

New Combinations in *Megalastrum* (Dryopteridaceae)

ALAN R. SMITH

Department of Botany, University of California, Berkeley, California 94720

ROBBIN C. MORAN

Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166

One of Carl Christensen's many important contributions to fern taxonomy was demonstrating that *Dryopteris*, as defined around the turn of the century, was a vast, unrelated assemblage of ferns (Christensen, 1913, 1920). He indicated this diversity by dividing *Dryopteris* into 11 subgenera, using characters such as pinnule arrangement, hair type, and scale type that were not widely employed or appreciated by his predecessors and contemporaries. Ever since his work on *Dryopteris*, the trend has been to raise Christensen's subgenera to the generic rank or to treat them as subgenera in genera other than *Dryopteris*. In some cases, even his informal species groups have received generic status. This paper deals with one such grouping: the *D. subincisa* group of *Dryopteris* subg. *Ctenitis*.

Nowadays, all pteridologists recognize Christensen's subgenus *Ctenitis* as a distinct genus, *Ctenitis*. Within *Ctenitis* s.l., one of Christensen's informal groups, comprising the species allied to *Ctenitis protensa*, was recently established as the genus *Triplophyllum* by Holttum (1986a). He provided evidence that *Triplophyllum* is more closely allied to *Tectaria* than to *Ctenitis*. Another informal group, that of *Dryopteris subincisa*, was made a section of *Ctenitis* by Tindale (1965) and a genus by Holttum (1986b), as *Megalastrum*. We agree with Holttum that *Megalastrum* deserves generic status, as it is phenetically and cladistically distinct from *Ctenitis*. Furthermore, we are not aware of any species that is ambiguous with regard to placement in either *Megalastrum* or *Ctenitis*.

The best characteristic to distinguish *Megalastrum* from *Ctenitis* is the type of hair present on the adaxial surface of the axes. In *Megalastrum*, these hairs are coarse, whitish, multiseptate, with pointed tips, and antrorsely strigose or spreading (Fig. 1D). When dried, these hairs either remain terete or, if the cell walls collapse laterally, they all collapse in the same plane. In *Ctenitis* (and all other genera of tectarioid ferns), hairs of the above type are lacking. Rather, *Ctenitis*-hairs are present, i.e., hairs that are fine, usually blunt, reddish, erect to spreading (never antrorsely strigose), which when dried have cells that often collapse in planes perpendicular to the adjacent cells thereby imparting a catenate appearance to the hair, i.e., adjacent cells appear twisted relative to each other (Fig. 1C). *Megalastrum* may have *Ctenitis*-hairs on the margins and/or abaxial surface of the lamina, but never on the adaxial surface of the axes, as in all other tectarioid ferns.

Another important difference in indument is that *Ctenitis* always has unicellular, cylindrical, glandular hairs on the stalks of the sporangia (Holttum, 1986b). These glandular hairs may also occur on the margins of the indusia or on the

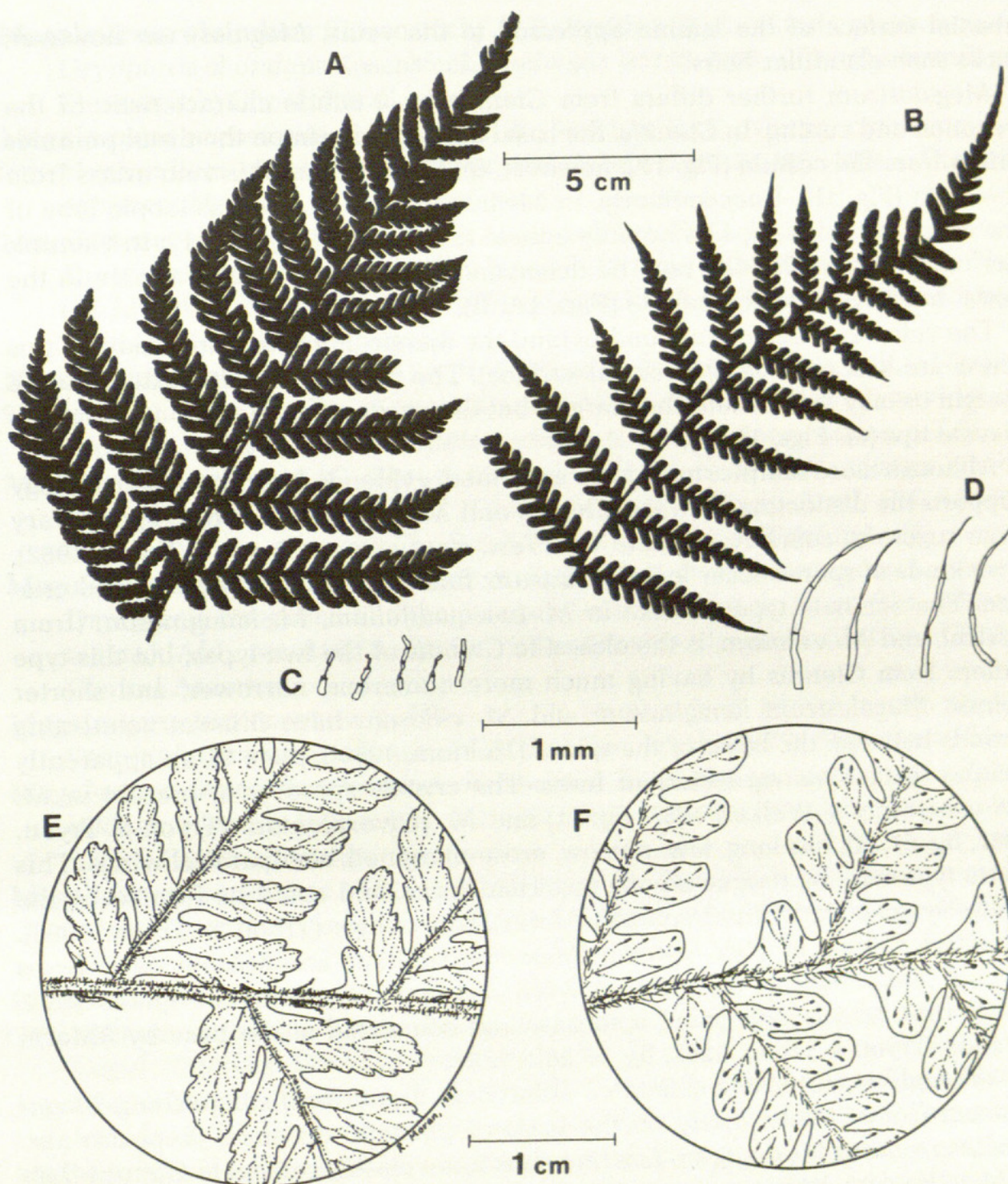


FIG. 1. Comparison of *Ctenitis sloanei* (Poeppig ex Sprengel) C. Morton and *Megalastrum acrosorum*. A, distal half of a proximal pinna, *C. sloanei*. B, Distal half of a proximal pinna, *M. acrosorum*; note position of the basal basiscopic lobes on the costa. C, typical *Ctenitis*-hairs from adaxial surface of the costa, *C. sloanei*. D, hairs from the adaxial surface of the costa, *M. acrosorum*. E, pinnule bases of *C. sloanei*; note the basiscopic veins arising from the costules and vein tips reaching the margin (pinna apex to the right). F, pinnule bases of *M. acrosorum*; note the basal basiscopic veins arising from the costa and clavate vein tips (pinna apex to the right). A, C, E: Killip 2678 (MO). B, D, F: Moran 3354 (MO).

abaxial surface of the lamina appressed to the veins. *Megalastrum* however, lacks such glandular hairs.

Megalastrum further differs from *Ctenitis* by a subtle characteristic of the venation and cutting. In *Ctenitis*, the basal basiscopic vein on the distal pinnules arises from the costule (Fig. 1E); however, in *Megalastrum* this vein arises from the costa (Fig. 1F). Concomitantly, in *Megalastrum* the basal basiscopic lobe of the distal pinnules appears broadly adnate to the costa (Figs. 1B, F). In *Ctenitis*, the basal basiscopic lobe may be decurrent on or only partially adnate to the costa, but never broadly adnate (Figs. 1A, E).

The veins in *Megalastrum* end behind the margin in conspicuous clavate tips (these are best seen on the adaxial surface). The veins in *Ctenitis* extend to the margin or may end behind the margin, but they never terminate in conspicuous clavate tips (cf. Figs. 1E, F).

Although more samples need to be examined, evidence from spore morphology supports the distinction between *Ctenitis* and *Megalastrum*. *Ctenitis* spores vary from rugose to coarsely echinate with few, stout spines (Tryon & Tryon, 1982). Two kinds of spores occur in *Megalastrum*: finely echinate (spinulose) and cristate. The echinate type, present in *M. inaequalifolium*, *M. lanuginosum* (from Africa), and *M. villosum*, is the closest to *Ctenitis* of the two types, but this type differs from *Ctenitis* by having much more numerous, narrower, and shorter spines. *Megalastrum lanuginosum* and *M. villosum* have filiform connecting strands between the bases of the spines (Holtum, 1986b, plate 3), an apparently unique feature among tectarioid ferns. The cristate spore type, present in *M. kallooi* (Jermy & Walker, 1985, fig. 11) and *M. pulverulentum* (Tryon & Tryon, 1982, fig. 67.24), has long, low, narrow, erose-margined, semiparallel wings. This spore type may be unique among tectarioid ferns, and could be formed by the coalescence of individual spines to form erose wings (Tryon & Tryon, 1982). Although distinct in their extreme forms, the echinate and cristate spore types are not fundamentally different, as evidenced by the intermediate spores of *M. connexum*, which have short, spinose wings connected at the base by filiform strands (Tryon & Tryon, 1982, fig. 67.26).

Although the foregoing character differences argue for distinguishing *Megalastrum* from *Ctenitis* solely on the basis of phenetic distance, there are also cladistic reasons for doing so. *Lastreopsis* is more closely related to *Ctenitis* than is *Megalastrum*, because *Lastreopsis* has *Ctenitis*-hairs on the adaxial surface of the axes and has unicellular, cylindrical, glandular hairs on the sporangial stalks and other parts of the plant (Tindale, 1965). Thus, since all present-day pteridologists recognize *Lastreopsis*, it would be inconsistent to subsume a more distant group, *Megalastrum*, in *Ctenitis*. Given the phenetic and cladistic arguments in favor of recognizing *Megalastrum* as distinct, we make the following combinations for the neotropical taxa. No doubt there are also a number of undescribed species, especially in South America. These are best dealt within a more critical revision of *Megalastrum*. Ranges are given in general terms, mostly following Christensen (1913, 1920).

Megalastrum Holtum, Gard. Bull. Straits Settlement. 39:161. 1986.—TYPE: *Megalastrum villosum* (L.) Holtum. - 10006

- 9935 **Megalastrum abundans** (Rosenstock) A. R. Smith & R. C. Moran, comb. nov.—
Dryopteris abundans Rosenstock, *Hedwigia* 46:133. 1906.—*Ctenitis abundans* 24847
(Rosenstock) Copel. Brazil.
- 9947 **Megalastrum acrosorum** (Hieron.) A. R. Smith & R. C. Moran, comb. nov.—
9934 *Nephrodium acrosorum* Hieron., *Bot. Jahrb. Syst.* 34:446. 1904.—*Ctenitis* 14890
acrosora (Hieron.) Copel. Costa Rica to Colombia.
- 9948 **Megalastrum adenopteris** (C. Chr.) A. R. Smith & R. C. Moran, comb. nov.—
Dryopteris adenopteris C. Chr., *Kongel. Danske Vidensk. Selsk. Skr., Naturvidensk Afd., ser. 8.* 6:85. 1920.—*Ctenitis adenopteris* (C. Chr.) Ching. 24843
Southern Brazil, N. Argentina.
- 9949 **Megalastrum andicola** (C. Chr.) A. R. Smith & R. C. Moran, comb. nov.—*Dryop-*
9938 *teris andicola* (C. Chr., *Kongel. Danske Vidensk. Selsk. Skr., Naturvidensk*
Afd., ser. 8. 6:88. 1920.—*Ctenitis andicola* (C. Chr.) Ching. Andes. -15111
- 9950 **Megalastrum aripense** (C. Chr. & Maxon) A. R. Smith & R. C. Moran, comb.
nov.—*Dryopteris aripensis* C. Chr. & Maxon, *J. Wash. Acad. Sci.* 14:143. 8852
1924.—*Ctenitis aripensis* (C. Chr. & Maxon) Lellinger. Trinidad. 8851
- 9951 **Megalastrum atrogriseum** (C. Chr.) A. R. Smith & R. C. Moran, comb. nov.—
Dryopteris atrogrisea C. Chr., *Kongel. Danske Vidensk. Selsk. Skr., Natur-* 9939
vidensk Afd., ser. 8. 6:70, fig. 15. 1920.—*Ctenitis atrogrisea* (C. Chr.) Ching. 14889
Central America.
- 9952 **Megalastrum bidecoratum** (Lellinger) A. R. Smith & R. C. Moran, comb. nov.—
Ctenitis bidecorata Lellinger, *Proc. Biol. Soc. Wash.* 98:373. 1985. Costa Rica. 9940
- 9953 **Megalastrum biseriale** (Baker) A. R. Smith & R. C. Moran, comb. nov.—*Poly-* 9941
podium biseriale Baker, *Syn. Fil.* 309. 1867.—*Ctenitis biserialis* (Baker) Lel-
lenger. Panama, Andes.
- 9954 **Megalastrum canescens** (Kunze ex Mett.) A. R. Smith & R. C. Moran, comb.
nov.—*Phegopteris canescens* Kunze ex Mett., *Abh. Senckenberg. Naturf.* 9942
Ges. 2:314. 1858.—*Ctenitis canescens* (Kunze ex Mett.) C. Morton. Brazil. 24844
- 9955 **Megalastrum connexum** (Kaulf.) A. R. Smith & R. C. Moran, comb. nov.—*Poly-*
9757 *podium connexum* Kaulf., *Enum. Fil.* 120. 1824.—*Ctenitis connexa* (Kaulf.) 9757
Copel. Southern Brazil to Paraguay.
- 9956 var. **lateadnatum** (Christ) A. R. Smith & R. C. Moran, comb. nov.—*Phegopteris*
lateadnata Christ, *Annuaire Conserv. Jard. Bot. Genève* 3:36. 1899. Paraguay. 9943
- 9957 **Megalastrum crenulans** (Fée) A. R. Smith & R. C. Moran, comb. nov.—*Aspidium* 9944
crenulans Fée, *Crypt. Vasc. Brés.* 1:139, tab. 47, fig. 1. 1869.—*Ctenitis cren-* 14003
ulans (Fée) Ching. Southern Brazil, Paraguay, Venezuela.
- 9958 **Megalastrum eugenii** (Brade) A. R. Smith & R. C. Moran, comb. nov.—*Dryopteris* 9945
eugenii Brade, *Rodriguésia* 13:298, tab. 2. 1940.—*Ctenitis eugenii* (Brade) 24846
Brade. Southern Brazil.
- 9959 **Megalastrum grande** (C. Presl) A. R. Smith & R. C. Moran, comb. nov.—*Poly-* 9946
podium grande C. Presl, *Del. Prag.* 1:171. 1822.—*Ctenitis grandis* C. Presl) 24848
Copel. Southern Brazil.—Holtum (1986b) excluded this species from *Mega-*
lastrum because it lacks hairs on the costae adaxially, but in all other respects
it belongs here: clavate vein tips, venation and cutting, spinulose spores with
a tendency for the spines to coalesce into subparallel ridges, and toothed
scales. Holtum's observation that the scales of *Ctenitis grandis* are funda-

mentally different from those of *Megalastrum* in that the teeth are the outgrowths of a single cell (vs. two or more cells in *Megalastrum*) is incorrect; many of the teeth in *M. grande* are formed at the base from parts of two adjacent cells. Certainly, *M. grande* is more closely related to other species of *Megalastrum* than to any other tectarioid genus, either Old World or New World.

- 9971 ***Megalastrum haitiense*** (Brause) A. R. Smith & R. C. Moran, comb. nov.—*Dryopteris subincisa* (Willd.) Urban var. *haitiensis* Brause, Ark. Bot. 17(7):67. 1922.—*Ctenitis haitiensis* (Brause) Lellinger. Haiti. 8854
- 9972 ***Megalastrum hirsutosetosum*** (Hieron.) A. R. Smith & R. C. Moran, comb. nov.—*Dryopteris hirsutosetosa* Hieron., Hedwigia 46:343, tab. 6, fig. 16. 1907. Andes. 8853
- 9973 ***Megalastrum honestum*** (Kunze) A. R. Smith & R. C. Moran, comb. nov.—*Polypodium honestum* Kunze, Linnaea 9:49. 1834.—*Ctenitis honesta* (Kunze) R. & A. Tryon. Andes. 15112
- 9974 ***Megalastrum inaequale*** (Kaulf. ex Link) A. R. Smith & R. C. Moran, comb. nov.—*Polypodium inaequale* Kaulf. ex Link, Hort. Berol. 2:107. 1833.—*Ctenitis inaequale* (Kaulf. ex Link) Copel. Brazil.
- 9975 ***Megalastrum inaequalifolium*** (Colla) A. R. Smith & R. C. Moran, comb. nov.—*Polypodium inaequalifolium* Colla, Mem. Reale Accad. Sci. Torino 36:49. 1836.—*Ctenitis inaequalifolia* (Colla) Ching. Juan Fernández. 5451
- 9976 ***Megalastrum kallooi*** (Jermy & T. Walker) A. R. Smith & R. C. Moran, comb. nov.—*Ctenitis kallooi* Jermy & T. Walker, Bull. Brit. Mus. (Nat. Hist.), Bot. 13:267, fig. 11. 1985. Trinidad. -9964
- 9977 ***Megalastrum lasiernos*** (Sprengel) A. R. Smith & R. C. Moran, comb. nov.—*Polypodium lasiernos* Sprengel, Syst. Veg. 4:61. 1827.—*Ctenitis lasiernos* (Sprengel) Copel. Brazil. 24849
- 9978 ***Megalastrum leptosorum*** (C. Chr.) A. R. Smith & R. C. Moran, comb. nov.—*Dryopteris leptosora* C. Chr., Ind. Fil. 274. 1905. Andes. 9966
- 9979 ***Megalastrum lunense*** (Christ) A. R. Smith & R. C. Moran, comb. nov.—*Aspidium lunense* Christ, Bull. Herb. Boissier, sér. 2. 6:55. 1906.—*Ctenitis lunensis* (Christ) Lellinger. Costa Rica, Andes? 9967 17061
- 9980 ***Megalastrum macrotheca*** (Fée) A. R. Smith & R. C. Moran, comb. nov.—*Phegopteris macrotheca* Fée, Mém. Fam. Foug. 11:56. 1866.—*Ctenitis macrotheca* (Fée) Ching. Lesser Antilles. 9968 24850
- 9981 ***Megalastrum mollicomum*** (C. Chr.) A. R. Smith & R. C. Moran, comb. nov.—*Dryopteris mollicoma* C. Chr., Kongel. Danske Vidensk. Selsk. Skr., Naturvidensk. Afd., ser. 8. 6:75. 1920.—*Ctenitis mollicoma* (C. Chr.) Ching. Andes. 9969 22388
- 9982 ***Megalastrum palmense*** (Rosenstock) A. R. Smith & R. C. Moran, comb. nov.—*Dryopteris subincisa* var. *palmensis* Rosenstock, Feddes Repert. Spec. Nov. Regni Veg. 22:11. 1925.—*Ctenitis palmensis* (Rosenstock) Lellinger. Costa Rica, Panama. 9970 7121
- 9983 ***Megalastrum pansamalense*** (C. Chr.) A. R. Smith & R. C. Moran, comb. nov.—*Dryopteris pansamalensis* C. Chr., Kongel. Danske Vidensk. Selsk. Skr., Naturvidensk. Afd., ser. 8. 6:72. 1920.—*Ctenitis pansamalensis* (C. Chr.) Lellinger. Southern Mexico to Costa Rica. 7120 7121
- 9996 ***Megalastrum platylobum*** (Baker) A. R. Smith & R. C. Moran, comb. nov.—

- 9984 *Polypodium platylobum* Baker, Syn. Fil. 307. 1867.—*Ctenitis platyloba* (Baker) C. Morton. Andes, Venezuela.
- 9997 **Megalastrum pleiosoros** (Hook. f.) A. R. Smith & R. C. Moran, comb. nov.—
- 9985 *Polypodium pleiosoros* Hook. f., Trans. Linn. Soc. London, ser. 2. 20:166. 1847.—*Ctenitis pleiosoros* (Hook. f.) C. Morton. Galapagos.
- 9260 **Megalastrum pulverulentum** (Poiret in Lam.) A. R. Smith & R. C. Moran, comb. nov.—
- 7122 *Polypodium pulverulentum* Poiret in Lam., Encycl. Méth. 5:555. 1804.—*Ctenitis pulverulenta* (Poiret) Copel. Greater Antilles, S. Mexico to N. Argentina.
- 9998 var. **heydei** (C. Chr.) A. R. Smith & R. C. Moran, comb. nov.—*Dryopteris*
- 7762 *karsteniana* var. *heydei* C. Chr., Kongel. Danske Vidensk. Selsk. Skr., Naturvidensk. Afd., ser. 8. 6:77. 1920.—*Ctenitis pulverulenta* var. *heydei* (C. Chr.) Stolze. Guatemala.
- 9999 **Megalastrum skutchii** (Lellinger) A. R. Smith & R. C. Moran, comb. nov.—*Ctenitis*
- 9986 *skutchii* Lellinger, Proc. Biol. Soc. Wash. 98:375. 1985. Costa Rica, Panama.
- 10000 **Megalastrum spectabile** (Kaulf.) A. R. Smith & R. C. Moran, comb. nov.—*Polypodium*
- 9987 *spectabile* Kaulf., Enum. Fil. 121. 1824.—*Ctenitis spectabilis* (Kaulf.) Kunkel. Chile.
- 24851 var. **phillippianum** (C. Chr.) A. R. Smith & R. C. Moran, comb. nov.—*Dryopteris*
- spectabilis* var. *phillippiana* C. Chr., Kongel. Danske Vidensk. Selsk. Skr., Naturvidensk. Afd., ser. 8. 6:70. 1920.—*Ctenitis spectabilis* var. *phillippiana* (C. Chr.) Rodriguez. Chile. 5456
- 10001 **Megalastrum squamosissimum** (Sodirol) A. R. Smith & R. C. Moran, comb. nov.—
- 9988 *Nephrodium squamosissimum* Sodirol, Anal. Univ. Quito 10(66):12. 1894. [Crypt. Vasc. Quit. 256. 1893.]—*Ctenitis squamosissima* (Sodirol) Copel. Andes. 24856
- 24855 var. **bogotense** (Hieron.) A. R. Smith & R. C. Moran, comb. nov.—*Dryopteris*
- 9989 *subincisa* var. *bogotensis* Hieron., Hedwigia 46:349. 1907.
- 10002 **Megalastrum subincisum** (Willd.) A. R. Smith & R. C. Moran, comb. nov.—
- 7128 *Polypodium subincisum* Willd., L. Sp. Pl. ed. 4, 5:202. 1810.—*Ctenitis subincisa* (Willd.) Ching. Antilles, Mexico to Bolivia. 2763
- 10003 **Megalastrum umbrinum** (C. Chr.) A. R. Smith & R. C. Moran, comb. nov.—
- 9990 *Dryopteris umbrina* C. Chr., Kongel. Danske Vidensk. Selsk. Skr., Naturvidensk. Afd., ser. 8. 6:81. 1920.—*Ctenitis umbrina* (C. Chr.) Ching. Southern Brazil, Paraguay. 24857
- 10004 **Megalastrum vastum** (Kunze) A. R. Smith & R. C. Moran, comb. nov.—*Polypodium*
- 9991 *vastum* Kunze, Linnaea 9:50. 1834. Costa Rica to Bolivia.
- 10005 **Megalastrum villosulum** (C. Chr.) A. R. Smith & R. C. Moran, comb. nov.—
- 9992 *Dryopteris villosula* C. Chr., Kongel. Danske Vidensk. Selsk. Skr., Naturvidensk. Afd., ser. 8. 6:89. 1920.—*Ctenitis villosula* (C. Chr.) Ching. Bolivia. 24858
- 10006 **Megalastrum villosum** (L.) Holttum, Gard. Bull. Straits Settle. 39:161. 1986.
- 9993 *Polypodium villosum* L., Sp. Pl. 1093. 1753.—*Ctenitis villosa* (L.) Copel. Greater Antilles. 24859
- 10007 **Megalastrum wacketii** (Rosenstock ex C. Chr.) A. R. Smith & R. C. Moran, comb. nov.—
- 9994 *Dryopteris wacketii* Rosenstock ex C. Chr., Kongel. Danske Vidensk. Selsk. Skr., Naturvidensk. Afd., ser. 8. 6:84. 1920.—*Ctenitis wacketii* (Rosenstock ex C. Chr.) Ching. Southern Brazil.
- 10008 **Megalastrum yungense** (Christ & Rosenstock) A. R. Smith & R. C. Moran, comb.

- 9995 nov.—*Dryopteris yungensis* Christ & Rosenstock, Feddes Repert. Spec. Nov. Regni Veg. 5:234. 1908. Bolivia.

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