# Rhopalotricha, a New Subgenus of the Fern Genus Lastreopsis (Dryopteridaceae)

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ABSTRACT.—A new subgenus of *Lastreopsis*, subg. *Rhopalotricha*, is here described based on the results of our recent phylogenetic analyses. Its species differ from others in the genus by having a distinctive type of hair within the grooves of the rachises and costae adaxially. These are 1-3(-4)-celled and clavate, whereas the remainders of the species in the genus have hairs that are 3-12-celled and non-clavate. Subgenus *Rhopalotricha* also differs by having spores with broadly folded perispores with echinulate surfaces (vs. tuberculate or spiny, and with smooth surfaces). Subgenus *Rhopalotricha* occurs in the Neotropics, islands of the southwestern Pacific (Samoa, Fiji, and Vanuatu), New Zealand, and Australia. A key is provided to distinguish the species, each of which is treated with synonymy, description, geographic distribution by country, elevation ranges, and discussions. Lectotypes are also designated for *Dryopteris amplissima* var. *subeffusa*, *Aspidium macrum* Fée, and *Aspidium latissimum* Fée.

KEY WORDS.—ferns, lastreopsids, taxonomy

Nested within the Dryopteridaceae (sensu Smith *et al.*, 2006) is a clade of about 150 species that we call the "lastreopsid ferns" (Labiak *et al.*, 2014a). The clade is pantropical with extensions into the temperate areas of the southern hemisphere. Members of the clade include *Lastreopsis* Ching, *Megalastrum* Holttum, *Parapolysticum* (Keyserl.) Ching, and *Rumohra* Raddi. The first genus is composed of two clades: a large clade of at least ten species, containing the type species of *Lastreopsis*, and a smaller clade – the *Lastreopsis amplissima* clade – whose relationship within the lastreopsids forms a polytomy with *Megalastrum*+*Rumohra* and the *Lastreopsis* s.s., clades (Labiak *et al.*, 2014a). The *L. amplissima* clade is composed of four species, three of which were included in our previous phylogenetic analysis; namely, *L. amplissima* (C. Presl) Tindale (South America), *L. hispida* (Sw.) Tindale (Australia and New Zealand), and *L. killipii* (Maxon) Tindale (Central and South America). One species not in our analyses, *L. davallioides* (Brack.) Tindale (Pacific Islands), is included here by us, in this taxonomic treatment, because it exhibits similar

morphology. The purpose of this paper is to describe the *L. amplissima* clade as a new subgenus of *Lastreopsis* and provide a synopsis of its species.

In her monograph of *Lastreopsis*, Tindale (1965) first pointed out the similarities among the four species, placed here in subg. *Rhopalotricha*. In fact, she separated these four species from their congeners in the first couplet of her key. The distinguishing characters used were rhizome scales with denticulate claw-like teeth, upper surfaces of the rachises provided with clavate-glandular hairs, suprabasal pinnae with the pinnules arranged catadromically, and spores that are finely echinulate. We confirm the usefulness and constancy of these characters except for pinnule arrangement, which we find variable in all four species.

In our phylogenetic analysis of lastreopsid ferns (Labiak *et al.*, 2014a), the three species (*L. amplissima, L. hispida*, and *L. killipii*) were resolved together as a strongly supported monophyletic group (Posterior Probability [PP] = 1.0, Maximum Likelihood Bootstrap [ML-BS] = 100%, and Maximum Parsimony Bootstrap [MP-BS] = 100%), but their relationship with the other clades within the lastreopsids remained ambiguous. In our Bayesian and Maximum Likelihood analyses it was recovered as sister to the rest of *Lastreopsis s.s* (PP = 0.91, and ML-BS = 66%). The Maximum Parsimony analysis, on the other hand, recovered it as sister to *Megalastrum+Rumohra* clade (MP-BS = 73%). Because of its strongly supported monophyly, morphological distinctiveness, and unique biogeographical history (Labiak *et al.*, 2014a), we believe it convenient to recognize the clade (*L. amplissima, L. hispida*, and *L. killipii*) as a new subgenus, for which we propose the name *Lastreopsis* subg. *Rhopalotricha*.

We also include a species not in our phylogenetic analysis, *Lastreopsis davallioides*, in subg. *Rhopalotricha*, because it shares the characters first pointed out by Tindale (1965). One of these characters—the echinulate perispore—can be compared to that of *L. amplissima*, *L. hispida*, and *L. killipii* (Fig. 1). The lamina dissection of *L. davallioides* greatly resembles that of *L. amplissima* (Fig. 2).

## MATERIALS AND METHODS

Herbarium specimens at B, MO, NY, P, UPCB, and VT were analyzed to write the key and comparative discussions. Geographic distributions were obtained primarily from Tindale (1965), as well as the list of synonyms and type information. The spores were imaged digitally at the New York Botanical Garden using a JEOL jSM-5410LV SEM. The images are also available at www. plantsystematics.org.

## Results

Lastreopsis subg. Rhopalotricha Labiak & R. C. Moran, subgen. nov. Type: Dryopteris killipii C. Chr. & Maxon, Amer. Fern J. 18(1):4. 1928.

## AMERICAN FERN JOURNAL: VOLUME 105 NUMBER 1 (2015)



FIG. 1. Spores of Lastreopsis subg. Rhopalotricha, Lastreopsis subg. Lastreopsis, and Parapolystichum. (A) Lastreopsis (subg. Rhopalotricha) killipii. (B) L. (subg. Rhopalotricha) amplissima. (C) L. (subg. Rhopalotricha) davallioides. (D) L. (subg. Rhopalotricha) hispida. (E) L. (subg. Lastreopsis) marginans. (F) Parapolystichum confine. Scale bars = 10 micrometers. (A from Venezuela, Beitel



FIG. 2. Silhouettes of the laminae and pinnae of *Lastreopsis* subg. *Rhopalotricha*. (A) *L. hispida*, complete leaf. (B) *L. amplissima*, basal pinna. (C) *L. davallioides*, basal pinna. (D) *L. killipii*, basal pinna. (A from New Zealand, *collector unknown s.n.*, NY; B from Brazil, *Webb s.n.*, NY; C from Samoa, *Vanpaul 336*, NY; D from Venezuela, *Beitel 85141*, NY).

85147, NY; B from Paraguay, *Hahn 756*, NY; C from Fiji, *Smith 275*, NY; D from Australia, *Coveny & Haegi 9942*, NY; E from Cuba, *Howard 5233*, NY). Figures A, C, D, and E originally published in Labiak et al., 2014a).

#### AMERICAN FERN JOURNAL: VOLUME 105 NUMBER 1 (2015)



FIG. 3. (A–E) Lastreopsis amplissima. (A) Basal pinna, showing a detail of the abaxial surface and the sori. (B) Adaxial side of a pinnule, showing the hairs on the axes. (C) Scale from the rachis. (D) Club-shaped hair from the adaxial side. (E) Glandular hair from the abaxial side of the lamina. (F–I). L. davallioides. (F) Basal pinna, showing a detail of the abaxial surface and the sori. (G) Adaxial side of a pinnule, showing the hairs on the axes. (H) Club-shaped hair from the adaxial side. (I) Scale from the rachis. (J–N) L. hispida. (J) Basal pinna, showing a detail of the abaxial surface and

Plants terrestrial; rhizomes short, stout, ascending, scaly, the scales denticulate; leaves up to 2 m long; petioles about as long as the laminae; laminae 3- to 5-pinnate-pinnatifid, deltate or pentagonal to broadly lanceolate, gradually tapered to a pinnatifid apex, buds on rachises absent; basal pinnae inequilateral prolonged on the basiscopic side; suprabasal pinnae equilateral or nearly so; *pinnules* of suprabasal pinnae anadromic; *rachises*, *costae*, and costules with a thickened marginal ridge surcurrent on the segments of the next higher order (i.e., "Lastreopsis-type" rachis-costa architecture), adaxially pubescent, the hairs 0.1–0.3 mm long, 1–3(–4)-celled, clavate, usually reddish brown, the apical cell sometimes swollen, apparently glandular and often darker than the others; veins free, ending at or very near the margins, abaxially glandular, the glands ca. 0.1 mm long, thick, oblong-cylindrical, shiny, yellow, orange or reddish, often appressed; sori round, indusiate, the indusia reniform, light brown to blackish, attached by a sinus; sporangia stalks glabrous or with a colored gland, the gland oblong-cylindrical; annulus of 14-17 indurated cells; spores monolete, achlorophyllous, the perispores finely echinulate, folded, the folds long, uninterrupted. x=41 (Brownlie, 1958).

Subgenus Rhopalotricha is characterized by denticulate rhizome scales, whereas those of subg. Lastreopsis are entire or nearly so. The rachises, costae, and costules are pubescent adaxially with 1-3(-4)-celled, clavate-glandular hairs, the apical cell of which is often darker than the others. This character is referenced in the name of the new genus (from the Greek, rhopalo, club, and tricho, hair) (Fig. 3). In contrast, species of subg. Lastreopsis and the genus Parapolystichum have slender, non-clavate hairs, composed of 3-12 cells. Subgenus Rhopalotricha has broadly folded perispores with the folds uninterrupted and finely echinulate surfaces. In contrast, Lastreopsis and Parapolystichum have perispores with folds interrupted to form a tuberculate pattern, and the surfaces are smooth or nearly so (Fig. 1; see this character optimized onto a phylogenetic tree depicting relationships of lastreopsid ferns in Fig. 6, Labiak et al., 2014a). Unlike many species of Parapolystichum (e.g., P. effusum (Sw.) Ching and P. excultum (Mett.) Labiak, Sundue & R. C. Moran), subg. Rhopalotricha lacks buds on rachises (see this character optimized onto a phylogenetic tree depicting relationships of lastreopsid ferns in Fig. 5, Labiak et al., 2014a).

Regardless of whether subg. *Rhopalotricha* will be confirmed as sister to subg. *Lastreopsis* or to *Rumohra+Megalastrum*, *Rhopalotricha* could be alternatively recognized at the rank of genus, since its monophyly is strongly

the sori. **(K)** Adaxial side of a pinnule, showing the hairs on the axes. **(L)** Glandular hair from the abaxial side of the lamina. **(M)** Club-shaped hair from the adaxial side. **(N)** Scale from the rachis. **(O–S)** *L. killipii.* **(O)** Basal pinna, showing a detail of the abaxial surface and the sori. **(P)** Adaxial side of a pinnule, showing the hairs on the axes. **(Q)** Glandular hair from the abaxial side of the lamina. **(R)** Club-shaped hair from the adaxial side. **(S)** Scale from the rachis. (A–E from Brazil, *Labiak et al. 4294*, UPCB; F–I from Fiji, *A.C. Smith 275*, NY; J–N from New Zealand, *Pichi-Sermolli 6240*, NY; O–S from Bolivia, *Altamirano 952*, NY).

supported. We prefer to recognize this monophyletic group in the rank of subgenus because of the morphological similarity with *Lastreopsis* subg. *Lastreopsis* in rhizome habit, lamina division, and sori. Using this rank fosters nomenclatural stability because the species of subg. *Rhopalotricha* have been classified in *Lastreopsis* by all pteridologists since Tindale's monograph of the group (1965).

The following key can be used to distinguish the new subgenus from *Lastreopsis* subg. *Lastreopsis* (corresponding to the clade *Lastreopsis* s.s., as termed by Labiak *et al.*, 2014a) and the morphologically similar *Parapolystichum*, in which many species formerly classified in *Lastreopsis* are now placed (Labiak *et al.*, 2014b). *Lastreopsis* and *Parapolystichum* cannot be consistently distinguished morphologically, and therefore only tendencies are given in the key.

KEY TO THE SUBG. RHOPALOTRICHA, SUBG. LASTREOPSIS, AND PARAPOLYSTICHUM

- 1. Hairs on the adaxial surfaces of the rachises and costae clavate, 1–3(–4)-celled, the apical cell often enlarged and apparently glandular; rhizome scales denticulate; perispores with uninterrupted folds and finely echinulate surfaces.......... Lastreopsis subg. Rhopalotricha
- 1. Hairs on the adaxial surfaces of the rachises and costae slender throughout, 3–12-celled, the apical cell not enlarged or glandular; rhizome scales entire or nearly so; perispores tuberculate or coarsely spiny, the surfaces of the tubercles or of the coarse spines otherwise smooth

The species of subg. *Rhopalotricha* may be distinguished by the following key. The synonymy, type information, and distribution data after each species largely follows that given by Tindale (1965).

# KEY TO THE SPECIES OF LASTREOPSIS SUBG. RHOPALOTRICHA

- 1. Leaves 1–2 m long, rachis scales thin, flat, loosely spreading to appressed; abaxial surfaces of rachises and costae without hairs; South Pacific Islands, Central and South America
  - 2. Rhizomes long-creeping; rachis scales 0.5–1.5 mm long, lanceolate, entire; Samoa, Fiji, Vanuatu ..... L. davallioides
  - 2. Rhizomes short-creeping to ascending; rachis scales 1–5 mm long, linear-lanceolate, erose to denticulate; Central and South America

Lastreopsis (subg. Rhopalotricha) amplissima (C. Presl) Tindale, Vict. Naturalist 73:185. 1957. Polystichum amplissimum C. Presl, Tent. Pterid.

84. 1836, nom. nud.; Epim. Bot. 58. 1849 [1851]. Aspidium amplissimum (C. Presl) Mett., Abh. Senckenberg. Naturf. Ges. 2(2):352. 1858. Nephrodium amplissimum (C. Presl) Hook., Sp. Fil. 4:145. 1862. Dryopteris amplissima (C. Presl) O. Kuntze, Rev. Gen. Pl. 2:812. 1891. Ctenitis amplissima (C. Presl) Copel., Gen. Fil. 124. 1947. Rumohra amplissima (C. Presl) Ching., Sinensia 5:35. 1934. Polystichopsis amplissima (C. Presl) Abbiatti, Revista Mus. La Plata, Secc. Bot. 37:19. 1958. TYPE: BRAZIL. [probably Rio de Janeiro or São Paulo]: exact locality unknown, s.d. [ca. 1822], F. Sellow & H. K. Beyrich (Holotype: PR n.v.; Isotype: B n.v.). Figs. 1B, 2B, and 3A–E.

- Aspidium macrum Fée, Crypt. Vasc. Brésil 1:141–142, t. 48, f. 1. 1869. TYPE: BRAZIL, Habitat in Brasilia fluminensi, *A. Glaziou 2390* (Lectotype, here designated: P! P02433921; isolectotype B!).
- Aspidium latissimum Fée, Crypt. Vasc. Brésil 1:142, t. 48, f. 2. 1869. TYPE: BRAZIL, Habitat in Brasilia fluminensi, A. Glaziou 979 (Lectotype, here designated: P! P00642655 Isolectotypes: P! P02433922, P00642654, P02433923).
- Dryopteris amplissima (C. Presl) O. Kuntze var. subeffusa C. Chr., Kongel.
  Danske Vidensk. Selsk. Skr., Naturvidensk. Afd., Ser. 8. 6:112. 1920.
  TYPE: VENEZUELA. Amazonas: Mt. Roraima, s.d., R. Schomburgk 1151 (Lectotype, here designated: P! P00642656).

*Rhizomes* short, thick, erect or ascending; *leaves* 1–2 m long; *petioles* slightly longer than the laminae, densely scaly toward the base and becoming less so distally, the scales lanceolate, appressed to slightly spreading, reddishbrown, thin, sharply toothed, the teeth often curved; *laminae* 0.5–1.0 × 0.7–0.9 m, 4-pinnate to 5-pinnate-pinnatifid, deltate-ovate, anadromous throughout; *rachises, costae, and costules* sparsely scaly abaxialy, the scales 1–3 mm long, linear-lanceolate, slightly tortuous, dark brown; *basal pinnae* 30–45 × 25–30 cm, ovate-oblong to triangular-oblong; *ultimate segments* 5–8 × 2–3 mm, obtuse to acute, often ascending and sometimes strongly so; *tissue between the veins* glabrous on both surfaces; *sporangial stalks* glabrous; *indusia* 1.0–2.2 mm long, glabrous.

*Distribution.*—southern Venezuela, Peru, Bolivia, Brazil, Argentina, and Paraguay; 150–1460 m.

This species greatly resembles *Lastreopsis davallioides* in dissection of the laminae but differs by ciliate scales on the rachis (the scales are entire in *L. davallioides*).

Lastreopsis (subg. Rhopalotricha) davallioides (Brack.) Tindale, Vict. Naturalist 73:184. 1957. Lastrea davallioides Brack., U.S. Expl. Exped., Filic. 16:202. 1854. Dryopteris davallioides (Brack.) O. Kuntze, Rev. Gen. Pl. 2:812. 1891. Parapolystichum davallioides (Brack.) Ching, Sunyatsenia 5:239. 1940. Ctenitis davallioides (C. Presl.) Copel., J. Arn. Arbor. 30:437. 1949. TYPE: TAHITI [but see below section Distribution]. "No. 19, U.S. South Pacific Exploring Expedition, under the command of Capt. Wilkes, 1838–42'' (Holotype: US 56405-56406, images seen). Figs. 1C, 2C, and 3F–I.

Dryopteris microtricha Copel., Bish. Mus. Bull. 59:10, 44. 1929. Ctenitis microtricha (Copel.) Copel., Gen. Fil. 124. 1947. TYPE: FIJI. Viti Levu, Voma Mountain, near the summit, 900 m, 1927, J. W. Gillespie 2742 (Holotype: BISH 1000481-1000482, images seen; Isotype UC 353779, image seen).

*Rhizomes* long-creeping; *leaves* 1.0–1.5 m long; *petioles* slightly longer than the laminae, densely scaly toward the base and becoming less so distally, the scales loosely spreading, linear, dark brown to golden brown, thin, sharply toothed, the teeth often recurved; *laminae* 0.3–0.6  $\times$  0.2–0.3 m, 4-pinnatepinnatifid to 5-pinnate, pentagonal, anadromous throughout; *rachises, costae, and costules* sparsely scaly abaxially, the scales 0.5–1.5 mm long, lanceolate, dark brown, entire; *basal pinnae* 20–40  $\times$  14–25 cm, ovate-oblong to triangular-oblong; *ultimate segments* 4–7  $\times$  1–2 mm long, obtuse to acute, sometimes strongly ascending and slightly falcate; *tissue between the veins* adaxially glabrous or nearly so, sparsely glandular abaxially, the glands minute, thick shiny, oblong, cylindrical, orange or yellowish, often appressed; *veins* glandular, the glands ca. 0.1 mm long, oblong, yellow or orange; *sporangia stalks* often with a colored glandular hair; *indusia* ca. 1 mm long, glabrous or with a few glandular hairs toward the center.

*Distribution.*—Samoa, Fiji, Vanuatu; 600–900 m. Although noted from Tahiti, the type specimen is likely from other islands in the Southern Pacific, given that the species has never been observed in Tahiti, and no collection is known from French Polynesia (including the island of Tahiti) in any of the herbaria relevant for these territories (J. Florence, pers. com.).

Christensen (1943) noted that the yellowish (sometimes orange) glands on the veins abaxially are so dense that the veins appear under magnification as yellow stripes. *Lastreopsis davallioides* greatly resembles *L. amplissima* in lamina size and cutting but can be distinguished by entire and lanceolate scales on the lamina (vs. erose and linear-lanceolate). If these two species are sister taxa as morphology suggests, it would be a remarkable example of a floristic relationship between the southwest Pacific Islands and southern South America.

Lastreopsis (subg. Rhopalotricha) hispida (Sw.) Tindale, Vict. Naturalist 73:183. 1957. Aspidium hispidum Sw., J. Bot. (Schrader) 1800(2):39. 1801. Polystichum hispidum (Sw.) J. Sm., J. Bot. (Hooker) 4:195. 1841. Lastrea hispida (Sw.) T. Moore & Houlston, Garden Mag. Bot. 3:88. 1851. Nephrodium hispidum (Sw.) Hook., Sp. Fil. 4:150. 1862. Dryopteris hispida (Sw.) O. Kuntze, Rev. Gen. Pl. 2:813. 1891. Rumohra hispida (Sw.) Copel., Gen. Fil. 114. 1947. TYPE: NEW ZEALAND. s.d., Forster s.n. (Lectotype, designated by Tindale (1965): S P6231, image seen; isolectotypes: BM 001048428, image seen, GOET n.v.). Figs. 1D, 2A, and 3J–N.

*Rhizomes* long-creeping; *leaves* 0.3–1.0 m long; *petioles* ca. as long as the laminae, densely scaly, the scales subulate, terete, thick, widely spreading, reddish-brown, entire; *laminae* 0.5–1.0  $\times$  0.7–0.9 m, 3–4-pinnate, deltate-ovate, the basal pinnae catadromous, suprabasal pinnae anadromous; *rachises, costae, and costules* pubescent and conspicuously scaly abaxially, the hairs 0.2–0.5 mm long, 3–5-celled, spreading, the scales like those of the petiole; *basal pinnae* 6–13  $\times$  5–10 cm, ovate-oblong to triangular-oblong; *ultimate segments* 2–12  $\times$  1.0–2.5 mm, narrowly lanceolate, slightly falcate, acuminate; *tissue between the veins* on both surfaces glabrous or with very sparse glands; *veins* glandular on both surfaces, more so abaxially, the glands ca. 0.1 mm long, oblong-cylindrical, colored, appressed; *sporangial stalks* glandular, the glands colored; *indusia* 1.0–2.2 mm long, with colored glands on the margins.

*Distribution.*—southeastern Australia, New Zealand, and Chatham Islands; 0–800 m.

Lastreopsis hispida differs from its congeners most conspicuously by leaves beset with dark, patent, bristle-like scales. Other distinguishing characteristics are given in the key. This is the only species of the subgenus that has had its chromosomes counted, with the result of n=41 (Brownlie, 1958).

In her description of this species, Tindale (1965) stated that laminae were "catadromous at the base, anadromous above." We find, however, the pinnules may be arranged either catadromously or anadromously, especially in the suprabasal pinnae.

Lastreopsis (subg. Rhopalotricha) killipii (C. Chr. & Maxon) Tindale, Vict. Naturalist 73:185. 1957. Dryopteris killipii C. Chr. & Maxon, Amer. Fern J. 18:4. 1928. Parapolystichum killipii (C. Chr. & Maxon) Ching, Sunyatsenia 5239. 1940. TYPE: PANAMA. Chiriquí: in humid forest of the Río Caldera watershed, W of El Boquete, 1900 m, 17–19 Feb 1917, E. P. Killip 5360 (Holotype: US 01100899, image seen; Isotype: MO! 122596). Figs. 1A, 2D, and 3O–S.

*Rhizomes* short, thick, ascending; *leaves* 1–2 m long; *petioles* slightly longer than the laminae, densely scaly throughout, the scales loosely spreading, lanceolate, reddish-brown, thin, flat, appressed, denticulate; *laminae* 0.5–1.0  $\times$  0.7–0.9 m, 4-pinnate-pinnatifid, deltate to broadly ovate; *rachises, costae, and costules* usually densely scaly abaxially, the scales 1–5 mm long, lanceolate, flat, reddish brown, denticulate; *basal pinnae* 30–45  $\times$  20–30 cm, ovate-oblong to triangular-oblong; *ultimate segments* 4–6  $\times$  2.5–4 mm, obtuse; *tissue between the veins* adaxially glabrous, glandular abaxially, the glands minute, thick shiny, oblong-cylindrical, yellowish, appressed; *sporangial stalks* glabrous; *indusia* 1.0–2.0 mm long, glabrous.

*Distribution.*—Costa Rica, Panama, Colombia, s. Venezuela, Ecuador, and Peru; 1300–2360 m.

*Lastreopsis killipii* is characterized by densely scaly petioles, rachises, and costae, especially abaxially (Fig. 3, O–R).

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