

A Revised Classification of *Thelypteris* Subgenus *Amauropelta*

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Thelypteris subgenus *Amauropelta* is a highly natural, probably monophyletic group occurring principally in the New World tropics and subtropics. The number of species is large; Christensen (1907, 1913) recognized about 120, and 55 have been described since then. Many undescribed species remain. The size of the subgenus in terms of both the number of "good" species (perhaps 200) and the number of basionyms assignable to the subgenus (ca. 400) makes it desirable that an infrasubgeneric classification be achieved before a revision of closely related species groups is undertaken and before additional species are described.

Christensen made no attempt to subdivide subg. *Amauropelta* (his *Dryopteris* subg. *Lastrea*), but he did recognize small groups of closely related species. As a result of my studies, I feel that the species fall naturally into nine more or less distinct groups, to be given the rank of section. There are relatively few basionyms that must remain unplaced, either because of intermediacy between sections or because type material has not yet been seen. I have attempted to account for all basionyms (based on New World specimens) that should be included within the circumscription of subg. *Amauropelta*. No doubt a few have been missed, especially infraspecific names. The search has been difficult because species have been described under so many different genera and because of the huge number of species in *Thelypteris* s.l. (perhaps 1000). An asterisk following a name in the enumeration of basionyms indicates that I have seen type material.

I thank R. E. Holttum for helping with the Latin diagnoses and curators of the following herbaria for loan of types: A, B, DS, F, GH, HB, K, M, R, SI, S, S-PA, US.

TAXONOMIC CHARACTERS

Rhizome.—Rhizome habit is preponderantly suberect to erect in all sections except sect. *Adenophyllum*, where it is usually decumbent. Creeping rhizomes occur in a few Andean species of sect. *Lepidoneuron* [e.g., *Thelypteris caucaensis* (Hieron.) Alston], and in a few rather aberrant species of sect. *Amauropelta* [*T. firma* (Bak. ex Jenm.) Proctor and allies]. I am uncertain which condition (Rhizome decumbent or erect) is ancestral for the subgenus. Probably evolution has proceeded in both directions within the subgenus and within individual sections.

Stipes.—The bases of stipes, and even entire croziers, of several species groups, i.e., sect. *Phacelothrix*, sect. *Blennocaulon*, and sect. *Amauropelta*, are coated with mucilage. Full development of this layer depends in part on microhabitat: extremely wet or humid conditions seem to favor greater production of mucilage. Microscopic examination of stipes coated with mucilage shows that this layer is the result of secretion by dense, glandular trichomes (Hennipman, 1968; Smith, unpublished).

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Aerophores.—The presence of aerophores at the bases of pinnae and sometimes pinnules is positively correlated with the production of mucilage. Aerophores occur in all species of sect. *Phacelothrix*, where they may be as much as 5 mm long, and in nearly all species of sections *Blennocaulon* and *Amauropelta*. They also occur in a few species of sect. *Uncinella* [*T. diplazioides* (Desv.) Proctor and allies] and sect. *Lepidoneuron* [*Polypodium crossii* Baker]. Aerophores are seemingly absent in species belonging to sections *Apelta*, *Adenophyllum*, and *Blepharitheca*.

Buds.—Many, but not all, species in sect. *Uncinella* produce buds in the axils of upper pinnae. While still attached to the parent plant, these bulblets may remain undeveloped, or they may develop only upon contact with the ground, or they may produce small plantlets. The presence or absence of such buds is usually constant for a given species. Bulblets are unknown in other sections of subg. *Amauropelta*, but do occur in another distantly related subgenus, *Goniopteris*.

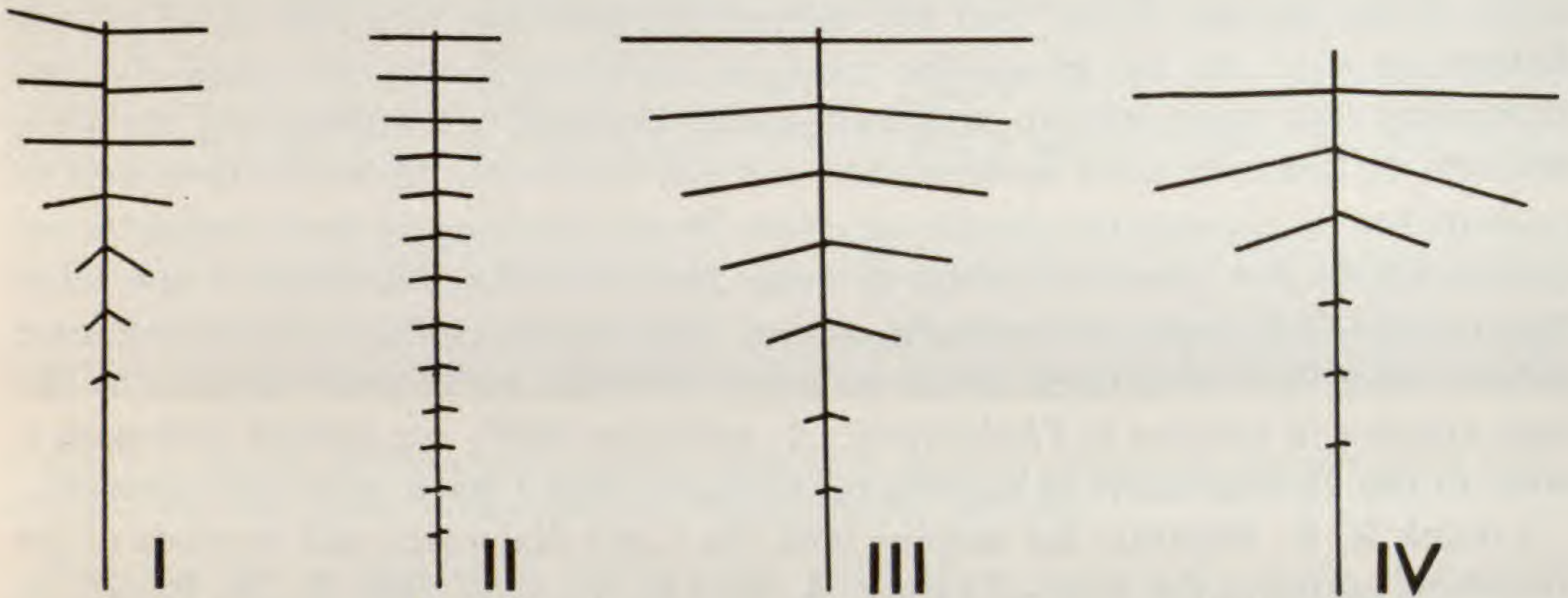


FIG. 1. Blade shapes in *Thelypteris* subg. *Amauropelta* (from Christensen, 1907).

Blade shape.—Christensen (1907) recognized five blade types, four of which I find useful for descriptive purposes (Fig. 1). Species belonging to sections *Lepidoneuron* and *Phacelothrix* consistently have blade type IV, with abruptly reduced lower pinnae and several, small, abortive glanduliform pinnae that are often overlooked. Most species of sect. *Uncinella* have blade type I, with 3–6 gradually reduced pinnae, the lowermost auriculiform. The species of sect. *Amauropelta* are preponderantly blade type II, but there is a line of evolution within the section culminating in a blade with few or even no reduced pinnae (*reducta*, *firma*). In subg. *Amauropelta*, the absence of reduced pinnae is, I believe, derived. Sections *Adenophyllum* and *Blennocaulon* contain species with blade type III.

Blade texture.—Blade texture is subject to great environmental influence, but nevertheless is of use in delimiting large groups of species. Section *Apelta* and species in sect. *Uncinella* related to *T. oligocarpa* (Willd.) Ching are thin-textured. Those species of sect. *Lepidoneuron* allied to *T. rudis* (Kunze) Proctor

generally have a very thick, even coriaceous, lamina. The species of sect. *Blennocaulon* have a subsucculent blade, with slightly impressed and darkened veins.

Sorus.—There is a tendency for sori to be somewhat elongate along the veins in several species of sect. *Uncinella* [e.g., *T. linkiana* (Presl) Tryon and allies]. This condition is certainly derived evolutionarily from species with round sori. Many species in sect. *Lepidoneuron* have slightly oblong sori. Sorus position varies greatly within most sections, but is consistently submarginal in species of sect. *Uncinella* related to *T. oligocarpa* and in *T. cheilanthoides* (sect. *Blennocaulon*).

Indusium.—The generalized and probably ancestral condition in subg. *Amauropelta* is indusiate. The indusium has been lost along several presumably separate evolutionary lines, however. Indusia are consistently absent in sect. *Apelta*, sect. *Blepharitheca*, and sect. *Lepidoneuron*, and absent in a few species of sect. *Blennocaulon* and sect. *Uncinella* [e.g., *T. linkiana*]. In the two last-named cases, the exindusiate species are clearly derived from indusiate ones. A reduced indusium has resulted in many species being described falsely as exindusiate.

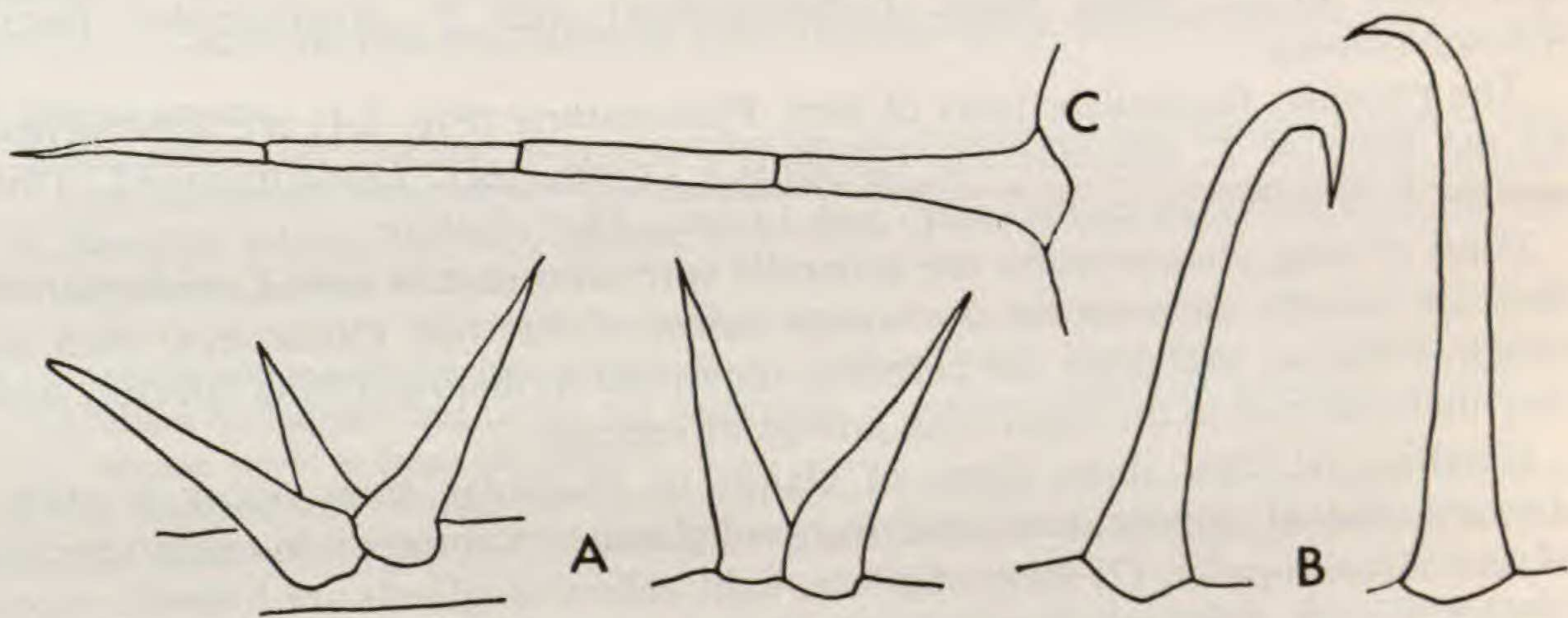


FIG. 2. Hair types in *Thelypteris* subg. *Amauropelta*. A, Fasciculate hairs in *Thelypteris thomsonii* (sect. *Phacelothrix*). B, Uncinate hairs in *Thelypteris melanochlaena* (sect. *Uncinella*). C, Septate hairs in *Thelypteris cheilanthoides* (sect. *Blennocaulon*).

Of the indusiate groups, the species of sect. *Pachyrachis* and most species of sect. *Blennocaulon* have the largest and most persistent indusia.

Indusial color can be important in distinguishing certain species groups. The species of sect. *Uncinella* allied to *T. diplazioides* have greenish indusia. A small group of species in sect. *Amauropelta* show dark, reddish-brown indusia (*sanctiformis*, *cooleyi*, *cornuta*, *brachypoda*).

Sporangia.—Paraphyses are known only from the sporangial walls of several species of sect. *Blepharitheca*, *T. firma* (sect. *Amauropelta*), *Dryopteris heineri* C. Chr., and *D. peruviana* Rosenst. (sect. *Lepidoneuron*), and in a few species of sect. *Adenophyllum* [e.g., *T. subandina*]. Sporangial setae are probably independently derived in all four sections.

Spores.—Wood's (1973) survey of spores in the Thelypteridaceae provides convincing evidence for the homogeneity of subg. *Amauropelta*. At the light microscope level, the spores appear to have a uniform, granular surface. Under the scanning electron microscope, the surface is a highly anastomosing, uniform reticulum which is very distinct from most other Thelypteridaceae. There seems to be very little variability within the subgenus, although Wood reports that *T. firma* has spores with only a partial reticulum and *T. aspidioides* has spores with a spiny reticulum. Both of these species, although somewhat atypical, are good members of *Amauropelta* on other morphological grounds.

Hairs.—Hair types are illustrated in Fig. 2. Again, convergent evolution has obscured the more basic pattern of divergent evolution. Septate hairs occur in nearly all species belonging to sect. *Blennocaulon*. But they occur also in a few species of other sections, as in *T. balbisii* (Spreng.) Ching (sect. *Amauropelta*) and in the species of sect. *Adenophyllum* related to *T. argentina* (Hieron.) Abbiatti.

The unciniate (hamate) hairs of sect. *Uncinella* (Fig. 2B) are nearly always diagnostic for the section, but a few such hairs can occasionally be found in some specimens of *T. rudis* (sect. *Lepidoneuron*) and *T. rivularioides* (sect. *Adenophyllum*).

The peculiar, fasciculate hairs of sect. *Phacelothrix* (Fig. 2A) are approached by the hairs of *T. phacelothrix* (Rosenst.) Tryon (sect. *Lepidoneuron*). This species is possibly an evolutionary link to sect. *Phacelothrix*.

Hairs of subg. *Amauropelta* are generally spreading, but in sect. *Lepidoneuron* they are usually antrorse on the costae below. Other hair characters, such as length, stiffness, and color are certainly important in distinguishing species, and may be important in distinguishing groups of species.

Glands.—At least three kinds of glands or glandular hairs occur in subg. *Amauropelta*: (1) sessile, hemispherical, red glands are common in many species of sect. *Amauropelta*; (2) short-stipitate, light yellowish glands are found in most species of sect. *Adenophyllum*; and (3) clavate, deep red glands are present in a small group of species of sect. *Adenophyllum* related to *T. argentina*. The absence of glands is nearly always diagnostic for sections *Uncinella*, *Apelta*, and *Lepidoneuron*.

TAXONOMIC TREATMENT

¹¹⁴³⁰ **Thelypteris subg. Amauropelta (Kunze) A. Reid Smith, Amer. Fern J. 63: 121. 1973.**

Amauropelta Kunze, Farnkr. 1: 86, 109. 1843. TYPE: *Amauropelta breutelii* Kunze [= *Thelypteris limbata* (Swartz) Proctor].

Oochlamys Fée, Gen. Fil. 297. 1852. TYPE: *Oochlamys rivoirei* Fée [= *Thelypteris opposita* (Vahl) Ching].

Dryopteris subg. *Lastrea sensu* C. Chr. Biol. Arb. tilg. Eug. Warming 79. 1911, and *sensu* C. Chr. K. Danske Vidensk. Selsk. VII, 10: 55-282. 1913.

Thelypteris subg. *Lastrea sensu* Alston, J. Wash. Acad. Sci. 48: 232. 1958, and *sensu* Morton, Amer. Fern J. 53: 153. 1963.

Rhizomes suberect to erect, occasionally decumbent; blades pinnate-pinnatifid (rarely pinnate or decomposed), with the lowermost pinnae reduced, sometimes nearly to the rhizome; aerophores present at the bases of pinnae, or absent; veins usually simple, occasionally furcate, meeting the margin of the segments, the lowermost veins of each segment running to the margin above the sinus; sori round to occasionally somewhat elongate, medial to submarginal on the veins, furnished with large to small indusia or indusia absent; sporoderm evenly granular (light microscope), finely reticulate (scanning electron microscope); $x=29$.

About 200 species, found mostly at middle to higher elevations on the margins of rain forests, along trails, wet roadside embankments, and the margins of streams, in tropical and subtropical America (Mexico, Florida, the Antilles, Central America, and South America to northern Argentina and Chile), with one species in Hawaii and one or a few in Africa, Madagascar, and the Mascarene Islands.

Some epithets have not yet been transferred to *Thelypteris*, and others need not be. I have cited names as basionyms or as epithets alone in some cases where the names are correct in *Thelypteris* but the combinations may or may not have been made.

KEY TO THE SECTIONS OF THELYPTERIS SUBG. AMAUROPelta

1. Indusia present.

2. Rhizomes usually creeping, suberect in a few species; laminae and axes with short-stipitate, light yellowish glands; veins often furcate; aerophores absent.....1. *Adenophyllum*
2. Rhizomes suberect to erect; laminae with sessile glands or eglandular; veins unbranched; aerophores present or absent.
 3. Hairs on rachises and costae fasciculate; prominent aerophores up to 5 mm long at base of costae and usually costules; blades abruptly reduced below (Type IV)2. *Phacelothrix*
 3. Hairs on rachises and costae not fasciculate, \pm evenly distributed; aerophores present or absent, never at bases of costules.
 4. Laminae with uncinata hairs; sori often submarginal, furnished with a very small indusium; blades with ca. 3-6 pairs of gradually reduced pinnae (Type I); blades and indusia without glands3. *Uncinella*
 4. Laminae with straight hairs or glabrous; sori medial to submarginal, the indusia easily visible; blades and often indusia glandular.
 5. Laminae usually gradually tapering nearly to the rhizome, with many pairs of reduced pinnae (Type II); laminae and axes pubescent, the hairs unicellular.....4. *Amauropelta*
 5. Laminae with usually fewer than 8 pairs of gradually reduced pinnae (Type III); laminae and axes glabrous or pubescent with septate hairs.
 6. Axes pubescent with septate hairs; veins slightly sunken below, often darkened; sori submarginal 5. *Blennocaulon*
 6. Axes without hairs; veins flush or slightly raised; sori medial6. *Pachyrachis*

1. Indusia absent.

7. Scales present on costae below, these sometimes clathrate or subclathrate; blades rather abruptly reduced below, with several abortive or auriculiform pinnae (Type IV).....7. *Lepidoneuron*
7. Scales absent on costae below; blades gradually reduced.
 8. Laminae and axes with uncinata hairs.....3. *Uncinella*
 8. Laminae and axes with straight hairs.
 9. Rachises and costae with dense, minute pubescence, the hairs less than 0.1 mm long; stipes and rachises darkened; sporangia glabrous or setose8. *Blepharitheca*
 9. Rachises and costae sparsely pubescent to glabrous; stipes and rachises stramineous; sporangia glabrous9. *Apelta*

15 **1. Thelypteris sect. Adenophyllum A. Reid Smith, sect. nov.**

Rhizomata repentia vel erecta; laminae deorsum sensim reductae (Typus II), pinnis infimis auriculiformibus, distantibus; bases pinnarum aerophoris destitutae; costae, venae et laminae glandulis stipitatis flavidis praeditae, paleis destitutae; indusia praesentia, saepe magna.

✓TYPE: *Aspidium rivularioides* Fée [≡ *Thelypteris rivularioides* (Fée) Abbiatti].

Perhaps 25 species, in southern Brazil, northern Argentina, Paraguay, Uruguay, Bolivia to Colombia, Venezuela, and north to southern Mexico. The only species occurring in North America is *T. pilosula* (Mett.) Tryon, from southern Mexico to Peru.

Aspidium achalense Hieron.*, *Aspidium arechavaletae* Hieron., *Aspidium argentinum* Hieron., *Thelypteris burkartii* Abbiatti*, *Polypodium camporum* Lindman, *Aspidium galanderi* Hieron.*, *Dryopteris glanduloso-lanosa* C. Chr.*, *Dryopteris hassleri* Christ*, *Dryopteris janeirensis* Rosenst.*, *Nephrodium juergensii* Rosenst.*, *Dryopteris juergensii* (Rosenst.) C. Chr. var. *hirsutula* Rosenst.*, *Aspidium lorentzii* Hieron.*, *Thelypteris minensis* Abbiatti, *Dryopteris mosenii* C. Chr.*, *Dryopteris neglecta* Brade & C. Chr.*, *Aspidium oligocarpum* (Willd.) H.B.K. var. *crassistipitatum* Hieron.*, *Dryopteris organensis* Rosenst.*, *Thelypteris pilosissima* Morton*, *Aspidium pilosulum* Mett.*, *Thelypteris platensis* Abbiatti*, *Aspidium pseudomontanum* Hieron., *Nephrodium pseudothelypteris* Rosenst.*, *Dryopteris rimbachii* Rosenst.*, *Aspidium rivularioides* Fée*, *Dryopteris rivularioides* (Fée) Rosenst. var. *crenata* Rosenst.*, *Dryopteris rivularioides* (Fée) Rosenst. var. *umbratica* Rosenst.*, *Dryopteris rojasii* Christ*, *Dryopteris rosei* Maxon*, *Dryopteris santae-catharinae* Rosenst.*, *Dryopteris scariosa* Rosenst.*, *Aspidium siambonensis* Hieron.*, *Dryopteris subandina* C. Chr. & Rosenst., *Dryopteris subandina* f. *minor* C. Chr. & Rosenst.*, *Dryopteris vattuonei* Hicken*.

This is perhaps the most heterogeneous of any of the sections that I recognize, but I believe that the species included within it are all more closely related to each other than to members of any of the other sections. Three elements can be discerned: (1) a group of very poorly circumscribed species with long-creeping rhizomes, occurring in southern Brazil, northern Argentina, Uruguay, and Paraguay (*achalense*, *hassleri*, *janeirensis*, *juergensii*, *mosenii*, *neglecta*, *platensis*, *rivularioides*, *rojasii*, *santae-catharinae*, *scariosa*, *siambonense*, *vattuonei*); (2) species allied to *T. argentina* (Hieron.) Abbiatti, with suberect rhizomes, stramineous stipes with blackened bases, and deep-red glands at the bases of costules and sometimes along the costules, distributed primarily in northwestern Argentina, Chile, Bolivia, and Peru (*argentina*, *burkartii*, *galanderi*, *glanduloso-lanosa*, *lorentzii*); and (3) species allied to *T. pilosula*, with long, dense, stiff, spreading hairs covering the rachis and costae, and an erect rhizome (*pilosissima*, *pilosulum*, *rimbachii*). The two last-named groups are connected through such species as *subandina*.

16 **2. Thelypteris sect. Phacelothrix A. Reid Smith, sect. nov.**

Rhizomata crassa, erecta; frondes volutae mucosae; pinnae versus basin laminarum abrupte reductae (Typus IV), pinnis infimis glandiformibus; aerophora usque 5 mm longa e basibus costarum costularumque exorientia; costae subtus paleis destitutae; laminae subtus (etiam venae) pilis fasciculatis glandulisque sessilibus rubris vestitae; indusia parva.

✓TYPE: *Polypodium thomsonii* Jenm. [≡ *Thelypteris thomsonii* (Jenm.) Proctor].

About 5 species, in montane cloud forests, at middle to higher elevations, from Hispaniola, Jamaica, southern Mexico (Oaxaca, Chiapas), Central America, and

Colombia to Bolivia.

Dryopteris andina Morton, *Dryopteris boliviensis* Morton, *Nephrodium cañadasii* Sod., *Nephrodium macradenium* Sod., *Dryopteris stubelii* Hieron., *Polypodium thomsonii* Jenm.

The species belonging to sect. *Phacelothrix* were formerly included in subg. *Glaphyopteris* by Christensen (1913) and in sect. *Glaphyopteris* by Morton (1938). However, *Glaphyopteris*, in my opinion, is an unnatural group, an idea first suggested to me a few years ago by R. E. Holttum. The type of *Glaphyopteris* [*T. decussata* (L.) Proctor] and its allies [*T. mapirensis* (Rosenst.) Alston, *T. comosa* (Morton) Morton, *T. polyphlebia* (C. Chr.) Morton, *T. brasiliensis* (C. Chr.) Morton, and *T. tatei* (Maxon & Morton) Morton] are all characterized by non-fasciculate septate hairs, the absence of reduced proximal pinnae, very close veins, and exindusiate sori. These species are all found at low to middle elevations, usually below 2000 m. *Thelypteris decussata* is the only species from which a chromosome count has been obtained, reported by Sorsa (in Fabbri, 1965) as $n=72$.

The remaining species in *Glaphyopteris sensu* Morton I include in sect. *Phacelothrix*; these are all characterized by having fasciculate, non-septate hairs, abruptly reduced basal pinnae, veins further apart, and indusiate sori. All of the species occur at higher elevations, generally above 2000 m. The sole species known chromosomally is *T. thomsonii*, reported by Walker (1966) as $n=58$.

Section *Phacelothrix* seems to me to be most closely related to sect. *Lepidoneuron*, through such species as *T. phacelothrix* (Rosenst.) Tryon, which bears costal scales like those of species of sect. *Lepidoneuron*, but shows a tendency toward the fasciculate hairs of sect. *Phacelothrix*.

24067 **3. Thelypteris sect. Uncinella A. Reid Smith, sect. nov.**

Rhizomata erecta vel repentia; laminae basin versus gradatim angustatae, 3-5 (raro pluribus) paribus pinnarum inferiorum reductis (Typus I); axillae pinnarum distalium saepe gemmiferae; costae subtus plerumque paleis destitutae; laminae eglandulosae, subtus (etiam venae) pilis uncinatis, supra pilis appressis vestitae; sori rotundi vel leviter elongati; indusia parva, saepe abscondita, vel nulla.

TYPE: *Polypodium oligocarpum* Willd. [≡ *Thelypteris oligocarpa* (Humb. & Bonpl. ex Willd.) Ching]. 27446

Perhaps 50 species, from the Antilles, southern Mexico (5 sp.) through Central America and South America to Bolivia and southern Brazil. At least one species, *T. bergiana* (Schlecht.) Ching, occurs in Africa.

Ceterach aspidioides Willd., *Dryopteris aspidioides* (Willd.) C. Chr. var. *subhastata* C. Chr., *Gymnogramma asplenioides* Swartz, *Polypodium asplenioides* Swartz, *Aspidium atrorubens* Mett.*, *Dryopteris atrovirens* C. Chr. in Christ*, *Nephrodium brachypus* Sod.*, *Dryopteris columbiana* C. Chr.*, *Nephrodium conforme* Sod.*, *Polypodium consanguineum* Klotzsch*, *Aspidium diplazioides* Moritz ex Mett.*, *Dryopteris diplazioides* (Desv.) Urban var. *brevisora* Rosenst.*, *Gymnogramma diplazioides* Desv., *Dryopteris dominicensis* C. Chr.*, *Phegopteris duchassaingiana* Fée, *Dryopteris dutrai* C. Chr. ex Dutra, *Aspidium fischeri* Mett., *Aspidium funckii* Mett.*, *Dryopteris funckii* (Mett.) Kuntze var. *angustiloba* Hieron., *Dryopteris funckii* var. *obtusa* Hieron., *Dryopteris funckii* var. *strigosa* Hieron., *Phegopteris germaniana* Fée, *Gymnogramma gracilis* Heward [≡ *Grammitis hewardii* Moore], *Gymnogramma gracilis* Heward var. *consimilis* Fée ex Baker, *Phegopteris gracilis* (Heward) Mett. var. *guadalupensis* Fée, *Polypodium heteroclitum* Desv., *Phegopteris hydrophila* Fée, *Polypodium induens* Maxon var. *subdentatum* Bosco, *Dryopteris irenae* Brade, *Aspidium kaul-*

fussii Link*, *Aspidium lasiesthes* Kunze, *Dryopteris leptogrammoides* Rosenst., *Dryopteris lindmanii* C. Chr.*, *Grammitis linkiana* Presl, *Dryopteris lomatosora* Copel.*, *Dryopteris melanochlaena* C. Chr.*, *Dryopteris mollicella* Maxon*, *Dryopteris moritziana* Urban, *Aspidium navarrense* Christ, *Nephrodium nimbatum* Jenm., *Polypodium oligocarpum* Humb. & Bonpl. ex Willd., *Polypodium oligosorum* Klotzsch, *Gymnogramme oppositans* Fée, *Gymnogramme polypodioides* Link, *Aspidium ptarmica* Kunze ex Mett., *Dryopteris ptarmiciformis* C. Chr. & Rosenst.*, *Aspidium pusillum* Mett., *Dryopteris raddii* Rosenst. var. *itatiayensis* Rosenst., *Dryopteris recumbens* Rosenst.*, *Dryopteris recumbens* var. *violacea* Rosenst., *Dryopteris regnelliana* C. Chr., *Polypodium retusum* Swartz [\equiv *Dryopteris raddii* Rosenst.], *Dryopteris retusa* (Swartz) C. Chr. f. *denticulata* Rosenst., *Dryopteris rioverdensis* C. Chr.*, *Dryopteris rivulariformis* Rosenst. [\equiv *Dryopteris stenophylla* Rosenst., 1908, non C. Chr., 1905], *Leptogramme rupestris* Klotzsch*, *Phegopteris rustica* Fée, *Polypodium saxicola* Swartz, *Aspidium scalare* Christ*.

At least three distinct groups of species can be recognized within sect. *Uncinella*: (1) the group of *T. linkiana* (Presl) Tryon, which includes species with exindusiate, often elongate sori, short-stipitate lower pinnae, and less deeply incised pinnae (e.g., *aspidioides*, *linkiana*, *ptarmica*); (2) the group of *T. diplazioides* (Moritz ex Mett.) Ching, with more numerous reduced pinnae, more or less prominent aerophores, relatively large indusia that are greenish in several species, more scaly axes culminating in the rather densely scaly costae of *T. funckii* (Mett.) Alston (e.g., *brachypus*, *diplazioides* Mett., *dominicensis*, *funckii*, *rustica*); and (3) the group of *T. oligocarpa*, with deeply cut pinnae, often falcate segments, submarginal sori furnished with minute indusia, and the absence of aerophores. This group contains the bulk of the species in the section. Groups 1 and 2 seem to me to be derived from Group 3.

Section *Uncinella* is evidently most closely related to sect. *Lepidoneuron*, on one hand, and sect. *Adenophyllum* on the other. Nearly all species can be readily placed by the character of uncinata hairs.

24074 4. *Thelypteris* sect. *Amauropelta*

Rhizomata erecta (vel speciebus paucis repentia); stipites perbreves; laminae plerumque basin versus sensim reductae (Typus II), pinnis reductis multis; aerophora parva, manifesta; laminae glandulosae vel eglandulosae, glandulis sessilibus, rubris vel aurantiacis; indusia praesentia, straminea vel brunneola, saepe glandulosa.

TYPE: Same as subg. *Amauropelta*.

Perhaps 50 species, from Florida (1 species), the Antilles, Mexico (4 species) through Central America, and tropical South America from Colombia to Bolivia and southeastern Brazil (1 species).

The center of evolution of the section is in the West Indies, where there are about 20 species, most of them endemic to one or a few islands. The species with red glands have been discussed by Morton (1963); however, not all these species belong in this section.

A single Hawaiian species, *Thelypteris globulifera* (Brack.) Reed, appears to belong in this section. It agrees with Neotropical members in having sessile, red glands, gradually decrescent lamina, relatively large, persistent indusia, and small aerophores. A chromosome count is highly desirable and, if based on 29, would provide nearly conclusive evidence of its New World affinities, in my opinion. According to Holttum (pers. comm.), a few African species may also belong in this section.

Phegopteris adenochrysa Fée, *Dryopteris aequatorialis* Copel.*, *Dryopteris aliena* C. Chr.*, *Nephrodium amphioxypteris* Sod.*, *Lastrea angustata* Presl, *Polypodium balbisii* Spreng., *Nephrodium basiattenuatum* Jenm., *Aspidium berteroanum* Fée, *Nephrodium brachypodium* Bak.*, *Amauropelta breutelii* Kunze, *Nephrodium caribaeum* Jenm.*, *Aspidium coarctatum* Kunze, *Dryopteris coarctata* (Kunze) C. Chr. var. *longipes* C. Chr., *Aspidium consanguineum* Fée, *Aspidium conterminum* Willd., *Thelypteris cooleyi* Proctor*, *Dryopteris cornuta* Maxon*, *Dryopteris crespiana* Bosco, *Aspidium exsudans* Fourn., *Nephrodium firmum* Bak. ex Jenm., *Dryopteris furva* Maxon*, *Aspidium ghiesbreghtii* Fourn., *Aspidium glanduliferum* Karst. ex Klotzsch*, *Dryopteris glutinosa* C. Chr.*, *Polypodium gracilentum* Jenm., *Dryopteris harcourtii* Domin, *Dryopteris hastiloba* C. Chr.*, *Nephrodium jamaicense* Bak. in Jenm., *Lastrea leiboldiana* Presl, *Dryopteris leucothrix* C. Chr.*, *Dryopteris leucothrix* C. Chr. var. *glanduligera* C. Chr. & Rosenst., *Aspidium limbatum* Swartz, *Polypodium litigiosum* Liebm.*, *Nephrodium longicaule* Baker*, *Dryopteris mercurii* A. Braun ex Hieron., *Thelypteris minutula* Morton*, *Thelypteris mortonii* A. Reid Smith*, *Nephrodium nockianum* Jenm., *Dryopteris novaeana* Brade, *Dryopteris opposita* (Vahl) Urban var. *geraensis* C. Chr., *Dryopteris opposita* var. *longissima* C. Chr., *Dryopteris opposita* var. *mettenii* Rosenst., *Dryopteris opposita* (Vahl) Urban var. *pubescens* Hieron., *Polypodium oppositum* Vahl, *Aspidium pachyklamys* Fée, *Nephrodium panamense* Presl, *Dryopteris panamensis* (Presl) C. Chr. var. *gonzalezii* C. Chr., *Dryopteris panamensis* var. *proxima* C. Chr.*, *Aspidium physematioides* Kuhn & Christ in Krug, *Dryopteris piedrensis* C. Chr.*, *Polypodium plumieri* Desv., *Aspidium polyphyllum* Kaulf., *Dryopteris pseudosancta* C. Chr.*, *Thelypteris randallii* Maxon & Morton*, *Dryopteris reducta* C. Chr.*, *Polypodium resiniferum* Desv., *Aspidium rigidulum* Mett. ex Kuhn*, *Oochlamys rivoirei* Fée, *Polypodium rivulorum* Raddi, *Dryopteris sanctiformis* C. Chr.*, *Aspidium sanctoides* Fée, *Acrostichum sanctum* L. [\equiv *Lastrea linnaeana* Copel.], *Nephrodium sanctum* (L.) Baker var. *hirtum* Jenm., *Dryopteris sancta* (L.) Kuntze var. *portoricensis* C. Chr., *Dryopteris sancta* var. *strigosa* C. Chr., *Dryopteris sancta* var. *terminalis* C. Chr., *Nephrodium sanctum* (L.) Baker var. *magnum* Jenm., *Phegopteris scalpturoides* Fée*, *Dryopteris scalpturoides* (Fée) C. Chr. var. *subbipinnata* C. Chr.*, *Dryopteris scalpturoides* var. *jamaicensis* C. Chr., *Dryopteris shaferi* Maxon & C. Chr.*, *Nephrodium sherringii* Jenm., *Aspidium sprengelii* Kaulf., *Dryopteris sprengelii* (Kaulf.) Kuntze var. *longipilosa* C. Chr., *Aspidium strigosum* Fée, *Dryopteris struthiopteroides* C. Chr.*, *Phegopteris tenella* Fée, *Dryopteris underwoodiana* Maxon, *Dryopteris vaccanea* Bosco.

I have included several primarily South American species in sect. *Amauropelta*; these differ from the bulk of the Antillean species in having a much smaller number of reduced basal pinnae, darkened (sometimes atropurpureous) stipes and rachises, lamina without bright sessile glands, and in indusia larger, more rotund, glabrous, and dark brown (*brachypodium*, *cooleyi*, *cornuta*, *furva*, *longicaule*, and *sanctiformis*).

Another natural group, perhaps deserving subsectional recognition, within sect. *Amauropelta* is the group that culminates in *Thelypteris firma* (Bak. ex Jenm.) Proctor. Allied species are *aliena* and *reducta*. This small group is connected to more typical members of sect. *Amauropelta* through such species as *scalpturoides*, *shaferi*, and *hastiloba*. Character trends in these species are the loss of glands (present, however, in *firma*), thickened subcoriaceous texture with prominent raised veins, reduced lower pinnae few or none, and creeping rhizome.

The most aberrant element in sect. *Amauropelta* and one that I place here only hesitatingly is *Thelypteris minutula* Morton, from the páramo of Ecuador. The fronds are very narrow, densely glandular, and nearly exindusiate, with small, wiry stipes. Its closest ally may be *glutinosa* from Haiti.

Section *Amauropelta* has close affinities only to sections *Pachyrachis* and *Blennocaulon*.

24075 5. *Thelypteris* sect. *Blennocaulon* A. Reid Smith, sect. nov.

Rhizomata crassa, erecta; frondes volutae mucosae; aerophora praesentia, saepe prominentia; costae rhachidesque pilis septatis elongatis praeditae; segmenta basalia basiscopica pinnarum prolongata; laminae subtus glandulis sessilibus praeditae; venae saepe fuscatae, subtus subimmersae; sori submarginales, indusiati vel interdum exindusiati.

✓TYPE: *Aspidium cheilanthoides* Kunze [≡ *Thelypteris cheilanthoides* (Kunze) Proctor] ⁷⁴³²

Perhaps 10 species, mostly at middle elevations, from southern Mexico, Jamaica, and Hispaniola to Bolivia, southeastern Brazil.

Nephrodium atomiferum Sod.*, *Dryopteris bañiensis* Rosenst.*, *Aspidium cheilanthoides* Kunze, *Dryopteris cheilanthoides* (Kunze) C. Chr. var. *eglandulosa* C. Chr. in Christ, *Thelypteris cheilanthoides* (Kunze) Proctor var. *mucosa* A. Reid Smith*, *Aspidium decrescens* Kunze ex Mett., *Dryopteris deflectens* C. Chr.*, *Dryopteris densa* Maxon*, *Lastrea grossa* Presl, *Aspidium kunzei* Fée [≡ *Dryopteris oochlamys* C. Chr.], *Dryopteris lanipes* C. Chr.*, *Dryopteris lanipes* f. *minor* C. Chr.*, *Dryopteris limaensis* Copel.*, *Dryopteris mertensioides* C. Chr., *Dryopteris multiformis* C. Chr., *Polypodium nitens* Desv., *Dryopteris opposita* (Vahl) Urban var. *mettenii* f. *major* Rosenst.*, *Dryopteris pabstii* Brade*, *Nephrodium resinoso-foetidum* Hook.*, *Nephrodium rigescens* Sod., *Polypodium ruizianum* Klotzsch*, *Nephrodium sprengelii* (Kaulf.) Hook var. *persicinum* Jenm., *Dryopteris supina* (Sod.) C. Chr. var. *biolleyi* Christ.

Section *Blennocaulon* is close to sect. *Pachyrachis* and also to certain species of sect. *Amauropelta* (*T. opposita*). From both of these, sect. *Blennocaulon* usually can be distinguished by the presence of pluricellular hairs on the veins and major axes, by the slightly immersed and blackened veins, and by the somewhat elongate basal basiscopic segments.

Certainly a few exindusiate species belong here, i.e., *deflectens*, *multiformis*, *nitens*, and *ruizianum*. These four are also somewhat atypical in having medial or inframedial sori. Within sect. *Blennocaulon*, I believe these characters (exindusiate, medial sori) are derived. A revision of the species is needed.

24076 6. *Thelypteris* sect. *Pachyrachis* A. Reid Smith, sect. nov.

Rhizomata erecta; frondes volutae mucosae; laminae deorsum gradatim angustatae (Typus III); aerophora praesentia, saepe prominentia; costae rhachidesque epilosae; costae subtus paleis appressis tenuibus stramineis vestitae; laminae subtus glandulis sessilibus rubris vel aurantiacis praeditae; sori mediales, indusiis magnis persistentibus glabris.

✓TYPE: *Aspidium pachyrachis* Kunze ex Mett. [≡ *Thelypteris pachyrachis* (Kunze ex Mett.) Ching] ⁹⁴⁴¹

About 10 species, at middle elevations, from the Greater Antilles (Jamaica, Hispaniola), southern Mexico (Oaxaca, Chiapas), Central America, Venezuela to Bolivia, and southeastern Brazil.

Aspidium berterioanum Fée, *Dryopteris consanguinea* (Fée) C. Chr. var. *aequalis* C. Chr.*, *Nephrodium crassipes* Sod., *Aspidium elatior* Fée*, *Dryopteris germaniana* (Fée) C. Chr. var. *glandulosa* C. Chr., *Aspidium helveolum* Fée*, *Dryopteris hieronymusii* C. Chr.*, *Dryopteris illicita* Christ, *Nephrodium jenmanii* Bak. ex Jenm.*, *Nephrodium jenmanii* Bak. ex Jenm. var. *sitorum* Jenm., *Dryopteris malangae* C. Chr., *Thelypteris oaxacana* A. Reid Smith*, *Aspidium pachyrachis* Kunze ex Mett., *Dryopteris pachyrachis* (Kunze ex Mett.) Kuntze var. *bogotensis* C. Chr., *Nephrodium palustre* Bak. in Hook & Bak. [≡ *Thelypteris metteniana* Ching], *Aspidium platyrachis* Fée*, *Dryopteris riopardensis* Rosenst.*, *Nephrodium sprucei* Bak. in Hook. & Bak.*, *Aspidium tablanum* Christ*, *Aspidium tenerrimum* Fée*.

The relationship of sect. *Pachyrachis* is certainly with sect. *Blennocaulon* and sect. *Amauropelta*. The lamina and axes are without hairs, but sessile, reddish glands similar to those found in sect. *Amauropelta* occur on the leaf tissue below in most species. The stramineous to tan, adpressed costal scales are wholly unlike those found in species of sect. *Lepidoneuron*. Indusia are generally larger and more easily seen than in any of the other sections of the subgenus.

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7. *Thelypteris* sect. *Lepidoneuron* A. Reid Smith, sect. nov.

Rhizomata plerumque erecta vel suberecta, raro repentia; pinnae inferiores abrupte reductae, remotae, glandiformes (Typus IV); costae subtus paleis brunneis, subclathratis et pilis appressis praeditae; laminae eglandulosae; sori indusiis destituti.

✓TYPE: *Polypodium rude* Kunze [\equiv *Thelypteris rudis* (Kunze) Proctor].

Perhaps 50 species, from Mexico (2 species) and the Greater Antilles (ca. 3 species) to Bolivia, and southeastern Brazil (2 species), but primarily Andean, with the greatest number of species at middle to higher elevations in wet, mountainous areas of Colombia, Ecuador, and Peru.

Dryopteris abbotiana Maxon*, *Dryopteris alfredii* Rosenst.*, *Thelypteris antillana* Proctor*, *Dryopteris arborea* Brause, *Dryopteris atropurpurea* Hieron.*, *Dryopteris bonapartii* Rosenst., *Dryopteris boqueronensis* Hieron.*, *Dryopteris bradei* Christ*, *Dryopteris bradei* var. *palmensis* Rosenst., *Dryopteris brausei* Hieron.*, *Dryopteris caeca* Rosenst., *Dryopteris canelensis* Rosenst., *Nephrodium caucaense* Hieron.*, *Dryopteris cochaensis* C. Chr.*, *Nephrodium corazonense* Baker*, *Polypodium crossii* Baker*, *Phegopteris ctenoides* Fée, *Polypodium demeraranum* Baker*, *Dryopteris dumetorum* Maxon*, *Nephrodium elegantulum* Sod., *Dryopteris engelii* Hieron., *Polypodium euchlorum* Sod., *Dryopteris euchlora* (Sod.) C. Chr. var. *inaequans* C. Chr.*, *Gymnogramme expansa* Fée, *Aspidium glaziovii* Christ, *Aspidium gleichenioides* Christ, *Dryopteris heineri* C. Chr.*, *Dryopteris herzogii* Rosenst.*, *Dryopteris horrens* Hieron., *Phegopteris impressa* Fée, *Dryopteris intromissa* C. Chr.*, *Dryopteris jimenezii* Maxon & C. Chr.*, *Phegopteris laevigata* Mett. ex Kuhn * [\equiv *Polypodium lechleri* Bak.], *Nephrodium lasiopteris* Sod., *Nephrodium lustratum* Hieron.*, *Dryopteris macbridei* C. Chr. & Maxon*, *Dryopteris millei* C. Chr., *Thelypteris muscicola* Proctor*, *Dryopteris muzensis* Hieron.*, *Polypodium nervosum* Klotzsch*, *Gymnogramme patula* Fée, *Polypodium pavonianum* Klotzsch*, *Dryopteris pavoniana* (Klotzsch) C. Chr. var. *contracta* Hieron., *Dryopteris perstrigosa* Maxon*, *Dryopteris peruviana* Rosenst., *Dryopteris phacelothrix* C. Chr. & Rosenst.*, *Alsophila pilosa* Mart. & Gal., *Nephrodium piloso-hispidum* Hook., *Dryopteris pittieri* C. Chr.*, *Aspidium pterifolium* Mett. ex Kuhn, *Polypodium pteroideum* Klotzsch, *Dryopteris pteroidea* (Klotzsch) C. Chr. var. *subsagittata* C. Chr., *Nephrodium retrorsum* Sod., *Dryopteris roraimense* Brause, *Dryopteris rosenstockii* C. Chr.*, *Polypodium rude* Kunze, *Dryopteris rudis* (Kunze) C. Chr. var. *gradata* C. Chr., *Dryopteris rusbyi* C. Chr., *Dryopteris rusbyi* var. *major* Rosenst., *Nephrodium semilunatum* Sod., *Dryopteris silviensis* Hieron.*, *Dryopteris strigifera* Hieron.*, *Aspidium subdecussatum* Christ, *Nephrodium tetragonum* Presl, *Dryopteris utanagensis* Hieron.

Two Lesser Antillean species (*muscicola*, *antillana*) are tentatively placed here, but they differ from most other members of sect. *Lepidoneuron* in having minute indusia.

Several evolutionary trends are discernible within sect. *Lepidoneuron*. The most noticeable is for the lamina to be more dissected (bipinnate-pinnatifid in *pteroidea* and *glaziovii*). Often correlated with this greater dissection is the tendency for the segments to be reflexed. Another trend is for loss of indument (hairs and/or scales). This can be seen in *caucaensis* and *laevigata*. Dark, sometimes polished stripes and rachises are yet another trend in several South American

species (*pavoniana*, *atropurpurea*, *laevigata*, *arborea*).

24078 8. *Thelypteris* sect. *Blepharitheca* A. Reid Smith, sect. nov.

Rhizomata erecta; stipites rhachidesque fuscae, pilis densis brevissimis uniformibus infra 0.1 mm longis vestitae; pinnae inferiores sensim reductae (Typus III); costae, costulae, venae et plerumque laminae utrinque pilis similibus praeditae, eglandulosae; costae paleis destitutae; indusia nulla vel minutissima; sporangia setulosa vel glabra.

✓ TYPE: *Polypodium concinnum* Willd. [≡ *Thelypteris concinna* (Willd.) Ching]. 7437

About 5 species, at middle elevations, on shady banks, in ditches, and along forest margins, from the Antilles, southern and eastern Mexico, Central America, Venezuela, Colombia to Bolivia and northwestern Argentina, and southeastern Brazil.

Dryopteris christensenii Christ, *Polypodium concinnum* Willd., *Phegopteris elongata* Fourn., *Phegopteris leptoptera* Fée, *Polypodium molliculum* Kunze ex Link, *Nephrodium stenophyllum* Sod.*, *Gymnogramme stierii* Rosenst.*.

The affinities of sect. *Blepharitheca* are uncertain. In some respects it approaches the *T. oligocarpa* group, especially *atrorubens* (sect. *Uncinella*). It is apparently not closely related to any of the other exindusiate sections.

24080 9. *Thelypteris* sect. *Apelta* A. Reid Smith, sect. nov.

Rhizomata erecta; stipites rhachidesque stramineae, glabrae, stipites basi denigrati; aerophora nulla; laminae tenues, eglandulosae pinnarum inferiorum 2-4 paribus gradatim reductis, pinnis infimis auriculiformibus; costae subtus epaleatae, glabrae vel pilis dispersis patentibus praeditae; indusia nulla. 7439

✓ TYPE: *Nephrodium deflexum* Presl [≡ *Thelypteris deflexa* (Presl) Tryon].

In wet mountainous areas at middle to higher elevations, from Hispaniola, southern Mexico, Central America, Venezuela, and British Guiana to Peru.

Dryopteris assurgens Maxon*, *Nephrodium deflexum* Presl [≡ *Dryopteris lindigii* C. Chr.], *Polypodium roraimense* Baker*, *Dryopteris sellensis* C. Chr.*, *Aspidium simplicissimum* Christ.

A small section of uncertain affinities, in need of critical study to determine the number of species. Section *Apelta* is closest to and perhaps derived from sect. *Lepidoneuron* or sect. *Uncinella*. In texture (thin) and blade shape it is closer to the latter, but in lack of any trace of an indusium and in its near glabrousness, it approaches species such as *T. caucaensis* (sect. *Lepidoneuron*).

NAMES OF UNCERTAIN POSITION

Aspidium alfarii Christ [= *Aspidium strigosum* Christ, non Willd.], *Lastrea aristeguietae* Vareschi, *Nephrodium crenulaeum* Jenm., *Aspidium confluens* Fée, *Lastrea cumingiana* Presl, *Phegopteris delicatula* Fée, *Nephrodium cinereum* Sod., *Aspidium eriosorum* Fée, *Aspidium frigidum* Christ, *Polypodium involutum* Desv., *Dryopteris tabraziensis* Christ, *Nephrodium negligens* Jenm., *Thelypteris nubicola* de la Sota, *Aspidium producens* Fée, *Dryopteris rudiformis* C. Chr., *Polypodium ruffum* Poir., *Dryopteris sancta* (L.) Kuntze var. *ecuadorensis* Bosco, *Nephrodium stramineum* Sod., *Nephrodium supinum* Sod., *Dryopteris tamandarei* Rosenst., *Aspidium tenuiculum* Fée, *Aspidium van-heurckii* Fourn.

EXCLUDED NAMES

Below are names that I exclude from *Thelypteris* subg. *Amauropelta* but that have been included by Christensen and other authors under what I regard as synonyms of the subgenus.

Phegopteris blanda Fée [≡ *Thelypteris* (*Goniopteris*) *blanda* (Fée) Reed], *Phegopteris caespitosa* Fourn. [= *Thelypteris* (*Goniopteris*) *blanda*], *Dryopteris cabreriae* Weatherby [= *Thelypteris*

(*Thelypteris*) sp.], *Nephrodium etchichuryi* Hicken [= *Thelypteris* (*Goniopteris*) sp.], *Dryopteris guentheri* Rosenst. [= *Polybotrya*? certainly not *Thelypteris*], *Dryopteris mexiae* C. Chr. [= *Thelypteris* (*Steiropteris*) sp.], *Polypodium pubescens* Raddi [probably a *Ctenitis*], *Dryopteris tremula* Christ [= *Thelypteris* (*Thelypteris*) sp.], *Aspidium velatum* Kunze ex Mett. [= *Ctenitis* sp.].

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SHORTER NOTE

ADIANTUM CAPILLUS-VENERIS IN PENNSYLVANIA.—On May 12, 1974, I discovered a colony of *Adiantum capillus-veneris* L., the Southern Maidenhair, growing on the walls of a storm drain on Drexel Avenue in Lansdowne, Delaware County, Pennsylvania. This colony probably represents a temporary occurrence of this subtropical species which, according to Wherry's "Fern Guide," in the eastern United States is known sporadically as far north as southern Virginia and Kentucky. Specimens have been deposited in the herbarium of the Academy of Natural Sciences of Philadelphia (PH).—Michael E. Kachur, Department of Botany, Academy of Natural Sciences, Nineteenth and the Parkway, Philadelphia, PA 19103.