




Original Article

The classification of the fern family Gleicheniaceae, with the description of a new genus, segregated from *Sticherus*

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ABSTRACT

Gleicheniaceae is an early diverging lineage of leptosporangiate ferns. Although the family can be readily recognized by the pseudodichotomous branching pattern of its fronds, generic circumscription has long been debated. Phylogenetic analyses based on genomic data supported the monophyly of six genera (*Dicranopteris*, *Diplopteridium*, *Gleichenella*, *Gleichenia*, *Rouxopteris*, and *Stromatopteris*) but indicate the paraphyly of *Sticherus*. To accommodate this latter result, we describe a new genus, *Sticheropsis*, **gen. nov.**, segregated from *Sticherus*. We provide a new taxonomic treatment of Gleicheniaceae, including an identification key to all eight genera, descriptions of the genera with comments and notes concerning geographic distributions and phylogenetic affinities, as well as an overview of the morphology of the family with a revised and unified terminology for the fronds. We recognize 149 species plus two hybrids for the family, distributed into eight genera, and propose six new combinations.

Keywords: Gleicheniales; morphology; new combinations; synopsis; taxonomy

INTRODUCTION

Phylogenetic studies based on molecular data have significantly influenced and rearranged plant taxonomy (APG 1998, APG II 2003, APG III 2009, APG IV 2016, PPG I 2016). Until recently, plastid data has been the main source of molecular information for phylogenetic reconstructions and classifications, especially for ferns and lycophytes (e.g. Pryer *et al.* 2004, Schuettpelz and Pryer 2007, Testo and Sundue 2016). Several premises have supported the use of that data, including uniparental heritage, the assumed behaviour of a single gene copy, a general lack of recombination, and the accessibility of universal primers (Palmer *et al.* 1988, Clegg and Zurawski 1992). Evidence has shown, however, that structural and functional features of the plastome may not

behave as a single locus (Gonçalves *et al.* 2019, Wang *et al.* 2022). The use of nuclear information may be a powerful ally in reconstructing the evolutionary histories of plant groups by providing a large source of data helping to improve the resolution of recovered topologies (Zimmer and Wen 2013). With increasing access to high-throughput sequencing, and the relatively low cost per sample for obtaining genomic-scale data to infer phylogenetic relationships (Park and Kim 2016), it has been possible to use multiple genome sources to reconstruct the evolutionary relationships within a group of interest (Zimmer and Wen 2015, Park and Kim 2016, Bloesch *et al.* 2022, Lima *et al.* 2023).

Generic circumscription of Gleicheniaceae has been debated since the first description of the family, with the number of genera

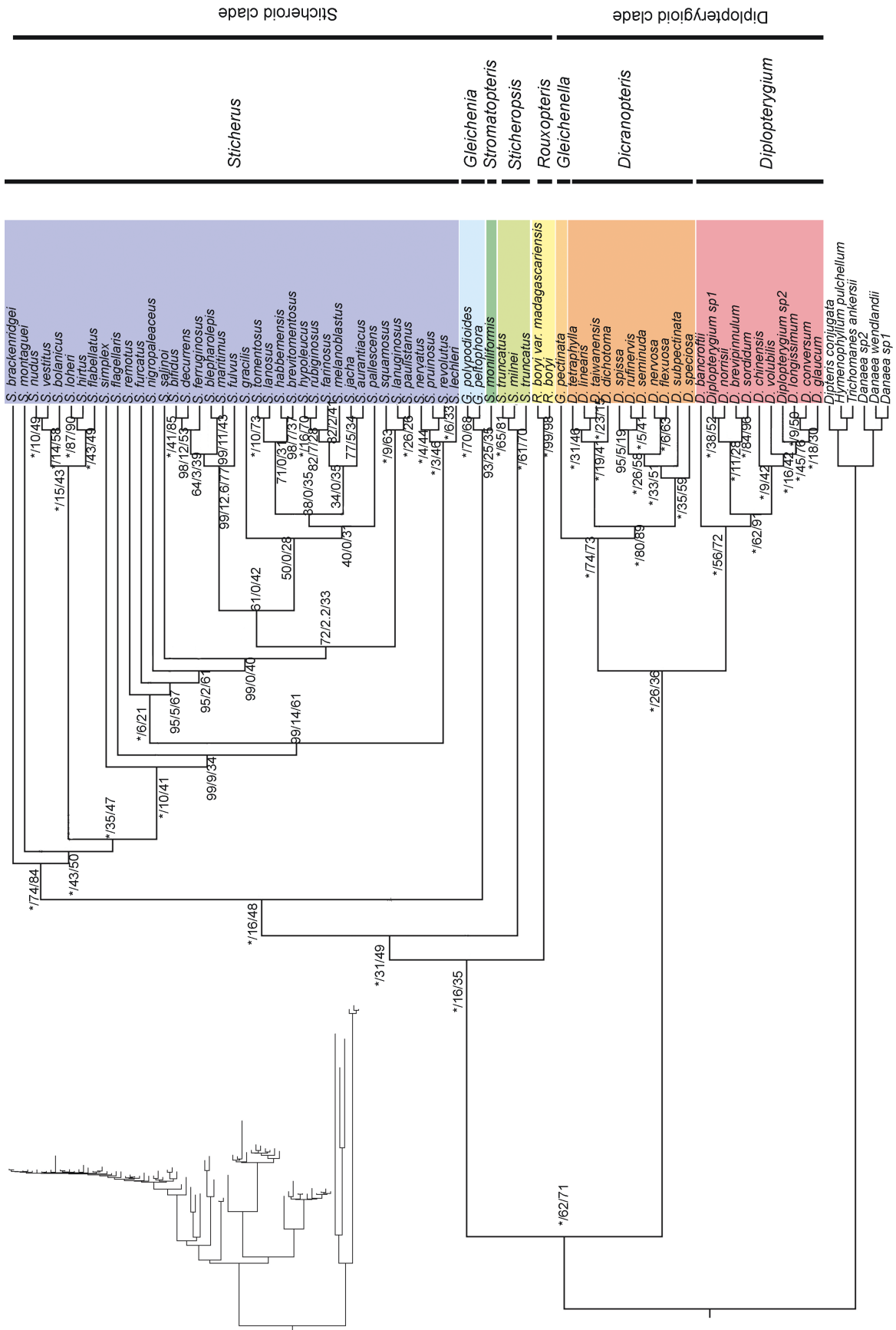


Figure 1. Phylogenetic hypothesis inferred from nuclear data (based on fig. 2 of Lima et al. 2023). Maximum likelihood phylogeny inferred from a partitioned nuclear matrix, with ultrafast bootstrap branch supports, gene concordance factor (gCF), and site concordance factor (sCF), respectively, listed at the nodes. * Indicates Ultrafast Bootstrap = 100.

recognized ranging from one to the currently accepted number of seven, i.e. *Dicranopteris* Bernh., *Diplopterygium* (Diels) Nakai, *Gleichenella* Ching, *Gleichenia* Sm., *Rouxopteris* Hong M.Liu, *Sticherus* C.Presl, and *Stromatopteris* Mett. (Christensen 1905, Ching 1940, Holttum 1947, 1957a, 1959, Nakai 1950, Smith *et al.* 2008, Li *et al.* 2010, PPG I 2016, Liu *et al.* 2020, Ohlsen *et al.* 2022). Even with many advances in DNA sequencing techniques, the monophyly of the genera is still questionable (Li *et al.* 2010, PPG I 2016, Liu *et al.* 2020, Ohlsen *et al.* 2022).

The first genomic-scale phylogenetic inference for Gleicheniaceae (Lima *et al.* 2023) recovered two main clades in the family: first, the diplopterygioid clade, formed by *Diplopterygium* sister to the clade formed by *Gleichenella* Ching plus *Dicranopteris* (Fig. 1); second, the sticheroid clade, formed by *Rouxopteris* as sister to a clade formed by *Sticherus truncatus* + *Sticherus milnei*, plus a clade formed by *Gleichenia* + *Stromatopteris* + the remaining species of *Sticherus* (Fig. 1). The monophyly of *Dicranopteris*, *Diplopterygium*, *Gleichenia*, *Gleichenella*, *Rouxopteris*, and *Stromatopteris* has therefore been supported, while *Sticherus* was found to be paraphyletic. The type assigned to *Sticherus* is *S. laevigatus* (= *S. truncatus*), requiring the establishment of a new genus to include the remaining species of *Sticherus*. However, to ensure nomenclatural stability within Gleicheniaceae and to avoid the need for 95 new combinations, a proposal has been made to conserve *Sticherus* with a different type (Lima *et al.*, 2024). Consequently, in light of these results, we propose a recircumscription of *Sticherus*.

In the present work, we revisit Gleicheniaceae taxonomy, describe a new genus, *Sticheropsis*, gen. nov. L.V.Lima, Salino & T.E.Almeida to accommodate *S. truncatus* and *S. milnei*, and provide the necessary new combinations, an identification key for the eight recognized genera, and notes concerning their distribution, ecology, and phylogenetic affinities, as well as a revision of frond morphology and terminology.

MATERIALS AND METHODS

More than 8200 specimens from 53 herbaria (ASE, ALCB, B, BHCB, BM, BR, CEN, CEPEC, CESJ, COL, E, EAC, ESA, FI, FLOR, FMB, FURB, HAL, HBRA, HUEFS, HSTM, INPA, JPB, K, LE, M, MBM, MG, MOSS, NX, NY, OUPR, P, PACA, PMA, PR, PRC, QCA, R, RB, RON, S, SP, SPF, UB, UEC, UFG, UFP, UFRPE, UPCB, US, VIC, and VIES; acronyms following Thiers 2022, continuously updated) were examined during visits (and/

or by loans) or evaluated as high-resolution images of type collections available in Jstor website (<https://plants.jstor.org/>).

Key morphological characters based on frond dissection were illustrated as silhouettes or line drawings for additional details. The terms used for the descriptions follow an extended literature review, with proposed updates to frond terminology as hereafter developed. The chromosome numbers referred to here were obtained from the Lima *et al.* (2021) compilation.

RESULTS

Taxonomic treatment

Gleicheniaceae C.Presl (as 'Gleicheniae') in Reliq. Haenk. 1: 70. 1825.

Gleichenae R.Br. in Prodr. Fl. Nov. Holl.: 160. 1810. Type: *Gleichenia* Sm. in Mém. Acad. Roy. Sci. 5: 419. 1793, **nom. cons.**

Dicranopteridaceae Ching in Acta Phytotax. Sinica 3: 94. 1954. Type: *Dicranopteris* Bernh. in Neues J. Bot. 1(2): 38. 1805.

Stromatopteridaceae Bierh. in Phytomorphology 18: 263. Type: *Stromatopteris* Mett. in Ann. Sci. Nat., Bot. 15: 84. 1861.

Plants terrestrial or epipetric, pendent or erect, perennials. **Rhizomes** slender, long-creeping, branched, rarely erect, protostelic, or solenostelic, with scales or hairs. **FronDs** monomorphic, c. 20 to 500 cm long, petiole long, rigid, not articulated with the rhizome, with a 'C' shaped transversal section of solid xylem or vascular bundle, indeterminate lamina growth, rarely determinate, one to several times pseudodichotomously forked, rarely simple, ultimate branches pinnate, pinnatisect, or bipinnate, ultimate segments linear, deltoid, or rounded. **Buds** absent or present, dormant, or latent in the branch axils, with or without pseudostipules, covered by scales or hairs, rarely glabrous, sometimes with opposite branches. **Veins** free, 1–4 times forked, prominent, or immersed. **Sori** round, abaxial, indusium absent, sporangia globose or piriform, with a transversal annulus not interrupted by a pedicel, simultaneously maturing, with or without multicellular hyaline paraphyses. **Spores** > 100 (–800) per sporangium, monolete or trilete, achlorophyllous, surface smooth, or granular. **Gametophytes** chlorophyllous, epigeal, obcordate to elongated, thickened at the centre, margins thin, with small hairs, archegonia on the ventral surface of the thick portion, antheridia with ~6–12 cells on the ventral surface.

Pantropical with eight genera and an estimated 149 species and two hybrids.

Key to the genera of Gleicheniaceae

- | | |
|---|--------------------------|
| 1. Fronds pinnatifid to pinnatisect | 2. |
| 2. Fronds pseudodichotomously branched | 3. |
| 3. Rhizomes erect; ultimate segments rounded | <i>Stromatopteris</i> |
| 4. Rhizomes long-creeping; ultimate segments rounded to linear | <i>Sticherus simplex</i> |
| 5. Ultimate branches bipinnate | 4. |
| 6. Ultimate branches pinnatisect | 6. |
| 7. Ultimate segments linear | <i>Diplopterygium</i> |
| 8. Ultimate segments rounded | 5. |
| 9. Laminae always with a resting bud at the main bifurcation; lateral branches opposite; fronds clearly pseudodichotomous | <i>Gleichenia</i> |
| 10. Laminae usually without a resting bud at the apex of the main axis; lateral branches alternate; fronds almost sympodial | <i>Rouxopteris</i> |

- | | |
|--|----------------------|
| 11. Rhizomes and buds covered with scales; veins 1-forked..... | 7. |
| 12. Rhizomes and buds covered with hairs; veins 2–4-forked..... | 8. |
| 13. Fronds isotomically branched, without a branching main axis..... | <i>Sticherus</i> |
| 14. Fronds anisotomically branched, each branch with a sympodial ramification, with a clear main axis..... | <i>Sticheropsis</i> |
| 15. Fronds anisotomically branched; accessory branches absent; spores monolete; rhizomes solenostelic..... | <i>Gleichenella</i> |
| 16. Fronds isotomically branched, occasionally anisotomically branched; accessory branches present; spores trilete, rarely monolete; rhizomes protostelic..... | <i>Dicranopteris</i> |

1. *Dicranopteris* Bernh. in Neues J. Bot. 1(2): 38. 1806. nom. nov. for *Mertensia* Willd. in Kongl. Vetensk. Acad. Nya Handl. 25(3): 165. 1804. nom. illeg. non Roth. \equiv *Mertensia* Willd. in Kongl. Vetensk. Acad. Nya Handl. 25(3): 165. 1804. nom. illeg. non *Mertensia* Roth in Catal. Bot. 1: 34. 1797. nom. cons. (Boraginaceae), nec *Gleichenia* subgen. *Mertensia* (Willd.) Hook. in Sp. Fil. 1. 1844. *Mesosorus* Hassk. In Fil. Jav. 1: 2. 1856. nom. nov. for *Mertensia* Willd. Type: *Polypodium dichotomum* Thunb. in Murray in Syst. Veg. 14: 938. 1784. \equiv *Mertensia dichotoma* (Thunb.) Willd. in Kongl. Vetensk. Acad. Nya Handl. 25: 167. 1804. \equiv *Dicranopteris dichotoma* (Thunb.) Bernh. in Neues J. Bot. 1(2): 38. 1806. \equiv *Dicranopteris linearis* (Burm.f.) Underw. in Bull. Torrey Bot. Club 34: 250. 1907.

\equiv *Hicriopteris* C. Presl in Epimel. Bot. 26. 1851: Type: *Hicriopteris speciosa* C.Presl in Epimel. Bot. 27. 1851. \equiv *Dicranopteris speciosa* (C.Presl) Holttum in Reinwardtia 4: 273. 1957.

\equiv *Gleichenia* sect. *Heteropterygium* Diels in Nat. Pflanzenfam. [Engler & Prantl] I(4): 355. 1900: Type: *Gleichenia linearis* (Burm.f.) Clarke in Trans. Linn. Soc. London, Bot. 1(7): 428. 1880. \equiv *Dicranopteris linearis* (Burm.f.) Underw. in Bull. Torrey Bot. Club 34: 250. 1907.

Plants terrestrial or epipetric. **Rhizomes** long-creeping, branched, protostelic, hairs rigid, multicellular, brown to red-brown; squamophores absent. **Fronds** erect or pendent, pseudodichotomously branched, branches frequently isotomic, occasionally anisotomic. **Laminae** abaxially glabrous or pubescent, with hairs multicellular, white, or reddish on rachises and midrib segments; secondary veins with or without hairs unicellular, globose, or bacilliform, or simple or stellate; adaxial surface glabrous or with hairs sparse, multicellular, white or reddish, restricted to the rachises; ultimate branches pectinate, segments linear. **Buds** with pseudostipule, usually entire or trifid, or rarely more divided, covered by hairs, rigid, reddish-brown, and multicellular. **Accessory branches** absent or present, entire to pinnatisect. **Veins** free, 2–3(–4)-forked. **Sori** round, with 6–15 sporangia per sorus, paraphyses present or absent. **Spores** usually trilete and tetrahedral globose, or rarely monolete and kidney-shaped, whitish, scabrous, rugulose, or perforate; $x = 39$.

Etymology: The name is a reference to the repeatedly forked fronds of the genus (from Greek, *dikranos* = two-headed; *pteris* = fern).

Diagnosis: *Dicranopteris* can be readily recognized by having a pair of branches opposite from the main bifurcations. *Dicranopteris* species usually have trilete spores, with the exception of *D. curranii*, which has monolete spores. The rhizomes are protostelic and covered by hairs.

Distribution and ecology: *Dicranopteris* is a pantropical genus comprising ~23 species. Its centres of diversity are in southern and south-eastern Asia, and Oceania, while the five neotropical endemic species comprise a clade. Occupies open sunny locations, with some species also occupying disturbed habitats, from sea level up to 2300 m.

Taxonomic and phylogenetic studies: Phylogenetic studies (Li et al. 2010, Liu et al. 2020, Lima et al. 2023) pointed to the monophyly of the genus. *Dicranopteris* is sister to *Gleichenella*, which was segregated by Ching (1940). The main difference between the two is the solenostelic rhizome in *Gleichenella*, whereas *Dicranopteris* has a protostelic rhizome (Ogura 1972).

Notes: *D. linearis* is an unresolved species complex, with many described varieties (Holttum 1959). Recently, Wei et al. (2022) demonstrated that *D. linearis* is polyphyletic, and seven species were separated from this complex based on phylogenetic inferences recovered from a few plastid loci. Worldwide sampling and the use of other sources of evidence, such as genomic, genetic populational structure, anatomical, and ontogenetic, in integrative approaches, will be needed before a comprehensive revision of the complex is possible.

Accepted species

1. *Dicranopteris alternans* (Mett.) Y.H.Yan & Z.Y.Wei in Front. Plant Sci. 12: 748562. 2021.
2. *Dicranopteris baliensis* Y.H.Yan & Z.Y.Wei in Front. Plant Sci. 12: 748562. 2021.
3. *Dicranopteris ampla* Ching & P.S.Chiu in Acta Phytotax. Sin. 8(2): 161. 1959.
4. *Dicranopteris austrosinensis* Y.H.Yan & Z.Y.Wei in Front. Plant Sci. 12: 748562. 2021.
5. *Dicranopteris cadetii* Tardieu in Bull. Mus. Natl. Hist. Nat., B, Adansonia, sér. 4, 4(1–2): 103. 1982
6. *Dicranopteris curranii* Copel. In Philipp. J. Sci. 81: 4. 1952.
7. *Dicranopteris emarginata* W.J.Rob. in Bull. Torrey Bot. Club 39: 240. 1912.
8. *Dicranopteris flexuosa* (Schrad.) Underw. In Bull. Torrey Bot. Club 34: 254. 1907.
9. *Dicranopteris gigantea* Ching in Chien & Chun in Fl. Reipubl. Popularis Sin. 2: 346. 1959.
10. *Dicranopteris inaequalis* (Rosenst.) Y.H.Yan & Z.Y.Wei in Front. Plant Sci. 12: 748562. 2021.
11. *Dicranopteris latiloba* (Holttum) Y.H.Yan & Z.Y.Wei in Front. Plant Sci. 12: 748562. 2021.
12. *Dicranopteris linearis* (Burm.f.) Underw. In Bull. Torrey Bot. Club 34: 250. 1907.

13. *Dicranopteris nervosa* (Kaulf.) Maxon in Contr. U.S. Natl. Herb. 24: 49. 1922.
14. *Dicranopteris pedata* (Houtt.) Nakaike in Enum. Pterid. Jap.: Filic. 114. 1975.
15. *Dicranopteris rufinervis* (Mart.) Ching in Sunyatsenia 5: 275. 1940.
16. *Dicranopteris seminuda* (Klotzsch) Maxon in Proc. Biol. Soc. Washington 46: 140. 1933.
17. *Dicranopteris speciosa* (C.Presl) Holttum in Reinwardtia 4: 273. 1957.
18. *Dicranopteris spissa* (Fée) L.V.Lima & Salino in Phytotaxa 533(1): 99. 2022.
19. *Dicranopteris splendida* (Handel-Mazzetti) Tagawa in Acta Phytotax. Geobot. 8(3): 164. 1939.
20. *Dicranopteris subpectinata* (Christ) C.M.Kuo in Taiwania 30: 54. 1985.
21. *Dicranopteris subspeciosa* (Holttum) Y.H.Yan & Z.Y.Wei in Front. Plant Sci. 12: 748562. 2021.
22. *Dicranopteris taiwanensis* Ching & P.S.Chiu in Fl. Reipubl. Popularis Sin. 2: 346. 1959.
23. *Dicranopteris tetraphylla* (Rosenst.) C.M.Kuo in Taiwania 30: 54. 1985.

2. *Diplopterygium* (Diels) Nakai in Bull. Natl. Sci. Mus. Tokyo 29: 47. 1950 ≡ *Gleichenia* sect. *Diplopterygium* Diels in Nat. Pflanzenfam. 1(4): 353. 1900 ≡ *Gleichenia* subg. *Diplopterygium* (Diels) Holttum in Reinwardtia 4: 261. 1957—Type: Lectotype (designated by [Christensen 1906](#)): *Polypodium glaucum* Thunb. Ex Houtt. In Nat. Hist. 2(14): 177. 1783. ≡ *Diplopterygium glaucum* (Thunb. ex Houtt.) Nakai in Bull. Natl. Sci. Mus. Tokyo 29: 51. 1950.

Plants terrestrial or epipetric. **Rhizomes** long-creeping, branched, protostelic, with scales rigid, brown, reddish-brown, basifixed; squamophores absent. **Fronds** scrambling, pseudodichotomously branched, with branches isotomic, rachises with lanceolate scales, and stellate hairs when young, being glabrescent or persistent. **Laminae** abaxially glabrescent, with scales red, brown, or whitish on rachises, midrib segments, secondary veins, and laminar tissue; adaxial surface glabrous, or with scales restricted to the rachises or midrib segments; ultimate branches bipinnate, pectinate, with linear segments. **Buds** covered with scales whitish or reddish, usually concolorous, occasionally with whitish margins, pseudostipules present. **Accessory branches** absent. **Veins** free, 1-forked. **Sori** round, 3–6 sporangia per sori, without paraphyses. **Spores** ellipsoidal, trilete, slightly rugose, and minimally perforated; $x = 56$.

Etymology: The genus's name is a reference to the appearance of their fronds as two wing-like pinnae (from the Greek *diploos* = double, *pterygium* = little wing).

Diagnosis: *Diplopterygium* differs from the other Gleicheniaceae genera by having ultimate branches bipinnate, with linear segments with midribs.

Distribution and ecology: *Diplopterygium* comprises ~21 species with amphi-Pacific distribution, with only a single species (*D. bancroftii*) occurring in the Neotropics. It occurs in tropical and subtropical areas along sunny forest edges or the forest

understory, at 500–2600 m a.s.l. The centre of diversity is in tropical Asia, especially the Malay Peninsula and China ([Holttum 1959](#), [Mickel and Smith 2004](#), [Jin et al. 2013](#)).

Taxonomic and phylogenetic studies: All *Diplopterygium* species were initially treated as members of the genus *Hicriopteris* C.Presl. However, [Holttum \(1957a\)](#) pointed out that the type of *Hicriopteris* (*Hicriopteris speciosa* C.Presl) belonged to *Dicranopteris*. Phylogenetic studies suggest the monophyly of the genus, with the neotropical *Diplopterygium bancroftii* as sister to a clade formed by all the other species, with an early divergence from the Asian species at 47–68 Mya ([Lima et al. 2023](#), [Fig. 1](#)). The genus is placed in the diplopterygioid clade alongside *Dicranopteris* and *Gleichenella* ([Lima et al., 2023](#)). [Shu et al. \(2017\)](#) demonstrated the existence of cryptic species in the genus using a DNA barcode technique, reestablishing *D. simulans* from synonymy. A comprehensive taxonomic revision of the genus is needed to clarify species boundaries and their morphological affinities, as well as phylogenetic inferences with expanded sampling.

Notes: *Diplopterygium* has its buds and rhizomes covered with scales and is placed in a clade with *Dicranopteris* and *Gleichenella*, whose rhizomes and buds are covered with hairs. Some species of *Diplopterygium*, however, have stellate hairs on their petioles and rachises, while some species of *Gleichenella* have stellate hairs abaxially on their rachises and segments. These stellate hairs may represent a shared morphological character in the diplopterygioid clade that was lost in some species or arose independently several times. Trilete spores are present in *Diplopterygium* and most of the *Dicranopteris* species of the diplopterygioid clade, whereas monolete spores are present in *Gleichenella* and *D. curranii*. *Diplopterygium* is the only genus in the clade with all its species having isotomic branching, whereas *Gleichenella* and several Asian species of *Dicranopteris* have anisotomic branching.

Accepted species and a new combination

1. *Diplopterygium angustilobum* (Holttum) Parris in Bull. Natl. Mus. Nat. Sci., Tokyo, B. 38(3): 119. 2012.
2. *Diplopterygium bancroftii* (Hook.) A.R.Sm. in Amer. Fern J. 70: 26. 1980.
3. *Diplopterygium blotianum* (C.Chr.) Nakai in Bull. Natl. Sci. Mus. Tokyo 29: 49. 1950.
4. *Diplopterygium brevipinnulum* (Holttum) Parris in Pl. Mt. Kinabalu: 59. 1992.
5. *Diplopterygium cantonense* (Ching) Nakai in Bull. Natl. Sci. Mus. Tokyo 29: 49. 1950.
6. *Diplopterygium chinense* (Rosenst.) De Vol in H.L.Li, Liu, T.C.Huang T.Koyama & De Vol in Fl. Taiwan 1: 92. 1975.
7. *Diplopterygium clemensiae* (Copel.) Parris in Bull. Natl. Mus. Nat. Sci., Tokyo, B. 38(3): 119. 2012.
8. *Diplopterygium deflexum* (Holttum) Parris in Bull. Natl. Mus. Nat. Sci., Tokyo, B. 38(3): 119. 2012.
9. *Diplopterygium elmeri* (Copel.) Nakai in Bull. Natl. Sci. Mus. Tokyo 29: 49. 1950.
10. *Diplopterygium giganteum* (Wall. ex Hook.) Nakai in Bull. Natl. Sci. Mus. Tokyo 29: 50. 1950.

11. *Diplopterygium glaucum* (Thunb. ex Houtt.) Nakai in Bull. Natl. Sci. Mus. Tokyo 29: 51. 1950.
12. *Diplopterygium irregulare* W.M.Chu & Z.R.He in Acta Bot. Yunnan. 22(3): 255. 2000.
13. *Diplopterygium laevisimum* (Christ) Nakai in Bull. Natl. Sci. Mus. Tokyo 29: 52. 1950.
14. *Diplopterygium longissimum* (Blume) Nakai in Bull. Natl. Sci. Mus. Tokyo 29: 53. 1950.
15. *Diplopterygium matthewii* (Holtum) L.V.Lima, Salino & T.E.Almeida, **comb. nov.** \equiv *Gleichenia matthewii* Holtum in Reinwardtia 4: 265. 1957.
16. *Diplopterygium maximum* (Ching) Ching & H.S.Kung in Fl. Sichuan. 6: 134. 1988.
17. *Diplopterygium norrisii* (Mett. ex Kuhn) Nakai in Bull. Natl. Sci. Mus. Tokyo 29: 54. 1950.
18. *Diplopterygium rufum* (Ching) Ching ex X.C.Zhang in Novon 14(1): 150. 2004.
19. *Diplopterygium simulans* Ching ex X.C.Zhang in Novon 14(1): 150. 2004.
20. *Diplopterygium sordidum* (Copel.) Parris in Malayan Nat. J. 50(4): 252. 1997.
21. *Diplopterygium volubile* (Jungh.) Nakai in Bull. Natl. Sci. Mus. Tokyo 29: 55. 1950.

3. *Gleichenia* Sm. In Mém. Acad. Roy. Sci. (Turin) 5: 419. 1793. Nom. Cons. \equiv *Gleichenia* subg. *Gleichenia* Sm., in Sp. Fil. 1. 1844: Type: *Onoclea polypodioides* L. in Mant. Pl. Altera 306. 1771 \equiv *Gleichenia polypodioides* (L.) Sm. in Mém. Acad. Roy. Sci. (Turin) 5: 419. 1793.

= *Calymella* C.Presl in Tent. Pterid. 48. 1836 \equiv *Gleichenia* sect. *Calymella* (C.Presl.) T.Moore in Index Fil. 108. 1857 \equiv *Gleichenia* subg. *Calymella* (C.Presl) Hook. In Gen. Fil. T. 41B. 1840: Type: *Calymella alpina* (R.Br.) C.Presl in Tent. Pterid. 49. 1836.

= *Gleicheniastrum* C.Presl. Gefässbündel Farn 30: 338. 1847: Type: *Gleichenia microphylla* R.Br. in Prodr. Fl. Nov. Holland. 161. 1810. Lectotype designated by Christensen (1906) \equiv *Gleicheniastrum microphyllum* (R.Br.) C.Presl in Abh. Königl. Böhm. Ges. Wiss. 5(2): 338. 1848.

Plants terrestrial or epipetric. **Rhizomes** long-creeping, branched, protostelic, sparsely to densely covered with scales entire to ciliate, occasionally with stellate hairs; squamophores absent. **FronDs** scrambling or erect, usually pseudodichotomously branched, with a resting bud at the bifurcation, rarely bifurcate without a resting bud (*G. abscida*), rachises glabrous or bearing hairs red-brown to dark blackish brown, stellate, and/or ciliate scales. **Laminae** abaxially glabrous, or sparsely to densely covered with ciliate scales round, orange-brown, whitish, or ferruginous, with or without an excrescence yellowish to white farinaceous; adaxial surface glabrous or sparsely to densely covered with whitish hairs; ultimate branches bipinnate, segments rounded, midrib absent. **Buds** present or absent, if present covered with scales pale to dark brown, lanceolate to ovate, with margins ciliate to erose, apex setose to acuminate, pseudostipule present or absent. **Accessory branches** absent. **Veins** free, 1-forked. **Sori** immersed, or not, in a soral chamber, rounded, 3–5 sporangia per sorus, without paraphyses. **Spores** trilete, tetrahedral globose, smooth, or rugose; $x = 20$ or 22 .

Etymology: The genus was named after Baron W.F. von Gleichen-Ruswurm (1717–1783), an amateur German naturalist (Pichi Sermolli 1972).

Diagnosis: *Gleichenia* is characterized by having ultimate branches bipinnate with rounded segments without a midrib. It differs from *Rouxopteris* by having a pseudodichotomous branching pattern.

Distribution and ecology: *Gleichenia* has a paleotropical distribution, with ~10 species in Africa, the western and southern Indian Ocean, Southeast Asia, and Oceania. It occurs in open sunny places, along roadsides, in open, wet habitats, near swamps, and colonizes rocky and poor substrates ranging from 0 to 1400 m a.s.l. (Perrie and Brownsey 2015).

Taxonomic and phylogenetic studies: *Gleichenia* was formerly more broadly circumscribed and comprised all Gleicheniaceae species in some circumscriptions (Holtum 1957a). Subsequent morphological and phylogenetic studies using molecular data supported the segregation of the other Gleicheniaceae genera, including the recent recognition of *Rouxopteris* (Liu et al., 2020). *Gleichenia* is monophyletic, and placed in the sticheroid clade, sister to *Stromatopteris* (Lima et al., 2023).

Notes: There is evidence for cryptic species and hybridization in *Gleichenia*. Ohlsen et al. (2022) demonstrated the polyphyly of *Gleichenia dicarpa* in a phylogenetic reconstruction using plastid regions. *Gleichenia abscida* shows a different frond branching, with fronds consisting of two undivided branches (single branch pair) and lacking a dormant vegetative bud at the bifurcation (Chinnock and Bell 1998). The remaining species of *Gleichenia* have fronds consisting of one or more bifurcations, with dormant vegetative buds (Chinnock and Bell 1998). However, the phylogenetic placement of *G. abscida* in *Gleichenia* was confirmed (Ohlsen et al. 2022).

Gleichenia has distinct chromosome numbers when compared to other Gleicheniaceae. The genus has the lowest basic count ($x = 22$) and shows aneuploidy series with different chromosome counts for the same species [e.g. *G. microphylla* (R.Br.) C.Chr with $n = 20$ and $n = 22$; Brownlie in Fabbri (1963), Brownlie (1961)] (Lima et al. 2021). To *G. elongata* see comments under *Rouxopteris*.

Accepted species

1. *Gleichenia abscida* Rodway in Tasman. Fl.: 289. 1903.
2. *Gleichenia alpina* R.Br. in Prodr. Fl. Nov. Holland.: 161. 1810.
3. *Gleichenia dicarpa* R.Br. in Prodr. Fl. Nov. Holland.: 161. 1810.
4. *Gleichenia inclusisora* Perrie, L.D.Sheph. & Brownsey in New Zealand J. Bot. 50(4): 406. 2012.
5. *Gleichenia mendellii* S.B.Andrews in Ferns of Queensland: 142. 1990.
6. *Gleichenia microphylla* R.Br. in Prodr. Fl. Nov. Holland.: 161. 1810.
7. *Gleichenia peltophora* Copel. in Philipp. J. Sci. 40: 291. 1929.
8. *Gleichenia polypodioides* (L.) Sm. in Mém. Acad. Roy. Sci. (Turin) 5: 419. 1793.

9. *Gleichenia rupestris* R.Br. in Prodr. Fl. Nov. Holland.: 161. 1810.
 10. *Gleichenia vulcanica* Blume in Enum. Pl. Javæ.: 251. 1828.

4. *Gleichenella* Ching in Sunyatsenia 5: 276. 1940 ≡ *Gleichenia* sect. *Acropterygium* Diels in Nat. Pflanzenfam. 1(4): 353. 1900 ≡ *Dicranopteris* sect. *Acropterygium* (Diels) Underw. In Bull. Torrey Bot. Club 34: 251. 1907 ≡ *Dicranopteris* subg. *Acropterygium* (Diels) Holttum in Reinwardtia 4: 261. 1957: Type: *Gleichenella pectinata* (Willd.) Ching in Sunyatsenia 5(4): 276. 1940. ≡ *Mertensia pectinata* Willd. in Kongl. Vetensk. Acad. Nya Handl. 25: 168. 1804.

Plants terrestrial. **Rhizomes** long-creeping, branched, solenostelic, pubescent with hairs brown, multicellular; squamophores absent. **Fronds** erect or scrambling, pseudodichotomously branched, with anisotomic branches. **Laminae** with hairs reddish, branched, usually stellate abaxially, rachis glabrous, secondary veins without glandular hairs; adaxial surface glabrous; ultimate segments linear. **Buds** covered with reddish hairs, pseudostipules present. **Accessory branches** absent. **Veins** free, 2–3(–4)-forked. **Sori** round, c. (6–)8–15(–25) sporangia per sorus, without paraphyses. **Spores** monolete, ellipsoidal, with rugose surfaces; $x = 43$.

Etymology: Ching (1940) did not provide an etymology for the genus name, but it is presumably derived from *Gleichenia* plus the Latin suffix -ellus (in its feminine allomorph form -ella), which indicates the diminutive form when added to a noun.

Diagnosis: *Gleichenella* is similar to *Dicranopteris*; it differs in having solenostelic rhizomes, whereas *Dicranopteris* has protostelic rhizomes, and without branches opposite to the main ramifications.

Distribution and ecology: *Gleichenella* is a monotypic genus endemic to the Neotropical region, where it is widely distributed. It occurs along roads, trails, and forest edges in all phytogeographic domains at 100–2300 m a.s.l.

Taxonomic and phylogenetic studies: Ching (1940) segregated *Gleichenella* from *Dicranopteris* based on the rhizome stele type (solenostelic in *Gleichenella* vs. protostelic in *Dicranopteris*), monolete spores, and anisotomic branching. Except for the stele type and the absence of a pair of branches opposite to the main bifurcation, the other characters are only useful for differentiating *Gleichenella* from neotropical *Dicranopteris*, as Asian *Dicranopteris* may have anisotomic branching (*D. speciosa*, *D. subpectinata*) and monolete spores (*D. curranii*). *Gleichenella* has a phylogenetic placement as sister to *Dicranopteris* in the diplopterygioid clade (Lima et al. 2023).

Accepted species

1. *Gleichenella pectinata* (Willd.) Ching in Sunyatsenia 5(4): 276. 1940.

5. *Rouxopteris* H.M.Liu in Pl. Syst. Evol. 306(2, 30): 9. 2020: Type: *Gleichenia boryi* Kunze in Farnkräuter 1: 162. 1844. ≡ *Rouxopteris boryi* (Kunze) H.M.Liu in Pl. Syst. Evol. 306(2, 30): 9. 2020.

Plants terrestrial. **Rhizomes** long-creeping, branched, protostelic, with hairs long, deciduous, brown, uniseriate, simple, or branched; squamophores absent. **Fronds** erect, lamina 1-pinnate-pinnatisect to 2-pinnate, with or without dormant apical buds, lateral branches alternate. **Laminae** abaxially glabrous or with hairs reddish, simple, or branched; adaxial surface glabrous or with hairs simple, whitish to reddish; ultimate branches bipinnate, with rounded segments, without a midrib. **Veins** free, 2–3-forked. Sori rounded, with 4–9 sporangia per sori, paraphyses absent. **Spores** trilete, globose.

Etymology: The genus is named after Jacobus Petrus Roux (1954–2013) (Liu et al. 2020).

Diagnosis: *Rouxopteris* morphologically resembles *Gleichenia* by having a rounded ultimate segment without a midrib, and bipinnate ultimate branches. It differs from *Gleichenia*, however, by always having superficial sori (vs. sori immersed in a soral chamber as in *G. inclusisora* and *G. polypodioides*), rachis with determinate growth, and a main axis from which the lateral branch emerges (vs. rachis with indeterminate growth, usually with a resting bud at the apex, pseudodichotomous branch fronds without the main axis in *Gleichenia*), and the lateral branches almost alternate (lateral branches of *Gleichenia* emerging at the same point from the main axis).

Distribution and ecology: *Rouxopteris* comprises three species endemic to continental Africa (Tanzania, Kenya, Uganda, Ruanda, Congo), Madagascar, and the Mascarene Islands (La Réunion). It occurs in open sunny locations at 0–1300 m a.s.l.

Taxonomy and phylogenetic relationships: The segregation of *Gleichenia boryi* from the other species of *Gleichenia*, and its phylogenetic placement in the diplopterygioid clade, was initially based on *rbcL* sequences (Liu et al. 2020). Phylogenomic data later supported the segregation of *G. boryi*; however, its placement is strongly supported in the sticheroid clade based on nuclear and plastid data (Lima et al. 2023).

Notes: We recognized three species in the genus. We elevate *Gleichenia boryi* var. *madagascariensis* to species level, based mainly on the indument of the segments in the abaxial surface. The type of *Rouxopteris madagascariensis* has a glabrescent abaxial surface, with no, or scarce, red hairs; the type of *R. boryi* has an abaxial surface pubescent to hirsute, with hairs long, catenate, and red.

Gleichenia elongata does not fit within the circumscription of *Gleichenia*. It has a blade branch pattern diagnostic of *Rouxopteris* with the frond apex usually without a bud (the only *Gleichenia* species without buds is *G. abscida*), and an almost sympodial architecture, with lateral branches slightly alternate. Although it has not yet been included in any phylogenetic study, we recognize this taxon in *Rouxopteris* based on its morphological characteristics.

Accepted species and new combinations

1. *Rouxopteris boryi* (Kunze) H.M.Liu in Pl. Syst. Evol. 306(2, 30): 9. 2020.
 2. *Rouxopteris elongatum* (Baker) L.V.Lima, Salino & T.E. Almeida, **comb. nov.** ≡ *Gleichenia elongata* Baker in Bull. Misc. Inform. Kew 1901(175–177): 137. 1901.

3. *Rouxopteris madagascariensis* (C.Chr.) L.V.Lima, Salino, T.E.Almeida, **comb. nov.** \equiv *Gleichenia madagascariensis* C.Chr. in Cat. Pl. Mad. Pter.: 64. 1932 (nom. nud.). \equiv *Gleichenia madagascariensis* C.Chr. in Dansk Bot. Ark. 7: 173, t. 69. 1932. \equiv *Gleichenia boryi* var. *madagascariensis* (C.Chr.) Tardieu in Bull. Mus. Natl. Adansonia sér. 4(1–2): 105. 1982. \equiv *Rouxopteris boryi* var. *madagascariensis* (C.Chr.) H.M.Liu in Pl. Syst. Evol. 306(2, 30): 9. 2020.

6. *Sticheropsis* L.V.Lima, Salino & T.E.Almeida, **gen. nov.**

Diagnosis: *Sticheropsis* is characterized by having rhizomes long-creeping, covered with scales, fronds with anisotomic branching, accessory branches absent, buds covered with scales, ultimate branches pinnatisect, segments with a midrib, and spores monolete. It is morphologically similar to *Sticherus*, from which it is distinguished by having anisotomic branching (vs. isotomic branching in *Sticherus*).

Type: *Sticheropsis milnei* (Baker) L.V.Lima, Salino & T.E.Almeida \equiv *Gleichenia milnei* Baker in Syn. Fil. 449. 1874 \equiv *Sticherus milnei* (Baker) Ching in Sunyatsenia 5: 284. 1940.

Plants terrestrial. **Rhizomes** long-creeping, branched, protostelic, with scales brown, basifixed, rigid; squamophores absent. **Fronds** scrambling, pseudodichotomously branched, with anisotomic branches. **Laminae** abaxially glabrescent, with brown scales on rachises, segments, midribs, secondary veins, and laminar tissue; adaxial surface with scales restricted to the rachises; ultimate branches pectinate, with linear segments bearing scales brown, ciliate, and substellate, and simple hairs, especially along the costae. **Buds** covered with brown scales, concolorous, with pseudostipule. **Accessory branches** absent. **Veins** free, 1-forked. **Sori** round, c. 3–6 sporangia per sorus, without hyaline paraphyses. **Spores** monolete ellipsoidal, rugose.

Etymology: *Sticheropsis* comes from *Sticher-* plus the Greek suffix ‘opsis’, which means resemblance. It is an allusion to the genus resemblance to *Sticherus*.

Distribution and ecology: *Sticheropsis* has two species (*S. milnei* and *S. truncata*) occurring in Australasia, in open sunny locations, forest edges, and along roadsides at 0–1600 m a.s.l.

Taxonomic and phylogenetic studies: We here propose the segregation of *Sticheropsis* from *Sticherus* based on their phylogenetic placement, depth of divergence, and frond architecture. The type designated for *Sticherus* is *S. laevigatus* (Willd.) C.Presl, which is synonymous with *S. truncatus* (Willd.) Nakai. The first author personally reviewed Willdenow’s collection housed at B, and there is no doubt about the synonymy between those two names (Lima et al. 2024). Lima et al. (2023) recovered a phylogenetic topology in which a clade formed by *S. truncatus* + *Sticherus milnei* is sister group of *Gleichenia* + *Stromatopteris* + the remaining species of *Sticherus*. The paraphyly of *Sticherus* is therefore evidenced on a phylogenomic scale, as the type of the genus is *S. truncatus*. The data points to a splitting of

the clade *Sticheropsis* from the clade *Gleichenia* + *Stromatopteris* + *Sticherus* at 114–117 Mya, while the separation of *Stromatopteris* from *Gleichenia* is ~108 Mya; *Sticherus* diverged from the *Stromatopteris* + *Gleichenia* clade ~112 Mya (Lima et al. 2023). Additionally, *Sticherus* is characterized by having an isotomic branching pattern, whereas *Sticheropsis* is characterized by having an anisotomic branching pattern. As no other generic name is available to accommodate the remaining species of *Sticherus*, a new generic name is necessary. However, aiming to prioritize the stability of Gleicheniaceae names, given the paraphyly of *Sticherus* (Lima et al. 2023, Fig. 1), a proposal to conserve *Sticherus* with a different type was made (Lima et al. 2024). Therefore, a new genus name is needed to accommodate *S. milnei* and *S. truncatus*.

Accepted species and new combinations

1. *Sticheropsis milnei* (Baker) L.V.Lima, Salino & T.E.Almeida, **comb. nov.** \equiv *Gleichenia milnei* Baker in Syn. Fil. 449. 1874 \equiv *Sticherus milnei* (Baker) Ching in Sunyatsenia 5: 284. 1940.

2. *Sticheropsis truncata* (Willd.) L.V.Lima, Salino & T.E.Almeida, **comb. nov.** \equiv *Mertensia truncata* Willd. in Kongl. Vetensk. Acad. Nya Handl. 25: 169. 1804 \equiv *Sticherus truncatus* (Willd.) Nakai in Bull. Natl. Sci. Mus. Tokyo 29: 30. 1950.

7. *Sticherus* C.Presl [Tent. Pterid.] in Abh. Königl. Böhm. Ges. Wiss., ser. 4, 5: 51. 1836 (ante 2 Dec), nom. cons.

Type: *S. gracilis* (Mart.) Copel. (Gen. Fil.: 27. 1947) (*Mertensia gracilis* Mart.), typ. cons. prop.

Plants terrestrial or epipetric. **Rhizomes** long-creeping, branched, protostelic, with scales rigid, brown, reddish-brown, or golden, peltate or basifixed; squamophores present or absent. **Fronds** erect or scrambling, pseudodichotomously branched, rarely pinnatifid, with isotomic branches; abaxial surface glabrous, glabrescent, or pubescent, with scales whitish, reddish, or nigrescent on the rachis, midrib segments, secondary veins, and/or laminar tissue; adaxial surface glabrous, or with scales restricted to the rachises or segment midribs, ultimate branches pectinate, with segments deltoid, lanceolate, or linear. **Buds** covered with scales whitish, reddish, or nigrescent, concolorous or bicolorous, if the latter, with apical, central, or basal cells with darkening, with or without a pseudostipule. **Accessory branches** absent. **Veins** free, 1-forked. **Sori** round, 3–6 sporangia per sorus, with or without a hyaline paraphyses. **Spores** monolete, ellipsoidal, slightly rugose, minimally perforated; $x = 34$.

Etymology: No etymology was given by Presl (1836); however, the name probably comes from the Greek *stichos*, which means ‘row or line’, which may be a reference to the sori arranged in a single row on either side of the midrib of the ultimate segment (Pichi Sermolli 1972).

Diagnosis: *Sticherus* can be readily distinguished by the pectinate ultimate branches, rhizomes, and buds covered with scales, and fronds with isotomic architecture.

Distribution and ecology: *Sticherus* is a pantropical genus with ~89 species and two hybrids. It occurs in open sunny locations, and anthropogenic habitats such as roadsides, ranging from sea level to 2600 m a.s.l. Its centres of diversity are the Neotropics, Southeast Asia, and Oceania.

Taxonomic and phylogenetic studies: Given the paraphyly of *Sticherus* (Lima *et al.* 2023), to assure the nomenclatural stability, avoiding 91 new combinations, we proposed the conservation of *Sticherus* with a new type (Lima *et al.* 2024).

Notes: We do not treat the varieties of *Sticherus hirta* recognized by Holttum (1959). Further studies should be conducted to better delimit the different species in this complex.

Accepted species and new combination

1. *Sticherus* × *pseudobifidus* (Jermy & T.G.Walker) J.Gonzales in Phytotaxa 31: 42. 2011.
2. *Sticherus* × *subremotus* (Jermy & T.G.Walker) J.Gonzales in Phytotaxa 31: 48. 2011.
3. *Sticherus albus* J.Gonzales in Phytotaxa 31: 14. 2011.
4. *Sticherus alstonii* (Holttum) L.V.Lima, Salino & T.E.Almeida, **comb. nov.** ≡ *Gleichenia alstonii* Holttum in Reinwardtia 4: 267. 1957.
5. *Sticherus antillensis* J.Gonzales in Phytotaxa 31: 16. 2011.
6. *Sticherus arachnoideus* Østergaard & Øllgaard in Fl. Ecuador 66: 121. 2001.
7. *Sticherus aurantiacus* Østergaard & Øllgaard in Fl. Ecuador 66: 124. 2001
8. *Sticherus bifidus* (Willd.) Ching in Sunyatsenia 5: 282. 1940.
9. *Sticherus blepharolepis* (Sodirol) Ching in Sunyatsenia 5: 282. 1940.
10. *Sticherus bolanicus* (Rosenst.) Copel. in Philipp. J. Sci. 75: 352. 1941.
11. *Sticherus bolivienis* (Maxon & C.V.Morton) J.Gonzales in Phytotaxa 31: 20. 2011.
12. *Sticherus brackenridgei* (E.Fourn.) St.John in Occas. Pap. Bernice Pauahi Bishop Mus. 17: 81. 1942.
13. *Sticherus brassii* (C.Chr.) Copel. in Philipp. J. Sci. 75: 357. 1941.
14. *Sticherus brevitomentosus* Østergaard Andersen & Øllgaard in Fl. Ecuador 66: 132. 2001.
15. *Sticherus brittonii* (Maxon) Nakai in Bull. Natl. Sci. Mus. Tokyo 29: 15. 1950.
16. *Sticherus chocoensis* J.Gonzales in Phytotaxa 31: 20. 2011.
17. *Sticherus compactus* (Christ) Nakai in Bull. Natl. Sci. Mus. Tokyo 29: 15. 1950.
18. *Sticherus cryptocarpus* (Hook.) Ching in Sunyatsenia 5: 282. 1940.
19. *Sticherus cubensis* (Underw.) J.Gonzales in Phytotaxa 31: 23. 2011.
20. *Sticherus cunninghamii* (Heward ex Hook.) Ching in Sunyatsenia 5: 283. 1940.
21. *Sticherus decurrens* (Raddi) J.Gonzales in Phytotaxa 31: 23. 2011.
22. *Sticherus erectus* (C.Chr.) Copel. in Philipp. J. Sci. 75: 353. 1942.
23. *Sticherus farinosus* (Kaulf.) Ching in Sunyatsenia 5: 283. 1940.
24. *Sticherus ferrugineus* (Desv.) J.Gonzales in Phytotaxa 31: 24. 2011.
25. *Sticherus flabellatus* (R.Br.) H.St. John in Occas. Pap. Bernice Pauahi Bishop Mus. 17: 81. 1942.
26. *Sticherus flabellatus* var. *compactus* (C.T.White & Goy) D.A.Sm. in N. Queensland Naturalist 14: 6. 1946.
27. *Sticherus flagellaris* (Bory ex Willd.) Ching in Sunyatsenia 5: 283. 1940.
28. *Sticherus fulvus* (Desv.) Ching in Sunyatsenia 5: 283. 1940.
29. *Sticherus furcatus* (L.) Ching in Sunyatsenia 5: 283. 1940.
30. *Sticherus fuscus* J.Gonzales in Phytotaxa 31: 25. 2011.
31. *Sticherus gnidioides* (Mett.) Nakai in Bull. Natl. Sci. Mus. Tokyo 29: 18. 1950.
32. *Sticherus gracilis* (Mart.) Copel. in Gen. Fil.: 27. 1947.
33. *Sticherus hastulatus* (Rosenst.) Nakai in Bull. Natl. Sci. Mus. Tokyo 29: 18. 1950.
34. *Sticherus hirtus* (Blume) Ching Sunyatsenia 5: 283. 1940.
35. *Sticherus hispidus* (Mett. ex Kuhn) Copel. in Gen. Fil.: 27. 1947.
36. *Sticherus holttumii* L.V.Lima & Salino in Phytotaxa 340: 182. 2018.
37. *Sticherus hooglandii* (Holttum) Perrie in Blumea 63: 120. 2018.
38. *Sticherus hypoleucus* (Sodirol) Copel. in Gen. Fil.: 28. 1947.
39. *Sticherus inflexus* Pic.Serm. in Webbia 27: 397. 1972.
40. *Sticherus interjectus* (Jermy & T.G.Walker) J.Gonzales in Phytotaxa 31: 28. 2011.
41. *Sticherus intermedius* (Baker) Chrysler in Amer. J. Bot. 31(8): 483. 1944.
42. *Sticherus jacha* J.Gonzales in Phytotaxa 31: 29. 2011.
43. *Sticherus jamaicensis* (Underw.) Nakai in Bull. Natl. Sci. Mus. Tokyo 29: 20. 1940.
44. *Sticherus lanosus* (Christ) J.Gonzales in Phytotaxa 31: 32. 2011.
45. *Sticherus lanuginosus* (Moric. ex Fée) Nakai in Bull. Natl. Sci. Mus. Tokyo 29: 20. 1950.
46. *Sticherus lechleri* (Mett. ex Kuhn) Nakai in Bull. Natl. Sci. Mus. Tokyo 29: 21. 1950.
47. *Sticherus leonis* (Maxon) Nakai in Bull. Natl. Sci. Mus. Tokyo 29: 21. 1950.
48. *Sticherus lepidotus* (R.A.Rodr.) R.A.Rodr. & Ponce in Darwiniana 45: 238. 2007.
49. *Sticherus littoralis* (Phil.) Nakai in Bull. Natl. Sci. Mus. Tokyo 29: 21. 1950.
50. *Sticherus lobatus* N.A.Wakef. in Victorian Naturalist 60: 110. 1943.
51. *Sticherus loheri* (Christ) Copel. in Gen. Fil. 27. 1947.
52. *Sticherus longipinnatus* (Hook.) Ching in Sunyatsenia 5: 283. 1940.
53. *Sticherus maritimus* (Hieron.) Nakai in Bull. Natl. Sci. Mus. Tokyo 29: 22. 1950.
54. *Sticherus melanoblastus* (Alston) Østergaard & Øllgaard in Fl. Ecuador 66: 144. 2001.
55. *Sticherus montaguei* (Compton) Nakai in Bull. Natl. Sci. Mus. Tokyo 29: 23. 1950.
56. *Sticherus moyobambensis* J.Gonzales in Phytotaxa 31: 34. 2011.

57. *Sticherus nervatus* J.Gonzales in Phytotaxa 31: 36. 2011.
58. *Sticherus nigropaleaceus* (J.W.Sturm) Prado & Lellinger in Amer. Fern J. 86: 101. 1996.
59. *Sticherus nudus* (Moritz ex Reichardt) Nakai in Bull. Natl. Sci. Mus. Tokyo 29: 23. 1950.
60. *Sticherus oceanicus* (Kuhn) Ching in Sunyatsenia 5: 284. 1940.
61. *Sticherus orthocladus* (Christ) Chrysler in Amer. J. Bot. 31(8): 483. 1944.
62. *Sticherus ovatus* J.Gonzales in Phytotaxa 31: 39. 2011.
63. *Sticherus owhyhensis* (Hook.) Ching in Sunyatsenia 5: 284. 1940.
64. *Sticherus pallescens* (Mett.) Vareschi in Fl. Venezuela 1: 180. 1969.
65. *Sticherus paulistanus* (Rosenst.) Copel. in Gen. Fil. 27. 1947.
66. *Sticherus peruvianus* (Maxon) A.R.Smith, M.Kessler & J.Gonzales in Amer. Fern J. 89(4): 260. 1999.
67. *Sticherus pruinosus* (Mart.) Ching in Sunyatsenia 5: 284. 1940.
68. *Sticherus pseudoscandens* (Alderw.) Copel. in Philipp. J. Sci 75: 356. 1941.
69. *Sticherus pteridellus* (Christ) Copel. in Gen. Fil.: 28. 1947.
70. *Sticherus pulcher* Copel. in Philipp. J. Sci. 75: 355. 1941.
71. *Sticherus quadripartitus* (Poir.) Ching in Sunyatsenia 5: 284. 1940.
72. *Sticherus reflexipinnula* (C.Chr.) Copel. In Philipp. J. Sci. 75: 355. 1941.
73. *Sticherus remotus* (Kaulf.) Chrysler in Amer. J. Bot. 31: 483. 1944.
74. *Sticherus retroflexus* (J.Bommer ex Christ) Copel. In Gen. Fil.: 28. 1947.
75. *Sticherus revolutus* (Kunth) Ching in Sunyatsenia 5: 285. 1940.
76. *Sticherus rubiginosus* (Mett.) Nakai in Bull. Natl. Sci. Mus. Tokyo 29: 28. 1950.
77. *Sticherus rufus* J.Gonzales & A.R.Sm. in Phytotaxa 31: 44. 2011.
78. *Sticherus salinoi* L.V.Lima in Phytotaxa 345: 80. 2018.
79. *Sticherus simplex* (Desv.) Ching in Sunyatsenia 5(4): 285. 1940.
80. *Sticherus squamosus* (Fée) J.Gonzales in Phytotaxa 31: 47. 2011.
81. *Sticherus squamulosus* (Desv.) Nakai in Bull. Natl. Sci. Mus. Tokyo 29: 28. 1950.
82. *Sticherus strictissimus* (Christ) Copel. In Gen. Fil. Copel.: 28. 1947.
83. *Sticherus tener* (R.Br.) Ching in Sunyatsenia 5: 285. 1940.
84. *Sticherus tepuiensis* A.R.Sm. in Ann. Missouri Bot. Gard. 77: 253. 1990.
85. *Sticherus tomentosus* (Cav. ex Sw.) A.R.Sm. in Ann. Missouri Bot. Gard. 77: 255. 1990.
86. *Sticherus umbraculifer* (Kunze) Ching in Sunyatsenia 5: 285. 1940.
87. *Sticherus underwoodianus* (Maxon) Nakai in Bull. Natl. Sci. Mus. Tokyo 29: 31. 1950.
88. *Sticherus urceolatus* M.Garrett, Kantvilas & Laws in Muelleria 11: 103. 1998.
89. *Sticherus velatus* (Kunze) Copel. in Gen. Fil.: 28. 1947.
90. *Sticherus venosus* Copel. in Philipp. J. Sci. 75: 356. 1941.
91. *Sticherus vestitus* (Blume) Ching in Sunyatsenia 5: 285. 1940.

8. *Stromatopteris* Mett. In Ann. Sci. Nat. 15: 84. 1861.

Type: *Stromatopteris moniliformis* Mett. In Ann. Sci. Nat. Bot. 15: 84. 1861.

Plants terrestrial. **Rhizomes** long-creeping, branched, with aerial branches dichotomous, protostelic, with scales dark, basifixed, rigid, and bristle-like hairs; squamophores absent. **Fronds** erect, pinnatifid. **Laminae** abaxially glabrescent, with scales restricted to the area of the sori; adaxial surface glabrous; segments ovate-rounded. **Buds** with pseudostipules, and accessory branches absent. **Veins** free, 1-forked. **Sori** round, c. 3–6 sporangia per sorus, without hyaline paraphyses. **Spores** monoletic, ellipsoidal, slightly rugose, nearly reticulate; $x = 39$.

Etymology: Mettenius (1861) did not provide an etymology for the genus name. It probably comes from the Greek *stromatos*, bed or mattress, and *pterus*, fern, and is presumably a reference to the long-haired cushion-like receptacle in which the sporangium is set.

Diagnosis: *Stromatopteris* is characterized by its rhizomes with erect branches and pinnatifid fronds, with segments lobed and without a midrib.

Distribution and ecology: *Stromatopteris* is an endemic monotypic genus from New Caledonia. It occurs on sandy soils including serpentine ones, in open places, in macchia-like vegetation, and occasionally in rain forests (Brownlie 1969, Kramer 1990), at 0–600 m a.s.l.

Taxonomic and phylogenetic studies: The affinities of *Stromatopteris* with Gleicheniaceae have long been debated (Pichi Sermolli 1972). Phylogenetic studies based on molecular datasets, however, firmly support its placement within the family (Li et al. 2010, Liu et al. 2020, Lima et al. 2023).

Accepted species

1. *Stromatopteris moniliformis* Mett. In Ann. Sci. Nat. Bot. 15: 84. 1861.

Morphology and growth habit of Gleicheniaceae

Gleicheniaceae stands out for its unique frond morphology. The indeterminate and almost modular growth pattern of the fronds, called pseudodichotomous, results from buds located at the bases of the branches (Holtum 1957b, 1959). The first step to better understanding the taxonomy of Gleicheniaceae is to accurately interpret its morphology. The last revision considering the morphology of the family was undertaken by Holtum (1957b) and demonstrates the need for a revision that embraces more recent information. The need for a simpler and more objective evaluation is evidenced by the several attempts to standardize frond terminology (e.g. Nakai 1950, Holtum 1957b, Tryon and Stolze 1989, Andersen and

Table 1. The main terminology systems of Gleicheniaceae morphology.

	Holtum (1957a)	Andersen and Øilgaard (1996)	Lellinger (2002)	Shaw and Ranker (2011)	Jin et al. (2013)	Gonzales and Kessler (2011); Kessler and Smith (2018)	Lima and Salino (2018) – Present work
frond	leaf	frond	frond	leaf	frond	leaf	frond
lamina	lamina	lamina	lamina	lamina	lamina	leaf	lamina/blade
stipe/petiole	rachis	stipe	stipe	stipe	stipe	petiole	petiole
rachis/main rachis	rachis bud/dormant rachis	rachis	rachis	rachis	rachis	rachis	rachis
dormant rachis-apex/leading rachis/dormant apex/permanent dormant apex	rachis bud/dormant rachis	dormant bud/latent bud	dormant bud/latent bud	rachis bud/pinna bud	apical bud	bud	bud
leaves/primary branches/lateral branches	pinna/branch/pair	pinna/branches	pinna/branches	pinna	pinna	first, second, third order branches	branches
primary rachis-branch/costa	costa	costa/costule/costule	costa/costule/costule	($\alpha, \beta, \gamma, \dots$) costa	costa/costule		
leaflet/axes of lower order that are leaf/leaf lamina	segments	segments	segments	costal segment	lateral pinnules	segments	segments
lateral branch/ultimate branch	ultimate branches	ultimate branches	ultimate branches	ultimate leaflet	ultimate pinna	ultimate branches/distal branches	ultimate branches
lobe/lamina-lobe/lateral/leaflet	segments	segments	segments	ultimate segments	lateral pinnules	segments/ultimate segments	ultimate segments
lobed leaflet covering bud	pseudostipules	pseudostipules	pseudostipules	pseudostipules	bracts	aphlebiae/pseudostipule	pseudostipules
accessory branch	accessory branches	sessile accessory branches	sessile accessory branches	accessory leaflet	pair of lateral pinnules at each dichotomy	accessory branches	accessory branches
midrib/costule	midvein	midvein	midvein	midvein	costa	midvein	midrib
vein	veinlet	vein	vein	vein	vein	vein	vein
branching pattern/branched/leaf branching/pseudodichotomy/forking/forks	pseudodichotomies/branchings/dichotomies	branched bifurcate	branched bifurcate	fork	dichotomy	pseudodichotomous branchings	pseudodichotomy/primary bifurcation/secondary bifurcation

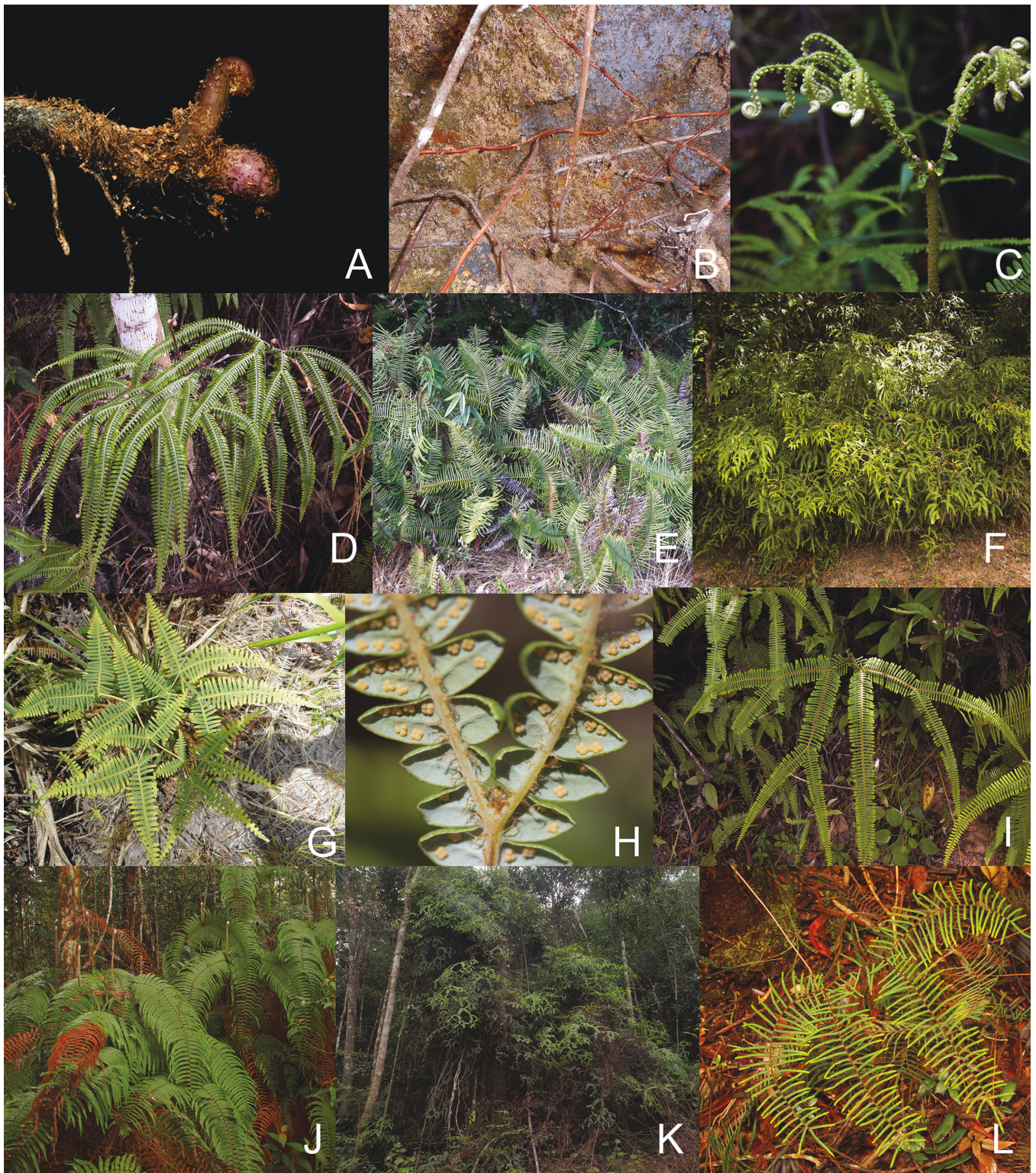


Figure 2. Gleicheniaceae habit and diversity. A, Rhizome tip of *S. squamosus*. B, Rhizomes of *D. flexuosa* forming nets on the soil surface. C, Erect frond of *S. lanuginosus*. D, Pendant blade of *S. bifidus*. E, Erect habit of *D. nervosa*. F, Scrambling habit of *G. pectinata*. G, *D. flexuosa*. H, Abaxial surface of *S. pruinosis*. I, *S. nigropaleaceus*. J, *D. clemensiae*. K, *S. truncata*. L, *G. microphylla*.

Øllgaard 1996, Lellinger 2002, Shaw and Ranker 2011, Table 1). These attempts have created difficulties for comparisons among the different descriptions and treatments (Shaw and Ranker 2011), as no single proposed system has been generally adopted. We here provide a revision of the morphology

and growth habits of the taxa, discuss and compare the different systems listed previously, and propose updates for some frond terminology. In this context, and focusing on structures of taxonomic interest, we chose what we consider the most suitable and simplest terms to describe frond structures

among the many names already proposed, thus avoiding the creation of new terms.

Habit: Gleicheniaceae shows two main growth habits: erect (Fig. 2E) and scrambling (Fig. 2F). The former refers to plants with fronds that are fully self-supporting and often of restricted growth. Typical examples are *S. simplex* and *Gleichenia vulcanica* Blume (Holttum 1959, Gonzales and Kessler 2011). In most cases, the rhizomes are creeping, and only the fronds are held erect. In *S. lanuginosus*, for example, the rhizome is fully creeping, and only the petiole is erect (Lima and Salino 2018). The ultimate branches are completely ascendant, conferring the fronds an erect aspect (Fig. 2C). Only in *S. moniliformis* are the pinnatifid fronds borne on short erect lateral branches of the rhizomes, from which the petioles also arise erectly (Kramer 1990).

In terms of the second growth habit, some authors have adopted the term ‘scandent’ as referring to a scrambling habit (e.g. Andersen and Øllgaard 2001, Mickel and Smith 2004), although that is not accurate. The definition of the term ‘scandent’, as stated by Lellinger (2002), refers to ‘climbing close on the other vegetation’ and points to *Polybotrya* (Dryopteridaceae) as an example. According to , ‘scandent’ refers to the plants that, with the help of specialized structures, climb a substrate like a wall, a fence, or other plants, which is not the case in Gleicheniaceae. The fronds in this family are usually large due to the rachis size and modular growth (which is a consequence of bud development) and they mostly lean on each other due to the projection of the petiole and rachis (Fig. 2D). New frond modules usually rest on older ones, or on what remains of the herbaceous subshrub layer.

In that context, we chose to use the term ‘scrambling’, as defined by Lellinger (2002), as plants that grow ‘loosely over other vegetation’. This term has already been adopted by various authors (e.g. Tryon and Tryon 1982, Proctor 1985, Jin *et al.* 2013), and it seems to be appropriate for describing the growth habit of Gleicheniaceae (Fig. 2F).

Gleicheniaceae often colonize disturbed and open habitats such as landslide scars, tree fall gaps, and burnt areas (Walker and Sharpe 2010). Some species will eventually climb the surrounding vegetation in response to competition for light by other colonizers, and some authors use the term ‘climbing’ for this growth habit (Mickel and Smith 2004). We also accept this term as a variation of the scrambling habit, as Gleicheniaceae do not have specialized structures for climbing on other plants, and they usually simply lean on the surrounding vegetation. Some species, especially those of *Gleichenia*, are very hard to disentangle from the vegetation thickets in which they grow. The stiff, resilient petioles are not articulated and remain on the rhizome even when the branches have died (Holttum 1957b). This architecture can be viewed as an adaptation or specialized structure for a self-supported climbing habit. The pinnate-pinnatisect branches of *Diplopterygium*, for example, frequently intertwine with twigs or lianas while growing, and some fronds can reach heights of 10 m or more (Holttum 1959). The opposite branches of *D. flexuosa*, associated with their long rigid fronds, help it to climb up on the surrounding vegetation (Lima and Salino 2018).

Rhizome: The rhizomes of Gleicheniaceae are usually short- to long-creeping, branched, and frequently form large mats. The

rhizomes can grow superficially, associated (or not) with the soil horizon top. By having this type of rhizome growth, specimens can easily be collected while preserving the indument and slender roots. The rhizomes of other species, such as *Dicranopteris*, *Gleichenella*, and *Stromatopteris*, grow deep in the soil, and while their rhizomes and indument can be harvested during field collections, the slender roots are not (Bower 1926, Holttum 1957b, Fig. 2A, B). The rhizome morphology of *S. moniliformis* is an exception within the family. It has both erect aerial rhizomes and creeping underground rhizomes. Fronds are arranged along both aerial and underground rhizomes, although they are more densely clustered just behind bifurcations of the aerial rhizome branches (Hagemann and Schulz 1978).

Anatomically, Gleicheniaceae rhizomes are circular in cross-section with a small stele in the centre, with a protosteles in *Dicranopteris*, *Diplopterygium*, *Gleichenia*, *Sticheropsis*, *Sticherus*, and *Stromatopteris*, and a solenosteles in *G. pectinata* (Ogura 1972).

The rhizome surface may be smooth, rugose, or muricate, glabrescent, or densely covered by dark brown, reddish, or orange scales, or hairs. Andersen and Øllgaard (2001) described projections of the rhizome epidermis that bear peltate or basifixed scales. They named these projections squamophores, a term adopted by Gonzales (2003) and Gonzales and Kessler (2011) in their revision of neotropical *Sticherus*. We accept this term and point out its taxonomic importance in separating close species such as *S. revolutus* with squamophores and *S. pruinosus* without squamophores.

Fronds: Fronds usually consist of a long petiole and a branched lamina. The elongation of the rachis is arrested by a dormant bud, while the lateral branches elongate in a sympodial pattern (Chrysler 1943, 1944, Fig. 3C). If the dormancy of the bud is broken, the main axis reinitiates its growth (Ogura 1972) (e.g. *Diplopterygium bancroftii*, *S. lanuginosus*, *S. montaguei*, and *Gleichenia dicarpa*). This branching pattern is called pseudodichotomous, as the bud may develop into a new branch, and these divisions may repeat indefinitely (Bower 1926). As that pattern is also observed on the lateral branches, the plant assumes a modular and seasonal frond growth pattern (Holttum 1957b). The only exceptions are *S. simplex* and *S. moniliformis*, which have unbranched fronds (Kramer 1990, Gonzales and Kessler 2011).

Side-branch architecture behaves in very different manners in different species (Holttum 1957b). The positions of the dormant buds and the arrangements of branches and segments are also variable, producing different frond patterns (Ogura 1972) (Figs 4–6). There are two main types of pseudodichotomy in the family: isotomic (Fig. 3A–C, E) and anisotomic (Fig. 3D, F) (Kramer 1990, Mickel and Smith 2004, Gonzales and Kessler 2011, Lima and Salino 2018). The former is most common in the family and occurs when all branches are equal in size, as in *Diplopterygium* (Holttum 1959, Mickel and Smith 2004). The latter type is known in *G. pectinata* (Lima and Salino 2018) and a few Asian species of *Dicranopteris*, such as *D. tetraphylla* (Holttum 1959, Wei *et al.* 2022). In these cases, the ramifications of the branches are unequal, and a dominant axis is observed (Figs 4G, 6B). The growth pattern of *Rouxopteris* is almost

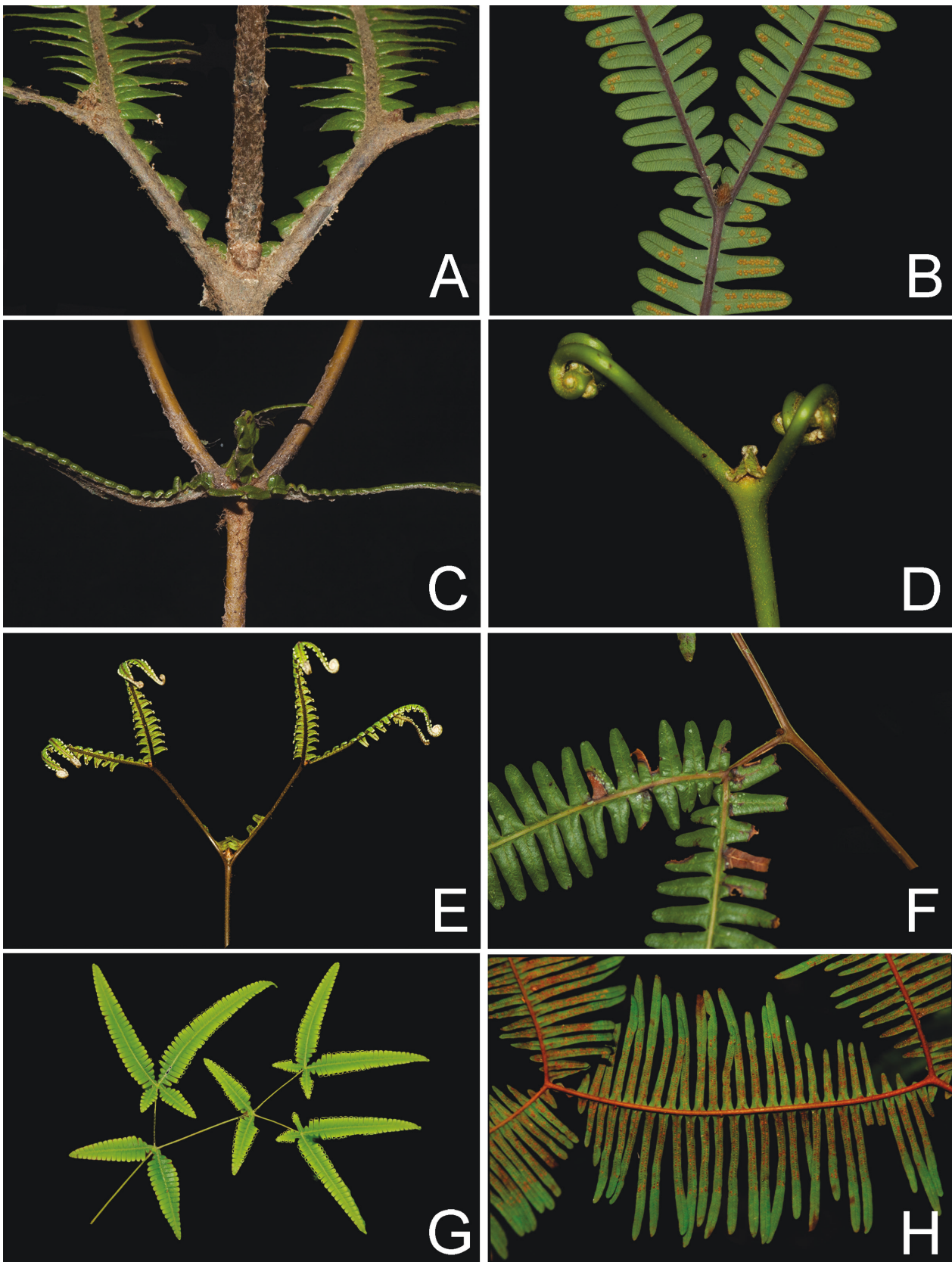


Figure 3. A, Detail of a pseudodichotomy in *S. bifidus*, primary ramification. B, Detail of a secondary ramification in *S. gracilis*. C, Detail of a primary ramification in *D. nervosa* showing the accessory branches and the pseudostipule. D, Early stage of development of an anisotomic ramification in *G. pectinata*. E, Isotomic ramification of *S. squamosus*. F, Anisotomic ramification in *G. pectinata*. G, Anisotomic ramification of *D. tetraphylla*. H, Anisotomic ramification of *S. truncata*.

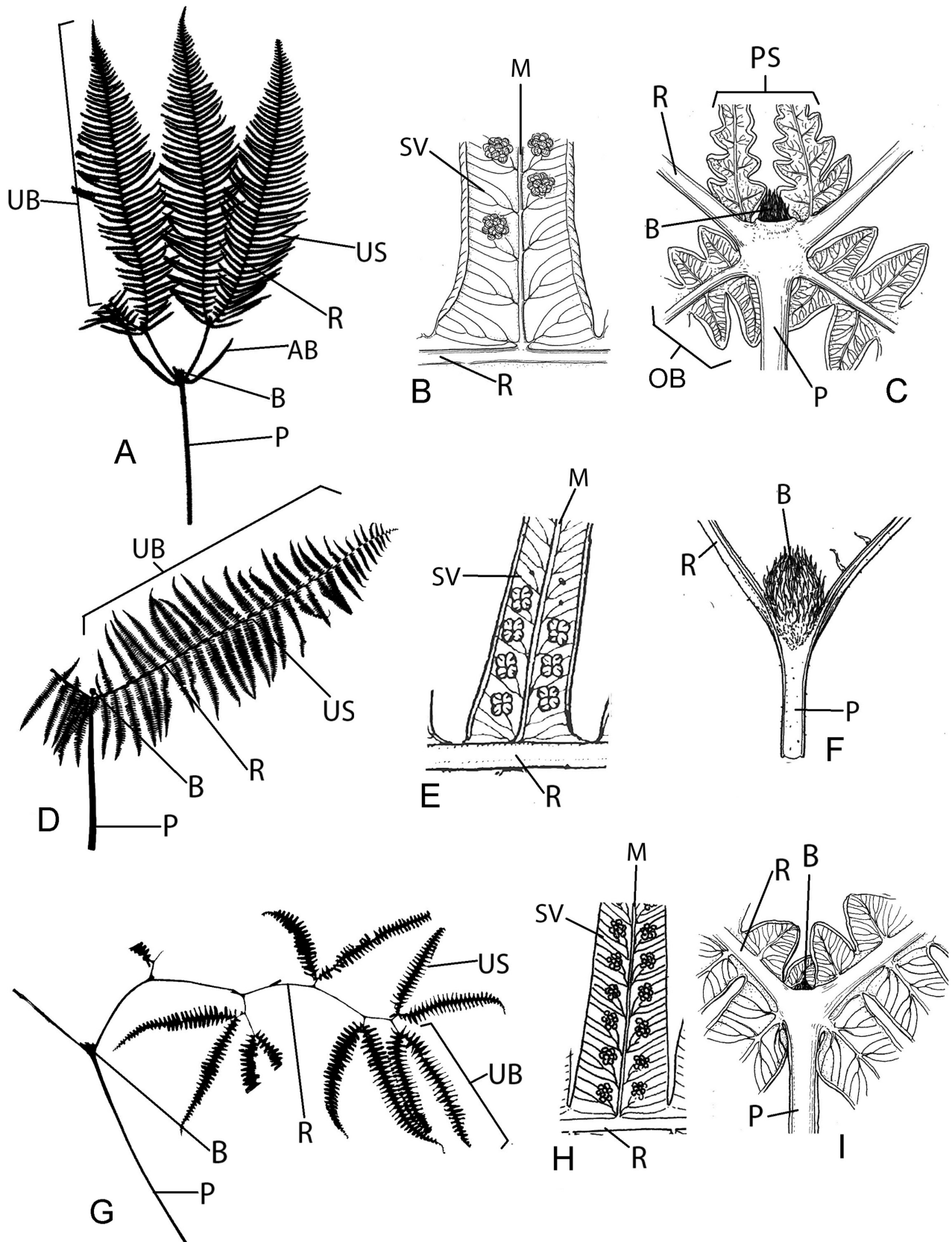


Figure 4. A, Schematic representation of *D. nervosa*. B, Abaxial surface detail of *D. flexuosa* segments, showing the sorus position and venation. C, Primary bifurcation detail, showing the bud position, accessory branches, and pseudostipule. D, Schematic representation of *Diplopterygium*. E, Abaxial surface detail of *D. bancroftii* segments, showing the sorus position and venation. F, Primary bifurcation detail, showing the bud position. G, Schematic representation of *G. pectinata*. H, Abaxial surface detail of *G. pectinata* segments, showing the sorus position and venation. I, Primary bifurcation detail, showing the bud position. B, bud; M, midrib; OB, opposite branches; P, petiole; PS, pseudostipule; R, rachis; SV, secondary vein; UB, ultimate branch; US, ultimate segment.

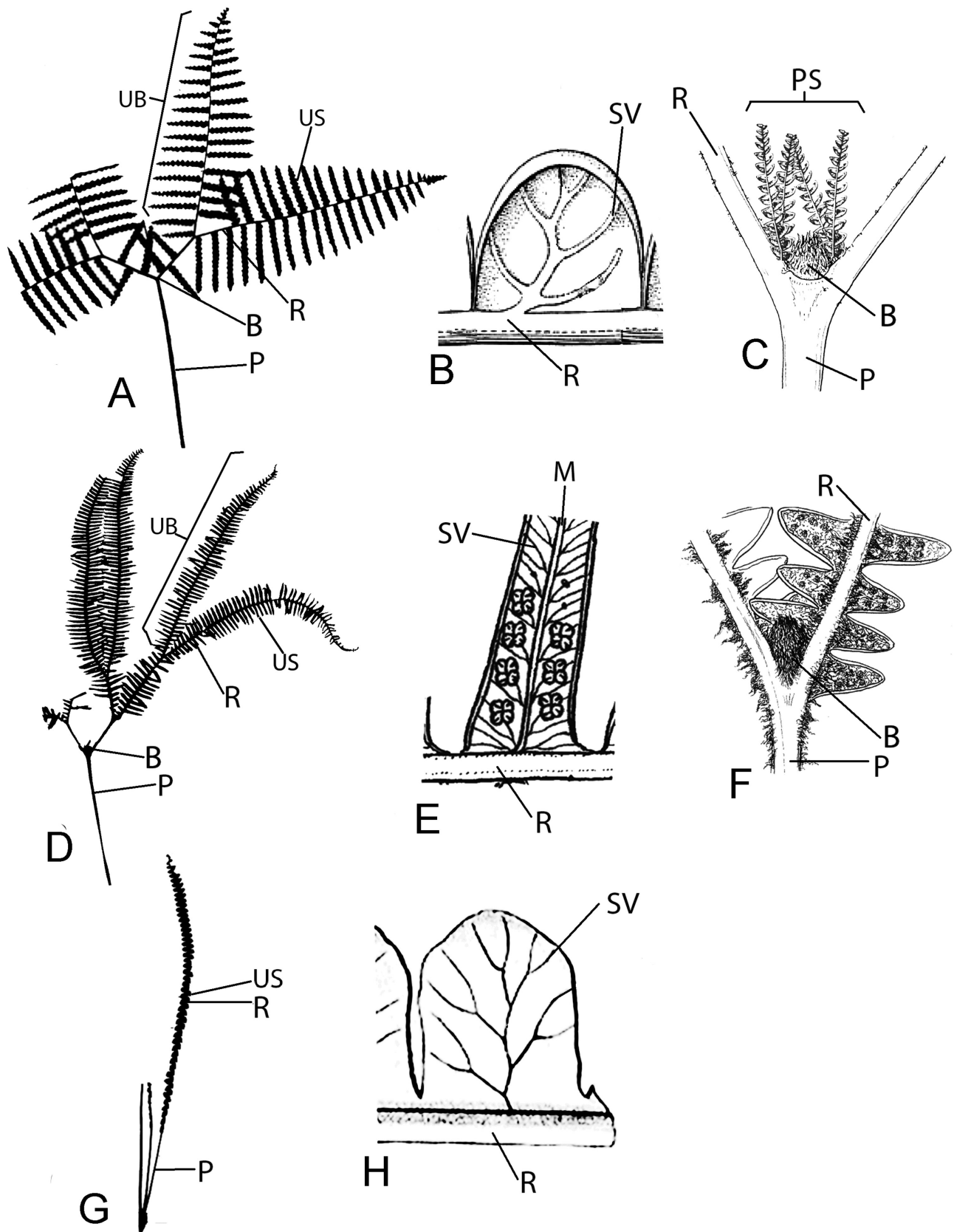


Figure 5. A, Schematic representation of *G. microphylla*. B, Abaxial surface detail of *G. microphylla* segments, showing the venation. C, Primary bifurcation detail, showing the bud position, and pseudostipule. D, Schematic representation of *S. paulistanus*. E, Abaxial surface detail of *S. paulistanus* segments, showing the sorus position and venation. F, Primary bifurcation detail, showing the bud position. G, Schematic representation of *S. moniliformis*. redrawn after Shaw and Ranker (2011). H, Abaxial surface detail of *S. moniliformis* segments, showing the venation. B, bud; M, midrib; P, petiole; PS, pseudostipule; R, rachis; SV, secondary vein; UB, ultimate branch; US, ultimate segment.

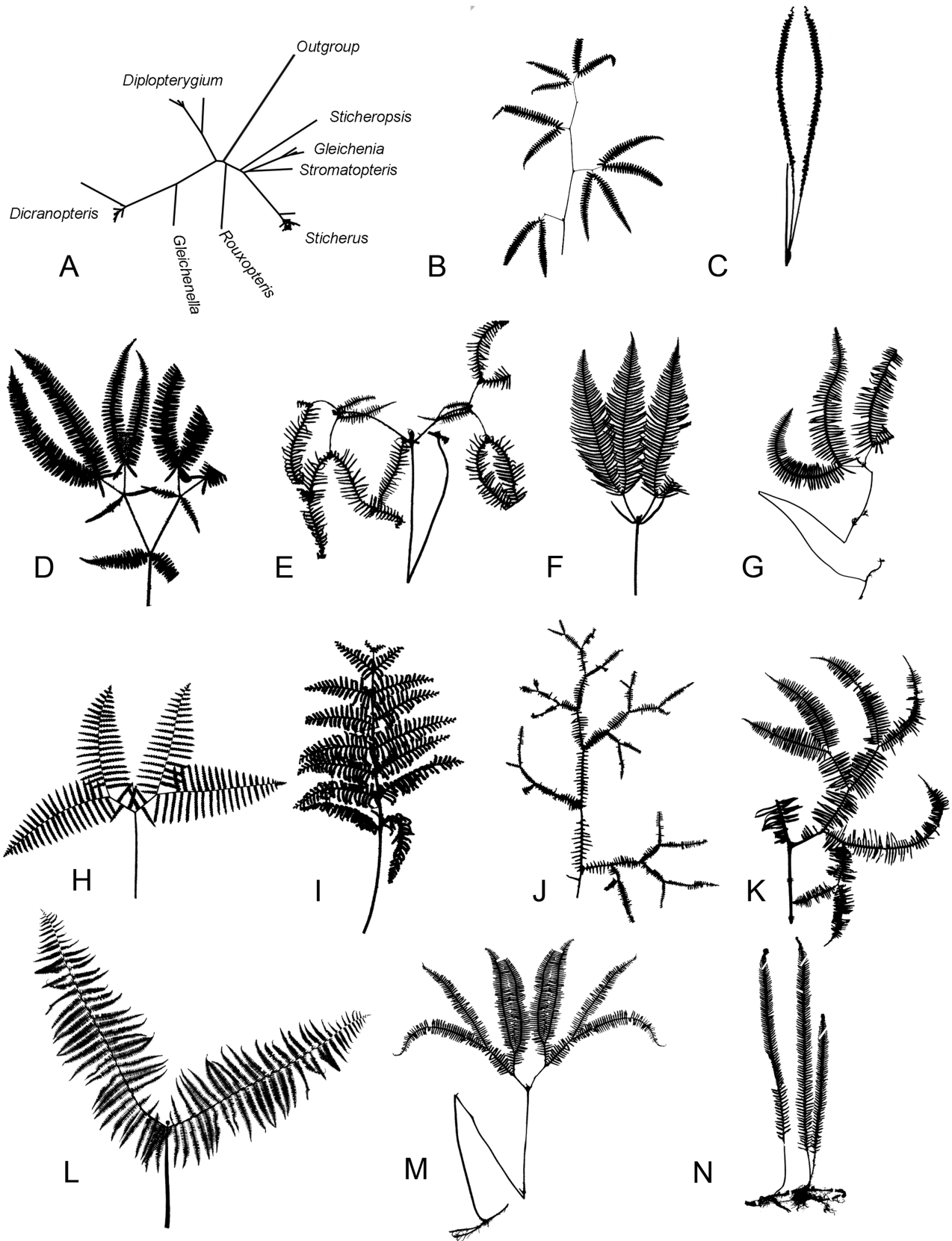


Figure 6. Gleicheniaceae genera silhouettes. A, Unrooted phylogenetic tree showing the relationship among the genera (Lima et al. 2023). B, *G. pectinata*. C, *S. moniliformis*. D, *D. flexuosa*. E, *D. seminuda*. F, *D. nervosa*. G, *D. spissa*. H, *G. microphylla*. I, *R. boryi*. J, *S. milnei*. K, *S. truncata*. L, *D. bancroftii*. M, *S. paulistanus*. N, *S. simplex*.

sympodial, and the bud (when present) is restricted to the main axis, with no lateral buds (Liu *et al.* 2020).

Additionally, the morphology of the ultimate branch also varies among the various genera. The fronds of *Stromatopteris* are unbranched (Holttum 1957b) (Figs 5G, 6C) and the lamina is pinnatifid, with its round segments lacking a midrib (Fig. 5H). In *Diplopterygium*, the ultimate branches are bipinnate (Figs 4D, 6L), and the pinnae may be sessile or subsessile, with the ultimate segments usually linear and with a midrib (Fig. 4E). *Gleichenia* and *Rouxopteris* also have bipinnate ultimate branches, with their usually round segments lacking a midrib (Figs 5A, B, 6H, I). *Dicranopteris*, *Gleichenella*, *Sticheropsis*, and *Sticherus* all have pinnatisect ultimate branches, with their ultimate segments usually being linear, with entire margins (Figs 4A, G, 5D, 6B, D–G, J–K, M).

Dicranopteris, unlike the other genera of Gleicheniaceae, has a pair of accessory branches opposite the main and secondary bifurcations (Figs 3C, 4A, 6D–G); these accessory branches may be simple (e.g. *D. nervosa*) or pectinate (e.g. *D. flexuosa*) (Lima and Salino 2018). The accessory branches may have sori and hairs. The differences from it to the regular branches are in terms of their positions and sizes, as they are frequently smaller (Lima and Salino 2018).

Fronn terminology

There is no consensus concerning terminology in Gleicheniaceae, and several nomenclatural systems have been proposed (Table 1). We discuss here some terms related to Gleicheniaceae fronds and present a terminology having taxonomic interest that focuses on these structures. It is not our goal to present new terms, but rather to summarize those available, and propose a unified terminology for the most suitable descriptors.

Accessory branch: One of a pair of branches emerging opposite to the bifurcations present in *Dicranopteris* species (Holttum 1959, Andersen and Øllgaard 1996, 2001) (Figs 3C, 4A).

Branch: The axis usually arises from a pseudodichotomy (except in *S. moniliformis* and *S. simplex*) and is formed in pairs almost opposite, designated by their order (ultimate, penultimate, or antepenultimate). It may or may not have segments. The branches can be pinnatisect (as in *Sticherus*, *Dicranopteris*, and *Gleichenella*) or pinnate (as in *Diplopterygium* and *Gleichenia*) (Figs 4–6). Several studies (e.g. Nakai 1950, Andersen and Øllgaard 1996, 2001, Shaw and Ranker 2011) have used the term ‘pinna’ to refer to the different portions of the Gleicheniaceae frond (structure) but, as highlighted by Holttum (1957b), previous authors made clear distinctions between the pseudodichotomous and pinnate patterns. The use of the term ‘pinna’ is therefore inadequate in Gleicheniaceae frond terminology. We have adopted here the term ‘branch’, as used by Holttum (1957b) and Gonzales and Kessler (2011), defining it following Lellinger (2002), with modifications.

Bud: It is formed usually at an axis apex at the base of a pseudodichotomy, flanked by two branches (Figs 4, 5). Several authors have used different terms when referring to the ramification buds. Tryon and Tryon (1982) used the term ‘axillary bud’. However, Andersen and Øllgaard (1996) argued that there is an

issue with applying the axillary concept as defined by Lellinger (1989). According to them, the term ‘dormant bud’, as used by Lellinger (2002), is also unsatisfactory. This is because Lellinger (2002) proposed two terms to describe the structure: ‘dormant bud’ and ‘latent bud’, which correspond to different developmental stages. Additionally, Holttum (1957c) used the term ‘apical bud’ and Proctor (1985), similarly, used ‘terminal bud’, although these terms are not suitable as they consider only the main ramification and not the lateral branches. An anisotomic branch is produced on the secondary branches of *G. pectinata*, for example, and the buds in these cases are almost lateral (Mickel and Smith 2004). In that context, we propose using simply the term ‘bud’, as it avoids any definitional conflict. This usage was also proposed by Andersen and Øllgaard (1996), followed by Gonzales and Kessler (2011) and Lima and Salino (2018).

Lamina: The expanded portion of the frond, composed of the rachis and laminar tissue. It begins at the first primary bifurcation (following Lellinger 2002).

Midrib/Midvein: The central axis of a segment, from which secondary veins arise (modified after Lellinger 2002) (Figs 4, 5).

Petiole: The frond structure that connects the base of the lamina to its attachment point on the rhizome (Lellinger 2002) (Figs 4, 5).

Primary Bifurcation: The bifurcation of the main axis of the rachis in a pseudodichotomy, forming two lateral branches. Occasionally, with the breaking of bud dormancy, the main axis may elongate and fork again.

Pseudostipule: The pair of modified segments that cover the buds (following Lellinger [2002], with modifications). They can be simple, trifold, pectinate, or lobate (Figs 4, 5). This structure was called the aplebiae by Gonzales and Kessler (2011), based on a misinterpretation of the original definition of the term, but that was not followed by Kessler and Smith (2018).

Rachis: We apply the definition of Lellinger (2002) to the structure: ‘the principal axis of a pinnatifid or more decompound lamina’, although the pseudodichotomy results in the rachis form three axes (Figs 4, 5).

Secondary bifurcation: The bifurcation of the secondary axis of the rachis in a pseudodichotomy, forming lateral branches at the end of the rachis.

Secondary vein: A vein that arises from the midrib in the segment and forks from one to three times (Figs 3, 4).

Segment: The portion of a blade with a base that is fully adnate to the rachis, having a deep sinus on each side that extends more than two-thirds of the distance from the segment apex to the rachis (following Lellinger [2002], with modifications) (Figs 4, 5).

Soral chamber: Depressions in the abaxial surfaces of the segments have been reported in a few *Gleichenia* species, such as *G. inclusora* and *G. polypodioides* (see Lima *et al.* 2020).

Squamophores: Projections of the rhizome epidermis that bear peltate or basifixed scales (Andersen and Øllgaard 2001).

Indument

Two types of epidermal appendages are observed in Gleicheniaceae: hairs and scales. Early phylogenetic interpretations of the family assumed the existence of only two distinct lineages, one with hairs on the rhizomes (*Dicranopteris*, *Gleichenella*, and *Stromatopteris*) and the other with scales (*Diplopterygium*, *Gleichenia*, and *Sticherus*) (Gonzales and Kessler 2011). The topologies of later phylogenetic studies indicated that hairs are most probably homoplastic in the family (Lima *et al.* 2023) (Fig. 1). Scales are present on the rhizomes of *Diplopterygium*, *Gleichenia*, *Sticheropsis*, and *Sticherus* (Gonzales and Kessler 2011), and show great morphological variations, providing many of the most important characteristics for defining species as well as the relationships between them (Holttum 1957b).

Among the genera with scaly rhizomes, *Gleichenia* stands out by also having stellate hairs on the rhizomes. As described by Holttum (1959), *G. microphylla* has small scales with ciliate margins as well as stiff stellate hairs on its rhizome.

The rhizomes of *Diplopterygium* are covered exclusively by scales, which are usually appressed, brown, or castaneous, linear-lanceolate with entire, dentate, or ciliate margins, persistent or deciduous (Holttum 1959, Mickel and Smith 2004). Stellate hairs may be present on the petioles of young fronds of some Asian species; these structures may be persistent or caducous at maturity (Jin *et al.* 2013). Bud scales are usually largely ovate to lanceolate, white to yellowish or brown, with margins entire to ciliate, with a cordate base. Stellate hairs can also occur on the abaxial surface of the rachis (Holttum 1959, Mickel and Smith 2004).

Sticheropsis and *Sticherus* also have rhizomes exclusively covered by scales but lack stellate hairs on the petiole or rachis; some species, however, such as *Sticherus pruinosus*, can have hairs on the abaxial surfaces of the secondary veins of their segments (Tryon and Stolze 1989, Gonzales and Kessler 2011, Kesler and Smith 2018, Lima and Salino 2018). Gonzales (2003) did not classify these structures as hairs, but rather as reduced scales. We follow here the definition of Lellinger (2002) of scales and hairs, classifying these structures as hairs as they have only one row of cells at their base. According to Gonzales (2003), the scales of *Sticherus* can be linear, lanceolate, ovate, orbicular, rhomboid, or triangular, their base can be truncate, rounded, sagittate, cordate, or auriculate, and their apex can be aristate, mucronate, setose, or long-aristate (with a single apical hair, a single apical gland, or a tuft of several hairs). The margins may either be entire, ciliate or have short, stiff setae. The cilia and setae can vary in their length and thickness and can be straight or curved. The bud scales can also show a darkening of some of their cells; according to Gonzales and Kessler (2011), the darkening pattern has taxonomic value.

Dicranopteris, *Gleichenella*, and *Stromatopteris* have rhizomes covered exclusively by hairs (Tryon and Stolze 1989, Gonzales and Kessler 2011, Kessler and Smith 2018, Lima and Salino 2018). The rhizome hairs on *Dicranopteris* are stiff and red-brown, leaving a scabrous surface when they abrade; the bud hairs are usually linear, rigid, and red. Some species, such as *D. nervosa*, may have long, whitish to red hairs on the abaxial

surface. *D. flexuosa* often has globular glandular hairs on the secondary veins of the segments, while these glandular hairs are bacilliform in *D. rufinervis* (Lima and Salino 2018).

The rhizome of *Gleichenella* is covered by unbranched, deciduous, reddish-brown, septate hairs; catenate hairs may also be present. The buds have reddish linear hairs, and the abaxial surfaces of the segments have pedicellate stellate hairs (Lima and Salino 2018).

Stromatopteris bears unique types of dermal appendages. The youngest parts of the rhizome are covered by peltate scales (with the surfaces of each cell being thickened and convex) as well as long simple hairs (Holttum 1957b, Kramer 1990), usually called 'bristle-like hairs' in the literature (e.g. Kramer 1990, Gonzales and Kessler 2011). Only hairs are found on mature sections of the rhizome (Kramer 1990).

Spores

The spores of Gleicheniaceae are achlorophyllous, and may be tetrahedral with a trilete aperture, or ellipsoidal with a monolete aperture. Their surfaces may be smooth, scabrous-perforate, faveolate, microflaveolate, granulose, or even rugulose, and may have Ubish bodies (Harris 1955, Tryon and Lugardon 1991, Farfán-Santillán *et al.* 2016). The exine is usually thick, and this feature may be linked to reductions of spore viability over time in *Sticherus* (Haufler and Adams 1982).

Spore morphology in Gleicheniaceae was defined by Tryon and Lugardon (1991) as specialized, having an exospore flange on the proximal face of both trilete and monolete spores with a complex foliated substructure that forms only between the aperture and the flange. The walls of this substructure appear to be three-layered on the proximal face and two-layered between the flange and the distal pole (Tryon and Lugardon 1991).

AUTHOR CONTRIBUTIONS

All authors made a substantial contribution to the concept and design of the study, to data collection, analysis, and interpretation, writing and revising the manuscript, and adding intellectual content.

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CONFLICT OF INTEREST

None declared.

DATA AVAILABILITY

The data underlying this article will be shared on reasonable request to the corresponding author.

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