



UNIVERSIDADE FEDERAL DE MINAS GERAIS
INSTITUTO DE CIÊNCIAS BIOLÓGICAS

Departamento de Botânica

Programa de Pós-Graduação em Biologia Vegetal



ANDRÉ LUÍS DE GASPER

**THE FERN FAMILY BLECHNACEAE: OLD AND NEW
GENERA RE-EVALUATED, USING MOLECULAR DATA**

**Tese apresentada ao Programa de Pós-Graduação em
Biologia Vegetal do Departamento de Botânica do Instituto
de Ciências Biológicas da Universidade Federal de Minas
Gerais, como requisito parcial à obtenção do título de
Doutor em Biologia Vegetal.**

Área de Concentração Taxonomia vegetal

BELO HORIZONTE – MG

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e a vida, que não se contém!*

*À Lucia Sevegnani, que não pode ver esta obra concluída, mas que
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A medida de todas as coisas. Ken Alder

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RESUMO GERAL

Blechnaceae é uma família monofilética de distribuição subcosmopolita, tendo *Blechnum occidentale* L. como espécie tipo. É caracterizada por pecíolos com dois ou mais feixes vasculares na base, veia comissural paralela a costa, onde nascem os cenosoros, indúcio que abre em direção a costa e frondes avermelhadas quando jovens. Tradicionalmente a família foi dividida em dois grandes grupos, as espécies monomórficas e as espécies dimórficas, contudo, tal divisão tem sido questionada. As primeiras propostas de classificação dividiam as espécies entre *Blechnum* L. e *Lomaria* Willd., seguindo o dimorfismo da lâmina, contudo outros autores chegaram e propor vários gêneros. A proposta até então adotada foi elaborada na década de 90, onde nove gêneros foram reconhecidos, em duas subfamílias, sendo *Blechnum*, *Brainea* J. Sm., *Doodia* R. Br., *Pteridoblechnum* Hennipman, *Sadleria* Kaulf., *Salpichlaena* J. Sm., *Steenisoblechnum* Hennipman e *Woodwardia* Sm. em Blechnoideae, e *Stenochlaena* Ching em Stenochlaenoideae. Boa parte da riqueza está no gênero *Blechnum* que também é subcosmopolita, com grande parte de sua diversidade concentrada no Neotrópico e Oceania. Mais recentemente um novo gênero foi reconhecido, *Telmatoblechnum* Perrie *et al.*, com a segregação de duas espécies antes em *Blechnum*, e *Doodia*, *Steenisoblechnum* e *Pteridoblechnum* foram inclusos em *Blechnum*. Contudo, mesmo assim, o gênero *Blechnum* permanecia polifilético. Neste sentido, com o intuito de testar a congruência dos gêneros, nós reunimos sequências de três regiões plastidiais (*rbcL*, *rps4-trnS*, *trnL-trnF*), focando na maior amostragem da família, com aproximadamente 60% das espécies reconhecidas. Foram amostradas 156 espécies com 180 novas sequências geradas. Nós reconhecemos três subfamílias, todas com elevado suporte nas três análises efetuadas: Máxima Parcimônia, Máxima Verossimilhança e Inferência Bayesiana. Os gêneros *Salpichlaena*, *Stenochlaena* e *Telmatoblechnum* são monofiléticos, contudo *Blechnum*, na sua circunscrição histórica não, pois *Brainea*, *Doodia* e *Sadleria* estão inclusos no mesmo. Com base nestes resultados, nós propomos o reconhecimento de 24 gêneros, sendo seis novos e os demais resgatados de propostas antigas, bem como a combinação para todas as espécies. Além das descrições, uma chave de identificação para os gêneros foi elaborada.

Palavras-chave: combinações, filogenia, nova classificação, samambaia, pteridófitas, *rbcL*, *rps4*, *trnL-trnF*.

ABSTRACT

Blechnaceae is a monophyletic family of worldwide distribution, having *Blechnum occidentale* L. as type species. The family is characterized by petioles with two or more vascular bundles at the base, commissural vein parallel to the costae, cenosori borne on these commissural veins, indusia opening inwardly, and reddish young fronds. The family was divided, traditionally, into two major groups, the monomorphic and dimorphic species, however, this division has been questioned. The first classification proposed follow this division and two genera was accepted: *Blechnum* L. and *Lomaria* Willd., but afterwards others proposes was made. The proposal so far adopted was elaborated in the 90s, where nine genera were recognized in two subfamilies, being *Blechnum*, *Brainea* J. Sm., *Doodia* R. Br., *Pteridoblechnum* Hennipman, *Sadleria* Kaulf., *Salpichlaena* J. Sm., *Steenisoblechnum* Hennipman and *Woodwardia* Sm. in Blechnoideae, and, *Stenochlaena* Ching in Stenochlaenoideae. The highest species richness is in the genus *Blechnum* that is also sub-cosmopolitan, with two main diversity centers in Neotropics and Oceania. More recently a new genus was recognized, *Telmatoblechnum* Perrie *et al.*, with the segregation of two species of *Blechnum*, and *Doodia*, *Steenisoblechnum* and *Pteridoblechnum* were included in *Blechnum* However, even then *Blechnum* remained paraphyletic. In order to test the congruence of the genera, we have assembled the broadest sequence dataset thus far (ca. 60%), including three plastid regions (*rbcL*, *rps4-trnS*, *trnL-trnF* intergenic spacer region) and with taxonomic sampling focused on both major diversity centers. Our sampling includes 160 taxa and 183 newly generated sequences. We recognize three subfamilies, all with high support in the three analyzes performed: Maximum Parsimony, Maximum Likelihood and Bayesian Inference. The genera *Salpichlaena*, *Stenochlaena*, and *Telmatoblechnum* are monophyletic, but *Blechnum*, in its current (historical) circumscription is polyphyletic, because *Brainea*, *Doodia*, and *Sadleria* all nest within it. Based on these results, we propose the recognition of 24 genera, been six new and the other resurrected, and new combinations for all species. In addition, descriptions an identification key for all genera was prepared.

Keywords: fern, new classification, phylogeny, pteridophyte, *rbcL*, *rps4*, *trnL-trnF*.

INTRODUÇÃO GERAL

O emprego de técnicas moleculares tem gerado grandes alterações na classificação das pteridófitas, tanto em nível supra família (Hasebe *et al.*, 1995; Pryer *et al.*, 1995, 2004; Smith *et al.*, 2006b), quanto a nível genérico (Pryer *et al.*, 2001; Korall *et al.*, 2007; Christenhusz *et al.*, 2008; Metzgar *et al.*, 2008; Moran *et al.*, 2010; Sundue *et al.*, 2010; Hirai *et al.*, 2011). Atualmente, são dois os grupos reconhecidos para as pteridófitas, um que engloba as licófitas (Kramer and Green, 1990; Øllgaard, 1992) e outro das samambaias (Smith *et al.*, 2006b).

Depois da classificação proposta por Tryon & Tryon (1982), baseada em caracteres morfológicos e esporos, Smith *et al.* (2006b) propôs uma classificação baseada em caracteres moleculares, deixando algumas famílias ainda parafiléticas/polifiléticas a serem resolvidas. Recentemente, Rothfels *et al.* (2012) revisaram parte das famílias do grupo “Eupolypods II” onde uma nova classificação, com novas famílias foi proposta. Na mesma análise, confirmaram que a família Blechnaceae (~200 espécies) é monofilética, bem como Thelypteridaceae (950), Onocleaceae (cinco) e Aspleniaceae (700). Estas famílias fazem parte das samambaias leptosporângiadas (Schuettpelz and Pryer, 2007) e têm sido estudadas recentemente pela elevada diversidade que compõe este grupo.

Dentre as famílias leptosporangiadas, Blechnaceae têm sido reconhecida como monofilética (Smith *et al.*, 2006b; Rothfels *et al.*, 2012), contudo, internamente, os gêneros atuais não se sustentam com base em análises moleculares previamente efetuadas (Shepherd *et al.*, 2007; Gabriel y Galán *et al.*, 2013; Perrie *et al.*, 2014), e o próprio número de espécies é controverso (Tryon and Tryon, 1982; Rolleri and Prada, 2006a).

Blechnaceae é uma família de samambaias de distribuição subcosmopolita, onde, atualmente, são reconhecidos entre seis a nove gêneros (Kramer *et al.*, 1990; Perrie *et al.*, 2014). As espécies são arborescentes, lianescentes, ervas terrícolas, escandentes, epífitas e até aquáticas (Rothfels *et al.*, 2012). A família é caracterizada pelos rizomas reptantes, ascendentes a eretos, com escamas não clatradas; pecíolos com dois a numerosos feixes vasculares distribuídos na forma de um anel; as frondes podem ser monomórficas a dimórficas (raramente trimórficas), com nervuras livres a anastomosadas; soros lineares, geralmente paralelos e adjacentes a costa, com indúcio linear abrindo em direção à costa; esporângios pedicelados; esporos reniformes e monoletes (Moran, 1995a; Mickel and Smith, 2004; Dittrich, 2005).

Dentre os gêneros reconhecidos por Kramer *et al.* (1990) temos: *Blechnum* L., *Brainea* J. Sm., *Doodia* R. Br., *Pteridoblechnum* Hennisman, *Sadleria* Kaulf., *Salpichlaena* J. Sm., *Stenochlaena* Ching, *Steenisoblechnum* Hennisman e *Woodwardia* Sm. Perrie *et al.* (2014) reconheceu *Blechnum*, *Brainea*, *Sadleria*, *Salpichlaena*, *Stenochlaena* e *Woodwardia*, além de segregar *Telmatoblechnum* de *Blechnum*. Os demais gêneros foram incluídos em *Blechnum*. Cranfill & Kato (2003), reconheceram *Woodwardia* como gênero irmão dos demais da família.

A diversidade de espécies varia bastante entre os gêneros, sendo *Doodia*, reconhecido com aproximadamente 15 espécies distribuídas a maior parte na Oceania (Parris, 1972; Smith *et al.*, 2006b). *Woodwardia* possui aproximadamente 14 espécies, distribuídas no hemisfério Norte, tanto na América quanto na Europa/Ásia (Cranfill and Kato, 2003; Mickel and Smith, 2004; Smith *et al.*, 2006b). Ainda, ocorrendo nas Américas, podemos encontrar *Salpichlaena*, com 3 espécies endêmicas do continente (Giudice *et al.*, 2008). Outro gênero, *Stenochlaena*, conta atualmente com seis a sete espécies de ocorrência Africana e Asiática (Holttum, 1971; Chambers, 2013). Os demais gêneros, possuem entre uma e seis espécies, e estão distribuídas, basicamente, na Ásia (Holttum, 1971; Tryon and Tryon, 1982; Wang *et al.*, 2013).

Atualmente, *Blechnum* é o maior gênero da família, com aproximadamente 150 a 200 espécies (Rothfels *et al.*, 2012), sendo 50 a 100 nas Américas (Tryon and Tryon, 1982; Rolleri and Prada, 2006a) e 29 no Brasil, das quais oito são endêmicas (Dittrich and Salino, 2012). Com base nas novas espécies descritas para os neotrópicos após a monumental obra de Tryon & Tryon (1982) – e.g. (Moran, 1992; Moran and Øllgaard, 1995; Moran and Smith, 2005; Kessler *et al.*, 2007; Rojas-Alvarado, 2008; Ramos Giacosa, 2010) e pelas enormes áreas ainda inexploradas ou pouco exploradas (p. ex., bacia amazônica e áreas extra-amazônicas na Colômbia, Equador, Brasil etc.), estima-se que o número de spp. nas Américas ultrapasse, em muito, o número apresentado por Tryon & Tryon (1982). Os principais centros de riqueza de espécies são os neotrópicos e a Oceania (Dittrich *et al.*, 2007). O gênero caracteriza-se pelos esporângios em cenosoros dispostos em uma comissura vascular, paralelos e contíguos à costa ou à nervura mediana, pelas folhas pinadas ou menos divididas (exceto por três táxons) e pelos indúsios introrsos, além das folhas avermelhadas quando jovens (Tryon and Tryon, 1982; Smith *et al.*, 2006b).

O gênero *Blechnum* foi estabelecido em 1753 por Linnaeus em sua *magna opus*, *Genera Plantarum* (Linnaeus, 1753). Desde então, a circunscrição do gênero alterou-se muito pouco. O gênero é, tradicionalmente, dividido em dois grupos, o grupo com folhas monomórficas e o com folhas dimórficas. Tal divisão, entretanto, é artificial (Kramer *et al.*, 1990), e não há classificação infragenérica recente para o gênero todo, exceto as propostas de Presl (1851) e Smith (1875). Entretanto, para as Américas, uma classificação artificial, foi estabelecida por Tryon & Tryon (1982).

O gênero foi tratado em vários trabalhos florísticos nos neotrópicos: México (Smith, 1981; Mickel and Beitel, 1988; Mickel and Smith, 2004), Antilhas (Kramer, 1962; Proctor, 1977, 1985, 1989), América Central (Stolze, 1981; Moran, 1995a), Venezuela (Vareschi, 1969; Smith, 1995), Peru (Tryon and Stolze, 1993), Uruguai (Legrand and Lombardo, 1958) e Chile (Marticorena and Rodríguez, 1995). Ademais, há listas de espécies para as Américas Central e do Sul na sua integridade (Rolleri and Prada, 2006a), para o Suriname (Kramer, 1978), para o Brasil (Dittrich and Salino, 2014) e para o Cone Sul – Chile, Argentina, Paraguai, sul do Brasil e Uruguai – (Zuloaga *et al.*, 2008). As espécies sul-americanas de folhas monomórficas foram revisadas por Murillo (1968), e as espécies centro-americanas, norte-americanas e antilhenses de folhas dimórficas foram monografadas por Broadhurst (Broadhurst, 1912a, 1912b).

Fora dos Neotrópico existem estudos das espécies, mais especificamente na Oceania e Austrália, devido a elevada diversidade, mas cabe destaque para a região Neártica o estudo de Cranfill (1993); para África os estudos de Schelpe (1952), Roux (2001, 2003) and Crouch *et al.* (2011); para a Ásia: Chiou *et al.* (1975), Boonkerd & Pollawatn (2004), Lu & Yang (2005), Austrey *et al.* (2008), Nooteboom (2012) and Wang *et al.* (2013); Oceania: Tindale (1960), Brownlie (1969, 1977), Chambers & Farrant (1993, 1995, 1996a, b, 1999), Chambers *et al.* (2005), Breitwieser *et al.* (2010) e Parris (2010).

Poucos trabalhos envolvendo biologia molecular com foco exclusivo em Blechnaceae foram efetuados até então, sendo os primeiros de Nakahira (2000), Cranfill (2001), ambos não publicados. O gênero *Woodwardia* ainda foi estudado, sendo sua classificação um pouco controversa, podendo ser reconhecido como um único gênero ou outros dois a três gêneros segregados: *Anchistea* C. Presl, *Lorinseria* C. Presl e *Chieniopteris* Ching. (Cranfill and Kato, 2003). Apesar de vários autores relatarem a necessidade de estudos em Blechnaceae, apontado para o possível reconhecimento de mais gêneros em

Blechnum (Smith *et al.*, 2006b; Rothfels *et al.*, 2012), poucos foram efetuados, como o de Shepherd *et al.* (2007), que avaliou as espécies da Nova Zelândia, e reforçava, mesmo com apenas um marcador, a necessidade de revisão de todo o grupo, e o de Perrie *et al.* (2014), que propôs um novo gênero e a combinação de outros em *Blechnum*. Além destes trabalhos, Tryon & Tryon (1982) propuseram uma classificação em grupos morfológicos para as espécies neotropicais, sendo avaliada posteriormente por Gabriel y Galán *et al.* (2013), que demonstraram não haver suporte molecular para tal classificação. Esta mesma classificação já havia sido questionada e adaptada por Dittrich (2005), ao estudar as espécies do Sul e Sudeste do Brasil.

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The fern family Blechnaceae: old and new genera re-evaluated, using molecular data

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Short running title: Inferring Blechnaceae phylogeny.

Abstract Blechnaceae, a leptosporangiate fern family nested within Eupolypods II, can be recognized by stipes with two or more vascular bundles at base, commissural veins parallel to the costae, cenosori borne on these commissural veins, indusia opening inwardly, and reddish young fronds. The family has been estimated to comprise 150--250 species, and seven to nine known genera have been recognized historically. Despite recent molecular studies for the family, it still lacks a modern taxonomic update based on broad sampling from the two centers of diversity - Neotropics and Australasia/Oceania. In order to test genera circumscription, we have assembled the broadest dataset thus far, from three plastid regions (*rbcL*, *rps4-trnS*, *trnL-trnF*) and with taxonomic sampling focused on both major diversity centers. Our sampling included 156 taxa and 178 newly generated sequences. We recognize three subfamilies, all corresponding to clades highly supported in all analyses (Maximum Parsimony, Bayesian Inference, and Maximum Likelihood). The genera *Salpichlaena*, *Stenochlaena*, and *Telmatoblechnum* are monophyletic, while *Blechnum*, in its current circumscription, is polyphyletic, because *Brainea*, *Doodia*, and *Sadleria* all nest within it. Based on currently available information, we recognize 24 genera in the family.

Keywords: *Blechnum*, Eupolypoids II, leptosporangiate ferns, Polypodiopsida, *rbcL*, *rps4-trnS*, *trnL-trnF*.

1. Introduction

Among leptosporangiate ferns, the family Blechnaceae has been by many authors, including Copeland (1947), Holttum (1947, 1949), Alston (1956), Crabbe *et al.* (1975), Pichi Sermolli (1977), Tryon and Tryon (1982), Kramer *et al.* (1990), Smith *et al.* (2006a), and many others. Blechnaceae species are terrestrial, epipetric, or scandent (by virtue of rachises or rhizomes) plants, rarely epiphytic, with long-creeping, short-creeping, ascending, or erect to arborescent stems (sometimes stoloniferous); rhizome apices and stipes/rachises bear non-clathrate scales; and bilateral, monolete, spores often with ridges or winged perispores (Tryon and Lugardon, 1991). Sundue and Rothfels (2014) characterized the family as having stipes with more than two vascular bundles at the base, commissural veins parallel to costae, cenosori borne along these commissural veins, and reddish young fronds. The family has been estimated to comprise ca. 200 species (Kramer *et al.*, 1990; Mickel and Smith, 2004; Perrie *et al.*, 2014); there are two major centers of diversity and endemism -- the Neotropics and Australasia/Oceania (Dittrich *et al.*, 2007) - with a preponderance of genera and species in the southern hemisphere.

Among modern classifications based on morphology, Copeland (1947) recognized eight genera for the world. Pichi Sermolli (1977) treated 12 genera in the family, Tryon and Tryon (1982) recognized nine genera (three in the New World), and Wang *et al.* (2013) recognized eight genera in China alone (Table 1). Smith *et al.* (2006a) placed the family in Polypodiales, Eupolypods II group, associated with low support to Aspleniaceae, Thelypteridaceae, Woodsiaceae *s.l.*, and Onocleaceae. This group was studied by Rothfels *et al.* (2012), who recognized a subclade comprising Onocleaceae and Blechnaceae.

Typically, Blechnaceae has been divided into two subfamilies. Kramer *et al.* (1990) recognized subfamily Blechnoideae, with eight genera, and Stenochlaenoideae, containing only *Stenochlaena* Ching. This segregation was proposed by Roux, (2001) and followed by

Chambers (2013). *Woodwardia* Sm. was shown to be sister-group to the rest of the family by Cranfill and Kato (2003).

Perrie *et al.* (2014) proposed recognition of seven genera in the family: *Blechnum* L., *Brainea* J.Sm., *Salpichlaena* J.Sm., *Sadleria* Kaulf., *Stenochlaena* J.Sm., *Telmatoblechnum* Perrie *et al.*, and *Woodwardia* Sm. Based on molecular analyses, circumscription of *Blechnum* was altered by Perrie *et al.* (2014) to include *Pteridoblechnum* Hennipman, *Steenisioblechnum* Hennipman, and *Doodia* R.Br. Perrie *et al.* (2014) also segregated two species of *Blechnum* in a new genus, *Telmatoblechnum*, comprising *T. serrulatum* (Rich.) Perrie *et al.* and *T. indicum* (Burm.f.) Perrie *et al.* However, *Blechnum* as circumscribed by Tryon and Tryon (1982) and others, still remains polyphyletic in all molecular analyses that have been conducted (Cranfill, 2001; Schuettpelz and Pryer, 2007; Shepherd *et al.*, 2007; Perrie *et al.*, 2014).

Blechnum L., as defined by Tryon and Tryon (1982), is by far the most diverse genus in the family and exhibits a wide variety of life forms, with predominantly terrestrial or epipetric species. The genus includes species with long-creeping rhizomes, stoloniferous rootstocks, ascending rhizomes, erect trunk-like stems, and climbing or scandent hemiepiphytes. Fronds may be monomorphic or dimorphic, with simple, pinnatifid, pinnate, or even pinnate-pinnatifid blades. Venation may be free or areolate. There are only a few infrageneric classifications of *Blechnum* (Presl, 1851; Smith, 1875), most likely because the genus was insufficiently known in the past, as mentioned by Tryon and Tryon (1982). Presl (1851) split *Blechnum* into nine genera, while Smith (1875) recognized 11 genera (including *Onoclea* L.) in his tribe Blechneae; these subdivisions have generally not been adopted by other authors, e.g., Copeland (1947), Tryon and Tryon (1982), and Kramer *et al.* (1990). Leaf dimorphism may have evolved independently at different times (Perrie *et al.*, 2014). This seems to be true, because *Blechnum* subg. *Blechnum* is a strongly supported clade (Perrie *et*

al., 2014) with monomorphic fronds, and the remotely related *Parablechnum* group has primarily dimorphic species but also a few of monomorphic ones, e.g., *B. monomorphum* R.C.Moran & B.Øllg., *B. obtusum* R.C.Moran & A.R.Sm. Reversions to monomorphy are known in several clades comprising mostly strongly dimorphic species, e.g., *Struthiopteris* [*Blechnum spicant* (L.) Sm.]. Some authors have noted that separation of *Blechnum* into groups based on dimorphism is rather artificial (e.g., Kramer *et al.* 1990: 64).

Two recent studies addressed the phylogeny of *Blechnum* and Blechnaceae. Gabriel y Galán *et al.* (2013), using a relatively small data set (18 spp.), showed incongruence between morphological and molecular data. In a larger phylogeny, incorporating 113 spp., Perrie *et al.* (2014) focused primarily on relationships of species from Australasia/Oceania. They attempted a redefinition of *Blechnum*, subsuming in *Blechnum* several traditional generic segregates including *Doodia*, *Steenisoblechnum*, and *Pteridoblechnum*, genera previously recognized by Kramer *et al.* (1990). Because two species traditionally included in *Blechnum s.l.* fell sister to core *Blechnum*, they segregated *Telmatoblechnum* as a new genus.

Gabriel y Galán *et al.* (2013) did not include Australasian species in their analysis, and Perrie *et al.* (2014) had only a meager sampling of Neotropical and African/Madagascan species. Therefore, we expand sampling from previously neglected areas, and combine data from the two major centers of diversity: Neotropics and Australasia/Oceania. The major aims of this study were (1) to test monophyly of *Blechnum s.l.*; and (2) to explore delimitation of genera based both on phylogenetic relationships, as gleaned from chloroplast DNA data and traditional data, as well as new morphological characters.

2. Material and methods

2.1 Taxon sampling

We included 151 ingroup species in seven historically recognized genera within Blechnaceae (all genera sampled by Perrie *et al.* 2014); this sampling represents about 60% of species in the family (Appendix 1). Our sampling includes 41 species heretofore not yet included in phylogenetic analyses, as well as samples from GenBank. We sampled material from type species of all genera recognized by Kramer *et al.* (1990) and Perrie *et al.* (2014), as well as from types or representative species of mostly unrecognized genera, subgenera, and sections (i.e., *Blechnidium* T.Moore, *Blechnopsis* C.Presl, *Blechnum* sect. *Lomariocycas* (J.Sm.) C.V.Morton, *Diploblechnum* Hayata, *Lomaridium* C.Presl, *Parablechnum* C.Presl, and *Struthiopteris* Scop.). Sampling included materials from personal collections, herbaria, and cultivated plants. Vouchers have been incorporated into the following herbaria: BHCB, FURB, QSA, MEXU, MO, K, P, PMA, SI, WELT (herbaria abbreviations according to Thiers, 2016).

2.2 Extraction, amplification and DNA sequencing

Samples were extracted using DNeasy Plant Mini Kit (QIAGEN Inc., Valencia, CA, USA) using field-collected silica gel-dried tissue or herbarium material. Amplifications were performed in 20 μ L reactions containing 1 μ L DNA template, 2 μ L buffer (Taq Quiagen 10x buffer), 2 μ L dNTP solution (10 mM), 0.5 μ L DMSO (100%), 0.5 μ L BSA (5 mg/mL), 0.2 μ L of each primer (10 μ M), 0.25 μ L Taq DNA Polymerase (5 U/ μ L) (Phoneutria, Belo Horizonte, Brazil or QIAGEN) and 14.35 μ L H₂O ultrapure. The sequences were amplified using primers designed for *rbcL* (Hafler and Ranker, 1995), for *rps4-trnS* (Nadot *et al.*, 1995; Smith and Cranfill, 2002), and for *trnL-trnF* (Taberlet *et al.*, 1991; Trewick *et al.*, 2002). The *rps4-trnS* region consisted of *rps4* gene and *rps4-trnS* intergenic spacer (IGS).

The *trnL-trnF* region consisted of *trnL* intron, *trnL-trnF* IGS, and short exon portions of the genes *trnL* and *trnF*. Amplification conditions were used for all primers: initial denaturation at 80°C for 5 min, followed by 30 cycles, 1 min at 95°C, 1 min at 50°C, 4 min at 65°C (with gradual temperature rise of 0.3 degree/s). The final extension temperature was 65°C for 5 min (adapted from Shaw *et al.*, 2007). PCR products were sequenced on High Throughput Genomics (www.htseq.org, University of Washington, Seattle, USA) on an ABI 3730xl DNA sequencer using the same primers described above. This study generated 335 new DNA sequences incorporated into GenBank (Appendix 1).

2.3 Alignment

DNA sequence electropherograms were edited in STADEN package software (Bonfield *et al.*, 1995). The sequences were aligned with MUSCLE (Edgar, 2004) using MEGA 6 (Tamura *et al.*, 2013), with manual adjustments when necessary. The data matrix was deposited in TreeBASE (<http://purl.org/phylo/treebase/phyloids/study/TB2:S19024>).

2.4 Phylogenetic analysis

Maximum Parsimony (MP), Maximum Likelihood (ML) and Bayesian Inference (BI) were performed using PAUP* v.4.0b10 (Swofford, 2002), IQ-TREE (Nguyen *et al.*, 2014), and MrBayes v.3.2.6 (Ronquist *et al.*, 2012), respectively. CIPRES (Miller *et al.*, 2010) was used to test all analyses. We included five species from the family Athyriaceae and Onocleaceae as outgroups: *Athyrium filix-femina* (L.) Roth, *Matteuccia struthiopteris* (L.) Tod., *Onoclea sensibilis* L., *Onocleopsis hintonii* F.Ballard, and *Pentarhizidium intermedium* (C.Chr.) Hayata (Smith *et al.*, 2006a; Rothfels *et al.*, 2012).

Maximum Parsimony (MP) was performed with heuristic searches, with 1,000 random sequence-addition replicates conducted with tree-bisection–reconnection (TBR) branch-

swapping. Support was calculated with 1,000 pseudoreplicates bootstrap.

Maximum Likelihood (ML) was performed with partitioned models selected automatically, and branches evaluated by 1000 ultrafast bootstrap replication (Minh *et al.*, 2013).

For Bayesian Inference (BI), evolutionary models were chosen through jModelTest 2.1.10 software (Darriba *et al.*, 2012), using BIC as selection criteria (Schwarz, 1978) (Table 2). Bayesian Inference (BI) consisted of two parallel races with four Markov Chain Monte Carlo (MCMC) each, for 5,000,000 generations, with a sample from a tree every 100 generations. Stationarity was assessed using Tracer v.1.5 (Rambaut and Drummond, 2009), and 25% of trees were discarded. The remaining trees were used to construct a 50% majority-rule consensus tree. Preliminary phylogenetic analyses indicated no significant incongruence between the loci, so they were concatenated.

3. Results

The resulting concatenated matrix had 3,350 characters, 1,181 from *rbcL*, 543 from *rps4* gene, 486 from the *rps4-trnS* IGS, 649 from *trnL*+intron *trnL* intron, and 391 from *trnL-trnF* IGS. The final matrix had 1,189 (35%) informative characters. The MP analysis retained 10,425 equally parsimonious trees with 5,010 tree length, consistency index (CI) 0.42, and retention index (RI) 0.79 (Fig. 1).

Three monophyletic major clades were resolved with strong support. These clades are recognized here as three subfamilies: Woodwardioideae Gasper, V.A.O.Dittrich & Salino *subfam. nov., ined.* (1.00 PP, 100% ML, 98% MP), Stenochlaenoideae Roux emend. Gasper, V.A.O.Dittrich & Salino (1.00 PP, 100% ML, 88% MP), and Blechnoideae Gasper, V.A.O.Dittrich & Salino *subfam. nov., ined.* (1.00 PP, 100% ML, 96% MP).

Subfamily Woodwardioideae comprised three genera: *Anchistea* C.Presl (1 sp.),

Lorinseria C.Presl (1 sp.), and *Woodwardia* (13 spp.). Subfamily Stenochlaenoideae also comprised three genera: *Stenochlaena* (ca. 7 spp.), *Salpichlaena* (3 spp.), and *Telmatoblechnum* (2 spp.). Subfamily Blechnoideae comprised the remaining genera in the family, and by far the most species in the family (ca. 230 spp.).

Subfamily Blechnoideae comprised 18 well-supported clades indicated in Figure 1. The relationship between *Brainea*+*Blechnidium*+*Struthiopteris* was not well recovered (0.59 PP, 78% ML, -- MP), but this clade is sister to all other Blechnoidea. The Blechnoideae clade (Fig. 1) includes the segregate *Lomaridium* (1.00 PP, 100% ML, 100% MP) as sister to the remaining recovered clades (1.00 PP, 100% ML, 94% MP).

The *Lomaria* clade (1.00 PP, 100 ML, 100% MP) was recovered as sister to two large clades, named here superclades A and B (Fig. 1). Superclade A (1.00 PP, 100% ML, -- MP) comprises *Icarus filiformis* (A.Cunn.) Gasper & Salino, *comb. ined.*, as sister to *Cranfillia ined.* (1.00 PP, 98% ML, 79% MP), *Blechnum* (1.00 PP, 100% ML, 100% MP), and *Austroblechnum ined.* (1.00 PP, 100%, ML, 100% MP).

Superclade B comprises *Parablechnum* (1.00 PP, 99% ML, 96% MP), *Doodia*, *Neoblechnum ined.*, *Oceanopteris ined.* (1.00 PP, 100% ML, 100% MP), *Lomariocycas comb. ined.* (1.00 PP, 100% ML, 100% MP), and *Diploblechnum* (1.00 PP, 99% ML, 88% MP).

4. Discussion

Our results are based on the largest data set thus far compiled for the family, with a comprehensive sampling of the two main diversity centers: Neotropics and Australasia/Oceania. With the inclusion of a large Neotropical sampling (about 80% of total species), we were able to expand on previous phylogenies (Gabriel y Galán *et al.*, 2013; Perrie *et al.*, 2014). Increased sampling (about 60% of species in the family) made it possible

to address critical unresolved issues regarding generic circumscription in Blechnaceae (Perrie *et al.* (2014).

Three major clades within Blechnaceae were first noted by Lehtonen (2011): one clade consisted of *Woodwardia*, including segregates *Anchistea* and *Lorinseria* (with about 15 species; Cranfill, 2001; Cranfill and Kato, 2003); another containing *Salpichlaena*, *Stenochlaena*, and *Telmatoblechnum*, with about 12 species; and a third clade comprising the remainder of *Blechnum s.l.*, *Brainea*, and *Sadleria*, totaling about 230 species.

Our results indicate that *Blechnum* as circumscribed by many authors (Copeland, 1947; Holttum, 1947; Pichi Sermolli, 1977; Tryon and Tryon, 1982; Kramer *et al.*, 1990; Perrie *et al.* 2014) is not monophyletic, because both *Brainea* and *Sadleria* are nested within it.

In order to summarize results and conclusions of phylogenetic analyses presented above, we outline below the substance of a new Blechnaceae classification (Gasper *et al.*, in prep.). Reference to previous published names to the various segregates, where applicable, is made in order to coincide with our forthcoming classification for the family. Morphological characteristics, synapomorphies when known, and cytological data characterizing the segregates are also mentioned.

4.1 Woodwardioideae clade

Woodwardia, typified by *W. radicans* (L.) Sm., was recovered with high support (1.00 PP; 100% ML, 100% MP), and together with *Anchistea* and *Lorinseria* it is clearly sister to the rest of Blechnaceae in all analyses performed thus far. *Woodwardia* is largely temperate and subtropical in northern hemisphere, and has about 13 species (nine sampled). It is considered a single genus by most authors (Cranfill and Kato, 2003; Smith *et al.*, 2006a), or with up to three small segregates by other authors, namely *Chieniopteris* Ching (Pichi Sermolli, 1977; Wang *et al.*, 2013), *Lorinseria* (Presl, 1851; Pichi Sermolli, 1977; Cranfill,

2001), and *Anchistea* (Presl, 1851; Pichi Sermolli, 1977; Cranfill, 2001). Despite similarities in venation pattern between *Woodwardia s.l.* (including segregates) and *Doodia*, in *Woodwardia* first-order areoles express the fertile vein, while areoles of second order do not, besides being irregular in shape and arrangement (Cranfill, 2001).

In our analyses, as well as ones presented by Cranfill and Kato (2003), there is support for separation of *Lorinseria areolata* (L.) T.Moore (1.00 P, 100% ML, 98% MP) and *Anchistea virginica* (L.) Sm. (0.98 PP, 99% ML, 9% MP) as segregate genera. These two species are distinguished by their long-creeping rhizomes, a characteristic also found in *Woodwardia kempii* Copel. and *W. harlandii* Hook. Additional characteristics of *Lorinseria* include the dimorphic fronds and sunken sori (Cranfill, 1993); *Anchistea* is further distinguished by having pinnae articulate to the rachis (Cranfill, 1993). Chromosome base numbers provide additional support for separation of *Lorinseria* and *Anchistea* from *Woodwardia*: the first two exhibit $x = 35$, while *Woodwardia s.s.* is $x = 31, 34$ (*W. japonica* (L. f.) Sm.; Takamiya *et al.*, 1992). Reports for several other species of *Woodwardia* [*W. fimbriata* Sm., *W. orientalis* Sw., *W. prolifera* Hook. & Arn., *W. radicans* (L.) Sm., *W. unigemmata* (Makino) Nakai] are also based on $x = 34$. Remarkably, *Woodwardia kempii* was reported as $2n = 124$ by Takamiya *et al.* (1992), and so is tetraploid, presumably based on $x = 31$, a base number in the family that is otherwise found in only distantly related genera (e.g., *Blechnum s.s.*; see below).

4.2 Stenochlaenoideae clade

Stenochlaenoideae is a small subfamily with about 12 species, distributed in three genera: *Stenochlaena* (about seven spp., three sampled), mostly from Southeast Asia; *Salpichlaena* (three spp. in the Neotropics); and *Telmatoblechnum* (two spp., one widespread in the Neotropics, the other in Southeast Asia, Australia, and the western Pacific). All three genera have strong support in our analysis.

Stenochlaena, typified by *S. scandens* J. Sm., has long-creeping, scandent, nearly glabrous rhizomes, and has long been considered problematic, in terms of its relationships, and also a unique chromosome number in the family, $x = 74$ [*Stenochlaena palustris* (Burm.f.) Bedd., Raj and Manickam, 1987]. Many authors have treated this taxon as a subfamily, Stenochlaenoideae, apart from other genera of Blechnaceae (Kramer *et al.*, 1990; Stevenson and Loconte, 1996; Roux, 2001; Chambers, 2013). It has even been regarded as sufficiently distinct to be considered a distinct family [Stenochlaenaceae Ching (Ching, 1978)]. Tryon and Tryon (1982) placed *Stenochlaena* in Blechnaceae, but admitted that it was very distant from other blechnoid genera. Pichi Sermolli (1977) considered some features of *Stenochlaena*, particularly the scandent habit and venation pattern, to indicate a relationship to *Blechnum s.l.* (e.g., *Lomaridium*). Our molecular analyses suggest that the scandent or climbing life form has arisen independently in subfam. Blechnoideae and subfam. Stenochlaenoideae.

Salpichlaena, typified by *S. volubilis* (Kaulf.) J.Sm., is characterized by having a climbing, twining rachis and an intramarginal commissural vein (Kramer *et al.*, 1990; Giudice *et al.*, 2008), as well as a unique base chromosome number in the family: $x = 40$ (Walker, 1985). Some authors admit only a single species, *Salpichlaena volubilis* (Murillo, 2001), while others recognize one or two others (Moran, 1995; Smith, 1995; Giudice *et al.*, 2008).

Telmatoblechnum, typified by *T. serrulatum* (Rich.) Perrie, D.J.Ohlsen & Brownsey, a newly segregated genus with two species, is characterized by having creeping, relatively scaleless rhizomes, and articulate pinnae (Perrie *et al.*, 2014). It also has a unique base chromosome number in the family, $x = 36$ (Tindale and Roy, 2002).

4.3 Blechnoideae clade

Subfamily Blechnoideae is the most diverse clade, with *ca.* 230 species, including many recently described species (e.g., Kessler *et al.*, 2007; Ramos Giacosa, 2010; Rakotondrainibe *et al.*, 2013). This clade includes six classically recognized genera: *Blechnum*, *Brainea*, *Doodia*, *Pteridoblechnum*, *Sadleria*, and *Steenisiolechnum* (Kramer *et al.*, 1990). However, our results and evidence from several studies (Cranfill, 2001; Shepherd *et al.*, 2007; Perrie *et al.*, 2014) show that *Blechnum* is polyphyletic, even with the segregation of *Telmatoblechnum* (Perrie *et al.*, 2014), because *Brainea*, *Doodia*, and *Sadleria* all nest within *Blechnum s.l.* Recognition that *Doodia* nests within *Blechnum s.l.* prompted Christenhusz *et al.* (2011) to subsume *Doodia* in *Blechnum*.

4.3.1 *Brainea* clade

Brainea, a monotypic genus typified by *Brainea insignis* (Hook.) J.Sm., is widespread in Asia and differs from *Blechnum* by having exindusiate sori, trunk-like rhizomes (Wang *et al.*, 2013), and sporangial disposition in fertile fronds following the veins (costal row of areolae), seemingly acrostichoid in mature fronds; in incompletely fertile leaves, sporangia are not confined to such veins (Kramer *et al.*, 1990). *Brainea* has been reported to have $n = 35$ (Bidin, 1995) and $2n = 66$ (Roy and Holttum, 1965), suggesting at least two different base chromosome numbers. According to Tryon and Lugardon (1991), the spores are slightly rugulate to plain with an irregular granulate deposit.

4.3.2 *Blechnidium* clade

Blechnidium T.Moore (1859), typified by *Blechnidium melanopus* (Hook.) T.Moore, is a monotypic genus from eastern Asia, and is newly sampled in our phylogenetic analyses. Wang *et al.* (2013) recognized *Blechnidium* as closely related to *Struthiopteris*. The genus is

characterized by long-creeping rhizomes, monomorphic fronds, anastomosing veins (Chiou *et al.*, 1975); and $2n = 124$ (Sankari Ammal and Bhavanandan, 1989), a tetraploid presumably based on $x = 31$. Brade (1966, 1967) considered *Blechnidium* related to *Blechnum heringeri* Brade from Brazil, but anastomosing veins appear to have evolved at least three times in subfam. Blechnoideae, appearing in *Blechnidium* and also in *Blechnum s.s.* and *Doodia* (Dittrich *et al.*, 2012).

4.3.3 *Struthiopteris* clade

Struthiopteris Scop. (Scopoli, 1754), typified by *S. spicant* (L.) Weiss, is a name used since 1561 (Broadhurst, 1912a, b). It is sometimes considered a synonym of *Lomaria*, *Spicantopsis*, or *Blechnopsis* (e.g., by Wang *et al.*, 2013), but we choose to apply it to a genus comprising about five spp. (two sampled here), distributed in north-temperate regions. Cranfill (2001) argued that species related to this clade have compact erect stems, with clustered frond rosettes at stem apices. Stems also produce a long-creeping rhizomes that grow and form new rosettes. Other morphological characteristics include having strongly dimorphic fronds, pinnatifid sterile blades having many pairs of gradually reduced proximal pinnae, free veins, and $x = 66$ (Tindale and Roy, 2002). *Struthiopteris* is closely allied to *Blechnidium* and *Brainea* (Fig. 1), similar agreeing with suggestions by Wang *et al.* (2013). Base chromosome number in this genus is $x = 31$ [$2n = 62$ for *S. amabilis* (Makino) Ching, *S. niponica* (Kunze) Nakai, *S. hancockii* (Hance) Tagawa, Ebihara *et al.*, 2014]; but *S. spicant* is reported as $2n = 68$, presumably $x = 34$. *Struthiopteris castanea* (Makino & Nemoto) Nakai was reported as $2n = 340$, probably a decaploid based on $x = 34$ (Nakato, 1987).

4.3.4 *Blechnopsis* clade

Blechnopsis C.Presl (1851), typified by *B. orientalis* (L.) C.Presl, comprises two species occurring in eastern Asia and Australia. Its species are characterized by monomorphic or slightly dimorphic fronds and proximal pinnae reduced to auricles, pinnae of the earliest fronds adnate to the rachis and with an obtuse apex, while slightly older plants have pinnae apically acute (Chambers and Farrant, 2001). Short-creeping to suberect rhizomes are also found in this clade (Cranfill, 2001). *Blechnopsis orientalis* has different chromosome numbers reported: $n = 32$ (Singh and Roy, 1988), $n = 66$, $2n = 66$ (Tindale and Roy, 2002), and $n = 34$ (Ghatak, 1977).

4.3.5. *Cleistoblechnum* clade

Cleistoblechnum eburneum (Christ) Gasper & Salino, *comb. ined.*, from China and Taiwan (Chiou *et al.*, 1975; Wang *et al.*, 2013), seems to be the sole representative of this clade. It differs from other species by having sporangia that remain enclosed by the indusium at maturity (Chambers and Farrant, 1996). Wang *et al.* (2013) treated *C. eburneum* as *Struthiopteris*, but our results, as well the ones presented by Perrie *et al.* (2014), did not support this option. The species is reported as $2n = 66$ (Wang *et al.*, 2013), another deviation from *Struthiopteris* ($x = 31, 34$)

4.3.6 *Sadleria* clade

Sadleria, typified by *Sadleria cyatheoides* Kaulf., is endemic to the Hawaiian Islands (Palmer, 1997) and comprises six species (five sampled; Appendix 1). It is related to *Blechnopsis*, *Struthiopteris*, *Blechnidium*, and *Cleistoblechnum* clade and has the base chromosome number $x = 33$ [Wagner, 1995, for *S. squarrosa* (Gaudich.) T. Moore]. The clade was recovered with high support (0.99 PP, 100% ML, 96% MP; Fig. 1). *Sadleria* is characterized by having trunk-like rhizomes and a pericostal arch uniting the veins; its

species grow mostly in lava-derived soils (Kramer *et al.*, 1990; Palmer, 1997).

4.3.7 *Lomaridium* clade

Lomaridium C.Presl (1851), typified by *Lomaridium plumieri* (Desv.) C. Presl, is a well-supported clade (1.00 PP, 100% ML, 100% MP) distinguished mainly by hemiepiphytic habit, long-creeping, climbing rhizomes, toothed rhizome scales, dimorphic, glabrous fronds, broadly adnate sterile pinnae, and decurrent or reduced proximal pinnae. According to Cranfill (2001), rhizomes grow erect for several meters in well lighted places in forests, as well in forest margins. Several Neotropical species climb preferentially on tree fern trunks. The clade is pantropical and comprises ca. 15 species; species are usually found in lower montane and montane forests (Mickel and Beitel, 1988; Mickel and Smith, 2004; Kessler and Smith, in prep.). At least some species of *Lomaridium* appear to have a unique chromosome number among species of Blechnaceae, $2n = 58$ [Smith and Foster, 1984, for *Lomaridium ensiforme* (Liebm.) Gasper & V.A.O.Dittrich, *comb. ined.*; and for *L. schottii* (Colla) Gasper & V.A.O.Dittrich, *comb. ined.* (Kurita, 1986)] presumably based on $x = 29$. *Lomaridium attenuatum* (Sw.) Gasper & V.A.O.Dittrich, *comb. ined.*, was reported as a tetraploid, $2n = 128$, so presumed based on $x = 32$ (Manton, 1959).

4.3.8 *Lomaria* clade

Lomaria Willd., synonym *Stegania* R. Br., is typified by *L. nuda* (Labill.) Willd. This clade, comprising ca. six spp. (four sampled), has representatives in Bolivia, Peru, Brazil, South Africa, Australia, and New Caledonia. The genus is distinguished by having strongly dimorphic fertile and sterile blades, once-pinnate or pinnatisect sterile fronds, a deeply grooved rachis adaxially, discoloured blades (adaxial side dark green, abaxial side silver-green), erect, sometimes trunk-like rhizomes, and $x = 28$ (*L. nuda*, Tindale and Roy, 2002). *Lomaria nuda* was reported as having green spores, an unusual condition in the family (Lloyd

and Klekowski Jr., 1970).

For many years, *Lomaria* comprised dimorphic *Blechnum* species. Broadhurst (1912a,b) transferred dimorphic species to *Struthiopteris*. Other authors proposed to treat *Lomaria* as a genus or subgenus of *Blechnum* (e.g., Christensen, 1906). However, since Copeland (1947), this segregation in *Blechnum* (species with monomorphic fronds) and *Lomaria* (species with dimorphic fronds) has not been followed, possibly because most authors believed that leaf dimorphism had evolved several times in the family (Tryon and Tryon, 1982; Kramer *et al.*, 1990; Dittrich, 2005).

4.3.9 *Icarus* clade

Icarus filiformis (A.Cunn.) Gasper & Salino, *comb. ined.*, endemic to New Zealand, is sister to superclade A (Fig. 1), (1.00 PP, 100% ML, -- MP). It is morphologically distinguished by the unique di- or trimorphic sterile fronds (Kramer *et al.*, 1990) and high-climbing rhizomes.

4.3.10 *Cranfillia* clade

The clade including *Cranfillia pilosa* (Brack.) Gasper & V.A.O.Dittrich, *comb. ined.*, is characterized by creeping, erect or erect to ascending rhizomes bearing long, acuminate, brown to blackish scales, dimorphic fronds, rachises and costae pilose (sometimes with small hairs) the hairs septate. Another characteristic that seems to be shared, at least for a few species, like *Cranfillia nigra* (Colenso) Gasper & V.A.O.Dittrich, *comb. nov.*, *C. sprucei* (C. Chr) Gasper & V.A.O.Dittrich, *comb. ined.*, *C. fluviatilis* (R. Br.) Gasper & V.A.O.Dittrich, *comb. ined.*, and *C. vulcanica* (Blume) Gasper & V.A.O.Dittrich, *comb. ined.*, is that the fertile fronds senesce rapidly after spore release (Cranfill 2001). The group has about eleven species (eight sampled), mostly from Australia and Oceania, with three species in

Neotropics. *Cranfillia sampaioana* (Brade) Gasper & V.A.O.Dittrich, *comb. ined.*, was previously considered related to *Austroblechnum divergens* (Kunze) Gasper & V.A.O.Dittrich, *comb. ined.* (Dittrich 2005), and *C. sprucei*, which has flagelliform, bud-bearing blade apices (Tryon & Stolze, 1993). Quinn (1961) reported $n = 99$ for *C. fluviatilis*, presumably a triploid based on $n = 33$, and $n = 33$ for *C. vulcanica*. A different number was reported for *C. fluviatilis* by Tindale and Roy (2002), $2n = 176$.

Chambers and Farrant (2001) suggested that *Austroblechnum membranaceum* (Colenso ex Hook.) Gasper & V.A.O.Dittrich, *comb. ined.*, is closely related to *C. fluviatilis* E.J.Lowe ex Salomon, because they share chromosome base number, $x = 33$. However, the phylogenetic topology shown in our analyses argues against this hypothesis.

4.3.11 *Blechnum sensu stricto*

Blechnum s.s. (Murillo, 1968; Dittrich *et al.*, 2015) comprises mostly Neotropical species, plus two species in Africa, and is typified by *Blechnum occidentale* L. This clade, with ca. 30 species (some of them hybrids; Dittrich *et al.*, 2015), is characterized by usually stoloniferous, monomorphic fronds with finely denticulate pinna margins (Dittrich *et al.*, 2015). In rare cases, fronds may be slightly dimorphic (e.g., Brazilian endemics *Blechnum heringeri* Brade, *B. areolatum* V.A.O.Dittrich & Salino, and *B. longipilosum* V.A.O.Dittrich & Salino, which have longer-stiped fertile fronds with slightly narrower fertile pinnae), or even subdimorphic, as in *Blechnum auriculatum* Cav. (Dittrich *et al.*, 2015). This clade also contains a few species with partially anastomosing veins [*B. areolatum*, *B. heringeri*, and *B. longipilosum*; Dittrich *et al.*, 2012)], a feature otherwise found in Blechnaceae only in Woodwardoideae, *Blechnidium melanopus*, and *Doodia*. Many of the species in this clade are weedy, growing in somewhat open habitats, along roadsides, and in disturbed areas; some species are widely naturalized outside their native range, e.g., *B. appendiculatum* Willd.,

(Palmer, 2003). Several species hybridize frequently (Walker, 1979), and the group is in need of a thorough taxonomic revision, despite of a recent review of southern and southeastern Brazil species (Dittrich *et al.*, 2015), and a monograph of the South American species by Murillo (1966); the group is considered by many (e.g., Mickel and Beitel, 1988) to be systematically and nomenclaturally difficult.

Many reports of chromosome number can found for *Blechnum s.s.* species, but mostly of them appear to be based on $x = 31$, with several hybrids being triploid (Smith and Foster, 1984).

4.3.12 *Austroblechnum* clade

This clade comprises *Austroblechnum penna-marina* (Poir.) Gasper & V.A.O.Dittrich, *comb. ined.*, and ca. 35 related species, with a tropical especially south-temperate occurrence. *Austroblechnum* species have strongly dimorphic fronds, and fertile fronds often have longer stipes than the sterile ones; fertile fronds can be similar in size or are often slightly taller than sterile fronds. The genus includes ca. 11 Neotropical species. *Austroblechnum penna-marina*, which has a circum-Antarctic distribution (Chambers and Farrant, 1996; Rolleri and Prada, 2006) as well as disjunct populations in northwestern Mexico (Mickel and Smith, 2004), is sister to *Austroblechnum microphyllum* (Goldm.) Gasper & V.A.O.Dittrich, *comb. ined.* (restricted to Argentina and Chile); the latter has often been considered a variety of *A. penna-marina* (Chambers and Farrant, 1996). Another group of species with Australasian/Oceanian distribution includes *A. chambersii* Tindale (from New Zealand, southeastern Australia, and Fiji) and allies. There is also a report of hybridization among Australasian species in this clade (Chambers and Farrant, 1999). Australian/Oceanian species occur at middle to high elevations (Brownlie, 1969), many of them above 2,000 m (Nooteboom, 2012). Base chromosome number has been reported as $x = 33$, for

Austroblechnum lanceolatum (R.Br.) Gasper & V.A.O.Dittrich, *comb. nov.* [*B. chambersii* Tindale] and *Austroblechnum patersonii* (R. Br.) Gasper & V.A.O.Dittrich subsp. *patersonii*, *comb. ined.* (Tindale and Roy, 2002), but a presumed dodecaploid number was reported for *Austroblechnum lehmannii* (Hieron.) Gasper & V.A.O.Dittrich, *comb. ined.* ($2n = 198$ II; $2n = 194$ -199 II; Smith and Mickel, 1977).

4.3.13 *Diploblechnum* clade

Diploblechnum Hayata (1.00 PP, 99% ML, 88% MP), typified by *Diploblechnum fraseri* (A.Cunn.) De Vol, comprises ca. six spp. (all sampled) occurring in Malesia, Australia, and Oceania. Species in this clade have dimorphic fronds and pinnate to pinnate-pinnatifid blades. *Diploblechnum fraseri* has unusual fronds with conspicuous, triangular, toothed wings adnate to the rachis, between adjacent pinnae (Chambers and Farrant, 2001). This clade also has erect rhizomes that may ultimately collapse and, when in contact to soil, new roots may be produced, thus mimicing long-creeping rhizomes (Cranfill, 2001). Species in this clade exhibit $2n = 54$ (in *Diploblechnum neglectum* (F.M.Bailey) Gasper & V.A.O.Dittrich, *comb. ined.*; Tindale and Roy, 2002) or $2n = 56$ (in *D. fraseri*; Murray and Lange, 2013), and so base number for the group is presumed to be $x = 27$, or 28. Likewise, *Pteridoblechnum* and *Steenisiolechnum* have similarities in spore ornamentation with *Diploblechnum fraseri*; all have tuberculate spores (Hennipman, 1966; Tryon and Lugardon, 1991).

4.3.14 *Lomariocycas* clade

This taxon was treated as a section of *Blechnum* by Morton (1959), and it is characterized by erect, arborescent caudices, stiff, thickened, curved stipe base and rhizome apex scales, and strongly dimorphic fronds. *Lomariocycas* has about 19 species (seven

sampled), and a reported chromosome number of $2n = 66$ (from *B. palmiforme* (Thouars) C. Chr.; Manton and Vida, 1968). Almost all species are Neotropical, or in mountains on the Juan Fernández Islands, Tristan da Cunha Islands, Madagascar, Réunion, Mauritius, and in South Africa (Tryon and Tryon, 1982; Austrey *et al.*, 2008). Tryon and Tryon (1982) included these species in the *Blechnum buchtienii* Rosenst. group, characterized by the subarborescent to arborescent caudices. This character is not exclusive from *Lomariocycas*, since a few species from other clades, like *Lomaria spannagelii* (Rosenst.) Gasper & V.A.O.Dittrich, *comb. ined.*, *Neoblechnum brasiliense* (Desv.) Gasper & V.A.O.Dittrich, *comb. ined.*, and *Oceanopteris gibba* (Labill.) Gasper & Salino, *comb. ined.*, also show similar caudices (Tryon and Tryon, 1982; Dittrich, 2005).

4.3.15 *Neoblechnum* and *Oceanopteris* clade

Neoblechnum brasiliense, an isolated species in Neotropics, is sister to *Doodia* and *Oceanopteris* (*B. gibbum* clade of Perrie *et al.*, 2014). In *Oceanopteris* (eight spp. sampled out of 10), plants have linear, black scales, free veins, and $2n = 66$, presumably $x = 33$; Abraham *et al.*, 1962). *Neoblechnum brasiliense* resembles morphologically species like Malesian *Oceanopteris egregia* (Copel.) Gasper & Salino, *comb. ined.*, and *O. gibba* (Labill.) Gasper & Salino, *comb. ined.* (Chambers and Farrant, 2001), and have spores similar to *O. cartilaginea* (Sw.) Gasper & Salino, *comb. ined.* (Passarelli *et al.*, 2010). *Oceanopteris cartilaginea* was reported as $n = 32$ or $2n = 132$ (Tindale and Roy, 2002), while *O. whelanii* (F.M. Bailey) Gasper & Salino, *comb. ined.* (Tindale and Roy, 2002) and *O. gibba* have $n = 32$ (Abraham *et al.*, 1962). This clade has broad variation in blade form, with some individuals from the same species (e.g., *O. gibba*; Cranfill, 2001) almost monomorphic, while others are dimorphic.

4.3.14 *Doodia* clade

Doodia (1.00 PP, 100% ML, 98% MP), typified by *Doodia aspera* R.Br., is a distinctive group that has been regarded historically as a genus (e.g., by Parris, 1972; Kramer *et al.*, 1990). It encompasses from 19 (12 sampled) to 30 species (Chambers, 2007), all in Australia, New Zealand, sparingly in Malesia, and the Pacific Islands, including Hawaii (Parris, 1972) and Juan Fernández islands. The genus can be recognized by having deeply pinnatifid to 1-pinnate blades and anastomosing veins (Kramer *et al.*, 1990; Nootboom, 2012). Tindale and Roy (2002) reported $n = 32$ in *Doodia aspera* R. Br. Shepherd *et al.* (2007) provided evidence that *Doodia* nested within *Blechnum s.l.*, which prompted Christenhusz *et al.* (2011) and Perrie *et al.* (2014) to subsume *Doodia* species within *Blechnum*.

4.3.16 *Parablechnum* clade

Parablechnum, the largest clade within subfam. Blechnoideae (ca. 65 spp.), has a pantropical, predominantly southern hemisphere distribution. Its species can be recognized mostly by having strongly dimorphic fronds, creeping to often suberect or erect rhizomes, stipe base scales large, tan to brown, occasionally blackish, concolorous or with darker streaks, numerous scales often extending to rachises, costae, costules, veins, and laminae. This clade can be further subdivided into three subclades based on geographical occurrence: *B. articulatum* (F. Muell.) Gasper & Salino, *comb. ined.*, from Australia, sister to the other two subclades; a second subclade represented by species from Oceania/Malesia; and a third subclade comprising Neotropical+African species. Neotropical species of *Parablechnum* sometimes have peg-like aerophores at pinna bases, and some produce copious amounts of mucilage on young croziers. Chambers and Farrant (1998), revising this complex species from New Zealand, highlighted differences among species of that area, as well as the frequent

occurrence of hybridization, a phenomenon that is possibly rampant among Neotropical species as well.

Parablechnum articulatum has $n = 31$ (Tindale and Roy, 2002), differing from other species like Australian *P. camfieldii* (Tindale) Gasper & Salino, *comb. ined.*, and *P. minus* (R.Br.) Gasper & Salino, *comb. ined.*, with $2n = 56$, presumably based on $x = 28$ (Tindale and Roy, 2002); the Neotropical *Parablechnum chilense* (Kaulf.) Gasper & Salino, *comb. ined.*, was reported as $n = 33$ (Jara-Seguel *et al.*, 2006).

4.4 Distribution

Several clades in our analyses exhibit interesting phylogeographic patterns, as discussed by Moran and Smith (2001), who argued that long-distance dispersal was a likely explanation for amphiatlantic occurrence of similar species. In particular, they noted this pattern in *Blechnum s.s.* [*B. australe* L. subsp. *auriculatum* (Cav.) de la Sota and *B. australe* L. subsp. *australe*], *Lomariocycas* [*L. magellanica* (Desv.) Gasper & A.R.Sm., *comb. ined.* and *L. tabulare* (Thunb.) Gasper & A.R.Sm., *comb. ined.*], and *Lomaridium* species [*L. fragile* (Liebm.) Gasper & V.A.O.Dittrich, *comb. ined.*, and *L. attenuatum* (Sw.) Gasper & V.A.O.Dittrich, *comb. ined.*]. There are also amphipacific distribution patterns involving South American and Australasian species, illustrated by the relationship of *Neoblechnum brasiliense* with *Oceanopteris cartilagea* and allies (discussed above), as well as Neotropical *Lomaria spannagelii*, allied to species related to *Lomaria oceanica* (Rosenst.) Gasper & V.A.O.Dittrich, *comb. ined.*, and relatives in Polynesia. Another trans-oceanic example occurs in *Parablechnum*, with one of the subclades occurring in Australasia/Oceania and the other mostly Neotropical. Of the genera and clades here recognized, only *Woodwardia* and *Struthiopteris* are widespread in the northern hemisphere.

Many of the more basal taxa in our phylogenetic analyses of extant Blechnaceae –

subfam. Woodwardioideae, *Struthiopteris*, *Blechnopsis*, *Brainea*, and *Sadleria* in subfam. Blechnoideae – appear to show a primarily northern hemisphere distribution. This might indicate that the predominance seen today of multiple clades and greater species richness in southern hemisphere is secondarily derived (Li *et al.*, 2014), an event that would have taken place during the Paleogene (Rothfels *et al.*, 2015).

5. Conclusions

The need for subdivision of *Blechnum* into smaller, more natural genera has previously been mentioned by several authors (Mickel and Smith, 2004; Smith *et al.*, 2006a; Rothfels *et al.*, 2012). Also, the unusually diverse cytological variation within Blechnaceae provides us with important clues regarding divergence and relationships among the various clades identified in this study (chromosome numbers summarized by Löve *et al.*, 1977; see also Walker, 1985; Tindale and Roy, 2002, for salient comments on the cytology of the family).

Recognition of main subclades within subfam. Blechnoideae as genera, many of them species-rich even in their reduced form, provides an improved and better supported classification of Blechnaceae. Inclusion of *Brainea*, *Doodia*, and *Sadleria* in *Blechnum s.l.*, although perhaps convenient for those accustomed to historically large fern genera, obscures relationships and creates an unwieldy, morphologically ill-defined genus *Blechnum*, cosmopolitan in distribution -- a genus that contains many strongly supported, monophyletic subclades, each having substantial morphological and cytological continuity.

The breakup of *Polypodium* L. into smaller, more natural genera like *Serpocaulon* A.R. Sm. (Smith *et al.*, 2006b), *Campyloneurum* C. Presl, *Pecluma* M.G. Price, and others, the segregation of numerous genera of grammitid ferns (Polypodiaceae - Hirai *et al.*, 2011; Kessler *et al.*, 2011), the fragmentation of cheilanthoid ferns [Pteridaceae; *Gaga* Pryer *et al.* (Li *et al.*, 2012); *Myriopteris* Fée (Grusz and Windham, 2013); *Doryopteris* J. Sm. (Yesilyurt

et al., 2015) etc.], and the dismemberment of *Thelypteris* Schmidel *s.l.* (Almeida *et al.*, 2016), all show parallels to the situation within Blechnaceae. Smaller genera, having stronger morphological and molecular support, are easier to study, allow for recognition of phylogeographic patterns, clarify relationships, and point the way toward other interesting avenues of research, involving character and character state evolution, chromosomal repatterning, reproductive biology, and ecological issues; they also facilitate more detailed monographic work. For these reasons, we chose to propose a full reclassification, resurrecting a number of existing names for some of the segregates, describing new genera, and making new combinations (Gasper *et al.*, in prep.). Further phylogenetic studies on this diverse family of ferns could prove interesting in resolving complex relationships among the various clades identified in this study.

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unpublished conclusions from newly sampled material, and accept full responsibility for them.

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Appendix

Appendix 1. List of sampled taxa with voucher information (herbarium), country, and GenBank accession numbers for *rbcL*, *rps4* and *trnL-trnF* sequences, respectively. New sequences in this study are indicated by *. Herbaria acronyms follow Thiers (2015).

Anchistea virginica (L.) C.Presl, *Cranfill s.n. (RBC 606)* (UC), USA: *rbcL* AY137660 (Cranfil and Kato, 2003), *rps4* AF533857 (Cranfil and Kato, 2003).

Athyrium filix-femina (L.) Roth, Groot (306), *Cranfill s.n. (RBC 356)*, cult: *rbcL* HQ676497 (Groot *et al.*, 2011), *rps4* AF425152 (Smith and Cranfill, 2002), *trnL-trnF* HQ676519 (Groot *et al.*, 2011).

Austroblechnum xaggregatum (Colenso) Gasper & V.A.O.Dittrich, *comb. ined.*, *Wilson 68* (MELU), Australia: *rbcL* KJ170817 (Perrie *et al.*, 2014), *rps4* KJ170790 (Perrie *et al.*, 2014), *trnL-trnF* KJ170844 (Perrie *et al.*, 2014); *Austroblechnum andinum* (Baker) Gasper & V.A.O.Dittrich, *comb. ined.*, *s.n. (BHCB)*, Brazil: *rbcL* KU898604*, *rps4* KU898550*, *trnL-trnF* KU925243*; *Austroblechnum blechnoides* (Keyserl.) Gasper & V.A.O.Dittrich, *comb. ined.*, *Perrie 3295* (WELT), New Zealand: *rbcL* KF975780 (Perrie *et al.*, 2014), *rps4* KF975736 (Perrie *et al.*, 2014), *trnL-trnF* DQ683374 (Shepherd *et al.*, 2007); *Austroblechnum colensoi* (Hook.f.) Gasper & V.A.O.Dittrich, *comb. ined.*, *Perrie 3572* (WELT), New Zealand: *rbcL* KF975783 (Perrie *et al.*, 2014), *rps4* KF975739 (Perrie *et al.*, 2014), *trnL-trnF* DQ683379 (Shepherd *et al.*, 2007); *Austroblechnum divergens* (Kunze) Gasper & V.A.O.Dittrich, *comb. ined.*, *Funez 1000* (FURB), Brazil: *rbcL* KU898605*, *rps4* KU898548*, *trnL-trnF* KU898664*; *Austroblechnum durum* (T.Moore) Gasper & V.A.O.Dittrich, *comb. ined.*, *Perrie 4023* (WELT), New Zealand: *rbcL* KF975788 (Perrie *et al.*, 2014), *rps4* KF975744 (Perrie *et al.*, 2014), *trnL-trnF* DQ683383 (Shepherd *et al.*, 2007); *Austroblechnum lehmannii* (Hieron.) Gasper & V.A.O.Dittrich, *comb. ined.*, *Almeida 3374* (BHCB), Brazil: *rbcL* KU898606*, *rps4*

KU898551*, *trnL-trnF* KU898665*; ***Austroblechnum melanocaulon*** (Brack.) Gasper & V.A.O.Dittrich, *comb. ined.*, *Perrie & Brownsey FJ2011182* (WELT), Fiji: *rbcL* KF975794 (Perrie *et al.*, 2014), *rps4* KF975750 (Perrie *et al.*, 2014), *trnL-trnF* KF975720 (Perrie *et al.*, 2014); ***Austroblechnum membranaceum*** (Colenso ex Hook.) Gasper & V.A.O.Dittrich, *comb. ined.*, *Perrie 3475* (WELT), New Zealand: *rbcL* KF975795 (Perrie *et al.*, 2014), *rps4* KF975751 (Perrie *et al.*, 2014), *trnL-trnF* DQ683391 (Shepherd *et al.*, 2007); ***Austroblechnum microphyllum*** (Goldm.) Gasper & V.A.O.Dittrich, *comb. ined.*, *Biganzoli 2141* (SI), Argentina: *rbcL* KU898607*, *rps4* KU898552*, *trnL-trnF* KU898666*; ***Austroblechnum mochaenum*** (G.Kunkel) Gasper & V.A.O.Dittrich **var. *achalense*** (Hieron.) Gasper & V.A.O.Dittrich, *comb. ined.*, *Larsen 252* (SI), Chile: *rbcL* KU898608*, *rps4* KU898553*, *trnL-trnF* KU898667*; ***Austroblechnum norfolkianum*** (Heward) Gasper & V.A.O.Dittrich, *comb. ined.*, *Parris 12358* (WELT), New Zealand: *rbcL* KF975801 (Perrie *et al.*, 2014), *rps4* KF975757 (Perrie *et al.*, 2014), *trnL-trnF* DQ683401 (Shepherd *et al.*, 2007); ***Austroblechnum patersonii*** (R.Br.) Gasper & V.A.O.Dittrich **subsp. *patersonii***, *comb. ined.*, *Wilson 70* (MELU), Australia: *rbcL* KJ170822 (Perrie *et al.*, 2014), *rps4* KJ170795 (Perrie *et al.*, 2014), *trnL-trnF* KJ170849 (Perrie *et al.*, 2014); ***Austroblechnum patersonii*** (R.Br.) Gasper & V.A.O.Dittrich **subsp. *queenslandicum*** (T.C.Chambers & P.A.Farrant) Gasper & V.A.O.Dittrich, *comb. ined.*, *Ohlsen BB144* (BRI), Australia: *rbcL* KJ170823 (Perrie *et al.*, 2014), *rps4* KJ170796 (Perrie *et al.*, 2014), *trnL-trnF* KJ170850 (Perrie *et al.*, 2014); ***Austroblechnum pennamariana*** (Poir.) Gasper & V.A.O.Dittrich, *comb. ined.*, *Gasper 3039* (FURB), Brazil: *rbcL* KU898609*, *rps4* KU898554*, *trnL-trnF* KU898668*; ***Austroblechnum squamipes*** (Hieron.) Gasper & V.A.O.Dittrich, *comb. ined.*, *Salino 14737* (BHCB), Brazil: *rbcL* KU898610*, *rps4* KU898555*, *trnL-trnF* KU898669*; ***Austroblechnum stoloniferum*** (Mett. ex E.Fourn.) Gasper & V.A.O.Dittrich, *comb. ined.*, *Campos Salas 12* (MEXU),

Mexico: *rbcL* KU898611*, *rps4* KU898556*, *trnL-trnF* KU898670*; ***Austroblechnum vieillardii*** (Mett.) Gasper & V.A.O.Dittrich, *comb. ined.*, *Perrie NC 2012 227* (WELT), New Caledonia: *rbcL* KF975814 (Perrie *et al.*, 2014), *trnL-trnF* KF975730 (Perrie *et al.*, 2014); ***Austroblechnum wardiae*** (Mickel & Beitel) Gasper & V.A.O.Dittrich, *comb. ined.*, *Salino 15367* (BHCB), Panama: *rbcL* KU898612*, *rps4* KU898557*, *trnL-trnF* KU898671*.

Blechnidium melanopus (Hook.) T.Moore, *Knapp 3355* (P), Taiwan: *rbcL* KU898627*.

Blechnopsis orientalis (L.) C.Presl, *Brownsey & Perrie FJ201190* (WELT), Australia: *rbcL* KF975806 (Perrie *et al.*, 2014), *rps4* KF975762 (Perrie *et al.*, 2014), *trnL-trnF* KF975726 (Perrie *et al.*, 2014).

Blechnum xcaudatum Cav., *Almeida 3371* (BHCB), Brazil: *rbcL* KU898618*, *rps4* KU898563*, *trnL-trnF* KU898677*; ***Blechnum xconfluens*** Schtdl. & Cham., *Kessler 13457* (LPB), Bolivia: *rbcL* KU898625*, *rps4* KU898569*, *trnL-trnF* KU898682*; ***Blechnum appendiculatum*** Willd., *Salino 15454* (BHCB), Panama: *rbcL* KU898613*, *rps4* KU898558*, *trnL-trnF* KU898672*; ***Blechnum areolatum*** V.A.O.Dittrich & Salino, *Salino 15184* (BHCB), Brazil: *rbcL* KU898614*, *rps4* KU898559*, *trnL-trnF* KU898673*; ***Blechnum asplenioides*** Sw., *Salino 14449* (BHCB), Brazil: *rbcL* KU898615*, *rps4* KU898560*, *trnL-trnF* KU898674*; ***Blechnum australe*** L., *unknown; Prada s.n.* (unknown/MA), Argentina: *rbcL* AB040557 (unknown), *trnL-trnF* JQ907366 (Gabriel y Galan *et al.*, 2013); ***Blechnum auriculatum*** Cav., *Funez 2162* (FURB), Brazil: *rbcL* KU898616*, *rps4* KU898561*, *trnL-trnF* KU898675*; ***Blechnum austrobrasilianum*** de la Sota, *Almeida 3372* (BHCB), Brazil: *rbcL* KU898617*, *rps4* KU898562*, *trnL-trnF* KU898676*; ***Blechnum glandulosum*** Kaulf. ex Link, *Yatskievych 83-157* (IND), Argentina: *rbcL* U62037 (Gastony and Ungerer, 1997); ***Blechnum gracile*** Kaulf., *Jiménez I. 1051*

(LPB), Bolivia: *rbcL* KU898620*, *rps4* KU898565*, *trnL-trnF* KU898678*; ***Blechnum gracilipes*** (Rosenst.) M.Kessler & A.R.Sm., *Jiménez I. 1485* (LPB), Bolivia: *trnL-trnF* KU898679*; ***Blechnum hastatum*** Kaulf., *Zuloaga 11322* (SI), Argentina: *rbcL* KU898619*, *rps4* KU898564*; ***Blechnum laevigatum*** Cav., *Canestraro 527* (MBM), Brazil: *rbcL* KU898621*, *rps4* KU898566*; ***Blechnum lanceola*** Sw., *Laurent 275* (BHCB), Brazil: *rbcL* KU898622*, *rps4* KU898567*, *trnL-trnF* KU898680*; ***Blechnum longipilosum*** V.A.O.Dittrich & Salino, *Salino 15570* (BHCB), Brazil: *rbcL* KU898626*, *rps4* KU898570*, *trnL-trnF* KU898683*; ***Blechnum occidentale*** L., *Funez 548* (FURB), Brazil: *rbcL* KU898623*, *rps4* KU898568*, *trnL-trnF* KU898681*; ***Blechnum polyodioides*** Raddi, *Salino 15334* (BHCB), Panama: *rbcL* KU898624*, *rps4* KU925241*, *trnL-trnF* KU925244*; ***Blechnum punctulatum*** Sw. var. *atherstonii* R.Sim, *cult., Parris 12683* (WELT), *cultivada: rbcL* KF975811 (Perrie *et al.*, 2014), *rps4* KF975767 (Perrie *et al.*, 2014), *trnL-trnF* DQ683412 (Shepherd *et al.*, 2007);

Brainea insignis (Hook.) J.Sm., *Averyanov 2702* (P 01568306), Vietnam: *rbcL* KU898628, *rps4* KU898571*, *trnL-trnF* KU898684*.

Cleistoblechnum eburneum (Christ) Gasper & Salino var. *eburneum*, *comb. ined.*, *S.G. LU/ZI* (PYU), China: *rbcL* JN168003 (Chunxiang *et al.*, 2011), *rps4* JN168071 (Chunxiang *et al.*, 2011).

Cranfillia fluviatilis (R.Br.) Gasper & V.A.O.Dittrich, *comb. ined.*, *Wilson 64* (MELU), Australia: *rbcL* KJ170818 (Perrie *et al.*, 2014), *rps4* KJ170791 (Perrie *et al.*, 2014), *trnL-trnF* KJ170845 (Perrie *et al.*, 2014); ***Cranfillia hirsuta*** (Rosenst.) Gasper & V.A.O.Dittrich, *comb. ined.*, *Perrie NC 2012 196* (WELT), New Caledonia: *rbcL* KF975792 (Perrie *et al.*, 2014), *rps4* KF975748 (Perrie *et al.*, 2014), *trnL-trnF* KF975718 (Perrie *et al.*, 2014); ***Cranfillia nigra*** (Colenso) Gasper & V.A.O.Dittrich, *comb. ined.*, *Perrie 3454* (WELT), New Zealand: *rbcL* KF975800 (Perrie *et al.*, 2014), *rps4* KF975756 (Perrie *et al.*,

2014), *trnL-trnF* DQ683399 (Shepherd *et al.*, 2007); ***Cranfillia opaca*** (Mett.) Gasper & V.A.O.Dittrich, *comb. ined.*, *Perrie NC 2012 167* (WELT), New Caledonia: *rbcL* KF975805 (Perrie *et al.*, 2014), *rps4* KF975761 (Perrie *et al.*, 2014), *trnL-trnF* KF975725 (Perrie *et al.*, 2014); ***Cranfillia pilosa*** (Brack.) Gasper & V.A.O.Dittrich, *comb. ined.*, *Perrie & Brownsey FJ2011181* (WELT), Fiji: *rbcL* KF975809 (Perrie *et al.*, 2014), *rps4* KF975765 (Perrie *et al.*, 2014), *trnL-trnF* KF975728 (Perrie *et al.*, 2014); ***Cranfillia sampaioana*** (Brade) Gasper & V.A.O.Dittrich, *comb. ined.*, *Salino 13818* (BHCB), Brazil: *rbcL* KU898629*, *rps4* KU898572*, *trnL-trnF* KU898685*; ***Cranfillia sprucei*** (C.Chr) Gasper & V.A.O.Dittrich, *comb. ined.*, *Jiménez I. 1743* (LPB), Bolivia: *rbcL* KU898630*, *rps4* KU898573*, *trnL-trnF* KU898686*; ***Cranfillia vulcanica*** (Blume) Gasper & V.A.O.Dittrich, *comb. ined.*, *Perrie 3461* (WELT), Australia: *rbcL* KF975816 (Perrie *et al.*, 2014), *rps4* KF975771 (Perrie *et al.*, 2014), *trnL-trnF* DQ683416 (Shepherd *et al.*, 2007);

Diploblechnum acuminatum (C.T.White & Goy) Gasper & V.A.O.Dittrich, *comb. ined.*, *Field et al. s.n.* (CNS), Australia: *rbcL* KJ170839 (Perrie *et al.*, 2014), *rps4* KJ170812 (Perrie *et al.*, 2014), *trnL-trnF* KJ170866 (Perrie *et al.*, 2014); ***Diploblechnum diversifolium*** (Mett.) Gasper & V.A.O.Dittrich, *comb. ined.*, *Perrie NC 2012 157* (WELT), New Caledonia: *rbcL* KF975787 (Perrie *et al.*, 2014), *rps4* KF975743 (Perrie *et al.*, 2014), *trnL-trnF* KF975716 (Perrie *et al.*, 2014); ***Diploblechnum fraseri*** (A.Cunn.) De Vol, *Perrie 3434* (WELT), New Zealand: *rbcL* KF975790 (Perrie *et al.*, 2014), *rps4* KF975746 (Perrie *et al.*, 2014), *trnL-trnF* DQ683390 (Shepherd *et al.*, 2007); ***Diploblechnum lenormandii*** (Baker) Gasper & V.A.O.Dittrich, *comb. ined.*, *Perrie NC 2012 169* (WELT), New Caledonia: *rbcL* KF975793 (Perrie *et al.*, 2014), *rps4* KF975749 (Perrie *et al.*, 2014), *trnL-trnF* KF975719 (Perrie *et al.*, 2014); ***Diploblechnum neglectum*** (F.M.Bailey) Gasper & V.A.O.Dittrich, *comb. ined.*, *van der Werff 17045* (MO), Australia: *rbcL* KU898631*, *rps4* KU898574*, *trnL-trnF* KU898687*.

Doodia aspera R.Br., *Perrie and Ohlsen BB113* (MELU), Australia: *rbcL* KJ170836 (Perrie *et al.*, 2014), *rps4* KJ170809 (Perrie *et al.*, 2014), *trnL-trnF* KJ170863 (Perrie *et al.*, 2014); *Doodia australis* Parris, *Ohlsen BB151* (MELU), Australia: *rbcL* KJ170837 (Perrie *et al.*, 2014), *rps4* KJ170810 (Perrie *et al.*, 2014), *trnL-trnF* KJ170864 (Perrie *et al.*, 2014); *Doodia brackenridgei* Carruth. ex Seem., *Perrie & al. FJ2011123* (WELT), Fiji: *rbcL* KF975818 (Perrie *et al.*, 2014), *rps4* KF975773 (Perrie *et al.*, 2014), *trnL-trnF* KF975732 (Perrie *et al.*, 2014); *Doodia caudata* (Cav.) R.Br., *Perrie and Ohlsen BB88* (MELU), Australia: *rbcL* KJ170838 (Perrie *et al.*, 2014), *rps4* KJ170811 (Perrie *et al.*, 2014), *trnL-trnF* KJ170865 (Perrie *et al.*, 2014); *Doodia kunthiana* Gaudich., *unknown* (unknown/WELT), USA: *rbcL* AB040578 (Nakahira, 2000), *rnl-trnF* DQ683424 (Shepherd *et al.*, 2007); *Doodia dives* Kunze, *Perrie et al. BB24* (BRI), Australia: *rbcL* KJ170831 (Perrie *et al.*, 2014), *rps4* KJ170804 (Perrie *et al.*, 2014), *trnL-trnF* KJ170858 (Perrie *et al.*, 2014); *Doodia linearis* J.Sm., *Ohlsen BB147* (MELU), Australia: *rbcL* KJ170833 (Perrie *et al.*, 2014), *rps4* KJ170806 (Perrie *et al.*, 2014), *trnL-trnF* KJ170860 (Perrie *et al.*, 2014); *Doodia media* R.Br., *Perrie NC 2012 120* (WELT), Australia: *rbcL* KF975819 (Perrie *et al.*, 2014), *rps4* KF975774 (Perrie *et al.*, 2014), *trnL-trnF* KF975733 (Perrie *et al.*, 2014); *Doodia milnei* Carruth., *Parris 12689* (WELT), New Zealand: *rbcL* KF975820 (Perrie *et al.*, 2014), *rps4* KF975775 (Perrie *et al.*, 2014), *trnL-trnF* DQ683425 (Shepherd *et al.*, 2007); *Doodia mollis* Parris, *Parris 12688* (WELT), New Zealand: *rbcL* KF975821 (Perrie *et al.*, 2014), *rps4* KF975776 (Perrie *et al.*, 2014), *trnL-trnF* DQ683427 (Shepherd *et al.*, 2007); *Doodia paschalis* C.Chr., *Christenhusz 5047* (P), Chile (Easter Island): *trnL-trnF* KU925245*; *Doodia squarrosa* Colenso, *Perrie 3517* (WELT), New Zealand: *rbcL* KF975822 (Perrie *et al.*, 2014), *rps4* KF975777 (Perrie *et al.*, 2014), *trnL-trnF* DQ683429 (Shepherd *et al.*, 2007).

Icarus filiformis (A.Cunn.) Gasper & Salino, *comb. ined.*, *Perrie 3459* (WELT), New

Zealand: *rbcL* KF975789 (Perrie *et al.*, 2014), *rps4* KF975745 (Perrie *et al.*, 2014), *trnL-trnF* DQ683385 (Shepherd *et al.*, 2007);

Lomaria nuda (Labill.) Willd., *Wilson 69* (MELU), Australia: *rbcL* KJ170821 (Perrie *et al.*, 2014), *rps4* KJ170794 (Perrie *et al.*, 2014), *trnL-trnF* KJ170848 (Perrie *et al.*, 2014);

Lomaria oceanica (Rosenst.) Gasper & V.A.O.Dittrich, *comb. ined.*, *Perrie NC 2012 105* (WELT), New Caledonia: *rbcL* KF975804 (Perrie *et al.*, 2014), *rps4* KF975760 (Perrie *et al.*, 2014), *trnL-trnF* KF975724 (Perrie *et al.*, 2014); *Lomaria raymondii* Gasper & V.A.O.Dittrich, *comb. ined.*, *Perrie 4015* (WELT), New Zealand: *rbcL* KF975786 (Perrie *et al.*, 2014), *rps4* KF975742 (Perrie *et al.*, 2014), *trnL-trnF* DQ683382 (Shepherd *et al.*, 2007);

Lomaria spannagelii (Rosenst.) Gasper & V.A.O.Dittrich, *comb. ined.*, *Almeida 3387* (BHCB), Brazil: *rbcL* KU898643*, *rps4* KU898584*, *trnL-trnF* KU898698*;

Lomaridium acutum (Desv.) Gasper & V.A.O.Dittrich, *comb. ined.*, *van der Werff 16799* (MO), Peru: *rbcL* KU898638*, *rps4* KU925242*, *trnL-trnF* KU925246*;

Lomaridium attenuatum (Sw.) Gasper & V.A.O.Dittrich, *comb. ined.*, *Hennequin R67* (BM), Réunion: *rbcL* KF992444 (Hennequin *et al.*, 2014); *Lomaridium biforme* (Baker)

Gasper & V.A.O.Dittrich, *comb. ined.*, *unknown* (unknown), Fiji: *rbcL* AB040561 (Nakahira, 2000); *Lomaridium contiguum* (Mett.) Gasper & V.A.O.Dittrich, *comb. ined.*,

Munzinger 651 (MO), New Caledonia: *rbcL* KF975804*, *rps4* KF975760*, *trnL-trnF* KF975724*;

Lomaridium ensiforme (Liebm.) Gasper & V.A.O.Dittrich, *comb. ined.*, *Jiménez I. 697* (LPB), Bolivia: *rbcL* KU898639*, *rps4* KU898581*, *trnL-trnF* KU898694*;

Lomaridium fragile (Liebm.) Gasper & V.A.O.Dittrich, *comb. ined.*, *Salino 15860* (BHCB),

Panama: *rbcL* KU898640*, *rps4* KU898582*, *trnL-trnF* KU898695*;

Lomaridium fuscocosquamosum (A.Rojas) Gasper & V.A.O.Dittrich, *comb. ined.*, *van der Werff 16823* (MO), Peru: *rbcL* KU898641*, *rps4* KU898583*, *trnL-trnF* KU898696*.

Lomariocycas aurata (Fée) Gasper & A.R.Sm., *comb. ined.*, *Jiménez I. 1852* (LPB),

Bolivia: *rbcL* KU898633*, *rps4* KU898576*, *trnL-trnF* KU898690*; ***Lomariocycas columbiensis*** (Hieron.) Gasper & A.R.Sm., *comb. ined.*, *van der Werff 16910* (MO), Peru: *rbcL* KU898634*, *rps4* KU898577*; ***Lomariocycas magellanica*** (Desv.) Gasper & A.R.Sm., *comb. ined.*, *unknown; Prada s.n.* (unknown/MA), Argentina: *rbcL* AB040559 (unknown), *trnL-trnF* JQ907376 (Gabriel y Galan *et al.*, 2013); ***Lomariocycas schomburgkii*** (Klotzsch) Gasper & A.R.Sm., *comb. ined.*, *Salino 15692* (BHCB), Brazil: *rbcL* KU898636*, *rps4* KU898579*, *trnL-trnF* KU898692*; ***Lomariocycas tabularis*** (Thunb.) Gasper & A.R.Sm., *comb. ined.*, *Hennequin R105* (BM), Reunion: *rbcL* KF992447 (Hennequin *et al.*, 2014); ***Lomariocycas werckleana*** (Christ) Gasper & A.R.Sm., *comb. ined.*, *Salino 15924* (BHCB), Panama: *rbcL* KU898637*, *rps4* KU898580*, *trnL-trnF* KU898693*; ***Lomariocycas yungensis*** (J.P.Ramos) Gasper & A.R.Sm., *comb. ined.*, *Jiménez I. 2383* (LPB), Bolivia: *rbcL* KU898635*, *rps4* KU898578*, *trnL-trnF* KU898691*.

Lorinseria areolata (L.) C.Presl, *Cranfill s.n. (RBC 170)* (unknown), USA: *rbcL* AF425102 (Smith and Cranfill, 2002), *rps4* AF425155 (Smith and Cranfill, 2002).

Matteuccia struthiopteris (L.) Tod., *Cranfill s.n. (RBC 460)*; *unknown* (UC), *cultivada*: *rbcL* U05930 (Cranfil and Kato, 2003), *rps4* AF425158 (Cranfil and Kato, 2003), *trnL-trnF* KC254425 (Wei *et al.*, 2013).

Neoblechnum brasiliense (Desv.) Gasper & V.A.O.Dittrich, *comb. ined.*, *unknown; Christenhusz 4968; Prada s.n.* (unknown/BM/MA), Argentina: *rbcL* AB040545 (unknown), *rps4* HQ157324 (Lehtonen, 2011), *trnL-trnF* JQ907369 (Gabriel y Galan *et al.*, 2013).

Oceanopteris cartilaginea (Sw.) Gasper & Salino, *comb. ined.*, *Bayly 2182* (MELU), Australia: *rbcL* KJ170816 (Perrie *et al.*, 2014), *rps4* KJ170789 (Perrie *et al.*, 2014), *trnL-trnF* KJ170843 (Perrie *et al.*, 2014); ***Oceanopteris ciliata*** (T.Moore) Gasper & Salino, *comb. ined.*, *Perrie NC 2012 146* (WELT), New Caledonia: *rbcL* KF975799 (Perrie *et al.*, 2014),

rps4 KF975755 (Perrie *et al.*, 2014), *trnL-trnF* KF975722 (Perrie *et al.*, 2014); ***Oceanopteris dentata*** (Brack.) Kuhn, Perrie & Brownsey FJ2011210 (WELT), Fiji: *rbcL* KF975815 (Perrie *et al.*, 2014), *rps4* KF975770 (Perrie *et al.*, 2014), *trnL-trnF* KF975731 (Perrie *et al.*, 2014); ***Oceanopteris francii*** (Rosenst.) Gasper & Salino, *comb. ined.*, Christenhusz 6198 (NOU), New Caledonia: *trnL-trnF* KU898688*; ***Oceanopteris gibba*** (Labill.) Gasper & Salino, *comb. ined.*, Perrie NC 2012 76 (WELT), New Caledonia: *rbcL* KF975791 (Perrie *et al.*, 2014), *rps4* KF975747 (Perrie *et al.*, 2014), *trnL-trnF* KF975717 (Perrie *et al.*, 2014); ***Oceanopteris obtusata*** (Labill.) Gasper & Salino, *comb. ined.*, McPherson 18146 (MO), New Caledonia: *rbcL* KU898632*, *rps4* KU898575*, *trnL-trnF* KU898689*; ***Oceanopteris whelanii*** (F.M.Bailey) Gasper & Salino, *comb. ined.*, Perrie *et al.* BB64 (BRI), Australia: *rbcL* KJ170827 (Perrie *et al.*, 2014), *rps4* KJ170800 (Perrie *et al.*, 2014), *trnL-trnF* KJ170854 (Perrie *et al.*, 2014).

***Onoclea sensibilis* L.**, *Weed s.n.* (UC), cultivada: *rbcL* U05936 (Cranfil and Kato, 2003), *rps4* AF425159 (unknown).

Onocleopsis hintonii F.Ballard, *Mickel s.n.* (UC), Mexico: *rbcL* U62033 (Cranfil and Kato, 2003), *rps4* AF425160 (unknown).

Parablechnum ambiguum C.Presl, *Ohlsen BB233* (MELU), Australia: *rbcL* KJ170813 (Perrie *et al.*, 2014), *rps4* KJ170786 (Perrie *et al.*, 2014), *trnL-trnF* KJ170840 (Perrie *et al.*, 2014); ***Parablechnum articulatum*** (F.Muell.) Gasper & Salino, *comb. ined.*, Perrie *et al.* BB36 (MELU), Australia: *rbcL* KJ170814 (Perrie *et al.*, 2014), *rps4* KJ170787 (Perrie *et al.*, 2014), *trnL-trnF* KJ170841 (Perrie *et al.*, 2014); ***Parablechnum bicolor*** (M.Kessler & A.R.Sm.) Gasper & Salino, *comb. ined.*, Jiménez I. 942 (LPB), Bolivia: *rbcL* KU898645*, *rps4* KU898586*, *trnL-trnF* KU898700*; ***Parablechnum bolivianum*** (M.Kessler & A.R.Sm.) Gasper & Salino, *comb. ined.*, Bach K. 1404 (LPB), Bolivia: *rbcL* KU898646*, *rps4* KU898587*, *trnL-trnF* KU898701*; ***Parablechnum camfieldii*** (Tindale)

Gaspar & Salino, *comb. ined.*, *Ohlsen BB216* (BRI), Australia: *rbcL* KJ170815 (Perrie *et al.*, 2014), *rps4* KJ170788 (Perrie *et al.*, 2014), *trnL-trnF* KJ170842 (Perrie *et al.*, 2014); ***Parablechnum capense*** (Burm.f.) Gaspar & Salino, *comb. ined.*, *unknown* (unknown), New Zealand: *rbcL* AB040547 (Nakahira, 2000); ***Parablechnum chiriquanum*** (Broadh.) Gaspar & Salino, *comb. ined.*, *Rojas & Gabriel y Galan CR 10419* (unknown), Panama: *trnL-trnF* KM001891; ***Parablechnum christii*** (C.Chr.) Gaspar & Salino, *comb. ined.*, *Salino 15459* (BHCB), Panama: *rbcL* KU898647*, *rps4* KU898588*; ***Parablechnum corbassonii*** (Brownlie) Gaspar & Salino, *comb. ined.*, *Perrie NC 2012 14* (WELT), New Caledonia: *rbcL* KF975785 (Perrie *et al.*, 2014), *rps4* KF975741 (Perrie *et al.*, 2014), *trnL-trnF* KF975715 (Perrie *et al.*, 2014); ***Parablechnum cordatum*** (Desv.) Gaspar & Salino, *comb. ined.*, *Gaspar 3051* (FURB), Brazil: *rbcL* KU898648*, *rps4* KU898589*, *trnL-trnF* KU898702*; ***Parablechnum falciforme*** (Liebm.) Gaspar & Salino, *comb. ined.*, *Salino 15430* (BHCB), Panama: *rbcL* KU898649*, *rps4* KU898590*, *trnL-trnF* KU898703*; ***Parablechnum glaziovii*** (Christ) Gaspar & Salino, *comb. ined.*, *Salino 15689* (BHCB), Brazil: *rbcL* KU898650*, *rps4* KU898591*, *trnL-trnF* KU898704*; ***Parablechnum gregsonii*** (Tindale) Gaspar & Salino, *comb. ined.*, *Ohlsen BB228* (MELU), Australia: *rbcL* KJ170819 (Perrie *et al.*, 2014), *rps4* KJ170792 (Perrie *et al.*, 2014), *trnL-trnF* KJ170846 (Perrie *et al.*, 2014); ***Parablechnum howeanum*** (T.C.Chambers & P.A.Farrant) Gaspar & Salino, *comb. ined.*, *Papadopulos et al. (2011)* (NSW), Australia: *rbcL* JF950804 (Papadopulos *et al.*, 2011), *trnL-trnF* JF950940 (Papadopulos *et al.*, 2011); ***Parablechnum lechleri*** (Mett.) Gaspar & Salino, *comb. ined.*, *Bach K. 1311* (LPB), Bolivia: *rbcL* KU898651*, *rps4* KU898592*, *trnL-trnF* KU898705*; ***Parablechnum lima*** (Rosenst.) Gaspar & Salino, *comb. ined.*, *Bach K. 1461* (LPB), Bolivia: *rbcL* KU898652*, *rps4* KU898593*, *trnL-trnF* KU898706*; ***Parablechnum loxense*** (Kunth) Gaspar & Salino var. *stenophyllum* (Klotzsch) Gaspar & Salino, *comb. ined.*, *Christenhusz 6777; Gabriel y Galán s.n.* (H; MA), Peru: *rbcL* KJ716414

(unknown), *trnL-trnF* JQ907375 (Gabriel y Galan *et al.*, 2013); ***Parablechnum marginatum*** (Kuhn) Gasper & Salino var. ***humbertii*** (Tardieu) Gasper & Salino, *comb. ined.*, *Hennequin R76* (BM), Reunion: *rbcL* KF992446 (Hennequin *et al.*, 2014); ***Parablechnum milnei*** (Carruth.) Gasper & Salino, *comb. ined.*, *Perrie & Brownsey FJ2011165* (WELT), Fiji: *rbcL* KF975796 (Perrie *et al.*, 2014), *rps4* KF975752 (Perrie *et al.*, 2014), *trnL-trnF* KF975721 (Perrie *et al.*, 2014); ***Parablechnum minus*** (R.Br.) Gasper & Salino, *comb. ined.*, *Wilson 72* (MELU), Australia: *rbcL* KJ170820 (Perrie *et al.*, 2014), *rps4* KJ170793* (Perrie *et al.*, 2014), *trnL-trnF* KJ170847* (Perrie *et al.*, 2014); ***Parablechnum montanum*** (T.C.Chambers & P.A.Farrant) Gasper & Salino, *comb. ined.*, *Perrie 3498* (WELT), New Zealand: *rbcL* KF975798 (Perrie *et al.*, 2014), *rps4* KF975754 (Perrie *et al.*, 2014), *trnL-trnF* KJ187000 (Perrie *et al.*, 2014); ***Parablechnum novae-zelandiae*** (T.C.Chambers & P.A.Farrant) Gasper & Salino, *comb. ined.*, *Perrie 3129 & Lovis* (WELT), New Zealand: *rbcL* KF975802 (Perrie *et al.*, 2014), *rps4* KF975758 (Perrie *et al.*, 2014), *trnL-trnF* DQ683403 (Shepherd *et al.*, 2007); ***Parablechnum pazense*** (M.Kessler & A.R.Sm.) Gasper & Salino, *comb. ined.*, *Jiménez I. 751* (LPB), Bolivia: *rbcL* KU898653*, *rps4* KU898594*, *trnL-trnF* KU898707*; ***Parablechnum procerum*** (G.Forst.) C.Presl, *Perrie 3127* (WELT), New Zealand: *rbcL* KF975810 (Perrie *et al.*, 2014), *rps4* KF975766 (Perrie *et al.*, 2014), *trnL-trnF* DQ683411 (Shepherd *et al.*, 2007); ***Parablechnum proliferum*** (Rosenst.) Gasper & Salino, *comb. ined.*, *Salino 15534 and Salino 13734* (BHCB), Brazil: *rbcL* KU898654*, *rps4* KU898595*, *trnL-trnF* KU898708*; ***Parablechnum schiedeanum*** (Schltdl. ex C.Presl) Gasper & Salino, *comb. ined.*, *Salino 15700* (BHCB), Panama: *rbcL* KU898655*, *rps4* KU898596*, *trnL-trnF* KU898709*; ***Parablechnum smilodon*** (M.Kessler & Lehnert) Gasper & Salino, *comb. ined.*, *Jiménez I. 1679* (LPB), Bolivia: *rbcL* KU898644*, *rps4* KU898585*, *trnL-trnF* KU898699*; ***Parablechnum stipitellatum*** (Sodirol) Gasper & Salino, *comb. ined.*, *van der Werff 16635* (MO), Peru: *rbcL* KU898656*, *rps4* KU898597*, *trnL-*

trnF KU898710*; ***Parablechnum subcordatum*** (E.Fourn.) Gasper & Salino, *comb. ined.*, *McPherson 18139* (MO), New Caledonia: *rbcL* KU898657*, *rps4* KU898598*, *trnL-trnF* KU898711*; ***Parablechnum triangularifolium*** (T.C.Chambers & P.A.Farrant) Gasper & Salino, *comb. ined.*, *Perrie 3416* (WELT), New Zealand: *rbcL* KF975813 (Perrie *et al.*, 2014), *rps4* KF975769 (Perrie *et al.*, 2014), *trnL-trnF* DQ683415 (Shepherd *et al.*, 2007); ***Parablechnum usterianum*** (Christ) Gasper & Salino, *comb. ined.*, *Salino 15688* (BHCB), Brazil: *rbcL* KU898658*, *rps4* KU898599*, *trnL-trnF* KU898712*; ***Parablechnum wattsi*** (Tindale) Gasper & Salino, *comb. ined.*, *Perrie and Ohlsen BB127* (MELU), Australia: *rbcL* KJ170826 (Perrie *et al.*, 2014), *rps4* KJ170799 (Perrie *et al.*, 2014), *trnL-trnF* KJ170853 (Perrie *et al.*, 2014); ***Parablechnum wurunuran*** (Parris) Gasper & Salino, *comb. ined.*, *Perrie et al. BB34* (MELU), Australia: *rbcL* KJ170828 (Perrie *et al.*, 2014), *rps4* KJ170801 (Perrie *et al.*, 2014), *trnL-trnF* KJ170855 (Perrie *et al.*, 2014).

Pentarhizidium intermedium (C.Chr.) Hayata, *Zhang 3394* (PE), China: *rbcL* KC254354 (Wei *et al.*, 2013), *rps4* KC254505 (Wei *et al.*, 2013), *trnL-trnF* KC254426 (Wei *et al.*, 2013).

Sadleria cyatheoides Kaulf., *Ornudff 8506*; *unknown* (UC; UC; WELT), USA: *rbcL* AF425103 (Cranfil and Kato, 2003), *rps4* AF425156 (Cranfil and Kato, 2003), *trnL-trnF* DQ683431 (Shepherd *et al.*, 2007); ***Sadleria pallida*** Hook. & Arn., *Ranker 1287* (COLO), USA: *rbcL* U05943 (Wolf *et al.*, 1994); ***Sadleria souleyetiana*** (Gaudich.) T.Moore, *unknown* (unknown), USA: *rbcL* AB040591 (Nakahira, 2000); ***Sadleria squarrosa*** (Gaudich.) T.Moore, *unknown* (unknown), USA: *rbcL* AB040592 (Nakahira, 2000); ***Sadleria unisora*** (Baker) W.J.Rob., *unknown* (unknown), USA: *rbcL* AB040593 (Nakahira, 2000).

Salpichlaena thalassica Grayum & R.C. Moran, *van der Werff 16278* (MO), Peru: *rbcL* KU898659*, *rps4* KU898600*, *trnL-trnF* KU898713*; ***Salpichlaena volubilis***

(Kaulf.) J. Sm., *Salino 14313* (BHCB), Brazil: *rbcL* KU898660*, *rps4* KU898601*, *trnL-trnF* KU898714*.

Stenochlaena milnei Underw., *UC Botanical Garden 55.0076* (UC), Philippines: *rbcL* AF425104 (Cranfil and Kato, 2003), *rps4* AF425157 (unknown); *Stenochlaena palustris* (Burm.f.) Bedd., *Ohlsen and Bayly BB197* (MELU), Australia: *rbcL* KJ170829 (Perrie *et al.*, 2014), *rps4* KJ170802 (Perrie *et al.*, 2014), *trnL-trnF* KJ170856 (Perrie *et al.*, 2014); *Stenochlaena tenuifolia* (Desv.) T.Moore, *Schuettpelz 504* (DUKE), cultivada: *rbcL* EF463163 (Schuettpelz and Pryer, 2007).

Struthiopteris castanea (Makino & Nemoto) Nakai, *H. Ohashi 49965* (LPB), Japan: *rbcL* KU898661*, *trnL-trnF* KU898715*; *Struthiopteris spicant* (L.) F.W.Weiss, *Windham 3395*; *cultivated* (DUKE; AK), cultivada: *rbcL* JF832059 (Rothfels *et al.*, 2012), *trnL-trnF* DQ683413 (Shepherd *et al.*, 2007).

Telmatoblechnum indicum (Burm.f.) Perrie, D.J.Ohlsen & Brownsey, *Perrie and Ohlsen BB107* (MELU), Australia: *rbcL* KJ170830 (Perrie *et al.*, 2014), *rps4* KJ170803 (Perrie *et al.*, 2014), *trnL-trnF* KJ170857 (Perrie *et al.*, 2014); *Telmatoblechnum serrulatum* (Rich.) Perrie, D.J.Ohlsen & Brownsey, *Funez 487* (FURB), Brazil: *rbcL* KU898662*, *rps4* KU898602*, *trnL-trnF* KU898716*.

Woodwardia auriculata Blume, *Cranfill s.n. (RBC 650)* (UC), Malaysia: *rbcL* AY137661 (Cranfil and Kato, 2003); *Woodwardia spinulosa* M.Martens & Galeotti, *Salino 15746* (BHCB), Mexico: *rps4* KU898603*, *trnL-trnF* KU898718*; *Woodwardia fimbriata* Sm., *unknown* (unknown), Japan: *rbcL* AB040597 (Nakahira, 2000), *rps4* AF533859 (unknown); *Woodwardia harlandii* Hook., *unknown* (unknown), Japan: *rbcL* AB040598 (Nakahira, 2000), *rps4* AF533860 (unknown); *Woodwardia japonica* (L.f.) Sm., *Kato s.n*; *unknown* (UC; UC; WELT), Japan: *rbcL* AY137664 (Cranfil and Kato, 2003), *rps4* AF533861 (Cranfil and Kato, 2003), *trnL-trnF* DQ683432 (Shepherd *et al.*, 2007);

Woodwardia kempii Copel, *Cranfill s.n. (RBC 023)* (UC), Taiwan/China: *rbcL* KM606992 (Li *et al.*, 2015), *rps4* KM606992 (Li *et al.*, 2015); *Woodwardia martinezii* Maxon ex Weath., *A. Cerón 420* (MEXU), Mexico: *rbcL* KU898663*, *trnL-trnF* KU898717*;
Woodwardia prolifera Hook. & Arn., *Cranfill s.n. (RBC 010)*; *unknown* (UC; UC; WELT), cultivada: *rbcL* AY137666 (Cranfil and Kato, 2003), *rps4* AF533864 (Cranfil and Kato, 2003), *trnL-trnF* DQ683433 (Shepherd *et al.*, 2007); *Woodwardia radicans* (L.) Sm., *RBG KEW*, *unknown* (UC; UC; WELT), Spain: *rbcL* AY137667 (Cranfil and Kato, 2003), *rps4* AF533865 (Cranfil and Kato, 2003), *trnL-trnF* DQ683434 (Shepherd *et al.*, 2007).

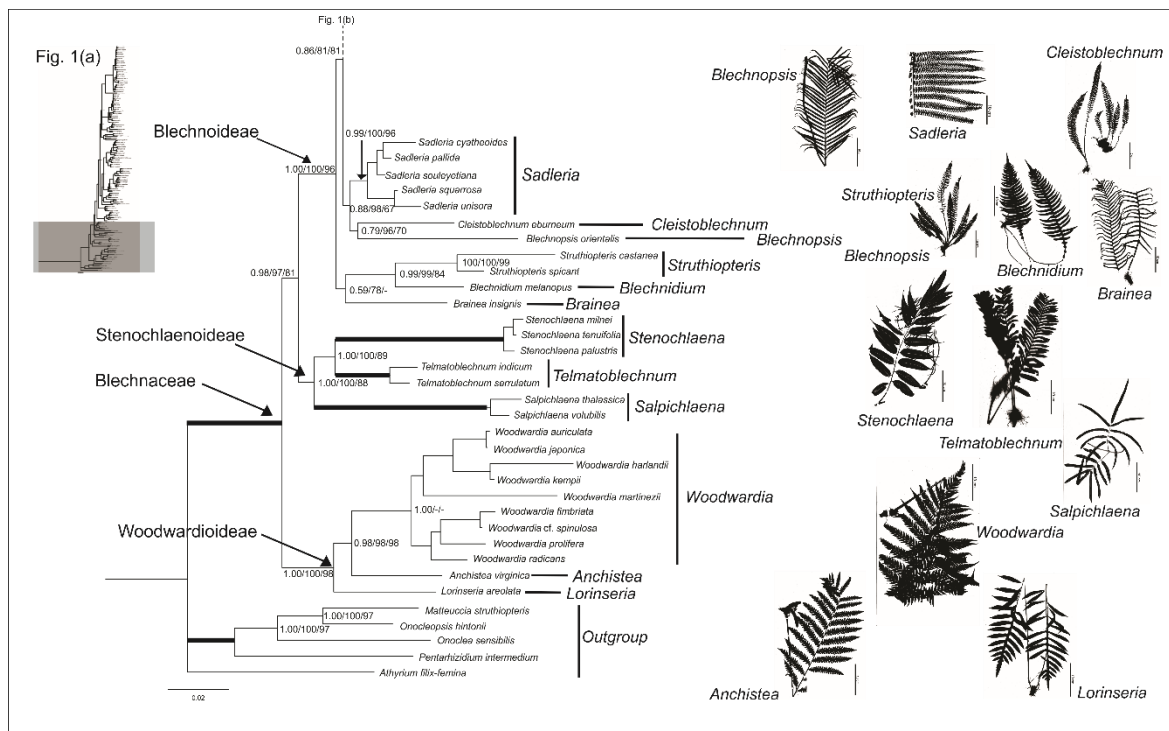


Figure 1. Majority-rule consensus phylogram from Bayesian Inference analysis from concatenated dataset, for three chloroplast regions (*rbcL*, *rps4*, *trnL-trnF*), showing phylogenetic hypothesis for relationship among Blechnaceae taxa. Bayesian Inference posterior probabilities, Maximum Likelihood bootstrap values and Maximum Parsimony bootstrap values (%) are indicated, respectively, on the branches. Thick lines indicate strong support (posterior probability = 1.00 and maximum likelihood bootstrap support and maximum parsimony = 100%)

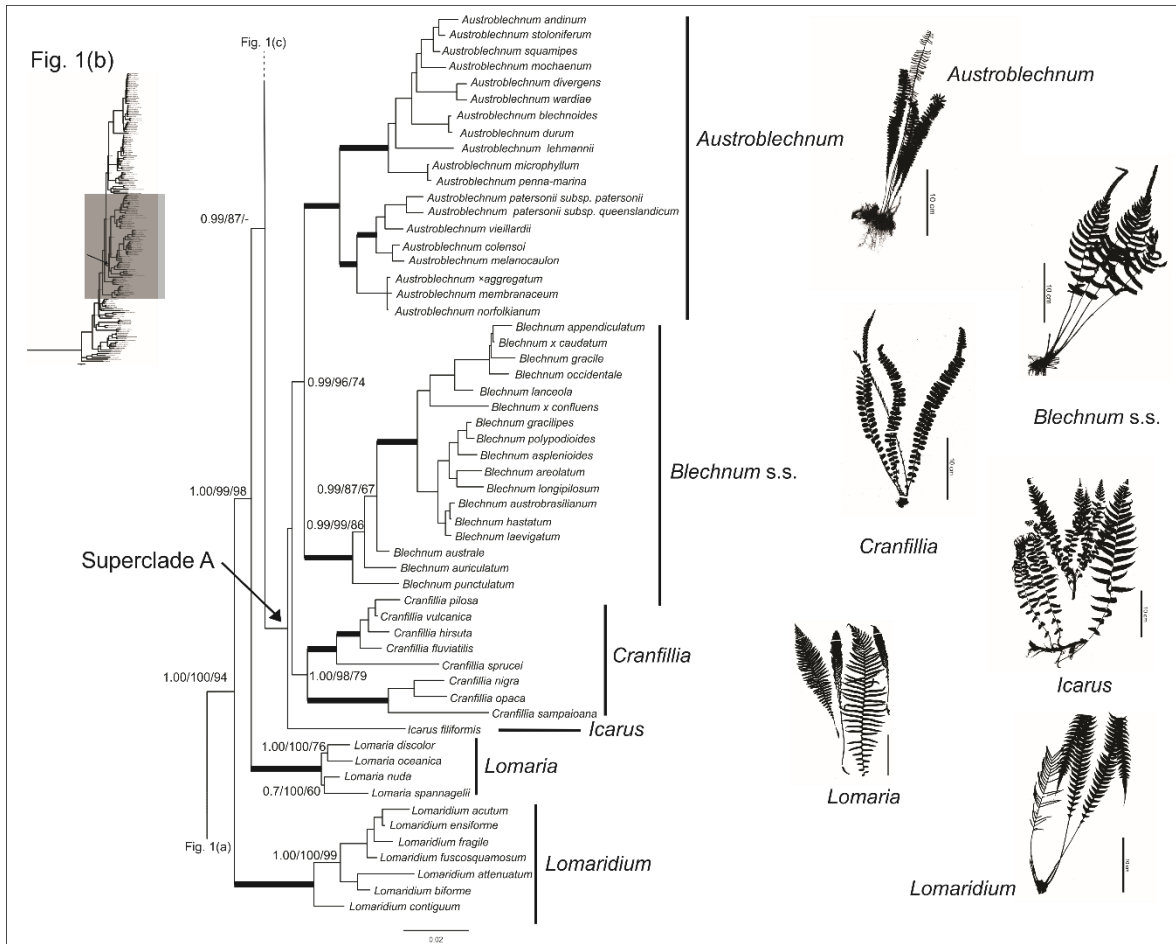


Figure 1. cont.

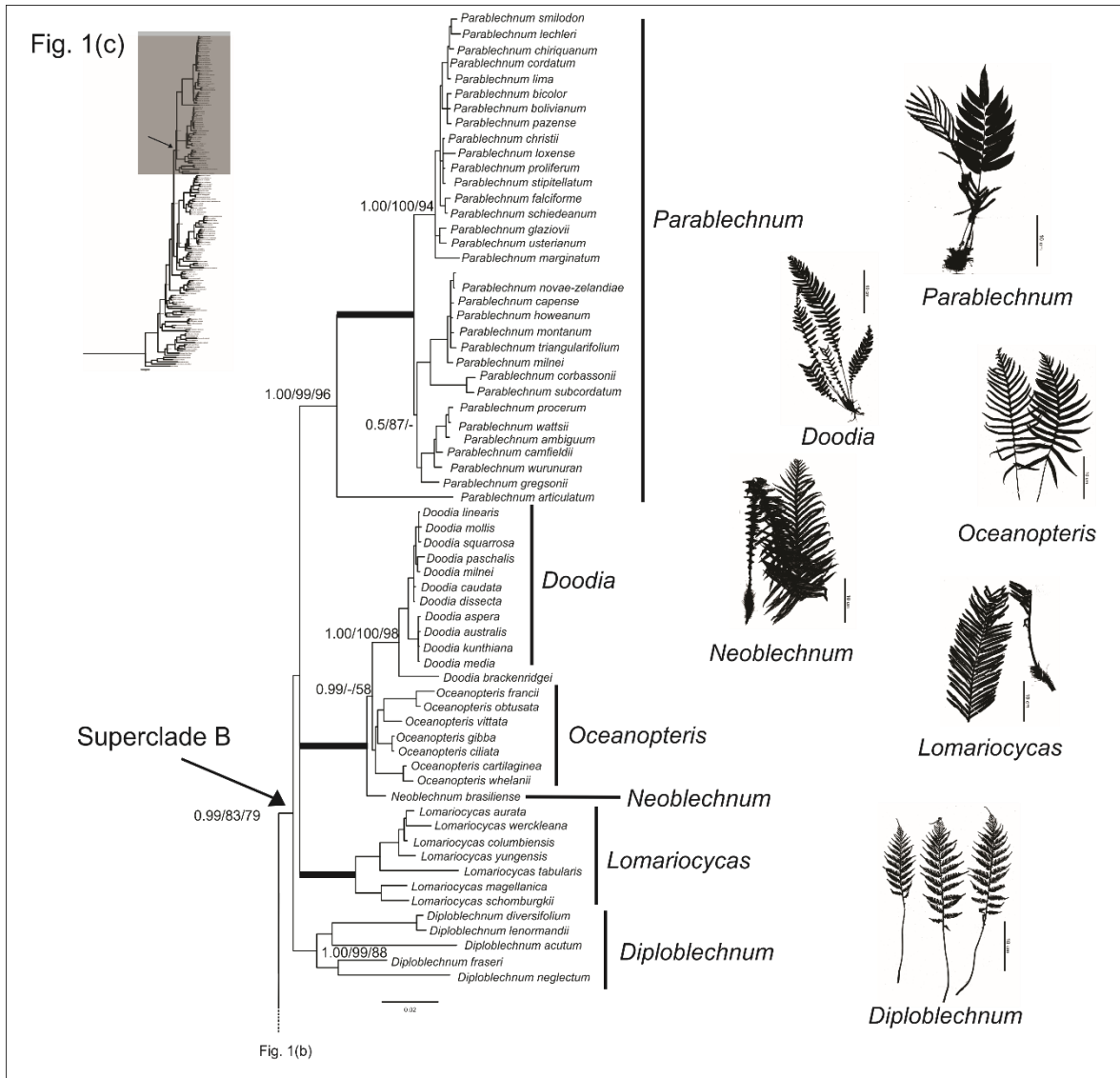


Figure 1. cont.

Table 1. Blechnaceae genera recognized in morphological classification systems and this study. Boldface indicates new genera.

Presl (1851)	Smith (1875)	Copeland (1947)	Pichi Sermolli (1977)	Holttum (1947, 1949, 1971)	Tryon & Tryon (1982)	Kramer <i>et al.</i> (1990)	This study
<i>Anchistea</i>	<i>Anchistea</i>	<i>Woodwardia</i>	<i>Anchistea</i>		<i>Woodwardia</i>	<i>Woodwardia</i>	<i>Anchistea</i>
<i>Lorinseria</i>	<i>Lorinseria</i>	<i>Lorinseria</i>	<i>Lorinseria</i>		<i>Woodwardia</i>	<i>Woodwardia</i>	<i>Lorinseria</i>
<i>Woodwardia</i>	<i>Woodwardia</i>	<i>Woodwardia</i>	<i>Woodwardia</i>	<i>Woodwardia</i>	<i>Woodwardia</i>	<i>Woodwardia</i>	<i>Woodwardia</i>
<i>Blechnum</i>	<i>Blechnum</i>	<i>Blechnum</i>	<i>Blechnum</i>	<i>Blechnum</i>	<i>Blechnum</i>	<i>Blechnum</i>	<i>Blechnum</i>
<i>Parablechnum</i>		<i>Blechnum</i>			<i>Blechnum</i>	<i>Blechnum</i>	<i>Parablechnum</i>
<i>Distaxia</i>		<i>Blechnum</i>			<i>Blechnum</i>	<i>Blechnum</i>	<i>Blechnum</i>
<i>Mesothema</i>		<i>Blechnum</i>			<i>Blechnum</i>	<i>Blechnum</i>	<i>Blechnum</i>
<i>Spicanta</i>		<i>Blechnum</i>			<i>Blechnum</i>	<i>Blechnum</i>	<i>Struthiopteris</i>
<i>Blechnopsis</i> sect.		<i>Blechnum</i>			<i>Blechnum</i>	<i>Blechnum</i>	<i>Blechnopsis</i>
<i>Eublechnopsis</i>							
<i>Sadleria</i>	<i>Sadleria</i>	<i>Sadleria</i>	<i>Sadleria</i>	<i>Sadleria</i>	<i>Sadleria</i>	<i>Sadleria</i>	<i>Sadleria</i>
<i>Orthogramma</i>		<i>Blechnum</i>			<i>Blechnum</i>	<i>Blechnum</i>	<i>Parablechnum</i>
<i>Salpichalena</i>	<i>Salpichalena</i>	<i>Salpichalena</i>	<i>Salpichalena</i>		<i>Salpichalena</i>	<i>Salpichlaena</i>	<i>Salpichalena</i>
<i>Lomaridium</i>		<i>Blechnum</i>			<i>Blechnum</i>	<i>Blechnum</i>	<i>Lomaridium</i>
<i>Blechnopsis</i> sect.					<i>Blechnum</i>	<i>Blechnum</i>	<i>Neoblechnum</i>

*Eublechnopsis**Blechnopsis* sect.*Diapnia*

				<i>Blechnum</i>		<i>Blechnum</i>	<i>Telmatoblechnum</i>
<i>Lomaria</i>	<i>Blechnum</i>		<i>Blechnum</i>	<i>Blechnum</i>		<i>Blechnum</i>	<i>Lomaria</i>
<i>Brainea</i>	<i>Brainea</i>	<i>Brainea</i>	<i>Brainea</i>	<i>Brainea</i>		<i>Brainea</i>	<i>Brainea</i>
<i>Doodia</i>	<i>Doodia</i>	<i>Doodia</i>	<i>Doodia</i>	<i>Doodia</i>		<i>Doodia</i>	<i>Doodia</i>
<i>Stenochlaena</i>	<i>Stenochlaena</i>	<i>Stenochlaena</i>	<i>Stenochlaena</i>	<i>Stenochlaena</i>		<i>Stenochlaena</i>	<i>Stenochlaena</i>
	<i>Blechnum</i>	<i>Blechnidium</i>		<i>Blechnum</i>		<i>Blechnum</i>	<i>Blechnidium</i>
		<i>Pteridoblechnum</i>		<i>Pteridoblechnum</i>		<i>Pteridoblechnum</i>	<i>Diploblechnum</i>
		<i>Chieniopteris</i>		<i>Woodwardia</i>		<i>Woodwardia</i>	<i>Woodwardia</i>
				<i>Blechnum</i>		<i>Steenisoblechnum</i>	<i>Diploblechnum</i>
				<i>Blechnum</i>		<i>Blechnum</i>	<i>Cleistoblechnum</i>
				<i>Blechnum</i>		<i>Blechnum</i>	<i>Oceanopteris</i>
				<i>Blechnum</i>		<i>Blechnum</i>	<i>Austroblechnum</i>
				<i>Blechnum</i>		<i>Blechnum</i>	<i>Icarus</i>
				<i>Blechnum</i>		<i>Blechnum</i>	<i>Cranfillia</i>
						<i>Blechnum</i>	<i>Diploblechnum</i>

Table 2

Best-fitting models and parameter values for separate *rbcL*, *rps4*, *rps4-trnS*, *trnL*, *trnL-trnF* IGS datasets in this study.

Data partition	Selected Model	Base frequencies				Substitution model (rate matrix)							
		A	C	G	T	A-C	A-G	A-T	C-G	C-T	G-T	ti/tv	gamma shape
<i>rbcL</i>	SYM+I+G	0.2518	0.2631	0.2423	0.2428	0.5643	8.3056	0.6531	0.2519	6.1826	1.0000	0.2041	0.7720
<i>rps4</i>	SYM+I+G	0.2822	0.2029	0.2339	0.2810	0.8494	6.6759	0.2612	0.3010	8.8669	1.0000	6.5339	0.7440
<i>rps4-trnS</i> IGS	GTR+G	0.2877	0.1965	0.1718	0.3441	0.8436	5.5681	0.3479	0.4328	4.9839	1.0000	3.9252	1.5090
<i>trnL intron</i>	HKY+G	0.2648	0.2072	0.2247	0.3033	1.2230	5.8872	0.8562	0.4030	5.8912	1.0000	3.3253	0.8060
<i>trnL-trnF</i> IGS	HKY+G	0.3023	0.1958	0.1678	0.3341	1.4541	4.9432	0.6332	0.5708	5.9361	1.0000	2.8218	1.2160

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A classification of Blechnaceae: New genera, resurrected names, and combinations

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Abstract: The fern family Blechnaceae, with about 250 species, has traditionally comprised one large genus, *Blechnum*, plus seven to nine smaller genera, most with fewer than 10 species. Several phylogenetic analyses strongly suggest that *Blechnum* in the traditional sense is not a monophyletic group. We propose a new classification for the family, with three subfamilies and 24 genera. All genera are described and new combinations are provided, with an estimate of species number for each genus. We also provide a key for the identification of the genera.

Key words: *Blechnum*, Eupolypods II, ferns, *Lomaria*, *Diploblechnum*, *Struthiopteris*, *Woodwardia*.

Introduction

Blechnaceae is a subcosmopolitan fern family, comprising about 250 species and between five and nine genera (Kramer *et al.* 1990, Perrie *et al.* 2014). The plants are mostly terrestrial herbs, sometimes rheophytic, aquatic, arborescent, or scandent, or even epiphytic (Rothfels *et al.* 2012). The family is characterized by creeping, ascending, or erect rhizomes, with non-clathrate scales; petioles with numerous vascular bundles forming a ring in cross section; fronds monomorphic to dimorphic; free to anastomosing veins; linear sori that are generally parallel and adjacent to midveins, with introrse indusia (rarely exindusiate); sporangia pedicellate; and spores reniform, monolete (Moran 1995a, Mickel & Smith 2004, Dittrich 2005).

Several classifications have been presented for the family, including one by Kramer *et al.* (1990), who recognized nine genera: *Blechnum* L., *Brainea* J.Sm., *Doodia* R.Br., *Pteridoblechnum* Hennipman, *Sadleria* Kaulf., *Salpichlaena* J.Sm., *Stenisioblechnum* Hennipman, *Stenochlaena* Ching, and *Woodwardia* Sm. Others treating Blechnaceae in a comprehensive way have been Copeland (1947), recognizing eight genera, and Pichi Sermolli (1977), with 12 genera. Tryon & Tryon (1982) admitted nine genera (only three in the New World), and Wang *et al.* (2013) treated eight genera in China alone. Largely on the basis of recent phylogenetic studies showing *Blechnum* to be polyphyletic (Nakahira 2000, Cranfill 2001, Shepherd *et al.* 2007, Perrie *et al.* 2014), several authors have acknowledged that the family needed a new classification (Smith *et al.* 2006, Rothfels *et al.* 2012).

Aside from *Blechnum s.l.*, by far the most species-rich genus, with 200 species, the existing recognized genera are mostly rather small. Using concepts adopted by Kramer *et al.* (1990), *Doodia* comprises ca. 15 species (Smith *et al.* 2006), most of these distributed in Oceania (Parris 1972). *Woodwardia* contains about 14 species, which are largely confined

to the northern hemisphere, in America and in Eurasia (Cranfill & Kato 2003).

Salpichlaena has three endemic species in the Neotropics (Giudice *et al.* 2008). Another small and rather isolated genus, *Stenochlaena*, comprises seven species in Africa and Asia (Holttum 1971, Chambers 2013). *Brainea* is monotypic (Kramer *et al.* 1990) and widely distributed in tropical Asia (Wang *et al.* 2013), while *Sadleria* comprises six species restricted to Hawaii (Palmer 1997). *Pteridoblechnum* and *Steenisoblechnum*, in Australia, have only one species each (Hennipman 1966, 1984, Kramer *et al.* 1990). *Stenochlaena* and *Pteridoblechnum* have been recognized only recently as Blechnaceae by Lovis (1978), Tryon & Tryon (1982), and Hennipman (1966); these genera were placed previously in Pteridaceae and Stenochlaenaceae by some authors.

Some genera are considered well established, as *Woodwardia*, which was revised by Cranfill (2001) and Cranfill & Kato (2003), who made one of early studies of Blechnaceae based on molecular data; *Woodwardia* was analyzed in more detail than other blechnoid genera, and they resolved it as sister to the other genera. Cranfill (2001) recognized *Anchistea* C.Presl and *Lorinseria* C.Presl, but Cranfill and Kato (2003) included both of these genera in *Woodwardia s.l.* Other genera having more detailed recent taxonomic treatments, mainly because they are small, are *Brainea* (Kramer *et al.* 1990), *Doodia* (Parris 1972), *Sadleria* (Palmer 1997), *Salpichlaena* (Giudice *et al.* 2008), *Stenochlaena* (Holttum 1971, Chambers 2013) and the recent segregate, *Telmatoblechnum* (Perrie *et al.*, 2014)

Blechnum, on the other hand, is treated in many floras and is currently the largest genus of the family with about 200 species (Rothfels *et al.* 2012). Tryon & Tryon (1982) estimated 50 species to the Americas, but based on the new species described for the Neotropics (e.g., by Moran 1992, 1995b, Moran & Smith 2005, Rojas-Alvarado 2006,

Kessler *et al.* 2007, Ramos Giacosa 2010, Dittrich *et al.* 2012), and considering the vast areas still unexplored or poorly explored (e.g., Amazon basin and extra-Amazonian areas in Colombia, Ecuador, Peru, Bolivia, and Brazil), we estimate that the number of species in the Americas exceeds, by far, the number presented by Tryon & Tryon (1982), as we show below.

Blechnum was established by Linnaeus (1753) in his *magnum opus*, *Species Plantarum*. Since then, the genus has traditionally been divided on the basis of form of the sterile and fertile fronds: one group with monomorphic fronds, another having dimorphic fronds. Such a division, however, is artificial (Dittrich 2005, Smith *et al.* 2006, Rothfels *et al.* 2012, Perrie *et al.* 2014, Gasper *et al.* in prep.), and the genus, as circumscribed today, is clearly polyphyletic (Cranfill & Kato 2003, Schuettpelz & Pryer 2007, Shepherd *et al.* 2007, Rothfels *et al.* 2012, Perrie *et al.* 2014, Gasper *et al.* in prep.).

Recently, proposals have been made to treat *Blechnum* in somewhat revised ways. Perrie *et al.* (2014) performed molecular phylogenetic analyses resulting in the naming of *Telmatoblechnum*, with two species, and subsuming *Pteridoblechnum* and *Stenisioblechnum* within *Blechnum* and recognized seven genera in the family. Using morphology alone, Wang *et al.* (2013) recognized eight genera for the Chinese species.

Based on molecular data (Gasper *et al.* in prep.), as well as morphological characters, spore ornamentation, and chromosome number, we here recognize 24 genera in the family (see below).

Methods

The identification key, notes, and synonyms are based on an analysis of type and non-type material from the following herbaria: B, BHCB, BM, CESJ, CRI, COL, ESA, FI, FURB, HB, HBR, HRCB, HUA, INPA, JOI, JPB, K, MBM, MEXU, MO, OUPR, P, PACA, PR, PMA, Q, QCA, QCNE, QPLS, R, RB, S, SI, SJRP, SP, SPF, UC, UEC, UPCB, WELT (on-line), as well JSTOR Plants (<http://plants.jstor.org/>). (herbaria abbreviations according to Thiers, 2015).

The characterization of the genera, as well the names recognized in this study, were made using both floras and taxonomic revisions, checklists or new described species. The names collected in those works were checked in Tropicos.org and IPNI.org. **Neotropical** floras and revisions consulted were: Antilles (Killip 1917, Kramer 1962, Proctor 1977, 1985, 1989), Argentina (de la Sota 1973, 1975), Brazil (Brade 1966, Sehnem 1968, Dittrich 2005, Dittrich *et al.* 2007, 2012, 2015), Central America (Stolze 1981, Moran 1995a), Chile (Marticorena & Rodríguez 1995, Aguiar *et al.* 2007, Ríos *et al.* 2009, Ríos 2015), Colombia (Alston 1957, Lellinger & de la Sota 1972), Ecuador (Sodirol 1883, 1893, Moran 1995b), French Guiana (Mori *et al.* 1997), Hawaii (Palmer 1997, 2003), Mexico (Smith 1981, Mickel & Beitel 1988, Mickel & Smith 2004), Peru (Tryon & Stolze 1993), Uruguay (Legrand & Lombardo 1958), Venezuela (Vareschi 1969, Smith 1995, Moran & Smith 2005, Akirov 2013). In addition, there are lists of species for Central and South America (Rolleri & Prada 2006a), Suriname (Kramer 1978), Brazil (Dittrich & Salino 2014), South Cone – Chile, Argentina, Paraguay, Uruguay, and Southern Brazil (Zuloaga *et al.* 2008). South American species with monomorphic leaves were reviewed by Murillo (1968), and the species with dimorphic leaves from Central and North America, as well as the Antilles, were studied by Broadhurst (1912a, b); the *Blechnum lherminieri* complex was revised by Rojas-Alvarado (2008); and a natural classification was proposed by Tryon

& Tryon (1982). **Nearctic:** North America north of Mexico (Cranfill 1993); **Africa:** Africa (Schelpe 1952), Southern African (Burrows 1990, Roux 2001, Crouch *et al.* 2011), Swaziland (Roux 2003). **Asia:** China (Wang *et al.* 2013), Taiwan (Chiou *et al.* 1975), Thailand (Boonkerd & Pollawatn 2004), Himalayas (Li *et al.* 2014), and Malesian regions (Chambers & Farrant 2001, Nootboom 2012). **Oceania:** Australia (Tindale 1960, Chambers & Farrant 1993, 1995, 1999, Brownsey & Smith-Dodsworth 2000, Chambers 2007, Parris 2010), Fiji (Brownlie 1977), Mascarene Islands (Austrey *et al.* 2008), Tasmania (Hooker & Ross 1860), New Caledonia (Brownlie 1969), New Zealand (Chambers & Farrant 1996a, 1998, Breitwieser *et al.* 2010).

There is also a global classification of Blechnaceae, proposal by Kramer *et al.* (1990), and a revision of circum-Antarctic species of *Blechnum penna-marina* complex (Chambers & Farrant 1996b).

Results

Characters

We discuss here some of the more important characters of the blechnoid genera, especially those used in the key and descriptions presented below. Many characters show great variation among and sometimes within the genera. Genera recognized in this treatment are similar to many other fern genera in that a single character is often insufficient for characterization; rather a suite of characters may be necessary to identify a particular plant to genus. In general, both vegetative and reproductive characters are highly plesiomorphic in the family, and homoplasy is rampant. This is similar to variation in many large fern families, e.g., the grammitids in the Polypodiaceae (Ranker *et al.* 2004).

Habit. Blechnaceae comprises mostly terrestrial species, with the exception of *Oceanopteris francii*, the only truly aquatic member (Brownlie 1969, Veillon 1981). Other

species are terrestrial or sometimes epipetric, or a few hemiepiphytic (starting on the ground, then climbing trees). A few species, e.g., *Lomariocycas werckleana* (Moran 1995a), *Stenochlaena areolaris* (Chambers 2013) or some species of *Blechnum* (Dittrich *et al.* 2015), have been reported as epiphytes or accidental epiphytes, and a few other species, especially the two species of *Telmatoblechnum*, are well known swamp-growing plants (Perrie *et al.* 2014).

Rhizomes. Rhizome habit shows great variation in the family, from long- to short-creeping, to ascending or suberect, or fully erect. These extremes can even be found in a single genus, e.g., *Diploblechnum*, in which *D. neglectum* has long-creeping, cord-like rhizomes and *D. fraseri* has narrow, erect rhizomes to 1 m tall; rhizome morphology in the latter species was discussed by Cranfill (2001). In the case of *Lomariocycas*, especially in paramo habitats, numerous species form erect, trunk-like caudices to 1 meter tall, resembling the habit of some cycads (hence the genus name). *Neoblechnum brasiliense* and *Oceanopteris gibba* in open habitats, specially under cultivation, may also have trunks to 1 m tall (Hoshizaki & Moran 2001). Several other species-rich genera also have predominantly ascending to erect rhizomes, with shorter, narrower trunks, e.g., *Parablechnum*, *Blechnum*, and *Austroblechnum*. However, even in these genera, certain species have long- to short-creeping rhizomes. In some of the basal lineages, particularly the woodwardioid lineage (*Anchistea*, *Lorinseria*, and some *Woodwardia* spp.), as well as the stenochlaenoid lineage (*Salpichlaena*, *Telmatoblechnum*), rhizomes are predominantly long-creeping, with sparse scales, or the rhizomes are climbing (*Stenochlaena*). Several other basal blechnoid lineage also have long-creeping rhizomes, e.g., *Blechnidium*, *Blechnopsis*, and some spp. of *Struthiopteris*. Three genera, *Lomaridium*, *Icarus*, and *Stenochlaena*, not closely related, are unusual in being hemiepiphytic, with plants beginning life on the ground and eventually climbing suitably erect, small or large trees,

especially genera of tree ferns (Cyatheaceae, Dicksoniaceae; see Mehltreter 2008). In most cases, the rhizomes maintain contact with the soil and produce fertile fronds only after climbing, apparently when light and plant mass requirements are fulfilled. In *Salpichlaena*, it is the leaf rachis that twines into the trees, not the rhizomes, and mature fronds can reach easily 15 m into the canopy (Moran 1995a).

Genera having predominantly or entirely long-creeping rhizomes generally are plants of temperate mesic forests or montane rain forests. In contrast, those genera having erect or suberect rhizomes, or stout, erect caudices, are generally plants of more open sites: *Neoblechnum* and *Brainea*, both monotypic, as well as *Sadleria*, *Oceanopteris*, and *Lomariocycas* all exemplify this habitat preference. Correspondingly, these five genera also generally have more coriaceous, leathery leaf blades than do species and genera that are predominantly forest-dwelling.

Stolons. Stolons are common only in *Blechnum* (Dittrich *et al.* 2015), where this condition seems to be a synapomorphy; but stolon-like outgrowths occur in a few species of *Austroblechnum*, e.g., *A. penna-marina*, especially in groups growing at middle to higher elevations or on rocks, and *Lomaria discolor*. Stolon-production is a useful characteristic for identifying *Blechnum*, and some species of *Austroblechnum*. *Cranfillia vulcanica* is exceptional, having been reported with two types of rhizomes: creeping to erect, sometimes forming a short caudex or, under some conditions, giving rise to slender, creeping, stoloniferous rhizomes borne from the growing rhizome apex (Chambers & Farrant 2001).

Rhizome scales. Rhizomes and stipe bases of members of Blechnaceae are always covered by triangular to acicular scales, and these are mostly entire; however, in *Lomaridium*, the scales can be denticulate, a good synapomorphy for that genus. Those genera having long acicular (needlelike) scales, like *Lomariocycas* and *Sadleria*, are quite

distinctive in also having these scales prominently thickened at their bases; when detached, such scales leave raised protuberances (stumps) on the stipe bases. Scales in some genera are prominently bicolorous, with a blackish mid-stripe, as in *Neoblechnum*, *Oceanopteris*, and *Lomariocycas*. Scales in other species (genera) may be peltate and blackish at the point of attachment, as in some members of the New Zealand *Parablechnum procerum* complex (Chambers & Farrant 1998). In most other genera the scales are tan or brown, broadly lanceolate, and concentrated on rhizome apices and stipe bases.

Leaf dimorphism. Traditionally, species of Blechnaceae have been divided into two main groups, having either monomorphic or dimorphic leaves. Dimorphic leaves are common in most genera, and the monomorphic condition is mostly restricted to species of *Blechnum*, the woodwardioid genera (*Woodwardia* and *Anchistea*), *Telmatoblechnum*, *Blechnidium*, *Blechnopsis*, *Sadleria*, *Neoblechnum*, *Oceanopteris*, and *Doodia*. However, in several ordinarily dimorphic genera, there are exceptions, plants or species having monomorphic leaves, like *Lomariocycas columbiense* and *Parablechnum loxense* (Tryon & Stolze 1993), *P. monomorphum*, and *P. obtusum*. In both genera, some plants or species can be subdimorphic, with laminae types somewhat (but not decidedly) dimorphic, i.e., the sporangia do not cover the entire surface of the lamina (dimorphic condition), but fertile blades are slightly different from the sterile ones. Trimorphy exists in *Icarus filiformis*, a monotypic genus. When in contact with soil, this species has small sterile leaves, and when climbing, much larger sterile leaves; the third leaf type, of fertile fronds, has greatly contracted pinnae (Allan 1961).

Blade dissection. Most members of Blechnaceae have pinnate or pinnatifid blades; the distal portion of the blades is usually pinnate (conform) or pinnatifid. There are a few species with simple, entire blades (e.g., *Blechnum lanceolatum* and *Austroblechnum difforme*), or bipinnatifid blades, e.g., certain species of *Sadleria*, *Diploblechnum*, or

Woodwardia unigemmata. *Salpichlaena* and *Stenochlaena* have pinnate-pinnatifid or bipinnate fertile blades, but the sterile blades are pinnate in *Stenochlaena* and bipinnate in *Salpichlaena*. According to Cranfill (2001), mostly species have persistent fertile fronds, but in *Cranfillia* and *Diploblechnum*, the fertile fronds senesce rapidly after spore release. Rapid senescence of fertile fronds of dimorphic species probably occurs in some species of *Austroblechnum*, e.g., *A. lehmannii*. Blades in various genera may be truncate (lacking reduced pinnae) as in most species of *Parablechnum*, *Sadleria*, and *Woodwardia*, or with proximal pinnae gradually to abruptly reduced to auricles, as in *Austroblechnum*, *Blechnidium*, *Blechnopsis*, *Doodia*, *Struthiopteris*, and other genera.

Articulate pinnae. There are four species in three genera reported with articulate pinna in Blechnaceae: *Anchistea* (monotypic), *Telmatoblechnum* (two species), and *Parablechnum articulatum* (Perrie *et al.* 2014). This last species is sister to two subclades in *Parablechnum* (Gasper *et al.* in prep), one represented by Neotropical+African species and the other one by Oceanian/Malesian species. Pinna articulation is not reported for other members of the family, and is likely independently derived in genera where it occurs, as an adaptation to seasonal climate fluctuation. When examining dried specimens, there is a discrete, slightly raised disarticulation ring at the bases of articulate pinnae (e.g., in *Telmatoblechnum serrulatum*).

Blade indument. Many kinds of hairs and scales can be found in Blechnaceae species, but mostly genera are essentially glabrous to glabrescent, e.g., the basal woodwardioid and stenochlaenoid lineages. Densely scaly species can be found in *Parablechnum* and *Lomariocycas*, with large scales on the laminae, sometimes covering a most of surface. In other genera, amorphous hyaline or tan scales are often present, but these may be deciduous, or lost in mature fronds. *Lomaridium* is glabrous, lacking hairs or scales, like mostly species of *Blechnum* s.s., but some species of the latter genus have

conspicuous hyaline hairs. When hairs are present in *Blechnum*, and other genera, they are mostly on the stipes and rachises. Species of *Cranfillia* have abundant hairs on the blades; the hairs may be blackish or hyaline, except in *C. sampaioana*, which has minute hairs in some plants.

Blade color and texture. Young leaves of Blechnaceae are often reddish, the color produced by an anthocyanin (Crowden & Jarman 1974); this is a synapomorphy for the family. When the leaves become adult, the laminae are generally green to yellow green, shiny, and opaque. Almost all species of Blechnaceae are concolorous when dried, but we note that species of *Lomaria* have discoloured blades, green above and brownish below. Some species of *Austroblechnum* also have discoloured blades, but less markedly than *Lomaria*. In *Lomaridium*, the blades are often dark green adaxially, silvery green abaxially

Coriaceous blades are found in *Lomariocycas*, but this condition may vary greatly in Blechnaceae, even among species in the same genus, e.g., *Austroblechnum*, where the species like *A. penna-marina*, that grow in full sun, have coriaceous to subcoriaceous blades, and *A. divergens*, a forest species, has chartaceous or herbaceous blades.

Pinna margins. Pinnae are generally slightly revolute at the margins, at least when dried, in most Blechnaceae, and strongly revolute (involute) in *Lomariocycas* and *Cleistoblechnum*. In *Struthiopteris* the pinna margins are entire and flat (not revolute), similar to species of *Neoblechnum*, *Oceanopteris*, *Icarus*, and *Doodia*, but in these last four genera the pinna margins are usually crenate to serrate. In *Blechnum*, the pinna margins are finely denticulate. In Stenochlaenoideae and Woodwardioideae, the laminae are flat, but the margins crenulate to serrulate.

Vivipary. Laminal buds are rare in Blechnaceae, occurring in few species in distantly related genera, e.g., *Woodwardia*, *Salpichlaena*, *Parablechnum*, and *Cranfillia*. *Woodwardia prolifera* is unique in bearing many small plants over the adaxial surface of

the blades.

Aerophores. Small tubercular or conical aeration structures, called aerophores (or pneumatophores; Bower 1923, 1926), are borne at the bases of pinnae, abaxial side; these seem to occur primarily on some (but not all) neotropical species of *Parablechnum* and one species of *Parablechnum acanthopodum*, from Goodenough Island, northeast coast of Papua. In addition, all, or nearly all, members of Blechnaceae have two whitish, lateral ventilation bands (Durchluftungstriefen) along the lengths of the stipes and continuing along the rachises; these bear copious stomata that presumably aid in aeration of young developing tissues (Davies 1991). In several species of Blechnaceae, especially those with prominent aerophores, copious amounts of mucilage cover the young croziers and early-developing fronds (Hennipman 1968). The taxonomic significance of these characters – aerophores and mucilage production – is poorly known and needs more study, as well the development of these structures in Blechnaceae.

Sori and indusia. Sori in the family are usually continuous or nearly so and protected by elongate indusia that open toward the costae. Only two genera, *Brainea* and *Stenochlaena* are exindusiate. When mature, the indusia often became lacerate and expose the sporangia, with two exceptions: *Salpichlaena* and *Cleistoblechnum* have reflexed indusia that remain entire or erose at maturity, covering the sporangia.

Anchistea, *Lorinseria*, *Woodwardia*, and *Doodia* (Kramer *et al.* 1990) have so-called chain-like sori, i.e., sori follow the areolar veins, and then are interrupted. At maturity, chain-like sori may appear to form a continuous row. Acrostichoid sporangia (covering the abaxial surfaces of pinnae) rarely occur in Blechnaceae, and are found in *Stenochlaena*. The acrostichoid condition is common in other genera outside Blechnaceae, e.g., in *Elaphoglossum* Schott ex J.Sm. (Dryopteridaceae) and *Acrostichum* L. (Pteridaceae), where the sori are borne not only on veins, but on laminar tissue, between

veins. This condition caused Holttum (1949, 1971) to relate *Stenochlaena* to other acrostichoid genera. Chambers (2013), in the review of the genus, stated that the pinna margins reflex at maturity and the sori appear acrostichoid, a condition common in most dimorphic species of Blechnaceae and easily seen in *Austroblechnum*, *Cranfillia*, *Parablechnum*, *Struthiopteris*, and other genera, but in these genera, the sporangia, as can be seen in young leaves and developing sori, appear to be borne only in commissural vein, not on laminar tissue. In most Blechnaceae with dimorphic fronds, the fertile pinna margins reflex to expose the sporangia when the sporangia mature. The development of sporangia in *Stenochlaena*, whether truly from laminar tissue, needs further investigation developmentally.

Chromosome numbers. The chromosome number in Blechnaceae, ranges from $x = 28-40$, with most genera having base numbers between 31-35. Base chromosome number appears to be a good synapomorphy for some genera, like *Salpichalena* ($x = 40$), *Diploblechnum* ($x = 27-28$), *Lomaridium* ($x = 28$), or the woodwardioid genera, like *Anchistea* and *Lorinseria*, with $x = 35$, and *Woodwardia* with $x =$ mostly 34. Other genera and even species have been reported to show variation in chromosome number, e.g., *Parablechnum* ($x = 28, 31, 33$), or *Brainea insignis* ($x = 33, 35$); however additional counts are needed to assess whether such variation is real or the result of miscounts. Chromosome base number helps to separate some otherwise similar genera like *Cleistoblechnum*, $x = 33$, from *Struthiopteris*, with $x = 31$ or 32. Diploids, triploids, tetraploids, and even higher ploidy levels (decaploids) are known in the family (see Nakato 1987, Tindale & Roy 2002). Hybridization also appears to be common in some genera, especially *Blechnum s.s.*; this often compounds the problem of delimiting species.

Taxonomic treatment

Blechnaceae Newman, Hist. Brit. Ferns (ed. 2) 8. 1844.

Plants perennial, terrestrials, epipetric, scandent or occasionally epiphytic, very rarely aquatic; **rhizomes** erect, decumbent, creeping, subarborescent to arborescent or scandent, slender to robust, sometimes stoloniferous, covered with non-clathrate scales, sometimes bearing mucilage; **fronds** monomorphic or dimorphic, rarely trimorphic, reddish when young; **stipes** not articulate, with two or more vascular bundles arranged in an arc, generally scaly proximally; **blades** entire to bipinnate; **rachises** grooved adaxially; **pinnae** articulate or not to the rachises, often reduced proximally, aerophores sometimes present at pinna bases, buds also sometimes present in pinna axils, rarely on adaxial laminar surfaces; **veins** free or anastomosing, lacking included veinlets, reaching the margins or ending a little before, tips sometimes enlarged, clavate (appearing as hydathodes) or rarely joined by a submarginal commissure (*Salpichlaena*); **sori** borne on a commissural vein parallel to the midvein or costa, or borne on the arches of the areolae; **sori** elongate, continuous or discontinuous; **indusia** usually present, introrse, absent in a few genera; **spores** monoletate, reniform, variously ornamented; $x = 27, 28, 29, 31, 32, 33, 34, 35, 36, 37, 40$.

Distribution: sub-cosmopolitan, with two main centers of distribution, Neotropics and Oceania/Australia, with about 266 spp.

Key to the Blechnaceae taxa

- 1a. Plants truly aquatic (submerged in water)..... *Oceanopteris francii*
- 1b. Plants terrestrial, epipetric, scandent or occasionally epiphytic, sometimes growing in swamps..... 2
- 2a. Sori exindusiate or with pseudoindusia (recurved pinna margins)..... 3
- 2b. Sori indusiate 4
- 3a. Rhizomes erect, stout, trunk-like or forming stout caudices to about 1 m tall; fronds subdimorphic..... *Brainea insignis*
- 3b. Rhizomes long-creeping, climbing; fronds dimorphic..... *Stenochlaena*
- 4a. Sterile blades with at least partially anastomosing veins..... 5
- 4b. Sterile blades with free veins..... 10
- 5a. Pinnae articulate to rachises..... *Anchistea virginica*
- 5b. Pinnae not articulate to rachises..... 6
- 6a. Blades pinnatisect, abruptly or subabruptly reduced proximally..... *Blechnidium melanopus*
- 6b. Blades simple, pinnate (at least proximally), or bipinnate.....7
- 7a. Pinna margins finely denticulate..... *Blechnum*
- 7b. Pinna margins entire, serrate, serrulate, crenate, or spinulose.....8
- 8a. Areoles arranged in a single order (row) on each side of costae, all areoles of similar size and shape..... *Doodia*
- 8b. Areoles clearly arranged in first and second order rows on each side of costae, the first order fertile, and the second order sterile ones of different shape and size.....9
- 9a. Fronds strongly dimorphic, the fertile with greatly contracted pinnae..... *Lorinseria areolata*

- 9b. Fronds monomorphic..... *Woodwardia*
- 10a. Blades climbing via twining rachises..... *Salpichlaena*
- 10b. Blades not climbing via twining rachises, if climbing via rhizomes..... 11
- 11a. Rhizomes stoloniferous 12
- 11b. Rhizomes not-stoloniferous..... 15
- 12a. Fronds monomorphic to subdimorphic..... *Blechnum*
- 12b. Fronds dimorphic..... 13
- 13a. Rhizome apices and stipe bases bearing linear-lanceolate scales; blades discolorous; rachises deeply grooved..... *Lomaria*
- 13b. Rhizomes bearing by lanceolate or ovate scales; blades concolorous; rachises shallowly grooved..... 14
- 14a. Pinnae each with an obtuse apex; rachises mostly glabrous or with diminute hairs; fertile fronds taller than sterile ones..... *Austroblechnum*
- 14b. Pinnae each with an acute apex; rachises pilose, with persistent, fine, uniseriate hairs; fertile and sterile fronds similar in size..... *Cranfillia vulcanica*
- 15a. Rhizomes long-creeping, climbing..... 16
- 15b. Rhizomes erect, short- or long-creeping, sometimes forming erect caudices, but not climbing..... 17
- 16a. Rhizomes clothed by long-lanceolate, denticulate or entire scales; blades deeply pinnatisect or pinnate in the proximal half, with vestigial or auricles pinnae proximally; sterile pinna margins entire..... *Lomaridium*
- 16b. Rhizomes clothed linear-lanceolate, squarrose scales; blades pinnate, with sterile terrestrial blades smaller than epiphytic ones (di- trimorphic), 2--6 pairs somewhat reduced proximally; sterile pinna margins serrulate *Icarus filiformis*
- 17a. Pinnae articulate to rachises..... 18

- 17b. Pinnae not articulate to rachises..... 19
- 18a. Pinna margins serrate; rhizomes long-creeping; fronds monomorphic to subdimorphic..... *Telmatoblechnum*
- 18b. Pinna margins entire to crenate; rhizomes erect; fronds dimorphic..... *Parablechnum*
- 19a. Blades pinnate-pinnatifid or bipinnatifid..... 20
- 19b. Blades simple, pinnatifid, or 1-pinnate..... 21
- 20a. Rhizomes erect, subarborescent, stout; fronds monomorphic..... *Sadleria*
- 20b. Rhizomes long-creeping to short-creeping, if caudices erect then slender; dimorphic or slightly dimorphic *Diploblechnum*
- 21a. Pinna margins revolute, sometimes strongly; veins immersed in leaf tissue, almost invisible..... 22
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- 22a. Rhizomes erect, stout, trunk-like; densely clothed with bicolorous, acicular, curved, basally thickened scales..... *Lomariocycas*
- 22b. Rhizomes short, ascending or suberect; bearing at apices a tuft of orange-brown, glabrous, lanceolate scales..... *Cleistoblechnum eburneum*
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- 25b. Fronds dimorphic or subdimorphic..... 26
- 26a. Rhizome scales linear-lanceolate or acicular, or scales sometimes pectinate and broadened only at the very base, otherwise acicular for nearly their entire length 27
- 26b. Rhizome scales lanceolate, ovate, sometimes acuminate 29
- 27a. Blades discolorous; rachises deeply grooved..... *Lomaria*
- 27b. Blades concolorous; rachises shallowly grooved..... 28
- 28a. Rhizomes short-creeping to erect, sometimes trunk-like, bearing black, entire scales; blades slightly reduced proximally; pinna margins entire to serrate or dentate..... *Oceanopteris*
- 28b. Rhizomes short-creeping or elongate, bearing brown to dark brown, entire or sparingly toothed scales; blades very gradually reduced proximally with proximal pinnae auriculate; pinnae margins entire..... *Struthiopteris*
- 29a. Stipes, rachises, costae, and veins pilose..... *Cranfillia*
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- 30a. Rhizomes erect, forming narrow trunks..... 31
- 30b. Rhizomes erect, but not forming narrow trunks..... 32
- 31a. Veins each ending in a clavate hydathode..... *Austroblechnum*
- 31b. Veins not ending in hydathodes, all running to the pinna margins..... *Lomaridium*
- 32a. Pinnae petiolulate; blade apices radicant..... *Cranfillia*
- 32b. Pinnae sessile or adnate; blade apices not radicant..... 33
- 33a. Blades truncate proximally, without auriculate pinnae below the longest pinnae..... *Cranfillia*
- 33b. Blades gradually or abruptly reduced to auricles proximally, or blades simple..... 34
- 34a. Blades simple, pinnatifid, or pinnate, if pinnate, then pinnae oblong to suborbicular and

margins crenate to serrate.....*Austroblechnum*
 34b. Blades pinnate; pinnae oblong-linear to linear-falcate; margins entire..... *Struthiopteris*

Blechnaceae subfamily Woodwardioideae Gasper, V.A.O.Dittrich & Salino, subfam.

nov. -- Type: *Woodwardia* Sm., Mém. Acad. Roy. Sci. Turin 5: 411. 1793.

Diagnosis: Plants with monomorphic or dimorphic fronds; blades pinnatifid, pinnate-pinnatifid or bipinnatifid, with margins serrulate to spinulose; veins anastomosing, forming a regular series of areoles along costae and costules, clearly visible in the first and second orders.

Plants terrestrial, rarely epipetric; **rhizomes** short- to long-creeping, erect or decumbent, slender to stout, densely clothed with brownish scales; **fronds** monomorphic or dimorphic; **stipes** scaly, at least proximally; **blades** pinnatifid, pinnate-pinnatifid, or bipinnatifid, rarely simple, truncate proximally, with margins serrulate; **buds** on blades present or not, if present then usually in axils of distal pinnae; **aerophores** absent; **rachises** and costae scaly to glabrescent; **veins** anastomosing and without included veinlets in both sterile or fertile fronds, forming a regular series of areoles along the costae and costules; **sori** arranged on each side of the costae and costules, in chain-like rows or sometimes confluent and long-linear, borne on the outer arc of costal areoles, usually immersed and covered by the paracostal indusia; $x = 31, 34, 35$.

Species number, comments, and distribution: Three genera and 15 species, with a largely north-temperate, amphioceanic distribution. Some authors segregate *Chieniopteris* Ching, from eastern Asia (Wang *et al.* 2013), but we have no molecular support to justify this. The genera were reviewed by Cranfill (2001) and Cranfill and Kato (2003).

***Anchistea* C.Presl**, Abh. Königl. Böhm. Ges. Wiss., ser. 5, 6: 431. 1851. -- **Type:**

Anchistea virginica (L.) C.Presl, Abh. Königl. Böhm. Ges. Wiss., ser. 5 6: 431. 1851.

Plants terrestrial; **rhizomes** long-creeping, non-stoloniferous, slender, clothed with dark brown, shiny, ovate, entire scales; **fronds** monomorphic; **stipes** 3--4 mm diam., about as long as blades, castaneous to dark purple-black proximally, tan to stramineous distally, with few scales proximally and glabrous abaxially; **blades** concolorous, lanceolate, 1-pinnate-pinnatifid, not reduced proximally, apices pinnatifid; **rachises** sparsely scaly to glabrescent; **buds** absent; **aerophores** absent; **pinnae** sessile to subpetiolulate, articulate to rachises, narrowly lanceolate, with margins denticulate or serrulate; **veins** anastomosing, without included veinlets in both sterile or fertile fronds, forming single rows of areoles along costae and costules, ultimate (marginal) veins free; **sori** oblong to linear, often borne along both sides of costal and costular areoles, chain-like but often appearing confluent in mature sori, indusia membranaceous, often hidden by sporangia; $x = 35$. Figure 1A; 5A.

Species number, comments, and distribution: One species in North America, U.S.A. and northeastern Canada. The genus is easily recognized by the long-creeping rhizomes, 1-pinnate-pinnatifid blades, pinnae articulate to the rachises, and areolate venation.

1. *Anchistea virginica* (L.) C.Presl, Abh. Königl. Böhm. Ges. Wiss., ser. 5, 6: 431. 1851. -- *Blechnum virginicum* L., Mant. Pl. 2: 307. 1771. -- *Woodwardia virginica* (L.) Sm., Mém. Acad. Roy. Sci. Turin 5: 412. 1793.

Lorinseria C.Presl, Abh. Königl. Böhm. Ges. Wiss., ser. 5, 6: 432. 1851, non *Lorinsera* Opiz, 1839, a genus that seems not to be generally recognized, in Apiaceae; if the two are considered homonymous, then *Lorinseria* needs conservation. -- **Lectotype** (chosen by J. Smith, Hist. Filic. 310. 1875): *Lorinseria areolata* (L.) C.Presl, Abh. Königl. Böhm. Ges. Wiss., ser. 5, 6: 432. 1851.

Plants terrestrial; **rhizomes** long-creeping, non-stoloniferous, slender (ca. 5 mm

diam.), densely clothed with brownish, ovate to broadly lanceolate, entire scales; **fronds** dimorphic; **stipes** slender, long, the fertile reddish brown, scaly at least proximally, distally sparsely scaly; **blades** concolorous, ovate to deltate, the sterile deeply pinnatifid, the fertile 1-pinnate, not reduced proximally, apices pinnatifid; **rachises** with scattered, ovate, light brown scales; **buds** absent; **aerophores** absent; **pinnae** not articulate to rachises, the sterile adnate, narrowly elliptic, margins serrulate, the fertile contracted, linear, attenuate at bases; **veins** anastomosing without included veinlets in areoles in both sterile or fertile fronds, forming a regular series of two or more rows of areoles between costae and pinna margins, veins free toward margins; **sori** linear-oblong, deeply sunken into blades, confined to costal areoles on each side of the costae, indusia membranaceous, the outer edge tucked around sporangia; $x = 35$. Figure 1B; 5B.

Species number, comments, and distribution: one species in eastern North America (U.S.A. and Nova Scotia, Canada). It is easily recognized by the long-creeping rhizomes and the deeply pinnatifid sterile blades. The fertile blades are 1-pinnate, and contracted.

1. ***Lorinseria areolata* (L.) C.Presl**, Abh. Königl. Böhm. Ges. Wiss., ser. 5 6: 432. 1851. -- *Acrostichum areolatum* L., Sp. Pl. 2: 1069. 1753. -- *Woodwardia areolata* (L.) T. Moore, Index Fil. xlv. 1857.

***Woodwardia* Sm.**, Mém. Acad. Roy. Sci. Turin 5: 411. 1793. **Lectotype** (chosen by J. Smith, Hist. Fil. 310. 1875): *Woodwardia radicans* (L.) Sm.

Chieniopteris Ching, Acta Phytotax. Sinica 9: 1964. -- Type: *Chieniopteris harlandii* (Hook.) Ching, based on *Woodwardia harlandii* Hook.

Plants terrestrial, rarely epipetric; **rhizomes** short- to long-creeping, erect or decumbent, slender to stout, non-stoloniferous, densely clothed by brownish, lanceolate to linear lanceolate, entire or with few teeth scales; **fronds** monomorphic; **stipes** stout, long,

dark brown proximally, stramineous distally, scaly at least proximally, then with sparse scales and/or hairs; **blades** concolorous, lanceolate, oblong-lanceolate, ovate-lanceolate, rarely simple, pinnatifid, pinnate-pinnatifid, or to bipinnatifid, not reduced proximally, apices pinnatifid; **rachises** scaly to glabrescent; **buds** present or not; **aerophores** absent; **pinnae** not articulate to rachises, oblong-lanceolate, margins entire to spinulose; **veins** anastomosing without veinlets in both sterile or fertile fronds, forming a regular series of areoles along the costae and costules, ultimate veins free; **sori** long-linear, sunken, usually confined to costular areoles, arranged on each side of the costae and costules, indusia membranaceous, discrete; $x = (31), 34$. Figure 1C; 5C.

Species number, comments, and distribution: *Woodwardia* is a north-temperate, amphioceanic genus comprising approximately 13 species. The species can be distinguished from the other by the monomorphic leaves, by the usually short-creeping to suberect rhizomes.

1. ***Woodwardia auriculata* Blume**, Enum. Pl. Javae 2: 196. 1828.
2. ***Woodwardia fimbriata* Sm.**, in Ress, Cycl. 38. 1818.
3. ***Woodwardia harlandii* Hook.**, Fil. Exot. 3: pl. 7. 1857.
4. ***Woodwardia japonica* (L.f.) Sm.**, Mém. Acad. Roy. Sci. Turin 5: 411. 1793. --
Blechnum japonicum L. f., Suppl. Pl. 445. 1781[1782].
5. ***Woodwardia kempii* Copel**, Philipp. J. Sci. 3: 280. 1908.
6. ***Woodwardia magnifica* Ching & P.S.Chiu**, Acta Phytotax. Sin. 12: 247-248. 1974.
7. ***Woodwardia martinezii* Maxon ex Weath.**, Amer. Fern J. 39: 88. 1949.
8. ***Woodwardia orientalis* Sw.**, J. Bot. (Schrader) 1800(2): 76. 1801.
9. ***Woodwardia prolifera* Hook. & Arn.**, Bot. Beechey Voy. 275, pl. 56. 1841[1838].

10. ***Woodwardia radicans* (L.) Sm.**, Mém. Acad. Roy. Sci. Turin 5: 412. 1793. --
Blechnum radicans L., Mant. Pl. 2: 307-308. 1771.
11. ***Woodwardia semicordata* Mickel & Beitel**, Mem. New York Bot. Gard. 46: 403.
1988.
12. ***Woodwardia spinulosa* M.Martens & Galeotti**, Nouv. Mém. Acad. Roy. Sci.
Bruxelles 15: 64. 1842.
13. ***Woodwardia unigemmata* (Makino) Nakai**, Bot. Mag. (Tokyo) 39(461): 103.
1925. -- *Woodwardia radicans* var. *unigemmata* Makino, J. Jap. Bot. 2: 7. 1918.

Blechnaceae subfam. Stenochlaenoideae (Ching) J.P.Roux, Conspect. South. Afr.
Pteridophyta, 156. 2001, emend. Gasper, V.A.O.Dittrich & Salino -- Stenochlaenaceae
Ching, Acta Phytotax. Sin. 16(4): 18. 1978. -- **Type:** *Stenochlaena* J.Sm., J. Bot. 3: 401.
1841.

Plants epiphytic or terrestrial; **rhizomes** long-creeping, scandent or not; **fronds**
monomorphic to dimorphic; **stipes** glabrous to hairy; **blades** pinnate to bipinnate,
sometimes pilose; **buds** absent (present in *Salpichalena hookeriana*); **rachises** with
determinate or indeterminate growth (*Salpichlaena*), glabrous; **pinnae** articulate to rachises
or not (*Salpichlaena*), glabrous or with a pair of glands at their bases (*Stenochlaena*); **veins**
free or with inconspicuous areoles near the costae, simple or furcate, with the ends
connected by a marginal vein in *Salpichlaena*; **sori (sporangia)** acrostichoid, without
indusia in *Stenochlaena*, indusia linear in other genera.

Species number, comments, and distribution: about 12 species, with *Salpichlaena*
in Neotropics, *Stenochlaena* in Asia, Malesia, Australia and Africa; *Telmatoblechnum* is
pantropical.

Salpichaena **J.Sm.**, in Hooker, Gen. Fil.: pl. 93. 1842. -- **Type:** *Salpichlaena volubilis* (Kaulf.) J.Sm., J. Bot. (Hooker) 4: 168. 1841.

Plants terrestrial, climbing; **rhizomes** long-creeping, non-stoloniferous, bearing dark brown, lanceolate, entire scales; **fronds** monomorphic to dimorphic, climbing, with indeterminate growth, reaching more than 15 m; **stipes** stout, long, stramineous, with few scales; **blades** linear, bipinnate, truncate proximally, apices conform, concolorous; **rachises** glabrous; **buds** present or absent; **aerophores** absent; **pinnae** not articulate to rachises, petiolulate, linear to linear-lanceolate, flat, margins entire to crenulate; **veins** simple or furcate, with the ends connected by a marginal vein; **sori** linear, parallel to commissural veins, protected by elongate indusia, these lacerate or strongly vaulted and virtually tubular, breaking up into narrow recurving strips as the mature spores are released; $x = 40$. Figure 2A; 5D.

Species number, comments, and distribution: *Salpichlaena* is a neotropical genus with three species, and is characterized by the rachises with indeterminate growth (reaching 15 m; Moran 1995a), and bipinnate blades.

1. *Salpichlaena hookeriana* (**Kuntze**) **Alston**, Bull. Misc. Inform. 1932: 312. 1932. -- *Spicanta hookeriana* Kuntze, Revis. Gen. Pl. 2: 821. 1891.
2. *Salpichlaena thalassica* **Grayum & R.C.Moran**, Ann. Missouri Bot. Gard. 77: 591. 1990.
3. *Salpichlaena volubilis* (**Kaulf.**) **J.Sm.**, J. Bot. (Hooker) 4: 168. 1841. -- *Blechnum volubile* Kaulf., Enum. Filic. 159. 1824.

Stenochlaena **J.Sm.**, in Hooker, J. Bot. 3: 401. 1841. **Lectotype** (designated by Pfeiffer, Nom. 2: 1274. 1874): *Stenochlaena scandens* J.Sm., nom. illeg. [= *Stenochlaena palustris* (Burm.f.) Bedd., 1876].

Lomariobotrys Fée, Mém. Foug., 5. Gen. Filic. 45. 1852 -- Type: *Lomariobotrys tenuifolia* (Desv.) Fée, Mém. Fam. Foug. 5: 46. 1852 = [*Stenochlaena tenuifolia* (Desv.) Moore]

Plants terrestrial, rarely epiphytic; **rhizomes** long-creeping, climbing, non-stoloniferous, stout, clothed when young by brown peltate or linear-acuminate scales, entire or almost entire; **fronds** dimorphic, determinate; **stipes** stout, long, stramineous, red-brown, sometimes with a few persistent scales, glabrous distally or slightly hairy adaxially; **sterile blades** ovate to oblong-lanceolate, pinnate, truncate proximally, apices conform, concolorous; **fertile blades** pinnate to bipinnate (in *S. tenuifolia*); **rachises** glabrous; **buds** absent; **aerophores** absent; **pinnae** not articulate to rachises, sessile to subsessile, oblong-ovate to lanceolate, serrate; **veins** with a unique series of inconspicuous areoles, the other ones simple to furcate; **sori** acrostichoid, exindusiate; $x = 37$. Figure 2B; 5E.

Species number, comments, and distribution: seven species, distributed in Asia and Africa. Rhizomes long-creeping, scandent, with dimorphic and pinnate blades. The acrostichoid condition as well the exindusiate sporangia, reported for this genus, need further investigation.

1. *Stenochlaena areolaris* (Harr.) Copel., Philipp. J. Sci., 2C: 406. 1908. -- *Lomaria areolaris* Harr., J. Linn. Soc., Bot. 16: 28. 1877.
2. *Stenochlaena cumingii* Holttum, Amer. Fern J. 71: 122. 1971.
3. *Stenochlaena mildbraedii* Brause, Bot. Jahrb. Syst. 53: 384. 1915.
4. *Stenochlaena milnei* Underw., Bull. Torrey Bot. Club 33: 38. 1906.
5. *Stenochlaena palustris* (Burm.f.) Bedd., Suppl. Ferns S. Ind., 26, pl. 201. 1876. -- *Polypodium palustre* Burm.f., Fl. Indica 234. 1768.
6. *Stenochlaena riauensis* Sofiyanti *et al.*, Bangl. J. Pl. Taxon. 22: 137. 2015.

7. *Stenochlaena tenuifolia* (Desv.) Moore, Gard. Chron. 193. 1856. -- *Lomaria tenuifolia* Desv., Ges. Naturf. Freunde Berlin Mag. Neuesten Entdeck. Gesamnten Naturk. 5: 326. 1811.

***Telmatoblechnum* Perrie, D.J.Ohlsen & Brownsey, Taxon: 63: 755. 2014. Type:**

Telmatoblechnum serrulatum (Rich.) Perrie, D.J. Ohlsen & Brownsey, Taxon 63: 755. 2014.

Blechnopsis sect. *Diapnia* C.Presl -- Epimel. Bot. 119. 1851.

Plants terrestrial, rarely epipetric; **rhizomes** long-creeping, non-stoloniferous, stout, clothed with bicolorous (atrocostate), lanceolate, entire scales; **fronds** monomorphic or slightly dimorphic, determinate; **stipes** stout, long, smooth and glabrous, with dark bases, stramineous distally, with a few scales similar to those of rhizomes; **blades** concolorous, pinnate, oblong to lanceolate, truncate proximally, apices conform; **rachises** glabrous or with amorphous, hyaline scales; **buds** absent; **aerophores** absent; **pinnae** articulate to rachises, linear to linear-oblong, margins serrate; **veins** free, 1--3-furcate, ending at the pinna margins; **sori** linear, close to costae, with narrow indusia, margins erose or lacerate; $x = 36$. Figure 2C; 5F.

Species number, comments, and distribution: *Telmatoblechnum* comprises two species, one in Neotropics and other in Australasia/Oceania. The genus is one of the few in the family with articulate pinnae; pinna margins are serrulate, and the rhizomes are long-creeping. Plants grow in swamps.

1. ***Telmatoblechnum indicum* (Burm.f.) Perrie, D.J.Ohlsen & Brownsey, Taxon 63: 755. 2014. -- *Blechnum indicum* Burm.f., Fl. Indica 231. 1768.**

2. ***Telmatoblechnum serrulatum* (Rich.) Perrie, D.J.Ohlsen & Brownsey, Taxon 63: 755. 2014. -- *Blechnum serrulatum* Rich., Actes Soc. Hist. Nat. Paris 1: 114. 1792.**

Blechnaceae subfam. Blechnoideae, Gasper, V.A.O.Dittrich & Salino, subfam. nov.

Type: *Blechnum occidentale* L., Sp. Pl 2: 1077. 1753.

Diagnosis: Rhizomes various, sometimes forming caudices, stoloniferous or not; fronds monomorphic to usually dimorphic (rarely trimorphic); blades rarely entire, pinnatifid, pinnate to bipinnate; buds and aerophores rare; veins free to areolate; sori linear, born along commissural veins, indusiate (rarely exindusiate).

Plants terrestrial, epiphytic, hemiepiphytic or rarely aquatic; **rhizomes** short- to long-creeping, erect, sometimes trunk-like, occasionally climbing, stoloniferous or not, clothed with basifixed scales; **fronds** monomorphic, subdimorphic, or dimorphic, rarely trimorphic, determinate; **stipes** not articulate to rachiseses, stramineous to dark brown, pilose, scaly, or glabrescent; **blades** pinnatisect, pinnate-pinnatifid, or bipinnate (rarely simple and entire), glabrous or rarely pilose; **rachises** glabrous or scaly, rarely densely pilose, but commonly very scaly; **buds** and **aerophores** absent or present in some species; **pinna** margins entire to serrate, not articulate (except *Blechnum articulatum*), adnate, sessile or petiolulate; **veins** free to areolate; **sori** linear, born on commissural veins, indusiate or rarely exindusiate.

Species number, comments, and distribution: About 239 species, most diverse in the southern hemisphere, but a few species in the north-temperate zone. We recognize 18 genera in this subfamily, with strong molecular and morphological support.

***Austroblechnum* Gasper & V.A.O.Dittrich, gen. nov. -- Type:** *Austroblechnum pennamarina* (Poir.) Gasper & V.A.O.Dittrich

Diagnosis: Rhizomes bearing concolorous or bicolorous scales; fronds dimorphic, blades with reduced pinnae proximally; pinnae partially or totally adnate, with veins ending in enlarged and readily visible hydathodes.

Plants terrestrial or epipetric; **rhizomes** erect, ascending, short- or long-creeping, stoloniferous or not, moderately stout, sometimes forming small caudices, apices with brown to reddish brown, concolorous, lanceolate or ovate, acuminate, entire scales (scales rarely bicolorous with pale margins), ; **fronds** dimorphic; **stipes** slender or stout, atropurpureus to dark or yellowish, usually longer in fertile fronds, proximally with scales similar to the rhizomes and sometimes with uniseriate hairs, mostly glabrous distally; **blades** concolorous, lanceolate-acuminate, narrowly elliptic or ovate, pinnatisect to pinnate, rarely entire, reduced proximally or blades truncate, sometimes with vestigial pinnae, apices pinnatifid or pinnatisect; **rachises** glabrous or bearing a few scales; **buds** rarely present; **aerophores** absent; **pinnae** partially or totally adnate to rachises, falcate, oblong or ensiform, entire or crenate to serrate, plane to slightly revolute at margins; **veins** free, rarely simple, 1-2 furcate, with clavate ends readily visible, forming hydathodes adaxially; **sori** linear, indusia entire to erose or fimbriate; $x = 33$. Figure 3A; 5G.

Species number, comments, etymology, and distribution: ca. 40 species with tropical to south temperate distributions. Most species from middle to high elevations are usually in forests, or in open rocky sites. Fronds are dimorphic, and usually stipes of the fertile fronds are longer than those of sterile ones; the sterile blades have reduced pinnae proximally. Pinnae are partially or wholly adnate, and the veins end in enlarged and readily visible hydathodes. The name, used by Ray Cranfill in preliminary notes, was adopted because of the austral distribution of the species.

1. *Austroblechnum aequatoriense* (A.Rojas) Gasper & V.A.O.Dittrich, *comb. nov.*
-- *Blechnum aequatoriense* A. Rojas, Mét. Ecol. Sist. 3(Supl. 1): 9-10, f. 1a-c. 2008.

2. ***Austroblechnum andinum* (Baker) Gasper & V.A.O.Dittrich, *comb. nov.*** --
Lomaria andina Baker, in Hooker & Baker, Syn. Fil., 2: 482. 1874. -- *Blechnum andinum*
(Baker) C.Chr., Index Filic. 150. 1905.
3. ***Austroblechnum ascendens* (A.Rojas) Gasper & V.A.O.Dittrich, *comb. nov.*** --
Blechnum ascendens A. Rojas, Mét. Ecol. Sist. 3 (Supl. 1): 10, f. 2a, b. 2008.
4. ***Austroblechnum asperum* (Klotzsch) Gasper & V.A.O.Dittrich, *comb. nov.*** --
Lomaria aspera Klotzsch, Linnaea 20: 344. 1847. -- *Blechnum asperum* (Klotzsch)
J.W.Sturm, Abh. Naturhist. Ges. Nürnberg 2: 172. 1858.
5. ***Austroblechnum bakeri* (C.Chr.) Gasper & V.A.O.Dittrich, *comb. nov.*** --
Blechnum bakeri C.Chr., Index Filic. 151. 1905.
6. ***Austroblechnum banksii* (Hook.f.) Gasper & V.A.O.Dittrich, *comb. nov.*** --
Lomaria banksii Hook.f., Fl. Nov.-Zel. 2:31, t. LXXVI. 1845. -- *Blechnum banksii*
(Hook.f.) Mett. ex Diels, Nat. Pflanzenfam. 1(4): 249. 1899.
7. ***Austroblechnum blechnoides* (Keyserl.) Gasper & V.A.O.Dittrich, *comb. nov.*** --
Lomaria blechnoides Bory, in Duperrey, Voy. Monde. 1: 273. 1829, non *Lomaria*
blechnoides Desv., Mém. Soc. Linn. Paris 6: 289. 1827. -- *Blechnum blechnoides* Keyserl.,
Polypodiacea et Cyatheacea Herbarii Bungeani 65. 1873.
8. ***Austroblechnum colensoi* (Hook.f.) Gasper & V.A.O.Dittrich, *comb. nov.*** --
Blechnum colensoi Hook.f., Victoria Naturalist 72: 159. 1956.
9. ***Austroblechnum corralense* (Espinosa) Gasper & V.A.O.Dittrich, *comb. nov.*** --
Blechnum corralense Espinosa, Revista Chilena Hist. Nat. 36: 92. 1932.
10. ***Austroblechnum difforme* (Copel.) Gasper & V.A.O.Dittrich, *comb. nov.*** --
Blechnum difforme Copel., Bernice P. Bishop Mus. Bull. 59: 13, t. 3. 1929.

11. ***Austroblechnum divergens* (Kunze) Gasper & V.A.O.Dittrich, comb. nov.** --
Lomaria divergens Kunze, *Linnaea* 9: 57. 1834. -- *Blechnum divergens* (Kunze) Mett.,
Ann. Sci. Nat. Bot., sér. 5, 2: 225. 1864.
12. ***Austroblechnum doodioides* (Brack.) Gasper & V.A.O.Dittrich, comb. nov.** --
Lomaria doodioides Brack., *U.S. Expl. Exped.*, *Filic.*, 16: 124. 1854, non *Blechnum*
doodioides Hook., *Fl. Bor.-Amer.* 2(12): 263. 1840.
13. ***Austroblechnum durum* (T. Moore) Gasper & V.A.O.Dittrich, comb. nov.** --
Lomaria dura T. Moore, *Gard. Chron.* 1866. 290. 1866. -- *Blechnum durum* (T. Moore)
C.Chr., *Index Filic.* 153. 1905.
14. ***Austroblechnum integrifrons* (Bonap. ex Rakotondr.) Gasper & V.A.O.Dittrich,**
comb. nov. -- *Blechnum integrifrons* Bonap. ex Rakotondr., *Adansonia*, sér. 3, 35: 171-
173, f. 12, 13[map]. 2013.
15. ***Austroblechnum jamaicensis* (Broadh.) Gasper & V.A.O.Dittrich, comb. nov.** --
Struthiopteris jamaicensis Broadh., *Bull. Torrey Bot. Club* 39: 266, t. 21. 1912. --
Blechnum jamaicense (Broadh.) *C.Chr.*, *Index Filic.*, *Suppl.* 1, 16. 1913.
16. ***Austroblechnum keysseri* (Rosenst.) Gasper & V.A.O.Dittrich, comb. nov.** --
Blechnum keysseri Rosenst., *Repert. Spec. Nov. Regni Veg.* 12: 527. 1913.
17. ***Austroblechnum lanceolatum* (R.Br.) Gasper & V.A.O.Dittrich, comb. nov.** --
Stegania lanceolata R.Br., *Prodr.* 152. 1810. -- *Blechnum lanceolatum* (R. Br.) J.W. Sturm,
Enum. Pl. Vasc. Crypt. Chil. 25. 1858, non Raddi (1819). -- *Blechnum chambersii* Tindale,
in Beadle et al., *Fl. Sydney Region.* ed. 2, 86. 1986.
18. ***Austroblechnum lehmannii* (Hieron.) Gasper & V.A.O.Dittrich, comb. nov.** --
Blechnum lehmannii Hieron., *Bot. Jahrb. Syst.* 34: 473. 1904.

19. ***Austroblechnum lherminieri* (Bory) Gasper & V.A.O.Dittrich, *comb. nov.*** -- *Lomaria lherminieri* Bory ex Kunze, Farrnkräuter 173. 1845. -- *Blechnum lherminieri* (Bory) C.Chr., Index Filic. 156. 1905.
20. ***Austroblechnum melanocaulon* (Brack.) Gasper & V.A.O.Dittrich, *comb. nov.*** - *Lomaria melanocaulon* Brack., U.S. Expl. Exped., Filic. 16: 122. 1854. -- *Blechnum melanocaulon* (Brack.) T.C.Chambers & P.A.Farrant, Blumea 46: 318. 2001.
21. ***Austroblechnum membranaceum* (Colenso ex Hook.) Gasper & V.A.O.Dittrich, *comb. nov.*** -- *Lomaria membranacea* Colenso ex Hook., Sp. Fil. 3. 1860. -- *Blechnum membranaceum* (Colenso ex Hook.) Mett., Nat. Pflanzenfam. 1(4): 249. 1899.
22. ***Austroblechnum microphyllum* (Goldm.) Gasper & V.A.O.Dittrich, *comb. nov.*** - *Lomaria microphylla* Goldm., Nov. Actorum Acad. Caes. Leop.-Carol. German. Nat. Cur. 16, Suppl. 1, 460. 1843. -- *Blechnum microphyllum* (Goldm.) C.V.Morton, Amer. Fern J. 60: 103. 1970.
23. ***Austroblechnum mochaenum* (G.Kunkel) Gasper & V.A.O.Dittrich, *comb. nov.*** -- *Blechnum mochaenum* G.Kunkel, Nova Hedwigia 13: 340. 1967.
24. ***Austroblechnum mochaenum* (G.Kunkel) Gasper & V.A.O.Dittrich var. *achalense* (Hieron.) Gasper & V.A.O.Dittrich, *comb. nov.*** -- *Blechnum lanceolatum* var. *achalense* Hieron., Bot. Jahrb. Syst. 22: 381. 1896.
25. ***Austroblechnum mochaenum* (G.Kunkel) Gasper & V.A.O.Dittrich var. *fernandezianum* (Looser) Gasper & V.A.O.Dittrich, *comb. nov.*** -- *Blechnum blechnoides* var. *fernandezianum* Looser, Revista Univ. (Santiago) 32(2): 61. 1947.
26. ***Austroblechnum norfolkianum* (Heward) Gasper & V.A.O.Dittrich, *comb. nov.*** -- *Lomaria norfolkiana* Heward, London J. Bot. 1. 122 nota. 1842. -- *Blechnum norfolkianum* (Heward) Maiden, Proc. Linn. Soc. New South Wales 28: 732. 1904.

27. *Austroblechnum nukuhivense* (E.D.Br.) Gasper & V.A.O.Dittrich, *comb. nov.* --
Blechnum nukuhivense E. Brown, Bernice P. Bishop Mus. Bull. 89: 69, f. 13. 1931
28. *Austroblechnum organense* (Brade) Gasper & V.A.O.Dittrich, *comb. nov.* --
Blechnum organense Brade, Arq. Inst. Biol. Veg. 2(1): 2-3, pl. 1, f. 3, pl. 3. 1935.
29. *Austroblechnum patersonii* (R. Br.) Gasper & V.A.O.Dittrich subsp. *patersonii*,
comb. nov. -- *Stegania patersonii* R. Br., Prodr. 152. 1810. -- *Blechnum patersonii* (R.Br.)
Mett. subsp. *patersonii*, Fil. Hort. Bot. Lips. 64, t. 4, f. 4-10. 1856.
30. *Austroblechnum patersonii* (R.Br.) Gasper & V.A.O.Dittrich subsp.
queenslandicum (T.C.Chambers & P.A.Farrant) Gasper & V.A.O.Dittrich, *comb. nov.*
-- *Stegania patersonii* R. Br., Prodr. 152. 1810. -- *Blechnum patersonii* (R.Br.) Mett. subsp.
queenslandicum T.C.Chambers & P.A.Farrant, Telopea 6: 177. 1995.
31. *Austroblechnum penna-marina* (Poir.) Gasper & V.A.O.Dittrich, *comb. nov.* --
Polypodium penna-marina Poir., in Lam., Encycl. 5: 520. 1804. -- *Blechnum penna-*
marina (Poir.) Kuhn, Filic. Afr. 92. 1868.
32. *Austroblechnum pinnatifidum* (A.Rojas) Gasper & V.A.O.Dittrich, *comb. nov.* -
- *Blechnum pinnatifidum* A.Rojas, Mét. Ecol. Sist. 3(Supl. 1): 20-21, f. 5a-c. 2008.
33. *Austroblechnum raiateense* (J.W.Moore) Gasper & V.A.O.Dittrich, *comb. nov.*
-- *Blechnum raiateense* J.W. Moore, Bernice P. Bishop Mus. Bull. 102: 9. 1933.
34. *Austroblechnum squamipes* (Hieron.) Gasper & V.A.O.Dittrich, *comb. nov.* --
Blechnum lanceolatum var. *squamipes* Hieron., Bot. Jahrb. Syst. 22: 381. 1896. --
Blechnum squamipes (Hieron.) M.Kessler & A.R.Sm., Amer. Fern J. 97: 80. 2007.
35. *Austroblechnum stoloniferum* (Mett. ex E. Fourn.) Gasper & V.A.O.Dittrich,
comb. nov. -- *Lomaria stolonifera* Mett. ex E.Fourn., Mexic. Pl. 1: 113. 1872. -- *Blechnum*
stoloniferum (Mett. ex E.Fourn.) C.Chr., Index Filic. 154. 1905.

36. *Austroblechnum vallegrandense* (M.Kessler & A.R.Sm.) Gasper & V.A.O.Dittrich, *comb. nov.* -- *Blechnum vallegrandense* M.Kessler & A.R.Sm., Amer. Fern J. 97: 79. 2007.
37. *Austroblechnum vieillardii* (Mett.) Gasper & V.A.O.Dittrich, *comb. nov.* -- *Blechnum vieillardii* Mett., Ann. Sci. Nat. Bot., sér. 4, 15: 70. 1861.
38. *Austroblechnum wardiae* (Mickel & Beitel) Gasper & V.A.O.Dittrich, *comb. nov.* -- *Blechnum wardiae* Mickel & Beitel, Mem. New York Bot. Gard. 46: 89, f. 122A,B, 125A. 1988.
39. *Austroblechnum ×aggregatum* (Colenso) Gasper & V.A.O.Dittrich, *comb. nov.* - - *Lomaria aggregata* Colenso, Trans. & Proc. New Zealand Inst. 20. 223. 1888. -- *Blechnum aggregatum* (Colenso) Tindale, Proc. Linn. Soc. New South Wales 85: 254. 1960. [*Blechnum chambersii* Tindale × *Blechnum membranaceum* (Colenso ex Hook.) Mett. ex Diels]
40. *Austroblechnum ×rodriguezii* (Aguiar *et al.*) Gasper & V.A.O.Dittrich, *comb. nov.* -- *Blechnum ×rodriguezii* Aguiar, Quintanilla & Amigo, Amer. Fern J. 97: 228, fig. 1. 2008. [*Blechnum corralense* Espinosa × *Blechnum mochaenum* G. Kunkel subsp. *mochaenum*]

Blechnidium T.Moore, Index. Fil. CLV. 1860; Brit. Ferns Nat. Pr. [Moore], octavo ed., 2. 210. 1860. -- **Type:** *Blechnidium melanopus* (Hook.) T.Moore, Brit. Ferns 210. 1860; Index Fil. CLV. 1860.

Plants terrestrial or epipetric; **rhizomes** long-creeping, slender (ca. 3--4 mm diam.), non-stoloniferous, bearing dense golden to dark-brown, lanceolate or ovate-lanceolate, entire scales; **fronds** monomorphic; **stipes** slender, long, dark brown to atropurpureous, with few scales proximally, glabrous toward apices; **blades** concolorous, lanceolate,

pinnatisect, abruptly or subabruptly reduced proximally, apices pinnatifid; **rachises** glabrous; **buds** absent; **aerophores** absent; **pinnae** adnate, usually falcate, entire, slightly revolute at margins; **veins** partially anastomosing, with costal areoles, ultimate veinlets free, usually forking; **sori** linear, adjacent and closely parallel to costae, indusia entire, linear; $x = 31$. Figure 3B; 5H.

Species number, comments, and distribution: One species in China (including Taiwan) and India. The genus is characterized by the discrete areoles adjacent to the costae, and the genus thus resembles *Blechnum* s.s., but the rhizomes are long-creeping and non-stoloniferous rhizomes, and phylogenetic analyses do not show them as closely related (Gasper et al., in prep.).

1. *Blechnidium melanopus* (Hook.) T.Moore, Brit. Ferns 2: 210. 1860. -- *Blechnum melanopus* Hook., Sp. Fil. 3: 64, pl. 161. 1859.

Blechnopsis C.Presl, Abh. Königl. Böhm. Ges. Wiss., ser. 5, 6: 475. 1851. -- **Type:**

Blechnopsis orientalis (L.) C.Presl, Abh. Königl. Böhm. Ges. Wiss., ser. 5, 6: 477. 1851.

Plants terrestrial; **rhizomes** erect to suberect, non-stoloniferous, stout, sometimes forming a caudices, densely clothed with concolorous or weakly bicolorous brown, linear, entire scales; **fronds** monomorphic; **stipes** stout, dark reddish or purple brown, bearing scales at bases similar to those of rhizomes, sometimes with very fine pale hairs distally; **blades** concolorous, ovate to deltate, pinnate, with many pairs (10+) of abruptly reduced, auriculate pinnae proximally, apices subconform; **rachises** glabrous or with sparse irregular hairs and slender reddish brown scales; **buds** absent; **aerophores** absent; **pinnae** sessile or subpetiolulate, linear to narrowly elliptic, entire, sometimes revolute at margins, often with a basisopic lobe; **veins** free, 1-furcate, each ending in a small hydathode adaxially; **sori** linear, indusiate, indusia entire at maturity, reflexed and not covering

sporangia; $x = 32, 33, 34$. Figure 3C; 5I.

Species number, comments, and distribution: Two species, in Asia, Malesia, Japan, Australia and Pacific islands. *Blechnopsis* is distinguished by the long stipes, with many auricles (more than 10), and usually with the basiscopic lobe adnate.

1. *Blechnopsis finlaysoniana* (Wall. ex Hook. & Grev.) C.Presl, Epimel. Bot. 116. 1851. -- *Blechnum finlaysonianum* Wall. ex Hook. & Grev., Pl. Voy. Russes Monde, t. 225. 1831.
2. *Blechnopsis orientalis* (L.) C.Presl, Abh. Königl. Böhm. Ges. Wiss., ser. 5, 6: 477. 1851. -- *Blechnum orientale* L., Sp. Pl. 2: 1077. 1753.

Blechnum L., Sp. Pl. 2: 1077. 1753. **Type:** *Blechnum occidentale* L., Sp. Pl. 2: 1077. 1753.

Distaxia C.Presl, Epimel. Bot. 110. 1851. -- Type: *Distaxia fraxinea* (Willd.)

C.Presl, based on *Blechnum fraxineum* Willd.

Mesothema C.Presl, Epimel. Bot. 111. 1851. -- *Blechnum* sect. *Mesothema* (C.Presl) J.Sm., Hist. Fil. 301. 1875. -- Type: *Mesothema australe* (L.) C.Presl, based on *Blechnum australe* L.

Plants terrestrial, epipetric, or rarely epiphytic; **rhizomes** erect to ascending, decumbent or short-creeping, stoloniferous, slender to rather stout, bearing linear or linear-oblong, pale brown or dark, concolorous or bicolorous, entire scales (or scales with few minute teeth); **fronds** monomorphic or subdimorphic; **stipes** slender, short (sometimes absent) or long, stramineous to pale brown or atropurpureus, scales similar to those of rhizomes proximally, scaly and sometimes with multicellular, catenate, hyaline hairs toward apices; **blades** concolorous, lanceolate to deltate-lanceolate, entire (rare), pinnatisect or 1-pinnate, gradually reduced or truncate proximally, apices pinnatifid or

conform; **rachises** glabrous or pilose, without scales; **buds** absent; **aerophores** absent; **pinnae** sessile, adnate or subpetiolulate, lanceolate, oblong-lanceolate, ensiform, margins entire, finely denticulate; **veins** rarely partially anastomosing, usually free and then 1--3 furcate, each ending near margins in an enlarged tip; **sori** linear, continuous or rarely interrupted along the costae, indusia slightly erose or ciliate; $x = 31$. Figure 3D; 6A.

Species number, comments, and distribution: Ca. 25 species, mostly Neotropical, a few in southern Africa. With the segregation of the other genera, *Blechnum s.s.*, redefined in a greatly restricted sense, is characterized by stoloniferous rhizomes, monomorphic to subdimorphic fronds, and finely denticulate pinna margins.

1. *Blechnum anthracinum* **R.C.Moran**, Novon 2: 132. 1992.
2. *Blechnum appendiculatum* **Willd.**, Sp. Pl., ed. 4, 5(1): 410. 1810.
3. *Blechnum arcuatum* **J.Rémy ex Gay**, Fl. Chil. 6: 477. 1853.
4. *Blechnum areolatum* **V.A.O.Dittrich & Salino**, Syst. Bot. 37: 40, figs. 1-3. 2012.
5. *Blechnum asplenioides* **Sw.**, Kongl. Vetensk. Acad. Handl. 1817(1): 72, t. 3, f. 3. 1817.
6. *Blechnum auriculatum* **Cav.**, Descr. Pl. 262. 1802.
7. *Blechnum australe* **L.**, Mant. Pl. 130. 1767.
8. *Blechnum austrobrasilianum* **de la Sota**, Bol. Soc. Argent. Bot. 16: 248. 1975.
9. *Blechnum fraxineum* **Willd.**, Sp. Pl., ed. 4, 5(1): 413. 1810.
10. *Blechnum gracile* **Kaulf.**, Enum. Filic. 158. 1824.
11. *Blechnum gracilipes* (**Rosenst.**) **M.Kessler & A.R.Sm.**, Amer. Fern J. 97: 80. 2007. -- *Blechnum blechnoides* var. *gracilipes* **Rosenst.**, Repert. Spec. Nov. Regni Veg. 9: 343. 1911.
12. *Blechnum guayanense* **A.Rojas**, Mét. Ecol. Sist. 3(1): 36-37, f. 1, 3C, D. 2008.
13. *Blechnum hastatum* **Kaulf.**, Enum. Filic. 161. 1824.

14. *Blechnum heringeri* **Brade**, Sellowia 18: 87. 1966.
15. *Blechnum laevigatum* **Cav.**, Descr. Pl. 263. 1802.
16. *Blechnum lanceola* **Sw.**, Kongl. Vetensk. Acad. Handl. 1817(1): 71, t. 3, f. 2.
1817.
17. *Blechnum longipilosum* **V.A.O.Dittrich & Salino**, Syst. Bot. 37: 40, figs. 1-3.
2012.
18. *Blechnum ludificans* **Herter**, Revista Sudamer. Bot. 8: 162. 1950.
19. *Blechnum malacothrix* **Maxon & C.V.Morton**, Bull. Torrey Bot. Club 66: 40.
1939.
20. *Blechnum meridense* **Klotzsch**, Linnaea 20: 349. 1847.
21. *Blechnum occidentale* **L.**, Sp. Pl. 2: 1077. 1753.
22. *Blechnum polypodioides* **Raddi**, Opusc. Sci. 3: 294. 1819.
23. *Blechnum punctulatum* **Sw.**, J. Bot. (Schrader) 1800(2): 74. 1801.
24. *Blechnum punctulatum* **Sw. var. atherstonii** **R.Sim**, Ferns S. Afr., ed. 2, 183, t.
79. 1915.
25. *Blechnum punctulatum* **Sw. var. intermedium** **R.Sim**, Ferns S. Afr, ed. 2, 185, t.
80. 1915.
26. *Blechnum punctulatum* **Sw. var. krebsii** **R.Sim**, Ferns S. Afr., ed. 2, 185, t. 81.
1915.
27. *Blechnum* ×*antillanum* **Proctor**, Brit. Fern Gaz. 9: 214. 1965. [*Blechnum*
appendiculatum Willd. × *Blechnum meridense* Klotzsch]
28. *Blechnum* ×*caudatum* **Cav.**, Descr. Pl. 262. 1802. [*Blechnum occidentale* L. ×
Blechnum gracile Kaulf.]
29. *Blechnum* ×*confluens* **Schldl. & Cham.**, Linnaea 5: 613. 1830. [*Blechnum*
occidentale L. × *Blechnum polypodioides* Raddi]

30. *Blechnum ×leopoldense* (Dutra) V.A.O.Dittrich & Salino, Phytotaxa 231: 217.
2015. [*Blechnum auriculatum* Cav. × *Blechnum occidentale* L.]

Brainea J.Sm., Cat. Kew Ferns 5. 1856. **Type:** *Brainea insignis* (Hook.) J.Sm., Cat. Kew Ferns 5. 1856.

Bowringia Hooker., Hooker's J. Bot. Kew Gard. Misc. 5: 237. 1853. -- Type:

Bowringia insignis Hook.

Plants terrestrial; **rhizomes** erect, stout, trunk-like, to about 1 m tall, caudices to 10 cm diam., non-stoloniferous, clothed with shiny dark brown, linear, entire scales, each with an attenuate or uniseriate tip; **fronds** subdimorphic; **stipes** stout, long, brownish, scales at bases similar to those of rhizomes, glabrous distally; **blades** bicolorous, elliptic- or deltate-lanceolate, pinnate, truncate or very slightly narrowed proximally, apices pinnatifid; **rachises** abaxially with small scales along costae and veins, or glabrescent; **buds** absent; **aerophores** absent; **pinnae** sessile or petiolulate, linear to narrowly oblong, crenate to serrulate, slightly revolute at margins; **veins** free or with a costal row of areoles in sterile and fertile pinna, then simple or 1- or 2-furcate; **sori** linear, borne along costal veins, exindusiate; $x = 33, 35$ both reported. Figure 3E; 6B.

Species number, comments, and distribution: Only one species, occurring in China and Malesia. This is a small "tree fern", with subdimorphic fronds and exindusiate sori.

Brainea insignis is one of the species in Blechnaceae with areolate venation, but the areoles are close to the costae and subtriangular, in contrast to the shapes of costal areoles in other genera in the family.

1. *Brainea insignis* (Hook.) J.Sm., Cat. Kew Ferns 5. 1856. -- *Bowringia insignis* Hook., Hooker's J. Bot. Kew Gard. Misc. 5: 237--238, pl. 2. 1853.

Cleistoblechnum* Gasper & Salino, gen. nov. -- Type: *Cleistoblechnum eburneum

(Christ) Gasper & Salino, Bull. Acad. Int. Géogr. Bot. 1902: 233 fig. c.

Plants terrestrial; **rhizomes** short, ascending or suberect, non-stoloniferous, slender, bearing at apices a tuft of orange-brown, glabrous, lanceolate, entire scales, some of these with a discrete, well-defined, darkened, atropurpureous mid-stripe; **fronds** slightly dimorphic, the fertile ones a bit longer, and with narrower, more widely spaced pinnae that are narrowed at their bases (vs. broader in sterile fronds); **stipes** short, ca. 5--10 cm long, slender, stramineous to tan, with scales confined to the very base, similar to those of rhizomes; **blades** thickened, concolorous, pinnatisect, linear-ob lanceolate, the pinnae reduced in the proximal 1/4--1/3 to small auricles ca. 1--2 mm long, 3--5 mm broad, apices pinnatifid; **rachises** glabrous; **buds** absent; **aerophores** absent; **pinnae** adnate, oblong to narrowly deltate, margins entire but strongly revolute; **veins** inconspicuous or completely hidden in the subcoriaceous laminae, free, furcate, not reaching laminar margins; **sori** linear, remaining enclosed by erose-margined indusia at maturity; $x = 33$. Figure 3F; 6C.

Species number, etymology, and distribution: One species with two varieties, endemic to Taiwan and mainland China. *Cleistoblechnum* resembles *Struthiopteris*, from which is distinguished by location (endemic to Taiwan and China), slightly dimorphic fronds, the segment margins strongly inrolled, and the much more coriaceous blades. Chambers and Farrant (1996b) reported that the sori remain enclosed by erose-margined indusia at maturity, a condition that suggests the generic name.

1. ***Cleistoblechnum eburneum* (Christ) Gasper & Salino var. *eburneum*, comb.**

nov. -- *Blechnum eburneum* Christ, Bull. Acad. Int. Géogr. Bot. 1902: 233, fig. c.

2. ***Cleistoblechnum eburneum* (Christ) Gasper & Salino var. *obtusum* (Tagawa)**

Gasper & Salino, comb. nov., Acta Phytotax. Geobot. 14: 192. 1952.

Cranfillia Gasper & V.A.O.Dittrich, *gen. nov.* -- **Type:** *Cranfillia fluviatilis* (R. Br.)

Gasper & V.A.O.Dittrich

Diagnosis: Rhizomes suberect or erect, bearing oblong-attenuate or acuminate, brown to black scales; fronds dimorphic; rachises and costae pilose with multicellular hairs, these black or hyaline, to 2 mm long.

Plants terrestrial; **rhizomes** short-creeping to usually suberect or erect, stoloniferous or not, slender to stout, clothed with reddish brown to blackish, sometimes bicolorous, lanceolate or oblong-attenuate, entire scales with acuminate tips; **fronds** dimorphic; **stipes** slender or stout, short to long, stramineous to dark brown, scaly proximally, often abundantly hairy, or hairs sometimes sparse or absent; **blades** concolorous, linear-oblong to deltate, pinnate or deeply pinnatifid proximally, pinnatifid distally, proximally truncate or with gradually to subabruptly reduced pinnae; **rachises** scaly and often pilose, the hairs uniseriate, septate, sometimes sparse; **buds** absent or rarely present (in *C. sprucei*); **aerophores** absent; **pinnae** subpetiolulate proximally or often becoming fully adnate distally, oblong to lanceolate, sometimes falcate, entire to crenate or dentate along margins; **veins** free, 1- or 2-furcate, terminating adaxially in small submarginal hydathodes; **sori** linear, indusia more or less entire, sometimes with uniseriate hairs; $x = 33$. Figure 3G; 6D.

Species number, etymology, and distribution: 11 species, three in the Neotropics, the remainder in Oceania. This genus is characterized by the usually pilose rachises and costae, with exception of *C. sampaiwana*, where hairs are very tiny and scarce. The genus honors Raymond Cranfill, one of the first researchers to study Blechnaceae, using molecular data; his notes advanced and inspired major portions of this work.

1. *Cranfillia fluviatilis* (R.Br.) Gasper & V.A.O.Dittrich, *comb. nov.* -- *Stegania fluviatilis* R. Br., Prodr. 1: 152. 1810. -- *Blechnum fluviatile* (R. Br.) Lowe ex Salomon, Nomencl. Gefässkrypt. 115. 1883.

2. ***Cranfillia fullagari* (F.Muell.) Gasper & V.A.O.Dittrich, *comb. nov.*** -- *Lomaria fullagarii* F.Muell., *Fragm.* 8: 157. 1874., as *Lomaria fullageri*. -- *Blechnum fullagarii* (F. Muell.) C.Chr., *Index Filic.* 154. 1905.
3. ***Cranfillia geniculata* (T.C.Chambers & P.A.Farrant) Gasper & V.A.O.Dittrich, *comb. nov.*** -- *Blechnum geniculatum* T.C.Chambers & P.A.Farrant, *Telopea* 5: 329. 1993.
4. ***Cranfillia hirsuta* (Rosenst.) Gasper & V.A.O.Dittrich, *comb. nov.*** -- *Blechnum hirsutum* Rosenst., *Repert. Spec. Nov. Regni Veg.* 9: 74. 1910.
5. ***Cranfillia longicauda* (C.Chr.) Gasper & V.A.O.Dittrich, *comb. nov.*** -- *Blechnum longicauda* C.Chr., *Ark. Bot.* 10(2): 10, pl. 1. 1910.
6. ***Cranfillia nigra* (Colenso) Gasper & V.A.O.Dittrich, *comb. nov.*** -- *Lomaria nigra* Colenso, *Tasm. Journ. Nat. Sci.* 1: 375. 1841. -- *Blechnum nigrum* (Colenso) Mett., *Ann. Sci. Nat. Bot.*, sér. 4, 15: 69. 1861.
7. ***Cranfillia opaca* (Mett.) Gasper & V.A.O.Dittrich, *comb. nov.*** -- *Blechnum opacum* Mett., *Ann. Sci. Nat. Bot.*, sér. 4, 15: 69. 1861.
8. ***Cranfillia pilosa* (Brack.) Gasper & V.A.O.Dittrich, *comb. nov.*** -- *Lomaria pilosa* Brack., *U.S. Expl. Exped., Filic.* 16: 125, t. 15. 1854. -- *Blechnum pilosum* (Brack.) Brownlie, *Beih. Nova Hedwigia* 55: 320. 1977.
9. ***Cranfillia sampaioana* (Brade) Gasper & V.A.O.Dittrich, *comb. nov.*** -- *Blechnum sampaioanum* Brade, *Arq. Inst. Biol. Veg.* 1: 225 1: 225. 1935.
10. ***Cranfillia sprucei* (C.Chr.) Gasper & V.A.O.Dittrich, *comb. nov.*** -- *Blechnum sprucei* C.Chr., *Index Filic.* 160. 1905.
11. ***Cranfillia vulcanica* (Blume) Gasper & V.A.O.Dittrich, *comb. nov.*** -- *Lomaria vulcanica* Blume, *Enum. Pl. Javae* 202. 1828. -- *Blechnum vulcanicum* (Blume) Kuhn, *Ann. Mus. Bot. Lugduno-Batavi* 4: 284. 1869.

***Diploblechnum* Hayata**, Bot. Mag. (Tokyo) 41: 702. 1927. **Type:** *Diploblechnum fraseri* (A.Cunn.) De Vol, Fl. Taiwan 1: 153. 1975.

Pteridoblechnum Hennipman, Blumea 13: 397. 1966. -- Type: *Pteridoblechnum neglectum* (F.M.Bailey) Hennipman

Steenisioblechnum Hennipman, Blumea 30: 17. 1984. -- Type: *Steenisioblechnum acuminatum* (C.T.White & Goy) Hennipman

Plants terrestrial; **rhizomes** slender, long-creeping to short-creeping, or caudices erect, densely clothed at apices by bicolorous, linear-acuminate or lanceolate, entire or sparingly toothed scales; **fronds** dimorphic or slightly dimorphic; **stipes** slender, short, brown to reddish, densely scaly proximally, fewer persistent scales distally; **blades** concolorous, ovate to narrowly elliptic, pinnate to deeply pinnatifid or bipinnatisect to bipinnate, usually becoming bipinnatifid, the proximal pinnae gradually to abruptly reduced with one or two pairs of pinnae, or abruptly reduced to winged lobes extending down rachis, the apical portions of the blades pinnatifid; **rachises** with sparse scales; **buds** sometimes present in axils of distal pinnae; **aerophores** absent; **pinnae** subpetiolulate to adnate, narrowly linear to narrowly elliptic, lanceolate, slightly revolute, margins subentire to crenate; **veins** free, 1-furcate, each ending in a clavate hydathode or (in *D. neglectum*) anastomosing and forming polygonal areoles, these in ca. 2 rows between costae and pinna margins; **sori** linear, indusiate, indusia subentire to erose, reflexed at maturity and not covering sporangia; $x = 27, 28$. Figure 3H; 6E.

Species number, comments, and distribution: Six species, in Malesia, Australia, and Oceania. The species usually have erect, narrow rhizomes that may eventually collapse and thus appear to be long-creeping, as reported by Cranfill (2001). The species are pinnate to deeply pinnatifid or bipinnatisect to bipinnate, usually becoming bipinnatifid, the basal pinnae gradually to abruptly reduced through one or two pairs of pinnae, or abruptly

reduced to winged lobes extending down rachis.

1. ***Diploblechnum acuminatum* (C.T.White & Goy) Gasper & V.A.O.Dittrich, *comb. nov.*** -- *Leptochilus acuminatus* C.T.White & Goy, Victoria Naturalist 54: 150. 1938. -- *Pteridoblechnum acuminatum* (C.T.White & Goy) Hennisman, Proc. Roy. Soc. Queensland 87: 98. 1976. -- *Blechnum reticulatum* R.K.Wilson & Bayly, Taxon 63: 755. 2014.
 2. ***Diploblechnum diversifolium* (Mett.) Gasper & V.A.O.Dittrich, *comb. nov.*** -- *Blechnum diversifolium* Mett., Ann. Sci. Nat. Bot., sér. 4, 15: 71. 1861.
 3. ***Diploblechnum fraseri* (A.Cunn.) De Vol, Fl. Taiwan 1: 153. 1975.** -- *Lomaria fraseri* A.Cunn., Companion Bot. Mag. 2: 364. 1836. -- *Blechnum fraseri* (A. Cunn.) Luerss., Fl. N. R. 34: 292. 1876.
 4. ***Diploblechnum lenormandii* (Baker) Gasper & V.A.O.Dittrich, *comb. nov.*** -- *Lomaria lenormandii* Baker, Syn. Fil. (Hooker & Baker) 181. 1867. -- *Blechnum lenormandii* (Baker) Diels, Nat. Pflanzenfam. 1(4): 249. 1899.
 5. ***Diploblechnum neglectum* (F.M.Bailey) Gasper & V.A.O.Dittrich, *comb. nov.*** -- *Acrostichum neglectum* F.M.Bailey, Proc. Linn. Soc. New South Wales 5: 32. 1880. -- *Pteridoblechnum neglectum* (F.M.Bailey) Hennisman, Blumea 13: 397. 1966. -- *Blechnum neglectum* (F.M.Bailey) R.K.Wilson & Bayly, Taxon 63: 755. 2014.
 6. ***Diploblechnum rosenstockii* (Copel.) Gasper & V.A.O.Dittrich, *comb. nov.*** -- *Blechnum rosenstockii* Copel., Univ. Calif. Publ. Bot. 12. 394. 1931, non *Blechnum rosenstockii* de la Sota, Darwiniana 18: 254. 1973.
- Doodia* R.Br.**, Prodr. Fl. Nov. Holl.: 151. 1810. -- **Lectotype** (designated by J. Smith, Hist. Fil. 309. 1875): *Doodia aspera* R.Br.

Plants terrestrial; **rhizomes** erect to ascending, sometimes stoloniferous, slender,

clothed with black to brown, lanceolate to linear-lanceolate, entire scales; **fronds** monomorphic or dimorphic; **stipes** slender, mostly short, usually dark proximally and stramineous on rachises, scaly, with scales similar to those of rhizomes, usually glabrescent; **blades** concolorous, linear-lanceolate, lanceolate-acuminate, deeply pinnatifid to pinnate, truncate or with reduced, auriculate pinnae proximally, apices pinnatifid or sub-conform; **rachises** sometimes with scales; **buds** absent; **aerophores** absent; **pinnae** sessile or adnate, lanceolate, sometimes falcate, ovate to linear, margins serrate-dentate; **veins** with one or three series of areoles, the first series between veinlets of different forks, the second between veinlets of the same fork and sometimes also like the first series, the third, if present, the same as the first; **sori** in a single or several rows on both sides of the costae, borne on areolar veins, indusia linear, entire to repand; $x = 32$. Figure 3I; 6F.

Species number, comments, and distribution: About 19 species, in Australia, New Zealand, Pacific Islands to Hawaii. *Doodia* is characterized by having erect to ascending rhizomes and by the areolate venation, forming distinct series; fronds are monomorphic or dimorphic.

1. *Doodia aspera* **R.Br.**, Prodr. 151. 1810.
2. *Doodia australis* **Parris**, Fl. Australia 48: 710. 1998.
3. *Doodia brackenridgei* **Carruth. ex Seem.**, Fl. Vit. 352. 1873.
4. *Doodia caudata* (**Cav.**) **R.Br.**, Prodr. 151. 1810. -- *Woodwardia caudata* **Cav.**, Descr. Pl. 264. 1802.
5. *Doodia dissecta* **Parris**, Fl. Australia 48: 711. 1998.
6. *Doodia dives* **Kunze**, Bot. Zeitung (Berlin) 6: 144. 1848.
7. *Doodia gracilis* **Copel.**, Univ. Calif. Publ. Bot. 14: 362. 1929.
8. *Doodia heterophylla* (**F.M.Bailey**) **Domin**, Bibliotheca Bot. 85: 121. 1915. -- *Doodia aspera* var. *heterophylla* **F.M. Bailey**, (Fern World Australia 51. 1881.

9. *Doodia hindii* Tindale ex T.C.Chambers, Telopea 12: 257. 2008.
10. *Doodia kunthiana* Gaudich., Voy. Uranie, Bot. 401, t. 14. 1829.
11. *Doodia linearis* J.Sm., Ferns Brit. For. 199. 1866.
12. *Doodia marquesensis* E.D.Br., Bernice P. Bishop Mus. Bull. 89: 73, t. 16. 1931.
13. *Doodia maxima* J.Sm. ex C.Chr., Index Filic. 243. 1906.
14. *Doodia media* R.Br., Prodr. 151. 1810.
15. *Doodia milnei* Carruth., Fl. Vit. [Seemann] 352. 1873.
16. *Doodia mollis* Parris, New Zealand J. Bot. 18: 145. 1980.
17. *Doodia paschalis* C.Chr., Nat. Hist. Juan Fernandez 2: 48, f. 1a-c 1920[1921].
18. *Doodia scaberula* Parris, Blumea 24: 505, f. 1. 1978.
19. *Doodia squarrosa* Colenso, Trans. & Proc. New Zealand Inst. 13: 382. 1881.

Icarus Gasper & Salino, *gen. nov.* -- **Type:** *Icarus filiformis* (A.Cunn.) Gasper & Salino

Diagnosis: Rhizomes long-creeping, climbing trees; fronds di- or trimorphic; larger pinnae short-stalked; veins free, furcate.

Plants terrestrial or hemiepiphytic; **rhizomes** long-creeping, climbing, non-stoloniferous, slender (2--4 mm diam.), densely clothed with bicolorous, dark brown, linear-lanceolate, squarrose scales; **fronds** di- or trimorphic, with different sterile fronds when hemiepiphytic; **stipes** slender, relatively short, but longer in ones borne hemiepiphytically, stramineous to tan, with a few scales similar to those of rhizomes proximally, with scattered scales to glabrescent distally; **blades** concolorous, lanceolate to narrow-oblong, with sterile terrestrial blades smaller than epiphytic ones, 2--6 pinna pairs somewhat reduced proximally, apices pinnatifid; **rachises** bearing scattered brownish scales and moderately dense, hyaline, flexuous, septate hairs 0.2--0.5 mm long; **buds** absent; **aerophores** absent; **pinnae** narrowly triangular, truncate at bases, sessile or short-

petiolate, dentate-serrulate or minutely crenulate along margins; **veins** free, simple or furcate, each ending in a submarginal hydathode; **sori** linear, indusia brown, continuous, erose at margins, reflexed at maturity; $x = 33$. Figure 4A; 6G.

Species number, comments, and distribution: One species, endemic to New Zealand.

This is a unique genus in the Blechnaceae, having trimorphic leaves. When in contact with soil, this species has small sterile leaves, and when climbing, much larger sterile leaves; the third leaf type, of fertile fronds, has greatly contracted pinnae (Allan 1961). The dentate-serrulate or minutely crenulate pinna margins and the presence of adaxial hydathodes are other distinguishing characters. This name was coined by Raymond Cranfill, in his unpublished notes, and we have decided to adopt this for it.

1. *Icarus filiformis* (A.Cunn.) Gasper & Salino, *comb. nov.* -- *Lomaria filiformis* A. Cunn., Companion Bot. Mag. 2: 363. 1837. -- *Blechnum filiforme* (A.Cunn.) Ettingsh., Denkschr. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl. 24: 21, t. 6 f. 5. 1864.

Lomaria Willd., Ges. Naturf. Freunde Berlin Mag. Neuesten Entdeck. Gesamten Naturk. 3: 160. 1809. -- **Lectotype** (designated by J. Smith, Hist. Fil. 303. 1875): *Lomaria nuda* (Labill.) Willd., Sp. Pl. ed. 4, 5(1): 289. 1810.

Stegania R. Br., Prod. Nov. Holl. 152. 1810. -- *Lomaria* sect. *Stegania* (R.Br.) J.Sm., Hist. Fil. 304. 1875. -- Type: *Stegania nuda* (Labill.) R. Br., based on *Onoclea nuda* Labill. [= *Blechnum nudum* (Labill.) Lueres.]

Plants terrestrial; **rhizomes** erect, stout, sometimes forming small trunks, stoloniferous or not, clothed by bicolorous or concolorous, dark brown or blackish, linear-lanceolate to acicular, entire scales, these brown with a blackened mid-stripe; **fronds** dimorphic; **stipes** stout, long, brown to blackish, with scales like those of rhizomes, but smaller, scaly, pilose, or glabrous; **blades** lanceolate or oblong-elliptic, pinnate or

pinnatisect, gradually reduced proximally, proximal pinnae auriculate, apices pinnatisect, discolorous (adaxial side dark green, abaxial side brownish in dried state); **rachises** with a few scales on abaxial surfaces, or glabrous; **buds** absent; **aerophores** absent; **pinnae** adnate to subpetiolulate, oblong, linear to lanceolate, plane to slightly revolute at the entire or minutely crenulate margins; **veins** free, 1- to 2-furcate, tips ending at pinna margins, sometimes ending in hydathodes adaxially, or slightly enlarged; **sori** linear, indusia continuous, lacerate or erose at maturity; $x = 28$. Figure 4B; 6H.

Species number, comments, and distribution: This widely dispersed genus comprises six species, and occurs in South America, South Africa, Australia, and New Caledonia.

Lomaria has historically been a name applied to species with dimorphic leaves, differing from *Blechnum*, which in the strict sense has monomorphic leaves. We characterize the genus by the deeply grooved rachises and the discolorous blades. One species has been reported with green spores (Lloyd & Klekowsky, 1970).

1. ***Lomaria brunea* (M.Kessler & A.R.Sm) Gasper & V.A.O.Dittrich, comb. nov.** -- *Blechnum bruneum* M.Kessler & A.R.Sm., Amer. Fern J. 97: 71. 2007.
2. ***Lomaria discolor* (G.Forst.) Willd.,** Sp. Pl., ed. 4, 5(1): 410. 1810. -- *Blechnum discolor* Keyserl., Polyp. Herb. Bunge 66. 1873.
3. ***Lomaria inflexa* Kunze,** Farrnkräuter 1: 150, t. 65. 1844. -- *Blechnum inflexum* (Kunze) Kuhn, Filic. Afr. 92. 1868.
4. ***Lomaria nuda* (Labill.) Willd.,** Sp. Pl., ed. 4, 5(1): 289. 1810. -- *Onoclea nuda* Labill., Nov. Holl. Pl. 2: 96, pl. 246. 1806. -- *Blechnum nudum* (Labill.) Mett., Flora 59: 292. 1876.
5. ***Lomaria oceanica* (Rosenst.) Gasper & V.A.O.Dittrich, comb. nov.** -- *Blechnum attenuatum* var. *oceanicum* Rosenst., Repert. Spec. Nov. Regni Veg. 10: 159. 1911. -- *Blechnum oceanicum* (Rosenst.) Brownlie, Fl. Nouv.-Calédonie & Dépend. 3: 245. 1969.

6. *Lomaria spannagelii* (Rosenst.) Gasper & V.A.O.Dittrich, *comb. nov.* --

Blechnum spannagelii Rosenst., Hedwigia 46: 93-94. 1907.

Lomaridium C.Presl, Abh. Königl. Böhm. Ges. Wiss., ser. 5, 6: 514. 1851. -- **Type:**

Lomaridium plumieri (Desv.) C.Presl, Abh. Königl. Böhm. Ges. Wiss., ser. 5, 6: 514-515. 1851.

Plants hemiepiphytic; **rhizomes** long-creeping, climbing trees or ascending to erect, non-stoloniferous, stout, clothed by mostly bicolorous, long-lanceolate, denticulate or entire (rare) scales; **fronds** dimorphic; **stipes** stout, long, stramineous, brown to dark brown, proximally with scales like those of rhizomes, glabrous or minutely but densely papillose; **blades** concolorous or bicolorous, the adaxial side dark green, abaxially silver-green, lanceolate or ovate-deltate, deeply pinnatisect or pinnate in the proximal half, usually with many pairs of greatly reduced, auriculate or vestigial pinnae proximally, distally pinnatifid, sometimes with an entire, acuminate blade tip; **rachises** glabrous or with scattered minute hairs, often atropurpureous; **buds** absent; **aerophores** absent; **pinnae** adnate, oblong-acute to linear-attenuate or narrowly triangular, sometimes falcate, margin entire, slightly revolute; **veins** free, 1-furcate proximally, terminating near margins in enlarged vein tips adaxially; **sori** linear, indusia linear, entire to subentire; $x = 29, 32$. Figure 4C; 6I.

Species number, comments, and distribution: 16 species in southern tropical regions, especially the Neotropics, eastern Africa, and Madagascar; a single species, *L. contiguum*, is known from Australasia. *Lomaridium* is easily distinguished from the other Blechnaceae by the denticulate rhizome scales, glabrous leaves, and hemiepiphytic condition.

1. ***Lomaridium acutum* (Desv.) Gasper & V.A.O.Dittrich, comb. nov.** -- *Lomaria acuta* Desv., Mém. Soc. Linn. Paris 6: 290. 1827. -- *Blechnum acutum* (Desv.) Mett., Ann. Sci. Nat. Bot., sér. 5, 2: 225. 1864.
2. ***Lomaridium attenuatum* (Sw.) Gasper & V.A.O.Dittrich, comb. nov.** -- *Onoclea attenuata* Sw., J. Bot. (Schrader) 1800(2): 73. 1801. -- *Blechnum attenuatum* (Sw.) Mett., Fil. Hort. Bot. Lips. 64, pl. 3, f. 1-6. 1856.
3. ***Lomaridium biforme* (Baker) Gasper & V.A.O.Dittrich, comb. nov.** -- *Lomaria biformis* Baker, J. Linn. Soc., Bot. 15: 415. 1876. -- *Blechnum biforme* (Baker) Christ, Farnkr. Erde 180. 1897.
4. ***Lomaridium binervatum* (Poir.) Gasper & V.A.O.Dittrich, comb. nov.** -- *Polypodium binervatum* Poir., in Lam., Encycl. 5: 521. 1804. -- *Blechnum binervatum* (Poir.) C.V.Morton & Lellinger, Amer. Fern J. 57: 67. 1967.
5. ***Lomaridium bonapartei* (Rakotondr.) Gasper & V.A.O.Dittrich, comb. nov.** -- *Blechnum bonapartei* Rakotondr., Adansonia, sér. 3, 35 167, f. 8, 9[map]. 2013.
6. ***Lomaridium contiguum* (Mett.) Gasper & V.A.O.Dittrich, comb. nov.** -- *Blechnum contiguum* Mett., Ann. Sci. Nat. Bot., sér. 4, 15: 70. 1861.
7. ***Lomaridium dendrophilum* (Sodirol) Gasper & V.A.O.Dittrich, comb. nov.** -- *Lomaria dendrophila* Sodirol, Anales Univ. Centr. Ecuador 8: 148. 1893. -- *Blechnum dendrophilum* (Sodirol) C.Chr., Index Filic. 153. 1905.
8. ***Lomaridium ensiforme* (Liebm.) Gasper & V.A.O.Dittrich, comb. nov.** -- *Lomaria ensiformis* Liebm., Kongel. Danske Vidensk. Selsk. Skr., Naturvidensk. Math. Afd., ser. 5, 1: 234. 1849. -- *Blechnum ensiforme* (Liebm.) C.Chr., Index Filic. 153. 1905.
9. ***Lomaridium fragile* (Liebm.) Gasper & V.A.O.Dittrich, comb. nov.** -- *Lomaria fragilis* Liebm., Kongel. Danske Vidensk. Selsk. Skr., Naturvidensk. Math. Afd., ser. 5, 1:

232. 1849. -- *Blechnum fragile* (Liebm.) C.V.Morton & Lellinger, Amer. Fern J. 57: 68. 1967.

10. ***Lomaridium fuscocosquamosum* (A.Rojas) Gasper & V.A.O.Dittrich, comb. nov.** - *Blechnum fuscocosquamosum* A.Rojas, Lankesteriana 5: 49, f. 1a, b. 2005.

11. ***Lomaridium nigrocostatum* (A.Rojas) Gasper, comb. nov.** -- *Blechnum nigrocostatum* A.Rojas, Mét. Ecol. Sist. 3: 38. 2008.

12. ***Lomaridium plumieri* (Desv.) C.Presl**, Abh. Königl. Böhm. Ges. Wiss., ser. 5, 6: 515. 1851. -- *Lomaria plumieri* Desv., Ges. Naturf. Freunde Berlin Mag. Neuesten Entdeck. Gesamten Naturk. 5: 325. 1811. -- *Blechnum plumieri* (Desv.) Mett., Fil. Hort. Bot. Lips. 61, t. 4, f. 19-20. 1856.

13. ***Lomaridium pteropus* (Kunze) Gasper & V.A.O.Dittrich, comb. nov.** -- *Lomaria pteropus* Kunze, Farnkräuter 1(4): 97, t. 46. 1842. *Blechnum pteropus* (Kunze) Mett., Fil. Hort. Bot. Lips. 61. 1856.

14. ***Lomaridium schottii* (Colla) Gasper & V.A.O.Dittrich, comb. nov.** -- *Lomaria schottii* Colla, Herb. Pedem. 6: 220. 1836. -- *Blechnum schottii* (Colla) C.Chr., Ark. Bot. 10(2): 7. 1910.

15. ***Lomaridium simillimum* (Baker) Gasper & V.A.O.Dittrich, comb. nov.** -- *Lomaria simillimum* Baker, J. Bot. 22: 141. 1884. -- *Blechnum simillimum* (Baker) Diels, Nat. Pflanzenfam. 1(4): 248. 1899.

16. ***Lomaridium xiphophyllum* (Baker) Gasper & V.A.O.Dittrich, comb. nov.** -- *Lomaria xiphophylla* Baker, J. Bot. 22: 142. 1884. -- *Blechnum xiphophyllum* (Baker) C.Chr., Index Filic. 161. 1905.

***Lomariocycas* (J.Sm.) Gasper & A.R. Sm., comb. nov.** -- *Lomaria* sect. *Lomariocycas* J.Sm., Hist. Fil. 305. 1875. -- *Blechnum* sect. *Lomariocycas* (J.Sm.) C.V. Morton, Amer.

Fern J. 49: 68. 1959. -- **Type:** *Lomaria boryana* (Sw.) Willd., based on *Onoclea boryana* Sw. = [*Blechnum boryanaum* (Sw.) Schltdl.] = *Lomariocycas tabularis* (Thunb.) Gasper & A.R.Sm.

Plants terrestrial, rarely epiphytic; **rhizomes** erect, stout, trunk-like, non-stoloniferous, densely clothed at apices by bicolorous, acicular, curved, multilayered, entire scales; **fronds** dimorphic, rarely monomorphic; **stipes** stout, long, yellowish to dark brown, with scales similar to those of rhizomes at base, distally glabrous or scaly; **blades** concolorous, oblanceolate to elliptic, pinnate, pinnatisect distally, pinnae gradually reduced proximally to small auricles, apices abruptly reduced to a large, entire segment; **rachises** with scales on both surfaces or only abaxially, these sometimes deciduous; **buds** absent; **aerophores** absent; **pinnae** sessile to subpetiolulate or partially adnate, linear to oblong, narrowly oblong-lanceolate, margins entire, strongly revolute; **veins** free, ending before the margins, immersed in blade tissue and practically invisible without clearing; **sori** linear, indusia linear, continuous, entire or erose; $x = 33$. Figure 4D; 7A.

Species number, comments, and distribution: About 19 species in the Neotropics, Africa, and Madagascar; the genus is absent in Australasia. *Lomariocycas* is reminiscent of species of *Cycas* (hence the name), a gymnosperm, because of the erect trunk-like rhizomes, and the rosetted disposition of the pinnate leaves. The veins are immersed in the blade tissue and practically invisible, and the pinnae are beset with scales.

1. ***Lomariocycas aurata* (Fée) Gasper & A.R.Sm., comb. nov.** -- *Lomaria aurata* Fée, Mém. Foug. 8: 71. 1857. -- *Blechnum auratum* (Fée) R.M.Tryon & Stolze, Fieldiana, Bot., n.s., 32: 67. 1993.
2. ***Lomariocycas buchtienii* (Rosenst) Gasper & A.R.Sm., comb. nov.** -- *Blechnum buchtienii* Rosenst., Repert. Spec. Nov. Regni Veg. 5: 231. 1908.

3. ***Lomariocycas columbiensis* (Hieron.) Gasper & A.R.Sm., *comb. nov.* --**
Blechnum columbiense Hieron., Hedwigia 47: 244. 1908.
4. ***Lomariocycas cycadifolia* (Colla) Gasper & A.R.Sm., *comb. nov.* -- *Lomaria*
cycadifolia Colla, Herb. Pedem. 6: 219. 1836. -- *Blechnum cycadifolium* (Colla)
J.W.Sturm, Abh. Naturhist. Ges. Nürnberg 2: 173. 1858.**
5. ***Lomariocycas decrescens* (Rakotondr.) Gasper & A.R.Sm., *comb. nov.* --**
Blechnum decrescens Rakotondr., Adansonia 35: 169. 2013.
6. ***Lomariocycas insularis* (C.V. Morton & Lellinger) Gasper & A.R.Sm., *comb.*
nov. -- *Blechnum insularum* C.V.Morton & Lellinger, Amer. Fern J. 57: 70. 1967.**
7. ***Lomariocycas longepetiolata* (Tardieu) Gasper & A.R.Sm., *comb. nov.* --**
Blechnum longepetiolatum Tardieu, Mém. Inst. Sci. Madagascar, Sér. B, Biol. Vég. 6: 230.
1955.
8. ***Lomariocycas longipinna* (Rakotondr.) Gasper & A.R.Sm., *comb. nov.* --**
Blechnum longipinum Rakotondr., Adansonia, sér. 3, 35 174-176, f. 15, 16[map]. 2013.
9. ***Lomariocycas madagascariensis* (Tardieu) Gasper & A.R.Sm., *comb. nov.* --**
Blechnum madagascariense Tardieu, Mém. Inst. Sci. Madagascar, Sér. B, Biol. Vég. 6:
230, f. 3, 1-4. 1955.
10. ***Lomariocycas magellanica* (Desv.) Gasper & A.R.Sm., *comb. nov.* -- *Blechnum*
magellanicum (Desv.) Mett., Fil. Lechl. 1: 14. 1856.**
11. ***Lomariocycas obtusifolia* (Ettingsh.) Gasper & A.R.Sm., *comb. nov.* -- *Lomaria*
obtusifolia C.Presl, Tent. Pterid. 143. 1836. -- *Blechnum obtusifolium* Ettingsh., Denkschr.
Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl. 23: 59, t. 8, f. 4. 1864.**
12. ***Lomariocycas palmiformis* (Thouars) Gasper & A.R.Sm., *comb. nov.* -- *Pteris*
palmiformis Thouars, Fl. Tristan d'Acugna 30. 1804. -- *Blechnum palmiforme* (Thouars)
C.Chr., Results Norweg. Sci. Exped. Tristan da Cunha no. 6: 10. 1940.**

13. *Lomariocycas rufa* (Spreng.) Gasper & A.R.Sm., *comb. nov.* -- *Lomaria rufa* Spreng., Nova Acta Phys.-Med. Acad. Caes. Leop.-Carol. Natur. Cur. 10: 230. 1821. -- *Blechnum rufum* (Spreng.) C.Chr., Index Filic., Suppl. 1, 17. 1913.
14. *Lomariocycas shaferi* (Broadh.) Gasper & A.R. Sm., *comb. nov.* -- *Struthiopteris shaferi* Broadh. -- Bull. Torrey Bot. Club 39: 374, t. 27. 1912. -- *Blechnum shaferi* (Broadh.) C.Chr., Index Filic., Suppl. 1, 17. 1913.
15. *Lomariocycas schomburgkii* (Klotzsch) Gasper & A.R.Sm., *comb. nov.* -- *Lomaria schomburgkii* Klotzsch, Linnaea 20: 346. 1847. -- *Blechnum schomburgkii* (Klotzsch) C.Chr., Index Filic. 159. 1905.
16. *Lomariocycas tabularis* (Thunb.) Gasper & A.R.Sm., *comb. nov.* -- *Pteris tabularis* Thunb., Prodr. Pl. Cap., 171. 1800. -- *Blechnum tabulare* (Thunb.) Kuhn, Filic. Afr. 94. 1868.
17. *Lomariocycas underwoodiana* (Broadh.) Gasper & A.R. Sm., *comb. nov.* -- *Struthiopteris underwoodiana* Broadh., Bull. Torrey Bot. Club 39: 377, t. 28. 1912. -- *Blechnum underwoodianum* (Broadh.) C.Chr., Index Filic., Suppl. 1, 17. 1913.
18. *Lomariocycas werckleana* (Christ) Gasper & A.R.Sm., *comb. nov.*, *Lomaria werckleana* Christ, Bull. Herb. Boissier, sér. 2, 4(11): 1091. 1904. -- *Blechnum werckleanum* (Christ) C.Chr., Index Filic. 161. 1905.
19. *Lomariocycas yungensis* (J.P.Ramos) Gasper & A.R.Sm., *comb. nov.* -- *Blechnum yungense* J.P.Ramos, Novon 20: 68. 2010.

Neoblechnum Gasper & V.A.O.Dittrich, *gen. nov.* -- **Type:** *Neoblechnum brasiliense* (Desv.) Gasper & V.A.O.Dittrich

Diagnosis: Rhizomes stout, erect, forming caudices, apices covered by long (2 cm) black, glossy, acicular, curved, entire scales; fronds monomorphic; pinnae adnate, strongly

decurrent at bases, margins serrulate; proximal pinnae (many pairs) gradually reduced to small triangular, obtuse lobes ca. 1 cm long, broader than long.

Plants terrestrial; **rhizomes** erect, stout, trunk-like, non-stoloniferous, clothed by black, glossy, acicular, curved, entire scales; **fronds** monomorphic; **stipes** stout, short, brown to blackish, proximally with smaller scales similar to those of the rhizomes, glabrous or glabrescent distally; **blades** concolorous, oblong-lanceolate, pinnate to pinnatisect, gradually reduced at base, with small auricles at the blade bases, apices pinnatifid; **rachises** glabrous or with tiny capitate hairs; **buds** absent; **aerophores** absent; **pinnae** adnate to rachises, decurrent, linear to linear-lanceolate, margins serrulate; **veins** free, 1-furcate, each ending at pinna margins; **sori** linear, indusia entire to subentire; $x = 66$. Figure 4E; 7B.

Species number, etymology, and distribution: One neotropical species. The species are monomorphic, with trunk-like rhizomes when old; pinna margins are serrulate. The name was coined from the exclusively Neotropical occurrence of the sole species *Neoblechnum brasiliense*.

1. *Neoblechnum brasiliense* (Desv.) Gasper & V.A.O.Dittrich, *comb. nov.* --

Blechnum brasiliense Desv., Mag. Neuesten Entdeck. Gesamten Naturk. Ges. Naturf. Freunde Berlin 5: 330. 1811.

Oceanopteris Gasper & Salino, *gen. nov.* -- **Type:** *Oceanopteris gibba* (Labill.) Gasper & Salino

Diagnosis: Rhizomes short-creeping to erect with black, acuminate, acicular scales, except when aquatic (*O. francii*); fronds dimorphic to subdimorphic; proximal pinnae only slightly shorter than others, or greatly reduced (e.g., *O. gibba*), veins free, furcate.

Plants terrestrial; **rhizomes** short-creeping to erect, non-stoloniferous, stout,

sometimes trunk-like, clothed with black, acuminate, acicular, entire scales (except when aquatic, as *G. francii*), or scales sometimes pectinate and broadened only at the very base, otherwise acicular for nearly their entire length (as in *G. gibba*); **fronds** dimorphic to subdimorphic, or hemidimorphic (only distal pinnae fertile); **stipes usually** stout (but very narrow, 0.5 mm diam. in *G. francii*), long or short, stramineous, brown, or blackish, with scales similar to those of rhizomes, fewer scales distally, scales sometimes deciduous, rarely with small hairs; **blades** concolorous, deltate to ovate (narrowly lanceolate in *G. francii*), pinnate or pinnate-pinnatisect, slightly reduced proximally (greatly reduced in *G. francii*), with pinnatifid apices; **rachises** glabrous or with sparse scales and hairs; **buds** absent; **aerophores** absent; **pinnae** adnate or petiolulate, linear to narrowly elliptic, entire to serrate-dentate; **veins** free, furcate, each ending in a clavate hydathode adaxially; **sori** linear, on both sides of costae, indusia entire (over-arching and covering sporangia at maturity in *G. francii*); $x = 32$. Figure 4F; 6C.

Species number, etymology, and distribution: About eight species, distributed in Malesia, Fiji, New Caledonia, Australia. This genus has trunk-like rhizomes, sometimes more than 1 m tall, with the exception of *O. francii*, an aquatic plant. The rhizomes have black, acuminate, acicular scales, and the fronds are dimorphic to subdimorphic. This is closely related to *Neoblechnum brasiliense*, which occurs only in the Neotropics, and has glossy, acicular, curved, entire scales and monomorphic fronds. The name was coined for the exclusively oceanic (in Oceania) distribution of all known species.

1. *Oceanopteris cartilaginea* (Sw.) Gasper & Salino, *comb. nov.* -- *Blechnum cartilagineum* Sw., Syn. Fil. 114. 1867.
2. *Oceanopteris ciliata* (T.Moore) Gasper & Salino, *comb. nov.* -- *Lomaria ciliata* T.Moore, Gard. Chron. 1866: 290, non *Blechnum ciliatum* C.Presl, 1925). -- *Blechnum moorei* C.Chr., Index Filic. 157. 1905.

3. *Oceanopteris egregia* (Copel.) Gasper & Salino *comb. nov.* -- *Blechnum egregium* Copel., *Fragm. Fl. Philipp.* 187. 1905.
4. *Oceanopteris francii* (Rosenst.) Gasper & Salino, *comb. nov.* -- *Blechnum francii* Rosenst., *Repert. Spec. Nov. Regni Veg.* 12: 191. 1913.
5. *Oceanopteris gibba* (Labill.) Gasper & Salino, *comb. nov.* -- *Lomaria gibba* Labill., *Sert. Austro-Caledon.* 3, t. 4. 5. 1824. -- *Blechnum gibbum* (Labill.) Mett., *Ann. Sci. Nat. Bot.*, sér. 4, 15: 68. 1861.
6. *Oceanopteris obtusata* (Labill.) Gasper & Salino, *comb. nov.* -- *Lomaria obtusata* Labill., *Sert. Austro-Caledon.* 4, t. 6. 1824. -- *Blechnum obtusatum* (Labill.) Mett., *Ann. Sci. Nat. Bot.*, sér. 4, 15: 68. 1861.
7. *Oceanopteris vittata* (Brack.) Gasper & Salino, *comb. nov.* -- *Blechnum vittatum* Brack., *U.S. Expl. Exped.*, *Filic.* 16: 131, t. 16. 1854. -- *Blechnum cartilagineum* Sw. var. *vittatum* (Brack.) Luer, *Fil. Graeff.* 132. 1871.
8. *Oceanopteris whelanii* (F.M. Bailey) Gasper & Salino, *comb. nov.* -- *Blechnum whelanii* F.M. Bailey, *Rep. Bellenden-Ker Range* 77. 1889.

Parablechnum C.Presl, *Abh. Königl. Böhm. Ges. Wiss.*, ser. 5, 6: 469. 1851. -- **Type:**

Parablechnum procerum (G. Forst.) C.Presl, *Epimel. Bot.* 109. 1851.

Orthogramma C.Presl, *Epimel. Bot.* 121. 1851 -- Type: *Orthogramma gilliesii* (Hook. & Grev.) C.Presl, based on *Lomaria gilliesii* Hook. & Grev. [= *Blechnum chilense* (Kaulf.) Mett.]

Lomaria subg. *Paralomaria* Fée, *Mém. Fam. Foug.* 5: 69 (Gen. Fil.). 1852. -- Type: *Lomaria procera* (G. Forst.) Spreng., based on *Osmunda procera* G. Forst. [= *Blechnum procerum* (G. Forst.) Sw.]

Plants terrestrial; **rhizomes** erect or suberect, sometimes subarborescent, to

decumbent, short-creeping, non-stoloniferous, stout, clothed by reddish to brown, bicolorous or concolorous, ovate or ovate-lanceolate, entire or denticulate scales one cell thick, sometimes covered by mucilage; **fronds** usually dimorphic, rarely monomorphic or subdimorphic; **stipes** stout, long, stramineous, light brown, or dark purplish, proximally with scales similar to those of rhizomes, scaly, rarely with twisted hairs; **blades** concolorous, oblong to lanceolate, 1-pinnate, bases truncate, apices conform; **rachises** glabrous or glabrescent to often densely scaly; **buds** absent or present in a few species; **aerophores** sometimes borne at the bases of pinnae abaxially; **pinnae** sessile or stalked, usually not articulate (articulate in *B. articulatum*), often falcate, oblong-linear, lanceolate, plane or revolute at margins, entire or finely denticulate; **veins** free, simple to 1-furcate, clavate at tips adaxially, near pinna margins; **sori** linear, indusia subentire to lacerate or erose; $x = 28, 31, 33$. Figure 4G; 7D.

Species number, comments, and distribution: About 65 species, pantropical. The species of *Parablechnum* are characterized by the truncate laminae, 1-pinnate blades and conform or subconform apices. Rhizomes are generally erect or suberect, sometimes subarborescent to decumbent, or rarely long-creeping; young croziers are sometimes covered by mucilage; aerophores are sometimes borne at the pinna bases, abaxially (Neotropical species).

1. ***Parablechnum acanthopodum* (T.C.Chambers & P.A.Farrant) Gasper & Salino, *comb. nov.* -- *Blechnum acanthopodum* T.C.Chambers & P.A.Farrant, *Blumea* 46: 290. 2001.**
2. ***Parablechnum ambiguum* C.Presl, *Epimel. Bot.* 109. 1851. -- *Blechnum ambiguum* (C.Presl) Kaulf. ex C.Chr., *Dansk Bot. Ark.*, 9, 3: 21. 1937.**
3. ***Parablechnum articulatum* (F.Muell.) Gasper & Salino, *comb. nov.* -- *Lomaria articulata* F.Muell., *Fragm.* 5: 187. 1866. -- *Blechnum articulatum* (F.Muell.) S.B.Andrews, *Austrobaileya* 1: 11. 1977.**

4. ***Parablechnum atropurpureum* (A.R.Sm.) Gasper & Salino, *comb. nov.* --**
Blechnum atropurpureum A.R.Sm., Acta Bot. Venez. 14(3): 5. 1984.
5. ***Parablechnum bicolor* (M.Kessler & A.R.Sm.) Gasper & Salino, *comb. nov.* --**
Blechnum bicolor M.Kessler & A.R.Sm., Amer. Fern J. 97: 66. 2007.
6. ***Parablechnum bolivianum* (M.Kessler & A.R.Sm.) Gasper & Salino, *comb. nov.***
-- *Blechnum bolivianum* M.Kessler & A.R.Sm., Amer. Fern J. 97: 69. 2007.
7. ***Parablechnum camfieldii* (Tindale) Gasper & Salino, *comb. nov.* --** *Blechnum*
camfieldii Tindale, Proc. Linn. Soc. New South Wales 85: 251. 1960.
8. ***Parablechnum capense* (Burm.f.) Gasper & Salino, *comb. nov.* --** *Blechnum*
capense Burm.f., Fl. Indica 28. 1768; see Roux (1982) for re-lectotypification. -- *Blechnum*
sylvaticum Schelpe, J. S. African Bot. 45: 221. 1979.
9. ***Parablechnum chauliodontum* (Copel.) Gasper & Salino, *comb. nov.* --**
Blechnum chauliodontum Copel., Univ. Calif. Publ. Bot. 14. 361. 1929.
10. ***Parablechnum chilense* (Kaulf.) Gasper & Salino, *comb. nov.* --** *Lomaria*
chilensis Kaulf., Enum. Filic. 154. 1824. -- *Blechnum chilense* (Kaulf.) Mett., Fil. Lechl. 1:
14. 1856.
11. ***Parablechnum chiriquanum* (Broadh.) Gasper & Salino, *comb. nov.* --**
Struthiopteris chiriquana Broadh., Bull. Torrey Bot. Club 39: 361. 1912. -- *Blechnum*
chiriquanum (Broadh.) C.Chr., Index Filic., Suppl. 1, 16. 1913.
12. ***Parablechnum christii* (C.Chr.) Gasper & Salino, *comb. nov.* --** *Blechnum*
christii C.Chr., Index Filic. 152. 1905.
13. ***Parablechnum cochabambense* (M.Kessler & A.R.Sm.) Gasper & Salino, *comb.***
***nov.* --** *Blechnum cochabambense* M.Kessler & A.R.Sm., Amer. Fern J. 97: 72. 2007.

14. ***Parablechnum confusum* (E.Fourn.) Gasper & Salino, comb. nov.** -- *Lomaria confusa* E. Fourn., Ann. Sci. Nat. Bot., sér. 5, 18: 316. 1873. -- *Blechnum confusum* (E.Fourn.) Brownlie, Fl. Nouv.-Calédonie & Dépend. 3: 249, t. 31, f. 5-6. 1969.
15. ***Parablechnum corbassonii* (Brownlie) Gasper & Salino, comb. nov.** -- *Blechnum corbassonii* Brownlie, Fl. Nouv.-Calédonie & Dépend. 3: 246, t. 31, f. 3, 4. 1969.
16. ***Parablechnum cordatum* (Desv.) Gasper & Salino, comb. nov.** -- *Lomaria cordata* Desv., Ges. Naturf. Freunde Berlin Mag. Neuesten Entdeck. Gesammten Naturk. 5: 330. 1811. -- *Blechnum cordatum* (Desv.) Hieron., Hedwigia 47: 239. 1908.
17. ***Parablechnum decorum* (Brause) Gasper & Salino, comb. nov.** -- *Blechnum decorum* Brause, Bot. Jahrb. Syst. 56: 156. 1920.
18. ***Parablechnum dilatatum* (T.C.Chambers & P.A.Farrant) Gasper & Salino, comb. nov.** -- *Blechnum dilatatum* T.C.Chambers & P.A.Farrant, Blumea 46: 292. 2001.
19. ***Parablechnum falciforme* (Liebm.) Gasper & Salino, comb. nov.** -- *Lomaria falciformis* Liebm., Kongel. Danske Vidensk. Selsk. Skr., Naturvidensk. Math. Afd., ser. 5, 1: 234. 1849. -- *Blechnum falciforme* (Liebm.) C.Chr., Index Filic. 154. 1905.
20. ***Parablechnum gemmascens* (Alston) Gasper & Salino, comb. nov.** -- *Blechnum gemmascens* Alston, Bull. Jard. Bot. État 27: 57, f. 4. 1957.
21. ***Parablechnum glaziovii* (Christ) Gasper & Salino, comb. nov.** -- *Blechnum glaziovii* Christ, Annuaire Conserv. Jard. Bot. Genève 3: 42. 1899.
22. ***Parablechnum gregsonii* (Tindale) Gasper & Salino, comb. nov.** -- *Blechnum gregsonii* Tindale, Proc. Linn. Soc. New South Wales 85: 253. 1960.
23. ***Parablechnum hieronymi* (Brause) Gasper & Salino, comb. nov.** -- *Blechnum hieronymi* Brause, Bot. Jahrb. Syst. 56: 155. 1920.
24. ***Parablechnum howeanum* (T.C.Chambers & P.A.Farrant) Gasper & Salino, comb. nov.** -- *Blechnum howeanum* T.C.Chambers & P.A.Farrant, Telopea 5: 331. 1993.

25. ***Parablechnum lechleri* (Mett.) Gasper & Salino, comb. nov.** -- *Blechnum lechleri* Mett., Fil. Lechl. 2: 17. 1859.
26. ***Parablechnum lima* (Rosenst.) Gasper & Salino, comb. nov.** -- *Blechnum lima* Rosenst., Repert. Spec. Nov. Regni Veg. 11: 53. 1912.
27. ***Parablechnum lineatum* (Sw.) Gasper & Salino, comb. nov.** -- *Osmunda lineata* Sw., Prodr. 127. 1788. -- *Blechnum lineatum* (Sw.) C.Chr., Index Filic. 156. 1905.
28. ***Parablechnum loxense* (Kunth) Gasper & Salino, comb. nov.** -- *Lomaria loxensis* Kunth, Nov. Gen. Sp. (quarto ed.) 1: 18-19. 1815[1816]. -- *Blechnum loxense* (Kunth) Hook. ex Salomon, Nomencl. Gefässkrypt. 117. 1883.
29. ***Parablechnum loxense* (Kunth) Gasper & Salino var. *stenophyllum* (Klotzsch) Gasper & Salino, comb. nov.** -- *Lomaria stenophylla* Klotzsch, Linnaea 20: 346. 1847. -- *Blechnum loxense* var. *stenophyllum* (Klotzsch) Lellinger, Amer. Fern J. 93: 147. 2003.
30. ***Parablechnum marginatum* (Kuhn) Gasper & Salino, comb. nov.** -- *Lomaria marginata* Fée, Mém. Foug. 5: 71. 1852, non *L. marginata* Schrad., 1824. -- *Blechnum marginatum* Kuhn, Filic. Afr. 92. 1868. -- *Blechnum montbrisonis* C.Chr., Index Filic. 157. 1905.
31. ***Parablechnum marginatum* (Kuhn) Gasper & Salino var. *humbertii* (Tardieu) Gasper & Salino, comb. nov.** -- *Blechnum humbertii* Tardieu, Mém. Inst. Sci. Madagascar, sér. B, Biol. Vég. 6: 232, f. 5. 1955. -- *Blechnum montbrisonis* var. *humbertii* (Tardieu) Rakotondr., Adansonia, sér. 3, 35: 178. 2013.
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33. ***Parablechnum minus* (R.Br.) Gasper & Salino, comb. nov.** -- *Stegania minor* R.Br., Prodr. 1: 153. 1810. -- *Blechnum minus* (R.Br.) Ettingsh., Denkschr. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl. 23: 63, t. 8, f. 5, 12. 1864.

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37. *Parablechnum nesophilum* (T.C.Chambers & P.A.Farrant) Gasper & Salino, *comb. nov.* -- *Blechnum nesophilum* T.C.Chambers & P.A.Farrant, *Blumea* 46: 322. 2001.
38. *Parablechnum novae-zelandiae* (T.C.Chambers & P.A.Farrant) Gasper & Salino, *comb. nov.* -- *Blechnum novae-zelandiae* T.C.Chambers & P.A.Farrant, *New Zealand J. Bot.* 36: 8. 1998.
39. *Parablechnum obtusum* (R.C.Moran & A.R.Sm.) Gasper & Salino, *comb. nov.* - *Blechnum obtusum* R.C. Moran & A.R. Sm., *Brittonia* 57: 237. 2005.
40. *Parablechnum pacificum* (Lorence & A.R.Sm.) Gasper & Salino, *comb. nov.* -- *Blechnum pacificum* Lorence & A.R. Sm., *PhytoKeys* 4: 8, figs. 1-2, 14A. 2011.
41. *Parablechnum pazense* (M.Kessler & A.R.Sm.) Gasper & Salino, *comb. nov.* -- *Blechnum pazense* M. Kessler & A.R. Sm., *Amer. Fern J.* 97: 73. 2007.
42. *Parablechnum procerum* (G.Forst.) C.Presl, *Epimel. Bot.* 109. 1851. -- *Osmunda procera* G. Forst., *Fl. Ins. Austr.* 414. 1786. -- *Blechnum procerum* (G. Forst.) Sw., *J. Bot. (Schrader)* 1800(2): 75. 1801.
43. *Parablechnum proliferum* (Rosenst.) Gasper & Salino, *comb. nov.* -- *Blechnum proliferum* Rosenst., *Hedwigia* 46: 91. 1906.

44. ***Parablechnum puniceum* (T.C.Chambers, P.J.Edwards & R.J.Johns) Gasper & Salino, *comb. nov.*** -- *Blechnum puniceum* T.C.Chambers, P.J.Edwards & R.J.Johns, Kew Bull. 60: 598, figs. 1-2. 2006.
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49. ***Parablechnum ryanii* (Kaulf.) Gasper & Salino, *comb. nov.*** -- *Lomaria ryanii* Kaulf., Enum. Filic. 155. 1824. -- *Blechnum ryanii* Hieron., Hedwigia 47: 245. 1908.
50. ***Parablechnum schiedeanum* (Schltdl. ex C.Presl) Gasper & Salino, *comb. nov.*** - *Blechnum schiedeanum* (Schltdl. ex C.Presl) Hieron., Hedwigia 47: 239. 1908.
51. ***Parablechnum sessilifolium* (Klotzsch ex Christ) Gasper & Salino, *comb. nov.*** -- *Lomaria sessilifolia* Klotzsch ex Christ, Bull. Herb. Boissier, sér. 2, 4: 1092. 1904. -- *Blechnum sessilifolium* (Klotzsch ex Christ) C.Chr., Index Filic. 159. 1905.
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53. ***Parablechnum squamatum* (M.Kessler & A.R.Sm.) Gasper & Salino, *comb. nov.*** -- *Blechnum squamatum* M.Kessler & A.R.Sm., Amer. Fern J. 97: 78. 2007.

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56. ***Parablechnum stuebelii* (Hieron.) Gasper & Salino, comb. nov.** -- *Blechnum stuebelii* Hieron., Hedwigia 47: 241, pl. 4, fig. 14. 1908, as "*stübelii*".
57. ***Parablechnum subcordatum* (E.Fourn.) Gasper & Salino, comb. nov.** -- *Lomaria subcordata* E.Fourn., Ann. Sci. Nat. Bot., sér. 5, 18: 316. 1873. -- *Blechnum subcordatum* (E.Fourn.) Brownlie, Fl. Nouv.-Calédonie & Dépend. 3: 248, t. 32, f. 1-2. 1969.
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60. ***Parablechnum usterianum* (Christ) Gasper & Salino, comb. nov.** -- *Lomaria usteriana* Christ, Fl. Umgebung São Paulo 135. 1911. -- *Blechnum usterianum* (Christ) C.Chr., Index Filic., Suppl. 2, 8. 1917.
61. ***Parablechnum venosum* (Copel.) Gasper & Salino, comb. nov.** -- *Blechnum venosum* Copel., Occas. Pap. Bernice Pauahi Bishop Mus. 14: 62. 1938.
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65. *Parablechnum wurunuran* (Parris) Gasper & Salino, *comb. nov.* -- *Blechnum wurunuran* Parris, Proc. Roy. Soc. Queensland 86: 157. 1975.

Sadleria Kaulf., Enum. Filic. 161. 1824. -- **Type:** *Sadleria cyatheoides* Kaulf., Enum. Filic. 161. 1824.

Plants terrestrial, epipetric in *S. squarrosa*; **rhizomes** erect, subarborescent, non-stoloniferous, stout, bearing brown, linear-acuminate or lanceolate scales, these entire or minutely toothed or ciliolate at the margins; **fronds** monomorphic; **stipes** stout, long, stramineous or darkened, with filiform brown scales proximally, glabrous or glabrescent distally; **blades** concolorous, lanceolate to elliptic, pinnate-pinnatifid or bipinnate, apices pinnatifid; **rachises** scaly, sometimes with glandular hairs, glabrous or glabrescent; **buds** absent; **aerophores** absent; **pinnae** sessile or short-stipitate, with segments falcate to obtuse, subentire to crenate; **veins** furcate near the costa, uniting to form a pericostal arch, ending in hydathodes; **sori** linear, continuous over vein arches, indusia continuous or not, sometimes glandular; $x = 33$. Figure 4H; 7E.

Species number, comments, and distribution: About six species, endemic to Hawaii.

The trunk-like rhizomes, pinnate-pinnatifid or bipinnate blades, and brown, linear-acuminate or lanceolate rhizome scales are typically present in species of this genus.

1. *Sadleria cyatheoides* Kaulf., Enum. Filic. 162. 1824.

2. *Sadleria pallida* Hook. & Arn., Bot. Beech. Voy. 75, 171. 1832.

3. *Sadleria souleyetiana* (Gaudich.) T.Moore, Index Fil. 26. 1857. -- *Blechnum souleyetianum* Gaudich., Voy. Bonite Bot. 134, t. 2, fig. 7-8. 1846.

4. *Sadleria squarrosa* (Gaudich.) T.Moore, Index Fil. 26. 1857. -- *Blechnum squarrosus* Gaudich., Voy. Bonite Bot. 42, t. 2, fig. 1-6. 1854.
5. *Sadleria unisora* (Baker) W.J.Rob., Bull. Torrey Bot. Club 40: 227. 1913. -- *Polypodium unisorum* Baker, in Hooker & Baker, Synops. Fil. 307. 1867.
6. *Sadleria wagneriana* D.D.Palmer & Flynn, Pacific Sci. 51: 302. 1997.

Struthiopteris Scop., Meth. Pl. 25. 1754. -- *Spicanta* C.Presl 114. 1851, nom. superfl. --

Type: *Struthiopteris spicant* (L.) F.W. Weiss., Pl. Crypt. Fl. Gott. 287. 1770.

Homophyllum Merino, Ann. Soc. Hist. Nat. 1898: 108. -- Type: *Homophyllum blechniforme* Merino [= *Blechnum spicant* (L.) Roth] = *Struthiopteris spicant* (L.) F.W. Weiss

Spicantopsis Nakai, Bot. Mag. (Tokyo) 47: 180. 1933. -- Type: *Spicantopsis niponica* (Kunze) Nakai, based on *Lomaria niponica* Kunze [= *Blechnum niponicum* (Kunze) Makino]

Plants terrestrial; **rhizomes** short-creeping or elongate, non-stoloniferous, stout, clothed by brown to dark brown, linear, lanceolate, or ovate-lanceolate, entire or sparingly toothed scales; **fronds** dimorphic or subdimorphic (*S. amabilis*); **stipes** slender, short, stramineous or dark purplish, scaly proximally, glabrous distally; **blades** concolorous, oblanceolate or lanceolate, pinnate to pinnatifid, very gradually reduced proximally to auricles, apices pinnatifid; **rachises** with a few filiform scales or glabrous; **buds** absent; **aerophores** absent; **pinnae** adnate, oblong-linear to linear-falcate, margins entire; **veins** free, inconspicuous, furcate, ending in submarginal hydathodes adaxially; **sori** linear, on both sides of costae, indusia linear, continuous or not, entire, usually enveloping sporangia at maturity; $x = 31, 34$. Figure 4I; 7F.

Species number, comments, and distribution: Five temperate species, mostly from China

and Japan, with *S. spicant* having a circumboreal distribution. Characterized by the subdimorphic to dimorphic fronds, adnate pinnae, free veins, and veins ending in submarginal hydathodes.

1. *Struthiopteris amabilis* (Makino) Ching, Sunyatsenia 5: 243. 1940. -- *Blechnum amabile* Makino, Bot. Mag. (Tokyo) 11: 83. 1897.
2. *Struthiopteris castanea* (Makino & Nemoto) Nakai, Bot. Mag. (Tokyo) 47: 186. 1933. -- *Lomaria castanea* Makino, Bot. Mag. (Tokyo) 6(60): 45. 1892, nom. nud. -- *Blechnum castaneum* Makino & Nemoto, Fl. Japan 1591. 1925.
3. *Struthiopteris hancockii* (Hance) Tagawa, Acta Phytotax. Geobot. 14: 192. 1952. -- *Blechnum hancockii* Hance, J. Bot. 21: 267. 1883.
4. *Struthiopteris niponica* (Kunze) Nakai, Report Veg. Daisetsusan 15. 1930. -- *Lomaria niponica* Kunze, Bot. Zeitung (Berlin) 6: 508. 1848. -- *Blechnum niponicum* Makino, Bot. Mag. (Tokyo) 11: 82. 1897, as “*nipponicum*”
5. *Struthiopteris spicant* (L.) F.W.Weiss, Pl. Crypt. Fl. Gott. 287. 1770. -- *Blechnum spicant* (L.) Sm., Mém. Acad. Roy. Sci. Turin 5: 411. 1793.

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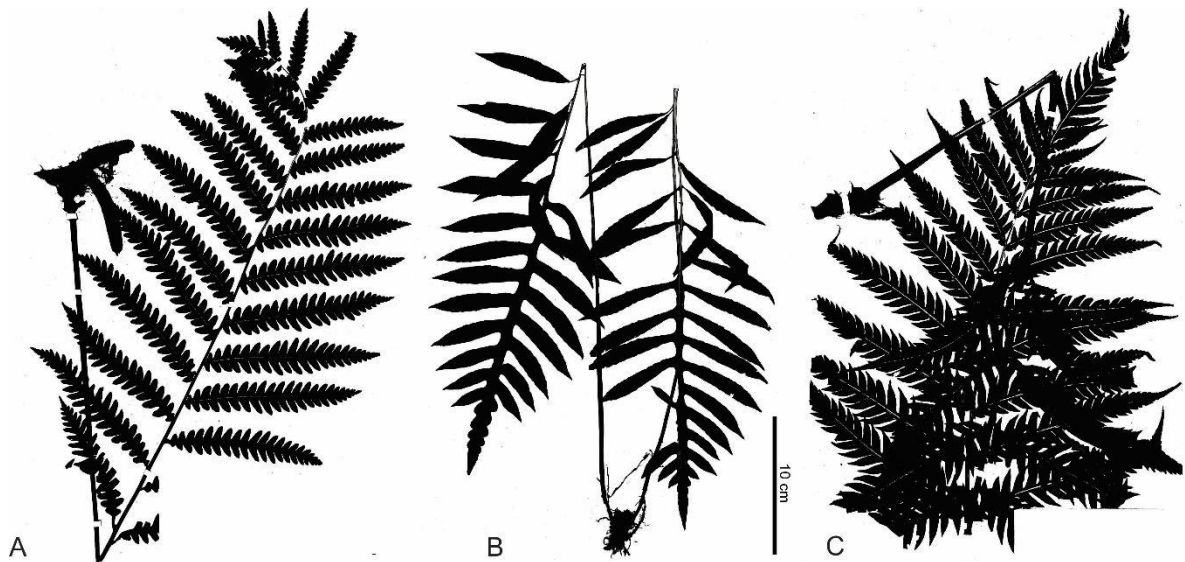


FIGURE 1. General appearance of the three genera of Blechnaceae subfamily Woodwardioideae. A: *Anchistea virginica* (P01513597); B: *Lorinseria areolata* (P01509531), C: *Woodwardia spinulosa* (P01557309). Vouchers are indicated by herbarium barcodes. Herbarium abbreviations according Thiers (2015).

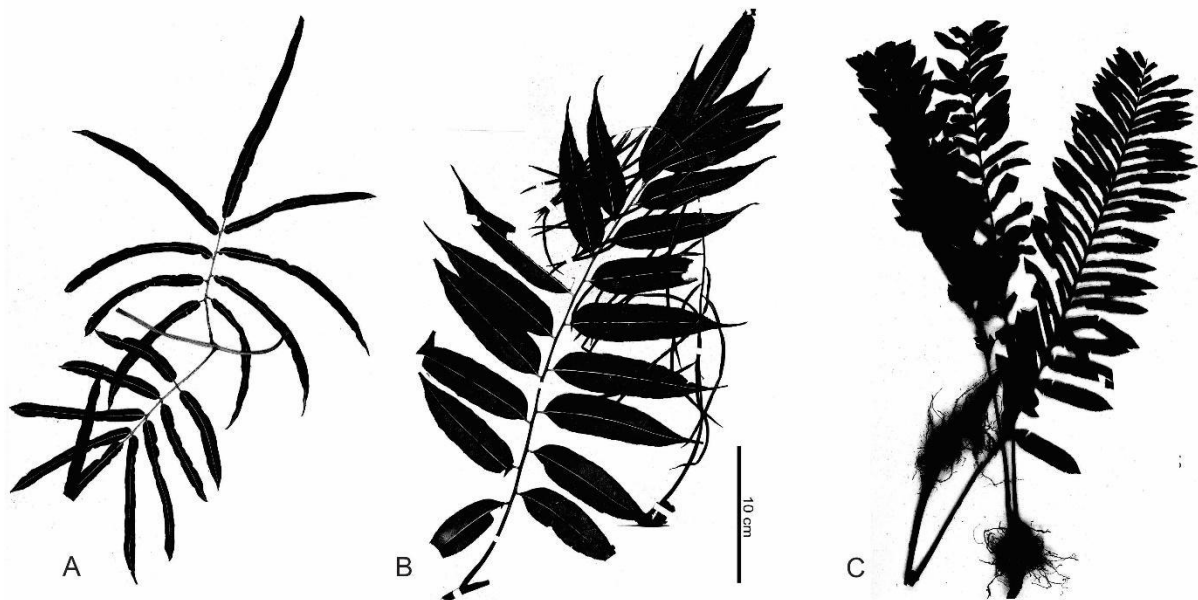


FIGURE 2. General appearance of the three genera of Blechnaceae subfamily Stenochlaenoideae. A: *Salpichlaena volubilis* (MO3588318); B: *Stenochlaena scandens* (P01420182); C: *Telmatoblechnum serrulatum* (MO2003917). Vouchers are indicated by herbarium barcodes. Herbarium abbreviations according Thiers (2015).

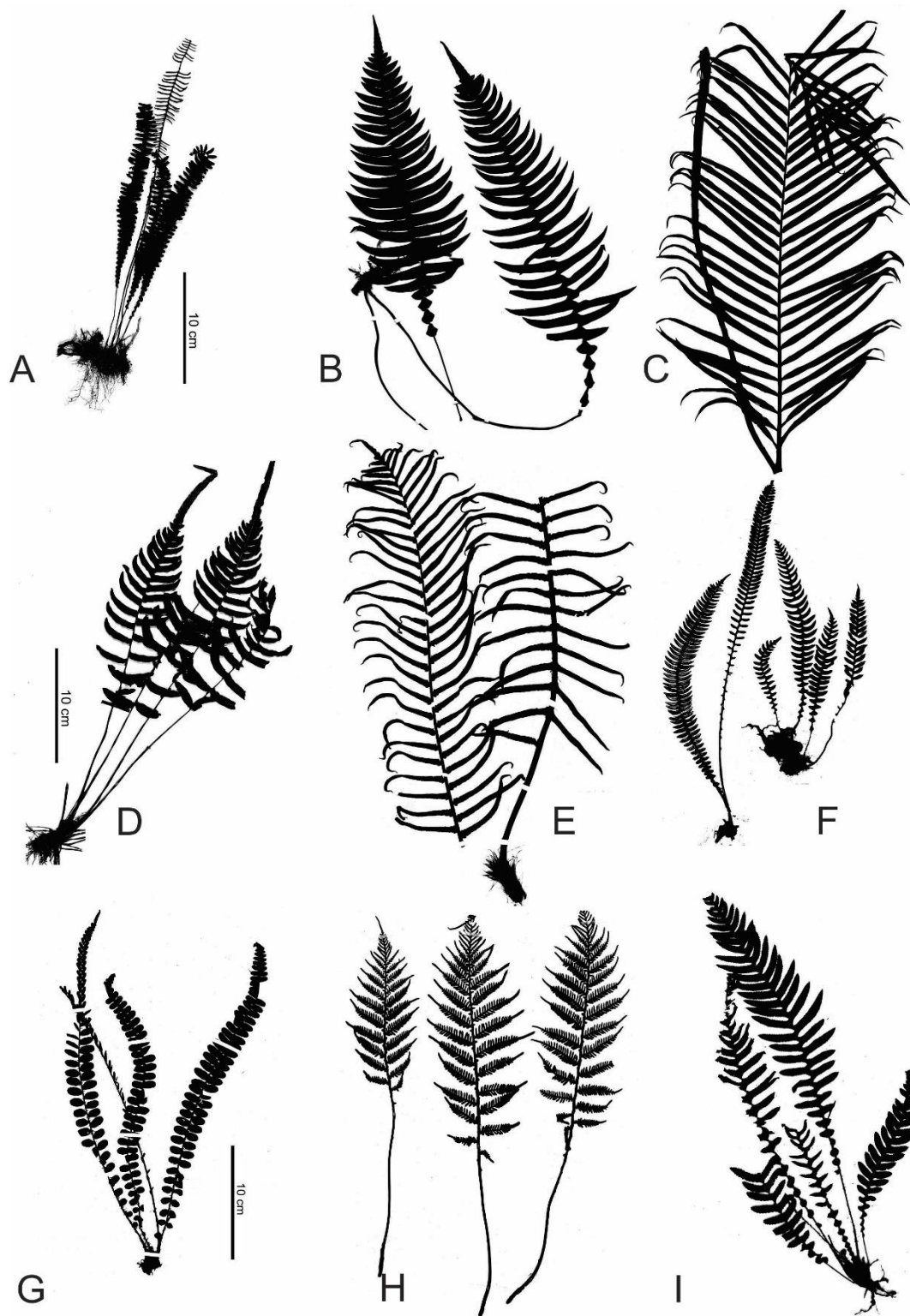


FIGURE 3. General appearance of the genera of Blechnaceae subfamily Blechnoideae (A-D). A: *Austroblechnum penna-marina* (FURB06706); B: *Blechnidium melanopus* (P02439094); C: *Blechnopsis orientalis* (P01406555); D: *Blechnum occidentale* (FURB06701); E: *Brainea insignis* (P01482127); F: *Cleistoblechnum eburneum* (P00627565); G: *Cranfillia fluviatilis* (P01606472); H: *Diploblechnum fraseri* (P01557366); I: *Doodia aspera* (P01618184). Vouchers are indicated by herbarium barcodes. Herbarium abbreviations according Thiers (2015).

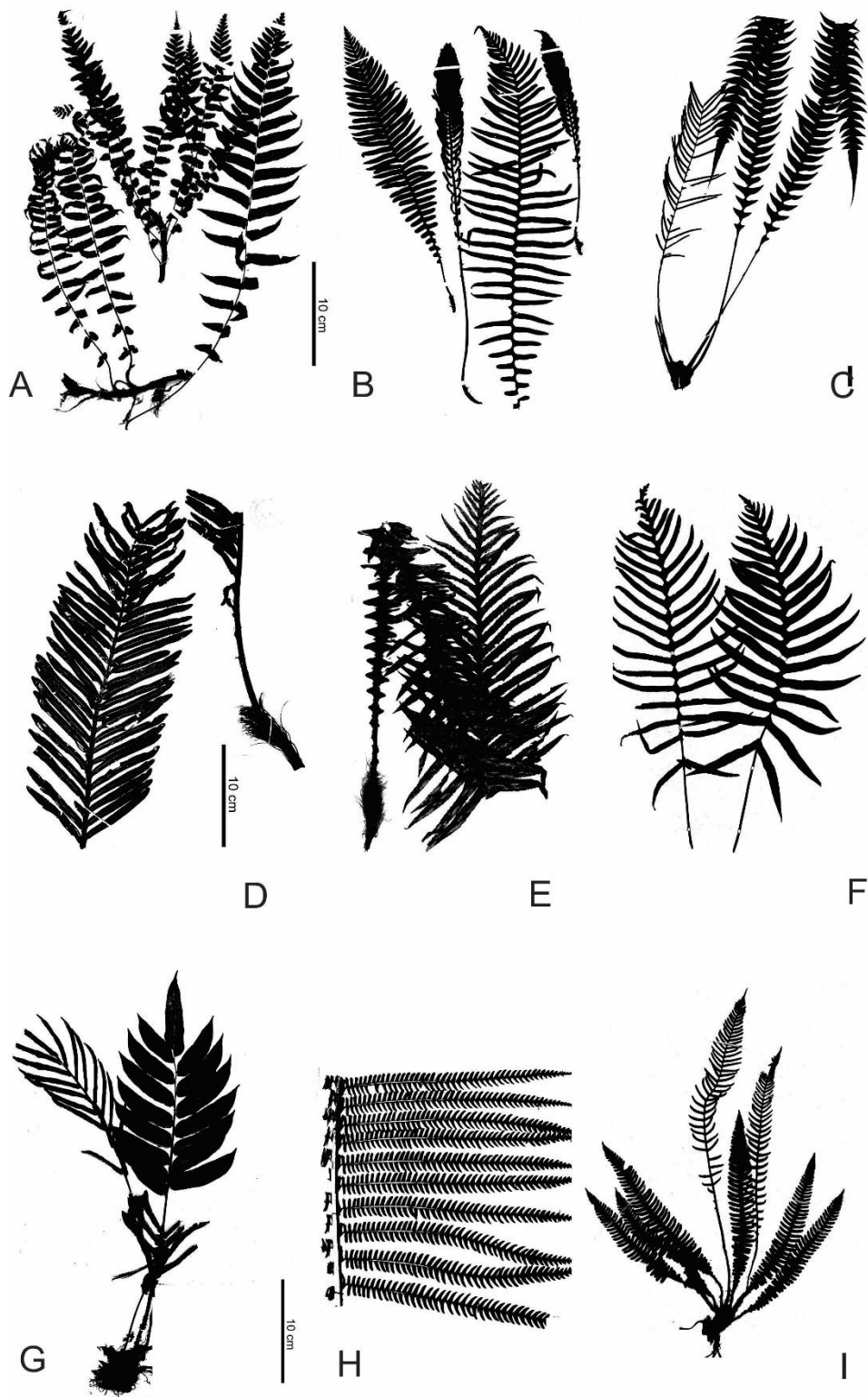


FIGURE 4. General appearance of the genera of Blechnaceae subfamily Blechnoideae (G-S). A: *Icarus filiformis* (WELT P009478); B: *Lomaria nuda* (P01557820); C: *Lomaridium fragile* (MEXU 149093); D: *Lomariocycas aurata* (QCA7004842); E: *Neoblechnum brasiliense* (FURB06585); F: *Oceanopteris cartilaginea* (P01630912). G: *Parablechnum cordatum* (FURB06639); H: *Sadleria pallida* (MEXU 956078); I: *Struthiopteris spicant* (P01658104); I: Vouchers are indicated by herbarium barcodes. Herbarium abbreviations according Thiers (2015).

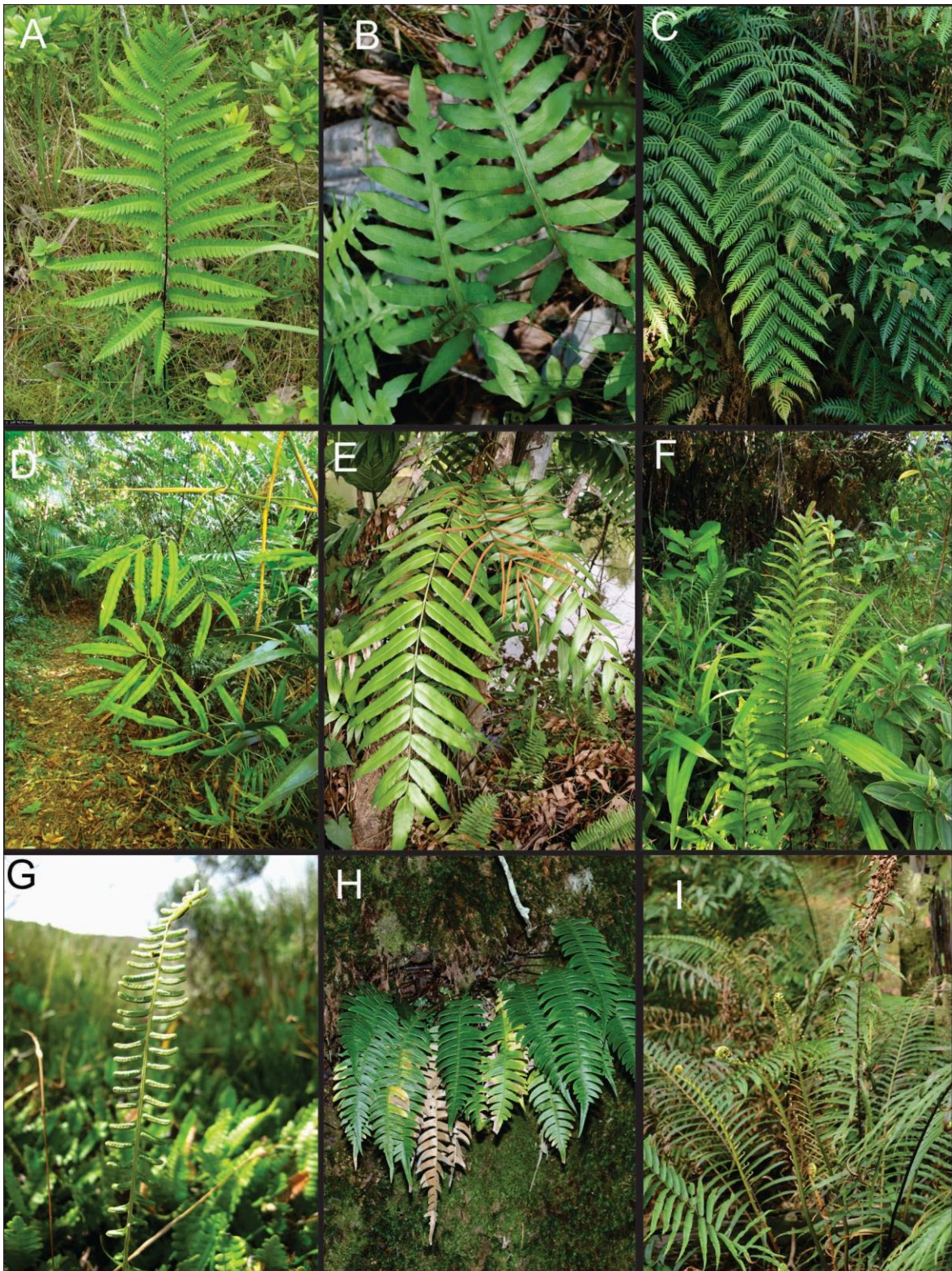


FIGURE 5. Habitat of Blechnaceae genera. A: *Anchistea virginica*; B: *Lorinseria areolata*; C: *Woodwardia unigemmata*; D: *Salpichalena volubilis*; E: *Stenochlaena milnei*; F: *Telmatoblechnum serrulatum*; G: *Austroblechnum penna-marina*; H: *Blechnidium melanopus*; I: *Blechnopsis orientalis*. Photos from: A: The PLANTS Database, USDA, NRCS. 2016; B: James Van Kley; C: Ralf Knap; D: Luis Adriano Funez; E: Julie F. Barcelona; F: Luis Adriano Funez; G: Vinícius A.O. Dittrich; H: Ralf Knap; I: Ralf Knap.

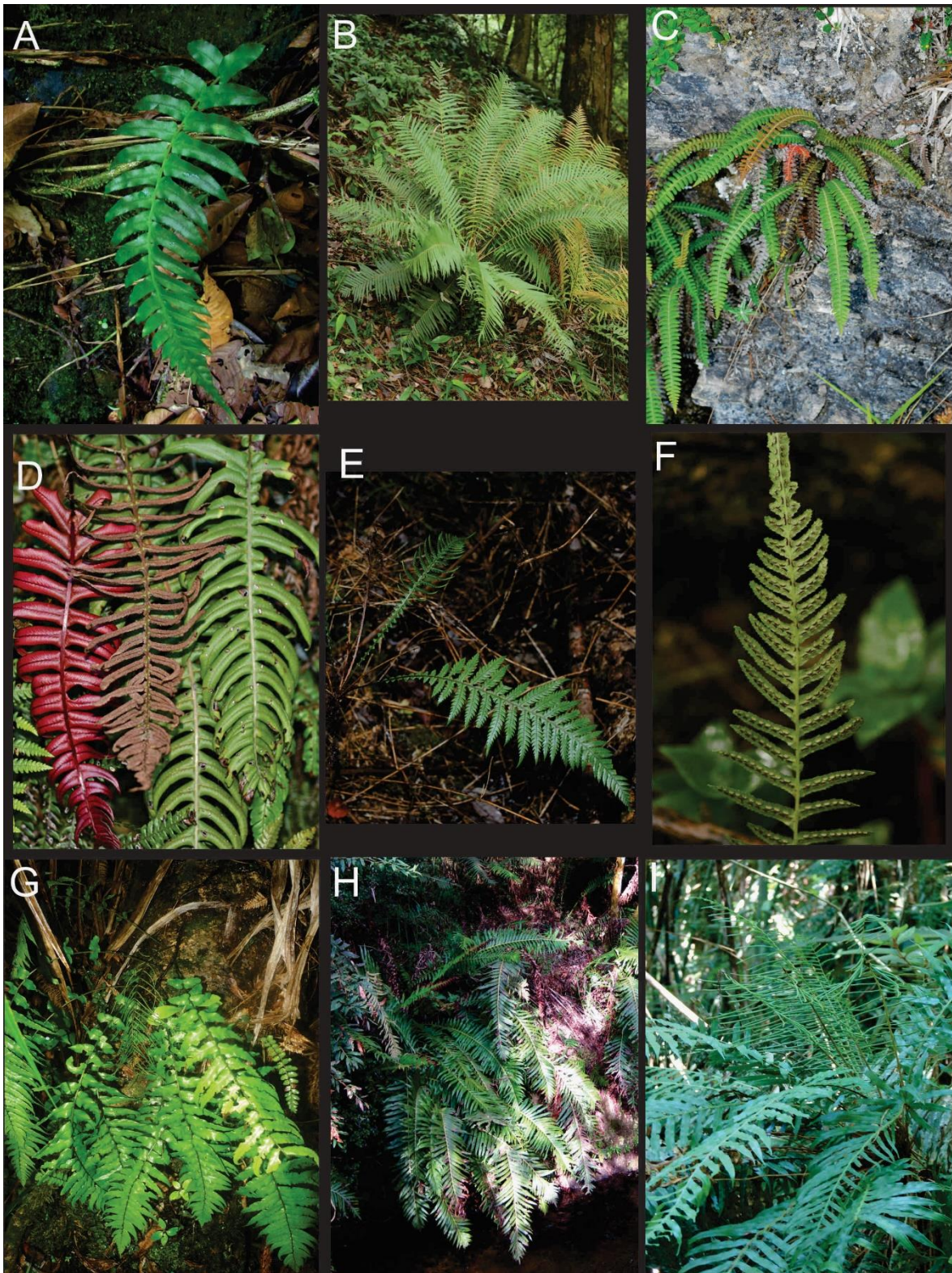


FIGURE 6. Habitat of Blechnaceae genera. A: *Blechnum occidentale*; B: *Brainea insignis*; C: *Cleistoblechnum eburneum*. D: *Cranfillia vulcanica*; E: *Diploblechnum fraserii*; F: *Doodia caudata*; G: *Icarus filiformis*; H: *Lomaria spannagelii*; I: *Lomaridium acutum*; Photos from: A: Luis Adriano Funez; B: Ralf Knap; C: Ralf Knap; D: Julie F. Barcelona; E: Michael Sundue; F: Paulo Araújo; G: WELT herbarium; H: Vinícius A.O. Dittrich; I: Tiago João Cadorin.



FIGURE 7. Habitat of Blechnaceae genera. A: *Lomariocycas schomburkii*. B: *Neoblechnum brasiliense*; C: *Oceanopteris gibba*; D: *Parablechnum glaziovii*; E: *Sadleria cyatheoides*; F: *Struthiopteris spicant*; F: Photos from: A-B: Luis Adriano Funez; C: Vojtěch Zavadil; D: Vinícius A.O. Dittrich; E: Kit Herring; F: Ralf Knap.

CONCLUSÕES GERAIS

A nova proposta de classificação aqui apresentada é resultado de uma ampla amostragem de espécies na análise filogenética. Foram amostradas 60 espécies de ocorrência neotropical, a maior amostragem até então efetuada para a família, dum total estimado de aproximadamente 83 espécies (Rolleri and Prada, 2006). Além disso, a amostragem de todas as espécies tipo possibilitou a tomada de decisões quanto a segregação ou não dos gêneros.

Além das espécies neotropicais, praticamente inexistentes em análises anteriores ou com poucas espécies e marcadores (Gabriel y Galán *et al.*, 2013; Perrie *et al.*, 2014), uma espécie de controversa foi amostrada, *Blechnidium melanopus* (Hook.) T. Moore, descartando definitivamente a possibilidade de tratar-se de uma espécie de *Blechnum*, confirmando as afirmações de Wang *et al.* (2013). Algumas espécies mostraram posicionamento inicial interessante, como o caso de *Lomaria spannagelii*, considerada por muitos como sinônimo de *Lamariocycas tabulare* (Rolleri and Prada, 2006), mas aqui tratada em um gênero distinto.

Diante do resultado apresentado pelas análises de inferência filogenética duas opções poderiam ser seguidas. 1) a inclusão de *Brainea* e *Sadleria* em *Blechnum*, ou 2) a segregação dos clados recuperados nas análises. Optou-se pela segunda opção, pois a primeira deixaria o gênero *Blechnum* sem identidade morfológica, com ampla variação de caracteres, desde o tipo de rizoma, que poderia ser curto, logo, ereto ou até formando cáudices, ao padrão de nervação, parcialmente anastomosado a livre, além dos números cromossômicos muitos díspares, que auxiliou na delimitação dos gêneros.

Apensar do reconhecimento final de 24 gêneros em Blechnaceae parecer um número muito elevado, cabe destacar que, nos últimos anos, vários gêneros têm sido segregados como o caso de *Polypodium* L. em *Serpocaulon* AR Sm. (Smith *et al.*, 2006b), *Campyloneurum* C. Presl, *Pecluma* M.G. Price etc.; do grupo gramitidoide [Polypodiaceae - Hirai *et al.* (2011), Kessler *et al.* (2011)], a segregação de numerosos gêneros no grupo cheilantoide (Pteridaceae): *Gaga* Pryer *et al.* (Li *et al.*, 2012); *Myriopteris* Fée; *Doryopteris* J. Sm etc.; e o mais recente reconhecimento de diversas linhagens de *Thelypteris* Schmidel *lato sensu* (Almeida *et al.*, 2016), todos casos similares a este. Gêneros menores, tem forte suporte morfológico e molecular, são mais fáceis de estudar, permitem o reconhecimento de padrões fitogeográficos, esclarecem relacionamentos, e apontam para outros caminhos interessantes de pesquisa, envolvendo evolução de caracteres, número cromossômico, biologia reprodutiva, questões ecológicas e permite a realização de monografias.

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