A Generic Classification of the Thelypteridaceae

Susan Fawcett and Alan R. Smith

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Phegopteris connectilis, Mosquito River, Alger County, Michigan. Photo by Susan Fawcett.

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A Generic Classification of the Thelypteridaceae

A Book to Promote Botanical and Environmental Education,
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***Plesioneuron attenuatum*, Lunga river, Guadalcanal, Solomon Islands. Photo by Cheng-Wei Chen.**

Coryphopteris subbipinnata, Mount Chaunapaho, Guadalcanal, Solomon Islands. Photo by Cheng-Wei Chen.

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***Pneumatopteris glandulifera*, Kolombangara, Solomon Islands. Photo by Cheng-Wei Chen.**

NEW NAMES AND NEW COMBINATIONS

Abacopteris birii (R.D. Dixit & Balkr.) S.E. Fawc. & A.R. Sm., **comb. nov.—22**
Abacopteris gardneri (Holttum) S.E. Fawc. & A.R. Sm., **comb. nov.—22**
Abacopteris gracilis (Ching ex Y.X. Lin) S.E. Fawc. & A.R. Sm., **comb. nov.—23**
Abacopteris hekouensis (Ching ex Y.X. Lin) S.E. Fawc. & A.R. Sm., **comb. nov.—23**
Abacopteris hirtisora (C. Chr.) S.E. Fawc. & A.R. Sm., **comb. nov.—23**
Abacopteris macrophylla (Ching ex Y.X. Lin) S.E. Fawc. & A.R. Sm., **comb. nov.—23**
Abacopteris nitida (Holttum) S.E. Fawc. & A.R. Sm., **comb. nov.—23**
Abacopteris nudata (Roxb.) S.E. Fawc. & A.R. Sm., **comb. nov.—23**
Abacopteris repanda (Fée) S.E. Fawc. & A.R. Sm., **comb. nov.—23**
Abacopteris setosa (Ching ex Y.X. Lin) S.E. Fawc. & A.R. Sm., **comb. nov.—23**
Abacopteris yunguiensis (Ching ex Y.X. Lin) S.E. Fawc. & A.R. Sm., **comb. nov.—23**
Amauropelta cystopteroides (D.C. Eaton) S.E. Fawc. & A.R. Sm., **comb. nov.—28**
Amauropelta grammitoides (Christ) S.E. Fawc. & A.R. Sm., **comb. nov.—28**
Amauropelta miyagii (H. Ito) S.E. Fawc. & A.R. Sm., **comb. nov.—28**
Amauropelta nevadensis (Baker) S.E. Fawc. & A.R. Sm., **comb nov.—27**
Amauropelta subg. **Nibaa** S.E. Fawc. & A.R. Sm., **subg. nov.—27**
Amauropelta noveboracensis (L.) S.E. Fawc. & A.R. Sm., **comb. nov.—27**
Amauropelta subg. **Parathelypteris** (H. Ito) S.E. Fawc. & A.R. Sm., **comb. nov.—27**
Amauropelta rechingeri (Holttum) S.E. Fawc. & A.R. Sm., **comb. nov.—28**
Amauropelta serrulata (Ching) S.E. Fawc. & A.R. Sm., **comb. nov.—28**
Amauropelta subg. **Venus** S.E. Fawc. & A.R. Sm., **subg. nov.—28**
Amblovenatum distinctum (Copel.) S.E. Fawc. & A.R. Sm., **comb. nov.—30**
Amblovenatum subattenuatum (Rosenst.) S.E. Fawc. & A.R. Sm., **comb. nov.—30**
Chingia marattioides (Alston) S.E. Fawc. & A.R. Sm., **comb. nov.—32**
Chingia lindleyi (W.N. Takeuchi) S.E. Fawc. & A.R. Sm., **comb. nov.—32**
Christella jinhongensis (Ching ex K.H. Shing) A.R. Sm. & S.E. Fawc., **comb. nov.—35**
Christella nanxiensis (Ching ex K.H. Shing) A.R. Sm. & S.E. Fawc., **comb. nov.—35**
Christella oblancifolia (Tagawa) A.R. Sm. & S.E. Fawc., **comb. nov.—35**
Christella shimenensis (K.H. Shing & C.M. Zhang) A.R. Sm. & S.E. Fawc., **comb. nov.—35**
Christella subacuta (Ching) A.R. Sm. & S.E. Fawc., **comb. nov.—35**
Christella wulingshanensis (C.M Zhang) A.R. Sm. & S.E. Fawc., **comb. nov.—35**
Coryphopteris caudata (Ching ex K.H. Shing) S.E. Fawc. & A.R. Sm., **comb. nov.—38**
Coryphopteris chinensis (Ching) S.E. Fawc. & A.R. Sm., **comb. nov.—38**
Coryphopteris chingii (K.H. Shing & J.F. Cheng) S.E. Fawc. & A.R. Sm., **comb. nov.—38**
Coryphopteris indochinensis (Christ) S.E. Fawc. & A.R. Sm., **comb. nov.—38**
Coryphopteris krayanensis (K. Iwats. & M. Kato) S.E. Fawc. & A.R. Sm., **comb. nov.—38**
Coryphopteris musashiensis (Hiyama) S.E. Fawc. & A.R. Sm., **comb. nov.—38**
Coryphopteris nigrescens (Ching ex K.H. Shing) S.E. Fawc. & A.R. Sm., **comb. nov.—38**
Coryphopteris nipponica (Franch. & Sav.) S.E. Fawc. & A.R. Sm., **comb. nov.—38**
Coryphopteris pauciloba (Ching ex K.H. Shing) S.E. Fawc. & A.R. Sm., **comb. nov.—39**
Coryphopteris sylva-nipponica (Ebihara & Nakato) S.E. Fawc., A.R. Sm. & Ebihara, **comb. nov.—39**
Coryphopteris trichochlamys (Ching ex K.H. Shing) S.E. Fawc. & A.R. Sm., **comb. nov.—39**
Goniopteris bermudiana (Baker) S.E. Fawc. & A.R. Sm., **comb. nov.—45**
Goniopteris fuertesii (Brause) S.E. Fawc., A.R. Sm. & Y.Y. Piña, **comb. nov.—45**
Goniopteris venusta (Heward) Pic.Serm. var. **usitata** (Jenman) S.E. Fawc. & A.R. Sm., **comb. nov.—45**
Grypothrix (Holttum) S.E. Fawc. & A.R. Sm., **gen. et stat. nov.—46**
Grypothrix crenulata (Holttum) S.E. Fawc. & A.R. Sm., **comb. nov.—47**
Grypothrix cuspidata (Blume) S.E. Fawc. & A.R. Sm., **comb. nov.—47**
Grypothrix longipetiolata (K. Iwats.) S.E. Fawc. & A.R. Sm., **comb. nov.—47**
Grypothrix megacuspis (Baker) S.E. Fawc. & A.R. Sm., **comb. nov.—47**
Grypothrix parishii (Bedd.) S.E. Fawc. & A.R. Sm., **comb. nov.—47**
Grypothrix pentapinnata (Fraser-Jenk.) S.E. Fawc. & A.R. Sm., **comb. nov.—47**
Grypothrix ramosii (C. Chr.) S.E. Fawc. & A.R. Sm., **comb. nov.—47**
Grypothrix rubicunda (Alderw.) S.E. Fawc. & A.R. Sm., **comb. nov.—47**
Grypothrix salicifolia (Wall. ex Hook.) S.E. Fawc. & A.R. Sm., **comb. nov.—47**
Grypothrix simplex (Hook.) S.E. Fawc. & A.R. Sm., **comb. nov.—48**
Grypothrix sulawesiensis (K. Iwats.) S.E. Fawc. & A.R. Sm., **comb. nov.—48**
Grypothrix triphylla (Sw.) S.E. Fawc. & A.R. Sm., **comb. nov.—48**
Hoiokula S.E. Fawc. & A.R. Sm., **gen. nov.—48**
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Menisorus blastophorus (Alston) S.E. Fawc. & A.R. Sm., **comb. nov.—56**
Menisorus unitus (Kunze) S.E. Fawc. & A.R. Sm., **comb. nov.—56**
Mesopteris attenuata (Kuntze) S.E. Fawc. & A.R. Sm., **comb. nov.—58**
Mesopteris ceramica (Alderw.) S.E. Fawc. & A.R. Sm., **comb. nov.—58**
Mesopteris kiauensis (C. Chr.) S.E. Fawc. & A.R. Sm., **comb. nov.—58**
Mesopteris paraphysophora (Alderw.) S.E. Fawc. & A.R. Sm., **comb. nov.—58**
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Pakau S.E. Fawc. & A.R. Sm., **gen. nov.—61**
Pakau pennigera (G. Forst.) S.E. Fawc. & A.R. Sm., **comb. nov.—62**
Pelazoneuron (Holttum) A.R. Sm. & S.E. Fawc., **gen. et stat. nov.—62**
Pelazoneuron abruptum (C. Presl) A.R. Sm. & S.E. Fawc., **comb. nov.—63**
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Pelazoneuron albicaule (Fée) A.R. Sm. & S.E. Fawc., **comb. nov.—63**
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A GENERIC CLASSIFICATION OF THE THELYPTERIDACEAE

ABSTRACT

Based on morphological, biogeographical, and phylogenomic data, a new generic classification system is proposed for the Thelypteridaceae. We give an overview of the previous classifications of the family, and a summary of the morphological, cytological, geographic and molecular data underlying these classifications is given. A synoptical phylogenetic tree, a key to genera, and a morphological description, a discussion of biogeography and ecology, and a list of constituent species for each genus are provided. Major taxonomic changes include the recircumscription of 14 genera, descriptions of four new genera and three subgenera, the elevation of three sections to generic status, the resurrection of one genus, the inclusion of two genera in synonymy, and 176 new names.

RESUMEN

Basado en datos morfológicos, biogeográficos y filogenómicos, se propone un nuevo sistema de clasificación genérico para Thelypteridaceae. Se ofrece una descripción general de las clasificaciones anteriores de la familia y los datos morfológicos, citológicos, geográficos y moleculares que informaron estas clasificaciones. Se incluye un árbol filogenético sinóptico, una clave para los géneros, y una descripción morfológica, una discusión de biogeografía y ecología, y una lista de especies constituyentes para cada género. Los principales cambios taxonómicos incluyen la recircumscripción de 14 géneros, descripciones de cuatro géneros nuevos, y tres subgéneros, la elevación de tres secciones subgenéricas, la resurrección de un género, la inclusión de tres géneros en la sinonomía y 176 nombres nuevas.

Key Words: *Pronephrium, Pneumatopteris, Sphaerostephanos, Christella, Thelypteris, Cyclosorus*, Fern

INTRODUCTION

The Thelypteridaceae is among the largest fern families, with 1190 species recognized here, and comprises about 10% of all fern diversity (PPG I 2016). The family is cosmopolitan and most diverse near the equator, although species range as far north as Greenland and Alaska, and as far south as southern New Zealand. Approaches to the classification of the family have varied, ranging from the recognition of a single genus, *Thelypteris* (Morton 1963), to as many as 32 genera (Pichi Sermolli 1977). The identification of taxa within the family is notoriously difficult. Ten of the 30 recognized genera (PPG I 2016) are either non-monophyletic as previously circumscribed or had not been included in molecular phylogenetic analyses. Many of these genera, especially in the Paleotropics, are not diagnosed by morphological synapomorphies, but rather by a combination of characteristics that frequently overlap with other genera (Holttum 1982). Furthermore, most of the diagnostic features needed to identify species are microscopic or require complete fertile fronds with rhizomes, making this an especially challenging group for field- and herbarium-botanists alike. The fact that many species appear superficially similar has no doubt contributed to neglect by most general plant collectors, who often overlook their diversity.

Since the last major effort to treat the most diverse and taxonomically complex groups within the Thelypteridaceae (Holttum 1982), many more collections have been made and the widespread use of molecular phylogenetics has provided novel lines of evidence for developing taxonomic hypotheses. Although the generic status of most New World Thelypteridaceae has reached a point of stability (Salino et al. 2015; PPG I 2016), the taxonomy of paleotropical groups is in need of major revision (He & Zhang 2012; Almeida et al. 2016; Patel et al. 2019a). The classification system proposed here benefits from a recent phylogenomic study that included approximately 600 of the approximately 1200 species in the family, nearly tripling the number of samples previously included in a molecular study (Fawcett et al. in press). The increased sampling, which emphasizes the most problematic taxa, helps resolve relationships within the family and enables us to propose important improvements to the classification system of Holttum (1971, 1974a, 1977b, 1982), which was largely adopted by PPG I (2016).

PREVIOUS CLASSIFICATIONS

The first major monograph treating a substantial proportion of the species of Thelypteridaceae was published by Carl Christensen (1913, 1920) who treated the American species within subgenera of *Dryopteris*, under a broadly circumscribed Dryopteridaceae. In spite of this, he recognized that "…it is in reality highly unnatural to unite them all under a single genus" and he identified the respective members of modern-day Dryopteridaceae and Thelypteridaceae as belonging to two distinct groups (Christensen 1913:59). His subgeneric concepts in many cases (e.g., subgenera *Goniopteris*, *Leptogramma,* and *Meniscium*) correspond perfectly to the prevailing generic taxonomy, while others (e.g., subgenera *Cyclosorus, Lastrea*, and *Steiropteris*) need relatively minor adjustments to represent clades. Christensen's pioneering work shaped the taxonomy of the family in the century that followed. His student, R.C. Ching (discussed below) expanded Christensen's system to develop thelypterid taxonomy for the Old World. The modern taxonomy, which centers around Holttum's initial conspectus of genera in the family (Holttum 1971) and subsequent treatment in

Flora Malesiana (Holttum 1982), was greatly influenced by Christensen, who corresponded frequently with Holttum and determined specimens for him early in Holttum's career.

Thelypteridaceae Pic.Serm., as it is currently recognized, was not fully conceived and circumscribed until the mid-20th century. The post-war proliferation of compound microscopy revolutionized systematic botany by facilitating chromosome counting. Chromosome number surveys in ferns, pioneered by Irene Manton (1950), provided powerful new data that solidified modern understanding of evolutionary relationships among ferns on multiple scales. Recognition that members of Dryopteridaceae have a base chromosome number of $x = 41$, while those of Thelypteridaceae have $x = 27$ to 36, went a long way towards settling any lingering disputes about family circumscriptions (Manton & Sledge 1954; Wagner 1955).

Meanwhile, Ching (1936, 1940) proposed that members of the Thelypteridaceae constituted a natural group within an expansive concept of Polypodiaceae. He later published a system of tribes and subtribes for the species of Thelypteridaceae occurring in mainland China (Ching 1963), which was the first attempt to develop a classification that proposed relationships among the Old World taxa using combinations of morphological characteristics. Important contributions to Old World Thelypteridaceae taxonomy were also made by Ito (1939), who described three new sections of *Thelypteris*: *Parathelypteris*, *Metathelypteris*, and *Macrothelypteris*; these are now widely recognized as genera. Further refinements of family circumscription, and generic and infrageneric taxonomy were proposed by Iwatsuki (1962, 1963, 1964a, 1964b). Among his contributions was the thoughtfully justified exclusion of several taxa previously included in Thelypteridaceae by others, such as *Gymnocarpium* (Christensen 1920) and *Hypodematium* (Ching 1963), resulting in the family-level circumscription still recognized today. The Thelypteridaceae was formally recognized at family rank by Pichi Sermolli (1970), following Ching and Iwatsuki.

Morton (1963), following Christensen (1913, 1920), recognized the taxonomic circumscriptions of American groups, but as subgenera of a broadly defined genus, *Thelypteris*. He suggested that members of *Thelypteris* sensu Morton were sufficiently uniform to be easily recognized by non-specialists, but not sufficiently distinct from each other to be treated as separate genera. However, his subgeneric treatment neglected the Old World members of the family, which are highly diverse morphologically, evolutionarily, and taxonomically. It is clear from his descriptions of *Thelypteris* s.l. that he was unfamiliar with this diversity, and he did not attempt to account for Old World taxa in his family-level classification (Morton 1963).

Morton (1963), Ching (1963), and others argued against "one character" genera, such as those defined by Copeland (1947) in his classification, believing that any good taxon will be defined by a combination of characteristics. Specifically, Morton (1963) cited *Goniopteris* as an example of a genus that should not be recognized strictly on the basis of stellate or furcate hairs. However, sometimes taxonomists are fortunate in that a single morphological synapomorphy suffices to define a clade, as is the case for *Goniopteris*. All taxa treated in *Goniopteris* so far represented by molecular data have proven to belong to this monophyletic genus, nearly all easily diagnosed by the presence of these specialized hairs. Species in which the characteristic has been secondarily lost (e.g., *Goniopteris macrotis*)—the generic placements of which were questioned by Christensen (1913) and Morton (1963)—sufficiently resemble the taxa with specialized hairs to have been rightly placed in the genus, as confirmed by subsequent molecular analyses (e.g., Fawcett et al. in press). Morton (1963) argued that a number of *Amauropelta* spp. also have furcate hairs, e.g., *Amauropelta thomsonii*, but careful examination of these hairs reveals that they are not stellate, but rather distinct hairs that are arranged tightly in groups, or fascicles.

Important contributions to our understanding of New World Thelypteridaceae since Christensen's monograph (1913, 1920) were made by Alan Smith, who published several monographs. These included the treatments of *Thelypteris* sect. *Cyclosorus s.l.* (which also included the American members of *Christella* and *Amblovenatum*) (Smith 1971), *Amauropelta* (Smith 1974), and *Steiropteris* (Smith 1980). The major changes from Christensen's system were the transfer of most species of *Lastrea* to *Amauropelta*, and of species in sect. *Glaphyropteris* to either *Steiropteris* or *Amauropelta*. Additionally, Smith authored or co-authored the Thelypteridaceae treatments in numerous regional floras, contributing a detailed understanding of species-level diversity, including Flora of North America (Smith 1993a), Flora Mesoamericana (Smith 1995a), The Pteridophytes of Mexico (Mickel & Smith 2004), Ferns and Fern Allies of Guatemala (Smith 1976), Pteridophyta of Peru (Smith 1992), Prodromus of a fern flora for Bolivia (Smith & Kessler 2017), Flora of the Venezuelan Guyana (Smith 1995b), Flora of Ecuador (Smith 1983), and Flora of China (Lin et al. 2013).

Other notable contributions to taxonomy of American thelypterids include the treatment of *Meniscium* by Maxon and Morton (1938), with subsequent refinements by Fernandes et al. (2020), the treatment of Caribbean *Amauropelta* by Alvarez-Fuentes (2010), and the study of New World *Stegnogramma* by Watkins and Farrar (2005). The definitive circumscription of *Goniopteris*, *Amauropelta*, *Meniscium*, and *Steiropteris*, and the new combinations necessitated by it, were published by Salino et al. (2015), and adopted by PPG I (2016).

Following the major contributions to our understanding of the family in continental and northern Asia by Ching (1936, 1963, 1978), Ito (1939), and Iwatsuki (1963), a foundational treatment for the family was provided in the *Flora of China* (Lin et al. 2013). Since then, the genus *Christella* (treated as *Cyclosorus* subgenus *Cyclosoriopsis*) was recently revised by Li et al. (2013), *Stegnogramma s.l.* by Kuo et al. (2019), and *Pseudocyclosorus* by Li et al. (2019).

Our current understanding of the diversity of paleotropical Thelypteridaceae is credited in large part to the meticulous, unrelenting efforts of R.E. Holttum, who published extensively on the family over the course of three decades. With the adoption of an initial conspectus of the genera (Holttum 1971), he contributed a series of taxonomic monographs (Holttum 1969, 1972, 1973a, 1973b, 1974b, 1975, 1976a, 1976b, 1977b, 1979, 1981; Holttum & Grimes 1980) and described seven new genera of Thelypteridaceae: *Amphineuron*, *Chingia*, *Coryphopteris*, *Mesophlebion, Nannothelypteris*, *Plesioneuron*, and *Trigonospora*; he also provided infrageneric classifications for *Christella* (Holttum 1974a) and *Pronephrium* (Holttum 1982). He published numerous regional floristic treatments of the family, including those for Malaya (Holttum 1954), Africa (Holttum 1974a), Europe (Holttum 1983), the Pacific (Holttum 1977b) and, ultimately, Malesia (Holttum 1982). The family treatment in Flora Malesiana, published eight years before his death, represented the synthesis of his career-long study of the family, and provided the basis for a taxonomic system that has remained little changed for the past half-century.

The Pteridophyte Phylogeny Group, or PPG (PPG I 2016), was established to develop a community-based classification system for ferns and lycophytes, informed by recent molecular phylogenetic research, following a model similar to that of the Angiosperm Phylogeny Group, or APG (Stevens 2001). For each family, a subcommittee of experts and interested parties was formed to collaborate on a classification system. For the Thelypteridaceae, this mostly involved developing a global taxonomic concept by merging the most recent treatment of New World taxa (e.g., Smith 1990; Salino et al. 2015) with the most recent Old World treatments, e.g., in Flora Malesiana (Holttum 1982) and in Flora of China (Lin et al. 2013). Problems with existing Thelypteridaceae taxonomy faced by the PPG included incongruence with recent molecular phylogenetic data, extremely limited sampling for the most problematic genera, and lack of recent taxonomic revisions. The best course of action was to follow Salino et al. (2015) and Almeida et al. (2016) for New World taxa, and to adopt Holttum's 1982 taxonomic concepts with minimal refinements for Old World taxa, pending further study (PPG I 2016).

Although alternative classification systems recognizing a small number of genera have been proposed and employed in regional floras (e.g., Fraser-Jenkins 2017), these systems have gained little traction. For example, Mazumdar proposed conservation of *Cyclosorus* to allow expansion of its circumscription to encompass most diversity within the family, but his proposal was withdrawn (Applequist 2016). Historically, gaps in the knowledge of evolutionary relationships among taxa have been the primary justification for conservative taxonomic circumscriptions (e.g., Christensen 1913, 1920; Reed 1968; Morton 1963; Smith 1990), but as understanding of phylogenetic relationships and diagnostic morphological characters has expanded, the prevailing approach has been to recognize more genera (Schuettpelz et al. 2018).

MORPHOLOGY

The Thelypteridaceae can be easily recognized by a combination of two characteristics—hyaline, acicular hairs most easily observed on adaxial rachis and costae, and two strap-shaped vascular bundles in the stipe, uniting into a U-shape distally (Holttum 1982; Smith 1990). Additional characters common to most members in the family include: monolete spores; sporangial stalks three cells thick; adaxial grooving of rachis and costae (most genera) with the groove not continuous from one axis to the next; catadromous laminae; and chromosome base numbers $x = 27–36$.

Macromorphology.—Rhizomes may be long-creeping (Figs. 3C, 6C, 10C), short-creeping (Figs. 8B, 8C), or erect (fronds fasciculate), forming caudices (Figs. 5B, 9A). In some genera, such as *Chingia*, these may be massive and up to a meter tall, resembling those of tree ferns. Although they are unusual in the family, scandent rhizomes are known in both *Amauropelta* and *Sphaerostephanos*. In some species, e.g., *Phegopteris*, the rhizomes are thin and branching, with the plants forming colonies. Like all members of the suborder Aspleniineae, or eupolypods II (with the exception of Blechnaceae), there are two more or less strap-shaped vascular bundles in the stipe, uniting to form a U-shape distally (Sundue & Rothfels 2013). Fronds may be only a few centimeters long (e.g., *Goniopteris minutissima*), to greater than 3 m (e.g., *Plesioneuron keysserianum*), with texture varying from membranaceous to thickly coriaceous. Species of a few genera (e.g., *Ampelopteris, Goniopteris, Gryopothrix*) bear proliferous buds. Stipes may be green, stramineous, castaneous, or black. In a few taxa (e.g., *Pneumatopteris, Pseudocyclosorus, Steiropteris*) prominent peg-like aerophores are present along the stipe and pinna-bases (Fig. 2C), and occasionally at the base of costules. The laminae are typically monomorphic, but may be weakly dimorphic (*Thelypteris s.s.*) or strongly dimorphic (*Pronephrium s.s.*, Fig. 8C). They may be simple (as in some species of *Goniopteris* and *Grypothrix*, Fig. 3C), to bipinnate-pinnatifid, as in species of *Macrothelypteris*. The most typical blade division, however, is pinnate-pinnatifid, which characterizes a majority of species across many genera. Thelypteridaceae is one of few families in which laminae are nearly always catadromous (Kramer 1987), a useful character in assigning fossils. The shape of the laminae is often taxonomically informative; the apex may taper gradually (Figs. 6C, 9A), or there may be a conform terminal pinna similar to the lateral pinnae (Figs. 3A, 10C). The proximal pinnae may be unreduced, abruptly reduced, or gradually reduced. These variations in laminar shape form a continuum wihin some genera. Occasionally, the color of the dried lamina is also informative, with a few genera (e.g., *Grypothrix, Menisciopsis, Mesopteris*) often drying reddish. The presence of pustules on the surface of the laminae is also a useful character (Fig. 8A).

Venation.—Venation has been greatly emphasized as an important diagnostic feature for genera in the family since the mid-19th century (Presl 1836; Fée 1852) and was also studied in detail by later workers (Iwatsuki 1962; Wagner 1979). Members of the family may have veins that are free (Figs. 6A, 6B), forked (Fig. 6D), or regularly (Fig. 4D, 5C, 10A) or irregularly anastomosing (e.g., the *Dictyocline* clade of *Stegnogramma*, Fig. 4E). Taxa defined entirely by venation (e.g., *Lastrea*, with free veins, *Cyclosorus sensu* Copeland (1947), with anastomosing veins) were later abandoned because they contained a “horrible mix” (Ching 1963) of non-monophyletic taxa. Although often insufficient as a stand-alone character, venation has proven useful in diagnosing clades and more narrowly circumscribed genera in combination with other characters. In the Neotropics, for example, simple, free veins that reach the margin above the sinus are a synapomorphy for the genus *Amauropelta* (Fig. 6B). Among species with anastomosing veins, subtle variations in architecture provide several useful characters to the trained eye. For example, whether veins meet at the sinus (Figs. 4C, 7C), are connivent just below it (Fig. 7D), unite to form an excurrent vein (Fig. 7B), or are united in multiple pairs below the sinus (Fig. 4A), are all diagnostic character states. A major criticism by Morton (1959, 1963), leading him to argue for the recognition of a single genus for all species of Thelypteridaceae, was the fact that members of *Cyclosorus* and *Goniopteris* both had united veins with an excurrent veinlet, while the character state was variable within the genus *Cyclosorus* (including *Christella*). It is true that some members of *Christella s.l.* (including *Pelazoneuron*) may exhibit both states on a single frond; however, these taxa can be recognized when other characters like indument, laminar shape, and rhizome morphology are also considered.

For species with regularly anastomosing veins, terms like ‘meniscioid’ and ‘goniopteroid’ have frequently been applied to describe the venation of several fern genera. Lellinger (2002) stated that such terms “…are imprecise in their application or meaning, are impossible to define other than tautologically, and are best avoided.” In spite of this, the taxa recognized as having these distinct venation types (Christensen 1913, 1920) have remained intact for a century, withstanding the taxonomic upheaval of the molecular era. The distinctive venation that was the basis of these generic concepts was precisely described, and accurately illustrated in early publications (e.g., Presl 1836; Fée 1852). Furthermore, the names themselves are intrinsically descriptive: *goni-* meaning angled, in reference to the anastomoses of intercostular veins where they unite to form an excurrent vein (Morton 1958), and meniscioid, a derivation of *meniscatus*, “shaped like a half-moon or crescent” (Stearn 1992), referencing the lunulate sorus along the arching intercostal anastomosis, which characterizes many members of the genus *Meniscium*. Although these morphologies have evidently arisen independently multiple times among distantly related members of the family, these terms are still useful descriptors. Rather than abandon them, we prefer to provide precise definitions, and apply them consistently.

Indument.—The taxonomic utility of trichomes in Thelypteridaceae was recognized by Christensen in his monograph more than a century ago:

> “…no doubt, [it is] the best and most constant character, by which groups of related species can be distinguished from each other … as a matter of fact I shall point out that all the 280 species, four or five perhaps excepted, could be determined to subgenus from an examination of the scales and hairs alone.” (Christensen 1913:59)

As discussed above, the taxonomic groups proposed by Christensen have changed primarily in rank, and only slightly in circumscription, which is a testament to his abilities as well as the utility of the character. The typical thelypterid hair is hyaline and acicular; however, the length, width, color, and distribution of hairs on the plant is highly variable and informative (Iwatsuki 1962). Certain lineages or genera can be recognized on the basis of unique hair morphology. For example, stellate (Fig. 2B) or otherwise compound hairs are synapomorphic for the ~120 species in the genus *Goniopteris* (see Previous Classifications). Hamate or hook-shaped hairs characterize *Amauropelta* sect. *Uncinella* (Smith 1974), *Cyclogramma*, and *Grypothrix* (Holttum 1982).

Scales are typically basifixed, and vary in shape, size, color, and presence and distribution of hairs along scale margins and surfaces (Figs. 2G, 2L). The presence of scales on laminae and costae (Figs. 6D, 7E) is a useful feature, and may be diagnostic at the species level. Glands are also highly variable in shape, color, and disposition. These may be spherical, hemispherical, oblate, pear-shaped, viscid, and may be sessile or stalked. The color may be clear, gold, amber, red, or bright sulphureous yellow, as in *Amblovenatum*. The presence and quantity of glands or hairs on indusia (Figs. 2A, 2D, 2E, 2J), sporangia (Figs. 2H, 2I), and sporangial stalks are useful at both generic and species rank.

Reproductive Morphology.—Sori of Thelypteridaceae are most typically small and round (Figs. 2A, 2C, 5D), but may be slightly elongate, as in *Amauropelta* and *Sphaerostephanos* (Fig. 2D), linear, as in *Leptogramma* (Fig. 4C), or tightly clustered and elongated along veins, as in *Meniscium*. Those species with round sori may be indusiate or not. In many species, the indusium is highly reduced and/or fugacious, and may be difficult to detect depending on the phenological stage at which the plant was collected, so it can be more challenging as a diagnostic character than it is in some other fern lineages. The sporangia may bear setae, glands, or both, and their presence and distribution (e.g., on stalk vs. on capsule), and whether they are unicellular or multicellular, are sometimes diagnostic.

Spores of Thelypteridaceae are monolete, with the exception of members of the genus *Trigonospora*, which are characterized by trilete spores (Nayar & Chandra 1966; Wagner 1979). The morphology of the perispore is highly variable within the family, and may be nearly smooth, echinate, or with broad folds or thin crests that may be free or anastomosing (Wood 1973; Tryon & Tryon 1982; Tryon & Lugardon 1991; Wang and Dai 2010; Patel et al. 2019a). The surface may have secondary structuring of papillae, or minute echinae or folds. Some genera, exemplified by *Amauropelta*, have perforate or fenestrate spore morphology. Although spore morphology is relatively consistent within some genera (e.g., *Steiropteris*; Smith 1980), it is remarkably variable within others and may vary between closely related members of a species complex (Tryon et al. 1980). In some cases, perine morphology provides reliable characters for distinguishing between members of a species complex (e.g., Nakato et al. 2002, 2004). See Patel et al. (2019a) and references therein for a synopsis and analysis of spore morphology in the family.

CYTOLOGY

Cytology has proven to be especially useful for developing taxonomic hypotheses for the Thelypteridaceae, since basic chromosome numbers are recognized as synapomorphic for several genera and major clades (Walker 1966; Mitui 1968; Smith 1971; Lovis 1978; Smith & Cranfill 2002; He & Zhang 2012). Based on counts reported for 217 taxa, assembled from 160 publications (Rice et al. 2015), the overall patterns within the family can be summarized. Slightly more than half, or 53% of species are strictly diploid and 70% of species are represented by a diploid cytotype. Twenty-two percent are strictly tetraploid, with 39% represented by a tetraploid cytotype. Higher polyploids are rare among thelypterids, as compared to other fern lineages, with only two reported hexaploids and four known octoploids. Although recent reviews have reported only five instances of apomixis in the Thelypteridaceae (Liu et al. 2012; Grusz 2016), twelve species of Thelypteridaceae are represented by triploid cytotypes (excluding known hybrids), warranting further investigation into their breeding systems. The genera *Phegopteris* and *Pseudophegopteris* are disproportionately represented by triploids compared to the rest of the family.

Although chromosome base numbers are generally highly stable within a genus and are useful diagnostic characteristics for major clades, there are apparently extreme examples of dysploid series, concentrated in the amauropeltoid clade, including several species in the genera *Amauropelta s.l.*, *Metathelypteris*, and *Coryphopteris* (Lovis 1978; Rice et al. 2015, references therein). Lovis (1978) noted different chromosome base numbers associated with various genera within Thelypteridaceae, and hypothesized that dysploidy may have played an important role in their differentiation. Lovis also inferred that all species with base number $x = 36$ represented a single radiation relatively late in the evolution of the family. This chromosome base number is a synapomorphy for the more recently diverged cyclosoroid clade, which encompasses a majority of the species diversity in the family. However, there appears to be a reduction to $x = 35$, exhibited in three species of *Pseudocyclosorus*.

Strikingly, 20% of all species with reported counts are represented by multiple cytotypes. The actual proportion could be considerably higher, since most species are represented by few independent counts, and material is often sampled from a small portion of the species range. Polyploidization, resulting in reproductive isolation, is an important driver of fern diversity, and an estimated 31% of fern speciation events are associated with a change in ploidy (Wood et al. 2009). Barker et al. (2016) estimated that 53% of angiosperms with multiple cytotypes are not recognized as distinct taxa, which has major implications for documenting, understanding, and, ultimately, conserving biodiversity. Few species complexes in Thelypteridaceae have been studied in sufficient detail to detect this type of cryptic diversity, but those that have been studied in depth frequently yield undescribed entities warranting recognition at species rank (e.g., Yatabe et al. 2002; Nakato et al. 2002, 2004; Patel et al. 2019b).

HYBRIDIZATION

Hybridization has been increasingly appreciated as an important driver of evolution in ferns (Manton 1950; Wagner 1954, 1968; Barrington et al. 1989; Haufler et al. 2000; Haufler 2007). Certain lineages of Thelypteridaceae, such as the Antillean calciphilic radiation of *Goniopteris* (Proctor 1985, 1989; Smith 1993b; Fawcett 2020), have an extraordinary propensity for hybridization, with more than a dozen putative F_1 hybrid combinations among a few dozen constituent species (Sánchez 2017; Fawcett, unpublished data), in addition to several species hypothesized to be of hybrid origin. Within the family, there are many examples of putative hybrids recognized on the basis of malformed spores and morphological intermediacy between presumed progenitors (e.g., Willis & Nester-Hudson 2006), and even suggestive evidence for hybrid introgression (Smith 1971). Comparatively few putative hybrids have been verified by other lines of evidence, however, such as cytology, isozymes, or molecular phylogenetics (but see Smith 1971). The genus *Christella s.l.*, which we now recognize as the phylogenetically distant genera *Christella* and *Pelazoneuron*, both include many infrageneric hybrids, many of which have been given binomial names (Mazumdar 2013).

There are also reports of intergeneric hybrids, although none has been verified by independent means. Three of these purported hybrids have been interpreted to involve the African species *Pneumatopteris afra* as one parent, with the other parent differing among the putative hybrids, involving two species of *Christella* sect. *Christella* and one species of what was treated by Holttum as an African member of *Christella* sect. *Pelazoneuron* (Viane 1985; Quansah & Edwards 1986). The pantropical *Christella dentata* has been implicated as a parent in many infrageneric hybrids, but is also purported to hybridize with two members of what we are newly recognizing as *Menisciopsis,* a segregate of the genus *Pronephrium* sensu Holttum. These putative parental taxa include the Hawaiian endemic *Menisciopsis cyatheoides* (=*Christella cyatheoides*) (Wagner 1993) and the closely related *Menisciopsis penangiana* (=*Pronephrium penangianum*) in mainland Asia (Fraser-Jenkins 2008a). Lastly, another species of *Christella* sect. *Christella* has been reported to hybridize with *Grypothix triphylla* (=*Pronephrium triphyllum*) (Fraser-Jenkins 2008b). If confirmed, these examples would represent multiple instances of intergeneric, or deep, hybridization, which has been definitively confirmed only rarely in ferns (summarized in Lehtonen 2018).

FOSSIL EVIDENCE

Recent analyses using fossil-calibrated fern phylogenies have all placed both stem- and crown nodes of Thelypteridaceae in the Cretaceous period, with age estimates ranging from 71 Ma to 117 Ma (Schuettpelz & Pryer 2007; Rothfels et al. 2015; Testo & Sundue 2016). Assignment of fossils to the family, and especially to extant taxa, is challenging, since fossils often do not preserve vascular anatomy of the stipe, or diagnostic microscopic features such as hairs or perine sculpture (Collinson 2001). To confidently place a fossil within an extant taxon, ideally, it should exhibit characteristics shared with, and unique to, that taxon. However, in many cases, fossils exhibit a combination of characteristics not shared with any extant genera, though each characteristic may be present among different genera within the family (Collinson 2001).

A mid-Cretaceous fossil recovered from Myanmar amber, *Holttumopteris burmensis*, has monolete, lophate spores, sporangia with a vertical annulus, round indusiate sori, adaxially grooved costae, and catadromous laminae, and is potentially, but not unequivocally, referable to Thelypteridaceae (Regalado et al. 2018). It may be placed with confidence in the eupolypod ferns, however, representing one of the oldest known fossils in that lineage.

The earliest fossil assigned to the Thelypteridaceae is *Aspidistes thomasii*, from the Jurassic (Holttum 1971; Lovis 1975). Holttum, who was experienced as a paleobotanist and a pre-eminent student of Thelypteridaceae, placed the fossil based on several features shared with extant thelypterids. He thought the glands resembled those of *Coryphopteris*, and the laminar division was like that of *Macrothelypteris* or *Pseudophegopteris*, and noted that the trilete spores were shared with *Trigonospora*. Trilete spores are very unusual in the Thelypteridaceae, however, and are restricted to small number of taxa where they likely represent a reversal from ancestors with monolete spores (Wagner 1974; Patel et al. 2019a). This hypothesis is also supported by the observation that they often occur in combination with monolete spores and have an atypical shape: although they bear a trilete laesura, they assume a form resembling a monolete spore, rather than the typical tetrahedral shape of trilete spores in other taxa (Nayar & Chandra 1966; Chandra 1973). Holttum believed that the Thelypteridaceae had close evolutionary affinities with the trilete-spored Cyatheaceae, on the basis of similarities in frond morphology, indument, aerating tissue along the rachis, and shape and placement of the sori (Holttum 1971). With the benefit of molecular phylogenetic evidence (e.g., Schuettpelz & Pryer 2007), we now understand these families to be quite distantly related and interpret these similarities as homoplasious. Although Holttum (1971) did recognize and enumerate the differences between these two families, we have a new perspective on the relative importance of vascular anatomy, soral morphology, and basic chromosome number in diagnosing major clades of ferns.

Speirsiopteris orbiculata (Stockey et al. 2006), recovered from 57 Ma sediments in Alberta, Canada, represents a distinct lineage, also reasonably assigned to Thelypteridaceae. This Paleocene fossil clearly exhibits features of Polypodiales, including a vertical annulus, and 64 monolete spores per sporangium. The deltate, catadromous pinnate-pinnatifid fronds with free or forked veins are most similar to those of non-cyclosoroid Thelypteridaceae. Since the fossil lacks details of hairs, scales, and perine, it cannot be assigned more precisely, although veins terminating at the margins are a feature shared with most early-diverging Thelypteridoideae, and lacking from most Phegopteridoideae (Smith 1990).

In light of the evolutionary significance of trilete spores and its implications for the placement of *Aspidistes thomasii*, and the lack of diagnostic details preserved in the fossils *Holttumopteris burmensis* and *Speirsiopteris orbiculata*, the earliest known fossil assignable with confidence to Thelypteridaceae is a cyclosoroid from the Cretaceous-Paleogene boundary, recovered from central Colorado (Berry 2019). Although the venation suggests affinity with extant neotropical genera *Goniopteris* or *Pelazoneuron*, the lack of preservation of microscopic features precludes more precise placement.

The Cenozoic era provides a wealth of Thelypteridaceae fossils, some of which have been assigned to extant lineages or genera. Recently, a Paleocene fossil from south China has been assigned to the genus *Christella* (Xu et al. 2019). This fossil was discovered within the modern geographic range of the genus, near its center of diversity (Li 2013), suggesting that, if correctly assigned, this lineage may have been in place 56 Ma, an order of magnitude longer than has been suggested by recent dated phylogenies (Testo & Sundue 2016).

An Eocene fossil representing *Cyclosorus s.l.* was recently described from southern China, but it could not be assigned more precisely due to lack of preservation of diagnostic features (Naugolnykh et al. 2016). The fossil taxon *Pronephrium stiriacum* (Unger) Knobloch & Kvacek is represented from Eocene and Miocene deposits across much of Europe, and has been compared to the extant Chinese taxon *Menisciopsis penangianum* (=*Pronephrium penangianum*) (Collinson 2001). Since many tropical and subtropical lineages would have been able to withstand the warmer climatic conditions that predominated in boreal latitudes during the Eocene, and could potentially have taken advantage of intercontinental migration corridors during that period, these fossils would be especially valuable to inform in-depth studies of the historical biogeography of the family. North American Eocene fossils that may be assignable to Thelypteridaceae have been recovered from Washington state (Pabst 1968; Davies-Vollum & Wing 1998), Yellowstone National Park (MacGinite 1974), and Louisiana (Berry 1917), but are in need of further study and possible re-interpretation in light of modern phylogenetic work and recircumscription of genera.

Miocene deposits have yielded multiple valuable examples of fossil Thelypteridaceae that may be reasonably assigned to extant lineages. Among these are a fossil *Pneumatopteris s.l.* from New Zealand (Pole 1992). Based on the present taxonomic treatment, there is currently a monotypic genus, represented by *Pakau pennigera* (=*Pneumatopteris pennigera*), on New Zealand, which is distantly related to all other taxa included in *Pneumatopteris* sensu Holttum (1982). The New Zealand fossil may represent a close relative of that extant taxon.

Additional Miocene fossils include *Meniscium*, described by Sanin (2016) from the Cauca Valley of Colombia, and unlikely to be misidentified due to the well-preserved and highly distinctive venation. Several fossils from Assam, India, dating to the mid-late Miocene have been convincingly compared to the monotypic genus *Ampelopteris* (Mehrotra et al. 2011). A fossil of *Christella* from the middle Miocene in southern China was described by Naugolnykh et al. (2016). Finally, a late Miocene fossil referable to *Cyclosorus interruptus* was described from Argentina (Robledo et al. 2015). This determination is further supported by the fact that the fossil was collected with a fossil of *Blechnum serratiformis,* whose modern analog, *Telmatoblechnum serrulatum*, often grows with *Cyclosorus interruptus* in low-elevation inundated environments, frequently near the ocean, which is a habitat not shared with most other neotropical Thelypteridaceae.

In her 2001 review, Collinson reported that many Cenozoic fossils previously reported as *Dryopteris s.l.* (e.g., Pabst 1968) may be correctly assigned to *Cyclosorus s.l.*, based on catadromous anatomy of the laminae and characteristic venation. Based on her assessment, there are fossil representatives of Thelypteridaceae from all continents except Africa and Antarctica, although no attempts have been made to classify them according to our current understanding of modern lineages.

GEOGRAPHICAL DISTRIBUTION

The family is globally distributed, with its constituent species occupying a wide range of habitats. Essentially all species are terrestrial or, less commonly, saxicolous, with few instances of epiphytism. Members of the family may be found in alpine meadows, boreal forests, tropical forests, and brackish wetlands near sea level. Habitat specialists include rheophytes in several genera, distributed in both the Neotropics and Paleotropics, and several lineages of diminutive rock-ferns, exemplified by the calciphilic *Goniopteris* of the Antilles (Proctor 1985, 1989) and some *Nannothelypteris* (=*Pronephrium s.s.*) of the Moluccas (Kato 1997).

Geographic distributions of genera within fern families exhibit strikingly different patterns. For example, genera of Cyatheaceae are distributed throughout the tropics and are generally present on multiple continents; this is interpreted as consistent with Gondwanan vicariance (Korall & Pryer 2014). The Polypodiaceae illustrate two different patterns, with the non-grammitid genera segregating cleanly into distinct neotropical and paleotropical radiations with few exceptions, while the biogeographic patterns of the grammitid clade display evidence of multiple long-distance dispersal events (Sundue et al. 2014). Distribution patterns within the Thelypteridaceae are likely explained by a combination of intercontinental migration and long-distance dispersal, although most genera show strong fidelity to a region or continent.

Although most genera tend to show relatively narrow geographic affinities, a few small genera of Thelypteridaceae are widely distributed, exemplified by the pantropical *Cyclosorus interruptus*. Other taxa, such as *Strophocaulon unitum* (=*Sphaerostephanos unitus*) and *Ampelopteris prolifera* are widespread in the Paleotropics and occur on both sides of the Indian Ocean. The genus *Leptogramma* is unusual within the family in that it is represented by species in Asia, Africa, and North America. Although the neotropical genera *Goniopteris*, *Meniscium*, and *Steiropteris* do not occur outside the Americas, the genus *Amauropelta*, which tends to occupy higher elevations than the other genera, has succeeded in colonizing Africa (Holttum 1974a) and several oceanic islands including Tristan da Cunha in the Atlantic (Christensen 1940) and Hawaii, Tahiti, and Rapa in the Pacific (Holttum 1977b).

Frost-prone northern latitudes have far fewer species of Thelypteridaceae than tropical regions, but a few genera have circumboreal distributions. Among temperate lineages, this pattern is exemplified by the triploid cytotype of *Phegopteris connectilis*, which is widespread throughout Asia, Europe, and North America (Patel et al. 2019b). *Oreopteris* occupies the most northerly and high-elevation habitats. *Oreopteris quelpartensis* extends from Korea to Washington State along the margins of the Bering Sea, including Siberia and Alaska, with a disjunct occurrence in Newfoundland. The other species are known from Europe (*O. limbosperma*) and from the eastern Himalayas at elevations of 4200 m in Sikkim (*O. elwesii*). The genus *Coryphopteris*, which is predominantly tropical-montane, includes temperate species in Asia, along with a single North American species, *C. simulata*, recently shown to belong in this clade (Fawcett 2018). As discussed by Wagner (1979), there is a strong positive relationship between the proportion of free-veined taxa with deeply divided leaves and higher latitudes and elevations, while reticulate-veined taxa with less divided leaves occur at lower latitudes and elevations; however, the biological implications of this pattern have yet to be addressed.

The aforementioned *Pakau pennigera* marks the most southerly distribution of any species in the family. It is widespread in temperate regions of New Zealand, and extends into Southeast Australia and Tasmania. *Thelypteris s.s.*, now recognized as having only two species, is widely distributed throughout boreal, temperate, tropical, and subtropical regions of all continents except Antarctica and Australia, although it does occur in New Zealand (Tryon 1971; Tryon et al. 1980).

Ferns are generally not considered especially weedy (with major exceptions, such as *Pteridium aquilinum* and *Salvinia molesta*), but a few paleotropical members of the Thelypteridaceae have become extremely widespread and have naturalized throughout the global tropics. These are *Amblovenatum opulentum, Macrothelypteris torresiana*, and *Christella dentata*. The appearance and subsequent spread of *Christella dentata* was documented in part though study of herbarium specimens (Strother & Smith 1970). Since it was first collected in the Americas in 1908, this species has spread to all regions of the tropics in the Americas, Africa, Asia, and the Pacific Islands, and is a common greenhouse weed. It is likely the most frequently collected fern in the New World, perhaps owing to its abundance in disturbed areas.

PREVIOUS PHYLOGENETIC STUDIES

Although the circumscription of the Thelypteridaceae was more or less established a century ago (Christensen 1913, 1920), relatively few hypotheses about relationships within the family have been proposed. Ching proposed a system of tribes and subtribes (1963), informed in large part by cytological data. Loyal (1963), Smith (1971), and Pichi Sermolli (1977) published dendrograms of hypothetical relationships among genera. Holttum (1982), who was most familiar with the diversity of the family, often commented on the affinities among what he believed to be allied genera.

The first molecular phylogeny of the family was published by Smith and Cranfill (2002). Their sampling design included samples of 27 genera represented by DNA sequence data from three chloroplast markers, which effectively established the backbone and overall structure within the family, including the recognition of two major clades, now classified as subfamilies Phegopteridoideae and Thelypteridoideae (PPG I 2016). The clade corresponding to Thelypteridaceae was perfectly concordant with the family circumscription proposed by Iwatsuki (1964a, 1964b), Holttum (1971), Pichi Sermolli (1977), and Smith (1990), which was demonstrated by the sampling of taxa historically treated as members of the family, but excluded by those authors, e.g., *Gymnocarpium* and *Hypodematium*, now widely recognized in the Cystopteridaceae and Hypodematiaceae, respectively (PPG I 2016).

Subsequent publications have contributed additional phylogenetic sampling, allowing the monophyly of generic concepts to be tested (Schuettpelz & Pryer 2007; Ebihara et al. 2011; He & Zhang 2012; Almeida et al. 2016). The most recent and densely sampled Sanger sequencing-based phylogeny includes 203 taxa and 11 gene regions, representing approximately 20% of the species diversity in the family (Patel et al. 2019a). Following the taxonomy proposed by PPG I, Patel et al. (2019a) found that of the 20 genera represented by more than one species, 12 were resolved as monophyletic, while eight were not, including *Amauropelta, Coryphopteris, Christella, Parathelypteris, Pneumatopteris, Pronephrium, Pseudocyclosorus, and Sphaerostephanos. Christella* was represented by two clades, corresponding to *Christella* sections *Pelazoneuron* and *Christella* (Holttum 1974a), as was first suggested by the data presented by Smith and Cranfill (2002). Additionally, Schuettpelz & Pryer (2007), He and Zhang (2012), and Patel et al. (2019a) found that *Pronephrium* is non-monophyletic; however, clades partly corresponding to the infrageneric taxa of *Pronephrium* recognized by Holttum (1982) were resolved. Due to limited sampling, and in anticipation of a phylogenomic nuclear dataset, taxonomic changes were not proposed.

The classification system proposed here benefits from a recent phylogenomic study that included 621 samples, representing nearly half of the 1206 minimum rank taxa here recognized in the family, more than tripling the number of accessions previously included in a molecular study (Fig. 1, Fawcett et al. 2020; Fawcett et al. in press). The data were generated using the *GoFlag 408* probe set designed by Breinholt et al. (2021) to generate genomic sequences for a diversity of flagellate plants (i.e., plants with flagellate sperm, including bryophytes, some gymnosperms, lycophytes, and ferns). The targeted enrichment dataset for Thelypteridaceae included 407 nuclear loci, resulting in an alignment of about 500,000 bp, with each taxon represented by 379 of the 407 loci, on average (Fawcett et al. 2020). This increased sampling, which emphasized the most problematic taxa, and expanded genomic coverage, resolved relationships within the family and enables important improvements to the classification system proposed by Holttum (1971, 1974a, 1977b, 1982), which was largely adopted by PPG I (2016).

TAXONOMIC TREATMENTS

Descriptions are provided for all 37 genera included in our classification. These are listed alphabetically and include generic etymology, a description of morphology, a diagnosis, a discussion of biogeography and ecology, and of taxonomic and phylogenetic studies, new combinations, and a list of constituent species and taxa that are *incertae sedis*. With a few exceptions, no combinations are made for taxa below species rank. This does not reflect a judgment on the taxonomic importance of these taxa, but rather insufficient data to support their recognition or rejection. Our species circumscriptions, especially for genera that have not been recircumscribed here, largely follow previous authors. Our focus is on generic delimitation, rather than a species-level revision. Accordingly, we do not list heterotypic synonyms unless we have studied the types ourselves, out of a desire not to perpetuate the inevitable oversights of earlier workers. In nearly all cases, complete synonymy has been provided by floristicians or monographers in recent treatments (e.g., Holttum 1974a, 1977b, 1982; Smith 1971, 1980; Palmer 2003, etc.). Instead of duplicating parts of their work, we reference their treatments herein. Apart from basionyms, older generic names that are no longer in use for extant taxa, e.g., *Aspidium, Nephrodium,* and *Lastrea*, are not given. Other synonyms, in genera such as *Dryopteris* and *Polypodium*, have not been used to refer to members of the Thelypteridaceae for 80 years (since Ching 1940) and are also excluded from synonymy. Most modern names in currently recognized genera of Thelypteridaceae are included for new combinations, though we have excluded some recently published names that have not been adopted in taxonomic or floristic literature, and have not gained currency. Chromosome counts are taken from Rice et al. (2015) and references therein, unless otherwise noted.

Although we have made an attempt to account for each species within the Thelypteridaceae, a number of taxa remain *incertae sedis*, listed under the treatment(s) where we believe they most likely belong. The two primary reasons for our difficulty in classifying these taxa are: type material is unavailable for study, is incomplete, and/or the original descriptions are lacking sufficient detail for confident placement; or that we believe the taxon warrants recognition, but the morphology is ambiguous, anomalous, or intermediate between our existing generic concepts. In both cases, our understanding is often limited because the species are rare, both in herbaria and in nature; they have not been included in molecular phylogenetic studies; descriptions fail to address the characters that we consider diagnostic; and few or no specimens have been digitized. There have been many new herbarium collections made since Holttum (1982); however, nearly a third of species in some genera (e.g., *Chingia, Plesioneuron*, *Sphaerostephanos*) remain known only from the type or one or two other collections, preventing an understanding of intraspecific variability and species boundaries. Especially for Afro-Madagascan and New Guinean taxa, a lack of both molecular data and herbarium collections inhibits an unequivocal assignment of certain species.

The goal of the present work is to develop a system of generic classification. Because our sampling of one representative per species was designed with this objective in mind, our data are ill-suited to addressing hypotheses of species circumscription. Nearly all genera of Thelypteridaceae lack modern monographs that incorporate molecular data with species sampled across their geographic ranges (but see Kuo et al. 2019). Our hope is that future work will include more detailed studies addressing species level circumscriptions, and incorporate careful study of the types of heterotypic synonyms not considered here.

Within the lists of constituent species, taxa included in the 407 nuclear locus phylogenomic study of Fawcett et al. (2020; in press) are indicated with an asterisk (*), and alignments, trees, and voucher information are available on Dryad: doi.org/10.5061/dryad.gxd2547j4. The raw data are archived at the NCBI Sequence Read Archive, BioProject 646399, available at: ncbi.nlm.nih.gov/bioproject/646399. Taxa not included in Fawcett et al. (in press), but represented by published Sanger sequence data are indicated by (**). In nearly all cases these taxa were included in Patel et al. (2019a), which incorporated sequence data from He & Zhang (2012) and Almeida et al. (2016), among other studies. For *Leptogramma* and *Stegnogramma*, (**) indicates inclusion in Kuo et al. (2019).

The key to genera presented here is not intended to be an exhaustive guide to the approximately 1200 species of Thelypteridaceae, but rather a general guide to be used in conjunction with the descriptions. The descriptions provide the most frequent character states for each genus, while also seeking to account for the variability within the genus.

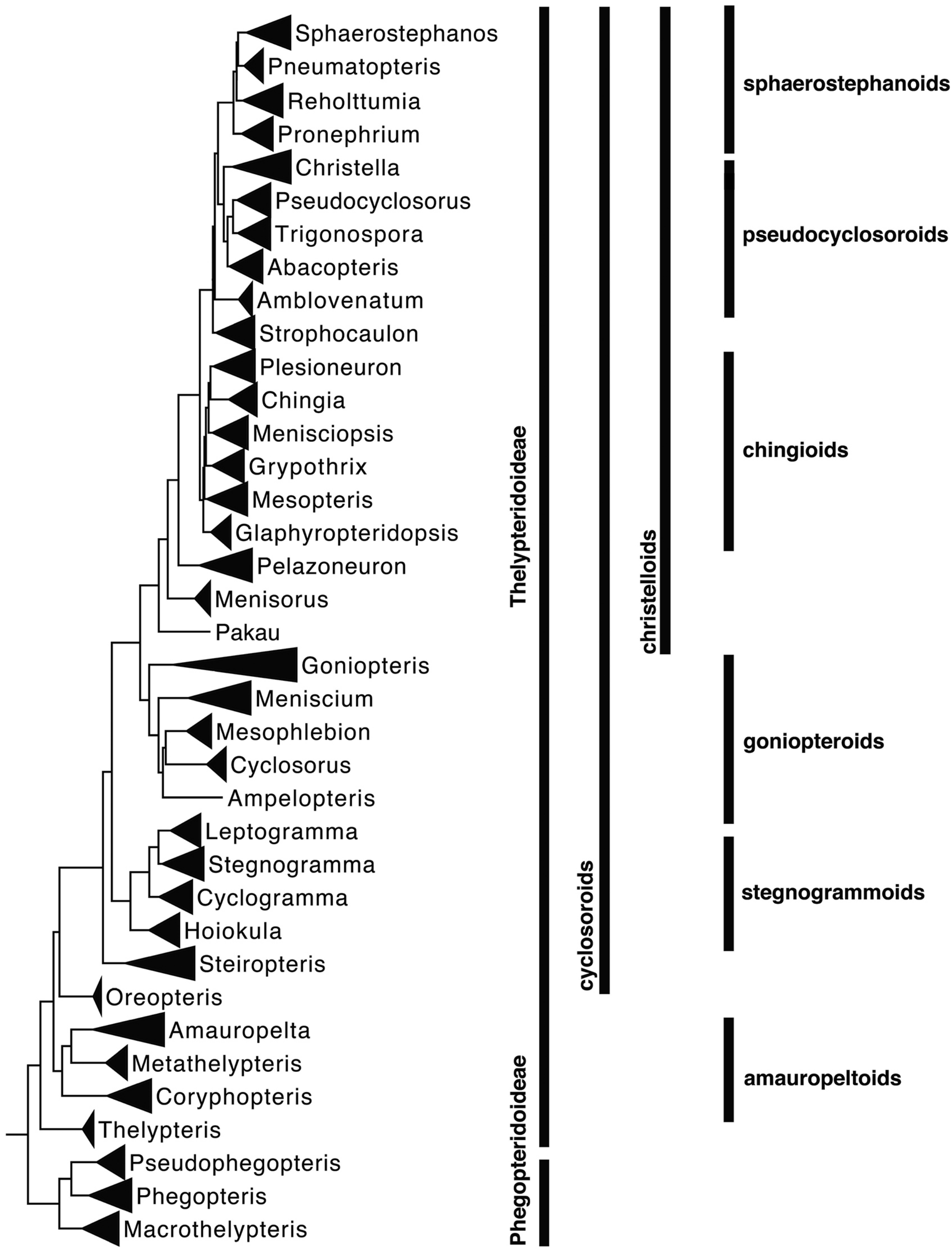

Fig. 1. A synoptical tree illustrating relationships among genera of Thelypteridaceae based on Fawcett et al. (in press).

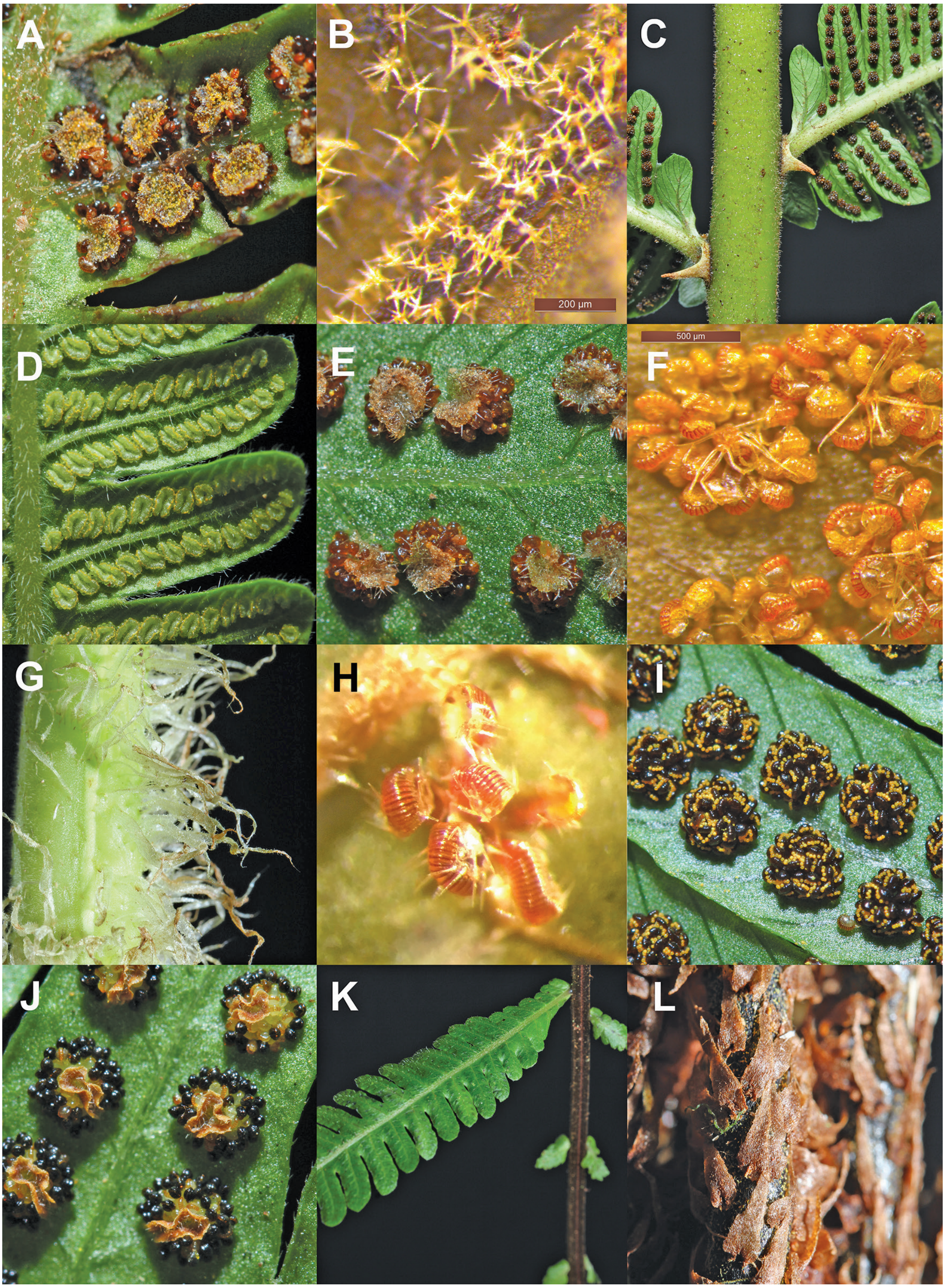

Fig. 2. Morphology of the Thelypteridaceae. **A.** *Coryphopteris kolombangarae, SITW07554* (TAIF), glandular indusia. **B.** *Goniopteris yaucoensis, Proctor 43584* (US), stellate hairs along adaxial costa. **C.** *Pneumatopteris glandulifera, SITW11069* (TAIF), peg-like aerophores at pinna bases. **D.** *Sphaerostephanos polycarpos, SITW11070* (TAIF), marginally glandular indusia. **E.** *Sphaerostephanos doodioides, SITW05702* (TAIF), setose indusia, spherical glands on indusia, sporangia, and laminar tissue. **F.** *Goniopteris reptans, Wright 813* (US), sori with shriveled, setose indusia, some hairs furcate. **G.** *Macrothelypteris polypodioides, SITW11122* (TAIF), stipe scales. **H.** *Hoiokula pendens, Hobdy 2664* (UC), setulose sporangia. **I.** *Plesioneuron imbricatum, SITW05370* (TAIF), exindusiate sori, sporangia with spherical glands. **J.** *Christella dentata, SITW10525* (TAIF), shriveled, setulose indusia. **K.** *Sphaerostephanos heterocarpos SITW11079* (TAIF), abruptly reduced proximal pinnae, adaxial surface with acicular hairs. **L.** *Coryphopteris subbipinnata, SITW11667* (TAIF), appressed stipe base scales, these marginally setulose. All photos by Cheng-Wei Chen except B, F, and H by Susan Fawcett.

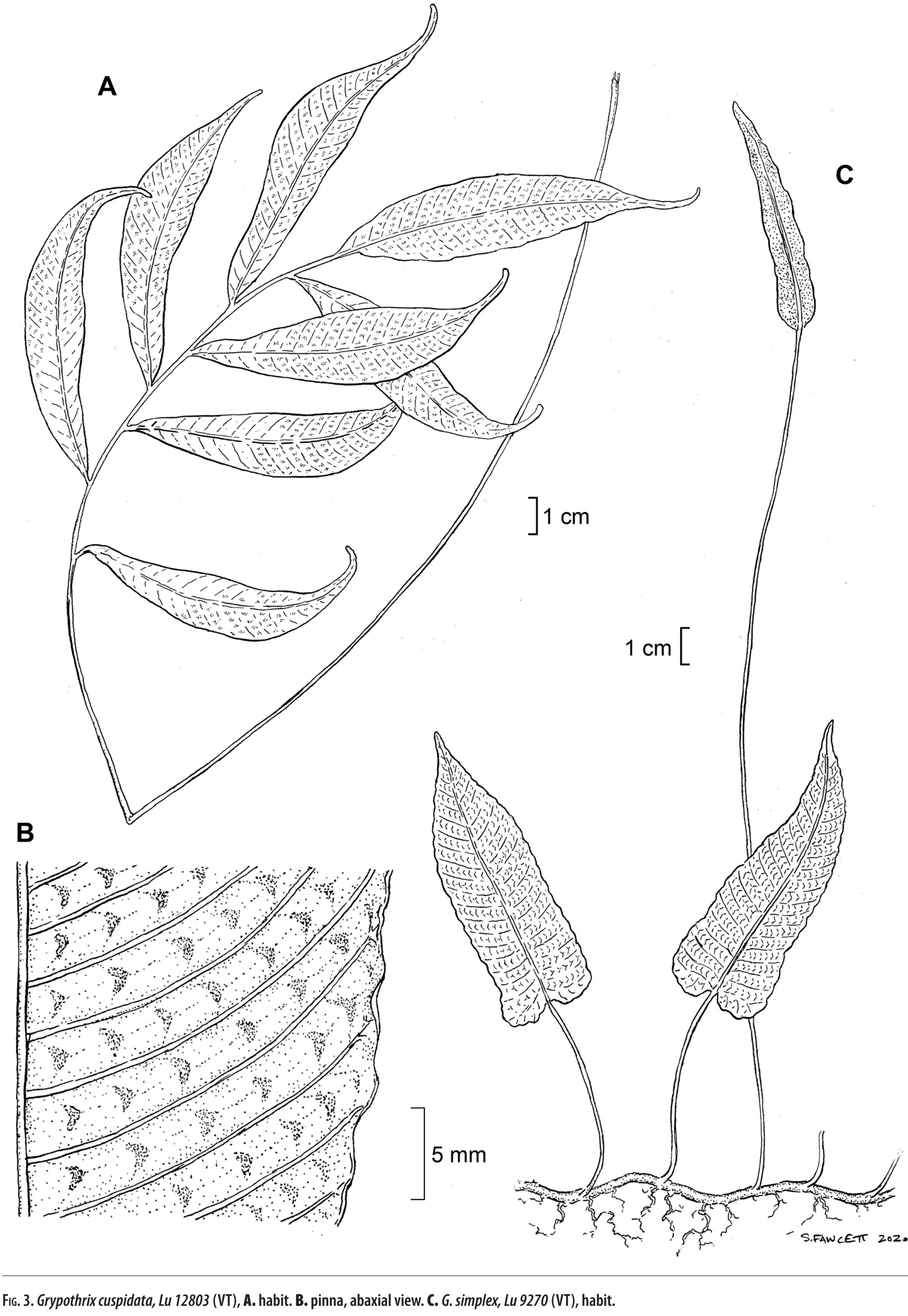

Fig. 3. *Grypothrix cuspidata, Lu 12803* (VT), **A.** habit. **B.** pinna, abaxial view. **C.** *G. simplex, Lu 9270* (VT), habit.

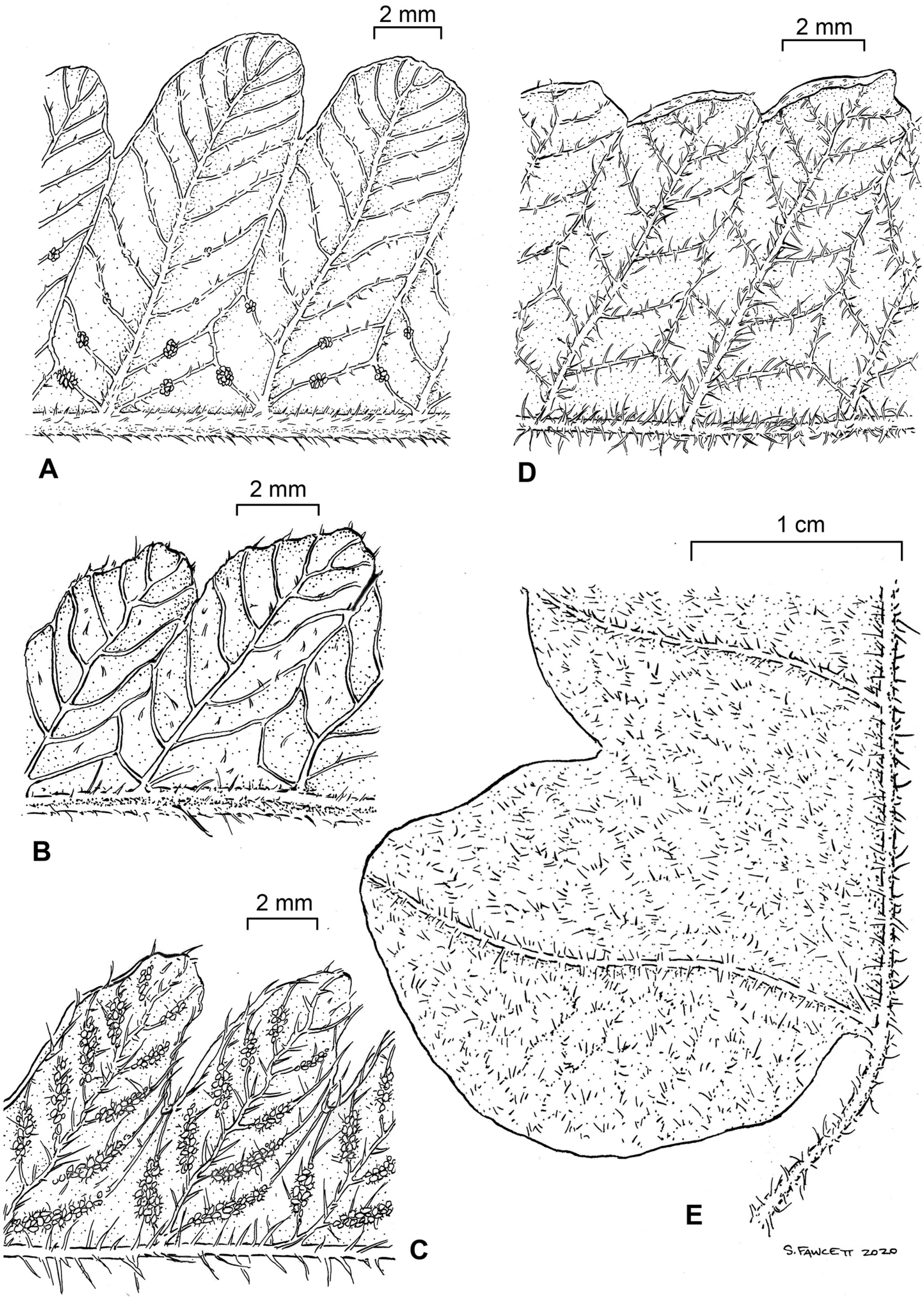

Fig. 4. A. *Hoiokula sandwicensis, Aborn s.n.* (VT), pinna lobes, abaxial view. **B.** *Hoiokula pendens, Hobdy 2664* (UC), pinna lobes, adaxial view. **C.** *Leptogramma pilosa, Diaz 6621* (UC), abaxial pinna lobes. **D.** *Stegnogramma aspidioides, Palmer 1035* (UC), abaxial pinna. **E.** *Stegnogramma wilfordii, Boufford 20159* (VT), proximal portion of lamina, abaxial view.

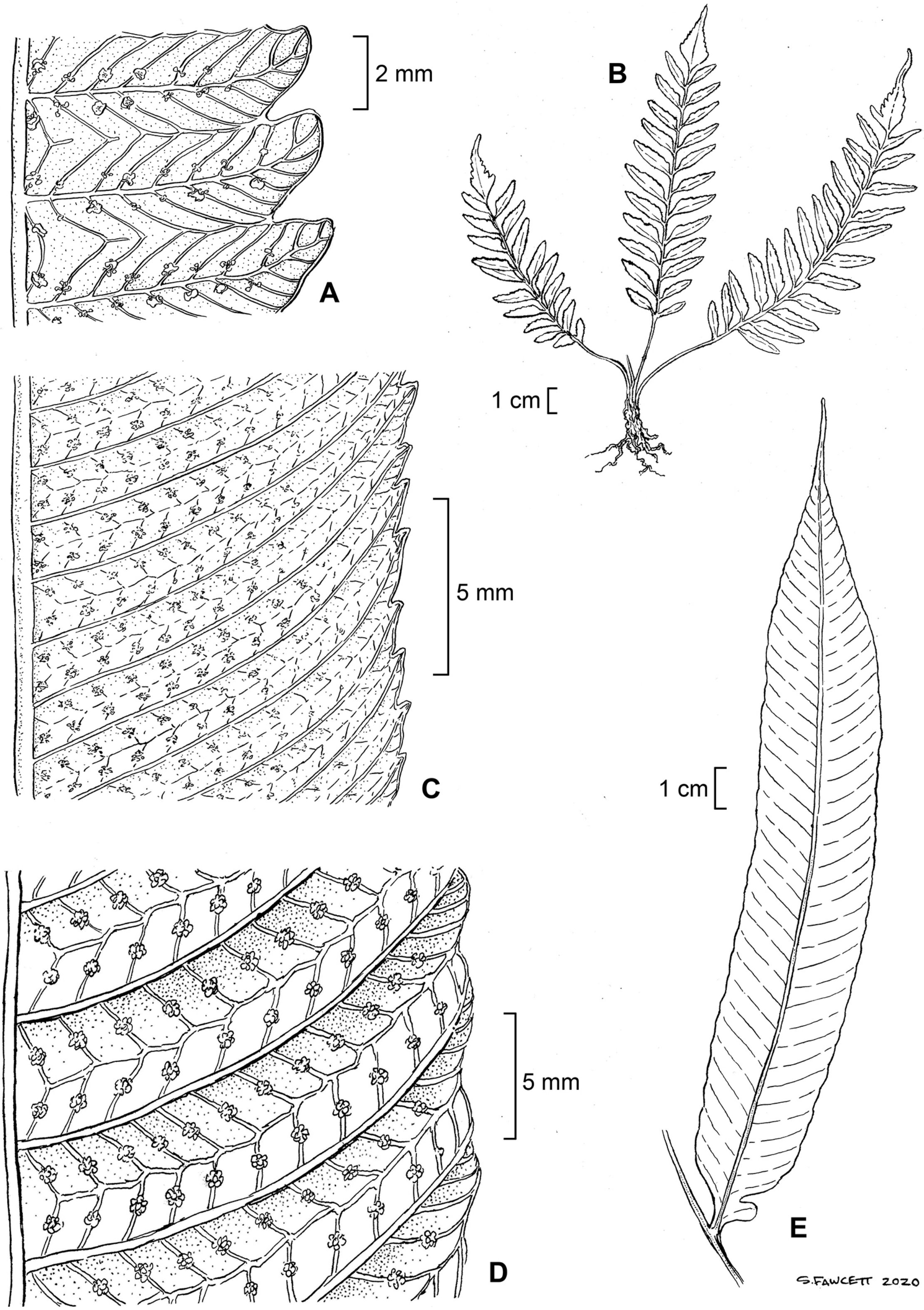

Fig. 5. A. *Menisciopsis cyatheoides, Takeuchi 1719* (UC), pinna lobes, abaxial view. **B.** *M. boydiae, Baldwin 116* (US), habit. **C.** *Menisciopsis rubrinervis, Fawcett 716* (VT), pinna, abaxial view. *Abacopteris aspera, James 1693* (VT). **D.** pinna. **E.** pinna, abaxial view.

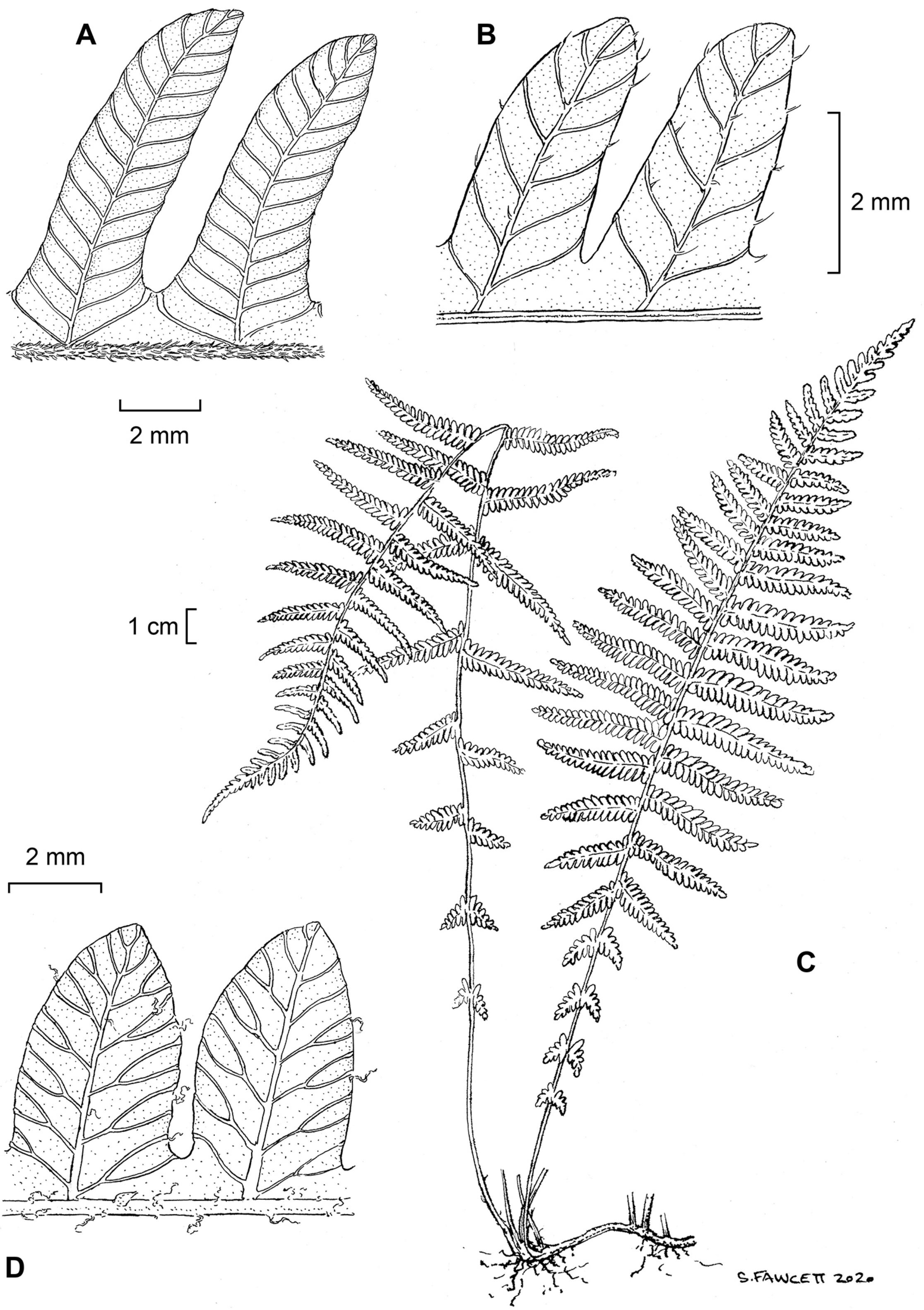

Fig. 6. A. *Plesioneuron hopeanum, Fawcett 613* (VT), pinna lobes, adaxial view. *Amauropelta* (subg. *Nibaa*) *noveboracensis, Fawcett 567* (MICH, VT), **B.** pinna-lobes, adaxial view. **C.** habit. **D.** *Thelypteris palustris, Fawcett 569* (VT), pinna lobes abaxial view.

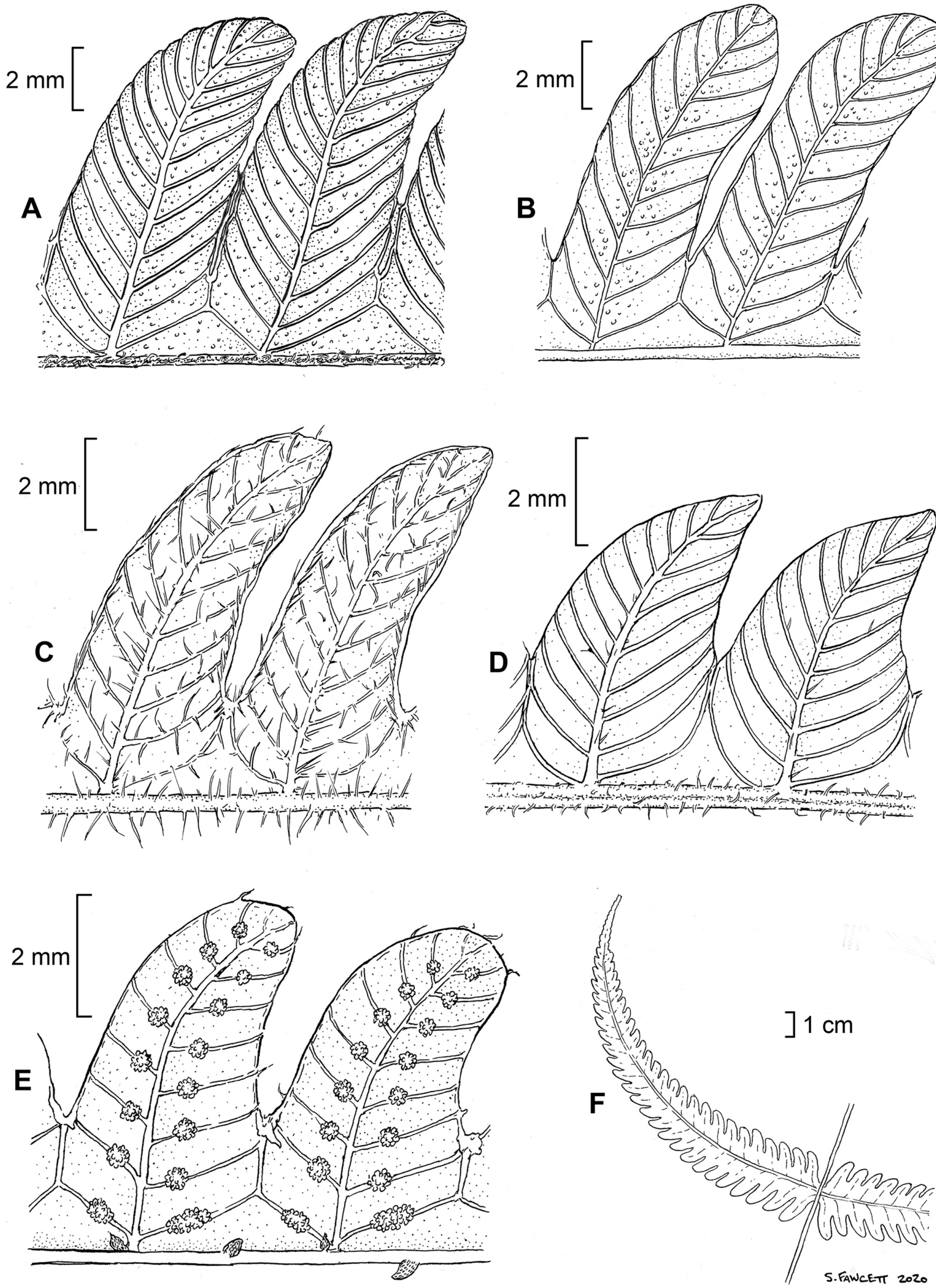

Fig. 7. A. *Pneumatopteris parksii, Fawcett 645* (UC), pinna lobes, adaxial view. **B.** *Reholttumia magnifica, Fawcett 676* (VT), pinna lobes, abaxial view. **C.** *Pelazoneuron patens, Fawcett 744* (VT), abaxial pinna-lobes. **D.** *P. serra, Fawcett 1034* (VT), adaxial pinna lobes. **E.** *Pakau pennigera, Given 11842* (VT), pinna lobes, abaxial view. **F.** *Pakau pennigera, Stuart s.n.* (VT), pinna.

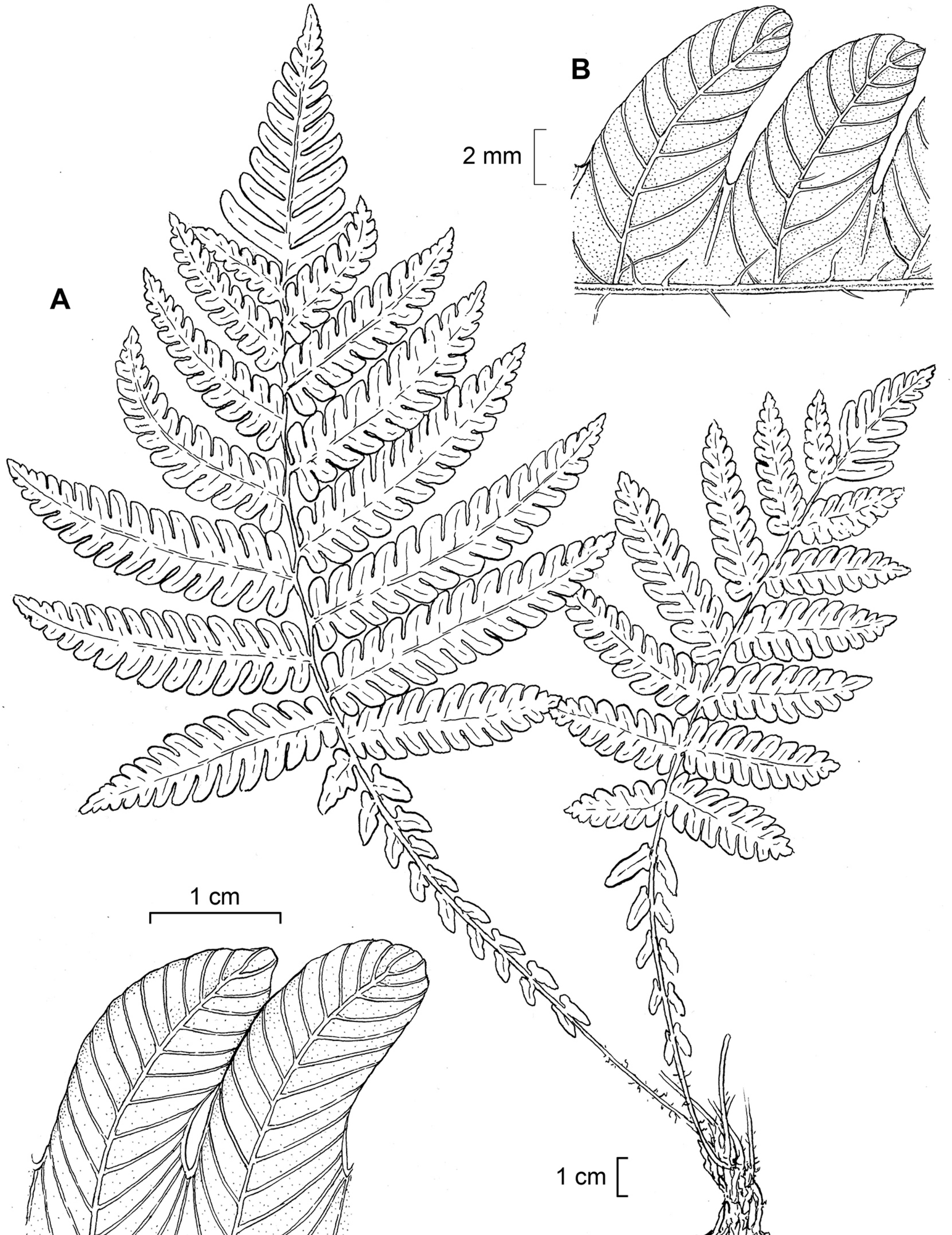

Fig. 9. ***Steiropteris deltoidea, Fawcett 464*** **(VT) A. habit. B. pinna lobes, adaxial view. C.** ***Mesophlebion*** **sp.,** ***Karger 1796*** **(VT), pinna lobes, abaxial view.**

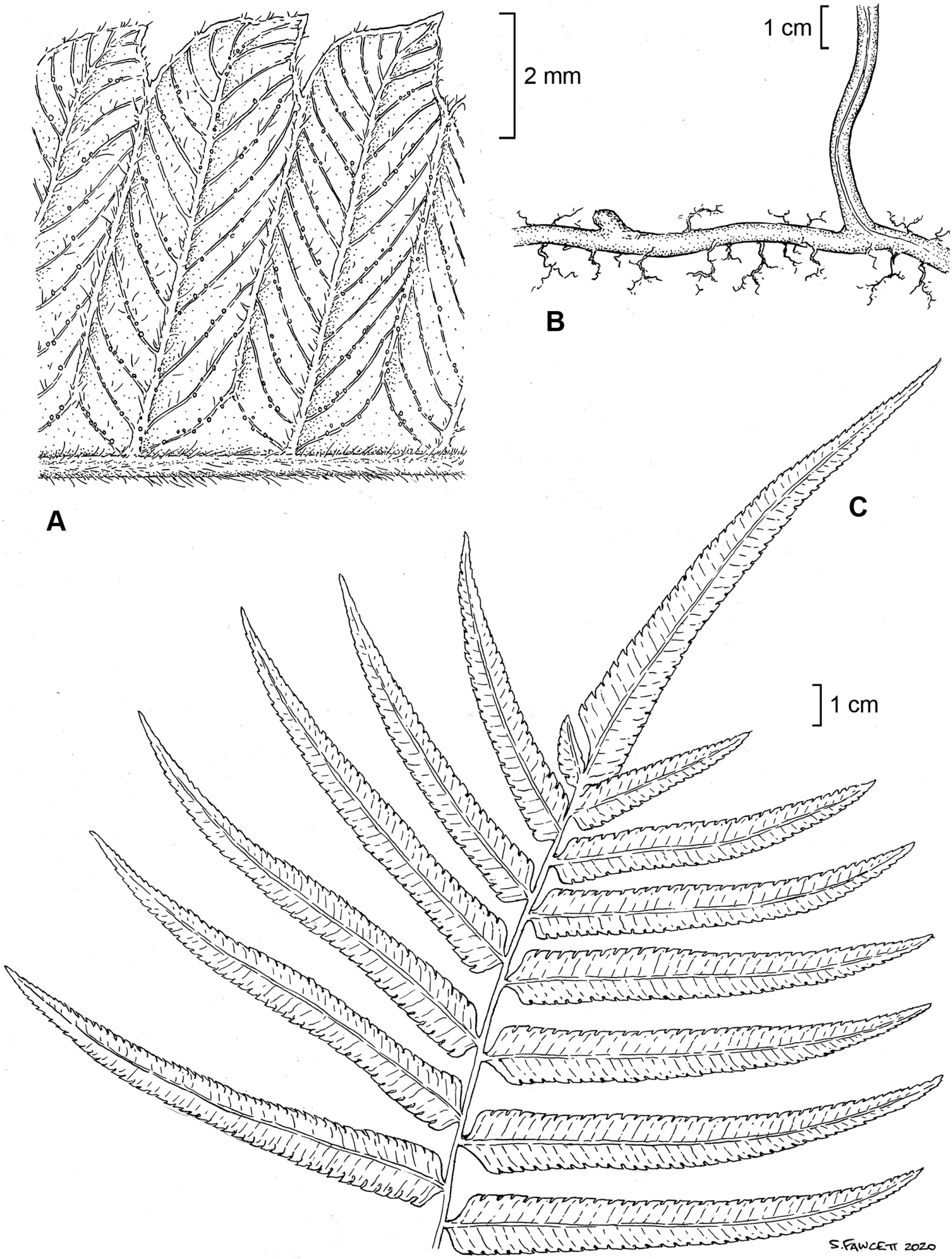

Fig. 10. ***Strophocaulon unitum, Fawcett 641*** **(VT), A. pinna lobes, abaxial view. B. rhizome. C. laminar apex.**

KEY TO GENERA OF THELYPTERIDACEAE

1. Adaxial costae not grooved; veins terminating before reaching laminar margins.
  2. Laminae ovate to lanceolate; sori indusiate; scales restricted to stipe bases ____ **Metathelypteris**
  2. Laminae deltate, ovate, or lanceolate; sori exindusiate or with very small indusia < 3 mm diam.; scales sometimes present on stipes and costae.
    3. Sori exindusiate, linear to elongate; sporangial capsules densely setulose; veins mostly simple; $x = 36$ ____ **Leptogramma**
    3. Sori indusiate or exindusiate, round to slightly oblong; sporangia glabrous or with few setae; veins mostly forking; $x = 30, 31$.
      4. Medial pinnae mostly adnate; laminae pinnatifid or pinnate-pinnatifid; stipe scales with marginal setae; $x = 30$; temperate or paleotropical-montane ____ **Phegopteris**
      4. Medial pinnae free (adnate only towards frond apices); laminae pinnate-pinnatifid to bipinnate or more divided; stipe scales with marginal and surperficial setae; $x = 31$; paleotropical.
        5. Medial pinnae mostly opposite; sori exindusiate; stipe scales brown, and of uniform thickness; hairs on laminae unicellular ____ **Pseudophegopteris**
        5. Medial pinnae mostly alternate; sori indusiate or exindusiate; stipe scales typically pale and thickened at base; hairs on laminae often septate ____ **Macrothelypteris**
1. Adaxial costae grooved; veins mostly reaching laminar margins.
  6. Veins free.
    7. Three or more pairs of proximal pinnae greatly reduced.
      8. Proximal pinnae abruptly reduced to a series of auricles subtended by peg-like aerophores; strictly paleotropical ____ **Pseudocyclosorus**
      8. Proximal pinnae gradually reduced, rarely abruptly reduced to auricles subtended by peg-like aerophores; mostly neotropical, temperate, or boreal.
        9. Stipe scales with papillose outgrowths along margins; boreal and paleotropical-montane; $x = 34$ ____ **Oreopteris**
        9. Stipe scales various, often marginally setulose; mostly neotropical, subtropical, or north-temperate; $x = 27, 29, 31$ ____ **Amauropelta**
    7. Fewer than three pairs of proximal pinnae greatly reduced, or none reduced.
      10. Fronds winter-deciduous; plants mostly of temperate regions; rhizomes creeping.
        11. Fronds weakly dimorphic; ovate scales present on abaxial costae; veins often forked; laminar glands lacking; $x = 35$ ____ **Thelypteris**
        11. Fronds monomorphic; scales absent on abaxial costae; veins almost always simple; sessile or stipitate glands sometimes present on lamina; $x = 27, 31, 32, 33$.
          12. Pinna segments subentire, often tapering, oblique to costae and apices acute; glands absent or orange-yellow, spherical or hemispherical; most spp. $x = 27, 31$ ____ **Amauropelta**
          12. Pinna segments entire, parallel sided, nearly perpendicular to costae and apices rounded or truncate; glands usually reddish, viscid and hemispherical; $x = 31, 32, 33$ ____ **Coryphopteris**
      10. Fronds not winter-deciduous; plants of tropical and subtropical regions; rhizomes various.
        13. Plants mostly of rocky riverbeds and streamsides; rhizomes (caudices) erect; spores trilete ____ **Trigonospora**
        13. Plants of various habitats; rhizomes creeping, ascending or erect; spores monolete.
          14. Pinnae with peg-like aerophores at bases; developing fronds covered in mucilage; neotropical ____ **Steiropteris**
          14. Pinnae without aerophores (except *Cyclogramma*), or these present as inconspicuous swellings; mucilage rare or unknown; paleotropical.
            15. Indument of abaxial axes and sporangia of hooked and straight setae; spores coarsely echinate or with reticulate crests ____ **Cyclogramma**
            15. Indument of abaxial axes lacking hooked hairs; sporangia usually lacking setae; spores variously ornamented.
              16. Plants mostly < 50 cm; rhizomes forming erect caudices; abaxial laminae with hemispherical resinous glands; scales often present on abaxial axes ____ **Coryphopteris**
              16. Plants mostly > 50 cm; rhizomes creeping to erect; glands absent or various; scales typically absent on abaxial axes.
                17. Abaxial laminae with amber to reddish translucent hemispherical glands; fronds drying reddish and bicolorous ____ **Mesopteris**
                17. Abaxial laminae lacking glands, or glands spherical, sulfur-colored and opaque; fronds drying greenish or brown and concolorous.
                  18. Sori inframedial, often overlapping costules; all pinnae opposite or subopposite ____ **Glaphyropteridopsis**
                  18. Sori medial to inframarginal; distal pinnae usually alternate.
                    19. Medial pinna with bases asymmetrical, cuneate or rounded; laminae chartaceous to stiffly coriaceous ____ **Plesioneuron**
                    19. Medial pinna with bases more or less symmetrical, truncate; laminae membranaceous to chartaceous ____ **Amblovenatum**
  6. Veins connivent at or near sinuses, or anastomosing below the sinuses and forming an excurrent vein to sinus.
    20. At least some veins connivent at sinuses or running to sinuses without merging.
      21. Veins running alongside non-vascularized cartilaginous keel below sinus.
        22. Sporangial stalks each with a multicellular stalk capped by a spherical reddish to orange gland; costae, costules, and veins abaxially bearing narrow scales; paleotropical ____ **Mesophlebion**
        22. Sporangial stalks lacking stalked glands; axes usually lacking scales abaxially; neotropical ____ **Steiropteris**
      21. Veins connivent at or just below sinuses, cartilaginous keel absent.
        23. Sessile glands absent from laminar axes and tissue, but short-stipitate light yellowish glands often present; all veins connivent at or just below sinuses; neotropical ____ **Pelazoneuron**

23. Glands present on abaxial laminae; veins connivent at or just below sinuses, anastomosing below sinuses, or sometimes free; paleotropical.
24. Adaxial laminar axes with hyaline acicular hairs; abaxial laminae with opaque sulfur-colored or pale yellow spherical glands; laminae drying concolorous green or olivaceous ____ **Amblovenatum**
24. Adaxial laminar axes glabrous, or with short-stipitate glands, abaxial laminae with translucent reddish to orangish hemispherical glands; laminae drying bicolorous and reddish ____ **Mesopteris**
20. At least one pair of veins anastomosing below the sinus, forming excurrent vein.
25. Pinnae entire, subentire, or shallowly lobed, typically incised less than 1/3 to costae.
26. Sori linear to slightly elongate, exindusiate; adaxial laminae with abundant simple hairs between veins; sporangial capsules densely setulose.
27. Spores winged; endemic to Hawaiian Islands ____ **Hoiokula**
27. Spores echinate; native to Eurasia, Africa, Mexico or Alabama.
28. Veins with two or fewer intersegmental areoles, or veins free ____ **Leptogramma**
28. Veins with at least three intersegmental areoles, or veins irregularly anastomosing ____ **Stegnogramma**
26. Sori mostly round (sometimes elongate), indusiate or exindusiate; adaxial laminae glabrous or sparsely hairy; sporangial capsules glabrous, glandular, or setulose.
29. Stellate or furcate hairs usually present, most easily observed on costae, rachis, and stipe base scales; neotropical ____ **Goniopteris**
29. Hairs all unbranched (some furcate in *Ampelopteris*); paleotropical (except *Meniscium*).
30. Sporangial stalks each with a multicellular stalk capped by a spherical reddish to orange gland; fronds abundantly proliferous; mature fronds continuing to elongate ____ **Ampelopteris**
30. Sporangia stalks all lacking a reddish to orange multicellular gland; fronds proliferous or not; mature fronds with determinate growth.
31. Hook-shaped (hamate) hairs present on laminae, these most easily observed on abaxial axes ____ **Grypothrix**
31. Hairs needle-shaped (acicular).
32. Fronds nearly always with proliferous buds in axils of distal pinnae; endemic to Africa ____ **Menisorus**
32. Fronds rarely proliferous; rare or absent in Africa.
33. Fronds strongly dimorphic to subdimorphic; pinnae mostly < 4 cm wide; 4 or fewer vein pairs usually anastomosing below sinuses; sessile yellowish glands typically present on laminae, sporangia, and/or indusia.
34. Proximal pinnae not reduced; hairs lacking from adaxial laminae between veins ____ **Pronephrium**
34. Proximal pinnae usually reduced; hairs sometimes present on adaxial laminae between veins ____ **Sphaerostephanos**
33. Fronds monomorphic to subdimorphic; pinnae often > 4 cm wide; 5 or more vein pairs usually anastomosing below sinuses; sessile yellowish glands usually absent.
35. Sporangial capsules usually setulose; sori usually medial and discrete ____ **Abacopteris**
35. Sporangial capsules usually glabrous; sori inframedial or coalescent along cross-veins.
36. Laminae often drying reddish; proliferous buds absent; Asian, Malesian, and Hawaiian ____ **Menisciopsis**
36. Laminae drying greenish, olivaceous, or brown; proliferous buds sometimes present in axils of pinnae; neotropical ____ **Meniscium**
25. Pinnae incised more than 1/3 to costae.
37. Stellate or furcate hairs usually present, most easily observed on adaxial costae, rachis, and stipe base scales; neotropical ____ **Goniopteris**
37. Hairs all unbranched; mostly paleotropical.
38. Rhizomes forming trunk-like erect caudices; pinnae opposite; endemic to New Zealand and Australia ____ **Pakau**
38. Rhizomes creeping, ascending or erect; pinnae mostly alternate, at least distally; mostly paleotropical.
39. Rhizomes long-creeping (internodes > 3 cm), subterranean; fronds sclerophyllous, often in full or partial sun.
40. Ovate scales present on abaxial axes of laminae; sporangial stalks each with a multicellular stalk capped by a spherical reddish to orange gland; plants aquatic, of freshwater marshes and swamps; pantropical ____ **Cyclosorus**
40. Scales absent from abaxial laminae; sporangial capsules with sessile glands or setae; plants not of permanently inundated habitats; paleotropical ____ **Strophocaulon**
39. Rhizomes creeping (internodes < 3 cm), ascending, or erect; fronds membranaceous to chartaceous.
41. Hairs usually appressed and often present on adaxial laminae between veins.
42. Proximal pinnae typically gradually reduced; glands, if present, typically orange and clavate or pear-shaped; most diverse and abundant in continental southeast Asia and Indian subcontinent ____ **Christella**
42. Proximal pinnae mostly abruptly reduced; glands, if present, sessile, typically yellowish and spherical or oblate; most diverse and abundant in Malesia ____ **Sphaerostephanos**
41. Hairs, if present on adaxial laminae, usually spreading, mostly restricted to costae and rachis.
43. Sori inframedial to costular; stipe scales terete or linear-lanceolate and thickened, dark brown to black, dense and persistent, spreading ____ **Chingia**
43. Sori medial to inframarginal; stipe scales not terete, ovate to lanceolate, brown, often caducous, often appressed.
44. Aerophores peg-like, projecting from pinna and sometimes pinnule bases; proximal pinnae abruptly reduced to vestigial laminar fringe; fronds drying bicolorous, reddish ____ **Pneumatopteris**
44. Aerophores inconspicuous; proximal pinnae gradually reduced; fronds mostly drying concolorous green or olivaceous ____ **Reholttumia**

ABACOPTERIS

Abacopteris Fée, Gen. Fil. 309, t. 18C. 1852.—Type: *Abacopteris philippinarum* Fée, Congr. Sci. France 10(sess. 1):178. 1843. [= *Abacopteris aspera* (C. Presl) Ching, Acta Phytotax. Sin. 8:332. 1963, based on *Goniopteris aspera* C. Presl] (**Figs. 5D, 5E**).

Etymology.—Gr. *abakos*, abacus + *pteris*, fern. The venation and sori resemble an abacus, or counting frame; a calculating tool.

Plants terrestrial, medium to large (> 1m); **rhizomes** long-creeping, rarely short-creeping; **fronds** monomorphic, pinnate, erect to ascending; **stipes** stramineous, dull brown, or reddish, with hairy or glabrous brown linear-lanceolate scales on stipe bases and rhizomes; **blades** membranaceous to chartaceous, drying green, each with conform or rarely subconform terminal pinna (*A. hirtisora*) and no proliferous buds, proximal pinnae not or only slightly reduced; **pinnae** entire to crenate or shallowly lobed < 1/3 to costae (*A. hirtisora*), bases cuneate or truncate, sessile or short-petiolulate; **veins** prominent abaxially, many pairs anastomosing between secondary veins (costules), with excurrent included veinlet, or continuous excurrent vein that is usually straight (occasionally zig-zag), costae adaxially grooved; **aerophores** present as darkened swellings at pinna bases; **indument abaxially** of hairs on and between veins, sometimes grading into small clear stipitate glands; **indument adaxially** of hyaline, unicellular, acicular hairs on costae and veins; **pustules** absent or sometimes present on adaxial lamina; **sori** round, medial, rarely coalescent (e.g., *A. gymnopteridifrons*), indusiate or exindusiate, indusia light brown and hairy when present (e.g., *A. aspera*); **sporangia** usually setulose, rarely glabrous; **spores** light brown or black, in *A. aspera* with fimbriate crests (Patel 2019a); $x = 36$, with diploids and tetraploids known.

Diagnosis.—*Abacopteris* is distinguished from *Pronephrium s.s.* and *Sphaerostephanos* by monomorphic fronds and lack of yellow spherical glands on indusia. It is distinguished from *Grypothrix* by lack of hamate hairs, and from *Menisciopsis* and *Grypothrix* by sori medial and discrete (rarely coalescent or inframedial), setulose sporangia, and fronds often membranaceous and rarely drying reddish. For complete synonymy, see Holttum (1972, 1974a, 1982) and Lin et al. (2013).

Biogeography and ecology.—*Abacopteris* comprises about 14 species. Most of the species diversity of *Abacopteris* is restricted to continental South Asia, at lower elevations up to about 1800 m. Several species were recently described by Lin et al. (1999) in *Pronephrium,* most of which are narrow endemics in China, and known only from the type collections at PE. *Abacopteris gymnopteridifrons* is distributed in southern China and the Philippines, and the variable and widespread *A. aspera* occurs throughout Malesia, northern Queensland, Australia, and into the Pacific (Holttum 1982) as far east as Fiji. The earliest diverging species in the genus is *A. hirtisora*, which occurs in Laos, India, and Thailand (Lin et al. 2013).

Taxonomic and phylogenetic studies.—Holttum (1971, 1982) treated *Abacopteris* as a synonym of *Pronephrium*, an earlier name. However, the type of *Pronephrium*, *P. lineatum*, shares many morphological features (e.g., dimorphic fronds, indusia with spherical yellow glands) with members of Holttum's *Pronephrium* sect. *Dimorphopteris*, and we believe it is allied more closely to those taxa than to the type of *Abacopteris*. In our view, the best solution is to resurrect the genus *Abacopteris*, and recognize a newly circumscribed *Pronephrium*, corresponding closely to Holttum's *Pronephrium* sect. *Dimorphopteris* (1982). Our current circumscription of *Abacopteris* includes members of Holttum's *Pronephrium* sect. *Pronephrium* (1972) and also some taxa he treated in sect. *Menisciopsis* (Holttum 1982). We also include here two species previously treated in *Sphaerostephanos* (*A. hirtisora, A. peltochlamys*). One of these, *A. peltochlamys*, was originally recognized in *Abacopteris* by Holttum (1954) but was later transferred to *Sphaerostephanos* (Holttum 1982). This species is unusual in having 2–4 pairs of proximal pinnae abruptly much reduced, and sporangia bearing stipitate glands. For further discussion on the treatment of *Pronephrium* sensu Holttum and our recircumscription, see our description of *Pronephrium*.

In the Thelypteridaceae phylogeny (Fawcett et al. in press) *Abacopteris* is a member of the pseudocyclosoroid clade, sister to a clade that includes all sampled members of *Pseudocyclosorus* and *Trigonospora*, in addition to African taxa recently treated in *Sphaerostephanos*, *Christella*, and *Pneumatopteris* by Holttum (1974a) but distantly related to the type species of those genera. *Amblovenatum* and *Christella s.s.* also fall within the pseudocyclosoroid clade, and are part of the larger christelloid clade, that also includes the sphaerostephanoids and *Strophocaulon* (**Fig. 1**).

New combinations.—

***Abacopteris birii** (R.D. Dixit & Balkr.) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Pronephrium birii* R.D. Dixit & Balkr., Indian Fern J. 7(1–2):20, f. 1–5. 1990. *Pronephrium hirsutum* Ching ex Y.X. Lin, Fl. Reipubl. Popularis Sin. 4:305, 351. 1999.

Abacopteris gardneri (Holttum) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Pronephrium gardneri* Holttum, Kew Bull. 26:81. 1971.

Abacopteris gracilis (Ching ex Y.X. Lin) S.E. Fawc. & A.R. Sm., **comb. nov.—***Pronephrium gracile* Ching ex Y.X. Lin, Fl. Reipubl. Popularis Sin. 4:308–310, 352. 1999.

Abacopteris hekouensis (Ching ex Y.X. Lin) S.E. Fawc. & A.R. Sm., **comb. nov.—***Pronephrium hekouense* Ching ex Y. X. Lin, Fl. Reipubl. Popularis Sin. 4:353. 1999.

Abacopteris hirtisora** (C. Chr.) S.E. Fawc. & A.R. Sm., **comb. nov.—Dryopteris hirtisora* C. Chr., Contr. U.S. Natl. Herb. 26:277. 1931.—*Cyclosorus hirtisorus* (C. Chr.) Ching—*Sphaerostephanos hirtisorus* (C. Chr.) Holttum—*Thelypteris hirtisora* (C. Chr.) K. Iwats.

Abacopteris macrophylla (Ching ex Y.X. Lin) S.E. Fawc. & A.R. Sm., **comb. nov.—***Pronephrium macrophyllum* Ching ex Y.X. Lin, Fl. Reipubl. Popularis Sin. 4:352. 1999.

Abacopteris nitida** (Holttum) S.E. Fawc. & A.R. Sm., **comb. nov.—Dryopteris urophylla* (Mett.) C. Chr. var. *nitida* Holttum, Gard. Bull. Straits Settlem. 7. 1934.—*Thelypteris urophylla* (Mett.) K. Iwats. var. *nitida* (Holttum) K. Iwats.—*Pronephrium nitidum* (Holttum) Holttum

Abacopteris nudata (Roxb.) S.E. Fawc. & A.R. Sm., **comb. nov.—***Polypodium nudatum* Roxb., Calcutta J. Nat. Hist. 4:491. 1844.—*Pronephrium nudatum* (Roxb.) Holttum—*Thelypteris nudata* (Roxb.) C.V. Morton

Abacopteris repanda** (Fée) S.E. Fawc. & A.R. Sm., **comb. nov.—Goniopteris repanda* Fée, Gen. Fil. 251. 1852.—*Pronephrium repandum* (Fée) Holttum

Abacopteris setosa (Ching ex Y.X. Lin) S.E. Fawc. & A.R. Sm., **comb. nov.—***Pronephrium setosum* Ching ex Y.X. Lin, Fl. Reipubl. Popularis Sin. 4:352. 1999.

Abacopteris yunguiensis (Ching ex Y.X. Lin) S.E. Fawc. & A.R. Sm., **comb. nov.—***Pronephrium yunguiensis* Ching ex Y.X. Lin, Fl. Reipubl. Popularis Sin. 4:352. 1999.

*Constituent species.—*Abacopteris aspera* (C. Presl) Ching (**Figs. 5D, 5E**); **A. birii* (R.D. Dixit & Balkr.) S.E. Fawc. & A.R. Sm.; *A. gardneri* (Holttum) S.E. Fawc. & A.R. Sm.; *A. gracilis* (Ching ex Y.X. Lin) S.E. Fawc. & A.R. Sm.; **A. gymnopteridifrons* (Hayata) Ching; *A. hekouensis* (Ching ex Y.X. Lin) S.E. Fawc. & A.R. Sm.; **A. hirtisora* (C. Chr.) S.E. Fawc. & A.R. Sm.; *A. macrophylla* (Ching ex Y.X. Lin) S.E. Fawc. & A.R. Sm.; **A. nitida* (Holttum) S.E. Fawc. & A.R. Sm.; *A. nudata* (Roxb.) S.E. Fawc. & A.R. Sm.; **A. peltochlamys* (C. Chr.) Holttum; * *A. repanda* (Fée) S.E. Fawc. & A.R. Sm.; *A. setosa* (Ching ex Y.X. Lin) S.E. Fawc. & A.R. Sm.; *A. yunguiensis* (Ching ex Y.X. Lin) S.E. Fawc. & A.R. Sm.

*Incertae sedis.—*Pneumatopteris afra* (Christ) Holttum, recognized by Holttum (1974a, 1973a) occurs in tropical West Africa, and is similar to *Abacopteris hirtisora* (distributed from India to Thailand) in having narrow pinnae (~2 cm wide) that are toothed or lobed; other species of *Abacopteris* typically have broader pinnae (> 3cm) with entire of crenate margins. Phylogenetic analyses (Fawcett et al. in press) place this taxon variably within *Abacopteris* or *Christella s.s.*, suggesting the possibility of hybrid origin. *Sphaerostephanos validus* may be closely related to *A. hirtisora*, or a synonym of it (Lindsay et al. 2009) but is treated as *incertae sedis* pending further study. An intergeneric hybrid has been reported between *Pneumatopteris afra* and *Christella dentata* (Quansah & Edwards 1986).

AMAUROPELTA

Amauropelta Kunze, Farrnkr. 1:86, 109, t. 51. 1843.—*Thelypteris* subg. *Amauropelta* A.R. Sm., Amer. Fern J. 63(3):121. 1973.—Type: *Amauropelta breutelii* Kunze = *A. limbata* (Sw.) Pic.Serm. [= *Thelypteris limbata* (Sw.) Proctor] *Oochlamys* Fée

Etymology.—Gr. *amauros*, dark + *pelte*, shield. Referring to the darkened indusia of the type species; most species in *Amauropelta*, if indusiate, have tan or stramineous indusia at maturity.

Plants mostly terrestrial, or occasionally cremnophilous or rheophytic, mostly from (10–)30–100(–200) cm tall; **rhizomes** long-creeping, short-creeping, suberect, or erect, rarely scandent; **fronds** once-pinnate to usually pinnate-pinnatifid, rarely 2-pinnate or slightly more divided, monomorphic, usually arching; **stipes** stramineous, brownish, or occasionally atropurpureous, dull to lustrous, stipe bases and rhizome scales dull brown to tan, ovate to lanceolate, rarely glabrous, usually with acicular, hyaline hairs 0.1–0.2 mm on margins and surfaces; **blades** chartaceous to subcoriaceous, usually drying green, lanceolate, ovate to broadly deltate, proximal pinnae usually greatly to sometimes subabruptly or abruptly reduced, often > 6 pairs, basal pair(s) sometimes auriculiform or glanduliform and < 5 mm long, blade apex gradually reduced, with distal pinnae not or only slightly decurrent, proliferous buds absent or infrequently present in axils of distal pinnae in a few spp. (e.g., *A. linkiana* and related spp. treated in sect. *Uncinella* by Smith 1974); **pinnae** shallowly lobed, usually pinnatifid or pinnatisect, rarely 1-pinnate or subentire, rarely entire (*A. reducta*), typically straight, less commonly falcate, sometimes with small acroscopic auricles; **veins** usually prominent abaxially and adaxially, lowermost pair from adjacent segments running to margin just above sinus between adjacent lobes, rarely running to sinus (*A. linkiana*), never united to form excurrent veins that run to sinuses, veins ending at pinna margins; **aerophores** absent or, if present, tuberculate or elongate, or with only or a small patch of darkened aerating tissue at pinna bases; **indument abaxially** usually of hyaline acicular hairs on rachises, costae, veins, and sometimes between veins, **indument adaxially** of hyaline acicular hairs on rachises and costae, sometimes also on veins and between veins, hairs sometimes appressed, hairs on stipes and rachises short 0.1–1(–2) mm, sparse to dense, plants rarely glabrous or glabrescent, hairs usually single-celled, rarely septate; glands, if present, resinous or hemispherical and translucent, orangish to reddish, sometimes capitate (short-stipitate), light yellowish, borne on laminae and veins; **pustules** absent on laminar tissue; **sori** inframedial, medial, or infrequently submarginal, usually round, occasionally oblong or elongate along veins, indusiate or exindusiate, indusia if present round-reniform (lunate in *A. decurtata*) or reduced to a fragment, usually whitish or tan when young, occasionally greenish (*A. germaniana*) or blackish (*A. melanochlaena*), persistent to evanescent, hairy and or glandular to glabrous; **sporangia** usually glabrous, rarely setulose; **spores** pale brown, lacking pronounced winglike ridges or echinae, reticulate and perforate (fenestrate), with secondary sculpturing of gemmulae (Tryon and Lugardon 1991; Alvarez-Fuentes 2010); x = 29, 27, 31. This heterogeneity in chromosome base numbers in a single genus is unusual in ferns, although it is common among genera of the amauropeltoid clade. The biological significance is yet to be determined; the numbers do not appear to be miscounts.

Diagnosis.—The genus *Amauropelta* is morphologically most similar to the other two genera of the amauropeltoid clade. It is distinguished from *Metathelypteris* (eastern Asia) by the veins running to the margins, adaxially grooved costae, base chromosome number of x = 27, 29, 31 (vs. usually x = 35 in *Metathelypteris*). From *Coryphopteris*, *Amauropelta* differs by the combination of usually greatly reduced proximal pinnae, lack of sessile, resinous, reddish glands on the lamina between veins (except in the *A. resinifera* group), usually creeping or suberect rhizomes (vs. upright and trunk-like, except in *Coryphopteris simulata*), and usual base chromosome number of x = 29, 27, 31 (vs. x = 31, 32, 33). Holttum (1974a) and Patel et al. (2019a) noted that the spores of species of the amauropeltoid clade are frequently perforate (a rare state elsewhere in the family) but those of *Amauropelta* are reticulate with low ridges, while spores of *Coryphopteris* often are winged and fimbriate.

By far the greatest species diversity of *Amauropelta* is in the Neotropics, but the earliest-diverging lineages are from the Old World. The genus is here broadly defined to include *Parathelypteris pro parte* (with some species transferred to *Coryphopteris*), and is subdivided into four subgenera; two are strictly Old World and two predominantly New World.

Most necessary combinations have been made in *Amauropelta*, by Holttum (1974a, 1977b), Salino et al. (2015), and Kuo et al. (2019), but new combinations in subgenera *Parathelypteris* and *Nibaa* are made below.

KEY TO SUBGENERA OF *AMAUROPELTA*

1. Proximal pinnae abruptly or little reduced; plants of temperate, or subtropical montane East Asia, mostly winter-deciduous with thin, branching long-creeping rhizomes 1–2.5 mm diam.; x = 27, 31 ____ subg. **Parathelypteris**
1. Proximal pinnae typically gradually reduced; plants widely distributed; rhizomes various; x = 27, 29, 31.
   2. Rhizomes typically erect, > 3 mm diam.; predominantly neotropical; x = 29 ____ subg. **Amauropelta**
   2. Rhizomes long creeping, < 3 mm diam.; temperate or paleotropical; x = 27, 31.
      3. Plants of temperate North America; glands yellowish or colorless; x = 27 ____ subg. **Nibaa**
      3. Plants of temperate East Asia to Malesia; glands resinous yellow-orange to red; x = 31 ____ subg. **Venus**

Amauropelta subg. **Amauropelta**

Diagnosis.—*Amauropelta* subg. *Amauropelta* may be distinguished from other subgenera of *Amauropelta* by x = 29, and rhizomes typically erect, and > 3 mm diameter.

Biogeography and ecology.—*Amauropelta* is the largest genus within the family, and subg. *Amauropelta* is by far its largest subgenus, with 223 of the 233 species recognized here (Almeida et al. 2016; Salino et al. 2015) (**Fig. 1**). The greatest center of diversity in the Neotropics is in the South American Andes, but important secondary centers are in the Antilles, Mesoamerica, Venezuela, and southern Brazil. It is likely that there remain dozens of undescribed species, especially in Andean countries—Colombia to Bolivia—and it is evident that much of the speciation has occurred concomitant with the recent uplift of the Andes. Species are found from near sea level to over 4000 m.

Members of this subgenus are globally distributed, representing complex biogeographical patterns (see below). Species of subg. *Amauropelta* are found generally in primary, undisturbed forests, partially disturbed forests, forest margins, and even sometimes in open areas; occasionally they grow on rocks, and on streamsides, where they tend to have smaller, more streamlined blades and can be considered rheophytes (e.g., *A. sancta*.) A few species are weedy and found especially along roadsides, trails, and wet ditches (e.g., *A. rudis*).

Taxonomic and phylogenetic studies.—The African and Pacific island species of subg. *Amauropelta* represented by molecular data are nested within the neotropical radiation (Almeida et al. 2016; Patel et al. 2019a; Fawcett et. al. in press). These include one species in Hawaii (*A. globulifera* (Brack.) Holttum) and two in Polynesia (*A. grantii* (Copel.) Holttum, Society Isl.; *A. margaretae* (E.D. Brown) Holttum, from Rapa) (Holttum 1977b). There are also nine species in southern and tropical Africa and offshore islands in the Indian Ocean: the six treated by Holttum (1974a) plus *A. odontosora* (Bonap.) Holttum from the Ivory Coast, *A. salazica* (Holttum) Holttum, from Réunion and initially placed by Holttum (1974a) in *Parathelypteris*, and *Amauropelta knysnaensis* (N.C. Anthony & Schelpe) Parris, from South Africa. A species described from Sri Lanka, *A. hakgalensis* Holttum, is related to the neotropical species *A. oligocarpa* (Fawcett et al. in press) and may be an escape from cultivation in the botanical garden nearby.

The neotropical species, treated by Smith (1974, 1982, 1990) as subg. *Amauropelta* within *Thelypteris s.l.*, have been recognized as a natural group for more than a century (Christensen 1907, 1913) and treated (usually as *Thelypteris*) in floristic accounts for many countries, e.g., Mexico (Mickel & Smith 2004), Mesoamerica (Smith 1995a), Jamaica (Proctor 1985), Puerto Rico (Proctor 1989), Lesser Antilles (Proctor 1977), Venezuelan Guayana (Smith 1995b), Ecuador (Smith 1983), Peru (Smith 1992), and Bolivia (Smith & Kessler 2017). Smith (1974) divided them into nine sections, based on morphological characters of the rhizomes, stipes, aerophores, buds, blade shape, sori, and indusia (or lack thereof). Some of these sections correspond to clades within *Amauropelta*, e.g., *Uncinella*, *Lepidoneuron*, and *Amauropelta*, but all will need either minor adjustments or major recircumscriptions as a result of recent molecular data (Almeida et al. 2016, Alvarez-Fuentes 2010, Fawcett et al. in press). Within subg. *Amauropelta*, molecular sampling is still inadequate to arrive at any meaningful infrageneric boundaries, with 59 of about 233 species sequenced by Fawcett et al. (in press), and an additional 14 species sampled by Almeida et al. (2016).

In broadly based molecular analyses, *Amauropelta s.s.* is either sister to, or intercalated with, species previously treated as *Parathelypteris*, from eastern Asia and North America, though with low support. The relationship among the four subgenera is not well resolved (e.g., in the coalescent analysis of Fawcett et al. in press), but each is monophyletic, as is the genus *Amauropelta s.l.* This combined clade is part of a larger clade that also includes *Metathelypteris* and *Coryphopteris*, the 'ACMP' clade sensu He & Zhang (2012) or amauropeltoid clade sensu Almeida et al. (2016), Fawcett et al. (in press). *Metathelypteris* and *Coryphopteris* are each monophyletic when certain species heretofore treated in *Parathelypteris* are transferred to *Coryphopteris*. All members of the amauropeltoid clade have free veins (not anastomosing to forming an excurrent vein to the sinus), usually rather thin-textured blades, sessile or resinous glands on the blades of many spp., and indusiate sori with round-reniform indusia (except many subgroups within *Amauropelta*, where indusia have been lost, probably along multiple evolutionary lines; see Smith 1990). Although *Parathelypteris* has long been recognized as a distinct genus, expanding the concept of *Amauropelta* to include part of *Parathelypteris* has recently gained favor (Chang et al. 2019).

Outside of the amauropeltoid clade, *Amauropelta* spp. are similar to the more distantly related *Pseudocyclosorus*, which also has free veins, and many pairs of gradually reduced proximal pinnae. Historically, many species of *Amauropelta* acquired names in *Aspidium*, *Nephrodium*, *Dryopteris*, and *Lastrea*, the last an illegitimate name now considered to be a synonym of *Oreopteris* (Holub 1969), native to north-temperate areas (which see for discussion). *Oreopteris* also has reduced proximal pinnae similar to many *Amauropelta* spp., but $x = 34$, different spore ornamentation (echinate or winged vs. reticulate and perforate in *Amauropelta*; Wood 1973; Tryon & Lugardon 1991).

Constituent species.—*Amauropelta achalensis* (Hieron.) Salino & T.E. Almeida; *A. aculeata* (A.R. Sm.) Salino & T.E. Almeida; *A. aliena* (C. Chr.) Salino & T.E. Almeida; *A. altitudinis* (Ponce) Salino & T.E. Almeida; **A. amambayensis* (Christ) Salino & A.R. Sm.; *A. amphioxypteris* (Sodiro) Salino & T.E. Almeida; *A. andicola* (A.R. Sm.) Salino & T.E. Almeida; *A. appressa* (A.R. Sm.) Salino & T.E. Almeida; *A. araucariensis* (Ponce) Salino & T.E. Almeida; *A. arborea* (Brause) A.R. Sm.; *A. arenosa* (A.R. Sm.) A.R. Sm.; *A. argentina* (Hieron.) Salino & T.E. Almeida; *A. arrecta* (A.R. Sm.) Salino & T.E. Almeida; **A. aspidioides* (Willd.) Pic.Serm.; *A. atrorubens* (Mett. ex Kuhn) Salino & T.E. Almeida; **A. atrovirens* (C. Chr.) Salino & T.E. Almeida; **A. aymarae* (A.R. Sm. & M. Kessler) Salino & T.E. Almeida; **A. balbisii* (Spreng.) A.R. Sm.; **A. barvae* (A.R. Sm.) Salino & T.E. Almeida; *A. basisceletica* (C. Sánchez, Caluff & O. Alvarez) Salino & T.E. Almeida; **A. bergiana* (Schltdl.) Holttum; *A. binervata* (A.R. Sm.) A.R. Sm.; *A. boliviana* A.R. Sm.; *A. bonapartii* (Rosenst.) Salino & T.E. Almeida; *A. brachypoda* (Baker) A.R. Sm.; *A. brachypus* (Sodiro) A.R. Sm.; **A. brausei* (Hieron.) A.R. Sm.; ***A. burkartii* (Abbiatti) Salino & T.E. Almeida; *A. campii* (A.R. Sm.) Salino & T.E. Almeida; *A. canadasii* (Sodiro) Salino & T.E. Almeida; *A. caucaensis* (Hieron.) A.R. Sm.; *A. chaparensis* (A.R. Sm. & M. Kessler) Salino & T.E. Almeida; **A. cheilanthoides* (Kunze) Á. Löve & D. Löve; *A. chiriquiana* (A.R. Sm.) Salino & T.E. Almeida; **A. christensenii* (C. Chr. in Christ) Salino & T.E. Almeida; **A. cinerea* (Sodiro) A.R. Sm.; *A. cochaensis* (C. Chr.) Salino & T.E. Almeida; *A. cocos* (A.R. Sm. & Lellinger) Salino & T.E. Almeida; **A. comptula* (A.R. Sm.) Salino & T.E. Almeida; **A. concinna* (Willd.) Pic.Serm.; *A. conformis* (Sodiro) Salino & T.E. Almeida; **A. consanguinea* (Fée) Salino & T.E. Almeida; *A. cooleyi* (Proctor) Salino & T.E. Almeida; **A. corazonensis* (Baker) Salino & T.E. Almeida; *A. cornuta* (Maxon) Salino & T.E. Almeida; *A. correllii* (A.R. Sm.) Salino & T.E. Almeida; *A. crassiuscula* (C. Chr. & Maxon) Salino & T.E. Almeida; *A.*

ctenitoides (A.R. Sm.) Salino & T.E. Almeida; *A. decrescens* (Proctor) Salino & T.E. Almeida; **A. decurtata* (Link) Salino & T.E. Almeida; *A. deflectens* (C. Chr.) Salino & T.E. Almeida; **A. deflexa* (C. Presl) Á. Löve & D. Löve; *A. demissa* (A.R. Sm.) Salino & T.E. Almeida; **A. delasotae* (A.R. Sm. & Lellinger) Salino & T.E. Almeida; *A. demerarana* (Baker) Boudrie & Cremers; *A. denudata* (C. Sánchez & Caluff) Salino & T.E. Almeida; *A. diplazioides* (Desv.) Pic.Serm.; *A. dodsonii* (A.R. Sm.) Salino & T.E. Almeida; *A. dudleyi* (A.R. Sm.) Salino & T.E. Almeida; *A. elegantula* (Sodiro) Salino & T.E. Almeida; *A. enigmatica* (A.R. Sm.) Salino & T.E. Almeida; ***A. eriosorus* (Fée) Salino & T.E. Almeida; **A. euchlora* (Sodiro) A.R. Sm.; *A. euthythrix* (A.R. Sm.) Salino & T.E. Almeida; *A. exuta* (A.R. Sm.) Salino & T.E. Almeida; *A. fasciola* (A.R. Sm. & M. Kessler) Salino & T.E. Almeida; *A. fayorum* (A.R. Sm.& M. Kessler) Salino & T.E. Almeida; *A. firma* (Baker ex Jenman) Salino & T.E. Almeida; *A. fluminalis* (A.R. Sm.) Salino & T.E. Almeida; *A. frigida* (Christ) A.R. Sm.; **A. funckii* (Mett.) A.R. Sm.; *A. furfuracea* (A.R. Sm.) Salino & T.E. Almeida; *A. furva* (Maxon) Salino & T.E. Almeida; **A. germaniana* (Fée) Salino & T.E. Almeida; *A. glabrescens* A.R. Sm.; *A. glandulosolanosa* (C. Chr.) Salino & T.E. Almeida; ***A. globulifera* (Brack.) Holttum; *A. glutinosa* (C. Chr.) Salino & T.E. Almeida; *A. gomeziana* (A.R. Sm. & Lellinger) Salino & T.E. Almeida; *A. gracilenta* (Jenman) Salino & T.E. Almeida; **A. gracilis* (Heward) A.R. Sm.; **A. grantii* (Copel.) Holttum; *A. grayumii* (A.R. Sm.) Salino & T.E. Almeida; **A. hakgalensis* Holttum; *A. harrisii* (Proctor) Salino & T.E. Almeida; *A. hastiloba* (C. Chr.) Salino & T.E. Almeida; *A. heineri* (C. Chr.) Salino & T.E. Almeida; **A. heteroclita* (Desv.) Pic.Serm.; ***A. heteroptera* (Desv.) Holttum; *A. hutchisonii* (A.R. Sm.) Salino & T.E. Almeida; *A. hydrophila* (Fée) Salino & T.E. Almeida; **A. illicita* (Christ) Salino & T.E. Almeida; *A. inabonensis* (Proctor) Salino & T.E. Almeida; **A. inaequans* (C. Chr.) Salino & T.E. Almeida; *A. inaequilateralis* (A.R. Sm. & M. Kessler) Salino & T.E. Almeida; *A. insignis* (Mett.) Salino & T.E. Almeida; *A. intromissa* (C. Chr.) Salino & T.E. Almeida; *A. ireneae* (Brade) Salino & T.E. Almeida; **A. jimenezii* (Maxon & C. Chr.) Salino & T.E. Almeida; ***A. juergensii* (Rosenst.) Salino & T.E. Almeida; *A. jujuyensis* (de la Sota) Salino & T.E. Almeida; *A. knysnaensis* (N.C. Anthony & Schelpe) Parris; *A. laevigata* (Mett. ex Kuhn) Salino & T.E. Almeida; *A. lanceolata* A.R. Sm.; *A. leoniae* (A.R. Sm.) Salino & T.E. Almeida; **A. lepidula* (Hieron.) A.R. Sm.; **A. limbata* (Sw.) Pic.Serm.; **A. linkiana* (C. Presl) Pic.Serm.; **A. longicaulis* (Baker) Salino & T.E. Almeida; *A. longipilosa* (Sodiro) Salino & T.E. Almeida; *A. longisora* (A.R. Sm.) Salino & T.E. Almeida; **A. loreae* (A.R. Sm.) Salino & T.E. Almeida; *A. loretensis* (A.R. Sm.) Salino & T.E. Almeida; **A. lumbricoides* (A.R. Sm. & M. Kessler) Salino & T.E. Almeida; *A. macra* (A.R. Sm.) Salino & T.E. Almeida; *A. madidiensis* (A.R. Sm. & M. Kessler) Salino & T.E. Almeida; **A. malangae* (C. Chr.) Salino & T.E. Almeida; **A. margaretae* (E. Br.) Holttum; **A. melanochlaena* (C. Chr.) Salino & T.E. Almeida; *A. membranifera* (C. Chr.) Holttum; *A. mertensioides* (C. Chr.) Salino & T.E. Almeida; *A. metteniana* (Ching) Salino & T.E. Almeida; **A. micula* (A.R. Sm.) Salino & T.E. Almeida; *A. minima* (A.R. Sm. & M. Kessler) Salino & T.E. Almeida; *A. minutula* (C.V. Morton) Salino & T.E. Almeida; *A. mombachensis* (L.D. Gómez) Salino & T.E. Almeida; *A. mortonii* (A.R. Sm.) Salino & T.E. Almeida; *A. mosenii* (C. Chr.) Salino & T.E. Almeida; *A. muscicola* (Proctor) Salino & T.E. Almeida; *A. namaphila* (Proctor) Salino & T.E. Almeida; *A. neglecta* (Brade & Rosenst.) Salino & T.E. Almeida; *A. negligens* (Jenman) Salino & T.E. Almeida; *A. nephelium* (A.R. Sm. & M. Kessler) Salino & T.E. Almeida; *A. nitens* (Desv.) Salino & T.E. Almeida; *A. nockiana* (Jenman) Salino & T.E. Almeida; *A. novaeana* (Brade) Salino & T.E. Almeida; **A. nubicola* (de la Sota) Salino & T.E. Almeida; *A. nubigena* (A.R. Sm.) Salino & T.E. Almeida; **A. oaxacana* (A.R. Sm.) Salino & T.E. Almeida; *A. odontosora* (Bonap.) Holttum; **A. oligocarpa* (Humb. & Bonpl. ex Willd.) Pic.Serm.; *A. ophiorhizoma* (A.R. Sm. & Lellinger) Salino & T.E. Almeida; **A. opposita* (Vahl) Pic.Serm.; **A. oppositiformis* (C. Chr.) Holttum; ***A. pachyrhachis* (Kunze ex Mett.) Salino & T.E. Almeida; *A. paleacea* (A.R. Sm.) Salino & T.E. Almeida; ***A. patula* (Fée) Salino & T.E. Almeida; *A. pavoniana* (Klotzsch) Salino & T.E. Almeida; *A. pelludia* (A.R. Sm. & M. Kessler) Salino & T.E. Almeida; *A. peradenia* (A.R. Sm.) A.R. Sm.; *A. peruviana* (Rosenst.) Salino & T.E. Almeida; *A. phacelothrix* (C. Chr. & Rosenst.) Salino & T.E. Almeida; *A. physematioides* (Kuhn & Christ ex Krug) Salino & T.E. Almeida; **A. piedrensis* (C. Chr.) Salino & T.E. Almeida; *A. pilosissima* (C.V. Morton) A.R. Sm.; *A. pilosohispida* (Hook.) A.R. Sm.; **A. pilosula* (Klotzsch & H. Karst. ex Mett.) Á. Löve & D. Löve; *A. pleiophylla* (Sehnem) Salino & T.E. Almeida; *A. podotricha* (Sehnem) Salino & T.E. Almeida; *A. proboscidea* (A.R. Sm.) Salino & T.E. Almeida; *A. proctorii* (A.R. Sm. & Lellinger) A.R. Sm.; *A. prolatipedis* (Lellinger) A.R. Sm.; **A. ptarmica* (Kunze ex Mett.) Pic.Serm.; *A. ptarmiciformis* (C. Chr. & Rosenst. ex Rosenst.) Salino & T.E. Almeida; **A. pteroidea* (Klotzsch) A.R. Sm.; **A. pusilla* (Mett.) A.R. Sm.; ***A. raddii* (Rosenst.) Salino & T.E. Almeida; *A. randallii* (Maxon & C.V. Morton ex C.V. Morton) Salino & T.E. Almeida; *A. recumbens* (Rosenst.) Salino & T.E. Almeida; **A. reducta* (C. Chr.) Salino & T.E. Almeida; ***A. regnelliana* (C. Chr.) Salino & T.E. Almeida; **A. resinifera* (Desv.) Pic.Serm.; *A. retrorsa* (Sodiro) Salino & T.E. Almeida; ***A. retusa* (Sw.) Salino & T.E. Almeida; *A. rheophyta* (Proctor) Salino & T.E. Almeida; *A. rigescens* (Sodiro) Salino & T.E. Almeida; ***A. rivularioides* (Fée) Salino & T.E. Almeida; *A. roraimensis* (Baker) A.R. Sm.; *A. rosenstockii* (C. Chr.) Salino & T.E. Almeida; *A. rosulata* (A.R. Sm. & M. Kessler) Salino & T.E. Almeida; *A. rudiformis* (C. Chr.) Salino & T.E. Almeida; **A. rudis* (Kunze) Pic.Serm.; *A. rufa* (Poir.)

Salino & T.E. Almeida; *A. ruiziana* (Klotzsch) Salino & T.E. Almeida; *A. rupestris* (Klotzsch) A.R. Sm.; **A. rupicola* (C. Chr.) Salino & T.E. Almeida; *A. rustica* (Fée) Salino & T.E. Almeida; *A. sabaensis* ***A. salazica* (Holttum) Holttum; **A. sancta* (L.) Pic.Serm.; *A. sanctae-catharinae* (Rosenst.) Salino & T.E. Almeida; ***A. saxicola* (Sw.) Salino & T.E. Almeida; **A. scalaris* (Christ) Á. Löve & D. Löve; *A. scalpturoides* (Fée) Salino & T.E. Almeida; *A. sellensis* (C. Chr.) Salino & T.E. Almeida; *A. semilunata* (Sodiro) Salino & T.E. Almeida; *A. shaferi* (Maxon & C. Chr.) Salino & T.E. Almeida; *A. soridepressa* (Salino & V.A.O. Dittrich) Salino & T.E. Almeida; *A. steyermarkii* (A.R. Sm.) Salino & T.E. Almeida; *A. stierii* (Rosenst.) Salino & T.E. Almeida; *A. straminea* (Sodiro) Salino & T.E. Almeida; *A. strigillosa* (A.R. Sm. & Lellinger) Salino & T.E. Almeida; *A. strigosa* (Willd.) Holttum; **A. struthiopteroides* (C. Chr.) Salino & T.E. Almeida; *A. subacrostichoides* A.R. Sm.; *A. subscandens* (A.R. Sm.) Salino & T.E. Almeida; *A. subtilis* (A.R. Sm.) Salino & T.E. Almeida; *A. supina* (Sodiro) Salino & T.E. Almeida; *A. supranitens* (Christ) Á. Löve & D. Löve; *A. tablana* (Christ) Salino & T.E. Almeida; **A. tamandarei* (Rosenst.) Salino & T.E. Almeida; *A. tapantensis* (A.R. Sm. & Lellinger) Salino & T.E. Almeida; *A. tenerrima* (Fée) Salino & T.E. Almeida; **A. thomsonii* (Jenm.) Pic.Serm.; ***A. tomentosa* (Thouars) Holttum; *A. trelawniensis* (Proctor) Salino & T.E. Almeida; *A. uncinata* (A.R. Sm.) Salino & T.E. Almeida; *A. vattuonei* (Hicken) Salino & T.E. Almeida; *A. venturae* (A.R. Sm.) Salino & T.E. Almeida; *A. vernicosa* (A.R. Sm. & Lellinger) Salino & T.E. Almeida; **A. villana* (L.D. Gómez) Salino & T.E. Almeida; *A. yungensis* (A.R. Sm. & M. Kessler) Salino & T.E. Almeida; **A. zurquiana* (A.R. Sm. & Lellinger) Salino & T.E. Almeida

Excluded species.—Amauropelta acunae (C. Sánchez & Zavaro) Salino & T.E. Almeida and *A. oviedoae* (C. Sánchez & Zavaro) Salino & T.E. Almeida are misplaced in *Amauropelta* (contrary to Salino et al., 2015); rather they belong in *Pelazoneuron,* and the latter is likely a sterile hybrid. We do not recognize them, pending further study.

Amauropelta subg. **Nibaa** S.E. Fawc. & A.R. Sm., **subg. nov.—**Type: *Amauropelta noveboracensis* (L.) S.E. Fawc. & A.R. Sm. [= *Polypodium noveboracense* L., Sp. Pl. 2:1091. 1753.]—*Thelypteris noveboracensis* (L.) Nieuwl. (**Figs. 6B, 6C**).

Etymology.—S/he sleeps, is asleep, in Anishinaabemowin (Ojibwe Peoples Dictionary 2015), a language of the first peoples of the Great Lakes region, where the type species occurs. The name refers to the winter-deciduous habit, which distinguishes it from its tropical evergreen sister clade, subg. *Amauropelta*.

Diagnosis.—Plants of temperate North America, winter-deciduous, with long-creeping rhizomes (**Fig. 6C**), often forming large colonies, proximal pinnae gradually reduced, $x = 27$. The two species of *Amauropelta* subg. *Nibaa* most closely resemble the Old World *Amauropelta* subg. *Venus*, ($x = 31$), but may be distinguished by glands yellow to colorless (vs. amber resinous orange-yellow to reddish).

Biogeography and ecology.—The two species are restricted to temperate North America, one to northeastern deciduous forests of the U.S.A. and Canada, and the other to lower montane habitats of the western cordillera. They occur in seasonally snowy environments, in mesic to moist forest understories or in seepy mountain meadows.

New combinations.—

***Amauropelta nevadensis** (Baker) S.E. Fawc. & A.R. Sm., **comb nov**.—*Nephrodium nevadense* Baker, Ann. Bot. (Oxford) 5:320. 1891.—*Parathelypteris nevadensis* (Baker) Holttum—*Thelypteris nevadensis* (Baker) Clute ex C.V. Morton

Amauropelta noveboracensis** (L.) S.E. Fawc. & A.R. Sm., **comb. nov.—Polypodium noveboracense* L., Sp. Pl. 2:1091. 1753.—*Parathelypteris noveboracensis* (L.) Ching—*Thelypteris noveboracensis* (L.) Nieuwl. (**Figs. 6B, 6C**).

*Constituent species.—*Amauropelta nevadensis* S.E. Fawc. & A.R. Sm.; **A. noveboracensis* (L.) S.E. Fawc. & A.R. Sm (**Figs. 6B, 6C**).

Amauropelta subg. **Parathelypteris** (H. Ito) S.E. Fawc. & A.R. Sm., **comb. nov.—***Thelypteris* sect. *Parathelypteris* H. Ito in Nakai & Honda, Nov. Fl. Jap. 4:127. 1939.—*Parathelypteris* (H. Ito) Ching—*Thelypteris* subg. *Parathelypteris* (H. Ito) R.M. Tryon & A.F. Tryon—Type: *Amauropelta glanduligera* (Kunze) Y.H. Chang [=*Aspidium glanduligerum* Kunze, Analecta Pteridogr. 44. 1837]—*Thelypteris glanduligera* (Kunze) Ching—*Amauropelta glanduligera* (Kunze) Y.H. Chang

Etymology.—Gr. *para*, beside + *Thelypteris*. A genus similar to, but distinct from, *Thelypteris*.

Diagnosis.—Plants of temperate, or subtropical montane East Asia, winter-deciduous with thin, branching long-creeping rhizomes, $x = 27, 31$. In addition to biogeographical distribution, the members of this genus can usually be distinguished from the other subgenera of *Amauropelta* by proximal pinnae typically abruptly- or little reduced.

Biogeography and ecology.—This clade includes about six species, of continental East Asia, Taiwan, Japan, and south to the Philippines. Recent studies have demonstrated remarkable cytological complexity among its species (Nakato et al. 2002), with diploids, triploids, tetraploids, hypotetraploids, hexaploids, and hyperhexaploids known from the *A. angustifrons* complex.

New combinations.—

Amauropelta cystopteroides** (D.C. Eaton) S.E. Fawc. & A.R. Sm., **comb. nov.—Athyrium cystopteroides* D.C. Eaton, Proc. Amer. Acad. Arts 4:110. 1858.—*Thelypteris cystopteroides* (D.C. Eaton) Ching—*Parathelypteris cystopteroides* (D.C. Eaton) Ching

Amauropelta grammitoides (Christ) S.E. Fawc. & A.R. Sm., **comb. nov.—***Aspidium grammitoides* Christ, Bull. Herb. Boissier 63:193. 1898.—*Thelypteris grammitoides* (Christ) Ching—*Parathelypteris grammitoides* (Christ) Ching

****Amauropelta miyagii** (H. Ito) S.E. Fawc. & A.R. Sm., **comb. nov.—***Dryopteris miyagii* H. Ito, Bot. Mag. Tokyo 49:360, f. 2, 4(2). 1935.—*Thelypteris miyagii* (H. Ito) Nakato, Sahashi & M. Kato—*Parathelypteris miyagii* (H. Ito) Nakaike

Amauropelta serrulata** (Ching) S.E. Fawc. & A.R. Sm., **comb. nov.—Thelypteris serrutula* Ching, Bull. Fan Mem. Inst. Biol. 6:319. 1936, spelling of epithet corrected by Ching (1963) to "serrulata".—*Parathelypteris serrulata* (Ching) Ching

*Constituent species.—*Amauropelta angustifrons* (Miq.) Y.H. Chang; **A. cystopteroides* (D.C. Eaton) S.E. Fawc. & A.R. Sm.; **A. glanduligera* (Kunze) Y.H. Chang; *A. grammitoides* (Christ) S.E. Fawc. & A.R. Sm.; ***A. miyagii* (H. Ito) S.E. Fawc. & A.R. Sm.; **A. serrulata* (Ching) S.E. Fawc. & A.R. Sm.

Amauropelta subg. **Venus** S.E. Fawc. & A.R. Sm., **subg. nov.**—Type: *Amauropelta beddomei* (Baker) Y.H. Chang [=*Nephrodium beddomei* Baker Syn. Fil. 267. 1867]—*Thelypteris beddomei* (Baker) Ching

Etymology.—Taken from the Chinese common name for *A. beddomei*, Venus fern, 长根金星蕨 chang gen jin xing jue.

Diagnosis.—Plants of the Paleotropics to subtropics, with long-creeping rhizomes, frequently forming colonies, proximal pinnae gradually reduced, $x = 31$. *Amauropelta beddomei* from tropical regions tends to be much smaller and more delicate than their more northerly counterparts, and to have more multicellular hairs on the axes; however there seems to be some intergradation, especially in Southern China. The North American *Amauropelta* subg. *Nibaa* is most similar, but has colorless or yellowish glands, unlike the resinous orange-yellow, amber or reddish glands of subg. *Venus*. This subgenus is also similar to some species of *Coryphopteris* that have creeping rhizomes and resinous glands (e.g., *C. nipponica*), but typically has more than three pairs of proximal pinnae gradually reduced (vs. three or fewer pairs).

Biogeography and ecology.—Amauropelta beddomei is widespread, perhaps representing a species complex, distributed in Sri Lanka, southern China, and throughout Malesia including New Guinea; it includes three varieties, var. *beddomei*, var. *eugracilis*, and var. *brassii* (Holttum 1982). We make no new varietal combinations at this time because of uncertainty in regard to their eventual rank. Plants from China frequently treated as *Parathelypteris nipponica* are most closely related to *Amauropelta beddomei* (He & Zhang 2012; Fawcett et al. in press) and are not closely related to the Japanese type of *P. nipponica*, which is here treated in *Coryphopteris*. A second species, *A. rechingeri*, presumably closely allied to *A. beddomei*, is of lower elevations on the Solomon Islands (Holttum 1977b).

New combinations.—

Amauropelta rechingeri (Holttum) S.E. Fawc. & A.R. Sm., **comb. nov.—***Parathelypteris rechingeri* Holttum, Allertonia 1:192. 1977.

*Constituent species.—*Amauropelta beddomei* (Baker) Y.H. Chang; *A. rechingeri* (Holttum) S.E. Fawc. & A.R. Sm

AMBLOVENATUM

Amblovenatum J.P. Roux, Strelitzia 23:200. 2009, a renaming of *Amphineuron* Holttum (1971), non *Amphineurion* (A. DC.) Pichon—Type: *Amblovenatum opulentum* (Kaulf.) J.P. Roux [= *Aspidium opulentum* Kaulf.]—*Thelypteris* subg. *Amphineuron* (Holttum) Fraser-Jenk.

For additional synonymy, see Holttum (1977a, 1977b, 1982).

Etymology.—Gr. *amphi*, of two kinds + *neuron*, nerve, pertaining to the venation of the type and some other species in the genus, which varies, even within the same frond, from free, meeting the margin at the sinus, or connivent with a sinus-membrane. *Amblovenatum*, although not explained by its author, appears to be an inelegantly formed Latin translation of *Amphineuron* meaning approximately the same thing.

Plants terrestrial, of forested or somewhat disturbed habitats, medium sized (to about 2 m tall); **rhizomes** long-creeping to erect, with brown setose linear-lanceolate scales; **fronds** monomorphic, arching to erect, pinnate-pinnatifid to pinnate-pinnatisect, **stipes** dull brown to stramineous; **stipe scales** tangled, spreading, linear-lanceolate, dark brown and setose, readily deciduous; **blades** membranaceous to chartaceous, drying bifacially concolorous green to pale-olivaceous, apex subconform to gradually reduced (*A. immersum*); proximal pinnae not reduced, or if reduced, then abruptly; proliferous buds lacking; **pinnae** short-petiolulate, with truncate bases, proximal pinnae gradually narrowed towards bases, not auriculate (except *A. subattenuatum*), margins lobed to within 1 mm of costae, or incised only 1/3 (*A. terminans*) to costae, segments nearly perpendicular to somewhat oblique and falcate, with rounded to broadly acute apices; **veins** free, connivent at or near sinuses, or with one or more pairs anastomosing below the sinus, and subsequent pairs running to sinus, with both states sometimes present within a single frond (*A. opulentum*), veins ending at margins or terminating prior to margins (*A. terminans*); **aerophores** present as inconspicuous swellings and/or discoloration at pinna bases; **indument abaxially** of long (0.5–1 mm), hyaline, acicular hairs along rachises, costae, and veins, short (< 0.1 mm) hairs along rachises, costae, veins, and sometimes laminae, small, clear stipitate glands abundant on laminae between veins, and sulfur-colored spherical, sessile or stipitate glands along costae and veins, most abundant towards segment apices, rarely with scales on costae (*A. distinctum*); **indument adaxially** of long (0.5–1 mm) hyaline acicular hairs along rachises, costae, and veins, sometimes with small, colorless stipitate glands on laminae; **pustules** absent; **sori** round, discrete to confluent, sometimes sunken in lamina (*A. immersum*), supramedial to inframarginal, often restricted to distal portion of segments, indusiate or exindusiate (*A. distinctum*), indusia thick, brown, sometimes bicolorous, dark in the center and pale towards margins, often bearing abundant sulfur-colored glands (*A. opulentum* and *A. immersum*) and/or setae (*A. terminans*); **sporangia** with thin stalks, which may bear stipitate glands, capsules glabrous; **spores** dark brown to black, rarely tan (*A. subattenuatum*), perine with low thin crests; x =36, two species counted: *A. opulentum* is tetraploid, but both diploid and tetraploid counts are reported for *A. terminans*. One collection from Timor may represent an infrageneric hybrid between *A. opulentum* and *A. immersum,* and *A. tildeniae*, of the Society and Cook islands, may represent an intergeneric hybrid between *A. opulentum* and *Christella dentata* (Holttum 1977b). Putative hybrids from the Cook Islands, between *A. opulentum* and *Christella dentata* (*Game 92/128*, !UC), and *A. opulentum* and *Strophocaulon invisum* (*Game 89/172A*, *89/173*, !UC) have been reported by Game and Smith (2014).

Diagnosis.—Amblovenatum s.s. is distinguished from *Mesopteris s.l.* by the presence of long (0.5–1 mm) hyaline acicular hairs on axes of abaxial or adaxial laminae (vs. only minute stipitate glands or hairs > 0.5 mm long); sori typically with large, persistent conspicuous indusia (vs. sori exindusiate, with small indusia, or indusia obscured by copious resinous glands); membranaceous to thin-chartaceous laminae drying bifacially concolorous green to olivaceous (vs. thick-chartaceous laminae sometimes drying bicolorous dark brown to reddish); by the presence of opaque whitish to sulfur-colored glands (vs. translucent red or amber resinous glands)—though both genera frequently have minute colorless or golden brown stipitate glands as well; sori often restricted to distal veins of segments (vs. sori distributed the length of segments, or restricted to proximal portion of segments); and sinus membranes rarely bearing an appendage (vs. sinus-membrane usually with conspicuous projecting appendage). *Christella* differs in having more abundant hairs, especially on laminar tissue between veins, and often having characteristic orangish pear-shaped glands.

Biogeography and ecology.—Amblovenatum is recognized herein as a genus of only six species. One of these, *A. opulentum*, is widespread throughout the tropics. Its native range is ostensibly Australasia south to Queensland, Asia north to Hainan, west to Sri Lanka, throughout Malesia, and east to Tahiti. The earliest records we have found outside this range are from 1948 in Mozambique (*Mendonza 4377*, L), and 1938 in Martinique (Smith 1971:110, *Stehle & Stehle 4986*, UC, US; GBIF.org). This species is now widespread throughout the Antilles, Central America, much of South America, and East Africa and Madagascar; it may be extirpated in Florida (Nelson 2000), where it was once established in Dade Co. Holttum (1982) noted that it was not common anywhere in Malesia, and of doubtful nativity in Java, but that cultivated plants in Singapore had a tendency to naturalize in the vicinity. Like *Christella dentata* and *Macrothelypteris torresiana*, it may be a successful weed where it has become established. *Amblovenatum terminans* occupies a native range similar to that of *A. opulentum*, but it extends east only as far Queensland and New Guinea; it is represented in Africa by few collections (Holttum 1974a) and may be introduced there. The species *A. queenslandicum* was described relatively recently (Holttum 1986) and is endemic to Queensland, Australia.

Taxonomic and phylogenetic studies.—Amphineuron was described by Holttum (1971) and its ten species were monographed by him a few years later (Holttum 1977a). His circumscription was adopted by Ching (1978), with the exception of the east Asian endemic species that Ching segregated in a newly described monotypic genus, *Mesopteris*, as *M. tonkinensis*. Because of some uncertainty regarding relationships among genera, the remaining species of *Amphineuron* were treated in a broad concept of *Cyclosorus* in the Flora of China, though *Mesopteris* was maintained based on morphological and molecular evidence (Lin et al. 2013). Because of its similarity to the older name *Amphineurion* (Apocynaceae), also native to southeast Asia, the name *Amphineuron* was rejected (Middleton in Brummitt 2007), and *Amblovenatum* was published as its replacement (Roux 2009).

In his revision of *Amphineuron*, Holttum (1977a: 206) recognized that the species "may be divided into two groups, one with conspicuous indusia, the other with indusia small or lacking." These two groups correspond to *Amblovenatum s.s.* and *Mesopteris s.l.* in our treatment. Despite some morphological similarities, these two groups are not closely related, based on molecular phylogenetic evidence, which was first demonstrated by He and Zhang (2012) and corroborated by subsequent analyses (Fawcett et al. in press). *Amblovenatum s.s.* is well supported as a member of the christelloid clade, but because of poor resolution of backbone nodes, its closest relatives within the clade are uncertain. The *Mesopteris* clade, which includes the Chinese/Vietnamese endemic, *M. tonkinensis*, and several Malesian and Australasian species, is in the chingioid clade, sister to a clade that includes *Grypothrix, Menisciopsis, Chingia,* and *Plesioneuron* (**Fig. 1**).

New combinations.—

Amblovenatum distinctum (Copel.) S.E. Fawc. & A.R. Sm., **comb. nov.—***Dryopteris distincta* Copel., Univ. Calif. Publ. Bot. 18:220. 1942.—*Amphineuron distinctum* (Copel.) Holttum—*Cyclosorus distinctus* (Copel.) Copel.—*Thelypteris distincta* (Copel.) C.F. Reed

Amblovenatum subattenuatum (Rosenst.) S.E. Fawc. & A.R. Sm., **comb. nov.—***Dryopteris subattenuata* Rosenst., Repert. Spec. Nov. Regni Veg. 10:332. 1912.—*Amphineuron subattenuatum* (Rosenst.) Holttum—*Thelypteris subattenuata* (Rosenst.) C.F. Reed

Constituent species.—Amblovenatum distinctum (Copel.) S.E. Fawc. & A.R. Sm.; **A. opulentum* (Kaulf.) J.P. Roux; **A. immersum* (Blume) Mazumdar; *A. queenslandicum* T.E. Almeida & A.R. Field; *A. subattenuatum* (Rosenst.) S.E. Fawc. & A.R. Sm.; **A. terminans* (Panigrahi) J.P. Roux

Excluded species.—Amblovenatum tildeniae (Holttum) T.E. Almeida & A.R. Field is likely to represent a hybrid involving *Amblovenatum opulentum* and *Christella dentata*, and we refrain from recognizing it, pending further study. Based on the description (Takeuchi 2005) and images of an isotype (!A) *Amphineuron lindleyi* W.N. Takeuchi is here transferred to *Chingia*.

Species transferred to Mesopteris.—Amblovenatum paraphysophorum (Alderw.) Parris; *A. pseudostenobasis* (Copel.) C.W. Chen; *Amphineuron attenuatum* (Kuntze) Holttum; *A. ceramicum* (Alderw.) Holttum; *A. kiauense* (C. Chr.) Holttum; *A. tonkinense* (C. Chr.) Holttum

AMPELOPTERIS

Ampelopteris Kunze, Bot. Zeit. 6:114. 1848.—Type: *Ampelopteris elegans* Kunze = *A. prolifera* (Retz.) Copel. [= *Cyclosorus proliferus* (Retz.) Tardieu & C. Chr.]

For additional generic synonymy, see Holttum (1974a).

Etymology.—Gr. *ampelos*, vine + *pteris*, fern, in reference to the indeterminate growth of the rachis, and vine-like habit.

Plants terrestrial, with proliferous fronds of indefinite growth, sometimes with climbing rhizomes, typically medium-sized, mostly (8–)15–75(–100+) cm tall; **rhizomes** short- to long-creeping, with scales primarily at apices, these setulose and/or glandular at margins, older parts of rhizomes becoming scaleless; **fronds** typically clustered, weakly dimorphic with fertile fronds often taller than non-fertile fronds and with narrower, shorter pinnae, erect or arching, once-pinnate; **stipes** 30–60 cm long, grooved adaxially, stramineous to dull brown, sometimes with short, blackish spines to 3 mm long; **stipe scales** ovate-deltate to lanceolate, appressed, brown, 2–3 mm long, typically with hairs on scales; **blades** chartaceous to subcoriaceous, with apex pinna-like, or blades ± indeterminate, rachises prolonged and whip-like, irregularly producing 20+ pairs of much reduced pinnae < 2 cm, and also bearing buds and plantlets in axils of pinnae, sometimes with clusters of plantlets in a single pinna axis, these proliferous plantlets sometimes well developed, fertile, and with fronds over 15 cm long; proximal pinnae of well-developed fronds not reduced or with a few pairs slightly reduced, but lacking greatly reduced or glanduliform pinnae; rachises adaxially grooved, bearing simple and sometimes forked or branched acicular hairs, often glabrescent; **pinnae** grooved adaxially, truncate or slightly cordate at bases, acute at tips, to ca. 15(–20) × 2(–3) cm wide, margins entire, subentire, crenate, or shallowly lobed about 1/4 the distance to costae, lacking acroscopic or basiscopic basal auricles, sessile or often short-petiolulate to ca. 1 mm, with truncate bases, symmetric, sometimes fertile at a very small size (ca. 3 × 0.6 cm); **veins** prominent adaxially and abaxially, with up to ca. 12 pairs of veins from a costule, 5–6 pairs alternately anastomosing with veins from an adjacent costule and producing a ± straight (toward the base) or often zig-zag (toward pinna margins) excurrent vein to sinus, areoles lacking included free veinlets; vein ends reaching margins; **aerophores** absent or at most a small darkened swelling at pinna bases; **indument abaxially**, if present, of sparse hyaline acicular hairs, shorter hairs sometimes shallowly forked or branched (most hairs restricted to costae), costae and sometimes also costules with scattered, tan, peltate, ovate, or lanceolate setulose scales, orangish spherical glands occasionally also present, blades often glabrescent with age; **indument adaxially** of hyaline acicular to ca. 0.5 mm long on costae, seldom with hairs on costules or ultimate veins, never on laminar tissue between veins; **pustules** absent on abaxial laminae between veins; **sori** ± medial to supramedial, round to often oblong or elongate, exindusiate, paired on either side of excurrent vein, not confluent, not appearing acrostichoid; **sporangia** glabrous or often with a reddish globose gland adjacent to annulus on the capsule; sporangial stalks short, with a stalked often reddish globose or pear-shaped gland(s) at the tip; **spores** tan, with numerous short and narrow ridges and small echinulate elements (Tryon & Lugardon 1991); $x = 36$, only diploids known. No hybridization with any other genus has been demonstrated.

Diagnosis.—The axillary plantlets of proliferous fronds produce rootlets that aid in clinging tightly to trees in thickets (Holttum et al. 1970). Other paleotropical genera with proliferous fronds include species of *Grypothrix* and *Menisorus s.l.*, and these genera appear to have no close affinity with *Ampelopteris*. *Ampelopteris* is unusual in Thelypteridaceae in having indeterminate growth of its fronds, a feature shared with the distantly related Hawaiian endemic *Pseudophegopteris keraudreniana,* and the Antillean *Goniopteris reptans*. The forked or branched hairs in *Ampelopteris* (see Holttum et al. 1970) are inconspicuous and easily abraded, and are not indicative of a close relationship with neotropical *Goniopteris*; the proliferous nature of the fronds of many *Goniopteris* has also been considered an indication of affinity to *Ampelopteris* by some, but this trait is likely independently derived in the two genera. Characteristics shared between *Ampelopteris* and *Cyclosorus s.s.* include the very similar spore morphology (Tryon & Lugardon 1991), stalked, multicellular glands with a globose, often reddish tip, and the presence of costal scales. Characteristics shared with *Mesophlebion* include the similar sporangial stalk glands, but spores of *Mesophlebion* have much broader, higher, and fewer ridges and lack the dense echinulate elements (Tryon & Lugardon 1991). *Ampelopteris* differs from both in having proliferous fronds, more copiously anastomosing veins, and short (to ca. 0.3 mm) forked, branched, or stellate hairs on the axes, these most easily seen along the adaxial ridges of young fronds.

Biogeography and ecology.—*Ampelopteris* comprises a single species, *A. prolifera* (Retz.) Copel., widely distributed from tropical West Africa to northeastern Australia and New Caledonia, including mainland southeastern Asia and throughout Malesia. It occurs on riverbanks, and in wet ditches, sometimes forming thickets, often in open places.

Taxonomic and phylogenetic studies.—Most workers have thought *Ampelopteris* to be most closely related to *Cyclosorus s.s.* and *Mesophlebion* (Holttum 1982; Smith 1990), and this hypothesis is now supported by molecular data, which show *Ampelopteris* forms a clade with these two genera (Almeida et al. 2016; Fawcett et al. in press; **Fig. 1**), though the relationship among them is poorly resolved. The sole species of *Ampelopteris* has sometimes been placed in a more broadly defined *Cyclosorus* or in *Goniopteris* (e.g., Christensen 1913), a neotropical genus having many proliferous species, as well as similar stellate hairs.

Notes.—Fossils of *Cyclosorus eoproliferus* (Prasad) Prasad et al. from mid-late Miocene strata in northeastern India (ca. 10 Ma), appear to be very similar to or conspecific with *Ampelopteris prolifera* (Mehrotra et al. 2011). The same or a similar taxon was previously described as *Goniopteris prolifera* (Retz.) C. Presl (Prasad 1991), a homotypic synonym of the extant species, and the fossil *Thelypteridaceophyllum tertiarum* Joshi & Mehrotra (2003).

Young tips of *Ampelopteris* are edible, but supposedly inferior to those of *Diplazium esculentum* (Retz.) Sw. (Copeland 1947).

Constituent species.—**Ampelopteris prolifera* (Retz.) Copel.

CHINGIA

Chingia Holttum, Blumea 19:31. 1971.—Type: *Chingia ferox* (Blume) Holttum [= *Aspidium ferox* Blume]

For complete synonymy, see Holttum (1974b, 1977b, 1982).

Etymology.—Named in honor of Chinese pteridologist Ren Chang Ching (1898–1986), who published extensively on the ferns of China and developed the first modern classification for Old World Thelypteridaceae.

Plants terrestrial, of open sites, with tree-fern habit, reaching heights of 5 m, though plants under 1 m tall may be fertile; **rhizomes** erect and caulescent, to 10 cm thick or greater, trunks to 1 m tall, stipe bases persistent; **fronds** monomorphic, erect, arching or spreading from caudex, usually pinnate-pinnatifid to pinnate-pinnatisect, rarely (*C. marattioides*) bipinnate; **stipes** stramineous to castaneous, with flat to terete scales, or hairs and scales; **stipe scales** proximally dense, thick, stiff, setiferous, dark brown to blackish, linear-lanceolate, to 2 cm long, transitioning to spreading, terete, spine-like scales distally, sometimes scales extending onto rachises, often breaking, leaving darkened stump-like scars, sometimes containing foul-smelling, irritating liquid (*C. urens, C. malodora*); **blades** chartaceous, drying green or reddish, ovate to lanceolate, proximally lacking greatly reduced or glanduliform proximal pinnae, with apex gradually reduced or conform, pinnae generally not greatly reduced distally, proliferous buds lacking; **pinnae** sessile or short-petiolulate, with bases truncate, rounded, or broadly cuneate, not or little dilated at the base, margins dentate to deeply lobed, with prominent sinus-membranes; **veins** of one or more pairs generally anastomosing below the sinus (free in *C. pricei* and *C. marattioides*), with many more pairs running along sinus membrane, large individuals with > 30 pairs of veins per segment, basalmost veins often arising from costae; **aerophores** absent; **indument abaxially** of rachises, costae, veins, and laminar tissue between veins of long and/or short hyaline acicular hairs, sometimes with clear stipitate glands or sessile yellow spherical glands, the young fronds sometimes sticky with a spicy-smelling, irritating glandular exudate (*C. australis,* Herbert 2006); **indument adaxially** primarily restricted to axes (rachises and costae), of hyaline acicular hairs; **pustules** absent; **sori** most often near costules, less commonly medial, discrete or coalescent, exindusiate or with small indusia; **sporangia** glabrous or with spherical yellow glands, stipitate glands, or setulae; **spores** nearly always black or dark brown, papillose, winged, or echinate (*C. marattioides*, Tryon & Lugardon 1991; *C. fijiensis*, Patel et al. 2019a); $x = 36$, two species counted, both diploids. No hybrids known.

Diagnosis.—As Holttum (1971, 1974b, 1977b, 1982) suggested, *Plesioneuron* is the closest relative of *Chingia*, and some species share the unusual stiff, terete stipe scales (otherwise unique in the family) and black to dark brown spores. *Plesioneuron* differs in having free veins, deeply pinnatisect pinnae, a tendency to be of much smaller stature, often creeping rhizomes, medial sori (vs. borne along costules), persistent indusia, pustular laminae, and swollen aerophores. *Plesioneuron marattioides* is here transferred to *Chingia.* This taxon differs from species in both genera in being fully bipinnate. However, with molecular evidence, it is nested within *Chingia*. Alston (1940:227) noted in his description of this species that it "seems allied to [*Chingia*] *imponens*", in spite of its free veins. Based on the description (Takeuchi 2005) and on observation of images of the type (A: both scanned specimens and photos of microscopic features, courtesy of A.V. Gilman), we believe a second species, described as *Amphineuron lindleyi*, should also be transferred to *Chingia*.

Biogeography and ecology.—The 25 species of *Chingia* are distributed throughout Malesia and the southeastern Pacific to elevations of 2000 m. One widespread species, *C. longissima*, extends eastward to the Caroline Islands, Society Islands, Solomon Islands, and Marquesas. They are largely absent from continental southeast Asia but reach Thailand and peninsular Malaysia. A single endangered endemic species, *C. australis*, reaches south to Queensland, Australia (Holttum 1986).

Taxonomic and phylogenetic studies.—The genus was described and its constituent taxa delineated by Holttum (1971). No previous authors had recognized these species as belonging to a natural group. Although initially suspecting a close affinity with *Mesophlebion* (Holttum 1971), he later concluded that the resemblance to that genus was superficial (1974a, 1977b, 1982) and that *Plesioneuron* (which Holttum, 1975, segregated from *Mesophlebion*) was the only close relative of *Chingia*. This conclusion is supported by the reciprocal monophyly and sister relationship of these two genera inferred from phylogenomic evidence (Fawcett et al. in press). Although this sister relationship generally has high support, some conflict exists among individual gene trees. *Chingia* plus *Plesioneuron* form the most highly nested clade within the chingioid (non-core christelloid) clade, which includes in descending order along a grade *Menisciopsis*, *Grypothrix*, *Mesopteris s.l.*, with *Glaphyropteridopsis* inferred either as sister to the rest of the chingioid genera or diverging from the backbone node before them, sister to the chingioids plus a large christelloid clade (**Fig. 1**). Although the monophyly of the chingioid clade, and crown nodes corresponding to each genus within it, are highly supported, support of backbone nodes is low, and uncertainty remains about the relationships of these genera to one other.

Notes.—Of the 18 species treated by Holttum (1982), eight were known only from the type, or the type and one other collection. Most species are narrowly restricted endemics, and further study may reveal that the current taxonomic concepts for widespread species, e.g., *C. ferox* and *C. longissima*, are too broad (e.g., see Game et al. 2018). *Chingia* species are often pioneers, dependent on disturbance and open habitats for their establishment, and their populations may be short-lived (Herbert 2006). Their dynamic population structure, ruderal nature, and narrow ranges make them a challenging target for conservation efforts. Furthermore, due to their exceptionally large size, narrow ranges, remote habitats, and, in some cases, foul-smelling, irritating secondary chemistry, our understanding of *Chingia* is impeded both by lack of collections and paucity of complete specimens.

New combinations.—

Chingia marattioides** (Alston) S.E. Fawc. & A.R. Sm., **comb. nov.—Dryopteris marattioides* Alston, J. Bot. 78:227. 1940.—*Plesioneuron marattioides* (Alston) Holttum

Chingia lindleyi (W.N. Takeuchi) S.E. Fawc. & A.R. Sm., **comb. nov.—***Amphineuron lindleyi* W.N. Takeuchi, Harvard Pap. Bot. 10:105. 2005.

Constituent species.—**Chingia acutidens* Holttum; **C. atrospinosa* (C. Chr.) Holttum; *C. australis* Holttum; *C. bewaniensis* Holttum; *C. christii* (Copel.) Holttum; **C. clavipilosa* Holttum; **C. ferox* (Blume) Holttum; **C. fijiensis* Game, S.E. Fawc. & A.R. Sm.; *C. horridipes* (Alderw.) Holttum; *C. imponens* (Ces.) Holttum; *C. lindleyi* (W.N. Takeuchi) S.E. Fawc. & A.R.

Sm.; **C. longissima* (Brack.) Holttum; *C. lorzingii* Holttum; **C. malodora* (Copel.) Holttum; **C. marattioides* (Alston) S.E. Fawc. & A.R. Sm.; *C. muricata* (Brause) Holttum; *C. paucipaleata* Holttum; *C. perrigida* (Alderw.) Holttum; *C. pricei* Holttum; *C. pseudoferox* Holttum; *C. sakayensis* (Zeiller) Holttum; **C. sambasensis* Holttum; *C. supraspinigera* (Rosenst.) Holttum; *C. tenerior* Holttum; *C. urens* Holttum

CHRISTELLA

Christella H. Lév., Flore de Kouy-tchéou 472. 1915.—Type: *Christella parasitica* (L.) H. Lév. [= *Polypodium parasiticum* L.].

Thelypteris subg. *Cyclosoriopsis* K. Iwats., Mem. Coll. Sci. Univ. Kyoto, ser. B, 31(1):28. 1964.—Type: *Thelypteris dentata* (Forssk.) E.P. St. John [= *Polypodium dentatum* Forssk.] = *Christella dentata* (Forssk.) Brownsey & Jermy

For complete synonymy, see Holttum (1976b, 1977b, 1982), Lin et al. (2013).

Etymology.—Honoring Swiss pteridologist Hermann Christ, 1833–1933 (Stewart et al. 1983).

Plants terrestrial, medium-sized (> 40 cm) to large (fronds to ca. 150 cm tall); **rhizomes** most often short- to long-creeping or suberect, occasionally erect; rhizome scales almost always lanceolate, brown, setulose on margins and surfaces; **fronds** monomorphic, occasionally weakly dimorphic with the fertile ones taller and longer-stiped, pinnate-pinnatifid, erect or arching; **stipes** stramineous to purplish, adaxially grooved, bearing scales at the base like those of rhizome apices; **blades** chartaceous to subcoriaceous, drying greenish, with proximal several 1–5(–10) pairs of pinna gradually reduced and almost always auricled at acroscopic base (the lowest not less than 2 cm long), less often blades truncate at base (e.g., *C. moluccana*, *C. parasitica*); blade apices usually not conform and generally pinnatifid or pinnatisect, infrequently subconform; **rachises** generally quite hairy, hairs 0.1–1.0 mm long, rarely also scaly (e.g., *C. crinipes*), lacking proliferous buds in axils of pinnae; **pinnae** usually alternate or becoming alternate distally, adaxially with a groove that is not continuous with the rachis groove, shallowly to often deeply pinnatifid; **veins** usually prominent on both sides, unbranched, 1–3 lowermost pairs from adjacent segments united at an obtuse angle below the sinus, and forming excurrent veins running to the sinus, rarely lowermost veins connivent at the sinus (e.g., *C. conspersa*) or meeting the segment margins above the sinus (e.g., *C. harveyi*), free vein ends reaching segment margins; **aerophores** absent at pinna bases, not swollen (pinnae abaxially sometimes with a slightly raised, darkened lunate ridge at attachment to rachis); **indument abaxially** of stipes, rachises, costae, veins, and often laminar tissue between veins of hyaline, acicular, spreading hairs (except *C. evoluta*, which is nearly glabrous), these short to long (0.1–1+ mm), generally unicellular, sometimes also with short capitate hairs, these usually with orangish to reddish, somewhat elongate (pear-shaped or clavate) glands on costules and veins, lacking sessile spherical glands and costal scales; **indument adaxially** of generally long (> 0.5 mm) hyaline, unicellular setae on stipes, rachises, and costae, sometimes also on veins, also often with scattered to rather dense, usually somewhat spreading (at least not closely appressed) hairs 0.2–0.3 mm between veins on most species; **pustules** absent on laminar tissue on both sides; **sori** medial or nearly so, not coalescent at maturity, indusiate (except *C. nana*), indusia usually setose on margins and surfaces, and somewhat persistent; **sporangia** usually without setulae or glands on the capsules, but often each with a unicellular, orangish, elongate gland on the stalk (such glands absent in many African spp.); **spores** dark brown, with perispore variously ridged, rugose, or tuberculate, lacking narrow wings; $x = 36$ (14+ spp. counted), diploids and several different tetraploids (*C. dentata*, *C. parasitica*, *C. subpubescens*) known, as well as many interspecific hybrids (see below).

Diagnosis.—Holttum (1976b) considered the essential characters of *Christella* to include the presence of an elongate, unicellular gland on the sporangial stalks (illustrated by Smith 1971), usually gradual reduction of auricled proximal pinnae (1–5 pairs), the universal presence of erect, acicular hairs on blades, including between the veins, and the absence of sessile spherical glands on the blades, as well as on the sporangial capsules. However, there are exceptions to some of these characters in particular species, e.g., the African species initially placed in sect. *Pelazoneuron* lack glands on the sporangial stalks, and *C. parasitica* lacks reduced proximal pinnae. Among related genera, *Christella* is distinguished from *Pseudocyclosorus* by the stipe base scales lanceolate, hairy on the margins and both sides, spreading (vs. stipe base scales often ovate, glabrous or with few hairs, appressed); generally anastomosing veins or pairs of veins that unite and produce an excurrent vein that runs to the sinus; the smaller number (or even absence) of reduced proximal pinnae at the base of the blades (vs. blade bases with as many as 12 pairs of abruptly reduced pinnae, the lowest < 5 mm and glanduliform); the presence of acicular hairs on and between the veins, both abaxially and adaxially (vs. hairs usually absent on veins and/or between veins, both sides of lamina); and the usual presence of an orangish, unicellular, clavate or tubular gland on each sporangial stalk as well as sometimes on the indusia and along the veins and costules abaxially. *Amblovenatum* differs from *Christella* in often bearing sulfur-yellow, sessile, spherical glands along the veins and costules, especially towards the tips of the segments.

Biogeography and ecology.—The 66 known species of *Christella* are mostly restricted to the Old World tropics and subtropics, from Africa through India and southeast Asia, China, Japan, and Malesia, Melanesia, and Polynesia. The center of diversity of the genus is clearly China and mainland southeast Asia to India (nearly 40 spp.), with a diminished number of species in Malesia, Melanesia, and Polynesia (17 species; Holttum 1977b), and even fewer in Africa (ca. four spp.; Holttum 1974a) and the Neotropics (two native, one naturalized; Smith 1971). The two native species in the Americas are *C. conspersa* and the pantropical *C. hispidula*; a third species, *C. dentata*, historically confused with *C. hispidula*, is very widely naturalized and is now one of the most commonly collected ferns in many parts of North and South America, from southeastern United States and Mexico to southern Brazil, Paraguay, and Bolivia (Smith 1971; Strother & Smith 1970). A group of species in eastern Malesia and Melanesia seems to be confined to limestone or coral rocks (e.g., *C. buwaldae*, *C. calcarea*, *C. gretheri*, *C. minima*, *C. moluccana*, *C. nana*, *C. perpubescens*; Chen et al. 2017:340–341) and were placed in *Christella* sect. *Leptochristella* by Holttum (1982).

Christella species are often widespread, locally common or even abundant, and sometimes weedy; the species generally occur at low to middle elevations, 0–1600(–2500) m. They are also quite variable morphologically, and this is reflected in the many heterotypic synonyms (> 10) for the most widespread species (see, e.g., Li et al. 2013; Lin et al. 2013). Species are commonly found along roadsides and trails, in ditches, ravines, and sometimes on limestone outcrops, often in slightly to heavily disturbed habitats. The ubiquitous *C. dentata* (**Fig. 2J**) is a common greenhouse weed. Circumscription of the genus herein is largely as treated in Holttum (1971, 1976b, 1982), except that we exclude some African and all American species recognized as *Christella* sect. *Pelazoneuron* by Holttum and allied either with *Pseudocyclosorus* (the African ones) or placed in *Pelazoneuron* (the American ones).

Some of the species accepted in the *Flora of China* (Lin et al. 2013; Li et al. 2013), e.g., *C. molliusculus* (Wall. ex Kuhn) Ching, *C. parvifolius* Ching, *C. procurrens* (Mett.) Copel., and *C. pygmaeus* Ching & C. F. Zhang, are known from relatively small areas in China and rather few specimens. We have not seen specimens or even photos of types. We prefer to await a more comprehensive treatment of the genus through its wide range to better evaluate the utility and consistency of the characters being used to define them, as well as their relationships to broadly variable and more widely distributed members of *Christella* in China and elsewhere, e.g., *C. parasitica*, *C. dentata*, and *C. subpubescens*.

Taxonomic and phylogenetic studies.—*Christella s.s.*, as defined here, including some of the African species of sect. *Pelazoneuron* discussed by Holttum (1974a), but not the type, is a member of the christelloid clade, which also includes *Sphaerostephanos*, *Pneumatopteris*, *Reholttumia*, and a few smaller genera (**Fig. 1**). In its redefined sense, the genus is sister to the clade including *Pseudocyclosorus*, *Trigonospora,* and *Abacopteris*, and this combined clade is sister to *Amblovenatum s.s.* A clade of African species, including *C. chaseana, C. gueintziana*, and *C. microbasis*, variously resolves as sister to *Christella s.s.*, or as sister to *Pseudocyclosorus* (Fawcett et al. in press). Species previously recognized as *Christella* are resolved in clades corresponding to *Pelazoneuron* and *Menisciopsis*.

The taxonomy and relationships within *Christella* are still preliminary, because of their widespread and variable nature, propensity to hybridize with related species (and perhaps also with species in other genera), the widespread polyploidy in the genus, and their tendency toward weediness. For general characterization and treatments of *Christella* in Asia see Holttum's seminal works (1971, 1976b) and the revision of Chinese taxa by Li et al. (2013); coverage for Pacific species is by Holttum (1977b), and for Malesian taxa by Holttum (1982). Holttum (1974a) also treated the African species, and those from adjacent islands.

Some authors, for example Lin et al. (2013) and Li (2013), have included *Christella s.l.* as part of a much larger genus *Cyclosorus s.l.*, which, thus defined, includes several other christelloid genera (especially *Sphaerostephanos*, *Pneumatopteris* sensu Holttum), and *Cyclosorus* itself, which we recognize as a small genus of two species. However, *Cyclosorus s.s.* is significantly different in several morphological characters and falls outside the christelloid clade (He & Zhang 2012; Almeida et al. 2016; Fawcett et al. in press). Definitions of *Cyclosorus s.l.* often exclude *Pronephrium s.l.*, which is now known to be polyphyletic, with two of its four segregates (*Menisciopsis* and *Grypothrix*) falling within the chingioid clade and the other two (*Pronephrium s.s.*, and *Abacopteris*) being within the christelloid clade and related to *Christella* (**Fig. 1**). As a consequence of new phylogenetic information, and reconsideration of the morphology, we here choose to recognize *Christella* in a more restricted sense.

Notes.—Hybrids between species of *Christella* abound, and many different infrageneric hybrids have been proposed (Shieh & Tsai 1987; Wagner 1993; Fraser-Jenkins 1997): *Thelypteris* ×*aculodentata* Fraser-Jenk. [*Christella dentata* × *jaculosa*]; *Thelypteris* ×*dentiarida* Fraser-Jenk. [*Christella arida* × *dentata*]; *Thelypteris* ×*gorkhalensis* Fraser-Jenk. [*Christella arida* × *clarkei*]; *Christella* ×*intermedia* (W.C. Shieh & J.L. Tsai) D.D. Palmer (= *Thelypteris* ×*incesta* W.H. Wagner) [*Christella dentata* × *parasitica*]; *Thelypteris* ×*inexpectata* Fraser-Jenk. [*Christella dentata* × *evoluta*]; *Cyclosorus*

×*intermedius* W.C. Shieh & J.L. Tsai [*Christella dentata* × *parasitica*]; *Thelypteris* ×*jaculodentata* Fraser-Jenk. [*C. dentata* × *jaculosa*]; *Christella* ×*kumaunica* Holttum [*Christella arida* × *procera*?]; *Thelypteris* ×*linii* Fraser-Jenk. [*Christella clarkei* × *dentata*]; *Thelypteris* ×*nareshii* Fraser-Jenk. [*Christella dentata* × *procera*]; *Thelypteris* ×*papilioides* Fraser-Jenk. [*Christella papilio* × *procera*]; *Thelypteris* ×*parahispidula* Fraser-Jenk. [*Christella hispidula* × *parasitica*]. *Christella* ×*altissima* Holttum, type from Natal, *Buchanan 103b* (K, isotype UC!) appears to be a sterile hybrid with malformed spores and involving *C. dentata*. Li et al. (2013) listed an additional 22 described species in *Cyclosorus* subg. *Cyclosoriopsis*, all with types from mainland China or Taiwan, that they consider putative hybrids, based on morphological intermediacy, lack of sori or no mature normal sori, and malformed spores. Hybrids within *Christella* can be expected whenever two species in the genus co-occur, but all suspected hybrids need substantiation by more than just morphological intermediacy and spore malformation: cytological, ecological, and nucleotide sequence evidence are also needed to confirm hybridity.

A few intergeneric hybrids, mostly from the Paleotropics, are also suspected, with one parent a *Christella*: *Thelypteris* ×*nepalensis* Fraser-Jenk. [*Christella dentata* × *Menisciopsis penangiana*]; *Thelypteris* ×*varievenulosa* Viane [*Pneumatopteris afra* × *Christella hispidula*], from the Ivory Coast (Viane 1985); another, given a hybrid generic name, is ×*Chrismatopteris holttumii* Quansah & D. S. Edwards, from Ghana [*Pneumatopteris afra* × *Christella dentata*; Quansah & Edwards 1986]. *Thelypteris* ×*palmeri* W.H. Wagner [*Christella dentata* × *Menisciopsis cyatheoides*]. *Christella* ×*wildemanii* (Christ) J.P. Roux, was accorded hybrid status by Roux (2009), but the putative parents were not indicated. By Holttum (1974a) and Viane (1985), this was thought to be a hybrid involving *Pneumatopteris afra*, which is apparently most closely related to *Abacopteris* and *Christella* (Fawcett et al. in press). Viane (1985) believed the other parent might be a species of Holttum's *Christella* sect. *Pelazoneuron*, which we consider members of the pseudocyclosoroid clade, since none of Holttum's (1974a) African taxa are related to the type of sect. *Pelazoneuron, P. patens*. In the Neotropics, Smith (1971) postulated a possible origin of tetraploid *Thelypteris kunthii* (treated by us herein as a species of *Pelazoneuron*) from an allopolyploid hybridization event between two diploids, *Thelypteris hispidula* (at the time treated as *Thelypteris quadrangularis* (Fée) Schelpe, now synonymized under *Christella hispidula*) and *T. ovata* (treated by us herein as *Pelazoneuron ovatum*). There is now some support for such a hypothesis based on topologies of discordant gene trees (Fawcett et al. in press).

Perhaps reflecting their penchant to hybridize, members of *Christella* have also been the subject of artificial hybridization experimentation, maybe more so than within any other genus of ferns. Results of experiments, by Panigrahi & Manton (1958) and Ghatak & Manton (1971), and conclusions derived from them, were summarized by Holttum (1976b: 295–297). Crosses were made between known diploids (especially *C. hispidula*) from many areas of Asia and Africa, and several tetraploids (e.g., *C. dentata*, *parasitica*), also from multiple sources. Chromosome pairing in the resultant triploids was often *n* pairs and *n* univalents, probably indicating a shared genome by the parents, as well as spore malformation (abortion). Other tetraploids used in attempted hybridizations with diploid *C. hispidula* failed, suggesting that the genome of the latter was not part of the makeup of the tetraploids. The authors concluded that some tetraploids in this group (placed by them in *Cyclosorus*) were allotetraploid and shared a genome with *C. hispidula*. Additional conclusions related to whether certain characters, i.e., ones frequently used in distinguishing species of *Christella* (and by extension, other thelypteroids), behaved as recessive or dominant in hybridizations, and the recessive characters included: 1) erect rhizomes (vs. creeping); 2) gradual reduction of proximal pinnae (vs. no reduction); 3) absence (vs. presence) of thick glandular hairs abaxially on laminae; and 4) verrucose perispore ornamentation (vs. irregular ridges). These findings have implications for erecting a usable taxonomy. In light of these discoveries, it is not surprising that *Christella* is especially confusing in the field and in the herbarium.

New combinations.—

Christella jinhongensis (Ching ex K.H. Shing) A.R. Sm. & S.E. Fawc., **comb. nov.—***Cyclosorus jinghongensis* Ching ex K.H. Shing, Fl. Reipubl. Popularis Sin. 4:337. 1999.

Christella nanxiensis (Ching ex K.H. Shing) A.R. Sm. & S.E. Fawc., **comb. nov.—***Cyclosorus naxiensis*, Fl. Reipubl. Popularis Sin. 4:343. 1999.

Christella oblancifolia (Tagawa) A.R. Sm. & S.E. Fawc., **comb. nov.—***Dryopteris oblancifolia* Tagawa, Acta Phytotax. Geobot. 5:190. 1936. *Thelypteris oblancifolia* (Tagawa) Fraser-Jenk.

Christella shimenensis (K.H. Shing & C.M. Zhang) A.R. Sm. & S.E. Fawc., **comb. nov.—***Cyclosorus shimenensis* K.H. Shing & C.M. Zhang, Keys Vasc. Pl. Wuling Mts. 565. 1995.

Christella subacuta (Ching) A.R. Sm. & S.E. Fawc., **comb. nov.—***Cyclosorus subacutus* Ching, Fl. Fujian. 1:598. 1982.

Christella wulingshanensis (C.M Zhang) A.R. Sm. & S.E. Fawc., **comb. nov.—***Cyclosorus wulingshanensis* C.M. Zhang, Keys Vasc. Pl. Wuling Mts. 567. 1995.

Constituent species and infrageneric taxa (generally following Holttum 1982; Li et al. 2013).—**Christella acuminata* (Houtt.) Lév.; *C. adenopelta* Holttum; ***C. arida* (D. Don) Holttum; *C. balansae* (Ching) Holttum; ***C. boninensis* (Kodama ex Koidz.) Holttum; *C. burmanica* (Ching) Holttum; *C. buwaldae* (Holttum) Holttum; **C. calcarea* D. Glenny, sp. ined.; *C. callensii* (Alston) Holttum; ***C. calvescens* (Ching) Holttum; *C. carolinensis* (Hosok.) Holttum; **C. chaseana* (Schelpe) Holttum; *C. clarkei* (Bedd.) Holttum; **C. conspersa* (Schrad.) Á. Löve & D. Löve; ***C. crinipes* (Hook.) Holttum; *C. cuneatus* Ching ex K.H. Shing; *C. cylindrothrix* (Rosenst.) Holttum; **C. dentata* (Forssk.) Brownsey & Jermy (**Fig. 2J**); **C. ensifera* (Tagawa) Holttum; *C. euphlebia* (Ching) Holttum; **C. evoluta* (C.B. Clarke & Baker) Holttum; *C. fukienensis* (Ching) Holttum; **C. gretheri* (W.H. Wagner) Holttum; **C. guamensis* Holttum; **C. gueintziana* (Mett.) Holttum [several authors, e.g., Schelpe (1964), Holttum (1974a), and Roux (2009, 2013), have used the altered spelling "gueinziana", but this is impermissible]; *C. gustavii* (Bedd.) Holttum [placement in *Christella* disputed by Li et al. 2013]; **C. harveyi* (Mett.) Holttum; *C. harveyi* var. *connivens* Holttum; **C. hispidula* (Decne.) Holttum; *C. hokouensis* (Ching) Holttum [placement in *Christella* disputed by Li et al.]; **C. jaculosa* (Christ) Holttum; *C. jinghongensis* (Ching ex K.H. Shing) A.R. Sm. & S.E. Fawc.; *C. kendujharensis* S.K. Behera & S.K. Barik.; *C. kumaunica* Holttum; **C. latipinna* (Benth.) H. Lév.; *C. lebeufii* (Baker) Holttum; *C. microbasis* (Baker) Holttum; *C. minima* Holttum; *C. modesta* Holttum; *C. moluccana* M. Kato; *C. mutifrons* (C. Chr.) Holttum; *C. namburensis* (Bedd.) Holttum; *C. nana* Holttum; ***C. nanxiensis* (Ching ex K.H. Shing) A.R. Sm. & S.E. Fawc.; *C. pacifica* Holttum; **C. papilio* (Hope) Holttum; *C. papyracea* (Bedd.) Holttum; **C. parasitica* (L.) Lév.; *C. peekelii* (Alderw.) Holttum; *C. perpubescens* (Alston) Holttum; *C. procera* (D. Don) Mazumdar, with heterotypic synonym *C. appendiculata* (C. Presl) Holttum (= *Thelypteris appendiculoides* Fraser-Jenk.); *C. prolixa* (Willd.) Holttum; *C. pseudogueintziana* (Bonap.) Alston; *C. rupicola* (Hosok.) Holttum; ***C. scaberula* (Ching) Holttum; *C. semisagittata* (Roxb.) Holttum; *C. shimenensis* (K.H. Shing & C.M. Zhang) A.R. Sm. & S.E. Fawc.; **C. siamensis* (Tagawa & K. Iwats.) Holttum; *C. sledgei* (Fraser-Jenk.) Ranil; *C. subdentata* Holttum; ***C. subelata* (Baker) Holttum; *C. subjuncta* (Baker) Holttum; **C. subpubescens* (Blume) Holttum; *C. taprobanica* (Panigrahi) Holttum; *C. timorensis* Holttum; *C. wulingshanensis* (C.M. Zhang) A.R. Sm. & S.E. Fawc.; *C. zeylanica* (Fée) Holttum.

Excluded names.—*Dryopteris albociliata* Copel. [= *C. parasitica*]; *Dryopteris assamica* Rosenst. [= *C. cylindrothrix*]; *Cyclosorus benguetense* Copel. [= *C. hispidula*]; *Polystichum benoitianum* Gaudich. [= *Sphaerostephanos benoitianus* (Gaudich.) Holttum—Holttum thought it possibly related to *Strophocaulon invisum* (G. Forst.) S.E. Fawc. & A.R. Sm.]; *Nephrodium biauritum* Bedd. [= *C. lebeuffii*]; *Dryopteris contigua* Rosenst. [= *C. hispidula*]; *Nephrodium didymosorum* Parish ex Bedd. [= *C. parasitica*]; *Dryopteris euaensis* Copel. [= *C. harveyi*]; *Nephrodium eurostotrichum* Baker = *Christella distans* (Hook.) Holttum, *incertae sedis*; *Cyclosorus falcatulus* (Christ) Copel. [= *C. hispidula*]; *Dryopteris hirtopilosa* Rosenst. [= *C. hispidula*]; *Cyclosorus jerdonii* Ching (excluded from *Christella* by Holttum 1976b: 336); *Dryopteris meeboldii* Rosenst. [= *C. malabariensis*]; *Dryopteris mindanaensis* Christ [= *C. dentata*]; *C. molliuscula* (Wall. ex Kuhn) Holttum [= *Pseudocyclosorus canus* (Baker) Holttum & Grimes]; *C. multiauriculata* Punetha [= *C. dentata*]; *Thelypteris novae-hiberniae* Holttum [= *C. harveyi*]; *Polypodium nymphale* Forst. [= *C. dentata*]; *Aspidium obliquatum* Mett. [= *C. prolixa*]; *Aspidium procurrens* Mett. [= *C. parasitica*]; *Dryopteris pseudoamboinensis* Rosenst. [= *C. subpubescens*]; *Nephrodium quadrangulare* Fée [= *C. hispidula*]; *Dryopteris repandula* Alderw. [= *C. hispidula*]; *Cyclosorus subaridus* Tatew. & Tagawa ex Tagawa [= *Christella jaculosa*]; *Dryopteris submollis* Alderw. [= *C. dentata*]; *Dryopteris sumatrana* Alderw. [= *C. subpubescens*]

Excluded species.—Three Hawaiian endemic species treated in *Christella* by Holttum (1977b) and Palmer (2003), *Christella boydiae, C. cyatheoides* and *C. wailele* are here transferred to the genus *Menisciopsis*. Based on a photo of the type of *Christella burundensis* Pic.Serm., and notes on the specimen by Holttum, this is not a *Christella*, and may be *Pelazoneuron kunthii* (Desv.) A.R. Sm. & S.E. Fawc.; it has free veins and the proximal pinnae are not reduced. If that species, it is likely introduced and not native to Burundi.

Incertae sedis.—*Christella afzelii* (C. Chr.) Holttum. Based on an image of the type, this appears to be bipinnate; veins are free and sometimes forked. It is unlikely to be a *Christella*.

Several Afro-Madagascan species (represented by *Pneumatopteris humbertii* and *Christella distans* in Fawcett et al. in press) are more closely related to *Pseudocyclosorus* and *Trigonospora* than to *Christella s.s.* Holttum (1976b) considered *Christella distans* the most aberrant species in *Christella*, in part because of the swollen aerophores; we agree, and its taxonomic placement remains uncertain. Two other species, *Christella friesii* (Brause) Holttum and *C. guineensis* (Christ) Holttum, may also belong to the *Pseudocyclorosus* + *Trigonospora* clade. Based on the original description (Rakotondrainibe & Jouy 2011) and images of the type (P!) of *Christella darainensis* Rakotondr., we note that the veins are free with the proximal one of a pair running to the sinus, the adjacent vein meeting the margin above the sinus, the rhizome is erect, and the stipe base scales are ovate and glabrous, unlike those of *Christella*, suggesting it may be more closely related to *Trigonospora*. The African Thelypteridaceae have been the most difficult taxonomically and have been subject to the greatest taxonomic upheaval as a result of our phylogenetic study (see *Menisorus* and *Pneumatopteris* for further discussion). This morphologically variable, and poorly studied species group cannot be confidently placed; additional molecular sampling and study of herbarium material will be necessary before taxonomic changes are made.

CORYPHOPTERIS

Coryphopteris Holttum, Blumea 19:33. 1971.—Type: *Coryphopteris viscosa* (Baker) Holttum [= *Nephrodium viscosum* Baker].

Wagneriopteris Á. Löve & D. Löve
For additional synonymy, see Holttum (1976a, 1977b, 1982), Lin et al. (2013).

Etymology.—Gr. *korupho*, latinized *Coryph*, summit, crest + *pteris*, fern, in reference to the propensity of species of this genus to grow on ridgetops in the Paleotropics.

Plants terrestrial (rarely epiphytic), of temperate forest understories, or tropical montane habitats, small to medium-sized (10 cm to 1 m tall); **rhizomes** erect and trunk-like (rarely creeping, e.g., in the temperate species *C. simulata*); **fronds** monomorphic to weakly dimorphic (fertile fronds slightly taller and with slightly narrower pinnae), pinnate-pinnatifid to pinnate-pinnatisect, rarely fully bipinnate (e.g., *C. habbemensis*); **stipes** stramineous, castaneous, or dull brown; **stipe scales** linear-lanceolate to ovate, thin to stiff, usually glabrous, these often transitioning to filiform scales, or uniseriate hairs on abaxial laminar axes (**Fig. 2L**); **blades** membranaceous to chartaceous, drying green or blackish, apex gradually reduced, proximal pinnae typically largest, not or only slightly reduced, often deflexed, rarely with a few to many pairs of proximal pinnae gradually reduced (e.g., *C. nipponica, C. fasciculata*); proliferous buds absent; **pinna** margins entire or slightly dentate, segments often parallel-sided and little tapered, with apices rounded, truncate, less often acute, often nearly perpendicular to costae (never strongly oblique), bases with one or more proximal pinna lobes sometimes free or sometimes with lobed acroscopic auricles; **veins** always free, mostly simple (rarely forking), reaching margins, costae grooved adaxially; **aerophores** absent or present as minor swellings; **indument abaxially** of hyaline acicular hairs, almost always also with glands, which may be stipitate or sessile, viscid or resinous, reddish, amber, or golden, never sulfur-colored (glands sometimes difficult to observe on dried specimens); scales often present abaxially along stipes and costae, transitioning to multicellular hairs; **indument adaxially** of unicellular or septate hyaline acicular hairs restricted to axes, or also present on laminar tissue between veins, sessile or stipitate glands sometimes present; **pustules** absent; **sori** usually round, sometimes slightly elongate on distal portion of segments, discrete, medial to costular, indusia typically present, these glabrous, or with acicular hairs or glands (**Fig. 2A**); **sporangia** short-stalked, capsule lacking hairs or glands, stalk sometimes with gland; **spores** typically pale, with perforate perine (Patel et al. 2019a), and often with fimbriate wings; $x = 31, 32, 33$ seven species counted, diploids, triploids and tetraploids known, although additional counts are needed to verify the base numbers. Infrageneric hybrids between *C. japonica* and *C. musashiensis* are well documented (Nakato et al. 2004).

Diagnosis.—*Coryphopteris* is most similar to *Amauropelta s.l.*, but it may be distinguished by its usually erect, trunk-like rhizomes, proximal pinnae largest or only slightly reduced, and by the presence of filiform scales or multicellular hairs along abaxial costae. *Metathelypteris* differs from both genera in having adaxial costae lacking a groove, and veins ending before the margins. The presence of abundant septate hairs on the adaxial axes of the laminae, frequent in *Coryphopteris*, is an unusual feature within the Thelypteridaceae (Holttum 1976a).

Biogeography and ecology.—*Coryphopteris* is widely distributed on mainland Asia from northeastern India to southern Russia. It is most diverse in the mountainous areas of Malesia, Melanesia, and Polynesia, usually above 1000 m. There is also a single species endemic to North America, and this has a primary distribution to the east from southern Canada to Virginia, and disjunct populations in the Great Lakes region (Smith 1993a). The genus includes 68 species and reaches its greatest diversity in the mountains of Papua New Guinea. Throughout their range, *Coryphopteris* species often occur in acidic or low-nutrient soils. In temperate North America, habitats include forest understories, often in mixed hardwood-conifer swamps, or wetland margins, frequently in association with *Sphagnum*. Holttum (1982) described tropical species as distributed exclusively on high elevation ridgetops, where the soils were leached, nutrient poor, and highly acidic, a habitat not normally shared with other members of Thelypteridaceae.

Taxonomic and phylogenetic studies.—The genus was first described by Holttum (1971) and monographed soon after (Holttum 1976a). Holttum's work dealt largely with the Malesian and Pacific species, and he described 50 of the 68 currently recognized species as new to science. Only three additional species belonging to this genus (Kato 2007; Lorence et al. 2011; Ebihara et al. 2020) have been described since Holttum (1982). Most Chinese species of *Coryphopteris* recognized here were treated by Ching (1963) in *Parathelypteris*. Holttum's (1976a) concept of *Coryphopteris* largely followed that of Ching for Chinese species in the group, recognizing only two species of *Coryphopteris* in mainland Asia: *C. hirsutipes* and *C. petelotii*. Despite rhizome differences—typically erect caudices in *Coryphopteris*, creeping rhizomes in *Parathelypteris* (=*Amauropelta* subg. *Parathelypteris* in our treatment)—Holttum noted the striking similarities (notably spores and sporangia) between some species of *Parathelypteris s.l.* and *Coryphopteris*, and expressed uncertainty about the taxonomic boundaries between the two genera in China and Japan (Holttum 1976a).

Holttum (1976a) considered *Coryphopteris angulariloba*, and *C. indochinensis* to be among seven heterotypic synonyms of a broadly variable *C. hirsutipes*, but he did not have access to type material for all of his synonyms. We follow Lin et al. (2013) and He & Zhang (2012) in recognizing these taxa as distinct. Pending further study, which may refine species delimitation, all necessary combinations in *Coryphopteris* are provided below.

Critical insights into the relationships among temperate and subtropical Asian *Parathelypteris s.l.* were provided by molecular phylogenetic studies (Ebihara et al. 2011; He & Zhang 2012); these resolved *Parathelypteris* in two distinct clades—one, including the type, resolving with *Amauropelta s.s.* (subg. *Amauropelta*), and the other, with *Coryphopteris*, which is sister to a clade that includes *Amauropelta s.s.*, *Parathelypteris*, and *Metathelypteris*. The sole North American species, *Coryphopteris simulata* (type of *Wagneriopteris*), was shown to be closely related to a Japanese accession of the East Asian species *Coryphopteris nipponica* (Fawcett 2018), both of which had been treated previously in *Parathelypteris*. Based on their molecular evidence, He and Zhang (2012) published new combinations in *Coryphopteris* for some species of *Parathelypteris*. We provide new combinations for an additional 11 species below, based on additional sampling (Fawcett et al. in press) and morphological study. In the present classification, the species of *Parathelypteris* (which has been shown to be polyphyletic) are treated in *Coryphopteris* in *Coryphopteris* or in three of the four subgenera of *Amauopelta*: subg. *Parathelypteris*, subg. *Nibaa*, and subg. *Venus*.

Based on certain morphological similarities to *Cyathea* (e.g., erect caudices, septate acicular hairs on adaxial axes, short-stalked sporangia), Holttum (1971, 1976a) hypothesized that *Coryphopteris* was "primitive" in the family and derived from a tree-fern lineage. All large-scale molecular studies of fern relationships (e.g., Testo & Sundue 2016) suggest that these groups are in fact quite distantly related.

Notes.—The name *Parathelypteris nipponica* has been broadly applied to plants from Japan, Korea, and China. The type is from Japan, and has been resolved in the *Coryphopteris* clade (Ebihara et al. 2011), while plants from China determined as such have been resolved near to *Parathelypteris s.s.* (He & Zhang 2012). Although they are strikingly similar—both have creeping rhizomes, sessile yellow glands on abaxial laminae, and several pairs of reduced proximal pinnae—typical *Coryphopteris nipponica* usually has three or fewer pairs of reduced proximal pinnae, while the Chinese plants, historically recognized as this, tend to have more than three pairs of gradually reduced proximal pinnae, and are most closely allied to *Amauropelta beddomei* (Fawcett et al. in press). This complex group of plants is in need of critical study and taxonomic revision (Ebihara & Nitta 2019). In tropical regions, as Holttum (1976a) noted, many of the localities that support *Coryphopteris* are difficult to access and have likely never been visited by botanical collectors. He further stated that anyone wishing "to make a general study of them would need to be very energetic and also have considerable resources for travel at his disposal" (Holttum 1976a:21).

New combinations.—

Coryphopteris caudata (Ching ex K.H. Shing) S.E. Fawc. & A.R. Sm., **comb. nov.—***Parathelypteris caudata* Ching ex K.H. Shing, Fl. Reipubl. Popularis Sin. 4:320. 1999.

****Coryphopteris chinensis** (Ching) S.E. Fawc. & A.R. Sm., **comb. nov.—***Thelypteris chinensis* Ching, Bull. Fan Mem. Inst. Biol. 6:311. 1936.—*Parathelypteris chinensis* (Ching) Ching

Coryphopteris chingii (K.H. Shing & J.F. Cheng) S.E. Fawc. & A.R. Sm., **comb. nov.—***Parathelypteris chingii* K.H. Shing & J.F. Cheng, Jiangxi Sci. 8:44. 1990.

Coryphopteris indochinensis (Christ) S.E. Fawc. & A.R. Sm., **comb. nov.—***Dryopteris indochinensis* Christ, J. Bot. (Morot), ser. 2, 1:263. 1908.—*Parathelypteris indochinensis* (Christ) Ching—*Thelypteris indochinensis* (Christ) Ching

Coryphopteris krayanensis (K. Iwats. & M. Kato) S.E. Fawc. & A.R. Sm., **comb. nov.—***Thelypteris krayanensis* K. Iwats. & M. Kato, Acta Phytotax. Geobot. 34(4–6):135(–136), f. 4. 1983.

****Coryphopteris musashiensis** (Hiyama) S.E. Fawc. & A.R. Sm., **comb. nov.—***Thelypteris japonica* var. *musashiensis* Hiyama, J. Jap. Bot. 26:155. 1950.—*Parathelypteris musashiensis* (Hiyama) Nakaike—*Thelypteris musashiensis* (Hiyama) Nakato, Sahashi & M. Kato

Coryphopteris nigrescens** (Ching ex K.H. Shing) S.E. Fawc. & A.R. Sm., **comb. nov.—Parathelypteris nigrescens* Ching ex K.H. Shing, Fl. Reipubl. Popularis Sin. 4:321. 1999.

****Coryphopteris nipponica** (Franch. & Sav.) S.E. Fawc. & A.R. Sm., **comb. nov.—***Aspidium nipponicum* Franch. & Sav., Enum. Pl. Jap. 2:242. 1879.—*Parathelypteris nipponica* (Franch. & Sav.) Ching—*Thelypteris nipponica* (Franch. & Sav.) Ching

Coryphopteris pauciloba (Ching ex K.H. Shing) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Parathelypteris pauciloba* Ching ex K.H. Shing, Fl. Reipubl. Popularis Sin. 4:321. 1999.

Coryphopteris sylva-nipponica (Ebihara & Nakato) S.E. Fawc., A.R. Sm. & Ebihara, **comb. nov.**—*Thelypteris sylva-nipponica* Ebihara & Nakato, Phytotaxa 477:239. 2020.

Coryphopteris trichochlamys (Ching ex K.H. Shing) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Parathelypteris trichochlamys* Ching ex K.H. Shing, Fl. Reipubl. Popularis Sin. 4:320. 1999.

Constituent species.—*Coryphopteris andersonii* Holttum; *C. andreae* Holttum; **C. angulariloba* (Ching) L.J. He & X.C. Zhang; *C. arthrotricha* Holttum; *C. athyriocarpa* (Copel.) Holttum; *C. athyrioides* Holttum; *C. atjehensis* Holttum; **C. badia* (Alderw.) Holttum; *C. borealis* Holttum; *C. brevipilosa* Holttum; **C. castanea* (Tagawa) Y.H. Chang; *C. caudata* (Ching ex K.H. Shing) S.E. Fawc. & A.R. Sm.; ***C. chinensis* (Ching) S.E. Fawc. & A.R. Sm.; *C. chingii* (K.H. Shing & J.F. Cheng) S.E. Fawc. & A.R. Sm.; *C. coriacea* (Brause) Holttum; **C. diaphana* (Brause) Holttum; *C. didymochlaenoides* (C.B. Clarke) Holttum; *C. diversisora* (Copel.) Holttum; *C. dura* (Copel.) Holttum; *C. engleriana* (Brause) Holttum; **C. fasciculata* (E. Fourn.) Holttum; **C. gymnopoda* (Baker) Holttum; **C. habbemensis* (Copel.) Holttum; **C. hirsutipes* (C.B. Clarke) Holttum; *C. horizontalis* (Rosenst.) Holttum; *C. hubrechtensis* Holttum; *C. indochinensis* (Christ) S.E. Fawc. & A.R. Sm.; *C. inopinata* Holttum; *C. iwatsukii* Holttum; **C. japonica* (Baker) L.J. He & X.C. Zhang; *C. klossii* (Ridl.) Holttum; **C. kolombangarae* Holttum (**Fig. 2A**); *C. krayanensis* (K. Iwats. & M. Kato) S.E. Fawc. & A.R. Sm.; *C. lauterbachii* (Brause) Holttum; **C. ledermannii* (Hieron.) Holttum; *C. marquesensis* (Lorence & K.R. Wood) A.R. Sm. & Lorence; *C. meiobasis* Holttum; *C. microlepigera* Holttum; *C. multisora* (C. Chr.) Holttum; ***C. musashiensis* (Hiyama) S.E. Fawc. & A.R. Sm.; **C. nigrescens* (Ching ex K.H. Shing) S.E. Fawc. & A.R. Sm.; ***C. nipponica* (Franch. & Sav.) S.E. Fawc. & A.R. Sm.; **C. obtusata* (Alderw.) Holttum; *C. oligolepia* (Alderw.) Holttum; *C. pauciloba* (Ching ex K.H. Shing) S.E. Fawc. & A.R. Sm.; **C. pectiniformis* (C. Chr.) Holttum; ***C. petelotii* (Ching) Holttum; *C. platyptera* (Copel.) Holttum; *C. plumosa* (C. Chr.) Holttum; *C. propria* (Alderw.) Holttum; **C. pubirachis* (Baker) Holttum; **C. quaylei* (E. Brown) Holttum; *C. raiateana* Holttum; **C. seemannii* Holttum; *C. seramensis* M. Kato; **C. simulata* (Davenp.) S.E. Fawc.; *C. squamipes* (Copel.) Holttum; *C. stereophylla* (Alderw.) Holttum; *C. subbipinnata* Holttum (**Fig. 2L**); *C. subnigra* (Brause) Holttum; *C. sulawesica* Holttum; *C. sylva-nipponica* (Ebihara & Nakato) S.E. Fawc., A.R. Sm. & Ebihara; *C. tahanensis* Holttum; *C. tanggamensis* Holttum; *C. trichochlamys* (Ching ex K.H. Shing) S.E. Fawc. & A.R. Sm.; *C. unidentata* (Bedd.) Holttum; *C. viscosa* (Baker) Holttum; *C. vitiensis* Holttum.

Incertae sedis.—Based on the descriptions and illustrations, we are unable to place *Parathelypteris changbaishanensis* Ching ex K.H. Shing and *Parathelypteris qinlingensis* Ching ex K.H. Shing with confidence in either *Amauropelta* or *Coryphopteris*. Study of the type material will be necessary to do so.

CYCLOGRAMMA

Cyclogramma Tagawa, Acta Phytotax. Geobot. 7:52. 1938.—*Thelypteris* subg. *Cyclogramma* (Tagawa) K. Iwats., Mem. Coll. Sci. Univ. Kyoto, ser. B, 31:26. 1964.—Type: *Cyclogramma simulans* (Ching) Tagawa [= *Thelypteris simulans* Ching] = *C. auriculata* (J. Sm.) Ching

For additional synonymy, see Holttum (1971, 1982).

Etymology.—Gr. *kyklos*, circle + *gramme*, line. The sori are small, round, and in lines (Stewart et al. 1983).

Plants terrestrial, small to medium-sized, evergreen; **rhizomes** short- to long-creeping, occasionally suberect (*C. auriculata*), mostly 3–5 mm diam.; **fronds** arching to erect, moderately sized to occasionally large, typically 35–130 (–220) cm, monomorphic, blades deeply pinnate-pinnatifid; **stipes** dull stramineous to brownish, blackened at bases, bearing basal scales and sparse to sometimes dense acicular and hooked hairs, the scales occasionally persistent distally (*C. squamaestipes*), even onto the rachis; **stipe scales** brown to blackish, ovate to lanceolate, bearing acicular hairs and sometimes also hooked hairs; **blades** herbaceous to chartaceous, drying dark green, olivaceous, or blackish (Ching 1963), proximal pinnae not noticeably or only slightly shorter than more distal pinnae, or sometimes several pairs (1–5) abruptly reduced, if gradually shortened then becoming a series of hastate auricles; blade apex gradually reduced; proliferous buds absent; **pinnae** with costae grooved adaxially, incised to 0.5–3 mm from costae, nearly symmetrical with segments spreading or slightly oblique and sometimes falcate, rounded at tips; margins entire, pinna bases sessile to short-petiolulate, truncate, acroscopic segment of greatly reduced pinnae often slightly elongate or auriculate; **veins** readily visible, free, simple or often forked, ending at margins of lobes just above sinuses, never united, sometimes with a raised non-vascularized keel abaxially just below sinuses (*C. auriculata*); **aerophores** at pinna bases at least swollen, greatly elongate in most species (0.5–4 mm); **indument abaxially** of unicellular, hooked (hamate) hairs on all axes (rachis, costae, and costules), lacking costal scales, tissue between veins glabrous and sometimes of acicular and/or hooked hairs; **indument adaxially** of usually long (> 1 mm), stout, hyaline acicular hairs restricted mostly to costae, with fewer, shorter ones also sometimes present on costules, veins, and (less often) on laminar tissue; **pustules** absent; **sori** typically round and discrete, not elongate or confluent at maturity, lacking receptacular hairs, medial, inframedial, or subcostular, indusia absent; **sporangia** usually bearing hooked hairs on capsules like those of laminae but shorter, lacking glandular hairs on sporangial stalks and capsules; **spores** pale, tan, bilateral, monolete, perispore often coarsely echinate or with reticulate crests (Tryon & Lugardon 1991; Patel et al. 2019a); $x = 36, 34?$, three spp. counted, *C. auriculata* diploid and tetraploid, *C. omeiensis* apparently octoploid (n = c. 136; Kurita 1966), the highest ploidy reported in Thelypteridaceae. There are at least three counts apparently based on $x = 34$, which, if true, is aberrant among cyclosoroid ferns (e.g., Wang & Sun 1982; Tsai & Shieh 1983).

Diagnosis.—*Cyclogramma* can be readily distinguished from other cyclosoroid genera by a combination of characters, including exindusiate sori, free veins, hooked hairs on the axes abaxially, as well as similar hairs on sporangial capsules. The only other paleotropical genus with hooked hairs is *Grypothrix*, which differs in having anastomosing veins and more shallowly incised pinnae. *Cyclogramma* usually has creeping rhizomes, but they are suberect or erect in *C. auriculata*, and that species, sister to the others, also has the longest aerophores, the greatest number of reduced proximal pinnae, and cristate spores. With *Leptogramma and Stegnogramma,* which are also exindusiate, *Cyclogramma* agrees in having creeping rhizomes, and blades often lacking reduced proximal pinnae; it differs from leptogrammoid genera in usually having pronounced, conspicuous, elongate aerophores, round sori, and in the hooked hairs on blades and sporangia.

Biogeography and ecology.—*Cyclogramma* comprises nine species, and these are mostly restricted to western and southern China, Bhutan, Nepal, northern India, continental southeastern Asia (Myanmar, Vietnam); a few extend their ranges into Taiwan, southern Japan, and the Philippines (Luzon; see Holttum 1976c). The most widely distributed species is *C. auriculata*, with outlying populations in the Philippines and perhaps Indonesia (Lin et al. 2013). Throughout its range, *Cyclogramma* occurs in moist lowland to montane forests, from 300–2800 m. Seven species are restricted to southern China, the center of diversity in the genus, and most of these are rather local; six spp. are known from Yunnan.

Taxonomic and phylogenetic studies.—*Cyclogramma* was recognized as a discrete natural group relatively early, by the Japanese pteridologist Tagawa (1938), who published combinations for eight species. Even before that, Ching (1936) recognized it as a natural group (his group 6) within *Thelypteris* subg. *Phegopteris*; later, Ching (1963) followed Tagawa's lead in treating it as a genus, while comparing it to *Leptogramma*. Prior to that, the species had usually been treated in a comprehensive genus *Dryopteris* or in an even more varied and unnatural genus *Polypodium* (because of lack of an indusium). Holttum (1971, 1982) adopted many of Ching's generic concepts in Thelypteridaceae, including that for *Cyclogramma*. An attempt at a taxonomic middle ground was offered by Smith (1990), who recognized *Cyclogramma* as one of 20 subgenera in a heterogenous genus *Cyclosorus s.l.*

All phylogenetic studies with broad sampling (He & Zhang 2012; Almeida et al. 2016; Fawcett et al. in press) recover *Cyclogramma* as sister to the clade *Leptogramma* + *Stegnogramma*, in Thelypteridoideae (**Fig. 1**). Even before molecular studies, the affinity of *Cyclogramma* with leptogrammoid ferns was recognized (e.g., see Smith 1990:270). *Cyclogramma* likely arose and diversified in Asia, along with its closest relatives.

Constituent species.—**Cyclogramma auriculata* (J. Sm.) Ching; *C. chunii* (Ching) Tagawa; *C. costularisora* Ching ex K.H. Shing; ***C. flexilis* (Christ) Tagawa; **C. leveillei* (Christ) Ching; *C. maguanensis* Ching ex K.H. Shing; **C. neoauriculata* (Ching) Tagawa; **C. omeiensis* (Baker) Tagawa; *C. squamaestipes* (C.B. Clarke) Tagawa

CYCLOSORUS

Cyclosorus Link, Hort. Reg. Bot. Berol. 2:128. 1833.—Type: *Cyclosorus gongylodes* (Schkuhr) Link [= *Aspidium gongylodes* Schkuhr] = *Cyclosorus interruptus* (Willd.) H. Ito

For additional synonymy, see Holttum (1982).

Etymology.—Gr. *kyklos*, circle + *sorus*, sori; ferns with round sori.

Plants terrestrial, medium-sized (> 40 cm) to large (fronds to ca. 100 cm tall); **rhizomes** very long-creeping, branching, blackish when dried; rhizome scales sparse or nearly absent back from the rhizome apex; **fronds** distant (to 10 cm apart), monomorphic, pinnate-pinnatifid, erect or arching; **stipes** blackish at bases, stramineous distally, adaxially grooved; **stipe scales** sparse, ovate-lanceolate, brown, setulose on margins and glabrous on surfaces; **blades** chartaceous to subcoriaceous (often somewhat leathery), drying greenish or reddish, pinnate-pinnatifid, with proximal pinnae not reduced or lowermost pair only slightly so, lacking auricles at acroscopic base; blade apices usually short, pinnatifid to subconform and pinna-like but usually much shorter than longest lateral pinnae; rachises generally hairy to glabrous or glabrescent, hairs if present 0.1–1.0 mm long, not scaly, lacking proliferous buds in axils of pinnae; **pinnae** 10–30 pairs, linear-lanceolate, short-stalked (1–4 mm), usually alternate or becoming alternate distally, lacking auricles, bases rounded to truncate, adaxially with a groove that is not continuous with the rachis groove, shallowly lobed ca. ¼–½ their width, or in *C. striatus* to ca. 5/6 their width; **veins** simple, 9–18(–30) pairs per segment, usually prominent on both sides, unbranched, basal pairs from adjacent segments united at an obtuse angle below the sinus, and forming an excurrent vein (usually 2–4 mm long) running to the sinus, next pair more oblique and meeting margin at or just above the sinus, free vein ends reaching segment margins; **aerophores** inconspicuous or absent at pinna bases, not swollen; **indument abaxially** of stipes, rachises, costae, veins, and often laminar tissue between veins lacking or of hyaline acicular, spreading hairs, these 0.1–0.4 mm, blades lacking capitate hairs, often (on *C. interruptus*) with orangish to reddish, sessile, spherical glands on costules, veins, and sometimes on laminar tissue between veins, also with scattered ovate, flat, pale brown scales on costae and sometimes on costules and veins in *C. striatus*; **indument adaxially** of generally short (ca. 0.2 mm) hyaline, unicellular setae on stipes, rachises, and costae, hairs lacking on veins and tissue between veins; **pustules** absent on laminar tissue on both sides; *sori* medial to supramedial, circular, often absent from proximal 1 or 2 pairs of veins, not coalescent at maturity, indusiate, indusia sparingly hairy or glabrescent on margins and sometimes on surfaces, caducous with age; **sporangia** without setae or glands on the capsules, but often each with orangish to reddish long-stalked (2–4 cells) gland on the sporangial stalk; **spores** dark brown, with perispore irregularly spinulose or with short perforate ridges, lacking thin wings; $x = 36$ (both spp. counted), diploids and tetraploids known (see *Notes*), intergeneric hybrids not known.

Diagnosis.—Holttum (1971, 1982) considered the essential characters of the genus to include the very long-creeping, nearly scale-less rhizomes, blades truncate at the base (without greatly reduced proximal pinnae), anastomosing veins (usually one pair), costae bearing persistent flat, ovate scales abaxially, the presence of long-stalked glands on the sporangial stalks and receptacle (illustrated by Holttum et al. 1970; Smith 1971), and often sessile orangish or reddish glands on the laminae. No other genus shares this combination of characters.

Biogeography and ecology.—*Cyclosorus s.s.*, as defined here, includes only two or three species (Holttum 1971, 1974a, 1982), plants of freshwater swamps and wetlands, in ponds, or along streams and rivers, tropics and subtropics, growing at generally low elevations, 0–1000(–1800) m. The type species of *Cyclosorus* is pantropical, extremely polymorphic, and not recently studied over its broad range. Smith (1971) tentatively recognized three varieties in the American tropics, from Florida, Antilles, southern Mexico to Bolivia, Uruguay, and Paraguay. This same species, perhaps comprising other varieties, occurs in Africa, southeastern Asia, Malesia, Melanesia, Australasia, and Polynesia (including Hawai'i). The second species, *C. striatus*, is restricted to tropical Africa and is clearly related, based on both morphology and nucleotide sequence data. A late Miocene fossil described by Robledo et al. (2015) from Argentina, is referable to *C. interruptus,* suggesting the species is at least 5 mya.

Taxonomic and phylogenetic studies.—Holttum (1971) provided a general characterization of the genus in its restricted sense and later (1974a, 1977b, 1982) offered treatments of *Cyclosorus* in Africa, the Pacific and Australasia, and Malesia. In his 1974a paper he also presented a tentative key to all species in *Cyclosorus*, separating the glabrous variants as *C. tottus* (Thunb.) Pic.Serm., with a South African type (many glabrous plants also occur in the Neotropics), and *C. interruptus s.s*., variously hairy, with a southern Indian type. In the same paper he also acknowledged that species intermediates existed. Because the elements and intricate interrelationships within this complex have been inadequately studied over their entire range, we prefer, in this work, to subsume *C. tottus* within *C. interruptus*, the oldest name in the complex.

Prior to Holttum's seminal works mentioned above, most authors included several other genera within *Cyclosorus*. This broad circumscription was adopted by Copeland (1947) and followed by many subsequent authors. Even after Holttum's studies, Lin et al. (2013) and Li (2013), working primarily with Chinese species, included *Christella* within *Cyclosorus*, as well as the genera *Sphaerostephanos*, *Pneumatopteris*, and *Amblovenatum*. All of these segregates are recognized as genera herein. By extension, the genera *Amblovenatum* (formerly *Amphineuron*), *Mesopteris*, *Pakau*, *Reholttumia*, *Strophocaulon*, and other genera as well, are often included in an expanded concept of *Cyclosorus*. Without providing new evidence, an extreme view was adopted by Mazumdar and Mukhopadhyay (2013), who subsumed all cyclosoroid genera within *Cyclosorus*. As discussed by Smith (1990), if one adopts that taxonomy, the earliest available generic name is *Meniscium* (*Stegnogramma* also preempts *Cyclosorus*). An even more extreme taxonomic view was taken by Christenhusz and Chase (2014), who included all thelypteroid genera—about 1200 species—in the single genus *Thelypteris*. As a consequence of recent phylogenetic insight (especially He & Zhang 2012; Almeida et al. 2016;

and Fawcett et al. in press), reconsideration of morphological characters, and a judgment that a more finely constructed taxonomy facilitates further evolutionary studies, we here choose to recognize *Cyclosorus* in its most restricted sense.

Cyclosorus belongs to the large cyclosoroid clade, which is defined by the synapomorphy of *x* = 36, and by most species having anastomosing veins. *Cyclosorus* forms a clade with the southeast Asian genus *Mesophlebion* plus the paleotropical *Ampelopteris*, and these three are in turn sister to the neotropical *Meniscium* (**Fig. 1**). Holttum (1977b, 1982) considered the closest relationship of *Cyclosorus* to be with predominantly temperate *Thelypteris s.s.*, which has only two species, and with monotypic *Ampelopteris*, but affinity with *Thelypteris s.s.* is now thought to be remote (He & Zhang 2012; Almeida et al. 2016; Patel et al. 2019a; Fawcett et al. in press). Possibly, the similar habitat—marshes and swamps—influenced Holttum to think the two genera were related.

Notes.—Spores of both *Cyclosorus* species were described as having "cavate folds with echinate elements" and "short, perforate ridges" by Tryon and Lugardon (1991), and spores of their Panamanian accession of *C. interruptus* and Ugandan *C. striatus* resemble *C. interruptus* material from New Zealand (Patel et al. 2019a), but differ from the spores observed in material from China, which have few broad crests and little secondary sculpturing (Dai et. al. 2002; Wang & Dai 2010). The spores of the related genus *Ampelopteris* (Tryon & Lugardon 1991, fig. 153.4) are virtually indistinguishable from the *Cyclosorus* spp. spores imaged in the same plate, while spores of *Mesophlebion* also have broadly winged spores with little secondary sculpturing (Tryon & Lugardon 1991, figs. 153.5, 153.6).

Chromosome counts are known from plants of *C. interruptus* growing in Ghana, Tanzania, Japan, India, Sri Lanka, and Japan. Manton and Sledge (1954) found meiotic irregularities, with both triploid and tetraploids from Sri Lanka, but most counts made from plants of the Paleotropics are diploid. Two counts from neotropical localities, Florida and Jamaica, are tetraploid. The taxonomic significance of these regional ploidy differences is unknown, but it seems quite possible, even likely, that *C. interruptus*, as construed herein, represents a species complex. The second species, *C. striatus*, has been counted as diploid.

Constituent species.—**Cyclosorus interruptus* (Willd.) H. Ito; **C. striatus* (Schum.) Pic.Serm.

Excluded species.—Many species in the family have combinations in *Cyclosorus* (see Mazumdar & Mukhopadhyay 2013), but only two species are included in our concept, which follows Holttum (1971) and PPG I (2016). Excluded species belong to many different genera in our treatment, especially, *Amblovenatum*, *Christella*, *Goniopteris*, *Meniscium*, *Mesopteris*, *Pelazoneuron*, *Pneumatopteris*, *Pronephrium* and its segregate genera, *Reholttumia*, and *Sphaerostephanos*.

GLAPHYROPTERIDOPSIS

Glaphyropteridopsis Ching, Acta Phytotax. Sin. 8:320. 1963.—*Thelypteris* sect. *Glaphyropteridopsis* (Ching) K. Iwats., Mem. Coll. Sci. Univ. Kyoto, ser. B, 31:29. 1964.—Type: *Glaphyropteridopsis erubescens* (Hook.) Ching [= *Polypodium erubescens* Hook.]

For additional synonymy, see Ching (1963) and Holttum (1971).

Etymology.—From *Glaphyropteris* (Gr. *glaphyros*, hollow + *pteris*, fern) + *-opsis*, like. Ching (1963) alluded to the general similarity in frond size and blade dissection of *Glaphyropteridopsis* to *Glaphyropteris* (= *Steiropteris* in our treatment) in the Neotropics. However, these two genera are not closely related, as understood by Ching.

Plants terrestrial or on (among) rocks, medium-sized to large, 50–150(–300 cm); **rhizomes** short and thick, sometimes massive, short-creeping or ascending, with sparse, ± glabrous scales at apices; **fronds** clustered or approximate, monomorphic, arching; **stipes** stramineous to tan, usually stout (2–)4–10+ mm diam., 30–100+ cm long, with sparse brown to tan, ovate, thin appressed scales at bases, with sparse acicular hairs or glabrescent; **blades** herbaceous, chartaceous or leathery, drying yellowish green to reddish brown, elliptic, with truncate bases (lacking greatly reduced pinnae), pinnate-pinnatifid, lacking pustules or glands, and generally lacking hairs between veins; **rachises** stramineous; **pinnae** sessile, opposite or subopposite, often large (to 50 × 5 cm in *G. erubescens*), linear-lanceolate, deeply pinnatifid or nearly pinnatisect (incised within 1(–2) mm of costae), lowermost pinnae often narrowed at their bases, deflexed, costae grooved adaxially and sparsely to densely hairy abaxially; segments large, falcate-lanceolate, those at the base of the larger pinnae often somewhat elongate and/or toothed, and reflexed to overlap the rachis; **aerophores** absent at pinna bases or with only a small darkened patch in dried fronds; **indument abaxially** of sparse to dense acicular hairs along rachis, costae, costules, and veins, seldom with hairs between veins, glands (both sessile and stipitate) and scales lacking; **indument adaxially** of usually dense hairs along costal grooves, costules, veins, and tissue between veins usually glabrous; **veins** free, pinnate on segments, veinlets simple, to 25 pairs per segment, prominent and reaching margins, proximal pair running alongside transparent membrane below sinus or to sinus, or to margins just above sinus; **pustules** absent on laminar tissue; **sori** orbicular, exindusiate or with small indusia, these glabrous or with acicular hairs, subcostular and attached at bases of veinlets in a row on each side, close to or overlapping costules at maturity, usually confluent into a line when mature; **sporangia** glabrous or with hyaline setulae near annulus, these sometimes numerous; **spores** brown, elliptic, bilateral, irregularly reticulate-echinate, with perforations (Tryon & Lugardon 1991) or with small tubercules on surfaces; *x* = 36. Two species counted, *G. erubescens*, both diploids and tetraploids, and *G. rufostraminea*, diploid.

Diagnosis.—*Glaphyropteridopsis* resembles *Chingia* in frond form and size, the truncate blade bases, and position of the sori, but the veins of the former are always free (vs. anastomosing below sinuses, except in *C. pricei*). Scales of *Chingia* are bristly, numerous, and spreading (vs. appressed, tan, ovate in *Glaphyropteridopsis*), and spores are sometimes reticulate and perforate (vs. echinate) (Holttum 1971, 1982). All species of *Glaphyropteridopsis* except *G. jinfushanensis* have subcostular sori, a character that sets it apart from most other thelypterid species and genera, except for some species of *Chingia*; however, this tendency for the sori to overlap the costules is most extreme in *Glaphyropteridopsis*. Another strong synapomorphy of the genus is the tendency to have strictly opposite or at least subopposite pinnae. This feature applies not only to the proximal pinnae but also to distal pinnae and is rather striking compared to the generally alternate pinnae (at least in the middle and distal parts of the blade) in most cyclosoroid genera. Species of *Glaphyropteridopsis* also resemble some neotropical *Pelazoneuron* spp., just outside the large clade containing the former, but *Pelazoneuron* has medial sori, more substantial indusia, more lanceolate, spreading, hairy stipe base scales, alternate pinnae above the blade base, and cristate or echinulate spores, rather than the reticulate spores of *Glaphyropteridopsis* (Patel et al. 2019a). The superficial resemblance of *Glaphyropteridopsis* to certain species of *Steiropteris* (the subgroup *Glaphyropteris*), particularly *S. decussata* and allies (Smith 1980), is not indicative of a close phylogenetic relationship; that species and relatives differ in having pronounced elongate aerophores, mucilaginous croziers, non-falcate segments with rounded apices, resinous laminar glands, and broadly winged spores.

Biogeography and ecology.—*Glaphyropteridopsis* is centered in, and nearly restricted to, South China, with all 11 known species occurring there, ten of them endemic, and several known only from the types or very few collections. The only species ranging outside of China is the type, *G. erubescens*, whose distribution extends into northern India, Nepal, Bhutan, northern Myanmar, Vietnam, Taiwan, and in Malesia only in the Philippines. The genus is absent from the rest of Malesia, Melanesia, and Polynesia, as well as Australasia and Africa and the New World. Species occur from 600–2000 m. They typically occur in forests or at forest margins, along streams, on rocks, or along roadsides.

Taxonomic and phylogenetic study.—Datasets based primarily on cpDNA sequences (He & Zhang 2012; Patel et al. 2019a) and coalescent nuclear phylogenomic analyses (Fawcett et al. in press) infer *Glaphyropteridopsis* as sister to a large clade of strictly paleotropical cyclosoroids—including *Amblovenatum*, *Chingia*, *Christella*, *Grypothrix*, *Menisciopsis*, *Plesioneuron*, *Pneumatopteris*, *Pronephrium*, *Pseudocyclosorus*, *Reholttumia*, and *Sphaerostephanos*, but excluding *Cyclosorus s.s.* and also excluding all neotropical cyclosoroid genera, except *Christella*. However, a concatenated analysis of the same nuclear dataset (Fawcett et al. in press) places *Glaphyropteridopsis* within the chingioid subclade (*Chingia*, *Grypothrix*, *Menisciopsis*, and *Plesioneuron;* Fig. 1). Low or conflicting support along backbone nodes in plastid and nuclear analyses suggest that the precise phylogenetic position of this lineage be interpreted with caution.

Notes.—Ching (1963), when describing the genus, surmised that his *G. eriocarpa* and *G. splendens* could be of hybrid origin, since they were rare and came from the same locality as *G. erubescens* and *G. rufostraminea*. This hypothesis has not been tested. Shieh & Tsai (1987) described *Thelypteris ×erubesquirolica*, which they believed to be a hybrid between *Glaphyropteridopsis erubescens* and *Pseudocyclosorus esquirolii*. This hypothesis needs re-examination.

About half of the known species are illustrated by Lin (1999). All necessary combinations have been made in *Glaphyropteridopsis*, by Ching (1963) and Lin (1999).

Constituent species.—*Glaphyropteridopsis emeiensis* Y.X. Lin; *G. eriocarpa* Ching; **G. erubescens* (Wall. ex Hook.) Ching; *G. glabrata* Ching & W.M. Chu ex Y.X. Lin; *G. jinfushanensis* Ching ex Y.X. Lin; *G. mollis* Ching ex Y.X. Lin; *G. pallida* Ching ex Y.X. Lin; **G. rufostraminea* (Christ) Ching; *G. sichuanensis* Y.X. Lin; *G. splendens* Ching; *G. villosa* Ching & W.M. Chu ex Y.X. Lin

GONIOPTERIS

Goniopteris C. Presl, Tent. Pterid. 181–183, pl. 7, f. 9–11. 1836.—*Thelypteris* subg. *Goniopteris* (C. Presl) Duek, Adansonia, n.s., 11:720. 1971.—*Thelypteris* sect. *Goniopteris* (C. Presl) C.V. Morton, Amer. Fern J. 53(4):154. 1963.—Lectotype (designated by J. Smith, Hist. Fil. 191. 1875): *Goniopteris crenata* (Sw.) C. Presl [= *G. poiteana* (Bory) Ching]

For additional generic synonymy, see Christensen (1913, 1920), Proctor (1985, 1989).

Etymology.—Gr. *gonia*, angle + *pteris*, fern, in reference to the angle of often acutely anastomosing veins below the sinus or these producing an excurrent vein joined by other connivent veins; this contrasts to the often obliquely united veins of *Meniscium*.

Plants terrestrial or epilithic, small to medium-sized (5–80 cm); **rhizomes** typically stout, short-creeping, ascending, or erect, scales generally with stellate or furcate hairs on surfaces and/or margins; **fronds** erect, arching, pendent, or prostrate, monomorphic, or weakly dimorphic (e.g., *Goniopteris tetragona*), typically pinnate-pinnatifid, rarely simple or pinnate-pinnatisect; **stipes** stramineous to dull brown, grooved adaxially; **stipe scales** brown, deltate-ovate to linear-lanceolate, typically with furcate or stellate hairs on surfaces and/or margins; **blades** membranaceous to thickly coriaceous, often drying dark green, apex conform or gradually reduced, base of blade unreduced, or, if reduced, without many pairs of gradually reduced pinnae, proliferous buds sometimes present adaxially along rachises, in axils of pinnae, sometimes also along costae (e.g., *G. alata*); **pinnae** petiolulate, sessile, or narrowly adnate (especially distally), margins simple, crenate to deeply lobed, bases dilated, truncate, rounded, hastate, or with acroscopic auricles; **veins** anastomosing, at an angle with veins from adjacent segments, forming an excurrent veinlet to the sinus, and creating one to a series of many areoles between costae and pinna margins (e.g., *G. tetragona*), or veins simple, free or forked in smaller 1-pinnate spp. (e.g., *G. abdita*); **aerophores** absent, rarely tuberculate at pinna bases (*G. lugubriformis*); **indument abaxially and adaxially** of stipitate or sessile, branched hairs, these furcate (T- or Y-shaped) or stellate (**Fig. 2B**), hairs occasionally bifurcate or multifurcate, branched hairs sometimes co-occurring with unicellular or pluricellular hyaline acicular hairs typical of other genera, branched hairs most easily observed along the adaxial groove of rachis, but sometimes also present on all axes and laminar tissue adaxially and abaxially, glands generally absent on axes and lamina in most spp. (except *G. redunca*), scales usually absent, except along costae abaxially in a few South American species; **pustules** rarely present (e.g., *G. juruensis*); **sori** round, typically medial, indusiate or exindusiate, discrete, indusia bearing hairs, these either acicular or variously branched (**Fig. 2F**); **sporangia** glabrous or with setulae (simple or branched); **spores** brown, consistently ornamented with reticulate crests (Patel et al. 2019a); $x = 36$, with 25 species counted, diploids and tetraploids, and a single triploid (*G. obliterata*) known. No intergeneric hybrids have been reported, but intrageneric hybrids are quite common, especially among the species of the calciphilic Antillean radiation (Smith 1993b), where more than a dozen have been reported in Cuba alone (Sánchez 2017).

Diagnosis.—The nearly invariable presence of stellate or branched hairs somewhere on the plant, especially along the axes and on stipe base and rhizome scales, is the most diagnostic feature of the genus, readily distinguishing it from all other genera in the family. The paleotropical *Ampelopteris* is similar in bearing proliferous buds and stellate hairs (see illustrations in Holttum et al. 1970), but the hairs are easily abraded, and less conspicuous than in *Goniopteris*. *Meniscium* differs in having exindusiate sori that are frequently coalescent, many more pairs of anastomosing veins, usually entire or only serrate pinnae, and often longer-creeping rhizomes. *Steiropteris* often differs in the presence of well-developed aerophores at the pinna (and sometimes costule) bases, and in most cases, a distinct cartilaginous, non-vascularized keel at the bases of the sinuses; it also lacks stellate or furcate hairs.

Biogeography and ecology.—Numbering 138 species, *Goniopteris* is strictly neotropical, ranging north to Florida, Mexico, through Mesoamerica and the Antilles, throughout Amazonia, and the foothills of the Andes, south to Bolivia and Argentina, and east through Brazil, the Guianas and Venezuela. They are predominantly plants of lower elevations, ranging to 1850 m in the Andes (Smith 1992), and to 1700 m in the Antilles. They are typically plants of shady forest understories, but a diverse clade of calciphiles, numbering ~30 species, has radiated in the karst regions of the Greater Antilles (Fawcett 2020). Two serpentine specialists, *G. crypta* and *G. brittoniae*, have likely independently arisen from calciphilic ancestors on Cuba, and Puerto Rico, respectively. As with many members of the family, they respond favorably to disturbance, may become weedy, and may be especially abundant on open roadcuts and in coffee and cacao plantations.

Taxonomic and phylogenetic studies.—Historically treated as a subgenus of *Dryopteris*, the circumscription of species of *Goniopteris* has remained essentially unchanged for more than a century (Christensen 1913, 1920). Christensen's treatment was the first to rely on close observation of microscopic features, and he united the species of *Goniopteris* largely on the basis of their striking stellate or branched hairs. Although the hairs have been secondarily lost on rare occasions (e.g., *G. macrotis*), the few taxa without them were still included by Christensen (1913) on the basis of other morphological similarities; their placement has now been supported by molecular data (Fawcett et al. in press). Christensen (1913, 1920) divided *Dryopteris* subg. *Goniopteris* into two sections—*Asterochlaena* and *Eugoniopteris*—recognized by apices gradually reduced, or by a conform terminal pinna, respectively. Phylogenetic analyses have shown these subdivisions to be non-monophyletic, and therefore artificial. Necessary combinations have been made for nearly all known members of the genus (Salino et al. 2015).

Molecular phylogenetic data support the monophyly of *Goniopteris* (Almeida et al. 2016; Patel et al. 2019a), and show strong biogeographical signal, with distinct radiations in the Antilles, the Andes, and Brazil (Fawcett et al. in press). The genus is in an early-diverging clade of cyclosoroids, and sister to a clade that includes the neotropical genus *Meniscium*, the pantropical *Cyclosorus s.s.*, the African and Southeast Asian *Ampelopteris*, and the Malesian *Mesophlebion* (Fawcett et al. in press). In contrast, in the less densely-sampled, mostly plastid dataset of Patel et al. (2019a), *Goniopteris* is inferred be sister to the aforementioned genera, plus the remaining cyclosoroids.

Most necessary combinations were made by Salino et al. (2015), except:

Goniopteris bermudiana (Baker) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Nephrodium bermudianum* Baker, in Hemsley, Rep. Challenger, Bot. 1:86, t. 13. 1884.

In light of its endangered status (only 185 individuals extant), and inclusion in the IUCN Red List of Threatened Species (Copeland & Malcom 2014), we provide the necessary combination in *Goniopteris* for the Bermuda Shield Fern, which is in need of more detailed taxonomic study. See Gilbert (1898) for a description.

Goniopteris fuertesii (Brause) S.E. Fawc., A.R. Sm. & Y.Y. Piña, **comb. nov.**—*Dryopteris fuertesii* Brause, in Urban, Symb. Antill. 7:485. 1913.

This taxon, previously known only from the type, was recently rediscovered by Yommi Piña (*Piña 1671*, FLAS, JBSD) near the type locality, after more than 100 years.

Goniopteris venusta (Heward) Pic.Serm. var. **usitata** (Jenman) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Nephrodium usitatum* Jenman, J. Bot. 17:261. 1879.—*Thelypteris venusta* var. *usitata* (Jenman) Proctor

Both varieties of *Goniopteris venusta* are endemic to Jamaica and are usually distinct from each other. However, intermediate forms are known, so we follow Proctor (1985) in recognizing this taxon at varietal rank, pending further study.

Constituent species.—**Goniopteris abdita* (Proctor) Salino & T.E. Almeida; **G. abrupta* (Desv.) A.R. Sm.; *G. affinis* Fée; **G. alan-smithiana* (L.D. Gómez) Salino & T.E. Almeida; **G. alata* (L.) Ching; **G. amazonica* (Salino & R.S. Fern.) Salino & T.E. Almeida; **G. ancyriothrix* (Rosenst.) Salino & T.E. Almeida; *G. anoptera* (Kunze ex Kuhn) Salino & T.E. Almeida; *G. asterothrix* Fée; *G. aureola* (A.R. Sm.) Salino & T.E. Almeida; **G. baorucensis* S.E. Fawc.; **G. beckeriana* (F.B. Matos, A.R. Sm. & Labiak) Salino & T.E. Almeida; *G. berlinii* (A.R. Sm.) Salino & T.E. Almeida; *G. bermudiana* (Baker) S.E. Fawc. & A.R. Sm.; **G. bibrachiata* (Jenman) Salino & T.E. Almeida; **G. biformata* (Rosenst.) Salino & T.E. Almeida; **G. biolleyi* (Christ) Pic.Serm.; **G. blanda* (Fée) Salino & T.E. Almeida; **G. bradei* Salino; **G. brittoniae* (Sloss.) Ching; **G. burkartii* Abbiatti; *G. calypso* (L.D. Gómez) Salino & T.E. Almeida; *G. chocoensis* (A.R. Sm. & Lellinger) Salino & T.E. Almeida; *G. clypeata* (Maxon & C.V. Morton) Salino & T.E. Almeida; **G. cordata* (Fée) Salino & T.E. Almeida; *G. costaricensis* Salino & T.E. Almeida; *G. crassipila* (Caluff & C. Sánchez) Salino & T.E. Almeida; **G. croatii* (A.R. Sm.) Salino & T.E. Almeida; *G. crypta* (Underw. & Maxon) Ching; **G. cumingiana* (Kunze) de Jonch. & U. Sen; *G. cuneata* (C. Chr.) Brade; **G. curta* (Christ) A.R. Sm.; *G. cutaitaensis* (Brade) Brade; *G. dissimulans* (Maxon & C. Chr.) Salino & T.E. Almeida; **G. eggersii* (Hieron.) Alston; *G. equitans* (Christ) Salino & T.E. Almeida; *G. erythrothrix* (A.R. Sm.) Salino & T.E. Almeida; **G. francoana* (E. Fourn.) Á. Löve & D. Löve; **G. fraseri* (Mett. ex Kuhn) Salino & A.R. Sm.; *G. fuertesii* (Brause) S.E. Fawc., A.R. Sm. & Y.Y. Piña; **G. gemmulifera* (Hieron.) Vareschi; *G. glochidiata* (Mett. ex C. Chr.) Brade; ***G. goeldii* (C. Chr.) Brade; **G. gonophora* (Weath.) Salino & T.E. Almeida; **G. hastata* Fée; **G. hatchii* (A.R. Sm.) Á. Löve & D. Löve; **G. hildae* (Proctor) Salino & T.E. Almeida; **G. holodictya* (K.U. Kramer) Salino & T.E. Almeida; *G. hondurensis* (L.D. Gómez) Salino & T.E. Almeida; *G. iguapensis* (C. Chr.) Brade; **G. imbricata* (Liebm.) Á. Löve & D. Löve; **G. imitata* (C. Chr.) Salino & T.E. Almeida; *G. indusiata* (Salino) Salino & T.E. Almeida; **G. jamesonii* (Hook.) Salino & T.E. Almeida; *G. jarucoensis* (Maxon ex Caluff & C. Sánchez) Salino & T.E. Almeida; **G. juruensis* (C. Chr.) Brade; *G. killipii* (A.R. Sm. & Lellinger) Salino & T.E. Almeida; **G. kuhlmannii* (Brade) Brade; *G. leonina* (Maxon ex Caluff & C. Sánchez) Salino & T.E. Almeida; **G. leptocladia* Fée; **G. levyi* (E. Fourn.) Salino & T.E. Almeida; **G. liebmannii* (Maxon & C.V. Morton) Salino & T.E. Almeida; **G. littoralis* (Salino) Salino & T.E. Almeida; **G. lugubriformis* (Rosenst.) Salino & T.E. Almeida; **G. lugubris* (Mett.) Brade; **G. macropus* (Blume) Ching (as "macropoda"); **G. macrotis* (Hook.) Pic.Serm.; *G. martinezii* (A.R. Sm.) Salino & T.E. Almeida; *G. megalodus* (Schkuhr) C. Presl; **G. minor* (C. Chr.) Salino & T.E. Almeida; *G. minutissima* (Caluff & C. Sánchez) Salino & T.E. Almeida; **G. mollis* Fée; **G. monosora* (C. Presl) Brade; *G. montana* (Salino) Salino & T.E. Almeida; **G. moranii* C. Sánchez; **G. multigemmifera* (Salino) Salino

& T.E. Almeida; *G. munchii* (A.R. Sm.) Salino & T.E. Almeida; **G. nephrodioides* (Klotzsch) Vareschi; **G. nicaraguensis* (E. Fourn.) Salino & T.E. Almeida; **G. nigricans* (Ekman & C. Chr.) Salino & T.E. Almeida; **G. obliterata* (Sw.) C. Presl; **G. oroniensis* (L.D. Gómez) Salino & T.E. Almeida; **G. paranaensis* (Salino) Salino & T.E. Almeida; **G. paucijuga* (Klotzsch) A.R. Sm.; **G. paucipinnata* (Donn.Sm.) Salino & T.E. Almeida; *G. pellita* (Willd.) A.R. Sm.; **G. pennata* (Poir.) Pic.Serm.; *G. peripae* (Sodiro) Salino & T.E. Almeida; *G. pilonensis* (A.R. Sm. & M. Kessler) Salino & T.E. Almeida; **G. pinnatifida* (A.R. Sm.) Salino & T.E. Almeida; **G. platypes* Fée; **G. poiteana* (Bory) Ching **G. praetermissa* (Maxon) Salino & T.E. Almeida; *G. pyramidata* Fée; *G. redunca* (A.R. Sm.) Salino & T.E. Almeida; *Goniopteris refracta* (Fisch. & C.A. Mey.) Brade; **G. reptans* (J.F. Gmel.) C. Presl (**Fig. 2F**); **G. resiliens* (Maxon) Salino & T.E. Almeida; **G. retroflexa* (L.) Salino & T.E. Almeida; **G. rhachiflexuosa* (Riba) Salino & T.E. Almeida; **G. riograndensis* (Lindm.) Ching; **G. ×rolandii* (C. Chr.) A.R. Sm.; **G. sagittata* (Sw.) Pic.Serm.; *G. salinoi* I.O. Moura & L.C. Moura; *G. sapechoana* (A.R. Sm. & M. Kessler) Salino & T.E. Almeida; **G. scabra* (C. Presl) Brade; **G. schaffneri* (Fée) Salino & T.E. Almeida; *G. schippii* (Weath.) Salino & T.E. Almeida; *G. schomburgkii* (A.R. Sm.) Salino & T.E. Almeida; *G. schunkei* (A.R. Sm.) Salino & T.E. Almeida; **G. schwackeana* (C. Chr.) Brade; **G. sclerophylla* (Poepp. ex Spreng.) Wherry; **G. scolopendrioides* (L.) C. Presl; *G. seidleri* Salino; *G. semihastata* (Kunze) Salino & T.E. Almeida; **G. semirii* (Salino & Melo) Salino & T.E. Almeida; *G. septemjuga* (C. Chr.) Salino & T.E. Almeida; **G. serrulata* (Sw.) J. Sm.; *G. skinneri* (Hook.) Salino & T.E. Almeida; *G. smithii* Salino; *G. stephanii* (A.R. Sm. & M. Kessler) Salino & T.E. Almeida; **G. stolzeana* (A.R. Sm.) Salino & T.E. Almeida; **G. straminea* (Baker) Ching; *G. strigosa* Fée; **G. subdimorpha* Salino; *G. subsagittata* (Maxon & C. Chr.) Salino & T.E. Almeida; *G. tenebrica* (Jenman) Salino & T.E. Almeida; *G. tenera* Fée; **G. tetragona* (Sw.) C. Presl; **G. toganetra* (A.R. Sm.) Á. Löve & D. Löve; **G. tristis* (Kunze) Brade; **G. tryoniorum* (A.R. Sm.) Salino & T.E. Almeida; **G. tuxtlensis* (T. Krömer, Acebey & A.R. Sm.) Salino & T.E. Almeida; **G. urbanii* (Sodiro) Salino & T.E. Almeida; *G. venusta* (Heward) Pic.Serm.; **G. verecunda* (Proctor) Salino & T.E. Almeida; **G. vivipara* (Raddi) Brack.; *G. windischii* Salino; **G. yaucoensis* (Proctor) Salino & T.E. Almeida (**Fig. 2B**).

GRYPOTHRIX

Grypothrix (Holttum) S.E. Fawc. & A.R. Sm., **gen. et stat. nov.—**Type: *Grypothrix cuspidata* (Blume) S.E. Fawc. & A.R. Sm. [= *Meniscium cuspidatum* Blume, Enum. Pl. Javae 2:114. 1828].—*Pronephrium* sect. *Grypothrix* Holttum

For complete synonymy, see Holttum (1982) and Lin et al. (2013).

Etymology.—Gr. *grupon*, hooked + *thrix*, hair, in reference to the hooked (hamate) hairs, which are diagnostic for the genus.

Plants terrestrial, small to medium-sized (10–)20–80(–120) cm tall, usually in forest understories or along streams at lower elevations; **rhizomes** short- to long-creeping; **fronds** monomorphic, weakly or strongly dimorphic (e.g., *G. simplex*, **Fig. 3C**), pinnate, trifoliolate or simple, erect or arching; **stipes** stramineous, dull brown or reddish, scales linear-lanceolate, brown, castaneous or black, often with hamate hairs on surfaces and margins; **blades** chartaceous, sometimes drying reddish, with conform apex (or expanded apex with smaller lateral lobes), proximal pinnae not reduced, proliferous buds rarely present at pinna bases (e.g., *G. cuspidata*, *G. ramosii*); **pinnae** margins usually entire, sometimes crenate, rarely shallowly lobed (*P. insularis*), bases cuneate, or sometimes cordate, sessile or short-petiolulate, pinnae generally broad (> 3cm), but quite narrow (< 1 cm) in *G. salicifolia*; **veins** usually prominent both adaxially and abaxially, reaching margins, several pairs regularly anastomosing to form a series of areoles, each with an included veinlet, or less commonly, a continuous excurrent vein; **aerophores** sometimes present in the form of a darkened swelling at pinna bases; **indument abaxially** of characteristic hyaline, hamate (hook-shaped) hairs, on costae and veins, present or absent between veins; **indument adaxially** of hamate hairs on costae and veins, present or absent between veins; **pustules** sometimes present on laminar tissue; **sori** exindusiate, elongate and coalescent along cross-veins, sometimes very dense, appearing acrostichoid (e.g., *G. simplex*), or, medial, round and discrete; **sporangia** glabrous or with hamate setulae or glands; spores brown or black, with fimbriate crests (Patel et al. 2019a); $x = 36$, five species counted, with diploids, triploids, and tetraploids known. Holttum (1982) believed *G. parishii* to be a hybrid based on its variable morphology and suggested that *G. triphylla* was one parent. Triploid counts ($n = 108$) in *G. simplex* suggest it may be a hybrid (Nakato 1987). See *Notes* for further discussion.

Diagnosis.—The most consistent character for distinguishing *Grypothrix* from other segregates of *Pronephrium* is the presence of hamate hairs somewhere on the body of the plant—scales, leaves, veins, or sporangia. Sometimes, however, these may be sparse, and difficult to observe (e.g., in *G. sulawesiensis*). Sori of all species of *Grypothrix* are exindusiate, whereas indusia are sometimes present in species of *Menisciopsis, Pronephrium s.s.*, and *Abacopteris*. The sori of most continental Asian species of *Grypothrix* are elongate and coalescent along cross-veins, which is less common among other *Pronephrium* segregates (but see *Menisciopsis lakhimpurensis*); members of the Malesian clade of *Grypothrix* more frequently have round, discrete sori. *Pronephrium s.s.* is generally highly dimorphic (**Fig. 7C**), and often bears spherical yellow glands on its sporangia or elsewhere, whereas most species of *Grypothrix* are monomorphic or weakly dimorphic (with the exception of *G. simplex*, which differs from nearly all *Pronephrium s.s.* in having simple blades, **Fig. 3C**) and do not bear such glands.

Biogeography and ecology.—The 12 species of *Grypothrix* are Malesian, Melanesian, Australasian, and southeast Asian in distribution, with species extending into India, Sri Lanka, Myanmar, Thailand, Vietnam, China, Japan, and Korea. *Grypothrix triphylla* is especially widespread, extending from subtropical east Asia, throughout Malesia, and into northern Queensland and Fiji (Holttum 1977b, 1982). A few species are restricted to continental Asia, and others are endemic to Taiwan (*G. longipetiolata)* or to Taiwan and Japan (*P. insularis*) (Iwatsuki 1959; Lin et al. 2013).

Taxonomic and phylogenetic studies.—Holttum (1982) treated *Grypothrix* as a section of *Pronephrium*; all species in this section (here elevated to genus) have hamate hairs on the scales, laminae, veins, and/or sporangia. No earlier workers had recognized the taxonomic utility of these unusual hairs. This is the only Holttum segregate of *Pronephrium* (or any of his infrageneric taxa) that we elevate in rank with identical circumscription. It can be distinguished from closely related genera on the basis of a single synapomorphy—the presence of hamate (hooked) hairs somewhere on the plant. Similar hairs also occur in distantly related taxa within Thelypteridaceae, e.g., in sect. *Uncinella* of the mostly neotropical genus *Amauropelta* (Smith 1974), and in *Cyclogramma*.

Grypothrix comprises two monophyletic subclades with different distributions: the species of one subclade are predominantly continental Asian, and the species of the other are Malesian. *Grypothrix* is a member of the chingioid clade which includes the monophyletic genera *Chingia*, *Menisciopsis* (also segregated from *Pronephrium s.l.*), *Mesopteris*, and *Plesioneuron*. *Grypothrix* and *Menisciopsis*, like the closely related *Mesopteris*, share a tendency to turn red when dry, as suggested by some of their specific epithets: *Grypothrix rubicunda, Menisciopsis rubida*, and *M. rubrinervis*.

Notes.—A hybrid between *G. triphylla* and *G. cuspidata* has been reported from Taiwan (Knapp 2011). *Pronephrium thwaitesii,* an unusual taxon from India and Sri Lanka treated in *Pronephrium* sect. *Grypothrix* by Holttum (1972), had not been collected for more than a century, and had been presumed extinct. Holttum suggested it might be a hybrid involving *G. triphylla* (Holttum 1972). The plant was relocated by Nayar and Geeverghese (1987), who conducted a careful examination of its morphology, including spore development, and agreed that it was a hybrid involving *G. triphylla*; they then suggested *Christella parasitica* is the second parent. A hybrid described from Taiwan, recently treated as *Pronephrium insulare,* is also triploid (n = 108), and postulated to represent a cross between *Christella dentata* and *Pronephrium triphyllum* (considered by us to belong to *Grypothrix*); it was given a name as a nothogenus, ×*Chrinephrium insulare* (K. Iwats.) Nakaike (Kuo et al. 2019). As noted by Iwatsuki (1959), in his taxonomic concept, *Abacopteris* (which included several species of *Grypothrix*) is distinguished from *Cyclosorus* (including *Christella s.s.*) by lacking sinus membranes, although these are present in this purported hybrid. As putative examples of intergeneric hybridization, these hypotheses warrant further investigation.

New combinations and constituent species.—

Grypothrix crenulata (Holttum) S.E. Fawc. & A.R. Sm., **comb. nov.—***Pronephrium crenulatum* Holttum, Blumea 20:123. 1972.

***Grypothrix cuspidata** (Blume) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Meniscium cuspidatum* Blume, Enum. Pl. Javae 2:114. 1828.—*Abacopteris cuspidata* (Blume) Ching.—*Cyclosorus cuspidatus* (Blume) Copel.—*Pronephrium cuspidatum* (Blume) Holttum (**Fig. 3A, 3B**).

***Grypothrix longipetiolata** (K. Iwats.) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Abacopteris longipetiolata* K. Iwats., Acta Phytotax. Geobot. 18:11. 1959.—*Cyclosorus longipetiolatus* (K. Iwats.) C.M. Kuo—*Thelypteris longipetiolata* (K. Iwats.) K. Iwats.—*Pronephrium longipetiolatum* (K. Iwats.) Holttum

***Grypothrix megacuspis** (Baker) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Polypodium megacuspe* Baker, J. Bot. 28:266. 1890.—*Pronephrium megacuspe* (Baker) Holttum

***Grypothrix parishii** (Bedd.) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Meniscium parishii* Bedd., Ferns Brit. Ind., t. 184. 1866.—*Abacopteris triphylla* (Sw.) Ching var. *parishii* (Bedd.) Ching—*Cyclosorus parishii* (Bedd.) Tardieu—*Pronephrium parishii* (Bedd.) Holttum—*Pronephrium triphyllum* (Sw.) Holttum var. *parishii* (Bedd.) Nakaike—*Thelypteris triphylla* (Sw.) K. Iwats. var. *parishii* (Bedd.) K. Iwats.

Grypothrix pentapinnata (Fraser-Jenk.) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Thelypteris pentapinnata* Fraser-Jenk., Annot. Checkl. Ind. Pterid. 1:476. 2016.

***Grypothrix ramosii** (C. Chr.) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Dryopteris ramosii* C. Chr., Philipp. J. Sci., Bot. 2:203. 1907.—*Pronephrium ramosii* (C. Chr.) Holttum

***Grypothrix rubicunda** (Alderw.) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Phegopteris rubicunda* Alderw., Bull. Jard. Bot. Buitenzorg. 2:162. 1920.—*Pronephrium rubicundum* (Alderw.) Holttum

***Grypothrix salicifolia** (Wall. ex Hook.) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Meniscium salicifolium* Wall. ex Hook., Icon. Pl. 10:t. 990. 1854.—*Pronephrium salicifolium* (Wall. ex Hook.) Holttum

***Grypothrix simplex** (Hook.) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Meniscium simplex* Hook., London J. Bot. 1:294. 1842.—*Abacopteris simplex* (Hook.) Ching—*Pronephrium simplex* (Hook.) Holttum—*Thelypteris simplex* (Hook.) K. Iwats. (**Fig. 3C**).

***Grypothrix sulawesiensis** (K. Iwats.) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Pronephrium rubicundum* (Alderw.) Holttum subsp. *sulawesiense* K. Iwats., Acta Phytotax. Geobot. 28:162, f. 2 (1977).—*Pronephrium sulawesiense* (K. Iwats.) Holttum

***Grypothrix triphylla** (Sw.) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Meniscium triphyllum* Sw. in Schrader, J. Bot. 1800:16. 1801.—*Abacopteris triphylla* (Sw.) Ching—*Cyclosorus triphyllus* (Sw.) Tardieu—*Pronephrium triphyllum* (Sw.) Holttum—*Thelypteris triphylla* (Sw.) K. Iwats.

Incertae sedis.—*Pronephrium insulare* (K. Iwats.) Holttum (= ×*Chrinephrium insulare* (K. Iwats.) Nakaike) and *Pronephrium thwaitesii* may represent triploid species of *Grypothrix* or, potentially, hybrids between *Christella* and *Grypothrix triphyllum*, but pending further study, we refrain from making new combinations.

HOIOKULA

Hoiokula S.E. Fawc. & A.R. Sm., **gen. nov.**—Type: *Hoiokula sandwicensis* (Brack.) S.E. Fawc. & A.R. Sm. [=*Stegnogramma sandwicensis* Brack., U.S. Expl. Exped., Filic. 16:26. 1854.]

Etymology.—*Ho'i'o kula* is the common name for *H. sandwicensis* in the native Hawaiian language (Palmer 2003), and it is valued for its edible fiddleheads (Pukui & Elbert 2003).

Plants terrestrial, cremnophilous or rheophytic, from 40 cm to > 1 m tall; **rhizomes** short-creeping; **fronds** once-pinnate, monomorphic, erect (*H. sandwicensis*) or pendent (*H. pendens*); **stipes** stramineous or dull brown, stipe bases and rhizome scales dull brown, glabrous or with short surficial hairs, ovate to linear-lanceolate; **blades** chartaceous, drying green, lanceolate to broadly deltate, apex gradually reduced, with distal pinnae somewhat decurrent, proximal pinnae not or only slightly reduced, basal pair sometimes somewhat deflexed, proliferous buds absent; **pinnae** crenate, dentate, shallowly lobed (< halfway to costae), or subentire, typically straight, less commonly falcate, with acroscopic auricles, grooved adaxially; **veins** prominent abaxially and adaxially, anastomosing with several pairs uniting below the sinus into a zig-zag excurrent vein, veins ending at pinna margins; **aerophores** absent, or a small patch of darkened aerating tissue, sometimes slightly swollen or tuberculate; **indument abaxially** of broad-based (stout), tapering hyaline acicular hairs on veins and between veins, or restricted to veins, **indument adaxially** of hyaline acicular hairs on and between veins, hairs on stipes and rachises short (< 1 mm) and sparse (*H. sandwicensis*), or long (> 1 mm) and abundant (*H. pendens,* **Fig. 4B**), single-celled or septate; glands usually absent, but when present, spherical, translucent yellow-orange, on laminae, veins, and sporangia; **pustules** absent on laminar tissue; **sori** medial, round or elongate along veins, exindusiate; **sporangia** abundantly to sparsely setulose (**Fig. 2H**), rarely glabrous; **spores** pale brown, with broad wings, in *H. sandwicensis* with secondary sculpturing of fimbriate microstructure (Tryon & Lugardon 1991). Ploidy and hybrids are unknown, but the basic chromosome number is likely to be $x = 36$, as is the case for its closest relatives.

Diagnosis.—In Hawaii, *Hoiokula* is distinguished from *Reholttumia hudsoniana* (formerly treated together with *Hoiokula* in *Pneumatopteris* (Holttum 1977b; Palmer 2003)), *Christella*, and *Menisciopsis* by having setulose sporangia and exindusiate sori. *Hoiokula* is distinguished from *Cyclogramma* by pinnae incised less than halfway to the costae (vs. more than half-way). Hamate hairs are absent in *Hoiokula*, but frequent in *Cyclogramma* and *Stegnogramma s.s.* Spores of most *Stegnogramma* and *Leptogramma* species are echinate, rather than winged, (a feature shared by *Hoiokula* and some species of *Menisciopsis*). *Hoiokula* further differs from *Leptogramma* in having costae prominently grooved adaxially, vein endings reaching margins, multiple areoles below the sinuses (except in very small individuals), and presence of zig-zag excurrent veins. Until 2005, both species of *Hoiokula* recognized herein were treated within *Pneumatopteris sandwicensis*; *Hoiokula pendens* represents one of the most recently recognized native species in the Hawaiian fern flora (Palmer 2005; Vernon & Ranker 2013; Ranker et al. 2019).

Biogeography and ecology.—*Hoiokula* is endemic to the Hawaiian Islands, distributed on all major islands (Palmer 2003, 2005). The two recognized species differ in habit and habitat, with the larger, erect *H. sandwicensis* occurring in forest understories and along stream margins, and the pendent *H. pendens* occurring on damp rocks and cliffs, often near streams (Palmer 2005).

Taxonomic and phylogenetic studies.—*Hoiokula* bears considerable resemblance to *Stegnogramma s.l.*, and the similarities must have been apparent to Brackenridge (1854), who described the type species in *Stegnogramma* and illustrated the elongate sori and setose sporangia in the protologue. Both of these features are shared by the three stegnogrammoid genera but are uncommon within Thelypteridaceae. Although Holttum (1977b) treated the plants recognized here in *Hoiokula* as a species of *Pneumatopteris*, he noted several characteristics that this "peculiar Hawaiian species" has in common with *Stegnogramma*, such as "…venation of the apical lamina and a few thick hairs between veins on the upper surface of pinnae, and … somewhat elongate sori" (Holttum 1982:540).

Based on both concatenated and coalescent analyses (Fawcett et al. in press), the phylogenetic position of *Hoiokula* is well-supported as sister to the stegnogrammoid ferns, which include the genera *Cyclogramma*, *Stegnogramma*, and *Leptogramma* (Kuo et al. 2019). These results should be interpreted with caution, however, since the analysis assumes a bifurcating tree. Preliminary evidence from plastid data (L.Y. Kuo, unpubl. data), and conflicting topologies among gene trees (Fawcett et al. in press) suggest the possibility that this lineage may be of hybrid origin involving *Leptogramma* and *Menisciopsis*, which occurs in Hawaii, Melanesia, and eastern Asia. *Leptogramma* is distributed throughout Asia and India, and is scattered in Africa, Europe, and North America, while the genera *Cyclogramma* and *Stegnogramma s.s.* are both restricted to Southeast Asia and Malesia. No species of these three genera have been collected in Hawaii. The hybrid origin hypothesis is currently under investigation (Fawcett, Kuo et al. in prep.).

New combinations and constituent species.—

***Hoiokula pendens** (D.D. Palmer) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Pneumatopteris pendens* D.D. Palmer, Amer. Fern J. 95:81. 2005.—*Cyclosorus pendens* (D.D. Palmer) N. Snow (**Fig. 2H, 4B**).

***Hoiokula sandwicensis** (Brack.) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Stegnogramma sandwicensis* Brack., U.S. Expl. Exped., Filic. 16:26. 185.—*Cyclosorus sandwicensis* (Brack.) Copel.—*Pneumatopteris sandwicensis* (Brack.) Holttum (**Fig. 4A**).

LEPTOGRAMMA

Leptogramma J. Sm., J. Bot. (Hooker) 4:51. 1842.—Lectotype (designated by Christensen, Ind. Fil. xxi. 1905): *Leptogramma totta* (Schltdl.) J. Sm. [= *Gymnogramma totta* Schltdl.]—*Thelypteris* sect. *Leptogramma* (J. Sm.) C.V. Morton

Craspedosorus Ching & W.M. Chu
For additional generic synonymy, see Kuo et al. (2019).

Etymology.—Gr. *lepto*, slender + *gramme*, line, in reference to the linear sori on the veins (Stewart et al. 1983).

Plants terrestrial or epipetric, of tropical and subtropical forest understories, streamsides and rocky banks, mostly small (10–50 cm); **rhizomes** short-creeping to erect, with ovate to lanceolate setose scales; **fronds** monomorphic to weakly dimorphic, erect to arching, pinnate to pinnate-pinnatisect; **stipes** stramineous to dull brown, terete (may not be visible upon drying), with long and/or short unicellular or multicellular hyaline acicular hairs; **stipe scales** ovate to lanceolate, castaneous, brown or pale, typically setose on margins and surfaces; **blades** membranaceous to chartaceous, drying green, olivaceous or dark brown, hastate, ovate to lanceolate, apex gradually reduced, never pinna-like, blades often widest at or near the base, never with many pairs of gradually reduced proximal pinnae; proliferous buds absent; **pinnae** typically shallowly to deeply lobed, sometimes entire (*L. cyrtomioides*) to pinnatisect (*L. sinensis*), pinna-bases adnate (especially distally) to short-petiolulate proximally, rounded or truncate, sometimes asymmetrical, but not strongly auricled; **veins** free, mostly simple to sometimes forking, or, if anastomosing (in sect. *Haplogramma*), then two pairs or fewer meeting below the sinus at an acute angle; veins reaching laminar margins, or terminating before (e.g., *L. tottoides*); **aerophores** inconspicuous or absent; **indument abaxially and adaxially** of stipes, rachises, costae, veins, and laminar tissue between veins with long and/or short hyaline acicular hairs, these unicellular (sect. *Leptogramma*) or multicellular (sect. *Haplogramma*); **pustules** absent; **sori** linear to slightly elongate along ultimate veins (**Fig. 4C**); indusia absent; **sporangia** with setulose capsules; **spores** echinate (Wood 1973; Tryon & Lugardon 1991), except in *L. pozoi*, which has broad wings similar to spores of *Cyclogramma* (Patel et al. 2019a) and one population of *L. pilosa*, in which the echinae anastomose into loops (Watkins & Farrar 2005); $x = 36$, diploids, triploids, and tetraploids known, eight species counted.

Diagnosis.—*Leptogramma* may be recognized by the combination of elongate exindusiate sori, setulose sporangia, and long hyaline acicular hairs on the adaxial laminae between veins. It is distinguished from its sister genus *Stegnogramma* by veins free, or if anastomosing, only one or two pairs united below the sinus between adjacent lateral veins (vs. usually three or more), and by the presence of long multicellular hairs on rachises.

Biogeography and ecology.—The 29 species of *Leptogramma* are most diverse in the Himalayan region, with numerous endemics in southern China, occurring from lower elevations up to 2700 m. Within Asia, species extend north to Japan, west and south to Sri Lanka, and into eastern Malesia, including the Philippines, Java, and Sulawesi. One species, *L. totta*, is native to South and East Africa, another, *L. pozoi*, to southern Europe and North Africa; two are endemic to North America—*L. pilosa* in Mexico and Central America, and *L. burksiorum,* in Alabama, in the southeastern United States (Watkins & Farrar 2005). They occur in shady forest understories and disturbed forest edges, or on rocky banks or cliffs, especially limestone.

This genus is unusual among tropical genera of the Thelypteridaceae for having such a broad amphioceanic tropical or subtropical distribution coupled with many local endemics. Other comparable groups include *Christella*, which is predominantly continental Asian with two native species in the Neotropics, or *Amauropelta*, which is most diverse in the Andes and Central America but has secondarily dispersed to Africa and several Pacific and Atlantic islands. Two genera, *Cyclosorus* and *Strophocaulon*, have diversified little, but are widely distributed in lowland tropics. Essentially all other genera are more regionally restricted.

Taxonomic and phylogenetic studies.—John Smith's (1842) original concept of *Leptogramma* included a diverse group of ferns with linear sori, including species now recognized in *Amauropelta*, *Athyrium*, and *Sphaerostephanos*. Ching (1936, 1963) united most of the species we recognize today in his concept of *Leptogramma*, which was treated within a broadly defined *Stegnogramma* by Iwatsuki (1964a, 1964b). The Flora of China (Lin et al. 2013) recognized Ching's genera *Stegnogramma*, *Leptogramma*, and *Dictyocline*, plus the monotypic *Craspedosorus*, while PPG I (2016) adopted a broad concept of *Stegnogramma,* including all of these genera. With the recent publication of a densely sampled phylogeny—the first to include the type of *Stegnogramma*—Kuo et al. (2019) chose to recognize a two-genus system, although either *Leptogramma s.s.* plus *Stegnogramma s.s.* or *Stegnogramma s.l.* is monophyletic. We adopt their classification here. For additional discussion, see our treatment of *Stegnogramma*.

Leptogramma can be divided into two sections, sect. *Leptogramma* and sect. *Haplogramma*, which are recognized by Kuo et al. (2019) and correspond closely to the infrageneric classification of *Stegnogramma* proposed by Iwatsuki (1964a, 1964b) with only minor revisions. Section *Haplogramma* is strictly Asian, and is recognized by septate hairs along the stipes, whereas sect. *Leptogramma* has a wider distribution (including Europe, Africa, and North America) and unicellular (vs. septate) hairs on stipes (Kuo et al. 2019). The species within this section tend to be smaller, with more deeply lobed pinnae, and with exclusively free veins. Most necessary combinations in *Leptogramma* and *Stegnogramma* have been made by Kuo et al. (2019), and we adopt their taxonomic concept here, including the inclusion of the monotypic genus *Craspedosorus* within *Leptogramma*.

Historically, the name *Leptogramma pozoi* had been broadly applied to plants of both Europe and East Asia, but that taxon is now recognized as restricted to southern Europe and northern Africa, with Asian plants now treated as *L. mollissima* (Kuo et al. 2019). However, considerable complexity in geographic, morphological, and ecological variation has been demonstrated within these taxa (Yatabe et al. 1998), as well as within the neotropical *Leptogramma* lineages (Watkins & Farrar 2005). Further detailed study of these groups may uncover unrecognized diversity deserving of species status.

New combination.—

Leptogramma crenata (Holttum) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Stegnogramma crenata* Holttum, Blumea 33:404. 1988.

Constituent species.—***Leptogramma amabilis* Tagawa; ***L. burksiorum* (J.E. Watkins & Farrar) Y.H. Chang & L.Y. Kuo; *L. celebica* Ching; ***L. centrochinensis* Ching ex Y.X. Lin; ***L. chandrae* (Fraser-Jenk.) Y.H. Chang & L.Y. Kuo; *L. crenata* (Holttum) S.E. Fawc. & A.R. Sm.; **L. cyrtomioides* (C. Chr.) Y.H. Chang & L.Y. Kuo; ***L. dissitifolia* (Holttum) Y.H. Chang & L.Y. Kuo; *L. gymnocarpa* (Copel.) Ching; **L. himalaica* Ching; *L. huishuiensis* Ching ex Y.X. Lin; ***L. intermedia* Ching ex Y.H. Chang & L.Y. Kuo; *L. jinfoshanensis* Ching & Z.Y. Liu; *L. jinyunensis* Y.H. Chang & L.Y. Kuo; **L. latipinna* (Ching ex Y.X. Lin) Y.H. Chang & L.Y. Kuo; **L. leptogrammoides* (K. Iwats.) Y.H. Chang & L.Y. Kuo; *L. liui* Y.H. Chang & L.Y. Kuo; **L. mollissima* (Fisch. Ex Kunze) Ching; ***L. petiolata* Ching; **L. pilosa* (M. Martens & Galeotti) Underw. (**Fig. 4C**); **L. pozoi* (Lag.) Heywood; ***L. scallanii* (Christ) Ching; *L. sinensis* (Ching & W.M. Chu) Y.H. Chang & L.Y. Kuo; *L. sinica* Ching ex Y.X. Lin; *L. subcalcarata* (Alderw.) Y.H. Chang & L.Y. Kuo; ***L. totta* (Schltdl.) J. Sm.; **L. tottoides* Hayata ex H. Ito; *L. xingwenensis* (Ching ex Y.X. Lin) Y.H. Chang & L.Y. Kuo; *L. yahanensis* Ching ex Y.X. Lin

MACROTHELYPTERIS

Macrothelypteris (H. Ito) Ching, Acta Phytotax. Sin. 8:308. 1963.—Type: *Macrothelypteris oligophlebia* (Baker) Ching [= *Nephrodium oligophlebium* Baker]

For additional generic synonymy, see Holttum, 1969, 1971.

Etymology.—Gr. *makros*, large + *Thelypteris*. This genus has some of the largest and most deeply dissected (tripinnate-pinnatifid) fronds in the family.

Plants terrestrial, fronds of determinate growth, mostly medium-sized to very large, 50–200+ cm tall; **rhizomes** short-creeping to ascending or suberect, to 1 cm diam., with brown to tan scales, these lanceolate, with scattered hairs along margins and sometimes sparingly on surface; **fronds** clustered, monomorphic, evergreen or dying in winter (*M. viridifrons*); **stipes** to 80 cm long, 12 mm diam., not grooved adaxially, green or stramineous, less often castaneous (e.g., *M. ogasawarensis*), sometimes glaucous (e.g., *M. torresiana*); **stipe scales** lanceolate, stramineous to brown, 2–20 mm long, thickened at their bases, usually with a hairlike tip, typically with marginal and superficial hairs and often with stipitate glands (**Fig. 2G**); **blades** herbaceous to chartaceous, broadly deltate, to 1 m long, usually broadest at bases or with proximal pinnae only slightly reduced (always lacking greatly reduced glanduliform pinnae), lacking buds or proliferations, pinnate-pinnatifid to bipinnate- or even tripinnate-pinnatifid, with blade apex gradually tapering and pinnatifid; rachises adaxially not grooved, bearing simple acicular, often septate hairs, sometimes with persistent scales that leave a stump or "wart" when breaking off (e.g., *M. banaensis*, *M. multiseta*, *M. ornata*, *M. setigera*); **pinnae** to 15–35cm, subopposite proximally to alternate distally, subsessile or stalked, distal pinnae increasingly adnate, spreading or obliquely spreading, not grooved adaxially, truncate at bases, acute at tips, to ca. 15(–20) × 2(–3) cm wide, pinnatifid or pinnate-pinnatifid with pinnules adnate and sometimes interconnected at their bases, in larger species free, with or without acroscopic and/or basiscopic, more lobed basal auricles, sessile or nearly so; **veins** free, often forking in ultimate segments, ± easily visible on both sides, vein ends clavate adaxially and not reaching segment margins; **aerophores** absent at pinna bases; **indument abaxially** usually of sparse to moderately dense unicellular or often septate hyaline acicular hairs 0.5–2 mm long, in some species also with costal scales (e.g., *M. ornata*, *M. setigera*), blades often glabrescent with age, short-stipitate pale yellowish glands sometimes present along costae and costules; **indument adaxially** of hyaline acicular hairs to ca. 1 mm long along costae, sometimes also with hairs and stalked glands on costules and ultimate veins, occasionally on laminar tissue between veins; **pustules** absent on laminae between veins; **sori** medial to supramedial, round, exindusiate (*M. ornata*) or usually with small indusia to ca. 0.3 mm diam. (often hidden in mature sori), sori not confluent at maturity; **sporangia** glabrous or with 1–3 short-stipitate glands ca. 0.05 mm long adjacent to annulus on capsule, sporangial stalks short; **spores** tan to brown, ± winged or with a fine reticulate network, but lacking a low polygonal network of ridges as in *Pseudophegopteris*. Perforations in the perine (resembling those of the distantly related *Amauropelta,* but generally coarser) characterize the genus (although lacking in *M. viridifrons*), and distinguish it from other Phegopteridoideae (Holttum 1969; Tryon & Lugardon 1991; Patel et al. 2019a). $x = 31$, diploids, triploids, and tetraploids known, with five spp. counted. No hybridization with any other genus has been demonstrated.

Diagnosis.—*Macrothelypteris* is most closely related to both *Pseudophegopteris* and *Phegopteris*, which all share the characteristic of lacking grooves along the rachis and costae adaxially. This separates them from all other genera of Thelypteridaceae, except *Metathelypteris* and some *Leptogramma*, both of which are generally much smaller plants than *Macrothelypteris*. The conspicuous septate hairs, more alternate pinnae, and usually indusiate sori easily separate *Macrothelypteris* from *Pseudophegopteris*. *Phegopteris* is a genus of temperate, and high tropical montane environments, not occurring with *Macrothelypteris*, and has medial pinnae adnate to rachis (vs. mostly free). Tryon and Lugardon (1991) photographed spores of four species of *Macrothelypteris*. Spores of *M. polypodioides* and *M. setigera* (Tryon & Lugardon 1991; figs. 151.1–151.4, respectively) are similar and show a fine reticulate perispore, somewhat similar to spores of many neotropical *Amauropelta* spp., e.g., *A. concinna* (fig. 149.5); spores of *M. ornata* and *M. torresiana* (figs. 152.5, 152.7, respectively) have coarser, irregular folds, with small perforations, more like those of the Asian amauropeltoids (fig. 149.16). Even considering this variation, and incomplete sampling, *Macrothelypteris* appears to be readily differentiated from both *Phegopteris* and *Pseudophegopteris* based on spore morphology.

Biogeography and ecology.—*Macrothelypteris* comprises about 10 species, which are confined to Madagascar and the Mascarene Islands in the Indian Ocean, India, and continental eastern Asia, Australia, Malesia, Melanesia, and Polynesia (to the Society and Austral Islands; Holttum 1969). A single species, *M. torresiana*, is widely introduced and abundantly naturalized in the New World tropics and subtropics, extending from South Carolina and Arkansas to Florida and Louisiana (Leonard 1972; Smith 1993a), southward into the Antilles, southern Mexico, and Central America, and further south through much of South America to northern Argentina and Bolivia; it is also naturalized in Natal, South Africa (Burrows 1990), Hawai'i (Palmer 2003), and perhaps elsewhere. The greatest diversity in the genus is in China, with six species (but only one endemic, *M. contingens*), one with two varieties (Lin et al. 2013). Species of *Macrothelypteris* occur mainly in forests (but not in deep shade) or along forest margins, along trails and streams, and in shaded wet places, often in areas with some sun or in disturbed areas, at low to middle elevations from 0–2100 m.

Taxonomic and phylogenetic studies.—Both *Macrothelypteris* and *Pseudophegopteris* were first recognized at generic rank by Ching (1963). Holttum's studies further clarified their distinction and differences (Holttum 1969, 1971, 1974a, 1977b, 1982). See comments under *Pseudophegopteris* for distinctions between the two genera. These two genera have retained their rank in publications on the family by Smith (1990), Smith et al. (2006), and in PPG I (2016), as well as in many recent floras.

In our analyses (Fawcett et al. in press), and also those of He and Zhang (2012), Schneider et al. (2013), and Almeida et al. (2016), *Macrothelypteris* is monophyletic and sister to the clade *Phegopteris* + *Pseudophegopteris*. These three genera form the subfamily Phegopteridoideae Salino, A.R. Sm. & T.E. Almeida. All are free-veined, often with forked veins, and the veins end before reaching the segment margins. They were clearly understood and delineated by Holttum (1969), who provided a revision/synopsis of these genera in the same paper. Holttum (1947, 1969, 1982) believed the phegopteroid genera in particular, but all of Thelypteridaceae, to be related to Cyatheaceae (Holttum 1947, 1969, 1982). The Phegopteridoideae do indeed form the earliest diverging branch in Thelypteridaceae in molecular analyses, but all recent evidence suggests that they are not closely related to, or derived from, Cyatheaceae.

All necessary combinations in *Macrothelypteris* have been made by Ching (1963) and Holttum (1969, 1982). One African species, heretofore included in *Macrothelypteris* by Pichi Sermolli (1983), is here transferred to *Pseudophegopteris*.

Constituent species.—Macrothelypteris banaensis (Tardieu & C. Chr.) Christenh.; **M. contingens* Ching; *M. multiseta* (Baker) Ching; ***M. ogasawarensis* (Nakai) Holttum; **M. oligophlebia* (Baker) Ching; ***M. ornata* (Wall. ex Bedd.) Ching; **M. polypodioides* (Hook.) Holttum (**Fig. 2G**); *M. setigera* (Blume) Ching; **M. torresiana* (Gaudich.) Ching; ***M. viridifrons* (Tagawa) Ching.

Excluded species.—Macrothelypteris rammelooi Pic.Serm. = *Pseudophegopteris rammelooi* (Pic.Serm.) A.R. Sm. & S.E. Fawc.; *M. uraiensis* (Rosenst.) Á. Löve & D. Löve = *Metathelypteris uraiensis* (Rosenst.) Ching

MENISCIOPSIS

Menisciopsis (Holttum) S.E. Fawc. & A.R. Sm., **gen. et stat. nov.**—*Pronephrium* C. Presl sect. *Menisciopsis* Holttum, Fl. Males, Ser. 2, Pterid. 1(5):530. 1982.—Type: *Menisciopsis lakhimpurensis* (Rosenst.) S.E. Fawc. & A.R. Sm.

Thelypteris subg. *Cyrtomiopsis* K. Iwats., Mem. Coll. Sci. Kyoto Imp. Univ., Ser, B, Biol. 31:36. 1964.
For complete synonymy, see Holttum (1977b, 1982; Lin et al. 2013).

Etymology.—Gr. *Meniscium* + *-opsis*, like. The type species, *M. lakhimpurensis*, often has sori coalescent along arching cross veins (meniscioid).

Plants terrestrial, rheophytic or cremnophilous, small (< 15 cm) to very large (> 2 m); **rhizomes** short-creeping, long-creeping, or forming massive erect caudices; **fronds** monomorphic and once-pinnate, erect, ascending, or pendent; **stipes** stramineous, dull brown, or reddish; **stipe scales** dull brown, broadly ovate-deltate to ovate-lanceolate; **blades** chartaceous to subcoriaceous, laminae sometimes drying reddish; **pinnae** entire, crenate, toothed, or shallowly lobed, proximal pinnae not or little reduced, distal pinnae gradually reduced, with conform or subconform frond apex; **veins** anastomosing, generally with several pairs united below the sinus, forming areoles; cross-veins generally more or less straight, excurrent veins free or continuous from one areole to the next, straight or zig-zag, vein endings reaching segment margins; **aerophores** absent or present at pinna bases as a darkened swelling of aerating tissue; **indument abaxially** lacking, or of sparse, short, hyaline acicular hairs, generally restricted to costae and veins; **indument adaxially** lacking, or with short hyaline acicular hairs restricted to costae, rarely on lamina between veins, scales sometimes present on costae; elongate orange resinous glands abaxially on veins in some species; **pustules** present or absent on laminar tissue abaxially and adaxially; **sori** inframedial, often along costae or costules, rarely coalescent along uniting cross-veins (*M. lakhimpurensis*), indusiate or exindusiate; indusia glabrous, and persistent, or shriveling at maturity; **sporangia** without setulae or glands; **spores** typically black, sometimes brown, with non-reticulate folds or short echinate crests (Patel et al. 2019a); $x = 36$, two of seven spp. counted, only diploids known. A sterile triploid hybrid between *M. cyatheoides* and *Christella dentata* (*Christella* ×*palmeri*) has been reported (Wagner 1993), and is supported by phylogenetic data (Fawcett et al., in press). The type (MICH!) resembles the tetraploid parent *C. dentata,* which presumably contributed 2/3 of the hybrid genome.

Diagnosis.—*Grypothrix* differs from *Menisciopsis* in the presence of hamate, or hook-shaped hairs, proliferous buds, and sometimes dimorphic fronds. *Abacopteris* differs in having setulose sporangia, and sori medial and discrete (*vs.* sori usually inframedial or coalescent in *Menisciopsis*). *Pronephrium* differs in dimorphic fronds, generally smaller size, frond apex gradually reduced (non-conform), and indusia sometimes bearing yellow glands. The neotropical genus *Meniscium* differs in the frequent presence of proliferous buds in axils of proximal pinnae, aerophores lacking, sori generally coalescent along arching cross-veins, and sporangial capsules or stalks sometimes bearing setulae.

Biogeography and ecology.—Among the seven species recognized in this genus, one is restricted to the Philippines, another is distributed in Fiji, New Hebrides, and New Ireland (Holttum 1977b, 1982), three are in the Hawaiian archipelago (Palmer 2003), and two are widespread in continental South Asia—one of these, *Menisciopsis penangiana*, reaches elevations of 3600 m (Lin et al. 2013), but its congeners are typically of low to middle elevations.

Taxonomic and phylogenetic studies.—Holttum described *Menisciopsis* as a section of *Pronephrium* (Holttum 1982), although within this section he recognized species we here transfer to *Sphaerostephanos* and *Abacopteris*. The three Hawaiian species were treated by Holttum (1977b) and Palmer (2003) as members of *Christella*. Iwatsuki (1964a, 1964b) treated *Menisciopsis boydiae* (**Fig. 5B**) in a new subgenus of *Thelypteris*, *Cyrtomiopsis*, based on its distinctive morphology and superficial resemblance to *Cyrtomium* (Dryopteridaceae). Based on molecular phylogenetic evidence (Fawcett et al. in press) the closest relatives to *Menisciopsis* are *Chingia* and *Plesioneuron*, and all three of these monophyletic genera are in turn sister to *Grypothrix*, which was treated by Holttum (1982) as another section of *Pronephrium* in subg. *Menisciopsis*.

New combinations and constituent species.—

***Menisciopsis boydiae** (D.C. Eaton) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Aspidium boydiae* D.C. Eaton, Bull. Torrey Bot. Club 6:361. 1879.—*Christella boydiae* (D.C. Eaton) Holttum—*Cyclosorus boydiae* (D.C. Eaton) W.H. Wagner—*Thelypteris boydiae* (D.C. Eaton) K. Iwats. (**Fig. 5B**).

***Menisciopsis cyatheoides** (Kaulf.) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Aspidium cyatheoides* Kaulf., Enum. filic. 234. 1824.—*Christella cyatheoides* (Kaulf.) Holttum—*Cyclosorus cyatheoides* (Kaulf.) Farw.—*Thelypteris cyatheoides* (Kaulf.) Fosb. (**Fig. 5A**).

***Menisciopsis lakhimpurensis** (Rosenst.) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Dryopteris lakhimpurensis* Rosenst., Meded. Rijks-Herb. 31:7. 1917.—*Cyclosorus lakhimpurensis* (Rosenst.) Copel.—*Pronephrium lakhimpurense* (Rosenst.) Holttum—*Thelypteris lakhimpurensis* (Rosenst.) K. Iwats.

***Menisciopsis penangiana** (Hook.) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Polypodium penangianum* Hook., Sp. Fil. 5:13. 1864.—*Abacopteris penangiana* (Hook.) Ching—*Cyclosorus penangianus* (Hook.) Copel.—*Pronephrium penangianum* (Hook.) Holttum—*Thelypteris penangiana* (Hook.) C.F. Reed

***Menisciopsis rubida** (J. Sm. ex Hook.) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Polypodium rubidum* J. Sm. ex Hook., Sp. Fil. 5:12. 1863.—*Cyclosorus rubidus* (J. Sm. ex Hook.) Copel.—*Pronephrium rubidum* (J. Sm. ex Hook.) Holttum

***Menisciopsis rubrinervis** (Mett.) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Phegopteris rubrinervis* Mett., Linnaea 36:116. 1869.—*Cyclosorus rubrinervis* (Mett.) Copel.—*Pronephrium rubrinerve* (Mett.) Holttum (**Fig. 5C**).

***Menisciopsis wailele** (Flynn) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Thelypteris wailele* Flynn, Contr. Univ. Michigan Herb. 20:245. 1995.—*Christella wailele* (Flynn) D.D. Palmer—*Cyclosorus wailele* (Flynn) W.H. Wagner

MENISCIUM

Meniscium Schreber, Gen. Pl., ed. 8(a), 2:757. 1791.—*Thelypteris* subg. *Meniscium* (Schreber) C.F. Reed—Type: *Meniscium reticulatum* (L.) Sw. [= *Polypodium reticulatum* L.]

For additional synonymy see Fernandes (2020).

Etymology.—Gr. *meniskos*, moon, in reference to the lunulate (crescent-moon shaped) sori that characterize this genus; these are coalescent or continuous along the arching cross-veins, which produce an excurrent vein at their union. This contrasts with *Goniopteris*, in which the discrete round sori are in pairs on the cross veins, on both sides of the origin of the excurrent veinlet, where the anastomosing cross-veins meet at an often acute angle.

Plants terrestrial, rarely rheophytic, medium-sized (ca. 50 cm) to very large (> 2 m); **rhizomes** short-creeping, sometimes ascending, thick, nearly scaleless back from the tip; **fronds** monomorphic or weakly dimorphic (fertile pinnae narrower and more densely hairy than sterile ones), infrequently fully dimorphic (if so, sporangia appearing acrostichoid at frond maturity), simple to usually 1-pinnate, erect or arching; **stipes** stramineous, dull brown, or rarely castaneous (*Meniscium giganteum*); **stipe scales** dull brown, broadly ovate-deltate to ovate-lanceolate, often abraded in mature fronds; **blades** chartaceous to subcoriaceous, laminae typically drying greenish; **pinnae** adaxially grooved, entire, crenate, or infrequently serrate (*M. consobrinum*; *M. serratum*), never lobed, proximal pinnae not or little reduced, distal pinnae gradually to often abruptly reduced, usually with a conform or subconform apex; buds often present in axil of a proximal pinna; **veins** regularly anastomosing, forming parallel rows of areoles, with (3–)10–25 pairs united and forming areoles; cross veins straight, arcuate, or subsigmoid, giving rise to excurrent veins that are generally free, but sometimes continuous and straight from one areole to the next; **aerophores** absent at pinna bases; **indument abaxially** lacking, sparse, or occasionally dense, of hyaline acicular, often curved hairs, generally restricted to costae, costules, and veins, less often on laminar tissue between veins, rarely of stipitate glands, scales lacking on costae; **indument adaxially** absent or of hyaline acicular hairs usually restricted to costae; **pustules** absent on laminar tissue abaxially and adaxially; **sori** along cross-veins, often coalescent and so oblong, linear, or lunate, mostly in single rows between main lateral veins, occasionally discrete and round or nearly round and forming two rows between main lateral veins (e.g., *M. lingulatum*), always exindusiate; **sporangia** usually without setulae (except in *M. macrophyllum*) or glands, but with setae or stalked red to orange spherical glands sometimes borne on sporangial stalks; receptacles bearing stalked, tubular, orangish glands in a few species (*M. andreanum*, *M. arcanum*); **spores** typically black or dark brown, perispore winged, the wings echinulate or fimbriate (Tryon & Lugardon 1991; Fernandes et al. 2014; Patel et al. 2019a); $x = 36$, $2n = 72$ (*M. serratum*), 144 (*M. reticulatum*), only two of 25 spp. counted. No intrageneric or intergeneric hybrids are known.

Diagnosis.—A few New World species with meniscioid venation are herein treated in *Goniopteris* (e.g., *G. clypeata*, *G. mollis*, *G. holodictya*, *G. liebmannii*, *G. poiteana*). *Meniscium* can be readily distinguished from *Goniopteris* by the lack of stellate or furcate hairs on the rhizome and stipe base scales, as well as on the blades, by the usually much greater number of areoles between the costae and pinna margins, by the sori usually arcuate, linear, or confluent at maturity (vs. sori round and in two discrete rows between main lateral veins in *Goniopteris*), by the usually 1-pinnate blades with entire, crenate or serrate, unlobed pinnae, and by the usually much larger frond size.

Biogeography and ecology.—The majority of the 26 species of *Meniscium* are either exclusively South American or largely South American with range extensions into Mesoamerica and/or the Antilles, and most occur in Andean countries, the center of diversity for the genus; *M. cocleanum*, *M. falcatum*, and *M. turrialbae* in Mesoamerica and *M. reticulatum* in the Antilles are the major exceptions to this pattern. The range of the genus is from peninsular Florida, the Antilles, and southern Mexico to Bolivia, southern Brazil, Paraguay, and northern Argentina, almost exactly the range of *M. serratum*, one of the more common and most widespread species in the genus. Most species of *Meniscium* tend to be widespread, but a few are narrow endemics (e.g., *M. cocleanum*, *M. consobrinum*). They are confined to low and middle elevations, from 0–1500(–2000) m, and are found along streams, in wet forests, and ditches. At least one, *M. serratum*, often occupies marshes and swamps, in open or partially open habitats.

Taxonomic and phylogenetic studies.—The species were first revised by Christensen (1913), later by Maxon and Morton (1938), and most recently by Fernandes (2020). The last author and coauthors (Fernandes et al. 2014; Fernandes & Salino 2016) described several new species (increasing the total to 26) and provided a key to the Brazilian species. Smith and Kessler (2017) treated the 13 Bolivian species.

Meniscium is monophyletic in all major phylogenetic studies (Almeida et al. 2016; Fawcett et al. in press) and is sister to a clade including *Ampelopteris*, *Mesophlebion*, and *Cyclosorus s.s.*, the first two of these paleotropical, the last pantropical. Holttum (1982) postulated a relationship among all three of these last genera, but not to *Meniscium*. *Goniopteris* is, in turn, sister to this combined 4-genus clade (Fawcett et al. in press). All five genera are sister to a huge clade comprising the remaining cyclosoroid genera (which includes *Pronephrium s.l.*) Thus, the so-called "meniscioid" venation in *Meniscium*, *Menisciopsis*, *Goniopteris*, *Pronephrium*, and a few other cyclosoroid genera appears to have evolved many times, independently.

Miocene deposits including a fossil *Meniscium* have recently been found in Colombia (Sanín et al. 2016); assignment of this fossil to an extant genus is likely correct based on venation and geographic location. The date of the fossil falls well within divergence estimates of the genus published by Testo and Sundue (2016).

Several genera here segregated from the Old World genus *Pronephrium* bear some resemblance to *Meniscium* in having large, one-pinnate fronds with many pairs of anastomosing veins between the costae and pinna margins. Several species in these genera have historically been included in *Meniscium* because of this similarity, but these are now treated in *Grypothrix*, *Pronephrium*, *Abacopteris*, or *Menisciopsis*. From *Grypothrix*, which sometimes mimics *Meniscium* in venation, *Meniscium* differs in lacking hamate hairs on the blades. *Abacopteris* differs in having setulose sporangia, and medial, discrete, round sori. *Pronephrium* differs in having more strongly dimorphic fronds, much smaller frond size, frond apex gradually reduced (non-conform), and sometimes yellow glands on indusia and/or laminae. *Menisciopsis* differs in typically having discrete sori, which may be indusiate. *Meniscium* generally differs from all of these in the frequent presence of proliferous buds in axils of proximal pinnae (though these are present in some *Grypothrix*), sori generally coalescent or continuous along arching or straight cross-veins, and usually by the much greater number of areoles between costae and pinna margins. *Meniscium* is strictly neotropical, whereas all of the genera segregated from *Pronephrium* are paleotropical.

Constituent species.—**Meniscium andreanum* Sodiro; **M. angustifolium* Willd.; **M. arborescens* Humb. & Bonpl. ex Willd.; **M. arcanum* (Maxon & C.V. Morton) Pic.Serm.; **M. chrysodioides* Fée; *M. cocleanum* (A.R. Sm. & Lellinger) R.S. Fern. & Salino; **M. consobrinum* (Maxon & C.V. Morton) Pic.Serm.; **M. delicatum* R.S. Fern. & Salino; *M. divergens* R.S.

Fern. & Salino; **M. falcatum* Liebm.; **M. giganteum* Mett.; **M. hostmannii* (Klotzsch) R.S. Fern. & Salino; **M. lanceum* (A.R. Sm.) R.S. Fern. & Salino; **M. lingulatum* (C. Chr.) Pic.Serm.; **M. longifolium* Desv.; **M. macrophyllum* Kunze; **M. maxonianum* (A.R. Sm.) R.S. Fern. & Salino; **M. membranaceum* (Mett.) Pic.Serm.; *M. minusculum* (Maxon) Pic.Serm.; **M. nesioticum* (Maxon & C.V. Morton) Jermy & T.G. Walker; **M. pachysorum* (Hieron.) R.S. Fern. & Salino; **M. reticulatum* (L.) Sw.; **M. serratum* Cav.; *M. standleyi* (Maxon & C.V. Morton) Pic.Serm.; *M. triangularis* R.S. Fern. & Salino; *M. turrialbae* (Rosenst.) Pic.Serm. Several species described in *Meniscium* in the Neotropics are heterotypic synonyms of species accepted above.

MENISORUS

Menisorus Alston, Bol. Soc. Brot., sér. 2, 30:20. 1956.—Type: *Menisorus pauciflorus* (Hook.) Alston [= *Meniscium pauciflorum* Hook.]

For complete synonymy, see Holttum (1974a).

Etymology.—Gr. *mene*, moon + *sorus*, sorus, in reference to the crescent-moon-shaped, or lunulate, sori on the cross-veins, similar to those of *Meniscium*.

Plants small to medium-sized, terrestrial, rheophytes of rocky streambeds in lowland tropical forests, or forest understory plants to ~1m tall; **rhizomes** erect, ascending, or short-creeping (*M. blastophorus*), rhizome scales caducous; **fronds** monomorphic, ascending or arching, pinnate to pinnate-pinnatifid; **stipes** stramineous; **stipe scales** appressed, sparse, glabrous, brown, ovate-deltate, to slightly elongate, apparently caducous; **blades** drying dark, sometimes grayish white abaxially in *M. pauciflorus*, proximal pinnae not or little-reduced, apex conform to subconform, frequently with proliferous buds, or persistent plantlets arising from distal rachis, just below frond apex; **pinnae** with crenate margins, obliquely dentate or shallowly lobed, bases truncate to narrowly cuneate; **veins** with one to several pairs anastomosing, these forming a zig-zag excurrent vein to sinus, with subsequent veins running along deep sinus-membrane; **aerophores** absent (*M. pauciflorus*) or elongate (*M. unitus*); **indument abaxially and adaxially** essentially lacking, or of short, erect hairs restricted to axes and occasional small scales on costae abaxially; **pustules** present in *M. unitus*; **sori** exindusiate, round to elongate, discrete or confluent along arching cross-veins (meniscioid sori); **sporangia** glabrous; **spores** papillose or winged (Holttum 1974a; Tryon & Lugardon 1991); x=36, diploid, based on a count of *M. unitus*. No hybrids are known.

Diagnosis.—*Menisorus* may be recognized by the combination of exindusiate sori, at least some of which are elongate along veins, and subapical proliferous buds. It shares these characteristics with *Ampelopteris prolifera*, but that monotypic genus may be distinguished by its forked hairs, indeterminate growth of frond apices, and stipitate glands on sporangial stalks.

Biogeography and ecology.—*Menisorus* is the only genus within Thelypteridaceae that is restricted to Africa. Its three constituent species are widespread in lowland and montane equatorial forests, up to about 2500 m, reaching Madagascar and the Comoros, and the Atlantic island of Bioko. *Menisorus pauciflorus* is quite distinctive and bears the narrow elongate pinnae with oblique costules characteristic of some other rheophytic, but distantly related, thelypteroids (e.g., *Sphaerostephanos cataractorum*, *Menisciopsis boydiae*, **Fig. 5B**); its typical habitat is rocky, forested streambeds (Lovett & Thomas 1986).

Taxonomic and phylogenetic studies.—*Menisorus*, segregated by Alston (1956) from *Meniscium*, was treated as a monotypic genus based solely on the highly distinctive *M. pauciflorus*. Until recently (Fawcett et al. in press) *Menisorus* remained one of only two of 337 genera of ferns (as recognized by PPG I 2016) yet to be included in a phylogenetic study—the last is *Thysanosoria* (Lomariopsidaceae) (Chen et al. 2018). Based on molecular evidence, *Pneumatopteris unita* (Kunze) Holttum is sister to *Menisorus pauciflorus,* and the two are well-supported on a long branch with no close relatives; therefore, we treat them as congeners. Based on morphological similarity, we expand *Menisorus* to also include *M. blastophorus,* recognizing the genus to include three species. The phylogenetic position of *Menisorus* is along a grade of cyclosoroid genera, after the divergence of *Pakau*, a monotypic genus endemic to New Zealand and Australia (described herein) and before the divergence of *Pelazoneuron*, a New World genus of 16 species (elevated to generic status herein) (**Fig. 1**).

Notes.—Thelypteridaceae is represented in Africa by only about 55 species (Holttum 1974a), far fewer than in the Neotropics or southeastern Asia; however, these species represent more than a dozen major lineages within the family (Fawcett et al. in press), a pattern that may have been greatly accentuated by recent extinctions (Aldasoro et al. 2004). The genus *Pneumatopteris* sensu Holttum has proven to be the most polyphyletic of his taxonomic concepts, resolving in 10 distinct lineages (see *Pneumatopteris* for further discussion). African species treated in *Pneumatopteris* by Holttum

(1974a) resolve in clades corresponding to *Abacopteris, Christella, Menisorus, Pseudocyclosorus,* or *Reholttumia*. While we have made new combinations for some of these, we remain uncertain about the placement of others, pending further study, and we treat two species which may have close affinities to *Menisorus* as *incertae sedis*.

New combinations.—

Menisorus blastophorus (Alston) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Cyclosorus blastophorus* Alston, Bol. Soc. Brot., ser. 2, 30:12. 1956.—*Pneumatopteris blastophora* (Alston) Holttum—*Thelypteris blastophora* (Alston) C.F. Reed

Menisorus unitus (Kunze) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Gymnogramma unita* Kunze, Linnaea 18:114. 1844.—*Goniopteris unita* (Kunze) J. Sm.—*Pneumatopteris unita* (Kunze) Holttum—*Phegopteris unita* (Kunze) Mett.

Constituent species.—*Menisorus blastophorus* (Alston) S.E. Fawc. & A.R. Sm.; **M. pauciflorus* (Hook.) Alston; **M. unitus* (Kunze) S.E. Fawc. & A.R. Sm.

Incertae sedis.—We suspect the following species may be most appropriately treated in *Menisorus* but refrain from making combinations pending further study; the Madagascar and Comoros endemic *Pneumatopteris subpennigera* (C. Chr.) Holttum, and *P. oppositifolia* (Hook.) Holttum, an endemic to the islands of Bioko, São Tomé, and Annobón, both of which resemble *M. unita*, but lack proliferous buds.

MESOPHLEBION

Mesophlebion Holttum, Blumea 19:29. 1971, a renaming of *Mesoneuron* Ching (1963), non *Mezonevron* Desf. (1818).—TYPE: *Mesophlebion crassifolium* (Blume) Holttum [=*Aspidium crassifolium* Blume]

For additional synonymy, see Holttum (1971, 1982).

Etymology.—Gr. *meso*, middle + *phlebion*, vein, in reference to basal basiscopic veins arising from costae between costules (**Fig. 9C**).

Plants terrestrial, mostly in wet forests, medium-sized; **rhizomes** short- to long-creeping, at apices with rather rigid (but never spine-like) dark scales bearing short acicular hairs; **fronds** mostly 35–150 cm tall, monomorphic to dimorphic (*M. oligodictyon*); **stipes** green when living, stramineous or reddish-flushed with age, scaly primarily at bases (except *M. echinatum* and a few other spp.), scales tan to brown, mostly 2–10 mm long, lanceolate, bearing short acicular hairs on margins and on surfaces; **blades** usually pinnate-pinnatifid with proximal pinnae not reduced, apices confluent and gradually tapering to subconform, or rarely, blades simple (*M. oligodictyon*); **pinnae** opposite or subopposite, often becoming alternate distally, shallowly to usually deeply lobed (to within 2 mm of costae); proximal pair narrowed at their bases, sessile to long-petiolulate (to 2 cm); rachises hairy to sometimes glabrescent, hairs acicular, sometimes with scales similar to those of stipes proximally, but scales shorter, blades lacking vegetative buds; **veins** free, rarely weakly united (*M. oligodictyon*), usually connivent at or just below the sinuses and touching sides of an often hairy ridge below sinus, simple in ultimate segments, ending at segment margins, basal basiscopic veins arising from costa midway between costules (**Fig. 9C**), near base of costule, or from costules (in smaller spp., e.g., *M. arenicola*) of ultimate segments; costae adaxially prominent, grooved; **aerophores** sometimes swollen on living fronds, collapsing on drying, never peg-like; **indument abaxially** on axes (rachises, costae, costules, and sometimes veins) of acicular, unicellular hairs, laminar tissue between veins usually glabrous, lacking stipitate glands, sometimes with spherical or hemispherical glands, scales sometimes present abaxially along costae; **indument adaxially** only along rachis and costae, of acicular hairs; **pustules** absent; **sori** round to sometimes elongate along veins, medial, indusiate (except *M. oligodictyon*), indusia round-reniform, thin, small to large, often caducous, glabrous or with short acicular setae; **sporangia** short-stalked, young ones often pale violet, glabrous or usually bearing a reddish or orangish stipitate spherical gland from the sporangial stalk, capsules lacking glands and hairs; **spores** dark brown, with long, continuous wings and a few cross-wings, ridges, or minutely papillose; $x = 36$ (3 species counted, both diploids and tetraploids); no intergeneric or infrageneric hybrids are known.

Diagnosis.—The genus is generally relatively easy to recognize because of the deltate pinnate-pinnatifid blades that are widest at the base, dark green thick-herbaceous blades, creeping rhizomes, free veins connivent at or near sinuses, and presence of large, stipitate, reddish spherical glands on the sporangial stalks, a characteristic shared with its closest relatives, *Cyclosorus s.s.* and *Ampelopteris*. *Mesophlebion* is easily distinguished from the latter by the more deeply incised pinnae, and the non-proliferous fronds. From *Cyclosorus*, *Mesophlebion* is distinguished by the free veins, shorter-creeping rhizomes, and forest habitat (vs. fresh-water marshes and swamps, often in partial to full sun).

Biogeography and ecology.—*Mesophlebion* comprises ca. 17 species, distributed from Myanmar and peninsular Thailand and Vietnam throughout Malesia, except eastern Java and the Lesser Sunda Islands (Holttum 1982); it is absent from Melanesia and Polynesia, and represented in Australasia by three species in New Guinea. Nearly half of the species are rare in collections, and the greatest diversity is in Borneo, with 13 species. Species are generally found in low- to mid-elevation forests, or among rocks in riverbeds, from 0–1800 m. Species seldom occur in open habitats, except for *M. arenicola* and *M. teuscheri*, which grow on wet sandstone in exposed places (Holttum 1982); as a likely consequence of this nutrient-deficient habitat, these two species are smaller (< 50 cm) than others in the genus. One other small species, *M. oligodictyon*, differs from others in the genus in its dimorphic blades, lack of acicular hairs abaxially, and irregularly anastomosing veins, somewhat resembling species of the *Sphaerostephanos beccarianus* group (**Fig. 7A**). Holttum treated it in *Mesophlebion* based on the stipitate gland on sporangial stalk, and venation; its placement needs verification.

Taxonomic and phylogenetic studies.—The genus *Mesoneuron* was published by Ching (1963) in his treatment of mainland Asian Thelypteridaceae. Because of its similarity to *Mezonevron* Desv. (a synonym of *Caesalpinia*, Fabaceae), Holttum (1971) published the replacement name *Mesophlebion*. Initially, Holttum (1971) included the genus *Plesioneuron* as a subgenus of *Mesophlebion*, but later Holttum (1975) accorded *Plesioneuron* generic rank. Prior to that, Christensen (1929) recognized species of *Mesophlebion* as a distinct group, in *Dryopteris*, and compared them to the neotropical group *Dryopteris* subg. *Steiropteris* (herein recognized as *Steiropteris*), which they superficially resemble in venation, blade architecture, and blade texture (**Fig. 9**). Holttum (1982) commented on the pale violet-purple color of young sporangia (and sometimes indusia) of some species, a character observed by us in this genus and also in *Steiropteris*. The cause of this coloration, or its taxonomic importance, is unknown. Certain species complexes, especially *M. crassifolium*, *M. chlamydophorum*, *M. motleyanum*, and close allies, are quite variable, and circumscription of taxa requires re-examination and detailed field study, a situation noticed by Holttum (1982) and by us.

Sequence data show that *Mesophlebion* is most closely related to *Cyclosorus s.s.* and *Ampelopteris*, the three genera forming a clade that is sister to the neotropical genus *Meniscium* (He & Zhang 2012; Almeida et al. 2016; Fawcett et al. in press). The relationship of *Mesophlebion* to *Steiropteris* and *Plesioneuron*, however, is more remote (He & Zhang 2012; Almeida et al. 2016; Fawcett et al. in press).

Constituent species.—*Mesophlebion arenicola* Holttum; *M. auriculiferum* (Alderw.) Holttum; *M. beccarianum* (Ces.) Holttum; *M. caroli* Holttum; **M. chlamydophorum* (Rosenst. ex C. Chr.) Holttum; **M. crassifolium* (Blume) Holttum; *M. dulitense* Holttum; **M. echinatum* (Mett.) Holttum; *M. endertii* (C. Chr.) Holttum; *M. falcatilobum* Holttum; *M. hallieri* (Christ) Holttum; **M. motleyanum* (Hook. ex Hook. & Baker) Holttum; *M. oligodictyon* (Baker) Holttum; **M. persquamiferum* (Alderw.) Holttum; **M. rufescens* Holttum; *M. teuscheri* (Alderw.) Holttum; **M. trichopodum* (C. Chr.) Holttum

MESOPTERIS

Mesopteris Ching, Acta Phytotax. Sin. 16:22. 1978.—Type: *Mesopteris tonkinensis* (C. Chr.) Ching [= *Dryopteris tonkinensis* C. Chr.]

For additional synonymy, see Wang et al. (2015) and Holttum (1977a, 1982).

Etymology.—Gr. *mesos*, middle + *pteris*, fern. A genus endemic to China and neighboring northern Vietnam. Ching (1978) did not explicitly state why he chose *Mesopteris* as the name of his new genus, but in Mandarin the name for China is Zhōngguó (中國/中国), in English, Middle Kingdom.

Plants terrestrial, medium-sized (to ca. 2 m tall), of lowland tropical forests or disturbed sites, or on limestone; **rhizomes** long-creeping (*M. tonkinensis*) to erect (*M. paraphysophora*); **fronds** monomorphic, arching to erect, pinnate-pinnatifid; stipes dull brown to castaneous, rarely stramineous; **stipe scales** tan, glabrous, tortuous, linear-lanceolate; **blades** chartaceous to sub-coriaceous, often drying dark brown to reddish brown, darker adaxially and paler abaxially, apex conform to subconform, proximal pinnae not or little reduced, proliferous buds absent; **pinnae** short-petiolulate, with truncate to cuneate bases, proximal pinnae often narrowed towards their bases, not auriculate, margins dentate, with sinuses reaching ca. 1/3 towards costae, to deeply lobed to 1 mm from costae; **veins** often obscure adaxially except for swollen vein endings, free, connivent below sinus, or with one or more pairs anastomosing below it, veins terminating before reaching margins, or ending at margins, sinus membrane sometimes with tooth-like projection abaxially; **aerophores** absent; **indument abaxially** essentially lacking, or of short (< 0.1 mm) hyaline acicular hairs on axes and laminae, and/or of minute spherical or stipitate glands, primarily restricted to axes, or red to amber resinous glands, which may be spherical and sessile, or viscid, sometimes abundant on laminae, these most easily observed on fresh material and not always apparent on dried specimens; **indument adaxially** essentially lacking, or of minute (< 0.1 mm) hairs or minute colorless, golden brown glands primarily restricted to costae; **pustules** often present on laminar tissue abaxially; **sori** round, discrete or confluent (*M. attenuata*), medial, distributed along length of segments or mostly towards segment base (never restricted to segment apices), exindusiate or with small indusia, which may be glabrous, or obscured by abundant resinous glands (*M. attenuata, M. ceramica*); **sporangia** glabrous, or with glands on capsules or on stalks; **spores** dark brown to black, with broad, non-reticulating crests; $x = 38$, based on a count of *M. tonkinensis* provided by Wang et al. 2015. This is an anomalous and unexpected number within the family and needs verification; nearly all members of the cyclosoroid clade (which includes the greatest diversity in the family) share the synapomorphy of $x = 36$. No hybrids have been reported.

Diagnosis.—*Mesopteris s.l.* is distinguished from *Amblovenatum s.s.* by indusia small, absent, or obscured by copious resinous glands (vs. indusia conspicuous, and persistent); presence of red to amber-colored translucent resinous glands (vs. opaque, sulfur-colored to pale glands); indument on axes essentially lacking, or of short (< 0.1 mm) stipitate-glandular and hyaline acicular hairs (vs. indument including long (0.5–1 mm) hyaline acicular hairs); and laminae drying bicolorous, dark, often reddish (vs. concolorous green to pale olivaceous). *Mesopteris* differs from *Grypothrix* and *Menisciopsis* in having more deeply incised pinnae; it also lacks the stiff, thickened, sometimes spine-like scales often present on stipes in *Chingia* and *Plesioneuron*.

Biogeography and ecology.—The six species of *Mesopteris*, five treated in this genus here for the first time, occur in humid tropical forest to elevations of about 1000 m. In contrast to species of *Amblovenatum s.s.*, several of which are extremely widespread, *Mesopteris* species tend to occupy more limited distributional ranges. The type species, *M. tonkinensis*, is restricted to the vicinity of the border area between China and Vietnam, where it occurs along roadsides and on limestone (Wang et al. 2015). The remaining species are primarily Malesian, with limited distributional ranges, extending as far east as the Solomon Islands.

Taxonomic and phylogenetic studies.—All species of *Mesopteris* were treated in *Amphineuron* (= *Amblovenatum s.l.*) by Holttum (1977a), a genus recognized by Ching but excluding *A. tonkinensis*, which he segregated in the monotypic genus *Mesopteris* in his classification of the ferns of China (1978). The Flora of China (Lin et al. 2013) followed Ching (1978) in recognizing *Mesopteris* as monotypic, but *Amphineuron s.l.* was subsumed under *Cyclosorus s.l.*

The first molecular evidence that *Amphineuron* sensu Holttum (1977a, 1982) was not monophyletic was published by He and Zhang (2012). This result was corroborated by subsequent analyses, which further infer a close phylogenetic relationship between a *Mesopteris tonkinensis* collection from China and specimens of *M. paraphysophora* and *M. pseudostenobasis* from Malaysia and the Solomon Islands, respectively (Fawcett et al. in press). The three sampled species of *Mesopteris* are sister to a clade that includes the genera *Grypothrix*, *Menisciopsis*, *Chingia*, and *Plesioneuron*. See *Amblovenatum* for further discussion of taxonomy and phylogenetic relationships.

New combinations.—

Mesopteris attenuata (Kuntze) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Dryopteris attenuata* Kuntze, Rev. Gen. Pl. 2:812. 1891.—*Aspidium attenuatum* Kunze ex Mett., Farngatt. 4:96. 1858, non Sw. (1801).—*Amphineuron attenuatum* (Kuntze) Holttum—*Thelypteris attenuata* (Kuntze) C.V. Morton

Mesopteris ceramica (Alderw.) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Phegopteris ceramica* Alderw., Bull. Dép. Agric. Indes Néerl. 18:15. 1908.—*Amphineuron ceramicum* (Alderw.) Holttum

Mesopteris kiauensis (C. Chr.) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Dryopteris kiauensis* C. Chr., Dansk Bot. Ark. 9:64. 1937.—*Amphineuron kiauense* (C. Chr.) Holttum

***Mesopteris paraphysophora** (Alderw.) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Dryopteris paraphysophora* Alderw., Bull. Jard. Bot. Buitenzorg., sér. 3, 2:143. 1920.—*Amblovenatum paraphysophorum* (Alderw.) Parris—*Amphineuron paraphysophorum* (Alderw.) Holttum

***Mesopteris pseudostenobasis** S.E. Fawc. & A.R. Sm., **comb. nov.**—*Dryopteris pseudostenobasis* Copel., J. Arnold Arbor. 10:176. 1929.—*Amblovenatum pseudostenobasis* (Copel.) C.W. Chen—*Amphineuron pseudostenobasis* (Copel.) Holttum—*Thelypteris pseudostenobasis* (Copel.) C.F. Reed

Constituent species.—*Mesopteris attenuata* (Kuntze) S.E. Fawc. & A.R. Sm.; **M. ceramica* (Alderw.) S.E. Fawc. & A.R. Sm.; *M. kiauensis* (C. Chr.) S.E. Fawc. & A.R. Sm.; **M. paraphysophora* (Alderw.) S.E. Fawc. & A.R. Sm.; *M. pseudostenobasis* S.E. Fawc. & A.R. Sm.; **M. tonkinensis* (C. Chr.) Ching

METATHELYPTERIS

Metathelypteris (H. Ito) Ching, Acta Phytotax. Sin. 8:304. 1963.—*Thelypteris* sect. *Metathelypteris* H. Ito, in Nakai & Honda—Type: *Metathelypteris gracilescens* (Blume) Ching [= *Aspidium gracilescens* Blume]

For additional synonymy see Lin et al. (2013).

Etymology.—Gr. *meta*, near, close to + *Thelypteris*. This genus is a distinct from, but close to, *Thelypteris*.

Plants terrestrial, small to medium-sized, usually 35–100 cm tall; **rhizomes** short-creeping to suberect or erect, often with tufted fronds; **fronds** monomorphic, arching to erect, pinnate-pinnatifid to barely bipinnate and with adnate pinnules (e.g., *M. flaccida*); **stipes** green when living, stramineous or reddish-flushed with age, scaly only at bases, scales tan to brown, mostly 2–7 mm long, lanceolate, bearing short acicular hairs on margins and on surfaces; **blades** membranaceous to chartaceous, ovate-deltate to lanceolate, proximal pinnae not or only slightly reduced, apices confluent, gradually tapering; **pinnae** opposite or subopposite, often becoming alternate distally, sessile, usually deeply lobed to ca. 1 mm from costae; rachises hairy to sometimes glabrescent, lacking vegetative buds, with acicular hairs; **veins** free, simple (*M. gracilescens*) or often forked in ultimate segments, with thickened ends (seen adaxially) ending short of segment margins; costae adaxially prominent, not grooved; **aerophores** absent; **indument abaxially** on axes (rachises, costae, costules, and veins) and sometimes on laminar tissue of acicular, unicellular hairs and/or stipitate glands, lacking spherical or hemispherical glands and scales; **indument adaxially** generally lacking, except along rachis and costae, but if present hairlike (uniseriate); **sori** round, often near tips of veins, and on acroscopic branch of forked veins, indusiate, indusia round-reniform, thin, glabrous or with short setulae and/or stipitate glands on margins and sometimes on surfaces; **sporangia** short-stalked, glabrous or sometimes bearing hairs of several cells on stalks, lacking glands and hairs on sporangial capsules; **spores** dark brown, with irregular, variously anastomosing ridges; $x = 31$ (*M. uraiensis*), 34 (*M. gracilescens*), 35 (*M. dayi*, *M. flaccida*, *M. singalanensis*), and 36 (*M. laxa*) (6 spp. counted), both diploids and tetraploids known. A base number of $x = 35$ is the predominant report (three species), and other base numbers need verification, as there are several cases of conflicting reports within a species.

Diagnosis.—*Metathelypteris* differs from *Amauropelta* (which see for additional discussion) and *Coryphopteris* in the costae and rachis lacking adaxial grooves, veins not reaching the segment margins (viewed adaxially), laminae truncate with proximal pinnae not greatly reduced (a characteristic shared with most members of *Coryphopteris*), and $x =$ usually 35 (vs. $x = 27$, 29, 31, 32, 33, rarely 35). There are also similarities with some species in the phegopteroid clade (*Phegopteris*, *Macrothelypteris*, *Pseudophegopteris*, which mostly lack or have relatively small indusia (as sometimes in *Macrothelypteris*), generally have larger, more broadly deltate, and more divided blades, and have different chromosome base numbers ($x = 30$, or 31, vs. $x =$ usually 34 or 35 in *Metathelypteris*. *Metathelypteris* shares with the phegopteroid genera the characteristics of often-forked veins that end before reaching the margin, the costae and main rachis adaxially lacking grooves, and generally the lack of reduced proximal pinnae.

Biogeography and ecology.—*Metathelypteris* comprises ca. 17 species, distributed from Bioko and São Tomé (both having endemic species), tropical Africa and South Africa (Holttum 1982; Pichi Sermolli 1983) and Madagascar, to India, Sri Lanka, China, continental southeast Asia, southern Japan, and Malesia, east to the Solomon Islands. It is most diverse in continental Asia, while seemingly absent from most of Melanesia, Australia, New Zealand, and all of Polynesia. Species occur in middle elevation forests, from ca. 1000–2000 m, often on steep earthy slopes or among rocks, occasionally in somewhat open places (*M. flaccida*), especially along trails.

Taxonomic and phylogenetic studies.—Ching (1963) first recognized *Metathelypteris* as a genus, and Holttum (1971) adopted a similar circumscription. Holttum (1976a, 1982) later expressed belief that *Metathelypteris* was most closely related to *Macrothelypteris* and especially *Pseudophegopteris*, agreeing with these genera in having free, often forking veins that end before reaching the segment margins and costae lacking adaxial grooves. Despite these morphological similarities, molecular evidence suggests that *Metathelypteris* is sister to *Amauropelta s.l.* (including *Parathelypteris s.s.*), with *Coryphopteris* sister to *Metathelypteris* + *Amauropelta* (He & Zhang 2012; Almeida et al. 2016; Fawcett et al. in press), and not ancestral to the phegopteroid clade, as Holttum (1976a) thought.

Notes.—Fraser-Jenkins et al. (2017) recently synonymized *M. deltoideofrons* Ching ex W.M. Chu & S.G. Lu under *M. decipiens*, *M. krameri* Sarn. Singh & Panigrahi under *M. flaccida*, and *M. tibetica* Ching & S.K. Wu under *M. uraiensis*. We have seen scant material of these heterotypic synonyms, but tentatively accept their conclusions, pending a much-needed modern monograph of *Metathelypteris*.

Constituent species.—**Metathelypteris adscendens* (Ching) Ching; *M. burrowsiorum* N.R. Crouch; *M. dassanayakei* (Fraser-Jenk.) Ranil; **M. dayi* (Bedd.) Holttum; *M. decipiens* (C.B. Clarke) Ching; **M. flaccida* (Blume) Ching; *M. fragilis* (Baker) Holttum; ***M. glandulifera* Ching ex K.H. Shing; *M. glandulosa* (H.G. Zhou & H. Li; **M. gracilescens* (Blume) Ching; ***M. hattori* (H. Ito) Ching; **M. laxa* (Franch. & Sav.) Ching; *M. petiolulata* Ching ex K.H. Shing; ***M. singalanensis* (Baker) Ching; **M. uraiensis* (Rosenst.) Ching; *M. vandervekenii* Pic.Serm.; *M. wuyishanica* Ching.

OREOPTERIS

Oreopteris Holub, Folia Geobot. Phytotax. 4:46. 1969.—Type: *Oreopteris limbosperma* (All.) Holub [= *Polypodium limbospermum* All.]

Thelypteris subg. *Lastrea* (Hook.) Alston, J. Wash. Acad. Sci. 48:232. 1958.

Etymology.—Gr. *oreos*, mountain + *pteris*, fern. A fern of the mountains.

Plants terrestrial, mostly (15–)25–100 cm tall; **rhizomes** brown, suberect or erect, 5–10 mm diam. (excluding old stipe bases); **fronds** seasonal, dying back in winter, crowded and tufted, pinnate-pinnatifid, monomorphic, arching; **stipes** stramineous to tan above the base; **stipe scales** persistent, light brown to stramineous, thin, ovate to lanceolate, these lacking acicular hairs but marginally papillose; **blades** chartaceous, drying yellowish green, elliptic or oblanceolate, middle pinnae the longest, with 5–10 pairs of proximal pinnae gradually reduced, basal pair(s) sometimes auriculiform or glanduliform and ca. 2–10 mm long, blade apex gradually tapered, with distal pinnae not decurrent, proliferous buds absent; **rachises** stramineous to pale castaneous (*O. elwesii*), usually with persistent ovate to lanceolate, glabrous scales abaxially, sometimes with hyaline acicular, unicellular hairs 0.2–0.4 mm long; **pinnae** sessile or nearly so, grooved adaxially, lobed about halfway to costae (*O. elwesii*) to deeply pinnatifid to ca. 1 mm or less from costa, sometimes with basal acroscopic crenulate-margined auricles, on basal segments on both sides somewhat elongate; **veins** (3–)5–12 pairs per segment, simple or 1-forked, usually prominent abaxially and adaxially, lowermost pair from adjacent segments running to margin just above sinus between adjacent lobes, veins ending at pinna margins or nearly so; **aerophores** absent or distinctly swollen (*O. elwesii*); **indument abaxially** along costae of tan, linear, lanceolate or ovate scales, also sometimes with acicular hairs along costae, veins and tissue between veins usually lacking hairs (except near costae) or nearly so, sometimes (in *O. limbosperma*) with numerous yellowish to occasionally orangish spherical glands ca. 0.1 mm diam., **indument adaxially** lacking or of hyaline acicular hairs on rachises and costae, sometimes also with short hairs or stipitate glands on and between veins, hairs on stipes and rachises 0.1–0.3 mm long, sparse to moderately dense, hairs if present single-celled; **pustules** absent on laminar tissue; **sori** inframarginal or medial, round, indusiate, indusia round-reniform, tan, persistent, glabrous or sometimes bearing minute capitate hairs, marginally toothed; **sporangia** glabrous or sometimes bearing glands; **spores** pale brown, echinate or with prominent irregular ridges that form a coarsely reticulate network (Tryon & Lugardon 1991); $x = 34$ (unique within the family), all three species counted, only diploids known; intrageneric and intergeneric hybrids unknown.

Diagnosis.—*Oreopteris* is distinguished from *Thelypteris s.s.* by having suberect to erect rhizomes (vs. long-creeping); presence of persistent scales on the stipes, rachises, and sometimes on the costae abaxially; thin, glabrous stipe base scales; proximal pinnae gradually reduced (vs. proximal pinnae not reduced); sessile (vs. short-stalked), broader pinnae; and base chromosome number of $x = 34$ (vs. $x = 35$). The two genera also occur in different habitats. Holub (1969) discussed at length the characteristics distinguishing *Oreopteris* from *Thelypteris s.s.*, but was unaware of a third species of *Oreopteris*, *O. elwesii*. From most *Coryphopteris*, which also usually has erect caudices, *Oreopteris* differs by the gradually reduced proximal pinnae, glabrous scales, and veins sometimes forked; *Amauropelta* subgenera *Parathelypteris* and *Venus*, both predominantly Asian, differ in the very narrow, almost filamentous long-creeping rhizomes. *Oreopteris* has reduced proximal pinnae similar to many *Amauropelta* spp., but very different spore ornamentation (echinate or broadly ridged vs. reticulate and perforate in *Amauropelta*; Wood 1973; Tryon & Lugardon 1991: fig. 149.24–149.26). All necessary combinations have been made in *Oreopteris* by Holub (1969) and by Holttum (1981).

Biogeography and *ecology.*—*Oreopteris* comprises three species, *O. limbosperma* of Eurasia, *O. quelpartensis* (Christ) Holub (often spelled *quepaertensis*) of eastern Asia and North America, and *O. elwesii* (Baker) Holttum (Holub 1969; Holttum 1971), confined to Sikkim (northeastern India) and Yunnan, China (Lin & Iwatsuki 2013). In North America, *O. quelpartensis* is noticeably disjunct, with western populations in Alaska, British Columbia, and Washington, and eastern populations in Newfoundland (Bouchard & Hay 1976; Smith 1993a). Species occur from near sea level to ca. 1800 m (–3100 m for *O. elwesii*). Species of *Oreopteris* are generally found in open, rocky woods and subalpine meadows, along streams, and in ditches in acidic soils.

Taxonomic and phylogenetic studies.—Ching (1963) was the first to recognize the two boreal species now recognized in *Oreopteris* as close relatives, treating them together within the genus *Lastrea* Bory. The name *Lastrea* historically has been variously applied to a great diversity of ferns with free veins, but Holub (1969) pointed out that the name was illegitimate because it was published with a list of type species that included the type of the earlier name *Thelypteris*. Accordingly, he proposed the name *Oreopteris* as a replacement for *Lastrea* sensu Ching. Holttum (1974e) later expanded the circumscription of the genus to include *Oreopteris elwesii*.

Most recent floras and fern classifications have followed Holub (1969) and Holttum (1981) in recognizing *Oreopteris* as distinct, e.g., Lin & Iwatsuki (2013), PPG I (2016). Older floras, e.g., *Flora Europaea* (1964) and *Flora of North America North of Mexico* (1993a), and classifications (e.g., Smith et al. 2006) often subsume *Oreopteris* in a broadly defined genus *Thelypteris*.

Oreopteris elwesii is rare in collections, poorly known, and divergent from the other two species on the basis of the following characteristics: short-creeping rhizomes (vs. erect or suberect); pale-castaneous stipe and rachis (vs. stramineous); distal portion of stipe and rachis lacking scales; swollen aerophores (vs. aerophores absent); narrower, less deeply incised pinnae (ca. ½ vs. ca. ⅘ their width or more); and its occurrence at higher elevation. The main characteristic keeping it in *Oreopteris* is its base chromosome number, $x = 34$. In the sum of its features, it resembles more some species of *Amauropelta*, which is an unlikely affinity on the basis of both geography and cytology ($x = 29$ in all *Amauropelta* subg. *Amauropelta*). Further study is needed to confirm placement of this unique taxon in the genus. *Oreopteris quelpartensis* in Asia and North America appears to lack the large, yellow, spherical glands that characterize most specimens of *O. limbosperma* from Europe, which is sometimes described as lemon-scented (Jermy 1964); most specimens of *O. quelpartensis* from North America are devoid, or nearly so, of acicular hairs of the sort found in most specimens of *O. limbosperma*. Holttum (1981) provided a key distinguishing the three known species.

In broadly based molecular analyses (He & Zhang 2012; Almeida et al. 2016; Patel et al. 2019a; Fawcett et al. in press), *Oreopteris* is sister to the entire cyclosoroid clade, including all christelloids, goniopteroids, and stegnogrammoids (**Fig. 1**). Holttum (1981) opined that *Oreopteris* was most closely related to *Amauropelta*, but in our analysis (Fawcett et al. in press), *Amauropelta* falls within the amauropeltoid clade, which is sister to all cyclosoroid genera plus *Oreopteris*. Both morphological and molecular evidence suggest that *Oreopteris* is nearly as evolutionarily isolated as *Thelypteris s.s.*, and neither genus is closely related to any element in the diverse cyclosoroid or amauropeltoid clades.

Constituent species.—*Oreopteris elwesii* (Hook. & Baker) Holttum; **O. limbosperma* (All.) Holub; **O. quelpartensis* (Christ) Holub

PAKAU

Pakau S.E. Fawc. & A.R. Sm., **gen. nov.**—Type: *Pakau pennigera* (G. Forst.) S.E. Fawc. & A.R. Sm. [= *Polypodium pennigerum* G. Forst., Fl. Ins. Austr. Prodr. 82. 1786.]

For complete species synonymy see Brownsey et al. (1985).

Etymology.—Pākau, or pākauroharoha, is the common name for this fern in the Māori language. The word may also refer to wing (Moorfield 2019), similar to the dual meanings of the Greek word *pteris* (fern or feather).

Plants large and terrestrial, from < 0.5 m to > 2.5 m in height; **rhizomes** sometimes forming massive erect caudices to 1 m tall, or decumbent; **fronds** monomorphic, pinnate-pinnatifid, arching; **stipes** light brown, with brown ovate to lanceolate glabrous scales on stipe bases; **blades** membranaceous to chartaceous, drying dull green, ovate to lanceolate; two to five pairs of proximal pinnae gradually reduced, the lowest 1–4(–6) cm long (never rudimentary or glanduliform); **pinnae** opposite or subopposite (**Fig. 7F**), even towards blade apex, grooved adaxially, (10–)15–30 pairs, lobes oblique, rounded with crenulate margins, incised halfway or a little more to costae, proximal pinnae frequently auricled, with acroscopic auricles often secondarily lobed; costules 5–7 mm apart; **veins** commonly about 6–9 pairs per segment, prominent both adaxially and abaxially, generally with one pair anastomosing below cartilaginous sinuses (sometimes forming a whitish, protruding apophysis to 0.5 mm long abaxially), and a second vein pair running to the sinus; **aerophores** absent; **indument abaxially** of brown, often lustrous, ovate to deltate scales (to 1 mm wide and about as long) along rachis and costae (**Fig. 7E**), hairs sparse and short, unicellular, acicular or capitate on costae, or lacking; **indument adaxially** of arching reddish brown hairs on rachis and costae, the hairs directed toward pinna and blade tips, short sparse capitate or acicular hairs present on costae, generally lacking on secondary veins and laminae; **pustules** absent; **sori** inframedial, exindusiate, the basal pair or two on each segment (larger fronds) often oval, to twice as long as wide (**Fig. 7E**); **sporangia** unadorned, each with a short stalk ca. 1/4–1/2 the capsule length; **spores** black, with small, irregular wings; $x = 36$, $2n = 144$ (only tetraploids known).

Diagnosis.—*Pakau* may be easily distinguished from *Christella* and *Macrothelypteris* by its essentially glabrous laminae, and from *Cyclosorus interruptus* by its erect or decumbent rhizomes (vs. long-creeping). *Pakau* differs from other segregates of *Pneumatopteris* in having persistent ovate to deltate scales on the abaxial costae, lack of aerophores at pinna bases, non-pustular laminae, laminae with proximal pinnae gradually reduced but lacking rudimentary pinnae, and black spores. Another distinctive feature of *Pakau* is its opposite pinnae; although some other Thelypteridaceae have opposite or subopposite proximal pinnae, these usually transition to an alternate arrangement towards the frond apex. The lobing of the acroscopic auricles on the pinna bases is also characteristic and unusual within the family (but see *Pelazoneuron patens*, and some *Christella* spp.). Holttum (1971:43) thought *Pneumatopteris pennigera* was possibly related to a species that we here treat as *Menisorus*, *Goniopteris madagascariensis* Fée (= *Pneumatopteris unita* (Kunze) Holttum), from Africa (Holttum 1974a). Molecular evidence (Fawcett et al. in press) suggests the two species diverged successively from the backbone of the phylogeny and are on long branches (**Fig. 1**).

Biogeography and ecology.—This monotypic genus is restricted to New Zealand, southeastern Australia, and Tasmania (Brownsey & Perrie 2016). *Pakau pennigera* is a plant of lowland (< 800 m), relatively undisturbed rain forests, especially of dark, heavily shaded gullies. It stands apart from other genera in the family in having a strictly austral distribution, but it does not extend to frost-prone latitudes. Fossil evidence suggests that *Pakau*, or its close relatives, were present in New Zealand at least since the early Miocene (Pole 1992).

Taxonomic and phylogenetic studies.—*Pakau* has been treated most recently in the genus *Pneumatopteris* (Holttum 1971, 1973a, 1974a, 1977b; Brownsey & Smith-Dodsworth 1989: fig. 112 A-B; Bostock 1998: fig. 121F-G), but even with this placement, Holttum realized that this species was somewhat apart from other *Pneumatopteris* in the exindusiate sori, presence of costal scales, and absence of rudimentary proximal pinnae. The highly polyphyletic genus *Pneumatopteris* is recircumscribed in the present work; see the *Pneumatopteris* treatment for further details. Based on recent molecular phylogenetic evidence (Fawcett et al. in press), *Pakau* is quite distinct from any extant genus of Thelypteridaceae; it resolves on a long branch, sister to the rest of the christelloid clade, which is a subclade of the cyclosoroid genera (including *Christella*, *Plesioneuron*, *Pneumatopteris*, *Pronephrium, Pseudocyclosorus*, and *Sphaerostephanos*) all sensu Holttum (1971), as well as a half dozen smaller genera (**Fig. 1**). The christelloid genera are almost exclusively Old World, primarily restricted to southeastern and southern Asia, Malesia, Melanesia, and Polynesia, with the exception of the three earliest-diverging lineages: The New Zealand and Australian *Pakau*, African *Menisorus*, and neotropical/subtropical *Pelazoneuron*.

New combination and constituent species.—

***Pakau pennigera** (G. Forst.) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Polypodium pennigerum* G. Forst., Fl. Ins. Austr. Prodr. 82. 1786.—*Cyclosorus pennigerus* (G. Forst.) Ching—*Pneumatopteris pennigera* (G. Forst.) Holttum—*Thelypteris pennigera* (G. Forst.) H.H. Allan (**Figs. 7E, 7F**).

PELAZONEURON

Pelazoneuron (Holttum) A.R. Sm. & S.E. Fawc., **gen. et stat. nov.**—*Christella* sect. *Pelazoneuron* Holttum, J. S. African Bot. 40:144. 1974.—Type: *Pelazoneuron patens* (Sw.) A.R. Sm. & S.E. Fawc. [= *Polypodium patens* Sw.]

For more complete synonymy, see Smith (1971).

Etymology.—Gr. *pelazo*, to approach + *neuron*, vein, in reference to the connivent veins at or just below the sinus, which are near each other, rather than anastomosing at an obtuse angle, as in *Christella s.s.* and many other related genera.

Plants terrestrial, or occasionally in rocky crevices, medium-sized to very large (fronds 40–250 cm long); **rhizomes** short- to long-creeping, or, in a few species, suberect to erect and forming small upright trunks (e.g., *P. patens*); **fronds** monomorphic, pinnate-pinnatifid, erect or arching; **stipes** stramineous to tan, darkened at the very base, adaxially grooved, bearing scales at the base like those of rhizome apices; **stipe scales** lanceolate to occasionally ovate-lanceolate, brown, setose on margins and surfaces, occasionally the scales ovate-lanceolate and glabrous (e.g., the type, *P. patens*); **blades** chartaceous to subcoriaceous, drying greenish, pinnae generally pinnatifid or pinnatisect, proximal ones the longest or nearly so, very rarely greatly reduced, distal ones gradually or sometimes abruptly reduced, blade apex not conform or rarely subconform (*P. serra*); rachises always lacking proliferous buds; **pinnae** opposite or nearly so proximally, becoming alternate distally, adaxially with a groove that is not continuous with the rachis groove, shallowly to often deeply pinnatifid; **veins** usually prominent on both sides, one or sometimes two pairs from adjacent segments connivent at an acute angle at or very slightly below the sinus (**Fig. 7D**), or the distal one or a pair meeting segment margin just above the sinus (veins not forming areoles) (**Fig. 7C**), rarely with a single pair truly obtusely united below the sinus and with an excurrent vein running to sinus, vein endings reaching segment margins; **aerophores** absent at pinna bases, or pinnae with a slightly raised and darkened lunate ridge at attachment to rachis; **indument abaxially** of stipes, rachises, costae, veins, and sometimes laminar tissue between veins of hyaline acicular, unicellular hairs, blades sometimes glabrescent with age, or blades sometimes lacking hairs on the lesser veins and between veins, most species lacking costal scales, but these scattered or more numerous in a few species (e.g., *P. serra*, *P. augescens, P. tuerckheimii*); **indument adaxially** of generally long (> 0.5 mm) hyaline, unicellular acicular hairs on stipes, rachises, and costae, sometimes also on veins, and in a few species (e.g., *P. kunthii*) with scattered hairs between veins; **pustules** absent on laminar tissue on both sides; **sori** medial or nearly so, not usually coalescent at maturity, indusiate, indusia glabrous to usually setose and somewhat persistent; **sporangia** without setulae or glands on the capsules, or each with a small clavate unicellular colorless glandular cell on the stalk; **spores** dark brown, with perispore variously ridged, rugose, or echinulate; *x* = 36 (10 of 16 spp. counted), diploids and tetraploids known, and several interspecific hybrids (Smith 1971).

Diagnosis.—*Pelazoneuron* differs from *Christella* in having the lowermost veins from adjacent segments connivent at an acute angle at the sinuses (vs. united at an obtuse angle below the sinus and with an excurrent vein to the sinus) and in having the proximal pinnae the longest or nearly so. *Pelazoneuron* differs from *Pseudocyclosorus*, which has similar venation, in the deltate blades with proximal pinnae the longest, or nearly so (vs. many pairs of abruptly reduced proximal pinnae). *Pelazoneuron* differs from many other cyclosoroid genera in one or often more of the following characteristics: lack of protruding aerophores at pinna bases; relatively large, ± persistent indusia; lack of areolate venation and included veinlets; monomorphic fronds; lack of laminar buds; lack of sessile, resinous glands on veins and laminar tissue; generally long-creeping rhizomes; and somewhat weedy nature in semi-open habitats.

Biogeography and ecology.—The 16 known species and four varieties are restricted to the New World tropics and subtropics, from the southern U.S.A. through the Antilles, Mexico, Central America, and South America to northern Argentina, Paraguay, Uruguay, and Bolivia (Smith 1971); one species (*P. kunthii*) is known to be naturalized in Spain and perhaps East Africa. Most species are at least locally common, if not weedy, and occur at low to middle elevations, to ca. 2600 m in the tropics, and are found along roadsides, trails, ditches, ravines, and limestone outcrops, often in slightly disturbed, somewhat open places.

Taxonomic and phylogenetic studies.—Holttum described *Christella* sect. *Pelazoneuron* in his treatment of the Thelypteridaceae of Africa (1974a) and considered most African species of *Christella* to belong to this section, in addition to many of the neotropical species; he selected one of these, *Christella patens*, as the type. Molecular data have shown *Pelazoneuron* to be rather distantly related to *Christella* (Smith & Cranfill 2002; Almeida et al. 2016; Patel et al. 2019a; Fawcett et al. in press). Other neotropical genera of the family (*Amauropelta*, *Cyclosorus*, *Goniopteris*, *Meniscium*, *Stegnogramma*, and *Steiropteris*) are also distantly related to *Pelazoneuron*, which is sister to a large clade that includes predominantly paleotropical genera. Although molecular data are not available for many African species of *Christella*, we find evidence that African members of *Christella* sect. *Pelazoneuron* sensu Holttum (e.g., *C. chaseana* and *C. gueinziana*) are more closely allied to *Christella s.s.* and *Pseudocyclosorus* than to the type of *Pelazoneuron* (Fawcett et al. in press). Our circumscription of the genus is largely as treated in Smith (1971) as *Thelypteris* sect. *Cyclosorus*, with the exclusion of a few species that are now placed in other genera. Among the neotropical taxa in that treatment, three are now included in *Christella* (*C. conspersa, C. dentata*, *C. hispidula*), one in *Cyclosorus s.s.* (*C. interruptus*), and another, the widely naturalized species *Thelypteris opulenta*, is now placed in the paleotropical genus *Amblovenatum*. All of the American species now placed in *Christella*, *Cyclosorus*, and *Amblovenatum* have the lowermost veins from adjacent segments truly united at an obtuse angle below the sinuses, producing an excurrent vein from this union that runs to the sinus, a condition largely absent in *Pelazoneuron*.

Notes.—Based on phylogenetic analyses (Fawcett et al. in press), two varieties, *Pelazoneuron ovatum* var. *lindheimeri* and *Thelypteris patens* var. *dissimilis*, are not sister to the typical varieties of their species. We refrain from making a combination for the latter, pending further study, but do provide one for *P. ovatum* var. *lindheimeri*. Additionally, Smith (1971) hypothesized that *P. kunthii* may be of hybrid origin, involving *Christella hispidula* and *Pelazoneuron ovatum*, based on its intermediate morphology (e.g., hairs on adaxial laminae between veins, and some veins anastomosing). Although this taxon is recovered with high support as a member of the *Pelazoneuron* clade in both concatenated and coalescent analyses (Fawcett et al. in press), we do find support for the hypothesis proposed by Smith (1971) based on the discordant topologies of individual gene trees. Two other taxa in the *Pelazoneuron* clade, *Thelypteris patens* var. *dissimilis* and *P. schizotis,* exhibit similar patterns of discordance, and all three taxa are currently the subject of further investigation.

New combinations, constituent species and intraspecific taxa.—

Pelazoneuron abruptum (C. Presl) A.R. Sm. & S.E. Fawc., **comb. nov.**—*Lastrea abrupta* C. Presl, Tent. Pterid. 75. 1836.—*Christella abrupta* (C. Presl) A.R. Sm.—*Thelypteris grandis* A.R. Sm. var. *kunzeana* (C. Chr.) A.R. Sm. (non *Thelypteris abrupta* (Desv.) Proctor)

Pelazoneuron abruptum (C. Presl) A.R. Sm. & S.E. Fawc. var. **pallescens** (C. Chr.) A.R. Sm. & S.E. Fawc., **comb. nov.**—*Dryopteris oligophylla* Maxon var. *pallescens* C. Chr., Kongel. Danske Vidensk. Selsk. Skr., Naturvidensk. Math. Afd., ser. 7, 10:188. 1913.—*Thelypteris grandis* A.R. Sm. var. *pallescens* (C. Chr.) A.R. Sm.

***Pelazoneuron abruptum** (C. Presl) A.R. Sm. S.E. Fawc. var. **grande** (A.R. Sm.) A.R. Sm. & S.E. Fawc., **comb. nov.**—*Thelypteris grandis* A.R. Sm., Univ. Calif. Publ. Bot. 59:76. 1971.

Pelazoneuron albicaule** (Fée) A.R. Sm. & S.E. Fawc., **comb. nov.—Aspidium albicaule* Fée, Mém. Foug. 8:102. 1857.—*Thelypteris albicaulis* (Fée) A.R. Sm.

Pelazoneuron augescens** (Link) A.R. Sm. & S.E. Fawc., **comb. nov.—Aspidium augescens* Link, Fil. Spec. 103. 1841.—*Christella augescens* (Link) Pic.Serm.—*Thelypteris augescens* (Link) Munz & I.M. Johnst.

***Pelazoneuron berroi** (C. Chr.) A.R. Sm. & S.E. Fawc., **comb. nov**.—*Dryopteris berroi* C. Chr., Kongel. Danske Vidensk. Selsk. Skr., Naturvidensk. Math. Afd., ser. 7, 10185. 1913.—*Christella berroi* (C. Chr.) Salino & A.R. Sm.—*Thelypteris berroi* (C. Chr.) C.F. Reed

Pelazoneuron blepharis (A.R. Sm.) A.R. Sm. & S.E. Fawc., **comb. nov.**—*Thelypteris blepharis* A.R. Sm., Proc. Calif. Acad. Sci, ser. 4, 40:227, f. 7F-H. 1975.

***Pelazoneuron clivale** (A.R. Sm.) A.R. Sm. & S.E. Fawc., **comb. nov.**—*Thelypteris clivalis* A.R. Sm., Fieldiana, Bot., n.s., 29:45. 1992.—*Christella clivalis* (A.R. Sm.) A.R. Sm.—*Thelypteris grandis* A.R. Sm. var. *aequatorialis* (C. Chr.) A.R. Sm.

Pelazoneuron cretaceum (A.R. Sm.) A.R. Sm. & S.E. Fawc., **comb. nov.**—*Thelypteris cretacea* A.R. Sm., Univ. Calif. Publ. Bot. 59:92. 1971.—*Christella cretacea* (A.R. Sm.) Á. Löve & D. Löve

Pelazoneuron depilatum (A.R. Sm.) A.R. Sm. & S.E. Fawc., **comb. nov.**—*Thelypteris depilata* A.R. Sm., Fieldiana, Bot., n.s., 29:45. 1992.

***Pelazoneuron kunthii** (Desv.) A.R. Sm. & S.E. Fawc., **comb. nov.**—*Nephrodium kunthii* Desv., Mém Soc. Linn. Paris 6:258. 1827.—*Thelypteris kunthii* (Desv.) C.V. Morton.

Dryopteris normalis C. Chr., Ark. Bot. 9:31. 1910.—*Christella normalis* (C. Chr.) Holttum—*Thelypteris normalis* (C. Chr.) Moxley

Pelazoneuron lanosum (C. Chr.) A.R. Sm. & S.E. Fawc., **comb. nov.**—*Dryopteris patens* (Sw.) Kuntze var. *lanosa* C. Chr., Kongel. Danske Vidensk. Selsk. Skr., Naturvidensk. Math. Afd., ser. 7, 10:180. 1913.—*Christella lanosa* (C. Chr.) Á. Löve & D. Löve—*Thelypteris lanosa* (C. Chr.) A.R. Sm.

***Pelazoneuron ovatum** (R.P. St.John) A.R. Sm. & S.E. Fawc., **comb. nov.**—*Thelypteris ovata* R.P. St.John, Ferns SE States 239. 1938.—*Christella ovata* (R.P. St.John) Á. Löve & D. Löve—*Dryopteris ovata* (R.P. St.John) Broun

***Pelazoneuron ovatum** (R.P. St.John) A.R. Sm. & S.E. Fawc. var. **lindheimeri** (C. Chr.) A.R. Sm., **comb. nov.**—*Dryopteris normalis* C. Chr. var. *lindheimeri* C. Chr., Kongel. Danske Vidensk. Selsk. Skr., Naturvidensk. Math. Afd., ser. 7, 10:182. 1913.—*Thelypteris ovata* var. *lindheimeri* (C. Chr.) A.R. Sm.

***Pelazoneuron patens** (Sw.) A.R. Sm. & S.E. Fawc., **comb. nov.**—*Polypodium patens* Sw., Prodr. 133. 1788.—*Christella patens* (Sw.) Holttum—*Thelypteris patens* (Sw.) Small (**Fig. 7C**)

Pelazoneuron puberulum (Baker) A.R. Sm. & S.E. Fawc., **comb. nov.**—*Aspidium puberulum* Fée, Mém. Foug. 10:40. 1865, non Gaudich. 1827.—*Nephrodium puberulum* Baker in Hook. & Baker, Syn. Fil., ed. 2., 495. 1874.—*Christella puberula* (Baker) Á. Löve & D. Löve—*Dryopteris puberula* (Baker) Kuntze

***Pelazoneuron puberulum** (Baker) A.R. Sm. & S.E. Fawc. var. **sonorense** (A.R. Sm.) A.R. Sm. & S.E. Fawc., **comb. nov.**—*Thelypteris puberula* (Baker) C.V. Morton var. *sonorensis* A.R. Sm., Univ. Calif. Publ. Bot. 59:91. 1971.

***Pelazoneuron schizotis** (Hook.) A.R. Sm. & S.E. Fawc., **comb. nov.**—*Nephrodium schizotis* Hook., Sp. Fil. 4:107. 1862.—*Christella schizotis* (Hook.) A.R. Sm.—*Thelypteris schizotis* (Hook.) M. Kessler & A.R. Sm.

Thelypteris patens (Sw.) A.R. Sm. var. *smithiana* Ponce

***Pelazoneuron serra** (Sw.) A.R. Sm. & S.E. Fawc., **comb. nov.**—*Polypodium serra* Sw., Prodr. 132. 1788.—*Christella serra* (Sw.) Holttum—*Thelypteris serra* (Sw.) R.P. St.John. (**Fig. 7D**).

***Pelazoneuron tuerckheimii** (Donn.Sm.) A.R. Sm. & S.E. Fawc., **comb. nov.**—*Nephrodium tuerckheimii* Donn.Sm., Bot. Gaz. 12:133, t. 11. 1887.—*Thelypteris tuerckheimii* (Donn.Sm.) C.F. Reed

PHEGOPTERIS

Phegopteris (C. Presl) Fée, Mém. Foug. 5:242–243. 1852.—Lectotype (designated by Ching, Acta Phytotax. Sin. 8(4):312. 1963): *Phegopteris polypodioides* Fée (based on *Polypodium phegopteris* L.) [= *Phegopteris connectilis* (Michx.) Watt]

Lastrella (H. Ito in Nakai & Honda) Nakai
For additional synonymy, see Holttum (1969).

Etymology.—Gr. *phegos*, beech + *pteris*, fern, a fern of beech forests.

Plants terrestrial, small to medium-sized (20–60 cm); **rhizomes** long-creeping, branching, subterranean, or short, ascending, or erect, with pale to brown, ovate scales with marginal hairs; **fronds** monomorphic, erect to arching; **stipes** dull-stramineous, terete to shallowly grooved adaxially; **stipe scales** stramineous to brown, ovate to lanceolate with marginal setulae; **blades** chartaceous to membranaceous, deciduous, with no clear articulations, broadly ovate-deltate, broadest at or near base of lamina (e.g., *P. hexagonoptera*) or lanceolate, tapering towards apex and base (*P. decursive-pinnata*), pinnate-pinnatifid to nearly bipinnate (e.g., *P. koreana*), with alate rachises (sometimes proximal pinna-pairs free), these often with small, vascularized extensions of laminar tissue connecting adjacent pinnae; **pinnae** deeply lobed, segments entire, or with crenate to lobed margins, pinna-bases adnate, with decurrent wings to next pinna-pair, sometimes bases of proximal one or two pinna-pairs narrowed and sessile (e.g., *P. connectilis*); **veins** free, often forking, reaching margin of lamina, or terminating near margin; **aerophores** absent; **indument abaxially and adaxially** of hyaline acicular hairs and narrow, hyaline, lanceolate scales with setulose margins, borne on rachises, costae, veins, and laminar tissue, or restricted to axes; **pustules** absent; **sori** medial, discrete, exindusiate, rarely with small indusium; **sporangia** sometimes with acicular or capitate hairs; **spores** smooth with essentially no ornamentation (e.g., *P. decursive-pinnata*), a low reticulum, or tubercules (Patel et al. 2019a; Kim et al. 2004), also with an adnate perine (a feature apparently unique within the family (Tryon & Lugardon 1991)); $x = 30$, with diploids, triploids, and tetraploids known, based on counts of five of the six species. For *Phegopteris decursive-pinnata*, all three cytotypes have been reported, suggesting further study is needed. *Phegopteris connectilis* is predominantly triploid throughout its circumboreal distribution, though diploid cytotypes are known from Japan (Matsumoto 1982). The North American allotetraploid, previously treated within *P. connectilis*, has been segregated as *Phegopteris excelsior* (Patel et al. 2019b). Apomixis is known to occur in *P. excelsior*, and both apomictic and sexual populations of *P. connectilis* and *P. decursive-pinnata* are reported. Although no hybrids are known, there is compelling evidence for hybrid speciation (Driscoll et al. 2003; Patel et al. unpubl. data). See Chandra (1963, 1974) for illustrations of anatomy and microscopic features.

Diagnosis.—The primarily north-temperate and montane *Phegopteris* may be distinguished from its mostly tropical sister genus, *Pseudophegopteris*, and closely related tropical genus *Macrothelypteris* by the adnate pinna-bases, and winged rachises with vascularized projections between pinnae (vs. pinnae mostly free, with only the distal pinnae adnate). Additionally, the stipe-scales of *Phegopteris* bear setulae restricted to the margins, while stipe-scales of *Pseudophegopteris* and *Macrothelypteris* also bear setulae on the scale surfaces (Lin et al. 2013; Holttum 1969).

Biogeography and ecology.—The six species of *Phegopteris* are primarily north-temperate, with a few subtropical montane occurrences as far south as Taiwan, occurring from near sea-level to 3600 m. They may be terrestrial or epipetric, in shady forest understories, or along streams, or in open, disturbed sites. The apomictic triploid, *Phegopteris connectilis*, has among the broadest geographic ranges of any vascular plant species, extending throughout the northern temperate and boreal forests of Europe, Asia, and North America. Two species, *P. hexagonoptera*, and *P. excelsior*, are endemic to eastern North America, and two are endemic to East Asia, *P. koreana* to Korea, and another, *P. tibetica*, known from the type, collected from montane conifer forests in Tibet and in neighboring Nepal (Fraser-Jenkins et al. 2015). *Phegopteris decursive-pinnata* is widespread in continental temperate and subtropical Asia, also extending to Taiwan and Japan. It has recently been reported as naturalized in the southeastern United States, where it likely escaped from cultivation (Florez-Parra & Keener 2016).

Taxonomic and phylogenetic studies.—When Fée (1852) elevated *Phegopteris* to generic status, his concept included over 50 species with morphologically similar sori and venation, and subsequently hundreds of combinations spanning a diversity of currently accepted fern families were published in that genus. More than a century later, Ching (1963) was the first to recognize the genus in its current, narrow circumscription, also recognizing the close affinity, but distinctness, of two segregate genera, *Pseudophegopteris* and *Macrothelypteris*. These three genera together constitute one of the two subfamilies, Phegopteridoideae. The remaining genera of Thelypteridaceae are within the Thelypteridoideae (PPG I 2016).

All molecular phylogenetic studies to date (Smith & Cranfill 2002; He & Zhang 2012; Schneider et al. 2013; Almeida et al. 2016; Patel et al. 2019a; Fawcett et al. in press) have corroborated the monophyly of Phegopteridoideae, and the monophyly of its three constituent genera. *Phegopteris* is sister to *Pseudophegopteris*, and that combined clade is sister to *Macrothelypteris*.

Notes.—*Phegopteris decursive-pinnata* has been the subject of several important studies on fern reproductive biology. Its study has contributed to our understanding of the functional differences in breeding systems in diploids vs. tetraploids (Masuyama 1979) and the mechanisms underlying gametophytic self-incompatibility (Masuyama 1986). It has also yielded insight into the pathways to autopolyploid speciation, which has been rarely studied in ferns (Nakato et al. 2012; Kawakami et al. 2019). Because of the ease of propagation, the diversity of ploidy and breeding systems, and strong foundational work, *Phegopteris* remains an excellent candidate for future experimental study.

Constituent species.—**Phegopteris connectilis* (Michx.) Watt; **P. decursive-pinnata* (H.C. Hall) Fée; **P. excelsior* N.R. Patel & A.V. Gilman; **P. hexagonoptera* (Michx.) Fée; *P. koreana* B.Y. Sun & C.H. Kim; *P. tibetica* Ching.

PLESIONEURON

Plesioneuron Holttum, Blumea 22:232. 1975.—Type: *Plesioneuron tuberculatum* (Ces.) Holttum [=*Nephrodium tuberculatum* Ces.]

Mesophlebion subg. *Plesioneuron* Holttum
For additional generic synonymy, see Holttum (1975, 1982, 1977b).

Etymology.—Gr. *plesio*, near + *neuron*, vein, the genus was segregated from *Mesophlebion*, from which it is distinguished by the basal basiscopic vein never arising far from its costule (**Fig. 6A**).

Plants terrestrial or epilithic, small to large (20–300 cm); **rhizomes** creeping to erect; **fronds** monomorphic, erect to pendent; **stipes** stramineous to dull brown, with ovate-lanceolate to linear, medium- to dark brown scales, these typically thin, sometimes thickened (e.g., *P. costulisorum*) at the base of stipe and rhizome apex, sometimes essentially lacking; dark projecting spines sometimes present along stipes (e.g., *P. dryopteroideum*); **blades** chartaceous to stiffly coriaceous, often drying dull-green or sometimes pale grayish, typically pinnate-pinnatisect, less often pinnate-pinnatifid, rarely pinnatifid (*P. fulgens*), proximal pinnae generally abruptly or subabruptly reduced, often deflexed, rarely gradually reduced (e.g., *P. imbricatum*), apex conform or gradually reduced, proliferous buds lacking; **pinnae** straight or falcate, sessile or petiolulate, typically strongly asymmetrical at the base, excavate basiscopically (e.g., *P. prenticei*), cuneate, rounded, or truncate, often with free basal lobe, but lacking expanded auricles; pinna apices frequently acuminate or caudate; sinus membranes often thickened, raised, and bearing hairs, forming a hairy ridge; **veins** generally free, running to the margin above the sinus or alongside sinus ridges, not forming areoles, basal basiscopic vein arising from or near costule; **aerophores** present as swollen discoloration, elongate in a few species (e.g., *P. croftii*); **indument abaxially** of short, unicellular, hyaline acicular hairs, usually restricted to veins and costae, sometimes also on laminar tissue, rarely lacking (e.g., *P. tuberculatum*), glands sometimes present, these yellow and spherical, sessile, or stipitate (e.g., *P. subglabrum*), scales occasionally present on costae; **indument adaxially** typically restricted to veins and costae, of hyaline acicular hairs and/or antrorsely arching reddish hairs along rachises and costae; **pustules** sometimes present on laminar tissue adaxially or abaxially (*P. prenticei*); **sori** round, discrete, typically medial or inframedial, usually indusiate, indusia typically large, dark, and persistent, glabrous or with hairs or glands; **sporangia** unadorned, or with spherical amber or yellow glands (e.g., *P. hopeanum, P. imbricatum,* **Fig. 2I**), or setulae; **spores** often black, often minutely spinulose (echinate) or occasionally winged; $x = 36$, all spp. diploid based on counts from four species, *P. fulgens* ($n = 36$), *P. caudatum* ($2n = 72$), *P. keysserianum* ($n = 36$), *P. wantotense* ($n = 36$). No hybrids are known.

Diagnosis.—*Plesioneuron*, which is predominantly found in New Guinea and the western Pacific, differs from the strictly Malesian *Mesophlebion* by the proximity of the origin of the basal basiscopic vein to the costule (Fig. 6) (vs. arising far from it; Fig. 9C), the presence of glandular or setulose sporangia (but never a reddish gland on sporangial stalks), and stiff, terete, spine-like scales along the stipe and rachis. These spines are often black and are also borne by species of *Chingia*, which differ from *Plesioneuron* in having less divided pinnae, veins generally anastomosing (vs. free), and by sori often inframedial or along costules (vs. medial to inframarginal; Holttum 1975). *Plesioneuron* may generally be distinguished from *Pneumatopteris s.s.*, *Reholttumia*, and *Sphaerostephanos* by its pinnate-pinnatisect frond division, frequently asymmetrical pinna-bases, and free veins. Its larger stature and coarser laminae distinguish it from *Coryphopteris* and Old World *Amauropelta*, which also have free veins.

Biogeography and ecology.—Totalling 60 species, *Plesioneuron* reaches its greatest diversity in the mountains of Papua New Guinea. A few species extend north and west in Malesia, and ca. 12 spp. (Holttum 1977b) occur in the Solomon Islands, Ponape, and northern Queensland to Melanesia (Fiji) and Polynesia from Samoa, the Society Islands, and the Marquesas Islands. The genus appears to be absent from mainland Asia (including India, China, Thailand, and Vietnam), as well as from peninsular Malaysia, and western Malesia (Sumatra, Java), and has only a single widespread species in the Philippines (*P. savaiense*). Species are epipetric or terrestrial and occur at low to middle elevations, but occasionally reach ~3000 m (Holttum 1982). They are found in forests, often along streams, and many species occur on limestone.

Taxonomic and phylogenetic studies.—Originally described as a subgenus of *Mesophlebion* (Holttum 1971), *Plesioneuron* was later elevated to generic status by Holttum (1975), who noted that it seemed to be most closely related to *Chingia*, an idea supported by morphological data and, now, molecular data. As treated by Holttum (1982), *Plesioneuron* comprised 49 species. We transfer one unusual species with bipinnate fronds, *Plesioneuron marattioides*, to *Chingia* based on morphology and molecular data (Fawcett et al. in press) and expand the genus to 60 by transferring thirteen species treated in *Pneumatopteris* by Holttum (1977b, 1982), and one by Takeuchi (2007), to *Plesioneuron* (listed below). These are almost entirely free-veined species, keyed by Holttum (1982:418) in the second half of his key to *Pneumatopteris*, couplet 1, and also in the second half of his key to *Pneumatopteris* (Holttum 1973a). A study of the pteridophyte flora of the east Indonesian islands of Ambon and Seram in the mid-1980's yielded two additional species and a variety to the genus (Kato 2007).

The eighteen samples, representing 15 of the 60 species of *Plesioneuron* (Fawcett et al. in press) are well-supported as monophyletic, and weakly supported as sister to *Chingia.* Together, these two genera form a clade with *Menisciopsis*, *Grypothrix*, and *Mesopteris s.l.* While each of these genera is well-supported as monophyletic, backbone support among these genera is weak.

Notes.—*Plesioneuron* is one of the least-studied genera of Thelypteridaceae, with many species known only from the type or a few collections. New Guinea, the center of diversity for the genus, remains poorly collected. A diverse and unusual group of diminutive epilithic calciphiles occurs at higher elevation karst terrains in Papua New Guinea and were treated within *Pneumatopteris* by Holttum (1982) (see *incertae sedis* under *Pneumatopteris* for further discussion, and an enumeration of these taxa), but may be most closely allied with *Plesioneuron*. We refrain from assigning these species to a genus, due to lack of material for both morphological and molecular study. Although several of these taxa share the asymmetrical pinna-bases, pinnatisect laminae, and free veins, some differ from typical *Plesioneuron* by proximal pinnae gradually reduced, and pinnae shallowly lobed, with a few anastomosing pairs of veins (vs. all veins free).

New combinations for species previously treated as Pneumatopteris.—

Plesioneuron angusticaudatum (Holttum) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Pneumatopteris angusticaudata* Holttum, Blumea 21:308. 1973.

Plesioneuron caudatum (Holttum) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Pseudocyclosorus caudatus* Holttum, Blumea 13:133. 1965.—*Pneumatopteris caudata* (Holttum) Holttum

Plesioneuron deficiens (Holttum) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Pneumatopteris deficiens* Holttum, Blumea 21:321. 1973.

Plesioneuron excisum (Holttum) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Pseudocyclosorus excisus* Holttum, Blumea 13:133. 1965.—*Pneumatopteris excisa* (Holttum) Holttum

Plesioneuron finisterrae (Brause) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Dryopteris finisterrae* Brause, Bot. Jahrb. Syst. 49:20. 1912.—*Pneumatopteris finisterrae* (Brause) Holttum—*Thelypteris finisterrae* (Brause) C.F. Reed

***Plesioneuron imbricatum** (Holttum) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Pneumatopteris imbricata* Holttum, Blumea 21:322. 1973.

***Plesioneuron keysserianum** (Rosenst.) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Dryopteris keysseriana* Rosenst., Repert. Spec. Nov. Regni Veg. 10:333. 1912.—*Pneumatopteris keysseriana* (Rosenst.) Holttum—*Thelypteris keysseriana* (Rosenst.) C.F. Reed

Plesioneuron ligulatum (J. Sm. ex C. Presl) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Lastrea ligulata* J. Sm. ex C. Presl, Epimel. Bot. 35. 1851.—*Pneumatopteris ligulata* (J. Sm. ex C. Presl) Holttum

Plesioneuron medlerae (W.N. Takeuchi) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Pneumatopteris medlerae* W.N. Takeuchi, Blumea 52:154. 2007.

Plesioneuron mingendense (Gilli) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Lastrea mingendensis* Gilli, Ann. Naturhist. Mus. Wien 81:24. 1978.—*Pneumatopteris mingendensis* (Gilli) Holttum

Plesioneuron obliquum (Holttum) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Pneumatopteris obliqua* Holttum, Blumea 21:309. 1973.

Plesioneuron regis (Copel.) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Dryopteris regis* Copel., Univ. Calif. Publ. Bot. 18:220. 1942.—*Pneumatopteris regis* (Copel.) Holttum

Plesioneuron walkeri (Holttum) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Pneumatopteris walkeri* Holttum, Blumea 21:323. 1973.

Constituent species.—Plesioneuron altum (Brause) Holttum; *P. angiense* Holttum; *P. angusticaudatum* (Holttum) S.E. Fawc. & A.R. Sm.; **P. archboldiae* (Copel.) Holttum; **P. attenuatum* (Brack.) Holttum; **P. belense* (Copel.) Holttum; *P. bipinnatum* (Copel.) Holttum; *P. caudatum* (Holttum) S.E. Fawc. & A.R. Sm.; * *P. costulisorum* (Copel.) Holttum; *P. crassum* (Copel.) Holttum; *P. croftii* Holttum; *P. cystodioides* Holttum; *P. deficiens* (Holttum) S.E. Fawc. & A.R. Sm.; *P. doctersii* Holttum; *P. dryas* Holttum; *P. dryopteroideum* (Brause) Holttum; *P. excisum* (Holttum) S.E. Fawc. & A.R. Sm.; **P. falcatipinnulum* (Copel.) Holttum; *P. finisterrae* (Brause) S.E. Fawc. & A.R. Sm.; *P. fuchsii* Holttum; *P. fulgens* (Brause) Holttum; **P. hopeanum* (Baker) Holttum (**Fig. 6A**); **P. imbricatum* (Holttum) S.E. Fawc. & A.R. Sm. (**Fig. 2I**); **P. keysserianum* (Rosenst.) S.E. Fawc. & A.R. Sm.; *P. kostermansii* Holttum; *P. kundipense* Holttum; *P. ligulatum* (J. Sm. ex C. Presl) S.E. Fawc. & A.R. Sm.; **P. marquesicum* Holttum; *P. medlerae* (W.N. Takeuchi) S.E. Fawc. & A.R. Sm.; *P. medusella* Holttum; *P. mingendense* (Gilli) S.E. Fawc. & A.R. Sm.; *P. murkelense* M. Kato; *P. myriosorum* (Copel.) Holttum; *P. notabile* (Brause) Holttum; *P. obliquum* (Holttum) S.E. Fawc. & A.R. Sm.; *P. ophiura* (Copel.) Holttum; *P. phanerophlebium* (Baker) Holttum; *P. platylobum* Holttum; **P. ponapeanum* (Hosok.) Holttum; **P. prenticei* (Carruth.) Holttum; *P. pullei* Holttum; *P. quadriquetrum* (Alderw.) Holttum; *P. regis* (Copel.) S.E. Fawc. & A.R. Sm.; *P. rigidilobum* Holttum; *Plesioneuron royenii* Holttum; *P. sandsii* Holttum; **P. savaiense* (Baker) Holttum; *P. saxicola* M. Kato; *P. septempedale* (Alston) Holttum; *P. stenura* Holttum; **P. subglabrum* Holttum; *P. subterminale* Holttum; * *P. tahitense* Holttum; *P. translucens* Holttum; **P. tuberculatum* (Ces.) Holttum; *P. varievestitum* (C. Chr.) Holttum; *P. walkeri* (Holttum) S.E. Fawc. & A.R. Sm.; *P. wantotense* (Copel.) Holttum; *P. wariense* (Copel.) Holttum; *P. woodlarkense* (Copel.) Holttum

Incertae sedis.—Trigonospora koordersii (Christ) Holttum was initially included in *Mesophlebion* subg. *Plesioneuron* (Holttum 1971), but later Holttum (1974c) decided that this taxon shared a close resemblance to *Trigonospora calcarata*. This plant is known only from the type collection (L, image!), and it is unclear whether that specimen may yield spores that could verify its placement in *Trigonospora*. At the present time, we cannot rule out its placement in *Plesioneuron*.

PNEUMATOPTERIS

Pneumatopteris Nakai in Bot. Mag. (Tokyo) 47:179. 1933.—Type: *Pneumatopteris callosa* (Blume) Nakai [= *Aspidium callosum* Blume]

For additional synonymy, see Holttum (1973a, 1977b, 1982).

Etymology.—Gr. *pneuma*, air, breath + *pteris*, fern. The peg-like pneumatophores (aerophores) extending from the stipe, and the bases of the pinnae (and sometimes the bases of the costules) are diagnostic for this genus (**Fig. 2C**).

Plants terrestrial, large (to 2 m tall), often along streams; **rhizomes** thick (> 1cm), creeping, or forming erect caudices with fronds densely clustered; **fronds** monomorphic, pinnate-pinnatifid, arching; **stipes** stramineous, scales brown, broadly ovate to ovate-lanceolate, glabrous, or often with hairs along margins; **blades** generally coarse in texture (chartaceous to subcoriaceous), often bicolorous, drying darker green adaxially; lamina apex gradually reduced or with subconform terminal pinna, proximal pinnae abruptly reduced to minute vestigial pinnae, with a fringe of laminar tissue surrounding aerophores (1–4 mm); **pinnae** sessile, with truncate bases, shallowly lobed (generally < ½ to costae), with pronounced cartilaginous sinus membranes that are grooved adaxially (**Fig. 7A**) and project out of the plane of the blade abaxially, segment tips generally acute; **veins** prominent above and below, often paler than lamina, with at least one pair anastomosing below each sinus, forming an excurrent vein to sinus, with more distal veins running to both sides of an elongate sinus membrane, veins closely spaced, (7–)11–12(–15) pairs per segment; **aerophores** prominent, peg-like (**Fig. 2C**), projecting through mucilage during early frond development, along stipes, and at pinna bases, frequently also with peg-like or swollen aerophores at the bases of costae; **indument abaxially** essentially lacking, or of generally short hyaline acicular hairs on veins and/or between veins; **indument adaxially** essentially lacking, or of abundant short hairs on and between veins (these sometimes glandular, or capitate, e.g., *P. glabra*), and long, antrorsely arching or curling reddish or brownish hairs in the adaxial grooves of the rachis and costae (hairs absent in *P. callosa*); **pustules** lacking, or present on lamina adaxially and abaxially (e.g., *P. stokesii*); **sori** round, medial to inframarginal, exindusiate, sometimes with receptacular hairs (*P. glandulifera*), or with a small indusia that may be glabrous or setose (e.g., *P. mesocarpa*), often shriveling or caducous upon maturation of sporangia; **sporangia** glabrous, setulose (e.g., *P. parksii*) or glandular (e.g., *P. glabra*), glands always colorless, setae acicular or capitate, unicellular or multicellular; **spores** yellow to light brown; likely $x = 36$, as is the case with all its close relatives, but no counts published. No hybrids have been formally documented, but certain specimens with malformed spores (e.g., *Fawcett 638*, Viti Levu, Fiji, UC, VT; *Game s.n.*, UC 1544285, Rarotonga, Cook Islands) represent possible hybrids.

Diagnosis.—*Pneumatopteris s.s.* is distinguished from most other christelloids by having prominent aerophores along the stipe, at the bases of pinnae (**Fig. 2C**), and at the bases of costae; pinnae abruptly reduced to vestiges subtending aerophores (not more than a few mm in length); fronds producing mucilage during early development; and veins closely spaced (ca. 12 per segment). The pinna segments of *Pneumatopteris s.s.* typically have about 11 veins per cm (vs. typically about 7 veins per cm in *Reholttumia*); laminae often strongly bicolorous, drying dark above and paler below; and prominent elongate sinus membranes concave adaxially and convex abaxially. *Sphaerostephanos* differs by having laminae sometimes gradually or subabruptly reduced, and having yellow spherical glands (glands in *Pneumatopteris* colorless, and usually capitate when present), and lacking mucilage on developing fronds. *Reholttumia* also differs in having laminae sometimes gradually or subabruptly reduced, pinnae often lobed more deeply (> halfway to costae), and segment apices usually truncate or obtuse rather than broadly acute in *Pneumatopteris s.s. Strophocaulon* differs in having long-creeping rhizomes (vs. erect or short-creeping with stipe bases closely clustered). *Hoiokula* differs in having a zig-zag excurrent vein, densely setulose sporangia (rare in *Pneumatopteris s.s.*), and hairs between veins on adaxial laminae. *Pakau* differs in having scales present on the abaxial costae, opposite or subopposite pinnae (vs. alternate), and lack of aerophores. *Christella s.s.* differs in generally having hairier laminae, on veins, and between veins.

Biogeography and ecology.—This relatively small clade, comprising just 11 species as defined here, is well represented in the Pacific, in Melanesia and Polynesia, with species occurring in the Solomon Islands, New Hebrides, Fiji, Samoa, Rarotonga, the Society Islands, and Rapa (but not in Hawaii). Several other species are Malesian, including the type, *P. callosa*, from Java. Species of *Pneumatopteris* occur primarily at low to middle elevations (0–2400 m) and are frequent along rocky rivers and streams (Holttum 1977b).

Taxonomic and phylogenetic studies.—*Pneumatopteris*, as recognized by Holttum (1973a, 1974a, 1977b, 1982; *in* Hovenkamp & De Joncheere 1988), with only two additional species described since then (by Palmer 2005; Takeuchi 2007), included about 90 species extending from Africa to New Zealand. In molecular phylogenetic analyses, *Pneumatopteris* sensu Holttum is by far the most heterogeneous and polyphyletic taxon in the Thelypteridaceae, with representatives in ten major clades (Fawcett et al. in press). Even so, Holttum was well aware of the diversity within his concept of the genus, recognizing most members of *Pneumatopteris s.s.* as close relatives of one another, but also describing the unique morphology of four aberrant taxa we now place in four different genera, three of which are newly described. Other species we exclude from *Pneumatopteris* are newly combined in several existing genera: *Abacopteris*, *Menisorus*, *Plesioneuron*, and *Sphaerostephanos*, or placed in one of three new genera, which see for details: *Pakau*, *Hoiokula*, and *Reholttumia*.

The African species of Thelypteridaceae are under-collected and remain poorly represented in molecular analyses. However, recent work (Fawcett et al. in press) has illuminated many of the problems with the current taxonomy and highlights the need for further study. The four African species treated in *Pneumatopteris* by Holttum (1974a) included in the molecular analysis each resolved in a distinct clade, corresponding to different genera: *Pneumatopteris afra* in *Abacopteris*, *Pneumatopteris unita* as sister to *Menisorus pauciflorus*, *Pneumatopteris remotipinna* in *Reholttumia*, and *Pneumatopteris humbertii* as sister to *Christella distans*, both of which resolve in a clade with *Trigonospora* and *Pseudocyclosorus*.

The closest relative of *Pneumatopteris s.s.* is the monophyletic genus *Sphaerostephanos*, redefined slightly herein. A majority of the remaining species treated as *Pneumatopteris* by Holttum (1977b, 1982) are in a clade sister to these two clades (herein named *Reholttumia*; **Fig. 1**). To preserve a monophyletic *Pneumatopteris*, *Reholttumia* must be segregated. Alternatively, *Sphaerostephanos* (the oldest name for the three groups) must be significantly expanded; this genus already includes nearly 200 species and is recognizable (albeit morphologically diverse). We prefer to recognize a smaller, well-defined *Pneumatopteris s.s.*, and segregate the sister clade to *Sphaerostephanos* as *Reholttumia*.

Constituent species.—*Pneumatopteris callosa* (Blume) Nakai; *P. dicranogramma* (Alderw.) Holttum; *P. dilatata* Holttum; *P. florencei* (A.R. Sm. & Lorence) A.R. Sm. & Lorence; *P. glabra* (Copel.) Holttum; *P. glandulifera* (Brack.) Holttum (**Fig. 2C**); *P. mesocarpa* (Copel.) Holttum; *P. obstructa* (Copel.) Holttum; *P. parksii* (F. Ballard) Holttum (**Fig. 7A**); *P. sibelana* Holttum; *P. stokesii* (E.D. Br. ex E.D. Br. & F. Br.) Holttum

Pneumatopteris as treated by Holttum (1974a, 1977b, 1982) includes about 90 species, but as we circumscribe it, only 11 species remain, one of which is newly combined. We transfer most of the others to other genera. Several species are excluded from *Pneumatopteris s.s.* but remain unplaced, pending further study.

Species transferred to Plesioneuron.—These taxa generally have petiolulate, deeply incised pinnae with asymmetric bases, and are often free-veined, or with few pairs of anastomosing veins, features characteristic of *Plesioneuron*. Several are small in stature and are epipetric calciphiles occurring in karst terrain (Kato 2007; Takeuchi 2007). These include: *Pneumatopteris angusticaudata* Holttum; *P. caudata* (Holttum) Holttum; *P. deficiens* Holttum; *P. excisa* (Holttum) Holttum; *P. finisterrae* (Brause) Holttum; *P. imbricata* Holttum; *P. keysseriana* (Rosenst.) Holttum; *P. ligulata* (C. Presl) Holttum; *P. medlerae* W.N. Takeuchi; *P. mingendensis* (Gilli) Holttum; *P. obliqua* Holttum; *P. regis* (Copel.) Holttum; *P. walkeri* Holttum

Species transferred to Reholttumia.—This newly described genus encompasses the greatest number of species treated as *Pneumatopteris* by Holttum (1971, 1982), and most of those he considered 'typical' of the genus. It is predominantly Malesian, but with representatives extending into Hawaii, Australia, Sri Lanka, and at least one species, with its affinities confirmed by molecular data, occurring in Africa: *Pneumatopteris basicurtata* Holttum; *P. boridensis* Holttum; *P. bryanii* (C. Chr.) Holttum; *P. christelloides* Holttum; *P. costata* (Brack.) Holttum; *P. ecallosa* (Holttum) Holttum; *P. glaberrima* (A. Rich.) Holttum; *P. hudsoniana* (Brack.) Holttum; *P. inclusa* (Copel.) Holttum; *P. jermyi* Holttum; *P. kerintjiensis* Holttum; *P. laevis* (Mett.) Holttum; *P. laticuneata* Holttum; *P. longipes* (Blume) Holttum; *P. macroptera* (Copel.) Holttum; *P. magnifica* (Copel.) Holttum; *P. michaelis* Holttum; *P. micropaleata* Holttum; *P. nitidula* (C. Presl) Holttum; *P. novae-caledoniae* Holttum; *P. oxyoura* (Copel.) Holttum; *P. papuana* Holttum; *P. pergamacea* Holttum; *P. psilophylla* Holttum; *P. remotipinna* (Bonap.) Holttum; *P. rodigasiana* (T. Moore) Holttum; *P. sogerensis* (Gepp) Holttum; *P. truncata* (Poir.) Holttum; *P. vaupelii* (C. Chr.) Holttum

Species recognized in Abacopteris.—A species, heretofore recognized in *Pronephrium*, was treated more recently in *Pneumatopteris*: *P. nudata* (Roxb.) Punetha & Kholia, J. Bombay Nat. Hist. Soc. 86:476. 1990.

Species transferred to Hoiokula.—Two Hawaiian endemics, most closely related to *Leptogramma, Stegnogramma*, and *Cyclogramma* in the phylogeny of Fawcett et al. (in press), are transferred to this new genus: *Pneumatopteris pendens* D.D. Palmer; *Pneumatopteris sandwicensis* (Brack.) Holttum.

Species transferred to Menisorus.—Previously recognized as monotypic, this genus now includes two species. Both share its proliferous buds, unusual among Thelypteridaceae: *Pneumatopteris blastophora* (Alston) Holttum; *Pneumatopteris unita* (Kunze) Holttum.

Pneumatopteris subpennigera (C. Chr.) Holttum, from Madagascar, is similar but lacks proliferous buds and has elongate sori; we consider it *incertae sedis*.

Species transferred to Pakau.—A single taxon, native to New Zealand and northern Australia, is transferred to this monotypic genus: *Pneumatopteris pennigera* (G. Forst.) Holttum.

Species transferred to Sphaerostephanos.—Three species have been transferred to *Sphaerostephanos*, which was recently demonstrated to be a large, mostly monophyletic, but morphologically heterogeneous genus (Fawcett et al. in press): *Pneumatopteris incisa* Holttum; *P. microloncha* (Christ) Holttum; *P. superba* (Brause) Holttum.

Incertae sedis.—Certain species stand out as especially problematic due to limited sampling, unique morphological features (or lack of diagnostic features), and distributions in poorly collected regions of high diversity, or some combination of these factors, and we are unable to place these with confidence.

The karst regions of Papua New Guinea host an extraordinary diversity of Thelypteridaceae, and these are known from few herbarium collections and very limited molecular data. Some of these can be transferred with confidence to the genera *Plesioneuron* or *Sphaerostephanos* (see above); however, we were unable to study diagnostic microscopic features of type material, or sample tissue for molecular analyses of others. The following species of Papua New Guinea all share the following characteristics: small stature; epipetric habitat, predominantly on calcareous rocks; proximal pinnae gradually reduced, and shallowly lobed pinnae, often with free, or forking veins, or with few anastomosing pairs: *Pneumatopteris cheesmaniae* Holttum; *P. egenolfioides* Holttum; *P. latisquamata* Holttum; *P. nephrolepioides* (C. Chr.) Holttum; *P. patentipinna* Holttum; *P. petrophila* (Copel.) Holttum (treated in *Pseudocyclosorus* by Holttum and Roy 1965); and *P. versteeghii* Holttum. The last taxon exhibits the asymmetrical pinna-bases typical of *Plesioneuron*, though its pinnae are not deeply incised. Outside of Papua New Guinea, several other diminutive rock ferns of diverse morphology are known and are also of uncertain placement: *Pneumatopteris lithophila* Holttum; *P. aberrans* Holttum; *P. sumbawensis* (C. Chr.) Holttum; and *P. brooksii* (Copel.) Holttum. Some of these calciphilic rock ferns demonstrate an interesting parallel to the diversity of the New World genus *Goniopteris* on Caribbean karst (Fawcett 2020).

An aberrant species with up to eight pairs of gradually reduced pinnae, *Pneumatopteris auctipinna*, resolves with support as sister to the four sphaerostephanoid genera, however, morphologically it is most similar to *Reholttumia*. Additional data are needed to confirm its placement.

The aforementioned *Pneumatopteris humbertii*, from Madagascar, as well as *Christella distans* and perhaps *Pronephrium fidelei* (Fawcett et al. in press), from the same area, are more closely related to *Pseudocyclosorus* and *Trigonospora* than either is to *Pneumatopteris* or any of its segregate genera; however, they are morphologically distinct from all species currently recognized in *Pseudocyclosorus*. We refrain from placing these taxa until a more complete understanding of the interrelationships of the African Thelypteridaceae can be achieved.

The African species *Pneumatopteris afra* (Christ) Holttum resolves variously with *Christella s.s.* or *Abacopteris* (Fawcett et al. in press), and our interpretation of its morphology is inconclusive; we refrain from making a combination, pending further study. The morphologically similar *Thelypteris glandafra* Viane was believed to be closely related to *Pneumatopteris afra* and *P. blastophora* (Viane 1985), but we treat the latter taxon in *Menisorus*. Further study is needed to place *T. glandafra* and an additional African taxon, *Pneumatopteris oppositifolia*, with confidence.

Finally, because of inadequate descriptions, incomplete type material, and/or aberrant morphology not corresponding closely to any current generic concept, we additionally treat the following taxa as *incertae sedis*: *Pneumatopteris eburnea* Holttum; *P. japenensis* Holttum; *P. lawakii* Holttum; *P. microauriculata* Holttum; *P. prismatica* (Desv.) Holttum; *P. subappendiculata* (Copel.) Holttum; *P. tobaica* Holttum; *P. transversaria* (Brack.) Holttum; *P. usambarensis* Holttum; and *P. venulosa* (Kuntze) Holttum.

Excluded species.—We exclude *Pneumatopteris lucida* (Baker) Holttum, which is likely to have been described from a mislabeled specimen of *P. laevis* (Mett.) Holttum from the Philippines, not from Madagascar, as it was labeled in the cultivated collection at Kew (Holttum 1973a).

PRONEPHRIUM

Pronephrium C. Presl, Abh. Königl. Böhm. Ges. Wiss., ser. 5, 6:618. 1851, Oct.; Epimel. Bot. 258. 185, Oct.—Lectotype (designated by Holttum, Blumea 19:36. 1971): *Pronephrium lineatum* (Blume) C. Presl [= *Aspidium lineatum* Blume]

Dimorphopteris Tagawa & K. Iwats. in Iwatsuki, Acta Phytotax. Geobot. 19:8. 1961.—*Pronephrium* sect. *Dimorphopteris* (Tagawa & K. Iwats.) Holttum, Blumea 19:36. 1971.—Type: *Dimorphopteris moniliformis* Tagawa & K. Iwats. in Iwatsuki, Acta Phytotax. Geobot. 19(1):8, f. 14. 1961. [= *Pronephrium moniliforme* (Tagawa & K. Iwats.) Holttum]

Nannothelypteris Holttum, Blumea 19:38. 1971.—Type: *Nannothelypteris aoristisora* (Harr.) Holttum, Blumea 19:38. 1971 [= *Pronephrium aoristisorum* (Harr.) S.E. Fawc. & A.R. Sm., based on *Polypodium aoristisorum* Harr.]

For complete synonymy, see Holttum (1977b, 1982).

Etymology.—Gr. *pro*, in front of + *nephros*, kidney, referring to the reniform indusia covering the sori (Stewart 1983); indusia in this genus may be round, or even absent.

Plants terrestrial, rheophytic or epipetric, typically small to medium-sized, mostly (8–)15–50(–70) cm tall; **rhizomes** short-creeping, ascending, or erect; **fronds** typically strongly dimorphic with fertile fronds often much taller (to 3×) than non-fertile fronds (**Fig. 7C**), erect or arching, and once-pinnate to pinnate-pinnatifid (rarely simple in juvenile plants); **stipes** stramineous to dull brown, with ovate-deltate to linear-lanceolate brown scales, typically with hairs on scales, rarely without; **blades** chartaceous to subcoriaceous, rarely membranaceous, with apex gradually reduced (e.g., *P. affine* C. Presl), pinna-like (e.g., *P. lineatum*), or much larger than lateral pinnae (e.g., *P. granulosum* (C. Presl) Holttum), proximal pinnae not, or only slightly, reduced, lacking proliferous buds; **pinnae** margins entire, crenate, or shallowly lobed (some irregular long lobes projecting outward in *P. xiphioides* (C. Chr.) Holttum, rarely deeply lobed (*P. philippinum*), frequently with acroscopic basal auricles, sometimes also with basiscopic auricles, sessile or short-petiolulate, with truncate or broadly cuneate bases, in some species the pinnae strongly asymmetric (*Nannothelypteris* group); **veins** prominent adaxially and abaxially, several pairs regularly anastomosing to form a straight, or somewhat zig-zag excurrent vein, less commonly with included veinlets (*P. menisciicarpon* (Blume) Holttum), in species with smaller pinnae (e.g., *P. aoristisorum*) veins forked rather than anastomosing; vein endings reaching margins; **aerophores** rare, when present, as darkened swelling of aerating tissue; **indument abaxially** of hyaline acicular hairs on costae, veins, and sometimes on laminar tissue between veins, yellow or golden spherical glands frequently present; **indument adaxially** of hyaline acicular hairs, these restricted to costae and veins; **pustules** usually present and often dense on abaxial and adaxial laminae; **sori** medial, round, with or without indusia, when present, indusia glabrous or with acicular hairs and/or golden spherical glands, generally paired on either side of excurrent vein, appearing acrostichoid on the most reduced fertile fronds; **sporangia** glabrous or with setae or yellow to golden spherical glands; **spores** light to dark brown, with fimbriate, anastomosing crests (e.g., *P. peltatum*) (Patel et al. 2019a); $x = 36$, with three species counted, representing two diploids (*P. hosei, P. camarinense*) and a tetraploid (*P. affine*). No hybridization has been formally demonstrated within the genus, but Holttum (1982) suggested that *Pronephrium xiphioides* may represent a hybrid (or a hybrid swarm) between *P. granulosum* and *P. rhombeum*.

Diagnosis.—Pronephrium s.s., as redefined here, is distinguished from the three other segregates of *Pronephrium s.l.* (*Menisciopsis, Abacopteris*, and *Grypothrix*) by its small stature (typically < 50 cm tall), strongly dimorphic fronds, small pinnae (usually < 4 cm wide), laminar apex sometimes gradually reduced, and yellow or golden spherical glands on abaxial lamina, indusia and/or sporangia. It also tends to grow at lower elevations than these taxa. *Pronephrium* lacks the hamate hairs on the blades and/or sporangia and has short-creeping to suberect rhizomes; hamate hairs occur on all known species of *Grypothrix*, and many species of that genus have long-creeping rhizomes. The yellow spherical glands found in some species of *Pronephrium* are shared with many species of *Sphaerostephanos*, but are lacking in *Pneumatopteris* and *Reholttumia*, to which *Pronephrium s.s.* is more closely related than it is to other species segregated from *Pronephrium s.l. Pronephrium s.s.* is generally distinguished from *Sphaerostephanos* by proximal pinnae not, or only slightly, reduced (vs. abruptly or gradually reduced), and appressed hairs lacking on the adaxial laminae between veins (present in *Sphaerostephanos glandulosum*). For complete synonymy, see Holttum (1982).

Biogeography and ecology.—Pronephrium includes approximately 37 species, is almost entirely Malesian in distribution, and is especially diverse in the Philippines. Some taxa extend into adjacent continental Asia (e.g., *P. affine* occurs in peninsular Thailand). One species, *Pronephrium palauense*, endemic to the island of Palau, extends the range of the genus into Micronesia. Most species occur at low elevations, many below 500 m, though some species reach 1800 m, along streams, or on calcareous rocks. Of the 45 species treated by Holttum (1982) in sect. *Dimorphopteris*, eight were known only from the type collection, and several others are known from only a few collections, suggesting that many may be rare, and therefore vulnerable to extinction; however, due in part to the subtle or microscopic characters needed to distinguish genera of Thelypteridaceae, this diverse family may be often overlooked by non-specialist collectors.

Taxonomic and phylogenetic studies.—Our observations suggest that *P. lineatum*, the type of *Pronephrium*, is distantly related to the other members of Holttum's (1971, 1972, 1982) small but heterogeneous *Pronephrium* sect. *Pronephrium*, which includes species we now recognize in *Abacopteris*, *Menisciopsis*, and *Sphaerostephanos* (based on molecular phylogenetic data; Fawcett et al. in press). Thus, *Pronephrium s.s.*, as defined herein, corresponds in large part to Holttum's concept of *Pronephrium* sect. *Dimorphopteris*. A collection at Leiden (L:0052355, image!), presumably studied by Blume, was designated as lectotype of *P. lineatum* by Holttum (1971). Contrary to Holttum's interpretation, we see this specimen as dimorphic, evidenced by the much longer stipe of the fertile frond. Holttum noted the spherical yellow glands and setulae on the sporangia, and glands on the indusia of the type, which, together with dimorphic fronds, are diagnostic for our concept of *Pronephrium s.s.* Holttum (1971) initially recognized *Haplodictyum* as a good genus, but later (Holttum 1982) placed it in synonymy under *Pronephrium*; we regard the type of *Haplodictyum*, and several similar species, to be part of *Sphaerostephanos*.

Based on the phylogeny in Fawcett et al. (in press), *Pronephrium* is a member of the sphaerostephanoid clade that also includes *Sphaerostephanos*, *Pneumatopteris s.s.*, and *Reholttumia* (which includes a majority of species formerly treated in *Pneumatopteris*). These four genera are together sister to the pseudocyclosoroid clade which includes *Abacopteris* (treated by Holttum as a heterotypic synonym of *Pronephrium* sect. *Pronephrium*). The larger christelloid clade includes both the sphaerostephanoids and the pseudocyclosoroids. *Pronephrium s.s.* (our sense, defined herein) is more distantly related to *Menisciopsis* and *Grypothrix*, the other two segregates of *Pronephrium sensu* Holttum (1982), which resolve in the chingioid clade. *Nannothelypteris aoristisora*, the type of *Nannothelypteris*, is nested within *Pronephrium s.s.*, and is here treated as a synonym. Holttum (1982) was aware of the similarity of *Nannothelypteris* to *Pronephrium* sect. *Dimorphopteris* and believed they were closely related. *Nannothelypteris*, as treated by Holttum (1973b, 1982), is restricted to the Philippines and its species are distinct from most *Dimorphopteris* in having lanceolate blades with many (> 30) pinna-pairs. Two additional species of *Nannothelypteris* were described by Kato et al. (1997), extending the known range to the Moluccas, but one of these, *N. seramensis* M. Kato, does not display morphology typical of *Nannothelypteris* because of its large size and deeply incised and gradually reduced proximal pinnae. Its affinity is uncertain, but its macromorphology, geographic location, and glandular sporangia suggest it may belong in *Sphaerostephanos*.

***Pronephrium aoristisorum** (Harr.) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Polypodium aoristisorum* Harr., J. Linn. Soc., Bot. 16:30. 1877.—*Cyclosorus aoristisorus* (Harr.) Copel.—*Nannothelypteris aoristisora* (Harr.) Holttum—*Thelypteris aoristisora* (Harr.) C.F. Reed

Pronephrium camarinense (Holttum) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Nannothelypteris camarinensis* Holttum, Kalikasan 5:119. 1976.

Pronephrium inaequilobatum (Holttum) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Nannothelypteris inaequilobata* Holttum, Kalikasan 2:67. 1973.

Pronephrium murkelense (M. Kato) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Nannothelypteris murkelensis* M. Kato, Acta Phytotax. Geobot. 48:50. 1997.

Pronephrium nervosum (Fée) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Phegopteris nervosa* Fée, Mém. Foug. 5:244 (Gen. Filic.). 1852.—*Nannothelypteris nervosa* (Fée) Holttum

Pronephrium philippinum (C. Presl) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Physematium philippinum* C. Presl, Epimel. Bot. 34. 1851.—*Nannothelypteris philippina* (C. Presl) Holttum—*Thelypteris philippina* (C. Presl) Ching

Constituent species.—**Pronephrium affine* (Blume) C. Presl; *P. amboinense* (Willd.) Holttum; *P. amphitrichum* Holttum; *P. aquatiloides* (Copel.) Holttum; **P. aoristisorum* (Harr.) S.E. Fawc. & A.R. Sm.; *P. borneense* (Hook.) Holttum; *P. camarinense* (Holttum) S.E. Fawc. & A.R. Sm.; **P. celebicum* (Baker) Holttum; *P. clemensiae* (Copel.) Holttum; *P. debile* (Baker) Holttum; *P. exsculptum* (Baker) Holttum; *P. firmulum* (Baker) Holttum; *P. giluwense* Holttum; **P. granulosum* (C. Presl) Holttum; *P. hewittii* (Copel.) Holttum; **P. hosei* (Baker) Holttum; *P. inaequilobatum* (Holttum) S.E. Fawc. & A.R. Sm.; *P. kjellbergii* Holttum; *P. lineatum* (Blume) C. Presl; **P. menisciicarpon* (Blume) Holttum; *P. merrillii* (Christ) Holttum; *P. millarae* Holttum; *P. minahassae* Holttum; *P. moniliforme* (Tagawa & K. Iwats.) Holttum; *P. murkelense* (M. Kato) S.E. Fawc. & A.R. Sm.; *P. nervosum* (Fée) S.E. Fawc. & A.R. Sm.; *P. palauense* (Hosok.) Holttum; **P. peltatum* (Alderw.) Holttum (**Fig. 7C**); *P. peramalense* Holttum; *P. philippinum* (C. Presl) S.E. Fawc. & A.R. Sm.; **P. rhombeum* (Christ) Holttum; *P. samarense* (Copel.) Holttum; *P. simillimum* (C. Chr.) Holttum; *P. solsonicum* Holttum; *P. thysanoides* Holttum; *P. trachyphyllum* Holttum; **P. xiphioides* (Christ) Holttum

Excluded species.—Several species included in *Pronephrium* sect. *Dimorphopteris* by Holttum (1982) are excluded here. *Pronephrium articulatum*, distributed in Sri Lanka, India, and southern China, is morphologically distinctive and may be nested within *Pseudocyclosorus* (Patel et al. 2019a). Several species are transferred to *Sphaerostephanos*; all other members of *Pronephrium* sensu Holttum not listed as constituents of *Pronephrium s.s.* (our new sense) here are treated in *Abacopteris*, *Grypothrix*, or *Menisciopsis*.

Species transferred to Sphaerostephanos.—*Pronephrium bakeri* (Harr.) Holttum; **P. beccarianum* (Ces.) Holttum; **P. brauseanum* Holttum; *P. bulusanicum* (Holttum) Holttum; *P. diminutum* (Copel.) Holttum; **P. glandulosum* (Blume) Holttum; *P. melanophlebium* (Copel.) Holttum; *P. micropinnatum* Holttum; **P. pentaphyllum* (Rosenst.) Holttum; **P. scopulorum* Holttum; **P. womersleyi* Holttum

Incertae sedis.—*Pronephrium acanthocarpum* (Copel.) Holttum was recognized by Holttum in subg. *Menisciopsis*. It has setose sporangia, which do not occur in members of that genus as treated here, but are common in species of

Abacopteris. Its short stature, trifoliolate laminae, and proliferous buds, however, agree with *Grypothrix*. Careful study of the type is needed to determine its taxonomic placement.

PSEUDOCYCLOSORUS

Pseudocyclosorus Ching, Acta Phytotax. Sin. 8:322–324. 1963.—Type: *Pseudocyclosorus tylodes* (Kunze) Ching [= *Aspidium tylodes* Kunze]—*Cyclosorus* subg. *Pseudocyclosorus* (Ching) Panigrahi—*Thelypteris* sect. *Pseudocyclosorus* (Ching) Fraser-Jenk.—*Thelypteris* subg. *Pseudocyclosorus* (Ching) Fraser-Jenk.

For synonymy, see Holttum (1974d), Holttum and Grimes (1980), Li et al. (2019).

Etymology.—Pseudocyclosorus Latin *pseudo*, false + *Cyclosorus* (Gr.); a distinct genus segregated from a broadly circumscribed *Cyclosorus*.

Plants terrestrial, often along streamsides, or shady forest understories, medium sized, 40–150 cm tall; **rhizomes** short-creeping or forming erect caudices (e.g., *P. tylodes*); scales light brown, glabrous; **fronds** monomorphic, arching to erect; **stipes** stramineous, castaneous, or dull brown; **stipe scales** often sparse or caducous, when present, brown, glabrous or with marginal hairs, ovate to lanceolate; **blades** chartaceous, drying green, brown, or olivaceous, gradually reduced towards apex, proximal pinnae abruptly reduced to a series of opposite auriculate pinnae, these often caudate and/or hastate (see fig. 2 in Li et al. 2019), or reduced to a series of peg-like aerophores (*P. tylodes*); proliferous buds absent; **pinnae** sessile, or short-petiolulate, bases truncate, margins deeply lobed, lobes nearly perpendicular (e.g., *P. esquirolii*) to strongly oblique (< 45 degrees from costae in *P. falcilobus*); **veins** free, reaching sinus, translucent sinus membrane often with tuft of hairs; **aerophores** swollen and conspicuous, protruding from mucilage in developing fronds; **indument abaxially** of spreading hairs restricted to axes, of various lengths, minute (< 0.1 mm) to medium-sized (0.5 mm), stipes often with long tangled hairs; small spherical, sessile or stipitate golden (but never sulfur-colored) glands sometimes present on axes; **indument adaxially** of hyaline acicular hairs, restricted to axes, and sometimes also abundant on laminae between veins (*P. canus*); **pustules** lacking; **sori** round, discrete, rarely confluent, medial, along costules, or inframarginal, sometimes restricted to distal portion of pinnae, always indusiate, indusium typically large, especially evident on young fronds, persistent, glabrous or with short hairs or glands; **sporangia** with capsules lacking glands or hairs, capitate hairs sometimes present on sporangial stalks; **spores** monolete with cristae or echinae (Grimes 1980; Li et al. 2019); $x = 36$ or 35, six species counted, diploids, triploids, and tetraploids known. A base number of 35 has been published for three species, based on several counts from multiple authors, and if correct this represents a dysploid change from the ancestral base number 36, which is synapomorphic for the cyclosoroid clade. Loyal (1961) reported a triploid *P. canus* with irregular meiosis from Darjeeling, representing a possible infrageneric hybrid. Shieh and Tsai (1987) reported a putative hybrid between *Glaphyropteridopsis erubescens* and *Pseudocylosorus esquirolii*, a finding that warrants further investigation.

Diagnosis.—The combination of deeply dissected pinnae, swollen aerophores (most easily observed in fiddleheads and fresh material), large indusia, and proximal pinnae abruptly reduced to auricles (or aerophores in *P. tylodes*) is diagnostic for *Pseudocyclosorus*. *Trigonospora* may be distinguished by its trilete spores and erect (vs. usually creeping) rhizomes. *Christella* rarely has deeply divided pinnae with free veins, and often bears orangish pear-shaped glands. *Plesioneuron* has similar deeply incised pinnae with free veins, and large persistent indusia, but does not overlap in geographic distribution, and often has more thickly chartaceous (and sometimes pustulate) laminae, pinna bases often short-petiolulate and rounded or cuneate (vs. sessile and truncate), and stipe scales usually thick and persistent (vs. thin and caducous). *Sphaerostephanos* and *Strophocaulon* both may have abruptly reduced auriculate pinnae, but often bear yellowish glands, and are largely non-overlapping with *Pseudocylosorus* geographically.

Biogeography and ecology.—Pseudocyclosorus, here circumscribed to include 14 species, is most diverse at middle elevations of the Pan-Himalayan region. *Pseudocyclosorus tylodes* occupies the most extensive range, occurring from Sri Lanka to the Philippines. Two species, *P. esquirolii* and *P. falcilobus,* reach as far north as Japan. Three species occur in Afro-Madagascar. Members of the genus are typically plants of streamsides and forest understories.

Taxonomic and phylogenetic studies.—Ching (1936, 1940) recognized the species now treated in *Pseudocyclosorus* as a natural group in early publications, but did not name the genus until later (Ching 1963). Based on similarities in venation, Ching (1963) believed *Pelazoneuron patens* and *P. kunthii* might also be allied, but this is not supported by molecular evidence (Smith & Cranfill 2002; Fawcett et al. in press). Species-level taxonomy of *Pseudocyclosorus* is highly variable among authors. *Pseudocyclosorus sensu* Ching (Ching 1963; Lin et al. 2013) included two Chinese species of *Trigonospora*, a genus that was segregated by Holttum (1971) based on having trilete spores and lacking abruptly reduced proximal pinnae. Holttum and Grimes (1980) recognized twelve species in their generic treatment of

Pseudocyclosorus. Later, the genus was greatly expanded, and 20 new species were described by Lin (in Shing & Lin 1999); 38 species are recognized in the Flora of China, including the two Chinese species of *Trigonospora* (Lin et al. 2013). However, in a recent revision of the species of the Pan-Himalayan region, Li et al. (2019) recognized only eight species, reducing 21 names to synonymy. It is apparent that *Pseudocyclosorus* would benefit from a densely sampled molecular study. For example, the species boundary between *P. subochthodes* and *P. esquirolii* is unclear (Li et al. 2019), and phylogenetic studies that have included multiple accessions of *P. esquirolii* (He & Zhang 2012; Fawcett et al. in press) have resolved that species as paraphyletic; these results suggest that further study, especially of widespread and variable taxa, is warranted.

Herein, we adopt a conservative, morphology-based classification largely following Li et al. (2019), pending further study and a greatly expanded phylogenetic dataset, preferably including taxa recognized by Lin et al. (2013). An even more conservative taxonomic concept of this group is favored for species of India by Fraser-Jenkins (1997, 2008b), who considered several species and varieties to be synonymous, and treated *Pseudocyclosorus* as a subgenus of *Thelypteris s.l.*

Pseudocyclosorus is sister to *Trigonospora* plus a clade of two species from Madagascar, *Pneumatopteris humbertii* and *Pronephrium fidelei*. This clade is in turn sister to *Abacopteris*, treated herein as a small genus of Southeast Asia and eastern Malesia. Two species here tentatively maintained in *Christella s.s.*, *C. chaseana* and *C. gueintziana*, resolve in *Pseudocyclosorus* in some individual gene trees (Fawcett et al. in press), suggesting possible hybrid origin. They are not closely related to other species of *Pelazoneuron*, where Holttum (1974a) treated them, despite striking superficial similarity (Moran & Smith 2001).

Constituent species.—Pseudocyclosorus camerounensis Holttum; **P. canus* (Baker) Holttum & J.W. Grimes; **P. esquirolii* (Christ) Ching; **P. falcilobus* (Hook.) Ching; *P. gamblei* Holttum & J.W. Grimes; *P. griseus* Holttum & J.W. Grimes; *P. johannae* Holttum; *P. ochthodes* (Kunze) Holttum; **P. ornatipes* Holttum & J.W. Grimes; *P. pseudofalcilobus* W.M. Chu; **P. pulcher* (Bory ex Willd.) Holttum; *P. stramineus* Ching ex Y.X. Lin; **P. subochthodes* (Ching) Ching; **P. tylodes* (Kunze) Ching

Taxa treated in Plesioneuron.—Pseudocyclosorus caudatus Holttum; *P. excisus* Holttum. These were both described in *Pseudocyclosorus* (Holttum & Roy 1965) and later transferred to *Pneumatopteris* (Holttum 1973a).

Names of uncertain status.—Pseudocyclosorus duclouxii was treated as dubious by Li et al. (2019); *P. furcovenulosus* Y.X. Lin, *P. guangxianensis* Ching ex Y.X. Lin, *P. pectinatus* Ching, and *P. submarginalis* Ching ex Y.X. Lin were treated in Flora of China, but are known from few collections that are unavailable for study, and were not included in the revision by Li et al. (2019). *Pseudocyclosorus tibeticus* Ching & Y.X. Lin was excluded from the Flora of China (Lin et al. 2013), pending further study.

Incertae sedis.—Pseudocyclosorus petrophila (Copel.) Holttum, from New Guinea (Holttum & Roy 1965), treated as *Pneumatopteris petrophila* (Copel.) Holttum in later works, shares the opposite, hastate-auricled reduced proximal pinnae of mainland *Pseudocyclosorus* and free veins shared among all species, but is a major geographic outlier. It may have closer affinities to *Plesioneuron* or *Sphaerostephanos*, but we do not believe it is close to *Pneumatopteris*, where Holttum (1973a) later treated it. *Pronephrium articulatum* (Houlston & T. Moore) Holttum was recovered as nested within *Pseudocyclosorus* in recent Bayesian phylogenetic analyses, with 99% posterior probability (Patel et al. 2019a). However, it differs in having up to four pairs of anastomosing veins below the sinus, proximal sori sometimes elongate, and unusual venation not seen elsewhere in the family: abaxially, veins are prominent until reaching sori, and obscure beyond them. The large, persistent indusia agree well with *Pseudocyclosorus* but, pending further data confirming its placement in *Pseudocyclosorus*, we refrain from making a new combination. A species of the Seychelles and São Tomé (see Holttum 1974a), *Sphaerostephanos elatus* (Bojer) Holttum is well supported as sister to *Pseudocyclosorus* in the nDNA analyses of Fawcett et al. (in press), but is well supported as sister to three species we now recognize as *Abacopteris* in studies relying primarily on cpDNA (e.g., Patel et al. 2019a). *Sphaerostephanos elatus* differs from all species in *Pseudocyclosorus* in having several pairs of veins anastomosing below the sinus, but it is alike in having the characteristic proximal pinnae abruptly reduced to triangular auricles, and large, persistent indusia. In our phylogenetic analysis (Fawcett et al. in press) the Afro-Madagascan *P. pulcher* is sister to all other *Pseudocyclosorus*, with the core clade of the genus all from the Pan-Himalayan region.

PSEUDOPHEGOPTERIS

Pseudophegopteris Ching, Acta Phytotax. Sin. 8:313. 1963.—Type: *Pseudophegopteris pyrrhorhachis* (Kunze) Ching [= *Polypodium pyrrhorhachis* Kunze]

Toppingia O. Deg., I. Deg. & A.R. Sm. ex O. Deg. & I. Deg.
For additional generic synonymy, see Holttum (1969, 1971).

Etymology.—Gr. *pseudo,* false + *phegos*, beech + *pteris* = fern; a distinctive relative of *Phegopteris*.

Plants terrestrial, fronds of determinate growth (except in *P. keraudreniana*, where growth is indeterminate), mostly medium-sized to very large, 50–300+ cm tall; **rhizomes** short- to long-creeping, or ascending, or erect, with thin scales, these brown to tan, lanceolate, with scattered hairs along margins and sometimes sparingly on surface; **fronds** clustered, or remote, monomorphic; **stipes** 30–60 cm long, not grooved adaxially, stramineous to red-brown, often glossy; **stipe scales** thin, lanceolate to ovate, light brown, 2–6 mm long, typically with superficial hairs; **blades** herbaceous to chartaceous, lacking buds or proliferations, pinnate-pinnatifid to bipinnate-pinnatifid or slightly more divided, with blade apex gradually tapering and pinnatifid; proximal pinnae of well-developed fronds not reduced or with 1–2 lowermost pairs somewhat reduced (sometimes to less than half the length of longest pinnae), but blades lacking greatly reduced, glanduliform pinnae; rachises adaxially not grooved, bearing simple and sometimes forked acicular hairs, some spp. glabrescent, typically lacking scales at maturity (except *P. dianae*, which is densely and persistently scaly); **pinnae** usually opposite to subopposite, sessile or increasingly adnate, especially more distal pinna (e.g., as in *P. rectangularis*), spreading or obliquely spreading, costae not grooved adaxially, truncate at bases, acute at tips, to ca. 15(–20) × 2(–3) cm wide, pinnatifid or pinnate-pinnatifid with pinnules strongly adnate and often connected at their bases, in larger species free, sessile or nearly so, with or without acroscopic and/or basiscopic, more lobed basal auricles; **veins** free, often forking in ultimate segments, ± prominent, at least readily visible on both sides, vein ends clavate adaxially and not reaching segment margins; **aerophores** absent at pinna bases; **indument abaxially**, if present, of sparse to moderately dense unicellular hyaline acicular hairs, lacking scales, blades often glabrescent with age; short-stipitate glands sometimes present along costae and costules; **indument adaxially** of hyaline acicular hairs to ca. 1 mm long along costae, sometimes also with hairs on costules and ultimate veins, occasionally on laminar tissue between veins; **pustules** absent on abaxial surfaces between veins; **sori** medial to supramedial, round to oblong (length 2 × width), exindusiate, not confluent at maturity; **sporangia** short-stalked, capsules glabrous or with short setulae 0.1–0.2 mm and/or yellowish short-stipitate glands ca. 0.1 mm adjacent to annulus; **spores** tan to brown, with numerous shallow and narrow ridges forming a reticulate network of polygonal areoles having a smooth or papillate surface (Holttum 1969; Tryon & Lugardon 1991; Patel et al. 2019a), lacking broad wings; $x = 31$, diploids and tetraploids known, about 10 spp. counted. No hybridization with any other genus has been demonstrated.

Diagnosis.—Characters used by Holttum (1969) to separate *Pseudophegopteris* from *Macrothelypteris* include: 1) thinner, brownish stipe base and rhizome apex scales on *Pseudophegopteris* (vs. pale thickened scales); 2) absence of septate hairs on axes and blades in *Pseudophegopteris* (vs. often septate); and exindusiate sori (vs. often with small indusia). In addition, ultimate segments and distal pinnae in *Pseudophegopteris* are more pronouncedly adnate, the pinnae are opposite (vs. alternate), and there are differences in spore ornamentation. These two genera have retained their rank in publications on the family by Smith (1990, 2006) and in PPG I (2016), as well as many recent floras.

Biogeography and ecology.—*Pseudophegopteris* comprises 28 species and is widely distributed from tropical West Africa (and offshore island endemic species on São Tomé and St. Helena), Madagascar, Réunion, India, southeast Asia, and Japan, through Malesia to Fiji and Hawaii (Holttum 1969). The greatest diversity in the genus is in China, with 12 species (including four endemics), one with two varieties (Lin et al. 2013). One of the oceanic island endemics, *P. dianae*, from St. Helena, is remarkable in its very dense, persistent, light brown, glabrous, ovate scales along the rachis. The other five Atlantic and Indian Ocean island species, *P. andringitrensis*, *P. aubertii*, *P. cruciata*, *P. henriquesii*, and *P. rammelooi* (see Holttum 1977b; Pichi Sermolli 1983), are much more similar to the larger, bipinnate-pinnatifid species such as *P. yunkweiensis* and *P. paludosa*, from southeast Asia and Malesia (Holttum 1974a). The sole species in Hawaii, *P. keraudreniana*, is quite rare and localized; it differs from all others in the genus in having indeterminate growth, with dormant tips growing intermittently after lower pinnae mature (Palmer 2003). Species of *Pseudophegopteris* occur mainly along streams, in thickets, and in rock crevices in dense lowland and montane forests, up to 3100 m; most species occur from 1000–2500 m.

Taxonomic and phylogenetic studies.—Both *Pseudophegopteris* and *Macrothelypteris* were first recognized at generic rank by Ching (1963). Holttum's studies further clarified their distinction and differences (Holttum 1969, 1971, 1974a, 1977b, 1982). *Pseudophegopteris* is most closely related to *Macrothelypteris* and *Phegopteris*, which together constitute the subfamily Phegopteridoideae (PPG I 2016). In our analyses (Fawcett et al. in press), and also those of He and Zhang (2012), Schneider et al. (2013), and Almeida et al. (2016), *Pseudophegopteris* is monophyletic and sister to a monophyletic *Phegopteris*, and this combined clade is in turn sister to *Macrothelypteris*. The close relationship of these three genera is evidenced by the fact they are all free-veined, often with forked veins that end before reaching the segment margins, and stipes, rachises, and costae not grooved adaxially. This separates them from all other genera of Thelypteridaceae, except *Metathelypteris* and some *Leptogramma*, which are not closely related. The phegopteroids were clearly understood and delineated by Holttum (1969), who provided a revision/synopsis of these genera, prior to their recognition as subfamily Phegopteridoideae (PPG I 2016). In part, because of the greater blade dissection in *Pseudophegopteris* and *Macrothelypteris,* but also because of a belief in the relationship of Thelypteridaceae to Cyatheaceae (Holttum 1947, 1969, 1982), Holttum thought these three genera showed the most primitive frond-form in the family. Although they are sister to all other taxa of Thelypteridaceae in molecular analyses, all evidence suggests that they are not closely related to, or derived from, Cyatheaceae.

Notes.—Based on a sample of five species, spores of *Pseudophegopteris* are very distinctive and consistently sculptured: low ridges forming a polygonal reticulate network, smooth papillose intra-areolar surfaces, and a gemmulate exospore (Tryon & Lugardon 1991). This is somewhat similar to *Phegopteris*, which has spores that differ in having a relatively unsculptured surface or a more coarsely reticulate network with a tuberculate intra-areolar surface. Spores of *Macrothelypteris* have a finer reticulate network of ridges with smaller, more rounded areoles (similar to spores of some species of *Amauropelta*), or a coarser, more irregular network of perforate folds (Tryon & Lugardon 1991).

All necessary combinations except one have been made in *Pseudophegopteris*, by Holttum (1969, 1982).

New combination.—

Pseudophegopteris rammelooi (Pic.Serm.) A.R. Sm. & S.E. Fawc., **comb. nov.**—*Macrothelypteris rammelooi* Pic.Serm., Bull. Jard. Bot. Natl. Belg. 53(1/2): 270(–272), fig. 16. 1983.

Constituent species.—Pseudophegopteris andringitrensis Rakotondr.; *P. aubertii* (Desv.) Holttum; **P. aurita* (Hook.) Ching; ***P. brevipes* Ching & S.K. Wu; **P. bukoensis* (Tagawa) Holttum; **P. cruciata* (Willd.) Holttum; *P. cyclocarpa* Holttum; *P. dianae* (Hook.) Holttum; *P. fijiensis* K.U. Kramer & Zogg; *P. henriquesii* (Baker) Holttum; **P. hirtirachis* (C. Chr.) Holttum; **P. keraudreniana* (Gaudich.) Holttum; *P. kinabaluensis* Holttum; **P. levingei* (C.B. Clarke) Ching; ***P. microstegia* (Hook.) Ching; *P. pallida* Ching; **P. paludosa* (Blume) Ching; *P. persimilis* (Baker) Holttum; **P. pyrrhorhachis* (Kunze) Ching; *P. rammelooi* (Pic.Serm.) A.R. Sm. & S.E. Fawc.; **P. rectangularis* (Zoll.) Holttum; ***P. subaurita* (Tagawa) Ching; *P. sumatrana* Holttum; *P. tenggerensis* Holttum; **P. tibetana* Ching & S. K. Wu; *P. yigongensis* Ching; **P. yunkweiensis* (Ching) Ching; ***P. zayuensis* Ching.

Schneider et al. (2013) sampled 10 species, and concluded that there has been a higher diversification rate in *Pseudophegopteris* (largely tropical), as compared with its sister genus *Phegopteris* (largely temperate), but that a latitudinal difference in the distribution of these genera might be a reflection of a greater extinction rate in the latter, and possibly a consequence of uplift of the Himalayas.

REHOLTTUMIA

Reholttumia S.E. Fawc. & A.R. Sm., **gen. nov.**—Type: *Reholttumia nitidula* (C. Presl) S.E. Fawc. & A.R. Sm. [≡ *Nephrodium nitidulum* C. Presl]

For species synonymy, see Holttum (1973a, 1974a, 1977b, 1982).

Etymology.—The name honors Richard Eric Holttum (1895–1990), whose keen insights, perseverance, and fundamental contributions to our knowledge of Thelypteridaceae enabled the present work. Holttum's focus was especially on species in the Old World tropics where the family is most diverse and least known. His careful examination of type material in numerous major herbaria resolved many problems that had plagued the taxonomy of the group for more than a century.

Plants terrestrial, medium-sized to large (to 2 m tall); **rhizomes** ascending, erect, short-creeping or rarely long-creeping, rhizome scales brown, often caducous; **fronds** monomorphic, erect to arching, rarely pendant, pinnate-pinnatifid; **stipes** stramineous, less often brown; **stipe scales** thick, brown, broadly ovate to linear-lanceolate, glabrous or with marginal setae, apparently caducous, rarely extending to rachis (*R. rodigasiana*); **blades** membranaceous to chartaceous, drying green, sometimes brown-olivaceous, but never reddish, blade apex gradually reduced, proximal pinnae not reduced, or gradually to subabruptly reduced to small, sometimes auriculate pinnae, the smallest typically at least 1 cm long, rarely less than 5 mm, proliferous buds absent; **pinnae** sessile to subsessile, pinna-bases truncate, margins usually incised 1/3–3/5 to costae, segment apices typically rounded, sometimes truncate (*R. truncata*), rarely acute (*R. costata*), proximal pinnae gradually tapered towards bases or with acroscopic auricles; **veins** of one to three pairs anastomosing to form an excurrent veinlet running to sinus membrane, or ending below it (*R. ecallosa*), subsequent veins ending at margin above sinus; **aerophores** absent, or present as swelling or discoloration at pinna-base, never peg-like; **indument abaxially** of short, erect hairs sometimes present on axes, laminar tissue typically glabrous, but erect acicular hairs sometimes present (*R. ecallosa*); **indument adaxially** often restricted to antrorsely arching hyaline or reddish hairs along rachis and costae, but short-erect hairs sometimes present on axes; **pustules** sometimes present on adaxial laminae, these large and irregular or minute, colorless, and glandular (*R. ecallosa*); **sori** round, discrete, typically medial on veins, sometimes inframedial, almost always indusiate (except *R. costata* sometimes exindusiate), though shriveled indusia in mature sori may be obscure, indusia dark brown, glabrous or with acicular hairs; **sporangia** glabrous, or with stipitate glands on capsules, these usually colorless, rarely bearing setulae (except *R. oxyoura*); **spores** tan to brown, perine with tubercles or robust echinae (Patel et al. 2019a; Tryon & Lugardon 1991); x = 36, based on five species counts, mostly diploid, but *R. truncata* has both diploid and tetraploid cytotypes. No interspecific or intergeneric hybrids are known.

Diagnosis.—*Reholttumia* is distinguished from *Pneumatopteris s.s.* by having inconspicuous or swollen (vs. peg-like) aerophores; segment apices typically rounded or truncate (vs. broadly acute); sporangia sometimes bearing stipitate glands, but rarely setulose; proximal pinnae gradually or subabruptly (vs. abruptly) reduced, rarely reduced to less than 5 mm long; and laminae drying green, or brown-olivaceous (vs. sometimes reddish). The pinna segments of *Reholttumia* typically have about 7 veins per cm (vs. about 11 veins per cm in *Pneumatopteris s.s.*), but species with smaller proportions, and narrower pinnae (e.g., *R. macroptera*, *R. kerintjiensis*) may have as many as 11 veins per cm. Another species, *R. laevis*, is atypical in the genus in having oblique, asymmetric pinnae, small stature, and a creeping rhizome; it is also the earliest-diverging species in our sample. *Christella* differs by generally having abundant hairs on axes and laminae, and often by having characteristic pear-shaped orangish laminar and sporangial glands; it also lacks laminar pustules. *Sphaerostephanos* differs in sometimes having yellow, sessile spherical glands. *Plesioneuron* differs by having dark (vs. tan) spores, and pinnae usually incised nearly to the costae.

Biogeography and ecology.—The 30 species of *Reholttumia* occur in forests and openings, often beside streams, generally at lower elevations, but some species reach about 2300 m. The greatest species diversity is in Malesia, but a dozen species occur in the Pacific and Australasia (Holttum 1977b), with one species reaching the Hawaiian Islands (*R. hudsoniana*). The western range of the genus nearly corresponds to that of its most widespread and highly variable species, *R. truncata*, which occurs in Australia, China, India, Japan, Laos, Malaysia, Malesia, Myanmar, Sri Lanka, Thailand, and Vietnam. The genus is represented on Madagascar by at least one species, *R. remotipinna*.

Taxonomic and phylogenetic studies.—All constituent species of *Reholttumia* were treated within *Pneumatopteris* by Holttum (1971, 1973a, 1974a, 1977b, 1982). However, his taxonomic concept of *Pneumatopteris* has proven to be extremely broad and heterogeneous, as it encompasses species from ten distinct lineages, which we treat herein within existing genera or in newly described genera (see *Pneumatopteris* for further discussion). Because the type of *Pneumatopteris*, *P. callosa,* is in a small clade that is sister to *Sphaerostephanos* (a genus of about 200 species; **Fig. 1**), we recognize *Pneumatopteris* in a greatly restricted sense, and segregate *Reholttumia*—a morphologically coherent and large clade that is sister to *Pneumatopteris s.s.* plus *Sphaerostephanos* (**Fig. 1;** Fawcett et al. in press). This new genus represents the largest segregate of *Pneumatopteris sensu* Holttum. In our phylogenetic analyses, *Reholttumia* is represented by 25 accessions, including 13 of 30 currently recognized species, and several undescribed species (Fawcett et al. in press).

New combinations and constituent species.—

Reholttumia basicurtata (Holttum) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Pneumatopteris basicurtata* Holttum., Blumea 21:309. 1973.

Reholttumia boridensis (Holttum) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Pneumatopteris boridensis* Holttum., Fl. Males., Ser. 2, Pterid. 1(5):434. 1982.

Reholttumia bryanii (C. Chr.) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Dryopteris bryanii* C. Chr., Bishop Mus. Bull. 177:89. 1943.—*Pneumatopteris bryanii* (C. Chr.) Holttum

Reholttumia christelloides (Holttum) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Pneumatopteris christelloides* Holttum, Blumea 21:311. 1973.

***Reholttumia costata** (Brack.) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Goniopteris costata* Brack., in Wilkes, U.S. Expl. Exp. 16:28. 1854.—*Cyclosorus costatus* (Brack.) Ching—*Pneumatopteris costata* (Brack.) Holttum—*Thelypteris costata* (Brack.) C.F. Reed

***Reholttumia ecallosa** (Holttum) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Cyclosorus ecallosus* Holttum, Gard. Bull. Singapore 11:269. 1947.—*Pneumatopteris ecallosa* (Holttum) Holttum—*Thelypteris ecallosa* (Holttum) C.F. Reed

Reholttumia glaberrima (A. Rich.) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Aspidium glaberrimum* A. Rich., Sert. Astrol. 18. 1834.—*Pneumatopteris glaberrima* (A. Rich.) Holttum

***Reholttumia hudsoniana** (Brack.) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Nephrodium hudsonianum* Brack., in Wilkes, U.S. Expl. Exp. 16:88. 1854.—*Cyclosorus hudsonianus* (Brack.) Ching—*Pneumatopteris hudsoniana* (Brack.) Holttum—*Thelypteris hudsoniana* (Brack.) C.F. Reed

Reholttumia inclusa (Copel.) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Dryopteris inclusa* Copel., Univ. Calif. Publ. Bot. 14:373. 1929.—*Cyclosorus inclusus* (Copel.) Copel.—*Pneumatopteris inclusa* (Copel.) Holttum—*Thelypteris inclusa* (Copel.) C.F. Reed

***Reholttumia jermyi** (Holttum) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Pneumatopteris jermyi* Holttum, Blumea 21:310. 1973.

Reholttumia kerintjiensis (Holttum) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Pneumatopteris kerintjiensis* Holttum, Blumea 21:312. 1973.

***Reholttumia laevis** (Mett.) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Aspidium laeve* Mett., Abh. Senckenberg. Naturf. Ges. 2(2):388(-389). 1858.—*Cyclosorus laevis* (Mett.) Ching—*Thelypteris laevis* (Mett.) C.F. Reed—*Pneumatopteris laevis* (Mett.) Holttum

Reholttumia laticuneata (Holttum) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Pneumatopteris laticuneata* Holttum, Blumea 21:312. 1973.

***Reholttumia longipes** (Blume) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Aspidium longipes* Blume, Enum. Pl. Jav. 155. 1828.—*Cyclosorus longipes* (Blume) Ching—*Pneumatopteris longipes* (Blume) Holttum—*Thelypteris longipes* (Blume) C.F. Reed

Reholttumia loyalii (Holttum) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Pneumatopteris truncata* (Poir.) Holttum var. *loyalii* Holttum, Blumea 21:314. 1973.—*Cyclosorus truncatus* (Poir.) Farwell var. *loyalii* (Holttum) Panigrahi, non *Cyclosorus loyalii* (Panigrahi & Sarn. Singh) Mazumdar & R. Mukhop.—*Thelypteris loyalii* (Holttum) Fraser-Jenk

***Reholttumia macroptera** (Copel.) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Dryopteris macroptera* Copel., Univ. Calif. Publ. Bot. 12:392. 1931.—*Cyclosorus macropterus* (Copel.) Ching—*Pneumatopteris macroptera* (Copel.) Holttum—*Thelypteris macroptera* (Copel.) C.F. Reed

***Reholttumia magnifica** (Copel.) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Dryopteris magnifica* Copel., Bull. Bernice P. Bishop Mus. 59:11. 1929.—*Cyclosorus magnificus* (Copel.) Ching—*Pneumatopteris magnifica* (Copel.) Holttum—*Thelypteris magnifica* (Copel.) C.F. Reed (**Fig. 7B**).

Reholttumia michaelis (Holttum) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Pneumatopteris michaelis* Holttum, Blumea 21:313. 1973.

Reholttumia micropaleata (Holttum) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Pneumatopteris micropaleata* Holttum, Blumea 21:319. 1973.

***Reholttumia nitidula** (C. Presl) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Nephrodium nitidulum* C. Presl, Epimel. Bot. 46. 1851.—*Cyclosorus nitidulus* (C. Presl) Copel.—*Pneumatopteris nitidula* (C. Presl) Holttum—*Thelypteris nitidula* (C. Presl) C.F. Reed

Reholttumia novae-caledoniae (Holttum) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Pneumatopteris novae-caledoniae* Holttum, Blumea 21:313. 1973.

Reholttumia oxyoura (Copel.) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Dryopteris oxyoura* Copel., Philipp. J. Sci. 60:107. 1936.—*Cyclosorus oxyourus* (Copel.) Copel.—*Pneumatopteris oxyoura* (Copel.) Holttum—*Thelypteris oxyoura* (Copel.) C.F. Reed

Reholttumia papuana (Holttum) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Pneumatopteris papuana* Holttum, Blumea 21:311. 1973.

Reholttumia pergamacea (Holttum) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Pneumatopteris pergamacea* Holttum, Blumea 21:315. 1973.

Reholttumia psilophylla (Holttum) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Pneumatopteris psilophylla* Holttum. Fl. Males., Ser. 2, Pterid. 1(5):427. 1982.

***Reholttumia remotipinna** (Bonap.) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Dryopteris remotipinna* Bonap., Notes Pterid. 5:57. 1917.—*Cyclosorus remotipinnus* (Bonap.) Ching—*Pneumatopteris remotipinna* (Bonap.) Holttum—*Thelypteris remotipinna* (Bonap.) C.F. Reed

***Reholttumia rodigasiana** (T. Moore) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Nephrodium rodigasianum* T. Moore in Linden, Ill. Hort. 29:27, t. 442. 1882.—*Cyclosorus rodigasianus* (T. Moore) Ching—*Pneumatopteris rodigasiana* (T. Moore) Holttum—*Thelypteris rodigasiana* (T. Moore) C.F. Reed

***Reholttumia sogerensis** (Gepp) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Dryopteris sogerensis* Gepp, J. Bot. 61(Suppl.): 61. 1923.—*Cyclosorus sogerensis* (Gepp) Ching—*Pneumatopteris sogerensis* (Gepp) Holttum—*Thelypteris sogerensis* (Gepp) C.F. Reed

***Reholttumia truncata** (Poir.) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Polypodium truncatum* Poir., Encycl. Meth. 5:534. 1804.—*Cyclosorus truncatus* (Poir.) Farw.—*Pneumatopteris truncata* (Poir.) Holttum—*Thelypteris truncata* (Poir.) K. Iwats.

Reholttumia vaupelii (C. Chr.) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Dryopteris vaupelii* C. Chr., Bull. Bernice P. Bishop Mus. 177:89, t. 3B. 1943.—*Pneumatopteris vaupelii* (C. Chr.) Holttum

Incertae sedis.—Several additional species treated as *Pneumatopteris* by Holttum are potentially referable to *Reholttumia*, but we treat them herein as *incertae sedis*, pending additional data. These include the Afro-Madagascan species *P. comorensis* Holttum, *P. prismatica* (Desv.) Holttum, *P. usambarensis Holttum*, and *P. venulosa* (Kuntze) Holttum, and several species from Malesia, including *Pneumatopteris japenensis* Holttum and *P. tobaica* Holttum. See the *Pneumatopteris* treatment for a complete list of *incertae sedis* in *Pneumatopteris s.l.*

SPHAEROSTEPHANOS

Sphaerostephanos J. Sm. in Hooker, Gen. Fil., t. 24. 1839.—*Thelypteris* subg. *Sphaerostephanos* (J. Sm.) K. Iwats., Mem. Coll. Sci Univ. Kyoto, ser. B, 31:32. 1964.—Type: *Sphaerostephanos asplenioides* J. Sm. [= *S. polycarpos* (Blume) Copel.]

Haplodictyum C. Presl
Mesochlaena(R. Br.) J. Sm.
Proferea C. Presl
For additional generic synonymy, see Holttum (1974a, 1977b, 1982).

Etymology.—Gr. *sphaera*, sphere + *stephanos*, crown, in reference to the spherical yellow glands adorning the sori; these may be borne on the receptacles, indusia (**Fig. 2D**), or sporangia, and are characteristic of the genus.

Plants mostly terrestrial, or occasionally cremnophilous or rheophytic, mostly from (10–)30–100(–200) cm tall; **rhizomes** mostly suberect or erect, occasionally short-creeping, rarely long-creeping or scandent (*S. scandens* Holttum); **fronds** monomorphic or with fertile fronds smaller and more erect (fronds subdimorphic to dimorphic, e.g., *S. dimorphus*), usually pinnate-pinnatifid or once-pinnate, rarely pinnae subentire, pinnatifid or weakly divided, with elongate apical lamina subtended by reduced lateral pinnae as in *S. beccarianus* (**Fig. 7B**) and related species (no simple-bladed or twice-pinnate species known), usually arching; **stipes** stramineous or brownish, usually dull, stipe bases and rhizome scales brown to tan, ovate to lanceolate, rarely glabrous, thin, usually with acicular, hyaline hairs 0.1–0.2 mm on margins and surfaces; **blades** usually chartaceous, less often thicker and subcoriaceous to coriaceous (species of more open areas, e.g., *S. lithophyllus*), usually drying green, lanceolate, ovate to deltate, proximal pinnae usually subabruptly or abruptly reduced (**Fig. 2K**), occasionally gradually reduced, often > 6 pairs (to 30+ pairs, e.g., in *S. sagittifolius*), basal pair(s) often auriculiform or glanduliform and < 5 mm long, blade apex gradually reduced, with distal pinnae not or only slightly decurrent, or subabruptly reduced and pinna-like; proliferous buds absent in axils of distal pinnae (no gemmiferous spp. known); **pinnae** entire (e.g., *S. debilis, S. dimorphus, S. mutabilis*) to subentire, crenate, shallowly lobed, or often pinnatifid to more than half their width, rarely pinnatisect or lobed within 1 mm of costae (e.g., *S. novoguineensis*, *S. williamsii*), typically straight, sometimes with small acroscopic auricles at pinna bases, adaxially grooved; **veins** usually prominent abaxially and adaxially (readily seen without transmitted light), lowermost pair from adjacent segments running to margin at a sinus between adjacent lobes, usually united to form an excurrent vein that runs to sinuses, or with 2–4 pairs (exceptionally 10 pairs united in *S. maximus*) united and forming a common excurrent vein (straight or zig-zag) that runs to a sinus, rarely lowermost veins meeting margins above sinuses (e.g., *S. novoguineensis*, *S. williamsii*), free veins ending at pinna margins; **aerophores** absent or often present at pinna bases, if present then swollen, tuberculate, or rod-like to 2 mm long (these species generally producing mucilage during development), or, forming a small patch of darkened aerating tissue at pinna bases; **indument abaxially** usually of hyaline acicular hairs on rachises, costae, veins, and sometimes between veins, rarely the blades glabrous or nearly so (e.g., *S. cataractorum*, a rheophyte from the Admiralty Islands), **indument adaxially** of hyaline or sometimes reddish acicular hairs on rachises and costae, sometimes also on veins and between veins, hairs often appressed between veins, scattered to dense, hairs on stipes and rachises short to long, 0.1–1(–2) mm, sparse to dense, rarely blades glabrous or glabrescent, usually single-celled, rarely septate; glands, if present, resinous or hemispherical and opaque, usually light yellowish to light orangish, seldom capitate (short-stipitate), borne on laminae and veins abaxially and sometimes also adaxially; **pustules** generally absent on laminar tissue (present in some spp., e.g., *S. beccarianus*, **Fig. 7A**); **sori** inframedial, medial, or infrequently submarginal, usually round, less often oblong or elongate along veins in a few spp. (e.g., the type), indusiate or exindusiate, indusia if present usually round-reniform or reduced to a fragment, usually whitish or tan when young, persistent to evanescent, hairy and/or glandular to glabrous (**Fig. 2D, 2E**); **sporangia** often setulose or with sessile glands just below the annulus like those of lamina; **spores** pale brown, lacking pronounced winglike ridges or echinae, reticulate and perforate (fenestrate), secondary sculpturing gemmulate (Tryon & Lugardon 1991); x = 36, ten species counted, mostly diploid, tetraploid counts few in comparison.

Diagnosis.—The most morphologically similar genera to *Sphaerostephanos* are other cyclosoroid genera, including the closest relatives, *Pneumatopteris s.s.*, *Reholttumia*, *Pronephrium s.s.*, and several other more distantly related christelloid genera—*Christella s.s.*, *Pseudocyclosorus*, *Amblovenatum*, and *Abacopteris*. Most of these, except for *Pseudocyclosorus* and some *Amblovenatum*, have at least a single pair of veins (if not many more) anastomosing below the sinuses and with an excurrent vein to the sinus. All have a base chromosome number of x = 36. All occupy large areas in continental Asia and Malesia, with extensions into India, Melanesia, Polynesia, and Australasia for some species. In the Flora of China (Lin et al. 2013), most of the christelloid genera mentioned above, including *Sphaerostephanos*, were treated as part of a greatly expanded concept of *Cyclosorus*, except for a separately treated *Pseudocyclosorus and Pronephrium s.l.* (which included *Abacopteris*). However, the Flora of China contains only four species of *Sphaerostephanos*, an extremely depauperate representation of the genus. Co-occurrence of many genera, recent and rapid diversification, and a lack of taxonomic experts in the group have made classification and identification of cyclosoroid Thelypteridaceae especially difficult and somewhat contentious. Rampant homoplasy in *Sphaerostephanos* and related genera has caused great difficulty in delineating taxa. As may be expected for a genus with more than two hundred species occupying diverse habitats, there is no single morphological character known that reliably holds the genus together—rather one must utilize a suite of characters, and have complete fertile specimens (including rhizomes) for identification to genus. Nevertheless, the circumscription of the genus by Holttum (1982) corresponds very closely to a clade, with only minor adjustments. The following characteristics are common to most (but by no means all) species: short-creeping to suberect or erect rhizomes, with lanceolate, brownish, hairy scales at apices (as well as at stipe bases); pinnate fronds with entire, subentire, crenate, or shallowly to deeply lobed pinnae, i.e., blades once pinnate to pinnate-pinnatifid; veins anastomosing, with at least the lowermost pair from adjacent segments uniting at an obtuse angle and producing an excurrent vein that runs to the sinus or to the excurrent vein in the next areole (thus bisecting the areole), i.e., veins sometimes meniscioid with as many as four pairs (10 pairs in *S. maximus*) joined in a file between costa and pinna margin; abruptly or subabruptly reduced proximal pinnae; costae abaxially with spreading to curved-appressed hairs, these often stout; the presence abaxially, and less often adaxially, of sessile, spherical or somewhat flattened, yellowish to light orangish, transparent glands on the laminar tissue between veins, on veins, and on costae and costules; often appressed or ascending (distally pointed) acicular, hyaline hairs between the veins adaxially, these often thin, mostly 0.1–0.3 mm long; the absence of pustules on laminar tissue; and $x = 36$.

Biogeography and ecology.—Species occur mostly at low and middle elevations, from near sea level to ca. 1500 m, with a few to 2000 m, and even fewer to 3000 m (to 3750 m, in subalpine shrublands and grasslands, e.g., *S. archboldii*, from New Guinea). Many of the 190 species of *Sphaerostephanos* are highly localized, endemic to relatively small areas, and found mostly in primary, undisturbed forests. However, as with many thelypteroid genera, some widespread spp. (e.g., *S. heterocarpos*, **Fig. 2K**) occur in disturbed forests, at forest margins, and sometimes in open areas; occasionally they grow on rocks or streamsides, where they tend to form smaller, less conspicuous adult plants. A few are rheophytes, e.g., *S. debilis*, *S. mutabilis*, with very narrow, streamlined, sometimes nearly glabrous pinnae. Some species are weedy and found especially along roadsides, trails, and wet ditches. The major center of diversity for *Sphaerostephanos* in the Paleotropics is unquestionably Malesia, with 150+ spp.; Melanesia and Polynesia are lesser centers of diversity. New Guinea is especially species-rich, with 60+ spp., most of them narrowly endemic and many of them poorly known.

Shortly after he expanded the concept of *Sphaerostephanos* from six species to more than 120, Holttum (1971, 1975, 1982) enlarged his concept still further, and described many new species, recognizing 152 spp. from Malesia, 12 species from tropical mainland Asia, 17 spp. from Polynesia and Australasia (Holttum 1977b), and four spp. from Africa and islands in the Indian Ocean (Holttum 1974a); most of the species he assigned to *Sphaerostephanos*, especially those from Malesia, Melanesia, and Polynesia, remain in that genus in our reclassification. However, we still include only two of the four species Holttum (1974a) recognized from Africa and islands of the Indian Ocean, *S. arbuscula* and *S. subtruncatus*, in *Sphaerostephanos*. About ten spp. are known from continental Asia including both of the African and Indian Ocean species, which also occur in India and Sri Lanka. The others are *S. gaudichaudii*, *S. heterocarpos*, *S. latebrosus*, *S. penniger*, *S. polycarpos*, *S. productus*, and *S. validus*, five of which also occur in western Malesia (see Holttum 1979). Species we exclude from *Sphaerostephanos*, where they were placed by Holttum, are noted below. No species are known from the New World.

With the addition of 15 species newly combined below, and placement of several species in other genera (see also below), there are about 190 known species in *Sphaerostephanos*, making it the second largest genus in the family, behind only *Amauropelta*. In Holttum's 1982 treatment, 66 taxa in *Sphaerostephanos* were known only from the type or one or two other collections, a testament to both their rarity and the paucity of herbarium collections. We are confident that there are dozens of undescribed species belonging to *Sphaerostephanos,* especially in eastern Malesia, where there are likely undiscovered narrowly distributed endemics; in addition, some more wide-ranging species, e.g., *S. heterocarpos*, are likely species complexes, in need of refinement and further study. Clearly, the genus is under-collected, because of the many superficially similar and highly local species and lack of specialists in the group.

Taxonomic and phylogenetic studies.—Until Holttum (1971) presented a new system of genera for Thelypteridaceae, *Sphaerostephanos* was a name applied to Old World species with elongate, indusiate sori, e.g., the type, *Sphaerostephanos asplenioides* J. Sm. [= *S. polycarpos* (Blume) Copel.]; this group comprised about six species. Holttum expanded his concept of *Sphaerostephanos* to include many species with round sori, and also some exindusiate species. Other salient characteristics of *Sphaerostephanos* included species with many pairs of gradually to often abruptly or subabruptly reduced proximal pinnae; veins mostly united below sinuses and forming a series of one to about four areoles, each with an included, excurrent veinlet, or with the excurrent veinlet continuous from one areole to the next; sessile, hemispherical, opaque, yellowish to light orangish glands usually present on the costules, veins, and often between the veins abaxially and sometimes also adaxially; sporangia slender-stalked and with sessile glands or setulae near the annulus; light brown spinulose spores; and $x = 36$. Although Holttum included species in *Sphaerostephanos* that were exceptional (deviated from the "norm") in some of these characteristics, most species could be comfortably placed in *Sphaerostephanos* on the basis of possessing a combination of these salient features.

Sphaerostephanos exhibits extremely wide variation in frond type, blade size, blade dissection, number and degree of reduction of proximal pinnae, and blade apex (conform or gradually reduced), with long aerophores or none at all, remarkably varied indument (glands and hairs), and presence or absence of indusia. There are diminutive species with few, small, entire pinnae, like *S. obtusifolius*, and *S. ddebilis* (pinnae ca. 10 × 2 mm), both from New Guinea, to large species with fronds > 1.5 m, pinnae to 30 × 2.5 cm (e.g., *S. braithwaitei*, from the Solomon Islands), species with 30+ pairs of small greatly reduced proximal pinnae (e.g., *S. sagittifolius*) and species with deltate blades—the lowest pinnae the longest and with reduced pinnae entirely absent. A group of related, pinnatifid or weakly divided species with just a few pinna pairs is exemplified by *S. beccarianus* (**Fig. 7B**), formerly included by Holttum (1972, 1982) in *Pronephrium* sect. *Pronephrium*. There are rheophytes with relatively few, entire pinnae 20+ times longer than wide and very narrow (< 5 mm), with only a single row of sori along each side of the costae (e.g., *S. mutabilis*). In short, just about any blade type imaginable can be found in the genus, short of forking gleicheniaceous blades or indeterminant ones. Some species have very long-creeping, narrow rhizomes, and bilaterally produced fronds, like *S. pentaphyllus*, thus mimicking some species of *Grypothrix* but lacking their hamate hairs; others form erect, relatively long trunks, e.g., *S. braithwaitei* and *S. archboldii*, to 60 cm tall in the latter.

In broadly based molecular analyses, *Sphaerostephanos* is monophyletic with minimal departure from previous classifications. Within the genus, there are two major clades, and a small clade of early diverging species (e.g., *S. larutensis* and *S. oosorus*; both are taxa with elongate sori). One of the two major clades includes many of the pinnate-pinnatifid taxa that tend to be hairy on both laminar surfaces (e.g., *S. heterocarpos*, **Fig. 2K**), while the second major clade includes several once-pinnate species to shallowly lobed species (e.g., *S. confertus*), including the taxa previously treated by Holttum (1982) in *Pronephrium* sect. *Pronephrium*. *Sphaerostephanos* is sister to newly redefined *Pneumatopteris s.s.* (Fawcett et al. in press; Fig. 1). This clade is in turn sister to *Reholttumia* and then *Pronephrium s.s.* (corresponding largely to Holttum's sect. *Dimorphopteris*). Together these four genera comprise the sphaerostephanoid clade. More distant relatives include members of the pseudocyclosoroid clade (*Abacopteris*, *Amblovenatum*, *Christella s.s.*, and *Pseudocyclosorus*), and *Strophocaulon* (whose two members include two very widespread spp. formerly placed in *Sphaerostephanos* by Holttum, 1982). All of these genera pertain to the christelloid clade, and most (except *Pseudocyclosorus*) contain species that usually have at least one pair of anastomosing veins, meeting at an obtuse angle below the sinuses and with an excurrent vein. Many, but not all, of these genera have reduced (sometimes greatly reduced) proximal pinnae, and most have sori with round-reniform indusia (but this lost in several evolutionary lines).

Most necessary combinations have been made in *Sphaerostephanos* by Holttum (1979, 1982), who included also homotypic and heterotypic synonyms in his revisions. We make combinations for the following species, placed by Holttum in other genera, especially *Pronephrium*.

New combinations.—

Sphaerostephanos bakeri (Harr.) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Nephrodium bakeri* Harr., J. Linn. Soc., Bot. 16:29. 1877.—*Cyclosorus bakeri* (Harr.) Copel.—*Haplodictyum bakeri* (Harr.) Ching—*Pronephrium bakeri* (Harr.) Holttum—*Thelypteris bakeri* (Harr.) C.F. Reed

***Sphaerostephanos beccarianus** (Ces.) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Meniscium beccarianum* Ces., Rendic. Acad. Napoli 16:27, 30. 1877.—*Cyclosorus beccarianus* (Ces.) Copel.—*Pronephrium beccarianum* (Ces.) Holttum (**Figs. 8A, 8B**).

***Sphaerostephanos brauseanus** (Holttum) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Pronephrium brauseanum* Holttum, Blumea 20:107. 1972.

Sphaerostephanos bulusanicus (Holttum) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Haplodictyum bulusanicum* Holttum, Kalikasan 2:61 1973.—*Pronephrium bulusanicum* (Holttum) Holttum

***Sphaerostephanos glandulosus** (Blume) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Aspidium glandulosum* Blume, Enum. Pl. Java, 144. 1828.—*Abacopteris glandulosa* (Blume) Fée—*Pronephrium glandulosum* (Blume) Holttum—*Thelypteris malayensis* (C. Chr.) C.F. Reed

Sphaerostephanos heterophyllus (C. Presl) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Haplodictyum heterophyllum* C. Presl, Epimel. Bot. 51. 1851.—*Pronephrium heterophyllum* (C. Presl) Holttum

***Sphaerostephanos incisus** (Copel.) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Pneumatopteris incisa* Holttum, Blumea 21:317. 1973.

Sphaerostephanos longbawanensis (K. Iwats. & M. Kato) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Thelypteris longbawanensis* K. Iwats. & M. Kato, Acta Phytotax. Geobot. 34(4–6):137(–138), f. 5. 1983.

Sphaerostephanos maximus (K. Iwats. & M. Kato) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Thelypteris maxima* K. Iwats. & M. Kato, Acta Phytotax. Geobot. 34(4–6):138. 1983.

Sphaerostephanos melanophlebius (Copel.) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Dryopteris melanophlebia* Copel., Philipp. J. Sci, Bot. 6:147. 1911.—*Cyclosorus melanophlebius* (Copel.) Ching—*Pronephrium melanophlebium* (Copel.) Holttum—*Thelypteris melanophlebia* (Copel.) C.F. Reed

Sphaerostephanos microlonchus (Christ) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Dryopteris microloncha* Christ, Philipp. J. Sci., Bot. 2:202. 1907.—*Cyclosorus microlonchus* (Christ) Copel.—*Pneumatopteris microloncha* (Christ) Holttum—*Thelypteris microloncha* (Christ) C.F. Reed

Sphaerostephanos micropinnatus (Holttum) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Pronephrium micropinnatum* Holttum, Blumea 20:108. 1972.

***Sphaerostephanos pentaphyllus** (Rosenst.) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Dryopteris pentaphylla* Rosenst., Repert. Spec. Nov. Regni Veg. 12:529. 1913.—*Pronephrium pentaphyllum* (Rosenst.) Holttum—*Thelypteris pentaphylla* (Rosenst.) C.F. Reed

Sphaerostephanos petiolatus (K. Iwats. & M. Kato) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Thelypteris petiolata* K. Iwats. & M. Kato, Acta Phytotax. Geobot. 34(4–6):139(–140), f. 7. 1983.

Sphaerostephanos pilosiusculis (Racib.) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Nephrodium pilosiusculum* Racib., Pteridoph. Buitenzorg 1:189. 1898.

Nephrodium debile Baker, J. Bot. 18:212. 1880.—*Pronephrium debile* (Baker) Holttum., non *Sphaerostephanos debilis* (Mett.) Holttum

Sphaerostephanos scopulorum (Holttum) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Pronephrium scopulorum* Holttum, Fl. Males., Ser. 2, Pterid., 1(5):532. 1981.

Sphaerostephanos subappendiculatus (Copel.) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Dryopteris subappendiculata* Copel., Univ. Calif. Publ. Bot. 18:220. 1942.—*Cyclosorus subappendiculatus* (Copel.) Copel.—*Pneumatopteris subappendiculata* (Copel.) Holttum

Sphaerostephanos superbus (Brause) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Dryopteris superba* Brause, Bot. Jahrb. Syst. 56:105. 1920.—*Cyclosorus superbus* (Brause) Ching—*Pneumatopteris superba* (Brause) Holttum

Sphaerostephanos womersleyi (Holttum) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Pronephrium womersleyi* Holttum, Blumea 20:108. 1972.

Constituent species.—*Sphaerostephanos acrostichoides* (Desv.) Holttum; *S. adenostegius* (Copel.) Holttum; *S. alatellus* (Christ) Holttum; *S. albosetosus* (Copel.) Holttum; **S. alcasidii* Holttum; *S. alpinus* Holttum; *S. alticola* Holttum; *S. angustibasis* Holttum; *S. angustifolius* (C. Presl) Holttum; **S. appendiculatus* (Blume) Holttum; *S. aquatilis* (Copel.) Holttum;* *S. arbuscula* (Willd.) Holttum; **S. archboldii* (C. Chr.) Holttum; *S. arfakianus* (Baker) Holttum; **S. atasripii* (Rosenst.) Holttum; *S. austerus* (Brause) Holttum; *S. baramensis* (C. Chr.) Holttum; *S. bakeri* (Harr.) S.E. Fawc. & A.R. Sm.; *S. batacorum* (Rosenst.) Holttum; **S. batjanensis* (Rosenst.) Holttum; *S. batulantensis* Holttum; **S. beccarianus* (Ces.) S.E. Fawc. & A.R. Sm. (**Figs. 7A, 7B**); *S. benoitianus* (Gaudich.) Holttum; **S. braithwaitei* Holttum; **S. brauseanus* (Holttum) S.E. Fawc. & A.R. Sm.; *S. bulusanicus* (Holttum) S.E. Fawc. & A.R. Sm.; **S. canescens* (Blume) Holttum; *S. carrii* Holttum; *S. cartilagidens* P.M. Zamora & Co; *S. castaneus* (A.R. Sm. & Lorence) A.R. Sm. & Lorence; **S. cataractorum* (W.H. Wagner & Grether) Holttum; *S. caulescens* Holttum; **S. confertus* (Brause) Holttum; *S. convergens* Holttum; *S. cyrtocaulos* (Alderw.) Holttum; *S. daymanianus* Holttum; *S. debilis* (Mett.) Holttum; **S. decadens* (Baker) Holttum; **S. dichrotrichoides* (Alderw.) Holttum; *S. dichrotrichus* (Copel.) Holttum; *S. dimidiolobatus* Holttum; *S. diminutus* (Copel.) M.G. Price; *S. dimorphus* (Brause) Holttum; *S. diversilobus* (C. Presl) Holttum; **S. doodioides* (Copel.) Holttum (**Fig. 2E**); *S. echinosporus* (Alderw.) Holttum; *S. efogensis* Holttum; *S. ekutiensis* Holttum; *S. ellipticus* (Rosenst.) Holttum; *S. eminens* (Baker) Holttum; *S. erectus* (Copel.) Holttum; *S. erwinii* Holttum; *S. exindusiatus* Holttum; *S. flavoviridis* Holttum; *S. foliolosus* Holttum; *S. foxworthyi* Holttum; *S. gaudichaudii* Holttum; **S. glandulosus* (Blume) S.E. Fawc. & A.R. Sm.; *S. grandescens* Holttum; *S. gregarius* (Copel.) Holttum; *S. gymnorachis* Holttum; *S. hamiferus* (Alderw.) Holttum; **S. hastatopinnatus* (Brause) Holttum; *S. hellwigensis* Holttum; *S. hendersonii* Holttum; *S. hernaezii* Holttum; **S. heterocarpos* (Blume) Holttum (**Fig. 2K**); *S. heterophyllus* (C. Presl) S.E. Fawc. & A.R. Sm.; **S. hirsutus* (Kunze ex Mett.) Holttum; *S. hispidifolius* (Alderw.) Holttum; *S. hispiduliformis* (C. Chr.) Holttum; *S. hoalensis* Holttum; *S. hochreutineri* (Christ) Holttum; *S. humilis* Holttum; *S. immucosus* Holttum; **S. incisus* (Copel.) S.E. Fawc. & A.R. Sm.; *S. inconspicuus* (Copel.) Holttum; *S. indrapurae* Holttum; *S. intermedius* S.J. Lin; *S. irayensis* (Copel.) Holttum; *S. isomorphus* Holttum; *S. kalkmanii* Holttum; **S. lamii* Holttum; **S. larutensis* (Bedd.) C. Chr.; **S. lastreoides* (C. Presl) Holttum; **S. latebrosus* (Kunze ex Mett.) Holttum; *S. lithophyllus* (Copel.) Holttum; *S. lobangensis* (C. Chr.) Holttum; *S. lobatus* (Copel.) Holttum; *S. loherianus* (Christ) Holttum; *S. longbawanensis* (K. Iwats. & M. Kato) S.E. Fawc. & A.R. Sm.; **S. maemonensis* (W.H. Wagner & Grether) Holttum; **S. magnus* (Copel.) Holttum; *S. major* (Copel.) Holttum; *S. makassaricus* Holttum; *S. maximus* (K. Iwats. & M. Kato) S.E. Fawc. & A.R. Sm.; *S. melanophlebius* (Copel.) S.E. Fawc. & A.R. Sm.; *S. melanorachis* Holttum; S.

menadensis Holttum; *S. mengenianus* Holttum; *S. metcalfei* (Baker) Holttum; *S. microlonchus* (Christ) S.E. Fawc. & A.R. Sm.; *S. micropinnatus* (Holttum) S.E. Fawc. & A.R. Sm.; *S. mindorensis* Holttum [name unaccounted for in Holttum, 1982]; *S. mjobergii* Holttum; *S. morotaiensis* Holttum; *S. moseleyi* Holttum; *S. multiauriculatus* (Copel.) Holttum; *S. muluensis* Holttum; *S. mundus* (Rosenst.) Holttum; *S. mutabilis* (Brause) Holttum; *S. nakaikei* Holttum; *S. neotoppingii* Holttum; *S. norrisii* (Rosenst.) Holttum; *S. novae-britanniae* Holttum; **S. novoguineensis* (Brause) Holttum; *S. nudisorus* Holttum; *S. obtusifolius* (Rosenst.) Holttum; *S. omatianus* Holttum; **S. oosorus* (Baker) Holttum; *S. paripinnatus* (Copel.) Holttum; *S. penniger* (Hook.) Holttum; **S. pentaphyllus* (Rosenst.) S.E. Fawc. & A.R. Sm.; *S. perglanduliferus* (Alderw.) Holttum; *S. petiolatus* (K. Iwats. & M. Kato) S.E. Fawc. & A.R. Sm.; *S. pilosissimus* Holttum; *S. pilosiusculis* (Racib.) S.E. Fawc. & A.R. Sm.; *S. pilososquamatus* (Alderw.) Holttum; *S. plurifolius* (Alderw.) Holttum; *S. plurivenosus* Holttum; *S. polisianus* Holttum; **S. polycarpos* (Blume) Copel. (**Fig. 2D**); **S. polyotis* (C. Chr.) Holttum; *S. porphyricola* (Copel.) Holttum; *S. posthumii* Holttum; *S. potamios* Holttum; **S. productus* (Kaulf.) Holttum; *S. pseudomegaphyllus* (Alderw.) Holttum; *S. pterosporus* (Alderw.) Holttum; *S. pullenii* Holttum; *S. pycnosorus* (C. Chr.) Holttum; *S. reconditus* Holttum; *S. reineckei* (C. Chr.) Holttum; *S. richardsii* (Baker) Holttum; *S. rigidus* (Ridl.) Holttum; *S. roemerianus* (Rosenst.) Holttum; *S. rudis* (Ridl.) Holttum; *S. sagittifolius* (Blume) Holttum; *S. sakayensis* (Zeiller) Holttum in B.K. Nayar & S. Kaur; *S. santomasii* Holttum; **S. sarasinorum* Holttum; *S. scandens* Holttum; *S. scopulorum* (Holttum) S.E. Fawc. & A.R. Sm.; *S. semicordatus* Holttum; *S. semimetralis* Holttum; **S. sessilipinna* (Copel.) Holttum; *S. simplicifolius* (J. Sm. ex Hook.) Holttum; *S. solutus* Holttum; *S. spenceri* (Christ) Holttum; *S. squamatellus* Holttum; *S. stenodontus* (Copel.) Holttum; **S. stipellatus* (Blume) Hottum; *S. stresemannii* Holttum; *S. subalpinus* (Alderw.) Holttum; *S. subappendiculatus* (Copel.) S.E. Fawc. & A.R. Sm.; *S. subcanescens* Holttum; *S. subcordatus* Holttum; **S. suboppositus* Holttum; **S. subpectinatus* (Copel.) Holttum; *S. subulifolius* (Alderw.) Holttum; *S. subtruncatus* (Bory) Holttum; *S. sudesticus* Holttum; *S. superbus* (Brause) S.E. Fawc. & A.R. Sm.; **S. taiwanensis* (C. Chr.) Holttum ex Kuo; *S. tandikatensis* (Alderw.) Holttum; *S. telefominicus* Holttum; *S. tephrophyllus* (Copel.) Holttum; *S. tibangensis* (C. Chr.) Holttum; *S. trichochlamys* Holttum; *S. trimetralis* Holttum; *S. uaniensis* Holttum; *S. uniauriculatus* (Copel.) Holttum; **S. urdanetensis* (Copel.) Holttum; **S. veitchii* Holttum; **S. vestigiatus* (Copel.) Holttum; **S. warburgii* (Kuhn & Christ) Holttum; *S. wauensis* Holttum; *S. williamsii* (Copel.) Holttum; *S. woitapensis* Holttum; *S. womersleyi* (Holttum) S.E. Fawc. & A.R. Sm.

Excluded species.—*Sphaerostephanos invisus* (G. Forst.) Holttum and *S. unitus* (L.) Holttum are both combined in *Strophocaulon*. *Sphaerostephanos cucullatus* (Blume) S.M. Almeida & M.R. Almeida was treated as a synonym of *S. unitus* by Holttum (1982), and so presumably is a synonym of *Strophocaulon unitum* (L.) S.E. Fawc. & A.R. Sm., or related to that. *Sphaerostephanos elatus* (Bojer) Holttum is inferred as sister to *Pseudocyclosorus* in Fawcett et al. (in press), but resolves with species of *Abacopteris* in earlier studies (e.g., Patel et al. 2019a). Two species, *Sphaerostephanos hirtisorus* (C. Chr.) Holttum and *Sphaerostephanos peltochlamys* (C. Chr.) Holttum are here combined in *Abacopteris*.

Incertae sedis.—We were unable to place *Sphaerostephanos kurzii* Holttum. *Sphaerostephanos validus* (Christ) Holttum, is considered a synonym of *Abacopteris hirtisora* by Lindsay et al. (2009) but is in need of further study. *Nannothelypteris seramensis* M. Kato may belong in *Sphaerostephanos* based on its morphology, although we treat all other species of *Nannothelypteris* in *Pronephrium*.

STEGNOGRAMMA

Stegnogramma Blume, Enum. Pl. Jav. 172. 1828.—Type: *Stegnogramma aspidioides* Blume—*Thelypteris* sect. *Stegnogramma* (Blume) Fraser-Jenk.—*Thelypteris* subg. *Stegnogramma* (Blume) C.F. Reed

Dictyocline T. Moore
For additional synonymy, see Kuo et al. (2019).

Etymology.—Gr. *stegnos*, cover, + *gramme*, line, in reference to the sori, which are borne along the veins (Stewart et al. 1983).

Plants terrestrial, frequently of steeply sloping tropical and subtropical forest understories and shaded streamsides, small to large (15–50 cm); **rhizomes** short-creeping to ascending or erect, with ovate to lanceolate setose scales; **fronds** monomorphic to weakly dimorphic, erect to arching, simply lobed to once-pinnate; **stipes** stramineous to dull brown, terete (lacking adaxial groove), with long and/or short unicellular to rarely septate (in *Dictyocline* group) hyaline acicular hairs; **stipe scales** ovate to lanceolate, castaneous, brown or pale, typically setose on margins and surfaces; **blades** membranaceous to chartaceous, drying green, olivaceous or dark brown, ovate, hastate to deltate, apex gradually reduced, never pinna-like, blades often widest at or near the base, never with several pairs of gradually reduced proximal pinnae; proliferous buds absent; **pinnae** entire to shallowly lobed, pinna-bases adnate (especially distally) to subsessile, bases rounded or truncate, sometimes asymmetrical, but never auricled; **veins** irregularly anastomosing (*Dictyocline* group, **Fig. 4E**), forming areoles with or without included veinlets, or regularly anastomosing (*S. aspidioides,* **Fig. 4D**), often with several pairs of veins united below the sinus with excurrent vein running to the sinus; veins reaching laminar margins; **aerophores** inconspicuous or absent; **indument abaxially and adaxially** of stipes, rachises, costae, veins, and frequently laminar tissue between veins with long and/or short hyaline acicular hairs, these usually unicellular, occasionally with septae in the *Dictyocline* group; **pustules** absent; **sori** linear and coalescent along lateral and/or excurrent or irregularly anastomosing veins; indusia absent; **sporangia** with abundantly setulose capsules; **spores** morphologically coherent within the genus, with non-reticulate echinae or short wings (Wood 1973; Tryon & Lugardon 1991; Patel et al. 2019a); $x = 36$, diploids and tetraploids known, three species counted. No hybrids have been reported.

Diagnosis.—*Stegnogramma* may be distinguished from all other Thelypteridaceae by the combination of elongate exindusiate sori, setiferous sporangia, indument on the adaxial laminae between veins, and veins irregularly anastomosing, or with at least three rows of intersegmental areoles below the sinus. The morphology of the *Dictyocline* group is quite distinctive within the family, with its irregularly anastomosing (pleocnemioid) venation, and laminae hastate and entire (*S. sagittifolia*), or deltate-pinnatifid (*S. wilfordii*, **Fig. 4E**), though these grade into somewhat more elongate laminae with up to six free pinna-pairs in the newly described Vietnamese endemic *S. australis* (Chen et al. 2019). The species of its sister genus, *Leptogramma*, tend to be small plants with many pairs of free pinnae, these sometimes incised halfway or more to the costae (vs. pinnae entire to crenate in *Stegnogramma*), and usually with free veins, or few pairs anastomosing. The terete rachis (lacking adaxial groove) is also rare in Thelypteridaceae, shared only among the stegnogrammoids, *Metathelypteris*, and the three genera of Phegopteridoideae, all of which tend to have laminae more dissected than those of *Stegnogramma* species.

Biogeography and ecology.—The seven species of *Stegnogramma* occur predominantly on steep forested slopes and shaded streamsides at lower to middle elevations (to 1750 m) of the Paleotropics and subtropics. Members of the genus are most diverse in southern China, but extend from East India, Myanmar, and Vietnam north to Taiwan and Japan. A single species, the type, *Stegnogramma aspidioides* (**Fig. 4D**), extends into Java, Sumatra, and Borneo.

Taxonomic and phylogenetic studies.—The genus was described by Blume in 1828, based on a once-pinnate species with regularly anastomosing veins from Java. In his classification of mainland Asian Thelypteridaceae, Ching (1963) recognized *Dictyocline*, *Stegnogramma*, and *Leptogramma* as separate genera, including *Leptogramma* in tribe Thelypterideae based on its free veins, and the others in tribe Goniopterideae based on their anastomosing veins, noting the clear affinities between *Dictyocline* and *Stegnogramma*, as demonstrated by the intermediate morphology of *Stegnogramma dictyoclinoides*.

In his insightful treatment of these taxa, Iwatsuki (1964a, 1964b) united all three genera under a broadly defined genus *Stegnogramma*, which he subdivided into four subgenera, based on characters of indument and venation; *Dictyocline, Leptogramma*, *Haplogramma*, *Stegnogramma*. His concept of *Stegnogramma* was adopted by PPG I (2016). Recent phylogenetic evidence (Kuo et al. 2019) supports the divisions proposed by Iwatsuki, with a few refinements, notably that *Dictyocline* is nested within *Stegnogramma*, and that the species of *Stegnogramma* plus *Dictyocline* are sister to *Leptogramma* plus a slightly revised *Haplogramma*. We adopt the two-genus classification proposed by Kuo et al. (2019), in which *Stegnogramma* (including *Dictyocline*) comprises seven species and is distinguished by irregularly anastomosing veins, or with regularly anastomosing veins, and three or more intersegmental areoles below the sinus. Thus defined, the genus is restricted to South and East Asia, while *Leptogramma* is recognized by free veins, or with up to two intersegmental areoles between main lateral veins, and is distributed in Asia, Africa, Europe, and North America.

In recent phylogenetic analyses (Luo et al. 2018; Patel et al. 2019a; Kuo et al. 2019; Fawcett et al. in press), *Stegnogramma* and *Leptogramma* are well-supported as sister to *Cyclogramma* on a long branch, together forming the stegnogrammoid subclade, which diverged early within the larger cyclosoroid clade (**Fig. 1**). The *Dictyocline* group (*Stegnogramma australis, S. griffithii, S. mingchegensis, S. sagittifolia*, and *S. wilfordii*) is subtended by a grade that includes the type, *S. aspidioides*, and *S. dictyoclinoides* (Kuo et al. 2019; Fawcett et al. in press), rendering subg. *Stegnogramma* sensu Iwatsuki (1964b) non-monophyletic.

In both coalescent and concatenated analyses of a large phylogenomic dataset (Fawcett et al. in press), two Hawaiian species, treated in the newly described genus *Hoiokula*, are sister to the rest of the stegnogrammoid clade. However, these trees were inferred using methods that assume bifurcating evolution. Evidence from individual gene trees, and plastid loci, suggests this lineage may be of deep hybrid origin involving *Leptogramma* and *Menisciopsis*; this hypothesis is the subject of ongoing investigation (Fawcett, Kuo, et al. in prep.).

Constituent species.—**Stegnogramma aspidioides* Blume (**Fig. 4D**); **S. australis* C.W. Chen & L.Y. Kuo; **S. dictyoclinoides* Ching; **S. griffithii* (T. Moore) K. Iwats.; **S. mingchegensis* (Ching) X.C. Zhang & L.J. He; **S. sagittifolia* (Ching), L.J. He & X.C. Zhang; **S. wilfordii* (Hook.) Seriz (**Fig. 4E**).

STEIROPTERIS

Steiropteris (C. Chr.) Pic.Serm., Webbia 28:449. 1973.—*Dryopteris* subg. *Steiropteris* C. Chr., Biol. Arb. til. Eug. Warming 81:1911.—*Thelypteris* subg. *Steiropteris* (C. Chr.) K. Iwats.—Lectotype (chosen by Christensen, Kongel. Danske Vidensk. Selsk. Skr., Naturvidensk. Math. Afd., ser. 7, 10:164. 1913): *Steiropteris deltoidea* (Sw.) Pic.Serm. [= *Dryopteris deltoidea* (Sw.) Kuntze]. (**Figs. 9A, 9B**).

Glaphyropteris C. Presl ex Fée, Crypt. Vasc. Brésil 2:40. 1873.—*Dryopteris* subg. *Glaphyropteris* (C. Presl. ex Fée) C. Chr.—*Thelypteris* subg. *Glaphyropteris* (C. Presl. ex Fée), Alston, nom. inval.—*Thelypteris* sect. *Glaphyropteris* (C. Presl ex Fée) C.V. Morton—*Steiropteris* subg. *Glaphyropteris* (Fée) A.R. Sm., nom. inval.—Lectotype (chosen by Christensen, Ind. Filic. XXI, 1906): *Steiropteris decussata* (L.) A.R. Sm., based on *Polypodium decussatum* L. [= *Dryopteris decussata* (L.) Urb.]

For additional synonymy, see Smith (1980).

Etymology.—Gr. *steira*, keel + *pteris*, fern. The keel, or false vein located abaxially, below the sinus (**Fig. 9B**), is a distinctive feature of many (but not all) species in this genus.

Plants terrestrial, or occasionally rheophytic, small (< 15 cm) to very large (> 2 m); **rhizomes** short-creeping to suberect; **fronds** monomorphic to rarely subdimorphic (e.g., *S. valdepilosa*) or weakly subdimorphic (*S. leprieurii*), pinnate to usually pinnate-pinnatifid, erect or arching; **stipes** stramineous to dull brown; **stipe scales** brown, lanceolate, setose; **blades** chartaceous, laminae drying dark green; rachises usually lacking buds in axils of distal pinnae (except in *S. seemannii*); **pinnae** shallowly to often deeply lobed, rarely subentire to crenate, proximal pinnae not or little reduced, or abruptly reduced to many pairs of auriculate pinnae (*S. deltoidea*, **Fig. 9A**), distal pinnae gradually to sometimes abruptly reduced and with subconform, or hastate apices (e.g., *S. insignis*, *S. setulosa*); **veins** running to sinuses or 1–several pairs anastomosing just below each sinus, forming a cartilaginous keel running to sinus (**Fig. 9B**), sometimes veins truly united below sinuses with an excurrent vein to the sinus, in a few species lowermost pair from adjacent segments meeting margins just above sinus and lacking a raised keel, vein endings reaching segment margins; **aerophores** often present at pinna bases, and sometimes at segment bases, these scale-like, tuberculate, or horny protuberances, persistent on old fronds; **indument abaxially** lacking or of sparse to dense, short to long, hyaline acicular hairs, these unicellular or septate, generally restricted to costae, costules, and veins, amorphous appressed scales often present on costae; **indument adaxially** lacking except along costae and rachises, rarely of hairs on lamina between veins; glands generally absent abaxially, but reddish, sessile, and resinous, in some spp. sometimes treated in subg. *Glaphyropteris*; **pustules** usually absent on laminar tissue abaxially and adaxially, except in a few species (*S. pennellii*, *S. seemannii*); **sori** round, subcostular, inframedial, or medial, not coalescent at maturity, indusiate or exindusiate; indusia, if present, glabrous, glandular, or short-hairy, sometimes vaulted, glandular, persistent or evanescent, hidden and/or shriveled at maturity in a few species; **sporangia** usually without setulae or glands, rarely setulose (*S. setulosa*) and rarely with orangish, stalked, globose glands from the receptacles (*S. valdepilosa*); **spores** monolete, brownish, narrowly winged with crenate or fimbriate crests, or rugose with closely packed, anastomosing ridges (Wood 1973; Smith 1980; Patel et al. 2019a); $x = 36$, two of 25 spp. counted, diploids and tetraploids known. No interspecific or intergeneric hybrids are known.

Diagnosis.—Certain species of *Steiropteris* (e.g., *S. decussata*) resemble some *Amauropelta* species (e.g., *A. thomsonii*); both genera may have mucilaginous croziers, peg-like aerophores, enormous fronds (> 2m), and free veins, and both occur in disturbed or open tropical montane habitats. These two groups are easily distinguished by the presence of fasciculate hairs in this subgroup of *Amauropelta* (vs. simple hairs in *Steiropteris*), tiny abortive pinnae at the blade bases in *Amauropelta* (vs. blades without abortive pinnae in *Steiropteris*), fewer pairs of widely placed (> 1 mm apart) veins in *Amauropelta* (vs. > 20 pairs of veins ca. 0.5 mm apart in the *Steiropteris decussata* and allies), and base chromosome number of $x = 29$ in *Amauropelta thomsonii* and allies (vs. $x = 36$ in *Steiropteris*).

Biogeography and ecology.—Among the 26 species recognized in *Steiropteris*, one is restricted to the Lesser Antilles (*S. clypeolutata*), four to the Greater Antilles (*S. deltoidea* (**Figs. 9A, 9B**), *S. hottensis*, *S. lonchodes*, *S. wrightii*—the last three narrowly endemic to Hispaniola or Cuba), and four are endemic to southern and Atlantic forests of Brazil (*S. hatschbachii*, *S. mexiae*, *S. polypodioides*, *S. villosa*). Three species are widespread and variable in the Neotropics (*S. decussata*, *S. gardneriana*, *S. leprieurii*), especially in South America, and the remaining 14 species occur in southern Central

America (Costa Rica, Panama) through the Andes to Bolivia and also the Coastal Cordillera of Venezuela (Smith 1980; Smith & Kessler 2017). Several species are quite rare, local, and known only from the types or from very few localities. Most species occur in low and middle elevation tropical and montane rain forests, below 2000 m and usually below 1000 m; they mostly occur in relatively undisturbed primary rain forests, but *S. decussata* may occur at forest margins in partially exposed situations. Two Antillean endemics have greatly reduced blades and occur on stream banks, and thus can be considered rheophytes.

Taxonomic and phylogenetic studies.—The species of *Steiropteris* were treated by Christensen (1913) in two subgenera of *Dryopteris*: subg. *Steiropteris* included the keeled species; and subg. *Glaphyropteris* included those with free veins. Based on a suite of shared morphological features (see below), Christensen (1913), in his treatment of *Glaphyropteris*, included species now more appropriately placed in *Amauropelta* (e.g., *Amauropelta thomsonii* and allies—*Thelypteris* sect. *Phacelothrix* of Smith 1974). However, he included them tentatively, recognizing their numerous similarities to his *Dryopteris* subg. *Lastrea* (= *Amauropelta*). The species circumscription of *Steiropteris* proposed in Smith's (1980) monograph relied on morphological and cytological data and has not needed adjustment in consideration of molecular evidence.

The genus *Steiropteris* is monophyletic, but its two subgenera do not form two monophyletic clades, based on molecular evidence. Both plastid (Almeida et al. 2016) and nuclear (Fawcett et al. in press) data indicate that *Steiropteris* is early diverging within the cyclosoroids, but the backbone relationship between *Steiropteris*, the stegnogrammoids, and a clade including all other cyclosoroid genera remains unresolved (**Fig. 1**).

Some keeled species of *Steiropteris* greatly resemble Old World members of the genus *Mesophlebion* (**Fig. 9**) in the convergent, connivent veins, conspicuous and cartilaginous sinus membrane, and presence of swollen aerophores at the bases of pinnae; but these similarities appear to be due to convergence or represent the plesiomorphic condition in the cyclosoroids (**Fig. 1**). Holttum (1982:378) commented on the "often pale violet-purple" color of young sporangia in *Mesophlebion*, a condition also seen in some species of subg. *Steiropteris*. There are morphological similarities, too, between *Steiropteris* and *Goniopteris*, especially in blade dissection and venation, but the latter genus is almost always distinguished by bearing furcate or stellate hairs (such hairs lacking in *Steiropteris*); *Goniopteris* is well removed from *Steiropteris* in the phylogenetic analysis of Fawcett et al. (in review) (Fig. 1). Several character states that are rare in *Steiropteris* are common in other cyclosoroid genera, e.g., rachis buds and pustular laminae.

Combinations for all known accepted species of *Steiropteris* have been made by Pichi Sermolli (1973), Salino et al. (2015), Smith and Kessler (2017), and by Salino and Smith (2018), except:

New combination.—

Steiropteris setulosa (A.R. Sm.) A.R. Sm. & S.E. Fawc., **comb. nov.**—*Thelypteris setulosa* A.R. Sm., Univ. Calif. Publ. Bot. 76:30. 1980.

Constituent species and infraspecific taxa.—Steiropteris alstonii Salino & A.R. Sm.; **S. buchtienii* (A.R. Sm.) Salino & T.E. Almeida; **S. clypeolutata* (Desv.) Pic.Serm.; *S. clypeolutata* var. *holmei* (Baker) Salino & T.E. Almeida; *S. comosa* (C.V. Morton) Salino & T.E. Almeida; **S. decussata* (L.) A.R. Sm.; *S. decussata* var. *brasiliensis* (C. Chr.) Salino & T.E. Almeida; *S. decussata* var. *costaricensis* (A.R. Sm.) Salino & T.E. Almeida; *S. decusssata* var. *mapiriensis* (Rosenst.) Salino & T.E. Almeida; *S. decussata* var. *velutina* (Sodiro) Salino & T.E. Almeida; **S. deltoidea* (Sw.) Pic.Serm. (**Figs. 9A, 9B**);**S. fendleri* (D.C. Eaton) Pic.Serm.; **S. gardneriana* (Baker) Pic.Serm.; *S. glabra* (A.R. Sm. & Kessler; **S. glandulosa* (Desv.) Pic.Serm.; **S. glandulosa* var. *brachyodus* (Kunze) Salino & T.E. Almeida; **S. glandulosa* var. *longipilosa* (A.R. Sm.) Salino & T.E. Almeida; **S. hatschbachii* (A.R. Sm.) Salino & T.E. Almeida; *S. hottensis* (C. Chr.) Salino & T.E. Almeida; *S. insignis* (Hook.) Pic.Serm.; *S. leprieurii* (Hook.) Pic.Serm.; *S. leprieurii* var. *costalis* (Baker) A.R. Sm.; *S. leprieurii* var. *glandifera* (A.R. Sm.) A.R. Sm.; *S. leprieurii* var. *incana* (Christ) A.R. Sm.; **S. leprieurii* var. *subcostalis* (A.R. Sm.) A.R. Sm.; *S. lonchodes* (D.C. Eaton) Pic.Serm.; **S. mexiae* (C. Chr. ex Copel.) Salino & T.E. Almeida; *S. parva* (A.R. Sm. & Kessler) Salino & T.E. Almeida; **S. pennellii* (A.R. Sm.) Salino & T.E. Almeida; **S. polyphlebia* (C. Chr.) Salino & T.E. Almeida; **S. polypodioides* (Raddi) Salino & T.E. Almeida; *S. praetervisa* (Kuhn) Pic.Serm.; **S. seemannii* (J. Sm.) Salino & T.E. Almeida; *S. setulosa* (A.R. Sm.) A.R. Sm. & S.E. Fawc.; **S. valdepilosa* (Baker) Pic.Serm.; **S. villosa* (Link) Salino & T.E. Almeida; *S. wrightii* (D.C. Eaton) Pic.Serm.

Excluded Species.—Steiropteris crassiuscula (C. Chr. & Maxon) Pic.Serm. = *Amauropelta crassiuscula* (C. Chr. & Maxon) Salino & T.E. Almeida; *Steiropteris fraseri* (Mett. ex Kuhn) Salino & T.E. Almeida = *Goniopteris fraseri* (Mett. ex Kuhn) Salino & A.R. Sm.

A new species, *Thelypteris nana* A. Rojas, was recently described as endemic to Cocos Island, Costa Rica (Rojas 2011). Although this taxon is likely a *Steiropteris*, we have not seen the type and are unable to evaluate its taxonomic status based on the description and illustration. It may be a diminutive specimen of *Steiropteris gardneriana*; most likely it is not very close to *S. leprieurii*, with which Rojas compared it.

STROPHOCAULON

Strophocaulon S.E. Fawc. & A.R. Sm., **gen. nov.**—Type: *Strophocaulon unitum* (L.) S.E. Fawc. & A.R. Sm. [= *Polypodium unitum* L.]

For additional species synonymy, see Holttum (1974a, 1977b, 1978, 1982).

Etymology.—Gr. *strophos*, twisted cord + *caulon*, stem, in reference to the tortuous, long-creeping subterranean rhizomes (**Fig. 10B**), which distinguish it from *Sphaerostephanos*.

Plants terrestrial, forming colonies in open sites, medium to large, to > 1.2 m tall; **rhizomes** thick (5+ mm), black, long-creeping, and subterranean, with internodes to 7+ cm long (**Fig. 10B**), bearing stramineous to brown, lanceolate, sometimes tortuous scales with setose margins; **fronds** arching to erect, monomorphic, pinnate-pinnatifid; **stipes** dull brown to dull stramineous; **stipe scales** lanceolate, stramineous, sometimes tortuous, bearing marginal setae; **blades** chartaceous to coriaceous, often bicolorous (drying paler below), often drying reddish-black adaxially, frond apex attenuate (*S. invisum*) or conform (*S. unitum*, **Fig. 10C**), frond base with pinnae abruptly reduced (*S. unitum*), with many pairs of pinnae reduced to auricles (sometimes only a few mm long), each subtended by an aerophore (auricles rarely lacking; Hayashi 2018), or blades truncate (*S. invisum*), proliferous buds absent; **pinnae** sessile to short-petiolulate, pinna bases truncate or broadly cuneate, sometimes slightly dilated; margins sharply dentate to incised to 1/3 towards costae; **veins** with at least one pair anastomosing at an angle < 90 degrees, with an excurrent veinlet running to the sinus, with several pairs of veins forming areoles, running along a deep, narrow sinus membrane, lowest veins sometimes arising from costae, not from costules (**Fig. 10A**); **aerophores** inconspicuous; **indument adaxially** of hyaline, spreading, acicular hairs, these restricted to axes, or also present on laminar tissue; **indument abaxially** of hyaline acicular hairs present on all axes (**Fig. 10A**), frequently abundant on laminar tissue, often forming a tangled mat of whitish hairs along rachises, spherical yellow or brown glands present on laminar surface, restricted to veins, or glands absent; **pustules** absent; **sori** round, discrete or somewhat coalescent with age, supramedial to costular, indusia stramineous to dark brown, persistent, bearing superficial hairs; **sporangia** bearing spherical yellow glands (*S. unitum*) or setulae (*S. invisum*) on capsules; **spores** brown, perine of low knobby ridges (Patel et. al. 2019a); $x = 36$, only diploids known based on eight counts, representing both species. No intra- or intergeneric hybrids have been reported.

Diagnosis.—Although Holttum (1978) treated the two species of *Strophocaulon* in *Sphaerostephanos*, he noted that they were unique in three respects. Unlike most *Sphaerostephanos* species, which are narrowly restricted, both have broad geographic ranges, occur in open habitats (vs. forested habitats), and have long-creeping rhizomes (vs. generally short-creeping, suberect, or erect rhizomes). This last character is the most reliable for distinguishing *Strophocaulon* from *Sphaerostephanos*. Although at least three species of *Sphaerostephanos*, *S. scandens* Holttum, *S. austerus* (Brause) Holttum, and *S. mundus* (Rosenst.) Holttum, may have long internodes, they have scandent, not subterranean rhizomes. As noted by Holttum (1977b), three other species of Thelypteridaceae share the coarse, long-creeping rhizomes, preference for open habitats, and tendency to form large colonies. These species have often been confused, because of their similar habit, widespread overlapping distributions, and problematic nomenclatural history. Among these, *Cyclosorus interruptus* can be distinguished by scales on the abaxial costae of laminae, and *Christella arida* (D. Don) Holttum and *Christella harveyi* (Mett.) Holttum both bear elongate or pear-shaped (vs. spherical) glands on abaxial laminae and often on sporangial stalks (characteristic of many species of *Christella s.s.*), and sporangial capsules lacking both glands and setulae (vs. glands present in *Strophocaulon unitum*, and setulae present in *Strophocaulon invisum*). As in *S. unitum*, bicolorous laminae abruptly reduced to many pairs of auriculate pinnae is a characteristic shared by species of *Pneumatopteris s.s.*, but these species frequently have pustulate laminae, always bear peg-like aerophores, and, when glands are present, they are colorless, not yellow or brown. Both yellowish glands and abruptly reduced, auriculate pinnae are commonly shared by *Sphaerostephanos s.s.*, but the rhizome morphology remains the most reliable character to distinguish them, illustrating the importance of complete herbarium specimens.

Biogeography and ecology.—Both species of *Strophocaulon* are widespread in the Paleotropics, and often occur in wet open areas, in partial sun, at low elevations; they frequently form extensive colonies near rivers or in disturbed sites, although *S. unitum* reaches elevations of 2000 m in New Guinea. *Strophocaulon unitum* is distributed in East Africa, in India, throughout Malesia, and into the Pacific, including the Mariana Islands, the Solomon Islands, New Caledonia, Fiji, and Samoa. *Strophocaulon invisum* has a partially overlapping distribution. It is widespread in the Pacific, and reaches its western range limit in Sulawesi, extending southward into New Guinea and Queensland (Holttum 1977b).

Taxonomic and phylogenetic studies.—Both species of *Strophocaulon* were recognized in *Sphaerostephanos* by Holttum (1974a, 1977b, 1978, 1982), a genus with which they share several morphological features. Based on recent molecular analyses (Patel et al. 2019a; Fawcett et al. in press), *Strophocaulon* is distantly related to *Sphaerostephanos s.s*., but has no close relatives; its two constituent species are on a long branch, with their position unresolved within the large christelloid clade. This clade includes *Strophocaulon,* plus two subclades, the pseudocyclosoroids (*Abacopteris*, *Amblovenatum s.s*., *Christella s.s*., and *Pseudocyclosorus*) and the sphaerostephanoids (*Pronephrium s.s*., *Pneumatopteris s.s*., *Reholttumia*, and *Sphaerostephanos*).

Notes.—Four varieties of *Sphaerostephanos unitus* have been described, but we make no combinations for them in *Strophocaulon*, pending more detailed study of the variation among these plants throughout their wide range. These include the unlocalized type, var. *unitus*, which exhibits brownish glands on and between veins, var. *mucronatus* (Christ) Holttum, which exhibits yellow glands restricted to veins, var. *papilliferus* Holttum, which has no glands, but a papillose lamina, and is restricted to higher elevations of New Guinea, and lastly, var. *dimorphophyllus* T. Hayashi et al., which includes plants with fertile fronds bearing peg-like (non-laminar) aerophores, known from a single location in Borneo (Hayashi et al. 2018). An unusual specimen from Singapore, *M. Tan 2011174* (VT), has a subconform terminal pinna, pinnae incised 2/5, large indusia, and ruby red glands on abaxial laminae.

New combinations and constituent species.—

***Strophocaulon invisum** (G. Forst.) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Polypodium invisum* G. Forst., Fl. Ins. Austr. 81. 1786.—*Cyclosorus invisus* (G. Forst.) Copel.—*Sphaerostephanos invisus* (G. Forst.) Holttum—*Thelypteris forsteri* C.V. Morton

***Strophocaulon unitum** (L.) S.E. Fawc. & A.R. Sm., **comb. nov.**—*Polypodium unitum* L., Syst. Nat., ed. 10, 2:1326. 1759.—*Cyclosorus unitus* (L.) Ching—*Sphaerostephanos unitus* (L.) Holttum—*Thelypteris unita* (L.) C.V. Morton (**Figs. 10A, 10B, 10C**).

THELYPTERIS

Thelypteris Schmidel, Icon. Pl., ed. Keller, 3, 45, t. 11B, 13. 1763, nom. cons.—Type: *Thelypteris palustris* Schott [based on *Acrostichum thelypteris* L., Sp. Pl. 2:1071. 1753]

Lastrea Bory nom. illeg. superfl.
Hemestheum Newman nom. illeg. superfl.

Etymology.—Gr. *thelys*, female + *pteris*, fern. An old Greek name for a fern more delicate than the male fern, *Dryopteris filix-mas* (Stewart et al. 1983).

Plants terrestrial, small to medium-sized, in wet ground (often marshes or swamps), dying back in winter (in temperate areas); **rhizomes** short- to often long-creeping, usually blackish, with relatively few roots between nodes, mostly 1.5–3 mm diam.; **fronds** moderately sized (typically 30–100 cm), monomorphic or weakly dimorphic, with fertile fronds narrower and having longer stipes and more constricted pinnae and segments, arching to erect, deeply pinnate-pinnatifid or often pinnatisect with pinnae incised to within 1 mm of costae; **stipes** dull stramineous, blackened at bases; **stipe scales** tan, ovate, glabrous or nearly so; **blades** chartaceous, drying green, proximal pinnae not reduced, or with 1–several pinna-pairs somewhat reduced, but never abruptly reduced to a series of hastate auricles or glanduliform pinnae; blade apex gradually reduced; proliferous buds absent; **pinnae** nearly symmetrical with segments spreading or only slightly oblique; margins entire, pinna bases sessile to short-petiolulate, truncate, acroscopic segment often slightly elongate but not auriculate; **veins** free, simple or often forked, ending at margins of lobes just above sinuses (**Fig. 6D**); **aerophores** absent; **indument abaxially** of hyaline acicular hairs restricted to axes (rachis, costae, and sometime costules), also with thin, flat, ovate tan scales along costae, tissue between veins glabrous or nearly so; **indument adaxially** of hyaline acicular or tortuous hairs restricted mostly to costae, veins and laminar tissue glabrous; **pustules** absent; **sori** typically round and discrete, or often confluent at maturity, medial or inframedial, indusia relatively large and persistent, glabrous or with a few short-stipitate glands; **sporangia** glabrous or often bearing short, stipitate glands < 0.1 mm; **spores** tan, bilateral, monolete, perispore variable, echinate in *T. confluens*, and granulate, papillate, irregularly tuberculate, or reticulate and perforate in *T. palustris* (Tryon 1971, Tryon et al. 1980, Tryon & Lugardon 1991); $x = 35$, two species, only one counted, always diploid. Reports of $n = 36$ for *T. palustris*, by Mitui (1968) and Hirabayashi (1969), from populations in Japan, are likely erroneous (see Tryon & Tryon 1973, for comments and a review of cytological information).

Diagnosis.—*Thelypteris* can be readily distinguished from the superficially similar, and sometimes co-occurring amauropeltoid genera by a combination of characteristics. It has consistently long-creeping, relatively narrow rhizomes (1.5–3 mm diam.); grows in persistently wet habitats in temperate areas; has largely scaleless rhizomes behind the apex;

has persistent ovate scales on the costae abaxially (**Fig. 6D**); lacks greatly reduced proximal pinnae; has frequently forked, free veins on the ultimate segments (**Fig. 6D**); and is often slightly dimorphic, with fertile fronds taller, and with confluent sori resulting in an almost acrostichoid appearance. *Thelypteris* may be distinguished from both *Amauropelta* and *Coryphopteris* in temperate latitudes by the presence of scales on the abaxial costae, the lack of glands on abaxial laminae, some veins forking (vs. simple), and fidelity to wetland habitats.

Biogeography and ecology.—Throughout their range, the two species of *Thelypteris s.s.* occur in perennially wet, often open areas, especially marshes, peat bogs, forested swamps, and edges of lakes. *Thelypteris palustris* is widespread in temperate wetlands of the northern hemisphere, while *Thelypteris confluens*, is south-temperate in sub-Saharan Africa, southern India, northern Thailand, parts of Malesia, Australia, New Zealand, and southern South America. Outlying populations of both *T. palustris* and *T. confluens* occur sporadically in suitable habitats in the tropics and subtropics.

Taxonomic and phylogenetic studies.—Historically, the genus *Thelypteris* has had many different circumscriptions. Beginning with Ching (1936), and continuing with Morton (1963), the genus was accepted in a broad sense, comprising all or most of the ca. 1000 species in the family Thelypteridaceae. Before that time, members of the family had usually been subsumed in an unwieldy genus *Dryopteris* (e.g., Christensen 1913, 1920). Ching (1963) recognized 18 genera within Thelypteridaceae for mainland Asia, and restricted *Thelypteris* to just three species. Shortly thereafter, Holttum (1969, 1971, 1982, 1983) adopted many of Ching's generic concepts and also segregated several new genera; a series of revisions and monographs culminated in recognition of 23 genera in Asia (Holttum 1982), and *Thelypteris s.s.* with either two or three species. An attempt at some middle ground was offered by Smith (1990) and later by Christenhusz et al. (2011). Smith recognized five genera in the family, with the largest genera being expanded concepts of both *Thelypteris* (ca. 280 spp,. in five subgenera, including subg. *Thelypteris* with two spp.) and *Cyclosorus* (ca. 525 spp. in 20 subgenera).

Holttum (1983) proposed a slightly different narrow classification of the genus, recognizing three species. In this, he distinguished European *T. palustris s.s.*, with glabrous indusia, from the North American taxon, having hairy indusia; he called the latter *T. thelypteroides* (Michx.) Holub. However, as shown earlier by Tryon et al. (1980), that name is based on a mistypification by Morton (1967) and applies to *Amauropelta noveboracensis* (see discussion under *Amauropelta*; see also comments regarding typification by Tryon et al. 1980). Regardless of the typification issue, we regard the European and North American variants as conspecific.

The two species of *Thelypteris* recognized by us and many others (e.g., Tryon et al. 1980) are only subtly different. *Thelypteris palustris* is largely restricted to north-temperate North America, Europe, and Asia. Fernald (1929) was the first to distinguish infraspecific variants within *Thelypteris palustris s.l.*—one in Eurasia (var. *palustris*), the other in North America and eastern Asia (var. *pubescens* (G. Lawson) Fernald). A third variant, var. *haleana* Fernald, in the southeastern U.S.A., Cuba, and Bermuda, was also distinguished by Fernald and others; however, it is only dubiously distinct, according to Tryon et al. (1980), and we concur. The southern hemisphere taxon, *T. confluens*, has been recognized as a distinct species by most recent authors, including Morton (1967), Tryon et al. (1980), and Holttum (1983), but was treated as *T. palustris* var. *squamigera* (Schlecht.) Weatherby by Tryon (1971) and Fernald (1929).

Thelypteris tremula Christ, type from Michoacán, Mexico, is probably only an outlier of the widespread Northern Hemisphere *T. palustris* var. *pubescens* (Mickel & Smith 2004), to which it is sister in the phylogenetic analysis of Fawcett et al. (in press). Most Mexican collections are more than 100 years old, and it seems likely that *T. tremula* is largely extirpated, with draining of its habitat; however, one recent collection is *Rzedowski 39234* (IEB, XAL). *Thelypteris fairbankii* (Bedd.) Y.X. Lin et al. was recognized by Lin et al. (2013) but seems likely to be a heterotypic synonym of *T. confluens*.

All phylogenetic studies with broad sampling (He & Zhang 2012; Almeida et al. 2016; Fawcett et al. in press) show *Thelypteris s.s.,* as treated here, sister to the rest of Thelypteridoideae (**Fig. 1**). This subfamily includes 900+ species, and is sister to the smaller subfam. Phegopteridoideae (*Macrothelypteris*, *Pseudophegopteris*, *Phegopteris*). *Thelypteris s.s.* represents an ancient lineage, diverged from its closest extant relatives by perhaps 86 Ma (Testo & Sundue 2016).

Constituent species.—**Thelypteris confluens* (Thunb.) C.V. Morton; **T. palustris* (Salisb.) Schott (**Fig. 6D**).

TRIGONOSPORA

Trigonospora Holttum, Blumea 19:29. 1971.—Type: *Trigonospora ciliata* (Wall. ex Benth.) Holttum [= *Aspidium ciliatum* Wall. ex Benth.]—*Cyclosorus* subg. *Trigonospora* (Holttum) Panigrahi—*Thelypteris* subg. *Trigonospora* (Holttum) Fraser-Jenk.—*Thelypteris* sect. *Trigonospora* (Holttum) Fraser-Jenk.

Etymology.—Latin *trigona*, three-angled + *spora*, spore; the genus is unusual among eupolypod ferns in having trilete tetrahedral spores (Holttum 1971).

Plants terrestrial, small to medium-sized (typically 20 cm–1+ m), rheophytes of rocky streambeds or of forest understories; **rhizomes** short, caudices erect, frequently with a tangle of thick roots that may serve as a 'holdfast'; **fronds** dimorphic, fertile fronds with longer stipes and more deeply lobed pinnae, or monomorphic, pinnate-pinnatifid to pinnate-pinnatisect, arching to erect; **stipes** dull stramineous to brown; **stipe scales** brown, caducous, often appressed, glabrous or with marginal hairs; **blades** chartaceous, drying green to black, proximal pinnae gradually reduced (e.g., *T. calcarata*) or only slightly reduced and reflexed (*T. ciliata*), never abruptly reduced to a series of hastate auricles; blade apex gradually reduced; proliferous buds absent; **pinnae** nearly symmetrical to asymmetrical and strongly oblique; margins subentire with dentate margins (*T. khamptorum, T. zeylanica*) to deeply pinnatisect (*T. calcarata*), pinna bases sessile to short-petiolulate, truncate to narrowly cuneate, acroscopic segment sometimes slightly enlarged or auriculate, in *T. angustifrons* basal segment free and enlarged, overlapping rachis; **veins** free, simple, ending at sinus, or with a single pair anastomosing and an excurrent vein running to shallow sinus (*T. khamptora, T. obtusiloba,* and *T. zeylanica);* **aerophores** inconspicuous or absent; **indument abaxially** nearly absent or with hyaline acicular hairs restricted to axes; **indument adaxially** of hyaline acicular hairs most frequently along costae; *T. glandulosa* with pale yellow subsessile glands; **pustules** absent; **sori** typically round and discrete, medial or inframedial, indusia large and persistent, glabrous to copiously hairy, rarely with glands (*T. glandulosa*); **sporangia** glabrous, or each with a stipitate gland arising from stalk; **spores** tan, trilete and tetrahedral, globose or bilateral, with echinulate or minutely papillose perine; $x = 36$, five species counted, both diploids and triploids known. Sledge (1981) suggested some of the taxonomic confusion of the *T. calcarata* group may be the result of infrageneric hybridization, and also suggested a potential intergeneric hybrid with *Christella parasitica* (Sledge 1981; *Sledge 752*).

Diagnosis.—*Trigonospora* is unique within the Thelypteridaceae in having trilete spores. However, it can also usually be distinguished from *Pseudocyclosorus* by having an erect rhizome (vs. often creeping); proximal pinnae little reduced or gradually reduced (vs. never reduced to auricles along stipes); and aerophores at pinna bases lacking or inconspicuous (vs. swollen). There is limited overlap in range or habitat with other free-veined Thelypteridaceae with persistent indusia, but *Plesioneuron*, which is most diverse in Papuasia, extends into western Malesia. *Trigonospora* differs from *Plesioneuron* by fronds usually drying dark (vs. dull green or pale); pinna bases sometimes auricled (vs. usually rounded or cuneate); and stipe scales thin and deciduous (vs. thick and persistent). The amauropeltoid genera (*Amauropelta, Metathelypteris*, and *Coryphopteris*) usually occur at higher elevations or more northern latitudes, and tend to have much more delicate laminae.

Biogeography and ecology.—The 12 species of *Trigonospora* are restricted to southeast Asia, and the genus is most diverse in south India and the island of Sri Lanka, where seven species occur, four of which are endemic. The Sri Lankan species are morphologically distinctive and occur at different elevational ranges, from low country to 2200 m (Sledge 1981). The genus extends through the Pan-Himalayan region into southern continental Asia, Java, Malaysia, and Sumatra, and possibly into Sulawesi (*T. koordersii*; Holttum 1974c, 1982). In China *T. ciliata* extends north to Guangxi and Guangdong. Throughout their range they frequently occur in rocky riverbeds and streamsides.

Taxonomic and phylogenetic studies.—Initially included within *Pseudocyclosorus* by Ching (1963), *Trigonospora* was recognized by Holttum (1971) as a distinct genus on the basis of its trilete spores. As noted by Wagner (1974), this characteristic is unusual within what we now classify as eupolypod ferns. Although trilete spores have also been observed in *Macrothelypteris torresiana* (Chandra 1973), and species of grammitids (e.g., *Alansmia*) in Polypodiaceae (Kessler et al. 2011), these may be spherical and/or with asymmetrical laesurae, and are unlike typical tetrahedral trilete spores. The same is sometimes true of spores in *Trigonospora*, which may be round or bilateral, occasionally occurring together with monolete spores (Nayar & Chandra 1966). Based on our understanding of its phylogenetic position, the spore morphology of *Trigonospora* should be interpreted as a reversal (Patel et al. 2019a), not as indication of a close relationship to other lineages with trilete spores, like Cyatheaceae, as Holttum (1971, 1974c) believed. Trilete spores are a diagnostic feature of the genus, however, and have been reported in several species, including *T. ciliata*, *T. caudipinna*, and *T. khamptorum* (Holttum & Chandra 1971; Lin et al. 2013), and are verified here for *T. calcarata, Gardette 559* (UC); *T. obtusifolia, Ballard 1393* (UC); *T. zeylanica, Ballard 1522* (UC); and *T. caudipinna*, *Mann s.n.* (UC).

He and Zhang (2012) and Patel et al. (2019a) inferred a close relationship between *Trigonospora ciliata* and *Pseudocyclosorus,* but with low support. The more densely sampled phylogeny of Fawcett et al. (in press.) recovers two Sri Lankan species of *Trigonospora* as sister to two morphologically distinctive taxa we determine as *Pneumatopteris humbertii* (Holttum 1974a) and *Pronephrium fidelei* (Rakotondrainibe & Jouy 2012), both once-pinnate species of

Madagascar. This clade is in turn sister to *Pseudocyclosorus* (**Fig. 1**). As discussed in the *Menisorus* treatment, a combination of limited collections and geologically recent extinctions may have shaped our understanding of the Afro-Madagascan fern flora, sometimes leaving isolated lineages that are difficult to place taxonomically. In light of these difficulties, and our own limited sampling, we refrain from making new combinations for these non-*Trigonospora* pseudocyclosoroid taxa. Although our understanding of *Trigonospora* has benefited from excellent floristic treatments (e.g., Holttum 1974c, 1982; Sledge 1981), the genus has never been monographed throughout its range. A critical study of widespread and morphologically variable species such as *T. ciliata* and *T. calcarata* would be especially helpful for improving our understanding of the group.

Constituent species.—*Trigonospora angustifrons* Sledge; *T. calcarata* (Blume) Holttum; *T. caudipinna* (Ching) Holttum; ***T. ciliata* (Wall. ex Benth) Holttum; *T. glandulosa* Sledge; *T. khamptorum* (Holttum) Irudayaraj & Manickam; *T. loyalii* Panigrahi & Sarn. Singh; **T. obtusiloba* Sledge; *T. sericea* (J. Scott ex Bedd.) Holttum in Nayar and Kaur; *T. subcaudipinna* Sarn. Singh & Panigrahi; *T. tenera* (Roxb.) Mazumdar; **T. zeylanica* Sledge.

Incertae sedis.—*Trigonospora koordersii* is a distinctive and unusual species, and known only from the type (Sulawesi), a considerable distance from the center of diversity of the lineage in Sri Lanka and southern India. It differs from all other *Trigonospora* species in having a conform terminal pinna, and is also distinctive in its elongate, nearly parallel-sided pinna segments or pinnules on an essentially bipinnate blade. This taxon was initially placed in *Mesophlebion* subg. *Plesioneuron* by Holttum (1971), though he later transferred it to *Trigonospora* (Holttum 1974b). Our concept of *Plesioneuron* is broader than Holttum's, and we cannot rule out the possibility that *T. koordersii* belongs that genus.

For additional synonymy, see Holttum (1974c), Sledge (1981), Singh and Panigrahi (2005), and Lin et al. (2013).

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The generic taxonomy of the Thelypteridaceae has proven to be exceptionally controversial, with some authors recognizing upwards of 30 genera, while others have treated the nearly 1200 species within a single genus, *Thelypteris*. With the benefit of a 600-taxon phylogenomic dataset and access to thousands of herbarium specimens, the authors have provided a revised generic classification that recognizes monophyletic genera. The present work includes the recircumscription of 14 genera, descriptions of four genera and three subgenera, and 176 new names. A dichotomous key, and detailed morphological description of each of the 37 genera recognized by the authors is provided, including a diagnosis, a discussion of previous taxonomic and phylogenetic studies, notes on ecology and biogeography, and a list of constituent species. Thirty-two original pen and ink illustrations and 15 color photographs provide examples of critical characteristics necessary for keying, and these represent much of the taxonomic and morphological diversity within the family. Extensive introductory material covers the history of classification in the group and provides a discussion on morphology, cytology, hybridization, fossil evidence, biogeography, and prior phylogenetic studies. This book will be a useful reference for professional and amateur botanists alike—all those hoping to familiarize themselves with one of the most diverse fern families. For anyone wanting to identify and classify ferns, especially in the most biodiverse and imperiled ecosystems, this will be an invaluable tool.

Susan Fawcett is a National Geographic Explorer and Research Botanist at the University and Jepson Herbaria at UC Berkeley. The Systematics of the Thelypteridaceae was the focus of her doctoral dissertation, completed at the University of Vermont. She is broadly interested in systematics and floristics, with an emphasis on ferns.

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