## II. A STUDY OF THELYPTERIS PALUSTRIS

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(Plate 180.)

In our current manuals the Marsh Fern, which has been passing variously as Aspidium Thelypteris (L.) Sw., Dryopteris Thelypteris (L.) Gray or Thelypteris palustris (Salisb.) Schott, is distinguished from its closest relatives by the forking veins of the segments or pinnules of the fertile pinnae. Thus, in Gray's Manual the species, as Aspidium Thelypteris, is distinguished in the key from A. simulatum Davenp. merely by "Fertile veins once forked" and in the fuller description emphasis is placed on "veins forked, bearing the . . . fruit dots near their middle; indusium minute, smooth and naked;" similarly in Britton & Brown's Illustrated Flora we find Dryopteris Thelypteris keyed out by "Veins once or twice forked," with the illustration clearly showing this point and the fuller text saying "veins regularly once or twice forked; . . . indusia small, glabrous." 2

The essential identity of these American accounts of the venation of the fertile segments and the descriptions in European floras is striking. For example, in such an authoritative European work as Moore's Nature-Printed British Ferns we find the genus Lastrea in Great Britain broken into two sections, Lastrea § Dryopteris and Lastrea § Thelypteris, the latter section including L. Thelypteris and characterized by "Veins usually forked, both branches (anterior and posterior venules) fertile:"3 while Moore's print from a fertile pinna shows the forking veins highly developed in all the median segments. Similar descriptions and illustrations of the venation of the fertile segments are found in all other detailed accounts of the European plant and the European specimens at hand clearly show many of the lateral veins of the fertile segments or pinnules to be forked (fig. 1). In fact, an actual count of the lateral veins of the anterior half of typical median fertile segments from median pinnae give a range of variation in the European plant as follows: from 2 forking and 4 simple to 7 forking and 3 simple, with an average of 4 veins forking and 4½ simple.

In northeastern America, however, from Newfoundland across

<sup>&</sup>lt;sup>1</sup> Robinson & Fernald, in Gray, Man. ed. 7: 41 (1908).

Maxon in Britton & Brown, Ill. Fl. ed. 2, i. 18, fig. 38 (1913).
Moore, Nat.-Pr. Brit. Ferns (Octavo), i. 163, t. xxix (1859).

southern Canada as far west as southeastern Manitoba and south across the northern states to Georgia, Tennessee and Oklahoma, it is difficult to find true fertile segments of our Marsh Fern with many forking veins. In sterile fronds the veins are mostly forking and so they are, also, in sterile segments (particularly the basal ones) of fertile fronds; but, when median and well-developed segments of median fertile pinnae of the plant of northeastern America are examined, it will be found that the veins of their anterior halves are usually all or nearly all quite simple (fig. 7). Actual count in more than 200 numbers examined shows a range as follows: from 0 forking veins and 4 to 8 simple ones up to 3 forking and 7 simple, with an average of ½ a vein forking and 6 simple.

This tendency of the fertile segments of the Marsh Fern of northeastern America to have few forking veins but more numerous simple ones, although overlooked by most modern botanists, was clearly recognized by those early students of our flora who were unembarrassed by a large number of European specimens and unprejudiced by the very uniform descriptions of the European plant. on the label of his specimen from Essex County, Massachusetts, William Oakes wrote, a full century ago, "the lowest pair of veins only is most commonly forked, frequently one of the lowest veins only is forked, often a pair and a half or two of the lowest pairs are forked." Again, the masterly American phytographer, John Torrey, working with New York specimens, correctly described them in his Flora of the State of New York, as having "veins mostly simple, sometimes forked;"1 and the late Charles Faxon, a modest but unusually keen observer, drawing the plate2 of Aspidium Thelypteris for Eaton's Ferns of North America and showing "the common form in New England," gave diagrams of the venation: the sterile pinna with most of the veins forked, the fertile pinna with them mostly unforked below the indusia. Lastly, on a Rhode Island sheet from Professor J. F. Collins, I find the following comment: "lower veins of pinnules forked, occasionally some others; but most of them simple." But, for the most part, the makers of modern descriptions of the plant of northeastern America have found the descriptions of the European plant more convenient to copy and the result is, that, by emphasis upon a character rarely found in the American

<sup>&</sup>lt;sup>1</sup> Torr. Fl. N. Y. ii. 497 (1843).

<sup>&</sup>lt;sup>2</sup>C. E. Faxon in Eaton, Ferns N. A. ii. t. 30 (1879).

plant, the real distinctions between our Thelypteris palustris and the endemic American T. simulata (Davenp.) Nieuwl. are rendered unnecessarily doubtful. The key-character now found in our manuals should be greatly modified and the following substitute is proposed:

T. PALUSTRIS. Lateral nerves of the segments of the sterile fronds mostly forked, of the fertile simple or forked: indusia glabrous or coarsely glandulartoothed or long-ciliate.

T. SIMULATA. Lateral veins of the segments of both sterile and fertile fronds simple: indusia minutely glandular-ciliate.

Although the plant of northeastern America has the venation of the fertile pinnae much simpler than in typical European material, we have in the extreme southeastern states and in Bermuda a plant with veins quite as generally forked as in the European. All the material I have seen from Louisiana, Florida and Bermuda has most of the veins of the fertile pinnae forked (fig. 5). This material shows a range of variation as follows: from 3 forking veins and 6 simple ones to 6 forking and 2 simple, with an average of 4 forking and 4 simple, an average not very unlike that of the European series. Some plants, with several forking fertile veins occur northward to southeastern Pennsylvania and occasional individuals from further north have a few fertile segments with numerous forking veins. But north of Louisiana and Florida the species certainly shows a general reduction in the number of forked veins. Typical segments of three of these plants, the European (fig. 1), the northeastern American (fig. 7) and the southeastern American (fig. 5) are shown in the outline drawings prepared by Miss Ethel C. Dansie.

The descriptions of the indusia in American manuals and in European handbooks are so different that, coupled with the difference in venation already discussed, they might very naturally be taken as characterizing distinct European and northeastern American species. The statements in Grav's Manual and in Britton & Brown's Illustrated Flora have already been quoted: "indusium minute, smooth and naked" and "indusia small, glabrous." Such characterizations are typical in America; and when we turn to European descriptions and illustrations we likewise find a remarkable uniformity of statement, but one seemingly incompatible with the American. Thus, the analytical drawings published by Schmidel<sup>1</sup> (see Pl. 179) with his original account of Thelypteris show the indusia with coarse glandtipped teeth; and in his description Schmidel strongly emphazised

Schmidel, Icones Plantarum, ed. 2, t xiii (1762).

them: "Quandiu peltae iuniores et vegetae adhuc sunt, apicibus lacinularum, non quidem omnium in omnibus, plurimarum tamen, inhaerere solent globuli parui, crocei dilutioris coloris, propter succum quem continent viscidulum splendidi. Ex his vnus post alterum sensim euanescunt, postquam ad aliquod tempus durauerunt." Similarly, in the very clear analytical plate in his incomparable Kryptogamische Gewächse, Christian Schkuhr showed the characteristic European plant with practically all the fertile veins forking and with the indusia bearing conspicuous glands at the tips of the coarse teeth: "Die Fruchtdecken . . . sind am Rande mit gestielten Drüsen besetzt." Or, again, in Moore's Nature-Printed British Ferns, already referred to, the illustration brings out the glandular ciliation and the text emphasizes it: "Indusium a small delicate roundish-reniform membrane, . . . the free margin lacerate and glandular"; and Luerssen goes still farther, describing not only the gland-tipped teeth, but also glands between the teeth and longer unicellular hairs occurring irregularly on the indusia.2 When the young and unshrivelled indusia of the European plant (fig. 2) are examined they are found to agree perfectly with the best European descriptions, in having coarse teeth tipped by conspicuous yellow or orange glands and only rarely (in a single collection seen by me, of Dryopteris Thelypteris, forma Rogaetziana (Bolle) Holmberg) do they have the very long cilia described by Luerssen. This European type, with fertile veins mostly forking and with indusia with coarse gland-tipped teeth, extends southward to the Mediterranean and eastward to India and southern China.

In the plant of northeastern America, on the other hand, the indusia (fig. 8) are mostly larger than in the European type (the best-developed measuring 0.7-1 mm. in diameter) and less lacerate or long-toothed. Only rarely are they so glandular-ciliate, occasionally they have a few glands, but the great majority of them examined (from a series of fully 200 numbers) are either quite glabrous and without ciliation or glabrous on the back and ciliate with few to many long slender trichomes. It is clear, then, that, although strikingly similar in aspect to European Thelypteris palustris, the

<sup>&</sup>lt;sup>1</sup> Schkuhr, Krypt. Gew. 52, t. 52 (1809).

<sup>2&</sup>quot;am Rande unregelmässig kurz-lappig bis stumpf-zähnig und auf der Spitze der Lappen oder Zähne sowie auch zwischen denselben mit kurzen, cylindrisch-keuligen bis keulenförmigen drüsigen Härchen und dazwischen längeren pfriemenförmigen, einzelligen Haaren in sehr wechselndem Verhältniss besetzt."—Luerrsen, Farnpfl. 364 (1889).

plant of northeastern America differs from it in having the veins of the fertile pinnae usually simpler and the larger indusia rarely so glandular-ciliate but more often glabrous or long-ciliate and without conspicuous glands. In one other tendency does it show a strong departure: in commonly having the rachis (at least when young), the midribs of the pinnae and the veins (especially beneath) minutely and rather densely pubescent, the frond of the European plant being nearly or quite glabrous. The pubescence is not always conspicuous in our plant but in nine-tenths of our material it is well developed and the plant of northeastern America is obviously what was intended by the late George Lawson when he designated "the plant of Gray's Manual" as

"Lastrea Thelypteris, a. pubescens.—Frond somewhat coriaceous, densely pubescent or downy throughout."

And naturally enough, though like all other such cases coming as a fresh surprise, when the venation of the fertile fronds (fig. 9) and the characters of the indusia (fig. 10) of all available material from northeastern Asia (5 collections from Manchuria and Amur) are examined, they show that the plant of Amur and Manchuria is indistinguishable from that of northeastern America. It is, furthermore, noteworthy that Christensen, studying the ferns brought back from Kamtchatka by Hultén, should have set off as "a most striking variety" the plant of South Kamtchatka: Dryopteris Thelypteris, "var. kamtschatica C. Chr. nov. var. . . . Frons longe stipitata rigida, lamina utrinque pubescente subtus squamis et glandulis destituta,"2 with the additional comment "indusia rather large and persistent." Christensen's D. Thelypteris, var. kamtschatica, like the plant of Amur and Manchuria, is pretty clearly the same as Lastrea Thelypteris, var. pubescens Lawson. Var. kamtschatica, besides its pubescent and esquamose and glandless character was "especially marked by . . . , short blade; frequently the stipe is 30 cm. or more, the lamina [fertile] 10 cm. long and only 5-6 cm. wide"

<sup>2</sup> Christens. in Hulten, Fl. Kamtch. and Adj. Isl. i. 38 (1927).

Lawson, Edinb. New Phil. Journ. n. s. xix. 277 (1864)—Reprinted as Syn. Can. Ferns and Fil. Pl. 21 (1864). Lawson's plant came from "Odessa, Hudson's Bay, & c." This does not mean that the fern reaches northward to Hudson Bay as might naturally be inferred. Hudson's Bay Territories in Lawson's day embraced all the vast unincorporated and undeveloped area now called Canada from the Atlantic to the Pacific and north of the St. Lawrence and the Great Lakes. It even included "the neighborhood of Montreal, up the Ottawa River," etc. (Lippincott's Gazetteer). The Odessa of Lawson, which may be taken as the type-station, is slightly north of latitude 44° N. in Addington Co., Ontario. His "Hudson's Bay" might have been anywhere in southeastern Ontario or southwestern Quebec.

and it was found only in "alkaline?" soil near a hot spring. In the plant of northeastern America it is not difficult to find stipes up to 7 dm. in length and in many plants the fertile lamina is but slightly more than one-third the length of the stipe. In fact, such a collection as Bissell & Linder, no. 19,402 from "brackish marsh," George River, Nova Scotia, must be a very close match for the type of var. kamtschatica; the George River specimen preserved in the Gray Herbarium having two fertile fronds: one with stipe 37 cm. long and lamina 13 cm. long and 7.5 cm. broad, the other with the lamina 15 cm. long and 6 cm. broad.

From Christensen's observation upon the Kamtchatkan plant, above quoted, one would infer that the proportions of stipe and lamina in the eastern Asiatic and the European plants are notably different. Without a larger and better-collected representation than I have seen from Europe I am unable to say whether the northeastern American and the European plants actually differ in these points. Lawson (l. c.) said: "In the Canadian plant the outline of the frond is a little different from Scotch and Irish specimens, being less narrowed at base." The European works, to quote from Moore's detailed account again, describe the "Stipes as long as or longer than the leafy portion in the fertile fronds. . . . Fronds . . from four to ten inches in breadth," and the European representation before me shows the fertile lamina ranging from 0.7 to 2 dm. in width (Moore's "ten inches" would be 2.45 dm.), with stipes up to 5 dm. long. In the plant of northeastern America the stipes often reach a length of 7 dm. (probably not really different in Europe) and the fertile laminas of the more than 200 numbers before me give a range in breadth of 0.4 to 1.7 dm. (with two collections from rich calcareous meadows showing the extraordinary breadth of 1.9 dm. and 2.1 dm. respectively), the average breadth of the 200 + laminas being 1.07 dm. Whether this average is less than in Europe I cannot say; judging from European descriptions and illustrations, apparently it is.

When we turn to the plant of the southeastern United States and Bermuda, with venation (fig. 5) as in the typical Thelypteris palustris of Europe and western and south-central Asia, we find an indusium (fig. 6) essentially like that of the northeastern American and northeastern Asiatic Lastrea Thelypteris, var. pubescens of Lawson, with few, if any, glands but with elongate non-glandular ciliation and in

size practically like the European indusia. This southern plant, it would seem, is as closely related to the more northern American extreme as it is to the European; and in the usual abundance of long cilia on the indusia they both strongly suggest the still more austral T. palustris, var. squamigera (Schlecht.) Weatherby1 of southern India, tropical and southern Africa and northern New Zealand. In var. squamigera (fig. 3) there is a greater development of broad brown scales on the lower side of the costa of the pinna than is common in the more northern plants; but small (though narrower) scales may be found on young and carefully preserved European and American specimens, and in the plants of Louisiana and Bermuda they are as abundant and nearly as broad as in African specimens. The plant of southeastern North America, however, can scarcely be referred to var. squamigera. Such material of the African and New Zealand plant as I have examined (only three or four of the sheets showing young indusia) has the indusia (fig. 4) with copious dorsal as well as marginal long trichomes; the southeastern American plants having the indusia essentially glabrous on the back and the frond more definitely bipinnate than in the other varieties.

Thelypteris palustris, a semi-cosmopolitan species, has, then, four strongly marked varieties which may be distinguished as follows.

T. PALUSTRIS (Salisb.) Schott, var. typica. Acrostichum Thelypteris L. Sp. Pl. ii. 1071 (1753). Polypodium Thelypteris (L.) Weis, Pl. Crit. Fl. Gott. 307 (1770). P. palustre Salisb. Prodr. 403 (1796). Polystichum Thelypteris (L.) Roth in Roem. Arch. ii. pt. 2: 106 (1799). Aspidium Thelypteris (L.) Sw. in Schrad. Journ. 1880, pt. 2: 33 (1801). Athyrium Thelypteris (L.) Spreng. Anleit. iii. 134 (1804). Aspid. palustre (Salisb.) S. F. Gray, Nat. Arr. Brit. Pl. ii. 9 (1821). Nephrodium Thelypteris (L.) Strempel, Fil. Berol. Synop. 32 (1822). Lastrea Thelypteris (L.) Bory, Dict. Class. ix. 233 (1826). T. palustris (Salisb.) Schott, Gen. Fil. in Obs. under t. 10 (1834). Aspid Thelyptera Wood, Class-Book, 459 (1845) as to name-bringing syn. Dryopteris Thelypteris (L.) Gray, Man. 630 (1848), as to name-bringing synonym. Hemestheum Thelypteris (L.) Newm., Phytol. iv. Append. xxii (1851). Lastrea palustris (Salisb.) J. Sm. Cat. Cult. Ferns, 56 (1857). T. Thelypteris (L.) Nieuwl. Am. Midl. Nat. i. 226 (1910), as to name-bringing synonym.—Fertile lamina 0.7-2.5 dm. wide, glabrous or only sparingly pubescent: scales on back of rachis and midribs lanceolate to oblong, caducous: segments of median fertile pinnae with about half the veins forking (of those of the anterior half 2-7 forking, 3 or 4 simple): indusia with coarse gland-tipped

Weatherby in Johnston, Contrib. Gray Herb. no. lxxiii. 40 (1924).

teeth, only rarely with long glandular ciliation.—Great Britain, southern Norway, central Sweden, northern European Russia (Perm) and lat. about 58° in western Siberia eastward in Asia and south to northern Spain, Algiers, central Italy, the Caucasus, the Himalayas and southern China. Figs. 1 and 2.

Var. squamigera (Schlecht.) Weatherby in Johnston, Contrib. Gray Herb. lxxii. 40 (1924). Aspidium Thelypteris, \u03b3. squamigerum Schlecht. Adumb. 23, t. 11 (1825). A. squamulosum Kaulf. ex Schlecht, l. c., in syn. (1825). Lastrea squamulosa Presl, Tent. 76 (1836). Nephrodium squamulosum (Presl.) Hook. f. Fl. N. Zeal. ii. 39 (1855). A. Thelypteris, B. squamuligerum Mett. Abh. Senckenb. Naturf. Ges. ii. 112 (1855). N. Thelypteris, B. squamulosum (Presl) Hook. Sp. Fil. iv. 88 (1862). Lastrea Fairbankii Bedd. Ferns Brit. Ind. t. 254 (1867). N. Thelypteris, var. β. squamuligerum (Mett.) Sim, Ferns S. Afr. 180 (1892). Dryopteris Thelypteris, var. 3. squamuligera [as um] Sim, l. c. ed. 2: 102 (1915).—Fertile lamina 0.5-1.5 dm. wide; scales of rachis and midribs reniform, suborbicular or broadovate, castaneous or fulvous, rather persistent: veins of median fertile pinnae mostly simple: indusia copiously long-ciliate and commonly with shorter glandular ciliation and often pilose-hirsute on the back.—India, tropical and southern Africa, northern New Zealand. Figs. 3 and 4.

Var. Haleana, n. var., frondibus plerumque bipinnatis medio 0.8-2 dm. latis; pinnarum costa media squamis paleaceis obtecta, squamis ovatis obtusis castaneis vel fulvis persistentibus vel caducis, pinnularum fructiferum nerviis plerumque furcatis; indusio longe ciliato vix glanduloso.—Southeastern United States and Bermuda Islands. Louisiana: marshes, Alexandria, Josiah Hale (Type in Gray Herb.). Florida: Palma Sola, S. M. Tracy, no. 6627; Deep Lake, Lee Co., A. A. Eaton, no. 1312; Miami, May, 1877, A. P. Garber (as Aspidium unitum); Black Point, Dade Co., A. A. Eaton, no. 277; Alapattah, A. A. Eaton, no. 1007; Biscayne Bay, E. Palmer, no. 652; New Smyrna, Palmer. Bermuda: Pembroke Marshes, June 21, 1905, Harshberger, August 23, 1913, F. S. Collins, no. 122; Devonshire Marshes, Brown & Britton, no. 84. Specimens from Georgia, eastern Virginia and southeastern Pennsylvania show more simple veins and seem to indicate transition to the next. Figs. 5 and 6.

Var. pubescens (Lawson), n. comb. Lastrea Thelypteris, α. pubescens Lawson, Edinb. New Phil. Journ. n. s. xix. 277—reprinted as Syn. Can. Ferns and Filic. Pl. 21 (1864). Lawson's L. Thelypteris, β. glabra likewise belongs here, but his γ. intermedia (judging from the locality) may be different. Dryopteris Thelypteris, var. kamtschatica C. Chr. in Hultén, Fl. Kamtch. and Adj. Isl. i. 38 (1927).—Fronds usually minutely pubescent, at least when young, on both surfaces and especially along the rachis and lower sides of the midribs, mostly without scales or when young with pale narrow caducous scales; fertile fronds 0.4–1.7 (rarely–2.1) dm. broad; the median fertile

segments with the veins all or nearly all simple: indusia when well developed 0.7-1 mm. in diameter, glabrous or long-ciliate, rarely glandular-ciliate.—Southeastern Newfoundland and the Magdalen Islands to the Ottawa Valley, Quebec, west to southeastern Manitoba and south to Georgia, Tennessee and Oklahoma (and Texas?); southern Kamtchatka, Amur and Manchuria. Type-station: Odessa, Addington Co., Ontario (Lawson). Figs. 7-10.

Phylogenetically the typical Eurasian plant, Thelypteris palustris, var. typica, seems to be farthest removed from the other varieties, in having the indusium more glandular-toothed but less often with long glandless ciliation than in the other three varieties. In this connection it is noteworthy that the European plant is distinctly not a boreal fern, there reaching its northern limit in Perm, central Sweden, southernmost Norway1 and Great Britain and Ireland, where, in the northern and western districts it is sufficiently local to have led Moore (in 1859) to write: "Though widely dispersed in the United Kingdom, the Marsh Fern is a comparatively rare plant, being local in occurrence . . . The only Scottish county in which there is certain information of its occurrence is Forfarshire; and the recorded habitats in Ireland are few."2 Other localities are now known, but the main point is clear, that in Europe the species is not primarily a boreal one. In Asia too, its northwestern limit (acc. to Christensen in Hultén) is near Tobolsk, and southward it reaches Algeria, central Italy, Crimea, the Caucasus, southern Turkestan, the Himalayas and southern China. In brief, var. typica belongs to temperate Eurasia.

Similarly, var. pubescens, the almost ubiquitous Marsh Fern of eastern America, is not boreal, reaching its northern limits near the southern borders of eastern Canada and Newfoundland but extending south into the Southern States; while var. Haleana is in a warm-temperate to sub-tropical belt, its northernmost extension on the Bermudas, its southernmost on the Florida Keys. The other variety, var. squamigera, occurs in southern India, tropical and southern Africa and on the North Island of New Zealand. In all three of these varieties, the plants of tropical, subtropical and temperate regions of the Southern Hemisphere and of eastern America and northeastern Asia, the preponderance of long glandless ciliation over short glandularity of the indusia is striking and it seems probable that the original form of the species was a plant of tropical or sub-

<sup>&</sup>lt;sup>1</sup> Holmb. Hartm. Handb. Skand. Fl. revised by Holmb. i. 11 (1922)

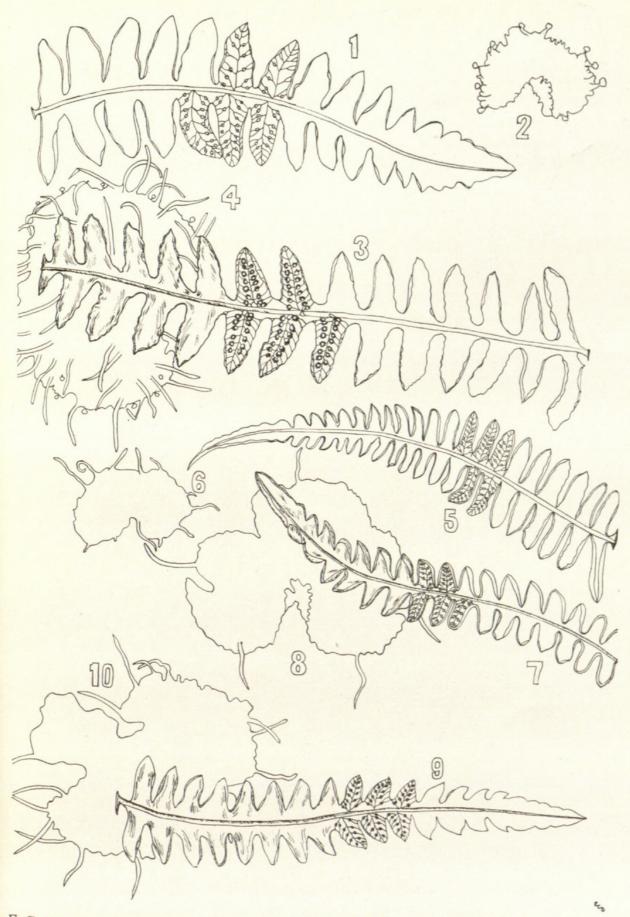
<sup>&</sup>lt;sup>2</sup> Moore, Nat.-Pr. Brit. Ferns (Octavo) i. 167, 168 (1859).

tropical regions, such as vars. squamigera and Haleana and that the more northern var. pubescens and still more extreme var. typica have been of later origin.

# EXPLANATION OF PLATE 180

Varieties of Thelypteris palustris; outlines and venations of pinnae × 1½, outlines of indusia × 50. Figs. 1 and 2, var. Typica; fig. 1 from Sweden, coll. Hugo Granvik, fig. 2 from Bavaria, Reinsch, no. 398. Figs. 3 and 4, var. squamigera, both from Natal, coll. S. L. Abraham, 1865-6. Figs. 5 and 6, var. Haleana, both from the type, Alexandria, Louisiana, J. Hale. Figs. 7-10, var. pubescens; fig. 7 from Shelburne, New Hampshire, coll. W. Deane, August 19, 1915, fig. 8 from Stottville, Quebec, coll. G. G. Kennedy, July 23, 1863, figs. 9 and 10 from Amur, coll. S. Korshinsky, 1891.

(To be continued)



E. C. Dansie del.

# VARIETIES OF THELYPTERIS PALUSTRIS

Figs. 1 and 2, var. Typica; 3 and 4, var. squamigera; 5 and 6, var. Haleana; 7-10, var. pubescens.



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