



Prodromus of a fern flora for Bolivia. VIII. Marattiaceae

HANNA TUOMISTO¹, MICHAEL KESSLER² & ALAN R. SMITH³

¹Department of Biology, University of Turku, FI-20014 Turku, Finland

²Systematic and Evolutionary Botany, University of Zurich, Zollikerstrasse 107, CH-8008 Zurich, Switzerland

³University Herbarium, 1001 Valley Life Sciences Bldg. #2465, University of California, Berkeley, CA 94720-2465, USA

Abstract

The Marattiaceae is a phylogenetically isolated family of eusporangiate ferns. Here we provide a synopsis to the family in Bolivia, where it is represented by five species in the genus *Danaea* and a single species of *Eupodium*.

Introduction

This is one in a series of family treatments that aims at providing a basis for a future, comprehensive fern and lycophyte flora of Bolivia.

Marattiaceae is a distinctive eusporangiate fern family that can easily be recognized by the presence of pulvini (swollen bases of the petioles) and two leathery or papery pseudostipules on the rhizomes on both sides of each petiole. In pinnate species, the pinnae and pinnules also have pulvinuli, and their attachment points on the rachises and costae are articulated with nodes that are often swollen. In many species, the petioles are also nodose. Both rhizomes and petioles are fleshy and secrete a gelatinous mucilage when cut. The vascular system is complex, and the nodes lack collenchyma in the internal tissue, with the result that the leaves and pinnae droop when the plants are under water stress. The venation is free, with a distinct midvein and parallel secondary veins that are either simple or once-forked. Members of the Marattiaceae can be recognized from all other ferns by unique characteristics of their reproductive structures, the synangia. Each synangium comprises many linear (*Danaea*) or \pm circularly arranged (all other Marattiaceae) eusporangia fused to form a structure that is much more robust than any sporangial structures in leptosporangiate ferns. In Marattiaceae, synangia are formed on the underside of the blade. In contrast, synangia in Psilotaceae consist of only 2 or 3 eusporangia associated with a microphyll, and in Ophioglossaceae they are produced on a specialized fertile part of the blade.

Marattiaceae are generally long-lived and slow-growing plants that occur mostly in non-disturbed habitats, often in shady and moist conditions (Sharpe 1993). Many species have the capacity to reproduce vegetatively, with adventitious buds most commonly found either on the pseudostipules or on the blades. In the latter, buds typically replace the terminal pinna or a part of it.

Phylogenetically, Marattiaceae is an isolated family that is sister to all extant ferns except Ophioglossaceae and Psilotaceae (Lehtonen 2011) and possibly Equisetaceae (Testo & Sundue 2016). The family has a rich fossil record and was much more diverse in earlier geological times (Vriese & Harting 1853, Bower 1908, Hill & Camus 1986, Taylor *et al.* 2009), back as far as the Carboniferous era. Today, Marattiaceae occurs throughout the tropics in sufficiently warm and wet areas. There are five genera and at least 150 species (Underwood 1909, Tuomisto & Moran 2001, Murdock 2008a, Christenhusz 2010a). In the Neotropics, there are three native genera (*Danaea* Sm., *Eupodium* J.Sm. and *Marattia* Sw.; Murdock 2008a) with a fourth, *Angiopteris* Hoffm., naturalized in a few areas (Christenhusz & Toivonen 2008).

Materials and Methods

Synonymy is here restricted to names commonly used for either Bolivian specimens (e.g., Foster 1958) or in literature from neighbouring countries (e.g., de la Sota 1977, Tryon & Stolze 1989–1994). In addition, we list all names having Bolivian types.

Citation of species names follows the standard format (<http://www.ipni.org/>), according to the allowed exception from the author guidelines of *Phytotaxa* for studies dealing with 30 or more taxa, like checklists or floras. We have applied this format to all parts of this series, even those that contain fewer taxa, in order to maintain uniformity. Geographical ranges are indicated by listing the countries (and within Bolivia, the province name abbreviations) in which each species is known to occur. Further details on the format of this series and a key to the families are provided by Kessler & Smith (2017).

Taxonomic treatment

Key to the Bolivian genera of *Marattiaceae*

- 1 Mature blades once pinnate, rarely simple or irregularly bipinnate, dimorphic with fertile blades contracted; all pinnae opposite; synangia sunken into the blades and covering most of their surface *Danaea*
 – Mature blades usually 3-pinnate-pinnatifid at base, monomorphic; ultimate pinnae alternate; synangia stalked, well-spaced, most of the abaxial surface of the blades visible between them *Eupodium*

Danaea Sm., Mem. Acad. Roy. Sci. (Turin) 5: 420, p. 9, f. 11. 1793.

Danaea is confined to the Neotropics. It is easily recognized as belonging to the Marattiaceae by the presence of pseudostipules on the rhizomes, pulvini, and rachis nodes, and can be differentiated from the other genera in Marattiaceae by the usually once-pinnate leaves (rarely simple or irregularly bipinnate) with opposite pinnae, and clearly dimorphic leaves with the fertile leaves having more contracted blades but longer petioles than the sterile ones (Brebner 1902, Underwood 1902, Tuomisto & Moran 2001). The fertile leaves are relatively short-lived and have sunken synangia, which are generally arranged along the secondary veins and cover almost the entire abaxial surface of the pinnae. Sometimes, aberrant leaves with partly fertile and partly sterile pinnae can be found. Individual sporangia within the synangia open by apical pores. Sterile leaves are long-lived and often covered in epiphyllous mosses and lichens.

Characteristics of the rhizomes are important for species identification and should always be documented when making herbarium specimens. The most widespread (and probably ancestral) kind of rhizome is an erect trunk, which has leaf bases arranged spirally and stilt-like roots on all sides. This is the only kind of rhizome found in the subg. *Arthrodanaea* C.Presl, and it is also present in several species of both other subgenera (subg. *Danaea* and subg. *Holodanaea* C.Presl). There are many interspecific differences in both the height (from 0.1 m to over 1 m) and the sturdiness of the trunks. Species of subg. *Danaea* that do not have erect trunks have instead short-creeping, compact rhizomes that are clearly dorsiventral: all leaf bases are on the upper side and are arranged in two or more rows, and all roots are on the lower side. Subg. *Holodanaea* is the most variable in terms of rhizome structure: some species have an erect trunk, others a dorsiventral creeping rhizome, and still others have an intermediate decumbent rhizome type, in which the rhizome itself is horizontal but leaf bases are arranged spirally and the very apex of the rhizome may be bent upwards. Species limits within *Danaea* are often difficult to define, but the subgenera are relatively easy to recognize. Therefore, subgeneric membership is indicated (in parentheses) for each species in the treatment below.

Phylogenetic analyses place *Danaea* as sister to the remainder of Marattiaceae (Murdock 2008a), but the isolated position of the family makes this conclusion tenuous (Murdock 2008b). We disagree with the very broad species circumscriptions of Rolleri (2004), who treated *Danaea* as including only 17 species. Instead, we apply a narrower taxonomic concept (mostly following, but not identical with, Tuomisto & Moran 2001; Christenhusz & Tuomisto 2005, 2006; Christenhusz 2010a). Our current estimate is that *Danaea* comprises at least 50 species. In Amazonia, where several species co-occur, there is a clear ecological separation of species by soil characteristics, especially nutrient concentration and drainage (Tuomisto & Poulsen 1996; Christenhusz & Tuomisto 2005), which presumably also played a role in the diversification of the genus (Christenhusz *et al.* 2008).

Key to the Bolivian species of *Danaea*

- 1 Rhizomes creeping, clearly dorsiventral with all leaf bases on the dorsal side in 2 parallel rows; petioles without nodes; adult leaves >1 m long 2
 – Rhizomes erect, leaf bases arranged spirally; petioles nodose; adult leaves <1 m long 3
 2 Pinnae 4–7(–10) pairs, 25–50 cm long, 5–9.5 cm wide, elliptic, all about the same size; pinna margins cartilaginous; pinna apices entire or with fine and very sharp serration that usually does not extend beyond the cartilaginous part *D. cartilaginea*
 – Pinnae (5–)9–16 pairs, 20–35 cm long, 3.5–6 cm wide, oblanceolate to elliptic, apical ones clearly smaller than basal ones; pinna margins not cartilaginous; pinna apices usually clearly serrate, serrations sharp or blunt *D. nigrescens*
 3 Blades abaxially whitish; pinnae 8–19 pairs, oblong, parallel-sided; pinna apices acute to acuminate, dentate to sharply serrate *D. moritziana*

–	Blades abaxially green; pinnae 4–7 pairs, elliptic, clearly widest at the middle; pinna apices acuminate to long-attenuate, entire ..	4
4	Pinnae 13–20 cm long, 3.5–6 cm wide, elliptic to obovate-oblongate ..	<i>D. arbuscula</i>
–	Pinnae 9–13 cm long, 1.5–4 cm wide, elliptic ..	<i>D. geniculata</i>

Bolivian species of *Danaea*

Danaea (subg. *Arthrodanaea*) *arbuscula* Christenh. & Tuomisto, Kew Bull. 61(1): 18, f. 1, 2. 2006.

Range:—Central America to Venezuela and the Antilles, along the Andes south to Bolivia, where known only from the Alto Beni region (LP).

Ecology:—Rare, known from four Bolivian collections; terrestrial in humid montane forests; 800–1500 m.

Notes:—The erect rhizome of this species becomes more than 0.5 m (or even 1 m) tall, which is unusual in *Danaea*.

Danaea (subg. *Danaea*) *cartilaginea* Christenh. & Tuomisto, Kew Bull. 61(1): 18, 21, 23, f. 3A–E. 2006.

Range:—Western Amazonia from southern Venezuela to northern Bolivia (PA).

Ecology:—Rare in Bolivia (known from a single collection: *Weigelt 90542*, GOET, LPB, TUR, Z), but widespread and relatively common in western Amazonia; terrestrial in humid forests on hilly or flat terrain, on well-drained loamy soil, often close to creeks or rivers (Christenhusz & Tuomisto 2006); 100–400 m.

Notes:—This is probably the largest species in the genus, with individuals reaching more than 2 m in height. Before the species was described in 2006, specimens belonging to it had been mistakenly referred to *D. ulei* (e.g., Tuomisto & Poulsen 1996, Tuomisto & Moran 2001).

Danaea (subg. *Arthrodanaea*) *geniculata* Raddi, Opusc. Sci. 3: 281. 1819.

Range:—Greater Antilles; southern Mexico to Bolivia (CO, SC) and southeastern Brazil.

Ecology:—Fairly common; terrestrial in humid forests, usually along streams or on steep slopes; 200–700 m in Bolivia, to 1300 m elsewhere.

Notes:—Specimens belonging to this species have traditionally been referred to *Danaea elliptica* Sm., together with most specimens of subg. *Arthrodanaea* (Smith *et al.* 1999, Tuomisto & Moran 2001). However, the type specimen of *D. elliptica* is a juvenile of *D. nodosa* (L.) Sm., which renders the former name a synonym of the latter (Christenhusz & Tuomisto 2006). *Danaea geniculata* is the oldest name that is available to replace *D. elliptica* for plants in this group, and is used here for the Bolivian material that is not referable to *D. arbuscula* or any of the other recently described segregate species. However, the type of *D. geniculata* is from the Atlantic forests of southeastern Brazil, and the species limits in this complex remain to be clarified. The possibility exists that there is an as yet undescribed species in Bolivia.

Danaea (subg. *Holodanaea*) *moritziana* C.Presl, Suppl. Tent. Pterid.: 35. 1845.

= *Danaea cuspidata* Liebm., Mexic. Bregn. 307. 1849.

Range:—Mountains from Mexico to Guianas and Bolivia (CO, LP, SC).

Ecology:—Fairly common; terrestrial in humid forests, often along streams; 800–2700 m. This is the common mid-sized *Danaea* in montane parts of Bolivia.

Notes:—Traditionally, South American material has been identified as *D. moritziana* (type from Venezuela) and Mexican/Central American material as *D. cuspidata* (type from Mexico). It is likely that more than one species are really involved, but here we treat *D. cuspidata* under *D. moritziana* mainly because species delimitation needs to be clarified before distributional limits can be defined between the two.

Danaea (subg. *Danaea*) *nigrescens* Jenman, Gard. Chron., ser. 3, 24: 413. 1898.

Range:—Amazonia from Colombia to French Guiana and Brazil, and south to Peru and Bolivia (BE, CO, LP, PA, SC).

Ecology:—Common; terrestrial in humid forests, usually on fertile clayey soil, often near streams; mostly 200–600 m, rarely to 1300 m. This is the common large *Danaea* in Bolivian lowlands.

Notes:—Young leaves often have a metallic-blue sheen. They become pinnate at a very early stage (usually when less than 15 cm long), unlike *D. cartilaginea*, whose smallest pinnate leaves are at least 20 cm long and simple leaves can exceed 40 cm. Bolivian specimens have previously been referred to *Danaea nodosa* Sm. (Smith *et al.* 1999,

Tuomisto & Moran 2001), described from the Greater Antilles, but the Amazonian and Guianan specimens belong to a different clade than specimens from the Caribbean (Christenhusz *et al.* 2008). Here we use the name *D. nigrescens*, which is the oldest name with an Amazonian or Guianan type.

Excluded species

Danaea (subg. *Holodanaea*) *humilis* T.Moore, Index Filic. 286. 1861.

Danaea humilis, distributed from Panama to Peru, has been cited for Bolivia (Tryon & Stolze 1989, Tuomisto & Moran 2001), but we have seen no specimens that would confirm this. *Danaea humilis* is easy to distinguish from other species in Bolivia by the combination of small size (plants fertile when only 30–40 cm tall), decumbent rhizomes, and narrow (<8 cm wide) blades that are clearly whitish abaxially and have many (12–24) pinna-pairs.

Eupodium J.Sm. in Hooker, Gen. Fil. (Hooker): t. 118. 1842.

Large ferns with massive, stout, globose rhizomes and large succulent stipules. Petioles thick and usually without nodes. Blades monomorphic, 2- to 4-pinnate, ultimate pinnae alternate, the rachises often winged. Sori are in distinct synangia that are raised to short-stalked and opening by apical slits. *Eupodium* is distinct in the family in having scattered awns adaxially along veins of pinnae. A neotropical genus with three species (Murdock 2008a, Christenhusz 2010b).

Species currently placed in *Eupodium* were long treated as members of the genus *Marattia* (e.g., Underwood 1909, Tuomisto & Moran 2001, Lavalley 2003), but molecular studies have shown that three distinct clades are involved, including *Marattia* in the strict sense, with 7 species in Mexico and the Caribbean region, southern Brazil, and Hawai'i, palaeotropical *Ptisana*, with 20 species, and neotropical *Eupodium* (sister to *Ptisana*) (Murdock 2008a). As thus treated, all three genera are monophyletic.

Eupodium pittieri (Maxon) Christenh., Kew Bull. 65: 120. 2010.

Range:—Costa Rica to Trinidad, south to Bolivia (CO, LP, SC) and northwestern Argentina.

Ecology:—Locally common; terrestrial in humid forests, usually along streams; 1500–3500 m.

Notes:—Long treated as *Eupodium laeve* (Sm.) Murdock (= *Marattia laevis* Sm.), but a recent taxonomic study has restricted that species to the Greater Antilles (Christenhusz 2010b).

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