

New insights into the relationships between *Paraboea*, *Trisepalum*, and *Phylloboea* (Gesneriaceae) and their taxonomic consequences

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Abstract The phylogenetic relationships between *Paraboea*, *Trisepalum* and *Phylloboea*, in the twisted-fruited clade of the advanced Asiatic and Malesian Gesneriaceae, were investigated using nuclear and chloroplast data. Maximum parsimony and Bayesian inference analyses demonstrated unambiguously that the three genera originated from a single common ancestor, that *Phylloboea* is nested deeply in *Trisepalum* and that in turn *Trisepalum* is nested in *Paraboea*. As *Paraboea* has been conserved against *Phylloboea* and *Trisepalum* the necessary new combinations in *Paraboea* are made here. The enlarged genus *Paraboea* comprises around 120 species. The phylogeny presented here will provide a valuable framework for future biogeographic and comparative studies in Gesneriaceae.

Keywords Gesneriaceae; molecular phylogeny; molecular systematics; new combinations; *Paraboea*; *Phylloboea*; taxonomy; *Trisepalum*.

Supplementary Material Diagnostics of the Bayesian inference analyses (Electronic Supplements 1–3), Figures S1–S4 (Electronic Supplement 4) and the alignments file are available in the Supplementary Data section of the online version of this article (<http://ingentaconnect.com/content/iapt/tax>).

■ INTRODUCTION

In this study we set out to investigate the relationships between *Paraboea* (C.B. Clarke) Ridl., *Trisepalum* C.B. Clarke and *Phylloboea* Benth. in the Gesneriaceae. Previous studies have already discussed relationships within the Old World Gesneriaceae (e.g., Mayer & al., 2003; Weber, 2004; Möller & al., 2009, 2011a) and have firmly established a strongly supported clade, including *Paraboea*, *Trisepalum* and *Phylloboea*, containing all Asian genera with twisted fruits. *Paraboea* was shown to be either paraphyletic, sharing a polytomy with *Trisepalum* (Möller & al., 2009), or monophyletic and sister to a clade in which *Phylloboea* was sister to *Trisepalum* (Möller & al., 2011a). There has, however, been insufficient research into relationships within this twisted-fruited group and into whether *Paraboea*, *Trisepalum* and *Phylloboea* should be maintained as distinct genera despite their evident similarities (see Burt, 1984).

The name *Paraboea* was first published by Clarke in 1883 as a section of the genus *Didymocarpus* Wall. *Didymocarpus* sect. *Paraboea* C.B. Clarke was characterised by dichotomous cymes with long peduncles, short and campanulate corolla tubes, large, round anthers and subfollicular capsules and was to be found in Billiton (Belitung, Indonesia), Borneo and Sulawesi. It was described as similar to *Boea* Comm. ex Lam., apart from the straight capsule valves (Clarke, 1883). In the same publication, *Trisepalum* was listed in the group of genera with straight capsules, like *Didymocarpus*, and *Phylloboea* was included in the twisted-fruited group, with *Boea*. Both *Trisepalum* and *Phylloboea* were only recorded from Burma. *Boea*,

defined by the short, 5-lobed, almost actinomorphic corolla, at that time consisted of 13 described species distributed between Western India and Australia (Clarke, 1883).

In his account of the Gesneriaceae of the Malay Peninsula, Ridley (1905) re-circumscribed the polymorphic *Didymocarpus* and excluded the short-flowered sections *Loxocarpus* R. Br. and *Paraboea*, which were consequently raised to generic status. At this point *Paraboea* (C.B. Clarke) Ridl. included about 20 species, mostly occurring in Malaysia but also in Thailand and Borneo. Its main morphological features were a short corolla tube, straight capsule, long style and two short stamens.

Paraboea was later typified by Burt (1948) with *P. clarkei* B.L. Burt. The genus was substantially re-circumscribed by Burt (1984), who decided to give higher taxonomic value to the indumentum rather than to the fruit morphology. As a consequence, many species with twisted valves, previously included in *Boea*, were transferred to *Paraboea*. This new circumscription of *Paraboea*, as an entity distinct from *Boea*, was subsequently supported by molecular studies (Möller & al., 2009, 2011a). *Dichiloboea* Stapf and *Trisepalum*, separated on the same straight vs. twisted fruit criterion that was applied to the groups of *Paraboea*, were also synonymised by Burt (1984), based on the common tripartite arrangement of the calyx (Burt, 1984). The alliance of genera highlighted by Burt (1984) was, therefore, defined as follows: *Boea* (simple hairs, 5-partite calyx), *Paraboea* (interwoven-matted hairs, 5-partite calyx) and *Trisepalum* (interwoven-matted hairs, tripartite calyx). As the author pointed out, however, *Paraboea* and *Trisepalum* could potentially be merged into one genus, a

question which needed further clarification. *Phylloboea* was not discussed by Burtt (1984). In the last taxonomic work on *Paraboea* (Xu & al., 2008) the distinction between *Paraboea* and *Trisepalum* was retained with some hesitation.

All but the type species of *Phylloboea* have previously been transferred to either *Paraboea* or *Trisepalum*. The only remaining species is *Phylloboea glandulosa* B.L. Burtt, previously only known from one collection from Burma (Burtt, 1960), but recently also found in western Thailand. Although not discussed as part of the *Boea* alliance by Burtt (1984), it appears to be part of this group based on flower characters even though it lacks the typical matted indumentum found in both *Paraboea* and *Trisepalum*. A collection of *Phylloboea glandulosa* from Thailand was included in the analysis of Möller & al. (2011a) and was shown to be sister to the only species of *Trisepalum*, *T. birmanicum* (Craib) B.L. Burtt, incorporated in the analysis. Further investigation of *Paraboea* and its relatives, therefore, needs to include *Phylloboea* and an increased taxon sampling of the aforementioned genera.

In the present study we use molecular sequence data from two sources, the internal transcribed spacers (ITS) of the nuclear ribosomal DNA (nrDNA) and the *trnL-trnF* intron-spacer region of the chloroplast DNA (cpDNA). Maximum parsimony and Bayesian inference analyses are applied on a greatly expanded sampling of *Paraboea*, *Trisepalum* and *Phylloboea* to address whether their phylogenetic relationships are reflected by the current taxonomy.

■ MATERIALS AND METHODS

Plant material. — Plant material for molecular analysis was collected by the authors and collaborators across China and Southeast Asia (Appendix). In some cases we sampled plants in cultivation at the Royal Botanic Garden Edinburgh. All associated vouchers from cultivated plants are deposited in E.

The ingroup taxa consisted of 42 samples, of which 32 were from the genus *Paraboea*, nine from *Trisepalum* and one from the monotypic *Phylloboea*. Eleven outgroups were sampled from eight other genera of the “twisted-fruited advanced Asiatic and Malesian genera” (Möller & al., 2009). Additionally, the straight-fruited *Didissandra frutescens* C.B. Clarke, *Microchirita involucrata* (Craib) Y.Z. Wang, *M. caliginosa* (C.B. Clarke) Y.Z. Wang and *M. hamosa* (R. Br.) Y.Z. Wang were included in the outgroup (Appendix). The trees were rooted on samples of *Microchirita* (C.B. Clarke) Y.Z. Wang (Möller & al., 2011a).

Molecular markers. — ITS and *trnL-trnF* are widely and successfully used in phylogenetic analyses of Gesneriaceae (Möller & al., 1999, 2009, 2011a, b; Zimmer & al., 2002; Smith & al., 2004; Roalson & al., 2005; Wei & al., 2010; Weber & al., 2011a, b, c) because of their complementary contributions to the tree resolution. Conservative regions, such as *trnL-trnF*, are more informative at higher taxonomic levels (Gielly & Taberlet, 1994), while faster evolving regions, such as ITS, provide resolution at genus or species level (Baldwin & al., 1995). In practical terms *trnL-trnF* provides backbone branch support, while ITS

provides resolution and support for near terminal relationships (Qiu & al., 1999; Long & al., 2000; Sinclair & al., 2002).

DNA extraction and PCR. — Total genomic DNA was extracted following a modified CTAB protocol (Doyle & Doyle, 1987) with no further purification. Two molecular markers were studied: the nuclear nrDNA ITS, with primers ‘2G’, ‘3P’, ‘5P’ and ‘8P’ (Möller & Cronk, 1997) and the cpDNA *trnL-trnF* intron-spacer region, with primers ‘c’, ‘d’, ‘e’ and ‘f’ (Taberlet & al., 1991). The internal primers ‘2G’, ‘3P’, ‘d’ and ‘e’ were only used in sequencing reactions when ambiguities needed clarification and confirmation.

The 20 µl PCR reaction contained 2 µl 10× NH₄ buffer, 2 µl dNTPs (2 mM), 0.6 µl MgCl₂ (50 mM), 2 µl of each primer (10 µM), 0.4 µl Biotaq polymerase (Biolone, London, U.K.), 0.2 µl BSA and 8.8 µl dH₂O, with 2 µl DNA template. For the ITS the PCR profile was: initial denaturation for three minutes at 94°C; 30 cycles of one minute at 94°C, one minute at 55°C and one and a half minutes at 72°C; and final elongation of five minutes at 72°C. The profile for *trnL-trnF* was: initial denaturation for four minutes at 94°C; 35 cycles of 45 seconds at 94°C, 45 seconds at 55°C; and three minutes at 72°C and final elongation of 10 minutes at 72°C. In some cases the annealing temperature in the *trnL-trnF* cycle was increased from 55°C to 65°C. This reduced the background noise in chromatograms previously found difficult to interpret.

Sequencing. — The PCR products were checked on agarose gels and purified with ExoSAP-IT (Affymetrix, Santa Clara, California, U.S.A.) following the manufacturer’s protocol. The 10 µl sequencing reaction was composed of: 0.5 µl BigDye Terminator v.3.1 (Applied Biosystems, Carlsbad, California, U.S.A.), 2 µl 5× sequencing buffer, 0.32 µl primer, 0.4 µl DMSO in some ITS reactions only, 0.5 µl to 2 µl purified PCR product and dH₂O to make up the final volume. The thermal profile consisted of 25 cycles of 30 seconds at 95°C, 20 seconds at 50°C and four minutes at 60°C. The products were sequenced at the GenePool laboratory of the University of Edinburgh on an ABI 3730 DNA Analyser (Applied Biosystems). Sequences were combined and edited in Sequencher v.4.7 (Gene Code Corporation, Ann Arbor, Michigan, U.S.A.) and aligned in MUSCLE v.3.8 (Edgar, 2004) under default settings, with adjustments made by eye in Mesquite v.2.74 (Maddison & Maddison, 2009).

Molecular phylogenetic analyses. — We applied two different phylogenetic approaches, maximum parsimony (MP, i.e., Fitch, 1971) and Bayesian inference (BI) on three datasets: ITS, *trnL-trnF* and a combined dataset. The combinability of ITS and *trnL-trnF* was tested with a partition-homogeneity test run in PAUP* v.4.0b10 (Swofford, 2002). The same software was employed for the MP analysis. The first part of the heuristic search consisted of a random addition sequence with 100,000 replicates; in the second, the most parsimonious trees saved were optimised with TBR branch swapping and MulTrees enabled (Möller & al., 2009, 2011a). A bootstrap analysis with full heuristic search with 10,000 replicates, TBR on and MulTrees off was run to obtain branch support values. Additionally, Autodecay (Eriksson, 1999), with default settings, was used to obtain Bremer branch support indices.

The BI was run in MrBayes (Huelsenbeck & Ronquist, 2001, 2007) using a model of evolution determined by MrModelTest (Nylander, 2004). Partitions were created in the ITS and combined matrices in order to better represent the different sections of the DNA. Specifically, we separated the *trnL-trnF* region from the ITS and the ITS1 and ITS2 spacers from the 5.8S gene. The best-fitting evolutionary models were GTR+G (*trnL-trnF*), GTR+I+G (ITS spacers) and K80+I+G (5.8S gene). The BI analyses were run over 10 million generations, in two independent runs of four chains (Electronic Supplements 1A, 2A, 3A), sampling every 500 generations. A burn-in of 5% was established from likelihood (LnL) vs. generation plots of preliminary runs and a chain temperature of 0.15 (Electronic Supplements 1B–E, 2B–E, 3B–E) was determined after test runs. Lowering the temperature from 0.20 to 0.15 resulted in more swapping among the chains, but otherwise did not alter the outcome of the analysis with respect to trees obtained under the default setting of 0.2 (results not shown). Convergence among runs was assessed in Are We There Yet (AWTY) (Electronic Supplements 1F, 2F, 3F) (Wilgenbusch & al., 2004) and Tracer (Rambaut & Drummond, 2007). Comparative plots of the posterior probabilities of all splits showed a very high correlation between the two parallel Bayesian runs (Electronic Supplements 1G, 2G, 3G).

As an estimate of the cost of enforcing the monophyly of *Paraboea* and *Trisepalum*, separate and combined, we used the constraint option in PAUP* to determine the tree-length increases (over unconstrained trees) for *trnL-trnF*, ITS and combined datasets. The heuristic search procedures were identical to the unconstrained searches. The statistical significance of the differences between constrained and unconstrained trees was tested with the Templeton (Wilcoxon signed-ranks) (Templeton, 1983) option (TW) in PAUP* (Swofford, 2002).

RESULTS

Individual datasets. — From the 830 base pairs (bp) long ITS matrix, 44 characters were excluded due to ambiguities in their alignment. Of the 786 included 361 were constant, 105 uninformative and 320 (40.7%) informative. The 140 best trees found by the MP analysis were 1673 steps long, with a consistency index (CI) of 0.4507 and a retention index (RI) of 0.6294. With respect to the *Paraboea*, *Phylloboea* and *Trisepalum* samples, the strict consensus MP tree (Fig. S1) and BI majority-rule consensus tree (Fig. S2) show the samples of the three genera in a highly supported clade (bootstrap value, BS = 100%; decay index, DI = 11; posterior probability, PP = 1.0). The *Paraboea* samples, except *P. incudicarpa* B.L. Burt, are found in two clades, clade 1 (BS = 96%; DI = 5; PP = 1.0) and clade 2 (BS = 55%; DI = 0; PP = 0.99), with the samples of *Trisepalum*, *Phylloboea* and *Paraboea incudicarpa* in a further clade, clade 3 (BS = 100%; DI = 10; PP = 1.0). Clade 3 is sister to the *Paraboea* clade 2 (BS = 81%; DI = 3; PP = 0.99).

The *trnL-trnF* matrix was 886 bp long. We excluded the initial 65 characters, as they were not available for all samples, and kept the remaining 821. Only 97 characters (11.8%)

were found to be informative in the parsimony analysis, 611 constant and 113 variable but uninformative. The MP analysis found two most parsimonious trees with a score of 282 steps, a CI of 0.8333 and an RI of 0.8873. The strict consensus MP tree (Fig. S3) and BI majority-rule consensus tree (Fig. S4) are identical. They are less well resolved than the ITS trees. All samples of *Paraboea*, *Phylloboea* and *Trisepalum* are in one well supported clade (BS = 85%; DI = 3; PP = 1.0). Clade 2 (BS = 81%; DI = 2; PP = 1.0) and clade 3 (BS = 100%; DI = 9; PP = 1.0) contain the same taxa as in the ITS analysis, while the taxa from clade 1 in the ITS trees appear in three clades on a polytomy with clades 2 and 3.

Combined data. — The combined dataset had 417 (25.9%) informative characters over a total of 1607 included in the analyses. The partition-homogeneity test confirmed a very high congruence between the ITS and *trnL-trnF* datasets ($P = 1.0$). The ILD test is known to occasionally result in errors, including Type-II errors where the false hypothesis of congruence between two datasets is accepted (e.g., Ramirez, 2006). We thus inspected the tree topologies of individual datasets manually and did not find evidence of conflict which would preclude combination of the data.

The MP analysis resulted in two most parsimonious trees, with a score of 1958 steps (CI = 0.5051 and RI = 0.6655). The strict consensus MP tree (Fig. 1) and the BI majority-rule consensus tree (Fig. 2) are congruent, except for the position of *Orchadocarpa lilacina* Ridl., *Paraboea suffruticosa* (Ridl.) B.L. Burt and *P. vulpina* Ridl., all involving cases with low or no branch support.

The ingroup samples form three major clades. The topology within these is more resolved than found in the individual ITS and *trnL-trnF* datasets, although not always supported. *Paraboea* is paraphyletic with respect to both *Trisepalum* and *Phylloboea* and samples are found in all three clades. The first, clade 1 (BS = 97%; DI = 7; PP = 1.0), contains two groups of Chinese and Thai *Paraboea* species. Clade 2 (BS = 82%; DI = 2; PP = 1.0) includes species of *Paraboea* from Thailand, Malaysia and Borneo. All sampled species of *Trisepalum*, the monotypic genus *Phylloboea* and *Paraboea incudicarpa* are in a strongly supported clade 3 (BS = 100%; DI = 20; PP = 1.0), which is sister to clade 2 (BS = 84%; DI = 4; PP = 0.97). *Paraboea incudicarpa* is deeply nested within the *Trisepalum* clade and is sister to three *Trisepalum* samples (BS = 82%; DI = 3; PP = 0.97); these four, in turn, are sister to *Phylloboea glandulosa* (BS = 96%; DI = 6; PP = 1.0).

Cost of enforced monophyly. — The MP trees with enforced monophyly of *Paraboea*, based on ITS, *trnL-trnF* and combined data, were respectively 1.6% ($P = 0.0001$), 4.3% ($P = 0.0005$) and 2% ($P < 0.0001$) longer than unconstrained trees (Table 1). The increase for trees constrained for monophyly of *Trisepalum* was lower at 0.6% (ITS), 1.1% (*trnL-trnF*) and 0.7% (combined) and consequently less significant ($P = 0.0253$ for ITS and $P = 0.0043$ for combined data) or not significantly different from that of the unconstrained trees ($P = 0.083$ for *trnL-trnF*). Enforcing monophyly on both genera together gave similar results to constraining the genus *Paraboea* alone (Table 1).

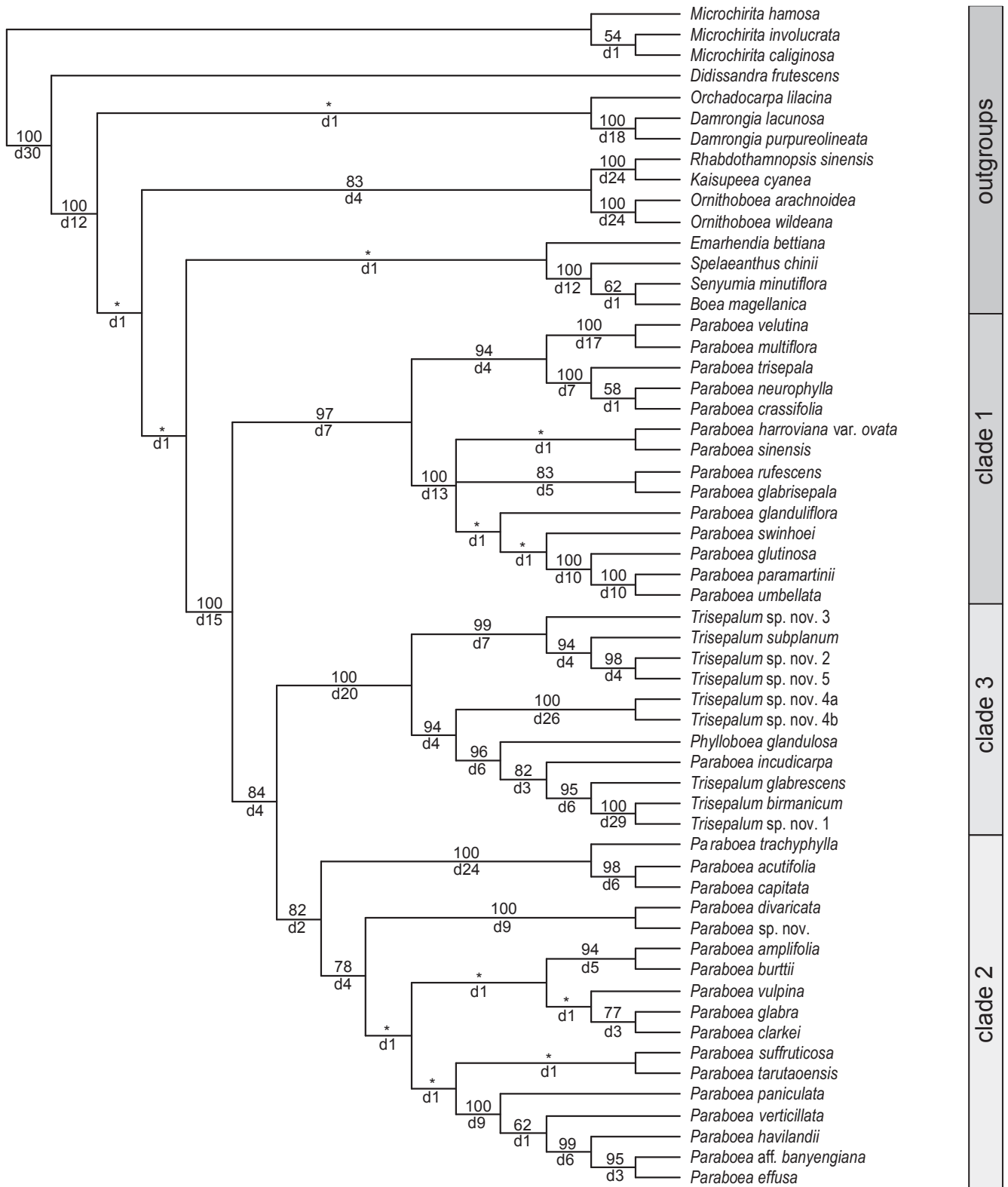


Fig. 1. Strict consensus tree of two most parsimonious trees of 1958 steps length, based on combined ITS and *trnL-trnF* sequences of 53 samples of the twisted-fruited dominated advanced Asiatic and Malesian didymocarpoid Gesneriaceae (CI = 0.5051, RI = 0.6655). Numbers above branches are bootstrap values, numbers below branches are decay indices. Asterisks indicate bootstrap values < 50%.

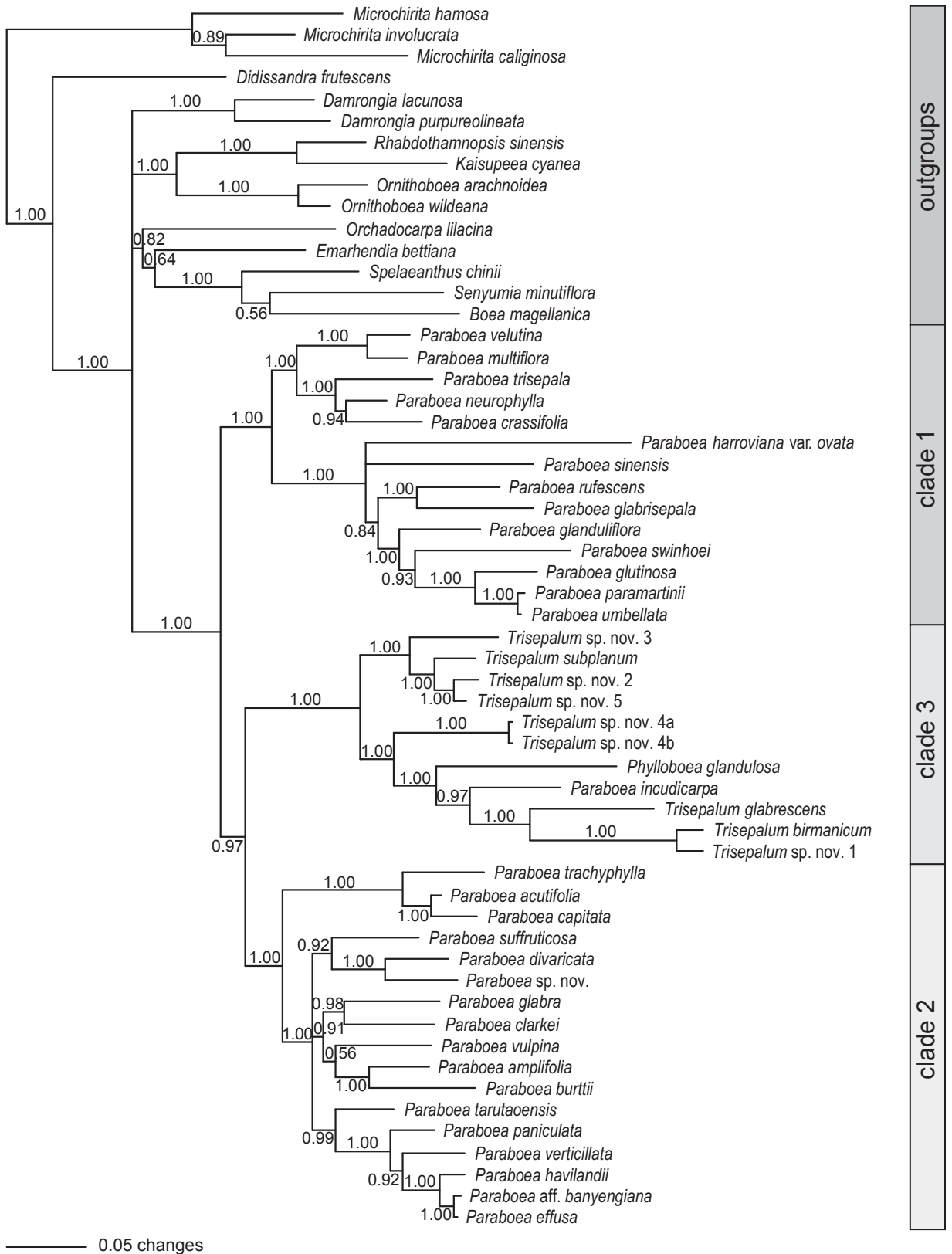


Fig. 2. Bayesian inference majority-rule consensus tree showing average branch lengths based on combined ITS and *trnL-trnF* sequences of 53 samples of the twisted-fruited dominated advanced Asiatic and Malesian didymocarpid Gesneriaceae. Numbers associated with the branches are posterior probabilities.

Table 1. The cost of enforcing monophyly for *Paraboea*, *Trisepalum* and both genera in parsimony analyses of ITS, *trnL-trnF* and combined datasets, using the Templeton (Wilcoxon signed-ranks) test (WT).

	ITS	<i>trnL-trnF</i>	Combined data
Unconstraint tree length	1673 steps	282 steps	1958 steps
Tree length with enforced monophyly of <i>Paraboea</i> (increase in steps / %)	1700 steps (+27 steps / 1.6%)	294 steps (+12 steps / 4.3%)	1997 steps (+39 steps / 2.0%)
WT-test result	$P = 0.0001^{***}$	$P = 0.0005^{***}$	$P < 0.0001^{***}$
Tree length with enforced monophyly of <i>Trisepalum</i> (increase in steps / %)	1683 steps (+10 steps / 0.6%)	285 steps (+3 steps / 1.1%)	1972 steps (+14 steps / 0.7%)
WT-test result	$P = 0.0253^*$	$P = 0.083^{ns}$	$P = 0.0043^{**}$
Tree length with enforced monophyly of both genera (increase in steps / %)	1708 steps (+35 steps / 2.1%)	297 steps (+15 steps / 5.3%)	2010 steps (+52 steps / 2.7%)
WT-test result	$P < 0.0001^{***}$	$P = 0.0013$	$P < 0.0001^{***}$

ns = not significant; * = significant difference at $P < 0.05$; ** = significant difference at $P < 0.01$; *** = significant difference at $P < 0.001$ or higher (two-tailed tests).

DISCUSSION

Phylogenetic findings. — The main result of our phylogenetic analyses is the non-monophyly of both *Paraboea* and *Trisepalum*. The critical branches, one leading to the *Paraboea/Trisepalum/Phylloboea* clade (BS = 100%; DI = 15; PP = 1.0), one tying the *Trisepalum* clade to the *Paraboea* clade 2 (BS = 84%; DI = 4; PP = 0.97) and one placing *Phylloboea* inside clade 3 (BS = 96%; DI = 6; PP = 1.00) are well supported, providing the confidence for our taxonomic conclusions. Additional support for our deductions comes from results of the enforced monophylies of the two genera *Paraboea* and *Trisepalum*. Whether they are constrained separately or together, using individual or combined data, enforcing monophyly always resulted in significantly longer trees except for the *trnL-trnF* data for *Trisepalum*. This, however, has no bearing on the overall conclusions.

Even though only about a third of all species of *Paraboea* (32 out of 91) and just under half (8 out of 19) of *Trisepalum* species described or to be described (Xu & al., 2008; Burtt, 1984) have been included in the present analyses, these species represent most of the morphological and geographical diversity observed in the genera. The type species of *Paraboea* (*P. clarkei*) and *Phylloboea* (*P. glandulosa*) were included, but we could not include any material for *Trisepalum obtusum* C.B. Clarke, the type species of *Trisepalum*, as it is currently known only from two nineteenth century specimens from Moulmein in Burma. We have, however, included *Trisepalum subplanum* B.L. Burtt, which is believed to be a close relative of *T. obtusum* (Burtt, 1984).

Morphology. — The nesting of *Trisepalum* within *Paraboea* was not necessarily to be expected given that there are morphological characters to separate the two genera. *Trisepalum* has a tripartite calyx, linguiform stigma and unequal pedicels, whereas *Paraboea* has a 5-partite calyx, a capitate stigma and \pm equal pedicels. A tripartite calyx, however, was observed in the recently described *Paraboea trisepala* W.H. Chen & Y.M. Shui (Chen & al., 2008), which is associated with the other Chinese *Paraboea* species in clade 1 (Figs. 1–2)

and not with *Trisepalum*. This suggests that trisepaly has arisen at least twice among the twisted-fruited advanced Asiatic and Malesian genera, and perhaps even more often in the Old World Gesneriaceae (Burtt, 1984). Its use as a taxonomic character, therefore, comes with some caveats. Furthermore, a nearly linguiform stigma was observed in *Paraboea dictyoneura* (Hance) B.L. Burtt, and *Trisepalum amplexicaule* (Parish ex C.B. Clarke) B.L. Burtt does not have unequal pedicels (Burtt, 1984), suggesting that the generic boundaries, at least morphologically, are blurred.

Paraboea incudicarpa was described from a fruiting specimen collected in Thailand (Burtt, 1984). It was ascribed to *Paraboea* because of its indumentum, but Xu & al., (2008) pointed out that the morphological characters known, particularly the capsule, would suggest a greater affinity with the genus *Hemiboea* C.B. Clarke than with *Paraboea*. Flowering material was collected only recently and the flowers resemble those of *Trisepalum* and *Phylloboea* rather than those of *Hemiboea*. Also, the dense inflorescence of *Paraboea incudicarpa* is comparable with *Phylloboea*. This study confirms the placement of this species within the *Trisepalum/Phylloboea* clade.

Apart from this rather distinct group with linguiform stigmas, it is difficult to define the expanded *Paraboea* clade and to separate clade 1 from clade 2 on macro-morphological characters. Our sampling indicates a strong geographical division between the two *Paraboea* clades, with all species included in clade 1 being from China and northern Thailand (except for the widespread *P. swinhoi* (Hance) B.L. Burtt and *P. harroviana* (Craib) Z.R. Xu var. *ovata* Z.R. Xu from the northern part of Peninsular Thailand) and all those in clade 2 from southern Thailand and Malaysia. Clade 3, which includes the *Trisepalum* species, *Phylloboea glandulosa* and *Paraboea incudicarpa*, spans this distribution from southern China to Peninsular Malaysia.

Further studies, including micro-morphological characters, might eventually provide more robust support for an infrageneric classification of *Paraboea*, but it is quite clear that *Trisepalum* and *Phylloboea* should not be recognised as distinct from *Paraboea*.

■ CONCLUSIONS

The present study defines the phylogenetic relationships among the genera *Paraboea* (C.B. Clarke) Ridl., *Trisepalum* C.B. Clarke and *Phylloboea* Benth. Together these genera form a monophyletic clade, with *Phylloboea* nested in *Trisepalum* and *Trisepalum* in turn deeply nested in *Paraboea*. Previous taxonomic treatments of *Paraboea* and *Trisepalum* have always highlighted the high degree of morphological similarity between the two genera, although a few distinguishing features (calyx and stigma) have always prevented authors from merging them into a single genus.

Phylloboea has received much less attention with most of its species having been progressively moved into *Paraboea* or *Trisepalum* and the delimitation of which has been difficult for some time (Burt, 1960). Taxonomists debate the relative merits of recognising monophyletic and paraphyletic taxa with an increasing presumption that monophyletic genera are preferable. In our case this would mean that *Paraboea*, *Trisepalum* and *Phylloboea* should be recognised as a single genus as otherwise *Paraboea* would be paraphyletic with respect to *Trisepalum* and *Phylloboea*. This accords well with the morphological similarities and even if one were to be relaxed about paraphyletic genera there has been ambivalence amongst classical taxonomists as to their distinction on morphological grounds (e.g., Burt, 1984; Xu & al., 2008). We can be confident these results would be found even with greater sampling as taxa with the range of morphological variation present in all three genera have been sampled. The phylogeny presented here will certainly provide a valuable framework for future biogeographic and comparative studies in Gesneriaceae.

The earliest published name at the rank of genus is *Phylloboea* but *Paraboea* has been conserved against both *Phylloboea* and *Trisepalum* (Middleton & al., 2010; Brummitt, 2011).

The new combinations are reported below.

■ TAXONOMIC IMPLICATIONS

- Paraboea* (C.B. Clarke) Ridl. in J. Straits Branch Roy. Asiat. Soc. 44: 63. 1905 – Type: *Paraboea clarkei* B.L. Burt (designated by Burt in Kew Bull. 3: 56. 1948).
- = *Phylloboea* Benth. in Bentham & Hooker, Gen. Pl. 2(2): 1020. 1876 – Type: *Phylloboea glandulosa* B.L. Burt (see Burt, 1960).
- = *Trisepalum* C.B. Clarke in Candolle & Candolle, Monogr. Phan. 5(1): 138. 1883 – Type: *Trisepalum obtusum* C.B. Clarke.
- = *Didymocarpus* sect. *Paraboea* C.B. Clarke in Candolle & Candolle, Monogr. Phan. 5(1): 71. 1883 – Type: *Didymocarpus Paraboea* C.B. Clarke.
- = *Roettlera* sect. *Paraboea* (C.B. Clarke) Fritsch in Engler & Prantl, Nat. Pflanzenfam. 4(3B): 150. 1894 – Type: *Roettlera paraboea* (C.B. Clarke) Kuntze
- = *Boea* sect. *Caulescentes* Fritsch in Engler & Prantl, Nat. Pflanzenfam. 4(3B): 150. 1894 – Lectotype: *Boea multiflora* R. Br. (designated by Burt in Notes Roy. Bot. Gard. Edinburgh 21: 194. 1954).

- = *Paraboea* sect. *Breviflores* Ridl. in J. Straits Branch Roy. Asiat. Soc. 44: 64. 1905 – Lectotype: *Paraboea capitata* Ridl. (designated by Burt in Notes Roy. Bot. Gard. Edinburgh 41: 422. 1984).
- = *Chlamydoboea* Stapf in Bull. Misc. Inform. Kew 1913: 354. 1913 – Type: *Chlamydoboea sinensis* (Oliv.) Stapf.
- = *Buxiphyllum* W.T. Wang & C.Z. Gao in Bull. Bot. Res., Harbin 1: 36. 1981 – Type: *Buxiphyllum velutinum* W.T. Wang & C.Z. Gao.

Paraboea acaulis (Barnett) C. Puglisi, **comb. nov.** ≡ *Dichiloboea acaulis* Barnett in Nat. Hist. Bull. Siam Soc. 20: 22. 1961 ≡ *Trisepalum acaule* (Barnett) B.L. Burt in Notes Roy. Bot. Gard. Edinburgh 41: 443. 1984 – Type: *Smitinand 4688*, Thailand, Chiang Mai, Doi Chiang Dao, 1100 m (lectotype E, designated by Barnett in Kew Bull. 15: 258. 1961).

Paraboea acuta (C.B. Clarke) C. Puglisi, **comb. nov.** ≡ *Trisepalum acutum* C.B. Clarke in Candolle & Candolle, Monogr. Phan. 5(1): 138. 1883 – Type: *Parish 435*, Burma, Moulmein, mouth of Pagut caves, limestone rocks, 1861 (lectotype K, designated by Burt in Notes Roy. Bot. Gard. Edinburgh 41: 443. 1984).

Paraboea albida (Barnett) C. Puglisi, **comb. nov.** ≡ *Dichiloboea albida* Barnett in Nat. Hist. Bull. Siam Soc. 20: 21. 1961 ≡ *Trisepalum albidum* (Barnett) B.L. Burt, Notes Roy. Bot. Gard. Edinburgh 41: 445. 1984 – Type: *Nai Noe 120*, Thailand, Saraburi, Khao Pang Sawang, Muak Lek (lectotype K, designated by Barnett in Kew Bull. 15: 257. 1961; isolectotypes ABD, BK, BKF).

Paraboea amplexicaulis (Parish ex C.B. Clarke) C. Puglisi, **comb. nov.** ≡ *Boea amplexicaulis* Parish ex C.B. Clarke, Commelyn. Cyrtandr. Bengal: t. 84. 1874 ≡ *Phylloboea amplexicaulis* (Parish ex C.B. Clarke) C.B. Clarke in Candolle & Candolle, Monogr. Phan. 5(1): 140. 1883 ≡ *Trisepalum amplexicaule* (Parish ex C.B. Clarke) B.L. Burt, Notes Roy. Bot. Gard. Edinburgh 41(3): 445. 1984 – Type: *Kurz 2998*, Burma, Pegu, Kambala Toung [ca. 18°30'N 96°E], 2nd highest point, ca. 960 m (lectotype CAL, designated by Burt in Notes Roy. Bot. Gard. Edinburgh 21: 207. 1954; photo E).

Paraboea barnettiae C. Puglisi, **nom. nov.** ≡ *Phylloboea speciosa* Ridl. in J. Linn. Soc., Bot. 32: 522. 1895 ≡ *Dichiloboea speciosa* (Ridl.) Stapf in Bull. Misc. Inform. Kew 1913: 356. 1913 ≡ *Trisepalum speciosum* (Ridl.) B.L. Burt in Notes Roy. Bot. Gard. Edinburgh 41: 445. 1984 – Type: *Curtis 2564*, Peninsular Malaysia, Kedah, Langkawi (lectotype SING, designated by Burt in Notes Roy. Bot. Gard. Edinburgh 41: 44. 1984).

Paraboea birmanica (Craib) C. Puglisi, **comb. nov.** ≡ *Boea birmanica* Craib in Bull. Misc. Inform. Kew 1913: 114. 1913 ≡ *Dichiloboea birmanica* (Craib) Stapf in Bull. Misc.

Inform. Kew 1913: 357. 1913 ≡ *Trisepalum birmanicum* (Craib) B.L. Burtt in Notes Roy. Bot. Gard. Edinburgh 41: 446. 1984 – Type: *Lace 5882*, Upper Burma, Maymyo, on bare hill near Pwedawng, ca. 1050 m (lectotype E, 1st step designated by Burtt in Notes Roy. Bot. Gard. Edinburgh 41: 446. 1984, 2nd step designated here; isolectotype K).

Paraboea glabrescens (Barnett) C. Puglisi, **comb. nov.** ≡ *Dichiloboea glabrescens* Barnett in Nat. Hist. Bull. Siam Soc. 20: 23. 1961 ≡ *Trisepalum glabrescens* (Barnett) B.L. Burtt in Notes Roy. Bot. Gard. Edinburgh 41(3): 444. 1984 – Type: *Put 175*, Thailand, Rachaburi, Baw Re (lectotype K, designated by Barnett in Kew Bull. 15: 259. 1961; isolectotypes ABD, BK, BKF).

Paraboea glandulifera (Barnett) C. Puglisi, **comb. nov.** ≡ *Dichiloboea glandulifera* Barnett in Nat. Hist. Bull. Siam Soc. 20: 23. 1961 ≡ *Trisepalum glanduliferum* (Barnett) B.L. Burtt in Notes Roy. Bot. Gard. Edinburgh 41(3): 448. 1984 – Type: *Kerr 6102*, Thailand, Tak, Umphang, Me Lamung, ca. 800 m (lectotype K, designated by Barnett in Kew Bull. 15: 258. 1961; isolectotypes ABD, BK, BKF).

Paraboea glandulosa (B.L. Burtt) C. Puglisi, **comb. nov.** ≡ *Phylloboea glandulosa* B.L. Burtt in Notes Roy. Bot. Gard. Edinburgh 23: 90. 1960 – Type: *Parish 445*, Burma, Moulmein (holotype K).

Paraboea longipetiolata (B.L. Burtt) C. Puglisi, **comb. nov.** ≡ *Trisepalum longipetiolatum* B.L. Burtt in Notes Roy. Bot. Gard. Edinburgh 41: 447. 1984 – Type: *Kostermans Khwae Noi River Basin Exped. 1380*, Thailand, Kanchanaburi, Rintin near Kin Sayok, ca. 140 km NW of Kanchanaburi, 100–150 m (holotype L).

Paraboea obtusa (C.B. Clarke) C. Puglisi, **comb. nov.** ≡ *Trisepalum obtusum* C.B. Clarke in Candolle & Candolle, Monogr. Phan. 5(1): 138. 1883; C.B. Clarke in Hook. f. Fl. Brit. Ind. 4: 363. 1884 – Type: *Lobb 368*, Burma, Moulmein (lectotype K, designated by Burtt in Notes Roy. Bot. Gard. Edinburgh 41: 443. 1984).

Paraboea prazeri (B.L. Burtt) C. Puglisi, **comb. nov.** ≡ *Trisepalum prazeri* B.L. Burtt in Notes Roy. Bot. Gard. Edinburgh 41: 447. 1984 – Type: *Prazer 93*, Burma, Kalai Hills adjoining N & S Chin Hills (holotype E; isotypes CAL, K).

Paraboea robusta (B.L. Burtt) C. Puglisi, **comb. nov.** ≡ *Trisepalum robustum* B.L. Burtt in Notes Roy. Bot. Gard. Edinburgh 41: 443. 1984 – Type: *Smitinand & Sleumer 1021*, Thailand, Chiang Mai, Doi Chiang Dao, Pine ridge, 1800 m (holotype E; isotype L).

Paraboea strobilacea (Barnett) C. Puglisi, **comb. nov.** ≡ *Dichiloboea strobilacea* Barnett in Nat. Hist. Bull. Siam Soc. 20: 25. 1961 ≡ *Trisepalum strobilaceum* (Barnett)

B.L. Burtt in Notes Roy. Bot. Gard. Edinburgh 41(3): 445. 1984 – Type: *Put 172*, Thailand, Kanchanaburi, Baw Re (lectotype K, designated by Barnett in Kew Bull. 15: 259. 1962; isolectotypes ABD, BK).

Paraboea subplana (B.L. Burtt) C. Puglisi, **comb. nov.** ≡ *Trisepalum subplanum* B.L. Burtt in Notes Roy. Bot. Gard. Edinburgh 41: 443. 1984 – Type: *Hansen & Smitinand 12027*, Thailand, Krabi, Khao Thong Lang, NW of Nai Chong (holotype C; isotypes BKF, K, L).

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Appendix. Taxa and vouchers for species sampled. Species, collector and number of collection (herbarium), country, GenBank accession numbers for *trnL-trnF*, ITS (resp.).

Boea magellanica Lam., *Lambinon* 87/830 (L), Papua New Guinea, Morobe, FJ501478, FJ501321; *Damrongia lacunosa* (Hook.f.) D.J. Middleton & A. Weber, *Weber* 870510-1/8 (WU), Malaysia, Pahang, FJ501458, FJ501308; *Damrongia purpureolineata* Kerr ex Craib, *Middleton & al.* 4812 (E), Thailand, Lamphun, JF912535, JF912562; *Dididssandra frutescens* C.B. Clarke, *Weber* 840805-1/2 (WU), Malaysia, Perak, FJ501522, JN934793; *Emarhendia bettiana* (M.R. Hend.) Kiew, *A. Weber & B.L. Burt*, *Kiew & al.* FRI 55716 (KEP), Malaysia, Pahang HQ632864, HQ632955; *Kaisupeea cyanea* B.L. Burt, *Larsen* 44272 [Cult. RBGE 19972918] (E), Thailand, Chachoengsao, FJ501459, FJ501309; *Microchirita caliginosa* (C.B. Clarke) Y.Z. Wang, ex *HB München-Nymphenburg-Kiehn & Pfosser* 2000-1 [Cult. HBV GS-96-02] (WU), Malaysia, state unknown, FJ501488, FJ501325; *Microchirita hamosa* (R. Br.) Y.Z. Wang, *Möller* MMO 05-753 (E), China, province unknown, JF912524, JF912551; *Microchirita involucreta* (Craib) Y.Z. Wang, *Rafidah* FRI 64447 (KEP), Malaysia, state

Appendix. Continued.

unknown, JF912525, JF912552; *Orchadocarpa lilacina* Ridl., *Kiew RK 5410* (KEP), Malaysia, Pahang, HQ632863, HQ632954; *Ornithoboea arachnoidea* Craib, *Middleton & al. 4538* (E), Thailand, Chiang Mai, JN934709, JN934751; *Ornithoboea wildeana* Craib, *Middleton & al. 4531* (E), Thailand, Chiang Mai, JN934710, JN934752; *Paraboea acutifolia* (Ridl.) B.L. Burtt, *Middleton & al. 4427* (E), Thailand, Trang, JN934711, JN934753; *Paraboea amplifolia* Z.R. Xu & B.L. Burtt, *Triboun s.n.* (EDNA 09-02281), Thailand, Trang, JN934712, JN934754; *Paraboea* aff. *banyengiana* B.L. Burtt, *Puglisi 28* (E), Malaysia, Sarawak, JN934713, JN934755; *Paraboea burttii* Z.R. Xu, *Middleton & al. 4425* (E), Thailand, Trang, JN934714, JN934756; *Paraboea capitata* Ridl., *Weber 870522-5/2* [Cult. HBV] (WU), Malaysia, Perak, AJ492298, FJ501315; *Paraboea clarkei* B.L. Burtt, *Puglisi 10* (E), Malaysia, Sarawak, JN934715, JN934757; *Paraboea crassifolia* (Hemsley) B.L. Burtt, *Möller MMO 01-83/2* (E), China, Yunnan, JN934716, JN934758; *Paraboea divaricata* (Ridl.) B.L. Burtt, *Middleton & al. 4437* (E), Thailand, Satun, JN934717, JN934759; *Paraboea effusa* B.L. Burtt, *Puglisi 32* (E), Malaysia, Sarawak, JN934718, JN934760; *Paraboea glabra* (Ridl.) B.L. Burtt, *Triboun s.n.* (EDNA 09-01765), Thailand, province unknown, JN934719, JN934761; *Paraboea glabripala* B.L. Burtt, *Middleton & al. 4533* (E), Thailand, Chiang Mai, JN934720, JN934762; *Paraboea glanduliflora* Barnett, *Middleton & al. 4545* (E), Thailand, Chiang Rai, JN934721, JN934763; *Paraboea glutinosa* (Hand.-Mazz.) K.Y. Pan, *Möller MMO 06-786a* (E), China, Guangxi, JN934722, JN934764; *Paraboea harroviana* (Craib) Z.R. Xu var. *ovata* Z.R. Xu, *Middleton & al. 4273* (E), Thailand, Prachuap Khiri Khan, JN934723, JN934765; *Paraboea havilandii* (Ridl.) B.L. Burtt, *Puglisi 18* (E), Malaysia, Sarawak, JN934724, JN934766; *Paraboea incudicarpa* B.L. Burtt, *Middleton & Triboun 4857* (E), Thailand, Tak, JN934725, JN934767; *Paraboea multiflora* (R. Br.) B.L. Burtt, *Wen 2010-01*, China, province unknown, JN934726, JN934768; *Paraboea neurophylla* (Collett & Hemsley) B.L. Burtt, *Middleton & al. 4557* (E), Thailand, Chiang Rai, JN934727, JN934769; *Paraboea paniculata* (Ridl.) B.L. Burtt, *FRIM staff FRI 65535* (KEP), Malaysia, state unknown, JN934728, JN934770; *Paraboea paramartinii* Z.R. Xu & B.L. Burtt, *Möller MMO 06-852b* (E), China, Guangxi, JN934729, JN934771; *Paraboea rufescens* (Franchet) B.L. Burtt, *Möller MMO 01-108/3* (E), China, Yunnan, JN934730, JN934772; *Paraboea sinensis* (Oliver) B.L. Burtt, *Möller MMO 06-949b* (E), China, Yunnan, JN934731, JN934773; *Paraboea suffruticosa* (Ridl.) B.L. Burtt, *Middleton & al. 4432* (E), Thailand, Satun, JN934732, JN934774; *Paraboea swinhoi* (Hance) B.L. Burtt, *Möller MMO 06-783c* (E), China, Guangxi, JN934733, JN934775; *Paraboea tarataoensis* Z.R. Xu & B.L. Burtt, *Middleton* [Cult RBGE 20082069] (E), Thailand, Satun, JN934734, JN934776; *Paraboea trachyphylla* Z.R. Xu & B.L. Burtt, *Middleton & al. 4310* (E), Thailand, Surat Thani, JN934735, JN934777; *Paraboea trisekala* W.H. Chen & Y.M. Shui, *Shui & al. CH153*, China, province unknown, JN934736, JN934778; *Paraboea umbellata* (Drake) B.L. Burtt, *Möller MMO 01-147/2* (E), China, Guangxi, JN934737, JN934779; *Paraboea velutina* (W.T. Wang & C.Z. Gao) B.L. Burtt, *Möller MMO 07-1105a* (E), China, Guangxi, JN934738, JN934780; *Paraboea verticillata* (Ridl.) B.L. Burtt, *Kiew & al. FRI 48225*, Malaysia, Selangor, JN934733, JN934781; *Paraboea vulpina* Ridl., *Middleton & al. 4442* (E), Thailand, Krabi, JN934740, JN934782; *Paraboea* sp. nov., *Triboun s.n.* (EDNA09-02285), Thailand, Krabi, JN934741, JN934783; *Phylloboea glandulosa* B.L. Burtt, *Middleton & Triboun 5202* (E), Thailand, Kanchanaburi, JN934742, JN934784; *Rhabdothamnopsis sinensis* Hemsli., Voucher from Cult. Kew 1988 4866 (K), China, province unknown, AJ492302, JN934794; *Senyumia minutiflora* (Ridl.) Kiew, A. Weber & B.L. Burtt, *Rafidah & al. FRI 55722* (KEP), Malaysia, Pahang, HQ632865, HQ632957; *Spelaeanthus chinii* Kiew, A. Weber & B.L. Burtt, *Weber 860709-2/2* (WU), Malaysia, Pahang, FJ501457, FJ501307; *Trisepalum birmanicum* (Craib) B.L. Burtt, *Möller MMO 06-862b* (E), China, Guangxi, HQ632866, HQ632958; *Trisepalum glabrescens* (Barnett) B.L. Burtt, *Middleton & Triboun 5203* (E), Thailand, Kanchanaburi, JN934743, JN934785; *Trisepalum subplanum* B.L. 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