

Phylogenetic affinities of *Polyalthia* species (Annonaceae) with columellar-sulcate pollen: Enlarging the Madagascan endemic genus *Fenerivia*

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Abstract The genus *Polyalthia* (Annonaceae) has been demonstrated to be polyphyletic, with the Asian species with columellar-sulcate pollen recently segregated to form a new genus, *Maasia*. The phylogenetic affinities of the other *Polyalthia* species with columellar-sulcate pollen, which occur in Madagascar, are investigated using maximum parsimony, maximum likelihood and Bayesian phylogenetic analyses of three chloroplast DNA markers (*trnL-F*, *matK*, *rbcL*). The species are shown to form a well-supported clade which warrants taxonomic recognition as a distinct genus. The name *Fenerivia* is adopted, considerably expanding the application of this formerly monotypic name, with nine new nomenclatural combinations validated. The genus is hypothesised to have undergone a homeotic mutation in which the outermost whorl of stamens develop as inner petals (presumed andropetals), and the calyx is reduced to a vestigial flange.

Keywords Annonaceae; *Fenerivia*; homeosis; *Maasia*; Madagascar; Malagasy; molecular phylogenetics; *Polyalthia*

Supplementary material The alignment is available in the Supplementary Data section of the online version of this article (<http://www.ingentaconnect.com/content/iapt/tax>).

■ INTRODUCTION

The genus *Polyalthia* Blume (Annonaceae) was first established by Blume (1830) following the transfer of species names from *Unona* L. f. and *Guatteria* Ruiz & Pav. Although only five species were initially recognised in the genus, over 300 species names have subsequently been published within the genus (International Plant Names Index, IPNI: <http://www.ipni.org/>), of which approximately 150 names are currently accepted (Global Index of Annonaceae Names: <http://herbarium.botanik.univie.ac.at/annonaceae/listTax.php>). *Polyalthia* is therefore currently one of the largest genera in Annonaceae.

Polyalthia has been described as a “default genus which is defined only by the absence of conspicuous synapomorphies” (Johnson & Murray, 1999), and this has resulted in it effectively becoming a “dustbin” genus for many Palaeotropical Annonaceae taxa of uncertain affinities. The inevitable morphological heterogeneity resulting from this prompted several authors to suggest that the genus is likely to be paraphyletic or polyphyletic (Rogstad & Le Thomas, 1989; Van Setten & Koek-Noorman, 1992; Doyle & Le Thomas, 1994, 1996; Doyle & al., 2000). The polyphyletic status of the genus has since been confirmed by Mols & al. (2004a, b), who used combined *matK*, *rbcL*, and *trnL-F* sequence data to show that *Polyalthia* species occur in at least five distinct clades. These clades furthermore included (or were ambiguously related to) species belonging to several smaller genera (*Enicosanthum* Becc., *Haplostichanthus* F. Muell., *Marsypopetalum* Scheff.), implying that these genera also need to be incorporated in taxonomic reassessments of *Polyalthia*. The unresolved phylogenetic status of the genus

Polyalthia is arguably the most significant current impediment to Annonaceae systematics research.

Hooker & Thomson (1872) recognised 25 species of *Polyalthia*, which they classified in three sections, sect. *Polyalthia* (as “*Eupolyalthia*”), sect. *Monoon* (Miq.) Hook. f. & Thomson, and sect. *Trivalvaria* (Miq.) Hook. f. & Thomson. The latter two sectional names were based on genera established by Miquel (1865). Another section, sect. *Afropolyalthia* Engl. & Diels, was subsequently added to the genus by Engler & Diels (1901) for two African species. The taxonomic scope of *Polyalthia* was later reduced following: (1) the reinstatement of *Trivalvaria* (Miq.) Miq. as a distinct genus (Sinclair, 1951; see also subsequent revision by Van Heusden, 1996); (2) the separation of *Polyalthia* sect. *Afropolyalthia* as the distinct genus *Greenwayodendron* Verdc. (Verdcourt, 1969); (3) the transfer of several *Polyalthia* species characterized by pollen octads to *Disepalum* Hook. f. (Sinclair, 1955) and *Enicosanthellum* Bân (Bân, 1975; species subsequently transferred to *Disepalum* by Johnson, 1989); (4) the removal of the Southeast Asian “*Polyalthia hypoleuca* complex” (sensu Rogstad, 1989, 1990, 1994; Rogstad & Le Thomas, 1989) as the new genus *Maasia* Mols & al. (Mols & al., 2008); and (5) the recent transfer of several *Polyalthia* species to *Marsypopetalum* (Xue & al., 2011).

Although *Polyalthia* is poorly represented in continental Africa, the genus appears to be considerably more diverse in Madagascar. Schatz & Le Thomas (1990) recognized 18 *Polyalthia* species in Madagascar, which they classified into five informal groups (referred to as groups A–E). Species in groups B and C are characterized by sulcate pollen with a columellar exine (Schatz & Le Thomas, 1990), typical of the “malmeoid”

clade (Doyle & Le Thomas, 1996). In contrast, species in groups A, D, and E are characterized by inaperturate pollen with a non-columellar exine (Schatz & Le Thomas, 1990), typical of many members of the “miliusoid” clade (Doyle & Le Thomas, 1996). It is noteworthy, however, that some of the miliusoid taxa previously regarded as inaperturate, including *Tri-valvaria* (Walker, 1971) and *Marsypopetalum* s.l. (Mols & al., 2004a), are now known to be disulculate (Xue & al., 2011), and that such pollen may be widespread within the miliusoid clade (Waha & Hesse, 1988; Waha & Morawetz, 1988; Chaowasku & al., 2008). The contrasting pollen characteristics of the different Madagascan representatives of *Polyalthia* suggest that they are unlikely to be congeneric and that those in groups B and C may share a closer phylogenetic affinity with *Maasia*, which comprises species formerly included in the *Polyalthia hypoleuca* complex (Mols & al., 2008). The present research clarifies the phylogenetic and taxonomic relationships between *Maasia* and the Madagascan *Polyalthia* species with columellar-sulcate pollen, and is based on extensive sampling of species from group B (*P. angustieliptica* Schatz & Le Thomas, *P. chapelieri* Baill., *P. emarginata* Diels, *P. madagascariensis* Cavaco & Keraudren) and group C (*P. capuronii* Cavaco & Keraudren, *P. ghesquiereana* Cavaco & Keraudren, *P. heteropetala* (Diels) Gesq., *P. humbertii* Cavaco & Keraudren, *P. oligosperma* (Danguy) Diels, *P. richardiana* Baill.).

Polyalthia heteropetala, a member of group C, was originally described as the sole representative of the genus *Fenerivia* Diels (Diels, 1925). This taxonomically isolated position was proposed because of the aberrant floral morphology evident in the only known flowering specimen: unlike the flowers of the great majority of Annonaceae species, which have a perianth of nine organs in three whorls (three sepals, three outer petals, three inner petals), *Polyalthia (Fenerivia) heteropetala* has a perianth of 12 organs. The homology of the latter organs has been the source of some discussion (Diels, 1925; Ghesquière, 1939; Schatz & Le Thomas, 1990; Derooin, 2007), but was interpreted by Saunders (2010) to be the result of a disruption to the homeotic control of organ identity during floral development. Molecular phylogenetic data is used in the present research to reassess putative homologies in the floral structure of *P. heteropetala* and related species with columellar-sulcate pollen.

■ MATERIALS AND METHODS

Taxon sampling. — The data matrix comprised a total of 123 species of Annonaceae representing all major clades in the family. The dataset was based on three chloroplast DNA regions: *trnL-F*, *matK*, and *rbcL*. Novel sequences were generated for the additional species from Madagascar, including all Madagascan species of *Polyalthia* belonging to groups B and C (sensu Schatz & Le Thomas, 1990), together with additional *Maasia* species. The samples, localities, and GenBank accession numbers are given in the Appendix.

DNA extraction, amplification, and sequencing. — Total genomic DNA was extracted from herbarium leaf samples using a modified cetyl trimethyl ammonium bromide (CTAB)

method (Doyle & Doyle, 1987; Erkens & al., 2008; Su & al., 2008), with DNA purified using the Wizard PCR Preps DNA Purification System (Promega, Madison, Wisconsin, U.S.A.), and eluted with 50 µl preheated TE (Tris-EDTA) buffer.

The following primers were used for amplification: *trnL-F* (*trnL* intron and *trnL-trnF* intergenic spacer)—primers *trnLF-12F/433R*, *trnLF-147F/508R*, *trnLF-413F/724R*, and *trnLF-597F/960R* (Su & al., 2008); *matK* gene—primers *matK-13F/515R*, *matK-424F/788R*, and *matK-449F/824R* (Su & al., 2008); and *rbcL* gene—primers *rbcL-7F/429R*, *rbcL-127F/734R*, *rbcL-656F/1100R*, and *rbcL-984F/1381R* (Su & al., 2008).

All PCR reactions were performed in a total volume of 50 µl using 1× PCR buffer, ca. 10 ng DNA, 3 mM MgCl₂, 0.2 mM dNTP, 0.3 µM of each primer, 2 U Taq DNA polymerase (Promega), and 0.5 µg/µl BSA (Promega). The PCR conditions consisted of 3 min at 94°C, followed by 35 cycles of 45 s at 94°C denaturation; 30 s at 49°C annealing for *trnL-F*, 52°C–55°C annealing for *matK* and *rbcL*; and 2 min extension at 72°C; and an additional final extension of 7 min at 74°C. Successfully amplified products were purified with the QIAquick PCR purification kit (Qiagen, Valencia, California, U.S.A.) following the manufacturer’s instructions.

Sequencing reactions were carried out for both forward and reverse strands using the same PCR primers, and the BigDye Terminator v.3.1 cycle sequencing kit (Applied Biosystems, Foster City, California, U.S.A.). Purified sequencing reactions were run commercially on an Applied Biosystems 3730XL DNA Analyzer.

Phylogenetic analyses. — Sequences were edited and assembled in SeqMan Pro using DNASTar Lasergene 8.0 (DNASTar, Madison, Wisconsin, U.S.A.), and aligned manually using BioEdit v.7.0.9 (Hall, 1999) and Se-AL v.2.0a11 (Rambaut, 1996). The combined three-region dataset consisted of 3186 aligned characters (*trnL-F*: 1054 bp; *matK*: 789 bp; *rbcL*: 1343 bp) following the removal of 65 bp ambiguously aligned positions in *trnL-F*.

Maximum parsimony (MP) analyses of the three combined datasets were conducted using PAUP* v.4.0b10 (Swofford, 2003). All characters were weighted equally and indels were treated as missing data. The most parsimonious trees were obtained with heuristic searches of 1000 replicates of random-addition-sequence, tree bisection-reconnection (TBR) branch swapping, and saving 10 trees from each random sequence addition. Bootstrap support (BS) values for the nodes were estimated using 1000 random-addition-sequence replicates with TBR branch swapping, and 10 trees saved per replicate.

Maximum likelihood (ML) analyses were conducted for the three-gene dataset using GARLI v.0.95 that implements a full heuristic tree search (Zwickl, 2006). The best-fitting nucleotide substitution model was determined by the Akaike Information Criterion (AIC) using the MrModelTest v.2.3 (Nylander, 2004). The analyses were performed using a random starting tree and the ML bootstrap (BS) values were estimated from 200 bootstrap replicates in GARLI.

Partitioned Bayesian analyses were performed on the three-gene combined dataset using MrBayes v.3.1.2 (Ronquist

& Huelsenbeck, 2003). Separate models of molecular evolution for individual gene partitions were determined by Mr-ModelTest v.2.3 (Nylander, 2004). Four Metropolis-coupled Markov Chain Monte Carlo (MCMC) runs, each with five heated chains and one cold chain, were run for 5 million generations with trees sampled every 100 generations. The final average standard deviation of the split frequencies was <0.01, indicating that the sampling of the posterior distribution was adequate. The convergence of the MCMC runs was also compared and checked using the online program AWTY (Nylander & al., 2008). The output AWTY plot displaying the posterior probabilities of splits between runs was linear, indicating that the runs had reached convergence. Effective sampling size (ESS) and burn-in were estimated using Tracer v.1.5 (Rambaut & Drummond, 2009); all parameters had ESS values above 200 and the first 10% of the sampled trees was discarded. The remaining trees were used to generate a 50% majority-rule consensus tree and calculate the posterior probabilities (PP). A more distant outgroup, *Anaxagorea silvatica*, was used to root the tree.

■ RESULTS

Of the 3186 included characters, 376 bp (11.8%) were variable but parsimony-uninformative and 438 (13.7%) were parsimony-informative. Parsimony analysis of the combined regions yielded 2310 most parsimonious trees of 1463 steps (consistency index, CI = 0.645; retention index, RI = 0.784; rescaled retention index, RC = 0.506). For the combined ML analyses, GTR+I+G was selected as the best-fitting model. Model parameter values were estimated as follows: base frequencies: A = 0.2885, C = 0.1946, G = 0.2125, T = 0.3043; rate matrix: A–C = 1.3785, A–G = 2.8460, A–T = 0.6622, C–G = 0.8091, C–T = 3.4410, G–T = 1.0; proportion of invariable sites (I) = 0.4708; and gamma shape parameter = 0.9649. The likelihood score of the optimal ML tree, $-\ln L$, was 14,622.2148. For the mixed-model Bayesian analyses, the best-fit model of sequence evolution for each gene partition was selected by AIC, as follows: GTR+G for *trnL-F* and *matK*, and GTR+I+G for *rbcL* data.

Parsimony, maximum likelihood, and Bayesian analyses of the combined cpDNA regions consistently recognized four *Polyalthia* clades (clades I–IV in Figs 1–2). Clade IV includes 10 *Polyalthia* species (viz.: *P. chapelieri*, *P. heteropetala*, *P. madagascariensis*, *P. angustil elliptica*, *P. oligosperma*, *P. richardiana*, *P. humbertii*, *P. ghesquiereana*, *P. emarginata*, *P. capuronii*). This clade received very strong statistical support (MP BS = 100%, ML BS = 100%, PP = 1.00; Fig. 1). *Maasia* is furthermore shown to form a well-supported clade (MP BS = 97%, ML BS = 97%, PP = 1.00). Clade IV shows a relatively rapid average rate of molecular evolution (Fig. 2), with 0.1533 substitutions per site; this is approximately 6 times faster than that of clade I (0.024 substitutions per site) and 2.5 times faster than clade II (0.060 substitutions per site), but is similar to that of clade III (0.1383 substitutions per site).

■ DISCUSSION

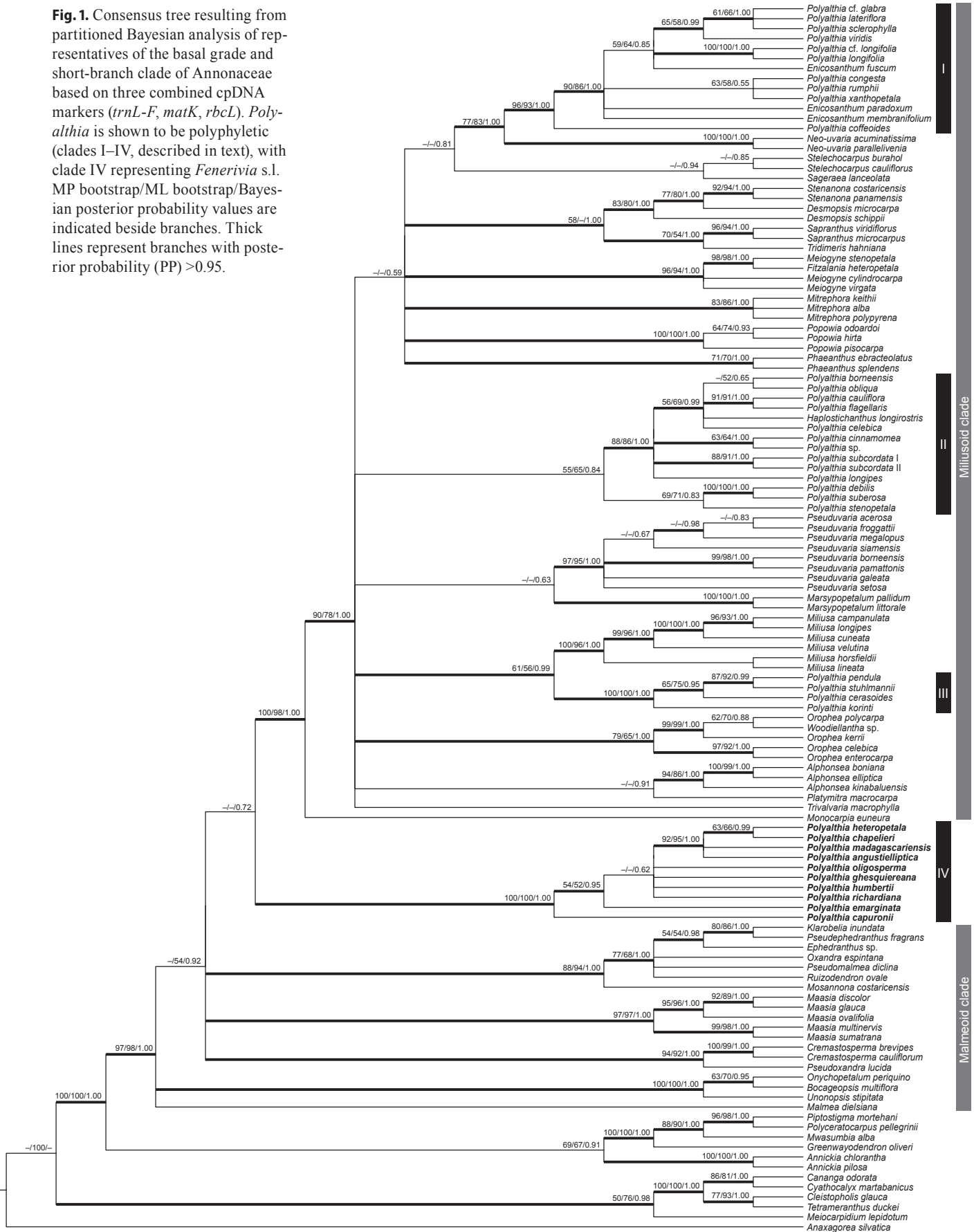
The results of the phylogenetic analyses presented here (Figs 1–2) reveal that the “*Polyalthia* columellar-sulcate group” (sensu Doyle & Le Thomas, 1994, 1995, 1996) is represented by two distinct and well-supported clades: an Asian clade with five *Maasia* species; and a Madagascan clade with all 10 *Polyalthia* species belonging to groups B and C (sensu Schatz & Le Thomas, 1990). Significantly, the latter clade has never been recovered in previous molecular phylogenetic analyses of the family. The phylogenetic relationships of these two “columellar-sulcate” clades are obscured, however, due to lack of adequate resolution and support. Only one other Madagascan *Polyalthia* species was included in the analysis: *P. pendula* Capuron ex Schatz & Le Thomas, belonging to group E (sensu Schatz & Le Thomas, 1990), is shown to be nested within *Polyalthia* clade III (Fig. 1), together with *P. cerasoides* (from Asia), *P. stuhlmannii* (from continental Africa), and *P. korinti* (from Asia). Although *Polyalthia* species in groups A and D and those occurring in East Africa were not included in the present analyses, they are known to be related to species in *Polyalthia* clade III based on palynological and macromorphological resemblances (Verdcourt, 1969; Vollesen, 1980a, b; Schatz & Le Thomas, 1990).

It is evident that the newly identified Madagascan clade of *Polyalthia* species (clade IV in Figs 1–2) is not congeneric with *Polyalthia* s.str. (represented by clade II), and the species therefore need to be reclassified. The species in *Polyalthia* clade IV are furthermore not congeneric with either of the other *Polyalthia* clades (I or III), nor any of the other genera which include species formerly classified in *Polyalthia*.

One of the species in clade IV, *P. heteropetala*, was originally described by Diels (1925) as the type of the monotypic genus *Fenerivia*. The name *Fenerivia heteropetala* was subsequently transferred to *Polyalthia* (Ghesquière, 1939), and although this approach was adopted in most later taxonomic treatments (Cavaco & Keraudren, 1957, 1958; Schatz & Le Thomas, 1990), others have maintained *Fenerivia* as a distinct genus (e.g., Fries, 1959; Van Heusden, 1992; Keßler, 1993). The recognition of *Fenerivia* as a distinct genus has recently received support based on interpretation of floral anatomy (Deroin, 2007). As the earliest generic name associated with the species in clade IV, *Fenerivia* is shown here to be the correct name for all species in this clade. Nine new nomenclatural combinations are consequently validated in this paper (see “Taxonomic treatment” section, below).

Diels (1925) originally segregated *F. heteropetala* from the Madagascan *Polyalthia* species because of its extraordinary floral structure, with what he interpreted as a highly reduced calyx of three vestigial sepals, and a corolla consisting of three broadly ovate outer petals and nine linear inner petals (Fig. 3). Ghesquière (1939) questioned this interpretation, however, suggesting that the “calyx” represents an extra-floral nectary, that the “outer petals” represent the true calyx, and that the nine “inner petals” actually represent both the inner and outer whorls of petals (with duplication of one of the whorls). Schatz & Le Thomas (1990) similarly doubted Diels’ interpretation of

Fig. 1. Consensus tree resulting from partitioned Bayesian analysis of representatives of the basal grade and short-branch clade of Annonaceae based on three combined cpDNA markers (*trnL-F*, *matK*, *rbcL*). *Polyalthia* is shown to be polyphyletic (clades I–IV, described in text), with clade IV representing *Fenerivia* s.l. MP bootstrap/ML bootstrap/Bayesian posterior probability values are indicated beside branches. Thick lines represent branches with posterior probability (PP) >0.95.



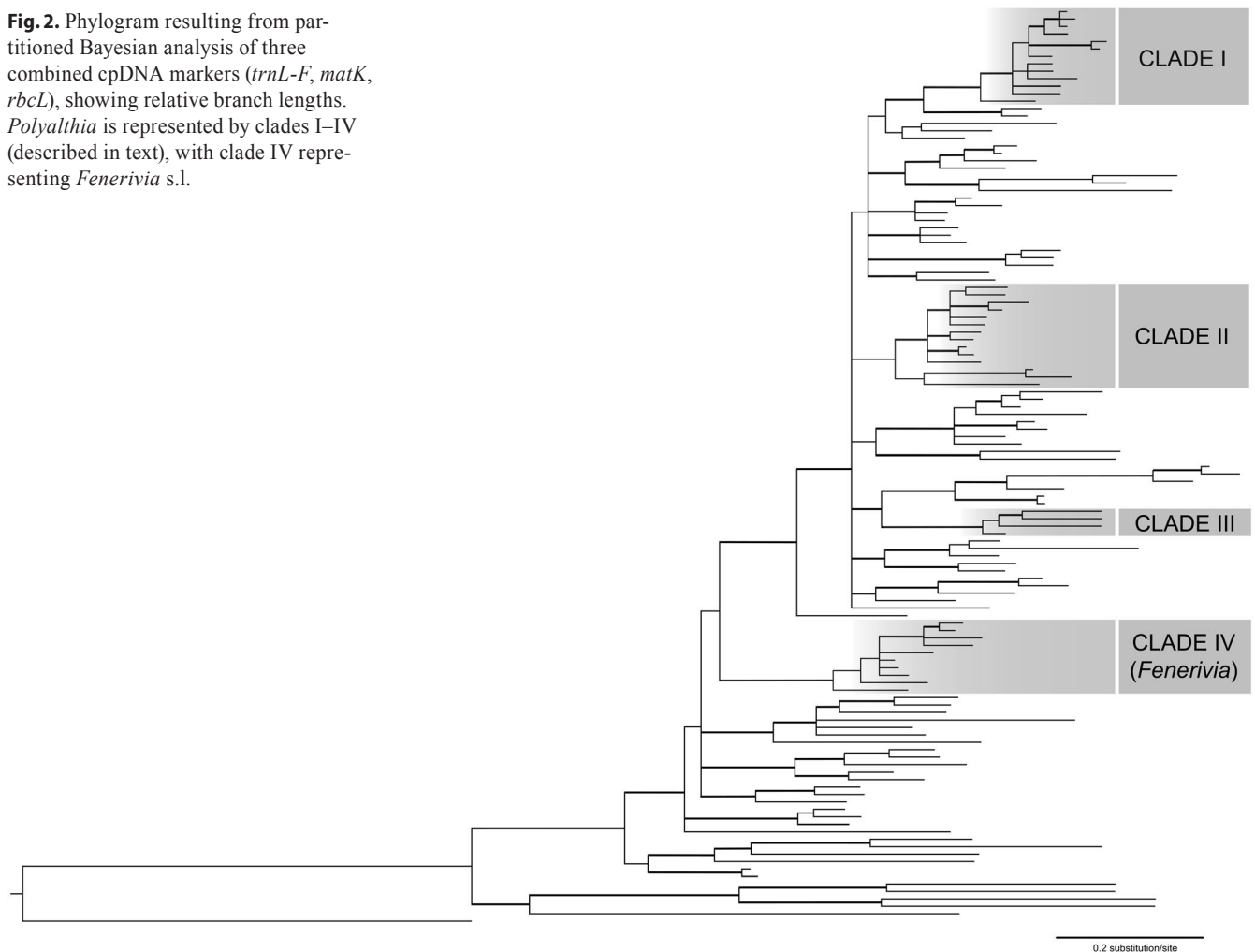
floral structure, but suggested that the calyx (sensu Diels) was merely an artefact resulting from dehydration of the receptacle.

Deroin (2007) published a detailed anatomical study of *F. heteropetala* and argued that Diels' original interpretation was correct. He demonstrated that the nine linear petals are of two types: three bracteopetals, homologous with the inner petals of other Annonaceae species; and six andropetals, derived from stamens. This was interpreted by Saunders (2010) to be the result of a substantial disruption of the homeotic control of floral organ identity during development, with a centrifugal shift so that the outermost whorl of six stamens develop as inner petals, the inner petals develop as outer petals, the outer petals develop to be sepal-like, and the sepals fail to develop significantly. Only one flowering specimen of *F. heteropetala* is known (the holotype, *H. Perrier de la Bâthie 4942*, P) and therefore it is not known whether the homeotic mutation occurred only in this individual (perhaps encouraging de la Bâthie to collect the sample) or whether the mutation has become fixed as a characteristic of the species as a whole.

The highly reduced calyx of three vestigial sepals (sensu Diels) is apparent in all species in the *Fenerivia* clade, and is visible in both living plants (Fig. 4A, E) and dried herbarium

specimens, and is noticeably persistent in fruiting material (Fig. 4B, F). This feature is therefore a valuable character for distinguishing *Fenerivia* from other Annonaceae genera and is a clear synapomorphy for the genus. Deroin (2007) demonstrated that the flange in *F. heteropetala* has a vascular system that is consistent with its interpretation as a calyx, hence confirming Diels' view of the flange as a reduced calyx. Other species transferred here to *Fenerivia* superficially have the standard number of petals and sepals for the family (Fig. 4C, E; Cavaco & Keraudren, 1958) but also possess the outermost "calyx" flange. Although the homology of the flange in *F. heteropetala* and other *Fenerivia* species has yet to be unequivocally demonstrated by examining the vascular supply in the latter, it seems likely that the structures are equivalent. If this interpretation is correct, the linear petals of species such as *F. angustieliptica* (Fig. 4C–E) would possibly represent two distinct whorls, of mixed bracteopetal and andropetal origin, consistent with the hypothesis of a disruption to the homeotic control of organ identity during floral development; unequivocal interpretation would require detailed anatomical research to reveal the vascular supply of the petals, however.

Fig. 2. Phylogram resulting from partitioned Bayesian analysis of three combined cpDNA markers (*trnL-F*, *matK*, *rbcL*), showing relative branch lengths. *Polyalthia* is represented by clades I–IV (described in text), with clade IV representing *Fenerivia* s.l.



On morphological grounds *Maasia* seems to be the closest relative of *Fenerivia*, although the relationships revealed by molecular data remain obscure due to lack of informative characters. Both genera share a number of characters, including inconspicuous leaf venation, axillary flowers, ovaries generally with a single ovule, seeds with a rib-like raphe and spiniform endosperm rumination, and monosulcate pollen grains with psilate-perforate ornamentation (Rogstad, 1989; Rogstad & Le Thomas, 1989; Schatz & Le Thomas, 1990; Mols & al., 2008). In addition to the presence of the calyx flange as described above, *Fenerivia* differs from *Maasia* in lacking a glaucous appearance on the abaxial surface of the leaves and in having significantly larger petals.

The polyphyletic genus *Polyalthia* has been significantly reduced in scope in recent years as a result of molecular phylogenetic analyses, with the transfer of six species to *Maasia* (Mols & al., 2008) and five species to *Marsypopetalum* (Xue & al., 2011). The transfer of nine Madagascan *Polyalthia* species to *Fenerivia*, as proposed here, further reduces the size of *Polyalthia*, although it does not render the genus monophyletic.

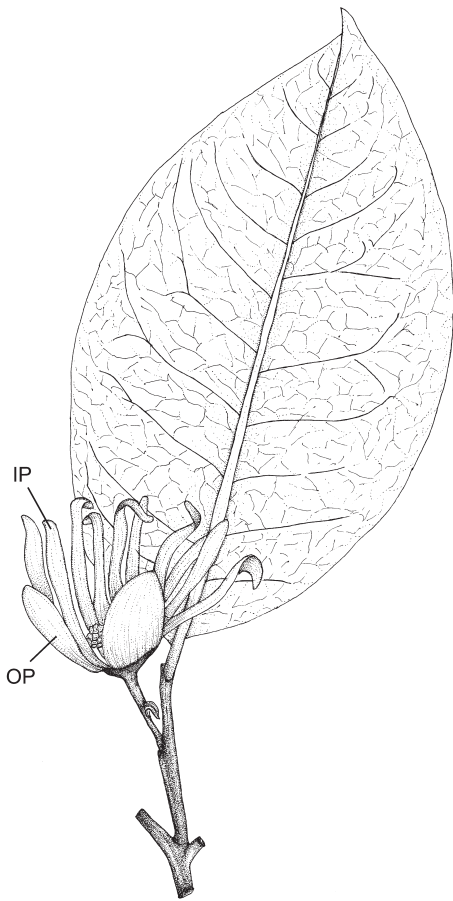


Fig. 3. *Fenerivia heteropetala*, showing ovate “outer petals” (OP) and linear “inner petals” (IP) of mixed origin (discussed in text). Although the drawing shows 10 linear petals, the type specimen and descriptions of the species indicate that there are only nine. Redrawn from Cavaco & Keraudren (1958: fig. XIV) by Vatsala Mirnaalini; reproduced from Saunders (2010).

Further research remains to address the status of *Haplostichanthus* species (associated with the “true” *Polyalthia* clade II, inclusive of the type species, *P. subcordata*) and also the *Polyalthia* species associated with *Enicosanthum* and *Miliusa* (clades I and III, respectively).

■ TAXONOMIC TREATMENT

Fenerivia Diels in Notizbl. Bot. Gart. Berlin-Dahlem 9: 355. 15 Jun 1925 – Type: *Fenerivia heteropetala* Diels.

Small to medium-sized trees. Leaves with inconspicuous venation, glabrous, not glaucous abaxially. Inflorescences axillary, reduced to a solitary flower; calyx highly reduced and vestigial, present as basal flange (sometimes 3-lobed); petals in 3 whorls; outer petals (presumed bracteopetals) 3 per flower, ovate, sepal-like; middle petals (presumed bracteopetals) 3 per flower, narrowly elliptic to linear; inner petals (presumed andropetals) generally 3 per flower (6 per flower in *F. heteropetala*), narrowly elliptic to linear. Stamens numerous per flower, dehiscence extrorse; connectives truncate. Carpels up to 45 per flower; ovule solitary, basal. Fruits with persistent calyx flange; monocarps stipitate, ellipsoid, with single seed.

Fenerivia angustieliptica (G.E. Schatz & Le Thomas) R.M.K. Saunders, **comb. nov.** \equiv *Polyalthia angustieliptica* G.E. Schatz & Le Thomas in Bull. Mus. Natl. Hist. Nat., B, Adansonia 12: 120–121, fig. 1 (7–15), 3 (5–6). 1990 (“*P. angusti-elliptica*”).

Fenerivia capuronii (Cavaco & Keraudren) R.M.K. Saunders, **comb. nov.** \equiv *Polyalthia capuronii* Cavaco & Keraudren in Bull. Jard. Bot. État Bruxelles 27: 75, t. 1, fig. 3. 1957.

Fenerivia chapelieri (Baill.) R.M.K. Saunders, **comb. nov.** \equiv *Polyalthia chapelieri* Baill. in Adansonia 8: 349. 1868 \equiv *Unona chapelieri* (Baill.) Baill. in Bull. Mens. Soc. Linn. Paris 1: 338. 1882.

\equiv *Polyalthia lucens* Baker in J. Linn. Soc., Bot. 21: 318–319. 1884 [synonymy according to Schatz & Le Thomas, 1990: 120].

\equiv *Polyalthia lamii* Cavaco & Keraudren in Bull. Jard. Bot. État Bruxelles 27: 76. 1957 [synonymy according to Schatz & Le Thomas, 1990: 120].

Fenerivia emarginata (Diels) R.M.K. Saunders, **comb. nov.** \equiv *Polyalthia emarginata* Diels in Notizbl. Bot. Gart. Berlin-Dahlem 9: 340–341. 1925.

Fenerivia ghesquiereana (Cavaco & Keraudren) R.M.K. Saunders, **comb. nov.** \equiv *Polyalthia ghesquiereana* Cavaco & Keraudren in Bull. Jard. Bot. État Bruxelles 27: 77, t. 1, fig. 2. 1957.

Fenerivia heteropetala Diels in Notizbl. Bot. Gart. Berlin-Dahlem 9: 356. 1925 \equiv *Polyalthia heteropetala* (Diels) Ghesq. in Rev. Zool. Bot. Africaines 32: 142. 1939.

Fenerivia humbertii (Cavaco & Keraudren) R.M.K. Saunders, **comb. nov.** \equiv *Polyalthia humbertii* Cavaco & Keraudren in Bull. Jard. Bot. État Bruxelles 27: 76, t. 1, fig. 1. 1957.

= *Polyalthia leandrii* Cavaco & Keraudren in Bull. Jard. Bot. État Bruxelles 27: 76. 1957 [synonymy according to Schatz & Le Thomas, 1990: 122].

Fenerivia madagascariensis (Cavaco & Keraudren) R.M.K. Saunders, **comb. nov.** \equiv *Polyalthia madagascariensis* Cavaco & Keraudren in Bull. Jard. Bot. État Bruxelles 27: 78. 1957.

Fenerivia oligosperma (Danguy) R.M.K. Saunders, **comb. nov.** \equiv *Artabotrys oligospermus* Danguy in Bull. Mus.

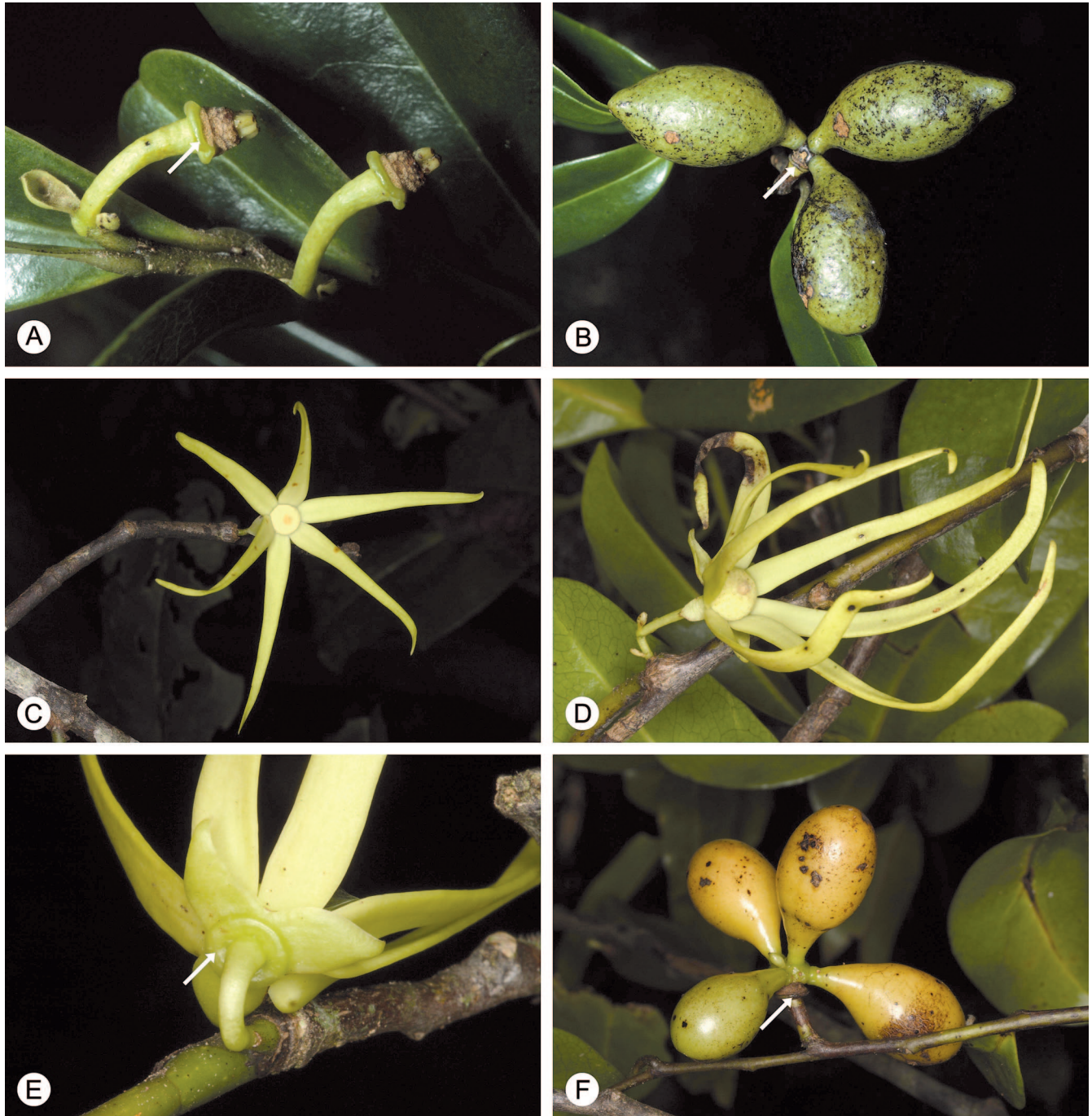


Fig. 4. Flower and fruit morphology in *Fenerivia*. **A–B**, post-fertilization flower (A) and fruit (B) of *Fenerivia angustieliptica*, showing flange lobes (arrowed) on receptacle. **C–F**, flowers (C–E) and fruit (F) of *Fenerivia capuronii*, showing flange lobes (arrowed) on receptacle. Voucher specimens: A, B, Poncy 1540 (MO); C, E, Chatrou 669 (TAN, WAG); D, Chatrou 667 (TAN, WAG); F, Chatrou 668 (TAN, WAG). Photographs: A, B, © Odile Poncy; C–F, © Lars Chatrou.

Natl. Hist. Nat. 28: 247. 1922 = *Polyalthia oligosperma* (Danguy) Diels in Notizbl. Bot. Gart. Berlin-Dahlem 9: 341–342. 1925.

Fenerivia richardiana (Baill.) R.M.K. Saunders, **comb. nov.**
= *Polyalthia richardiana* Baill. in Adansonia 8: 350. 1868
= *Unona richardiana* (Baill.) Baill. in Bull. Mens. Soc. Linn. Paris 1: 339. 1882.
= *Polyalthia dielsii* Cavaco & Keraudren in Bull. Jard. Bot. État Bruxelles 27: 77. 1957 [synonymy according to Schatz & Le Thomas, 1990: 124].

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Appendix. Voucher information and GenBank accession numbers for samples used in this study (*newly sequenced data).

Species, origin, voucher, GenBank accession number (in following order: *trnL-F*, *matK*, *rbcL*)

Alphonsea boniana Finet & Gagnep.: Vietnam, P.J.A. Keßler 3116 (L), AY319077, AY518809, AY318965; *Alphonsea elliptica* Hook. f. & Thomson: cultivated, Kebun Raya, Bogor [X-F-52], Van Balgooy 5141 (L), AY319078, AY518807, AY318966; *Alphonsea kinabaluensis* J. Sinclair: Malaysia, Ridsdale DV-S-3048 (L), AY319080, AY518811, AY318968; *Anaxagorea silvatica* R.E. Fr.: Brazil, P.J.M. Maas & al. 8836 (U), AY743458, AY743477, AY743439; *Annickia chlorantha* (Oliv.) Setten & Maas: Gabon, M.S.M. Sosef 1877 (WAG), AY841671, AY841393, AY841594; *Annickia pilosa* (Exell.) Setten & Maas: Gabon, M.S.M. Sosef 1803 (WAG), AY743469, AY743488, AY743450; *Bocageopsis multiflora* (Mart.) R.E. Fr.: Guyana, M.J. Jansen-Jacobs & al. 5789 (U), AY841678, DQ018262, AY841600; *Cananga odorata* (Lam.) Hook. f. & Thomson: Costa Rica, L.W. Chatrou & al. 93 (U), AY841680, AY841394, AY841602; *Cleistopholis glauca* Engl. & Diels: Gabon, J.J. Wieringa & al. 3278 (WAG), AY841681, AY841395, AY841603; *Crematosperma brevipes* (DC.) R.E. Fr.: French Guiana, U. Scharf 76 (U), AY743573, AY743550, AY743527; *Crematosperma cauliflorum* R.E. Fr.: Peru, L.W. Chatrou & al. 224 (U), AY743565, AY743542, AY743519; *Cyathocalyx martabanicus* Hook. f. & Thomson: cultivated, Kebun Raya, Bogor, J.B. Mols 11 (L), AY841683, DQ125054, AY841605; *Desmopsis microcarpa* R.E. Fr.: Costa Rica, L.W. Chatrou & al. 85 (U), AY319173, AY518804, AY319059; *Desmopsis schippii* Standl.: Costa Rica, L.W. Chatrou & al. 94 (U), AY319174, AY518805, AY319060; *Enicosanthum fuscum* (King) Airy-Shaw: Thailand, P.J.A. Keßler 3222 (L), AY319085, AY518787, AY318973; *Enicosanthum membranifolium* J. Sinclair: Thailand, P.J.A. Keßler 3198 (L), AY319086, AY518788, AY318974; *Enicosanthum paradoxum* Becc.: Borneo, P.J.A. Keßler & Arifin PK 2746 (L), AY319087, AY518789, AY318975; *Ephedranthus* sp.: Brazil, Maas & al. 8826 (U), AY841694, AY841396, AY841616; *Fenerivia angustieliptica* (G.E. Schatz & Le Thomas) R.M.K. Saunders (= *Polyalthia angustieliptica* G.E. Schatz & Le Thomas): Madagascar, O. Poncy 1540 (P),* JF810397, JF810373, JF810385; *Fenerivia capuronii* (Cavaco & Keraudren) R.M.K. Saunders (= *Polyalthia capuronii* Cavaco & Keraudren): Madagascar, P.P. Lowry II 4436 (WAG),* JF810398, JF810374, JF810386; *Fenerivia chapelieri* (Baill.) R.M.K. Saunders (= *Polyalthia chapelieri* Baill.): Madagascar, Ludovic & Rallotoarivony 221 (P),* JF810399, JF810375, JF810387; *Fenerivia emarginata* (Diels) R.M.K. Saunders (= *Polyalthia emarginata* Diels): Madagascar, J.S. Miller 3527 (WAG),* JF810400, JF810376, JF810388; *Fenerivia ghesquiereana* (Cavaco & Keraudren) R.M.K. Saunders (= *Polyalthia ghesquiereana* Cavaco & Keraudren): Madagascar, R. Randrianaivo 282 (WAG),* JF810401, JF810377, JF810389; *Fenerivia heteropetala* Diels (= *Polyalthia heteropetala* (Diels) Ghesq.): Madagascar, G. Cours 2606 (P),* JF810402, JF810378, JF810390; *Fenerivia humbertii* (Cavaco & Keraudren) R.M.K. Saunders (= *Polyalthia humbertii* Cavaco & Keraudren): Madagascar, S.T. Malcomber & A.J.M. Leeuwenberg 1173 (WAG),* JF810403, JF810379, JF810391; *Fenerivia madagascariensis* (Cavaco & Keraudren) R.M.K. Saunders (= *Polyalthia madagascariensis* Cavaco & Keraudren): Madagascar, J. Rabenantoandro & A. Monja 1590 (P),* JF810404, JF810380, JF810392; *Fenerivia oligosperma* (Danguy) R.M.K. Saunders (= *Polyalthia oligosperma* Danguy): Madagascar, Ursch s.n. (WAG),* JF810405, JF810381, JF810393; *Fenerivia richardiana* (Baill.) R.M.K. Saunders (= *Polyalthia richardiana* Baill.): Madagascar, P. Antilahiema 157 (WAG),* JF810406, JF810382, JF810394; *Fitzalania heteropetala* (F. Muell.) F. Muell.: Australia, T.H. Kemp 7267 (L), AY773282, AY773280, AY773281; *Greenwayodendron oliveri* (Engl.) Verdec.: Ghana, C.C.H. Jongkind & al. 1795 (WAG), AY743470, AY743489, AY743451; *Haplostichanthus longirostris* (Scheff.) Heusden: New Guinea, W. Takeuchi & D. Ama 15656 (L), AY319091, AY518826, AY318979; *Klarobelia inundata* Chatrou: Peru, L.W. Chatrou & al. 205 (U), AY743471, AY743490, AY743452; *Maasia discolor* (Diels) Mols & al.: New Guinea, W. Takeuchi & D. Ama 16394 (L), AY319135, AY518872, AY319021; *Maasia glauca* (Hassk.) Mols & al.: cultivated, Kebun Raya, Bogor [XX-D-81], J.B. Mols 20 (L), AY319137, AY518871, AY319023; *Maasia multinervis* (Diels) Mols & al.: New Guinea, S.H. Rogstad 819 (WAG),* JF810407, JF810383, JF810395; *Maasia ovalifolia* (S.H. Rogstad) Mols & al.: Borneo, P.S. Ashton 7863 (WAG),* JF810408, JF810384, JF810396; *Maasia sumatrana* (Miq.) Mols & al.: Borneo, unknown collector SAN 143918 (SAN), AY319153, AY518873, AY319039; *Malmeea dielsiana* R.E. Fr.: Peru, L.W. Chatrou & al. 122 (U), AY231288, AY238964, AY238955; *Marsyppetalum littorale* (Blume) B. Xue & R.M.K. Saunders: cultivated, Kebun Raya, Bogor [IV-H-53], Rastini 153 (L), AY319140, AY518835, AY319026; *Marsyppetalum pallidum* (Blume) Backer: Thailand, P.J.A. Keßler 3192 (L), AY319092, AY518834, AY318980; *Meiocarpidium lepidotum* Engl. & Diels: Gabon, F.J. Breteler 13947 (WAG), EU169776, EU169687, EU169754; *Meiogyne cylindrocarpa* (Burck) Heusden: Borneo, C.E. Ridsdale DV-M1-1930 (L), AY319093, AY518796, AY318981; *Meiogyne stenopetala* (F. Muell.) Heusden: Australia, L. Jessup 706 (L), AY319083, AY773279, AY318971; *Meiogyne virgata* (Blume) Miq.: Borneo, P.J.A. Keßler 2751 (L), AY319094, AY518798, AY318982; *Milusa campanulata* Pierre: Thailand, P. Chalermglin 440407-11 (TISTR), AY319096, AY518842, AY318984; *Milusa cuneata* Craib: Thailand, P. Chalermglin 440214-7 (L), AY319097, AY518844, AY318985; *Milusa horsfieldii* (Benn.) Pierre: cultivated, Kebun Raya, Bogor, J.B. Mols 1 (L), AY319098, AY518849, AY318986; *Milusa lineata* (Craib) Ast: Thailand, P.J.A. Keßler 3202 (L), AY319099, AY518848, AY318987; *Milusa longipes* King: Thailand, P. Pholsena 2651 (L), AY319100, AY318988, AY318988; *Milusa velutina* (Dunal) Hook. f. & Thomson: Thailand, P. Pholsena 2842 (L), AY319105, AY518847, AY318993; *Mitrephora alba* Ridl.: Thailand, P. Chalermglin 440304-1 (Thailand Institute of Scientific and Technological Research, Bangkok), AY319106, AY518855, AY318994; *Mitrephora keithii* Ridl.: Thailand, P.J.A. Keßler 3190 (L) & D.J. Middleton & al. 877 (L), AY319108, AY518857, AY318995; *Mitrephora polypyrena* (Blume) Miq.: cultivated, Kebun Raya, Bogor, J.B. Mols 7 (L), AY319110, AY518858, AY318997; *Monocarpia euneura* Miq.: Borneo, F. Slik 2931 (L), AY319111, AY518865, AY318998; *Mosannona costaricensis* R.E. Fr.: Costa Rica, L.W. Chatrou & al. 90 (U), AY743496,

Appendix. Continued.

AY743503, AY743510; *Mwasumbia alba* Couvreur & D.M. Johnson: Tanzania, *T.L.P. Couvreur 85* (WAG), EU747674, –, EU747680; *Neo-uvaria acuminatis-sima* (Miq.) Airy-Shaw: Borneo, *C.E. Ridsdale DV-SR-4671* (L), AY319112, AY518793, AY318999; *Neo-uvaria parallelivenia* (Boerl.) H. Okada & K. Ueda: cultivated, Kebun Raya, Bogor, *P.J.A. Keßler sub IV-H-73* (L), AY319113, AY518794, AY319000; *Onychopetalum periquino* (Rusby) D.M. Johnson & N.A. Murray: Bolivia, *L.W. Chatrou & al. 425* (U), AY319179, AY518876, AY319065; *Orophea celebica* Miq.: Sulawesi, *P.J.A. Keßler 2953* (L), AY319117, AY518814, AY319004; *Orophea enterocarpa* Maingay ex Hook. f.: Thailand, *P. Chalermglin 440403* (Thailand Institute of Scientific and Technological Research, Bangkok), AY319119, AY518815, AY319006; *Orophea kerrii* P.J.A. Kessler: Thailand, *P. Chalermglin 440416-1* (L), AY319121, AY518818, AY319008; *Orophea polycarpa* A. DC.: Thailand, *P.J.A. Keßler 3234* (L), AY319123, AY518819, AY319010; *Oxandra espitana* (Spruce ex Benth.) Baill.: Peru, *L.W. Chatrou & al. 133* (U), AY319180, DQ018260, AY319066; *Phaeanthus ebracteolatus* (Presl) Merr.: New Guinea, *T.M.A. Utteridge 17* (K), AY319125, AY518863, AY319012; *Phaeanthus splendens* Miq.: Borneo, *P.J.A. Keßler B 1564* (L), AY319126, AY518864, –; *Piptostigma mortehani* De Wild.: Gabon, *J.J. Wieringa 2779* (U), AY743473, AY743492, AY743454; *Platymitra macrocarpa* Boerl.: cultivated, Kebun Raya, Bogor [IV-G-53], *H. Okada 3457* (L), AY319127, AY518812, AY319013; *Polyalthia borneensis* Merr.: Borneo, *C.E. Ridsdale DV-SR-7921* (L), AY319128, AY518821, AY319014; *Polyalthia cauliflora* Hook. f. & Thomson: cultivated, Singapore Botanical Garden, *P.J.A. Keßler 3114* (L), AY319129, AY518803, AY319015; *Polyalthia celebica* Miq.: cultivated, Kebun Raya, Bogor [IV-C-97], *J.B. Mols 9* (L), AY319130, AY518827, AY319016; *Polyalthia flagellaris* (Becc.) Airy-Shaw: Borneo, *P. Chalermglin 440214-4* (L), AY319131, AY518854, AY319017; *Polyalthia cinnamomea* (Hook. f. & Thomson) Hook. f. & Thomson: Borneo, *C.E. Ridsdale DV-M1-347* (L), AY319132, AY518828, AY319018; *Polyalthia coffeoides* (Thwaites ex Hook. f. & Thomson) Thwaites: Sri Lanka, *R.M.C.S. Ratnayake 1/03* (HKU), EU522178, EU522233, EU522288; *Polyalthia congesta* (Ridl.) J. Sinclair: Borneo, *C.E. Ridsdale DV-S-5105* (L), AY319133, AY518790, AY319019; *Polyalthia debilis* (Pierre) Finet & Gagnep.: Thailand, *P.J.A. Keßler 3228* (L) & Thomson: cultivated, Kebun Raya, Bogor [XX-D-82] (L), AY319139, AY518785, AY319025; *Polyalthia longipes* (Miq.) Koord. & Valetton: Borneo, *C.E. Ridsdale DV-M2-11443* (L), AY319142, AY518829, AY319028; *Polyalthia obliqua* Hook. f. & Thomson: Borneo, *Ambriansyah & Arifin AA 1694* (L), AY319143, AY518822, AY319029; *Polyalthia pendula* G.E. Schatz & Le Thomas: Madagascar, *Rabevohitra 2386* (K, WAG), AY319144, AY518852, AY319030; *Polyalthia rumphii* (Hensch.) Merr.: Sumatra, *M.M.J. van Balgooy & A.K. van Setten 5654* (L), AY319145, AY518791, AY319031; *Polyalthia sclerophylla* Hook. f. & Thomson: cultivated, Kebun Raya, Bogor [XX-D-82] (L), AY319147, AY518783, AY319033; *Polyalthia stenopetala* (Hook. f. & Thomson) Finet & Gagnep.: Thailand, *P. Chalermglin 440302* (Thailand Institute of Scientific and Technological Research, Bangkok), AY319148, –, AY319034; *Polyalthia stuhlmannii* (Engl.) Verd.: Kenya, *Luke & Robertson 1424* (K, WAG), AY319149, AY518853, AY319035; *Polyalthia subcordata* (Blume) Blume (I): Java, *B. Gravendeel & al. 549* (L), AY319150, AY518830, AY319036; *Polyalthia subcordata* (Blume) Blume (II): Java, *B. Gravendeel & al. 678* (L), AY319151, AY518831, AY319037; *Polyalthia suberosa* (Roxb.) Thwaites: India, *L.W. Chatrou 480* (U) & cultivated, Botanical Gardens Kaiserslautern, anonymous s.n., AY319152, AY518833, AY319038; *Polyalthia viridis* Craib: Thailand, *P. Chalermglin 440214-3* (L), AY319154, AY518784, AY319040; *Polyalthia xanthopetala* Merr.: Borneo, *C.E. Ridsdale DV-S-5107* (L), AY319155, AY518792, AY319041; *Polyalthia* sp.: Borneo, *C.E. Ridsdale DV-M1-12314* (L), AY319084, AY518825, AY318972; *Polyceratocarpus pellegrinii* Le Thomas: Cameroon, *J.J.E. de Wilde 8718* (WAG), EU747678, –, EU747684; *Popowia hirta* Miq.: Borneo, *P.J.A. Keßler B 1628* (L), AY319156, AY518860, AY319042; *Popowia odoardoii* Diels: Borneo, *C.E. Ridsdale DV-SR-7422* (L), AY319157, AY518861, AY319043; *Popowia pisocarpa* (Blume) Endl.: Java, *M.M.J. van Balgooy & A.K. van Setten 5683* (L), AY319158, AY518862, AY319044; *Pseudephe-dranthus fragrans* (R.E. Fr.) Aristeg.: Venezuela, *P.J.M. Maas & al. 6878* (U), AY841729, –, AY841651; *Pseudomalmea diclina* (R.E. Fr.) Chatrou: Peru, *L.W. Chatrou & al. 211* (U), AY319128, AY841398, AY319068; *Pseudoxandra lucida* R.E. Fr.: Peru, *L.W. Chatrou & al. 213* (U), AY319190, AY319190, AY319076; *Pseuduvaria acerosa* Y.C.F. Su & R.M.K. Saunders: New Guinea, *J.S. Womersley NGF 43899* (L), EU522181, EU522236, EU522291; *Pseuduvaria borneensis* Y.C.F. Su & R.M.K. Saunders: Borneo, *P.S. Ashton S 18415* (L), EU522184, EU522239, EU522294; *Pseuduvaria fragrans* Y.C.F. Su & al.: Thailand, *T. Chaowasku 27* (L), EU522231, EU522286, EU522341; *Pseuduvaria froggattii* (F. Muell.) Jessup: Australia, *A. Ford & L. Cinelli 4776* (HKU), EU522196, EU522251, EU522306; *Pseuduvaria galeata* J. Sinclair: Peninsular Malaysia, *J. Sinclair 10689* (L), EU522197, EU522252, EU522307; *Pseuduvaria megalopus* (K. Schum.) Y.C.F. Su & J.B. Mols: New Guinea, *W. Takeuchi & D. Ama 16235* (L), EU522208, EU522263, EU522318; *Pseuduvaria pamattonis* (Miq.) Y.C.F. Su & R.M.K. Saunders: Philippines, *A.C. Podzorski SMHI 520* (L), EU522217, EU522272, EU522327; *Pseuduvaria setosa* (King) J. Sinclair: Thailand, *J.F. Maxwell 86-208* (L), EU522224, EU522279, EU522334; *Ruizodendron ovale* (Ruiz & Pav.) R.E. Fr.: Ecuador, *P.J.M. Maas & al. 8600* (U), AY841735, –, AY841657; *Sageraea lanceolata* Miq.: Borneo, *C.E. Ridsdale DV-M2-1692* (L), AY319164, AY518799, AY319050; *Sapranthus microcarpus* (Donn. Sm.) R.E. Fr.: Honduras, *P.J.M. Maas & al. 8457* (U), AY319166, AY518806, AY319052; *Sapranthus viridiflorus* G.E. Schatz: Costa Rica, *L.W. Chatrou & al. 55* (U), AY319165, AY743493, AY319051; *Stelechocarpus burahol* (Blume) Hook. f. & Thomson: cultivated, Kebun Raya, Bogor, *J.B. Mols 13* (L), AY319167, AY518803, AY319053; *Stelechocarpus cauliflorus* (Scheff.) R.E. Fr.: cultivated, Kebun Raya, Bogor [XV-A-196] (L), AY319168, AY518800, AY319054; *Stenanona costaricensis* R.E. Fr.: Costa Rica, *L.W. Chatrou & al. 67* (U), AY319183, AY518801, AY319069; *Stenanona panamensis* Standl.: Costa Rica, *L.W. Chatrou & al. 100* (U), AY319184, AY518802, AY319070; *Tetrameranthus duckei* R.E. Fr.: Brazil, *D.W. Stevenson & al. 1002* (U), AY841736, –, AY841658; *Tridimeris hahniana* Baill.: Mexico, *G.E. Schatz 1198* (K), AY319169, –, AY319055; *Trivalvaria macrophylla* (Blume) Miq.: Java, *M. Chase 1207* (K), AY319170, –, AY319056; *Unonopsis stipitata* Diels: Peru, *L.W. Chatrou & al. 253* (U), AY841740, AY841400, AY841662; *Woodiellantha* sp.: Borneo, *Lugas 311* (K), AY841743, –, AY841665.