

INVITED SPECIAL ARTICLE

For the Special Issue: *The Tree of Death: The Role of Fossils in Resolving the Overall Pattern of Plant Phylogeny*

# Assessing the evolutionary history of the fern family Dipteridaceae (Gleicheniales) by incorporating both extant and extinct members in a combined phylogenetic study

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**PREMISE OF THE STUDY:** Dipteridaceae is a lineage of ferns that has existed from the early Mesozoic and is known for its extensive fossil record. By integrating information from all described extant and extinct genera into a single phylogenetic study, this paper aims to examine the taxonomy of the group on a whole and explore character evolution within the lineage across time.

**METHODS:** A morphological matrix of 51 characters was developed for 72 species (43 extinct and 29 extant) based on published information. Morphological characters were combined with nucleotide sequences for four chloroplast genes (*rbcl*, *atpA*, *atpB*, and *rps4*) for extant taxa, and combined parsimony analyses were conducted to infer evolutionary trends in the group.

**KEY RESULTS:** Dipteridaceae was found to be monophyletic and characterized by highly anastomosing minor veins forming a meshwork of areoles with free-included veinlets. Based on our analyses, we recognize six previously described genera (i.e., *Goeppertella*, *Thaumatopteris*, *Clathropteris*, *Digitopteris*, *Dipteris*, and *Cheiropleuria*) and one new genus (i.e., *Sewardalea*). Fossils currently described as *Dictyophyllum*, *Kenderlykia*, *Hausmannia*, and *Protorhipis* are ambiguously placed on the tree and are recognized as possibly unnatural morphogenera.

**CONCLUSIONS:** Overall, the evolutionary trend in Dipteridaceae has been toward increasing complexity in the venation pattern and laminal fusion. Only the *Hausmannia*-type frond with dichotomizing primary veins and relatively fused lamina persisted in the later part of the Mesozoic to the present. Within the crown group, we see evidence of re-radiation of frond forms in *Dipteris* and *Cheiropleuria*.

**KEY WORDS** dipterid ferns; frond evolution; Gleicheniales; leaf evolution; systematics; total evidence.

Dipteridaceae is one of three families in Gleicheniales (Kramer et al., 1990; Christenhusz et al., 2011; Pteridophyte Phylogeny Group [PPG] I, 2016), an early-diverging leptosporangiate fern lineage (Schuettelpelz and Pryer, 2007; Lehtonen, 2011; PPG I, 2016).

Most members of this family are large terrestrial ferns that colonize open areas, commonly forming dense thickets on exposed road cuts or cliffs (Holttum, 1954; Kramer et al., 1990; Gonzales and Kessler, 2011; T. Y. S. Choo, personal observation). Today, the

largest of the three families is Gleicheniaceae, which is composed of over 140 species in six extant genera and has a pantropical distribution (Holtum, 1954; Kramer et al., 1990; Christenhusz et al., 2011; Gonzales and Kessler, 2011). In contrast, extant Dipteridaceae and Matoniaceae are rare components of the extant flora, comprising only four genera and fewer than 12 species (Holtum, 1954; Kramer et al., 1990; Kato et al., 2001), and are mainly restricted to mid to high elevation areas in the warm tropics of the Asia-Pacific region (Holtum, 1954; Kramer et al., 1990).

One of the most distinctive features of Dipteridaceae is its venation pattern. Extant Dipteridaceae (i.e., *Dipteris* and *Cheiropleuria*) have a reticulated venation network with numerous internally directed veinlets (Seward and Dale, 1901; Bower, 1923; Bierhorst, 1971; Boyce, 2005). The family is also known for one of the highest vein densities ( $\sim 5 \text{ mm mm}^{-2}$ ) outside of the angiosperm clade (mean  $\sim 8 \text{ mm mm}^{-2}$ , but up to  $25 \text{ mm mm}^{-2}$ ), more than twice that of other ferns (mean  $\sim 1.5 \text{ mm mm}^{-2}$ ; Boyce et al., 2009). This hierarchical, reticulate venation pattern, coupled with other apomorphic characters such as the lack of indusia and sporangia with approximately vertical annuli (Seward and Dale, 1901; Bower, 1923; Bierhorst, 1971) led early botanists to consider *Dipteris* and *Cheiropleuria* as part of the derived Polypodiaceae (e.g., Blume, 1828; Hooker, 1853; Hooker and Baker, 1868).

In 1882, paleobotanist Charles René Zeiller first drew attention to the resemblance of fronds of *Dipteris* to certain fossil ferns of Mesozoic age (Zeiller, 1882; Seward and Dale, 1901). This observation spurred further investigation by paleobotanist A. C. Seward and botanist Elizabeth Dale, which led to the description of a new family, “Dipteridinae” (Seward, 1900a). In their seminal paper on the family, Seward and Dale (1901) detailed the characters that separated *Dipteris* from Polypodiaceae: an oblique annulus with no stomium, a solenostele, and a C-shaped (or horseshoe-shaped) petiolar vascular strand. Seward and Dale (1901) also placed several fossil genera (i.e., *Dictyophyllum*, *Clathropteris*, *Thaumatopteris*, *Camptopteris*, *Hausmannia*, and *Protorhipis*) that were prominent across the globe in the Late Triassic and Early Jurassic in Dipteridaceae (see also Corsin and Waterlot, 1979; Wing and Sues, 1992; Tidwell and Ash, 1994).

The advent of molecular phylogenies resolved many of the previously unclear relationships between the major fern groups. Extant Dipteridaceae were firmly placed within the early-diverging Gleicheniales group (e.g., Pryer et al., 2001, 2004; Schneider et al., 2004; Schuettpelz and Pryer, 2007; Lehtonen, 2011; PPG I, 2016), making it apparent that the similar venation and soral characters in extant members of Dipteridaceae and Polypodiaceae were a case of convergent evolution. The relationships between the various extinct and extant genera within Dipteridaceae are poorly understood. Over the years, numerous Mesozoic fossils, many of which are merely fragments of sterile fronds, have been assigned to the family on the basis of the distinctive dipterid venation pattern (e.g., Zeiller, 1903; Nathorst, 1906b; Berry, 1918; Oishi and Yamasita, 1936; Frenguelli, 1941; Harris, 1961; Corsin and Waterlot, 1979; Webb, 1982; Cantrill, 1995; Stockey et al., 2006; Bomfleur and Kerp, 2010; Kustatscher and van Konijnenburg-van Cittert, 2011; Choo et al., 2016). Several authors have discussed the taxonomy of the group and proposed different classification systems (e.g., Seward and Dale, 1901; Nathorst, 1906b; Oishi and Yamasita, 1936; Harris, 1961; Herbst, 1992); however, none of the taxonomic proposals have been based on explicit phylogenetic analyses. Today, most workers follow the classification scheme proposed by Oishi and Yamasita (1936), which mostly

agrees with that of Seward and Dale (1901), except for the addition of *Goepfertella* for highly dissected frond fragments with the characteristic Dipteridaceae venation, and the recognition of *Protorhipis* as a synonym of *Hausmannia* (Oishi and Yamasita, 1936). Since then, another genus *Kenderlykia* was described for a single fossil species from Kazakhstan (Turutanova-Ketova, 1962), although few workers have since used that name, and more recently, a new genus *Digitopteris* was described for a fossil species from Austria (Pott et al., 2018). Overall, some confusion remains with regard to generic delimitations because various diagnostic characters are not clearly defined and/or fall on a spectrum that overlap and intergrade with another (e.g., *Dictyophyllum* and *Thaumatopteris*; see Nathorst, 1906b; Harris, 1961; Webb, 1982). There are also certain nomenclatural issues (e.g., *Camptopteris*; see Nathorst, 1906b).

This paper takes an integrative approach to studying the systematics of Dipteridaceae. By incorporating both extinct and extant members of a family in a single cladistic study, we provide the first testable phylogenetic hypothesis of the evolution of the family. The phylogenetic trees are then used to clarify the taxonomy of the group and demonstrate the morphological development and evolutionary history of this clade over the past 250 million years.

## MATERIALS AND METHODS

### Taxonomic sampling

Thirty-eight (33 extinct and 5 extant) Dipteridaceae species, 9 (7 extinct and 2 extant) Matoniaceae species, 9 (3 extinct and 6 extant) Gleicheniaceae species, and 16 (extant only) other outgroup taxa were chosen for the study (Appendix S1 for full list and references; see the Supplemental Data with this article). All the extinct genera were represented by the type species, and as many informative non-type species as possible. Outgroups to Gleicheniales represented members from all the major fern lineages (see Christenhusz et al., 2011; Lehtonen, 2011) including several other reticulate-veined ferns (see Boyce et al., 2009).

### Terminology

Although members of Dipteridaceae share the same basic frond architectural plan, past authors have used different terms for describing the various parts of the frond (e.g., Seward and Dale, 1901; Nathorst, 1906b; Oishi and Yamasita, 1936; Holtum, 1954; Rees, 1993). To avoid confusion, we have adopted the following set of descriptive terms, which can be used consistently across different Dipteridaceae forms. The stipe dichotomizes into two rachial axes termed rachial arms. Each rachial arm dichotomizes unequally and catadromously, giving rise to primary segments (i.e., “pinnae” of Oishi and Yamasita, 1936; “lobes” of Holtum, 1954; “frond members” of Rees, 1993). The main vein of each primary segment is termed the primary vein, which can be simple or dichotomizing. Subsequent orders of veins are named accordingly. Specific areoles are referred to by specifying the surrounding vein orders (e.g., areoles bounded by secondary and tertiary veins), and the areoles bounded by the highest order veins are termed ultimate areoles.

### Scoring of characters

A matrix of 51 morphological characters was developed (Appendix 1). As most known Dipteridaceae fossils are preserved

as compressions and impressions, the majority of characters are based on directly observable morphological features, with few anatomical or developmental characters used. Gametophytic characters were also excluded because this life stage is not usually captured in the fossil record. Where possible, complex characters were broken down into several characters representing likely distinct biological processes (e.g., the presence/absence of peltate indusia was broken down into two separate characters, the first for presence/absence of indusia, regardless of type because all true indusia are taken to be homologous structures, followed by a second character on the type of indusium, as opposed to a single character with three character states of no indusium, peltate indusium, nonpeltate indusium), and quantitative characters were divided into roughly equal ranges that best represented the total variation. All taxa were scored based on published information, and the full morphological matrix can be accessed on Morphobank (<http://morphobank.org/permalink/?P1192>). For fossil species, emphasis was placed on the re-examination of photographs, figures, and descriptions used in the original protologues. Specimens from the Paleobotanical Collection of the Museo Paleontológico Egidio Feruglio (Trelew, Chubut) were also examined for taxa from the Early Jurassic of Patagonia (e.g., Choo et al., 2016). For the extant species, herbarium materials from the L. H. Bailey Hortorium Herbarium (BH) were examined. Photographs of extant *Dipteris* were taken by the primary author from the Western Catchment of Singapore (1.357°N, 103.643°E), and two sites in Sarawak, Malaysia—Lambir Hills National Park (4.204°N, 114.043°E) and Mulu National Park (4.051°N, 114.915°E).

As all published *Goeppertella* fossils are frond fragments (e.g., Schenk, 1867; Zeiller, 1903; Oishi, 1940; Oishi and Huzioka, 1941; Herbst, 2000; Schweitzer et al., 2009), it is impossible to assign orders of veins (and hence to score many of the vegetative characters) with certainty. In this context, three separate morphological matrices were created: (1) All\_genera, with *Goeppertella* venation characters scored as unknown and only the two *Goeppertella* species with fertile characters included; (2) Reduced, with all *Goeppertella* species excluded; (3) Reconstructed, with *Goeppertella* species (two without fertile characters) included and assigned vein orders based on the reconstruction of Rees (1993). All specimens of *Hausmannia* and *Protorhipis* that are unknown for spore type were scored the same as other *Hausmannia* and *Protorhipis* specimens (i.e., trilete spores).

All characters, regardless of the number of character states or whether they were ordered or unordered, were weighted equally. Where homologies between the ingroup and more distantly related groups were unclear (e.g., the numeric order of veins in fronds with vastly different architectural plans), Dipteridaceae fossils were taken as the reference point and outgroups were scored as unknown to maximize the comparable information within the ingroup.

All molecular characters were scored as missing for all fossils. For the extant taxa, DNA sequences of four chloroplast genes (*rbcl*, *atpA*, *atpB*, *rps4*) were downloaded from GenBank (Benson et al., 2012; See Appendix S1 for GenBank references).

### Sequence alignment and phylogenetic analyses

All four genes were aligned separately using MUSCLE (Edgar, 2004). The aligned gene sequences were concatenated and mopped for non-parsimony informative characters using WinClada (Nixon, 2015), leaving a final molecular matrix of 2202 parsimony informative molecular characters. The three alternative morphological data sets (see above) were concatenated with the molecular data set

using WinClada to form the final three combined data sets used in the analyses.

Parsimony analyses were performed using TNT (Goloboff et al., 2008). In the TNT analyses, 200 sets of 200 iterations using a 10% perturbation of characters were used for the ratchet analyses (Nixon, 1999), and default values for drift, sectorial search, and tree fusion were used. WinClada was used to view all the most parsimonious trees and to identify synapomorphies by optimizing unambiguous characters onto the strict consensus tree.

Bootstrap analyses were not conducted as fossil species have no molecular information and, depending on the quality and type of material preserved, are often only scored for a subset of the total number of morphological characters. Support values for fossil clades are thus expected to be extremely low (clades can theoretically be supported by a single morphological character), rendering bootstrap analyses meaningless.

## RESULTS

For the All\_genera data set, 178 most parsimonious trees of 81,308 steps, 0.58 RI and 0.47 CI were found, and the strict consensus tree is shown in Fig. 1. The Reduced data set yielded 168 most parsimonious trees of 81,308 steps, 0.58 RI and 0.47 CI, and the Reconstructed data set yielded 415 most parsimonious trees of 81,319 steps, 0.58 RI and 0.47 CI (Fig. 2).

The overall topologies of all three trees are concordant with published trees (Schuettpelz and Pryer, 2007; Lehtonen, 2011; PPG I, 2016; see Figs. 1, 2), with the Gleicheniales falling out in its expected position as an early-diverging leptosporangiate lineage. The analyses place all Dipteridaceae fossils within a monophyletic clade, and all extant Matoniaceae and most Matoniaceae fossils are placed in a clade that is sister to Dipteridaceae. *Selenocarpus* is placed outside the Dipteridaceae and Matoniaceae s.s. clade, making Matoniaceae as is currently defined, paraphyletic. The Dipteridaceae and Matoniaceae s.l. clade is sister to a monophyletic Gleicheniaceae clade.

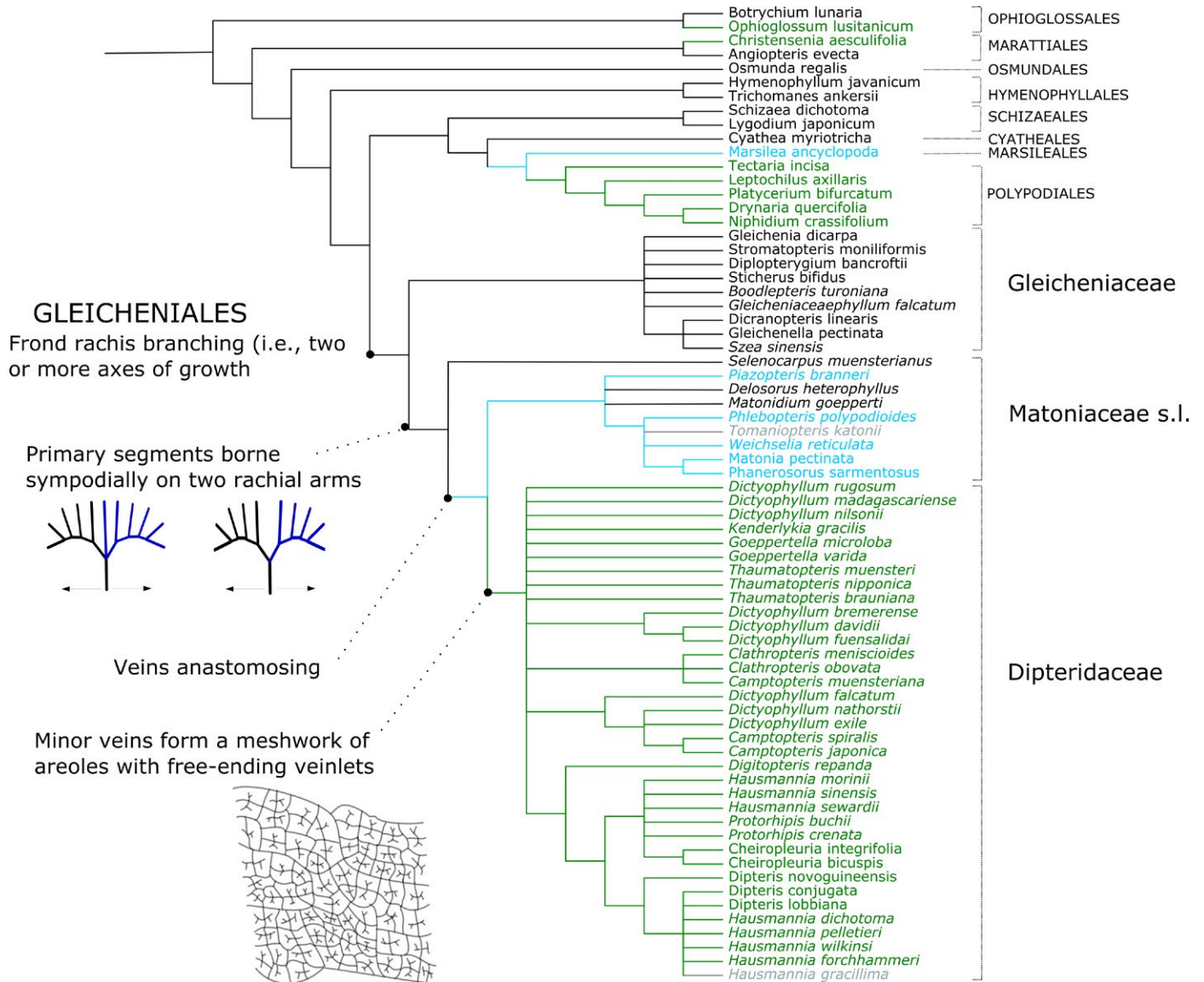
Within Dipteridaceae, the following clades were recovered in all three trees: *Clathropteris*, *Sewardalea* (*Camptopteris* sensu Nathorst (1906b), and some *Dictyophyllum* species); a clade including *Digitopteris*, *Hausmannia*, *Protorhipis*, *Dipteris*, and *Cheiropleuria*; *Dipteris* (with the inclusion of *Hausmannia* fossils in two of three of the analyses) and *Cheiropleuria* (Figs. 1, 2).

*Goeppertella* came out as a distinct clade in the Reconstructed data set (Fig. 2) but not in the All\_genera data set (Fig. 1), due largely to uncertain assignment of venation characters. This basal polytomy of the All\_genera data set consisted of *Goeppertella*, *Clathropteris*, *Sewardalea*, various *Dictyophyllum* species, and all *Thaumatopteris* species. *Dictyophyllum* as currently recognized is polyphyletic. Some members fall into the *Sewardalea* clade, whereas others (including the type *D. rugosum*) are part of this large polytomy.

In the Reduced data set, *Thaumatopteris* was placed as the earliest-diverging Dipteridaceae lineage; followed by *Sewardalea*; followed by a polytomy including *Clathropteris*, *Kenderlykia*, various *Dictyophyllum* species, and a clade composed of *Digitopteris* and the crown clade (i.e., *Hausmannia*, *Protorhipis*, *Dipteris*, and *Cheiropleuria*).

*Digitopteris* was placed as sister to the crown clade in all three trees. In the All\_genera and Reduced data sets (Figs. 1, 2), some *Hausmannia* and *Protorhipis* species (including the type *P. buchii*)





**FIGURE 1.** Strict consensus tree obtained from the All\_genera data set. Major clades and important frond architectural synapomorphies within Gleicheniales are illustrated. Fossil specimens are indicated by italics, and taxa are colored according to venation type: free veins (black); anastomosing veins without free-ending veinlets (blue); anastomosing veins with free-ending veinlets (green); unknown (grey). For *Goepertella*, only specimens with both sterile and fertile characters were included, and the most conservative scoring regarding vein orders was used (see Methods).

fall out in a polytomy with *Cheiropleuria* (*Cheiropleuria* s.l.), whereas others (including the type *H. dichotoma*) nest within *Dipteris* on the basis of frond dissection levels. In the Reconstructed data set, fossils that were nested in *Dipteris* in the All-genera and Reduced trees move to either a polytomy at the base of the crown clade with *Dipteris* and *Cheiropleuria* s.l., or into the polytomy with *Cheiropleuria* (Fig. 2).

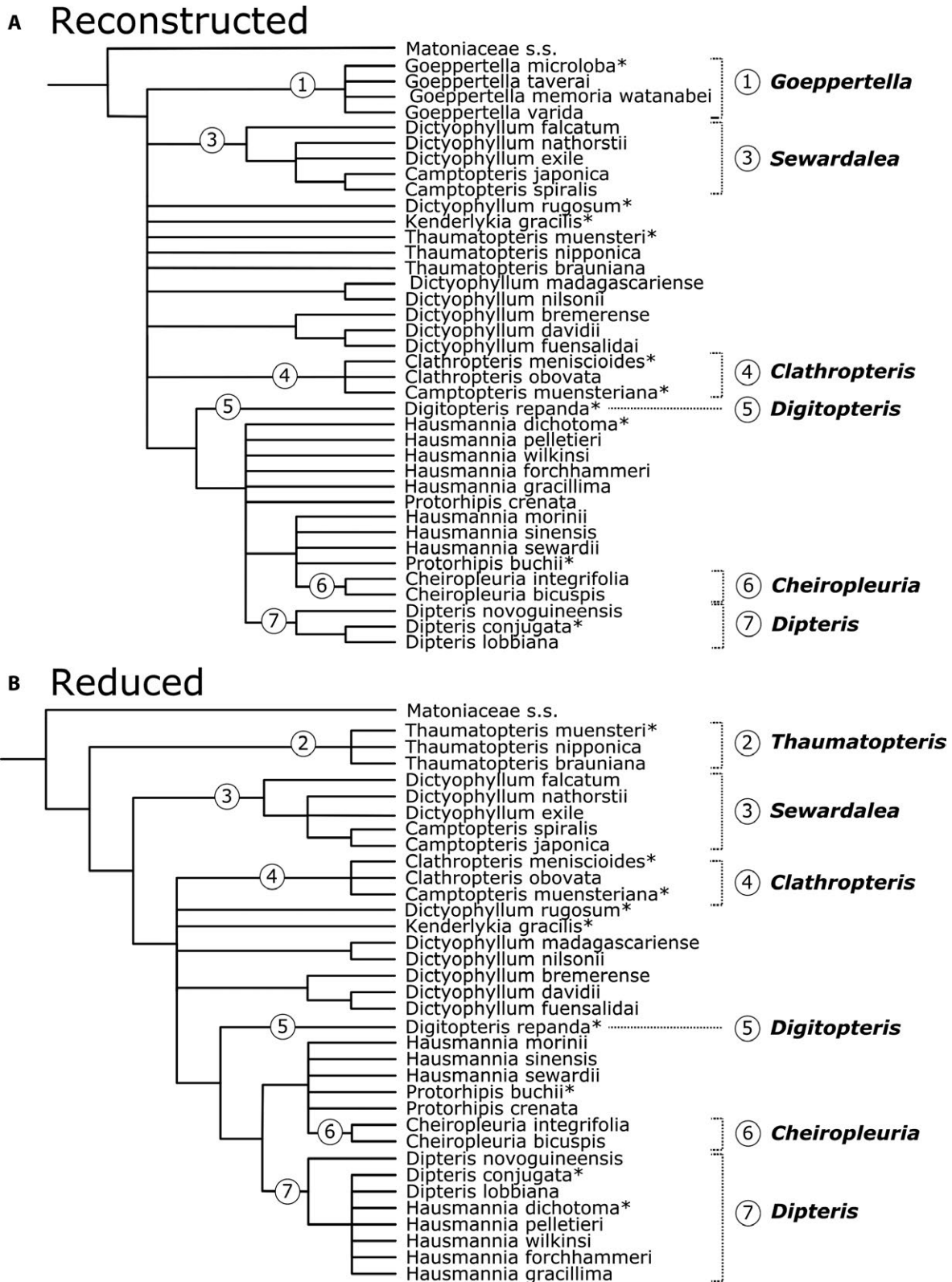
**DISCUSSION**

**Phylogeny and character evolution of the Gleicheniales**

Incorporating fossils into our understanding of systematics is always desirable. However, for lineages such as Dipteridaceae, which

have a very early origin and where extant members represent only a very small proportion of the overall diversity within the family, considering the total evidence provided by both extinct and extant taxa is imperative in understanding the morphological evolution of the group. This study is the first to combine a large number of extinct and extant Gleicheniales members in a single cladistic study, and the resultant phylogenetic trees provide an insightful character-based look into the evolution of Gleicheniales as a whole, and Dipteridaceae in particular.

Overall, most fossils that have been ascribed to the various families in Gleicheniales are recovered within their respective families (Figs. 1, 2). All members of this monophyletic order share the synapomorphy of fronds with a branching main rachis, resulting in the frond having two or more main axes of growth, whereas most outgroups have fronds where the main rachis remains unbranched



**FIGURE 2.** Phylogenies of Dipteridaceae with clades corresponding to the seven genera recognized in this paper numbered and labeled. Type species of genera are indicated by an asterisk. (A) Strict consensus tree obtained using the Reconstructed data set, where *Goepfertella* vein orders are scored based on the reconstruction of Rees (1993), and all *Hausmannia* and *Protorhipis* fossils are scored as having trilete spores. (B) Strict consensus tree obtained using the Reduced data set, where *Goepfertella* is excluded and all *Hausmannia* and *Protorhipis* fossils are scored based on known information (i.e., either trilete or unknown for spore type). Unnatural groups “*Dictyophyllum*” and “*Hausmannia*” are also indicated.

and the frond has a single main axis of growth. All Dipteridaceae and Matoniaceae fossils fall into a monophyletic clade that is sister to Gleicheniaceae and is characterized by a distinctive frond architectural plan. In particular, the stipe dichotomizes into two rachial arms, which themselves branch catadromously, giving rise to anadromous primary segments and resulting in a pedate frond. This synapomorphy is key to the interpretation of the incomplete fronds of *Goepfertella*, as discussed below.

Unlike Gleicheniaceae and Dipteridaceae, which come out in our analyses as monophyletic, the inclusion of various fossils in the analysis suggests that Matoniaceae, as currently defined, is paraphyletic. The monotypic fossil genus *Selenocarpus* is classically considered to be a member of Matoniaceae, but is placed as sister to the clade containing the remaining Matoniaceae and Dipteridaceae in our analyses, as it has a unique combination of plesiomorphic and derived features. In addition to plesiomorphic characters, such as free veins and exindusiate sori (Schenk, 1867; Czier, 1994) *Selenocarpus* also has unique crescent-shaped sori, compared with circular sori in the rest of Matoniaceae (Czier, 1994; Nagalingum and Cantrill, 2006). It should be noted that although no other Matoniaceae fossil in our analyses has both the plesiomorphic characters of *Selenocarpus*, some Matoniaceae fossils (e.g., *Delosorus heterophyllus* and *Matonidium goeperti*) have free veins (Schenk, 1871; Skog, 1988) and others (e.g., *Piazopteris branmeri* and *Phlebopteris smithii*) lack the typical peltate indusium typical of most Matoniaceae (Ash, 1972; Ash et al., 1982). However, these specific examples of exindusiate species differ from *Selenocarpus* in that both have sori with a prominent central receptacle (Ash, 1972; Ash et al., 1982), which could be interpreted as a “protoindusium” or the remnant of an indusium that was shed at maturity and, hence, not preserved (Ash et al., 1982).

Since the focus of our study was on Dipteridaceae, sampling of the Matoniaceae was broad but not deep, and few Matoniaceae-specific characters were included. As such, we view the current placement of *Selenocarpus* as merely suggestive that a greater, in-depth study of the fossil genera of Matoniaceae is necessary. Whether or not *Selenocarpus* is eventually found to be in its own monotypic family outside of the Matoniaceae or within a monophyletic Matoniaceae, it is unlikely to change the overall relationship of Dipteridaceae to the majority of Matoniaceae (Matoniaceae s.s. in our analyses), or of the infrageneric relationships within Dipteridaceae.

### Phylogeny and character evolution of Dipteridaceae

Dipteridaceae was found to be monophyletic and is diagnosed by highly anastomosing minor veins that form a meshwork of areoles with free-included veinlets across the frond lamina. Within Dipteridaceae, the relationships between groups are only partially resolved. This result is not unexpected, as our analysis includes a very large number of fossil species, many of which have ambiguous or missing characters.

Nevertheless, even in the All\_genera analysis, several clades are recovered (i.e., *Clathropteris*, *Sewardalea*, the clade comprising *Digitopteris* and the crown clade, and *Cheiropleuria*). When the trees from the Reduced and Reconstructed data sets and character optimizations are considered, we are able to piece together a reasonable hypothesis on the evolution of the family as a whole (Fig. 3), which is largely congruent with the classification scheme of Oishi and Yamasita (1936) and the stratigraphic record of the fossils (see Oishi and Yamasita, 1936). We recognize five existing genera on the

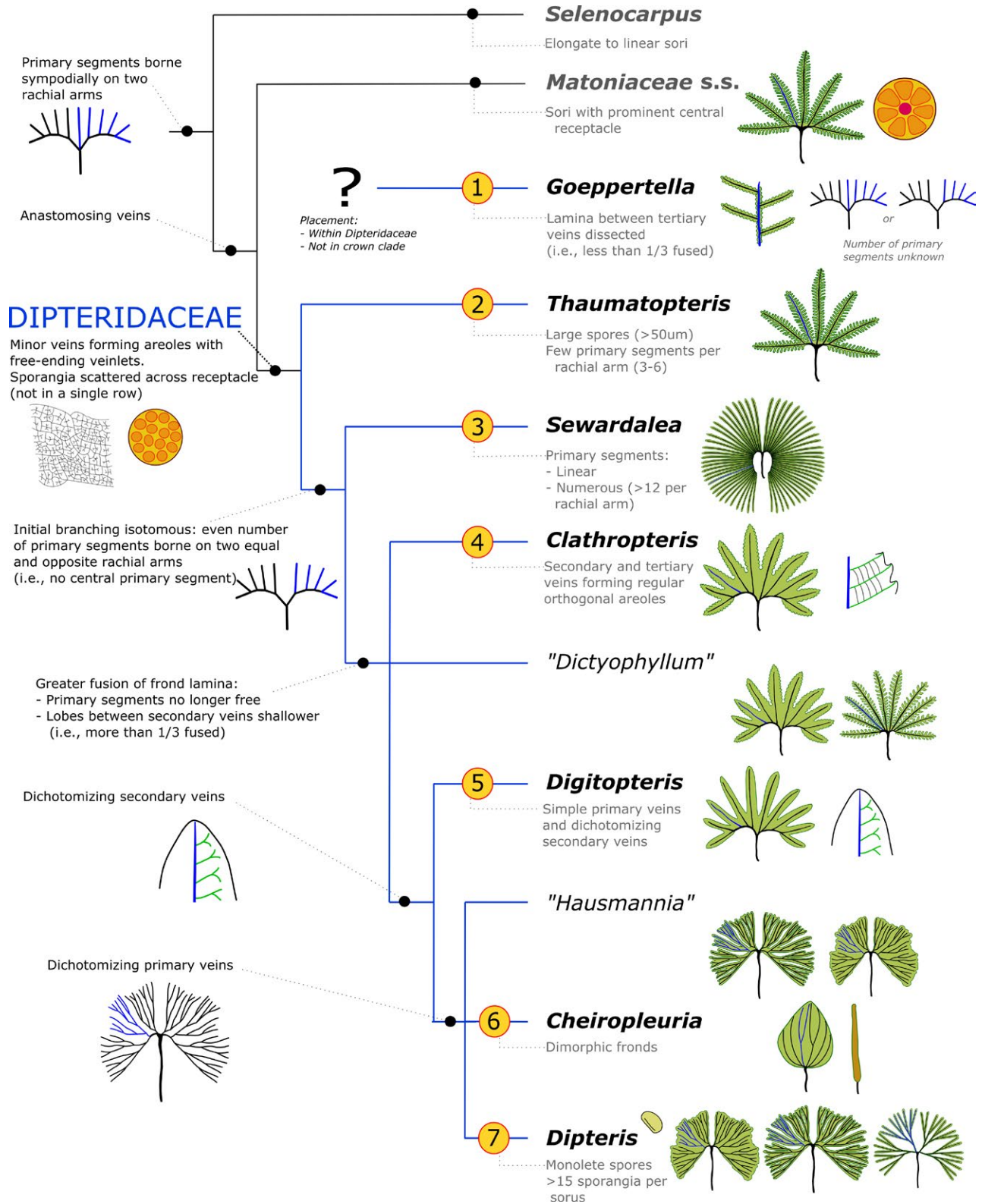
basis of clear synapomorphic traits: *Goepfertella*, *Thaumatopteris*, *Clathropteris*, *Dipteris*, and *Cheiropleuria*. We recognize the fossil currently described as *Digitopteris* (Pott et al., 2018) to be in its own unique genus and holding an intermediate position between the basal and crown groups in Dipteridaceae (Figs. 1, 2). We also describe the new genus *Sewardalea*, which can be seen as an expanded *Camptopteris* sensu Nathorst, but is given a new name and type because continuing to use the name *Camptopteris* would go against nomenclatural rules (see section on *Sewardalea* below). Fossils currently described as *Dictyophyllum*, *Kenderlykia*, *Hausmannia*, and *Protorhipis* cannot be resolved into clear clades. Hence, until such time as more characters are discovered that either place these fossils into existing clades or enable their separation into their own clades, we propose that workers continue to use the existing names, but be very mindful that these morphogenera likely do not represent natural groups.

Despite the ambiguity in the overall phylogeny of Dipteridaceae, general evolutionary trends can be detected. Rachial architecture switches from an anisotomous initial branching resulting in two unequal rachial arms with a central primary segment (as in Matoniaceae and *Thaumatopteris*), to an isotomous initial branching resulting in the typical bilaterally equal fronds represented in the rest of Dipteridaceae. The main veins of the fronds also become more complex, with first the secondary, and then the primary veins, changing from a simple to dichotomizing form. There also appears to be a general trend of increasing fusion of the frond lamina segments: the earlier-diverging lineages show a greater degree of dissection (e.g., *Thaumatopteris* with deep lobes between secondary veins, *Sewardalea* with primary segments that are free to the base); the fossils in the middle of the trees have a more transitional form (e.g., *Clathropteris* and many *Dictyophyllum* fossils have primary segments that are up to 1/3 fused at the base and have shallow lobes between secondary veins); and the crown group consists of species with highly fused frond lamina (e.g., *Cheiropleuria*, *Dipteris novoguineensis* and many *Hausmannia* species). Interestingly, while there exist many dissected forms within *Dipteris* and *Hausmannia* (e.g., *D. lobbiana*, *D. conjugata*, and *H. dichotoma*), these laminal “segments” are derived from lobing both within and between primary segments (Fig. 4), which is different from other dissected fossil genera (e.g., *Goepfertella* and *Thaumatopteris*; see Fig. 3).

### Evolutionary history of Dipteridaceae

Put together, the phylogeny, fossil record, and optimization of characters provide a much more complete picture of the evolutionary history of the family. The earliest-known Dipteridaceae fossils are from the Middle Triassic (e.g., *Dictyophyllum* and *Thaumatopteris*; Webb, 1982; Kustatscher et al., 2012), suggesting that the origin of the family likely dates back to the Early Triassic or Late Paleozoic (Tidwell and Ash, 1994). The family then reached its peak in generic diversity in the Late Triassic to Early Jurassic, and fossils of all six genera recognized in this paper have been found in Mesozoic deposits across the world (e.g., Zeiller, 1903; Nathorst, 1906b; Berry, 1918; Oishi and Yamasita, 1936; Frenguelli, 1941; Harris, 1961; Corsin and Waterlot, 1979; Stockey et al., 2006; Turner et al., 2009; Bomfleur and Kerp, 2010; Zhou et al., 2015; Choo et al., 2016). Paleoecological reconstructions show that Dipteridaceae fossil species occupied moist localities in the temperate-warm to tropical zones across the world (van Konijnenburg-van Cittert, 2002), and at least some species were very large, formed monotypic





**FIGURE 3.** Inferred evolution of characters in Dipteridaceae. Composite tree summarizes the possible relationships between the genera recognized in this paper (numbered 1–7) and outgroup clades (*Matoniaceae s.s.* and *Selenocarpus*) as inferred by the different phylogenetic analyses. Unambiguous synapomorphies are mapped and labeled, and generalized leaf forms and important characters are illustrated. For all illustrations, the primary vein of a single primary segment is highlighted in blue to indicate homology across different leaf forms. Simplified representations of the morphogenera *Dictyophyllum*, *Kenderlykia*, *Protorhipis*, and *Hausmannia* are included in the tree, but current data suggest these are unnatural groups.



**FIGURE 4.** Photographs of extant Dipteridaceae. (A) *Dipteris conjugata* growing in the Western Catchment of Singapore. (B) *D. conjugata* frond. (C) *D. lobbiana* growing in the Lambir Hills National Park, Sarawak, Malaysia. (D) *D. lobbiana* frond. (E) *D. novoguineensis* growing on the summit of Gunung Mulu, Sarawak, Malaysia. (F) *D. novoguineensis* frond. (G) *Cheiropleuria bicuspis* growing along the summit trail of Gunung Mulu, Sarawak, Malaysia. (H) Single fertile frond and two sterile fronds of *C. bicuspis*.

colonies and were likely a prominent part of disturbed, floodplains of the Mesozoic (Stockey et al., 2006; Gee and Kranz, 2010; Choo et al., 2016).

Past physiological studies have linked vein density with transpiration rates and carbon assimilation (Brodribb et al., 2007; Boyce et al., 2009). Given that Dipteridaceae had some of the highest vein densities outside of the angiosperm clade (Boyce, 2005; Boyce et al., 2009), it seems likely that Dipteridaceae had a competitive edge in open, wet environments, allowing the family to become a prominent part of the vegetation. The overall trends of increasing venation complexity and progressive fusion of lamina within Dipteridaceae could possibly have been driven by the competitive advantage of a higher photosynthetic capacity brought about by maximizing frond laminal area through greater fusion of parts.

The Cretaceous and Paleogene fossil record of Dipteridaceae is sparse and consists only of various species of *Hausmannia* (Cantrill, 1995; Stockey et al., 2006). The decline in the family has been attributed to the increasing aridity brought about during the onset of the Late Jurassic and Cretaceous (Skog, 2001; van Konijnenburg-van Cittert, 2002; Choo et al., 2016) and the reduction of open habitats brought about by the rise in angiosperms in the Cretaceous (Moran, 2004). However, the story behind the family's decline is likely to be more complex because it is unlikely that increasing aridity affected the entire globe equally. Spore evidence from Australia also suggests that Dipteridaceae had already declined by the Late Jurassic, before the rise of the angiosperms, and maintained very low and stable levels of relative diversity and abundance throughout the Cretaceous (Nagalingum et al., 2002). Nevertheless, under hot and dry environments, large, highly irrigated fronds would have been disadvantageous, and

most Dipteridaceae species would have been unlikely to tolerate such conditions. Why the *Hausmannia*-form with dichotomizing primary veins survived is unclear. However, the fact that many *Hausmannia* fossils recovered from this period are very small (e.g., Walkom, 1928; Sukh-Dev, 1972; Stockey et al., 2006) suggests that smaller, tougher fronds were selected for. The two extant genera, *Dipteris* and *Cheiropleuria*, seem to have subsequently evolved from this relictual lineage, and the diversity in frond type evident in the extant lineages are all built on the basic *Hausmannia* frond architectural pattern (Figs. 3, 4).

Although the highly irrigated fronds of Dipteridaceae likely had a growth advantage over many non-angiosperm plants during the Jurassic, extant *Dipteris* and *Cheiropleuria* are relatively slow-growing when compared to the fast-growing angiosperms with extremely high vein densities of today's flora (Boyce et al., 2009). As such, *Dipteris* and *Cheiropleuria* are only minor parts of extant floras and are mostly restricted to open patches in the higher elevations of the Asia-Pacific tropics (Holttum, 1954; Kramer et al., 1990) where warm temperatures and constant humidity allow them to thrive. In terms of gross morphology, both these extant lineages have continued to diversify, but in seemingly opposite directions (Fig. 3). *Cheiropleuria* has remained relatively small and has an even greater degree of laminal fusion than the *Hausmannia* frond type, with sterile fronds appearing simple, lobed, or trilobed (Kato et al., 2001). *Dipteris* species have a range of frond dissection levels (Fig. 4). The high-elevation *D. novoguineensis* is small, bipartite, and the lamina on each frond half almost completely fused, much like many *Hausmannia* species (Fig. 4.). The most extreme level of laminal dissection occurs in *D. lobbiana*, where the frond lamina is restricted to just a thin layer flanking the dichotomizing primary



veins (Fig. 4). *Dipteris lobbiana* is a rheophyte, and the dissected leaf form is typical of plants growing in similar environments to minimize damage inflicted by fast-flowing water (Kato and Imaichi, 1992). Other species of *Dipteris* (i.e., *D. conjugata*, *D. quinquefurcata*, *D. wallichii*, *D. nieuwenhuisii*, and *D. chinensis*) have laminal dissection levels that fall within this spectrum.

### Synopsis of the generic classification of Dipteridaceae

The following synopsis highlights the diagnostic characters (i.e., the most important characters that distinguish a taxon from other closely related taxa) of the various groups within Dipteridaceae, as derived from the distribution of characters in this phylogenetic study. Other, nondiagnostic characters are excluded from the descriptions.

#### Dipteridaceae Seward

**Diagnosis**—Fronds pedate, the stipe dichotomizing into two rachial arms that branch catadromously, bearing few to numerous anadromous primary segments. Venation highly ordered, minor veins anastomosing copiously to form a meshwork of ultimate areoles with free-included veinlets. Sporangia short stalked, with an oblique annulus.

##### 1. *Goepfertella* Oishi & Yamasita

**Type**—*Goepfertella microloba* (Schenk) Oishi & Yamasita

**Diagnosis**—Frond lamina highly dissected; the degree of dissection between tertiary veins at least 2/3 the total length of the tertiary vein.

**Remarks**—Despite the absence of gross morphological characters, minor vein and reproductive characters are sufficient to place fossil species of *Goepfertella* (including the type *G. microloba*) into Dipteridaceae (Fig. 1). By optimizing characters onto the phylogenetic tree (Fig. 1), we can infer that *Goepfertella* had the synapomorphic pedate frond architecture of the Dipteridaceae and Matoniaceae s.l. clade, similar to the reconstruction of Rees (1993), although key characters, such as whether or not the initial dichotomy was isotomous or anisotomous, and number of primary segments per rachial arm, are still unknown (Fig. 3). This interpretation would mean that the “bipinnate” fossils of *Goepfertella* represent fragments of primary segments, and the central vein (or rachis) in each *Goepfertella* fossil is homologous to the primary vein in other Dipteridaceae fossils (Fig. 3). When *Goepfertella* fossil fragments are re-scored based on this reconstruction, all *Goepfertella* specimens, even those without reproductive characters (e.g., *G. taverai* and *G. memoria-watanabei*), are recovered as a monophyletic clade within Dipteridaceae (Fig. 2A). We, thus, recognize the clade *Goepfertella* based on the synapomorphy of frond lamina having a degree of dissection between tertiary veins of 2/3 or more, which is consistent with the original description of the genus by Oishi and Yamasita (1936).

##### 2. *Thaumatopteris* Goepfert

**Type**—*Thaumatopteris muensteri* Goepfert

**Diagnosis**—Initial stipe dichotomy anisotomous, forming two unequal rachial arms with a central primary segment. Frond lamina

dissected, forming deep lobes between secondary veins (more than 2/3 the length of the secondary vein). Spores large (>50 µm).

**Remarks**—No Dipteridaceae genus has been met with as much controversy as *Thaumatopteris*, and Webb (1982) provided a very good overview of the history of the genus and its confused relations with *Dictyophyllum*. Authors have held differing views on the validity of *Thaumatopteris*; some considered it indistinguishable from *Dictyophyllum* (e.g., Schenk, 1867; Seward, 1900b; Seward and Dale, 1901; Webb, 1982; Guignard et al., 2009), whereas others considered *Thaumatopteris* and *Dictyophyllum* different enough to be recognized as separate genera (e.g., Nathorst, 1907; Oishi and Yamasita, 1936; Harris, 1961; Cleal and Rees, 2003) or *Thaumatopteris* as a subgenus of *Dictyophyllum* (Herbst, 1992). Characters that have been used to distinguish the two genera include variation in laminal dissection, arrangement of primary segments, sporangial diameter, and spore number (Oishi and Yamasita, 1936; Harris, 1961; Schweitzer, 1978; Webb, 1982; Cleal and Rees, 2003; Guignard et al., 2009). However, all these characters are problematic because the variation exhibited by fossils either falls into a continuum or the characters are not readily observable in most fossils (Webb, 1982). More importantly, many of the generic descriptions of both *Thaumatopteris* and *Dictyophyllum* are invalid as they were based on groups that excluded the type specimens (e.g., Nathorst, 1878, 1907; Harris, 1931; Oishi and Yamasita, 1936; see Webb, 1982).

Upon re-examination of the original protologue of the type species, *T. muensteri*, we found that the *T. muensteri* as illustrated by Goepfert (1841) has an anisotomous initial branch, resulting in an odd number of primary segments. This character is represented in the picture of *T. muensteri* of Seward (1910) and descriptions and illustrations of other *Thaumatopteris* fossils where gross morphology is preserved (e.g., Oishi, 1932; Schweitzer, 1978). This plesiomorphic character and the character of large spores (>50 µm in diameter) define the *Thaumatopteris* clade in our analysis of the Reduced data set. Unfortunately, if these characters are not preserved in a fossil, it is impossible to assign it with certainty to *Thaumatopteris*. One character that is shared among the members in our *Thaumatopteris* clade, but is not diagnostic on its own as it is also shared with other *Dictyophyllum* specimens, is a relatively dissected frond, the lamina between secondary veins lobing to 2/3 or more the total length of the vein.

##### 3. *Sewardalea* Choo & Escapa gen. nov.

**Type**—*Sewardalea spiralis* (Nathorst) Choo & Escapa comb. nov.

Basionym: *Camptopteris spiralis* Nathorst

**Etymology**—This name honors Sir Albert Charles Seward (1863–1941) and Elizabeth Dale (1868–1956) for their seminal paper on Dipteridaceae. Sir Albert Charles Seward was a renowned British paleobotanist who was working at the University of Cambridge at the time of his study of Dipteridaceae. Elizabeth Dale was a botanist at the same university and would have provided important contributions to that paper on understanding and drawing links between the fossil and extant genera.

**Diagnosis**—Stipe with an isotomous initial dichotomy. Two equal and opposite rachial arms bearing numerous (>12, but up to over 100) primary segments. Primary segments linear and free.

**Remarks**—This clade contains species that traditionally have been placed in *Camptopteris* sensu Nathorst (1878). Nathorst (1878) emended the original generic description by Presl for fossil species that had numerous linear primary segments that were borne spirally, but excluded the type *C. muensteriana*, which was regarded as a *Clathropteris* species (Nathorst, 1878, 1906b; Seward, 1900b; Seward and Dale, 1901; Oishi and Yamasita, 1936). Because our analysis firmly places the type *C. muensteriana* in the *Clathropteris* clade, the continued use of the name *Camptopteris* would be illegitimate based on the code of nomenclature. We, thus, describe this diagnosable clade as *Sewardalea* and designate *Sewardalea spiralis* as the type. *Sewardalea* is more inclusive than *Camptopteris* sensu Nathorst (1878) because several species previously recognized as *Dictyophyllum* are also placed in this clade on the basis of the diagnostic characters of numerous (>12) linear primary segments. The spiraling of primary segments, which was previously cited as an important feature (Nathorst, 1878, 1906b; Seward, 1910; Oishi and Yamasita, 1936), is not recognized as a diagnostic feature. Extant *Dipteris* shows a slight spiraling of primary segments, resulting in a twisted frond lamina that does not naturally fall into a single plane (see Fig. 4). The “funnel-like” disposition of primary segments on *Thaumatopteris* (Oishi and Yamasita, 1936) is another result of the slight spiraling of primary segments. The spiraling of primary segments in Dipteridaceae appears to be a natural consequence of the unequal, catadromous branching of the rachial arms. Thus, the exaggerated spiraling represented in *Sewardalea spiralis* is probably due to the much greater number of primary segments.

**New combinations**—*Sewardalea exile* (Brauns) Choo & Escapa, comb. nov.  $\equiv$  *Camptopteris exilis* Brauns, Palaeontograph, ix, p. 54, 1862.  $\equiv$  *Dictyophyllum exile* (Brauns) Nathorst, Kgl. Svenk. Vet.-Akad. Handl., Bd. XVI, No. 17, p. 13, 1878.

*Sewardalea falcata* (Naito) Choo & Escapa, comb. nov.  $\equiv$  *Dictyophyllum falcatum* Naito, Kon’no, J. Linn. Soc. (Bot.) 61: 93–105, 1968.

*Sewardalea japonica* (Yokoyama) Choo & Escapa, comb. nov.  $\equiv$  *Dictyophyllum japonicum* Yokoyama, J. Coll. Sci. Imp. Univ. Tokyo, 4: (1), 1891.  $\equiv$  *Camptopteris japonica* (Yokoyama) Kon’no J. Linn. Soc. (Bot.) 61: 93–105, 1968.

*Sewardalea nathorstii* (Zeiller) Choo & Escapa, comb. nov.  $\equiv$  *Dictyophyllum nathorstii* Zeiller, Flore fossile des gites de charbon du Tonkin, 1903.

*Sewardalea spiralis* (Nathorst) Choo & Escapa, comb. nov.  $\equiv$  *Camptopteris spiralis* Nathorst, Kgl. Svenk. Vet.-Akad. Handl., Bd. XVI, No. 17, p. 13, 1878.

#### 4. *Clathropteris* Brongniart

**Type**—*Clathropteris meniscioides* (Brongniart) Brongniart

Basionym: *Filicites meniscioides* Brongniart

**Diagnosis**—Stipe with an isotomous initial dichotomy. Two equal and opposite rachial arms each bearing 3–12 primary segments. Frond lamina between primary segments fused up to 1/3 the total length of the primary vein. Secondary and tertiary veins forming regular orthogonal areoles in the free distal portion of each primary segment.

**Remarks**—When first describing the genus, Brongniart (1828) erroneously interpreted the type specimen as having a typical

hierarchical, pinnatifid structure. However, after restudying the protologue and tracking the original specimen, Nathorst (1906a) provided a convincing argument that the type illustration of *C. meniscioides* was inaccurate in its depiction of gross morphology, and reinterpreted the type as having the typical dipterid pedate architecture (Nathorst, 1906a; Choo et al., 2016).

In the past, authors have held differing views on the taxonomic rank of *Clathropteris*. Although always viewed as a natural group, its similarity in gross morphology and reproductive characters to other *Dictyophyllum* species led some authors to advocate for the merging of *Clathropteris* into a subgenus of *Dictyophyllum* (e.g., Seward and Dale, 1901; Herbst, 1992). Our analyses consistently recover this clade as a monophyletic group that has close but unresolved relations with *Kenderlykia* and other *Dictyophyllum* species. Because this clade is highly distinctive, it is useful to continue recognizing it as a separate genus, as many authors have done in the past (e.g., Nathorst, 1906a; Berry, 1918; Oishi and Yamasita, 1936; Schweitzer et al., 2009; Choo et al., 2016). This clade also includes the type species of the later-described *Camptopteris* (i.e., *C. muensteriana*), and *Camptopteris* is thus recognized as a synonym of *Clathropteris*.

#### 5. *Digitopteris* C.Pott & Bomfleur gen. nov. ined

**Type**—*Digitopteris repanda* C.Pott & Bomfleur

**Diagnosis**—Stipe with isotomous initial dichotomy. Primary vein simple. Secondary veins dichotomizing and anastomosing, forming loops.

**Remarks**—This recently described genus is based on a single fossil specimen from the Upper Triassic of Lunz am See, Lower Austria (Pott et al., 2018). Because of its unique combination of plesiomorphic (i.e., simple primary veins) and apomorphic (i.e., dichotomizing secondary veins, few primary segments that are fused at the base) characters, it comes out in our analyses as a transitional form between the basal Dipteridaceae lineages and the crown group.

#### 6. *Cheiropleuria* C.Presl

**Type**—*Cheiropleuria bicuspis* (Blume) C.Presl

Basionym: *Polypodium bicuspe* Blume

**Diagnosis**—Fronds dimorphic. Rhizomes protostelic, with an indument of uniseriate hairs. Frond lamina between primary segments highly fused: the sterile fronds simple, bilobed or tetralobed; the fertile fronds simple and linear. Sporangia acrostichoid.

**Remarks**—This extant clade of three species (Kato et al., 2001) has been recovered as sister to extant *Dipteris* in published phylogenetic studies (e.g., Schuettpelz and Pryer, 2007; Lehtonen, 2011). The group differs sufficiently from *Dipteris* that some past authors have placed it in a separate family, the Cheiropleuriaceae (e.g., Kramer et al., 1990; Laferriere, 1998). Our analyses consistently find the extant species forming a monophyletic clade within the crown group of Dipteridaceae (Figs. 1, 2). Synapomorphies of this clade include sterile–fertile dimorphism, sterile fronds being reduced in width and having acrostichoid sporangia, extreme fusion of primary segments, and dichotomous primary veins commonly anastomosing at the distal portions of the frond. We recognize *Cheiropleuria* as a genus within the monophyletic Dipteridaceae, as recognizing the family *Cheiropleuriaceae* would

entail describing new families for all other Dipteridaceae fossil genera to avoid making Dipteridaceae paraphyletic.

## 7. *Dipteris* Reinwardt

**Type**—*Dipteris conjugata* Reinwardt

**Diagnosis**—Fronds bipartite. Primary veins dichotomizing. Many (>15) sporangia per sorus. Sporangia arranged in circular sori across frond lamina. Spores monolete.

**Remarks**—*Dipteris*, as currently described, is an extant group of several species (Kramer et al., 1990) that is sister to extant *Cheiropleuria* (Schuettpelz and Pryer, 2007; Lehtonen, 2011). Our analyses consistently place extant *Dipteris* specimens within a monophyletic clade in the crown group (Figs. 1, 2), but depending on the various interpretations of certain fossil *Hausmannia* specimens (Figs. 1, 2), this clade may include various fossils specimens as well. Based on our analyses, two synapomorphic characters are unambiguously optimized for *Dipteris*. The first is monolete spores (Fig. 4), and the second is having many (>15) sporangia per sorus, versus very few (3–8) to few (9–15) in the outgroups. Although the character of monolete spores is relatively easy to observe and verify, the number of sporangia per sorus is a character that is difficult to measure and should be regarded with caution, especially when applied to fossil specimens. *Dipteris conjugata* is known to have mixed maturation of sporangia (Seward and Dale, 1901; Armour, 1907), so a count at any single stage of development is likely to be an underestimate. In contrast, *D. lobbiana* has simultaneous sporangial maturation (Armour, 1907), but determining the number of sporangia per sorus is still difficult because sori are covered in a gummy substance before maturity (Hooker, 1853). At present, the only species that can definitively be placed in this genus on the basis of spore type are all extant; no fossils with monolete spores have been described. However, we recognize that several fossil specimens cannot be placed within or outside this clade with certainty, due to missing characters.

### **Unnatural, unresolved groups**—“*Dictyophyllum*”

*Dictyophyllum* Lindley and Hutton and *Kenderlykia* Turutanova-Ketova

**Characters**—Initial stipe dichotomy isotomous, resulting in an even number of primary segments, but fewer than 15 primary segments on each rachial arm. Primary segments lanceolate or oblanceolate, not linear. Primary and secondary veins simple. Areoles formed between secondary and tertiary veins irregularly polygonal, never forming regular orthogonal shapes.

**Remarks**—Neither *Dictyophyllum* nor *Kenderlykia* form clear clades in our analysis; both these genera have the above-described mixture of general Dipteridaceae characters. The name *Dictyophyllum* was established by Lindley and Hutton (1834, p. 65) for “doubtful dicotyledonous leaves of common reticulated structure” from the Oolitic formation in Yorkshire (1834). The accepted reinterpretation of the type species is that it represents a fragment of a dipterid frond that has simple primary and secondary veins, and where the frond lamina forms deep lobes between the secondary veins (2/3 or more of the total length), similar to the dissection levels seen in *Thaumatopteris*. Since then, numerous *Dictyophyllum* species

have been recorded from the Mesozoic from Europe, Asia, South and North America, Greenland and Australia (Oishi and Yamasita, 1936; Webb, 1982; Skog, 2001; Guignard et al., 2009).

Our analyses finds *Dictyophyllum*, as currently defined, polyphyletic, with some species belonging to the *Sewardalea* clade, and others forming an unresolved polytomy with *Clathropteris*, *Kenderlykia*, and the clade comprising *Digitopteris* and the crown clade (Figs. 1, 2). Among the *Dictyophyllum* specimens examined in this study, two smaller monophyletic clades are recovered. The first includes *D. bremerense*, *D. davidii*, and *D. fuensalidai* on the basis of having many (>15) sporangia per sorus. The second includes *Dictyophyllum madagascariense* and *D. nilsonii* as both species have fronds with deep lobes between secondary veins (dissected to 2/3 or more of the total length of the secondary vein) and are recorded as having very small and crowded sori, giving the appearance of sporangia being scattered across the lamina (Webb, 1982; Appert, 2002; Guignard et al., 2009). We do not recognize either of these monophyletic clades as their own genera as the characters that define them are weak and/or unreliable. As discussed earlier in the paper, the number of sporangia per sorus is difficult to interpret with certainty and prone to underestimation. Moreover, based on the observations of extant *Dipteris* (T. Y. S. Choo, personal observations), the density of sori can vary significantly depending on the maturity of the fronds. Deep lobing between the secondary veins is not diagnostic alone, and other *Dictyophyllum* specimens that do not fall into this clade (e.g., the type species *D. rugosom*) also share this character. It should be noted that it is also possible that some dissected *Dictyophyllum* specimens could actually be *Thaumatopteris*, but the lack of spore and rachial characters would prevent them from being resolved with the other *Thaumatopteris* species.

*Kenderlykia* was named for Dipteridaceae fossils in Kazakhstan (Turutanova-Ketova, 1962). Most workers consider *Kenderlykia* to be indistinguishable from *Dictyophyllum*.

### **“*Hausmannia*”**—*Hausmannia* Dunker and *Protorhipis* Andrae

**Characters**—Monomorphic fronds. Primary veins dichotomizing.

**Remarks**—Although clearly placed in the crown clade, no characters conclusively resolve the crown group fossils into one or more clades. In the All\_genera and Reduced analyses (Figs. 1, 2), the fossils appear to fall into two monophyletic clades that correspond to an expanded *Dipteris* and an expanded *Cheiropleuria* (neither the names *Hausmannia* nor *Protorhipis* have priority over the extant names).

However, this result is based on a combination of weak characters and is unconvincing. Five *Hausmannia* species (including the type *H. dichotoma*) are placed in the *Dipteris* clade on the basis of having dissected fronds, but all have unknown states for the diagnostic *Dipteris* characters of monolete spores and more than 15 sporangia per sorus. When these fossils are scored as having the plesiomorphic character of trilete spores, as represented in other *Hausmannia* and *Protorhipis* specimens (Stockey et al., 2006; Schweitzer et al., 2009; Wang and Zhang, 2010), they change position on the tree and form a polytomy at the base of the crown clade (Fig. 4).

The placement of the remainder of the *Hausmannia* and *Protorhipis* fossils tested in our analyses (including the type *P. buchii*) is more stable, consistently forming a polytomy with *Cheiropleuria*. Because they do not form a clade themselves, they can only be considered as part of an expanded *Cheiropleuria*. However, the characters that define this expanded *Cheiropleuria*



clade are also unconvincing: each laminal half having primary segments that are completely fused, a character shared with *D. novoguineensis*; and spores that are less than 30 µm long, a character that is unknown in *P. buchii* and *H. sewardii*, and results in the larger spores of *C. integrifolia* having to be explained as a reversion.

Recently, Stockey et al. (2006) described the anatomically preserved *H. morinii* as having anomocytic stomata and suggested that stomatal type could be an important distinguishing character between *Dipteris* and *Hausmannia* (Stockey et al., 2006). In their paper, Stockey et al. (2006) listed both *H. morinii* and *H. pachyderma* (Sukh-Dev, 1972) as having anomocytic stomata (Stockey et al., 2006). In contrast, extant *Dipteris* and *Cheiropleuria* (van Cotthem, 1970; Kramer et al., 1990; T. Y. S. Choo, personal observation) and *Dictyophyllum madagascariense* (Appert, 2002) have paracytic stomata. We re-examined the published illustration of *H. pachyderma* (Sukh-Dev, 1972) and are of the opinion that this species has a paracytic stomatal arrangement similar to extant *Dipteris*. It is also difficult to clearly determine whether *H. morinii* has anomocytic or paracytic stomata from the published picture (Stockey et al., 2006). Regardless, since most Dipteridaceae fossils (including most other *Hausmannia* species) are not preserved with stomatal detail, we do not consider there to be sufficient evidence for stomatal type to be a distinguishing feature of *Dipteris*.

Although inconclusive, our phylogeny is suggestive of a split between the various crown group fossils into a *Hausmannia* group, typified by *H. dichotoma* and characterized by dissected fronds; and a *Protorhipis* group, typified by *P. buchii*, characterized by each laminal half having primary segments that are completely fused, and having a closer affiliation to *Cheiropleuria* than to *Dipteris*. This is reminiscent of Cantrill's (1995) classification of *Hausmannia*, in which species were classified on the basis of frond dissection. However, evidence to support this classification is very weak. Hence, we find it more prudent to conclude that, until further characters are known, the relationships between the crown group fossils are unresolved and that both *Hausmannia* and *Protorhipis* (often synonymized as the single genus *Hausmannia*; e.g., Oishi and Yamasita, 1936; Cantrill, 1995; Stockey et al., 2006) are unnatural groups.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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**APPENDIX 1. List of morphological characters used in the phylogenetic analysis.**

No.	Character description
1	Sterile/fertile dimorphy: Fronds monomorphic (0), Fronds dimorphic (1)
2	Degree of dimorphism: Holodimorphic (0), Hemidimorphic (1)
3	Position of sporangia: On leaf lamina (0), Along leaf margin (1)
4	Percentage of frond lamina covered by sporangia: <50% (0), 50–90% (1), >90% (2)
5	Shape of sori: Circular to oval (0), Oblong to linear (1)
6	Arrangement of sporangia within sorus: In a single row (0), In multiple rows (1)
7	Indusium: Absent (0), Present (1)
8	Indusium peltate: No (0), Yes (1)
9	Presence of prominent central receptacle in sorus: No (0), Yes (1)
10	Number of sporangia per sorus: Very few 3–8 (0), Few 9–15 (1), Many >15 (2)
11	Sporangial maturation: Simultaneous (0), Mixed (1)
12	Diameter of sporangial capsule: <200 $\mu\text{m}$ (0), 200–400 $\mu\text{m}$ (1), 400–600 $\mu\text{m}$ (2), >600 $\mu\text{m}$
13	Number of cell files in sporangial stalk: 0 (0), 1 (1), 2 (2), 3 (3), 4 (4), >4 (5)
14	Ratio of length of sporangial stalk to diameter of sporangial capsule: $\leq 1$ (0), >1 (1)
15	Presence of annulus: Absent (0), Present (1)
16	Annulus type: Patch (0), Ring (1)
17	Annulus orientation: Lateral (0), Oblique to vertical (1)
18	Ring-type annulus interrupted at stalk: No (0), Yes (1)
19	(for Gleicheniales) Spore size: <30 $\mu\text{m}$ (0), 30–50 $\mu\text{m}$ (1), >50 $\mu\text{m}$ (2)
20	Spore shape: Trilete (0), Monolete (1)
21	Rhizome: Upright (0), Creeping (1)
22	Rhizome vasculature: Protostele (0), Solenostele (1), Dictyostele (2)
23	Solenostele: Single (0), Polycyclic (1)
24	Rhizome indument: Absent (0), Present (1)
25	Rhizome indument type: Uniseriate hairs (0), Bristles [multiseriate but not flattened] (1), Scales (2)
26	Stipe vasculature: Single bundle (0), Multiple bundles (1)
27	Stipe vasculature shape: C-shaped (0), Omega (1), Ring (2), Solid central bundle (3)
28	Rachial architecture: Branching rachis resulting in two or more axes of growth (0), unbranched rachis, i.e., one axis of growth (1)
29	Initial rachial dichotomy: Isotomous (0), Anisotomous (1)
30	Subsequent rachial dichotomies: Isotomous (0), Anisotomous (1)
31	Directionality of anisotomous dichotomies: Catadromous (0), Alternate (1)
32	Dichotomizing axis reduced to rachial bud: Never (0), Yes (1)
33	For pedate fronds, number of primary segments on each rachial arm: 1–2 (0), 3–6 (1), 7–12 (2), 13–20 (3), 20–50 (4), >50 (5)
34	For pedate fronds, degree of laminal fusion between primary segments: None (0), Up to 1/3 fused (1), 1/3–2/3 fused (2), 2/3 to almost fully fused (3), Fully fused (4)
35	For pedate fronds with simple veins, degree of laminal fusion between secondary veins: None (0), Up to 1/3 fused (1), 1/3–2/3 fused (2), 2/3 to almost fully fused (3), Fully fused (4)
36	For pedate fronds, degree of fusion between tertiary veins: None (0), Up to 1/3 fused (1), 1/3–2/3 fused (2), 2/3 to fully fused (3)
37	For pedate fronds, primary veins: Simple (0), Dichotomizing (1)
38	For pedate fronds with simple primary veins, primary segment shape: Linear (0), Lanceolate–oblanceolate (1)
39	For pedate fronds with dichotomizing primary veins, primary veins anastomosing: Never (0), Yes (1)
40	For pedate fronds, secondary veins: Simple (0), Dichotomizing (1)
41	For pedate fronds, maximum width of frond: <50 cm (0), 50–100 cm (1), >100 cm (2)
42	For pedate fronds without free primary segments, overall leaf lamina bipartite: No (0), Yes (1)
43	For pedate fronds, lamina dissecting within primary segment between branched primary veins: No (0), Yes (1)
44	Venation type: Free (0), Anastomosing (1), Anastomosing with free-ending veinlets (2)
45	For free-veined taxa, ultimate veins showing multiple sympodial dichotomizing venation pattern: No (0), Yes (1)
46	Proportion of ultimate areoles with free-ending veinlets: <50% (0), >50% (1)
47	Areolar free-ending veinlets branched: Mostly not branched (0), Mostly branched (1)
48	Arrangement of ultimate areoles: Areoles only found locally on frond (0), Meshwork of areoles throughout leaf lamina (1)
49	Size of ultimate areoles: <1 mm <sup>2</sup> (0), 1–3 mm <sup>2</sup> (1), >3 mm <sup>2</sup> (2)
50	Secondary and tertiary veins forming regular orthogonal areoles: Yes (0), No (1)
51	Stomata type: Anomocytic (0), Paracytic (1), Cyclocytic (2), Other (3)