A global phylogeny of *Stegnogramma* ferns (Thelypteridaceae): generic and sectional revision, historical biogeography and evolution of leaf architecture

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Abstract

The thelypteroid fern genus *Stegnogramma* s.l. contains around 18–35 species and has a global, cross-continental distribution ranging from tropical to temperate regions. Several genera and infrageneric sections have been recognized previously in *Stegnogramma* s.l., but their phylogenetic relationships are still unclear. In this study, we present a global phylogeny of *Stegnogramma* s.l. with the most comprehensive sampling to date and aim to pinpoint the phylogenetic positions of biogeographically and taxonomically important taxa. Based on the reconstructed historical biogeography and character evolution, we propose a new (infra)generic classification and discuss the diversification of *Stegnogramma* s.l. in a biogeographical context. New names or combinations are made for 12 (infra)species, including transferring the monotypic species of *Craspedosorus* to *Leptogramma*. Finally, we discuss a possible link between leaf architecture and ecological adaptation, and hypothesize that the increase in leaf dissection and free-vein proportion is an adaptive feature to cool climates in *Stegnogramma* s.l.

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Introduction

The thelypteroid fern genus *Stegnogramma* Blume (subfamily Thelypteridoideae; family Thelypteridaceae; order Aspleniineae), in the broad sense (e.g. Holttum, 1971; PPG I, 2016), contains around 18–26 species (or 35 based on the estimate in this study) and has a global, cross-continental distribution ranging from tropics to temperate regions. The centre of *Stegnogramma* s.l. diversity is in Asia, with a few (sect. *Leptogramma*) species scattered in North and Central America, Europe and Africa. Taxonomically, *Stegnogramma* s.l. can be further divided into four sections (Iwatsuki, 1963): sect. *Stegnogramma*, sect. *Dictyocline* (T. Moore) K. Iwats., sect. *Leptogramma* (J. Sm.) K. Iwats. and sect. *Haplogramma* K. Iwats., and the first three have been recognized as different genera by some authors (e.g. Ching, 1963; Fig. 1). More recently, the genus *Craspedosorus* Ching & W.M. Chu was transferred to *Stegnogramma* (He and Zhang, 2012a)

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but has not yet been assigned to any section. Past taxonomic division relied mainly on morphological features, such as leaf venation and indument. Patterns of leaf venation are particularly useful in *Stegnogramma* s.l.: sects. *Stegnogramma*, *Dictyocline* and *Haplogramma* include species with anastomosing venation. Of these, *Dictyocline* is the most unusual in that areoles of *Dictyocline* form irregularly reticulated hexagons with included veinlets (Ching, 1936, 1963; Iwatsuki, 1963; Lin et al., 2013). In contrast, leaves of sect. *Leptogramma* species are free-veined (Ching, 1936, 1963; Iwatsuki, 1963; Lin et al., 2013). In spite of such morphological variation, current phylogenetic evidence supporting previous generic or infrageneric delimitation is weak.

Phylogenetically, *Stegnogramma* s.l. is monophyletic and sister to the genus *Cyclogramma* (He and Zhang, 2012b; Almeida et al., 2016; Luo et al., 2018). Within *Stegnogramma* s.l., sect. *Dictyocline* forms a clade, and is sister to the clade mixed with the sects. *Haplogramma* and *Leptogramma* (He and Zhang, 2012b; Almeida et al., 2016; Luo et al., 2018). All previous phylogenetic sampling lacks a number of key taxa, particularly the type of *Stegnogramma*, *S. aspidioides* Blume, and the type of (sect.) *Leptogramma*, *L. totta* (Schltdl.) J. Sm. from South Africa. Apart from Yatabe et al. (2002) and He and Zhang (2012b), previous phylogenies have sampled only Asian taxa. Such narrow taxon sampling limits our understanding of the biogeography and the global phylogenetics of the lineage. In addition, there might be an interesting Tertiary relictual biogeographical pattern in *Stegnogramma* s.l., but our current phylogenetic understanding of the group is insufficient to test this.

In this study, we present a global phylogeny of *Stegnogramma* s.l. with the most comprehensive sampling to date. This sampling covers around 70% of the species diversity, including the type species of all previously recognized (infra)generic groups, and all of the known species outside Asia. Based on our results from character state reconstruction and biogeographical analysis, we further present: (i) new (infra)generic revision of *Stegnogramma* s.l.; and (ii) biogeographical scenario for its Tertiary vicariance. Finally, by examining the evolution of leaf venation and dissection in the context of historical biogeography, we propose a link between leaf architectural changes and adaptation in cold climates in ferns.

Materials and methods

Taxon sampling, DNA extraction and PCR amplification

A total of 28 ingroup (*Stegnogramma* s.l.) taxa were sampled, which includes all previously recognized (infra)generic groups, and was estimated to cover ~71% (25 of 35) species diversity. For the outgroup, we sampled a species from *Cyclogramma* (the genus most closely related to *Stegnogramma* s.l.), eight representatives from the other major clades in the subfamily Thelypteridoideae (Thelypteridaceae; Almeida et al., 2016), one from the subfamily Phegopteridoideae (Thelypteridaceae), and one from a closely related family Woodsiaceae.

A modified CTAB protocol (Kuo, 2015) was used to extract DNA. For the plastid regions, we sequenced *rps16-ycf94-matK* intergenic spacer (IGS) and *trnL-L-F* (*trnL* intron + *trnL-F* IGS), *ycf94*, *matK* and *rbcL*. For PCRs, each reaction was performed in 15-µL volume containing 20 ng genomic DNA, 1× PCR buffer, 200 µM dNTP, 15 pmol of each primer and 1 U polymerase (GENETBIO ExPrime Taq DNA Polymerase, Korea). Some primers used in this study were newly designed and are specific to *Stegnogramma* s.l. (Appendix S1).

The voucher information and GenBank accession numbers of our samples are provided in the Appendix S2. A few sequences of the outgroup taxa came from previous studies (Appendix S2).

Phylogenetic analyses

The plastid DNA matrix was aligned using MUSCLE (Edgar, 2004) implemented in Aliview (Larsson, 2014). The maximum-parsimony (MP) phylogeny was inferred using PAUP* 4.0 (Swofford, 2003) under the setting of TBR swapping, gaps as missing data and equal weighting. Heuristic bootstrap analysis was performed under the same setting. W-IQ-TREE (Nguyen et al., 2015; Trifinopoulos et al., 2016) and MRBAYES 3.2.6 (Ronquist and Huelsenbeck, 2003; on CIPRES, Miller et al., 2010) were used to infer the maximum-likelihood (ML) and Bayesian phylogenies, respectively. PARTITIONFINDER 2 (Lanfear et al., 2017; on CIPRES, Miller et al., 2010) was first used to find the best partition scheme (by regions and codon positions) and the associated nucleotide substitution models based on the Aikake Information Criterion (AICc). For the ML phylogeny, 1000 replicates with the same setting were performed to generate standard bootstrap trees. For the Bayesian phylogeny, two simultaneous runs were carried out with four chains each for five million generations. Markov Chain Monte Carlo (MCMC) results were sampled every 1000 generations. The first 25% of the samples were discarded as burn-in, and the rest were used to generate a 50%-majority-rule consensus tree. TRACER v.1.6 (Rambaut and Drummond, 2013) and RWTY (Warren et al., 2017) were used to inspect whether all the post-burn-in MCMC parameters reached convergence.

Molecular dating

In the dating analyses, we focused only on taxa of Thelypteridaceae (excluding Woodsiaceae). Because
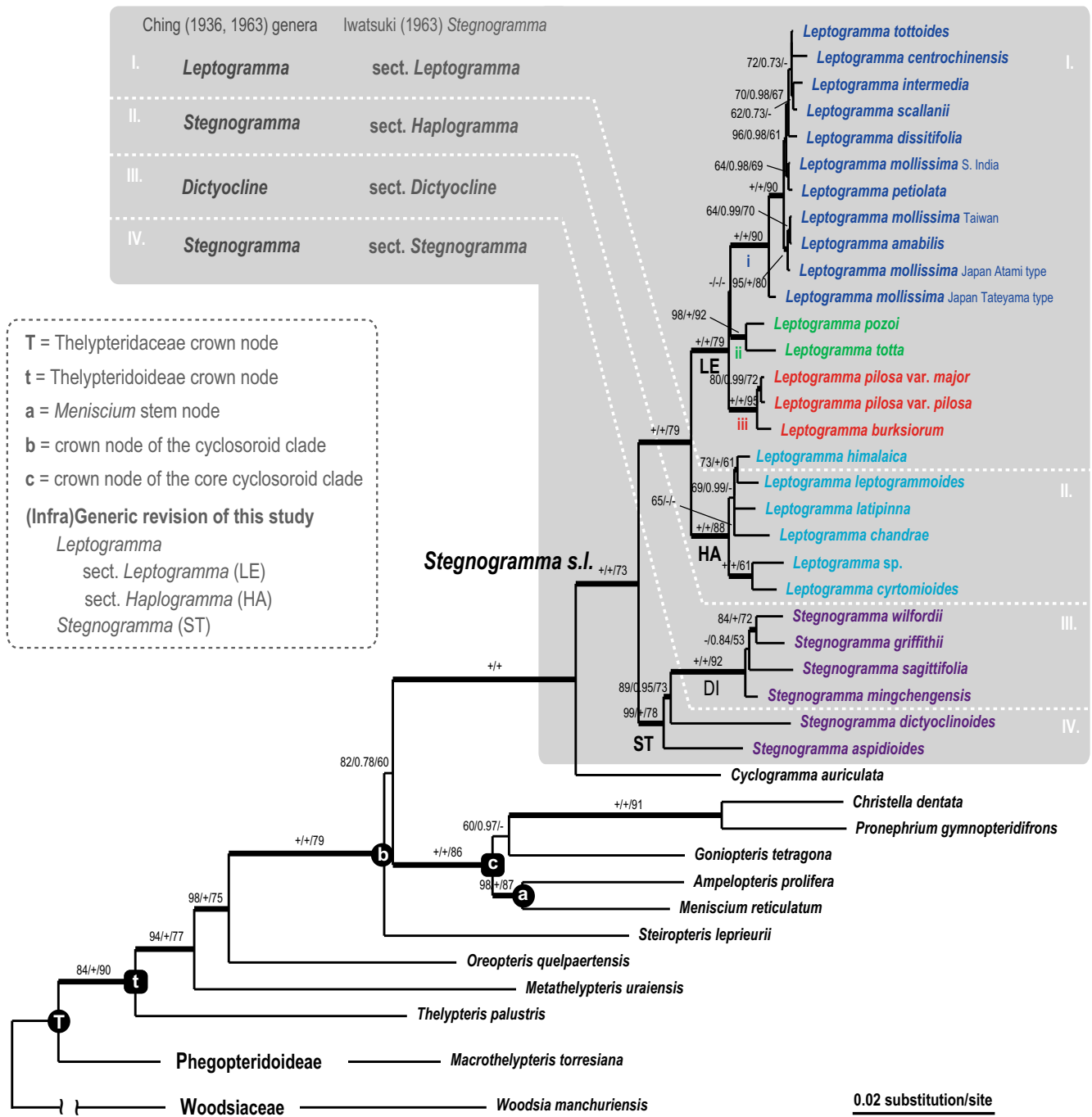
Fig. 1. The maximum-likelihood (ML) phylogeny of *Stegnogramma* s.l. based on the plastid DNA matrix of *rps16-ycf94-matK* IGS + *trnL-L-F* + *ycf94* + *matK* + *rbcL*. ML bootstrap support (ML BS) values, Bayesian inference posterior probabilities (BI PP) and MP bootstrap supports (MP BS) are indicated on each branch of the phylogram, as ML BS/BI PP/MP BS. The plus (+) sign represents ML BS = 100 or BI PP = 1.00; the minus (–) sign represents ML BS < 50, BI PP < 0.5, or MP BS < 50. Three major clades under *Stegnogramma* s.l., "ST", "HA" and "LE", and three subclades under the LE clade, "i", "ii" and "iii", are indicated below the branches. The grey box at the left upper side shows the (infra)generic divisions by Ching (1936, 1963) and Iwatsuki (1963). DI = the *Dictyocline* group. [Colour figure can be viewed at wileyonlinelibrary.com]

merging partitions likely leads to incorrect age estimation due to combining genetic regions with different substitution rates (Angelis et al., 2018), we used the finest partitions possible (by regions and by codon positions). Each of these partitions was applied with its own best substitution model inferred by PartitionFinder 2 (Lanfear et al., 2017; on CIPRES, Miller et al., 2010).

MᴦBᴀʏᴇs 3.2.6 (Ronquist and Huelsenbeck, 2003; on CIPRES, Miller et al., 2010) was used to reconstruct our time-calibrated phylogenies with a relaxed clock model, a uniform prior of branch lengths (prset brlenspr = clock:uniform), and a prior of independent gamma rates (prset clockvarpr = igr). For the clock rate prior, a normal distribution with mean of 0.0001 and standard deviation of 0.1 was applied. Because there is no confirmed fossil of *Stegnogramma* s.l., we applied only age priors on the outgroups. We applied exponential priors on the stem node of *Meniscium* ("a" in Fig. 1; minimum age = 5.333 and mean age = 21.06 Ma) and the crown node of the cyclosoroid clade (sensu Almeida et al., 2016; "b" in Fig. 1; minimum age = 33.9 and mean age = 35.54 Ma). The minimum ages of *Meniscium* and cyclosoroids (i.e. the lineage includes species with both joined venation and round sori) were based on the fossil records published previously (Collinson, 2001; Naugolnykh et al., 2016; Sanín et al., 2016), and the mean ages were set according to the median ages inferred by Testo and Sundue (2016). The root age (= crown age of Thelypteridaceae) was set with a uniform prior between 47.7 and 104.43 Ma, which are the minimum and maximum inferred dates, respectively, from previous studies (Schuettpelz and Pryer, 2009; Kuo et al., 2016; Testo and Sundue, 2016). Two simultaneous runs were carried out with four chains (20 million generations each). In each chain, MCMC results were sampled every 1000 generations. The first 25% of the samples were discarded as burn-in. TRACER v.1.6 (Rambaut and Drummond, 2013) and RWTY (Warren et al., 2017) were used to inspect convergence. Post-burn-in MCMC trees were summarized to obtain the 50%-majority-rule consensus tree as our final chronogram.

Three well-supported clades—ST, HA and LE—were resolved under *Stegnogramma* s.l. (Fig. 1). Moreover, in the LE clade, three geo-subclades (i, ii and iii) were identified but their subclade relationships were still unresolved in the current phylogeny (Fig. 1). To account for all of the possible topologies, we additionally carried out three runs with different topological constraints. This allowed us to test how the different topologies could affect divergence estimates and reconstruction of historical biogeography. A total of 40 million MCMC generations was run for each of the topology-constrained analyses.

Historical biogeography

Only *Stegnogramma* s.l. taxa and their most closely related outgroup, *Cyclogramma*, were included in the following biogeographical analyses. Four biogeographical regions were defined here: (i) East Asia/continental Asia, (ii) North and Central America, (iii) South Europe/Africa, and (iv) Southeast Asia (Fig. 2a). Coding

for their biogeographical distribution mostly followed Watkins and Farrar (2005) and several floras (Holttum, 1982; Mickel and Smith, 2004; Lin et al., 2013; Ebihara, 2016). For *Leptogramma pozoi*, we coded this species with a distribution of South Europe/Africa. The Asian records of "*L. pozoi*" actually belong to a different taxon, and should be treated as *L. mollissima* or its relatives (see more details in Discussion).

Ancestral biogeographical states were reconstructed using the S-DEC (statistical dispersal-extinction-cladogenesis) model (Beaulieu et al., 2013; Yu et al., 2015) implemented in RASP v.4.0 beta (Yu et al., 2015). We did not include the parameter "jump" (J) in our S-DEC reconstruction because the implementation of J in DEC model appears to have some conceptual problems (Ree and Sanmartín, 2018). The maximum area number was set to four. We subsampled 1% of the post-burn-in, ultrametric MCMC trees from the molecular dating analysis as the input for S-DEC. The same biogeographical analysis was carried out for each of the four dating analyses (i.e. those with/without a topology constraint; see Molecular dating section above).

Character coding and ancestral state reconstruction

Only *Stegnogramma* s.l. taxa and their most closely related outgroup, *Cyclogramma*, were included in the analyses here. In total, we analyzed ten discrete and two continuous morphological characters, including indument, rhizome habitat, leaf features and venation. The discrete characters are (1) (presence or absence) multicellular hairs on stipe, (2) (creeping or erect/ascending) rhizome habit, (3) (irregularly reticulate, joined, or free) venation, (4) (stalked or sessile) basal pinnae, (5) (obviously auriculate, slightly auriculate, or nonauriculate) lateral pinnules, (6) (decreasing, nearly equal or increasing) lengths of proximal pinnae, (7) maximum and (8) minimum areole row number, (9) minimum and (10) maximum leaf dissection. The two continuous characters are (11) minimum and (12) maximum proportion of free vein pairs to leaf margin. Coding of these characters was based on documentation in floras (Holttum, 1982; Mickel and Smith, 2004; Lin et al., 2013; Ebihara, 2016), and/or observation of collections in herbaria K, P, PE, TNS and TAIF (see Index Herbariorum for acronyms; http://sweetgum.nybg.org/science/ih/). For the venation characters (9)–(11), we observed the intersegmental parts (i.e. sinuses) at the broadest basiscopic portions of the longest pinnules, and recorded row numbers of areoles (i.e. anastomosing vein pairs) and free vein pairs to leaf margin; for the simple-leaved taxon, *S. sagittifolia*, we recorded these characters from its basal lobes. The proportions of free vein pairs to leaf margin were calculated as number of free vein pairs / total number of vein pairs. The details of our character coding are shown in Appendix S3.
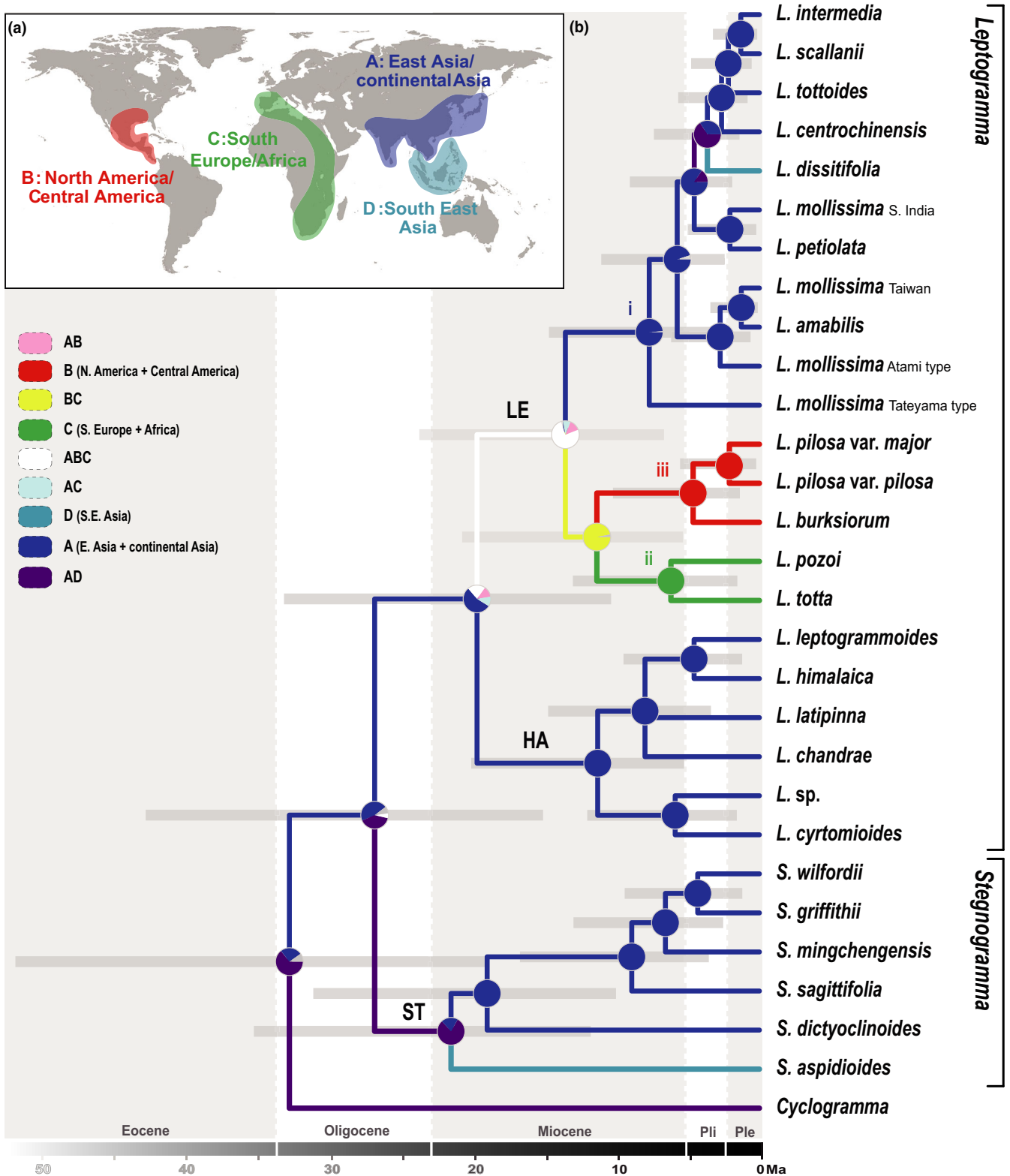
Fig. 2. Present distribution of *Stegnogramma* s.l. (a) and its ancestral state reconstruction of biogeographical regions (b). The pie charts on nodes summarize the state reconstruction based on a S-DEC model, and the colour in each of the branches shows only state inferred with the highest probability. The bars on nodes are 95% HPD age estimates. The new generic division is indicated behind the tip names. Names of different clades and subclades are indicated on the branches. Pli, Pliocene; Ple, Pleistocene. [Colour figure can be viewed at wileyonlinelibrary.com]

All of the subsequent analyses were performed in R v.3.5.1 (R Development Core Team, 2008). To reconstruct ancestral states of the discrete characters, we used simulations of stochastic character mapping (i.e. marginal reconstruction). The input ultrametric trees are the same as the ones used in the S-DEC biogeographical analysis (but only those without topological constraint were used). For the characters (5)–(10), transitions of their character states were set to be ordered because we believe these discrete characters likely evolved in a stepwise manner along a high-to-low or low-to-high direction. In each of these characters, we set only one forward and one reverse rate. For characters (1)–(4), we allowed for all transition rates to be different. Because characters (4)–(6) were applicable only to pinnate species, simple-leaved *S. sagittifolia* was removed from the analyses. When a tip had multiple character states, we set each of the states with an equal probability. To calculate the transition rates of discrete characters [(1)–(9)], we used the "fitMk" function in R/PHYTOOLS (Revell, 2012) with our tip coding states (Appendix S3) and the majority-consensus phylogeny of the input MCMC trees. The "make.simmap" function (Paradis et al., 2004; Revell, 2012) was used for stochastic character mapping with five simulations per MCMC tree. For the continuous characters [(10) and (11)], we used two methods to reconstruct their ancestral states: (A) "ace" function (in R/APE; Paradis et al., 2004) with a Brownian motion model (model = "BM", method = "ML"), and (B) "fastAnc" and "contMap" function (in R/PHYTOOLS). The continuous character states were reconstructed over the majority-consensus ultrametric tree (without topological constraint).

Results

Phylogeny, molecular dating and historical biogeography

Our ML phylogeny is shown in Fig. 1 with ML bootstrap supports (ML BS) and Bayesian (not time-calibrated) posterior probabilities (BI PP), and MP bootstrap supports (MP BS). The dated phylogenies are shown in Fig. 2b (the no-topology-constrained one) and Fig. S1 (with different topological constraints). All post-burn-in effective sampling size values (including the ones for tree topology) are larger than 200, except for those of "igrvar{all}" and "TH{all}" in a few analyses that have values between 156 and 172. Overall, no conflict with a strong branch support was found between different phylogenies except for where a topological constraint was applied. The monophyly of *Stegnogramma* s.l. is highly supported (ML BS = 100; BI PP = 1.00; MP BS = 73) in all of the resulting

phylogenies (Fig. 1), and *Stegnogramma* s.l. is, in turn, sister to *Cyclogramma*, as reported previously (Smith and Cranfill, 2002; He and Zhang, 2012b; Almeida et al., 2016; Luo et al., 2018). Within *Stegnogramma* s.l., three well-supported (ML BS ≥ 99; BI PP = 1.00; MP BS ≥ 78) clades—ST, HA and LE—were identified (Fig. 1). Similar groupings have also been found in previous studies, but ours is the first to pinpoint the positions of *S. aspidioides* (the type of *Stegnogramma*) and *S. dictyoclinoides*. These two species are successive sisters to the *Dictyocline* group in the ST clade (the clade noted with "DI" in Fig. 1). In contrast, the *Dictyocline* group previously was not found to form a clade with any other sister taxon in that clade (He and Zhang, 2012b; Almeida et al., 2016; Luo et al., 2018). In the LE clade, three subclades (i, ii and iii) were identified (Fig. 1), and these clades have distinct geographical distributions (Fig. 2). The type species of *Leptogramma*, *L. totta*, was found in subclade LEii. This represents the first molecular evidence for the position of *L. totta*. However, relationships among the three subclades are still unclear (Fig. 1), and all of the resulting topologies were weakly supported. The Bayesian nondated phylogeny was unable to resolve subclade relationship (i.e. BI PP < 0.5). The ML and MP phylogenies inferred a sister relationship between the two subclades LEi and ii (Fig. 1), whereas the Bayesian dated phylogeny without a topological constraint inferred that the two subclades LEii and iii are sister (Fig. 2b).

Our molecular dating results are summarized in Figs 2b and S1, and for several important nodes, more details are provided in Table 1. Generally, the inferred dates from different analyses (with/without a topological constraint) are similar, although those from the topology-constrained runs are slightly older (Figs 2b and S1).

The reconstructed distribution ranges based on different input trees were nearly identical for their most likely states (Figs 2b and S1). All four analyses supported an Asian origin (A or A + D) of *Stegnogramma* s.l. with subsequent dispersals to North and Central America (B), and South Europe/Africa (C) (Figs 2b and S1). The main difference among these analyses is their inferred biogeographical scenarios for the subsequent range contractions/extinctions after the broad distribution (A + B + C) of the LE crown node (Figs 2b and S1; summarized in Table 1).

Morphological character evolution

The ancestral state reconstructions of morphological characters are shown in Figs 3 and 4. Some discrete characters such as "multicellular hairs on stipe", "rhizome habit" and "venation", are less homoplasious and thus more useful to characterize the clades morphologically (Fig. 3a–c). However, characters for lateral and proximal pinnae are evidently more

Table 1
Summary of biogeographical reconstructions from different dating analyses

Analysis	Stem node of LE clade		Crown node of LE clade		Second diverged node under LE clade	
	Biogeographical region*	Age: median [95% HPD] Ma	Biogeographical region*	Age: median [95% HPD] Ma	Biogeographical region*	Age: median [95% HPD] Ma
No constraint (Fig. 2)	A	20.43 [10.73–34.40]	A + B + C	14.04 [6.90–24.61]	B + C	11.78 [5.52–21.51]
Sister constraint of ii + iii (Fig. S1)	A	22.74 [10.85–39.22]	A + B + C	15.66 [6.91–28.17]	B + C	13.12 [5.45–23.84]
Sister constraint of i + iii (Fig. S1)	A	22.34 [11.18–38.87]	A + B + C	15.16 [7.05–27.53]	A + B	13.96 [6.26–25.16]
Sister constraint of i + ii (Fig. S1)	A	22.80 [11.58–39.47]	A + B + C	15.56 [7.07–28.42]	A + C	13.84 [6.35–25.57]

*A, East Asia/continental Asia; B, North and Central America; C, South Europe/Africa.

homoplasious (Fig. 3d–f). One interesting pattern inferred here is that venation characters (i.e. "areole row number" and "proportion of free vein pairs to leaf margin") and "leaf dissection" are likely linked. The decrease of "areole row number", increase of "proportion of free vein pairs to leaf margin" and increase of "leaf dissection" appear to be linked (Fig. 4).

Discussion

Phylogeny, systematics and character evolution

Our phylogeny is the first to place all of the type taxa in previously recognized sections/genera in *Stegnogramma* s.l., except for *Craspedosorus* [= *Stegnogramma sinensis* (Ching & W.M. Chu) L.J. He & X.C. Zhang = *Leptogramma sinensis* (Ching & W.M. Chu) Y.H. Chang & L.Y. Kuo]. We found that *Stegnogramma* s.l. can be divided into three major clades: ST, HA and LE (Fig. 1). The division by these clades differs from previous circumscriptions of sections/genera (Fig. 1), and only (sect.) *Dictyocline* was found to be monophyletic.

Previous generic or sectional classifications (Ching, 1936, 1963; Iwatsuki, 1963; Lin et al., 2013) have relied mostly on characteristics of venation, which is free for (sect.) *Leptogramma*, joined for (sect.) *Stegnogramma* and irregularly reticulate for (sect.) *Dictyocline*. Our reconstruction of character evolution suggests that joined venation evolved into irregularly reticulate venation once and into free veins several times (Figs 3c and 4a–d). In other words, the joined-vein *Stegnogramma* s.l. [i.e. (sect) *Stegnogramma* sensu Ching (1936, 1963) and Iwatsuki (1963)], as well as the free-veined group [i.e. (sect.) *Leptogramma* sensu Ching (1936, 1963) and Iwatsuki (1963)] are polyphyletic. Nonetheless, the number of areole rows is different for each clade (Fig. 4a–d). Evolution of indument characters, by contrast, is conserved in *Stegnogramma* s.l. The presence of multicellular hairs on the stipe evolved once at the crown node of the HA clade, and serves as a synapomorphy for this clade (Fig. 3a). Because of this character, *Craspedosorus* most likely belongs to this clade, and unpublished phylogenetic data (J. Nitta, pers. comm.) also support this idea. For the remaining characters investigated here, we find that all tend to be homoplasious (Fig. 3d–f), and are less useful for systematics use. By revisiting the three major clades morphologically, we here provide a revised classification of *Stegnogramma* s.l. with two genera and two sections (see Taxonomy section below).

In addition, the current phylogeny reveals several cryptic taxa that are worthy of taxonomic reevaluation. Particularly for East Asian *Leptogramma*, several
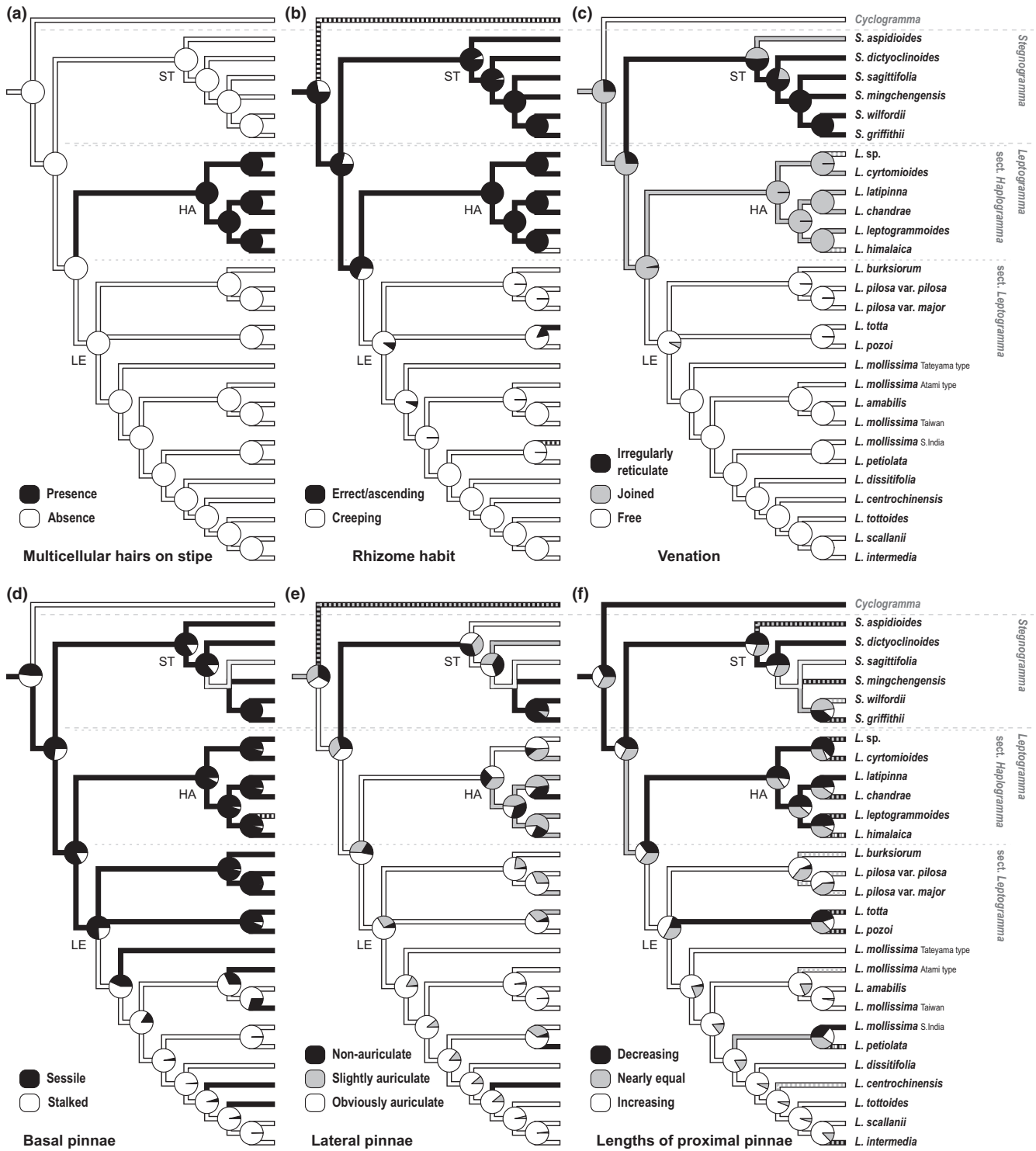
Fig. 3. The ancestral state reconstruction of stipe indument (a), rhizome habitat (b), venation types (c) and pinna characters (d–f) in *Stegnogramma* s.l. The pie charts on nodes summarize results of stochastic character mapping, and the colour in each of the branches shows only the state inferred with the highest probability. The dashed lines of terminal branches indicate the equally possible character states coded for tip taxa. The new generic and section-level division are indicated behind the tip names.
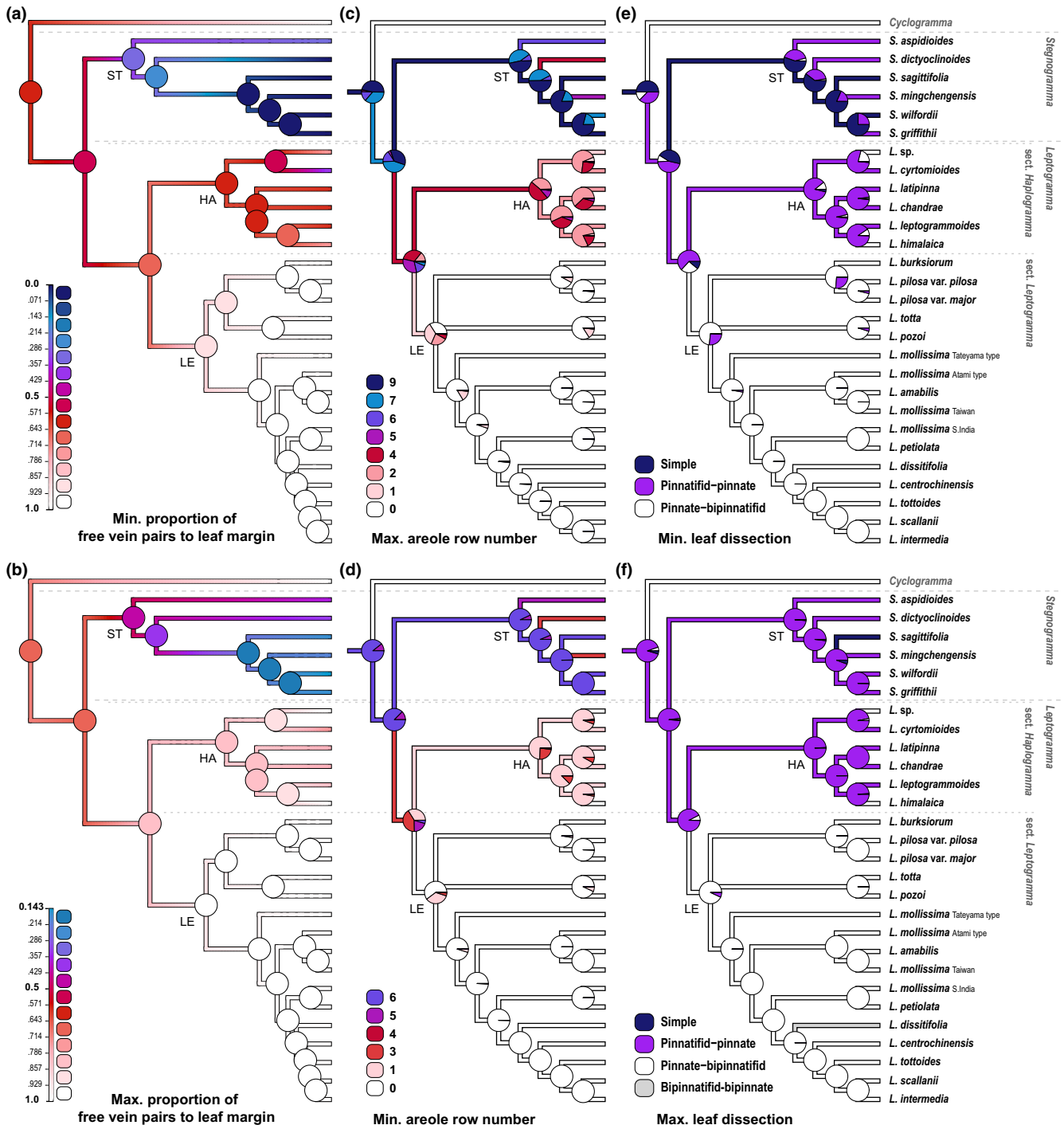
Fig. 4. The ancestral state reconstruction of venation characters (a–d) and leaf dissection (e–f) in *Stegnogramma* s.l. For continuous characters of venation (a & b), the pie charts on nodes show the results by "ace" function with a Brownian motion model, and the colours on branches show the results from "fastAnc" function. For the discrete characters (d–f), the pie charts on nodes summarize results of stochastic character mapping, and the colour in each of the branches shows only the state with the highest probability. The new generic and sectional division are indicated behind the tip names. [Colour figure can be viewed at wileyonlinelibrary.com]

phylogenetically distinct taxa have been synonymized under *L. mollissima* (Fig. 1), or sometimes misapplied as *L. pozoi* (e.g. Kuo, 1975; Tsai and Shieh, 1994; Lin et al., 2013), which is a species endemic to South Europe and Northern Africa, and has elongate sori (vs. shorter ones in Asian *L. mollissima*). The "true"

L. mollissima is likely distributed only in southern India (i.e. its type locality), and is apparently a tetraploid (Ghatak, 1977; Irudayaraj et al., 1996). In contrast, East Asian "*L. mollissima*" is known only from diploids (reviewed in Ebihara, 2016). In East Asia, "*L. mollissima*" has at least two distinct morphological forms, Atami and Tateyama type, but these two forms exhibit a continuous morphological cline similar to *L. pilosa* var. *major* and var. *pilosa* (Watkins and Farrar, 2005), and may form fertile hybrids and introgress (Yatabe et al., 1998, 2002). Together with *L. amabilis* in Japan, further genetic evidence is needed to clarify species boundaries among these Asian *Leptogramma* taxa.

The pattern of leaf venation has long been recognized as an important taxonomic character in the thelypteroid ferns. There are different venation types in subfamily Thelypteridoideae, and, among and within different major clades, transitions between different venation types have been found (Iwatsuki, 1962; He and Zhang, 2012b). *Stegnogramma* s.l., for example, has three major types—free, joined and irregularly reticulate patterns (Fig. 3c). The previous hypothesis is that the irregularly reticulate veins in *Stegnogramma* s.l. evolved from a free-veined ancestor through joined venation (Iwatsuki, 1962), and is generally supported by our character reconstruction (Fig. 3c). However, free veins in the LE clade are more likely a reversal from joined veins. Although most outgroup lineages were excluded from our character state reconstruction, they (together with *Cyclogramma*) are mostly free-veined except for the core cyclosoroid clade (i.e. the lineage with the crown node "c" in Fig. 1). In other words, instead of being joined, the ancestral state of *Stegnogramma* s.l. + *Cyclogramma* is more likely to be free-veined along with the cyclosoroid crown node, as suggested in He and Zhang (2012b; in which they coded this type of free venation as "veins connivent at sinuses"). Interestingly, Iwatsuki (1962) observed a transition in leaf venation through different juvenile stages in *S. wilfordii* (in the *Dictyocline* group), being free-veined during the early stages of sporeling leaf development but subsequently shifting to irregularly reticulate venation without an intermediate joined venation stage. Together with the evolutionary pattern inferred here, Iwatsuki's (1962) finding further implies that a developmental transition of vein formation may occur in very young stages. Given the importance of venation pattern in this family, such developmental transition warrants further study with careful examinations of additional taxa from the ST clade.

Vicariance, recent dispersals and diversification in Asia

Stegnogramma s.l. arose in Asia and subsequently dispersed to North and Central America, and South Europe/Africa (Figs 2b and S1). These intercontinental expansions (7–40 Ma) in the LE clade were estimated to have occurred during the Tertiary. This was followed by cladogenesis with range contractions (5–20 Ma) during the Miocene (Table 1). Age estimates of the biogeographical splits leading to the South European/African subclade LEiii corroborate disconnection of the North Atlantic land bridge and/or formation of climatological barriers since the Middle Miocene (~15 Ma; Tiffney and Manchester, 2001), and imply vicariant speciation in the LE clade.

Our vicariance time estimates fall in the known range of previously studied cases (reviewed in Tiffney and Manchester, 2001; Xiang et al., 2015; Wen et al., 2016) but are on average older than those known from most fern examples studied previously (Table 2). Previous estimates for ferns predominantly were for disjunct taxa in eastern Asia and western North America, and fell between 2.4 and 9.68 Ma (95% HPDs ranged from 0.5 to 20.12 Ma; Table 2), except for *Diplazium* subgen. *Diplazium* (Wei et al., 2015). Reconstruction by our dated phylogeny without a topological constraint, however, favours a vicariant origin through the North Atlantic land bridge that gave rise to a disjunct descendants in North (and Central) America and Europe/Africa (Fig. 2b; with a BI PP branch support of 0.62, data not shown). Some fern genera, such as *Polypodium* and *Dryopteris*, have also been reported to have such a North Atlantic disjunction but their biogeographical divergences were estimated to be younger than the land bridge disconnection, and thus more likely resulted from long-distance dispersal (Sessa et al., 2012; Sigel et al., 2014). A more probable example of North Atlantic vicariance in ferns was suggested in *Cryptogramma* sect. *Cryptogramma* (Metzgar et al., 2013, 2016) with a biogeographical split estimated to 8.64 Ma (95% HPD of 5.22–9.6 Ma; Testo and Sundue, 2016). Among these cases, the divergence estimate in *Stegnogramma* s.l. presented here is the most ancient one, and represents a rare case for ferns in the context of North Atlantic vicariance. Still, many other ferns, such as *Culcita* spp., exhibit a similar disjunct distribution pattern (Pichi Sermolli, 1979). Clearly, these taxa are in need of further phylogenetic investigation to better understand the biogeography of North Atlantic vicariance in ferns.

The Asian subclade LEi was found to be the most species-rich among the three geo-subclades. Such a pattern supports the hypothesis that, when compared to North America or Europe, the refugia in East Asia may have provided as a more stable climate leading to the diversification of Tertiary relictual plants (Tiffney and Manchester, 2001; Wen et al., 2016; Tang et al., 2018). In this Asian subclade, species such as *Leptogramma dissitifolia* (possibly also *L. gymnocarpa*, *L. subcalcarata*, *L. celebica* and *L. crenata* that were

Table 2
Fern genera inferred with a pattern of Tertiary vicariance

Genus	Specific lineage	Distribution	Divergence estimates (Ma): median [95% HPD(s) range]	References
Diplazium	subgen. *Diplazium*	E.Asia/N.America	29.3–31.2 [23.9–38.4], 18.78 [17.72–22.16]*	Wei et al. (2015)
Leptogramma	the LE clade (= sect. *Leptogramma*)	Europe (+ Africa)/N.America	11.78–13.12 [5.45–23.84]	This study (Figs 2 and S1a)
Cystopteris	*chinensis/bulbifera* clade	E.Asia/N.America	9.68 [4.36–13.26][a]	Wei and Zhang (2014)
Asplenium	*ruprechtii/rhizophyllum*	E.Asia/N.America	9.29 [7.69–20.12][a]	Xiang et al. (2015)
Polypodium	*glycyrrhiza* clade	E.Asia/N.America	8.81 [5.06–13.08]	Sigel et al. (2014)
Cryptogramma	sect. *Cryptogramma* (*crispa/cascadensis*)	Europe (+ Africa)/N.America	8.64 [5.22–9.6][a]	Metzgar et al. (2016)
Deparia	the LU clade (= sect. *Lunathyrium*)	E.Asia/N.America	7.61–9.38 [4.39–16.17]	Kuo et al. (2016)
Polystichum	sect. *Polystichum*, subclade A1	E.Asia/N.America	7 [2–16]	Le Péchon et al. (2016)
Dryopteris	*ludoviciana* + *celsa/tokyoensis*	E.Asia/N.America	5.6 [2.2–9.4]	Sessa et al. (2012)
Adiantum	*pedatum* complex	E.Asia/N.America	2.47–2.87 [1.17–4.63]	Lu et al. (2011)

[a] Ages from Testo and Sundue (2016).

not sampled by us), have expanded and further colonized high mountains in southeast Asian islands via long-distance dispersals (Fig. 2b). For the HA clade, because the majority of the species are found distributed in the Himalayas, the radiation that began in the late Miocene was presumably driven by the rise of the Qinghai-Tibetan Plateau, as already suggested for several Himalayan ferns (Wang et al., 2011; Li et al., 2012; Chen et al., 2017) and many other plant groups (reviewed in Wen et al., 2014).

Evolution of leaf architecture and its implication for ecological adaptation

Leaf architecture and morphology play crucial functional roles in plant ecophysiology and there have been several studies of angiosperms that link leaf form with function (Boyce et al., 2009). For example, venation patterns are crucial to efficiently deliver water to the sites of photosynthesis in order to maintain assimilation, and a higher vein density tends to have a higher carbon assimilation rate (Roth-Nebelsick et al., 2001; Brodribb et al., 2007; Boyce et al., 2009). In angiosperms, serration/dissection of leaves is strongly and negatively correlated with annual mean temperature, and has been used as a climatic indicator for extant and palaeofloras by some authors (Bailey and Sinnott, 1916; Peppe et al., 2011, and references therein). It has been hypothesized that plants from higher latitudes develop thinner leaves with greater dissection, marginal serration and/or increased number of lobes. This may potentially maximize the leaf surface:volume ratio and impact gas exchange (Baker-Brosh and Peet, 1997; Royer and Wilf, 2006; Royer et al., 2012; McKee, 2017). Similar attention has not been paid to ferns, a lineage that is remarkable for variation in overall leaf morphology (Vasco et al., 2013), and the association between leaf architecture and ecological adaptation in ferns has remained unexplored.

From our results of reconstructions of character evolution, leaf architectural traits—venation and dissection—appear to be linked in *Stegnogramma* s.l. Specifically, more highly dissected leaves produced fewer areole rows and an increased proportion of free veins (Fig. 4). When the "closed" inter-segmental lamina becomes more lobed/dissected, areoles "break" into free veins. As suggested previously, these two characters in ferns are generally associated with each other (Wagner, 1979). A similar evolutionary pattern was found in some fern lineages (e.g. the ER + DI clade in *Deparia*; Kuo et al., 2018), and such linkage is particularly obvious in thelypteroid ferns (Smith, 1971). Furthermore, in *Stegnogramma* s.l., we found that more dissected species produce higher proportions of free vein pairs and tend to be distributed in higher latitudes. For example, in the LE clade, all members

that produce bipinnate free-veined leaves are distributed in the highest latitudinal records of *Stegnogramma* s.l. (i.e. *L. mollissima* record in Japan, Hokkaido, N44°). The ST clade, which produces less dissected (simple to pinnate) leaves with anastomosing veins, has the lowest latitudinal records in *Stegnogramma* s.l. (i.e. *S. aspidioides* record in Indonesia, N3.4° to S7.2°) and the most northern distribution to N28.3° (i.e. for *S. mingchegensis* record in China, Jiangxi) (accessed in GBIF 2019/2/5). These patterns imply a shift in venation and dissection along a latitudinal gradient in *Stegnogramma* s.l. This corresponds to an overall and previously reported pattern where the proportion of free-veined taxa increases along latitudinal gradients between North and Central American ferns (Wagner, 1979).

Taken together, we here hypothesize that increases in leaf dissection and the proportion of free vein pairs (and decrease of areole rows) in *Stegnogramma* s.l. are adaptive features for cold temperate climates with a greater seasonality. During the early growing season, more dissected leaves with a greater leaf surface:volume ratio may better enhance assimilation and leaf-level hydraulics compared to less dissected leaves, a pattern similar to functionalities assumed in angiosperm leaves (see Discussion above). Moreover, we found that, in the HA clade, more dissected species with higher proportions of free vein pairs and fewer areole rows tend to occur at higher elevations. *Leptogramma himalaica* produces bipinnatifid leaves with no areoles or a single areole row (i.e. the highest leaf dissection degree and the lowest number of areole rows in the HA clade; Fig. 4) and is distributed at a higher elevational range (2100–2500 m a.s.l.), whereas *L. cyrtomioides* produces pinnate leaves with one to two areole rows (i.e. the lowest leaf dissection degree and the highest numbers of areole rows in the HA clade; Fig. 4) and occurs at lower elevations (600–1500 m a.s.l.; Lin et al., 2013). These observations support our hypothesis that in *Stegnogramma* s.l. leaf traits are associated with adaptations to different climatic environments. It also is likely that following the Paleocene–Eocene Thermal Maximum, features of free-veined and bipinnatifid leaves of the LE clade may have facilitated range expansion to cold temperate regions, particularly the high-latitude land bridge in the early Miocene (Table 1; Fig. 2; Tiffney and Manchester, 2001; Tiffney, 2008).

In conclusion, using the case of *Stegnogramma* s.l., we propose some characteristics of leaf architecture that are possibly adaptive for temperate vs. tropic, and cold vs. warm climates in ferns. We believe that this hypothesis warrants further investigation with phylogenetic correlation and evidence from ecophysiological experiments. Analyses of phylogenetic correlation between these functional traits and habitat preferences would be worthwhile in order to work on a broader scale of taxon sampling, such as a dataset of whole subfamily Thelypteridoideae. In addition to the leaf characteristics mentioned above, there might be other adaptive strategies for ferns in different climates. For example, prolific growth (Watkins and Farrar, 2005) and cold-tolerance (Sato and Sakai, 1981) of gametophytes have been suggested to be important for the adaptation of temperate ferns. We also noticed that the evolution of included veinlets in the *Dictyocline* group possibly increases vein density in these ferns (C.-W. Chen, pers. comm.), and thereby may enhance their photosynthetic rates in adapting to warmer habitats. More surveys in ferns are needed to study adaption of these growth habits and morphological traits.

Taxonomy

Key to genera and sections of Stegnogramma s.l.

1.. Veins irregularly or joined-anastomosing, included veinlets present or not; more than three rows of intersegmental areoles .... genus *Stegnogramma*
2.. Veins free or joined-anastomosing, included veinlets absent; not more than two rows of intersegmental areoles .... 2 (genus *Leptogramma*)
3.. Multicellular hairs present on stipes .... *Leptogramma* sect. *Haplogramma*
4.. Multicellular hairs absent on stipes .... *Leptogramma* sect. *Leptogramma*

Genus ***Stegnogramma*** Blume, Enum. Pl. Javae 2: 172. 1828. *Dryopteris* subgen. *Stegnogramma* (Blume) C. Chr., Index Filic. [C. Chr.] xxii, 250. 1906.—*Gymnogramma* subgen. *Stegnogramma* (Blume) Hook., Sp. Fil. 5: 150. 1864, "*Stegnogramme*".—*Thelypteris* sect. *Stegnogramma* (Blume) Fraser-Jenk., Taxon. Revis. Indian Subcontinental Pteridophytes 590. 2008.—*Thelypteris* subgen. *Stegnogramma* (Blume) C.F. Reed, Phytologia 17(4): 254. 1968.—Type: *St. aspidioides* Blume (from INDONESIA, Java).

HETEROTYPIC SYNONYMS: *Dictyocline* T. Moore, Gard. Chron. 1855: 854. 1855.—*Stegnogramma* sect. *Dictyocline* (T. Moore) K. Iwats., Acta Phytotax. Geobot. 19(4–6): 115. 1963.—*Syneuron* J. Sm., *mss.*; in Hook. f., Ic. Pl. t. 950. 1854.—Type: *Di. griffithii* T. Moore (from INDIA, Assam).

Generic characters

Rhizomes short creeping or suberect, sparsely scaly, scales lanceolate, rufous to brown, thick, more or less setose; fronds caespitose or approximate. Laminae

oblong to ovoid, simple, pinnatifid or pinnate, generally herbaceous, entire, covered by acicular unicellular hairs on all parts; stipes mainly stramineous with blackish base, terete, hairy throughout but slightly scaly at bases. Venation reticulated, goniopteroid [in *Stegnogramma* sensu Ching (1936)] or copiously anastomosing (in *Dictyocline* group), areolae with included veinlets (in *Dictyocline* group) or not. Sori linear, exindusiate, borne along all veins (in *Dictyocline* group) or only lateral veinlets and the related excurrent ones [in *Stegnogramma* sensu Ching (1936)]; sporangia generally setiferous near the top; spores bilateral.

Taxa included

1. **Stegnogramma aspidioides** Blume, Enum. Pl. Javae 2: 173. 1828.—*Gymnogramma aspidioides* (Blume) Hook., Ic. Pl. t. 950. 1854, *non* Kaulf. 1824, *nec* Desv. 1827, *nor* Blume 1828.—*Grammitis aspidioides* (Blume) Hook. f. in Thwait., Enum. Pl. Zeyl. 383. 1864.—*Syneuron aspidioides* (Blume) J. Sm., *mss.* (info. from Hook. f., Ic. Pl. t. 950. 1854).—*Thelypteris merryi* Christenh., Global Fl. 1(4): 33. 2018; *non Th. aspidioides* (Willd.) R.M. Tryon, Rhodora 69(777): 5. 1967.—*Gy. stegnogramma* Blume, Fl. Javae Fil. 98, t. 44. 1828.—*Dryopteris stegnogramma* (Blume) C. Chr., Index Filic. [C. Chr.] 294. 1906.—*Nephrodium stegnogramma* (Blume) Diels in Engler & Prantl, Nat. Pflanzenf. 1(4): 181. 1899.—*Phegopteris stegnogramma* (Blume) Mett., Fil. Hort. Bot. Lips. 84. 1856.—*Th. stegnogramma* (Blume) C.F. Reed, Phytologia 17: 466. 1968.—TYPE: *anonymous (C.L. Blume?) s.n.*, INDONESIA, Java, in L; *C.L. Blume 44*, INDONESIA, Java, in K.
   HETEROTYPIC SYNONYM: *Phegopteris stegnogramme* (Blume) Mett. var. *meniscioides* Alderw., Bull. Jard. Bot. Buitenzorg, ser. 2, 16: 27. 1914.—Type: *C.G. Matthew 584* (from INDONESIA, Sumatra), in BO & K.
   DISTRIBUTION: Indonesia (Borneo, Java and Sumatra), Vietnam and Malaysia (Sabah).

2. **Stegnogramma dictyoclinoides** Ching, Sinensia 7 (1): 92, pl. 1. 1936.—*Cyclosorus dictyoclinoides* (Ching) C.M. Kuo, Taiwania 47(2): 171. 2002.—*Thelypteris dictyoclinoides* (Ching) C.F. Reed, Phytologia 17: 465. 1968.—TYPE: *H.T. Tsai 62728*, CHINA, Yunnan, in PE?.
   DISTRIBUTION: China (Yunnan) and Taiwan (Pingtung, Taitung).

3. **Stegnogramma griffithii** (T. Moore) K. Iwats., Mem. Coll. Sci. Kyoto Imp. Univ., Series B, Biol. 31(1): 20. 1964.—*Dictyocline griffithii* T. Moore, Index Fil. [T. Moore] lix, 316. 1857.—*Aspidium griffithii* (T. Moore) Diels in Engler & Prantl, Nat. Pflanzenf. 1(4): 186. 1899.—*Cyclosorus griffithii* (T. Moore) C.M. Kuo, Taiwania 47(2): 171. 2002.—*Gymnogramma griffithii* (T. Moore) Hance, J. Bot. 25: 14. 1887.—*Hemionitis griffithii* (T. Moore) Hook. f. & Thomson, Sp. Fil. [Hooker] 5: 193. 1864.—*Thelypteris griffithii* (T. Moore) C.F. Reed, Phytologia 17(4): 280. 1968.—TYPE: *W. Griffith s.n.*, INDIA, Meghalaya (part of Assam before 1970), in K.
   HETEROTYPIC SYNONYM: *Hemionitis griffithii* (T. Moore) Hook. f. & Thomson var. *pinnata* Hook., Sp. Fil. [Hooker] 5: 193. 1864.—Type: *J.D. Hooker et T. Thomson s.n.* (from INDIA, Assam), in K?
   DISTRIBUTION: China (Yunnan), India, Myanmar, Taiwan and Vietnam.

4. **Stegnogramma mingchegensis** (Ching) X.C. Zhang & L.J. He, Glossary Lycopods Ferns 166. 2015.—*Dictyocline mingchegensis* Ching, Acta Phytotax. Sin. 8(4): 334. 1963.—*Di. griffithii* T. Moore var. *tenuissima* Ching, Bull. Fan Mem. Inst. Biol. 1: 146, f. 1. 1930.—TYPE: *K.K. Tsoong s.n.*, CHINA, Zhejiang, in PE.
   DISTRIBUTION: China (Fujian, Zhejiang and Guangdong).

5. **Stegnogramma sagittifolia** (Ching), L.J. He & X.C. Zhang, Lycophytes Ferns China 346. 2012.—*Dictyocline sagittifolia* Ching, Acta Phytotax. Sin. 8(4): 335. 1963.—TYPE: *C.L. Tso 20932*, CHINA, Guangdong, in PE.
   DISTRIBUTION: China (Guangdong, Guangxi, Guizhou, Hunan, Jiangxi).

6. **Stegnogramma wilfordii** (Hook.) Seriz., J. Jap. Bot. 50: 17. 1975.—*Hemionitis wilfordii* Hook., Fil. Exot. t. 93. 1859.—*Dictyocline wilfordii* (Hook.) J. Sm., Hist. Fil. 149. 1875.—*Di. griffithii* T. Moore var. *wilfordii* (Hook.) T. Moore, Index Fil. [T. Moore] 317. 1861.—*St. griffithii* (T. Moore) K. Iwats. var. *wilfordii* (Hook.) K. Iwats., Acta Phytotax. Geobot. 19(4-6): 117. 1963.—*Thelypteris griffithii* (T. Moore) C.F. Reed var. *wilfordii* (Hook.) C.F. Reed, Phytologia 17(4): 280. 1968.—*He. griffithii* (T. Moore) Hook. f. & Thomson var. *pinnatifida* Hook., Sp. Fil. [Hooker] 5: 193. 1864.—*Di. griffithii* T. Moore var. *pinnatifida* (Hook.) Bedd., Ferns Brit. India 155. 1866.—TYPE: *C. Wilford 503*, TAIWAN, Keelung, in K.
   DISTRIBUTION: China, Japan and Taiwan.

Genus **Leptogramma** J. Sm., J. Bot. [Hooker] 4: 51. 1842. *Dryopteris* subgen. *Leptogramma* (J. Sm.) C. Chr., Index Fil. [C. Chr.] xxi, 250. 1906.—*Grammitis* sect. *Leptogramma* (J. Sm.) T. Moore, Index Fil. [T.

Moore] lxiii. 1857.—*Stegnogramma* sect. *Leptogramma* (J. Sm.) K. Iwats., Acta Phytotax. Geobot. 19(4–6): 115. 1963.—*Thelypteris* subgen. *Cyclosorus* sect. *Leptogramma* (J. Sm.) C.V. Morton, Amer. Fern J. 53 (4): 153. 1963.—Type: *Le. totta* (Schltdl.) J. Sm. (from SOUTH AFRICA), lectotypified by C. Chr., Index Fil. [C. Chr.] xxi. 1906.

HETEROTYPIC SYNONYMS: *Craspedosorus* Ching & W.M. Chu, Acta Phytotax. Sin. 16(4): 24. 1978.— Type: *Cr. sinensis* Ching & W.M. Chu (from CHINA, Yunnan). *Stegnogramma* sect. *Haplogramma* K. Iwats., Acta Phytotax. Geobot. 19(4–6): 115. 1963.—Type: *St. cyrtomioides* (C. Chr.) Ching (from CHINA, Sichuan).

Generic characteristics

Rhizomes short erect or ascending, sparsely scaly, scales ovate-oblong or lanceolate, rufous to brown, thick, more or less setose; fronds caespitose. Laminae oblong, hastate, ovate-lanceolate or lanceolate, pinnate-pinnatifid, herbaceous or papery, covered by long acicular hairs (or mixed with shorter setae) in all parts; stipes stramineous or darker, rarely pale green (in *Leptogramma sinensis*), terete, hairy throughout but scaly only at bases; pinnae 6–25 pairs, pinnatifid and usually reaching 1/2–2/3 of distance to costae, oblique or spreading, oblong to lanceolate, bases rounded or truncate, usually sessile but in some taxa with short stalks, apices obtuse or acuminate; proximal 1 to several pairs of pinnae free, distal ones usually adnate to rachises; costae grooved adaxially; segments ovate or oblong, usually entire, rounded or sometimes obtuse at apices. Venation pinnately forked, 3–10 pairs per segment, tips of veinlets reaching to leaf margin but rarely not (in *Leptogramma sinensis*); all free, occasionally reticulated, or regularly anastomosing with 1- or 2-jugate costal areolae. Sori oblong, elongate or linear, borne along veinlets but shorter than veinlets, exindusiate; sporangia generally setiferous (1–6 setae; dependent upon species) near the top; spores bilateral.

Section **Haplogramma** (K. Iwatsuki,) L.Y. Kuo & Y.H. Chang, **comb.n**.
Type species: *Dryopteris stegnogramma* C. Chr. var. *cyrtomioides* C. Chr. (= *Leptogramma cyrtomioides*; from CHINA, Sichuan).

Section characteristics

As "*Generic characteristics*" described above; but differs from section *Leptogramma* by their long acicular hairs being multicellular (vs. unicellular in section *Leptogramma*), and venation being occasionally reticulated, or regularly anastomosing with 1- or 2-jugate costal areolae (vs. all free in section *Leptogramma*).

Taxa included

1. **Leptogramma chandrae** (Fraser-Jenk.) Y.H. Chang & L.Y. Kuo, **comb.n.**; *non Le. asplenioides* (Sw.) J. Sm., J. Bot. [Hooker] 4: 52. 1842.—*Dryopteris stegnogramma* (Blume) C. Chr. var. *asplenioides* C. Chr., Acta Horti Gothob. 1(2): 56. 1924.—*Stegnogramma asplenioides* (C. Chr.) Ching, Sinensia 7(1): 94. 1936.—*Thelypteris chandrae* Fraser-Jenk., Taiwania 53(2): 191. 2008.— TYPE: *W. Griffith s.n.*, INDIA, Meghalaya (part of Assam before 1970), in GH and K.
DISTRIBUTION: China (Yunnan?) and India (Assam, Meghalaya, and Sikkim).

2. **Leptogramma cyrtomioides** (C. Chr.) Y.H. Chang & L.Y. Kuo, **comb.n.**—*Dryopteris stegnogramma* (Blume) C. Chr. var. *cyrtomioides* C. Chr., Acta Horti Gothob. 1(2): 56. 1924.—*Stegnogramma cyrtomioides* (C. Chr.) Ching, Sinensia 7: 95. 1936.—TYPE: *H. Smith 2104*, CHINA, Sichuan, in BM & S.
DISTRIBUTION: China (Hunan, Guizhou, Sichuan and Yunnan).

3. **Leptogramma himalaica** Ching, Sinensia 7: 100. 1936.—*Stegnogramma himalaica* (Ching) K. Iwats., Acta Phytotax. Geobot. 19(4–6): 122. 1963.—*Thelypteris himalaica* (Ching) C.F. Reed, Phytologia 17(4): 283. 1968.—*Th. pozoi* (Lag.) C.V. Morton subsp. *himalaica* (Ching) C.V. Morton, Amer. Fern J. 56(4): 179. 1966.—TYPE: *R.R. Stewart s.n.*, INDIA (NW Himalaya), Simla, in PE, NW, and US.
HETEROTYPIC SYNONYM: *Leptogramma yunnanensis* Ching, Icon. Filic. Sin. 5: pl. 228. 1958.—Type: *K.M. Feng 4474* (from CHINA, Yunnan), in PE.
DISTRIBUTION: China (Yunnan), NW (Simla) & S (Kodiakanal) India (Morton, 1966).

4. **Leptogramma jinyunensis** Y.H. Chang & L.Y. Kuo, **comb. & nom.n.**; *non Le. diplazioides* (Desv.) Underw., Bull. Torrey Bot. Club 29: 626. 1902.—*Stegnogramma diplazioides* Ching ex Y.X. Lin, Fl. Reipubl. Popularis Sin. 4(1): 288, 351. 1999.—TYPE: *C.Z. Liu 10047*, CHINA, Chongqing, Mt. Jinyun.
DISTRIBUTION: China (Chongqing).
NOTE: The new name of this species under *Leptogramma* refers to its type location, i.e. Mt. Jinyun.

5. **Leptogramma latipinna** (Ching ex Y.X. Lin) Y.H. Chang & L.Y. Kuo, **comb.n.**—*Stegnogramma latipinna* Ching ex Y.X. Lin, Fl. Reipubl. Popularis Sin. 4(1): 350. 1999.—TYPE: *K.M. Feng*

7578, CHINA, Yunnan, in PE.
DISTRIBUTION: China (Yunnan).

6. ***Leptogramma leptogrammoides*** (K. Iwats.) Y.H. Chang & L.Y. Kuo, **comb.n.**—*Stegnogramma leptogrammoides* K. Iwats., Acta Phytotax. Geobot. 19(4–6): 119. 1963.—*Thelypteris kingii* C.F. Reed, Phytologia 17: 465. 1969.—TYPE: *G. King s.n.*, Oct. 1883, INDIA, Sikkim, in K & US.
DISTRIBUTION: China (Yunnan; Luo et al., 2018) and India (Sikkim).

7. ***Leptogramma liui*** Y.H. Chang & L.Y. Kuo, **comb. & nom.n.**; *non Le. jinfoshanensis* Ching & Z.Y. Liu, Bull. Bot. Res., Harbin 4(3): 17. 1984.—*Stegnogramma jinfoshanensis* Ching & Z.Y. Liu, Bull. Bot. Res., Harbin 3(4): 13. 1983.—TYPE: *Z.Y. Liu 3464*, CHINA, Chongqing, in PE (?) & IMC.
DISTRIBUTION: China (Chongqing, Sichuan and Yunnan).
NOTE: The new name of this species under *Leptogramma* is dedicated to its type collector, i.e. Mr. Zheng-Yu Liu.

8. ***Leptogramma sinensis*** (Ching & W.M. Chu) Y.H. Chang & L.Y. Kuo, **comb.n.**—*Craspedosorus sinensis* Ching & W.M. Chu, Acta Phytotax. Sin. 16(4): 26. 1978.—*Stegnogramma sinensis* (Ching & W.M. Chu) L.J. He & X.C. Zhang, Lycophytes Ferns China 32. 2012.—TYPE: *W.M. Chu 4938*, CHINA, Yunnan, in YUNU.
DISTRIBUTION: China (Yunnan).

9. ***Leptogramma xingwenensis*** (Ching ex Y.X. Lin) Y.H. Chang & L.Y. Kuo, **comb.n.**—*Stegnogramma xingwenensis* Ching ex Y.X. Lin, Fl. Reipubl. Popularis Sin. 4(1): 286, 350. 1999.—TYPE: *Sichuan Economy Bot. Exped. 420*, CHINA, Sichuan, Xingwen, in PE.
DISTRIBUTION: China (Sichuan).

Section **Leptogramma** J. Sm., *loc. cit.* Type species: *Leptogramma totta* (Schltdl.) J. Sm. (= *Le. pozoi*), *loc. cit.* (from SOUTH AFRICA).

Section characteristics

As "*Generic characteristics*" described above; but differs from section *Haplogramma* by their long acicular hairs being unicellular (vs. multicellular in section *Haplogramma*), and venation being all free (vs. reticulated venation in section *Haplogramma*).

Taxa included

1. ***Leptogramma amabilis*** Tagawa, Acta Phytotax. Geobot. 7: 76. 1938.—*Le. totta* (Schltdl.) J. Sm. var. *amabilis* (Tagawa) H. Itô, Bot. Mag., Tokyo 52: 642. 1938.—*Le. gymnocarpa* (Copel.) Ching subsp. *amabilis* (Tagawa) Nakaike, Enum. Pterid. Jap., Fil. 282. 1975.—*Stegnogramma gymnocarpa* (Copel.) K. Iwats. subsp. *amabilis* (Tagawa) K. Iwats., Acta Phytotax. Geobot. 19(4-6): 122. 1963.—*Thelypteris gymnocarpa* (Copel.) C.V. Morton subsp. *amabilis* (Tagawa) C.V. Morton, Amer. Fern J. 56(4): 179. 1966.—TYPE: *G. Koidzumi s.n.*, May 1923, JAPAN, Ryukyu, in KYO.
DISTRIBUTION: Japan.

2. ***Leptogramma burksiorum*** (J.E. Watkins & Farrar) Y.H. Chang & L.Y. Kuo, **comb.n.**—*Thelypteris burksiorum* J.E. Watkins & Farrar, Amer. Fern J. 92(2): 172. 2002.—*Cyclosorus burksiorum* (J.E. Watkins & Farrar) Mazumdar & R. Mukhop., Bionature 33(1): 16. 2013.—*Stegnogramma burksiorum* (J.E. Watkins & Farrar) Weakley, J. Bot. Res. Inst. Texas 5(2): 451. 2011.—TYPE: *J.E. Watkins 797*, U.S.A., Alabama, in NY [holotype], ISC, UC, UF, UNA.
HETEROTYPIC SYNONYMS: *Thelypteris pilosa* (M. Martens & Galeotti) Crawford var. *alabamensis* Crawford, Amer. Fern J. 41: 19. 1951.—*Leptogramma pilosa* (M. Martens & Galeotti) Underw. var. *alabamensis* (Crawford) Wherry, S. Fern Guide 346. 1964.—*Stegnogramma pilosa* (M. Martens & Galeotti) K. Iwats. var. *alabamensis* (Crawford) K. Iwats., Amer. Fern J. 54(3): 142. 1964.—Type: *L.C. Crawford 241* (from U.S.A., Alabama), in UNA [holotype & isotype] & US.
DISTRIBUTION: U.S.A. (Alabama).

3. ***Leptogramma celebica*** Ching, Sinensia 7: 99, t. 5. 1936.—*Stegnogramma celebica* (Ching) Holttum, Fl. Males., ser. 2, Pterid. 1(5): 543. 1982.—*St. gymnocarpa* (Copel.) K. Iwats. subsp. *celebica* (Ching) K. Iwats., Acta Phytotax. Geobot. 19(4–6): 123. 1963.—*Thelypteris bunnemeyeri* C.F. Reed, Phytologia 17(4): 265. 1968.—TYPE: *Bunnemeyer 12073*, INDONESIA, Sulawesi, Bonthain ("Banthain"), in NY [holotype], BO and L.DISTRIBUTION: Indonesia (Sulawesi).

4. ***Leptogramma centrochinensis*** Ching ex Y.X. Lin, Fl. Reipubl. Popularis Sin. 4(1): 120, 323. 1999.—TYPE: *G.X. Fu* et al*., 1732*, CHINA, Hubei, Lichuan, in PE & LBG.
DISTRIBUTION: China (Hubei).

5. ***Leptogramma dissitifolia*** (Holttum) Y.H. Chang & L.Y. Kuo, **comb.n.**—*Stegnogramma dissitifolia* Holttum, Fl. Males., ser. 2, Pterid. 1(5): 543. 1982.—*Thelypteris dissitifolia* (Holttum) Christenh., Global Fl. 1(4): 29. 2018.—TYPE: *M.G. Price 1668*, THE PHILIPPINES, Luzon, in K.DISTRIBUTION: The Philippines.

6. ***Leptogramma gymnocarpa*** (Copel.) Ching, Acta Phytotax. Sin. 8(4): 318. 1963.—*Dryopteris*

gymnocarpa Copel., Leafl. Philipp. Bot. 3: 807. 1910.—*Lastrea gymnocarpa* (Copel.) Copel., Gen. Fil. [Copel.] 139. 1947.—*Stegnogramma gymnocarpa* (Copel.) K. Iwats., Acta Phytotax. Geobot. 19(4-6): 122. 1963.—*Thelypteris gymnocarpa* (Copel.) C.V. Morton, Amer. Fern J. 56 (4): 179. 1966.—TYPE: *A.D.E. Elmer 11508*, PHIPPLINES, Mindanao, in BO, E, F, K, L, MICH and MO.
DISTRIBUTION: The Philippines (Mindanao).

7. ***Leptogramma huishuiensis*** Ching ex Y.X. Lin, Fl. Reipubl. Popularis Sin. 4(1): 122, 323. 1999.—TYPE: *J. Cavalerie 378*, CHINA, Guizhou, in PE.DISTRIBUTION: China (Guizhou).

8. ***Leptogramma intermedia*** Ching ex Y.H. Chang & L.Y. Kuo, **sp.n.**—*Le. intermedia* Ching in Y.L. Zhang et al., Spor. Pterido. Sin., 286. 1976, *nom. nud.*; Ching ex Y.X. Lin, Fl. Zhejiang 1: 154. 1993, *nom. illeg.* (without Latin descriptions and type designation).—TYPE: *P.S. Chiu 109*, CHINA, Fujian, in PE [holotype].
DIAGNOSIS: Within genus *Leptogramma* sect. *Leptogramma*, only *L. intermedia* and *L. tottoides* have proximal pinnae that are longer than the remaining distal ones, thus providing an apparently hastate lamina. *Leptogramma intermedia* differs from *L. tottoides*, *L. intermedia* by having lager fronds usually >30 cm and acuminate lateral pinnae (vs. fronds usually 14–32 cm and the obtuse lateral pinnae in *L. tottoides*).
MORPHOLOGY: Terrestrial plants, usually 30–65 cm tall. Rhizomes short and erect, loosely covered by long acicular hairs and castaneous, entire, lanceolate scales that are hairy on both sides; stipes bases also covered by the same epidermal appendages. Fronds clustered; stipe 20–35 cm long, stramineous, densely covered by long acicular hairs and mixed with a few caducous scales. Laminae pinnate, long hastate, thin-papyraceous to herbaceous, 15–30 cm long, widest at base and within the range of 8–20 cm, distal portion pinnatifid and long acuminate, both sides of leaf surfaces covered with greyish white short setae and long acicular hairs, these more dense on rachises and costae; pinnae 15–18 pairs, lobate with entire round lobes, sessile, alternate, nearly patent, acuminate or obtuse at ends and truncate at bases, the ones of distal portion adnate to rachis, the most proximal pair apparently longer than the upper ones. Venation all free, pinnately-forked, tips of veinlets reaching to leaf margin. Sori oblong to short linear, dorsal on the veinlets, exindusiate; near top of per sporangium always scattered with 3–7 setae.

DISTRIBUTION: China (Fujian, Guizhou and Zhejiang).

9. ***Leptogramma jinfoshanensis*** Ching & Z.Y. Liu, Bull. Bot. Res., Harbin 4(3): 17. 1984.—TYPE: *Z.Y. Liu 4414*, CHINA, Chongqing, in IMC.
DISTRIBUTION: China (Chongqing).

10. ***Leptogramma mollissima*** (Fisch. ex Kunze) Ching, Sinensia 7(1): 102. 1936, s.l.—*Gymnogramma mollissima* Fisch. ex Kunze, Linnaea 23: 255, 310. 1850.—*Gy. totta* Schltdl. var. *mollissima* (Fisch. ex Kunze) Kunze, Linnaea 24: 249. 1851.—*Lastrea mollissima* (Fisch. ex Kunze) Akasawa, Bull. Kochi Wom. Univ. 8: 34. 1960.—*Le. pozoi* (Lag.) Ching subsp. *mollissima* (Fisch. ex Kunze) Nakaike, Enum. Pterido. Jap., Fil. 283. 1975.—*Stegnogramma mollissima* (Fisch. ex Kunze) Fraser-Jenk., New Sp. Syndr. Indian Pteridol. Ferns Nepal 237. 1997.—*St. pozoi* (Lag.) K. Iwats. subsp. *mollissima* (Fisch. ex Kunze) K. Iwats., Acta Phytotax. Geobot. 19(4-6): 125. 1963.—*Thelypteris mollissima* (Fisch. ex Kunze) Thapa, Pterid. Nepal 95. 2002.—*Th. pozoi* (Lag.) C.V. Morton subsp. *mollissima* (Fisch. ex Kunze) C.V. Morton, Amer. Fern J. 56(4): 178. 1966.—TYPE: *Schmidt-Koch s.n.*, *8*, *79 &145*, S. INDIA, Mt. Nilagaria; *Weigle-Schaeffer 39*, S. INDIA, Mt. Nilagaria.
HETEROTYPIC SYNONYMS: *Leptogramma totta* (Schltdl.) J. Sm. form. *cristata* Nakai, Bot. Mag., Tokyo 45: 105. 1931.—*Lastrea mollissima* (Fisch. ex Kunze) Akasawa form. *cristata* (Nakai) Okuyama, Col. Ill. Wild Pl. Jap. 6 (Index): 19. 1962.—*Le. mollissima* (Fisch. ex Kunze) Ching form. *cristata* (Nakai) Namegata & Sa. Kurata, Enum. Jap. Pterid. 306, 341. 1961.—*Le. pozoi* (Lag.) Heywood subsp. *mollissima* (Fisch. ex Kunze) Nakaike monstr. *cristata* (Nakai) Nakaike, Enum. Pterid. Jap., Fil. 284. 1975.—Type: In hortus Japonensibus culta, in TI.
Leptogramma totta (Schltdl.) J. Sm. var. *pilosissima* H. Itô, Bot. Mag., Tokyo 49: 434. 1935.—*Le. mollissima* (Fisch. ex Kunze) Ching var. *pilosissima* (H. Itô) Sa. Kurata, J. Geobot. [Kanazawa] 7: 41. 1958.—*Le. pozoi* (Lag.) Heywood subsp. *mollissima* (Fisch. ex Kunze) Nakaike form. *pilosissima* (H. Ito) Nakaike, Enum. Pterido. Jap., Fil. 284. 1975.—*Le. totta* (Schltdl.) J. Sm. form. *pilosissima* (H. Itô) H. Itô in Nakai & Honda, Nova Fl. Jap. 4: 165. 1939.—*Stegnogramma pozoi* (Lag.) K. Iwats. subsp. *mollissima* (Fisch. ex Kunze) K. Iwats. form. *pilosissima* (H. Itô) Sugimoto, Keys Herb. Pl. Jap. Pterid. 323, 407. 1966.—Type: *H. Itô s.n.*, Nov. 1928 (from JAPAN, Honshu), in TI.

Leptogramma totta (Schltdl.) J. Sm. var. *yakusimensis* H. Itô, Bot. Mag., Tokyo 49: 434. 1935.—*Le. mollissima* (Fisch. ex Kunze) Ching form. *yakusimensis* (H. Itô) Namegata & Sa. Kurata, Enum. Jap. Pterid. 306, 341. 1961.—*Le. pozoi* (Lag.) Heywood subsp. *mollissima* (Fisch. ex Kunze) Nakaike var. *yakusimensis* (H. Itô) Nakaike, Enum. Pterid. Jap., Fil. 284. 1975.—*Stegnogramma pozoi* (Lag.) K. Iwats. subsp. *mollissima* (Fisch. ex Kunze) K. Iwats. form. *yakusimensis* (H. Itô) Sugimoto, Keys Herb. Pl. Jap. Pterid. 322, 407. 1966.—Type: *G. Masamune s.n.*, 2 Jul. 1926 (from JAPAN, Kyushu, Isl. Yakusima), in TI.

DISTRIBUTION: Southern India, Japan, southern Korea and Taiwan (Lanyu).

11. ***Leptogramma petiolata*** Ching, Acta Phytotax. Sin. 8: 319. 1963; *non Thelypteris petiolata* K. Iwats. & M. Kato, Acta Phytotax. Geobot. 34(4–6): 139. 1983.—*Stegnogramma pozoi* (Lag.) K. Iwats. var. *petiolata* (Ching) Sledge, Bull. Brit. Mus. [Nat. Hist.], Bot. 8: 49. 1981.—*Thelypteris stipitata* Fraser-Jenk., Taxon. Revis. Indian Subcontinental Pteridophytes 196. 2008.—TYPE: *G. Wall* (misnamed "*Wallich*" in Ching, 1963) *s.n.*, SRI LANKA, in PE [holotype]; *Thwaites 481*, SRI LANKA, in PE [paratype].

DISTRIBUTION: Sri Lanka.

NOTE: This is a diploid sexual species (Fraser-Jenkins, 2008).

12. ***Leptogramma pilosa*** (M. Martens & Galeotti) Underw. var. ***pilosa***, Bull. Torrey Bot. Club 29: 626. 1902.—*Gymnogramma pilosa* M. Martens & Galeotti, Nouv. Mém. Acad. Roy. Sci. Bruxelles 15(5): 27. 1842.—*Dryopteris pilosa* (M. Martens & Galeotti) C. Chr., Index Fil. [C. Chr.] 284. 1906.—*Phegopteris pilosa* (M. Martens & Galeotti) Mett., Abh. Senckenberg. Naturf. Ges. 2: 302. 1858, *non* Fée, *mss.* 1857.—*Stegnogramma pilosa* (M. Martens & Galeotti) K. Iwats., Amer. Fern J. 54: 141. 1964.—*Thelypteris pilosa* (M. Martens & Galeotti) Crawford, Amer. Fern J. 41: 16. 1951.—TYPE: *Galeotti 6267*, MEXICO, Veracruz, Pico de Orizaba, in BR [syntype], K, and P; *Galeotti 6268*, MEXICO, Veracruz, Pico de Orizaba, in BR [syntype], K and P.

DISTRIBUTION: Guatemala, Mexico, Nicaragua and Panama.

13. ***Leptogramma pilosa*** (M. Martens & Galeotti) Underw. var. ***major*** (E. Fourn.), Y.H. Chang & L.Y. Kuo, **comb.n.**—*Gymnogramma pilosa* M. Martens & Galeotti var. *major* E. Fourn., Mexic. Pl. 1: 73. 1872.—*Thelypteris pilosa* (M. Martens & Galeotti) Crawford var. *major* (E. Fourn.) Crawford, Amer. Fern J. 41: 19.

1951.—*Gy. procurrens* Fée, Mém. Foug. 8: 78. 1857.—*Dryopteris pilosa* (M. Martens & Galeotti) C. Chr. var. *procurrens* (Fée) C. Chr., Kongel. Danske Vidensk. Selsk. Skr., Naturvidensk. Math. Afd., ser. 7, 10(2): 197. 1913, *comb. illeg.*—*Gy. totta* Schltdl. var. *procurrens* (Fée) Baker in Hook. & Baker, Syn. Fil. (ed. 2) 515. 1874.—TYPE: *W. Schaffner 293*, MEXICO, Popocatepetl.

DISTRIBUTION: Guatemala and Mexico.

14. ***Leptogramma pozoi*** (Lag.) Heywood, Feddes Repert. Spec. Nov. Regni Veg. 64: 19. 1961.—*Hemionitis pozoi* Lag., Gen. Sp. Pl. 33. 1816.—*Ceterach pozoi* (Lag.) A. Br. ex Milde, Bot. Zeitung [Berlin] 24: 310. 1866.—*Cyclosorus pozoi* (Lag.) C.M. Kuo, Taiwania 47(2): 172. 2002.—*Gymnogramma pozoi* (Lag.) Desv., Mém. Soc. Linn. Paris 6(3): 216. 1827.—*Pleurosorus pozoi* (Lag.) Diels in Engler & Prantl, Nat. Pflanzenf. 1(4): 245. 1899, *excl. descr. et fig. 129.*—*Stegnogramma pozoi* (Lag.) K. Iwats., Acta Phytotax. Geobot. 19(4–6): 124. 1963.—*Thelypteris pozoi* (Lag.) C.V. Morton, Bull. Soc. Bot. France 106(5/6): 234. 1959.—TYPE: *D.G. del Pozo s.n.*, N. SPAIN, Cantabria, in S-PA.

HETEROTYPIC SYNONYMS:

Gymnogramma lowei Hook. & Grev., Icon. Filic. t. 89. 1831.—*Leptogramma lowei* (Hook. & Grev.) J. Sm., J. Bot. [Hooker] 4: 52. 1842.—Type: *R.T. Lowe s.n.*, PORTUGAL, Island of Madeira, in K?.

Acrostichum pilosiusculum Wikstr., Kongl. Vetenskaps Academiens Handlingar, ser. 3. 1825: 439. 1826.—*Leptogramma pilosiuscula* (Wikstr.) Alston, Bol. Soc. Brot., ser. 2, 30: 17. 1956.—Type: *Masson s.n.*, PORTUGAL, Madeira (= Madera), in BM.

DISTRIBUTION: Portugal (Madeira and Azores), N. Spain and S. France (Pyrénées-Atlantiques department).

15. ***Leptogramma scallanii*** (Christ) Ching, Sinensia 7: 101. 1936.—*Aspidium scallanii* Christ, Boll. Soc. Bot. Ital. 1901: 296. 1901.—*Dryopteris scallanii* (Christ) C. Chr., Index Fil. [C. Chr.] 291. 1905.—*Stegnogramma scallanii* (Christ) K. Iwats., Acta Phytotax. Geobot. 19(4–6): 124. 1963.—*Thelypteris scallanii* (Christ) C.V. Morton, Amer. Fern J. 56(4): 179. 1966.—TYPE: *Scallan s.n.*, CHINA, Sichuan.

DISTRIBUTION: China, India (Assam) and N. Vietnam.

16. ***Leptogramma sinica*** Ching ex Y.X. Lin, Flora Reipubl. Popularis Sin. 4(1): 323. 1999.—*Cyclosorus sinicus* (Ching ex Y.X. Lin) Mazumdar & R. Mukhop., Bionature 33(1): 30. 2013.—TYPE:

G.Z. He 4734, CHINA, Guizhou, in PE.
DISTRIBUTION: China (Guizhou and Hunan).

17. ***Leptogramma subcalcarata*** (Alderw.) Y.H. Chang & L.Y. Kuo, **comb.n.**—*Phegopteris totta* Mett. var. *subcalcarata* Alderw., Malayan Ferns Fern Allies, Suppl. 1: 515. 1916.—*Stegnogramma subcalcarata* (Alderw.) Holttum, Fl. Malesiana, ser. 2, Pterid. 1(5): 543. 1982.—*Thelypteris subcalcarata* (Alderw.) Christenh., Global Fl. 1(4): 38. 2018.—TYPE: *Beccari 430*, INDONESIA, Sumatra, in BO [holotype], FI, K and MEL.
DISTRIBUTION: Indonesia (Kerinci and Singgalang).

18. ***Leptogramma totta*** (Schltdl.) J. Sm., J. Bot. [Hooker] 4: 52. 1842.—*Polypodium tottum* Willd., Sp. Pl. [Willdenow] 5: 201. 1810, *non Po. tottum* Thunb., Prodr. Pl. Cap. 172. 1800.—*Gymnogramma totta* Schltdl., Adumbr. Pl. 1: 15. 1825.—*Aspidium tottum* (Schltdl.) Engler, Hochgeb. Fl. Trop. Afr. 99. 1892.—*Grammitis totta* (Schltdl.) C. Presl, Tent. Pterid. 209. 1936.—*Lastrea totta* (Schltdl.) Ohwi, Bull. Nation. Sci. Mus. Tokyo, ser. 2. 3(2): 98. 1956.—*Nephrodium tottum* (Schltdl.) Diels in Engler & Prantl, Nat. Pflanzenf. 1(4): 170. 1899.—*Phegopteris totta* Mett., Abh. Senckenberg. Naturf. Ges. 2(2): 302. 1858.—*Po. africanum* Desv., Mém. Soc. Linn. Paris 6(3): 239. 1827.—*Dryopteris africana* (Desv.) C. Chr., Index Fil. [C. Chr.] 4: 251. 1906.—*La. africana* (Desv.) Ching, Contrib. Biol. Lab. Sc. Soc. China 9(1): 37. 1933.—*Le. africana* (Desv.) Ching, Sinensia 7(1): 101. 1936.—TYPE: *Herb. Willdenow no. 19697*, SOUTH AFRICA, Cape of Good Hope, in B.
DISTRIBUTION: Ethiopia (= Abyssinia), Comores and South Africa.

19. ***Leptogramma tottoides*** Hayata ex H. Itô, Bot. Mag. [Tokyo] 49(583): 434. 1935.—*Cyclosorus tottoides* (Hayata ex H. Itô) C.M. Kuo, Taiwania 47(2): 172. 2002.—*Le. totta* (Schltdl.) J. Sm. var. *tottoides* (Hayata ex H. Itô) H. Itô, Nova Fl. Jap. 4: 166. 1938.—*Stegnogramma tottoides* (Hayata ex H. Itô) K. Iwats., Acta Phytotax. Geobot. 19(4-6): 121. 1963.—*Thelypteris tottoides* (Hayata ex H. Itô) C.V. Morton, Amer. Fern J. 56(4): 179. 1966.—TYPE: *Hayata & Sasaki s.n.*, 1912, TAIWAN, Arisan, in TI.
HETEROTYPIC SYNONYMS:
Leptogramma caudata Ching, Sinensia 7(1): 98. 1936.—*Thelypteris caudata* (Ching) C.F. Reed, Phytologia 17(4): 266. 1968.—Type: *Metcalf 5002c*, CHINA, Fujian, in PE [holotype].DISTRIBUTION: S. China and Taiwan.

20. ***Leptogramma yahanensis*** Ching ex Y.X. Lin, Fl. Reipubl. Popularis Sin. 4(1): 324. 1999.—TYPE: *D.H. Zhang 1138*, CHINA, Sichuan, Ya'an, in PE.
DISTRIBUTION: China (Chongqing).

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Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Fig. S1 Dating results with topological constraints.

Appendix S1-S3. Voucher information, GenBank accession numbers, primer information, and character coding of the taxa used in this study.