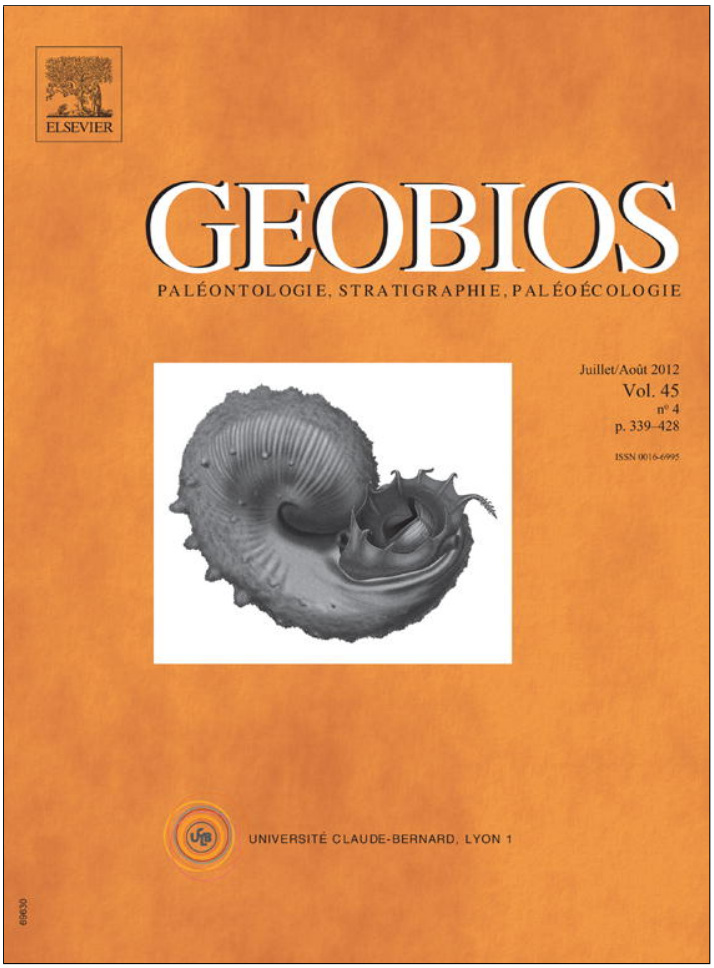

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Original article

Korallipteris, a new genus for Mesozoic *Gleichenia*-like fern fronds☆

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ABSTRACT

A new morphogenus, *Korallipteris*, is proposed to accommodate fertile or sterile fern fronds possessing essentially *Gleichenia*-like morphology (e.g., pinnate fronds with small pecopteroid pinnules) but lacking diagnostic features that allow their classification at fern family-level. The aim is thus, to solve an old nomenclatural problem that involves the use of illegitimate genera, such as *Gleichenites* Goeppert and *Microphyllopteris* Arber. Several species of *Gleichenites* described from the Mesozoic of Argentina and Chile, and *Microphyllopteris unisora* Cantrill and Nagalingum from Antarctica are here reassigned to *Korallipteris* gen. nov. The proposal of Nagalingum and Cantrill to preserve *Gleicheniaceaephyllum* Crabtree emend. Nagalingum and Cantrill for true Gleicheniaceous ferns, diagnosed by having an arrested laminar bud, is here accepted.

1. Introduction

Gleichenia-like fronds are abundant constituent of global Mesozoic floras. We include within this informal group all those simple or once- to twice-forked fronds, pinnately divided, with numerous, very small pinnules, having a midvein and a few lateral veins. Fossil foliage with these gross-features has been described since the earliest paleobotanical studies. In the past, different generic names have been proposed to accommodate these remains, the oldest being *Gleichenites* Goeppert (e.g., *Gleichenites gleichenoides* Oldham and Morris, 1863). Historically, fossil fronds identified as *Gleichenites* were mostly linked to the extant fern family Gleicheniaceae. Unfortunately, this botanical affinity has been assumed even for fronds lacking fertile structures (or any other characteristic that might relate them to the Gleicheniaceae). However, fossil foliage with *Gleichenia*-like frond morphology but bearing fertile structures similar to other families of ferns has also been described. These include the Aptian ferns *Lophosoria cupulata* Cantrill (1998) (Dicksoniaceae sensu Smith et al., 2006) and *Eocyathea remesaliae* Césari (2006) (Cyatheaceae), which clearly widen the phylogenetic range of this frond morphology within the Pteridophyta.

A nomenclatural problem began when the original species of *Gleichenites* Goeppert (*G. linkii* Goeppert, *G. neesii* Goeppert, *G. artemisiaefolius* Goeppert, *G. crithmifolius* Goeppert and *G. neuropteroides* Goeppert), Paleozoic forms which were the syntypes of the genus, were removed from it and transferred in other previously recognized pteridosperm genera (e.g., *Neuropteris*, *Sphenopteris*, and *Eremopteris*), precluding the use of this genus name for true ferns (e.g., Unger, 1845; Schimper, 1869). Nevertheless, the genus continued to be used. At the same time, amendments of *Gleichenites* and the formulation of alternative morphogenera (e.g., *Microphyllopteris* Arber) were proposed as a mean of solving this nomenclatural problem. However, as explained below, this process became progressively more complex and confusing regarding the legitimacy of the genera involved, their morphological features and the possible botanical affinities of the fossil fronds included in each of them.

Here, a new morphogenus is proposed to include fossil fern foliage with *Gleichenia*-like physiognomy but whose family-level affinity, is impossible to establish. This proposal should resolve the successive nomenclatural problems within this artificial group.

2. Systematic paleontology

Division PTERIDOPHYTA
INCERTAE SEDIS
Morphogenus **Korallipteris** nov. gen.
Figs. 1, 2

Derivation of name: The name derives from the Greek words "*Koralli*", meaning coral, and "*Pteris*", fern; in reference to *Gleichenia microphylla* R. Br., the scrambling coralfern, which

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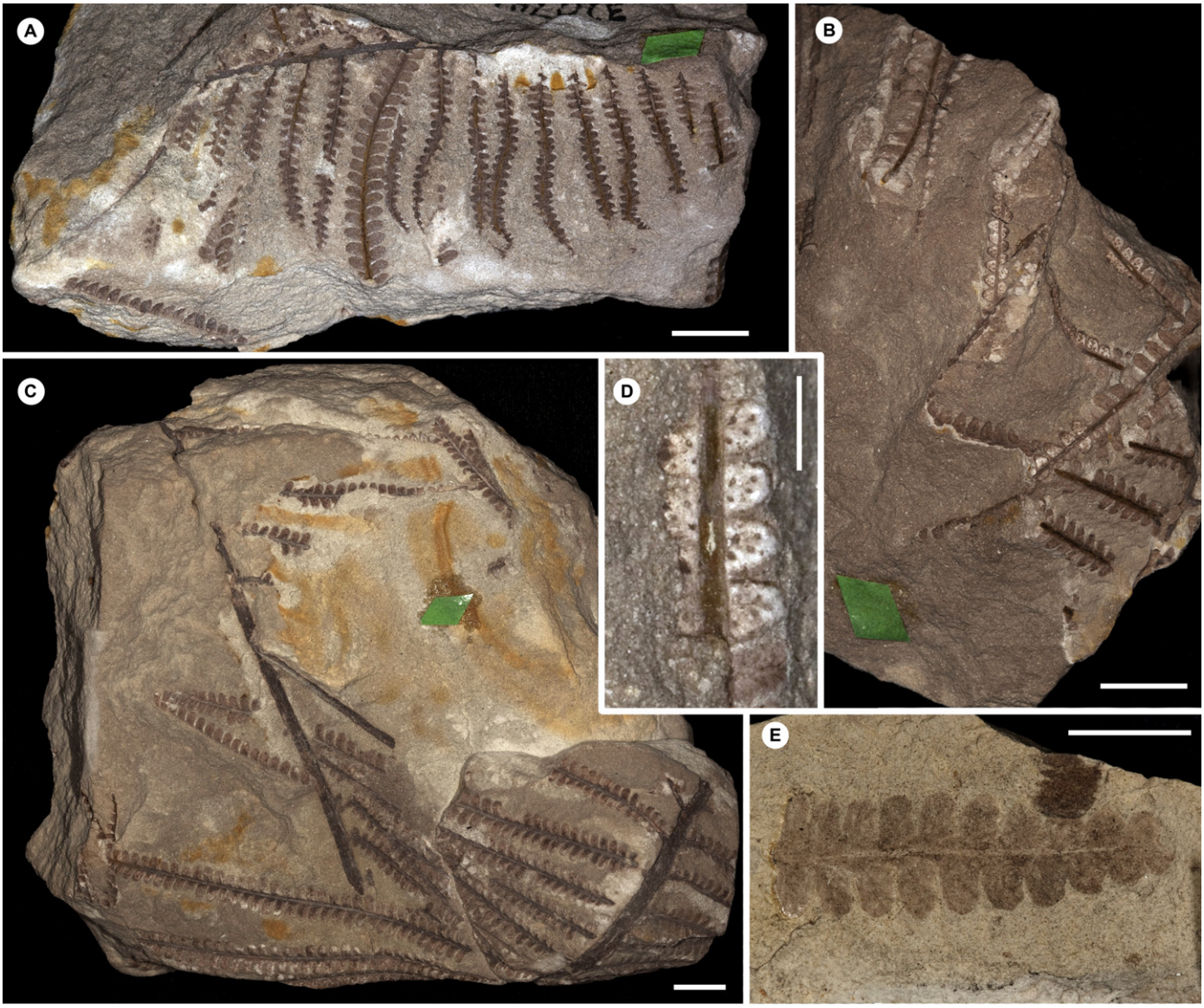

Fig. 1. A–D. *Korallipteris argentinica* (Berry emend. Herbst) nov. comb. [= *Gleichenia argentinica* Berry], Meseta Baqueró, Santa Cruz Province, Baqueró Group, general view of sterile and fertile pinnae. A. syntype USNM PAL 320741. B. lectotype USNM PAL 320740. C. syntype USNM PAL 320742. D. detail of B, showing fertile pinnules. Sori appear as little points at both sides of the midvein, and were interpreted by Herbst (1962a) as immature. **E.** *Korallipteris piatnitzkyi* (Berry) nov. comb. [= *Gleichenites piatnitzkyi* Berry], Cerro Baguales, Santa Cruz Province, Mata Amarilla Formation, general view of sterile pinnae, lectotype USNM PAL 315223. Scale bars: 1 cm in A–C, 0.5 cm in D, E.

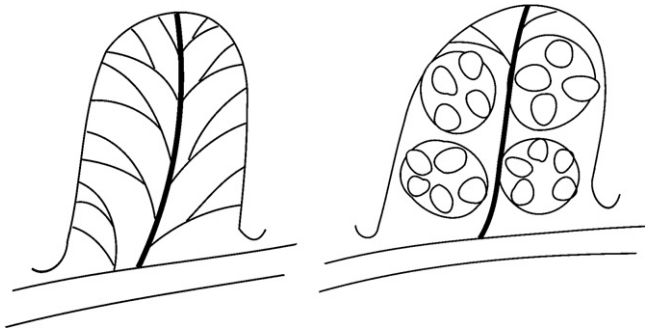

Fig. 2. Schematic representation of sterile (left) and fertile (right) pinnules of *Korallipteris argentinica* (Berry emend. Herbst) nov. comb., the latter presenting mature sori.
Modified from Herbst (1962a).

possesses pinnate fronds, bearing small pinnules similar to the fossil specimens referred to this morphogenus.

Type species: *Gleichenia argentinica* (Berry) emend. Herbst, 1962a, from the Early Cretaceous of Santa Cruz Province, Patagonia, Argentina.

Included species: *Korallipteris argentinica* (type species designed here), *Korallipteris cachivaritensis*, *Korallipteris feruglioi*, *Korallipteris gallegoi*, *Korallipteris juliensis*, *Korallipteris medinae*, *Korallipteris piatnitzkyi*, *Korallipteris potrerillensis*, *Korallipteris quilacoyensis*, *Korallipteris unisora* and *Korallipteris vegagrandensis*. Although this genus probably encompasses several more species than the ones presented in this work (see section 3.2), we restricted the new systematic treatment to those taxa from the Mesozoic of Argentina, Chile and Antarctica, described originally as different species of *Gleichenites*, as well as to *Microphyllopteris unisora*. *Gleichenites taquetrensis* Herbst and Anzótegui (1968), from the Middle Jurassic of Chubut, Argentina, is not included in the genus, since it has pinnules all along the length of the rachis, and the

particular shape and size of its pinnules clearly indicates that this fern frond should be referred to a different morphogenus.

Occurrence: In this work, from the Triassic to the Cretaceous of Argentina, Chile and Antarctica, but almost certainly having a worldwide distribution (see section 3.2).

Diagnosis: Fertile or sterile fronds, pinnate, bipinnate, tripinnate or dichotomously branched, without an arrested laminar bud; primary pinnae variable in size and shape; secondary pinnae alternate to sub-opposite; pinnules small (ca. 5 mm wide and long), alternate to opposite, elliptic or deltoid to falcate or rhombic, apex round to acute; pinnule venation consisting of a midvein and two to five pairs of lateral veins, simple and/or branched once or twice; when fertile, having one to numerous circular sori in the abaxial side of the pinnules.

Korallipteris argentinica (Berry emend. Herbst) nov. comb.
Figs. 1(A–D), 2
1924. *Gleichenia argentinica* Berry - Berry, p. 18, pl. 1, figs. 1–5.
(?)1951. *Gleichenites argentinica* Berry - Feruglio, p. 54.
1962a. *Gleichenites argentinica* (Berry) emend. Herbst - Herbst, p. 144, pl. 2, figs. 6–10.

Basionym: *Gleichenia argentinica* Berry, 1924 (p. 18, pl. 1, figs. 1–5).

Repository data: Not indicated in the protologue, but the three specimens illustrated by Berry (1924: pl. 1, fig. 1) are registered in the Smithsonian Institution, National Museum of Natural History, United States of America, with the collection numbers USNM PAL 320740–320742.

Lectotype: Berry (1924) did not designate a type. In accordance with the ICBN (McNeill et al., 2006: Art. 9.2), we designate here as the lectotype the fertile specimen USNM PAL 320740 (Fig. 1(B, D)), illustrated in the protologue by Berry (1924: pl. 1, fig. 1).

Syntypes: Specimens USNM PAL 320741 (Fig. 1(A)) and USNM PAL 320742 (Fig. 1(C)) illustrated in the protologue by Berry (1924: pl. 1, figs. 2 and 3 respectively).

Type locality and unit: Meseta Baqueró, Santa Cruz Province, Argentina; Baqueró Group (Aptian).

Remarks: Sterile and fertile fronds are known (Fig. 2); Feruglio's (1951) record is included with reservation because the author did not illustrate the specimens nor gave repository data. This taxon is here proposed as the type species of *Korallipteris* nov. gen.

Korallipteris cachivaritensis (Herbst) nov. comb.
1996. *Gleichenites cachivaritensis* Herbst - Herbst, p. 71, pl. 1, figs. 1, 6.
1998. *Gleichenites cachivaritensis* Herbst - Herbst et al., p. 95, pl. 1, figs. 4–6.
(?)2005. *Gleichenites cachivaritensis* Herbst - Herbst et al., p. 382, text-fig. 3, D.

Basionym: *Gleichenites cachivaritensis* Herbst, 1996 (p. 71, pl. 1, figs. 1, 6).

Holotype: SGO-PB 1310; designated in the protologue by Herbst (1996: pl. 1, figs. 1, 6); housed in the Museo Nacional de Historia Natural, Santiago, Chile.

Type locality and unit: Quebrada de la Cachivarita, area of Cerro La Ternera, Copiapó Province, III° Región, Chile; La Ternera Formation (Upper Triassic).

Remarks: Sterile and fertile fronds are known, the latter bearing four to five sori per pinnule; the record of Herbst et al. (2005) is preceded by a question mark due to the lack of fertile structures to allow an accurate assignment.

Korallipteris feruglioi (Herbst) comb. nov.

Basionym: *Gleichenites feruglioi* Herbst, 1966 (pp. 80–81, pl. 1, figs. 1, 2).

Holotype: PB-LP 2335, as designated in the protologue by Herbst (1966: pl. 1, figs. 1, 2); housed in the División Paleobotánica, Museo de La Plata, Argentina.

Type locality and unit: Meseta Baqueró, Santa Cruz Province, Argentina; Baqueró Group (Aptian).

Remarks: Sterile and fertile fronds are known, the latter with poorly preserved reproductive structures.

Korallipteris gallegoi (Herbst) nov. comb.
1988. *Gleichenites* sp. - Herbst, p. 376, pl. 1, figs. 7–10; pl. 4, figs. 30–32.
1996. *Gleichenites gallegoi* Herbst - Herbst p. 70, pl. 1, figs. 2, 3.
(?)2005. *Gleichenites gallegoi* Herbst - Herbst et al., p. 382, figs. 3, B–C.

Basionym: *Gleichenites gallegoi* Herbst, 1996 (p. 70, pl. 1, figs. 2, 3).

Holotype: CTES-PB 10120, as designated in the protologue by Herbst (1996: pl. 1, fig. 2), housed in the Facultad de Ciencias Exactas, Naturales y Agrimensura, Universidad Nacional del Nordeste, Corrientes, Argentina.

Type locality and unit: Ea. Cañadón Largo, Santa Cruz Province, Argentina; Cañadón Largo Formation (Upper Triassic), El Tranquilo Group.

Remarks: Sterile and fertile fronds are known, the latter bearing six to seven sori per pinnule; Herbst et al. (2005) stated that there is no doubt about the taxonomic assignment of their specimens to *Gleichenites gallegoi*. However, based on the illustrated material of Herbst et al. (2005: figs. 3B, C), their placement in *Gleichenites* (*Korallipteris*) is equivocal. For this reason, they are included here with reservation.

Korallipteris juliensis (Herbst) nov. comb.
(?)1913. *Gleichenites* cf. *G. micromerus* Heer - Halle, p. 22, pl. 1, figs. 14, 15.
1962b. *Gleichenites juliensis* Herbst - Herbst, p. 188, pl. 1, figs. 1–5.
(?)2007. *Gleichenites juliensis* Herbst - Passalia, p. 568, pl. 3, figs. 5–9.

Basionym: *Gleichenites juliensis* Herbst, 1962 (b, p. 188, pl. 1, figs. 1–5).

Holotype: MACN (BAPB) 1915, as designated in the protologue by (Herbst, 1962b: pl. 1, fig. 1), housed in the División Paleobotánica, Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires, Argentina.

Type locality and unit: Ea. El Mineral, Gran Bajo de San Julián, Santa Cruz Province, Argentina; La Matilde Formation (Middle Jurassic).

Remarks: Sterile and fertile fronds are known, the latter bearing eight to ten sori per pinnule; the synonymy entries of Halle (1913) and Passalia (2007) are preceded by a question mark due to the lack of fertile fronds which impels to assign accurate taxonomic position.

Korallipteris medinae (Ruiz) nov. comb.

Basionym: *Gleichenites medinensis* Ruiz, 1984 (p. 449, pl. 2, fig. 3; text-fig. 1 C, D).

Holotype: CIRGEO Pb 423, as designated in the protologue by Ruiz (1984, pl. 2, fig. 3; text-fig. 1 C, D), housed in the División Paleobotánica, Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires, Argentina.

Type locality and unit: Lago Cardiel, Santa Cruz Province, Argentina; Piedra Clavada Formation (mid-Cretaceous).

Remarks: Sterile and fertile fronds are known, the latter bearing numerous sori per pinnule; Ruiz (1984) pointed out the presence of 10–16 sori per pinnule in the diagnosis, but in text-fig. 1 C, drew up to twenty.

Korallipteris piatnitzkyi (Berry) nov. comb.
Fig. 1(E)

Basionym: *Gleichenites piatnitzkyi* Berry, 1937 (p. 21, pl. 1, figs. 1, 2).

Repository data: Not indicated in the protologue, but the few specimens studied by Berry (1937) are deposited in the Smithsonian Institution, National Museum of Natural History, United States. Among them, only the specimen illustrated by the author has a collection number (USNM PAL 315223).

Lectotype: Berry (1937) did not designate a type. In accordance with ICBN (McNeill et al., 2006: Art. 9.2), we designate the sterile specimen USNM PAL 315223 (Fig. 1(E)) as the lectotype, illustrated in the protologue by Berry (1937: pl. 1, figs. 1, 2).

Type locality and unit: Cerro Baguales, Santa Cruz Province, Argentina; Mata Amarilla Formation (Cenomanian–Coniacian).

Korallipteris potrerillensis (Herbst) nov. comb.

Basionym: *Gleichenites potrerillensis* Herbst, 1972 (p. 19, text-fig. 1A–C).

Derivation of name: No derivation of the specific epithet *potrerillensis* was provided in the protologue, but it certainly was derived from the name of the type locality, Potrerillos (Argentina).

Holotype: PB-LP 10691 (and its counterpart 10692) was designated in the protologue by Herbst, 1972 (text-fig. 1A–C), housed in the División Paleobotánica, Museo de La Plata, La Plata, Argentina.

Type locality and unit: Cerro Bayo, Potrerillos, Mendoza Province, Argentina; Las Cabras Formation (Middle Triassic).

Remarks: Although the pinnules are somewhat elongate, they can be referred to *Korallipteris* nov. gen. because of the morphology of the pinnae and the size of the pinnules; a single fertile specimen, bearing up to eight sori per pinnule, is known; no photographs were included in the protologue.

Korallipteris quilacoyensis (Leppe and Moisan) nov. comb.

1996. *Gleichenites* sp. - Herbst, p. 71, pl. 1, figs. 4, 5.

2005. *Gleichenites* sp. - Nielsen, p. 555, pl. 5, fig. 1.

2006. *Gleichenites quilacoyensis* Leppe and Moisan - Leppe et al., p. 90, pl. 2, figs. 9–11; pl. 5., fig 22.

2010. *Gleichenites quilacoyensis* Leppe and Moisan - Moisan et al., p. 93, pl. 3, figs. D, E; pl. 7, fig B.

Basionym: *Gleichenites quilacoyensis* Leppe and Moisan in Leppe et al., 2006 (p. 90, pl. 2, figs. 9–11; pl. 5, fig. 22).

Holotype: STJU 2, as designated in the protologue by Leppe et al. (2006: pl. 2, figs. 9–11; pl. 5, fig. 22), housed in the Laboratorio de Paleobotánica del Departamento Ciencias de la Tierra, Universidad de Concepción, Concepción, Chile.

Type locality and unit: Cerro Calquinhue, Concepción Province, Biobío Region, Chile; Santa Juana Formation (Upper Triassic).

Remarks: Sterile and fertile fronds are known, the latter bearing five sori per pinnule; the synonymy list is in accordance with Moisan et al. (2010).

Korallipteris unisora (Cantrill and Nagalingum) nov. comb.

1981. Brevipteris-Elongat - Jefferson, p. 63, pl. 4.1, fig. 12 (pars), (non pl. 4.1, figs. 13, 14).

1981. Brevipteris-Semicirc - Jefferson, p. 65, pl. 4.1, fig. 9.

2005. *Microphyllopteris unisora* Cantrill and Nagalingum - Cantrill and Nagalingum, p. 90, pl. 2, figs. A–C.

Basionym: *Microphyllopteris unisora* Cantrill and Nagalingum, 2005 (p. 90, pl. 2, figs. A–C).

Derivation of name: No derivation of the specific epithet *unisora* was provided in the protologue, but the name likely derives from the presence of a single sorus per pinnule.

Holotype: KG 2815.195, as designated in the protologue by Cantrill and Nagalingum (2005: pl. 2, fig. B), housed in the British Antarctic Survey, Cambridge, United Kingdom.

Type locality and horizon: Coal Nunatak, Alexander Island, Antarctic Peninsula, Antarctica; Triton Point Formation (late Albian).

Remarks: Sterile and fertile fronds are known, the latter being smaller, and bearing a single circular or elliptic sorus per pinnule; the synonymy list is in accordance with Cantrill and Nagalingum (2005).

Korallipteris vegagrandensis (Herbst) nov. comb.

Basionym: *Gleichenites vegagrandis* Herbst, 1962 (a, p. 145, pl. 3, figs. 11, 14, 15).

Derivation of name: No derivation of the specific epithet *vegagrandis* was provided in the protologue, but certainly derived from the name of the type locality, Estancia Vega Grande.

Holotype: LIL-PB 936, as designated in the protologue by Herbst (1962a: pl. 3, figs. 14, 15), housed in the Fundación Miguel Lillo, Tucumán, Argentina.

Type locality and horizon: Ea. Vega Grande, Santa Cruz Province, Argentina; Baqueró Group (Aptian).

Remarks: Sterile and fertile fronds are known, the latter with pinnules bearing a single sorus, incorporating more than twenty sporangia.

3. Discussion

3.1. *Genera used for* Gleichenia*-like fronds*

Several morphogenera have been proposed to include fern pinnate fronds bearing small, pecopteroid pinnules, similar to that of the extant *Gleichenia microphylla*. Many of these proposed names are currently illegitimate, whereas others are still legitimate, but do not allow the inclusion of all known specimens of ferns with *Gleichenia*-like morphology. For clarity's sake, we provide hereafter a list of these genera, with comments about their nomenclatural status.

3.1.1. Gleichenites *Goeppert, 1836*

This morphogenus was proposed by Goeppert (1836) to encompass five fossil species of sterile fronds with dichotomous branching pattern (*Gleichenites linkii* Goeppert, *G. neesii* Goeppert, *G. artemisiaefolius* Goeppert, *G. crithmifolius* Goeppert, and *G. neuropteroides* Goeppert), similar to the extant *Gleichenia*. Goeppert's species were later recognized as pteridosperms, and transferred to other genera (*Sphenopteris*, *Neuropteris* and *Eremopteris*; Schimper, 1869). As a result, Goeppert's *Gleichenites* became a junior nomenclatural synonym.

3.1.2. Gleichenia *Smith, 1973*

Berry (1924) preferred to use the extant genus *Gleichenia* for several specimens he placed in *Gleichenia argentinica*. However, the referral of a fossil of unknown familial affinities (i.e., lack of diagnostic features of Gleicheniaceae) to an extant fern genus is questionable, and thus is not recommended.

3.1.3. "Gleichenites *Seward, 1927" (in Andrews, 1955)*

Seward (1927) criticized Berry's use of *Gleichenia*, arguing that *Gleichenites* Goeppert was still available for material related to the Gleicheniaceae, despite the assignment of Goeppert's species to the pteridosperms. In his Index of Generic Names of Fossil Plants, Andrews (1955, 1970) pointed out that Seward "described five species (of *Gleichenites*) which do not conform to modern usage" and suggested one of the taxa described by Seward (1927), *Gleichenites porsildii*, as the type species for *Gleichenites*. However, this procedure is not permitted by the International Code of Botanical Nomenclature (McNeill et al., 2006), since Andrews never did a formal proposal to conserve the name *Gleichenites*, with

an epitype, for specimens with no relationships to the pteridosperms. Unfortunately, Seward's position was repeatedly followed later in the literature (e.g., Van der Burgh and van Konijnenburg-van Cittert, 1984; Herbst, 1996; Herbst et al., 2005; Wang et al., 2009).

3.1.4. Gleichenites *Bolkhovitina, 1959 and* Gleichenites *Agranovskaya in Pokrovskaya and Stelmak, 1960*

Apart from fossil fronds, Bolkhovitina (1959) and Agranovskaya in Pokrovskaya and Stelmak (1960) independently proposed the generic name *Gleichenites* for disperse palynomorphs (Farr and Zijlstra, 2011). Under regulations of the ICBN, Article 53.1, these names are illegitimate, since they are later homonyms of *Gleichenites* Goeppert.

3.1.5. Microphyllopteris *Arber, 1917*

Arber (1917) also recognized the problems of using *Gleichenites* Goeppert for fern remains, and proposed *Microphyllopteris* as a replacement for pinnate, bipinnate or dichotomous fronds bearing small pinnules similar to the extant *Gleichenia*. However, in 1981, Retallack discussed several species of *Pachydermophyllum* Thomas and Bose, 1955, and proposed the new combination *Pachydermophyllum pinnatum* (Walkom) Retallack to include many specimens described as *Microphyllopteris pectinata* (Hector) Arber, 1917, the type species of *Microphyllopteris*. Although Arber (1917) did not explicitly defined a holotype for this species, he stated "Types: New Zealand Geological Survey Collection" (Arber, 1917: 41). A revision of the specimens reassigned by Retallack (1981) to *Pachydermophyllum*, reveals that those left in *Microphyllopteris* (Arber, 1917: pl. 7, figs. 5, 9) are housed in the British Museum of Natural History, which means that all the "types" proposed by Arber (i.e., the specimens housed in the New Zealand Geological Survey) of *Microphyllopteris pectinata* were transferred to *Pachydermophyllum pinnatum*, transforming *M. pectinata* into a junior synonym of *P. pinnatum*. Furthermore, since *Microphyllopteris pectinata* is the type species of *Microphyllopteris*, this genus name should be considered illegitimate. More recently, the specimens of *Microphyllopteris pectinata* referred by Retallack to *Pachydermophyllum pinnatum* were placed in *Rintoulia pectinata* (Hector) McLoughlin, Tosolini, Nagalingum and Drinnan, 2002, whereas the rest of Arber's specimens remain without a clear taxonomic placement, and a revision is pending.

3.1.6. Microphyllopteris *Arber emend. Miller and Hickey, 2008*

Recently, Miller and Hickey (2008) discussed the use of the morphogenera *Microphyllopteris* and *Gleichenites*, among others. They suggested that *Microphyllopteris* should be used for true gleicheniaceous fronds. Furthermore, they emended the diagnosis of this genus, to include fertile foliage with single (or rarely two) circular sori per pinnule (Miller and Hickey, 2008). Unfortunately, this proposal has some problems. Miller and Hickey (2008) relied on the identification of Gleicheniaceous affinities based on the presence of dichotomous or pseudodichotomous fronds, but in their emended generic diagnosis, they allowed inclusion of "pinnate, bipinnate or dichotomously branched" fronds (Miller and Hickey, 2008: 151). Thus, even if they claim that *Microphyllopteris* should be used for Gleicheniacean ferns, their diagnosis allows the inclusion of non-Gleicheniacean ferns (e.g., in absence of preserved spores, *Lophosoria cupulata* Cantrill, 1998). Although nomenclaturally this is not a problem, the type material of *Microphyllopteris* has been transferred to a gymnosperm taxon, and thus their use for Gleicheniacean or non-gleicheniacean ferns should be rejected.

3.1.7. Gleicheniaceaephyllum *Crabtree, 1988*

Crabtree (1988) did not agree with the use of *Gleichenites*, even with the proposal of a new type species made by Andrews (1955, 1970). He concluded that the best way for dealing with this nomenclatural problem was the establishment of new morphogenera, to encompass the previously published Mesozoic-Cenozoic "*Gleichenites*". Thus, he proposed *Gleicheniaceaephyllum*, a genus diagnosed by the presence of indeterminate, tripinnate or pseudodichotomous fronds, having an arrested laminar bud between the primary pinnae, and lacking fertile structures (Crabtree, 1988). It is important to note that the presence of a resting bud is a character shared by extant representatives of the fern family Gleicheniaceae. Crabtree's new genus did not allowed the inclusion of fertile, fragmentary (i.e., without preserved dichotomies), or dichotomously branched fronds without arrested laminar buds. Fertile fronds of this family would be referred to *Gleicheniopsis*, *Didymosorus* or *Gleichenioides* (Crabtree, 1988), whereas fragmentary remains, or fronds lacking laminar buds, still presented an undetermined generic placement.

3.1.8. Gleicheniaceaephyllum *Crabtree emend. Nagalingum and Cantrill, 2006*

In an attempt to clarify the systematics of these fossil plants, Cantrill and Nagalingum (2005) proposed the use of *Microphyllopteris* Arber as a morphogenus to include fronds similar to the extant *Gleichenia*, with unknown or absent resting buds, small pinnules and exindusiate sori, with complete transverse or obliquely transverse sporangia (although the original diagnosis of the genus provided by Arber (1917) did not include specifically characters of the fertile structures). The same authors (Nagalingum and Cantrill, 2006) summarized their proposal, extending it to true gleicheniaceous fossil fronds. They stated that *Microphyllopteris* should be used for *Gleichenia*-like fronds presenting an unknown branching pattern or a dichotomous branching without resting buds. Furthermore, they slightly emended the form-genus *Gleicheniaceaephyllum* Crabtree, narrowing it to gleicheniaceous fronds with a resting bud between a two-to-four branching dichotomy, both genera being able to include fertile or sterile remains (Nagalingum and Cantrill, 2006). Although this proposal is rather logical, and would clarify notably the systematics of this kind of ferns, it faces the problem that *Microphyllopteris* is an illegitimate name, the type species of the corresponding genus being a junior synonym of the gymnosperm *Rintoulia pectinata* (McLoughlin et al., 2002).

3.1.9. Korallipteris *nov. gen. Vera and Passalia*

We contend that the proposal of Nagalingum and Cantrill (2006) would lead to a more effective classification scheme for these fossil ferns, allowing their identification as gleicheniaceans (*Gleicheniaceaephyllum*) or ferns without known affinities ("*Microphyllopteris*"). However, since the latter genus cannot be used for fossil ferns, we propose *Korallipteris* nov. gen. as a "replacement", with *Korallipteris argentinica* nov. comb. (originally described as *Gleichenia argentinica* Berry, 1924) as its type species. The selection of this type, which has fertile fronds bearing sori on the abaxial surface of the pinnules, allows their placement in the Pteridophyta, and precludes their referral to other groups of plants.

3.2. Spatiotemporal distribution of "korallipteroid" ferns

In this work, we refer to the new genus *Korallipteris* nov. gen. several species recorded in Mesozoic strata from Argentina, Chile and Antarctica, formerly described as *Gleichenites* and *Microphyllopteris*. However, numerous taxa which also share a "korallipteroid" gross morphology (e.g., pinnate fronds with small pecopteroid pinnules) have been identified in localities placed both in the Northern and Southern Hemispheres, with ages ranging from the Triassic to the Cretaceous and probably extending into the Paleogene. In Table 1, a selection of fossil species with "kor-

Table 1
List of selected fossil species characterized by having a "korallipteroid" frond morphology.

Species	Age	Localization	References
Gleicheniaceaephyllum acutum Nagalingum and Cantrill	Lower Cretaceous	Antarctica	Nagalingum and Cantrill (2006)
G. falcatum Crabtree	Lower Cretaceous	USA	Crabtree (1988)
Gleicheniopsis erlansonii Miner	Upper Cretaceous	Greenland	Miner (1934)
Gleichenites gracilis (Heer) Tanai	Upper Cretaceous-Paleogene	China	Tanai (1979)
	Cretaceous	Greenland	From Tanai (1979)
G. porsildi Seward[a]	Cretaceous	Greenland	Seward (1927)
G. (?) waltoni Seward	Cretaceous	Greenland	Seward (1927)
G. coloradensis (Knowlton) Andrews	Cretaceous	USA	Andrews and Pearsall (1941)
G. medinensis Ruiz[b]	Cretaceous	Argentina	Ruiz (1984)
G. piatnitzkyi Berry[b]	Cretaceous	Argentina	Berry (1937)
G. gieseckiana (Heer) Seward[a,c]	Cretaceous	Greenland	Seward (1927)
	Lower Cretaceous	China	FromWang et al. (2009)
	Lower Cretaceous	Canada	Bell (1956)
	Lower Cretaceous	USA	Miller and Hickey (2008)
G. jixiensis Yang	Lower Cretaceous	China	Yang (2002)
G. monosoratus Zhang	Lower Cretaceous	China	Zhang et al. (1980)
G. nipponensis Oishi	Lower Cretaceous	Japan, China, Korea	From Cantrill (1998); Kimura (2000); Wang et al. (2009)
G. vegagrandis Herbst[b]	Lower Cretaceous	Argentina	Herbst (1962a)
G. argentinica (Berry) Herbst[b]	Lower Cretaceous	Argentina	Berry (1924); Feruglio (1951); Herbst (1962a)
G. sanmartinii Halle emend. Herbst[d]	Lower Cretaceous	Argentina	Halle (1913); Herbst (1962a)
G. feruglioi Herbst[b]	Lower Cretaceous	Argentina	Herbst (1966)
G. rewahensis Feistmantel	Lower Cretaceous	India	From Surange (1966)
G. cycadina (Schenk) Seward	Lower Cretaceous	Germany	From Cantrill (1998)
	Lower Cretaceous	China	Wang et al. (2009)
	Upper Jurassic	Scotland	Van der Burgh and van Konijnenburg-van Cittert (1984)
G. nordenskioldi (Heer) Seward[c]	Cretaceous	Greenland	Seward (1927)
	Lower Cretaceous	Canada	Bell (1956)
	Jurassic-Lower Cretaceous	China	From Wang et al. (2009)
	Middle-Upper Jurassic	Madagascar	Appert (1973)
G. boodlei (Schenk) Seward	Upper Jurassic	Scotland	van Konijnenburg-van Cittert, 2007
G. juliensis Herbst[b]	Middle Jurassic-Cretaceous	Argentina	Herbst (1962b); Passalia (2007)
G. nitida Harris	Lower Jurassic	Greenland	Harris (1931)
	Lower Jurassic	China	From Wang et al. (2009)
G. chaoyangensis Zhang and Zheng	Upper Triassic	China	From Wang et al. (2009)
G. cachivaritensis Herbst[b]	Upper Triassic	Chile	Herbst (1996); Herbst et al. (1998, 2005)
G. gallegoi Herbst[b]	Upper Triassic	Argentina	Herbst (1996); Herbst et al. (2005)
G. quilacoyensis Leppe and Moisan[b]	Upper Triassic	Chile	Leppe et al. (2006); Moisan et al. (2010)
G. yipinglangensis Li and Cao	Upper Triassic	China	From Wang et al. (2009)
G. potrerillensis Herbst[b]	Middle Triassic	Argentina	Herbst (1972)
Microphyllopteris unisora Cantrill and Nagalingum[b]	Cretaceous	Antarctica	Cantrill and Nagalingum (2005)
M. delicata Miller and Hickey	Lower Cretaceous	USA	Miller and Hickey (2008)
M. gleichenoides (Oldham and Morris) Walkom[e]	Lower Cretaceous	Australia	McLoughlin (1996)
	Upper Jurassic-Lower Cretaceous	India	Surange (1966)

[a] Seward (1927) mentioned the presence of a dichotomously branched rachis with a probable resting bud, allowing to place it in the genus *Gleicheniaceaephyllum*.
[b] Combined here to *Korallipteris* gen. nov.
[c] Combined in part to *Microphyllopteris gieseckiana* by Miller and Hickey (2008).
[d] Due to the presence of a dichotomously branched rachis with resting buds, this species should be placed in the genus *Gleicheniaceaephyllum*.
[e] Mentioned by Surange (1966) as *Gleichenites gleichenoides* (Oldham and Morris) Seward and Sahni.

allipteroid" morphology is provided. Most of these species were included in the genus *Gleichenites*, but other generic denominations have also been used (e.g., *Gleichenia*, *Gleicheniaceaephyllum*, *Gleicheniopsis*, *Microphyllopteris*). The oldest representative of this group is *Korallipteris potrerillensis* nov. comb. (*Gleichenites potrerillensis* sensu Herbst, 1972), from the Middle Triassic of Argentina. Upper Triassic species referred to *Gleichenites* have been also recognized in areas as far away as southern South America (Argentina, Chile) and Southeast Asia (China). Among the Jurassic *Gleichenites* species, stands *G. nordenskioldi* (Heer) Seward, which has been identified at several localities around the world. However, the greatest number of species referred to *Gleichenite*s has been described from Cretaceous (in particular Lower Cretaceous) deposits, possibly surpassing the total number of species of the two previous periods. Specimens referred to the genera *Gleicheniopsis*, *Gleicheniaceaephyllum* and *Microphyllopteris* also were mostly found in Cretaceous strata. With few exceptions (e.g., *Gleichenites gracilis* (Heer) Tanai), Cenozoic "korallipteroid" fern fronds have not been referred to any of these morphogenera (i.e., *Gleichenites*, *Microphyllopteris*, etc.).

Among the many species of *Gleichenites*, few were recognized as presenting dichotomies with a resting bud, a feature that allows their placement in the genus *Gleicheniaceaephyllum* (e.g., *Gleichenites gieseckiana* (Heer) Seward, *G. porsildi* Seward, *G. sanmartinii* Halle emend. Herbst). The remaining species of *Gleichenites*, as well as those species of *Microphyllopteris* (and maybe those mentioned as *Gleicheniopsis*), whose branching pattern is unknown, or which present dichotomies without an arrested laminar bud, may be possible associated to the new genus *Korallipteris* nov. gen., as was made here to those species recorded from Southwestern Gondwana strata. Regarding this topic, Kimura (1975) pointed out that more than 115 species consonant with *Gleichenites* had been

described in the literature, and since Kimura's work was published more than 35 years ago, the number of species is probably greater. To this respect, an extensive review of all published taxa falls outside the scope of this contribution, and future contributions will deal with the pertinent systematic treatment of these taxa.

4. Conclusions

The proposal of Nagalingum and Cantrill (2006) for classifying *Gleichenia*-like fern fronds in two genera, depending on whether they can be referred to the Gleicheniaceae or should be regarded as Pteridophyta incertae sedis owing to the lack of diagnostic features of this family is here accepted. The genus *Gleicheniaceaephyllum* Crabtree emend. Nagalingum and Cantrill should be used for true Gleicheniacean ferns, diagnosed by having an arrested laminar bud.

A new morphogenus, *Korallipteris* nov. gen., is proposed to include fertile or sterile fern fronds, possessing essentially *Gleichenia*-like morphology (e.g., pinnate fronds with small pinnules) and, if dichotomously branched, lacking arrested laminar buds. This proposal is intended to clarify the systematics of these problematic fern remains, which have been historically referred to several form-genera, such as *Gleichenites* Goeppert and *Microphyllopteris* Arber. Furthermore, the election of a type species where the type specimens possess filicalean affinities (e.g., fertile structures positioned on the pinnules) should guarantee that this genus will not be synonymized or referred to other group of plants (e.g., gymnosperms), as has previously occurred with *Gleichenites* and *Microphyllopteris*.

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