A REVIEW OF THE GENUS DENNSTAEDTIA IN AMERICA

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Some twenty species of *Dennstaedtia* are currently recognized in the Americas; however, there has been no recent survey of them and several have not been adequately defined. The treatment of the genus by Maxon¹ is an excellent one but includes only four (two of his species I place together) of our ten tropical species. During preparation of an account of *Dennstaedtia* in Peru, it become apparent that to treat the genus adequately it would be necessary to consider all of the American species. I have found reasons to maintain only eleven of the species previously recognized; however, these conclusions are sometimes tentative, for a number of problems remain which must be studied in the field and with more adequate collections.

Most of the species of *Dennstaedtia* are of common occurrence and of these I have cited only a selection from the many specimens examined. I have not cited any specimens of the well known and distinctive *D. punctilobula*. A few species are rare and in their treatment I have cited all of the material I have seen. The specimens in the Gray Herbarium and the United States National Herbarium have formed the principal basis for this study. I am indebted to Conrad V. Morton for the loan of material and also to Bassett Maguire of the New York Botanical Garden for making certain specimens available for my study. Mr. Richard van Frank has taken the photographs.

I have considered all of the names that seemed pertinent to the nomenclature of the species and some others that are rather widely used in the literature or in the herbarium. I have not listed combinations made under segregates of *Dennstaedtia*, none of which is currently considered seriously: *Patania* Presl, *Sitolobium* Desv., *Adectum* Link and *Litolobium* Newm.

THE GENUS DENNSTAEDTIA

The definition of *Dennstaedtia* has, through the years, been increasingly clarified. Species were often originally described in such genera as *Polypodium*, *Dicksonia*, *Deparia* and *Microlepia*. Most of these have been transferred to

¹ Maxon, W. R. Pteridophyta in Sci. Surv. Porto Rico and the Virgin Islands, 6³: 491-494, 1926.

Dennstaedtia. The genus is particularly close to Microlepia and the relation of these two genera will be discussed. Other related genera, with hairs on the rhizome, are Oenotrichia and Leptolepia of the Old World; they seem distinct from Dennstaedtia but I have not especially considered them.

In relation to Microlepia, I have surveyed the species of it and of Dennstaedtia readily available to me, which included 12 American species, 54 Old World species and one pan-tropic one. On the basis of this study it is evident that the two genera are indeed closely related and evidently intergrade. However, of the 67 species studied, nearly all clearly belong in either one genus or the other, and the species that would tend to unite the genera are few. These major groups of species are each sufficiently homogeneous and distinct so that it does not seem a justifiable course, or a practical one, to unite them. I have assessed the genera and maintained them on the basis of their soral characters and a thorough revision of all species of Microlepia and Dennstaedtia may support this course. Such a study may indicate, however, that other and better characters exist and should be used either to unite the two genera or to maintain them.

In *Dennstaedtia* the sorus is marginal, the indusium being formed of an inner (true) indusium and an outer indusium which is the opposed leaf tissue, modified in form and texture; these are fully joined (connate) beyond the margin of the segment to form a reflexed saucer-, purse- or cupshaped, or globular or cylindrical whole indusium; or they are joined as far as the margin and extend separately beyond it to form a moderately to strongly bilabiate indusium.

The following species described in or sometimes transferred to other genera I would place in *Dennstaedtia*: *D. pilosella* (Hook.) Moore, *Microlepia stenoloba* Prantl, *Saccoloma Wercklei* Christ and *D. Wilfordii* Moore. The last species is not maintained in *Dennstaedtia* with any great confidence. It does not appear to be a *Microlepia* and, although perhaps rightly segregated as the genus *Coptidipteris* by Nakai & Momose, I would prefer to retain it in *Dennstaedtia* until its removal is suggested by a study of broad scope. The American *Saccoloma Wercklei* has recently been placed in *Microlepia* on the basis of several similarities with *Microlepia Hookeriana*. The generic (soral) characters presented here separate the two species and I am inclined to regard their similarities as due to convergent evolution. Each is a 1-pinnate species in a genus of species with decompound leaves and the sorus has perhaps been modified in each case by the alignment of adjacent sori along an entire margin, so that neither species has a sorus quite typical for its genus. Saccoloma Wercklei is closely related, in its pubescence, to several American species (nos. 7-10) and in its sorus especially to one of these, D. arborescens (Compare figs. 32 and 38). The indusium of M. Hookeriana shows a relation to the form sometimes present in M. pilosula where the edges of the indusium attached to the leaf tissue may be attenuated toward the margin of the segment.

In *Microlepia* the sorus is abaxial, borne well back of, or near, the margin of the segment, the indusium is fully attached (rarely only partially) to the leaf tissue along its sides, these sometimes approaching and rarely reaching the margin; it is usually half cup-shaped, with the sides and apex extended rather equally, or rarely the sides are attenuated well beyond the apex toward or to the margin.

I would place the following critical species in Microlepia: Dennstaedtia concinna Rosenst. (illegit.), Microlepia dennstaedtioides Copel., Microlepia melanorhachis Rosenst., and Dennstaedtia resinifera (Bl.) Mett. In Dennstaedtia concinna the sorus is rather close to the margin and only a moderate degree of modification of it and of the indusium would make it, by definition, a Dennstaedtia. In Microlepia jamaicensis and a species from New Caledonia (Rosenst. Fil. Nov. Caled. exsicc. 131) the sides of the indusium are only partially attached to the leaf tissue. If some of the species listed above are placed in the genus I suggest, nomenclatural changes are necessary. I am not willing to make these, without a greater familiarity with the species, except in the case of the single American one.

SPECIES IN DENNSTAEDTIA

The species of *Dennstaedtia* have been difficult to define. This difficulty, I believe, is due more to the fragmentary nature of most herbarium specimens than to an inherent lack of defining characters. Most, if not all, of the remaining problems exist where there is a lack of sufficient information. The leaves of *Dennstaedtia* are usually large and the specimens prepared from them commonly consist of such a part as may readily be accommodated on an herbarium sheet and they are not often accompanied by notes on the portion of the lamina represented or its shape. There is considerable uncertainty involved in relating these pieces to a whole lamina so that one may compare characters of comparable portions of the leaf. There are so few collections that provide data on the shape of the lamina that, although evidently an important character, it has not been possible to emphasize it. When a sufficient number of adequate specimens exists it will also be possible to know if specific characters are to be found in the petiole and rhizome. There may be differences between juvenile and adult leaves of the same species and there is a possibility that the juvenile type may persist in large leaves.

The key presents the species as less well defined than they actually are. A key that utilized lamina shape and characters of the basal pinnae more prominently would reflect the difference between the species to better advantage but would be impractical to use with most specimens. A major difficulty in the construction of the key, and one that will hardly fail to pass unnoticed by its users, is that of the characters available for a practical key some are variable and others, although constant, are not unique. The identification of a single fragment then often depends on a combination of its characters and will not always be either easy or perhaps possible.

GEOGRAPHY AND RELATIONSHIP OF THE SPECIES

The American species of *Dennstaedtia* have, with the exception of *D. punctilobula* and *D. Wercklei*, large and complex leaves. The lamina is frequently 1-1.5 (-2) m. long and the petiole is of similar length. The leaves are borne singly on an extensively creeping rhizome and the species often form large and conspicuous colonies. They grow predominantly in moist and usually shaded places. The tropical species are most frequent in forests but also grow along forest margins, or in clearings and other open habitats.

The most pronounced group within the American representatives of the genus is formed by species 7-11 which share the characters of enlarged sterile vein tips and a closely crispate, persistent pubescence on the under surface of the axes. Of these five species, *Dennstaedtia Sprucei* and *D. Wercklei* each have one or more unique characters. The former species is known only from Ecuador and Peru, the latter from Costa Rica, Colombia and Peru. The other three species of this group are more closely related and the problems of their definition are discussed under their treatments. All three are known to bear proliferous buds in the axils of the pinnae and are the only American species that have such buds. *D. arborescens* is distributed from Mexico to Panama, the Greater Antilles, and in the Andes south to Bolivia. D. dissecta has a similar range but is more widely distributed in northern South America and extends, in the south, to southern Brazil. D. obtusifolia is the most widely distributed of the three; its range is similar to that of D.dissecta except that it also occurs throughout the Lesser Antilles and is the only species of the genus in that area.

Dennstaedtia globulifera and D. bipinnata are evidently related, sharing a similar type of pubescence and decurrent herbaceous wings on the minor axes. Both species are distributed widely in tropical America, from Mexico to Panama, the Greater Antilles, northern South America to Bolivia. The former, D. globulifera, has a wider range in the south, extending to Argentina, Uruguay, and Brazil; while the latter, D. bipinnata, extends north to Florida.

The three species, *Dennstaedtia cicutaria*, *D. distenta* and *D. glauca* are not clearly closely related but do share characters of pubescence and of slender sterile vein tips. *D. cicutaria* is the most widely distributed of the three, growing from Mexico to Panama, the Greater Antilles, and in South America southward to Bolivia and southern Brazil. *D. distenta* has a relatively restricted range from Mexico to Panama; Jamaica and Hispaniola. *D. glauca*, the only species of Chile, also occurs from northwestern Argentina to southern Peru.

Dennstaedtia punctilobula, the only species of temperate to boreal regions, has no close relations with the other American species. Rather, it is related to certain species of eastern and southeastern Asia. It occurs in eastern and midwestern United States, north to Newfoundland. The gland-tipped trichomes on the lamina are distinctive among the American species.

The occurrence of six of the American species in Central America and Mexico and also in the Greater Antilles, but not the Lesser Antilles, lends emphasis to the well known floristic affinity between those two regions.

KEY TO THE SPECIES

- a. Axis of the penultimate segments, as in figs. 8, 9, lacking perpendicular herbaceous wings on the upper surface or perpendicular wings present but the one on the basiscopic side not decurrent onto the axis of the next order; trichomes on the under surface of the pinnules, when present, whitish to brownish and usually subopaque. b.
 - b. Sterile vein tips, on the upper surface, slender, as in fig. 17, not enlarged, ending well back of the glabrous margin; tertiary axes glabrous to sparsely or densely pubescent beneath with straight to tortuous, more or less spreading trichomes. c.
 - c. Trichomes on the under surface of the pinnules gland-tipped, or many of them so, fig. 2. 1. D. punctilobula.
 - c. Trichomes on the under surface of the pinnules not glandtipped, or absent.² d.
 - d. Pinnae alternate, the lower ones stalked, with the basal pinnules not or scarcely reduced, as in fig. 4. e.
 - e. Many or most of the sori borne in a sinus, fig. 5; pinnules more or less pubescent beneath, fig. 5; lamina deltoid. (Trichomes usually abundant on the under surface of the pinnules, some of them short, acicular, rigid, or rarely these absent and only larger, sometimes lax and subtortuous ones present; cells of the trichomes, except sometimes the lower ones, mostly several times longer than broad).
 - d. Pinnae opposite or rarely subopposite, the lower ones sessile, each with a pair of usually much reduced basal pinnules, fig. 6 (a detached pinna). (Major axes straw colored on the under surface; trichomes sparse, rarely absent, to usually rather abundant on the under surface of the pinnules, rather tortuous, their cells mostly about twice as long as broad, or shorter; lamina ovate to perhaps deltoid).3. D. distenta.
 - b. Sterile vein tips, on the upper surface, enlarged, as in fig. 30, clavate to punctate, or rarely (in *D. obtusifolia*) slender; tertiary axes glabrate to usually subappressed ascending pubescent beneath with the trichomes more or less curled. (Pinnae subopposite to alternate, the lower ones subsessile or less often short stalked). f.
 - f. Lamina pinnate-pinnatifid or more complex. (Basal pinnules of the lower pinnae more or less reduced, often strongly so, as in fig. 6, a detached pinna). g.
 - g. Sterile veins ending well back of the glabrous margin, as in fig. 30. h.

² Rarely, specimens of D, obtasifolia have slender sterile vein tips and are also glabrate: they may be separated from D, cicutaria by the subopposite, nearly sessile lower pinnae with reduced basal pinnules, from D, glauca by the sori borne predominantly in a since, from D, distenta by the major axes that are brownish beneath.

- h. Pinnules 1-pinnate to pinnate-pinnatifid, figs. 23, 25-28, apical segments of the pinna separate or nearly so to the prolonged apex, the separate ones closest to the tip obtuse; obtuse pinnules on the apical pinnae deeply pinnatifid; lamina deltoid. i.
- f. Lamina 1-pinnate, the pinnae entire, fig. 39. (Sterile veins ending well back of the glabrous margin) 11. D. Wercklei
- a. Axis of the penultimate segments bordered on each side, on the upper surface, by a pronounced herbaceous wing perpendicular to the plane of the segment, fig. 21, the wing on the basiscopic side decurrent onto the axis of the next order either as an herbaceous wing, fig. 22, or as a pronounced ridge; trichomes on the under surface of the pinnules wholly clear brown or tan, rarely subopaque or whitish. (Trichomes relatively straight and rather rigid, with all or many of their cells several times longer than broad; pinnae alternate, rarely subopposite, the lower stalked with the basal pinnules not or scarcely reduced, as in fig. 4; sterile vein tips, on the upper surface, slender, fig. 17, to rarely clavate, ending well back of the glabrous margin). j.

766-00125 1. Dennstaedtia punctilobula (Michx.) Moore, Ind. Fil. xcvii. 1857. FIGS. 1-2.

216-04070 Nephrodium punctilobulum Michx. Fl. Bor.- Am. 2: 268. 1803. Holotype: Canada, "Polypodium punctilobulum", Hb. Michaux, P. (D. C. Eaton, Can. Nat. 13: 28. 1870, comments on the identity of the type).

The gland-tipped trichomes on the lamina (Fig. 2) distinguish this species from all other American ones. It is related, rather, to certain species of eastern and southeastern Asia, especially to D. appendiculata, and D. scabra but also to D. pilosella and Microlepia stenoloba (this last species has not been transferred to Dennstaedtia).

The named forms, f. cristata, f. nana, f. Poyseri and f. schizophylla, are fully treated in Gray's Manual of Botany, ed. 8.

In the eastern portion of its range this species grows in a variety of habitats, especially in open pastures, in meadows, in woods, on rocky hillsides, streams banks and moist road banks; from Indiana westward it becomes restricted to sandstone cliffs.

Newfoundland southwestward through the southern parts of Ontario, Indiana and Illinois, to Iowa (US), Missouri and Arkansas, and southward to Georgia and Alabama (US).

I do not believe it is necessary to cite specimens of this well known and distinctive species.

266-01780 2. Dennstaedtia cicutaria (Sw.) Moore, Ind. Fil. xcvii.

1857. FIGS. 3-5.

- 14-ollob Dicksonia cicutaria Sw. Schrad. Jour. 18002: 91. 1801. Holotype: Jamaica, Swartz, S-PA, fragment and photographs US!.
- 266-06207 Dicksonia rubiginosa Kaulf., Enum. Fil. 226. 1824. Holotype: Rio de Janeiro, Brazil, Hb. Mertens.
- 56352 Dicksonia apiifolia var. dissecta Desv. Mém. Soc. Linn. Paris 6: 318. 1827. Holotype: none cited, presumably Brazil, Raddi.

500 -94355 Dicksonia angustidens Presl, Tent. Pterid. 136. 1836. Based, indirectly, on Dicksonia apiifolia var. dissecta Desv.

- 14-21357 Dicksonia umbrosa Liebm. Vid. Selsk. Skr. V, 1: 262 (reprint 101). 1849. Holotype: Colipa to Misantla, Mexico, March, Liebmann, C; isotype, US!.
- 145-dilel Dennstaedtia rubiginosa (Kaulf.) Moore, Ind. Fil. xcvii. 1857.

166-01755 Dicksonia decomposita Christ, Bull. Soc. Bot. Belg. 35: 180. 1896. Holotype: Costa Rica, Tonduz 8644, P; isotype, "Tonduz in Pittier 8644", US !.



PLATE 1. Dennstaedtia punctilobula: Fig. 1, central portion of a lamina, \times $\frac{1}{2}$. Massachusetts, Stevens in 1892; Fig. 2, sori, \times 10, Quebec, Marie-Victorin 20734. Dennstaedtia cicutaria: Fig. 3, central portion of a pinna, \times $\frac{1}{2}$. Haiti, Leonard 4956; Fig. 4, basal portion of a pinna, \times $\frac{1}{2}$. Panama, Mazon 4967.

266-07796 Dennstaedtia decomposita (Christ) Christ, Bull. Herb. Boiss. II, 5: 732. 1905.

> Dennstaedtia cicutaria is apparently most closely related to D. distenta and D. glauca. It may be distinguished from the first, D. distenta, by its alternate rather than opposite or subopposite pinnae, by its stalked, rather than sessile, lower pinnae each bearing a basal pair of little or scarcely reduced pinnules, rather than strongly reduced ones. In addition, the major axes of D. cicutaria are usually brownish while those of D. distenta are usually straw colored. The pubescence is also different; the cells of the trichomes of D. cicutaria are mostly several times as long as broad (except sometimes the lower ones) while those of D. distenta are mostly about twice as long as broad. The differences from D. glauca are discussed under that species.

> The pubescence of *D. cicutaria* is usually dimorphic and the presence of short, one-celled, acicular trichomes is characteristic. However, sometimes these are absent and only the larger, multicellular trichomes are present.

> I have not been able to maintain D. rubiginosa although it has traditionally been recognized as a species. The only difference between it and D. cicutaria that I have found is in the distribution and abundance of the trichomes on the under surface of the pinnules. In D. rubiginosa they are only on the axes and veins while in D. cicutaria (sens. str.) they are also on the leaf tissue. This is correlated to a certain degree with the abundance of trichomes. The more pubescent specimens have them on the leaf tissue and the less pubescent (or glabrate) ones have them only on the axes or also on the veins. However, the correlation between abundance and distribution is only a general one and there is a complete gradation from one extreme to the other. These characters do not seem to be important ones, especially since other species of Dennstaedtia, for example D. distenta, exhibit a similar variation in extent and abundance of trichomes. The two extremes do not have distinct ranges and they are often collected in the same local area. Local field studies are needed to determine if D. rubiginosa and D. cicutaria (sens. str.) may be correlated with differences in habitat.

> Wet forests, river and stream banks, moist wooded hillsides and open places, borders of forest, clearings and moist thickets, 100-2600 m.

> Central Mexico to Panama; Greater Antilles; Venezuela and Colombia to Bolivia and southern Brazil.



PLATE 2. Dennstaedtia cicutaria: Fig. 5, sori, \times 10, Mexico. Conzatti & Gonzales 573. Dennstaedtia distenta: Fig. 6, basal portion of a lower pinna (detached). \times 1/2. Mexico. Pringle 10253; Fig. 7, upper pinnae. \times 1/2. Jamaica. Maxon 9913; Fig. 8, base of penultimate segments and base of pinnules (upper surface). \times 5, Mexico. Pringle 10253; Fig. 9, base of penultimate segments and base of pinnule. \times 5, Mexico. Copeland 69.

Representative specimens: Mexico: SAN LUIS POTOSÍ: Pringle 3824 (GH, US). VERACRUZ: Conzatti & Gonzales 573 (GH, US); Copeland 70 (GH, US); Fink 9 (GH, US); Purpus 2936 (GH, US); Seaton 463 (GH, US); C. L. Smith 2222 (GH). MICHOACAN: Hinton 16254 (US). OAXA-CA: Conzatti 3164 (US); Makrinius 488 (US). CHIAPAS: Ghiesbreght 367 (GH); Purpus 7228 (US). Guatemala: J. D. Smith 1542 (GH), 2426; (GH, US); Steyermark 51849 (US), 51849a (GH); Türckheim II 1328 (GH). British Honduras: Schipp S-802 (GH). Honduras: Ames 143 (US); Yuncker 4592 (US). Nicaragua: C. F. Baker 2469 (GH, US); Maxon et al. 7530 (GH, US). Costa Rica: Holm & Iltis 884 (US); Pittier 7729 (US); Scamman 5893, 7022, 7023, 7611, 7612 (GH); Tonduz 8631 (GH, US). Panama: Maxon 4967 (GH, US). Cuba: Britton & Wilson 5250 (GH, US); Caldwell & Baker 7110 (GH, US); Ekman 4355, 16633 (US); Morton & Acuna 3633 (GH, US); Shafer 533 (GH, US); Wright 3946 (GH, US). Jamaica: Clute 227 (US); Howard & Proctor 15074 (GH); Maxon 8801, 8975, 10044, 10292, 10374, 10431 (GH, US); Maxon & Killip 408, 1254, 1486 (GH, US); Orcutt 6243 (GH); Proctor 4151 (US); Wilson & Webster 504 (GH). Hispaniola. HAITI: Ekman H2094, H7176 (US), H8591 (GH, US); Eyerdam 453, 454 (GH); Leonard 4956, 8092, 9259 (GH, US); Leonard & Leonard 13742, 14522 (GH, US). DOMINICAN REPUBLIC: Ekman H3194 (US), H11803 (GH, US); Fuertes 1516 (GH, US). Porto Rico: Britton et al. 4526 (GH, US), 6451 (US); Heller & Heller 921 (US); Sintenis 2711 (GH, US). Venezuela: Chardon 183 (US); Fendler 58 (GH). Colombia: Barkley & Gutiérrez 1902 (GH); Karsten 17 (US); Killip 7849 (GH, US); Killip & Smith 17000, 18855, 19030 (GH, US); Pennell et al. 8605 (GH, US); H. H. Smith 1070 (GH, US). Ecuador: Eggers 14355 (US); Haught 3094 (GH, US); Rimbach 32 (GH, US); Sydow 656 (US). Peru: Killip & Smith 22440, 23072, 23699 (GH, US); Klug 3553 (GH, US); Mexia 6128, 8218 (GH, US); Spruce 4338 (GH); Tryon & Tryon 5372 (BM, F, GH, U, US, USM). Bolivia: Buchtien 3379 (GH, US), 3607 (US); Cárdenas 859 (GH, US). Brazil. SANTA CATHARINA: Haerchen (Ros. exsicc. 173) (US). PARANÁ: Dusén 15288 (GH). SAO PAULO: Luederwaldt 21350 (GH). RIO DE JANE-IRO: Claussen 121 (US). MINAS GERAES: Claussen 2114 (US); Mexia 4846, 4866 (GH, US). BAHIA: Blanchet 305 (GH).

3. Dennstaedtia distenta (Kze.) Moore, Ind. Fil. 306. 1861. FIG. 6-10.

246-07/38 Dicksonia distenta Kze. Analect. Pterid. 39. 1837. Holotype: Jalapa, Mexico, May, 1829, Schiede; isotype, NY!.

 244-21090 Dicksonia antillensis Jenm. Jour. Bot. 24: 267. 1886. Holotype: Jamaica, Morris. (I have accepted Jamaican specimens collected and identified by Jenman, NY!, as authentic).
 244-21399 Dennstaedtia antillensis (Jenm.) C. Chr. Ind. Fil. 216. 1905.

> "Dennstaedtia mexicana Rosenst." has never been properly published but has been used by some authors, for example, Matuda, Anal. Instit. Biol. México 27: 66. 1956. See note by Morton, Am. Fern Jour. 48: 124. 1958.

266-07137

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PLATE 3. Dennstaedtia distenta: Fig. 10. sori, × 10. Mexico, Mexia 9085. Dennstaedtia glauca: Fig. 11, central portion of a large pinna, × ½, Argentina, Lillo 2658; Fig. 12, central portion of a pinna, × ½, Chile, Morrison 17076; Fig. 13, sori, × 5. Argentina, Schreiter 5783.

Dennstaedtia distenta is evidently most closely related to the previous species, D. cicutaria, and the principal differences are discussed under that treatment. Especially in specimens that are abundantly publication on the under surface of the pinnules, there are both short and long trichomes and some of intermediate length. The major axes are usually straw colored beneath and in this character the species shows a relation to the following, D. glauca.

The material from Jamaica, Fig. 7, and Hispaniola previously considered to be a distinct species is a glabrate form with narrow lobes. These characters occur in a few specimens from Mexico and Central America although most of the continental material is publicated and has broader lobes. Since several of the other species have, within the range of D. distenta, a similar distribution — Mexico and Central America and the Greater Antilles — it does not seem justifiable to recognize D. antillensis unless definite differences between it and D. distenta can be established.

Banks of streams and brooks, and other wet places, or in wet woods; 100-2500 m. usually above 1000 m. in Mexico, elsewhere confined to mountains, 1200-2850 m.

Western and central Mexico to Panama; Jamaica and Hispaniola.

Representative specimens: Mexico: CHIHUAHUA: LeSueur 1132 (GH, US). SONORA: Gentry 1395 (GH, US). DURANGO: Sanchez 736 (US). SINALOA: Gentry 7300 (GH, US). SAN LUIS POTOSÍ: Cottam 10462 (US). VERACRUZ: Bourgeau 2343, 2605 (GH, US); Copeland 69 (GH, US). HIDALGO: March 21, 1938, Copeland (GH). MÉXICO: Hinton 3637 (GH), 3776, 4046 (US), 7372 (GH, US). MICHOACÁN: Arsène 6044, 6098 (GH, US). GUERRERO: Hinton 14046 (GH, US), 14187 (GH); Mexia 9085 (GH, US). OAXACA: Conzatti 2232 (GH); Pringle 10253 (GH, US). CHIAPAS: Little & Sharp 9877 (US); Purpus 9196 (GH, US). Guatemala: Skutch 741 (US); J. D. Smith 1542 (US); Standley 67466, 85831, 85852 (US); Steyermark 42386 (GH, US); Türckheim II 2196 (US). Salvador: Tucker 726 (US). Costa Rica: Chrysler 5473 (US); Standley & Valerio 49449 (GH, US). Panama: Killip 5175 (US). Jamaica: Maxon 9913 (GH, US), 9914 (US); Sherring (US). Hispaniola. HAITI: Ekman H7980 (US).

344-05505 4. Dennstaedtia glauca (Cav.) C. Chr. ex Looser, Rev. Hist. Geog. Chile 69: 184. 1932. FIG. 11-13.

246-062°) Davallia glauca Cav. Descr. Pl. 278. 1802. Holotype: Cordillera de Planchon, Chile, Neé, MA. (Looser, loc. cit., and C. Chr. Dansk. Bot. Ark. 9³:28. 1937, discuss the identity of the type).

216- 0(2/o Dicksonia Lambertiana Remy, Gay Fl. Chil. 6: 523. 1853. Holotype: Chile, Hb. Bonpland, P. Dennstaedtia Lambertiana (Remy) Christ, Farnkr. 312. 1897.

Dennstaedtia glauca is the only species of the genus in Chile. In adjacent countries where *D. cicutaria* also occurs, the two species may be separated by the following characters. The under surface of the pinnules of *D. glauca* is glabrous or nearly so, the sori are borne predominantly on lobes and the lamina is ovate- to deltoid-lanceolate. The under surface of the pinnules of *D. cicutaria* is pubescent (rarely glabrate), the sori are borne predominantly in sinuses and the lamina is deltoid. The major axes of *D. glauca* are usually straw colored while those of *D. cicutaria* are usually brownish.

In canyons, ravines, stream borders and other locally wet places, 700-3200 m.

Chile, northeast to adjacent Argentina, north to Bolivia and southern Peru.

Representative specimens: Peru: Herrera 279 (GH, US); Vargas 2320 (US). Bolivia: Cárdenas 153 (GH). Argentina. TUCUMÁN: Lillo 1491, 2658 (GH); Schreiter 4351, 5783 (GH); Venturi 4204 (GH). CAT-AMARCA: Castillon 1474 (GH). LA RIOJA: Jan. 25, 1928, Castellanos (GH). Chile: Looser 346 (GH, US), 637 (GH); Mexia 7872 (GH, US); Morrison 17076 (GH, US).

266- 02 98/ 5. Dennstaedtia globulifera (Poir.) Hieron. Bot. Jahrb.

34: 455. 1904. FIGS. 14-16.

266- 6625/ Polypodium globuliferum Poir. Lam. Encycl. 5: 554. 1804. Holotype: Santo Domingo, Plumier, Fil. t. 30.

- 246-16532 Dicksonia altissima Sm. Rees Encycl. 11. 1808. Based on Polypodium globuliferum Poir.
- 244-75533 Dicksonia punctulata Poir. Lam. Encycl. Suppl. 2: 475. 1811. Holotype: Hb. Desfontaines, P.
- Rio de Janeiro, Brazil.
- 26-65253 Dicksonia exaltata Kze. Bot. Zeit. 8: 59. 1850. Holotype: Plumier, Fil. t. 30.
- 266- 66256 Dennstaedtia tenera (Presl) Mett. Ann. Sci. Nat. V, 2: 261, 1864.

246-14539 Dicksonia Lagerheimii Sod. Crypt. Vasc. Quit. 50. 1893. Holotype: Volcán El Corazón, 2000-2800 m., Ecuador, Sodiro; isotype or authentic specimen, NY! US (fragment)!

- 378, 1898.
- 266-66257 Dennstaedtia exaltata (Kze.) Hieron. Bot. Jahrb. 34: 454. 1904.
- 246-16535 Dennstaedtia Lagerheimii (Sod.) C. Chr. Ind. Fil. 217. 1905.

⁵³⁵⁶ Dennstaedtia Tamandarei Rosenst. Hedwigia 56: 359. 1915. Syntypes: Brazil, Legru in 1913; Brazil, Tamandaré 5421. Rosenst. Fil. Bras. exsicc. marked "n. sp. original", "Tamand" & Brade 5421, NY !.

244-AS32 Dennstaedtia Bradeorum Rosenst. Repert. Sp. Nov. 22: 3. 1925. Holotype: Costa Rica, Brade 634; isotype, NY!, US!.

> Dennstaedtia globulifera is closely related to the next species, D. bipinnata, in the characters mentioned in the key. Of these, perhaps the most important is the character of the perpendicular herbaceous wings that border the axes of the penultimate segments and are decurrent onto the next axis. The differences between the two are discussed under D. bipinnata.

> The distinctive characters of the basal segments of the pinnules (nearly opposite, rather equal is size and the inferior not or slightly ascending) may be developed only in certain portions of the lamina. They are present in the central portion of basal pinnae and progessively more basal portions of the pinnae above. In the apical pinnae, where the pinnules are not large enough to have basal segments, the same characters are developed in the basal pinnules. The apical portions of the pinnae and the basal portions of the lower pinnae may have the basal segments of the pinnules similar to those in *D. bipinnata*.

> Wet forests, moist shaded hillsides, forest borders, stream banks, canyons, and ravines, 200-2300 m.

Eastern and central Mexico to Panama; Greater Antilles; Venezuela and Colombia south to Bolivia, Argentina, Uruguay and southern Brazil.

Representative specimens: Mexico. TAMAULIPAS: Sharp 5077 (US). SAN LUIS POTOSÍ: Pringle 3824 (GH, US). VERACRUZ: Bourgeau 1941, 2342 (GH, US); Conzatti & Gonzales 613 (GH, US); Copeland 72 (GH, US); Fink 14, 140 (GH, US); Purpus 6192 (GH, US); Spence 64 (GH). HIDALGO: Nov. 27, 1937, Kenoyer (GH): Kenoyer & Crum 4108 (GH). MORELOS: Lyonnet 2801 (US); Rose & Painter 6879 (GH, US). Guatemala: Skutch 973 (GH); J. D. Smith 2709 (GH, US); Standley 58877, 78350, 81027 (US); Türckheim II 1328 (US). Honduras: Williams & Molina 14486 (GH); Yuncker et al. 6216 (GH, US). Nicaragua: Grant 982 (US); Standley 8753 (GH, US). Costa Rica: Brade 634 (NY, US); Haupt 42 (GH, US); Scamman & Holdridge 7896 (GH); Standley 43336 (US). Panama: Killip 5252, 5487 (US); Maxon 4969, 5725 (GH, US). Cuba: Clément 1185 (US); Ekman 14359 (US); Howard 5198 (GH, US); Jack 7037 (US), 7272, 7937 (GH, US). Jamaica: Webster & Goldberg 20 (US), 23 (GH, US), 92 (US). Hispaniola. HAITI: Ekman H3117, H5598 (US); Holdridge 1981 (US); Leonard 3768, 4026 (GH, US). DOMINICAN REPUBLIC: Ekman H11634, H11778 (US); Miller 1222 (US); Türckheim 3075 (GH, US). Porto Rico: Hioram 256 (US). Venezuela:



PLATE 4. Dennstaedtia globulifera: Fig. 14. basal portion of a central pinna, \times 1/2. Colombia, H. H. Smith 1118; Fig. 15. central portion of a pinna, \times 1/2. Argentina, Rodriguez 1033; Fig. 16, sori, \times 5, Cuba, Howard 5198. Dennstaedtia bipinnata: Fig. 17. a sterile pinnule (upper surface), \times 8, Jamaica, Hunnewell & Griscom in 1936.

Linden 140 (GH). Colombia: Holton 70 (GH); Killip & Smith 19111 (GH, US); H. H. Smith 1118 (GH, US); Triana 48 (US). Ecuador: Camp E-3462 (GH, US); GALAPAGOS ISLANDS: Stewart 882, 883, 959 (GH, US). Peru: Killip & Smith 24648 (US), 25473 (GH, US). Bolivia: Buchtien 3382 (GH, in part); Cárdenas 2853 (US); Herzog 2232 (US); Steinbach 8939 (GH, US). Argentina. JUJUY: Lillo 3123 (GH). SALTA: Rodriguez 1033 (GH). TUCUMÁN: Lillo 2875 (GH); Venturi 255, 2516, \$136 (GH, US). CHACO: Schulz 714 (GH). MISIONES: Gozalbo 38 (GH); Hindobro 5435 (GH); Rodriguez 664 (GH). Paraguay: Hassler 6842 (GH), 12244 (US); Morong 571 (US). Uruguay: Osten 6541 (US). Brazil. RIO GRANDE DO SUL: Leite 154 (GH). SANTA CATHARINA: Dusén 11806 (US); Luederwaldt 705 (GH). PARANÁ: Annies (Ros. exsicc. 56) (US); Dusén 16388 (GH). RIO DE JANEIRO: Regnell II 59 (US); L. B. Smith 2246 (GH, US); L. B. Smith & Brade 2278 (GH, US). MINAS GERAES: Regnell II 322c (US). 266-02779

 Dennstaedtia bipinnata (Cav.) Maxon, Proc. Biol. Soc. Wash. 61: 39. 1938. FIGS. 17-22.

- Dicksonia bipinnata Cav. Descr. Pl. 174. 1802. Holotype: Porto Rico, Ventenat, MA; isotype, Hb. Willd. B, fragment US!. (Maxon, loc. cit., discusses the Hb. Willdenow specimen accepted as an isotype).
- 244-21396 Polypodium bacciferum Poir. Lam. Encycl. 5: 554. 1804. Holotype: Port-de-Paix, Santo Domingo, Plumier, Fil. t. 31 and the identical Plumier, Amer. t. 45.
 244-04073 Dicksonia adjantoidee Hondow P. Dickso
 - ⁶⁴⁶⁷³ Dicksonia adiantoides Humb. & Bonpl. ex Willd. Sp. Pl.
 5: 488. 1810. Holotype: Caripe, Venezuela, Humboldt & Bonpland, Hb. Willd., B, fragment US!.
- 246-21397 Dicksonia globuligera Desv. Mém. Soc. Linn. Paris 6: 317. 1827. Based on Polypodium bacciferum Poir.
- 246-04.69 Dennstaedtia adiantoides (Humb. & Bonpl. ex Willd.) Moore, Ind. Fil. xcvii. 1857.

Dennstaedtia bipinnata is most closely related to the previous species, D. globulifera. In addition to the differences brought out in the key, the texture of the lamina is usually different, that of D. bipinnata being typically coriaceous to firmly herbaceous, while that of D. globulifera is usually softly herbaceous. The apex of the ultimate segments of D. bipinnata, (Figs. 17, 20) is shallowly to deeply toothed or laciniate, the more pronounced teeth being acute to subacute, while those of D. globulifera (Fig. 16) are entire to usually shallowly and bluntly (rarely subacutely) toothed. In D. bipinnata the trichomes on the under surface of the pinnules are more often deciduous than those in D. globulifera (or perhaps not as abundant) and they most often occur in the axils of the tertiary segments and of the pinnules.

The South American specimens (Fig. 18) are usually of a firmer texture and more deeply laciniate than those from



PLATE 5. Dennstaedtia bipinnata: Fig. 18, basal portion of a central pinna. \times 1½. Bolivia, R. S. Williams 1259; Fig. 19, basal portion of an upper pinna (detached). \times 1½. Cuba, Maxon 4400; Fig. 20, sori, \times 10. Peru, Mexia 6127; Fig. 21, portion of penultimate segment (upper surface). \times 8, Mexico, Ghiesbreght 356; Fig. 22, base of penultimate segment (pinnule) and portion of pinna-rachis (upper surface). \times 8, Jamaica, Hunnewell & Griscom in 1936.

Central America and the West Indies (Fig. 19). This variant is not sufficiently distinctive, however, to deserve recognition.

Wet forests or forest borders, road banks, rocky slopes and open habitats, sea level to 2000 m.

Southern Florida; central Mexico to Panama; Greater Antilles; Trinidad to Colombia, south to Peru and Bolivia.

Representative specimens: United States. FLORIDA: Palm Beach Co., May 14, 1926, Small et al. (GH, US). Mexico. HIDALGO: Kenoyer 710 (GH, US); H. E. Moore 3402 (GH). CHIAPAS: Ghiesbreght 356 (GH); Münch 155 (US). Guatemala: Heyde & Lux 4667 (GH, US). Honduras: Standley 18621, 55545 (US); Thieme 5639b (GH, US). Salvador: Standley 19760, 20207 (GH, US). Costa Rica: Pittier 6925, 7494, 10347 (US); Scamman 5892, 7018, 7019, 7608 (GH); Scamman & Holdridge 7895 (GH); Skutch 3031 (GH, US); Standley & Valerio 45186, 45895 (US). Panama: Killip 4538 (US), 5003 (GH, US); von Wedel 718 (US). Cuba: Britton & Shafer 2096 (US); Clément 1419, 5224 (US); Eggers 4938 (US); Hioram 6299, 6404 (GH); Linden 1747 (GH); Maxon 3960, 4144, 4400 (GH, US); Morton & Acuña 3613 (GH, US); Pollard & Palmer 174 (US); Shafer 7868, 8499 (GH, US); Wright 895 (GH), 962 (GH, US). Jamaica: Maxon 10330 (US), 10368, 10371 10385, (GH, US); Orcutt 5770 (GH). Hispaniola. HAITI: Ekman H8199 (GH, US); Leonard 7919 (GH, US); Leonard & Leonard 12149, 14324 (GH, US). DOM-INICAN REPUBLIC: Abbott 1592 (GH, US); Ekman H11466 (US); Fuertes 1554 (GH, US); Valeur 739 (GH, US). Porto Rico: Britton 5214 (GH, US); Britton & Marble 446 (US); Britton et al. 6189 (US); Eggers 35 (US); Garber 77 (GII); Sintenis 401 (GH, US), 2391 (US). Trinidad: Broadway 6020, 7265 (US); Fendler 157 (GH). Venezuela: Fendler 448 (GH); Moritz 109 (US). Colombia: Seifriz 157 (US); H. H. Smith 2431 (GH, US). Ecuador: Haught 3368 (GH, US). Peru: Killip & Smith 22651 (GH, US), 22875, 26799, 27796 (US); Mexia 6127 (GH, US); Spruce 4890 (NY). Bolivia: Buchtien 313, 3378 (US); Herzog 321 (US); Krukoff 10331 (GH, US); Steinbach 3036 (GH); R. S. Williams 1259, 1267 (GH, US).

266-06262

Dennstaedtia dissecta (Sw.) Moore, Ind. Fil. 305. 1861. FIGS. 23-25.

- 266.06269 Polypodium dissectum Sw. Prod. 134. 1788, not Forst. 1786.
- 266-06166 Dicksonia dissecta Sw. Schrad. Jour. 1800²: 91. 1801. Holotype: Jamaica, Swartz, S-PA, photograph and fragment US!.
 - 266- 6226 ⁺ Dicksonia cornuta Kaulf. Enum. Fil. 227. 1824. Holotype: Brazil, "ex Spreng.".
- 500-56357 Dicksonia Millefolium Desv. Mém. Soc. Linn. Paris 6: 318. 1827. Holotype: Hb. Desv., P, photograph GH !.
- 266-6268 Dennstaedtia cornuta (Kaulf.) Mett. Ann. Sci Nat. V, 2: 260. 1864.

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PLATE 6. Dennstaedtia dissecta: Fig. 23, central portion of a pinna, × ½, Haiti, Leonard 4740; Fig. 24, sori, × 5, Guatemala, Türckheim 8629; Fig. 25, upper pinnae, × ½, Costa Rica, J. J. Cooper. Dennstaedtia obtusifolia: Fig. 26, central portion of a pinna, × ½, Tobago, Broadway in 1911; Fig. 27, central portion of a pinna, × ½, Panama, Killip 12141.

The shape and size of the mature sori distinguish D. dissecta (Fig. 24) from D. obtusifolia (Fig. 29). In the key I have expressed this difference in terms of the breadth and the thickness. There is a simular relation of breadth and length, although this is not as constant. However, it may be useful for identification of immature specimens. In D. dissecta the sorus is about twice as broad as long, while in D. obtusifolia it is about as broad as long. The basal acroscopic sori of a segment are especially distinctive in D. dissecta; the apical ones may resemble those of D. obtusifolia. I have not been able to discover any means of identifying sterile specimens of these species, but fortunately they are few.

The close relation of *D. dissecta* and of *D. obusifolia*, their similar ranges and the occurrence of at least a few mixed collections³ suggest that perhaps they are variants of a single species. However, *D. dissecta* is not known from Cuba, Porto Rico or the Lesser Antilles, while *D. obtusifolia* eccurs in all of those areas.

Scamman 7609 and 7610 from Costa Rica have proliferous buds in the axils of the pinnae.

Wet forests, shady woods and forest openings, 30-2600 m. Southern Mexico to Panama; Jamaica and Hispaniola;

Trinidad to Colombia, south to Bolivia and southern Brazil. Representative specimens: Mexico: VERACRUZ: Copeland 71 (GH, US). CHIAPAS: Ghiesbreght 368 (GH). Guatemala: Heyde & Lux 3212 (GH, US); Münch 151 (US); Türckheim 8629 (GH, US), II 2367 (US). British Honduras: Schipp S-921 (GH). Nicaragua: Standley 10919 (US). Costa Rica: Maxon 305 (US); Maxon & Harvey 8053 (US); Pittier 63 (GH); Scamman 7021, 7609, 7610 (GH); Standley 37173, 51247, 51258 (US). Panama: Cornman 1195 (US); Killip 5175 (GH). Jamaica: Clute 108 (US); Hart 162 (US); Maxon 9828 (GH, US); Orcutt 5139 (GH); Underwood 3155 (US); Wilson 532 (GH). Hispaniola. HAITI: Ekman H7527, H7528, H10185 (US); Leonard 4279, 4740 (GH, US). Trinidad: Lockhart (GH). Venezuela: Fendler 59 (GH); Moritz 283 (GH, US). Colombia: Killip & Smith 16057 (GH, US); Linden 1043 (US); Pennell 4424, 7602 (GH, US); Stübel 438 (US). Ecuador: Eggers 15313 (US); Rimbach 105 (GH, US). Peru: Killip & Smith 24546 (US); Macbride 4844 (US); Mexia 8248 (GH, US). Bolivia: Bang 2423 (GH, US); Herzog 2260 (US); Rusby 127 (US). Brazil: RIO GRANDE DO SUL: Leite 3048 (US). SANTA CATHARINA: Luederwaldt 1821 (US). PARANÁ: Dusén 14116 (US). SAO PAULO: Brade 8351 (US). RIO DE JANEIRO: Glaziou 1232 (US).

246-01782 8. Dennstaedtia obtusifolia (Willd.) Moore, Ind. Fil. 306. 1861. FIGS. 26-29.

266-0 62 70 Dicksonia obtusifolia Willd. Sp. Pl. 5: 483. 1810. Holo-

³ Maxon 9375 and 9901, Maxon & Killip 1189 from Jamaica, and Leite 3048, Brazil, are all D. dissecta at US and D. obtusifolia at GH.

type: Caracas, Venezuela, Bredemeyer, Hb. Willd., B, photograph us!.

- 266-66177 Dicksonia ordinata Kaulf. Enum. Fil. 226. 1824. Holotype: Porto Rico, Ventenat. (Kze. Farnkr. t. 106b is evidently drawn from the holotype).
- 246-06224 Dennstaedtia ordinata (Kaulf.) Moore, Ind. Fil. 306. 1861.
- 500-56358 Dennstaedtia producta Mett. Ann. Sci. Nat. V, 2: 260. 1864. Syntypes: Colombia, Lindig 329, B, photographs and fragment US!, P, photograph GH!; Colombia, Lindig 333, B, GH!, NY!, US!.
- 500-96309 Dicksonia incisa Fée, Mém. Fam. Foug. 11:94, t. 25, fig 1. 1866. Holotype: Guadeloupe, L'Herminier in 1864; authentic specimen, L'Herminier 172 in 1862, P, photograph GH!.
- 246-07767 Dicksonia cicutarioides Fée, Mém. Fam. Foug. 11: 95, t. 25, fig. 2. 1866. Holotype: Guadeloupe, L'Herminier in 1864.
- 500-51260 Dennstaedtia incisa (Fée) Kuhn, Linnaea 36: 146. 1869.
 146-10508 Dicksonia scandens Baker, Jour. Bot. 15: 162. 1877, not Bl. 1828; illustrated in Ic. Pl. t. 1605. Holotype: Andes of Quito, Ecuador, Sodiro, K, photograph and fragment US!
- Soo-Stor Dicksonia pubescens Baker, Jour. Bot. 19: 203. 1881, not Schkuhr, 1809. Holotype: Antioquia, Colombia, Kalbreyer 1859, K, photograph and fragment US!.
- Soc-offes Dennstaedtia Sodiroi Diels, Nat. Pflanz. 14: 218. 1899. Based on Dicksonia scandens Baker.
- Costar. 3: 38. 1901. Holotype: Costa Rica, Tonduz 11785, P, isotype, GH!, US!.
- 245 -0739? Dennstaedtia cicutarioides (Fée) Hieron. Bot. Jahrb. 34: 454. 1904.
- 56365 Dicksonia cicutaria var. deparioides Rosenst. Hedwigia 43:214. 1904. Holotype: Toledo, São Paulo, Brazil, Ulbricht 73, PA!
- 500-56342 Dennstaedtia pubescens (Baker) C. Chr. Ind. Fil. 218. 1905.
- 5-o-56366 Dennstaedtia deparioides (Rosenst.) Rosenst. Hedwigia 46: 71. 1906.
- 244-17926 Dennstaedtia Kalbreyeri Maxon, Proc. Biol. Soc. Wash. 51: 40. 1938. Based on Dicksonia pubescens Baker.

Dennstaedtia obtusifolia is most closely related to D. dissecta and their distinguishing characters and problems of separation are discussed under the latter treatment.

This species and *D. ordinata* have commonly been maintained as distinct but I have been unable to find any reliable characters by which to separate them. Three other species have been less often recognized as distinct from *D. obtusi*-

folia. Dennstaedtia producta Mett. is an unusually laciniate form. Dennstaedtia incisa (Fée) Kuhn is a form with especially small and narrow lobes. Dennstaedtia Kalbreyeri Maxon I can interpret only as an unusual variation of D. obtusifolia with a fine, stiff and abundant pubescence, and the pinnules nearly at right angles to the pinna-rachis and with very uniform tertiary segments. The type of D. Kalbreyeri has some trichomes on the under surface of the costa that resemble (although they are longer) those usually occurring in D. obtusifolia. Another specimen (Cuatrecasas 9382, US) has the aspect of D. Kalbreyeri and the typical pubescence of D. obtusifolia.

Fée (*loc. cit.*, t. 25. fig. 2) illustrates a specimen of this species with proliferous buds in the axils of the pinnae.

Wet forests, forest clearings, wet banks and hillsides, sea level to 2100 m.

Guatemala to Panama; Greater and Lesser Antilles; Trinidad to Colombia, south to Peru, Paraguay and southern Brazil.

Representative specimens: Guatemala: Türckheim 1053 (GH), 8629 (US). Honduras: Ames 105 (US). Nicaragua: C. F. Baker 2468 (US); Levy 453 (GH). Costa Rica: Scamman & Holdridge 7899, 7900 (GH); Skutch 5357 (US); Tonduz 11785 (GH, US); COCOS ISLAND: Pittier 16230 (GH); Snodgrass & Heller 952 (GH). Panama: Killip 2832 (GH), 12141 (GH, US). Cuba: Clément 1178 (GH, US), 1497, 1557, 1609 (GH); Ekman 3937 (US); Pollard & Palmer 165 (GH, US); Wright 895 (GH, US). Jamaica: Clute 292 (US); Maxon 8836 (GH, US); Wilson & Murray 581 (GH). Hispaniola. HAITI: Leonard & Leonard 12280 (GH, US). DOMINICAN REPUBLIC: Abbott 320 (US), 486 (GH, US); Ekman H11473 (GH, US); Howard & Howard 9394 (GH, US). Porto Rico: Britton & Cowell 1023, 2205 (US); Scamman 6524 (GH); Sintenis 1789 (US), 5443 (GH, US), 6536 (US). Guadeloupe: Duss 4184, 4341 (US); L'Herminier 172 (GH); Stehlé 1464 (US). Dominica: Lloyd 900 (US). Martinique: Duss 1685, 4164 (GH, US), 4686 (US). St. Lucia: Box 469, 470 (US); Proctor 17905 (GH). St. Vincent: H. H. Smith 1723 (GH, US). Grenada: Broadway 1862 (GH). Tobago: Broadway 4219 (GH, US), 9223 (GH). Trinidad: Britton et al. 1353 (GH, US); Broadway 5354 (GH), 5914 (US), 9961 (GH,US); Fendler 84 (GH, US). Venezuela: Fendler 374 (GH); MARGARITA ISLAND: Johnston 185 (GH, US), Miller & Johnston 160 (GH, US). Colombia: Lindig 333 (GH, NY, US); Pennell 4472 (US), 8918 (GH, US); Pennell et al. 8665 (GH, US). Ecuador: Hitchcock 21764 (GH, US); Stübel 947 (US). Peru: Kanehira 160 (US); Killip & Smith 22647 (GH, US), 23915, 24916 (US); Schunke 154 (US). Paraguay: Hassler 6840, 12244 (GH). Brazil. RIO GRANDE DO SUL: Leite 3048 (GH). SANTA CATHARINA: Spannagel (Ros. exsicc. 241) (US). PARANÁ: Dusén 14678 (GH, US). SAO PAULO: Luederwaldt 21351 (GH). RIO DE JANEIRO: Glaziou 5256 (US).



PLATE 7. Dennstaedtia obtusifolia: Fig. 28, central portion of a pinna, X ½. Nicaragua, C. F. Baker 2468; Fig. 29, sori, X 5, Porto Rico. Scamman 6524. Dennstaedtia arborescens: Fig. 30, portion of a sterile pinnule (upper surface). X 5, Bolivia, Buchtien 3593; Fig. 31, portions of upper pinnae, X ½, Costa Rica, Scamman 7020; Fig. 32, sori, X 5, Costa Rica, Maxon & Harvey 3006. 9. Dennstaedtia arborescens (Willd.) Ekman ex Maxon, Proc. Biol. Soc. Wash. 43: 88. 1930. FIGS. 30-35.

266-06278 Davallia arborescens Willd. Sp. Pl. 5: 470. 1810. Holotype: 266-062 79 Damali

Davallia concinna Presl, Rel. Haenk. 1: 66. 1825, not Schrad. 1818. Syntypes: "Chile, 1790, Haenke", 2 sheets PR, photographs GH!, US!. The species is not known from Chile; Presl, Epim. Bot. (reprint) 102, was undoubtedly correct in citing the Haenke collection as from Peru.

266-21401 Dicksonia macrophylla Desv. Mém. Soc. Linn. Paris 6: 317. 1827. Based on Davallia arborescens Willd.

24 -04281 Dicksonia Pavonii Hook. Sp. Fil. 1: 74. 1844. Based on Davallia arborescens Willd., not Dicksonia arborescens L'Hérit. The specimen cited is Dennstaedtia Sprucei. 266-0778/ Dicksonia concinna (Presl) Hook. Sp. Fil. 1: 74. 1844. 266-06285 Deparia Mathewsii Hook. Sp. Fil. 1: 85, t. 30B. 1844.

Holotype: Peru, Mathews 1782, K, photograph and fragment US!; isotype, US!.

- 244- o7 #2 Dicksonia consanguinea Kl. Linnaea 20: 445, 1847. Holotype: Puerto Cabello, Columbia, Karsten.
- 266-21402 Dicksonia recognita Kze. Bot. Zeit. 8: 57. 1850. Holotype: Plumier, Fil. t. 6.

500-5637/ Patania triangularis Presl, Epim. Bot. (reprint) 261. 1852. Holotype: Colombia, Linden 1042, PR; isotype, GH !.

246-06287 Dennstaedtia concinna (Presl) Moore, Ind. Fil. xcvii. 1857.

500-17506 Dennstaedtia macrophylla (Desv.) Moore, Ind. Fil. xcvii, 1857.

24-0629/ Dennstaedtia Pavonii (Hook.) Moore, Ind. Fil. 307. 1861.

264- of 733 Dennstaedtia consanguinea (Kl.) Moore, Ind. Fil. 305. 1861.

Sov- 09/69 Dicksonia adiantoides var. coronata Sod. Rec. Crypt. Vasc. Quit. 23. 1883. Holotype: Ecuador, Sodiro; Corazón, Sodiro, US!, K, photograph US! and Canzacoto, Sodiro, NY! are presumably authentic.

166-22372 Dicksonia coronata (Sod.) Sod. Crypt. Vasc. Quit. 48. 1893.

Soo-5635/ Dennstaedtia coronata (Sod.) C. Chr. Ind. Fil. 216. 1905.

266-06283 Dennstaedtia Mathewsii (Hook.) C. Chr. Ind. Fil. 218. 1905.

266 - 07294 Dennstaedtia grossa Christ, Bull. Herb. Boiss. II, 6: 192. 1906. Holotype: Navarro, Costa Rica, Wercklé 9, P; authentic specimens collected by Wercklé, NY !. US !.

Maxon (loc. cit.) has discussed the application of Willdenew's name and the confusion that led to the inappropriate epithet. The Plumier plate is not an entirely satisfactory

266-06277

match for material recently collected in Hispaniola, or elsewhere, but unless it can be shown that it represents a different species it seems best to accept its identity as Maxon determined it.

Some forms of *D. arborescens* with deeply pinnatifid pinnules and some of the previous species, *D. obtusifolia*, with 1-pinnate pinnules are rather similar and fragmentary specimens may be difficult to identify.

In the shape and size of the ultimate segments, *D. arborescens* is the most variable of the American species. The three principal variations are illustrated in Figs. 31, 33 and 34. The form with broadly obtuse segments illustrated in Fig. 33 may occur in both fertile and sterile pinnae, or the sterile ones may be truncate, as in Fig. 35. It is with some uncertainty that I treat these all as one species and do not give them some intraspecific status.

My conclusion that D. arborescens should be considered a polymorphic species is based on the following considerations. Dennstaedtia Sprucei, a distinctive species, exhibits some of the variability in shape and size of the ultimate segments that D. arborescens does. Some specimens, Fig. 36, are similar to those of D. arborescens in Fig. 33; others are substantially the same as those of D. arborescens in Fig. 31. None of the forms has a distribution that would favor its recognition. There are no other characters (or at least I have found none) to support those of size and shape of the ultimate segments. Finally, complete intergradation exists between the forms, although these intermediate specimens are not as numerous as the others. The lack of a distinctive geographic range and the parallel variation in D. Sprucei indicate, I believe, that no geographic subspecies or varieties are involved in the variation of D. arborescens. However, adequate field studies may bring out facts of correlation with habitat or local geography that may result in a reevaluation of this conclusion.

This species has, more often than the two preceeding ones, proliferous buds in the axils of the pinnae. They are not, however, common. Evidently they are readily detached and leave no observable scar; thus it is not possible to determine if specimens formerly bore them.

Wet forests, ravine banks, forest borders; 100-1500 m. in Central America, 1200-2200 m. in the Greater Antilles and 400-2800 m. in South America.

Southern Mexico to Panama; Cuba, Jamaica and Hispaniola; Venezuela to Colombia, south to Bolivia. Representative specimens: Mexico. CHIAPAS: Münch 60 (US). Guatemala: Hatch & Wilson 114 (US); Salvin (GH). Costa Rica: Maxon & Harvey 8006 (GH, US); Scamman 7020, 7897, 7898 (GH); Standley 44096 (GH, US). Panama: Cornman 1226 (GH, US); Maxon 4968 (GH, US); Pittier 5338 (GH, US). Cuba: Ekman 5499, 7145, 7146 (US). Jamaica: Chrysler 2055 (GH, US). Hispaniola. HAITI: Ekman H1682, H3122, H5446 (US), H7633 (GH). Venezuela: Fendler 60 (GH, US); Moritz 386 (US). Colombia: Killip & Hazen 8987 (GH, US); Killip & Smith 19970, 20414, 20462 (GH, US); Linden 1042 (GH); H. H. Smith 1072, 2218 (GH, US). Ecuador: Mexia 7208 (GH, US); Rimbach 66 (US). Peru: Macbride 4176, 4842 (F, US); Mathews 1782 (US); Killip & Smith 24642 (F, GH, US); Spruce 4346 (GH). Bolivia: Buchtien 314, 3593 (GH, US); R. S. Williams 1243 (GH, US).

10. Dennstaedtia Sprucei Moore, Ind. Fil. 308. 1861.

Holotype: Ecuador, Spruce 5350; isotype, GH!, C, photograph and fragment US!. FIGS. 36-37.

500-05%3 Dicksonia Sprucei (Moore) Baker, Jour. Bot. 15: 162. 1877.

This is one of the most distinctive species; the sterile veins that nearly reach the margin of the segment and the persistently pubescent margin (Fig. 37) are unique characters among the American species. Specimens have sometimes been identified as *D. Pavonii*, but that name is based on *Davallia arborescens* (=*Dennstaedtia arborescens*) rather than the specimen of *D. Sprucei* (Peru, *Ruiz & Pavon*) cited and illustrated by Hooker (Sp. Fil. 1: 74, t. 26A).

Wet forests and moist open places, 1500-2000 m.

Ecuador and Peru.

Specimens seen: Ecuador: Mille 165 (US); 1873, Sodiro (NY); Spruce 5350 (GH). Peru: Killip & Smith 25848 (GH, US); Soukup 1826 (GH, US).

11. Dennstaedtia Wercklei (Christ) Tryon, comb. nov. FIGS, 38-39.

266 - 0429² Saccoloma Wercklei Christ, Bull. Herb. Boiss, II, 4: 1100. 1904. Holotype: Costa Rica, Wercklé 320, P, photograph and figures in Am. Fern. Jour. 48: pl. 13 and 14, 1958.

Dennstaedtia arcuata Maxon, Am. Fern Jour. 35: 22, 1945. Holotype: Colombia, Killip 5565, US!; isotype: GH. (Paratypes: Colombia, Dryander 2446, GH!, US!, Juzepczuk 6570, US!; Peru, Bryan 674, US!).

Microlepia Wercklei (Christ) Kramer, Am. Fern Jour. 48: 116. 1958.

The 1-pinnate lamina with entire, slightly auriculate pinnae is sufficient to distinguish *D. Wercklei* from all other species. The closely crispate pubescence on the under sur-

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PLATE 8. Dennstaedtia arborescens: Fig. 33, central portion of a pinna, X ¹/₂. Haiti. Ekman H7633; Fig. 34, pinnules, X ¹/₂ Panama, Pittier 5338; Fig. 35, pinnules, X ¹/₂, Colombia. Daniel 1899. Dennstaedtia Sprucei: Fig. 36, pinnules X ¹/₂. Peru, Soukup 1826; Fig. 37, portion of a sterile pinnule (upper surface). X 10, Peru, Killip & Smith 25848. Dennstaedtia Wercklei: Fig. 38, sori, X 5, Colombia, Dryander 2446; Fig. 39, central pinnae, X ¹/₂, Colombia, Dryander 2446.

face of the costa and the enlarged sterile vein tips relate this species to *D. dissecta*, *D. obtusifolia*, *D. arborescens* and *D. Sprucei*.

Kramer (loc. cit.) has discussed and illustrated the previously obscure Saccoloma Wercklei and has (in herb.) identified D. arcuata as conspecific with it.

Forests, about 2000 m.

Costa Rica, Colombia and Peru.

Specimens seen: Colombia: Dryander 2446 (GH, US); Juzepczuk 6570 (US); Killip 5565 (GH, US). Peru: Bryan 674 (US).

DUBIOUS AND EXCLUDED NAMES

Some of the following names are undoubtedly based on specimens of *Dennstaedtia* but, not having seen the types, I have not been able to place them in synonymy. From some portion of the protologue, it is reasonably certain that none of them could be the correct name for any of the species recognized in this treatment. Other names are included that have been placed in *Dennstaedtia* but are referable to another genus.

Dennstaedtia apiifolia (Sw.) Moore, Ind. Fil. xcvii. 1857. Dicksonia apiifolia Sw. Schrad. Jour. 1800²: 91. 1801. = MAXONIA APHIFOLIA.

Dennstaedtia divaricata (Sod.) C. Chr. Ind. Fil. 217. 1905. Dicksonia divaricata Sod. Crypt. Vasc. Quit. 48. 1893. Holotype: Volcán Pululahua, 2000 m., Ecuador, Sodiro.

Dennstaedtia erosa (Kze.) Moore, Ind. Fil. 306. 1861. Dicksonia erosa Kze. Linnaea 9: 88. 1834. Holotype: Pampayaco, Peru, July, 1829, Poeppig. The petiole and upper surface of the rachis are described as scaly and this would exclude it from Dennstaedtia; however, the description may be erroneous for the name has been applied to specimens of Dennstaedtia arborescens.

Dennstaedtia fluminensis (Fée) C. Chr. Ind. Fil. 217. 1905. Microlepia fluminensis Fée, Crypt. Vasc. Brésil 1: 151, t. 51, fig. 1. 1869. Holotype: Brazil, Glaziou 2378. = MICROLEPIA sp.

Dennstaedtia grandifrons Christ, Prim. Flor. Costar. 3: 38. 1901. Holotype: Costa Rica, Tonduz 11931, P.

Dennstaedtia lindsayiformis (Fée) C. Chr. Ind. Fil. 217. 1905. Microlepia lindsayiformis Fée, Crypt. Vasc. Brésil 1: 152, t. 51, fig. 2. 1869. Syntypes: Brazil, Glaziou 2379, 3332. = MICROLEPIA SPELUNCAE?

Dennstaedtia Munchii Christ, Bull. Herb. Boiss. II, 5: 732. 1905. Holotype: Chiapas, Mexico, Münch 137, P.

Dennstaedtia Orbignyana Kuhn, Linnaea 36: 146. 1869; Chaetopt. 348. 1882. Holotype: Bolivia, D'Orbigny 278, B.

Dennstaedtia Pearcei (Baker) C. Chr. Ind. Fil. 218. 1905. Dicksonia Pearcei Baker, Ann. Bot. 5: 197. 1891. = LOXSOMOPSIS PEARCEI.

Dennstaedtia rubicaulis Christ, Bull. Herb. Boiss. II, 5: 258, 782. 1905. = HYPOLEPIS sp.

Dennstaedtia vagans (Baker) Diels, Nat. Pflanz. 1⁴: 218. 1899. Dicksonia vagans Baker, Jour. Bot. 15: 162. 1877. Holotype: Andes of Quito, Ecuador, Sodiro, K. - GRAY HERBARIUM, HARVARD UNIVERSITY.



Tryon, Rolla M. 1960. "A review of the genus Dennstaedtia in America." *Contributions from the Gray Herbarium of Harvard University* (187), 23–52. <u>https://doi.org/10.5962/p.336394</u>.

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