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MOLECULAR AND
MORPHOLOGICAL EVIDENCE
SUPPORTS THE INCLUSION
OF *DEINOSTIGMA* INTO
METAPETROCOSMEA
(GESNERIACEAE)^{1,2}

Peng-Wei Li,^{3,4} Fang-Pu Liu,^{3,4} Meng-Qi Han,^{3,4}
James F. Smith,⁵ and Yin-Zheng Wang^{3,4*}

ABSTRACT

Metapetrocosmea W. T. Wang and *Deinostigma* W. T. Wang & Z. Y. Li were originally monotypic with *M. peltata* (Merr. & Chun) W. T. Wang and *D. poilanei* (Pellegr.) W. T. Wang & Z. Y. Li, respectively. Recent molecular phylogenetic research expanded *Deinostigma* to include several species previously transferred from *Chirita* D. Don to *Primulina* Hance. However, the relationship between *Metapetrocosmea* and *Deinostigma* has not been well addressed. In the present study, the type species of *Metapetrocosmea* and *Deinostigma* were sampled together with related taxa, and the systematic relationships were reexamined using the nuclear ribosomal internal and external transcribed spacer regions (ITS and ETS) and four chloroplast regions (*rpL32-trnL*, *rps16*, *trnH-psbA*, *trnL-F*). Phylogenetic analyses demonstrate that *M. peltata* is embedded in the species of *Deinostigma* and sister to *D. poilanei*. All of these species form a highly supported branch, i.e., *Metapetrocosmea–Deinostigma* clade, which is sister to *Oreocharis* Benth. Morphological analyses show that species in the *Metapetrocosmea–Deinostigma* clade share a series of morphological traits, i.e., alternate leaves, arcuate filaments, densely lanate anthers with the hair surface covered with granular or vermiform appendages, bilobed stigma that vary from dorsal to ventral and almost equal in size to a dorsal-ventral oblique lamella with the dorsal one sterile, hooked hairs and T-shaped glandular hairs occurring on the whole plant, and riblike seed surfaces. Both molecular and morphological evidence strongly suggest that the *Metapetrocosmea–Deinostigma* clade is monophyletic and should be combined into a single genus, i.e., *Metapetrocosmea* W. T. Wang. Therefore, we present a taxonomic treatment for this group.

Key words: *Deinostigma*, *Metapetrocosmea*, morphology, phylogeny, taxonomic treatment.

Metapetrocosmea W. T. Wang is a monotypic genus endemic to Hainan Island, China, erected by Wang (1981) for a small perennial herb, *M. peltata* (Merr. & Chun) W. T. Wang, that was removed from *Petrocosmea* Oliv. *Metapetrocosmea* was distinguished from *Petrocosmea* by its somewhat elongated rhizome, subfiliform and longer filaments, villous anthers, divaricate thecae, and subspheroidal capsule (Wang, 1981). *Deinostigma* W. T. Wang & Z. Y. Li was originally another monotypic genus distributed in southern Vietnam, described by Wang and Li (1992) for *D. poilanei* (Pellegr.) W. T. Wang & Z. Y. Li, and previously placed in *Hemiboea* C. B. Clarke. The perennial herb *D. poilanei* is characterized by alternate leaves, free bracts, gradually widening fil-

aments, velutinous anthers, divaricate thecae, and a stigma with two dorsal-ventral subequal lobes (but see Results), which are morphologically different from *Hemiboea* species (Wang & Li, 1992).

Primulina Hance, originally a monotypic genus established by Hance (1883), has become the largest genus of Gesneriaceae in China after being expanded to include most species of *Chirita* D. Don sect. *Gibbosaccus* C. B. Clarke, *Chiritopsis* W. T. Wang, and two species of *Wentsaiboea* D. Fang & D. H. Qin (Wang et al., 2011; Weber et al., 2011a; Xu et al., 2012). The redefined *Primulina* is characterized by rosulate plants with stout rhizomes, somewhat fleshy leaves, free calyx lobes, broad corolla tubes, two ventrally fertile stamens,

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² Yin-Zheng Wang, James F. Smith, and Peng-Wei Li conceived of the presented idea. Peng-Wei Li performed the fieldwork, lab work, and analysis. Peng-Wei Li and Yin-Zheng Wang wrote the manuscript with support from James F. Smith. Fang-Pu Liu and Meng-Qi Han participated in the lab work. All authors discussed the results and contributed to the final manuscript.

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and a dorsal-ventral obliquely laminar stigma (Wang et al., 2011). A few morphologically distinctive species, i.e., *Chirita cynostyla* B. L. Burtt, *Chirita cyrtocarpa* D. Fang & L. Zeng, *Chirita eberhardtii* Pellegr., *Chirita minutihamata* D. Wood, and *Chirita tamiana* B. L. Burtt, with usually slender rhizomes and alternate and somewhat peltate leaves, were also transferred to *Primulina* based on available evidence then (Weber et al., 2011a). In fact, the systematic positions of these species have long been controversial. Burtt (1960) had pointed out that *Chirita cynostyla* was not at first considered a member of *Chirita* sect. *Gibbosaccus* or even the genus *Chirita*. Wood (1974) noted that *C. cynostyla*, *C. eberhardtii*, and *C. minutihamata* are characterized by small, hooked hairs on the pedicels, and he believed that the three species together with three other species of *Chirita* (*C. balansae* Drake, *C. poilanei* Pellegr., and *C. semicontorta* Pellegr.) endemic to Vietnam formed a natural group, which had been proven to be inaccurate (Möller et al., 2016; Xu et al., 2021). Boggan (1999) also proposed that *C. eberhardtii* and *C. tamiana*, together with one or two other related species, were not similar to any other species in *Chirita* sect. *Gibbosaccus* and their proper placement awaited further study. Christie et al. (2012) found that *C. tamiana* ($2n = 32$) has a different chromosome number from other *Primulina* species ($2n = 36$).

Möller et al. (2016) observed that the five morphologically distinctive species that had been transferred from *Chirita* to *Primulina* by Weber et al. (2011a), i.e., *P. cynostyla* (B. L. Burtt) Mich. Möller & A. Weber, *P. cyrtocarpa* (D. Fang & L. Zeng) Mich. Möller & A. Weber, *P. eberhardtii* (Pellegr.) Mich. Möller & A. Weber, *P. minutihamata* (D. Wood) Mich. Möller & A. Weber, and *P. tamiana* (B. L. Burtt) Mich. Möller & A. Weber, were similar to *Deinostigma poilanei* (Pellegrin) W. T. Wang & Z. Y. Li in a number of morphological traits, including alternate leaf arrangement, hooked hairs on many plant parts, and flowers with the pedicel inserted at an angle and off-center on the receptacle (Möller et al., 2016). Then, they conducted a phylogenetic reconstruction using ITS and *trnL-F* DNA sequence data and found that the several morphologically distinctive *Primulina* species sampled form a moderately supported clade with *D. poilanei*, and together they are sister to the monotypic *Metapetrocosmea* with maximum support. Meanwhile, other *Primulina* species are resolved as a monophyletic clade remote from *Deinostigma*. Therefore, Möller et al. (2016) expanded *Deinostigma* to include the five aforementioned *Primulina* species but excluded the monotypic *Metapetrocosmea*. In addition, they also revived the name *Chirita cicatricosa* W. T. Wang, a heterotypic synonym of *C. minutihamata*. Later, Möller et al. (2020) provided additional morphological and molecular phy-

logenetic data to support the distinct status between *C. minutihamata* and *C. cicatricosa*. Recently, a new species of *Deinostigma*, *D. fasciculatum* W. H. Chen & Y. M. Shui, was described by Shui et al. (2020), which brings the number of recognized species in *Deinostigma* to eight.

The limited number of DNA markers resulted in most major branches being poorly resolved in the molecular phylogenetic trees by Möller et al. (2016), and only five of the eight *Deinostigma* species were confirmed by the molecular phylogenetic reconstruction (Möller et al., 2020). Furthermore, the single most parsimonious tree and Bayesian tree are wholly the same in Möller et al. (2020), which is probably a careless mistake. Therefore, it is desirable to conduct further study using more DNA sequence data and more comprehensive sampling. In addition, *Metapetrocosmea* was excluded from the expanded *Deinostigma* due to its specific morphological characters, i.e., unilocular ovary, free anthers, and capitate stigma (Möller et al., 2016). Nevertheless, some trait descriptions are inaccurate, such as the capitate stigma, whereas it clearly is a bilobed stigma instead (see Results for details). In addition, the locule number is frequently variable within a genus in many taxa across Gesneriaceae (Wang et al., 1997, 2002; Wang & Pan, 1998) and is not a reliable taxonomic marker for the delimitation of genera. Further careful examination of morphological characters of *Metapetrocosmea* and *Deinostigma* would provide more accurate knowledge about the two closely related genera.

To address these questions, we conducted a broad range of investigations relating to the phylogenetic relationship between *Metapetrocosmea* and *Deinostigma* by using multiple DNA sequences with additional extensive sampling in the genera across the Old World Gesneriaceae, i.e., *Didymocarpus* Wall., *Henckelia* Spreng. (Weber et al., 2011a), *Liebigia* Endl. (Wang et al., 2011; Weber et al., 2011a), *Microchirita* (C. B. Clarke) Yin Z. Wang (Wang et al., 2011; Weber et al., 2011a), *Oreocharis* Benth. (Möller et al., 2011b), *Petrocodon* Hance (Wang et al., 2011; Weber et al., 2011b), and *Primulina* (Wang et al., 2011; Weber et al., 2011a; Xu et al., 2012). In addition, we also carried out comprehensive morphological and anatomical analyses that ranged from vegetative to reproductive organs in *Metapetrocosmea* and the expanded *Deinostigma*.

The aim of this research is to: (1) investigate the phylogenetic relationship between *Metapetrocosmea*, *Deinostigma*, and their allies; (2) clarify the morphological character states of *Metapetrocosmea* and *Deinostigma*, and uncover morphological features that unify the two genera; and (3) provide a taxonomic treatment based on molecular phylogenetic and comparative morphological analyses.

MATERIALS AND METHODS

SAMPLING, AMPLIFICATION, AND SEQUENCING

Using previous studies as a guide to sample closely related taxa (Möller et al., 2009, 2011a, 2016, 2020; Wang et al., 2010, 2011; Weber et al., 2011a), we included 66 samples representing 13 genera (Wen et al., 2019; Weber et al., 2020) and 61 species with *Deinostigma cicatricosum* (W. T. Wang) D. J. Middleton & Mich. Möller, *D. cyrtocarpum* (D. Fang & L. Zeng) Mich. Möller & H. J. Atkins, and *D. poilanei* (Pellegr.) W. T. Wang & Z. Y. Li represented by two, two, and three accessions, respectively. According to Weber et al. (2013, 2020), the genus *Deinostigma* and its allies belong to Didymocarpaceae. However, the phylogenetic relationships within this subtribe are not well resolved (Möller et al., 2009, 2011a). Therefore, we chose four genera in Loxocarpaceae, including *Boea* Lam., *Damrongia* Kerr ex Craib, *Orniuhoboea* C. B. Clarke, and *Paraboea* (C. B. Clarke) Ridl., as outgroup based on the phylogenetic results of Möller et al. (2009). The full list of sampled species is presented in Appendix 1.

We obtained dry leaves of *Deinostigma poilanei* from the isotype housed in the National Herbarium of the Institute of Botany, Chinese Academy of Sciences (PE), and collected *D. tamianum* (B. L. Burtt) D. J. Middleton & H. J. Atkins in a greenhouse of the Institute of Botany, Chinese Academy of Sciences; all other samples were gathered in the field. Total genomic DNA was extracted using a modified CTAB method (Doyle & Doyle, 1987), and the genomic DNA of *D. poilanei* was repaired to improve the amplification efficiency following Xu et al. (2015). Two nuclear ribosomal DNA regions (ITS, ETS) and four chloroplast DNA regions (*rpL32-trnL*, *rps16*, *trnH-psbA*, *trnL-F*) were amplified. The PCR conditions for the six regions included initial denaturation at 94°C for 3 min., followed by 35 cycles at 94°C for 30 sec., 52°–54°C for 30 sec., and 72°C for 50 sec., with a final extension at 72°C for 5 min. Primers used to amplify ITS, ETS, *rpL32-trnL*, *trnH-psbA*, *rps16*, and *trnL-F* were ITS1/4 (White et al., 1990) and ITS p5/p2, p3/u4 (Cheng et al., 2016), ETS-B/18S-IGS (Beardsley & Olmstead, 2002), *rpL32/trnL* (Shaw et al., 2007), *trnH/psbA* (Hamilton, 1999), *rps16-2F/R3* (Bremer et al., 2002), *trnL-F-cff* (Taberlet et al., 1991), respectively. The PCR products were purified using Tian quick Midi Purification Kit (Tiangen Biotech, Beijing, China) following the manufacturer's protocol and sequenced with a 3730xl automated sequencer in BGI (BGI Group, Beijing, China) with the same primers as amplification. Sequences for six samples were retrieved from GenBank, i.e., *Damrongia lacunosa* (Hook. f.) D. J. Middleton & A. Weber, *Damrongia purpureolineata* Kerr ex Craib, *Deinostigma minutihama-tum* (D. Wood) D. J. Middleton & H. J. Atkins, two ac-

cessions of *Deinostigma poilanei*, and *Liebigia speciosa* (Blume) DC.; other sequences used in this study were newly acquired (see Appendix 1 for detail).

SEQUENCE ALIGNMENT AND PHYLOGENETIC ANALYSES

Contigs were edited and assembled in Geneious v7.1.8 (Kearse et al., 2012). Individual regions were aligned with Clustal W (Larkin et al., 2007), followed by manual adjustment in Geneious v7.1.8 (Kearse et al., 2012). We analyzed four data sets, i.e., nrDNA (ITS and ETS), cpDNA (*rpL32-trnL*, *rps16*, *trnH-psbA*, *trnL-F*), combined data matrix (concatenated nrDNA and cpDNA), and concatenated ITS and *trnL-F*. The two accessions of *Deinostigma poilanei* retrieved from GenBank were not included in the former three data sets and incorporated only in the concatenated ITS and *trnL-F* in order to be comparable with Möller et al. (2016). Indels also contain phylogenetic signals useful in phylogenetic reconstruction (Andersson, 2006; Weber et al., 2011b; Ren et al., 2017; Hanusch et al., 2020). Therefore, they were coded as binary characters in the present study. Fastgap v.1.2 (Borchsenius, 2009) was employed for indel coding, using the simple method of Simmons and Ochoterena (2000).

MrModeltest v2.3 (Nylander, 2004) was used to find the best-fit model of nucleotide substitution. All four data sets were analyzed with maximum likelihood (ML) and the Bayesian inference (BI) method. All phylogenetic analyses were conducted on the CIPRES Science Gateway (Miller et al., 2010). Tests for incongruence as an indicator of among-data partition conflict play an important role in data combination (Yoder et al., 2001). However, the incongruence length difference (ILD) test is prone to suggest significant conflict between character partitions (Quicke et al., 2007) and only has limited power to detect incongruence caused by differences in the evolutionary conditions or in the tree topology (Darlu & Lecointre, 2002). Thus, measures of incongruence should not be used as indicators of data set combinability (Yoder et al., 2001). Tree-based comparisons can be used to visually identify incongruence between phylogenies obtained from cpDNA and nrDNA data sets (Wiens, 1998; Wang et al., 2014). Thus, we evaluated the incongruence manually by comparing trees constructed from nuclear and chloroplast data sets.

Maximum likelihood analysis was carried out in RAxML v8.2.12 (Stamatakis, 2014) with 1000 rapid bootstrap (BS) inferences to assess uncertainty in the topology using the GTR+GAMMA and BIN+GAMMA models for DNA sequences and binary characters, respectively. Bayesian inference analysis was performed in MrBayes v3.2.7 (Ronquist & Huelsenbeck, 2003). DNA sequence data was partitioned according to gene regions, using the best-fit model suggested by MrModel-

Table 1. Summary of the alignments used in the phylogenetic analysis.

Region	Accessions	Alignment length	Constant sites	PuI	PI	Model by AIC	Indel coding sites
ETS	58	546	137	89	320	GTR+I+G	155
ITS	66	863	331	147	385	GTR+I+G	334
<i>rpl32-trnL</i>	60	1131	734	211	186	GTR+G	110
<i>rps16</i>	59	1004	683	187	134	GTR+G	105
<i>trnH-psbA</i>	60	658	329	169	160	F81+G	195
<i>trnL-F</i>	66	905	662	136	107	GTR+G	41
nrDNA	64	1407	471	231	705	—	477
cpDNA	64	3698	2413	699	586	—	450
Combined	64	5105	2884	930	1291	—	927
ITS+ <i>trnL-F</i>	66	1768	993	283	492	—	375

AIC, Akaike information criterion; PI, parsimony-informative sites; PuI, parsimony-uninformative sites.

test v2.3 (Nylander, 2004). The binary characters were treated as separate partitions using the binary model with ascertainment bias corrections (coding=variable). Ten million generations were run in two independent analyses each with four Markov chain Monte Carlo (MCMC) chains. One tree was sampled every 1000 generations (= 10,000 trees). An average standard deviation of split frequencies of less than 0.01 was assumed to show that the two runs converged to a stationary distribution. After discarding the first 25% trees as burn-in, a 50% majority-rule consensus tree and posterior probabilities (PP) for node support were calculated.

MORPHOLOGICAL ANALYSES

The monotypic genus *Metapetrocosmea* and all the species of *Deinostigma* were included in the morphological studies. Specimens (or specimen images) including the types deposited in E, GXMG, GXMI, IBK, IBSC, KUN, NYBG, P, PE, and VNM were consulted (herbarium acronyms according to Thiers, 2022). Living plants in the field or cultivated in the greenhouse were carefully observed. Morphological characters were photographed with a Nikon Digital Camera (D7200 or DXM1200F; Nikon, Tokyo, Japan).

The micromorphology of *Metapetrocosmea* and *Deinostigma* was also examined. Fresh, well-developed flowers and leaves were taken from living plants and fixed using a mixture of ethanol (70%), glacial acetic acid, and formalin (18:1:1). Preparations for the SEM observation were as follows: first, fixed specimens were dehydrated in graded ethanol (70%, 80%, 90%, 100%) and then critical point dried; next, all the samples were mounted on double-sided tape affixed to aluminum stubs and sputter-coated with gold powder; finally, prepared samples were observed and photographed in a Hitachi S-4800 Field Emission SEM (Hitachi, Tokyo, Japan). The terminology of seed coat ornamentations

in this study follows Beaufort-Murphy (1983) and Liu et al. (2004).

RESULTS

PHYLOGENETIC ANALYSES

Except for *Deinostigma poilanei* (four DNA regions) and *Oreocharis fargesii* (five DNA regions), we successfully amplified all six DNA regions for the remaining species (see Appendix 1 for detail), and in total, 357 DNA sequences were newly generated for this study and have been deposited in GenBank (Appendix 1). Results of MrModeltest suggest the best fit models were GTR+I+G for ETS and ITS, GTR+G for *rpl32-trnL*, *rps16*, and *trnL-F*, and F81+G for *trnH-psbA* (Table 1). Data matrixes of the combined data set and concatenated ITS and *trnL-F* are available as Supplementary Appendices S1–S2.

The nrDNA matrix included 64 samples with an aligned length of 1407 bp, of which 705 were parsimony informative. The inferred ML tree was generally congruent with the majority rule BI tree (Supplementary Fig. S1, Supplementary Appendix S3). *Primulina* is strongly supported as a monophyletic clade and sister to *Petrocodon* with maximum support (bootstrap [BS] = 100%, posterior probability [PP] = 1.0). A clade comprising two species of *Didymocarpus* and one *Liebigia* species is resolved as sister to *Primulina* and *Petrocodon* with maximum support. The *Metapetrocosmea-Deinostigma* clade and *Oreocharis* form a branch with strong support (BS = 98%, PP = 1.0), and together they are strongly supported as sister to all aforementioned taxa (BS = 99%, PP = 1.0). Finally, *Henckelia* and *Microrchirita* are successively recovered as highly supported clades sequentially sister to the remainder of the taxa in the nuclear tree (Supplementary Fig. S1).

The chloroplast DNA matrix also contained 64 sequences with a total length of 3698 bp, of which 586

were parsimony informative. The intergeneric relationships are congruent between the chloroplast tree (Supplementary Fig. S2, Supplementary Appendix S4) and nuclear tree (Supplementary Fig. S1). Regarding the infrageneric relationships, conflicts exist mainly in nodes receiving weak support (Supplementary Figs. S1, S2). As a result, we concatenated nuclear and chloroplast matrices directly.

The combined data matrix had aligned sequences of 5105 bp, and a summary of the matrix composition is presented in Table 1. The combined data set yields a fairly well-resolved phylogenetic tree (Fig. 1, Supplementary Appendix S5). *Primulina* and *Petrocodon* are recovered as sister genera with maximum support. The two *Didymocarpus* species are paraphyletic and form a highly supported clade with *Liebigia speciosa*, and together they are resolved as sister to *Primulina/Petrocodon* with maximum support. The *Metapetrocosmea-Deinostigma* clade and *Oreocharis* are another pair of highly supported sister clades and together they are clustered with the clade comprised of the four aforementioned genera with maximum support. *Henckelia* and *Microchirita* are resolved as two sequential clades with strong to maximum support, respectively, to the remainder of the taxa in the tree (Fig. 1). The *Metapetrocosmea-Deinostigma* clade, which is the focus of this study, consists of nine species with maximum support and splits into two branches. In the first strongly supported branch (BS = 94%, PP = 0.99), the two samples of *Deinostigma cyrtocarpum* and the two accessions of *D. cicatricosum* are sister to each other with strong support (BS = 83%, PP = 0.99), and together they successively form a clade with *D. fasciculatum*, *D. minutiamatum*, and *D. cynostylum* with high support. The second branch with maximum support consists of four species. *Metapetrocosmea peltata* and *Deinostigma poilanei* as a pair of sister species are grouped with *D. eberhardtii* (BS = 67%, PP = 0.76). The two samples of *D. tamianum* are sister to the above-mentioned three species with maximum support (Fig. 1).

The concatenated ITS and *trnL-F* data matrix with 66 samples is composed of 1768 bp, of which 492 (27.83%) were parsimony informative (Table 1). The inferred phylogenetic tree contains three accessions of *Deinostigma poilanei*, i.e., *D. poilanei*_HB222 (Möller et al., 2016), *D. poilanei*_463 (this study), and *D. poilanei*_POIL (Xu et al., 2021). However, the three accessions are recovered in different positions of the phylogenetic tree (Fig. 2, Supplementary Appendix S6). *Deinostigma poilanei*_HB222 is recovered as sister to the sample that resembles *D. tamianum* (BS = 76%, PP = 1.0), and *D. poilanei*_463 is sister to *Metapetrocosmea peltata* (BS = 92%, PP = 1.0), whereas *D. poilanei*_POIL is sister to the remaining samples in the *Metapetrocosmea-Deinostigma* clade (BS = 100, PP = 1.0).

MORPHOLOGICAL OBSERVATIONS

According to our observations, the species in the *Metapetrocosmea-Deinostigma* clade share a series of unique morphological characters and character combinations in comparison to its allies (*Oreocharis*, *Henckelia*, *Petrocodon*, and *Primulina*) in the phylogeny. The rhizomes of *Deinostigma cicatricosum*, *D. cyrtocarpum*, *D. poilanei*, and *D. tamianum* are slender while the rhizomes of *M. peltata* are relatively short (Fig. 3, A1–E1, A2–D2). Leaves in species of this clade are all alternate with often peltate to subpeltate blades (Fig. 3, A3–E3). The bracts are usually ovate or obovate, or linear-triangular. The filaments of fertile stamens are arcuate and usually inflated at the middle (*D. cicatricosum*, *D. cyrtocarpum*, and *D. tamianum*) or near the apex (*M. peltata* and *D. poilanei*) (Fig. 3, A4–E4). The divaricate thecae are usually laterally oriented due to filamentous bending at the apex (Fig. 3, A4–E4). The anthers are densely lanate (Fig. 3, A4–E4) with the surface of hairs covered with granular or vermiform appendages (Fig. 4, A1–D1). The styles are all longer than the ovaries. Hooked hairs and T-shaped glandular hairs are distributed in almost all parts of the plant, such as the young stems, leaves, inflorescences, and different flower organs (Fig. 4, A2–D2, A3–D3). The capsules are usually falcate and loculicidal, except those of *M. peltata* are subglobose (Fig. 3, A5–E5).

The *Metapetrocosmea-Deinostigma* clade is characterized by somewhat riblike seed coat ornamentations (Fig. 4, A4–D4, A5–D5). In *D. cicatricosum*, seed coat sculpture is composed of primary longitudinal ribs, which are secondarily more or less corrugated with alternating concavity and horizontal ridges (Fig. 4, A4–A5). The seed surface of *D. cyrtocarpum* consists of longitudinal ridges and distorted small ribs with blurred edges (Fig. 4, B4–B5). On the seed surface of *D. tamianum*, longitudinal prominent ribs are further linked to become somewhat reticulate (Fig. 4, C4–C5). In *M. peltata*, the seed coat is featured by primary longitudinal ridges and small ribs that are broadly reticulate with distorted and connected ribs (Fig. 4, D4–D5).

It is unexpected that there are two stigmatic lobes in species of the *Metapetrocosmea-Deinostigma* clade, and the stigmas can be variable both at the intra- and interspecific levels. In *D. cicatricosum*, there exist dorsal-ventral oblique lamellar stigma with the ventral lobe enlarged and dorsal one becoming aborted (Fig. 5A1), dorsal-ventral oblique lamellar stigma with dorsal one slightly developed (Fig. 5A2–A3), and two unequal stigmatic lobes with the dorsal one well developed (Fig. 5A4). The ventral stigma lobe of *D. cicatricosum* is slightly bifid or not (Fig. 5A1–A4). The stigma of *D. cyrtocarpum* is generally dorsal-ventral oblique lamellar with the ventral lobe enlarged and slightly bifid and

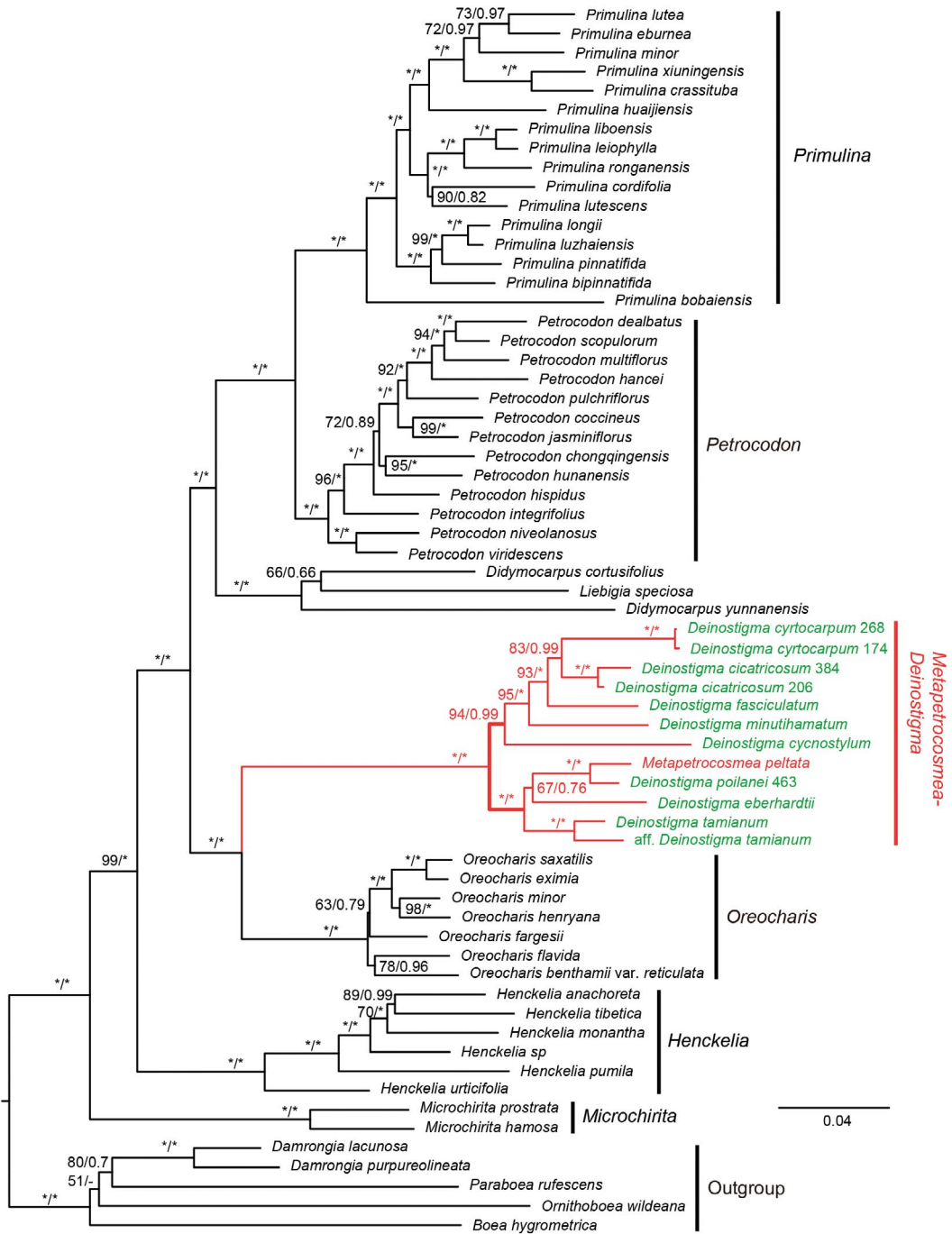


Figure 1. Maximum likelihood (ML) tree inferred from combined nuclear (ETS, ITS) and chloroplast (*rpl32-trnL*, *rps16*, *trnH-psbA*, *trnL-F*) data sets. ML bootstrap values and Bayesian inference (BI) posterior probabilities are indicated on the left and right sides of slashes, respectively. Asterisks indicate maximum support and hyphens represent no support. Bold branches indicate the two lineages in the *Metapetrocosmea* W. T. Wang–*Deinostigma* W. T. Wang & Z. Y. Li clade.

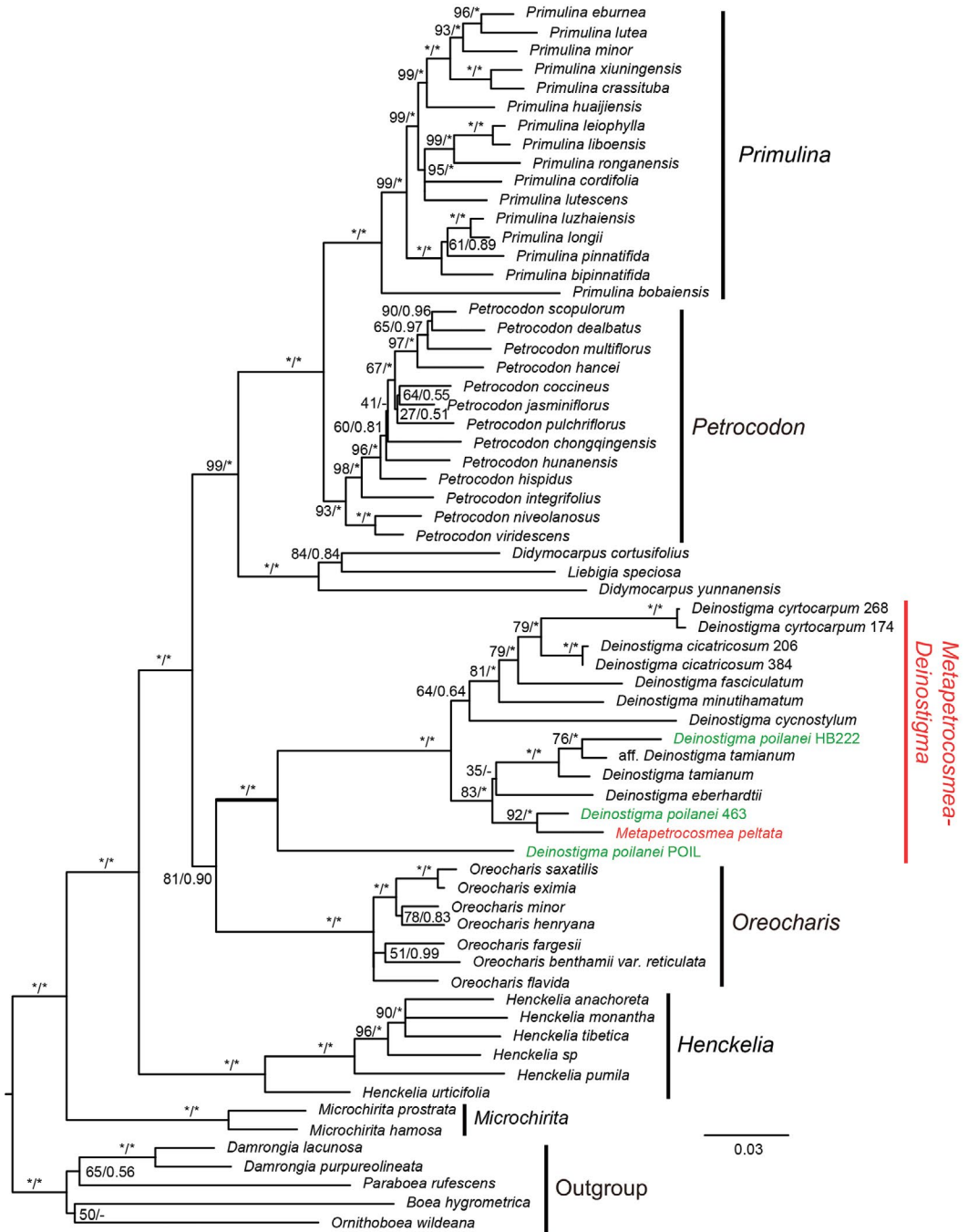


Figure 2. Maximum likelihood (ML) tree inferred from combined ITS and *trnL-F* data sets. ML bootstrap values and Bayesian inference (BI) posterior probabilities are indicated on the left and right sides of slashes, respectively. Asterisks indicate maximum support and hyphens represent no support. Sequences of *Deinostigma poilanei*_HB222, *D. poilanei*_463, and *D. poilanei*_POIL are from Möller et al. (2016), this study (isotype), and Xu et al. (2021), respectively. Bold branch indicates the *Metapetrocosmea* W. T. Wang–*Deinostigma* W. T. Wang & Z. Y. Li clade.

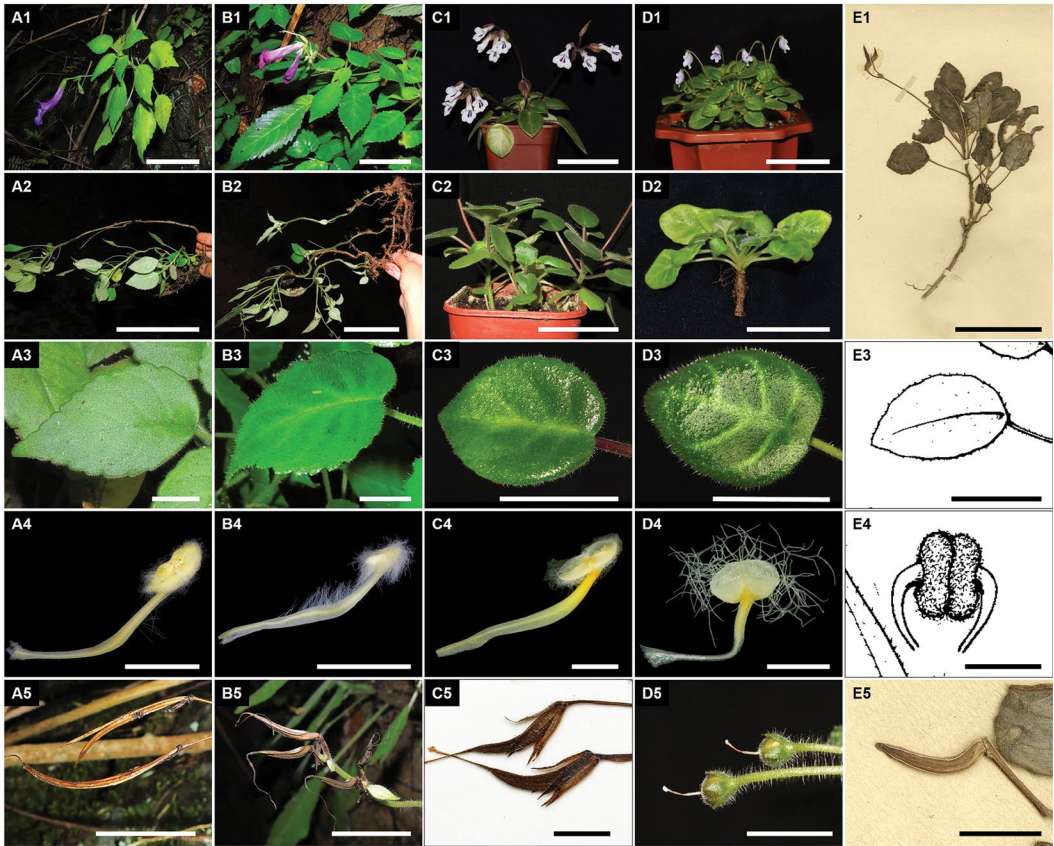


Figure 3. Macro-morphological characters of species in the *Metapetrocosmea* W. T. Wang–*Deinostigma* W. T. Wang & Z. Y. Li clade. A1–A5. *Deinostigma cicatricosum* (W. T. Wang) D. J. Middleton & Mich. Möller. B1–B5. *Deinostigma cyrtocarpum* (D. Fang & L. Zeng) Mich. Möller & H. J. Atkins. C1–C5. *Deinostigma tamianum* (B. L. Burt) D. J. Middleton & H. J. Atkins. C5. Modified from the image of a specimen of *D. tamianum* from the Royal Botanic Garden Edinburgh (RBGE) (E00254848). D1–D5. *Metapetrocosmea peltata* (Merr. & Chun) W. T. Wang. E1, E3–E5. Holotype of *Deinostigma poilanei* (Pellegrin) W. T. Wang & Z. Y. Li. E3, E4 are modified from Wang and Li (1992). A1–E1. Habit. A2–D2, E1. Slender rhizome. A3–E3. Peltate or subpeltate leaves. A4–E4. Stamens, showing lanate anthers, angles made by divaricate thecae and filament, and filament shape. A5–E5. Falcate or subglobose and loculicidal capsules. Scale bars: A1–E1, C2–D2 = 5 cm; A2, B2 = 10 cm; A3–E3, A5 = 2 cm; A4, B4 = 5 mm; C4, E4 = 2 mm; D4 = 1 mm; B5–E5 = 1 cm.

dorsal one aborted (Fig. 5B1) or slightly developed (Fig. 5B2). *Deinostigma tamianum* has a relatively uniform stigma with only an enlarged and slightly bifid ventral lobe (Fig. 5C1–C2). The stigma of *Metapetrocosmea peltata* is also variable with the dorsal stigma lobe aborted (Fig. 5D1), slightly developed (Fig. 5D2), or distinctly developed (Fig. 5D3). We examined the isotype of *D. poilanei* available to us and the only flower showed that *D. poilanei* has a dorsal-ventral oblique stigma with dorsal one aborted and ventral one an entire oblong lamella (Fig. 5E1). It should be noted here that the stigma of *D. poilanei* observed in the present study and that in Wang and Li (1992) are from different individuals. Wang and Li (1992) dissected a flower of

the holotype and specially pointed out that there are two stigma lobes with the dorsal one 0.6 mm long and the ventral one 0.8 mm long (Fig. 5E2). However, the holotype is not available to us and our observation here recovered a lamellar stigma with an aborted dorsal lobe. Although it might be reasonable to question their observation, variable stigmas indeed occur in the genus *Deinostigma*. As shown by us, stigmas of *D. cicatricosum* and *D. cyrtocarpum* are both dorsal ventrally bilobed, albeit differing in degree. We noted Möller et al. (2016) described the “stigma of only lower lip developing” in their taxonomic treatment of *Deinostigma*. However, considering the results presented here, it seems that Möller et al. (2016) had missed the stigmas

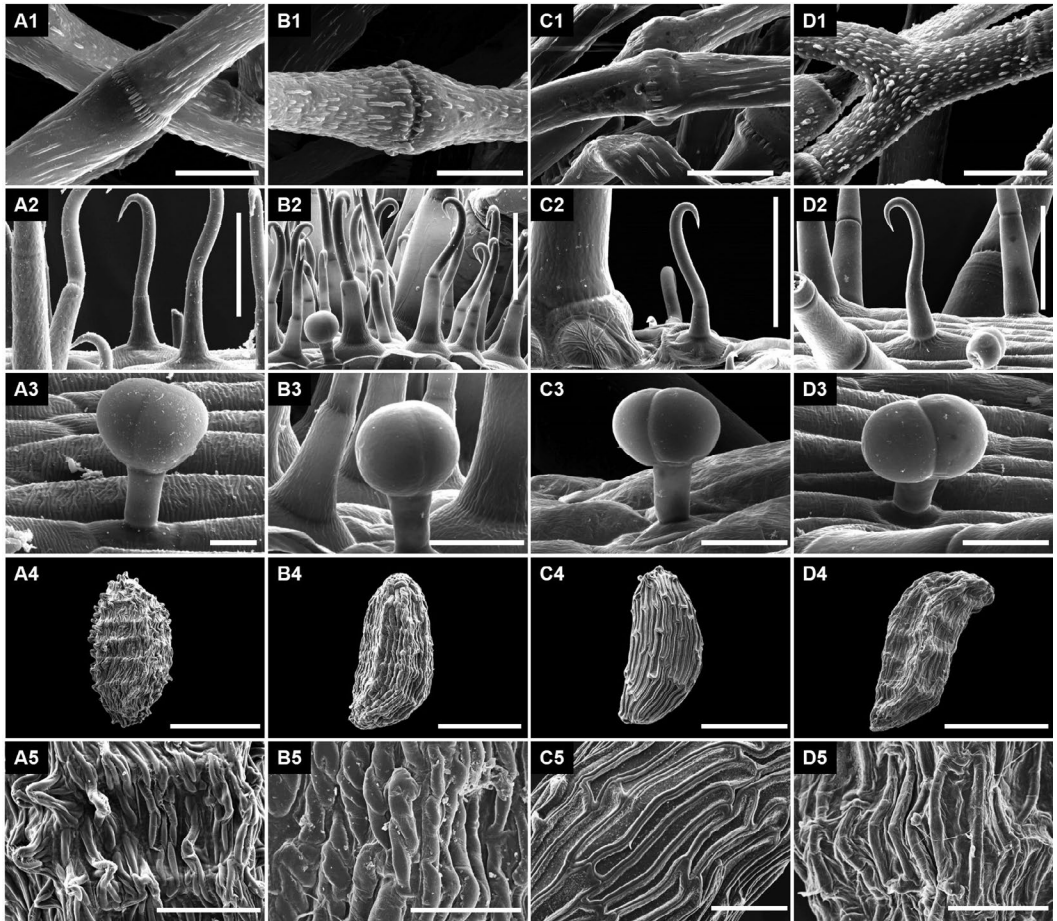


Figure 4. Micro-morphological characters of species in the *Metapetrocosmea* W. T. Wang–*Deinostigma* W. T. Wang & Z. Y. Li clade. A1–A5. *Deinostigma cicatricosum* (W. T. Wang) D. J. Middleton & Mich. Möller. B1–B5. *Deinostigma cyrtocarpum* (D. Fang & L. Zeng) Mich. Möller & H. J. Atkins. C1–C5. *Deinostigma tamianum* (B. L. Burt) D. J. Middleton & H. J. Atkins. D1–D5. *Metapetrocosmea peltata* (Merr. & Chun) W. T. Wang. A1–D1. Granular or vermiform appendages on hair surface of lanate anthers. A2, D2. Hooked hair on pedicle. B2. Hooked hair on ovary. C2. Hooked hair on sepal. A3, D3. T-shaped glandular hair on pedicle. B3. T-shaped glandular hair on ovary. C3. T-shaped glandular hair on style. A4–D4, A5–D5. Seed coat micromorphology, showing longitudinal ribbed ornamentations. Scale bars: A1–D1, A3–D3 = 20 μ m; A2–D2, A5–D5 = 50 μ m; A4–D4 = 200 μ m.

with somewhat developed dorsal lobes (Fig. 5A3–A4, B2). Therefore, we choose to follow the observation of Wang and Li (1992).

DISCUSSION

The phylogenetic reconstruction here reveals that *Metapetrocosmea peltata* is embedded in the clade consisting of *Deinostigma* species otherwise and is sister to *D. poilanei* with maximum support (Fig. 1). In contrast, phylogenetic reconstruction by Möller et al. (2016) showed that *M. peltata* was sister to all the *Deinostigma* species sampled and *D. poilanei* and *D. tamianum* were

sister species with strong support. However, it should be noted that the four species of *Deinostigma* included in Möller et al. (2016) were recovered in a monophyletic clade with relatively low support (BS = 73%, PP = 0.88; see Möller et al., 2016) and the pair of sister genera, i.e., *Metapetrocosmea* and *Deinostigma*, together form a clade with maximum support. Our further phylogenetic analysis with the data set containing only ITS and *trnL-F*, which is comparable to Möller et al. (2016), confirmed that *D. poilanei*_HB222 (Möller et al., 2016) is closely related to *D. tamianum* (Fig. 2). *Deinostigma poilanei*_463, i.e., the isotype, is sister to *M. peltata* with strong support (Fig. 2). Another acces-

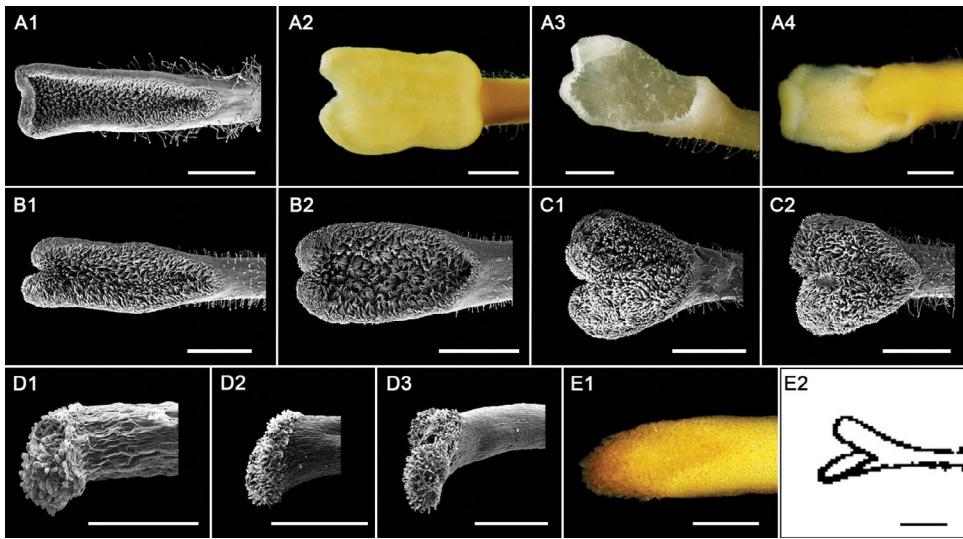


Figure 5. Stigmas in *Metapetrocosmea* W. T. Wang–*Deinostigma* W. T. Wang & Z. Y. Li clade. A1–A4. *Deinostigma cicatricosum* (W. T. Wang) D. J. Middleton & Mich. Möller. B1, B2. *Deinostigma cyrtocarpum* (D. Fang & L. Zeng) Mich. Möller & H. J. Atkins. C1, C2. *Deinostigma tamianum* (B. L. Burt) D. J. Middleton & H. J. Atkins. D1–D3. *Metapetrocosmea peltata* (Merr. & Chun) W. T. Wang, side view. E1, E2. *Deinostigma poilanei* (Pellegrin) W. T. Wang & Z. Y. Li, top view and side view, respectively. E2 is modified from Wang and Li (1992). A1, B1, C1, C2, D1, E1. Stigma with the dorsal lobe aborted and ventral lobe enlarged and slightly bifid or not. A2, A3, B2, D2. Stigma with inconspicuous dorsal lobe and enlarged bifid or not ventral lobe. A4, D3, E2. Dorsal-ventrally bilobed stigma with well-developed dorsal lobe. Scale bars: A1–A4, B1, B2, C1, C2 = 1 mm; D1–D3, E1, E2 = 500 μ m.

sion of *D. poilanei*, i.e., *D. poilanei_POIL* (Xu et al., 2021), is resolved as sister to all the remaining species in the *Metapetrocosmea–Deinostigma* clade (Fig. 2). There is no voucher for *D. poilanei_POIL*, and we are not able to examine the morphology of this sample. It seems that the three accessions of *D. poilanei* represent different species based on the phylogenetic results. Although the identifications of *D. poilanei_HB222* and *D. poilanei_POIL* are unclear, *D. poilanei_463* was sampled from the isotype and represents the correct “*Deinostigma poilanei*.” In our results, *M. peltata* is embedded in the *Metapetrocosmea–Deinostigma* clade with strong support rather than sister to the genus *Deinostigma*.

The genus *Oreocharis*, as the sister group of the *Metapetrocosmea–Deinostigma* clade, is characterized by hairy leaves without hooked hairs, four (rarely two or five) fertile stamens with parallel thecae, glabrous stamens and pistils, non-lamellar stigma, and straight capsules (Wang et al., 1998; Möller et al., 2011b). These character combinations are clearly different from those of the *Metapetrocosmea–Deinostigma* clade. The longitudinally ribbed seed coat observed in some species of *Oreocharis* (Li & Wang, 2004) might indicate the close affinity between the two sister groups. But it should be noted here that the longitudinally ribbed seed had originated independently multiple times since

it occurs in many other distantly related genera of Gesneriaceae (Beaufort-Murphy, 1983; Li & Wang, 2004).

SYNAPOMORPHIC TRAITS SHARED IN THE *METAPETROCOSMEA–DEINOSTIGMA* CLADE

In an evolutionary scenario, synapomorphies represent the products of unique evolutionary events, reflecting a common evolutionary history of given plant lineages (Simpson, 2010). Morphological analyses herein show that there is a series of novel morphological traits unique to the *Metapetrocosmea–Deinostigma* clade, including mostly peltate or subpeltate leaves, arcuate filaments, anthers densely lanate with the hair surface covered with granular or vermiform appendages, a dorsal-ventral bilobed stigma to a dorsal-ventral oblique bifid or entire laminar stigma with the dorsal lobe sterile, hooked hairs and T-shaped glandular hairs distributed in almost all parts of the plant, and generally falcate capsules with the seed coat longitudinally ribbed. Some of these morphological traits are peculiar. The granular or vermiform appendages on the surface of the hairs have not been reported in other species of the Old World Gesneriaceae to date. This specific trichome strongly indicates that species in the *Metapetrocosmea–Deinostigma* clade are derived from a most recent com-

mon ancestor. Hooked hairs rarely occur in Gesneriaceae and have been only observed in *Epithema* Blume and *Loxonia* Jack (Herat & Theobald, 1979; Li & Wang, 2004). The two genera are affiliated with the tribe Epithemateae, whereas the species in the *Metapetrocosmea–Deinostigma* clade belong to the tribe Trichosporeae (Weber et al., 2013, 2020). Therefore, the hooked hairs originated independently in the *Metapetrocosmea–Deinostigma* clade. The variability of dorsal-ventral stigmatic lobes had been observed in *Henckelia* (Burt, 1965) and *Rhabdothamnopsis* Hemsl. (Wang et al., 1998). In parallel, we also find a sequence of morphological variation in stigmas in this clade from two stigmatic lobes of dorsal-ventrally subequal size or unequal size to a ventrally much enlarged lamellar stigma with the dorsal lobe completely repressed (Fig. 5). The peltate leaves are frequently found scattered across several groups in Old World Gesneriaceae, such as *Glabrella* Mich. Möller & W. H. Chen (Möller et al., 2014), *Paraboea* (C. B. Clarke) Ridl., and *Petrocosmea* (Wang et al., 1998). Similarly, a series of variants from peltate to subpeltate (sometimes obscure peltate) leaves are observed in the *Metapetrocosmea–Deinostigma* clade. All of these morphological correlative transitions are unique in the *Metapetrocosmea–Deinostigma* clade, which indicate a common evolutionary history.

METAPETROCOSMEA–DEINOSTIGMA CLADE, ONE OR TWO GENERA?

It is widely accepted that morphological features are vital in determining systematic position or establishing taxonomical framework for certain taxa (Kong, 2001; Zarre, 2003; Moon et al., 2010; Górnjak et al., 2014; Yu et al., 2016) and therefore could enhance our understanding of the relationships revealed by molecular phylogeny (Qiu et al., 2015). Thus, it is crucial and necessary to reevaluate the morphological characters related to the *Metapetrocosmea–Deinostigma* clade in a phylogenetic context.

Möller et al. (2016) expanded the previously monotypic genus *Deinostigma* to include several species removed from *Primulina* and left the monotypic genus *Metapetrocosmea* out of *Deinostigma*. They believed *M. peltata* with the unilocular ovary, free anthers, capitate stigma, and subglobose capsule was different from *Deinostigma*, which has a bilocular ovary at least at the base, adherent anthers, lamellar stigma, and falcate capsules. These morphological differences together with the phylogenetic relationship recovered convinced the authors to maintain two genera (Möller et al., 2016).

Generally, there are three types of placentation in Gesneriaceae, including typical axile placentation with a bilocular ovary (one of the two ovary locules usually becomes sterile), typical parietal placentation with

a unilocular ovary, and a transitional type with the lower part bilocular and upper part unilocular in an ovary (Li, 2019). The axile placentation with two ovary locules is rare, while the latter two types are rather common. In addition, the placentation can be different in a given genus among different species. In *Whytockia* W. W. Sm. and *Rhynchoglossum* Blume, both the axile and transitional types had been observed (Wang et al., 1997, 2002; Wang & Pan, 1998). In *Primulina*, all three types of placentation have been observed, in which the axile placentation is scattered among different species (Wang et al., 2011). For example, placentation in *P. pinnatifida* (Hand.-Mazz.) Yin Z. Wang is typically axile and *P. luzhaiensis* (Yan Liu, Y. S. Huang & W. B. Xu) Mich. Möller & A. Weber is typically parietal, whereas a transitional form exists in *P. lutea* (Yan Liu & Y. G. Wei) Mich. Möller & A. Weber. Hence, it would be misguided to take the number of ovary locules as a standard for the delimitation of genera. In addition, the anthers of *Metapetrocosmea peltata* are not free, but actually connivent according to our own observation of living plants. Here, we recover that *M. peltata* is sister to *Deinostigma poilanei* with maximum support in our molecular phylogenetic analyses (Fig. 1), consistent with their obvious peltate leaves, oblique campanulate corollas, as well as incrassate filaments near the apex (Fig. 3). Furthermore, the capsules are all loculicidal in the *Metapetrocosmea–Deinostigma* clade despite that the subglobose capsule of *M. peltata* is remarkably different. Thus, there are no essential morphological differences between *M. peltata* and the species of *Deinostigma*.

The species in the *Metapetrocosmea–Deinostigma* clade show obvious differences in corolla shape and size, and the subglobose capsule of *M. peltata* is also very peculiar. Morphological traits related to reproductive organs had been attached greater importance than vegetative characters since Linnaeus's time. But, if we accept the precept that the taxonomic value of a character rests upon its correlation value, then vegetative characters are as valid as floral ones in the delimitation of genera (Davis & Heywood, 1963). In the present study, a series of morphological characters including both vegetative characters (slender rhizomes, alternate and peltate leaves, hooked hairs) and floral or fruit traits (lanate anthers, falcate capsules, and ribbed seed) are correlated with each other in a strongly supported clade (Fig. 1), and these specific character combinations may represent targets favored by natural selection. The exceptional morphological characters, such as relatively short rhizomes, leaves that are not peltate, or a subglobose capsule, simply represent autapomorphies that occasionally occurred in different species in the *Metapetrocosmea–Deinostigma* clade. In addition, variation of floral traits or capsules within the same

genus can be numerous in Gesneriaceae, which had been recovered in *Didymocarpus* (Nanggam & Maxwell, 2013), *Oreocharis* (Möller et al., 2011b), *Paraboea* (Xu et al., 2008; Triboun & Middleton, 2012), *Petrocodon* (Weber et al., 2011b), *Streptocarpus* Lindl. (Nishii et al., 2015), and several Neotropical genera (Clark et al., 2012). Thus, it is undoubted that all the species in the *Metapetrocosmea-Deinostigma* clade form a natural group.

Geographically, the species in the *Metapetrocosmea-Deinostigma* clade are distributed from southern Vietnam to southern China. However, *M. peltata*, endemic to Hainan Island, China (Xu et al., 2017; Li et al., 2020; Tan et al., 2020), shows a relative disjunction to other members of this clade (Fig. 6). Nevertheless, geological research show that Hainan Island was separated from Beibu Gulf (Replumaz & Taponnier, 2003) and rotated about 150° counterclockwise from the original position to the current location, which was confirmed by multiple lines of evidence, such as geographic geomorphology, strata, ore belt distribution, seismic exploration profile, and paleontology (Yan, 2006; Zhu, 2016; Liang, 2018). That is to say, Hainan Island had been linked together with the mainland in close proximity to northeastern Vietnam and southern Guangxi Province of China, where *D. cicatricosum* and *D. tamianum* are distributed at the present time. Floristic investigations also demonstrate a close connection of the flora between Hainan Island and northern Vietnam (Metcalfe, 1945; Wu, 1979; Lu & Liang, 1983; Fang et al., 1995). Thus, distribution of *M. peltata* had been within the common geographic range of the *Metapetrocosmea-Deinostigma* clade, and the present geographic disjunction between *M. peltata* and other species of this clade is attributed to plate movement that occurred in geological history.

CONCLUSION

Metapetrocosmea peltata and *Deinostigma poilanei* are the type species for their genera, but *M. peltata* is embedded in a clade consisting of otherwise *Deinostigma* species and is sister to *D. poilanei*. Species in this clade are characterized by a series of morphological traits, i.e., slender rhizomes, alternate leaves with mostly peltate or subpeltate blades, arcuate filaments, anthers densely lanate with the hair surfaces covered with granular or vermiform appendages, style longer than ovary, two stigmatic lobes from dorsal to ventral almost equal size to a dorsal-ventral oblique lamella with the dorsal lobe becoming sterile, hooked hairs and T-shaped glandular hairs occurring on the whole plant, generally falcate capsules, and a riblike seed surface. Thus, we propose that the species in the *Metapetrocosmea-Deinostigma* clade should be combined

into a single genus. According to the principle of priority in biological nomenclature, *Metapetrocosmea* W. T. Wang will be expanded to accommodate all species in the *Metapetrocosmea-Deinostigma* clade.

TAXONOMIC TREATMENT

Metapetrocosmea W. T. Wang, Bull. Bot. Res., Harbin 1(4): 38. 1981. TYPE: *Metapetrocosmea peltata* (Merr. & Chun) W. T. Wang.

Deinostigma W. T. Wang & Z. Y. Li, Acta Phytotax. Sin. 30(4): 356. 1992, syn. nov. TYPE: *Deinostigma poilanei* (Pellegri) W. T. Wang & Z. Y. Li.

Perennial herbs. Rhizomes slender or inconspicuous. Leaves alternate or basal with long straight hairs and short hooked hairs, leaf blades oblong, narrowly ovate, or broadly ovate, peltate, subpeltate, or not, apex acuminate or obtuse, margin entire or serrate, pubescent. Inflorescences dichasially branched or scorpioid-like cyme, lax or dense, axillary. Bracts 2 or 3, linear-triangular, lanceolate-ovate to ovate or obovate, sometimes caducous. Calyx 5-parted from base, segments narrowly triangular, lanceolate-triangular, or oblanceolate-triangular. Hooked hairs occurring on bracts, sepals, and corolla. Corolla white, pale yellow, pink, or purple, ventricose or narrowly infundibuliform. Limb bilabiate, adaxial lip 2-parted, shorter than abaxial lip; abaxial lip 3-lobed, lobes subequal, apex rounded. Stamens 2, adnate to abaxial side of corolla tube, included; anthers densely woolly with the surface of hairs covered with granular or vermiform appendages, thecae divaricate, dehiscing by longitudinal slits or rarely by apical pores. Staminodes 3, adnate to the adaxial side and two lateral sides of the corolla tube. Disc ringlike, rarely absent, dorsal-ventrally subequal, glabrous, margin repand or slightly lobed. Ovary linear or ovoid, densely pilose with hooked hairs, shorter than style. Two stigmatic lobes from dorsal to ventral almost equal size to a dorsal-ventral oblique lamella with the dorsal lobe aborted. Capsules usually falcate, occasionally straight or subglobose, loculicidal. Seed coat ornamentation riblike.

Distribution and habitat. *Metapetrocosmea* includes nine species distributed from southern Vietnam to southern China. These species grow on shady and moist rock along riverbanks or in the understory of subtropical or tropical rainforests.

Notes. The taxonomic status of the undescribed species, i.e., aff. *Deinostigma tamianum*, is still uncertain, and we need more morphological data to ascertain its specific rank. Therefore, we will identify it as *Metapetrocosmea tamiana* temporarily in the present study.

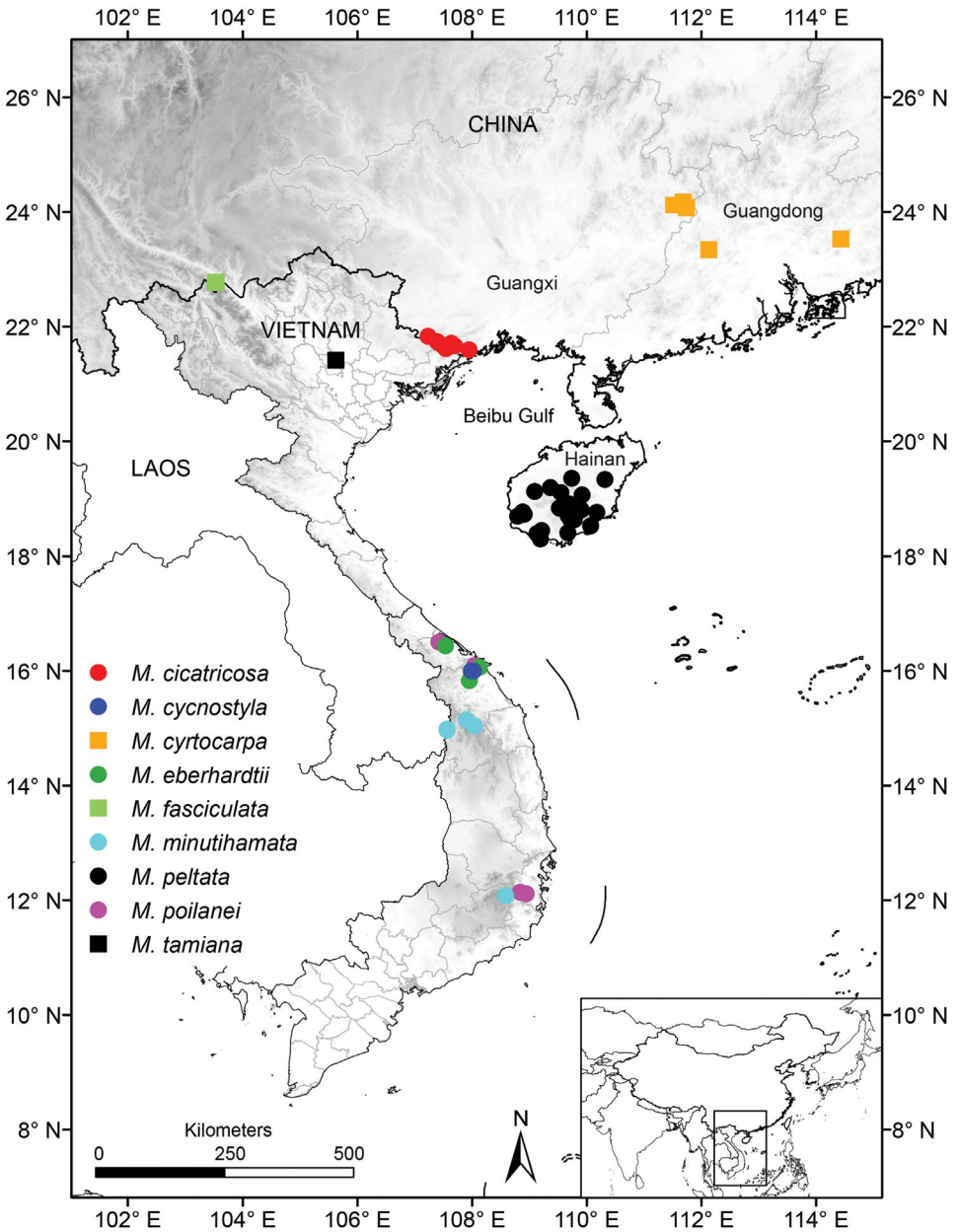


Figure 6. Distribution map for *Metapetrocosmea* W. T. Wang.

KEY TO THE SPECIES OF *METAPETROCOSMEA*

- 1a. Leaves basal; rhizome inconspicuous 2
 - 2a. Leaves somewhat fleshy, narrowly ovate to elliptic, base often cordate; inflorescence lax; corolla slightly gibbous, ca. 1 cm long, purple-striped inside; capsules subglobose..... 7. *M. peltata* (Merr. & Chun) W. T. Wang
 - 2b. Leaves distinctly fleshy, narrowly elliptic, base round; inflorescence dense; corolla narrowly campanulate, more than 1 cm long, slightly constricted at the orifice, stripes absent inside the tube; capsules falcate 2. *M. cynostyla* (B. L. Burt) Yin Z. Wang & P. W. Li
- 1b. Leaves alternate; rhizome distinct 3
 - 3a. Corolla less than 3 cm long 4

- 4a. Rhizome more than 10 cm long; corolla ca. 1 cm long, obliquely campanulate; ovary bilocular throughout with the ventral locule sterile 8. *M. poilanei* (Pellegr.) Yin Z. Wang & P. W. Li
- 4b. Rhizome less than 10 cm long; corolla more than 2 cm long, funnellform; ovary bilocular in the lower part, both locules fertile 5
- 5a. Leaves elliptic, margin dentate; sepals ca. 5 mm; capsules ca. 3 cm 4. *M. eberhardtii* (Pellegr.) Yin Z. Wang & P. W. Li
- 5b. Leaves broadly ovate, margin entire; sepals more than 1 cm; capsules ca. 2 cm long 9. *M. tamiana* (B. L. Burtt) Yin Z. Wang & P. W. Li
- 3b. Corolla more than 3 cm long 6
- 6a. Filaments densely villous; axile placentation with the ventral locule sterile 7
- 7a. Cymes scorpioid-like, lax; bracts lanceolate-triangle; sepals less than 1 cm long 3. *M. cyrtocarpa* (D. Fang & L. Zeng) Yin Z. Wang & P. W. Li
- 7b. Cymes fasciculate; bracts ovate; sepals more than 1 cm long 5. *M. fasciculata* (W. H. Chen & Y. M. Shui) Yin Z. Wang & P. W. Li
- 6b. Filaments sparsely villous at apex; ovary with the lower part bilocular and upper part unilocular 8
- 8a. Corolla purple; filaments geniculate at middle; capsules falcate 1. *M. cicatricosa* (W. T. Wang) Yin Z. Wang & P. W. Li
- 8b. Corolla pale blue to violet with few darker lines inside the ventral side of tube; filaments slightly arcuate; capsules straight 6. *M. minutihamata* (D. Wood) Yin Z. Wang & P. W. Li

1. *Metapetrocosmea cicatricosa* (W. T. Wang) Yin Z. Wang & P. W. Li, comb. nov. *Chirita cicatricosa* W. T. Wang, Bull. Bot. Res., Harbin 1(4): 69, Photo. 14. 1981. *Deinostigma cicatricosum* (W. T. Wang) D. J. Middleton & Mich. Möller, Gard. Bull. Singapore 68(1): 155. 2016. TYPE: China. Guangxi: Dongxing, Banba, 3 Oct. 1976, *D. Fang et al.* 1525 (holotype, GXMI-050619!; isotype, GXMI-050620!).

Distribution. *Metapetrocosmea cicatricosa* is found in southern Guangxi (Dongxing, Fangchenggang, Ningming), China, in the vicinity of the Sino-Vietnam border (Fig. 6).

Additional specimens examined. CHINA. **Guangxi:** Dongxing, Banba, Renbei, 21°42'47.69"N, 107°38'17.00"E, 18 Oct. 1973, *C. F. Liang* 33988 (IBSC-0548985); Fang Cheng Distr., Taan Faan, Kung Ping Shan & vic. (now propre Dongxing Town), 21°39'48.74"N, 107°41'57.81"E, 25 Aug. 1936, *W. T. Tsang* 26711 (IBSC-0548984; E-00627703 image); Shiwandashan, Dongzhong, 21°39'48.74"N, 107°41'57.81"E, alt. 520 m, 24 Mar. 2010, *Shiwandashan Exped.* 2277 (IBK-00234498); Shiwandashan, Dongzhong, 21°37'16.19"N, 107°32'24.92"E, alt. 390 m, 23 Mar. 2010, *Shiwandashan Exped.* 2167 (IBK-00234499); Fangchenggang, Dongzhong, Nali, 21°38'19.76"N, 107°32'41.45"E, alt. 360 m, 17 July 2014, *P. W. Li LPW2014056* (PE); Fangchenggang, Dongzhong, Banba, 21°40'45.83"N, 107°39'31.71"E, alt. 670 m, 15 Oct. 2016, *P. W. Li LPW2016121* (PE); Fangchenggang, Dongzhong, Ban'an, 21°39'26.31"N, 107°37'16.41"E, alt. 700 m, 15 Oct. 2016, *P. W. Li LPW2016124* (PE); Ningming, Tongmian, Nali, 21°44'11.86"N, 107°23'45.44"E, alt. 400 m, 13 July 2011, *W. B. Xu* 11221 (IBK-00207087); Ningming, Tongmian, Shunfeng'ao, 21°39'46.83"N, 107°29'48.46"E, alt. 300–650 m, 13 July 2011, *W. B. Xu et al.* NM1084 (IBK-00207089); Ningming, Tongmian, Gu'nian, 21°43'01.53"N, 107°26'58.25"E, alt. 737 m, 9 Dec. 2012, *Y. D. Peng et al.* 451422121209073LY (GXMG-0101485).

2. *Metapetrocosmea cynostyla* (B. L. Burtt) Yin Z. Wang & P. W. Li, comb. nov. *Chirita cynostyla*

B. L. Burtt, Notes Roy. Bot. Gard. Edinburgh 23: 96. 1960. *Primulina cynostyla* (B. L. Burtt) Mich. Möller & A. Weber, Taxon 60(3): 781. 2011. *Deinostigma cynostylum* (B. L. Burtt) D. J. Middleton & H. J. Atkins, Gard. Bull. Singapore 68(1): 156. 2016. TYPE: Vietnam. Ba-Na, près Tourane, 1000–1500 m, 27 Feb. 1939, *E. Poilane* 29123 (holotype, P-00602510 image!).

Distribution. *Metapetrocosmea cynostyla* is endemic to Da Nang, Vietnam, according to our knowledge (Fig. 6).

Additional specimens examined. VIETNAM. **Da Nang:** Mt. Bana, 15°59'47.50"N, 107°59'17.71"E, 13 July 1927, *J. & M. S. Clemens* 3463 (P-04526453 image); Hoa Vang Distr., Hoa Ninh municipality, Ba Na-Nui Chua protected area, around point 16°00'05"N, 108°01'15"E, alt. 800–900 m, 16 May 2011, *L. Averyanov et al.* 3320 (E-00547466 image).

3. *Metapetrocosmea cyrtocarpa* (D. Fang & L. Zeng) Yin Z. Wang & P. W. Li, comb. nov. *Chirita cyrtocarpa* D. Fang & L. Zeng, Acta Phytotax. Sin. 31(5): 468. 1993. *Primulina cyrtocarpa* (D. Fang & L. Zeng) Mich. Möller & A. Weber, Taxon 60(3): 781. 2011. *Deinostigma cyrtocarum* (D. Fang & L. Zeng) Mich. Möller & H. J. Atkins, Gard. Bull. Singapore 68(1): 156. 2016. TYPE: China. Guangxi: Hexian (now Hezhou), Daguishan, 130–140 m, 16 June 1991, *L. S. Zhou & L. Zeng* 1263 (holotype, GXMI-050608!; isotypes, GXMI-050609!, GXMI-050610!, GXMI-050611!, PE-00032261!).

Distribution. *Metapetrocosmea cyrtocarpa* occurs in eastern Guangxi (Hezhou) and Guangdong (Heyuan, Zhaoqing), China (Fig. 6).

Additional specimens examined. CHINA. **Guangdong:** Heyuan, Zijin, Dongjiang forestry center, 23°31'48.2"N,

114°42'38"E, 1 June 2022, S. W. Deng 2881 (IBSC); Zhaoqing, Deqing, Yongfeng, 23°20'29.92"N, 112°07'32.58"E, alt. 385 m, 12 July 2016, B. Pan P835 (IBK not seen). **Guangxi:** Hezhou, Daguishan, 24°10'26.92"N, 111°42'39.36"E, 170 m, 16 Oct. 1989, D. Fang et al. 80899 (GXMI-050618); *ibid.*, 130–140 m, 14 Aug. 1990, D. Fang et al. 81138 (paratypes, GXMI-050612, GXMI-050613, GXMI-050614, GXMI-050615, GXMI-050616, PE-00032262); *ibid.*, 220–240 m, 16 June 1991, L. S. Zhou & L. Zeng 1278 (paratype, GXMI-050617); *ibid.*, 27 May 2010, N. F. Li & C. H. Lu 22563 (GXMG-0052380); Daguishan, Guabang, 24°07'36.78"N, 111°45'21.36"E, alt. 137 m, 10 July 2014, P. W. Li LPW2014047 (PE); Daguishan, Gandong, 24°08'03.29"N, 111°41'14.53"E, alt. 350 m, 12 June 2015, P. W. Li LPW2015037 (PE).

4. *Metapetrocosmea eberhardtii* (Pellegr.) Yin Z.

Wang & P. W. Li, comb. nov. *Chirita eberhardtii* Pellegr., Bull. Soc. Bot. France 73: 418. 1926. *Primulina eberhardtii* (Pellegr.) Mich. Möller & A. Weber, Taxon 60(3): 782. 2011. *Deinostigma eberhardtii* (Pellegr.) D. J. Middleton & H. J. Atkins, Gard. Bull. Singapore 68(1): 156. 2016. TYPE: Vietnam. Thua Thien-Hue: Baïka, 300–500 m, P. A. Eberhardt 2466 (lectotype, designated by Middleton & Atkins in Möller et al. [2016: 156], P-00602512 image!; isolectotype, VNM-00021366 image!).

Distribution. *Metapetrocosmea eberhardtii* is distributed in Da Nang City (Lien Chieu) and Thua Thien-Hue Province, Vietnam (Fig. 6).

Notes. The herbarium sheet (L. Averyanov et al. CPC2780, E-00634296) labeled as *Primulina eberhardtii* is apparently misidentified and probably represents an undescribed species of *Metapetrocosmea*.

Additional specimens examined. VIETNAM. **Da Nang:** Linh Chiên, près Tourane, 16°04'05.05"N, 108°07'37.56"E, 8 Aug. 1923, M. Poilane 7389 (P-03511166 image). **Quang Nam:** Dai Loc Distr., Dai Hong Municipality, environs of Dai Hong town, 15°49'44"N, 107°57'19"E, 20 May 2011, L. Averyanov et al. CPC3473 (E-00634297 image).

5. *Metapetrocosmea fasciculata* (W. H. Chen &

Y. M. Shui) Yin Z. Wang & P. W. Li, comb. nov. *Deinostigma fasciculatum* W. H. Chen & Y. M. Shui, PhytoKeys 157: 201. 2020. TYPE: China. Originally introduced from Yunnan Province, Jinping County, Ma-an-di Town, 11 Aug. 2018, collected from the living plants at Kunming Botanical Garden, Y. M. Shui & S. W. Guo B2018-493 (holotype, KUN-1519975 image!).

Distribution. *Metapetrocosmea fasciculata* occurs only at the type locality: Jinping County, Yunnan Province, China (Shui et al., 2020).

Notes. *Metapetrocosmea fasciculata* is morphologically very similar to *M. cyrtocarpa*; it can be distinguished from the latter by its fasciculate cymes, ovate bracts, and long sepals judging from the plates in the protologue (Shui et al., 2020). *Metapetrocosmea fasciculata* is also confirmed by our molecular phylogenetic analyses, which demonstrates that *M. fasciculata* is an independent lineage (Figs. 1, 2; Supplementary Figs. S1, S2). However, the type of *M. fasciculata* was collected from a living plant cultivated in KUN. The range of variation of the cymes, bract shape, and sepal length of *M. fasciculata* is largely unknown and needs further investigation.

Additional specimens examined. CHINA. **Yunnan:** Jinping County, Ma'an'di Town, 22°46'15.98"N, 103°31'36.67"E, alt. 500 m.s.m., with fruits, 22 Jan. 2016, Y. M. Shui & W. H. Chen B2016-084 (KUN-1519974 image); the same county, Ma'an'di town, Maguaitang village, 22°46'43.41"N, 103°30'39.95"E alt. 520–850 m.s.m., with buds, 1 May 2019, Z. Y. Yu B2019-001 (KUN not seen).

6. *Metapetrocosmea minutihamata* (D. Wood) Yin

Z. Wang & P. W. Li, comb. nov. *Chirita minutihamata* D. Wood, Notes Roy. Bot. Gard. Edinburgh 31: 370. 1972. *Primulina minutihamata* (D. Wood) Mich. Möller & A. Weber, Taxon 60(3): 783. 2011. *Deinostigma minutihamatum* (D. Wood) D. J. Middleton & H. J. Atkins, Gard. Bull. Singapore 68(1): 158. 2016. TYPE: Vietnam. Kon Tum: Ngok Pan, 2300 m, 12 Dec. 1946, E. Poilane 35803 (holotype, P-00602518 image!; isotypes, E-00279065 image!, P-00602519 image!).

Distribution. *Metapetrocosmea minutihamata* is found in Kon Tum, Lam Dong, and Quang Nam, Vietnam (Fig. 6).

Additional specimens examined. VIETNAM. **Kon Tum:** Ngok Pan, 15°08'31.14"N, 107°53'50.93"E, 2300 m, 12 Dec. 1946, E. Poilane 35781 (P-03884219 image); evergreen dry primary forest at 1700–1900 m on northwest slope of Ngoc Linh mountain system above Long Nam village, 14°58'50.38"N, 107°33'46.72"E, 4 Apr. 1995, L. Averyanov et al. VH1165 (E-00267299 image, HN not seen, P-03884218 image); evergreen primary forest at 1900–2000 m on W slope of Ngoc Linh mountain system on elevation to Ngoc Gua peak, 14°58'14.38"N, 107°33'43.12"E, 4 Oct. 1995, L. Averyanov et al. VH1316 (HN not seen, P-03884217 image). **Lam Dong:** Lac Duong Distr., Da Chay Municipality, 29 km to NE from Dalat City, 12°04'46.62"N, 108°35'23.65"E, alt. 2150 m, 1 May 1997, Averyanov et al. VH4492 (HN not seen). **Quang Nam:** Nam Tra My Distr., Tra Linh commune, Tra Cang village, 15°02'37.5"N, 108°02'19.9"E, 692 m, 18 June 2018, Quang 218 (HN not seen).

7. *Metapetrocosmea peltata* (Merr. & Chun) W. T.

Wang, Bull. Bot. Res., Harbin 1(4): 39. 1981. *Petrocosmea peltata* Merr. & Chun, Sunyatsenia

2(3–4): 320, pl. 70. 1935. TYPE: China. Hainan: Ngai Yuen, ca. 700 m, 23 Feb. 1933, *F. C. How* & *N. K. Chun 70183* (holotype, IBSC-0004925!; isotype, NYBG-00063205 image!).

Distribution. *Metapetrocosmea peltata* is endemic to Hainan Island, China, and can be found in Baoting, Baisha, Ding'an, Changjiang, Dongfang, Gan'en, Ledong, Lingshui, Qiongzong, and Wuzhishan (Fig. 6).

Additional specimens examined. CHINA. **Hainan:** 19 Dec. 1934, *H. Y. Liang 64959* (IBK-00054780); Baoting, Taiping, Jiatong, 18°48'09.01"N, 109°54'18.64"E, 21 Apr. 1934, *F. C. How 72048* (IBK-00054781, IBSC-0550689); Baoting, Chengxing, 18°38'11.14"N, 109°46'58.67"E, 29 Nov. 1936, *C. K. Lau 28267* (IBK-00054782, IBSC-0550698); Baoting, Qizhiling, 18°42'24.89"N, 109°40'27.22"E, 12 Apr. 1989, *B. H. Chen 365* (IBSC-0550703); Baoting, Miaoren church, 18°38'17.72"N, 109°43'01.97"E, Feb. 1952, *S. H. Chun 7701* (IBSC-0550696); Baisha, Nabang, 19°11'32.60"N, 109°22'04.21"E, 24 Feb. 1936, *C. K. Lau 25429* (IBK-00054783, IBSC-0550690); Baisha, Yuanmen, 19°06'36.06"N, 109°33'06.38"E, 14 Apr. 1936, *C. K. Lau 26262* (IBSC-0550706); Dingan, Wuzhi Mtn., 19°31'49.71"N, 110°18'50.68"E, 21 Dec. 1933, *Z. Huang 35753* (IBK-00054880); Changjiang, Bawangling, Dongsi, 19°07'39.04"N, 109°05'23.84"E, 27 Apr. 1988, *Z. X. Li & F. W. Xing 3866* (IBSC-0550686); Dongfang, Jianfengling, 18°46'15.03"N, 108°52'59.61"E, 17 Dec. 1955, *Hainan Veg. Exped. 337* (IBSC-0550697); Gan'en, Shamo, 18°41'37.94"N, 108°47'45.84"E, 13 Dec. 1934, *C. K. Lau 5106* (IBSC-0550702); Gan'en, Chunbailing, 19°04'06.75"N, 109°55'00.58"E, 19 Oct. 1933, *H. Y. Liang 63502* (IBSC-0550705); Ledong, Jianfengling, 18°43'49.70"N, 108°54'32.99"E, alt. 1316 m, 26 Apr. 2014, *T. Zhang et al. 14CS8688* (KUN-1385422); Lingshui, 18°31'33.27"N, 110°04'08.55"E, alt. 433 m, 2 Aug. 2011, *Y. M. Shui et al. B2011-114* (KUN-1385423); Qiongzong, Chengpo, 19°21'29.40"N, 109°44'24.13"E, 5 Dec. 1956, *L. Deng 3539* (IBSC-0550695); Wanning, Xinglong forest park, 18°45'55.02"N, 110°10'32.12"E, 20 Mar. 1995, *F. W. Xing et al. 5734* (IBSC-0550701); Wuzhishan, Tongshi, A'tuoling, 18°50'26.23"N, 109°31'31.61"E, alt. 760 m, 5 Sep. 2017, *C. Liu et al. 17CS15926* (KUN-1450855); Wuzhishan, Maoxiangshan, 18°48'02.33"N, 109°39'28.80"E, 16 Jan. 1934, *H. Y. Liang 64728* (IBSC-0550694); Wuzhishan, Fanyi, 18°24'24.11"N, 109°40'13.63"E, 7 Oct. 1932, *C. L. Tso & N. Q. Chen 44039* (IBSC-0550685); Wuzhishan forest park 18°54'49.27"N, 109°41'17.47"E, 19 Nov. 2013, *Z. W. Wang & Y. X. Su wzw00622* (CSH-0073415); Yazhou, 18°26'53.51"N, 109°12'50.72"E, 23 Feb. 1933, *N. Q. Chen & F. C. How 70183* (IBSC-0550691); Yazhou, Yanglin, 18°23'29.93"N, 109°07'44.18"E, 14 Mar. 1933, *F. C. How 70350* (IBSC-0550693); Yazhou, Nanlinling, 18°18'11.65"N, 109°11'43.93"E, 27 Sep. 1933, *Z. Huang 34301* (IBSC-0550692).

8. *Metapetrocosmea poilanei* (Pellegr.) Yin Z. Wang & P. W. Li, comb. nov. *Hemiboea poilanei* Pellegr., Bull. Soc. Bot. France 73: 421. 1926. *Deinostigma poilanei* (Pellegr.) W. T. Wang & Z. Y. Li, Acta Phytotax. Sin. 30(4): 357. 1992. TYPE: Vietnam. Khánh Hòa: Nhatrang, 300 m, 29 Oct. 1922, *M. Poilane 3846* (holotype, P-00606338 image!;

isotypes, P-00634330 image!, PE!, VNM-00021378 image!).

Distribution. *Metapetrocosmea poilanei* occurs in Da Nang, Khanh Hoa, and Thua Thien-Hua, Vietnam (Möller et al., 2016, 2020) (Fig. 6).

Additional specimens examined. VIETNAM. Originally collected as *R. Rybkova HB-222* from Vietnam, Khanh Hoa, primary forest, 12°07'4.5"N, 108°56'46.8"E under accession number 20132216*A, vouchered for the herbarium as *H. J. Atkins No. 54* (E-00743552 image).

9. *Metapetrocosmea tamiana* (B. L. Burt) Yin Z. Wang & P. W. Li, comb. nov. *Chirita tamiana* B. L. Burt, Gloxinian 49(4): 20. 1999. *Primulina tamiana* (B. L. Burt) Mich. Möller & A. Weber, Taxon 60(3): 785. 2011. *Deinostigma tamianum* (B. L. Burt) D. J. Middleton & H. J. Atkins, Gard. Bull. Singapore 68(1): 158. 2016. TYPE: Originally collected as Soviet-Vietnam Expedition 0/114 from Vietnam, Vinh Phuc, Tam Dao National Park, cultivated in RBGE under accession number 19981743*A, vouchered for the herbarium as *CULTE 15738* (holotype, E-00269898 image!).

Distribution. *Metapetrocosmea tamiana* occurs in Vinh Phuc Province, Vietnam (Fig. 6).

Notes. *Metapetrocosmea tamiana* is easy to cultivate and propagate, and it has been widely grown by Gesneriad growers or botanical gardens. However, we know little about this charming plant in the wild.

Additional specimens examined. Cultivated in FairyLake Botanical Garden, Shenzhen & CAS, China, vouchered for the herbarium as *P. W. Li LPW2015065* (PE). Cultivated in Royal Botanic Garden Edinburgh, collected by *M. Möller s.n.* (E-00254848 image).

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Appendix 1. Taxa included in the phylogenetic analyses, voucher information, locality, and GenBank accession numbers for ETS, ITS, *rpl32-trnL*, *rps16*, *trnH-psbA*, *trnL-F*, re-

spectively. The codes in square brackets after the scientific names correspond to those in Figures 1 and 2. Sequences not obtained are designated by an em dash; sequences downloaded from the National Center for Biotechnology Information (NCBI) are labeled with an asterisk; herbarium acronyms follow Thiers (2021).

Ingroup: *Deinostigma cicatricosum* (W. T. Wang) D. J. Middleton & Mich. Möller [206], *P. W. Li LPW2014056* (PE), Fangchenggang, Guangxi, China, MN637023, MN627934, MN637186, MN637306, MN637446, MN637585. *Deinostigma cicatricosum* (W. T. Wang) D. J. Middleton & Mich. Möller [384], *P. W. Li LPW2016121* (PE), Fangchenggang, Guangxi, China, MN637022, MN627933, MN637185, MN637305, MN637445, MN637584. *Deinostigma cynostylum* (B. L. Burtt) D. J. Middleton & H. J. Atkins, *P. W. Li LPW2021004* (PE), Da Nang, Vietnam, MZ325319, MZ265312, MZ325306, MZ325313, MZ325315, MZ325308. *Deinostigma cyrtocarpum* (D. Fang & L. Zeng) Mich. Möller & H. J. Atkins [174], *P. W. Li LPW2014047* (PE), Hezhou, Guangxi, China, MN637021, MN627932, MN637184, MN637304, MN637444, MN637583. *Deinostigma cyrtocarpum* (D. Fang & L. Zeng) Mich. Möller & H. J. Atkins [268], *P. W. Li LPW2015037* (PE), Hezhou, Guangxi, China, MN637020, MN627931, MN637183, MN637303, MN637443, MN637582. *Deinostigma eberhardtii* (Pelleg.) D. J. Middleton & H. J. Atkins, *M. Q. Han HMQ215182* (PE), Vietnam, MZ325320, MZ265313, MZ325303, MZ325311, MZ325316, MZ325310. *Deinostigma fasciculatum* W. H. Chen & Y. M. Shui, *M. Q. Han HMQ215181* (PE), Jinping, Yunnan, China, MZ325321, MZ265314, MZ325304, MZ325314, MZ325317, MZ325309. *Deinostigma minutiamatum* (D. Wood) D. J. Middleton & H. J. Atkins, *B. H. Quang 218* (HN), Quang Nam, Vietnam, —, MT066216*, —, —, MT075730*. *Deinostigma poilanei* (Pelleg.) W. T. Wang & Z. Y. Li [463], *M. Poilane 3846* (PE), Nha trang, Vietnam, —, MN627950, MN637202, —, MN637462, MN637601. *Deinostigma poilanei* (Pelleg.) W. T. Wang & Z. Y. Li [HB222], *R. Rybková HB222* (E), Hon Ba, Vietnam, —, KU990892*, —, —, KU990888*. *Deinostigma poilanei* (Pelleg.) W. T. Wang & Z. Y. Li [POIL], *M. Z. Xu et al. POIL*, Vietnam, —, MK747169*, —, —, MK746224*. *Deinostigma tamianum* (B. L. Burtt) D. J. Middleton & H. J. Atkins, *P. W. Li LPW2015065* (PE), cultivated in Fairy Lake Botanical Garden, Shenzhen & CAS, China, MN637025, MN627936, MN637188, MN637308, MN637448, MN637587. aff. *Deinostigma tamianum*, *P. W. Li LPW2021003* (PE), Thua Thien-Hue, Vietnam, MZ325322, MZ265315, MZ325305, MZ325312, MZ325318, MZ325307. *Didymocarpus cortusifolius* (Hance) H. Lévl., *M. T. Liu LMT2012010* (PE), Leqing, Zhejiang, China, MN637013, MN627924, MN637176, MN637296, MN637436, MN637575. *Didymocarpus yunnanensis* (Franch.) W. W. Sm., *P. W. Li LPW2012028* (PE), Miyi, Sichuan, China, MN637012, MN627923, MN637175, MN637295, MN637435, MN637574. *Henckelia anachoreta* (Hance) D. J. Middleton & Mich. Möller, *P. W. Li LPW2013143* (PE), Maguan, Yunnan, China, MN637027, MN627938, MN637190, MN637310, MN637450, MN637589. *Henckelia monantha* (W. T. Wang) D. J. Middleton & Mich. Möller, *P. W. Li LPW2015046* (PE), Yongshun, Hunan, China, MN637029, MN627940, MN637192, MN637312, MN637452, MN637591. *Henckelia pumila* (D. Don) A. Dietr., *R. B. Mao MRB201076* (PE), Zhenfeng, Guizhou, China, MN637030, MN627941, MN637193, MN637313, MN637453, MN637592. *Henckelia* sp., *J. M. Li LJM200488* (PE), cultivated in Kunming Institute of Botany, CAS, China, MN637028, MN627939, MN637191, MN637311, MN637451, MN637590. *Henckelia tibetica* (Franch.) D. J. Middleton & Mich. Möller, *P. W. Li LPW2012025* (PE),

Miyi, Sichuan, China, MN637026, MN627937, MN637189, MN637309, MN637449, MN637588. *Henckelia urticifolia* (Buch.-Ham. ex D. Don) A. Dietr., *J. M. Li LJM200481* (PE), Lüchun, Yunnan, China, MN637031, MN627942, MN637194, MN637314, MN637454, MN637593. *Liebigia speciosa* (Blume) DC., *P. Woods 1071* (E), Java, Indonesia, —, FJ501359*, —, —, FJ501538*. *Metapetrocosmea peltata* (Merr. & Chun) W. T. Wang, *J. Wen 16378* (PE), Qiongzong, Hainan, China, MN637024, MN627935, MN637195, MN637307, MN637447, MN637586. *Microchirita hamosa* (R. Br.) Yin Z. Wang, *P. W. Li LPW2013079* (PE), Fengshan, Guangxi, China, MN637032, MN627943, MN637195, MN637315, MN637455, MN637594. *Microchirita prostrata* J. M. Li & Z. Xia, *J. M. Li 057291* (PE), Hekou, Yunnan, China, MN637033, MN627944, MN637196, MN637316, MN637456, MN637595. *Oreocharis benthamii* C. B. Clarke var. *reticulata* Dunn, *Z. J. Qiu QZJ2008006* (PE), Zhaoqing, Guangdong, China, MN637019, MN637442, MN637182, MN637302, MN637442, MN637581. *Oreocharis eximia* (Chun ex K. Y. Pan) Mich. Möller & A. Weber, *C. Y. Feng FCY2013017* (PE), Jinyang, Sichuan, China, MN637015, MN627926, MN637178, MN637298, MN637438, MN637577. *Oreocharis fargesii* (Franch.) Mich. Möller & A. Weber, *C. Y. Feng FCY2013002* (PE), Chengkou, Chongqing, China, —, MN627949, MN637201, MN637321, MN637461, MN637600. *Oreocharis flavida* Merr., *X. R. Zhou ZXRO41124* (PE), Lingshui, Hainan, China, MN637018, MN627929, MN637181, MN637301, MN637441, MN637580. *Oreocharis henryana* Oliv., *P. W. Li LPW2012033* (PE), Butuo, Sichuan, China, MN637016, MN627927, MN637179, MN637299, MN637439, MN637578. *Oreocharis minor* (Craib) Pelleg., *P. W. Li & C. Y. Feng PWCY2013048* (PE), Lijiang, Yunnan, China, MN637017, MN627928, MN637180, MN637300, MN637440, MN637579. *Oreocharis saxatilis* (Hemsl.) Mich. Möller & A. Weber, *R. H. Liang LRH011* (PE), Nanchuan, Chongqing, China, MN637014, MN627925, MN637177, MN637297, MN637437, MN637576. *Petrocodon chongqingensis* F. Wen, B. Pan & L. Y. Su, *P. W. Li LPW2014098* (PE), Chongqing, China, MN637007, MN627918, MN637170, MN637290, MN637430, MN637569. *Petrocodon coccineus* (C. Y. Wu ex H. W. Li) Yin Z. Wang, *P. W. Li LPW2013090* (PE), Napo, Guangxi, China, MN637005, MN627916, MN637168, MN637288, MN637428, MN637567. *Petrocodon dealbatus* Hance, *M. T. Liu LMT2012017* (PE), Shibing, Guizhou, China, MN636999, MN627910, MN637162, MN637282, MN637422, MN637561. *Petrocodon hancei* (Hemsl.) A. Weber & Mich. Möller, *M. T. Liu LMT2012005* (PE), Xinning, Hunan, China, MN637002, MN627913, MN637165, MN637285, MN637425, MN637564. *Petrocodon hispidus* (W. T. Wang) A. Weber & Mich. Möller, *P. W. Li LPW2012010* (PE), Xichou, Yunnan, China, MN637004, MN627915, MN637167, MN637287, MN637427, MN637566. *Petrocodon hunanensis* X. L. Yu & Ming Li, *P. W. Li LPW2014014* (PE), Dong'an, Hunan, China, MN637008, MN627919, MN637171, MN637291, MN637431, MN637570. *Petrocodon integrifolius* (D. Fang & L. Zeng) A. Weber & Mich. Möller, *P. W. Li LPW2013040* (PE), Longzhou, Guangxi, China, MN637009, MN627920, MN637172, MN637292, MN637432, MN637571. *Petrocodon jasminiflorus* (D. Fang & W. T. Wang) A. Weber & Mich. Möller, *M. T. Liu LMT2012002* (PE), Napo, Guangxi, China, MN637006, MN627917, MN637169, MN637289, MN637429, MN637568. *Petrocodon multiflorus* F. Wen & Y. S. Jiang, *P. W. Li LPW2018034* (PE), Cangwu, Guangxi, China, MN637001, MN627912, MN637164, MN637284, MN637424, MN637563. *Petrocodon niveolanosus* (D. Fang & W. T. Wang) A. Weber & Mich. Möller, *P. W. Li LPW2013119* (PE), Longlin, Guangxi, China, MN637011, MN627922, MN637174, MN637294, MN637434, MN637573. *Petroco-*

- don pulchriflorus* Y. B. Lu & Q. Zhang, *P. W. Li LPW2018018* (PE), Daxin, Guangxi, China, MN637003, MN627914, MN637166, MN637286, MN637426, MN637565. *Petrocodon scopulorum* (Chun) Yin Z. Wang, *P. W. Li LPW2018003* (PE), Pingba, Guizhou, China, MN637000, MN627911, MN637163, MN637283, MN637423, MN637562. *Petrocodon viridescens* W. H. Chen, Mich. Möller & Y. M. Shui, *Y. M. Shui 85339* (KUN), Maguan, Yunnan, China, MN637010, MN627921, MN637173, MN637293, MN637433, MN637572. *Primulina bipinnatifida* (W. T. Wang) Yin Z. Wang, *P. W. Li LPW2013016* (PE), Lingui, Guangxi, China, MN636997, MN627847, MN637160, MN637217, MN637358, MN637497. *Primulina bobaensis* Q. K. Li, Qiang Zhang & Wen L. Li, *P. W. Li LPW2015024* (PE), Bobai, Guangxi, China, MN636998, MN627848, MN637161, MN637218, MN637359, MN637498. *Primulina cordifolia* (D. Fang & W. T. Wang) Yin Z. Wang, *P. W. Li LPW2013021* (PE), Liujiang, Guangxi, China, MN636993, MN627843, MN637156, MN637213, MN637354, MN637493. *Primulina crassituba* (W. T. Wang) Mich. Möller & A. Weber, *P. W. Li LPW2016003* (PE), Shuangpai, Hunan, China, MN636985, MN627835, MN637148, MN637205, MN637346, MN637485. *Primulina eburnea* (Hance) Yin Z. Wang, *P. W. Li LPW2013105* (PE), Pingle, Guangxi, China, MN636984, MN627834, MN637147, MN637204, MN637345, MN637484. *Primulina huaijiensis* Z. L. Ning & Jing Wang, *P. W. Li LPW2014129* (PE), Huaiji, Guangdong, China, MN636988, MN627838, MN637151, MN637208, MN637349, MN637488. *Primulina leiophylla* (W. T. Wang) Yin Z. Wang, *P. W. Li LPW2013082* (PE), Jingxi, Guangxi, China, MN636989, MN627839, MN637152, MN637209, MN637350, MN637489. *Primulina liboensis* (W. T. Wang & D. Y. Chen) Mich. Möller & A. Weber, *P. W. Li LPW2016027* (PE), Libo, Guizhou, China, MN636990, MN627840, MN637153, MN637210, MN637351, MN637490. *Primulina longii* (Z. Y. Li) Yin Z. Wang, *P. W. Li LPW2013017* (PE), Yongfu, Guangxi, China, MN636995, MN627845, MN637158, MN637215, MN637356, MN637495. *Primulina lutea* (Yan Liu & Y. G. Wei) Mich. Möller & A. Weber, *P. W. Li LPW2013100* (PE), Zhongshan, Guangxi, China, MN636987, MN627837, MN637150, MN637207, MN637348, MN637487. *Primulina lutescens* B. Pan & H. S. Ma, *P. W. Li LPW2014055* (PE), Lingshan, Guangxi, China, MN636991, MN627841, MN637154, MN637211, MN637352, MN637491. *Primulina luzhaiensis* (Yan Liu, Y. S. Huang & W. B. Xu) Mich. Möller & A. Weber, *P. W. Li LPW2013019* (PE), Yongfu, Guangxi, China, MN636994, MN627844, MN637157, MN637214, MN637355, MN637494. *Primulina minor* F. Wen & Y. G. Wei, *P. W. Li LPW2014018* (PE), Daoxian, Hunan, China, MN636983, MN627833, MN637146, MN637203, MN637344, MN637483. *Primulina pinnatifida* (Hand.-Mazz.) Yin Z. Wang, *P. W. Li LPW2016072* (PE), Tianlin, Guangxi, China, MN636996, MN627846, MN637159, MN637216, MN637357, MN637496. *Primulina ronganensis* (D. Fang & Y. G. Wei) Mich. Möller & A. Weber, *P. W. Li LPW2013020* (PE), Rong'an, Guangxi, China, MN636992, MN627842, MN637155, MN637212, MN637353, MN637492. *Primulina xiuningensis* (X. L. Liu & X. H. Guo) Mich. Möller & A. Weber, *P. W. Li LPW2017007* (PE), Xiuning, Anhui, China, MN636986, MN627836, MN637149, MN637206, MN637347, MN637486. **Outgroup:** *Boea hygrometrica* (Bunge) R. Br., *P. W. Li LPW2015033* (PE), Shaoguan, Guangdong, China, MN637037, MN627948, MN637200, MN637320, MN637460, MN637599. *Damrongia lacunosa* (Hook. f.) D. J. Middleton & A. Weber, *Imin FR163238* (KEP), Malaysia, —, KU203801*, —, —, KU203801*. *Damrongia purpureolineata* Kerr ex Craib, *Triboun.s.n. CH111* (BK), Lamphun, Thailand, —, KU203798*, —, —, KU203893*. *Ornithoboea wildeana* Craib, *P. W. Li LPW2013078* (PE), Fengshan, Guangxi, China, MN637034, MN627945, MN637197, MN637317, MN637457, MN637596. *Paraboea rufescens* (Franch.) B. L. Burt, *J. M. Li LJM2003124* (PE), Longzhou, Guangxi, China, MN637035, MN627946, MN637198, MN637318, MN637458, MN637597.