



Fig. 53.4. Venation, groups of sporangia on and between the veins, stippled, *A. citrifolium*, $\times 0.75$.

The genus occurs (Fig. 3) from Chiapas in southern Mexico through Central America, in the West Indies, and is widely scattered in South America south to Bolivia, and Santa Catarina in southeastern Brazil; also on Cocos Island.

Spores

Anetium spores (Fig. 5) have a relatively uniform papillate surface as in other vittarioid genera but additional deposits are formed on this layer as in Fig. 6. The surface is partly to entirely covered with strands that become fused into a dense, sheathlike formation as in the spores of *Doryopteris* or *Pellaea*.

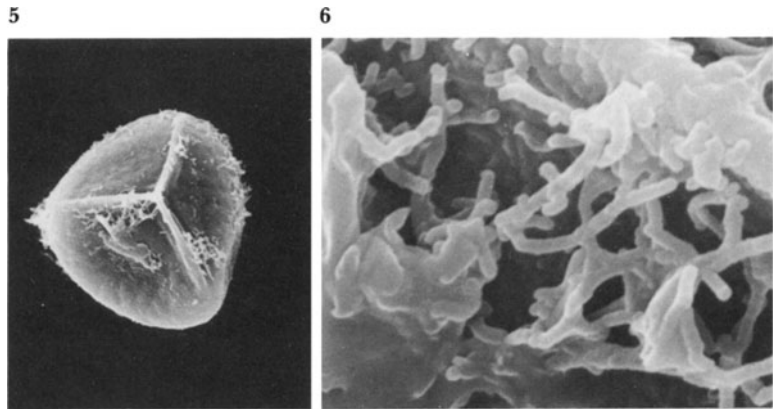
Cytology

Anetium citrifolium is reported (as *Pteridanetium*) from Trinidad with $n = 60$, and regarded as a tetraploid by Walker (1966).

Literature

Walker, T. G. 1966. Reference under the family.

Figs. 53.5, 53.6. *Anetium citrifolium* spores, Peru, *Schunke 3203*. **5.** Spore with strand remnants, $\times 1000$. **6.** Detail of the strands and part of the outer sheathlike formation lower left, papillate surface of laesura, above, $\times 10,000$.



Family 16. Dennstaedtiaceae

Dennstaedtiaceae Pic.-Ser., *Webbia* 24: 704. 1970. Type: *Dennstaedtia* T. Moore.

Family synonyms are placed under the tribes, where they correspond more closely to the taxonomy.

Description

Stem erect, rarely arborescent, to short- or very long-creeping (to ca. 60 m or more), small to stout or slender, protostelic with internal phloem, sphenostelic or rarely dictyostelic, usually indurated or (in *Lonchitis*) succulent, bearing trichomes or scales, or both; leaves ca. 20 cm to 7 m long, usually pinnate or (in *Lindsaea*) rarely simple and cordate to sagittate, circinate in the bud, petiole without stipules; sporangia borne in marginal, submarginal or rarely abaxial sori, at a vein end, receptacle elevated or not, or on a vascular commissure connecting vein ends, indu-

siate, the indusium cup- or purse-shaped, or formed by the modified, recurved margin, or abaxial and laterally more or less extended, or rarely (in *Paesia* and sometimes in *Pteridium*) both a marginal and abaxial indusium present, or (in *Hypolepis*) exindusiate; sporangia short- to usually long-stalked, the stalk 1- to 3-rowed below its apex, the annulus vertical to slightly oblique, at least the indurated portion interrupted by the stalk, homosporous, spores lacking chlorophyll. Gametophyte epigeal, with chlorophyll, obcordate to reniform, slightly thickened centrally, glabrous, archegonia borne on the lower surface, usually in the central region, antheridia 3-celled, borne on the lower surface, mostly apart from the archegonia.

Comments on the Family

The Dennstaedtiaceae are a pantropical family of 17 genera, with a few of them extending to boreal and (or) south temperate regions. The group is characterized by long-creeping stems bearing large, decomposed leaves with marginal or submarginal, indusiate sori. Many species have epipetiolar buds which develop into branches. The chromosome numbers are diverse and usually high, ranging from $n = 26$ to $n = 220$. Since there is little information on the gametophytes, they cannot be adequately described.

Fossil records are meager and represent rather late periods as *Dennstaedtia americana* Knowlton from the Paleocene and Miocene and *Dennstaedtiopsis* Arnold & Daugherty from the Eocene.

The family undoubtedly includes a number of evolutionary lines from an ancient complex, as shown by the several distinctive genera without close affinities to others. There are similarities to several primitive families but it is difficult to assess their phyletic value.

Each of the genera of the Dennstaedtiaceae have distinctive types of spores except for the Lindsaeae, and *Hypolepis* and *Blotiella*. The chromosome numbers are also diverse including a large range indicative of both polyploid and aneuploid changes. The discordant reports known for *Dennstaedtia*, *Hypolepis* and *Lindsaea* suggest cytological complexities that possibly involve more than a single base number in each of these genera.

The tribe **Dennstaedtieae** is characterized by a typical although sometimes polycyclic siphonostele, and the indusium is either purse- or cup-shaped as in *Dennstaedtia*, or formed by the more or less modified, reflexed margin, or an abaxial as well as a marginal indusium is present as in *Paesia* and *Pteridium*. The spores have various but usually prominent architecture. Spores, chromosome numbers and other characters indicate that the relationships of the genera are complex and that they represent isolated elements.

The tribe **Lindsaeae** is characterized by a special type of stele, a protostele with internal phloem. Found in nearly all members of the tribe it is often referred to as the Lindsaea-type. The abaxial indusium is laterally short to very long and the opposed leaf margin is little if at all modified. The surface architecture of the spores is generally less elaborate than in the spores of the Dennstaedtieae. Within the tribe, *Odontosoria* and *Lindsaea*

are closely related and are not clearly separable because of intermediate species. *Ormoloma* is clearly allied to *Lindsaea*. The other two paleotropical genera *Tapeinidium* and *Xyopteris* are not closely related to each other nor to other genera of the tribe.

The tribe **Monachosoreae** (Ching) R. & A. Tryon, *Rhodora* 84:126. 1982 includes *Monachosorum* Kze., an unusual small genus of uncertain affinity. It has a dictyostele, unique, small trichomes on the stem, two vascular bundles in the petiole, an exindusiate sorus, irregularly tuberculate spores and a chromosome number of $n = 56$ or 84 . Its morphology and relations have been reviewed by Nair and Sen (1974). It has been allied to the dennstaedtioid ferns, the davallioids, thelypteroids and taenioids, and Ching (1978) has placed it in a separate family, Monachosoraceae Ching, *Acta Phytotax. Sinica* 14 (4): 17. 1978. Type: *Monachosorum* Kze.

Key to Genera of Dennstaedtiaceae in America

- a. Indusium cup- or purse-shaped, the abaxial and adaxial portions joined, recurved, spores tuberculate-verrucate, reticulate, or coarsely ridged. 55. *Dennstaedtia*, p. 377
- a. Indusium formed only by the modified, recurved margin, or a separate abaxial indusium may also be present. b. (see third a).
- b. Sori 1-nerved 59. *Hypolepis*, p. 398
- b. Sori few to many nerved. c.
- c. Sterile segments and sterile portions of fertile segments with a modified, recurved margin similar to the indusium but not as broad. 57. *Pteridium*, p. 387
- c. Only the fertile portion of segments with a modified, recurved margin (indusium). d.
- d. Abaxial indusium present. 58. *Paesia*, p. 395
- d. Abaxial indusium absent. e.
- e. Lamina glabrous, or with a very few scales, usually glaucous beneath, stem long-creeping, slender, indurated, spores mono-lete. 62. *Histiopteris*, p. 410
- e. Lamina pubescent, not glaucous beneath. f.
- f. Stem decumbent to erect, indurated, veins fully anastomosing, spores mono-lete. 60. *Blotiella*, p. 403
- f. Stem short-creeping, succulent, veins free or casually anastomosing, spores trilete. 61. *Lonchitis*, p. 406
- a. Indusium abaxial, the opposed margin not or hardly modified, flat or nearly so. g.
- g. Stem erect, spores dichotomously ridged. 56. *Saccoloma*, p. 383
- g. Stem creeping to ascending. h.
- h. Stem with trichomes, sori at or near sinuses of the fertile segments, spores regularly and prominently echinate. 54. *Microlepia*, p. 373
- h. Stem with scales and sometimes also with trichomes, or if only with trichomes then the sori terminal on the fertile segments, spores smooth or with granulate or spherical deposition, or with strands forming an irregular, low echinate surface. i.
- i. Lamina 1-pinnate and the sori 1-nerved. 65. *Ormoloma*, p. 429
- i. Lamina entire, or 2-pinnate or more complex, or 1-pinnate and the sori many nerved. j.
- j. Sori laterally short, with the indusium attached at the base and at least partially on the sides. 63. *Odontosoria*, p. 414
- j. Sori laterally short with the indusium attached only at the base, or sori laterally elongate. 64. *Lindsaea*, p. 421

Literature

- Ching, R. C. 1978. The chinese fern families and genera: Systematic arrangement and historical origin (cont.). *Acta Phytotax. Sinica* 16 (4): 16-37.

- Lugardon, B. 1974. La structure fine de l'exospore et de la périspore des Filicinées isosporées, 2. Filicales, Commentaries. Pollen et Spores 16: 161–226.
- Nair, G. B. and U. Sen. 1974. Morphology and anatomy of *Monachosorum subdigittatum* (Bl.) Kze. with a discussion of its affinities. Ann. Bot. 38: 749–756.
- Smith, A. R., and J. T. Mickel. 1977. Chromosome counts for Mexican ferns. Brittonia 29: 391–398.
- Walker, T. G. 1966. A cytotaxonomic survey of the pteridophytes of Jamaica. Trans. Roy. Soc. Edinburgh 66: 169–237.
- Walker, T. G. 1973. Evidence from cytology in the classification of ferns, in: A. C. Jermy et al., The phylogeny and classification of the ferns, pp. 91–110. Bot. Jour. Linn. Soc. 67, Suppl. 1.

16a. Tribe Dennstaedtieae

- Hypolepidiaceae Pic.-Ser., Webbia 24: 705. 1970. Type: *Hypolepis* Bernh.
- Pteridiaceae Ching, Acta Phytotax. Sinica 13: 96. 1975. Type: *Pteridium* Scop.

Nine genera of America and the paleotropics; also *Leptolepia* Diels of New Zealand, Queensland and New Guinea, *Coptidipteris* Nakai & Momose of eastern Asia and Japan, and *Oenotrichia* Copel. of New Caledonia. *Coptidipteris* has coarsely tuberculate spores and a chromosome number of $n = 31$. The only species, *C. Wilfordii* (Moore) Nakai & Momose, has been placed in both *Dennstaedtia* and in *Microlepia* but may not be closely related to either. *Oenotrichia maxima* (Fourn.) Copel, the type species, of *Oenotrichia* and *O. MacGillivrayi* (Fourn.) Brownlie, both of New Caledonia, have trilete, coarsely ridged spores that are clearly dennstaedtioid. Spores of *Oenotrichia tripinnata* (F. v. Muell.) Copel. of Queensland and an apparently undescribed species of New Caledonia are bilateral and echinate. These two species also have scales rather than trichomes on the stem; their relation is uncertain, they do not belong in *Oenotrichia* and the spores suggest an alliance with *Thelypteris* or *Ctenitis*.

54. *Microlepia*

Figs. 54.1–54.9

- Microlepia* Presl, Tent. Pterid. 124. 1836. Type: *Microlepia polypodioides* (Sw.) Presl (*Dicksonia polypodioides* Sw.) = *Microlepia speluncae* (L.) Moore.
- Dennstaedtia* Bernh., Jour. Bot. (Schrad.) 1800 (2): 124. 1802. Type: *Dennstaedtia flaccida* (Forst.) Bernh. (*Trichomanes flaccida* Forst.) = *Microlepia flaccida* (Forst.) Fée.
- Scypholepia* J. Sm., Hist. Fil. 261. 1875. Type: *Scypholepia Hookeriana* (Hook.) J. Sm. (*Davallia Hookeriana* Hook.) = *Microlepia Hookeriana* (Hook.) Presl.

Description

Terrestrial, very rarely rupestral; stem long-creeping to sometimes short-creeping, slender to rather stout, bearing trichomes or rarely bristles and few to many fibrous roots; leaves monomorphic, ca. 20 cm to 3 m, rarely to 7 m long, usually distant, or sometimes closely spaced, lamina 1- to 4-pinnate, usually pubescent, veins free; sori abaxial to marginal, 1-nerved, receptacle not or somewhat elevated, sometimes paraphysate, indusium half cup-shaped, attached at its base and sides or rarely only along a broad base, directed outward, or rarely cup-shaped and directed downward; spores tetrahedral-globose, prominently lobed, trilete, the laesurae short, usually about $\frac{1}{2}$ the radius, the surface of slender rods or strands forming a fine, echinate structure. Chromosome numbers: $n = 43, 44, 84-87, 86, 129$; $2n = 84, 86, 160, \text{ca. } 170, 172$.

The sori of *Microlepia* are at or near the margin (Fig. 2) and are typically covered by an arching indusium. The leaves vary from decompose (Fig. 3) to 1-pinnate in the Old World *Microlepia Hookeriana* (Hook.) Presl.

Systematics

Microlepia is a pantropical and somewhat extratropical genus of about 45 species with only one, *M. speluncae* (L.) Moore, in America. It is usually distinct from *Dennstaedtia* in characters of the sorus and indusia but in the paleotropics it grades into that genus except in spore architecture. *Microlepia flaccida* (Forst.) Fée has the sorus and indusium cup-shaped and directed downward as in *Dennstaedtia* and species such as *M. concinna* R. & A. Tryon and *M. Hooveri* Christ sometimes have a somewhat recurved, shallow, cup-shaped indusium. These species have large, decompose leaves and, except for their delicately echinate spores, resemble species of *Dennstaedtia* more than some *Microlepia* species as *M. strigosa* (Thunb.) Presl and *M. marginata* (Panzer) C. Chr.

The earliest name for the genus, *Dennstaedtia* Bernh., is not adopted in order to avoid confusing changes of the species names.

Tropical American Species

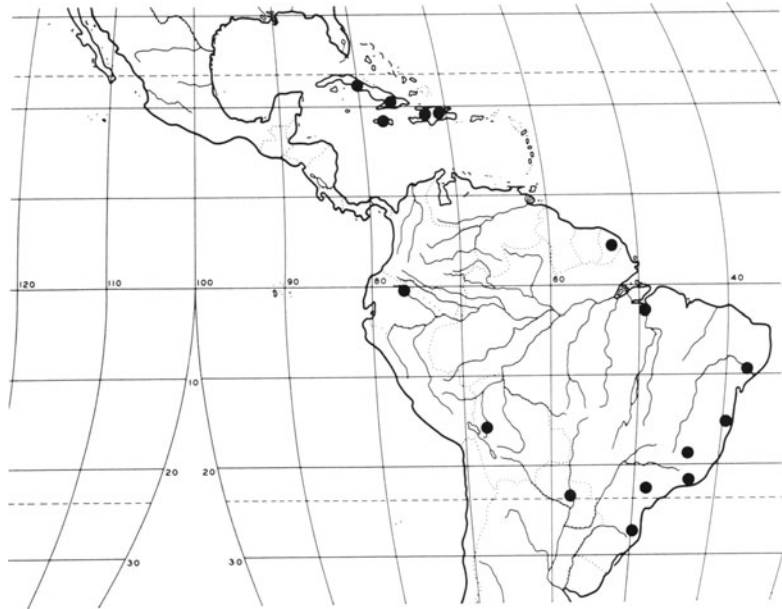
The pantropical *Microlepia speluncae* (L.) Moore is variable through its range, and *Microlepia jamaicensis* (Hook.) Fée is one of the many local variations. It differs from typical *M. speluncae* in that the indusium is only partly attached at the sides rather than fully fused, a condition that also occurs in plants of the Old World.

Ecology

Microlepia is usually a genus of moist to wet forests, where it grows on mountain slopes, in ravines or along streams. It also grows in dry forests, on lightly shaded hillsides, less often in thickets, along roadsides or in open places.

In America it grows in shady forested ravines and on mountain sides in forests at ca. 400–850 m.

Fig. 54.1. Distribution of *Microlepia* in America.



Geography (Fig. 1)

Microlepia grows in the American tropics, in tropical Africa and Madagascar, India, Ceylon, China, and eastward through Malasia across the Pacific to the Hawaiian Islands and Easter Island, north to Korea and Japan, and south to Queensland, Australia. It is adventive in the Hawaiian Islands and perhaps elsewhere.

In America the distribution of *Microlepia* is widely scattered. It grows in the Greater Antilles except Puerto Rico, and in South America in eastern and southeastern Brazil, also Paraguay, Bolivia, Ecuador, and French Guiana. It lacks a coherent range in America which suggests that it may be adventive.

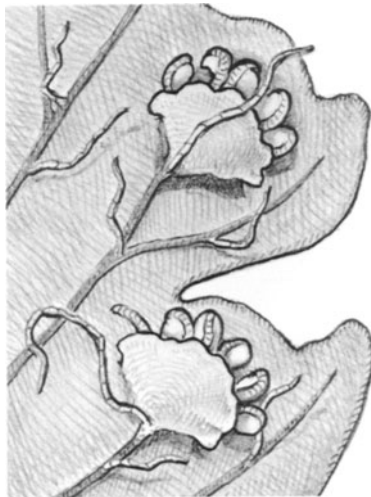


Fig. 54.2. Sori of *Microlepia speluncae*,
× 15.

Spores

Microlepia spores are relatively small and finely echinate. The characteristic surface is best developed on the lowest spore (Fig. 5) and on the proximal surface of the spore at higher magnification (Fig. 6). Young spores are usually strongly 3-lobed and each lobe appears to fit into depressed areas of adjacent spores of the tetrad. These associations are evident in spores somewhat displaced from the tetrad (Fig. 4). *Microlepia* spores are described as lacking perispore by Erdtman and Sorsa (1971) but SEM micrographs of abraded surfaces show three types of perispore structure. The outer echinate formation overlays a granulate stratum (Fig. 7) and below this is a meshwork of strands (Fig. 8). *Microlepia* spores are consistently echinate as in *M. speluncae* and in species of the Old World as *M. marginata* from Japan (Fig. 9). These clearly differ from the coarsely ridged or reticulate spores of *Dennstaedtia*.

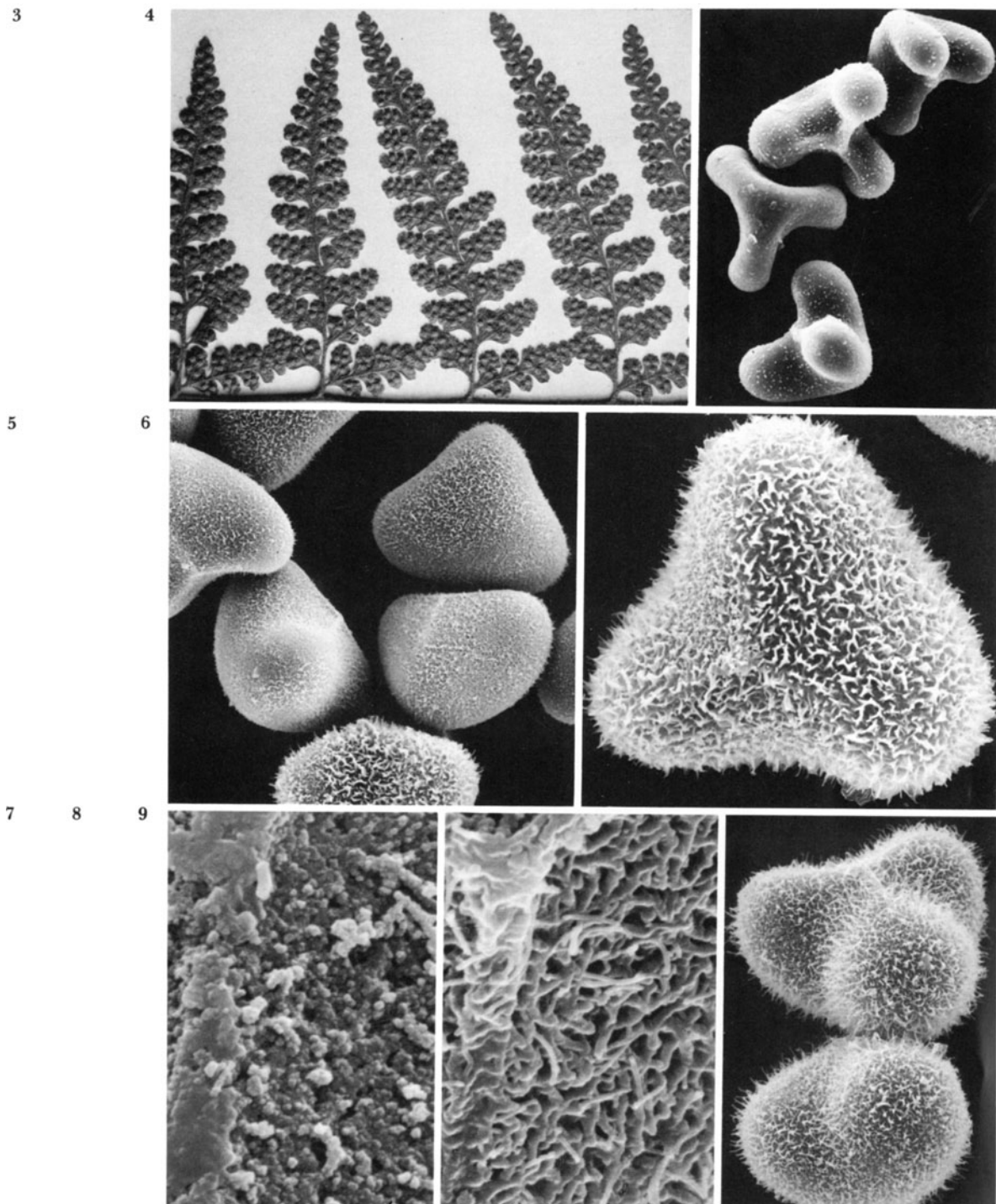


Fig. 54.3–54.9. *Microlepidia*. 3. Portion of a pinna of *M. speluncae*, $\times 1.5$. 4–9. Spores. 4. *M. dennstaedtioides* Copel, four spores of a young tetrad, strongly lobed with concave areas adjacent to laesurae, Philippines. Edaño, in 1932, $\times 700$. 5–8. *M. speluncae*. 5, 6. Cuba, Smith & Hodgdon 3241. 5. The complete echinate surface on spore at base, $\times 1000$. 6. Echinate, proximal face, $\times 2000$. 7, 8. Lower perispore deposition, Paraguay, Rojas 1051, $\times 10,000$. 7. Granulate perispore deposit below echinate surface, part of laesura at left. 8. Fused strands of lowest perispore deposit, part of laesura at left. 9. *M. marginata*, proximal face, above, lateral view, below, Taiwan, Chuang 4766, $\times 1000$.

Cytology

There are no reports of chromosome numbers for *Microlepia* in America. Records of *M. speluncae* from India and Ceylon include several ploidy levels ranging from $n = 43, 84-87, 86,$ and 129, while other species of the Old World are mostly 43 or 86.

Literature

Erdtman, G., and P. Sorsa. 1971. Pollen and Spore Morphology/Plant Taxonomy. Pteridophyta. Almqvist & Wiksell, Stockholm.

55. *Dennstaedtia*

Figs. 55.1–55.13

- Dennstaedtia* Moore, Ind. Fil. xcvi. 1859. Type: *Dennstaedtia cicutaria* (Sw.) Moore (*Dicksonia cicutaria* Sw.).
- Sitobolium* Desv., Mém. Linn. Soc. Paris 6: 262. 1827, altered to *Sitobolium* by J. Sm., Jour. Bot. (Hook.) 3: 418. 1841. Type: *Sitobolium punctilobulum* (Michx.) Desv., as *punctilobum* (*Nephrodium punctilobulum* Michx.) = *Dennstaedtia punctilobula* (Michx.) Moore.
- Patania* Presl, Tent. Pterid. 137. 1836. Type: *Patania obtusifolia* (Willd.) Presl (*Dicksonia obtusifolia* Willd.) = *Dennstaedtia obtusifolia* (Willd.) Moore.
- Aeductum* Link, Fil. Sp. 42. 1841. Type: *Aeductum pilosiusculum* (Willd.) Link (*Dicksonia pilosiuscula* Willd.) = *Dennstaedtia punctilobula* (Michx.) Moore.
- Litolobium* Newm., Phytologist 5: 236. 1854, *nom. superfl.* for *Sitobolium* Desv. and with the same type.
- Costaricia* Christ, Bull. Soc. Bot. Genève, 11, 1: 229. 1909. Type: *Costaricia Werckleana* Christ = *Dennstaedtia* sp.
- Fuziifilix* Nakai & Momose, Cytologia, Fujii Jub. Vol. 365. 1937. Type: *Fuziifilix pilosella* (Hook.) Nakai & Momose (*Davallia pilosella* Hook.) = *Dennstaedtia hirsuta* (Sw.) Mett.
- Paradennstaedtia* Tagawa, Jour. Jap. Bot. 27: 213. 1952. Type: *Paradennstaedtia glabrata* (Ces.) Tagawa (*Dicksonia glabrata* Ces.) = *Dennstaedtia glabrata* (Ces.) C. Chr.
- Emodiopteris* Ching, Acta Phytotax. Sinica 16: 21. 1978. Type: *Emodiopteris appendiculata* (Hook.) Ching (*Dicksonia appendiculata* Hook.) = *Dennstaedtia appendiculata* (Hook.) J. Sm.

Description

Terrestrial or rarely rupestral; stem long-creeping or rarely short-creeping, slender to moderately stout, bearing trichomes and a few to many long fibrous roots; leaves monomorphic, ca. 20 cm to 4 m, rarely to 7 m long, borne at intervals to sometimes loosely clustered, lamina 1-pinnate, imparipinnate to 4-pinnate-pinnatifid, glabrous or pubescent, veins free; sori marginal, 1-nerved, the receptacle more or less elevated, sometimes paraphysate, indusium cup- or purse-shaped, directed more or less

Fig. 55.1. *Dennstaedtia circuitaria*, central cordillera, Puerto Rico. (Photo D. S. Conant.)



downward, sometimes slightly bilabiate; spores tetrahedral-globose with prominent lobes, usually somewhat compressed, trilete, the laesurae $\frac{3}{4}$ the radius, often obscured by adjacent surface features, the surface prominently verrucate-tuberculate, reticulate or ridged. Chromosome number: $n = 30, 33-34, 34, 46, 47, 60, 64, 65, 94$; $2n = 60, \text{ca. } 94, 120, 128$.

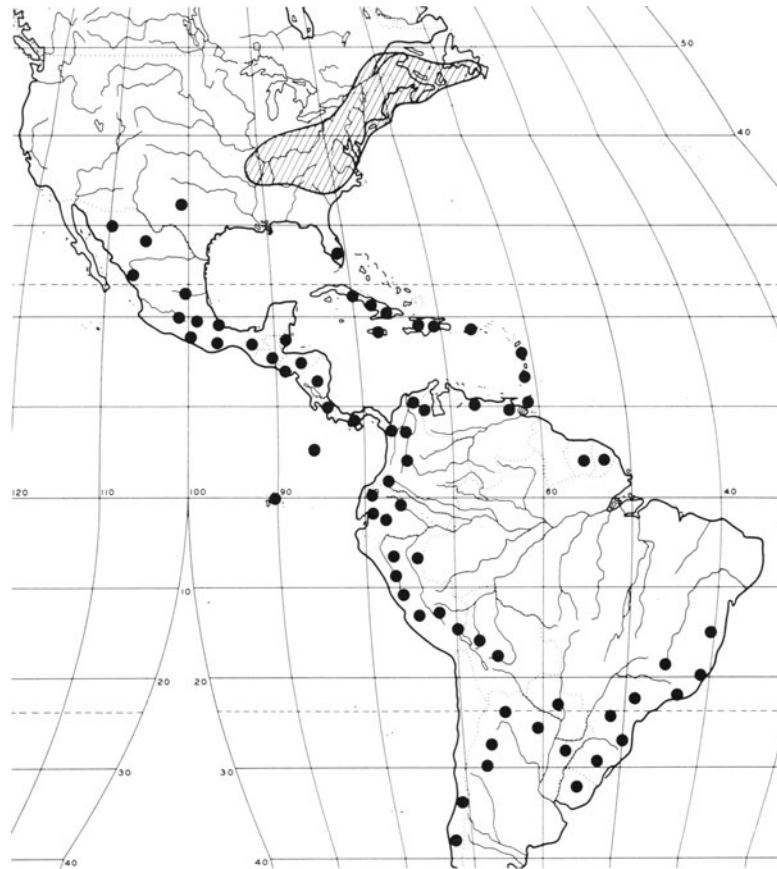
Dennstaedtia typically has the indusium bent downward (Figs. 3–6) and it is sometimes bilabiate as in Fig. 3. The stem is usually slender but may be up to 2.5 cm in diameter and rarely is nearly devoid of indument. The pinnules of *D. bipinnata* in Fig. 7 show details of leaf architecture typical of many species.

Systematics

Dennstaedtia is a genus of tropical and extratropical regions with about 45 species, 12 of them in America.

Similarities in many characters indicate a close relation to *Microlepia* although there are differences in the indusium, and the verrucate-tuberculate, reticulate or coarsely ridged spores are quite different from the echinate ones of *Microlepia*. In tropical America the genus is relatively homogeneous in characters of the spores and leaves except for *D. Wercklei* with a 1-pinnate lamina. The morphological diversity is greater in the paleotropics, where species as *Dennstaedtia scandens* (Bl.) Moore have spines on

Fig. 55.2. Distribution of tropical species of *Dennstaedtia* in America.



the petiole and rachis, and others as *D. glabrata* (Ces.) C. Chr. have articulate pinnae.

The most divergent elements in the genus are extratropical species as *Dennstaedtia appendiculata* (Hook.) J. Sm., *D. punctilobula* (Michx.) Moore and *D. hirsuta* (Sw.) Mett. These are sometimes segregated as genera but seem better placed in *Dennstaedtia*; further study may indicate that an infrageneric classification is needed.

Costaricia was based on sterile specimens that have trichomes on the stem and elongate leaves similar to juvenile ones of *Dennstaedtia*. They undoubtedly represent juvenile plants of *Dennstaedtia dissecta* or *D. obtusifolia*. Fertile specimens collected later and referred to *Costaricia* (Tryon, 1961) represent a variant of *D. obtusifolia*.

Scyphofilix Thouars, Nov. Gen. Madagas. (Melanges Bot. 2): 1. 1806, of Madagascar was published without an included species. Kunze (1837, p. 38) suggested it might be *Dicksonia madagascariensis* Kze. (= *Dennstaedtia madagascariensis* (Kze.) Tard.). It could as well be a *Davallia* (*D. chaerophylloides* (Poir.) Steud.) as Thouars indicated and it is best placed there until an authentic specimen is found, since *Davallia* is the older name.

Since the type of *Dennstaedtia* Bernh. is a *Microlepia*, the name *Dennstaedtia* is taken from a later publication and with a different type in order to avoid confusing name changes.

The American species of *Dennstaedtia* have been revised by Tryon (1960).



Fig. 55.3. Sori of *Dennstaedtia globulifera*, $\times 10$.

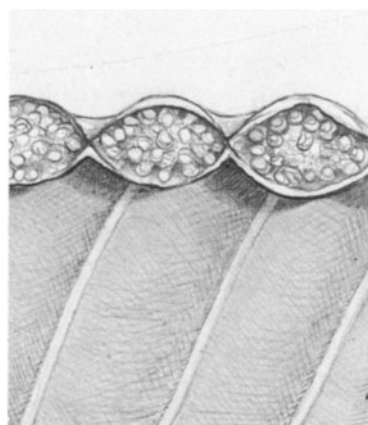


Fig. 55.4. Sori of *Dennstaedtia Wercklei*, $\times 10$.

Tropical American Species

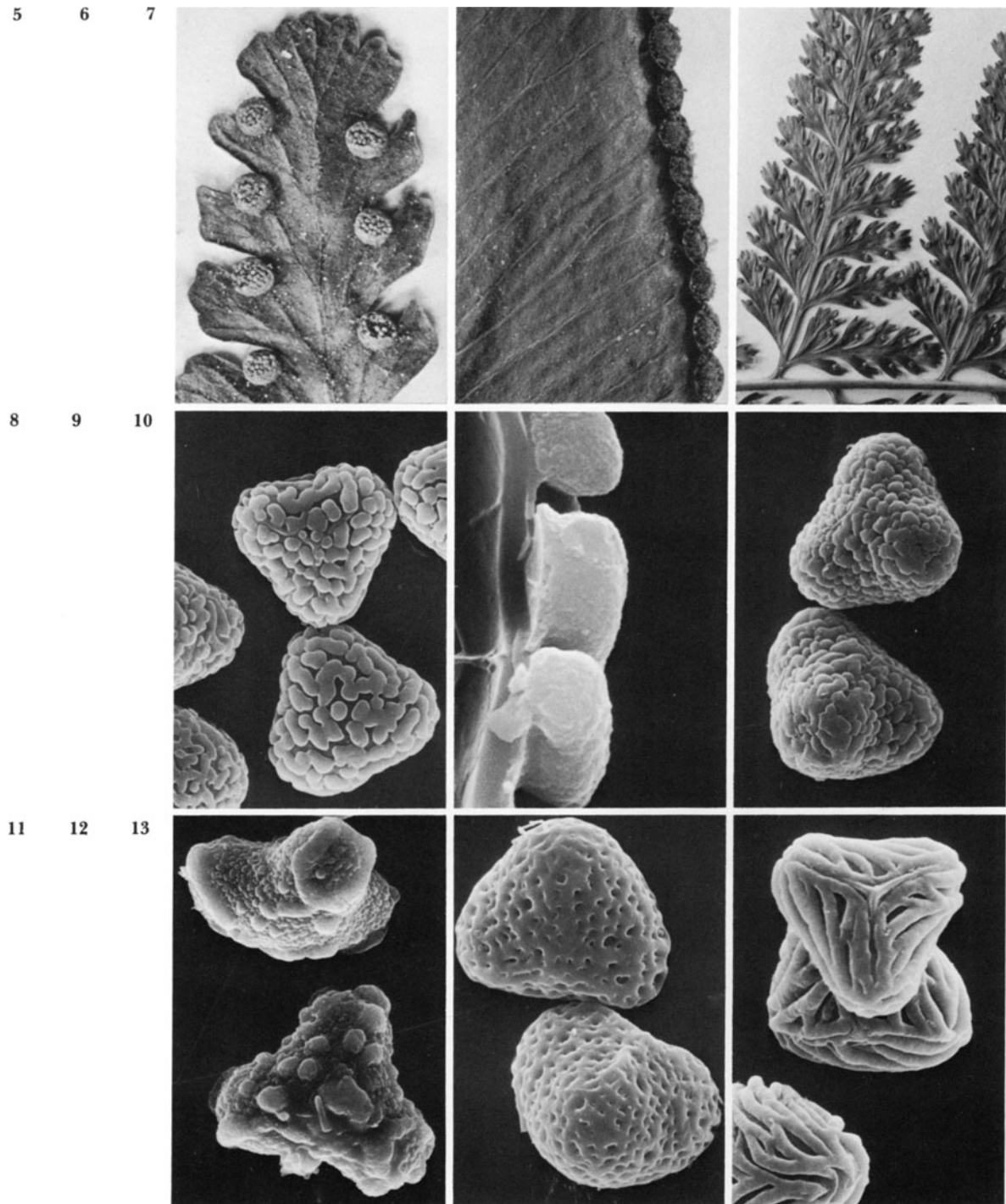
Tropical American species of *Dennstaedtia* are relatively well known, but additional field work is needed to determine the relationship between *D. dissecta* and *D. obtusifolia*. They evidently differ only in quantitative characters of the indusium and sorus and may be variations of a single species. Further study is also needed to adequately separate *D. arborescens* from *D. Kalbreyeri* which was long known from limited material but has recently been collected several times in Ecuador.

The large leaves in most species are developed through heteroblastic series from elongate leaves of juvenile plants to broadly ovate or deltoid leaves on adult plants. Study of these developmental series may provide new species characters and better evidence for their relations.

The following key has been adapted from the more detailed one in Tryon (1960).

Key to Species of *Dennstaedtia* in Tropical America

- a. Upper surface of axis of the penultimate segments bordered on each side by a pronounced herbaceous wing perpendicular to the plane of the segment, the wing on the basiscopic side decurrent onto the axis of the next order as a wing or a pronounced ridge.
 - b. Basal segments of the pinnules of the central pinnae usually subopposite to nearly opposite, rather or quite equal in size, the inferior not or slightly ascending. *D. globulifera* (Poir.) Hieron.
 - b. Basal segments of the pinnules of the central pinnae definitely alternate, quite unequal in size, the inferior slightly to strongly ascending. *D. bipinnata* (Cav.) Maxon.
- a. Upper surface of axis of the penultimate segments lacking perpendicular herbaceous wings, or if these present, the one on the basiscopic side not decurrent onto the axis of the next order.
 - c. Sterile vein-tips on the upper surface slender, ending well back of the glabrous margin.
 - d. Pinnae alternate, the lower ones stalked with the basal pinnules not or hardly reduced.
 - e. Many or most of the sori borne in a sinus, pinnules more or less pubescent beneath, lamina deltoid. *D. cicutaria* (Sw.) Moore.
 - e. All or most of the sori terminal on lobes, lamina ovate or deltoid-lanceolate. *D. glauca* (Cav.) Looser.
 - d. Pinnae opposite or rarely subopposite, the lower ones sessile with a pair of usually much reduced basal pinnules. *D. distenta* (Kze.) Moore.
 - c. Sterile vein-tips on the upper surface enlarged, clavate to punctate or rarely (in *D. obtusifolia*) slender.
 - f. Lamina 1-pinnate, the pinnae entire. *D. Wercklei* (Christ) Tryon.
 - f. Lamina 1-pinnate-pinnatifid or more complex.
 - g. Sterile veins nearly reaching the persistently pubescent margin. *D. Sprucei* Moore.
 - g. Sterile veins ending well back of the glabrous margin.
 - h. Pinnules entire to deeply pinnatifid; apical segments of the pinnae confluent back of the prolonged apex.
 - i. Segments persistently and prominently pubescent on both surfaces. *D. Kalbreyeri* Maxon.
 - i. Segments glabrous to glabrate on both surfaces. *D. arborescens* (Willd.) Maxon.
 - h. Pinnules 1-pinnate to 1-pinnate-pinnatifid, apical segments of the pinnae distinct, or nearly so, up to the prolonged apex.
 - j. Mature sori mostly 1.0–1.5 mm broad and about half as thick, especially the acroscopic one on a segment. *D. dissecta* (Sw.) Moore.
 - j. Mature sori mostly 0.5–1.0 mm broad and about as thick. *D. obtusifolia* (Willd.) Moore.



Figs. 55.5–55.13. *Dennstaedtia*. 5. Fertile segment of *D. obtusifolia* $\times 5.0$. 6. Portion of a fertile pinna of *D. Wercklei*, $\times 5.0$. 7. Pinnules of *D. bipinnata*, $\times 1.5$. 8–13. Spores, $\times 1000$. 8–9. *D. cicutaria*, Panama, *Burch 218*. 8. Verrucate elements more or less fused into ridges, proximal face above. 9. Wall profile with a thin outer perispore over the verrucate exospore, $\times 10,000$. 10. *D. obtusifolia*, verrucate, proximal faces tilted, Colombia, *Pennell et al. 8665*. 11. *D. bipinnata* somewhat compressed, irregularly papillate and tuberculate, Colombia, *Killip 5003*. 12. *D. Smithii*, coarsely reticulate, Moluccas, *Burwald 5734*. 13. *D. samoensis*, coarsely ridged proximal face, above, part of distal face lower left, New Hebrides, *Braithwaite 2479*.

Ecology (Fig. 1)

Dennstaedtia is predominantly a genus of wet mountain forests, forest openings and secondary vegetation. The northern species such as *D. hirsuta* grow in woods, pastures, rocky slopes, on shaded banks and roadsides, and along streams. *Dennstaedtia punctilobula* grows in a variety of usually moist habitats, such as woods and forest borders, rocky hillsides, meadows; in the southwestern portion of its range it is restricted to sandstone cliffs.

In tropical America, *Dennstaedtia* usually grows in rain forests or cloud forests on mountain slopes, in ravines or on stream banks. It may also grow in forest borders or clearings and rarely in rocky places, on road banks, or open sunny habitats. It is sometimes a weed or persists in coffee plantations.

Species are usually colonial from the long-creeping, frequently branching stems. The leaves may be semiscandent in tall shrubs or among the branches of small trees.

Dennstaedtia grows from near sea level to 3200 m, usually from 500 to 2500 m.

Geography (Fig. 2)

Dennstaedtia occurs in America, in Madagascar and the Mascarenes, and eastward through Malesia and in the Pacific to Samoa and Tonga, south to eastern Australia and north to Japan and the adjacent mainland.

In America the genus occurs in the eastern United States and adjacent Canada (*D. punctilobula*) and from southern Florida (*D. bipinnata*) and Texas (*D. globulifera*) through Mexico and Central America, the West Indies, and in South America from French Guiana west to Colombia, south to Bolivia, central Chile (*D. glauca*) and Argentina to southeastern Brazil and Uruguay; also on Cocos Island and in the Galápagos Islands.

Most of the species have typical pan-Andean ranges, from the Greater Antilles, southern Mexico and Central America, Venezuela, Colombia to Bolivia and sometimes in southeastern Brazil. A few, as *D. obtusifolia*, are somewhat more widely distributed and also occur in the Lesser Antilles. Several have rather restricted ranges as *D. distenta* from Mexico to Panama and in the Greater Antilles, *D. glauca* from Chile, northwest Argentina to southern Peru, *D. Sprucei* in Ecuador and Peru, *D. Kalbreyeri*, Ecuador and Colombia, and *D. Wercklei* in Costa Rica, Colombia and Peru.

Spores

Three main types of spores in *Dennstaedtia* are generally correlated with geography. The American species have tuberculate to verrucate spores as *D. obtusifolia* (Fig. 10) or the verrucate elements may be more or less fused into rugae as in *D. cicutaria* (Fig. 8). The spores are often somewhat compressed rather than spheroidal as in *D. obtusifolia* (Fig. 10) and in *D. bipinnata* (Fig. 11) which has an unusually irregular surface. Spore wall sections

of *D. bipinnata* by Lugardon (1974) show a thin perispore formed above a compact exospore layer which is traversed by exceptionally large canals. The profile of the wall of *D. cicutaria* (Fig. 9) shows a thin outer perispore layer conform to the verucate exospore. The paleotropical species have spores with two main types of surface—reticulate as in *D. Smithii* (Hook.) Moore (Fig. 12), or ridged as in *D. samoensis* (Brack.) Moore (Fig. 13). Temperate species as *D. punctilobula* have shallowly tuberculate spores with a slightly raised equatorial ridge.

Cytology

There appear to be two distinct cytological groups in *Dennstaedtia*. The American tropical species with $n = 46$ or 47 , and 94 based on records from Jamaica and Trinidad (Walker, 1966, 1973) and Chiapas, Mexico (Smith and Mickel, 1977), represent one group. The record from the paleotropics of the *D. glabrata* complex with $n = 46$, reported from New Guinea by Walker (1973) may also belong here. The temperate species *D. punctilobula* with $n = 34$ represents a second group with lower chromosome numbers between 30 and 34 that appear to center in Asia. A scheme involving polyploid and aneuploid changes to accommodate the many chromosome numbers based on 15 , 16 and 17 was proposed by Walker (1973). However, it was noted that further sampling of species from all parts of the range is required to clarify the cytological complexities of the genus.

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56. Saccoloma

56.1–56.12

- Sacoloma* Kaulf., Berl. Jahrb. Pharm. 1820: 51. Type *Sacoloma elegans* Kaulf.
- Neuropteris* Desv., Mém. Linn. Soc. Paris 6: 292. 1827. Type: *Neuropteris elegans* Desv. = *Sacoloma elegans* Kaulf.
- Orthiopteris* Copel., Bishop Mus. Bull. 59: 14. 1929. Type: *Orthiopteris ferulacea* (Moore) Copel. (*Davallia ferulacea* Moore, Ind. Fil. 294. 1861, *nom. nov.* for *D. trichomanoides* Hook. 2nd Cent. t. 64. 1861, not Bl., 1828) = *Sacoloma ferulaceum* (Moore) R. & A. Tryon.
- Ithycaulon* Copel., Univ. Cal. Publ. Bot. 16: 79, 1929. Type: *Ithycaulon moluccanum* (Bl.) Copel. (*Davallia moluccana* Bl.) = *Sacoloma moluccanum* (Bl.) Kuhn.

Fig. 56.1. *Saccoloma inaequale*, Toro Negro, west of Barranquitas, Puerto Rico. (Photo D. S. Conant.)



Description

Terrestrial; stem erect to decumbent, moderately stout, bearing scales and many fibrous roots; leaves monomorphic, ca. 50 cm to 2.5 m long, borne in a cluster, lamina 1-pinnate, imparipinnate, to 5-pinnate, glabrous or nearly so, veins free; sori marginal or submarginal, 1-nerved, receptacle not to slightly elevated, not paraphysate, indusium half-conical, attached at its cuneate base and sides, or half cup-shaped, or purse-shaped and slightly bilabiate and more or less directed downward; spores tetrahedral-globose, trilete, the laesurae $\frac{2}{3}$ to $\frac{3}{4}$ the radius, the surface with generally parallel, dichotomous ridges usually partly obscured by spherical deposit. Chromosome number: $n = 188$; $2n = 63 \pm 2$ II, ca. 376.

Characteristic sori of *Saccoloma* are shown in Fig. 3, and those of the 1-pinnate *S. elegans* in Fig. 4. In the latter, simplification of the lamina to pinnae with entire margins brings the sori in close alignment. Stem scales with a basal peltate attachment have been described in *S. elegans* (Nair, 1979).

Systematics

Saccoloma is a tropical genus of about 10 species with three present in America. It is distinguished by its usually erect or sometimes decumbent stem bearing scales and the unusual delicately ridged spores. *Saccoloma elegans* is sometimes distinguished as a monotypic genus. However, except for the 1-pinnate lamina architecture it is similar to other species. A 1-pinnate lamina has also developed in other genera as in *Microlepia Hookeriana* (Hook.) Presl and *Dennstaedtia Wercklei*.

Ithyaulon has been considered a synonym of *Tapeinidium*, but the type specimen of *Davallia moluccana* Bl. is a *Saccoloma* (Kramer, 1967).

Fig. 56.2. Distribution of *Saccoloma* in America.

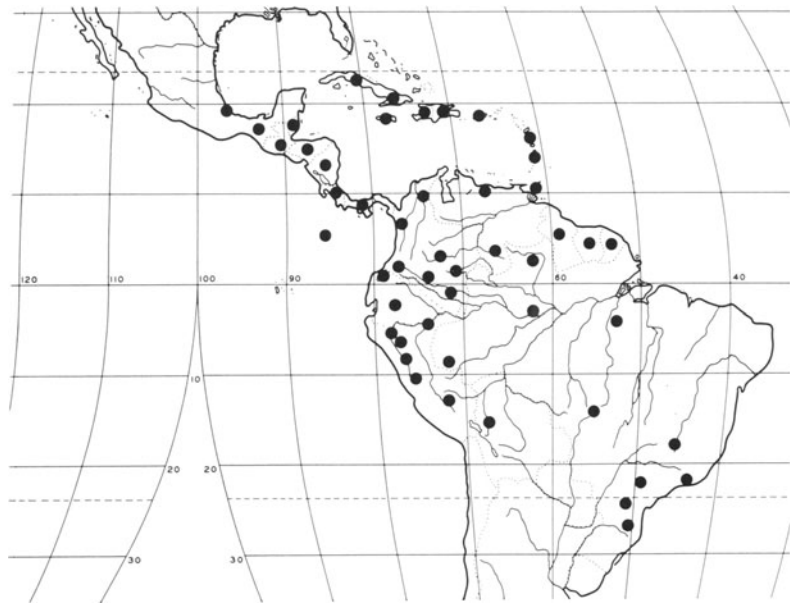


Fig. 56.3. Sori of *Saccoloma inaequale*, ×15.

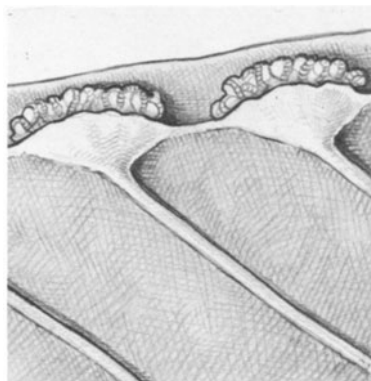


Fig. 56.4. Sori of *Saccoloma elegans*, ×10.

Tropical American Species

Saccoloma inaequale and *S. domingense* differ in chromosome number and evidently are valid species. They are also distinguished by differences in lamina architecture, sorus and indusium, but there are some specimens that appear intermediate. Some of these may represent hybrids, but others are from areas where only one species is known.

The following key has been adapted from the treatment of the genus by Tryon (1962).

Key to American Species of *Saccoloma*

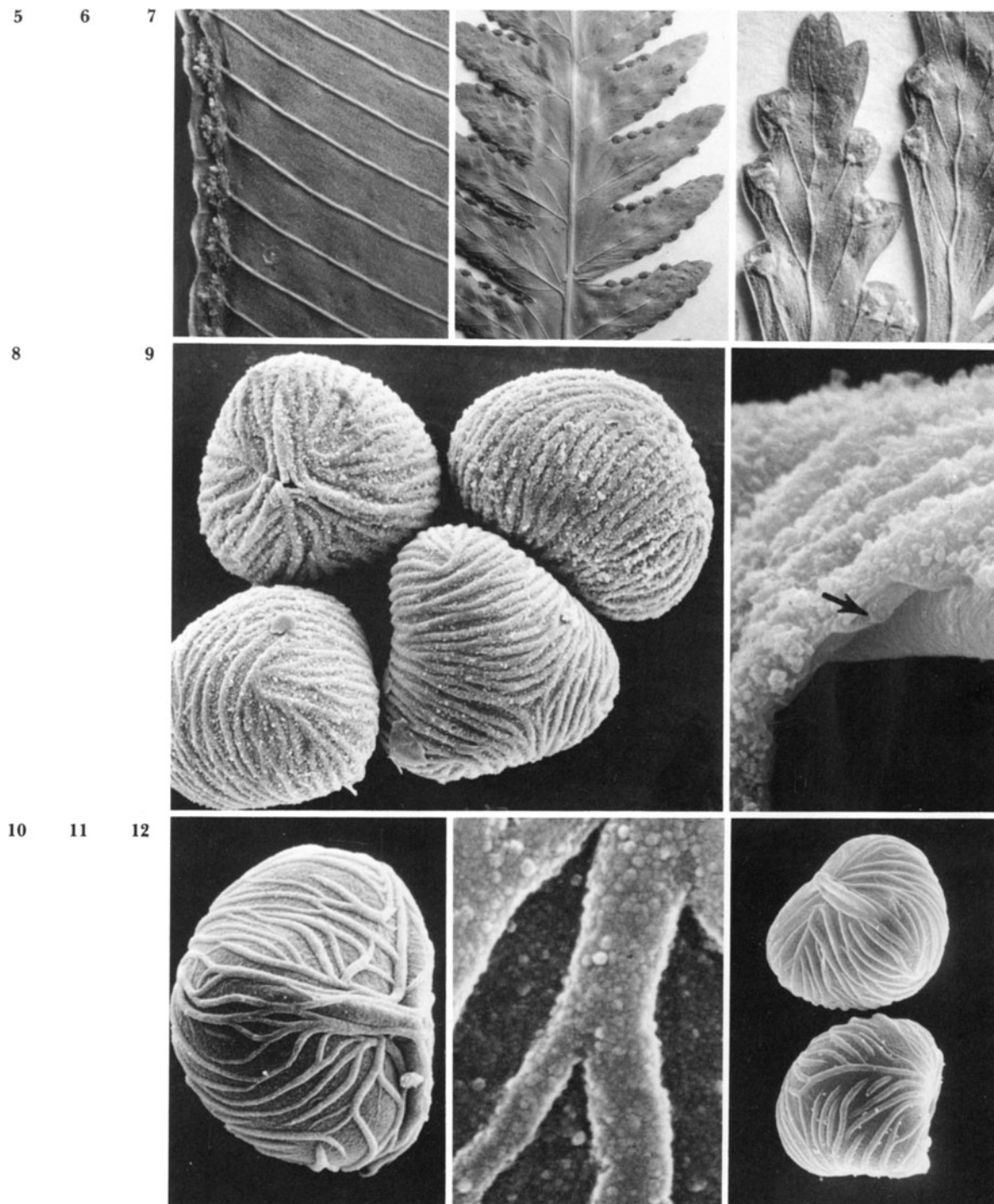
- a. Lamina 1-pinnate (Figs. 4, 5) *S. elegans* Kaulf.
- a. Lamina 2-pinnate or more complex. b.
- b. Ultimate segments mostly large, entire to shallowly toothed, apices of lamina and of the larger pinnae pinnatifid, sori mostly close on adjacent vein-tips, indusium broadly cuneate (Fig. 6) *S. domingense* (Spreng.) Prantl
- b. Ultimate segments mostly small, strongly toothed or lobed, apices of lamina and of the larger pinnae more or less pinnatisect, sori distant, indusium narrowly cuneate (Figs. 3, 7) *S. inaequale* (Kze.) Mett.

Ecology (Fig. 1)

Saccoloma is a forest genus, often growing in dense shade. In America it grows in rain forest and cloud forest on steep mountain slopes, in ravines, less often in secondary forest, or rarely in swamps or on rocks; the genus grows from ca. 50 to 2000 m altitude.

Geography (Fig. 2)

Saccoloma occurs in the American tropics, in Madagascar and in Malesia eastward to Samoa. In America it ranges from Veracruz in Mexico, through Central America, the West Indies, and in northern South America to Bolivia and Santa Catarina in Brazil; also on Cocos Island.



Figs. 56.5–56.12. *Saccoloma*. 5. Portion of a pinna of *S. elegans*, $\times 5$. 6. Portion of a pinnule of *S. domingense*, $\times 1.5$. 7. Pinnules of *S. inaequale*, $\times 5$. 8–12. Spores. 8, 9. *S. elegans*, Colombia, *Schultes & Idrobo 795*. 8. Ridged spores with granulate deposit, proximal face upper left, distal face, lower right, lateral view, lower left and upper right, $\times 1500$. 9. Wall strata, the granulate perispore above, ridges formed by lower perispore (arrow) above the exospore, lower right, $\times 10,000$. 10, 11. *S. elegans*, British Honduras, *Schipp 90*. 10. Lateral view, ridges with sparse granulate deposit, $\times 2000$. 11. Surface detail of ridges and granulate deposition, $\times 20,000$. 12. *S. moluccanum*, the proximal face, above, distal below, Solomon Islands, *Brass 2914*, $\times 1000$.

Spores

The dichotomous ridges enveloping the spores of *Saccoloma* form an unusual type of surface that is consistent in American tropical species such as *S. elegans* (Fig. 8) and those of the paleotropics as *S. moluccanum* (Bl.) Kuhn (Fig. 12). The ridges are formed by the lower perispore, exposed as in Fig. 10, and are underlaid by a thick exospore (Fig. 9). An upper, dense granulate perispore deposit forms the surface (Figs. 9, 11). The wall is often peculiarly cracked or chipped suggesting it may be brittle. The thin, scarcely raised ridges differ from those of other ridged spores among the dennstaedtioid genera. *Saccoloma* spores resemble those of the paleotropical genus *Cystodium* of the Dicksoniaceae and suggest a possible link with that family.

Cytology

Reports of $n = 188$ and $2n = 376$ for *Saccoloma domingense*, (as *Orthiopteris*) from Jamaica were regarded by Walker (1966) as probably an octoploid level based on 47. Another high but discordant record of $2n = \text{ca. } 63 \pm 2 \text{ II}$ or ca. 63 for *S. inaequale* is reported from Chiapas, Mexico, by Smith and Mickel (1977). On the basis of this record, they question the octoploid level proposed for the Jamaican plants and the close relationship of *Saccoloma* to the dennstaedtioid ferns. The high chromosome numbers known in *Saccoloma* and the complex ridged spore architecture indicate that the genus represents a specialized element among the dennstaedtioids. It is perhaps best treated in this alliance until there is clear evidence for placing it elsewhere.

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57. *Pteridium*

Figs. 57.1–57.12

- Pteridium* Scop., *Fl. Carn.* 169. 1760. Type: *Pteridium aquilinum* (L.) Kuhn (*Pteris aquilina* L.).
Cincinnatiensis Gled., *Syst. Pl.* 290. 1764. Type: “*Cincinnatiensis aquilina* Gled.” (Scop. *Fl. Carn.* 2: 290. 1772) = *Pteridium aquilinum* (L.) Kuhn.
Eupteris Newm., *Phytologist* 2: 278. 1845. Type: *Eupteris aquilina* (L.) Newm. (*Pteris aquilina* L.) = *Pteridium aquilinum* (L.) Kuhn.
Ornithopteris (Ag.) J. Sm., *Hist. Fil.* 297. 1875, not Bernh. 1806 (= *Aneimia*). *Pteris* section *Ornithopteris* Ag., *Rec. Gen. Pterid.* 45. 1839. Type: *Pteris aquilina* L. = *Pteridium aquilinum* (L.) Kuhn.

Fig. 57.1. *Pteridium aquilinum* var. *Feei*, north of Jalapa, Veracruz, Mexico. (Photo W. H. Hodge.)

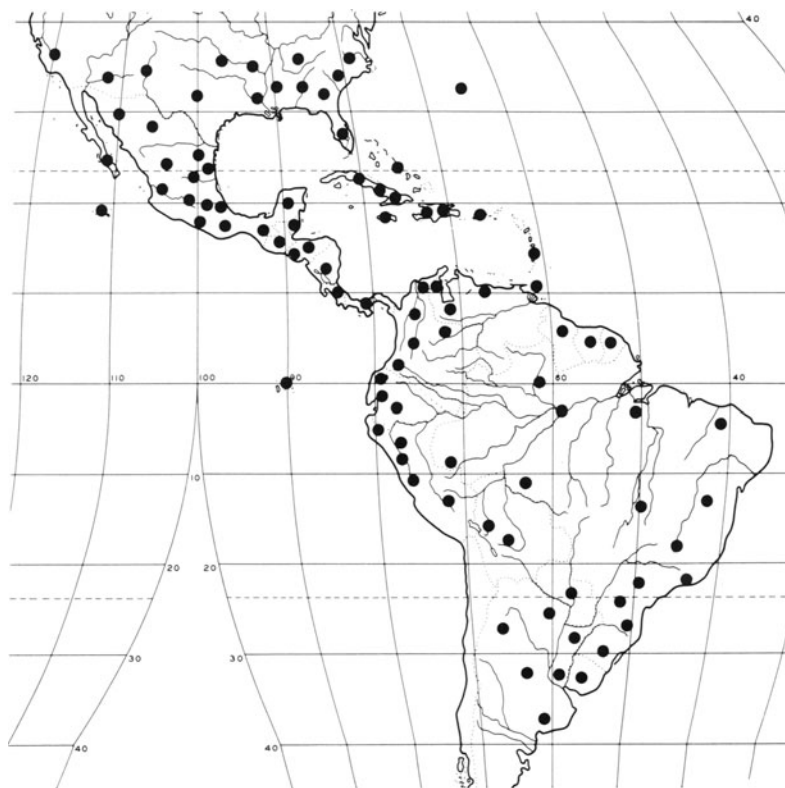


Description

Terrestrial; stem long-creeping, rather slender, bearing trichomes and a few fibrous roots; leaves monomorphic, ca. 40 cm to 3 m, rarely to 7 m long, borne at intervals, lamina 2-pinnate-pinnatifid to 4-pinnate, pubescent to rarely glabrous, veins free; sori marginal, the sporangia on a vascular commissure between the apex and sinus of a segment, not paraphysate, the adaxial indusium formed by the recurved, modified margin, the abaxial indusium membranous, or hardly to not developed, the sterile margins modified similarly to the adaxial indusium; spores tetrahedral-globose, the distal face well rounded, the laesurae $\frac{2}{3}$ the radius, irregularly granulate with particles fused into masses, or more or less fused into short rods. Chromosome number: $n = 52$; $2n = 52, 208$.

Pteridium has several anatomical and morphological features that are unusual in ferns. There are true vessels in the stem, which rarely occur in pteridophytes. There are two types of stems: one is a long shoot that branches but does not bear leaves, the other is a short shoot that usually bears a single leaf during a

Fig. 57.2. Distribution of *Pteridium aquilinum* in America, south of lat. 35° N.



growing season. Glandular areas, often called nectaries, occur at the base of the pinnae and exude a substance attractive to ants. *Pteridium* is unique in having the sterile segments with a modified margin (Fig. 6) similar to that of the adaxial indusium of the fertile margins. This may be narrower or the same width as the adaxial indusium. The abaxial indusium is variously developed, is sometimes a continuous membrane, or is only partially developed as in Fig. 4, or it may be absent.

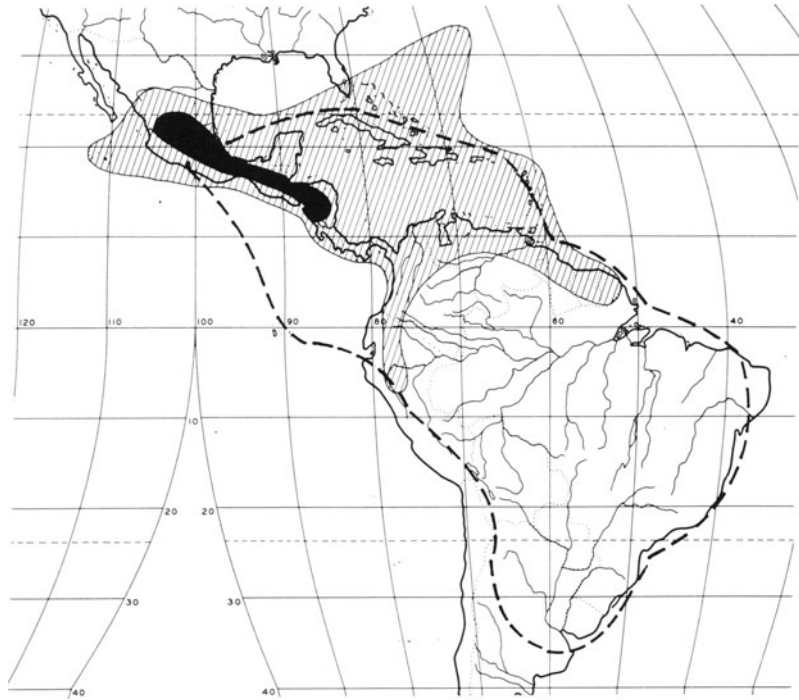
Systematics

Pteridium is a genus of one species, *P. aquilinum* (L.) Kuhn, of worldwide distribution except in regions that are extremely dry or cold. It is morphologically isolated, but its closest affinities are with the dennstaedtioid ferns. *Pteridium aquilinum* is a complex species consisting of 12 geographic varieties. Subspecies *aquilinum* has eight varieties and ssp. *caudatum* has four. While these have distinctive characters, they are difficult to define precisely because they are both phenotypically and genetically variable.

Seven varieties occur in the Old World: subspecies *aquilinum* var. *aquilinum* in Europe and Africa, var. *africanum* Bonap. in central Africa, var. *Wightianum* (Ag.) Tryon in southeastern Asia to Ceylon and New Guinea, var. *decompositum* (Gaud.) Tryon in the Hawaiian Islands, and var. *latiusculum* of America which extends from northern Europe across Asia to China and Kamchatka; in subspecies *caudatum* there are var. *esculentum* (Forst.) Kuhn, distributed from Australia to Tahiti, and var. *yarrabense* Domin from northern India to Australia.

Pteridium has been revised by Tryon (1941).

Fig. 57.3. General distribution of the tropical varieties of *Pteridium aquilinum* in America: solid area, var. *Feei*; dashed line, var. *arachnoideum*; hatched area, var. *caudatum*.



Key to Varieties of *Pteridium aquilinum* in America

- a. Ultimate segments not decurrent at the base, or decurrent and equally surcurrent; subspecies *aquilinum*. b.
- b. Adaxial indusium and modified sterile margin ciliate and (or) pubescent on the adaxial surface. c.
- c. Modified sterile margin ca. 0.25 mm broad, the adaxial indusium broader on the same segment. var. *pubescens* Underw.
- c. Modified sterile margin ca. 0.4 mm or more broad, the adaxial indusium at least as broad on the same segment. (Fig. 6) var. *Feei* (Fée) Maxon
- b. Adaxial indusium and modified sterile margin glabrous. d.
- d. Ultimate segments moderately pubescent at the base of the indusium, the longest about four times as long as broad. var. *latiusculum* (Desv.) Heller.
- d. Ultimate segments glabrous or subglabrous at the base of the indusium, the longest about nine times as long as broad. var. *pseudocaudatum* (Clute) Heller.
- a. Ultimate segments, at least some of them, more strongly decurrent than surcurrent at the base; subspecies *caudatum* (L.) Bonap. e.
- e. Free lobes present on the axes between the ultimate or penultimate segments. (Fig. 5) var. *arachnoideum* (Kaulf.) Brade.
- e. Free lobes absent on the axes between the ultimate and penultimate segments. (Fig. 7) var. *caudatum* (L.) Sadeb.

Ecology (Fig. 1)

Pteridium grows in a variety of habitats as woods, forests and scrublands, in thickets and along open borders of woods, and especially in disturbed places as pastures, abandoned fields and burned or cut-over land. It usually grows in poor, more or less acid soils but also in fertile and sometimes calcareous soils.

In tropical America, var. *Feei* grows most commonly in oak and pine woods in mountaneous areas, often in calcareous soils, in rocky places, old pastures or clearings. The varieties *caudatum* and *arachnoideum* grow in open forests especially along the bor-

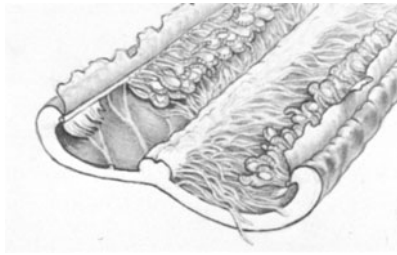


Fig. 57.4. Sorus and indusia of *Pteridium aquilinum* var. *caudatum* $\times 8$. The adaxial indusium is bent to show the sorus, and the sporangia removed, at left, to show the partly developed abaxial indusium.

ders, in thickets, grasslands, and rarely in wetlands. Variety *caudatum* rarely grows around limestone sinks. *Pteridium* grows from sea level to ca. 3000 m.

The species can be a pernicious weed in tropical America, as in most parts of the world, for it invades lands cleared for agriculture or pasture and often develops into pure stands. Allelopathy appears to be involved in the promotion and maintenance of this dense growth as shown in the studies of Gliessman and Muller (1978).

The leaves of *Pteridium* are usually one to two meters tall but those growing in thickets or under small trees may be semiscandent on the branches and reach a length of 4 or rarely up to 7 m. The stem is wide creeping, it frequently branches, usually well below the soil surface, and it can be very long lived. Stems examined by Watt (1940) were 60 m long including the branches, but this is probably not the maximum for a fully developed living system. A study of Oinonen (1967a, 1967b) on bracken clones in Finland estimated the age of the oldest to be about 1500 years. Established plants may survive considerable change and a major environmental alteration is probably necessary to completely exterminate a colony. The capacity for survival of the plants at one locality over a long period reflects the broad ecological tolerance of the species.

There are few reports of *Pteridium* gametophytes and sporelings in nature but these stages appear to occur especially in areas that have been burned (Oinonen, 1967a; Gliessman, 1978).

Geography (Figs 2, 3)

Pteridium grows in North and South America, Europe and Africa, and eastward across Asia, through Malesia and in the Pacific to Tahiti and the Hawaiian Islands; it extends northward to Scandinavia and southward to Tasmania and New Zealand.

In America it occurs from Newfoundland to southern Alaska, south to Buenos Aires in Argentina, and Uruguay (Fig. 2); also on the Revillagigedo Islands, and the Galápagos Islands.

The general distribution of the tropical American varieties is shown in Fig. 3. In addition to these, var. *pubescens* is in the western United States, north to southern Alaska, and south in the mountains of Mexico to Hidalgo; var. *latiusculum* of eastern North America and the Rocky Mountains occurs at Monterrey, Nuevo Leon, Mexico; and var. *pseudocaudatum* ranges from Massachusetts to southern Indiana and Illinois, south to Florida and Texas.

Five of the six American varieties occur in eastern Mexico, but this is probably not a center of evolution since all of the varieties are evidently quite old.

Spores

The granulate surface deposit is relatively uniform in spores of several varieties of *Pteridium* from widely distant areas (Figs. 8–12). The often partly eroded surface, as on the distal face in Fig.

8, exposes a compact stranded formation. The section in Fig. 10 shows that the exceptionally thin wall consisting of a somewhat thicker exospore below the granulate perispore surface. In this section of the wall the surface appears to be quite uniformly granulate. This is also shown at greater magnification in the TEM study of the wall by Lugardon (1974). The detail, in Fig. 12, shows the meshwork of rods or strands is formed below the granulate surface deposit.

Cytology

A meiotic chromosome number of 52 is consistently reported for plants of North America, Europe, Asia and New Zealand. However there is a record of $2n = 52$ for a plant from Spain by Löve and Kjellquist (1972) that was proposed as possibly an ancient element surviving in calcareous areas of southern Europe. The range of this cytotype and its age in relation to other elements in the species need to be substantiated. A plant from the Galápagos Islands with $2n = 208$ (Jarrett et al., 1968) was considered tetraploid but a second collection had the usual number 52. The base number of 26 established for *Pteridium* is an uncommon one in ferns, but this or its multiples are also known in *Paesia* and *Hypolepis*. A close relationship of these three genera has been proposed on the basis of the chromosome number, but marked differences in the spores do not confirm a close alliance.

Observations

There are more studies covering a diversity of topics on *Pteridium* than on any other fern. This is due in part to the wide distribution of the species and its abundance as well as unusual anatomical and morphological features. It is also the most economically important fern and there is considerable literature pertaining to its useful and detrimental qualities. The latter seem to predominate at present but formerly the fern was employed for many purposes as a source of potash for making glass and soap, for thatch, swine food, bedding material for animals and man, and as packing material for fruits. It is still used in rural regions of Venezuela for packing and especially for wrapping heads of curing cheese.

A major undesirable aspect of bracken is its poisonous effect when consumed as fodder by animals or when eaten by man. The young leaves contain a nerve poison and are also carcinogenic (Evans, I. A., 1976; Evans, W. C., 1976). In regions where large quantities of bracken croziers are consumed, as in Japan (Hodge, 1973), they may be implicated in the high incidence of stomach cancer. Bracken is regarded as a pernicious weed in some areas where it takes over land intended for cultivation or grazing. It often forms dense colonies over large areas excluding all or most other plants. Eradication of bracken has met with only limited success because of the high cost of effective control measures on the poorer land that it usually invades.

Two major publications on bracken, including about 1000 references covering most of the extensive work, are by Braid (1959)

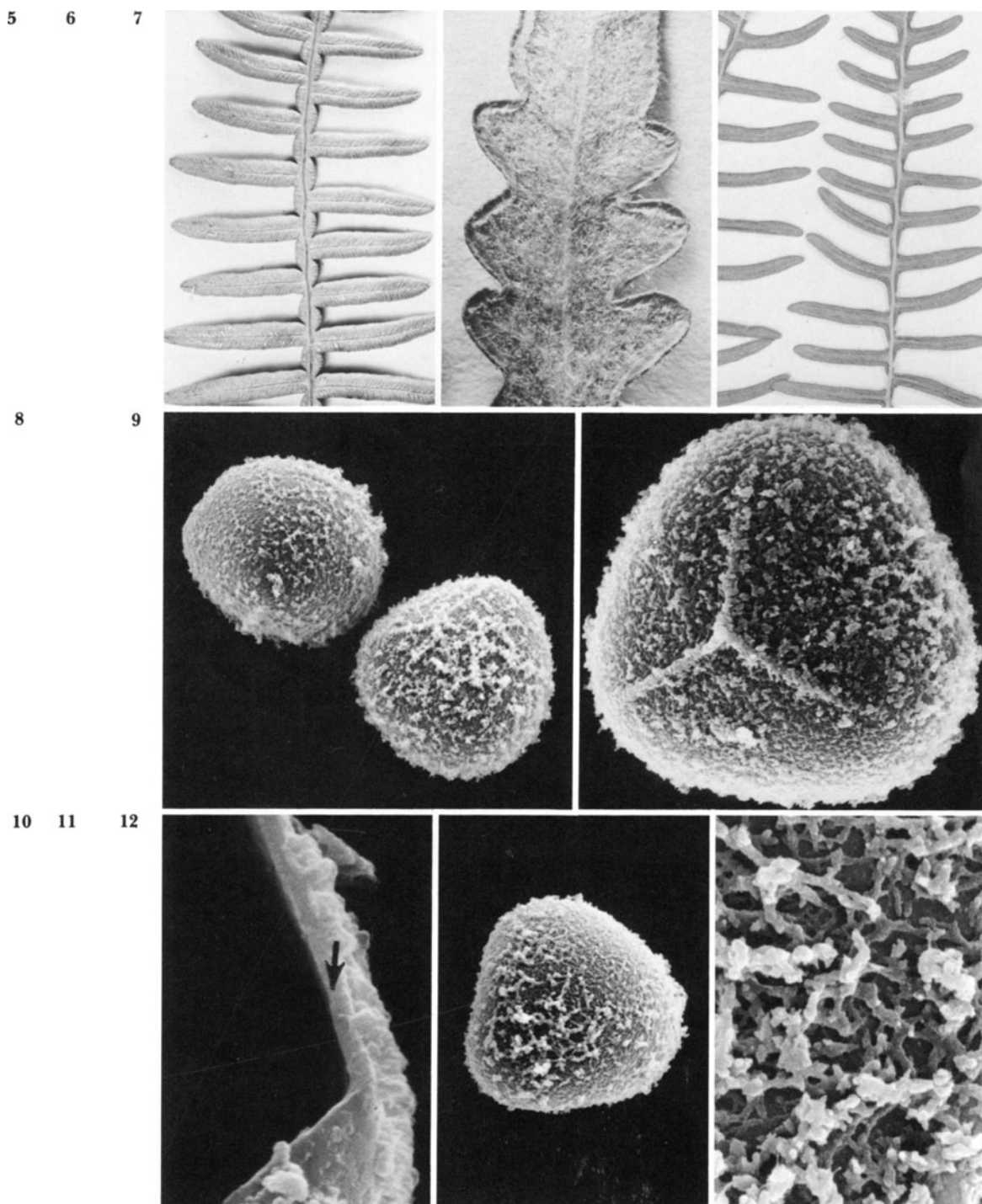


Fig. 57.5–57.12. *Pteridium aquilinum*. 5. Portion of a pinnule of var. *arachnoideum*, $\times 1.5$. 6. Sterile pinnule of var. *Feei* with modified margin, $\times 5$. 7. Portion of pinnules of var. *caudatum*, $\times 1.5$. 8–12. Spores. 8. var. *arachnoideum*, the distal face above with surface partially eroded showing lower reticulate stratum, Colombia, *Little 8781*, $\times 1000$. 9. var. *aquilinum*, granulate proximal face, Uganda, *Lovage 473*, $\times 2000$. 10. var. *arachnoideum*, wall section, the exospore (at arrow) below granulate perispore deposit, Brazil, *Irwin & Soderstrom 5301*, $\times 10,000$. 11. var. *caudatum*, distal face, Dominican Republic, *Fuertes 1053*, $\times 1000$. 12. var. *esculentum*, detail of more or less granulate deposit on proximal face, New Zealand, *Hunnewell 13360*, $\times 6000$.

and Perring and Gardner (1976). Some special areas of research on the species include genetics, by Wilkie (1956), Klekowski (1973) and Chapman et al. (1979), and flavonoid chemistry by Cooper-Driver (1976). Studies of ecdysones by Kaplanis et al. (1967) have found two major insect molting compounds in bracken that may explain the general resistance of the plants to insect predation. Some basic studies on the development and growth of *Pteridium* are by Webster and Steves (1958), O'Brien (1963) and Watt (1940).

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58. *Paesia*

Figs. 58.1–58.10

Paesia St.-Hil., Voy. Distr. Diamans 1: 381. 1833. Type: *Paesia viscosa* St.-Hil. = *Paesia glandulosa* (Sw.) Kuhn.

Description

Terrestrial, rarely rupestral; stem long-creeping, rather slender, bearing trichomes and few to many fibrous roots; leaves monomorphic, ca. 20 cm to 2.5 m long, borne at intervals, lamina to 4-pinnate-pinnatifid, glabrate, glandular-pubescent or pubescent, veins free; sori marginal, the sporangia on a short to long vascular commissure, not paraphysate, the adaxial indusium formed by the modified, recurved margin, the abaxial indusium firmly membranous; spores somewhat ellipsoidal, monolete, the laesura ca. $\frac{3}{4}$ the spore length, usually in a furrow formed by adjacent rugae, the surface coarsely rugose. Chromosome number: $n = 26, 104$.

Paesia is characterized by a well-developed abaxial indusium as well as a marginal indusium (Fig. 3). The abaxial one is invariably present and of a firm, membraneous texture, contrasting with the structure in *Pteridium* that is often poorly developed or absent. The rachis, especially in large leaves, is usually somewhat fractiflex and appears to be adapted for a scandent or scrambling habit. The segment architecture is shown in Figs. 4 and 5.

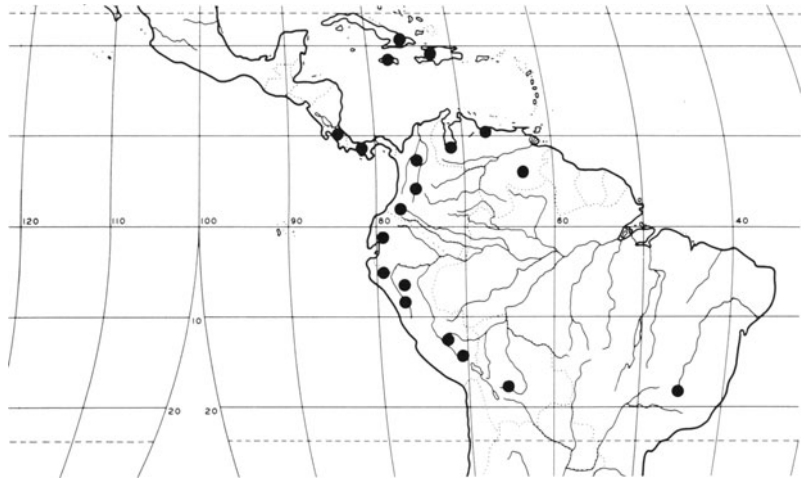
Systematics

Paesia is a predominantly tropical genus of about 12 species, two of them in tropical America. It has been related to *Pteridium* on the basis of characters such as the vascular commissure, abaxial indusium and the chromosome number based on $n = 26$. The



Fig. 58.1. *Paesia anfractuosa*, south of Cartago, Costa Rica. (Photo W. H. Hodge.)

Fig. 58.2. Distribution of *Paesia* in America.



rugose, monolete spores suggest that the alliance may not be close.

Hypolepsis bivalvis vAvR. with an abaxial indusium, is correctly placed as *Paesia bivalvis* (vAvR.) R. & A. Tryon.

Tropical American Species

The marked variability of *Paesia glandulosa* has led to its recognition under several names which are based on local variants not sufficiently constant for taxonomic recognition. The name *Paesia viscosa* has been commonly used for this species, but examination of the type material of *Cheilanthes glandulosa* Sw. at Stockholm showed this to be an earlier name, contrary to Tryon (1964).

Key to American Species of *Paesia*

- a. Basal segment of the pinnae and secondary segments on the acroscopic side.
P. glandulosa (Sw.) Kuhn
- a. Basal segment of the pinnae and secondary segments on the basispic side.
P. anfractuosa (Christ) C. Chr.

Ecology (Fig. 1)

Paesia is a genus of montane forests and occurs in natural forest openings. In America, *Paesia* most often grows in cloud forests or wet, montane forests, usually in shrubby places, at the edge of woods, and in rocky woods; occasionally it invades road banks in forest zones. It occurs at altitudes between 1400 and 3600 m. *Paesia* may form large colonies and probably has a long, creeping and branching stem; however, data are not available on the stem system. The leaves are semiscandent, on and among branches when plants grow among shrubs and small trees.

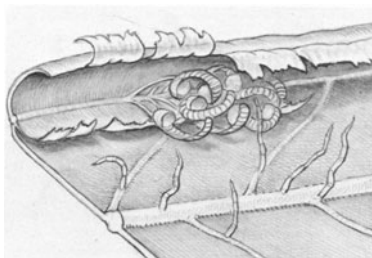
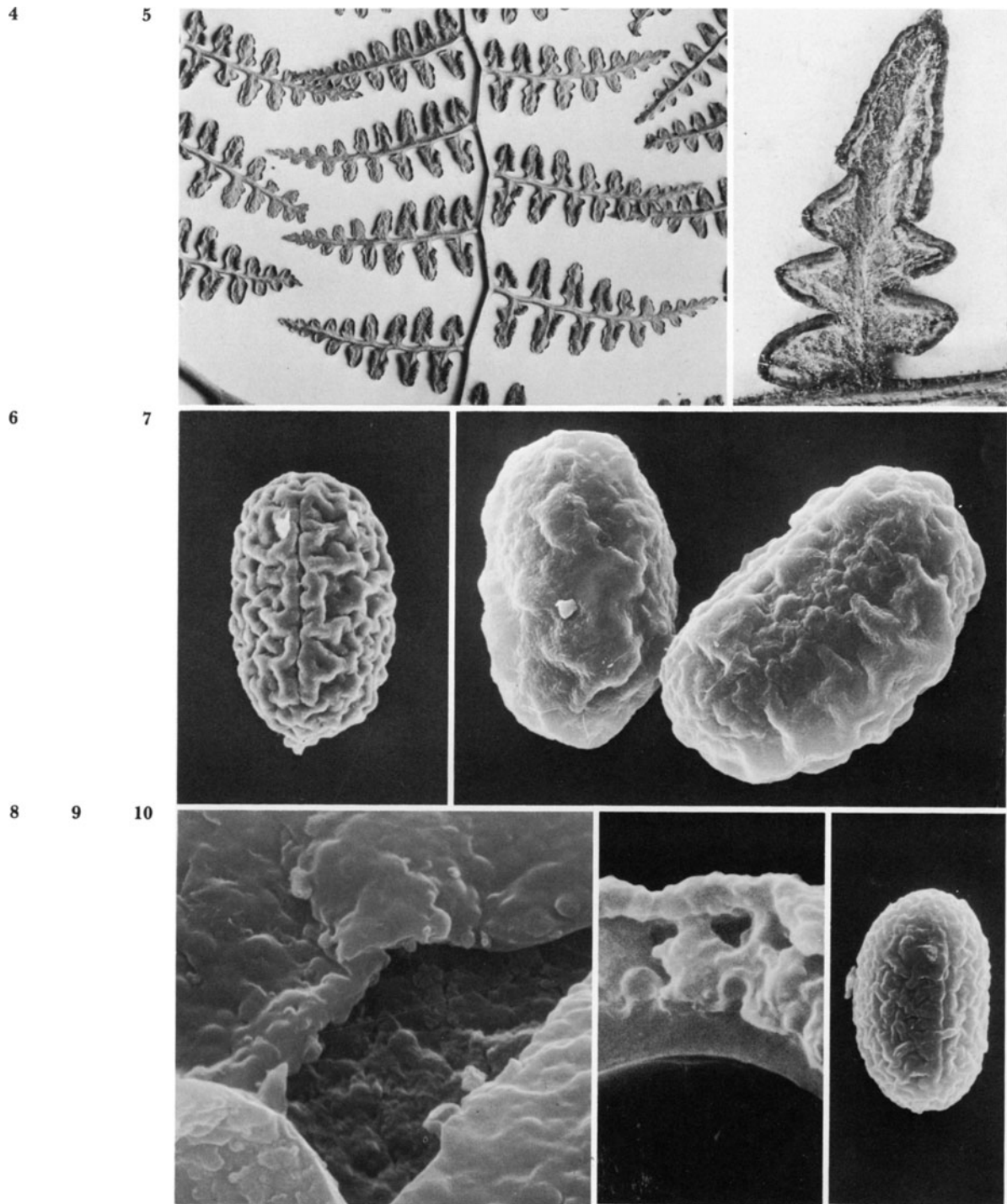


Fig. 58.3. Sorus of *Paesia glandulosa*, showing the adaxial and abaxial indusia, $\times 20$.

Geography (Fig. 2)

Paesia is present in the American tropics and in the Old World tropics from Malesia to Tahiti, and south to New Zealand.

In America the genus occurs in Costa Rica and Panama, Cuba, Jamaica, Hispaniola, Venezuela to Colombia, south to Bolivia,



Figs. 58.4–58.10. *Paesia*. 4. Tertiary segments of *P. anfractuosa*, $\times 1.5$. 5. Abaxial surface of segment of *P. glandulosa*, $\times 5$. 6–10. Spores, $\times 1000$. 6–9. *P. glandulosa*. 6. Proximal face with rugae obscuring the central laesura, Colombia, Daniel 660. 7–9. Peru, Pennell 14024. 7. Coarsely rugose, laesura across top of the spore, right. 8. Part of abraded perispore and the lower papillate exospore, $\times 10,000$. 9. Wall profile with thick, ridged perispore above a denser, more or less papillate exospore, $\times 10,000$. 10. *P. scaberula*, rugose proximal face the rugae obscuring the central laesura, New Zealand, Craig 157.

and disjunct in Minas Gerais in Brazil; this is also the range of *Paesia glandulosa*. The other American species, *P. anfractuosa* is endemic to Costa Rica.

Spores

The spores of *Paesia* are consistently rugose but vary in density and prominence of the rugae (Figs. 6–10). There are marked size differences between specimens of *Paesia glandulosa* from Colombia (Fig. 6) and those from Peru (Fig. 7). The species is reported as octoploid in Jamaica thus the larger spored material from Peru may represent a higher ploidy level. The abraded surface (Fig. 8) and section of the wall (Fig. 9) show that the thick outer rugose perispore overlays a more or less papillate exospore. Spores of *P. scaberula* (A. Rich.) Kuhn from New Zealand (Fig. 10) are rugose but smaller than those of the American tropics. The alliance of *Paesia*, *Pteridium* and *Hypolepis* is proposed on the basis of similar chromosome numbers. However, marked differences in shape and surface of the spores suggest the relationships may not be close.

Cytology

The record of $n = 26$ in *Paesia anfractuosa* from Costa Rica (Gómez Pignataro, 1971) is consistent with that of *P. scaberula* from New Zealand (Brownlie, 1957). The report of $n = 104$ for *P. glandulosa*, (as *P. viscosa*) from Jamaica was regarded as an octoploid by Walker (1966). Differences in spore size of specimens from distant portions of the range may reflect the changes in ploidy levels within the species.

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 Walker, T. G. 1966. Reference under the family.

59. *Hypolepis*

Figs. 59.1–59.12

Hypolepis Bernh., *Neues Jour. Bot.* (Schrad.) 1 (2) 34. 1806. Type: *Hypolepis tenuifolia* (Forst.) Presl (*Lonchitis tenuifolia* Forst.).

Description

Terrestrial; stem long-creeping, rather slender, bearing trichomes and long, fibrous roots; leaves monomorphic, ca. 10 cm to 3 m, rarely to 7 m long, borne at intervals, lamina 2-pinnate-pinnatifid to 4-pinnate-pinnatifid, usually pubescent, or nearly glabrous, veins free; sori submarginal, 1-nerved, usually borne in a sinus, not paraphysate, indusium slightly to strongly dif-



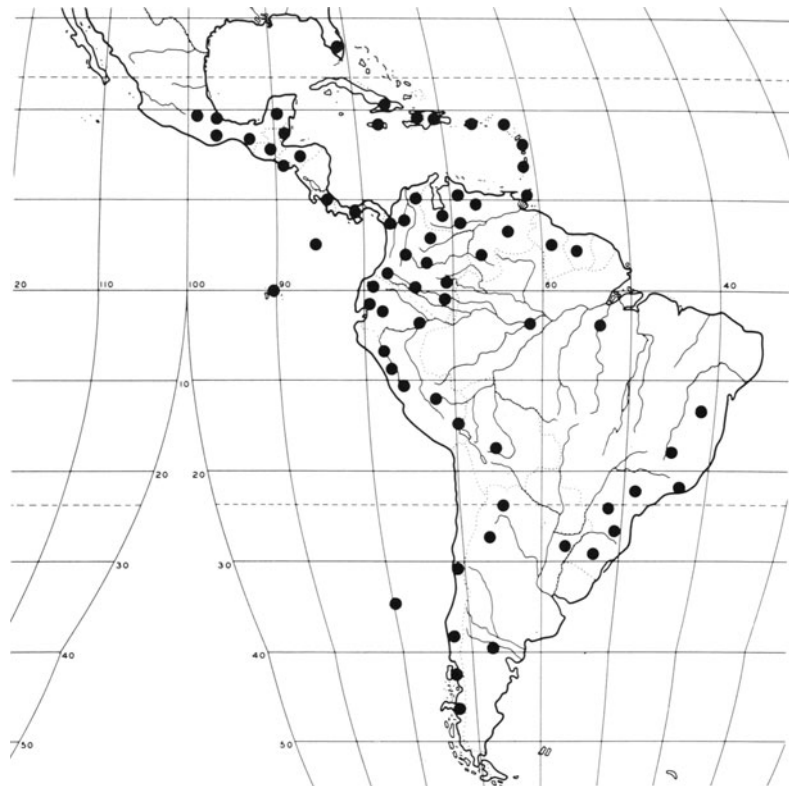
Fig. 59.1. *Hypolepis repens*, north of Jalapa, Veracruz, Mexico. (Photo W. H. Hodge.)

ferentiated from a recurved marginal lobe, or lacking and the lobe flattened and unmodified; spores somewhat ellipsoidal, monolete, the laesura $\frac{2}{3}$ the length, the surface echinate, often with more or less reticulate strands connecting the echinate elements. Chromosome number: $n = 29, 39, 51-53, 52, \text{ca. } 92, 98, \text{ca. } 100, 104; 2n = \text{ca. } 92, 104, \text{ca. } 150, 208.$

Hypolepis has a marginal or submarginal sorus (Fig. 4) usually covered by a modified, recurved, marginal indusium (Figs. 3). The lamina is usually 3-pinnate or more complex (Figs. 1, 5), but the smallest species in the genus, *H. obtusata*, may be only 2-pinnate-pinnatifid at the base and 2-pinnate above (Fig. 6). The margin is unmodified in some species, as *H. rugulosa* and *H. pulcherrima*.

Systematics *Hypolepis* is a tropical and extratropical genus of perhaps 40 species with about 15 in America. Relationships of *Hypolepis* with other dennstaedtioid ferns are not close. There are similarities in chromosome numbers to *Paesia* and *Pteridium*, and to *Blotiella* in the spores, but other characters do not support a close alliance with these genera. Species lacking an indusium, as *H. pulcherrima* suggest a possible distant relationship to the taenitoid ferns of the Pteridaceae.

Fig. 59.2 Distribution of *Hypolepis* in America.



Tropical American Species

Over 20 species have been recognized in America but there are probably fewer; a modern revision of these and of the paleotropical species is needed. Some of the American species are: *Hypolepis bogotensis* Karst., *H. crassa* Maxon, *H. hostilis* (Kze.) Presl, *H. melanochlaena* A. R. Smith, *H. nigrescens* Hook., *H. obtusata* (Presl) Hieron., *H. parallelogramma* (Kze.) Presl, *H. pulcherrima* Maxon, *H. repens* (L.) Presl, *H. rugulosa* (Labill.) J. Sm., *H. Stuebelii* Hieron., and *H. viscosa* Karst.

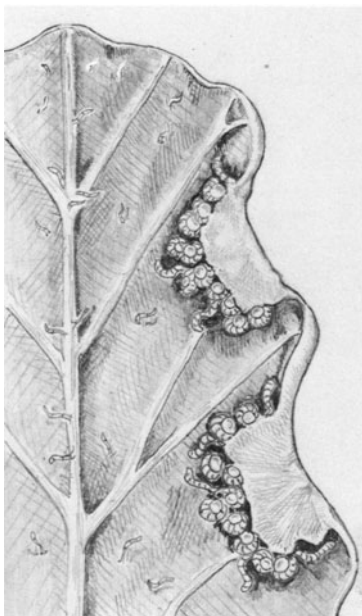


Fig. 59.3. Sorus of *Hypolepis parallelogramma*, $\times 15$.

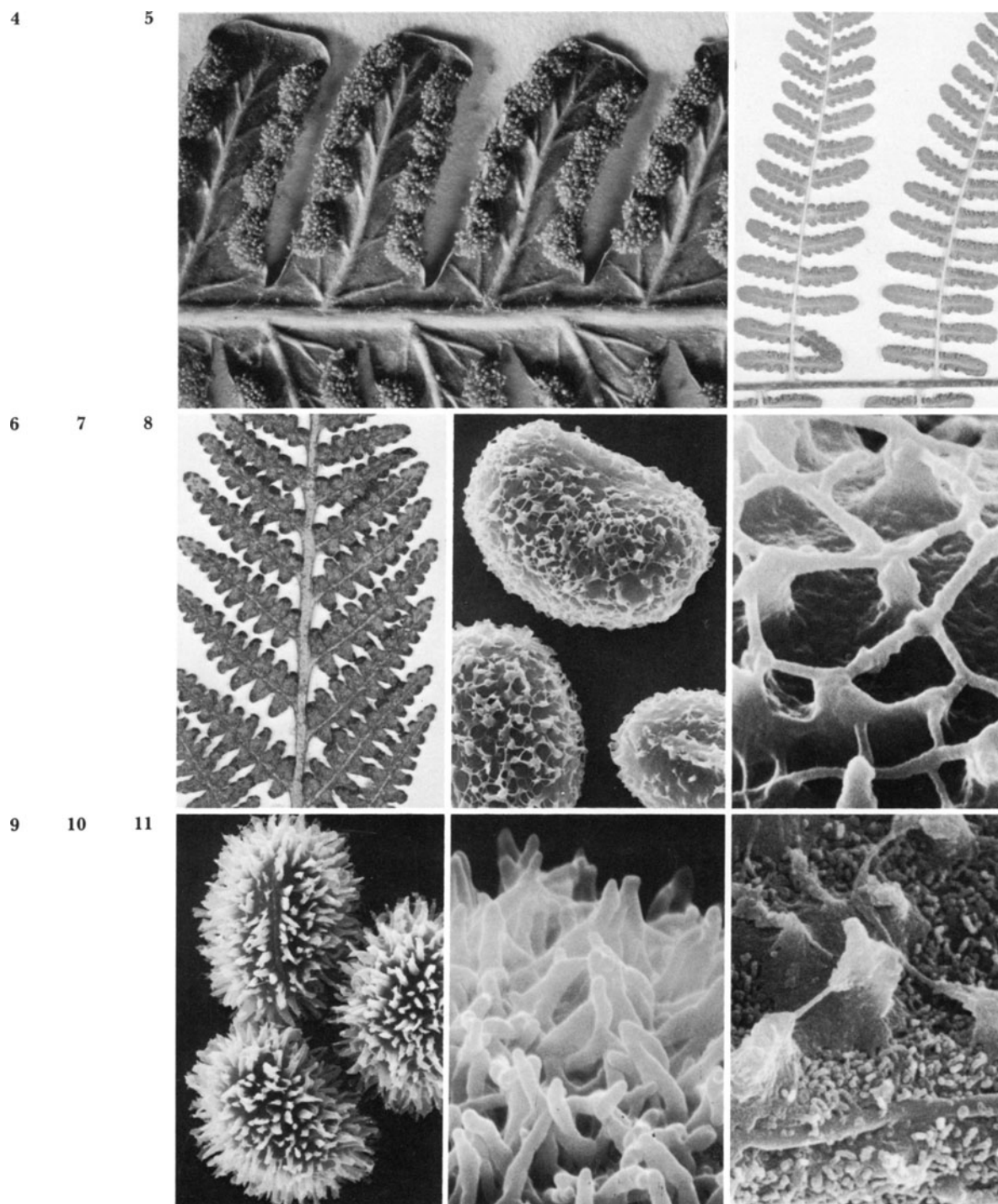
Ecology (Fig. 1)

Hypolepis usually grows in forests or along their borders, in clearings and thickets, sometimes in moist to wet, open habitats.

In America it grows in rain or montane forests, páramillo thickets, brushy places, forest borders or clearings, in fields, open pastures, and less often in open, rocky places or on cliffs. A few species in the Andes may extend into the páramo.

Hypolepis usually grows from sea level to 2500 m; with *H. crassa* at altitudes to 3900 m and *H. obtusata* to 4200 m.

Hypolepis may form dense colonies in shrubby vegetation and among small trees. The leaves may be long and subscaudent and the stem may be very long and frequently branched. The excavated stem system of a plant in *Hypolepis repens* studied by Gruber (1981) is about 22 m in length, although incomplete (Fig. 12). The extensive development and numerous apices show the potential for growth of these plants.



Figs. 59.4–59.11. *Hypolepis*. 4. Fertile segments of *H. parallelogramma*, $\times 5$. 5. Pinnules of *H. repens*, $\times 1$. 6. Segments of *H. obtusata* (central portion of lamina), $\times 1$. 7–11. Spores, $\times 1000$, surface detail, $\times 10,000$. 7–8. *H. crassa*, reticulate, Ecuador, *Øllgaard & Balslev 8155*. 7. Echinete-reticulate surface, the laesura at top of upper spore. 8. Detail of particulate strands connecting echinate elements. 9. *H. hostilis*, with dense echinate-reticulate elements, Costa Rica, *Berger & Liesner 7038*. 10. *H. nigrescens*, detail of echinate surface, Jamaica, *Maxon & Killip 1139*. 11. *H. bogotensis*, echinate-reticulate elements and papillate surface, part of laesura at base, Colombia, *Pennell & Hazen 10068*.

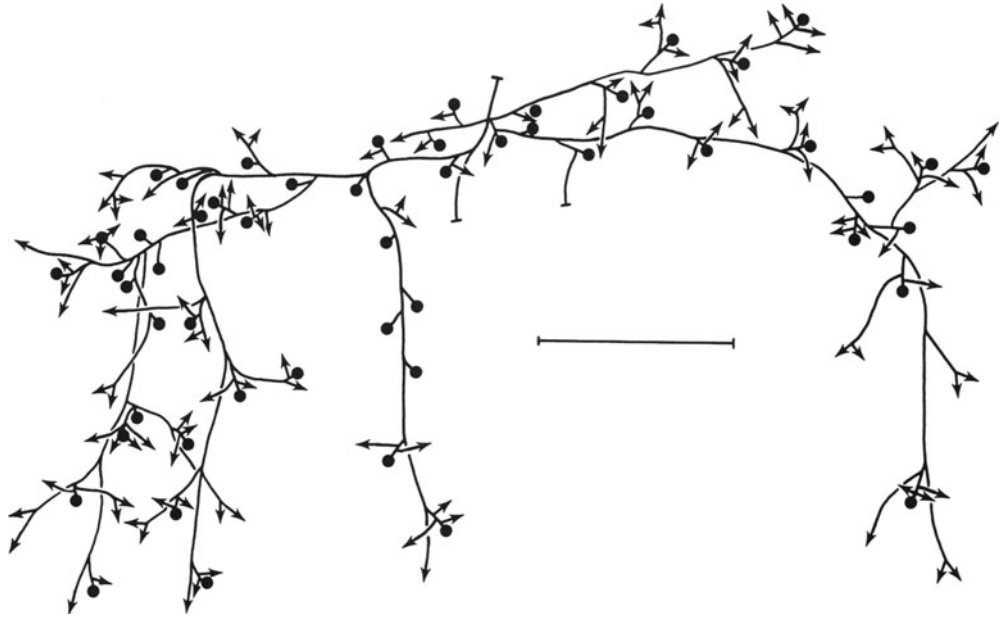


Fig. 59.12. Stem system of *Hypolepis repens*, mapped in situ in a cloud forest north of Jalapa, Mexico, (Gruber, 1981). Solid dots indicate the position of leaves, arrows the stem apices, and short bars the decayed stem ends; the scale is shown by a 1 m bar.

Geography (Fig. 2)

Hypolepis grows in tropical America and temperate South America, in Africa eastward to southeastern Asia and Malesia, east through the Pacific to Pitcairn Island and the Hawaiian Islands, south to Tasmania, New Zealand and Auckland Island.

In America *Hypolepis* grows from Puebla and Veracruz in Mexico to Panama, southern Florida, the West Indies, and in South America from Surinam, to Colombia, south to southern Chile, northeastern Argentina and southeastern Brazil; also on Cocos Island, the Galápagos Islands and the Juan Fernandez Islands.

The greatest diversity of species is in the Andes from Colombia to Peru. There are several species in Central America and in the Greater Antilles, and fewer elsewhere. *Hypolepis rugulosa* occurs in Chile, the Juan Fernandez Islands, and also in Australia and New Zealand.

Spores

Hypolepis spores are basically echinate-reticulate, with slender strands forming a reticulum incorporating the echinate formation as in *H. crassa* (Figs. 7, 8) and *H. bogotensis* (Fig. 11). The echinate elements may be dense as in *H. hostilis* (Fig. 9). Spores of *H. nigrescens* lack the reticulate strands (Fig. 10) and the species is also distinguished by its divergent chromosome number. *Hypolepis* spores have one of the most complex types of surface structure among the dennstaedtioid ferns, suggesting that the genus may represent a derived element in the group.

Cytology

The large range of chromosome numbers reported for *Hypolepis* indicates complex cytological changes, although several species have meiotic numbers of 52 or 104. Reports of putative hybrids involving *H. viscosa* from Oaxaca, Mexico, and *H. repens* from Costa Rica are based upon study of chromosome pairing in triploid plants (Smith and Mickel, 1977). The record of $n = 29$ in *H. nigrescens* from Jamaica (Walker, 1966), and from Oaxaca, Mexico (Smith and Mickel, 1977), is a divergent number for the genus. However, Walker (1973) suggests that the basic numbers 26 and 29 may represent a short aneuploid series.

Literature

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 Walker, T. G. 1973. Reference under the family.

60. *Blotiella*

Figs. 60.1–60.11

Blotiella Tryon, Contrib. Gray Herb. 191: 96. 1962. Type: *Blotiella glabra* (Bory) Tryon (*Lonchitis glabra* Bory).

Description

Terrestrial; stem erect, to 4.5 m tall, to decumbent, stout, bearing trichomes and many long, fibrous roots; leaves monomorphic, ca. 50 cm to 6 m long, borne in a crown or cluster, lamina 1-pinnate-lobed to 2-pinnate-pinnatifid, more or less pubescent, veins partially to usually wholly anastomosing, without included free veinlets; sori marginal, continuous around base of narrow sinuses, sporangia borne on a vascular commissure, paraphysate, indusium well differentiated from the recurved margin; spores somewhat ellipsoidal, monolet, the laesura $\frac{1}{2}$ to $\frac{2}{3}$ the spore length, the surface coarsely echinate, sometimes with connecting reticulate strands, or granulate. Chromosome number: $n = 38, 76$.

The lamina indument is somewhat variable but is usually dense as in Fig. 4. It may be sparse and, especially with age, the lamina may be glabrate. Reduced (stipular) pinnules may occur at the base of the lower pinnae as in *Histiopteris*. The marginal sori are continuous around the sinuses of the ultimate segments as in Fig. 3 and the veins are anastomosing as in Figs. 4 and 5.

Systematics

Blotiella is a genus of about 15 species, one in America and the others in Africa and Madagascar. The American *Blotiella Lindeniana* (Hook.) Tryon is variable especially in the color, density and distribution of the lamina indument. However, there seems to be no basis for the recognition of more than one taxon. The African and Madagascar species require additional study be-

Fig. 60.1. *Blotiella Lindeniana*. Tapanti, Cartago, Costa Rica, pinnae of a scandent leaf. (Photo Alice F. Tryon.)



Fig. 60.2. Distribution of *Blotiella* in America.

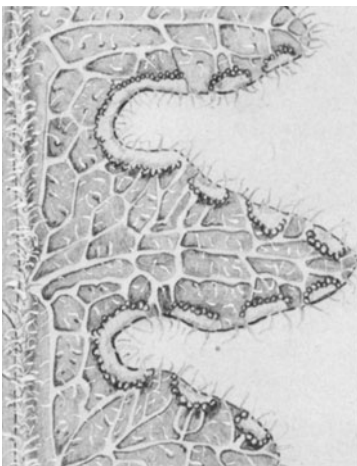
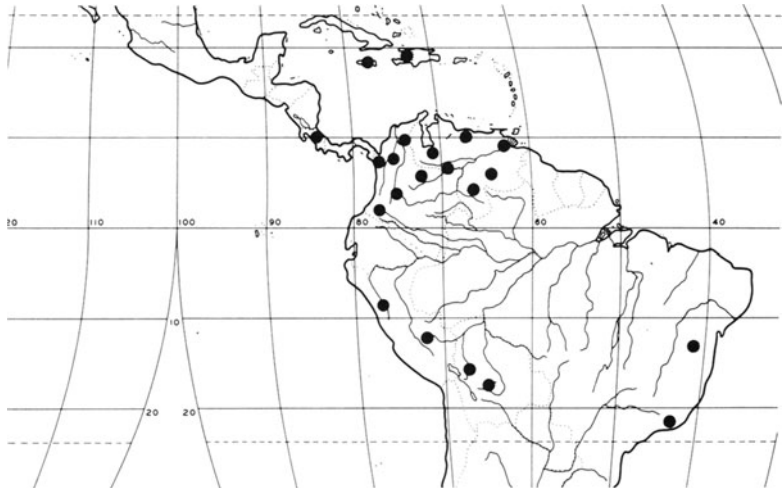


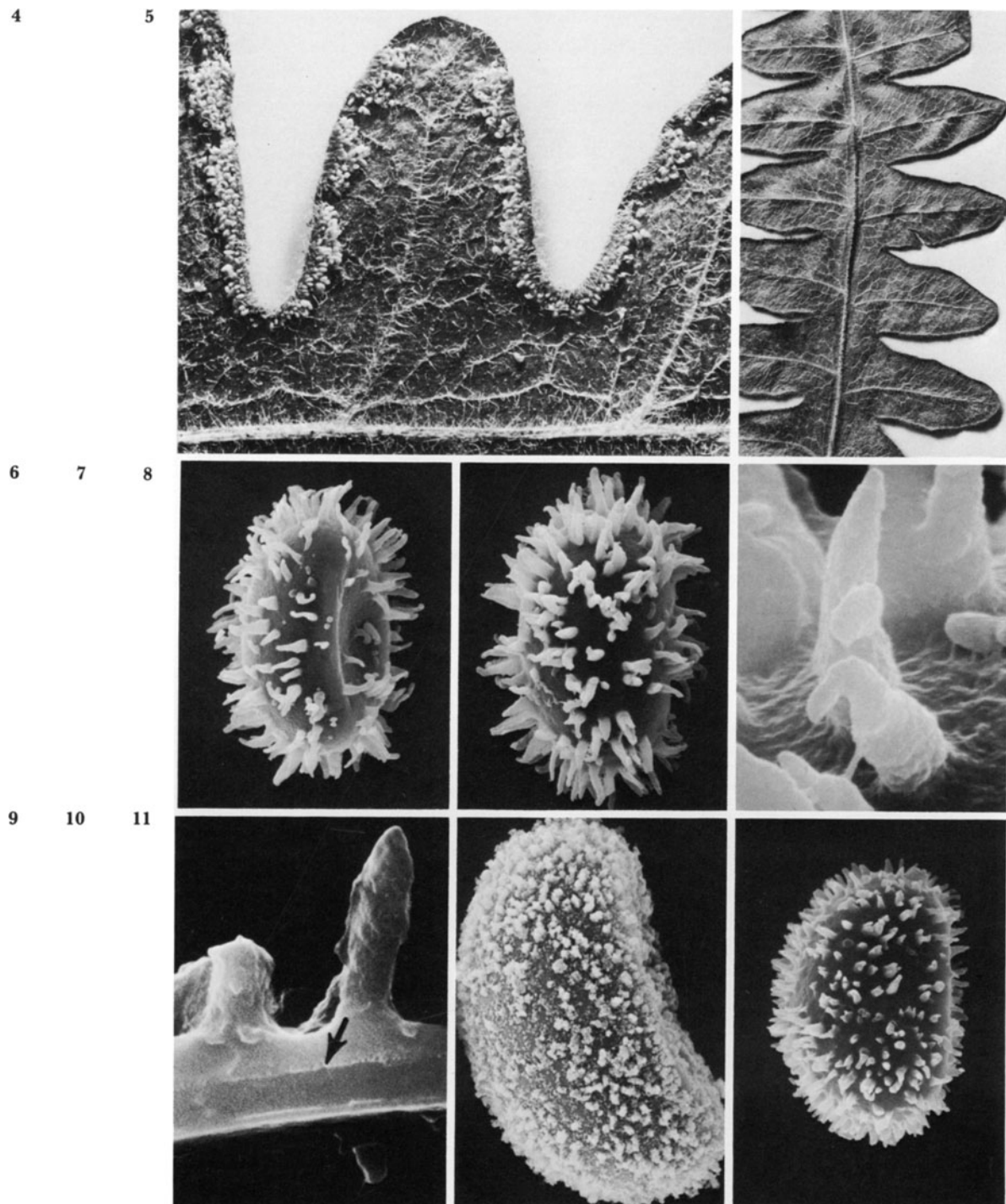
Fig. 60.3. Sori of *Blotiella Lindeniana*, $\times 2$.

cause of variability of the lamina architecture and precocious fertility.

Although they are very distinctive, the genera *Blotiella*, *Lonchitis*, and *Pteris* have been confused (Copeland, 1947) primarily because of similarities of the sorus and indusium. *Blotiella* is a new name for some species previously called *Lonchitis* (Kümmerle, 1915). The type of *Lonchitis* has erroneously (Proctor, 1977) been considered to be *Lonchitis aurita* L. It is actually *Lonchitis hirsuta* L. which belongs in the genus often called *Anisosorus* (Lellinger, 1977), while *Lonchitis aurita* is a synonym of *Pteris arborea* L.

Ecology and Geography (Figs. 1, 2)

Blotiella grows in wet forest, in ravines and along streams. In America *B. Lindeniana* grows in cloud forests, wet, montane forests (Fig. 1) and sometimes in more open, wet sites. The leaf is



Figs. 60.4–60.11. *Blotiella*. 4. *B. Lindeniana* sori with lobed, marginal indusia, abaxial leaf surface pubescent, $\times 5.0$. 5. *B. Lindeniana* areolate venation of sterile segment, $\times 1.5$. 6–11. Spores, $\times 1000$. 6–8. *B. Lindeniana*, Brazil, *Brade 18285*. 6. Echiniate proximal face with laesura. 7. Distal face. 8. Surface detail with strand connecting echinate elements, $\times 10,000$. 9. *B. Lindeniana*, wall profile, the coarse echinate elements formed by upper perispore, lower perispore at arrow, above the exospore. Costa Rica, *Burger & Stolze 5698*, $\times 10,000$. 10. *B. glabra*, granulate spore, laesura, right, Tanganyika, *Richards 6320*. 11. *B. glabra*, echinate spore, laesura, right, Swaziland, *Schelppe 6320* (US).

sometimes scandent on shrubs and small trees. *Blotiella* ranges in altitude from 1500 to 2300 m.

The genus is in tropical America, tropical and subtropical Africa and in Madagascar and the Mascarenes. In America it occurs uncommonly in Costa Rica, Jamaica and Hispaniola, and in South America from Venezuela and Colombia south to Bolivia and eastern Brazil.

Spores

Spores of the American *Blotiella Lindeniana* are coarsely echinate (Figs. 6, 7) often with slender strands connecting the echinate elements (Fig. 8). The wall profile of this species (Fig. 9) shows the echinate structure is formed by an outer perispore, and below this a slightly rougher, thin granulate stratum overlays a thick exospore. Spores of the African species vary from granulate to echinate as in *B. glabra* (Bory) Tryon (Figs. 10, 11). The echinate material appears to be organized from the less structured granulate form. Variance in size of these spores indicates possible differences in ploidy levels. The echinate-reticulate spores of *B. Lindeniana* are similar to those of *Hypolepis* and are considered to represent a specialized, derived form among the dennstaedtioid ferns.

Cytology

Chromosome numbers are not reported for the American *Blotiella Lindeniana* but two diploids and a tetraploid based on $n = 38$ are known for species in Africa. This number is quite different from that of $n = 100$ reported for *Lonchitis* from Jamaica and supports recognition of the two as distinct genera.

Literature

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61. *Lonchitis*

Figs. 61.1–61.9

Lonchitis L., Sp. Pl. 1078. 1753; Gen. Pl. ed. 5, 485. 1754. Type: *Lonchitis hirsuta* L. (Chosen by Brongn., Dict. Class. Hist. Nat. (Bory) 9: 490. 1826).

Anisosorus Maxon, Sci. Surv. Porto Rico & Virg. Isls. 6: 429. 1926, *nom. superfl.* for *Lonchitis* L. and with the same type.



Fig. 61.1. *Lonchitis hirsuta*, a small plant, Spring Garden, Jamaica. (Photo W. H. Hodge.)

Description

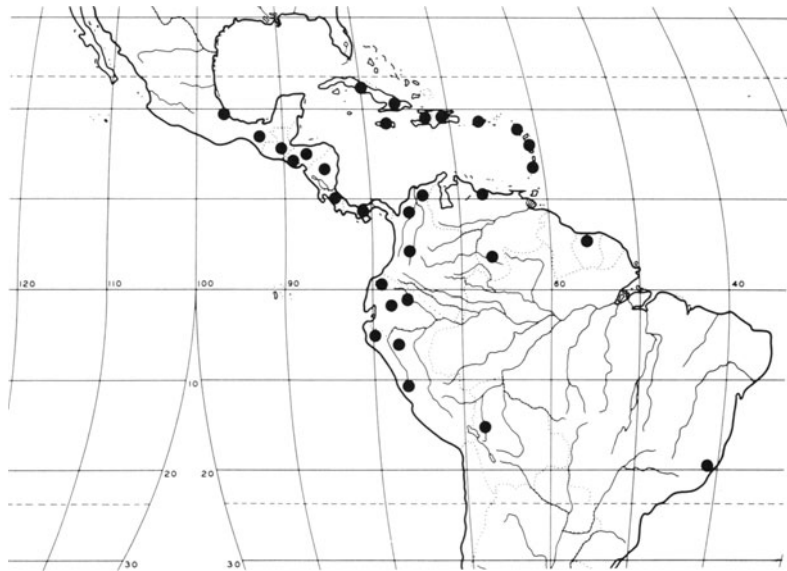
Terrestrial or sometimes rupestral; stem more or less short-creeping, moderately stout, bearing trichomes and many long, fibrous roots; leaves monomorphic, ca. 40 cm to 2.5 m long, rather closely spaced, lamina 2-pinnate-pinnatifid to 3-pinnate-pinnatifid, more or less pubescent, veins free or partly anastomosing without included free veinlets; sori marginal, sporangia on a vascular commissure between the apex and sinus of segment or sometimes at the base of the sinus, sometimes paraphysate, the indusium well differentiated from the recurved margin; spores spheroidal, trilete with broad, raised laesurae $\frac{3}{4}$ the radius with diffuse, spherical material irregularly deposited on a slightly granulate surface. Chromosome number $n = 50, 100$.

The stem of *Lonchitis* is crisp and fleshy, and bears succulent leaves in two ranks. It is often reported as bearing scales but these are true trichomes that may be flattened and laterally coherent appearing as narrow scales. The sorus and modified marginal indusium are shown in Figs. 3–5, and the scattered lamina pubescence on the abaxial surface in Fig. 5.

Systematics

The two species of *Lonchitis* are geographically distinct with *L. hirsuta* L. in America and *L. occidentalis* Baker in tropical Africa and Madagascar. *Lonchitis* has often been allied to *Pteris*, and Copeland (1947) placed it in that genus. Several characters including the spores and chromosome numbers, clearly relate it to

Fig. 61.2. Distribution of *Lonchitis* in America.



the dennstaedtioid rather than the pteroid ferns. The name *Lonchitis* has usually been applied to the previous genus, *Blotiella*, while the genus *Lonchitis* has usually been called *Anisosorus*.

The typification of *Lonchitis* was conclusively established by Lellinger (1977).

Ecology (Fig. 1)

Lonchitis grows in wet forests, especially in ravines, on stream banks and near waterfalls, it grows less often on wet rocks or ledges of wet cliffs. In America it occurs between about 100 to 1800 m.

Geography (Fig. 2)

Both of the species are wide ranging, one in tropical America and the other in tropical Africa and Madagascar.

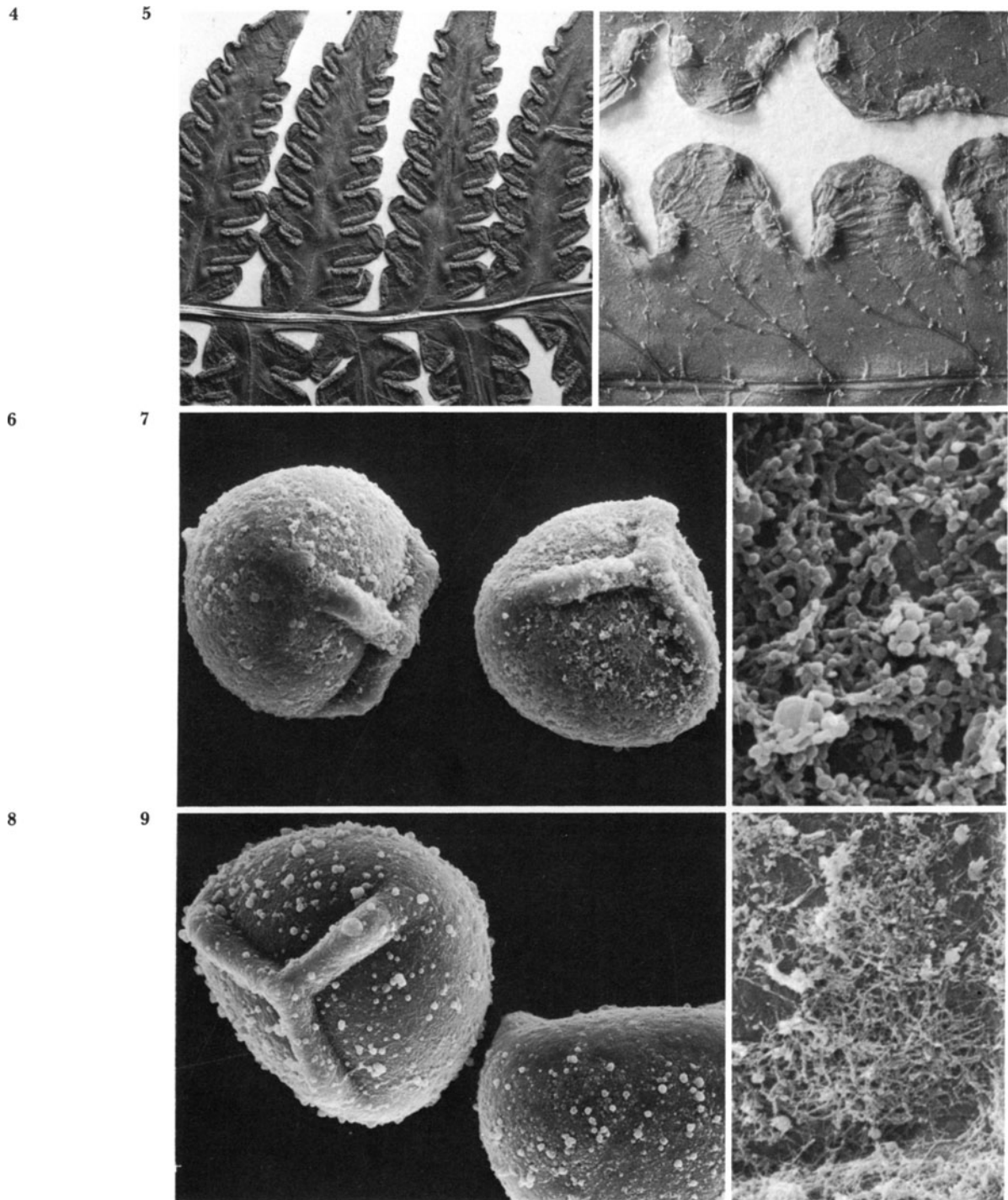
In America *Lonchitis* occurs from Veracruz in Mexico, south to Panama; in the Greater Antilles and many of the Lesser Antilles; in South America from Surinam to Colombia, south to Bolivia and also disjunct in Rio de Janeiro, Brazil.



Fig. 61.3. Fertile segments of *Lonchitis hirsuta* with free veins, sori and marginal indusia, $\times 4$.

Spores

Lonchitis spores are spheroidal with a relatively simple granulate surface as in Figs. 6–8. Slender strands form a basal meshwork (Fig. 9) on which a granulate deposit is coalesced into a thick layer forming the main part of the wall, and coarse, irregular spheres are formed on the surface as in Fig. 7. Size differences are evident in spores from distant geographic areas. Those from Veracruz, Mexico, (Fig. 6) are smaller than spores from Ecuador (Fig. 8), possibly reflecting different ploidy levels within the species. These trilete spores are unlike those of other genera of the dennstaedtioids, especially the complex, monolete, echinate spores of *Blotiella*, a genus formerly associated with *Lonchitis*.



Figs. 61.4–61.9. *Lonchitis hirsuta*. 4. Portion of fertile pinna with marginal sori, $\times 1.5$. 5. Sori and trichomes on abaxial surface of fertile segments, $\times 5.0$. 6–9. *Lonchitis hirsuta*, spores, $\times 1000$. 6–7. Mexico, *Purpus 2928*. 6. Granulate spores with prominent laesurae. 7. Detail of spherical surface deposit, $\times 10,000$. 8. Proximal face left, and part of distal face right, Ecuador, *Holm-Nielson 547*. 9. Detail of slender strands below the spherical surface deposit, Guatemala, *Skutch 1861*, $\times 5000$.

The prominent, raised laesurae and spherical surface deposit most closely resemble that of *Odontosoria* spores. These similarities provide a connection between the tribes Dennstaedtieae and Lindseeae that otherwise have discrete kinds of spores.

Cytology

The report of $n = 100$ for *Lonchitis* from Jamaica was considered a tetraploid by Walker (1966). The record of $n = \text{ca. } 50$ for *L. occidentalis* (as *Anisosorus occidentalis*) from Ghana by Manton (1958) is consistent with this. The distinction between *Lonchitis* and *Blotiella* is reinforced by the meiotic chromosome reports of 38 and 76 in African species of *Blotiella*.

Literature

- Copeland, E. B. 1947. General Filicum. 247 pp. Chronica Botanica. Waltham, Mass.
- Lellinger, D. B. 1977. The identity of *Lonchitis aurita* and the generic names *Anisosorus* and *Lonchitis*. *Taxon* 26: 578–580.
- Manton, I. 1958. Chromosomes and fern phylogeny with special reference to "Pteridaceae." *Jour. Linn. Soc. Bot.* 56: 73–92.
- Walker, T. G. 1966. Reference under the family.

62. *Histiopteris*

Figs. 62.1–62.8

- Histiopteris* (Ag.) J. Sm., *Hist. Fil.* 294. 1875. *Pteris* section *Histiopteris* Ag., *Rec. Gen. Pterid.* 76. 1839. Type: *Pteris vespertilionis* Labill. (as *Histiopteris vespertilionis* (Labill.) J. Sm.) = *Histiopteris incisa* (Thunb.) J. Sm.
- Lepidocaulon* Copel., *Univ. Cal. Publ. Bot.* 8: 218. 1942. Type: *Lepidocaulon caudatum* Copel. = *Histiopteris caudata* (Copel.) Holtt.

Description

Terrestrial; stem long-creeping, slender to rather stout, bearing scales and sometimes also trichomes, or only trichomes, and long, fibrous roots; leaves monomorphic, ca. 50 cm to 3 m, rarely to 6 m or more long, borne at intervals, lamina 2- to 4-pinnate, glabrate, veins free to usually anastomosing without included free veinlets; sori marginal, the sporangia on a vascular commissure, sometimes around a sinus, paraphysate, the indusium well differentiated from the recurved margin; spores ellipsoidal, monolete, the laesura $\frac{1}{2}$ to $\frac{2}{3}$ the spore length, the surface tuberculate to rugose, usually less prominent near the laesura. Chromosome number: $n = 48, 96$.

The position and structure of the sorus in *Histiopteris* (Figs. 3, 5) resembles that of *Pteris* and the sometimes fully anastomosing veins (Fig. 6) are likewise similar to *Pteris*. The leaves are unusual in the development of stipule-like reduced pinnules (Fig. 4) especially at the base of large pinnae. These may also be formed at the base of pinnules. The lamina is usually glaucous beneath and glabrous or sometimes with a few large trichomes.



Fig. 62.1. *Histiopteris incisa*, near El Empalme, Costa Rica, (Photo W. H. Hodge.)

Fig. 62.2. Distribution of *Histiopteris incisa* in America.

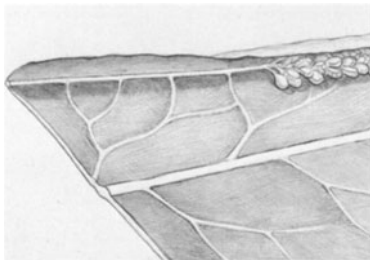


Fig. 62.3. Sorus of *Histiopteris incisa* with continuous commissure and marginal indusium, $\times 12$.

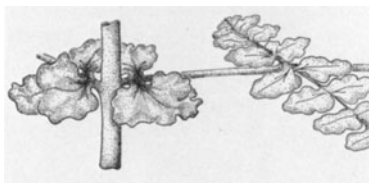
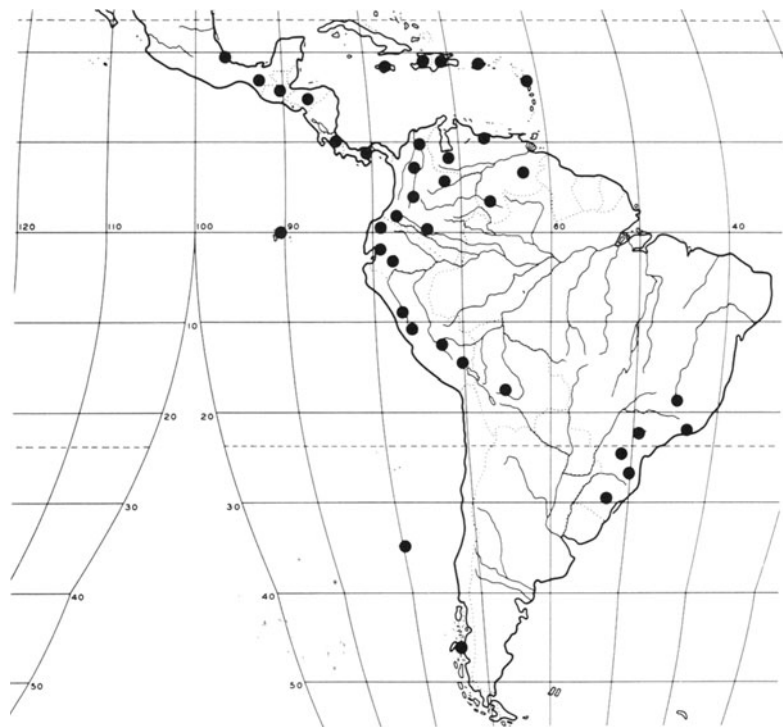
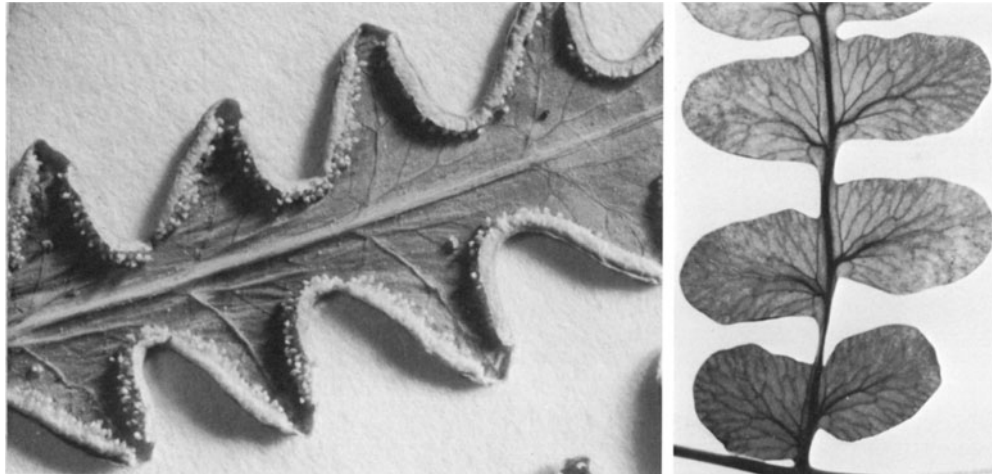


Fig. 62.4. Laminar stipules at base of pinna, $\times 0.5$.



5

6



Figs. 62.5, 62.6. *Histiopteris incisa*. 5. Fertile segments, $\times 5$. 6. Sterile pinnule with anastomosing veins, $\times 0.5$.

Systematics

Histiopteris is a pantropical and temperate genus of one or perhaps a few species. *Histiopteris incisa* (Thunb.) J. Sm. occurs throughout the range of the genus. Other species sometimes recognized in the paleotropics are: *Histiopteris caudata* (Copel.) Holtt., *H. estipulata* vAvR., *H. sinuata* (Brack.) J. Sm., and *H. stipulacea* (Hook.) Copel. Revisionary work on the group is necessary to confirm the status of these segregate species.

Ecology (Fig. 1)

Histiopteris is a genus of wet forests and especially occurs along the borders, in clearings and natural openings in forested areas.

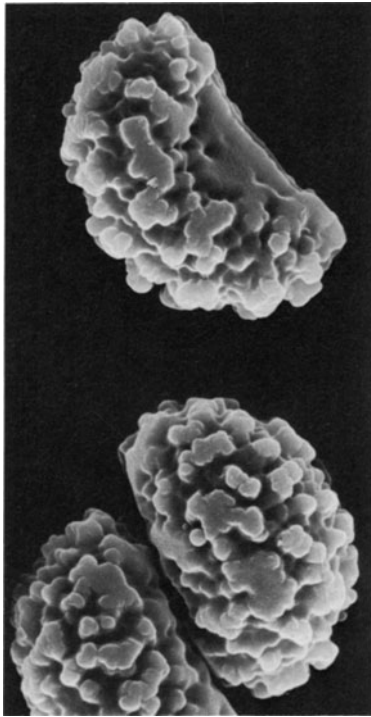
In tropical America it grows in montane forests, cloud forests, and higher páramillo thickets, in clearings of dense forests, open woodlands, and grassy places, it is less often on rocky slopes and rarely on cliffs. *Histiopteris* usually grows from 1500 to 3000 m, less often to 3600 m.

Geography (Fig. 2)

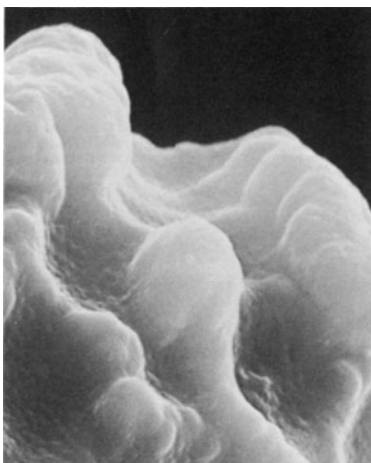
Histiopteris grows in tropical and south temperate America, in Africa and east to China and Australia, and in the Pacific to Tahiti and Rapa, north to Japan and south to Tasmania; it is also in the Auckland Islands.

In America, *Histiopteris* is distributed from Veracruz in Mexico, through Central America, in the Greater Antilles, except Cuba, and some of the Lesser Antilles (Guadeloupe, Dominica), and in South America from Venezuela and Colombia south to Bolivia; it is disjunct in southeastern Brazil, and in Aisén in Chile; also on the Galápagos and on the Juan Fernandez Islands.

7



8



Figs. 62.7, 62.8. *Histiopteris incisa* spores, Costa Rica, *Allen 623*. 7. Tuberculate the laesura, right, upper spore, $\times 1000$. 8. Detail of tuberculate surface, $\times 5000$.

Spores

The coarsely tuberculate, monolete spores of *Histiopteris* (Fig. 7) have a coalescent, papillate surface deposit (Fig. 8). The contours appear to be formed by a lower layer of the perispore, although Erdtman and Sorsa (1971) indicate that the perine is lacking. The tuberculate surface resembles that of the trilete spores in the American tropical species of *Dennstaedtia*. The monolete form of *Histiopteris* spores and the relatively high chromosome numbers in the American plants suggest the species represents a derived element among the dennstaedtioid ferns.

Cytology

Plants of *Histiopteris* are reported with $n = 96$ from Jamaica and there are tentative records probably representing this number from Tristan da Cunha, and for species of Ceylon and New Zealand. A record of $n = 48$ for plants of the Bonin Islands is reported and a base number of 48 or 24 suggested by Mitui (1973).

Literature

- Erdtman, G., and P. Sorsa. 1971. Pollen and Spore Morphology/Plant Taxonomy. 4. Pteridophyta. 302 pp. Almqvist & Wicksell, Stockholm.
 Mitui, K. 1973. A cytological survey on the Pteridophytes of the Bonin Islands. *Jour. Jap. Bot.* 48: 247–253.

16b. Tribe Lindsaeae

Lindsaeae Hook., *Sp. Fil.* 1: 202. 1846. Type: *Lindsaea* Sm.
 Lindsaeaceae Pic.-Ser., *Webbia* 24: 707. 1970. Type: *Lindsaea* Sm.

Three American genera, two of them also paleotropical, and *Xyopteris* Kramer and *Tapeinidium* (Presl) C. Chr. confined to the paleotropics.

This treatment of the genera of the tribe Lindsaeae is based on the work of Karl U. Kramer, and his review of our manuscript. In reference to indument there are two differences between the terminology used here and that in the work of Kramer. The uniseriate stem indument that is referred to as

scales in the work of Kramer is designated here as trichomes. The minute, usually 2- to 3-celled trichomes, often born on the receptacle, are considered as paraphyses by Kramer, while the sorus is considered as nonparaphysate here since similar 2- to 3-celled trichomes are also borne on other parts of the lamina.

63. *Odontosoria*

Figs. 63.1–63.18

Odontosoria Fée, Mém. Fam. Foug. 5 (Gen. Fil.): 325. 1852. Type: *Odontosoria uncinella* (Kze.) Fée (*Davallia uncinella* Kze.).

Stenoloma Fée, Mém. Fam. Foug. 5 (Gen. Fil.): 330. 1852. Type: *Stenoloma dumosa* (Sw.) Fée (*Davallia dumosa* Sw.) = *Odontosoria aculeata* (L.) J. Sm. (Internat. Code Bot. Nomencl. ed. 8, 220. 1956). [Incorrectly changed in ed. 9, 231. 1961 to *Stenoloma clavata* (L.) Fée = *Odontosoria clavata* (L.) J. Sm; see Kramer 1971, p. 179.].

Odontosoria (Presl) J. Sm., Hist. Fil. 263. 1875, not Fée, 1852. *Davallia* section *Odontosoria* Presl, Tent. Pterid. 129. 1836. Type: *Davallia tenuifolia* (Lam.) Sw. (*Odontosoria tenuifolia* (Lam.) J. Sm., *Adiantum tenuifolium* Lam.) = *Odontosoria chinensis* (L.) J. Sm.

Sphenomeris Maxon, Jour. Wash. Acad. Sci. 3: 144. 1913. Type: *Sphenomeris clavata* (L.) Maxon (*Adiantum clavatum* L.) = *Odontosoria clavata* (L.) J. Sm.

Description

Terrestrial or rupestral; stem short- to long-creeping, slender to rather stout, bearing scales that sometimes intergrade to trichomes, or (in *O. clavata*) often only trichomes, and few to many, long, fibrous roots; leaves monomorphic, ca. 20 cm to 6 m long, borne in a loose cluster or at intervals, lamina 2- to 5-pinnate, glabrous, veins free; sori marginal, 1-nerved or sometimes 2- to 8-nerved and then borne on a vascular commissure connecting the vein-ends, not paraphysate, covered by an abaxial indusium attached at the base and at least partly on the sides, the opposed margin not or slightly modified; spores usually spheroidal, trilete, the laesurae $\frac{2}{3}$ to $\frac{3}{4}$ the radius (usually broad and raised), or sometimes ellipsoidal, monolete with laesura $\frac{3}{4}$ the length (broad and raised), the surface granulate, with spherical deposit, or nearly smooth. Chromosome number: $n = 38, 39, 47, 48$, ca. 88, 94, ca. 96, 100, 145–147; $2n = 76$; apogamous 47, 48, 94.

The spines that are borne along the axes of most species (Fig. 6) are an unusual development in ferns. The terminal sori at the ends of single veins (Fig. 5) are characteristic of the genus, although in a few species two or more veins extend to the sorus (Fig. 9).

Systematics

Odontosoria is a pantropical and partly extratropical genus of about 20 species, with some 12 of them in America. The genus is related to *Lindsaea*, especially section *Schizoloma*.

Although *Sphenomeris* has been widely accepted as a genus since its recognition by Maxon, the difficulties of separating it from *Odontosoria* were pointed out by Kramer (1972) and since then he has expressed the opinion that a single genus should be recognized. The species with large leaves with periodic growth



Fig. 63.1. *Odontosoria gymnogrammoides*, Tapanti, Cartago, Costa Rica. (Photo W. H. Hodge.)

and dormancy of the apex and with spines represent a specialized element in the genus, but one that is not clearly distinguished from the species with smaller and normally expanded leaves.

The American species of *Odontosoria* were revised by Maxon (1913) and the ones previously placed in *Sphenomeris* by Kramer (1957).



Fig. 63.2. *Odontosoria clavata*, Retreat, St. Mary, Jamaica. (Photo W. H. Hodge.)

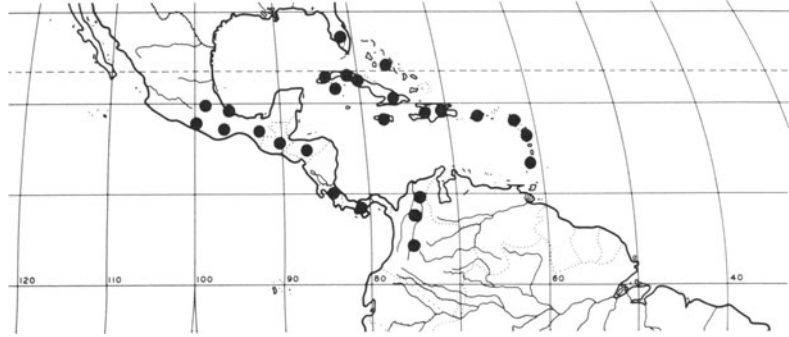
Tropical American Species

The revision of Maxon recognized 10 species. However, specimens collected since his study indicate that most of the characters used to distinguish the species, such as segment size and shape, and type and orientation of the spines are sometimes variable in a species and do not always correlate. Several of the species need a modern assessment employing new characters. *Odontosoria Wrightiana* Maxon (Fig. 7), for example, is surely only a narrow-segmented form of *O. aculeata*, and *O. fumarioides* of Jamaica needs to be more clearly distinguished from *O. gymnoqrammoides* of Costa Rica.

There are three species in Colombia: *O. colombiana*, *O. Killipii* (*Sphenomeris Killipii* (Maxon) Kramer), and *O. spathulata* (*Sphenomeris spathulata* (Maxon) Kramer). These are all very rare and poorly known and their status should be reassessed when adequate materials are available.

The following key has been adapted and simplified from Maxon (1913) and Kramer (1957).

Fig. 63.3. Distribution of *Odontosoria* in America.



Geographic-Morphological Key to American Species of *Odontosoria*

- a. Sori 2- to 4-nerved (Fig. 9) at least on the larger segments, stem mostly or wholly with trichomes. *O. clavata* (L.) J. Sm.
- a. Sori 1-nerved, stem with scales, sometimes intergrading to trichomes. b.
 - b. Mexico and Central America. c.
 - c. Leaves lacking spines on the axes. d.
 - d. Ultimate lobes long and narrow (Fig. 4), hardly broader than the alate axes to which they are attached; Mexico to Honduras. *O. Schlectendahlü* (Presl) C. Chr.
 - d. Ultimate lobes mostly rather short, many somewhat to rather deeply bifid, mostly broader than the alate axes to which they are attached; Guatemala. *O. guatemalensis* Christ.
 - c. Leaves with some of the axes spiny; Costa Rica and Panama. *O. gymnogrammoides* Christ.
 - b. Greater Antilles. e.
 - e. Axes with long often acicular, mostly spreading spines (Fig. 6). *O. aculeata* (L.) J. Sm.
 - e. Axes with stout, conical, mostly retrorse spines, these sometimes few. f.
 - f. Pinnæ with a few, elongate, 1-pinnate pinnules and an elongate conform terminal segment. *O. uncinella* (Kze.) Fée.
 - f. Pinnæ with many 2- to 3-pinnate pinnules, the apex more or less gradually reduced. g.
 - g. Ultimate segments deeply flabellate or bifid (Fig. 8), nearly all fertile lobes with one sorus. *O. fumaroides* (Sw.) J. Sm.
 - g. Ultimate segments mostly with shallow lobes, many fertile lobes with 2-3 sori. *O. Jenmaniü* Maxon.
 - b. Lesser Antilles. *O. flexuosa* (Spreng.) Maxon.
- b. Colombia. h.
 - h. Rachis spiny. *O. colombiana* Maxon.
 - h. Rachis lacking spines. i.
 - i. Ultimate segments spatulate. *O. spathulata* (Maxon) R. & A. Tryon.
 - i. Ultimate segments linear or slightly cuneate. *O. Killipii* (Maxon) R. & A. Tryon.

Ecology (Figs. 1, 2)

Odontosoria most commonly grows in regions of rain forests, montane forests, and cloud forests, but also in oak and pine woods. It especially grows in secondary vegetation, on brushy slopes, in thickets and clearings and in disturbed sites such as roadsides, landslips and sometimes in plantations. Rarely it grows in swampy places or on mossy rocks near streams or waterfalls. *Odontosoria clavata* (Figs. 2, 9-11) grows in limestone sinks and on limestone outcrops, especially in pinelands, also along streams and on river banks in shaded situations. It sometimes also grows on serpentine rocks. *Odontosoria* occurs from near sea level to ca. 2500 m, most commonly from 500 to 1500 m.

Many species of *Odontosoria* in America are thicket-forming ferns with long, scandent leaves scrambling on other vegetation. The pinnae are usually opposite and often flexuous, and the axes spiny; these characters appear to be adaptations for a scandent habit. In addition, the apical leaf-bud is dormant during the time that the last pair of pinnae expand, following which growth is resumed to produce another pair of pinnae. This periodic growth pattern of the leaf is probably also an adaptation that allows the pinnae to gain support from surrounding plants prior to further development of the leaf. The leaf of *Odontosoria* is often reported to be indeterminate, but a determinate apex is apparently eventually produced.

Geography (Fig. 3)

Odontosoria is distributed in tropical and subtropical America, in Africa, and eastward to southeastern Asia, Malesia, and through the Pacific to Rapa, Tahiti, the Marquesas and the Hawaiian Islands, and northward to Korea and Japan. It is notably absent from Australia and New Zealand.

In America it occurs from Puebla in Mexico, south to Panama, southern Florida and the Bahamas, in all of the Greater Antilles and some of the Lesser Antilles, and in Colombia.

Spores

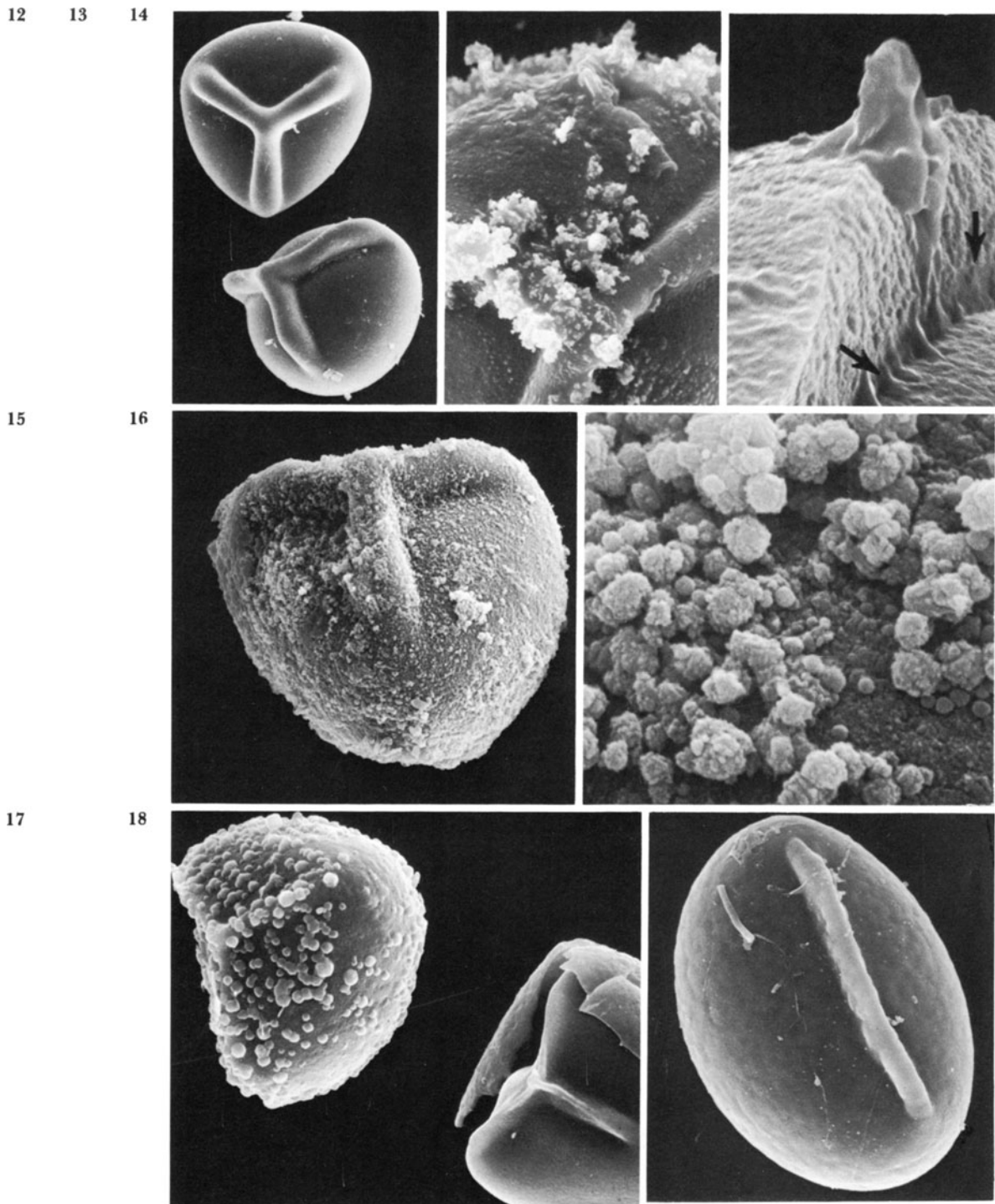
Odontosoria spores are generally larger than those of *Lindsaea* and the trilete spores of some species are the largest in the family. The surface may be relatively smooth as in the large spores of *O. guatemalensis* at half the usually magnification (Fig. 12) and also in the monolete spores of the Old World *O. chinensis* (L.) J. Sm. (Fig. 18). The granulate surface may be sparsely and irregularly deposited as in *O. aculeata* (Fig. 13) or denser as in *O. Killipii* (Figs. 15, 16) but without surface strands as in spores of *Lindsaea* or *Ormoloma*. The profile of a portion of the wall of *O. aculeata* (Fig. 14) shows two perispore strata consisting of a thick outer layer appressed to a thinner, somewhat denser lower one adjacent to the exospore. The spores of *O. clavata* (Fig. 17) differ from other species in having a somewhat rougher surface with coarse, spherical deposit.

Cytology

Records of $n = 38$ and $2n = 76$ for *Odontosoria clavata* (as *Sphenomeris*) from Jamaica (Walker, 1966) clearly document these numbers. A report of $n = 39$ from Florida (Wagner, 1963) may also represent 38. *Odontosoria fumarioides* and *O. Jenmanii* are reported with $n = \text{ca. } 96$ from Jamaica (Walker, 1966). There are records for several paleotropical species of numbers ranging between $n = 47$ and $n = 147$ that have been considered to be based on 47, 48 or 50. The discrete numbers of neotropical species as compared to those from the paleotropics suggests that more than one lineage may be included in *Odontosoria*.



Figs. 63.4–63.11. *Odontosoria*. 4. Segments of *O. Schlechtendahlü*, $\times 2$. 5. Ultimate segments of *O. fumaroides* with marginal sori, $\times 5$. 6. Spines on rachis of *O. aculeata*, $\times 8.5$. 7. Narrow segments of *O. aculeata* (the form described as *O. Wrightiana*), $\times 2$. 8. Segments of *O. fumaroides*, $\times 2$. 9. Fertile segments of *O. clavata*, $\times 4$. 10. Sterile segments of *O. clavata*, $\times 3$. 11. Portion of a leaf of *O. clavata*, $\times 0.75$.



Figs. 63.12–63.18. *Odontosoria* spores. **12.** *O. guatemalensis*, nearly smooth with raised laesurae, Guatemala, *Muenscher 12130* (F), $\times 500$. **13, 14.** *O. aculeata*. **13.** Detail of granulate proximal face, part of laesura, below, Dominican Republic, *Valeur 291*, $\times 1600$. **14.** Wall profile with thick outer and thinner inner perispore strata (arrow), the exospore below, right, Cuba, *Maxon 4131*, $\times 10,000$. **15, 16.** *O. Killipii*, Colombia *Killip 7947* (isotype). **15.** Proximal face, tilted, granulate, the laesurae at top, $\times 1000$. **16.** Detail of granulate surface, $\times 10,000$. **17.** *O. clavata*, spherical surface deposit on spore, at left, part of abraded spore with smooth exospore exposed, right, Nassau, Bahama Islands, *A. Wight 137*, $\times 1000$. **18.** *O. chinensis*, monolete spore, shallowly rugose, Hong Kong, *C. Wright* in 1853–56, $\times 1000$.

Literature

- Kramer, K. U. 1957. See reference under *Lindsaea*.
 Kramer, K. U. 1972. The Lindsaeoid ferns of the Old World, IX. Africa and its islands. Bull. Jard. Bot. Nat. Belg. 42:305–345.
 Maxon, W. R. 1913. Studies of tropical American ferns, 4. Contrib. U.S. Nat. Herb. 17: 133–179.
 Wagner, W. H. 1963. A biosystematic study of United States ferns. Preliminary abstract. Amer. Fern Jour. 53: 1–16.
 Walker, T. G. 1966. Reference under the family.

64. *Lindsaea*

Figs. 64.1–64.24

- Lindsaea* Sm. Mém. Acad. Turin 5: 413. 1793. Type: *Lindsaea trapeziformis* Dryand. = *Lindsaea lancea* (L.) Bedd.
Schizoloma Gaud., Ann. Sci. Nat. 3: 507. 1824. Type: *Schizoloma Billardieri* Gaud. = *Lindsaea ensifolia* Sw. *Lindsaea* subgenus *Schizoloma* (Gaud.) Hook. Sp. Fil. 1: 219. 1846. *Lindsaea* section *Schizoloma* (Gaud.) Kramer, Acta Bot. Neerland. 15: 571. 1967. [Subgenus *Lindsaea*].
Isoloma J. Sm., Jour. Bot. (Hook.) 3: 414. 1841. Type: *Isoloma divergens* (Hook. & Grev.) J. Sm. = *Lindsaea divergens* Hook. & Grev. [Subgenus *Lindsaea*].
Odontoloma J. Sm., *ibidem* 3: 415. 1841, not HBK., 1820 (Compositae). Type: *Odontoloma Boryana* (Presl) J. Sm. (*Davallia Boryana* Presl) = *Lindsaea repens* (Bory) Thwaites.
Synaphlebiium Hook., Gen. Fil. t. 101. 1842. Type: *Synaphlebiium recurvatum* Hook. = *Lindsaea cultrata* (Willd.) Sw. [Subgenus *Lindsaea*].
Davallia subgenus *Odontoloma* Hook., Sp. Fil. 1: 174. 1846. Type: the same as that of *Odontoloma* J. Sm. *Lindsaea* subgenus *Odontoloma* (Hook.) Kramer, Blumea 15: 561. 1968.
Lindsaenium Fée, Mém. Mus. Hist. Nat. Strassburg 4: 201. 1850. Type: (Fée, Mém. Fam. Foug. 5 (Gen. Fil.): 333. 1852.) *Lindsaenium rigidum* (Hook.) Fée (as *Lindsaynium*) = *Lindsaea rigida* Hook. [Subgenus *Odontoloma*].
Lindsaea section *Paralindsaea* Keys., Polypod. Cyath. Herb. Bung. 3, 21, 70. 1873. Type: *Lindsaea linearis* Sw. [Subgenus *Lindsaea*].
Sambirania Tard., Mém. Instit. Sci. Madagas. ser. B, 7: 34. 1956. Type: *Sambirania plicata* (Baker) Tard. = *Lindsaea plicata* Baker [Subgenus *Lindsaea*].
Humblotiella Tard., *ibidem* 7: 38. 1956. Type: *Humblotiella odontolabia* (Baker) Tard. (*Davallia odontolabia* Baker) = *Lindsaea odontolabia* (Baker) Kramer. [Subgenus *Odontoloma*].
Lindsaea section *Pseudosphenomeris* Kramer, Acta Bot. Neerland. 6: 165. 1957. Type: *Lindsaea bifida* (Kaulf.) Mett. (*Davallia bifida* Kaulf.) = section *Schizoloma*.
Lindsaea section *Crematomeris* Kramer, *ibidem* 171. 1957. Type: *Lindsaea pendula* Kl. [Subgenus *Lindsaea*].
Lindsaea section *Temmolindsaea* Kramer, *ibidem* 176. 1957. Type: *Lindsaea Klotzschiana* Ettingsh. [Subgenus *Lindsaea*].
Lindsaea section *Haplolindsaea* Kramer, *ibidem* 260. 1957. Type: *Lindsaea sagittata* (Aubl.) Dryand. (*Adiantum sagittatum* Aubl.) [Subgenus *Lindsaea*].
Lindsaea section *Tropidolindsaea* Kramer, *ibidem* 267. 1957. Type: *Lindsaea Seemannii* J. Sm. [Subgenus *Lindsaea*].

Description Terrestrial, rupestral or epiphytic; stem decumbent and very short-creeping, moderately stout to slender, or long-creeping and slender, bearing scales that usually intergrade to stiff trichomes, and usually many, long, fibrous roots; leaves monomorphic or (in *L. cubensis*) somewhat dimorphic (with the fertile larger and more erect), ca. 15–100 cm long, borne in a cluster or at intervals, lamina simple to ca. 4-pinnate, glabrous, veins free or sometimes anastomosing without included free veinlets; sori marginal, rarely 1-nerved, usually 2- to many-nerved and borne on a vascular commissure connecting the vein-ends, not paraphysate, covered by an abaxial indusium attached at the base and sometimes the sides, the opposed margin unmodified; spores usually trilete, spheroidal or 3-lobed, the laesurae $\frac{2}{3}$ to $\frac{3}{4}$ the radius, often broad and raised or sometimes ellipsoidal, monolete, and the laesura nearly as long as the spore, broad and raised, the surface often smooth or granulate or with curled strands. Chromosome number: $n = 34$, ca. 40, 42, 44, 44 or 45, 47, ca. 50, ca. 84, ca. 87, 88, ca. 100, ca. 150, ca. 153, 155, ca. 220; $2n =$ ca. 100, ca. 176; ? apogamous 47, 80, 94, ca. 130.

The sorus of *Lindsaea* is sometimes short laterally, as on narrow segments of species such as *L. bifida* (Fig. 3). More typically it extends along the upper and outer sides of a segment as in *L. guianensis* (Fig. 4). In species with long, entire pinnae or a simple lamina, the sorus extends along nearly all of the margin (Fig. 6). When the sorus is mature, the indusium becomes more or less bent backward (Fig. 5). The lamina architecture is diverse in *Lindsaea*, and a selection of the types among the American species is shown in Figs. 11–24. The minute trichomes, mentioned by Kramer (1957) as probably occurring on the leaves of all *Lindsaea* species, are too small to be recognized as pubescence.

Systematics *Lindsaea* is a pantropical and extratropical genus of about 150 species, with about 45 in America.

The genus is a complex one, with two subgenera and 23 sections (Kramer, 1971). This classification provides a basis for further detailed studies, especially of species relations and of the polyploid complexes that undoubtedly exist. Section *Schizoloma* is closest to *Odontosoria* and is probably the most primitive element in the genus.

Lindsaea has a series of lamina forms that often closely resemble some of those in *Adiantum*.

The American species of *Lindsaea* have been revised by Kramer (1957).

Synopsis of Subgenera of *Lindsaea*

Subgenus *Lindsaea*

Terrestrial or only casually epiphytic, stem short- to only moderately long-creeping, the stele radially symmetrical or nearly so.

A subgenus of 17 sections, seven of them America. The subgenus *Schizoloma* in Kramer (1957) was later altered to a section of subgenus *Lindsaea*.



Fig. 64.1. *Lindsaea portoricensis*, Mason River savannah, Jamaica. (Photo W. H. Hodge.)

Subgenus *Odontoloma*

Epiphytic, stem very long-creeping, the stele strongly dorsiventral. A subgenus of six sections, all paleotropical.

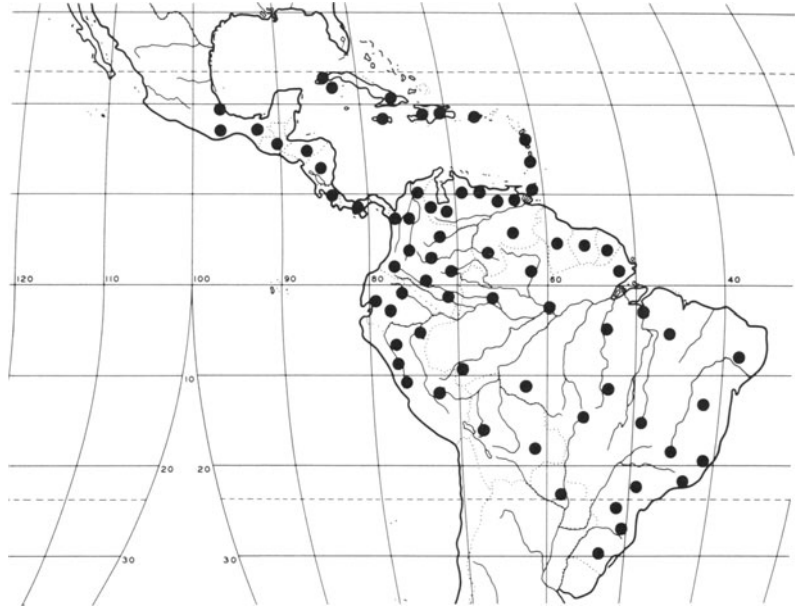
Tropical American Species

The following enumeration provides some of the characteristics of the American sections of subgenus *Lindsaea* and includes all or a selection of the species.

Section *Schizoloma*

Lamina usually gradually reduced apically and often decompose. It has about 40 species, with four of them American: *L. bifida* (Kaulf.) Kuhn (Fig. 11), *L. macrophylla* Kaulf., with a 1-pinnate lamina and some anastomosing veins, *L. sphenomeridopsis* Kramer, and *L. virescens* Sw. (Fig. 12).

Fig. 64.2. Distribution of *Lindsaea* in America.



Section *Crematomeris*

Twisted axes that result in pendulous segments. It has two species: *L. meifolia* (HBK.) Kuhn and *L. pendula* Kl. (Fig. 16), both American.

Section *Temnolindsaea*

2-pinnate lamina and incised pinnules. It has eight species, five of them American, including *L. Klotzschiana* Ettingsh., *L. tetraptera* Kramer, and *L. Parkeri* (Hook.) Kuhn. The three Old World species may not belong with the American ones.

Section *Lindsaea*

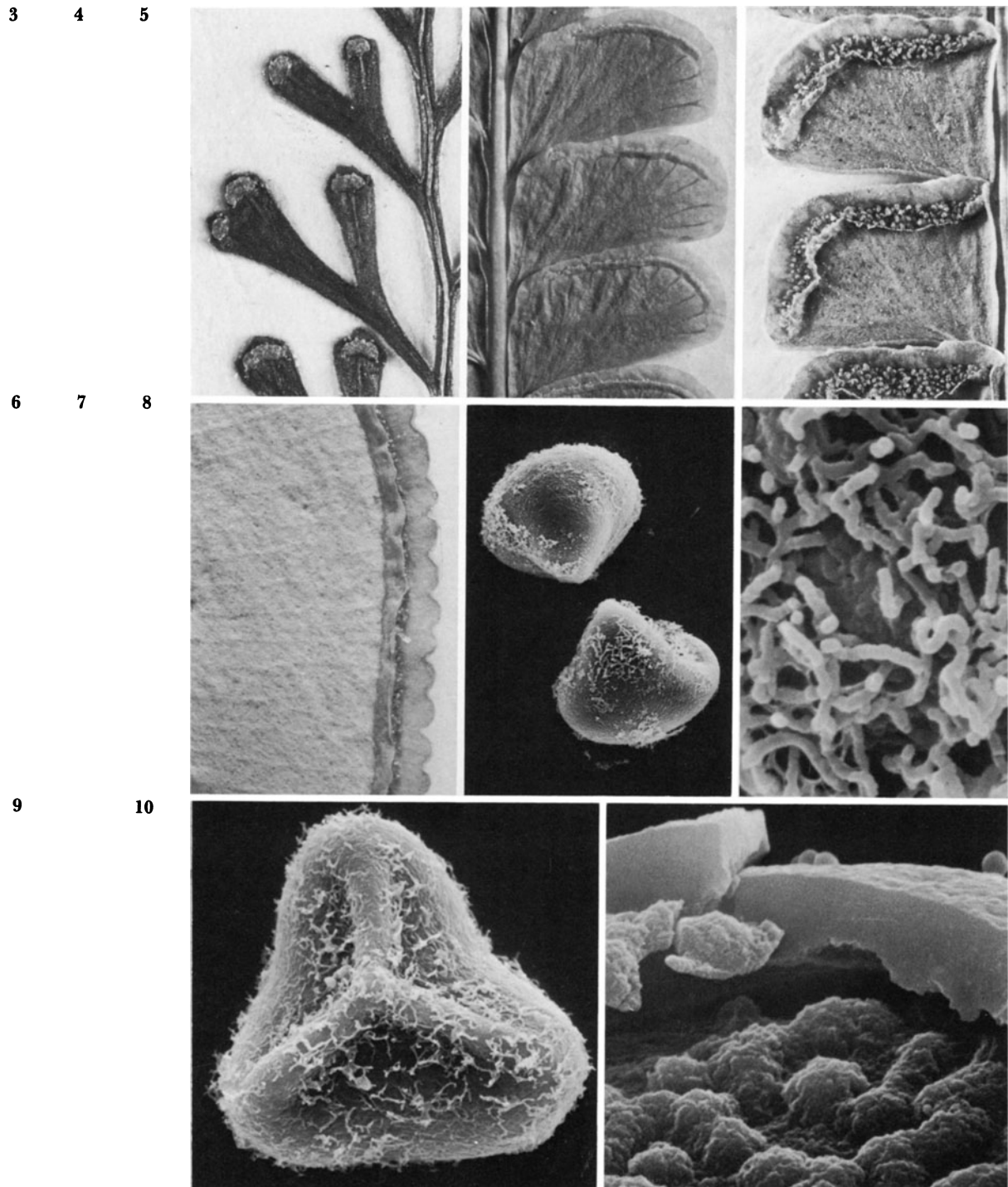
1- to 2-pinnate lamina and a conform terminal pinna-segment. It has 28 species, 26 of them American, including: *L. arcuata* Kze., *L. botrychioides* St.-Hil. (Fig. 14), *L. dubia* Spreng. (Fig. 13), *L. guianensis* (Aubl.) Dryand., *L. hemiglossa* Kramer (Fig. 21), *L. lancea* (L.) Bedd. (Figs. 17, 18), *L. portoricensis* Desv., *L. quadrangularis* Raddi, *L. Schomburghkii* Kl., *L. stricta* (Sw.) Dryand. (Figs. 19, 20), and *L. Ulei* Hieron. (Fig. 22). The two Old World species may not belong with those in America.

Section *Haplolindsaea*

Reniform, cordate or sagittate lamina. It has three species: *L. cyclophylla* Kramer, *L. reniformis* Dryand. (Fig. 23), and *L. sagittata* (Aubl.) Dryand. (Fig. 24), all American.

Section *Paralindsaea*

Small, somewhat dimorphic leaves. It has four species, with one of them, *L. cubensis* Underw. & Maxon (Fig. 15), American. This species is only doubtfully related to the Old World ones.



Figs. 64.3–64.10. *Lindsaea*. 3–6. Segments and sori. 3. Fertile ultimate segments of *L. bifida*, $\times 8$. 4. Fertile pinnules of *L. guianensis* with immature indusium, $\times 5$. 5. Fertile pinnules of *L. stricta* with mature sori and indusia, $\times 8$. 6. Portion of fertile lamina of *L. cyclophylla* with continuous sorus and indusium, $\times 5$. 7–10. Spores. 7. *L. guianensis*, lateral view of two young spores with fused strands, Brazil, *Dusén* in 1908, $\times 1000$. 8. *L. lancea* var. *lancea*, surface detail of strands, Dominican Republic, *Valeur 548*, $\times 10,000$. 9. *L. portoricensis* proximal face of young spore with sparse strands, Jamaica, *Gastony 77*, $\times 2000$. 10. *L. philippensis*, part of wall section with thick outer perispore, above, and tuberculate inner perispore, below, Philippines, *Elmer 12416*, $\times 10,000$.

Section *Tropidolindsaea*

1-pinnate lamina reduced both apically and basally. It has three species: *L. pratensis* Maxon, *L. protensa* C. Chr., and *L. Seemannii* J. Sm., all American. The Philippine *L. adiantoides* Hook. is probably closely related.

Ecology (Fig. 1)

Lindsaea is primarily a genus of moist or wet forests, but species also grow in grasslands, marshes, and open rocky places.

In America the genus grows in low rain forests, in montane and in elfin forests, sometimes in pine lands, in savannahs, in thickets and low scrub, and in shaded or exposed rocky sites. Sometimes it grows in clearings or on exposed clay road banks. The genus grows on a great variety of soil and rock types. Several species are sometimes low epiphytes on mossy tree trunks or branches but these (subgenus *Lindsaea*) are not adapted, as subgenus *Odontoloma* is, for a truly epiphytic habit. *Lindsaea* grows from near sea level up to about ca. 2300 m, most commonly below 1500 m.

Geography (Fig. 2)

Lindsaea occurs through the American tropics, in Africa and eastward to Malesia and southeastern Asia, north to Japan and south to Tasmania and New Zealand, it extends eastward in the Pacific to the Marquesas and the Hawaiian Islands.

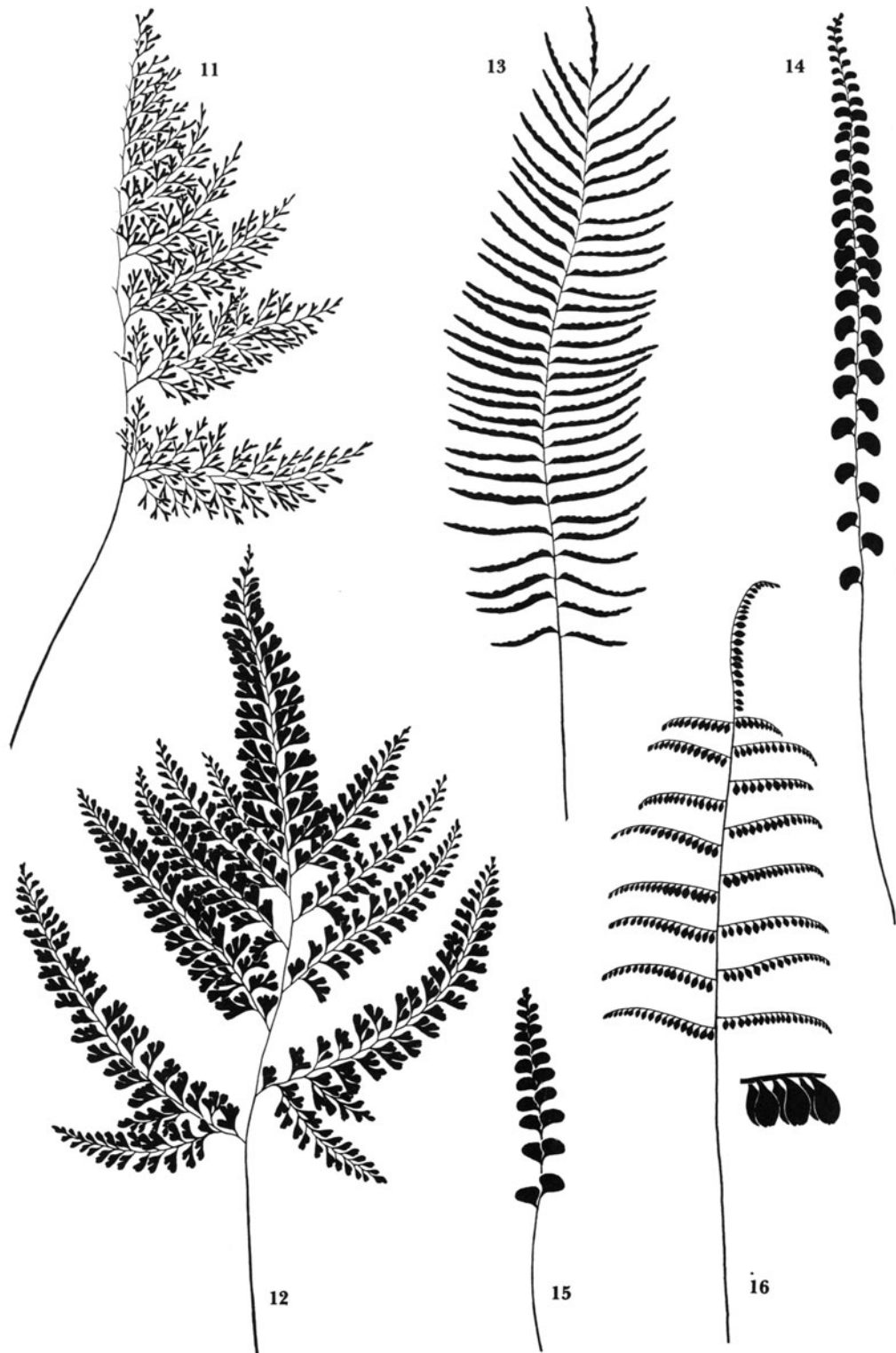
In American *Lindsaea* grows from Veracruz in Mexico, through Central America, in the West Indies, and generally through South America south to Bolivia, Paraguay and Rio Grande do Sul in Brazil.

A few species have ranges that extend nearly throughout that of the genus in America: *L. guianensis*, *L. portoricensis*, *L. stricta* and *L. lancea*. Most have moderate-sized ranges, but seven are local endemics: *L. pratensis* of Costa Rica; *L. stenomeris* Kramer of Cerro Neblina, Amazonas, Venezuela; *L. Spruceana* Kuhn of Mt. Guayrapurima, Tarapoto, Peru; *L. Herminieri* Fée of Guadeloupe, *L. taeniata* Kramer of Antioquia, Colombia; *L. cubensis* of Cuba and the Isle of Pines; and *L. protensa* of Hispaniola.

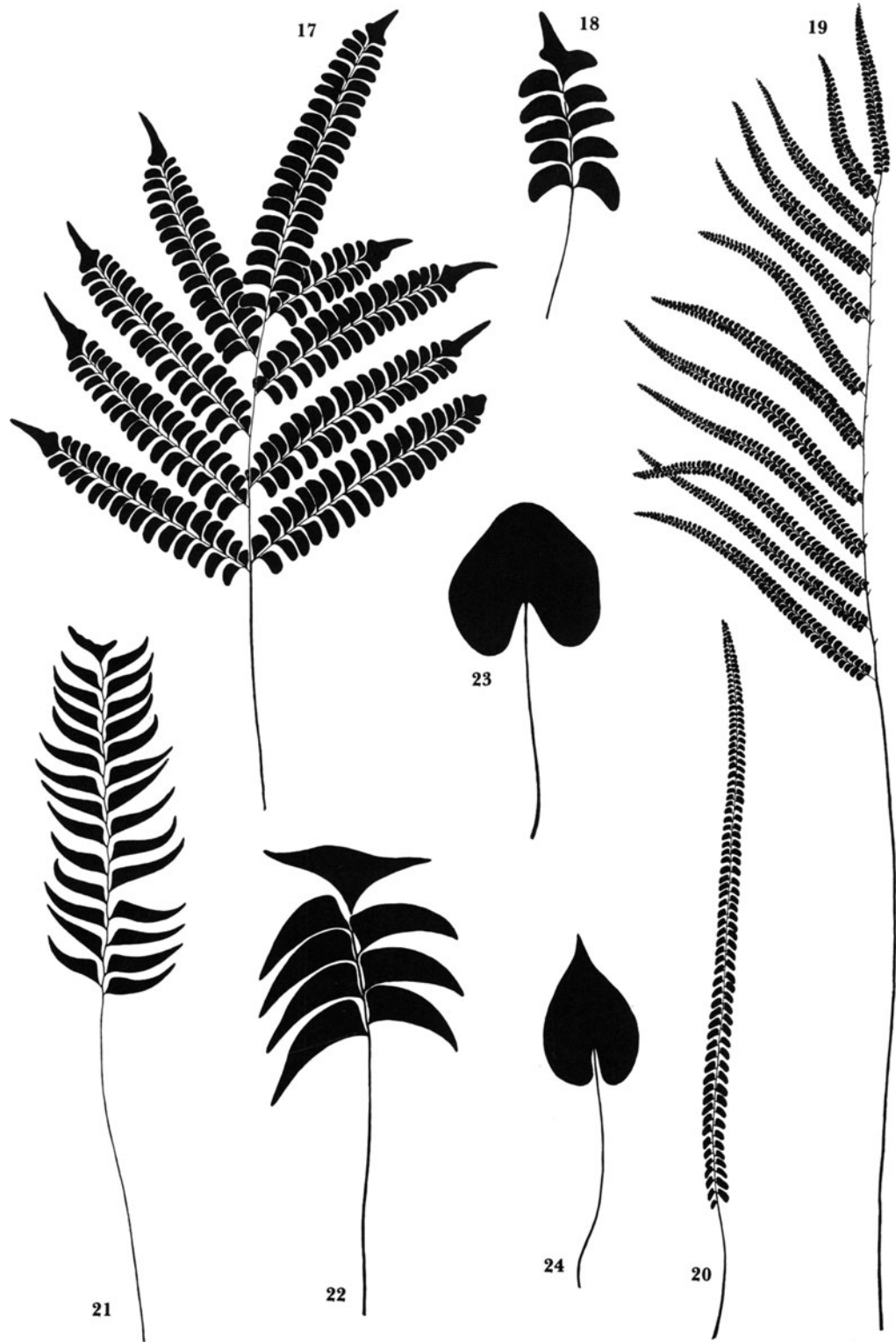
The center of diversity and endemism of *Lindsaea* is in the area of the Roraima sandstone formation in northern South America where 27 of the 45 species occur and 14 of them are endemic. Southeastern Brazil is a secondary center, with 13 species, three of them endemic, and also Panama and Andean Colombia with 12 species and one endemic. *Lindsaea* is one of three fern genera with a dominant geographic center in Guayana; the others are *Hymenophyllopsis* and *Pterozonium* which are endemic or nearly endemic to the region.

Spores

Lindsaea spores that have strands or dense granulate surface deposits are usually strongly lobed (Fig. 7) and have concave areas between the laesurae. Those with a nearly smooth surface are



Figs. 64.11–64.16. Lamina architecture of *Lindsaea*. 11. *L. bifida*, $\times 0.5$. 12. *L. virescens*, $\times 0.5$. 13. *L. dubia*, $\times 0.5$. 14. *L. botrychioides*, $\times 2.5$. 15. *L. cubensis*, fertile leaf, $\times 0.5$. 16. *L. pendula*, $\times 0.5$, detail enlarged.



Figs. 64.17–64.24. Lamina architecture of *Lindsaea*. 17. *L. lancea*, 2-pinnate form, var. *lancea*, $\times 0.25$. 18. *L. lancea* var. *falcata* (Dryand.) Ros., $\times 0.25$. 19. *L. stricta*, 2-pinnate form, $\times 0.25$. 20. *L. stricta*, 1-pinnate form, $\times 0.25$. 21. *L. hemiglossa*, $\times 0.25$. 22. *L. Ulei*, $\times 0.25$. 23. *L. reniformis*, $\times 0.25$. 24. *L. sagittata*, $\times 0.25$.

usually spheroidal or ellipsoidal. The surface strands (Figs. 8, 9) appear to be incorporated in the outer part of the wall as the spores develop. Although the surface structure of *Lindsaea* spores is relatively smooth the wall stratification is complex. A section of the wall of *Lindsaea philippensis* Kramer (Fig. 10) shows the thick, outer perispore layer is closely appressed to a lower thin, tuberculate perispore above the exospore. The lobed form of the spores and surface strands are similar to those of *Ormoloma*. The paleotropical genera *Tapeinidium* and *Xyopteris* have monolet spores with smooth, thick outer walls, prominent laesurae and generally resemble the ellipsoidal spores of *Lindsaea*.

Cytology

Species of *Lindsaea* from the American tropics are reported as $n = \text{ca. } 88$ from Jamaica (Walker, 1966); $2n = \text{ca. } 88$ II, from Chiapas, Mexico (Smith and Mickel, 1977), and $n = 42$, $n = \text{ca. } 84$ from Brazil (Tryon et al., 1975). The diverse numbers of *Lindsaea*, between $n = 34$ and 220 are assessed by Kramer (1971) and several approximate records are considered as equal to or derived from 44 to 47 or possibly 94. At least three discrete series of numbers involving 34, 44 and 47 are also evident in the arrangement made by Walker (1973) based on reports of species in six sections of the genus. The Old World species with monolet spores including *Lindsaea viridis* Colenso and *L. odorata* Roxb. have high numbers ranging from $n = 88$ to 220 that suggest they represent derived elements.

Literature

- Kramer, K. U. 1957. A revision of the genus *Lindsaea* in the New World with notes on allied genera. Acta Bot. Neerland. 6: 97–290.
 Kramer, K. U. 1971. *Lindsaea*-group. Fl. Malesiana 1:177–254. (This is the author's major paper, among six, on paleotropical *Lindsaea*.)
 Smith, A. R., and J. T. Mickel. 1977. Reference under the family.
 Tryon, A. F., H. P. Bautista, and I. Araujo. 1975. Chromosome studies of Brazilian ferns. Acta Amazonica 5: 35–43.
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 Walker, T. G. 1973. Reference under the family.

65. *Ormoloma*

Figs. 65.1–65.6

Ormoloma Maxon, Proc. Biol. Soc. Wash. 46: 143. 1933. Type: *Ormoloma Imrayanum* (Kze.) Maxon (*Saccoloma Imrayanum* Kze.).

Description

Terrestrial or casually epiphytic; stem rather long-creeping, slender, bearing scales and many, long, fibrous roots; leaves monomorphic, ca. 20–60 cm long, borne at intervals, lamina 1-pinnate, glabrous, veins free; sori marginal, 1-nerved, not paraphysate, covered by an abaxial indusium attached only at the base, the opposed margin unmodified; spores trilete, somewhat 3-lobed, the laesurae $\frac{2}{3}$ the radius, with slender, more or less coalescent strands. Chromosome number: $n = 42$.

Fig. 65.1. *Ormoloma Imrayanum*, Cloud forest, Monteverde, Costa Rica, (Photo L. D. Gómez.)



Ormoloma is a distinctive genus among the lindsaeoid ferns in having 1-nerved sori (Fig. 4) borne on nearly entire pinnae. These are not connected by a vascular commissure except occasionally where a vein branches very near the margin (Fig. 3).

Systematics

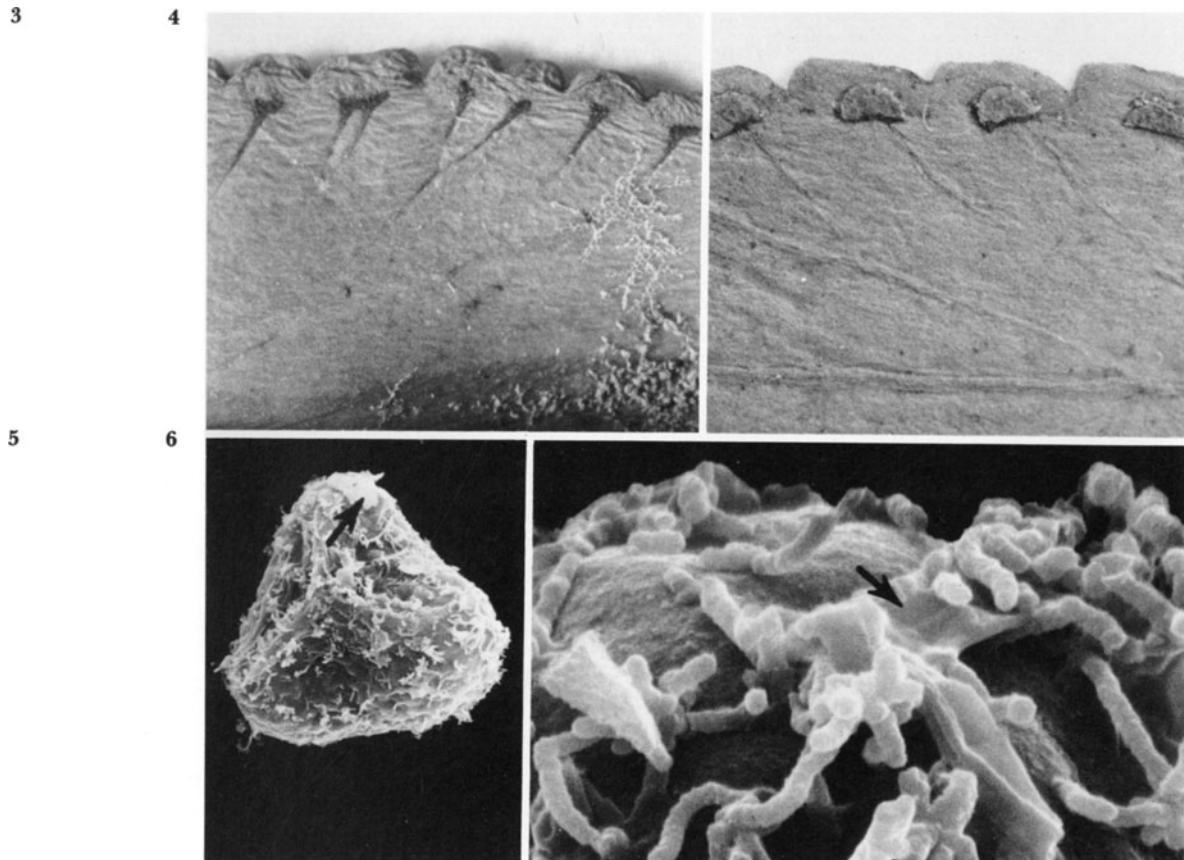
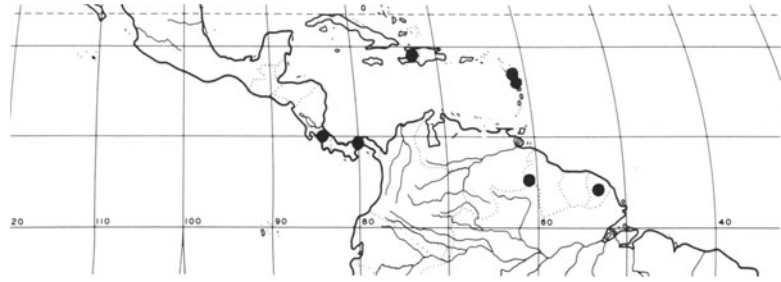
Ormoloma is a monotypic genus based on *O. Imrayanum* (Kze.) Maxon. While it is clearly related to *Lindsaea* its affinity to a particular group within the genus is uncertain.

Maxon (1933) described a second species, *Ormoloma Standleyi* of Costa Rica, on the basis of the color of the petiole, the shape of the stem scales, and size of the indusium, but later collections show that all of these characters are variable.

Ecology (Fig. 1)

Ormoloma grows in moist or wet forests, in deep shade or in somewhat open forests. It is terrestrial and also grows on old logs and tree stumps and rarely is a low epiphyte on mossy tree trunks. *Ormoloma* grows from ca. 750 to 1800 m.

Fig. 65.2. Distribution of *Ormoloma*.



Figs. 65.3–65.6. *Ormoloma Imrayanum*. **3.** Portion of a fertile pinna, adaxial side, with discrete fertile vein-ends, except where a vein has branched close to the margin, $\times 8$. **4.** Portion of a fertile pinna, abaxial side, $\times 8$. **5–6.** Spores. Dominica, *Lellinger 485*. **5.** Proximal face slightly tilted, with strands more or less coalescent in plates (at arrow), $\times 1000$. **6.** Detail of strands, coalescent at arrow, $\times 10,000$.

Geography (Fig. 2)

Ormoloma occurs in Haiti, Guadeloupe, and Dominica, in French Guiana and on Mount Roraima, and in Costa Rica and Panama.

Spores

The strands on the spores of *Ormoloma Imrayanum* appear to coalesce and form compact plates, at the arrow near the top of the whole spore in Fig. 5. This and other compact fragments suggest that the strands become incorporated into a denser surface. At

higher magnification (Fig. 6) the sparse strands are more or less fused and form a denser plate, at the arrow. The general form of the spores and especially the stranded elements composing the wall most closely resemble spores of *Lindsaea* species such as *L. lancea* (Fig. 64.8).

Cytology

The record of $n = 42$ for *Ormoloma* from Costa Rica (Wagner, 1980) is the same number as in some species of *Lindsaea* and is consistent with the close relationship of these genera as noted in the spores as well as other characters reviewed by Kramer (1957).

Literature

- Maxon, W. R. 1933. A second species of *Ormoloma*. Proc. Biol. Soc. Wash. 46: 157–158.
 Kramer, K. U. 1957. Reference under *Lindsaea*.
 Wagner, F. S. 1980. New basic chromosome numbers for genera of neotropical ferns. Amer. Jour. Bot. 67: 733–738.

Family 17. Thelypteridaceae

Thelypteridaceae Pic.-Ser., *Webbia* 24: 711. 1970. Type: *Thelypteris* Schmidel.

Description

Stem erect, decumbent or to very long-creeping, stout to slender, with a dictyostele, usually indurated, bearing scales; leaves ca. 10 cm to 5 m long, entire or usually pinnate, circinate in the bud, petiole without stipules; sporangia borne in roundish to elongate abaxial sori or rarely also on the leaf-tissue, indusiate, the indusium usually reniform, or exindusiate, mostly rather short-stalked, the stalk 2- to 3-rowed below its apex, the vertical annulus interrupted by the stalk; homosporous, spores lacking chlorophyll. Gametophyte epigeal, with chlorophyll, more or less obcordate, slightly thickened centrally, often with unicellular, rarely multicellular trichomes and (or) glands, archegonia borne on the lower surface, mostly in the central region, antheridia 3-celled, borne on the lower surface, mostly among the archegonia.

Comments on the Family

The Thelypteridaceae are essentially a worldwide family. The generic classification has been diverse, some authors recognizing a single genus *Thelypteris*, as we do, while others such as Iwatsuki (1964) recognize three genera, and some recognize many, for example, Pichi-Sermolli (1977) has 32 genera, and Holttum (1971) has 23 genera in the Old World. These ferns were formerly placed in the large genus *Dryopteris* and much of the literature concerning them uses that name.

The family is characterized by two vascular bundles at the base