UNIVERSIDAD COMPLUTENSE DE MADRID

FACULTAD DE CIENCIAS BIOLÓGICAS

TESIS DOCTORAL

Sinopsis global y aproximación a la filogenia molecular del género *Parablechnum* C.Presl (Blechnaceae, Polypodiopsida)

A global synopsis and molecular phylogenetic approach of the genus *Parablechnum* C.Presl (Blechnaceae, Polypodiopsida)

MEMORIA PARA OPTAR AL GRADO DE DOCTOR

PRESENTADA POR

Sonia Molino de Miguel

Directores

Rafael Medina Bujalance
Weston Testo
María Vicent Fernández

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Madrid, 2022

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Los corderos baladores
van en grupos triscadores
asaltando los repechos,
coronando los cerrillos
y brincando los helechos.

J.M. Gabriel y Galán.

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Nothing in Biology makes sense except in the light of Evolution.

T. Dobzhansky

That you are here—that life exists and identity. That the powerful play goes on, and you may contribute a verse.

W. Whitman

1. ABSTRACT

Abstract

The family Blechnaceae is a lineage that includes about 280 species in 25 genera, and together with the Onocleaceae is the most recent family of ferns. Within this family, *Parablechnum* is the most diverse genus, with about 65 species. The distribution of this genus reflects very well the distribution of the most diverse areas of the family: Central and South America, the Austropacific and some representatives in southern Africa, Madagascar and the Mascarene archipelago.

The distribution of this genus reflects a disjunction that could easily be explained by Gondwanan vicariance, but the available dating indicates that the genus underwent a rapid radiation after the separation from Gondwana, which would imply that its distribution is due to long-distance dispersal (LDD). In addition, the intra-continental dispersal of the genus together with other problems such as poor representation in herbaria has made the taxonomy of *Parablechnum* unclear to date.

In this context, a revision of the systematics of the genus has been proposed using herbarium material and some field collections to elucidate the taxonomy and evolutionary history of the genus.

For this purpose, 3,738 specimens from 52 herbariums of all the species of *Parablechnum* conceived to date have been examined physically and digitally. Where possible, the anatomy of the fertile pinnae and epidermis was studied, and spores and sporangia were observed by light and electron microscopy. In addition, DNA was extracted from 127 individuals and five chloroplastic markers were sequenced for maximum likelihood phylogenetic trees and Bayesian inference. In addition, a dating have been carried out. For this purpose, 582 sequences were used, 469 of which were newly created in this work.

The anatomical results have shown cross-sections with relatively constant characteristics in the genus, showing variations in receptacle length, complexity, epidermal pattern and margin of the indusia, monomorphy of the fronds and curvature of the margin. Likewise, we show as a novelty the characterization of the parasagittal

sections for Parablechnum, which show congruence with some of the classical hypotheses of the arrangement of veins in the family.

Spore ornamentation has shown variation that has allowed the characterisation of five morphological groups based on the formation of folds in the perisporium and the arrangement of these and the presence of filamentous processes. Sporangia have also been characterised and the presence of paraphyses and sporangiasters have been detected in several Austropacific species, structures that had been overlooked to date.

The phylogeny shows that *Parablechnum* is a monophyletic genus, with the species *P. articulatum* being the sister to all other species in the genus. However, the resolution of all trees has been generally low, with only three more or less well-supported clades detected in the different phylogenies, with a backbone forming a large polytomy. One of the clades shows geographic structure, but the other two show a mixture of taxa from all centres of diversity of the genus, so that the previous conception of an American and an Austropacific clade is ruled out. This lack of resolution is related to unexplored cryptic diversity in *Parablechnum*, polyploidy and hybridisation processes, and rapid radiation in the Americas.

On the other hand, the dating shows an origin of the genus approximately 38 million years ago, which would indicate that the genus has reached its global distribution by LDD events. Likewise, it shows a diversification in America with several cladogenesis events in the Late Miocene, coinciding with the rise of the Andes, which could explain the rapid American radiation.

All morpho-anatomical data have allowed the generation of a taxonomic synopsis of the genus that begins with the first global identification key for the genus Parablechnum and continues with detailed descriptions of its component species, as well as distribution and habitat data. Sixty-eight species are considered in this treatment.

The diversity and evolutionary history of *Parablechnum* is thus unresolved, and this work provides an unprecedented starting point for the study of the genus. The morphoanatomical data presented here combined with genomic techniques that can be applied in the future will serve to resolve the real diversity of *Parablechnum*, which is likely to be greater than previously thought.

Resumen

La familia Blechnaceae es un linaje que incluye unas 280 especies en 25 géneros, y junto con las Onocleaceae es la familia más reciente de helechos. Dentro de esta familia, *Parablechnum* es el género más diverso, con alrededor de 65 especies. La distribución de este género refleja muy bien la distribución de los puntos más diversos de la familia: América Central y del Sur, el Austropacífico y algunos representantes en el sur de África, Madagascar y el archipiélago mascareno.

La distribución de este género refleja una disyunción que podría explicarse fácilmente por la vicarianza gondwánica, pero las dataciones disponibles indican que el género tuvo una radiación rápida tras la separación de Gondwana, lo que implicaría que su distribución se debe a la dispersión a larga distancia (LDD). Además, la dispersión dentro de los distintos continentes del género junto con otros problemas como la escasa representación en los herbarios ha hecho que la taxonomía de *Parablechnum* no esté clara hasta la fecha.

En este contexto, se ha propuesto una revisión de la sistemática del género utilizando material de herbario y algunas colecciones de campo para dilucidar la taxonomía y la historia evolutiva del género.

Para ello, se han examinado 3.738 pliegos provenientes de 52 herbarios de todas las especies concebidas hasta hoy de *Parablechnum*, de forma física y presencial. En los taxones en los que ha sido posible se ha estudiado de la anatomía de las pinnas fértiles, la epidermis y se han observado las esporas y los esporangios con microscopía óptica y electrónica. Así mismo, se ha extraído ADN de 127 individuos y se han secuenciado cinco marcadores cloroplásticos para la realización de árboles filogenéticos de máxima verosimilitud e inferencia bayesiana. Además, se ha realizado una datación. Para este fin se han utilizado 582 secuencias de las cuales 469 son de nueva creación en este trabajo.

Los resultados anatómicos han mostrado cortes transversales con características relativamente constantes en el género, mostrando variaciones en la longitud del receptáculo, la complejidad, modelo epidérmico y margen de los indusios, monomorfía de las frondas y curvatura del margen. Así mismo, mostramos como novedad la

caracterización de los cortes parasagitales para *Parablechnum*, que muestran congruencia con algunas de las hipótesis clásicas de la disposición de las venas en la familia.

La ornamentación de las esporas ha presentado una variación que ha permitido la caracterización de cinco grupos morfológicos basados en la formación de pliegues en el perisporio y la disposición de estos y la presencia de procesos filamentosos. Los esporangios también han sido caracterizados y se ha detectado la presencia de paráfisis y esporangiastros en varias especies del Austropacífico, estructuras que habían sido pasadas por alto hasta la fecha.

La filogenia muestra que *Parablechnum* es un género monofilético, siendo la especie *P. articulatum* la hermana de todas las demás especies del género. No obstante, la resolución de todos los árboles ha sido, en general, baja, habiendo podido detectar sólo tres clados más o menos bien apoyados en las diferentes filogenias, con una columna vertebral formando una gran politomía. Uno de los clados muestra estructura geográfica, pero los otros dos muestran una mezcla de taxones de todos los centros de diversidad del género, por lo que la concepción previa de un clado americano y otro austropacífico queda descartada. Esta falta de resolución se relaciona con una diversidad críptica aún sin explorar en *Parablechnum*, procesos de poliploidía e hibridación y una radiación rápida en América.

Por otra parte, la datación muestra un origen del género hace aproximadamente 38 millones de años, lo que indicaría que el género ha alcanzado su distribución global por eventos de dispersión a larga distancia. Así mismo, se muestra una diversificación en América con varios eventos de cladogénesis en el Mioceno Tardío, coincidiendo con la elevación de los Andes, lo que podría explicar la radiación rápida americana.

Todos los datos morfo-anatómicos han permitido la generación de una sinopsis taxonómica del género que comienza con la primera clave de identificación global para el género *Parablechnum* y continúa con descripciones detalladas de las especies que lo componen, así como con datos de distribución y hábitat. En este tratamiento se consideran 68 especies.

La diversidad e historia evolutiva de *Parablechnum* queda, por tanto, sin resolver, mostrando este trabajo un punto de partida para el estudio del género sin precedentes. Los

datos morfoanátomicos aquí expuestos combinados con técnicas genómicas que puedan aplicarse en el futuro servirán para resolver la diversidad real de *Parablechnum* que apunta a ser mayor de lo que se concebía hasta hoy.

2. INTRODUCTION

Taxonomy and Biodiversity crisis

Taxonomy can be defined as the science of naming and classifying all living things on the planet and is considered a key tool for conservation (Thomson *et al*., 2018). Most of the world's biodiversity is undescribed, so we are in a situation of taxonomic urgency (Wheeler, 2004; Dubois, 2010) in which we have an obligation to reduce the taxonomic gap as much as possible and to document all (or the majority) of planet Earth's biodiversity (Engel *et al.,* 2021).

However, despite being one of the most integrative disciplines within the life sciences (de Carvalho *et al*., 2008), taxonomy is in a real crisis. The discipline is often mistakenly seen as a nineteenth-century, old-fashioned science, but nothing could be further from the truth. Taxonomy follows the scientific method, is based on all kinds of characters (morphological, anatomical, behavioural, ecological, chorological, chemical...), and at the same time is an alive science, which is constantly re-evaluated and undergoes exhaustive revisions in search of the greatest possible rigour (Löbl, 2018; Engel *et al.*, 2021). However, this misperception of taxonomy is leading to fewer and fewer taxonomists, and the lack of professionals with sufficient practical and theoretical training to practise this science as well as the decline of natural history is becoming increasingly apparent (Schmidly, 2005; Tewksbury *et al.*, 2014). This situation leads to a difficult loop, in which taxonomic treatises offer their authors few citations, which in an academic system measured by impact factor is a problem, as in the end the top quartile journals reject this type of work. This ultimately makes it more difficult to get funding for taxonomic work and leads to less interest from emerging researchers.

There are some techniques that have brought a more modern approach to the study of the classification of living organisms, such as DNA studies. These revolutionary techniques are an indisputable tool in the study of living organisms, but we are gradually

running the risk that they will be used as the sole resource for the classification of living organisms. To understand the delimitation of species, their evolution, and the relationships between them, it is essential to continue using, together with the new techniques, the rest of taxonomic approaches such as morphology, anatomy, behaviour, ecology, etc. (Engel *et al.*, 2021; Meier *et al.*, 2021). Although taxonomy has been criticised for requiring expert criterion, this is also necessary in evolutionary approaches when establishing the parameters and assumptions of an evolutionary model. The truth is that as long as we recognise homologous characters as informative, we can complement information from different disciplines. At the same time, taxonomy is essential for recognising taxa *in situ*. This is useful for a more immediate understanding of biodiversity for scientific, management and/or conservation purposes. It does not matter how much molecular techniques evolve; we will always need to identify species in the field with morphological criteria (Haufler, 1996).

In this context, the most important integrative taxonomic works are monographs. Monographs are a systematic treatment of a group of organisms based on their observation in their natural habitat or in scientific collections, and with data obtained in the laboratory. Usually, these treatises cover all the taxa of a family or genus, although there are also regional monographs for a particular part of the planet. They are an indispensable resource for taxonomists and can be used as the first pillar in any work dealing with living beings, from ecology, genetics, evolutionary biology, conservation, management, physiology... (Grace *et al*., 2021). One of the great advantages of monographs is that they stimulate taxonomic rigour and the actual diversity of a group of organisms, as well as the discovery of new species, which helps to fill the problematic taxonomic gap that exists in the current biodiversity crisis (Marhold *et al*., 2013; Ripple *et al*., 2019).

Along with the decline of natural history and taxonomy, there is an increasing lack of new monographs, as difficulties in obtaining funding for such studies coupled with the arduousness of their execution enhance their abandonment, amplifying the risk of losing species before they are described, studied, and conserved (Grace *et al*., 2021). It is essential to recover and promote monographs as the first basis for the management of the planet's biodiversity (Díaz *et al*., 2019; Grace *et al.*, 2021). In fact, it is interesting and necessary to apply new techniques (phylogenetics and phylogenomics) in these works, so

that an integrative view of a group of organisms of unquestionable importance can be given (Tautz *et al*., 2003; Muñoz-Rodríguez *et al*., 2019).

We are facing an alarming decline and extinction of biodiversity, mainly due to habitat destruction (Brook *et al*., 2003). There are studies that indicate that we have entered a period of mass extinction (Myers, 1990; Cowie *et al.*, 2022), having already altered more than half of the habitable land surface for humans (Daily, 1995). It is documented that there have been at least five mass extinctions in the history of life. The difference with the present one is that, whereas past mass extinctions occurred over a period of millions of years or less, now it could occur over a period of about 200 years (Jablonski, 1991). It is predicted that up to 50% of current species will be extinct within the next 50 years (Myers, 1990; Pimm & Raven, 2000; Thomas *et al*., 2004). These extinction rates are 1,000-10,000 times greater than those inferred from the fossil record (Singh, 2002).

Estimates of the number of living species range from 2 to 100 million (May, 1988; 1992; Ehrlich & Wilson, 1991; Lambshead, 1993; Hawksworth & Kalin-Arroyo, 1995; Costello *et al.*, 2012), or even 1 billion (Larsen *et al*., 2017) or 1 trillion (Locey & Lennon, 2016). Despite May's predictions (May, 1994) that said that by 2044 we would know virtually every species on the planet, only about 1.76 million species have been described (Singh, 2002), Therefore, we can conclude that most biodiversity is currently undescribed (González-Oreja, 2008; Costello *et al*., 2013).

These data, coupled with estimates of extinction rates, tell us that we are losing species before they are even discovered.

Hence, the need to protect biodiversity has become one of the major concerns of the 21st century (Dirzo & Raven, 2003; Ceballos *et al*., 2015). However, in this panorama of biodiversity loss, only a few lineages are considered while most of the eukaryotic diversity remains ignored or even unknown (Feeley *et al*., 2016, Di Marco *et al*., 2017). In fact, some vertebrate groups such as birds account for 53% of the occurrences in GBIF, even though birds represent only 1% of the total number of species catalogued on this platform (Troudet *et al*., 2017). This is called taxonomic bias or taxonomic chauvinism, and studies show that this has been the case, with some variation, at least since the 1950s (Troudet *et al*., 2017; Bonnet *et al*., 2002).

Among many others, there has been a tendency to neglect plant organisms in comparison with animals. This is what Wandersee & Schussler (1998, 1999) defined as "plant blindness": “the inability to see plants in the environment, to recognise the importance of plants in the biosphere and human affairs, to appreciate the aesthetics and unique biological characteristics of plants and the misguided anthropocentric ranking of plants as inferior to animals and thus, as unworthy of consideration”. Other terms have been proposed for this problem as plant awareness disparity (PAD) in order to avoid ableism using “blindness” as something negative (Parsley, 2020).

This PAD can be found in many different fields as society, education (at all levels) and science (Drea, 2011; Jose *et al.*, 2019; Mayoral García-Berlanga, 2019). PAD is probably the reason why conservation initiatives are biased against plants and towards animals, especially mammals and birds (Metrick & Weizman, 1996; Martin-Lopez *et al*., 2011; Havens *et al*., 2014; Balding *et al.*, 2016). For example, when comparing protected species in Spain, it was found that animal groups such as amphibians, reptiles, mammals, and birds had 54-85% of the country's species under a state of protection, compared to 5.4% for plants, even though, for example, reptiles account for 1.3% of total biodiversity, compared to 12.5% for plants (Martínez *et al*., 2021). Even in the most conspicuous and well-studied groups of plants, such as trees, it is estimated that there are still around 9,200 species to be described, which is about 13% of the planet's tree species richness (Cazzolla Gatti *et al*., 2022). However, as can also be seen in the work of Troudet *et al*. (2017) inside each different group of organisms there are important biases, and so happens regarding terrestrial plants.

Terrestrial plants represent the largest segment of biomass on the planet (Bar-On *et al*., 2018), are the fundamental node of all biogeochemical cycles (Schimel, 1995), and a critical structural component of continental ecosystems. Therefore, in-depth knowledge of plant biodiversity, including that of the evolutionary processes and underlying patterns, is a fundamental goal of Life Sciences research. However, our knowledge of their evolutionary biology is clearly biased towards angiosperms, limiting a general perspective on plant evolution and biodiversity. For instance, since the sequencing of the first plant genome, belonging this to *Arabidopsis thaliana* Schur, many plant genomes have been sequenced, but more than the 95% are angiosperms, so our knowledge of plant evolution can be dangerously distorted (Rensing, 2017). In recent years, the need to

broaden the focus of evolutionary studies beyond flowering plants to understand plant evolution in depth is becoming apparent (Rensing, 2017; Petlewski & Li, 2019). As a result, the number of model organisms within spore-dispersed land plants (those whose fertilization is mediated by flagellated sperm cells; primarily bryophytes, lycophytes, and ferns) is expanding (e.g. One Thousand Plant Transcriptomes Initiative, 2019; Breinholt *et al*., 2021).

The application of new techniques for phylogenetic and phylogenomic studies are revealing a much more dynamic picture that goes beyond the traditional view of flagellated plants as primitive and slowly evolving organisms, demonstrating that they experience recent evolutionary radiations (e.g. Dauphin *et al*., 2018; Medina *et al*., 2018; Testo *et al*., 2019) responsible for a relevant portion of biodiversity yet to be described. Despite a dispersal capacity (spore-mediated) theoretically far superior to that of seed plants, flagellated plants are particularly vulnerable to global change (e.g. Zanatta *et al.*, 2020) and to the destruction of tropical habitats (e.g. Pouteau *et al*., 2016). Consequently, deepening the study of the evolution and diversity of ferns, the second most diverse group of vascular plants, is part of an essential ambition of the study of biodiversity. For example, studying ferns has shown us important discoveries regarding the evolution of physiological mechanisms in vascular plants such as stomata control (McAdam *et al.*, 2016), the history of shoot development and leaf evolution (Plackett *et al.*, 2015; Vasco *et al*., 2016) and symbiosis with other organisms as cyanobacteria (Li *et al.*, 2018). However, this group of plants is still neglected with respect to angiosperms. Hen, referring to the above example, in 2018 there were 236 sequenced angiosperm genomes (Chen *et al*., 2018), while only three fern genomes have been sequenced to date (Li *et al*., 2018; Huang *et al*. 2022).

We are in urgent need of continuing the exploration of plant diversity using up to date tools. Monographs informed by molecular phylogenetics constitute a long-term legacy that achieve this role.

Regarding plants, we need to fight the bias and to expand the study of plants to flagellated models to overcome biases. In this sense, ferns could constitute the “last frontier” in terms of plant systematics research.

Here we use the genus *Parablechnum* C.Presl (Blechnaceae) as a case study of plant taxonomy and systematics in a fern genus that could become a good model to overcome the above-mentioned issues.

General overview of ferns

Ferns are seedless vascular plants. There are between 12,000-15,000 fern species worldwide, which makes them the second most diverse group of vascular plants after the angiosperms (Smith, 1972; Ross, 1996; Barker & Wolf, 2010). Ferns are cosmopolitan and can be found in all types of habitats (terrestrial, epiphytic, rupicolous, aquatic...), as well as appearing on all continents except Antarctica. However, their maximum diversity is found in tropical areas, where they find the humidity and temperature conditions most favourable for their development (Salvo, 1990; Wolf *et al*., 2015). It is estimated that approximately 80% of fern diversity can be found in the tropics (Ross, 1996; Weigand *et al.*, 2020; Suissa *et al.*, 2021). They present a unique life cycle (together with lycophytes), in which there are two fully independent gametophyte and sporophyte generations (Haufler *et al*., 2016). This unique life cycle could shed light on the transition between the haploid-dominant and sporophyte-dominant life cycle models (Petlewski & Li, 2019), an issue that has been of transcendental importance in plant evolution (Gerienne & Gonez, 2011; Haufler *et al.*, 2016; Qiu *et al*., 2012).

Morphological and anatomical studies

The first generic classifications of ferns by Linnaeus (1754) were based on macromorphological characters such as shape, size, and location of sori. Later, finer characters such as stelar anatomy, venation, sporangium development, indumentum or spores started to be considered when classifying pteridophytes (Brown, 1960). It has been observed that more inconspicuous morpho-anatomical characters, what Haufler (1996) calls "cryptic morphology" are usually more informative in fern systematics. In many cases, aspects such as sporangium development, anatomy or spores have been more reliable for species delimitation than more obvious aspects such as frond shape or venation.

One of the structures that has shown the greatest taxonomic importance in ferns in the last decades are the spores. Spores are composed of three layers: the endosporium, of

cellular origin, the exosporium, of mixed origin between the cell and the sporangium, and the perisporium, originated from the sporangium mat. They can be classified into trilete (tetrahedral, with triradiate laesurae) and monolete (bilateral, with linear laesurae) (Brown, 1960). Spores, together with stomata, frequently show relevant traits to distinguish species and hybrids, as they are cells with shape and size that is constant within species and variable between species (Barrington *et al*., 1986, 2020). The ornamentation of their perispores has been a very important feature in supra- and infrageneric classifications (McVaugh, 1935; Brown, 1960; Warren & Wagner, 1974; Tryon & Lugardon, 1990).

The ontogeny of sporangia has also shown importance in the classification of ferns (Bower 1914, 1925; Copeland, 1947; Haider, 1954, Wilson 1958a, b, 1959a, b, 1960). These structures have been shown to be well conserved within species and to provide important information, although they have generally been more neglected than spores (Edwards, 1996).

Phylogeny and classification

Seedless vascular plants have two clearly distinct evolutionary lineages that share a unique life cycle: ferns and lycophytes, which have traditionally been referred to by the term pteridophytes (e.g., Kenrick & Crane, 1997; Pryer *et al*., 2001; Haufler *et al*., 2016).

For decades, the classification of pteridophytes was controversial, there being little consensus on relationships based on morphological characters (e.g., Kramer & Green, 1990). In this regard, molecular biology shed much light on this question. In the mid-1980s, the first works on the classification of ferns using molecular techniques began to appear (Stein, 1985) and expanded in the 1990s (e.g. Hasebe *et al*., 1993, 1994, 1995; Manhart, 1994; Wolf *et al.*, 1994; Wolf, 1995...). Further on, the first major classification of pteridophytes based on molecular techniques was published by Smith *et al.* (2006a), which laid a new fundamental basis for the classification of ferns and lycophytes. From this moment on, new phylogenetic works started to appear and refined the classification (e.g. Christenhusz *et al*., 2011; Rothfels *et al*., 2012a...). Hennipman (1996) proposed to create a consensus on the classification of ferns, which he provisionally called the "Scientific Consensus Classification" (SCC), which could be reviewed every five to ten years. However, this initiative was not very successful in subsequent years. Later, in 2016

the Pteridophyte Phylogeny Group (PPG I, 2016) was founded based on the consortia already formed for the classification of angiosperms (APG, 1998; APG II, 2003; APG III, 2009; APG IV, 2016). In this project, nearly 100 pteridologists proposed a consensus classification for seedless vascular plants. The PPG took into consideration all studies examining the monophyletic relationships of pteridophytes published until mid-2016. Two classes of seedless vascular plants were recognized in this work: Lycopodiopsida (lycophytes) and Polypodiopsida (ferns), the last one sister to the spermatophytes. The term pteridophyte, despite representing a paraphyletic group , is still used to refer to these two classes. In the latter, four subclasses are recognized: Equisetidae (horsetails); Ophioglossidae; Marattiidae; and Polypodiidae (leptosporangiates). Of these subclasses, the Polypodiidae contains the greatest biodiversity of ferns, with seven orders: Osmundales, Hymenophyllales, Gleicheniales, Schizaeales, Salviniales, Cyatheales, and Polypodiales. Altogether, it has been estimated that there are about 11,916 species, 337 genera, 51 families, 14 orders and 2 classes (PPGI, 2016).

This result was based on the most recent classifications for ferns at that time (e.g., Smith *et al.,* 2006a; Chase & Reveal, 2009; Christenhusz *et al*., 2011; Rothfels *et al.*, 2012a; Ruggiero *et al.,* 2015), but rejected a previous work more conservative that reduced the number of taxa recognized (Christenhusz & Chase, 2014). However, some later works completely rejected using the PPG I classification (Christenhusz & Chase, 2018; Christenhusz *et al.,* 2018). The work of Christenhusz *et al.* (2018) proposed a classification that decreased the number of genera in ferns and required an extraordinary number of nomenclatural changes: 1,107 new combinations, compared to 42 in the PPG I (Schuettpelz *et al*., 2018). The main reason why these authors decided not to follow the international convention of pteridologists proposed in the PPG I was mainly that the number of genera in ferns was too high (Christenhusz & Chase, 2018). However, in the response work carried out by Schuettpelz *et al*. (2018) it is presented how the trend of increasing numbers of fern genera since the publication of *Species Plantarum* (Linnaeus, 1754) has followed a gradual and steady increase as more information on global fern diversity has become available. In fact, the number of species per genus in other lineages of living beings such as birds, reptiles or mosses is shown to be much lower than in the case of ferns. Furthermore, the unprecedented number of nomenclatural changes presented in Christenhusz *et al*. (2018) clashes head-on with the previous desire expressed

by some of these authors for a more stable classification of ferns (Christenhusz & Chase, 2014). For all these reasons, we prefer to follow here the classification proposed by the PPG I.

Evolution and Biogeography

The origin of ferns dates to the Middle Devonian (c.a. 390 MY; Scheckler, 1974; Rothwell & Stockey, 1989). These plants acquired remarkable levels of diversity and abundance from the Carboniferous to the Jurassic, which is considerably well documented in the fossil record (Smith, 1972; Rothwell, 1996; Collinson, 1996). From this point several diversifications occurred across the globe: the first in the Carboniferous (c.a. 360 MY), resulting in six now extinct families (Röβler, 2000); the second between the upper Palaeozoic and early Mesozoic (c.a. 200 MY), with several families, some still extant, and a third at the beginning of the Cretaceous (c.a. 145 MY; Schneider *et al.*, 2004b; Tomescu *et al.*, 2006). The divergence between the present-day fern lineages took place between the Cretaceous and the Cenozoic (c.a. 145-66 MY; Taylor *et al*., 2009b; Vera, 2010). However, the amount of fossil record of seedless vascular plants drops dramatically in the Cretaceous (Lupia *et al.*, 1999; Nagalingum *et al.*, 2002; Lethtonen *et al.*, 2017). For a long time, this was linked to the emergence and rapid diversification of angiosperms (Crane, 1987; Haufler, 1996).

Nevertheless, subsequent molecular studies have shown that the most recent groups of ferns, the so-called polypoids, which comprise 80% of the current diversity diversified during the Cretaceous (Pryer *et al*., 2004; PPG I, 2016). This had gone unnoticed due to the tendency of palaeobotanical studies towards angiosperms, the epiphytic habit of many of these pteridophytes (which makes their preservation more difficult), and the excision of the spore perispores from the fossil palynological record, which makes their analysis more complicated (Schneider *et al.*, 2004b). In addition, some authors suggest that the radiation of angiosperms created new niches that had not been generated by gymnosperms, which may have favoured an opportunistic diversification of ferns and lycophytes, without losing sight of the large-scale abiotic events that may have had an influence (Wikström & Kenrick, 2001; Schneider *et al*., 2004b; Schuettpelz & Pryer, 2009; Testo & Sundue, 2016). These same studies have also shown that the nesting sequence of the current lineages of pteridophytes is as follows: osmundaceous ferns,

Hymenophyllaceae, gleichenioids, schizaeoids, aquatic ferns, tree ferns and polypods (Schneider *et al.*, 2004b).

The fact that ferns are dispersed by spores, which are much smaller structures than most seeds and therefore more easily transported by wind, has led to the idea that long-distance dispersal (LDD) is the most common colonisation strategy in ferns (Korall & Pryer, 2014), allowing the possibility of establishing new populations following a successful dispersion event of a single spore. For example, on islands there is a higher proportion of ferns to angiosperms than on mainland areas (Tryon, 1970; Smith, 1972; Kreft *et al*., 2010). Also, fern endemicity levels on islands are lower compared to angiosperms, suggesting that dispersal of pteridophytes occurs frequently enough that these populations do not become sufficiently distinct from those on the mainland (Smith, 1972; Ranker *et al*., 1994). However, many studies have shown that the biology of these plants is more complicated. For example, many diploid ferns have compulsory intergametophytic outcrossing, requiring male and female gametes to come from different gametophytes originating from spores of different sporophytes (Klekowski, 1973; Soltis & Soltis, 1987; Haufler, 2007; Haulfer *et al.*, 2016). This implies that the germination of a single spore it is not enough for the recruitment of a new population (Korall & Pryer, 2014). However, studies have shown that some ferns disperse more efficiently than seed plants.

The first divergences between the current main pteridophyte lineages occurred before the separation of the supercontinent Gondwana, approximately 145–110 MY ago (Schuettpelz & Pryer, 2009), which would support, in this case, that the first divergences and distribution patterns were explained by a scenario of Gondwanan vicariance (Dubuisson *et al*., 2003; Hennequin *et al*., 2008). Polypods diverged from their closest relatives in the Triassic, but many subgroups diverged from the Eocene onwards, after the separation from Gondwana (Schuettpelz & Pryer, 2009). In these cases, the most plausible explanation is transoceanic dispersal (Korall & Pryer, 2014).

For these reasons, when explaining the distribution and biogeographic history of a fern group we must consider both scenarios: LDD or vicariance (Wolf *et al*., 2001; Haufler, 2007), but there appear to have been events after the break-up of Gondwana that have affected the distributions we see today (Perrie *et al.*, 2007).

Comparable studies focusing on the biogeographic history of different pteridophyte clades are crucial to understanding the distribution of ferns on the planet from an evolutionary perspective, and thus to test the vicariance hypothesis against the long-distance dispersal hypothesis (Korall & Pryer, 2014). Some work of this type has already been carried out. For example, a study focused on the family Cyatheaceae showed that both types of evolutionary scenarios existed within the clade: there were lineages such as *Cyathea* Sm. and *Sphaeropteris* Bernh. that had probably acquired their current distribution by vicariance at the separation of South America and Australasia and younger ones, such as *Alsophila* R. Br., and *Gymnophaera* Blume, whose distribution was better explained by LDD (Korall & Pryer, 2004).

Similar results were found by Noben *et al*. (2017) in a study focusing on another lineage of tree ferns: the family Dicksoniaceae. The biogeography of some genera of this family, such as *Lophosoria*, could be explained by Gondwananic vicariance, as there is a fossil record from 125-50 MY However, other clades, such as *Dicksonia*, are too young to think of such an event, with LDD being more likely and suggesting that the evolutionary history of this family, as in the case of the Cyatheaceae (Korall & Pryer, 2014), is explained by a combination of vicariance and long-distance dispersal.

In conclusion, sometimes ferns are considered an ancient group with monotonous biogeography, but fern evolutionary history cannot be reconstructed based on a single narrative and they show a high number of patterns (Testo *et al.*, 2016). The Blechnaceae is an optimal study system due to morphological, phylogenetic, and biogeography, as we will discuss further on.

Family Blechnaceae

Generalities

The family Blechnaceae is a diverse lineage of leptosporangiate ferns with about 250 species (Smith *et al*., 2008). It is subcosmopolitan and has two major centres of diversity, one in Central and South America and the other in the Austropacific region, although it is also represented in cold and temperate areas of the northern hemisphere (Christenhusz *et al*., 2011; Rothfels *et al*., 2012) (**Figure 1**). It has a wide variety of growth habits, ranging from small creeping plants to large arborescent ferns. Its habitat is mainly

terrestrial, but there is also a large representation of epiphytic, saxicolous, and even one aquatic species, *Oceaniopteris francii* (Rosenst.) Gasper & Salino. Diagnostic characters to identify this family are presence of numerous conducting bundles at the base of the petiole, unlike the rest of the eupolypods II (Sundue & Rothfels, 2014), costal coenosori (sometimes discrete sori, e.g. *Doodia* R.Br. or *Woodwardia* Sm.), with a lateral indusium opening towards the costa (sometimes exindusiate, e.g. *Brainea* J.Sm.) (Kramer *et al.*, 1990; Gasper *et al.*, 2016; Moran, 2017) (**Figure 2**).

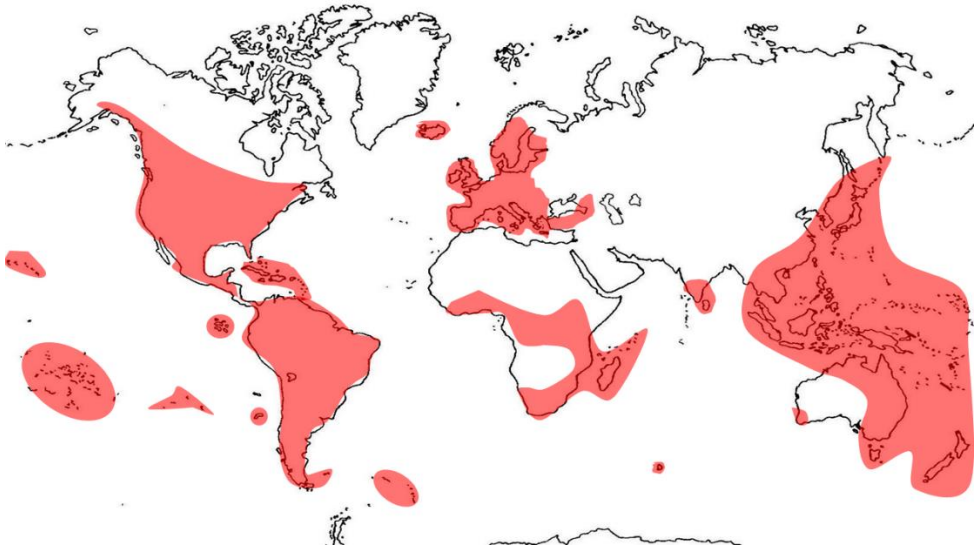

Figure 1. Global distribution of the family Blechnaceae, modified from GBIF (2022).

Some authors point out that the etymology of Blechnaceae comes from the term *bléchnon*, which was the Greek name for some ferns, synonymous with *pteris* (Castroviejo *et al.*, 1986). Other authors say that it comes from another Greek term, *blax*, which means without virtue, referring to ferns without virtues or medicinal use (Gunckel, 1984; Aguiar, 2003). The geographical, and morphological complexity of the family Blechnaceae make it a particularly interesting group in terms of phylogeny (Cranfill, 2001).

Morphology and anatomy

Genera in the family can be distinguished by some macromorphological characters such as habit, rhizome scales, dimorphism of fronds, venation and continuous or discrete sori and palynological characters (Tryon & Tryon, 1982; Gasper *et al.*, 2016; Moran *et al.*, 2018).

The anatomy of the family has attracted interest, especially the arrangement of vascular tissues in the fertile pinnae (eg. Presl, 1849; de la Sota & Gouvêa Labouriou, 1961). The first to distinguish groups within the family based on venation was Presl (1849). Since that time, the configuration of venation into trophophyles and sporophyles has been a much-studied character.

Figure 2. A. *Lomariocycas schomburgkii*, arborescent habit (Cerro de la Muerte, Costa Rica); B. *Lomaridium fragile*, epifitic habit (Monteverde, Costa Rica); C. *Neoblechnum brasiliense*, reddish fiddlehead (Cultivar, Real Jardín Botánico de Madrid, Spain); D. *Blechnum punctulatum*, saxicolous habit (Table Mountain National Park, South Africa); E. *Struthiopteris spicant*, terrestrial habit (Asturias, Spain); F. *Woodwardia radicans*, fragmented coenosori (La Palma, Spain); G. *Blechnum arcuatum*, continuous coenosori (Puyehue, Chile); H. *Anchistea virginica*, petiole cross section. Pictures: A, B & G: Jose María Gabriel y Galán; C & E: Sonia Molino; D & F: Mario Mairal; H: Michael Sundue, Vinson Doyle, and Robbin Moran.

Cranfill (2001) coined the term blechnoid veins to refer to the typical arrangement of veins in Blechnaceae, defining them as "a fertile vein deflecting from the base of the pinna or lamellar segment towards the apex". This type of fertile vein is a synapomorphy for

the whole family. Veins in Blechnaceae form areoles, as in *Brainea* or *Woodwardia*, or or free. Sometimes the receptacle may be semi-acrostichoid. Anastomosing veins have been found in the trophophylls of all woodwardioid ferns, as well as in other genera such as *Brainea* or *Blechnidium* T. Moore (Cranfill, 2001).

A study by Prada *et al*. (2016) defined the characters in cross-sections of fertile pinnae in Blechnaceae, demonstrating that these had a high diagnostic value at the generic level, which has in fact been used in subsequent publications (Molino *et al*., 2019b; Bauret *et al*., 2020).

Numerous authors have shown the importance of ontogeny and structures of the sporangia, the importance of some characters and the variation between different groups of leptosporangiate ferns such as the Blechnaceae (Bower 1914, 1925; Copeland, 1947; Haider, 1954, Wilson, 1959a). In fact, the study by Prada *et al*. (2016) demonstrated that sporangium characters were useful for differentiating taxa at the species level in the family Blechnaceae, which has been applied in several subsequent studies (Molino *et al*., 2020; Wal *et al*., 2021).

As in all other leptsporangiate ferns, spores have been an important taxonomic tool. There have been numerous studies that have focused on the description of the spores of the family Blechnaceae (Lugardon, 1965, 1974; Erdtman & Sorsa, 1971; Morbelli, 1974, 1976, 1980; Lloyd, 1976; Tryon & Tryon, 1982; Tryon & Lugardon, 1991; Ramos Giacosa *et al*., 2006, 2009; de la Sota *et al*, 2006; Passarelli, 2007), and others more recently have demonstrated the systematic importance of spore characters this family, where they have proven to be useful at genus and species level (Passarelli *et al*., 2010; Moran *et al*., 2018; Silva *et al*., 2019, 2021; Molino *et al*., 2020; Wal *et al*., 2021; Molino *et al.*, submitted). To date, all spores of the family Blechnaceae studied are monolete, as is common in Eupolypods (Moran *et al*., 2018). The spores of this family are mostly brownish, only two species have been reported with chlorophytic spores: *Lomaria nuda* (Labill.) Willd. and *Lomaria discolor* (G Forst.) Willd. (Stone, 1961; Sundue & Rothfels, 2014); no cryptochlorophytic spores have ever been reported (Sundue *et al.*, 2011).

Moran *et al*. (2018) studied the evolution of spores in this family. In this work, they deduce that the ancestral condition of the perispore in the family was that of high and wide folds, from which it changed to a non-folded perispore at least eight times

independent. On the outside of the perisporium the granular ornamentation appears to be a synapomorphy for the whole family, and the spherical deposits a synapomorphy for the subfamily Stenochlaenoideae. The subfamilies Blechnoideae and Woodwardioideae have perispores with three layers, whereas the family Stenochlaenoideae has only one. These data suggest that the ancestral state for the family is three-layered perispores, having been reduced to one in the subfamily Stenochlaenoideae. As for the exosporium, it appears that the earliest Blechnaceae had a smooth exosporium, with some genera having secondarily tuberculate, verrucate or contoured exospores.

Phylogeny and classification

The group was first mentioned about 200 years ago (Kaulfuss, 1827) based on the arrangement of sori, and was considered a natural group from its very early circumscription, and subsequently monophyletic (Kramer *et al*., 1990; Kenrick & Crane, 1997; Cranfill, 2001; Pryer *et al*., 2001; Rothfels *et al*., 2012; Schuettpelz *et al.*, 2006; Schuettpelz & Pryer, 2007, 2008; Gabriel y Galán *et al.*, 2013; Gasper *et al.*, 2016, 2017; PPG I, 2016). After this, the group was proposed as a family for the first time by Newman (1844) on the basis, again, of the position of the sori on the veins.

Bower (1925) inferred for the first time that the Onocleaceae is the closest group to the Blechnaceae family. However, it is curious that Bower inferred this relationship for reasons that turned out to be wrong. He believed the family Blechnaceae derived from a strongly dimorphic *Matteuccia*-like ancestor with *Blechnum s.l.*-like coenosori, the monomorphic species and those with discrete sori being derived from it. However, phylogenetic and cladistic studies by Cranfill (2001) and Cranfill & Kato (2003) showed that in fact it may have been the other way around: the first species to derive from a proto-blechnoid ancestor would show discrete sori and would probably be monophyletic, and the dimorphic species in the family do not form a monophyletic group but have derived independently several times. Ching (1940, 1978) related the family Blechnaceae to the onocleoid ferns and to the asplenioids, but failed to justify why, seeming rather to follow the approach of Bower (1925). Copeland (1947) defined the Blechnaceae as an isolated family distantly related to *Athyrium* Roth. He further argued that they radiated in Antarctica because of the Gondwanic distribution of *Blechnum* s.l. and *Doodia*, and that the dimorphic species arose several independent times from the monomorphic ones, being

this therefore the ancestral character. Holttum (1947, 1949) made a very detailed review in which he discussed the observations of Bower (1925). Like Copeland (1947), he considered the Blechnaceae to be an isolated family that could be derived from asplenioid ancestors. He also did not believe that dimorphism was the ancestral state and thought that the first lineage to appear was *Woodwardia*.

Pichi Sermolli (1977) was the first to publish an explicit phylogeny of the family. It was based on morphological characters and cytology. He created a specific order for the Blechnaceae (Blechnales), which he considered sister to the order Aspidiales. He based it on the fact that cytological numbers were low in Blechnales and on morphological differences, considering as primitive characters the presence of free veins, coenosori, sporangia only in the fertile vein and indusium, and as derived characters the presence of anastomosed veins, interrupted coenosori, acrosticoid sporangia and absence of indusium.

At genera level there has been several controversies. Ching (1940) considered *Doodia* to be derived from or related to *Woodwardia*, while dividing the blechnoid species into monomorphic (*Blechnum* L.) and dimorphic (*Struthiopteris* Scop.). Holtum (1949) considered *Woodwardia* to be the basal group of the family and constructed a larger genus *Blechnum* in which dimorphic and monomorphic species coexisted. Like Copeland (1947), he also considered *Doodia* to be derived from *Blechnum* and not from *Woodwardia*. The position of the genus *Salpichlaena* J. Sm. was controversial too, some authors considered part of the Blechnaceae (Copeland, 1947) and others did not (Ching, 1940). Pichi Sermolli (1977) concluded that *Stenochlaena* J. Sm. was the first to derive from a proto-blechnoid ancestor, followed by *Brainea*, and above this arose two clades: one with the *Woodwardia*-type ferns with *Doodia* and the other with *Sadleria* Kaulf., *Pteridoblechnum* Hennipman, *Salpichlaena* and *Blechnum*. It was based on chromosome numbers and the presence of discrete or continuous sori. The controversy over the relationship between *Woodwardia* and *Doodia* is solved in the studies of Cranfill (2001), where it was shown that, although both possess anastomosed veins and discrete sori, *Woodwardia* and *Doodia* are not sister genera, and these characters probably are evolutionary convergences. In fact, in other characters analysed such as habit, petiole vascular tissue, scales, frond architecture, venation patterns, sori configuration, perispore ornamentation and chromosome number, the two groups are very different. Kramer *et al*. (1990) considered nine genera in two subfamilies: Blechnoideae (*Blechnum*, *Doodia*,

Pteridoblechnum, *Sadleria*, *Salpichlaena*, *Steenisioblechnum* Hennipman and *Woodwardia*) and Stenochlaenoideae (*Stenochlaena*), and ruled out their relationship with asplenioid or athyrioid ferns. Since the 1990s, therefore, the family was always considered to consist of no more than eleven genera, of which *Blechnum* comprised about 200 species, approximately 80% of the diversity of the entire family (Kramer *et al*., 1990; Kasmirczak, 1999; Cranfill, 2001; Rothfels *et al*., 2012).

When DNA studies came into play, several molecular and morphological studies were carried out to evaluate the monophyly of clades within the family (Cranfill, 2001; Rolleri & Prada, 2006; Shepherd *et al*., 2007; Passarelli *et al*., 2010; Rolleri *et al*., 2012b, 2013; Gabriel y Galán *et al*., 2013; Perrie *et al*., 2014; Dittrich *et al*., 2015; Gasper *et al*., 2016, 2017; Molino *et al*. 2019a). The position of the family Blechnaceae within the order Aspleniineae has been confirmed by several works carried out with Sanger sequencing technology (Schuettpelz & Pryer, 2007; Kuo *et al*., 2011; Rothfels *et al*., 2012a, b), as well as by subsequent studies with high-throughput sequencing (Wei *et al*., 2017; Breinholt *et al*., 2021). The most unexpected result from molecular phylogenetics in the Blechnaceae was that the genus *Blechnum* was not monophyletic (Cranfill, 2001; Shepherd *et al*., 2007; Gabriel y Galán *et al*., 2013; Perrie *et al*., 2014). These results are not entirely surprising, as other authors have been considering the existence of different groups within *Blechnum s.l.* based on morphology, anatomy, and cytology since the 19th century. Some, such as Presl (1849), even segregated many of these groups into new genera. In fact, since Bower (1925) hypothesised on the possible matteuccioid origin of the Blechnaceae, many authors tried to form groups within the genus *Blechnum* according to whether they were dimorphic or monomorphic (e.g. Broadhurst, 1912a, b). The abovementioned molecular studies showed that there is not one clade encompassing all the dimorphic species of the family Blechnaceae and another the monomorphic ones, but there were numerous monophyletic lineages of groups of species that were entirely dimorphic.

On this basis, a new classification was published between 2016 and 2017 in which the family was restructured into 24 genera, some newly created, such as *Cranfillia* Gasper & V.A.O. Dittrich or *Oceaniopteris* Gasper & Salino, and others resurrected, such as *Parablechnum* C. Presl or *Struthiopteris* (Gasper *et al*., 2016, 2017). This new classification was accepted in the PPG I (2016). This study was followed by further

research aimed to explore and assess the diversity of the family under the new taxonomic treatment, often expanding it. For example, a study came to light that resurrected one more genus in the family Blechnaceae, the genus *Spicantopsis* Nakai, which was separated from the genus *Struthiopteris* considering morpho-anatomical and molecular results (Molino *et al*., 2019a, Molino *et al*., 2020). Likewise, several nomenclatural combinations and new descriptions have been made at the infrageneric level within the family in recent years (Bauret, 2017; Ditrich *et al*., 2017; Vicent *et al*., 2017, 2018; Smith & Kessler, 2018; Cárdenas *et al*., 2019; Chambers & Wilson, 2019; Lange & Parris 2019; Molino *et al*. 2019b; Bauret *et al*. 2020).

Currently, in summary, the family is considered monophyletic and sister to the family Onocleaceae, within the order Polypodiales and suborder Aspleniiae. Within the family, diversity is usually organised into three subfamilies: Woodwardioideae Gasper, V.A.O. Dittrich & Salino, Stenochlaenoideae J.P. Roux, and Blechnoideae Gasper, V.A.O. Dittrich & Salino, the latter concentrating most genera and species (Smith *et al*., 2006a; Rothfels *et al*., 2012; Gabriel y Galán *et al*., 2013; Perrie *et al*., 2014; Gasper *et al*., 2016, 2017; PPG1, 2016). **Figure 3** summarises the current phylogenetic landscape at the generic level.

Biogeographic history

The eupolypod II group (Aspleniineae *sensu* PPG I, 2016), which comprises approximately one-third of the total diversity of ferns (Smith *et al*., 2006a; Rothfels *et al*., 2012a; Sundue & Rothfels, 2014), is remarkable for its worldwide distribution, with species specialised to very diverse environmental conditions (Rothfels *et al*., 2012a; Sundue & Rothfels, 2014). Phylogenetic relationships within this group have been difficult to infer due to a very rapid radiation in their evolutionary history, with great heterogeneity in the rate of substitution, with respect to the rest of lineages within Pteridophyta (Rothfels *et al*., 2012b). This type of rapid radiation implies that there are few apparent synapomorphies within each clade, and thus phylogenetic analyses are difficult to interpretate (Jian *et al*., 2008). On the other hand, a heterogeneous rate such as that found in the eupolypod II clade can cause convergence between sister groups, and thus lead to erroneous inferences regarding relationships between groups with similar substitution rates (Ho & Jermin, 2004; Soubrier *et al*., 2012). All this has led to the deeper

relationships within eupolyplods II still showing some uncertainty (Rothfels *et al*., 2012b).

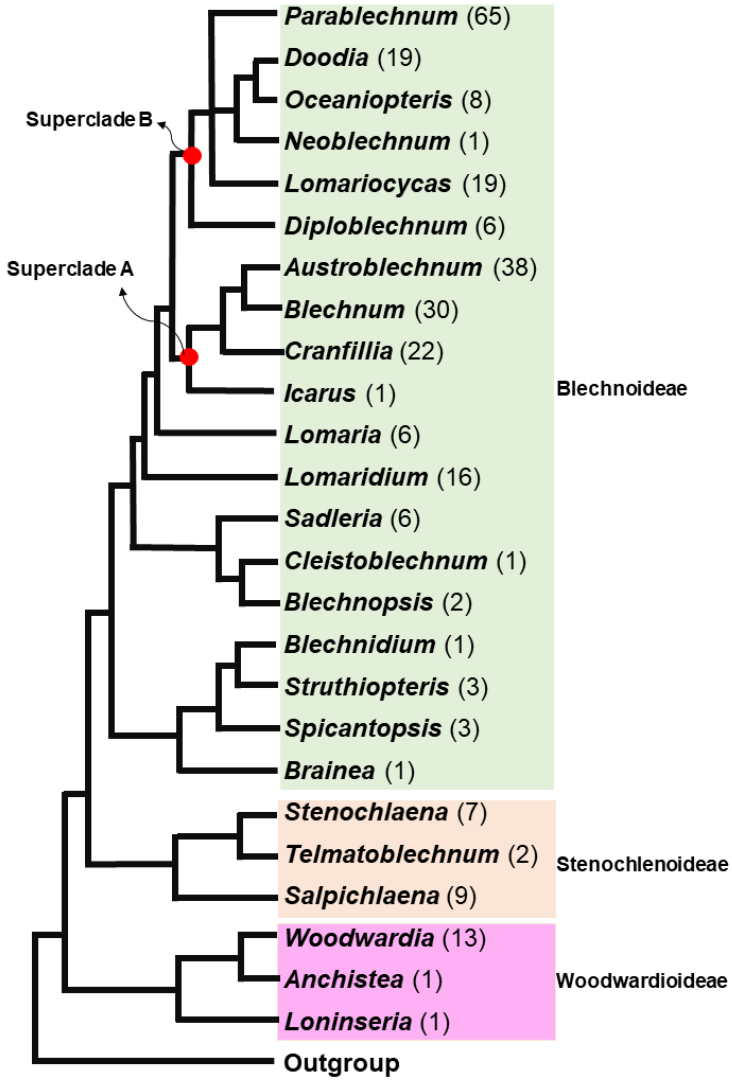

Figure 3. Summary of the molecular phylogeny of the family Blechnaceae proposed by Gasper *et al*. (2017) with the addition of *Spicantopsis* by Molino *et al*. (2019a). Each box corresponds to a subfamily indicated on the right, and next to each genus the number of its component species is included in parentheses *sensu* Gasper *et al*. (2017), Cardenas *et al*. (2018), Lange & Parris (2019), Molino *et al*. (2019a) & Bauret *et al*. (2020).

Copeland (1947) was the first to note that groups within the Blechnaceae tend to be split in distribution between Laurasia and Gondwana. In particular, he noted that *Anchistea* C. Presl, *Lorinseria* C. Presl and *Woodwardia* show a classic Arcto-Tertiary distribution, while species of *Blechnum* s.l. are almost restricted to continental fragments that were once part of Gondwana. It was further noted that several lineages within *Blechnum* s.l. are also restricted in their distribution within Laurasia, such as *Brainea*,

Struthiopteris, *Spicantopsis*, *Blechnidium*, *Blechnopsis* C. Presl or *Cleistoblechnum* Gasper & Salino, which would imply that both the species within the Woodwardioideae and the first branching groups of the Blechnoideae subfamily would be Laurasian (Copeland, 2011). On the other hand, the rest of the subfamily Blechnoideae (superclades A and B together with *Lomaridium* C. Presl and *Lomaria* Willd.) are almost entirely restricted to Gondwana, although some of these lineages have migrated from areas such as South America and Papua New Guinea or Australia to typically Laurasic regions of North America and Southeast Asia, e.g. *Blechnum* s.s. or *Parablechnum*. Considering that onocleoid ferns are restricted entirely to Laurasia, it has been hypothesised that the ancestor of the family Blechnaceae originated and diversified in Laurasia, and then dispersed across Gondwana (Cranfill, 2011). Moreover, more modern divergence time estimates suggest that the family is too young to be of Gondwanan origin (Testo & Sundue, 2016).

Several fossils of putative Blechnaceae taxa have been described. For example, a fossil of *Anchistea virginica* (L.) C. Presl with relatively well-preserved anatomy was discovered in Yakima Canyon, Washington, USA, dated to the middle Miocene (Pigg & Rothwell, 2001). However, the earliest fossil record unequivocally belonging to the Blechnaceae dates to the Mesozoic, the now extinct species *Mildandia nishidae* Serbet & Rothwell, which was found in Canada along with other related species of the families Dennstaedtiaceae Lotsy and Dryopteridaceae Herter (Serbet & Rothwell, 2003). Another Blechnaceae fossil has also been discovered in Princeton, Canada, described as *Trawetsia princetonensis* Smith (extinct), this time more recent, from the middle Eocene (Smith *et al*., 2006b). Fossils similar to the present-day genus *Salpichlaena* from the Palaeocene have been found in western North America, to which various genera have been attributed (Lesquereux, 1878; Knowlton, 1930; Pabst, 1962). The Colorado fossils (Knowlton, 1930) are the most complete, and provide a detailed comparison with the extant species *Salpichlaena volubilis* (Kaulf.) J.Sm. *Woodwardia* is the genus with the larger fossil record in the family. There are reliable fossil records reported from the Paleocene (Knowlton, 1919; Hickey, 1977; Collinson, 2001; Quing et al., 2006; Manchester, 2014), the Eocene (Knowlton, 1899, 1919; Endo, 1962; Collinson, 2001, Song et al., 2021) and the Oligocene (Tanai, 1970; Kvaček et al., 2018).

Several studies on biogeographic history and ancestral range reconstruction have been conducted in the Blechnaceaes, specifically in the genera *Lomaridium* C.Presl (Vicent *et al.*, 2017), *Struthiopteris* and *Spicantopsis* (Molino *et al.*, 2019b). A recent study of the family has estimated that the origin of the Blechnaceae was in Eurasia, and its diversification started in the Late Cretaceous, splitting the three subfamilies before the K-Pg boundary (Testo *et al*., submitted). Although the origin of the family post-dates the break-up of Gondwana (Sanmartín & Ronquist, 2004), some lineages of the Blechnaceae can be explained by vicariance, such as the subfamily Woodwardioideae, which would have reached North America from Asia via Beringia, with subsequent isolation (Testo *et al.*, submitted). This was previously reported by Li *et al.* (2016), except that they proposed reverse migration. The distribution of the subfamily Stenochlaenoideae could also be explained by a migration from Asia to America across Beringia or the North Atlantic Land Bridge, but palaeobotanical information is more limited in this case.

In the subfamily Blechnoideae some genera such as *Lomaridium*, *Lomariocycas* (J.Sm) Gasper & V.A.O. Dittrich or *Austroblechnum* Gasper & V.A.O. Dittrich could result from a trans-Antarctic linkage that connected most southern landmasses and South America after the breakup of Gondwana, although more specific studies are needed to confirm this hypothesis (Testo *et al*., submitted). That connection lasted from the beginning of the Late Cretaceous between New Zealand and America until the end of the Paleocene (Ladiges & Cantrill, 2007) and until the end of the Eocene in the case of Australia, Antarctica, and South America (Stickley *et al*., 2004).

Most fern families show their highest diversity and speciation rates in montane forests near the equator (Kessler *et al.*, 2011; Weigand *et al.*, 2020; Suissa *et al.*, 2021). However, species richness of the family Blechnaceae occurs at ca. 20ºS, and the highest speciation rates between ca. 20-40ºS. Diversity at these latitudes is mostly in the Central Andes, southeastern Brazil, eastern Australia, and New Zealand, especially in rainforests (Testo *et al*., submitted). This speciation rate and species richness are especially high in Australia and New Zealand, where they constitute 7% and 11% (McCarthy, 1998; Breitwieser *et al*., 2010) of the pteridoflora, respectively, which is an overrepresentation of the family considering the global diversity of ferns (Testo *et al*., submitted). This could be explained by the colonization of several lineages of the subfamily Blechnoideae since 50 MY In addition, species of the family Blechnaceae have been found to be among the few cold-

tolerant fern families in Australia (Nagalingum *et al*., 2015), so ferns of this family could be particularly well adapted to these conditions (Testo *et al*., submitted).

The Blechnaceae still pose several unresolved questions, and its most species-rich genus remains largely understudied.

Genus *Parablechnum*

Generalities

Parablechnum C. Presl is the most diverse genus of the family Blechnaceae, with about 65 species. It was first described by Presl (1851), who defined it by having clearly dimorphic fronds, which he considered a character of extreme importance in the separation of genera in the Blechnaceae, the arrangement of the sori and the nature of the indusium. The genus subsequently fell into disuse. It was considered a group inside *Blechnum* by most authors until recently, within which it was informally considered as a fairly well delimited morphological group (Tryon & Tryon, 1982; Kramer *et al*., 1990; Gabriel y Galán *et al*., 2013). Finally, it was resurrected by Gasper *et al*. (2016, 2017) considering its phylogenetic position and morphological synapomorphies that had little to do with those proposed at the time by Presl, but whose genus he had to keep because of the principle of priority (Turland *et al.*, 2018).

Parablechnum is generally characterized by being terrestrial plants with erect or suberect rhizomes, that are sometimes subarborescent; ovate or ovate-lanceolate rhizome scales; fronds usually dimorphic, 1-pinnate, with truncate base and conform apex; stalked pinnae; monolete spores with cristate-reticulate perispore, with a tendency to form polygonal areoles, occasionally with filamentous processes (Passarelli *et al*., 2010; Rothfels *et al*., 2012; Gasper *et al*., 2016; Moran *et al.*, 2018; Moran, 2022; **Figure 4**). Although there are known chromosome counts for the genus (n=28, 31 and 33), they are based on very limited knowledge and the incidence of polyploidy is unknown (Chambers & Farrant, 1998a, b; Jara-Seguel *et al*. 2006).

Figure 4. *Parablechnum* specimens in the field. A. *Parablechnum loxense*, terrestrial habit, trophophylls and sporophylls with contracted pinnae (Cerro de la Muerte, Costa Rica); B. *Parablechnum schiedeanum*, dimorphic fronds, trophphylls with expanded pinnae and sporophylls with contracted pinnae (Monteverde, Costa Rica); C. *Parablechnum stipitellatum*, rachis and costa with numerous scales (Pichincha, Ecuador); D. *Parablechnum cordatum*, young frond with reddish fiddleheads, mucus and aerophores (arrow) (Morona-Santiago, Ecuador); E. *Parablechnum schiedeanum*, terrestrial, with young reddish fronds (Monteverde, Costa Rica); F. *Parablechnum falciforme*, stalked pinnae with old non-functional, low aerophores (arrow) (Cuerici Biological Station, Costa Rica) (Canar, Ecuador). Pictures: A, C, D & F: Robbin Moran; B & E: José María Gabriel y Galán.

Parablechnum remains understudied, despite presenting obvious taxonomic challenges. The stated number of 65 species is the number given in the recent classification by Gasper *et al*. (2016), with some later combinations and descriptions of new species (Dittrich et al. 2017; Smith & Kessler, 2018; Lange & Parris, 2019, Wal *et al.,* 2021; Molino *et al.,* submitted). However, because of the work of Gasper *et al.* focused on the entire Blechnaceae, they did not explore the taxonomy of *Parablechnum* in depth. The current number of recognized species in the genus is suspect for the following reasons:

- Many species have a restricted local distribution, and some are only known from the type or a handful of collections. An example is *Parablechnum rheophyticum* (R.C. Moran) Gasper & Salino, collected only twice in Ecuador at two neighbouring localities (Moran & Øllgaard, 1995).
- Strongly conflicting taxonomic concepts applied to some widespread and variable taxa. For example, *Parablechnum cordatum* (Desv.) Gasper & Salino has sometimes been considered as a single, variable species distributed from Central America to Chile, or segregated into different entities such as the Central American *Parablechnum schiedeanum* (C. Presl) Gasper & Salino, the South American *P. cordatum,* and the southern Chilean *Parablechnum chilense* (Kaulf.) Gasper & Salino (Prada *et al*., 2008; Vicent, 2017).
- The presence of a lot of incomplete herbarium material, due to the large size of some plants, or with only fertile or sterile frond material. This problem is aggravated when it affects type specimens.
- The broad pantropical distribution of the genus and large number of species has prevented the completion of a comprehensive taxonomic treatment. Regional treatments do exist, e.g., for Mesoamerica (Moran, 1995b) or Malaysia (Chambers & Farrant, 2001), and there are, of course, a multitude of treatments in floras and local studies or lower circumscription works. Taxonomic studies have also been undertaken, e.g., the complexes *Parablechnum procerum* (G. Forst.) C. Presl (Chambers & Farrant, 1998) and *P. cordatum* (Prada *et al*., 2008; Wal *et al*., 2020).

Therefore, there is a clear need for a global monographic study of this complex genus, as has already been suggested by other authors (Tryon & Stolze, 1993; Moran, 1995a; Dittrich *et al*., 2017, 2020).

Phylogeny

Regarding the relationships between species, there is no global phylogenetic hypothesis for *Parablechnum*, beyond partial studies with few species, carried out in the context of the phylogeny of the family (Gabriel y Galán *et al*., 2013; Perrie *et al*., 2014; Testo & Sundue, 2016; Gasper *et al*., 2017; Bauret, 2017). The most complete phylogeny of the genus to date is found in the work of Gasper *et al.* (2017) with the additions of Bauret (2017). In this work, 34 species were included (one individual per species except two in *Parablechnum humbertii* (Tardieu) S.Molino & Bauret). The resulting topology showed three major clades, two of them Austropacific and one American, with one species from continental Africa (*Parablechnum capense* (Burm.f.) Gasper & Salino) nested within one of the Austropacific clades and one from Reunion Island (*Parablechnum marginatum* (Feé) Gasper & Salino) and from Madagascar (*P. humbertii*) within the American clade (**Figure 5**). However, bootstrap and posterior probability results were, in many cases, low.

The scarce information available points to a recent radiation and diversification of the genus —exceptional among ferns— impossible to elucidate and reconstruct with current data due to a scarce sampling of taxa and a very limited availability of genetic information. It is necessary and urgent to deepen the phylogeny of the genus in order to, on the one hand, help the infrageneric systematic delimitation, and on the other hand, to undertake new challenges in the field of evolutionary biology (e.g. evolutionary analysis of morphological characters, or biogeographical studies).

Biogeography

Parablechnum has two major centres of diversity, one in tropical-subtropical America and the other in Australasia, both with similar numbers of species (**Figure 6**). These ferns inhabit ecosystems of high biological diversity and scientific interest that are also particularly vulnerable to global change, such as montane cloud forests and wetlands (e.g. Pouteau *et al*., 2016). It also occurs in South Africa, Madagascar and Reunion and reaches

southern temperate forests in South America. Some species of *Parablechnum*, especially in South America, present very small geographic ranges (Kessler *et al.*, 2007) and evidence of unclear species delimitation (Smith & Kessler, 2018).

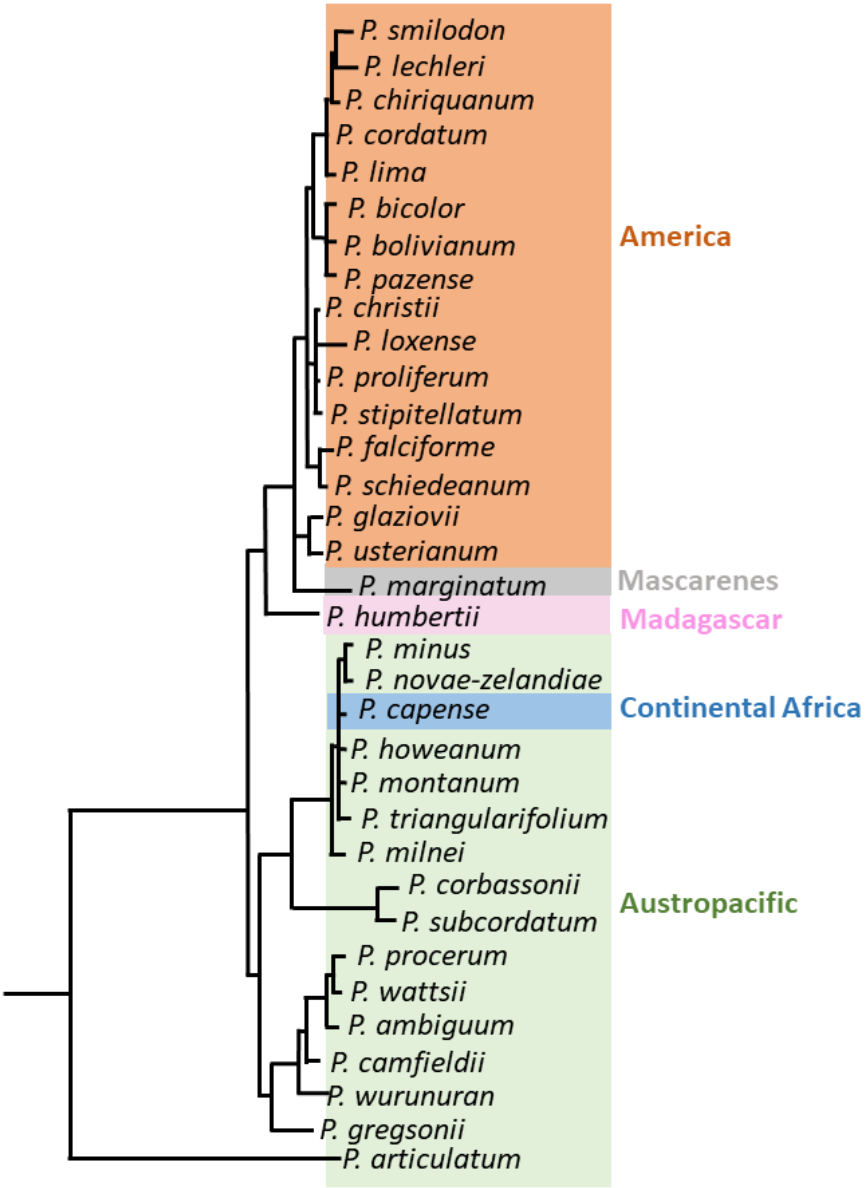

Figure 5. Summary of the molecular phylogeny of the genus *Parablechnum* proposed by Gasper *et al*. (2017) with the additions of Bauret (2017). Each box corresponds to a region indicated on the right.

The origin of *Parablechnum* has been dated to around 30 MY, and it is the most striking example of rapid radiation within the Blechnaceae family, with at least six LDD events since its ancestral origin in New Zealand (Testo *et al*., submitted). One of the most notable migrations of the genus is that which took place in the middle Miocene to America. There it diversified very rapidly in tropical and south temperate America,

especially in the Andes. The time of diversification of *Parablechnum* in America corresponds to the Andes uplift (Gregory-Wodzicki, 2000; Garzione *et al*., 2008), an event that has involved the rapid speciation of several groups of organisms (Madriñán *et al*., 2013; Lagomarsino *et al*., 2016; Testo *et al*., 2019). This relationship between montane uplift and lineage diversification remains unexplored in ferns at present, so *Parablechnum* could constitute an exceptional study model for this type of research (Testo *et al*., submitted).

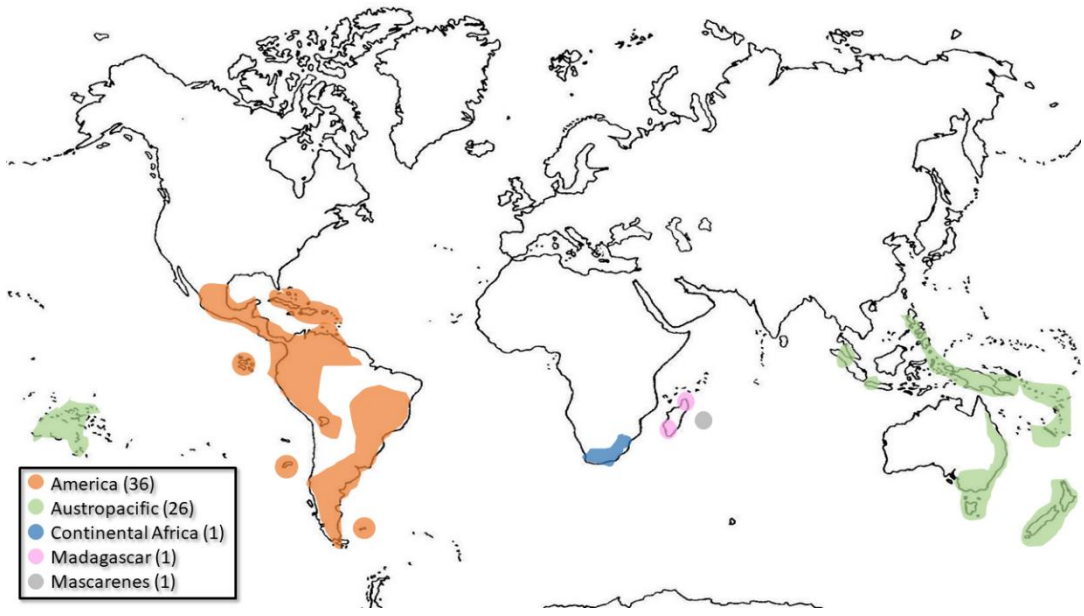

Figure 6. Global distribution of *Parablechnum* modified from GBIF (2022). The legend indicates the centres of diversity and the approximate number of species in parentheses.

The study of Gondwanan disjunctions in spore-dispersed plants, often counterintuitive in explanation, is an active source of knowledge on the phenomenon of long-distance dispersal (Vanderpoorten *et al*., 2010; Noben *et al*., 2017), and a detailed phylogeny of *Parablechnum* would be a substantial advance in cryptogamic biogeography.

The large America-Australasia biogeographic disjunction has not yet been studied for the genus *Parablechnum* as a whole. Given the size and importance of the genus in terms of biodiversity, a biogeographical hypothesis of the genus would be a significant step towards a solidly based biogeography of the entire family. The limited phylogenetic data available suggest that the genus *Parablechnum* is of very recent appearance (Testo & Sundue, 2016; Gasper *et al*., 2017). The only dated phylogeny today is the one presented by Testo *et al*. (submitted), which dates the origin of *Parablechnum* at about 30 MY ago

in New Zealand. However, this is based on the phylogeny published by Gasper *et al*. (2016) in order to study the biogeographical history of the whole family, and a more detailed phylogeny is necessary to investigate the genus in concrete. In addition, even at that moment, Gondwana was already separated, suggesting thus an event of LDD, the Antarctic corridor between New Zealand and America was still present 30 My, so a more precise date is needed to decide whether that could have played a role.

In summary: the study of *Parablechnum* presents a unique potential among ferns as a genus of very recent emergence, which has undergone a rapid evolutionary radiation yet to be studied and shows a biogeographic pattern that remains unexplained. The remarkable taxonomic complexity of these ferns, the lack of knowledge of the influence of polyploidy phenomena, and the scarcity of genetic data have limited the progress needed to reveal the biodiversity housed in this taxon. The present work aims to make a contribution in the systematic knowledge of this genus and to establish future lines of work.

3. OBJECTIVES

The general objective of this thesis is to carry out a global systematic treatment of the genus *Parablechnum* that improves the current state of the art and advance towards the phylogenetic reconstruction of the genus increasing the available sequence information. To achieve this, the following specific objectives are proposed:

1) To explore the taxonomic and systematic significance of microanatomical traits of spores and pinnae ultrastructure.

2) To conduct a broader phylogenetic analysis of the genus expanding the coverage of taxa and exploring new loci to be sequenced.

3) To summarize the current systematic knowledge of the genus in a global taxonomic synopsis.

4. MATERIAL AND METHODS

Biological material

The study is based on the study of 3,748 herbarium specimens of all *Parablechnum* taxa from the following institutions included in Index Herbariorum (Thiers, 2022. Continuously updated): Botanischer Garten und Botanisches Museum Berlin, Zentraleinrichtung der Freien Universität Berlin, Germany (B), Facultad de Ciencias Biológicas, Universidad Complutense de Madrid, Spain (MACB), Real Jardín Botánico, Madrid, Spain (MA), Missouri Botanical Garden, U.S.A. (MO), Muséum National d'Histoire Naturelle, Paris, France (P), The New York Botanical Garden, U.S.A. (NY), Smithsonian Natural Institution, Washington D.C., U.S.A. (US) and University of Vermont, U.S.A. (VT), as well as field surveys in Costa Rica, Chile and Peru, in which material was collected and deposited in the MACB herbarium. In addition, high-resolution digital material from the following herbaria has been analysed: Harvard University, Massachusetts, U.S.A. (A), Aarhus University, Denmark (AAU), Auckland War Memorial Museum, Auckland, New Zealand (AK), The Natural History Museum, London, U.K. (BM), Buffelskloof Nature Reserve, Mpumalanga, South Africa, Meise Botanic Garden, Meise, Belgium (BR), Queensland Herbarium, Brisbane, Australia (BRI), Australian National Herbarium, Australia (CANB), Australian National Herbarium, Canberra, Australia (CBG), Museo Nacional de Costa Rica, San José, Costa Rica (CR), Royal Botanic Garden Edinburgh, Scotland, U.K. (E), Universidade Regional de Blumenau, Santa Catarina, Brazil (FURB), Conservatoire et Jardin botaniques de la Ville de Genève, Switzerland (G), Harvard University, Massachusetts, U.S.A (GH), Universität Göttingen, Germany (GOET), University of Helsinki, Finland (H), Martin-Luther-Universität, Halle, Germany (HAL), Royal Botanic Gardens, Kew, U.K. (K), Naturalis, Leiden, The Netherlands (L), Fundación Miguel Lillo, San Miguel de Tucumán, Argentina (LIL), Linnean Society of London, England, U.K. (LINN), Museo de La Plata, Buenos Aires, Argentina (LP), Herbario Nacional de Bolivia, Universidad Mayor de San Andrés, La Paz, Bolivia (LPB), Museu Botânico Municipal, Paraná, Brazil (MBM), Royal Botanic Gardens Victoria, Australia (MEL), University of Michigan, U.S.A. (MICH), Royal Botanic Gardens & Domain Trust, Sydney, Australia (NSW), Università di Pisa, Italy (PI), Universidad de Panamá, Panamá (PMA), BioCentro-

UNELLEZ, Mesa de Cavacas, Venezuela (PORT), National Tropical Botanical Garden, Hawaii, U.S.A. (PTBG), Pontificia Universidad Católica del Ecuador, Quito, Ecuador (QCA), Museu Nacional, Rio do Janeiro, Brazil (R), Jardim Botânico do Rio de Janeiro, Brazil (RB), Universidad de Santiago de Compostela, Galicia, Spain (SANT), Swedish Museum of Natural History, Stockholm, Sweden (S), The Bergius Foundation at the Royal Swedish Academy of Sciences, Stockholm, Sweden (SBT), Sichuan Institute of Natural Resources, Sichuan, China (SR), Taiwan Forestry Research Institute, Taipei, Taiwan (TAIF), Trinity College, Dublin, Ireland (TCD), Naturalis, Leiden, Netherlands (U), Universidade de Brasília, Brasília, Brazil (UB), The University of California, U.S.A. (UC), Union College, New York, U.S.A., (UCS), Universidade Federal do Paraná, Brazil (UPCB), Universidad Nacional Mayor de San Marcos, Lima, Perú (USM), Universidad Central de Venezuela, Caracas, Venezuela (VEN). These images have been consulted in the official web pages of the herbaria, in GBIF.org (2022), JSTOR Global Plants platform (Ryan, 2018), and in PteridoPortal (2022). The specimens studied can be consulted in the **Taxonomic Synopsis** section. Additional pictures of the plants in the field have been consulted on PlantSystematics (2022) and iNaturalist (2022).

Nomenclature

Nomenclature followed the floristic treatments cited in the corresponding sections, complementing them with the information present on IPNI (2022), and Tropicos.org (2020). For the nomenclatural decisions, we followed what is stated in the last version of the International Code of Nomenclature for algae, fungi and plants (Turland *et al*., 2018). The backbone phylogeny of the Blechnaceae and the systematic starting point of this work is the one published by Gasper *et al.* (2016).

Information of antique publications and from author and collectors has been consulted on Biodiversity Heritage Library (Gwinn & Constance, 2009), Bionomia (2022) and Botanicus (2022).

Morphological and anatomical study

A study of the general morphology of the plants (i.e. fronds, scales, rhizomes, epidermis etc.), anatomy of the fertile pinnae, sporangia and spores was carried out for all species of *Parablechnum* to which access has been obtained. These characters were

chosen as they have proved to be of great taxonomic importance in pteridology in general (e.g. Kramer *et al.*, 1990) and in the Blechnaceae in particular (e.g. Rolleri & Prada, 2006b). **Appendix I** summarises the data collection for each species. Photographs of details at a more macromorphological level were taken with a *Leica Stereozoom S9i* with *Swing Arm Stand* stereomicroscope and all the microscopic pictures were taken with a *Nikon Eclipse Ci* microscope with a *Nikon DS-Fi2* camera.

General morphological characters observed

For the terminology we used Lellinger (2002). Here we summarize the morphological taxonomic characters that have been observed on the herbarium specimens or in the literature and used for the descriptions of the taxa of *Parablechnum*. A summary of these characters can be found in **Figure 7**.

- Habit: usually terrestrial plants, although some may appear as saxicolous or epiphytic. To recognise this, we have usually had to refer to the bibliography or the notes on the herbarium labels, as we have not worked with specimens in the field.
- Rhizome: usually erect, sometimes forming trunks, sometimes short or long creeping, with or without the ability to form stolons. The scales have also been observed.
- Fronds: the level of dimorphism (monomorphic, subdimorphic, or dimorphic) has been observed.
- Axes: on petioles, rachises, and costae we have observed length (in the case of petioles), colour, ornamentation, and indumentum (ie. scales and/or hairs).
- Lamina: size, shape and degree of division have been observed. The possible shapes are illustrated in **Figure 8**.
- Pinnae: number of pairs, general shape, base, apex, margin, insertion into the rachis, ornamentation (i.e. scales and/or hairs). The possible shapes of base, apex, and margin can be found in **Figure 8**.
- Venation: division and direction (catadromous or anadromous).
- Aerophores: presence and shape.
- Hydathodes: presence and shape.
- Sori: arrangement in the pinna and shape.

- Indusium: arrangement on pinna and shape of margin and cells (**Figure 9**).
- Indumentum: the indumentum can appear on different parts of the plant, usually in the form of scales and occasionally hairs.

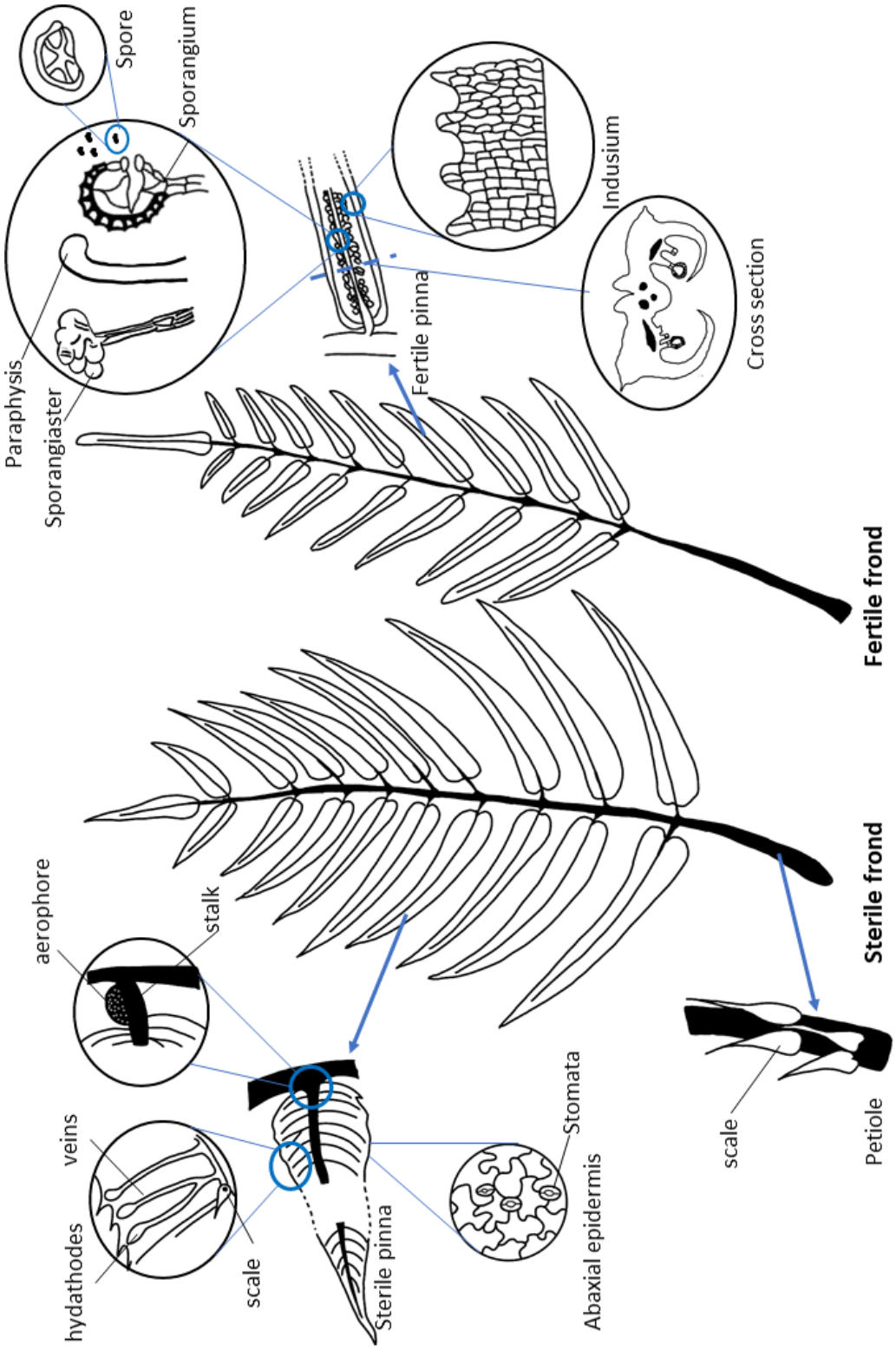

Figure 7. Summary of the characters observed in the specimens.

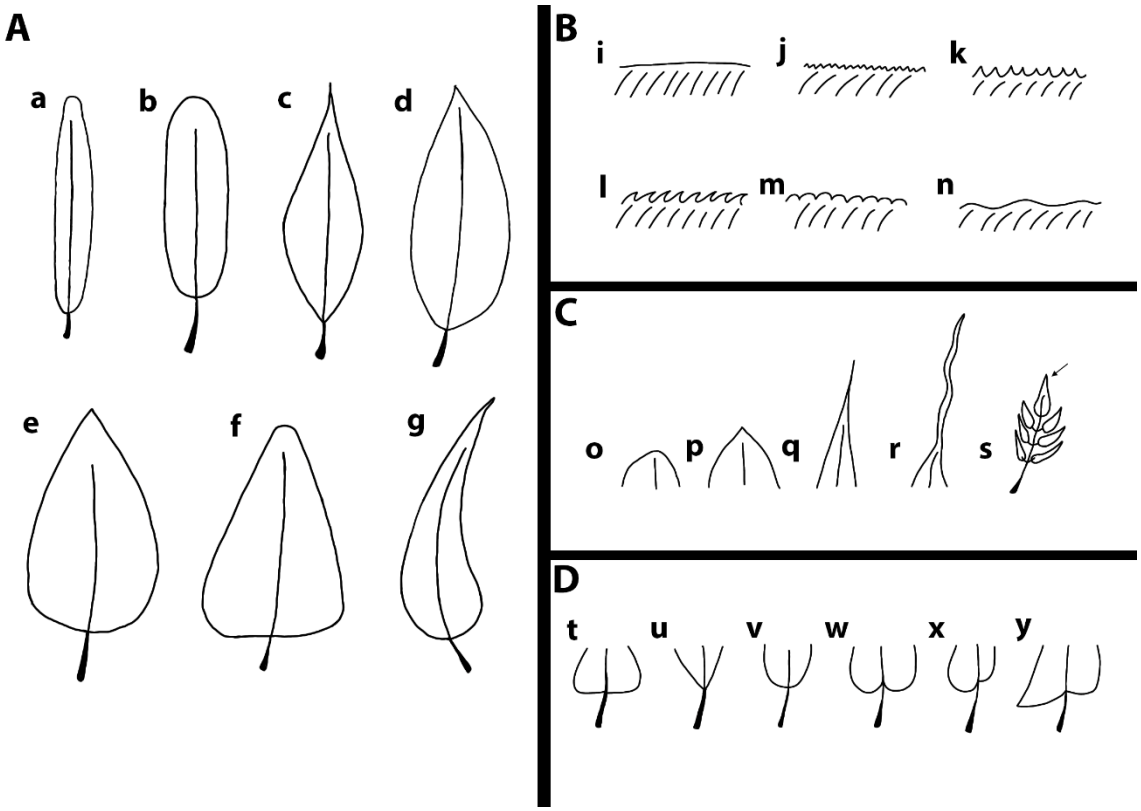

Figure 8. Summary of the terminology used to describe shapes, margins, apex and bases. A. Shapes: a. linear; b. Oblong; c. Lanceolate; d. Elliptic; e. Ovate; f. Deltoid/triangular; g: falcate. B. Margins: i. entire; j. Denticulate; k. Dentate; l. Serrulate; m. Crenate; n. wavy. C. Apexes: o. Obtuse; p. Acute; q. Acuminate; r: Filiform; S. Conform. D. Bases: t. Truncate, u. Cuneate; v. Rounded; w. Cordate; x. Subcordate; y. Hastate.

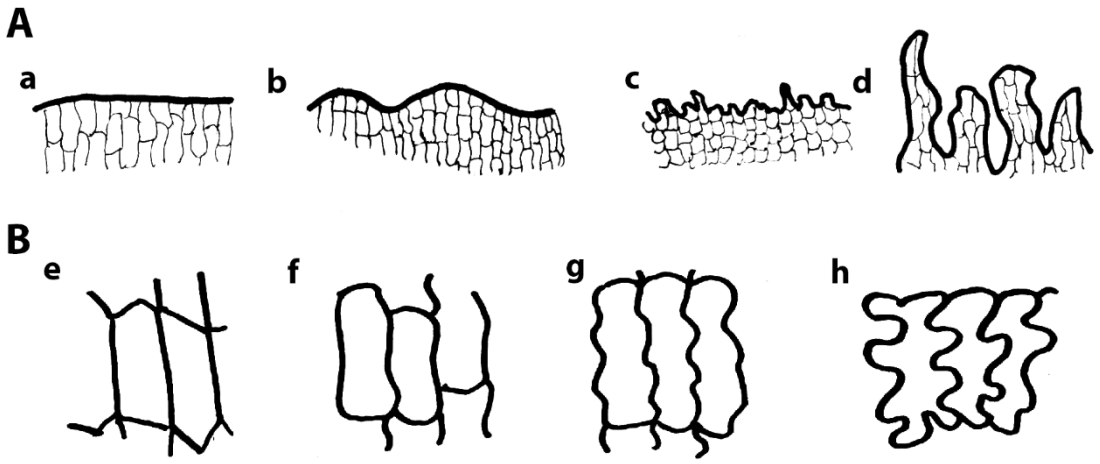

Figure 9. A. Indusia in surface view. A. Margins: a. straight; b. repand; c. erose; d. lacerate. B. Epidermical models based on the anticlinal cell walls: e. polygonal; f. subpolygonal; g. subsinuous; h: sinuous.

Anatomy of the fertile pinnae and epidermis

For the microscopical procedures we followed the general techniques used by Gurr (1966) and Ruzin (1999). The samples were softened for approximately 5 minutes in water and then sections were made freehand in the middle area of the fertile pinnae. We made both cross and parasagittal sections to check the anatomical characters of each specimen (**Figure 10A**). The characters observed are based on the publication Prada *et al.* (2016).

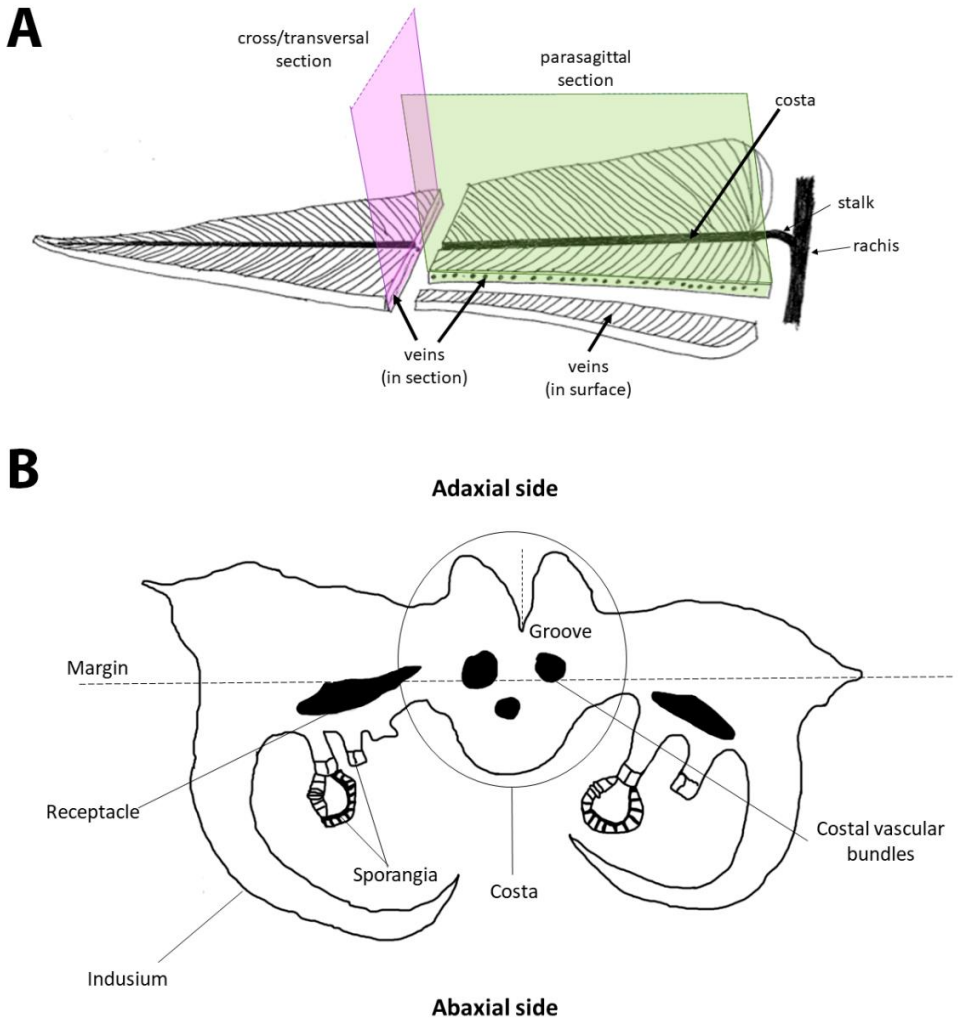

Figure 10. A. Diagram of a pinna and the orientation of the cross (pink) and parasagittal (green) sections. B. Diagram of the main characters observable in a cross section of fertile pinna.

The most important characters available in a cross section are summarised in **Figure 10B**. The sections were then rinsed by immersing them in a 50% solution of diluted commercial sodium hypochlorite (between 2 and 5 minutes). After several washes with

water, the sections were stained with 0.1% aqueous toluidine blue (TBO) or floroglucinol, both widely used in anatomical studies in ferns (Prada *et al*., 2016; Molino *et al*. 2019a, b). The photographs were edited with *Adobe Photoshop 2022* for background and contrast removal, all original photos are available for consultation.

For the observation of the epidermis, the sterile tissue was softened for at least 10 minutes in water and scraped until a single layer of cells was obtained on both the abaxial and adaxial sides. In the case of the underside, stomata were measured with the software *Piximètre* (Henriot & Cheype, 2022).

Spores and sporangia

The terminology used for sporangia was taken from the compendium of Lellinger (2002), Wilson (1959a) and Prada *et al*. (2016) proposed in Molino *et al*. (2020) **(Figure 11**).

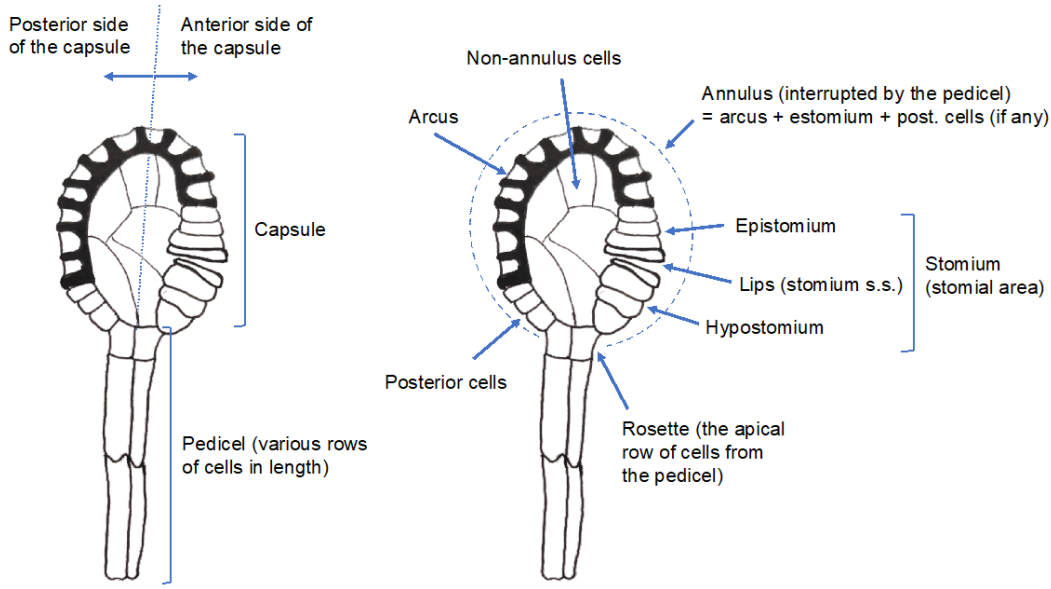

Figure 11. Schematic of a leptosporangiate vertical sporangium with indication of the main traits considered in this work. Extracted from Molino *et al.* (2020).

Sporangia analysis was carried out by scraping the sori from the previously softened and rinsed pinnae. At least 3 measurements of the following sporangial characters were taken for each individual: capsule length and width; number of arch cells; number of lip, hypo- and epistomial cells, and length of pedicel and rosette. These were based on

previous work studying sporangia of the family Blechnaceae (Prada *et al*., 2016; Molino *et al*., 2020; Wal *et al*., 2021; Molino *et al*., submitted).

Spores were studied by optical microscopy to establish their dimensions mounted in untreated water. At least 30 measurements of polar and equatorial diameter were taken on each individual, excluding the perispore. With these measures we calculated the shape and volume of each spore following the formulae of Barrington *et al.* (1986, 2020). The measures were made with the software *Piximètre* (Henriot & Cheype, 2022).

In order to observe the ornamentation of the perispores and exospores of all species in more detail, a scanning electron microscope (SEM) study was carried out. The samples were mounted in a sample holder with carbon adhesive. Before observation, each sample was coated with a gold layer and observed under a JSM 6400 JEOL SEM operating at 20 kv. The observations were carried out at the Centro Nacional de Microscopía Electrónica (CNME) of the Universidad Complutense de Madrid.

Statistical analysis

The biometric data obtained were analysed with *IBM SPSS Statistics 27* to obtain the means, maximum and minimum values, and standard deviation of each variable.

Molecular study

Phylogeny

We extracted genomic material using different commercial kits from *Qiagen*©, *Norgen Biotek Corp*© and *NZYTech*©. SANGER sequencing was outsourced and carried out by Eurofins Genomics and the Genomics Unit within the Research Support Centre (CAI) and Singular Scientific and Technological Facility (ICTS) of the Universidad Complutense de Madrid. DNA was extracted from 127 individuals which are listed on **Appendix 2**.

The following chloroplast markers were amplified: *rbc*L, *trn*L-*trn*F and *rps*4, which are widely known and have been previously used in phylogenetic studies of ferns (e.g. Pryer *et al.*, 2001; Schuettpelz & Pryer, 2007) and, specifically, of Blechnaceae (e.g. Gabriel y Galán *et al.*, 2013; Gasper *et al.*, 2017). In addition, we used the FERN ch1B fYAA primer designed by Kuo *et al*. (2011) for the chloroplast region *mat*K and designed

a complementary primer for it. We also designed a complementary primer for chlB rTRK of region *mat*K but discarded it due to lack of variation and problematic sequencing. All the information regarding primers is summarised on **Table 1**.

A total of 582 sequences were used, of which 469 are new sequences obtained in this work (pending publication in GenBank) and the remaining correspond to sequences previously published by other authors from GenBank (Benson *et al*., 2005) (**Appendix 2**). Contig assemblage and sequence alignment was done in *Geneious R11* (Kearse *et al*., 2012) using the *ClustalW* (Larkin *et al*., 2007) plugin and then manually adjusted. Sequences were concatenated after ruling out among-site conflict performing single-locus FastTrees. Three alternative datasets varying in number of accessions were produced with decreasing number of specimen accessions aiming to minimize the effect of missing data 165, 133, and 76. For each of these datasets, an extra alignment was made with an adjacent binary block containing the coded indels according to the Simple Coding algorithm (Simmons & Ochoterena, 2000) implemented in SeqState (Muller, 2005). Hence, six datasets were ultimately produced and analysed.

All alignments were partitioned according to a 4 (datasets without coded indels) or 5 (with coded indels) partition scheme: One partition for codon positions 1 and 2; a second partition for codon position 3; third partition for tRNA genes; fourth partition for non-coding spacers; and a last partition, when applicable, for the binary block of coded indels. Each dataset was analysed to produce a phylogenetic reconstruction using two optimality criteria: Maximum Likelihood (ML) and Bayesian Inference (BI) ML analyses of the alignments without indels were performed using RAxML (Stamatakis, 2006) under the GTRCAT model and assessing branch support with 1000 bootstrap pseudorreplicates. Indel-coded datasets were analysed with Garli (Zwickl, 2006) under GTR+G+I models in the CIPRES Science Gateway. Phylogenetic analyses under BI were performed using MrBayes (Ronquist & Huelsenbeck, 2005), implementing GTR+G+I models for each nucleotide partition and an F81 model for the indel blocks (Ronquist et al., 2011). The MCMC was run for 10 million generations (20 million for the 165 accessions dataset) with 2 runs and 4 chains on the CIPRES Science Gateway (Miller *et al.,* 2010). Trees were stored each 1000th generation and the first 20% of each run was discarded as burn-in. Trees were first imaged on FigTree v1.4.4. (Rambaut, 2017).

Table 1. Markers used in the study together with their 5'-3' primers. Under each marker, the cycle followed in the thermocycler is indicated.

Marker	Primer	Sequence	Refference
***rbc*L**	1F	ATGTCACCACAAACGGAGACTAAAGC	Hasebe *et al*. (1994)
	654R	GAARCGATCTCTCCAACGCAT	Schuettpelz & Pryer (2007)
	628F	CCATTYATGCGTTGGAGAGATCG	Schuettpelz & Pryer (2007)
	1361R	TCAGGACTCCACTTACTAGTCTCACG	Pryer *et al*. (2001)
Cicle	95ºC 5’ + 35x[95ºC 45’’ + 55ºC 1’+ 72ºC 1’] + 72ºC 10’		
***trn*L-*trn*F**	F	ATTTGAACTGGTGACACGAG	Trewick *et al.* (2002)
	fern1	GGCAGCCCCCARATTCAGGGRAACC	Taberlet *et al.* (1991)
Cicle	94ºC 5’ + 35x[94ºC 30’’ + 53ºC 1’ + 72ºC 30’’] + 72ºC 7’		
***mat*K**	FERN ch1B fYAA	GATGTRAYGTATGCRGCYAAAGA	Kuo *et al*. (2011)
	FERN ch1B rYAA	CGCGAAGCCGTATATGAAAC	Designed here
Cicle	94ºC 5’ + 35x[94ºC 1’ + 55ºC 1’ + 72ºC 1’30’’] + 72ºC 1’		
***rps*4-*trn*S**	trnS	ATGAATTATTAGTTGTTGAG	Shaw *et al*. (2005)
	rps4	TACCGGGGTTCGAATC	Souza-Chies *et al*. (1997)
Cicle	95ºC 3’ + 35x[94ºC30’’ + 42ºC30’’ + 72ºC 1’30’’] + 72ºC7’		

Several species of *Oceaniopteris* and the species *Doodia linearis* were used as outgroups in all trees as these are the closest genera to *Parablechnum* (Gasper *et al*., 2017).

Dating

A molecular dating analysis was carried out using *BEAST v.1.10.4* software (Suchard *et al.*, 2018). For this analysis, a pruned version of the 76-sequence alignment was used, eliminating those taxa that belonged to the same species and formed a monophyletic clade in the Bayesian analysis, since the dating analyses will be based on interspecific processes. One individual of *Parablechnum articulatum* (F.Muell.) Gasper & Salino was also included, as it is sister to all other *Parablechnum*, as well as the species *P. humbertii* and *P. marginatum* in order to cover the whole distribution of the genus. In addition to *Oceaniopteris gibba* (Labill.) Gasper & Salino, *Austroblechnum melanocaulon* (Brack.)

Gasper & V.A.O. Dittrich, *Brainea insignis* (Hook.) J.Sm., *Woodwardia japonica* (L.f.) Sm. and *Woodwardia unigemmata* (Makino) Nakai were used as outgroups to have more calibration points. The result was an alignment of 68 sequences.

A log-normal, uncorrelated relaxed clock model was implemented with a priority Yule process tree and a Birth Death process tree and using GTR+G+I substitution model. We used a uniform prior for the ucld.mean within values commonly observed in plant plastid markers (10^{-4}–10^{-2} substitutions/site/MY, Wolfe *et al*., 1987) and a default exponential prior for the standard deviation (SD). As calibrations points, we used the results of Testo *et al.* (submitted). The split between *Woodwardia* and *Brainea, Austroblechnum, Oceaniopteris* and *Parablechnum* was calibrated using a normal distribution spanning the confidence interval in the aforementioned study (mean = 73.78 MY, SD = 4, 95% high posterior density (HPD) = 61–86.57 MY), the split between *Brainea* and *Austroblechnum, Oceaniopteris* and *Parablechnum* to mean = 59.99 MY (SD = 4, 95% HPD = 47.84–72.15 MY), the split between *Austroblechnum* and *Oceaniopteris* and *Parablechnum* to mean = 47.33 MY (SD = 4, 95% HPD = 36.92–57.74 MY) and the split between *Oceaniopteris* and *Parablechnum* to mean = 41.66 MY (SD = 4, 95% HPD = 31.51–51.81 MY). The *Parablechnum* clade was forced into monophyly in view of previous Bayesian phylogenetic analyses.

The analysis was run for 300 million generations, saving trees every 1,000 generations and other parameters every 1,000 generations. The posterior distribution and estimated sample size (ESS) of all parameters was examined using *Tracer v.1.7* (Rambaut *et al.*, 2018). The analysis performed with Yule was selected because it was the one that showed the best ESS values. The analysis was determined to have run long enough when all ESS values were above 200, except coefficient of variation which was 189. *TreeAnnotator v.1.10.4* (Suchard *et al.,* 2018) was used to combine and summarise the tree samples, calculate the maximum 95% posterior density (HPD) intervals for all age nodes, and generate a maximum clade credibility chronogram and visualized in Figtree v1.4.4 (Rambaut, 2017).

5. MORPHO-ANATOMY AND PALYNOLOGY

Results

Fertile pinnae cross sections

Within *Parablechnum* species range from monomorphic to dimorphic through subdimorphism. In this work, species are defined as monomorphic when the sterile and fertile pinnae have the same degree of contraction, as dimorphic when it differs, and as subdimorphic when the contraction is intermediate. Within monomorphism we distinguish two types, "flat" monomorphism, with species showing uncontracted pinnae, with flat lamina, and "contracted" monomorphism, which includes species with strongly contracted sterile and fertile pinnae.

The margin is generally plain, sometimes curving recurved or incurved. Receptacles are generally extended, although there are some examples of defined receptacle in the axil of the indusium. All species have an indusium located on the hypophyll along a distinct commissural vein and recurved above the sporangia. This is always complex, this is, consisting of more than one layer of cells at least at the base, although the thickness of this indusium varies among species, some of them tending to a typical thin (monostratose) indusium, as in *P. ambiguum*. The costa is always grooved adaxially and prominent abaxialy. The prominence of the costa abaxially, however, varies from rounded, rectangular, keeled to flat or almost so. Some examples can be found in **Figure 12**. The number of vascular bundles in the costa goes from (1) 2–3 (5). In addition, we found incomplete extensions of the circumendodermal band into the costae on the species *Parablechnum nesophilum* (T.C. Chambers & P.A. Farrany) Gasper & Salino and *Parablechnum chauliodontum* (Copel.) Gasper & Salino (**Figure 12D**).

Some examples of the variation of fertile pinnae cross-section in *Parablechnum* can be seen in **Figure 13.** The characteristics of the fertile pinna cross section for each studied taxon is shown on **Table 2**.

Fertile pinna parasagital section

In the parasagittal sections of the sori we have observed two types of veins. First, we found a commissural vein that irrigates the sorus, formed by short and wide tracheids that can be defined as scaleriform veins. Below these veins, towards the abaxial side, are the

lateral veins perpendicular to the commissural veins. These veins are composed of long and thin tracheids. Likewise, there are arches of scaleriform tracheids that join the lateral veins with the commissural veins. In areas where the arches join the commissural vein to the lateral vein the receptacle tends to cluster into discrete units, although the sporangia still occupy the entire receptacle. These characteristics can be seen in **Figure 14**.

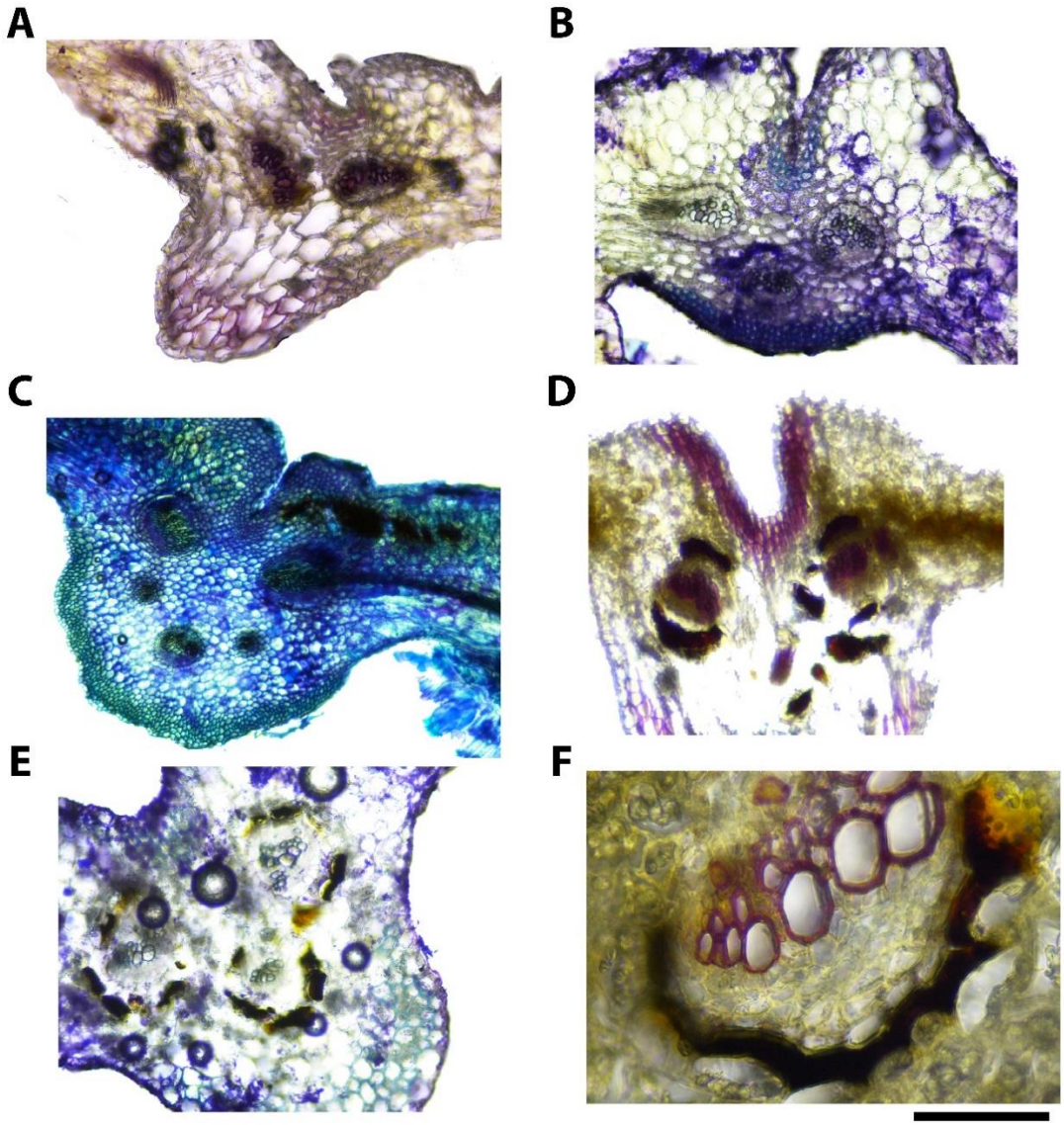

Figure 12. Cross section of various species of *Parablechnum*. A. *P. confusum*, two vascular bundles, abaxially keeled (*E. Rosenstock 90*, US01527826); B. *P. lima*, three vascular bundles, abaxially flat (*G.W. Harling 23590*, M04938179); C. *P. humbertii*, five vascular bundles, abaxially rounded (*F. Rakotondrainibe & F. Raharimalala 2519*, P00904704); D. *P. chauliodontum*, three vascular bundles (two visible in the image) with interrumped circumendodermal band (*M. Baumann 13963*, US2425971); E. *P. corbassonii*, three vascular bundles with interrumped circumendodermal band, abaxially rounded (*H. van der Werff & G. McPherson 16085*, UC1740315); F. *P. nesophilum*, detail of a costal vascular bundle with an interrupted circomendodermal band (*Sundue 4251*, MACB). Scale: 258 µm in A, 271 µm in B, 623.5 µm in C, 265 µm in D, 257 µm in E, 61 µm in F.

Indusia

Parablechnum indusia have a margin that varies from repand to lacerate, sometimes erose, rarely straight. The epidermal pattern varies from polygonal to subsinuous, with anticlinal walls being more sinuous in the area closer to the insertion, but not showing a clearly sinuous epidermal pattern. Some examples of the indusium characteristics can be found on **Figure 14C-F**, and the specific characteristics of each taxon studied can be consulted in **Table 2**.

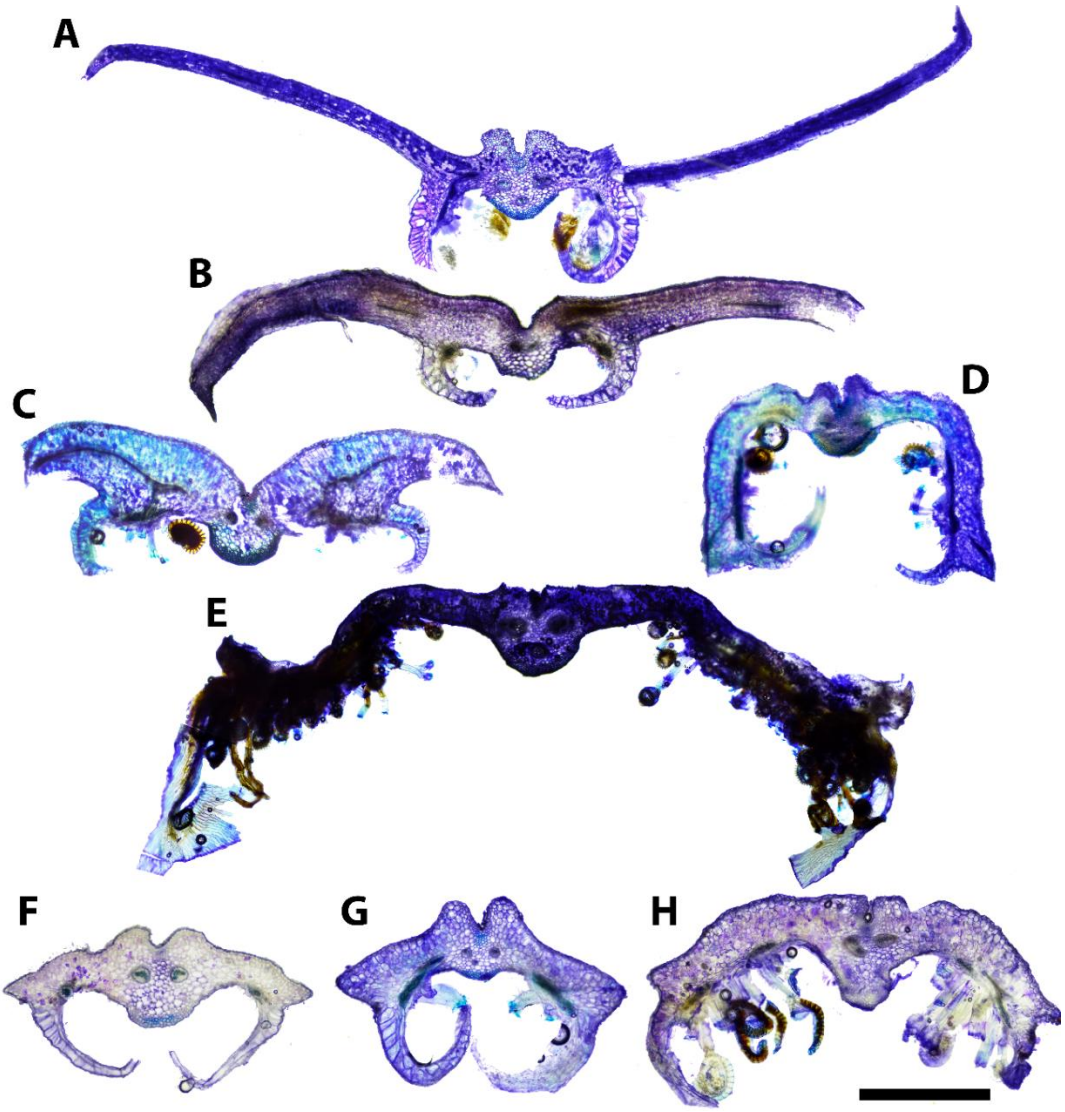

Figure 13. Fertile pinnae cross sections of several *Parablechnum* species. Monomorphic taxa ("flat" type): A. *P. monomorphum* (*I. Jimenez Pérez 5107*, MO6157390); B. *P. obtusum* (*E. Forero et al 526*, NY04187103). Monomorphic taxa ("contracted" type): C. *P. loxense* (*H. Churchill 3370*, VT198691); D. *P. stipitellatum* (*Escobar 5568*, NY); E. *P. chilense* (*J.M. Gabriel y Galán s.n.*, MACB109257). Dimorphic taxa: F. *P. ambiguum* (*Coveny 9135*, NY); G. *P. ryanii* (*R. Hill & L.R. Phillippe 29004*, VT198716); *P. vestitum* (*T. Maatschappij et al 7277*, US3100967). Scale: 1.5 mm in A, 1.3 mm in B, D & G, 1 mm in C & H, 587.5 µm in E, 893 µm. in F.

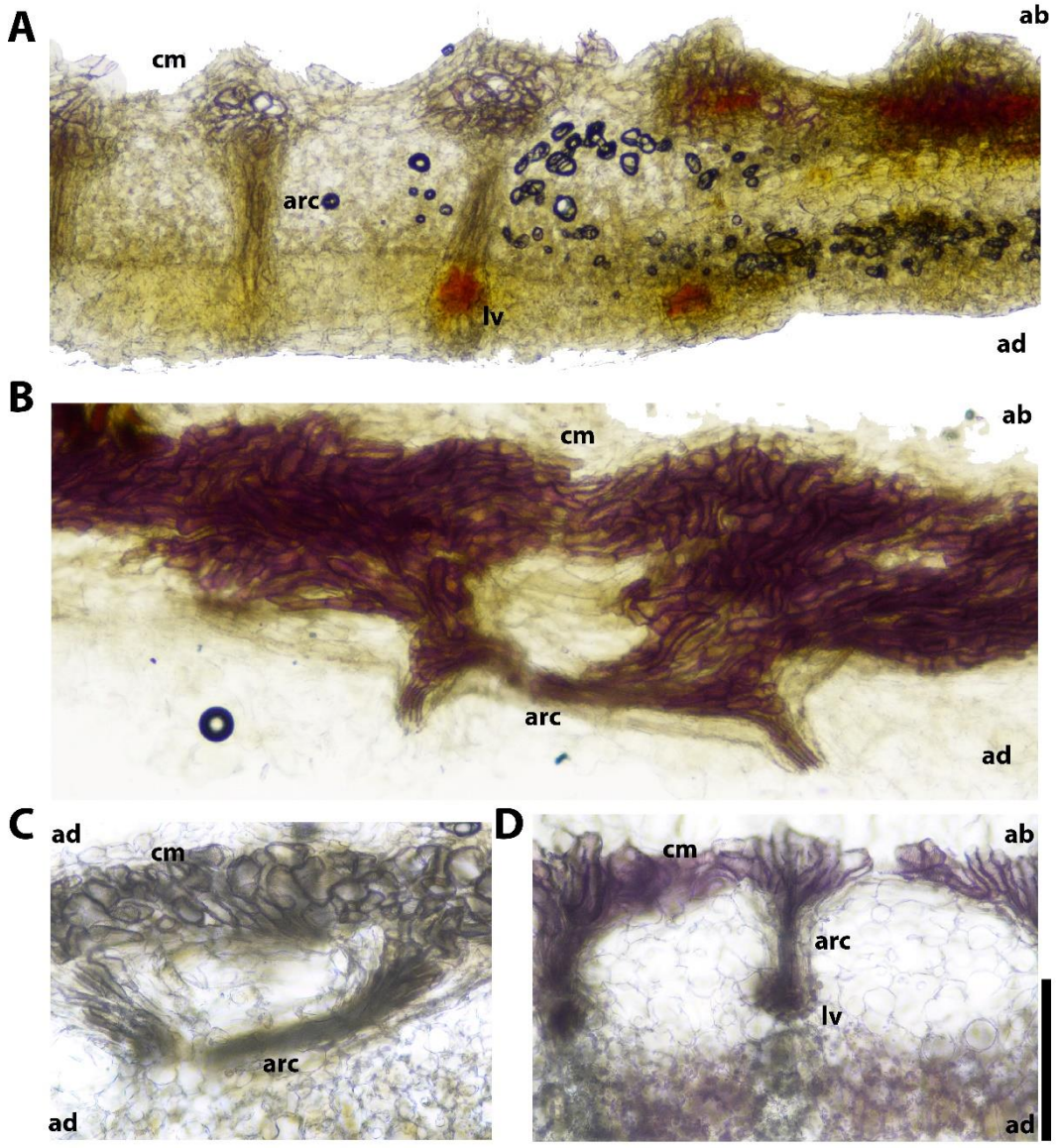

Figure 14. Fertile pinna parasagittal sections of *Parablechnum*. A. *P. loxense* (*B. Stergios et al 20544,* US449754); B. *P. ambiguum* (*E.F. Constable P8186,* US2361403); C. *P. humbertii* (*F. Rakotondrainibe & F. Raharimalala 2519,* P00904704); D. *P. lineatum* (*S. Fawcett & A.A. Reznicek 477,* VT198703). ab = abaxial side; ad : adaxial side; arc = arch linking commissural vein and lateral vein; cm = commissural vein; lv = lateral vein. Scale: 317 µm in A, 1.7 mm in B, 303 µm in C, 275 µm in D.

Epidermis

The epidermis of *Parablechnum* has epiphyll and hypophyll with elongated cells with anticlinal walls with many U- or V-shaped undulations and apparently flat periclinal walls, with ellipsoid stomata occurring only on the abaxial side, with narrower accompanying cells that are sometimes shared between more than one stoma. In addition, patent hydathodes develop on the epiphyllum. Sometimes a whitish layer was found over

the hydathodes. We have not found any taxa with any patent difference to this model, and some examples can be seen in **Figure 14A-B**. The stomatal length for each taxon can be found in **Table 2**.

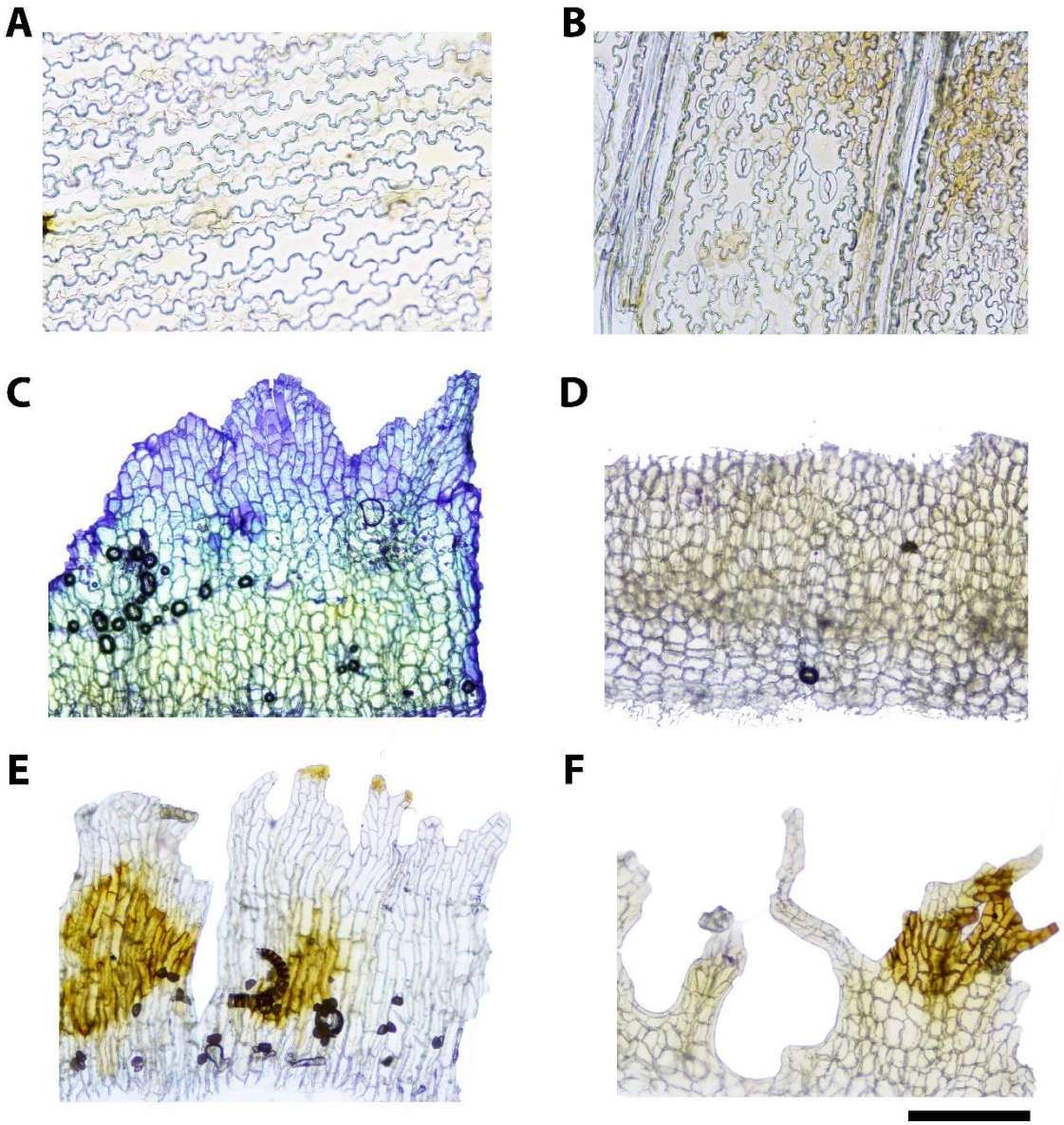

Figure 14. *Parablechnum* epidermis A adaxial side, *P. glaziovii* (*Y. Mexia 4546*, US1482144); B. Abaxial side, *P. glaziovii* (*Y. Mexia 4546*, US148244). *Parablechnum* indusia: C. *P. bicolor*, margin repand to erose, polygonal to subpolygonal epidermical model (*A.F. Fuentes 13724*, MO6255006); D. *P. lineatum*, margin repand, polygonal to subpolygonal epidermical model (*S. Fawcett & A.A. Reznicek 477*, VT198703); E. *P. montanum* margin lacerate, polygonal to subpolygonal epidermical model (*illegible collector*, UC313104); F. margin lacerate, subpolygonal to subsinuous epidermical model *P. moranianum* (*H. Churchill 3374*, VT198689). 231.5 µm in A, 242.5 µm in B, 569 µm in C, 490.5 µm in D, 451 µm in E, 433.5 µm in F.

Table 2. Summary table of the main characters of fertile pinnae cross-sections and epidermis of *Parablechnum* species. Species whose anatomy or epidermis could not be observed are marked with a dash.

Taxon	Dimorphism	Margin	Indusium		Receptacle	Costa		Stomata length (µm)
			Cross section	Margin and epidermic model		# stelles	Abaxial	
P. ambiguum	Dimorphic	Straight	Thin	Repand to lacerate Polygonal	Defined	2	Keeled	53.7±4
P. articulatum	Dimorphic	Straight to incurved	Thin	Straight to repand Polygonal	Extended	2	Rounded	48.6±5.2
P. atropurpureum	Dimorphic	Straight	Complex	Repand Polygonal	Extended	3	Rounded	56.5±5.3
P. bicolor	Dimorphic	Straight	Complex	Repand to erose Polygonal to subpolygonal	Extended	3	Rounded	58.9±5
P. camfieldii	Dimorphic	Straight to incurved	Complex	Straight to repand Polygonal to subpolygonal	Extended	2	Keeled	43.8±5.1
P. capense	Dimorphic	Straight	Complex	Repand to erose Polygonal	Extended	2	Rounded. almost flat	57.4±6.7
P. chauliodontum	Dimorphic	Straight to recurved	Complex	Repand Subpolygonal	Extended	3	Rounded	53.7±5.6
P. chilense	Dimorphic	Recurveds	Complex	Repand to erose Polygonal to subpolygonal	Extended	3	Rounded	57.9±3.5
P. chiriquanum	Dimorphic	Incurved	Complex	Repand Polygonal to subsinuous	Extended	3	Rounded	49.5±6.2
P. confusum	Dimorphic	Recurved	Complex	Repand Polygonal to subpolygonal	Extended	2	Keeled	58±5.5

Taxon	Dimorphism	Margin	Indusium		Receptacle	Costa		Stomata length (µm)
			Cross section	Margin and epidermic model		# stelles	Abaxial	
P. corbassonii	Dimorphic	Straight	Thin	Repand Polygonal to subsinuous	Extended	3	Rounded	61.6±5.6
P. cordatum	Dimorphic	Straight to incurved	Complex	Repand to erose Polygonal to subpolygonal	Extended	3	Rounded	71.8±5
P. falciforme	Dimorphic	Straight	Complex	Lacerate Polygonal to subpolygonal	Extended	3	Rounded	56.2±4.8
P. glaziovii	Dimorphic	Straight	Complex	Repand Polygonal	Extended	3	Rounded. almost flat	54±4.7
P. hieronymi	Dimorphic	Straight	Complex	Straight to repand Polygonal	Defined	2	Rounded	46.9±4.8
P. humbertii	Dimorphic	Straight to incurved	Complex	Repand to erose Polygonal to subpolygonal	Extended	5	Rounded	57.6±5.6
P. lechleri	Dimorphic	Recurved	Complex	Lacerate Subpolygonal	Extended	3	Rounded	60±5.9
P. lima	Dimorphic	Straight to recurved	Complex	Straight to repand Polygonal to subsinuous	Extended	3	Rounded. almost flat	47±5.7
P. lineatum	Dimorphic	Straight to recurved	Complex	Repand Polygonal to subpolygonal	Extended	3	Rounded	47.1±4.3
P. loxense	Contracted monomorphic	Straight to recurved	Complex	Lacerate. papillose Subsinuous to subpolygonal	Extended	3	Rounded	49±8.2
P. loxense var. stenophyllum	Contracted monomorphic	Straight to recurved	Complex	Lacerate. papillose Subpolygonal to subsinuous	Extended	3	Rounded	58.4±4.6

Taxon	Dimorphism	Margin	Indusium		Receptacle	Costa		Stomata length (µm)
			Cross section	Margin and epidermic model		# stelles	Abaxial	
P. marginatum	Dimorphic	Straight to recurved	Complex	Repand to erose Polygonal to subpolygonal	Extended	3	Rounded	58.5±5.8
P. milnei	Dimorphic	Straight to recurved	Complex	Straight to repand Subpolygonal to subsinuous	Extended	3	Rounded	48.3±5.1
P. minus	Dimorphic	Straight to recurved	Complex	Repand to erose Polygonal to subpolygonal	Extended	2	Rounded. almost flat	54.4±5.9
P. monomorphum	Flat monomorphic	Straight	Complex	Repand Polygonal to subpolygonal	Extended	3	Keeled	45.7±5.2
P. montanum	Dimorphic	Straight	Thin to complex	Lacerate Polygonal to subpolygonal	Extended	2	Keeled	40.6±33.7
P. moranianum	Subdimorphic to contracted monomorphic	Straight to recurved	Thin to complex	Lacerate Subpolygonal to subsinuous	Extended	3	Rounded. almost flat	51.3±8.5
P. nesophilum	Dimorphic	Straight	Thin to complex	Erose to lacerate Subpolygonal to subsinuous	Extended	3	Keeled	
P. novae-zelandiae	Dimorphic	Straight to recurved	Thin	Lacerate Subpolygonal to subsinuous	Extended	3	Keeled	35±5.4
P. obtusum	Flat monomorphic	Straight	Complex	Lacerate Polygonal to subpolygonal	Defined	2	Rounded	70.4±14.4
P. pacificum	Dimorphic	Straight to incurved	Thin	Lacerate Polygonal to subpolygonal	Extended	2	Rounded	47.8±4.5
P. pazense	Flat monomorphic	Straight	Complex	Repand	Extended	3	Rounded	53.9±6.4

Taxon	Dimorphism	Margin	Indusium		Receptacle	Costa		Stomata length (µm)
			Cross section	Margin and epidermic model		# stelles	Abaxial	
				Polygonal to subpolygonal				
P. procerum	Dimorphic	Straight	Complex	Erose to lacerate Polygonal to subpolygonal	Extended	1	Rounded. almost flat	54.7±7.7
P. proliferum	Dimorphic	Straight	Complex	Repand Polygonal	Extended	5	Rounded	–
P. revolutum	Subdimorphic to contracted monomorphic	Straight	Thin	Repand Polygonal to subpolygonal	Extended	2	Keeled	55.7±5.5
P. rheophyticum	Dimorphic	Straight to recurved	Complex	Repand to erose Polygonal	Extended	3	Rounded. almost flat	56.9±6.1
P. ryanii	Dimorphic	Straight to recurved	Complex	Repand Polygonal	Extended	3	Rounded. almost flat	48.3±5.8
P. schiedeanum	Dimorphic	Straight to incurved	Complex	Repand to lacerate Polygonal to subpolygonal	Extended	2	Rounded	63.8±5.7
P. sessilifolium	Dimorphic	Straight to incurved	Complex	Repand Polygonal to subpolygonal	Extended	3	Rounded	38.3±4.3
P. squamatum	Dimorphic	Straight	Complex	Repand to lacerate Polygonal to subpolygonal	Extended	3	Rounded. almost flat	64.5±5.9
P. stipitellatum	Subdimorphic to contracted monomorphic	Recurved	Complex	Repand to lacerate Polygonal to subpolygonal	Extended	3	Rounded	33.7±5.9
P. stuebelii	Subdimorphic to contracted monomorphic	Recurved	Complex	Repand to lacerate Polygonal	Extended	3	Rounded	68.6±7.3

Taxon	Dimorphism	Margin	Indusium		Receptacle	Costa		Stomata length (µm)
			Cross section	Margin and epidermic model		# stelles	Abaxial	
P. subcordatum	Dimorphic	Recurved	Complex	Repand Subpolygonal to subsinuous	Extended	3	Rounded	53.7±5.6
P. triangularifolium	Dimorphic	Straight to incurved	Complex	Repand to lacerate Subpolygonal to subsinuous	Extended	3	Rounded	52.1±5.1
P. tuerckheimii	Dimorphic	Straight	Complex	Repand Polygonal to subpolygonal	Extended	3	Rounded	44.3±4.6
P. usterianum	Dimorphic	Straight	Thin to complex	Polygonal Repand	Extended	3	Rounded. almost flat	46.4±5.9
P. varians	Dimorphic	Straight to incurved	Complex	Polygonal Lacerate	Extended	3	Rounded	78.7±11.7
P. vestitum	Dimorphic	Recurved	Complex	Lacerate Polygonal	Extended	2	Keeled	48.5±6.4
P. wattsii	Dimorphic	Recurved	Complex	Repand Polygonal to subpolygonal	Extended	3	Keeled	47.3±5.1
P. werffii	Dimorphic	Straight	Complex	Repand Polygonal	Extended	2	Flat	61.2±5.3
P. wohlgemuhii	Dimorphic	Straight to recurved	Thin to complex	Repand Subpolygonal to subsinuous	Defined	2	Rounded	–

Spores

In general, *Parablechnum* spores are monolete, flat-convex in longitudinal equatorial view and elliptical in polar view, with a size that ranges from (8–)42(–79) µm wide and (24–)58(–100) µm long, with a densely folded or cristate-reticulate perispore, with more or less high muri delimiting polygonal areolae, forming reticules or, rarely, not folded, reticulate, with walls sometimes fenestrated. Sometimes, there are short (shorter than the walls) to long filamentous processes (longer or as long as the walls) that vary in their presence and density and granules, granulate exospore, usually with low, irregular verrucae with granules above. It is usual to find aborted spores or spores whose perispore has fallen or broken.

Considering the perispore macro and micro-ornamentation we have been able to distinguish three major morphological groups: Group 1 comprises species with not folded perispore, reticulate, with more or less fenestrated walls (**Figure 15A-B**); Group 2 have species with cristate-reticulate perispores, densely folded, with acute or obtuse folds, without defined areolae, with spreading or moderately dense short filamentous processes (**Figure 15C-F**); Group 3 presents cristate-reticulate perispores, with long folds, (scarce, acute or obtuse), delimiting polygonal or irregular areolae (**Figure 16-24**). The first group presents three subgroups: Group 1.1 with filamentous processes rather long and twisted, sometimes welded on the base, from dense to moderately dense (**Figure 16-19**); Group 1.2 without or with scarce short filamentous processes, scattered on the areolae, sometimes welded laterally forming short crests (**Figure 20-22**); Group 1.3 without filamentous processes and perispore surface rugulose (**Figure 23-24**). The taxa belonging to each group can be checked on **Table 3**.

The spores of all studied species are described below in alphabetical order. The size of the spores represents the minimum and maximum values in brackets and the mean in the middle (major equatorial diameter × polar diameter). These are rounded values, the exact values can be found in **Table 3.**

Parablechnum ambiguum C. Presl: spores (50–)59(–72) × (37–)41(–48) µm, perispore rugulose, cristate-reticulate, with sharp low walls forming irregular sharp ridges, with a short supralesural fold, about 2/3 the length of the spore, with short, sparse filamentous processes; exospore granulose (**Figure 15C**).

Table 3. Summary of the morphological groups formed with the spore ornamentation with the measures (mean ± standard deviation) of each taxa presented as major equatorial diameter × polar diameter. The taxa marked with * have not been seen here but on previously published works.

Group		Taxa	Spore measure (µm)
Group 1: perisporium without folds. reticulate. with more or less fenestrated walls.		*P. nesophilum*	46.6±5 × 60.4±5.7
		P. vestitum	44.3±5.3 × 56.7±6
Group 2: perispores densely folded. with short acute or obtuse folds. without defined areoles. with scattered or moderately dense short filaments		*P. ambiguum*	41.2±3.6 ×58.9±6.6
		P. camfieldii	34.5±5.9 ×49.6±5.4
		P. capense	39.1±3.8 × 54.3±4.8
		*P. puniceum**	
Group 3: perisporium with long. sparse. acute. or obtuse folds. delimiting polygonal or irregular areolae	**Group 3.1:** filamentous processes rather long and twisted. sometimes laterally welded at the base. dense to moderately dense	*P. atropurpureum*	47.6±5.2 × 65.4±5.2
		P. bicolor	35.5±5 × 50±5
		P. chilense	36.5±3.2 × 51.2±3.2
		P. chiriquanum	50.2±3.3 × 66.3±6.5
		P. falciforme	42.4±3.2 × 56.3±4.5
		P. glaziovii	37.2±8.2 × 51.5±10.2
		P. lechleri	33.2±4.2 × 48±4
		P. loxense	44.8±7.6 × 60.4±8.9
		P. loxense var. *stenophyllum*	43.7±4.5 × 59.8±5.8
		P. marginatum	45.7±6.8 × 64.3±7.2
		P. pazense	46.7±4.6 × 64.6±6
		P. rheophyticum	47.1±5.6 × 62.7±6
		P. ryanii	53.7±7 × 68.8±7.3
		P. sessilifolium	44±4.7 × 58.3±6.6
		P. squamatum	44.4±5 × 56.8±5.2
		P. stipitellatum	37.5±3.4 × 54.6±10.5
		P. stuebelii	39.1±3.5 × 56.1±5.8
		P. subcordatum	39.1±5.9 × 61.8±4.8
		P. usterianum	43.4±4.8 × 64.7±4.3
		P. varians	42.2±3.4 ×55.4±5.1
		P. wattsi	40.3±3.3 × 56.1±3.8
	Group 3.2: without filament processes or very few short filaments scattered along the areoles. sometimes laterally welded to form short ridges.	*P. cordatum*	46.2±9 × 60.2±9.5
		*P. dilatatum**	
		P. humbertii	48.7±5.6 × 66.1±5.4
		P. hieronymi	47.3±4 × 63.8±5.3
		P. lima	38.1±4 × 54.3±4.2
		P. lineatum	41.2±5.4 × 57.1±4.8
		P. milnei	53.4±4.4 × 75.4±5.9
		P. moranianum	47.8.2±5.2 × 65.3±7.1
		P. proliferum	44.2±5.6 × 57.9±5.4
		P. revolutum	43.5±5.4 × 58.7±5.7
		P. schiedeanum	44.1±3.8 × 58.8±5
		P. triangularifolium	36.1±3.9 × 51.7±5.0
		P. werffii	49.4±3.7 × 67.7±4.1
		P. wholgemuthii	36.5±4.4 × 49.4±5.2
	Group 3.3: Without filamentous processes or very few short filaments scattered along the areoles and with roughened perispore surface	*P. chauliodontum*	33.9±4.5 × 47.5±4.3
		P. corbassonii	36.1±13.8 × 50±15.6
		P. minus	37.4±6.1 × 53.1±8.3
		P. monomorphum	56.8±9.5 × 81.8±12.5
		P. montanum	31±4.4 × 47.8±4.6
		P. novae-zelandiae	36.8±3.9 × 53.1±4.5
		P. obtusum	42.8±5.7 × 57.7±6.2
		P. pacificum	39±4 × 56.5±4.7
		P. procerum	34.7±4.2 × 48.9±6.1
		P. tuerckheimii	46.2±4.6 × 60.7±5.1
		*P. wurunuran**	

Parablechnum atropurpureum (A.R.Sm.) Gasper & Salino: spores (56–)65(–74) × (39–)48(–55) µm, perispore smooth, cristate-reticulate, with low, thick walls forming large polygonal areoles, with a supralesural fold running the entire length of the spore, with long, very dense filamentous processes over the entire surface, spongy internal structure; exospore densely granular (**Figure 16A**).

Parablechnum bicolor (M.Kessler & A.R.Sm.) Gasper & Salino: spores (40–)50(–61) × (26–)36(–46) µm, perispores smooth or slightly rugulose, cristate-reticulate, with more or less high, sharp walls, forming large to medium areoles, with more or less long moderately dense filamentous processes, spongy internal structure; exospores densely granular. (**Figure 16B**).

Parablechnum camfieldii (Tindale) Gasper & Salino: spores (38–)50(–69) × (23–)35(–63) µm µm, perispores smooth, cristate-reticulate, forming short abundant ridges, with more or less long filamentous processes not very abundant, spongy internal structure; smooth exospores to which the fibrous-filamentous sculptural elements of the internal perispores remain attached. (**Figure 15D-E**).

Parablechnum capense: spores (39–)54(–70) × (32–)39(–51) µm, perispore smooth, cristate-reticulate, forming a reticulum of low, sharp walls delimiting small areoles, supralesural fold long and thin, subterminal, with long filamentous processes not very dense, spongy internal structure, granular exospore (**Figure 15 F**).

Parablechnum chauliodontum: spores (39–)47(–59) × (27–)33(–42) µm, perispore granular, cristate-reticulate, with high and thick walls forming large polygonal areoles, with more or less long filamentous processes not very abundant, internal structure spongy, exospore granular. (**Figure 23A**).

Parablechnum chilense: spores (43–)51(–57) × (29–)36(–45) µm, perispores cristate-reticulate, with thin, sharp walls, delimiting small areoles, with long, moderately abundant filamentous processes, located in the areole lacunae, internal structure spongy; exospores smooth or slightly granular. (**Figure 16C-D**).

Parablechnum chiriquanum (Broadh.) Gasper & Salino: spores (44–)51(–57) × (29–)37(–45) µm, perispore-cristate-reticulate, with thin, sharp walls, delimiting small polygonal areoles, with very abundant long filamentous processes, spongy internal

structure; exospore with a base of irregular low warts and abundant granules above (**Figure 16E**).

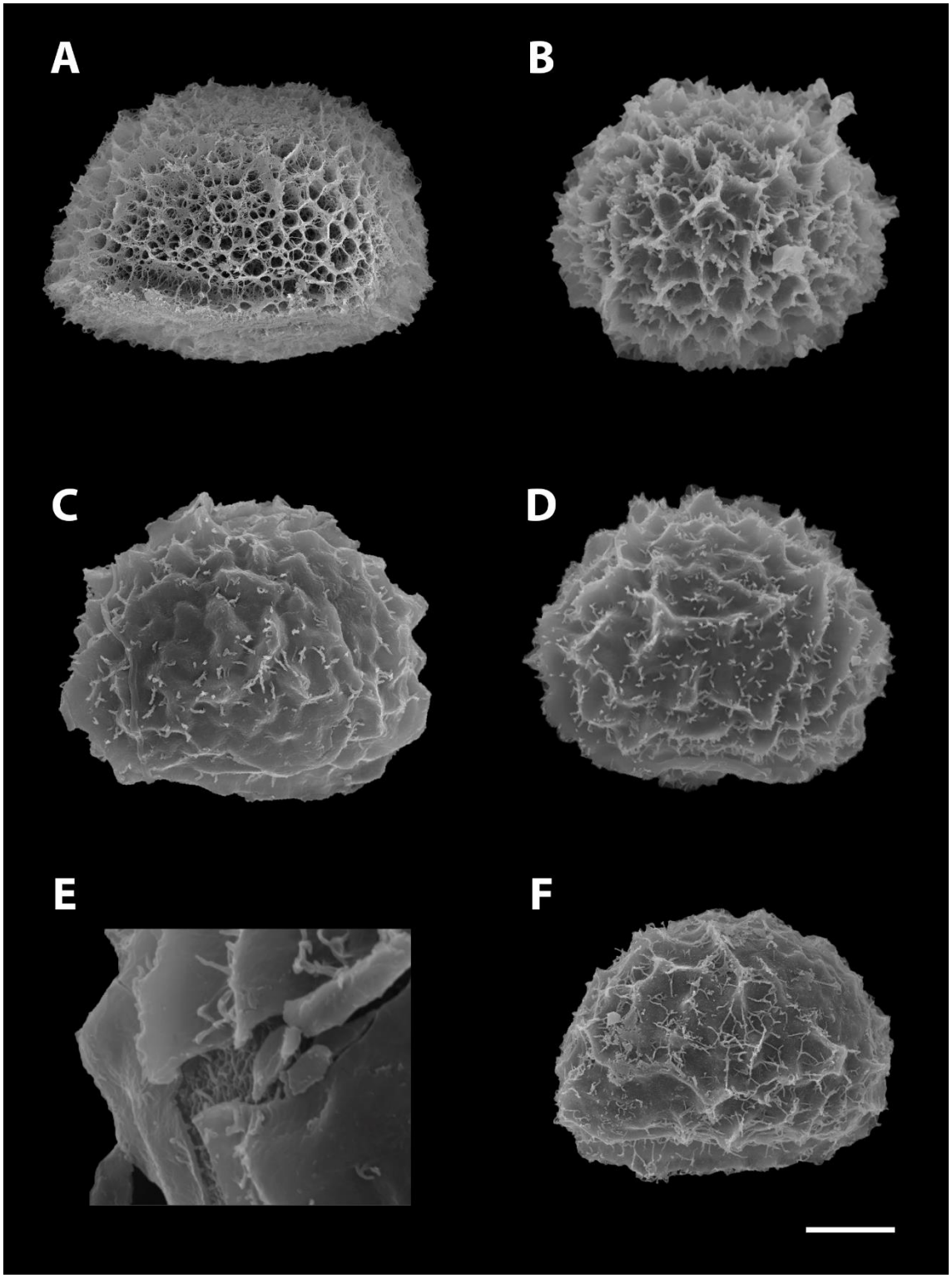

Figure 15. *Parablechnum* spores of group 1: A. *P. nesophilum* (*Sundue 4251*, MACB); B. *P. vestitum* (*J.F. Barcelona 3173*, US3563129). *Parablechnum* spores of group 2: C. *P. ambiguum* (*Coveny 9133*, NY); D & E. *P. camfieldii* (*Coveny 10191*, NY); F. *P. capense* (*R.J. Rodin 1141*, MO1606356). Scale: 16 µm in A & F, 15 µm in B, 12 µm in C, 14 µm in D, 4.5 µm in E.

Parablechnum corbassonii (Brownlie) Gasper & Salino: spores (39–)48(–58) × (22–)34(–43) µm, perispores rugulose, cristate-reticulate, with high, thin, sharp walls, forming medium to large polygonal areoles, with filamentous processes in the areoles and on the fold ridges, spongy internal structure; exospores granulose (**Figure 23B**).

Parablechnum cordatum: spores (43–)60(–75) × (25–)46(–62) µm, perispores smooth, cristate-reticulate, with high, thin, sharp walls, forming large polygonal areoles, without filamentous processes, spongy internal structure; exospores granular exosporium (**Figure 20A-B**).

Parablechnum falciforme (Liebm.) Gasper & Salino: spores (43–)56(–67) × (35–)42(–52) µm, perispores smooth, cristate-reticulate, with high, thin, sharp walls, forming small polygonal areoles, with more or less long filamentous processes in the lacunae of the areoles and at the edge of the walls, spongy internal structure; exospores with irregular low verrucous base and abundant granules above. (**Figure 16F**).

Parablechnum glaziovii (Christ) Gasper & Salino: spores (24–)52(–92) × (16–)37(–70) µm, perispores smooth, with low, thin, tapering walls, forming small polygonal areoles or reticules, with moderately abundant filamentous processes, spongy inner structure; exospores granular (**Figure 17A**).

Parablechnum hieronymi (Brause) Gasper & Salino: spores (47–)64(–75) × (30–)47(–55) µm, perispores smooth or slightly roughened, cristate-reticulate, with tall thin walls delimiting large polygonal areoles, with short, moderately abundant, moderately abundant filamentous processes, distributed evenly over the entire spore surface, internal structure and exospores not observed (**Figure 20D**).

Parablechnum humbertii: spores (49–)66(–78) × (35–)49(–62) µm, perispores rugulose, cristate-reticulate, with thick, high walls forming medium to large polygonal areoles, without filamentous processes or with moderately abundant sporadic filamentous processes in the areole lacunae, with granules, spongy internal structure; exospores granulose (**Figure 20C**).

Parablechnum lechleri (Mett.) Gasper & Salino: spores (40–)48(–62) × (23–)33(–43) µm, perispore smooth, cristate-reticulate, with low, thin walls, forming small areoles or a reticulum, with moderately abundant long filamentous processes over the entire surface,

spongy internal structure; exospore with a warty base with granules on top (**Figure 17B-C**).

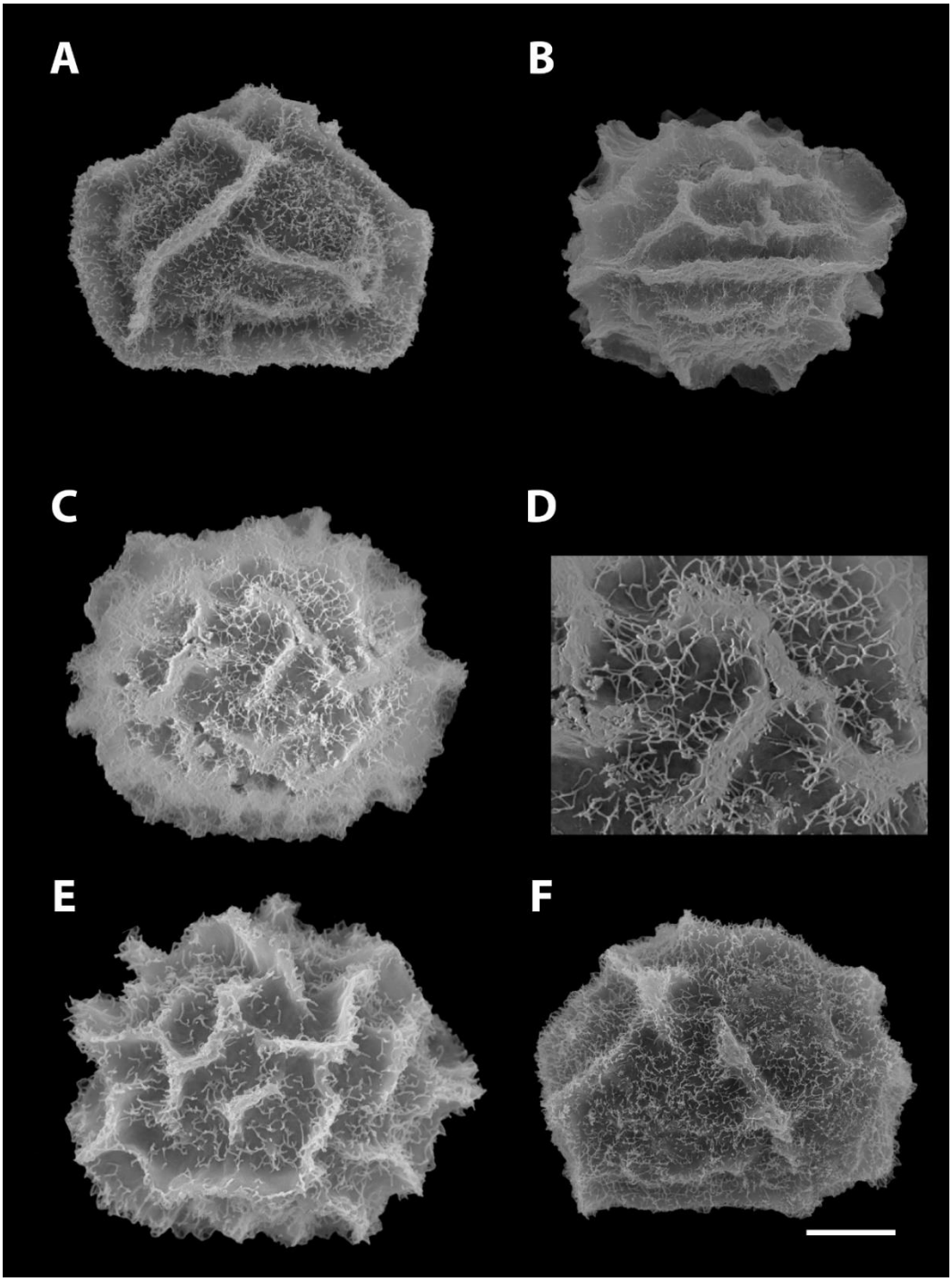

Figure 16. *Parablechnum* spores of Group 3.1: A. *P. atropurpureum* (*G.S. Jenman 286*, NY04187107); B. *P. bicolor* (*A.F. Fuentes 13724*, MO6255006); C & D. *P. chilense* (*J.M. Gabriel y Galán s.n.*, MACB109257); E. *P. chiriquanum* (*UG. Davidse et al. 28674, C1509051*); F. *P. falciforme* (*R. Torres et al 17654*, VT198685). Scale: 23 µm in A, 20 µm in B, 14.5 µm in C, 7 µm in D, 12.5 µm in E, 15 µm in F.

Parablechnum lima (Rosenst.) Gasper & Salino: spores (40–)54(–67) × (27–)38(–50) µm, perisporium smooth to granular, cristate-reticulate, with low, thick walls, forming large polygonal areoles, with few or no filamentous processes, internal structure spongy; exosporium finely granular (**Figure 20E-F**).

Parablechnum lineatum (Sw.) Gasper & Salino: spores (43–)57(–66) × (29–)41(–52) µm, perispores smooth to granular, with possible globules, cristate-reticulate, with high, thin, sharp walls, forming a reticulum or large areoles, without filamentous processes or with some scattered long filaments in areole lacunae, internal structure and exosporium not observed (**Figure 21A**).

Parablechnum loxense var. *loxense* (Kunth) Gasper & Salino: spores (37–)60(–86) × (7–)45(–67) µm, perispore smooth, cristate-reticulate, low walled, thick, forming large polygonal areoles, with very abundant long filamentous processes over the entire surface, spongy internal structure; exospore with a base of irregular low verrucae and abundant granules above. (**Figure 17D-E**).

Parablechnum loxense var. *stenophyllum* (Klotzsch) Gasper & Salino: spores (42–)60(–73) × (42–)60(–73) µm with no notable differences with the *loxense* variety (**Figure 17F**).

Parablechnum marginatum: spores (41–)64(–81) × (27–)46(–60) µm; perispores smooth, cristate-reticulate, high-walled, thin, tapering, forming large polygonal areoles or reticules, with long filamentous processes in the areole lacunae and at the edges of the walls, moderately abundant; internal structure spongy; exosporium granulose (**Figure 18A**).

Parablechnum milnei (Carruth.) Gasper & Salino: spores (60–)75(–85) × (37–)53(–62) µm, perispores smooth, cristate-reticulate, with broad, obtuse, high folds, the terminal supralesural, forming large polygonal areoles, with no or very few filamentous processes, spongy internal structure; exospores granulose (**Figure 21B**).

Parablechnum minus (R.Br.) Gasper & Salino: spores (31–)53(–69) × (23–)37(–51) µm, perisporium rugulose, cristate-reticulate, with broad, acute, more or less high folds, forming medium to large polygonal areoles, without or with only a few very short

filamentous processes scattered in the areoles and on the edges of the walls, internal structure and exosporium not observed (**Figure 23C**).

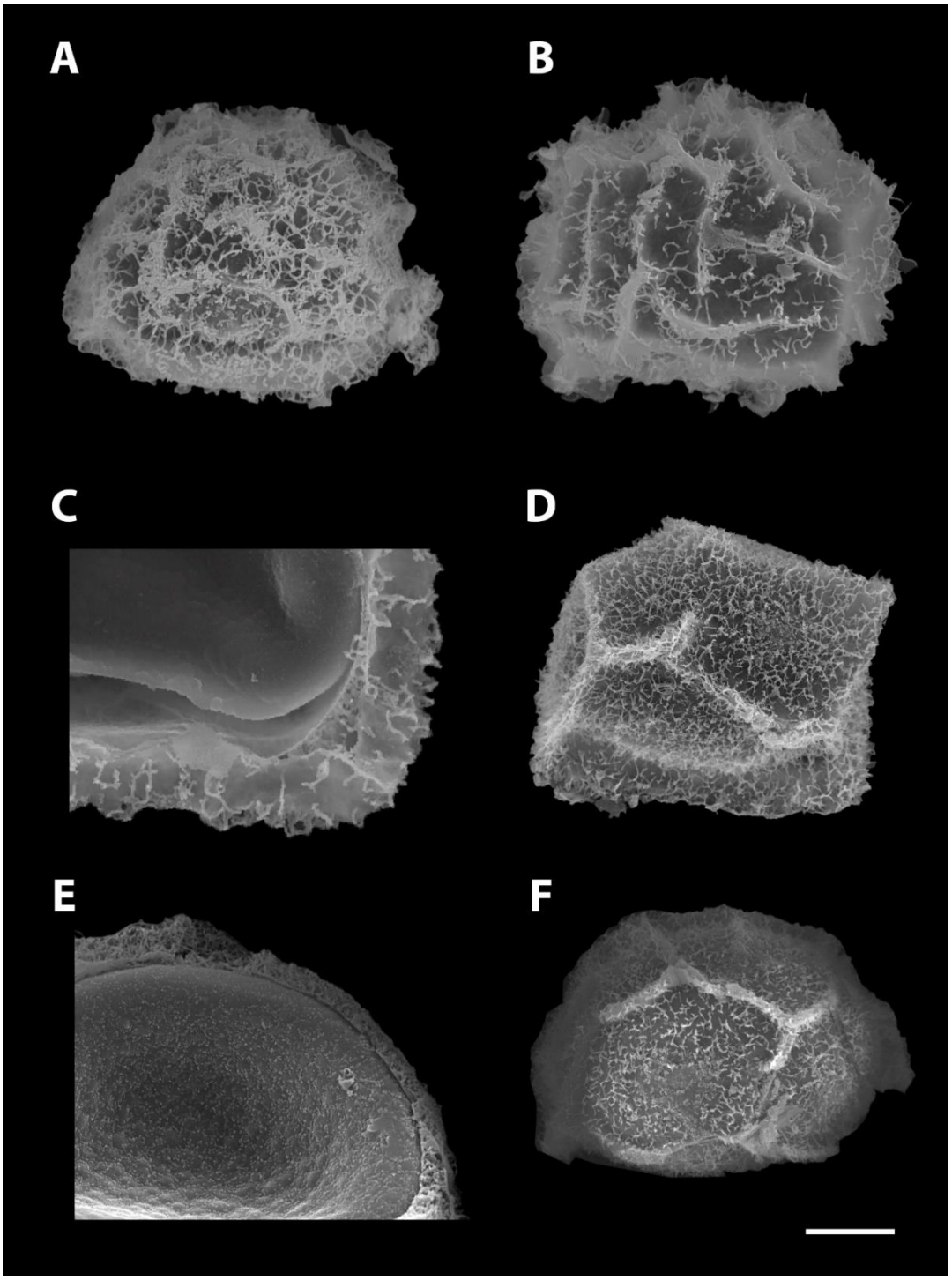

Figure 17. *Parablechnum* spores of Group 3.1: A. *P. glaziovii* (*R.F. Novelino 1031, J.E. Oliveira 246, P.B. Pita 131, D. Gragano 48*, NY02597230); B & C. *P. lechleri* (*L. Valenzuela Gamarra 10166*, MO6560309); D. *P. loxense* (*D. Barrington 353*, VT198692); E. *P. loxense* (*H. Churchill 3370*, VT198691); F. *P. loxense* var. *stenophyllum* (*Vázquez & Monteagudo 29947*, NY). Scale: 15 µm in A, 12.5 µm in B, 9 µm in C, 17 µm in D, 8 µm in E, 17.5 µm in F.

Parablechnum monomorphum (R.C.Moran & B.Øllg.) Gasper & Salino: spores (48–)82(–100) × (38–)57(–79) µm; perispores rugulose, cristate-reticulate, low-walled, thick, forming large polygonal areoles, without filamentous processes, spongy internal structure; exospores granulose (**Figure 23D**).

Parablechnum montanum (T.C.Chambers & P.A.Farrant) Gasper & Salino: spores (41–)48(–62) × (21–)31(–43) µm; perisporium rugulose, cristate-reticulate, forming large polygonal areoles, without filamentous processes, internal structure not observed; exosporium granulose (**Figure 23E**).

Parablechnum moranianum (A.Rojas) Gasper & Salino: spores (49–)65(–84) × (37–)48(–58) µm; perispores with granules on the surface, cristate-reticulate, with low and thick walls, forming large polygonal areoles, without filamentous processes or with some short filaments scattered in the areole lacunae and on the edges of the walls, internal structure and exosporium not observed (**Figure 21C**).

Parablechnum nesophilum: spores (47–)60(–72) × (37–)47(–57) µm; perispores not folded, reticulate, with fenestrated walls, without filamentous processes, spongy internal structure; exospores granulsose (**Figure 15A**).

Parablechnum novae-zelandiae (T.C.Chambers & P.A.Farrant) Gasper & Salino: spores (39–)53(–61) × (25–)37(–50) µm, perispore rugulose, weakly folded, without filamentous processes, internal structure narrow, spongy; exospore densely granular (**Figure 23F**).

Parablechnum obtusum (R.C. Moran & A.R.Sm.) Gasper & Salino: spores (48–)58(–70) × (31–)43(–58) µm; perispores rugulose, cristate-reticulate, with low, thick walls, delimiting large polygonal areoles, without filamentous processes, internal structure not observed; exospores granulose (**Figure 24A**).

Parablechnum pacificum (Lorence & A.R.Sm.) Gasper & Salino: spores (48–)57(–69) × (31–)39(–50) µm, perispores rugulose, cristate, with thick, low walls, forming two or three large areoles, without filamentous processes, internal structure spongy; exospores granulose (**Figure 24B**).

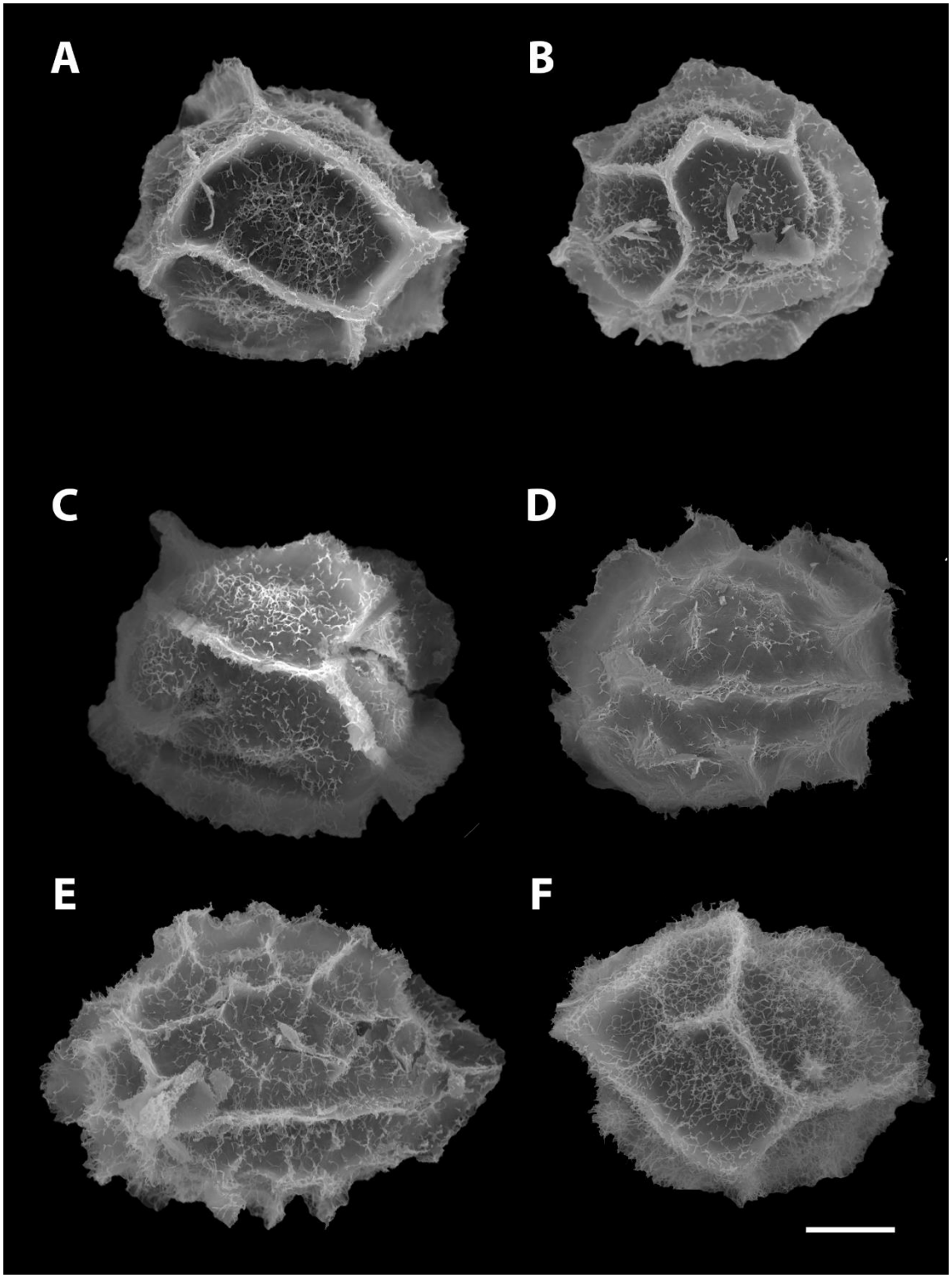

Figure 18. *Parablechnum* spores of Group 3.1: A. *P. marginatum* (*no collector 357*, P01462831); B. *P. pazense* (*A.F. Fuentes Claros 11620*, MO6136888); C. *P. rheophyticum* (*W.A. Palacios Cuenca 6934*, MO4303680); D. *P. ryanii* (*R. Hill & L.R. Phillippe 29004*, VT198716); E. *P. sessilifolium* (*D.B. Lellinger 976*, MO2139852); F. *P. squamatum* (*I. Jiménez Pérez 2828*, MO6112550). Scale: 21 µm in A, 20 µm in B, 18.5 µm in C, 19 µm in D, 14.5 µm in E, 17 µm in F.

Parablechnum pazense (M.Kessler & A.R.Sm.) Gasper & Salino: spores (48–)64(–71) × (38–)47(–55) µm, perispores smooth or slightly rugulose, cristate-reticulate, with low, thick walls, delimiting large polygonal areoles, with long, twisted filamentous processes moderately abundant on the entire surface, internal structure and exosporium not observed (**Figure 18B**).

Parablechnum procerum: spores (35–)49(–65) × (27–)35(–52) µm; perispores rugulose, cristate-reticulate, with low, thick walls, delimiting large polygonal areoles, without filamentous processes or with some scattered short filaments in the areole lacunae, compact internal structure; exospores granulose (**Figure 24C**).

Parablechnum proliferum (Rosenst.) Gasper & Salino: spores (46–)58(–74) × (30–)44(–64) µm; perispores smooth, cristate-reticulate, with low, thick, slightly tapering walls, deflected at apex, delimiting large polygonal areoles, without filamentous processes or with some scattered filament in areole lacunae, internal structure spongy; exospores granular, with low verrucae (**Figure 21D**).

Parablechnum revolutum (Alderw.) Gasper & Salino: spores (41–)59(–69) × (33–)43(–56) µm; perispore rugulose, cristate-reticulate, thick-walled, low, forming medium to small polygonal areoles, with moderately abundant short filamentous processes over entire spore surface, internal structure and exospore not observed (**Figure 21E**).

Parablechnum rheophyticum: spores (50–)63(–72) × (37–)47(–57) µm; perispores smooth, cristate-reticulate, high-walled, thin, sharp, forming large polygonal areoles, without filamentous processes, internal structure spongy; exospores smooth or granular (**Figure 18C**).

Parablechnum ryanii (Kaulf.) Gasper & Salino: spores (53–)76(–100) × (37–)57(–81) µm; perispore, smooth or slightly roughened, cristate-reticulate, with thin, low walls, forming large polygonal areoles, with sparse to moderately abundant long filamentous processes over the entire spore surface, spongy internal structure; exospore granulose (**Figure 18D**).

Parablechnum schiedeanum: spores (47–)59(–75) × (37–)44(–55) µm; perispore smooth, cristate-reticulate, high-walled, thin, sharp, delimiting large polygonal areoles,

without filamentous processes, spongy internal structure; exospore with low warts (**Figure 21F**, **Figure 22A**).

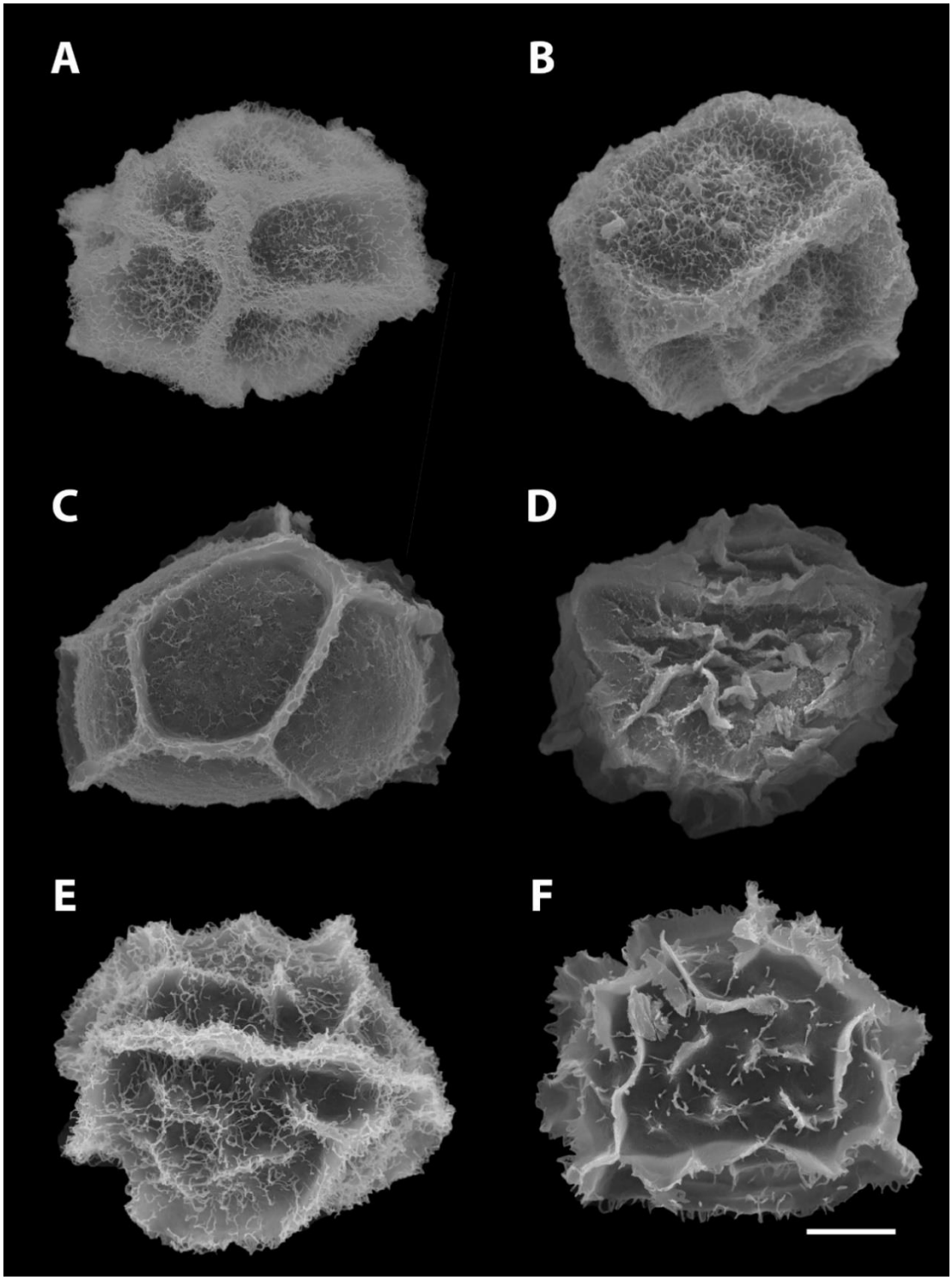

Figure 19. *Parablechnum* spores of Group 3.1: A. *P. stipitellatum* (*R.B. Foster 10304*, US3221253); B. *P. stuebelii* (*van der Werff 23230*, NY); C. *P. subcordatum* (*J.T. Buchholz 1346*, US2082441); D. *P. usterianum* (*Y. Mexia 4782*, P01395987); E. *P. varians* (*Mickel 95-M077*, NY04187113); F. *P. wattsi* (*E.F. Constable 6910*, US2596731). Scale: 23.5 µm in A, 19 µm in B, 15.5 µm in C, 17.5 µm in D, 14.5 µm in E, 13.5 µm in F.

Parablechnum sessilifolium (Klotzsch ex Christ) Gasper & Salino: spores (48–)58(–70) × (32–)44(–52) µm; perispore smooth, cristate-reticulate, high-walled, thick, forming a reticulum, with abundant long filamentous processes on the entire spore surface, spongy internal structure; exospore not observed (**Figure 18E**).

Parablechnum squamatum (M.Kessler & A.R.Sm.) Gasper & Salino: spores (47–)57(–69) × (34–)44(–54) µm; perispores smooth, cristate-reticulate, with high, thick walls, forming large polygonal areoles, without filamentous processes, with granules, internal structure and finely granular exospores (**Figure 18F**).

Parablechnum stipitellatum (C.Chr.) Gasper & Salino: spores (38–)55(–83) × (30–)38(–44) µm; perispores smooth, cristate-reticulate, with low, thick walls, forming large polygonal areoles, with very long and abundant filamentous processes on the entire spore surface, spongy interior; exospores granular (**Figure 19A**).

Parablechnum stuebelii (Hieron.) Gasper & Salino: spores (47–)57(–69) × (34–)44(–54) µm; perispores smooth, cristate-reticulate, with low, thick walls, forming large polygonal areoles, with very abundant long filamentous processes on the entire spore surface, internal structure not observed; exospores granular (**Figure 19B**).

Parablechnum subcordatum (E.Fourn) Gasper & Salino: spores (52–)62(–74) × (38–)47(–62) µm; perispores smooth, cristate-reticulate, with low, thin walls, forming medium to large polygonal areoles, with moderately abundant long filamentous processes in areole lacunae, spongy internal structure; exospores granular (**Figure 19C**).

Parablechnum triangularifolium (T.C.Chambers & P.A.Farrant) Gasper & Salino: spores (39–)52(–66) × (28–)36(–52) µm; perispores rugulose, cristate-reticulate, with high, thick walls, forming medium to large polygonal areoles, without filamentous processes or with some sporadic short, thick filaments, spongy internal structure; exospores granulose (**Figure 22B**).

Parablechnum tuerckheimii (Brause) Gasper & Salino: spores (51–)61(–69) × (35–)46(–53) µm; perispore smooth, cristate-reticulate, with very low, thin walls, forming very large polygonal areoles, with moderately abundant long filamentous processes, spongy internal structure; exospore with low verrucae (**Figure 24D**).

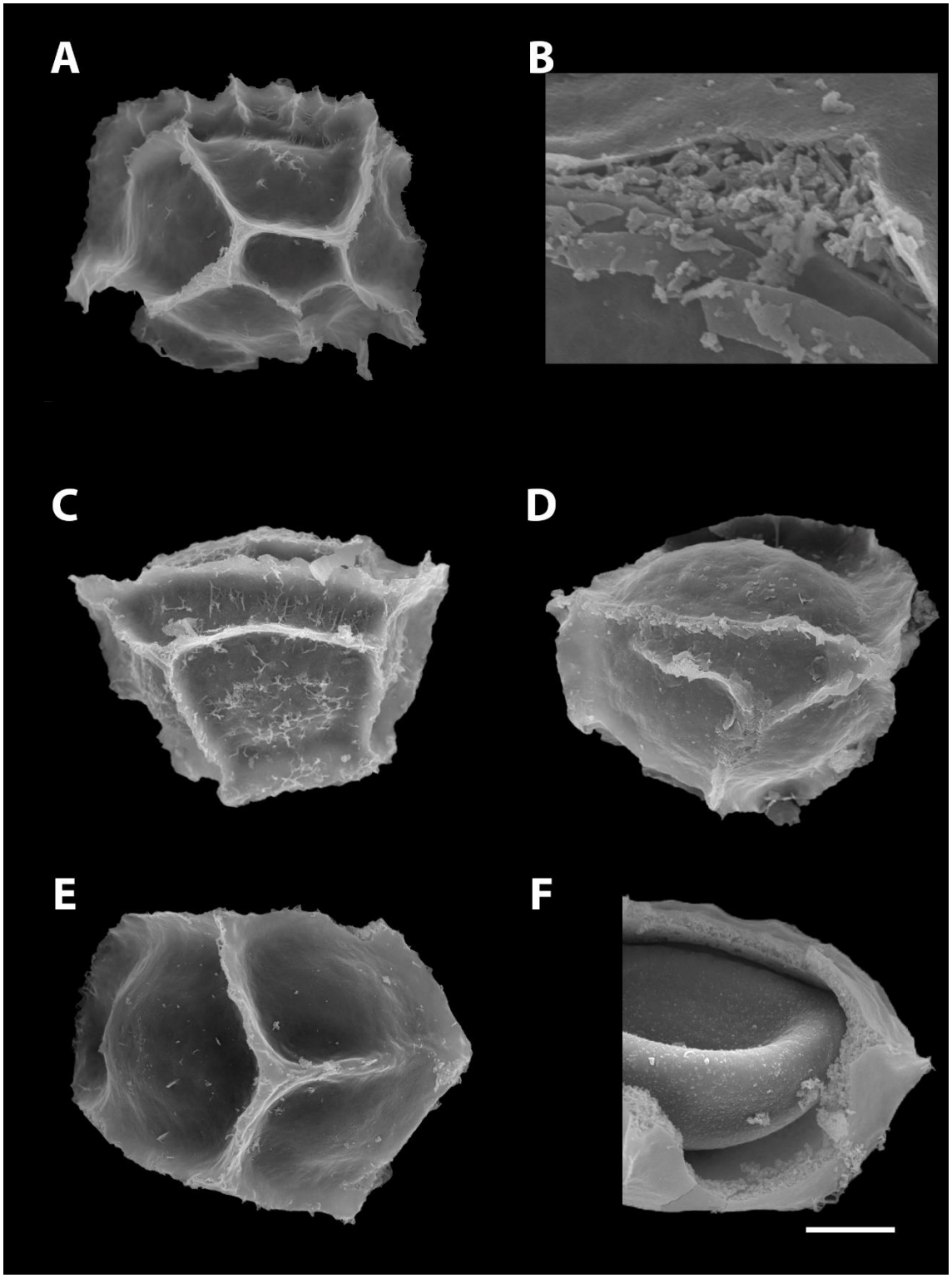

Figure 20. *Parablechnum* spores of Group 3.2: A. *P. cordatum* (*P.A. Silverstone-Sopkin 10189*, MO4806421); B. *P. cordatum* (*Skilman 12893*, NY); C. *P. humbertii* (*F. Rakotondrainibe & F. Raharimalala 2519*, P00904704); D. *P. hieronymi* (*M. Sundue et al 3711*, VT198739); E & F. *P. lima* (*B. Ollgaard 23590*, MO4666586). Scale: 18.5 µm in A, 2.5 µm in B, 19.5 µm in C, 14 µm in D, 15 µm in E, 11 µm in F.

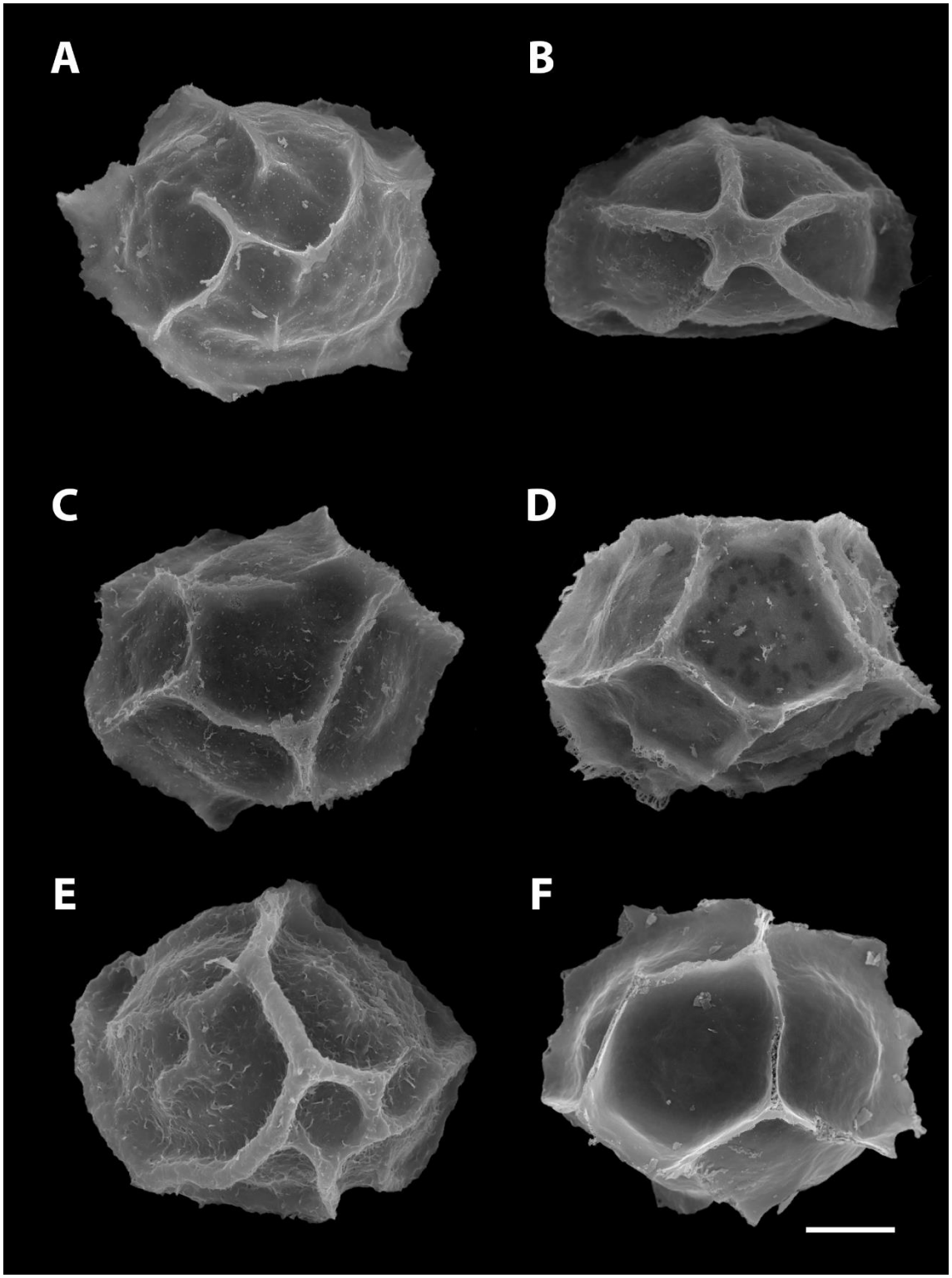

Figure 21. *Parablechnum* spores of Group 3.2: A. *P. lineatum* (*S. Fawcett & A.A. Reznicek 477*, VT198703); B. *P. milnei* (*M. Schmid 3101*, P01573192); C. *P. moranianum* (*H. Churchill 3374*, VT198689); D. *P. proliferum* (*Lellinger & de la Sota 9196*, NY); E. *P. revolutum* (*W. Vink 17260*, NY04187080); F. *P. schiedeanum* (*T.G. Yuncker 5936*, US1637799). Scale: 16.5 µm in A & E, 22 µm in B, 19.5 µm in C, 14.5 µm in D, 16 µm in F.

Parablechnum usterianum (Christ) Gasper & Salino: spores (56–)65(–75) × (34–)43(–58) µm; perispore smooth, cristate reticulate, with high, thin walls, forming small polygonal areoles, with abundant to moderately abundant long filamentous processes in the areolar lacunae; internal structure spongy; exospore densely granular (**Figure 19D**).

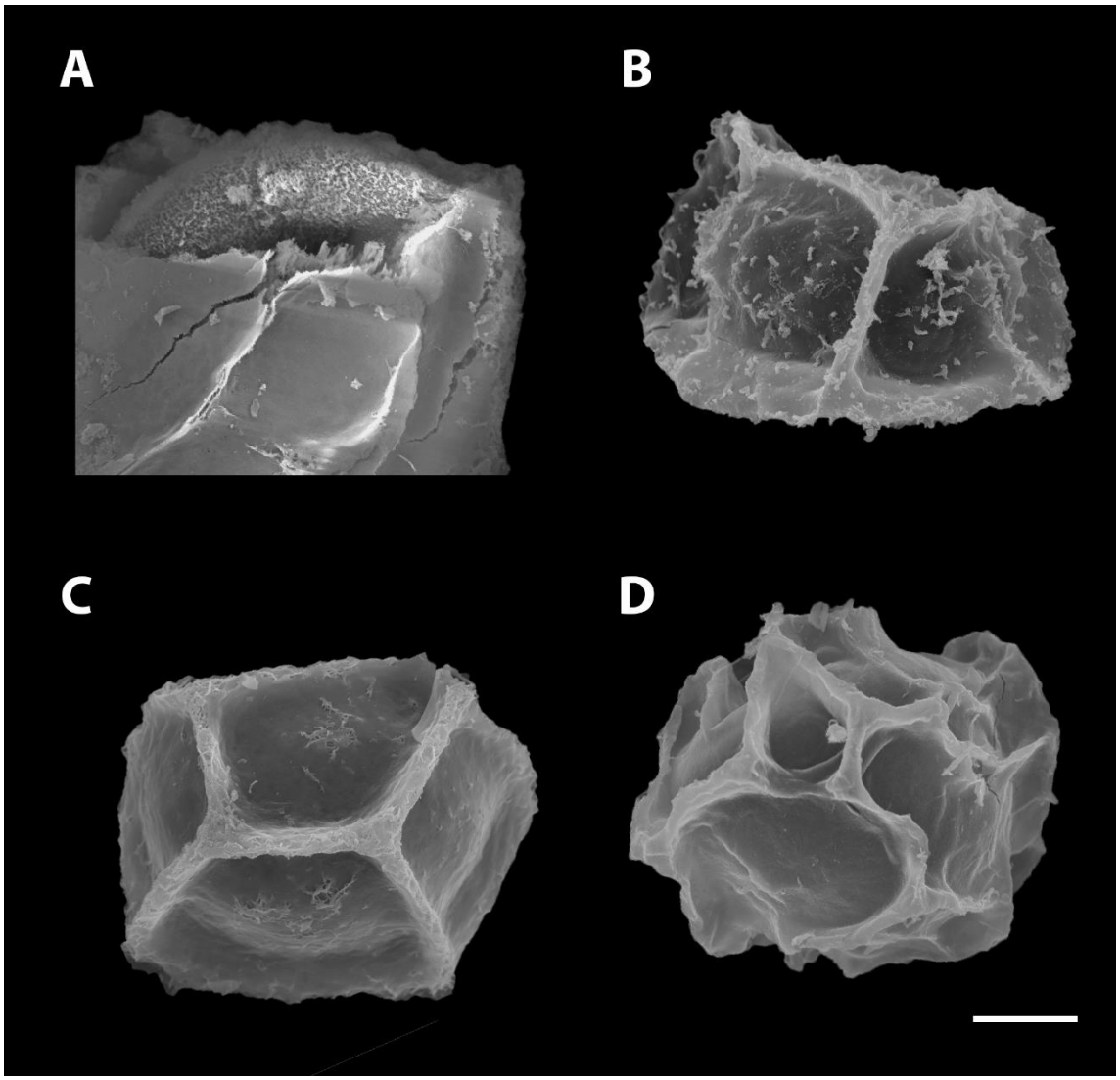

Figure 22. *Parablechnum* spores of Group 3.2: A. *P. schiedeanum* (*A. Rojas y J.M Gabriel y Galán 10418*, MACB109259); B. *P. triangularifolium* (*no collector,* VT198734); C. *P. werffii* (*R. Caballero 141*, MO3126356); D. *P. wholgemuthii* (*O. Buchtien s.n.*, P01546453). Scale:11.53 µm in A, 16.5 µm in B, 19 µm in C, 13 µm in D.

Parablechnum varians (C.Chr.) A.Wal, S.Molino & Gabriel y Galán: spores (46–)55(–65) × (37–)42(–50) µm; perispore smooth to granular, cristate-reticulate, with high, thin walls, forming large polygonal areoles, with abundant long filamentous processes in the areolar lacunae; internal structure spongy; exosporium granular (**Figure 19E**).

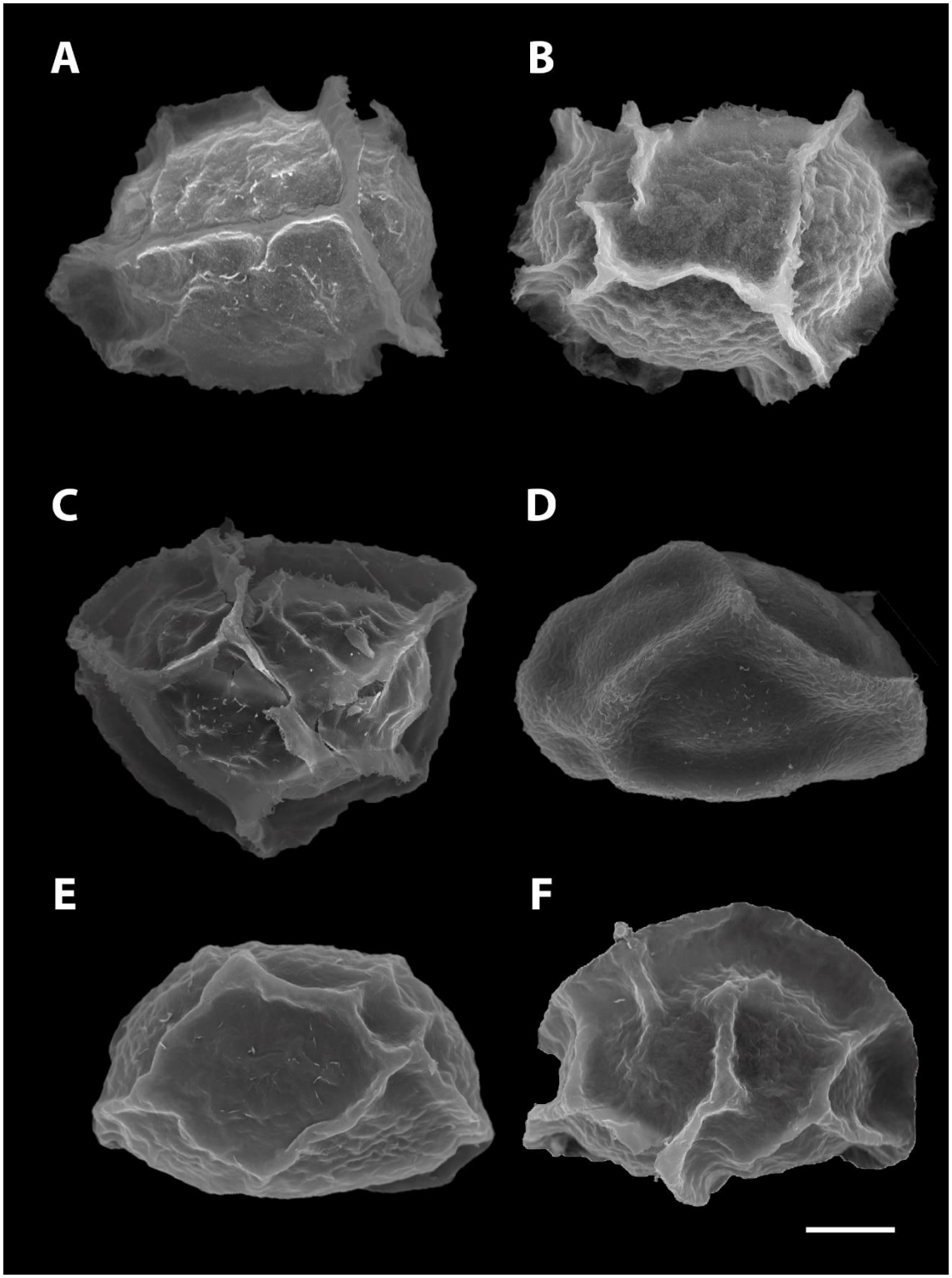

Figure 23. *Parablechnum* spores of Group 3.3: A. *P. chauliodontum* (*M. Baumann 5435*, US2425966); B. *P. corbassonii* (*H. van der Werff & G. McPherson 16085,* UC1740315); C. *P. minus* (*Védel s.n.*, P01462532); D. *P. monomorphum* (*Rodriguez et al 4662,* NY); E. *P. montanum* (*illegible collector*, UC313104); F. *P. novae-zelandiae* (*Védel s.n.*, P01462530). Scale: 13 µm in A, 11.5 µm in B, C & E, 29 µm in D, 15.5 µm in F.

Parablechnum vestitum (Blume) Gasper & Salino: spores (42–)57(–71) × (32–)44(–55) µm; perispore not folded, reticulate, with moderately abundant coarse filamentous processes running from wall to wall in the areoles, spongy internal structure; exosporium granulose (**Figure 15B**).

Parablechnum wattsii (Tindale) Gasper & Salino: spores (46–)56(–66) × (33–)40(–47) µm; perispores smooth, cristate-reticulate, low-walled, thin, sharp, forming small irregular areoles or a reticulum, with abundant thick and short filamentous processes, internal structure and exosporium not observed. (**Figure 19F**).

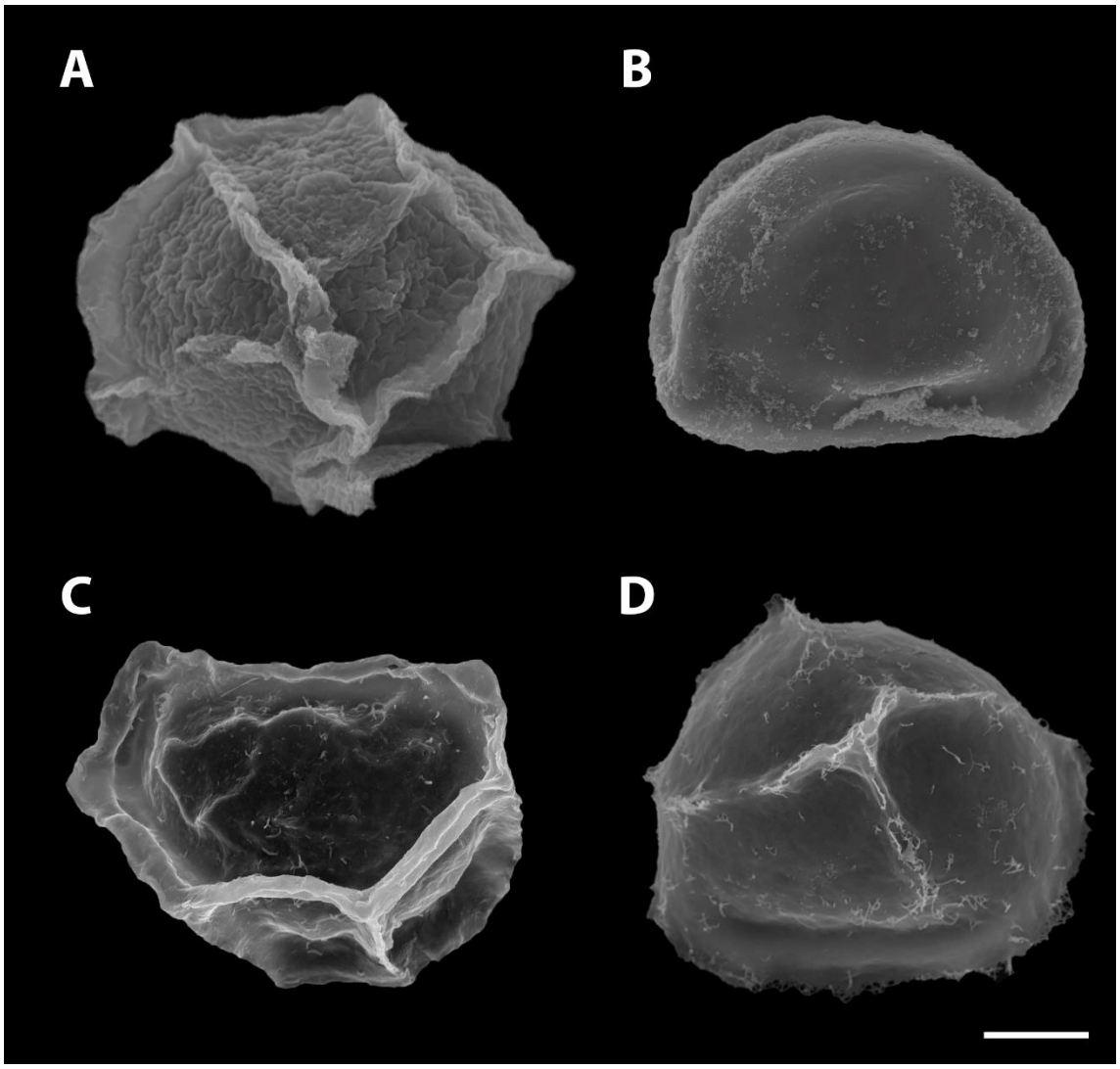

Figure 24. *Parablechnum* spores of Group 3.3: A. *P. obtusum* (*Forero et al 526,* NY); B. *P. pacificum* (*A. Mouly 534*, P00746714); C. *P. procerum* (*R.O. Gardner 8365*, MO5316089); D. *P. tuerckheimii* (*P. Acevedo-Rodríguez 12498*, US3487178). Scale: 14.5 µm in A, 16 µm in B, 14 µm in C, 15 µm in D.

Parablechnum werffii (R.C. Moran) Gasper & Salino: spores (56–)68(–76) × (39–)49(–57) µm; perispores rugulose, cristate-reticulate, low-walled, thick, forming large areoles, with small, perforated ridges that appear to be laterally attached filamentous processes, internal structure and exosporium not observed. (**Figure 22C**).

Parablechnum wolhgemuthii M. Kessler & A. R. Sm.: spores (40–)49(–61) × (30–)37(–44) µm, perispores smooth, crested-reticulate, high-walled, thick, forming medium to large areoles, no filamentous processes, internal structure, and exospores not observed (**Figure 22D**).

Sporangia

The sporangia of *Parablechnum* are of the Polypodialean type: a capsule with a vertical annulus interrupted by a pedicel that attaches it to the surface of the pinna (**Figure 15A-B**). The species of the genus present pedicels of (56–)496(–1,967) µm in length with 2-3 rows of cells, there are species with very short pedicels like *P. confusum* (**Figure 15A**) and others with very long pedicels like *P. chilense* (**Figure 15B**). All taxa have a rosette that differs from the rest of the pedicel cells in shape and size, and ranges from (19–)59(–536) µm. The pedicel in transverse section is composed of three cells in all cases observed in this work.

The capsules are spheroidal or ovoid, (213–)389(–656) × (111–)270(–519) µm. The annulus is composed of an arch with (12–)21(–37) cells and a complex stomial area in the anterior part of the capsule. In this area there is a lip of (2–)4(–7) cells where the sporangium opens, an epistomium of (1–)3(–7) cells and a hypostomium of (1–)3(–6) cells. We have not found in any case basal posterior cells; in all taxa the arc emerges in direct contact with the pedicel.

In several taxa we have found paraphyses mixed with the sporangia in the sori. We have differentiated two types: “simple paraphyses”, which are long, linear paraphyses, similar in appearance to the pedicels of the sporangia but emerging above them (**Figure 25E**), as in the case of *P. confusum, P. chauliodontum* or *P. subcordatum*, and sporangia composed of a pedicel similar to that of the sporangia culminating in an amorphous capsule, of greater length than the sporangia in *P. nesophilum* (type 1, **Figure 25C**) or of similar length in *P. humbertii* and *P. milnei* (ty pe2, **Figure 25D**). Measurements taken

for the sporangia of each taxon as well as the presence of paraphyses can be found in **Table 4.**

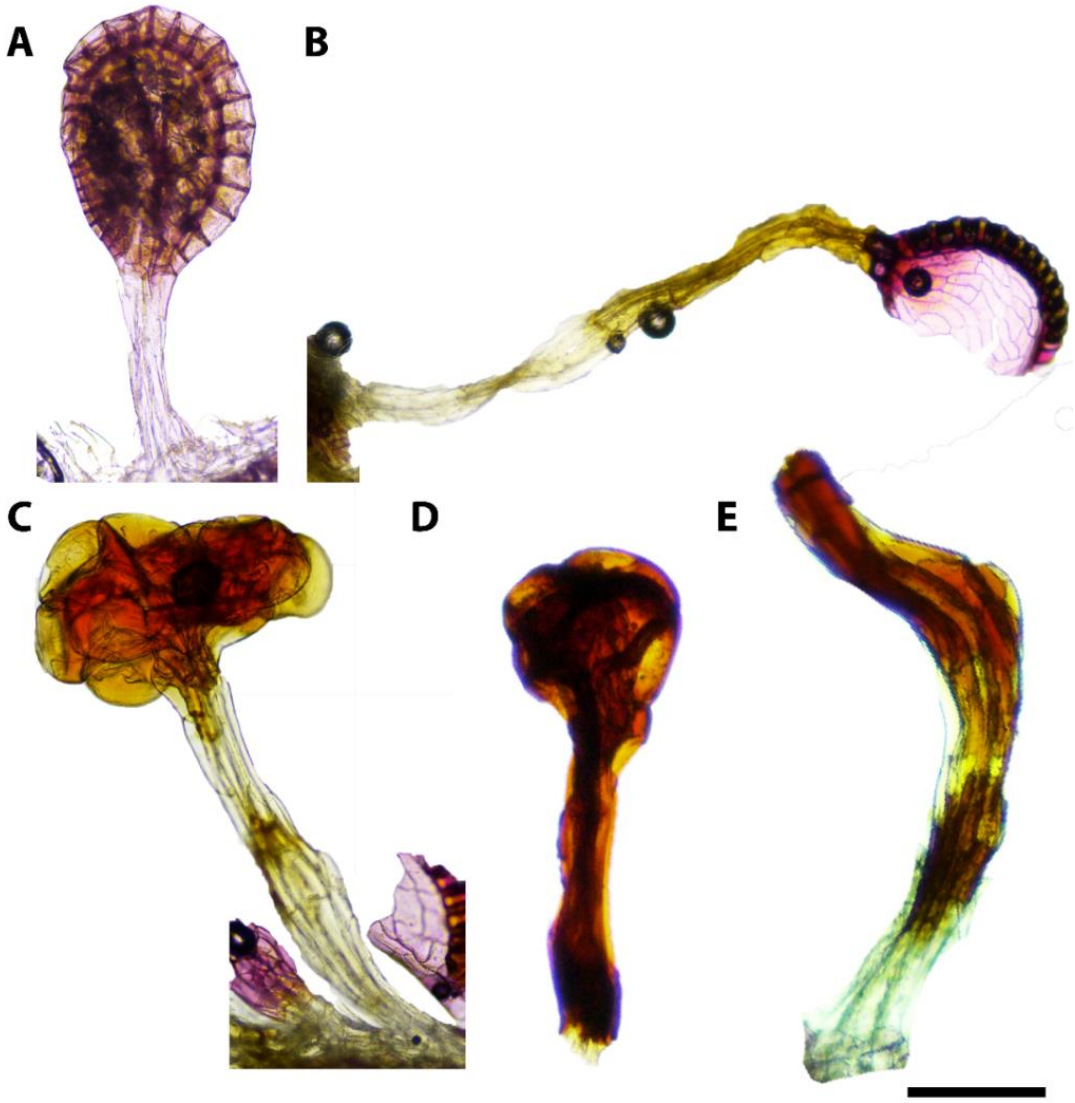

Figure 25. Sporangia and paraphyses of *Parablechnum.* A. Sporangium with short stalk (*P. confusum* US01527826); B. Sporangium with long stalk (*P. chilense, J.M. Gabriel y Galán*, MACB109257); C. Sporangiaster longer than the sporangia (*P. nesophilum, Sundue4251*, MACB); D. Sporangiaster with similar size than the sporangia (*P. milnei, G. Bourdy 123*, P01576209); E. Paraphysis (*P. corbassonii, H. van der Werff & G. McPherson 16085*, UC1740315). Scale: 135 µm in A, 291 in B, 2.5 mm in C, 242 µm in D, 177 µm in E.

Table 4. Summary table of the main characters of the sporangia of *Parablechnum* species. The continuous variables are given as the mean value ± standard deviation, the categorical variables are given as a rank or as (minimum) mean (maximum). All the measures are given in µm.

Taxon	Arch	Capsule	# cells stomium			Pedicel length		Paraphyses
	# cells	Length × width	Lips	Epistomium	Hypostomium	Rosette	Pedicel	
P. ambiguum	(24) 29 (26)	439.5±30.2 × 291±36.7	2	3	1–2	81.6±42	330.5±36.7	No
P. articulatum	17	277.1±17.5 × 223.9±23.6	2–3	2–3	1	30.8±5.4	507.1±198.2	No
P. atropurpureum	(16) 18 (22)	465.4±44.4 × 267.3±28	3	2–3	3	79.1±28	413.1±206.7	No
P. bicolor	19–21	368.2±62.8 × 272±26.4	5	3–4	2–3	58.8±10.9	603.8±113.2	No
P. camfieldii	(16) 18 (20)	338.5±52.5 × 210.4±21.4	3–4	2–4	3	53±15.7	417.5±83.9	No
P. capense	(17) 22 (26)	305.9±36.8 × 216.4±25.3	4–6	1–3	1–4	65.3±118.2	423.8±167.1	No
P. chauliodontum	18–20	296±34.5 × 197±13.3	5	2	1	72.3±35.5	313.5±62	Simple paraphysis
P. chilense	(16) 20 (24)	367.7±20.6 × 329.5±24.0	3–4	3–5	3–5	51.8±9.3	985.3±246.6	No
P. chiriquanum	(15) 25	308.1±66.3 ×183.0±51.7	2–5	1–5	1–4	58.5±12.2	336.8±61.8	No
P. confusum	(17) 21 (24)	385.4±51.7 × 225.2±27.9	3–5	1–3	2–4	52.0±18.6	590.5±303.4	Simple paraphysis

Taxon	Arch	Capsule	# cells stomium			Pedicel length		Paraphyses
	# cells	Length × width	Lips	Epistomium	Hypostomium	Rosette	Pedicel	
P. corbassonii	(16) 19 (21)	306.1±55.6 × 195.5±38.9	3–6	2–3	2–3	33.0±5.3	748.0±326.3	Sporangiasters type 2
P. cordatum	(17) 21 (26)	494.0±59.1 × 371.5±59.3	2–4	2–5	2–5	76.7±16.3	376.1±112.3	No
P. falciforme	(19) 22 (26)	475.7±64.1× 363.6±29.2	2–5	2–5	2–4	68.1±16.1	517.6±116.1	No
P. glaziovii	(16) 24 (30)	325.9±52.4 × 216.5±23.1	3–5	2–3	1–3	53.8±13.0	706.8±421.5	No
P. hieronymi	(21) 23 (26)	416.4±37.7 × 264.3±21.8	3–6	1–4	2–4	51.6±17.9	415.6±110.3	No
P. humbertii	(18) 21 (24)	414.8±73.4 × 278.1±27.9	4–7	2–5	1–4	55.4±18.8	514.3±189	Sporangiasters type 2
P. lechleri	(17) 18 (22)	307.1±35.8 × 183.1±25.7	2–5	1–4	1–4	43±9.4	424.4±9.4	No
P. lima	(18) 21 (25)	363.4±43.6 × 203.2±19.8	2–5	1–5	1–4	51.8±16.3	287.4±32.2	No
P. lineatum	(17) 24 (32)	410.7±51 × 236.4±31.3	4–5	2–6	1–4	72.2±16.3	288.8±52.6	No
P. loxense	(17) 22 (37)	368.8±75.2 × 230.5±51.8	2–6	1–7	1–3	58.2±17.1	282.7±69	No
P. loxense var. stenophyllum	(18) 20 (23)	495.4±39.3 × 315.8±56.8	3	2	3	395.5±72	56.4±11.1	No

Taxon	Arch	Capsule	# cells stomium			Pedicel length		Paraphyses
	# cells	Length × width	Lips	Epistomium	Hypostomium	Rosette	Pedicel	
P. marginatum	(19) 23 (28)	441±71.3 × 258.5±26.6	2–6	2–6	1–4	59.3±17.7	561.7±110.7	No
P. milnei	(21) 23 (26)	462.2±82.9 × 303.1±60.6	3–4	3–6	2–3	65.4±16	320.3±120.9	Sporangiasters type 2
P. minus	(16) 18 (22)	317.3±62.9 × 206.5±37.7	2–4	2–5	1–4	44.2±13.3	372.6±159	No
P. monomorphum	26	480.3±120.9 × 306.7±63.4	3	4–5	3–4	57.4±25.3	319.4±44.4	No
P. montanum	(16) 19 (21)	270.9±19.1 × 175.1±13.4	3	2–3	3–5	54.6±9.6	320.8±55.2	Simple paraphysis
P. moranianum	(19) 21 (24)	484.7±52 × 313.4±44.9	3–5	3–4	3–4	90.6±19.9	310.5±47.9	No
P. nesophilum	(20) 23 (24)	396±58.4 × 238±45.9	3–5	3–4	1–2	87.2±20.9	432±203.7	Sporangiasters type 1
P. novae-zelandiae	(14) 19 (23)	337.8±60.2 × 192.5±20.9	2–4	2–4	2–5	47±11.6	368.8±284	Simple paraphysis
P. obtusum	(22) 25 (31)	396.6±139.8 × 222.3±28.5	3	4	4	72.2±11.1	186.3±19.7	No
P. pacificum	(17) 20 (21)	348.7±27.3 × 219.4±12.2	2–5	2–4	2–3	37.1±3.3	886.8±231.8	Simple paraphyses
P. pazense	(15) 18 (20)	391.4±25.2 × 239.6±16.5	3	3–5	3–4	67.4±2	208.2±31.5	No
P. procerum	(16) 18 (19)	311.2±28.4 × 177.9±25	2–4	3–4	3–5	33.8±7	690.1±167.4	Simple paraphyses

Taxon	Arch	Capsule	# cells stomium			Pedicel length		Paraphyses
	# cells	Length × width	Lips	Epistomium	Hypostomium	Rosette	Pedicel	
P. proliferum	(20) 24 (28)	399±67.2 × 251.1±44	3–6	1–6	1–5	63.5±22.3	280.8±98.6	No
P. revolutum	19–21	373.4±22 × 234.1±11.9	3	3	3	69±6.6	301.4±101.5	No
P. rheophyticum	18–19	449.6±17.5 × 258.3±18.5	3	2	2	83.4±11.7	426.4±69	No
P. ryanii	19–20	343.3±25.8 × 283.2±27.8	3	3	2	74.5±7.1	469.2±63.1	No
P. schiedeanum	(17) 22 (30)	475.9±38.9 × 349.7±37.5	2–5	2–6	3–6	58.2±7.4	400.2±85.8	No
P. sessilifolium	(22) 25 (26)	233.8±25.8 × 392.7±41.5	3	1–5	1–5	59.8±24	430±137.6	No
P. squamatum	(17) 19 (20)	378.7±19.6 × 288.8±24.2	3	3	3–4	76.5±11.7	550.3±57	No
P. stipitellatum	(19) 20 (23)	313.5±28.6 × 198.8±20.1	3	4	4	66.3±11.1	270.6±85	No
P. stuebelii	(24) 26 (31)	469.2±23.1 × 334.9±26.2	4–5	3	3–4	88.7±18.3	151.8±40.9	No
P. subcordatum	(17) 19 (20)	278.9±71.9 × 357.3±84.3	3–4	3	2–3	117±14.9	607.9±246.7	Simple paraphyses
P. triangularifolium	(12) 16 (20)	285.6±18.5 × 206.5±17.7	3–4	1–4	1–5	43.6±9.8	554.3±184.3	Simple paraphyses
P. tuerckheimii	20–23	248.4±24.4 × 388.6±21.7	3	5	3	88.1±21.4	358±56.5	No

Taxon	Arch	Capsule	# cells stomium			Pedicel length		Paraphyses
	# cells	Length × width	Lips	Epistomium	Hypostomium	Rosette	Pedicel	
P. usterianum	(21) 23 (24)	409.2±14.8 × 262±31.7	3–5	1–3	1–3	54±11.3	361.7±78.9	No
P. varians	(17) 21 (24)	438.4±36.7 × 351.7±22.4	2–4	2–4	2–4	65.5±13.7	429.6±88	No
P. vestitum	19–22	381.7±29.8 × 252.1±22.4	3–4	1–5	1–3	46.4±9.1	493.4±166.3	No
P. wattsii	(15) 17 (19)	344.5±15.5 × 194.7±13.2	3–5	1–3	3–5	39.2±6.7	695.3±400.9	Simple paraphyses
P. werffii	(18) 21 (23)	327.4±6.3 × 262.1±52.6	3–4	4	2–3	70.2±15.3	290.6±87.5	No
P. wohlgemuhii	16–17	307.3±8.4 × 179.4±23.3	2–4	2–4	3–5	27.2±2.8	450.4±0.2	No

Discussion

Fertile pinnae anatomy

Anatomical studies of ferns have allowed comparison and separation of families, genera, and species (Ogura, 1972; Lin & DeVol, 1977, 1978; Moran, 1987; Hernandez *et al*., 2006). The cross section of the fertile pinna is a character that has proven to be very informative and that allows us to separate genera and sometimes species in the family Blechnaceae (Prada *et al*., 2016; Vicent, 2017; Molino *et al*., 2019a, b; Bauret *et al*., 2021). The anatomy for *Parablechnum* had already been partially studied in the work of Prada *et al*. (2016). The species of *Parablechnum* included in their study were ascribed to group 3.2., defined as cordatoid species, and were defined as species with contracted fertile pinnae, reduced in width, with complex indusium and defined or extended receptacle. The observations in this work match those of Prada *et al*., (2016) but we have been able to record that the variability within the genus is greater due to the inclusion of a larger number of species, 51 taxa, which constitutes approximately the 78% of the diversity of the genus.

Parablechnum plants are, in general, dimorphic, although there are some monomorphic taxa. Some are classically monomorphic, such as *P. monomorphum*, *P. obtusum* or *P. pazense*, although in cases such as *P. monomorphum* and *P. pazense* it has been hypothesized that this could be a variable character, and that dimorphic species could revert to a monomorphic state under certain environmental conditions, as happens in *Struthiopteris spicant* (Smith & Kessler, 2018). However, in the specimens we have observed this, monomorphism is fairly constant, with completely straight, identical pinnae in sterile and fertile specimens, whereas when a dimorphic species of *Parablechnum* tends to monomorphism it does so in a clearly aberrant manner, with subdimorphic intermediate stages, so we believe that it could indeed be a good diagnostic character for these species.

The monomorphic character is also interesting in the group of *Parablechnum loxense*, where we could include the species *P. moranianum*, *P. loxense*, *P. revolutum*, *P. stipitellatum* and *P. stuebelii*. There have been authors who have defined these species as dimorphic due to the high level of contraction of their pinnae (e.g. Sundue, 2010; Dittrich *et al*., 2018). However, this level of contraction occurs in both fertile and sterile pinnae,

both having the same appearance, so in this work we consider these species subdimorphic or monomorphic. It does appear, however, that these taxa tend to dimorphism in exposed environments, with those specimens presenting less contracted sterile pinnae.

The presence of circumendodermal bands is a character that has only been observed recently in Molino *et al.* (2021), on the species *P. nesophilum*. Here, we report this feature also for *P. chauliodontum* and *P. corbassonii*. These bands are common in petiole sections and are comprised of sclerenchyma, and the dark colour of the cells is probably caused by the deposition of phlobaphene in the secondary walls (Ogura, 1972). They have already been observed in several petiole cross sections of Blechnaceae, including the species *P. vestitum* (Noraini *et al*., 2014). The presence of these bands on the costae of *P. nesophilum*, *P. chaulidontum* and *P. corbassonii* seems to indicate that, occasionally, these may extend to the costa, and appears to be a distinctive feature of these three species.

In view of the fact that the anatomy of the fertile pinnae seems a constant character within the different groups of Blechnaceae, and that many of the groups generated by Prada *et al*. (2016) correspond to the genera subsequently described or resurrected by Gasper *et al*. (2016, 2017), it would be interesting to make a global study of the fertile pinnae of this family to contrast it with the molecular phylogeny, something that was slightly outlined in Vicent (2017).

In addition, the presence of solid diagnostic characters in the Blechnaceae pinnae cross sections is particularly relevant, since it is common to find herbarium specimens of which only fertile fronds are preserved, and even cases in which sterile and fertile material of different species are mixed in the same voucher.

The photographic illustration of the parasagittal sections of the fertile pinnae of *Parablechnum* is, to the best of our knowledge, a novelty of this work. The composition of venation in the family Blechnaceae has been long discussed since the 19th century (Mettenius, 1856; Bower 1914, 1928; de la Sota & Gouvêa Labouriou, 1961). In Bower's studies on blechnoid ferns it was determined that the origin of the commissural vein was mixed, involving both scaleriform and typical lateral vein tracheids. However, de la Sota & Gouvêa Labouriou contradicts this in his study of the venation of *Blechnum occidentale* L., illustrating that the commissural veins are composed only of scaleriform tracheids. In our study, de la Sota & Gouvêa Labouriou's view is confirmed, since in the worked

species of *Parablechnum* only scaleriform tracheids have been observed in the receptacle. It would be interesting to continue this type of section in the rest of the genus family to see if it is consistent at the generic level, and to determine the anatomical condition of the family as a whole.

Indusia

In general, the anticlinal walls of the indusia cells in *Parablechnum* are, at least, a little bit curved. We have called the walls subpolygonal if the curve is slight and subsinuous if it is more pronounced, as reported in Prada *et al*. (2016). However, we have not found any *Parablechnum* taxon whose indusial cells have distinctly sinuous walls, as seen for example in *Neoblechnum brasiliense* (Desv.) Gasper & V.A.O. Dittrich (Prada et al., 2016). The tendency is for the cells to be more polygonal in the distal zone and more sinuous towards the insertion zone, which is probably due to the epidermal origin of the indusium, which explains why basal cells look, indeed, epidermal (with very sinuous anticlinal walls).

Epidermis

The epidermal pattern found in Parablechnum with strongly sinuous cells, with U- or V-shaped anticlinal walls, is the usual pattern previously observed in species of the family Blechnaceae (Lavalle *et al.*, 2005, 2007; Rolleri & Prada, 2006b; Prada *et al.*, 2008; Cortizo *et al*., 2009; Molino *et al*., 2019a, b).

The presence of hydathodes was found to be shared by all *Parablechnum* species. Hydathodes are secretory structures whose function is to remove excess water, a process known as guttation. The presence of whitish layers on them that we have observed in some specimens is formed by the deposition of calcium carbonate when exuding water with calcium oxalate salts react with carbon dioxide from the environment (Ogura, 1972). These structures are common in several Blechnaceae (e.g. Sperry, 1983; Lavalle *et al.*, 2005; Molino *et al.*, 2019b).

Regarding stomatal size, studies have shown that stomatal length and spore shape and volume tend to have a direct relationship with the size of the fern genome (Barrington *et al*., 1986, 2021). The chromosome number of *Parablechnum* species is highly unknown,

so characterization of this trait may be helpful in future studies to elucidate the genome size of the taxa involved in the genus.

Spores

This work constitutes the study in which the largest number of spores of different taxa of *Parablechnum* has been reviewed to date. Spores are a character of extreme importance when making taxonomic classifications in ferns (Tryon & Lugardon, 1991). In fact, it has been shown that spore size can be closely related to ploidy in ferns (Barington *et al*., 1986, 2021). Considering that we are dealing with a genus whose hybridization and polyploidy events are largely unknown, the data provided in this work may help in the future to shed light on these issues in *Parablechnum*. It would be interesting to see if there is a correlation between stomata size and ploidy in the few taxa where ploidy is known.

The spores of *Parablechnum* had been described in works of wider range for the family Blechnaceae (Passarelli *et al*., 2010; Moran *et al*., 2018; Silva *et al*., 2019, 2021), some Floras (e.g. Chambers & Farrant, 2012) and in other specific to some special complexes of *Parablechnum* taxa (Wal *et al*., 2021; Molino *et al.,* submitted). The work with the largest number of species contributed was that of Moran *et al*. (2018), where spores of 30 species of *Parablechnum* were studied. In that work, perispores were defined as folded with filaments varying from sparse to dense, with some species lacking these. This corresponds to our groups 2 and 3, but neither of the two species included in group 1 was studied by Moran *et al*. which may be why this variant was not included in their work. Also, it is commented that filaments are usually always present, giving as an example the species *P. schiedeanum*, where they state to find filaments on the edges of the wall. In this work we consider that these structures are deflections of the folds that form the walls, and do not have a defined structure of filamentous processes. It is also commented that the presence of these filamentous processes is an exceptional case within the Blechnaceae family, however we cannot consider it a synapomorphy of the whole genus since we have found species that do not present these structures in groups 1, 3.2 and 3.3.

The study by Passarelli *et al*. (2010) includes several species of *Blechnum s.l.* that they group according to their spore morphologies. Some of those groups correspond to the genera segregated by Gasper *et al*. (2017) later, corroborating the systematic importance of these structures. Of these species 12 correspond to *Parablechnum*, which are included

in their groups 6 and 7, corresponding to our groups 3.1 and 3.2 respectively. In general, the descriptions of these spores correspond to ours except for *P. cordatum*, *P. schiedeanum* (sub. *Blechnum costarricense*) and *P. stuebelii*. We could not find the specimen from which the spores of *P. cordatum* were extracted (*Jügens & Ittier 69*, BA), so we cannot confirm whether this is due to intraspecific variation or a different taxonomic criterion. We have also reviewed the case of *P. stuebelii* and found that the individual examined by Pasarelli *et al*. (MA610969) does not correspond to this species; it is, however, more like some of the syntypes of the species that were rejected as such in the lectotypification of Dittrich *et al*. (2017). We have not been able to ascribe this voucher to any current taxon of *Parablechnum*, and it may be a new species. In the case of *P. schiedeanum*, we have noted that the specimen reviewed by Passarelli *et al*. (MA702487) is *P. varians*, taxa considered conspecific at that time.

The studies of Silva *et al.* (2019, 2021) include five species of *Parablechnum*. The description of their spores matches our observations except, again, *P. schiedeanum*, whose spore appears described with filaments in Silva *et al.* (2021). However, we could not see the herbarium material in which they based this information (*Salino 15418*, BHBC). Considering the location of this individual, it could be again *P. varians*, which was considered a synonym at that moment too. These cases in which the presence or absence of filamentous processes help to discern between *P. schiedeanum* and *P. varians* confirm the view of Wal *et al* (2021), where it is proposed as a key character to reject the co-specificity of these two species.

There are some spores that we could not observe but whose images under the SEM have been already published, that is the case of *Parablechnum dilatatum* (T.C.Chambers & P.A.Farrant) Gasper & Salino and *Parablechnum puniceum* (T.C.Chambers, P.J.Edwards & R.J.Johns) Gasper & Salino (Chambers & Farrant, 2001; Chambers *et al.*, 2005, respectively). *Parablechnum dilatatum* presents a smooth, cristate-reticulate perispore, with thick and low walls that form big polygonal areolae, without filaments, which falls into Group 3.2. *Parablechnum puniceum* present a folded perispore, with numerous folds which do not form areolae, and abundant filamentous processes, which falls into Group 2. In addition, there is a specimen of *Parablechnum wurunuran* (Parris) Gasper & Salino (sub. *Lomaria eximia* F.Muell.) in the MEL herbarium that include SEM pictures of the spores (*J. Dallachy s.n.*, MEL54065). These spores present a rugulose

perispore, cristate reticulate, with thin walls which form big polygonal areolae and some short and sparce filamentous processes, which would be in Group 3.3

We have found some cases in which the spore of the same species varies significantly among individuals, as is the case of *P. loxense*, *P. ryanii* or *P. stipitellatum*, where the density of filaments or the size of the areolae differs considerably. These variations could be due to the coexistence of several otherwise very similar or cryptic species that are being considered as one, as has already occurred in other *Parablechnum* complexes (Chambers & Farrant, 1998a; Wal *et al*., 2021).

It is intriguing that the perispores of *Parablechnum* spores are easily detached and broken, or that aborted spores appear so frequently. This has already been emphasized in other studies of Blechnaceae spores (eg. Mitui, 1979; Molino *et al*., 2020) and is probably what led some authors to erroneously state that the perisporium is non-existent in some Blechnaceae (Ching, 1940; Tagawa, 1959). The reason for this phenomenon is still unknown, although it could be indicative of high levels of polyploidy or hybridization in the family.

The ability of spore ornamentation to influence dispersal ability is a field yet to be discovered. Some authors suggest that fluid mechanics does not act on such small scales (Tryon & Lellinger, 1991), but there are studies with mosses that show that the variation in shape and ornamentation could affect the balance between density and drag (Zanatta *et al*., 2016). *Parablechnum* is an interesting model in this respect as it has centres of diversity throughout the southern hemisphere and species with both wide and very restricted distributions.

In addition, here it has been observed that there are *Parablechnum* species with close distributions and quite different spores (e.g. *P. nesophilum* and *P. pacificum*, both Austropacific species but with different types of ornamentation), and species from distant areas with very similar spores such as *P. camfieldii* and *P. capense*, with the same type of ornamentation, one being Austropacific and the other African or *P. minus* and *P. werffii*, one being Austropacific and the other American. This leads us to think that the biometry and ornamentation of the spores could be a character related to the occupation of one ecological niche or another, and/or to the ecological strategy of the species.

Sporangia

Sporangia are structures whose ontogeny and variation in characters have been studied for many groups of leptosporangiate ferns (e.g. Bower, 1928, 1928; Copeland, 1947; Haider, 1954; Wilson 1959). In fact, there have been specific studies in the family Blechnaceae where sporangia have been key in the separation of genera and species (González *et al*., 2010; Prada *et al*., 2016; Molino *et al*., 2020; Wal *et al*., 2021). We have seen that *Parablechnum* sporangia are, in general, relatively uniform, although they can vary greatly in pedicel length, there being some with extremely short pedicels such as *P. loxense*, and others very long such as *P. chilense*, which had already been observed in the work of Prada *et al*. (2016) and Wal et al. (2021).

The finding of paraphyses in several taxa of *Parablechnum* is relevant. Paraphyses are sterile structures that are mixed with sporangia and whose function has usually been attributed to the protection of the sporangia (Wagner, 1964, 1965; Parris, 1997). These structures are relatively common in leptosporangiate ferns, and may be diagnostic of some groups (Copeland, 1947; Wilson, 1959a). Often these paraphyses are similar to the indumentum of the fronds, but at other times they resemble modified sporangia, with a pedicel and an irregular capsule that does not carry spores, in which case they are called sporangiasters. These sporangiasters are less common than the other paraphyses and have only been found in a few groups of leptosporangiate ferns (Martens & Pirard, 1943). According to Peterson & Kott (1979), these structures develop precociously, and their modified capsules remain above the growing sporangia, serving as protection.

The presence of sporangiasters in the Blechnaceae was recently observed for the first time in *Parablechnum nesophilum*, a species from Papua New Guinea (Molino *et al*., 2021). No type of paraphyses had been previously reported in the family (Rolleri *et al*., 2008; Rothfels *et al*., 2012; Prada *et al*., 2016). These structures had probably gone unnoticed because they are more inconspicuous in dry material, as already indicated in Molino *et al*., and due to the lack of anatomical studies discussed by Prada *et al*. (2016).

Sporangiasters have been seen in exindusiate genera of the family Polypodiaceae (Brinton & Taylor, 1902; Martens & Pirard, 1943; Wagner & Farrar, 1976; Price, 1990) and in genera with indusia such as *Alsophila* (Janssen & Rakotondrainibe, 2006), *Meniscium* Schreb (Fernandes & Salino, 2016). However, the application of the term

sporangiaster has not always been clear, having occasions in which it is applied without being clearly these structures, and other occasions in which it could be applied and is not, so the study of the homology of these structures is necessary to determine when to use this term. In this work we have used the term sporangiaster whenever we have found paraphyses with a pedicel ending in an irregular capsule, clearly a modified sporangium. This is the case for *Parablechnum nesophilum*, already reported in Molino *et al*. (2021), and also for *P. humbertii* and *P. milnei*. On the other hand, in the rest of the taxa where paraphyses have been found these were elongated structures, with pedicel-like appearance but without a defined capsule at the apex, so for these cases we have decided to use only the term paraphyses.

The function of sporangiasters has usually been defined as protective, and in fact they occur much more frequently in ferns without indusium (Wagner, 1964). However, as we have observed in *Parablechnum*, the presence of these structures may be underestimated, and more anatomical studies in ferns would be necessary to assess the frequency of the presence of sporangia in indusiated ferns as well. In these cases, their functionality is not clear. It is hypothesized that they could serve as protection in ferns whose indusial opening is early. It has also been speculated that they may act as spore dispersal limiters, maximizing local recruitment and minimizing spore loss to potentially unfavourable conditions (Carlquist, 1966; Molino *et al*., 2021). This second scenario is especially interesting in the case of *Parablechnum* since all the species in which we have found them are Austropacific species restricted to more or less large islands, which would reinforce this hypothesis. However, specific studies in this direction, including the observation of fresh specimens in the field, are needed before reaching solid conclusions.

6. MOLECULAR PHYLOGENY AND DATING

Results

Phylogeny

We worked with three datasets from least to most pruned, hereafter, datasets 165, 133, and 76 depending on their number of accessions. The length of each set and the percentage of parsimony informative sites (% PIS) can be found in **Table 5**. Likewise, the basic structure of each marker can be found in **Figure 26.**

The coding sites of all markers had typical start codons (ATG) except for some samples that had an ACG start codon in the CDS *rps*16 of the *mat*K FERN chlB YAA marker (**Figure 26**).

As the individual trees of each marker separately in all the data sets were not incongruent, they were concatenated and four trees were obtained for each set, two ML (one with coded indels and one without) and two BI (one with coded indels and one without). The ML and BI showed can be checked in **Figure 27** and **Appendix III.** In general, indel codification did not result in an increased node support.

Table 5. Summary of the characteristics of the three data sets showing the percentage of parsimoniously informative sites (% PIS) for each marker, the length in base pairs of each marker and the total base pair length of the set.

Dataset	Marker	% PIS	Length (bp)	Total length (bp)
165	*trn*L-*trn*F	22.79 %	974	3680
	*rbc*L	30.77 %	1326	
	*rps*4-*trn*S	44.28 %	411	
	*mat*K FERN chlB YAA	28.17 %	969	
133	*trn*L-*trn*F	18.08 %	968	3671
	*rbc*L	29.79 %	1326	
	*rps*4-*trn*S	40.14 %	411	
	*mat*K FERN chlB YAA	27.43 %	966	
76	*trn*L-*trn*F	10.60 %	906	3601
	*rbc*L	26.02 %	1326	
	*rps*4-*trn*S	23.11 %	411	
	*mat*K FERN chlB YAA	25.37 %	958	

In all the trees obtained, the genus *Parablechnum* was found to be monophyletic with maximum bootstrap and posterior probability. The accession of *Parablechnum articulatum* is resolved as sister to all other *Parablechnum* in those sets in which it is present (133 and 165) with maximum support. Likewise, in dataset 165 a sample of *P. varians* also appears as sister to the rest of *Parablechnum* with strong support regardless of the analysis type, and in turn, an accession of *P. lechleri* is resolved as sister of the reminder of the genus, but this node is only strongly supported in the analysis without

indels. All analyzed *Parablechnum* accessions excluding these three species remain as a strongly supported monophyletic clade regardless of the analysis type.

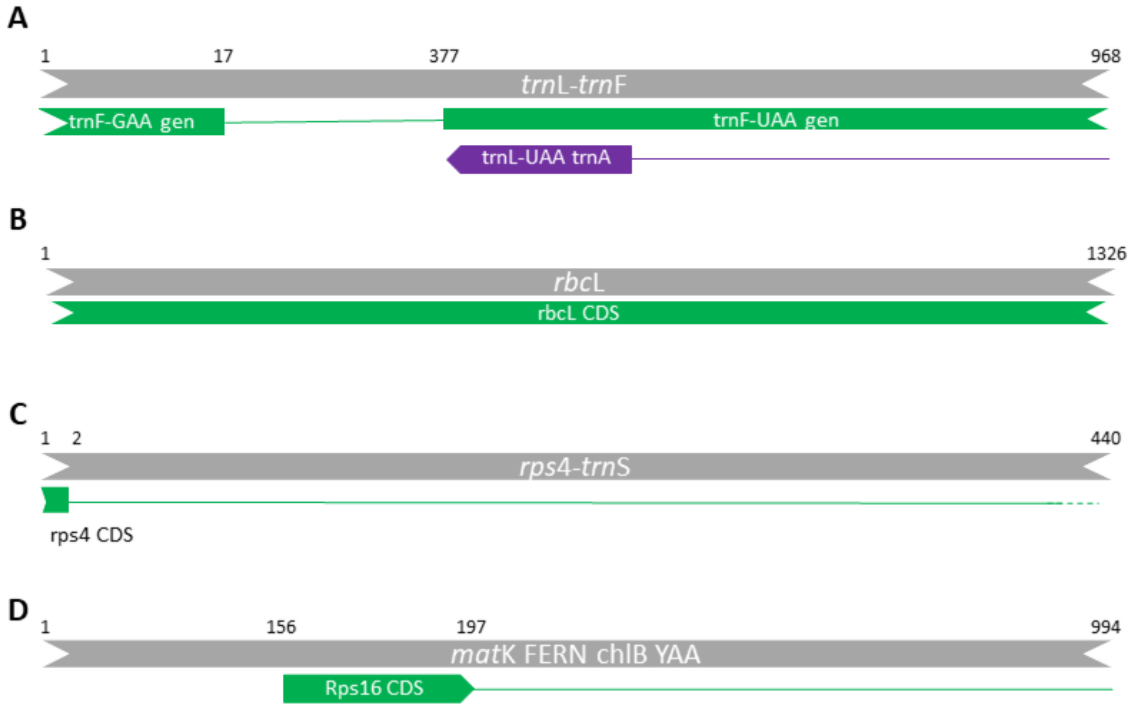

Figure 26. Basic structure of the markers used in this study. Grey = name of the marker; green = coding region; purple: tRNA. A. *trn*L-*trn*F; B. *rbc*L; C. *rps*4-*trn*S; D. *mat*K FERN chlB YAA.

The backbone phylogeny of the genus remains unresolved in all the resulting topologies. Several clades with strong support can be found in all analyses, with a general trend of lower bootstrap and posterior probability values in larger datasets. Within the backbone unresolved polytomy, three relatively large clades that can be identified across datasets and analyses can be found, named here Clade A, Clade B, and Clade C. The support of these clades tends to be stronger in the most pruned datasets and decreases in those with higher percentage of missing data. To facilitate the interpretation of the results, the general topology of dataset 76 is described here with more detail **Figure 27**, all trees are shown in the **Appendix III.**

Clade A comprises American species such as *P. atropurpureum, P. cordatum, P. lechleri, P. lineatum, P. loxense, P. stipitellatum, P. varians* or *P. werffii*, Austropacific species such as *P. procerum* or *P. subcordatum*, the African species such as *P. capense* and *P. marginatum* from Madagascar (**Figure 28C**). This clade is strongly supported in all analyses, except in the trees obtained from dataset 165, where it remains in the

topology with maximum likelihood (with low bootstrap values) and and posteriors of 0.83 and 0.84 in the Bayesian analyses Clade A stands out by a long branch in all analyses.

Clade B comprises accessions of strictly American species, such as *P. loxense* or *P. proliferum* and Austropacific species such as *P. chauliodontum, P. minus, P. montanum* and *P. subcordatum* (**Figure 28D**). This clade is strongly supported in all trees except the one made with ML with coded indels from Set 165. Accessions from taxa already present in clade A can also be found in this one, such as *P. atropurpureum* or *P. lechleri*.

Clade C appears in all the trees but only with strong support (bootstrap over 90 and posterior over 0.9) in the Bayesian inferences of Set 76. In these trees, clade C shows strictly Austropacific species such as *P. triangularifolium, P. wattsii, P. camfieldii, P. hieronymi, P. revolutum* and *P. vestitum* (**Figure 28E**). Clade C appears in datasets 133 and 165, both in the topologies with the highest likelihood and maximum posterior probability, but without strong support and with one American species from Ecuador still undescribed.

Several smaller clades with a low number of accessions but high bootstrap and/or posterior support are also resolved nested on the backbone polytomy. They include clusters of 2-4 accessions of the same species, for example *Parablechnum moranianum, P. glaziovii, P. vestitum, P. pacificum, P. nesophilum, P. stuebelii, P. tuerckheimii* and *P. revolutum*. Other small clades, similarly, with high support values, include accessions belonging to different morphospecies, such as a clade with accessions of *P. glaziovii* and *P. usterianum*. These small clades are not necessarily consistent across datasets and given the lack of a backbone general structure and support in the resulting analyses, they are not thoroughly named here. These smallest clades are also subject to the general trend of lower supports in the datasets with the higher number of accessions with missing data.

Regarding the consistency of morphological species concepts, there are several species that are polyphyletically distributed throughout the phylogeny, not only nested in the unresolved backbone polytomy but also in different well-supported clades. This is the case of *P. loxense, P. proliferum, P. stipitellatum, P. subcordatum, P. atropurpureum, P. lineatum, P. cordatum, P. lechleri* and *P. capense*.

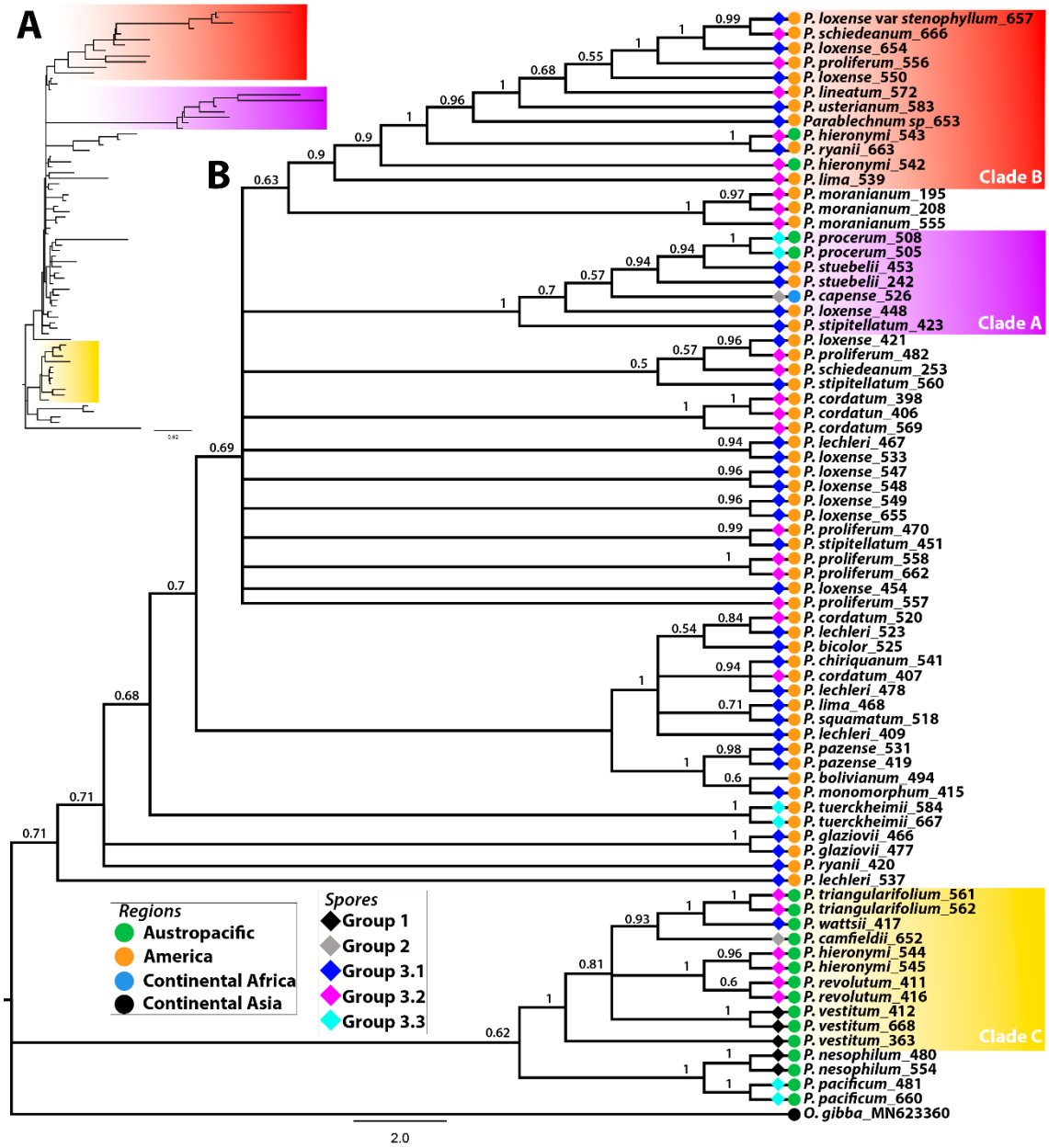

Figure 27. BI phylogenetic tree with coding of indels in set 76. A. Real tree topology, Clade A purple, Clade B red, Clade C yellow. B. Cladogram with posterior probability values at branch nodes, Clade A purple, Clade B red, Clade C yellow. At the ends of the branches the spore type of the species is indicated with a diamond and the geographical region with a circle, the color legend is indicated at the base of the figure.

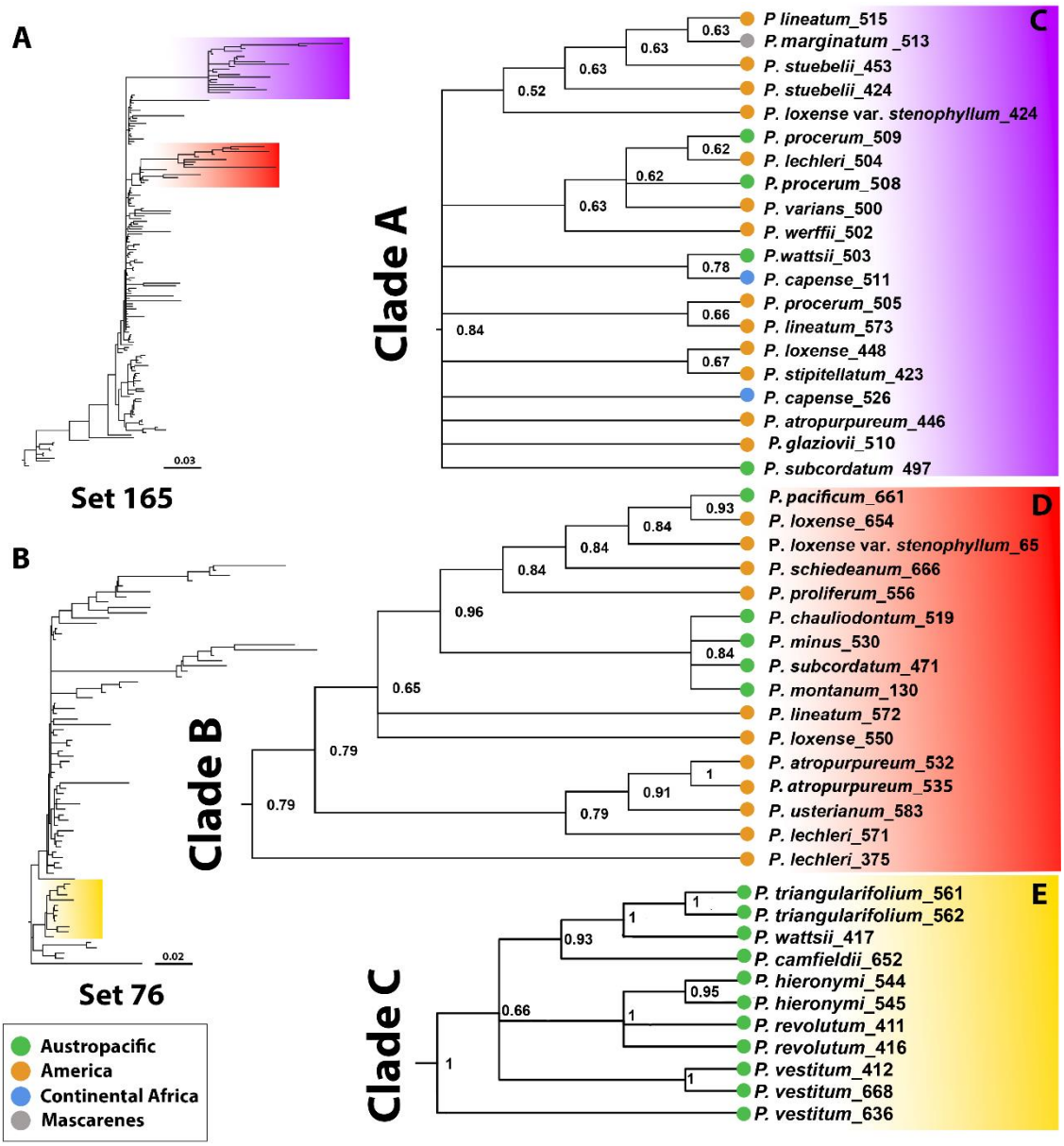

Figure 28. Details of the Clades detected in the phylogenies at. Each clade is presented in the tree of the dataset that provides the highest number of nested taxa in the clade with the best posterior probability support (over 0.7). A. Real topology of the BI phylogenetic tree without indels coding from dataset 165, Clade A purple, Clade B red; B. Real topology of the BI phylogenetic tree with indels coding from dataset 76, Clade C yellow; C. Clade A of the BI phylogenetic tree without indels coding from dataset 165; D. Clade B of the BI phylogenetic tree without indels coding from dataset 165; E. Clade C of the BI phylogenetic tree with indels coding from dataset 76. At the tip of each branch the geographical region of the taxon is indicated by a circle, the legend is indicated in the lower left of the figure.

Dating

Beast analysis of the *Parablechnum* dataset resulted in a phylogeny that was congruent with the ML and BI trees (**Figure 27**, **Appendix III**). The phylogeny resulted can be checked in **Figure 29**, and the tree with the HPD intervals in **Appendix IV**. We obtained

good posterior probability values for the main clades (pp ≥ 0.99), while some of the most recent divergences showed not so strong values, thus, they should be interpreted carefully.

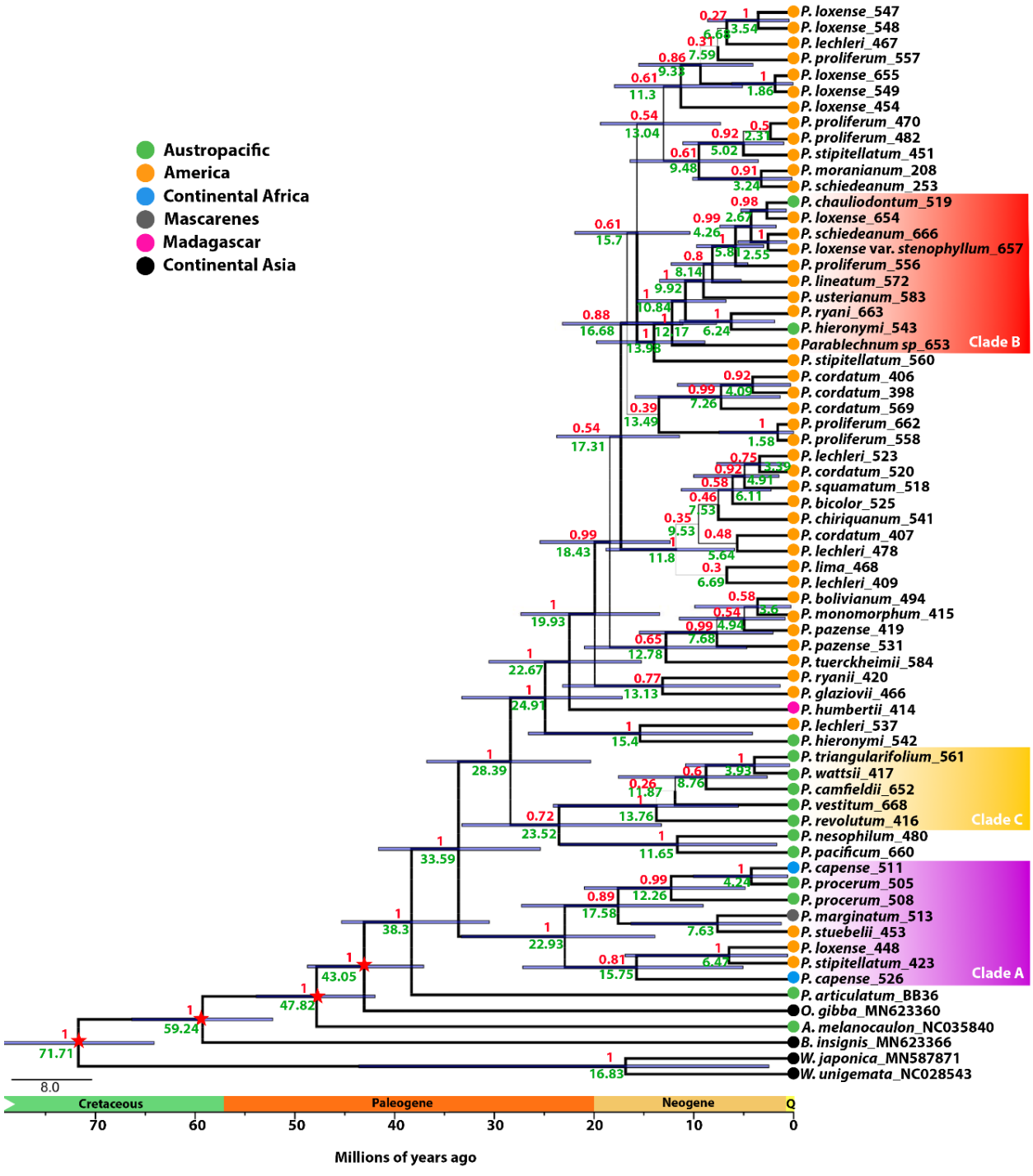

Figure 29. Phylogeny resulting from the dating for *Parablechnum*. At each node the confidence bars are indicated and, above them, the posterior probability values (red) and below the mean age in MY (green). At the tip of the branches the geographical region of the taxon is marked with a circle, the legend is at the top left of the figure. The main Clades of *Parablechnum* detected here are shaded (Clade A purple, Clade B red, Clade C yellow). Calibration points are marked with stars. At the bottom there is a geological time scale.

Divergence of *Parablechnum* and *Oceaniopteris gibba* is dated in 47.82 MY (95% HPD = 37.07 – 48.75), while the crown age of *Parablechnum* is dated in 38.3 MY (95% HDP = 30.48 – 45.33). *Parablechnum articulatum* was the sister species of all the other *Parablechnum* taxa, which is congruent with our previous phylogenetic analysis, being the earliest diverging species. Within *Parablechnum*, Clade A, including taxa from four diversity centers of the genus, showed an early divergence in the Middle Paleogene (stem age 33.59 MY (HPD 95 % = 25.39 – 41.63); crown age 22.93 MY (HPD 95 % = 13.9 – 33.3)). Clade C together with *P. nesophilum* and *P. pacificum*, showed a geographic structure, grouping taxa from the Austropacific diversity center. This clade was the next diverging one in the Upper Paleogene (stem age 28.39 MY (HPD 95 % = 20.32 – 36.78); crown age 23.52 MY (HPD 95 % = 13.25 – 33.24)).

A large clade including three Austropacific species, one Malagasy species and numerous American species diverged 24.91 MY ago (HPD 95 % = 17.18 – 33.25). Within this large clade it is interesting to note the early divergence of *P. humbertii* from Madagascar from a clade including a large diversification in America 22.67 MY ago (HPD 95 % = 15.26 – 30.52). The crown age of the American diversification is dated at 19.93 MY (HPD 95 % = 13.4 – 27.35). It is interesting to note that in the Late Miocene there are numerous cladogenesis events for the American radiation. In addition, there are two individuals belonging to the taxa *P. chauliodontum* and *P. hieronymi* of Austropacific distribution nested within the American radiation, showing more recent divergence times (6.24 MY for *P. hieronymi*; 2.67 MY for *P. chauliodontum*).

Discussion

The systematics of the Blechnaceae is experiencing deep changes following recent studies based on molecular phylogenetics, and particularly the one published by Gasper *et al*. (2017). Under the new generic circumscription, *Parablechnum* became the most speciose genus of the family, however, little could be said about the infrageneric phylogenetic relationships since the scope of that study was broad and only a limited accessions of *Parablechnum* were included. This study was aimed to provide the most comprehensive phylogenetic reconstruction of the genus to date, both, by expanding the selection of taxa (including for the first-time multiple accessions from each of them when possible) and by expanding the number of molecular loci.

We have used the same chloroplast markers used in the most complete phylogenies of *Parablechnum* (Gasper *et al.,* 2017; Bauret, 2018), which are markers widely used in vascular plant taxonomy in general and in ferns in particular (eg. Shepherd *et al.*, 2007; Gabriel y Galán *et al.,* 2013). In addition, we have added an additional marker, the *mat*K region FERN chlB YAA. The *mat*K marker has been widely used in angiosperms, as despite being a chloroplast marker it evolves fast enough to be useful in taxonomic studies (e.g., Hilu *et al*., 2003; Döring *et al*., 2007; Xie *et al*., 2010). It has even been proposed as a DNA barcoding region for land plants. In ferns, however, this marker has been less used, as primers designed for angiosperms bind to exons that have been lost in leptosporangiate ferns (Wolf *et al.,* 2003; Duffy *et al*., 2009; Gao *et al*., 2009). Kuo *et al*. (2011) designed a set of primers from different regions of *mat*K that could serve to amplify these regions in leptosporangiate ferns. We designed a complementary primer to FERN chlB fYAA proposed by Kuo *et al*. (2011), thus obtaining *Parablechnum* sequences that included intergenic spacers and the *rps*16 coding region. In this region we found in several samples an ACG start codon instead of the classical ATG codon. It is known that RNA editing can occasionally create an AUG initiation codon from an ACG codon by C-to-U edit (Hoch *et al.,* 1991; Sugiura 2008; Wolf *et al.,* 2004). This has been found in several vascular plant's chloroplasts (eg. Hoch *et al.,* 1991; Kudla *et al.,* 1992), including ferns (Wolf *et al.,* 2003; Gao *et al.,* 2009; Kim *et al.,* 2014; Ruiz-Ruano *et al.*, 2019). However, this event of RNA editing seems to be more frequent in the mitochondria (Knie *et al.,* 2016). Although the %PIS of *mat*K in our case is lower than in other markers such as *rbc*L and *rps*4, it would be expected that by increasing the number of markers, samples, and taxa the phylogenetic picture would be more robust, but we have found the opposite.

All the analyses from all datasets included in this study resolve *Parablechnum* as a strongly supported clade, confirming the circumscription of all the currently recognized species of the genus except *P. acanthopodum*, *P. cochabambense, P. confusum, P. dilatatum, P. gemmascens, P. obtusum, P. paucipinna, P. puniceum, P. reflexum, P. repens, P. roraimense* and *P. wolhgemuthii,* which could not be sequenced. Most of this species are known from very restrictive distribution and the representation of them in the herbaria is very low. For example, *P. puniceum* is only known by its type material from a remote location in Papua New Guinea (Chambers *et al.,* 2005), and the same happens

with *P. acanthopodum* in Indonesia (Chambers & Farrant, 2001). This is similar on the Americas, by instance *P. cochabambense, P. reflexum, P. repens,* and *P. wolhgemuthii*, which are endemic to Bolivia and have almost not been collected since its original descriptions (Kessler *et al.,* 2007; Smith & Kessler, 2018), or *P. roraimense* and *P. paucipinna*, which have been recently described so there are almost not material yet (Dittrich *et al.,* 2017). Others have relatively wider distribution, as *P. confusum*, which appears all over New Caledonia, but all the specimens reviewed here are from the 19th century or early 20th century. This reflects one of the main problems of the genus: there are many species described that still needs collection efforts to evaluate their phylogenetic position.

The position of *P. articulatum* as sister to the remaining species of the genus was also shown in Gasper *et al*. (2017) and Bauret *et al.* (2018). This taxon is morphologically distinct by its articulated pinnae, and it might represent the only extant species of a now mostly extinct lineage (depauperon). *Parablechnum varians* is also resolved as a depauperon, sister to the rest of *Parablechnum*, but given the some of the studied loci could not be sequenced for this accession, confirmation of this status should be considered provisional pending further data retrieval. In addition, the origin of the genus dates approximately 38 MY ago, which confirms that it would have reached its current distribution by LDD, as this date is after the separation of Gondwana or the presence of the corridor that existed between Antarctica and the Americas (Sanmartín & Ronquist, 2004).

The results of Gasper *et al*. (2017) regarding the bulk of *Parablechnum* showed a straightforward and simple interpretation of the genus phylogeny: one clade composed of mostly Austropacific taxa, and another one including the Neotropical species, leading to a simple biogeographic interpretation with a single colonization event of the Neotropics, assuming an Austropacific origin of the genus (Testo *et al.,* submitted). This interpretation had, however, two caveats: the low support of said clades, and the relatively low number of accessions. The present study increased substantially the number of accessions and enriched the amount of molecular data by including an additional locus. The interpretation obtained by this phylogenetic study presents a radically different prospect of the phylogeny of the genus, reflecting an evolutionary history more complex than expected. Despite the rise in the number of accessions and the additional locus, there

is no clearly resolved backbone topology. Instead, only three larger clades (A, B, and C) and several smaller clusters have support, and a considerable admixture of Neotropical and Paleotropical taxa can be seen in some of them. In general, support values are higher in more stringent datasets, the Bayesian analyses, and analyses without indels. In part, this may be due to the uncertainty resulting for the missing data and a scarce phylogenetic signal resulting from a rapid radiation, as discussed below. Most pruned datasets (133 and 76) were made to obtain a clearer signal and consequently the trees obtained with those datasets are discussed and illustrated in more detail. Indel coding are often used to increase clade resolution (e.g. Boltenkov *et al.,* 2021; Frohlich *et al.,* 2022). In our data, however, the inclusion of indels coding has resulted in a decreased support. The reasons behind this effect deserve further investigation.

One of the phenomena that would explain an unresolved backbone phylogeny is a rapid radiation early in the history of the genus. The effects of recent rapid radiations obscuring Sanger-based phylogenies is a well-documented phenomenon in flowering plants (Lagomarsino *et al*., 2016), and bryophytes (Liu *et al.*, 2012) but perhaps not as expected in ferns (Schneider *et al.,* 2010). The Blechnaceae constitute one of the most recently evolved fern families and with one of the highest diversification rates (Testo *et al.*, submitted) and seem a good candidate for recent explosive species radiations. In recent times it has become clear that Sanger sequencing data might turn insufficient to resolve these radiations, while phylogenomic approaches can be successful where few-loci attempts failed in the past (Medina *et al.,* 2018; Pouchon *et al.*, 2018; Fawcett *et al*. 2021).

Many *Parablechnum* species inhabit montane tropical areas, where other fern groups have diversified intensely. Some of the best documented examples are from the same Andean centers of diversity, including *Jamesonia* Hook. & Grev. (Sánchez-Baracaldo & Thomas, 2014), *Polystichum* Roth (McHenry & Barrington, 2014), and *Diplazium* Sw. (Wei *et al*., 2018). Himalayan cases have also been documented such as in the family Athyriaceae (Wei *et al*., 2018) or in the genus *Lepisorus* (J.Sm.) Ching (Wang *et al*., 2012). It has been postulated that the basic mechanisms that could explain this type of pattern would be a rapid mountain uplift that creates new habitats that are then colonized, leaving the lineages isolated on "sky islands" (Peyre *et al*., 2020). The divergence time of the great American diversification coincides with the Andean Uplift. Specifically, a 2.5±1

km uplift of the Andes took place in the Late Miocene (Gregory-Wodzicki, 2000; Garzione *et al*., 2008), which coincides with several cladogenesis events in our dating.

The phylogenetic reconstructions of this study resolve many of the species of the genus as polyphyletic. This might be explained by the presence of many cryptic taxa, by non-tree-like evolutionary processes (incomplete lineage sorting, reticulate evolution, hybridization…) and by a combination of both. Recent work in some fern groups has shown complex biogeographic patterns resulting from the detection of morphologically cryptic taxa. Examples of this can be seen in *Cystopteris* Bernh. (Ekrt *et al*., 2022), *Notholaena* R.Br. (Kao *et al*., 2020), *Astrolepis* D.M.Benham & Windham (Beck *et al*., 2010, 2012) and *Salpichlaena* (Cardenas *et al*., 2019). Resolving these complexes generally requires an integrative approach that includes examination of geography, morphology, cytology, and DNA sequencing. The "polyphyletic species" found in the phylogeny of *Parablechnum* could be species complexes, whereby the actual diversity of *Parablechnum* would still be unknown and would likely be greater than 65 species as conceived today. Interestingly, some of the taxa that appear polyphyletic in the phylogenies also showed remarkable variation in spores between individuals, as for example *P. loxense* or *P. stipitellatum*, which reinforces the idea that more than one species could be involved. The existence of species complexes in *Parablechnum* has already been mentioned by other authors, and the importance of monographic work on this subject is always stressed, although there is still little available (Tryon & Stolze, 1993; Moran, 1995a; Chambers & Farrant, 1998a; Dittrich *et al*., 2017, 2020).

In addition, there is good reason to suspect that reticulate evolution has played an important role in the history of *Parablechnum*, as hybrids and polyploidy are very common in the family and have hardly been studied in the genus. Reticulate evolutionary events are incompatible with bifurcating tree-based phylogenetic models and may lead to under-supported and misleading representations (Linder & Rieseberg, 2004). Again, Sanger-based data might be limiting the ability of this study to resolve the evolutionary history of *Parablechnum*, but a different approach combining phylogenomic data and considering conflict among different loci would be instrumental to move towards the reconstruction of the evolution of the genus. In fact, the two Austropacific specimens that appear nested in the great American diversification clade in our dating tree could point to a genetic exchange between the two centres of diversity, which could be intensifying

hybridisation. To confirm this hypothesis, more robust data would be needed to allow a reconstruction of geographic areas.

Regarding hybridization, the only known work that studies and proposes with solid data hybrids in *Parablechnum* was carried out by Chambers & Farrant (1998a). This work reviews the number of species involved in the so called "*Blechnum procerum* complex" in New Zealand. It was concluded that there were four species in the complex, three of them recognized in this treatment, producing up to four different hybrids. In the development of this work, the chromosome numbers of the four species forming the complex were published. Only 4 additional chromosome numbers are documented for *Parablechnum* (**Table 6**), leading to an extremely limited knowledge in terms of ploidy levels. Of these eight taxa only one is from the American center of diversity, and none from Africa, Madagascar, or the Mascarenes. This illustrates how precarious the cytogenetic knowledge of this genus is, and the critical importance of exploring ploidy levels to detect the hybridization events within *Parablechnum*. Considering that a single detailed study of a species complex in a relatively small area such as New Zealand revealed the presence of four distinct and well delimited species that could produce up to four confirmed different hybrids, cryptic diversity and hybridization can be rampant in *Parablechnum* and essential to explain its evolutionary history. The Blechnaceae already have a record of studies in which, when delving into a particular group, species that had been overlooked in floras and hybridization events appear, as is the case with *Salpichlaena* (Cárdenas *et al*., 2019) and *Cranfillia* (Chambers & Wilson, 2019; de Lange & Parris, 2019).

Table 6. Summary of the chromosome numbers known in *Parablechnum* to date.

Taxon	Chromosome number	Reference
P. ambiguum	n = 56	Chambers & Farrant (1998b)
P. chilense	2n = 66	Jara-Seguel *et al.* (2006)
P. minus	n = 28	Brownlie (1954), Quinn (1961)
	2n = 56	Dawson *et al*. (2000)
P. montanum	2n = 56	Chambers (1954), Chambers & Farrant (1998a)
P. novae-zelandiae	2n = 56	Chambers (1954), Chambers & Farrant (1998a)
P. procerum	2n = 112	Chambers (1954), Chambers & Farrant (1998a)
P. triangularifolium	2n = 56	Chambers & Farrant (1998a), Dawson *et al.* (2000)
P. wattsii	n = 28	Quinn (1961)

The inclusion of nuclear loci, which are inherited biparentally, is critical in order to fill this gap in our knowledge. However, in a context of a genus in which hybridization, reticulate evolutions, and incomplete lineage sorting might be obscuring the early cladogenetic events of the genus, chances are that a Sanger-based approach of a few nuclear loci will be insufficient to illuminate the phylogeny. Alternative approaches capable to retrieve hundreds of loci, such as Target capture, seem more promising for this purpose, as the large number of loci recovered allows hybridization and other sources of conflict to be assessed more efficiently. The use of nuclear data requires that copies inherited from different parents can be analyzed and achieving this with a large number of loci and with short-read sequence data has, in other works, been a major challenge. However, new analytical approaches such as those seen in Freyman *et al*. (2020) or Nauheimer *et al*. (2021) show that this is now possible and has been successfully applied in projects such as GoFlag (Bloesch *et al*., 2021).

7. TAXONOMIC SYNOPSIS

The following is a general description of the genus *Parablechnum* and all its known species. The descriptions are based on the herbarium sheets observed and checked by previous descriptions in various works cited after the descriptions. Likewise, the distribution of each species is indicated based on what has been observed in herbaria and in previous publications. In addition, notes on chromosome number, uses and other points of interest are provided.

Symbology and acronyms used:

- !: sheet seen.
- n.s.: sheet not seen.
- ! photo: sheet seen in photo.
- ≡: homotypic synonym.
- =: heterotypic synonym.

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

Synonyms –

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.].

Type – *Parablechnum procerum* (G.Forst.) C.Presl, Epimel. Bot. 109. 1851. Figs. 4G, 7D. (*Osmunda procera* G.Forst.)

Diagnosis – *Parablechnum* species are characterised by 1-pinnate laminae, conform or subconform apices and stalked to substalked pinnae.

Description – *plants* terrestrial; *rhizomes* erect or suberect, rarely subarborescent or short to long creeping, scaly, scales concolorous or bicolorous, membranaceous or coriaceous, brown, pale brown, reddish or blackish, non-stolonifeorus; *fronds* dimorphic, sometimes monomorphic; *lamina* 1-pinnate, base truncate, apex ending in a conform pinna similar to the lateral ones, usually longer; *veins* free, simple or 1-furcated, catadromous; *buds* present only in two species (*P. proliferum* and *P. sessilifolium*); *pinnae* alternate to subopposite, stalked; *aerophores* often present, axillar, tuberculiform or conical; *hydathodes* usually patent, rounded to ovate; *fertile fronds* in the dimorphic species usually longer, more erect; *fertile pinnae* contracted, linear; *sori* linear, continuous, forming coenosori on both sides of the costa; *indusia* linear continuous, repand to lacerate margins, open towards the costa; *sporangia*; *spores* monolete, flat-convex in longitudinal equatorial view and elliptical in polar view, with a densely folded or cristate-reticulate perispore, with more or less high muri delimiting polygonal areolae, forming reticules or, rarely, not folded, reticulate, with walls sometimes fenestrated, sometimes with filamentous processes.

Chromosome number – x = 28, 31, 33.

Distribution – pantropical, in Central and South America, South of Africa, Madagascar and the Mascarenes and the Austropacific.

Notes – the Blechnaceae genera closest to *Parablechnum* are *Neoblechnum*, *Oceaniopteris*, and *Doodia* (Gasper *et al.*, 2017).

Parablechnum identification key

1a. Petioles with dark, spiny excrescences ..... *P. acanthopodum*
1b. Petioles without dark, spiny excrescences.....2

2a. Buds present.....3
2b. Buds absent.....4

3a. Bulbils in the axils of the pinnae or mostly in distal pinnae, sterile pinnae margins flat or only slightly revolute ..... *P. proliferum*
3b. Bulbils on lateral pinnae, all over the lamina, sterile pinnae revolute . *P. sessilifolium*

4a. Pinnae articulate to the rachis ..... *P. articulatum*
4b. Pinnae not articulate to the rachis..... 5

5a. Rhizomes stoloniferous 6
5b. Rhizomes non-stoloniferous..... 7

6a. Sterile pinnae strongly revolute ..... *P. revolutum*
6b. Sterile pinnae not or only slightly revolute ..... *P. puniceum*

7a. Pinnae hastate, at least the proximal ones with a basiscopic auricle, in both sterile and fertile fronds..... *P. camfieldii*
7b. Pinnae not hastate 8

8a. Sterile pinnae with revolute margins (sterile pinnae sometimes weakly revolute in *P. stipitellatum*)..... 9
8b. Sterile pinnae with margins not or only slightly revolute 16

9a. Rhizome and laminar scales dentate in all the plant, sometimes sterile pinnae less revolute when the plant is in an exposed position..... *P. stipitellatum*
9b. Rhizome and laminar scale margins variable, but never dentate 10

10a. Veins very prominent ..... *P. lima*
10b. Veins not or only slightly prominent 11

11a. Rhizomes erect but not forming trunks, usually long-creeping and ascendent ..... *P. stuebelii*
11b. Rhizomes forming trunks up to 1 m 12

12a. Aerophores absent 13
12b. Aerophores present ..... *P. moranianum*

13a. Petiole, rachis and costa scales strong, coriaceous, always concolorous ..... *P. revolutum*
13b. Petiole, rachis and costa scales papyrose, fragile, concolorous or bicolorous 14

14a. Pinnae clearly stalked, about 5 times longer than wide ..... *P. reflexum*
14b. Pinnae shortly stalked, about 10-15 times longer than wide 15

15a. Petiole and rachis scales concolorous ..... *P. loxense* var. *loxense*
15b. Petiole and rachis scales bicolorous ..... *P. loxense* var. *stenophyllum*

16a. Aerophores absent 17
16b. Aerophores present 36

17a. Paraphyses or sporangiasters present 18
17b. Paraphyses or sporangiasters absent 24

18a. Spore perispore not folded, reticulate, with walls usually fenestrated .*P. nesophilum*
18b. Spores perispore cristate-reticulate or folded, with walls not fenestrated 19

19a. Basal pinnae reduced in size 20
19b. Basal pinnae not reduced in size 22

20a. Basal pinnae reduced to auricles, rachis with peltate scales with a distinctive black spot ..... *P. novae-zelandiae*
20b. Basal pinnae smaller than the distal ones but not reduced to auricles, rachis with peltate scales with or without a distinctive black spot 21

21a. Pinnae falcate, with acute or attenuate apices, scales with black dot on abaxial side of costa and sometimes on rachis and petiole ..... *P. montanum*
21b. Pinnae straight, with obtuse or acute apices, with concolorous or slightly bicolorous scales, but never with well-developed black spot. .....*P. procerum*

22a. Fertile pinnae with proximal portion of fertile pinnae expanded and sterile..... *P. chauliodontum*
22b. Fertile pinnae without proximal portion of fertile pinnae expanded and sterile, at least in non-aberrant specimens 23

23a. Lamina deltoid ..... *P. triangularifolium*
23b. Lamina lanceolate ..... *P. milnei*

24a. Fertile pinnae with marginal band of laminar tissue lacking sporangia.. *P. ambiguum*
24b. Fertile pinnae without marginal band of laminar tissue lacking sporangia, or only visible in aberrant specimens 25

25a. Basal pinnae clearly reduced in size 26
25b. Basal pinnae not reduced in size 27

26a. Petiole, rachis, and costa scales without a distinctive black spot at the point of attachment ..... *P. minus*
26b. Petiole, rachis, and costa scales with a distinctive black spot at the point of attachment ..... *P. howeanum*

27a. Fronds monomorphic ..... *P. gregsonii*
27b. Fronds dimorphic or subdimorphic 28

28a. Rachis and costa scales serrate 29
28b. Rachis and costa scales entire 30

29a. Petiole stramineous, only atropurpureous at base, lamina lanceolate, ovate to deltoid, lanuginose hairs sometimes present, pinnae in 2-17 pairs ..... *P. wattsii*
29b. Petiole atropurpureous or shiny brown, lanuginose hairs absent, pinnae in 21-28 pairs ..... *P. cochabambense.*

30a. Rhizome long-creeping ..... *P. usterianum*
30b. Rhizome erect or short-creeping 31

31a. Sterile pinnae bases clearly cuneate ..... *P. glaziovii*
31b. Sterile pinnae bases cordate, subcordate or ovate 32

32a. Rachis and costa scales bicolorous .....*P. bicolor*
32b. Rachis and costa scales concolorous 33

33a. Sterile pinnae margins strongly undulate..... *P. chilense*
33b. Sterile pinnae margins straight or only slightly wavy 34

34a. Plant very densely scaly, scales from pale brown to black.....*P. squamosissimum*
34b. Plant from densely to moderately scaly, brown or reddish brown, rarely bicolored 35

35a. Fertile fronds clearly longer than the sterile ones..... *P. capense*
35b. Fertile fronds approximately the same size as the sterile ones..... *P. wurunuran*

36a. Aerophores conical 37
36b. Aerophores various, but not conical 39

37a. Petiole brown or pale brown, but never atropurpureous, rachis and costa glabrous or sparsely scaly ..... *P. proliferum*
37b. Petiole brown, pale brown or atropurpureous, rachis and costa densely scaly, sparsely scaly or glabrous..... 38

38a. Petiole, rachis, and costa atropurpureous, glabrous o sparsely scaly ..... *P. lechleri*
38b. Petiole, rachis, and costa pale brown, densely scaly ..... *P. chiriquanum*

39a. Glandular hairs present on the pinnae surface, mostly on the abaxial side ..... *P. wolhgemuthii*
39b. Glandular hairs absent 40

40a. Plants monomorphic 41
40b. Plants dimorphic or subdimorphic.....43

41a. Axis atropurpureous..... *P. pazense*
41b. Axis brown or pale brown 42

42a. Lamina 10-19 cm long, petioles equal in length or longer ..... *P. obtusum*
42b. Lamina >20 cm long, petioles clearly shorter ..... *P. monomorphum*

43a. Fertile pinnae with a sterile basal portion, wider than longer..... 44
43b. Fertile pinnae without a sterile basal portion, or only in aberrant specimens 47

44a. Pinnae bases subcordate ..... *P. subcordatum*
44b. Pinnae bases rounded or cordate 45

45a. Pinnae in <10 pairs, clearly ascendent (New Caledonia) .....*P. confusum*
45b. Pinnae in >10 pairs, straight or only slightly ascendent (not New Caledonia) 46

46a. Rhizome scales linear to oblong-ovate, brown, concolorous, 19-30 pinnae pairs, margins slightly revolute ..... *P. pacificum*
46b. Rhizome scales linear to elliptic-triangular, reddish brown, concolorous or sometimes bicolorous, 14-32 pinnae pairs, margins never revolute .....*P. dilatatum*

47a. Petiole with conspicuous scars left by fallen scales, sporangiasters present ..... *P. humbertii*
47b. Petiole lacking scars, sporangiasters absent 48

48a. Petiole, rachis and costa strongly atropurpureous 49
48b. Petiole, rachis and costa brown or pale brown, or only in basal portions 50

49a. Scales dentate, laminar tissue extremely coriaceous .....*P. atropurpureum*
49b. Scales entire, laminar tissue chartaceous or coriaceous ..... *P. varians*

50a. Rhizomes long-creeping 51
50b. Rhizomes erect, ascendent or short-creeping 52

51a. Sterile pinnae in less than 9 pairs, lamina deltoid (Bolivia) ..... *P. repens*
51b. Sterile pinnae in more than 9 pairs, lamina elliptic (Austropacific).....*P. hieronymi*

52a. Laminar tissue herbaceous..... 53
52b. Laminar tissue chartaceous or coriaceous 54

53a. Fronds >30 cm long (New Caledonia)..... *P. corbassonii*
53b. Fronds <30 cm long (Venezuela) ..... *P. paucipinna*

54a. Rachis densely scaly 55
54b. Rachis glabrous or sparsely scaly 58

55a. Rachis scales persistent (Austropacific) ..... *P. vestitum*
55b. Rachis scales deciduous (Neotropical) 56

56a. Raised dark dots on rachis (scars from fallen scales) absent .....*P. squamatum*
56b. Raised dark dots on rachis (scars from fallen scales) present 57

57a. Petioles on the sterile frond as long as the lamina, 18-40 pinna pairs, buds absent *P. lineatum*
57b. Petioles on the sterile frond shorter than the lamina, 27-70 pinna pairs, buds present .....*P. sessilifolium*

58a. Rachis and costa scales dentate 59
58b. Rachis and costa scales entire or weakly dentate 60

59a. Pinna pairs 20-40 ..... *P. smilodon*
59b. Pinna pairs 7-10..... *P. roraimense*

60a. Rhizome scales orange to pale brown, concolorous 61
60b. Rhizome scales dark reddish brown to blackish, concolorous or bicolorous.....69

61a. Pinnae margin serrulate 62
61b. Pinnae margins entire or crenulate 64

62a. Pinnae 1.5–3 x 0.6–1 cm, petioles very long, usually longer than the lamina ..... *P. werffii*
62b. Pinnae 5–20 x 1–2.5 cm, petiole usually not longer than the lamina 63

63a. Spores perisporium without filaments on the areolae surface .....*P. cordatum*
63b. Spores perisporium with filaments on the areolae surface .....*P. falciforme*

64a. Pinnae bases cuneate, plants rheophytic ..... *P. rheophyticum*
64b. Pinnae bases ovate or cordate, terrestrial habitat.....65

65a. Spore perispore with filamentous processes.....66
65b. Spore perispore without filamentous processes.....68

66a. Lamina linear-ovate, sterile pinnae revolute, spores with sparse filaments ..... *P. tuerckheimii*
66b. Lamina elliptic-acuminate or oblong-lanceolate 67

67a. Lamina oblong-lanceolate, spores with sparse, short filamentous processes (Neotropical) .....*P. ryanii*
67b. Lamina elliptic-acuminate, sterile pinnae slightly revolute, spore perispore with a net of long filamentous processes (Madagascar).....*P. marginatum*

68a. Sporangium rosette length and equatorial spore diameter >60 mm .....*P. cordatum*
68b. Sporangium rosette length and equatorial spore diameter <60 mm . *P. schiedeanum*

69a. Rhizome scales bicolorous (Austropacific) ..... *P. hieronymi*
69b. Rhizome scales concolorous (Bolivia) ..... *P. bolivianum*

Parablechnum species

Parablechnum acanthopodum (T.C.Chambers & P.A.Farrant) Gasper & Salino, Phytotaxa 275(3): 215. 2016.

Basionym – *Blechnum acanthopodum* T.C.Chambers & P.A.Farrant, Blumea 46: 290. 2001.

Type – Papua New Guinea, Milne Bay District, Goodenough Island, E slopes, wet rocky bank of stream in forest, 1600 m, 4th Archbold Expedition to New Guinea, *L.J. Brass 24859,* 21 October 1953 (holotype: CANB84030–1! photo; isotypes: A00112052! photo, BM001048316! photo, GH n.s.).

Description – *rhizome* unknown; *fronds* subdimorphic or monomorphic, more or less erect; *sterile fronds* up to 2.5 m long and 50 cm wide; *petioles* up to 84 cm, atropurpureous, grooved adaxially and prominent abaxially, with dark, spiny excrescences 0.1 cm in diameter at base and 0.1–0.35(–0.5) cm long, scales at base broadly triangular, 0.7 × 0.2–0.3 cm wide, entire, brown, membranaceous and concolorous, persistent; *lamina* linear-triangular, 1-pinnate, *rachis* brown or atropurpureous at base, brown towards apex, glabrous, with petiole–like spines; *sterile pinnae* in at least 40 pairs, linear-elliptic, 25 × 1.5 cm, sessile or sub–stalked, base asymmetrical, subcordate or truncate, apices acuminate, margins serrate to dentate towards apex, basal pinnae slightly reduced, falcate, alternate to subopposite, *costae* similar in colour to rachis, grooved adaxially, prominent abaxially, glabrous, sometimes with some spine–like structures similar to those on basal third of rachis; *veins* free, simple or 1-furcate, catadromous; *aerophores* present, axillary; *hydathodes* not observed*; fertile*

fronds similar in size to sterile ones; *fertile pinnae* slightly narrower, usually 0.8 cm wide but up to 1 cm towards base and then narrowing abruptly at insertion with rachis, resembling sterile pinnae; *sori* linear, continuous, forming coenosori on both sides of costa, occupying at least the proximal two–thirds of pinna; *indusia* linear, continuous, open on both sides of costa; *spores* 71.3 × 60 µm, perispore folded, with a scabrous to minutely rugulate surface (**Figure 30**).

Reference: Chambers & Farrant (2001).

Chromosome number – unknown.

Distribution and habitat – Known from one collection from Goodenough Island (a high island) in the D'Entrecasteaux Islands off the northeast coast of Papua. (Chambers & Farrant, 2001).

Etymology – The epithet refers to the spiny petioles.

Notes – Chambers & Farrant (2001) described the spore ornamentation as similar, but more markedly folded, than that of *Oceanopteris whelanii*. The presence of spines on the petioles, the subdimorphic fronds, and the almost sessile pinnae suggest that this species may belong to the genus *Oceaniopteris* rather than *Parablechnum*. However, the scarce amount of herbarium material (only the types) hampers the settlement of this issue without further field collections and molecular work.

Reviewed material:

INDONESIA. Goodenough Island: Milne Bay District, *L.J. Brass 24859*, 21 October 1953 (A00112052! photo, isotype; BM001048316! photo, isotype; CANB84030! photo, syntype; CANB84031! photo, syntype).

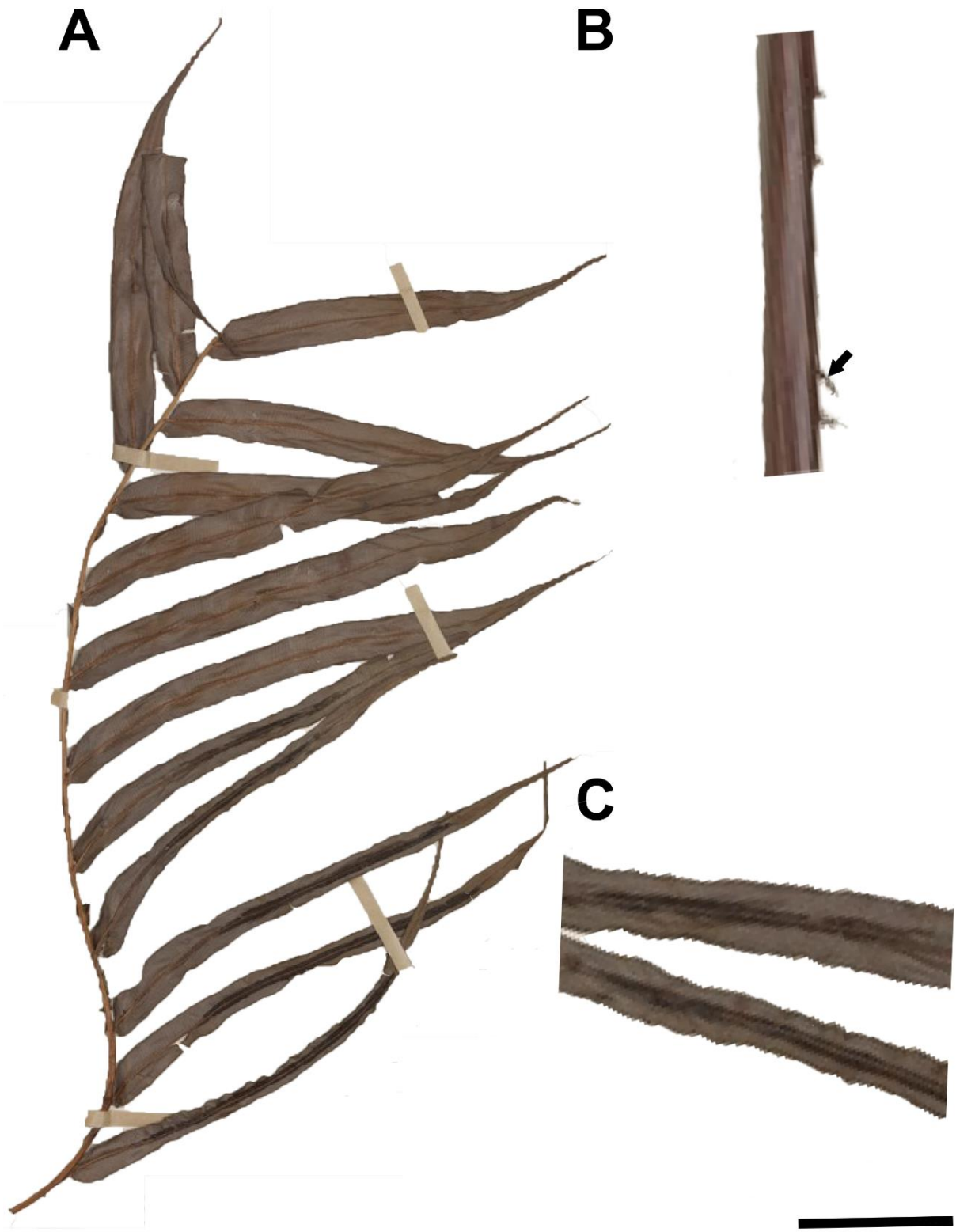

Figure 30. *Parablechnum acanthopodum*. A. Lamina; B. Petiole with spines (arrow); C. Fertile pinnae, abaxial side. (A-C: *L.J. Brass 24859*, CANB84031, holotype). Scale: 4 cm in A, 1.4 cm in B, 2 cm in C.

Parablechnum ambiguum C.Presl, Epimel. Bot. 109. 1851.

Synonyms –

≡*Lomaria ambigua* (C.Presl) Fée, Gen. Fil. 5: 68.1852. *Blechnum ambiguum* (C.Presl) Kaulf. ex C.Chr., Dansk Bot. Ark., 9, 3: 21. 1937.

=*Parablechnum procerum* var. *acuminata* C.Presl, Epimel. Bot. 109. 1849. ≡*Blechnum capense* var. *acuminatum* (C.Presl) Domin, Biblioth. Bot. 20(85): 115. 1913. Type: New Holland [Australia], Sieber 105, 1835 (NSW n.s.)

=*Doodia caudata* var. *lomarina* F.Muell., Fragm. 5: 130. 1866. Type: Australia, New South Wales, Parramatta, *W. Woolls s.n.* (syntype: MEL5427! photo).

=*Blechnum procerum* var. *blechnoides* Luerss., Flora 59: 292. 1876. ≡*Lomaria procera* var. *blechnoides* (Luerss.) Wawra, Itin. Princ. S. Coburgi 2: 121. 1888. Type: Australia, Blau Berge [Blue Mountains] *C.R. 376,* (nod found).

–*Orthogramma laevigata* (Cav.) C.Presl, Epimeliae Botanicae: 121. 1851, misapplication; ≡*Spicanta laevigata* (Cav.) Kuntze, Revisio Generum Plantarum 2: 821. 1891, misapplication; ≡*Blechnum capense* subsp. *laevigatum* (Cav.) Domin, Beitrage zur Flora und Pflanzengeographie Australiens. Bibliotheca Botanica 20(85): 117–118. 1914, misapplication; ≡*Blechnum capense* var. *laevigatum* (Cav.) Melvaine, A check list of the New South Wales pteridophytes. Proceedings of the Linnean Society of New South Wales 61: 119. 1936, misapplication.

–*Blechnopteris ambiguum* Trevis., Atti Reale Ist. Veneto Sci. Lett. Arti 2: 166. 1851. nom. nud.

–*Blechnum ambiguum* C.Presl, Tentamen Pteridographiae sue Genera Filicacearum. 1836. nom. invalid., nom. nud.

Type – New Holland [Australia], *Sieber 106,* 1835 (holotype: B200031542! photo; isotypes: B200031541-2! photo, BM001048226! photo, NSW n.s., NY!, S2049! photo)

Description – *plants* terrestrial; *rhizome* short, erect or shortly creeping, non-stoloniferous, with ovate–lanceolate scales, cordate at base, acuminate, margin entire or very slightly toothed, brown or reddish; *fronds* dimorphic or subdimorphic, pendulous; *sterile fronds* 7–50 × 3–15 cm; *petioles* 3–15(–47) cm long, straw-coloured or brown, sometimes atropurpureous at base, with scales on the base similar to those of the rhizome; *lamina* deltoid, truncate, 1-pinnate, *rachis* straw-coloured, grooved adaxially, granulose ornamentation, with linear, acuminate, brown or reddish-brown scales, sometimes interspersed with woolly indumentum, *sterile pinnae* on 5–14 pairs, 1.5–14 cm long, obtuse to acute apex, rounded bases, becoming adnate towards apex, shortly stalked, basal pinnae similar to or slightly shorter than middle ones, alternate to subopposite, terminal pinnae longer, with an asymmetric base, sometimes with a basal auricle, margins serrulate; *costae* similar to the rachis, grooved adaxially, prominent abaxially; *veins* free, simple or 1-furcate, catadromous; *aerophores* not present; *hydathodes* elongated, ovate to linear; *fertile fronds* longer than sterile ones, petioles similar in appearance to sterile

fronds but longer, *lamina* deltoid, truncate, 1-pinnate, *fertile pinnae* linear, variably wide, usually with photosynthetic tissue on edges of abaxial side; *sori* linear, continuous, on both sides of costa, forming coenosori; *indusia* linear, continuous, open towards costa, brownish; *sporangia* with (24) 26 (29) arch cells; *spores* monolete, (50) 59 (72) × (37) 41 (48) µm, perispore rugulose, cristate-reticulate, with sharp low walls forming irregular sharp ridges, with short, sparse filamentous processes (**Figure 31**).

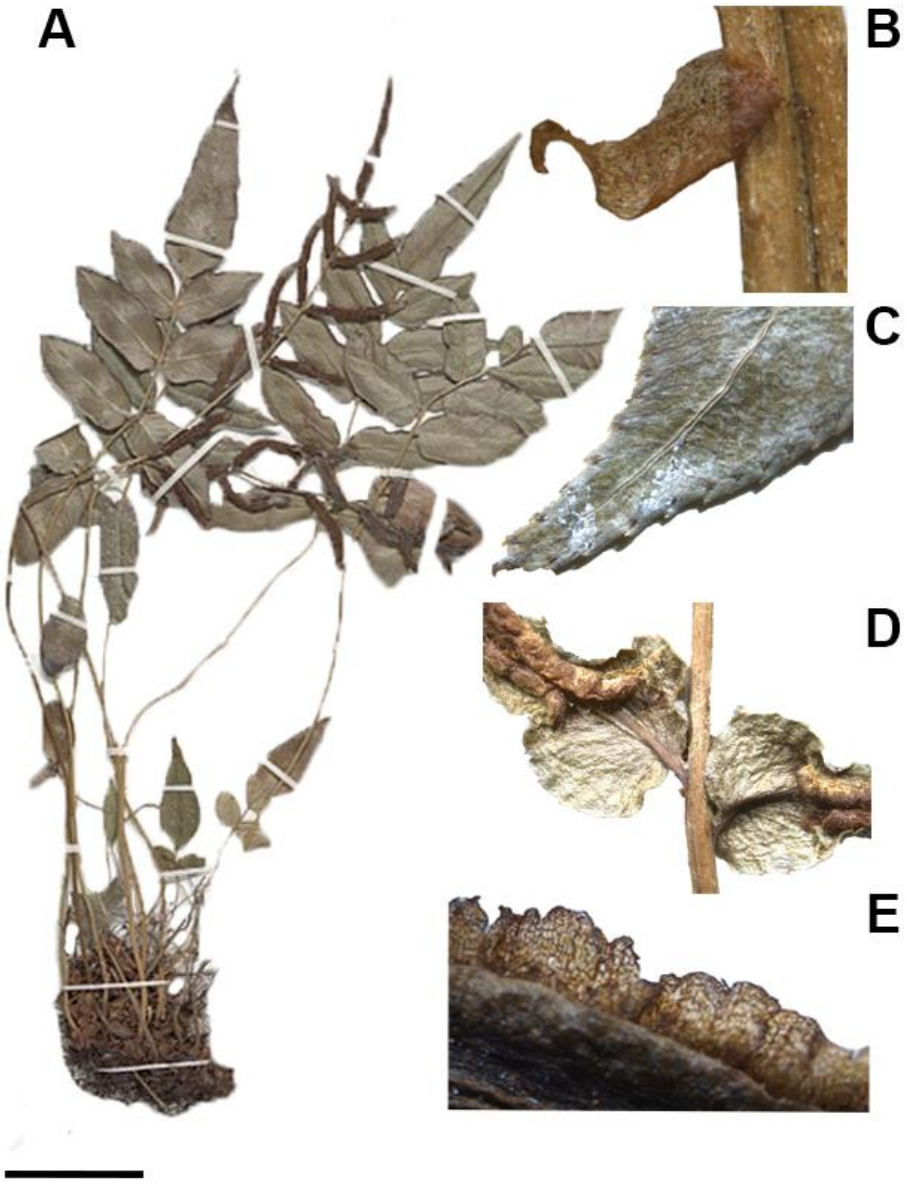

Figure 31. *Parablechnum ambiguum*. A. Plant; B. Petiole scale; C. Sterile pinna apex, adaxial side; D. Fertile pinnae bases, abaxial side; E. Indusium. (A, B & E: *E.F. Constable s.n.*, US2361403; C & D: *M. Tindale s.n.*, US2359587). Scale: 4 cm in A.

Chromosome number – n = 56 (Chambers & Farrant, 1998b).

Distribution and habitat – Endemic from the Eastern coastal regions and plateaus of Australia, scattered from the middle of Queensland to the south coast of New South Wales. Growing on rocks and wetland shores, sometimes in tropical forests and humid evergreen forests (Chambers & Farrant, 1998b).

Etymology – Ambiguous, referring to the variability of pinnae morphology.

Notes – According to Chambers & Farrant (1998b), *P. ambiguum* may hybridise with *Parablechnum wattsii* in New South Wales. It is distinguished from this species by its pendulous habit, photosynthetic margins on most fertile pinnae and entire or almost entire scales on petiole, rachis and/or costa. *Parablechnum wattsii* is usually erect, has no sterile margins on fertile pinnae and often has bicolorous scales on the rhizome and dark, toothed scales on the rachis and costa.

Several authors have used the name *Blechnum laevigatum* Cav. to refer to this taxon (Brown, 1810; Hooker, 1859; Bentham, 1878; Moore, 1893; Christensen, 1905). *Blechnum laevigatum* is a species of *Blechnum s.s*. from South America and is not related to *Parablechnum ambiguum*. This error was probably due to the fact that the sterile tissue of the fertile pinnae of *P. ambiguum* could be interpreted belonging to a nearly monomorphic plant, like true *Blechnum* species.

Reviewed material:

AUSTRALIA. New South Wales: *E.F. Constable P1284,* 25 November 1956 (UC194885! Photo); *R. Brown s.n.,* 1825 (P01463085!); Central Coast, Junction of Woolshed gully and Colo River below Boorai ridge 20.4 km (12.7 miles) E along Culoul Range road, *R.G. Coveny & P.D. Hind 9135*, 12 February 1976 (NY!); Federal Falls, Lawson, *R. Coveny 10190,* 1 August 1978 (NY!; UC1523286! photo); Hazelbrook, near Recreaton Reserve, Blue Mountains, *M. Tindale P8124,* 26 March 1960 (US2359587!); New Juntion, ca. 5 miles north–east of Lithgow, *E.F. Constable P8186,* 21 February 1961 (UC1225106! Photo; US2361403!); Northbridge, *H.S. Mckee s.n.,* 10 December 1950 (P01579169!; P01579170!); Stanwell Park, *J.L. Boorman s.n.* (P01463075!; P01463076!); Sydney, *S. Helms 751,* 10 April 1922 (US1348784!). **Queensland:** Lamington National Park, Q–on Elabana Falls track, *L.S. Smith & M.D. Tindale P7446,* 3 August 1956 (US3259584!). **South Australia:** Mt. Lofty Range, Mt. Lofty Botanic

Garden, ca. 12 km South–East of Adelaide, *R.H. Kuchel 1270*, 16 October 1963 (US2541441!). **Tasmania:** *Astrolabe s.n.*, 1828 (P01463050!); *van Diemen 14*, 1828 (P01463080!); *Oldfield s.n.*, no date (NY!); *ibidem* (NY!); *ibidem* (NY!); *Verreaux 86*, 1844 (P01462488!); Hobart, *G.F. Rome s.n.*, 1862 (NY!); Jordan River Jorge, *O. Degener & I. Degener 36026*, 30 August 1981 (NY!). **Victoria:** Mt. Buch, *E.E. Pescott s.n.*, 2.1901 (P01462491!). **Unknown area:** *A.N. Desvaux s.n.*, no date (P01463063!); *JPV 471*, 4.1845 (P01567011!; P01567012!); *M. Verrenux 78*, 1844 (US0071269!); *Sieber 105*, 1827 (P01462492!); *Sieber 106*, 1835 (B200031537! Photo, isotype; B200031542! photo, holotype; B200031541! photo, isotype; B200031542! photo, isotype; BM001048226! photo, isotype; NY!, isotype; S2049! photo, isotype); *Verreaux 78*, 1844 (P01463049!).

Parablechnum articulatum (F.Muell.) Gasper & Salino, Phytotaxa 275(3): 215. 2016

Basionym – *Lomaria articulata* F.Muell., Fragm. 5: 187. 1866.

Type – Australia, Queensland, Head of MacKay River, *J. Dallachy s.n.*, 12 August 1866 (MEL59536! photo).

Synonyms –

≡*Blechnum articulatum* (F.Muell.) S.B.Andrews, Austrobaileya 1: 11. 1977.
=*Lomaria euphlebia* F.M.Bailey, Lithogr. Ferns Queensland 87. 1892. non *Plagiogyria euphlebia* (Kunze) Mett., in K.Domin, Biblioth. Bot. 20(85): 147. 1913. Type: not found.

Description – *plants* terrestrial; *rhizome* short and erect, not stoloniferous, sometimes forming a small trunk, with scales narrow, triangular, acuminate, entire, reddish brown, darker at base; *fronds* dimorphic 12–50(–165) × 4–25(–80) cm; *sterile fronds* with *petioles* 4–82 cm long, straw-coloured or slightly reddish, with sparce scales on the base similar to those on the rhizome; *lamina* ovate, 1-pinnate; *rachis* straw-coloured or slightly reddish, glabrous, *rachis* straw-coloured or slightly reddish, glabrous, without ornamentation; *sterile pinnae* on 5–20 pairs, narrowly lanceolate, 2.5–36 × 1–2.5 cm, base cuneate, stalked, stalks articulate, becoming adnate towards apex, alternate to subopposite, apices acute to acuminate, margins cuneate, serrulate at the apex, basal pinnae similar to or slightly shorter than middle pinnae; *costa* similar to the rachis, grooved adaxially, prominent abaxially; *aerophores* absent; *veins* free, simple or 1-

furcate, catadromous, dark, patent; *hydathodes* subtle, round or ovate; *fertile pinnae* linear, 6–27 × 0.15–0.7 cm, with an sterile acute apex; *sori* linear, continuous, on both sides of costa, forming coenosori; *indusium* linear, continuous, wavy-edged or lacerate at maturity, open towards costa, brownish; *sporangia* with 17 arch cells; *spores* monolete, 47 × 34 µm (**Figure 32**).

References – Chambers & Farrant (1998b).

Chromosome number – unknown.

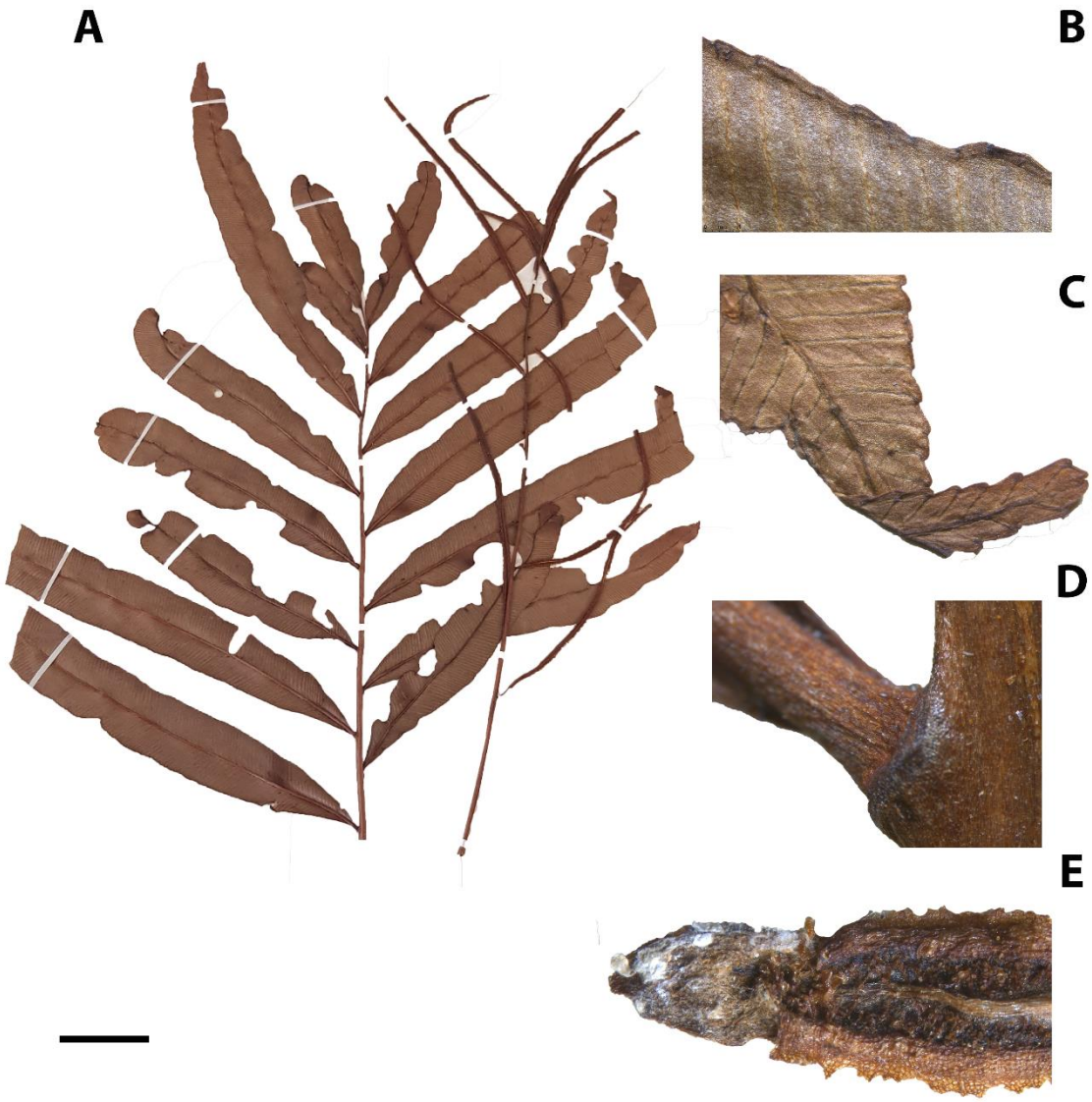

Figure 32. *Parablechnum articulatum*. A. Fragment of sterile frond (left) and fertile frond (right). A. Sterile pinna margin, abaxial side; C. Sterile pinna apex, abaxial side; D. Sterile pinna articulated stalk; E. Fertile pinna apex, abaxial side.). (*Dallachy s.n.*, US1371885). Scale: 4 cm in A, 3.4 mm in B; 2.6 mm in C, 1 mm in D, 1 mm in E.

Distribution and habitat – endemic to the mountain ranges of north–east Queensland. Grows along wet stream banks in rainforests. (Chambers & Farrant, 1998b).

Etymology – the specific epithet refers to the articulate stalks of the pinnae.

Notes -- *P. articulatum* as appear in all the phylogenies as the sister to the rest of species of the genus (Gasper *et al*., 2017; Bauret *et al.* 2018 and in the present work). This taxon is morphologically distinct by its articulated pinnae, and it might represent the only extant species of a now mostly extinct lineage.

Reviewed material:

AUSTRALIA. Queensland: Head of MacKay River, *J. Dallachy s.n.*, 12 August 1866 (MEL59536! Photo, holotype); Rockingham Bay, *Dallachy s.n.,* no date (K001092693! Photo; US1371885!).

Parablechnum atropurpureum (A.R.Sm.) Gasper & Salino, Phytotaxa 275(3): 215. 2016.

Basionym– *Blechnum atropurpureum* A.R.Sm., Acta Bot. Venez. 14(3): 5. 1984.

Type – Venezuela, Macizo de Chimantá, pequeñas altiplanicies en la base septentrional de los farallones superiores del Amurí-tepui (Sector W del Acopán-tepui), 5°10'N, 62°07' W, Distrito Piar, Bolívar, Venezuela, 1950 m, 2-5 February 1983, *Julian A. Steyermark, Otto Huber & Victoriano Carreño 128970* (holotype: VEN218673! photo).

Description – *plants* terrestrial or epiphytic; *rhizome* erect; *fronds* dimorphic, 30–40 × 9 cm; *sterile fronds* with *petioles* the same length than the lamina or longer, atropurpureous from the basal portion to the middle part, verrucose, scales ovate–lanceolate or lanceolate, up to 8 × 3 mm, ferruginous, irregularly dentate; *lamina* 1-pinnate, ovate, ending in a conform terminal pinna, coriaceous; *rachis* atropurpureous, lustrous, rugose, scally, scales similar to those of the petiole; *sterile pinnae* in 7–10 pairs, up to 5 × 1 cm, ascending, stalked, alternate to subopposite, apex acute, base cordate, margin serrate, especially in the apex, revolute; *costae* grooved adaxially, prominent abaxially, scaly abaxially, scales ovate to lanceolate, ferruginous, deeply dentate; *veins* free, simple or 1-furcate, catadromous, prominent, blackish; *aerophores* axillary,

atropurpureous, tuberculiform; *hydathodes* ovate, whitish; *fertile fronds* longer and more erect; *petioles* longer without verrucose ornamentation; *fertile pinnae* in up to 10 pairs, ascending; *costae* densely scaly; *sori* linear, continuous, forming coenosori on both sides of the costa; *indusia* linear, continuous, open towards the costa, margin erose or lacerate; *sporangia* with (16) 18 (22) arch cells*; spores* monolete (56) 65 (74) × (39) 48 (55) µm, perispore smooth, cristate-reticulate, with low, thick walls forming large polygonal areoles with long, very dense filamentous processes over the entire surface (**Figure 33**).

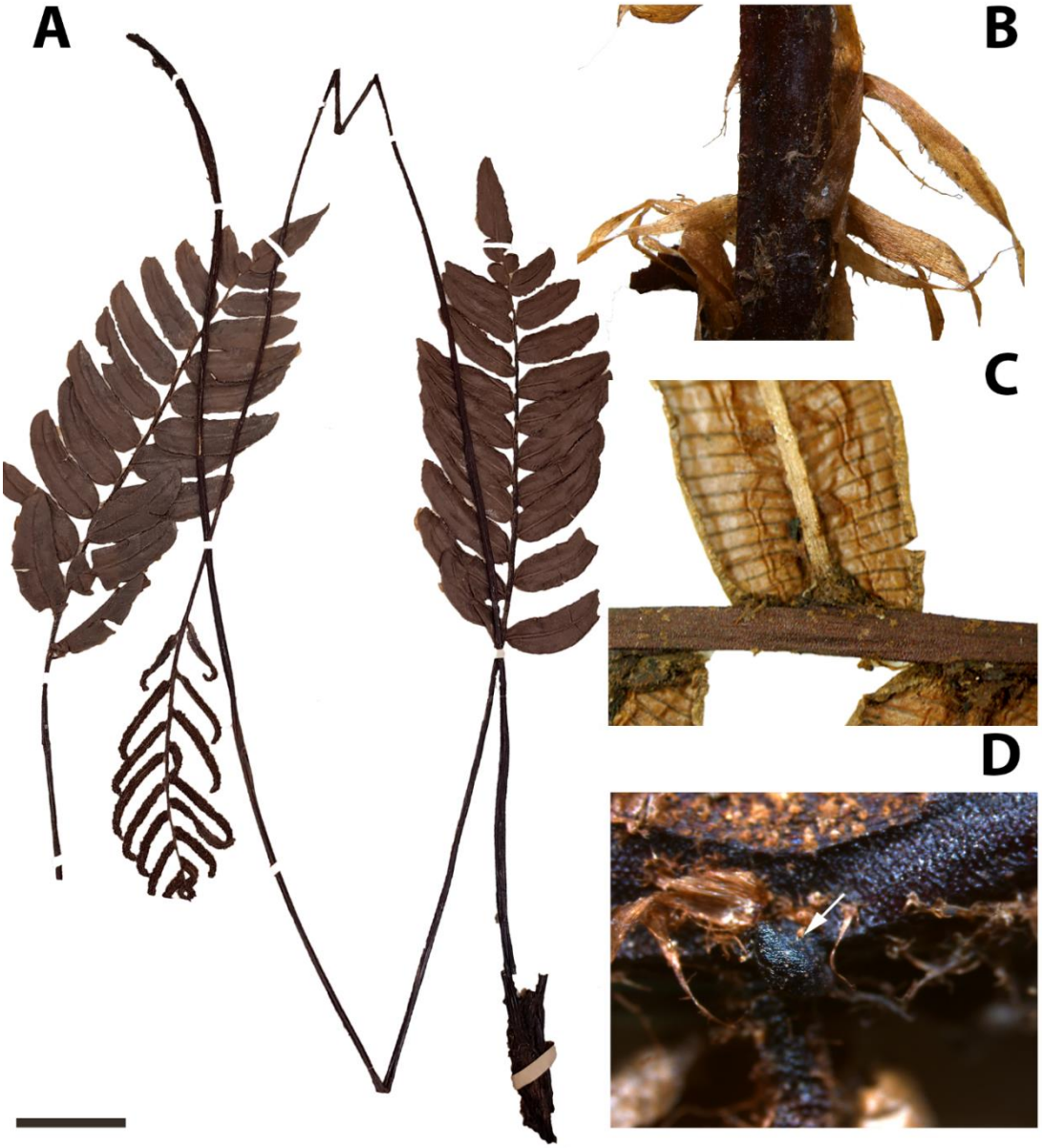

Figure 33. *Parablechnum atropurpureum*. A. Plant; B. Petiole base; C. Sterile rachis, abaxial side; D. Stalk with an aerophore (arrow) (A: *J. Steyermark et al. 126052*, NY; B & D: *H.D. Clarke et al 9488*, US3460185; C: *R. Liesner 25215*, UC1557245). Scale: 4.5 cm in A, 3.4 mm in B, 1 cm in C, 1.3 mm in D.

References – Steyermark & Maguire (1984).

Chromosome number – unknown.

Distribution and habitat – endemic to Venezuela and Venezuelan Guyana. Terrestrial, saxicolous or epiphytic. Montane and cloud forests, 1,800–2,700 m (Smith, 1985, 1995).

Etymology – the epithet probably refers to the atropurpureous axis of this species.

Notes – *Parablechnum atropurpureum* it is similar to *Parablechnum lineatum* and *Parablechnum cordatum*, but it is distinguished by its black to atropurpureous axes, smaller fronds with fewer pinnae, strongly coriaceous laminar tissue and the strongly dentate margins of the costal scales. It is similar to *Parablechnum lechleri* as both present very dark petioles, rachises and costae, but *P. lechleri* is larger and has conical aerophores.

It is interesting that the holotype was found growing as an epiphyte, an atypical habitat for *Parablechnum*, which is usually terrestrial (Steyermark & Maguire, 1984).

Reviewed material:

BRITISH GUYANA. Demerara, slopes of Roraima, *G.S. Jenman s.n.,* 1895 (NY!); Potaro-Siparuni, Mt. Ayanganna, camp on Summit plateat, *H.D. Clarke et al 9488,* 23 June 2001 (NY!; US3460185!); Region Cuyuni-Mazaruni, ±2-5 km NW of northern "prow" of Roraima, *W. Hahn & D. Gopaul 5455,* 24 February 1989 (NY!; US3272739!); Roraima, *G.S. Jenman 286,* 1911 (NY04187107!). **VENEZUELA. Amazonas:** Dept. Atabapo, Cerro Marahuaca, cumbre, extremo noreste, *J. Steyermark & F. Delascio 129261,* 30 March – 1 April 1983 (MO3240326!, paratype; MO3250201!, paratype; NY04187109!, paratype; UC1489182! Photo, paratype); *ibidem, J. Steyermark et al. 129252,* 30 March 1982 (NY04187108!); Dept. Atabapo, Cerro Marahuaca, summit, SW side of center, *R. Liesner 25215,* 22 October 1988 (MO3684930!; UC1557245! Photo). **Bolivar:** Dist. Piar, Murisipan-tepui, Summit, second of 4 tepuis W to E in Aparaman range, *B.K. Holst 3529,* 22 March 1987 (MO3469063!); Macizo de Chimantá, pequeñas altiplanicies en la base septentrional de los farallones superiores del Amurí-tepui (Sector W del Acopán-tepui), Distrito Piar, *J.A. Steyermark, et al. 128970,* 2-5 February 1983, (VEN218673! photo, holotype). **Lara:** Dept. Iribarren, Via El Palmar a 2 Kms. De Río

Claro, *Rivero et al R007,* 14 November 1982 (UC1503275! Photo; UC1503276! Photo); Dept. Morán, Caserto "Buenos Aires", *R. Rivero 788A,* 5 December 1984 (UC1508674! Photo). **Mérida:** *Funcke & Schlein 980,* 1846 (P01623220!; P01623221!); *Funcke & Schlein 1008,* 1846 (P01466406!); Tovar, *Moritz 298,* no date (P01462417!; P01462418!); Tovar, *Moritz s.n.*, no date (P01462413!). **Sucre:** Cumaná, *Aundz 658,* 8.1843 (P01466407!). **Tachira:** along highway between Pregonero and La Fundación, 5 km S of Pregonera, *T.B. Croat 54932,* 9 August 1982 (MO3106715!; UC1488925! Photo); Dist. Lobatera, La Cazadora, *H. van der Werff & R. Ortiz 5631,* 24 July 1983 (UC1524961! Photo). **Trujillo:** Distr. Boconó, Montalas de Misisí, carretera vieja Trujillo-Boconó, ca. 12 km by air NW od Boconó, *L.J. Dorr et al 7312,* 6 July 1990 (NY04187099!).

Parablechnum bicolor (M.Kessler & A.R.Sm.) Gasper & Salino, Phytotaxa 275(3): 215. 2016.

Basionym – *Blechnum bicolor* M.Kessler & A.R.Sm., Amer. Fern J. 97: 66. 2007.

Type – Bolivia. La Paz: Prov. Nor Yungas, Unduavi, 3400 m, November 1910, *Buchtien 2690* (holotype: UC477686! photo).

Description – *plants* terrestrial; *rhizomes* erect, dark ca. 3 cm in diameter including petiole base, with scales 6–10 × 1–2.2 mm, lanceolate, membranaceous, reddish brown or blackish with lighter margins, entire; *fronds* dimorphic or subdimorphic, 90 × 15 cm, *sterile fronds*, erect; *petioles* up to 45 × 0.3 cm, reddish brown at base, distally straw–like, moderately scaly, base scales similar to those of the rhizome, distally mixed with smaller, lighter coloured scales, 2–10 × 0.2–2 mm, lanceolate, membranaceous, yellowish-brown, entire or slightly denticulate, and others more or less ovate, appressed, yellowish-brown, ciliate, 0.1–0.8 × 0.1–0.7 mm; *lamina* broadly lanceolate, 1-pinnate, abruptly reduced at base, gradually reduced towards apex with a terminal conform pinna, coriaceous, glabrous adaxially and with minute scales on abaxial side, arachnoid, light brown, 0.05 × 0.2 mm; *rachis* straw-coloured, similar to petiole, with similar scales, *sterile pinnae* in 15–28 pairs, 9 × 1 cm, straight or slightly ascending, stalked, falcate, acuminate apices, bases ovate, margins hyaline, serrulate, reddish brown; *costae* straw-coloured, with scales similar to those of the rachis; *veins* free, simple or 1-furcate,

catadromous; *aerophores* absent; *hydathodes* rounded or ovoid; *fertile fronds* similar to sterile ones, but with narrower pinnae, 3–5 mm wide; *sori* linear and continuous, forming coenosori on both sides of costa, limited to the central zone of the pinna, lacking in the proximal 5–10 mm and distal 10–20 mm; *indusia* linear, continuous, opening towards costa, dark, entire to irregular at maturity; *sporangia* with 19-21 arch cells; *spores* monolete, (40) 50 (61) × (26) 36 (46) µm, perispores smooth or slightly rugulose, cristate-reticulate, with more or less high, sharp walls, forming large to medium areoles, with more or less long moderately dense filamentous processes (**Figure 34**).

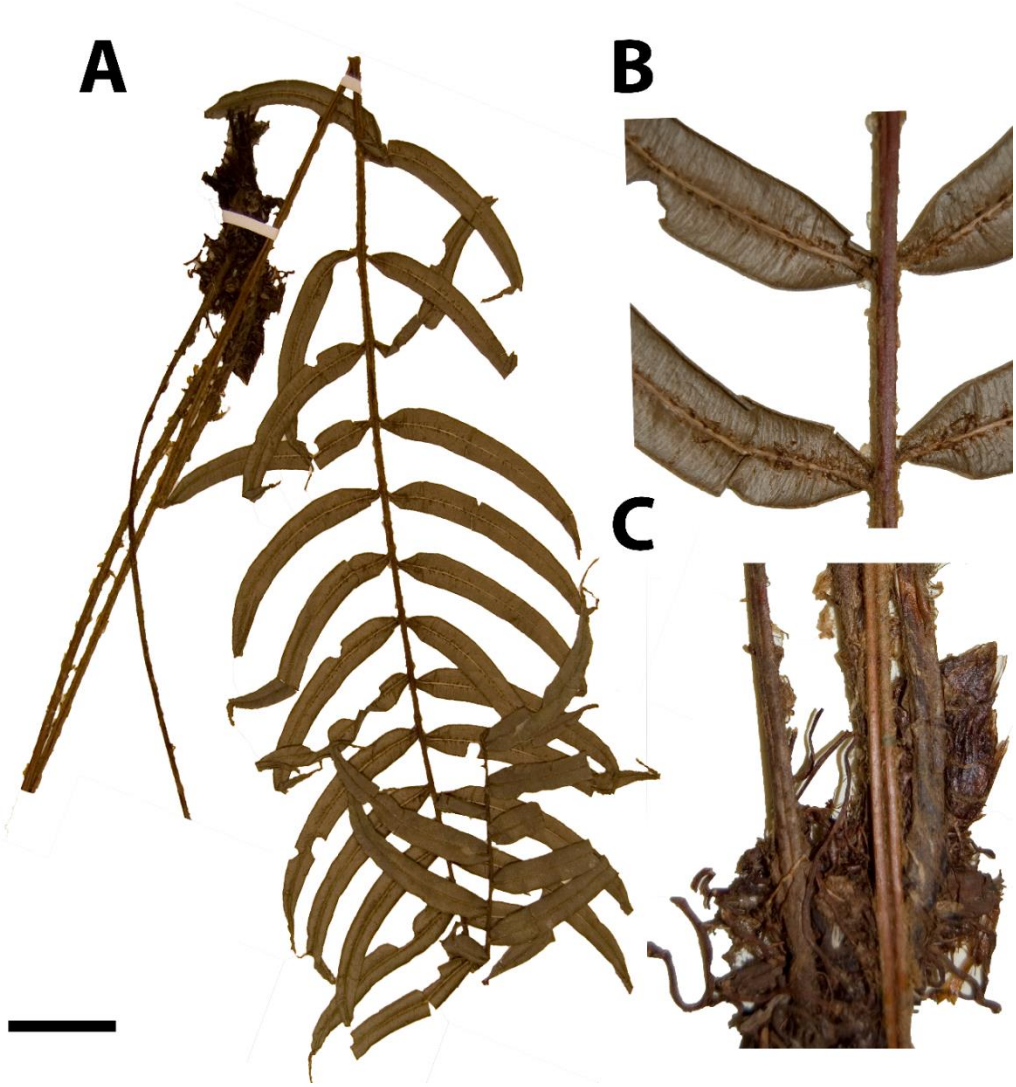

Figure 34. *Parablechnum bicolor*. A. Sterile frond; B. Sterile pinna bases, abaxial surface; C. Rhizome and petiole bases. (A-C: *E. García et al. 4479*, UC1749617). Scale: 4 cm in A, 3.5 cm in B, 7 cm in C.

References – Kessler *et al.*, (2007)

Chromosome number – unknown.

Distribution and habitat – endemic to Bolivia. Terrestrial in humid montane forests at 2150–3400 m. Locally relatively common. (Kessler *et al*., 2007; Smith & Kessler, 2018).

Etymology – the epithet alludes to the bicolorous scales of the petioles and the rhizome (Kessler *et al*., 2007).

Notes – this species is related to the Bolivian endemics *P. bolivianum* and *P. pazense* described by Kessler *et al*. (2007). It differs from *P. pazense* by having a more compact rhizome, bicolorous scales and straw-coloured costa and rachis. It differs from *P. bolivianum* in the bicolorous costal scales and darker rhizome scales. In the type, Buchtien indicated that this species had a trunk of up to 1 m, but as noted by Kessler *et al*. (2007) this is probably due to confusion with one or both two trunk–forming species that coexist with *P. bicolor* in the type locality: *Parablechnum loxense* and *Lomariocycas aurata* (Fée) Gasper & A.R.Sm..

Reviewed material:

BOLIVIA. Dept. Cochabamba: Prov. Ayopaya, Comunidad Pampa Grande, entre Achira y Pampa Grande, 09 November 2002, *Jiménez 1552* (GOET007143! photo, paratype; UC s.ph, paratype). **Dept. La Paz:** Bautista Saavedra, Area Natural de Manejo Integrado Apolobamba, sector Chaka, bosque al NO del campamento, por el antiguo camino Sorapata.Apolo, *A.F. Fuentes 13724*, 31 March 2009 (MO6255006!); Prov. Nor Yungas, camino desde Unduavia a Chulumani, *Schmit 168*, 22 December 1991 (UC! photo, parartype); Prov. Nor Yungas, Estación Biólogica de Tunquini, Bajo Hornuni, senda del campo de Don Pedro al camino de la mina, 16º12'S, 67º53'W, 2300 m, 25 July 2000, *Garcia 4479* (GOET007143! photo, LPB n.s., UC1749617! photo) ;Prov. Nor Yungas, Unduavi, 11.1910, *Buchtien 2690* (UC477686! photo, holotype).

Parablechnum bolivianum (M.Kessler & A.R.Sm.) Gasper & Salino, Phytotaxa 275(3): 215. 2016.

Basionym – *Blechnum bolivianum* M.Kessler & A.R.Sm., Amer. Fern J. 97: 69. 2007.

Type – Bolivia. La Paz: Prov. Nor Yungas, Estación Biológica de Tunquini, senda cafetal (cerca del campamento de Don Pedro) al camino de la mina, 16º12'S, 67º53'W, 2500 m, *Bach 1332*, 8 March 2001 (holotype: UC1762926! photo; isotypes: GOET007144! photo, LPB0000014! photo).

Description – *plants* terrestrial; *rhizomes* dark, erect, scales 4–6 × 1.2–2.5 mm, ovate–lanceolate, dark brown to blackish, margins pale brown, entire, irregular or slightly toothed, narrow; *fronds* probably dimorphic or subdimorphic, *sterile fronds* 120 × 26 cm, erect; *petioles* 60 cm, basally reddish brown, distally straw-coloured, moderately scaly, scales basally rhizome-like, graduating to a mixture of two types of smaller, paler scales, some 1.5–4 × 0.5–1.2 mm, ovate to ovate–lanceolate, dull pale brown, finely denticulate, the others 0. 3–1 × 0.2–0.8 mm, ovate, dense, dull pale brown, ciliate; *lamina* narrowly deltoid, 1-pinnate with an abruptly reduced base and gradually reducing towards the apex, with a conform terminal pinna, coriaceous, adaxially glabrous, abaxially with minute scales, arachnoid, pale brown, 0.05 × 0.2 mm; *rachis* reddish brown or straw–brown, adaxially grooved, abaxially prominent, moderately scaly, with petiole–like but slightly smaller scales; *sterile pinnae* in 25–30 pairs, 14 cm × 16 mm, stalked, slightly curved towards the apex, apices broadly acuminate, bases ovate, margins hyaline, serrulate, very slightly revolute; *costa* reddish-brown to straw–brown, adaxially grooved, abaxially prominent, densely scaly on abaxial side, scales ovate–lanceolate, denticulate, pale brown, 0.5–1.2 × 0.3–0.8 mm, adaxially glabrous; *veins* free, simple or 1-furcate, catadromous; *aerophores* present, tuberculiform; *hydathodes* rounded or ovate; *fertile fronds* unknown (**Figure 35**).

References – Kessler *et al.* (2007).

Chromosome number – unknown.

Distribution and habitat – endemic to Bolivia, in the departments of La Paz and Cochabamba, at 2400–2600m. It is terrestrial common in humid montane forests. (Kessler *et al.*, 2007; Smith & Kessler, 2018).

Etymology – the epithet refers to its type locality.

Notes – This species is related to the Bolivian endemics *P. bicolor* and *P. pazense* described by Kessler *et al*. (2007). It differs from *P. pazense* in that the latter species has long creeping rhizomes with light-coloured, denticulate scales, bicolorous costal scales, and narrower, lanceolate pinna margins.

Figure 35. *Parablechnum bolivianum. K. Bach 1332,* GOET007144, isotype. Scale = 4 cm

Reviewed material:

BOLIVIA. **Dept. Cochabamba:** Prov. Carrasco, km 10 desde Siberia a Comarapa, *Kessler 9166,* 20 October 1996 (UC! photo, paratype). **Dept. La Paz:** Prov. Nor Yungas, Estación Biológica de Tunquini, senda cafetal (cerca del campamento de Don Pedro) al camino de la mina, *Bach 1332*, 8 March 2001 (UC1762926! photo, holotype; GOET007144! photo, isotype; LPB0000014! photo, isotype).

Parablechnum camfieldii (Tindale) Gasper & Salino, *Phytotaxa* 275(3): 215. 2016.

Basionym – *Blechnum camfieldii* Tindale, Proc. Linn. Soc. New South Wales 85: 251. 1960.

Type – Fraser Island, Wide Bay district, in scanty forest, in swampy grey sandy soil amongst shrubs and sedges (*Gleichenia* sp.); common, fertile fronds dark brown, rachis black, sterile fronds green, *C.E.Hubbard 4576* 17 October 1930 (holotype: NSW.P8046 n.s.; isotype: K n.s.).

Synonyms –

=*Blechnum capense* var. *scabrum* Domin, Biblioth. Bot. 20(85): 116. 1913. Type: Australia, *Sieber 107* (holotype: not found; isotypes: BM001048223–4! photo, P01463051!, US3128051!); ≡*B. minus* subsp. *scabrum* (Domin) Tindale, Amer. Fern J. 50: 117. 1960.

Description – *plants* terrestrial; *rhizome* slightly creeping, forming an erect stem, densely scaly, scales long, linear to narrowly lanceolate, acuminate, with a twisted fibrillose apex, coriaceous, entire margin, very shiny, castaneous to atropurpureous, with light brown margins, 2.5 × 0.3 cm; *fronds* dimorphic; *sterile fronds* 45–100(–150) × 4–30 cm; *petioles* 12–60 cm long, atropurpureous, brown or reddish brown, linear basal scales lanceolate, acuminate, entire, brown, reddish brown or bicolorous, with scars at the insertion of the fallen scales distally; *lamina* ovate to lanceolate, 1-pinnate; *rachis* similar in colour to petiole, ribbed, prominent abaxially, rugulose ornamentation, with fine scales and woolly indumentum in the grooves; *sterile pinnae* in 6–37 pairs, oblong-lanceolate, acuminate at apex, auriculate–hastulate at base, especially basiscopically, 7–25 × 0.8–2 cm, shortly stalked, becoming adnate towards apex, margins serrate, basal pinnae gradually reduced and more widely spaced; *costae* similar to the rachis, grooved adaxially, prominent abaxially, granulate ornamentation; *veins*, free, simple or 1-furcate,

catadromous; *aerophores* absent; *hydathodes* rounded; *fertile fronds* usually longer than sterile ones, *pinnae* narrower, 7–17 × 0.3–0.5 cm, base hastulate, especially basal pinnae, apex acuminate; *sori* linear, continuous, forming coenosori on both sides of costa, occupying the entire pinna; *indusia* linear, continuous, opening towards the costa, brownish, margin repand; *sporangia* with (16) 18 (20) arch cells; *spores* monolete (38) 50 (69) × (23) 35 (63) µm µm, perispores smooth, cristate-reticulate, forming short abundant ridges, with more or less long filamentous processes not very abundant (**Figure 36**).

References – Chambers & Farrant (1998b).

Chromosome number – unknown.

Distribution and habitat – endemic to south–east Queensland and the northern and central coastal regions of New South Wales, possibly extending into Tasmania. Grows in low–lying swampy areas, usually in coastal habitats. (Chambers & Farrant, 1998b).

Etymology – taxon dedicated to J.H. Camfield, a naturalist who collected this species in large numbers in the Oatley–Kogarah district (Australia) between 1893 and 1902. This fern seems to be extinct in that area, as the swamps were drained for construction before 1960 (Tindale, 1960b).

Notes – Tindale (1960a) first wrote about this species as a subspecies of *Parablechnum minus* (as *Blechnum minus*), combining the variety described by Domin (1913) *Blechnum capense* var. *scabrum*, erroneously ascribed to the species *Blechnum capense* (= *Parablechnum capense*). He did not elevate it to species rank because he thought that there were intermediate individuals between this plant and *Parablechnum minus*, but later he saw that these individuals were young plants of *Parablechnum camfieldii*. After this finding he decided to elevate the status of the taxon to species, and since the name *Blechnum scabrum* already existed he changed it to *Blechnum camfieldii* in honour of J.H. Camfield (Tindale, 1961b).

This species seems to be related to *Parablechnum minus* and *P. wattsii*. It is easily distinguished by the hastate bases on sterile and fertile pinnae. Young plants, however, can be difficult to identify, as noted by Tindale (1960a, b). In this case, Chambers & Farrant (1998b) recommend paying attention to the basal pinnae, which are markedly reduced in *P. camfieldii*, reduced to auricles in *P. minus* and only slightly reduced in *P.*

wattsii. The same authors suggest that, although the species is widely distributed, it is probably an endangered species.

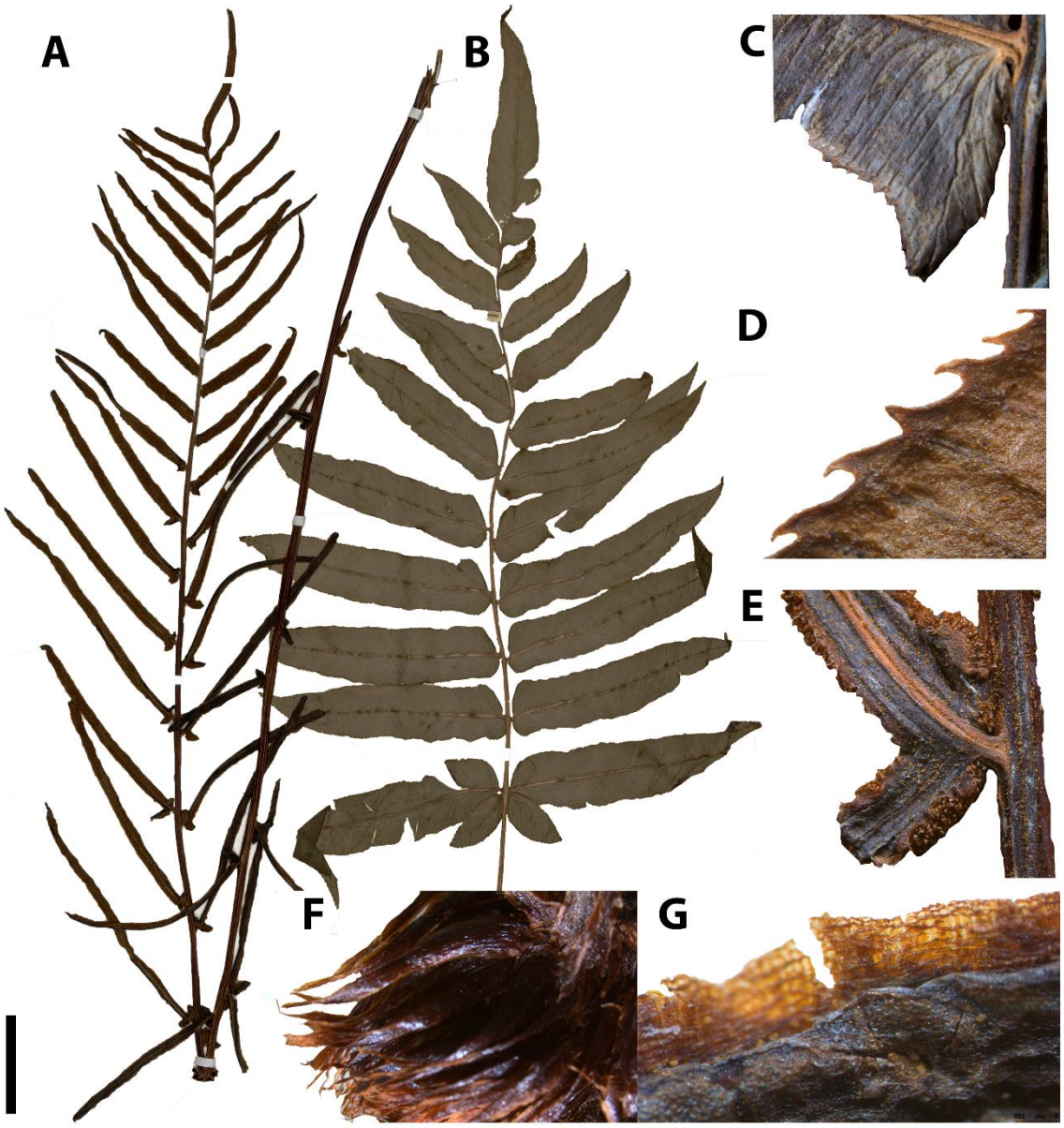

Figure 36. *Parablechnum camfieldii*. A. Fertile frond; B. Sterile frond; C. Sterile pinna base, adaxial surface; D. Sterile pinnae margin, abaxial surface; E. Fertile pinnae base, adaxial surface; F. Rhizome scales; G. Indusium (A: *R. Brown s.n.*, P01573180; B: *E. Cosson s.n.*, P01463052; C-G: *R. Coveny 4947*, US2840927). Scale: 4 cm in A & B, 4.5 mm in C, 1 mm in D, 3 mm in E, 3.5 mm in F, 560 in µm G.

Reviewed material:

AUSTRALIA. New South Wales: 5.5 miles (8.9km) SSW. Of Port Macquarie on the Lake Cathie Road, *R. Coveny 4947*, 21 August 1973 (US2840927!); 6.4 km SSW of

Bryon Bay, *R. Coveny 9383*, 2 August 1977 (NY!, two specimens); Botany Bay, *no collector*, no date (P01463079!); Captain Cook's Historical Landing Site, Kurnell, *R. Coveny 10195*, 2 August 1977 (NY!, two specimens); Dist. Port Jackson, *R. Brown s.n.*, 19 January 1884 (P01463045!; P01463046!); *ibidem*, *J.H. Camfield s.n.*, March 1897 (P01572091!); *ibidem*, *J.H. Camfield s.n.*, 1899 (P01463059!); *ibidem*, *E. Dainel 112*, 1869 (P01618454!); Federal Falls, Lawson, *R. Conveny 10191*, 1 August 1978 (NY!); Kurnell, Botany Bay, *J.L. Boorman s.n.*, May 1906 (US0654107!). **Unknown area:** *no collector*, no date (P01463052!); *ibidem* (P01573180!); *A. Sodiro s.n.*, 5 November 1920 (P01462497!); *Banks & Solander s.n.*, 1770 (P01463048!); *Brame s.n.*, no date (NY!); *Daimel 77*, 1866 (P01565122!); *Damels s.n.*, no date (P01662158!; P01662159!); *D. D'Urville s.n.*, no date (P01557666!); *Labillardiere s.n.*, 1808 (P01463047!); *Sieber s.n.*, 1827 (P01463054!); *Sieber 107*, 1 January 1827 (BM001048223! photo, isotype of *Blechnum capense* var. *scabrum*; BM001048224! photo, isotype of *Blechnum capense* var. *scabrum*; P01463051!, isotype of *Blechnum capense* var. *scabrum*; US3128051!, isotype of *Blechnum capense* var. *scabrum*).

Parablechnum capense (Burm.f.) Gasper & Salino, Phytotaxa 275(3): 215. 2016.

Basionym – *Blechnum capense* Burm.f., Fl. Indica 28. 1768.

Type – Cape, *sine coll. s.n.* (lectotype: G! photo, designated by Roux, 1982).

Synonyms –

=*Osmunda capensis* L. Mant. Pl. Alt.: 306.1771, illegitimate. Type: Habitat inter montes Cap b. Spei, inter montem tabularem et Diaboli, ad rivulum, *Koenig 22* (lectotype: LINN 1244/II! photo). ≡*Lomaria capensis* (L.) Willd. Sp. pl., 4th edn, 5: 291. 1810; ≡*Spicanta capensis* (L.) Kuntze Revis. gen. pl. 2: 821. 1891; ≡*Blechnum capense* (L.) Schltdl. Jacobsen, Ferns Sthn. Afr.: 464, fig. 350, map 176. 1983.

=*Blechnum sylvaticum* Schelpe J. S. African Bot. 45: 221. 1979. Type: as for in *Osmunda capensis.*

=*Lomaria duplicata* Potts T.N.Z.I. 9, 491. 1877. Type: Malvern Hills near the gorge of the Rakaia, *T. H. Potts* (holotype: K n.s.)

=*Lomaria latifolia* Col. in Tasm. J. nat. Sci. 2, 175. 1846. Type: Africa, Te Waiiti District, *W. Colenso*, January 1842 (lectotype: WELTP3240! Photo).

Vernacle names – Kaapse vleivaring (afrikaans), palm leak fern.

Description – *plants* terrestrial; *rhizome* erect or slightly creeping, up to 40 cm, with scales ovate–lanceolate, apex more or less filiform, concolorous, brownish,

membranaceous, up to 2 cm long; *fronds* dimorphic, rosette–forming; *sterile fronds* up to 1 m long; *petioles* light brown, grooved, unornamented, up to 50 cm long, with scales in the basal zone decreasing in density distally, similar to those of the rhizome but more filiform; *lamina* 1-pinnate, elliptic, up to 65 cm long, leathery; *rachis* light brown, adaxially grooved, abaxially prominent, without ornamentation, scales similar to those of the petiole, more abundant adaxially; *sterile pinnae* in up to 30 pairs, lanceolate–elliptic, stalked, becoming adnate towards the apex of the frond, base asymmetric, subcordate to obtuse, apex acute, margins slightly serrate, alternate or subopposite, slightly smaller at the base, the longest pinnae at the middle part, reducing towards the apex, terminal pinna similar to the pinnae closer to the apex, but usually longer, sometimes with a basal auricle; *costae* light brown, grooved adaxially, prominent abaxially, without some darker spots, with scales at base similar to those of rachis, mixed with fibrillose scales mostly in the stalk; *veins* free, simple or 1-furcate, catadromous; *aerophores* absent; *hydathodes* rounded to elongate; *fertile fronds* larger than sterile and more erect, up to 150 cm; *lamina* up to 50 cm or sometimes more, lanceolate–oblong; *fertile pinnae* in up to 40 pairs, linear, with slightly broader, asymmetrical, cordate, base, margins slightly toothed, apex acute; sori linear, continuous, forming coenosori on both sides of costa; *indusia* linear, continuous, opening towards costa, dark brown, membranaceous, usually lacerate; *sporangia* with (17) 22 (26) arch cells; *spores* monolete, (39) 54 (70) × (32) 39 (51) µm, perispore smooth, cristate-reticulate, forming a reticulum of low, sharp walls delimiting small areoles, with long filamentous processes not very dense (**Figure 37**).

References – Roux (2001, 2003).

Chromosome number – unknown.

Distribution and habitat – restricted to eastern parts of southern tropical and southern Africa (Malawi, Mozambique, South Africa, Swaziland, and Zimbabwe). Terrestrial, on swampy ground and in perennial streams in open grasslands, or along forest margins, in exposed conditions or in light shade, pyrophytic plant. 150–2,250 m (Roux, 2001; 2003).

Etymology – the epithet refers to Cape Town, South Africa (Roux, 2003).

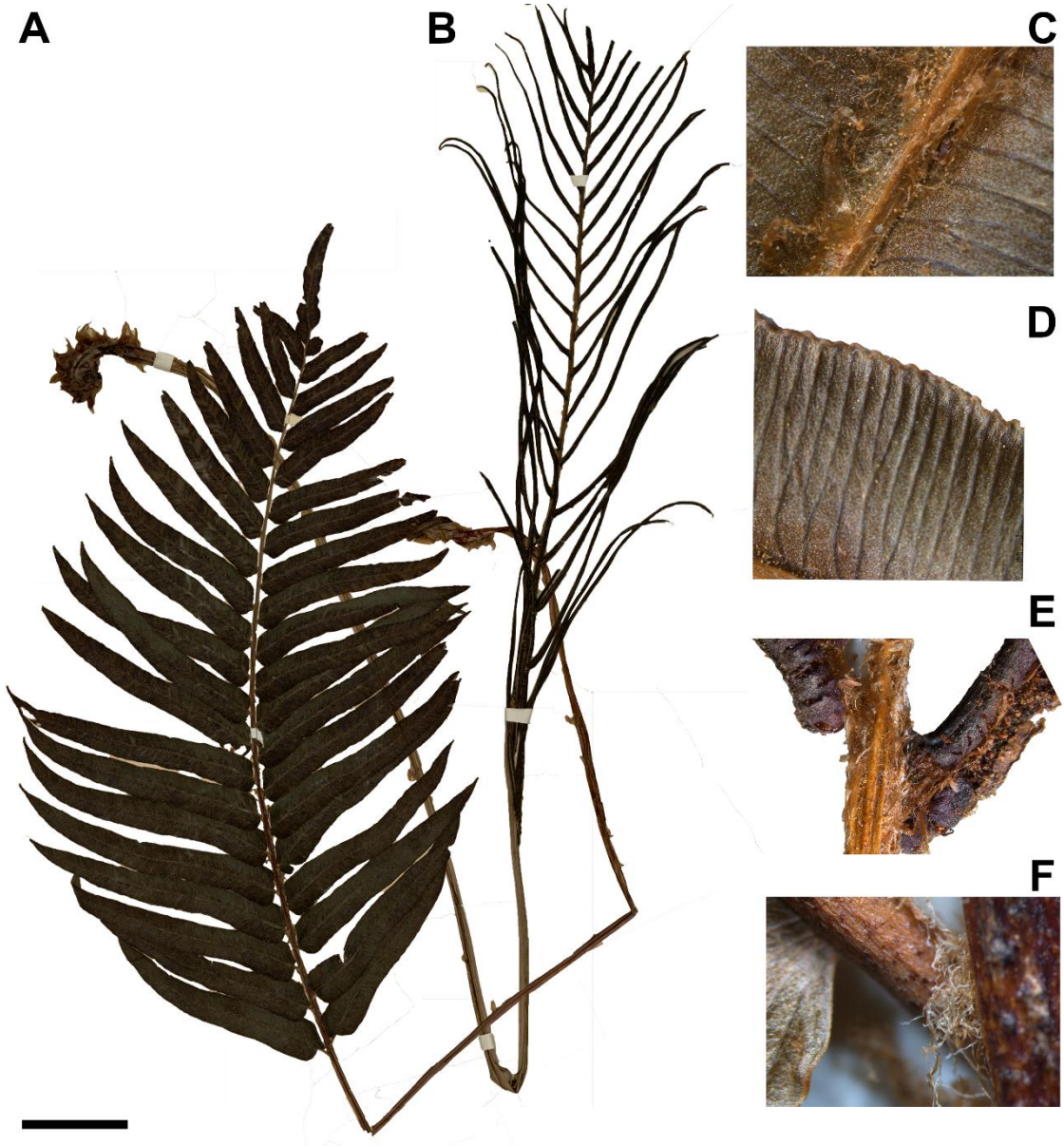

Figure 37. *Parablechnum capense*. A. Sterile frond; B. Fertile frond; C. Sterile costa, adaxial surface; D. Sterile pinnae margin, abaxial surface; E. Fertile pinnae bases, adaxial surface; F. Sterile pinnae stalk; (A: *J. Buchanan*, P01662430; B: *Deserès s.n.*, P01662421; C-F: *J. Thode 2585*, US1627374). Scale: 4 cm in A & B, 3.5 mm in C, 2 mm in D, 4.5 mm in E, 1.5 mm in F.

Notes – is a taxon in need of detailed revision because this name has been ascribed to numerous different taxa, many of them referring to plants from the Austropacific, where this species is not found. Indeed, our molecular results suggests that it could constitute a complex of species.

The valid basonym has also been debated, and Roux (1982) provides clarification. The first to propose a name for this species was Burmann (1768). Three years later, Linnaeus published the name *Osmunda capensis* L. (Linnaeus, 1771). This name was illegitimate,

as Burmann had published it earlier. However, some authors considered Burmann's description invalid, for example Christensen, who cites it in his *Index Filicum* as "nomen = *B. australe* L" (Christensen, 1905). Schelpe (1979), after reviewing the type material of Burmann's species, concluded that the name was superfluous, and as Linnaeus' name was illegitimate he proposed *Blechnum sylvaticum*. However, Roux (1982) states that the type material cited by Schelpe was not the only one attributable to Burmann's description, but that there was a second specimen he overlooked that corresponds to Burmann's description, which would rule out that the published name was superfluous. Roux proposed this second sheet as a lectotype, confirming the validity of *Blechnum capense* Burn.f., which would therefore be the basionym of *Parablechnum capense*. It is common to find aberrant specimens with partly fertile and partly sterile pinnae.

Reviewed material:

MALAWI. Reg. South: Mt. Mulanje, Phalombe Gorge, *J.D. Chapman & E.G. Chapman 7939*, 15 August 1986 (MO04565429!). **SOUTH AFRICA. Prov. Cape Town:** Cape of Good Hope, *no collector*, no date (P01662428!); *ibidem, no collector*, 1838-1842 (US0092904!); *ibidem, A. Rehmann s.n.*, 1 January 1875 (P01662369!); *ibidem*, 1834 (P01662438!); *ibidem, Bojer s.n.*, no date (P01662408!); *ibidem, Descrez s.n.*, no date (P00674777!; P00674778!); *ibidem, Deserès s.n.*, no date (P01662418!; P01662421!; P01662445!); *ibidem, Drége s.n.* (P01662416!; P01662359!; P01662362!; P01662368!); *ibidem, Drége 2668*, no date (P01662345!); *ibidem, Ecklon s.n.*, no date (P01662414!; P01662434!); *ibidem, J.G. Koening s.n.*, no date (LINN-HL1244-11! Photo, lectotype of *Osmunda capensis*) *Lahaie s.n.*, 1.1792 (P01662357!); *Sieber s.n.*, 1827 (P01662411!); *Sieber 4*, 1825 (P01662346!; P01662350!; P01662367!; P01662371!; P01662372!; P01662423!; P01662427!; P01662429!); *Sonnerat s.n.*, no date (P01662363!; P01662422!; P01662435!); *ibidem, Zeyher s.n.*, 1847 (P01662375!; P01662415!; P01662448!); *ibidem, Zeyher 4614*, 1847 (P01662361!); Humansdorp Dist., *J. Thode 2585*, 1930 (US1627374!); Knysna area, a few miles north of Blattenberg Bay, *R.J. Rodin 1186*, 5 September 1947 (MO1606391!; P01618217!); Luisikisiki, near Magwa waterfall, *Venter & Vorster 70*, 23 August 1976 (MO4344676!); near Port Elizabeth, North about 30 miles on Otterford Forest Reserve, *R.J. Rodin 1141*, 31 August 1947 (MO1606356!). **Prov. Eastern Cape:** *T.R. Sim s.n.*, 1898 (P01662331); Albany, Hourrisonsport, in montosis prope Grahonstuwn, *Drége s.n.*, no date (P01662342!);

Dolne Hill, Kaffraia, *T.R. Sim 2994*, 1898 (P01662425!; P01662431!); *Zeyher s.n.*, 1847 (P01662442!). **Prov. Gauteng:** Johannesburg, Transeval, *A. Wertheman s.n.*, 1897 (P01662352!); **Prov. KwaZulu–Natal:** *no collector*, no date (P01623251!); *ibidem* (US barcode 1528564!); *Bolton s.n.*, no date (P01662412!); *ibidem*, 1872 (P01623360!); *Brown & Shapiro 211*, 18 December 1975 (MO2468498!); *Buchanan 71*, no date (P01662353!; P01662354!); *Gueinzius s.n.*, no date (P01662348!); *McHew s.n.*, no date (US barcode 1528568!); Kloof, *F. de Casteliau s.n.*, 7.1856 (P01662341!); near springs, *C.E. Beusher s.n.*, 03.1888 (US barcode 1528569!). **Prov. Western Cape:** *no collector*, 1 February 1855 (P01662347!; P01662349!); *D.F. Wilms 3911 s.n.*, 19 July 1883 (P01662410!); *F. de Castelnau s.n.*, 1 July 1856 (P01662441!; P01662364!); *F. de Castelnau 33*, July 1856 (P01662424!); *F. Wilms s.n.*, 19.7.1883 (P01662407!); *J. Buchanan s.n.*, no date (US0816239!); *ibidem* (US0816243); *J. MacGillivray 378*, 12.1832 (P01662351!; P01662413!); *O. Debeaux s.n.*, 26 February 1860 (P01662358!); *Zeyher & Ecklon s.n.*, no date (P01662439!); Buffelskloof Nature Reserve, Transuaal, *JEB 2530BC*, 28 March 1988 (BNRH0016167! Photo). **Unknown province:** *no collector*, no date (LINN-HS1624-7! Photo); *ibidem* (NY!); *ibidem* (P01619773!); *ibidem* (P01662365!); *ibidem* (P01662426!); *ibidem* (P01662440!); *ibidem* (P01662443!); *ibidem* (P01662446!); *ibidem* (P01662447!); *ibidem* (P01662355!); *ibidem* (P01662366!); *ibidem* (P01662379!); *ibidem* (P01662340!); *ibidem* (P01662343!); *ibidem* (US, barcode 1528570!); *ibidem* (US barcode 1528575!); *Breutel 3719*, no date (P01662373!); *B.B.S. s.n*, no date (NY!); *Browning 595*, no date (MO1877438!); *Burchell s.n.*, no date (P01662360!); *C. Bojer s.n.*, no date (P01662409!); *C. Gaudichaud s.n.*, 1818 (P01662344!; P01662444!); *C.P. Thunberg s.n.*, no date (SBT10626! Photo) *Du Petit-Thouars s.n.*, no date (P01662356!); *Kühn 18721*, 1869 (P01662374!); *J. Buchanan s.n.*, no date (P01662432!); *J. Buchanan 22*, no date (P01662430!); *R.J. Rodin 4522*, 19 May 1948 (MO2261321!); *S.F. Venter 70*, 23 August 1976 (MO4344676!); *Sieber 25*, 1835 (NY!); *T. Bernhardi s.n.*, no date (P01482942!); *Verreaux s.n.*, no date (P01662433!). **ZIMBABUE. Prov. Manicalandia:** Umtali [now Mutare], *N.C. Chase 4268*, 29 November 1951 (MO1637809!).

Parablechnum chauliodontum (Copel.) Gasper & Salino, Phytotaxa 275(3): 215. 2016.

Basionym – *Blechnum chauliodontum* Copel., Univ. Calif. Publ. Bot. 14. 361. 1929.

Type – New Caledonia, *Franc 915* (holotype: MICH1190149 s.ph).

Description – *plants* terrestrial; *rhizome* short, erect, covered with linear scales, dark brown with light margins; *fronds* dimorphic; *sterile fronds* with *petioles* light brown, up to 50 cm long, without ornamentation, scaly near the base, with scales of two types, some similar to those of the rhizome, others narrower, brownish, some light cilia, glabrous distally; *lamina* up to 30 × 20 cm, 1-pinnate, coriaceous, glabrous on adaxial side; *rachis* similar to petiole, sometimes with some scattered scales on abaxial side; *sterile pinnae* in 5–13 pairs, linear-acuminate, base irregular, obtusely rounded, apex acute or shortly acuminate, the base of the terminal pinna clearly irregular, sometimes auriculate, margin serrulate, the most developed ones ca. 10 × 1,5 cm; *costae* similar in colour to the rachis, grooved adaxially, very prominent abaxially; *veins*, free, simple or 1-furcate, catadromous; *aerophores* absent; *hydathodes* rounded or ovate; *fertile fronds* larger; *petiole*, up to 60 cm; *fertile pinnae* ca. 10 × 0.4 cm, base rounded, asymmetrical, apex acuminate, sterile; *sori* linear, continuous, forming coenosori on both sides of the costa, leaving a sterile fragment at the apex and another at the base, sterile fragments as wide as the rest of the pinna or narrower; *indusia* linear, continuous, open towards costa, brownish, margin entire or lacerate at maturity; *sporangia* 18-20 arch cells, interspersed with longer paraphyses, reddish, similar in appearance to sporangial pedicels; *spores* monolete, (39) 47 (59) × (27) 33 (42) µm, perispore granular, cristate-reticulate, with high and thick walls forming large polygonal areoles, with more or less long filamentous processes not very abundan (**Figure 38**).

References – Brownlie (1969).

Chromosome number – unknown.

Distribution and habitat – endemic to New Caledonia. It is found throughout the island, in bush and open dry forest areas from sea level to 600 m (Brownlie, 1969).

Etymology – the epithet is usually applied in zoology to an open mouth with teeth and refers to the pinnae margins.

Notes – according to Brownlie (1969) the number of scales on the distal petiole and rachis varies considerably between individuals, being denser on plants in lightly shaded sites. It is sometimes confused with the species *Lomaridium contiguum* (Mett.) Gasper & V.A.O. Dittrich, but they can be easily distinguished by the pinnae, which are stalked in *P. chauliodontum* and adnate in *L. contiguum*.

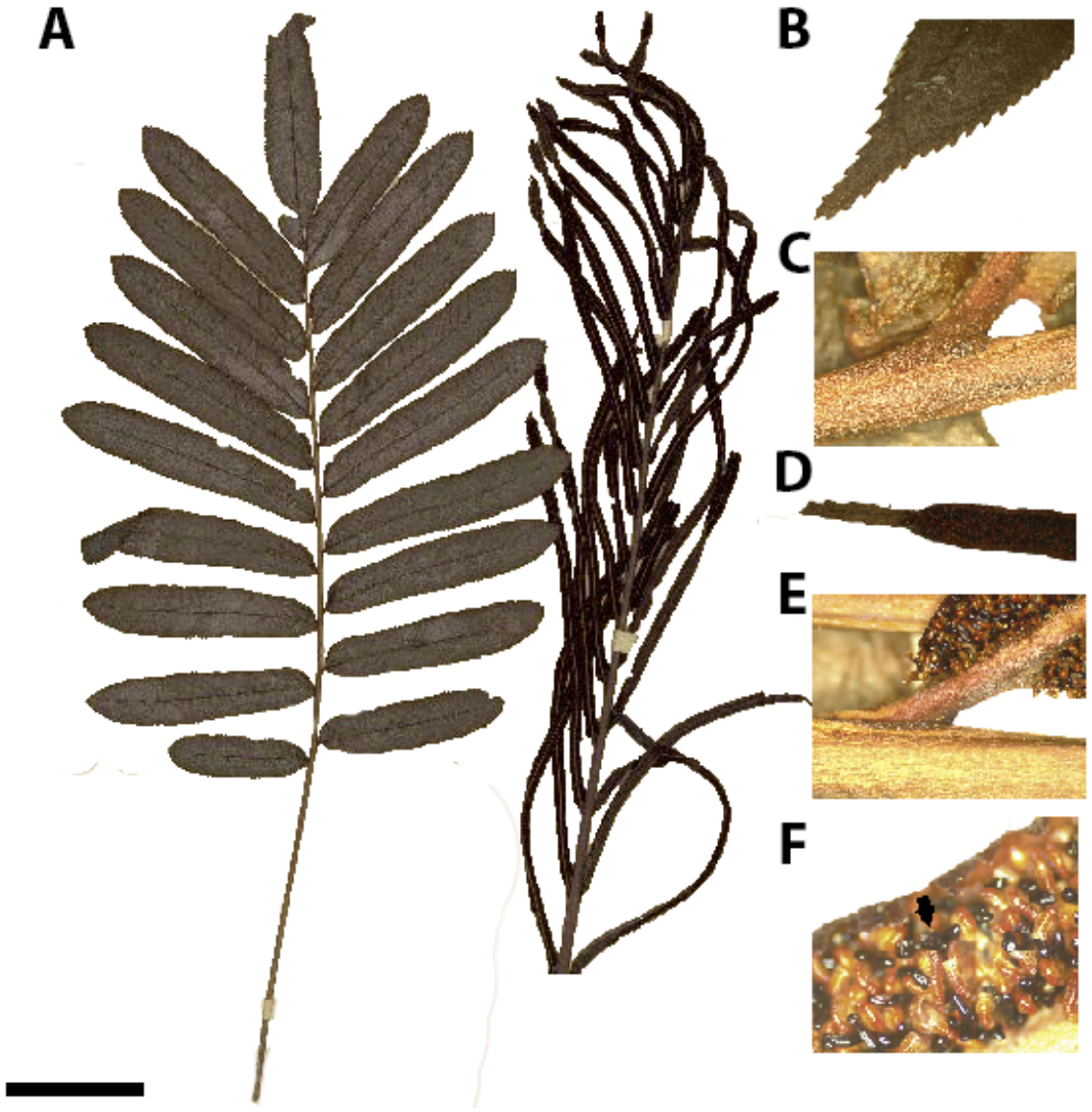

Figure 38. *Parablechnum chauliodontum.* A. Sterile (left) and fertile (right) fronds fragments; V. Sterile pinna apex, adaxial side; C. Sterile pinna base, abaxial side; D. Fertile pinna apex, abaxial side; E. Fertile pinna base, abaxial side; F. Sori with paraphyses (arrow). (A: *Cribs 438*, P01534971; B-F: *J.K. Munzinger 1042*, P00229724). 5 cm in A, 11.5 mm in B, 12 mm in C, 10 mm in D, 3.5 mm in E, 1.5 mm in F.

Reviewed material:

NEW CALEDONIA. Prov. Northern: Kouaoua, Dahi, *H.S. MacKee 4495*, 26 July 1990 (P01557791!; P01557792!). **Prov. Southern:** Forêt de Sailles, près du sommet du Pwénari, *J.K. Munzinger 1294*, 7 December 2001 (MO5843881!; MO5843882!); Prony, *I. Franc s.n.*, May 1916 (P01576153!); *ibidem, I. Franc 115*, May 1916 (P01534972!); Doret Nord, Baie du Sud, *Cribs 438*, March 1900 (P01534971!); Riviere Bleue, enverious des village de la Mine du "Bori Secours", Plaine des acas, *R. Vitor 574*, 3 April 1942 (P01557789!); Thio, Port Bouquet, Rivière Koum, *J.K. Munzinger 1042*, 25 November 2001 (MO5737840!; P00229724!); Yaté, *H.S. MacKee 43572*, 31 May 1987 (P01557790!). **Unknown province:** *de Pompéry s.n.*, 04.1880 (P01534970!); *I. Franc 915* (MICH1190149! photo, holotype); *J. Pancher & J. Hennecart s.n.*, 1879 (P01534928!); *MacGillivray 733*, 1858 (P01468149!; P01468150!; P01468151!; P01468162!); *M. Baumann 5435*, 13 August 1950 (US2425966!); *M. Baumann 13963*, 22 June 1951 (US2425971!); *Mazagot s.n.*, 21 December 1889 (P01534973!); *Vieillard 1520*, 1855 (P01468158!).

Parablechnum chilense (Kaulf.) Gasper & Salino, Phytotaxa 275(3): 215. 2016.

Basionym – *Lomaria chilensis* Kaulf., Enum. Filic. 154. 1824.

Type – Habitat in Chile, *Chamisso* (not found).

Synonyms –

≡*Blechnum chilense* (Kaulf.) Mett., Fil. Lechl. 1: 14. 1856.
=*Blechnum chilense* f. *imbricatum* Kunkel, Nova Hedwigia 13(3–4): 337. 1967. Type: Chile Mocha, Quebrada de las Casas, 80 m; Quebrada Ortigas. *G. Kunkel 6390*, October 1958 (hologype: PTER n.s.).
=*Blechnum raddianum* Mold., Lilloa 6: 288. 1941, non Rosenstock 1906. Type: Nahuel Huapí, *A.L. Cabrera & M.M. Job 239*, 10 January 1935 (holotype: N n.s.)
=*Lomaria gilliesii* Hook. et Grev., Icon. Filic. 2: tab. 207. 1831. Type: Chile, *Gillies s.n.*, no date (K, photo US Morton, negative 11355, n.s.); ≡*Blechnum gilliesii* (Hook. Et Grev.) Mett., Fil. Hort. Bot. Lips. 64. 1856.
=*Lomaria reedei* Phil., Anales Univ. Chile 43: 581. 1873; ≡*Blechnum reedii* (Phil.) Espinosa, Revista Chilena Hist. Nat. 41: 337. 1938. Type: Chile, Juan Fernández Archipiélago, *E.C. Reed s.n.*, January 1872 (holotype: SGO, n.s.; isotype: BM000769806! Photo); ≡*B. chilense* var. *reedei* (Phil.) Looser, Revista Univ. (Santiago) 32(2): 47. 1947.

Vernacular names – añü (Mapudungún), cül–cül (Mapudungún), iquide (Mapudungún), quiquil (Mapudungún), costilla de vaca (Spanish), palmilla (Spanish).

Description – *plants* terrestrial, subarborescent, not stoloniferous; *rhizome* erect, 3–5 cm in diameter, scaly, with broad straw–like scales, 0.2–0.5 × 1.5–2 cm; *fronds* dimorphic; *sterile fronds* 50–150 × 10–40 cm; *petioles* 20–40 cm long, somewhat woody, grooved adaxially, prominent abaxially, at base with abundant, broad, light brown scales, similar to those of the rhizome; *lamina* 1-pinnate, very leathery, ovate–lanceolate, apex with a conformal terminal pinna; *rachis* similar to petiole, with more or less filiform scales, caedulous at maturity; *sterile pinnae* in approximately 11–30 pairs, coriaceous, rugose, margin wavy and serrulate, apex acute, base cordate, overlapping the rachis adaxially, 5–20 × 1–3 cm, shortly stalked, becoming adnate towards the apex; *costae* similar to rachis, grooved adaxially, prominent abaxially; *veins*, free, simple or 1-furcate, catadromous; *aerophores* absent; *hydathodes* rounded or ovate; *fertile fronds* longer and more erect; *fertile pinnae* linear 0.3–1 cm, directed towards apex; *sori* linear, continuous, forming coenosori on both sides of costa, entirely covering abaxial side of pinna; *indusia* linear, continuous, submarginal, entire or lacerate–edged, opening towards costa; *sporangia* with arcs of 19–21 cells; *spores* monolete, (44–)51(–57) × (44–)47(–57) μm, perispore with more or less high walls forming small areoles with abundant filaments in the areole lacunae; *gametophyte* cordate, without indument (**Figure 39**).

References – Looser (1955); Rodríguez-Ríos, (1995), Pérez-García *et al*. (1996), Rodríguez-Ríos *et al*. (2009).

Chromosome number – 2n = 66 (Jara–Seguel *et al*., 2006).

Distribution and habitat – Native to Chile and the southern Andean region of Argentina, rare in the Falkland Islands. In Chile it is found from the coast of the province of Limarí and the Andean region of the province of Santiago to the province of Magallanes. It also grows in the Juan Fernández Archipelago, where it is quite common (Christensen & Skottsberg 1920; Rodríguez-Ríos, 1995; Rodríguez-Ríos *et al*., 2009). Its populations are in constant decline, due to the presence of introduced species through displacement and substitution, as well as extraction for foraging and alteration of the vegetation by fire (Baeza *et al*., 1998). It grows in very humid places, along watercourses,

in the interior of shady and swampy forests, especially in waterfalls (Rodríguez-Ríos *et al*. 2009). It is an invasive species in Sintra, Portugal (Sanchez Gullon *et al.,* 2017).

Etymology – the specific epithet for this species refers to Chile, where it was described as endemic, although it was later found in Argentina.

Notes – There has been controversy as to whether this species and *Parablechnum schiedeanum* are synonyms of *P. cordatum* (Tryon & Stolze, 1993; Prada *et al*., 2008) or whether it is instead a different species (de la Sota, 1972; Moran, 1995a; Rodríguez-Ríos, 2015; Gasper *et al*., 2016). Indeed, several authors have indicated the need for a monographic study in this regard (Tryon & Stolze, 1993; Moran, 1995a; Dittrich *et al*., 2017, 2020). Tryon & Stolze (1993) included *Blechnum chilense* under the synonymy of *B. cordatum* and this same view is adopted by Prada *et al*. (2008) giving a large distribution that includes Mesoamerica, West Indies, South America, Juan Fernández Archipelago, and SE Australia. In an earlier work Rolleri & Prada (2006a) consider *B. chilense* as a member of the floras of Ecuador, southern Brazil (doubtful), Chile, Uruguay, and Argentina. Some authors support the separation of the species of the *P. cordatum* complex based on morphological characteristics, for example, Rodríguez-Ríos (2015) argues that *P. cordatum* and *P. chilense* differ in the shape and distribution of petiole and rachis scales, aerophores (absent in *P. chilense*, present in *P. cordatum*) and palynology (filamentous spores in *P. chilense*, without filaments in *P. cordatum*), allowing the morphological separation between the two species. De la Sota (1972) considers *P. chilense* to be an Austral–Antarctic element, vicariant of *P. capense* (South African), living in continental Chile, Juan Fernández and Argentina, an opinion shared by Rodríguez (2015). Recent phylogenetic and palynological studies suggest that these are different species, as it differs from *Parablechnum cordatum* and the other species of the complex at the molecular level and in numerous sporangial and spore characters (Wal *et al*., 2021).

During the specimen review for this work, it has been observed that the specimens from the Juan Fernández archipelago and Falkland Islands are identical to those from the mainland except for the fact that they have aerophores. It has not been possible to extract DNA because the material reviewed was very old, but it would be interesting to assess a potential taxonomical relevance of this local variation. If the specimens of Juan Fernández are a different species, the recovery of the name *Lomaria reedei* should be considered,

since the type material was collected there. Here it was only possible to examine pictures of this material, so the combination is still uncertain.

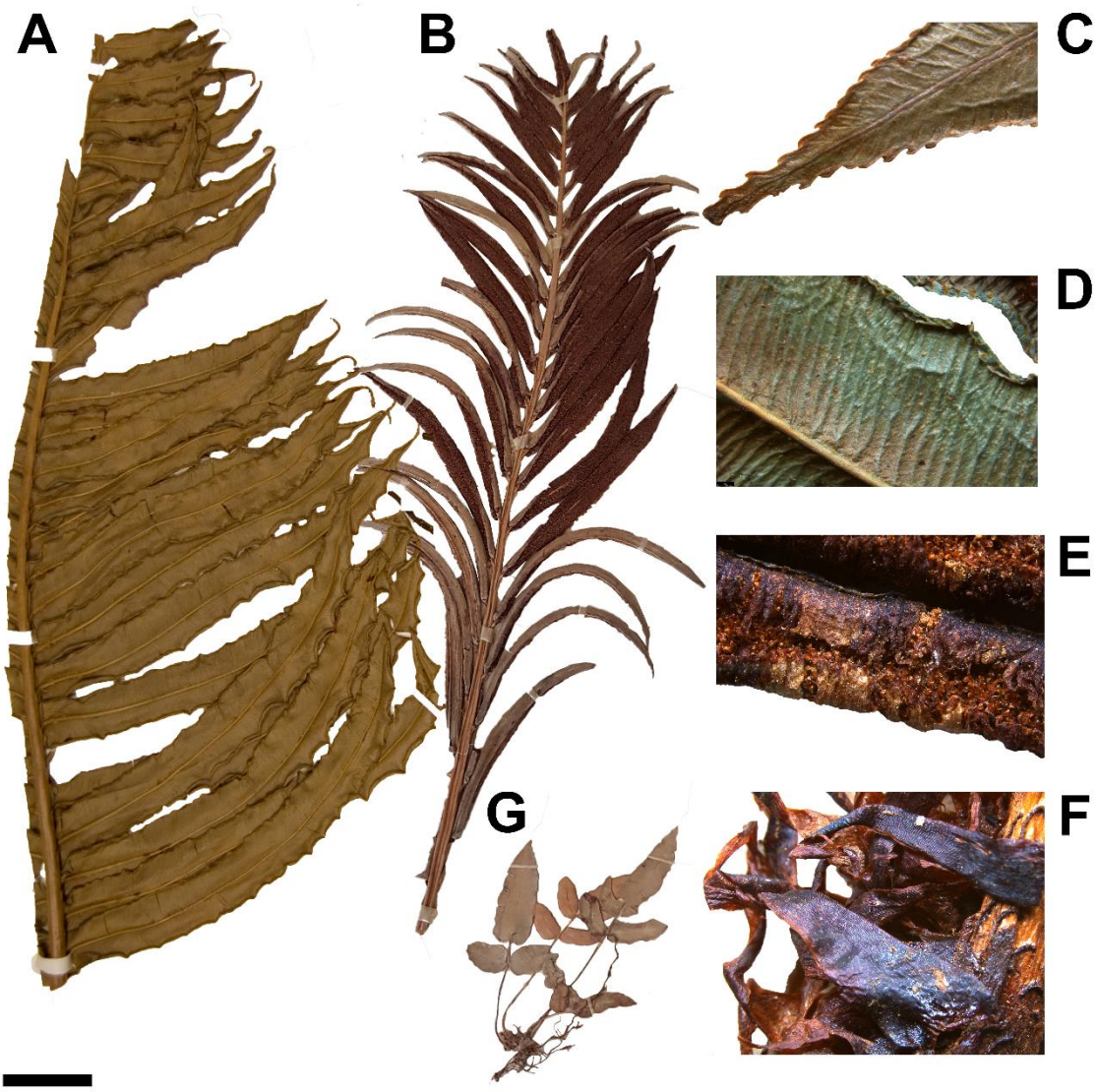

Figure 39. *Parablechnum chilense*. A. Sterile frond; B. Fertile frond; C. Sterile pinna apex, abaxial surface; D. Sterile pinnae margin, abaxial surface; E. Fertile pinnae, abaxial surface; F. Rhizome scales; G. Juvenile plant. (A: *A. Bryan 360*, UC1613597; B & G: *C. Joseph 2662*, US1198588; C & F: *C. o I. Skottsberg 565*, US1055778; D & E: *D.J. Layton 131*, US3590585). Scale: 4 cm in A, B & G, 4 mm in D, 3 mm in E & F.

Since hybridisation phenomena are known within the Blechnaceae, this aspect should be studied in greater detail within this complex, specifically in the geographical areas of contact, given that, if this phenomenon occurs among the plants of this complex, the difficulty of identifying the species would increase considerably (Tryon & Stolze, 1993; Moran, 1995a; Chambers & Farrant, 1998b).

The holotype only indicates that it was collected in Chile, it must have been collected in the region around Talcahuano–Concepción, as this is the only part of Chile visited by Chamisso (Looser, 1955; Rodríguez-Ríos, 2015).

Although it is a species resilient to human activity and is frequent in disturbed habitats, (Looser, 1955), it has been catalogued as vulnerable in Chile (Baeza *et al*., 1997).

This species has been reported as an invasive plant in Sintra, Portugal (Sanchez Gullón *et al*., 2017). It was cited as *Blechnum cordatum,* but after reviewing the photographs provided in the paper and the records of iNaturalist (2022) we have concluded that it is *Parablechnum chilense*. Apparently, it was first planted in the lake cascades in the historic garden of Quinta of Monserrate (Archer, 1870; Daveau, 1878, Bacelar *et al.*, 1987). Some authors considered it occasional or even extinct (Almeida, 1999), but according to Sanchez Gullón *et al*. (2017) it is forming extensive populations and competing with native plants.

Various uses have been recorded for this species, such as medicinal, ornamental and food. It is used as an ornamental plant, in soils with high humidity (Gunckel, 1983; Rodríguez-Ríos *et al*., 2009), it is used for eye diseases and umbilical cord wounds (Muñoz *et al*., 1980) and the pith of the rhizomes is used for food (Möesbach, 1992).

Reviewed material:

ARGENTINA. Prov. Buenos Aires: Partido de Tornquist, Sierra de la Ventana, Cerro de la Ventana, Vertientes, *A.L. Cabrera 5768,* 17 January 1940 (NY!); Sierras Pampeanas, Penfana, *G.P. Lorentz s.n.*, 1881 (P01410486!); Sierras Pampeanas, Sierra Ventana, *G.P. Lorentz s.n.,* February-April 1881 (US1095281!); *ibidem*, *G.P. Lorentz 105,* February-April 1881 (US691724!). **Prov. Chubut:** Parque Nacional de los Alerces, riva orientale del lago Situación, *R.E.G. Pichi Sermolli & P. Bizzarri 7402*, 8 January 1974 (P01410493!; P01410494!). **Prov. Córdoba:** Cuesta de Arjel, Sierra Achala, *G. Hieronymus 12,* 26 March 1875 (P01466389!). **Prov. Neuquén:** Correntoso, Región del lago Nahuel, camino al aserradero, *Á.L. Cabrera 239,* 10 January 1935 (NY00814187!); Lago Nahuel Huapi, *E. Ljungner 1002,* 4 April 1934 (NY!); Northside of Lago Correntoso, near the road from Traful to Villa la Angostura, *T.M. Pedersen 221,* 11 March 1949 (US2083168!; US2083169); Parque Nacional Lanín, Hua Hum, *C. Prada A33,* 12 December 2003 (MA803378!); *ibidem, C. Prada s.n.,* 30 November 2005

(MACB109261!); Ruca Maléu, Lagos Pichilaufquén y Calcú, *R. Sconlnik 328,* 29 March 1946 (US2082971!); *ibidem, R. Sconlnik 345,* 29 March 1946 (US2082984!). **Prov Rio Negro:** Puerto Blest, Rio Neuquen, *A.L. Cabrera & M.M. Job 252,* 12 January 1935 (NY!); Región del Lago Nahuel Huapí, Lago Espejo, *A.L. Cabrera 5975,* 7 November 1940 (NY!); Rio Manss (antes de llegar al Jibess), *T. Meyer 8221,* 5 February 1945 (NY!). **CHILE**. **Prov. Acanagua:** Zuintero, *H.A. Garaventa 1671,* 03.1930 (US2609975!). **Prov. Biobío:** Dpto. La Laja, Salto del Trubunleo, *Boelcke et al 6565,* 23 January 1969 (VT285853!); Trapa-Trapa, *Parra 8837088370,* 23 December 1944 (NY!). **Prov. Cachapoal:** Punta, *C. Joseph 2148,* 03.1923 (US1189599!). **Prov. Chiloe:** *F.W. Pennell 12610,* 8-9 February 1925 (NY). **Prov. Concepción:** *Dombey s.n.,* no date (P01466402!; P01466403!; P01466394!); *Dombey 18,* no date (P01531088!); *Dombey 48,* no date (P01410490!); *Dunville s.n.,* no date (P01410496!); Región Bío–Bío, Concepción, Hualpén, *J.M. Gabriel y Galán s.n.,* 11 July 2014 (MACB109257!); Rocoto, *E. de la Sota 6020,* 20 April 1970 (NY!). **Prov. Llanquihue:** La Ensenada *K. W. Wolffhügel s.n.,* no date (B200165280!); Lago de Todos los Santos, Cayutué–Ost, *K. W. Wolffhügel s.n.,* no date (B200165212!); *Ibidem* (B200165212); *Ibidem* (B200165222!); Puerto Montt, *E. Wall s.n.,* 8 January 1947 (NY!). **Prov. Malleco:** Angol, *O. Kuntze s.n.,* 10 February 1992 (NY!); *ibidem* (NY!). **Prov. Ñuble:** VIII Región, Playa Purema, *L. Cavieres et al 3531*, December 2001 (MA774731!). **Prov. Palena**: Región de Los Lagos, Hurinay, next to power station, *D.J. Layton 131,* 23 October 2008 (US3590585!); × Región de Los Lagos, 22 km SE of Chaiten on gravel road to Pto. Cárdenas, *J. Furlow et al. 7087*, 8 March 1985 (MA723449); × Región de Los Lagos, Comuna de Hualaihué, Hornopirén, San Ignacio de Huinay, *J.L. Fernández Alonso et al. RM2772*, 7 December 2013 (MA887207); *ibidem* (MA887208); *ibidem* (MA887255); *ibidem, Fernández Alonso et al. RM2688,* 8 December 2013 (MA887209); *ibidem* (MA887254). **Prov. Osorno:** Región de los Lagos, Puyehue, *J.M. Gabriel y Galán s.n.,* 08.2014 (MACB109256). **Última Esperanza:** Island Harbor [now Evan Island], *R.D. Cumingliau s.n.,* no date (NY!); Patagonia, Island Harbor [now Evan Island], *"the Albatross"*, no date (US0050830!); *ibidem*, February 1888 (US0050827!). **Prov. Valdivia**: *no collector*, no date (P01623357!); *Hohemacker 210*, no date (P01410463!); *Hohemacker 510*, no date (P01410453!; P01623356!); *Hohemacker 11560a*, no date (P01410481!); *Hohemacker 11564*, no date (P01410464!); *P.A. Hollermayer 1007*, March 1942 (UC1333995! Photo); *O. Buchtien s.n.,* 9 April 1897 (P01410457!; P01410458!); *O. Buchtien s.n.*, July 1902

(P01410459!); *O. Buchtien 11211,* 1904 (US1095260!); *R.A. Philipi 210*, no date (P01466399!; P01466400!); along Pan-American high-way, 15,2 km S of Rio Calle-Calle bridge in Valdivia, *R. Schmid s.n.,* December 1980 (NY!); Huachocopihue, *G.W.H. Kunkel 2740 (1021)*, 27 July 1958 (B200165420!); along Pan-American highway, 15.4 km S of Río Calle–Calle bridge in Valdivia, *R.Schmid s.n.*, December 1980 (US barcode 1525489!); Isla Teja, *G.W.H. Kunkel 2741b (1021)*, 11 June 1958 (B200165416); Panguipulli, *C. Joseph 2662*, January 1924 (US1198588!); *ibidem, C. Joseph 2365,* April 1923 (US1189117!); Santo Domingo, *G.W.H. Kunkel 2737*, 6 July 1958 (B200165421); *Ibidem, G.W.H. Kunkel 2741 (1021),* 27 July 1958 (B200165417!); *Ibidem, G.W.H. Kunkel 2741a (1021)*, 4 September 1958 (B200165418!); *Ibidem, G.W.H. Kunkel 2740a (1021)*, 27 July 1958 (B200165419!). **Prov. Valparaiso:** *no collector*, no date (NY!); *no collector*, 1819 (P01410472!); *Bertero 1109*, 1829 (P01410471!; P01410488!; P01466397!; P01466398!); *Bertero 1209,* no date (P01410455!); *Diar 45,* no date (P01466419!; P01410479!); *Gaudicham 28*, 1834 (P01410454!; P01466392!; P01466395!); *Jaramillo 28,* no date (P01410482!); *H.H. Rusby, M.D. 310*, June 1885 (NY!, 2 sheets); *Jelinck 44*, no date (P01410487!); *Kunze 142*, no date (P01410480!); Archipiélago Juan Fernández, *Bertero 1544*, no date (P01410465!; P01410466!; P01410467!); *E.C. Reed s.n.*, January 1872 (holotype: not found; isotype: BM000769806! Photo, isotype of *Lomaria reedei*); *ibidem, M. Moseley s.n.,* 1875 (P01466388!; P01466396!); *ibidem, G.T. Hastings 202,* 10–14 January 1901 (US530135!); Archipiélago Juan Fernández, Masafuera, *O.T. Solbrig 3762*, 4 December 1965 (US2421543!); *ibidem, J.P. Chapin 1056*, 30 January 1935 (NY!); *ibidem, Wm.A. Bryan 360,* 3 March 1920 (UC1613597! Photo); Archipiélago Juan Fernández, Isla Masatierra, along the road to Portezuelo, *C.J.F. Skottsberg 565*, 25 March 1907 (US1055778!); Archipiélago Juan Fernández, Isla Masatierra, *J.L. Morrison 17346*, 1 March 1939 (US2609974!); *ibidem, C. & I. Skottsberg s.n.,* 23 March 1917 (NY!); *ibidem, J.P. Chapin 1088,* 31 January 1935 (NY!); Archipiélago Juan Fernández, Isla Masatierra, Quebrada Damajuana, *I. & C Skottsberg 272*, 3 March 1955 (US2751089!; US2751090!); Archipiélago Juán Fernández, Isla Masatierra, down from Mirador Selkirk into Villagra, *Stuessy & D. Crawford 12160*, 1 February 1991 (MA775505!); Archipiélago Juán Fernández, Isla Más a Tierra, pendiente norte del Portezuelo, *C. Skottsberg 565*, 25 March 1917 (P01410468!; P01410469!; P01410470!). **Prov. Talca:** Maule (Región VIII), Constitución, Playa el Cable, *C. Aedo Pérez 7164*, 8 March 1985

(MA686813!). **Prov. Unknown province:** *no collector*, no date (P01409517!); *ibidem* (P01410456!); *ibidem* (P01410461!); *ibidem* (P01410462!); *ibidem* (P01410474!); *ibidem* (P01410475!); *ibidem* (P01410476!); *ibidem* (P01410477!); *ibidem* (P01410491!); *ibidem* (US0050818!); *ibidem* (US0594553!); *no collector 12*, no date (US0050806!); *ibidem* (US0050808!); *ibidem* (US0050817!); *Bertero s.n.*, no date (P01410495!); *Bertero 1115*, no date (P01410489!); *Chuntien s.n.*, 1878 (P01410478!); *Hourtig 435* (interpreted), no date (P01410460!); *Kaulf 609*, no date (P01410492!); *Lepin s.n.*, no date (P01466393!); *Poeppig s.n.*, 1827 (NY!); *Poortman s.n.*, no date (P01410473!); *Quillota 29*, 1879 (P01466390!); *Shilippi 269*, no date (P01466387!); on trouse ce gougére quan el les Savanne, de "Boldo" se trouve arretés par des Camps marécageux, *J. Elliot 254*, 20 December 1903 (P01623832!); Patagonia, *F.P. Moreno & Tovinirvi 431*, 1882 (NY!). **FALKLAND ISLANDS.** *R. Cove 8p79*, March 1901 (P01212622!; P01571514!; P01571517!; P01571518!).

Parablechnum chiriquanum (Broadh.) Gasper & Salino, Phytotaxa 275(3): 215. 2016.

Basionym – *Struthiopteris chiriquana* Broadh., Bull. Torrey Bot. Club 39: 361. 1912.

Type – Panamá, humid forests of the upper Caldera watershed between “Camp I” and the Divide, Holcomb’s trail, above El Boquete, Chiriquí altitude 1650–1925 m, *W.R. Maxon 5650*, 23 March 1911 (holotype: US676110-4!).

Synonyms –

≡*Blechnum chiriquanum* (Broadh.) C.Chr., Index Filic., Suppl. 1, 16. 1913.

Description – *plants* terrestrial; *rhizomes* erect, not stoloniferous, scales lanceolate, long, dark brown, 0.4–1 cm; *fronds* dimorphic; *sterile fronds* with *petioles* 27–86 cm, dark brown to atropurpureous, without ornamentation, densely scaly, especially on the adaxial side, scales of two types, the first, irregular, fibrillose, forming a deciduous indumentum, the second 3–10 mm, patent, lanceolate, brown to whitish; *lamina* 50–123 cm, 1-pinnate, truncate at the base, gradually reduced towards the conform apex, with a terminal pinna similar in shape to the lateral pinnae and almost half the length of them, herbaceous; *rachis* dark brown to atropurpureous, without ornamentation, indumentum like that of the petiole; *sterile pinnae* in 30–50 pairs, 10–25 × 1.3–3 cm, linear-lanceolate,

bases asymmetric, obliquely rounded, apices acute or acuminate, shortly stalked, becoming gradually adnate distally, margins slightly revolute, serrate, more deeply serrate towards apex; *costae* yellowish-brown to brownish, grooved adaxially, prominent and scaly abaxially, with scales similar to those of rachis; *veins* free, simple or 1-furcate, catadromous; *aerophores* 2–5 mm, conical to cylindrical, deciduous in dry specimens; *hydathodes* rounded or ovate; *fertile fronds* longer than sterile ones, 100–240 cm; *petiole* 50–122 cm, dark brown to atropurpureous, slightly lighter than sterile ones; *lamina* 98–124 cm long, base slightly or abruptly reduced, gradually reduced towards apex; *rachis* with 49–52 pairs of pinnae; *fertile pinnae* linear, narrow, with rounded base and acuminate apex, 15–25 × 0. 3–0. 5 cm; *sori* linear, continuous, forming coenosori on both sides of the costa occupying the whole pinna except a small fragment of the apex; *indusia* linear, continuous, opening towards the costa, dark brown, lacerate, deciduous; *sporangia* (15) 25 arch cells; *spores* monolete, (44) 51 (57) × (29) 37 (45) µm, perispore-cristate-reticulate, with thin, sharp walls, delimiting small polygonal areoles, with very abundant long filamentous processes (**Figure 40**).

References – Broadhurst (1912b), Moran (1995a), Passarelli *et al*. (2010).

Chromosome number – unknown

Distribution and habitat – endemic to Mesoamerica. Humid forests, 1500–2500 m (Dadvise *et al*., 1995).

Etymology – the specific epithet refers to the region of Chiriqui, Panama, where the holotype was collected.

Notes – this species is similar to *Parablechnum sessilifolium*, but differs in the brightly coloured petioles, partially adnate distal pinnae, adaxially glabrous costae, deciduous indusia, and conical aerophores. Aberrant individuals with fronds intermediate between trophophylls and sporophylls are sometimes found.

Reviewed material:

COSTA RICA. Prov. Cartago: Cordillera de Talamanca, *L.O. Williams 16104*, 30 March 1949 (US2019155!; US2019156!); Interamerican Hwy, along the Cerro de la Muerte, *K. Lems 640115-60*, 15 January 1964 (NY!). **Prov. Heredia**: Barba, Cerro Chompipe nr. Ermita Sta. Cruz, *K. Lems 650130-01*, 30 January (NY!); Braului Carillo

National Park, *E. Hennipman et al 6731,* 6 November 1986 (UC1586682! Photo); ca. 10 km N of San Rafael de Heredia on Volcán Barba, *D.B. Lellinger 664,* 13 July 1967 (US2589670A!; US2589671A!); *ibidem, J.T. Mickel 2653,* 13 July 1967 (NY!); *ibidem, J.T. Mickel 3016,* 30 July 1967 (NY!); Cerro Chompipe, 5 km SE of Volcán Barba, *D.B. Lellinger 1704,* 15 April 1971 (US3264638!; US3264639!); Yerba Buena, northeast of San Isidro, *P.C. Standley & J. Valerio 50185,* 22–28 February 1926 (US1308368!; US1308369!); Forest of Rio Vueltas, *L.D. Gomez P. 2253,* 23 May 1969 (NY!). **Prov. Limón:** Cordillera de Talamanca, Atlantic slope, Valle de Silencio, área just N of Cerro Hoffman, 4 ½ airline km W of the Costa Rican-Panamaian border, *G. Davidse et al. 28674,* 8 September 1984 (UC1509051! Photo). **Prov. Puntarenas:** high ridge north of the television relay tower above Monteverde and bordering the Monteverde Cloud Forest Nature Reserve. Near the juncture of the Provinces of Alajuela Guanacaste, and Puntarenas, *Wm. Burger et al 10841,* 27 February 1977 (NY!, 2 sheets); Monte Verde, Estación Biológica Monteverde, Cordillera de Tilarán, *M. Sundue & W. Testo 4792,* 1 September 2017 (MACB!, 2 sheets; VT285874!). **Prov. San José:** along carretera Interamericana, 15 to 18 km SE of Empalme, *R.G. Stolze 1519,* 17&26 March 1973 (NY!; US2776188!); Cerro de la Muerte, bog a km 73 algon interamerican highway , *J.T. Mickel 1230,* 24 March 1967 (NY!, 3 sheets); *ibidem, J.T. Mickel 2130,* 24 March 1967 (LP9220276! Photo); Cerro de la Muerte, km 73 along de Interamerican Highway, *D.B. Lellinger 863,* 9 August 1967 (US2589672A!); *ibidem, J.T. Mickel 3240,* 9 August 1867 (NY!; US2589185!); Dota, Carretera Interamericana, km 66, ca. 3 km después de La Trinidad, *A. Rojas et al 10319,* 15 July 2013 (MACB!); San Jerónimo, *L. Brade 755,* 22 April 1916 (NY!). **HONDURAS. Dept. Intibucá:** between Perla Nariz and Calaberas, 12 km. From La Esperanza, *A. Molina R. 24118,* 7 March 1969 (US3695437!; US3695438!). **PANAMA. Prov. Chiriqui:** 2–3 km W of the town of Cerro Punta along trail beyond quarry, *D.B. Lellinger 1919,* 28 June 1975 (US3275442!; US3275443!); Cuesta de Las Palmas, southern slope of Cerro de la Horqueta, *W.R. Maxon 5442,* 18 March 1911 (US675825!, paratype; US675826!, paratype; US675827!, paratype; US675828!, paratype); Dist. Bugaba, Cerro Punta, *H. van der Werff & J. Herrera 6460,* 26 January 1985 (UC1509307! Photo; UC1509308! Photo); Upper Caldera River, between Camp 1 and divide, Holcomb's Trail, above El Boquete, *W.R. Maxon 5650,* 23 March 1911 (US676110!, syntype; US676111!, syntype; US676112!, syntype;

US676113!, syntype; US676114!, syntype); Vicinity of Bajo Chorro, *R.E. Woodson Jr & R.W. Schery 697*, 20-22 July 1940 (US1792549!).

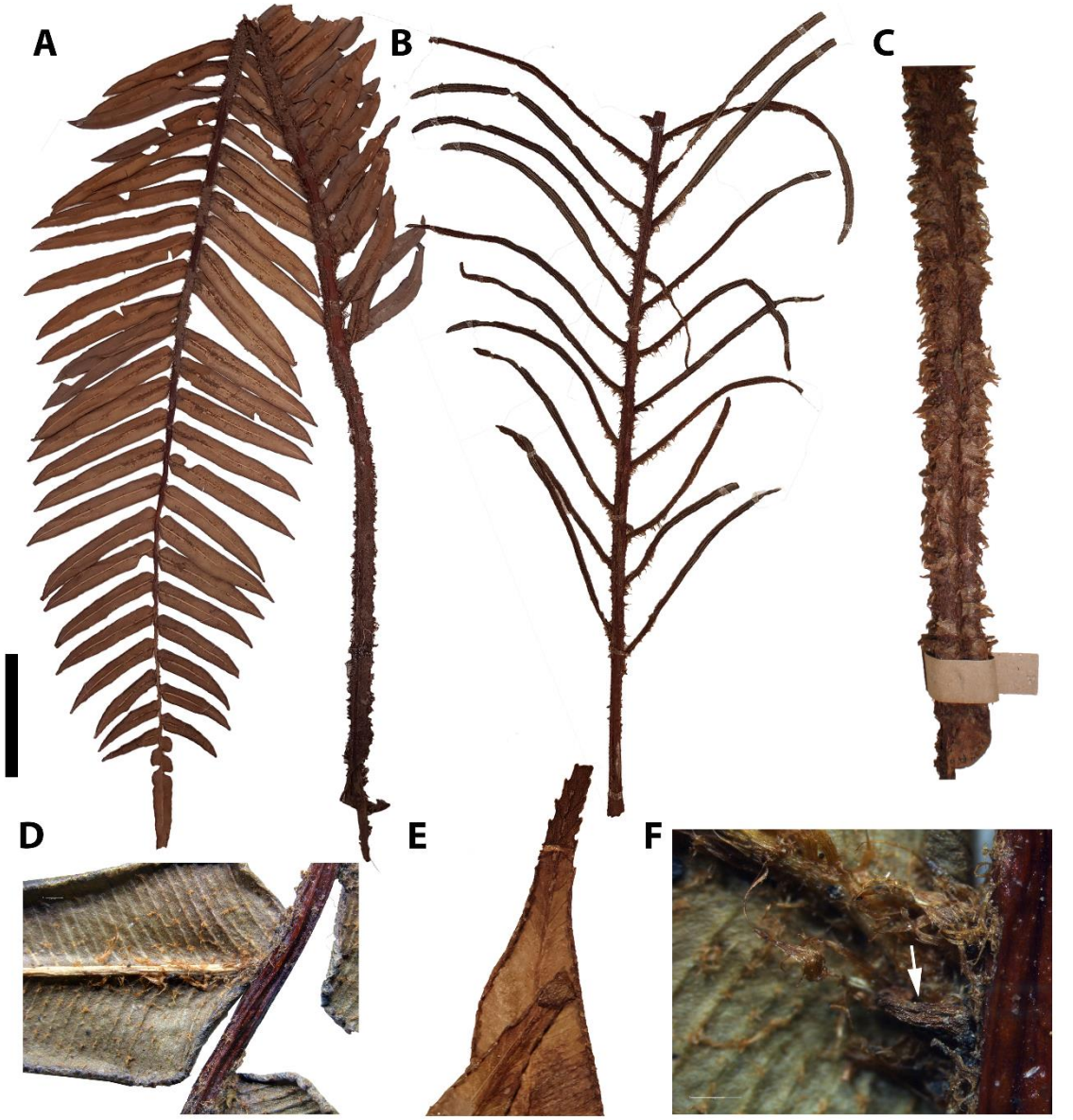

Figure 40. *Parablechnum chiriquanum*. A. Sterile frond; B. Fertile frond; C. petiole; D. Sterile pinnae base, abaxial surface; E. Sterile pinnae apex, abaxial surface; F. Sterile pinnae base detail with an aerophore (arrow); (A: *J.T. Mickel 2130*, NY; B: *D.B. Lellinger 664*, US2589670A; C: *J.T. Mickel 2130*, LP; D: *L.O. Williams 16104*, US2019156; E: *L.D. Gómez 2253*, NY; F: *D.B. Lellinger 863*, US2589672A). Scale: 4 cm in A & B, 1.5 cm in C, 5.5 mm in D, 6 mm in E, 2 mm in F.

Parablechnum cochabambense (M.Kessler & A.R.Sm.) Gasper & Salino, Phytotaxa 275(3): 215. 2016.

Basionym – *Blechnum cochabambense* M.Kessler & A.R.Sm., Amer. Fern J. 97: 72. 2007.

Type – Bolivia. Cochabamba: Prov. Carrasco, Km 95–96 on old road between Cochabamba and Villa Tunari, 17'12.64'S, 65041.95'W, 3400 m, 24 October 1999, *Stahl 5156B* (holotype: AAU24276! Photo; isotypes: BOLV n.s., S n.s.).

Description – *plants* terrestrial; *rhizomes* erect, scales 14–30 × 2–3 mm, linear-lanceolate, reddish-brown with narrow paler margins, entire; *sterile fronds* to 70 × 15 cm, erect or arching; *petioles* to 30 × 0.5 cm, atropurpureous or shiny brown, densely scaly, scales of two kinds, one similar to the ones on the rhizomes but smaller, basally irregular and deciduous except at base of petiole, the others ovate to lanceolate, 1–3 × 0.3–1.5 mm, dull pale brown, margin irregular–denticulate; *lamina* lanceolate, 1-pinnate, apices gradually reduced with a conform apical pinna, coriaceous, adaxially sparsely scaly, the scales 0.1–0.7 × 0.1–0.5 mm, ovate, dark, margin irregular or ciliate; *rachis* reddish brown to straw–brown, grooved adaxially, prominent abaxially, densely scaly, scales of two kinds, the first 1–3 × 0.3–0.6 mm, spreading, lanceolate, brown, margin entire or denticulate, the second 0.3–1 × 0.2–0.8 mm, ovate, dark, margin irregular or ciliate; *sterile pinnae* in 21–28 pairs, 9 × 0.11 cm, stalked, falcate, bases cordate, apices acuminate, margins narrowly hyaline, serrulate, revolute; *costa* adaxially grooved, abaxially prominent, straw-coloured, moderately scaly, the scales similar to those of the rachis but smaller; *veins* free, simple or 1-furcate, catadromous; *aerophores* tuberculiform, dark; *hydathodes* small, ovate; *fertile fronds* unknown (**Figure 41**).

References – Kessler *et al.* (2007).

Chromosome number – unknown.

Distribution and habitat – endemic to Bolivia, at 3100–3400 m in a limited area of Cochabamba department. Locally uncommon, it is known from two collections of terrestrial plants in humid montane forests (Kessler *et al.*, 2007; Smith & Kessler, 2018).

Etymology – the specific epithet refers to the Bolivian Department of Cochabamba, where the plant is endemic (Kessler *et al*. 2007).

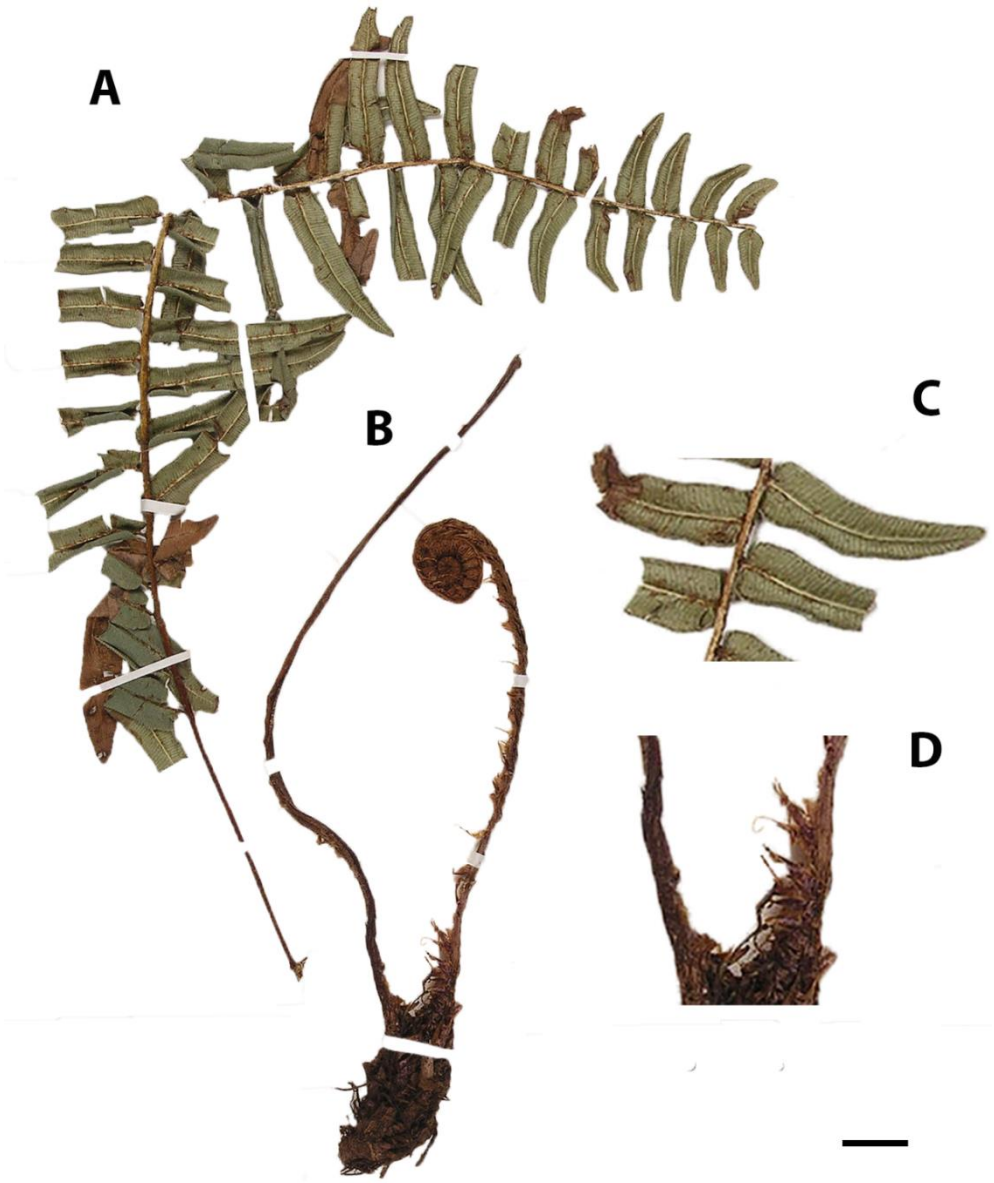

Figure 41. *Parablechnum cochabambense. B. Staal 5156B,* AUU, holotype. Scale: 2 cm in A, 1 in C & D.

Notes – this species is recognisable by its erect rhizomes with bicolorous, lanceolate, entire scales that are 14–30 mm long, dark, denticulate costa scales; coriaceous, falcate, basally cordate pinnae with adaxially sunken veins; and dense scales on the lamina. It is probably related to *P. cordatum s.l.*, but the latter has concolorous, dark, translucent rhizome scales and whitish to pale brown, entire to irregular costa scales, and broader, flatter, finer–textured pinnae. Other related species could be *Parablechnum lima*, which has similar leathery pinnae with sunken veins, but much larger, denticulate costa scales, and *Parablechnum squamatum* (which co–occurs with *P. cochabambense*), which is

larger overall and has wider, finer textured pinnae and much smaller rhizome scales (Kessler *et al.*, 2007).

Reviewed material:

BOLIVIA: Dept. Cochabamba: Prov. Carrasco, Km 95–96 on old road between Cochabamba and Villa Tunari, *Stahl 5156B* 24 October 1999 (AAU24276! Photo, holotype).

Parablechnum confusum (E.Fourn.) Gasper & Salino, Phytotaxa 275(3): 216. 2016

Basionym – *Lomaria confusa* E.Fourn., Ann. Sci. Nat. Bot., sér. 5, 18: 316. 1873.

Type – New Caledonia, Balade, *Vieillard 1520*, 1913 (lectotype: P01468161!, designed here).

Synonym –

≡*Blechnum confusum* (E.Fourn.) Brownlie, Fl. Nouv.–Calédonie & Dépend. 3: 249, t. 31, f. 5–6. 1969.

Description – *plants* terrestrial; *rhizome* more or less erect, scaly, scales linear, reddish-brown; *fronds* dimorphic; *sterile fronds* 30–40 × 15–20 cm; *petioles* up to 75 cm, grooved, finely rugulose, with some scales at base, shiny, straw-coloured or reddish brown; *lamina* leathery, 1-pinnate, base truncate, ending in a conform apical pinna; *rachis* straw-coloured, glabrous, petiole-like, grooved, ribbed, finely rugulose; *sterile pinnae* in 5–10 pairs, slightly overlapping, 10–12 × 1.5 cm, linear-acuminate, stalked, becoming adnate distally, apex acute or slightly acuminate, base slightly asymmetric, rounded or cuneate, margins crenulate, terminal pinnae similar to lateral, but with a more irregular base; *costae* similar to rachis, glabrous, grooved adaxially, prominent abaxially; *veins* free, simple or 1-furcate, catadromous; *aerophores* dark, tuberculiform; *hydathodes* rounded or ovate; *fertile fronds* with slightly longer petioles; *fertile pinnae* generally more numerous than in the sterile frond, linear, straight, 8–12 cm long, with a sharp sterile apex, and a sterile basal portion 1 × 1 cm, similar in shape to that of the sterile pinna; *sori* linear, continuous, forming coenosori on both sides of the costa occupying the entire pinna except for the sterile apical and basal fragments; *indusia* linear, continuous, opening

towards the costa, brownish, repand; *sporangia* (17) 21 (24) arch cells; *spores* monolete, perispore not seen (**Figure 42**).

References – Brownlie (1969).

Chromosome number – unknown.

Distribution and habitat – endemic to New Caledonia, mostly in the South half of the island. Common in dry zones, among brush (Brownlie, 1969).

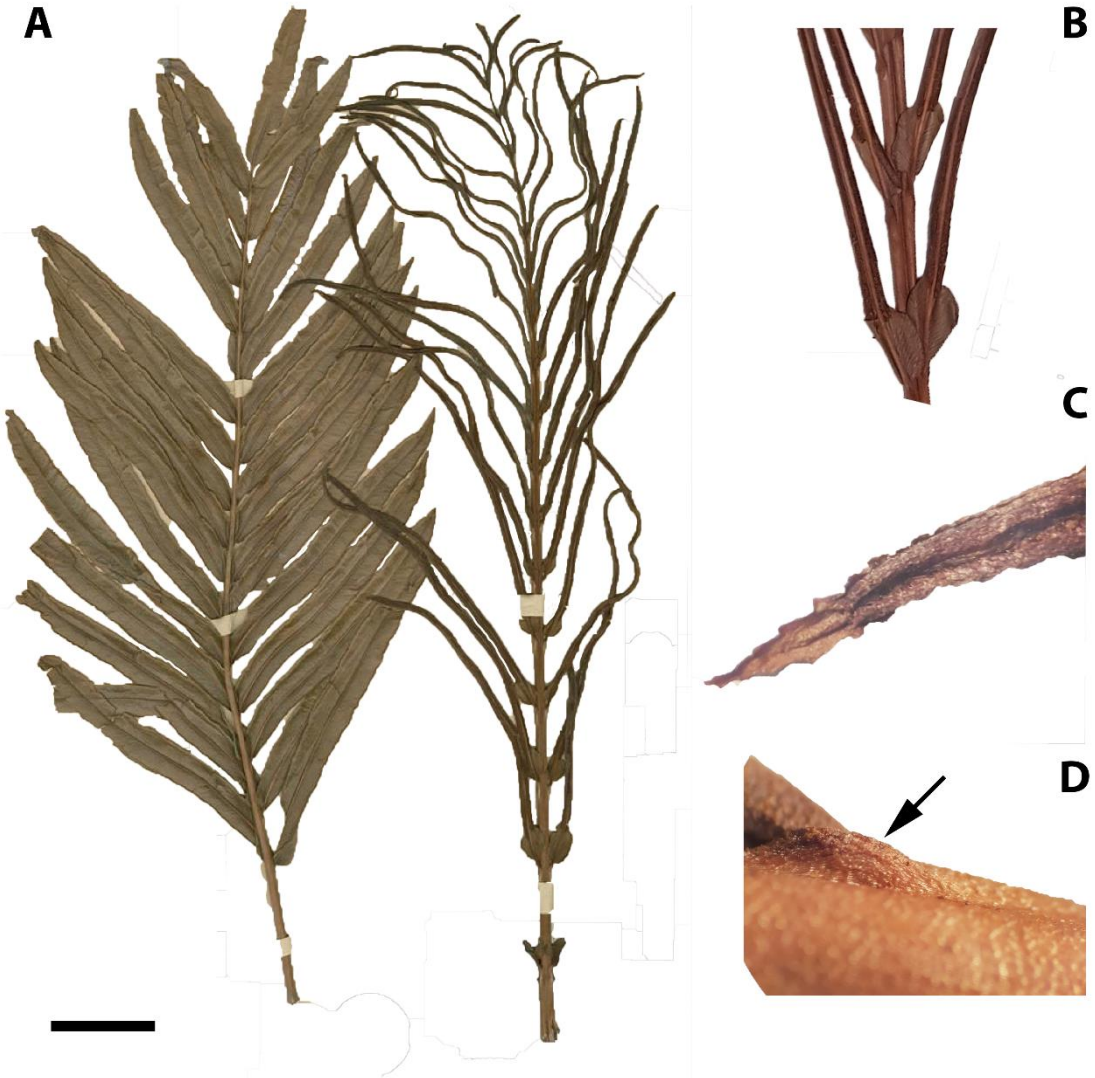

Figure 42. *Parablechnum confusum.* A. Sterile frond fragment (left) and fertile (right). B. Fertile pinnae bases; C. Fertile pinna apex, abaxial side; D. Aerophore (arrow). (A & B: *E. Veillard 1520*, P00627674, lectotype; C & D: *Franc 90*, US01527826). Scale: 50 mm in A, 2.5 cm in B, 400 µm in C, 1.3 mm in D, 1 in mm E.

Notes – this species is similar to *Parablechnum chauliodontum* and *P. subcordatum*. It can be distinguished from the former by the base of the fertile pinnae, which are wider

than the rest of the pinna in *P. confusum* and narrower in *P. chauliodontum*, and from the latter by the subcordate pinnae bases of *P. subcordatum*, as well as by the larger size of this species compared to *P. confusum*. According to Brownlie (1969) there may, however, be intermediate forms between the latter two species.

Brownlie (1969) designed a specimen from Kanala as lectotype labelled as *Veillard 1520*. However, Veillard used a confusing code for the collections, and there are several collections of him numbered as 1520 from different places of New Caledonia, sometimes they are even different species. In the protologue of the species the location is Balade (Fournier, 1873). Hence, we propose P01468161 as the lectotype, which was collected in Balade and is labelled as *Veillard 1520*.

Reviewed material:

NEW CALEDONIA. Prov. Northern: Balade, *Veillard 1520,* 1913 (P01468161!, lectotype); Kanala, *Vieillard 1520*, 1913 (P00627674!; P01468155!, P01468157!; P01468159!; BR0000006959999! Photo; BR0000006960520! photo; BR0000006960100! Photo). **Prov. Southern:** base du Pic du Pin, prés de la Mine Auci Madeleine, explotation forestiere La fleux, *R. Vitor 594*, 1 April 1942 (P01534951!); Goro, *C.–W. Hope 18*, no date (P01468154!); Ile des Pins, Plateau, Marais du port d'Onignon, *M.R. Germain s.n.*, 1868 (P01557359!); *ibidem*, 1874 (P01571860!); Lemoral, *I. Franc 115*, May 1912 (P01576154!; P01576155!; P01566769!; P01566770!); Les Dalmates, route de Yaté, *H.S. MacKee 43706*, 20 September 1987 (P01579714!; P01579715!; P01579716!); Mt. Dore, *G. Denizot s.n.,* 7 July 1961 (P01534955!); Mt. Koghi, *E. Rosenstock 90,* 1911 (US01527826!); *ibidem, Franc 90,* January 1911 (P01467841!); Mt. Mon, pentes ouest, *R. Virot 288,* 21 August 1940 (P01534952!; P01557784!); Plaine des Lacs, at 22 km Station (railway distance from Pirogue bay), *J.T. Buchholz 1346*, 4 November 1947 (P01468147!); Plum, Landes boussailleuses, *I. Franc 115*, May 1912 (P01534934!); Provy, Marecages, *I. Franc 115,* 1 May 1916 (P01534936!); Riviere Bleue, envirous du village de la Mine du Bou–Secours, *R. Virot 574*, 3 April 1942 (P01534956!); *ibidem, R. Vitor 585*, 3 April 1942 (P01534944!). **Unknown area:** *no collector*, no date (US01527827!); *no collector*, 1861-67 (NY!); *A. Baudouin s.n.*, 1865 (P01534924!; P01534925!; P01534937!); *A. Baudouin 47*, 1865 (P01534938!); *A. le Rat s.n.*, 01.1909 (P01468111!; P01468112!); *B. Balansa s.n.*, 1868 (P01534942!; P01534943!); *E. Veillard s.n.*, no date (P01534940!); *E. Vieillard 1520*, no

date (P01571506!; P01581273!; P01618501!); *I. Franc 115*, 18 July 1909 (P01534931!; P01534933!); *J. Pancher s.n.*, 1830 (P01534929!; P01534930!); *J. Pancher 221*, no date (P01534939!; P01534941!); *M. Pancher*, 1879 (US0483256!); *Mazagot s.n.*, 1889 (P01468152!; P01468153!); *M. Cribs s.n.*, no date (P01575737!; P01575738!); *Pancher s.n.*, 1870 (P01467834!; P01467835!); *R. Germain s.n.*, 1874 (P01534948!; P01534949!; P01534950!); Wai, *MacGillivray 733*, 1 August 1858 (P01534926!; P01534927!); Wogap, *Vieillard 1520*, 1864 (P01534932!).

Parablechnum corbassonii (Brownlie) Gasper & Salino, Phytotaxa 275(3): 216. 2016.

Basionym – *Blechnum corbassonii* Brownlie, Fl. Nouv.–Calédonie & Dépend. 3: 246, t. 31, f. 3, 4. 1969.

Type – New Caledonia: Messioncoué, *Balansa 1584*, October 1869 (P01662716!, lectotype, designed in Brownlie, 1969).

Description – *plants* terrestrial; *rhizome* erect, with the upper part densely covered with brown or reddish, linear, sometimes filiform scales; *fronds* dimorphic; *sterile fronds* with *petioles* up to 60 cm long, sometimes scaly at base, scales similar to those of the rhizome; *lamina* linear-ovate, 30–50 × 25–40 cm, 1-pinnate, herbaceous texture; *rachis* grooved adaxially, rugulose, glabrous or with some scattered scales, straw-coloured, shiny; *sterile pinnae* in up to 20 pairs, linear, 1–3 cm apart, never overlapping, stalked, becoming basally adnate distally, the largest 20 × 2 cm, base cuneate, asymmetrical, apex acute or shortly acuminate, surfaces glabrous, margins serrulate, terminal pinnae similar to lateral pinnae; *costae* rugulose, adaxially grooved, abaxially prominent, straw, glabrous; *veins* free, simple or 1-furcate, catadromous; *aerophores* poorly developed, dark; *hydathodes* ovate, yellowish; *fertile fronds* same size as sterile; *fertile pinnae* narrower, reaching 20 × 2–3 cm, linear, widely spaced, apex attenuate, sterile, with only the lower pairs sterile at base; *sori* linear, continuous, forming coenosori on both sides of costa occupying the entire pinna except for the sterile apical and basal fragments; *indusia* linear, continuous, opening towards the costa, brownish; *sporangia* with (16) 19 (21) arch cells; *spores* monolete, (39) 48 (58) × (22) 34 (43) µm, perispores rugulose, cristate-reticulate, with high, thin, sharp walls, forming medium to large polygonal areoles, with filamentous processes in the areoles and on the fold ridges (**Figure 43**).

References – Brownlie (1969).

Chromosome number – unknown.

Distribution and habitat – endemic to New Caledonia. Common fern in shady and humid forests and riverbanks in forests from sea level to 500 m, rare in open areas. (Brownlie, 1969).

Notes – differs from other New Caledonian endemic *Parablechnum* species by its herbaceous texture and closely spaced pinnae.

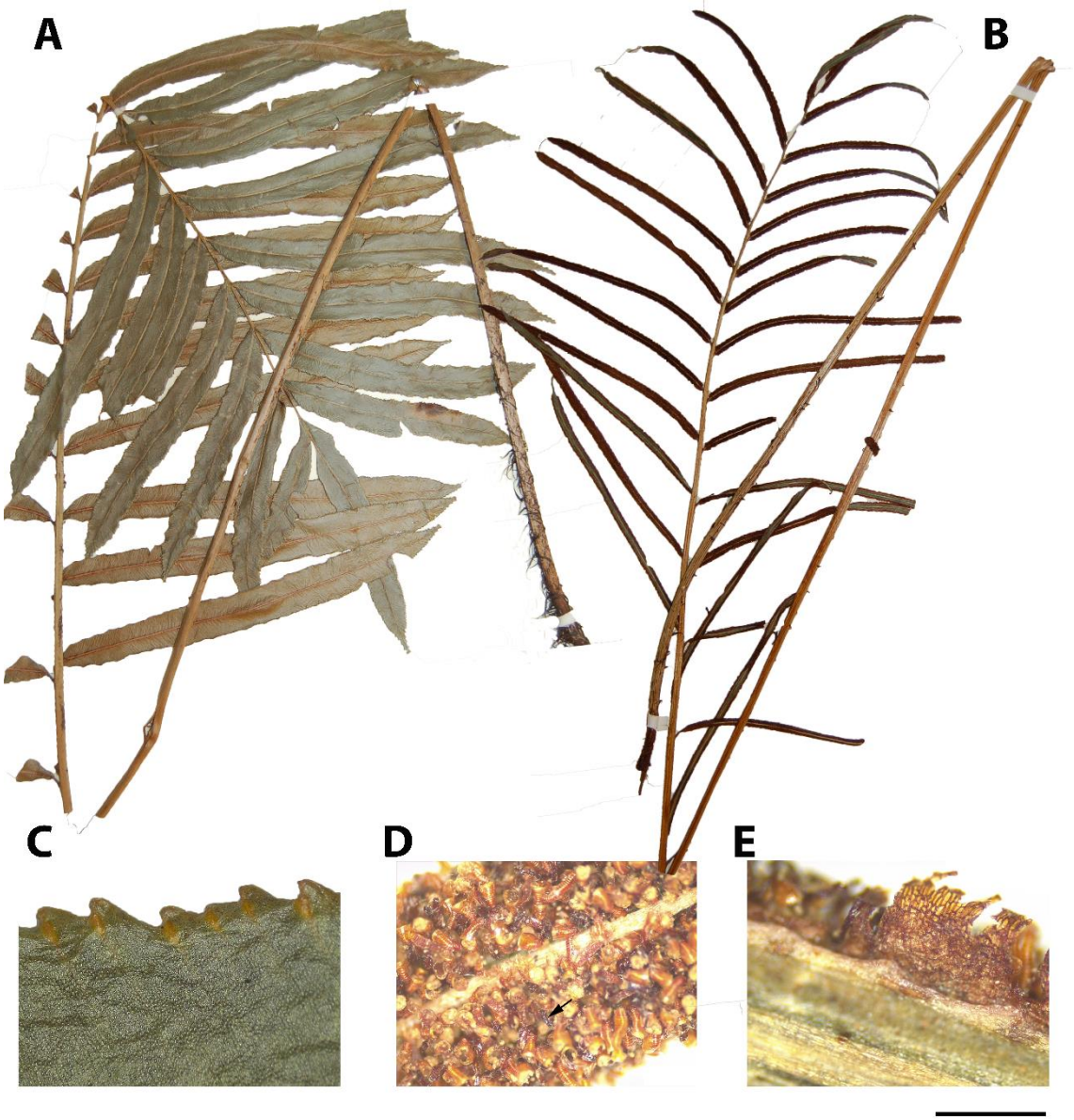

Figure 43. *Parablechnum corbassonii*. A. Sterile frond; B. Fertile frond; C. Sterile pinna margin, adaxial side; D. Sori with paraphyses (arrow); E. Indusium. (A & C: *H. van der Werff & G. McPherson 16085*, UC1740314; B, D & E: *H. van der Werff & G. McPherson 16085*, UC1740315). Scale: 50 mm in A, 2.5 cm in B, 400 µm in C, 1.3 in mm D, 1 mm in E.

Reviewed material:

NEW CALEDONIA. Prov. Northern: Balade, *E. Vieillard 1520,* 1855 (P01662712!; P01662715!); *ibidem,* 1861 (P01662713!); Mt. Panie, *D.R. Hodel et al 1438*, 15 December 1995 (UC1606653! Photo; UC1606654! Photo). **Prov. Southern:** along road to Yabé, E of Col Mouirange, *H. van Werff & G. McPherson 16085*, 9 November 1999 (UC1740314! Photo; UC1740315! Photo); at the northerm region of Rivier Bleue, Mous de Mai, *H. Koyama et al 4217*, 12 March 1992 (P01572084!; P01572085!; P01572086!), auf den Hüngen bei Paita, un Bachen, *R. Schlechter 14880*, 2 October 1902 (P01662265!); Faux Bon Secours, *M. Schmid 2053*, 1 June 1867 (P01576210!; P01576211!); Messioncoué, près de Port Bouquet *Balansa 1584*, October 1869 (P01662716!); *ibidem, B. Balansa 1586,* 1.101869 (P016626720!); Mt. Koghi, *Fran 118*, 8 January 1911 (P01468160!). **Unknown Province:** *Balansa 1584*, 1 October 1869 (P01662264!); forib lombres des bords de la Caricoigé, *I. Franc 115*, January 1906 (P01662260!; P01662267!); *J. Pancher s.n.*, no date (P01571732!; P01662707!; P01662719!; P01662721!; P01662722!); *Mazagot s.n.*, no date (P01662255!; P01662268!); *M. Savès s.n.*, 07.1879 (P01662266!); *M.T. Lécard s.n.*, 25 September 1876 (P01557213!; P01557358!; P01662256!; P01662259!); *Veillard 1520,* no date (P01468134!).

Parablechnum cordatum (Desv.) Gasper & Salino, Phytotaxa 275(3): 216. 2016

Basionym – *Lomaria cordata* Desv., Ges. Naturf. Freunde Berlin Mag. Neusten Entdeck Gesammten Naturk. 5: 330. 1811.

Type – Perú. Concepción, *J. Dombey s.n.* (Herb. Jussieu 1368; holotype: P00307042!; isotypes: P00627581!, P01466404!, BM000769804! photo).

Synonyms –

≡*Blechnum cordatum* (Desv.) Hieron., Hedwigia 47: 239. 1908
=*Blechnum euraddianum* Brade, Annais Reunião Sul–Amer. Bot. 2: 7. 1940. Type: not found.
=*Blechnum itiaiense* Brade, Arq. Inst. Biol. Veg. 1(3): 225, f.3, pl.4. 1935. Type: Brazil, Rio do Janeiro, Serra do Itatiaia, *Brade 10115,* 1933 (syntypes: R000021796! Photo; RB0035050! Photo).
= *Blechnum macahense* Brade, Annais Reunião Sul–Amer. Bot. 2: 6, t.3. 1940. Type: Brazil, Rio do Janeiro, Frade de Macahé, *M. Brade 15801*, 19 November 1937 (holotype: RB n.s.; isotype: HB33994! Photo).

=*Blechnum simile* Sehnem in Dsitz, Fl. Ilustr. Catarin. 1(fasc. Blec): 56, f.1. 1968. Type: Brazil, Rio Grande do Sul, Aparados da Serra, Passo do Guarda, 800 m, *Sehnem 5861*, no date (holotype: PACA, n.s.).

=*Blechnum raddianum* Rosenst., Hedwigia 46: 91. 1907. Type: Brasilia, Invenitur saepissime ad margmes nemorum humidorum in vallibus prope Tijuccam., *Raddi s.n.*, 1825 (PI010198! Photo).

=*Lomaria arborescens* Klotzsch & H. Karst., Linnaea 20: 347. 1847. Types: Colombia, *Karsten 25*, no date (syntypes: B200030107-8!); *Karsten 58*, no date (syntype: B200030107!); Venezuela, Caracas et Cumana *Mortiz 116*, no date (not found), Mérida, *Moritz 299*, no date (syntypes: B200030106!, US2456199!); *Moritz 300*, no date (syntypes: P00627570-2!, P01466410!, P01466420!); ≡*Blechnum arborescens* (Klotzsch & H. Karst.) Hieron., Hedwigia 47: 239. 1908.

=*Lomaria brasiliensis* Raddi, Pl. Bras. Nov. Gen. 1: 50 t.72, 72 bis. 1825; ≡*Struthiopteris brasiliensis* (Raddi) Maxon & C.V. Morton, Bull. Torrey Bot. Club 66: 43. 1939. Type:Brazil, Rio de Janeiro, Tijuca, *G. Raddi s.n.*, no date (holotype: PI! Photo).

=*Lomaria ornifolia* C. Presl, Reliq. haenk. 1: 51. 1825; ≡*Blechnum ornifolium* (C. Presl) Ettingsh., Denkschr. Kaiserl. Akad. Wiss. Wien. Math.-Naturwiss. Kl. 23: 61. 1864. Type: Hab. In Peruvia? [*Haenke*] (not found).

=*Lomaria regnelliana* Kunze, Linnaea 22(5): 576. 1849; ≡*Blechnum regnellianum* (Kunze) C.Chr., Index Filic., Suppl. (1906–1912), 17. 1913. Type: Brazil, Minas Gerais, *Regnell 490*, 1846 (B200033168! Photo).

=*Lomaria serrulosa* Desv., Mém. Soc. Linn. Paris 6: 290. 1827. Type: Crescit in Peruvia (Holotype: P!).

Description– *plants* terrestrial; *rhizomes* erect or suberect, not stoloniferous, scaly, scales light brown, concolorous, membranaceous, triangular–lanceolate, 3–25 × 0.9–3.5 mm, margins entire; *fronds* dimorphic, reddish and secreting mucus when young; *sterile fronds* 20–250 cm, arching; *petioles* from stramineous distally to dark brown at the base, 8–112 × 0.4–0.6 cm, scaly throughout the length or only near the base, scales similar to those of the rhizome; *lamina* 12–56 × 6.7–37 cm, coriaceous, 1-pinnate, oblong-lanceolate, base truncate, reducing towards the apex ending in a conform pinna; *rachis* grooved, stramineous, scaly, scales brown to light brown, concolorous, 5 × 1.4 mm, lanceolate or triangular–lanceolate, margins entire, sometimes with some elongated processes; *sterile pinnae* in 5–18 pairs, 10–30 × 1.3–3.5 cm, stalked, becoming basiscopically adnate towards the apex, margins entire or serrulate, elliptic, base subcordate, cordate or rounded, apex acute or acuminate, margin serrulate; *costae* similar to the rachis, grooved abaxially, prominent abaxially, scaly, mostly proximally, scales similar to those on the rachis but smaller; *veins* free, simple or 1-furcate, catadromous; *hydathodes* patent, rounded or elliptic; *fertile fronds* longer than the sterile and normally more erect; *petiole* 20–75 cm long; *lamina* 32–45 × 5.1–27 cm; *fertile pinnae* contracted, linear, 3–7 mm wide; *sori* linear, continuous, forming coenosori on both sides of the costa;

indusia subentire to lacerate, continuous opening towards the costa; *sporangia* with (16) 21 (–26) arc cells; *spores* monolete, (52–) 66 (–75) × (41–) 52 (–62) µm, perispore cristate-reticulate, delimiting polygonal areolae without filaments; *gametophytes* cordate, without indument (**Figure 44**).

References – Ramos Giacosa *et al.* (2006), Prada *et al.* (2008), Dittrich *et al.* (2018, 2020), Sundue (2010).

Chromosome number – unknown. Prada *et al.* (2008) state that the chromosome number is 2n = 66, but they refer to an individual identified as *P. chilense* since they considered it a synonym, a view that we do not follow in this work.

Distribution and habitat – common in South America: Venezuela, Colombia, Ecuador, Perú, Bolivia, SE and centre of Brazil, Paraguay, Uruguay, and Argentina (Ramos Giacosa *et al*., 2006, Dittrich *et al.*, 2018, 2020). There are some reports in Chile but they might be due to its resemblance to *P. chilense*. The species may also occur in Mexico (Mickel & Smith, 2004), Central America and the West Indies (Smith & Kessler, 2018), the range is uncertain due to taxonomic difficulties. It inhabits tropical rainforests and seasonal forests, as well as riparian forests in areas dominated by rocky fields. However, the plants are much more common in open areas such as roadside ravines, on the edge of wide roads, on well–lit riverbanks and in wetlands, 50–3,300 m (Dittrich *et al.*, 2018; Smith & Kessler, 2018).

Notes – this is a highly variable species that could comprise a species complex, analysis of material from a limited area is insufficient to solve the taxonomic problem in this species (Prada *et al*., 2008; Dittrich *et al*. 2018, 2020). Tryon & Stolze (1993) and Smith (1995) drew attention to the difficulties in this species. Both adopted a broad species definition, and Smith (1995) stated that even other taxa may in fact be morphological variations of *P. cordatum*. Our phylogenetic results show a topology for this species that also points to a complex of species.

There are some synonyms that had led controversy concerning this taxon. For instance, pteridologists split *B. regnellianum* from *P. cordatum*, without clarifying the diagnostic characters for this distinction. Sehnem (1968), when referring to *B. regnellianum*, said that it could be differentiated from similar species by veins close together, juxtaposed ("20–25 cm", which is 20 to 25 veins per cm). In descriptions of other species, at least

two have, according to Sehnem (1968), up to 20 veins per cm. In herbaria, until the last decade, smaller individuals with fewer pinnae were generally called *B. regnellianum*, while larger individuals with more pinnae were called *B. cordatum*. In the study by Dittrich *et al*. (2018), they verify that there is a continuum between these two forms, making it impossible to separate these materials into more than one taxon. Therefore, the concept of *P. cordatum* used there includes what is often treated as *B. regnellianum*. *Blechnum regnellianum* is based on *Lomaria brasiliensis*, as the epithet "brasiliense" was not available in *Blechnum*, since *Blechnum brasiliense* (now *Neoblechnum brasiliense* (Desv.) Gasper & V.A.O. Dittrich) was described in 1811. *Blechnum raddianum* is a later homonym for the same taxon and *Blechnum euraddianum* is a *nomen novum* for the same taxon, and consequently superfluous. Although Dittrich *et al*. (2018) did not observe authentic material of *Lomaria brasiliensis*, the illustration of Raddi (1825) led them to believe that *L. brasiliensis* and *P. cordatum* are the same species. (Dittrich *et al*., 2018).

Parablechnum cordatum can be distinguished from other dimorphic species by its large size, concolorous rhizome scales and lack of arborescent habit. (Sundue, 2010). Spores have proved to be constant and useful characters to distinguish this taxon from its related ones, among all the size of the areolae and the absence of filaments (Prada *et al*., 2008; Wal *et al*., 2021).

Of the species of the "*Parablechnum lineatum* group" reviewed by Tryon & Tryon (1982) *Parablechnum proliferum*, which grows in Mesoamerica (Costa Rica and Panama) and South America (from Venezuela and Colombia to Brazil) seems to be the most closely related to *P. cordatum*, from which it is distinguished by the presence of buds on the apical portions of the fronds, lanceolate pinnae with rounded bases, acroscopically cuneate, the venation pattern, conical aerophores, epidermal patterns and crested spores without filamentous micro–ornamentation (Prada *et al.*, 2008).

Species of the *P. lineatum* group (Tryon & Tryon, 1982) or *P. cordatum* group (Dittrich, 2005), need to be better studied to establish their boundaries and analyse their affinity with *P. cordatum*. Moran (1995a) treated *P. schiedeanum* for Mesoamerica, included *B. costaricense* among its synonyms and considered it very similar *to P. cordatum*. That author also treated *P. falciforme* as a distinct species. Mickel & Smith (2004) noted the similarities between *P. falciforme, P. schiedeanum, P. varians* and *P. cordatum*, although they retained them as distinct taxa.

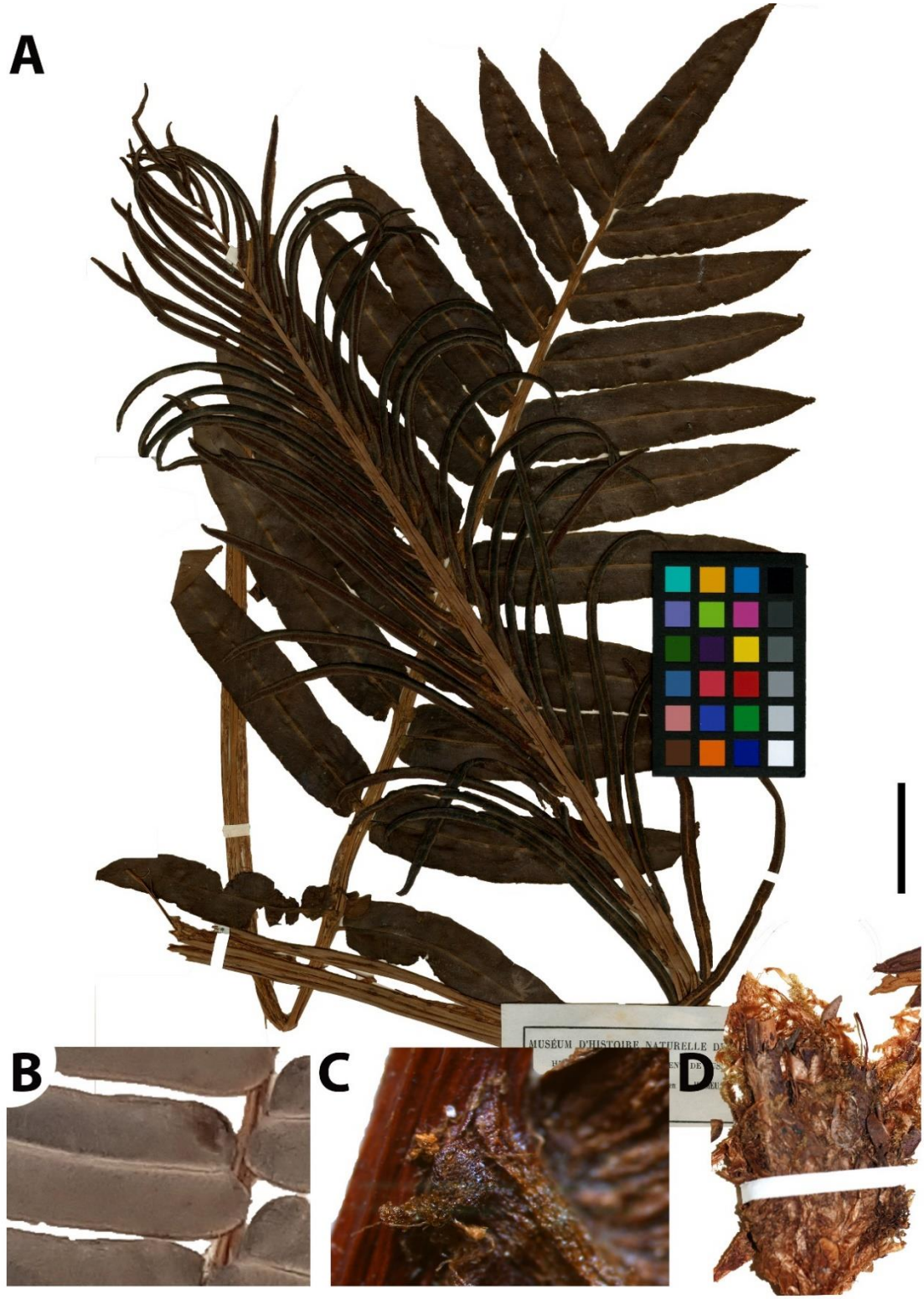

Figure 44. *Parablechnum cordatum.* A. Sterile (back) and fertile (front) fronds; B. Sterile pinnae bases, adaxial side; C. Stalk with an aerophore; D. Rhizome. (A. *Domby s.n.*, P00307042, lectotype; B. *E. Hassler 6368*, NY; B. *J.A. Steyermark 89586*, US2419607 US; C. *B. Stergios & L. Zambrano 17683*, UC1735032). Scale: 4 cm in A; 2.3 cm in B; 2.3 mm in C; 2 cm in D.

Regarding distribution, there are two individuals from Australia that have led Prada *et al*. (2008) to think that the distribution of this species could reach the Austropacific. The individual from Australia considered in that work (MA213373) has been reviewed for this monograph. It is a specimen collected by Luís Neé and revised by Cavanilles, who identified it only as *Blechnum*. It was subsequently given the identification *of Parablechnum cordatum*, but it seems to be rather its Australian relative *Parablechnum wattsii*.

Reviewed material:

BOLIVIA. Dept. Chuquisaca: Prov. Belisario Boeto, 1 km de Nuevo Mundo a Padilla, *M. Kessler et al 5140,* 5 July 1995 (NY!). **Dept. Cochabamba:** Prov. Chapare, *R.S. Williams 1186,* 23 January 1929 (US1803883!); *ibidem, J. Steinbach 8912,* 23 January 1929 (US1859963!); Prov. Chapare, Incachaca, *J. Steincach 8912,* 23 January 1929 (NY!); *ibidem, J. Steincach 8913,* 23 January 1929 (NY!); Sailapata, Azopaza, *M. Cardenas 3151,* December 1935 (US1742475!); Prov. José Carrasco Torrico. 7 km de Siberia hacia karahuasi, *M. Kessler et al 9103,* 17 October 1996 (NY!, 2 sheets); Prov. Tiraque, localidad El Limbo, *M.A. Zabalaga 224,* 16 February 2004 (NY!). **Dept. La Paz:** *O. Buchtien s.n.,* 1912 (P01396001!); Apolo, *R.S. Williams 1186,* 5 March 1902 (US1832087!; US1832088!); Franz Tamayo, Parque Nacional Madidi, Sector Pilcobamba, por el antiguo camino Pelechuco Apolo, *R. Jaramillo–Mejía & T. van der Hammen 4177,* 23 November 1967 (MA882533!); Nor Yungas, Parque Nacional Anmi Cotapata; Estación Biológica Tunquini, NW of Coroico, NNE of La Paz: vix. Of Chairo, 23 km W of Yolosa, *T.B. Croat et al 84752*, 21 August 2000 (NY!); Nord Yungas, Polo-Polo bei Coroico, *O. Buchtien 3367,* 10–11.1912 (US1096205!); Nor Yungas Provincias, 15.4 km from Yolosa towards Chuspipata, *A. Fay & L. Fay 2164,* 27 June 1989 (US3250865!); Polo-Polo bei Coroico, Nordyungas, *O. Buchtien s.n*., 1912 (NY!); *ibidem* (P01395998!); Región de Mapiri San Carlos, *O. Buchtien 271,* 23 January 1927 (NY!); Sirupaya bei Yanacachi, *O. Buchtien 466,* 24 December 1906 (US1096157!; US1096158!); Subandine Region, Milluguaya, *O. Buchtien 5016,* December 1917 (NY00813957!; US1099001!; US1096212!); Sud Yungas, Chulumani road, 15,1 km W of Chulumani, 93 km from Huancané, *A. Fay & L. Fay 2512*, 2 August 1989 (US3250886!); Sud Yungas, Provincia La Paz-Chulumani road, 12 km E of Chuspipata (77 km from La Paz) *A. Fay & L. Fay 2491*, 1 August 1989 (US3250867!); Sud Yungas,

Yomoicochi, *O. Buchtien 467*, 11 November 1906 (P01389557!); Unduavi River, between la Paz and Coroico, *Julio 220*, March 1924 (US1997709!). **Dept. Larecaja:** Cordillera Real Okara, *G.H.H. Tate 938*, 26-29 April 1929 (NY00814188!); Hacienda Casama sobre camino a Tipuani, *O. Buchtien 7003*, 3 April 1923 (US1499156!); Hacienda Simanco, sobre el camino a Tipuani, *O. Buchtien 5131*, January 1920 (US1096219!; US109620!). **Dept. Santa Cruz:** Manuel M. Caballera, *R. Núñez C. 728*, 23 April 2004 (NY!, 2 sheets); Prov. Caballero. 6 km (by air) N of Comarapa along road to Cerro Bravo and Tinqui Laguna, *M.A. Sundue et al 806*, 30 August 2003 (NY!); Prov. Caballero, 6,5 km (by air) N of Comarapa. Lower reaches of Cerro Bravo, *M.A. Sundue et al 803*, 3 August 2003 (NY!; UC1792958! Photo); Prov. Florida, 7 km (by road) NE crossing of Río Paredones north of Achiras Camping resort, on trail to Abra Los Toros, *M. Nee 49703*, 7 June 1998 (NY000309614!); Prov. Florida, Parque Nacional Amboró, 8 km (by air) NE of Mairana, along trails and near ridgetop. 5,5 km N of Campamento "La Yunga" park station, *M. Sundue et al 546*, 30 March 2002 (NY!, 2 sheets). **Unknown Department:** *D. Eberhardt 108*, 19 August 2000 (MO6280923!); *R.S. Williams 1186*, 1902 (NY!); Cañamine, *H.H. Rusby 261*, 1921 (US1069682!). **BRAZIL. Bahía:** Ilhéus, *no collector*, no date (NY00814184!); Rio de Contas, 17 km ao N da cidade na estrada para o povoado de Mato Grosso. Perto do rio, *R.M. Harley et al 26068*, 9 November 1988 (NY01114005!); Rio de Contas, Pico das Almas Vertente leste, Margem leste do Campo do Queiroz, *R.M. Harley et al. 26219*, 20 November 1988 (NY01114004!; UC1871917! Photo). **Brasilia:** Federal District, Fazenda Agua Limpa (University of Brasilia field station), near Vargem Bonita, c. 18 km. SSW of Brasilia TV tower, at the crossing at the upper end of the Corrego Capitinga, *J.A. Ratter 4766*, 12 September 1982 (K000954311! Photo; NY00908717!). **Golás:** Chapada dos Veadeiros, 1 m E of Alto Paraíso on road to Nova Roma, *W.R. Anderson 6299*, 5 March 1973 (K000954312! Photo; NY00908655!; P01389549!). **Minas Gerais:** *no collector*, 06.1879 (P01395982!); *M. Claussen 201*, 1 November 1843 (P01466429!; P01466450!); *Schwacke 3096*, August 1896 (P01575347!); *Regnell 490*, 1846 (B200033168! Photo, holotype of *Lomaria regnelliana*); *Schwacke 12322*, 10 August 1896 (P01624911!); Bocaina de Minas, Parque Nacional do Itatiaia, Alto dos Brejos, *J.P.S. Condack & E. Cortines 301*, 30 October 2004 (NY2480438!); ca. 17 km E. of Diamantina, *H.S. Irwin et al 28023*, 21 March 1970 (NY00908659!); Caldas, *H. Mosén 4602*, 1876 (P01395989!); Carasa, *M. Claussen 261*, 1 November 1843 (P01466430!); Fonseea, *L. Emygdio et al. 3496*, 20 July 1972

(NY00908720!); Gandarela, *L. Emygdio et al 3433,* 17 July 1972 (NY00908718!); *ibidem, L. Emygdio et al 3491*, 18 July 1972 (NY00908719!); Lima Duarte, Parque Estadual do Ibitipoca, *R.C. Forzza et al. 4149,* 6 March 2012 (NY!);S. Sebastião do Paraiso, Baú de Sta Cruz, *Brade & Altamiro 257,* 16 July 1945 (P01389551!); *ibidem, Brade & Altamiro 261,* 16 July 19445 (P01389580!); Mun. Serro, Estrada entre Milho Verde e São Gonçalo do Rio das Pedras, *A.L. de Gasper & F.C. Assis 2846,* 10 April 2011 (FURB35873! Photo); Serra do Cipó, ca. Km 120 (ca. 145 km N. of Belo Horizonte), *H.S. Irwin et al 20093,* 14 February 1968 (NY00908658!); Viçosa, Agricultura College Valley, road to Chacha valley, *Y. Mexia 4546* 1 April 1930 (P01395988!; UC476340! Photo). **Paraná:** *D. Parodi 81,* April 1883 (K000954315! Photo); Campina Grande do Sul, Parque Estadual Pico Paraná, *J.B.S. Pereira et al 268,* 22 May 2008 (VT198659!; VT198669!); Juariaiva, Parque Estadual do Cerrado, *P.H. Labiak 51,* 28 August 1993 (UPCB54850! Photo); Ponta Grossa, Parque Estadual de Vila Velha. *P.B. Schwartsburd & F.B. Matos 431*, 14 December 2004 (NY!, 2 sheets); Ponta Grossa, Parque Estadual de Vila Velha. Campos proximo aos Capao da Fortaleza. Campos Gerais, *P.B. Schwartsburd & M. Nogueira Jr 795*, 16 March 2005 (NY01015457!; NY01015458!). **Río de Janeiro:** *A. Glaziou 2425,* 1870 (P01466433!; P01466434!; P01631360!; P01631361!); *A. Saint–Hilaire 450*, 1816 (P01466453!; P01466454!; P01466455!); *Brade 3479,* September 1929 (NY00814182!); *E.R. Wagner s.n.,* no date (P01325336!; P01325337!); *H.A. Weddell 863,* 1844 (P01466432!); *J. Díaz s.n.,* 1 February 1923 (P01623189!); Campo Bello, bords du Riberão de Ustatiaia, *Glaziou 7009*, 25 March 1873 (P01395991!; P01395992!; P01546438!); *ibidem, E.R. Wagner s.n.,* 7 March 1901 (P01546441!); Corcovado, *A. Glaziou 72/bis*, 1 September 1867 (P01466425!); *ibidem, A. Glaziou 368,* 8 September 1867 (P01466424!); entre Corcoravo e Tijuca, *M. Nadeaud s.n.*, November 1860 (P01466448!; P01466449!); Estrella, *H.A. Weddell s.n.,* 1844 (P01466456); Frade de Macahé, *M. Brade 15801,* 19 November 1937 (HB33994! Photo, 2 sheets, isotype of *Blechnum macahense*); Guapimirim, Parque Nacional da Serra dos Órgãos, Trilha do São Pedro, *Rolf A. Engelmann et al 769,* 13 July 2010 (NY02681784!); Ilha Grande, Distrito Federal, *J.N. Rose & P.G. Russell 20360,* 22-24 July 1915 (NY01016736!); Itatiaia, *Brade 350,* 26 March 1940 (P01410445!, topotype of *Blechnum itatiaiense*); Itatiaia, *Brade 10115,* 1933 (R000021796! Photo, syntype of *Blechnum itatiaiense*; RB0035050! Photo, 2 sheets, syntype of *Blechnum itatiaiense*); Itatiaia, *E. Pereira 350,* 26 March 1946

(NY00814035!; NY00814036!; P01410443!); Itaiaia, Parque Nacional do Itatiaia, Planalto-Abrigo Macena, *J.P.S. Condack 235*, 8 September 2004 (NY02480422!); Itatiaia, Reg. Rio d'Ouro, *Brade 15506*, March 1937 (NY00814037!; NY00814038!); Miguel Pereira, Reserva Biológica do Tinguá. Orbel 2. Proximidades do km 29, *L.S. Sylvestre et al 2103*, 18 July 2007 (NY02711692!); Montagnes des Orgues, *Wagner s.n.*, 16 November 1904 (P01389554!); Mun. De Carandaf, Hermilo Alves, *A.P. Duarte & A.C. Brade 6312*, 14 February 1963 (NY00814186!); near Rio Janeiro and Bahia, *Mrs. J.W. Webb s.n.*, 1867-1868 (NY00814093!); Organ Mountains, *illegible collector*, no date (NY00814181!); Organ Mountains, Petropolis, *J.N. Rose & P.G. Russell 20754*, 12 August 20754 (NY01016737!); Petropolis, *T.A. Preiter s.n.*, 1872 (K000954316! Photo); *ibidem* (K000954317! Photo); Petropolis, *W. Herter 4300*, 10 September 1907 (P01466444!); *ibidem, W. Herter 4317*, 10 September 1907 (P01466445!); Pr. José Dias. Serra da Estrella, *no collector*, 1 February 1823 (P01631761!); São Fidélis, Parque Estadual do Desengano. Serra do Itacolomi, Subida para a Pedra do Macaco, *C. Baez et al 1038*, 31 August 2016 (NY03489013!); Serra da Estrella, *Brade 2825*, June 1929 (UC441983! Photo); Serra dos Orgãos, *Casaresso s.n.*, May 1839 (P01630875!); Teresópolis, Parque Nacional da Serra dos Órgãos, Trilha para a cachoeira Véu de Noiva e Pedra do Sino, *P. Fiaschi & G.M. Antar 2888*, 6 March 2012 (NY!). **Rio Grande do Sul:** Caixas do Sul, Vila Oliva, estrada para Gramado, *F. Gonzatti 2404*, 24 April 2014 (P00963816!); Cerro Largo, Sierra de Fouza, *J. Arechavaleta 466*, January 1877 (P01395994!); man Venancio Ryres, Compeste dos terrães, *L.C. Jüngens s.n.*, December 1905 (P01546456!); Sta. Cruz, *I.C. Jürgens 69*, 1 October 1904 (P01546440!); *ibidem, I.C. Jürgens & A. Stier 17177*, 1 October 1904 (P01546439!); Tambie São Francisco de Paula, *A. Sehnem 6452*, 16 November 1953 (MBM106456! Photo, paratype of *Blechnum simile*); Valley of the Rio Campo Bello, vicinity Monte Serrat, Mt. Itatiya, Estaçao Biologica, *L.B. Smith 1647*, 3 January 1929 (NY00814190!; UC419639! Photo); Vicinity of São Leopoldo, *J. Eugenio 20*, 1941 (NY01016739!). **Santa Catarina;** *no collector 2342*, April 1891 (P01410444!); Apiuna, *A. Korto & A. Kniess 2160*, 17 March 2010 (FURB22367! Photo); Blumeau, Parque Nacional da Serra do Itajai, Spitzkopf, *A.L. de Gasper 578*, 17 August 2007 (FURB6533! Photo); Jainville, *A. Schmalz 82*, 19 November 1903 (NY00813953!; NY00814076!); Orleans, Triha Pedra Furada, *A. Kassner et al 2599*, 11 March 2018 (FURB58560! Photo); Santo Amaro, *C. Spannagel 347*, 1921 (NY00814185!); Serra do Jacu, Massaranduba, *A. Korto & M.J. Rigon-JR 5908*, 4

February 2011 (FURB34048! Photo). **São Paulo:** *no collector 298,* 1859 (P01389555!); *Guillemin s.n.,* 1839 (P01466451!); *Uster 25,* 1905 (P01389553!); between Sanlós and São Paulo, *C. Sandeman s.n.,* May 1942 (K000954313! Photo); *ibidem* (K000954314! Photo); entre San Pãulo et Santos. Serra do Mar, *R. Schnell 8605,* 1 August 1958 (P01531020!; P01531021!); Iguape, Reserva Ecológica de Juréia trilha para campo do alto do morro próximo ao alojamento, *J. Prado et al. 361,* 16 August 1990 (P00904676!); Iporanga, área da Fazenda Intervales, *J. Prado et al. 917,* 22 May 1996 (P00904677!); S. José do Barreiro, *Hoehne & A. Gehrt 17679,* 1 May 1926 (NY00813954!); Sumaré, *A.C. Brade 8585,* November 1928 (NY00814183!). **Unknown state:** *illegible collector,* no date (K000954321! Photo); *A. Glaziou s.n.,* no date (P01466440!); *A. Glaziou 12345,* 1880 (P01466436!; P01466437!; P01466438!; P01466439!); *Appun 12345,* no date (P01630874!); *Burchell 2245,* no date (K000954322! Photo; P01466443!); *Gardner 143* (P01466446!); *M. Nadeaud s.n.,* no date (P01466447!); *Raddi s.n.,* 1825 (PI010198! Photo, 2 sheets, holotype of *Blechnum raddianum*); *Schwace s.n.,* September 1895 (P01630873!); *Riedel s.n.,* no date (P01466452!); *Riedel s.n.,* no date (P01546437!). **COLOMBIA. Dept. Antioquia:** 10 km al Este de Sonsón, *R. Scolnik et al 19An250,* 18. March 1949 (US3145388!); Alto de Minas, entre Caldas y Santa Barbara, *M. de Garganta 2001,* 4 April 1955 (US2816077!); Cocorná, *Daniel 1212,* 30 July 1937 (US1742807!); Chocó-Antioquia, at an both sides of the principal ridge W of La Mansa, al ca. Km. 105.5 of the Ciudad Bolivar–Quibdo Road, *D.B. Lellinger & E.R. de la Sota 919,* 4 April 1971 (LP9190197! Photo; US2723494!; US2723495!; US2723496!); Chocó, W of El Siete along the Ciudad Bolivar-Quibdo Road, *D.B. Lellinger & E.R. de la Sota 872,* 2 April 1971 (US2723490!; US2723491!); Cordillera Central, 2 km. E. Medellín, foot of Santa Elena, *J.A. Ewan 15694,* 22 May 1944 (UC1077896! Photo; US2254134!); Cordillera Central, Páramo de Sonsón, above Sonsón, *J.A. Ewan 15711,* 23 May 1944 (US2254140!; US2254141!); en Chaparral del paramo diez kilómetros al norte de Sonsón, *G. Gutiérrez V et al. 18C236,* 6 March 1948 (US3186600!); Frontino, Corregimiento Carauta, Parque Nacional Natural Las Orquídeas, sector Tres Bocas, camino hacia mina San Francisco, marge izquierda del río San Francisco, *M.A. Sundue et al 3352,* 11 September 2012 (NY02058070!; NY02058122!; VT198666!); Mpio. Angelópolis, Sector Bocatoma acueducto, Quebrada Las Animas, *W.D. Rodriguez et al 5104,* 6 February 2005 (NY!, 2 sheets); Mpio. Jericó, Límites entre los municipios Jericó-Pueblo Rico, *W.D. Rodriguez et al 4797,* 13 December 2004 (NY!); Municipio de Mesopotamia. Carretera entre San

Miguel y Mesopotamia, *A.L. Arbeláez et al 77*, 7 July 1987 (NY!); Paramo de Sonsón, *M. de Garganta 2051*, 8 January 1956 (US2816144!); *ibidem, M. Gargante 2052*, 8 January 1956 (US2816145!); Río Negro, *W.A. Archer 246*, 22 June 1930 (US1544619!); vicinity of Medellin, *S.J. Charetier 20*, 1911 (US602774!). **Dept. Bocayá:** Camino del Alto de Onzag a Soatña en el Valle Lateral, *R. Jaramillo-Mejía, T. van der Hammen 4177*, 23 November 1967 (MA381520!); Mun. Villa de Leyva, SFF de Iguaque, cerca al centro de visitantes, *M. Sundue & A. Vasco 1280*, 29 April 2007 (NY!; VT198664!; VT198665!). **Dept. Caldas:** Laguneta to Magana, Old Quindio Trail, Cordillera Central, *F.W. Pennell & E.P. Killip 9465*, 1 August 1922 (US1144826!); Río Boquia, Salento, Cordillera Central, *F.W. Pennell & E.P. Killip 8842*, 27 July 1992 (US1191806!); Río Santa Rita, Salento, Cordillera Central, *F.W. Pennell & E.P. Killip 8977*, 28 July 1922 (NY!; US1144742!; US1144743!). **Dept. Cauca:** *Hartweg 459*, no date (P01546375!); *Hartweg 1483*, no date (P01546376!); 4 km N of Popayán, Río Cauca drainage, *J.A. Ewan 15862*, 5 July 1944 (US2254165!); *ibidem, J.A. Ewan 15882*, 5 July 1944 (UC1077898! Photo; US2254169!; US2254170!); Caanan, Mt. Purace, Cordillera Central, *F.W. Pennell & E.P. Killip 6617*, 11-13 June 1912 (US1144420!; US1144421!); *ibidem, F.W. Pennell & E.P. Killip 6690*, 11-13 June 1912 (US1144437!); Chocó–El Valle, at and on both sides of the principal ridge of the Serranía de Los Paraguas, along the trail from El Cairo to Río Blanco, ca. 8 km SW of El Cairo, *D.B. Lellinger & E.R. de la Sota 855*, 28 March 1971 (US2723492!; US2723493!): Corregimiento de Santa Marta, *W. Rodriguez et al 7947*, 25 October 2013 (NY01487518!; NY01487519!); Highland y Pohayán, *Lehmannianum KK55*, March 1884 (US1424524!); Mpio. de El Tambo. Abajo del Munchique (arriba de Fondas, cerca km. 54), *Steven P. Churchill & Julio Betancur 18092*, 13 May 1991 (NY!, 4 sheets); Mpio. Popayán, ca. 8 km E de Popayán, *S.P. Churchill & W. Rengifo M. 17315*, 12 January 1991 (NY!, 3 sheets); Papayan, Cordillera Central, vertiente occidental, *K. von Sneidern 5613*, 20 June 1946 (US2018045!; US2018046!); Río Sucio to Río Piedras, West of Popayan, Cauca Valley, *F.W. Pennell & E.P. Killip 8233*, 3 July 1922 (US1144660!). **Dept. Chocó:** S. ridge of Cerro Mecana, *A. Juncosa 1800*, 8 January 1984 (UC1505117! Photo)**Dept. Cundinamarca:** above Bogotá, *H.H. Rusby & F.W. Pennell 1254*, 16 August 1917 (NY!); below Alto de Cuchuco, 7 km southwest of Sibate, *R.M. Tryon & A.F. Tryon 6114*, 19 October 1961 (P01466411!); Bogotá, *Apollinaire s.n.*, March 1905 (NY!); Bogotá, *J. Goudot 5*, 1844 (P01462410!); *ibidem, Lindig 197*, 1862 (P01462415!; P01462416!); Bogotá, Cordillera Oriental, *E.L. Little & R.R. Little 7829*, 7

May 1944 (US2419373!); Bogotá, Cordillera Oriental, between Sebastopol and Analaima, *E.L. & R.R. Little 8585,* 3 September 1944 (US2419457!); Bogotá, Cordillera Oriental, low ridge east of Calle 55, *E.L. Little Jr 7830,* 7 May 1944 (US2604561!); Bogotá D.C., La Mesa, Prov. De Bogotá, *Apollinaire s.n.,* May 1905 (US0464106!); *ibidem* (US0464107!); Bogotá, near La Gruta canyon, E. of Calle 57, *E.L. & R.R. Little 7849,* 14 May 1944 (US2419461!); Bogotá, Guadalupe, *O. Haught 5004,* 22 September 1946 (US2016671!); de Bogotá hacia la Aguadita, *M.T. Murillo & R. Jaramillo Mejía 942*, 2 December 1966 (NY!); from Bogotá to El Salto (Tequendama), Cordillera Oriental, Monserrate, at E. edge of Bogotá, *E.L. Little & R.R. Little 8185,* 2 July 1944 (US2419400!; US2419401!); falls of Río Bogotá, vicinity of El Salto, *E.L. & R.R. Little 7867,* 18 May 1944 (US2419402!; US2419408!; US2419399!); Quebrada la Vieja, near Chafainero, *Ariste–Joseph 354A,* June 1919 (US1040030!); region of Bogotá, *Ariste-Joseph s.n.,* no date (US1040143!); San Francisco, *Apollinaire & Arthur 134,* September 1915 (US537738!). **Dept. Huanuco:** *P.S. Coronado 59,* 12 December 1953 (US2255964!). **Dept. Huila:** along mule Trail from Garzón SE, about 15 km to Estrella (finca), *E.L. Little Jr. 9328,* 31 January 1945 (US2419451!); Cordillera Oriental, vertiente occidental, bosques más arriba de Guadalupe en Resina, *E. Pérez Arbelaiez & J. Cuatrecasas 8369,* 20 March 1940 (US1850662!; US1850663!); Macizo colombiano; Hoya del Magdalena, San Agustín, K. 17 carretera a Santa Rosa, "La Candela", *Idrobo et al 2878,* 27 August 1958 (NY!); Resinas near Altamira, *T. Plowman 2231*, 20 January 1969 (P01623219!); ridge s. of Quebrada Cascajosa, 9 km. e.s.e. of Garzón above Finca los Cedros. Cordillera oriental, *F.R. Fosberg 1982,* 31 January 1943 (US2203883!). **Dept. Monserrat:** Santa Marta, *H.H. Smith 1076,* 1898 (US0601013!). **Dept. Nariño:** above pueblo of Miraflores, Volcán de Cumbal, vía Laguna Bolsa, *J.J. Ewan 16147,* 11 August 1944 (UC1077824! Photo; US2254229!; US2254230!); Cordillera Oriental, Headwaters of Río Guapuscal, above pueblo of Caballo Rucio, *J.A. Ewan 16558,* 5 December 1944 (US2254361!); Ricaurte, sobre el sendero del la Posada al sitio de estudio de borde de bosque, *P. Sánchez Baracaldo 40,* 22 June 1995 (UC1606865! Photo). **Dept. Putumayo:** Comisaría del Putumayo, vertiente oriental de la Cordillera, *J. Cuatrecasas 1140,* 29 December 1940 (US1851928!); Comisaria of Putumayo, Cordillera Oriental (E. slope), 3 km E. of El Cano, Laguna de la Cocha basin, *J.A. Ewan 16662,* 5 January 1945 (US2254390!; US2254391!); Comisaria of Putumayo, Cordillera Oriental (E. slope), upper Río Mocoa drainage, on the Trail from San Francisco to Sachamate, *J.A. Ewan*

16674, 6 January 1945 (US2254400!); Municipio de San Miguel de Agreda de Mocoa, carretera Mocoa, San Francisco (Valle del Sibundoy). *W. Rodriguez et al 7994*, 26 October 2013 (NY01487514!); Paramo de San Antonio, road from Pasio of Sibundoy, *R.E. Schultes & I. Cabrera 18873*, 13 March 1955 (US2136902!). **Dept. Quindío:** Bosque Quindío, *E. André 2216*, 10 March 1876 (NY!); *ibidem*, *E. André 2382*, March 1876 (NY!, 2 sheets); Quindío Pass, 35 km. West of Ibague on road to Armenia, *R.M Tryon & A.F. Tryon 6015*, 7 October 1961 (P01662902!). **Dept. Santander:** between Piedecuesta and Las Vegas, Eastern Cordillera, *E.P. Killip & A.C. Smith 15490*, 19–24 December 1926 (US1351363!); norte de Santander, Eastern Cordillera, Vicinity of Toledo, *E.P. Killip & A.C. Smith 20519*, 3–11 March 1927 (US1355549!); western slope of Páramo Rico, *E.P. Killip & A.C. Smith 17363*, 15–19 January 1927 (US1353299!); Vicinity of Vetas, *E.P. Killip & A.C. Smith 17383*, 16 January 1927 (US1352992!); Vicinity of Vetas, Eastern Cordillera, *E.P. Killip & A.C. Smith 17891*, 16–20 January 1927 (US1353404!; US1353405!). **Dept. Tolima:** along Quindio Highway, between Cajamarca and summit of Divide, *E.P. Killip & Guillermo Varela 34570*, 27–28 March 1939 (US1772561!; US1772562!); Cordillera Central, La Línea, Cerro El Campanario, *J. Cuatrecasas & R. Echverry 27676*, 4 March 1969 (US2651397!); Quindio Pass, 35 km, west of Ibague on road to Armenia, *R.M. Tryon & A.F. Tryon 6015*, 7 October 1961 (US2722291!). **Dept. Valle:** Cordillera Central, vertiente occidental, Hoya del río, Bugalagrande, Barragán, Quebrada de la Chorrera, *J. Cuatrecasas 20990*, 22 April 1946 (US2018958!); Cordillera Central, vertiente oriental, Hoya del río Cali, Pichindé, Alto de las Brisas, *J. Cuatrecasas 18289*, 27 October 1944 (US1918285!; US1918286!; US1918287!); Cordillera Occidental, Hoya del río Albán, Quebrada Robada, Alto Bonito, *J. Cuatrecasas 22380*, 21 October 1946 (US2019025!; US2019026!); La Cumbre, Cordillera occidental, *E.P. Killip 5709*, 14–19 May 1922 (US1144348!); Prov. El Valle, *F.E. Dryander 1044*, January 1931 (US1594250!); *ibidem*, *F.E. Dryander 1045*, January 1931 (US1594251!); San Antonio (Cerro La Horqueta), Cordillera Occidental, vertiente oriental, *F.A. Silverstone-Sopkin et al. 3622*, 28 February 1968 (UC1565367! Photo; UC1565368! Photo); San Antonio, esto f Cali, near Summit of Cordillera Occidental, *E.P. Killip & H. García 33647*, 26 February to 2 March 1939 (US1772477!; US1772478!; US1772479!). **Unknown Department:** *H. Smith 1076*, no date (P01410484!; P01466417!); *H. Smith 1092*, 1898–1901 (P014664112!); *J.C. Mutis 3112*, no date (US1563575!); *Karsten 25*, no date (B200030107!, syntype of *Lomaria arborescens*;

B200030108!, syntype of *Lomaria arborescens*); *Karsten 58*, no date (B200030107!, syntype). *Moritz 1156,* no date (P01396000!); Cruz Verde, *Apollinaire & Arthur 23,* November 1913 (US0603080!). **ECUADOR. Prov. Azuay:** the Eastern Cordillera, 1–8 km north of the village of Sevilla de Oro, *W.H. Camp 4276,* 27 July 1945 (NY!, 2 sheets, US2080230!; US2080231!). **Prov. Bolivar:** *O. Haught 3300,* 3 May 1992 (US1708246!; US1708247!); road above Balzapamba, *O. Haught 3333*, 3 May 1942 (P01389552!); San Miguel, Along Guaranda-Babahoyo road, from 2 km west of Las Guardias, wotking westward, *A. Fay et al 4617,* 8 July 1995 (NY!); *ibidem, A. Fay & L. Fay 4623,* 8 July 1995 (UC1742418! Photo). **Prov. Carchi:** Montufar Cantón, Within 3 km of the pueblo of Colonia Huaqueña, *A. Fay & L. Fay 4296,* 26 June 1994 (NY!, 2 sheets); *ibidem, A. Fay & L. Fay 4297,* 26 June 1994 (NY!); *ibidem, A. Fay & L. Fay 4310,* 26 June 1994 (NY!); Tulcan Cantón, Turfino, 18 km west of Tulcan, within 1 km of town center, *A. Fay & L. Fay 4266*, 13 August 1993 (NY!, 2 sheets). **Prov. Chimborazo:** along ravine in mountains between Banos and Riobamba, *D.S. Correll E321,* 12 March 1958 (US2256312!); Riobamba, *Rimbach s.n.,* no date (US1197093!). **Prov. Cotopaxi:** Cantón Sigchos, entre Rio Escaleras y zona Escaleras, *J. Ramos et al 6142*, 17 July 2003 (UC1792399! Photo); Cantón Sigchos, finca del señor Marco Silio, *J.Ramos et al 6504*, 24 July 2003 (NY04187096); km 78 Quevedo-Latacunga, *C.P. Dodson & W.P. Clendenin 1066,* 9 May 1981 (US2977954!); Vu uilv. Suband occid. Vulc. Corazón, *Sodiro s.n.*, December 1907 (US1196742!). **Prov. Imbabura:** Lago San Marcos, Cayambe, *K.N.Y. Wash et al 5461,* 2 December 1961 (US2421260!); *ibidem, P.C.D. Cazalet & T.D. Pennington 5461,* 2 December 1961 (NY!, 2 sheets; US2421261!). **Prov. Loja:** Five km east of Vilcabamba, on Rio Yambala or hills above it, *A. Fay & L. Fay 4503*, 27 July 1994 (NY!); Zamora–Huaico (SE, Loja), *R. Espinosa 2273,* 15 December 1947 (US2018298!). **Prov. Napo:** Quijos Cantó.n, within 5 km of the town Baeza, *A. Fay & L. Fay 3844*, 8 May 1992 (NY!); San Francisco de Borja, *G.L. Sobel & J. Strudwick 2400*, July 1980 (NY!). **Prov. Pastaza:** 5 km NW de Mera, *N. Trushell 1104,* 16 March 1985 (NY02065294!; NY02065295!); Mera, *Schimpff 673,* 31 January 1934 (US1740117!); Pastaza Canton, South-east of Puyo ca. 1 km, toward Indian village, then southwest. Los Angeles area, *A. Fay & L. Fay 3701,* 19 July 1992 (NY!). **Prov. Pichincha:** *A. Mille s.n.,* no date (P01546382!; P01546385!; P01546386!); *A. Sodiro s.n.,* no date (P01546362!); *A. Sodiro s.n.,* July 1907 (P01546352!; P01546354!); *L. Sodiro s.n.,* 04.1974 (P01546351!); Andes of Quito, *Sodiro s.n.,* no date (US050828!); *ibidem*

(US050829!); Dos Puentes, *Liebmnn s.n.,* no date (P01409537!); *ibidem* (P01409538!); In reg. interand. et sglv. suband. Prope Quito ad Cotocollao, *L. Mille s.n.,* no date (US1192015!); Quito Cantón, Bellavista Lodge, next to Mindo, Nambillo Reserce, ca. 10 km S of Tandayapa, *J.L. Clark et al 3437,* 3 December 1996 (NY!; UC1744707! Photo); Quito, Cordillera Central, quebrada above Quinta Miraflores, *J.A. Ewan 16469,* 12 November 1944 (US2254325!); Quito-Santo Domingo via Chiriboga (old road), *C.P. Dodson & W.P. Clendenin 10901,* 15 May 1981 (US2977878!); Quito, Tichimancho, *Börtzkes 19856,* 1897 (P01396002!; P01396003!); San Francisco de Borja, *G.L. Sobel & J. Strudwick 2400,* July 1980 (US3249513!); Vicinity of Quito, *L.R. Holdridge 1520,* 26 February 1943 (US1833988!). **Prov. Tungurahua:** *A. Sodiro s.n.,* August 1901 (P01546357!; P01546358!; P01546361!); *ibidem*, 07.1907 (P01546355!); Baños Canton, On trail south from 'La Cruz', above and south-east of town of Baños, *A. Fay & L. Fay 3495,* 1 July 1992 (NY!); Baños Cantón, Rio Verde, on hillside above road, east of town, *A. Fay & L. Fay 3560,* 8 July 1992 (NY!);Río Manoto, Had. San Francisco, *C.W. Penland & R.H. Summers 267,* 24 March 1939 (US1779097!). **Prov. Zamora Chinchipe:** Bombuscaro, Podocarpus National Park, Matrix plot, Mirador M1, *M. Lehnert 2574,* 13 October 2011 (VT198660!); Parque Nacional Podocarpus, Reserva Biologica San Francisco, T2, along trail, below plot A4, *M. Lehnert 2457,* 27 January 2011 (VT198662!); road between Loja & Zamora ca. km 16–18, *J.L. Luteyn et al 6579,* 31 December 1978 (US2902082!); within 3 km of the town of Zamora, *A. Fay & L. Fay 4350,* 7 July 1994 (NY!). **Unknown Province:** *A. Sodiro s.n.,* no date (P01557686!); *ibidem* (P01557687!); *ibidem* (P01557688!); *ibidem* (US2786104!); *A. Sodiro 20,* no date (NY!); *J. Verleysen s.n.,* no date (P01546359!); *ibidem* (P01546371!); *ibidem* (P01546372!); *Rimbach s.n.,* (P01546356!); *S.J. Verleysen s.n.,* no date (US2786110!); *ibidem* (US2786114!); *ibidem* (US2786122!); a reg. subtrop. Ad andinam ad Balza, *A. Mille 759,* no date (US1120470!); Vulc. Alacatzo, *Sodiro 20380,* 07.1807 (US2550369!). **PARAGUAY. Dept. Cordillera:** Valenzuela, *B. Balansa s.n.,* 1883 (P01546451!; UC934815! Photo). **Unknown area:** *no collector 6368,* no date (NY!). **PERU. Dept. Amazonas:** Bagua District, along road from Chiriaco towards Bagua, *H. van der Werff et al 16269,* 20 March 2001 (NY!; UC1778060! Photo); Campo Seis, between Bagua and Imacita, *H. van der Werff et al 14467,* 7 March 1998 (NY04187097!; UC1728866! Photo). **Dept. Cajamarca:** Prov. Chota, Laguna Yahuarcocha (arriba de Incahuasi), *D. Skillman et al. 12893,* 14 September 1985 (NY!, 2 sheets); Prov. Contumaza, Bosque de

Cachil, *A. Sagastegui 14863*, 25 December 1992 (NY!). **Dept. Cusco:** Cusco, La Convención, Dist. Huayopata, Huyro, Calquiña, *E. Bonino et al 767*, 27 June 2003 (NY! 2 sheets); Cusco, Paucartambo Province, Cusco, Wariquichas DD, *B.R. Chambi et al 311*, 4 July 2006 (NY!, 2 sheets); Cusco, Santa Isabel, Valle Cosuipata, *R. Sconlnik 931*, 23-31 July 1948 (US2083017!; US2083018!); Urubamba Valley, *O.F. Cook & G.B. Gilbert 1117*, 7 June 1915 (US604363!); Valle de Pillahuate, Prov. de Paucartambo, *F.L. Herrera 1618*, February 1928 (US1343829!). **Dept. Huánuco:** 10 km S of Chinchao on Tingo María – Huánuco road, *A. Gentry et al 19293*, 13 April 1977 (NY!); Distr. Churubamba, Hacienda Mercedes, Balsa-plays, above Río Cayumba, *Y. Mexia 8174*, 11 September 1936 (NY!; UC644737! Photo; US1706675!). **Dept. Junin:** Concepción, *J. Dombey s.n.*, 1811 (Herb. Jussieu 1368; P00307042!, lectotype; P00627581!, isolectotype; P01466404!, isolectotype; BM000769804! photo, isolectotype); Mito, San Juan, *Macbride & Featherstone 1522*, 8-22 July 1922 (US1121905!). **Dept. Loreto:** Pumayacu, between Balsapuerto and Moyobamba, *G. Klug 3243*, August-September 1933 (NY!; US1457626!). **Dept. Pasco:** Oxapampa, along road Chatarra-Pto. Bermudez, *H. van der Werff et al. 18175*, 9 July 2003 (NY!); *ibidem, H. van der Werff et al. 18201*, 9 July 2003 (NY!); Oxapampa, Chacos, *H. van der Werff et al. 17690*, 22 June 2003 (UC1791016! Photo; UC1791017! Photo); Oxapampa, Prov. Chontabamba valley, 23 km west of Oxapampa, *D.N. Smith & J. Canne 5883*, 26 January 1984 (NY!, 2 sheets); Oxapampa, Santa Clara, Sector Grapanazu, *H. van der Werff et al 20226*, 18 May 2005 (NY!). **Dept. San Martín:** Dist. Huallaga, Valley of Río Apisoncho, 30 km above Jucusbamba, *A.C. Hamilton & P.M. Holligan 916*, 9 September 1965 (US2994818!). **Unknown Department:** *J. Soukup 5015*, 30 July 1963 (US2425139!); *Pópping s.n.*, no date (P01546446!); *Pópping s.n.*, no date (P01546447!); *Pópping s.n.*, 1829 (NY!); *Pópping 138*, no date (NY!). **URUGUAY. Dept. Cerro Largo:** *Lhecharaleti 466*, 01.1875 (P01395993!). **Dept. Montevideo:** Canalones, *Fruchard s.n.*, March 1867 (P01546452!); Montevideo, *no collector*, no date (P01410485!). **Dept. Riviera-Frontera:** Loc. Dict. Livramento, *W.G. Herter 1641a*, 20-23 September 1937 (NY!); *ibidem, W.G. Herter 1641b*, 20-23 September 1937. **VENEZUELA. Amazonas:** Cerro de la Neblina, 5.1 km. NE Pico Phelps (=Neblina) (21.5 km. E Neblina Base Camp), *D. Bell 368*, 30 November 1984 (NY02730077!); Sierra Parima, vecindades de Simarawochi, Rio Matacuni, a unos 6-7 km de la frontera Venezolana-Brasilera, *J.A. Steyermark 107151*, 18 April – 23 May 1973 (NY!). **Caracas:** *M. Linden 123*, 1842

(P01466408!); *O. Kuntze 1654*, 20 May 1874 (NY!). **Aragua:** Cordillera de la Costa, Serrania del Litoral, Monumento Natural Pico Codazzi, 4 km al SO-O (en línea recta) del centro de la Colonia Tovar en la Carretera Los Anaucos, 1,5-2 km de la intersección con la carretera Colonia Tovar-La Victoria, cerca del Peñón de Gabante, *J. Mostacero et al 468*, 8 February 2000 (UC1746808! Photo). **Bolivar:** Cabeceras de Río Chicanán, 80 km (en línea recta) al suroeste de El Dorado, *J.A. Steyermark 89586*, 28 August 1961 (US2419607!); Chimantá Massif, Torono–tepui, *J.A. Steyermark & J.J. Wurdack 961*, 20 February 1955 (US2200327!; US2200328!); Gran Sabana, 5 km south of San Ignacio de Yuruani, *F. Ortega & B. Stergios 1529*, 28 September 1982 (NY!, 2 sheets); Meseta de Jaua, Cerro Jáua, Cumbre de la porción Central–Occidental de la Meseta, 36 millas nauticas o 60 km noroeste de la misión de Campamento de Sanidad del Río Kanarakuni; *J.A. Steyermark 98166*, 22-27 March 1967 (US2571318A!; US2571319A!); Río Chicanán, Sierra de Lema, *J.A. Steyemark 89586*, 28 August 1961 (US2414060!). **Guaira:** Galipan, *Moritz* 300, no date (B200030109!, syntype of *Lomaria arborescens*); **Mérida:** *Moritz s.n.*, no date (B200030114!; B200030115!); *Moritz 116*, no date (P01546424!); *Moritz 299*, no date (B200030106!, syntype of *Lomaria arborescens*; US2456199!, syntype of *Lomaria arborescens*); *Moritz 300*, no date (P00627570!, syntype of *Lomaria arborescens*; P00627571!, syntype of *Lomaria arborescens*; P00627572!, syntype of *Lomaria arborescens*; P01466410!, syntype of *Lomaria arborescens*; P01466420!, syntype of *Lomaria arborescens*). Dtto. Campo Elías. Bosque La Carbonera, *A. Fernandez & B. Bracamonte 75*, 24 October 1981 (NY!); hautes Andes de Truxillo et de Merida, *M. Linden 523*, 1842 (P01466423!). **Tachira:** Distr. Uribante, ±3 km outside Siberia on road to Pegonero, *H. van der Werff & A. González 5361*, 11 July 1983 (NY!). **Trujillo:** Dept. Boconó, Parque Nacional Guaramacal, *L.J. Dorr et al 8309*, 27 October 1998 (UC1735033! Photo); entre El Batatal y Boca de Monte, *F. Ortega & B. Stergios 1529*, 28 September 1982 (NY!, 2 sheets); Mpio. Boconó, Parque Nacional Guaramacal, slope forests od El Pumar, SE of Boconó, *L.J. Dorr et al 8637*, 26 December 2000 (UC1750275! Photo); Parque Nacional Guaramacal, Fila de Agua Fria, *B. Stergios & L. Zambrano 15584*, January-February 1996 (UC1735031! Photo); *ibidem, B. Stergios & L. Zambrano 17683*, January-February 1996 (UC1735031! Photo). **Unknown State:** *A. Fendler 119*, 1854 (NY!; P01410483!); *A. Fendler 283*, 1854 (NY!); *Luerfsen s.n.*, no date (P01623230!); Sarvén–tepui, *J.J. Wurdack 34119*, 13 January 1952 (US2359245!;

US2359246!). **WITHOUT LOCATION.** *no collector*, no date (P01546396!); *ibidem* (P01546427!); *A.N. Devaux s.n.*, no date (P01409519!).

Parablechnum dilatatum (Brause) Gasper & Salino, Phytotaxa 275(3): 216. 2016

Basionym – *Blechnum decorum* var. *dilatatum* Brause, Bot. Jahrb. Syst. 56: 157. 1921 (sub. '*dilatata'*).

Type – Nordostl. Neu–Guinea: Kaiserin–Augusta–FluB (Sepik–)Gebiet, *Ledermann 11168*, 1 August 1913 (holotype B200030881-2!),

Synonyms –

≡*Blechnum dilatatum* (Brause) T.C.Chambers & P.A.Farrant, Blumea 46: 292. 2001.

Vernacular names – Iobion (Tomba), wongare (Enga) (Chambers & Farrant, 2001).

Description – *plants* terrestrial; *rhizome* short creeping and sometimes forming a stout, erect stem, with linear, narrowly elliptic or triangular scales, 1.6 × 0.4 cm, entire, brown to reddish brown, tending to bicolorous, sometimes shiny; *fronds* dimorphic; *sterile fronds* 80–200 × 12–44 cm; *petioles* 10–120 × 2.5 cm, about twice the length of the lamina, smooth, brown, light brown or beige when dry, densely scaly, scales linear to narrowly elliptic or triangular, acuminate, 1.3–2.5 × 0.15–0.3 cm, almost entire, with some outgrowths, brown to bright reddish-brown, sometimes tending to bicolorous with lighter margins; *lamina* ovate-deltoid, 1-pinnate, similar colour adaxial and abaxially, young fronds reddish; *rachis* brown, green or light beige, with scales 0.2–0.7 × 0.5–2 mm, irregular, linear, narrowly elliptic or triangular, light whitish or brownish, sometimes darker at attachment, deciduous; *sterile pinnae* in 14–32 pairs, oblong-elliptic, base rounded, apex acuminate, margins straight, wavy, serrulate, more denticulate towards the apex, 5–22 × 0.8–2 cm, stalked, becoming basiscopically adnate towards the apex, basal pinnae only slightly reduced, the lower ones slightly inflexed, terminal pinna slightly longer than subterminal pinnae; *costae* similar to the rachis, scales similar to those on the rachis but smaller, adaxially grooved and abaxially prominent, without ornamentation; *veins* free, simple or 1-furcate, catadromous; *aerophores* tuberculate, dark brown; *hydathodes* rounded or ovate; *fertile fronds* about the same size as sterile fronds; *petioles* longer than lamina, *fertile pinnae* linear, 11–22 × 0.2–0.7 cm, stalked, with an expanded

sterile region, base cordate, the proximal pinnae with a sterile zone no wider than the base of the sterile pinnae; *sori* linear, continuous, forming coenosori on both sides of the costa, covering the lower part of the fertile pinnae except in the sterile region of the apices and at base of proximal pinnae; *indusia* linear, continuous, opening on both sides of costa, dark, lacerate; *sporangia* intermingled with atropurpureous paraphyses, longer than these, similar in appearance to sporangial pedicels; *spores* monolete, flat-convex in equatorial view, elliptic in polar view, 77 × 59.7 µm, perispores muricate, forming a reticulum, walls broad, low and rounded, surface smooth, scabrous or microrreticulate, exospores smooth to scabrous (**Figure 45**).

References – Chambers & Farrant (2001).

Chromosome number – unknown.

Distribution and habitat – endemic to Papua New Guinea. In fully sunny to semi–shaded areas, in reed swamps withstanding water, growing among tall clumps of sedges, anthropogenic grasslands resulting from shifting cultivation and fire; occasionally occurs in submontane grassland thickets and, more rarely, in rainforest on mountain ridges, 1,500–2,700 m. (Chambers & Farrant, 2001).

Etymology – the epithet refers to the lamina which is considerably wider than those of related species such as *Parablechnum hieronymi* (Chambers & Farrant, 2001).

Notes – following the review of various collections and types by Chambers & Farrant (2001) it was concluded that *Blechnum decorum* var. *dilatatum*, basionym of this species, is not closely related to *Parablechnum decorum*. In fact, the latter was narrowed down as a synonym of *P. hieronymi*.

Parablechnum dilatatum consistently possesses a clear petiole and rachis and usually much longer fronds and broader lamina than those in *P. hieronymi*. Another species that may be related to *P. dilatatum* is *P. nesophilum*, which seems to replace *P. dilatatum* in the mountain ranges of the Admiralty Islands, New Britain, and New Ireland. They differ in numerous details such as the presence of sporangiasters in *P. nesophilum* instead of paraphyses (Molino *et al*., 2021). Specimens collected from woodland habitats have thinner pinnae, more widely spaced on the rachis, and may appear at first glance to be different plants when compared to plants collected from open meadows and marshes.

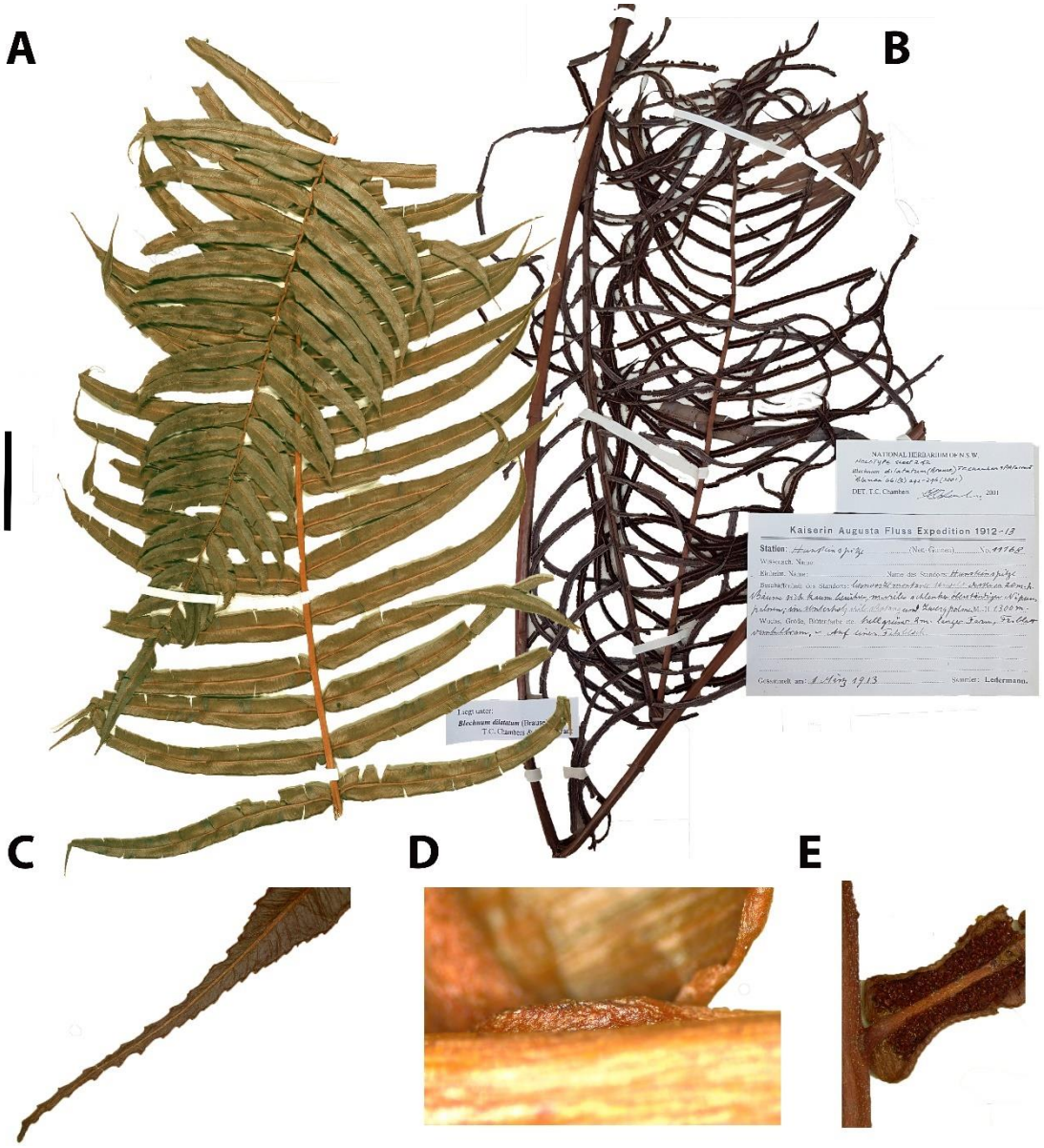

Figure 45. *Parablechnum dilatatum.* A. Fragment of a sterile frond; B. Fertile frond; C. Sterile pinnae apex, abaxial side; D. Aerophore; E. Fertile pinnae base, abaxial side. (A,C&D: *C. Ledermann 11168,* B200030881, syntype; B&E: *C. Ledermann 11168,* B200030881, syntype). Scale: 5 cm in A&B; 7 mm in C; 1.4 mm in D; 7.3 mm in E.

Plants from exposed habitats usually have thicker, leathery pinnae, usually crowding and overlapping the rachis; fresh specimens are brighter green on the upper surface of the lamina and lighter green below. Juvenile plants of *P. dilatatum* usually have 6–10 small fronds 5–10 cm long with 1–3 pairs of short, rounded pinnae 1 cm long, with a terminal pinna 2–2.5 cm long and narrowly elliptic, acuminate to attenuate. Several intermediates indicate a continuous gradient towards large mature plants. Intermediates 25–40 cm tall and with 6–10 pairs of pinnae usually produce fertile fronds, basal pinnae usually have a

wider sterile zone contiguous to the rachis while pinnae towards the apex may possess a small decurrent sterile zone; closer to the apex pinnae have no sterile zone; the terminal pinna on fertile and sterile fronds is 10 or more cm long, which is twice as long as the lateral pinnae. (Chambers & Farrant, 2001).

Reviewed material:

PAPUA NUEVA GUINEA. *Ledermann 11168*, 1 March 1913 (B200030881!, syntype); *Ibidem* (B200030882!, syntype)

Parablechnum falciforme (Liebm.) Gasper & Salino, Phytotaxa 275(3): 216. 2016

Basionym – *Lomaria falciformis* Liebm., Kongel. Danske Vidensk. Selsk. Skr., Naturvidensk. Math. Afd., ser. 5, 1: 234. 1849.

Type – México, *Liebmann 2343* (lectotype: C n.s., designated by Smith, 1981; isolectotypes: B200031041!; BM00769807! photo, P00627589!).

Synonyms –

≡*Blechnum falciforme* (Liebm.) C.Chr., Index Filic. 154. 1905. *Struthiopteris falciformis* (Liebm.) Broadh. Bull. Torrey Bot. Club 39: 365. 1912.
=*Lomaria deflexa* Liebm. Vid. Selsk. Skr. V. 1: 234. 1849. nom. invalid. type – México, Oaxaca, between Totontepec & Trapiche de la Concepción, *Liebmann 770*, no date (holotype: C n.v.; isotypes: UC v.f.; US1406165!).
=*Lomaria spissa* H. Christ. Bull. Boiss. II. 4: 1902. 1904. nom. invalid. type– Costa Rica, *C. Weckle s.n.*, no date (syntypes: P01623169–70!).
=*Blechnum christii* C.Chr., Index Filic. 152. 1905 – type: Costa Rica, *Braveas 143* (holotype: US0600721!); ≡*Struthiopteris christii* (C. Chr.) Broadh. Bull. Torrey Bot. Club 39: 361. 1912; ≡*Parablechnum christii* (C.Chr.) Gasper & Salino, Phytotaxa 275(3): 191–227. 2016.

Description – *plant* terrestrial; *rhizome* erect, non-stoloniferous, with scales 4–25 × 1–4 mm, lanceolate to ovate–lanceolate, orange-brown to blackish, entire; *fronds* dimorphic; *sterile fronds* with *petiole* 30–80 cm, yellowish-brown or straw–brown, densely scaly to glabrescent on both surfaces, scales deciduous, varying from straw, chestnut to reddish–ochre similar in shape to those of rhizome; *lamina* to 37–150 × 18–50 cm, 1-pinnate, oblong, truncate at base, gradually reduced towards apex, with a conform terminal pinna, scaly or glabrescent on underside, with small, arachnoid, membranaceous, brownish, scales, membranaceous to herbaceous laminar tissue; *rachis* straw-coloured, papillose, densely scaly or glabrescent, scales similar to those of the

petiole; *sterile pinnae* in 13–35 pairs, 10–23 × 1–2.5 cm, linear-lanceolate, falcate, bases cordate, slightly asymmetric, apices acuminate, margins flattened or only slightly and irregularly involuting, strongly serrate, teeth often curved, cartilaginous, tapering slightly towards apex, shortly stalked, becoming basiscopically adnate distally; *costae* similar to the rachis, grooved adaxially, prominent abaxially, papillose, densely scaly or glabrescent; *veins* free, simple or 1-furcate, catadromous; *aerophores* low, rounded, oblong, very dark, with stomata forming white dots; *hydathodes* brownish ovate; *fertile fronds* longer and more erect, 0. 5–1 m; *petiole* 30–50 cm, straw-coloured or brown; *fertile pinnae* narrow, linear, cordate base and acuminate apex 10–22 × 0.3–0. 6 cm; *sori* linear, continuous, forming coenosori on both sides of the costa, covering the lower part of the fertile pinnae except for an apical region; *indusium* linear, continuous, opening on both sides of costa, dark, lacerate dark brown; *sporangia*, with arc of 21–23 cells; *spores* monolete, (43–)56(–67) × (34–)42(–52) μm, with crested–reticulate perispores delimiting small polygonal areoles, up to 10 μm, with scattered filaments in areole gaps, interior of perispores spongy, exospore smooth or slightly rough (**Figure 46**).

References – Broadhurst (1912b), Moran (1995a), Passarelli *et al.* (2010).

Chromosome number – unknown.

Distribution and habitat – México, El Salvador, Costa Rica, Guatemala, Honduras, Panamá, Colombia and Ecuador. Cloud forests, 1100–3200 m (Moran, 1995a).

Notes – authors have suggested that this taxon may be conspecific with *Parablechnum schiedeanum* (Moran, 1995a). However, palynological studies suggest that they are different species (Wal *et al*., 2021). It is easily distinguished from this species by its serrate margins as opposed to the smooth margins of *P. schiedeanum*.

It has been compared to the taxon *Parablechnum christii* and is usually separated from it in floras by the number of pinnae, that of *P. falciforme* being 13 or more and that of *P. christii* 10 or less (Moran, 1995a). However, after reviewing the nomenclatural history of *P. christii* we consider it to be a synonym. The basionym of this taxon, *Blechnum christii*, was proposed Christensen for a species previously described by Christ as *Lomaria spissa*, a name that is invalid, as there was already an African plant with that name described by Feé (Broadhurst, 1912b). We have found the holotypes of both names, *Lomaria spissa* (**Figure 47A-B**) and *Blechnum christii* (**Figure 47C**), which were unannotated as such at

P and US, respectively. The number of pinnae on these individuals is that normally assigned to *P. falciforme* in floras. We have concluded that this is not a constant or reliable character, and that specimens with less than 10 pairs of pinnae are probably actually small *P. falciforme* specimens, as we have not found any further differences after checking individuals under both names. As the basionym of *Parablechnum falciforme* was proposed before the one for *Parablechnum christii*, we have decided to consider *Parablechnum christii* a synonym of it.

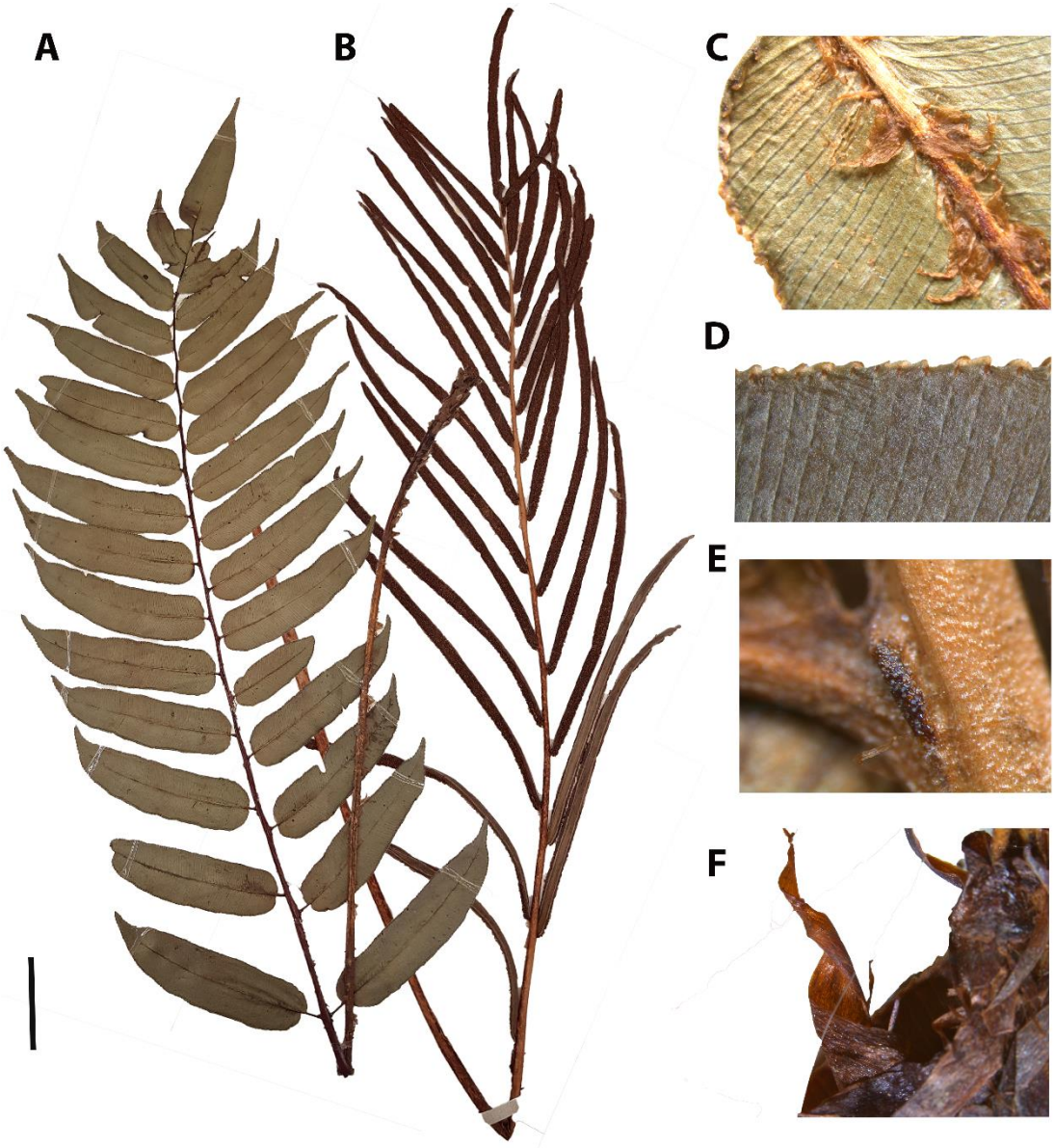

Figure 46. *Parablechnum falciforme.* A. Sterile frond; B. Fertile frond; C. Sterile pinna abaxial side; D. Sterile pinna margin, adaxial side; E. Aerophore; F. Rhizome scales. (A: *A.M. Evans et al 26,* US2589677A; B: *H.H. Smith s.n.,* NY; C&E: *J.T. Mickel 989* US420216; D: *Gonzatti & Gonzalez 4* US0371512; F: *J.T. Mickel 1521,* US2550240). Scale: 4 cm in A&B; 3.3 mm in D; 0.7 mm in E; 4 mm in F.

Reviewed material:

COLOMBIA. Dept. Bocaya: Santa María, *H.H. Smith 1076,* 22 August 1898 (NY!, 3 sheets). **Dept. Cauca:** 1.5 km north of El Paramo, betw. Río Ñambi and Río Napi, *J.A. Ewan 16819,* 1 February 1945 (US2254463!); Caanan, Mt. Purace, Cordillera Central, *F.W. Pennell & E.P. Killip 6690*, 11-13 June 1922 (NY!). **Dept. Cundinamarca:** below Alto de Cuchuco, 7 km southwest of Sibate, *R.M. Tryon & A.F. Tryon 6114*, 19 October 1961 (US2722289!). **Dept. el Valle:** Cordillera Occidental, Los Farallones, extremo N, vertiente oriental, Alto Buey, *J. Cuatrecasas 18064*, 13 October 1944 (US1918253!; US1918254!). **Dept. Quindío:** Cordillera Oriental, Buenavista, a small abandoned clearing in the valley of the Río Tigre, on the Colombia–Uribe trail, 26 km e.s.e. of Colombia, Int. Del Meta, *F.R. Fosberg 19539,* December 1942 (US2203858!; US2203859!). **Dept. Santander:** between Piedecuesta and Las Vegas, eastern cordillera, *E.P. Killip & Albert C. Smith 1590*, 19-24 December 1926 (NY!); *ibidem, E.P. Killip & Albert C. Smith 17891,* 16-20 January 1927 (NY!, 2 sheets); Vicinity of Toledo, eastern cordillera, *E.P. Killip & A.C. Smith 20519,* 3-11 March 1927 (NY!). **COSTA RICA. Prov. Alajuela:** around, Summit and old crater lake of Volcán Poás, *J.T. Mickel 2423,* 6 July 1962 (US2589072A!); La Cañada, *C.H. Lankester s.n.,* 6 September 1925 (US1266789!); *ibidem* (US1266790!); Palmia, Canton Alfaro Ruiz, *A. Smith 1409*, 4 January 1939 (NY!); Poás Lake, Volcán Poás, *H.E. Stork 2354,* 3 June 1928 (UC1206727! Photo); Volcán de Poas, *Alfaro 16455*, 1 February 1902 (P01546409!; P01546410!); *ibidem, H.E. Stork 3346,* 29 July1932 (UC1355963! Photo). **Prov. Cartago:** Cerro de la Muerte, "Madre Selva", 24.5 km NW of La Asunción near km 67 on Interamerican highway *D.B. Lellinger 888,* 11 August 1967 (US2589678A!; US2589679A!); entre El Empalme y la Chonta, en km. 54, *A. Jiménez M. 1997*, 17 May 1964 (NY!); N of Irazu, *H.E. Stork 1291,* 27 March 1928 (UC1214980! Photo); ravine at La Pastora, near Irazu Volcano, *H.E. Stock 2375*, 17 May 1928 (US2421758!); Valle de la Estrella, Rio Sombrero between Vara de Roble and Muneco, *H. Churchill 3303,* 29 January 1980 (VT198679!; VT198680!; VT198686!); Volcán Turrialba, *K. Mehltreter 447,* 16 June 1993 (CR187302! Photo); Volcán Turrialba, *Wercklé s.n.,* 1905 (P01579724!). **Prov. Guanacaste:** Liberia, Parque Nacional Guanacaste, sendero casa Frank, entre el cruce a Cerro Cacao y la quebrada, *A. Rojas & G. Araya 7823,* 10 August 2007 (CR263286! Photo); southwestern slopes of Volcán Rincon de la Vieja and Volcan

Santa Maria along the trail from Hda. Guachipelin, *W.C. Burger & R.W. Pohl 7775*, 30 July 1971 (NY!, 2 sheets). **Prov. Heredia:** Braulio Carillo National Park, *E. Hennipman et al 6730,* 6 November 1986 (UC1586645! Photo); ca. 3 km, N of Los Cartagos on the road from Heredia to Vara Blanca, *D.B. Lellinger & J.J. White 964*, 5 July 1970 (US2726510!; US2726512!); along the cart-road from Varablanca (between Poás and Barba volcanoes) to La Concordia, *W.R. Maxon & A.D. Harvey 8386,* 23 July 1923 (US1182006!); N of Heredia, ca. 1 km beyond Porrosati, *D.B. Lellinger & J.J. White 1687*, 18 August 1970 (US3276195!; US3276196!); Varablanca, north slope of the Central Cordillera, *M.A. Chrysler & W.E. Roever s.n.,* 10 July 1940 (US1806146!); *ibidem* (US1806147!); Volcan Barbas, *H. Pittier 1921*, 1890 (NY!). **Prov. Limon:** Cerro Chrripó, *A.M. Evans et al 158,* 25 August 1967 (US2589685A!; US2589686A!). **Prov. Puntarenas:** La Palma, *Lehmann 115,* 5 June 1926 (CR38520! Photo). **Prov. San José:** Alajuelita, San Antonio Z.P. Cerros de Escazú, Cima de cerro Cedral, Estación del Instituto costarricense de Electricidad, *R. Chacón et al. 890,* 2 July 2007 (CR255424! Photo); along Panamerican Highway in the Cordillera de Talamanca, Villa Mills, *C. Weber 6241,* 25 September 1961 (US2722149!); Cantón de Dota, Cordillera de Talamanca, Camino a San Gerardo de Dota. Entrada por Jaboncillo, *A. Rojas 2715,* 16 July 1996 (NY!; UC1618580! Photo); Cantón de Pérez Zeledón, Cuenca Térraba-Sierpe, Estación Cuericí, Sendero a la Piedra, 5 km este de Villa Mills, *B. Gamboa R. 784*, 9 October 1996 (UC1740699! Photo); Cerro Chirripó, lower SW slopes, along trail from Canaan to Summit, *A.M. Evans et al 26*, 21-27 August 1967 (US2589677A!); *ibidem*, *A.M. Evans et al 96*, 28 August 1967 (US2589687A!); Cerro de las Vueltas, *P.C. Standley & J. Valerio 43786,* 1 January 1926 (US1307875!); Dota, Carretera Interamericana, km 66, cerca de 3 km después de La Trinidad, *A. Rojas et al. 10418*, 15 July 2013 (MACB!); Tablazo, *C. Brade 65,* 1 July 1908 (P01410451!; P01410452!); *ibidem, C. Brade 143*, no date (NY!; UC405792! Photo); road from Cartago to San Isidro del General (Pan American Hwy, Rt 2), Km 72-73, or 21-22 km SE of El Empalme, *A.R. Smith & T. Béliz 2090*, 30 January 1986 (CR122741! Photo; UC1522809! Photo; UC1522810! Photo). **Unknown province:** *Maxon s.n.*, no date (NY!). **ECUADOR. Prov. Galapagos Islands:** Mt. Crocker, indefatigable island, *J.T. Howell 9253,* 10 May 1932 (US2256235!). **Prov. Pichincha:** Quito–Santo Domingo via Chirboga (old road) km 82, *C.P. Dodson & W.P. Clendenin 10984,* 17 May 1981 (US2977838!). **Prov. Sucumbíos:** en el camino desde La Bonita hacia La Sofía después de cruzar el primer río grande por un puente, *A.*

Garmendía & P. Jaramillo 181, 16 September 1995 (MA630215!). **EL SALVADOR. Dept. Santa Ana:** Bosque Montecirsto, *R. Seiler 478*, 1 July 1978 (NY!); *ibidem*, *R. Seiler 863*, 1 February 1979 (UC1489960! Photo); Cerro Monte Cristo, ca. 14 miles NE of Metapán, along trail to Punto Trifinio (frontier of El Salvador, Honduras, and Guatemala), *T.B. Croat 42454*, 31 July 1977 (UC1510369! Photo); Cordillera Miramundo, mountan of Montecristo, *A. Molina R. 16759*, 27-31 January 1966 (NY04187117!; NY04187118!; NY!, 2 sheets; US2689336!). **Unknown Department:** *R. Seiler 990*, 28 March 1979 (NY!); Crescit in silv. suband. occid. vale. Cusiguahua, *A. Sodiro s.n.*, August 1901 (US2783459!). **GUATEMALA. Dept. Alta Verapaz:** Río Chió about 2-4 km. SW of Cobán, *L.O. Williams et al 40722*, 31 January – 8 February 1969 (NY!, 2 sheets). **Dept. Chimaltenago:** Chichavac, *A.F. Skutch 77*, 11–12.1930 (US1494381!); Volcano Acatenango, *W.A. Kellerman 6481*, 8 February 1907 (US575493!; US575494!; US575495!); *ibidem*, *W.A. Kellerman 6482*, 8 February 1907 (US575496!). **Dept. Chiquimula:** middle slopes of Montana Norte to El Jutal, on Cerro Brujo, southeast of Concepción de las Minas, *J.A. Steyemark 31004*, 2 November 1939 (US2138012!); *ibidem*, *L.O. Williams & A. Molina R. 12099*, 2 March 1947 (US1919966!). **Dept. Quetzaltenango:** Mun. De Zunil, along dirt road above Aldea Chuimucubal, northwest slopes of Pico Zunil, *T.S. Quedensley 2791*, 3 January 2006 (NY!); Mun. de Zunil, road to Fuentes Georginas, 4 km south of Zunil, northwest slopes of Volcán Zunil, *T.S. Quedensley 692*, 15 May 2004 (UC1797563! Photo) Vicinity of Fuentes Georginas, slopes of Volcán de Zunil, *P.C. Standley 86026*, 3 February 1941 (UC1444357! Photo). **Dept. San Marcos:** Cerro Tumbador, Sierra Madre Mountains, about 15 k, west of San Marcos, *L.O. Williams et al 23057*, 15 December 1962 (US2425331!; US2425337!). **HONDURAS. Dept. Francisco Morazán:** Cerro de Uyuca, *C.V. Morton 7214*, 10-20 March 1951 (US2017120!); *ibidem*, *M.J. Howard 47*, 4 July 1952 (US2081482!); *ibidem*, *M.J. Howard 50*, 4 July 1952 (US2081476!); eastern slopes of Peña Blanca, San Juancito Mountains, *C.V. Morton 7282*, 22 March 1951 (NY!). **Dept. La Paz:** between Florida and El Ceron, 7 km from Marcala, *A. Molina R. 24092*, 6 March 1969 (US3695436!). **Dept. Morazán:** mountains above San Juancito, *E.D. Merril et al 15626*, 22 February 1949 (US2015244!); Mt. Uyuca, *L.O. Williams & A. Molina R. 12083*, 2 March 1947 (US1917549!; US1917550!). **MÉXICO. Chiapas:** *G. Mínch 27*, 1902 (P01623361!; P01623362!); 45-50 km NE of Huixtla along road to Motozintla, Municipio of Motozintla de Mendoza, *D.E. Breedlove & A.R. Smith 22665*,

17 November 1971 (NY!, 2 sheets); Cerro de Boquerón, *C.A. Purpus 6739,* September 1913 (NY!; UC173831! Photo; US464862!; US567096!); east side of Zonthehuitz near summit, Mun. Of San Cristobal de Las Casas, *D.E. Breedlove & A.R. Smith 22050*, 8 November 1971 (NY!, 2 sheets); Gueytepee, *G. Müch 17,* 1902 (US1791665!); Paraje Banabil, Municipio of Tenejapa, *D.E. Breedlove & A.R. Smith 21990*, 7 November 1971 (NY!, 3 sheets); San Juán Chamula, Sak Tzu', *C. Santíz Ruiz 152*, 17 September 1987 (NY!; UC1728332! Photo). **Chihuahua:** E. of Monserrat, *Liebmann s.n.,* 05.1841 (US0474921!). **Guerrero:** Barranco de Chinantla, *Liebmann s.n.*, no date (B200031041, isolectotype); Dist. Mina, Gro., Toro Muerto, *G.B. Hinton 14207,* 1 May 1939 (US1748786!). **Hidalgo:** 11 km al S de Tenango de Doria, sobrre carretera a Metepec, *Rzedowski 30211,* 14 January 1973 (NY!); near Zacualtipán, *M. Martinez 8*, 5 December 1939 (US1790321!); Mpio. De Tenango de Doria, camino de Tenango de Doria a Metepec, a 2 km al S de Tenango, *D.H. Lorence & R. Hernández M. 4943,* 10 November 1985 (NY!). **Jalisco:** Barranca de Chinanila, *F. Liebmann s.n.*, May 1871 (P00627589!). **Mexico:** Dist. of Telmascaltepec, La Sierrita, *G.B. Hinton 3470*, 3 July 1933 (NY!; UC1162741! Photo; US1792099!); *ibidem, G.B. Hinton 6252*, 24 November 1933 (US1792105!). **Nuevo León:** Dist. Galeana, Gro., Teotepec, *G.B. Hinton 14204,* 21 May 1939 (US1748806!). **Oaxaca:** *C. Conzatti & D. González 4*, 1900 (P01623231!); *L.B. de Karwinski s.n.,* 1830 (US2258885!); *ibidem* (US0213046!); along highway 175 through Sierra de juarez between Tuxtepec and Oaxaca, 21.5 miles S of bridge at Valle Nacional, *T.B. Croat 48085,* 20 February 1979 (UC1505460! Photo); between Totontepec & Trapiche de la Concepción *Liebmann 770,* no date (US1406165!, isotype of *Lomaria deflexa*); Cerro de San Felipe, *C. Couzatti & V. González 529,* 14 November 1897 (US327322!); Ixtlan de Juarez, *Krueger & Gillespie 37,* 12 June 1940 (UC1036929! Photo); Mpio. Comaltepec, Loc. Dto. Ixtlán, La Esperanza, 18 km al SW, sendero de la Capilla, *R. Torres Colín et al. 17654,* 24 March 2014 (VT198677!); Cuyamelcalco, Cuicatlan, *G. Aguirre B. 15,* December 1945 (NY!); Distr. Itlán, Cerro de Malacate, N of Capulapan, ca. 8 km E of Ixtlán from 10000 to 7600 ft on NE side of Cerro, *J.T. Mickel & S.W. Leonard 5242,* 5 October 1970 (NY!; UC1496128! Photo); *ibidem, J.T. Mickel & S.W. Leonard 5265*, 5 October 1970 (NY!); Distr. Ixtlán, 2-6 km ne of Natividad on trail from San Pedro Nolasco to the Llano Verde, *J.T. Mickel & L. Pardue 7018,* 5 October 1972 (NY!, 2 sheets); *ibidem*, *J.T. Mickel & R.L. Hellwig 3755,* 4 October 1969 (NY!, 2 sheets; UC1503072! Photo; US3124177!); Distr. Ixtlán, 56 km N of Ixtlán on rte 175,

J.T. Mickel 5599, 25 July 1971 (NY!; UC1496141! Photo; US3124191!); Distr. Ixrlán, 76 km n of Itxtlán de Juárez on Rte 175, 4 km a Esperanza, *J.T. Mickel 7112,* 30 September 1987 (NY!, 2 sheets; UC1503040! Photo); Distr. Ixtlán, Cerro de Malacate, N of Capulapan, ca. 8 km E of Itxtlán from 10000 to 7600 ft on NE side of Cerro, *J.T. Mickel & S.W. Leonard 5241,* 5 October 1970 (NY!); Distr. Ixtlán, Mun. De Comaltepec, S. Comaltepec, *L. López López & G.J. Martin 467,* 15 May 1990 (NY!); Distr. de Ixtlán, Municipio de Santiago Comaltepec, La Esperanza, *R. López Luna 40,* 30 September 1987 (NY!); Distr. Mixes, E slope of Cerro Zempoaltepetl, 2-3 hrs SW of Zacatepec on trail to Tamazulapam, *J.T. Mickel & S.W. Leonard 4871,* 22 September 1970 (NY!; UC1496142! Photo; US3124192!); Distr. Mixes, Mun. De Totontepec, Santiago Amaepec, *W. Ruiz S. 89,* 4 December 1987 (NY!); Distr. Mixe, Municipio Totontepec, Villa de Morelos, Pup jo yup, na payi, *J. Riviera Reyes 2567,* 2 March 1991 (NY!); Distr. Mixes, NW slope of Cerro Zempoaltepetl, trail from Yacoche to Totontepec, *J.T. Mickel & S.W. Leonard 4666,* 19 September 1970 (NY!; UC1503073! Photo); Distr. Mixes, West slope of Cerro Zempoaltepetl to Yacoche, *J.T. Mickel & S.W. Leonard 4607,* 18 September 1970 (NY!); *ibidem, J.T. Mickel & S.W. Leonard 4607,* 18 September 1970 (NY!); Distr. Sola de Vega, Municipio: Santiago Textilán, arriba de las Juntas, *A. Zarate Marcos 638,* 29 September 2006 (NY!); Distr. Teotiltán, 26-29 km NE of Teotitlán del Camino, vicinity of pass at Puerto Soledad, *J.T. Mickel & R.L. Hellwig 4112,* 18 September 1970 (NY!; UC1496143! Photo); Distr. Villa Alta, Moist woods along trail from Yetzelalag toward Lovani, *B. Hallberg 1512,* 2 December 1971 (NY!, 2 sheets); Distr. Villa Alta, valley of the Yelagago River, ca. 20 mi. N e of Villa Alta, *J.T. Micel 989,* 26 July 1962 (US2420216!); Dto. Ixtlán, Sierra Norte, MEX Rt. 175 Oaxaca to Valle Naional, Mun. Comaltepec, El Relampago forest reserve, SW of La Esperanza, *M. Sundue & R. Torres 3463,* 15 April 2013 (VT198682!; VT198683!); Itxtal–Tuxtepec road, 35-39 km south of Valle Nacional, *J.T. Mickel 1521,* 27 July 1964 (NY!; US2550240!); Mpio. Comaltepec, Loc. Dto. Ixtlán, La Esperanza, 18 km al SW, sendero de la Capilla, *R. Torres et al 17654,* 24 March 2014 (VT198684!; VT198685!); Mpio. Oaxaca, *C. Conzatti & A. Gonzalez 4,* 07–08.1900 (US371512!); on the Hwy 175, between Oaxaca and Uxtepec. 11,7 mi south of Villa Hermosa, *K. Torke et al 508,* 15 August 1975 (NY!); Región Sierra Sur, Dto. Juxtlahuaca, Mpio. Coicoyán, Loc. Orilla SW de Coicoyán, *A. de Ávila 701,* 18 August 1989 (NY!); Rancho Tejas, above Ixtlan, *M. Sundue 147,* February 2000 (VT198678!); road fro Oaxaca to Tuxtepec, km 112-127 (94-84 mi. N of Oaxaca), *R.L. Hellwig 317,* 8 July 1967

(NY!); Sierra de Clavellinas, *C.G. Pringle 5599,* 25 October 1895 (VT198687!); Sta. Inés del Monte Zimatlán-Oaxaca, *C. Conzatti 1313,* 8-9 December 1905 (US570910!). **Puebla:** Distr. Galeana, Gro, Loc. Teotepec, *G.B. Hinton 14303,* 21 February 1939 (NY!, 2 sheets). **Sinaloa:** Mun. Mazatlan Villa de Flores, San Pedro de los Encinos, Sierra Mazateca, *X. Munn-Estrada & F. Mendoza 1681*, 22 November 2001 (NY!, 2 sheets). **Veracruz:** Totula, Zacuapan, *C.A. Purpus 4370,* January 1910 (UC150725! Photo; US841495!). **Unknown State:** *Arsène et al s.n.*, no date (P01325531!); *Hye 431*, (P01527644!); *Karumalky 1315*, no date (NY!); *Liebmann 2343* (B200031041!, isolectotypes; P00627589!, isolectotypes; US1406167!, isolectotypes). **NICARAGUA. Dept. Zelaya:** Bluefields, *C.E. Nichols 386,* 11 December 1968 (VT198681!). **PANAMA. Prov. Chiriqui:** El Potrero Camp, Chiriqui Volcano, *W.R. Maxon 5335,* 12 March 1911 (NY!, 2 sheets; US675688!; US675689!; US675690!; US675691!) Dist. De Bugadaba, Alrededores de Las Nubes, *G. Galdames et al 2940,* 17 May 1996 (US3450278!; US3450279!): road to ridge top, near Rual Castro's house, Guadalupe, above Cerro Punta, *J.P. Folsom 6025,* 22 October 1977 (UC1505466! Photo). **UNKNOWN LOCATION:** *B.T. 442*, no date (NY!).

Figure 47. A. Syntype of *Lomaria spissa* (*C. Weckle s.n.,* P01623169); B. Syntype of *Lomaria spissa* (*C. Weckle s.n.*, P01623170); C. Holotype of *Blechnum christii* (*Braveas 143*, US0600721!). Scale: 4 cm.

Parablechnum glaziovii (Christ) Gasper & Salino, Phytotaxa 275(3): 216. 2016

Basionym – *Blechnum glaziovii* Christ, Annuaire Conserv. Jard. Bot. Genève 3: 42. 1899.

Type – Brasil. Rio de Janeiro, Petrópolis, 1885, A.F.M. *Glaziou 15717* (lectotype: P00347404!, designed in Dittrich *et al.* 2018); Isolectotypes: MACB!; P00347401-3!, BM000769809! photo, K000633399! photo, RB00543443! photo).

Description – *plants* saxicolous, rarely terrestrial; *rhizomes* erect, scaly, with narrowly triangular, brown, concolorous scales, 12–13 × 1.5–2.6 mm, margins entire or slightly dentate; *fronds* dimorphic; *sterile fronds* 24–67 cm long; *petioles* atropurpureous to straw-coloured, scales at base similar to those of rhizome, distally similar to those of rachis, 10.1–12.2 × 0.13–0.26 cm; *lamina* ovate, truncate at base and gradually reducing towards apex, with in a terminal conform pinna 12–27 × 9.4–16 cm, 1-pinnate, papyraceous to coriaceous; *rachis* straw-coloured with atropurpureous spots, grooved adaxially, prominent abaxially, glabrous or, especially at the insertion of the pinnae, with a few narrowly triangular scales with expanded or linear bases, with filiform apex, brown, concolorous, membranaceous, margins entire or with long projections; *sterile pinnae* in 2–14 pairs, 6.1–10 × 1.3–1.7 cm, strongly to slightly ascending, rarely patent, stalked, lanceolate, margins entire or serrulate, flat or slightly revolute, apices acute to acuminate, bases cuneate; *costa* adaxially grooved, abaxially prominent, with slightly granular ornamentation, glabrous adaxially, glabrous abaxially or with brownish, concolorous scales, with expanded bases and filiform apices; *veins* free, simple or 1-furcate, catadromous, with minute, almost filiform scales, with long lateral expansions, with or without scattered multicellular hairs on lamina between veins; *aerophores* absent or slightly developed; *hydathodes* rounded, whitish; *fertile fronds* shorter or longer than sterile ones; *petioles* 16–30 cm long; *lamina* 11–16 × 8, 3–10 cm, broadly ovate, truncate at base, *fertile pinnae* 65–88 × 2.1–3 mm, linear, narrowly contracted; *sori* linear, continuous, forming coenosori on both sides of costa, covering the entire pinna; *indusium* linear, continuous, open towards costa, brownish, entire or lacerate at maturity; *sporangia* with (16) 24 (30) arch cells; *spores* monolete, (24) 52 (92) × (16) 37 (70) µm, perispores smooth, with low, thin, tapering walls, forming small polygonal areoles or reticules, with moderately abundant filamentous processes (**Figure 48**).

References – Dittrich *et al*. (2018, 2020).

Chromosome number – unknown.

Distribution and habitat – according to Dittrich *et al*. (2018) this species is endemic to Brazil, in the southeast of the country. However, we have also found specimens from Paraguay (P01530996). Specimens of this species grow on rocks and sometimes on the ground, in mountainous areas bordering streams, in well–lit places, between 800–2060 m, in high altitude fields or rock fields and riparian forests and tropical rainfor It is considered a relatively common, non-threatened species. (Dittrich *et al*., 2018, 2020).

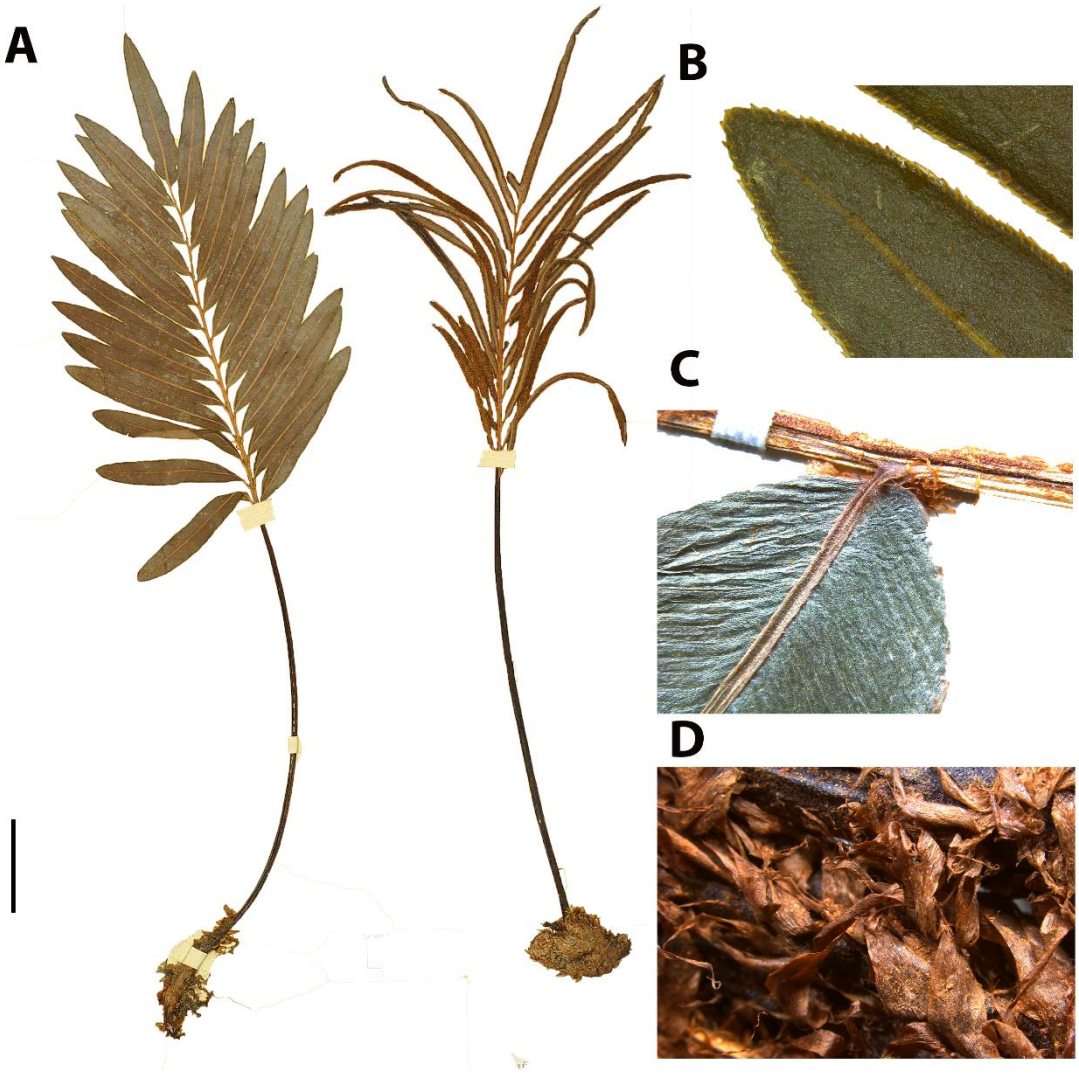

Figure 48. *Parablechnum glaziovii*. A. Sterile frond (left) and fertile frond (right); B. Sterile pinna apex, adaxial side; C. Sterile pinna base, adaxial side; D. Rhizome scales. (A: *A. Glaziou 15717*, P00347401, isolectotype; B: *J. Prado et al 2058*, NY02330524; C: *E.Y. Dawson 14744*, US2291496; D: *Y. Mexia 4546*, US1482144). Scale: 4 cm in A, 2.6 mm in B, 3 mm in C, 3.3 mm in D.

Etymology – the epithet refers to A.F.M. Glaziou (1828–1906), the botanist who collected the holotype of this species.

Notes – in the area where *P. glaziovii* occurs it can be confused with *P. cordatum* and *P. usterianum*. It differs from the former in the base of the sterile pinnae, clearly cuneate in *P. glaziovii* and cordate in *P. cordatum*, and from the latter in the rhizome, erect in *P. glaziovii* and creeping in *P. usterianum*. Christ (1899) cited only one collection (*Glaziou 15717*) in the protologue of *Blechnum glaziovii* and did not designate a holotype. Therefore, Dittrich *et al*. (2018) designated the best specimen in P (where Glaziou's original collections are located), annotated as "holotype" by T.C. Chambers, as the lectotype.

Reviewed material:

BRAZIL. Minas Gerais: Caldas, *H. Mosén 4601*, 1876 (P01395986!; P01395990!); MG Parque Forestal Estadual de Ibitipoca, debaixo da Ponte de Pedra, Paredão rochoso à esquerda do Rio do Salto, *R.F. Novelino 1031, J.E. Oliveira 246, P.B. Pita 131, D. Gragano 48*, 15 May 1993 (NY02597230!); Ouro Preto, *P. Campos Porto & Brade 1210*, 26 November 1926 (NY00908716!); Prope S. João d'El Rei, *A. Silveira 568*, 1 March 1896 (P01662916!; P01662917!); Riviere de le Serra de Saramenia praos d´Ouro Preto, *A. Glaziou 20581*, 28 October 1983 (P01466426!; P01466427!; P01466428!); Santo Antònio do Itambè, Serra do Espinhaço, about 3 km W of Santo Antônio do Itambé, near the Cachoeira da Fumaça, *E. Schuettpelz et al 1422*, 14 January 2010 (MO6209223!; NY01039737!); Serra do Espinhaço, Serra do Cipo, km 132 (ca. 153 km N of Belo Horizonte, *H.S. Irwin et al 20319*, 17 February 1968 (NY00814072!; UB103492! Photo; US2967412!); Serra de Ouro Preto, *Schwacke 12574*, 1 October 1896 (P01662918!); Vicosa, *M.A. Chase 9719*, 18 April 1925 (US1282260!); Vicosa, Agricultural College land, Road to Chacha Valley, *Y. Mexia 4546*, 1 April 1930 (US1482144!). **Paraná:** Prefeitura Municipal de Curitiba, Tabatinga (Mun. ijucas do Sul), *Y.S. Kuniyoshi & R. Kummrow 4594*, 11 January 1983 (US3044585!). **Rio de Janeiro:** *M. Glaziou 1941*, September 1876 (K000954319! Photo); Corcovado, *J.N. Rose & P.G. Russell 21276*, July 1915 (US763107!); Petropolis, sur les rochers du Rio Itamaraty, *Glaziou 15717*, 7 July 1883 (BM000769809! photo, isolectotype; K000633399! photo, isolectotype; MACB!, isolectotype; P00347401!, isolectotype; P00347402!, isolectotype; P00347403!, isolectotype; P00347404! Lectotype; RB00543443! photo isolectotype;); Valley of the

Rio Campo Bello, vicinity Monte Serrat, Mt. Itatiaya, Estaçao Biologica, *L.B. Smith 1647*, 3 January 1929 (US1497968!). **Rio Grande do Sul:** Estrada do Cassino, *F. Gonzattii 1249ª*, 15 May 2014 (UCS41510! Photo); man Venancio Ryres, Compeste dos terrães, *L.C. Jüngens 378*, December 1905 (P01546455!); Mostardas, Balneário Mostardense, *F. Gonzattii 895*, December 2013 (UCS40886! Photo). **Santa Catarina:** *E. Ule 200*, May 1886 (P01546443!; P01546444!); Garopaba, Ouvidor, *A. Kassner et al 3031*, 7 July 2018 (FURB60429! Photo); Garuva, Alto Quiriri, *L.A. Funez & A.E. Zermiani 4302*, 5 May 2015 (FURB50077! Photo). **São Paulo:** Mun. Caraguatatuba, Parque Estadual da Serra do Mar, Núcleo Caraguatatuba. Estrada da Intermediária próximo ao Rio Pardo, *J. Prado et al 2000*, 8 March 2003 (NY01018584!); Mun. Salesópolis, Estação Biológica de Boracéia, margem do Rio Guaratuba, Mata Atlântica, *J. Prado et al 2009*, 10 December 2008 (NY02240840!); Mun. Salesópolis, Reserva de USP, *J. Prado & P.H. Labiak 1672*, 10 June 2007 (NY02422577!); Prope Rio Grande ad "São Paulo Railway", *Wettstein & Schillner s.n.*, no date (P01531131!). **Goiás:** Región of the Chapada dos Veadeiros, streambed 4 km, north of Veadeiros, *E.Y. Dawson 14744*, 30 April 1956 (US2291496!). **Unknown State:** *F. Sellow s.n.*, no date (NY02597206!); *Glaziou 20581*, 8 December 1892 (P01546445!).

Parablechnum gregsonii (Watts) Gasper & Salino Phytotaxa 275(3): 216. 2016.

Basionym – *Blechnum capense* var. *gregsonii* Watts, Journal and Proceedings of the Royal Society of New South Wales. 1915.

Type – Australia, New South Wales, C. Tablelands, 33º30'S 150º23'E, *J. Gregson s.n.*, Apr 1902 (lectotype: NSW241413! photo; isolectotypes: K001092749! photo, NSW241411! photo, NSW241414! photo).

Synonyms –

≡*Blechnum gregsonii* (Watts) Tindale, Proc. Linn. Soc. New South Wales 85: 253. 1960.

Description – *plants* terrestrial or epiphytic; *rhizome* short to long creeping, non-stoloniferous, scales usually ovate, entire, light brown to reddish brown, papyrose or membranaceous; *fronds* monomorphic, pendulous; *sterile fronds* 17–81 × 7–26 cm; *petioles* 7–42 cm long, straw-coloured, sometimes with atropurpureous spots, scales similar to those on the rhizome, more abundant on the base; *lamina* ovate to deltoid,

truncate at base and gradually reducing towards apex, with in a conform terminal pinna, similar to mid–lateral pinnae but longer, *rachis* straw-coloured, sometimes with atropurpureous spots, glabrous, *sterile pinnae* in 2–12 pairs, mostly lanceolate, acuminate, 5–15 × 0.7–0.24 cm, shortly stalked, margins crenulate, becoming serrate towards apex; *costae* similar to the rachis; *veins* free, simple or 1-furcate, catadromous; *aerophores* absent; *hydathodes* rounded, whitish; *sori* linear, continuous, forming coenosori on both sides of the costa, occupying the middle part of the pinna only; *indusia* linear, continuous, open towards the costa; *sporangia* not seen; *spores* monolete, flat-convex in equatorial view, elliptic in polar view, 60 × 44 µm, perispore verrucose, fenestrated, exospore smooth (**Figure 49**).

References – Chambers & Farrant (1998b).

Chromosome number – unknown.

Distribution and habitat – endemic to Australia. It is known from several localities in the Blue Mountains and Minnamurra Falls in southeastern New South Wales. It grows in rocky bank crevices, on rocks and ledges, near waterfalls and caves in rainforests or ravines, sometimes epiphytic on trees. (Chambers & Farrant, 1998b).

Etymology – the epithet refers to the botanist J. Gregson, collector of the type.

Notes – although this species was annotated in the erratum submitted by *Dittrich et al*. (2017), the valid combination for *Parablechnum*, in which the author of the basionym should appear in brackets, i.e. Watts and not Tindale, was still missing. Considering so, the correct combination should be *Parablechnum gregsonii* (Watts) Gasper & V.A.O. Dittricht. It is distinguished from the rest of *Parablechnum* species in Australia because it is clearly monomorphic, while the rest of the species there are dimorphic or subdimorphic.

Reviewed material:

AUSTRALIA. New South Wales: C. Tablelands, *J. Gregson s.n.*, Apr 1902 (NSW241413! photo, lectotype; K001092749! photo, isolectotype; NSW241411! photo, isolectotype; NSW241414! photo, isolectotype).

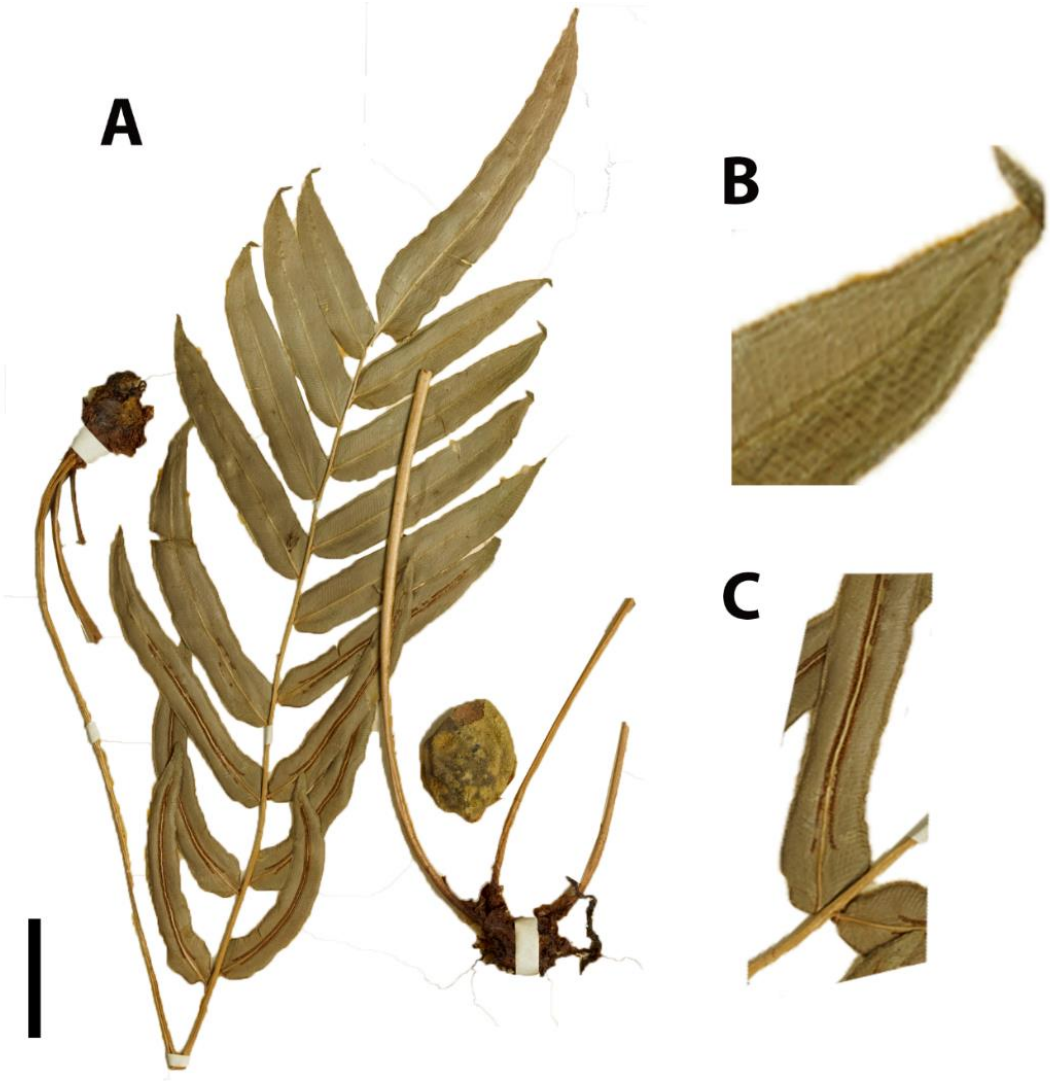

Figure 49. *Parablechnum gregsonii.* A. Fertile frond; B. Sterile pinna apex, abaxial side; C. Sori. (A-C: *J. Gregson 4326,* K001092749) Scale: 4 cm in A; 2 cm in B; 1 cm in C.

Parablechnum hieronymi (Brause) Gasper & Salino, Phytotaxa 275(3): 216. 2016

Basionym – *Blechnum hieronymi* Brause, Bot. Jahrb. Syst. 56: 155. 1920.

Type – *Ledermann 12217b* 'Nordöstl. Neu Guinea: Kaiserin Augusta Fluβ Sepik Gebiet: Schraderberg, Gebirgswald', epiphytic, 2000 m, June 1913 (syntypes: B200031476-7!).

Synonyms –

=*Blechnum brassii* Copel., Univ. Calif. Pub. Bot. 18: 222. 1942. Type: New Guinea, Irian Jaya, Idenburg, 15 km SW of Bernhard Camp, Idenburg River, *L.J. Brass 12287,* January 1939 (holotype: not foun; isotypes: BRI-AQ0024614! Photo, L0064513! Photo).

=*Blechnum decorum* Brause, Bot. Jahrb. Syst. 56: 156. 1921; ≡*Parablechnum decorum* (Brause) Gasper & Salino, Phytotaxa 275(3): 191–227. 2016. Type: Papua New Guinea, *C. Lederman 12459a*, 1 August 1913 (syntypes: B200030879-80!).

= *Lomaria acutiuscula* Alderw., Nova Guinea 14: 31. 1924. Type: Papua New Guinea, mountain ridge near Doorman Summit, epiphytic, 1420 m, *Lam 1543*, October 1920 (BO n.s.); ≡*Blechnum acutiusculum* (Alderw.) C. Chr., Ind. Fil. Suppl. 3, 45. 1934.

Vernacular names – Djaholiha (Asaro: Defamo), korrungel (Wahgi: Minj), gag (Hagen: Togoba) (Chambers & Farrant, 2001).

Description – *plants* terrestrial, rarely epiphytic; *rhizome* erect or creeping, non-stoloniferous, scaly, scales elliptic to subdeltoid, acuminate, entire, reddish, brown or black, bicolorous, usually with lighter margins, 1.9 × 0.4 cm; *fronds* dimorphic, forming a rosette, sometimes spaced fronds due to creeping rhizome; *sterile fronds* with *petioles* ca. 20 cm long, brown, reddish, sometimes atropurpureous in the abaxial area of the base, scaly, scales at the base similar to those of the rhizome, distally smaller, straw-coloured, concolorous, sometimes with a dark central insertion point, bases cordate, mixed with woolly indumentum; *lamina* elliptic, acuminate, truncate at base, up to 50 cm long, with reddish hairs abaxially; *rachis* light brown, with scattered scales, similar to those of the petiole but smaller; *sterile pinnae* in up to 17 pairs, alternate or subopposite, coriaceous, glabrous, stalked, becoming basiscopically adnate towards the apex, bases rounded, apices acuminate or acute, margins slightly revolute, serrate; *costae* grooved adaxially, prominent abaxially, similar to rachis; *veins* free, simple or 1-furcate, catadromous; *aerophores* rounded; *hydathodes* patent, ovate; *fertile fronds* taller and more erect than sterile ones; *petiole* up to 70 cm; *fertile pinnae* in up to 14 pairs, linear, base rounded, apex acute or acuminate, stalked, apical pinnae smaller, similar to those of the basal and middle zone, sometimes with a basal auricle; *sori* linear, continuous, forming coenosori on both sides of the costa, occupying the entire length of the pinna except for an apical sterile zone; *indusia* linear, continuous, open towards the costa, dark brown, lacerate; *sporangia* with (21) 23 (26) arch cells; *spores* monolete, (47) 64 (75) × (30) 47 (55) µm, perispores smooth or slightly roughened, cristate-reticulate, with tall thin walls delimiting large polygonal areoles, with short, moderately abundant filamentous processes, distributed evenly over the entire spore surface, (**Figure 50**).

References – Chambers & Farrant (2001).

Chromosome number – unknown.

Distribution and habitat – Papua New Guinea, Fiji, and Seram, Indonesia. Here we also report a specimen from Philippines (P01630640). It occurs in many of the montane regions from 1200–3500 m, usually in mossy forests, forest edges and stream edges in subalpine meadows. Occasionally this species is found in more exposed situations in alpine grass fields and vegetation ridges, but more frequent in protected habitats, sometimes epiphytic, but more usually terrestrial (Chambers & Farrant, 2001).

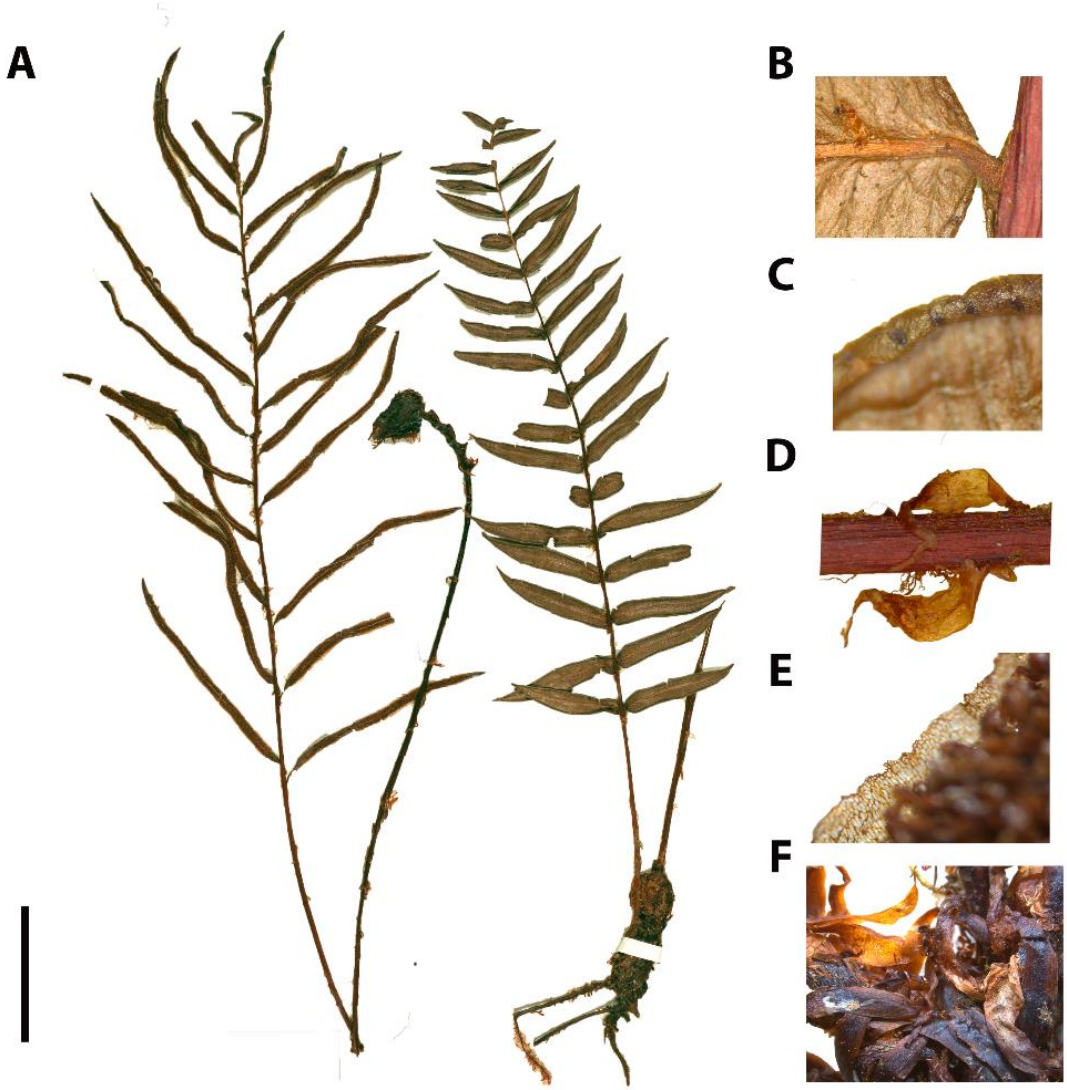

Figure 50. *Parablechnum hieronymi*. A. Fertile (left) and sterile (right) fronds; B. Sterile pinna base, adaxial side; C. Sterile pinna hydathodes; D. Fertile rachis with scales; E. Indusium; F. Rhizome scales. (A,C&D: *C. Ledermann 12217b*, B200031477, syntype; B: *C. Ledermann 12217b*, B200031476, syntype; E&F: *R.D. Hoogland & R. Pullen 5466*, US2291936). Scale: 5 cm in A; 4.3 mm in B; 2 mm in C; 0.4 mm in D; 1.3 mm in E & 6.7 mm in F.

Notes – the work of Chambers & Farrant (2001) concluded that this taxon cannot not be segregated from *Parablechnum decorum*, and after reviewing the syntypes of that

taxon it has been concluded that they are indeed synonyms. This species has similarities to forest edge specimens of *Parablechnum revolutum*, where the sterile pinnae are less revolute, but are easily distinguished by the rhizome scales and petiole base, which are more robust in *P. revolutum*.

Reviewed material:

INDONESIA. Celebes: Sualawesi Utara, Bolaang Mongondow, Gunung Ambang Nature Reserve, Bolirang slfatara area, *de Vogel & Vermeulen 7277*, 19 April 1985 (P01571491!). **New Guinea Occidental:** Irian Jaya, Idenburg, 15 km SW of Bernhard Camp, Idenburg River, *L.J. Brass 12287*, January 1939 (BRI-AQ0024614! Photo, isotype of *Blechnum brassi*; L0064513! Photo, isotype of *Blechnum brassii*). **PAPUA NUEVA GUINEA**. **Eastern Highlands**: Distr, near Daulo camp. Asaro–Mairi, Divide, Goroka subdistrict, *R.D. Hoogland & R. Pullen 5466*, 26 June 1956 (US2291936!). **Madang:** Bundi, *M. Sundue et al 3799*, 8 August 2014 (VT198737!); Bundi, Bundi Station, *M. Sundue et al. 3711*, 8 April 2014 (VT198739!); Bundi, Forest accesible from road to Mundia pass, near Kiagimangi, *M. Sundue et al 3596*, 28 July 2014 (VT198738!). **Oro:** Akupe Camp, Kuriae River, Sibium Mountains, Umate Village, *S.A. James & M. Sundue 1639*, 13 February 2013 (VT198733!). **Unknown area:** *C. Lederman 12217*, 1 August 1913 (B200031476!, syntype, B200031477!, syntype); *C. Lederman 12459a*, 1 August 1913 (B200030879!, syntype of *Blechnum decorum*, B200030880!, syntype of *Blechnum decorum*). **PHILIPPINES. Mindanao:** Mt. Apo, *C. Copeland 1511*, 2 April 1904 (P01630640!).

Parablechnum howeanum (T.C.Chambers & P.A.Farrant) Gasper & Salino, Phytotaxa 275(3): 216. 2016.

Basionym – *Blechnum howeanum* T.C.Chambers & P.A.Farrant, Telopea 5: 331. 1993.

Type – Lord Howe Island: Erskine Valley, *A.N. Rodd 3700*, 1 September 1981 (holotype: NSW281343! photo).

Description – *plants* terrestrial; *rhizome* shortly erect to suberect or shortly creeping, non-stoloniferous, scales acuminate, 20 × 3 mm, reddish brown, margins entire and

sometimes lighter, being more or less bicolorous; *fronds* dimorphic, erect; *sterile fronds* 100 × 44 cm; *petioles* 43 cm, atropurpureous at base, brown, pinkish brown or straw-brown distally, densely scaly at base, with scales similar to rhizome scales, distal scales more scattered, shorter, finer, pale reddish brown, acuminate and mostly entire, sometimes with clusters of fine pale matted hairs and scattered scales on the upper petiole; *lamina* lanceolate, ovate or deltoid, 1-pinnate, base truncate, with basal auricles, gradually reducing towards the apex, with in a conform terminal pinna; *rachis* straw or pale pinkish brown, sometimes darker, with pale or reddish brown scales, variable in shape, broad at the base, arachnoid, some or most of the longer scales with a distinct black dot covering part of the broad scale base; *sterile pinnae* in up to 24 pairs, linear-lanceolate, base slightly auriculate basally, apex acuminate, those towards the stalked, becoming basiscopically adnate distally, adjacent often overlapping, coriaceous, up to 22 × 2.5 cm, basal pinnae becoming reduced to simple auricles, terminal pinna usually longer than subterminal pinnae, margins finely crenulate and sometimes dentate, especially towards apices; *costae* similar to rachis, grooved adaxially, prominent abaxially, with small scales extending from costa to lower surface of pinnae, sometimes clusters of fine, matted hairs and scales; *veins* free, simple or 1-furcate, catadromous; *aerophores* absent; *hydathodes* ovate, whitish; *fertile fronds* similar in size to sterile ones; *fertile pinnae* linear apices long-acuminate and sterile, bases broadening to become decurrent along rachis and markedly auriculate and sterile in lower half of frond 26 × 0.5 cm; *sori* linear, continuous, forming coenosori on both sides of costa covering the lower part except for sterile apices and broadened bases; *indusia* linear, continuous, opening towards costa, brown with lacerate margins; *sporangia* not seen; *spores* monolete, flat-convex in equatorial view, elliptic in polar view, ca 40–50 μm × 50–70 μm (**Figure 51**).

References – Chambers & Farrant (1993).

Chromosome number – unknown.

Distribution and habitat – endemic to Lord Howe Island, where it occurs on Mt Gower, Mt Lidgbird, and some low–lying areas such as those in the Erskine Valley. It lives in submontane mixed woodland and scrub (Chambers & Farrant, 1993).

Etymology – the specific epithet refers to Lord Howe Island, where the plant is endemic.

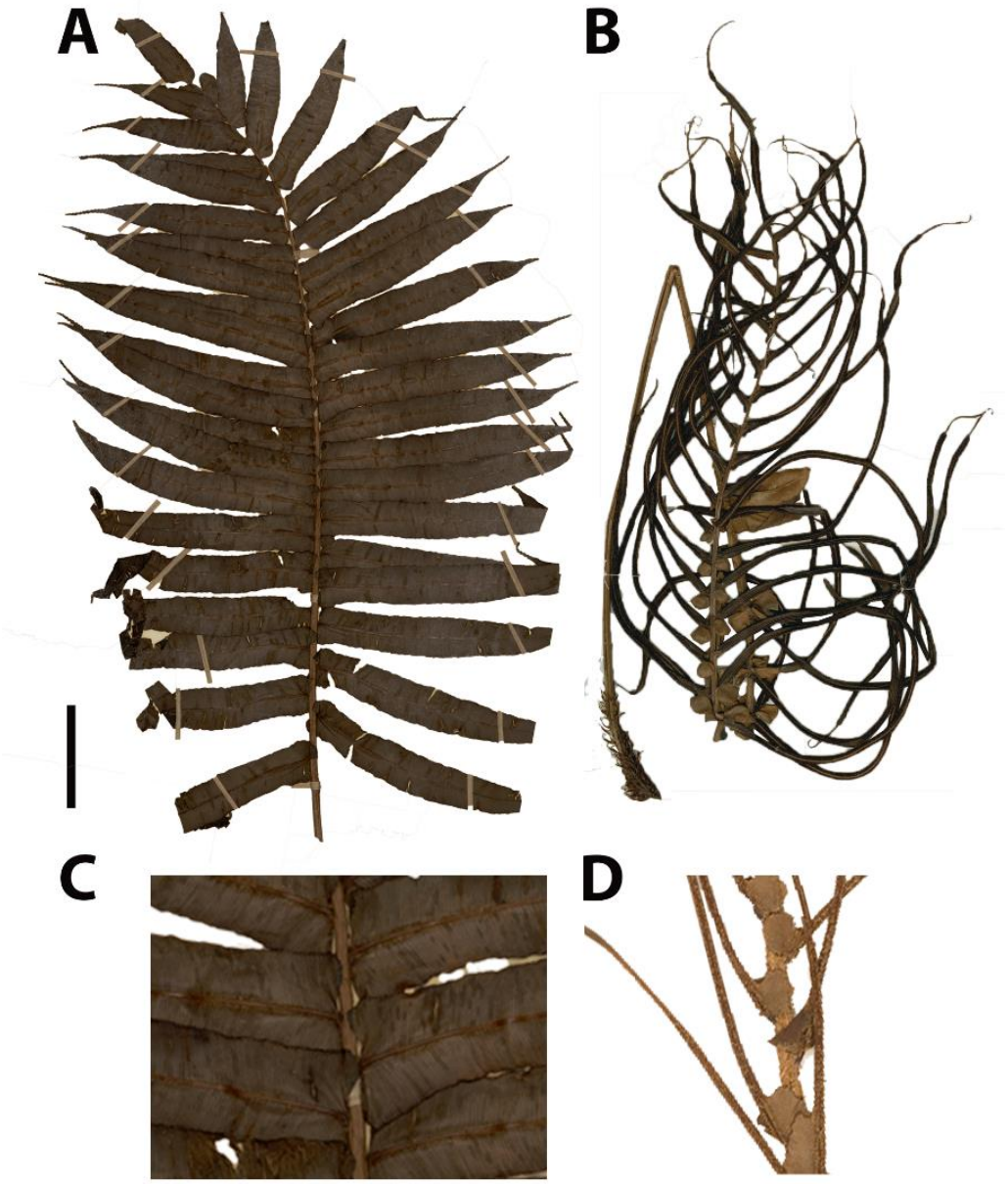

Figure 51. *Parablechnum howeanum*. A. Sterile frond; B. Fertile frond; C. Detail of the sterile pinnae bases, adaxial side; D. Detail of the fertile proximal pinnae. (A&C: *Moore s.n.*, P01662370; B: *A.N. Rodd 3700*, NSW281343, holotype; D: *J.M. Le Cussan 1004*, NSW606986). Scale: 5 cm in A&B; 1.6 cm in C; 2.6 cm in D.

Notes – *Parablechnum howeanum* belongs to a group of *Parablechnum* species in Australia and New Zealand. *Parablechnum wattsii* differs from *P. howeanum* in having toothed scales, without black dots, and slightly or not at all reduced basal pinnae. *Parablechnum procerum* is a New Zealand species which is much smaller than *P. howeanum* and in which the basal pinnae are not reduced. *Parablechnum minus* has scales without a black spot, in which the base of the fertile pinna does not widen to the point of being auriculate in the lower half of the frond. It can be distinguished from New Zealand

species such as *Parablechnum novae-zelandiae* and *P. montanum* in that *P. howeanum* has the pinnae reduced to auricles suddenly, rather than gradually in several pairs. Chambers and Farrant (1993) examined some specimens of *P. milnei* from Fiji, collected and determined by Brownlie, and concluded that the materials from Lord Howe Island do not appear to refer to this taxon; the bases of the pinnae in *P. milnei* do not become auriculate–hastened to any significant degree. The sheets reviewed in this paper seem to confirm this fact (Chambers & Farrant, 1993).

Reviewed material:

AUSTRALIA. New South Wales: Lord Howe Island, *no collector*, no date (US0654068!); *ibidem, J.L. Boorman s.n.*, May 1920 (US1370789!); *ibidem, Moore s.n.*, no date (P01662370!); Lord Howe Island, about 350 m east of Goathouse cave on track along base of Mt. Lidgbird cliffs, *J.M. Le Cussan 1004*, 11 November 2000 (NSW606985! Photo; NSW606986! Photo); Lord Howe Island, Erskine Valley, *A.N. Rodd 3700*, 1 September 1981 (NSW281343! Photo, holotype).

Parablechnum humbertii (Tardieu) S. Molino & Lafuente, Phytotaxa (submitted).

Basionym – *Blechnum humbertii* Tardieu, Mém. Inst. Sci. Madagascar, sér. B, Biol. Vég. 6: 232, f. 5. 1955.

Type – Madagascar. 'Vallée de la Lokoho, mont Beondroka, au Nord de Maroambihy, sylve à Lichens, sur gneiss et quartzite', *H. Humbert 23554* (holotype: P00483200!).

Synonyms –

≡*Blechnum montbrisonis* var. *humbertii* (Tardieu) Rakontondr. Adansonia, série 3, 35(2): 178. 2013; *Parablechnum marginatum* var. *humbertii* (Tardieu) Gasper & Salino Phytotaxa 275(3): 216. 2016.

Description – *plants* terrestrial; rhizome erect or suberect, non-stoloniferous, with ovate–lanceolate scales with elongated apex, more or less filiform, concolorous, brownish, membranaceous, with entire margins, up to 20 mm long; fronds dimorphic, sterile fronds with petioles 20–30 cm long, dark brown at base, straw–greyish distally, smooth, grooved, with scales in the basal zone decreasing in density distally, similar to those of the rhizome, leaving a black scar after falling off; lamina 1-pinnate, elliptic-acuminate, up to 30 cm, sometimes longer, rachis light brown, smooth, grooved adaxially,

scales similar to those of the petiole but more filiform, more abundant in the adaxial side, pinnae in up to 20 pairs, alternate or subopposite, slightly smaller at the base, lanceolate–oblong, stalked, becoming basiscopically adnate towards the apex of the frond, 10 × 1.5 cm, base asymmetric, subcordate to truncated, apex long acuminate, margins serrate, with a conform terminal pinnae similar to the lateral ones; veins free, simple or 1-furcate, catadromous; fertile frond longer than sterile and more erect, petiole similar to sterile fronds, lamina 30 cm long, sometimes longer, lanceolate–oblong, rachis similar to sterile fronds, pinnae usually in more pairs than in the sterile ones, linear, narrow, 12 × 0.2 cm, slightly broader based, asymmetrical, cordate, apex long acuminate; aerophores present in both sterile and fertile fronds, tuberculiform, atropurpureous; hydathodes present in both sterile and fertile fronds, rounded or ovate; sori linear, continuous, forming coenosori on both sides of the costa; indusium linear, continuous, open towards the costa, dark brown, membranaceous, sometimes lacerate; *sporangia* long-pedicellate, simple, 3–seriate below capsule, capsule broadly elliptic in lateral view, with (18) 21 (24) cells in the arc, mixed with sporangiasters slightly shorter than the sporangia, darker; *spores* monolete, (49) 66 (78) × (35) 49 (62) µm, perispores rugulose, cristate-reticulate, with thick, high walls forming medium to large polygonal areoles, without filamentous processes or with moderately abundant sporadic filamentous processes in the areole lacunae, with granules (**Figure 52**).

References – Tardieu–Bolt (1955, 1960), Roux (2009), Rakotondrainibe *et al*. (2013), Molino *et al*. (submitted).

Chromosome number – unknown.

Distribution and habitat – Endemic to Madagascar. Fairly frequent in the north of the island, only one collection in the south–central region of Fianarantsoa; dense humid forest, on rocky or sandy soil, 1,250–1,940 m (Roux, 2009; Rakotondrainibe *et al.*, 2013).

Etymology – the epithet refers to the botanist H. Humbert (1887-1967), the collector of the holotype specimen.

Figure 52. *Parablechnum humbertii*. A. Plant with fertile frond (left) and sterile (right); B. Detail of the petiole surface with scars left by the fallen scales (arrow); C. Detail of a sterile pinna apex, abaxial side; D. Detail of an aerophore (arrow); E. Detail of fertile pinna apex abaxial side; F. Detail of a sorus with sporangiasters (arrow). (A: *H. Humbert 23554*, P00483200, holotype; B: *R.N. Rabarijaona et al. 1053*, P00783078; C: *F. Rakotondrainibe 1673*, P00100192; D: *F. Rakotondrainibe 2743*, P00059958; E&F: *F. Rakotondrainibe 2743*, P00059959). Scale: 4 cm in A, 1.6 mm in B, 12 mm in C, 4 mm in D, 9 mm in E, 1 mm in F.

Notes – the phylogenetic differences noted by Bauret (2017), and a morphological comparison with *P. marginatum* (Molino *et al.*, submitted) led the authors to propose this former variety of *P. marginatum* to again be recognized as a distinct species. It can be easily distinguished from *P. marginatum* by the long-acuminate rather than obtuse or acute apices and the scars left by the scales on the petioles, as well as spore size and ornamentation.

Reviewed material:

MADAGASCAR: Anjanaribe, *M.G. Cours 3772,* 19 December 1950 (P01625801!); Antsiranana, *L. Bauret et al. 102,* 24 September 2015 (P02435082!); Antsiranana, Andapa, Parc National de Marojejy. Aux alentours du Camp 4, au bord de la rivière Andranomifototra, *G. Rouhan et al. 1209,* 25 October 2011 (P02432741!; P02432742!; P02432743!; P02432744!); Antsiranana, Andapa, Befingotra, RS d'Anjanaharibe–Sub, sur le versant Sud–Est, à 12. 2 km à l'Ouest-Sud-Ouest de Befingra, *F. Rakotondrainibe & F. Raharimalala 2519*, 25 November 1994 (P00904704; P00046988); *ibidem*, *F. Rakotondrainibe & F. Raharimalala 2534*, 27 November 1994 (P00046998); Antsiranana, Andapa, RNI 12 du Marojejy. A 11 km au Nord-Ouest de Manantenina, *F. Rakotondrainibe 3571*, 27 October 1996 (P00085122!; P00085123!; P00085124!; P00085125!); Antsiranana, Ambanja, Massif du Manongarivo, Mt d'Antsatrotro, berges de la rivière Ankaramihely, *F. Rakotondrainibe 1673*, 19 May 1992 (P00100192!; P00100193!; P00100194!); Antsiranana, Iharana (Vohémar), Marojejy, route, vers campement 3, R.N. *Rabarijaona et al. ROM 1053*, 13 May 2015 (P00783078!; P00783098!); Eboulis sableux Ambondrombe, *P. Boiteau 4635,* 11 April 1941 (P02284987!; P01632222!); Fianarantsoa, Ambalavao, Ambatomboay, RNI d'Andringitra versant E; à environ 38 km au Sud d'Ambalavao, près de la source de la rivière Sahavatoy, *F. Rakotondrainibe 2743*, 30 May 1995 (P00059958!; P00059959!; P00059960!; P00059961!); Vallée de la Lokoho (nord–est), Mont Beondroka au Nord de Maroambihy, *H. Humbert 23554,* 17-22 March 1949 (P00483200!, holotype).

Parablechnum lechleri (Mett.) Gasper & Salino, Phytotaxa 275(3): 216. 2016.

Basionym – *Blechnum lechleri* Mett., Fil. Lechl. 2: 17. 1859.

Type – Peruvia (Peru): Tatanara; *W. Lechler 2534* (lectosyntypes: B200031630–2!).

Synonyms –

=*Lomaria violacea* Fée Hist. Foug. Antil. 11, t. 5. 1866; ≡*Blechnum violaceum* (Fée) C.Chr. Index Filic. 161. 1905. Type: Guadelupe, *L'Herminieri s.n*., 1846 (syntypes: US2019932!, US2703206-7!; isotype: MACB!).

Description – *plants* terrestrial; *rhizomes* erect or suberect, non-stoloniferous, scaly, scales 20–30 × 2–4 mm, lanceolate, brownish, concolorous, often shiny, the apices acute,

the margins entire or with some ciliate processes; *fronds* dimorphic; *sterile fronds* 55–118 × 12–30 cm; *petioles* atropurpureous throughout their length, or sometimes becoming mottled or straw-coloured above the base and continuing to the proximal portion of the rachis, scaly when young, glabrescent at maturity; *laminae* oblong-lanceolate, 1-pinnate, with a conform terminal pinna; *rachis* atropurpureous, with verrucous ornamentation, scaly, with scales of two types, some linear-lanceolate, light brown, concolorous, membranaceous, more or less cordate at base, apex filiform, margin entire or with some ciliate processes, others stellate, smaller, light brown, membranaceous, concolorous; *sterile pinnae* 9–15 × 1–1.5(–2) cm, elliptic, shortly stalked, sometimes becoming basiscopically adnate distally, base rounded, truncate or subcordate, apices acute or acuminate; *costae* atropurpureous, grooved adaxially, abaxially prominent, with verrucose ornamentation, more straw–like adaxially; *veins* free, simple or 1-furcate, catadromous; *aerophores*, 1–5 mm long, vermiform; *hydathodes* rounded or ovate; *fertile fronds* longer and more erect than sterile, 58–150 × 6–36 cm; *fertile pinnae* narrower, 3–6 mm wide; *sori* linear, continuous, forming coenosori on both sides of the costa, *indusia* linear, continuous, open towards the costa; *sporangia*; *spores* monoecious, flat-convex in equatorial view, elliptic in polar view, (50–)53(–55) × (38–)49(–43) µm, with perispores, 6. 0–8.0 µm thick, cristate-reticulate, delimiting polygonal areoles with more or less long filaments abundant in areole lacunae and wall walls, spongy interior, exospore smooth (**Figure 53**).

References – Passarelli *et al*. (2010), Sundue (2010)

Chromosome number – unknown

Distribution and habitat – Lesser Antilles, Guyana Highlands, Andes from Venezuela, Ecuador to Bolivia, Peru, and Brazil. Common, terrestrial in moist forests, especially in open habitats and edges, in streams, roadsides and secondary habitats. 850–3600 m (Mettenius, 1859; Sundue, 2010; Smith & Kessler, 2018).

Etymology – the epithet refers to W. Lechler (1814–1856), collector of the specimens constituting the syntypes of the species.

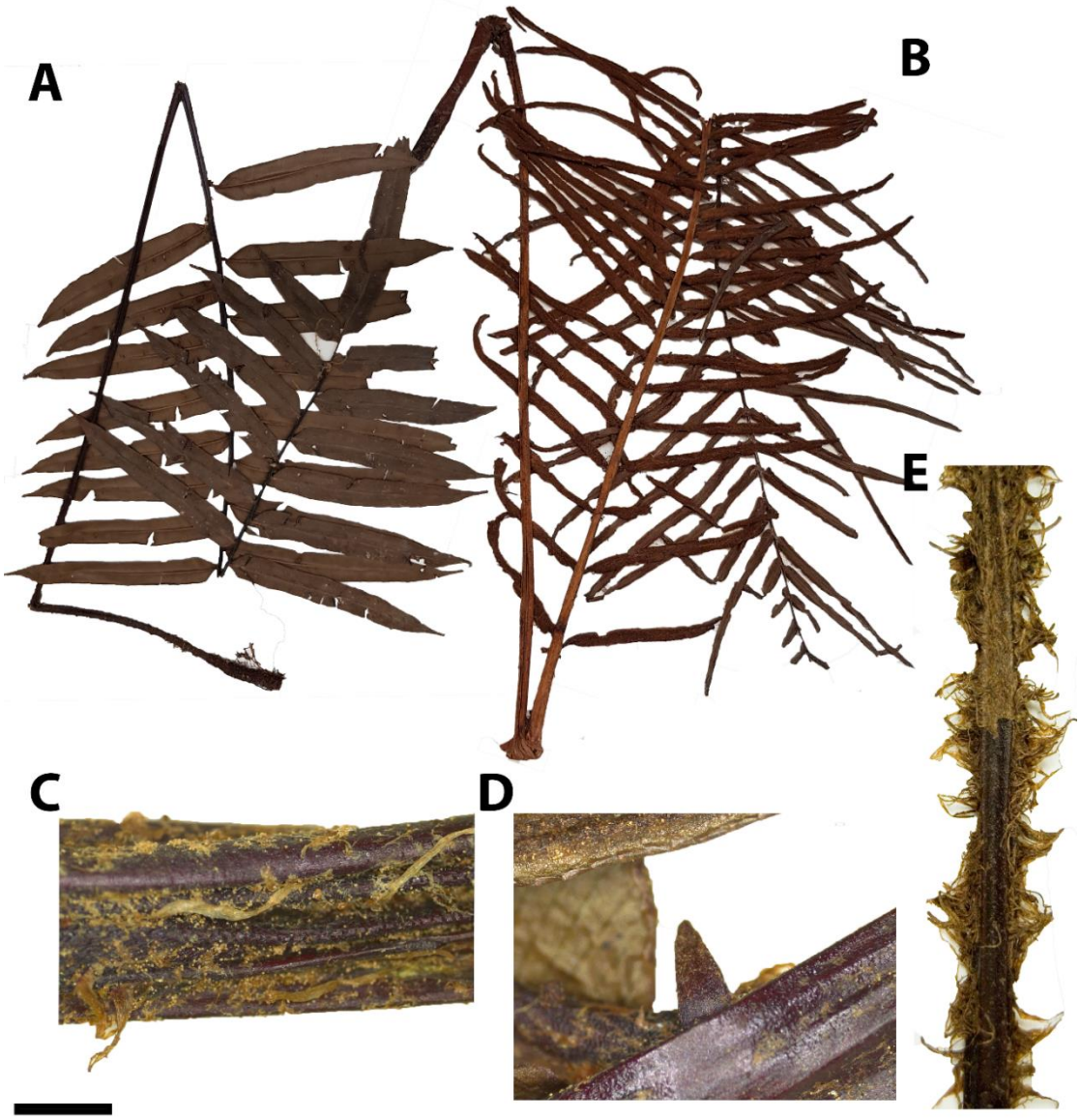

Figure 53. *Parablechnum lechleri.* A. Sterile frond; B. Fertile frond; C. Detail of the rachis; D. Conical aerophore; E. Detail of a fertile petiole, proximal portion. (A: *Sundue & Vasco 1220*, NY; B: *Sundue et al. 661*, NY; C: *Lechler 2534*, B200031632, syntype; D: *Lechler 2534*, B200031630, syntype; E: *H. van der Werff et al 19781*, UC1872874). Scale: 5 cm in A&B; 1.7 mm in C; 2 mm in D; 1.3 cm in E.

Notes – it can be distinguished from other *Parablechnum* species of the area by its strongly atropurpureous axes and vermiform aerophores. It is common to find aberrant specimens with fronds partially fertile and partially sterile. It has been discussed if the name *Blechnum violaceum* is a synonym of this species or not. Here there has been some differences found as the shape of the lamina and the spore ornamentation, but information is still not enough to take a decision. The phylogenetic results presented here suggest that it could constitute a complex of species.

Reviewed material:

BOLIVIA. Dept. Cochabamba: Prov. Jose Carrasco Torrico, 110 km antigua carretera Cochabamba-Villa Tunari, *M. Kessler et al 6803,* 29 June 1996 (UC1603989! Photo); Prov. Jose Carrasco Torrico, 3 km de Siberia hacia Karahuasi, *M. Kessler et al 8134,* 18 October 1996 (NY!); Prov. Tiraque, Localidad El Limbo, *M.A. Zabalaga 1095,* 19 August 2003 (NY04178932!); *ibidem, S. Altamirano et al 918,* 16 June 2003 (NY!). **Dept. Potosí:** San Antonio, *O. Buchtien 1054,* December 1907 (UC477682! Photo). **Dept. La Paz:** *G. Mandon s.n.,* no date (P01546450!); Franz Tamayo, Área Natural de Manejo Integrado Apolobamba, Pelechuco, *A.F. Fuentes 15068,* 1 July 2009 (MO6348190!); Mapiri, Región tropical, Charopampa, *O. Buchtien 1051,* November 1907 (US1096165!; US1096166!); Murillo Province, Zongo Valley, *A. Fay & L. Fay 2902,* 5-6 August 1990 (UC1593452! Photo); near Yungas, *H.H. Rusby 311,* 1885 (NY!, 2 sheets); Noryungas, 46 km N of Caranavi, *A. Fay & L. Fay 2145,* 26 June 1989 (US3250868!); Mapiri, San Antonio, *O. Buchtien 18,* 12.1907 (P01389532!; P01389533!; P01389534!); Prov. Larecaja, Hacienda Simaco, on road to Tipuani *O. Buchtien 5132,* 1920 (NY!; P01389530!; P01389531!; US1096221!; US1096222!); Sud Yungas, 9 km de Huancané en la carretera hacia San Isidro, *D.N. Smith & J.F. Smith 13102,* 2 May 1989 (NY4178934!; UC1585080! Photo; UC1585081! photo). **Dept. Santa Cruz:** Huertas, Comarapa, *J. Steinbach 8567,* 26 October 1928 (NY!); Prov. Caballero, *R. Nuñez 564,* 23 March 2004 (NY!); *ibidem, R. Nuñez 710,* 22 April 2004 (NY!); Prov. Caballero, 1,5 km down from Empalme (on Comarapa-Cochabamba highway) on road to Khara Huasi, *M.A. Sundue et al. 788,* 2 August 2003 (NY!); Prov. Caballero, 4,5 km (by road) eastwards from school at village of Siberia towards Comarapa, 6,5 km (boa road) westwards from "El Empalme" at the turnoff to Kara Huasi, *M.A. Sundue et al 828,* 5 August 2003 (NY!); *ibidem, M.A. Sundue et al 829,* 5 August 2003 (NY!); Prov. Caballero, along road from Cochabamba to Comarapa, 3 km E of turnoff to Karahuasi, *M. Sundue et al. 661,* 16 April 2002 (NY!, 2 sheets; US3479181!); Prov. Caballero, tramo entre Bella Vista y Siberia, 26 km desde Comarapa sobre la carretera hacia Cbba, *I.G. Vargas & C.G. Jordán 6879,* 13 April 2003 (NY!); Prov. Valle Grande, 6 km de Loma Larga a Valle Grande, *M. Kessler et al 6332,* 7 June 1996 (UC1603987! Photo). **Unknown Department:** *O. Kuntze s.n.,* 1-4 April 1892 (NY!); *ibidem* (NY!); *ibidem* (NY!); *ibidem* (NY!). **BRAZIL. Unknown State:** *Duos & L.*

Giraudias s.n., no date (P01546404!). **COLOMBIA. Dept. Antioquia:** Mun. Amalfi, 8-15 kms., de Amalfi a Rumazón, sitios “Salazar” y “La Playa”, Cordillera Central, *J. Betancur et al 831*, 28 Septembre 1988 (MO3650111!; MO3650112!; UC1564534! Photo); Mun Frontino, corregimiento Carauta, Parque Nacional Natural Las Orquídeas, sector Tres Bocas, bosques a la orilla del río Santiago, minas del río Santiago ("Mina La Salada"), finca La Pradera, *M.A. Sundue et al 3281*, 8 September 2012 (NY02058146!; NY02058147!; NY02058148!; VT198672!; VT198673!). **Dept. Bocaya:** Cordillera Oriental, Vertiente Oriental, carretera Sogamoso Pajarito, Valle del río Cusiana, *R. Jaramillo Mejía et al 3733*, 19 October 1967 (NY!); en la carretera Tunja Arcabuco, quebrada afluente del río Pómeca, en El Boquerón, *R. Jaramillo Mejía et al 3719*, 17 October 1967 (NY!). **Dept. Cauca:** Mount Santa Ana, *F.W. Pennell 7467*, 29–30 June 1922 (US1144552!; US1144553!); Popayán, *no collector 4422*, no date (P01631385!). **Dept. Chocó:** Cerro del Torá, Mun. San José del Palmar, *A. Silvierstone-Sopkin et al 4649*, 21 August 1988 (UC1565369! Photo). **Dept. Hulia:** above Finca Miravalles, on ridge between Río Blanco drainage and Quebrada la Cuandinosa drainage, 21 km E of Gigante, *F.R. Fosberg 19862*, 28 January 1943 (US2202879!; US2202880!); *ibidem, F.R. Fosberg 19863*, 28 January 1943 (US220869!). **Dept. Nariño:** La Planada Biological Reserve, ca. 7 km S of Chucunez, along Road to Pialapi, *J.L. Luteyn & S. Sylva S. 13992*, 10 August 1990 (NY!, 2 sheets); Mun. De Piedrancha, Corregimiento de Chucunés, Reserva Natural La Planada, *S.P. Churchill et al 18244*, 18 May 1991 (NY!, 2 sheets); Río San Juan at pueblo of San Antonio, near junction of Río San Juan drainage, *J.A. Ewan 16057*, 3 September 1944 (UC1077964! Photo; US2254201!; US2254202!). **Dept. Risaralda:** Mun. Apia, Pueblo Rico, Cuchilla de la línea, sector Quebrada Risaralda, PNN Tatamá, *Sundue & A. Vasco 1220*, 16 April 2007 (VT198676!); *ibidem, Sundue & A. Vasco 1224*, 16 April 2007 (NY!; VT198675!); Mun. Santuario, PNN Tatamá, camino que lleva al páramo de Tatamá, subiendo hacia Morro Zancudo, *Sundue & A. Vasco 1250*, 17 April 2007 (NY!; VT198674!). **Dept. Valle:** Cerro del Inglés, Cordillera Occidental, Serranía de los Paraguas, a 1 hora en jeep de El Cairo, *F.A. Silverstone Sopkin et al. 2757*, 30 December 1986 (UC1603722! Photo). **ECUADOR. Prov. Carchi:** Cerro Golondrinas, *B. Boyle et al. 3328*, 20 July 1994 (UC1619182! Photo); Maldonado, Qba. Naranjo, near the waterfall (First Qba. W of the market in Maldonado), *L.J. Dorr & L.C. Barnett s.n.*, 13 November 1988 (NY4178924!); *ibidem* (NY4178925!); *ibidem* (NY!); Río Chingual drainage, Cordillera Oriental, in vicinity of Pun, *J.A. Ewan 16312*, 9

October 1944 (US2254288!; US2254289!). **Prov. Morona-Santiago:** San Juan Bosco, Cordillera del condor, Comunidad Shuar Numpatkaim, sendero que conduce hacia la cima del cerro más alto de la Cordillera del Cóndor, *C. Morales & T. Embrey 1374* (MO4785306!; MO4785307!; UC1869110! Photo). **Prov. El Oro:** 21 ½ mi. west Portovelo, *I.L. 10937,* 7 October 1944 (NY!). **Prov. Pastaza:** along road from Mera to Rio Anzu, 7 km N of Rio Alpayacu, *T.B. Croat et al 88785,* 8 May 2003 (UC1793324! Photo); Canton Mera, North northwest of Shell, *A. Fay & L. Fay 3695,* 22 July 1992 (NY!, 2 sheets); Canton Quito, Rio Guajalito Reserve, 10 km W of Chiriboga, km 59 of old road Quito-Santo Domingo, *A. Fay & L. Fay 3354,* 10 July 1991 (NY!). **Prov. Pichincha:** cerca de Maldonado, subiendo aprox. 1 km por la quebrada del puente que hay a la salida de Maldonado hacia Chingal, *A. Garmendia & P. Jaramillo 76,* 11 September 1995 (MA630263!). **Prov. Zamora-Chinchipe:** in the vicinity of the mining camp at the Río Tundaime, along road from mining camp to military base El Condor, *H. van der Werff et al 19073,* 30 October 2004 (UC1796225! Photo; UC1796226! Photo); Reserva Tapichalaca, nearby Ventanilla, *M. Lehnert 986,* 16 October 2003 (UC1791960! Photo). **GUADALOUPE.** *No collector,* 1861 (P01623720!); *A. Baudouin 610,* no date (P01531049!); *L'Herminier s.n*., no date (P01557755!); Bains Jaunes, *Questel 1097,* no date (P06491240!). **GUYANA. Reg. Potaro–Siparuni:** Mt. Wokomung, Little Ayanganna, upper slopes of highest point of Mt. Wokomunfg massif, *H.D. Clarke et al 10533*, 5 July 2003 (P00904703!); Pakaraima Mts, Mt. Wokomung, summit plateau, N escarpment, exposed sandstone cliffs, adj. Terrain, *T.W. Henkel et al 1526*, 20 February 1993 (NY!); upper Potaro River region, upper slopes of Mt. Wokomung, *B.M. Boom & G.J. Samuels 9154,* 10 July 1989 (NY!). **MARTINIQUE ISLAND.** *no collector,* no date (P01466477!); Monte Pelée, *M. Hahn 6,* 1867 (P01557749!); St. Pierre, *Stehlé s.n.*. 13 August 1936 (P01466460!). **PERÚ**. **Dept. Cusco:** La Convención, above Quillouno, *H. van der Werff et al 21062,* 18 April 2006 (NY!); La Convención, Dist. Quellouno, Lacco, Bellavista, *L. Valenzuela 10166,* 23 August 2007 (MO6560309!; MO6560310!; NY02701906!; NY02701907!). **Dept. Pasco:** Dist. Oxapampa, from Antenna past Chacos to the Laguna, *H. van der Werff et al. 19639,* 5 May 2005 (UC1872859! Photo); *ibidem, H. van der Werff et al 19718,* 5 May 2005 (UC1872873! Photo; UC1872874! Photo); Dist. Oxapampa, Parque Nacional Yanachaga-Chemillen, Abra Yanachaga, *R. Vasquez et al 28423,* 1 August 2003 (NY!). **Unknown Department:** *Lechler 2534*, August 1854 (B200031630!, syntype); *ibidem* (B200031631!, syntype); *ibidem*

(B200031632!, syntype). **VENEZUELA. Bolivar:** Distr. Piar, Macizo del Chimantá, valle amplio ubicado en sección SE del Apacará-tepui, en la zona de contacto entre areniscas de la Formación Roraima y extensas intrusiones metamórficas (diabasas) halladas en el sector N del Macizo, *O. Huber et al 8826*, 6-9 February 1984 (NY!, 2 sheets). **Mérida:** *Funk & Schlim 980*, 09.1846 (P01466421!; P01466422!); *J. Linden 980*, 1 September 1846 (P01557743!). **Zulia:** Maracaibo, *Plée s.n.*, no date (P01466413!); *ibidem* (P01466414!); *ibidem, Plée 786*, no date (P01466415!);

Parablechnum lima (Rosenst.) Gasper & Salino, Phytotaxa 275(3): 216. 2016.

Basionym – *Blechnum lima* Rosenst., Repert. Spec. Nov. Regni Veg. 11: 53. 1912.

Type – Bolivia, región andina, Unduavi, Nordyungas, 3400 m, *O. Buchtien 2691* 11.1990 (holotype: US1096191!, isotype: UC477679! photo).

Description – *plants* terrestrial; *rhizome* erect, subarborescent, stem–forming, non-stoloniferous, scaly, scales linear-lanceolate, coriaceous, discoloured, atropurpureous, with lighter brown, entire margins; *fronds* dimorphic or subdimorphic; *sterile fronds* with *petioles* smooth, reddish at base, straw-coloured distally, 30 × 5 cm, densely scaly with triangular–lanceolate scales, cordate at base and acuminate at apex, membranaceous, brown, concolorous, denticulate margin; *lamina* 1-pinnate, triangular–lanceolate, base truncate, gradually reducing distally, with in a conform terminal pinna; *rachis* ribbed, dark reddish brown, with scales similar to those of the rhizome but smaller and lanose indument; *sterile pinnae* in 35 pairs, alternate or subopposite, triangular–linear, base strongly truncate, apex acute or acuminate, margins revolute, serrulate, stalked; *costae* dark reddish brown, smooth, grooved adaxially, with very small ciliate scales, prominent abaxially with scales similar to those of the rachis, more abundant at the base; *veins* catadromous, free, simple or 1-furcate, very prominent adaxially; *aerophores* not observed; *hydathodes* rounded, covered with minute scales; *fertile fronds* similar in size to sterile ones; *fertile pinnae* narrower, linear, truncate base and acute or acuminate apex; *sori* linear, continuous, forming coenosori on both sides of costa, covering the entire pinna except sometimes a small region of the apex; *indusia* linear, continuous, opening towards costa, light brown, entire or slightly lacerate; *sporangia* with (18) 21 (22) arch cells; *spores* monolete, (40) 54 (67) × (27) 38 (50) µm, perisporium smooth to granular, cristate-

reticulate, with low, thick walls, forming large polygonal areoles, with few or no filamentous processes (**Figure 54**).

Chromosome number – unknown.

Distribution and habitat – Peru, Bolivia, Ecuador, Colombia, Venezuela, and Cuba. Locally common, terrestrial in moist forest margins, scrub, and grassland; 2200–3500 m (Smith & Kessler, 2018).

Etymology – the epithet refers to the lime–like texture of the pinnae due to the very prominent veins (R. Moran, pers. com.).

Notes – It can be distinguished from other similar Bolivian species such as *Parablechnum smilodon*, *P. bolivianum*, *P. pazense* or *P. cochabambense* by the very prominent veins. Our molecular results suggest that this species could be a complex of several species.

Reviewed material:

BOLIVIA. Prov. La Paz: Prov. Franz Tamayo, PN-ANMI Madidi, senda Pelechuco-Mojos, localidad Tambo Quemado, *I. Jimenez 1783*, 29 April 2003 (MO5950468!; UC1781481! Photo); Prov. J. Bautista Saavedra M., 15 km de Charazani hacia Chullina, *M. Kessler et al. 10609*, 5 July 1997 (UC1621922! Photo); Prov. Nor Yungas, 0.7 km W of Chuspipata, *J.C. Solomon 13697*, 15 May 1985 (UC1550536! Photo); región andina, Unduavi, Nordyungas, *O. Buchtien 2691* November 1990 (US1096191!, holotype; UC477679! photo, isotype). **ECUADOR. Prov. Chimborazo:** Trail Alao - Huamboya, around the pass, between Cuspipaccha abs alt. 3700 m on E slope, *B. Ollgaard 38218*, 7 May 1982 (NY04187100!). **Prov. Loja:** Nudo de Sabanilla, W slope c. 10 km above Yangana on road to Valladolid, *G. Harling & L. Andersson 23590*, 3 April 1985 (MO4938179!); Parque Nacional Podocarpus, at pass on road Yangana-Valladolid, *B. Ollgard & J.E. Madsen 74285*, 21 May 1984 (MO6021443!; NY04187101!); Parque Nacional Podocarpus, above Nudo de Cajanuma, *J.E. Madsen et al 74479*, 25-26 May 1988 (MO4666586!); Limon Idanza, cordillera de Huaracayo, east of cordillera del Cóndor and Río Cangos; Parque Nacional Podocarpus, Cajanuma, *M. Lehnert 2193*, 27 November 2010 (VT198726!); *ibidem*, *M. Lehnert 2248*, 2 December 2010 (VT198728!). **Prov. Morona-Santiago:** Cerro Ijiach Naint, flat-topped sanstone mountain, east of

Shuar village of Tinkimints, *D. Neill & J. Manzanares 13118*, 22 March 2001 (NY04187187!; UC1750642! Photo); Comunidad Shuar "Wisui", below top of El Torre, *J. Michel 13*, 6 March 2013 (VT198671!); Trail Alao-Huamboya, eastern slopes above and around La Magdalena, *B. Ollgaard et al. 38318*, 7 May 1982 (NY!); *ibidem*, *B. Ollgaard et al. 38324*, 7 May 1982 (NY!; UC1539399! Photo). **Prov. Napo:** slopes of Guagra Urcu, on the loma above upper Río Borja, *L.B. Holm–Nielsen et al. 2709*, 25 September 1980 (P00904691!).

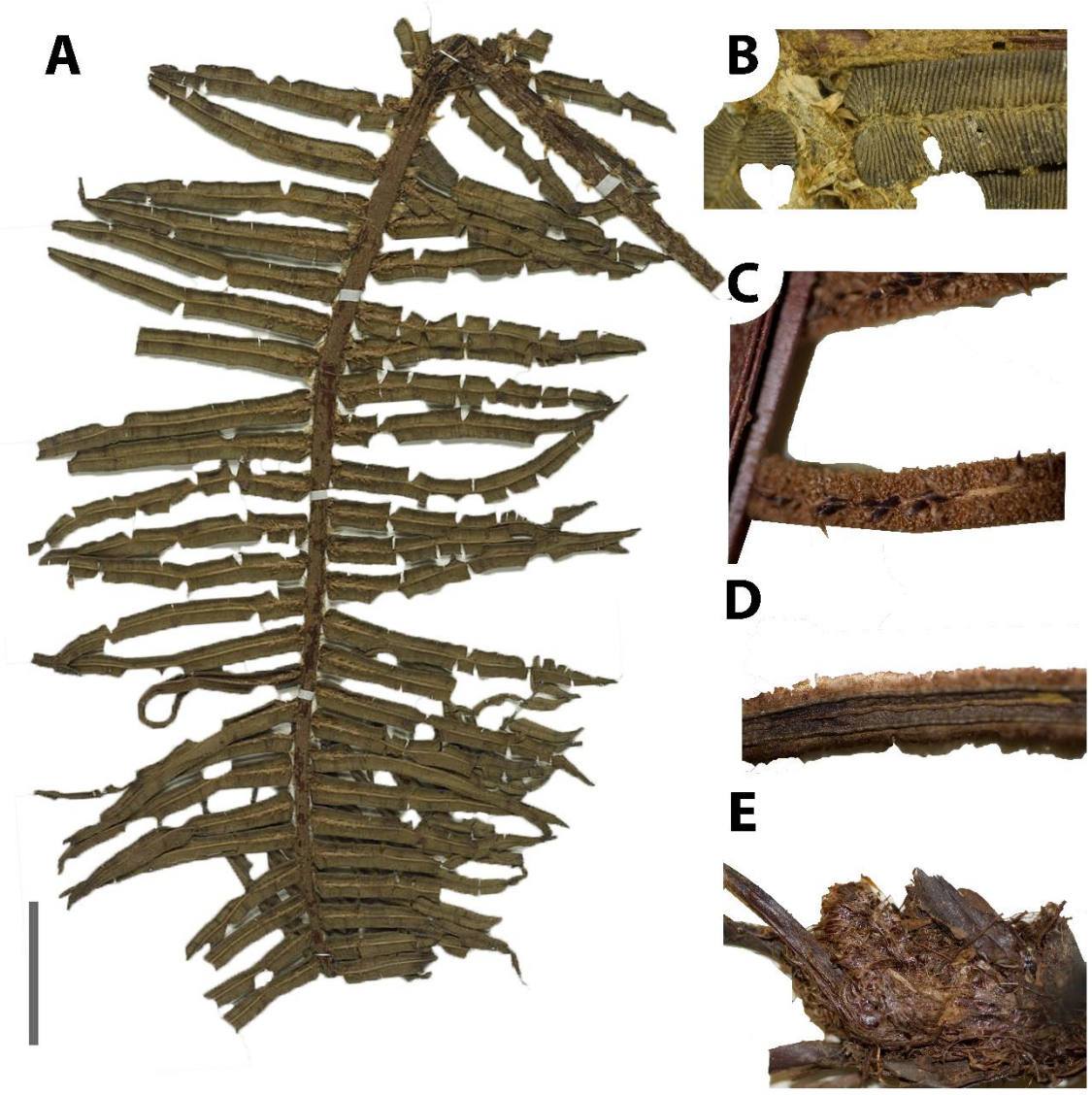

Figure 54. *Parablechnum lima.* A. Fragment of a sterile frond; B. Detail of sterile pinnae, adaxial side; C. Detail of fertile pinnae, abaxial side; D. Detail of a fertile pinna, adaxial side; E. Detail of a rhizome. (A: *O. Buchtien 2691*, US00067430, holotype; B: *O. Buchtien 2691*, UC477679, isotype; C-E: *I. Jimenez 1783*, UC1781481). Scale: 5 cm in A; 1.3 cm in B; 0.7 cm in C; 0.8 cm in D; 3 cm in E.

Parablechnum lineatum (Sw.) Gasper & Salino, Phytotaxa 275(3): 216. 2016.

Basionym – *Osmunda lineata* Sw., Prodr. 127. 1788.

Type – Jamaica, *Swartz s.n.* (holotype: S167175 v.ph.; isotypes: SR3823 v.ph., SR678 v.ph., US!).

Synonyms –

≡*Blechnum lineatum* (Sw.) C.Chr., Index Filic. 156. 1905; *Lomaria lineata* (Sw.) Willd. In L., Sp. Pl. 5: 290. 1810; *Onoclea lineata* (Sw.) Sw. in J. Bot. Schrader 1800(2): 73. 1802; *Struthiopteris lineata* (Sw.) Broadh. In Bull. Torrey Bot. Club 39: 366. 1912.

Description – *plants* terrestrial; *rhizome* ascending or erect, non-stoloniferous, densely scaly, scales oblong-lanceolate, 1–2 cm long, light reddish brown, very thin and membranaceous; *fronds* dimorphic, clustered; *sterile fronds* 50–170 cm long; *petioles* usually as long as lamina, light yellowish brown, densely covered at base with scattered, deciduous, rhizome-like scales; *laminae* leathery, oblong to narrowly lanceolate, 30–100 × 10–50 cm, 1-pinnate, slightly narrowed at base, apex with a more or less elongate conform terminal pinna; *rachis* rugulose–papillose, deciduously scaly like petiole, the position of the fallen scales marked with raised dark dots; *sterile pinnae* in 18–40 pairs, linear-oblong, 5–25 × 0.9–2.2 cm, falcate–acuminate at apex, base cordate, shortly stalked, becoming basiscopically adnate distally, margins finely denticulate especially towards apex and often minimally revolute, alternate to subopposite; *costae* and sometimes the tissue with fibrillose scales on abaxial side, grooved adaxially, prominent abaxially; *veins* free, simple or 1-furcate near base, slightly grooved adaxially, prominent abaxially, catadromous; *aerophores* elongate, tuberculiform, dark; *hydathodes* round, ovate, inconspicuous in dry specimens; *fertile fronds* erect, equal to or longer than sterile ones; *fertile pinnae* narrowly linear, 5–18 × 0.3–0.4 mm, with long acuminate sterile apices; *sori* linear, continuous, forming coenosori on both sides of costa, covering the entire pinna except for the apex; *indusia* linear, continuous, open towards costa, irregularly lacerate; *sporangia* with (18–) 18 (–22) arch cells; *spores* monolete, (43–) 57 (–66) × (29–) 41 (–52) µm, perispores smooth to granular, with possible globules, cristate-reticulate, with high, thin, sharp walls, forming a reticulum or large areoles, without filamentous processes or with some scattered long filaments in areole lacunae (**Figure 55**).

References – Proctor (1985).

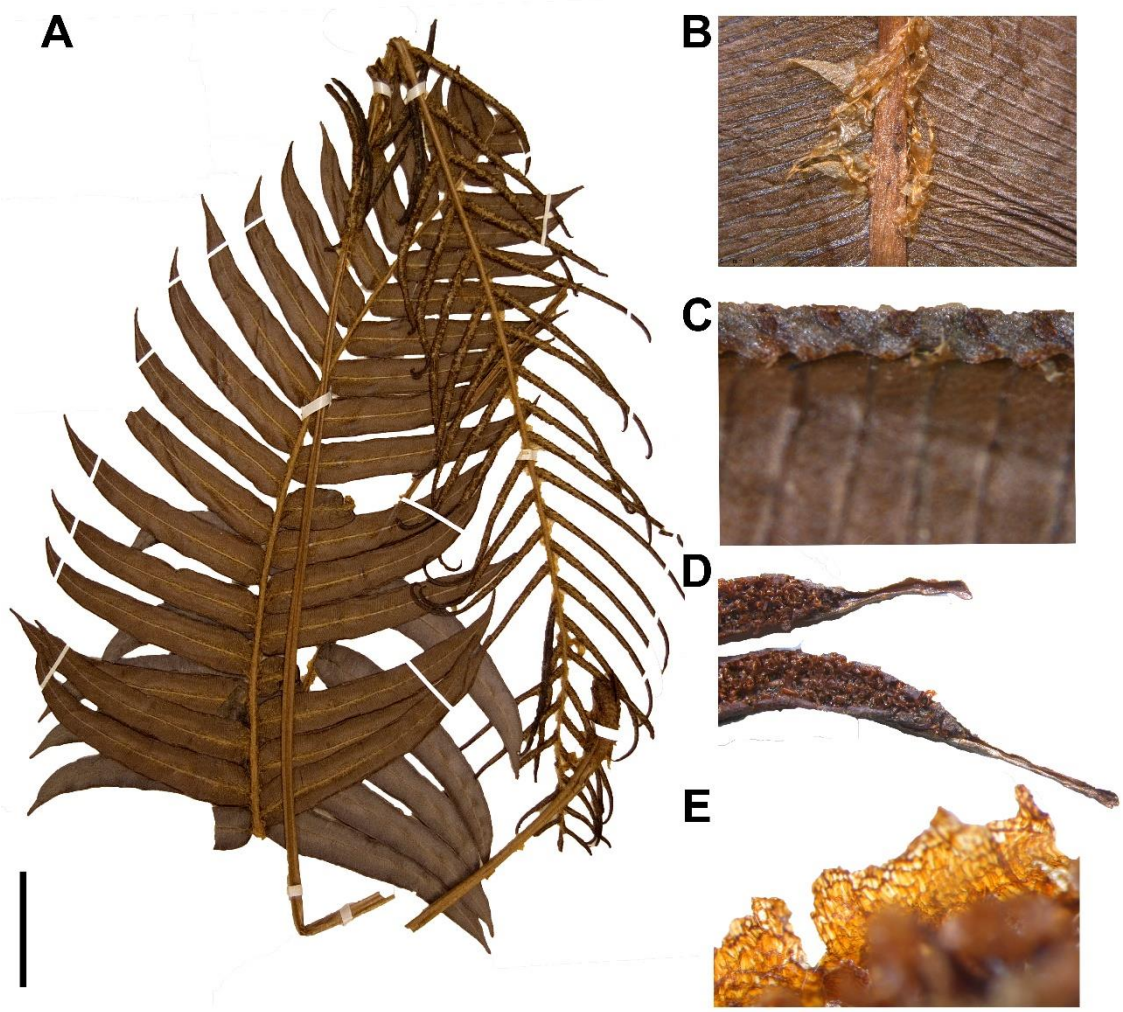

Figure 55. *Parablechnum lineatum.* A. Sterile frond (left) and fertile frond (right); B. Detail of pinnae surface, abaxial side; C. Detail of sterile pinna margin; D. Detail of fertile pinnae apexes, abaxial side; E. Indusium. (A: *G.F.P. s.n.*, UC1043051; B&C. *W.R. Maxon 1049*, US427309; D: *W.R. Maxon & E.P. Killip 610*, US1045373); E: *G.R. Proctor 4363*, US2017954). Scale: 5 cm in A; 3.6 mm in B; 1.2 mm in C; 4 mm in D; 571 µm in E.

Chromosome number – unknown.

Distribution and habitat – Cuba, Jamaica, and Puerto Rico. Here we have found specimens from Guadeloupe (P01546405) and Dominican Republic (P01409496; P01623188; US3564862). Found on exposed banks, rocky slopes, and humid montane forests at mid to high elevations, 503–2257 m. Common (Swartz, 1788; Proctor, 1985).

Etimology – the epithet "lineatum" refers to a surface covered by parallel lines (the veins).

Notes – according to Proctor (1985) there are plants growing in exposed situations which may be much smaller when mature.

Reviewed material:

CUBA. Prov. Granma: Oriente, camp La Gloria, South of Sierra Moa, *J.A. Shafer 9038*, 23-30 December 1910 (US657905!); Oriente, road from Aserrado San Antonio de los Cumbres to La Bayamesa, crest of Sierra Maestra, *C.V. Morton 9315*, 22 January 1956 (US2418020!); Sierra Maestra, at top of Loma Giganta, *E.L. Ekman 16094*, 4 January 1923 (US1301511!). **Prov. Guantánamo:** Oriente, trail Camp Toa to Camp La Barga, *J.A. Shafer 4150*, 22-26 February 1910 (NY02007531!; US657796!). **Prov. Oriente:** Camp La Gloria of Sierra Moa, *J.A. Shafer 8059*, 24-30 December 1910 (NY02007532!); Sierra Maestra, La Bayamesa, *C.V. Morton 9315*, 21 September 1960 (UC1181593! Photo); Sierra Maestra, on the ascent from Finca Reunión to the top of Loma del Gato, *E.L. Ekman 6972*, 29 March 1916 (NY02007528!; UC618038! Photo; US1476859!). **Prov. Santiago de Cuba:** around Sierra Maestra, Loma del Gato, *Frére Clement 1354*, 08.1924 (US1148272!); debajo de la Gran Piedra, *Bro. Clement 6677*, July 1949 (US2016145!); *ibidem*, *Bro. Clement 6678*, July 1949 (US2016146!); El Cobre, Loma del Gato et environs, Sierra Maestra, *Frére Clement 844*, August 1923 (US1148219!); *ibidem*, *Frére Clément 2415*, August 1938 (US1713132!); La Gran Piedra, *J.A. Shafer 8059*, 4-5 March 1911 (US658095!); *ibidem*, *J.A. Shafer 9038*, 4 March 1911 (NY02007529!); Loma del Gato and environments, Sierra Maestra, *Bro. Hioram & Bro. Clement 6393*, August 1903 (US1146232!); Loma del Gato, Srra. Maestra, Oriente, *Bro. Clement 1073*, December 1923 (US1147539!); Loma del Gato, *Clément 844*, August 1923 (P01623250!; P01623260!); *ibidem*, *Bro. Clément 2090*, no date (US1559771!); Pico Turquino, north saddle, *Ekma 5451*, no date (US1476856!); Pico Turquino, on very top of the mountain, *E.L. Ekman 14552*, 22–24 July 1922 (US1301476!); Southern oriente and Pico Turquino, *Fre. Leon 11124*, July 1922 (NY!; US1049925!); *ibidem*, *Fre. Leon 11129*, July 1922 (NY00814151!). **Unknown area:** Linden, *ex herb. Horti*, no date (US1786159!).. **DOMINICAN REPUBLIC.** *Toepffer 709*, 02.1882 (P01409496!; P01623188!); **Prov. La Vega:** Reserva Científica Ébano Verde, *P. Acevedo–Rdgz et al 12630*, 28 May 2003 (NY02007578!; US3564862!). **GUADALOUPE.** *Leprieur 24*, no date (P01546405!). **JAMAICA.** *no collector*, no date (NY02007546!); *C.F. Baker s.n.*, 1902 (P01624652!); *ibidem* (P01624653!); *Ebbeke s.n.*, 1885 (P01546407!); *Ebbeke 709*, 1880 (P01409489!; P01409490!; P01409491!; P01409492!; P01409493!); *J. Hart 134*, no date (US0834088!; US0834089!); *Eggers 3659*, 25 January 1888 (P01575944!); *G.L.*

Fisher 152, 30 July 1907 (NY02007523!); *G.S. Jenman s.n.*, 1874-1879 (NY02007542!); *ibidem* (NY02007547!); *ibidem* (NY02007571!); *ibidem* (NY02007573!); *ibidem* (NY!); *Swartz s.n.*, no date (P01396004!, SR678! Photo, isotype); *ibidem* (P01396005!, SR3823 v.ph., isotype); *ibidem* (P01396006!, S167175! photo, fertile frond right holotype, the sterile frond at left is *Cyclopeltis semicordata* and is probably part of the type of *Polypodium semicordatum*); Blue Mountain Peak, *L.M. Underwood 1446*, 11-12 February 1903 (NY02007539!; NY02007540!; NY02007545!); *ibidem*, *W.R. Maxon & D.P. Killip 1125*, 16 March 1920 (NY02007566!); Chesterdale, near Newcastle in the Blue Mountains, *M. Carhart s.n.*, 15 March 1909 (NY2007522!); Cinchona, *Killip s.n.*, 18 January 1917 (P01396011!); *ibidem*, *W.N. Clute 71*, 6 February 1900 (NY02007570!; NY02007572!; US349371!); Cuna Gap, St. Thomas, forested ridge east of Cuna, *W.R. Maxon 9440*, 22 June 1926 (NY02007574!); Cuna Gap, St. Thomas, Mountain trail between House Hill and Cuna, *W.R. Maxon 8939*, 7 June 1926 (NY02007568!); crest of Gossamer peat, St. Thomas, *W.R. Maxon 9275*, 16 June 1926 (US1182770!); deep ravine in mountain forest above House Hilla, St. Thomas, *W.R. Maxon 9115*, 6-12 June 1926 (US1182635!; US1182636!); eastern ridge of Stone Hole Bump, St. Thomas, *W.R. Maxon 9510*, 23 June 1926 (US1182988!); Filabess River, *M.D. Walt 78*, 27 April 1909 (P01396009!; P01396010!); flamstead and vicinity, Port Royal Mountains, *W.R. Maxon 8632*, 31 May 1906 (NY02007538!; US1182227!); forested ridge east of Cuna Cuna Gap, St. Thomas, *W.R. Maxon 9440*, 22 June 1926 (US1182921!); John Crow Mountains, southwest end, ridge from Corn Puss Gap to Crown Peak, *K.A. Wilson & W. Murray 578*, 14 August 1954 (US2254537!); John Crown Peak, *N. Faucett s.n.*, 8 August 1889 (US521810!); Linchona, *L.M. Underwood 2586*, April 1903 (NY02007553!); lower slopes of Mt. Moses, *W.R. Maxon 1049*, 14 April 1903 (US427308!; US427309!; US427310!); Mabess River, *M.D. Watt 78*, 27 April 1909 (US2703289!; US2703312!); "main ridge gap" and vicinity (East of Mossman's Peak), *W.R. Maxon 10242*, 15 July 1926 (US1183616!; US1183617!); Morse's Gap, *C.H. Farr s.n.*, November-December 1915 (NY02007554!); *ibidem*, *E.H. Day s.n.*, no date (NY02007556!); *ibidem* (NY02007557!); *ibidem*, *E.H. Day s.n.*, 1891 (NY02007535!); *ibidem*, 4 June 1891 (NY02007536!); *ibidem*, *L.M. Underwood 522*, 2 February 1903 (NY02007550!; NY02007551!; NY02007552!; U0S521194!); *ibidem*, *L.M. Underwood 1534*, 14 February 1903 (NY02007567!); Mountain trail between House Hill and Cuna, Cuna Gap, St. Thomas, *W.R. Maxon 8938*, 7 June 1926 (US1182481!); New Haven gap, *L.M.*

Underwood 1017, 4 February 1903 (NY02007541!; NY02007543!); Perk forest, Blue Mountain, *R.C. Alexander s.n.,* 28 March 1950 (US1411347!); Portland, Hardwar Gap, Hollywell Recreational Park, ravine of Hollywell, near parking and load down to the waterfall, *M.J.M. Christenhusz et al 3043,* 13 January 2004 (NY02007534!); Portland, Sugar loaf peak, *G.R. Proctor 4363,* 28 April 1950 (US2017954!); road to Cinchona to Morse's gap, *L.M. Underwood 258,* 30 January 1903 (NY02007555!; NY02007569!); Saint Andrew, *W.N. Clute 71,* 6 February 1900 (P01546402!); Saint Andrew, in opening summit of Mt. Horeb, above Woodcutter's Gap, *T.G. Yunker 17547,* 23 November 1957 (NY02007549!; NY02007559!); Saint Thomas, deep ravine in mountain forest above House Hill, *W.R. Maxon 9115,* 6-12 June 1926 (NY02007575!); Silver Hill Gap, *W.R. Maxon 10280,* 20 July 1926 (US1183650!); summit of Blue Mountain Peak, *W.R. Maxon 9988,* 79 July 1926 (NY02007561!; NY02007562!; US1183392!); trail between Portland Gap and Blue Mountain, *E.B. Copeland s.n.,* 15 July 1932 (UC1043051! Photo); trail from St. Helens Gap to Latimer River, *W.R. Maxon & E.P. Killip 911,* 9 March 1920 (NY02007564!; US1045516!); Tweebide, *L.M. Underwood 2047,* 10-13 April 1903 (NY02007544!); *ibidem, L.M. Underwood 2098,* 10-13 April 1903 (NY02007548!; NY02007558!; NY02007560!); upper slopes of Blue Mountain Peak, *W.R. Maxon & E.P. Killip 1125,* 16 March 1920 (NY02007566!; US1045620!); upper southern slopes and summit of Maccasucker Bump, St. Thomas, *W.R. Maxon 9587,* 25 June 1926 (US1183047!); vicinity of Cinchona, New Haven Gap, *L.M. Underwood 3134,* 2 September 1906 (NY02007533!); vicinity of House Hill, St. Thomas, *W.R. Maxon 9115*, June 1926 (P01396008!); vicinity of St. Helens Gap, St. Andrew, *W.R. Maxon & E.P. Killip 610,* 4 March 1920 (NY02007563!; NY02007565!; US1045372!; US1045373!). **PUERTO RICO.** Catalina-Yunque trail, Luquillo mountains, El Yunke, *N.L. Britton & E. Murray Bruner 7632,* 23-26 February 1923 (NY00901731!; US1145573!); Cerro de Punta, Jayuya, *H.A. Liogier et al 37154,* 2 September 1993 (MO4901087!); El Yunque, *C.F. Carroll 10,* 30 March 1987 (VT198700!); *ibidem, F.H. Sargent 282,* 10 April 1938 (US1713109!); El Yunque, N branch of Rio Sonadora, *D.S. Conant 210,* 12 July 1992 (VT198699!); Ponce, Bosque Estatal de Toro Negro, ~km 20 on hwy 143, border with Jayuya, *S. Fawcett & A.A. Reznicek 477,* 12 January 2016 (VT198703!; VT198696!); rt 143, Monte Jayuya, *C.F. Carroll 54B,* 3 April 1987 (VT198697!; VT198698!); Saint Andrew, *P.N. Fraser s.n.,* 1896 (P01546401!); *ibidem* (P01546403!); Naguabo, Rio Blanco, Caribbean National Forest, Dwarf forest, near radio antennas at Pico del Este, *J.*

Vélez-Gavilán et al 287, 21 March 1997 (NY02330087!); Sierra Luquillo, *M.A. Sundue 8,* August 1999 (VT198701!); *M.A. Sundue 9,* August 1999 (VT198702!); Sierra de Luquillo, El Yunque, *C. Sanchez & A. Liogier 119,* 18 August 1994 (NY01044186!); Sierra de Luquillo in monte Jimenez, *M. Kuhn 1337,* 9 July 1885 (P01409497!; P01409498!; P01409499!; US0827935!); *ibidem, P.E.E. Sintesis 1337,* 9 July 1885 (NY00901718!); Sierra de Naguabo, Monte El Duque, Mountain Junker, *J.A. Shafer 2247,* 8 March 1914 (NY00901729!; NY00901730!); Sierra de Naguabo, Quebrada Grande to Cuchilla Firme, *J.A. Shafer 3595,* 6 August 1914 (NY00901714!; NY00901717!); Sierra de Naguabo, summit of Loma La Mina, *J.A. Shafer 3324,* 20 July 1914 (VT285878!); *ibidem, J.A. Shafer 3334,* 20 July 1914 (NY00901715!; NY00901716!). **UNKNOWN LOCATION:** *no collector,* 1 January 1898 (P01546406!).

Parablechnum loxense (Kunth) Gasper & Salino, Phytotaxa 275(3): 216. 2016.

Basionym – *Lomaria loxensis* Kunth, Nov. Gen. Sp. (quarto ed.) 1: 18–19. 1815 [1816].

Type – Ecuador, Loja, *Humboldt & Bonpland s.n.* (holotype: P00669195!; isotypes: B200031696!).

Synonyms –

≡*Blechnum loxense* (Kunth) Hook. ex Salomon, Nomencl. Gefässkrypt. 117. 1883.

Description – *plants* terrestrial; *rhizome* erect, subarborescent, forming a massive stem up to 1 m high, non-stoloniferous, densely scaly, scales 10–30 × 2–6 mm, ovate to lanceolate, concolorous, light orange or brownish, margins entire, sometimes discoloured, with darker and leathery centre; *fronds* monomorphic or subdimorphic, but appearing dimorphic because of narrow, strongly revolute pinnae; *petioles* 6–21 cm, brown or slightly reddish, base scaly with rhizome-like scales, distal portions glabrous or scaly, with scales 2–5 × 1–2 mm, lanceolate, straw–like, always concolorous; *lamina* 18–30 × 4–8 cm, narrowly ovate, 1-pinnate, abruptly reduced at base, the apex ending in a conform terminal pinna similar in shape to the lateral pinnae; *rachis* smooth, straw to yellowish-brown, densely scaly; *pinnae* in 18–25 pairs, 2.5–7 × 0.3–0.7 cm, ascending, linear, bases subcordate, apices rounded, strongly revolute, with wavy margins, ciliate, stalked, the basal ones sometimes slightly reduced; *costae* straw-coloured, grooved adaxially,

prominent abaxially, densely scaly abaxially, the scales concolorous, brownish to light orange; *veins* free, simple or 1-furcate; *aerophores* absent; *hydathodes* rounded or ovate; *fertile fronds* similar or equal to sterile ones, sometimes longer, with petioles up to 30 cm long; *sori* linear, continuous, forming coenosori on both sides of costa, occupying the entire pinna; *indusia* linear, continuous, open towards the costa, strongly lacerate, *sporangia* with 16–21 cells in the arc; *spores* monolete, (45–)47(–50) × (35–)38(–43) µm, with perispores 1.9–2.0 µm thick, crested–reticulate delimiting polygonal areoles with long filaments very abundant in the areole lacunae and on the walls (**Figure 56**).

References – Moran (1995a), Passarelli *et al.* (2010), Sundue (2010), Rolleri *et al.* (2012a), Prada *et al.* (2016).

Chromosome number – unknown.

Distribution and habitat – Costa Rica, Panamá, Colombia, Venezuela, Ecuador, Perú, Bolivia. Locally common, terrestrial in humid forests, scrub, and grasslands near the forest line, in paramos and cloud forests. 2800–4100 m (Moran, 1995a, Sundue, 2010; Smith & Kessler, 2018).

Etymology – The epithet makes reference to Loja, Ecuador, where the type was collected.

Notes – specimens with abundant mucilage have been seen in young circines (Moran, 1995a). *Parablechnum loxense* has sometimes been confused with other arborescent species of the genus *Lomariocycas* such as *L. aurata* and *L. schomburgkii* and can be distinguished by the size of the scales at the base of the stipe. *Parablechnum loxense* has scales 10–25 × 2–5 mm, broad and lanceolate, while *Lomariocycas aurata* and *Lomariocycas schomburgkii* have scales 20–50 × 1–2 mm, narrow and acicular. Our phylogenetic results together with the variation found on the spores suggests that this taxon is a complex of several species.

Reviewed material:

BOLIVIA. Dept. Cochabamba: Sailapata, Ayopaya, *M. Cárdenas 3140,* December 1935 (LIL536181! Photo). **Dept. La Paz:** vicinis Lorata, Cuchipata, Marcamarcani, *G. Mandon 1579,* 7 September 1887 (NY!); Vicinis Sorata, Cochipata, *G. Mandon 1579,* 7 November 1857 (P01462421!; P01462422!; P01462423!; US2786069!). **Dept. Santa**

Cruz: Prov. Caballero, Loc. Cerro Curucucho, cerca de 1 km ENE de Siberia, *M. Saldias & M. Fernández 4563*, 24 July 1996 (NY!). **Unknown Department:** *R.S. Williams 2580*, 30 April 1902 (NY!). **COLOMBIA. Dept. Antioquia:** en una meseta a 1 kilómetro al norte de Santa Rosa de Osos, *S. Pesada S. & F. A. Barkley W. 18AD01*, 25 September 1948 (US3147920!); Mun. Belmira, Sitio El Yerbal, camino hacia el páramo de Santa Inés (área de reserva sistemá de páramos), *W. Rodríguez et al 3426*, 19 June 2002 (NY!); Mun. Ituango, camino entre El Retiro y Cerro Paramillo, *H. Cuadros 4977*, 25 February 1993 (US3346280); Páramo Frontino, near Llano Grande, *J.D. Boeke & J.B. McElroy 233*, 25 October 1976 (NY!, 2 sheets). **Dept. Boyacá:** beside path to Raton, Sierra Nevada de Cocuy, *P.J. Grubb & D.A. Guymer 47*, 15 August 1957 (US2295593!); Cordillera Oriental, Vertiente Oriental, carretera Sogamoso a Pajarito, en el Valle del río Cusiana, cerca de Vadohondo, *R. Jaramillo et al 3740*, 19 October 1967 (NY!); Mun. Duitama, corregimiento El Cármen, vía a Virolín, páramo de La Rusia, *J. Betancur et al 5602*, 19 November 1994 (NY!). **Dept. Caldas:** Carretera entre Manizales y El Hotel Termales del Ruiz, *E. Forero et al. 534*, 8 June 1966 (NY!). **Dept. Cundinamarca:** 4 m northwest of Zipaquirá, Pantano Redondo, *R.M. Tryon & A.F. Tryon 6057*, 14 October 1961 (P01395964!; US2722275!); Bogotá, *Apollinaire s.n.*, 1 July 1905 (P01546432!); *ibidem*, 1 June 1906 (P01546428!); Bogotá, páramo de Monserrate, El Granizo, *J.L. Fernández Alonso et al. 5134*, 8 February 1986 (MA517122!); Cordillera Oriental, ersait Sud da Paramo Cruz Verde su Bogotá, *E. Mayor 19ª*, 14–15 October 1910 (US1197103!); Delicias, *B.T. 944*, no date (NY!); Dist. Especial de Bogotá, Páramo de Chisacá, lomas cerca a la Laguna, *M.T. Murillo & L.S. Fayad 47*, 10 February 1961 (NY!); Dist. Especial, Valle del río Tunjuelo en el Páramo de Chisacá, alrededores de la Laguna Grande, *M.T. Murillo et al.772*, 21 May 1964 (NY!; P01395968!; US2850951!); entre Zipaquirá y Pacho, Páramo de Guerrero, *M.T. Murillo & M. Villarreal 1358*, 9 June 1970 (P01395967!); Fusaguasua, *J. Dwyer & J. Idrobo 8176*, 35 August 1978 (NY!); Mun de la Calera, Páramo de la Siberia, *H. Humbert et al 26859*, 25 October 1952; *ibidem*, *H. Humbert et al 26877 bis*, 25 October 1952 (P01395972!; P01395973!); Mun. Madrid, autopista Bogotá-Medellín, bosques en contorno a la casa de L. Richter, *M.T. Murillo & L. Sandoval 538*, 23 November 1961 (NY!); Mun. Usme, Páramo de Sumapaz, pp-SA, *J. Betancur & O. Marulanda 153*, 26 July 1986 (NY!); near San Miguel, along road from Bogotá to Fusagasugá, Eastern Cordillera, *E.P. Killip 38085*, 30 April 1944 (US1856456!); Páramo de Coachi, near Bogotá, *E.P. Killip & Bro. Ariste–Joseph 11932*,

8 August 1922 (NY!; US1140015!); Páramo de Chisacá, *R.E. Schultes 22422*, 8 July 1960 (NY!); Páramo de Cruz Verde, *M.T. Murillo 415*, 17 October 1967 (NY!); Páramo de Cruz Verde, 8 km east of Bogotá, *R.M. Tryon & A.F. Tryon 6079*, 16 October 1961 (NY!; US2722276!); Páramo de Cruz Verde, Alto de La Viga, flanco N, *A.M. Cleff 2842*, 12 April 1972 (US2949609!); Páramo de Palacio, 10 km. East of La Calera, 20 m northeast of Bogotá, *R.M. Tryon & A.F. Tryon 6027*, 10 October 1961 (NY!; P01395963!; US1722288!). **Dept. Huila:** "Balsillas" on Rio Balsillas, *H.H. Rusby & F.W. Pennell 750A*, 3-6 August 1917 (NY!); *ibidem, H.H: Rusby & F.W: Pennell 768*, 3-5 August 1917 (NY!). **Dept. Magdalena:** Sierra de Perijá, east of Manaure, Sabana Rubia, *J. Cuatrecasas & R. Romero Castaneda 25051*, 7 November 1959 (US2294877!). **Dept. Nariño:** Mun. De Pasto. Entre km 29-30, carretera Pasto-San Francisco (Putumayo), *S.P. Churchill & W. Rengifo M. 17495*, 15 January 1991 (NY!). **Dept. Santander:** Cordillera Oriental, Páramo del Almorzadero, extremo sur Peralonso, *J. Cuatrecasas & H. Garcia Barriga 9884*, 19 July 1940 (US1851879!); edg of Páramo de Santurbán, near Vetas, *E.P. Killip & A.C. Smith 17947*, 17 June 1927 (NY!); Páramo de las Coloradas, above La Baja, *E.P. Killip & A.C. Smith 18463*, 27 January 1927 (NY!; US1353876!); Eastern Cordillera, edge of Páramo de Santurbán, near Vetas, *E.P. Killip & A.C. Smith 17947*, 17 January 1927 (US1353452!); Páramo de Chisacá, *T.R. Soderstrom 1328*, 8 September 1966 (US3136710!). **Dept. Sonsón:** Mpio. Sonsón, vereda Chaverras, vertiente de la quebrada "El Padre Sanchéz", ascenso al alto "La Paloma", *R. Callejas & F.J. Roldán 10644*, 19 August 1992 (NY!). **Dept. Tolima:** Cordillera Central, La Línea, Cerro El Campanario, *J. Cuatrecasas & R. Echeverry 27677*, 4 March 1969 (NY!; P01623173!; US2651398!). **COSTA RICA. Prov. Cartago:** Cerro de la Muerte, *D. Barrington 353*, 28 December 1970 (VT198692!); Cerro de la Muerte (Cerro Sakina), Paramo Buenavista, *H. Churchill 3370*, 20 February 1980 (VT198691!; VT198695!). **Prov. San José:** along Interamerican Hwy. (Rt. 2), Cerro Chirripó, *A.M. Evans et al 139*, 24-26 August 1967 (MO2612371!)Cerro de la Muerte, SE of road to radio towers, *S.R. Hill et al 17559*, 2 January 1987 (NY!; VT020021!; VT289536!). **ECUADOR. Prov. Carchi:** about 1/2 hr. E of Huaca, past Colonia Huaceña, *H. van der Werff & W. Palacios 10620*, 18 February 1989 (NY!); Canton Espejo, paramo del Azufral, east of Angel, *Y. Mexia 7533*, 17 July 1935 (US1663955!); Páramo de El Ángel, *F. Hekker & W.H.A. Hekking 10295*, 29-30 November 1987 (NY!); Páramo de El Ángel, *Padilla & Proaño 43*, 2 July 1975 (NY!); road Julio Andrade-Palestina, *L. Holm-Nielsen et al 29614*, 27 December 1980 (NY!);

San Gabriel in ref. "paramo", *I. Holmgren 876,* 18 August 1920 (US1284949!). **Prov. Cañar:** Azogues, Gualleturo, vertiente occidental de los Andes, 20 km al oeste de Cañar, Sector Ventanas, km 6 del cruce la via Purbín-Buquiar, *H. Vargas & W. Defas 6090,* 30 July 2005 (MO6389461!); Páramo, *J.N. Rose & R.G. Russell 22692,* 15 September 1918 (US1022328!). **Prov. Chimborazo:** along ravine in mountains between Baños and Riobamba, *D.S. Correll E22,* 12 March 1958 (US2256313!); road ca 4 km E of Alao, *B. Ollgaard et al. 37946,* 5 May 1982 (NY!); sudl. Riobamba, Paramogebiet, *H.J.F. Schimpff 880,* 22 March 1934 (US2015621!; US1740131!); Trail Alao - Huamboya, around the pass, between Cuspipaccha abs alt. 3700 m on E slope, *B. Ollgaard et al 38216,* 7 May 1982 (NY!). **Prov. Cotopa:** Paramo along Salcedo-Napo Road, *B. Ollgaard 52530,* 3 February 1985 (NY!). **Prov. Imbabura:** Lago San Marcos, *Cayambe, P.C.D. Cazalet & T.D. Pennington 5458,* 1 December 1961 (NY!). **Prov. León:** railway station Cotopaxi, *E. Asplund 6503,* 16 May 1939 (US3192297!). **Prov. Loja:** *Bonpland s.n.*, no date (B200031696!, isotype; P00669195!, holotype). **Prov. Napo:** Archidona Canton, Sumaco, Napo-Galeras, National Park, *J.L. Clark 2226,* 16 March 1996 (NY!, US3597815!); junction of Río Chalupas and Río Aguas Buenas, cataract at the E end of the upper Chalupas valley, *L. Holm-Nielsen 19097,* 11 August 1979 (NY!); Oyacachi, Pot 3TE-05, *M. Lehnert 3189,* 4 March 2015 (VT198694!); Papallacto, *L. Mille s.n.,* no date (US1192045!); *ibidem, L. Mille 2,* 1917 (NY!); Quijos, Laguna de Papallacta, sector SW, *A. Álvarez 1564,* 29 July 1995 (NY!); road Quito-Baeza, at Laguna de Papallacta, *B. Ollgard & H. Balselv 8045,* 17 July 1976 (NY!). **Prov. Pichincha:** Andes Quitenses, *A. Sodiro 17/93,* no date (P01624674!; P01624675!); Cayambe, *T.D. Pennington s.n.,* 19 October 1960 (NY!); Guamaní, *A. Mille 51,* no date (P01396008!). **Prov. Tungurahua:** around Lago Pisayambo, 1 hour from Ambato by car, *D.H. Knight 264,* 26 December 1964 (NY!). **Unknown Province:** *A. Sodiro s.n.,* no date (P01462850!); *ibidem* (US2786111!); *Bonpland s.n.,* no date (P01409529!); *ibidem* (US2361969!); *J.N. Rose & G. Rose 22692,* 15 September 1918 (NY!). **Prov. Azuay:** Cuenca, Cuenca-Loja Rd. about 50 km S. of Cuenca, just N. of La Paz, *Mirabai R. McCarthy & Eric Tepe 230,* 30 July 2011 (NY!); Cuenca, Parque Nacional Cajas, km 32,1 desde redondel Cuenca-Molleturo. Bosque de Polylepirs debajo de la casa de información, Laguna La Toreadora, *C. Ulloa et al 1058,* 9 January 2003 (NY!, 2 sheets); Páramo de Soldados, at highest point of road W of Soldados, *B. Ollgaard et al 58520,* 3 March 1985 (NY!); *ibidem, B. Ollgaard et al 58521,* 3 March 1985 (NY!). **PANAMÁ. Prov. Chiriqui:** Loma Larga to summit, Volcán

de Ciriquí, *R.E. Woodson et al 1067*, 4-6 July 1938 (NY!). **PERÚ. Dept. Ayacucho:** Pampalca, between Huanta and Río Apurimac, *E.P. Killip & A.C. Smith 23258*, 4, 5, 18 May 1929 (NY!). **Dept. Cajamarca:** Hualganca, *Soukup–Carmona 5011*, 28 June 1968 (LP9190250! Photo; US2849507!; US2828652!). **Dept. Cusco:** Calca, Dist. Yanatile, *I. Huamantupa 9788*, 10 June 2007 (MO6560300!); Paucartarmo, *C. Vargas Calderón 2219*, no date (US1803634!); Paucartambo, Hacienda Cluru, *F.L. Herrera 1028a*, January 1926 (US1281815!). **Dept. Junín:** Mito, *Macbride & Featherstone 1790*, 1922 (MA467910!). **Dept. Lamayeque**, Prov. Ferreñafe, Laguna Tembladera, Distrito Incahuasi, *D. Skillman et al. 12781*, 11 September 1985 (NY!). **Dept. Lucanas:** Agapata, *W. Lechler 2025*, June 1854 (P01462409!; P01462419!). **VENEZUELA. Lara:** Parque Nacional Dinira, ladera del Páramo de Jabón, vertiente hacia el Tocuyo, sector "Los Charquitos", *R. Riina et al 702*, 15 August 1999 (NY!; US3402332!); Parque Nacional Dinira, laderas nororientales del Páramo de Cendé, Sector "Las Lajitas", *R.Riina & R.Duno 1232*, 10 January 2001 (NY!); wet meadow at Las Sabanetas, above Los Aposentos, west of Humocaro Bajo, *J.A. Steyermark 55286*, 5 February 1944 (US1916349!). **Mérida:** 75 km N.E. of Mérida along road to Barina, *F.J. Breteler 3360*, 20 November 1963 (US2599353!); Dist. Libertador, Sierra de Culata 20 km al NE de Mérida, *J.J. Pipoly et al 6473*, 19 December 1983 (NY!); Páramo de Pozo Negro, between San José and Berguilla, *J.A. Steyermark 56270*, 3 May 1944 (US1916417!); Sierra Nevada de Santo Domingo, Versant N.W., Laguna Negra, *H. Humbert 26445*, 21 September 1952 (P01395970!). **Táchira:** Páramo de Tamá, *F. Cardona 297*, July 1939 (US1779004!). **Trujillo:** Dept. Boconó, Mpio. Ribas, alrededores de la finca Guirigay, hacia el río Burate, páramo de Guirigay, *L. Ruiz–Terán & M. López–Figueiras 13102*, 20 December 1975 (US3064059!); Dept. Trujillo, el atajo, cabeceras de la quebrada El Riecito, vertiente suroccidental del páramo de La Crisalina, *L. Ruiz–Terán 9007*, 4 August 1973 (US3064058!); El Atajo, cabeceras de la quebrada El Riecito, vertiente suroccidental del gran páramo de La Cristalina, distrito Trujillo, *L. Ruiz-Terán 9007*, 4 August 1973 (NY!); Mpio. Boconó, aguna Larga, vía Laguna Las Parias, to Laguna Eco, Páramo de Motumbo, Monumento Natural Teta de Niquitao-Guirigay, *B. Stergios et al 20421*, 15 September 2003 (NY!; UC1785091! Photo; US3449599!); Prov. Mérida, Mpio. Rangel, Páramo Motumbo, SW of Laguna Larga (Trujillo state) along border of divide to Laguna Las Parias (Trujillo state), Monumento Natural Teta de Niquitao-Guirigay, *B. Stergios et al 20544*, 17 September 2003 (US3449754!); vertiente larense

del páramo de El Jabón, *L. Ruiz-Terán & M. López-Figueiras 1012*, 4 October 1970. **UNKNOWN LOCATION:** *Moritz 298*, no date (US2361968!).

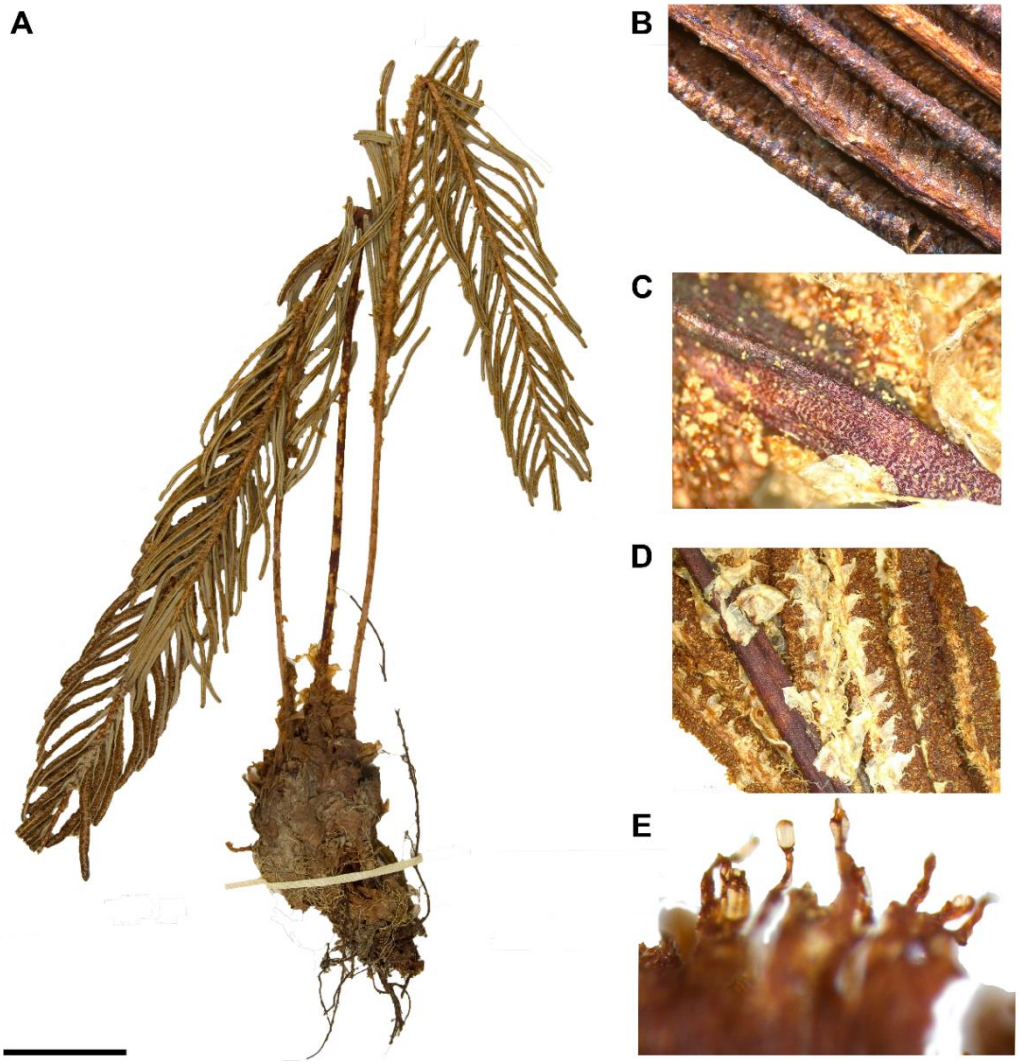

Figure 56. *Parablechnum loxense*. A. Plant of *P. loxense*; B. Detail of sterile pinna, abaxial side; C. Detail of fertile rachis, abaxial side; D. Detail of fertile pinnae, abaxial side; Detail of the indusium. (A: *D.S. Barrington 353*, VT198692; B&D: *Bonpland s.n.*, B200031696, holotypus; C&E: *S.M.F. Fa5011*, US2828652). Scale; 5 cm in A; 3 mm in B; 1.8 mm in C; 9 mm in D; 0.4 mm in E.

Parablechnum loxense var. ***stenophyllum*** (Klotzsch) Gasper & Salino, Phytotaxa 275(3): 216. 2016.

Basionym – *Lomaria stenophylla* Klotzsch, Linnaea 20: 346. 1847.

Type – Peru, *Dombey s.n.* (holotype: B200031699!; isotype: P00627602!, US!).

Synonyms –

≡*Blechnum loxense* var. *stenophyllum* (Klotzsch) Lellinger, Amer. Fern J. 93: 147. 2003.

≡*Lomaria squamulosa* Desv., Mem. Soc. Linn. Paris 6:290. 1827.
=*B. sociale* Sodiro, Recens. Crypt. Vasc. Quit. 30. 1883; ≡*Lomaria socialis* (Sodiro) Sodiro, Anales Univ. Centr. Ecuador 8: 152. 1893. Type: Ecuador, *L. Sodiro S.J. 34,* 27 July 1871 (K000633423! Photo; K000633424!).

Figure 57. *Parablechnum loxense* var. *stenophyllum*. A. Plant of *P. loxense* var. *stenophyllum*; B. Detail of the rachis; C. Detail of sterile pinnae, abaxial side; D. Detail of fertile pinna, abaxial side; E. Rhizome scales. (A-D: *Macbride & Featherstone 2179,* US1121934; E: *A. López M. 1183,* US2539765). Scale: 4 cm in A, 4 mm in B-E.

Description – the general characters coincide with the type variety except for the petiole and rachis scales, which in this variety are clearly discoloured, with a darker, leathery texture centre (**Figure 57**).

Chromosome number – unknown.

Distribution and habitat – distributed from Venezuela to Chile.

Notes – Lellinger (2003) decided to retain the epithet *stenophylla* (sub. *Lomaria stenophylla)* as this was much more widely used than *squamulosa*.

Reviewed material:

BOLIVIA. Dept. Cochabamba: Prov. Chapare, Lago Corani (represa Santa Elena) en la ruta Cochabamba–Villa Tunari, *C. Rolleri 236,* July to August 1978 (US3364777!). **Dept. La Paz:** Inquisivi, walk along the trail between Mina Chambillaya and Quime on slope W of Río Khuyuna, ca. 1-2 km S from Quime, *M. Lewis 35245,* 18 February 1989 (LP! Photo; NY!); Prov. Larecaja, *P.V. Le Roy,* no date (NY!);Prov. Larecaja, Viciniis orata, cerro del Iminape in sepulosis fontis del Cacique, *G. Mandon 1582,* 1 January 1854 (P01462424!); Prov. Murillo, 3,5 km W of Pongo on road from Unduavi to La Paz, *J.C. Solomon 14886,* 20 February 1986 (NY!); Pongo, Cordillera Real, *G.H.H. Tate 120,* 17 February – 1 March 1926 (NY!, 2 sheets); Prov. Murillo, Valle del Río Zongo, 20 km al N de la cumbre, *J.C. Solomon 17274,* 8 November 1987 (NY!); Prov. Sud Yungas, 1,4 km W of Unduavi, on new road between Chuspipata and La Paz, *J.C. Solomon 15378,* 2 July 1986 (LP! Photo; NY!); Viciniis Sorata, Cochipata, *G. Mandon 1579,* 7 November 1857 (P01462425!; P01462426!; P01462429!). **Prov. Nord Yungas:** Undani, *Buchtien 47,* November 1910 (P01395974!; P01395976!). **Unknown Department:** *Williams 1378,* no date (NY!). **CHILE.** *Richay s.n.,* no date (P01462420!). **COLOMBIA. Dept. Boyacá:** Cordillera Oriental, Páramo between Duitama and Charalá, *J.A. Ewan 15659,* 7 May 1944 (US2254122!); Mun. Chisacá-San Pedro de Iguaque, SFF de Iguaque, sendero subiendo a la laguna de Iguaque, *Sundue & A. Vasco 1283*, 3 April 2007 (NY!; VT198693!). **Dept. Cauca:** 5 km. East of Puarce, *E.L. Core 223,* 20 January 1944 (US2200874!); Distr. Cauca, Cordillera Central, Puracé, *K. von Sneidern 1688,* February 1938 (US2081048!); Páramo de Puracé, Central Cordillera, *E.P. Killip & F.C. Lehmann V 38586,* 26 May 1944 (US2608573!). **Dept. Cundinamarca:** *Apollinaire s.n.,* 05.1905 (P01546423!); carretera a Choachí, *C.E. Acosta–Arteaga et al 499,* 15 June 1974 (NY!; US2801378!); Cordillera Oriental, Cruz Verde, 14 km south–southeast of Bogotá, *M.L. Grant & F.R. Fosberg 9228,* 19 May 1944 (US2203508!); Cordillera Oriental, entre Bogotá y La Calera, *F.A. Barkley et al. 17@7a5,* 27 November 1947 (US3186606!);

Cordillera Oriental, Páramo de Chocontá, *J. Cuatrecasas 9645*, 29 June 1940 (US1796338!); Macizo de Bogotá, páramo de Usaquén, *J. Cuatrecasas 9440*, 22 May 1940 (US1852072!); Mun de la Calera, Páramo de la Siberia, *H. Humbert et al. 26877 bis*, 25 October 1952 (P01395971!); Mun. Madrid, autopista Bogotá–Medellin, bosques en contorno a la casa de L. Richter, *M.T. Murillo & L. Sandoval 530*, 23 November 1961 (US2801416!). **Dept. Huila:** "Balsillas" on Río Balsillas, *H.H. Rusby & F.W. Pennell 768*, 3-6 August 1917 (US1041484!). **Dept. del Meta:** Incidencia del Meta, Villavicencio, *B. Guevara Amótegui 430*, no date (US1484949!); **Dept. Nariño:** km 15 de la via que conduce de Pasto a la Laguna de la Cocha. Margen derecha de la carretera , *A.L. Arbelaez & S. Churchill 394*, 5 November 1988 (NY!, 2 sheets). **ECUADOR. Prov. Azuay:** along the río Matadero, west of Cuenca, *W.H. Camp 2003*, 2 March 1945 (NY!; US2080067!); road between Cuenca and Molleturo, División Continental de aguas. Páramo, vegetation, *E. Zogg & H. Gassner 13189*, 13 October 1989 (NY!, 2 sheets). **Prov. Cañar:** headwaters of Río Mangán, 20–22 km e.n.e of Azogues, *F.R. Fosberg & F. Prieto 22799*, 5 February 1945 (US2203985!); road between Cañar and Biblian, *O. Haught 3333*, 30 May 1942 (P01395977!; US1708251!). **Prov. Carchi:** Canton Espejo, east of Angel, Paramo del Azufral, *Y. Mexia 7533*, 17 July 1935 (NY!); Cordillera Oriental, 5 km S. of Tulcán, Altos de Boliche, *J.A. Ewan 16301*, 9 October 1944 (US2254286!); páramo El Ángel, 2 km before the pass on road El Ángel to Tulcán, *L. Holm-Nielsen 18233*, 14 June 1979 (NY!). **Prov. Imbabura:** boggy slope about 2–3 km east of Río Arturo along to Las Toldadas, N.E. of Cayambe Pk., *I.L. Wiggins 10393*, 11 July 1944 (US1859525!); Lago San Marcos, Cayambe, *P.C.D. Cazalet & T.D. Pennington 5448*, 1 December 1961 (NY!; US2421329!). **Prov. Loja:** Amaluza, Yicusura, *Izco et al s.n.*, 11 July 2006 (SANT58023! Photo). **Prov. Napo:** Papallacta, *A. Mille 161*, no date (US1120472!); Volcán Cayambe, N slopes, *B. Ollgaard et al 34208*, 9 July 1980 (P00904701!). **Prov. Nariño:** Mpio. De Pasto, Páramo de Bordoncillo, *S. Espinal T 1020*, 5 March 1963 (US2552129!). **Prov. Pichincha:** Cayambe, Reserva Ecologica Cayambe Coca, collections made along dirt road 3 km W of La Laguna San Marcos, *J.L. Clark 448*, 11 March 1995 (NY!); in pascuis andinis, *Sodiro s.n.*, no date (US1196740!); old road Quito–Sto. Domingo, *H. van der Werff & W. Palacios 10585*, 16 February 1989 (NY; UC1596735! Photo; US3273643!). **Prov. Tungurhua:** *A. Sodiro s.n.*, August 1901 (P01623233!). **Prov. Zamora-Chichipe:** *Izco et al s.n.*, 12 July 2006 (SANT58021! Photo); Zumba, próximo al límite provincial con Loja en Amalaza, *Izco et*

al. s.n., 14 July 2006 (SANT58022! Photo). **Unknown Province:** *A. Sodiro s.n.,* no date (NY!); *ibidem* (P01462859!); *ibidem,* 03.1900 (P01462848!); *ibidem,* 1856-1857 (TCD0009457! Photo); *A. Sodiro 40,* 01.1901 (P01462848!); *ibidem* (P01462860!); *L. Sodiro s.n.,* 11 October 1876 (P01395966!); *L. Sodiro S.J. 34,* 27 July 1871 (K000633423! Photo, syntype of *Blechnum sociale*; K000633424! Photo, syntype of *Blechnum sociale*); *R. Spruce s.n.,* no date (P01395965!); *ibidem,* 1857 (P01546369!); *R. Spruce s.n.,* 1857-9 (NY!); *ibidem* (NY!); *Spruce 10038,* no date (P01462856!). **PERÚ. Dept. Ancash:** Prov. Pallasca, Consuzo, Pampas, *A. López M. 1183,* 31 August 1955 (US2539765!). **Dept. Cajamarca:** Jaén, Sallique, Localidad La Cocha, *J. Campos et al 4995,* 16 June 1998 (NY!). **Dept. Cusco:** Prov. La Convención, bajando del Pto. de Málaga, *J.M. Gabriel y Galán s.n.,* 29 April 2008 (MACB109263); Prov. Umbamba, Puympatamarca ancient ruins, *C. Vargas Calderón 2786,* 29 March 1942 (US1830075!). **Dept. Huanuco:** 15 miles N.E. of Huanuco, *Macbride & Featherstone 2179,* 12-22 June 1922 (US1121934!). **Dept. Pasco:** Oxapampa, Distr. Huancabamba, P.N. Yanachaga-Chemillen, Sector Santa Barbara, *R. Vásquez & A. Monteagudo 29947,* 11 March 2006 (NY!). **Dept. San Martin:** Prov. Mcal. Cáceres, "Tampi de zorro" Pajonal, Río Abiseo, *B. León & K. Young 1461,* 11 March 1988 (USM214608! Photo). **Unknown Department:** *no collector 63.38,* 08.1818 (P01462427!); *Dombey s.n.,* no date (B200031699!, holotype of *Lomaria stenophylla* var. *α;* P00627601!, isotype of *Lomaria stenophylla* var. *α*; P00627602!, isotype of *Lomaria stenophylla* var. *α*); *Dombey s.n.,* 1829 (B200031700, holotype of *Lomaria squamulosa*). **VENEZUELA. Prov. Mérida**: 75 km NE of Mérida along road to Barinas, *F.J. Breteler 3360,* 20 November 1963 (P01395975!); Páramo de la Culata, *Moritz 298,* no date (B200031695!, holotype of *Lomaria stenophylla* var. *β*). **UNKNOWN LOCATION:** *no collector,* no date (P01409526!); *no collector 1579,* July 1857 (P01462428!).

Parablechnum marginatum (Kuhn) Gasper & Salino Phytotaxa 275(3): 216. 2016.

Basionym – *Blechnum marginatum* Kuhn. Filic. Afr. 92. 1868.

Type – Habitat in insulâ Borboniâ, *de Montbrison s.n.* (not found).

Synonyms –

≡*Blechnum montbrisonis* C. Chr. Index Filic. 157. 1905.

–*Lomaria marginata* Fée (nom. illeg. hom.) (non *L. marginata* Schrad.) Mém. Foug. 5: 71. 1852. Type: same as the basyonim.

Description – *plants* terrestrial; *rhizome* erect, suberect or slightly creeping, non-stoloniferous, with ovate–lanceolate scales with elongated apex, more or less filiform, concolorous, brownish, membranaceous, up to 2 cm long; *fronds* dimorphic; *sterile fronds* with *petioles* light brown, grooved, smooth, up to 50 cm long, with scales in the basal zone decreasing in density distally, similar to those of the rhizome, *lamina* 1-pinnate, elliptic-acuminate, up to 1 m long, sometimes longer, *rachis* light brown, smooth, adaxially grooved, scales similar to those of the petiole, more abundant in the adaxial side, *pinnae* in up to 30 pairs, alternate or subopposite, slightly smaller at the base, lanceolate–oblong, stalked, becoming basiscopically adnate towards the apex of the frond, 11 × 2 cm, base asymmetric, subcordate to truncated, apex acute or obtuse, margins entire, with a conform terminal pinna similar to the lateral ones, costa light brown, grooved adaxially, prominent abaxially, with scales at base similar to those of the rachis; veins simple or 1-furcate, patent, catadromous; *fertile fronds* larger than sterile and more erect, *petiole* similar to sterile fronds, *lamina* up to 50 cm or sometimes longer, lanceolate–oblong, *rachis* similar to sterile fronds, *pinnae* usually in more pairs than in the sterile ones, linear, narrow, 13 × 0.2 cm, slightly broader based, asymmetrical, cordate, apex acute; *aerophores* present in both sterile and fertile fronds, tuberculiform, atropurpureus; *hydathodes* present in both sterile and fertile fronds, rounded or ovate; *sori* linear, continuous, on both sides of costa forming a coenosori; *indusia* linear, continuous, opening towards costa, dark brown, membranaceous, usually lacerate; *sporangia* long-pedicellate, simple, 3–seriate below capsule, capsule broadly elliptic in lateral view, with 18–23 cells in the arc; *spores* monolete, (41–)64(–81) × (27–)46(–60) µm, perispore muriform cristate-reticulate, with protruding ridges and with large areas between them (areolae), measuring approximately 30 µm, covered with filamentous micro–ornamentation forming a kind of net that is arranged on a more or less smooth surface; internal structure of the perispore of spongy appearance and irregularly granular exospore (**Figure 62**).

References – Roux (2009).

Chromosome number – unknown

Distribution and habitat – Réunion and Mauritius islands.

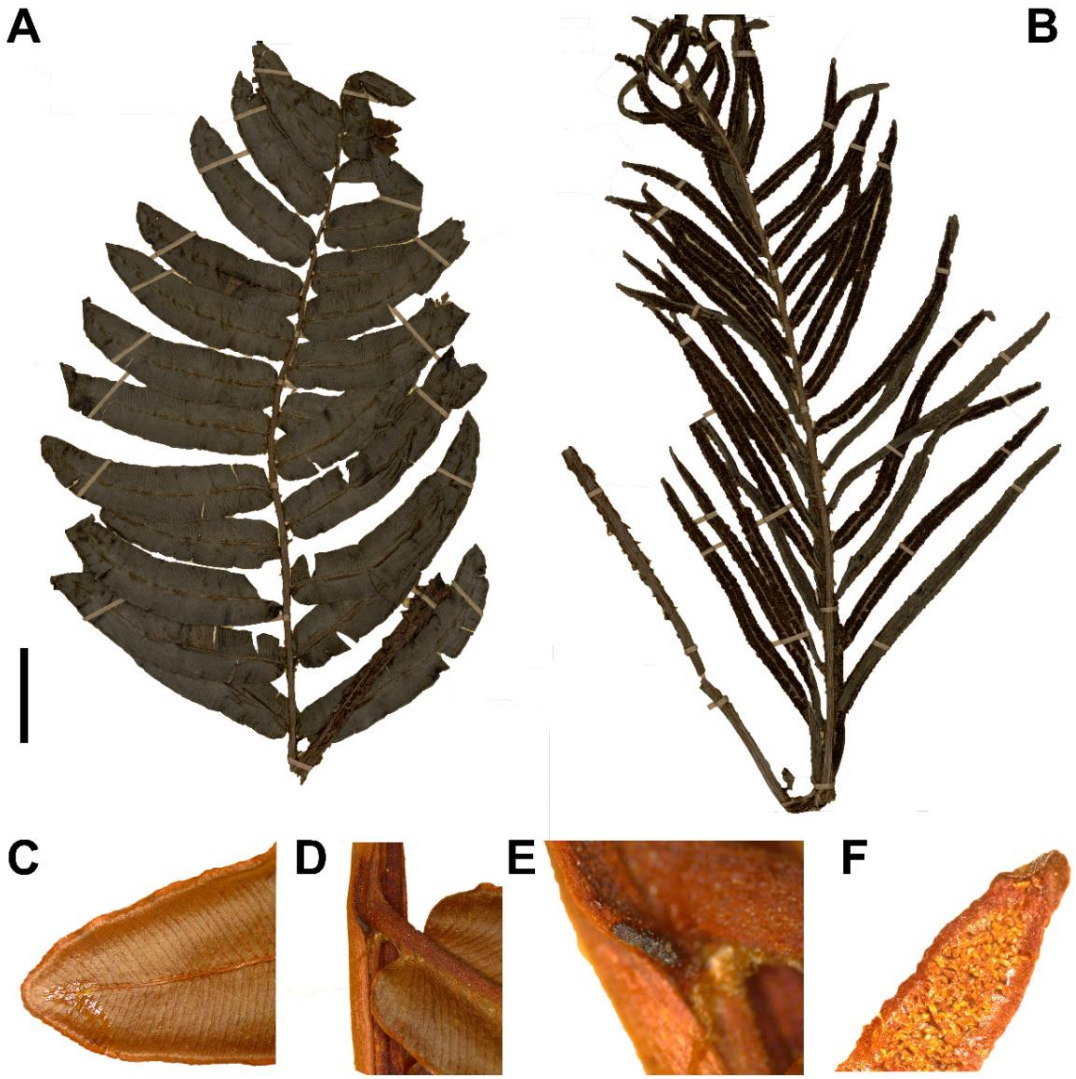

Figure 62. *Parablechnum marginatum.* A. Sterile frond; B. Fertile frond; C. Detail of sterile pinna apex, abaxial side; D. Detail of sterile pinna base, abaxial side; E. Aerophore; F. Detail of fertile pinna pinna, abaxial side. (A: *L. de Cordemoy s.n.*, P01462834; B: *L. de Cordemoy s.n.*, P01462832; C-E: *Th. Cadet 4050B2*, P01462767; F: *Th. Cadet 4050B1*, P01462768). Scale: 5 cm in A&B; 6.4 mm in C; 7 mm in D; 1.5 mm in E; 2.2 mm in F.

Notes – differs from *Parablechnum humbertii* in the obtuse or slightly acute rather than attenuate apices and in the absence of scale scars on the petiole.

Christensen (1905) proposed the name *Blechnum montbrisonis* as a replacement name, as the name *Blechnum marginatum* proposed by Kuhn (1868) was based on an illegitimate basionym, *Lomaria marginata* Feé. This name was proposed by Feé (1852) after this combination had already been used by Scharder (1824) for what is now known as *Lomariopsis marginata* (Schrad.) Kuhn. However, according to the rules of the current code (see Art. 6.14 Ex. 18, Turland, 2018), *Blechnum marginatum* would be a validly

published replacement name for *Lomaria marginata* Feé, and therefore *Blechnum montbrisonis* would be a nomenclaturally superfluous and illegitimate name.

Reviewed material:

MAURITIUS. *Belanger 98C*, no date (P01462824!); *Bonpland s.n.*, no date (P01532252!); *ibidem* (P01532253!); *Meller 6*, 3 December 1909. **RÉUNION.** *no collector*, no date (P01462821!); *ibidem* (P01462829!); *ibidem* (P01462833!); *ibidem* (P01557677!); *ibidem* (P01557678!); *no collector 113*, no date (BM000769811! Photo); *Cowemoy s.n.*, 1892 (P01462832!); *ibidem* (P01462834!); *D.H. Lorence s.n.*, 8 March 1979 (MO3156135!; MO3156136!)**;** *M.G. de Isle 606*, 1875 (P01462825!; P01462826!; P01462827!); *M. Lépervanche–Mézière s.n.*, 1842 (P01462830!); *M. Lépervanche–Mézière 17*, 1898 (P01462771!); *M. Lépervanche–Mézière s.n.*, no date (P01462820!; P01462823!; P01462828!); Berge de la Riviére des Marsouins prés Coserne des Hirondelles Nébom, *Th. Cadet 4050B1*, 22 July 1973 (P01462768!); *ibidem*, *Th. Cadet 4050B2*, 22 July 1973 (P01462767!); Bourbon, *M. Richard 99*, no date (P01462822!); cirque de Salazie, sentier vers La Nouvelle, *F. Bradé 1052 bis*, 29 November 1973 (P01462769!); *ibidem*, *F. Bradé 1055*, 29 November 1973 (P01462836!; P01462837!); Fourré à Philippia, sentier de la Mare à Joseph au coteau Kerveguen, cirque de Cilaos, *F. Bradé 935*, 16 November 1973 (P01462835!, P00917036!, P00917037!); *ibidem*, *F. Bradé 958*, 16 November 1973 (P00917032!; P00917033!; P00917034!; P00917035!); Nationale 3, Bord de route, entre le Col de Bellevue et la Plaine des Palmistes, *F. Rakotondrainibe & E. Grangaud 6910*, 5 November 2004 (P00411889!); Sentie de Bélome à la caunne Munard, *J. Bosser 12208*, 1957 (P01625974!).

Parablechnum milnei (Carruth.) Gasper & Salino, Phytotaxa 275(3): 216. 2016.

Basionym – *Lomaria milnei* Carruth., Fl. Vit. 351. 1873.

Type – Fiji, *Milne 284*, 1855 (holotype: BM001048222! photo).

Synonyms –

≡*Blechnum milnei* (Carruth.) C.Chr., Index Filic. 156. 1905.

Description – *plants* terrestrial; *rhizome* erect, scaly, scales lanceolate, acuminate, bicolorous, dark brown with paler margins; *fronds* dimorphic; *sterile fronds* with *petioles* up to 70 cm long, pale brown, densely scaly proximally, similar to those on the rhizome;

lamina lanceolate, 1-pinnate, 80 × 40 cm, ending in a conform pinnae similar to the lateral ones; *rachis* glabrous or with some scales, similar to those of the petiole but smaller; *pinnae* shortly stalked, alternate to subopposite, 10–20 × 2.5 cm, apex acuminate, base asymmetrical, rounded, margins serrulate and cartilaginous, coriaceous; *veins* free, simple or 1-furcate, catadromous; *aerophores* present, globose; *hydathodes* present, round to ovate; *fertile fronds* usually similar in size to the sterile ones and more erect; *fertile pinnae* linear, contracted; *sori* linear, continuous, forming coenosori on both sides of the costa; *indusium* linear, continuous, open towards the costa; *sporangia* (18–) 20 (–23) cells in the arc; mixed with sporangiasters; *spores* monolete, (60–) 75 (– 85) × (37–) 53 (– 62) µm, perispores smooth, cristate-reticulate, with broad, obtuse, high folds, the terminal supralesural, forming large polygonal areoles, with no or very few filamentous processes (**Figure 58**).

References – Brown & Brown (1931), sub. *Blechnum capense*, Brownlie (1977).

Chromosome number – unknown.

Distribution and habitat – Marquesas Islands, Society Islands, Rapa, Fiji, Cook Islands and Kermedec (Brown & Brown, 1931). It generally occurs on forest margins at low elevaions, but it can also be found on mountain clearings or exposed sites on ridges (Brownlie, 1977).

Etymology – this species in named after G.R. Milne, the botanist who collected the type material.

Notes – a specimen under the name *Blechnum societatum* T.C. Chambers, was found in the K herbarium (K001089684) annotated as a new species. However, we have found no publication of this name, and after reviewing the picture we believe that this specimen belongs to *Parablechnum milnei.* It can be distinguish from other similar *Parablechnum* of the region for the presence of sporangiasters, with an smaller capsule than those on *P. nesophilum*.

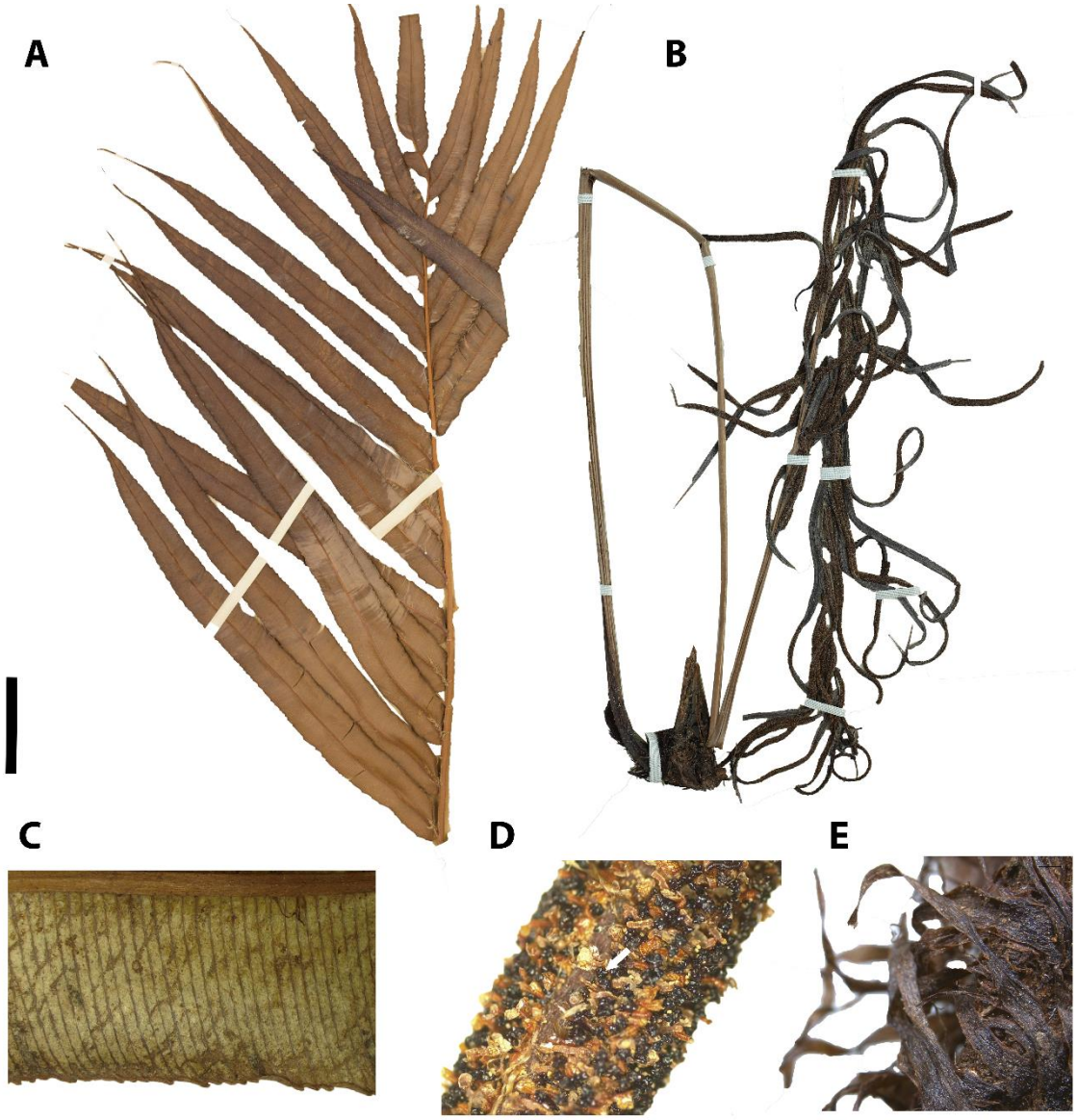

Figure 58. *Parablechnum milnei*. A. Fragment of sterile frond; B. Fertile frond; C. Sterile pinna margin, abaxial side; D. Fertile pinnae, abaxial side with sporangiasters (arrow); E. Rhizome scales. (A: *J.W. Gillespie 2714*, BISH99619; B: *J.W. Gillespie 3884*, UC353392; C: *M. Schmid 3101*, P01573191; D: *P. Cabalion 2382*, P01571513; E: *A.C. Smith 7710*, US2257570). Scale: 4 cm in A&B, 5 mm in C, 2 mm in D, 4 mm in E.

Reviewed material:

COOK ISLANDS. Rarotonga, Te Kou, *W.R. Sykes 1471/CI*, 8 July 1974 (US2951140!). **FIJI. Ovalau:** summit of Mt. Tana Lailai and adjacent ridge, *A.C. Smith 7710*, 1 June 1953 (US2257570!; US2257571!; US2257572!). **Viti Levu:** *H.E. Parks 20813*, March to July 1927 (US1273464!); SE Viti Levu, Tamavua–Sawani road, *W.A. Setchell & H.E. Parks 15055*, 23 May 1926 (US1275978!; US1275979!); Viti Levu, *J.W. Gillesple 3337*, 1927 (NY!, 2 sheets). **Unknown area:** *Milne 284*, 1855 (BM001048222!

photo, holotype). **FRENCH POLYNESIA. Rapa:** *H. St. John & F.R. Fosberg 15293,* 1 July 1934 (K001089684! Photo); S. slope, ridge between Morongota and Vaitan, *F.R. Fosberg 11605,* 20 July 1934 (US1919843!). **SOCIETY ISLANDS. Tahiti:** *Wilkes Explor. Exped s.n.,* 1838-1842 (US0095752!); *ibidem* (US0095753!). **VANUATU. Unknown area:** *G. Bourdy 123,* 23 September 1985 (P01576208!; P01576209!). **Tanna:** rte E.O. vers le col, *Schmid 3107,* 7 May 1970 (P01573190!; P01573191!; P01573192!); Tafea Province, Southeast Tonna, Iatukei area, at Mount Mamkuiri, *G.M. Plunkett et al 3065,* 6 March 2015 (NY03599600!); Tafea Province, Southwest Tanna, Mount Tukosmera area (upper slopes), *G.M. Plunkett et al. 3312,* 25 April 2016 (NY!; P00864658!); Tafea, Rantop, *P. Cabalion 2382,* 28 June 1984 (P01571513!).

Parablechnum minus (R.Br.) Gasper & Salino, Phytotaxa 275(3): 216. 2016.

Basionym – *Stegania minor* R.Br., Prodr. 153. 1810.

Type – Australia, Queensland, Dalrymple, *R. Borwn 47,* 1 July 1804 (lectotype: BM001048221! Photo; isolectotypes: BM000093974! Photo, E00080328! Photo; K001092747! Photo).

Synonyms –

≡*Lomaria minor* (R.Br.) Spreng., Syst. Veg. 4: 65 .1827; *Blechnum minus* (R.Br.) Ettingsh., Denkschr. Kaiserl. Akad. Wiss., Math.–Naturwiss. Kl. 23: 63, t. 8, f. 5, 12. 1864; *Blechnum capense* var. *minus* (R.Br.) Domin, Biblioth. Bot. 20(85): 116. 1913.
=*Lomaria alta* Heward ex T.Moore, Index Fil. (T.Moore) 1: xxiv. 1857. Type: New Zelanad, *no collector,* no date (holotype: not found; isotype: BM001048220! photo).
=*Lomaria procera* var. *paludosa* Rodway, Tasmanian Fl. 283 .1903. Type: Australia, Tasmania, Sorell Creek, *L.Rodway s.n.,* March 1895 (HO n.s.).
–*Lomaria minor* (R.Br.) Desv., nom. illeg. homon. Mém. Soc. Linn. Paris 6: 288 .1827.

Vernacular names – Swamp kiokio (Chambers & Farrant, 1998b).

Description – *plants* terrestrial; *rhizomes* erect or shortly creeping, non-stoloniferous, scaly, scales narrowly ovate, 3–10 × 1–2 mm, chestnut brown, concolorous or occasionally slightly discoloured with paler margins; *fronds* dimorphic; *sterile fronds* 10–140 cm long; *petioles* 2–42.5 cm long, yellowish brown, sometimes darker at base, scales narrowly ovate concolorous, chestnut–brown, entire or slightly toothed, often darker at base; *laminae* 8–75(165) × 2–20(44) cm, 1-pinnate, lanceolate to ovate, with in a conform terminal pinna, reddish when young; *rachis* yellowish brown, adaxially grooved, scaly;

sterile pinnae in 3–37 pairs, widely spaced, alternate or subopposite, narrowly oblong, reduced to small rounded lobes at the base of the lamina, 1–19 × 0.6–1.8 cm, apices acute, obtuse or rounded, margins entire or slightly serrulate, bases truncate, shortly stalked, becoming adnate distally; *costae* straw-coloured, grooved adaxially, prominent abaxially, scaly abaxiallty, scales concolorous, pale chestnut–brown; *veins* free, simple or 1-furcate, catadromous; *aerophores* absent; *hydathodes* present, rounded or oval; *fertile fronds* equal to or longer than sterile fronds, 10–170 cm long; *petioles* 4–76 cm; *laminae* 3.5–60 × 0.6–20 cm; *fertile pinnae* in 4–28 pairs, linear, straight, 1–14 cm, with suprabasal pinnae with an expanded sterile region at base, 1–4 pairs of pinnae at base of lamina replaced by short, rounded, sterile lobes; *sori* linear, continuous, on both sides of costa forming a coenosori; *indusia* linear, continuous, opening towards costa, dark brown, membranaceous, usually lacerate; *sporangia* with 16–22 arch cells; *spores* monolete, (31–) 53 (–69) × (23–) 37 (–51) µm, perisporium rugulose, cristate-reticulate, with broad, acute, more or less high folds, forming medium to large polygonal areoles, without or with only a few very short filamentous processes scattered in the areoles and on the edges of the wall (**Figure 59**).

References – Allan (1961), Chambers & Farrant (1998b), Brownsey & Perrie (2021).

Chromosome number – n = 28 (Brownlie, 1954; Quinn, 1961), 2n = 56 (Dawson *et al.*, 2000).

Distribution and habitat – in Australia from southeast Queensland to the plateau, in coastal regions of New South Wales, Victoria and Tasmania. In New Zealand on the three main islands, the Chatham Islands and Stewart Island, in an altitudinal range from sea level to 1040 m. It grows in streams and riverbanks, as well as in other wet places such as springs, waterlogged areas, swamps, bogs, and wet rocks, in crevices near waterfalls and caves, ravines, forests and open fields and river plains. (Allan, 1961; Chambers & Farrant, 1998b; Brownsey & Perrie, 2021).

Etymology – the specific epithet comes from the Latin *minor* (smaller), as a reference to the small plants of this species that were first collected by Robert Brown (Brownsey & Perrie, 2021).

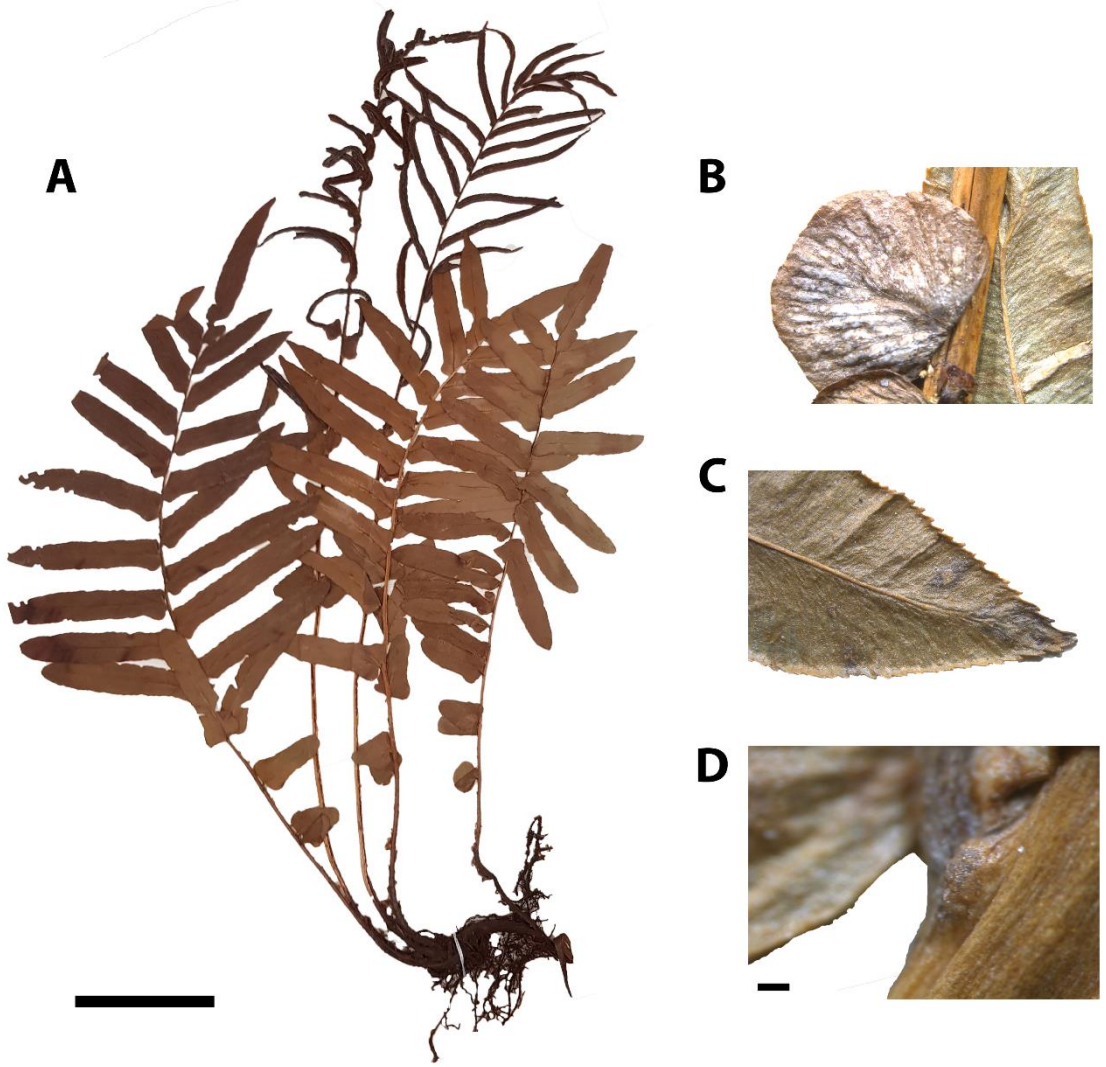

Figure 59. *Parablechnum minus*. A. Plant of *P. minus*; B. Basal sterile pinna; C. Detail of sterile pinna apex, abaxial side; D. Detail of sterile pinna stalk with an aerophore. (A: *M.C. Ferguson 135*, NY; B-D: *Hj. Eichler 14471*, US2563068). Scale: 4 cm in A, 6 mm in B, 5 mm in C, 1 mm in D.

Notes – it can be confused with *Parablechnum novae-zelandiae*, but is easily distinguished by its narrower lamina, generally smaller size, widely spaced pinnae and concolorous scales.

There is controversy as to whether this plant is endemic to Australia or also grows in New Zealand. Plants identified as this species were first collected in New Zealand by Colenso (1893; sub. *Lomaria procera* var. *gracilis*). Chambers & Farrant (1998b) determined that tese plants were a swamp–restricted form of *Parablechnum novae-zelandiae*, and that the species *Parablechnum minus* did not occur in New Zealand. Other authors do consider this swamp form to be *P. minus* rather than *P. novae-zelandiae* because, unlike *P. novae-zelandiae*, it has concolorous scales (Brownsey & Smith–

Dodsworth, 1989, 2000; Brownsey & Perrie, 2021) which has been confirmed by the specimens reviewed in this work. Chambers & Farrant (1998b) indicated that some of the plants they ascribed to a swamp form of *P. novae-zelandiae* did have scales with the distinctive black spot of this species, or at least a tendency to have it. We did not observe this in any of the specimens, but this observation could be due to the tendency of these species to hybridise (Chambers & Farrant, 1998b; Brownsey & Perrie, 2021).

Reviewed material:

AUSTRALIA. New South Wales: *Daimel 79,* 1869 (P01463090!); *Daimel 90,* 1866 (P01463088!; P01463089!); *G. Caley s.n.*, 1804 (P01566767!); *ibidem*, 1 February 1804 (P01662376!); Adelina Falls, *R. Coveny 10194*, 1 August 1978 (NY!); Batlow, *L. Boorman s.n.*, October 1916 (US0719653!); Blue Mountains, Lake Meldow, ca. 2 miles south-east of Blackheath, *E.F. Constable 6773*, 20 April 1966 (P01618508!); Fitzroy falls, *Meebold 3005*, September 1929 (NY!); Paddy's River, Goulburn–Sydney Road, *E.F. Constable P7289*, 25 January 1956 (US2414193!); top of Victoria Falls, ca. 2 miles east of Mount Victoria (Blue Mountains) *E.F. Constable P8006*, 6 May 1959 (US2414196!; US2414197!). **Queensland:** Dalrymple, *R. Brown s.n.*, January 1882 (K001092748! Photo); Dalrymple, *R. Borwn 47*, 1 July 1804 (BM000093974! Photo, isolectotype; BM001048221! Photo, lectotype; E00080328! Photo, isolectotype; K001092747! Photo, isolectotype). **South Australia:** Claredon, *O. Tepper 1882*, no date (NY!); Mt. Compass, *Meebold 1615*, December 1928 (NY!); Peninsula, between Cape Jervis and Victor Harbour, Tapanappa Creek, near a Waterfall ca. 2 km north of the seacoast, *Hj. Eichler 14471*, 17 November 1955 (US2563068!); Southern Mt. Lofty Range, Square Waterhole, ca. 2.5 km south of Mt. Compass, ca. 50 km south of Adelaide, *Hj. Eicher 13859*, 30 June 1957 (UC1222084! Photo). **Tasmania:** Nieka, *D.A. Ratkowsky & A.V. Ratkowsky s.n.*, 7 February 1975 (MO109861!). **Victoria:** Australian Alps., Bogong, near the bridge of Pretty Valley Creek above Bogong, *Hj. Eichler 14759*, 6 February 1955 (US2541444!). **Unknown area:** *E. Daimel 82*, 1866 (P01576207!); *Limminghe s.n.*, 1859 (P01463053!). **NEW ZEALAND. North Island:** ARA Waitakere, *R. Cooper & H.H. Nickerson 6027*, 18 December 1965 (US2942489!); Auckland, *Hay & Schnwartz 337*, no date (P01462518!); Auckland, *P. Serre s.n.*, 1931 (P01462587!); Bay of Islands, *no collector*, no date (US0095745!); *ibidem, L.A. Doore & T.T. Earle 228*, 18 January 1935 (NY!; UC1368922! Photo); Northland, *Védel s.n.*, 1847 (P01462573!);

ibidem (P01462531!); *ibidem* (P01462532!); Warakei, *M.C. Ferguson 135*, 20 March 1921 (NY!). **South Island:** Akaroa, *T. Kirk 607*, no date (US816200!); Canterbury, *Flchtus 69*, no date (P01568444!); Canterbury, Ashley Gorge near Oxford, valley of first stream north of Ashley River, *H. Lamoureux 3253*, 18 December 1965 (US3584984!); Canterbury, Hoods Bush, west of White Cliffs, *R. Mason 13325*, 12 March 1977 (MO4388611!); Richmond upon, *no collector*, no date (P01462585!). **Southland:** Malven Hills near the gorge of the Rahaia, *T.H. Potts s.n.*, 1876 (K001092715! Photo); Stewart Island, Half-moon Bay, Glory Cove, on trail between Glory Cove and Golden Beach, *T.T. Earle et al 372*, 26 February 1935 (NY!; UC1368903! Photo). **Unknown area:** *no collector*, no date (BM001048220! Photo, isotype of *Lomaria alta*); *ibidem* (P01462549!); *ibidem* (P01630904!); *W. Colenso 323*, no date (K001092716! Photo); *no collector 457*, no date (P01462556!); *A. Cunningham s.n.*, no date (US barcode 1527773!); *E. Craig 56*, no date (UC553122! Photo); *Travers*, no date (UC678365! Photo); *Walker*, 1875 (P01462543!); *W. Hooker s.n.*, 1860 (P01462578!). **CULTIVAR.** New Zealand, Christchurch, *Dutton s.n.*, September 1890 (K001092774!).

Parablechnum monomorphum (R.C.Moran & B.Øllg.) Gasper & Salino, Phytotaxa 275(3): 216. 2016.

Basionym – *Blechnum monomorphum* R.C.Moran & B.Øllg., Nordic J. Bot. 15: 177. 1995.

Type – Ecuador. Imbabura: Road Cotacachi–Apuela, 22.5 km from Cuicocha entrance, wet road banks, 00"20'N, 78"23'W, 3000 m, *Øllgaard 100667*, 27 February 1993 (holotype: AAU100667! Photo, 6 sheets; isotype: QCA108068! photo).

Description – *plants* terrestrial; *rhizome* ascending to erect, non-stoloniferous; *fronds* monomorphic or very slightly subdimorphic; *sterile fronds* up t 3 m long, erect, the fiddleheads with a coarse mucilage; *petioles* 150 cm, proxially darkened and scaly, scales ca. 1 cm long, lanceolate to ovate, light brown, thin, membranaceous; *lamina* 1-pinnate, gradually reducing in size distally, apex with a terminal pinna conformal or subconformal, coriaceous, glabrous to sparsely scaly abaxially, the scales light brown, thin, inconspicuous; *rachis* straw-coloured, sparsely scaly, adaxially grooved; *sterile pinnae* 31 × 4.5 cm, ascending, shortly stalked, alternate or subopposite, margins slightly

cartilaginous, thickened and serrulate, base broadly rounded to subtruncate, apex slightly acuminate; *costa* similar to the rachis, grooved adaxially, prominent abaxially; *veins* free, simple or 1-furcate; *aerophores* blackened, elliptical, low, rounded; *hydathodes* brownish in tooth axils; *fertile fronds* more or less equal to sterile ones; *fertile pinnae* 31 × 3.5 cm, ascending, basal auriculate, auricula overlapping on rachis; *sori* linear, continuous, forming a coenosori on both sides of costa, with 6–8 mm of laminar tissue between sorus and margin; *indusia* linear, continuous, opening towards costa, pale yellowish brown, slightly lacerate; *sporangia* with 26 arch cells; *spores* monolete, (48–) 82 (–100) × (38–) 57 (–79) µm; perispores rugulose, cristate-reticulate, low-walled, thick, forming large polygonal areoles, without filamentous processes (**Figure 60**).

References – Moran & Øllgaard (1994).

Chromosome number – unknown.

Distribution and habitat – scattered collections in the Andes from Ecuador, Peru, and Colombia. Rare, terrestrial in humid forests, 2100–3100 m. At type locality occurs in moist road cuts with tall scrub and is locally frequent along the road (Moran & Øllgaard, 1994; Smith & Kessler, 2018).

Etymology – the specific epithet refers to the monomorphic fronds, which is unusual for *Parablechnum* species.

Notes – Similar to other large *Parablechnum* species such as *P. cordatum*, *P. schiedeanum* or *P. proliferum*, but is distinguished from all of them by its monomorphic fronds. Smith & Kessler (2018) suggest that there is a possibility that this plant could be a dimorphic species of *Parablechnum* that sometimes reverts to a monomorphic condition, which has been seen in other species of the family such as *Struthiopteris spicant*.

Reviewed material:

BOLIVIA. Dept. La Paz: Prov. Franz Tamayo, Parque Nacional Madidi, senda Mojos-Keara, trayecto Chunkani – Ichu Korpe, *I. Jiménez 5107*, 7 March 2008 (MO6157390!). **COLOMBIA. Dept. Antioquia:** Mpio. Ciudad Bolivar, Corregimiento San Bernardo de los Farallones, Cerro San Nicolas, Farallones del Citará, sector La Peña,

W.D. Rodriguez et al 4662, 9 November 2004 (NY04187102!). **ECUADOR**. **Prov. Imbabura**: Road Cotacachi–Apuela, 22.5 km from Cuicocha entrance, *Øllgaard 100667*, 27 February 1993 (AAU100667! Photo, 6 sheets, holotype; QCA108068! photo, isotype).

Figure 60. *Parablechnum monomorphum. A. Fertile frond. B. Fertile pinna, abaxial side. W.D. Rodriguez et al 4662* (NY). Scale: A. 4 cm in A, 2.3 cm in B.

Parablechnum montanum (T.C.Chambers & P.A.Farrant) Gasper & Salino, Phytotaxa 275(3): 216. 2016.

Basionym – *Blechnum montanum* T.C.Chambers & P.A.Farrant, New Zealand J. Bot. 36: 11. 1998.

Type – Wairau Valley, Morse's Mountain, now called Red Hill, *P. Hynes*, 16 Apr 1965 (AK104893! photo).

Synonyms –

=*Lomaria procera* var. *tegmentosa* Hombron, Voy. Pole Sud. Bot, 80, t. 2E, E'. 1853. Type: New Zealans, North Island, Auckland, *J.B. Hombron s.n*., 1841 (syntypes: P00627663-4!).

Vernacular names – dunedin–cass blechnum; mountain kiokio (Chambers & Farrant, 1998a).

Description – *plant* terrestrial; *rhizome* shortly creeping, non-stoloniferous, scaly, scales 12–20 × 3 mm, linear to lanceolate, acuminate, light reddish brown, sometimes tending to be bicolorous with a slightly darker central zone, entire to finely toothed, 8–14 × 1.5–2.6 mm; *fronds* dimorphic, erect; *sterile fronds* 10–115 × 3–25 cm; *petioles*, light brown or reddish brown, darkening at base, sometimes with dark spots, 7–62 cm, scaly, scales variable in size, 2–8 × 0.5–2 mm, but mostly small, linear, ovate or cordate, light brown, brown, reddish brown, some with a dark spot, entire or toothed, sometimes branched at base; *lamina* ovate to narrowly deltoid, reddish when young, 1-pinnate, gradually decreasing in size towards the apex with in a conform terminal pinna, 13–73 × 6–28 cm; *rachis* reddish brown, grooved adaxially; *sterile pinnae* in 3–27 pairs, oblong to lanceolate, often falcate, apices usually acuminate, sometimes acute, becoming more acute proximally, bases truncate or rounded–cordate at the rachis, shortly stalked, becoming basiscopically adnate and decurrent at the apex, coriaceous, margins dentate and often markedly crenulate, basal pinnae as long as or slightly shorter than medial pinnae, more deflexed and with more obtuse to rounded apices, terminal pinna more elongate; *costae* reddish brown, grooved adaxially, prominent abaxially, with moderately dense scales and irregularly branched hairs, scales 1–10 × 0.5–1 mm, mostly inconspicuous, linear, branched or stellate, with black dot, 2–3 × 1 mm, ovate–lanceolate, with attenuate apices; *veins* free, simple or 1-furcate, catadromous; *aerophores* absent; *hydathodes* ovate; *fertile fronds* similar in length to sterile ones, 18.5–97 cm long; *petioles* often longer than those of sterile ones, with dark spots more frequently than sterile ones; *rachis* darker than in the sterile fronds; *fertile pinnae* narrow, linear, acuminate, 4–16 × 0.25–0.5 cm; *sori* linear, continuous, forming coenosori on both sides of costa covering the whole pinna except apex; *indusium* linear, continuous, opening towards costa, brown, lacerate; *sporangia* with (16–)19(–21) arc cells mixed with paraphyses; *spores* monolete, flat-convex in equatorial view, elliptic in polar view, (42–)48(–60) × (23–)33(–46) µm, perispore from costa to costa–winged, loosely reticulate, exospore smooth or granular (**Figure 61**).

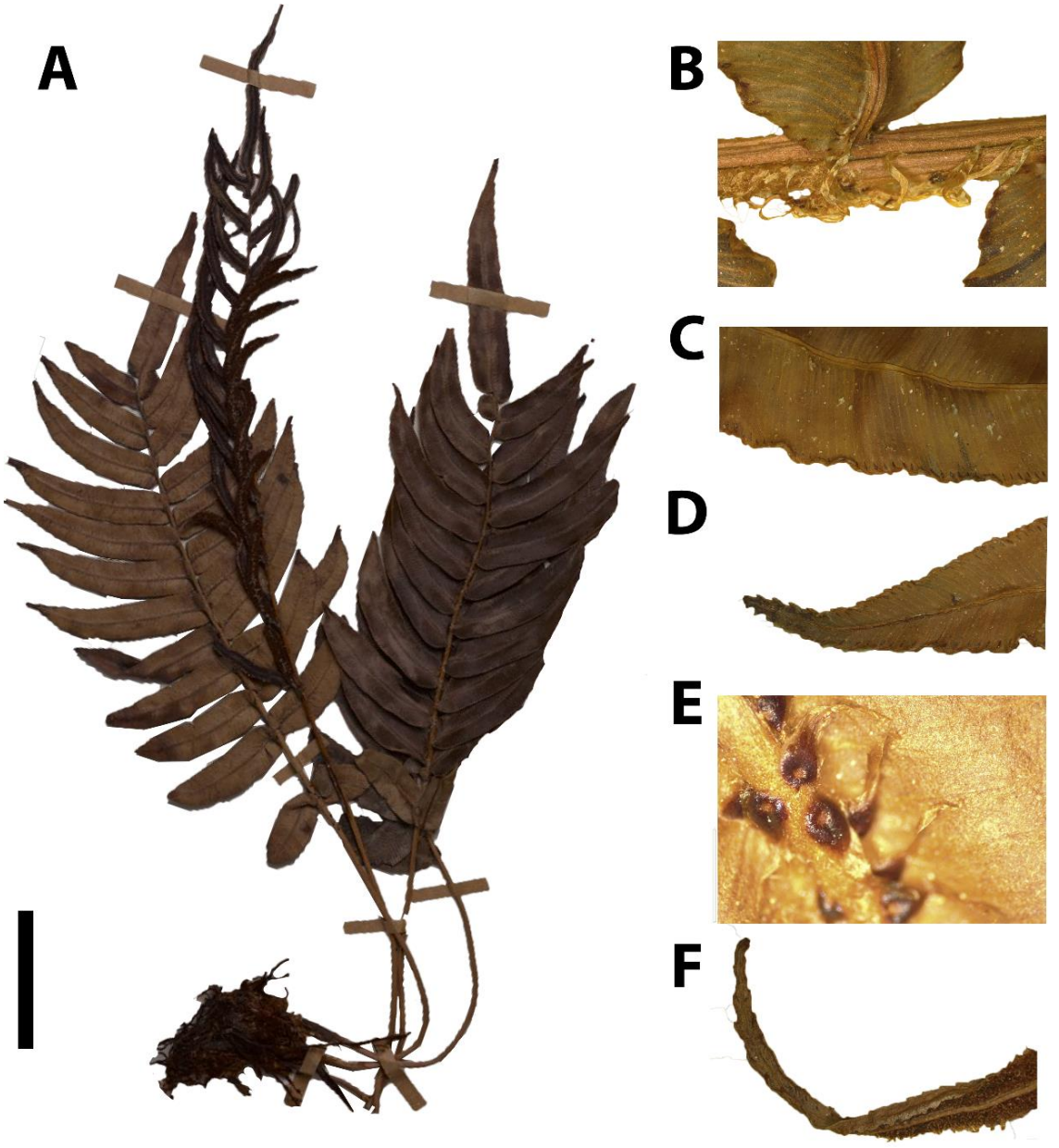

Figure 61. *Parablechnum montanum*. A. Plant; B. detail of the fertile rachis; C. Detail of sterile pinna margin, adaxial side; D. Detail of sterile pinna apex, adaxial side; E. Detail of sterile costa, abaxial side; F. Detail of fertile pinna apex. (A: AK104893, *P. Hynes*, holotype; B-D: *Filhol s.n.*, P01532233; E-F: *Filhol s.n.*, P01532234). Scale: 4 cm in A, 5.7 mm in B, 9.4 mm in C&D, 2 mm in E, 7 mm in F.

References – Chambers & Farrant (1998a), Brownsey & Perrie (2021).

Chromosome number – 2n = 56 (Chambers, 1954; Chambers & Farrant, 1998a).

Distribution and habitat – endemic to New Zealand. It occurs in montane and subalpine regions south of North Island and across much of South Island, where it is found along the shores, and in swampy and disturbed terrain, in forests, forest clearings and

scrub. In the sub–Antarctic region, the species is widespread on Chatham Islands and the Antipodes, Auckland and Campell Islands. 10–1375 m (Chambers & Farrant, 1998a; Brownsey & Perrie, 2021).

Etymology – the epithet refers to its occurrence in mountainous areas (Brownsey & Perrie, 2021).

Notes – amongst the New Zealand species of *Parablechnum*, *P. montanum* can be confused with *P. novae-zelandiae,* from which *P. montanum* has a narrowly deltoid lamina without basal pinnae reduced to auricles and in the distal pinnae being falcate. It is distinguished by these same characters from *Parablechnum minus*, which also lacks black–dotted scales. According to Chambers & Farrant (1998a) there are two forms of *P. montanum* in the field, one in alpine meadows, smaller, similar to *P. procerum*, but distinguishable by the black–dotted scales. Here it forms patches where it grows together with *P. procerum*, similar to the patches formed by *P. novae-zelandiae* in exposed situations. The other form is forest, which is the most similar to small individuals of *P. novae-zelandiae*. In many localities, this species grows intermixed with *P. procerum*; *P. montanum* tends to dominate in cooler, more exposed habitats. It also sometimes grows with *P. novae-zelandiae*; there is evidence that it hybridises with both species (Chambers & Farrant, 1998a).

Reviewed material:

NEW ZEALAND. North Island: Auckland, *J.B. Hombron s.n.,* 1841 (P00627663!, syntype of *Lomaria procera* var. *tegmentosa*; P00627664!, syntype of *Lomaria procera* var. *tegmentosa*); Auckland**,** Wairau Valley, Morse's Mountain, now called Red Hill, *P. Hynes s.n.,* 16 April 1965, (AK104893! photo). **Subantartic Islands:** Campbell Island, *M. Filhol s.n.,* 1874 (P01532233!; P01532234!). **Unknown area:** illegible location, *illegible collector,* no date (UC313104! Photo).

Parablechnum moranianum (A.Rojas) Gasper & Salino, Phytotaxa 275(3): 216. 2016.

Basionym – *Blechnum moranianum* A.Rojas, Brittonia 58: 388, 392, f. 1A, 2A. 2006.

Type – Costa Rica. San José: Pérez Zeledón, Páramo, Villa Mills, entre La Georgina y Las Torres, 9º23’15’’N, 83º45’00’’W, 3270 m, *Rojas & Frias 6345,* 8 Jan 2005

(holotype: CR237193! Photo.; isotypes: F n.s., K n.s., MO6378459! photo, UC! n.s., USJ n.s.).

Description – *plants* terrestrial; *rhizome* 7–10 mm in diameter, erect, non–arborescent, non-stoloniferous, scaly, with scales 10–20 × 2–5 mm, ovate to lanceolate, concolorous, light brown to yellowish brown, entire; *fronds* dimorphic, *sterile fronds* curving to revolute, 25–70 cm long, petiole 4.5–40 cm long, straw-coloured, basally atropurpureous, scaly, scales 3–15 × 1–3 mm, lanceolate, yellowish, with entire to shortly ciliate margin; *lamina* 20–35 × 5.5–11.5 cm, pinnate, elliptic to oblong-elliptic, slightly to strongly reduced at base, without vestigial pinnae, with a conformal terminal pinna, the terminal pinna similar in shape to the lateral ones, *rachis* smooth, straw to yellowish brown, densely scaly, the scales 1–5 × 0.5–2 mm, stellate to lanceolate, yellowish, margins dentate to ciliate, *sterile pinnae* in 22–26 pairs, 1.5–6 × 0.5–1 cm, the basal ones commonly reflexed, the middle and distal ones perpendicular to the rachis, sometimes falcate at the apex, strongly involute, shortly stalked, margins entire, *costa* straw-coloured, densely scaly, the scales 1–3 mm long, similar to the rachis scales; *veins* free, simple or 1-furcate, impressed, catadromous; *aerophores* present, low; *hydathodes* ovate; *fertile fronds* erect slightly longer than sterile ones, *petiole* (10–)20–45 cm long, *fertile pinnae* 3–5.5 × 0.2–0.4 cm, adaxially dark brown, arching at apex; *sori* linear, continuous, forming coenosori on both sides of costa, covering entire pinna; *indusium* linear, continuous, open towards costa, lacerate; *spores* monolete, flat-convex in equatorial view, elliptic in polar view, costal–reticulate, with thick walls more or less high forming large areoles, with scattered filaments on the walls, sometimes also on the surface of the areole lacunae, exospore smooth (**Figure 63**).

References – Rojas (2006).

Chromosome number – unknown.

Distribution and habitat – Costa Rica, Cordillera Central and Cordillera de Talamanca, from 2800 to 3270 m elevation (Rojas, 2006).

Etymology – the epithet refers to Dr Robbin C. Moran, former curator of ferns at the New York Botanical Garden, in recognition of his many contributions to the study of

ferns and because he first noted the differences between this species and *Parablechnum loxense* (Rojas, 2006).

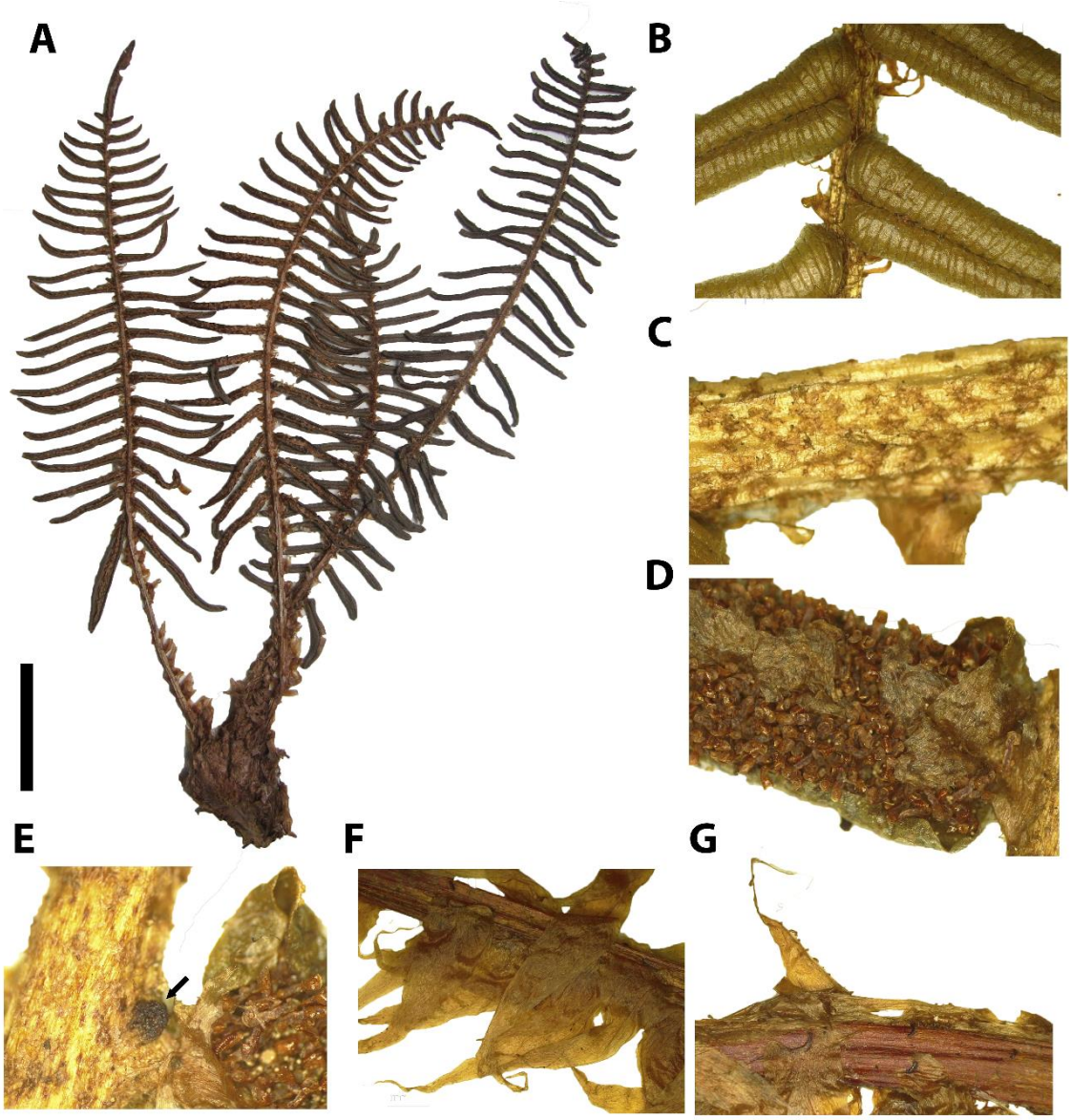

Figure 63. *Parablechnum moranianum*. A. Plant; B. Detail of sterile pinnae bases, adaxial side; C. Detail of sterile rachis; D. Detail of fertile pinna base, abaxial side; E. Detail of stalk with aerophore (arrow); F. Detail of sterile petiole scales; G. Detail of fertile petiole base. (A: *A. Rojas & H. Gómez 5895*, CR240690; B,D,E,G: *H. Churchill 3374*, VT198689; C,F: *Churchill 3374*, VT198690). Scale: 5 cm in A, 8 mm in C&G, 2 mm in C&E, 2.5 mm in D, 9.4 mm in F.

Notes – the species is similar to *Parablechnum loxense*. It differs from this species in having dimorphic rather than monomorphic or subdimorphic fronds, sterile fronds arching rather than erect, laminae elliptic to oblong-elliptic rather than ovate or oblong, sterile pinnae slightly revolute rather than strongly revolute, fertile pinnae not revolute, adaxial lamina surface dark brown instead of green (in the field), basal pinnae reflexed

and the others perpendicular to the rachis instead of all ascending) and the presence of aerophores. It is also similar to *P. sessilifolium* but has shorter sterile laminae (20–70 cm vs. 70–120 cm), elliptic to oblong-elliptic instead of oblong-lanceolate, 11–16 pairs of pinnae (vs. 27–70), reflexed basal pinnae instead of perpendicular, shorter middle pinnae (1.5–6 cm vs. 6.1 cm) and absence of buds (Rojas, 2006). Our phylogenetic results shows that this is a very well supported species, forming a clear monophyletic clade.

Reviewed material:

COSTA RICA. Prov. Cartago: Cantón Paraiso, Dist. Orosi, Cerro de la Muerte, North of Cuerici Biological Station along Panamericana, in the vicinity of the powerlines, *A.L. Grusz 118,* 23 June 2008 (CR4212342! Photo); Prov. Villa Mills. 4 km. West on road to Oja de Agua, *H. Churchill 3374,* 2 February 1980 (VT198689!; VT198690!). **Prov. Heredia:** Cantón Barva, *M. Valerio s.n.,* 29 July 1926 (CR28522! Photo); Cantón Barva, Dist. San José de la Montaña, *M. Valerio s.n.,* 29 July 1926 (CR28523! Photo). **Prov. San José:** Cantón Pérez Zeledón, Dist. Páramo, km 72-73, or 21-22 km SE of El Empalme, *A.R. Smith et al 2084,* 30 January 2006 (CR122722! Photo); Cantón Pérez Zeledón, Dist. Páramo, Villa Mills, entre La Georgina y Las Torres, *Rojas & Frias 6345,* 8 Jan 2005 (CR237193! Photo, holotype)**;** Dota, Copey, Ojo de Agua, 0.5-3 km del cruce rumbo a Providencia, *A. Rojas & H. Gómez 5895,* 24 August 2004 (CR0240690! Photo).

Parablechnum nesophilum (T.C.Chambers & P.A.Farrant) Gasper & Salino, Phytotaxa 275(3): 216. 2016.

Basionym – *Blechnum nesophilum* T.C.Chambers & P.A.Farrant, Blumea 46: 322. 2001.

Type – Papua New Guinea, Manus Island (Admiralty Islands, Bismarck Archipelago), summit region Mt Dremsel, 700 m, *Croft 1224,* 26 March 1981 (holotype: CBG8904708! Photo, 8 sheets; isotype: NSW n.s., K000519008–10! photo).

Vernacular names – referred as 'Buna–Bona' in San Cristobal in Solomon Islands (Chambers & Farrant, 2001).

Description – *plants* terrestrial; *rhizome* erect, non-stoloniferous, scaly, scales narrowly elliptic c. 3 × 0.3 cm, entire, brown to reddish brown, sometimes shiny; *fronds*

dimorphic; *sterile fronds* scattered and arching, mature ones 110–250 × 20–62 cm; *petioles* 50–100 cm, smooth, smooth, green, brown or light beige, densely covered with persistent scales, above 20 cm from base, linear-elliptic narrowly 1–2 × 0.2–0.3 cm at base, tapering from a short basal region to an attenuate hair–like apex, almost entire, pale to dark brown; *lamina* ovate–deltoid, 1-pinnate, in living material medium or dark green and shiny or semi–glossy on the adaxial surface, slightly lighter and not so shiny on the abaxial, young fronds reddish, *rachis* green, brown to light brown, scales narrowly linear-elliptic to triangular, 0.6–1.6 × 0.1–0.2 cm, tapering towards the apex, almost entire, varying from white to reddish brown, occasionally with some cells with a slightly darker spot at the point of attachment, *sterile pinnae* in 28–60 pairs, narrowly oblong-elliptic, with rounded base and attenuate apices in mature fronds, 20–33 × 1.3–2.6 cm, shortly stalked, distally some basiscopically adnate pairs, papyraceous to coarsely papyraceous, margins usually wavy, not revolute, finely toothed for most of their length becoming serrate to toothed towards the apex, basal pinnae slightly reduced in length, terminal pinnae usually slightly longer than subterminal pairs, *costa* similar to rachis, grooved adaxially, prominent abaxially, with scales up to 1 cm long; *veins* free, simple or 1-furcated, catadromous; *aerophores* absent; *hydathodes* ovate, mostly in axils of serrations; *fertile fronds* erect and with longer petioles but usually smaller lamina, *lamina* smaller in size and dark brown, with little or no photosynthetic surface, *fertile pinnae* linear, 11–22 × 0.3–0.55 cm, shortly stalked, sometimes basiscopically adnate in several pairs below frond apex, *costae* with pale scales; *sori* linear, continuous, forming coenosori on both sides of the costa, covering the whole pinna except the apex; *indusia* linear, continuous, opening towards costa, brownish, lacerate at maturity; *sporangia* with arc of 20–24 cells; *spores* monolete, (47–)60(–72) × (37–)47(–57) µm; perispores not folded, reticulate, with fenestrated walls, without filamentous processes (**Figure 64**).

References – Chambers & Farrant (2001, 2012), Chen *et al.* (2017), Molino *et al*. (2021).

Chromosome number – unknown.

Distribution and habitat – Manus Islands (Admiralty group), New Britain, New Ireland, Lihir Island, and the Solomon Islands (Kolombangara, east of San Cristobal, Guadalcanal). Most common on disturbed ridges in low forest, sometimes in meadows

dominated by small forest trees, 700–1300m. Occurs on limestone and volcanic soils in areas of high rainfall (Chambers & Farrant, 2001; 2012; Chen *et al.*, 2017).

that *P. milnei* is the lowland rainforest species. (Chambers & Farrant, 2001; 2012).

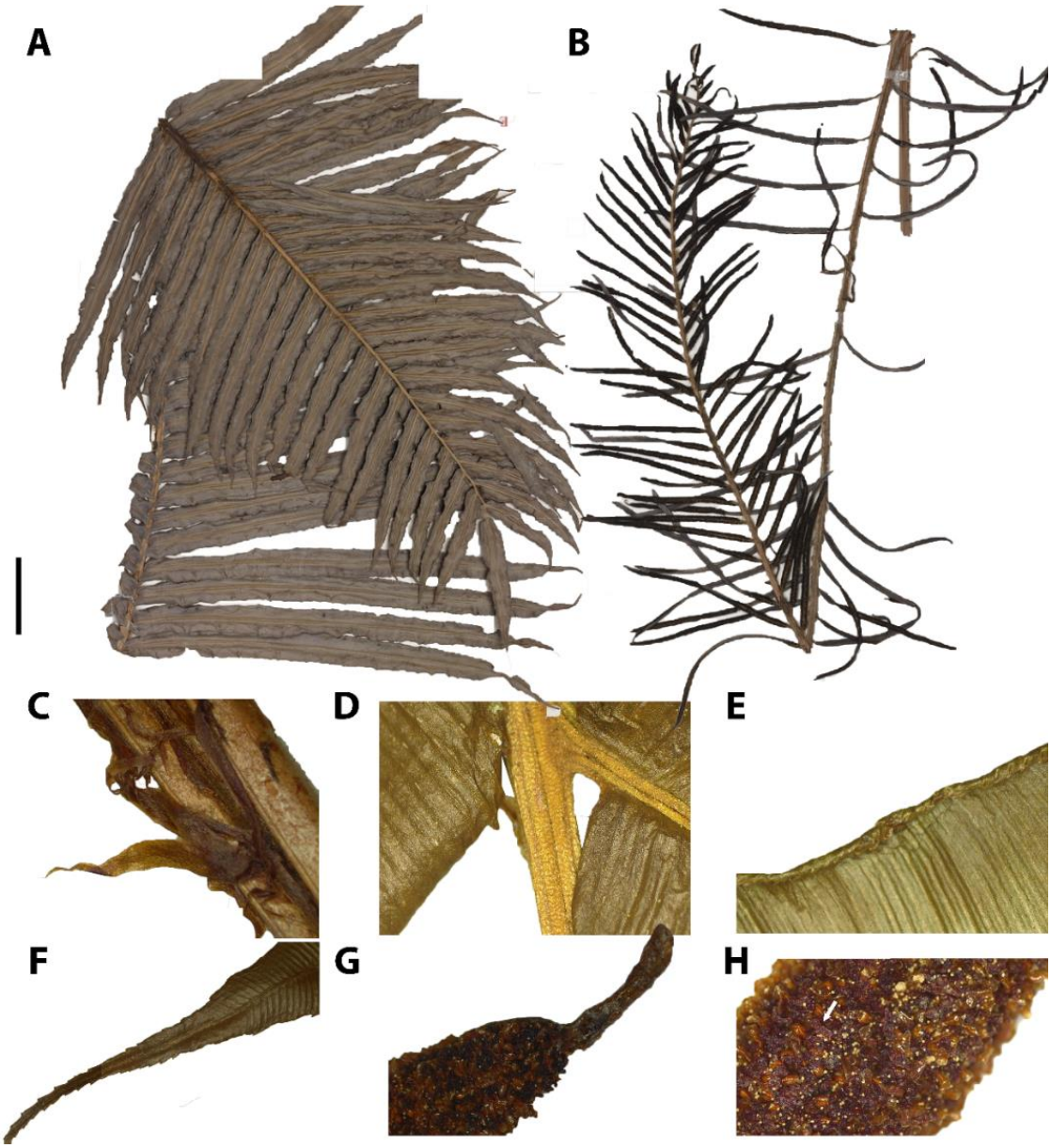

Figure 64. *Parablechnum nesophilum*. A. Fragment of sterile frond; B: Fregment of fertile frond; C. Fertile petiole base; D. Sterile rachis, adaxial side; E. Sterile pinna margin, abaxial side; F. Sterile pinna apex, adaxial side; G. Fertile pinna apex, abaxial side; H. Fertile pinna surface with sori and sporangiasters (arrow), abaxial side. (A-B: *J.R. Croft 1224*, CANB8904708, holotype; C-H: *Sundue 4251*, MACB). Scale: 4 cm in A&B, 6 mm in C, 2 mm in D, 3.5 mm in E, 8 mm in F, 2.5 mm in G, 1.5 mm in H.

Etymology – the epithet means "affinity to islands" in Latin (Chen *et al.*, 2107; Molino *et al*., 2021).

Notes – resembles *P. dilatatum*, but most specimens of *P. nesophilum* have an erect radial stem, the dry lamina is papyraceous, the sterile pinnae are long, elliptic, markedly attenuate, very finely toothed for most of their length, with toothed margins towards the apex, the pinnae of the lower half of the lamina are set at right angles to the rachis while the more distal ones are at an angle of c. 45–60º, the spores are distinct and have coralline ornamentation and are not costate–reticulate like the rest of the genus, the fertile pinnae of *P. nesophilum* lack distinctive sterile base often present in *P. dilatatum*. In addition, *Parablechnum dilatatum* lacks sporangiasters.

Parablechnum nesophilum could be confused with *P. milnei*. It is possible that both *P. nesophilum* and *P. milnei* occur on the main islands of Fiji and

Reviewed material:

PAPUA NEW GUINEA. Manus Island: Mount Dremsl region, Tjajiak Mountain, *D.F. Grether & W.H. Wagner Jr. 4180*, 25 November 1945 (P01532230!; US1915946!). Manus Island, Admiralty Islands, Bismarck Archipelago, summit region Mt Dremsel, *Croft 1224*, 26 March 1981 (CBG8904708! Photo, holotype, 8 sheets; K000519008! Photo, isotype; K000519009! Photo, isotype; K000519010! Photo, isotype). **SOLOMON ISLANDS. Kolombangara Island:** Western Province, Kongu Rano Crater, *C.–W. Chen et al. Wade2750 SITW02996*, 5 August 2005 (TAIF444962! photo); *ibidem* (TAIF444963! photo). **Makira Island:** Materato village to Mt Gasi, Makira Prov., *C.-W. Chen et al SITW06893*, 1 July 2015 (VT284040!). **Nggatokae Island:** Western Province, Mbiche Village to Mt. Mariu, *C.-W. Chen et al. Wada3287 SITW03868*, 9 October 2013 (TAIF452439! photo); *ibidem, C.-W. Chen et al. Wade3314 SITW04855*, 9 October 2013 (TAIF463384! photo; TAIF463385! photo). **Ranogga Island:** Western Province, Qiloe Village, *C-W. Chen et al. Wade2808 SITW03054*, 16 August 2013 (TAIF445010! photo; TAIF445011! photo). **Rendova Island:** Western Province, Ughele Village, *C.-W. Chen et al Wade2977 SITW03415*, 26 August 2013 (TAIF448471! Photo; TAIF448472! Photo; TAIF448473! photo). **San Cristobal Island:** Makira, Hinuahaoro, *L.J. Brass 2875*, 16 September 1932 (P01557786!; P01557787!; P01557788!). **Vella Lavella, Island:** Western Province, Boro Village to Mt. Tambisala, *C.-W. Chen et al. Wade3502 SITW03947*, 28 October 2013 (TAIF459957! photo; TAIF459958! photo; TAIF459958! photo; TAIF459959! photo; TAIF459960! photo; TAIF459961! photo).

Parablechnum novae-zelandiae (T.C.Chambers & P.A.Farrant) Gasper & Salino, Phytotaxa 275(3): 216. 2016.

Basionym – *Blechnum novae-zelandiae* T.C.Chambers & P.A.Farrant, New Zealand J. Bot. 36: 8. 1998.

Type – New Zealand: Auckland, Waitakere Ranges, Swanson, banks of stream in University of Auckland property, *T.C. Chambers s.n.*, April 1961 (syntypes: AK 232038–45! photo; isotypes: NSW281651! photo, NSW404071–76! photo, NSW 281655–56! photo).

Synonyms –

=*Lomaria procera* var. *flagelliformis* Szyszyl. In Wawra, Itin. princ. Coburgi, 121. 1888. Type: New Zealand, Auckland, *no collector 294*, no date (not found).
=*Lomaria procera* var. *gracilis* Colenso, Trans. N.Z. Inst. 25: 323. 1893. Type: New Zealand, south of Dannevirke, County of Waipawa, *no collector*, 1892 (holotype: K n.s.).
=*Stegania procera* (G.Forst.) R.Br. var. *stipulosa* A.Rich. Essai Fl. N.Z., 86, t. 13. 1832. Type: New Zealand, Bay of Islands, *no collector*, no date (not found).

Vernacular names – kiokio, korokio, horokio, koropui, piupiu, tupari, uruuruwhenua. The most used is kiokio (Chambers & Farrant, 1998a).

Description – *plants* terrestrial; *rhizome* shortly creeping, very stout in larger specimens, suberect or erect, non-stoloniferous, scaly, scales up to 5–21 × 1–3 mm, linear or lanceolate, acuminate, light reddish-brown, sometimes dark at base, more or less entire; *fronds* dimorphic; *sterile fronds* arching upwards or outwards, 18.5–350 × 3.5–50 cm;, *petioles* 3.5–115 cm long, yellow-brown, sometimes darker at the base, scaly, especially at the base, with narrowly ovate, discoloured, chestnut–coloured scales with a dark spot around the point of insertion, 2–20 × 1–3 mm; *lamina* 15–212.5 × 6.5–74 cm, 1-pinnate, elliptic to ovate, decreasing in size towards the apex, with in a conform terminal pinna, similar to subterminal, laminar tissue bright green, reddish when young, coriaceous; *rachis* yellow-brown, adaxially striate, sparsely to moderately scaly, with linear to ovate, sometimes stellate, light brown or reddish brown scales, often with a black spot, 3–15 × 1–1.5 mm, mixed with some irregular, fine, tangled hairs, with 5–53 pairs of pinnae, pinnae narrowly spaced, narrowly oblong, straight or very slightly falcate, markedly reduced to small rounded lobes at base of lamina; *sterile pinnae* 3.2–40 × 0.9–3 cm, bases cordate, apices acuminate, margins narrowly crenulate, basal pinnae opposite, subopposite distally, stalked; *costae* similar in colour to rachis, grooved adaxially,

prominent abaxially, scales on abaxial pinnae costae discoloured, with a dark spot around insertion point, concolorous towards pinnae apices and on distal pinnae; *veins* free, simple, 1-furcate, catadromous; *aerophores* absent; *hydathodes* ovate; *fertile fronds* equal to or shorter than sterile ones, 21–225 cm long; *petioles* 10–90 cm long; *lamina* 13.5–135 × 6.5–28 cm; *rachis* with 8–45 pairs of pinnae, *fertile pinnae* linear, 4.8–32 × 0.2–0.6 cm, sterile, proximally rounded bases present on the middle pinnae, 2–9 pairs of pinnae at the base of the lamina replaced by short, rounded, sterile lobes; *sori* linear, continuous, forming coenosori occupying the whole pinna except those with sterile bases and sometimes a small region of the apex; *indusia* linear, continuous, open towards the costa, brown, lacerate; *sporangia*; *spores* monolete, flat-convex in equatorial view, elliptic in polar view, (40–)52(–60) × (32–)37(–43) μm, perispores costulate, rarely costulate–winged, slightly reticulate, smooth, granulate, scabrous or rugulate between walls, exospores smooth to granulate (**Figure 65**).

Chromosome number – 2n = 56 (Chambers, 1954; Chambers & Farrant, 1998a).

Distribution and habitat – it occurs on both the North and South Islands of New Zealand, on Stewart Island, and on the outlying islands, including the Chatham and Kermadec Islands. Probably the most widespread fern in New Zealand. It has been discussed if it is present in Australia, we have found one individual from Victoria (P01462496) and another from Tasmania (US0050340) that coincide with the description of this species. It is at its optimum in regions of high rainfall, along riverbanks and in deep ravines in forested areas. Also colonises road cuts and cliffs, especially in areas of high rainfall (Chambers & Farrant, 1998a).

Etymology – the epithet refers to New Zealand, where the species was considered endemic.

Notes – this species has often been referred to as *Blechnum capense* or *Lomaria capense* (= *Parablechnum capense*) in New Zealand botanical literature, but it is now acknowledged that this name refers to an African species which, although clearly related, is not the same species.

It is related to the rest of the New Zealand species of *Parablechnum* but differs from all of them by the black–dotted scales, the sterile bases of the basal pinnae and the auricles

at the base of the lamina. It is a species in which aberrant specimens with fronds between trophophyls and sporophyls are often found. We have not observed plants with this shape and bicolorous scales as indicated by Chambers & Farrant (1998a), although it should be considered that, if these do exist, they may be hybrids, as the species of this complex tend to hybridise. These authors also found triploid plants (3n = 84) intermediate between *Parablechnum novae-zelandiae* and *Parablechnum procerum* in the South Maitai Valley, the mineral belt near Nelson, which are most likely hybrids of these two species, which grow together at this site.

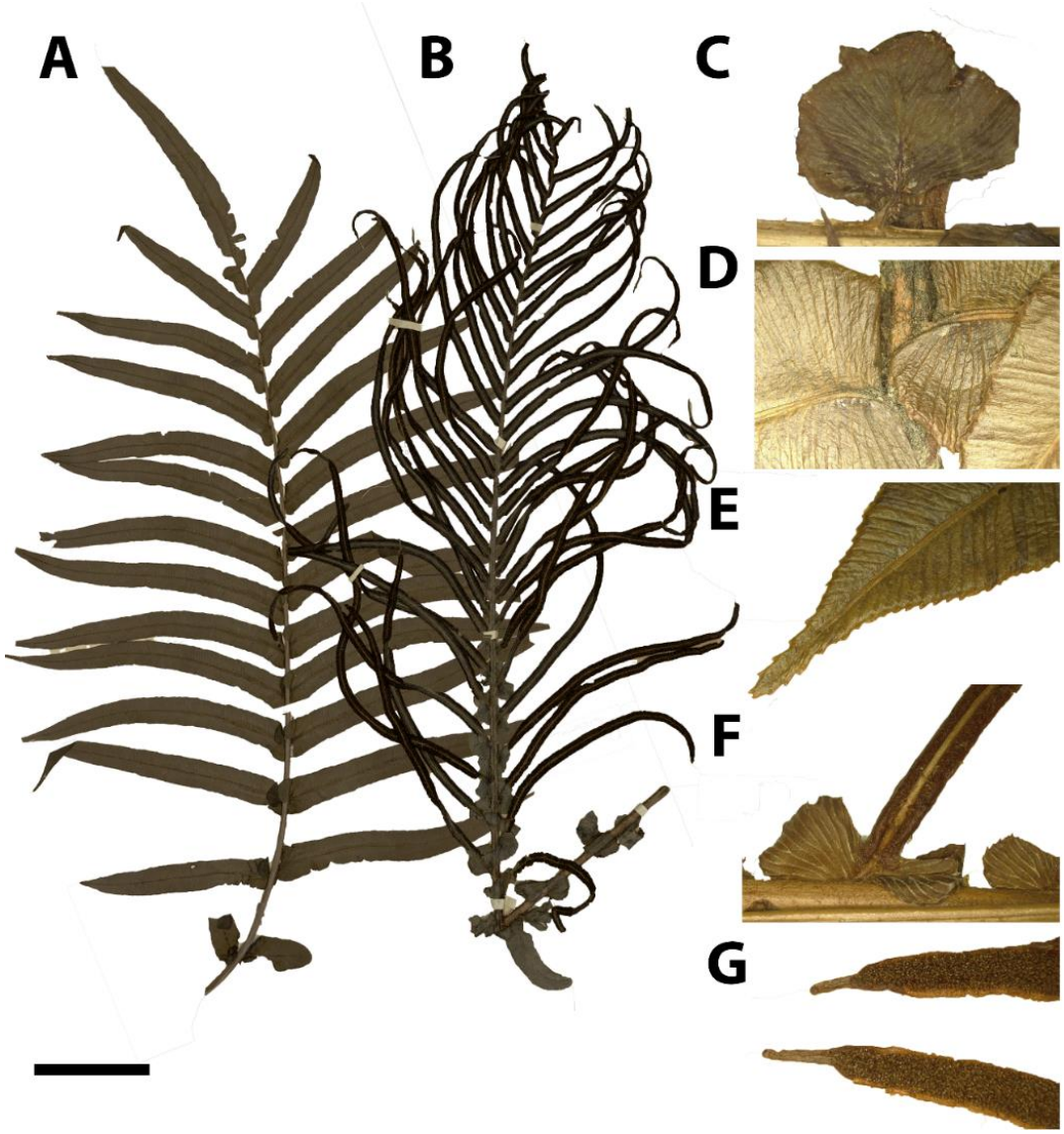

Figure 65. *Parablechnum novae-zelandiae*. A. Sterile frond fragment; B. Fertile frond fragment; C. Basal pinna of a sterile frond; D. Detail of sterile pinnae bases, adaxial side; E. Detail of sterile pinna apex, adaxial side; F. Detail of fertile pinna base, abaxial side; G. Detail of fertile pinnae apices, abaxial side. (A: *W. Gourlie s.n.*, P01462546; B: *R. Helms s.n.*, P01462568; C&E: *E. Deplanche s.n.*, P01571505; F&G: *H. Carse s.n.*, P01462540). Scale: 5 cm in A&B, 8 mm in C-G.

Chambers & Farrant (1998a) state that the normal form occurs in woodlands, stream banks and cliffs, and that there is an ecological variant in smaller swamps, with more widely spaced pinnae and basal auricles. Here, and after observing several such specimens lacking black–dotted scales, we have adopted the position of Brownsey & Smith–Dodsworth (1989) and Brownsey & Perrie (2021) concluding that these plants can be ascribed to *Parablechnum minus*.

The fronds are widely used by Maori to wrap food in their traditional pit ovens, called "hangi" (Chambers & Farrant, 1998a).

Reviewed material:

AUSTRALIA. Victoria: Cape Otway, *H. Mariner s.n.,* 1889 (US1371884!); Dayleford, *R. Wallace 12,* 1880 (P01462496!). **Tasmania:** Alta Heward, Van Dieman's Land, *no collector,* 1832 (US0050340!). **NEW ZEALAND. North Island:** *A. Cunningham 182,* 1830 (NY!; US2416302!; US barcode 1527770!); Auckland, *H. Carse s.n.,* 25 March 1922 (P01462540!); Auckland, *B. Leland et al 202,* December 1909 (NY!; US0653017!; US2567060!; US2567061!); Auckland, *J.E. Tenison–Woods 1022*, no date (P01462504!; P01462505!); Auckland, *Sinclair 293,* 1872 (P01462515!); Auckland, between Green and Blockhouse Bay, *H. Carse 16,* 23 March 1922 (US3016881!); Auckland, Waikakerei Range, *W.R.B. Oliver s.n.,* 28 October 1912 (P01462554!); Auckland, Wairakere Ranges, Cascade Cauri Forest, *L. Bernardi 12362,* 13 March 1968 (P01611550!); Auckland, Waitakere Ranges, Swanson, banks of stream in University of Auckland property, *T.C. Chambers s.n.,* April 1961 (AK232038! Photo, syntype; AK232039! Photo, syntype; AK232040! Photo, syntype; AK232041! Photo, syntype; AK232042! Photo, syntype; AK232043! Photo, syntype; AK232044! Photo, syntype; AK232045! Photo, syntype; NSW281651! Photo, isotype; NSW404071! Photo, isotype; NSW404072! Photo, isotype; NSW404073! Photo, isotype; NSW404074! Photo, isotype; NSW404075! Photo, isotype; NSW404076! Photo, isotype; NSW281655! Photo, isotype; NSW281656! Photo, isotype); Bay of Islands *no collector,* no date (US0095743!); *ibidem* (US0095744!); National Park Pokaka, *W.A. Grace 1017 (bis),* 23 April 1940 (US1756247!; US1756248!); near Memorial to Chief Tukarehe, Mamaku Forest, west of Rotorua, *O. Degener & I. Degener 36454,* 22 September 1981 (NY!); Northland, *A. Sinclair s.n.,* no date (P01462546!); Wellington Province, near the spiral in the National Park near Raurimu, *E.H. Walker 4320,* 9 February 1949 (US2015818!; US2015819!;

US2015820!). **South Island:** Canterbury, *de Belligny s.n.,* no date (P01462534!); Canterbury, *Comte s.n.,* 1855 (P01462542!); Canterbury, *M. Raoul s.n.,* 1843 (P01462560!); *ibidem* (P01462584); Otago, *C. Wilhelmi 30,* 1869 (P01462523!); Greymouth, North of Rich Helms, *R. Helms s.n.,* no date (P01462568!); West Coast, Greymouth, *R. Helms s.n.,* 1885 (P01462499!); *ibidem, R. Helms s.n.,* no date (P01462507!); *ibidem* (P01462561!); *ibidem* (P01462562!). **Southland:** Stewart Island, Oban, One mile northwest of Oban on "Bush road" to Horseshoe Bay, *P.J. Philson et al 299,* 15 February 1935 (NY!); Stewart Island, Ulva Island in Pattersln Inlet. Primeval, *E.H. Walker 4851,* 15 March 1948 (US2015864!). **Unknown area:** *no collector,* no date (P01462558!); *ibidem* (P01557665!); *ibidem* (P01568443!); *ibidem* (P01618452!); *ibidem* (P01662129!); *ibidem* (US2416303!); *no collector 86145,* no date (P01576201!); *no collector,* 1835 (NY!); *no collector 15,* 1835 (NY!); *Craig s.n.,* 24 August 1920 (P01462576!); *Cuming s.n.,* no date (P01462512!); *de Limminghe s.n.,* 1859 (P01571507!); *D. Jaun 15,* no date (P01462588!); *E. Craig s.n.,* no date (P01462583!); *E. Deplanche s.n.,* no date (P01571504!); *ibidem* (P01571505!); *E. Deplanche 57,* 1864 (P01566771!; P01566772!); *F. Mueller 10961,* 1882 (P01618451!); *Hannaford s.n.,* no date (P01462513!); *ibidem* (P01462519!); *ibidem* (P01462520!); *JDH s.n.,* no date (P01662147!); *J.D. Hooker s.n.,* no date (P01462508!); *ibidem* (P01462580!); *ibidem* (P01462581!); *S. Mossman 635,* 1854 (P01462533!); *Védel s.n.,* 1847 (P01462526!); *ibidem* (P01462530!); *ibidem* (P01462570!); *ibidem* (P01462571!); *ibidem* (P01462577!); *Walker s.n.,* 1875 (P01462537!); *W. Stephenson s.n.,* no date (P01618461!); *W. Stephenson 10,* 1943 (P01462538!; P01462555!); *W.T.L. Travers s.n.,* no date (P01462516!); *ibidem* (US barcode 1527772!).

Parablechnum obtusum (R.C.Moran & A.R.Sm.) Gasper & Salino, Phytotaxa 275(3): 217. 2016.

Basionym – *Blechnum obtusum* R.C.Moran & A.R.Sm., Brittonia 57: 237. 2005.

Type – Venezuela. Lara: Parque Nacional Dinira, laderas NW del páramo de Cendé, borde de Quebrada Las Lajitas, 09º 33’ 17’’N, 70º 05’ 50’’W. 2640 m, *Riina & Duno 1171*, 9 Jan 2001, (Holotype: NY00951457!; isotypes: UC n.s., VEN n.s.).

Description – *plants* terrestrial or saxicolous; *rhizomes* suberect or erect, non-stoloniferous, scaly, with scales 10–15 × 1.0–2.5 mm, linear-lanceolate, ferruginous to chestnut, concolorous to discoloured, with lighter margins, entire or nearly so; *fronds* monomorphic; *petioles* 10–25 cm long, brown, lustrous, smooth, scaly especially proximally, with scales light to dark brown; *lamina* 10–18 × 3–7 cm, 1-pinnate, coriaceous, broadest or slightly reduced at base, tapering towards apex and ending in a conform terminal pinna, laminar tissue between veins sparsely and minutely scaly or glabrescent, adaxially glabrous; *rachis* brown, rough on both surfaces, with short narrow ribs, sparsely scaly, with linear-lanceolate, denticulate, light or dark brown scales; *pinnae* in 10–14 pairs, 1.5–3.6 × 0.4–1, 1 cm, oblong, slightly falcate, bases truncate or subcordate, apices obtuse, margins serrulate, revolute, stalked, becoming basiscopically adnate towards apex; *costae* straw–like, smooth, sparsely scaly, grooved adaxially, prominent abaxially; *veins* free, simple or 1-furcate, sometimes dark and slightly sunken, catadromous; *aerophores* reduced and dark at insertion of pinnae; *hydathodes* ovate, prominent; *sori* linear, continuous, forming coenosori on both sides of costae; *indusia* linear, continuous, opening towards costa, with irregular margin, brown; *sporangia* (22–)25(–31) arc cells; *spores* monolete, (48–)58(–70) × (31–)43(–58) µm; perispores rugulose, cristate-reticulate, with low, thick walls, delimiting large polygonal areoles, without filamentous processes **Figure 66**).

References – Moran & Smith (2005).

Chromosome number – unknown.

Distribution and habitat – Western Venezuela. Terrestrial and saxicolous in paramo, 2600–3500 m (Moran & Smith, 2005). Here we extend the distribution to Colombia since we found a specimens from Caldas (*E. Forero et al 526*, NY) and Risaralda (US1144925).

Etymology – the epithet refers to the obtuse apices of the pinnae of this species (Moran & Smith, 2005).

Notes – it is distinguished from the species in its group by having monomorphic fronds. The fronds are distinctive for having very long petioles, longer than the length of the lamina. In addition, short pinnae with obtuse apices are characteristic. It resembles *Parablechnum werffii*, which is known from Costa Rica and Panama at lower elevations

(2000–2200 m). Both species have long petioles, leathery laminae, obtuse pinnae and a similarly shaped lamina, but differ in that *P. obtusum* is monomorphic, the pinnae bases do not overlap the rachis, the rachises are transversely rugose and generally have fewer pairs of pinnae (10–14 vs. 11–25) (Moran & Smith, 2005).

Figure 66. *Parablechnum obtusum*. A. Plant; B. Detail of a pinna stalk with an aerophore (arrow); C. Detail of fertile pinnae bases, abaxial side; D. Detail of the rhizome. (A, B &D: *A. Fay 1572*, UC1547754; C: *F.W. Pennell 10546*, US114925). Scale: 4 cm in A, 1.3 mm in B, 1 cm in C, 1.3 cm in D.

Reviewed material:

COLOMBIA. Dept. Caldas: Carretera entre Manizales y el Hotel Termales del Ruiz, *E. Forero et al 526*, 8 June 1966 (NY!). **Dept. Risaralda:** Cerro Tatamá, Cordillera Occidental, *F.W. Pennell 10546*, 8–10 September 1922 (US1144925!). **VENEZUELA. Caracas:** *Stergios 19227*, 1 Jun 2001 (PORT77556! Photo, paratype); *Stergios et al.*

20546 (PORT46356! Photo, paratype). **Lara:** Parque Nacional Dinira, laderas NW del páramo de Cendé, borde de Quebrada Las Lajitas, *Riina & Duno 1171*, 9 January 2001 (NY00951457!, holotype). **Trujillo:** peak above Bocono Municipal Park, *A. Fay 1572*, 24 December 1986 (UC1547754! Photo). **Unknown area:** *Moritz 116*, no date (P01395999!).

Parablechnum pacificum (Lorence & A.R.Sm.) Gasper & Salino, Phytotaxa 275(3): 217. 2016.

Basionym – *Blechnum pacificum* Lorence & A.R.Sm., PhytoKeys 4: 8, figs. 1–2, 14A. 2011.

Type – Marquesas Islands: Ua Pou: Poumaka Summit Trail, 690 m elevation, 9°23'33"S, 140°04'59"W, 19 June 2004, *L. M. Dunn and D. H. Lorence 481* (syntypes: PTBG041866–7! photo; isotypes: BISH n.s., P01576151!, PAP n.s., US!).

Description – *plants* terrestrial; *rhizomes* erect or suberect, non-stoloniferous, dark, scales linear-subulate to oblong-ovate, 20–30 × 1–5 mm, thin, brown, concolorous but thicker and darker basally and in the centre, base rounded or truncate, apex sinuous, margins entire or subentire; *fronds* dimorphic; *sterile fronds* with *petioles* 41–102 × 0.4–1 cm, straw–like, densely scaly towards the base, with scales similar to those of the rhizome, sparse distally, glabrescent, smooth, grooved adaxially; *laminae* 1-pinnate, oblong-ovate to oblong-elliptic, 35–100 × 20–60 cm, coriaceous to coriaceous, reducing in size towards the apex, with a conform terminal pinna; *rachis* straw-coloured, dark brown, when young scaly with fine, brown to dark brown, oblong-ovate to subulate, contoured-sinuate scales, 10 mm long with subentire or sometimes basally lacerate margins; *sterile pinnae* in 19–30 pairs proximal pinnae only slightly or not at all reduced, apices acute or acuminate, shortly stalked, subopposite to alternate, becoming basally adnate distally, terminal pinna free, conform, mid pinnae 11–30 × 1.5–2.5 cm, linear, margins serrulate, often wavy, apices, acroscopically bases oblique–cuneate, basiscopically truncate or rounded; *costa* similar to the rachis, with same kind of scales, grooved adaxially, prominent abaxially; *veins* free, simple or 1-furcate, prominent, catadromous, with the same kind of scales that the rachis and costa; *aerophores* slightly swollen and mammiform; *hydathodes* ovate; *fertile fronds* similar in size or slightly

smaller than sterile ones; *fertile pinnae* in up to 40 pairs, about the same length as sterile ones but narrower, 2.5–5 mm wide, margins strongly revolute; *sori* linear, continuous, forming coenosori on both sides of costa covering most of abaxial surface, but usually with some expanded green tissue at base; *indusia* linear, continuous, scarious and eroded; *sporangia* with (17–)20(–21) arc cells; *spores* monolete, (48–)57(–69) × (31–)39(–50) µm, perispores rugulose, cristate, with thick, low walls, forming two or three large areoles, without filamentous processes (**Figure 67**).

References – Lorence *et al.* (2011).

Chromosome number – unknown.

Distribution and habitat – known from the Marquesas Islands, Society Islands and Austral Islands. Occurs in clearings or in shade from 380–1500 m elevation in lowland to humid forests and montane plateaus, thickets, or fern fields, in valleys, on slopes or ridge crests and rocky banks. (Lorence *et al.*, 2011).

Etymology – the specific epithet refers to its distribution in the islands of the Pacific Ocean.

Notes – The name *Blechnum capense* has been erroneously applied to this Polynesian species (Brown & Brown, 1931; Copeland, 1932). The true *Blechnum capense* (= *Parablechnum capense*) is confined to southern Africa. The name *Blechnum procerum* (= *P. procerum*) has also been erroneously applied to this plant, and that taxon is only found in New Zealand. *Parablechnum procerum* has the lower pinnae only slightly reduced (not less than half the length of the middle pinna), the fertile fronds are up to 50% longer than the sterile fronds, and the fertile pinnae do not show expanded green tissue at the base as in *Parablechnum pacificum*.

In New Zealand, the closest relatives appear to be *P. novae-zelandiae* and *P. minus*. *Parablechnum novae-zelandiae* is superficially similar but differs in having reduced proximal pinnae and discoloured rhizome and petiole scales with a distinct black spot (Chambers & Farrant, 1998). It may also be related to the New Caledonian species *Parablechnum confusum*, *P. chauliodontum* and *P. subcordatum*. *Parablechnum subcordatum* differs in smaller fronds with less scaly petioles and rachises, fewer pairs of pinnae (5–15), and sterile pinnae not as wavy at the margins. *Parablechnum confusum*

differs in its strongly ascending, more strongly serrulate and less scaly pinnae (sterile laminae are almost glabrous). *Parablechnum chaliodontum* lacks the sterile expanded bases on the fertile fronds.

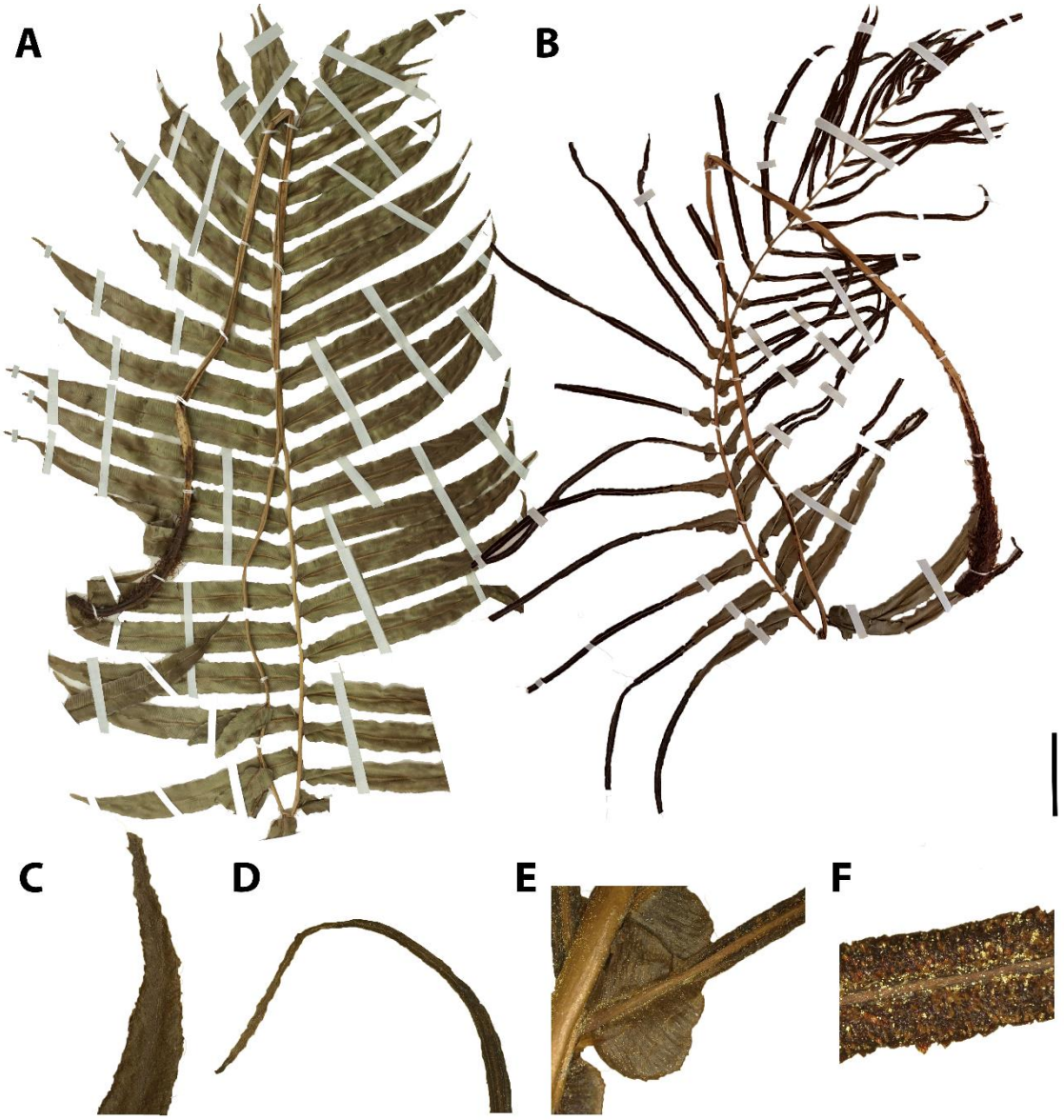

Figure 67. *Parblechnum pacificum*. A. Sterile frond; B. Fertile frond; C. Sterile pinna apex, adaxial side; D. Fertile pinna apex, adaxial side; E. Basal fertile pinna base; F. Fertile pinna surface, abaxial side. (A: *L. Dunn 481*, US3522077, syntype; B: *L. Dunn 481*, US3522076, syntype; C: *J. Nadeaud 136*, P00746654; D&F: *J. Nadeaud 136*, P00746655; E: *J. Nadeaud 136*, P00746656). Scale: 4 cm in A & B, 6.5 mm in C & E, 8 mm in D, 3 mm in F.

The closest species in Malaysia appears to be *Parablechnum vestitum* but differs in the absence of sporangiasters in *Parablechnum pacificum*, which also distinguishes it from the Fijian species *Parablechnum milnei*. In addition, neither of these two species has expanded sterile bases on the fertile pinnae. The Papua New Guinean species *P. dilatatum*

is similar to *P. pacificum* in the fertile pinnae with an expanded sterile basal region, but in the latter the margins are never revolute, and the rhizome scales are thin, concolorous and pale to medium brown.

The suitable habitat for *P. pacificum* on most of the islands where it occurs is indicated as a declining or endangered environment, threatened by human activity (deforestation, fire), feral animals and invasive plants, that are reducing the extent of the forest, making this species Vulnerable (VU) according to the IUCN Red List (Lorence *et al*., 2011).

Reviewed material:

FRENCH POLYNESIA. Marquesas Islands: *no collector,* 1 August 1922 (P00746646!); *E. Jardin 202,* 1855 (P00746643!); Fatu Iva, Sentier d'Ouia, W du col, lieu-dit Tahuna, *P.A. Schäfer 5803,* 19 September 1975 (US3149808!); Henua Enana, Ua Pou, Tekohepu, *K.R. Wood & S. Perlman 6455,* 4-5 July 1997 (US3391245!; US3391246!); Hiva'Oa, Atuona-Feani trail, ridge crest, *M.H. Sachet & B.G. Decker 1160,* 24-26 September 1963 (US3149831!; US3149832!); Hiva'Oa, Feani ridge to upper slopes of dry side of island, *R.L. Oliver & P.A. Schäfer 3130,* 12 February 1975 (US3149958!; US3149959!); Hiva'Oa, montagnes NW du Temetiu, entre la haute vallée de Hanamenu et la crête de Temetiu-Feani, *P.A. Schäfer 5932,* 23 October 1975 (US3149806!); Hiva'Oa, Puamau, along Puamau-Atuona trail, *B.G. Decker 1190,* 14 December 1963 (US3590941!); Hiva'Oa Island, road from Atuona to Puamau, just below Mt. Ootua, *M.H. Sachet & B. Decker 1904,* 23 November 1974 (US3590948!); Nuku Hiva, *Le Batard 9,* 1 January 1844 (P01532254!); Nuku Hiva, Pic au Nord du village de Toovii, crête NO, *A. Mouly 534,* 27 July 2004 (P00592146!; P00746713!; P00746714!); Nuku Hiva, Spur of Mt. Ooumu, Toovii Plateau, *B. Gagné 1039,* 16 July 1977 (P00746640!; US3149804!); Nuku Hiva, Toovii, épaulement S du Mt Ooumu, *J. Florence 4269,* 3 December 1982 (P00746636!); Nuku Hiva, Toovii, sommet du Mt Akaupe, *J. Florence 8537,* 10 August 1987 (P00746638!; P00746639!); Nuku Hiva, Toovii, Terre Deserte, km 4 après le col, *Florence 6905,* 5 June 1984 (P00746637!); Tahuata, De Hamatea à la crête centrale de l'île, *J.-C. Thibault 64,* 26 May 1975 (US3149886!); Ua Pou, drainage and forest patch to the northwest of Teavahaakiti, *K.R. Wood 10458,* 27 November 2003 (P01566768!); Ua Pou drainage and forest patch to the northwest of Teavahaaiti, *K.R. Wood 10458,* 27 November 2003 (US3463807!); Ua Pou,

Poumaka summit Trail, *L. Dunn & D.H. Lorence 481*, 19 June 2004 (P01576151!, isotype; US3522076!, syntype; US3522077!, syntype); Ua Pou, slope below Oave, *E. Schuettpelz et al 1893*, 5 November 2017 (US3717580!). **Rapa:** *H. St. John & F.R. Fosberg 15293*, 1 July 1934 (NY!; P00746633!; US1919777!); Flanc W de la baie d'Agairao, *J. Florence 6315*, 30 January 1984 (P00746645!; P00776644!); Hiri side below Maitua ridge, peak west of TeVaitau Pa (fortress) (maybe more correctly be called Maitua nako and Vaitau is smaller Pa on next south ridge), *T.J. Motley & R. Fenstemacher 2754*, 13 April 2002 (NY!); Kaukauamoo, *F.R. Fosberg 11567*, 18 July 1934 (NY!); S slope, ridge between Morongota and Vaitau, *F.R. Fosberg 11605*, 20 July 1934 (P00746631!). **Society Islands:** Moorea, *J. Nitta & S. Vinette 212*, 10 September 2008 (P00746664!; P00746665!); Moorea, pass between Mt Tiura and Mt. Tatiri, *J. Nitta 616*, 17 August 2010 (P00847391!); Tahiti, *M.J. Lépine 83*, 1847 (P00746651!; P00746652!; P00746674!); Tahiti, *Nadeaud 136*, no date (P00746653!; P00746654!; P00746655!; P00746656!; P00746657!; P00746658!); Tahiti, *Nadeaud 515*, 1896 (P00746659!; P00746660!; P00746661!; P00746662!; P00746663!); Tahiti, route du Mt Marau, crête de l'OPT, *J. Florence 3283*, 5 June 1982 (P00746647!; P00746648!); Tahiti, Mt. Marau road, crest between Tapaerui and Punaruu valleys, *F.R. Fosberg 62647*, 5 June 1982 (P00746649!; P00746650!; US3353090!; US3353091!); Tahiti, Orohena, *Raynal 18070*, 11 July 1973 (P00746666!; P00746667!; P00746668!; P00746669!; P00746670!). **Unknown area:** *Vesco s.n.*, no date (P00746671!); *ibidem* (P00746672!); *ibidem* (P00746673!).

Parablechnum paucipinna A.R.Sm. Phytotaxa, 292(1): 66. 2017.

Type – Venezuela. Edo. Bolívar: Sierra de Lema, sector La Escalera, al Este de la carretera, a unos 200 m del salto El Danto en dirección N–S, 05°57'54"N, 61°23'42"W, bosque de galería muy húmedo, 1250–1300 m, *Y. Vivas, B. Holst, J. Tillet & S. Fawcett 1553*, 23 Apr 2006 (holotype: UC2044673! photo; isotypes: SEL n.s., VEN n.s.).

Description – *plants* saxicolous; *rhizomes* erect, forming a small stem, scaly, scales concolorous, brown to dark brown, lanceolate to ovate–ovate, attenuate apex, 8–10 × 1–2.5 mm, margins entire or nearly so; *fronds* dimorphic; *sterile fronds* with straw-coloured *petioles*, darker at maturity, axially grooved, verrucose ornamentation, 20 × 0.2–0.3 cm,

about the same length as the laminae, glabrous except in the base, scales 6 × 2 mm, margins entire, with apices resembling those of the rhizome but lighter brown, concolorous; *laminae* herbaceous, ca. 20 × 15 cm, deltoid, 1-pinnate; *rachis* straw-coloured or brownish, with transverse ribs like those of the petioles, adaxially grooved, with some scattered brown near costae scales ca. 0.5–3 × 0.3 cm, with a few scattered brown scales. 0.5–3 × 0.1–0.4 mm; *sterile pinnae* in 4–5 pairs, stalked, bases rounded to cuneate, apices abruptly attenuate and finely toothed at tips, margins not revolute; *costae* abaxially with shiny, filiform to lanceolate tan scales, the larger ones broadened and pectinate at their bases, mostly 0.5–1.5 mm long; *veins* free, simple or 1-furcate, impressed, darker abaxially, catadromous; *aerophores* low, blackish and tuberculiform; *hydathodes* not visible; *fertile fronds* similar in size to the sterile ones; *petioles* 25 cm long, twice as long as the laminae; *fertile pinnae* delicate, ca. 4 pairs per frond, narrow, ca. 5 × 0.1 cm; *costae* with filiform scales on abaxial side; *sori* linear, continuous, forming coenosori on both sides of the costa; *indusia* linear, continuous, very narrow, entire, at least at maturity; *sporangia* not observed; *spores* not observed (**Figure 68**).

References – Dittrich *et al*. (2017).

Chromosome number – unknown.

Distribution and habitat – Venezuela, ca. 1300 m. It grows in rocks, with clustered fronds in montane rainy forest (Dittrich *et al*., 2017).

Etymology – the specific epithet refers to the low number of pinnae and relatively small fronds (*paucus* = few) (Dittrich *et al*., 2017).

Notes – according to Dittrich *et al*. (2017), this could be the most delicate species within *Parablechnum* because its fine and herbaceous laminar texture. However, this is also characteristic of *Parablechnum corbassonii* in New Caledonia, although this species is larger. It seems remarkable the low number of pinnae compared to the rest of the Venezuelan species. Dittrich *et al*. (2017) also point the remarkably low number of scales, which could be deciduous, something common in this genus. It is similar in shape to *Parablechnum glaziovii*, but that species has a stronger laminar tissue.

Figure 68. *Parablechnum paucipinna. Y. Vivas et al 1553,* UC2844673, holotype. Scale: 4 cm.

Reviewed material:

VENEZUELA: **Bolívar**: Sierra de Lema, sector La Escalera, al Este de la carretera, a unos 200 m del salto El Danto en dirección N–S, *Y. Vivas et al. 1553*, 23 March 2006 (UC2044673! Photo, holotype).

Parablechnum pazense (M.Kessler & A.R.Sm.) Gasper & Salino, Phytotaxa 275(3): 217. 2016.

Basionym – *Blechnum pazense* M.Kessler & A.R.Sm., Amer. Fern J. 97: 73. 2007.

Type – Bolivia. La Paz: Prov. Franz Tamayo, PNANMI Madidi, sendero Keara–Mojos, a 1 hora y media aproximadamente de caminata desde Tokuaqe por la senda del

inciensal, 14'36'S, 68057'W, 2490 m, *Jiménez 752*, 11 March 2001 (holotype: UC1764475! photo; isotype: LPB0000018! photo).

Description – *plants* terrestrial; *rhizomes* elongate, creeping to suberect, scaly, scales 5–8 × 1.2–2 mm, lanceolate, dark reddish brown, denticulate; *fronds* monomorphic or subdimorphic, 175 × 21 cm, erect to arching; *petioles* 100 × 0.5 cm, dark reddish brown, densely scaly on adaxial side, scales basally similar to those of the rhizome but distally intermixed with ovate to lanceolate scales, pale dull brown, denticulate, 1–3.5 × 0.3–1 mm; *laminae* lanceolate, 1-pinnate, with a gradually reduced apex, with in a conform terminal pinna, laminar tissue chartaceous, adaxially glabrous, abaxially with scattered minute scales mostly on the veins, the scales 0.05–0.2 × 0.05 × 0.2 mm, arachnoid, appressed, pale brown; *rachis* adaxially dull brown, grooved, glabrous, abaxially dark reddish brown to atropurpureous, densely scaly, scales 1–3 × 0.3–1 mm, ovate to lanceolate, pale brown, dull, denticulate; *pinnae* in ca. 40 pairs, 11 × 1.25 cm, stalked, falcate, apices broadly acuminate, margins hyaline, serrulate, slightly revolute, alternate to subopposite; *costae* adaxially straw-coloured, grooved, glabrous, abaxially atropurpureous, bearing scales dense, 0.5–1 × 0.3–0.7 mm, ovate, entire to denticulate, pale brown to bicolorous at costa base, with dark brown centres and whitish margins; *veins* free, simple or 1-furcate, abaxially slightly raised and slightly paler than laminar tissue, catadromous; *aerophores* axillary, tuberculiform; *hydathodes* patent, ovate; *sori* linear, continuous, forming coenosori on both sides of costa, leaving 2–4 mm of green laminar tissue between sori and pinna margins, usually not reaching apex; *indusia* linear, continuous, opening towards costa, translucent, brown, entire to slightly irregular; *sporangia* with (17–)20(–21); *spores* (48–)64(–71) × (38–)47(–55) µm, perispores smooth or slightly rugulose, cristate-reticulate, with low, thick walls, delimiting large polygonal areoles, with long, twisted filamentous processes moderately abundant on the entire surface (**Figure 69**).

References – Kessler *et al.* (2007).

Chromosome number – unknown.

Distribution and habitat – endemic to Bolivia, at 2400–2850 m in the department of La Paz. In this work we also found a specimen from the department of Cochabamba (*M.A.*

Zabalaga 196, NY04187077). Locally common, terrestrial in montane rainforests (Kessler *et al*., 2007; Smith & Kessler, 2018).

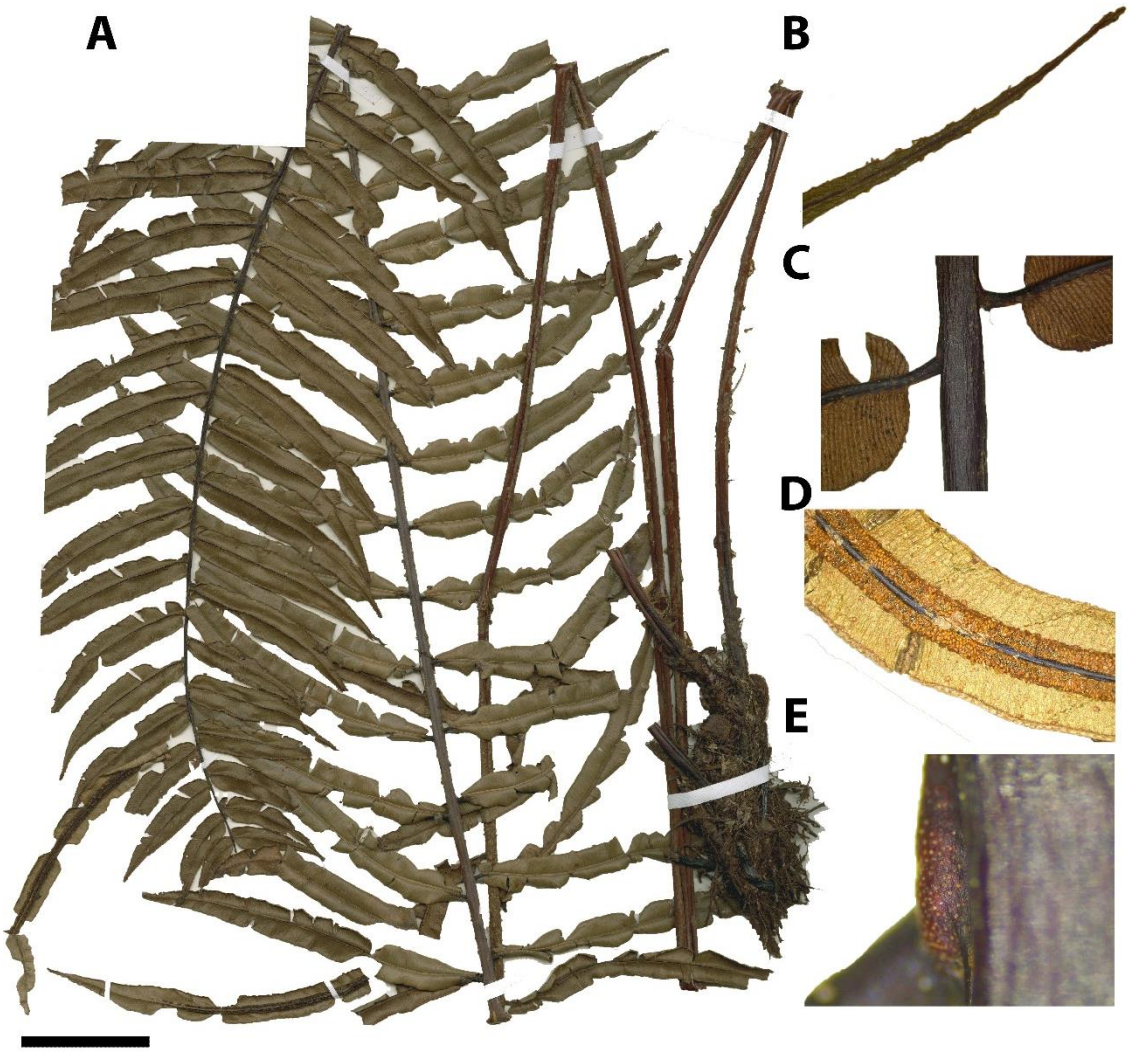

Figure 69. *Parablechnum pazense.* A. Plant. B. Pinna apex, adaxial side; C. Pinnae bases, abaxial side; D. Pinna surface with sori, abaxial side; E. Aerophore. (A: *I. Jiménez 752*, UC176445, holotype; B-E: *M.A. Zabalaga 196*, NY04187077).4 cm in A, 9 mm in B, 9.5 mm in C & D, 1 mm in E.

Etymology – the epithet refers to the Bolivian Department of La Paz, where the species is endemic.

Notes – this species is recognisable by its creeping to suberect, slightly dark reddish-brown rhizomes, denticulate rhizome scales and partially bicolorous scales about 1 mm long. It is similar to *P. bolivianum*, which differs by having shorter, erect rhizomes, darker, entire, irregular, or dentate rhizome scales, wider and abruptly reduced lamina and concolorous costal scales. (Kessler *et al*., 2007).

Reviewed material:

BOLIVIA: Dept. Cochabamba: Prov. Tiraque. Localidad El Limbo, *M.A. Zabalaga 196*, 13 February 2004 (NY04187077!). **Dept. La Paz:** Prov. Franz Tamayo, Parque Nacional Madidi, Mojos, sector Lagunillas, por el camino a Queara, *A. Fuentes et al. 11620*, 30 April 2007 (MO6136888!); Prov. Franz Tamayo, Parque Nacional Madidi, sector Tocoaque (entre Keara y Mojos), *A.F. Fuentes et al 15484,* 2 October 2009 (MO6587657!; MO6461269!); Prov. Franz Tamayo, PNANMI Madidi, sendero Keara–Mojos, *Jiménez 752*, 11 March 2001 (UC1764475! photo, holotype; LPB0000018! photo, isotype); *ibidem, Jiménez 751,* 11 March 2001 (UC1764728! photo, paratype); Prov. Nor Yungas, Estación Biólogica de Tunquini, Bajo Hornuni, *Garcia 4460*, 25 July 2000, (UC! photo, paratype).

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

Basionym – *Osmunda procera* Forst.f., Prodr., 78, no. 414 (1786)

Type – New Zealand, *Forster s.n.* (lectotype: K001092705! photo).

Synonyms –

≡*Blechnum procerum* (G.Forst.) Sw., J. Bot. (Schrader) 1800(2): 75. 1801; *Lomaria procera* (G.Forst.) Spreng., Syst. Veget., IV: 65. 1827; *Onoclea procera* (G.Forst.) Spreng., Schrad. Journ. 2: 267. 1799 [–1800]; *Stegania procera* (G.Forst.) R. Br., Prodr., 153. 1810.

=*Lomaria latifolia* Colenso, Tasm. J. Nat. Sci. 2: 175. 1846. Type: New Zealand, near Waikare Lake and Ruatahuna, Te Waiiti District, *W. Colenso s.n.*, January 1842 (holotype: WELT P3240! Photo).

=*Lomaria procera* var. *minor*, Hook.f., Fl. Nov. Zel. 2: 27, t. 75. 1855. Type: Noua Zeelandia [New Zealand], *Forster s.n.*; (lectotype: K! phot; isolectotypes: BM! photo, GOET! photo).

=*Lomaria duplicata* Potts, Trans. N.Z. Inst. 9:491. 1877. Type: New Zealand, Malvern Hills near the gorge of the Rakaia, *T. H. Potts s.n.;* (holotype: K! photo).

Vernacular names – small kiokio (Chambers & Farrant, 1998a).

Description – *plants* terrestrial; *rhizomes* erect or short to long creeping, non-stoloniferous, scaly, scales ovate to narrowly ovate, 3–11 × 1–2.7 mm, chestnut brown, concoloured or slightly discoloured with paler margins; *fronds* strongly dimorphic; *sterile fronds* 7–100 cm long, rarely up to 140 cm long, prostrate or semi-erect; *petioles* 1.5–58 cm long, rarely up to 83 cm long, blackish proximally, yellowish brown distally, with shiny, uniformly chestnut-brown or dark brown scales with paler margins; *lamina* 4.5–57

× 2–28 cm, 1-pinnate, elliptic or oblong, with a conform terminal pinna, sometimes reddish when young, coriaceous; *rachis* yellow–brown, adaxially striate, scaly; *sterile pinnae* in 1–12 pairs, closely spaced, oblong, straight, not reduced or hardly reduced at the base of the lamina, longest about half the length of the lamina, 1–19.5 × 1–3.5 cm, apices acute or obtuse, margins narrowly crenulate, bases truncate or rounded, shortly stalked, basal pinnae opposite, subopposite distally; *costa* grooved adaxially, prominent abaxially, scaly, scales on abaxial costa dark brown with paler margins, without a clearly defined dark spot, sometimes becoming chestnut–brown and concolorous towards pinnae apices; *veins* free, simple or 1-furcate, catadromous; *aerophores* absent; *hydathodes* ovate; *fertile fronds* longer and more erect, 12.5–114 cm, or rarely up to 143 cm long, centrally positioned; *petioles* 8.5–86 cm long, rarely only 5 cm or up to 104 cm long; *lamina* 9–44 × 2–23 cm; *rachis* with 2–14 pairs of *fertile pinnae*, linear, straight, 18–17 × 0.2–0.6 cm; *sori* linear, continuous, forming coenosori on both sides of costa; *indusia* linear, continuous, opening towards costa, brownish, entire or lacerate at maturity; *sporangia* with 16–19 arc cells mixed with longer paraphyses, dark; *spores* monolete, flat-convex in equatorial view, elliptic in polar view, (45–)56(–70) × (25–)39(–52) µm, perispores costate–reticulate, forming large areoles, surface of areole lacunae granular, without filaments (**Figure 70**).

References – Chambers & Farrant (1998a), Brownsey & Perrie (2021).

Chromosome number – 2n = 112 (Chambers, 1954). It appears to be an autotetraploid that could have originated from *P. novae-zelandiae* or *P. montanum* by chromosomal duplication. (Chambers & Farrant, 1998a).

Distribution and habitat – endemic to New Zealand and the Subantarctic Islands, scattered in isolated localities; most common in the southern parts of the region, 10–1375 m. In the North Island it is generally found on ridges above 300 m, although there are some records from lower elevations. Occurs in mixed montane forest in the north, and in woodland and subalpine grassland in the south (Chambers & Farrant, 1998a; Brownsey & Perrie, 2021).

Etymology – from the Latin, *procerus* (very high or long), referring to the long erect fertile fronds (Brownsey & Perrie, 2021).

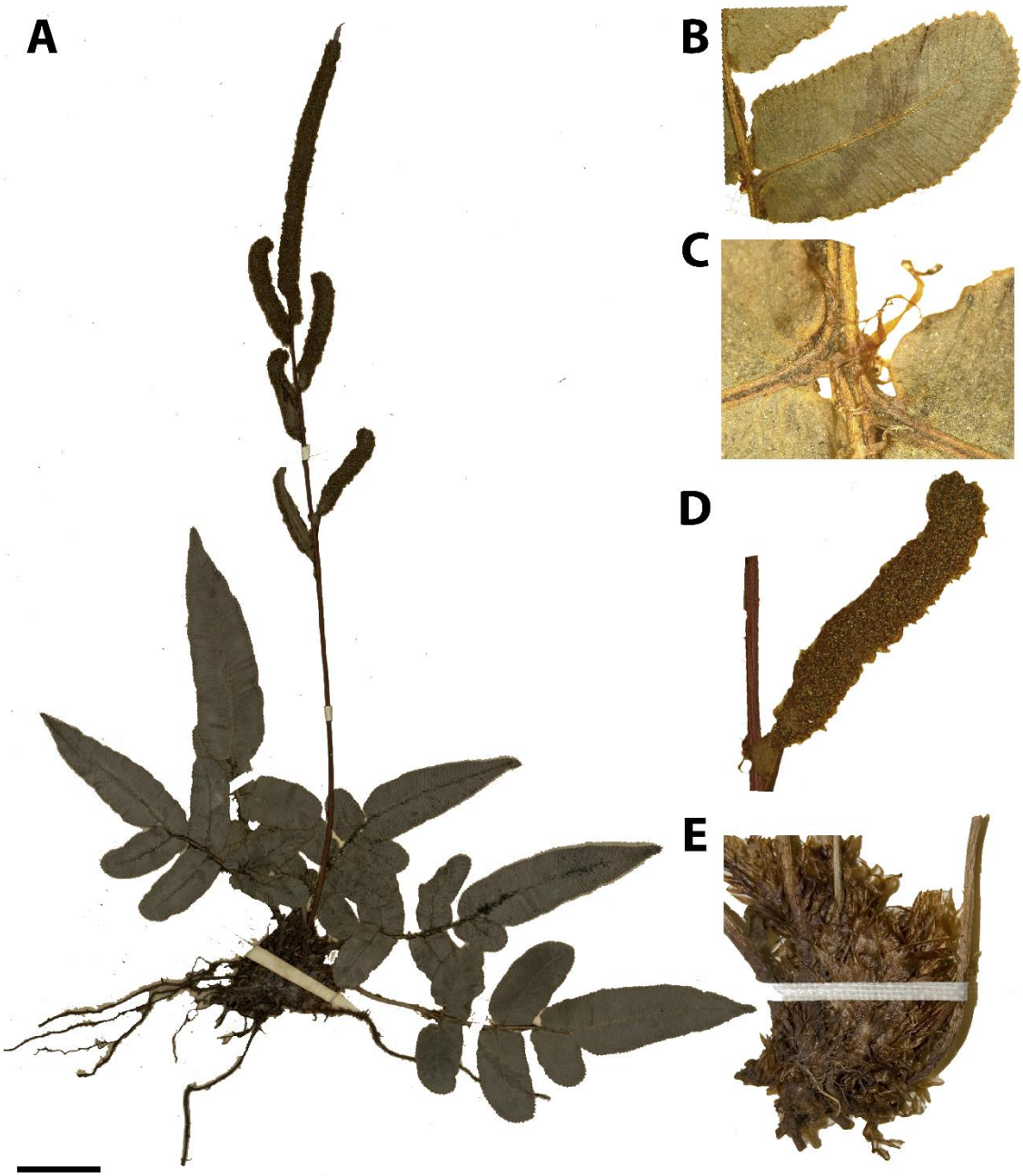

Figure 70. *Parablechnum procerum.* A. Plant; B. Sterile medium pinna, adaxial side; C. Sterile rachis, adaxial side; D. Fertile pinna, abaxial side; E. Rhizome. (A-D: *R.Helms s.n.*, P01463055; E: *R.m.h. 92044*, UC497725). Scale: 2.5 cm in A, 6.5 mm in B, 2 mm in C, 6.7 mm in D, 1 cm in E.

Notes – *Parablechnum procerum* has been referred to as *Blechnum minor* or *Blechnum minus* in some New Zealand floras and vegetation notes. It has also been listed as *Parablechnum capense*, now recognised as an African species that does not occur in Australia or New Zealand. *Parablechnum procerum* can be confused with *P. montanum*, with which it appears to hybridise in some areas. *Parablechnum procerum* tends to have fewer, more obtuse pinnae and its basal pinnae are not reduced. The pinnae of *P.*

montanum are usually attenuate and falcate, and it has black–dotted scales. *Parablechnum procerum*, although morphologically very different, also hybridises with *P. novae-zelandiae*. It can also be confused with *Parablechnum minus* but is easily distinguished because *P. procerum* lacks pinnae reduced to lobes at its base. *Parablechnum procerum* is similar in its coarse morphology and comparable in its ecological preferences, especially in its forest habitats, with *P. wattsii* in eastern Australia. However, the latter can become a much more robust plant, with fronds up to 140 × 26 cm, up to 17 pairs of pinnae and with conspicuously toothed and larger costal scales. Australian plants formerly recognised as *P. procerum* (Tindale, 1960) are now recognised as *P. wattsii*.

Reviewed material:

NEW ZEALAND. North Island: Auckland, *H. Carse s.n.,* May 1919 (P01462548!); Auckland, *H. Carse 14,* 23 March 1922 (P01462552!); Auckland, *Le Guillou 72,* 1841 (P01462579!); Auckland, *P. Serre s.n.,* June 1931 (P01462525!); Auckland, Waikakerei Range, *J.W. Brame s.n.,* March 1925 (US1371330!); *ibidem*, *W.R.B. Oliver s.n,* 28 October 1912 (P01462547!); Cape Terawhiti, *T. Kirk 609,* no date (US0816201!); Coromandal, *T.F. Cheesman s.n.,* December 1884 (US0060839!); near Waikare Lake and Ruatahuna, Te Waiiti District, *W. Colenso s.n.*, January 1842 (WELT P3240! Photo, holotype of *Lomaria latifolia*); North Cape, *T. Kirk 604*, no date (US0816202!); Taranki, slopes of Pouakai, *R.O. Gardner 5354*, 28 September 1987 (US343278!); Te Aroha, *B. Leland et al 266,* February 1919 (NY!; US0653058!); Titirangi Ranges, *T.F. Cheesman 234*, 1872 (US barcode 1527776!); Wellington, *C.K. Jeffs 69*, 1868 (P01462524!); Wilton's Bush, nr. Wellington, *R. Ornduff s.n.*, July 1954 (UC1093824! Photo). **South Island:** Canterbury, *de Belligny s.n.*, no date (P01462529!); Canterbury, Malvern Hills near the gorge of the Rakaia, *T. H. Potts s.n.*, no date (K! photo, holotype of *Lomaria duplicata*); Canterbury, Presqu'île de Banes, *M. Raoul s.n.*, 1843 (P01462572!); *ibidem* (P01462559!); Christchurch, Lyttelhon Hills, *R.m.h. s.n.*, no date (UC497725! Photo); just south of Big Totara River, 5 mi. South of Westport, Westland, *F.R. Fosberg 30697*, 27 February 1949 (US269644!); Otago, *C. Wilhelm 33*, 1869 (P01462539!; P01462541!); Otago, *C. Wilhelm 624*, no date (P01462536!); Paparoa Range, SW of Sewell Peak, *A. Strid 22240*, 5 February 1983 (MO3412985!); Richmond, upon Thames, *no collector 457*, no date (P01462563!); West Coast, Greymouth, *Helms s.n.* no date (P01462564!); *ibidem* (P01462565); *ibidem* (P01462569); *ibidem* (P01463055!); *ibidem* 04.1878(P01462521!);

ibidem, 1879 (P01462500!); Waiuta, Westland County, *J. Thompson 535*, 19 January 1973 (MO2225320!); Westland, Auld Creek, near Reefton, *R.O. Gardner 8365*, 12 May 1997 (MO5316089!); Westland, Jacksons Creek on Hwy. 7 between Springs Junction and Maruia Springs, *C.H. Lamoureux 3316*, 10 January 1966 (US3584976!). **Unknow area:** *no collector*, no date (P01462522!); *ibidem* (P01658107!); *ibidem* (P06491234!); *illegible collector*, 11 March 1927 (UC313093! Photo); *A. Cunningham s.n.*, 1838 (US barcode 1527771!); *Craig, s.n.*, no date (P01532240!); *Craig s.n.*, 24 August 1924 (P01462517!); *ibidem* (P01462553!); *Daemel s.n.*, no date (P01462502!); *Hannaford s.n.*, no date (P01462514!); *Forster s.n.* (K001092705! Photo, lectotype); *ibidem* (BM! photo, isolectotype of *Lomaria procera* var. *minor*; GOET! photo, isolectotype of *Lomaria procera* var. *minor*; K! photo, lectotype of *Lomaria procera* var. *minor*); *Helms s.n.*, 1870 (US2416305!); *Helms s.n.*, 1887 (P01462503!); *Mueller s.n.*, 1882 (P01462545!); *Pictor 40*, no date (P01462510!); *R. Hawkins s.n.*, no date (P01462511!); *W. Hooker s.n.*, 1854 (P01462567!); *Wilkes Explor. Exped. s.n.*, 1838-1842 (US0095751!); *W. Stephenson 2*, 1843 (P01462506!; P01462535!); *W.T.L. Travers s.n.*, no date (US barcode 1528186!). **UNKNOWN LOCATION:** *P. Meiepnur* [interpreted], 1876 (NY!).

Parablechnum proliferum (Rosenst.) Gasper & Salino, Phytotaxa 275(3): 217. 2016.

Basionym – *Blechnum proliferum* Rosenst, Hedwigia 46: 91. 1906.

Type – Brazil, São Paulo: Santo André, Rio Grande, *M. Wacket 132* [Rosenstock Filices Austrobrasilienses, no. 338] (synlectotypes: P01573198!, P00627617–21!; designed by Dittrich *et al*., 2018); isolectotypes: B200033012!; US600227!).

Synonyms –

=*Struthiopteris vivipara* Broadh. Bull. Torrey Bot. Club 39: 381. 1912. Type: Costa Rica, San José, vicinity of La Palma, 1450–1550 m, *W.R. Maxon 435* 06–08 May 1906 (syntypes: US00067454-5!), isotypes: NY149790-1!); ≡*Blechnum viviparum* (Broadh.) C.Chr. Index Filic., Suppl. (1906–1912): 17. 1913.

Description – *plants* terrestrial; *rhizomes* erect to decumbent, non-stoloniferous, scaly, scales lanceolate–ovate to lanceolate, yellowish-brown, brown, concolorous, 5.3–25 × 0.4–2.6 mm, margins entire; *fronds* dimorphic, mucilaginous when young; *sterile fronds* 88–194 cm long; *lamina* 57–125 × 19–43 cm, 1-pinnate, papyraceous, narrowly oblong, tapering towards apex to a conform terminal pinna similar to lateral pinnae,

truncate at base, sparsely scaly on underside; *bulbils* present at bases of some pinnae, especially on distal ones, adaxially; *rachis* smooth; *sterile pinnae* in 10–22 pairs, 12–28 × 2.3–4 cm, stalked, becoming sessile or basiscopically adnate distally, ascending, narrowly elliptic to nearly linear, apices acuminate, margins dentate, flat to slightly revolute; *costae* grooved adaxially, prominent abaxially, with brown, concolorous, twisted scales, margins with elongate teeth, narrowly triangular with a broader base; *veins* free, simple or 1-furcate, with scales similar to those of costa but minute, catadromous; *aerophores* axillary, conical; *hydathodes* rounded or ovate; *fertile fronds* longer than sterile, 122–220 cm long; *petioles* 69–136 cm long; *lamina* 53–85 × 11–22 cm; *rachis* petiole–like, atropurpureous, with light brown to whitish scales; *fertile pinnae* in 17–20 pairs, narrower, 12.8–19 × 0.55–0.7 cm, linear; *sori* linear, continuous, forming coenosori on both sides of costa; *indusia* linear, continuous, opening towards costa, brownish, entire or lacerate at maturity; *sporangia* with 24–30 arc cells; *spores* monolete (46–)58(–74) × (30–)44(–64) µm; perispores smooth, cristate-reticulate, with low, thick, slightly tapering walls, deflected at apex, delimiting large polygonal areoles, without filamentous processes or with some scattered filament in areole lacunae (**Figure 71**).

References – Moran (1995a), Passarelli *et al.* (2010), Prada *et al.* (2016), Dittrich *et al*. (2018, 2020).

Chromosome number – unknown.

Distribution and habitat – Brazil, Panama, Costa Rica, and Bolivia. Uncommon, terrestrial in humid forests, especially at forest edges. In mountainous areas between 300–1300 m according to Dittrich *et al*. (2018), 900–2700 m according to Smith & Kessler (2018), usually in forest edges, humid, cloud and disturbed forests (Moran, 1995a).

Etymology – its epithet refers to the bulbils present in the species.

Notes – this species can be confused with other large *Parablechnum* species such as *P. cordatum*, *P. falciforme* or *P. schiedeanum*, but is distinguished by its atropurpureous petioles, conical aerophores, presence of bulbils at the bases of the distal pinnae and more scaly rachises. *Parablechnum varians* also has atropurpureous axes, but no bulbils and no conical aerophores. It is also similar to *Parablechnum lechleri* in its dark axes and conical aerophores, but again this species lacks bulbils.

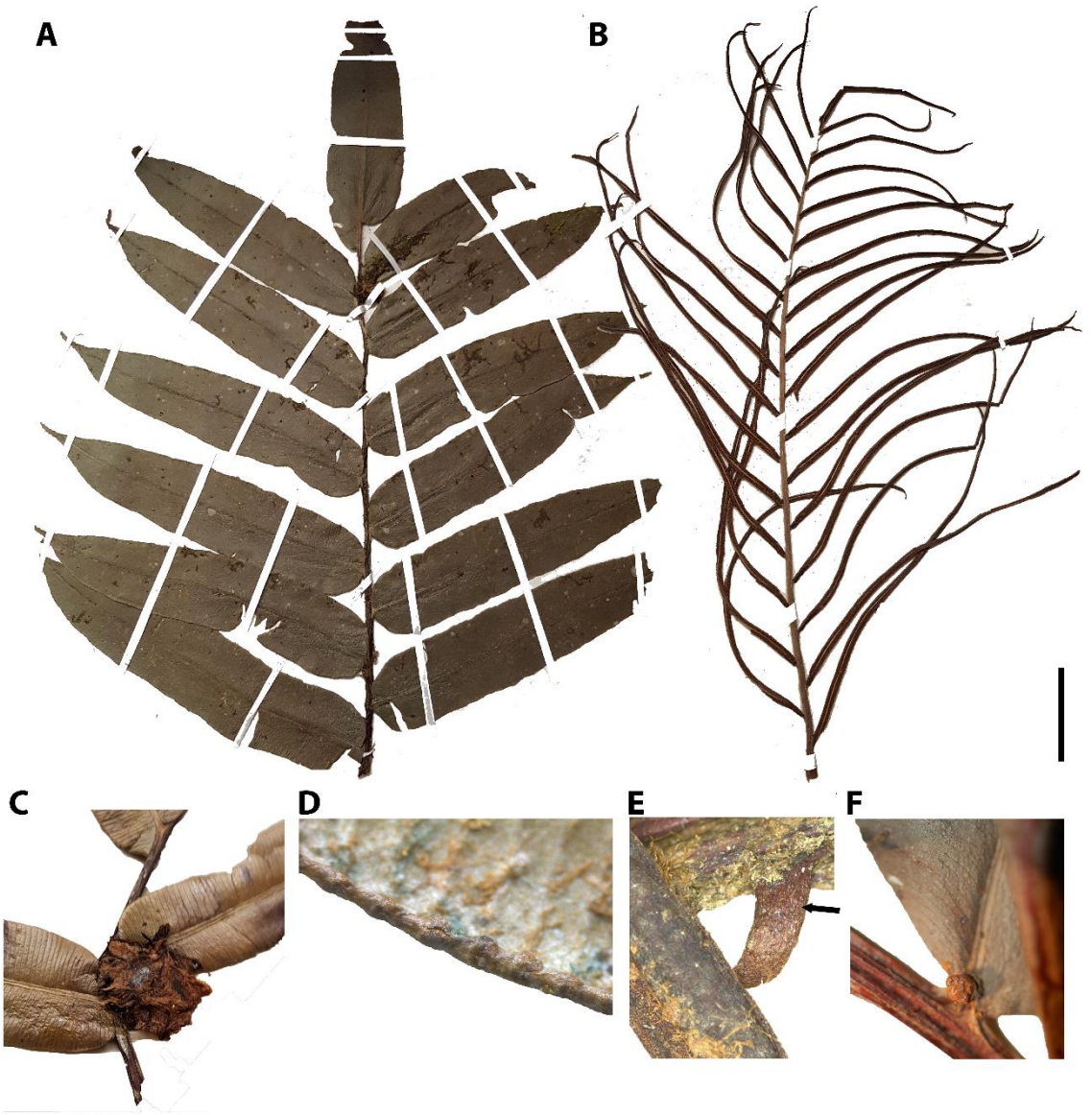

Figure 71. *Parablechnum proliferum.* A. Sterile frond fragment with a bud in the apical pinna base; B. Fertile frond fragment; C. Bud; D. Sterile pinna margin, abaxial side; E. Aerophore (arrow); F. Sterile pinna base with an axillar bud (adaxial side). (A: *A.M. Evans & D.B. Lellinger 291*, US3265374; B: *J.J. Cooper s.n.*, US50337; C: *W.R. Maxon & A.D. Harvey 8078*, US1181753; D: *W.R. Maxon 8079*, US1181754; E: *M. Wacket 132*, B200033012, isolectotype; F: *M. Kessler et al., 6970*, UC1603998). Scale: 4 cm in A & B, 1.5 cm in C, 1.5 mm in D, 2 mm in E,1 cm in F.

In Mesoamerica this species has long been known as *Blechnum viviparum*, but no differences appear between the Mesoamerican plants and those of South America, which include the type of *P. proliferum*. Broadhurst (1912b) was apparently unaware of the previous epithet, *proliferum*, as his new species *B. viviparum* was not compared to that taxon (Moran, 1995a).

There is another species with buds, *P. sessilifolium*¸ which differs from *P. proliferum* in being smaller, with revolute sterile pinnae margins and with buds usually al along the frond, not only in the apical part. The phylogenetic results presented here suggest that this taxon is a complex of species. Maybe, as the presence of buds is unusual in this genus, there has been a tendency to give this name to all the individuals with buds and big size.

Reviewed material.

BOLIVA. Dept. Cochabamba: Prov. De Chapare, road to San Onofre, 3.3 +- km, + N of road to Villa Tunari at point 97.5 km, from Cochabamba, *M.S. Foster 79-159,* 4 November 1979 (UC1475865! Photo); Prov. José Carrasco Torrico, 115 km Antigua Carretera Cochabamba-Villa Tunari, *M. Kessler et al 6970,* 4 July 1996 (UC1603998! Photo). **Dept. La Paz:** Hacienda Casama sobre el camino a Tipuani, *O. Buchtien 7006,* 2 December 1922 (UC477678! Photo): Prov. Nor Yungas, along eoad between Unduavi and Chulumani, 12 km E of Unduavi, *T.B. Croat 51496,* 25 November 1980 (UC1482717! Photo). **BRAZIL. Sao Paulo:** A. da Serra, *H. Luederwaldt 21720,* April 1912 (NY00814180!); Mun. Jundiaí, Serra do Japi, na trilha à esquerda antes de chegar na base da Reserva, indo para a Cachoeira Paraíso, *J. Prado et al 2066,* 13 November 2009 (NY01415312!); Rio Grande, Serra do Mar, *Wacket 132,* 10 August 1907 (B200033012!, isolectotypes, NY00149779!, isolectotypes; P01573198!, synlectotype; P00627617!, synlectotype; P00627618!, synlectotype; P00627619!, synlectotype; P00627620!, synlectotype; P00627621!, synlectotype; UC441992! Photo, isosynlectotype). **Unknown State:** *M. Wacket 338,* no date (US600227!, isolectotype); *Glaziou 2425,* 1868 (BR0000005912605! Photo; P01389410!; P01389411!). **COLOMBIA. Dept. Nariño:** Ricaurte, *P. Sánchez Baracaldo 122,* 30 June 1995 (UC1606866! Photo). **COSTA RICA. Prov. Alajuela:** 11 km of San Ramón, *J.T. Mickel 2925,* 28 July 1967 (NY!, 3 sheets; US2588737A!); Los Ángeles de San Ramón, *A.M. Brenes 16242a,* 2 August 1932 (NY!, 2 sheets); north slope of ridge along quebrada draining eastward to Río Cataratitas, ca. 20 km NW of San Ramón, *A.R. Smith et al 2271,* 3 February 1986 (UC1524445! Photo; UC1524446! Photo); Volcan Poas, about 1 km from the top, *K. Lems 64090604,* 6 September 1964 (NY!, 2 sheets). **Prov. Cartago:** along trail leading eastward into mountains from road into Tapanti Reserve ca. 1 km S of jct. of Quebrada Salto and Rio Grande de Orosi. Also known as "Quebrada Val Verde", *A.R. Smith et al. 2168,* 1 February 1986 (NY!; UC1526053! Photo; UC1526054! Photo);

Cantón de Paraíso, P.N. Tapantí, Cord. De Talamanca, Río Grande de Orosi, *J.F. Morales & G. Carnevale 2881,* 2 June 1994 (UC1605893! Photo); Navarrito, old logging Trail, *C.H. Lankester 749,* 6 December 1923 (US1207152!; US1207153!; US1207154!; US1207155; US1207152!). **Prov. Heredia:** Road to la Hondura, 5.8 km beyond S. Jerónimo, *A.M. Evans & D.B. Lellinger 291,* 18 July 1987 (US3265374!; US3265375!). **Prov. Puntarenas:** evergreen cloud forest and wet wind-gap formation (lower montane and premontane rain forest life zone) on and near the Continental Divide about 2 to 5 km. east and SE of Monteverde, *W.C. Burger & J.L. Gentry Jr. 8745*, 17-20 March 1973 (NY!, 2 sheets); La Palma, *L. Brade 89,* 17 March 1902 (UC405790! Photo); Monteverde, Canadian Biological Station, *R.C. Moran & C.K.R. Moran 5860,* 18 May 1992 (UC1595146! Photo); Monteverde, Estación Biológica Monteverde, Cordillera de Tilarán, *M. Sundue & W. Testo 4787,* 1 September 2017 (MACB!, 2 sheets; VT285873!); vicinity of La Palma, on the road to La Hondura, *W.R. Maxon & A.D. Harvey 8039,* 17-18 July 1923 (US1181711!; US1181713!; US1181714!). **Prov. San José:** *L.A. Brade 121*, no date (US3091707!); between La Palma and La Hondura (1-4 km S of La Hondura) on Rte 220 between Volcán Irazú and Volcán Barba, *J.T. Mickel 2529*, 9 July 1967 (NY!, 2 sheets); old cart road to Limon, 5.6 km N of San Jeronimo, near La Palma, *S.R. Hill et al 17786,* 13 January 1987 (VT020022!; VT198729!; VT291817!; VT291818!); Vásquez de Coronado, carretera a Guápiles, sendero al Río Patria, *A. Rojas & J.M. Gabriel y Galán 10433*, 17 July 2013 (MACB!); Farêt de La Palma, *A. Tonduz 12568*, September 1898 (US1507514!); La Palma área, northeast of San Jerónimo, above La Hondura valley, *W.C. Burger & R.G. Stolze 5300,* 27 May – 1 June 1968 (US2588578A!); P.N. Braulio Carrillo, Estación Tránsito Zurqui, trail opposite the highway from the station, ca. 500 km from the tunnel, *M. Sundue & J. Nitta 1813*, 12 February 2008 (NY!); vicinity of La Hondura (4 km S to 1 km N on Rte 220) between Volcán Irazú and Volcán Barba, *J.T. Mickel 2225*, 25 March 1967 (NY!, 2 sheets); vicinity of La Palma, 1450–1550 m, *W.R. Maxon 435* 06–08 May 1906 (US00067454!, syntype of *Struthiopteris viviparum*; US00067455!, syntype of *Struthiopteris viviparum*); NY149790! isotype of *Struthiopteris viviparum*; NY149791! isotype of *Struthiopteris viviparum*). **Unknown province:** *J.J. Cooper s.n.*, no date (US0050336!), *ibidem* (US0050337!). **ECUADOR. Prov. Napo:** Cascada San Rafael, Campamento San Rafael, INECEL/Proyecto Coca, km 101 via Lago Agrio, 14 km by road SW of Reventador, S of main road at Km 101, *M.S. Foster 85-128,* 21-24 February 1985 (UC1505306! Photo). **Prov. Zamora-Chinchipe:** Estación Científica San

Francisco, *M. Lehnert 1440,* 16 October 2000 (UC1794340! Photo; UC1794341! Photo). **ILLEGIBLE LOCATION:** *Galeotti 255*, no date (P01409516!).

Parablechnum puniceum (T.C.Chambers, P.J.Edwards & R.J.Johns) Gasper & Salino, Phytotaxa 275(3): 217. 2016.

Basionym – *Blechnum puniceum* T.C.Chambers, P.J.Edwards & R.J.Johns, Kew Bull. 60: 598, figs. 1–2. 2006.

Type – Indonesia, West Papua (Irian Jaya), Mt Jaya, PT–Freeport Indonesia Concession of Work Area: 2620 m, *Edwards 4161,* 17 March 1999, (holotype: K000475923–5! photo; isotypes: BO n.s., NSW! photo).

Description – *plants* small, terrestrial; *rhizome* long creeping, at least 40 cm, stoloniferous, dark brown to black and shiny beneath the persistent indumentum, bearing fronds at 3–9 cm intervals and occasionally small clusters of fronds, densely scaly, relatively persistent scales, membranaceous, more or less entire and with slightly wrinkled margins with a few small outgrowths of irregular marginal growth, narrowly triangular to lanceolate, 1–9.5 × 0.2–1.6 mm, varying from pale concolorous to reddish brown to discoloured with a dark reddish brown base and central region and paler margins, apices long acuminate, twisted, hairs sparse, small, 2–3-celled, translucent, deciduous; *fronds* dimorphic; *sterile fronds* with glossy dark red-brown *petioles*, atropurpureous to black at base, but in young stages pale brown to yellowish orange, pink or purple, deeply grooved adaxially prominent abaxially, keeled towards rachis, up to 17 × 0.2 cm, rhizome-like scales, basally dense, becoming smaller, spreading and deciduous towards the rachis, bases persistent, forming a raised scar, hairs sparse, small, 2–3-celled, adpressed and deciduous; *lamina* ovate to triangular, 1-pinnate, 9.5–16 × 4.5–12 cm; *rachis* strongly grooved adaxially and strongly keeled abaxially, dark reddish brown, glossy, bearing scattered, small, 2–3–celled, translucent, adpressed and deciduous hairs; *sterile pinnae* in 1–5 pairs, subopposite, linear-lanceolate, coriaceous, 2.5–7 × 0.7–2.3 cm, slightly falcate, entire to slightly revolute, apices acuminate to shortly attenuate, bases rounded, truncate to slightly cordate, stalked, terminal pinna usually larger, 13 × 2.4 cm; *costae* with indumentum of small, 2–3–celled adpressed hairs, less than 0.5 mm long and scales less than 1 mm long; *veins* free, simple or 1-furcate, catadromous; *aerophores* not

observed; *hydathodes* ovate, slightly sunken and visible only on adaxial side; *fertile fronds* with petioles usually longer than sterile ones; *fertile pinnae* shortly stalked, narrowly linear, 5.5–10 × 0.25–0.4 cm, longer than sterile ones and with a sterile zone at acuminate apices, basally 1–5 mm sterile, terminal pinna 10–13.5 cm, usually longer than lateral ones; *sori* linear, continuous, forming coenosori on both sides of costa; *indusia* linear, continuous, opening towards costa, entire, membranaceous, becoming slightly eroded at maturity; *sporangia* not observed; *spores* monolete, flat-convex in equatorial view, elliptic in polar view, (63–)70(–82) × (52–)63(–67) µm, perispores fenestrated to densely reticulate, the fenestrations and more continuous ribs formed by dense aggregations of fine reticulate material, in a coral-like whole, exospore not observed (**Figure 72**).

References – Chambers *et al*. (2005).

Chromosome number – unknown.

Distribution and habitat – known for the moment from localities of its description in the Freeport Concession of Work area in Mt Jaya in two neighbouring localities at 2630 m and 2780 m altitude. The long creeping rhizomes grow either near or above the soil surface, through bryophytes at the base of tree trunks in disturbed and regenerating, wide open, mixed broadleaf, and coniferous montane forests (Chambers *et al*., 2005).

Etymology – the specific epithet is related to the intense red colour in the young lamina (Chambers *et al*., 2005).

Notes – the species is known to grow in an area of ca. 1000 m^2 scattered in two localities. The habitat where they occur is considered rare. Although there are no obvious threats to the two known sites and there is a lot of unexplored land around, it is probably correct to consider this taxon as vulnerable (Chambers *et al.*, 2005).

Reviewed material:

INDONESIA. West Papua: Mt Jaya, *P.J. Edwards et al. 4161*, 17 March 1999, (K000475923! photo, syntype); *ibidem* (K000475924! photo, syntype); *ibidem* (K000475925! photo, syntype).

Figure 72. *Parablechnum puniceum.* A. Plant with two sterile fronds and one fertile in the middle; B. Plant with three sterile fronds. (A: *P.J. Edwards 4161,* K000475924, syntype; B: *P.J. Edwards 4161,* K000475925, syntype). Scale: 4 cm.

Parablechnum reflexum (Rosenst. ex M.Kessler & A.R.Sm.) Gasper & Salino, Phytotaxa 275(3): 217. 2016.

Basionym – *Blechnum reflexum* Rosenst. ex M.Kessler & A.R.Sm., Amer. Fern J. 97: 74. 2007.

Type – Bolivia. Cochabamba: Prov. Carrasco, Km 104 antigua carretera Cochabamba– Villa Tunari, 17'11'S, 65040'W, 3250 m, *Kessler 6697a*, 25 June 1996, (holotype: UC1603974! Photo, mixed collection, *P. reflexum* marked with an "A", the other plant probably *P. lechleri*; isotype: GOET007146! Photo; LPB0000019! photo).

Description – *plants* terrestrial or saxicolous; *rhizomes* erect, scales 3–7 × 0.6–2.2 mm, lanceolate to oblong-lanceolate, sparse, flaccid, translucent, dull, orange-brown, with finely toothed margins; *sterile fronds* up to 33 cm long, arching; *petioles* 18 × 0.25 cm, slightly longer than lamina, dark reddish brown, densely covered with scales at base with similar to those of the rhizome but smaller and scattered; *lamina* 15 × 5 cm, lanceolate, 1-pinnate, with a conform terminal pinna, elongate, laminar tissue coriaceous, glabrous; *rachis* dark reddish brown, grooved adaxially, densely scaly, scales 1.5–5 × 0.2–1.2 mm, lanceolate to oblong-lanceolate, flaccid, translucent, orange-brown, with finely toothed margins; *sterile pinnae* in 15 pairs, 2.6 × 0.55 cm, oriented at right angles to the rachis, ovate–lanceolate, stalked, bases asymmetrical, apices rounded, margins slightly cartilaginous, lighter, serrulate and strongly revolute; *costae* light brown, deeply grooved adaxially and prominent abaxially, moderately scaly, the scales similar to those of the rachis but smaller and relatively wider; *veins* free, simple or 1-furcate, impressed on both sides, abaxially darker than laminar tissue, catadromous; *aerophores* not observed; *hydathodes* small, rounded; *fertile fronds* unknown; *sporangia* and *spores* unknown (**Figure 73**).

References – Kessler *et al*. (2007).

Chromosome number – unknown.

Distribution and habitat – endemic to Bolivia. An apparently rare and local species found between 3150–3300 m on the eastern Andean slope in Bolivia, so far only known from two sterile collections. Terrestrial, on rock surfaces (one collection is from a rocky outcrop) in moist open habitats around the forest edge (Kessler *et al*., 2007; Smith & Kessler, 2018).

Etymology – the specific epithet refers to strongly reflexed pinnae.

Notes – to date it is known only from two sterile collections. Therefore, the measurements given in the description may not reflect the potential size of this species. Nevertheless, the authors decided to describe it as new because no other *Parablechnum* species has similar reflexed pinnae The pinnae are reminiscent of *Lomariocycas aurata* (Fée) Gasper & A.R.Sm., but that species has very different rhizome scales, which are long, falcate, and shiny (Kessler *et al*., 2007).

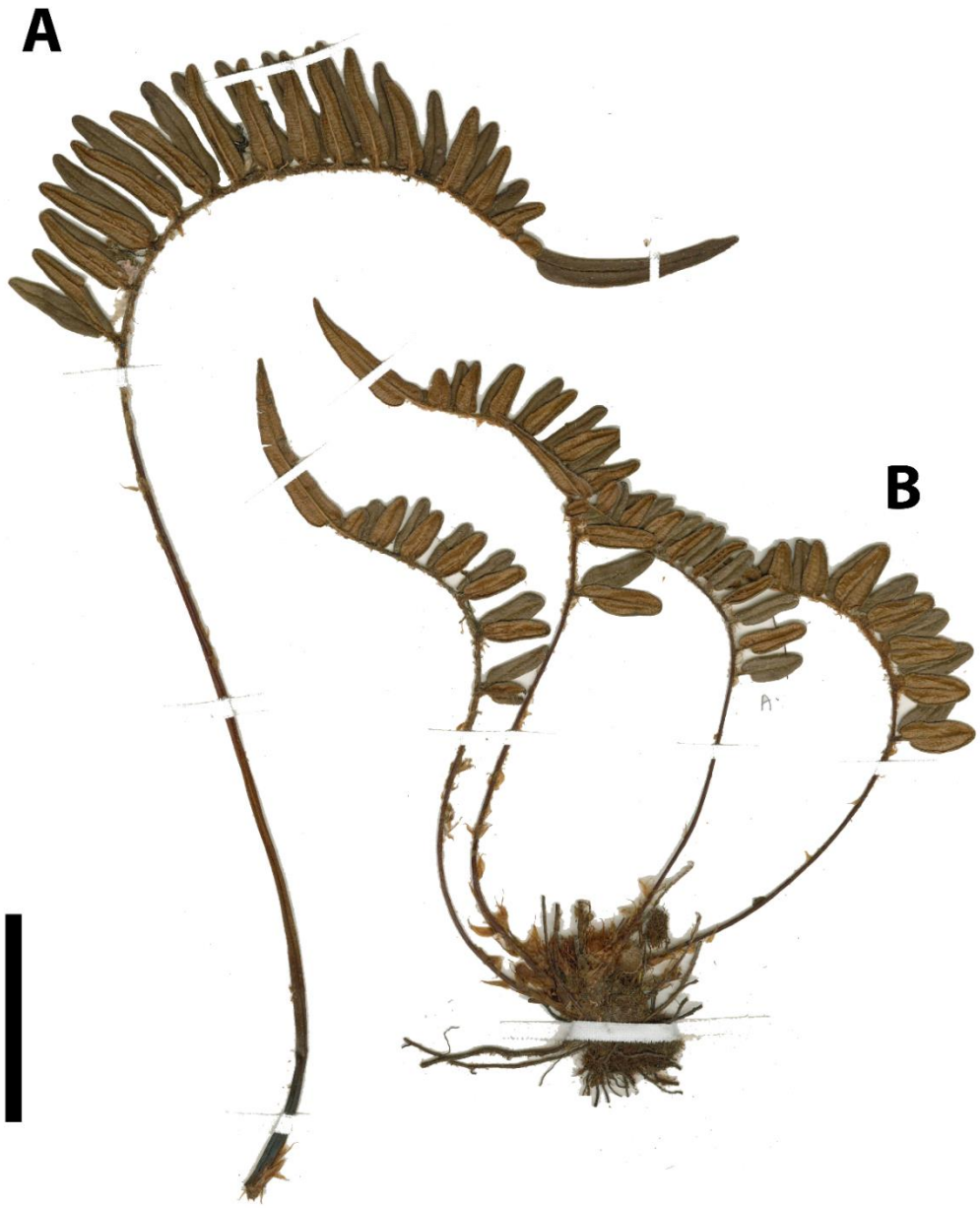

Figure 73. *Parablechnum reflexum.* A. Sterile frond; B. Plant. (*Kessler et al 6697*, UC1603974, holotype). Scale: 4 cm.

Reviewed material:

BOLIVIA. Dept. Cochabamba: Prov. Carrasco, Km 104 antigua carretera Cochabamba– Villa Tunari, 17'11'S, 65040'W, 3250 m, *Kessler 6697a*, 25 June 1996, (UC1603974! photo, holotype; GOET007146! Photo, isotype; LPB0000019! Photo, isotype). **Dept. La Paz:** Prov. Nor Yungas, Unduavi, 3300 m, *Buchtien 2681*, November 1910 (UC477676! photo, paratype).

Parablechnum repens (M.Kessler & A.R.Sm.) Gasper & Salino, Phytotaxa 275(3): 217. 2016

Basionym – *Blechnum repens* M.Kessler & A.R.Sm. Amer. Fern J. 97: 75. 2007.

Type – Bolivia. La Paz: Prov. Nor Yungas, Estación Biológica de Tunquini, Bajo Hornuni, senda del campo de Don Pedro al camino de la mina, 16'12'S, 67053'W, 2200 m, *Jiménez 453*, 16 August 2000 (holotype: LPB0000020! photo).

Description – *plants* epiphytic; *rhizomes* long-creeping, 3–4 mm thick, atropurpureous, moderately scaly, scales 4–5 × 0.8–1.4 mm, linear to lanceolate, shiny, orange-brown or reddish-brown with slightly lighter margins, margins subentire to remotely denticulate; *sterile fronds* 75 cm long, *petioles* ca. 45 cm × 0.15 cm, sparsely scaly, scales similar to those of the rhizome, but smaller; *lamina* ca. 30 × 15 cm, deltoid, 1-pinnate, with a conform terminal pinna, laminar tissue chartaceous, glabrous; *rachis* dark reddish brown, grooved adaxially, sparsely scaly, the scales firm, 0.2–1 mm long, orange; *sterile pinnae* in 7–9 pairs, 8 × 0.16 cm, the proximal pinnae longer, lanceolate, with elongate, falcate apices, margins finely serrate, very narrowly cartilaginous, not revolute; *costa* straw-coloured, slightly raised on both sides, basally with some rachis-like scales; *veins* free, simple or 1-furcate, impressed adaxially, raised abaxially, catadromous; *aerophores* tuberculiform; *hydathodes* small; *fertile fronds* unknown (**Figure 74**).

References – Kessler *et al.* (2007).

Chromosome number – unknown.

Distribution and habitat – endemic to Bolivia, known only from the type collection. Rare, epiphytic in humid forests 2200 m (Kessler *et al.*, 2007; Smith & Kessler, 2018).

Etymology – the epithet (creeping) refers to the rhizome growth.

Notes – this species has slender, 3–4 mm wide, blackish, long-creeping rhizomes, unlike most other species of the genus. No fertile material was available in its description, but the laminar appearance and scale characters suggest that it is a *Parablechnum*. It is perhaps close to *P. pazense* but this species has erect to shortly creeping rhizomes, 2–3 cm thick, and ca. 40 pairs of pinnae (vs. 7–9 pairs in *P. repens*).

Figure 74. *Parablechnum repens. I. Jiménez et al 453,* LPB0000020, holotype. Scale: 4 cm.

Another epiphytic Blechnaceae species with blackish, creeping rhizomes, *Blechnum anthracinum* R.C. Moran, has been described about 1 km south of the type locality of *P. repens* (Moran, 1992). Despite the apparent similarity in rhizome characters, *B. anthracinum* does not belong to *Parablechnum*. It has sterile and fertile monomorphic fronds, fully adnate pinnae, and different scale characters. Another epiphytic Blechnaceae species with blackish, creeping rhizomes, *B. anthracinum* R.C. Moran, has been described from a single collection made about 10 km south of the type locality of *P. repens* (Moran, 1992). Despite the apparent similarity in rhizome characters, *B. anthracinum* is not related to *P. repens*, and in fact belongs to another genus. It has sterile

and fertile monomorphic fronds, fully adnate pinnae, and different scale characters. The apparent independent and convergent evolution of these two species remains to be elucidated (Kessler *et al*., 2007).

Reviewed material:

BOLIVIA: Dept. La Paz: Prov. Nor Yungas, Estación Biológica de Tunquini, Bajo Hornuni, senda del campo de Don Pedro al camino de la mina, *Jiménez 453*, 16 August 2000 (LPB0000020! photo, holotype).

Parablechnum revolutum (Alderw.) Gasper & Salino, Phytotaxa 275(3): 217. 2016.

Basionym – *Lomaria revoluta* Alderw., Nova Guinea 14: 31. 1924

Type – Papua New Guinea, at foot of Doorman summit, terrestrial in sunny ravine, 3230 m, *Lam 1708*, 24 Oct. 1920 (holotype: BO n.s.; isotype: BM n.s., fragment).

Synonyms –

≡*Blechnum revolutum* (Alderw.) C.Chr., Index Filic., Suppl. 3, 46. 1934.
=*Blechnum archboldii* C. Chr., Brittonia 2: 288. 1937. Type: Papua New Guinea, Prov. Central, Mt. Albert Edward, *J. Brass 4318*, May 1933 (syntypes: BM001048304-5! Photo; isotypes: BRIAQ0024618! Photo)

Vernacular names – Kangermabeh (Wahri: Minj), pingkama (Mairi: Mondo), teda (Mendi) (Chambers & Farrant, 2001).

Description – *plants* terrestrial, *rhizome* both creeping and erect on the same plant, the slender creeping one 0.3–0.4 cm in diameter, internodes 2–3 cm apart, and an erect or suberect one usually forming a massive stem, topped by a rosette usually of 5–8 stout fronds, with bases of old petioles and densely covered with leathery, broadly acuminate, entire, shiny brown to dark tawny, 1–3 × 0.25–0.7 cm, varying from concolorous to distinctly discoloured scales, with an atropurpureous central region and a reddish margin; *fronds* monomorphic or subdimorphic; *sterile fronds* with *petioles* 14–70 cm, strongly grooved adaxially, keeled abaxially, variable in colour from light straw-coloured to more often atropurpureous, the scales at the base of the petioles are persistent, similar to those of the rhizome, those 10 cm above the base are similar in shape and colour or sometimes lighter in colour, but smaller, up to 1.5 × 0.1–0.3 cm, interspersed with irregularly distributed lanuginous scales, more densely scaly when

the plant is young; *lamina* narrowly elliptic to narrowly ovate, 1-pinnate, 60 cm or more in length, longer than petiole, but sometimes shorter, darker on adaxial side, decreasing in size towards the apex with in a conform terminal pinna; *rachis* brown, reddish brown or dark brown, sometimes straw-coloured, densely scaly, especially at costal bases, with conspicuous, persistent, acuminate, entire scales similar to those of the petiole but smaller and paler, some up to 1 × 0.2 cm with darker centres mixed with irregularly distributed, lanuginous, paler, linear scales at costal bases; *sterile pinnae* in 6–55 pairs, narrowly oblong-elliptic acuminate, sometimes falcate, 4–7 × 0.4–0.8 cm, stalked, distant, more crowded and basiscopically adnate distally, coarsely coriaceous, margins entire, strongly revolute, basal pinnae becoming shorter to about half the length of those of the middle region, the terminal pinna usually longer than the subterminal pairs; *costa* deeply grooved on adaxial face, prominent on abaxial face; *veins* free, simple or 1-furcate, sunken adaxially, prominent abaxially, covered with dense scales, catadromous; *aerophores* absent; *hydathodes* ovoid or clavate, adaxial; *fertile fronds* with longer petioles, erect, 30–130 × 4–15 cm, *fertile pinnae* narrowly elliptic, obtuse, 4–10 × 0.3–0.5 cm, at maturity less revolute or not revolute, reaching almost to the width of sterile revolute pinnae, though usually slightly shorter and set closer and at a more acute angle to the rachis, decreasing in size towards the apex; *sporangia* with 19–21 arc cells; *spores*, monolete (41–)59(–69) × (33–)43(–56) µm; perispore rugulose, cristate-reticulate, thick-walled, low, forming medium to small polygonal areoles, with moderately abundant short filamentous processes over entire spore surface (**Figure 75**).

References – Chambers & Farrant (2001; 2012).

Chromosome number – unknown.

Distribution and habitat – widely distributed in Papua New Guinea. Also reported from the Philippines. Common in mountainous regions above 2500 m, in exposed alpine areas and subalpine grasslands, and at the edge of alpine shrub borders and montane forests. Occasionally abundant in meadows and fire-affected, often waterlogged, and peaty soils. There are also records from mountainous areas, where it grows on the margins of lakes and streams and on rocky ground in and around stream beds. (Chambers & Farrant, 2001; 2012).

Etymology – its name y refers to its revolute pinnae.

Notes – this species is capable of repeated vegetative reproduction through the decay of creeping rhizomes and the persistence of separate plants, which probably explains the localised, sometimes dominant, abundance of this species (Chambers & Farrant, 2001).

Parablechnum revolutum is readily distinguished from other species of the genus in Papua New Guinea by the strongly revolute sterile pinnae and the scaly, dense, and persistent nature of almost the entire plant. These general characters are also found in the South American species *P. loxense* but can be distinguished by the nature of the scales. The South American species, although it has more variability, has much finer, more fragile, papery and generally paler basal petiole scales, while those of the rachis and costa tend to have paler, more fragile margins and sometimes darker centres.

Some New Guinean specimens of *P. revolutum*, especially when growing in protected areas such as rainforest edges, low subalpine and montane forests, have sterile pinnae that are not markedly revolute or may only be finely revolute at the margin. These specimens can be confused as well with *P. hieronymi*, but the long, broad, atropurpureous scales at the base of the petioles indicate that they belong to *P. revolutum* (Chambers & Farrant, 2001).

Reviewed material:

PAPUA NEW GUINEA. Prov. Eastern Highlands: Mt. Wihelm, E of Lake Aunde in Pindunde Creek, *M.M.J. v. Balgooy 247,* 16 May 1965 (NY04187081!); Terr. Of New Guinea, near Kerigomna camp, Goroka subdistrict, *R.D. Hoogland & R. Pullen 5526*, 5 July 1956 (P01618074!). **Prov. Central:** Mt. Albert Edward, *J. Brass 4318,* May 1933 (BM001048304! Photo; syntype of *Blechnum archboldii*; BM001048305! Photo; syntype of *Blechnum archboldii*; BRIAQ0024618! Photo, isotype of *Blechnum archboldii*); Murray Pass, Wharton Range, *L.J. Brass 4590,* June 1933 (BM001048197! Photo, paratype of *Blechnum archboldii*; BM001048198! Photo, paratype of *Blechnum archboldii*; K000537525! Photo, paratype of *Blechnum archboldii*; NY04187078!, paratype of *Blechnum archboldii*). **Prov. Chimbu:** Mt. Wilhelm, E slopes, Pindue-Aunde valley, *M. Sundue et al. 3690,* 1 August 2014 (VT198732!); Osthäge des Mt Wilhelm oberhalb Denglagu, in Bereich, *E. Borgmann 812,* May-July 1960 (NY!). **Prov. South Highlands:** Tari Subdistr., Ibiwara, *W. Vink 17260,* 23 July 1966 (NY04187080!;

P01623358!); Tari Subdistr., pass between Mt. Ne and Mt. Kerewa, *C. Kajman 4877*, 13 July 1966 (P01623359!). **PHILIPPINES.** *Cumming 15b*, no date (P01558317!). **Luzon:** *Cuming 156*, 31 August 1908 (P01662189!; P01662193!); Albay, Mt. Mayor, *C.B. Robinson 6499*, 4–6 September 1908 (P01558315!). **Gran Manila:** Manila, *Cumming 141*, no date (P01558316!). **Mindanao:** Mt. Apo, *E.B. Copeland 1511*, 1904 (P01558300!; P01558302!).

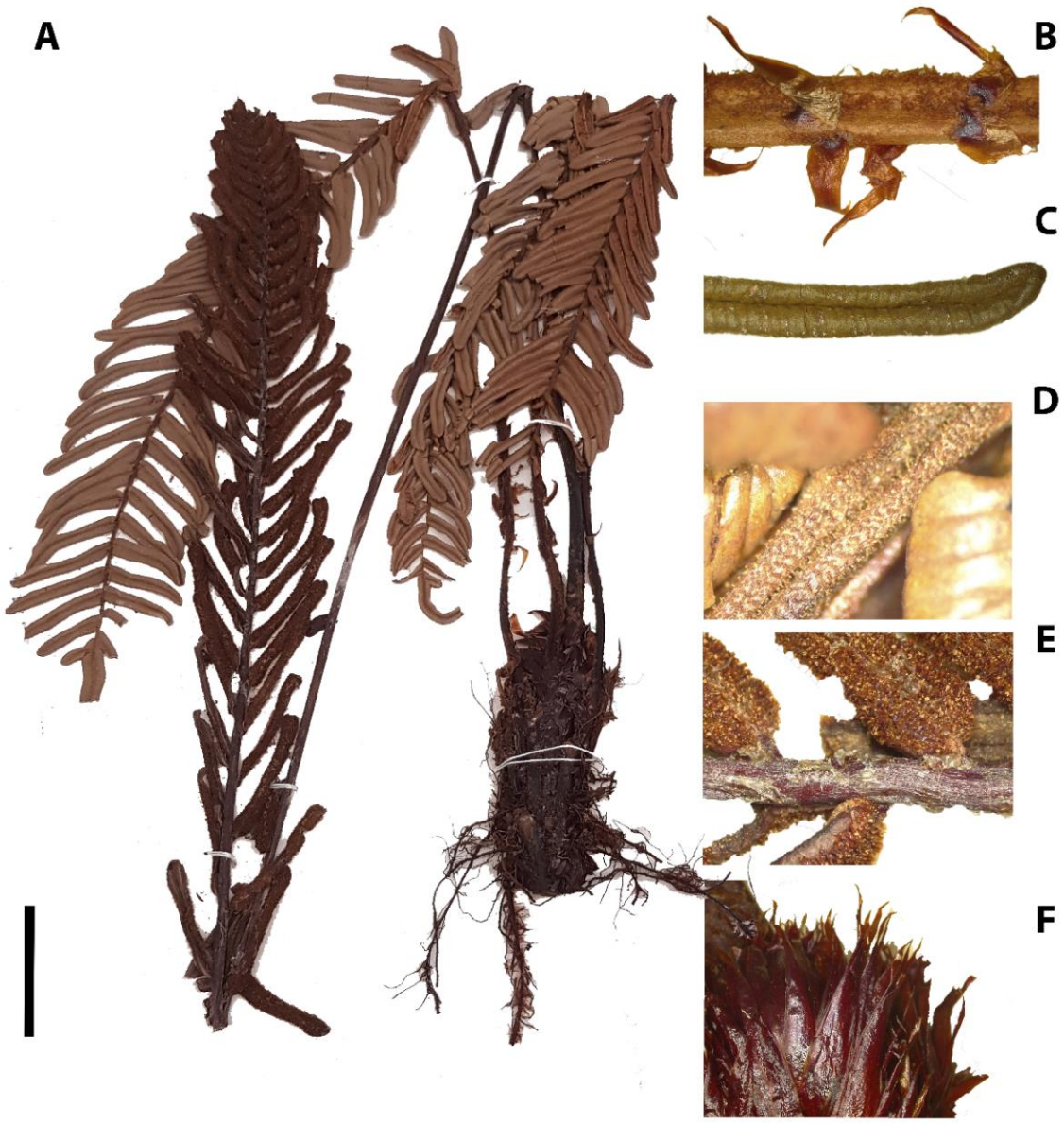

Figure 75. *Parablechnum revolutum.* A. Plant with three sterile fronds and one fertile in the middle; B. Petiole; C. Sterile pinna, adaxial side; D. Sterile rachis, adaxial side; E. Fertile rachis, abaxial side; F. Rhizome scales. (A, C-E: *W. Vink 17260*, NY04187080; B&F: *Brass 4590*, NY). Scale: 4 cm in A, 9.5 mm in B & E, 8 mm in C, 2 mm in D, 6 mm in F.

Parablechnum rheophyticum (R.C.Moran) Gasper & Salino, Phytotaxa 275(3): 217. 2016.

Basionym – *Blechnum rheophyticum* R.C.Moran, Nordic J. Bot. 15: 52. 1995.

Type – Ecuador. Carchi: border area between Prov. Carchi and Prov. Esmeraldas, about 20 km past Lita on road to Alto Tambo, selectively logged forest, 550 m, *van der Werff et al. 12014*, 25 Jun 1991 (holotype: MO289393! photo; isotypes: AAU n.s., QCNE63! photo, UC1611294! photo, US3278304!; US478879!).

Description – *plants* rheophytic; *rhizome* erect, scaly, scales 7–12 × 2–4 mm, lanceolate to oblong-lanceolate, flaccid, bright orange-brown, entire or nearly so; *fronds* dimorphic; *sterile fronds* with *petioles* 15–20 × 0.4–0.5 cm, about the same length as the lamina, light to dark brown, scaly basally, with scales similar to those of the rhizome, glabrous distally; *lamina* 18–30 × 7–17 cm, lanceolate to oblong-lanceolate, 1-pinnate, the apex similar in size and shape as the lateral pinnae, laminar surface glabrous; *rachis* dark to light brown, scaly to glabrous, transversely papillose; *sterile pinnae* in 9–17 pairs, 8–12 × 9–1.3 cm, ascending, linear, entire, stalked, base narrowed, *costae* glabrous with a few scattered scales, grooved adaxially, prominent abaxially; *veins* free, simple or 1-furcate, catadromous, glabrous; *aerophores* axillary, low and rounded; *hydathodes* patent; *fertile fronds* with longer *petioles*, 20–32 cm long; *fertile pinnae* 3–4 mm wide; *sori* linear, continuous, forming coenosori on both sides of the costa; *indusia* linear, continuous, open through the costa, margins entire or lacerate in maturity; *sporangia* with 18–19 arc cells; *spores* monolete, (50–)63(–72) × (37–)47(–57) µm; perispores smooth, cristate-reticulate, high-walled, thin, sharp, forming large polygonal areoles, without filamentous processes (**Figure 76**).

References – Moran (1995b), Passarelli *et al.* (2010).

Chromosome number – unknown.

Distribution and habitat – the species grow among rocks in streams that overflow their banks. It is endemic to the Pacific side of the Andes in northwestern Ecuador (Moran, 1995b).

Etymology – the specific epithet refers to the plant's rheophytic habitat.

Notes – It may be related to *Parablechnum glaziovii* and *P. paucipinna*, but differs from both in the riparian habitat, the very fragile texture of *P. paucipinna* and in the more linear lanceolate frond shape and more pairs of pinnae of *P. glaziovii*.

Figure 76. *Parablechnum rheophyticum*. A. Sterile (right) and fertile (left) fronds; B. Sterile pinna apex; C. Sterile pinnae bases; D. Fertile rachis; E. Rhizome scales. (A-E: *W. Palacios 6934*, MO04303680, paratype). Scale: 4 cm in A, 13.5 mm in B, 9.5 mm in C, 3.3 mm in D, 9 mm in E.

Reviewed material:

COLOMBIA. Dept. Nariño: Mpio. de Ricaurte. Resguardo Indigena Nulpe Medio. Orillas del rio Nulpe, *R. Ramirez & M.S. González 9438*, 6 January 1996 (UC1732585! photo). **ECUADOR**. **Prov. Carchi:** Carchi, border área between Prov. Carchi and

Esmeraldas, about 20 km past Lita on road Lita-Alto Tambo, *van der Werff et al. 12014*, 25 June 1991 (MO289393! Photo; QCNE63! Photo, isotype; UC1611294! Photo, isotype; US3278304!, isotype; US478879!, isotype) **Prov. Esmeraldas**: San Lorenzo Canton, Río Negro, a 2 km de El Placer, *Palacios 6934* (MO4303680!, paratype; MO503130! Photo, paratype; NY!, paratype). **Prov. Pichincha:** Cayambe, *K95*, 23 May 1876 (NY!).

Parablechnum roraimense V.A.O.Dittrich & Gasper, Phytotaxa 292(1): 69. 2017.

Basionym – *Parablechnum roraimense* V.A.O.Dittrich & Gasper, Phytotaxa 292(1): 65–73. 2017.

Type – Guyana. Cuyuni–Mazaruni: Mt. Roraima, 2,130 m, *R. Persaud 160*, 02 November 1973 (holotype: K! photo; isotype: BRG n.s.).

Description – *plants* terrestrial; *rhizomes* erect, up to 10 cm long, non-stoloniferous, rhizome apex scales brown, concolorous, basifixed, linear-lanceolate or lanceolate, margins entire or sparsely toothed, apices acute to acuminate, 12–12.5 × 2–3.3 mm; *sterile fronds* clustered at rhizome apex, 21–30 cm long; *petioles* dark straw-coloured or brownish, almost black, proximally with sparse rhizome-like scales, distally with sparse rachis-like scales, deeply grooved adaxially, smooth, 8–12.5 cm, proportionally very long, 2/5–1/2 of total length, 1.9–2.4 mm in diameter; *lamina* leathery, 10–17 × 4–10 cm, ovate or ovate–lanceolate, truncate at base, apex conform, 1-pinnate, laminar tissue with very few scales, mostly stellate, on adaxial side or more or less linear, strongly ciliate, all minute, less than 1 mm long, but absent in older leaves; *rachis* straw-coloured, light or dark brown, adaxially grooved, more or less scaly on both sides, ovate, lanceolate or linear, 0.1–1.1 × 2.5–5.6 mm, abaxially slightly verrucose; *sterile pinnae* in 7–10 pairs, strongly ascending, 4–7 cm × 3–8 mm, linear, falcate, revolute, shortly stalked, bases rounded, cuneate or cordate, slightly asymmetric, with one side sometimes partially overlapping the rachis, becoming basiscopically adnate distally, sometimes completely so, apices acuminate, serrate; *costae* adaxially grooved, abaxially prominent, covered with scales sparse, brown, deltoid, lanceolate or stellate, ciliate, 0.4–0.8 × 0.6–2.1 mm; *veins* free, simple or 1-furcate, darkened abaxially, weakly visible adaxially, catadromous; *aerophores* axillary, blackish, tuberculiform; *hydathodes* clavate, blackish; *fertile fronds* unknown (**Figure 77**).

References – Dittrich *et al.* (2017).

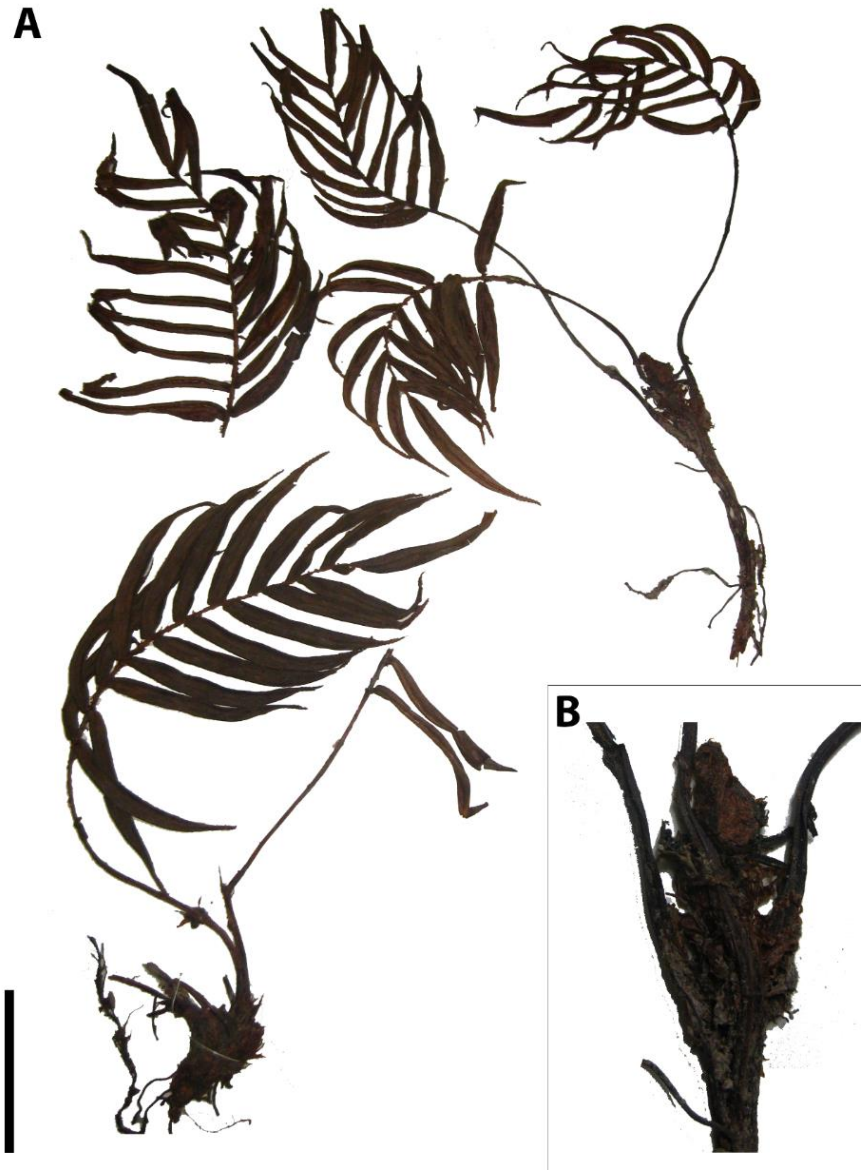

Figure 77. *Parablechnum roraimense.* A. Plants; B. Rhizome (A-B: *R. Peraaud 160*, K). Scale: 4 cm in A, 1.5 cm in B.

Chromosome number – unknown

Distribution and habitat – Guyana, 2130 m, known only from the type. Muddy soil on cliff. (Dittrich *et al.*, 2017).

Etymology – the epithet refers to Mount Roraima, the type locality.

Notes – it is distinguished from the other species of the genus by the long, ascending rhizomes, the few pairs of strongly ascending pinnae (up to 10), the tuberculate aerophores at the base of the pinnae, the leathery fronds with revolute-margined pinnae

and the strongly abaxially elevated costa. Its closest relatives are not known, but the revolute margins are reminiscent of *P. stipitellatum* and *P. loxense*, although they are not necessarily closely related. (Dittrich *et al.*, 2017).

Reviewed material:

GUYANA. **Reg. Cuyuni–Mazaruni**: Mt. Roraima, *R. Persaud 160*, 2 November 1973 (K! photo, holotype).

Parablechnum ryanii (Kaulf.) Gasper & Salino, Phytotaxa 275(3): 217. 2016.

Basionym – *Lomaria ryanii* Kaulf., Enum. Filic. 155. 1824.

Type – Habitat in Monserrat insula, *Ryan s.n.*, no date (syntypes: BM000769812! photo, BM000769813! photo).

Synonyms –

≡*Blechnum ryanii* (Kaulf.) Hieron., Hedwigia 47: 245. 1908.
=*Onoclea striata* Swartz. Syn. Fil. 304, 422. 1806. Type: St. Christopher [St. Kitts], *B. W. I., Forstrom s.n.* (holotype: S-PA, n.s., 3 sheets,). ≡*Blechnum striatum* (Swartz) C.Chr. Ind. Fil. 160. 1905 nom. illeg. *Blechnum nesioticum* Kramer, Acta Bot. Neerl. 9: 299. 1960.

Description – *plants* terrestrial, *rhizome* decumbent to erect, woody, densely scaly with light brown, papyrose, ovate or oblong scales, 20 × 5 mm; *fronds* dimorphic; *sterile fronds* 125 cm or more; *petioles* as long as or longer than the laminae, straw-coloured or light brown, with numerous scales, deciduous, papyrose, leaving small scars when drooping; *laminae* broadly lanceolate or oblong, 12–35 cm wide, base truncate, apex acute, with a conformal terminal scale, laminar tissue coriaceous, usually glabrous, straw-coloured, with decumbent scales; *rachis* similar in colour and shape to the petiole; *sterile pinnae* in 7–23 pairs, lanceolate or linear-oblong, slightly falcate, 1.5–3 cm wide, base cordate, margins revolute; *costae* grooved adaxially, prominent abaxially, with fibrillose scales abaxially, light brown; *veins* free, simple or 1-furcate, sometimes with minute whitish, deciduous scales, catadromous; *aerophores* axillary, low, blackish; *hydathodes* ovate, not reaching margin; *fertile fronds* longer and more erect than sterile ones, up to 175 cm; *fertile pinnae* linear, contracted, 3–6 mm wide; *sori* linear, continuous, forming coenosori on both sides of costa, covering entire abaxial side of pinna; *indusia* linear, continuous, opening towards costa, irregular and strongly lacerate; *sporangia* with 19–20

arch cells; *spores* monolete, (53–)76(–100) × (37–)57(–81) µm; perispore, smooth or slightly roughened, cristate-reticulate, with thin, low walls, forming large polygonal areoles, with sparse to moderately abundant long filamentous processes over the entire spore surface (**Figure 78**).

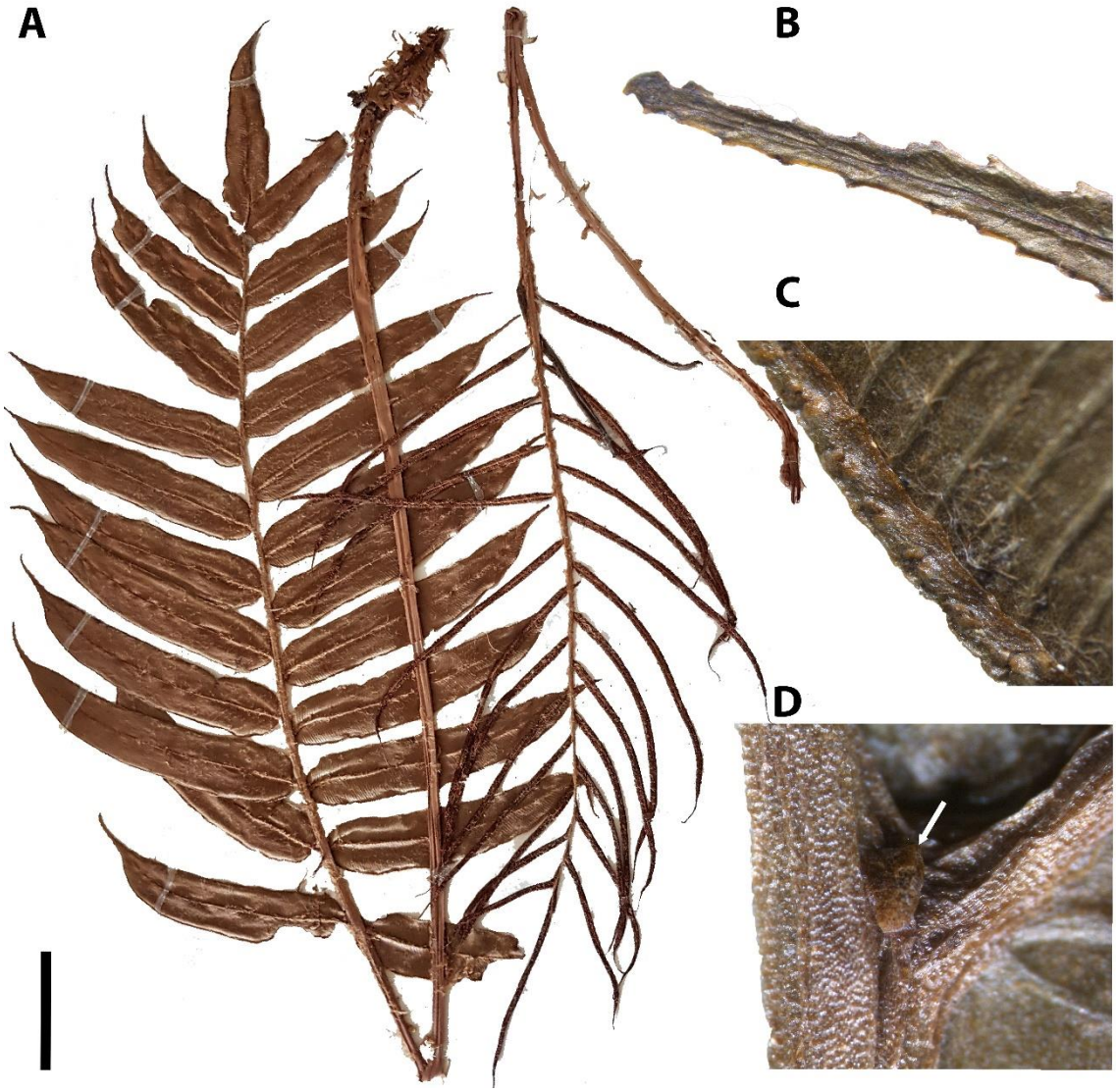

Figure 78. *Parablechnum ryanii*. A. Sterile (left) and fertile (right) fronds. B. Sterile pinna apex; C. Sterile pinna margin; D. Aerophore (arrow). (A: *F.R. Fosberg 48279*, US2554163; B-D: *D.B. Lellinger 391*, US2683749). Scale: 4 cm in A, 3.5 mm in B, 1.5 mm in C & D.

References – Morton & Lellinger (1967), Proctor (1977).

Chromosome number – unknown.

Distribution and habitat – endemic the Lesser Antilles, Saba, St Kitts, Nevis, Montserrat, Guadeloupe, Martinique, St Lucia, St Vincent, Jamaica, and Grenada.

Terrestrial in humid areas and mossy soils, in elevated areas, common. (Morton & Lellinger, 1967; Proctor, 1977).

Etymology – the epithet refers to Elling Ryan, Norwegian pharmacist, factory manager, politician and botanist (1849-1905), who collected the type specimen of this species.

Notes – this fern gets larger size and produces more sporophylls in cloud montane rainforest than in exposed locations (Graveson, 2022).

It is common to find specimens of this taxon named as *Blechnum striatum*. This is an illegitimate name, but other authors as Kramer (1960) believed that *B. striatum* and *B. ryanii* were different species, and thus he proposed the replacement name *B. nesioticum* for *B. striatum*. However, later publications as Morton & Lellinger (1967) reviewed specimens under both names and concluded that they can be considered synonyms, being *Lomaria ryanii* the valid basionym for the species. Here, the view of Morton & Lellinger is followed.

However, the phylogenetic results and palynological variation within the samples processed in this work suggest that *P. ryanii* could constitute a complex of species. A more detailed study would be necessary, and in case more than one taxon is involved in the name *P. ryanii* the recovery of the epithet *striatum* should be considered.

Reviewed material:

DOMINICA. Laudat, *Filic Luerssen 709,* February 1882 (US2703205!); Morne Trois Pitons, *W.H. Hodge 86,* 15 August 1938 (US1780798!); Parish of St. George, Morne Trois Pitons Nat'l Park. Freshwater Lake, *H.T. Beck 2067,* 4 May 1993 (NY00088722!); rainforest borders between Laudat and freshwater laker, *W.H. Hodge & B.T. Hodge s.n.,* 8-9 March 1940 (US1780873!); St. David Parish, trail between Boeri Lake and Freshwater Lake above Laudat, at St. George Parish line, *S.R. Hill & L.R. Phillipe 29004*, 4 March 1997 (NY0200777!; UC1619257! Photo;; VT198716!; VT198717! VT198721!); *ibidem, S.R. Hill & L.R. Philippe 29014*, 4 March 1997 (VT289541!; VT289542!); St. George Parish, Vicinity of the Fresh Water Lake, NE of Laudat, E side of Morne Macaque, *S.R. Hill et al 22103,* 10 March 1991 (VT289546!); *ibidem, S.R. Hill et al 22116*, 20 March 1991 (NY0200778!; NY0200779!; VT289544!; VT289545!);

south slope of Morne Macaque (Micotrin) on road Fresh Water Lake, *W.R. Ernst 1498*, 28 April 1964 (US2538921!); St. Joseph, elfin woodland, peak of Morne Couronne, *G.I. Webster 13209*, 4 June 1965 (US2419104!); St. Paul Parish, frequent along clay banks of the Rivière Deux Branches where it crosses the road 0.8 mi. E of Pont Cassé, *D.B. Lellinger 391*, 27 September 1965 (US2683748!; US2683749!; US2683750!; US2683751!); St. Paul Parish, trail to summit of Morne Trois Pitons SE of Pont Casse, *S.R. Hill 27949*, 27 May 1996 (VT289543!);Vicinity of Fresh Water Lake, near Laudat, *A.C. Smith 10287*, 26 March 1956 (US2256422!; US2256423!). **Unknown area:** *F.R. Fosberg 48279*, 10 March 1967 (P01623185!; US2554163!; US2643539!). **FRENCH ANTILLES.** *no collector*, no date (P00674774!); *Burquet s.n.*, 1878 (P01466473!). **GUADELOUPE.** *no collector*, no date (P01466501!); *ibidem* (P01409483!); *ibidem* (P01466502!); *ibidem* (P01466503!); *no collector*, 1908 (VT198722!); *ibidem* (VT198724!); *A. Père Duss 1196*, no date (VT!); *A. Père Duss 1197*, 1908 (VT198720!); *A. Père Duss 4353*, 1899 (US524251!); *Baudouin 622*, no date (P01466500!); *Chiebaut 31*, 12 March 1876 (P01466496!; P01466497!; P01466499!); *C. Legallo 2964*, 18 January 1960 (P01573412!); *L.C. Richard s.n.*, no date (P01409472!); *ibidem* (P01409473!); *Leprieur 24*, no date (P01546374!); *L'Herminier s.n.*, no date (P01466442!); *ibidem* (P01466485!); *ibidem* (P01466504!); *ibidem* (P01466505!); *ibidem* (P01466506!); *ibidem* (P01409475!); *ibidem* (P01409478!); *ibidem* (P01409479!); *ibidem* (P01409480!); *ibidem* (P01557725!); *ibidem* (P01557726!); *ibidem* (P01623187!); *ibidem*, 1840 (P01409474!); *ibidem* (P01409482!); *ibidem* (P01409485!); *ibidem* (US0483224!); *ibidem* (US0483225!); *ibidem* (US0483226!); *ibidem* (US0483227!); *ibidem*, 1862 (P01466494!); *M. Marie 72*, no date (P01466498!); *M. Merie s.n.* (P01409476!); *ibidem* (P01409477!); Bains-Jannes, *A. Questal 1097*, 24 July 1934 (US1780544!); *ibidem*, *A. Questal 1120*, 6 September 1939 (US1780551!); Basse Terre, comm. Basse–Terre/Capesterre, massif de La Souffrière, Carmichaël and Grande Savane, *M.J.M. Christenhusz & F. atzer 3927*, 6 March 2005 (P01389543!); *ibidem, M.J.M. Christenhusz & F. atzer 3934*, 6 March 2005 (P01389542!); Basse Terre, massif de la Soufriere, Partie NW, trace Victor Huguej, 500 m de la savane aux ananas, *C. & F. Sastre 2876*, 5 May 1974 (MO2340838!; P01618056!); Bois superieurs des Bains-Jaunes, Bois des Bains Chauds et du Morne Papaye, *A. Père Duss 4354*, May 1896-May 1898 (US524250!); Camp des Anglais, chemis conduisanrt, a norme, *Capitaine Bena 5490*, 9 December 1944 (US1881403!); Capesterre, Foret dense de la valle du Cabet, au–dessus

de Routhiers, *J. Fournet 4643*, 21 June 1990 (P01466483!); Foret des Bains Jaunes, Region Superieure, *P. Allorge s.n.,* 22 April 1936 (P01466486!); *ibidem* (P01466487!); *ibidem* (P01466488!); *ibidem* (P01466490!); *ibidem* (P01466491!); Iceland, *A. Questal 1818,* 29 September 1938 (US1780499!); la citerne, *J. Fedmann s.n.*. 23 April 1936 (P01466480!); *ibidem* (P01466481!); *ibidem* (P01466482!); le long du canal de Mer Aubin, *A. Père Duss 1198,* November 1908 (VT198718!; VT198719!); Matouba, Bords de cana, *Thiebaut 31,* February 1876 (US2703204!); Rivier Range, *A. Questal 3149,* 14 April 1943 (US2084021!; US2084022!); *ibidem, A. Questal 3180,* 14 April 1943 (US2084023!); Saint Claude, foret de Bains Jaunes, Sentier du Pas du Roi, *J. Fournet & Ph. Feldmann 5145*, 8 March 1992 (P01466484!); Savane aux Ananas, Trois-Rivieres (Madeleine), Matouba, Vallee de St. Louis, Bouillante, *A. Père Duss 3710,* May 1896-May 1898 (US524245!); Soufiere, *A. Questal 1091,* 24 July 1939 (US1780541!); summit of Mt. Peléz, *W. Seifriz s.n.,* August 1939 (US1714765!); Vallée de la Matilis, *J. Fedmann s.n.*. 23 April 1936 (P01466478!); *ibidem* (P01466479!). **MARTINIQUE.** *no collector,* no date (P01409484!); *ibidem* (P01466457!); *ibidem* (P01466476!); *ibidem* (P01466470!); *no collector 2,* no date (US1430031!); *no colector 245,* no date (US2703212!); *Belanger s.n.,* 1860 (P01466471!); *Belanger s.n.,* 1863 (P01546415!); *Belanger s.n.,* 1869 (P01546435!); *ibidem* (P01546436!); *Belanger 102,* 1857 (P01624670!); *Belanger 51,* 1858 (P01466474!; P01466475!); *Belanger 779,* 1863 (P01546416!); *Husnot 300,* 1868 (P01466469!); *Husnot 303,* 1868 (P01466465!; P01466466!; P01466467!; P01466468!; P01631353!; P01631354!; P01631355!; P01631356!; P01631357!; P01631358!; P01631359!; P01631362!; P01631363!; P01631364!; P01631365!; P01631366!); *Leprieur s.n.,* no date (P01546420!); *L. Hahn 60,* 12. 1867 (P01466458!); *L. Hahn 75,* 12.1867 (P01466459!); *Sieber 245,* no date (P01466461!; P01466462!; P01466463!; P01466464!; P01546413!); *Sieber 3720,* no date (P01546397!); Ayoupa-Boullon interieur des bois, *L. Hahn 6,* December 1867 (US2703129!); Bois de la Montangne Peler, du camp Colson des Deuz-Choux, *A. Père Duss 1555,* 1884 (US524242!; US524243!); Firet de la Cabessa, *L. Hahn s.n.,* 11.1870 (P01546417!); *P. Duss 1554,* 1883 (P01466492!; P01466493!); Matsubay R. Rouge, *A. Questel 1818,* 1938 (P01409481!); *Belanger s.n.,* no date (P01546412!); *ibidem* (P01546414!); *ibidem* (P01546421!); *ibidem* (P01546422!); Mt. Peleé, *M. Privault 169,* 13 August 1936 (P01546419!); Mt. Pelée, above Morne Lacroix, *J. Ewan 17099,* 19 March 1945 (US2019328!); près Capesterre, sur le chemin des Chutes du Carbet, *B. de*

Retz 90060, 21 March 1992 (P01624730!): *ibidem, B. de Retz 90061*, 21 March 1992 (P01624731!); *ibidem, B. de Retz 90064*, 21 March 1992 (P01624732!); *ibidem, B. de Retz 90070*, 21 March 1992 (P01624729!). **MONSERRAT.** *Ryan s.n.*, no date (BM000769812! photo, isotype; BM000769813! Photo, isotype); Chianers Mountain, Martha top, *J.A. Shafer 293*, February 1907 (US657443!; US065744!). **SAINT KITTS AND NEVIS. St. Kitts:** forest slopes of Mt. Misery, *N.L. Britton & J.F. Cowell 511*, 8 September-5 October 1901 (US428804!); ridge above The Crater, *H.E. Box 284*, 1 August 1932 (US1557194!; US1557195!); summit of Mt. Misery, *H.E. Boxx 296* 1 August 1933 (US1557202!). **SAINT VINCENT AND THE GRENADINES. Grenade:** *D.O. Mills s.n.*, 1903 (NY00814015!); *R.V. Sherring 137*, 1890-1891 (US0834091!); *W. Elliott s.n.*, 1887 (US0050338!); *ibidem* (US0050338!). **Saint Vicent:** *H.H. & G.W. Smith s.n.*, March 1890 (NY02007292!); *Bory 1*, no date (P01409523!); *Bory 42*, no date (P01409522!); *Bory 168*, no date (P01409471!); *Bory 298*, no date (P01466441!); Cumberland Mountain, *C.V. Morton 5857*, 14 May 1947 (US2358427!; US2358428!; US2358429!; US2358430!; US2358431!); Grand Bonhomme, *C.V. Morton 6138a*, 24 May 1947 (US2358483!); in Morne au Camp, *Eggers 6220*, 6 December 1889 (US2255747!); Richmond Peak, Morne Garou Mountains, *C.V. Morton 5080*, 15 April 1947 (US2358171!) Souffriere, *no collector 6911*, no date (P01466495!); Soufriere, *P. Beard 1367*, 26 November 1945 (US1916135!); Soufriere in Lava, *Eggers 6911*, January 1890 (US834092!). **UNKNOWN LOCATION:** *Filic Luerssen s.n.*, no date (US1786160!).

Parablechnum schiedeanum (C.Presl) Gasper & Salino, Phytotaxa 275(3): 217. 2016.

Basionym – *Lomaria schiedeana* C. Presl, Tent. Pterid. 143. 1836.

Type – México,in sylvis umbrosis pr. Jalapam, *Schiede 781*, August 1928 (holotype: HAL0112469! photo; isotypes: K ex B n.s., NY!).

Synonyms –

≡*Blechnum schiedeanum* (C.Presl) Hieron., Hedwigia 47: 239. 1908; *Struthiopteris schiedeana* (C. Presl) Broadh. Bull. Torrey Bot. Club 39: 363. 1912.

=*Lomaria costaricensis* H. Christ, Bull. Boiss. 11.4: 1092. 1904. Type: Costa Rica, *Oersted s.n.*, no date (holotype: C n.s.); ≡*Blechnum costarricense* (H. Christ) C. Chr., Ind. Fil. 152. 1905; ≡*Struthiopteris costarricensis* (H. Christ) Broadh., Bull. Torrey Bot. Club 39: 363. 1912.

=*Lomaria danaeacea* Kze. Linnaea 18(3): 326. 1845. Type: México, Veracruz, *F.E. Leibold 125*, no date (holotype: B200030876! Photo).
=*Lomaria longifolia* Schlecht ex Mart. & Galeoti, Mem. Ac. Bruz. 15: 49. 1842. Type: México, Veracruz, *M. Galeotti 6406*, 1840 (Syntypes P01409501!, P01409503-7!, P01409521!, P01531081-2!; isotypes: K000974394! Photo).
=*Lomaria spectabilis* Liebm. Kongel. Danske Vidensk. Selsk. Skr., Naturvidensk. Math. Afh., ser. 5, 1: 235. 1849. Type: México, *Liebmann s.n.*, no date (syntypes: US591311!, US591312!).

Description – *plants* terrestrial; *rhizome* erect, not subarborescent, scaly, scales 10–25 × 2–4 mm, lanceolate, light brown or rarely black, entire; *fronds* dimorphic; *sterile frond* 60–80 cm long; *petiole* 30–160 cm, yellowish-brown or straw-coloured and often with brownish spots, densely scaly to glabrescent on both surfaces, scales lanceolate, 1.5 × 0.4 cm, smooth, deciduous, mixed with other fibrillose; *lamina* up to 160 × 28 cm, 1-pinnate, scaly to glabrescent on the abaxial side, broadly oblong, truncate at base, gradually reducing towards apex and with in a conform terminal pinna, leaf tissue stiff–herbaceous, brittle and yellowish-green when dry; *rachis* straw–like, papillose, densely scaly, with petiole–like scales, or glabrescent; *sterile pinnae* in 12–25 pairs, 10–22 × 1.5–2.5 cm, stalked or substalked, sometimes becoming basiscopically adnate towards the distal lamina, entire margin, often narrowly revolute, bases subcordate, apex acute or acuminate; *costae* straw-coloured, adaxially grooved, abaxially prominent, sometimes scaly abaxially, with rachis-like scales; *veins* free, simple or 1-furcate, catadromous; *aerophores* low, rounded, oblong; *hydathodes* ovate; *fertile fronds* longer and more erect than sterile fronds, 50–150 cm; *petiole* 30–80 cm, straw or brown; *rachis* similar to sterile fronds; *fertile pinnae* in 16–24 pairs, linear, narrow 12–22 × 0.2–0.5 cm, bases cordate; *sori* linear, continuous, forming coenosori on both sides of the costa, covering the entire abaxial side of the pinna except the apices; *indusia* linear, continuous, opening towards the costa, brownish, lacerate; *sporangia* yellowish brown or dark brown, with arcs of 22–25 cells; *spores* monolete, (47–)59(–74) × (37–)44(–55) μm, perispores costate–reticulate, with walls delimiting large areoles, without filaments, edges of walls sometimes somewhat deflected, exospores smooth (**Figure 79**).

References – Moran (1995a), Broadhurst (1912b).

Chromosome number – unknown.

Distribution and habitat – Southern Mexico and Mesoamerica, cloud forests, *Pinus–Liquidambar* forests and swamps, 900–2400 m (Moran, 1995a).

Etymology – the epithet refers to C.J. Wilhelm Schiede, the collector of the type specimen.

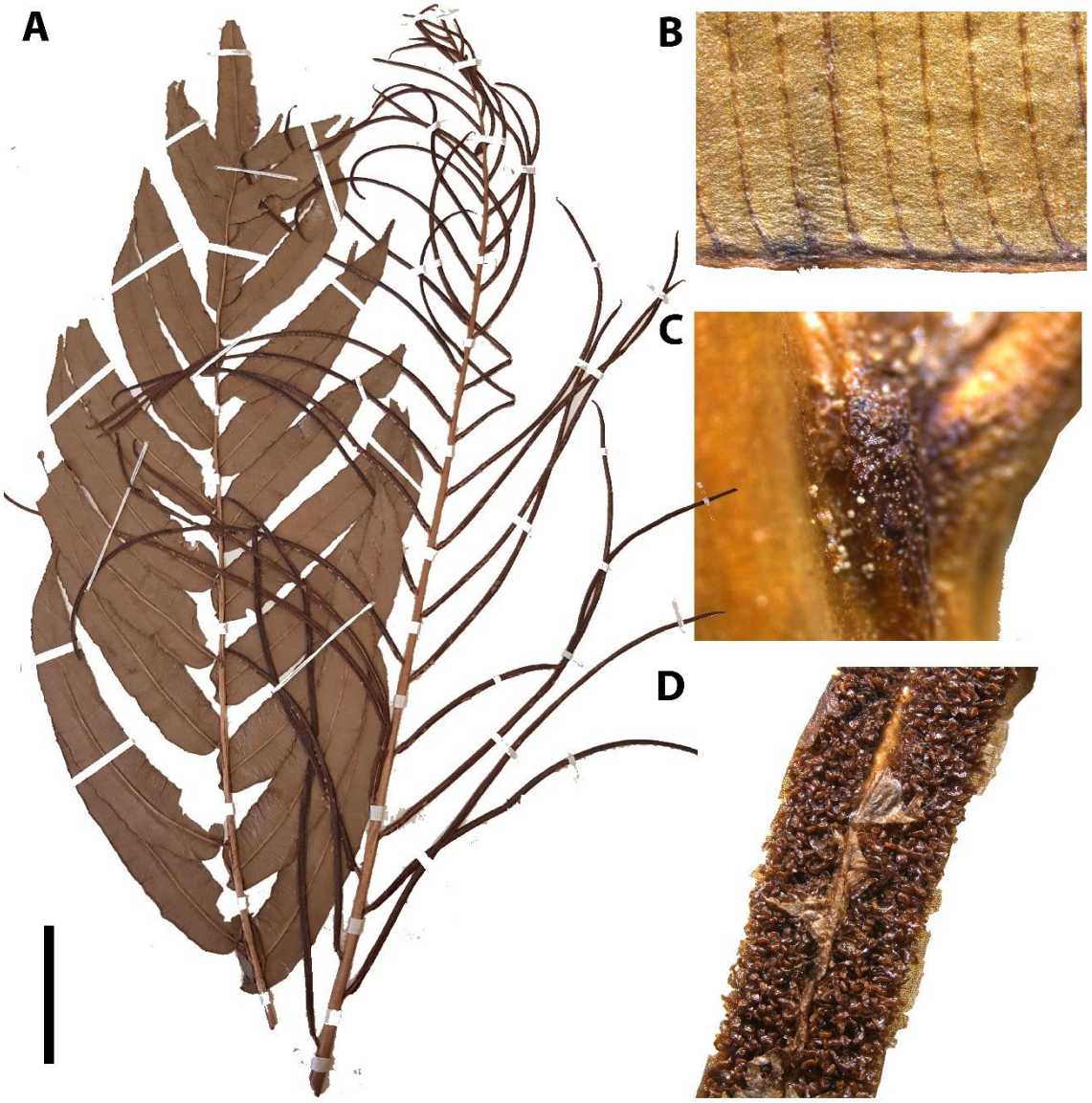

Figure 79. *Parablechnum schiedeanum*. A. Fragment of a sterile (left) and fertile (right) fronds; B. Sterile pinna margin, abaxial side; C. Aerophore; D. Fertile pinna surface, abaxial side. (A: *F.W. Johnson s.n.*, US1621301; B-C: *J.D. Smith 2427*, US50343; D: *H. Johnson 941*, US1082068). Scale: 4 cm in A, 2 mm in B, 1.5 mm in C, 3.5 mm in D.

Notes – there has been controversy as to whether this species is a synonym of *P. cordatum* (Tryon & Stolze, 1993; Prada *et al*., 2008) or whether it is a different species (de la Sota, 1972; Moran, 1995a; Rodríguez Ríos, 2015; Gasper *et al*., 2016, 2017), and in fact several authors have indicated the need for a specific study (Tryon & Stolze, 1993; Moran, 1995a; Dittrich *et al*., 2017). First molecular results as well as palynological study

suggest that they are different species, with *P. schiedeanum* having smaller spores (< 60 μm) (Vicent, 2017; Wal *et al*., 2021).

Some authors such as Mickel & Smith (2004) and Moran (1995b) indicate *that P. schiedeanum* may also be conspecific with *Parablechnum varians*; they were treated as synonyms by Gasper et al. (2016, 2017). A subsequent study focusing on the spores revealed substantial differences between the ornamentation of *P. schiedeanum* and *P. varians*. The presence of filaments on the spores of the latter and absence in the former, and it was decided to consider them as different species (Wal *et al*., 2021). This character, together with the atropurpureous axes and the crenate apices of *P. varians,* allow differentiation between the two species.

Parablechnum schiedeanum is also similar to the Mesoamerican species *Parablechnum falciforme,* but they are distinguished by the margins of the pinnae (entire in *P. schiedeanum* and serrate in *P. falciforme*), and in the spores (with filaments in *P. falciforme* and without filaments in *P. schiedeanum*).

Reviewed material:

COSTA RICA. Prov. Alajuela: 11 km N of San Ramón, *J.T. Mickel 2923,* 28 July 1967 (NY!); 12 km N of San Ramón, *D.B. Lellinger 732,* 27 July 1967 (US2589684A!); area of Balsa de San Ramon, *J. Taylor 17752*, 29 December 1974 (NY!); near Zapote on the road to Villa Quesada, *E. Scanman 7715*, 24-27 March 1955 (US2356529!); slopes near crater of Volcán Poás, *R.G. Stolze 1460,* 24 March 1973 (UC1444332! Photo; US2849674!); Volcán Poás, *Tonduz 10710,* September 1896 (P01631379!; P01631380!). **Prov. Cartago:** about 15 km south of Tapantí along the new road on the east slope above the Río Grande de Orosi near the concrete bridge, *W.C. Burger & J.L. Gentry Jr. 9197*, 14 April 1973 (NY!, 2 sheets); between Navarro and El Muñeco, *H.E. Stork 4711*, May 1929 (US2080649!); Cerro de la Muerte, 1 km NW of Villa Mills on Interamerican Highway, behinf Hotel La Georgina, *J.T. Mickel 3232,* 8 August 1967 (NY!, 2 sheets); El Muñeco, on the Rio Navarro, *P.C. Standley & R. Torres R. 50968,* 6-7 March 1926 (US1308455!; US1308456!; US1308457!); Girara, *R. Torres R. 89,* 12 December 1923 (US1315596!); Lowermost slope of Alto Perlas at northern end, talpanti, *M.H. Grayum & B. Jacobs 3812,* 12 August 1984 (UC1505457! Photo; UC1505458! Photo); mountains South of Cartago, *H.E. Stork 368,* 23 June 1923 (US1167820!); *ibidem, H.E. Stork 384,*

26 June 1923 (UC1215005! Photo; US1167822!); Navarro, *Wercklé s.n.,* 1905 (P01389535!); SE of Turrialba, ca. 4 km NE of La Suiza, *D.B. Lellinger & J.J. White III 1423*, 3 August 1970 (US2726492!); Tapaní, ca. 15 km S of Paraíso, *J.T. Mickel 1843,* 20 March 1967 (NY!); *ibidem, J.T. Mickel 1844,* 20 March 1967 (NY!, 3 sheets); *ibidem, J.T. Mickel 2318,* 3 July 1967 (NY!; US2589030A!); *ibidem, J.T. Mickel 2320,* 3 July 1967 (NY!). **Prov. Guanacaste:** *J.M. Gabriel y Galán s.n.,* 17 July 2013 (MACB109260!). **Prov. Heredia:** along the cart-road from Vara Blanca (between Poás and Barba volcanoes) to La Concordia, *W.R. Maxon & A.D. Harvey 8458,* 23 July 1923 (US1182065!; US1182066!; US1182067!; US1182068!; US1182069!); falls of Chinchona, near Vara Blanca, *C.A. Brown 210,* 30 July 1961 (US2414654!; US2414655!); on Atlantic slope of Volcán Barbam *R.R. Woodruff s.n.,* 14 August 1964 (US2551977!); Vara Blanca, between Poás and Barba Volcanoes, *E. Scanman 7178,* 22 March 1953 (US2356416!). **Prov. Navarro:** *Wercklé s.n.,* 1905 (US2577842A!). **Prov. Puntarenas:** Monteverde, Cloud Forest Reserve, *P.L. Fiedler 136,* 2 July 1980 (UC1446325! Photo); Monteverde, Santa Elena, *J.M. Gabriel y Galán s.n.,* 13–14 July 2013 (MACB!). **Prov. San José:** 10 km N of San Rafael de Heredia on Volcán Barba, *J.T. Mickel 3015,* 30 July 1967 (NY!); about 3 km. Northwest of Cascajal near the union of the Cascajal and Bajo Maquina Rivers, *J. Taylor & C. Taylor 11309,* 9 August 1971 (NY!); along unnamed north fork of Río Zurquí (upstream from highway, north of tunnel), Cantón de Moravia, P.N. Braulio Carrillo, Cuenca del Sarapiquí, Tunel Zurqui hasta 5 km, camino a Guapiles, *A. Rojas & M. Coto 3562,* 12 June 1997 (UC1740598! Photo); Cordillera Central , *A.R. Smith et al. 1662,* 18 January 1986 (NY!; UC1524429! Photo; UC1524430! Photo); de San José a Guápiles, *J.M. Gabriel y Galán s.n.,* 17 July 2013 (MACB109258!); Dota, Slopes od Cerro de la Muerte, below the hotel La Georgina, *M. Sundue & W. Testo 3885,* 1 January 2015 (VT198704!; VT198705!); La Palma, *P.C. Standley 33026,* 3 February 1924 (US1154699!); Las Nubes, La Palma, *W. Knight 29354,* 30 January 1938 (US1713078!); San Cristobal, *Wercklé s.n.,* no date (US690910!); Tablazo, *Brade 210,* 28 August 1908 (UC405791! Photo); Tablazo, *R.L. Rodríguez 110,* 21 February 1954 (UC1095631! Photo); Vásquez de Coronado, carretera a Guápiles, sendero al Río Patria, *A. Rojas & J.M. Gabriel y Galán 10418* (MACB109259!); Vicinity of La Palma, on the road to La Hondura, *W. Maxon & A. Harvey 8091,* 17-18 July 1923 (US1181771!; US1181772!; US1181773!; US1181774!; US1181775!); Vicinity of Tarbaca (1 km S and 2 km N), *J.T. Mickel 2400,* 5 July 1967 (NY!, 2 sheets). **Unknown**

province: *no collector,* no date (NY!); *C. Wercklé s.n.,* 1904 (NY!, isotype of *Lomaria costarricensis*); *ibidem* (P01624671!, isotype of *Lomaria costarricensis*); *ibidem* (P00627594! Holotype of *Lomaria costarricensis*); *W. Ceuviez 46,* no date (NY!). **EL SALVADOR. Dept. Chalatenago:** Dulce Nombre de María, carretera y cerros aledaños a Cooperativa, *J. Monterrosa & A. Soto 1219,* 25 August 2006 (NY!, 2 sheets). **Dept. Morazan:** near El Zancudo, *R. Seiler 1034,* 28 March 1979 (NY!); west Cerro de la Cruz, *R. Seiler 1051,* 9 April 1979 (NY!). **GUATEMALA. Dept. Alta Verapaz:** *H. von Türckheim s.n.,* 1906 (VT198715!); *H. von Türckheim 353,* 1879 (P01546388!; P01546389!); *H. von Türckheim 92295,* 1906 (P01623363!; P01623364!); Chihob, *H. Johnson 941,* 23 February 1920 (US1082068!; US1082069!); Coban, *H. von Türckheim 353,* December 1886 (US0834095!; US834096!; US834097!; US834098!); Coban, *von Türckheim 1384,* September 1907 (NY!; P01546392!; P01546394!; P01546395!); entre Tactic y Santa Cruz, Río Frío, *A. Molina 12201,* 14 May 1963 (US2631085!; US2631086!); large swamp just east of Tactic, *J.A. Steyermark 43975,* 20 February 1942 (US1916901!); near Tactic, above the bridge across Río Frío, *P.C. Standley 90483,* 30 March 1941 (US1840684!; US1840685!); near the Finca Sepacuite, *O.F. Cook & R.F. Griggs 161,* 16 March 1902 (US407951!); *ibidem, O.F. Cook & R.F. Griggs 578,* 8 April 1902 (US408222!); Río Chio, 2-4 km SW of Cobán, *L.O. Williams et al. 40722,* 8 February 1969 (US2642366!). **Dept. Baja Verapaz:** Mun. Purulha, along highway CA14 between El Progreso and Coban, 3 mi S of Purulhá, 17 mi N of junction with Hwy. 17 to Salamá and San Jerónimo vic. Km marker 160, *T.B. Croat & D.P. Hannon 63769,* 26 January 1987 (UC1539685! Photo; UC1539686! Photo; UC1539687! Photo); Sierra de las Minas, 3 km, SE of Purulhá, *L.O. Williams et al. 43414,* 6 January 1974 (US2795012!). **Dept. El Progreso:** between Calera and middle slopes of quebradas of Volcán Siglo, *J.A. Steyermark 43003,* 20 January 1942 (US1916823!). **Dept. Guatemala:** *J.D. Smith 2427,* February 1890 (US0050343!; US0050344!; US834099!; US834100!; US0834101!). **Dept. Huehuetenango:** Cerro Chiblac, between Finca San Rafael and Ixcan, Sierra de los Cuchumatanes, *J.A. Steyermark 49164,* 22 July 1942 (US1917175!; US1917176!); Río Mérida–río Hondo, *Bernoulli & Cario 252,* October 1876 (P01624727!; P01624728!). **Dept. Jalapa:** *F.W. Johnson s.n.,* 22 September 1906 (US1621301!); *Halm s.n.,* no date (P01409509!); *ibidem* (P01409510!). **Dept. Quetzaltenango:** Mun. de Zunil, road to Fuentes, Georginas, 4 km south of Zunil, northwest slopes of Volcán Zunil, *T.S. Quedensley 635,* 13 May 2004 (UC1789837!

Photo). **Dept. Zacapa:** along Rillito del Volcán de Monos, *J.A. Steyermark 42372*, 10 January 1942 (US1916761!). **HONDURAS. Dept. Comayagua:** Cordillera Montecillos 20 km al sur de Siguatepeque, *A.R. Molina 8028*, 6 April 1957 (US2358932!); near El Achote, hills above plains of Sigateyeque, *K.G. Tunder et al 5936*, 27 July 1936 (NY!); orillas del Barranco El Socorro, 5 km, al norte de Siguatepeque, *L.O. Williams & A.R. Molina 18137*, 18 April 1951 (US2202489!; US2202490!). **Dept. Copán:** 5 kms SO de Santa Rosa de Copán, *A.R. Molina 11686*, 29 March 1963 (US1631074!; US1631076!). **Dept. Cortes:** P.N. Cusuco, Montana San Idelfonso, dense wet cloud forest above Estación El Cusuco, *D.R. Hodel et al 1278*, 17 February 1994 (UC161604! Photo); Pulapanzack, 45 km SO de San Pedro Sula, *C. Bendeck 135*, 20 April 1985 (NY!). **Dept. Francisco Morazán:** along Río Agua Amarilla, northeastern slopes of Cerro de Uyuca, *C.V. Morton 7555*, 31 March 1951 (US2017292!; US2017293!; US2017294!; US2017295!; US2017296!; US2017297!); along road to Parque Nacional La Tigra, 22-25 km NE of Tegucigalpa, *T.B. Croat & D.P. Hannon 64004*, 1 February 1987 (UC1540592! Photo); Eastern slopes of Peña Blanca, San Juancito Mountains, in lower cloud-forest, *C.V. Morton 7282*, 22 March 1951 (US2017162!; US2017163!); vicinity of Las Mesas, *J.R. Swallen 11421*, 7 November 1951 (US2360148!; US2360149!; US2360150!; US2360151!). **Dept. Lempira:** Mount Celaque National Park, 8 km SW of Coracias, along road 500 m NE of Visitors Center and between river and Visitors Center, *J. Renfrow & D. Renfrow 31*, 1 April 1989 (US3210283!). **Dept. Morazán:** drainage of the Rio Yeguare, abundante en pantano de Valle Encantado, Montaña Uyuca, *A.R. Molina 4099*, 28 August 1951 (US2019850!; US2019851!). **Dept. Ocotepeque:** common in forest El Moral on Cordillera Merendón, *A. Molina R. 22286*, 27 August 1968 (NY!). **MÉXICO. Chiapas:** habitat inter pago San Bartolo et Las Nubes, *J.N. Rovirosa 836*, 31 July 1890 (NY!); Mun. of San Cristóbal las Casas, steep heavily wooded northeast slope of Zontehuitz near summit, *D.E. Breedlove 14033*, 1 November 1965 (US2416683!; US2416695!; US2416696!). **Guerrero:** Dist. Mina, Gro., Toro Muerto, *G.B. Hinton 14207*, 5 January 1939 (NY!); Mun. Alcozauca, aprox. 2 km. al S de Tzilacayotitlan camino de Tlaxco a San Miguel Amoltepec, *F.G. Lorea 1944*, 29 March 1982 (NY!, 2 sheets); Mun. Chichihualco, aprox 2 km N de Yerba Santa por el camino que va desde F. de Caballos a P. del Gallo, *F.G. Lorea 2103*, 17 July 1982 (NY!; UC1612760! Photo); Mun. Xalpatlahuac. Totopec - San Miguel Amoltepec, aprox 6 km al S de Tototepec, camino, *F. Lorea 2785*, 9 November 1983 (NY04187111!; NY04187112!). Mexico:

Mpio. Tejupilco, El Salto de Nanchititla (Nanchititla), *J.D. Tejero Díez 2443*, 14 July 1986 (NY04187115!). **Mexico:** Mun. Tejupilo, Nanchititla, El Salto de Nanchititla, *J.D. Tejero Díez 2443*, 14 July 1986 (NY!); Mun. Tejupilco, Palos Prietos y Cañadas en la Sierra de Nanchichitla, Río Cañada Nanachichitla-Salto de los Santos, *D. Tejero-Díez 3143b*, 10 August 1990 (NY!); Pungarancho, Dist. Temascaltepec, *G.B. Hinton 5252*, 24 November 1933 (NY!). **Morelos:** Dist. Mixes, Vicinity of Zacatepec, along trail north of city for ca. 1 mile, *J.T. Mickel 1561*, 30 July 1964 (NY!, 2 sheets). **Oaxaca:** Cerro San Felipe, *C. Conzatti 529*, 14 November 1897 (P01546448!; P01546449!); Dist. Cuicatlán, Vicinity of Teutila, *J.T. Mickel 7245*, 25 September 1973 (NY!; UC1503041! Photo); Dist. Ixtlán, 2-3 km S of Vista Hermosa, 75-76 km N of Ixtlán de Juárez on Rte 175, *J.T. Mickel & L. Pardue 6546*, 17 September 1972 (NY!); Dist. Ixtlán, 79 km W of Ixtlán de Juárez on Rte 175, 1 km S of Campamento Vista Hermosa, ca. 1 hour hike on trail toward Tarabundí, *J.T. Mickel 5661*, 27 July 1971 (NY!); *ibidem, J.T. Mickel 5708*, 27 July 1971 (NY!; UC1503037! Photo); Dist. Ixtlan, Mun. de Comaltepec, La Esperanza, *R. Lopez Luna 405*, 25 November 1988 (NY!); Dist. Ixtlan, Mpio. Ixtlán de Juarez, *M. Sundue & R. Torres 3075*, 1 March 2012 (VT198706!; VT198709!); *ibidem, J.T. Mickel & R. Torres 3075b*, 1 March 2012 (VT198711!; VT198712!); Dto. Juquila, 24-25 km N of San Gabriel, *J.T. Mickel 6167*, 10 August 1971 (NY!; UC1503034! Photo); Dist. Juquila, 96 km S of Sola de Vega, 41 km S of bridge at Juchatengo, 33 km N of San Gabriel, *J.T. Mickel 6042*, 9 August 1971 (NY!; UC1496042! Photo); Dist. Mixes, moist ridge between Camotlan and Quetzaltepec Mixe, *B. Hallberg 1801*, 29 July 1972 (NY!, 2 sheets); Dist. Mixes, Northeast slope of Cerro Zempoaltepetl, trail from La Candelaria to Zacatepec, *J.T. Mickel & S.W. Leonard 4827*, 19 September 1970 (NY!); Dist. Mixes, Vicinity of Zacatepec, along trail of city for ca. 1 mile, *J.T. Mickel 1561*, 30 July 1964 (US2550284!); Dist. Pochtla. 181 jm S of Oaxaca, 64 km N of Ponchutla, *J.T. Mickel & S.W. Leonard 5075*, 29 September 1970 (NY!; UC1496043! Photo); Dist. Teotitlan, Mun. San José de Tenago, San Martín Caballero, Sierra Mazateca, *Mickel 95-M077*, 2 March 1995 (NY04187113!); Dist. Villa Alta, 5-8 mi. N. ov Betaza on Camino Real, *J.T. Mickel 891*, 22 July 1962 (NY!, 2 sheets; US2420287!; US2420298!); Mpio. Ayotzintepec, 30 km despues de Valle Nacional Rumbo a Oaxaca, entre Vista Hermosa y La Esperanza, *A. Mendoza R. et al 484*, 1 August 2000 (NY!); Mpio. San Juan Quiotepec, Dto. Ixtlán, Rancho Arriero, recorrido de Santa María Totomoxtla, *R. Torres Colín et al. 16656*, 25 June 2002 (MACB!; VT198714!); *ibidem, R. Torres et al. 16690*, 25 June 2002 (MACB!;

VT198713!); Mpio. Santiago Xiacui, Dto. Ixtlán, Llano Verde, a 20.3 km de Xuacui, *R. Torres & M. Sundue 17239,* 27 February 2012 (VT198710!). **Puebla:** 4 km después de Petaltecoya, *B. Pérez-García et al 1179,* 5 July 2003 (NY!); 12 km de Teziutlan rumbo a Tlapacoyan, *A. Ramos & J.M. Fernández R128,* 27 July 1974 (NY!); Mun. Atzalan, Alceseca, cerca del río y el puente, *F. Ventura A. 89,* 22 November 1969 (NY!); Mun. De Atzalan, La Calavera, *F. Ventura A. 9366,* 5 December 1973 (NY!); Loc. Xicotepec de Juárez, *F. Ventura 4522,* 18 November 1971 (NY!); *ibidem, R. Cruz Cisneros 1498,* 27 July 1974 (NY!); Mun. Teziutlán, Agua de Obispo, *F. Ventura A. 404,* 1 November 1966 (NY!); near Villa Juárez, *H. Sánchez M. 626,* December 1950 (US2204120!; US2204122!); Tlacotepec, cercanias de Puerto del Gallo, *F.G. Lorea 2378,* 13 March 1983 (NY!; NY04187114; UC1612785! Photo); Villa Juarez, on grounds of Mi Ranchita Motel, *I.W. Knobloch 2172,* 9 August 1966 (US2424455!; US2593600A!). **Veracruz:** *F.E. Leibold 73,* no date (P00627590!); *F.E. Leibold 121,* no date (P01410437!); *F.E. Leibold 125,* no date (B200030876! Photo, syntype of *Lomaria danaeaceum*); *M. Galeotti 6406,* 1840 (K000974394! Photo, isotype of *Lomaria longifolia*; P01409501!, syntype of *Lomaria longifolia*; P01409503!, syntype of *Lomaria longifolia*; P01409504!, syntype of *Lomaria longifolia*; P01409505!, syntype of *Lomaria longifolia*; P01409506!, syntype of *Lomaria longifolia*; P01409507!, syntype of *Lomaria longifolia*; P01409521!, syntype of *Lomaria longifolia*; P01531081!, syntype of *Lomaria longifolia*; P01531082!, syntype of *Lomaria longifolia*); Camino vecinal Chocamán-Tetla, *L. Esperón Muñoz 16123,* 13 September 1985 (UC1526306! Photo); Inter Totula at Huatusco, *Liebmann 767 (2320),* no date (US1406169!); Jalapa, *C.L. Smith 2176,* 1894-6 (UC995564! Photo; UC995565!); Jalapam, *C.W.J. Schiede 764,* August 1828 (HAL0112469! Photo, holotype); Jalapa, *J.N. Couch M27,* 18 February 1940 (US1791189!); La Perla, *M. Copeland 52,* 3 March 1938 (NY!; P01662923!; UC600172! Photo); Llave, Coatepec, *J. Sánchez 69,* December 1943 (US1843386!; US1843387!); Llave, near Orizaba, *C.G. Pringle 5581,* 3 February 1895 (P01546387!; P01546408!; P01546411!); Llave, Zacuapan, *C.A. Purpus 16581,* March 1933 (US1637325!); near Orizaba, *C.G. Pringle s.n.,* 3 February 1881 (VT198707!); Región Orizaba, *E.B. 2790,* 7 August 1866 (P01409513!; P01409514!; P01409515!); *ibidem, Miller 436,* no date (NY!); Salto del Gato, along Rio Sendeño, about 3 km NE of Xalapa, *J. Dorante et al. 709,* 31 December 1973 (VT198708!); Zacuapan, *C.A. Purpus s.n.,* November 1906 (UC150512! Photo). **Unknown state:** *F.W. Johnson s.n.,* no date (NY!); *Halm 384,* no date (P01409511); *J.J. Linden 66,* 185¡41 (BR0000013071837!

Photo; BR0000013071844! Photo); *Legbold 125*, no date (B200030876!); *Lévide s.n.*, 1859 (P01409512!); *Liebmann s.n.*, no date (US591311!, syntype of *Lomaria spectabilis*, US591312!, syntype of *L. spectabilis*); *M. Galeotti s.n.*, 06.1840 (P01409502!); *M. Galeotti 255*, no date (P01409500!); *Sartorius 137*, no date (NY!); *Schnutz 64*, no date (NY!). **NICARAGUA. Dept. Jinotega:** San Rafael del Norte, *W. de Miller & L. Griscom 149*, 25-26 March 1917 (US989091!). **PANAMA. Prov. Chiriquí:** along Holcomb's Trail, 10-11 miles above El Boquete, *E.P. Killip 5201*, 11 February 1918 (US922421!); trail to Cerro Pate Macho, *G. de Nevers & G. McPherson 6832*, 17 January 1986 (UC1533352! Photo; UC1533353! Photo); vicinity of El Boquete, *L.R. Cornman 846*, 6 February 1918 (UC1185559! Photo; US1082417!); *ibidem, L.R. Cornman 1153*, 17 March 1918 (US1082668!; US1082669!). **MESOAMERICA.** *Poeppig 34*, 1868 (P01409520!).

Parablechnum sessilifolium (Klotzsch ex Christ) Gasper & Salino, Phytotaxa 275(3): 191–227. 2016.

Basionym – *Lomaria sessilifolia* Klotzsch ex Christ, Bull. Herb. Boissier, sér. 2, 4: 1092. 1904.

Type – Costa Rica: Sommet du Poàs, 2644 m *Tonduz 10710*, 1896 (syntypes: P01631379–80!) isotypes: US00067444!, US00472015–6! US01081292!).

Synonyms –

≡*Blechnum sessilifolium* (Klotzsch ex Christ) C.Chr., Index Filic. 159. 1905; *Struthiopteris sessilifolia* (Klotzsch ex H. Christ) Broadh. Bull. Torrey Bot. Club 39: 373. 1912.

Description – *plants* terrestrial; *rhizome* erect, not subarborescent, non-stoloniferous, scaly, scales 10–20 × 3–6 mm, lanceolate, concolorous, golden to light brown, entire; *fronds* dimorphic; *sterile fronds* size with *petiole* 15–28 cm, yellowish-brown or straw–brown, densely scaly on both surfaces; *lamina* 28–50 × 12–20 cm, 1-pinnate, glabrous or with scattered scales on the upper side, truncate at the base, tapering distally, with in a conform terminal pinna about half the length of the lateral pinnae; *buds* present on the upper side in the sinuses at the base of the lateral pinnae; *rachis* straw to yellowish-brown, papillose, moderately to densely scaly; *sterile pinnae* in 27–70 pairs, 6–10 × 0.7–1.5 cm, shortly stalked, the base strongly cordate and overlapping slightly with the rachis, entire

or serrulate, flattened to narrowly revolute; *costa* straw-coloured, grooved adaxially, prominent abaxially, with scales on abaxial face similar to those of the rachis; *veins* free, simple or 1-furcate, catadromous; *aerophores* low, rounded, reniform; *hydathodes* ovate; *fertile fronds* longer and more erect, 1–1.5 × 10–20 cm; *buds* small, on the upper side of the base of the pinnae; *petiole* 20–50 cm, yellowish-brown to straw-coloured; *fertile pinnae* linear, narrow, 10–15 × 0.3–0.5 cm; *sori* linear, continuous, forming coenosori on both sides of the costa; *indusia* linear, continuous, open towards the costa, brownish, lacerate at maturity; *sporangia* (22–)25(–26); *spores* monolete, spores (48–)58(–70) × (32–)44(–52) µm; perispore smooth, cristate-reticulate, high-walled, thick, forming a reticulum, with abundant long filamentous processes on the entire spore surface (**Figure 80**).

References – Moran (1995a).

Chromosome number – unknown

Distribution and habitat – Costa Rica, in this work it was found also a specimen from Panama (MO3520233). Near small streams on recent volcanic soils, pastures, secondary forest margins. 800–2600 m (Moran, 1995a).

Etymology – the epithet, meaning "sessile leaf", refers perhaps to the relative short length of the stalks.

Notes – this is the only known species of the genus *Parablechnum* with bulbils or vegetative buds along with *P. proliferum*. It differs from this species in that *P. proliferum* has only one bulbil on the terminal pinna, whereas *P. sessilifolium* has buds on the lateral pinnae.

Reviewed material:

COSTA RICA. Prov. Arajuela: around summit and old crater lake of Volcán Poás, *J.T. Mickel 2423*, 6 July 1967 (NY!); *ibidem, J.T. Mickel 2424*, 6 July 1967 (NY!; US2589073A!); *ibidem, J.T. Mickel 2425*, 6 July 1967 (NY!; UC1507670! Photo); Cantón de Poás, P.N. Volcán Poás, Cuenca del Sarapiquí, orillas del crater, Laguna Botos y sendero de regreso, *A. Rojas & A. Soto 4817*, 15 December 1998 (NY!); upper slopes of Volcán de Poás, between the Hotel and the crater, *P.C. Standley 34892*, 17 February

1924 (US1154874!); Volcán Poás, *Tonduz 10710*, 9.1896 (P01631379!, syntype); *ibidem* (P01631380, syntype); *ibidem* (US00067444!); *ibidem* (US00472015!, isotype); *ibidem* (US00472016!); *ibidem* (US01081292!). **Prov. Cartago:** Cerro de la Muerte, 1 km NW of Villa Mills on Interamerican Highway, behinf Hotel La Georgina, *J.T. Mickel 3299a*, 8 August 1967 (NY!); Navarro, *Wercklé s.n.*, 1905 (P01557691!); Interamerican Highway, vicinity of Villa Mills and 1 km NW (vicinity Hotel La Georgina), *J.T. Mickel 2159*, 24 March 1967 (NY!); Southern slope of Volcán de Turrialba, near the Finca del Volcán de Turrialba, *P.C. Standley 35280*, 22 February (US1154959!). **Prov. Guanacaste:** Liberia, Parque Nacional Guanacaste, Sendero al Volcán Cacao, *A. Rojas 7690*, 7 August 2007 (MO6387305!); Parque Rincón de la Vieja Hacienda Santa María, sendero desde la casita de Las Pailas hasta el cráter del Volcán Von-Seebach, *G. Herrera & R. Robles 793*, 6 October 1987 (UC1747714! Photo). **Prov. Heredia:** Ca. 3 km N of Los Cartagos on the road from Heredia to Vara Blanca, *D.B. Lellinger & J.J. White 976*, 5 July 1970 (MO2139852!; UC1386894! Photo; US2726490!); Cerro de las Caricias, north of San Isidro, *P.C. Standley & J. Valerio Rodríguez 52086*, 11 March 1926 (US1308596!); Cerros de Zurqui, northeast of San Isidro, *P.C. Standley & J. Valerio Rodríguez 50543*, 3 March 1926 (US1308423!); Cut-over forest along Río Vueltas (upper Rio Patrio), at end of Rte. 113,9 km. N of Angeles, *R.G. Stolze 1629*, 1 April 1973 (US2849675!; US2849676!); end of road from San Rafael at Rio Patrio, *R.B. Faden 203*, 9 August 1964 (US3736536!; US3736537!); second river crossing further up path, Calle Leones, road from Conception de San Isidro to Cerro Zurqui, *R.B. Faden s.n.*, 16 July 1965 (US3663813!); Volcán Barva, *M. Valerio 112*, 29 July 1926, (US1316842!); Yerba Buena, northeast of San Isidro, *P.C. Standley & J. Valerio Rodríguez 50057*, 22-18 February 1926 (US1308365!). **Prov. San José:** Dota, Carretera Interamericana, km 66, cerca de 3 km después de Trinidad, *A. Rojas et al. 10417*, 15 July 2013 (MACB!); Interamerican Highway, vicinity of Villa Mills and 1 km NW (vicinity Hotel La Georgina), *J.T. Mickel 2158*, 24 March 1967 (NY!, 2 sheets). **PANAMA. Prov. Cocle:** above El Valle, along Trail to top of Cerro Gaital, *G. McPherson 12146C*, 24 February 1988 (MO3520233!).

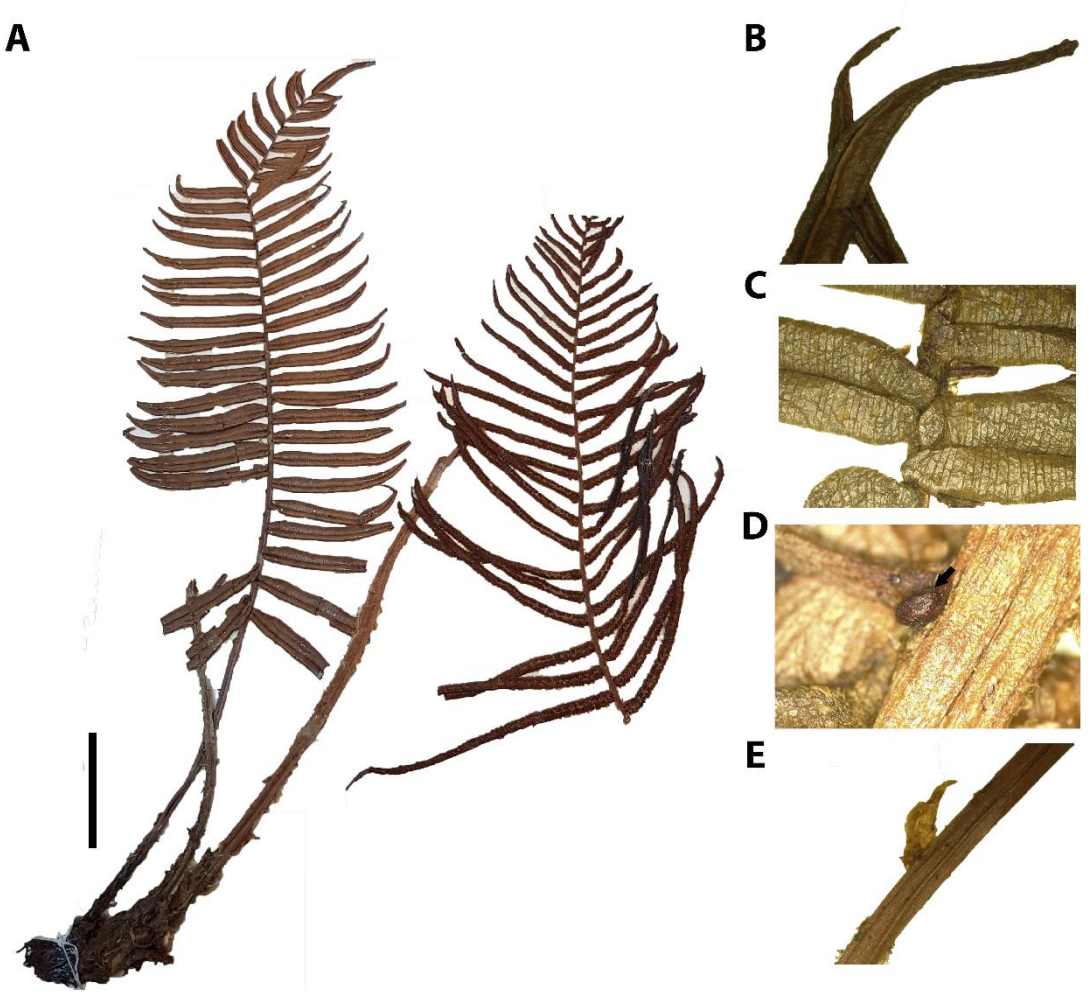

Figure 80. *Parablechnum sessilifolium.* A. Sterile frond (left) and fertile frond fragment (right); B. Sterile pinnae apices, abaxial side; C. Sterile pinnae bases, adaxial side; D. Aerophore (arrow); E. Fertile petiole. (A: *D.B. Lellinger & J.J. White 976*, MO2139852; D-E: *G. McPherson 12146C*, MO3520233). Scale: 4 cm in A, 7.5 mm in B, 9 mm in C & E, 2 mm in D.

Parablechnum smilodon (M.Kessler & Lehnert) Gasper & Salino, Phytotaxa 275(3): 191–227. 2016.

Basionym – *Blechnum smilodon* M.Kessler & Lehnert, Amer. Fern J. 97: 76. 2007.

Type – Bolivia. La Paz: Prov. Nor Yungas, Trocha al Valle de Coscapa, Parque Nacional Cotapata, 16012'S, 67053'W, 3250 m, 11 September 1997, *Kessler 11814* (holotype: GOET007568! photo; isotypes: LPB0000021! photo, UC1621924! photo).

Description – *plants* terrestrial; *rhizomes* dark, erect, scaly, scales 8–12 × 1.5–2 mm, lanceolate, translucent, blackish brown or reddish brown with slightly lighter margins, margins irregularly toothed; *sterile fronds* 90 × 13 cm, erect; *petioles* 45 × 0.6 cm, dark

reddish brown with atropurpureous bases, sparsely scaly, basal scales similar to those of rhizomes; *laminae* lanceolate, 1-pinnate, abruptly reduced base and gradually reduced apex, laminar tissue finely coriaceous, adaxially glabrous, abaxially with minute, scattered scales on the veins, the scales 0.05–0.2 × 0.05 × 0.2 mm, arachnoid, adpressed, brown or light-brown; *rachis* atropurpureous, reddish brown or straw–brown, adaxially grooved, densely scaly, scales of two types, one 3–7 × 0.2–0.8 mm, lanceolate, sparse, translucent, yellowish brown with midlines of dark reddish brown cells, margins setose, the others 0.2–2 × 0.1–0.8 mm, ovate to broadly lanceolate, appressed, yellowish to dark brown, setose, with setae about as wide as the scale body; *sterile pinnae* in 40–55 pairs, 7.5 cm × 9 mm, stalked, slightly falcate, apices acuminate, margins narrowly hyaline, serrulate, slightly to strongly revolute; *costa* straw-coloured, adaxially grooved, on both sides with sparse scales resembling the smaller ones of the rachis; *veins* free, simple or 1-furcate, flush with tissue or slightly raised on both sides, catadromous; *aerophores* tuberculiform; *hydathodes* small; *fertile fronds* unknown (**Figure 81**).

References – Kessler *et al*. (2007), Smith & Kessler (2018)

Chromosome number – unknown.

Distribution and habitat – found only in Bolivia, at 2500–3350m. Fairly common, terrestrial, located in the humid ecotone of the forest edge in cloud forests (Kessler *et al.*, 2007; Smith & Kessler, 2018).

Etymology – the epithet evokes the extinct saber–toothed tiger, *Smilodon* Lund, due to the strongly dentate scales of this species (Kessler *et al.*, 2007).

Notes – this species is similar to *Parablechnum stipitellatum*, and in fact it was previously identified as such. *Parablechnum smilodon* differs from *P. stipitellatum* mainly in its smaller size (fronds 90 × 13 cm vs. 120 × 22 cm), the greater number of pinnae per frond (40–55 vs. 20–40 pairs) and much more strongly toothed rachis scales (Kessler *et al*., 2007). Amongst Bolivian species, it is quite similar to *P. lima*, but that species has strongly truncated, broader pinna bases and less deeply toothed rachis scales, as well as very prominent veins (Kessler *et al*., 2007; Smith & Kessler, 2018).

Reviewed material:

BOLIVIA. **Dept. La Paz:** Prov. Nor Yungas, Trocha al Valle de Coscapa, Parque Nacional Cotapata, *Kessler 11814*, 11 September 1997 (GOET007568! photo, holotype); LPB0000021! Photo, isotype; UC1621924! photo, isotype); Estación Biológica de Tunquini, senda nueva del camino de la mina (curva al lado oeste) al pantanón, *Bach 1038*, 14 September 2000 (GOET007147! photo, paratype; UC1749602! Photo, paratype); *Ibidimen*, *Bach 1839*, 13 July 2002, (GOET007226! photo, paratype; UC1780589! Photo, paratype); *ibidem* (GOET007227! photo, paratype); *ibidem* (GOET007228! photo, paratype); Bajo Hornuni, senda del campo de Don Pedro al camino de la mina, *Jiménez 474*, 17 August 2000 (GOET007225! photo, paratype; UC1749603! Photo, paratype).

Figure 81. *Parablechnum smilodon* (*M. Kessler et al. 11814*, UC1621924, isotype). Scale: 4 cm.

Parablechnum squamatum (M.Kessler & A.R.Sm.) Gasper & Salino, Phytotaxa 275(3): 217. 2016.

Basionym – *Blechnum squamatum* M.Kessler & A.R.Sm., Amer. Fern J. 97: 78. 2007.

Type – Bolivia, Cochabamba, Carrasco, 94 km antigua carretera Cochabamba–Villa Tunari, 17º08'S, 65º38'W, 3500 m, *Kessler 6790*, 28 June 1996 (holotype: UC1602976! photo; isotypes: GOET007169! photo, LPB0000022! photo).

Description – *plants* terrestrial; *rhizomes* erect, scaly, scales 8–14 × 2–24.5 mm, lanceolate, light orange-brown, in some specimens with darker centres, margins entire or very slightly and remotely denticulate; *fronds* dimorphic, *sterile fronds* ca. 100 × 30 cm, erect; *petioles* 50 × 0.4 cm, proximally reddish-brown, distally straw-coloured, moderately scaly, scales of two types, some similar to those of the rhizome, but smaller, the others 0.2–1.2 × 0.2–0.9 mm, ovate to broadly lanceolate, adpressed, brownish, ciliate; *lamina* broadly lanceolate, 1-pinnate, abruptly reduced base and a gradually reduced apex with an apical conform pinna, laminar tissue chartaceous, adaxially glabrous, abaxially with scattered small scales on the veins, the scales 0.05–1 × 0.05 × 0.5 mm, arachnoid to triangular, appressed, light brown; *rachis* light reddish brown to straw-coloured, adaxially grooved, moderately to densely scaly, scales similar to petiole scales, but smaller, with partly fibrillose and arachnoid scales; *sterile pinnae* in ca. 15–18 pairs, 21 × 2.5 cm, stalked, falcate, apices long acuminate and serrulate, margins narrowly hyaline, entire, flat; *costae* reddish brown to straw-coloured, adaxially grooved, glabrous, abaxially with scattered scales 1–3.5 × 0.4–1.7 mm, triangular to lanceolate with cordate to truncate bases, margins denticulate to ciliate, light orange-brown, the longer scales usually with dark reddish-brown centres; *veins* free, simple or 1-furcate, slightly immersed adaxially, catadromous; *aerophores* reddish brown, peg–like, 1–5 × 1–2 mm; *hydathodes* small; *fertile fronds* known only from fragments; *fertile pinnae* 9 × 0.4 cm, linear, coarse–textured and drying darker than sterile ones; *sori* linear, continuous, forming coenosori on both sides of costa, covering the entire pinna except 1–3 mm distally; *indusia* linear, continuous, open towards the dark brown costa, entire but irregular after opening; *sporangia* with (17–)19(–20) arc cells; *spores* monolete, (47–)57(–69) × (34–)44(–54) µm; perispores smooth, cristate-reticulate, with high, thick walls, forming large polygonal areoles, without filamentous processes, with granules (**Figure 82**).

References – Kessler *et al.* (2007).

Chromosome number – unknown.

Distribution and habitat – endemic to Bolivia, at (1150–)2600 – 3500 m. Uncommon, terrestrial in open montane moist forest and scrub (Kessler *et al.*, 2007; Smith & Kessler, 2018).

Etymology – the epithet refers to the diagnostic costal scales (Kessler *et al*., 2007)

Notes – this species differs from *P. cordatum* in that the costa scales are much larger, much denser and the rachis scales are larger and partially bicolorous; it also has larger aerophores. More material is needed to assess the variability of this species. (Kessler *et al.*, 2007).

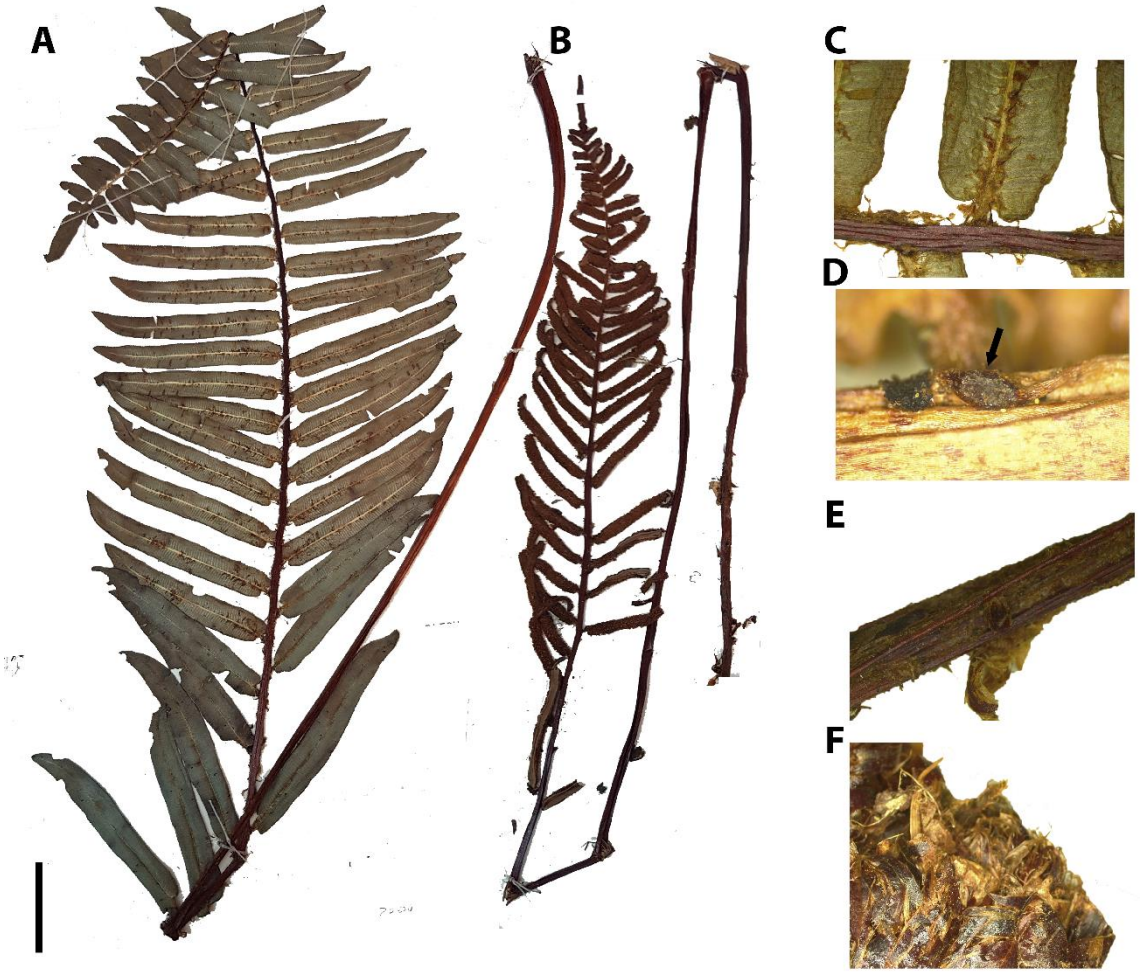

Figure 82. *Parablechnum squamatum.* A. Sterile frond; B. Fertile frond; C. Sterile pinnae bases abaxial side; D. Aerophore (arrow); E. Sterile petiole; F. Rhizome scales. (A & C: *A.F. Fuentes & H. Huaylla 13638*, MO6218541; B, D-F: *I. Jiménez et al 2828*, MO6112550). 4 cm in A & B, 11 mm in C, 1.5 mm in D, 4.5 mm in E, 2.5 mm in F).

Reviewed material:

BOLIVIA. Dept. Cochabamba: Carrasco, 94 km antigua carretera Cochabamba–Villa Tunari, *Kessler 6790*, 28 June 1996 (UC1602976! photo, holotype; GOET007169! photo, isotype; LPB0000022! photo, isotype). **Dept. La Paz:** Prov. Bautista Saavedra, Area Natural de Manejo Integrado Apolobamba, sector Chaka, bosque continuo al SE del campamento cerca de la Cueva, por el antiguo camino Laji Sorapata-Apolo, *A.F. Fuentes & H. Huaylla 13638,* 30 March 2009 (MO6218541!); Prov. Franz Tamayo, bajando desde Puina (pueblo antiguo), *I. Jiménez et al. 2828*, 20 June 2005 (MO6112550!).

Parablechnum squamosissimum (A.Rojas) Gasper & Salino, Phytotaxa 275(3): 217. 2016

Basionym – *Blechnum squamosissimum* A.Rojas, Mét. Ecol. Sist. 3(1): 37, f. 2, 3A, B. 2008.

Type – El Salvador. Santa Ana: Trifinio, Hacienda Montecristo, Metapán, *B. Hernández s.n.*, 16 Dec 1971 (holotype: MO2903897! photo).

Description – *plants* terrestrial; *rhizome* erect, scaly, scales 5–15 × 1.5–3 mm, lanceolate, dark brown to black, entire; *fronds* dimorphic; *sterile fronds* 1.5–2.4 m long, *petiole* 60–90 cm long, straw-coloured to dark brown basally, scaly, denser at base, the scales 5–15 × 1–2.5 mm, lanceolate to linear-lanceolate, dark brown to blackish, marginally entire, mixed with small, marginally ciliate, mainly at the base; *rachis* straw-coloured, adaxially grooved, moderately to densely scaly, scales of two types, some ca. 0.5–2 × 0.5 × 0.5 mm. 0.5–2 × 0.5 mm, upright, orange, marginally dentate or ciliate, the others ca. 3–5 × 1 mm, ovate to lanceolate, orange, discoloured, with reddish or dark brown centre, margins entire; *sterile pinnae* in 26 pairs, 15–22 × 2–3 cm, linear-oblong, basally rounded to truncate, apically acuminate, marginally denticulate, costa similar to rachis, with the same type of scales abaxially, grooved adaxially, prominent abaxially; *veins* free, simple or 1-furcate, glabrous on adaxial surface, moderately to densely scaly on abaxial surface, scales 0.5–1.5 mm long, ovate, marginally ciliate, catadromous; *aerophores* absent; *hydathodes* ovoid; *fertile fronds* ca. 1.5–2 m long. 1.5–2 m long, *fertile pinnae* 8–12 × 0.3–0.7 cm, linear, adaxially glabrous, abaxially with costal scales ca. 3–5 × 1 mm, whitish to yellowish, apex brown, marginally entire; *sori* linear,

continuous, forming coenosori on both sides of costa occupying entire pinna; *indusia* linear, continuous, opening towards costa brown, eroded; *sporangia* not observed; *spores* not observed (**Figure 83**).

References – Rojas (2008).

Chromosome number – unknown.

Distribution and habitat – known only from Cerro de Montecristo in El Salvador and Chiapas in the State of Mexico, at 2000–2800 m (Rojas, 2008).

Etymology– the name of this species refers to the medium to dense abaxial laminar scales (Rojas, 2008).

Figure 83. *Parablechnum squamosissimum*. (*B.A. Hernández s.n.,* MO207689, holotype). Scale: 4 cm.

Notes – the species is similar to *Parablechnum falciforme* but differs in the scales at the base of the petiole, which are darker in *P. squamossisimum*, wider pinnae and denser scales on costae and rachis.

Reviewed material:

EL SALVADOR. **Santa Ana**: Trifinio, Hacienda Montecristo, Metapán, *B. Hernández s.n.,* 16 December 1971 (MO2903897! photo, holotype); Cordillera Miramundo, Mountain of Montecristo, *A. Molina et al. 16759*, 27–31 January 1966 (US2689336!, paratype). **MÉXICO. Est. Chiapas:** Cerro Hueytepec, 5 km NW of Ciudad de Las Casas (San Cristobal), *E.L. Little Jr & A.J. Sharp 9928*, 22 April 1945 (UC910165! Photo; US1919334!; US1919335!); Mpio. Tenejapa, *D. Breedlove & A. Smith 21990*, 7 November 1971 (NY!, paratype); north of San Cristobal las Casas at top of Cerro Zontehuitz, *J.T. Mickel 1238*, 27 July 1963 (NY!; UC1507698! Photo; US2550188!).

Parablechnum stipitellatum (Sodiro) Gasper & Salino, Phytotaxa 275(3): 217. 2016

Basionym – *Lomaria stipitellata* Sodiro. Recens. Crypt. Vasx. Quit. 29. 1883.

Type – Ecuador, Corazon y Atacazo, 2500–3400 m. *Sodiro s.n.*, Jul 1882 (syntypes: P00627643–46!).

Synonyms –

≡*Blechnum stipitellatum* (Sodiro) C.Chr. Ind. Filic. 160. 1905.
=*Blechnum rubicundum* Hieron., Hedwigia 47. 242, /. 4,f. 16. 1908. Type: Colombia, weg nach La Ceja, *Stübel 347*, no date (B200033183!).

Description – *plants* terrestrial; *rhizomes* erect or sometimes shortly creeping, scaly, scales lanceolate, entire, concolorous or discoloured, brown, up to 1.5 cm long, with or without a dark central area; *fronds* dimorphic; *sterile fronds* 50–100 cm long, narrowly lanceolate, arched, *petioles* stiff, grooved, from 20 cm to almost as long as half the frond in some specimens, scaly, with very denticulate scale; *lamina* narrowly lanceolate, up to 100 cm long, 1-pinnate, with attenuate acuminate apex, with in a conform terminal pinna, base almost straight; *rachis* dark brown or light brown, scaly, scales concolorous, distinctly denticulate, light brown to reddish brown, 2–3 mm long and unicellular glands; *sterile pinnae* in 20–60 pairs, linear-lanceolate, up to 10 cm long, narrow, margin more or less revolute, stalked, becoming basiscopically adnate towards the apex, terminal pinna lanceolate to lanceolate attenuate, longer than the laterals and sometimes with a basal

auricle; *costae* similar to rachis, with the same type of scales, grooved adaxially, prominent abaxially; *veins* free, simple or 1-furcate, catadromous; *aerophores* dark, globose; *hydathodes* large, elliptic; *fertile fronds* similar in size to sterile ones, longer and erect, *lamina* lanceolate or linear, *fertile pinnae* ascending(size?); *sori* linear, continuous, forming coenosori on both sides of costae; *indusia* linear, continuous, opening towards costa, lacerate with irregular margin; *sporangia* with (19–)20(–23) arc cells; *spores* monolete, (38–)55(–83) × (30–)38(–44) µm; perispores smooth, cristate-reticulate, with low, thick walls, forming large polygonal areoles, with very long and abundant filamentous processes on the entire spore surface (**Figure 84**).

References – Tryon & Slotze (1993), Passarelli *et al.* (2010), Rolleri *et al.* (2012a).

Chromosome number – unknown.

Distribution and habitat – from Venezuela and Colombia to Peru and southern Bolivia. Terrestrial, in humid montane forests, on rocks, páramo, rock edges, clayey or volcanic soils and in areas under waterfalls, 2400–3700 m (Tryon & Stolze, 1993; Rolleri *et al.*, 2012a).

Etymology – the specific epithet, could mean "bearing a small trunk", making reference to the sometimes-erect rhizome, or to the pinnae which are stipitate.

Notes – this species is similar to *Parablechnum loxense*, and also occupies similar habitats, but its sterile pinnae are less strongly revolute than in this species, and also easily distinguished by the serrate scales (entire in *P. loxense*). It is also similar to *P. lima*, from which it differs mainly in the blackish to reddish-brown rhizome scales (*vs*. tan) and less deeply sunken petioles, rachises, costae and veins. According to Kessler *et al*. (2007) these two species appear to replace each other geographically, with *P. lima* being known only from Bolivia, and *P. stipitellatum* from southern Peru to northern Colombia, however in subsequent work, as well as in this treatment, specimens of *P. stipitellatum* from Bolivia have been observed (Rolleri *et al*., 2012).

Tryon & Stolze (1993) suggested that it is similar to specimens of *Parablechnum cordatum* with less revolute pinnae. However, this species is quite different from *P. cordatum* and it is easy to differentiate them by the linear-lanceolate lamina of *P. stipitellatum* and its denticulate scales. These authors also suggest the possibility that the

forms with less revolute margins of this species are those found in locations with lower light.

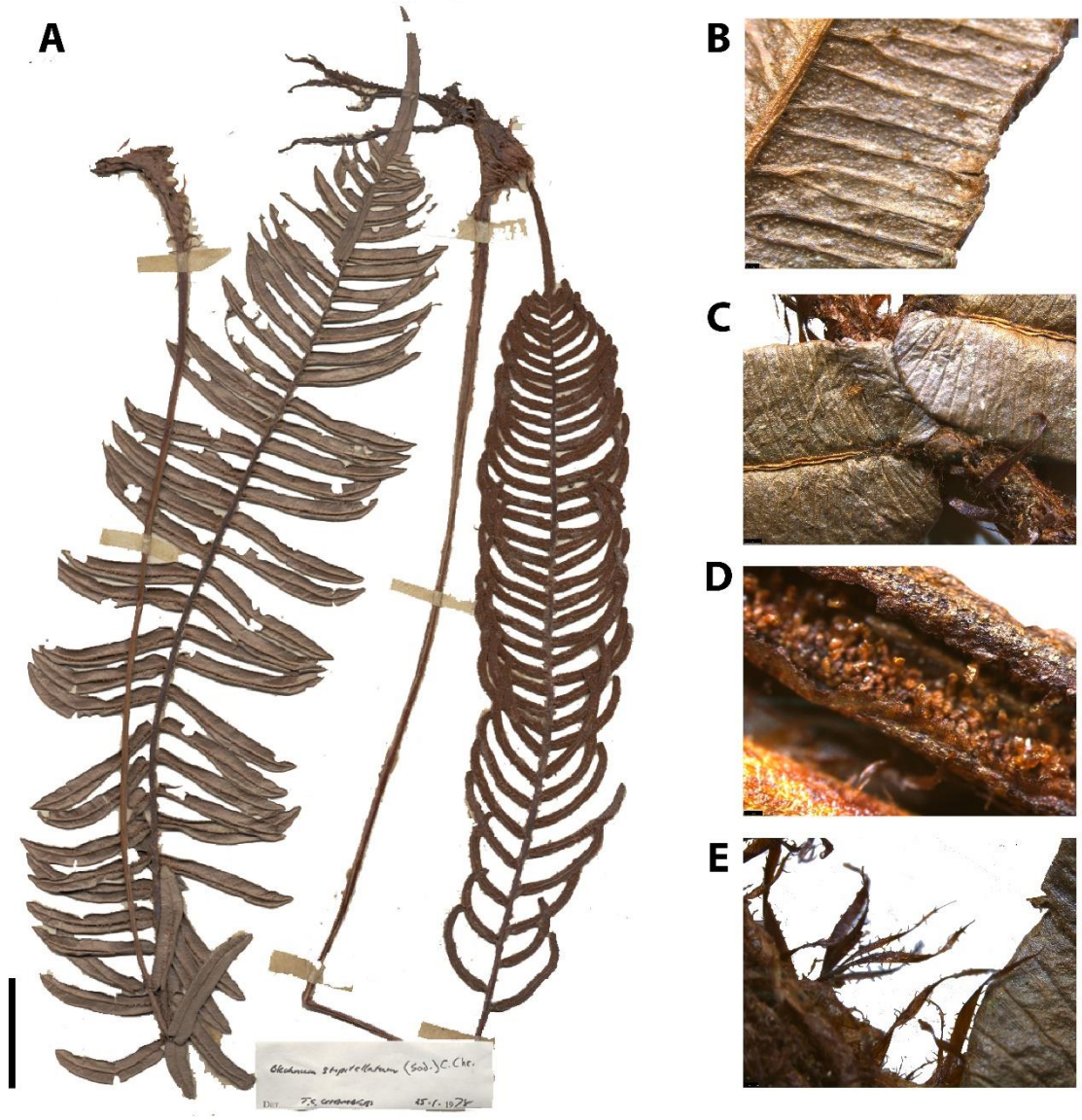

Figure 84. *Parablechnum stipitellatum.* A Sterile (left) and fertile (right) fronds; B. Sterile pinna margin, abaxial side; C. Sterile pinnae bases, adaxial side; D. Fertile pinna surface, abaxial side; E. Rachis scales. (A: *no collector 5328*, K000006845; B-F: *Bro Daniel 672*, US1592401). 4 cm in A,2.5 mm in B, 5 mm in C, 1.5 mm in D, 2 mm in E.

Reviewed material:

BOLIVIA. Dept. La Paz: Unduavi, Nord yungas, *Buchtien 2691* (UC477679! photo); Juan Bautista Saavedra, 15 km de Charazani hacia Chullina, *Kessler et al. 10629* (UC1621922! photo). **COLOMBIA. Dept. Antioquia:** Chocó–Antioquia, at and on both sides of the principal ridge W of La Mansa, at ca. Km. 105.5 of the Ciudad Bolivar–

Quibdo Road, *D.B. Lellinger & E.R. de la Sota 949,* 4 April 1971 (US2723497!; US2723498!; US272399!); Cordillera Central, *E. Mayor 142,* 8 August 1910 (US1197142!); Cordillera Central, 25 km n. Sonson, Rio Buey drainage basin, w. of Cerro de los Parados, *J.A. Ewan 15698,* 22 May 1944 (US2254137!); Laguna de Juarez, *Bro. Daniel 672,* 27 September 1935 (US1592401!); La Sierra, 18 kilometers north of Medellín, *W.A. Archer 1541,* January 1931 (US1544668!); Medellín, *Bro. Henri-Stanislas 1694,* July 1915 (US1044754!); Mpio. Belmira, Vereda La Salazar (parte baja), quebrada el Diablo, *W. Rodríquez & M. Arboleda 3442,* 20 June 2002 (NY!); Santa Elena, *W.A. Archer 1219,* 1 January 1931 (US1544649!); vicinity of Medellín, *S.J. sn.n,* 1911 (US0602754!); *ibidem* (US0602755!); *ibidem, S.J. 37,* 1911 (US0602792!). **Dept. Boyacá:** *R. Jaramillo Mejía et al. 2784*, 28 August 1967 (MA379749!); *R. Jaramillo Mejía et al. 2943* (MA380798!). **Dept. Caldas:** Mpio. de Caldas, Vereda La Corrala, Finza "La Zarza", al lado del camino sombreado en área de Axinea, *L.A. de Escobar et al 5568,* 12 August 1985 (NY!). **Dept. Chocó:** Mun. San José del Palmar, Cerro del Torrá, vertiente oriental, *P.A. Silverstone Sopkin et al 4518,* 17 August 1988 (UC1565479! Photo). **Dept. Cundinamarca:** Bogotá, *Apollinaire s.n.,* 1 April 1905 (P01546433!); *ibidem*, 05.1906 (P01546431!); entre Zipaquirá y Pacho, Páramo Guerrero, *M.T. Murillo & M. Villarreal 1358,* 9 June 1970 (MA228370!). **Dept. El Valle:** Chocó–El Valle, at and on both sides of the principal ridfe of the Serranía de Los Paraguas, along the trail from El Cairo to Río Blanco, ca. 8 km SW of El Cairo, *D.B. Lellinger & E.R. de la Sota 864*, 28 March 1971 (US2723503!). **Dept. Huila:** Comisaría del Caquetá, Cordillera Oriental sobre el filo divisorio, en Gabinete, *J. Cuatrecasas 8408,* 21 March 1940 (US1850664!); Cordillera Oriental, 15-20 km SE of Garzón, *E.L. Little Jr. 9405,* 7 February 1945 (US2420560!; US2420569!; US2420570!); Cordillera Oriental, Caquetá side of Huila-Caquetá divide, 20 km SE of Garzón, *E.L. Little Jr. 9388,* 6 February 1945 (US2419440!; US2419444!; US2419445!). **Dept. Nariño:** Ceja de Mayasquer, *Stübel 347*, 1934 (B200033183!, holotype of *Blechnum rubicundum*); Cordillera Oriental, Río Chingual at San José, below La Victoria, *J.A. Ewan 16207,* 25 September 1944 (US2254255!). **Dept. Tolima:** Andes, Cordillera Central, Vert. SE del Tolina en las Mesetas, *J. Cuatrecasas 2067,* 15 May 1932 (MA213338!). **Unknown Department:** *B.T. 467,* no date (NY!); *S.J. s.n.,* no date (NY!). **ECUADOR. Prov. Canar:** Inganilla Pass on Pan-American Highway between Cañar and Biblian, *L. Holm-Nielsen et al 29003*, 12 December 1980 (NY!; UC1535914! Photo). **Prov. Carchi:** about 1/2 hr. E of Huaca, past

Colonia Huaceña, *H. van der Werff & W. Palacios 10632,* 18 February 1989 (NY!); Espejo, Reserva Ecológica El Ángel, El Gritadero, *W. Palacios 11724*, 1 November 1993 (UC1742409! Photo); road Tulcán-Maldonado, 53 km from Tulcán., *B. Ollgaard & H. Balslev 8263,* 31 July 1976 (NY!); Valle de Maldonado, km 53 on the road Tulcán-Maldonado, *L. Holm-Nielsen et al 6251,* 22 May 1973 (UC1477915! Photo); Tulcan, camino Tufiño, aguas Hediondas en la base del volcán Chiles, *W. Palacios 11820,* 8 November 1993 (UC1744490! Photo). **Prov. Chimborazo:** Parque Nacional Sangay, Carretera Chambo-Pungalá, junto al río Alao, *R. Valencia 106,* 9 August 1987 (NY!). **Prov. Loja:** Yangana, Yangana-Valla Rd. 11 km S. of Yangana., *M.R. McCarthy & E. Tepe 249,* 31 July 2011 (NY!). **Prov. Napo:** Llanganati, steep slope along Río Topo, inmediately SE of Aucacocha, *B. Ollgaard & L. Holm-Nielsen 38772,* 18 May 1982 (UC1535836! Photo); road Olmedo-Laguna San Marcos, E of the pass, *B. Ollgaard et al 34432,* 10-11 July 1980 (UC1539134! Photo). **Prov. Pichincha:** Atacazo, *L. Mille s.n.*, 1917 (P01462403!); Quito, Corazon y Atacazo, *Sodiro s.n.*, 07.1882 (P00627643!, syntype; P00627644!, syntype; P00627645!, syntype; P00627646!, syntype); in silv. M. Corazón et Atacazo, *A. Mille 160,* no date (US1120471!); in Sylvis subland occidentalibus, in olectiv mts. Atacazo, *A. Mille s.n.*, 1917 (US1192046!); Salvador, about 25 kms. West of Quito, *P.R. Bell 658,* 25 April 1951 (UC1085354! Photo). **Prov. Tungurahua:** Andes Quitenses, *Spruce 5328,* no date (P01546366!; P01546368!); Baños Canton. On trail south from 'La Cruz', above and south-east of town of Baños, *A. Fay & L. Fay 3528,* 4 July 1992 (NY!; UC1597660! Photo). **Prov. Zamora-Chinchipe:** Chinchipe, P.N. Podocarpus, along new Loja-Zanira rd., 4 km E of the pass "El Tiro", *M. Sundue 1150,* 15 December 2006 (NY!, 2 sheets; US3520553!); Estación Científica San Francisco, above refuge, along trail "Antennenbergweg", just below junction with trail T1, *M. Lehnert 922,* 26 September 2003 (UC1791920! Photo); Parque Nacional Podocarpus, plot C7 (AG Gradstein FOR 402), Quebrada Los Lumos, *M. Lehnert 2340,* 7 January 2011 (VT198727!); road between Loja & Zamora ca. 16-18 km, *J.L. Luteyn et al 6611,* 21 December 1978 (NY!). **Unknown province:** *A. Mille S.J. s.n.*, 1917 (NY!); *A. Sodiro s.n.*, 1857 (TCD0009468! Photo); *ibidem,* 1887 (UC678371! Photo); *S.A. Sodiro 87903,* 5 November 1920 (P01466401!); *Spruce 532d,* 1857 (P01546363!); Andibus, *R. Spruce 5320,* 1857-9 (NY!, 2 sheets). **PERU. Dept. Amazons:** near the border with Dept. San Martin, *H. van der Werff et al. 16635,* 3 April 2001 (UC1778093! Photo). **Dept. Cajamarca:** Dist. San José de Lourdes, Loc. De Buenos Aires (Cerro El

Parco), Cajamarca, San Ignacio, *R. Bonino 235*, February 2002 (NY!); San Ignacio, Cerro Coyona, Santuario Nacional Tabaconas namaballe, *J. Campos et al 5808*, 21 November 2998 (UC1763244! Photo); San José de Lourdes, Picorana, *J. Campos et al. 5579*, 18 August 1998 (NY!). **Dept. Pasco:** Dist. Oxapampa, Río San Alberto, Abra Esperanza, *R. Foster et al 10304*, 28 June 1985 (US3221253!). **Unknown Department:** *Dombey 50*, no date (P01462408!). **VENEZUELA. Bolivar:** Gran Sabana, alrededores del Salto del Aponguao, 42.5 kms al noreste de la Misión de Santa Teresita de Kavanayén, *J.A. Steyermark et al 115580*, 22 February 1978 (UC1480966! Photo). **AMERICA. Unknown location:** *ex herbarium Lehmannianum, BT467*, no date (US1424452!).

Parablechnum stuebelii (Hieron.) Gasper & Salino, Phytotaxa 275(3): 217. 2016.

Basionym – *Blechnum stuebelii* Hieron., Hedwigia 47: 241, pl. 4, fig. 14. 1908, sub. "*stübelii*".

Type – Colombia. Cundinamarca: Excursion nach den Llanos de San Martín, Páramo de Guasca Gegend), *M.A. Stübel 717*, 1934 (lectotype: B200034236!, designated by Dittrich *et al.*, 2017).

Description – *plants* terrestrial; *rhizomes* creeping, ascending or semi–erect, entirely covered with concolorous or faintly discoloured scales, with darker bases and centres, margins straw-coloured or light brown, basifixed or nearly so, atropurpureous at attachment point, lanceolate to ovate–lanceolate with caudate apex, 8–10 × 1–2.5 mm, margins entire or nearly so, often slightly setose at base, setae 0,1 mm; *fronds* monomorphic or subdimorphic; *sterile fronds* 1–8 × 15–45 cm; *petioles* atropurpureous, shiny, flattened or slightly grooved adaxially, rugulose ornamentation, 3–10 × 0.2–0.4 cm, 1/3 to about equal to or slightly longer than lamina length, with persistent ascending scales, scales of two types, larger, entire or subentire or slightly setose towards the base, similar to those of the rhizome but lighter brown, and smaller, lanceolate, brownish, usually conspicuously setose at the margins, 0.1–0.3 mm long, all scales, especially the small ones, often pectinate or irregularly ciliate basally; *laminae* very thick, coriaceous, 10–30 × 2.5–5.5 cm, alternate to subopposite, lanceolate, 1-pinnate, more or less truncate at base, lamina apices gradually attenuate, with a terminal pinna elongate, lanceolate, ca. 2–4 × 0.5 cm. 2–4 × 0.5 cm; *rachis* atropurpureous, ornamentation similar to petiole,

adaxially grooved, scaly, scales 5–10 mm, with some smaller ones below the larger ones, scales gradually decreasing in size distally; *sterile pinnae* in 18–25 pairs, 1.2–3 × 0.3–0.6 cm, shortly petiolate, bases subcordate, apices rounded, margins very strongly revolute, *costa* grooved adaxially, prominent abaxially, scaly on both surfaces, scales mostly 2–5 mm, distinctly setose at margins; *veins* free, simple or 1-furcate, with scales similar to those of costa, catadromous; *aerophores* blackish, tuberculiform; *fertile pinnae* very similar to sterile ones but slightly longer, *sori* linear, continuous, forming coenosori on both sides of costa, often hidden by scales; *indusia* linear, continuous, opening towards the costa, dark brown, glabrous, strongly lacerate or strongly dentate, at least at maturity, teeth often blackish; *sporangia* with (24–)26(–31) arc cells; *spores* monolete, (47–)57(–69) × (34–)44(–54) µm; perispores smooth, cristate-reticulate, with low, thick walls, forming large polygonal areoles, with very abundant long filamentous processes on the entire spore surface (**Figure 85**).

References – Hieronymus (1908), Dittrich *et al.* (2017).

Chromosome number – unknown.

Distribution and habitat – Colombia, Ecuador, and Venezuela. This species grows on steep rocky slopes, in open paramo vegetation, in primary montane forest and scrub vegetation, and on low forest ridges (up to 4 m), at 2400–2850 m (Dittrich *et al*., 2017).

Etymology – the epithet refers to A. Stübel (1835–1904), collector of the plants that Hieronymus, the descriptor of the species, selected as type material.

Notes – Hieronymus (1908) described this species (sub. *Blechnum stübelii*), citing five syntypes from Colombia and one from Ecuador. In the opinion of Dittrich e*t al*. (2017), these represent at least two (if not more) different species. The only syntype with rhizome is *Stübel 717* (B200034236). In the original description, Hieronymus described the rhizome and rhizome scales of this species, being congruent with what they saw in Peruvian and Ecuadorian plants – long creeping (fronds arising at 1–8 cm intervals) or ascending and densely scaled rhizomes. Since *Stübel 717* is the most complete specimen, and the only one with a rhizome, it was chosen for lectotypification of the species. The identification of the other five syntypes is unclear and may be difficult to ascribe because of their incompleteness (no rhizomes or rhizome scales). In fact, Hieronymus relied on

these rhizome-less specimens heavily (and perhaps primarily) in issuing his description of the fronds of *Blechnum stübelii*. What is clear is that these five syntypes include one or several additional *Parablechnum* species other than *P. stuebelii*. On the basis that Hieronymus' description was based on multiple taxa, Dittrich *et al*. (2017) redescribed and illustrated it based on specimens seen from Peru and Ecuador.

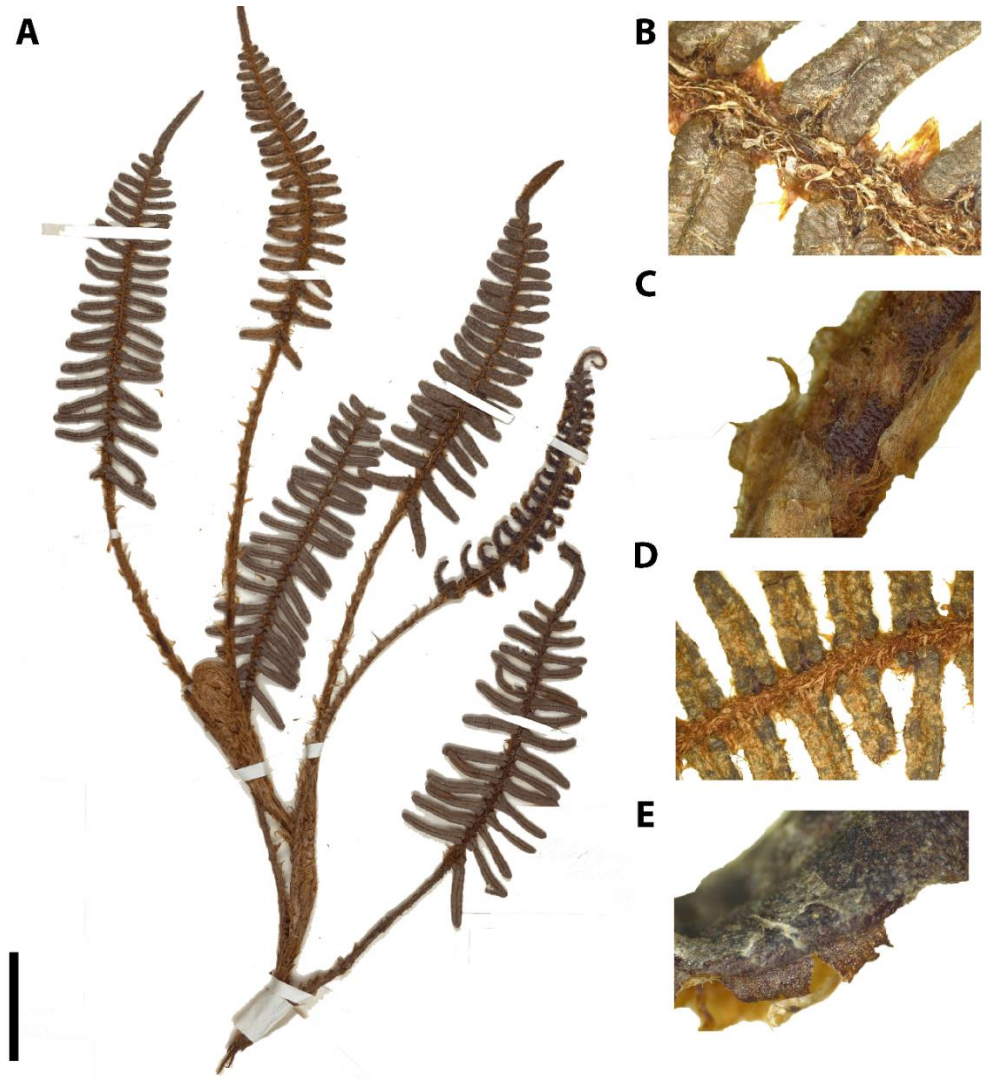

Figure 85. *Parablechnum stuebelii.* A. Plant; B. Sterile pinnae bases, adaxial side; C. Petiole; D. Fertile pinnae, adaxial side; E. Fertile pinnae. (A-E: *Stübel 717*, B200034236, lectotype). 4 cm in A, 5 mm in B, 2 mm in C, 8.5 mm in D, 1.7 mm in E.

Parablechnum stuebelii appears to be related to *P. loxense*, common in paramo vegetation from Costa Rica to Bolivia, as was also acknowledged by Hieronymus (1908). The lectotype is, in fact, the only one of the three syntypes in which paramo vegetation is clearly indicated as the habitat of the specimen. *Parablechnum loxense*, although scalier than most other *Parablechnum* species, is less scaly than *P. stuebelii*, and also differs in

having trunks up to 1 m high. Dittrich *et al*. (2017) also note that the level of dimorphism is higher in *P. loxense*, but this could be a confusing character as this species is often practically monomorphic, just like *P. stuebelii*. They also differ in the rhizome, *P. stuebelii* having more or less creeping rhizomes, while *P. loxense* forms erect trunks. A more distant relative may be *P. stipitellatum*, which grows from Colombia to Bolivia. It shares with *P. stuebelii* a very leathery laminae with revolute pinnae, with serrated scales on rachises and costae, but differs in the much larger fronds, with much stronger dimorphism, attenuated pinnae tips, serrulate margins and generally darker and dentate petiole and rhizome scales.

After reviewing the sheet from which the spores were observed in Passarelli *et al*. (2010) (MA610969) it has been concluded that this specimen does not correspond to *P. stuebelii*, so the description of the spores presented in this paper is not ascribable to this species. The identification of the specimen is uncertain, and it is possible that it is an undescribed taxon. Dittrich *et al*. (2017) note that the spores and sporangia of *P. stuebelii* appear unusually large, reaching 0.1 mm, which together with sporangia with a high number of cells in the arc (> 30) could suggest that it is a polyploid.

Reviewed material:

COLOMBIA. Dept. Cauca: Mount el Derrumbo, cordillera occidental, *F.W. Pennell 7505*, 29 June 1922 (NY04187105!). **Dept. Meta:** Llanos de San Martín, Páramo de Guasca Gegend, *Stübel 717*, 1934 (B200034236!, lectotype). **PERU. Dept. Pasco:** Oxapampa, Chacos, *H. van der Werff et al 23230*, 6 November 2009 (NY02715793!); Oxapampa, road to Chacos, *H. van der Werff et al 18523*, 17 July 2003 (NY04187106!).

Parablechnum subcordatum (E.Fourn.) Gasper & Salino, Phytotaxa 275(3): 217. 2016.

Basionym – *Lomaria subcordata* E.Fourn., Ann. Sci. Nat. Bot., sér. 5, 18: 316. 1873.

Type – New Caledonia, *Balansa 37*, Ferme modèle (P00627677!).

Synonyms –

≡*Blechnum subcordatum* (E.Fourn.) Brownlie, Fl. Nouv.–Calédonie & Dépend. 3: 248, t. 32, f. 1–2. 1969.

Description – *plants* terrestrial; *rhizome* erect, sometimes forming a trunk, with the upper part covered with brown linear scales; *fronds* dimorphic; *sterile fronds* with *petioles* close together, reaching 60 cm in length, finely rugulose ornamentation, with a base with scales similar to those of the rhizome, very rigid, resembling thorns, becoming glabrescent distally; *laminae* 30–40 × 10–30 cm, 1-pinnate, oblique, base truncate, apex ending in a conform pinna; *rachis* with some reddish brown scales; *sterile pinnae* in 5–15 pairs, glabrous, coriaceous, shortly stalked, alternate or suboposite, sometimes becoming adnate basiscopically towards the apex, oblique, linear, 12 × 1.5 cm, apex subacute, base rounded, subcordate, sometimes overlapping the rachis, margin finely serrulate, terminal pinna stalked, with unequal bases, not subcordate; *veins* free, simple or 1-furcate, catadromous; *aerophores* axillary, elongate, low, tuberculiform, dark; *hydathodes* ovoid; *fertile fronds* slightly longer and more erect; *petiole* similar to sterile; *lamina* 1-pinnate, lanceolate; *fertile pinnae* linear, apex acuminate and base subcordate, as long as sterile or longer, up to 0.3 cm wide, basal portion of pinnae sterile by about 1 cm, at least the most proximal; *sori* linear, continuous, forming coenosori on both sides of costa, covering pinna completely except basal sterile portion and part of apex; *indusia* linear, continuous, open towards costa, brownish, continuous or somewhat lacerate at maturity; *sporangia* with (17–)19(–20) arc cells; *spores* monolete, (52–)62(–74) × (38–)47(–62) µm; perispores smooth, cristate-reticulate, with low, thin walls, forming medium to large polygonal areoles, with moderately abundant long filamentous processes in areole lacunae (**Figure 86**).

References – Brownlie (1969).

Chromosome number – unknown.

Distribution and habitat – endemic to New Caledonia. Abundant in bush and forest edge, in full sunlight, at about 1000 m and above. This species seems to have spread in parallel with the deforestation (Brownlie, 1969).

Etymology– the epithet refers to the subcordate bases of the pinnae, a character that distinguishes this species from the rest of the New Caledonian *Parablechnum*.

Notes – the type specimen is a small plant with the apex of the pinnae more rounded than in more developed specimens but shows the typical subcordate base and pinnae overlapping the petiole, especially in the fertile frond (Brownlie, 1969).

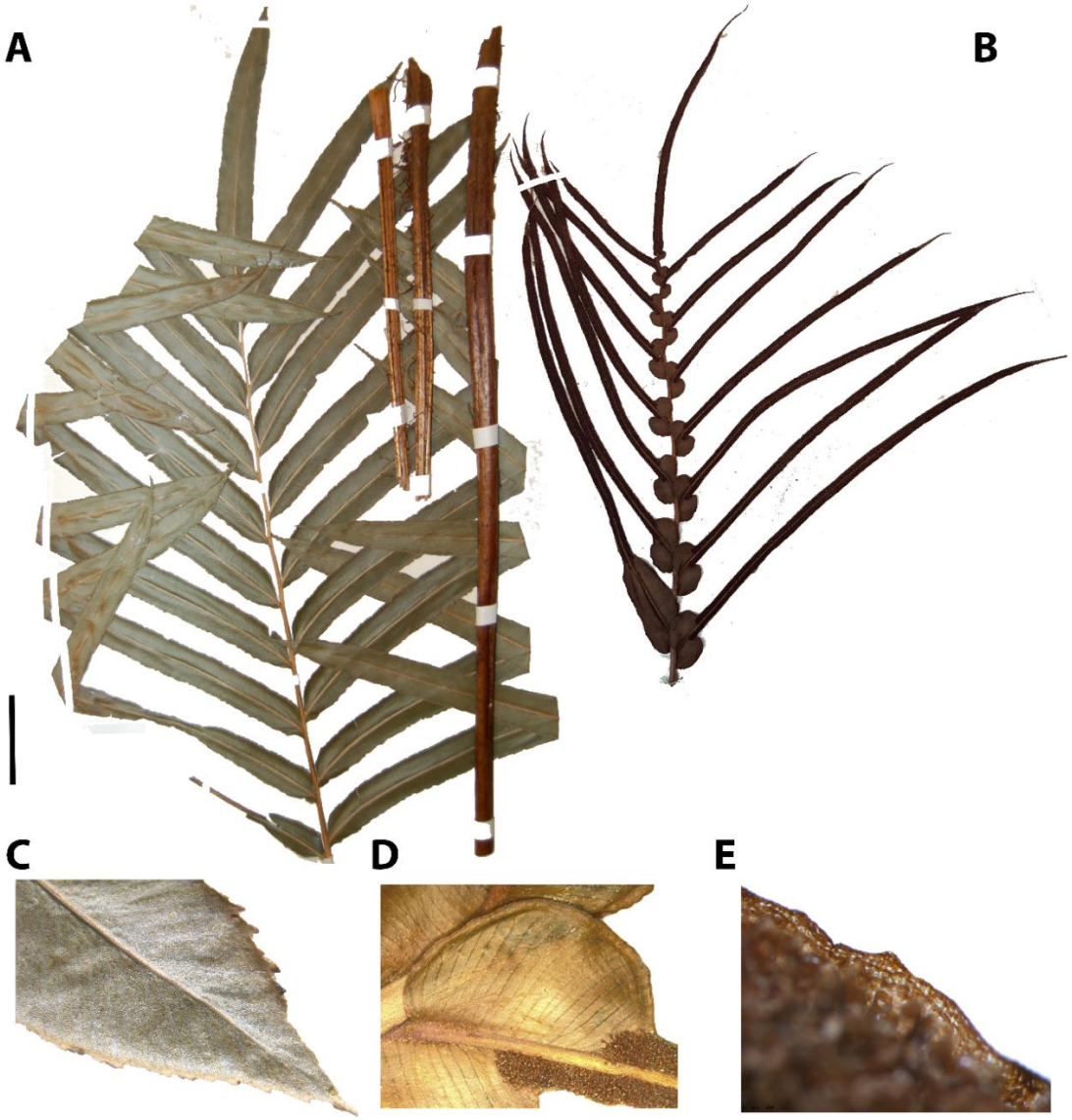

Figure 86. *Parablechnum subcordatum.* A. Sterile frond fragment; B. Fertile frond fragment; C. Sterile pinnae apex, adaxial side; D. Fertile pinnae bases, abaxial side; E. Indusium. (A: *J.-C. Pintaud 380*, UC1614696; B & D: *G. McPherson & J. Munzinger 18139*, MO5307448; C: *J.T. Buchholz 1056*, US2082412; E: *J.T. Buchholz 1346*, US2082441). 5 cm in A & B, 3.5 mm in C, 7 mm in D, 775 µm.

Reviewed material:

NEW CALEDONIA. Nord Province: Massif de Tchingou, *G. McPherson & J. Munzinger 18139*, 3 April 2001 (MO5307448!; MO5307449!; MO5307450!; P01558330!); Massif de Tchingou, Face East, *G. Munzinger & G. McPherson 631*, 2 April 2001 (MO5570071!; MO5570072!; MO5570073!; P00275266!; P00217101!;

P00275267!); Mt. Paéoua, contrebas du pic, *J.M. Veillon 6096*, 16 October 1986 (P01573188!); Négropo, Ouen Kono, *H.S. MacKee 23868*, 28 June 1971 (P01213097!; P01213098!; P01213099!). **Sud Province:** 22 km Station (railway distance from Pirogue bay), Plaine des Lacs, *J.T. Buchholz 1346*, 4 November 1947 (US2082441!); Baie des Pirogues, *C.T. White 2263*, 31 October 1923 (P01534953!); Basse Vallee de Thio, *H.S. MacKee 15445*, 6 August 1966 (P01576218!; P01576219!; P01558328!; P01558329!); Circ. Paita, W slopes of Mt. Ouin, *G.L. Webster & R. Hildreth 14612*, 7 August 1968 (P01468123!); Foret de Sailles, *J. Muzinger et al 1191*, 4 December 2001 (P00239188!; P01558331!; P01558332!; P01558333!); Houte Ouinne, *H.S. MacKee 11816*, 6 December 1964 (P01558324!; P01576220!; P01576221!); Ilê-des-pins, Plateau, marais du font d'Avignon, *R. Germain s.n.*, 1874-1876 (US0483250!); Mareeages, Prony, *I. Franc 115*, 05.1906 (NY!; P01467836!; P01467837!; P01467838!; P01467839!; P01557785!); Massiff de Ton–Ton, *H.S. MacKee 18528*, 21 March 1968 (P01579204!); *ibidem, H.S. MacKee 196*, 21 March 1968 (P01573164!; P01573165!; P01573166!); Messioncomé, pres du Port–Bouquet, *B. Balansa 1585*, 28 September 1869 (P01534946!); Mont Humboldt, *B. Balansa 1583*, 12 October 1869 (P01534945!); Mont Humboldt, *F. Sarasin 163*, 18 September 1911 (P01467829!; P01467830!); Mont Humboldt, pente Nord–Ouest, *J.M. Veillon 7682*, 8 June 1993 (P01576217!); Mont. Koghi, *Franc 90*, 1911 (P01468156!); Mont Mou, *B. Balansa 2717*, 03.1870 (P01534947!; P01558338!; P01558339!); Mont Mou, *H.S. MacKee 2290*, 27 March 1955 (P01323909!); Mont Mou, *M.G. Baumann–Bodenheim 5585*, 22 August 1950 (P01558334!; US2425923! US2425924!; US2425928!); Mont Mou, *M.G. Baumann–Bodenheim 5652*, 23 August 1950 (P01558337!; US2425967!); Plume, *M. Baumann 5585*, 22 August 1950 (NY!); Prony, *I. Franc 115*, April 1918 (US1273183!); Riviere Blanche, *A. Guillaumin & M.G. Baumann–Bodenheim 13963*, 22 June 1951 (P01558340!); Riviere Blanche, *M.G. Baumann–Bodenheim 14287*, 25 June 1951 (P01558336!; US2425968!); Riviere Bleue, *A. Guillaumin & M.G. Baumann–Bodenheim 10885*, 22 February 1951 (P01558341!; US2082441!); Rivière Bleue Provincial Park, *J.-C. Pintaud 380*, 1 August 1996 (UC1614694! Photo; UC1614695! Photo; UC1614696! Photo); road leading toward Plume, at SW slope of Mt Dore, *J.T. Bucolz 1056*, 17 September 1947 (P01468146!); Thio, *J.T. Buchholz 1035*, 15 September 1947 (P01468148!); Thy River valley, a 12 air–km NE of Nouméa, G. McPherson 1659, 21 May 1979 (P01618028!). **Unknown area:** *B. Balansa 37*, 11.1870 (P00627677!,

holotype); *Brousmiche s.n.,* 15 August 1881 (P01558327!); *E. Vieillard s.n.,* 1865 (P01573172!); *E. Vieillard 1522*, 1863 (P01468141!); *J. Pancher s.n.,* no date (P01558325!); *ibidem* (P01558326!); *ibidem* (P01619972!); *ibidem*, 1870 (P01534935!); *J. Pancher 671*, no date (P01619973!); *J.T. Buchholz 1056*, no date (NY!; US2082411!; US2082412!); *M.G. Baumann–Bodenheim & A. Guillaumin 8771*, 28 November 1950 (P01558335!).

Parablechnum triangularifolium (T.C.Chambers & P.A.Farrant) Gasper & Salino, Phytotaxa 275(3): 217. 2016 .

Basionym – *Blechnum triangularifoliu*m T.C.Chambers & P.A.Farrant, New Zealand J. Bot. 36: 14. 1998.

Type – New Zealand, Green Bay, Manukau Harbour, *T. C. Chambers s.n.*, Apr 1961, (syntypes: AK232046–49! photo; isotypes: NSW405685! Photo, NSW405688! Photo).

Synonyms –

=*Lomaria capense var. carsi* Dobbie, New Zealand Ferns ed. 3, 222, f. 76c. 1931. [as *L. australis* var. *carsi* changed in errata to *L. capense* var. *carsi*]. Type: New Zealand, Manukau Harbour, *no collector*, no date (holotype: ex icon pl. 76c).

Vernacular names – green bay kiokio (Chambers & Farrant, 1998a).

Description – *plants* terrestrial; *rhizome* shortly creeping to erect, covered with the bases of old petioles and scales 10–13 × 0.5–2 mm, lanceolate, acuminate, light brown, reddish brown or sometimes discoloured, entire or slightly toothed; *fronds* dimorphic; *sterile fronds* usually pendulous, 20–192 × 9–55 cm, broadest at base of lamina; *petioles* straw to light brown, darkening only proximally, 6.5–108 cm, scaly especially at base, distal portion almost glabrous at maturity, scales up to 10 × 1–1.5 mm, ovate, cordate or linear, acuminate, often appressed, concolorous brown or with a distinct central black spot, shiny, entire or finely toothed; *lamina* broadly deltoid, pale green, 1-pinnate; *rachis* light brown or reddish brown, grooved adaxially, with sparse to moderately dense scales and a few small, fine, irregular hairs, scales up to 3 mm long, 1.5 mm wide, ovate to cordate, peltate, appressed, shortly acuminate, shiny and discoloured with a central black spot, entire or finely toothed, also some larger scales, up to 10 × 1 mm, narrow, linear, acuminate, twisted, concolorous light brown or reddish brown, entire or finely toothed;

sterile pinnae in 6–34 pairs, 7–28 × 1, 4–2 cm, lanceolate, slightly falcate, acuminate to attenuate at the apices, rounded at the base, shortly stalked, sometimes basoscopically adnate at the base of the lamina and completely adnate towards the apex, coriaceous to papyrose, margins finely serrate, often crenulate or wavy, terminal pinna usually slightly longer than subterminal, basal pinnae slightly longer or similar to upper pair of pinnae and longer than middle pinnae, sometimes deflexed; *costae* rachis-like, grooved adaxially, prominent abaxially, especially scaly on abaxial side; *veins* free, simple or 1-furcate, catadromous; *aerophores* not present; *hydathodes* patent, ovoid; *fertile fronds* smaller than sterile ones; *petioles* 10–123 cm, similar in length or longer than those of sterile ones; *fertile pinnae* 11–24 × 0.2–0.6 cm, narrow, linear, shortly stalked at base becoming basiscopically adnate or completely adnate towards apex; *sori* linear, continuous, forming coenosori on both sides of costa, covering the lower part of the pinna except for attenuated sterile apices and small sterile lobes appearing at the base of the lower pairs of pinnae in some specimens; *indusia* linear, continuous, opening towards costa, brownish; *sporangia* with (12–)16(–20) arch cells; *spores* monolete, flat-convex in equatorial view, elliptic in polar view, (46–)55(–64) × (29–)40(–50) µm, perispores narrowly reticulate with rounded lower walls, smooth to granular in areolar lacunae, exospores smooth granular (**Figure 87**).

References – Chambers & Farrant (1998a), Brownsey & Perrie (2021).

Chromosome number – 2n = 56 (Chambers & Farrant, 1998a; Dawson *et al*., 2000).

Distribution and habitat – endemic to New Zealand, throughout the North Island from Te Paki to Wellington, but rare north of Auckland and in the Bay of Plenty. Occurs in lowland and coastal areas, reaching 750 m near Mangaweka. It also occurs in low–lying and coastal areas throughout the South Island, but is rare in southern Canterbury, Otago and Southland, reaching 300 m in the Awatere Valley. It is also widespread on Chatham and Stewart Islands. In exposed areas, forest margins, coastal habitats, dry slopes, roadside slopes, riverbanks, cliffs, rock faces and in dune areas. (Chambers & Farrant, 1998a; Brownsey & Perrie, 2021).

Etymology – the specific epithet probably refers to the deltoid shape of the lamina.

Notes – this species is similar to other species of *Parablechnum* occurring in New Zealand. It is distinguished by the non–reduced basal pinnae (unlike *P. minus* and *P. novae-zelandiae*). It is also larger than *P. procerum*, with falcate pinnae (vs. straight in *P. procerum*). *Parablechnum montanum* differs in having a wider sterile lamina with more pairs of pinnae and *P. triangularifolium* is a lowland species whereas *P. montanum* is a montane or subalpine species.

Figure 87. *Parablechnum triangularifolium.* A. Sterile frond; B. Fertile frond fragment; C. Sterile pinna apex, adaxial side; D. Sterile pinna margin, adaxial side; E. Sterile pinna base, adaxial side; F. Sterile pinna costa, abaxial side; G. Indusium. (A, E & F: *M. Howard 4120,* VT198735; B & G: *M. Howard 4120,* VT198736; C & D: *M. Howard 4095,* VT198734). 4 cm in A & B, 6.5 cm in C, 2 mm in D, 6.5 mm in E, 3 mm in F. 1 mm in G.

Reviewed material:

NEW ZEALAND. North Island: Green Bay, Manukau Harbour, *T. C. Chambers s.n.*, Apr 1961, (AK232046! Photo, syntype; AK232047! Photo, syntype; AK232048! Photo, syntype; AK232049! Photo, syntype; NSW405685! Photo, isotype; NSW405688! Photo, isotype). **South Island:** Greymouth, *R. Helms s.n.*, no date (P01463056!); Leith Saddle, Dunedin, *M. Howard 4095*, 2 November 1978 (VT198734!); Tautuku, *M. Howard 4120*, 5 November 1978 (VT198735!; VT198736!).

Parablechnum tuerckheimii (Brause) Gasper & Salino, Phytotaxa 275(3): 217. 2016.

Basionym – *Blechnum tuerckheimii* Brause, Symb. Antill. 7(1): 159. 1911.

Type – Dominican Republic, Hab. In Sto. Domingo prope Constanza 1200 m. alt. in paludibus sylvaticis, *H. v. Türckheim n. 2976*, m. Febr. 1910 (holotype: K000633394! photo; isotypes: BM000769815! Photo; E00417618! Photo; GH00020671! Photo; NY00127312!; P00627650!; U0007277! Photo; US00067452!).

Description – *plants* terrestrial; *fronds* dimorphic; *sterile fronds* ca 92 cm, *petiole* upt to 25 cm, pale brown to brown, with daker spots, ribbed, scaly, scales ferruginious, ciliate, forming a dense tomentum, mixed with smaller scales, long acuminate, entire; *lamina* 1-pinnate, laceolate, conform apex, up to 58 × 12.4 cm; *rachis* similar to the petiole but more scaly; *pinnae* in about 58 pairs, patent, alternate to subopposite, falcate-linear, acute apex, stalked to substalked, entire but more serrate at the apex, margins revolute; *costa* similar to the rachis; *veins* free, simple or 1-furkated, catadromous; *aerophores* axillar, tuberculiform, dark; *fertile fronds* longer than the sterile, *petiole* ca. 37 cm; *lamina* ca 60 × 20 cm; *sori* continuous, linear, forming coenosori on both sides of the costa; *insusium* linear, continuous, margin repand, open towards the costa; *sporangia* with 20–23 arch cells; *spores* monolete, (51–)61(–69) × (35–)46(–53) µm; perispore smooth, cristate-reticulate, with very low, thin walls, forming very large polygonal areoles, with moderately abundant long filamentous processes (**Figure 88**).

References – Rolleri *et al.* (2012a).

Chromosome number – unknown.

Distribution and habitat – this species can be found in Hispaniola and Puerto Rico. Terrestrial in marshy areas, it is occasional or locally common in upper elevation forest in wet areas with rocky soils. (Maxon, 1924; Howard, 1950; Testo, pers. com.).

Etymology – this species honours H. von Türckheim (1853–1920), collector of the type specimen.

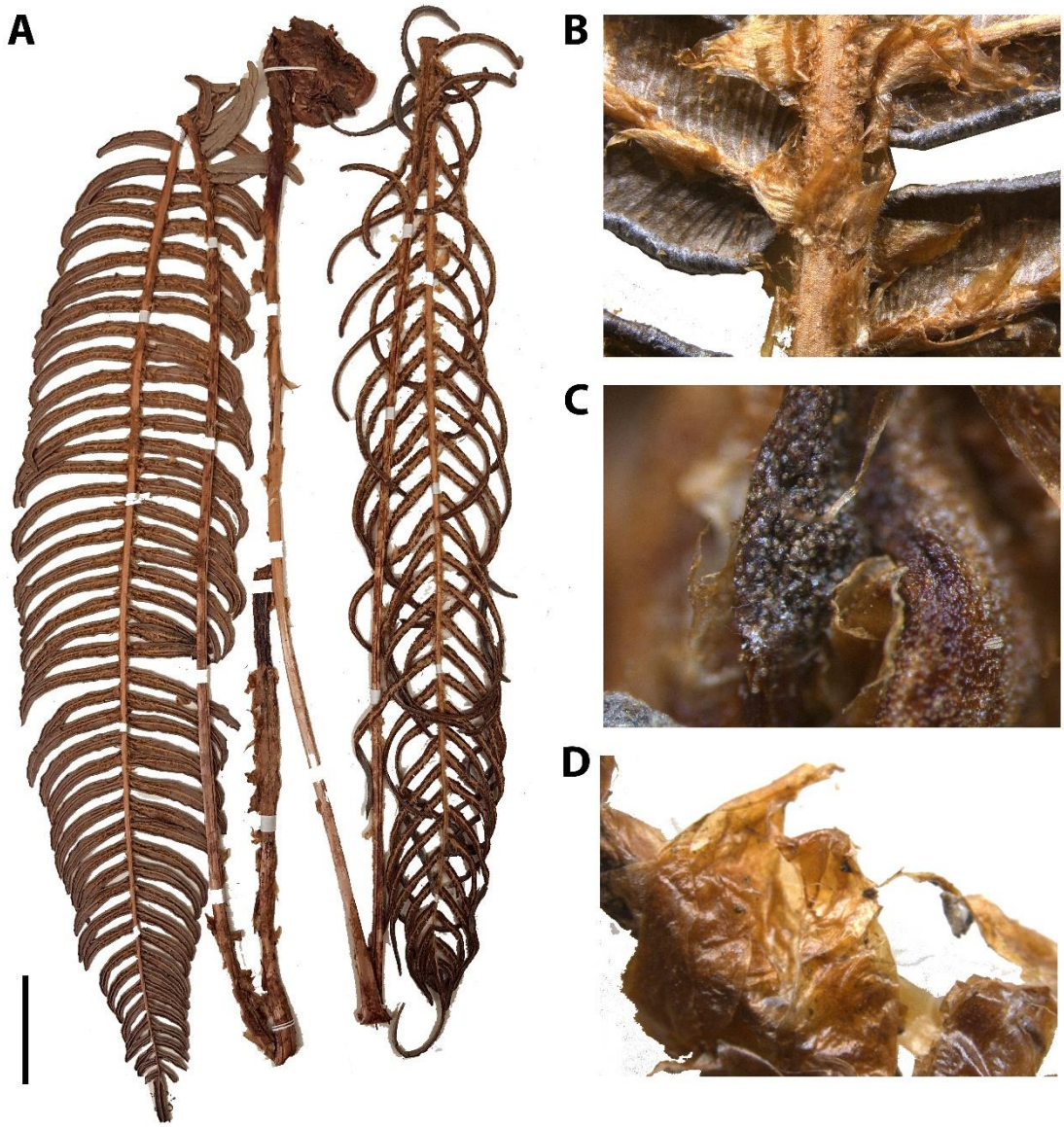

Figure 88. *Parablechnum tuerckheimii*. A. Sterile (left) and fertile (right); B. Sterile pinnae bases, abaxial side; C. Aerophore; D. Rhizome scales. (A: *E.L. Ekman 1496*, US1559827; B-D: *E.C. Leonard 3945*, US1076291). 4 cm in A, 3.5 mm in B & D, 1 mm in C.

Notes – this species is similar to *Parablechnum lechleri* but differs in having straw colored petiole (vs. atropurpureous in *P. lechleri*) and in the aerophores, rounded in *P. tuerckheimii* and conical in *P. lechleri*. It is similar to *P. stipitellatum* too, but it can be easily distinguished by the scales, which are dentate in *P. stipitellatum* and entire in *P. tuerckheimii*.

Reviewed material:

DOMINICAN REPUBLIC. *M. Canela s.n.,* 10 October 1946 (P01531870!). **Prov. El Seibo:** alrededores o antes de la Laguna, *M. Canela 2269,* 30 December 1942 (P01531871!). **Prov. Azua:** between Valle Nuevo and Azua, *G.C. Jones & D:H: Norris 1125,* 24 December 1964 (NY02007860!; NY02007861!); Civ. Santo Domingo, Sierra de Ocoa, San José de Ocoa, Loma del Rancho, *E.L. Ekman 11642,* 23 February 1929 (US1710583!); El Montazo, *J.S. Jiménez 2530,* 26 January 1953 (US2135274!); road between Valle Nuevo and San José de Ocoa, *G.C. Jones & D.H. Norris 1126,* 24 December 1964 (NY02007875!). **Prov. Barouco:** Sierra de Neibe (subsite 1), *P. Acevedo-Rdgz et al 13218,* 21 June 2003 (NY02007862!; US3564753!). **Prov. Duarte:** vicinity San Frqancisco de Macorís, Quita Espuela, *W.L. Abbott 2041,* 5-17 April 1922 (US1079934!; US1079935!; US1079936!); *ibidem, W.L. Abbott 2044,* 5-17 April 1922 (US1145263!; US1145264!); *ibidem, W.L. Abbott 2050,* 5-17 April 1922 (US1079942!; US1079943!). **Prov. Independencia:** Sierra de Baoruco, Prov. Independencia, 12 km Sur del Puesto Militar El Aguacata en la Carretera Internacional a Los Arroyos y Pedernales, *T. Zanoni et al 27089,* 8 September 1983 (NY02007851!; US3129410!). **Prov. La Estrelleta:** Sierra de Neiba, 31-34 km by road NNW of La Descubierta, 11-14 km N of Angel Felix. *J.T. Mickel et al 8749,* 21 February 1983 (NY02007852!). **Prov. La Vega:** 5-5,4 km W of La Culata de Constanza, area called Agua Fría, on road between La Culata to (Cienaga de), *J.T. Mickel et al 8288,* 23 February 1982 (NY02007879!); along road from Constanza to La Nevera, by the entrance to Parque Nacional Juan Bautista Perez (Valle Nuevo), *P. Acevedo-Rdgz et al 11595,* 23 March 2001 (US3593228!); *ibidem, P. Acevedo-Rdgz et al 11607,* 24 March 2001 (US3592897!); al sureste del poblado de Pinalito, Constanza, en el lugar que los campesinos llaman "Madre Vieja", *R. García & S. Peláez 998,* 7 February 1986 (NY02007857!); Costanza-Valle Nuevo road, *G.C. Jones & D.H. Norris 1039,* 22 December 1964 (NY02007874!); in monte Barrero, *M. Fuertes 1689,* 06.1913 (NY02007871!; P01531874!); La Nevera, *P. Acevedo-Rdgz et al 12498,*

24 May 2003 (NY02007863!; US3487178!); prope Constanza, *H. v. Türckheim n. 2976*, m. 02.1910 (BM000769815! Photo, isotype; E00417618! Photo, isotype; GH00020671! Photo, isotype; K000633394! photo, holotype; NY00127312! isotype; P00627650!, isotype; U0007277! Photo, isotype; US00067452!, isotype). **Prov. Monseñor Nouel:** en la subida de Jayaco (de Bonao) a El Río (de Constanza), aprox. 8 km al oeste de la Carretera Duarte (Santo Domingo-Santiago), orilla del Río Jatubey, *T. Zanoni & F. Jiménez 40451,* 8 September 1987 (NY02007884!). **Prov. Monte Cristi:** subiendo Cabeza Cotorra, rancho 31, ladera este Piquito, *M. Canela 2269,* 12.1942 (P01531872!). **Prov. Pedernales:** Sierra de Baoruco, 45 road km S of Jimaní-Duverge hwy (Cruce del Escondido) and 8 km S of El Aguacate, 7,2 km N of the ridge top, *J.T. Mickel et al 8821,* 22 February 1983 (NY02007877!); *ibidem, J. T. Mickel et al 8851,* 22 February 1983 (NY02007854!); *ibidem, J.T. Mickel 8905,* 23 February 1983 (NY02007878!). **Prov. Peravia:** 14,2 km Norte del Parque Central de San José de Ocoa y 4,1 km desde el cruce de Los Arroyos, en el camino a Carmona, en una zona rural "El Caliche" o "La Brusca", *J.T. Mickel et al 8236,* 22 February 1982 (NY02007880!; UC1733553! Photo); *ibidem, T. Zanoni et al 19828,* 7 April 1982 (NY02007881!); 15 km. Norte desde el Parque Central y 8 a 10 km. Desde el cruce de Los Arroyos en el camino a Carmona, zona rural denominada "El Caliche" o "Carrao", *T. Zanoni et al 21842,* 21 July 1982 (US3058888!); *ibidem, T. Zanoni & M. Cabral 35844,* 23 December 1985 (NY02007883!); 48 km S. of Constanza (on road to San José de Ocoa), en las cimas de Loma del Rancho, al SE de San José de Ocoa, subida por el lado de "Tumbaca", *T. Zanoni & J. Pimentel 40238,* 14 August 1987 (NY02007867!); entre "Dieciseis" y "La Peñita", 9 km. Desde Rancho Arriba en la carretera a Juan Aldian y Piedra Blanca, *T. Zanoni et al 22652,* 13 August 1982 (NY02007876!; NY02007885!); in area of La Nevera, *T. Zanoni & M. Mejía 12206,* 2 April 1981 (NY02007866!; US3211957!); *ibidem, T. Zanoni & M. Cabral 35844,* 2 April 1981 (NY02007865!). **Prov. San Cristobal:** broad-leaved forestr (much cut over) along Río Mahoma, 5,3 km E of Piedra Blanca-Rancho Arriba road, (from point 19 km SW of Piedra Blanca, 11,2 km NE of Rancho Arriba, 0,7 km NE of La Penita, *J.T. Mickel et al 9084,* 28 February 1983 (NY02007853!; UC1733573! Photo); *ibidem T. Zanoni et al 22494,* 12 August 1982 (NY02007882!). **Prov. San José de Ocoa:** Piedra del Aguacate to Rio del Oro, *R.A. Howard & E.S. Howard 9396,* 10 October 1946 (NY02007858!; NY02007859!); sitio llamado El Firme, aprox. 8 km noreste de Rancho Arriba (línea recta) por la carretera Sabana Larga-Arroyo Vuelta, *W. Testo et al. 2275,* 17 May 2019

(VT296572! Photo). **Prov. San Juan:** *R.A. Howard & E.S. Howard 9396,* 10 October 1946 (US2017723!; US2017724!). **Prov. Santiago:** at the base of La Cotorra, *E. Marcano 4862,* 26 March 1964 (US2566449!); Bassin du Río Bao, *H. Humbert 27738,* 12.1952 (P01531056!; P01531057!; P01531058!); Cordillera Central, en el poblado rural "Las Lagunas de Cenoví" aprox. 3,5 hr. Por mulo al Sur de El Aguacate (de Monción): en las laderas del arroyo Caña, *T. Zanoni et al 43758,* 29 November 1989 (NY02007855!; NY02007856!). **Prov. Santo Domingo:** a lo largo del río Tablones, *D. Alain & P. Liegier 23554,* 15 July 1975 (NY02007864!); in monte Barrero, *Eggers 2041b,* 23 May 1887 (NY02007872!; NY02007873!). **HAITI. Dept. Artibonito:** vicinity of Mission, fonds Varrettes, *E.C. Leonard 3915,* 17 April – 4 May 1920 (US1076290!; US1076291!). **Dept. Ouest:** massif de la Selle, Pétionville, Fourcy, Riv. Thébaud, *E.L. Ekman 1225,* 31 July 1924 (US1559786!); Massif de la Selle, Pétionville, M. La Visite, *E.L. Ekman 1496,* 15 August 1924 (NY02007869!; US1559827!); vicinity of Furcy, *E.C. Leonard 4319,* 20 May – 15 June 1920 (US1076776!; US1076777!); *ibidem, E.C. Leonard 4461,* 20 May – 15 June 1920 (US1076942!); *ibidem, E.C. Leonard 4496,* 20 May – 15 June 1920 (NY02007870!; US1076989!). **Dept. Sud Est:** Morne des Commissaires, *L.R. Holdridge 870,* 22 November 1941 (NY02007868!; US1781739!). **PUERTO RICO.** *no collector,* no date (P01546400!); Sierra de Luquillo in monte Jimenez, *P. Jinertes 1689,* 26 May 1913 (P01409486!; P01409487!); Sierra de Naguabo, Summit of Loma la Miña, *J.A. Shafer 3334,* 20 July 1914 (P01409494!).

Parablechnum usterianum (Christ) Gasper & Salino, Phytotaxa 275(3): 217. 2016.

Basionym – *Lomaria usteriana* Christ ex A. Usteri, Fl. Umgebung São Paulo 135. 1911.

Type – Brazil. São Paulo: Ipiranga, *H. Luederwaldt s.n.*, June 1912 (neotype: SPF94516 n.s., designated on Dittrich *et al.*, 2018); isoneotype: BM000787908! photo).

Synonyms –

≡*Blechnum usterianum* (Christ) C.Chr., Index Filic., Suppl. 2, 8. 1917.
=*Blechnum capense* (L.) Schltdl. var. *limosa* Rosenstock Hedwigia 56: 362. 1915. Type: Brazil, São Paulo, Campo Grande, Sumpf. *A.C. Brade 6906,* 24 May 1914 (syntypes: S0510151! Photo; S05-10153! Photo).

Description – *plants* terrestrial; *rhizomes* long-creeping, dark, scaly, scales lanceolate, light brown, concolorous, 6.5–8.1 × 1.8–2 mm, margins entire; *fronds* dimorphic; *sterile fronds* 41–80 cm long; *petioles* stramineous, blackish proximally, 17–65 cm × 2.1–3.4 mm, with scales similar to those of rhizomes; *lamina* 22–38 × 11–14 cm, chartaceous to coriaceous, 1-pinnate, narrowly oblong, base truncate, terminal pinna conform; *rachis* abaxially glabrous or scaly, adaxially more or less scaly, the scales lanceolate or linear, whitish to light brown, concolorous, margins entire or dissected; *sterile pinnae* in 3–17 pairs, 2–10 × 0.8–1.7 cm, slightly to strongly ascendant, stalked, becoming basiscopically adnate towards the apex, narrowly oblong, margins entire to denticulate, plane to strongly revolute, apices obtuse, acute or acuminate; *costae* grooved adaxially, prominent abaxially, scaly abaxially, scales whitish, twisted, triangular, margins denticulate, on the adaxial costa with twisted, linear, whitish scales, the apices filiform; *veins* free, simple or 1-furcated, catadromous; *aerophores* absent; *hydathodes* clavate; *fertile fronds* longer than the sterile; *petioles* 66–77 cm long, basal scales similar to those on the rhizome; *lamina* 22–65 × 5.6–8.2 cm, 1-pinnate, elliptical, base truncate, reduced towards the apex, terminal pinna conform, *fertile pinnae* linear, contracted; *sori* linear, continuous, forming coenosori on both sides of the costa; *indusia* linear, continuous, open towards the costa; *sporangia* with 21–24 arc cells; *spores* monolete, (56–)65(–75) × (34–)43(–58) µm; perispore smooth, cristate reticulate, with high, thin walls, forming small polygonal areoles, with abundant to moderately abundant long filamentous processes in the areolar lacunae (**Figure 89**).

References – Dittrich *et al*. (2018, 2020)

Chromosome number – unknown.

Distribution and habitat – southeaster and southern Brazil., here we also report one collection from Paraguay (P01530996!; P01530997!6) Tropical rainforests and grasslands, mostly in marshy terrains, sometimes in river ravines and roadsides, always in exposed places. 40–1400 m. Relatively common (Dittrich *et al.*, 2018, 2020).

Etymology – The name is dedicated to Alfred Usteri (1869-1948), Swiss botanist, horticulturalist and professor at São Paulo Polytechnic who lived an collected plenty of plant specimens in Brazil.

Figure 89. *Parablechnum usterianum*. A. Plant; B. Sterile pinna apex, adaxial side; C. Sterile pinnae bases, abaxial side; D. Sterile petiole; E. Rhizome scales. (A-E: *B. Balansa 4462*, P000904675). 5 cm in A, 10 mm in B & C, 3.5 mm in D, 9 mm in E.

Notes – this species is easily distinguishable from other Brazilian *Parablechnum* species by the long-creeping rhizome. However, this is not always so obvious because the fronds do not grow widely spaced, and it is common to find herbarium specimens without rhizomes. In these cases, it can be distinguished from other Brazilian species such as *P. cordatum* and *P. glaziovii* by the longer and narrower pinnae which are ascending and scalier on the costa and lamina abaxially.

Dittrich *et al*. (2018) designated a neotype for this species, as the material that would serve as lectotype (Brazil, Villa Marianna, *Usteri*) was not found (Stafleu & Cowan, 1976).

Reviewed material:

BRAZIL. Minas Gerais: *A. Glaziou 11703,* 1879 (P01462852!; P01462853!; P01462855!; P01466435!); Serra do Espinhaço, Serra do Cipó, ca. Km 120 (ca. 145 km N of Bello Horizonte), *H.S. Irwin et al. 20093,* 14 February 1968 (P01389550!); Viçosa, Agricultura College Valley, *Y. Mexia 4782,* 3 June 1930 (P01395987!; UC476354! Photo; US1482150!). **Paraná:** Pira do Sul, *B.K. Canestrato & P.H. Labiak 352,* 30 April 2012 (MBM393650! Photo). **Rio Grande do Sul:** *C. Furgens & A. Stier 69,* 10.1904 (P01546442!); *W. Herter 2628,* 1 May 1907 (P01389522!); Serra de Santa Anna do Livramento, *W. Herter 3016,* 26 May 1907 (P01389513!). **São Paulo:** *Usteri s.n.,* 1907 (UC417797! Photo); Ipiranga, *H. Luederwaldt s.n.*, 06.1912 (BM000787908! photo, isoneotype); Campo Grande, Sumpf. *A.C. Brade 6906*, 24 May 1914 (S0510151! Photo, syntype of *Blechnum capense* var. *limosa*; S05-10153! Photo, syntype of *Blechnum capense* var. *limosa*); Mun. Bofete, Morro das Três Pedras (gigante deitado), *J. Prado et al 1693*, 24 July 2007 (P00904675!); Mun. Jundiaí, Serra do Japi, *J. Prado et al 2058*, 13 November 2009 (NY02330524!). **PARAGUAY. Dept. Valenzuela:** Cordillera de Valenzuela, *B. Balansa 4462*, 1883 (P01530996!; P01530997!). **Unknown State:** *Usteri 26,* 24 June 1907 (P01389556!).

Parablechnum varians (Fourn.) A. Wal, S. Molino & J.M. Gabriel y Galán Bot. Complut. 45(1): 5. 2021.

Basionym – *Lomaria varians* Fourn. Mex. pl. 1. 113. 1872. 1872.

Type – México. Veracruz: Orizaba, in valle Cordobensi; *Bourgeau 1826*, 4 Feb 1866, in herb. Van Heurck, no. 1420 (syntypes: P00627651–4!, P02142467–8!, P02142468!, P01624641!; isosyntypes: BR0000013343200! photo, K000633393! photo, NY00214901–2!; US2427572!).

Synonyms –

≡*Blechnum varians* (Fourn.) C.Chr., Index Filic. 161. 1905; *Struthiopteris varians* (Fourn.) Broadh., Bull. Torrey Bot. Club 39: 379. 1912.

Description – *plants* terrestrial; *rhizome* erect, non-stoloniferous, scaly, scales triangular to linear, yellowish, membranaceous, entire, 10–25 × 2–4 mm; *fronds* dimorphic; *sterile fronds* size? with *petioles* of 30–160 cm, atropurpureous, scaly, mostly

proximally, scales similar to those on the rhizomes, mixed with fibrillose ones, *lamina* 48–160 × 25–30 cm, oblong, 1-pinnate, base truncate, reducing towards the apex, ending with a terminal conform pinna, *rachis* similar to the petiole, papillose, scales similar to those of the petiole, *sterile pinnae* in 9–20 pairs, oblong-lanceolate, base rounded, apex acuminate, serrate, stalked, margins cartilaginous, erose–crispate, no revolute, 10–15 × 1.5–3 cm, *costae* similar to the rachis, grooved adaxially, prominent abaxially; *veins* free, simple or 1-furcated, catadromous; *aerophores* axillary, globose, stomata visible as white dots; *fertile fronds* longer and more erect 50–150 cm, *petioles* 25–50 cm, *fertile pinnae* narrower, linear; *sori* linear, continuous, forming coenosori on both sides of the costa; *indusia* continuous, linear, open towards the costa, entire or erose on maturity; *sporangia* with 20–22 arc cells; *spores* monolete, flat-convex in longitudinal equatorial view and elliptical in polar view (46–)55(–65) × (37–)42(–50) µm, perispore folded forming walls that frame large areolae, with filaments (**Figure 90**).

References – Broadhust (1912b), Moran (1995a)

Chromosome number – unknown.

Distribution and habitat – endemic to Mexico and Mesoamerica, terrestrial in wet montane forest (Mickel & Beitel, 1988).

Etymology – likely refers to the intraspecific variation of some characters.

Notes – this taxon has been widely regarded as conspecific with *Parablechnum schiedeanum*, but differs from this species in the atropurpureous axes, the crenulate pinnae margins and the spores with large areoles and filaments (Smith, 1981; Mickel & Beitel, 1988; Moran, 1995a; Wal *et al*., 2020).

The phylogenetic results presented here suggest that this taxon could be a complex of several species. One of the analysis placed it as the sister group of the rest of the genus, but the individual holding that position presented a lot of missing data, so it is probably a mistake.

Figure 90. *Parablechnum varians*, A. Fertile (left) and sterile (right) fronds; B. Sterile pinna apex, adaxial side; C. Sterile pinna margin, adaxial side; D. Sterile pinna base, adaxial side; E. Fertile pinna surface, abaxial side; F. Fertile petiole. (A: *Krueger & Gillespie 37*, US1843362; B-F: NY04187113). Scale: 4 cm in A, 6.5 mm in B, 3 mm in C, 7 mm in D, 4.5 mm in E, 5.5 mm in F.

Reviewed material:

COSTA RICA. Prov. Guanacaste: Parque Nacional Guanacaste, sendero al Volcán Orosí, *A. Rojas & M. Grayum 8020*, 22 August 2007 (MO6387272!). **Prov. Puntarenas:** La Palma, *Ad. Tonduz 12568*, 09.1898 (P01624646!). **Prov. San José:** Escazú, San Antonio, Z.P. Cerros de Escazú, Pico Blanco, *A. Rojas et al. 6252*, 11 November 2004 (MO6397010!); *ibidem*, *A. Rojas & C. Frias 6316*, 5 January 2005 (MO6397065!). **Unknown Province:** *C. Wercklé s.n.*, 1903 (P01624647!). **HONDURAS. Dept. Comayagua:** near el Achote, hills above plains of Siguatepeque, *T.G. Yuncker et al. 5936*, 17 July 1936 (UC1013393! Photo; US1637798!; US1637799!). **Dept. Santa**

Bárbara: 7 km N of El Mochito, on the E slopes of Mt. Santa Bárbara, *R.C. Moran 5692*, 23 November 1991 (MO4224729!; MO4224730!; MO4224731!). **MEXICO. Chiapas:** Municipio of Cintalapa, Oaxaca - Chiapas border. 4 km west of La Cienaga along a logging road 38 km west of Las Cruces, *D.E. Breedlove 25131*, 10 May 1972 (NY04187110!). **Oaxaca:** Dto. Mixes, NE slope of Cerro Zempoaltepec, *J.T. Mickel & S.W. Leonard 4826*, 21 September 1970 (NY04187116!). **Veracruz:** Córdova [Córdoba], *H. Zink 64*, no date (UC678358! Photo); Orizaba, in valle Cordobensi, *Bourgeau 1826 (*in herb. *Van Heurck, no. 1420*), 4 February 1866 (BR0000013343200! photo, isosyntype; K000633393! photo, isosyntype; NY00214901!, isosyntype; NY00214901!, isosyntype; P00627651!, syntype; P00627652!, syntype; P00627653!, syntype; P00627654!, syntype; P02142467!, syntype; P02142468!, syntype; P01624641!, syntype; US2427572!, isosyntype). **PANAMÁ. Prov. Chiriquí:** Holcomb's Trail, along Río Caldera 8 to 10 miles above El Boquete, *E.P. Killip 5074*, 6 February 1918 (US1842660!; US1842661!; US1842662!; US0887842!); Pila, Las Nubes, Cerro Punta, *I. González 12*, 14 October 1994 (MA702487!).

Parablechnum vestitum (Blume) Gasper & Salino, Phytotaxa 275(3): 217. 2016.

Basionym – *Lomaria vestita* Blume, Enum. Pl. Javae 203. 1828.

Type – *crescit in montibus altissimis Javae.Blume s.n.* (holotype: L0051111; isotype: P01532244!)

Synonyms –

≡*Blechnum vestitum* (Blume) Kuhn, Ann. Mus. Bot. Lugd.–Bat. 4. 284. 1869 *non Blechnum vestitum* T. Moore, Index Fil. 207. 1857, nom. rej. prop.
=*Lomaria glandulifera* Heward in Houlston & Moore, Gard. Mag. Bot. 3, 227. 1851. Type: Indonesia, Java, *Lobb 274*, no date (BM n.s.)
=*L. pyrophila* Blume, Enum. PI. Javae 2, 204. 1828 *non Blechnum pyrophyllum* Blume, Enum. PI. Javae 2, 197. 1828. Type: 'crescit in fissuris lapidum ejectorum in summo monte ignivomo Ternates', *Reinwardt s.n.*, no date (holotype: L n.s.).
=*L.rotundifolia* Blume, Enum. PI. Javae 2, 204. 1828. Type: Indonesia, montibus Javae altissimis, *Reinwardt s.n.*, no date (holotype: L n.s.).

Vernacular names – Kalang Kalang (Moluccas) (Chambers & Farrant, 2001).

Description – *plants* terrestrial; *rhizome* erect or suberect, non-stoloniferous, dark, covered with lanceolate–acuminate scales, ca. 1.5 × 0.3 cm, usually discoloured, with atropurpureous centre and lighter margins; *fronds* dimorphic; *sterile fronds* with *petioles* 20–100 cm long, dark brown, reddish or atropurpureous, covered with scales, at the base similar to those of the rhizome and becoming broader and browner distally, some concolorous or slightly discoloured, with the central zone darker, mixed with woolly indumentum; *lamina* elliptic-deltoid, 1-pinnate, darker in the adaxial zone than in the abaxial zone, tapering to the apex ending in a conform pinna; *rachis* grooved adaxially and prominent abaxially, with verrucose ornamentation on the adaxial side and smooth on the abaxial side, with scales similar to those of the petiole, but becoming smaller and filiform towards the apex, usually concolorous, light brown; *sterile pinnae* in 7–42 pairs, closely spaced, oblong-elliptic, alternate to subopposite, base slightly asymmetric, cordate, apex acute, sometimes acuminate, shortly stalked, becoming adnate towards apex, coriaceous, margins finely serrulate, sometimes slightly revolute, similar in length but becoming shorter towards apex, terminal pinnae longer than subterminal pinnae, sometimes with a basal auricle; *costae* of the same colour as rachis or slightly paler, grooved adaxially and prominent abaxially, sometimes with verrucose ornamentation on the adaxial side and smooth on the abaxial side, with persistent, fine, narrowly elliptic scales, cordate at the base, acuminate or attenuate at the apex, much smaller than those of the rachis, and more or less entire; *veins*, free, simple or bifurcate, catadromous; *aerophores* axillary, atropurpureous, elongate; *hydathodes* rounded, patent, in the axil of each serration on the adaxial side; *fertile fronds* longer and more erect than sterile fronds, *petioles* longer, sometimes as long as lamina; *fertile pinnae* linear, 9–20 × 0.4–0.6 cm; *sori* linear, continuous, forming coenosori on both sides of costa, covering underside except for a small sterile segment at apex; *indusia* linear, continuous, opening towards costa, light brown, entire or slightly lacerate; *sporangia* with 19–22 arc cells; *spores* monolete, spores (42–)57(–71) × (32–)44(–55) µm; perispore not folded, reticulate, with moderately abundant coarse filamentous processes running from wall to wall in the areoles (**Figure 91**).

References – Chambers & Farrant (2001).

Chromosome number – unknown.

Distribution and habitat – in Peninsular Malaysia, Sumatra, Java, Borneo, Sulawesi, Flores, Philippines, Moluccas, Bougainville, New Ireland. Usually in low and high primary forests, also in open areas, near mountain peaks, near craters and on edges of streams, lakes, and swamps. (Chambers & Farrant, 2001).

Etymology – specific epithet probably referring to the abundancy of scales.

Notes – *Parablechnum vestitum* can be confused with the African species *P. capense* and also with some species from Central and South America and the Australasian and Pacific region but is usually easily distinguishable by the abundant amount of scales on the petiole, rachis and costa, as already noted by Chambers & Farrant (2001).

There was some controversy as to whether the name to be used was *Blechnum vestitum* (Blume) Kuhn or *B. vestitum* T. Moore. The name *B. vestitum* (Blume) Kuhn has been used extensively in taxonomic and ecological notes for known species of *Blechnum s.l.* with a distribution in the Malayan region but apparently absent from New Guinea. It is the name used in the regional and local floras of the region for about 150 years. The only exception has been the occasional inappropriate use of the name *Blechnum capense* (a species from Africa) by some authors. Informally in ecological work, *Blechnum procerum*, has also been used, but its taxonomic status has been clarified (Chambers & Farrant, 1998a). The name *B. vestitum*, however, was previously occupied, which was overlooked by Chambers & Farrant (2001) revision of *Blechnum s.l.* from the Malasian region. Therefore, Chambers (2004) proposes that the illegitimate name *B. vestitum* (Blume) Kuhn, referring to Malaysian specimens, be retained against *B. vestitum* T. Moore, in order to avoid the need to create a new name for a widely known taxon and thus avoid the disadvantageous change that would result from strict application of the rules.

Also, Christensen (1905) indexed *B. vestitum* T. Moore based on a collection from Venezuela (*Fendler 108*, n.s.). This had been overlooked by Holttum (1968) and treatments of Venezuelan ferns do not mention this taxon either (Smith, 1995). However, Chambers (2004) reviewed Moore's footnote descriptions and stated that this could be one of the many variants of *Blechnum occidentale* or even a hybrid *B. occidentale* × *B. polypodioides* Raddi.

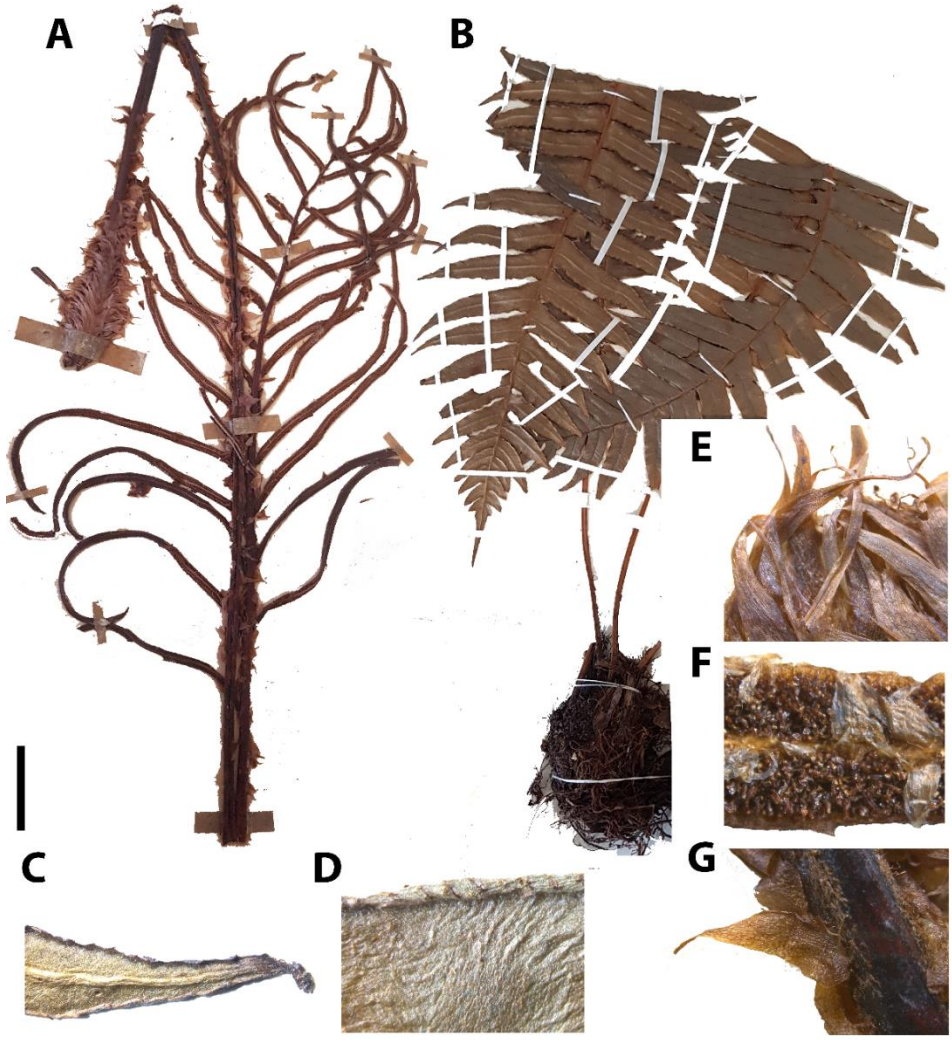

Figure 91. *Parablechnum vestitum*. A. Fertile frond; B. Plant with two sterile fronds; C. Sterile pinna apex, abaxial side; D. Sterile pinna margin, abaxial side; E. Rhizome scales; F. Fertile pinna surface, abaxial side; G. Scale. (A, E & G: *Fr. Scortechini 343*, US263958; B: *Meijer 136304*, US3462349; C: *Allen 3921*, US2293666; D: *T. Shimizu M13556*, US2552645; F: *B.E.G. Molesworth-Allen 3921*, US2293665). Scale: 5.5 cm in A, 4 cm in B, 3.5 mm in C, 2.5 mm in D & F, 4 mm in E & G.

Reviewed material:

INDONESIA. Celebes: Sulawesi, Roroka Timbu, *E. Hennipman 5362*, April 1914 (P01571490!; US3098130!); Sulawesi Utara, Bolaang Mongondow, Gunung Ambang Nature Reserve, Bolirang solfatara area, *T. Maatschappij et al 7277*, 19 April 1985 (US3100967!). **Java:** *no collector*, no date (B200034398! Photo); *ibidem* (NY!); *ibidem*, (P01532243!); *Blume s.n.*, 1836 (L0051111! Photo, holotype; P01532244!, isotype); *Lefebre 74*, no date (P01575950!); *Ploem s.n.*, 1867 (P01532246!); *Zollinger 337*, no date (P01532247!); Bodas, *C.M. Gandager s.n.*, 1897 (P01558299!); Cibodas, from garden to Waterfall, *A. Nitta 15166*, 31 December 1977 (MO2723768!); Dreng-Prahu, *C.E.O.*

Kuntze 5738, 18 August 1875 (NY!, 2 sheets); Gedeh, *H. Möller s.n.*, 11 September 1897 (NY!); northwestern slopes of Mount Salak, above Goenoeng Boender, Batavia province, *W. Palmer & O. Bryant 396*, 5 May 1909 (US0651839!); *ibidem*, *W. Palmer & O. Bryant 486*, 14 May 1909 (US0651927!); Pangerango, *C.E.O. Kuntze 4650*, 30 May 1875 (NY!); Saddle between Gedeh and Pangarango volcanoes, *F.R. Fosberg 44598*, 11 December 1963 (US2638465!); Southeast Java, *H.O. Forbes 742*, 1880 (P01532245!; P01558303!); summit of Mount Pangranggo, *W. Palmer & O. Bryant 963*, 26 August 1909 (US0652499!); Tjiboeroem, forested middle slopes of Mount Gede, Preanger province, *W. Palmer & O. Bryant 279*, 23 September 1909 (US0651718!; US0651719!; US0651720!); West Java, *Forbes s.n.*, no date (P01532258!); West Java, *M. Fleischt 739*, 28 August 1912 (P01575942!; P01575943!); West Java, Gunung Gede Pangrango National Park, *C.–W. Chen Wade1788*, 22 October 2011 (TAIF388744! photo); *ibidem* (TAIF388745! photo); *ibidem* (TAIF388746! photo); *ibidem* (TAIF388747! photo); *ibidem* (TAIF388748! photo); *ibidem* (TAIF388749! photo); West Java, Mt Gede, *M. Fleicher 638*, 28 September 1912 (P01558304!). **Moluccanas:** *G.H. Vriese & J.E. Teijsmann 450*, 1859-1860 (US1579260!); Abolukken Halmahera, P. Tidore Kie Abatoehoe, *H.J. Sam 3750*, 8 July 1926 (NY!). **Sumatra:** *Winkler 126*, 1912 (P01532256!; P01532257!; P01575932!); Deleng Si Bajak, Karoland, *H.H. Bartlett 6520*, 28 January 1927 (US1429051!); *ibidem*, *H.H. Bartlett 8491*, 21 June 1927 (US1429232!); Si Bajak, Berastafi, *H.N. Ridley s.n.*, 11 February 1991 (US1277704!). **MALESIA. Pahang:** en route from Tanah Rata to Gunong Jasar, Cameron Highlands, *T. Shimizu et al. 13556*, 20 October 1967 (US2552645!; US2552646!); Gumong Jahan, *Hamiff & Nur 7946*, 13 June 1922 (P01558306!; P01558308!). **Perak:** *King 8065*, 08.1885 (P01532255!); *Scortechini 343*, no date (P01406634!); Gunong Jasah, Cameron Highlands, *B.E.G. Molesworth Allen 3921*, no date (US2293665!; US2293666!; US2293667!); *Revd. Father Scortechini 343*, no date (US0263958!). **Sabah**: Borneo**,** *G.F. Singapore & Sarawak s.n.*, 1894 (P01557682!); *ibidem* (P01557683!); Borneo, *Halleés s.n.*, 1701 (P01558313!); Borneo, Gurulau spur, upper Kinabalau, *J. Clemens & M.S. Clemens 50753*, 5 December 1932 (NY!); Borneo, Kamburanga, Mt. Kinabalu, *J. Clemens & M.S. Clemens 28883*, 1931 (NY!; US1673321!); Borneo, Sarawak, *Native collector 749*, no date (P01558312!; US1290608!); Borneo, Sarawak, Mount Matang, *M. Clemens & J. Clemens 21012*, 28 October 1929 (NY!); Dept. Sandakan, Raleigh platean, Tongod, *Meijer 136304*, 27 July 1992 (US3462349!); Island or Province B.B.B.

Kinbalau, Upper Mt. Kamburanga Oaka, upper Kinabalu, *J. Clemens & M.S. Clemens 27755*, 8 January 1932 (US1673165!); Mt. Kinabalu, Trail to submit, *C.–W. Chen Wade3894*, 4 March 2016 (TAIF490671! photo; TAIF490672! photo); Mt. Kinabalu, upper Kinataki R., *J. Clemens & M.S. Clemens 31773,* 24 February 1933 (US1715045!); Mt. Malang, *C.J. Brooks s.n.*, February 1910 (P01406635!); *ibidem* (P01406636!); Mt. Trusmadi, Nuluhon Trusmadi Forest Reserve, *C.–W. Chen Wade4308*, 10 April 2015 (TAIF468106! photo; TAIF468107! photo; TAIF468108! photo; TAIF468109! photo); North Borneo, State of Sabah, southern slope of Mt. Kinabalu, eastern route, *S. Collenette 21553*, 31 March 1905 (US2467135!). **PHILIPINES. Luzon:** *H. Cumingg 141,* 1814 (P01462509!; US0853727!); Benguet, Mt., Sub-Province, *M. Ramos & G. Edaño 40370*, September 1921 (US1261459!; US1261460!); Benguet Mt. Pulogloco, *M. Ramos & G. Edano 40370*, September 1912 (P01558305!; P01558309!); Laguna, Mt. Bonahao, *I.A. Loher s.n.*, February 1906 (P01558311!); Mountain Prov., Barlig Mun., Mt. Amuyao, Barlig View, *J.F. Barcelona & P. Puchana 3173*, 28 February 2007 (US3563129!); Mountain Prov., Barlig Municipality, Lubfon rice terraces vicinity (Firafiag loco dicto), *J.F. Barcelpona & N. Losao-na 3032,* 10 February 2007 (US3563130!); Prov. Albay, Luzon, Mayon Volcano, *M. Ramos & G. Edaño 75697*, September 1928 (NY!); Quezon Prov., Tayabas Municipality, Brgy. Lalô approach, Mt. Banahaw de Tayabas, *J.D. Barcelona 1490,* 23 October 2002 (US3629912!). **Mindanao:** Camiguin, *M. Ramos 1146*, April 1912 (NY!, 2 sheets; P01558314!; P01558318!; P01558320; P01558321!; US0775931!; US0775932!; US0901332!; US0901333!; US1096496!); Mt. Apo, *E.B. Copeland s.n.*, 24 October 1904 (NY!); *ibidem, R.S. Wiliams 2476,* 31 March 1905 (NY!, 2 sheets; US0448154!); Mt. Apo, middle peak, *Dr. Edgar & A. Mearns s.n.,* 1 July 1904 (US0447687!); *ibidem* (US0447691!); *ibidem* (US0447693!); Mt. Halcon, *E.D.Merrill 5904*, November 1906 (P01558319!; P01575941!; P01558322!). **Mindoro:** Prov. Mimaropa, Mt. Halcon, *E.D. Merrill 5904*, November 1906 (NY!; US0710946!; US0710947!). **Negros Oriental:** Dumaguete, Mts. Cuernos, *A.D.E. Elmer 9913*, April 1908 (NY!; P01558301!; US0705572!; VT198731!); Sibulan Municipality, Balinsasayao Twin Lakes Natural Park to Mt. Guinsayawan, *C.–W. Chen Wade3894*, 7 April 2014 (TAIF455378 v.f; TAIF455379! photo; TAIF455380! photo; TAIF455391! photo). **Unknown area:** *E.B. Copeland s.n.*, 5 January 1909 (P01558323!). **UNKNOWN LOCATION:** *Fil 49* (interpreted), 1908 (P01558307!).

Parablechnum wattsii (Tindale) Gasper & Salino, Phytotaxa 275(3): 217. 2016

Basionym – *Blechnum wattsii* Tindale, Contr. New South Wales Natl. Herb. 3: 247. 1963.

Type – Lyrebird Glen, Hazelbrook, Blue Mountains, N.S.W., *M.D. Tindale*, 22 April 1960 (holotype: NSW244165! photo; isotypes: K000665353! photo, UC1499328! photo, US2551332!).

Synonyms –

=*Blechnum capense* var. *vestitum* (Blume) Domin, Biblioth. Bot. 20(85): 116 1913. Australia, Tasmania, *R.C. Gunn s.n.*, no date (holotype: not found).

Description – *plants* terrestrial; *rhizome* shortly erect to creeping, non-stoloniferous; *fronds* dimorphic; *sterile fronds* 9–140 cm long; *petioles* 5–65 cm long, atropurpureous at base, stramineous above, scales linear to lanceolate, subulate to acuminate, entire to finely dentate, brown to reddish brown to bicolorous, more abundant in the proximal region; *lamina* 1-pinnate, lanceolate, ovate to deltoid; *rachis* stramineous to pale pinkish brown, sometimes darker, scales variable in shape, acuminate, dentate, often with irregular, marginal outgrowths (especially the narrower scales), stramineous to dark red-brown sometimes bicolorous, lanuginose hairs sometimes present; *sterile pinnae* in 2–17 pairs, oblong-lanceolate, 1.5–15 cm × 9–34 mm, shortly stalked, becoming adnate basiscopically towards apex; margins serrate to crenate; basal pinnae very slightly reduced; *costae* similar to the rachis, grooved adaxially, prominent abaxially; *veins* free, simple or 1-furcate, catadromous; *aerophores* absent; *hydathodes* very small, rounded; *fertile fronds* usually larger; *fertile pinnae* narrowly linear; *sori* linear, continuous, forming coenosori on both sides of the costa; *indusia* linear, continuous, dark brown, entire margin, sometimes lacerate; *sporangia* with (15–)17(–19) arc cells; *spores* monolete (46–)56(–66) × (33–)40(–47) µm; perispores smooth, cristate-reticulate, low-walled, thin, sharp, forming small irregular areoles or a reticulum, with abundant thick and short filamentous processes (**Figure 92**).

References – Chambers & Farrant (1998b).

Chromosome number – n = 28 (Quinn, 1961).

Distribution and habitat – endemic to eastern Australia, in mountainous regions of Queensland, New South Wales, Victoria and Tasmania. Usually forming large colonies in deep humid soils and, occasionally, on rocks in wet forests (Chambers & Farrant, 1998b.

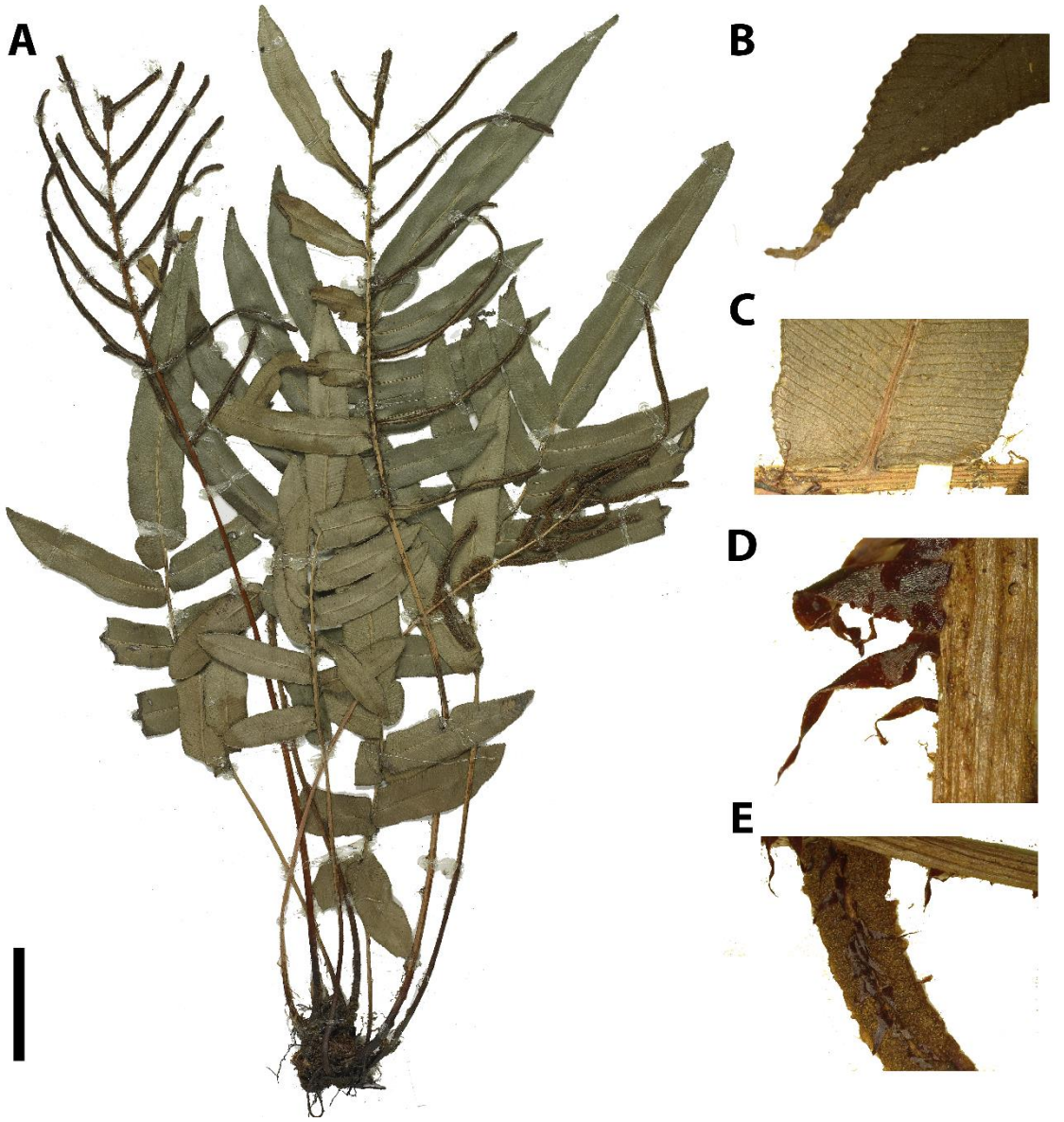

Figure 92. *Parablechnum wattsii.* A. Plant; B. Sterile pinna apex adaxial side; C. Sterile pinna base, adaxial side; D. Rachis scales; E. Fertile pinna surface, abaxial side. (A: US2551332, isotype; B-E: *M.D. Tindale 610, no collector* P00526897). Scale: 4 cm in A, 8.5 mm in B, 9.5 in C, 3 mm in D, 9 mm in E.

Notes – see note on *P. ambiguum*. This species is sometimes confused with *P. minus*, but that species presents much more reduced basal pinnae. Jones & Clemesha (1981) and Chambers & Farrant (1998b) pointed out that there are some individuals of Otway Range

(Victoria) very similar to *P. wattsii* but with narrower and more acuminate sterile pinnae and papery stramineous to pale brown scales on the petiole and rachis. Even though it seems a considerable variation there is still insufficient evidence to consider this form a different taxon.

Reviewed material:

AUSTRALIA. New South Wales: *no collector,* no date (P00526897!); *D. Werner 1*, 12 January 1954 (UC1052948! Photo); *F. Mueller s.n.*, no date (P01463073!); *ibidem* (P01463074!); *ibidem* (P01463084!); *ibidem* (P01463087!); *G. Caby s.n.*, no date (P01557667!); *ibidem* (P01557668!); *J.P. Verreaux 471*, April 1845 (P01463078!); *W.C.B. Selitieel s.n.*, 21 February 1927 (UC312382! Photo); Botany–Bay, *Neé s.n.*, no date (MA213373!); Govetts Leap, Blackheath, *E.F. Constable 8026*, 8 March 1957 (MO2007376!; US2551331!); Head of Moruya River, Dampier State Forest, 15 miles west of Bodalla, *E.F. Constable 6910*, 11 May 1966 (US2596731!); Lyrebird Glen, Hazelbrook, Blue Mountains, *M.D. Tindale*, 22 April 1960 (NSW244165! Photo, holotype; K000665353! photo, isotype; UC1499328! photo, isotype; US2551332!, isotype); Jenolan Cavez, *W.F. Blakely s.n.*, September 1900 (UC417963! Photo); Mt. Banda Banda, 44 km (27,5 miles) NW of Wauchope in Mt. Boss State Forest, *R. Coveny et al 6381*, 31 May 1975 (NY!); Noona, Walcha, *A.R. Crawford s.n.*, February 1885 (US2987096!); Victoria Falls, ca. 2 mileas east of Mount Victoria, Blue Mountains, *E.F. Constable 8007*, 6 May, 1959 (UC1251870! Photo; US2359585!); within 125 miles of Sydney, *no collector*, 1844 (P01618450!); Zircon Creek, Mount Wilson, Blue Mountains, *J.D. Lovis 233*, 25 August 1955 (NY!, 2 sheets). **Norfolk Island:** *no collector 125*, no date (P01462494!). **Queensland:** Rockingham bay, *Dallachy s.n.*, no date (P01463068!). **South Australia**: *Behr s.n.*, no date (P01463064!); Aldgake, *Koch 817*, September 1902 (P01463065!). **Tasmania:** *Leschenault s.n.*, no date (P00526899!); *R.C. Gunn & J.D. Hooker s.n.*, no date (P01463060!); *ibidem* (P01463082!); *ibidem* (P01463083!); *R. Schlechter s.n.*, 1830 (P01463062!); Hobart town, *E. Kershner s.n.*, January 1875 (US0653641!); Lowhead, Launceston, *L.M. Jones 134*, December 1934 (NY!); Mt. Bischoff, *G. Renner s.n.*, 1891 (P01462493!). **Victoria:** Alpen, *O. Kuntze 20100*, March 1904 (NY!); Coleraine, *A. MacCaskill s.n.*, 1927 (P01662152!); Emu Creek, road up north side of Mt Emu, *T.J. Entwisle & S. Bodsworth 1739*, 10 October 1990 (MO3893784!; MO3893785!); Mt. Kitchener, S. side near Marysville, *D.M. Glynne 11*,

8 July 1928 (US2292203!; US2292204!); North-east, Emu Creek, road up north side of Mt Emu, *T.J. Etwisle & S. Bodsworth 1739,* 10 October 1990 (MO3892784!; MO3892785!); Sunday Island, *no collector,* no date (P01532232!); Warburton, *illegible collector,* November 1929 (US1525422!); York Town, *R.C. Gunn s.n.,* October 1844 (VT198730!); *Illegible collector,* November 1929 (NY!);. **Unknown area:** *no collector,* no date (NY!); *no collector 22,* no date (P01462490!); *no collector 670,* no date (P01463058!); *M. Verreaux 268,* no date (P01662185!); *S.O. Labillardiere s.n*., no date (P01462487!).

Parablechnum werffii (R.C.Moran) Gasper & Salino, Phytotaxa 275(3): 217. 2016.

Basionym – *Blechnum werffii* R.C.Moran, Novon 2: 132, f. 2. 1992.

Type – Panama. Chiriquí: Distrito Bugaba, Cerro Punta, around STRI house, cloud forest, rich in epiphytes, 8º52'N, 82º33'E, 2,220 m, *van der Werff & Herrera 6500*, 27 Jan. 1985, (holotype: MO207394! photo; isotype: UC1509306! Photo; PMA2! Photo, NY04187119!).

Description – *plants* terrestrial; *rhizomes* erect, not subarborescent, non-stoloniferous, scaly, scales 10–15 × 2–3 mm, lanceolate to ovate, concolorous, light yellow–brown, entire; *fronds* dimorphic; *sterile fronds* with *petioles* 8–20 cm, yellowish-brown with brown or atropurpureous spots; *lamina* 9–21 × 3–6 cm, 1-pinnate, glabrous on both surfaces, apex attenuate, 1-pinnate; *rachis* pale yellowish-brown or atropurpureous, not papillose, glabrous or sparsely scaly, the scales ovate, pale orange-brown, adpressed; *sterile pinnae* in 11–25 pairs, 1.5–3 × 0.6–1 cm, shortly stalked, with the base overlapping the rachis, narrowly involuting, serrate; *costae* pale yellowish-brown, grooved adaxially, prominent abaxially, glabrous or with scales similar to those on the rachis; *veins* free, simple or 1-furcate, catadromous; *aerophores* axillary, oblong; *hydathodes* ovate; *fertile fronds* longer, 25–57 cm; *petiole* 17–35 cm, yellowish-brown with brownish or atropurpureous spots; *fertile pinnae* linear, narrower, 1.2–2.5 × 0.2–0.3 cm; *sori* linear, continuous, forming coenosori on both sides of the costa; *indusia* linear, continuous, dark brown, entire margin, sometimes lacerate; *sporangia* with (18–)21(–23) arc cells; *spores* monolete, (56–)68(–76) × (39–)49(–57) µm; perispores rugulose, cristate-reticulate, low-

walled, thick, forming large areoles, with small, perforated ridges that appear to be laterally attached filamentous processes (**Figure 93**).

References – (Moran, 1992; 1995a).

Chromosome number – unknown.

Distribution and habitat – endemic to Costa Rica and Panama, where it grows in cloud forest, 2000–2200 m (Moran, 1992; 1995a).

Figure 93. *Parablechnum werffii.* A. Plant; B. Sterile pinnae apices, abaxial side; C. Sterile pinna base with an aerophore (arrow); D. fertile pinnae bases, abaxial side; E. Petiole base. (A: *R. Caballero 141*, US3077717, paratype; B-E: *H. van der Werff & J. Herrera 6500*, NY04187119, isotype). 4 cm in A, 9.5 mm in B, 3.5 mm in C & E, 11 mm in D.

Etymology – the species is named after Henk van der Werff, Dutch pteridologist and botanist who collected the type specimens.

Notes – the petiole of the fertile frond is distinctly long compared to other species of the genus, from as long as the apex of the sterile fronds to longer than it, up to twice as long. The pinnae are distinctive in being glabrous on both surfaces, small, obtuse and coriaceous (Moran, 1992; 1995a).

Reviewed material:

COSTA RICA. Prov. Heredia: on the road N of San Rafael, ca. 6 mi. above Monte de la Cruz, cloud forest, *Moran 2269* (MO! Photo, paratype). **PANAMA**. **Prov. Chiriquí:** Distrito Bugaba, Cerro Punta, *H. van der Werff & J. Herrera 6500*, 27 January 1985 (MO207394! photo, holotype; PMA2! Photo, isotype; UC1509306! Photo, isotype; NY04187119!, isotype); Guadalupe, Cerro Punta, Finca Alfaro, *Caballero 141* (MO3126356!, paratype; PMA3! Photo, paratype; US3077717!, paratype; US386238!, paratype).

Parablechnum wohlgemuthii K. Kessler & A.R. Sm, Phytotaxa 334(2): 113. 2018.

Type – Bolivia. La Paz: Prov. Franz Tamayo, Parque Nacional Madidi, entre Chuncani e Ichocarpa, por el camino Mojos–Queara, 3200 m, *A. Fuentes 11864*, 13 May 2007 (holotype: UC1930701! photo; isotypes: LPB n.s., MO2122524! photo).

Description – *plants* terrestrial; *rhizome* dark, erect, non-stoloniferous, scaly, scales 6–10 × 1.2–2 mm, lanceolate, dark reddish brown, margins entire; *sterile fronds* 32 × 6.5 cm, erect; *petioles* 15 cm × 1.5 mm, proximally dark reddish brown, distally straw–like, glabrous proximally bearing some reduced rhizome-like scales; *lamina* broadly lanceolate, 1-pinnate truncate base and a gradually reduced apex with a conform apical pinna, scattered hairs on the laminar faces, the hairs 0.05–0.15 mm long, mostly 2 or 3–celled, with a whitish glandular apical cell; *rachis* straw-coloured, with scattered scales, scales 0.5–1.5 × 0.2–0.8 mm, broadly lanceolate, margins strongly toothed, pale to medium brown, the larger scales with darker bases, adaxially glabrous, abaxially; *sterile pinnae* in ca. 12–15 pairs, 37 cm long, stalked, alternate to subopposite, slightly falcate, apices acuminate, bases cordate, margins narrowly hyaline, finely serrulate; *costae*

grooved adaxially, prominent abaxially, similar to the rachis, with scattered scales, 0.2–1.5 × 0.1–0.8 mm, broadly lanceolate, margins strongly toothed, light brown, the larger ones with darker bases; *veins* free, simple or 1-furcated, not immersed, with sparce scales similar to those on the costa, catadromous; *aerophores* axillary, small, tuberculate; *hydathode* small, ovate; *fertile fronds* similar to sterile ones, but longer, 38 cm long;, *fertile pinnae* narrower and longer, 50 × 5 mm, the rachis scales longer, darker and denser than in sterile pinnae, extending more towards the lamellar surfaces, fewer and darker hairs; *sori* linear, continuous, forming coenosori on both sides of the costa, absent in the proximal 1–4 mm and distal 12–20 mm of the pinna, with green laminar tissue extending beyond the indusium; *indusia* linear, continuous, open towards the costa, brown, entire to eroded at maturity; *sporangia* with 16–17 arc cells; *spores* monolete (40–)49(–61) × (30–)37(–44) µm, perispores smooth, crested-reticulate, high-walled, thick, forming medium to large areoles, no filamentous processes (**Figure 94**).

References – Smith & Kessler (2018).

Chromosome number – unknown.

Distribution and habitat – endemic to Bolivia, known only from the type locality, at 3200 m in humid montane forest (Smith & Kessler, 2018), and from three specimens collected by O. Butchtien (P01546453, P01546454, US1096159), reported here.

Etymology – this species is dedicated to Dr. T. Wohlgemuth, in recognition of his important ecological and plant floristic research (Smith & Kessler, 2018).

Notes – *Parablechnum wohlgemuthii* differs in the other species of *Parablechnum* primarily by the glandular–tipped hairs on the lamellar surface. In addition, the rachis and costa scales are more strongly toothed than in its Bolivian relatives (*P. bolivianum*, *P. cochabambense*, *P. pazense*).

Reviewed material:

BOLIVIA. **Dept. La Paz:** Prov. Franz Tamayo, Parque Nacional Madidi, entre Chuncani e Ichocarpa, por el camino Mojos–Queara, 3200 m, *A. Fuentes 11864*, 13 May 2007 (MO2122524! Photo, isotype; UC1930701! photo, holotype); Las Yungas, Sirnpaya verde Yanacachi, *O. Buchtien 467*, 24 December 1906 (US1096159!); *ibidem*, *O.*

Buchtien 506, 11 December 1906 (P01546454!); Near Yungas, *H.H. Rusby 312,* 1885 (NY!). **Unknown Department:** *O. Buchtien s.n.*, July 1902 (P01546453!).

Figure 94. *Parablechnum wholgemuthii*. A. Sterile frond fragment; B. Fertile fronds; C. Sterile pinna apex, adaxial side; D. Sterile pinna margin, abaxial side, with hairs (arrows); F. Fertile pinnae bases, adaxial side; G. Fertile pinna apex, abaxial side; H. Rhizome. (A, C-E: *O. Buchtien 467,* P01546453; B, F-H: *O. Buchtien s.n.,* P01546453). 4 cm in A, 4.5 cm in B, 9.5 mm in C, 700 µm, in D, 11 mm in F, 9.5 mm in G, 11.5 mm in H.

Parablechnum wurunuran (Parris) Gasper & Salino, Phytotaxa 275(3): 217. 2016.

Basionym – *Blechnum wurunuran* Parris, Proc. Roy. Soc. Queensland 86: 157. 1975.

Type – Bellenden Ker Range, Qld, *L.J.Webb & J.G.Tracey*, Aug. 1959 (holotype: BRI148845! photo; isotype: CANB n.s.).

Synonyms –

=*Blechnum capense* var. *appendiculatum* Domin, Biblioth. Bot. 20(85): 115, t. 8, fig. 3. 1913. Type: Australia, Queensland, Mt Bellenden Ker, *K.Domin* 1909–1910 (holotype: PR 249/523499 n.s., sterile frond; isotype: PR 246/523496 n.s., fertile frond).

=*Lomaria eximia* F.Muell., Fragm. 5: 188. 1866. Type: Australia, Queensland, Mount Pleasant Creek, Rockinghams Bay, *J. Dallachy s.n.*, 9 June 1866 (holotype: MEL54065! photo).

Description – *plants* terrestrial; *rhizome* shortly creeping to erect, non-stoloniferous; *fronds* dimorphic; *sterile fronds* 43–135 × 13–43 cm; *petioles* 22–70 cm long, dark brown to reddish brown at base, often straw-coloured above, scaly, scales lanceolate, acuminate, entire or sometimes with marginal excrescences, brown to reddish brown, sometimes bicolorous, lanuginose hairs also present; *lamina* lanceolate to ovate, 1-pinnate; *rachis* reddish brown to straw–brown, the larger scales lanceolate, acuminate, reddish brown, mostly entire, often also present fine matted scales and lanuginose hairs, grooved adaxially, prominent abaxially, papillae sometimes present, especially near the groove; *sterile pinnae* in up to 29 pairs, narrowly ovate to linear oblong, 7–27 cm long, 12–23 mm wide, shortly stalked, becoming basiscopically adnate distally, margins crenulate and serrate, basal pinnae similar or slightly shorter, alternate to subopposite; *veins* free, simple or 1-furcated, catadromous; *aerophores* not seen; *hydathodes* patent; *fertile fronds* longer; *fertile pinnae* linear, 10–21 cm long, 3–4 mm wide; *sori* linear, continuous, forming coenosori on both sides of the costa; *indusia* linear, continuous, open towards the costa; *sporangia* not observed; *spores* monolete, 59 × 43 µm, perispore alate–costate, walls with ciliate margins, exine scaberulose (**Figure 95**).

References – Chambers & Farrant (1998b).

Chromosome number – unknown.

Distribution and habitat – endemic to northeast of Queensland, Australia. In lowland or montane rainforest, up to 1800 m, sometimes on rocks near streams. (Chambers & Farrant, 1998b).

Figure 95. *Parablechnum wurunuran.* (*L.J. Webb & J.G. Tracey 6421,* BRI-AQ0022374). Scale: 4 cm.

Notes – usually found in shaded conditions, but there is a "sunny" form of the species which has narrower, lighter fronds, with narrower, shorter, and less widely spaced pinnae. It is mostly similar to *P. wattsii* and occupies the same ecological niche but in more northerly latitudes. It has finer, lighter fronds than *P. wattsii* and tends to have reddish-brown, serrate to entire scales on rachis and costa, while those of *P. wattsii* are much

darker and usually serrate with marginal excrescences. *Parablechnum wurunuran* also tends to have more numerous and matted fine hairs and scales than *P. wattsii*. (Chambers & Farrant, 1998b).

Reviewed material:

AUSTRALIA. Queensland: Bellenden Ker Range, *L.J.Webb & J.G.Tracey s.n.*, 08. 1959 (BRI148845! photo, holotype); Mount Pleasant Creek, Rockinghams Bay, *J. Dallachy s.n.*, 9 June 1866 (MEL54065! photo, holotype of *Lomaria eximia*).

Taxa with uncertain status:

Parablechnum gemmascens (Alston) Gasper & Salino, Phytotaxa 275(3): 217. 2016

Basionym – *Blechnum gemmascens* Alston, Bull. Jard. Bot. État 27: 57, f. 4. 1957.

Type – Colombia: Cundinamarca: Paraiso (cerca de Sumapaz), 1400 m, *Køie 4584*, 5 June 1952 (holotype: BM001079672! photo).

Description – *rhizome* erect, about 8 cm high; *fronds* about 45 cm long, *petioles* 20 cm long, purple, inclusive, some gemmae in the upper zone, with pale brown scales at the base, membranous, 1 cm × 3 mm, with oblong pinnae on each side, *pinnae* in 15 pairs, stalked, narrowly oblong, c. 8 cm long, 1 cm wide, minutely serrate-crenulate, glabrous, with mostly simple veins, white–tipped at apex, *costae* lined with a few small scales; *fertile fronds* with narrower pinnae, ca. 3 mm wide; *sori* completely covering the abaxial face, covered with a few small scales on the costa, tapering at apex; *sporangia* usually with 20 arch cells; *spores* are usually smooth.

References – Alston (1957).

Chromosome number – unknown.

Distribution and habitat – Colombia: Cundinamarca: Paraiso, 1400 m (Alston, 1957).

Etymology – the specific epithet probably refers to the gemmae mentioned in the diagnosis in the upper zone of the petiole.

Notes – According to Alston (1957) it has affinity with *Parablechnum glaziovii* but differs in the numerous sterile pinnae and the more acuminate fertile pinnae, although in this work specimens of *P. glaziovii* have been found with up to 14 pairs of pinnae, which does not differ much from this species (15 pairs of pinnae). However, as also noted by A. Smith in Bernal *et al*. (2016), this species has not been observed again and its status is uncertain. In the plants reviewed in this work, nothing similar has been observed in Cundinamarca, so the validity of this species is doubtful. Also, it is not clear the meaning of "gemmae" by the author, he could be referring to bulbils, which is a rare character in *Parablechnum* only found in *P. proliferum* and *P. sessilifolium*, or to aerophores.

Reviewed material:

COLOMBIA. Dept. Cundinamarca: Paraiso (cerca de Sumapaz), *Køie 4584*5 June 1952 (BM001079672! photo).

New species

There have been detected three taxa which constitute possible new species. The specimens are cited here, and the species will be described in further publications.

New species #1

ECUADOR. Prov. Azuay: the Eastern Cordillera, 1–8 km, north of the village of Sevilla de Oro, *W.H. Camp 4299*, 27 July 1945 (NY04187088!; US2080228!). **Prov. Zamora Chinchipe:** Nangaritzaq, Cordillera del Cóndor region. Along upper Rio Nangaritza between Las Orquídeas and Shaime, *H. van der Werff et al 21926*, 5 November 2006 (NY04187079!).

New species #2

COLOMBIA. Dept. Cauca: Macizo Colombiano, páramo de Las Papas, El Boquerón, *Idrobo et al. 3222*, 7 September 1958 (P01531010!; P01531012!). **VENEZUELA: Prov. Mérida:** *Funck & Schlim 1008*, August 1846 (P01546425!).

New species #3

COLOMBIA. Dept. Cundinamarca: Bogotá, above Usaquén, *A.H.G. Alston 7467*, 13 March 1939 (BM001079543! Photo; BM001079544! Photo).

Material that could not be ascribed to any taxon

Sub. *Blechnum sp.*

BOLIVIA. Dept. La Paz: Prov. Unduavi, *C. Aedo et al 14541*, 12 August 2007 (MA759404!). **BRAZIL. Rio Grande do Sul:** *E. Leite 672*, December 1941 (NY00813980!). **Santa Catarina:** São Bento do Sul, Sertaozinho, em beira de estrada, após a capelinha, *P. Schwirkowski 1990,* 23 October 2016 (FURB52094! Photo). **São Paulo:** Campos do Jordão, caminho PI S. José dos Alpes, *A. Santos 234 & T. Silva-Oliveira 4*, 1 July 1984 (RB224247! Photo); Iporanga/Apiai, near Parque Estadual Turístico do Alto Ribeira (PETAR), núcleo Santana, *F.F.F. Mazziero & A. Soller 692*, 21 September 2011 (NY02423743!). **COLOMBIA. Dept. Antioquia:** Municipio de San Luis, hacia la Vereda Manisales, *C.I. Orozco et al 526*, 11 October 1981 (NY!). **Dept. Cauca:** Páramo de Puracé, Central Cordillera, *E.P. Killip & F.C. Lehmann V 38591*, 26 May 1944 (US2608554!). **Dept. Chocó:** San José, Mun. del Palmar, Cerro del Torra, *J.E. Ramos et al. 1522*, 25 August 1988 (NY!). **Dept. Cundinamarca:** Carretera entre Cogua y San Cayetano, *M.T. Murillo et al. 1058*, 9 May 1967 (NY!, 3 sheets), Carretera entre Cogua y San Cayetano, *M.T. Murillo et al 1047*, 9 May 1967 (NY!); Mun. De Gachetá, km 87.7, *C.E. Acosta-Arteaga 538*, 22 June 1974 (NY!, 2 sheets); Mun. De Sibaté, Alto de San Miguel, km. 31 de la carretera a Fusagasugá, *C.E. Acosta-Arteaga 136*, 3 February 1974 (NY!); Zipaquirá, en el páramo Alto de Águila, *M.T. Murillo 590*, 23 June 1962 (NY!). **Dept. Santander del Sur:** entre Bucaramanga y Pamplona, arriba de la Corcova, *M.T. Murillo & R. Jaramillo 1152*, 5 November 1969 (NY!). **Unknown Department:** Manecillo, *C.E. Knoth 3166*, 11 March 1951 (NY!). **ECUADOR. Prov. Carchi:** Huaca, Parroquia Mariscal Sucre, Estación Biológica GUandera, Sendero Oso, *A. Álvarez & C. Padilla 2946*, 30 May 2002 (NY!). **Prov. Zamora:** Nangaritza, Cordillera de Nanguipa, Cerro Colorado, Ridge 8 km SSE of Nambija, 20 km ESE of Zamora, *C.J. Cole et al 282*, 20 February 2002 (NY!). **GUADALUPE. Unknown area:** *A. Duss 4158a*, no date (NY02007973!); *M. L'Herminier 2,* 1944 (NY02480618!). **GUYANA.** Mt. Roraima, NW facing slopes of Mt. Roraima, vicinity of Camp 6 (near the end of the 'Waruma Trail'). C.lml. N. of the 'prow', *J.R. Woodhams et al 1078*, 1978 (NY!); Mt Roraima, ond the "Ledge" above Rondon Camp, *G.H.H. Tate 470*, 1 December 1927 (NY02597332!). **JAMAICA. St. Thomas Parish:** vicinity of Blue Mountain Peak, *R. Chambers J75*, August 1976 (VT198489!). **MALESIA. Borneo:** Sarawak, Mt. Poï, *E. Mjöberg s.n.*, no

date (P01630642!). **PANAMA. Prov. Chiriquí:** Dist. Boquete, Fortuna dam site, *H. van der Werff & C. van Hardeveld 6724,* 8 February 1985 (US3126020!). **PARAGUAY. Dept. Amambay:** National Park Cerro Corá, along Aceite-i-creek, *E.M. Zardini & P. Báez 52623,* 12 November 1999 (NY!); Prov. Yungay, alrededores Laguna Llanganuco, *J. Mostacero L. et al 1402,* 9 August 1986 (NY!). **Dept. Paraguai:** Parque Nacional Ybycu'i, Gallery forest along tributaries of Arroyo Minas in NE corner of the Park, *E. Zardini 8720,* 14 December 1988 (NY!). **PERÚ. Dept. Ancash:** Caraz, Laguna Porón, Huaylas, *A. López et al. S.n.,* 17 May 1976 (NY!). **Dept. Pasco:** Oxapampa, along old road Oxapampa-Cerro de Pasco, *H. van der Werff et al. 17969,* 3 July 2003 (NY!, 2 sheets). **PUERTO RICO.** Monserrat, Gages near the Soufriere, *J.A. Shafer 202a,* 23 January 1907 (NY02007972!). **VENEZUELA. Bolivar:** Chimantá Massif, Abácapa-tepuí, *J. Steyermark 74916,* 13 April 1953 (NY!, 2 sheets) **Merida:** *A.L. Bernardi 6221,* 17 February 1957 (NY!, 2 sheets); 75 km N.E. of Mérida along road to Barinas, *F.J. Breteler 3360,* 20 November 1963 (NY!). **Tachira:** Uribante, en los alrededores del campamento Siberia (CADAFE), *F. Ortega & H. van der Werff 2844,* 21 November 1985 (NY!).

Sub. *Blechnum ambiguum*

MAURICE. *no collector,* 1955 (P01565266!).

Sub. *Blechnum arborescens*

COLOMBIA. Unknown department: *F.C. Lehman 4422,* no date (US834104!). **Dept. Antioquia:** Santa Elena, *W.A. Archer 1192,* 28 December 1930 (US1544648!). **Dept. Cauca:** Caanan, Mt. Purace, Cordillera Central, Río Aguablanca, *E.P. Killip 6749,* 11-16 June 1922 (US1144458!); Miranda, Pico de Naiguatá, *Silince 793,* 26 May 1940 (MA284295!). **Dept. Cundinamarca:** Bogotá, old Spanish road from San Cristobal to Tibagua, *H. Schiefer 337,* 7 January 1945 (US2543412!); low ridge easte of Calle 55, Bogotá, Cordillera Oriental, *E.L. Little & R.R. Little 7828,* 7 May 1944 (US2419372!); *ibidem, E.L. Little & R.R. Little 7829,* 7 May 1944 (US2419460!); hills at west base of Monserrate, east of Bogotá, Cordillera Oriental, *S. Galen Smith 1012,* 13 June 1950 (US2019869!); Marizo La Bogotá, Quebrada de Chicó, *J. Cuatrecasas 5393,* 8 June 1939 (US1795483!); Mun La Calera, W del Páramo de la Siberia, valle de Sopó, carretera a guasea El salitre, *H. Humbert et al 26876,* 25 October 1952 (P01462397!); Usaquén, near

Bogotá, *M. González & Bto Daniel 1847*, January 1939 (US1743128!). **Dept. Santander:** Páramo de las Puentes, above La Baja, Eastern Cordillera, *E.P. Killip & A.C. Smith 18252*, 25 January 1927 (NY!; US1353699!); Páramo de Romeral, Eastern Cordillera, *E.P. Killip & A.C. Smith 18611*, 29-30 January 1927 (US1353995!); Quebrada de País, north of La Baja, *E.P. Killip & A.C. Smith 18826*, 31 January 1927 (US1354175!). **ECUADOR. Prov. Pichincha:** Corazón PEak (N. slope) and Corazón Pass (W. side), Cordillera Occidental, *A.E. Joseph 16415*, 8 November 1944 (US2254311!). **UNKNOWN LOCALITY:** *no collector*, no date (P01662904!).

Sub. *Blechnum capense*

AUSTRALIA. *Daemel s.n.*, no date (P01463067!); *Koch s.n.*, 09.1902 (P01463066!); *M. Verreaux*, no date (P01532248!). **New South Wales:** *R. Brown s.n.*, no date (P01532237!); *R. Brown s.n.*, 1802 (P01462486!). **Queensland:** *Dallachy s.n.*, no date (P01463069!). **South Australia:** *Baudin s.n.*, 1801 (P00526898!); *Koch 817*, 09.1902 (P01463071!; P01463072!). **Tasmania:** *Jacquinot 16*, 1838 (P01463081!); *Verreaux s.n.*, 1844 (P01463061!). **Victoria:** *Toepffer 126*, 25 November 1886 (P01463086!); near Mt. Ellery, East Guippoland, *E. Merrah s.n.*, 1887 (P01462495!). **COLOMBIA. Dept. Cundinamarca:** Bogorá, *Apollinaire s.n.*, 04.1906 (P01546431!); *ibidem*, 03.1906 (P01546434!). **ECUADOR. Prov. Pichincha:** *A. Mille s.n.*, 08.1897 (P01546383!); *ibidem* (P01546384!). **Unknown área:** *J. Verleysen s.n.*, no date (P01546373!). **FIJI. Unknown area:** *no collector*, no date (NY!). **FRENCH POLYNESIA. Tahiti:** Mahina, Ahonu-Tuauru, with motu purata, mamau, *E.B. Copeland 4394*, 5 November 1930 (NY!). **INDONESIA. Java:** *Eulofatá 274*, no date (P01532259!); *Reinwardt s.n.*, no date (P01532251!); Mt. Malabon, *T. Anderson s.n.*, 19 October 1861 (P01532236!). **NEW ZEALAND.** *no collector*, no date (P01462550!); *Cuming s.n.*, no date (P01462566!); *Craig s.n.*, no date (P01462544!); *J.D. Hooker s.n.*, no date (P01532235!); *Tescott s.n.*, 1901 (P01463070!); *Védel s.n.*, 1847 (P01462527!); *ibidem* (P01462528!). **North Island:** Astrolabe, *D. Jaun 17*, no date (P01462582!); Auckland, *E. Nielsen 383*, 30 December 1928 (US2290861!); Auckland, *E. Nielsen 384*, 30 December 1928 (US2290862!); Auckland, *H. Carse 18*, 15 May 1923 (P01462557!); Auckland, *P. Serre s.n.*, 1931 (P01462586!). **AMERICA.** *no collector*, no date (P01662903!); *ibidem* (P01482940!); *ibidem* (P01482941); *ibidem* (P01482943!); *ibidem* (P01546377!); *ibidem* (P01546378!); *ibidem* (P01546381!); *H. Christ 11559b*, no date

(P01546379); *H. Christ 11560b,* no date (P01546379); *Luersen s.n.*, 1873 (P01482946!); *Luersen s.n.,* 08.1870 (P01482951!); *ibidem* (P01482952!); *ibidem* (P01482953!); *ibidem* (P01482954!); *Luersen s.n.,* 11.1870 (P01482948!); *Luersen 1745,* 11.1870 (P01482947!). **ASIA.** *no collector,* no date (P01406633!); *ibidem* (P01532242). **OCEANIA.** *no collector*, no date (P01532231!); *ibidem* (P01532238!); *ibidem* (P01532239!). **CULTIVAR.** America, *Luersen s.n.,* 06.1872 (P01482950!); America, *P. Molesworth s.n.,* no date (P01546393!); *ibidem* (P01546399!).

Sub. *Blechnum chilense*

ECUADOR. Prov. Loja: Yangana, Yangana-Valla Rd. 11 km S. of Yangana, *M.R. McCarthy & E. Tepe Z249,* 31 July 2011 (NY04187089!).

Sub. *Blechnum cordatum*

BOLIVIA. Dept. Cochabamba: Prov. De Chapare, road to San Onofre, 3.2-3.5 km. ±N of road to Villa Tunari at point 97.5 km from Cochabamba, *M.S. Forest 79-178,* 14 November 1979 (UC1475860! Photo). **Dept. Santa Cruz:** Cascadas del agua, road Santa Cruz, Samaipata, *H.T. Kuhn 144,* 11 July 1976 (VT198670!); Manuel Caballero, *R. Núñez 593,* 26 March 2004 (NY!); Prov. Florida, near bottom of valley of Quebrada Guapurucillo, steep slopes, between mountains of massive red sandstone of Serranía de la Cruz road to Bella Vista, 2 km SE from turnoff (the turnoff ca. 3 km E of Cuevas from highway from Santa Cruz to Samaipata), *M. Nee 48370,* 16 February 1998 (NY00306231!). **BRAZIL. Espirito Santo:** Castelo, Parque Estadual do Frono Grande, Trilha para o Forninho, *P.H. Labiak et al 4556,* 12 February 2008 (RB463333! Photo). **Minas Gerais:** *Weddell 1554*, 1 November 1843 (P01466431!); Bocaina de Minas, Parque Nacional do Itatia, Caminho para o Alto dos Brejos, *L.S. Sylvestre & J.P.S. Condack 1735*, 16 June 2004 (RB0040783! Photo). **Parana:** Mun. Porto Amazonas, Lajeado, *O.S. Ribas et al 3614,* 12 June 2001 (MBM259117! Photo; UCS32313! Photo); Ponta Grossa, Nascente do rio Tibagi, campos higrófilos sobre Organossolo, *B.O. Andrade 303,* 29 March 2009 (MBM360624! Photo); Ponta Grossa, Parque Estadual de Vila Velha, Próximo a Lagoa Dourada, Campos Naturais, *P.B. Schwartsburd et al 746*, 23 April 2005 (NY01015456!); Rio dos Papagaios, Palmeira, *M.G. Caxambu et al 2165*, 20 April 2008 (MBM347294! Photo). **Rio de Janeiro:** *M.E.R. Wagner s.n.*, no date (P01212519!). **Santa Catarina:** Mun. São Bento do Sul, *A.L. de Gasper & L. Sevegoani*

94, 30 March 2007 (FURB5639! Photo); Mun. São Bento do Sul, Rio Vermelho, *A. Korte 5938,* 16 February 2011 (FURB34084! Photo); Urubici, Morro da Igreja, *L.L. Almeira & A.L. de Gasper,* 8 April 2010 (FURB35521! Photo). **São Paulo:** São José do Barreiro, Parque Nacional da Serra da Bocaina, Cachoeira São Izidro, *P.H. Labiak et al 4287,* 6 January 2008 (UPCB61097! Photo). **COLOMBIA. Dept. Antioquia:** Frontino, Corregimiento Carauta, Parque Nacional Natural Las Orquídeas, sector Tres Bocas, bosques a la orilla del río Santiago, minas del río Santiago ("Mina La Salada), finca La Pradera, *M. Sundue et al. 3316,* 10 September 2012 (VT198668!); Mpio. Bello, corregimiento de San Félix, Alto de Las Baldias, sector Antenas de el Colombiano, W.D. Rodríguez et al. 5477, 30 September 2005 (NY!). **Dept. Cauca:** Parque Nacional Munchique, El Tambo, Vereda la Romelia, *F. González et al. FG1950,* 18 July 1993 (MA610969!). **Dept. Cundinamarca:** Monserrate, 1 km. East of Bogotá, *R.M. Tryon & A.F. Tryon 5911,* 27 September 1961 (NY04187098!; US2722290!). **Unknown department:** *J.C. Mutis 3120,* 1760-1808 (US1563581!). **ECUADOR. Prov. Cotopatxi:** Reserva Ecológica Los Ilinizas, Sector Tilipulo, Cordellera Tilinche, Cordellera Occisental, veriente occidental, *P.A. Silverstone-Sopkin 10189,* 20 August 2003 (MO4806421!; UC1792400! Photo; UC1792401! Photo). **Prov. Loja:** Parque Nacional Podocarpus, Cajanume, *M. Lehnert 2297,* 3 December 2010 (VT198663!). **Prov. Napo:** Oyacachi, Pot 3TE-05, *M. Lehnert 3203,* 4 March 2015 (VT198667!). **Prov. Pichincha:** *A. Sodiro s.n.,* 7.1907 (P01546353!). **PERU. Dept. Ancash:** Prov. Huaylas, *A. López et al 8378,* 17 May 1976 (UC1482722! Photo). **Dept. Cajamarca:** Jaén, Sallique, Localidad La Concha, *J. Campos et al. 5060,* 23 June 1998 (NY!). **VENEZUELA. Amazonas:** Dpto. Río Negro, Cerro de la Neblina, CAMP VII, 5,1 m NE Pico Phelps (=Neblina) (21,5 km E Neblina Base Camp), *J. Beltel 85116,* 1 February 1985 (NY!, 2 sheets). **Anzoátegui:** Dist. Freites, Cerro Peonía, above Los Pajaritos, 31 airline km NE of Bergantín and N of Mundo Nuevo, Serranía de Turimiquire, *G. Davidse & A.C. González 19901,* 2-3 December 1981 (NY!). **Aragua:** Colonia Tovar, *A. Fendel 118,* 1854 (NY04187095!); Colonia Tovar and vicinity, *H. Pittier 9380,* 1921 (NY!). **Caracas:** *O. Kuntze 1661,* 25 May 1874 (NY!).

Sub. *Blechnum costarricense*

PANAMA. Prov. Chiriqui: N.O. del campamento Fortuna, *M.D. Correa et al. 2599,* 23 September 1976 (NY!).

Sub. *Blechnum divergens*

BRAZIL. Paraná: Telêmaco Borba, Parque Ecológico da Klabin, Trilha Ecológica, *C.R. Sakagami & K. Sakagami 45,* 28 June 2004 (VT198725!).

Sub. *Blechnum euraddianum*

BRAZIL. Paraná: Morretes, *G. Hatschbach 2081 & J.P. Fontella 390,* April 1969 (UC1389082! Photo).

Sub. *Blechnum falciforme*

GUYANA. Mount Roraima and Vicinity, lower part of Pilipp Brook, *G.H.H. Tate 353,* 1927 (NY02497205!); Rio das Mortes (Mun. Jaguariaiva), *E. Barbosa & E.F. Costa 1313,* 4 May 2006 (UC1872166! Photo).

Sub. *Blechnum lechleri*

COLOMBIA. Huila: Macizo Colombiano, páramo de Las Papas, Cerros y alrededores de la laguna La Magdalena, *Idrobo et al. 3244,* 16 October 1958 (US3360681!).

Sub. *Blechnum lineatum*

BRAZIL. Paraná: *Besto 2541,* no date (P01395983!); Boa Vista (Mun. Adrianópolis), *G. Hatschbach 43618,* 19 February 1981 (UC1493584! Photo). **Rio do Janeiro:** Campo Bello, *Glaziou 7009,* 4 March 1893 (NY00814073!; NY00814074!); Theresopolis [interpreted], *illegible colector 20824,* 11 March 1917 (UC441986! Photo). **Rio Grande do Sul:** Santa Cruz, *C. Jürgens 261,* November 1904 (NY00814078!). **Santa Catarina:** Joinville, *E.O. Muller 124,* 1906 (NY00814077!); Pirabeirada [interpreted], *Illegible collector 82,* November 1903 (UC441984! Photo). **São Paulo:** Campos de Bocaina, *Gaziou 7941,* 11 February 1876 (P01395995!; P01395996!; P01395997!); Moira, *Brade 5821,* February 1913 (NY00814073!); Moira, *Brade 6390,* January 1913 (UC441985! Photo). **Unknown State:** *Cetropoli 2394,* 02.1881 (P01395984!). **AMERICA.** *Puiggari s.n.,* no date (P01395985!).

Sub. *Blechnum loxense*

COLOMBIA. Dept. Nariño: Mpio. Pasto, entre km 29-30, carretera Pasto, San Francisco (Putumayo), *S.P. Churchill & W. Rengifo s.n.,* 15 January 1991

(NY04187094!). **ECUADOR. Prov. Pichincha:** Mun. Cantón Machachi, reserva Ecológica Los Ilinizas, hacienda del Sr. Segundo Verachucha, por el camino que de la casa va al oeste, ca. 400 m de la casa, *J.E. Ramos et al 7397*, 18 August 2003 (NY04187093!).

Sub. *Blechnum montbrisonis*

REUNIÓN. *F. Bradé 9*, no date (P00917031!).

Sub. *Blechnum procerum*

BRAZIL. Unknow State: *Luersen 12740*, no date (VT198688!). **ECUADOR. Prov. Pichincha:** *Sodiro & M. Gandoger s.n.*, 1899 (P01575951!). **SAMOA. Savail Island:** above Matavanu, *E. Christophersen 799*, 24 September 1929 (US1919527!). **UNKNOWN LOCATION:** *Underwood s.n.*, no date (NY!).

Sub. *Blechnum regnellianum*

BRAZIL. Bahía: Serra de Agua de Rega, ca. 26 km N of Seabra, road to Agua de Rega, near Rio Riachão, *H.S. Irwin et al 30822*, 23 February 1971 (NY00814191!). **Brasilia:** Distr. Federal, ca. 25 km S.W. of Brasilia D.F., *H.S. Irwin et al 13029*, 19 February 1966 (NY00908657!). **Espírito Santo:** Victor Hugo, Mun. Marechal Floriano, *G. Hatschbach et al. 71380*, 18 October 2000 (UC1747760! Photo). **Minas Gerais:** *illegible collector 614*, 1854 (K000954320! Photo); S. Sebastião do Paraiso, *Brade 17969 & A. Barbosa 52555*, 24 April 1945 (K000954318! Photo); Serra do Espinhaço, ca. 11 km N of Gouveia, Municipio de Datas; km. 286 on M.G. 256, *W.R. Anderson et al 35577*, 6 February 1972 (K000954310! Photo; NY00908656!). **Paraná:** Fazenda Santa Rita, Palmeira, *Dombronski 13066*, 28 January 1981 (MBM320166! Photo); Mun. Jaguariaiva, Vale do Codó, *E.F. Costa & L. von Linsingen 1084*, 13 July 2005 (MBM307916! Photo); Rio Laranjinha, Mun. Ventania, *G. Hatschbach et al 68308*, 3 September 1998 (UC1732299!); Rod. BR-277, lm 156, próximo ao pedagio, Mun. Palmeira, *E. Barbosa et al. 471*, 20 April 2000 (UC1746541! Photo). **Rio do Janeiro:** Mun. Guapimirim, Parque Nacional da Serra dos Oroãnos, estrada para Teresópolis, base do Dedo de Deus, "Santinha", *J.M.A. Braga & M.G. Bovini 988*, 22 January 1994 (RB00545795! Photo!); Teresopolis, Parque Nacional da Serra dos Órgãos, near the road between entrance and Barragem, R. Engelmann RE243, 24 February 2005 (NY01015588!; RB00421574! Photo). **Santa Catarina:** Morro do Pinheiro Seco, Lajes, *Reitz & Klein 14891*, 14 April

1963 (NY00814192!). **São Paulo:** Campos de Jordão, *P. Campos Porto 3078*, 20 February 1937 (RB0032259! Photo, 2 sheets); Bauru, Jardim Botanico Municipal de Bauru, queda d'água do Botánico (cahoerinha), *G.A. Nóbrega & M. Andrade 96*, 14 April 2005 (NY02425750!). **Unknown area:** *illegible collector 5934*, March 1841 (K000954323! Photo).

Sub. *Blechnum schiedeanum*

COLOMBIA. Unknown area: *R.G. Fonnegra 3515*, 23 April 1991 (MO4566326!).

Sub. *Blechnum stenophyllum*

BRAZIL. São Paulo: *Brade 5155*, 9 February 1912 (UC441991! Photo). **COLOMBIA. Dept. Cundinamarca:** Bogotá, *J. Goudot 73*, no date (P01462411!); Bogotá, *J. Triana s.n.*, 1857 (P01462412!); *ibidem* (P01462405!) *ibidem* (P01462412!). **AMERICA.** *no collector*, no date (P01462406!); *Lindig 97*, no date (P01462414!).

Sub. *Blechnum stipitellatum*

COLOMBIA. Dept. Antioquia: Mpio. Belmira, Vereda La Salazar (parte baja), quebrada el Diablo, *W. Rodriguez & M. Arboleda 3442*, 20 June 2002 (NY04187090!); Mpio. Jericó, Límites entre los municipios Jericó-Pueblo Rico, *W.D. Rodriguez et al 4791*, 13 December 2004 (NY04187091!; NY04187092!). **ECUADOR. Prov. Pichincha:** Quito-Santo Domingo via Chiriboga (old-road), *C.P. Dodson & W.P. Clendenin 10844*, 15 May 1981 (US2977887!). **PERÚ. Prov. Bagua:** Cordillera Colan NE of La Peca, *P. Barbour 3467*, 9 September 1978 (US3366618!).

Sub. *Blechnum striatum*

BRAZIL. Rio do Janeiro: *Brade 9479*, September 1929 (UC441988! Photo). **São Paulo:** *Brade 8585*, November 1928 (UC441989! Photo); Rio Grande, *Brade 6626*, August 1913 (UC441989! Photo). **COLOMBIA**. *J. Linden 307*, no date (P01466416!). **Dept. Boacá:** Carretera entre Chiquinquirá y Pauna, arriba de San Antonio, *M.T. Murillo et al. 3325*, 3 September 1967 (P01466418!). **Dept. Cundinamarca:** *R. Jaramillo Mejía et al. 4704*, 16 December 1967 (MA380282!; NY!); Bogotá, *J. Triana 126*, no date (P01466409!). **Dept. Magdalena:** Santa Marta, *H.H. Smith s.n.*, 1898 (P01623186!). **COSTA RICA. Unknown Province:** *J.M. Greenman 5383*, 30 January 1922

(MO906728!). **ECUADOR.** *M.A. Bonpland s.n.,* no date (P01409495!). **Prov. Pichincha:** Dos Puentes, *Liebmann s.n.,* no date (P01409536!). **MARTINIQUE.** Morne de la Cabbasse, *Belanger 412,* 02.1853 (P01466472!). **JAMAICA.** Ouaiamaca, *Vaillaud 784,* no date (P01409518!). **PARAGUAY.** Caaguazu, *B. Balansa 665,* 1874 (P01466391!). **PERU.** *Dombey s.n.,* no date (P01466405!). **AMERICA.** *no collector,* no date (P01409524!); *ibidem* (P01409525!); *ibidem* (P01409527!); *ibidem* (P01409535!); *L. Savatier 268,* 1876 (P01409528!); *Wildeman s.n.,* 8 April 1909 (P01409531!); *ibidem* (P01409532!); *ibidem* (P01409533!); *ibidem* (P01409534!).

Sub. *Blechnum stuebelii*

BRASIL. Roraima: *E. Ule 8509,* 02.1910 (B200034237!); *ibidem* (B200034238!). **COLOMBIA. Dept. Cundinamarca:** Bogotá, *Stübel 415,* 1934 (B200034235); Bogotá, *Stübel 435,* 1934 (B200034231!). **Dept. Meta:** Mun. Llanos de San Martin, Salto del Diablo, *Stübel 683,* 1934 (B200034234!). **Dept. Tolima:** Pandano, *Stübel 59,* 1934 (B200034233!). **ECUADOR. Prov. Tungurahua:** *Stübel 841,* no date, (B200034232!). **PERU. Prov. Cusco:** La Convención, bajando del Pto de Málaga, *J.M. Gabriel y Galán s.n.,* 29 April 2008 (MACB!); *ibidem* (MACB!).

Sub. *Blechnum varians*

MEXICO. Veracruz: *Wolfe s.n.,* 31 March 1976 (VT285880!).

Sub. *Blechnum violaceum*

BOLIVIA. Prov. Santa Cruz: Manuel M. Caballero, *R. Núñez 564,* 23 March 2004 (NY!); Manuel M. Caballero, Colecta a 2 km al Suroeste de la comunidad de Siberia, *R. Núñez 617,* 8 April 2004 (NY!); *ibidem, R. Núñez 650,* 9 April 2004 (NY!). **COLOMBIA. Dept. Antioquia:** Mpio. Ciudad Bolivar, Corregimiento San Bernardo de los Farallones, Farallones del Citará, sector La Peña, base del cerro Cabeza de Indio, *W.D. Rodríquez et al 4702,* 11 November 2004 (NY!). **Dept. Cundinamarca:** entre Zipaquirá y Pacho, Páramo de Guerrero, *M.T Murillo & M. Villarreal 1369,* 9 June 1970 (P01662198!); Mpio. De Subachoque, páramo El Tablazo, *M. Hernández–Schmidt 1450,* 12 December 2003 (MA850400!). **DOMINICA. St. Andrew Parish:** Morne Diablotin, *G.L. Webster 13377,* 11 June 1965 (US2419099!). **St. George Parish:** Boiling Lake trail from Laudat, between Titou Gorge and Breakfast river, *S.R. Hill & L.R. Philippe 29089,* 6 March 1997 (UC1619273! Photo; VT291815!; VT291816!); common along trail up

Morne Micotrin, *D.B. Lellinger 484,* 18 October 1965 (US2683955!). **St. Patrick Parish:** top of Morne Nicholls, *D.H. Nicolson 1950,* 9 November 1964 (US2419036!; US2419056!). **DOMINICAN REPUBLIC. Unknown area:** *Lloyd 315,* 1903 (NY02007906!; NY02007908!). **ECUADOR. Prov. Napo:** Tena Cantón, Parque Nacional Llanganates. Cordillera Nor-Occidental del nacimiento del Río Mulatos, Río Mulatos, *H. Vargas et al 2489,* 16 September 1998 (NY!; UC1740385! Photo). **FRENCH ANTILLES. Unknown region:** *F. Bena s.n.,* 1944 (P01618058!); *Fourner 1286,* no date (P01662227!). **GUADELOUPE:** *no collector,* July 1844 (P01662213!); *ibidem* (P01662217!); *Buequet s.n.,* no date (P01662241!); *A. Questel 1091,* 24 July 1934 (US2084104!); *J. Fieldmann s.n.,* 23 April 1936 (P01662215!); *L. Roddriguez 4807, 23 April 1936* (P01662199!); *Leprieur 25,* no date (P01662202!; P01662208!; P01662214!); *L'Herminier s.n.,* no date (NY02007907!); *ibidem* (P00627655!); *ibidem* (P00627656!); *ibidem* (P00627657!); *ibidem* (P01662203!); *ibidem* (P01662205!); *ibidem* (P01662204!); *L'Herminier 3,* 1840 (P01662216!); *Mazé s.n.,* no date (P01662200!); *ibidem* (P01662201); *M. Beaupertuis s.n.,* no date (P01662219!); *ibidem* (P01662220!); *ibidem* (P01662221!); *ibidem* (P01662222!); *M. Beaupertuis s.n.,* 1839 (P01662224!); *ibidem* (P01662225!); *M. Marie 83,* no date (P01662196!; P01662197!); *M. Perrier s.n.,* no date (NY02007910!); *M. Picard s.n.* (P01662195!); *P. Duss 861,* September 1893 (P01662212!); *P. Duss 3710,* 1894 (NY02007911!); *P. Duss 4163,* 1900 (P01662218!); *P. Duss 4165,* 1894 (NY02007913!; NY02007914!; NY02007915!; P01623232!); *T. Husnot 304,* 1868 (P01662209!; P01662210!; P01662211!; P01631387!; P01631389!; P01631388!); Basse Terre/Capesterre, massif de La Souffrière, Carmichaël and Grande Savane, *M.J.M. Christenhusz & F. Katzer 3933*, 6 March 2005 (P01389544!); Forêt des Banis Jaunes, *P. Allorge s.n.,* 22 April 1936 (P01662226!); Plateau de la Saulfrieie et cune, *R.P. Quentin 851,* no date (P01662194!). **GUYANNA.** Potaro.Siparuni Region, Mt. Ayanganna, east face, *H.D. Clarke et al 9426,* 21 June 2001 (US341716!); *ibidem*, Pakaraima Mts., Mt. Wokomung, *T.W. Henkel et al 1536,* 20 February 1993 (US3333343!). **MARTINIQUE:** lules plus hautes montagnes La Dacouverte, fitons de la montagna Pellé, *P. Duss 4163,* 1900 (P01546418!). **PERÚ. Cusco:** Paucartambo Province, Cusco, Wariquichas DD, *Chambi et al 314*, 7 April 2006 (NY!, 2 sheets). **Pasco:** Oxapampa, La Suiza Nueva, *H. van der Werff et al 17545*, 21 June 2003 (NY!, 3 sheets; UC1791015! Photo); Oxapampa, near antenna past Chacos, *H. van der Werff et al 18717*, 21 June 2003 (NY!; (MO5831116!; MO5831117!; UC1790852! Photo).

PUERTO RICO. Sierra de Luquillo in monte Jimenez, *P. Sintenis 1337*, 9 July 1888 (P01623183!). **VENEZUELA. Trujillo:** Distr. Boconó. Montalas de Misisí, ca. 12 km by air NW od Boconó, *Dorr 7257*, 5 July 1990 (NY!, 2 sheets). **AMERICA.** *no collector*, no date (P01662228!); *M. Beaupertuis 1344*, no date (P01662223!).

Sub. *Lomaria alta*

AUSTRALIA. Unknown area: *no collector*, September 1909 (NY!).

Sub. *Lomaria arborescens*

AMERICA: *no collector*, no date (P01662207!).

Sub. *Lomaria obtusifolia*

COLOMBIA. Boyaca: Sierra Nevada de Cocuy, State of Boyaca, Valle de San Jose, towards El Playon over the Boqueron de Cusiri, *P.J. Grubb & D.A. Guymer P109*, 10 September 1957 (US2295639!).

Sub. *Lomaria polyphylla*

UNKNOWN LOCATION: *Presl s.n.*, no daye (NY02007769!).

Sub. *Lomaria procera*

GUYANA. Cuyuni-Mazaruni, Mt. Roraima Expedition, *E.F. Thurn 167*, 10 December 1884 (US0050825!).

Sub. *Lomaria rapcusis*

AUSTRALIA. New South Wales: Neusudioales, Fitzroy Falls, *Meebold 2969*, February 1929 (NY!).

Sub. *Lomaria socialis*

COLOMBIA. Dept. Cundinamarca: Bogotá, *V. Apollinaire s.n.*, 1908 (P01462857!); Bogotá, *V. Apollinaire 202*, 1908 (P01462858!).

Sub. *Lomaria stenophylla*

AMERICA. *no collector*, no date (P01462407!).

Sub. *Lomaria violacea*

GUADELUPE: *L'Herminieri s.n.,* 1846 (MACB!, isotype; US2019932!, syntype; US2703206!, syntype; US2703207!, syntype).

Sub. *Parablechnum sp*

BRAZIL. Santa Catarina: Agua Doce, *A. Kassner 2479,* 23 March 2018 (FURB66893! Photo); Florianópolis, Trilha Praia Matadero, Lagoinha do Leste, *N.P. Smith 645,* 24 February 2019 (FURB63240! Photo); Urubici, Corvo Branco, *A.L. Gasper & J.M. Gabriel y Galán 540,* 10 September 2019 (FURB66894! Photo). **VENEZUELA. Tovar:** *J.W.K. Moritz 298,* no date (NY!, 2 sheets; P01631374!).

Sub. *Struthiopteris sp.*

BOLIVIA. Dept. La Paz: Cañamina: *H.H. Rusby 361,* Jly 1921 (NY!); Cocopunto, *G.H.H. Tate 308,* March 1924-1929 (NY!); *ibidem, G.H.H. Tate 350,* 24-29 March 1926 (NY!); *ibidem, G.H.H. Tate 378,* 24-29 March 1926 (NY!); Ticunhueaya, *G.H.H. Tate 1071,* April 1920-1934 (NY!). **COLOMBIA. Dept. Cauca:** Mount el Derrumbo, Cordillera Occidental, *F.W. Pennell 7495,* 29 June 1922 (US1144559!). **Dept. Santander:** Mesa de los Santos, Eastern Cordillera, *E.P. Killip & A.C. Smith 15121,* 11-15 December 1926 (NY!; US1351056!). **VENEZUELA. Uribante:** en los alrededores del campamento Siberia (CADAFE), *F. Ortega & H. van der Werff 2849,* 21 November 1985 (NY!, 2 sheets).

Sub. *Struthiopteris lineata*

BRAZIL. Rio Grande do Sul: Porto Alegre, *C. Jürgens 219,* 1904 (NY00814075!; UC441987! Photo).

Sub. *Struthiopteris violacea*

DOMINICAN REPUBLIC. Unknown region. *Lloyd 315,* no date (US429270!; US429271!).

No name label

ECUADOR. Unknown Province: *Sodiro s.n.,* no date (NY!). **PUERTO RICO.** Monte Jayuya, Rt. 143, Km 18.5 near Cerro de Punta, ca. 60 km s.w. of San Juan, *D.S. Conant 2211,* 22 August 1975 (VT198491!).

8. CONCLUSIONS AND FUTURE LINES / CONCLUSIONES Y LÍNEAS DE FUTURO

Conclusions

After carrying out this work, the following conclusions have been reached:

1) Morphoanatomical characters have a high importance in the characterization of the different species of *Parablechnum*, the spore ornamentation has been particularly useful, with five different types being established throughout the genus.
2) The anatomy of the fertile pinnae is critical in the description of the Blechnaceae, yet few recent works have studied it. In *Parablechnum* the classical patterns seem to be maintained, and the genus has been characterized almost entirely in this respect.
3) Sporangia have been typically overlooked in the Blechnaceae taxonomy. This work provides the first description of these structures for many species. Paraphyses and sporangiasters, characters never observed in other genera of the family, are relatively common in *Parablechnum*. They could have taxonomic relevance and play a role in dispersal, as they have only been observed in islandic species.
4) *Parablechnum* is a well-supported monophyletic genus, with *Parablechnum articulatum* being the sister species to the reminder of the genus.
5) The geographic consistency of the phylogeny of *Parablechnum* shown in previous work was unrealistic, and the picture given here shows that the diversity within *Parablechnum* is the result of one or several rapid radiations that obscures the backbone phylogeny of the genus. Three relatively well-supported clades have been found, one exclusive to the Austropacific region, and two present in both centers of diversity.
6) Several well-delimited morphospecies are resolved as polyphyletic in the phylogeny, which could indicate extensive hybridization via polyploidy, incomplete lineage sorting, and morphological homoplasy among other phenomena linked to a dynamic evolution landscape.

7) High levels of cryptic diversity are suspected within this genus with at least three undescribed species newly detected. Targeted field work aimed to find new populations in tropical areas will be essential to improve the resolution of this treatment.
8) The origin of *Parablechnum* occurred approximately 38 million years ago, which would indicate that the genus has reached its present distribution by several events of Long-Distance Dispersal.
9) There is a large diversification of the genus in the Americas in the Late Miocene, with several cladogenesis events matching the uplift of the Andes, which could be related to the rapid radiation of the genus.
10) The first comprehensive taxonomic synopsis of the genus *Parablechnum* as defined by current evidence has been completed, resulting in a treatment of 68 different species.
11) The co-specificity of the Mascarene and Malagasy taxa has been rejected, concluding that there is one species in Madagascar (*P. humbertii*) and another in Mauritius and Réunion (*P. marginatum*). The Central American species *P. chirstii* and *P. falciforme* have been synonymized.
12) The detailed evolutionary history of *Parablechnum* remains largely unresolved, its diversity being probably much greater than currently shown here. This work constitutes a starting point providing the most comprehensive morpho-anatomical characterization to date and 469 newly generated plastid sequences that will become instrumental in subsequent studies to elucidate the unknowns that remain open in the genus.

Future lines

1) Morpho-anatomy and palynology:
    a. It would be interesting to extend the study of the anatomy of the fertile pinnae to the whole family to check whether the morphological groups make phylogenetic sense. Likewise, the addition of the para-sagittal section can also be transferred to the rest of the genera of the family to check if the classical statements of the characteristics of the veins in the family Blechnaceae are congruent in all of them.

b. *Parablechnum* is an interesting model for studying the relationship of spore ornamentation to dispersal ability, as the genus has considerable variation in perispore ornamentation and has both widely and narrowly distributed species.
c. It would be interesting to correlate spore volume, spore shape and stomatal size with ploidy levels.
d. A more detailed study of sori in Blechnaceae is needed to determine the real incidence of paraphyses and sporangiasters, and it remains to be determined whether these influence spore dispersal in taxa where they are present.
e. There is only one gametophyte described in the genus *Parablechnum*, so the diversity and morphology of gametophytes in the genus is completely unexplored. It would be interesting to produce a gametophytic monograph of the genus showing the morphological characteristics of this stage of development and how they grow.

2) Molecular study
   a. Traditional Sanger sequencing methods are insufficient to resolve the evolutionary history of *Parablechnum*, which has been shown to be much more complicated than previous publications have indicated. More complex genomic techniques will be necessary to unravel the phylogeny and evolutionary relationships between the different taxa of *Parablechnum*.
   b. When a more robust phylogeny is available, an ancestral range reconstruction study for the genus is needed to demonstrate reliably the LDD events that the genus has undergone.
   c. A global cytological study is needed to reveal the ploidy levels of the different species of the genus.

3) Monographic study:
   a. Morphoanatomical and molecular results show a high cryptic diversity in the genus. Case studies focusing on the species complexes detected in this work are vital to unravel the true diversity of the genus using both approaches.

Conclusiones

Después de la realización de este trabajo se han alcanzado las siguientes conclusiones:

1) Los caracteres morfoanatómicos tienen una gran importancia en la caracterización de las diferentes especies de *Parablechnum*, la ornamentación de las esporas ha sido particularmente útil, estableciéndose cinco tipos diferentes en todo el género.
2) La anatomía de las pinnas fértiles es fundamental en la descripción de la familia Blechnaceae, pero pocos trabajos recientes la han estudiado. En *Parablechnum* parecen mantenerse los patrones clásicos, y el género se ha caracterizado casi por completo en este aspecto.
3) Los esporangios han sido típicamente pasados por alto en la taxonomía de las Blechnaceae. Este trabajo proporciona la primera descripción de estas estructuras para muchas especies. Las paráfisis y los esporangiastros, caracteres nunca observados en otros géneros de la familia, son relativamente comunes en *Parablechnum*. Podrían tener relevancia taxonómica y desempeñar un papel en la dispersión, ya que sólo se han observado en especies insulares.
4) *Parablechnum* es un género monofilético bien apoyado, siendo *Parablechnum articulatum* la especie hermana del recordatorio del género.
5) La consistencia geográfica de la filogenia de *Parablechnum* mostrada en trabajos anteriores era poco realista, y la imagen que se ofrece aquí muestra que la diversidad dentro de *Parablechnum* es el resultado de una o varias radiaciones rápidas que oscurecen la filogenia vertebral del género. Se han encontrado tres clados relativamente bien soportados, uno exclusivo de la región austropacífica y dos presentes en ambos centros de diversidad.
6) Varias morfoespecies bien delimitadas se resuelven como polifiléticas en la filogenia, lo que podría indicar una amplia hibridación por poliploidía, una ordenación incompleta de los linajes y una homoplasia morfológica, entre otros fenómenos vinculados a un paisaje evolutivo dinámico.
7) Se sospecha que existen altos niveles de diversidad críptica dentro de este género, con al menos tres especies no descritas detectadas recientemente. El trabajo de campo dirigido a encontrar nuevas poblaciones en zonas tropicales será esencial para mejorar la resolución de este tratamiento.

8) El origen de *Parablechnum* tuvo lugar hace aproximadamente 38 millones de años, lo que indicaría que el género ha alcanzado su distribución actual mediante varios eventos de dispersión a larga distancia.
9) Hay una gran diversificación del género en las Américas en el Mioceno tardío, con varios eventos de cladogénesis que coinciden con el levantamiento de los Andes, lo que podría estar relacionado con la rápida radiación del género.
10) Se ha completado la primera sinopsis taxonómica exhaustiva del género *Parablechnum* tal y como se define en las evidencias actuales, dando lugar a un tratamiento de 68 especies diferentes.
11) Se ha rechazado la coespecificidad de los taxones mascarenos y malgaches, concluyendo que hay una especie en Madagascar (*P. humbertii*) y otra en Mauricio y Reunión (*P. marginatum*). Las especies centroamericanas *P. chirstii* y *P. falciforme* han sido sinonimizadas.
12) La historia evolutiva detallada de *Parablechnum* sigue sin resolverse en gran medida, siendo su diversidad probablemente mucho mayor de lo que aquí se muestra. Este trabajo constituye un punto de partida que proporciona la caracterización morfo-anatómica más completa hasta la fecha y 469 secuencias del cloroplasto recién generadas que serán fundamentales en estudios posteriores para dilucidar las incógnitas que siguen abiertas en el género.

Líneas de futuro

1) Morfoanatomía y palinología:
    a. Sería interesante extender el estudio de la anatomía de los pabellones fértiles a toda la familia para comprobar si los grupos morfológicos tienen sentido filogenético. Igualmente, la adición de la sección parasagital puede trasladarse al resto de géneros de la familia para comprobar si las afirmaciones clásicas de las características de las venas en la familia Blechnaceae son congruentes en todos ellos.
    b. *Parablechnum* es un modelo interesante para estudiar la relación de la ornamentación de las esporas con la capacidad de dispersión, ya que el género presenta una considerable variación en la ornamentación de los perisporios y tiene especies de distribución amplia y estrecha.

c. Sería interesante correlacionar el volumen de las esporas, su forma y el tamaño de los estomas con los niveles de ploidía.
d. Es necesario un estudio más detallado de los soros en Blechnaceae para determinar la incidencia real de las paráfisis y los esporangiastros, y queda por determinar si éstos influyen en la dispersión de las esporas en los taxones donde están presentes.
e. Sólo hay un gametofito descrito en *Parablechnum*, por lo que la diversidad y morfología de los gametofitos en el género está completamente inexplorada. Sería interesante realizar una monografía de los gametofitos del género en la que se mostraran las características morfológicas de este estadio de desarrollo y su crecimiento.

2) Estudio molecular
   a. Los métodos tradicionales de secuenciación de Sanger son insuficientes para resolver la historia evolutiva de Parablechnum, que ha demostrado ser mucho más complicada de lo que indicaban las publicaciones anteriores. Serán necesarias técnicas genómicas más complejas para desentrañar la filogenia y las relaciones evolutivas entre los diferentes taxones de Parablechnum.
   b. Cuando se disponga de una filogenia más robusta, será necesario realizar un estudio de reconstrucción del áreas ancestrales del género para demostrar de forma fiable los eventos dispersión a larga distancia que ha sufrido el género.
   c. Se necesita un estudio citológico global para revelar los niveles de ploidía de las diferentes especies del género.
3) Estudio monográfico:
   a. Los resultados morfoanatómicos y moleculares muestran una alta diversidad críptica en el género. Los estudios de caso centrados en los complejos de especies detectados en este trabajo son vitales para desentrañar la verdadera diversidad del género utilizando ambos enfoques.

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10.- APPENDIXES

Appendix I: material used in the morpho-anatomical study

Table S1. Summary of the specimens reviewed ant the characters seen and/or measured on each. #specimens Ph. = number of specimens seen physically; #specimens Dig. = number of specimens seen digitally: Spores MO Ind = individuals whose spores has been measured under the optical microscope; Spores MO # = number of spores measured for that individual; Spores SEM = individuals whose spores has been observed under the Scanning Electron microscope; Sporangia Ind = individuals whose sporangia has been measured under the optical microscope; Sporangia # = number of sporangia measured for that individual; Stomata Ind = individuals whose stomata has been measured under the optical microscope; stomata # = number of stomata measured for that individual; Cross sections Ind. = individuals whose fertile pinnae cross section has been observed.

Taxon	# specimens		Spores			Sporangia		Stomata		Cross sections
			MO		SEM					
	Ph.	Dig.	Ind.	#		Ind.	#	Ind.	#	Ind.
P. acanthopodum	—	4	—	—	—	—	—	—	—	—
P. ambiguum	30	8	US2361403	10	*Coveny 9133* (NY) US2361403	US2361403	3	*Coveni 9135* (NY)	41	*Coveny 9135* (NY) UC1225106 US2361403
P. articulatum	1	2	—	—	—	US1371885	6	US1371885	40	US1371885
P. atropurpureum	22	7	US3460185	13	*Hann 5455* (NY) NY04187107 US3460185	US3460185	15	US3460185	40	UC1557245 US3460185
P. bicolor	1	1	MO6255006	58	MO6255006	MO6255006	12	MO6255006	42	MO6255006
P. bolivianum	—	3	—	—	—	—	—	—	—	—

Taxon	# specimens		Spores			Sporangia		Stomata		Cross sections
			MO		SEM					
	Ph.	Dig.	Ind.	#		Ind.	#	Ind.	#	Ind.
P. camfieldii	26	2	P01462497	30	*Coveny 9383* (NY)	P01462497	3	*Coveny 10195* (NY)	39	US2840927
					Coveny 10191 (NY)					
			US2840927	42	*Coveny 10195* (NY)	US02840927	3			
					P01462497					
P. capense	105	4	MO1606356	58	MO1606356	MO1606356	7	MO4565429	71	MO1877438
			MO1606391	32	MO01606391	MO01606391	13			UC417797
			MO1877438	62	MO1877438	MO1877438	11			
P. chauliodontum	22	1	US2425966	20	US2425966	US2425971	4	MO5737840	64	US2425971
			US2425971	58						
P. chilense	138	3	MACB109256	15	MACB109256	MACB109256	15	MACB109256	14	MACB109256
					MACB109257					
			MACB109257	37	P01410469	MACB109257	30			MACB109257
					P01571518					
P. chiriquanum	42	5	US3264638	40	UC1509051	*A.Rojas at al. 10491* (MACB)	10	UC1509051	46	US2776188
			US3275443	38	US2776188	US3264638	8			
P. cochabambensse	—	1	—	—	—	—	—	—	—	—
P. confusum	59	3	P01534941	30	P01534941	P01467835	22	US01527827	50	US01527826
						P01534941	2			

Taxon	# specimens		Spores			Sporangia		Stomata		Cross sections
			MO		SEM					
	Ph.	Dig.	Ind.	#		Ind.	#	Ind.	#	Ind.
						P01467835	8			
			P01566769	22	P01566769	P01566769	1			
						US1527826	3			
P. corbassonii	41	4	P01576210	30	P011576210	P01576210	16	UC1740315	57	UC1740315
					UC1740315	UC1740315	2			
P. cordatum	438	50	*Campos et al 5060* (NY)	15	MO04806421	*Campos et al 5060* (NY)	15	*Sundue et al 2002* (NY)	60	*Sundue et al 2002* (NY)
					Skillman 12893 (NY)					
			Skillman 12893 (NY)	15	*van der Werff 18201* (NY)	*Skillman 12893* (NY)	15			
			van der Werff 18201 (NY)	15	VT198667	*van der Werff 18201* (NY)	15			
					VT198685					
P. dilatatum	2	—	—	—	—	—	—	—	—	—
P. falciforme	194	33	*AZM 638* (NY)	15	P01623170	*AZM 638* (NY)	15	*Prupus 6739* (NY)	46	*Rojas et al 10418* (MACB)
					Prupus 6739 (NY)					
					Rojas 2715 (NY)					UC1505460
					US2551967	*Prupus 6739* (NY)	15			US2726493
			Prupus 6739 (NY)	15	US2726493					
					US3276195					
					VT198685					
P. gemmascens	—	1	—	—	—	—	—	—	—	—

Taxon	# specimens		Spores			Sporangia		Stomata		Cross sections
			MO		SEM					
	Ph.	Dig.	Ind.	#		Ind.	#	Ind.	#	Ind.
P. glaziovii	34	10	MO6209223	34	*J. Prado & P. H. Labiak 1672* (NY)	MO6209223	7	US148244	48	US0148244
					MO6209223					
			US3044585	30	NY02597230	US3044585	3			
					US3044585					
P. gregsonii	—	3	—	—	—	—	—	—	—	—
P. hieronymi	9	2	US2291936	31	US2291936	P01571491	10	US2291936	66	US2291936
			P01571491	54	VT198739	US2291936	4			
P. howeanum	2	3	—	—	—	—	—	—	—	—
P. humbertii	25	—	P00085125	41	P00085125	P00085125	9	P02432744	146	P00904704
			P00904704	44	P00904704	P00904704	12			
P. lechleri	103	20	MO6560309	46	MO3650111	MO6560309	9	UC1593452	35	MA850400
					MO4785306					
					MO583116					
					MO6560309					
					NY02007914					
			US3250868	54	NY04187097	US3250868	8			UC1565369
					P01662203					
					UC018691					
					US3250868					

Taxon	# specimens		Spores			Sporangia		Stomata		Cross sections
			MO		SEM					
	Ph.	Dig.	Ind.	#		Ind.	#	Ind.	#	Ind.
					van der Werff 17545 (NY)					
P. lima	14	6	MO0466586	61	MO0466586	MO0466586	10	MO0493179	81	MO0493179
			MO493179	48	MO493179	MO493179	14			
			MO6021443	65	MO6021443	MO6021443	4			UC17811481
					UC1781481					
P. lineatum	156	6	MO3106715	43	MO3106715	MO3106715	11	VT198697	82	VT198703
					NY02007523					
			NY02007523	43	NY02007531	VT198703	15			
					NY02007578					
					VT198703					
P. loxense	132	4	*Callejas & Roldan 10644* (NY)	38	*Callejas & Roldan 10644* (NY)	*Callejas & Roldan 10644* (NY)	5	VT198691	10	*Callejas & Roldán 10655* (NY)
					Hekker & Hekking 10295 (NY)					MA1358
			Hekker & Hekking 10295 (NY)	30	MO6560300					US3449754
			MO6560300	39	NY04187094	MO6560300	13			
					US3597815					
			VT198691	77	VT020021	VT198691	17			
					VT198691					VT198691

Taxon	# specimens		Spores			Sporangia		Stomata		Cross sections
			MO		SEM					
	Ph.	Dig.	Ind.	#		Ind.	#	Ind.	#	Ind.
			VT198692	49	VT198692	VT198692	16			
					VT289536					
P. loxense var. stenophyllum	81	9	P01462848	38	MACB	*Vazquez & Monteagudo 29947* (NY)	4	*Vazquez & Monteagudo 29947* (NY)	40	*J.M. Gabriel y Galán s.n.* MACB
					US1121934					
			P01462851	44	*Vazquez & Monteagudo 29947* (NY)	P01462851	3			*Vazquez & Monteagudo 29947* (NY)
					P01462851					
P. marginatum	37	1	MO2715099	61	MO2715099	P01462834	8	P00917032	50	P00917035
			P01462834	41		P00917035	9			
			P00917035	38	P01462834	P01462838	11			
			P01462838	34		MO2715099	13			
P. milnei	21	2	P01573192	33	P01573192	P01573191	11	P0157319	44	P01573192
					P01576209					P01576208
					US1273464					P01576209
P. minus	41	14	P01462532	35	MO2225320	P0462585	3	MO5423204	83	P0462585
					MO4388611	P01462556	11			
			P01462556	16	P01462532	P01462532	16			
					P01462556					
P. monomorphum	2	2	*Rodriguez et al 4662* (NY)	37	*Rodriguez et al 4662* (NY)	*Rodriguez et al 4662* (NY)	3	MO6157390	73	MO6157390
P. montanum	4	4	UC313104	43	P01532234	UC313104	12	UC313104	56	UC313104

Taxon	# specimens		Spores			Sporangia		Stomata		Cross sections
			MO		SEM					
	Ph.	Dig.	Ind.	#		Ind.	#	Ind.	#	Ind.
					UC313104					
P. moranianum	2	7	CR240690	15	VT198689	CR240690	4	VT198689	38	VT198689
			VT198689	32		VT198689	4			
P. nesophilum	8	18	*Sundue 4251* (MACB)	27	*Sundue 4251* (MACB)	*Sundue 4251* (MACB)	4	*Sundue 4251* (MACB)	56	*Sundue 4251* (MACB)
						US2291936	5			
P. novae-zelandiae	75	17	P01462530	54	P01462530	P01462530	30	P01462568	11	P01611550
			P01462568	64	P01462568	P01462568	19			
P. obtusum	4	4	NY04187103	30	NY04187103	NY04187103	3	NY04187103	113	NY04187103
P. pacificum	70	—	P00746649	33	*Motley 2754* (NY)	P00746649	12	US3463807	25	US3391245
					P00746649					
					P00746714					
					US3149886	P00746714	8			
					US3391245					
					US3717580					
P. paucipinna	—	1	—	—	—	—	—	—	—	—
P. pazense	4	3	NY4187077	38	MO63136888	NY4187077	7	MO6136888	52	MO6136888
					NY04187077			NY4187077	58	NY4187077
P. procerum	52	10	P01462567	38	MO5316089	P01462567	7	MO536089	20	MO5316089
					P01462567					

Taxon	# specimens		Spores			Sporangia		Stomata		Cross sections
			MO		SEM					
	Ph.	Dig.	Ind.	#		Ind.	#	Ind.	#	Ind.
P. proliferum	63	17	*Lems 64090604* (NY)	34	*Lellinger & de la Sota 919* (LP)	VT291818	14	*Lellinger & de la Sota 919.* (LP)	59	*Lellinger & de la Sota 919.* (LP)
			US2588578A	43	*Lems 64090604* (NY)	US2588578A	10			
			VT291818	47	US2588578A	*Lems 64090604* (NY)	4			
					US2588737A					
P. puniceum	—	3	—	—	—	—	—	—	—	—
P. reflexum	—	3	—	—	—	—	—	—	—	—
P. repens	—	1	—	—	—	—	—	—	—	—
P. revolutum	15	6	NY0418780	36	NY04187078	NY0418780	4	NY0418780	65	NY04187078
					NY04187080					NY04187080
P. rheophyticum	5	4	*Palacios 6934* (NY)	31	MO4303680	*Palacios 6934* (NY)	5	*Palacios 6934* (NY)	50	*Palacios 6934* (NY)
					UC1732585					
P. roraimense	—	1	—	—	—	—	—	—	—	—
P. ryanii	185	3	NY0088722	15	NY0088722	VT198716	4	P01389543	39	VT198716
					VT198716					
			VT198716	37	VT198723					
P. schiedeanum	220	35	MACB109259	31	CR10418	MACB109259	15	VT198709	71	MACB109259
					MACB109259					
			MACB109260	15	MO04566325					VT198705

Taxon	# specimens		Spores			Sporangia		Stomata		Cross sections
			MO		SEM					
	Ph.	Dig.	Ind.	#		Ind.	#	Ind.	#	Ind.
			UC995564	15	US1637799 VT198707	MACB109260	15			
P. sessilifolium	19	3	MACB	32	MO2139852	MO2139852	4	MO6387305	50	MO2139852
P. smilodon	—	—	—	—	—	—	—	—	—	—
P. sqamosissimum	4	3	—	—	—	—	—	—	—	—
P. squamatum	2	2	MO6112550	38	MO6112550	MO6112550	5	MO6112550	44	MO6112550
P. stipitellatum	66	16	*Escobar 5568* (NY)	50	*Escobar 5568* (NY) *Fay 3528* (NY) NY04187091 US3221253	*Escobar 5568* (NY)	5	*Escobar 5568* (NY)	11	MA213338 *Escobar 5568* (NY)
P. stuebelii	4	—	*van der Werff et al 23230* (NY)	22	¨*van der Werff et al 23230* (NY)	*van der Werff et al 18523* (NY)	6	*van der Werff et al 18523* (NY)	37	*van der Weff et al 23230* (NY)
P. subcordatum	78	3	MO5570071	32	US2082441	MO5570071	8	MO5570071	51	MO5570071
P. triangularifolium	4	6	VT198734 VT198736	35 35	VT198734 VT198736	VT198734 VT198736	10 8	VT198734	62	VT198734
P. tuerckheimii	76	7	P01531058	38	NY02007863 NY02007878 US3487178	P01531058	3	US3487178	44	UC1733553 US3487178
P. usterianum	15	6	P01395987	51	P01395987	P01395987	10	*Prado et al 2058* (NY)	17	P01395987

Taxon	# specimens		Spores			Sporangia		Stomata		Cross sections
			MO		SEM					
	Ph.	Dig.	Ind.	#		Ind.	#	Ind.	#	Ind.
P. varians	25	4	US1637799	15	MO4224730 NY04187110	US1637799	15	US1843362	19	CR255423
			US1843362	15	NY04187113 US1843362	US1843362	15			MA702487
P. vestitum	102	18	US3100967	34	US3100967	US3563129	8	US3100967	74	US3100967
			US3563129	58	US3563129	US2293665	10			
					VT198731	US3100967	6			
P. wattsii	45	7	P01532232	29	MO3893784 P01532232	P01532232	11	US2596731	50	US2596731
			P01532233	55	US2596731					
P. werffii	4	4	MO3126356	63	NY04187119 MO3126356	MO3126356	5	MO312356	60	MO3126356
P. wohlgemuhii	3	2	P01546453	20	P01546453	P01546453	6	—	—	P01546453
P. wurunuran	1	2	—	—	—	—	—	—	—	—
Parablechnum sp. nov. 1	3	—								
Parablechnum sp. nov. 2	3	—								
Parablechnum sp. nov. 3	—	—								
Incertae sedis	317	46								
TOTAL	3,252	496								
	3,748									

Appendix II: material used in the molecular study

Table S2. Sequences used in molecular analysis. For each row the species is indicated (*A.* = *Austroblechnum*, *B.* = *Brainea*, *D.* = *Doodia*, *P.* = *Parablechnum*, *O.* = *Oceaniopteris*, *W.* = *Woodwardia*), the identification given in the analyses, the voucher of provenance if known (collector with collection number and/or herbarium code), the locality to which it belongs at the country level and the markers used. For each marker the GenBank voucher is indicated or if publication is pending (P.S.). and a dash if the marker was not available for that sample. In those samples whose GenBank voucher is identical for all markers. we are dealing with sequences of complete chloroplasts from which the desired area has been extracted for our study.

Taxon	ID	Voucher	Locality	*mat*K-*YAA*	*rbc*L	*rps*4-*trn*S	*trn*L-F
A. melanocaulon	NC035840	*WR0329* (PE)	Indonesia	NC035840	NC035840	NC035840	NC035840
B. insignis	MN623366	—	China	MN623366	MN623366	MN623366	MN623366
D. linearis	BB146	MELUP109816	Australia	—	KJ170833	KJ170806	KJ170860
O. cartilaginea	MJB2182	MELU P109811	Australia	—	KJ170816	KJ170789	KJ170843
O. ciliate	P026067	WELT P026067	New Caledonia	—	KF975799	KF975755	KF975722
O. gibba	MN623360	—	China	MN623360	MN623360	MN623360	MN623360
O. gibba	P026063	WELT P026063	New Caledonia	—	KF975791	KF975747	KF975791
O. obtusata	18146	*McPherson 18146* (MO)	New Caledonia	—	KU898632	KU898575	KU898689
O. obtusata	P026059	WELT P026059	New Caledonia	—	KF975803	KF975759	KF975723
O. vitatta	P023770	WELT P026059	Fiji	—	KF975815	KF975770	KF975731

Taxon	ID	Voucher	Locality	*mat*K-*YAA*	*rbc*L	*rps*4-*trn*S	*trn*L-F
O. vittate	360	TAIF448600	Solomon Islands	P.S.	P.S.	—	P.S.
O. whelanii	BB64	*Perrie et al BB64* (BRI)	Australia	—	KJ170827	KJ170800	KJ170854
W. japonica	MN587871	NIBRVP0000524323	South Korea	MN587871	MN587871	MN587871	MN587871
W. unigemata	NC028543	*Liu et al.* (KUN)	China	NC028543	NC028543	NC028543	NC028543
P. ambiguum	BB233	MELUP109808	Australia	—	KJ170813	KJ170786	KJ170840
P. articulatum	BB36	MELUP109809	Australia	—	KJ170814	KJ170787	KJ170841
P. atropurpureum	446	*Clake 9488* (NY)	British Guyana	P.S.	P.S.	—	P.S.
P. atropurpureum	532	MO3469063	Venezuela	P.S.	P.S.	P.S.	P.S.
P. bicolor	525	MO6255006	Bolivia	P.S.	P.S.	P.S.	P.S.
P. bicolor	LPB942	*I. Jiménez 942* (LPB)	Bolivia	—	KU898645	KU898586	KU898700
P. bolivianum	405	*K. Bach 1332* (LPB)	Bolivia	P.S.	P.S.	P.S.	P.S.
P. bolivianum	494	*K. Bach 1404* (LPB)	Bolivia	P.S.	P.S.	P.S.	P.S.
P. bolivianum	LPB1404	*K. Bach 1404* (LPB)	Bolivia	—	KU898646	KU898587	KU898701

Taxon	ID	Voucher	Locality	*mat*K-*YAA*	*rbc*L	*rps*4-*trn*S	*trn*L-F
P. camfieldii	652	*Coveny 9383* (NY)	Australia	—	P.S.	P.S.	P.S.
P. camfieldii	BB216	*Ohlsen BB216* (BRI)	Australia	—	KJ170815	KJ170788	KJ170842
P. capense	511	MO4344676	South Africa	P.S.	P.S.	P.S.	—
P. capense	526	MO4565429	South Africa	P.S.	P.S.	P.S.	P.S.
P. capense	527	MO2468498	South Africa	P.S.	P.S.	—	P.S.
P. chauliodontum	519	MO5737840	New Caledonia	—	P.S.	P.S.	P.S.
P. chiriquanum	541	VT285874	Costa Rica	P.S.	P.S.	P.S.	P.S.
P. corbassonii	P026057	WELTP026057	New Caledonia	—	KF975785	KF975741	KF975715
P. cordatum	398	NY03489013	Brazil	P.S.	P.S.	P.S.	P.S.
P. cordatum	406	*I. Jiménez 1037*	Bolivia	P.S.	P.S.	P.S.	P.S.
P. cordatum	407	*M. Kessler 12986*	Bolivia	P.S.	P.S.	P.S.	P.S.
P. cordatum	520	MO6280923	Bolivia	P.S.	P.S.	P.S.	P.S.
P. cordatum	569	VT198660	Ecuador	P.S.	P.S.	P.S.	P.S.

Taxon	ID	Voucher	Locality	*mat*K-*YAA*	*rbc*L	*rps*4-*trn*S	*trn*L-F
P. cordatum	Gasper3051	*Gasper 3051* (FURB)	Brazil	—	KU898648	KU898589	KU898702
P. cordatum	394	*Quednsley 2791* (NY)	Guatemala	P.S.	P.S.	P.S.	P.S.
P. falciforme	408	*M.L. Silva 54*	México	P.S.	—	P.S.	P.S.
P. falciforme	476	*M.A. Zabalaga 224* (NY)	Bolivia	P.S.	P.S.	P.S.	P.S.
P. falciforme	BHCB15430	*Salino 15430* (BHCB)	Panamá	—	KU898649	KU898590	KU898703
P. glaziovii	510	MO6209223	Brazil	P.S.	P.S.	P.S.	—
P. glaziovii	395	NY02597230	Brazil	—	P.S.	P.S.	P.S.
P. glaziovii	466	NY01039737	Brazil	P.S.	P.S.	P.S.	P.S.
P. glaziovii	477	NY02240840	Brazil	P.S.	P.S.	P.S.	P.S.
P. glaziovii	BHCB15689	*Salino 15689* (BHCB)	Brazil	—	KU898650	KU898591	KU898704
P. gregsonii	BB228	MELUP109815	Australia	—	KJ170819	KJ170792	KJ170846
P. hieronymi	413	*M. Kessler 13859*	Indonesia	P.S.	P.S.	P.S.	P.S.
P. hieronymi	542	VT198733	Papua New Guinea	P.S.	P.S.	P.S.	P.S.

Taxon	ID	Voucher	Locality	*mat*K-*YAA*	*rbc*L	*rps*4-*trn*S	*trn*L-F
P. hieronymi	543	VT198737	Papua New Guinea	P.S.	P.S.	P.S.	P.S.
P. hieronymi	544	VT198738	Papua New Guinea	P.S.	P.S.	P.S.	P.S.
P. hieronymi	545	VT198739	Papua New Guinea	P.S.	P.S.	P.S.	P.S.
P. howeanum	AP804	*Papadopulos AP804* (NSW)	Australia	—	JF950804	—	JF950940
P. humbertii	414	*Kluge 7947*	Madagascar	P.S.	P.S.	P.S.	P.S.
P. lechleri	409	*K. Bach 1311*	Bolivia	P.S.	P.S.	P.S.	P.S.
P. lechleri	467	*Sundue & Vasco 1224* (NY)	Colombia	P.S.	P.S.	P.S.	P.S.
P. lechleri	478	*Kluge 9254*	Guadelupe	P.S.	P.S.	P.S.	P.S.
P. lechleri	522	MO6348190	Bolivia	P.S.	P.S.	P.S.	—
P. lechleri	523	MO6560310	Perú	P.S.	P.S.	P.S.	P.S.
P. lechleri	537	MO4785307	Perú	P.S.	P.S.	P.S.	P.S.
P. lechleri	571	VT198675	Colombia	P.S.	P.S.	P.S.	—
P. lechleri	LPB1461	*K. Bach 1311* (LPB)	Bolivia	—	KU898651	KU898592	KU898705

Taxon	ID	Voucher	Locality	*mat*K-*YAA*	*rbc*L	*rps*4-*trn*S	*trn*L-F
P. lechleri sub *violaceum*	375	MA850400	Colombia	P.S.	P.S.	P.S.	—
P. lechleri sub *violaceum*	504	MO5831117	Perú	P.S.	P.S.	P.S.	—
P. lechleri sub *violaceum*	563	VT291815	Dominica	P.S.	P.S.	P.S.	—
P. lima	410	*K. Bach 1461*	Bolivia	P.S.	P.S.	P.S.	P.S.
P. lima	468	UC1781481	Bolivia	P.S.	P.S.	P.S.	P.S.
P. lima	514	MO5950468	Bolivia	P.S.	P.S.	P.S.	—
P. lima	539	MO4666586	Ecuador	P.S.	P.S.	P.S.	P.S.
P. lima	540	MO4938179	Ecuador	—	P.S.	P.S.	P.S.
P. lima	LPB1461	*K. Bach 1461* (LPB)	Bolivia	—	KU898652	KU898593	KU898706
P. lineatum	515	MO4901087	Puerto Rico	P.S.	P.S.	P.S.	—
P. lineatum	535	MO3106715	Venezuela	P.S.	—	P.S.	P.S.
P. lineatum	572	VT198697	Puerto Rico	P.S.	P.S.	P.S.	P.S.
P. lineatum	573	VT198699	Puerto Rico	P.S.	P.S.	P.S.	—

Taxon	ID	Voucher	Locality	*mat*K-*YAA*	*rbc*L	*rps*4-*trn*S	*trn*L-F
P. loxense	421	*Hekker & Hecking 10295* (NY)	Ecuador	P.S.	P.S.	P.S.	P.S.
P. loxense	448	*Stergios 20421* (NY)	Venezuela	P.S.	P.S.	P.S.	P.S.
P. loxense	452B	*Callejas & Roldán 10644* (NY)	Colombia	P.S.	P.S.	P.S.	P.S.
P. loxense	454	*Riina et al 702* (NY)	Venezuela	P.S.	P.S.	P.S.	P.S.
P. loxense	533	MO6560300	Perú	P.S.	P.S.	P.S.	P.S.
P. loxense	536	MO6289461	Ecuador	—	P.S.	P.S.	P.S.
P. loxense	547	VT020021	Costa Rica	P.S.	P.S.	P.S.	P.S.
P. loxense	548	VT198695	Costa Rica	P.S.	P.S.	P.S.	P.S.
P. loxense	549	VT198694	Ecuador	P.S.	P.S.	P.S.	P.S.
P. loxense	550	VT198692	Costa Rica	P.S.	P.S.	P.S.	P.S.
P. loxense	552	VT198691	Costa Rica	P.S.	P.S.	P.S.	P.S.
P. loxense	654	US3597815	Ecuador	P.S.	P.S.	P.S.	P.S.

Taxon	ID	Voucher	Locality	*mat*K-*YAA*	*rbc*L	*rps*4-*trn*S	*trn*L-F
P. loxense	655	US3449754	Venezuela	P.S.	P.S.	P.S.	P.S.
P. loxense var. stenophyllum	422	Sundue & Vasco 1283 (NY)	Colombia	P.S.	P.S.	P.S.	P.S.
P. loxense var. stenophyllum	449	Vasquez & Monteagudo 29947 (NY)	Perú	P.S.	P.S.	P.S.	P.S.
P. loxense var. stenophyllum	657	*Churchill 394* (NY)	Colombia	P.S.	P.S.	P.S.	P.S.
P. marginatum	513	MO2715098	Rèunion	—	P.S.	P.S.	—
P. milnei	P023769	WELTP023769	Fiji	—	KF975796	KF975752	KF975721
P. minus	530	MO4388611	New Zealand	—	P.S.	P.S.	P.S.
P. minus	P021187	WELTP021187	New Zealand	—	KF975797	KF975753	DQ683395
P. minus	RW72	MELUP109818	Australia	—	KJ170820	KJ170793	KJ170847
P. monomorphum	415	*Jimenez 2943*	Bolivia	P.S.	P.S.	P.S.	P.S.
P. montanum	P21189	WELP021189	New Zealand	—	KF975798	KF975754	KJ187000
P. moranianum	195	CR240690	Costa Rica	P.S.	P.S.	P.S.	P.S.
P. moranianum	208	CR240690	Costa Rica	P.S.	P.S.	P.S.	P.S.

Taxon	ID	Voucher	Locality	*mat*K-*YAA*	*rbc*L	*rps*4-*trn*S	*trn*L-F
P. moranianum	555	VT198689	Costa Rica	P.S.	P.S.	P.S.	P.S.
P. nesophilum	362	TAIF444962	Solomon Islands	P.S.	P.S.	P.S.	P.S.
P. nesophilum	480	TAIF445010	Solomon Islands	P.S.	P.S.	P.S.	P.S.
P. nesophilum	554	VT284040	Solomon Islands	P.S.	P.S.	P.S.	P.S.
P. novae-zelandiae	P020793	WELTP20793	New Zealand	—	EF469957	KF975758	DQ683403
P. pacificum	661	US3353090	French Polynesia	—	P.S.	P.S.	P.S.
P. pacificum	481	US3717580	French Polynesia	P.S.	P.S.	P.S.	P.S.
P. pacificum	660	*Motley & R. Fentemacher 2754* (NY)	French Polynesia	P.S.	P.S.	P.S.	P.S.
P. pazense	528	MO6587657	Bolivia	—	P.S.	P.S.	P.S.
P. pazense	LPB751	*I Jimenez 751* (LPB)	Bolivia	—	KU898653	KU898594	KU898707
P. pazense	419	*I Jimenez 752* (LPB)	Bolivia	P.S.	P.S.	P.S.	P.S.
P. pazense	531	MO6136888	Bolivia	P.S.	P.S.	P.S.	P.S.
P. pazense	397	NY04187077	Bolivia	—	P.S.	P.S.	P.S.

Taxon	ID	Voucher	Locality	*mat*K-*YAA*	*rbc*L	*rps*4-*trn*S	*trn*L-F
P. procerum	508	MO225320	New Zealand	P.S.	P.S.	P.S.	P.S.
P. procerum	505	MO5316089	New Zealand	P.S.	P.S.	P.S.	P.S.
P. procerum	509	MO3412985	New Zealand	P.S.	P.S.	P.S.	—
P. proliferum	252	*JMGyG s.n.* (MACB)	Costa Rica	—	P.S.	P.S.	P.S.
P. proliferum	470	NY01415312	Brazil	P.S.	P.S.	P.S.	P.S.
P. proliferum	482	*Sundue & Nitta 1813* (NY)	Costa Rica	P.S.	P.S.	P.S.	P.S.
P. proliferum	556	VT291817	Costa Rica	P.S.	P.S.	P.S.	P.S.
P. proliferum	557	VT020022	Costa Rica	P.S.	P.S.	P.S.	P.S.
P. proliferum	558	VT285873	Costa Rica	P.S.	P.S.	P.S.	P.S.
P. proliferum	662	*Moran & Moran 5860* (NY)	Costa Rica	P.S.	P.S.	P.S.	P.S.
P. proliferum	BHCB15534	*Salino 15534* (BHCB)	Brazil	—	KU898654	KU898595	KU898708
P. revolutum	411	*D.N. Krager 2550*	Papua New Guinea	P.S.	P.S.	P.S.	P.S.
P. revolutum	416	*D.N. Krager 2610*	Papua New Guinea	P.S.	P.S.	P.S.	P.S.

Taxon	ID	Voucher	Locality	*mat*K-*YAA*	*rbc*L	*rps*4-*trn*S	*trn*L-F
P. rheophyticum	483	*Palacios 6934* (NY)	Ecuador	P.S.	P.S.	—	P.S.
P. ryanii	420	*Kluge 9257*	Guadelupe	P.S.	P.S.	P.S.	P.S.
P. ryanii	663	VT198721	Dominica	P.S.	P.S.	P.S.	P.S.
P. schiedeanum	253	MACB109259	Costa Rica	—	P.S.	P.S.	P.S.
P. schiedeanum	393	LAGU 812007	Costa Rica	P.S.	P.S.	P.S.	—
P. schiedeanum	666	US3210283	Honduras	P.S.	P.S.	P.S.	P.S.
P. schiedeanum	BHCB15700	*Salino 15700* (BHBC)	Panamá	—	KU898655	KU898596	KU898709
P. sessilifolium	254	*A. Rojas et al. 10417* (MACB)	Costa Rica	P.S.	—	P.S.	P.S.
P. smilodon	LPB1679	*I. Jiménez 1679* (LPB)	Bolivia	—	KU898644	KU898585	KU898699
P. squamatum	518	MO6218541	Bolivia	P.S.	P.S.	P.S.	P.S.
P. stipitellatum	423	*Campos et al 5579* (NY)	Perú	P.S.	P.S.	P.S.	P.S.
P. stipitellatum	450	*Escobar 5568* (NY)	Colombia	P.S.	P.S.	P.S.	—
P. stipitellatum	451	*Sundue 1150* (NY)	Bolivia	P.S.	P.S.	P.S.	P.S.

Taxon	ID	Voucher	Locality	*mat*K-*YAA*	*rbc*L	*rps*4-*trn*S	*trn*L-F
P. stipitellatum	Werff16635	*van der Werff 16635* (MO)	Perú	—	KU898656	KU898597	KU898710
P. stuebelii	424	NY02715793	Perú	P.S.	P.S.	P.S.	P.S.
P. stuebelii	453	NY04187106	Perú	P.S.	P.S.	P.S.	P.S.
P. subcordatum	471	NY03599421	New Caledonia	—	—	P.S.	P.S.
P. subcordatum	497	MO5570071	New Caledonia	P.S.	P.S.	P.S.	—
P. subcordatum	McPherson18139	*McPherson 28139* (MO)	New Caledonia	—	—	KU898598	KU898711
P. subcordatum	P026061	WELTP026061	New Caledonia	—	KF975812	KF975768	KF975729.1
P. triangularifolium	561	VT198734	New Zealand	P.S.	P.S.	P.S.	P.S.
P. triangularifolium	562	VT198735	New Zealand	P.S.	P.S.	P.S.	P.S.
P. triangularifolium	P021198	WELTP021198	New Zealand	—	KF975813	KF975769	DQ683415
P. tuerckheimii	472	NY02007862	Dominican Republic	P.S.	—	P.S.	P.S.
P. tuerckheimii	584	NY02007863	Dominican Republic	P.S.	—	P.S.	P.S.
P. tuerckheimii	667	US3487178	Dominican Republic	P.S.	P.S.	P.S.	P.S.

Taxon	ID	Voucher	Locality	*mat*K-*YAA*	*rbc*L	*rps*4-*trn*S	*trn*L-F
P. usterianum	583	NY02330524	Brazil	P.S.	P.S.	P.S.	P.S.
P. varians	218	CR255423	Costa Rica	P.S.	P.S.	—	P.S.
P. varians	500	MO637272	Costa Rica	P.S.	P.S.	P.S.	—
P. vestitum	363	TAIF490671	Malaysia	P.S.	P.S.	P.S.	P.S.
P. vestitum	412	*D.N. Kager 341*	Philippines	P.S.	P.S.	P.S.	P.S.
P. vestitum	668	TAIF455378	Philippines	P.S.	P.S.	P.S.	P.S.
P. wattsii	417	*M. Kessler 14235*	Australia	P.S.	P.S.	P.S.	P.S.
P. wattsii	503	MO3893785	Australia	—	P.S.	P.S.	P.S.
P. wurunuran	BB34	MELUP109832	New Zealand	—	KJ170828	KJ170801	KJ170855
Parablechnum sp	653	NY04187094	Colombia	P.S.	P.S.	P.S.	P.S.
Parablechnum sp	110	MACB	Perú	P.S.	P.S.	P.S.	P.S.
Parablechnum sp	118	MACB	Perú	P.S.	—	P.S.	P.S.
Parablechnum sp	371	MACB	Perú	P.S.	P.S.	P.S.	P.S.

Taxon	**ID**	**Voucher**	**Locality**	***mat*K-*YAA***	***rbc*L**	***rps*4-*trn*S**	***trn*L-F**
Parablechnum sp	418	*Jimenez 1128*	Bolivia	P.S.	P.S.	P.S.	P.S.
Parablechnum sp.	374	MA759404	Bolivia	P.S.	P.S.	P.S.	P.S.
Parablechnum sp. nov. #1	459	NY04187079	Ecuador	—	P.S.	P.S.	P.S.

Appendix III: molecular phylogenetic trees generated

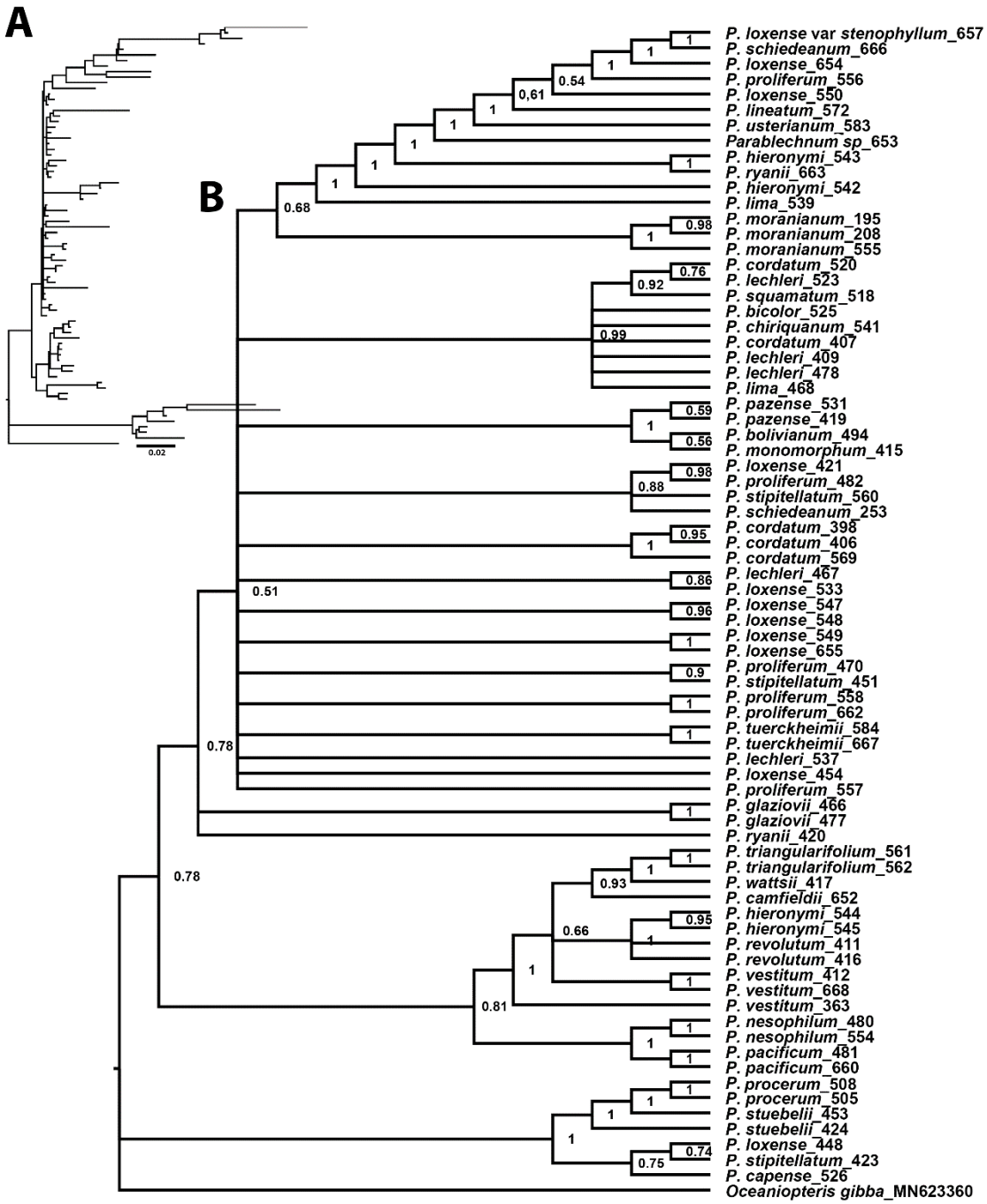

Figure S1. BI tree with no indel coding of Set 76. A. Real topology of the tree; B. Tree cladogram with posterior probability values.

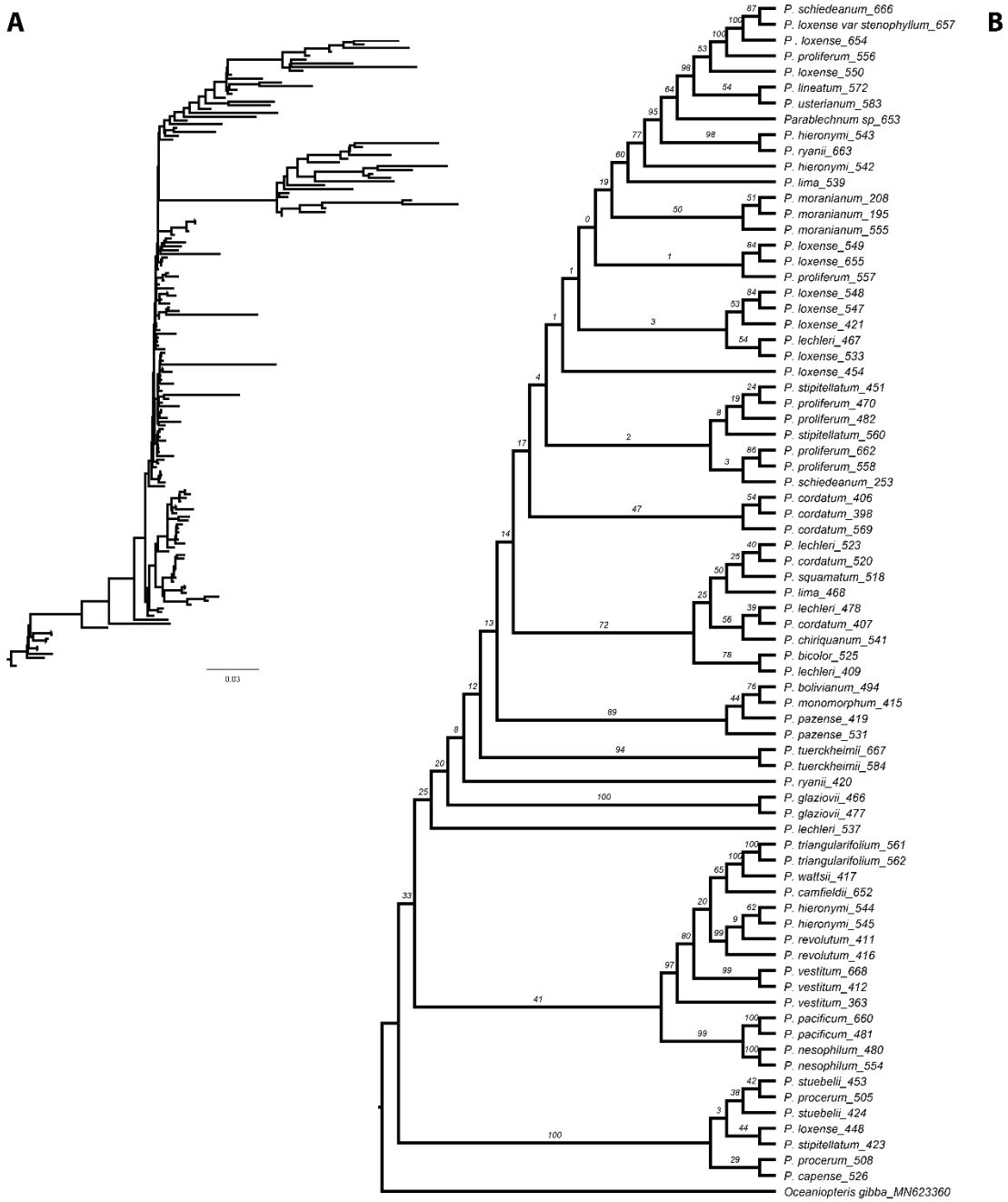

Figure S2. ML tree with no indel coding of set 76. A. Real topology of the tree; B. Tree cladogram with posterior probability values.

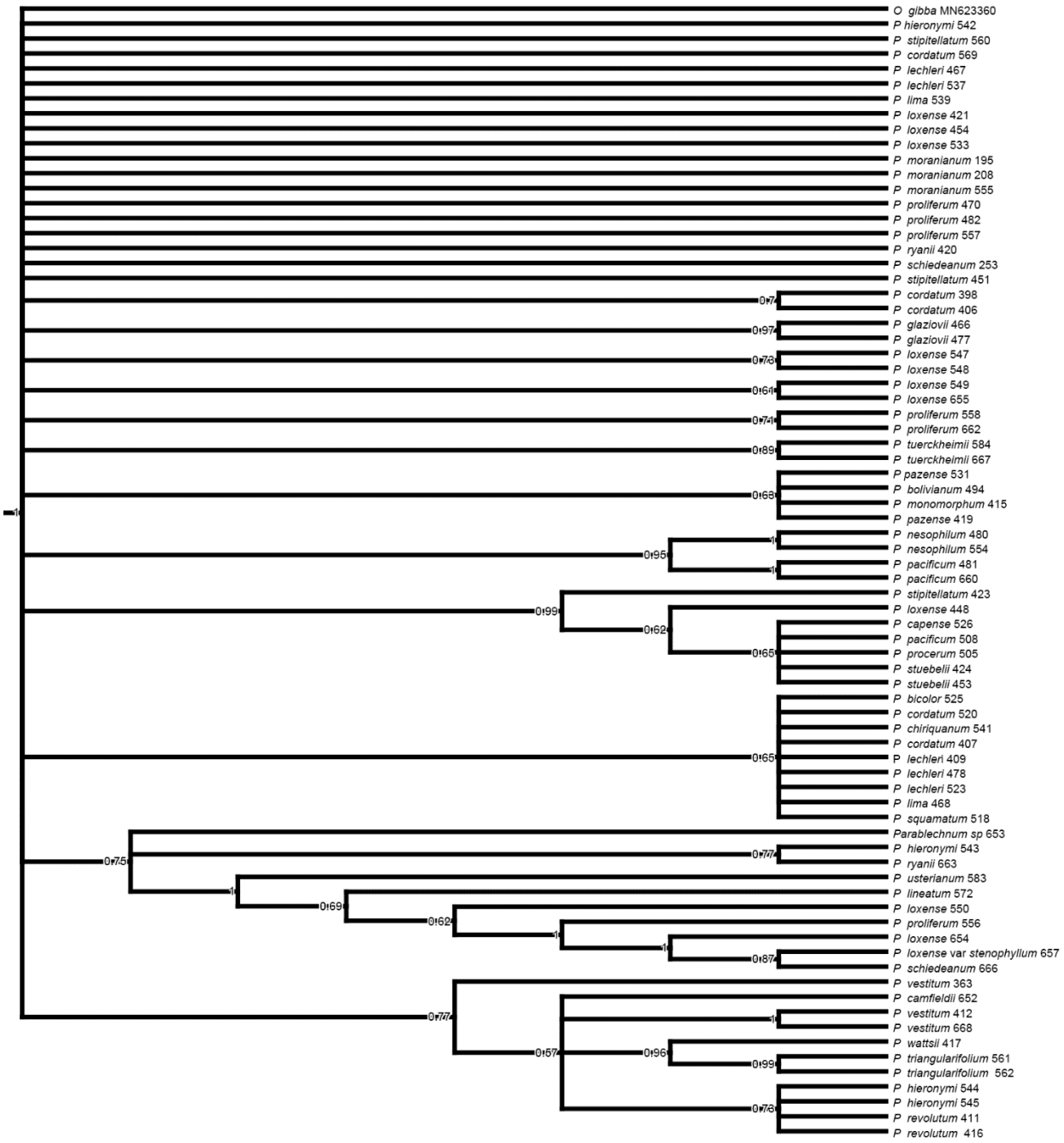

Figure S3. ML consensus tree with indel coding of set 76 with bootstrap values.

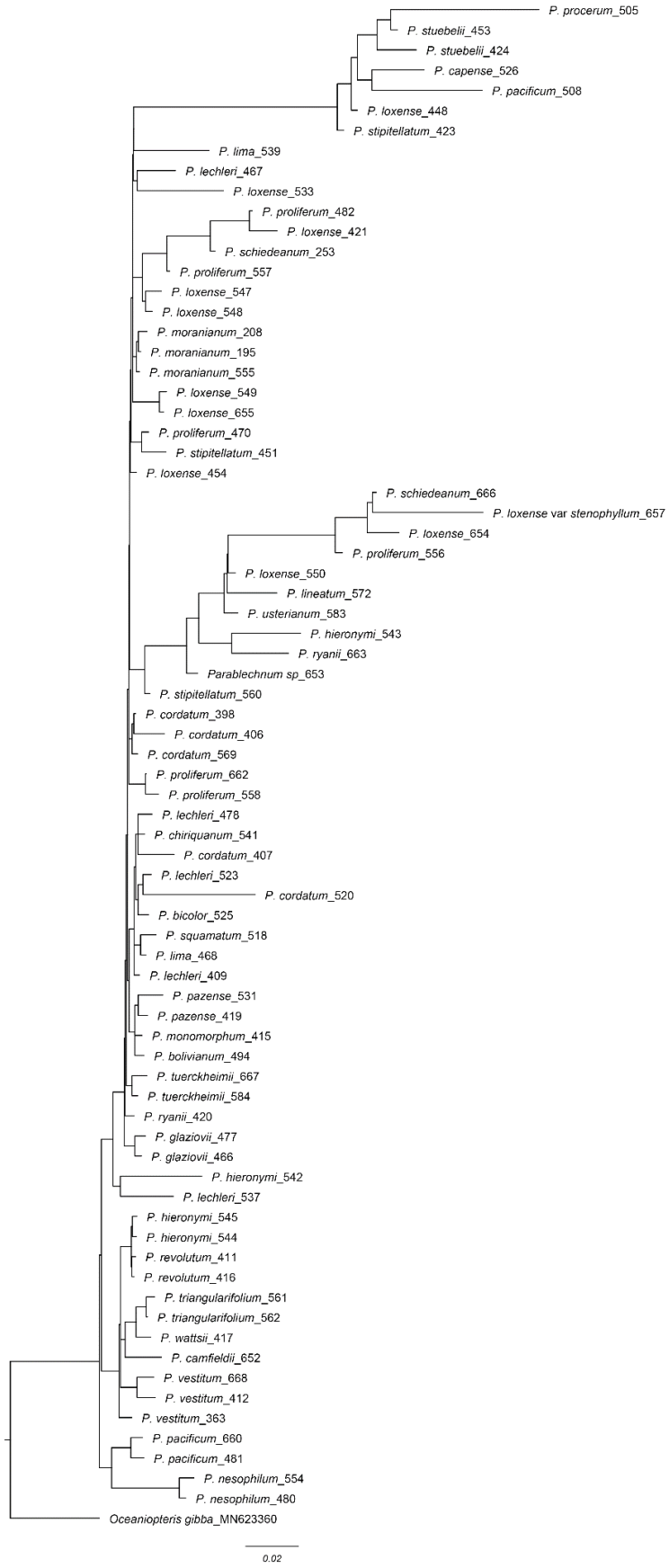

Figure S4. ML tree topology with indel coding of set 76.

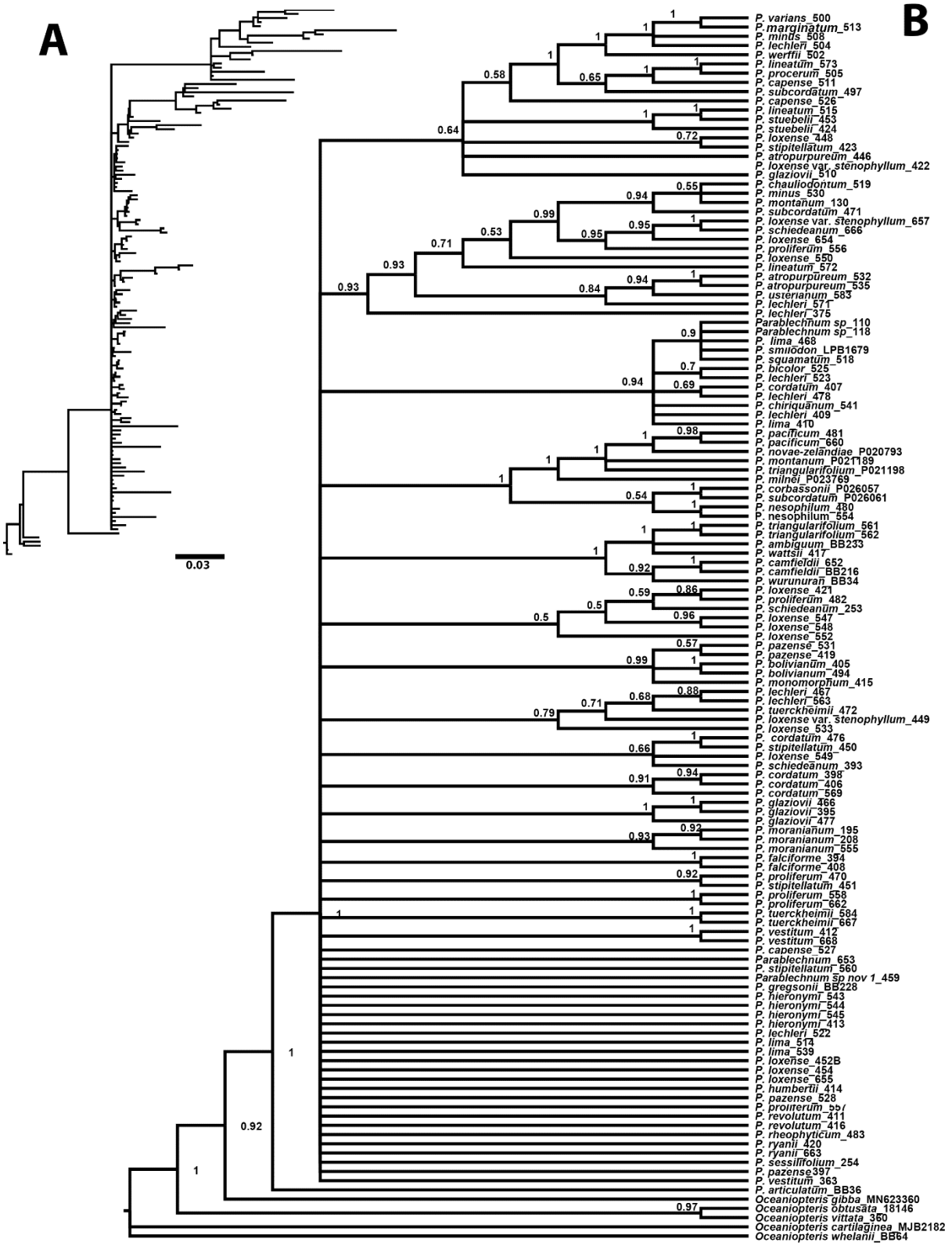

Figure S5. BI tree with no indel coding of Set 133. A. Real topology of the tree; B. Tree cladogram with posterior probability values.

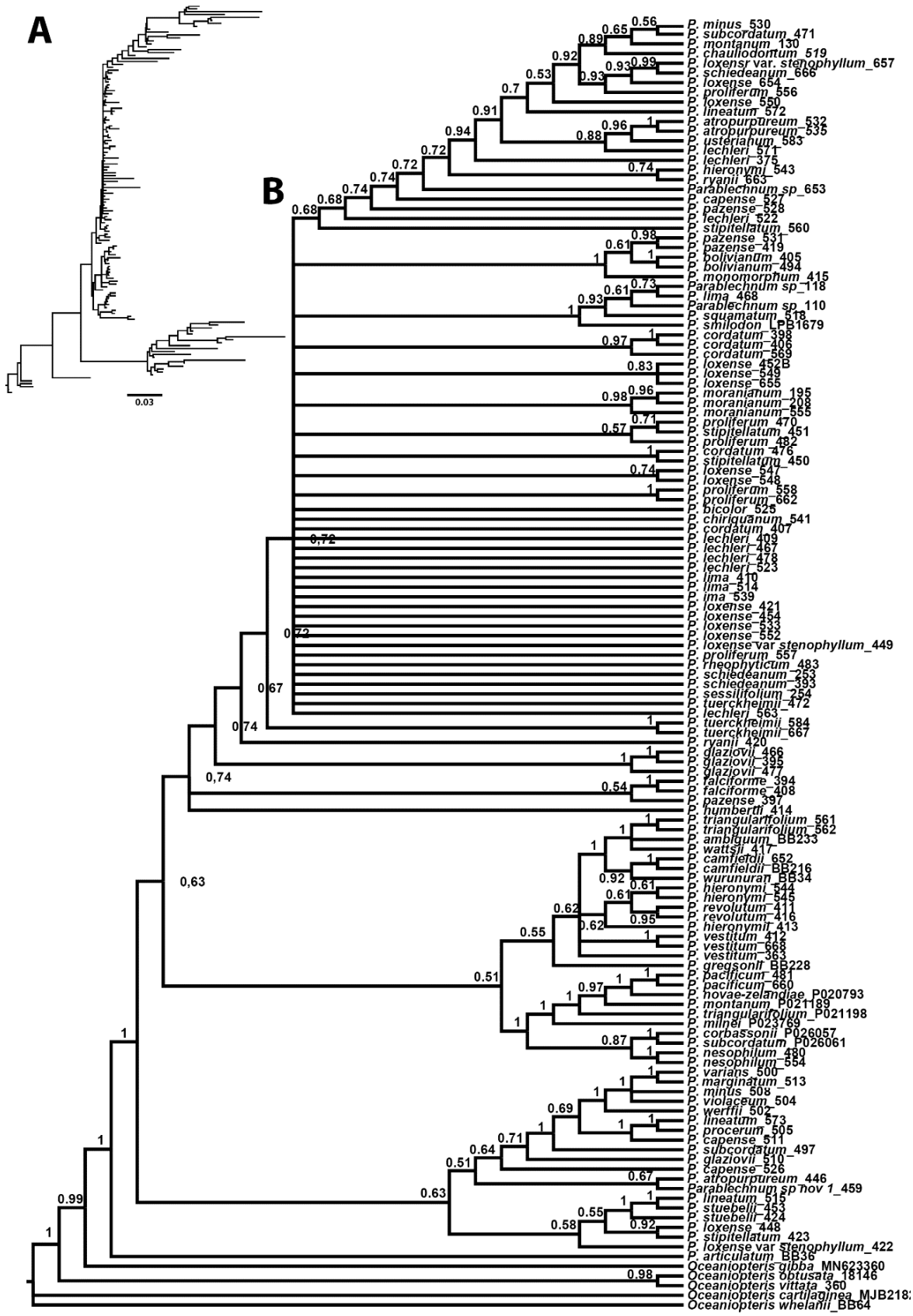

Figure S6. BI tree with indel coding of Set 133. A. Real topology of the tree; B. Tree cladogram with posterior probability values.

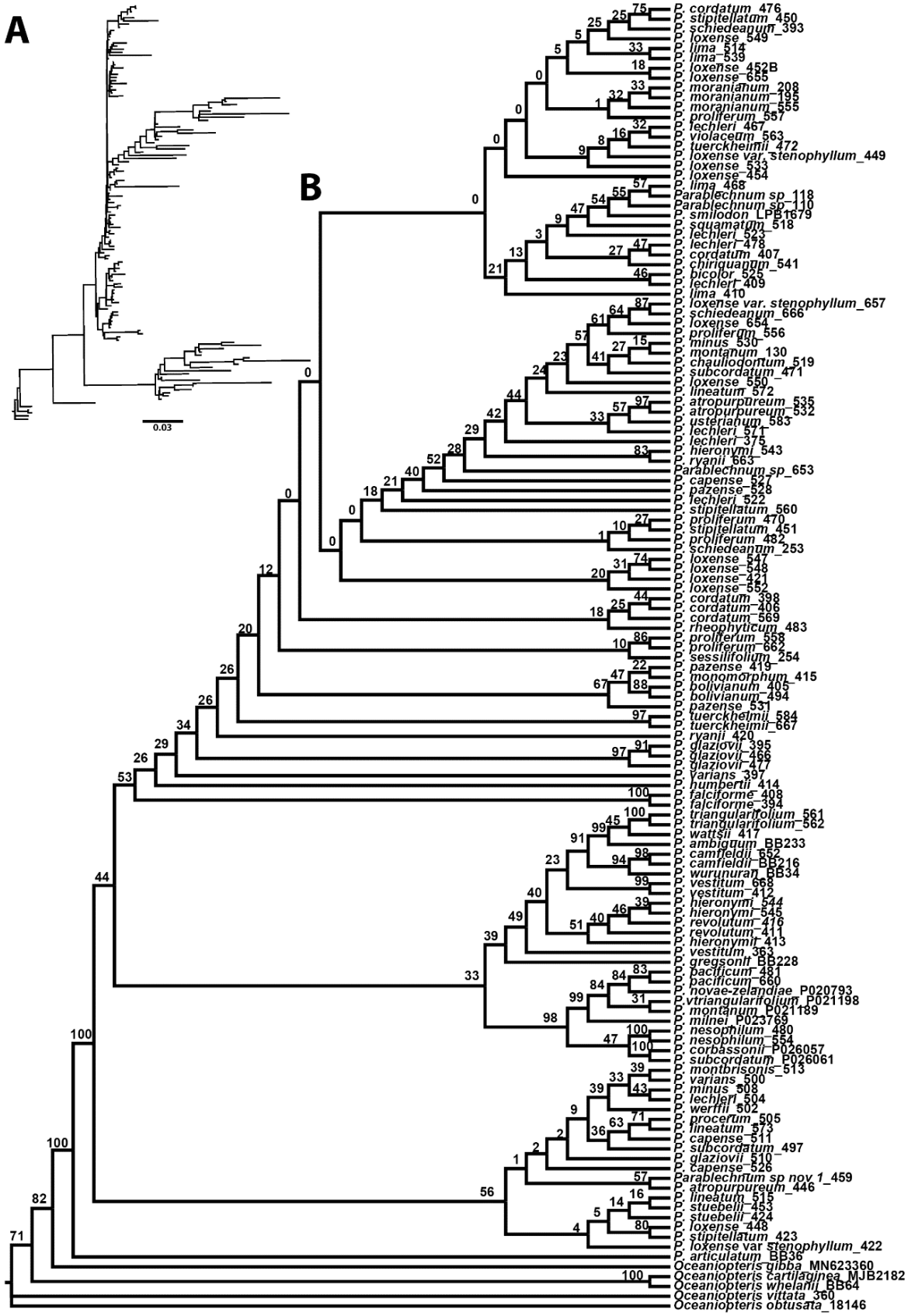

Figure S7. ML tree with no indel coding of set 133. A. Real topology of the tree; B. Tree cladogram with posterior probability values.

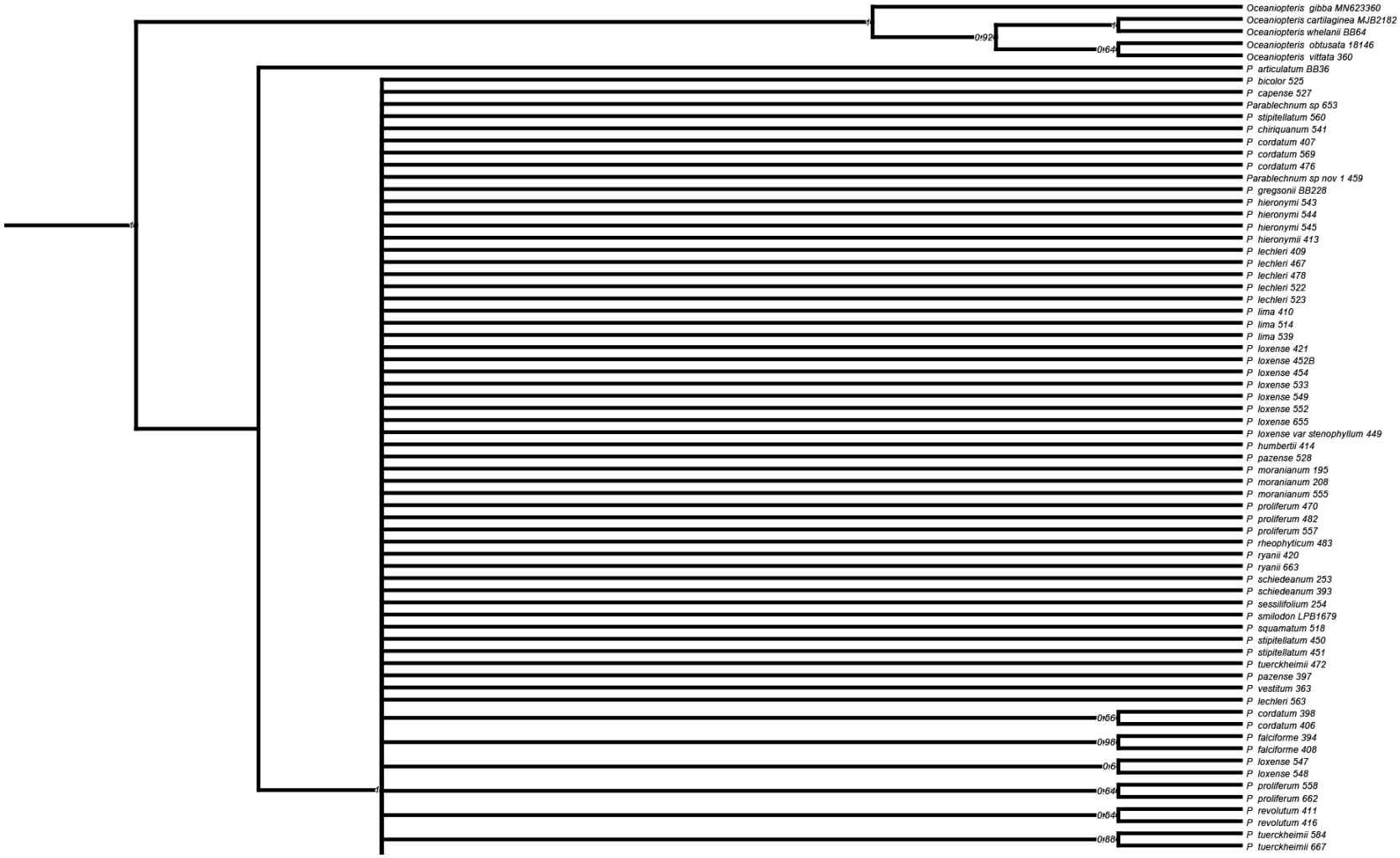

Figure S8. ML consensus tree with indel coding of set 133 with bootstrap values.

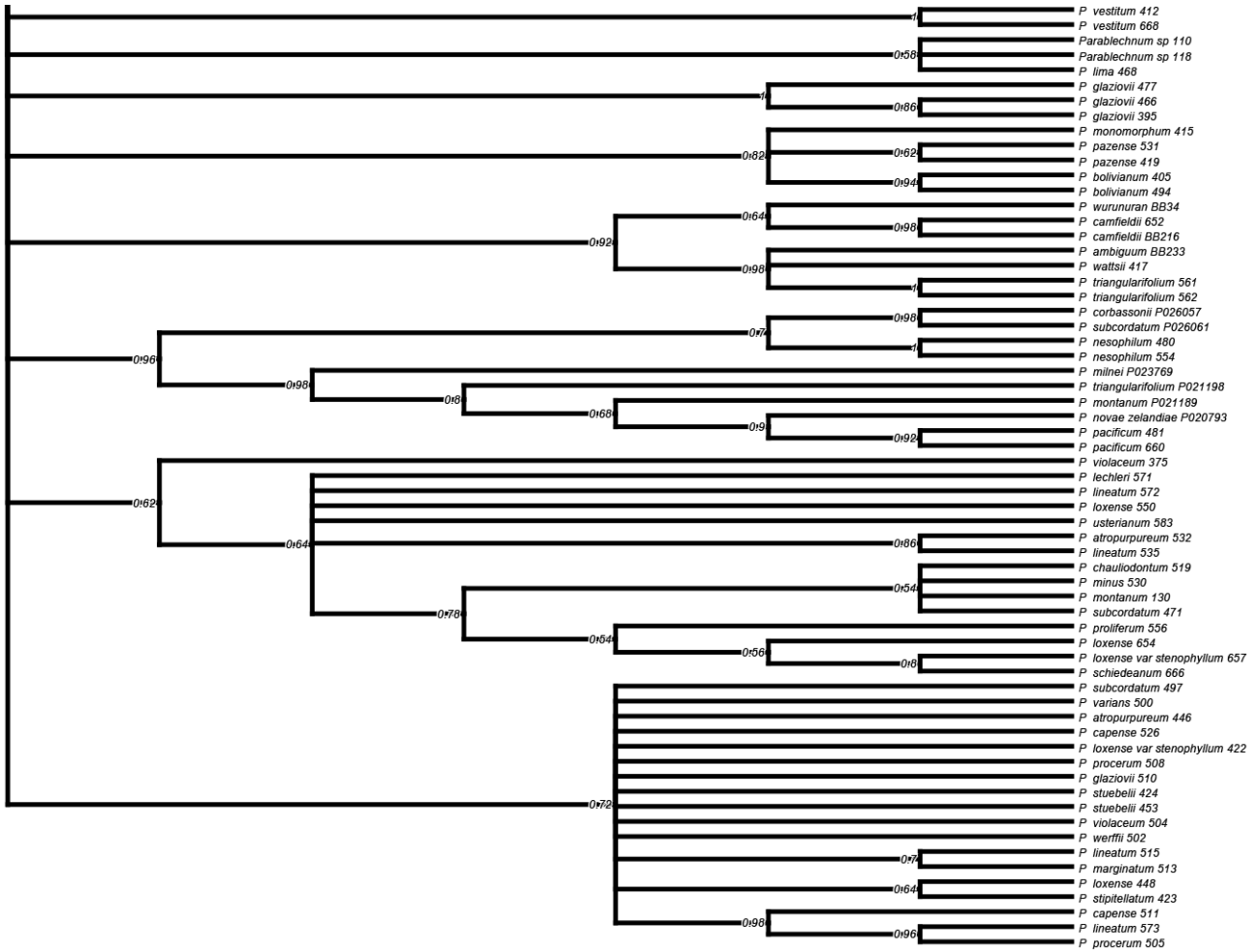

Figure S8. ML consensus tree with indel coding of set 133 with bootstrap values (cont).

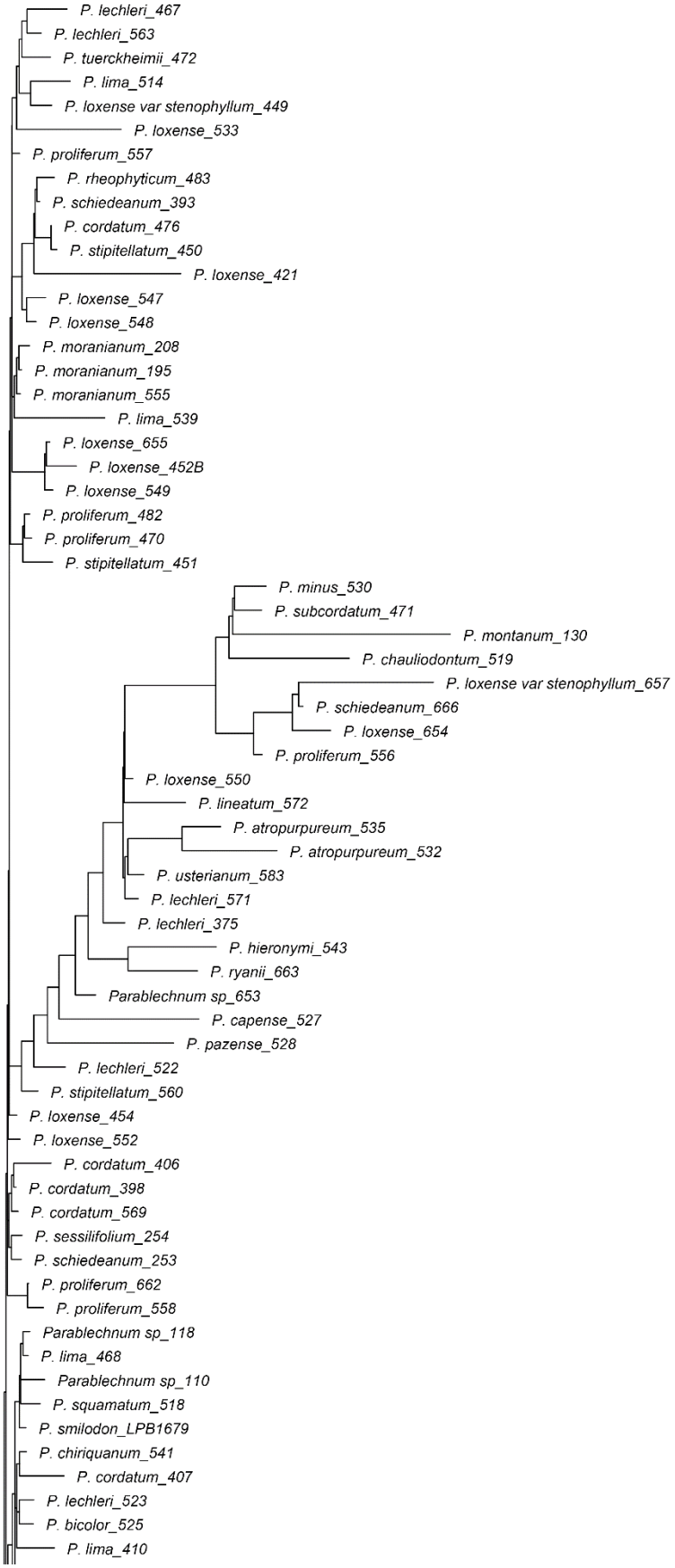

Figure S9. ML tree topology with indel coding of set 133.

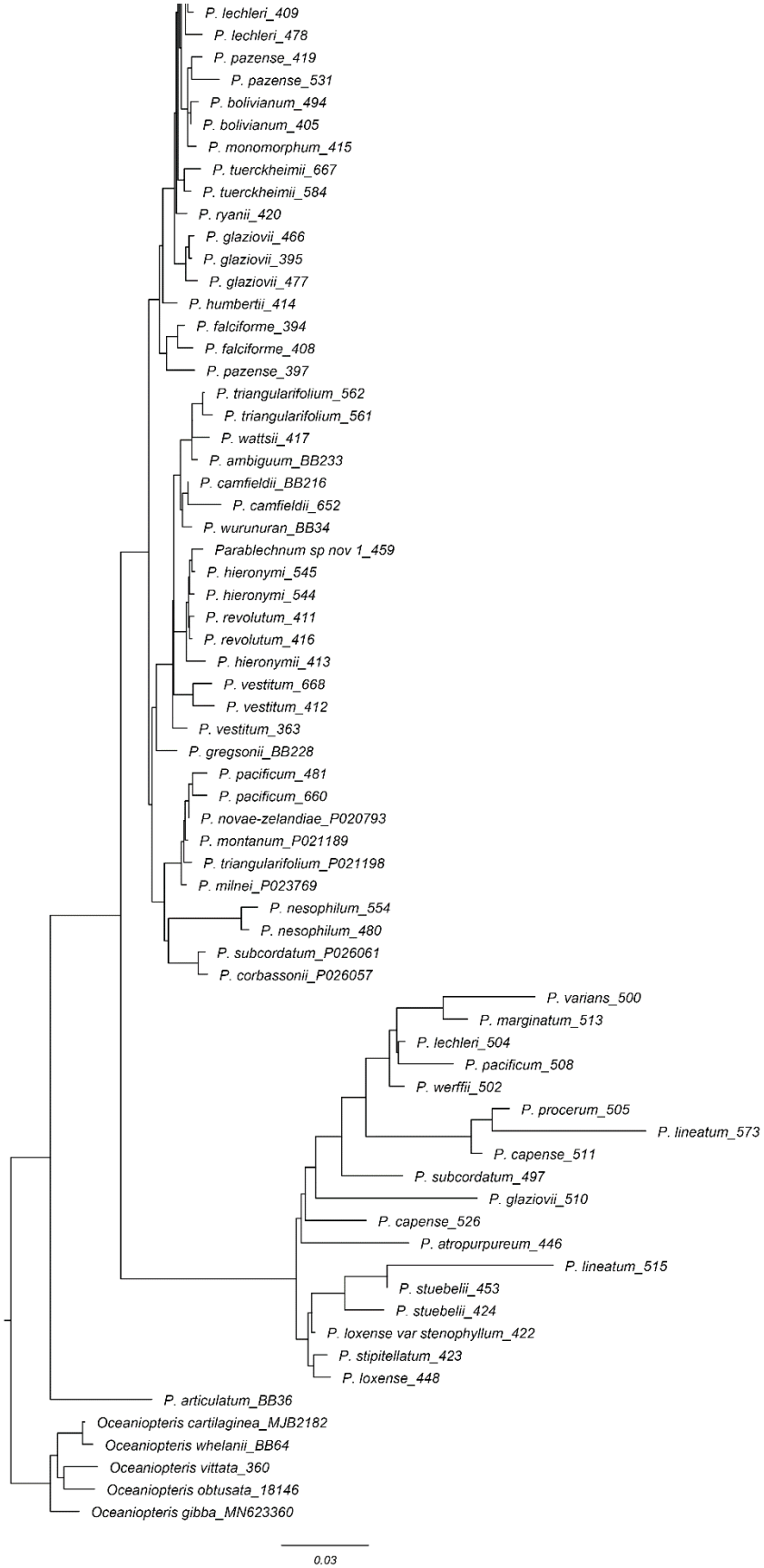

Figure S9. ML tree topology with indel coding of set 133. (cont).

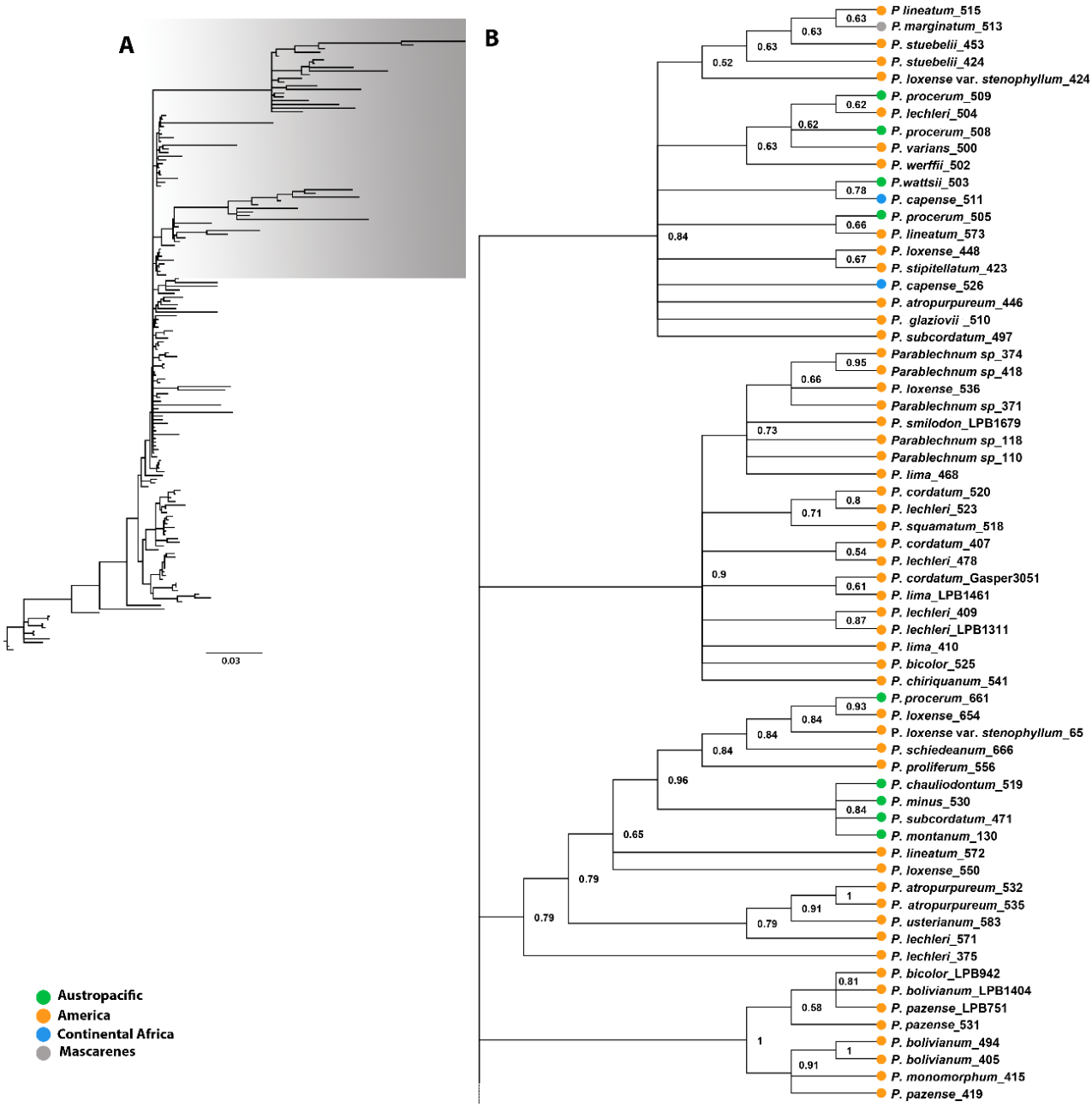

Figure S10. BI tree with no indel coding of Set 165. A. Real topology of the tree; B. Tree cladogram with posterior probability values.

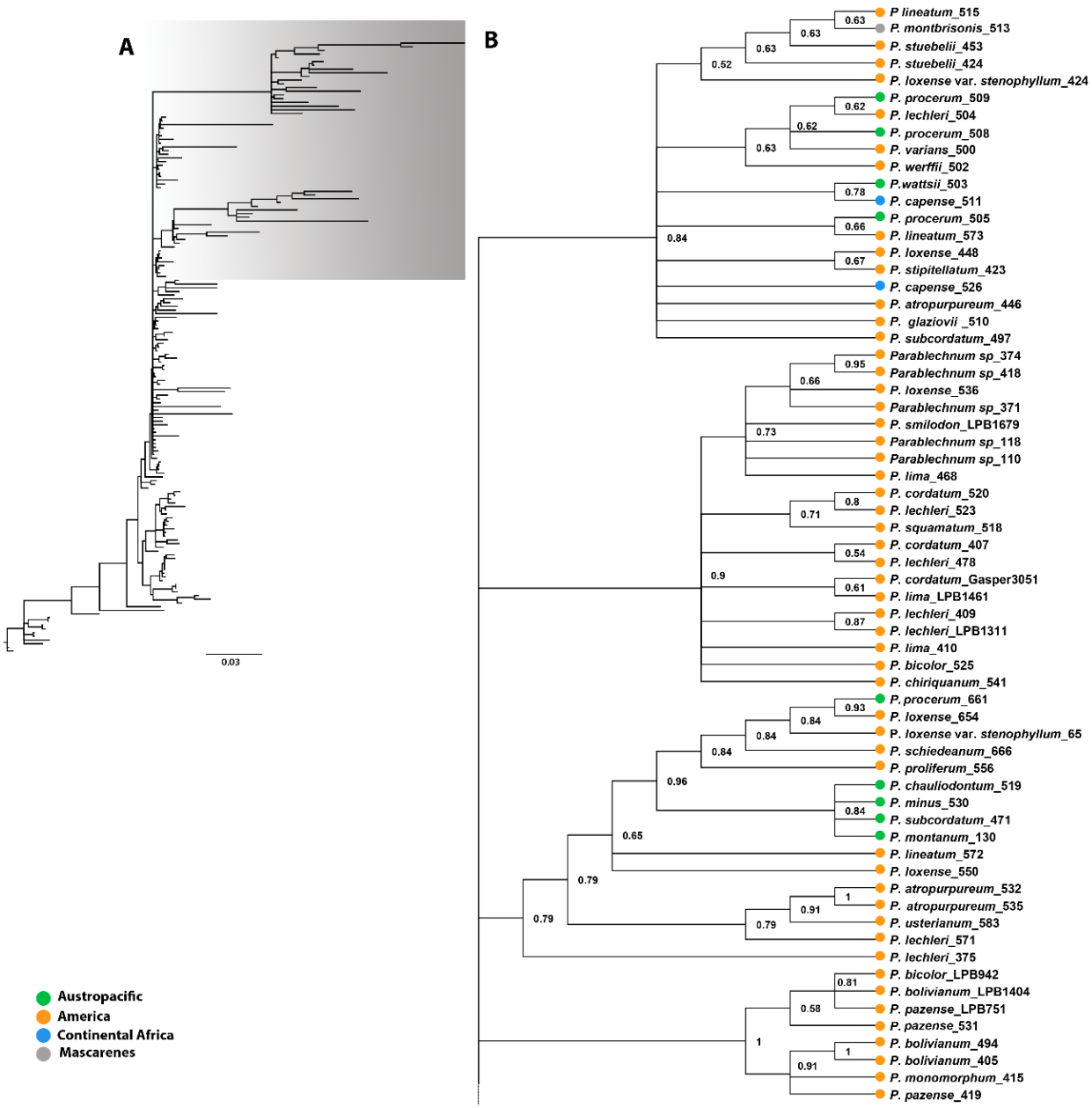

Figure S10. BI tree with no indel coding of Set 165. A. Real topology of the tree; B. Tree cladogram with posterior probability values (cont).

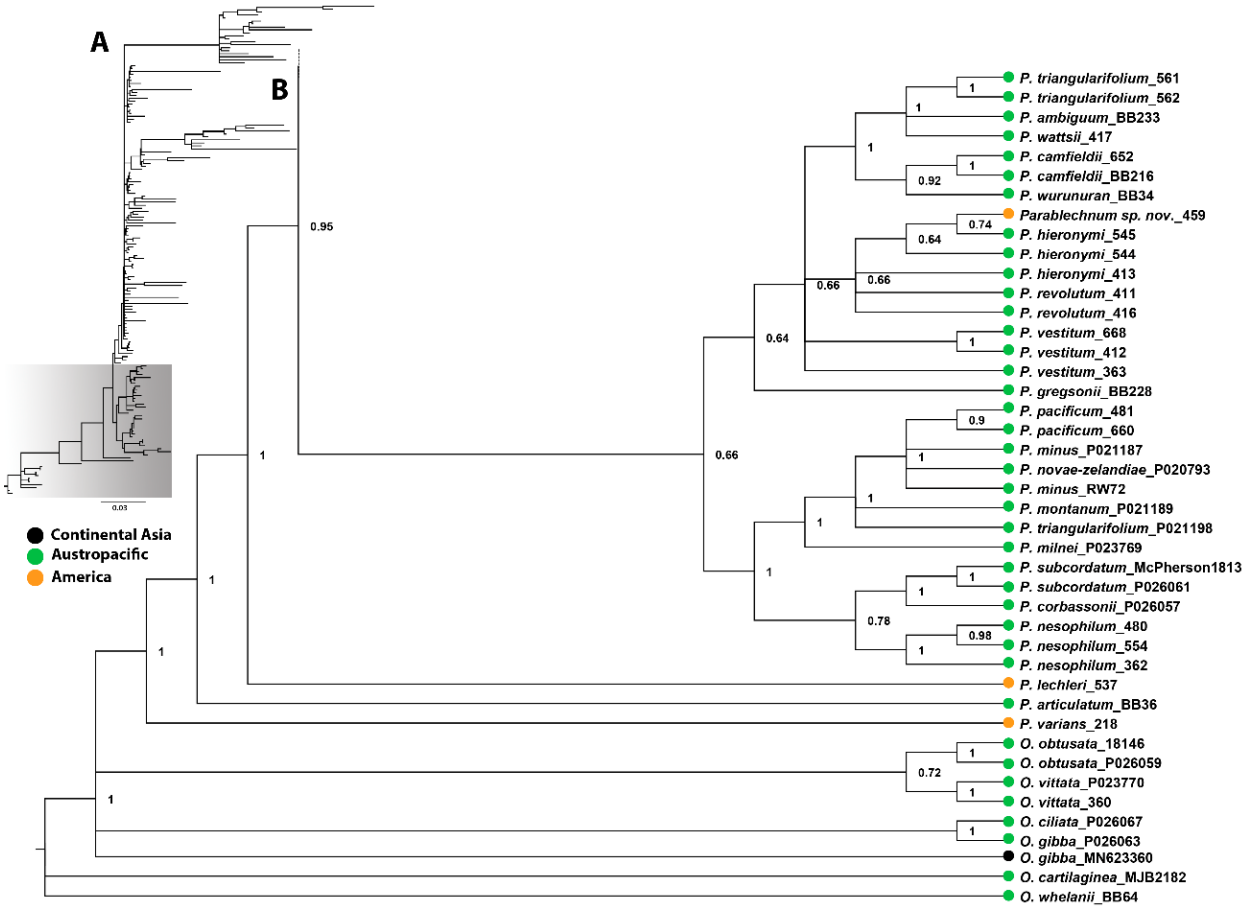

Figure S10. BI tree with no indel coding of Set 165. A. Real topology of the tree; B. Tree cladogram with posterior probability values (cont).

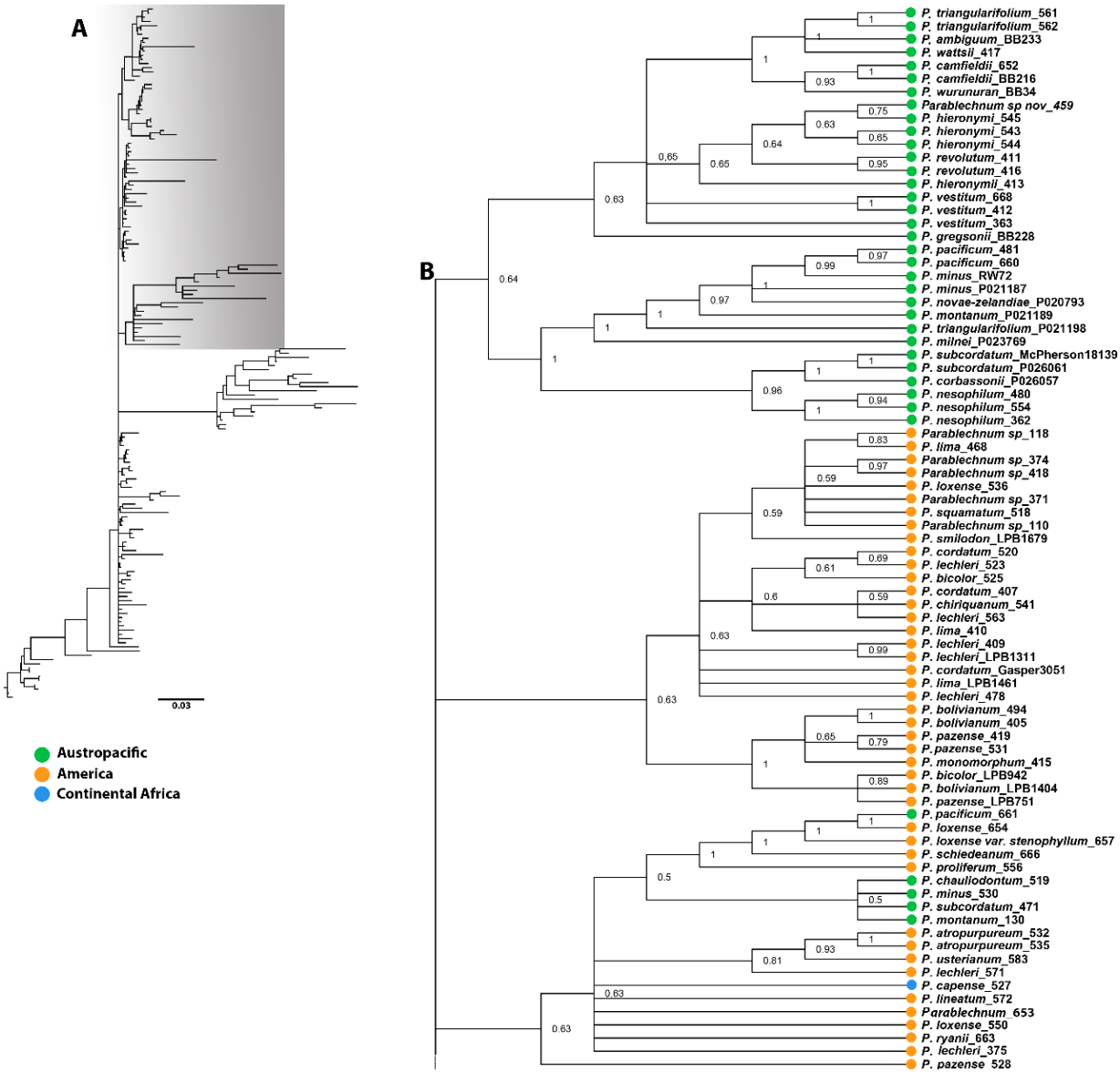

Figure S11. BI tree with indel coding for set 165. A. Real topology of the tree; B. Tree cladogram with posterior probability values.

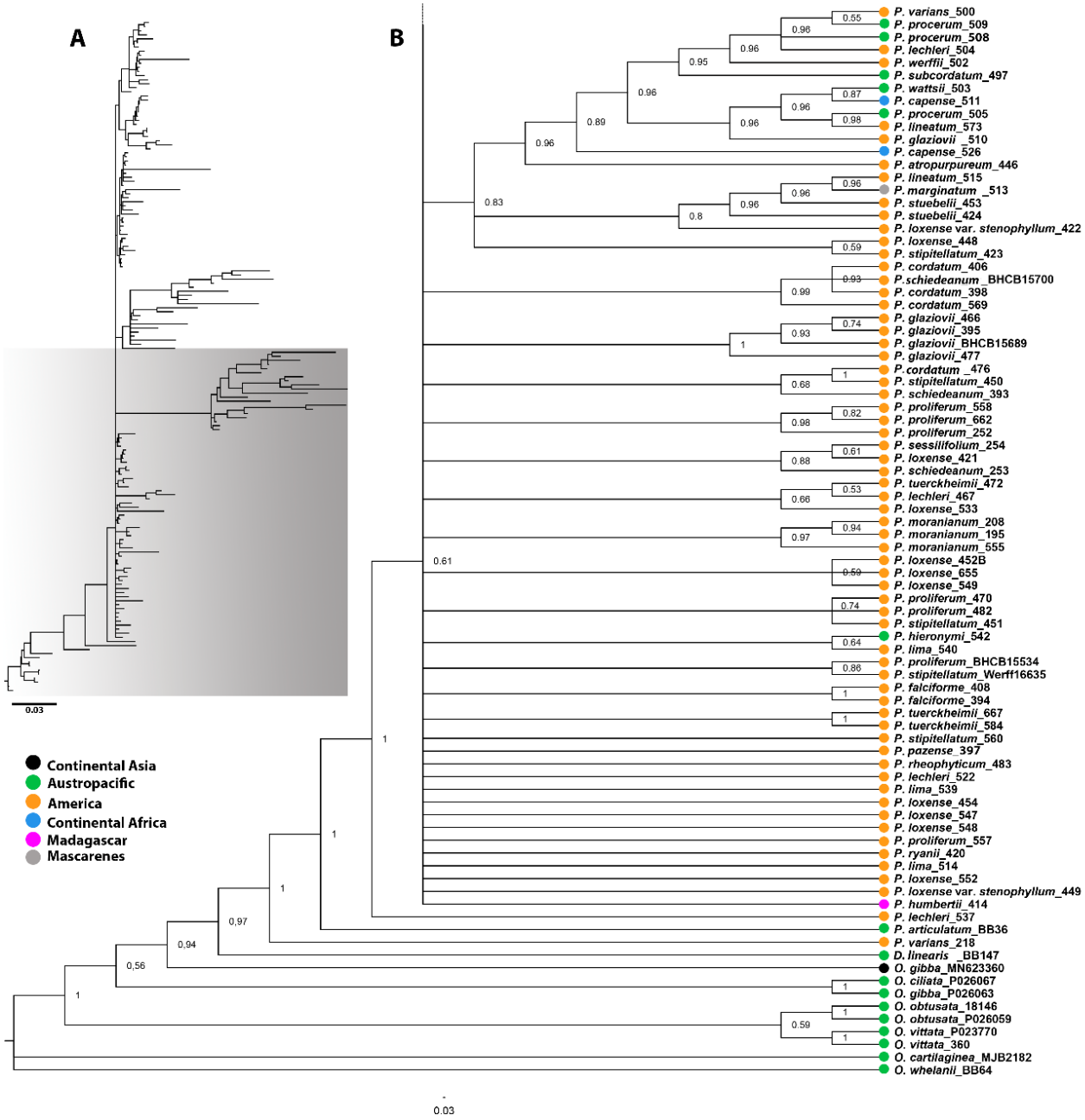

Figure S11. BI tree with indel coding for set 165 A. Real topology of the tree; B. Tree cladogram with posterior probability values. (cont.).

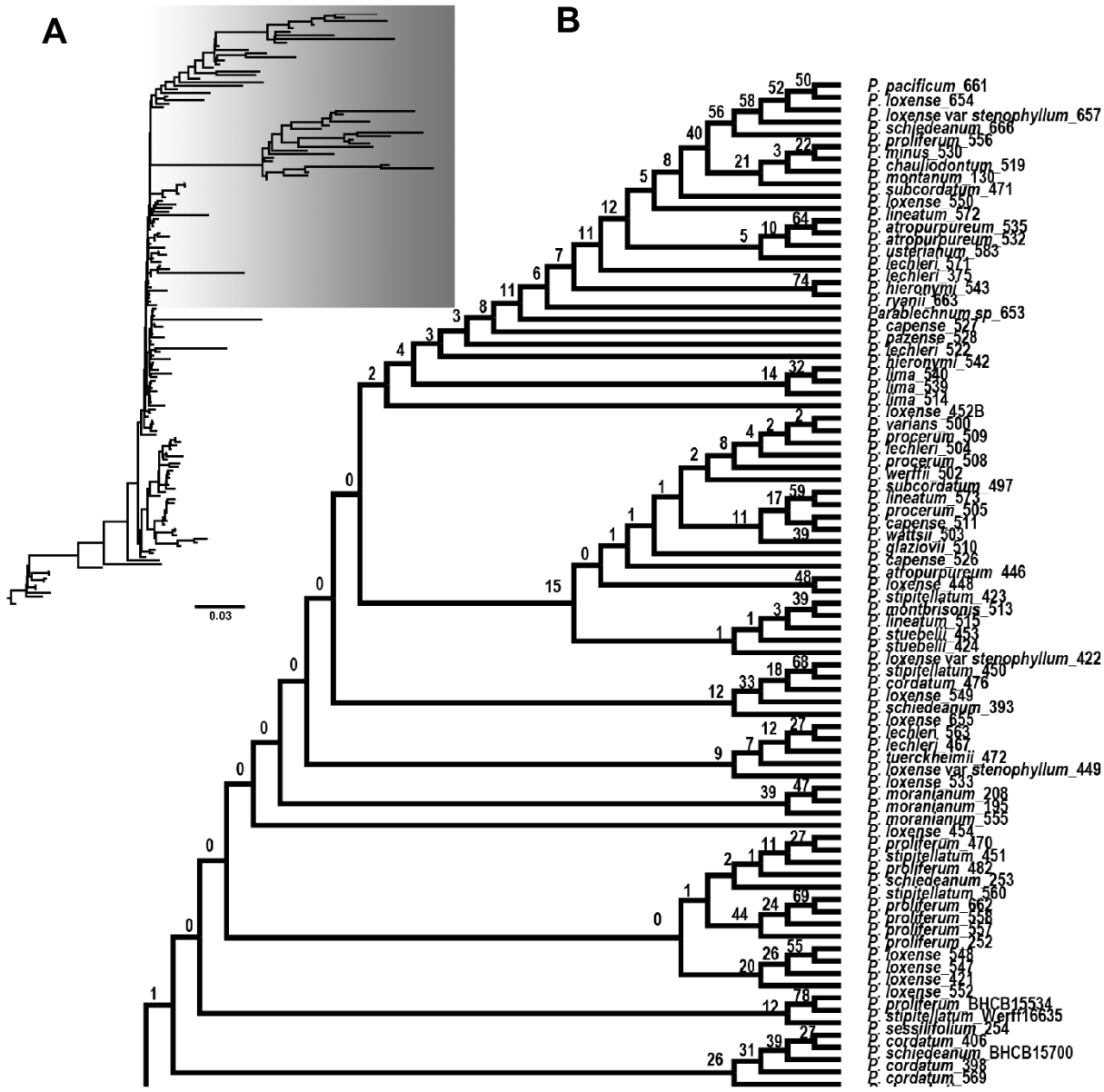

Figure S12. ML tree with no indel coding of set 165. A. Real topology of the tree; B. Tree cladogram with posterior probability values.

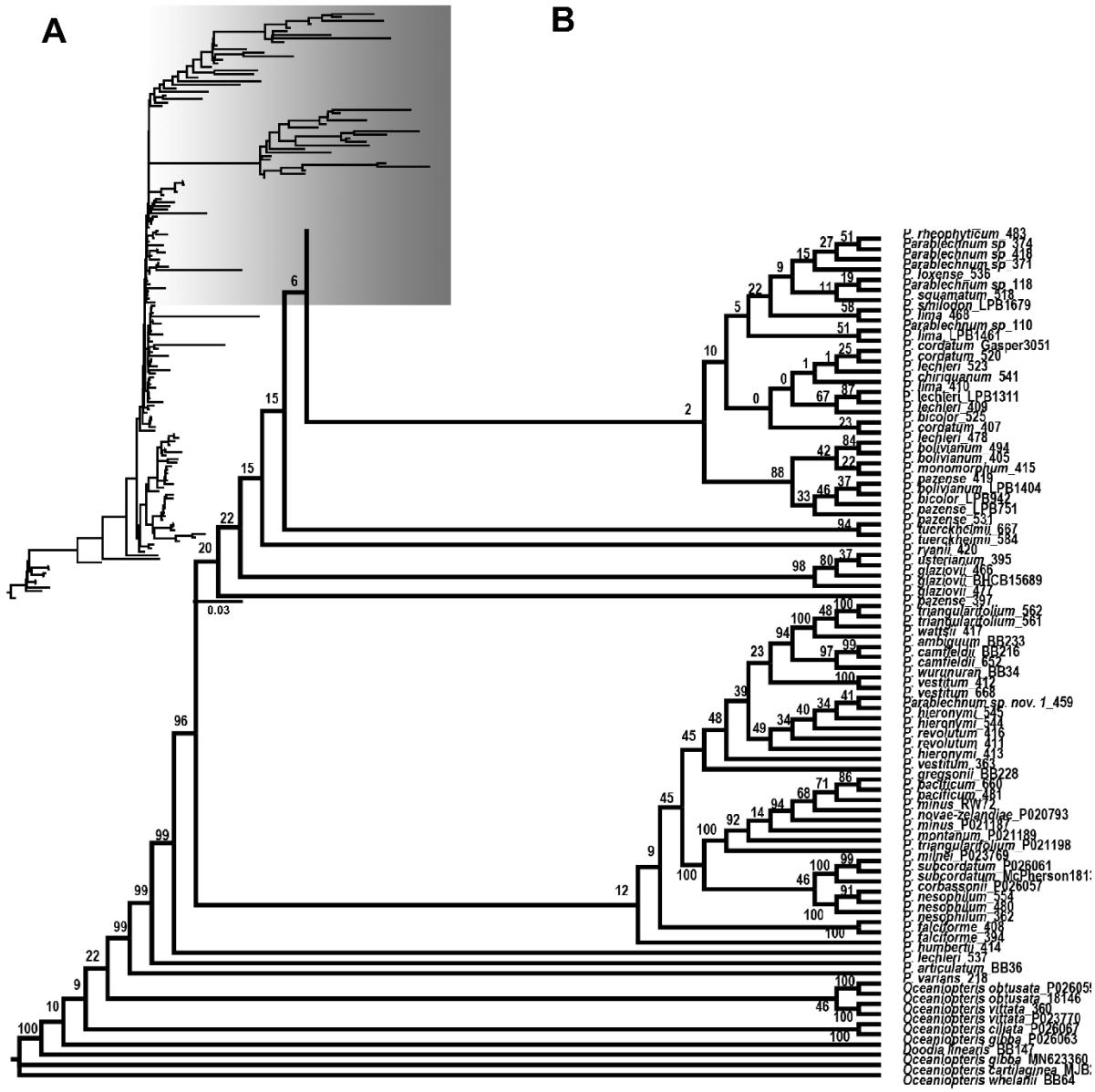

Figure S12. ML tree with no indel coding of set 165 A. Real topology of the tree; B. Tree cladogram with posterior probability values (cont).

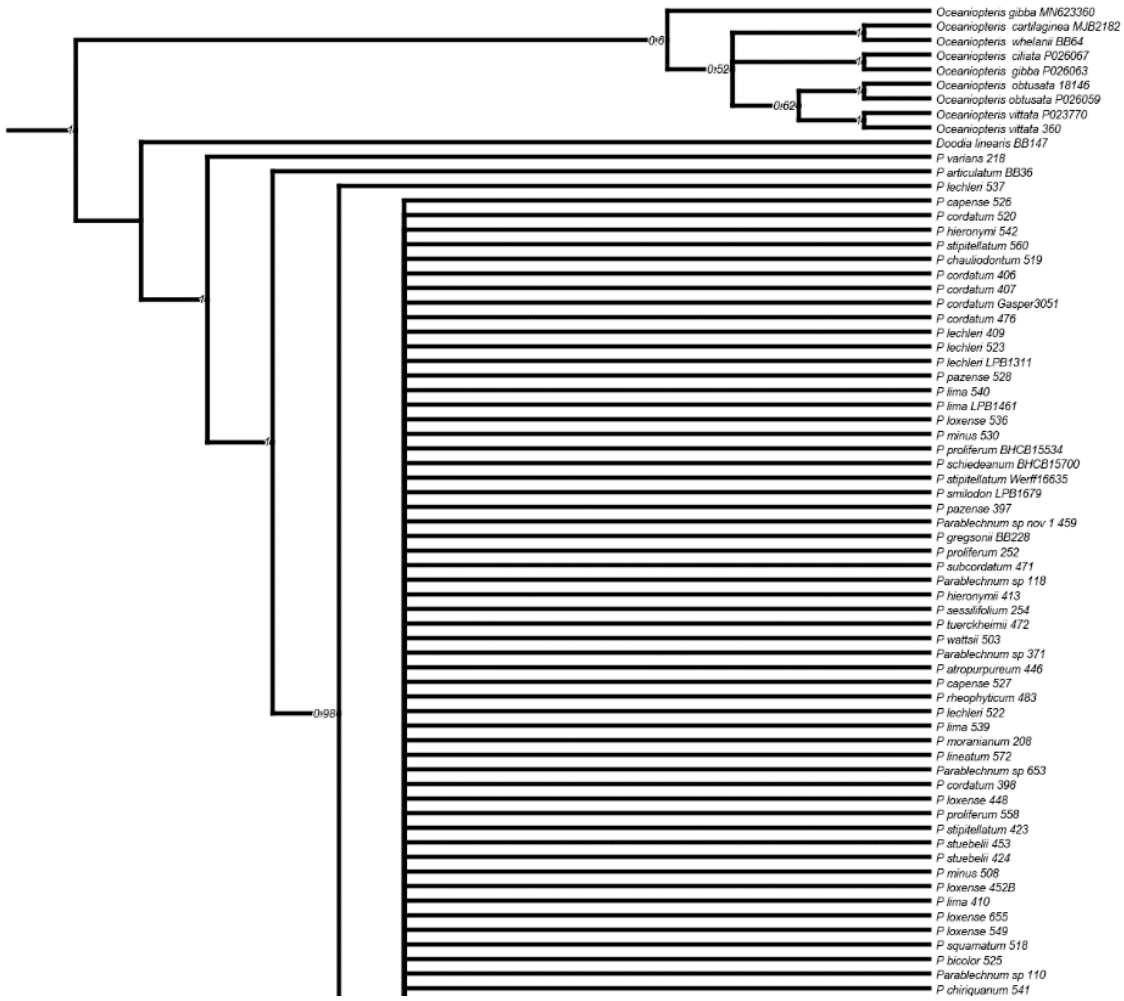

Figure S13. ML consensus tree with indel coding of set 165 with bootstrap values.

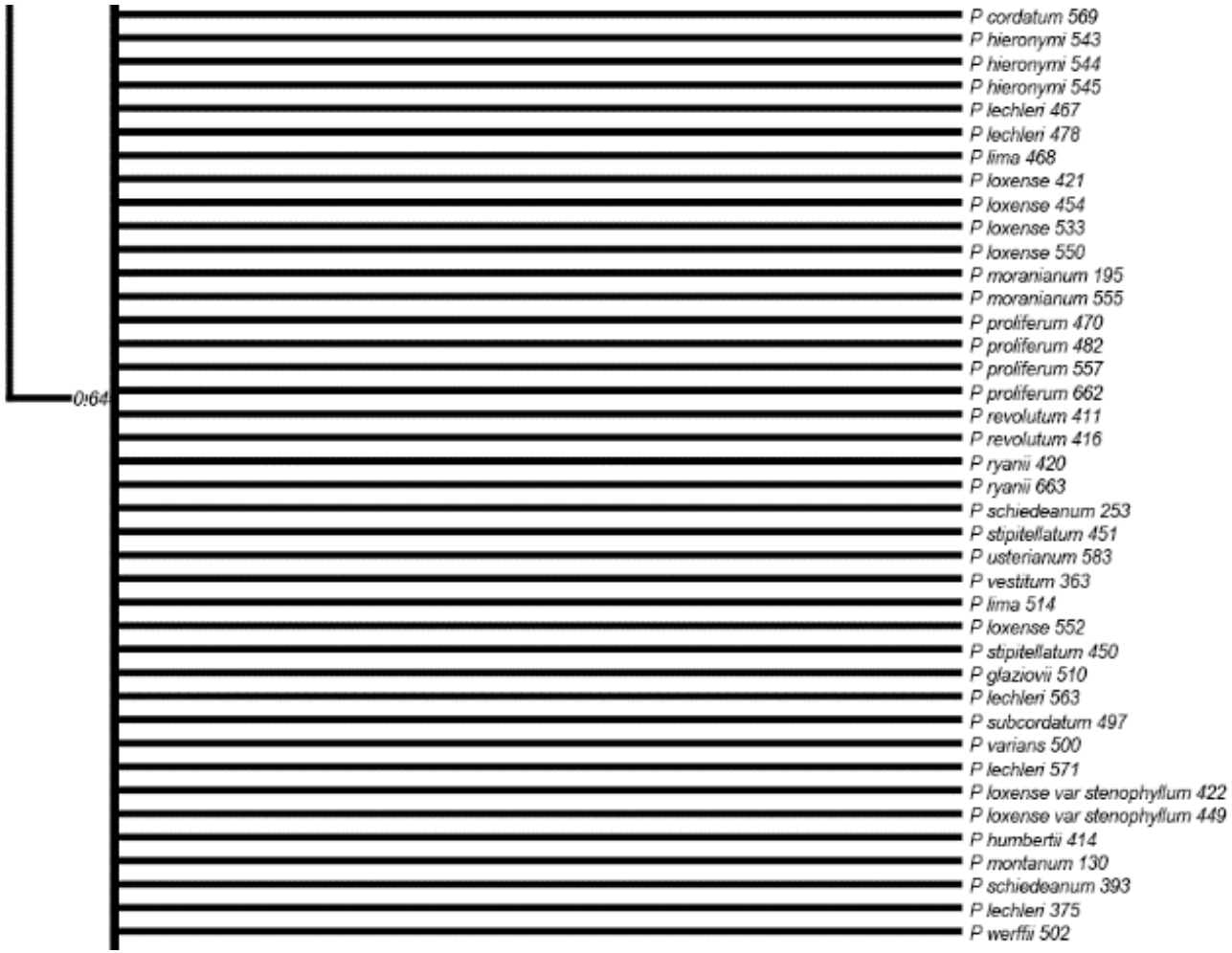

Figure S13. ML consensus tree with indel coding of set 165 with bootstrap values (cont).

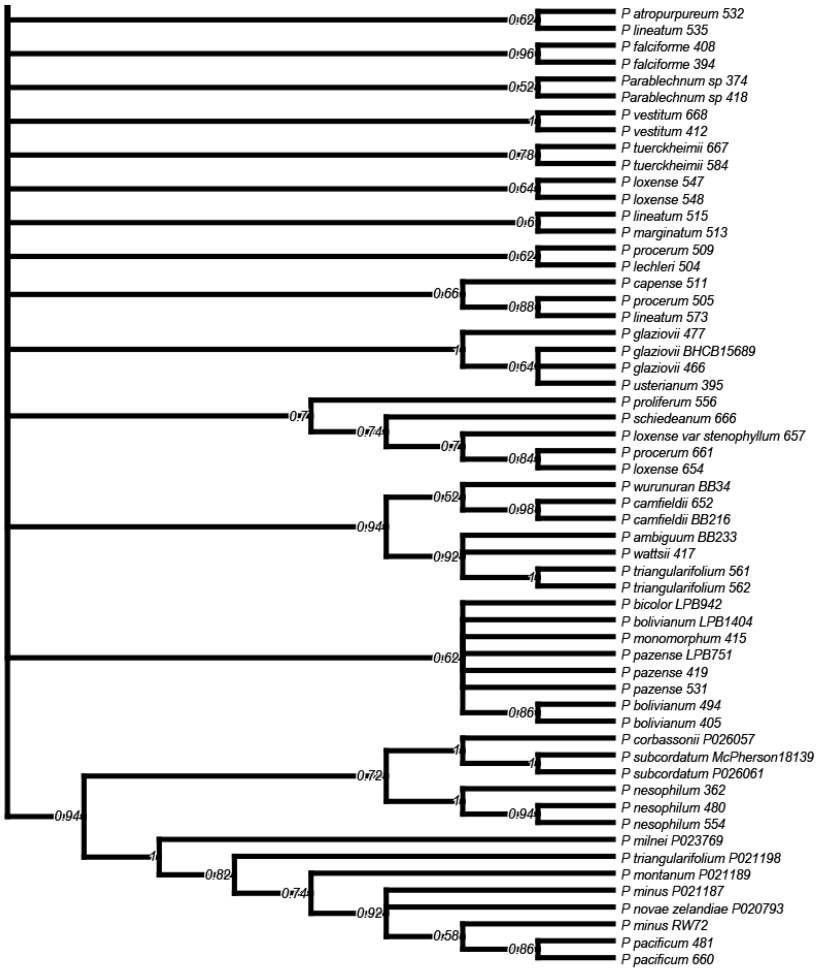

Figure S13. ML consensus tree with indel coding of set 165 with bootstrap values (cont).

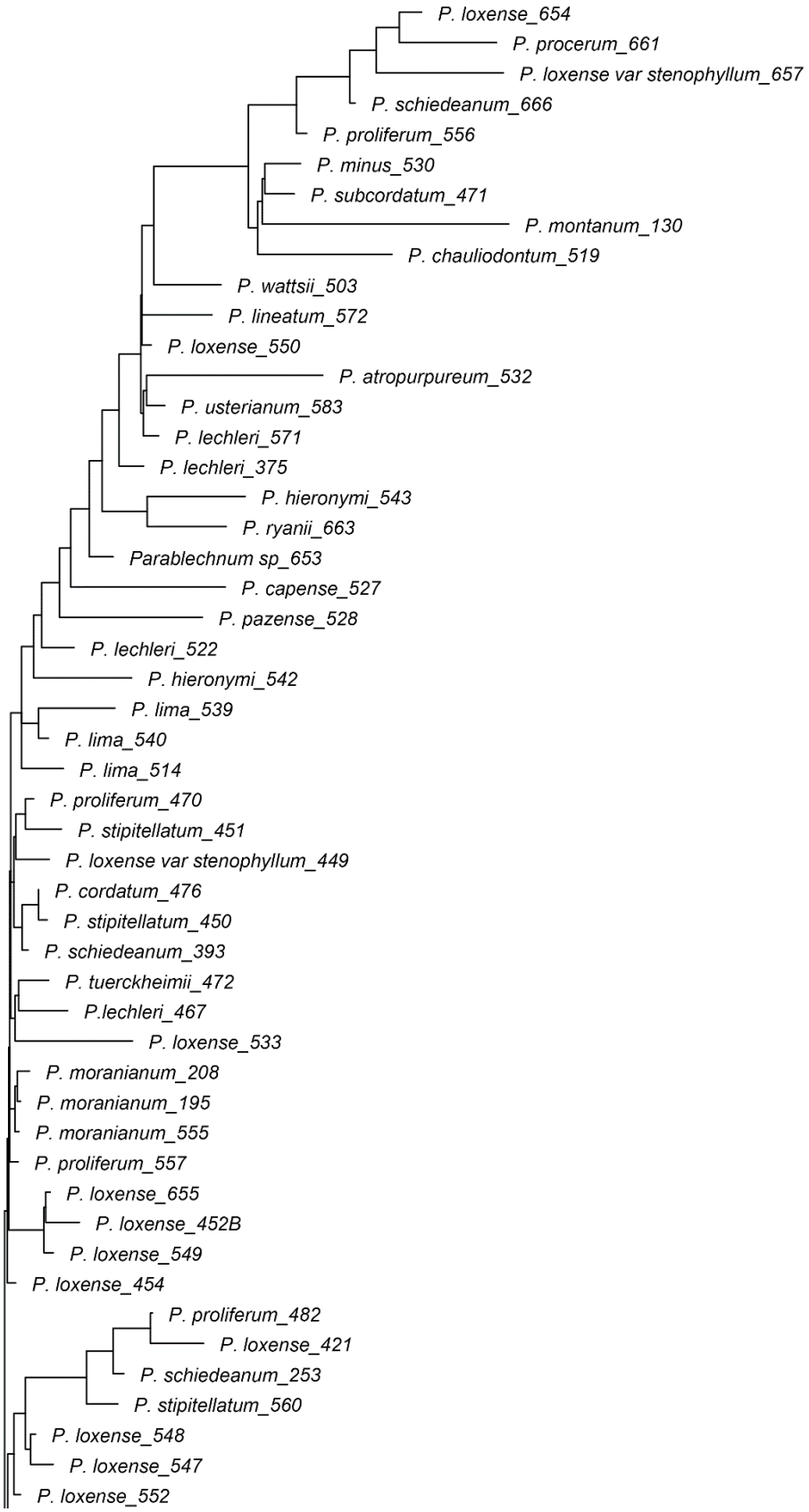

Figure S14. ML tree topology with indel coding of set 165.

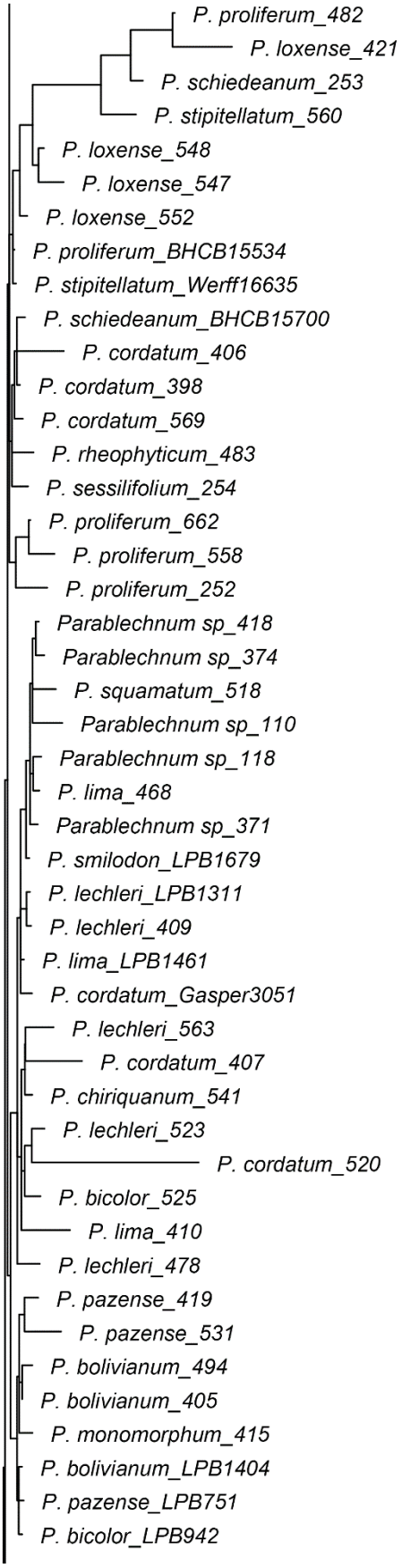

Figure S14. ML tree topology with indel coding of set 165 (cont).

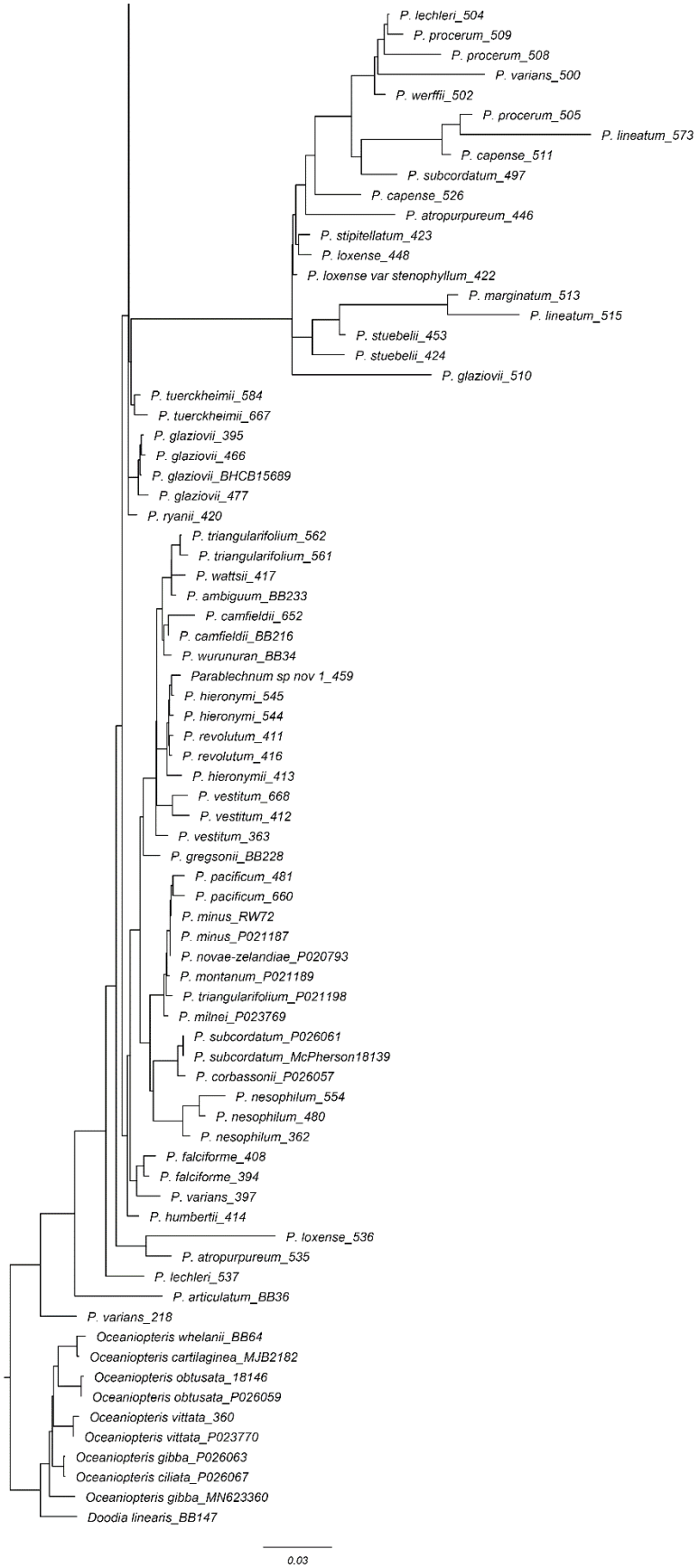

Figure S14. ML tree topology with indel coding of set 165 (cont).

Appendix IV: mean ages and 95% HPD confidence intervals for the Beast analysis represented in Figure 29.

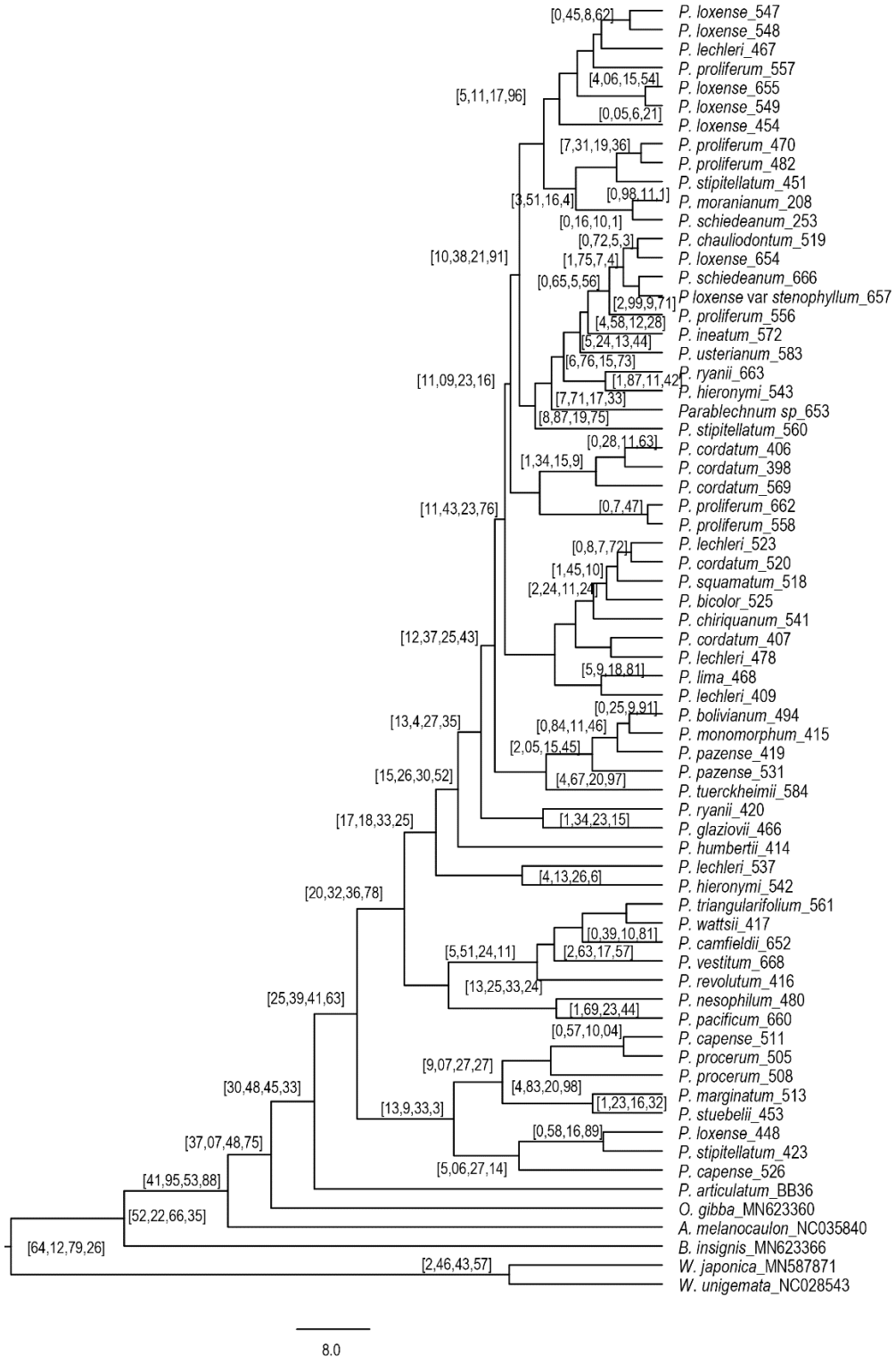

Figure S15. Phylogenetic tree resulting from the dating of Parablechnum with 95% HPD intervals.

TESIS DOCTORAL

MADRID, 2022.