pinna-apices often absent in dried specimens, probably remaining immature for a long time and lost in pressing or mounting. Sporangia ca. 195 × 158 μ; annulus with 13–15 indurated cells.

This description applies to the commonest form. In South America,



Maps 31–33: *L. stricta;* map 31: var. *stricta* f. *stricta;* map 32: complete dots: f. *moritziana;* half dots: intermediates between f. *stricta* and f. *moritziana;* map 33: var. *jamesoniiformis.*

particularly in south-eastern Brazil, a large, mostly bipinnate or subtripinnate form occurs with chartaceous or quite herbaceous pinnules which are distinctly crenate or sharply dentate when sterile, often sharply erose-denticulate when fertile; the pinnae are more spreading than mostly in the other form (fig. 73). These specimens have been described as *L. brasiliensis* Desv. and *L. dentata* Fée, and have often been misidentified as *L. guianensis;* because of this, Lindman considered

L. stricta to be only a form of *L. guianensis*. The latter species has, however, narrower, entire or minutely erose indusia, and ssp. *guianensis*, which may be more or less like *L. stricta*, has long-caudate or acuminate pinna-apices. Extreme specimens of the lax form of *L. stricta* look rather different, but there is a large series of intermediates with the typical form, and both are united here under var. *stricta*. Typical specimens of the lax form are marked with an * in the enumeration of specimens.

Distribution: Widespread and common almost throughout tropical America, but rare in most regions where the following variety occurs (map 31). On campos and savannas, on rocky slopes, in scrub, in forest-clearings, in crevices of rocks (sandstone, granite, rarely limestone); the lax form in more shaded situations, in light forests; from sea-level to almost 2000 m.

Vern. name: cumyaic (Boz, Brit. Guiana).

Representative or widely distributed specimens:

MEXICO. OAXACA: Between Comaltepec and Trapiche de la Concepcion, Liebmann 2448 (C); without loc., Galeotti 6470 in part (P, HOLOTYPE of *L. multifrondulosa*; Isotypes in B, G, LE).

VERA CRUZ: Chinameca, Orcutt 3197 (BM, GH, K, MO, US).

BRITISH HONDURAS: Stann Creek Railway, Schipp S 28 (B, F, US); Pine Ridge, Yaccos Lagoon, Peck 677 (F, GH, K, US).

NICARAGUA: Wuonta-Haulover, Schramm 27 (S-PA).

COSTA RICA: Los Palmares, Pittier s.n. (BR, US); Buenos Aires-Osa, Valerio 1822 (US).

PANAMÁ: Las Margeritas-El Valle, Woodson, Allen & Seibert 1278 (MO, NY, US); below Bismark, R. S. Williams 505 (NY, US); Hacienda de la Joya, Panamá prov., Dodge, Hunter, Steyermark & Allen 16883 (G, MO, US).

CUBA. ORIENTE: Airport, vic. of Moa, Acuña 12352 (US).

JAMAICA: Frankfield to Cave Valley, Orcutt 7833 (G, K, MO, UC, US); Bunker's Hill Savanna, Harris 11171 (BM, F, K, MO, NY, US); Bull Head Mountain, Sherring s.n. (K, Paratype of *L. portoricensis* var. *brachypoda*); without loc., Swartz s.n. (S-PA, HOLOTYPE; Isotype in M; fragment and photogr. in US).

ISLA DE PROVIDENCIA (to Colombia, 13°21′ N, 81°23′ W): Summit of highest peak, Proctor 3392 (PH, US).

COLOMBIA. MAGDALENA: Sierra Nevada, Bolinder s.n. (C, S-PA).

CHOCÓ: La Oveja-Quibdó, Archer 1761 (GH, US).

EL VALLE: Buenaventura, Killip 5320 (GH, K, NY, PH, US); Pavas, Pennell 5498 (GH, NY, PH, US); Cali, André 448 (F, K, NY).

CAUCA: Aganche, Pennell & Killip 6283 (US); El Ramal-Río Sucio, w. of Popayan, Pennell & Killip 8134 (GH, NY, PH, US); El Hatico, Lehmann 6076 (B, K, LE, US); Río Piendamo, André 2743 (F, GH, K, NY, US).

NORTE DE SANTANDER: Ocaña, Karsten s.n. (W).

SANTANDER: Mesa de los Santos, Killip & A. C. Smith 15337 (GH, NY, US); Socorro, Lindig 47 (K).

META: Llanos de San Martín, Stübel 710 (B).

CUNDINAMARCA: Cerinza, e. of Gutiérrez, Grant 9762 (US); Bogotá, Karsten 47, 62 (B).

TOLIMA: El Convenio, w. of San Lorenzo, Pennell 3485 (F, GH, K, MO, NY, US).

CAQUETÁ: Florencia-Cordoba, Juzepczuk 6486 (US).

ANTIOQUIA: Canoas, Kalbreyer 1423 (B, K).

Without loc., Cuming 1101 (K, HOLOTYPE of *L. elegans* Hook.).

VENEZUELA. SUCRE: Valley of Cocollar, Steyermark 62382 (F, US).

D.F.: Caracas, Aldridge s.n. (NY); ibid., Bredemeyer s.n. (W, very probably type-material of *L. rigescens*); Cerro de Macarao, Tamayo 4174 (U, US).

MÉRIDA: Near Tovar, Fendler 377 (B, BR, C, F, G, GH, GOET, K, MO, PH, US); ibid., id. 479 (G, GH, GOET, K, MO, PH).

Monagas: La Sabana de las Piedras–Cerro Negro, n.w. of Caripe, Steyermark 61806 (F, US).

Bolívar: La Gran Sabana, R. Uairén, Sta. Elena, Tamayo 2836 (US).

Amazonas La Esmeralda, Upper Orinoco, Ll. Williams 15390, 15432 (US); Esmeralda Ridge, Tate 232 (NY).

State?: Near San Antonio, Otto 695 (B, BM, G, K, L, LE, S–PA, W).

Trinidad: Without loc., Fendler 89 (B, BM, F, G, GH, IA, K, LE, M, NY, PH, UC, US); Lockhart s.n. (GH, K).

British Guiana: Paramacutoi Savanna, Ireng Distr., Boz 523 (C, K); Mazaruni Station, Fanshawe M 240 (BM, K, U); Mt. Roraime, Tate 310 (NY, US).

Suriname: Palaime Savanna, Paloemeu R., Geyskes s.n. (U).

French Guiana: Montsinéri near Cayenne, Leprieur 50 (B, LE, US), 161 (FI, G).

Brazil. Bahia: São Bento, von Lützelburg 113 * (M, NY); Ilheos, Riedel s.n. * (B, GH, S–PA); ibid., Blanchet 3471 (K, MO); ibid., Riedel s.n. (B, FI, G, LE, S–PA, UPS, W).

Rio Branco: Igarapé, Rio Quinô, von Lützelburg 21356, 21536 (M).

Amazonas: Manáos, Cachoeira Grande, Schwacke III 189 (GOET).

Pará: Upper Parú, Sampaio 5578 (B).

Amapá: Cunani, Huber 1113 (G).

Goias: Without loc., Glaziou 22640 (B, G, NY).

Minas Gerais: Viçosa, Mexía 5486 * (B, BM, C, F, G, GH, K, MO, NY, PH, S, U, UC, US); São João del Rei, Lindman A 141 * (K, S, S–PA, UPS); near Cocaes, Gardner 5323 * (K, Holoytpe of var. *tripinnata*; Isotypes in B, BM, FI, G, W); Ouro Preto, Itacolomi, Macedo 2765 * (MO, US); Caraça, Mendonça 420 (B); Serra do Ouro Branco, Schenck 3538 (B).

Rio de Janeiro: Near Rio, Mosén 74 * (B, BR, FI, K, LE, M, S, U); Serra de Estrella, Brade s.n. (NY, UC); Serra dos Orgãos, von Lützelburg 487 (M, S–PA); Corcovado, Mosén 2640 * (C, S, S–PA, UPS); ibid., Pohl sn. * (W).

São Paulo: Rio Grande, Wacket s.n. (Rosenstock-exs. 67) (B, F, M, S, S–PA, US, W); Retiro da Lagem near Cajurú, Regnell III 1474 (B, BR, C, LE, S, S–PA, UPS, US); Ilha de São Amaro near Santos, Wettstein & Schiffner s.n. (W); Santa Anna, Brade 5176 * (NY, UC); Campinas, Heiner s.n. * (S, S–PA); São José do Barreiro, Hoehne & Gehrt 17697 * (BM, GH), near Santos, Burchell 3240 (B, FI, GH, K, L, LE, US, W).

Matto Grosso: Without loc., H. Smith Jr. s.n. * (UC).

Santa Catarina: Without loc., Macrae s.n. (B).

Perú. San Martín: San Roque, Ll. Williams 7760 (F, GH); Lamas, Ll. Williams 6382 (F, US); Zepelacio near Moyobamba, Klug 3418 (B, F, G, GH, K, MO, NY, S, US).

Bolivia: Songo, Bang 905 (B, BM, G, GH, K, LE, M, MO, NY, PH, US, W); near Atan, R. S. Williams 1332 (GH, NY, UC, US); n. of Santiago de Chiquitos, Cutler 7029 (US); San Antonio near Mapiri, Buchtien 1106 * (NY, S–PA, US); Tipuani Valley, Hacienda Casana, Buchtien 7068 * (G, MO, NY, S–PA, UC); Apolo, R. S. Williams 1330 * (GH, NY, UC, US); Cerro Amboró, Herzog 576 * (B).

A specimen collected by Tweedie labelled "Tucumán" in LE; this locality is probably incorrect, as the species has never again been found in this rather well-collected part of Argentina.

Another aberrant form is found in Central and north-western South America (map 32). It differs from the typical form in several characters considered characteristic of *L. stricta* and would be excluded from that species if it were not for a number of intermediates in the same area which link it with typical *stricta*. It may be distinguished as forma **moritziana** (Klotzsch) Kramer, comb. nov.

Basionym: *L. Moritziana* Klotzsch, Linnaea 18:548 (1844), in part.

Lectotype: Moritz 164 in part from Caripe, Venezuela (B!); of the other specimens cited, the second, Schomburgk 272 from British

Guiana was not seen by the present author; the third, Schomburgk 273 in part, also from British Guiana, belongs to *L. guianensis*. Homotypic synonym: *L. guianensis* (Aubl.) Dryand. var. *β major* Hooker, Spec. Fil. I:217 (1844).

Petiole stramineous or pale brown, abaxially often obtusely or even sharply angular or sulcate above, rarely close to the base, then castaneous; *primary rachis* abaxially at least obtusely, often sharply angular, or sulcate; *lamina* bipinnate or subtripinnate, with mostly patent, often decurved pinnae; secondary rachises abaxially terete at the extreme base only, otherwise flattened, angular or sulcate, often more slender than in the typical form; *pinnules* herbaceous or chartaceous, never coriaceous, not rarely more elongate than in the typical form; indusium often less erose, often subentire.

Typical specimens are:

MEXICO. OAXACA: Without loc., Galeotti s.n. (FI).
JALISCO: Sierra Madre Occidental, Hacienda del Ototal w. of San Sebastian, Mexía 1837 (F, G, GH, MO, NY, UC, US).
BRITISH HONDURAS: Gracie Rock Pine Ridge, Sibun R., Gentle 1536 (GH, K, MO, NY, UC, US).
COSTA RICA: Without loc., Endres 16 (BM, W).
PANAMÁ: Cerra Vaca, Chiriquí prov., Pittier 5368 (US); Boquete, ibid., Davidson 837 (F, GH, MO, US).
COLOMBIA. MAGDALENA: Santa Marta, Mt. Cuaco, H. H. Smith 938 (BM, F, GH, K, MO, NY, PH, S-PA, US); ibid., Las Partidas, H. H. Smith 1089 (NY); ibid., Dos Aguas, Carriker 27 (US); Santa Marta, Purdie s.n. (BM).
CAUCA: Tetilla near Popayan, Stübel 88 (B); El Tambo, Kj. von Sneidern 2181 (G, S).
NORTE DE SANTANDER: Ocaña, Kalbreyer 399 (B, K).
SANTANDER: Socorro, Karsten s.n. (W); ibid., Lindig 62 (B, BM, K).
CUNDINAMARCA: Bogotá, Karsten 63 (B).
BOYACA: Puente Nacional, Karsten s.n. in part (LE); Cune, Lindig 63 (B, BM).
Without loc., Lehmann 5030 (F, K, US).
VENEZUELA. MÉRIDA: Between Maracas and Chorona, near Tovar, Fendler 378 in part (BR, G, K); ibid., id. 380 (B, GOET, K).
MONAGAS: Caripe, Moritz 164 in part (B, HOLOTYPE; Isotype in BM).

As intermediates between f. *moritziana* and f. *stricta* may be cited (map 32):

MEXICO. OAXACA: Choapam, Yaveo, Mexía 9138 (B, F, G, GH, K, MO, NY, Pic.-Ser., S-PA, U, UC, US).
BRITISH HONDURAS: Manatee Pine Ridge, Belize distr., Gentle 89 (US); Sarawee Pine Ridge, Stann Creek distr., Gentle 2698 (NY, US); Monkey River, Toledo distr., Gentle 3687 (GH, K, MO, NY).
GUATEMALA: N. of Quiriguá, Weatherwax 225 (MO).
HONDURAS: Without loc., Berry s.n. (IA).
COSTA RICA: Near El General, San José prov., Skutch 4105 (BM, K, MO, NY, S-PA, US).
COLOMBIA. NORTE DE SANTANDER: Ocaña, Schlim 53 p.p. mai (BR, FI, G, GH, L, W).
VENEZUELA. ARAGUA: Near Choroni, Vogl s.n. (M).
BRAZIL. RIO BRANCO: Igarapé of Rio Quinô, von Lützelburg 21364 in part (M); summit of Mt. Roraima, von Lützelburg 21609 (M).
HISPANIOLA. SAN DOMINGO: Bayaguana, slope of Loma Managuá, prov. San Domingo, Ekman H 11100 (B, F, GH, K, NY, S, UC, US).

b. var. **parvula** (Fée) Kramer, comb. nov. **Fig. 74**

Basionym: *L. parvula* Fée, 11^{e} mém. 17 (1866), Hooker & Baker, Syn. Fil. 1st ed. 452 (1868), 2^{dn} ed. app. 471 (1874); Jenman, Jo. Bot. 25:98 (1887); W. Ind. Gui. F. 78 (1899); Diels, N. Pfl. I^{4}:221 (1902); Knuth, Fedde Rep. Beih. 43 (1):32 (1926).
Type: Germain s.n. from Trinidad (P!).

Heterotypic synonyms: *L. gracilis* Klotzsch, Linnaea 18:549 (1844), non Blume 1828. Type: Schomburgk 273 from British Guiana (B!).

L. aquatica Jenman, W. Ind. Gui. F. 78 (1899). Type: Jenman s.n. from Macouria Creek, Essequibo R., British Guiana (NY!, 2 sheets).

Petioles ca. 10–60(–80) cm long, slightly shorter than to almost 3 × as long as the lamina, $^{2}/_{3}$–1$\frac{3}{4}$, mostly 1–1$\frac{1}{2}$ mm in diam. near the apex, stramineous or less often reddish-brown, dull or somewhat shining, adaxially flattened almost to the base, broadly and shallowly sulcate above, with obtuse angles, abaxially terete but often flattened above, near the apex with lateral ridges as described for the rachises. *Lamina* bipinnate, rarely simply pinnate on mature rhizomes, ca. 10–35(–60) cm long, firmly herbaceous to chartaceous or mostly coriaceous, dark brownish to dark yellowish-green, paler on the dorsal side, with from one odd to 9 primary pinnae to a side and a conform terminal one. *Primary rachis* adaxially mostly with a deeper groove than the petiole, abaxially terete or slightly flattened with rounded angles, laterally near the adaxial surface with a groove which runs below the edges of the adaxial groove which are visible as ledges from the abaxial side (Fig. 7); these may be evident at the nodes only, sometimes only in the lower part of the primary rachis, and are occasionally conceiled by the bulging lateral surfaces (see also p. 114 and fig. 74). Axillary cushions hardly or not swollen but usually visible as small dark dots. *Pinnae* mostly subopposite, mostly strongly ascending, often contiguous, 2–7(–9) cm apart, the upper ones sometimes closer, mostly about 7–12(–30) cm long, 0.5–1(–1.5) cm wide, the upper ones shorter in plurijugate leaves, the terminal longest in paucijugate ones, practically sessile or the terminal one with a stalk of 0.5–2 cm, linear, gradually narrowed from just above the base to the long-acuminate apex. Secondary rachises (and rachis of simply pinnate leaves) adaxially with a rather wide and deep channel, abaxially round at the base, then angular, finally narrowed and sulcate, the relative length of these portions quite variable; lateral surfaces channelled in the same way as described in the primary rachis at least at the base. *Pinnules* ca. 25–60 (rarely up to ca. 100) to a side, alternate or the lower ones subopposite, mostly not contiguous, roughly oval, 3–6 mm long, 2–4.5 mm wide, spreading, often laxly ascending or the lower ones slightly deflexed; a strongly reduced axillary pinnule present, one or two additional pinnules on the acroscopic side may be slightly reduced. Basal pinnules of simply pinnate blades not reduced. Inner margin straight or somewhat convex, often touching or overlapping the rachis, lower base very shortly cuneate, hardly stalk-like, upper base of pinnules shortly rounded, lower margin mostly shallowly S-shaped, rarely more strongly concave, upper margin evenly rounded or more convex towards the apex; apex of pinnules rounded. Marginal thickening stramineous, conspicuous, especially on the abaxial side, erose in fertile pinnules, subentire to faintly sinuate or repand along the upper/outer margin in sterile ones. Veins sometimes slightly elevated. Terminal segment up to 7 mm long, 3 mm wide. Sori not rarely conceiled by the incurved margin; indusium strongly reflexed and conceiled at full maturity. Sporangia ca. 185 × 160 μ; annulus with 11–13 indurated cells; spores 32?

Distribution: Mostly confined to northern South America; most common in Trinidad and the Guianas (map 34). Almost always in moist places in savannas, in bogs, and along watercourses; rarely in forests or among rocks. Elevations not indicated, but probably restricted to lower altitudes (below 1000 m).

Vern. name: Koeliki kaloeabandikoro (Arowakkan, Suriname).

Representative specimens:

CUBA. ORIENTE: S. side of Bahia de Moa, Howard 5897 (GH, MO, NY, U).
BRITISH HONDURAS: All Pines, Schipp S 197 (B).
NICARAGUA: Wuonta–Haulover, Schramm 34 (S–PA); Mosquito-coast, Wullschlaegel s.n. (B).
COLOMBIA. CHOCÓ: Quibdó, Río Atrato, Archer 1770 (NY, US).
META: R. Zanza–R. Güejar, n. end of Cordillera Macarena, S. G. Smith & Idrobo 1547 (UC, US).
TRINIDAD: Aripo Savanna, Britton & Britton 2927 (GH, K, NY, US); ibid., Broadway 2406 (BR, G, MO, S–PA, US), 5283 (F, MO, U, UC); ibid., Fendler 89β (B, GH, LE, MO, NY, US), and several other collections; Arima, Woodford 58 (K); without loc., Germain s.n. (P, HOLOTYPE).
BRITISH GUIANA: Kamakusa, Upper Mazaruni R., de la Cruz 4066 (F, GH, MO, NY, PH, UC, US); Mazaruni Station, Sandwith 1014 (BM, K); ibid., Fanshawe M 332 (K); Macouria Creek, Essequibo R., Jenman s.n. (NY, 2 sh., HOLOTYPE of *L. aquatica*); without loc., Schomburgk 273 (B, 3 sh., HOLOTYPE of *L. gracilis* KL.; Isotype in BM).
SURINAME: Line Moengo tapoe–Grote Zwiebelzwamp, Lanjouw & Lindeman 568, 726, 767, 795, 1012 (U); Couroupina Creek, Kappler 1737 (B, C, FI, G, MO); Cordonpad near Joden-Savanna, Kegel 1052 (GOET).
FRENCH GUIANA: Montsinéri, Leprieur 72 in part (FI, G, L), 167 (FI, G, NY); Mana, Perrottet s.n. (G); without loc., Leprieur s.n. (B, F, FI, K, L, NY).
BRAZIL. AMAZONAS: Bella Vista, R. Uaupés, Baldwin 3544 (US).
AMAPÁ: Cunani, Huber 1110 (G).
PARÁ: Barra do Rio Tapajoz near Santarem, Spruce 931 (B, BM, C, G, GH, GOET, K, L, LE, NY, US, W).
MARANHÃO: Without loc., G. Don 142 (BR).
PERNAMBUCO: Malti da Caxanga, Ridley, Lea & Ramage s.n. (BM); Malti da Iguarassa, id. s.n. (B, BM).
BAHIA: Ilheos, Riedel s.n. (LE, NY); Marians, Riedel s.n. (L, LE).
RIO DE JANEIRO: Near Nova Friburgo, Beyrich s.n. (L); near Rio, Beyrich 1 (GOET); ibid., Chamisso s.n. (LE).
PERÚ. SAN MARTÍN: Pacasmayo–Moyobamba, Stübel 1061 (B).
A specimen labelled „Panama" from R. W. Rawson's herb. in BM; specimens collected by L'Herminier said to have come from Guadeloupe in BM and G, this locality probably incorrect, never again found on that island.

Generally var. *parvula* can easily be separated from var. *stricta*, especially in the Guianas and Trinidad. There are, however, a few specimens which, though in size and shape of pinnules much like var. *parvula*, have only traces of the rachis-ridges or none at all which characterize that variety, and can be said to be intermediates between the two varieties. Because of their existance *L. parvula* Fée is reduced here to a variety. The following intermediates may be cited:

VENEZUELA. AMAZONAS: Maroa, R. Guainía, Ll. Williams 14331 a (US); Yavita, id. 13902 (F, US), 14065 (F, GH, US); La Esmeralda, Croizat 123 (MO, U).
BOLÍVAR: Cerro Guaiquínima, Upper R. Paragua, Cardona 949 (US).
BRAZIL. AMAZONAS: Içana, Pirauána, von Lützelburg 22692 (M, NY, UC).
PIAUI: Boqueirão near São João do Piaui, von Lützelburg 226 (M, US).
BAHIA: Moritiba, Blanchet 3471 (BR, C, G, W); Marians, Riedel s.n. (B, GH, L, S–PA).

They are mostly restricted to the Amazon region, and their total number, as compared with that of typical specimens of var. *parvula*, is small.

c. var **jamesoniiformis** Kramer, var. nov. **Fig. 76**

Lamina percoriacea, pinnata vel bipinnata, pinnis valde adscendentibus, rhachide primaria laminae simpliciter pinnatae et rhachidibus secundariis facie abaxiali usque ad basin constanter angularibus, pinnulis rigidis, rotundatis, longitudine latitudinem sesquies vel minus superante, approximatis vel laxe imbricatis (interdum infimis exceptis), soris margine pinnularum recurvata saepe obtectis.

Typus: Maguire 24377 from Tafelberg, Suriname (US).

Petioles 5–54 cm long, from about half (rarely less) as long to more than 3 × as long as the lamina, $^2/_3$–1½(–2) mm in diam. near the apex, dark red to black dull, abaxially terete or with short lateral ridges at the extreme apex. *Lamina* once or twice pinnate, very coriaceous and rigid, medium green to dark greenish-brown, greyish or blackish, dull or slightly lustrous, ca. 10–35 cm long, linear when simply pinnate, otherwise with one odd to 3 (rarely to 5) pinnae to a side and a conform terminal one. *Primary rachis* of bipinnate leaves abaxially terete or angular above, of simply pinnate leaves as the secondary rachises of bipinnate ones. Axillary cushions not seen. *Pinnae* subopposite or almost so, strongly ascending (less so in plurijugate leaves), 5–20 cm long, ca. 3?4–1½ cm wide, widest at or slightly above the base, gradually narrowed to the apex, subsessile or the terminal short-stalked, the terminal by far the longest in paucijugate leaves. Secondary rachises (and primary rachis of simply pinnate leaves) red to blackish, abaxially laterally sharply angled, the angles extending almost to the base (or to the upper part of the petiole in simply pinnate leaves), the surface between them convex towards the base (and then sometimes almost conceiling the lateral angles) or for the greater part flattened. Rachis of terminal pinna abaxially often terete in a considerable basal portion. *Pinnules* ca. 30–100 to a side, close to slightly imbricate (succubous) or a few basal ones more remote, spreading or rarely slightly deflexed, mostly alternate throughout, roundish or occasionally slightly falcate, from 3 × 2 — 7 × 5 mm, a slightly reduced axillary pinnule mostly present. Inner margin slightly convex, touching or overlying the rachis, lower base shortly cuneate, hardly stalk-like, upper base rounded, lower margin shallowly S-shaped, the concavity mostly shallow, upper margin ± evenly convex, apex broadly rounded. Marginal thickening stramineous to medium brown, distinct throughout, entire or minutely repand along the upper/outer margin; margin of sterile pinnules entire or shallowly crenate in leaves of juvenile rhizomes. Terminal pinnule roundish, fertile along the distal edge. Sporangia ca. 215 × 165 μ; annulus with 10–12 indurated cells (fig. 21); indusium strongly reflexed at full maturity; sori often conceiled by the incurved margin.

Distribution: Northern South America (mostly Guayana) and Puerto Rico (map 33). In thickets and open forests or on exposed rocks (mostly sandstone), from ca. 1000–2300 m.

Vern. name: ari-epana-ú (Venezuela, Steyermark).

PUERTO RICO: Sierra de Luquillo, Sintenis 1398 (B, BM, GH, GOET, K, L, LE, M, NY, S-PA, US); ibid., P. Wilson 96 (NY, US); ibid., Blauner 299 (B, BM, G); Mt. El Yunque, Sargent 307 (US); without loc., Schwanecke s.n. (B, GH); Palacky s.n. (W).

COLOMBIA. MAGDALENA: Santa Marta, Purdie s.n. (NY).

SANTANDER: Mesa de los Santos, Killip & A. C. Smith 15035 in part (US).

VENEZUELA. AMAZONAS: Cerro Yavé, Phelps & Hitchcock 9 (NY, US); Mt. Duida, summit, Tate 777 (NY); ibid., Steyermark 58246, 58282 (F, MO, NY, US).

BOLÍVAR: Auyan-tepuí, Tate 1269 (NY); Uaipan-tepuí, Phelps & Hitchcock 374 (NY); Ptari-tepuí, Steyermark 59502 (F, US), 59735 (F, MO, NY, US); Chimantá-Massif, summit of Abácapa-tepuí, Steyermark 74846 (US); Gran Sabana, Steyermark 58576 (F, NY, US).

BRITISH GUIANA: Kaieteur Savanna, Jenman s.n. (NY); ibid., Sandwith 1284 (BM, K, U); ibid., Jenman 1387 (K); ibid., Im Thurn s.n. (K); Kaieteur plateau, Maguire & Fanshawe 23159 (A, F, G, K, MO, NY, U, UC, US); Potaro R., Santini s.n. (L); Mt. Roraima, McConnell & Quelch 76 (BM); ibid., Im Thurn 149, 150 (BM, K, US); ibid., summit' McConnell & Quelch 497, 557 (K); without loc., Jenman s.n. (US).

SURINAME: Tafelberg, Maguire 24377 (US, HOLOTYPE; Isotypes in A, F, G, K, MO, NY, S-PA, U, UC).

The combination of very coriaceous pinnules, strongly ascending pinnae, dark axes, and abaxially angular rachises of the highest order characterize this variety very well, although these characters occur also in other varieties of *L. stricta*, but not together. Var. *jamesoniiformis* is, as a whole, very clear-cut and could perhaps be raised to subspecific or specific rank, but it is very close to typical *L. stricta;* intermediates have hardly been found, not even in the few localities where both varieties occur side by side (Santa Marta, Mt. Roraima). Simply pinnate leaves and pinnae of paucijugate bipinnate ones resemble a species of the genus *Jamesonia;* the specimens from Puerto Rico are smaller, not unlike *Polypodium moniliforme* Lag.

The closest relative of *L. stricta* is *L. portoricensis;* the differences are discussed under that species. *L. javitensis* is also allied (see there). *L. pallida* is sometimes confused with *L. stricta;* it has more strongly erose indusia, sori not covered by the reflexed margin, and monolete spores.

28. **Lindsaea javitensis** Humboldt & Bonpland ex Willdenow, Sp. Pl. V:424 (1810); Poiret in Lamarck, Encycl. Suppl. III:448 (1813); Kunth in H. B.K., Nov. Gen. & Spec. I:18 (1815); Desvaux, Prodr. 313 (1827); Sprengel, Syst. Veget. IV: 80 (1827); Presl, Tent. Pterid. 131 (1836); not of Raddi, Plant. Bras. Nov. Gen. 56 (1825). **Fig. 66, 67**

Type: Humboldt & Bonpland s.n. from Yavita, Venezuela (Willdenow-herbarium in B, not seen; photographs in BM and U!).

Misapplied name: *L. stricta* of Hooker, Spec. Fil. I:216 (1844), in part, non Dryand.

Petioles reddish brown, abaxially terete; lamina bipinnate with conform terminal pinna, coriaceous; secondary rachises abaxially angular; pinnules subovate to tongue-shaped, almost 2 × as long as wide, the upper ones gradually and strongly reduced; veins immersed or slightly elevated; sori continuous; indusium irregularly repand-erose; spores trilete.

Rhizome creeping, ca. 4 mm in diam.; scales pale castaneous, shining, lanceolate, long-acuminate, up to 2 mm long and 0.4 mm wide, with up to 10 rows of cells at the base. *Petioles* close, (15–)25–50 cm long, 1.5–2 mm in diam. near the apex, of a very characteristic reddish-brown colour suffused with purple, darker at the extreme base, rather glossy, terete, only the upper part of the adaxial surface flattened to shallowly sulcate, the borders not sharp. *Lamina* roughly as long as the petiole, yellowish to brownish green, with 6–15 pinnae to a side and a conform terminal one; lateral pinnae subopposite, or the upper ones (rarely all) alternate, 3–5 cm apart, or the upper ones closer, patent under an angle of ca. 30–50°, short-stalked, the lateral a few mm, the terminal up to 1 cm; lower pinnae about 10–15 cm long, 1–1.5 cm wide, the terminal longer than the slightly reduced upper lateral ones. *Primary rachis* similar to the upper part of the petiole. Upper half or two-thirds of the pinnae very gradually narrowed, the apex thus acuminate, the base shortly narrowed. Secondary rachises flattened abaxially and adaxially, with sharp borders, shallowly sulcate towards the apex, only a short basal portion terete on the abaxial side. *Pinnules* ca. 35 to 50 to a side, subopposite to alternate, spreading or slightly ascending, a few somewhat reduced ones at the base, a strongly reduced axillary one sometimes present, rather close and regularly spaced but not contiguous, 5–7 mm long, 2.5–4 mm wide. Inner margin straight, parallel, often touching the rachis, upper edge rounded, especially towards the apex, where it gradually passes into the straight lower margin; upper base rounded, lower base hardly stalk-like. All edges, also in sterile pinnules, entire. Marginal thickening strong and conspicuous along the lower edge, otherwise slightly weaker, pale brown. Veins on both surfaces elevated near their bases, sometimes inconspicuously raised throughout, not stramineous, simple or once forked, ca. ½–¾ mm apart at the margin; main vein for ¼ or ⅓ of its length united with the marginal strand, for the rest slightly divergent from it. Upper pinnules gradually and strongly reduced, the uppermost about 1 mm long, but hardly confluent, with a slightly larger (2–3 mm), almost free terminal segment with blunt apex. *Sori* along the upper/outer margin; indusium rigid, ca. 0.2 mm wide, almost equalling the margin, ± reflexed at full maturity. Sporangia 200–205 × 160 μ; annulus with 10–13 indurated cells; spores rather pale brown, ca. 32–40 μ.

Distribution: North-western South America; apparently uncommon (map 30). On campos and savannas, in gravel and among boulders in sandy soil, up to 250 m.

COLOMBIA. VAUPÉS: Río Kananarí, trib. of R. Apaporis, Cerro Isibukuri, Schultes & Cabrera 14528 (US).

AMAZONAS–VAUPÉS: Cachivera de Jirijirimo, R. Apaporis, Schultes & Cabrera 12965 (US).

VENEZUELA. AMAZONAS: Yavita, Humboldt & Bonpland s.n. (Type, herb. Willdenow in B, not seen; photographs in BM and U); "Caracas", prob. incorrect, without coll. or number (S-PA).

BRITISH GUIANA: Amatuk Portage, Potaro R., Sandwith 1255 A in part (K; juv.).

BRAZIL. AMAZONAS: Rio Negro, São Felippe, von Lützelburg 22605 (NY, UC); ibid., id. 22387 (M, UC); Rio Negro, Tapacal, von Lützelburg 22902 (M, UC).

Probably most closely allied to *L. rigidiuscula*, which differs by larger pinnules and abaxially sharply angular petiole; also to *L. stricta*, which has more strongly immersed veins, fewer, more strongly ascending pinnae (except in the herbaceous, mainly, s.e. Brazilian form), and upper margins often incurved around the sorus. The three species agree in their small, rigid pinnules, which is in accordance with their preference for open habitats. *L. javitensis* was incorrectly referred to *L. guianensis* by Christensen (Ind. Fil. p. 394).

29. **Lindsaea rigidiuscula** Lindman, Hedwigia 43:308 (1904); Knuth, Fedde Rep. Beih. 43 (1):32 (1926); Sampaio, Arch. Mus. Nac. Rio de Jan. 32:35 (1930). **Fig. 68**

Type: without collector or number, said to be from Caracas, Venezuela (S-PA!).

Homotypic synonym: *L. nervosa* Lindman, Ark. f. Bot. 1:199 (1903) pl. 8 fig. 5, non Mettenius, 1861.

Petioles dull olivaceous with paler angles, quadrangular; lamina bipinnate with conform terminal pinna, chartaceous; primary and secondary rachises abaxially angular; pinnules semi-ovate or subfalcate, ca. 2½ × as long as wide, the upper ones gradually reduced; veins elevated; terminal pinnule distinct but small; sori continuous; indusium subentire or slightly repand; spores trilete.

Rhizome creeping, 2–3 mm in diam.; scales lanceolate, long-acuminate, up to 1¾ cm long, 0.3 mm wide, with up to 9 rows of cells at the base. *Petioles* close, 6–43 cm long, from half as long as to slightly longer than the lamina, 1–2 mm in diam. at base of lamina, a short basal portion (a few cm) terete, otherwise quadrangular. *Lamina* brownish to yellowish green, with 1–8 pinnae to a side and a conform terminal one. *Primary rachis* similar to the upper part of the petiole. Axillary cushions present, inconspicuous. *Pinnae* subopposite or the upper ones alternate, the lower 3–7 cm apart, the upper closer, short-stalked (up to 8 mm) to sessile, forming an angle of 30–45° (rarely more) with the primary rachis, up to 30 cm long, the upper ones much shorter in plurijugate leaves, up to only 5 cm long, 15–37 mm wide, mostly ca. 20–30 mm, very shortly narrowed at the base, the upper two-thirds very gradually tapering to the apex. Secondary rachises abaxially terete at the extreme base, otherwise angular, adaxially with a narrow dark or reddish brown channel bordered by stramineous ridges. *Pinnules* 15 to 50 to a side, subopposite or alternate, spreading or, especially the upper ones, laxly ascending, never decurved, the larger ones 9–17 × 4–8 mm, subsessile, 1–3 basal ones on each side reduced, a strongly reduced axillary pinnule usually present. Inner margin ± parallel to the sec. rachis, often touching it, lower margin substraight or concave, upper margin rather strongly convex, especially towards the apex which is subacute, rounded in sterile or incompletely fertile pinnules. Margins entire in fertile pinnules, very shallowly crenate in sterile ones, the incisions not over 0.4 mm deep, the lobes uni- or binerval, rounded or subacute. Marginal strand narrow and stramineous except at the base of the lower edge where it is thick and often reddish. Veins very close, 0.5–0.75 mm apart at the margin, conspicuously elevated on both surfaces, stramineous to pale green, two to three times forked; the pinnules are stiff through the close veins and indurated margin. Upper pinnules gradually reduced, but not confluent; terminal pinnule always distinct, oblong-lanceolate, obtuse, mostly lobed at the base, 5–10 mm long, often soriferous. *Sori* along the upper/outer margin. Indusium rigid, ca. 0.2 mm wide, not reaching the margin by a distance equalling its width, reflexed and conceiled at full maturity. Sporangia ca. 160 × 115 μ; annulus with 10–13 indurated cells; spores medium brown, ca. 34 × 30 μ.

Distribution: Northern South America; apparently uncommon (map 36). On campos, glades, and forest clearings and in light secondary forest, often on sand, up to 130 m.

COLOMBIA. VAUPÉS: Río Kananarí, Cerro Isibukuri, Schultes & Cabrera 15070 (US).
VENEZUELA. AMAZONAS: Maroa, Río Guainía, Ll. Williams 14329 (F, GH, US); ibid., id. 14263 (F, US); Yavita, Upper Atabapo, Ll. Williams 16126 (US). "Caracas", probably coll. in southern Venezuela, without collector or number (S–PA, HOLOTYPE; fragment in C. Chr. in BM).
BRAZIL. AMAZONAS: R. Uaupés, Iutica, von Lützelburg 23601 (M); Tunuy, R. Içana, Koch 65 (B).
GOIAS: Sucuriu on Rio das Femeas, von Lützelburg 1509 in part (UC).

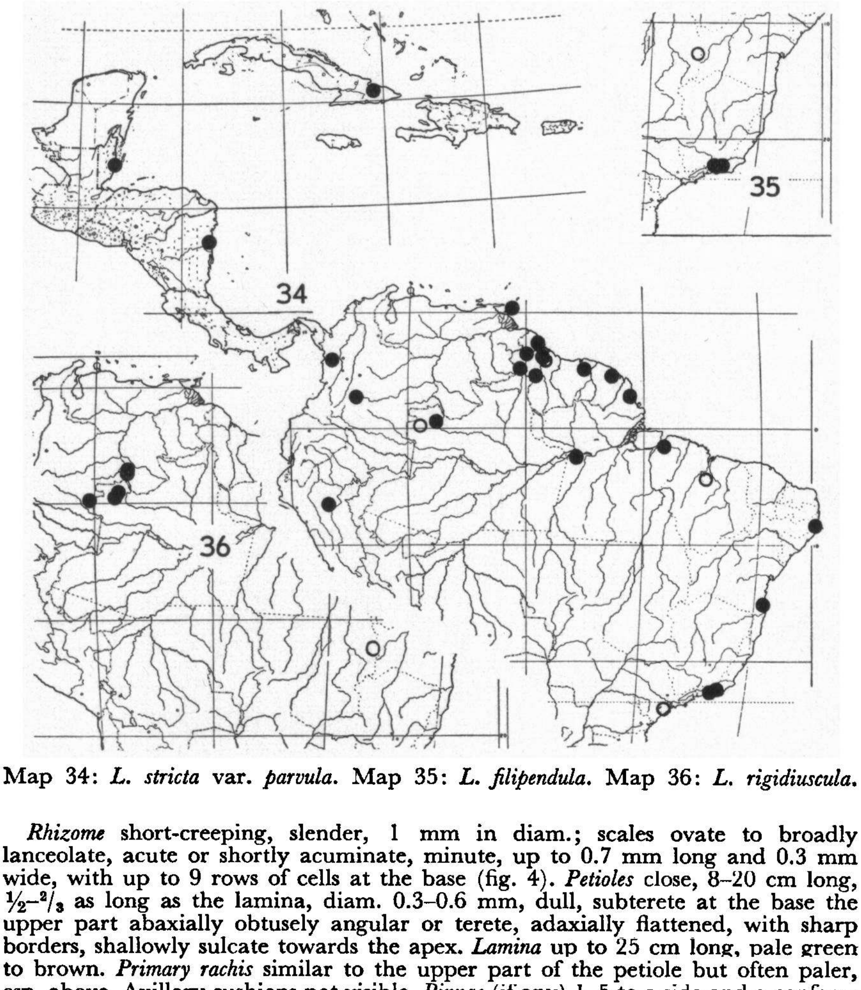
The combination of rigid pinnules with raised veins and abaxially angular axes serves to distinguish this species easily. Its closest relative seems to be *L. javitensis;* the differences are discussed under that species. It is unlikely that the type was collected near Caracas, as it was never found again in that vicinity, and all other collections are from the Guianan or Brazilian shields.

30. **Lindsaea filipendula** (Rosenstock) Kramer, comb. nov. **Fig. 72**

Basionym: *L. guianensis* (lapsu: *gnianensis*) (Aubl.) Dryand. var. *filipendula* Rosenstock, Fedde Rep. 20:93 (1924); *L. filipendula* Ros., ibid., nom. provis.

Lectotype: von Lützelburg 141 from Sucuriu, Rio das Femeas, Goias, Brazil (M!).

Petioles reddish brown to blackish, very delicate, wiry; lamina simply pinnate, bipinnate with conform terminal pinna, or rarely subtripinnate, herbaceous; pinnules dimidiate-ovate to dimidiate-elliptic or subtriangular, ca. 1½ × as long as wide, the upper ones gradually reduced; upper/outer margin conspicuously and very irregularly erose-lacerate in fertile pinnules; sori continuous; indusium very wide, equalling or surpassing the margin, irregularly lacerate; spores trilete.



Map 34: *L. stricta* var. *parvula*. Map 35: *L. filipendula*. Map 36: *L. rigidiuscula*.

Rhizome short-creeping, slender, 1 mm in diam.; scales ovate to broadly lanceolate, acute or shortly acuminate, minute, up to 0.7 mm long and 0.3 mm wide, with up to 9 rows of cells at the base (fig. 4). *Petioles* close, 8–20 cm long, ½–²/₃ as long as the lamina, diam. 0.3–0.6 mm, dull, subterete at the base the upper part abaxially obtusely angular or terete, adaxially flattened, with sharp borders, shallowly sulcate towards the apex. *Lamina* up to 25 cm long, pale green to brown. *Primary rachis* similar to the upper part of the petiole but often paler, esp. above. Axillary cushions not visible. *Pinnae* (if any) 1–5 to a side and a conform terminal one, the lower ones (and simply pinnate laminae) 10–15 cm long, 1–1.5(–2) cm wide; lateral pinnae somewhat decurrent, subopposite or alternate, short-stalked to subsessile, laxly spreading under an angle of 40–50°, rather widely spaced, 2–3 cm apart, the upper ones closer and shorter, sometimes considerably reduced, terminal pinna mostly distinctly stalked, longer than the lateral ones. Secondary rachises abaxially stramineous to pale brown, with a sudden transition from the darker colour of the primary rachis at the point of insertion, in the terminal pinna more gradual, terete, adaxially with a narrow groove, concolorous with the primary rachis. *Pinnules* ca. 20–35 to a side, mostly alternate throughout, the larger ones rather constant in size, 6–7 mm long, 4–5 mm wide, widest at the base, the basal ones hardly reduced, even the axillary one which is invariably present but little reduced but somewhat adnate, the other pinnules short-stalked, more or less spreading, the lower ones their width or more apart, the upper ones closer but not contiguous. Inner margin ± straight, mostly touching or slightly overlying the sec. rachis, upper base shortly rounded, lower base long-cuneate, lower margin convex, upper margin slightly and evenly convex, conspicuously and very irregularly erose-lacerate in fertile pinnules, superficially crenate or sinuous to subentire in sterile ones, this difference even observed between sterile and fertile parts of the upper margin of a single pinnule; apex broadly rounded, no outer margin developed. Marginal thickening not conspicuous but evident, stramineous to pale reddish, virtually absent in the lacerate upper margin of fertile pinnules. Veins once or the basal one twice forked, immersed, ¾–1 mm apart at the margin; main vein distinctly intramarginal, ca. ½ mm above the lower margin near the apex. Upper pinnules (in the upper ²/₃ or more or the pinna) gradually reduced, the uppermost ones ca. 2–5 mm long, confluent into a lobed spathulate often soriferous terminal segment. *Sori* along the upper margin; indusium 1–1.5 mm wide, very irregularly and (under the lens) conspicuously lacerate, sometimes cleft, in addition often plicate, pale, often with reddish margin, not reflexed at maturity. Sporangia 210–220 × 150 μ; annulus with 11–14 indurated cells; spores almost globose, medium to dark brown, ca. 32 μ, 32?

Distribution: Eastern Brazil (map 35). No ecological data extant.

BRAZIL. GOIAS: Sucuriu on Rio das Femeas, von Lützelburg 141 (M, LECTOTYPE; Isotypes in NY, UC).

RIO DE JANEIRO: Serra d'Estrella, Cortisso, von Lützelburg 252 (C, M, NY, UC, US, W, Paratypes); Serra dos Orgãos, Morro Assú, von Lützelburg 13751 (M, Paratype).

Not at all close to *L. guianensis* and generally of doubtful alliance among the American species; possibly distantly related to *L. stricta* or *L. ovoidea*, perhaps to *L. tenuis* with which it shares the wiry axes and the minute broad scales. The very delicate axes and the extremely wide, lacerate indusia are most distinctive.

31. **Lindsaea tenuis** Klotzsch, Linnaea 18:550 (1844); Hooker, Spec. Fil. I:218 (1844); Baker, Fl. Bras. I²:353 (1870); Kuhn, Chaetopt. 26 (1882); Jenman, W. Ind. Gui. F. 79 (1899); Diels, N. Pfl. I⁴:221 (1902); Posthumus, Fl. Surin. Suppl. 72 (1928). **Fig. 28**

Type: Schomburgk 1185 from British Guiana (B!).

Heteroptypic synonym: *Lindsaea filiformis* Hooker, Spec. Fil. I:218 (1844): Hooker & Baker, Syn. Fil. 1st ed. (1868), 2nd ed. (1874) 106. Type: Schomburgk 1185 from Mt. Roraima, British Guiana (K!).

Petioles dark, very delicate, wiry; primary rachis similar, flexuose; lamina bipinnate with conform terminal pinna, chartaceous; pinnules obliquely triangular, ca. 2 × as long as wide, not over 6 × 3 mm, the upper ones somewhat reduced, the terminal segment sometimes distinct; sori continuous; indusium rather wide, minutely erose to laciniate, about equalling the margin; spores trilete.

Rhizome creeping (short?), delicate, ca. ¾ mm in diam.; scales minute, ovate, obtuse, acute, or apiculate, up to 0.35 mm long and 0.2 mm wide, with up to 4 rows of cells at the base. *Petioles* 5–12 cm long, much shorter than the lamina, 0.4–0.5 mm in diam., shining, subterete except for the upper part of the adaxial side which has a flattened portion with sharp paler borders, the surface between them somewhat sunken. *Lamina* bipinnate (very rarely simply pinnate), ca. 10–85 cm long, 4–10 cm wide, medium to brownish green, with 4–? pinnae to a side and a conform terminal one. Axillary cushions not seen. Pinnae in subopposite pairs, the members of a pair up to 1(–2) cm apart, the lower pairs in large leaves very remote, up to 12 cm apart, the upper ones gradually closer; mostly laxly ascending, forming with the primary rachis an angle of ca. 45°, subsessile to short-stalked (–7 mm), 3.5–6 cm long, 1–1.5 cm wide, mostly not strongly narrowed to the apex, often narrowed at the base. Secondary rachises similar to the primary but paler in their upper part, mostly reddish, ca. 0.2 mm in diam. *Pinnules* 7–13 to a side (in the terminal pinna of paucijugate leaves, which is the largest, up to 35), alternate, subsessile, not close, separated by spaces approximately equal to their width, never contiguous, the largest 4–6 mm long, 2–3 mm wide, narrowed-obtuse at the apex. Lower base with a short stalk-like base, inner margin convex, divergent from the sec. rachis, upper base obtuse, lower margin straight or slightly convex, upper margin subentire or in some of the sterile pinnules crenate, in addition mostly minutely erose. Marginal thickening obsolete except at the base of the lower margin where it is reddish. Veins immersed, hidden, simple or once forked, their ends 1–1.5 mm apart; small pinnules with only 2 veins. Lower pinnules sometimes very gradually reduced, the basal ones then minute; upper pinnules somewhat, but not very strongly, reduced, one of them sometimes connected by a wing with the terminal segment (pinnule) which is about the same size as one of the larger lateral ones, asymmetric, lanceolate, soriferous. *Sori* along the upper margin; indusium ca. 0.5 mm wide, ± reflexed at full maturity. Sporangia ca. 170 × 120 μ; annulus with 9–10 indurated cells; spores pale brown, ca. 26–31 μ.

Distribution: Venezuela and British Guiana; apparently extremely rare (map 26).

VENEZUELA. BOLÍVAR: Lower slopes of Carrąo-tepuí; climbing, appressed to mossy tree-trunks; woods, 1675–1980 m; Steyermark 60959 (F, K, MO, NY, US). BRITISH GUIANA: Roraima, Schomburgk 18 (BM); without loc., prob. ibid., Schomburgk 1185 (B, HOLOTYPE; BR; K, HOLOTYPE of *L. filiformis*).

The elongate, flexuose, wiry rachis is unique among the neotropical species and perhaps in the whole genus. The only species to which it is perhaps allied is *L. filipendula*.

Subsectio 3. **Terminales** Kramer, subsect. nov.

Pinnulae fertiles ut in subsectione *Decrescentes*, sed superiores paullum vel paene decrescentes, pinnula terminalis magna, libera. Lamina in speciebus omnibus interdum, in nonnullis semper simpliciter pinnata.

Species typica: *Lindsaea lancea* (L.) Bedd.

As has been pointed out above (p. 138), it is not certain whether this subsection is a phyletic entity, as it may have been developed from subsection *Decrescentes* along several lines. For this there is, however, no conclusive evidence.

32. **Lindsaea lancea** (L.) Beddome, Ferns Brit. India Suppl. 6 (1876); Kuhn, Chaetopt. 26 (1882); Christ. Farnkr. d. E. 292 (1897), as to New World specimens only; Krug in Urban, Engl. Bot. Jb. 24:91 (1897); Diels, N. Pfl. I^4:221 (1902), as to New World specimens only; Kuhn in Urban, Symb. Ant. 4:30 (1903); Lindman, Ark. f. Bot. 1:198 (1903); not pl. 8 fig. 2 and 3; Rosenstock, Hedwigia 46:79 (1906); Hieronymus, Hedwigia 47:209 (1908); Bonaparte, Notes Ptérid. II:150 (1915), VII:374 (1918); Hieronymus, Hedwigia 62:14 (1920); Urban, Symb. Ant. 9:321 (1925); Knuth, Fedde Rep. Beih. 43 (1):32 (1926); Maxon, Pterid. Port. 490 (1926);

Hassler, Trab. Inst. Bot. Farm. Buenos Aires 45:36 (1928), in part; Posthumus, Fl. Surin. Suppl. 75 (1928); Domin, Pterid. Domin. 244 (1929); Sampaio, Arch Mus. Nac. Rio de Jan. 32:35 (1930), pl. 12 fig. 1, 2, 4; Standley & Record, Field Mus. Publ. 350:64 (1936); Christensen, Kungl. Sv. Vet.-Ak. Handl. 3e Ser. 16 (2):46 (1937); Stehlé, Caribb. For. 4 (2): 92 (1943); Dutra, An. Prim. Reun. S. —Am. Bot. 2:29 (1938); Capurro, ibid.: 106 (1938); Maxon & Morton in Maguire, Bull. Torr. Bot. Cl. 75:73 (1948); Hodge, Lloydia 17 (2): 102 (1954).

Basionym: *Adiantum lancea* L., Spec. Pl. ed. 2, II:1557 (1763); Willdenow, Spec. Pl. V:440 (1810); Poiret in Lamarck, Encycl. Suppl. I:136 (1810); not of Baker, Fl. Bras. I²:373 (1870).

Type: no specimen extant (see below).

Homotypic synonym: *Lindsaea falcata* Dryand. var. *lancea* (L.) Jenman, W. Ind. Gui. F. 74 (1899).

Heterotypic synonyms: *L. trapeziformis* Dryander, Trans. Linn. Soc. 3:43 (1797) pl. 9; Roem. Arch. 2 (II):236 (1801), t. IV fig. 4; Swartz, Syn. Fil. 119 (1806); Willdenow, Spec. Pl. V:424 (1810); Sprengel, Syst. Veg. IV:79 (1827); Desvaux, Prod. 313 (1827); Kunze, Linnaea 9:87 (1835); Presl, Tent. Pterid. 131 (1836); J. Smith, Lond. Jo. Bot. 1:200 (1842); Hooker, Spec. Fil. I:214 (1844), in part; Klotzsch, Linnaea 18:546 (1844); Kunze, Linnaea 21:226 (1848); Bot. Zeit. 8:348 (1850); J. Smith in Seemann, Bot. Voy. Herald 239 (1854); Ettingshausen, Farnkr. 212 (1865), in part, t. 146, fig. 4, 5; Fée, 11e mém. 15 (1866); Grisebach, Catal. Plant. Cub. 274 (1866); Hooker & Baker, Syn. Fil. 1st ed. (1868), 2nd ed. (1874) 107, excl. of almost all synon.; Fée, Crypt. vasc. Brés. I:29 (1869); Baker, Fl. Bras. I²:355 (1870), in part, excl. of most synon. and var., t. 41 fig. 5; J. Smith, Hist. Fil. 268 (1875); Eaton, Bot. Gaz. 3 (11): 89 (1878); Britton, Bull. Torr. Bot. Cl. 15:248 (1888); Sodiro, Crypt. Vasc. Quit. 56 (1893); Bommer & Christ, Prim. Fl. Costar. (Bull. Soc. Roy. Bot. Belg. 35): 115 (1896); Shimek, Ferns Nicar. 151 (1897), pl. XI fig. 1, 4, 5, 6, 7; Krug in Urban, Engl. Bot. Jb. 24:91 (1897), p.p. min.; Rosenstock, Hedwigia 43:216 (1904), in part; Duss, Fl. Crypt. Ant. franç. 58 (1904), p.p. mai. Type: Smeathman s.n. from Grenada (not seen).

L. nitidissima Richard ex Willdenow, Spec. Pl. V:423 (1810); Poiret in Lamarck, Encycl. Suppl. III:447 (1813); Presl, Tent. Pterid. 131 (1836); Klotzsch, Linnaea 14:287 (1840); Alston Kew Bull. 1932: 311. Type: unknown coll., "habitat in Gujana (v.s.)", in herb. Willdenow (B, not seen; photograph in U!).

Pteris adiantoides Vellozo, Fl. Flumin. 11 t. 88 (1827), teste C. Christensen, Ind. Fil. 591 (1906), non Bory, 1810.

L. imbricata Liebmann, Vid. Selsk. Skr. 5 (1): 269 (1849), non Devaux, 1811. Type: Liebmann 2447 from San Pedro Tepinapa, Oaxaca, Mexico (C!).

L. lancea (L.) Bedd. var. *subtripinnata* Rosenstock, Hedwigia 46:79 (1906). Type: Goeden 22 from Blumenau, Santa Catarina, Brazil (UC!).

L. Abbottii Brause, Fedde Rep. 18:245 (1922); Urban, Symb. Ant. 9:322 (1925). Type: Abbott 824 from Cotuy, San Domingo, Hispaniola (US!).

Misapplied names: *L. montana* auct. non Fée; Urban, Symb. Ant. 9:322 (1925).

L. schomburgkii of Posthumus, Fl. Surin. Suppl. 71 (1928), p.p. mai.

Petioles pale or dark, abaxially angular or rounded; lamina simply pinnate or bipinnate with conform terminal pinna, herbaceous; pinnules subtrapeziform to subfalcate of falcate, angular at the apex, up to 3 × as long as wide; upper pinnules somewhat or hardly reduced, terminal pinnule quite free, large, triangular-lanceolate; sori continuous; indusium rather narrow, mostly entire; spores trilete.

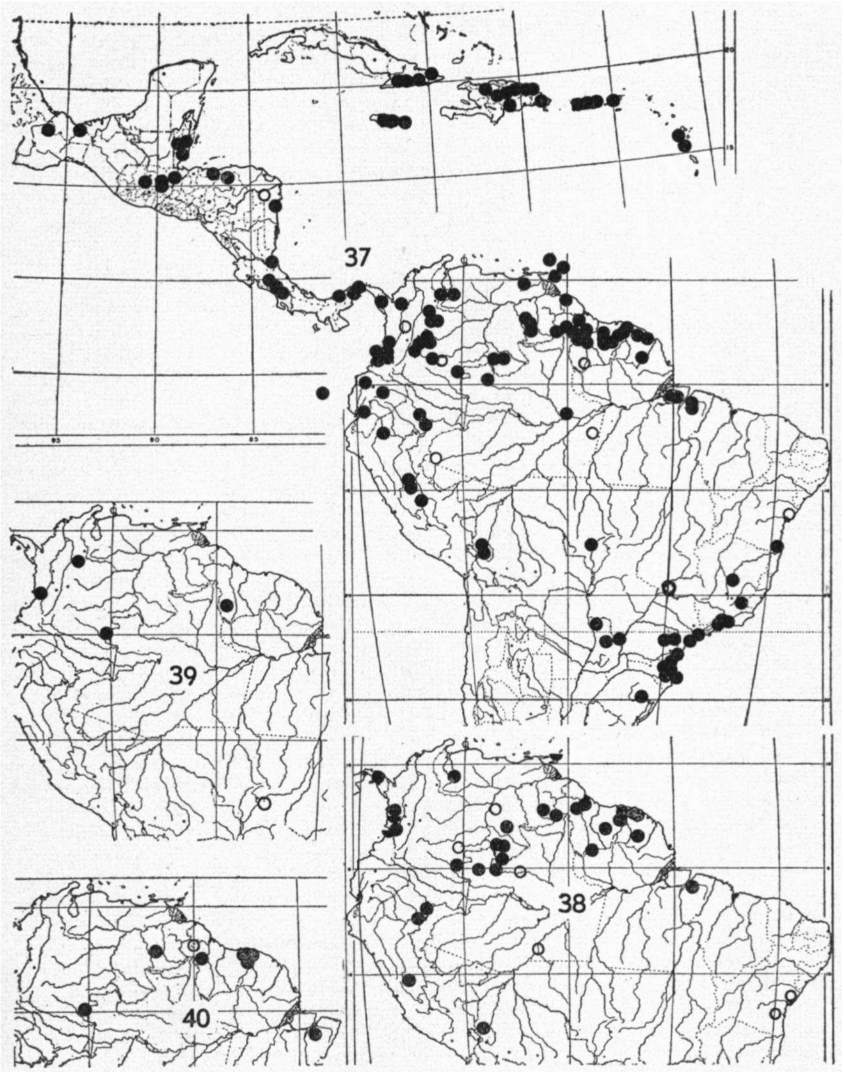
This very polymorphous species consists of five more or less distinct varieties, which can be distinguished as follows:

1\. a. Terminal pinnule very obtuse; leaves simply pinnate, with numerous pinnules, the upper ones gradually and rather strongly reduced . . . . c. var. *elatior*
b. Terminal pinnule acute or subacute; leaves bipinnate, or, if simply pinnate, the upper pinnules but little reduced . . . 2
2\. a. Pinnules small, 10–16 mm long, 5–8 mm wide, gradually narrowed to the apex which is mostly subacute; a distinct outer margin mostly not developed. . . . b. var. *remota*
b. Pinnules 11–45 mm long, 6–20 mm wide, mostly of equal width close to the apex, which is ± rectangular, or, if subacute, points obliquely downwards; a distinct outer margin mostly present 3
3\. a. Pinnules about 2–2½ × as long as wide, 11–37 mm long, 6–14 mm wide, the upper ones about half as long as the lower ones; terminal pinnule longer than wide, or, if as long as wide, not very asymmetrical; pinnate or bipinnate a. var. *lancea*
b. Pinnules up to 3 × as long as wide, up to 45 mm long and 20 mm wide, the upper ones little or not reduced; terminal pinnule about as long as wide, very asymmetrical . . . 4
4\. a. Petiole reddish-brown to blackish, abaxially in at least about the upper half with pale, slightly wing-like angles d. var. *falcata*
b. Petiole black, abaxially terete throughout or angular at the extreme apex only . . . . e. var. *leprieurii*

a. var. **lancea.** **Fig. 79**

Misapplied names: *L. falcata* auct. non Dryand.; Krug in Urban, Engl. Bot. Jb. 24:91 (1897); Jenman, W. Ind. Gui. F. 74 (1899), in part; Posthumus, Fl. Surin. Suppl. 71 (1928), p.p. mai.; Graham, Ann. Carnegie Mus. 22:87 (1934); Standley & Record, Field Mus. Publ. 350:64 (1936); Maxon & Morton in Maguire, Bull. Torr. Bot. Cl. 75:73 (1948), in part; Alston, Mutisia 7:6 (1952).

L. trapeziformis Dryand. var. *falcata* Baker of Eaton, Bot. Gaz. 3



Maps 37–40: *L. lancea;* map 37: var. *lancea;* map 38: complete dots: var. *falcata;* half dots: intermediates between var. *falcata* and var. *lancea;* map 39: var. *elatior;* map 40: var. *remota.*

(11):91 (1878), not *L. falcata* Dryand.

L. lancea (L.) Bedd. var. *falcata* Rosenstock, Hedwigia 46:79 (1906), as to specimen cited, not *L. falcata* Dryand.

This variety, the most variable of the species, consists of two extreme forms, which, although they are connected by a large number of intermediates, can best be described separately in order to avoid too many alternatives in the descriptions.

The bipinnate form.

Rhizome creeping, mostly with several short lateral branches, sometimes long-creeping, rather stout, 2–3 mm in diam.; scales narrowly lanceolate, long-acuminate, up to 2 mm long, 0.2 mm wide, with up to 8 rows of cells at the base. *Petioles* close, ca. 10–50 cm long, mostly about as long as the lamina, not infrequently up to 1½ × as long or more, 1–1.5(–2) mm in diam. near the apex, dark brown at the base, for the rest stramineous or pale brown, rarely raddish or olivaceous-brown throughout, then above with paler angles, more or less shining, adaxially sharply angular almost to the base, the surface flat or, especially above, sulcate, abaxially sharply angular almost to the base or sometimes below obtusely angular or subterete. *Lamina* mostly bipinnate (very rarely subtripinnate; this form was described as a variety by Rosenstock but can hardly be kept apart), dark green on the ventral, dark or medium green on the dorsal side, herbaceous, 11–52 cm long, with 1–8, mostly 3 or 4 pinnae to a side and a conform terminal one. *Primary rachis* similar to the upper part of the petiole, abaxially at least above sulcate. Axillary cushions visible as swellings but usually not discoloured. *Pinnae* alternate or the lower subopposite, angle with the primary rachis rather variable but mostly ca. 45–60°, the lower ones ca. 3–7 cm apart, the upper ones in plurijugate leaves gradually closer, subsessile or short-stalked (the terminal often longer, up to 2 cm), lanceolate, 10–32 cm long, 1–5 cm wide, the upper ones in plurijugate leaves about $^{2}/_{3}$ as large as the lower ones, the terminal not smaller, widest around the middle or just above the base, slightly narrowed towards the base, more gradually but not strongly narrowed to the apex, not acuminate. Secondary rachises adaxially sulcate, abaxially terete at the extreme base, two ridges appearing abruptly at the level of the 1st–3rd pinnule which soon occupy a lateral position, the portion between them flat or mostly at least below sulcate, the ridges often paler, sometimes obscurely wing-like, merging into a keel in or just below the terminal pinnule. *Pinnules* ca. 12–35 to a side, alternate or sometimes subopposite, spreading or the upper ones laxly ascending, the basal ones occasionally decurved, rather close to contiguous or slightly overlapping, mostly subtrapezoidal, occasionally dimidiate-ovate or subfalcate, ca. 11–23(–29) mm long, 6–11 mm wide, mostly from slightly less than 2–2½ × as longas wide, equally wide from the base close to the apex, rarely more gradually narrowed. Inner margin straight, parallel to the sec. rachis or slightly divergent, lower base cuneate, hardly stalk-like, upper base shortly rounded, often subangular, upper margin almost straight, connected by a short convex portion with the substraight outer margin, rarely more evenly rounded, gradually passing into the outer margin, lower margin straight, sometimes faintly concave, or in basal pinnules more strongly so. Apex usually aproximately rectangular, less often obtuse or apiculate. Marginal thickening stramineous, inconspicuous but visible throughout, or indistinct along the soriferous margins. All margins entire in fertile pinnules, in sterile ones the upper and outer mostly shallowly sinuate or crenate, with incisions up to 1 mm deep, rarely quite entire. Veins immersed or the bases sometimes elevated, readily discernible, mostly twice forked, ca. ¾–1 mm apart at their ends, Main vein hardly connected with the marginal strand, ca. ½–¾ mm above it near the apex. Upper pinnules not strongly reduced, about $^{2}/_{3}$ or ½ the size of the lower ones. Terminal pinnule quite free, lanceolate, mostly broadly so or even triangular, asymmetrical at the often shallowly lobed base, obtuse or mostly acute, acuminate, or even caudate, ca. (10–)25–70 mm long, (4–)10–25 mm wide, at least 1½ × as long as wide, with a percurrent midrib, soriferous in the basal lobes, rarely throughout. *Sori* continuous along the upper and outer margin; indusium narrow, ca. 0.2–0.3 mm wide, entire, not reaching the margin by 2–4 times its own width, reflexed and conceiled at full maturity. Sporangia ca. 135 × 105 μ; annulus with 10–12 indurated cells; spores trilete, pale yellowish-brown, 22–25 μ, 32?

The simply pinnate form. (All characters not mentioned are as in the bipinnate form).

Rhizome 1.5–2.5 mm in diam.; *petioles* sometimes not very close, 7–22 cm long, half as long to as long as the lamina, mostly dark reddish-brown to atropurpureous, occasionally olivaceous or stramineous, the abaxial side usually terete below, sometimes close to the apex, the angles often distinctly wing-like in the upper part. *Lamina* 6–30 cm long, 2.5–6(–8) cm wide. *Rachis* with sharp or wing-like angles throughout. *Pinnules* ca. 7–25(–30) to a side, subopposite or alternate, spreading or slightly deflexed, the basal ones often more strongly so, up to 37 mm long (rarely) and 14 mm wide, often more falcate than in the bipinnate forms, with more acute apex. Terminal pinnule often long-acuminate. Indusium sometimes closer to the margin.

The pinnate form is more variable than the bipinnate form. The extremes look rather different, and it is not difficult to understand that the two forms were regarded as separate species for a long time; the simply pinnate form was included in *L. falcata*. Study of the very large number of specimens available at present shows, however, that such a distinction is artificial, even when additional characters such as colour and structure of the stipe are used. Both forms are sometimes found together on the same rhizome; they occur side by side in the same habitats almost throughout the range of the species. Generally the bipinnate form is more common; the simply pinnate form seems to be commonest in Trinidad. It has so far not been found in the West Indies, except Puerto Rico, Jamaica, and Grenada.

Distribution: Throughout the range of the genus in the New World (map 37). Common and often abundant. Mostly in forests, sometimes in thickets, palm-groves or in swamps, on sandy or clayey soil, occasionally on trunks of trees or on decaying logs, from sea-level to 1500 m (rarely at higher altitudes).

Vern. names: avenca (Pará, Brazil, Miles Moss); warakoewirie (Suriname).

Representative or widely distributed specimens:

Mexico. Vera Cruz: Coatzacoalcos, Ch. L. Smith 2078 in part (GH, IA, UC).

Oaxaca: Tepinapa, Galeotti 6496 (BR, LE); San Pedro Tepinapa, Chimantla, Liebmann 2447 (C, Holotype of *L. imbricata*).

British Honduras: Mountain Pine Ridge, El Cayo Distr., Bartlett 11713 (F, MO, UC, US); Big Creek, Schipp 100 (B, BM, F, G, GH, K, NY, UC, US).

Guatemala: Cubilquitz, Alta Verapaz, von Türckheim II 27 (Donnell Smith-exs. 7707) (B, BR, S–PA, US); Izabal, near Puerto Barrios, Standley 25006 (NY, US); near Entre Rios, Standley 72761 (F, US).

Honduras: Lancetilla Valley, near Tela, Dept. Atlántida, Standley 53133 (F, US); near Ceiba, Dyer A 194 (US).

Nicaragua: Karatá, Schramm 29 (S–PA); Sangsangta Distr., Schramm 38 (US); Camp Menocal near Greytown, Shimek s.n. (IA).

Costa Rica: El General, Skutch 4127 (BM, GH, MO, NY, US); Buenos Aires, Kupper 1363 (M); Cocos Island, Pittier 12356 (GH).

Panamá: East of Las Cascadas, C.Z., Maxon 4894 (GH, NY, S, US); Chepigana, Cana-Cuasi-trail, Darien, M.E. & R.A. Terry 1551 (F, US); Orange River, Killip 2631 (S–PA, US).

Cuba. Oriente: Baracoa, Lomas de Cuaba, Ekman 3602 (BM, G, GH, NY, S, US); along Río Buey, n. slope of Sierra Maestra, Morton & Acuña 3687 (GH, K, UC, US); near Monte Verde, Wright 976 in part (B, BM, BR, F, G, GOET, IA, L, LE, MO, S–PA, US).

Hispaniola. Haïti: Near Plaisance, Dept. du Nord, Leonard 9330 (GH, NY, UC, US).

San Domingo: Las Cidras, Sabaneta, prov. Monte Cristy, Valeur 548 p.p. mai. (C, F, G, GH, K, MO, US); La Cumbre, Cordillera Central, prov. San Domingo, Ekman H 12361 (B, NY, S, US); Cotuy, prov. de la Vega, Abbott 824 (US, Holotype of *L. Abbottii;* Isotypes in GH, NY); Jato Viejo R., Samaná-penins., Abbott 1404 (GH, NY, US).

Jamaica: Crown Lands near Troy, Maxon 2925 (NY, S, US); ibid., Harris 8731 (BM, NY); Catalina near Chepstow, A. Moore s.n. (NY, US).

Puerto Rico: El Yunque, Big Tree Trail, Blomquist 13156 (UC, US); Rio Piedras near San Juan, Hioram s.n. (L, M, S–PA, US); Sierra de Luquillo, P. Wilson 204 (GH, NY, US); Utuado, Santa Isabel, Sintenis 6154 (B, G, GH, GOET, K, LE, M, S–PA, US); Fajardo, Heller & Heller 994 (F, K, NY, US).

Guadeloupe: Duss 4240 (NY, US), id. s.n. (C, F, GH, MO, US); L'Herminier s.n. (B, BM, F, G, K, L, LE, MO, NY); Husnot 270 (BM).

Dominica: Eggers 900 (C, F, K, US); id. 647 in part (B, BR, GOET, NY, S–PA, W).

Grenada: Sherring 183 (C, US); Broadway s.n. (GH, NY, US).

Colombia. El Valle: Córdoba, Dagua Valley, Pittier 518, 534 (US); ibid., Killip 5104 (GH, NY, PH, US); Buenaventura, Lehmann 98 (K).

Cundinamarca: Buena Vista, Gazaguan Valley, Grant 10415 (US).

Meta: Sierra Macarena, Philipson 2340 (BM); Puerto Lopez, Little & Little 8314 (US).

Antioquia: Peñas Blancas, Woronow & Juzepczuk 4544 (US); Guadalito, Kalbreyer 1387 in part (B, K).

Santander: Puerto Wilches–Puerto Santos, Killip & A. C. Smith 14837 (NY, US); Barranca Bermeja, Haught 1293, 1352 (GH, US).

Vaupés: R. Guayabero, Cuatrecasas 7552 (US).

Bolívar: Boca Antizales, R. Esmeralda, Pennell 4482 (NY).

Boyaca: Puente Nacional, Karsten s.n. in part (LE).

Chocó: Bay of Chocó, Seemann 979 in part (BM, K).

Venezuela. Amazonas: Tamatama, Upper Orinoco, Ll. Williams 15097 (F, G, US); Yavita, id. 13964 (F, G, US); Capihuara, Upper Casiquiare, id. 15529 (G, US), 15546 (US).

Bolívar: Guaiquinima, R. Paragua, Killip 37479 (GH, US); La Prisión, R. Caura, Ll. Williams 11631 (F, US).

Anzoátegui: Montaña de las Palomas, R. Neverí, Steyermark 61456 (F, NY, US), 61457 (F, US).

Trinidad: Aripo Road, Arima, Broadway 5408 (F, MO, UC, US), 5409 (F, MO, US); Sangre Grande, Broadway 6095 (BM, K); ibid., Britton & Hazen 369 (GH, K, NY, US); ibid., Britton 2838 (GH, NY, S–PA, US); Quare Road-Valencia Forests, Broadway 6299 (BM, F, K, MO, S, W); without loc., Fendler 24 (B, BM, F, G, GH, IA, K, LE, M, MO, NY, PH, S, UC, US); id. 110 (B, BM, F, GH, IA, K, LE, M, MO, NY, UC, US).

Tobago: Eggers 5814 (US), Broadway 3883 (BM).

British Guiana: Tumatumari, Potaro R., Gleason 85 (NY, US); ibid., Linder 22 (GH, NY); ibid., Hitchcock 17356 (GH, NY, US); Kamuni Creek, Groete Creek, Essequibo R., Maguire & Fanshawe 22917 (A, K, NY, U, US); Moraballi Creek near Bartica, Essequibo R., Richards 21, 32, 281, 467 (K), 156, 351 (BM, K); Kamwatta, Pomeroon distr., de la Cruz 1172 (GH, MO, NY, PH, US); Mt. Roraima, Schomburgk 9 (BM); without loc., Schomburgk 148 (BM, G), 251 (B, L), 347 in part (B, BM, G, K, L, US).

Suriname: Nassau Mts., Lanjouw & Lindeman 2312 (BM, U); Upper Nickerie R., Tulleken 512 (L, U); plant. Bergendaal, Focke 1081 (K, U); Tafelberg, Maguire 24244 (A, F, K, MO, NY, S–PA, U, UC, US); Para R. region, Wullschlaegel 693 in part, 1717 (BR); without loc., Hostmann 96 in part (B, BM), 108 (BM, FI, K), 1352c (B).

French Guiana: Near R. Saï, Leprieur 6 (GH, LE, US); Acarouany, Sagot 733 (B, BM, K, NY, S–PA), 841 (B, BM, G, GOET, K, LE, S–PA); without loc., Leprieur 22 (B, GH, LE, NY, US), 162 (FI, P, U), 547 (P, UPS).

Brazil. Amazonas: Manáos, Killip & A. C. Smith 30178 (GH, NY, US); Humayta, between Rs. Livramento and Ipixuna, Krukoff 7302 (GH, NY).

Pará: Acará, Thomé Assú, Mexía 6016 in part (BM, MO, UC, US); Villa Aramá, Huber 1824 (G); Tanaii, R. Acará, Spruce 50 (B, BM, K), 385 (M); near Pará, Miles Moss 14 (BM).

Goias: without loc., Glaziou 22639 in part (B, G, NY).

Bahia: Ilheos, Martius 367 (BR, M, NY); ibid., Riedel 3, 12 (LE); Jacobina, Blanchet 2511 (C, FI, G, K, L, M, S–PA); without loc., Blanchet 2252 (BM, G, US).

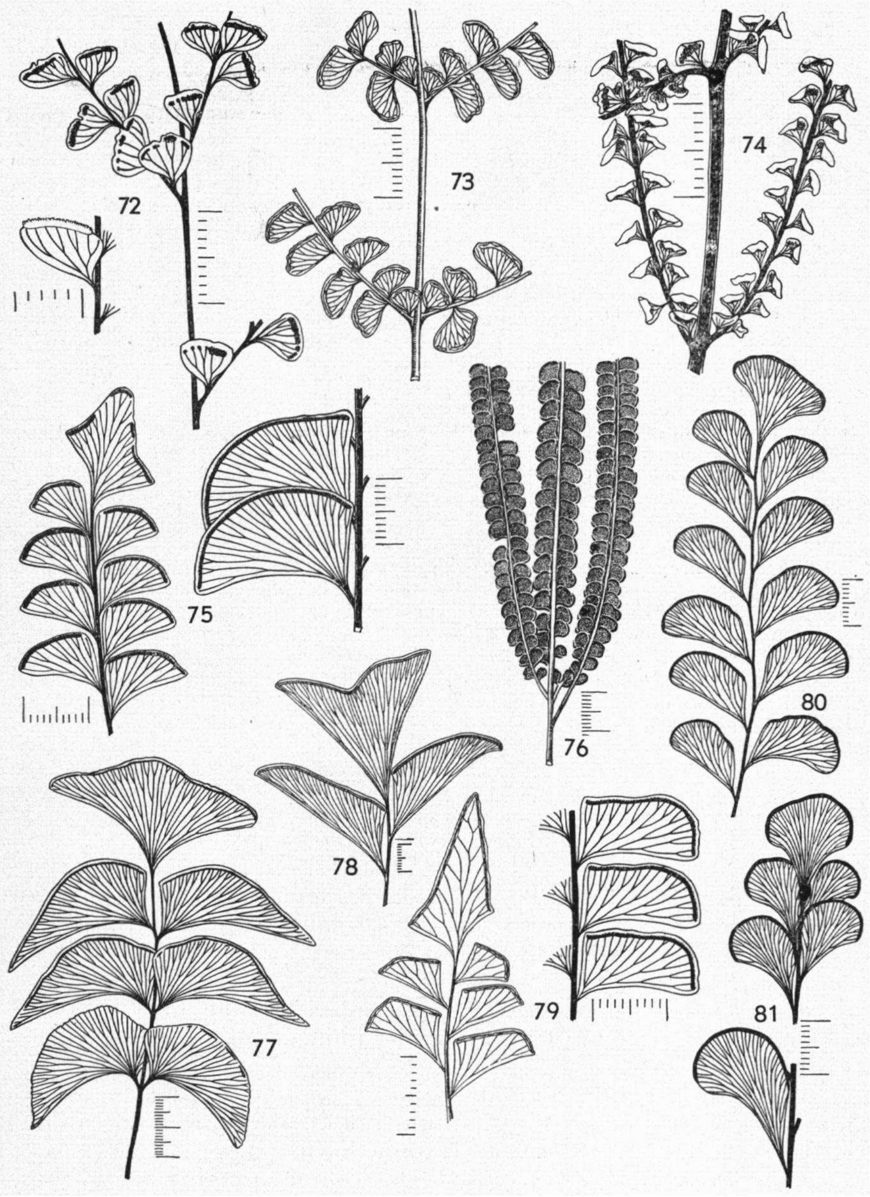


Fig. 72: *Lindsaea filipendula;* middle portion of lamina and pinnule (left) (v. Lützelburg 252). Fig. 73: *L. stricta* var. *stricta* (the lax form); portion from base of lamina (Mosén 74). Fig. 74: *L. stricta* var. *parvula;* portion from base of lamina (Kappler 1737). Fig. 75: *L. lancea* var. *elatior;* apex of lamina (left), pinnules from lower part of lamina (right) (Haught 1364). Fig. 67: *L. stricta* var. *jamesoniiformis;* portion from base of lamina (Maguire 24377). Fig. 77–78: *L. ulei;* fig. 77: complete, largely fertile lamina (Killip 37406); fig. 78: apex of lamina (Ule 5756). Fig. 79: *L. lancea* var. *lancea;* apex (left) and pinnules from base of lateral pinna (right) (Gaudichaud s.n.). Fig. 80: *L. schomburgkii* f. *coriifolia;* upper part of lamina (v. Lützelburg 22956). Fig. 81: *L. schomburgkii* f. *densa;* apex of lamina and pinnule from base (below) (Steyermark 59474). (Scales in mm).

Minas Gerais: Viçosa, Mexía 4639a (GH, UC, US); Lagôa Santa, Warming 61 (C).

Rio de Janeiro: Serra d'Estrella, Beyrich s.n. (L); Rezende, Hoehne & Gehrt 17585 (GH).

São Paulo: Santos, Rio Boturoca, Mosén 3527 (B, BR, S); Sorocaba, Mosén 3056 (S), 3734 (C, L, LE, S, S–PA, UPS); Apiahy, Puiggarí s.n. (GOET).

Matto Grosso: Serra do Itapirapuan, Affonso, Lindman A 3341 (BM, K, S, S–PA); Poaia, Grillos, Lindman A 3253 (S, S–PA); Santa Anna da Chapada, Robert 562 (BM).

Paraná: Jacarehy, Dusén 14643 (C. Chr. in BM, F, NY, PH, S); Paranagua, Herter 20037 (B); Serra do Mar, Volta Grande, Dusén 749a (S, US).

Santa Catarina: Blumenau, Goeden 22 (UC, Holotype of var. *subtripinnata*); ibid., Reitz & Klein 2186 (HBR); ibid., Viereck 76 (M); Joinville, Schmalz 83 (F, MO); Isla Santa Catarina, Gaudichaud 51 (B, FI); Peninsula da Gloria, Ule 30 (B).

Rio Grande do Sul: Porto Alegre, Stier s.n. (Rosenstock-exs. 324) (B, M, S–PA, US); Santa Cruz, Jürgens 315 (NY).

Ecuador: Sapote–Milagro, Crespi s.n. (US); near Quininde, Holdridge 1638 (GH, US); Baños-Pintuo, Stübel 993 (B).

Perú. Loreto: Pongo de Manseriche, Mexía 6207a (GH, UC, US); Iquitos, Killip & A. C. Smith 27021 (NY, US).

Huánuco: Hac. Mercedes, distr. Churubamba, Mexía 8178a (UC).

Junín: Schunke Hacienda above San Ramon, Killip & A. C. Smith 24698 (NY, US); ibid., Schunke A 233 (US); Chanchamayo Valley, Schunke 458 (F, US); Quimiri, Tarma, Esposto s.n. (USM).

San Martín: Near Tingo María, Allard 21369, 21491 (US); ibid., R. M. & A. F. Tryon 5291, 5296, 5297 (U).

Bolivia. La Paz: Mapiri, Rusby 161 (B, BM, G, GH, K, LE, MO, NY, PH, US, W); Choropampa near Mapiri, R. S. Williams 1329 (GH, NY, UC, US); ibid., Buchtien 1101 (B, F, LE, M, S–PA, US); San Carlos near Mapiri, Buchtien 8 in part (MO), 11 (NY, S–PA, UC), 12 (NY, UC), 1002 (NY, US), 1102 (B, S–PA); Copacabana, Larecaja Prov., Krukoff 11264 (F, GH, K, MO, NY, S, U, US).

Paraguay: Yerbales, Sierra de Maracayú, R. Curuguatuy, Hassler 4614 (B, BM, G, GH, NY, S–PA); Paraguari, Cerros de Tobaty, Hassler 6373 (B, BM, G, GH, K, NY, S); Vista Alegre, Rojas 3824, 3851 (C).

Most specimens from Bolivia and Paraguay are atypical, with strongly reduced upper pinnules and a small, not always quite free terminal pinnule; there is perhaps some introgression with *L. quadrangularis* ssp. *terminalis*.

There is no specimen of *Adiantum lancea* L. in the Linnaean herbarium or in the Hortus Cliffortianus. Linnaeus' original description reads as follows:

"Adiantum frondibus pinnatis: pinnis oppositis oblongis: terminalibus triangulari hastatis. +. Adiantum album maximum americanum. Seb. thes. 2. p. 65. t. 64. f. 7, 8. Habitat Surinami.

Stipes laevis. Frons pinnata: foliolis lateralibus oppositis, brevioribus, saepe duorum parium: impari longiore. Pinnae recurvatae, oblongae, obtusae: terminales majores, cordato s. hastato-triangulares, oblongae, acutae."

Seba's plate (1735) shows two almost identical bipinnate leaves which are in exact agreeance with this description. His comment is: "Adiante, ou Capillaire, d'Amerique, blanc, à grandes feuilles. Cette Plante qu'on m'a envoyée de Surinam, pousse des tiges menues, rondes, garnies de feuilles opposées, d'un verd-pâle. Ses vertus sont pectorales, telles que celles du Capillaire de nos climats, dont l'usage si efficace contre la Toux & les autres maladies du Poumon, est connu de tout le monde . . ." It is not entirely certain whether this really applies to *Lindsaea lancea.* The petiole of the bipinnate form of that species is not round, and the base of the terminal pinnule is never cordate or hastate. This may, however, be an exaggeration of the plate. Furthermore, there is no species of *Adiantum* occurring in Suriname known to the writer which the plate might represent; all have even more different terminal pinnules. Therefore it seems reasonably safe to assume that Seba's plant was really *Lindsaea lancea.* Linnaeus' description was presumably drawn from Seba's plate—all characters mentioned by him can be observed there—and it is best to regard this plate as the type of the species.

b. var. **remota** (Kunze) Kramer, comb. nov. **Fig. 29**

Basionym: *L. pumila* Klotzsch var.? *remota* Kunze, Linnaea 21:226 (1848).

Type: Kegel 1066 from Sornau Creek near Joden-Savanne, Suriname (GOET!).

Heterotypic synonym: *L. pusilla* Splitgerber, Tijdschr. Nat. Gesch. Physiol. 7:423 (1840); Kuhn, Chaetopt. 25 (1882); Posthumus, Fl. Surin. Suppl. 75 (1928). Type: Splitgerber 108 from the vic. of Paramaribo, Suriname (L!).

Rhizome slender, ca. 1 mm in diam.; scales as in var. *lancea* but smaller, up to 1 mm long, 0.15 mm wide, with up to 4 rows of cells at the base. *Petioles* close, ca. 3–18 cm long, half as long to about as long as the lamina, ½–1 mm in diam. near the apex, reddish-brown to atropurpureous, ± shining, adaxially sharply angular almost to the base, the angles paler above, the surface channelled, abaxially similar above, below mostly subterete. *Lamina* pinnate or bipinnate, dark brownish-green or olivaceous, herbaceous, ca. 5–16 cm long, with up to 2 pinnae to a side and a conform terminal one. *Primary rachis* similar to the upper part of the petiole, pale above; axillary cushions not seen. *Pinnae* (and, mutatis mutandis, simply pinnate laminae) subopposite, ascending under an angle of ca. 30–45°, 6–12 cm long, 2–3 cm wide, the terminal mostly longest, widest slightly above the base, gradually narrowed to the apex. Secondary rachises similar to the primary but abaxially with a terete portion at the base; rachis of terminal pinna and of simply pinnate laminae abaxially channelled throughout. *Pinnules* 6–15 to a side, alternate or the lower ones subopposite, spreading or slightly ascending, the lower ones often somewhat deflexed, subsessile, rather far apart, not contiguous, 10–16 mm long, 5–8 mm wide, mostly ca. 12 × 6 mm, ca. 2 × as long as wide, semi-elliptic or mostly semi-oval, more strongly narrowed to the apex than in var. *lancea,* mostly subacute. Inner margin straight, divergent or parellel to slightly overlapping the sec. rachis, lower base cuneate, somewhat stalk-like, upper base shortly rounded or angular, lower margin straight of faintly convex, concave in deflexed pinnules, upper margin straight at the base, convex towards the apex, mostly without a separate outer margin, sometimes minutely erose. Marginal thickening stramineous, inconspicuous except at the base of the lower margin. Upper/outer margin of sterile pinnules shallowly crenate, the incisions up to ½ mm deep, the lobes broadly rounded or flattened. Veins immersed, once or twice forked, their ends ca. ¾–1 mm apart. Upper pinnules not strongly reduced, 5–8 mm long. Terminal pinnule triangular-lanceolate, acute or mostly obtuse, cuneate-narrowed at the asymmetrical base, 1–1.5 cm long, soriferous in the lobes at the base or throughout. *Sori* as in var. *lancea,* but the indusium mostly superficially erose, but little reflexed at full maturity. Sporangia ca. 175 × 160 μ; annulus with 10–12 indurated cells; spores trilete, pale yellowish-brown, ca. 23–28 μ.

Distribution: Northern South America; apparently uncommon (map 40). In moist forests at lower elevations; almost always along watercourses.

COLOMBIA. AMAZONAS/VAUPÉS: Sorotama, Río Apaporis, above mouth of R. Kananarí, Schultes & Cabrera 16073 (US).
VENEZUELA. BOLÍVAR: R. Tonoro, above junction with R. Paragua, Killip 37411 (US).
BRITISH GUIANA: Sheenabowa, Potaro R., Jenman s.n. (NY); Porato R., Jenman s.n. (NY); Kurupung, Leng 268 (NY); Kaieteur Falls, Appun s.n. (B); ibid., Jenman 1392 in part (K); Essequibo R., Persaud 355 in part (F); without loc., Drake s.n. in part (NY).
SURINAME: Forest near Paramaribo, Splitgerber 108 (L, HOLOTYPE of *L. pusilla*); Sornau Creek near Joden-Savanne, Kegel 1066 (GOET, HOLOTYPE); along Wane creek between Moengo tapoe and Grote Zwiebelzwamp, Lanjouw & Lindeman 516 (BM, U); plant. Berlijn (Compass), Para R., Wullschlaegel 693 in part (BR).
BRAZIL. PARÁ: Acará, Thomé Assú, Mexía 5948a (C, K); ibid., id. 6016 in part (B, C, F, G, GH, K, NY, PH, S, U, UC).

The combination of dark petioles and small, more strongly narrowed, less close pinnules serves to distinguish this variety. Transitions to var. *lancea* are quite rare; an example is Killip & Cuatrecasas 38883a from Agua Clara, El Valle, Colombia (F), an epiphytic, perhaps depauperate specimen.

c. var. **elatior** (Kunze) Kramer, comb. nov. **Fig. 75**

Basionym: *L. falcata* Dryand. var. *β elatior* Kunze, Linnaea 21:225 (1848).

Type: Kegel 1068 from Sornau Creek near Joden-Savanne, Suriname (GOET!).

Rhizome 1.5–2 mm in diam.; scales up to 1.5 mm long, otherwise as in var. *lancea*. *Petioles* close, 10–37 cm long, half as long to about as long as the lamina, ¾–1¼ mm in diam. near the apex, dark olivaceous to dark reddish brown or castaneous, rather dull, adaxially flattened or sulcate almost to the base, abaxially at least in the upper third sharply angular, the surface between the angles flattened or shallowly sulcate, below gradually obtusely angular or subterete; the angles mostly paler when sharp. *Lamina* simply pinnate, medium or brownish green, herbaceous, linear, 16–ca. 40 cm long, 3–5 cm wide, mostly widest at the base or just above the base, with (20–)25–40 pinnules to a side and a separate terminal one. Primary rachis reddish or castaneous, sharply angled, the angles mostly paler, and ± sulcate. *Pinnules* alternate or the lower ones subopposite, close, sometimes contiguous or slightly overlapping, subsessile, spreading, the basal ones sometimes slightly deflexed, resembling ¼ of an ellipse, not rarely subfalcate, the largest 15–25 mm long, 8–14 mm wide, 1½ to almost 2 × as long as wide. Inner margin approximately straight, lower base cuneate, ± stalk-like, upper base shortly rounded or subangular, upper margin evenly convex or less so towards the base, lower margin ± concave, apex obtuse or subacute; no separate outer margin developed. Marginal thickening present throughout, inconspicuous except at the base of the lower margin; all margins entire, the upper/outer margin of sterile pinnules very shallowly crenate. Veins immersed but often visible as wrinkles in the leaf-tissue, 2–3 times forked, about 1 mm apart at the margin; main vein hardly united with the marginal strand, often reddish at the base. A few lower pinnules sometimes slightly shortened, the upper ones more strongly reduced, 9–10(–12) mm long, about ½ the size of the lower ones. Terminal pinnule asymmetrically-triangular or rhombic, ca. 1–2 cm long, lobed at the base, very obtuse, with an almost percurrent midvein, soriferous in the lobes, sometimes also in the apical part. *Sori* as in var. *lancea*, but the indusium often closer to the margin. Sporangia ca. 165 × 120 μ; annulus with 9–11 indurated cells; spores as in var. *lancea*, ca. 28 μ.

Distribution: Northern and central South America (map 39). In forests, sometimes in bogs, at lower elevations.

COLOMBIA. EL VALLE: Buenaventura, André 275 (K).
SANTANDER: Vic. of Barranca Bermeja, Magdalena Valley, Haught 1364 (GH, UC, US).
VAUPÉS: Cerro Isibukuri, Río Kananarí, Schultes & Cabrera 14446 (US).
BRITISH GUIANA: Essequibo R., Appun 54 (B); Upper Rupununi R., near Dadanawa, de la Cruz 1556 (F, GH, K, MO, NY, PH, UC, US).
SURINAME: Sornau-Creek near Joden-Savanne, Kegel 1068 (GOET, HOLOTYPE); perhaps also Hostmann 108 without loc. (FI, GOET, K; mat. incomplete, doubtful).
BRAZIL. MATTO GROSSO: Campo Teles Pires, Sick B 535 (RB).

There are a few simply pinnate specimens of var. *lancea* that approach var. *elatior* in general habit; they differ in acute or subacute terminal pinnule and less reduced upper pinnules; an example is Riedel 18a from Castelnovo, Brazil (B, C, FI, GOET, LE, M, S-PA). These specimens are not numerous, and var. *elatior* is sufficiently distinct from the very large series of specimens of var. *lancea* now extant to be maintained as a variety.

d. var. **falcata** (Dryand.) Rosenstock, Hedwigia 46:79 (1906), as to type only; incorrectly publ. as new comb. by Hassler, Trab. Inst. Bot. Farm. Buenos Aires 45:36 (1928). **Fig. 30**

Basionym: *L. falcata* Dryander, Trans. Linn. Soc. 3:41 (1797),t. 7 fig. 2; Roem. Arch. 2 (II):236 (1801), t. V fig. 5; Swartz, Syn. Fil. 118 (1806); Willdenow, Spec. Pl. V: 422 (1810); Sprengel, Syst. Veget. IV:79 (1827); Desvaux, Prodr. 313 (1827); Klotzsch, Linnaea 18:545 (1844); Kunze, Linnaea 21:224 (1848); Bot. Zeit. 8:348 (1850); J. Smith, Hist. Fil. 268 (1875); Jenman, W. Ind. Gui. F. 74 (1899), in part; Hieronymus, Hedwigia 47:209 (1908); Bonaparte, Notes Ptérid. VII:374 (1918); Posthumus, Fl. Surin. Suppl. 71 (1928), p.p. min.; Sampaio, Arch. Mus. Nac. Rio de Jan. 32:34 (1930); A. C. Smith in Gleason, Bull. Torr. Bot. Cl. 58:303 (1931); Alston, Kew Bull. 1932:311; Posthumus, Rec. trav. bot. néerl. 31:469 (1934); Maxon & Morton in Maguire, Bull. Torr. Bot. Cl. 75:73 (1948), in part.

Type: Aublet s.n. from French Guiana (P? not seen).

Homotypic synonyms: *L. trapeziformis* var. *δ falcata* (Dryand.) Baker, Fl. Bras. I/:355 (1870), in part, excl. synon.

L. lancea (L.) Bedd. f. *falcata* (Dryand.) Lindman, Ark. f. Bot. 1:201 (1903).

Rhizome creeping, often widely and much branched, 1–2 mm in diam.; scales up to 1 mm long, otherwise as in var. *lancea*. *Petioles* close, (5–)7–22, mostly about 10–16 cm long, $^2/_3$–1½ × as long as the lamina, 0.5–1 mm in diam. near the apex, reddish-brown to atropurpureous or almost black, shining, adaxially sharply angular almost to the base, above with pale sometimes wing-like angles which evasnesce downwards, abaxially with similar angles above, these rather abruptly evanescing about halfway, the lower half obtusely angular or subterete; the surfaces between the angles slightly convex to concave. *Lamina* simply pinnate, yellowish to olivaceous, herbaceous, broadly ovate to narrowly lanceolate, (5–)10–25, mostly 12–20 cm long, 4–7½ cm wide, relatively widest in short specimens, with 3–15 (rarely more, in atypical specimens) pinnules to a side and a large separate terminal one. *Rachis* similar to the upper part of the petiole, the pale angles more pronounced, sometimes distinctly wing-like, the surfaces sulcate. *Pinnules* alternate or the lower ones subopposite, spreading or, especially the upper ones, somewhat ascending, the lower ones mostly deflexed, the basal pair often strongly, separated by spaces equal to half their width to contiguous or slightly overlapping, subsessile, subtrapeziform to elongate-dimidiate-elliptic, faintly to strongly falcate, at least the basal ones, the largest 21–45 mm long, 11–20 mm wide, 2–3 × as long as wide, mostly widest at base or in the basal $^2/_8$. Inner margin ± straight and parallel to the rachis, lower base cuneate, slightly stalk-like, upper base shortly rounded to subangular, lower margin mostly concave, in the basal pinnules often strongly so, upper margin straight at the base, increasingly convex towards the apex, in the basal pinnules often evenly convex, a separate outer margin sometimes present; apex subacute or almost obtuse, mostly pointing obliquely downwards, the pinnules slightly hamate. Marginal thickening stramineous, present throughout, inconspicuous. All margins entire, upper/outer margin of sterile pinnules subentire to shallowly crenate. Veins immersed except at their extreme bases, mostly 2 or 3 times forked, lax, 1–1.5 mm apart at the margin. Main vein hardly or not united with the marginal strand, ca. ¾ mm above it almost from the base. Lower pinnules not reduced, but, as they are often deflexed, the lamina slightly narrowed at the base; upper pinnules not at all or slightly reduced (in extreme cases not quite $^2/_3$ the length of the lower ones). Terminal pinnule large, very asymmetrical, approximately triangular, trilobed, one basal lobe of ca. 2 cm, another about half as long, opposite and above the other, the central lobe as large as the basal one or larger, the whole pinnule 3–5 cm long and broad, acute or shortly acuminate, the base below the lobes long-cuneate, a percurrent midvein present. *Sori* continuous along the upper/outer margin, and in the basal lobes of the terminal pinnule, sometimes also in the central lobe. Indusium and sporangia as in var. *lancea.*

Distribution: Panamá and tropical South America; less common than var. *lancea* (map 38). In moist forests, occasionally in swamps, terrestrial or on decaying wood, rarely epiphytic, from sea-level to ca. 1000 m.

Representative specimens:

PANAMÁ: Southern Darien, Seemann s.n. (BM).

COLOMBIA. EL VALLE: Buenaventura, Killip 11740 (GH, PH, US).

CHOCÓ: La Concepción, east of Quibdó, Archer 1992 (GH, US).

VAUPÉS: Cerro de Circasia, Cuatrecasas 7175 (F, US), 7184 (F); Sorotama, Río Apaporis, Schultes & Cabrera 15999 (US).

VENEZUELA. AMAZONAS: Slopes of Mt. Duida, Tate 904 (NY, US); Tamatama, Upper Orinoco, Ll. Williams 15096 (F, G, US), 15843 (US); Yavita, Ll. Williams 13970 (F, US); Capihuara, Upper Casiquiare, Ll. Williams 15534 (G, US).

BOLÍVAR: Ptari-tepuí, Steyermark 59427 (F, MO, NY, US); Chimantá Massif, slopes of Abácapa-tepuí, Steyermark 74742 (US).

BRITISH GUIANA: Essequibo R., Appun 67 (B); Macouria Creek, Essequibo R., Jenman s.n. (NY); ibid., Fanshawe M 312 (BM); Bartica-Potaro Road, Sandwith 1141 (BM, K, NY); near mouth of Onoro Creek, Essequibo basin, A. C. Smith 2783 (GH, K, NY).

SURINAME: Coppename R. headwaters, Maguire 24181 (A, F, K, MO, NY, U, US); Tafelberg, Maguire 24736 in part (K, NY, U, US); Wilhelmina Mts., Top 1200, Boschwezen 7088 (U); Rikanau near Moengo, Lindeman 6001 (U).

FRENCH GUIANA: Acarouany, Sagot 734 in part (B, BM, GH, GOET, K, W); Saï R. headwaters, Leprieur 35 (C. Chr. in BM, F, GH, LE, US); Mana, Perrottet s.n. (FI, G); Saï and Conana, Leprieur 160 (FI, P, U); without loc., Jelsky 24 (LE).

BRAZIL. AMAZONAS: Humayta, basin of Rio Madeira, Krukoff 7298 (BM, F, GH, K, LE, MO, NY, S, U, US); São Gabriel da Cachoeiras, Rio Negro, Spruce 2356 in part (K, LE); Cucuí, Rio Negro, Baldwin 3206 (US); British Guiana Boundary, Akarai Mts., A. C. Smith 2973 (GH, NY); Venezuelan Boundary, foothills of Serra Imeri near Salto de Huá, Holt & Blake 493 (NY, US).

PARÁ: Pará, Pételot s.n. (F); ibid., Spruce 47 (K); São Joaquim near Pará, Schwacke 4090 (GOET); Utinga waterworks near Pará, Miles Moss 7 (BM).

BAHIA: Blanchet 2226 (B).

PERÚ. LORETO: Mishuyacu near Iquitos, Klug 379 (F, NY, US), 1510 (F, NY, US); Timbuchi, Upper R. Nanay, Ll. Williams 954 (F); Pongo de Manseriche, Upper Marañon, Tessmann 4850 (B).
JUNÍN: Near La Merced, Killip & A. C. Smith 23966 in part (F, US).
BOLIVIA. LA PAZ: San Carlos near Mapiri, Buchtien 8 in part (NY, S-PA, UC, US), 1104 (S-PA, US).

Generally, this variety can be distinguished by its elongate, ± falcate pinnules, the upper ones being hardly reduced, and the very broad, very asymmetrical terminal pinnule. These characters are clearly visible in Dryander's plate of the type specimen, which has not been examined itself by the author. If applied to this form only, not to all simply pinnate specimens otherwise agreeing with *L. lancea* var. *lancea*, *L. falcata* can be maintained as a variety. There are, however, a few intermediates between these two varieties, e.g. Killip & Cuatrecasas 39083 from Chocó, Colombia (F, K, MO, Pic.-Ser., UC), Lehmann 98 from Buenaventura, Colombia (B, BM, LE, US), and Broadway 5377 from Trinidad (F). Their number in comparison with the large series of specimens of both varieties is very small. Their distribution is also shown on map 38.

e. var. **leprieurii** (Hooker) Kramer, comb. nov. **Fig. 31**

Basionym: *L. Leprieurii* Hooker, Spec. Fil. I:208 (1847), t. 62 D; Kunze, Linnaea 21:225 (1848); Bot. Zeit. 8:325 (1850); Kuhn, Chaetopt. 26 (1882); not of Ettingshausen, Farnkr. t. 145 fig. 9 (1865); prob. not of Wawra, Bot. Ergebn. Reise Max. Südbras. 192 (1866). Type: Leprieur s.n. from French Guiana (K!).
Homotypic synonym: *L. falcata* Dryand. var. *leprieurii* (Hooker) Jenman, W. Ind. Gui. F. 74 (1899).

Heterotypic synonym: *L. Pittieri* Underwood & Maxon, Smithson. Misc. Coll. 62:17 (1920). Type: Pittier 533 from Córdoba, Dagua Valley, El Valle, Colombia (US!).

Rhizome delicate, ca. 1 mm in diam.; *petioles* abaxially terete and black throughout or angular and ± winged near the apex. *Lamina* simply pinnate, herbaceous, dark brownish-green, 3–16 cm long, with 1–14 pinnules to a side which are dimidiate-oblong to falcate, 9–30 mm long, 3–10 mm wide, 2–3 × as long as wide, often decurved, especially the lower ones, the upper ones ± reduced; apex rounded, acute, or apiculate, inner margin not rarely overlapping the rachis. Terminal pinnule relatively large, strongly lobed and asymmetrical at the base. For the rest as the simply pinnate form of var. *lancea*.

Distribution: Northern South America; rare (map 41). Often in mountain forests.

COLOMBIA. EL VALLE: Córdoba, Dagua Valley, Pittier 533 (US, HOLOTYPE of *L. Pittieri;* Isotype in GH); Agua Clara, between Buenaventura and Cali, Killip & Cuatrecasas 38908 (US).
ANTIOQUIA: Guadalito, Kalbreyer 1387 in part (B).
SURINAME: Near plant. Victoria, Kappler 1353 in part (B, GOET, K, L. S-PA, U, W).
FRENCH GUIANA: Mountains along Upper Oyapok R., Leprieur 159 in part (B, FI, P); without loc., Leprieur s.n., prob. same coll. (K, HOLOTYPE).

This variety in the shape of the terminal and lateral pinnules approaches var. *falcata*, in structure of the petiole the simply pinnate form of var. *lancea*; it is not always easily separated from the latter variety. The specimen described as *L. Pittieri* is apparently depauperate.

Many different, often not at all closely related forms have been put in *L. lancea* (or *trapeziformis*) in the course of time, and many good species that had been described before have been made varieties or synonyms of that voracious species. The most extreme case of this encountered by the author is Baker's treatment in Flora Brasiliensis, whose *L. trapeziformis* contains at least ten different species. Several of his errors appear in Christensen's Index Filicum, though some were corrected in subsequent supplements.

In spite of its great variability, *L. lancea* can be easily distinguished in most cases. Simply pinnate forms can be told apart from other species with once-pinnate leaves and a free terminal pinnule by their triangular or lanceolate terminal pinnule with a distinct apex. The same character serves to distinguish bipinnate forms; in addition, these have a very characteristic structure on the abaxial side of the secondary rachises, where a groove starts abruptly just above the base. This character is shared by *L. arcuata* and *L. quadrangularis* ssp. *antillensis*, which have, however, gradually and strongly reduced, finally ± confluent upper pinnules, and by *L. divaricata*, which has much darker, distinctly winged axes and a not entirely free terminal segment; *L. quadrangularis* ssp. *terminalis* may occasionally have a practically free terminal segment, but here also the axes tend to be darker, and the structure of the abaxial side of the secondary rachises is different. There are, however, a few aberrant specimens of *L. lancea* which have more strongly reduced upper pinnules and a small, not quite free terminal segment; they are much like *L. quadrangularis* ssp. *antillensis*, but differ mainly in the shape of the pinnules (see figs. 53 and 79). The author does not share HODGE's view (1954, p. 102) that these two taxa may be combined. It is not easy to decide which species is the closest relative of *L. lancea*. The most likely one is *L. quadrangularis* (especially ssp. *antillensis* and *terminalis*); *L. divaricata* is perhaps also allied. Relatives in the sub-section *Terminales* are *L. schomburgkii* and *L. ulei*.

For a long time an Asiatic species was included in *L. lancea* (e.g. by BACKER & POSTHUMUS, 1939), which was listed as *L. scandens* Hooker by HOLLTUM (1930, 1954); HIERONYMUS (1920) was of the opinion that its correct name was *L. parasitica* Wall. This author pointed out the principal differences between the Asiatic and the American species very clearly, but even without paying attention to them, the trained eye can tell the two species apart quite readily, although they are similar in general sapect. The writer does not believe that they are at all closely allied; *L. scandens* belongs probably to the group of *L. pectinata*, from which species it can sometimes be separated only with difficulty (HOLTTUM, 1954, p. 328). Nevertheless, the resemblance between *L. lancea* and *L. scandens* presents a case of very striking convergent evolution.

HIERONYMUS (l.c.) argued that Beddome, when making the new combination *Lindsaea lancea* for the Asiatic species, misconstrued

Linaeus' species, as his type was from Suriname, and that he was therefore not the correct author of the combination, which should be ascribed to Mettenius (in Urban, Engl. Bot. Jb. 24:91, 1897). This is, however, not in accordance with our present Code of Nomenclature based on the type-method; Beddome's transfer applied in the first place to Linnaeus' type-specimen, no matter what other specimens were included in the same species.

33. **Lindsaea schomburgkii** Klotzsch, Linnaea 18:545 (1844); Kunze, Farrnkr. II:67, t. 128 (1850); Bot. Zeit. 8:349 (1850); Ettingshausen, Farnkr. 211, t. 143 fig. 4, 5 (1865); Hieronymus, Hedwigia 47:209 (1908); Posthumus, Fl. Surin. Suppl. 71 (1928) in part; Sampaio, Arch. Mus. Nac. Rio de Jan. 32:35 (1930), pl. VI; pl. XII fig. 5.

Type: Schomburgk 278 from British Guiana (B!).

Misapplied names: *L. trapeziformis* auct. non Dryand.; Hooker, Spec. Fil. I:214 (1844), in part.

L. trapeziformis var. *δ falcata* of Baker, Fl. Bras. I^2:355 (1870) in part, pl. 21 fig. 18, 19; not *L. falcata* Dryand.

L. botrychioides auct. non St. Hilaire; Jenman, W. Ind. Gui. F. 75 (1899); Goebel, Flora N.F. 24 fig. p. 371 (1930).

Petioles reddish to dark purplish brown, quadrangular; lamina simply pinnate, firmly herbaceous to coriaceous; pinnules variable in shape, ca. 2⅓–2½ × as long as wide, rarely more, the upper ones but little reduced; veins elevated; terminal pinnule large, free, very obtuse; sori continuous; spores trilete.

Rhizome short-creeping, 2–3 mm in diam.; scales lanceolate, acuminate, up to 1.5 mm long, 0.3 mm wide, with up to 10 rows of cells at the base. *Petioles* close, ca. 10–35, mostly ca. 15–20 cm long, ¾–1½ × as long as the lamina, 0.5–1.5, mostly ca. 1 mm in diam. near the apex, subterete at the base, adaxially above with a shallow groove, the angles towards the apex sharper, paler, and more protruding, but hardly ever wing-like. *Lamina* 5–50, mostly about 20–30 cm long, 3–10, mostly 4–6 cm wide, with 2–32, mostly about 10 pinnules to a side and a distinct terminal one. *Rachis* similar to the upper part of the petiole but often paler, abaxially sulcate above, the margins of the groove fusing to form a keel in the stalk-like base of the terminal pinnule. *Pinnules* very variable in texture, size, and shape, pale yellowish-green to olivaceous or rather dark brown, semi-ovate, semi-elliptic, subtrapeziform, or broadly falcate, the lower ones subopposite, the upper ones alternate, spreading or mostly more or less ascending, the largest 18–35 mm long, 9–15 mm wide, the greatest width in the lower third or in the middle, sometimes in the upper third. Lower base long-cuneate, somewhat stalk-like, upper base mostly rounded, lower margin straight or shallowly convex or concave, upper margin convex, apex rounded or acute; fertile margin entire or very inconspicuously repand-erose, sterile margin shallowly crenate, the incisions shallow, acute, the lobes rounded, uni- or binerval. Marginal strand present throughout, not very conspicuous except at the lower base, stramineous to pale brown or reddish. Veins raised at least for the basal two-thirds, especially adaxially, 2–3 × forked, their ends ½–1 mm apart, often reddish at the base. Main vein hardly continuous with the marginal strand, ca. 0.2 mm above it near the apex. Terminal pinnule flabellate, resembling undivided leaves of *Ginkgo*, 20–35 mm long, 15–45 mm wide, mostly about as wide as long, slightly convex or subtruncate at the apex, there often soriferous, the sides rounded, rarely acute, the lateral margins concave, the base long-cuneate, venation as in *L. ulei*. *Sori* along the upper/outer margin; indusium rather firm, 0.2 mm wide, entire or minutely erose-sinuate, not quite reaching the margin, ± reflexed at full maturity. Sporangia ca. 195–200 × 140–150 μ; annulus with 11–13 indurated cells; spores pale brownish-yellow, ca. 27–33 μ.

Distribution: Northern and central South America (map 42). Rather euryoeceous; often in exposed situations, on withered rocks, in savannas, in swamps, or in scrub, sometimes also in forests, up to ca. 1600 m.

a. forma **schomburgkii**.

Pinnules acute, strongly ascending, close, overlying the rachis and often also one another, usually firmly herbaceous, venation rather lax.

BRITISH GUIANA: Swamp behind Oreala, Corantyne R., Im Thurn s.n. (K); ibid., Jenman 435 (K); Essequibo R., Appun 2 (B, W); without loc., Schomburgk 27 (BM, FI, G, W), 278 (B, HOLOTYPE), s.n. (L); Appun s.n. (K), 730 (K); Lobscheid s.n. (W).

PERÚ. SAN MARTIN: Pacasmayo–Moyobamba, Pajonal, between Rio Negro and Rioja, Stübel 1059 (B).

b. forma **coriifolia** (Lindman) Kramer, comb. nov. **Fig. 80**

Basionym: *Lindsaea coriifolia* Lindman, Ark. f. Bot. 1:201 (1903), pl. 8 fig. 1; Knuth, Fedde Rep. Beih. 43 (1):31 (1926); Maxon & Morton in Maguire, Bull. Torr. Bot. Cl. 75:73 (1948).

Type: unknown coll., "Caracas", Venezuela (S-PA!).

Pinnules acute or obtuse, ascending or spreading, not overlying the rachis, at most touching it, separated by spaces equalling their width or half as wide, or the upper ones contiguous, firmly herbaceous to coriaceous, venation rather close.

COLOMBIA. AMAZONAS–VAUPÉS: Río Apaporis, Cachivera de Jirijirimo, Schultes & Cabrera 12459 (US).

VENEZUELA. BOLÍVAR: Cerro Tonoro, Upper R. Paragua, Cardona 852 (US).

AMAZONAS: Maroa, R. Guainía, Ll. Williams 14330 (F, US); id. 14264 in part (F); between Esmeralda Savanna and base of Mt. Duida, Steyermark 57819 (F, NY, US); without loc., van Lansberge s.n. (B, L); unknown coll., "Caracas", prob. from southern Venezuela (S–PA, HOLOTYPE).

BRITISH GUIANA: Essequibo, right bank, Guppy 156 (BM); Kaieteur Savannas, Maguire & Fanshawe 23394 (NY, US); Mt. Roraima, Schomburgk 23 (BM); without loc., Jenman (?) s.n. (US).

BRAZIL. AMAZONAS: Rio Negro, Içana, Serra de Tunuý, Fróes 22422 (U); Manáos and Flores, Ule 5418 (B, G, K, L); ibid., Miss Solomon s.n. (BM); Içana, Tunuy, von Lützelburg 22956 (M); ibid., Piranana, id. 22988 (M); Rio Uaupés, Panuré, Spruce 2648 (G, GH, GOET); Rio Uaupés, Iutica, Varadouro, von Lützelburg 22762 (M), von Lützelburg 23631 (M); Cachoeira da Turumá, Traill 1355 (K); Flores, von Lützelburg 21980 (M, NY, UC, US); Barra do Rio Negro, Spruce 1371 (K); ibid., id., s.n. (W); São Gabriel da Cachoeiras, Rio Negro, Spruce 2356 in part (LE).

MATTO GROSSO: Juruana, Hoehne 1817/1818 (NY; unusually large).

PERÚ. Dept.?: Chamicuras, Bartlett s.n. (W).

c. forma **densa** Kramer, f. nov. **Fig. 71**

Exstat pinnulis approximatis, plus minusve contiguis, valde coriaceis, multum adscendentibus, margine superiore valde convexa, apice obtuso vel rotundato.

Typus: Steyermark 59474 from Ptari-tepuí, Bolívar, Venezuela (F).

Colour pale yellowish-green; marginal strand reddish-brown; veins close.

Only known from Type-collection:

VENEZUELA. BOLÍVAR: Ptari-tepuí, vic. of Misa Kathy camp, low scrubby growth on flat portion of south-facing shoulder, Steyermark 59474 (F, HOLOTYPE; Isotypes in MO, NY, US).

The differences between *L. schomburgkii* and *L. coriifolia*, which were pointed out by Lindman as he described the latter species, break down when more ample material is studied. The form with rather thin, lax, acute, close pinnules to which the type belongs is however rather different in aspect and can be more or less sharply distinguished from the commonest form, f. *coriifolia*, which in itself is quite variable. F. *densa* also is rather outstanding, but as the characters used to separate these forms are all of rather little importance, they are maintained here as *formae* only. It is feasible that eventually they will prove to be quite untenable. In spite of this variability, *L. schomburgkii* can easily be recognized by its simply pinnate lamina with a large, very obtuse terminal pinnule and elevated veins. It is probably closest to *L. semilunata*, which differs mainly by more elongate pinnules.

A series of specimens from the basin of the Kuyuwini R., British Guiana, A. C. Smith 2622 (F, G, GH, MO, NY, S-PA, U, US) is aberrant by very long simply pinnate or rarely subbipinnate leaves, the terminal pinnule approximately rhombic, with an obtuse apex; the spores are abortive. Probably a hybrid, perhaps *L. schomburgkii* × *lancea*. A rather similar specimen, Jenman s.n. (NY) from the Hooroobia Creek, British Guiana, may be of similar origin.

34. **Lindsaea semilunata** (C. Christensen) C. Christensen, Index Filicum 397 (1906). **Fig. 82**

Basionym: *L. lancea* (L.) Bedd. [err.: (L.) Mett.] var. *semilunata* C. Chr., Bot. Tidsskr. 25:81 (1902).

Type: Glaziou 12352, "Brazil", which is Appun (prob. 962) from British Guiana (C. Chr. in BM!).

Misapplied name: *L. trapeziformis* var. *δ falcata* of Baker, Fl. Bras. I^2:355 (1870), in part, excl. syn.; non *L. falcata* Dryand.

Petioles castaneous, terete below, quadrangular above; lamina simply pinnate, herbaceous to chartaceous; pinnules elongate-triangular to lanceolate-subfalcate, 3–3½ (– over 4) × as long as wide, the upper ones little or not reduced; veins elevated; terminal pinnule large, free, truncate or concave on the distal side; sori continuous; indusium narrow, entire; spores trilete.

Rhizome creeping, ca. 2 mm in diam.; scales lanceolate, acuminate, up to 0.9 mm long and 0.3 mm wide, with up to about 10 rows of cells at the base. *Petioles* close, rather shining, above with stramineous angles, the surfaces slightly convex, flattened towards the apex, 10–40 cm long, as long as to 1½ × as long as the lamina, 0.5–1 mm in diam. at the apex. *Lamina* 10–25 cm long, 5–10 cm wide, with 4–11 pinnules to a side, the overall number mostly odd, and a large terminal pinnule. *Rachis* similar to the petiole, the angles broader but not wing-like, the surfaces concave. *Pinnules* opposite to alternate, dull olivaceous, 30–45(–70) mm long, 10–14 mm wide, 1–3 cm apart, subsessile, with a long-cuneate, somewhat stalk-like base, broadest just above the base. Inner margin straight or slightly concave, upper margin straight or concave towards the apex, slightly crenate in sterile pinnules, sometimes superficially sinuate or notched in fertile ones, upper base angular or subauriculate, lower edge straight or convex towards the apex; apex subacute to acute, often falcately upcurved, rarely faintly deflexed. Marginal strand stramineous, inconspicuous. Veins, especially abaxially, elevated to about ½ cm from the margin, two to three times forked, ca. 1 mm apart at the margin; main vein not very close to the lower margin, ca. 0.2–0.3 mm above it. Terminal pinnule 2–5 cm long, 3–6 cm wide, triangular to crescent-shaped, as long as wide or wider, the base long-cuneate, passing into a stalk of 0.5–1 cm, the lateral edges concave, the distal edge strongly concave, V-shaped, or straight, soriferous, the sides mostly prolonged into long acute to subacute horns that point to the sides or obliquely upwards; no median main vein present, but two stronger unequal short basal marginal veins can be observed; the keel formed by the fusion of the sides of the channel on the abaxial side of the rachis evanescing in the stalk of the terminal pinnule or running into one of the stronger basal veins. *Sori* along the upper margin, indusium ca. 0.15 mm wide, almost equalling the margin, ± reflexed at full maturity. Sporangia ca. 185 × 140 μ; annulus with 11–12 indurated cells; spores very pale brown, ca. 28–32 μ.

Distribution: Northern South America; apparently rare (map 43). In savannas and forests; very few data extant.

VENEZUELA. BOLÍVAR: Río Tonoro, Upper R. Paragua, Cardona 829 (NY, US). AMAZONAS: Yavita, Ll. Williams 13944 (F; slightly aberrant, prob. juvenile). BRITISH GUIANA: Cucuyu Creek, Appun 962 (K); Glaziou 12352, "Brazil", almost certainly a duplicate of the preceding number (C. Chr. in BM, HOLOTYPE; Isotypes in B, C); id. 12353 (B, C, K; Paratypes).
BRAZIL. AMAZONAS: São Gabriel de Cachoeiras, Rio Negro, Spruce 2338 (B, BR, K, W).

To be recognized by simply pinnate leaves with large triangular or crescent-shaped terminal pinnule and elevated veins. It is not closely allied to *L. lancea* var. *falcata* (*L. falcata*), with which Christensen compared it. Closer relatives are *L. ulei*, which has immersed veins and an abaxially largely terete petiole, *L. schomburgkii*, which has more numerous, shorter pinnules and a smaller terminal pinnule, and probably also *L. hemiglossa*, which also has immersed veins and a petiole that is quadrangular almost throughout.

35. **Lindsaea latifrons** Kramer, spec. nov. **Fig. 73**

Folia pinnata, raro bipinnata, petiolo stramineo vel pallide fusco quadrangulari; lamina statu sicco pullo-olivacea, firme herbacea; pinnulis dimidiato-lanceolatis, longitudine latitudinem vulgo ter vel quater superante, apice acuto vel caudato-acuminato, saepe curvato-adscendente, superioribus vix redactis, segmento terminali magno, libero, triangulari vel fere semilunato; soris continuis, indusio angustissimo, integro, marginem paene aequante; sporis tetraedriformibus.

Typus: Klug 2890 from Balsapuerto, dept. Loreto, Perú (US).

Rhizome short-creeping, 2–3 mm in diam.; scales as in the following species. *Petioles* closely subdistichous, 15–45 cm long, slightly longer than to 1½ × as long as the lamina, ca. 1½ mm in diam. near the apex, quadrangular, the surfaces channelled or the lateral ones flat, ± shining. *Lamina* ca. 15–38 cm long, 9–16 cm wide (wider when bipinnate), when bipinnate with one patent lateral pinna to a side which is up to 15 cm long, with ca. 6 pinnules to a side, otherwise as simply pinnate laminae, which have 5–14 pinnules to a side and a separate terminal one, equally wide in the lower half, little narrowed towards the apex. *Primary rachis* similar to the petiole, the bottom of the abaxial groove sometimes darker than the rest. Secondary rachises, if any, similar, apart from the terete base of the abaxial side. *Pinnules* subopposite to alternate, subsessile, spreading, or, especially the upper ones, somewhat ascending, the lower ones separated by spaces about equal to their width, the upper ones gradually closer but not contiguous, the lowermost somewhat decurved, 6–9 cm long, 1½–2½ cm wide, broadest at their base or in the lower third. Inner margin ± straight, lower margin often somewhat concave, especially near the base, often concave towards the upcurved apex, upper margin convex, or straight to concave towards the apex, which is acute, rarely obtuse, usually caudate-acuminate and often upcurved; upper base rounded or ± angular, lower base cunate, hardly stalk-like. Marginal thickening not very conspicuous except at the base of the lower margin; all edges entire. Veins immersed, only at the extreme base slightly raised, 2–3 times forked, lax, ca. 1.5–2 mm apart at the margin. Main vein close to the margin but everywhere distinct from it, ca. 0.1–0.2 mm above it. Terminal pinnule variable in size and shape, 2–6 cm long, 3.5–8 cm wide, mostly wider than long, usually asymmetric, the base long-cuneate, with a stalk of ½–1½ cm, the sides straight or concave, the apical margin straight, concave, or sinuous, its apices usually acute or acuminate, sometimes protracted into long upcurved horns; venation about as in *L. ulei*. *Sori* along the upper margin and along the apical margin of the terminal pinnule; indusium 0.1–0.2 mm wide, almost reaching the margin, reflexed at full maturity. No completely sterile pinnules seen. Sporangia ca. 120–130 × 90–100 μ; annulus with 10–12 indurated cells; spores very pale yellowish-brown, ca. 20–23 μ.

Distribution: North-eastern Perú (map 45). In forests, at lower elevations.

PERÚ. LORETO: Balsapuerto, basin of Lower Río Huallaga, Klug 2890 (US, HOLOTYPE; Isotypes in B, BM, F, G, GH, K, MO, NY, S); ibid., Killip & A. C. Smith 28614 (NY, US); ibid., id. 28596 (US); ibid., id. 28614 (NY, US); Tierra Doble, Río Nanay, Ll. Williams 1068 (F).
Dept.?: Chamicuras, Bartlett s.n. (W; immature, somewhat dubious).

Closely related to *L. hemiglossa*, which is distinguished by more slender, elongate pinnules and mostly bright-green colour; perhaps they will eventually prove to be conspecific. The resemblance to *L. ulei* may be due to coindence and not to close alliance; the same is perhaps true for *L. semilunata*. It is possible that the inclusion of *L. hemiglossa* and *L. latifrons* in the present subsection is artificial; they may be more closely related to *L. arcuata* than to *L. lancea* and its allies.

36. **Lindsaea hemiglossa** Kramer, spec. nov. **Fig. 84**

Folia simpliciter pinnata, petiolo rachideque stramineis vel pallide fuscis quadrangularibus, lamina firme herbacea, statu sicco vulgo laetevirens; pinnulis dimidiato-lanceolatis, subacutis, acutis vel longe acuminatis, apice saepe incurvato, longitudine latitudinem quater usque ad sexies superante, pinnulis superioribus vix redactis, segmento terminali magno, libero, fere triangulari vel semilunato; soris continuis; indusio angustissimo, integro, marginem non attingente; sporis tetraedriformibus.

Typus: Schunke A 324 from the Schunke Hacienda above San Ramón, dept. Junín, Perú (UC).

Rhizome creeping, 2–3 mm in diam.; scales narrowly lanceolate, long-acuminate, up to 1½ mm long and 0.25 mm wide, with up to 8 rows of cells at the base. *Petioles* rather close to close, ca. 10–40, mostly 25–30 cm long, roughly as long as the lamina, rarely much shorter, 1–1½ mm in diam. near the apex, quadrangular except at the extreme base, with channelled surfaces, ± shining. *Lamina* ca. 20–40 cm long, 5–17, mostly 7–9 cm wide, with 7–25, mostly 17–20 pinnules to a side and a separate terminal one, widest at the base or just above it, but little narrowed to the apex. *Rachis* similar to the upper part of the petiole. *Pinnules* subopposite to alternate, subsessile, spreading or mostly more or less ascending, up to 45° in the upper part of the lamina, the lower ones separated by spaces equalling their width or larger, the upper ones closer but not contiguous, often falcately upcurved, 3½–6(–9½) cm long, 0.9–1.5(–1.9) cm wide, broadest at the more or less truncate base. Inner margin straight, lower margin concave at the base, for the rest straight or more often somewhat convex, upper margin convex at the base, thence straight or concave, rarely evenly convex throughout; apex acute (the extreme top often obtuse) to long-acuminate; upper base rounded or ± angular, lower base cuneate, slightly stalk-like. Marginal thickening not conspicuous, stramineous; all edges entire. Veins hidden except at their bases, 2–3 times forked, not close, ca. 1 mm apart at their ends. Main vein close to the margin but everywhere distinct from it, ca. 0.2 mm above it. Terminal pinnule variable in size and shape, 1–6 cm long, 1.5–8.5 cm wide, mostly roughly as long as wide, the base long-cuneate, subsessile or with a stalk of ca. 0.5 mm, the sides straight, concave or S-shaped, the upper margin straight, concave, V-shaped or sinuous, the apices subacute or often protracted into horns that point sideways or upwards; venation mostly as in *L. ulei*. *Sori* along the upper margin and along the apical margin of the terminal pinnule, sometimes leaving the apex free; indusium ca. 0.1 mm wide, not reaching the margin by about its own width, reflexed at full maturity. Sporangia ca. 120 × 95 μ; annulus with 10–12 indurated cells; spores hyaline, almost colourless, ca. 25 μ.

Distribution: Ecuador and Perú (map 45). In dense forests at higher elevations, ca. 1100–1700 m.

ECUADOR. Cuenca, east of the Andes, Pearce 319 (K, W).
PERÚ. JUNÍN: Schunke Hacienda above San Ramón, Schunke A 234 (UC, HOLOTYPE; Isotypes in GH, US); ibid., Killip & A. C. Smith 24571 (F, NY, US); ibid., La Merced, Macbride 5624 (F, US); Chanchamayo Valley, Schunke 511 (F); ibid., id. 806 (F, US); ibid., id. 102 (F, US); Cumbassummun (?) Mts., collector illegib. (K).
SAN MARTÍN: Tarapoto, Spruce s.n. (K).

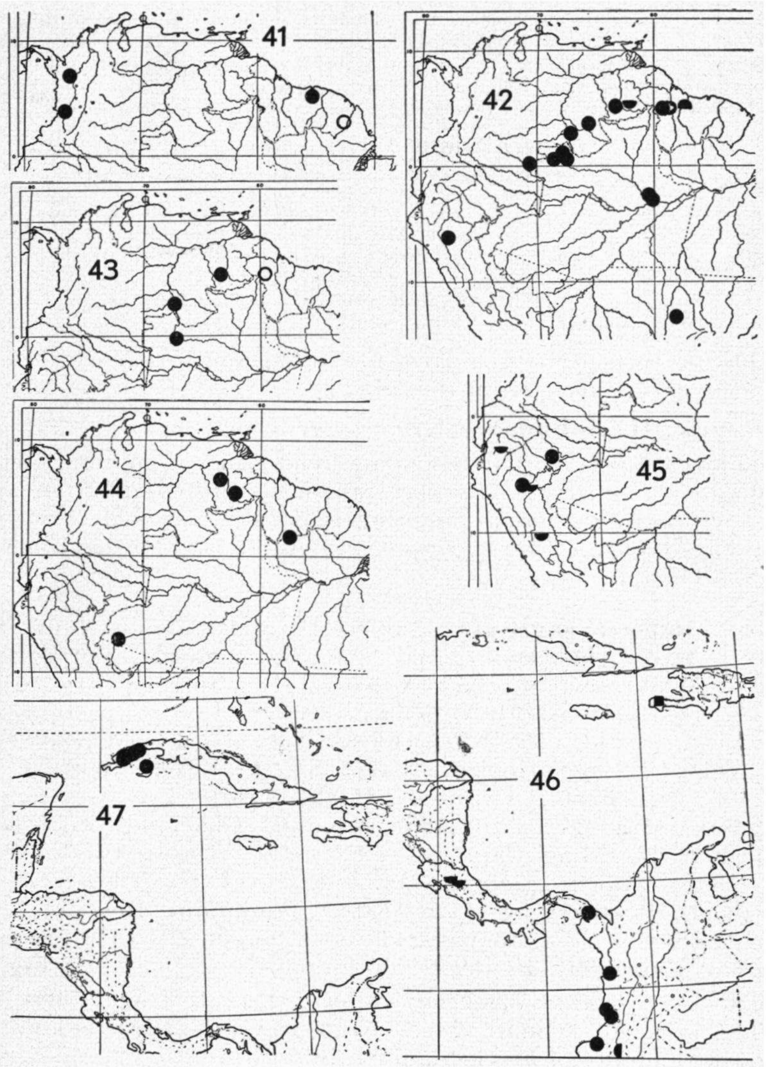
This species is very closely allied to the preceding, where the differences are discussed.

37. **Lindsaea ulei** Hieronymus in Christ, Hedwigia 44:365 (1905); Sampaio, Arch. Mus. Nac. Rio de Jan. 32:35 (1930). **Fig. 77, 78**

Type: Ule 5756 from Puritisal, Juruá Miry, Rio Juruá, Amazonas, Brazil (B!).

Petioles dark, abaxially terete below, above with pale membranous wings; lamina simply pinnate, herbaceous; pinnules subfalcate-triangular to falcate, 2–2½ × as long as wide, the upper ones little or not reduced; terminal pinnule large, free, asymmetrically flabellate, the distal margin evenly and faintly convex or sinuous; sori continuous; indusium narrow, entire or subentire; spores trilete.

Rhizome creeping, 1–2 mm in diam.; scales narrowly lanceolate, acuminate, up to 1 mm long, 0.2 mm wide, with up to 6 or 7 rows of cells at the base. *Petioles* not very close, 8–30 cm long, 1½–2 × as long as the lamina, ½–1 mm in diam. near the apex, rather lustrous, adaxially flattened, the margins in the upper part pale, membranous, wing-like. *Lamina* dark, dull greenish-brown, ca. 6–20 cm long, 5–13 cm wide, with 1–7 pinnules to a side and a large terminal one. *Rachis* similar to the apical part of the petiole, often paler, more reddish. *Pinnules* subopposite or alternate, subsessile, spreading or the lower ones somewhat deflexed, not contiguous, 2–3 cm apart, 4–7 cm long, 1½–2½ cm wide, acute or shortly acuminate, rarely obtuse, often with a small ± upturned apiculus. Inner margin straight or slightly concave, slightly divergent to slightly overlying the rachis, lower base cuneate, somewhat stalk-like, upper base angular or shortly rounded, lower margin straight or, especially near the base, concave, sometimes slightly



Map 41: *L. lancea* var. *leprieurii*. Map. 42: *L. schomburgkii;* complete dots: f. *coriifolia;* half dots (upper half): f. *schomburgkii;* half dots (lower half): f. *densa*. Map 43: *L. semilunata*. Map 44: *L. ulei*. Map 45: complete dots: *L. latifrons;* half dots: *L. hemiglossa*. Map 46: complete dots: *L. seemannii* var. *seemannii;* half dot (left half): var. *serrigera;* half dots (lower half): *L. pratensis;* square: *L. protensa*. Map 47: *L. cubensis*.

convex near the apex, upper margin convex, mostly less so towards the apex and at the base. Marginal thickening stramineous to pale brown, rather inconspicuous. Upper/outer margin entire in fertile pinnules, shallowly crenate in sterile ones. Veins immersed, mostly twice, rarely three or four times forked, their ends 1–1 ½ mm apart. Terminal pinnule very large, as large as or larger than the lateral ones, with a stalk of ½–2 cm, 3–5 cm long, 5–11 cm wide, 1 ½ to more than 2 × as wide as long, the sides straight or somewhat concave. the distal margin entire when soriferous, crenulate when sterile, the sides acute or rounded. No main vein present; for details of the venation see p. 129. *Sori* along the upper/outer margin; indusium ca. 0.2 mm wide, not reaching the margin by about twice its width, reflexed and conceiled at full maturity. Sporangia ca. 135 × 90 μ; annulus with 9–11 indurated cells; spores very pale brownish-yellow, ca. 20–23 μ.

Distribution: Northern South America; apparently rare (map 44). Terrestrial or on tree-trunks, in moist forests, ca. 300–800 m.

VENEZUELA. BOLÍVAR: Río Tonoro, above junction with R. Paragua, Killip 37406 (GH, US); Chimantá Massif, Abácapa-tepuí, Steyermark 74756 (F).
BRAZIL. AMAZONAS: Rio Juruá, Puritisal, Juruá Miry, Ule 5756 (B, HOLOTYPE; Isotypes in G, K, L).
PARÁ: Acarai Mts., Boundary of British Guiana, between drainage of Rio Mapuera and Shodikar Creek, A. C. Smith 2973a (GH, NY).

This species is probably related to *L. lancea* on the one hand and to the section *Haplolindsaea* on the other.

Sectio V. **Haplolindsaea** Kramer, sect. nov.

Lamina simplex, cordato-rotundata, reniformis vel sagittata, petiolo atrato abaxialiter tereti vel superne angulari, soris continuis vel apice laminae interruptis, indusio angusto, valde intramarginali.

Species typica: *Adiantum sagittatum* Aublet (=*Lindsaea sagittata* (Aubl.) Dryand.).

38. **Lindsaea sagittata** (Aublet) Dryander, Trans. Linn. Soc. 3:40 (1797); Roem. Arch. 2 (II):235 (1801); Swartz, Syn. Fil. 118 (1806); Willdenow, Spec. Pl. V:420 (1810); Sprengel, Syst. Veget. IV:79 (1827); Hooker & Greville, Icon. Fil. I t. 87 (prob. 1828); Presl, Tent. Pterid. 131 (1836); Hooker, Spec. Fil. I:203 (1844); Fée, 11^{me} mém. 17 (1866); Hooker & Baker, Syn. Fil. 1st ed. (1868), 2nd ed. (1874) 109; Baker, Fl. Bras. I^{2}:357 (1870), pl. 41 fig. 6; J. Smith, Hist. Fil. 267 (1875); Kuhn, Chaetopt. 25 (1882); Krug in Urban, Engl. Bot. Jb. 24:92 (1897); Christ, Farnkr. d. E. 295 (1897), with fig.; Jenman, W. Ind. Gui. F. 72 (1899); Goebel, Organogr. d. Pfl. II fig. 1126 (1918); Posthumus, Rec. trav. bot. néerl. 23:397 (1927), in part; Fl. Surin. Suppl. 69 (1928), in part; Rec. trav. bot. néerl. 31:469 (1934), in part. **Fig. 88**

Basionym: *Adiantum sagittatum* Aublet, Hist. Pl. Gui. II:964, IV, pl. 366, 1 (1775); J. Smith, Mém. Acad. Roy. Sci. Turin 413 (1793); Poiret in Lamarck, Encycl. Suppl. I:139 (1810).

Type: Aublet s.n., from French Guiana (prob. P, not seen; Isotype in BM!).

Homotypic synonym: *Schizoloma sagittatum* (Aublet) Diels, N. Pfl. I^{4}:218 (1902); Bonaparte, Notes Ptérid. IV:87 (1917); ibid. VII:374 (1918); Knuth, Fedde Rep. Beih. 43 (1):31 (1926); Sampaio, Arch. Mus. Nac. Rio de Jan. 32:42 (1930).

Petioles dark, abaxially terete; lamina simple, sagittate, hastate, or acuminate-cordate, herbaceous; sori continuous or mostly interrupted in the acumen; indusium entire or slightly sinuous, strongly intramarginal; spores trilete.

Rhizome short-creeping, slender, ca. 1–1.3 mm in diam.; scales lanceolate to almost linear, long-acuminate, up to 0.8 mm long but mostly much shorter, usually 0.4–0.6 mm, up to 0.15 mm wide, with up to 4 rows of cells at the base. *Petioles* rather close, 4–21 cm long, mostly longer than the lamina, up to three times its length, in small leaves of equal length or shorter, ¾–1 mm in diam. below the base of the lamina, the extreme apex sometimes broadened; shining, abaxially terete up to the base of the lamina, where the sclerotic tissue is divided, the lateral parts evanescing in the basal portion of the edge of the lamina, the middle portion depressed, V-shaped, prolonged into a tapering point which extends some distance along the midrib; adaxially terete at the base, the upper half or two-thirds with concolorous or paler lateral ridges, these more pronounced towards the apex where the portion between them is flattened or concave. Apparently the petiole is of delicate structure as it is often crushed in dried specimens. *Lamina* dark brownish green, 4–12 cm long, 3.5–10 cm wide, mostly somewhat longer than wide, short- to mostly long-acuminate, the acumen 1–6 cm long, its apex acute or subacute. Sides of the lamina rather evenly convex except towards the apex where they are straight to concave; the same holds for the basal lobes when they are acute. Base deeply cordate, the sinus 1.5–3 cm deep, mostly shortly rounded at the point of attachment of the petiole. The lateral lobes show all transitions from broadly rounded via angular to acuminate, the acumen up to 2 cm long, obtuse to subacute, mostly pointing to the sides; rounded basal lobes sometimes overlapping. Acute or acuminate lobes are generally more common than obtuse ones. Leaves with one acute and one obtuse lobe are extremely rare. Edge entire or very slightly sinuous or crenulate, especially in sterile leaves or portions of leaves, not thickened, except at the base of the sinus. Veins 2–3(–4) times dichotomously forked, a median, flexuose midrib present which extends into the apex and gives off 5–9 lateral veins at each side, apparently not homologous to the submarginal main vein of dimidiate pinnules. Veins immersed, lax, their ends 1–1.5 mm apart, free, but in large leaves often a few anastomoses present. *Sori* leaving the sinus free or reaching about halfway down; indusium thin, greyish or brownish, 0.2–0.4 mm wide, not reaching the margin by 1.5–2.5 mm, bulging or reflexed at maturity. Sporangia ca. 150 × 100–110 μ, annulus with 10–12 indurated cells; spores pale yellowish, ca. 20–25 μ.

Distribution: Guianas (map 48). Terrestrial in forests, from ca. 500–1000 m; very few ecological data extant. Not often collected, but according to Jenman common in the interior of British Guiana.

BRITISH GUIANA: Kaieteur Falls, Appun s.n. (BM); Pacatout, below the Kaieteur, Jenman 1393 (K); Essequibo R., Appun 42 (B, W); Tiger's Leap, Demerara R., Jenman s.n. (NY); Mazaruni R. below Kalacoon, Jenman s.n. (NY); Amacuro, Goebel s.n. (B, M, P); without loc., Mrs. Gordon s.n. (BM); Appun s.n. (K); Jenman 930 (US); Winter s.n. (UC).
SURINAME: Wilhelmina Mts., Top 1200, Stahel 7087 (U); Hendriktop, Boschwezen 5724 (Pic.-Ser., U); Brownsberg, Boschwezen 587 (P, U, US).
FRENCH GUIANA: without loc., Aublet s.n. (BM, Isotype); Poiteau s.n. (K).

Erroneously reported from Guadeloupe by Sprengel, l.c., and by some other authors, apparently on his authority. Said to occur in Venezuela by Knuth, l.c., and in Trinidad by Krug, l.c.; no specimens seen by the writer.

L. sagittata is not likely to be confused with any other species; the simple acuminate lamina is quite unique. POSTHUMUS (1927) united it with *L. reniformis;* for arguments against this, see under the latter species.

39. **Lindsaea reniformis** Dryander, Trans. Linn. Soc. 3:40 (1797), t. 7 fig. 1; Roem. Arch. 2 (II):235 (1801), t. IV f. 1; Swartz, Syn. Fil. 118 (1806); Willdenow, Spec. Pl. V:420 (1810); Sprengel, Syst. Veget. IV:79 (1827); Desvaux, Prod. 312 (1827); Kunze,

Farrnkr. I:31 (1840); t. 16 fig. 2; J. Smith, Lond. Jo. Bot. 1:200 (1842); Klotzsch, Linnaea 18:544 (1844); Hooker, Spec. Fil. I:203 (1844); Ettingshausen, Farnkr. 211 (1865), t. 145 fig. 10; Hooker & Baker, Syn. Fil. 1st. ed. (1868), 2nd ed. (1874) 109; Baker, Fl. Bras. I^2:357 (1870), in part; J. Smith, Hist. Fil. 267 (1875); Christ, Farnkr. d. E. 294 (1897); Jenman, W. Ind. Gui. F. 72 (1899); Maxon & Morton in Maguire, Bull. Torr. Bot. Cl. 75:73 (1948).

Type: Alex. Anderson s.n. from Suriname (BM!).

Homotypic synonyms: *Schizoloma reniforme* (Dryand.) Diels, N. Pfl. I^4:218 (1902); Sampaio, Arch. Mus. Nac. Rio de Jan. 32:42 (1930). *Adiantum emarginatum* Poiret in Lamarck, Encycl. Suppl. I:139 (1810), non Bory, 1810, nec Hooker, 1851.

Misapplied name: *L. sagittata* auct. non Dryand.; Posthumus, Rec. trav. bot. néerl. 23:397 (1927), in part; Fl. Surin. Suppl. 69 (1928), in part; Rec. trav. bot. néerl. 31:469 (1934), in part; Wagner, Am. Jo. Bot. 39 fig. 9 I (1952).

Petioles dark, abaxially terete or with short, irregular, interrupted lateral ridges below the apex; lamina simple, bean-shaped, reniform or suborbicular, herbaceous to subcoriaceous; sori continuous; indusium subentire, strongly intramarginal; spores trilete.

Rhizome short-creeping, 1½–2 mm in diam.; scales narrowly lanceolate, long-acuminate, up to 1 mm long and 0.2 mm wide, with up to 5 rows of cells at the base, the greater part of 1 or 2 rows of cells only. *Petioles* rather close to close, subdistichous, 6–ca. 30 cm long, 2–3 times as long as the lamina, 0.6–1 mm in diam. at the base of the lamina, very shining, abaxially terete or with short, irregular, interrupted lateral ridges below the apex which are not or hardly discoloured, adaxially terete in the lower half, in the upper half flattened, with lateral ridges which are pale and wing-like towards the apex where they are continuous with the margin of the blade. *Lamina* (1.5–)3–10 cm long, (3–)4.5–10 cm wide, mostly about 1 cm wider than long, sometimes as long as wide, or, in small bean-shaped leaves up to twice as wide as long, greatest width lying at the middle or at the level of the insertion of the petiole, medium to dark or brownish green on the ventral, paler on the dorsal surface; margin more or less equally rounded, but often with a more protruding portion at the distal side, the sinus rather narrow, about 1.5–3(–4) cm deep extending to about ⅓ of the length of the lamina, in small leaves sometimes almost absent, the base shallowly concave; rarely the basal lobes, which are always broadly rounded, overlap in very large leaves. The sclerotic patch at the base of the lamina adaxially as in *L. sagittata*, abaxially with two lateral more or less truncate portions and a middle shank which is linear, tapering, and extends up to 8 mm into the blade. Veins all dichotomous *), two to three (rarely to five) times forked, rather lax, 1–1.5 mm apart at the margin, immersed, free, but in large leaves a few anastomoses may be found. Margin with a whitish thickened border at the bottom of the sinus, otherwise indistinctly thickened, stramineous to brownish, entire to very faintly and minutely erose-crenate, sometimes slightly more in sterile leaves, occasionally slightly crispate; no sterile leaf of normal size seen. *Sori* leaving the whole sinus or its proximal half free. Indusium ca. 0.5 mm wide, concolorous with the dorsal surface, not reaching the margin by 0.5–1.5 mm, reflexed and conceiled at full maturity. Sporangia ca. 185 × 138 *μ*; annulus with 8–10 indurated cells; spores ca. 23–30 *μ*, pale brown to yellow; a small number of monolete spores sometimes found intermingled, these ca. 30 × 17 *μ*.

---

*) The writer's observations do not agree with WAGNER's figure (cited above), which shows a short basal midrib, for which he may have mistaken the extension of the sclerotic patch.

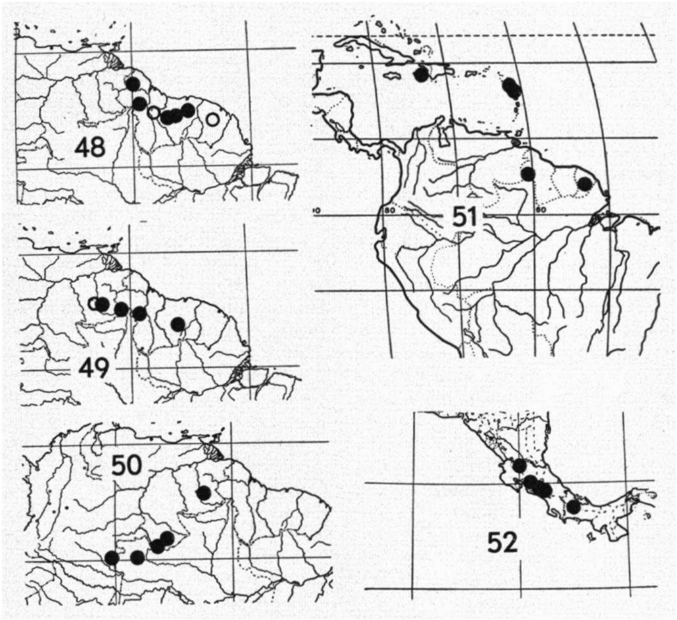
Distribution: Guayana (map 49). In forests, in moist localities, sometimes along streams, up to ca. 1000 m.

Venezuela. Bolívar: Vic. of Salto de Pacairao, n.e. of Santa Teresita de Kavanayén, Steyermark 60518 (F, NY, US); Chimantá-Massif, slopes of Toronotepuí, Steyermark 75416 (US); Mt. Roraima, Venezuelan side, Schomburgk s.n. (K).

British Guiana: Essequibo R., Appun 42 in part (B); Essequibo and Rupununi Rs., Schomburgk 533 (B, BM, BR, K, L, NY, US, W); Pacatout below the Kaieteur, Potaro R., Jenman 1394 (K, NY); without loc., Winter s.n. (C. Chr. in BM, UC), Schomburgk 367 (B, BR), Schomburgk 68 (BM, BR, C. Chr. in BM, FI, K, W).

Suriname: Tafelberg, top, Maguire 24243 (A, F, K, MO, NY, U, UC, US); ibid., id. 24817 (A, F, K, NY, U, US); without loc., Anderson s.n. (BM, Holotype).

French Guiana: without loc., Martin s.n. (BM).



Map 48: *Lindsaea sagittata*. Map 49: *L. reniformis*. Map 50: *L. cyclophylla*. Map 51: *Ormoloma imrayanum*. Map 52: *O. standleyi*.

Most closely allied to *L. cyclophylla;* the differences are discussed under that species.

Posthumus (1927) claimed to have proved that *L. reniformis* could not be separated from *L. sagittata*. His conclusion was mainly based on the fact that the basal lobes in the latter species are not always acute but may be rounded, as in the former, a fact already known to Dryander; and on an abnormal leaf of *L. sagittata*, were the leaf-apex was not developed because of damage, apparently at an early stage. It is quite clear that this is not sufficient evidence; the present author has not seen a single dubious or intermediate specimen. The only other author who reported specimens of *L. reniformis* tending towards *L.*

sagittata was JENMAN (l.c., p. 72); his observations of "an occasional frond to become pointed" probably refer to leaves where the distal margin has an outstandingly protruding portion. The present author has probably seen all of Jenman's specimens and has not found any specimens of *reniformis* with pointed leaf-top.

40. **Lindsaea cyclophylla** Kramer, spec. nov. **Fig. 90, 91**

Misapplied names: *L. reniformis* auct. non Dryand.; Baker, Fl. Bras. I^2:357 (1870), in part; Wagner, Am. Jo. Bot. 39: fig. 9H (1952).

L. reniformi valde affinis, differt petiolo facie abaxiali superne usque ad cacumen angulari; lamina potius orbiculari vel in plantis juvenilibus reniformi, sporisque diplanatis.

Typus: Holt & Blake 494 from Serra Imeri, terr. Amazonas, Venezuela (US).

Rhizome short-creeping, ca. ½ mm in diam.; scales narrowly lanceolate, long-acuminate, up to 1 mm long and 0.15 mm wide, with up to 6 rows of cells at the base. *Petioles* rather close, subdistichous, 10–20 cm long, 2–4(–6), mostly about 3 × as long as the lamina, ca. 0.6 mm in diam. at the base of the lamina, dark brown to atropurpureous, rather shining, adaxially terete in the lower third, above with lateral ridges that become narrow pale wings between which the surface is more or less flattened in the upper part, abaxially the same happens roughly halfway, the petiole thus being quadrangular in its upper part, with four often pale narrowly winged angles. The angles of the adaxial side are continuous with the marginal strand of the lamina, those of the abaxial surface extend up to or into the sclerotic patch at the base of the lamina. This patch is adaxially as in the preceding species; abaxially it is smaller, more regular in shape, mostly without a central extension but with several short ones extending not more than about 0.5 mm along the veins, giving the patch a stellate appearance. *Lamina* almost circular in large leaves, reniform or bean-shaped in small leaves of juvenile plants, chartaceous, medium green on the ventral, paler on the dorsal side, 2.5–7 cm long, 3.5–8 cm wide, 0.5–2 cm wider than long, rarely approximately isodiametric, deeply cordate (or in small leaves shallowly emarginate), the sinus 1.5–3 cm deep, reaching to about $^2/_5$ of the length of the lamina, mostly narrow, the basal lobes sometimes overlapping. Margin very evenly rounded except at the sinus, marginal thickening stramineous or pale brown, visible throughout but strongest at the base, slightly more distinctly and more irregularly erose-denticulate than in *L. reniformis*, in addition distinctly crispate-undulate, crenate in sterile leaves except in the sinus, the incisions ca. 0.5–1 mm deep, separating one or two vein-ends. Veins regularly dichotomously 3–4(–5) times forked, rather lax, ¾–1½ mm distant at the margin, immersed except for the base where they are slightly elevated just beyond the sclerotic patch; no main vein developed. *Sori* continuous to the edge of the sinus but not extending into it; indusium concolorous with the lamina, ca. 0.5 mm wide, subentire or mostly minutely erose-denticulate, not reaching the margin by 0.5–1.5 mm, reflexed and conceiled at full maturity. Sporangia ca. 160–165 × 125 μ annulus with 9 or 10 indurated cells; spores bean-shaped, very pale brownish, almost colourless, ca. 33 × 21 μ, 16?

Distribution: North-western borderlands of the Amazon basin (map 50). In forests, along creeks, on sandstone or igneous boulders, at about 600–800 m.

BRAZIL. AMAZONAS: Panuré on Rio Uaupés, Spruce 2916 (K).
VENEZUELA. AMAZONAS: Western foothills of Serra Imeri, near Salto de Huá, ca. 800 m, Holt & Blake 494 (US, HOLOTYPE; Isotypes in GH, NY, US); Cerro de la Neblina, Rio Yatua, Maguire, Wurdack & Bunting 36806 (US; juvenile).

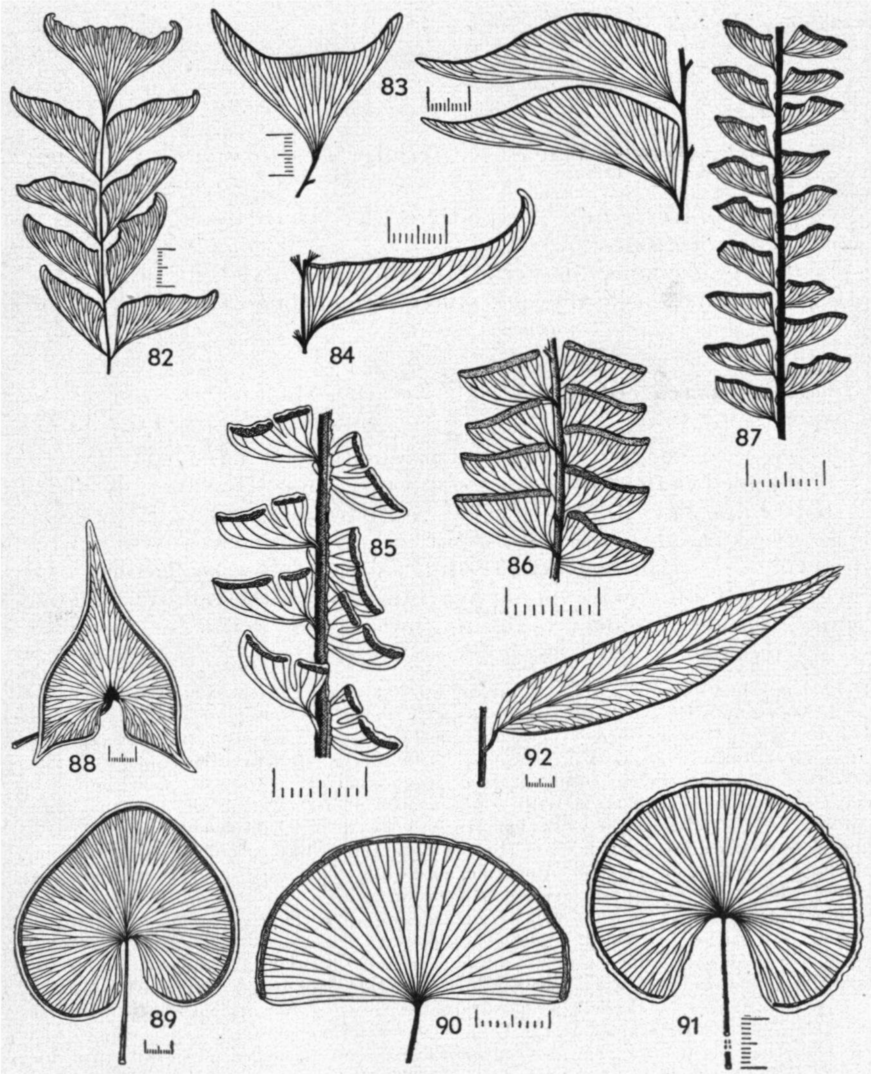


Fig. 82: *Lindsaea semilunata;* complete lamina (Appun s.n., Glaziou 12353). Fig. 83: *L. latifrons;* terminal pinnule (left) and lower pinnules from bipinnate leaf (Klug 2890). Fig. 84: *L. hemiglossa;* upper pinnule (Spruce s.n.). Fig. 85: *L. seemannii* var. *serrigera;* middle of lamina (Lehmann 737). Fig. 86: *L. pratensis;* middle of lamina (Wercklé s.n.). Fig. 87: *L. protensa;* middle of lamina (Ekman H 10243). Fig. 88: *L. sagittata;* lamina (Boschwezen 587). Fig. 89: *L. reniformis;* lamina (Maguire 24817). Fig. 90–91: *L. cyclophylla;* fig. 90: lamina of juvenile plant (Steyermark 74800); fig. 91: lamina of mature plant (Holt & Blake 494). Fig. 92: *L. macrophylla;* lateral pinna (Riedel s.n.). (Scales in mm).

Bolívar: Chimantá Massif, western sides of Apácara-tepuí, Steyermark 74663, 74800 (US).
Colombia. Vaupés: Rio Kananarí, Cerro Isibukuri, Schultes & Cabrera 15064 (US).

Closely related to *L. reniformis.* for the diffierences, see the latin description.

Sectio VI. **Paralindsaea** (Keyserling) C. Christensen, Ind. Fil. xxx (1906).

Paralindsaya Keyserling, Polypod. & Cyath. Herb. Bung. 3, 21 (1873), as subgenus of *Lindsaea.*

Leaves dimorphous, the sterile ones short, decurved, simply pinnate, always present, the fertile ones longer, erect, once or twice pinnate.

Type species: *Lindsaea linearis* Swartz.

41. **Lindsaea cubensis** Underwood & Maxon, Smithson. Misc. Coll. 50:336 (1907). **Fig. 33, 71**

Type: Wright 3947, from Loma pelado, Cuba (NY!)

Misapplied name: *L. portoricensis* auct. non Desvaux; Krug in Urban, Engl. Bot. Jb. 24:91 (1897), in part.

Petioles stramineous or reddish brown; leaves herbaceous, somewhat dimorphous; sterile leaves spreading, simply pinnate; fertile leaves erect, simply pinnate or sometimes bipinnate with conform terminal pinna; sori continuous; indusium rather wide, erose or laciniate; spores monolete.

Rhizome short-creeping, ca. 1 mm in diam.; scales almost linear, up to 1 mm long, 0.2 mm wide, with up to 4 rows of cells at the base, for the greater part consisting of 2 or 1 row only. *Petioles* rather close, adaxially shallowly sulcate, abaxially obtusely angular to rounded; often crushed, the structure not easily observed; primary rachis similar to the upper part of the petiole. *Leaves* more or less dimorphous. *Sterile leaves* with a petiole 0.5–4 cm long, ca. ¼ mm in diam.; lamina 3–7(–9) cm long, ca. ½–1½ cm wide, with 6–12 pinnules to a side, these subopposite to alternate, delicate, pale green, somewhat ascending or spreading, the lower ones widely spaced, interstices equalling their width or larger, the upper ones closer, subcontiguous; roundish or dimidiate-ovate to subtriangular, ca. 4–8 mm long and 3–6 mm wide, from as long as wide to ca. 1½ × as long as wide, subsessile, subentire to shallowly undulate-crenate, the upper margin mostly minutely erose, the inner margin often touching or even overlapping the rachis, all margins more or less equally and not strongly convex, or all but the upper straight, but little thickened; veins simple or mostly once forked, lax, their ends ca. 1 mm apart, the main vein ca. ½ mm above the lower margin. Upper pinnules little or not reduced; terminal segment large, often larger than any pinnule, ¾–1 cm long, lobed-incised at the base, confluent with one or two lateral pinnules, lanceolate to lozenge-shaped or even square, obtuse. *Fertile leaves* with a petiole (3–)6–13 cm long, ½–1 mm in diam.; lamina with one to two up to 6 cm long primary pinnae to a side, (3½–)5–18 cm long, 10–22 mm wide, with 8–25 pinnules to a side, these subopposite to alternate, pale to medium green, herbaceous, spreading or laxly ascending, the lower ones up to 3 cm apart, the upper ones gradually closer but mostly not contiguous, very variable in shape, subtriangular, dimidiate-ovate, flabellate, cuneate, or even dimidiate-tongue-shaped, ca. 6–12 mm long and 3–9 mm wide, mostly about twice as long as wide, sometimes less, subsessile to short-stalked (up to 1 mm), entire, the inner margin straight, often touching or overlapping the rachis, the upper margin convex, sometimes only near the apex, subentire to minutely erose or superficially incised, lower margin straight, convex towards the apex, the upper base truncate or mostly shortly rounded, the apex rounded; veins or once or twice forked. Otherwise as the sterile leaves. *Sori* along the upper/outer margin, also in the terminal segment; indusium greyish, ca. ½ mm wide, not reaching the margin by ¼-½ mm, mostly little or not reflexed at full maturity. Sporangia ca. 125–130 × 105 × 110 μ; annulus with 10–13 indurated cells; spores semi-elliptic to bean-shaped, medium brown, ca. 19 × 31 μ, 32?

Distribution: Western Cuba and Isla de Pinos (map 47). In pinelands and scrub, almost always along watercourses; altitude not noted.

CUBA. PINAR DEL RIO: Herradura, Shafer 427 (NY, Paratype); Los Palacios to Herradura, Shafer 11698 (NY); near El Guama, Palmer & Riley 287 (BM, C, GH, NY, US); ibid., id. 550 (BM, C. Chr. in BM, MO, NY, S–PA, Paratypes); Sierra de Cabra, Britton, Britton & Cowell 9785 (NY, US); ibid., Guane road, Britton, Britton & Gager 7290 (NY), 7222 (NY, US); east of Viñales, Ekman 18008 (G, NY, S, US). Prov.?: Loma pelado, in dense bunches under overhanging rocks, Wright 3947 (NY, HOLOTYPE; Isotypes in B, GH, K, MO, NY, S–PA, U, US).

ISLA DE PINOS: near Managua, Palmer & Riley 1060 (US, Paratype); near Nueva Gerona, Palmer & Riley 1027 (C, NY, US, Paratypes); ibid., Curtiss s.n. (NY, Paratype); La Cunagua, Britton, Britton & Wilson 14553 (F, NY, US); Swetland Ranch, San Francisco de la Piedras, Killip 34547 (US); Santa Bárbara–Mina de Oro, Killip 43866 (US); without loc., Jennings 418 (NY).

In spite of the great variability of the pinnules, this species can be easily recognized by its delicate stipes, small size, large terminal segment, and the almost universal presence of sterile leaves. The dimorphism is not absolute, as transitions between sterile and fertile leaves do occasionally occur, and leaves of the fertile shape are sometimes only incompletely fertile; but in most cases it can be readily observed. There is no obvious relative in the New World, but there is a striking resemblance to *L. linearis* Sw. from Australia, New Zealand, and New Caledonia. The latter agrees in its dimorphism, with small spreading sterile and large erect fertile leaves, in the lower pinnules being remote but not reduced, in similar pinnules and erose indusia. Points of difference are the larger and wider rhizome scales, the dark petiole and rachis, the wider indusia, always simply pinnate leaves, and trilete spores of *L. linearis*. For these reasons, *L. cubensis* is placed with misgivings in the present section, and the phytogeographical implications of the supposed relationship are not discussed at length. It may be pointed out here that a parallel case is found in the section *Tropidolindsaea*, also of the Caribbean region, whose closest relative is beyond doubt *L. viridis* from New Zealand.

Sectio VII. **Tropidolindsaea** Kramer, sect. nov.

Lamina simpliciter pinnata, pinnulis superioribus et inferioribus sensim redactis; petiolo rhachideque facie abaxiali carinatis vel angustato-rotundatis; cellulis induratis annuli pedunculum sporangii non attingentibus; sporis oblongis.

Species typica: *Lindsaea seemannii* J. Smith.

The species of this section are quite outstanding among the neotropical Lindsaeas by the lamina being gradually reduced above *and* below, the abaxially keeled or narrowed-rounded petiole and rachis, and the annulus, the indurated part of which does not reach the stalk of the sporangium, the latter character also observed in some species of *Sphenomeris*. In addition, the rhizome-scales are large and ovate or broadly lanceolate and in one species clathrate, unlike any American species, and the spores are always monolete. A related species, to be placed in an allied section, or perhaps in the same section, is *Lindsaea viridis* Col. from New Zealand. The section *Tropidolindsaea* should perhaps be raised to the rank of subgenus.

42. **Lindsaea seemannii** J. Smith, Bot. Voy. Herald 239 (1854); Hist. Fil. 268 (1875), non Carruthers, 1873. **Fig. 32**

Type: Seemann 976 from the Bay of Chocó, "Panama" (now Colombia) (BM!).

Rhizome-scales clathrate; petioles reddish to dark brown, abaxially keeled; lamina simply pinnate, linear, herbaceous; rachis abaxially keeled; pinnules ca. 2 × as long as wide, the upper margin incised; upper and lower pinnules gradually reduced; sori interrupted, mostly binerval, usually three per pinnule; spores monolete.

Rhizome short-creeping, ca. 1.5 mm in diam.; scales ovate to broadly lanceolate, acuminate, up to 2.4 mm long, 0.75 mm wide, with up to 15 rows of cells at the base, clathrate, the tangential and marginal longitudinal walls very pale, the other longitudinal and all transversal walls medium brown (fig. 5); the cells relatively regular in shape, the median ones hardly more elongate; reduced scales only in small numbers present near the rhizome-apex. *Petioles* close, very lustrous, ca. 3–8 cm long, ¾–1 mm in diam., adaxially narrow, channelled, roughly triangular in cross-section, the lateral surfaces flattish or convex. *Lamina* obtuse, ca. 15–35 cm long, two to more than five times as long as the petiole, ca. 1.5–2 cm wide, pale to brownish green, with 30 to more than 50 pinnules to a side. *Rachis* adaxially with a narrow groove with paler edges, abaxially keeled below, the keel becoming wing-like and pale in the upper ⅔ or ½ of the rachis. *Pinnules* subopposite or the upper ones alternate, the middle ones rather close but not contiguous, the lower ones gradually remote and strongly reduced, sometimes auriculiform, the upper ones gradually but not very strongly reduced, the leaf-apex rather suddenly pinnatifid with a few confluent cuneate segments. Largest pinnules ca. 10 mm long, 5–6 mm wide, in outline resembling ¼ of an ellipse, subsessile, spreading, the upper ones slightly ascending, the reduced basal ones often somewhat deflexed. Lower margin evenly convex, inner margin ± straight, often touching or slightly overlapping the rachis, lower base very shortly stalk-like, inserted on a brown protuberance of the rachis where it is easily detached but not truly articulate, upper margin incised with at least one incision 2–3 mm deep, the sinus rounded, ca. 0.5 mm wide at the margin, the lobes mostly about 2–5 mm wide, often not equal in length, their outer margins not in one line, sinuate or sometimes erose. Marginal strand almost absent, except at the extreme lower base. Veins immersed or very slightly protruding; the vein at the basiscopic side (hardly to be called a main vein) ca. 3 mm above the lower margin; lateral veins once forked, (1–)2(–4) per lobe. *Sori* laterally extending beyond the vein-ends. Indusium membranous, ca. 0.5 mm wide, sinuous-erose, mostly not quite reaching the margin, not reflexed at full maturity. Sporangia ca. 250 × 200 μ; annulus with 12–15 indurated cells (fig. 20); spores subelliptic, rather pale brownish-yellow, 50–55 × 37 μ.

a. var. **seemannii**.

Wing on the abaxial side of the rachis entire or sinuous, usually not wider than 0.1 mm; pinnules mostly with two or three incisions.

Distribution: Eastern Panamá and western Colombia; on cliffs and rocky bands, near sea-level (map 46).

PANAMÁ. DARIEN: Isthmus of Darien, Seemann s.n. (US, Paratype).
COLOMBIA. CHOCÓ: Bay of Chocó, Seemann 976 (BM, HOLOTYPE; Isotypes in B, K, photogr. in US); between La Oveja and Quibdó, Archer 1670 (US).

El Valle: Punta Magdalena, Haught 5581 (S–PA, US); Colorada, n. shore of Buenaventura Bay, Killip & Cuatrecasas 38695 (US).

b. var. **serrigera** Kramer, var. nov. **Fig. 85**

Recedit a varietate typica pinnulis minus incisis, ala carinae faciei abaxiali rhachidis petiolique valde prominente, conspicue et irregulariter eroso-repanda vel serrata.

Typus: Lehmann 737 from Sucre, Cauca, Colombia (US).

Pinnules mostly with only one incision near the base; some sori occupying six or even eight veins; wing-like borders of the adaxial groove also irregularly erose-sinuate.

Distribution: Colombia; on banks in very moist forest, 200 m. Only known from type-collection (map 46).

Colombia. Cauca: Near Sucre, Río Dagua, Lehmann 737 (US 826432, Holotype; Isotypes in B, BM, C. Chr. in BM, G, K, LE, US).

Most closely allied to *L. pratensis*, where the differences are discussed It has nothing to do with *L. cultrata*, with which it was compared by Hooker & Baker (1868, 1874, p. 105).

43. **Lindsaea pratensis** Maxon, Am. Fern Jo. 23:73 (1933). **Fig. 86**

Type: Wercklé s.n. from Costa Rica (US).

Rhizome-scales not clathrate; petioles reddish to dark brown, abaxially obtusely keeled; lamina simply pinnate, linear, mostly coriaceous; rachis abaxially keeled below, winged above; pinnules 30–50 to a side, 1½–2 × as long as wide, not or hardly incised; upper and lower pinnules gradually reduced; sori continuous or rarely slightly interrupted; spores monolete.

Rhizome creeping, ca. 2 mm in diam.; scales yellowish brown, ovate to broadly lanceolate, acuminate, ca. 4 mm long and 1 mm wide, with up to 20 rows of cells at the base; the cells very irregular, those of the apex more elongate than the basal ones. *Petioles* not very close, 7–15 cm long, one half to two-thirds the length of the blade, ca. ¾ mm in diam. near the apex, rather dull, adaxially with a shallow rather broad groove or flattened below, approximately triangular in cross-section, the lateral sides convex. *Lamina* ca. 12–25 cm long, 1.5–3.5 cm wide, coriaceous or rarely chartaceous, brownish green. *Rachis* below similar to the petiole, above abaxially with a pale often very coarsely and irregularly erose-dentate wing, the borders of the adaxial groove never erose. *Pinnules* subopposite, the upper alternate, the middle and upper ones very close, contiguous or mostly somewhat overlapping (succubous), ± spreading, sessile, ca. 8–13 mm long, 5–8 mm wide, subtriangular, semi-crescent-shaped or ¼-elliptic, those of the lower ⅔ of the lamina very gradually reduced and remote, 2–5 cm apart, in the upper ⅓ of the lamina gradually reduced to the pinnatifid leaf-top. Apparently the leaves develop very slowly; in otherwise mature leaves the apex is still involute and quite immature and very often lost; perhaps the lamina develops intermittently, as in *Jamesonia*. Lower edge of pinnules straight or usually somewhat convex, inner edge more or less concave, touching or slightly overlying the rachis, lower base not stalk-like, inserted on a protuberance of the rachis as in the preceding species, upper edge straight or slightly convex or concave, the apex blunt or often slightly apiculate and upturned. All edges entire, or the upper edge with one incision up to 2 mm deep near the middle. Marginal thickening indistinct, except at the lower base. Veins immersed, mostly somewhat impressed adaxially, simple or once forked, their ends ca. ¾–1 mm apart; main vein ca. 0.2–0.3 mm above the lower margin. *Sori* along the upper margin; indusium delicate, ca.

0.4 mm wide, subentire or erose, almost equalling the margin, hardly reflexed at full maturity. No full-size sterile pinnules seen, the basal reduced ones usually incompletely fertile. Sporangia ca. 250 × 200 μ; annulus with 14–16 indurated cells; spores subelliptic, pale brownish-yellow, ca. 52 × 39 μ.

Distribution: Endemic in Costa Rica (map 46). On wet, open, grassy bank, (1400?–) 2000–2400 m.

COSTA RICA. Cerro de las Caricias, north of San Isidro, Heredia prov., Standley & Valerio 52245 (GH, US, Paratypes); Carillo region, Lankester s.n. (BM); garden at San José, originally from La Palma, Wercklé s.n. (US, Paratype); without exact loc., Wercklé s.n. (US, HOLOTYPE).

Most closely allied to *L. seemannii*, from which it differs by the non-clathrate scales, closer and firmer pinnules, and mostly not incised upper margin. *L. protensa*, which is more remotely related, has smaller, thinner, more numerous pinnules.

44. **Lindsaea protensa** C. Christensen, Kungl. Sv. Vet.—Akad. Handl. Ser. III, 16 (2): 45 (1937), pl. XI fig. 1–3. **Fig. 87**

Type: Ekman H 10243 from Massif de la Hotte, Hispaniola (C. Chr. in BM!).

Rhizome-scales not clathrate; petioles reddish brown, abaxially narrowed-rounded; lamina simply pinnate, linear, herbaceous; pinnules ca. 80–100 to a side, ca. 1½ × as long as wide, not over 8 × 5 mm, entire; upper and lower pinnules gradually reduced; sori continuous; spores monolete.

Rhizome creeping, ca. 2–3 mm in diam.; scales yellowish-brown, broadly lanceolate, acuminate, up to ca. 3 mm long, ¾ mm wide, with about 16 rows of cells at the base. *Petioles* rather close, ca. 3–6, mostly about 4 cm long, ¾–1 mm in diam., rather shining, adaxially with a sharply delimited flat portion. *Lamina* elongate, ca. 35–80 cm long, 1–2 cm wide near the middle, pale green. *Rachis* similar to the petiole. *Pinnules* subopposite, the upper ones alternate, spreading, the upper ones ascending, the largest rather close but not contiguous, 5–8 mm long, 3–5 mm wide, in the lower half or one-third of the lamina gradually reduced and farther apart, the lowest ca. 2 cm apart, in the upper third of the lamina also gradually reduced, a few linear segments connected by a wing; no well-developed terminal segment present, the leaf-top incurved, immature, or missing in most leaves which apparently develop quite slowly, perhaps intermittently. Largest pinnules obliquely triangular to ¼-elliptic in outline; lower margin convex, inner margin S-shaped to straight, ± parallel to the rachis, upper edge straight, slightly concave, or with a shallowly concave portion in the basal half, often somewhat erose-sinuate, apex bluntish to subacute, lower base cuneate, with a stalk-like portion of ca. ½ mm, with hardly any trace of an articulation as in the two preceding species, but the dark colour of the rachis suddenly fading at the base of the pinnules. Veins immersed but readily visible, once or twice forked, their ends ca. ½ mm apart; main vein close to the lower edge; marginal thickening externally not visible. *Sori* along the upper margin; indusium delicate, ca. 0.4 mm wide, sinuate-erose, equalling the margin, hardly reflexed at full maturity. No full-size sterile pinnules seen, reduced lower pinnules usually at least incompletely fertile. Sporangia ca. 230 × 185 μ; annulus with 15–16 indurated cells; spores subelliptic, pale brownish-yellow, ca. 45–50 × 37–41 μ, 16?

Distribution: Endemic in the south-western peninsula of Hispaniola (map 46). On lateritic soil, 150 and 900 m.

HISPANIOLA. HAÏTI: Massif de la Hotte, western group, Jérémie, between La Source Chaude and Source Cahouane, Ekman H 10243 (C. Chr. in BM, HOLOTYPE;

Isotypes in B, GH, K, NY, S, UC, US); ibid., near Lopineau, Ekman H 10402 (B, C, F, S, Paratypes).

Not as close to *L. pratensis* as Christensen supposed, but apparently most closely related to that species. The abaxially almost terete petiole and rachis and the small very numerous pinnules distinguish it quite readily.

Subgenus B. **Schizoloma** (Gaud.) Hooker, Spec. Fil. I:219 (1844). *Schizoloma* Gaudichaud, Ann. sci. nat. 3:507 (1824), as genus.

Veins anastomosing, without included veinlets; lamina simply pinnate, with large equal-sided pinnae with a median main vein, or, when bipinnate, with large undivided pinna-apices; sori continuous.

Type species: *Schizoloma billardieri* Gaudichaud (= *Lindsaea ensifolia* Swartz).

45. **Lindsaea macrophylla** Kaulfuss, Enum. 218 (1824); Sprengel, Syst. Veget. IV:79 (1827); Kunze, Anal. 37 (1837), pl. 25; Hooker, Ic. Fil. II t. 193 (1837); Hooker & Bauer, Gen. Fil. t. 63 B (1840); Hooker, Spec. Fil. I:220 (1844); Klotzsch, Linnaea 20:445 (1847); Kunze, Bot. Zeit. 8:404 (1850); Hooker & Baker, Syn. Fil. 1st ed. (1868); 2nd ed. (1874) 112; Baker, Fl. Bras. I^2: 358 (1870), pl. 42 fig. 1; Christ. Farnkr. d. E. 298 (1897); Jenman, W. Ind. Gui. F. 72 (1899). **Fig. 92**

Type: Chamisso (?) s.n. from French Guiana, not seen (prob. P). Homotypic synonym: *Schizoloma macrophyllum* (Kaulfuss) Presl, Tent. Pterid. 132 (1836); J. Smith, Hist. Fil. 271 (1875); Kuhn, Chaetopt. 26 (1882); Diels, N. Pfl. I^4:219 (1902); Knuth, Fedde Rep. Beih. 43 (1):31 (1926); Sampaio, Arch. Mus. Nac. Rio de Jan. 32:42 (1930).

Lamina simply pinnate, chartaceous; pinnae almost equal-sided, broadly lanceolate, the upper and the terminal one not reduced; veins reticulate; sori continuous, interrupted at the pinna-apex; spores monolete.

Rhizome not seen. *Petioles* (only one complete specimen seen) up to 52 cm long, rather stout, 1.5–2 mm in diam. near the apex, castaneous to greyish-brown, rather shining, adaxially sulcate, with sharp, often somewhat paler angles, abaxially obtusely angular below, sharply angular above, there flattened or sulcate. *Lamina* ovate in outline, 30–35 cm long, medium green to olivaceous, paler on the dorsal side, with 3–4 pinnae to a side and a conform terminal one. *Rachis* similar to the upper part of the petiole, but adaxially flattened with raised borders, not concave. Axillary cushions indistinct, slightly swollen and discoloured. *Pinnae* alternate or subopposite, ascending under an angle of ca. 30–60°, rather wide-spaced to moderately close, the lower ones 5–6 cm apart, the upper ones closer, not contiguous, 13–17 cm long, 3–4 cm wide, 4–5 × as long as wide, broadest in the middle or mostly in the lower third, the terminal pinna always relatively broadest, with a stalk of 2–3 cm, lateral pinnules with a stalk-like base of ca. ½ cm, the basiscopic half often more strongly convex than the acroscopic, the cuneate base also unequal, the leaf-tissue extending farther down on the acroscopic side, in addition often somewhat folded over at the basiscopic side; base of the terminal pinna equal or almost so. All pinnae gradually narrowed from the broadest point, the apex often somewhat acuminate, the very top blunt or subacute. Margins with a strong, often revolute, entire, stramineous strand that extends around the apex (the sterile apex of the pinnae figured as being serrate in Hooker & Bauer's plate). Veins immersed or very slightly elevated, very oblique near the midrib, less so towards the margin, 3–5 times forked, usually with one or two anastomoses between midrib and margin, the meshes exappendiculate; vein-ends very irregularly spaced, ca. 1–3 mm apart. Midrib strong, approximately median, slightly flexuose, percurrent, abaxially elevated, stramineous, adaxially immersed, except near the base. *Sori* along both margins from about 1 cm above the base, interrupted in the apex, where the receptacle may be nevertheless continuous; no sterile pinnae seen. Indusium greyish, entire, ca. 0.4 mm wide, not reaching the margin by approximately its own width, strongly reflexed and conceiled at full maturity. Sporangia ca. 140 × 115 μ; annulus with ca. 10–14 indurated cells; spores bean-shaped, hyaline, almost colourless, ca. 23 × 27 μ.

Distribution: North Brazil and French Guiana, also reported from other regions, but probably confused with species of *Adiantum*. No ecologidal data extant.

BRAZIL. PARÁ: Bay of Esperara (or Esperança), Riedel s.n. (GH, K, U, W, fragment, prob. of this coll., in F).

This very remarkable and apparently extremely rare species has no relatives in the Western Hemisphere. It is most closely allied to *L. ensifolia*, which is widespread in the tropics of the Eastern Hemisphere, and the only species occurring on the African continent. The two species agree in such diverse characters as leaf-pattern, unequal pinna-bases, venation, structure of the petiole, etc.; but *L. macrophylla* has broader pinnae, smaller sporangia, and monolete spores.

Most specimens in herbaria determined as *Lindsaea macrophylla* belong to *Adiantum dolosum* Kunze. HOOKER (1844, p. 220/221) admitted to have made a similar mistake; KUNZE (1850, see above) believed Hooker-Bauer's plate to represent the same species, but in the present author's opinion this is not certain. Incidentally, the plate incorrectly shows the veins to be free. The specimen from Cumana, Venezuela, cited by Klotzsch and Knuth (see above) (Moritz 155), not seen by the author, may also be an *Adiantum*. On the other hand, it is hardly likely that *Kaulfuss*' type itself is an *Adiantum*, not a *Lindsaea*, although the author cannot confirm this on the base of his own observations.

SPECIES OF UNCERTAIN STATUS

Lindsaea falciformis Hooker, Spec. Fil. I:208 (1844), t. 64 B; Hooker & Baker, Syn. Fil. 1st ed. (1868), 2nd ed. (1874) 104; Baker, Fl. Bras. I^2:351 (1870); J. Smith, Hist. Fil. 268 (1875); Kuhn, Chaetopt. 26 (1882); Jenman, W. Ind. Gui. F. 72 (1899); Posthumus, Fl. Surin. Suppl. 71 (1928); Maxon & Morton in Maguire, Bull. Torr. Bot. Cl. 75:74 (1948).

Type: Schomburgk s.n. from Mt. Roraima, British Guiana (K!, Isotype in BM).

This species is unlike any species from the Guianas except *L. surinamensis;* from this it differs by smaller, more numerous pinnules which are more falcate, but it may be an abnormal form of that species. It has never again been collected.

Lindsaea mazaruniensis Jenman, W. Ind. Gui. F. 75 (1899); Posthumus, Fl. Surin. Suppl. 76 (1928).

Type: Jenman 2265 from the falls of the Mazaruni River, British Guiana (K!); a specimen which may be a duplicate in NY.

Not unlike a bipinnate specimen of *L. lancea*, but differing by dark, abaxially quite terete primary rachis, more strongly intramarginal sori, and much more rounded pinnules which are often broadest near the apex, not unlike those of *L. botrychioides*. Almost all sporangia (in the K specimen) abortive, the few normal ones with abortive spores. Another specimen: Appun 831 from British Guiana (K) is ± similar, but simply pinnate, with more elongate pinnules; the sporangia are normal, but the spores also abortive. Probably a hybrid; one of the parents almost certainly *L. lancea*, the other perhaps *L. divaricata*.

Lindsaea montana Fée, 11^e mém. 17 (1866), t. 6 fig. 2; non Copeland, 1905.

Type: L'Herminier s.n. from Guadeloupe (P!).

Almost all authentic specimens, including the type, are mixtures of *L. guianensis* ssp. *guianensis* and the form described above as *L. quadrangularis* ssp. *antillensis*, with which the name has almost universally been associated. Neither Fée's description nor his plate make it possible to decide to which of the two forms the name should preferably be applied; therefore it seems best to regard it as a *nomen confusum*. For more complete citations see under *L. quadrangularis* ssp. *antillensis*.

Lindsaea pumila Klotzsch, Linnaea 18:545 (1844); Hooker, Spec. Fil. I:209 (1844); Kunze, Linnaea 21 :225 (1848); Kunze, Bot. Zeit. 8:325 (1850); Jenman, W. Ind. Gui. F. 73 (1899); Sampaio, Arch. Mus. Nac. Rio de Jan. 32:35 (1930); not of C. Christensen, Dansk Bot. Ark. 6:97 (1929), nor *L. pumila* (Brack) Hooker & Baker, Syn. Fil. 1st ed. 113 (1868), which is *Diellia erecta* Brack. f. *pumila* (Brack.) Wagner.

Type: Schomburgk 1138 from British Guiana (B!).

The type-specimen has small rhizomes with small scales like those of *L. lancea* and simply pinnate leaves up to 11 cm long; the petioles are dark, sharply quadrangular almost to the base, the pinnules ca. 10–15, not unlike those of *L. lancea* var. *remota* but firmer, up to 9 × 5 mm, the terminal segment broadly lanceolate, free or connected with 1 or 2 lateral ones; the indusia are continuous, entire or subentire, 0.4–0.5 mm wide, almost reaching the margin. Schomburgk 47 from Mt. Roraima, British Guiana (BM) is similar. This is probably a depauperate form of some other species, but it is impossible to say of which. Posthumus referred it to *L. guianensis* which is, however, not close. CHRISTENSEN (l.c.) referred to the same species a specimen from Taracuá, Amazonas, Brazil, Roman nr. 26 (C. Chr. in BM, S-PA); this differs by the abaxially terete lower half of the petiole, thinner, more rounded pinnules, and narrower erose indusia. A third collection referred to *L. pumila* by Christensen is Spruce 3064 (B, BM, BR, G, K, L, LE, W) from San Carlos, Rio Negro, Amazonas, Venezuela. This is approximately intermediate between the two collections just described, but the pinnules are more strongly reduced above, confluent with a small terminal segment, and the indusia are ca. 0.5 mm wide and strongly erose-denticulate; a very similar specimen is

Baldwin 3507 (US) from the junction of Rio Uaupés with Rio Negro, Amazonas, Brazil, also von Lützelburg 22238 (M) from São Felippe, Rio Negro, and id. 22280 (M) from Marabitana, Rio Negro. These specimens represent perhaps an undescribed species. Steyermark 58095 (F, MO, NY, US) from Mt. Duida, Amazonas, Venezuela, differs by narrower, less erose indusia, larger terminal segment, and often wing-like ridges on the petiole and rachis; von Lützelburg 22529 (M, NY, UC) from Cururú, Rio Ayarí, and id. 22679 (M) from Tunuý, Rio Içana, both Amazonian Brazil, are similar but have narrow erose indusia with erose fertile margin and strongly wing-like angles of the axes.

Unnamed forms

Of the comparatively very few specimens which the author has not been able to determine, the following are discussed because they may represent new taxa.

Two collections from Venezuela: Tate 430 (K, NY, US) from Mt. Duida, Amazonas, and Maguire, Wurdack & Bunting 37158 (US) from Cerra de la Neblina, Río Yatua, Amazonas, belong to a form allied to *L. klotzschiana*, differing by abaxially terete petioles, firmer texture, and darker colour; in general habit they are not unlike more amply bipinnate forms of *L. stricta* var. *jamesoniiformis*. The spores are trilete, most of them abortive, a few giant spores and some monolete ones were observed in the same sorus with the others; all this points to hybrid origin. A third specimen: Steyermark & Wurdack 637 (US) from Torono-tepuí, Chimanta Massif, Bolívar, Venezuela, with normal spores, is more like *L. klotzschiana* and is perhaps a backcross with that species which is almost certainly one of the parent-species. The author cannot suggest which would be the other one.

Steyermark 59409 (F, MO, NY, US) from the Gran Sabana, Bolívar, Venezuela, is intermediate between *L. schomburgkii* and *L. portoricensis;* the leaves are simply pinnate or bipinnate, with small pinnules, the upper ones reduced, but the veins are elevated, the texture coriaceous, and there is small terminal pinnule shaped as in *L. schomburgkii.* The spores are dark and wrinkled, apparently abortive, and hybrid origin is very likely, *L. schomburgkii* being probably one of the parent-species, the other perhaps *L. portoricensis.*

Steyermark 75665 (U, US) from the Chimantá Massif, Bolívar, Venezuela, has pinnules and pinna-apices not unlike those of small forms of *L. arcuata;* the petioles are stramineous to fawn, very stout, and abaxially terete, the secondary rachises are on the abaxial side more like those of *L. portoricensis.* The spores are trilete, pale yellowish. Presumably a new species, but hardly sufficiently distinct to be described on the base of only one collection.

Two collections of von Lützelburg from northern Amazonas, Brazil: 23605 (M, NY) from Varadoura, Iutica, R. Uaupés, 23674 (M) from Uapuý, R. Ayari, and a third, 23826 (M) from the Colombian side of R. Uaupés near Iutica almost certainly represent a new species. The leaves are rather long, simply pinnate, the pinnules are not unlike those of *L. hemiptera*, but the upper part of the dark brown petiole is sharply quadrangular, and the angles of the abaxial side of the rachis are pale and somewhat wing-like. The spores are trilete, pale yellowish-brown. As there is not a single full-grown leaf with a complete apex, its relationships remain uncertain, and it cannot be described here as new. Rosenstock annotated all sheets "*Lindsaya quadrangularis* Raddi v. *amazonica* Ros. n.v. (an spec. propr.)", a name that was never published; fortunately, because there is certainly no close relationship to *L. quadrangularis*.

NAMES OF UNCERTAIN APPLICATION

Lindsaea caudifera Fée, Gen. Fil. 106 (1852). Type: L'Herminier s.n. from Guadeloupe (P? not seen). Not recognized.

Lindsaea consanguinea Fée, 11^e mém. 16 (1866). Two collections cited; the first, L'Herminier s.n. from Guadeloupe, is shown on pl. 6 fig. 3 of the above-cited work. It is probably a form of *L. lancea* with reduced upper pinnules and a small terminal segment, but may also represent *L. quadrangularis* ssp. *antillensis*. The authentic specimen has not been examined. The second collection, Luschnath 22 from Bahia, Brazil (B, MO!) belongs to *L. lancea* var. *lancea*.

Lindsaea falcata Dryander var. *subrotundifolia* Jenman, W. Ind. Gui. F. 74 (1899). No type specimen, or any other specimen, cited. Belongs perhaps to *L. lancea* var. *elatior*, or possibly to *L. schomburgkii*.

Lindsaea guianensis (Aubl.) Dryander var. *venosa* Jenman, W. Ind. Gui. F. 77 (1899). "In the forest near the Kaieteur Savannah", British Guiana. No specimen seen. Said to be well marked by the interrupted sori. Perhaps an incompletely fertile specimen of *L. portoricensis*.

Lindsaea ripidoteris Kunze, Bot. Zeit. 8:328 (1850). "fl. Bras. ined.", not typified. Kunze compared it with *L. flabellulata*. Perhaps a sterile specimen of *L. stricta*.

Lindsaea serrata Goldmann, Nova Acta Leop. 16 Suppl. 2:464 (1843). Type from Mt. Corvocado near Rio de Janeiro, "ad Aquaeductum", not seen. The description is most incomplete, apparently a sterile specimen, perhaps of *L. quadrangularis*.

EXCLUDED SPECIES

L. aculeata (L.) Mettenius, Ann. sci. nat. IV, 15:65 (1861). – *Odontosoria aculeata* (L.) J. Smith, Cult. Ferns 67 (1857).

L. clavata (L.) Mettenius, Ann. sci. nat. IV, 15:64 (1861). – *Sphenomeris clavata* (L.) Maxon, Jo. Wash. Acad. Sci. 3:144 (1913).

L. colombiana (Maxon) Pérez Arbeláez, Bot. Abh. Goebel 14:55 (1928). – *Odontosoria colombiana* Maxon, Contr. U.S. Nat. Herb. 17 (2):165 (1913).

L. divaricata (Schlecht. & Cham.) Mettenius ex Kuhn, Jo. Bot. 15:231 (1877), non Klotzsch 1844. – *Odontosoria schlechtendalii* (Presl) C. Chr., Ind. Fil. 209 (1906).

L. fumarioides (Swartz) Mettenius, Ann. sci. nat. V, 2:217 (1864). – *Odontosoria fumarioides* (Swartz) J. Smith, Hist. Fil. 264 (1875).

L. imrayana (Hooker) Pérez Arbeláez, Bot. Abh. Goebel 14:55 (1928). – *Ormoloma imrayanum* (Hook.) Maxon, Proc. Biol. Soc. Wash. 46:144 (1933).

L. (?) *Killipii* Maxon, Contr. Gray Herb. 165:74 (1947). – *Sphenomeris killipii* (Maxon) Kramer, Acta Bot. Neerl. 6: 153 (1957).

L. Michleriana Eaton, Mem. Amer. Acad. n.s. 8:213 (1860). – *Pleuroderris michleriana* (Eaton) Maxon, Jo. Wash. Acad. Sci. 24:550 (1934).

L. panamensis (Hooker) Mettenius, Fil. Lips. 105 (1856). – *Dictyoxiphium panamense* Hooker, Gen. Fil. t. 20 (1840).

L. schlechtendalii (Presl) Christ, Farnkr. d. E. 296 (1897). – *Odontosoria schlechtendalii* (Presl) C. Chr., Ind. Fil. 209 (1906).

L. sectorifolia Goldmann, Nova Acta Leop. 16 suppl. 1:464 (1843). – Not Lindsaeoid; according to C. Christensen, Ind. Fil. 397 (1906) *Adiantum flabellulatum* L.

L. (?) *spathulata* Maxon, Contr. Gray Herb. 165:74 (1947). – *Sphenomeris spathulata* (Maxon) Kramer, Acta Bot. Neerl. 6: 153 (1957).

L. uncinella (Kunze) Krug, Engl. Bot. Jb. 24:92 (1897) (perhaps antedated by Christ, Farnkr. d. E. 297, 1897). – *Odontosoria uncinella* (Kunze) Fée, Gen. Fil. 326 (1852).

4. ORMOLOMA

Ormoloma Maxon, Proc. Biol. Soc. Wash. 49:143 (1933); Christensen Man. Pterid. 534 (1938); Copeland, Gen. Fil. 55 (1947).

Davallia J. E. Smith; Hooker & Baker, Syn. Fil. 1st ed. (1868), 2nd ed. (1874) 88; Baker, Fl. Bras. I^2:343 (1870), in part.

Lindsaea Dryand.; Pérez Arbeláez, Bot. Abh. Goebel 14:53 (1928), in part.

Rhizome long-creeping, with a Lindsaeoid protostele provided with a large internal phloem-strand. Scales ovate or lanceolate. Leaves not very close, subdistichous; petiole and rachis dark. Lamina simply pinnate, with a conform terminal pinna; pinnae non-articulate, petiolulate, lanceolate, crenate, approximately equal-sided, with a median main vein and free furcate secondary venation. Sori terminal on the veins or extending slightly along the vein-ends which may run parallel to the margin for a short distance; indusium semi-circular or semi-ovate, fixed at its base, otherwise free, opening outwardly; sporangia numerous, the head up to ca. 200 μ long, annulus with 10–14 indurated cells which reach the stalk; spores trilete.

Two species in Central and northern South America.

Type species: *Ormoloma imrayanum* (Hooker) Maxon (*Saccoloma Imrayana* Hooker in Kunze).

Key to the species:

1.a. Petiole atropurpureous to blackish; sori mostly 1½–2 mm long; scales lanceolate, up to 2½ × 0.6 mm . . . . 1. *O. imrayanum* (West Indies, Guiana)

b. Petiole castaneous to dark reddish brown; sori ½–1 mm long; scales ovate to lanceolate, up to 1½ × 1 mm . . . . 2. *O. standleyi* (Costa Rica, Panamá)

1. **Ormoloma imrayanum** (Hooker) Maxon, Proc. Biol. Soc. Washington 46:144 (1933); Christensen, Kgl. Sv. Vet.-Akad. Handl. 3e ser. 16 (2):44 (1937); Copeland, Gen. Fil. 55 (1947).

Basionym: *Saccoloma Imrayana* Hooker in Kunze, Farrnkr. I:86 (1841/42); Hooker, Gen. Fil. t. 58 B (1839), nom. nud.; J. Smith, Hist. Fil. 260 (1875); Diels, N. Pfl. I^2:211 (1902); Duss, Fl. Crypt. Ant. franç. 73 (1904); Bonaparte, Notes Ptéridol. VII:342 (1918); Knuth, Fedde Rep. Beih. 43 (1):29 (1926); Posthumus, Fl. Surin. Suppl. 68 (1928); Domin, Pterid. Domin. 62 (1929), pl. VI fig. 2; Sampaio, Arch. Mus. Nac. Rio de Jan. 32:42 (1930); Stehlé, Caribb. For. 4 (2):93 (1943); Hodge, Lloydia 17 (2):103 (1954).

Type: Imray 84, Couliabon Mountain (= Morne Anglais?), Dominica (K!)

Homotypic synonyms: *Davallia Imrayana* (Hooker) Hooker, Spec. Fil. I:171 (1844), t. 49 A; Klotzsch, Linnaea 18:544 (1844); Hooker & Baker, Syn. Fil. 1st ed. (1868), 2nd ed. (1874) 90; Baker, Fl. Bras. I²:347 (1870); Krug in Urban, Engl. Bot. Jb. 24:90 (1897); Jenman, W. Ind. Gui. F. 66 (1899).

Humata ? Imrayana (Hooker) Moore, Ind. Fil. I:xcii (1857).

Acrophorus Imrayanus (Hooker) Moore, Ind. Fil. II:295 (1861).

Schizoloma Imrayanum (Hooker) Kuhn, Chaetopt. 26 (1882).

Lindsaya Imrayana (Hooker) Pérez Arbeláez, Bot. Abh. Goebel 14:55 (1928), fig. 33 a–g.

Rhizome rather long-creeping, branched, 1–2½, mostly 2 mm in diam.; scales narrowly to broadly lanceolate, acuminate to long-acuminate, up to 2½ mm long and 0.6 mm wide, with up to 12 rows of cells at the base. *Petioles* rather close, ½–1 cm apart, sometimes less, ca. 10–30 cm long, ⅔–1½ × the length of the lamina, diam. 1–1½ mm at base of lamina, atropurpureous to blackish, shining; adaxial side channelled almost to the base, abaxial side bluntly angular above, gradually less so downwards, subterete at the base. *Lamina* simply pinnate, 9–36 cm long, 6–14, mostly about 10 cm wide, truncate-ovate to broadly lanceolate in outline, herbaceous, dark green at the ventral, paler at the dorsal side, with 2–10 lateral pinnae and a conform terminal one. *Rachis* similar to the upper part of the petiole, abaxially sharply quadrangular and occasionally shallowly sulcate in its upper part. *Pinnae* alternate, the basal ones mostly subopposite, lanceolate, 4–8½ cm long, 11–19 mm wide, ca. 4 × as long as wide, rarely less, 1½–4 cm apart, laxly ascending; upper pinnae but little reduced, ca. ⅔ the size of the lower ones, somewhat closer. All pinnae with a short stalk, which is ca. 3 mm long in the lower, ca. 1 mm in the upper ones; the dark colour of the rachis rather abruptly fading in the base of the stalk. Base of pinnae unequal, the lower base narrowly cuneate or slightly excavate, passing gradually into the lower margin, the upper base more broadly cuneate to almost truncate, passing into the upper margin by the way of a shortly rounded to almost angular portion; the stalk at the upper side winged to the base or almost to the base, unwinged at the lower side. Pinnae gradually narrowed from just above the base to the apex which is sometimes acuminate but blunt at the extreme end. Lower half of pinnules mostly a little wider than the upper, the lower margin more convex in its basal part, rarely the whole pinna is somewhat falcate-upcurved. Terminal pinna with a longer stalk (1–2 cm), mostly larger than the adjacent lateral pinna, sometimes confluent with a reduced pinna at its base, mostly slightly curved to the side opposite the highest lateral pinna. Margins of pinnae except at the narrowed base crenate, the incisions regular, ½–1 mm deep, alternating with the ends of the veins, the teeth rounded, sometimes slightly oblique, or flattened; margins of sterile pinnules, which are uncommon, similar. Thickened strand of the margin very inconspicuous. Axillary cushions not seen. Midrib almost median, percurrent, slightly flexuose, somewhat raised and stramineous at the dorsal, very slightly raised and channelled at the base of the ventral side. Lateral veins immersed, oblique, once or rarely twice forked, very lax, their ends 1½–3 mm apart at the margin. *Sori* terminal on the veins in a line that does not quite extend to the top of the pinna; indusia inserted somewhat below the level of the incisions, semi-circular or semi-elliptic, fixed at the flattish or somewhat concave base, entire, (¾–)1½–2 mm long, ½–¾ mm wide and about as far from the edge, hardly reflexed at full maturity, but the sporangia bulging from under its margin. Sporangia ca. 205 × 160 μ, annulus with 12–14 indurated cells; spores trilete, very pale brown, ca. 27–30 μ.

Distribution: Hispaniola, Guadeloupe, Dominica, and Guianas. (Erroneously reported from Costa Rica by Hodge (1954) and others) (map 51). In moist forests, from 750 to 1225 m (Domin 1929).

Hispaniola. Haïti: Massif de la Hotte, Ekman H 7425 (US).
Guadeloupe: Duss 4176 (MO, NY, US); Mazé 612 (K); Husnot 269 (BM, G, K, M); L'Herminier 167 (G, GH, K); L'Herminier s.n. (BM, C, G, K, L, MO, NY, UC, US).
Dominica: F. E. Lloyd 881 (NY, US); Hodge 2279 (GH, NY, US); Imray 84 (K, Holotype).
British Guiana: Mt. Roraima, Im Thurn 120 (BM, K, US); ibid., Appun 1144 (K).
French Guiana: Rivière St. Louis, Leprieur 117 (GH, US).

2. **Ormoloma standleyi** Maxon, Proc. Biol. Soc. Washington 46:157 (1933).

Type: Standley & Valerio 50039, Yerba Buena, prov. Heredia, Costa Rica (US!).

Rhizome long-creeping, sparingly branched, 1½–2 mm in diam.; scales broadly ovate and obtuse or subacute to lanceolate and acute, up to 1½ mm long and 1 mm wide, when broadly ovate with up to 25 rows of cells at the base. *Petioles* rather close, ½–2 cm apart, 9–24 cm long, diam. 1 mm at base of lamina, castaneous to dark reddish brown, shining; adaxial side angular and channelled almost to base, the borders not discoloured, abaxial side also sharply angular, or bluntly below, subterete only at the very base. *Lamina* simply pinnate, 9–24 cm long, usually as long as the petiole, 5–10 cm wide, truncate and broadly lanceolate in outline, herbaceous, dark green on the ventral, paler on the dorsal side, with 7–11 lateral pinnae and a conform terminal one. *Rachis* similar to the upper part of the petiole, the edges of the adaxial groove often pale. *Pinnae* alternate or the lower ones subopposite, lanceolate, often more elongate than in *O. imrayanum*, 2.5–7 cm long, 7–13 mm wide, 3–6½ × as long as wide, ca. 2–4 cm apart, laxly ascending; upper pinnae often considerably reduced, gradually closer. All pinnae with a short stalk, 3–4 mm long in the lower, 1–2 mm in the upper ones; the dark colour of the rachis fading in this stalk. Base of pinnae mostly, not always, less unequal than in the preceding species, the upper base being usually more narrowly cuneate, the leaf-tissue of the upper base decurrent as a narrow wing on the stalk. Top of pinnae often long acuminate, the very end blunt or subacute. Structure of leaf-top, pinnae, and venation as in the preceding species, but the basal veins not rarely twice or even three times forked. Incisions of the margin ca. 1½–2 mm apart, very shallow, ca. ½ mm deep, the teeth rounded. *Sori* as in the preceding species; indusia semi-circular or semi-elliptic, entire, ½–1 mm long, ca. ½ mm wide and as far from the margin, often reflexed and conceiled at full maturity. Sporangia ca. 160 × 115 μ, annulus with 10 or 11 indurated cells (fig. 19); spores trilete, very pale brown, ca. 23–27 μ.

Distribution: Costa Rica and western Panamá (map 52). In moist forests at 1400–1800 m, terrestrial or epiphytic, probably on mossy tree trunks and stumps.

Costa Rica: Navarrito, in forest, Lankester 755 (BM, S-PA, US, Paratypes); La Palma, A. & C. Brade 51 (Rosenstock-exs. 146) (M, NY, S-PA, UC); south of Cartago, Maxon 514 (NY, US, Paratypes); near El Copey, Cordillera de Talamanca, L. O. Williams & Allen 16485 (US); Orosi, Kupper 762 (M); Cerro de las Lajas, north of San Isidro, Standley & Valerio 57434 (US, Paratype); Yerba Buena, north-east of San Isidro, id. 50039 (US, Holotype); without exact loc., Cooper s.n. (K, US, Paratypes).
Panamá: Cordillera above El Boquete, Chiriquí prov., Killip 5267 (BM, S-PA, US, Paratypes).

The two species are very closely allied. The genus *Ormoloma* is outstanding among the Lindsaeoid ferns by the highly simplified leaf-pattern but strictly uninerval sori, a condition otherwise approached among the members of this group only by *Tapeinidium pinnatum.* Its closest ally seems to be *Lindsaea;* but the author is unable to suggest to which group or species of that genus it is closest.

REFERENCES

Publications cited only in the taxonomic part with the synonymy are not listed here in extenso. The full titles can be found in Christensen's Index Filicum.

ALDERWERELT VAN ROSENBURGH, C. A. W. K. VAN, 1908. Malayan Ferns. Batavia.

ALSTON, A. H. G., 1944. Pteridophyta, *in* A. W. EXELL: Catalogue of the vascular plants of S. Tomé. London.

ALSTON, A. H. G., 1956. New African ferns. Bol. Soc. Brot. 2e ser. *30*:5.

AUBLET, F., 1775. Histoire des plantes de la Guyane françoise. Vols. II & IV. London–Paris.

BACKER, C. A., & O. POSTHUMUS, 1939. Varenflora voor Java. Buitenzorg.

BAKER, J. G., 1870. Cyatheaceae & Polypodiaceae, *in* MARTIUS: Flora Brasiliensis, Vol. 1^2. Munich.

BEARD, J. S., 1949. The natural vegetation of the Windward & Leeward Islands. Oxford.

BLACK, J. M., 1922. Flora of South Australia. Part 1. Adelaide.

BOWER, F. O., 1923. The Ferns. Vol. I: Analytical examination of the criteria of comparison. Cambridge.

BOWER, F. O., 1928. Id. Vol. II: The Leptosporangiate Ferns.

BRADE, A. C., 1942. A composicão da flora Pteridófita do Itatiaia. Rodriguesia *6* (15):29.

BROUN, M., 1938. Index to North American Ferns. Orleans, Mass.

CAPURRO, R. H., 1938. Catálogo de las Pteridofitas Argentinas. An. Prim. Reun. Sul–Am. Bot. *2*:69.

CHING, R. C., 1940. On natural classification of the family "Polypodiaceae". Sunyatsenia *5* (4):201.

CHRIST, H., 1897. Die Farnkräuter der Erde. Jena.

CHRIST, H., 1910. Die Geographie der Farne. Jena.

CHRISTENSEN, C., 1906. Index Filicum. Copenhagen. Supplements I (1913), II (1917), III (1934).

CHRISTENSEN, C., 1925. Revised list of Hawaiian Pteridophyta. B. P. Bishop Mus. Bull. *25*:1.

CHRISTENSEN, C., 1932. The Pteridophyta of Madagascar. Dansk Bot. Ark. *7*:1.

CHRISTENSEN, C., 1937. The collection of Pteridophyta made in Hispaniola by E. L. Ekman 1917 and 1924–1930. Kungl. Sv. Vet.-Akad. Handl. Ser. III. *16* (2):3.

CHRISTENSEN, C., 1938. Chapter XX, Filicinae, *in* F. VERDOORN: Manual of Pteridology. The Hague.

COPELAND, E. B., 1929. The oriental genera of Polypodiaceae. Univ. Calif. Publ. Bot. *12*:375.

COPELAND, E. B., 1939. Fern evolution in Antarctica. Philipp. Jo. Sci. *70* (2):157.

COPELAND, E. B., 1941. Comment on natural classification of the family Polypodiaceae by R. C. CHING. Sunyatsenia *6* (2):159.

COPELAND, E. B., 1947. Genera Filicum. Waltham, Mass. (Publ. by Chronica Botanica).

CORRELL, D. S., 1938. A county check-list of Florida ferns and fern-allies. Am. Fern Jo. *28*:11; 46;91.

DICKASON, F. G., 1946. A phylogenetic study of the ferns of Burma. Ohio Jo. Sci. *46*:73.

DIELS, L., 1902. Polypodiaceae, *in* ENGLER & PRANTL: Die natürlichen Pflanzenfamilien, Vol. I^4:139. Leipzig.

DOBBIE, H. B. & M. CROOKES, 1952. New Zealand Ferns. 5th ed. Auckland.

DRYANDER, J., 1797. Lindsaea, a new genus of ferns. Trans. Linn. Soc. *3*:39.

DUTRA, J., 1938. A flora Pteridofita do estado do Rio Grande do Sul. An. Prim. Reun. Sul.-Am. Bot. *2*:19.

EWART, A. J., 1930. Flora of Victoria. Melbourne.

Fée, A. L. A., 1852. Genera Filicum (5e mémoire). Paris/Strasbourg.

Fée, A. L. A., 1865. 10e mém. Mém. Soc. Sci. nat. Strasbourg *6* (1): 1.

Fée, A. L. A., 1869. Cryptogames vasculaires du Brésil. I. Paris.

Gaudichaud-Beaupré, C., 1824. Description de quelques nouveaux genres de Plantes recueillies dans le voyage autour du monde sous les ordres du capitaine Freycinet. Ann. sci. nat. *3*: 507.

Gerth, H., 1941. Geologie Südamerikas. I. Berlin.

Hieronymus, G., 1920. Kleine Mitteilungen über Pteridophyten. III. Hedwigia *62*: 12.

Hodge, W. H., 1954. Flora of Dominica, B.W. I., part I. Lloydia *17*: 1.

Holttum, R. E., 1930. The genus Lindsaya in the Malay Peninsula. Gardens' Bull. (Singapore) *5*: 58.

Holttum, R. E., 1947. A revised classification of leptosporangiate ferns. Jo. Linn. Soc. (Bot.) *53*: 123.

Holttum, R. E., 1949. The classification of ferns. Biol. Reviews (Cambridge) *24*: 267.

Holttum, R. E., 1954. A revised Flora of Malaya. Vol. II: Ferns of Malaya. Singapore.

Hooker, W. J., 1844. Species Filicum. Vol. I (1844–46). London.

Hooker, W. J., & J. G. Baker, 1868. Synopsis Filicum. 1st ed.

Hooker, W. J., & J. G. Baker, 1874. Idem, 2nd ed.

Hooker, W. J., & F. Bauer, 1842. Genera Filicum. London.

Jenman, G. S., 1899. West Indian and Guiana Ferns, 2nd part. Bull. misc. inf. Bot. Dept. Trinidad *4*: 33.

Kaulfuss, G. F., 1827. Das Wesen der Farrnkräuter, etc. Leipzig.

Keyserling, A., 1873. Polypodiacea et Cyatheacea Herbarii Bungeani. Leipzig.

Klotzsch, J. F., 1844. Beiträge zu einer Flora der Aequinoctial-Gegenden der neuen Welt. Linnaea *18*: 545.

Kryshtofovich, A., 1935. Hymenophyllum and Trichomanes in the Ussuriland of the U.S.S.R. Sunyatsenia *3* (1): 22.

Kuhn, M., 1882. Die Gruppe der Chaetopterides unter den Polypodiaceen. Festschr. z. 50j. Jubil. d. kgl. Realschule, Berlin.

Kunze, G., 1840. Die Farrnkräuter. I, 1–2. Leipzig.

Kunze, G., 1851. Id. II, 14.

Lötschert, W., 1954. Ferns of the Republic of El Salvador. Ceiba *4* (4): 241.

Manton, I., 1950. Problems of cytology and evolution in the Pteridophyta. Cambridge.

Manton, I., & W. A. Sledge, 1954. Observations on the cytology and taxonomy of the Pteridophyte flora of Ceylon. Philos. Trans. Roy. Soc. London Ser. B *654* (Vol. 238): 127.

Martens, M., & H. Galeotti, 1842. Mémoire sur les fougères du Mexique. Mém. Acad. Brux. *15*: 1.

Maxon, W. R., 1913. The genus Odontosoria. *In* Studies of tropical American ferns 4. Contr. U.S. Nat. Herb. *17* (2): 157.

Maxon, W. R., 1926. Pteridophyta of Porto Rico and the Virgin Islands. *In* Sci. Surv. P. Rico Virg. Isl. *6* (3): 373.

Maxon, W. R., & P. C. Standley, 1930. Ferns of the Republic of El Salvador. Proc. Biol. Soc. Wash. *43*: 167.

Mettenius, G., 1856. Filices horti botanici Lipsiensis. Leipzig.

Moore, Th., 1857. Index Filicum. London.

Ogura, Y., 1938. Anatomie der Vegetationsorgane der Pteridophyten, *in* K. Linsbauer: Handbuch der Pflanzenanatomie, Vol. VII pt. 2 B. Berlin.

Pérez Arbeláez, H., 1928. Die natürliche Gruppe der Davalliaceen (Sm.) Klfs. Bot. Abh. Goebel 14. Jena.

Pichi-Sermolli, R. E. G., 1954: The nomenclature of some fern-genera. Webbia *9* (2): 387.

Posthumus, O., 1927. Notes on Guiana ferns. Rec. trav. bot. néerl. *23*: 396.

Posthumus, O., 1928. The ferns of Surinam and of French and British Guiana. (Supplement of Pulle: Flora of Suriname). Malang.

Posthumus, O., 1934. Notes on Guiana ferns. Rec. trav. bot. néerl. *31*: 466.

Presl, C. B., 1825. Pteridophyta, *in* Reliquae Haenkeanae, etc., I (1). Prague.

Presl, C. B., 1836. Tentamen Pteridographiae, seu Genera Filicearum. Prague.

ROSENSTOCK, E., 1906. Beiträge zur Pteridophytenflora Südbrasiliens. II. Hedwigia *46*:57.

SANTAMARIA, F. J., 1942. Diccionario general de Americanismos. 3 vols. México.

SCHUCHERT, CH., 1935. Historical geology of the Antillean–Caribbean region. New York.

SEBA, A., 1735. Locupletissimi rerum naturalium thesaurus, etc. II. Amsterdam.

SEWARD, A. G., 1922. A study in contrasts: The present and past distribution of certain ferns. Jo. Linn. Soc. *46*:219.

SIM, TH. R., 1915. The ferns of South Africa. 2nd ed. Cambridge.

SMALL, J. K., 1920. The land of ferns. The habitats and distribution of the fernworts of Florida. Contr. N.Y. Bot. Gard. 222.

SMALL, J. K., 1938. Ferns of the southeastern States. Lancaster, Pa.

SMITH, J., 1842. An arrangement and definition of the genera of ferns with observations on the affinities of each genus. Lond. Jo. Bot. *1*:419.

SMITH, J., 1875. Historia Filicum. London.

SMITH, J. E., 1793. Tentamen Botanicum de filicum generibus dorsiferarum. Mém. Acad. Roy. Sci. Turin *5*:401.

STANDLEY, P. C., & S. CALDERÓN, 1925. Lista preliminar de las plantas de El Salvador. San Salvador.

STOKEY, I. G., 1951. The contribution by the gametophyte to the classification of the homosporous ferns. Phytomorphology *1*:39.

TAGAWA, M., 1937. The genus Lindsaya in Japan. Acta Phytotax. Geobot. (Kyoto) *6* (1):24.

TANSLEY, A. G., & R. B. LULHAM, 1902. On a new type of fern-stele and its probable phylogenetic relations. Ann. Bot. *16*:157.

TARDIEU-BLOT, M., 1952. Sur le genre "Isoloma J. Sm." et l'"Isoloma lanuginosum J. Sm.". Not. Syst. *14* (4):330.

TARDIEU-BLOT, M., & C. CHRISTENSEN, 1939. Cryptogames vasculaires, *in* HUMBERT & GAGNEPAIN: Flore générale de l'Indo-Chine, Vol. VII pt. 2. Paris.

TINDALE, M. D., 1956. The Cyatheaceae of Australia. Contr. N.S.W. Nat. Herb. *2* (4):327.

TRYON, R. M., Jr., 1942. A revision of the genus Doryopteris. Contr. Gray Herb. *143*:1.

TRYON, R. M., Jr., 1944. Dynamic phytogeography of Doryopteris. Am. Jo. Bot. *31*:470.

WAGNER, W. H., Jr., 1952a. Types of foliar dichotomy in living ferns. Am. Jo. Bot. *39*:578.

WAGNER, W. H., Jr., 1952b. The fern-genus Diellia. Univ. Calif. Publ. Bot. *26* (1):1.

WAGNER, W. H., Jr., 1953. An Asplenium prototype of the genus Diellia. Bull. Torr. Bot. Cl. *80*:76.

WAGNER, W. H., Jr., 1954a. Reticulate evolution in the Appalachian Aspleniums. Evolution *8* (2):103.

WAGNER, W. H., Jr., 1954b. The evidence used in recent classifications of the ferns. Rapp. & Commun. 8me Congr. intern. Bot. Paris Sect. 4:9.

WEEKS, L. G., 1948. Paleogeography of South America. Bull. Geol. Soc. America *59*:249.

WYLIE, R. B., 1948. The dominant role of the epidermis in leaves of Adiantum. Am. Jo. Bot. *35*:465.

INDEX OF EXSICCATAE
(Lindsaea only)

The numbers in parentheses correspond with the species-numbers of the present treatment. Only numbered collections have been listed.

Buchtien, O., 8 (32a, d), 10, 11, 12 (32a), 23 (27a), 1002 (32a), 1098, 1100 (16), 1101, 1102, 1103 (32a), 1104 (32d), 1106 (27a), 2798, 5116, 7028 (16), 7068 (27a).
Bues, C., 894 (27a), 1739 (16).
Burchell, W. J., 947 (27a), 2457 (16), 2663 (26), 3240 (27a), 3551 (3a), 3732, 4402 (13), 5201 (24b).

Cárdenas, M., 1264 (32a).
Cardona, F., 829 (34), 852 (33), 899 (10), 949 (27a), 969, 1530 (7).
Carriker, M. A., 26 (7), 27 (27a).
Chase, A., 9173½ (27a).
Chrysler, M. A., 5456 (16).
Chrysler, M. A., & W. E. Roever 5216 (14a), 5222 (32a).
Claussen, P., 77 (27a).
Clement, Bro., 4611 (32a).
Cook, O. F., & R. F. Griggs 837 (16), 844 (32a).
Cooper, J. J., s.n. (Donnell Smith-exs. 6022, 6023) (16).
Cornman, L. R., 651 (14a).
Crisostomo, Bro., 122 (32a).
Croizat, L., 123 (27a/b), *164 (26), 663 (32a).
Crüger, H., 48 (27a), 125 (32a), 150 (27b), 182 (26).
Cruz, J. S. de la, 1172 (32a), 1556 (32c), 4066 (27b).
Cuatrecasas, J., 6775–A (32a), 7175, 7184 (32d), 7189 (20), 7552, 15812, 17394, 21029 (32a).
Cuming, H., 1100 (27a).
Curran, H. M., & M. Haman, 681 (14d).
Cutler, H., 7029 (27a).

Dale, E. E., 14 (32a).
Damazio, L., 1111 (27a), 1938 (1).
Daniel, Bro., 654 (27a).
Davidson, M. E., 837 (27a).
Day, J., 343, 344 (32a), 345 (27a), 390 (14d).
Deam, Ch. C., 489 (14a), 490 (32a).
Dodge, C. W., A. A. Hunter, J. A. Steyermark & P. H. Allen, 16883 (27a).
Don, G., 142 (27b).
Duarte, A. P., 2562 (23).
Dusén, P., 35, 599a, 677 (1), 2537 (3a), 3730, 3733 (12), 4424 (24b), 8334 (13), 9872 (24b), 11393 (32a), 13213 (24b), 14117 (13, 24b), 14139 (14c, 24b), 14643 (32a), 15013 (24b, 32a), 15298 (14b), 18036 (13).
Duss, A., 826, 829, 1707 (14d), 4129 (24a), 4232 (14d), 4237 (21), 4239 (14d, 24a), 4240, 4241 (32a), 4242 (14d, 24a), 4243 (14d).

Dyer, F. J., A 194 (32a).

Eggers, H. F. A., 647 (14d, 32a), 900 (32a), 1691 (26), 4991, 5814 (32a), 6095, 6191 (14d), 13405, vi (27a).
Ekman, E. L., 3602 (32a), 3770, 3856, 4364 (14a), 5107 (32a), 18008 (41), H 7427 (16), H 9021 (26), H 10243 (44), H 10380 (16), H 10402 (44), H 10984 (26), H 11091 (32a), H 11100 (27a), H 12361 (32a), H 12751 (26), H 14756, H 15555 (32a), H 15869 (26).
Endres, E., 16 (27a).
Engel, F., 208 (7).
Eugenio, J., 48 (14c).

Fanshawe, D. B., M 240 (27a), M 312 (32d), M 325 (23), M 326 (32a), M 327 (24a), M 329 (11a), M 332 (27b), M 334 (26), 2558 (24a).
Fendler, A., 24 (32a), 63 (7), 89 (27a), 89b (27b), 110 (32a), 377 (27a), 378 (27a, 32a), 380 (27a), 412 (14a), 479 (27a), 7346 (32a).
Fiebrig, K., 5252 (23), 6343 (24b).
Focke, H. C., 88, 150, 913 (26), 1081 (32a), 1082 (27b).
Forestry Dept. (Brit. Guiana) 6896 (26).
Forssell, N. E., 225, 231 (14b).
Fosberg, F. R., 19899 (16).
Foster, M. & R., 608 (1), 750 (26).
Fox, 242 (32a).
Fróes, R. L., 22422 (33).
Funck, N., 647 (27a).
Funck, N., & L. Schlim, 7 (14d), 598 (16).

Galeotti, H., 6469 (16), 6470 (26, 27a), 6489 (16), 6495 (14a, 26, 32a), 6496 (32a).
Gardini, A., 72 (24a), 77 (32a), 78 (16).
Gardner, G., 155 (1), 156 (3a), 157 (16), 1225 (15), 2987 (26), 5295, 5323, 5324 (27a).
Gaudichaud-Beaupré, C., 51 (32a), 58 (1).
Gehrt, A., 7830 (13).
Gentle, P. H., 89, 1536 (27a), 1560 (26), 2698 (27a), 2838 (32a), 3687 (27a), 3832 (32a), 4128 (26).
Gerdes, 25 (16), 27 (13), 28 (3a), 29 (27a), 35 (1).
Ginés, Bro., 211 (15), 1523, 1524 (32a).
Glaziou, A., 1644 (3a), 1653 (14b), 2323 (16), 2324 (3a), 2325 (3b), 2326 (1), 2805 (26), 4315, 4381 (12), 5254, 5255 (1), 5357 (27a), 7010 (32a), 7260 (16), 7892 (12), 7956 (24b), 7957 (12), 7958 (13), 7959 (3a, 3a × 12?), 9063 (27a), 10164 (27b), 11701 (12), 11708, 12348 (26,

INDEX OF NAMES

(New names or combinations are in **bold face,** synonyms in *italics*)