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The curious distribution of the dwarf Brazilian tree fern, *Neoblechnum brasiliense* (Blechnaceae): New country records and a significant range extension

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Abstract. *Neoblechnum brasiliense* (Blechnaceae) is common and widespread in South America but has been known from Mesoamerica by only one collection from Guatemala by Julian Steyermark in 1939. We discovered two new occurrences of the species, in Belize and Mexico, extending the range of the species over 1000 km north and west into northern Mesoamerica. We discuss possible explanations for the rarity of the species in Mesoamerica and its disjunction from South America.

Keywords: Belize, *Blechnum*, floristics, Mexico.

The Blechnaceae comprises ca. 250 species of ferns worldwide (Kramer et al., 1990 Smith et al., 2006; Rothfels et al., 2012; Perrie et al., 2014; Gasper et al., 2016, 2017), of which about 200 have been classified in *Blechnum*. This genus is well known to be polyphyletic (e.g., Cranfill & Kato, 2003; Schuettpelz & Pryer, 2007; Rothfels et al., 2012; Perrie et al., 2014; Gasper et al., 2017), and recently 25 genera have been recognized for the family (Molino et al., 2019). Five of these genera may have trunk-like, arborescent rhizomes: the monotypic *Brainea* J. Sm. (China, southeast Asia, Malesia) and *Neoblechnum* Gasper & V.A.O. Dittrich (Neotropical), plus *Oceaniopteris* Gasper & Salino [*O. gibba* (Labill.) Gasper & Salino of Oceania], some *Lomaria* Willd. (South America, South Africa, Australia, New Caledonia), *Lomariocycas* (J. Sm.) Gasper & V.A.O. Dittrich (Neotropics, Africa, and Madagascar), and *Sadleria* Kaulf. (Hawaii).

Neoblechnum brasiliense (Desv.) Gasper & V. A. O. Dittrich (*Blechnum brasiliense* Desv.) differs from other Blechnaceae by the combination of stout, erect rhizomes forming caudices to c. 1 m, monomorphic sterile and fertile fronds, free veins, indusiate sori, serrulate pinnae adnate to and strongly decurrent onto the leaf rachis, and linear-lanceolate, bicolored but mostly glossy-black scales at the base of the stipe (Gasper et al., 2016).

Distribution

Neoblechnum brasiliense has an unusual distribution: it is almost exclusively South American except for one disjunct occurrence in Guatemala that was first documented by a collection by Julian Steyermark in 1939. In his description of the species for Guatemala, Stolze (1981) remarked that "The species is aptly named, as it is far more abundant in Brazil than anywhere else. It is found as far north as Colombia but heretofore has not been found in the West Indies, or in Central America except for the one Steyermark specimen collected in Chiquimula in 1939. This is curious, in that the plants are large and conspicuous and not likely to be overlooked even by general collectors. It should not be confused with any other

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Guatemalan species." *Neoblechnum brasiliense* is collected most often in lowlands < 1000 m but up to 1800 m and is most common in southern Brazil, southeastern Paraguay, and northeastern Argentina, with far fewer collections in each of Bolivia, Colombia, Ecuador, Peru, Uruguay, and Venezuela, plus the small cluster of specimens in northern Mesoamerica including our recent collections (Fig. 1).

To our knowledge, no other collections of this species for Mesoamerica have been made until our recent collections over 69 (in Mexico) and 79 (in Belize) years after Steyermark's collection. The first author discovered the species in the Mountain Pine Ridge Forest Reserve of Belize in 2018 (*Brewer 8518* BRH, MO) and identified it as *Blechnum brasiliense* using Stolze's (1981) and Moran's (1995) keys for the genus and by matching the specimen to images of type specimens (JSTOR, 2018). In late 2018, while perusing a photographic field guide to the Las Margaritas field station, Hueytamalco, Puebla, Mexico (Cornejo-Tenorio & Ibarra-Manríquez, 2014), the first author recognized that the photographs of a *Blechnum* in the guide matched *Neoblechnum brasiliense*. This plant was collected in 2008 (*G. Cornejo-Tenorio & G. Ibarra-Manríquez 2478* MEXU, MO) and it was misidentified as *Blechnum polypodioides* Raddi. The first author confirmed the identity of the plant by examining a duplicate specimen at the Missouri Botanical Garden (Tropicos.org, 2019) and an image of another duplicate through Portal de Datos Abiertos UNAM (UNAM, 2019).

Habitat

Neoblechnum brasiliense has a somewhat broad ecological amplitude. Although it is mostly associated with some disturbance, the species can be found in tropical rainforests to seasonally deciduous and semideciduous tropical forest, on sub-mesic to wet soils where light availability is moderate to high, less commonly in shaded areas under forest canopy (Dittrich et al., 2017). Most of the collections in South America have been from mesic-to-wet ground associated with disturbed areas and edge habitat, including stream banks, forest edges, vegetation openings, degraded vegetation, trails, roadsides, etc. All three collections in Mesoamerica were from disturbed, mesic-to-wet habitats.

In Guatemala, *Neoblechnum* was found in "swampy thickets with *Osmunda* at the base of slopes" along the Río Lucía Saso between 1200 and 1500 m (Field Museum of Natural History, 2018; Smithsonian Institution, 2018). In Belize, a small population of five individuals was located in a remote, hurricane-disturbed, broadleaved gallery forest within a pine-oak-*Byrsonima* savanna, in wet soil derived from granite, beside and near a small stream at ca. 700 m (Figs. 2). Characteristic taxa in this area of the gallery forest included *Blechnum gracile* Kaulf., *Casearia arborea* (Rich.) Urb., *Cyathea myosuroides* (Liebm.) Domin, *Euterpe precatoria* Mart., *Ficus obtusifolia* Kunth, *Geonoma interrupta* (Ruiz & Pav.) Mart., *Hieronyma alchorneoides* Allemão, *Hymenophyllum hirsutum* (L.) Sw, *Lacistema aggregatum* (P.J.Bergius) Rusby, *Machaerium floribundum* Benth., *Meniscium serratum* Cav., *Polybotrya caudata* Kunze, *Psychotria panamensis* Standl., *Sloanea tuerckheimii* Donn.Sm., *Symphonia globulifera* L.f., and *Xylopia frutescens* Aubl.

In Mexico, this species was found 11 years ago (*G. Cornejo-Tenorio & G. Ibarra-Manríquez 2478*) in mesic soil in young (3–5 years old) Acahual (successional vegetation) derived from evergreen tropical forest at 480 m (Figs. 1, 2). Recently it was observed again, in the same general area, along the edge of a small riverbed (1–2 m wide) in secondary forest (c. 12–25 years old) also derived from evergreen tropical forest, at 560 m (*G. Cornejo-Tenorio & G. Ibarra-Manríquez 5220*; *G. Ibarra-Manríquez & G. Cornejo-Tenorio 7140*). In the latter habitat there were at least 30 individuals of *N. brasiliense* found in the understory of the forest. This population shared habitat with *Bursera simaruba* Sarg., *Cecropia obtusifolia* Bertol., *Cnidoscolus multilobus* (Pax) I.M.Johnst., *Conostegia xalapensis* D.Don, *Costus scaber* Ruiz & Pav., *Croton draco* Schltdl., *Dieffenbachia seguine* Schott, *Cupania dentata* Moc. & Sessé, *Cyathea divergens* Kunze, *Cymbopetalum baillonii* R.E.Fr., *Hampea nutricia* Fryxell, *Philodendron sagittifolium* Liebm., *Piper aduncum* L., *P. hispidum* M.Martens & Galeotti, *Psychotria limonensis* K.Krause, *P. flava* Oerst., *Scleria secans* Urb., *Selaginella stenophylla* A.Braun, *Syngonium podophyllum* Schott, *Trichospermum mexicanum* (DC.) Baill., *Trophis mexicana* (Liebm.) Bureau, *Vernonia patens* Kunth and *Vismia camparaguey* Sprague & L.Riley.

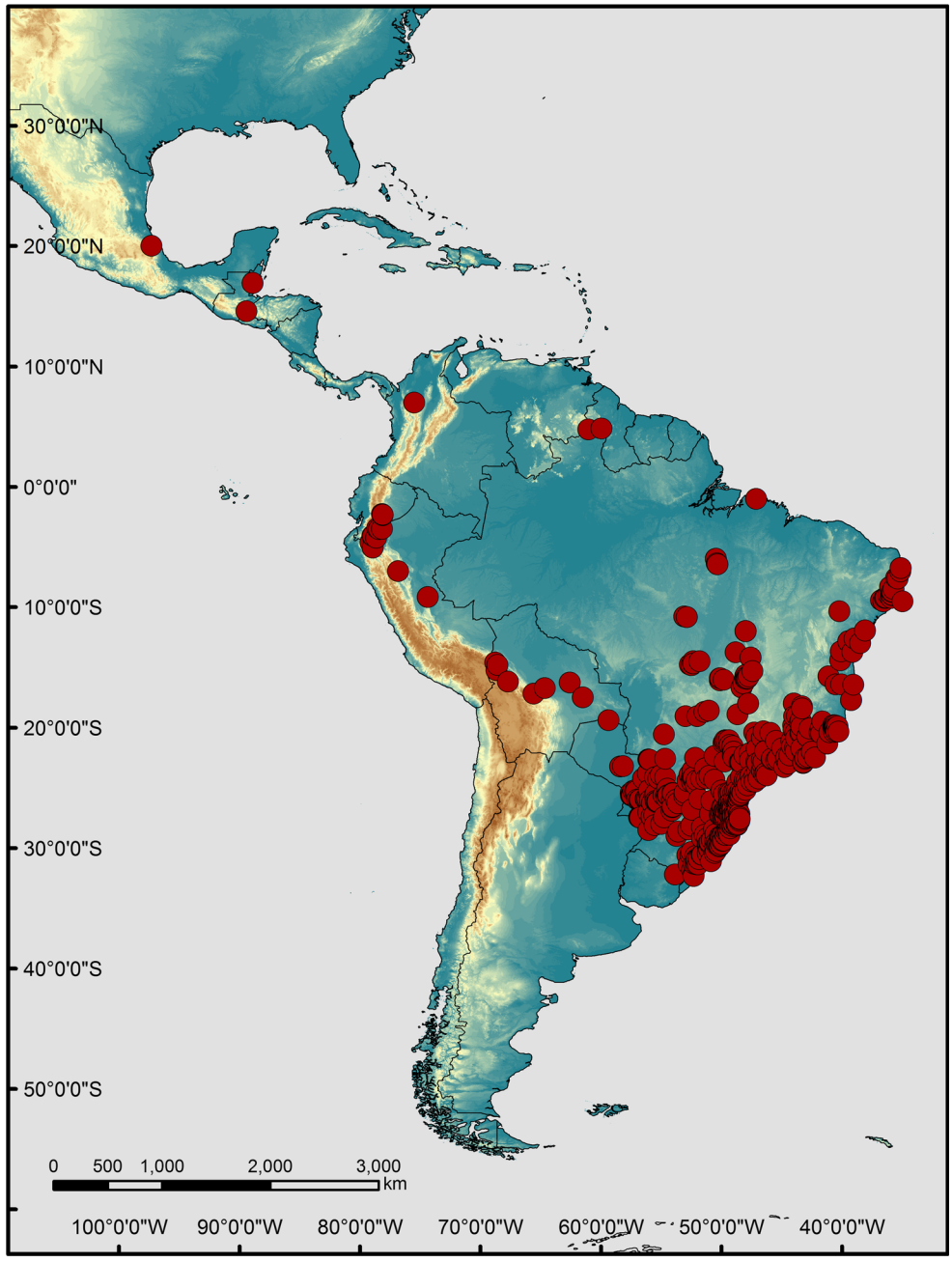

FIG. 1. Distribution of *Neoblechnum brasiliense* represented by collections locality data (red dots) from IDigBio (2019).

Discussion

Why no other collections of *Neoblechnum brasiliense*, a rather large, conspicuous, and distinctive fern often growing in accessible habitats, have been made in Mesoamerica is indeed curious. The most parsimonious explanation is that the species is very rare in Mesoamerica and has eluded collection. These conclusions are based in part on the assumption that variation in local abundance of collections of *N. brasiliense* is proportional to the true local abundance of

Fig. 2. *Neoblechnum brasiliense*. **a**–**b**. Habit (year 2008 and 2019, respectively). **c**. Frond (adaxial surface). **d**. Midleaf (abaxial surface). **e**. Young crozier with scales similar to those of stipes and rhizomes. **f**. Basal stipe scales. **g**. Detail of sori, venation, and margin of pinna. **h**. Young frond. Photographic credits: from Mexico G. Cornejo-Tenorio (**a**, **b**, **e**, **h**), from Belize S. Brewer (**c**, **d**, **f**, **g**).

populations of this species, rather than an artifact of differences in collecting intensity. Record densities for ferns, with records obtained by searching the iDigBio database using the general search term "Polypodiopsida" (IDigBio, 2019), and area coverage of fern collections are generally similar for southern and northern Mesoamerica, with Costa Rica (0.46/km^2) ranked first in fern density collection, followed by Panama (0.16/km^2), Belize (0.11/km^2), El Salvador (0.09/km^2), Nicaragua (0.07/km^2), Guatemala (0.05/km^2), Honduras (0.05/km^2), and southern Mexico (0.04/km^2). Although collections of ferns and other vascular plants in Mesoamerica are spatially inconsistent in intensity, and some areas remain under-collected in general, historically extensive collecting for vascular plants in Mexico, Belize, Guatemala, Nicaragua, and Costa Rica should have returned some or more specimens of *N. brasiliense* if the species were more common.

Furthermore, the nearly 2000 km gap (Fig. 1) in the known distribution of *N. brasiliense* between northern Mesoamerica and South America

appears to represent a true and recent disjunction in the range of this species. Disturbed and otherwise open, mesic-wet habitats are common and often readily accessible throughout Mesoamerica, as they are in South America, where *N. brasiliense* is often frequent and found among a variety of vegetation types (Dittrich et al., 2017). Therefore, a limitation in habitat availability and/or habitat restriction appear to be unlikely explanations for the species' rarity and distribution in Mesoamerica. Vicariance as an explanation for the disjunct distribution of *N. brasiliense* is not viable; South America was well separated from what is now northern Mesoamerica by the early Cretaceous (e.g., Coney, 1982; Bally et al., 1989), before the Eupolypod II clade (including Blechnaceae) arose in the late Cretaceous (Pryer & Schuettpelz, 2009).

It seems likely that the populations in Belize and Mexico have been relatively recently established. Although Central America is geologically young, the closing of the Central American Isthmus occurred 2.8 MYA (O'Dea et al., 2016), providing plenty of time for the development of a robust Mesoamerican population of *N. brasiliense*. The Belize population, though small, is notable in that it appears to be growing; two of the five individuals were quite small, without well-developed stems and were not reproductive, one was of intermediate size and not reproductive, and two individuals were moderately robust and reproductive. All were located within an area < 300 m^2. In the Mexican locality, the second and third authors worked on a regional checklist of vascular plants (G. Ibarra-Manríquez & G. Cornejo-Tenorio, unpubl. data) covering an area ca. 2500 ha (360–640 m) for three years. In 2008 the species was seen and collected only once. This population was small, about eight individuals, of which at least half were reproductive. After 11 years (2019), they returned to the original collection area but could not find the population; the collection site was not recognizable due to successional changes in the vegetation, and the original population did not have precise GPS coordinates. During a follow up search of the general area one month later, they found another population of *N. brasiliense* with ca. 30 young and mature individuals within an area of around of 600 m^2.

Dispersal from cultivation in botanical or home gardens is highly unlikely. The Guatemalan collection was made in a remote area less than 20 years after and 75 km due east of the oldest and most likely potential source (the botanical garden now at Universidad de San Carlos de Guatemala) at the time. Prevailing winds in this part of Guatemala are predominantly northerly and easterly, rarely westerly (Weatherspark, 2019). Belize has only two small, and relatively young botanical gardens, neither of which cultivate nor know of any cultivation of *N. brasiliense* anywhere in Belize (R. Aguilar, Belize Botanic Garden, pers. comm.; Brewer, pers. obs.). The Belize population of *N. brasiliense* is in an uninhabited area of the north-central Maya Mountains, 32, 40 and 100 km to the south and east of the nearest major settlements San Ignacio, Belmopan and Belize City, respectively. Prevailing winds in Belize are primarily easterly, with stronger winds associated with northeasterly winter storms and hurricanes tracking from the east or southeast (Wright et al., 1959; Weatherspark, 2019). The same situation occurs in Mexico. The species was collected in the Sierra Norte de Puebla region, which is an area where the main productive activities are agriculture (mainly orange and banana plantations) and livestock (for milk and meat production). This fern was not observed as ornamental plants in family gardens, government buildings or hotels, where species of Araceae, Orchidaceae, or ferns like *Nephrolepis* spp. are usually registered. The Xoxoctic Botanical Garden in Cuetzalán municipality, about 25 km northwest of the Mexican population of *N. brasiliense*, lacks specimens of this species. Northeasterly to southwesterly trade winds are predominant in this sierra. During winter, strong, cold winds ("nortes") come from the northeast (Valera et al., 2011).

The remoteness and rarity of the species in northern Mesoamerica may best be explained by a rare long-distance dispersal (LDD) event and/or irregular events limiting the propagule load necessary to sustain infrequent and small populations. The importance and ubiquity of such improbable events as mechanisms of colonization of remote habitats by plants were recognized at least as early as Darwin (1859). Over the last two decades with the advent of modern molecular and computational techniques (e.g., Avise, 2000), the biogeographical importance of LDD events in plant distributions has received significant attention and support (Cain et al., 2000; Horn et al., 2001; Nathan, 2006; Nathan et al., 2008). Recent attention to the importance of LDD events has been placed on distributions of ferns in general (Moran, 2008) and for the Blechnaceae in

particular (Shepherd et al., 2007; Vicent et al., 2017).

Successful dispersal and establishment of *Neoblechnum brasiliense* spores from South America to northern Mesoamerica is plausible and would require production of a sufficiently large numbers of spores, long-distance air transport, viable propagules after dispersal, landing in sites suitable for successful recruitment of a sporophyte, and establishment of reproductive individuals in a stable population (Wolf et al., 2001). Long distance transport is possible via hurricanes and prevailing winds tracking from the east to the west/northwest across northernmost South America (NOAA, 2019). The lightweight, windblown spores of ferns can survive long periods of time under extreme conditions and, due to their small size, can be produced in great abundance and be dispersed up to thousands of kilometers through the air (Tryon, 1970; Ranker et al., 1994; Perrie et al., 2010). Such events have been attributed to the establishment of significant fern lineages in remote islands such as Hawaii (Tryon, 1970; Geiger et al., 2007). Once successfully dispersed, homosporous ferns are capable of self-fertilization, and establishment of a population from just a single spore is possible.

The conditions for a successful LDD event establishing *N. brasiliense* would appear to be more likely to occur from northwest South America, which is closer to Mesoamerica and within the reach of hurricanes, but where the propagule pool of this species would be much smaller than in eastern Brazil. The core and largest propagule pool of *N. brasiliense* in southeastern Brazil and immediate environs is also the farthest pool from northern Mesoamerica and from hurricane lanes across the Atlantic (Fig. 1). We suggest a phylogeographic study of *N. brasiliense* to test this hypothesis.

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Literature cited

Avise, J. C. 2000. Phylogeography: the history and formation of species. Harvard University Press, Cambridge.

Bally, A. W., C. R. Scotese & M. L. Ross. 1989. North America-Plate-tectonic setting and tectonic elements. Pp. 1–16. *In:* A. W. Bally & A. R. Palmer (eds.), The geology of North America v. A. The geology of North America–an overview. Geological Society of America, Boulder.

Cain, M. L., B. G. Milligan & A. E. Strand. 2000. Long-distance seed dispersal in plant populations. American Journal of Botany 87: 1217–1227.

Coney, P. J. 1982. Plate tectonic constraints on the biogeography of Middle America and the Caribbean region. Annals of the Missouri Botanical Garden 69: 432–443.

Cornejo-Tenorio, G. & G. Ibarra-Manríquez. 2014. Municipio de Hueytamalco, Puebla, México. Plantas de Las Margaritas. Field Museum Field Guide no. 650, versión 1. https://fieldguides.fieldmuseum.org/sites/default/files/rapid-color-guides-pdfs/650_plantas_de_las_margaritas.pdf.

Cranfill, R. B. & M. Kato. 2003. Phylogenetics, biogeography and classification of the woodwardioid ferns (Blechnaceae). Pp. 25–48. *In*: S. Chandra & M. Srivastava (eds.). Pteridology in the new millennium. Kluwer Academic Publishers, Dordrecht.

Darwin, C. 1859. The origin of species. John Murray, London.

Dittrich, V. A. O., A. Salino, R. Monteiro & A. L. Gasper. 2017. The family Blechnaceae (Polypodiopsida) in Brazil: Key to the genera and taxonomic treatment of *Austroblechnum*, *Cranfillia*, *Lomaridium*, *Neoblechnum* and *Telmatoblechnum* for southern and southeastern Brazil. Phytotaxa 303: 1–33.

Field Museum of Natural History. 2018. Department of Botany. https://fm-digital-assets.fieldmuseum.org/1120/651/C0615952F.jpg. (Accessed 14 April 2018).

Gasper, A. L., T. E. Almeida, V. A. O. Dittrich, A. R. Smith & A. Salino. 2017. Molecular phylogeny of the fern family Blechnaceae (Polypodiales) with a revised genus-level treatment. Cladistics 33: 429–446.

Gasper, A. L., V. A. O. Dittrich, A. R. Smith & A. Salino. 2016. A classification for Blechnaceae (Polypodiales: Polypodiopsida): New genera, resurrected names, and combinations. Phytotaxa 275: 191–227.

Geiger, J. M. O., T. A. Ranker, J. M. R. Neale & S. T. Klimas. 2007. Molecular biogeography and origins of the Hawaiian fern flora. Brittonia 59: 142–158.

Horn, H. S., R. Nathan & S. R. Kaplan. 2001. Long-distance dispersal of tree seeds by wind. Ecological Research 16: 877–885.

IDigBio. 2019. Integrated digitized biocollections. National Science Foundation. https://www.idigbio.org/ (Accessed 12 February 2019).

JSTOR. 2018. JSTOR Global Plants. http://plants.jstor.org/ (Accessed 12 April 2018).

Kramer, K. U., T. C. Chambers & E. Hennipman. 1990. Blechnaceae. Pp. 60–68. *In*: K. U. Kramer & P. S. Green

(eds.), The families and genera of vascular plants. Volume 1. Pteridophytes and gymnosperms. Springer-Verlag, Wien, Berlin.

Molino, S., J. M. Gabriel y Galán, E. B. Sessa & P. Wasowicz. 2019. A multi-character analysis of *Struthiopteris* leads to the rescue of *Spicantopsis* (Blechnaceae, Polypodiopsida). Taxon 68: 185–198.

Moran, R. C. 1995. Blechnaceae. Pp. 325–333 *In*: G. Davidse, M. Souza, S. & Knapp (eds.), Flora Mesoamericana, Volume 1: Psilotaceae a Salviniaceae. Universidad Autónoma de México, D.F.; Missouri Botanical Garden, St. Louis; The Natural History Museum, London.

Moran, R. C. 2008. Diversity, biogeography, and floristics. Pp. 367–394. *In:* T. A. Ranker & C. H. Haufler (eds.), Biology and evolution of ferns and lycophytes. Cambridge University Press, Cambridge.

Nathan, R. 2006. Long-distance dispersal of plants. Science 313: 786–788.

Nathan, R., F. M. Schurr, O. Spiegel, O. Steinitz, A. Trakhtenbrot & A. Tsoar. 2008. Mechanisms of long-distance seed dispersal. Trends in Ecology and Evolution 23: 638–647.

National Oceanic and Atmospheric Administration (NOAA). 2019. National Hurricane Center Data Archive. https://www.nhc.noaa.gov/data/ (Accessed 1 January 2019).

O'Dea, A., H. A. Lessios, A. G. Coates, R. I. Eytan, S. A. Restrepo-Moreno, A. L. Cione, L. S. Collins, A. de Queiroz, D. W. Farris, R. D. Norris, R. F. Stallard, M. O. Woodburne, O. Aguilera, M.-P. Aubry, W. A. Berggren, A. F. Budd, M. A. Cozzuol, S. E. Coppard, H. Duque-Caro, S. Finnegan, G. M. Gasparini, E. L. Grossman, K. G. Johnson, L. D. Keigwin, N. Knowlton, E. G. Leigh, J. S. Leonard-Pingel, P. B. Marko, N. D. Pyenson, P. G. Rachello-Dolmen, E. Soibelzon, L. Soibelzon, J. A. Todd, G. J. Vermeij, & J. B. C. Jackson. 2016. Formation of the Isthmus of Panama. Science Advances 2: e1600883.

Perrie, L. R., D. J. Ohlsen, L. D. Shepherd, M. Garrett, P. J. Brownsey & M. J. Bayly. 2010. Tasmanian and Victorian populations of the fern *Asplenium hookerianum* result from independent dispersal from New Zealand. Australian Systematic Botany 23: 387–392.

Perrie, L. R., R. K. Wilson, L. D. Shepherd, D. J. Ohlsen, E. L. Batty, P. J. Brownsey & M. J. Bayly. 2014. Molecular phylogenetics and generic taxonomy of Blechnaceae ferns. Taxon 63: 745–758.

Pryer, K. M. & E. Schuettpelz. 2009. Ferns (Monilophyta). Pp. 153–156 *In*: S. B. Hedges & S. Kumar (eds.), The timetree of life. Oxford University Press, New York.

Ranker, T. A., S. K. Floyd & P. G. Trapp. 1994. Multiple colonizations of *Asplenium adiantum-nigrum* onto the Hawaiian Archipelago. Evolution 48: 1364–1370.

Rothfels, C. J., M. A. Sundue, L. Y. Kuo, A. Larsson, M. Kato, E. Schuettpelz & K. M. Pryer. 2012. A revised family-level classification for eupolypod II ferns (Polypodiidae: Polypodiales). Taxon 61: 515–533.

Schuettpelz, E. & K. M. Pryer. 2007. Fern phylogeny inferred from 400 leptosporangiate species and three plastid genes. Taxon 56: 1037–1050.

Shepherd, L. D., L. R. Perrie, B. S. Parris & P. J. Brownsey. 2007. A molecular phylogeny for the New Zealand Blechnaceae ferns from analyses of chloroplast *trn*L-*trn*F DNA sequences. New Zealand Journal of Botany 45: 67–80.

Smith, A. R., K. M. Pryer, E. Schuettpelz, P. Korall, H. Schneider & P. G. Wolf. 2006. A classification for extant ferns. Taxon 55: 705–731.

Smithsonian Institution. 2018. National Museum of Natural History, Department of Botany collections database. http://n2t.net/ark:/65665/399420a81-d942-4548-9a7c-84ba79e00ba2 (Accessed 14 April 2018).

Stolze, R. G. 1981. Fern and fern allies of Guatemala. Part II. Polypodiaceae. Fieldiana: Botany 6: 1–522.

Tropicos.org. 2019. Missouri Botanical Garden. http://www.tropicos.org/Image/100589760 (Accessed 09 Mar 2019).

Tryon, R. M. 1970. Development and evolution of fern floras of oceanic islands. Biotropica 2: 76–84.

Universidad Nacional Autónoma de México (UNAM). 2019. Portal de datos abiertos UNAM. Departamento de Botánica, Instituto de Biología (IBUNAM), *Blechnum polypodioides* Raddi, ejemplar de: Herbario Nacional de México (MEXU), Plantas Vasculares. https://datosabiertos.unam.mx/IBUNAM:MEXU:1408764 (Accessed 09 March 2019).

Valera, M. A., C. Arreguín & E. Torres. 2011. Clima. P. 31. *In:* Comisión nacional para el conocimiento y uso de la biodiversidad (CONABIO) (ed.), La biodiversidad en Puebla: Estudio de estado. México. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, Gobierno del Estado de Puebla, Benemérita Universidad Autónoma de Puebla, Puebla.

Vicent, M., J. M. Gabriel Y Galán, & E. B. Sessa. 2017. Phylogenetics and historical biogeography of *Lomaridium* (Blechnaceae, Polypodiopsida). Taxon 66: 1304–1316.

Weatherspark. 2019. https://weatherspark.com/. (Accessed 10 November 2019).

Wolf, P. G., H. Schneider & T. A. Ranker. 2001. Geographic distributions of homosporous ferns: does dispersal obscure evidence of vicariance? Journal of Biogeography 28: 263–270.

Wright, A. C. S., D. H. Romney, R. H. Arbuckle, & V. E. Vial. 1959. Land in British Honduras. Colonial Research Publication, Her Majesty's Service Office London.

Appendix 1. List of specimens examined.

BELIZE. Cayo: Mountain Pine Ridge Forest Reserve, 16°55′05"N, 88°54′23"W, 700 m, 11 Apr 2018, *S. W. Brewer 8518* (BRH, MO).

GUATEMALA. Chiquimula: Montaña Castilla, vicinity of Montaña Cebollas, along Rio Lucía Saso, 3 miles southeast of Quezaltepeque, [14°40′0.12"N, 89°25′0.12"W], 1200–1500 m, 6 Nov 1939, *J. A. Steyermark 31,347* (F, US).

MEXICO. Puebla: Hueytamalco, Campo Experimental "Las Margaritas", Instituto Nacional de Investigaciones Forestales, Agrícolas y Pecuarias (INIFAP), without coordinates, 480 m, 2 Mar 2008, *G. Cornejo-Tenorio & G. Ibarra-Manríquez 2478* (MEXU, MO); ibid., [20°00′32.06"N, 97°19′08.17"W], 562 m, 13 Aug 2019, *G. Cornejo-Tenorio & G. Ibarra-Manríquez 5220* (MEXU); *G. Ibarra-Manríquez & G. Cornejo-Tenorio 7140* (MEXU).