

FIRST RECORD OF THE FERN *AMBLOVENATUM OPULENTUM* (THELYPTERIDACEAE) IN NATURAL ENVIRONMENTS OF ARGENTINA AND TYPIFICATION OF THE NAME

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The occurrence, establishment and spread of invasive plant species represent one of the major threats to the conservation of natural ecosystems. This paper reports for the first time the presence of *Amblovenatum opulentum* (Thelypteridaceae) growing in the wild in Argentina and provides the typification of the name. The species is native to tropical Africa and Asia and has been reported as naturalized and widely invasive across the tropical and subtropical Neotropics. During field trips conducted in 2025 and 2026 in the Punta Lara Nature Reserve, Buenos Aires Province, Argentina, two populations of *A. opulentum* were discovered. They were found growing terrestrially in the understory of the mixed riparian forest, a microhabitat that supports most reserve's native fern populations. Given *Amblovenatum opulentum* is widely cultivated in central and eastern Argentina, it has the potential to become invasive in the absence of appropriate monitoring and management measures.

Key words. Alien species; Ferns; Lectotype; Polypodiales; Protected areas; Thelypteroids.

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La aparición, establecimiento y propagación de especies de plantas invasoras representan una de las principales amenazas para la conservación de los ecosistemas naturales. Este trabajo da a conocer por primera vez la presencia de *Amblovenatum opulentum* (Thelypteridaceae) creciendo de forma silvestre en Argentina y presenta la tipificación del nombre. La especie es nativa de África tropical y Asia, y ha sido reportada como naturalizada y ampliamente invasora en las regiones tropicales y subtropicales del Neotrópico. Durante relevamientos de campo realizados en 2025 y 2026 en la Reserva Natural Punta Lara, provincia de Buenos Aires, Argentina, se descubrieron dos poblaciones de *A. opulentum*. Estas fueron halladas creciendo en forma terrestre en el sotobosque del bosque ribereño mixto, un microhábitat que alberga la mayor parte de las poblaciones de helechos nativos de la reserva. Dado que *Amblovenatum opulentum* es ampliamente cultivada en el centro y el este de Argentina, presenta el potencial de convertirse en una especie invasora en ausencia de medidas adecuadas de monitoreo y manejo.

Palabras clave. Especies exóticas; Helechos; Lectotipo; Polypodiales; Áreas protegidas; Thelypteroides.

INTRODUCTION

Invasive species are usually defined as those introduced by humans (intentionally or unintentionally) into regions outside their historical native distribution range, and that have then established self-sustaining populations (“naturalized”) and spread widely, negatively impacting on biodiversity and natural ecosystems (Convention on Biological Diversity, 2023). The intentional or unintentional dispersal of these species is facilitated by various human-mediated introduction pathways (Wilson et al., 2009). In particular, horticultural and gardening trades have been indicated as the primary source of introductions of invasive alien plants worldwide (Pyšek et al., 2011; Seebens et al., 2015; van Kleunen et al., 2018). Terrestrial ferns have been popular plants in gardening trade for centuries to this day (de Winter & Amoroso, 2003; Whittingham, 2010). Alien ferns are generally understudied and therefore poorly represented in official inventories of plant species and regulatory lists of invasive exotic plants. Of over 12,000 described fern species, about 60 are problematic due to their invasive behaviour, which affects the use of damaged resources, human health, and plant communities (Robinson et al., 2010). Remarkable examples include some species of *Lygodium* Sw. (“climbing fern”), the tuber-forming *Nephrolepis cordifolia* (L.) C. Presl (“tuberous sword fern”), and water ferns as *Azolla filiculoides* Lam. (“mosquito fern”), and *Salvinia molesta* D.S. Mitch. (“giant Salvinia”, “kariba weed”); these water ferns, beyond their natural areas, can double surface coverage in a few days, blocking light to waterways and reducing oxygen for fish (Coetzee & Hill, 2020; Pinero-Rodríguez et al., 2021). Another example is the ornamental tree fern *Sphaeropteris cooperi* (Hook. ex F. Muell.) R. M. Tryon, which was introduced in Hawaii and became invasive, displacing native populations of the also tree fern *Cibotium glaucum* (Sm.) Hook. & Arn. (Chau et al., 2013).

Some of the most widespread invasive fern species belong to Thelypteridaceae (Walker & Sharpe, 2010; Akomolafe & Rahmad, 2018; Fawcett & Smith, 2021), a family distributed in tropical and subtropical zones around the world, with highest species richness in Asia and less representation in temperate zones. Members of Thelypteridaceae are distinguished by their conspicuously pubescent indument distributed over the vegetative organs and the presence of grayish-white unicellular acicular trichomes (Lin et al., 2013). Among Thelypteridaceae, the genus *Amblovenatum* J. P. Roux includes six species characterized by having veins united below, or connivent to, the sinuses; relatively large,

persistent indusia; laminae lacking greatly reduced proximal pinnae, and sessile, sulfur-yellow glands on the lamina abaxially, especially along the veins and costules (Fawcett & Smith, 2021). The type species, *Amblovenatum opulentum* (Kaulf.) J. P. Roux, is native to Tropical Africa and Asia, and has become widely naturalized and reported as invasive in the neotropics, in Antilles, Costa Rica, Guatemala to northern and central Brazil, and Bolivia (Rojas Alvarado, 2011; FLEPPC, 2017; Smith & Kessler, 2017; Govaerts et al., 2021; Jiménez Barrios, 2025; see also <https://www.gbif.org/es/species/5275254>). Although knowledge of the richness and general status of non-native species in South America has increased in recent years, the extent of the distribution, abundance and ecological impacts of invasive plants throughout the Americas remain largely unknown (Zenni et al., 2022). The absence of continuous documentations of local floras, including sampling, long-term monitoring and maintenance of voucher specimens in herbaria, can lead to the overlooked establishment of non-native species. The documentation of newly introduced species in the Argentine flora, together with continued monitoring of the spread of previously recorded non-native species, provides an essential basis for implementing managing actions to their control and eradication, before they become invasive and cause significant impacts (Arana et al., 2020). The aims of this study are to report the recent discovery of *Amblovenatum opulentum* growing in the wild in Argentina, thereby updating its known distribution in South America, and to present the typification of the name. We also provide illustrations of the species’ morphological diagnostic characters, together with information on its habitat and ecological characteristics.

MATERIALS & METHODS

Field trips carried out during 2025 and 2026 in diverse habitats of the Punta Lara Nature Reserve (Buenos Aires Province, Argentina, 34° 47’ S - 57° 59’ W), revealed the presence of two populations of *Amblovenatum opulentum* growing terrestrially. The voucher specimens were deposited in LIL. Specialized taxonomic literature was used to confirm the identification of the species and to compile information on its distribution, particularly in the Neotropical region (Holttum, 1971, 1977a, b, 1980, 1981; Fosberg & Sachet, 1972; Du Puy, 1993; Green, 1994; Lin et al., 2013). Additional data were obtained from POWO (2026), Tropicos (<https://www.tropicos.org/>), Pteridoportal (<https://www.pteridoportal.org/portal/index.php>), and Govaerts et al. (2021). Herbarium collections and databases from the following institutions were also consulted: BA,

CORD, CTES, JUA, LIL, LP MCNS, RCVC, and SI. The potential status of *A. opulentum* within the introduction-naturalization-invasion (INI) continuum was assessed following the criteria proposed by Richardson et al. (2011) and Divíšek et al. (2025).

RESULTS

Amblovenatum opulentum (Kaulf.) J. P. Roux, *Strelitzia* 23: 201. 2009. *Aspidium opulentum* Kaulf., Enum. Filic.: 238. 1824. *Nephrodium opulentum* (Kaulf.) C. Presl, Tent. Pterid.: 81. 1836. *Amphineuron opulentum* (Kaulf.) Holttum, Blumea 19(1): 45-46. 1971. *Thelypteris opulenta* (Kaulf.) Fosberg, Smithsonian Contr. Bot. 8: 3-6. 1972. *Cyclosorus opulentus* (Kaulf.) Nakaike, Enum. Pterid. Jap., Fil.: 277. 1975. TYPE: GUAM. "habitat in Guahan", L. K. A. von Chamisso s.n. (lectotype, LECB 0001317!, designated here, is lectotype presumably at LE, not found). Figs. 1-2.

Terrestrial, 60-100 cm tall. Rhizome short-creeping, branched, with dark brown linear-lanceolate, attenuate minutely ciliate scales $\pm$ 9 mm long. Fronds tufted, approximate. Stipe 30-70 cm long, minutely pubescent and with dark brown scales similar to those to rhizome scales at the base. Laminae herbaceous, green turning to yellowish green when dried, broadly oblong-ovate, 0.8-1 m $\times$ 20-30 cm, pinnate-pinnatifid, pinnae 10-20 pairs, almost sessile, the proximal pair of pinnae slightly reduced; the largest pinnae are in the middle of the lamina, which are linear-lanceolate to narrowly oblong, 15-30 $\times$ 1-2 cm, apices long acuminate with several acicular hairs above on costa, with short trichomes and sulfur-colored spherical, sessile or stipitate glands along costae and veins abaxially (Fig. 2F), most abundant towards segment apices, deeply lobed 1/2-2/3 toward costae; segments 25-40 pairs, narrowly oblong, oblique, slightly falcate, 4-8 $\times$ 2-3 mm; veinlets 8-10 pairs, proximal pair varies, even within the same frond, from free, meeting the margin at the sinus, or connivent with a sinus-membrane (Fig. 2E). Sori orbicular, submarginal, appearing marginal because of revolute margins of lobes; indusia with small yellow glands on edges and often with acicular trichomes (Figs. 1C, 2G). Sporangia bearing golden spherical glands on stalks. Spores brown to dark brown, perispore folded.

Distribution, habitat and invasion status. The populations of *A. opulentum* occur in the Punta Lara Nature Reserve, located along the coast of the Río de La Plata estuary in Buenos Aires Province, in close proximity to major urban

centers comprising several million inhabitants. The climate is temperate and sub-humid, with average annual temperatures between 16.7°C to 18°C, annual rainfall of 1,000 mm and a relative humidity of 79% (Luna et al., 2025).

Biogeographically, the Punta Lara Nature Reserve is included in the Paraná Delta district, which belongs to the Esteros del Iberá Province of the Neotropical Region (Arana et al., 2021; Arana, 2023). Two populations of *A. opulentum*, each consisting of at least four to five individuals in the reproductive stage, were found growing beneath the canopy of a mixed riparian forest dominated by *Tessaria integrifolia* Ruiz & Pav. (Asteraceae), *Myrsine laetevirens* (Mez) Arechav. (Primulaceae) and *Nectandra angustifolia* (Schrad.) Nees & Mart. (Lauraceae), accompanied by other arborescent species as *Inga uraguensis* Hook. & Arn. (Fabaceae), *Blepharocalyx salicifolius* (Kunth) O. Berg (Myrtaceae) and *Sambucus australis* Cham. & Schltdl. (Viburnaceae) (Fig. 2A).

The introduction-naturalization-invasion (INI) continuum classifies alien species according to the stage of invasion they have reached, distinguishing among casual, naturalized and invasive species (Richardson et al., 2000). Following Richardson et al. (2011) and Divíšek et al. (2025), *Amblovenatum opulentum* can be tentatively considered a casual species (a subset of alien species) within the INI continuum, as no evidence of gametophyte establishment was observed in the habitat.

Typification

When Kaulfuss described *Aspidium opulentum*, he cited the provenance of the type as "Habitat in Guahan. Chamisso". In his first report to Romanzoff, Chamisso (1818) estimated that they had collected approximately 2,500 plant species, with about one-third of them being previously undescribed. To date, the full extent of their collections, including duplicate specimens, remains unknown (Berger, 2018). In particular, the ferns specimens were distributed to specialists such as Georg Friedrich Kaulfuss for study, a practice that partly explains the dissemination of many Chamisso's specimens.

In 1833, Chamisso succeeded von Schlechtendal as curator of the Royal Herbarium Berlin (B), and deposited a complete set of specimens from his expedition in that Herbarium. Unfortunately, this collection was destroyed during a bombing raid on the herbarium during the Second World War (Hiepko, 1987). In 1840, two years after Chamisso's death, his private herbarium comprising approximately 60,000 specimens, was purchased by the Botanical Museum of the St. Petersburg Academy of Sciences. This collection is now housed at the Komarov Botanical Institute in St. Petersburg (LE), where it is maintained

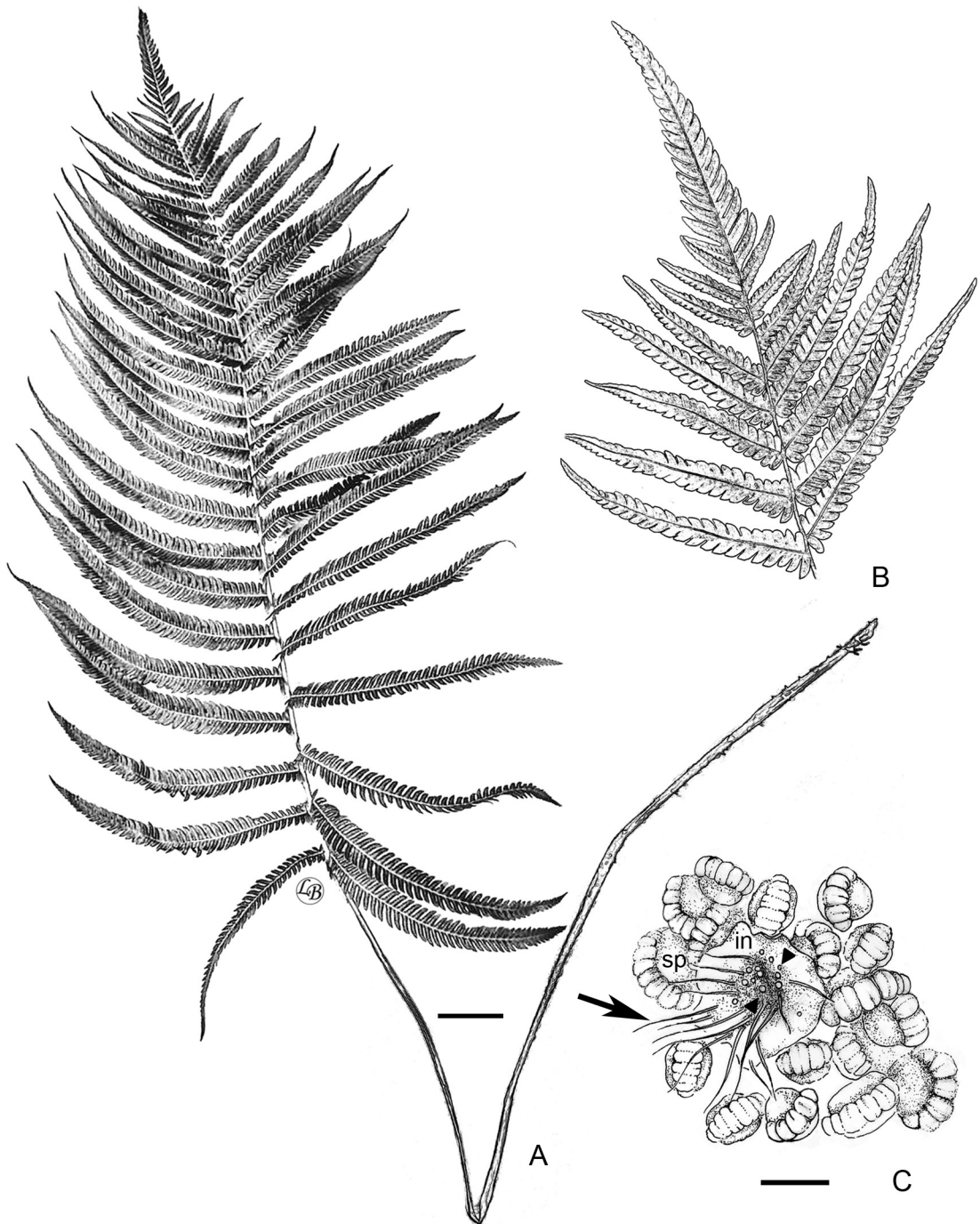


Fig. 1. *Amblovenatum opulentum*. **A**, frond. **B**, apical portion of the frond. **C**, sorus showing indusium with glands (arrowheads) and trichomes (arrow). References: **in**, indusium; **sp**, sporangia. From Martinenco, Arana & Luna 33 (LIL). Scales: A, 3.5 cm; C, 0.5 cm.



Fig. 2. *Amblovenatum opulentum*. **A**, population growing in Punta Lara Nature Reserve. **B**, scale of stipe with ciliate margins. **C**, apical portion of the frond. **D**, abaxial surface of the last segment of a pinna showing sori position (arrowheads). **E**, detail of venation meeting the margin at the sinus (arrows). **F**, abaxial pinna surface showing trichomes (arrow) and glands on the veins (arrowhead). **G**, sorus with indusium bearing glands (arrowhead) and trichomes (arrow). References: **in**, indusium; **sp**, sporangia; **so**, sorus; **vn**, vein. From Martinenco, Arana & Luna 33 (LIL). Scales: A, 25 cm; B, 2 mm; C, 1.5 cm; D, 2.5 mm; E, 1.5 mm; F, 1 mm; G, 0.2 mm.

as a separate collection (Berger, 2018). Holttum (1977b), when transferring *Aspidium opulentum* to the genus *Amphineuron*, stated that he had examined a specimen preserved in LE which he regarded as the holotype. However, after an exhaustive search of the LE collections, the specimen could not be located and presumably no longer exists (Dorofeyev, pers. comm.). As a syntype is preserved in LECB, this specimen (LECB 0001317!) is here selected as lectotype in order to fix the application of the name.

Selected specimen examined. ARGENTINA. Buenos Aires. Pdo. Ensenada: Reserva Natural Punta Lara, en sotobosque próximo al arroyo de la entrada a la reserva, 20-III-2026, *L. Martinenco, M. Arana & M. L. Luna* 33 (LIL). Sendero “el burrito”, 15-IV-2025, *L. Martinenco & L. Luna* 28 (LIL).

DISCUSSION AND CONCLUSIONS

According to the Global Register of Introduced and Invasive Species (GRIIS) (Pagad et al., 2018), 553 naturalized plant species have been recorded in Argentina (Zenni et al., 2022), among a total of 1,401 non-native plant species documented in Argentine National Parks (Gantchoff et al., 2018). Although ferns are usually valued for their ornamental and medicinal uses, over 157 species worldwide have been reported as naturalized in regions outside their native ranges, and approximately 39% of these are considered invasive (Jones et al., 2019). In Argentina, 25 fern species are currently listed as “weeds” (Yañez et al., 2020). Among them, Thelypteridaceae as *Christella dentata* (Forssk.) Brownsey & Jermy and *Macrothelypteris torresiana* (Gaudich.) Ching were reported as both, “ruderal and ecological weeds”. In the present study, *Amblovenatum opulentum* (Thelypteridaceae), is documented for first time as a casual alien species for the Argentine flora. Previously, *A. opulentum* had been recorded in Bolivia (Smith & Kessler, 2017) and northern and central Brazil (Salino et al., 2020), with no reported occurrences in other regions or countries of the Southern Cone (which comprises southern Brazil, Chile, Argentina, Paraguay and Uruguay). This taxon was not included in the recent work by Luna et al. (2025), as it was detected during subsequent floristic monitoring field trips focused on ferns and lycophytes within the Punta Lara Nature Reserve. Particularly in the last two years up to the present, the habitats regularly surveyed by our team have undergone modifications associated with infrastructure maintenance activities within the Reserve, which has facilitated the appearance of previously unrecorded plant species, such as *Amblovenatum opulentum*.

Another possible reason that may explain why the species had remained unnoticed is its frequent misidentification as *Christella hispidula*. This confusion was clarified through a detailed re-examination of herbarium specimens and field observations.

Exotic species occur in most ecosystems worldwide, and their impacts on protected areas may be particularly significant due the fundamental role of these areas in preserving native biodiversity and maintaining essential services for many communities (Foxcroft et al., 2014). Human activities in the vicinity of protected areas can have numerous negative impacts, including the introduction and establishment of alien species (Gantchoff et al., 2018; Zenni et al., 2022). In Argentina, the establishment of *A. opulentum* is likely to have originated from the gardening trade, a well-recognized pathway that directly contributes to the invasion success of alien ferns (McCulloch-Jones et al., 2021). *Amblovenatum opulentum* has been widely cultivated for centuries and possesses an efficient reproductive strategy, propagating both through rhizomes and via spores.

Invasive ferns often exhibit adaptations to prolonged drought, resistance to fire, pathogens or herbivory and continuous spore production and dispersal, all traits considered responsible to the difficulty of their control and management during biological invasion (Schneider, 2004; Jones et al., 2019). Since biodiversity is continuously modified by biotic and abiotic processes and environmental pressures, documenting its status across temporal and spatial scales is essential to identify the changes in species composition and to evaluate their ecological impacts. This may require the implementation of management and mitigation measures to safeguard native biodiversity (Arana et al., 2020). This is particularly recommended for the case of the alien species *Amblovenatum opulentum*, given that it is widely cultivated in central and eastern Argentina (Arana & Luna, pers. obs.) which may facilitate its introduction and subsequent spread in natural environments. As occurred with *Christella dentata* and *Macrothelypteris torresiana*, it could become a successful invasive species once established (Rojas Alvarado, 2011; Fawcett & Smith, 2021). Accordingly, *Amblovenatum opulentum* is included in Category I: “invasive exotics that are altering native plant communities by displacing native species, changing community structures or ecological functions, or hybridizing with native species”, in the Florida State, USA (FLEPPC, 2017). Therefore, early control and eradication measures should be implemented in the Punta Lara Nature Reserve to prevent its establishment and spread.

Identification key of Thelypteridaceae of Punta Lara Reserve

1. Laminae pinnate.....	2
1. Laminae pinnate-pinnatifid	3
2(1). Proliferous buds absent in proximal pinnae.....	<i>Cyclosorus interruptus</i>
2. Proliferous buds present adaxially in proximal pinnae.....	<i>Goniopteris burkartii</i>
3(1). Three or more pairs of proximal pinnae greatly reduced.....	<i>Amauropelta platensis</i>
3. Proximal pinnae not reduced.....	4
4(3). Abaxial laminae without opaque sulfur-colored or pale yellow spherical glands.....	<i>Christella hispidula</i>
4. Abaxial laminae with opaque sulfur-colored or pale yellow spherical glands	<i>Amblovenatum opulentum</i>

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BIBLIOGRAPHY

- Akomolafe, G. F. & Z. B. Rahmad. 2018. A review on global ferns invasions: mechanisms, management and control. *Journal of Research in Forestry, Wildlife & Environment* 10(3): 42-54.
- Arana, M. D. 2023. Caracterización biogeográfica de los Esteros del Iberá. *Bonplandia (Corrientes)* 32(2): 147-164.
- Arana, M. D.; E. Natale, G. Martínez & A. J. Oggero. 2020. The first register of the weed fern *Pteris cretica* var. *laeta* (Pteridaceae) in central Argentina. *Lilloa* 57(2): 99-109. DOI: <https://doi.org/10.30550/j.lil/2020.57.2/2>
- Arana, M. D.; E. Natale, A. Oggero, N. Ferreti, G. Romano, G. Martínez, P. Posadas & J. J. Morrone. 2021. Esquema biogeográfico de la República Argentina. *Opera lilloana* 56. Tucumán: Fundación Miguel Lillo. Available at: <http://www.lillo.org.ar/editorial/index.php/publicaciones/catalog/book/253>
- Berger, A. 2018. Rediscovery of Chamisso's type specimens of Hawaiian *Psychotria* (Rubiaceae, Psychotriaceae) in the herbarium of the Natural History Museum, Vienna. *PhytoKeys* 114: 27-42. DOI: <https://doi.org/10.3897/phytokeys.114.29426>
- Chamisso, L. K. A. von 1818. Voyage de Kotzebue. Lettre écrite à M. le comte de Romanzoff, par M. de Chamisso, naturaliste français, qui a fait le voyage autour du monde, avec M. de Kotzebue, sur le bric le Rurick. *Journal des Voyages, Découvertes et Navigations Modernes* 1818(1): 201-208.
- Chau, M. M.; L. R. Walker & K. Mehlreter. 2013. An invasive tree fern alters soil and plant nutrient dynamics in Hawaii. *Biological Invasions* 15(2): 355-370. DOI: <https://doi.org/10.1007/s10530-012-0291-0>
- Coetzee, J. A. & M. P. Hill. 2020. *Salvinia molesta* D. Mitch. (Salviniaceae): impact and control. *CABI Reviews* 15: 1-11. DOI: <https://doi.org/10.1079/PAVSNNR202015033>
- Convention on Biological Diversity. 2023. Invasive Alien Species, Glossary of Terms. <https://www.cbd.int/invasive/terms.shtml>
- de Winter, W. P. & V. Amoroso. 2003. *Plant Resources of South-East Asia. Cryptogams: Ferns and Fern allies*. Leiden: Backhuys Publishers.
- Divišek, J.; P. Pyšek, D. M. Richardson, N. J. Gotelli, B. Beckage, J. Molofsky, Z. Lososová & M. Chytrý. 2025. Naturalized and invasive species integrate differently in the trait space of local plant communities. *Ecology Letters* 28(11): e70235. DOI: <https://doi.org/10.1111/ele.70235>
- Du Puy, D. J. 1993. Thelypteridaceae. *Flora of Australia* 50, *Oceanic Islands* 2: 551-553. Canberra: Australian Government Publishing Service.
- Fawcett, S. & A. R. Smith. 2021. *A generic classification of the Thelypteridaceae*. BRIT Press, Fort Worth.
- FLEPPC (Florida Exotic Pest Plant Council). 2017. Florida Exotic Pest Plant Council's 2017 List of Invasive Plant Species. Available at: https://www.wbdg.org/FFC/AF/AFIFS/FLEPPC_Invasive_Plant_List_2017.pdf
- Fosberg, F. R. & M. H. Sachet. 1972. Three Indo-Pacific *Thelypteris* species reinterpreted and a new African species described. *Smithsonian Contributions to Botany* 8: 1-10.
- Foxcroft, L.C.; P. Pysek, D. M. Richardson, J. Pergl & P. E.

- Hulme. 2014. Chapter 2: Impacts of alien plant invasions in protected areas. In L. C. Foxcroft et al. (eds.), *Plant invasions in protected areas: patterns, problems and challenges* pp. 19-41. Dordrecht: Springer.
- Gantchoff, M. G.; C. M. Wilton & J. L. Belant. 2018. Factors influencing exotic species richness in Argentina's national parks. *PeerJ* 6:e5514. DOI: <https://doi.org/10.7717/peerj.5514>
- Govaerts, R.; E. N. Lughadha, N. Black, R. Turner & A. Paton. 2021. The World Checklist of Vascular Plants, a continuously updated resource for exploring global plant diversity. *Scientific Data* 8: 215. DOI: <https://doi.org/10.1038/s41597-021-00997-6>
- Green, P. S. 1994. Thelypteridaceae. *Flora of Australia* 49, *Oceanic Islands* 1: 583-585. Canberra: Australian Government Publishing Service.
- Hiepko, P. 1987. The collections of the Botanical Museum Berlin-Dahlem (B) and their history. *Englera* 7: 219-252.
- Holttum, R. E. 1971. Studies in the family Thelypteridaceae III. A new system of genera in the Old World. *Blumea* 19: 17-52.
- Holttum, R. E. 1977a. The family Thelypteridaceae in the Pacific and Australasia, *Allertonia* 1: 169-223.
- Holttum, R. E. 1977b. XII. The genus *Amphineuron* Holttum. *Blumea* 23: 205-218.
- Holttum, R. E. 1980. The fern-family Thelypteridaceae in Malaya. *Gardens' Bulletin (Singapore)* 33:1-30.
- Holttum, R. E. 1981. Thelypteridaceae, *Flora Malesiana* ser. II, 1(5): 331-560.
- Jiménez Barrios, J. 2025. Nuevos Registros del Helecho *Amblovenatum opulentum* (Thelypteridaceae) en el Sur de Guatemala. *Ciencia, Tecnología y Salud* 12(2): 133-138. DOI: <https://doi.org/10.36829/63CTS.v12i2.1878>
- Jones, E. J.; T. Kraaij, H. Fritz & D. Moodley. 2019. A global assessment of terrestrial alien ferns (Polypodiophyta): species' traits as drivers of naturalization and invasion. *Biological Invasions* 21(4): 861-873. DOI: <https://doi.org/10.1007/s10530-018-1866-1>
- Lin, Y. X.; Z. Y. Li, K. Iwatsuki & A. R. Smith. 2013. Thelypteridaceae. In Z. Y. Wu, P. H. Raven & D. Y. Hong (eds.). *Flora of China*, Vol. 2-3 (Pteridophytes), pp. 319-396. Beijing: Science Press; St. Louis: Missouri Botanical Garden Press.
- Luna, M. L.; M. L. Martinenco, E. Santellán, J. P. Ramos Giacosa & M. D. Arana. 2025. Helechos y licófitas de la Reserva Natural Punta Lara (Buenos Aires, Argentina): actualización florística, taxonómica y aspectos biogeográficos. *Lilloa* 62 (1): 237-266. DOI: <https://doi.org/10.30550/j.lil/2090>
- McCulloch-Jones, E. J.; T. Kraaij, N. Crouch & H. Fritz. 2021. The effect of horticultural trade on establishment success in alien terrestrial true ferns (Polypodiophyta). *Biological Invasions* 23(11): 3583-3596. DOI: <https://doi.org/10.1007/s10530-021-02599-0>
- Pagad, S.; P. Genovesi, L. Carnevali, S. Dimitri & M. A. McGeoch. 2018. Introducing the Global Register of Introduced and Invasive Species. *Scientific Data* 5: 170202. DOI: <https://doi.org/10.1038/sdata.2017.202>
- Pinero-Rodríguez, M. J.; R. Fernández-Zamudio, R. Arribas, I. Gomez-Mestre & C. Díaz-Paniagua. 2021. The invasive aquatic fern *Azolla filiculoides* negatively impacts water quality, aquatic vegetation and amphibian larvae in Mediterranean environments. *Biological Invasions* 23: 755-769. DOI: <https://doi.org/10.1007/s10530-020-02402-6>
- POWO (Plants of the World Online). 2026. Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew. Published on the Internet; <https://powo.science.kew.org/> (Accessed 13 April 2026).
- Pyšek, P.; V. Jarošík & J. Pergl. 2011. Alien plants introduced by different pathways differ in invasion success: Unintentional introductions as a threat to natural areas. *PLoS ONE* 6(9): e24890. DOI: <https://doi.org/10.1371/journal.pone.0024890>
- Richardson, D. M.; P. Pyšek, M. Rejmánek, M. G. Barbour, D. F. Panetta & C. J. West. 2000. Naturalization and invasion of alien plants: concepts and definitions. *Diversity and Distributions* 6: 93-107. DOI: <https://doi.org/10.1046/j.1472-4642.2000.00083.x>
- Richardson, D. M.; P. Pyšek & J. T. Carlton. 2011. A compendium of essential concepts and terminology in invasion ecology. In D. M. Richardson (ed), *Fifty years of invasion ecology: the legacy of Charles Elton*, pp: 409-420, Blackwell Publishing, Chichester.
- Robinson, R. C.; E. Sheffield & J. M. Sharpe. 2010. Problem ferns: their impact and management. In: K. Mehltreter, L. R. Walker, J. M. Sharpe (eds.), *Fern ecology*, pp. 255-322. Cambridge University Press, New York.
- Rojas Alvarado, A. F. 2011. New species and new records of ferns (Pteridophyta: Polypodiales) from Cocos Island, Costa Rica. *Brenesia* 75-76: 7-15.
- Salino, A.; R. S. Fernandes, I. O. Moura, L. C. Moura, T. E. Almeida, L. C. Paixão & M. I. Souza. 2020. Thelypteridaceae in Flora do Brasil 2020. Jardim Botânico do Rio de Janeiro.
- Schneider, L. C. 2004. Bracken fern invasion in Southern Yucatan: a case for land change science. *The Geographical Review* 94 (2): 229-241.
- Seebens, H.; F. Essl, W. Dawson, N. Fuentes, D. Moser, J. Pergl, P. Pyšek, M. van Kleunen, E. Weber, M. Winter & B. Blasius. 2015. Global trade will accelerate plant invasions in emerging economies under climate change. *Global Change Biology* 21(11): 4128-4140. DOI: <https://doi.org/10.1111/gcb.13021>

- Smith, A. R. & M. Kessler. 2017. Prodromus of a fern flora for Bolivia. XXX. Thelypteridaceae. *Phytotaxa* 331 (1): 1-34. DOI: <https://doi.org/10.11646/phytotaxa.331.1.1>
- van Kleunen, M.; F. Essl, J. Pergl, G. Brundu, M. Carboni, S. Dullinger, R. Early, P. González-Moreno, Q. J. Groom, P. E. Hulme, C. Kueffer, I. Kühn, C. Máguas, N. Maurel, A. Novoa, M. Parepa, P. Pyšek, H. Seebens, R. Tanner, J. Touza, L. Verbrugge, E. Weber, W. Dawson, H. Kreft, P. Weigelt, M. Winter, G. Klöner, M. V. Talluto & K. Dehnen-Schmutz. 2018. The changing role of ornamental horticulture in alien plant invasions. *Biological Reviews of the Cambridge Philosophical Society* 93(3): 1421-1437. DOI: <https://doi.org/10.1111/brev.12402>
- Walker, L. R. & J. M. Sharpe. 2010. Ferns, disturbance and succession. In K. Mehlreter, L. R. Walker & J. M. Sharpe (eds.), *Fern Ecology*, pp. 177-219. Cambridge University Press.
- Whittingham, S. 2010. *The Victorian Fern Craze*. Shire, Oxford.
- Wilson, J. R. U.; E. E. Dormontt, P. J. Prentis, A. J. Lowe & D. M. Richardson. 2009. Something in the way you move: Dispersal pathways affect invasion success. *Trends in Ecology & Evolution* 24(3): 136-144. DOI: <https://doi.org/10.1016/j.tree.2008.10.007>
- Yañez, A.; D. G. Gutiérrez & M. M. Ponce. 2020. Weedy ferns (Polypodiopsida) in Argentina: diversity, distribution and impact on human activities and ecosystems. *Anais da Academia Brasileira de Ciências* 92(01): e20180983. DOI: <https://doi.org/10.1590/0001-3765202020180983>
- Zenni, R. D.; I. Herrera, M. de Sá Dechoum, S. R. Ziller, A. C. L. de Matos, C. Núñez, M. A. Núñez & A. Pauchard. 2022. Plant invasions in South America. In: D. R. Clements, M. K. Upadhyaya, S. Joshi, A. Shrestha (eds.), *Global Plant Invasions*, pp. 187-208. Springer, Cham. DOI: https://doi.org/10.1007/978-3-030-89684-3_9