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https://doi.org/10.1080/14772000.2010.542497

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*Systematics and Biodiversity* (2011), **9(1)**: 17–26

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## Research Article

# Further fragmentation of the polyphyletic genus *Polyalthia* (Annonaceae): molecular phylogenetic support for a broader delimitation of *Marsypopetalum*

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(Received 23 May 2010; revised 10 November 2010; accepted 11 November 2010; printed 30 March 2011)

The species-rich genus *Polyalthia* has previously been shown to be highly polyphyletic, with species represented in at least five different clades. The *Polyalthia* species that are associated with *Marsypopetalum* and *Trivalvaria* (as revealed either by previous phylogenetic studies or inferred on the basis of comparative morphology) were included in a molecular phylogenetic study based on three chloroplast DNA regions (*matK*, *rbcL* and *trnL-F*). Maximum parsimony, maximum likelihood and Bayesian analyses consistently revealed that several *Polyalthia* species form a well-supported clade with *Marsypopetalum pallidum*, and that this clade is sister to *Trivalvaria*. Diagnostic morphological characters for the clades are re-evaluated and shown to be congruent with the molecular phylogeny. Five *Polyalthia* species (*P. crassa*, *P. littoralis*, *P. lucida*, *P. modesta* and *P. tristis*) are accordingly transferred to *Marsypopetalum*.

**Key words**: Annonaceae, *Marsypopetalum*, molecular phylogenetics, nomenclature, *Polyalthia*, systematics, taxonomy, *Trivalvaria*

## Introduction

The genus *Polyalthia* Blume is one of the largest palaeotropical genera in the Annonaceae, with over 300 published names (International Plant Name Index, IPNI: http://www.ipni.org/index.html), of which *c.* 150 are currently in use (Global Index of Annonaceae Names: http://herbarium.botanik.univie.ac.at/annonaceae/listTax.php). *Polyalthia* has been the source of considerable taxonomic confusion due to the absence of morphological synapomorphies (Johnson & Murray, 1999), and several taxonomists have accordingly suggested that it is likely to be paraphyletic or polyphyletic (Rogstad & Le Thomas, 1989; van Setten & Koek-Noorman, 1992; Doyle & Le Thomas, 1994, 1996; Doyle *et al.*, 2000). The polyphyletic status of *Polyalthia* was subsequently confirmed in a molecular phylogenetic study based on combined *rbcL* and *trnL-F* plastid DNA sequences (Mols *et al.*, 2004*b*), in which representative *Polyalthia* species were scattered in at least five distinct clades.

Research aimed at dividing *Polyalthia* into separate monophyletic groups effectively began with the segregation of African species formerly classified in *Polyalthia* sect. *Afropolyalthia* as a new genus, *Greenwayodendron* (Verdcourt, 1969). More recently, species in the Southeast Asian '*Polyalthia hypoleuca* complex' (sensu Rogstad, 1989, 1990, 1994; Rogstad & Le Thomas, 1989) have been recognized as the new genus *Maasia* (Mols *et al.*, 2008). Removal of these species from *Polyalthia* has not rendered the genus monophyletic, however, as the genus is still represented by species in several distinct clades.

The present research focuses on the monotypic genus *Marsypopetalum*, which was previously shown to form a strongly supported clade (maximum parsimony bootstrap support = 99%; Bayesian posterior probability = 1.00) with *Polyalthia littoralis* (Mols *et al.*, 2004*b*). We have undertaken a new molecular phylogenetic analysis, based on a larger plastid DNA dataset and a larger number of taxa (including species that are morphologically similar to *Marsypopetalum pallidum* and *P. littoralis*), with the objective of recircumscribing the genus *Marsypopetalum*.

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ISSN 1477-2000 print / 1478-0933 online

DOI: 10.1080/14772000.2010.542497

# Materials and methods

## Taxon sampling

The data matrix comprised a total of 123 species of Annonaceae representing all major clades in the family, including 28 species of *Polyalthia*, the single species of *Marsypopetalum*, two species of *Trivalvaria* and 92 outgroup taxa. *Polyalthia crassa* R. Parker, *P. lucida* Merr. and *P. tristis* (Pierre) Finet & Gagnep. were specifically included in the analyses as they were identified as likely to be closely related to the clade that includes *Marsypopetalum pallidum* and *Polyalthia littoralis* based on morphological criteria (van Heusden, 1992; Mols *et al.*, 2004*b*; and pers. obs.); although morphologically very similar, *Polyalthia modesta* was not included due to the lack of availability of material. The samples, localities and GenBank accession numbers are listed in the Appendix (see supplementary material which is available on the Supplementary tab of the article's Informaworld page at http://dx.doi.org/10.1080/14772000.2010.542497)

## DNA extraction, amplification and sequencing

Total genomic DNA was extracted from herbarium leaf samples or fresh materials using a modified cetyl trimethyl ammonium bromide (CTAB) method (Doyle & Doyle, 1987; Erkens *et al.*, 2008; Su *et al.*, 2008), with DNA purified using the Wizard PCR Preps DNA Purification System (Promega, Madison, Wisconsin), and eluted with 50 $\mu$l preheated TE (Tris-EDTA) buffer.

Three chloroplast DNA regions, *matK*, *rbcL* and *trnL-F*, were sequenced, using the following primers for amplification: (1) *matK* gene: primers matK-13F/515R, matK-424F/788R and matK-449F/824R (Su *et al.*, 2008); (2) *rbcL* gene: primers rbcL-7F/429R, rbcL-127F/734R, rbcL-656F/1100R and rbcL-984F/1381R (Su *et al.*, 2008); and (3) *trnL-F* (*trnL* intron and *trnL-trnF* intergenic spacer): primers trnLF-12F/433R, trnLF-147F/508R, trnLF-413F/724R and trnLF-597F/960R (Su *et al.*, 2008).

All PCR reactions were performed in a total volume of 50 $\mu$l using 1 × PCR buffer, *c.* 10 ng DNA, 3 mM $MgCl_2$, 0.2 mM dNTP, 0.3 $\mu$M of each primer, 2 U Taq DNA polymerase (Promega, Madison, Wisconsin) and 0.5 $\mu$g/$\mu$l BSA (Promega). Reactions were performed using the following cycling conditions: 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*, and 52–55°C annealing for *matK* and *rbcL*; and 2 min extension at 72°C; with an additional final extension of 7 min at 74°C. Successfully amplified products were purified with the QIAquick PCR purification kit (Qiagen Inc., Valencia, California) following the manufacturer's instructions.

Sequencing reactions were carried out for both forward and reverse strands using the same PCR primers, and a BigDye Terminator ver. 3.1 cycle sequencing kit (Applied Biosystems, Foster City, California). 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), and aligned manually using BioEdit ver. 7.0.9 (Hall, 1999) and Se-Al ver. 2.0a11 (Rambaut, 1996).

Maximum parsimony (MP) analyses of the three combined regions were conducted using PAUP* ver. 4.0b10 (Swofford, 2003). All characters were weighted equally and gaps treated as missing data. The most parsimonious trees were obtained with heuristic searches of 1000 replicates of random stepwise sequence addition, tree bisection-reconnection (TBR) branch swapping with no limit to the number of trees saved. Bootstrap support (BS) was calculated with 1000 simple stepwise addition replicates with TBR branch swapping, and 10 trees saved per replicate.

Maximum likelihood (ML) analyses were conducted for the three-region dataset using GARLI ver. 0.95 which 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 ver. 2.3 (Nylander, 2004). The analyses were performed using a random starting tree and the ML bootstrap (BS) values were estimated from 100 bootstrap replicates in GARLI.

Partitioned Bayesian analyses were performed on the combined three-region dataset using MrBayes ver. 3.1.2 (Ronquist & Huelsenbeck, 2003). Separate models of molecular evolution for individual gene partitions were determined by MrModelTest ver. 2.3 (Nylander, 2004). Two independent runs of six MCMCMC chains were run for 5 million generations and 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 effective sample size (ESS) values of all parameters were greater than 100, indicating convergence of the runs. Burn-in was estimated using Tracer ver. 1.4 (Rambaut & Drummond, 2007), with the first 10% of the sampled trees discarded. The remaining trees were used to generate a 50% majority rule consensus tree and calculate the posterior probabilities (PP). A distant outgroup, *Anaxagorea silvatica*, was used to root the tree.

## Scanning electron microscopy

Pollen and stamens of available material (*Polyalthia crassa*, *Polyalthia littoralis*, *Trivalvaria dubia* and *Trivalvaria macrophylla*) were obtained from air-dried herbarium specimens and were directly attached to metal stubs using adhesive carbon tabs. All stub preparations were then

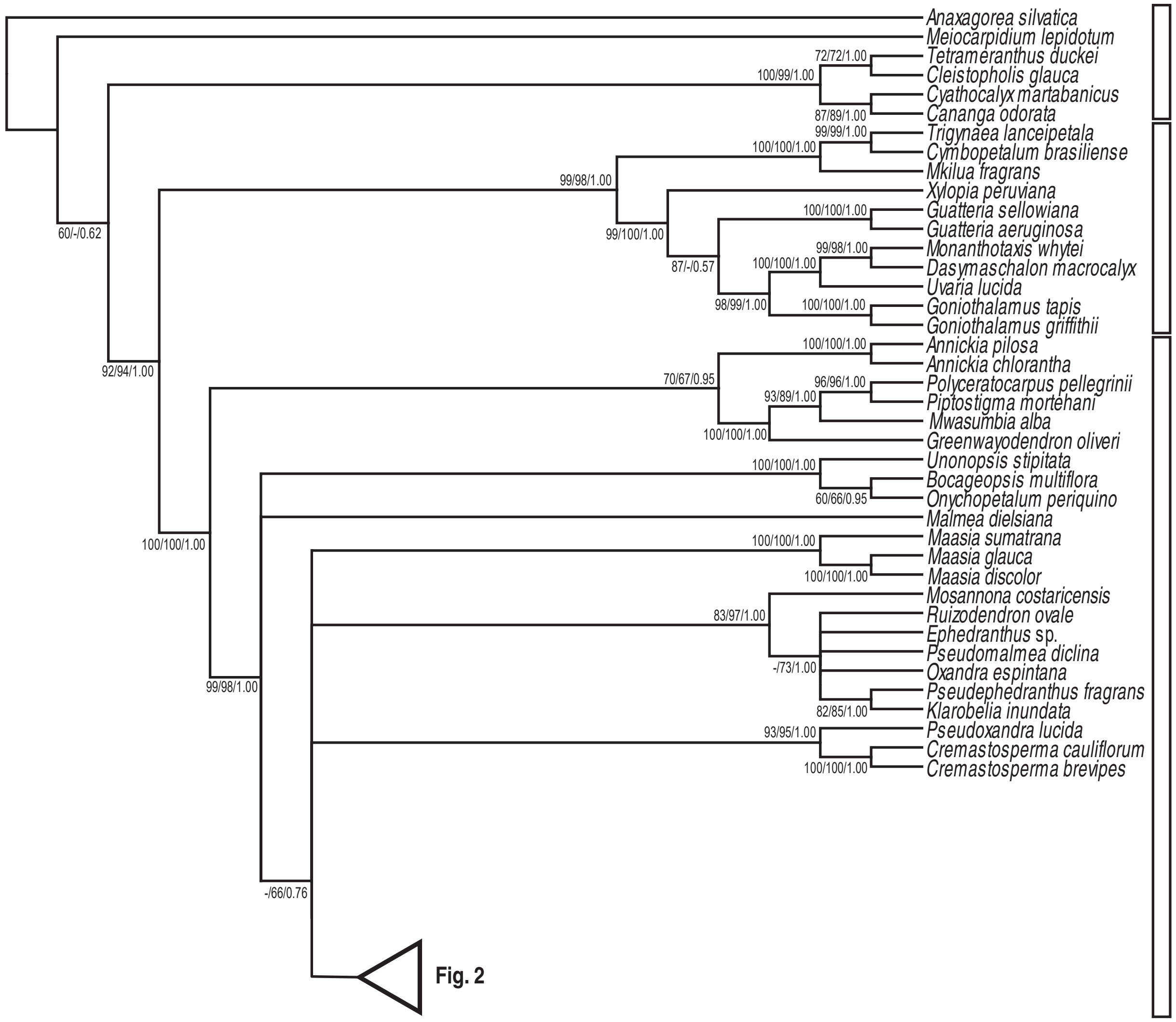


**Fig. 1.** Bayesian phylogeny inferred from combined *matK*, *rbcL* and *trnL-F* data under partitioned models (showing basal lineages only; *Monocarpia* and the 'miliusoid' clade shown in Fig. 2). Numbers at the nodes indicate MP, ML bootstrap values (>50%) and Bayesian posterior probabilities in that order.

sputter-coated with gold/palladium, and viewed using a Hitachi S-3400 VP scanning electron microscope at 5 kV.

## Results

The combined three-region dataset consisted of 3187 aligned characters (*trnL-F*: 1055 bp; *matK*: 789 bp; and *rbcL*: 1343 bp) following the removal of 65 bp of ambiguous regions in *trnL-F*. Of the total, 1062 bp (33.3%) were variable and 643 bp (20.2%) were parsimony informative.

GTR + I + G was selected as the best-fitting model for the ML analyses. Model parameter values were estimated as follows: base frequencies A = 0.2868, C = 0.1907, G = 0.2131, T = 0.3094; rate matrix: A–C = 1.4812, A–G = 3.2020, A–T = 0.6756, C–G = 0.8211, C–T = 3.7110, G–T = 1.0000; proportion of invariable sites (I) = 0.3592; and gamma shape parameter = 0.9608. The likelihood score of the optimal ML tree, –InL, was 18203.02. 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.

The MP, ML and Bayesian analyses of the combined regions consistently revealed four strongly supported *Polyalthia* clades (Clades I–IV, as numbered in Fig. 2). Clade I (MP BS = 74%; ML BS = 72%; PP = 0.98; corresponding with clades F2 and F3 as recognized by Mols *et al.*, 2004*b*) represents 'true' *Polyalthia* as it includes the type species (*P. subcordata*), but also includes *Haplostichanthus longirostris*. Clade II (MP BS = 100%; ML BS = 100%; PP = 1.00; corresponding with clade F1 as recognized by Mols *et al.*, 2004*b*) consists of four *Polyalthia*

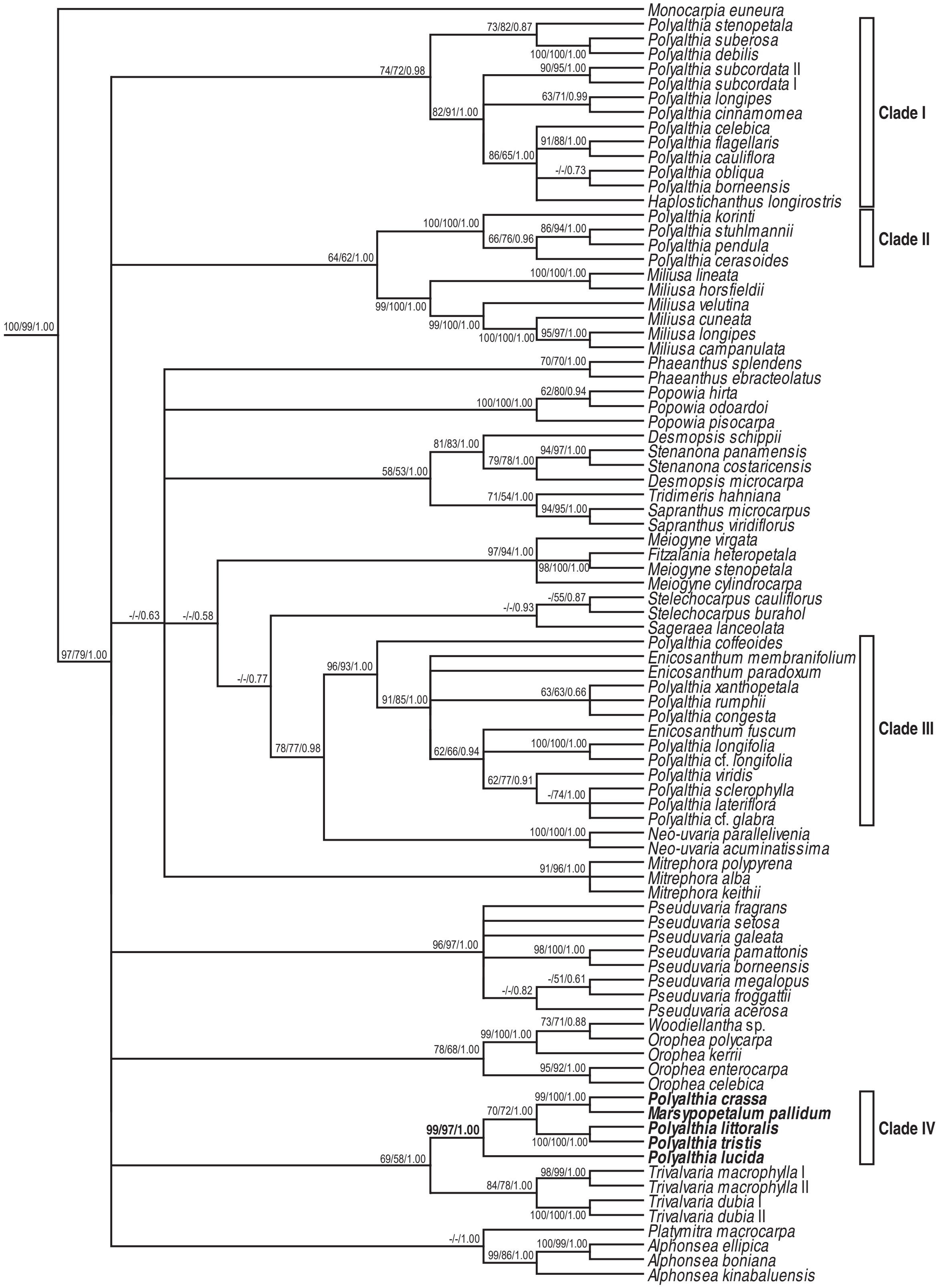


**Fig. 2.** Bayesian phylogeny inferred from combined *matK*, *rbcL* and *trnL-F* data under partitioned models (showing *Monocarpia* and the 'miliusoid' clade only; basal lineages shown in Fig. 1). Numbers at the nodes indicate MP, ML bootstrap values (>50%) and Bayesian posterior probabilities in that order. Clades I–IV discussed in text.

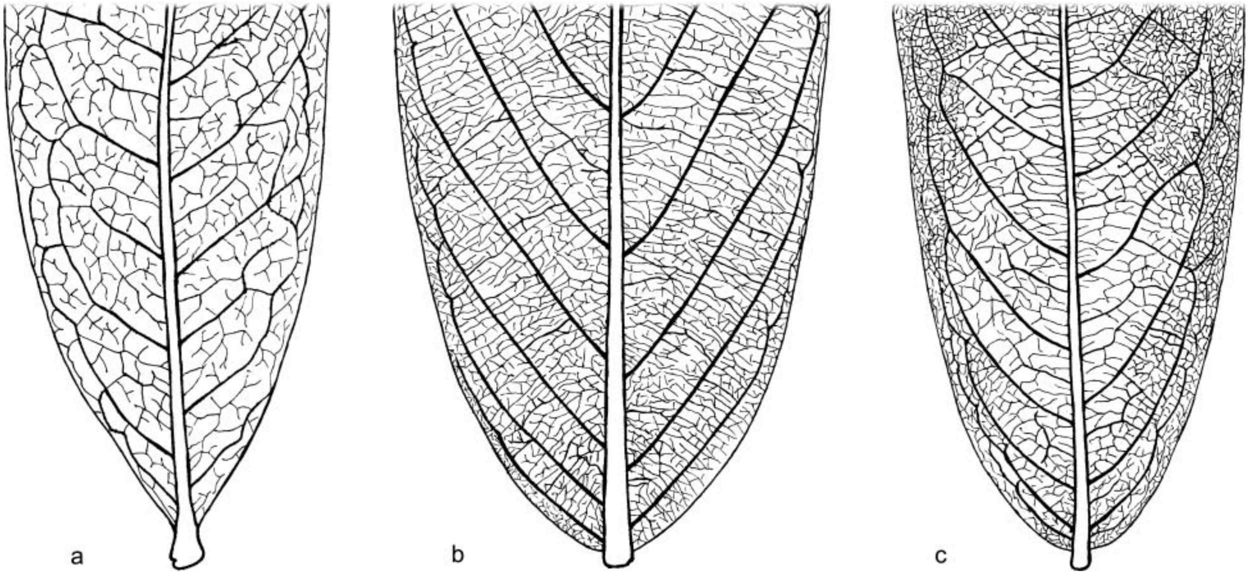


**Fig. 3.** Leaf venation patterns in selected Annonaceae species. a, *Marsypopetalum pallidum* (Clade IV), showing brochidodromous venation with prominent intermarginal veins, straight secondary veins, and reticulate tertiary veins. b, *Trivalvaria macrophylla*, showing eucamptodromous venation with parallel and curved secondary veins, and scalariform tertiary veins. c, *Polyalthia flagellaris* (Clade I), showing brochidodromous venation with prominent intermarginal veins, curved secondary veins and reticulate tertiary veins. Redrawn from Klucking (1986).

species, with moderate to strong support for a sister-group relationship with *Miliusa* (MP BS = 64%; ML BS = 62%; PP = 1.00). Clade III (MP BS = 96%; ML BS = 93%; PP = 1.00; corresponding to clade F4 as recognized by Mols *et al*., 2004*b*) consists of a combination of *Polyalthia* and *Enicosanthum* species, and is sister to a small *Neo-uvaria* clade, with strong support for the combined clade (MP BS = 78%; ML BS = 77%; PP = 0.98). Clade IV (MP BS = 99%; ML BS = 97%; PP = 1.00; corresponding with clade L as recognized by Mols *et al*., 2004*b*) consists of *Marsypopetalum pallidum* and four *Polyalthia* species (*P. crassa*, *P. littoralis*, *P. lucida* and *P. tristis*); this clade is sister to a small *Trivalvaria* clade, with the combined clade with weak to moderate support in the MP and ML analyses (MP BS = 69%; ML BS = 58%), but strong support in the Bayesian analysis (PP = 1.00).

## Discussion

The phylogenetic analyses (Figs 1, 2) confirm once again the polyphyletic status of *Polyalthia*, with species distributed in four main clades, although unequivocal resolution of the higher-level relationships between these clades cannot be achieved with the available data. The presence of four *Polyalthia* species in the same clade as the monotypic genus *Marsypopetalum* (Clade IV in Fig. 2) suggests that the taxonomic delimitation of the latter genus should be expanded.

Clade IV is characterized by the following morphological features: (1) leaves with very straight secondary veins and arcuate brochidodromous loops (*c.* 3–8 mm from the edge of the leaf) that are almost as prominent as the secondary veins; (2) generally extra-axillary inflorescences; (3) short pedicels, less than 1 cm long; (4) petals that are green at anthesis; (5) thick, fleshy petals; (6) inwardly curved inner petals, forming a partially enclosed floral chamber; and (7) a single, basal ovule in each carpel, and hence a solitary seed in each monocarp. Determination of the potential synapomorphic status of these morphological characteristics is constrained by the suboptimal resolution of the phylogeny.

Leaf venation in Clade IV (character 1) is strictly brochidodromous (*sensu* Hickey, 1979), with secondary veins linking together to form a series of prominent arches (e.g., *Marsypopetalum pallidum*: Fig. 3a; Klucking, 1986); the brochidodromous loops and the generally straight secondary veins form box-like intercostal areas. This type of venation is also seen in *Anaxagorea*, and has been interpreted as plesiomorphic for the family (Scharaschkin & Doyle, 2006). This contrasts with species in Clade III (inclusive of *Enicosanthum*), and *Trivalvaria* (e.g. *Trivalvaria macrophylla*: Fig. 3b; van Heusden, 1997), which all have eucamptodromous venation (sensu Hickey, 1979), with secondary veins that are upturned and gradually diminishing towards the apex, connected to the super-adjacent secondaries by a series of cross veins without forming prominent marginal loops. The venation pattern in species of Clade I (‘true’ *Polyalthia*) and Clade II varies in the extent to which the veins anastomose and the continuity of the brochidodromous loops; most of them bear a closer resemblance to those in Clade IV, however,

**Figs 4–9.** Flowers and fruits of *Polyalthia* species from Clade IV and *Trivalvaria*. Fig. 4. *Polyalthia cf. modesta*. Figs 5, 6. *Polyalthia crassa*. Fig. 7. *Trivalvaria macrophylla*. Fig. 8. *Trivalvaria nervosa*. Fig. 9. *Trivalvaria macrophylla*. Photographs: Figs 4, 7, 8, © Simon Gardener; Figs 5, 6, 9, © Piya Chalermglin; Figs 5, 6, reproduced from Chalermglin (2001).

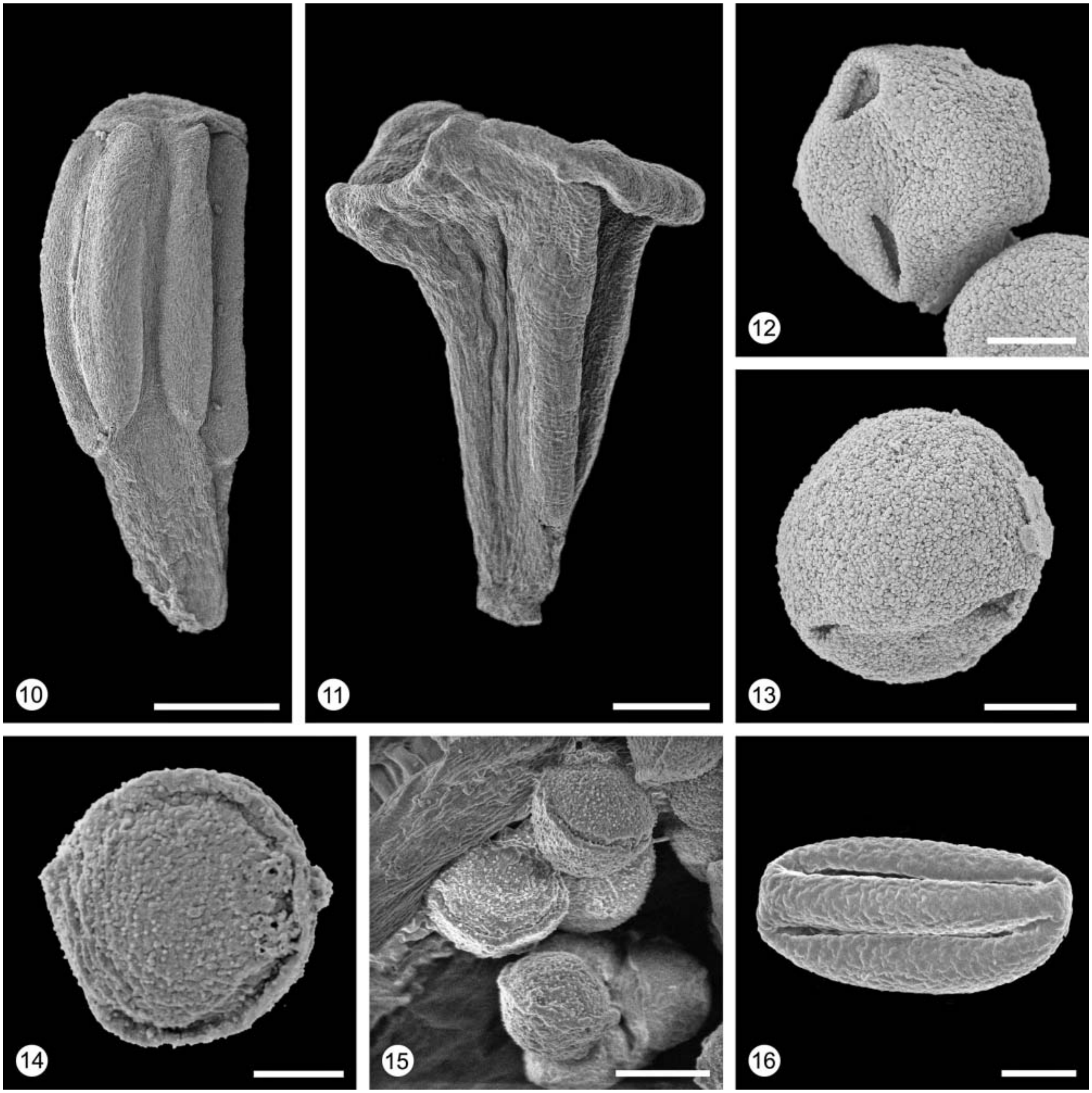
with 'festooned brochidodromous' venation (*sensu* Hickey & Wolfe, 1975) in which secondary loops exist outside the main brochidodromous arch (e.g. *Polyalthia flagellaris*: Fig. 3c). Although the secondary veins also anastomose away from the margin, they generally do not form a continuous series of brochidodromous loops as in Clade IV; the shape of the intercostal areas is furthermore different since the secondary veins are curved upwards.

The extra-axillary inflorescence position (character 2) and flowers with short pedicels (character 3), typical of most species in Clade IV, are features that are also observed in *Trivalvaria* (van Heusden, 1997). These characters are potential synapomorphies for Clade IV and *Trivalvaria* collectively since they are rare in other miliusoid taxa: the inflorescences are more commonly axillary in Clades I–III (Mols *et al.*, 2004*a*), for example, with pedicels generally longer than 1 cm (pers. obs.). *Polyalthia lucida* is a significant exception, however: it has axillary inflorescences despite being located within Clade IV, although its pedicels are nevertheless short (*c.* 8 mm; Merrill, 1915).

Although the retention of chlorophyll in the petals at anthesis (character 4) is common in *Polyalthia*, there is a marked contrast between species in Clade IV, with green petals (e.g. *P. modesta*: Fig. 4; and *P. crassa*: Fig. 5), and *Trivalvaria*, with cream-coloured petals (e.g. *T. macrophylla*: Fig. 7; and *T. nervosa*: Fig. 8). Species in Clade IV furthermore have thick and fleshy petals (character 5; Figs 4, 5), whereas those of *Trivalvaria* are comparatively thin and membranous (Figs 7, 8; van Heusden, 1992).

The inner petals of species in Clade IV (e.g. *Polyalthia modesta*: Fig. 4; and *Polyalthia crassa*: Fig. 5) are inwardly curved (character 6), forming a partially enclosed floral chamber (cf. Type IV *sensu* Saunders, 2010), which presumably functions as a pollination chamber. This feature is not observed in the other *Polyalthia* clades (Mols *et al.*, 2004*a*), nor does it occur in *Trivalvaria*, although *T. macrophylla* has apically connivent inner petals (Fig. 7; van Heusden, 1997), forming a Type III pollination chamber (*sensu* Saunders, 2010). Structurally distinct but functionally similar pollination chambers are widespread in the Annonaceae, reflecting extensive evolutionary convergence (Saunders, 2010).

The presence of only one, basal ovule per carpel and hence a solitary seed per monocarp (character 7; Fig. 6) is



**Figs 10–16.** Stamen and pollen morphology of selected species (scanning electron micrographs). Fig. 10. Stamen of *Polyalthia crassa*, showing reduced connective that does not extend over the thecae (*Chalermglin 521212-1*, HKU). Fig. 11. Stamen of *Trivalvaria macrophylla*, showing broad connective, extending over the thecae (*Djoemadi 116*, SING). Figs 12, 13. Modified disulculate pollen of *Trivalvaria dubia* (*Wong 0805*, HKU). Figs 14, 15. Zonasulculate pollen of *Trivalvaria macrophylla* (*Chalermglin 530212*, HKU). Fig. 16. Disulculate pollen of *Polyalthia crassa* (*Chalermglin 521212-1*, HKU). Scale bars: Fig. 10: 0.5 mm; Fig. 11: 0.25 mm; Figs 12–14, 16: 10 $\mu$m; Fig. 15: 20 $\mu$m.

less important diagnostically for Clade IV as it also occurs in *Polyalthia* Clades II and III as well as in *Trivalvaria* (Fig. 9). The 'true' *Polyalthia* clade (Clade I) is distinct, however, as all constituent species possess at least two lateral ovules per carpel (Mols *et al.*, 2004*a*).

There are several other characters of taxonomic importance although they are not specifically diagnostic for Clade IV. The staminal connectives of *Polyalthia crassa* (Fig. 10) and *Marsypopetalum pallidum* (Sinclair, 1955; van Heusden, 1992) differ from those of the other *Polyalthia* species in Clade IV and *Trivalvaria* (Fig. 11) as they do not extend over the thecae. This 'miliusoid' stamen type therefore appears to be synapomorphic for the *Polyalthia crassa*–*Marsypopetalum pallidum* lineage within Clade IV, and parallels similarly reduced connectives in *Alphonsea*, *Miliusa*, *Orophea*, *Platymitra*, *Sageraea* and *Stelechocarpus* pro parte (Mols *et al.*, 2004*a*).

Walker (1971) interpreted the pollen of *Trivalvaria* as inaperturate on the basis of light microscopy studies, although this seems to be contradicted by scanning electron micrographs (Figs 12–15) which indicate that it may be disulculate. *Trivalvaria dubia* (Figs 12, 13) possesses modified disulculate pollen with four short apertures, all slightly elongated in the same plane (equatorial or parallel to it) with a line of thinner exine connecting two adjacent apertures. This condition might be derived from the disulculate type, with the centre of each sulculus reduced and the ends modified into the four conspicuous apertures. The pollen of *Trivalvaria macrophylla* appears to be zonasulculate (Figs 14, 15), and might also be derived from the disulculate type by extension and connection of the ends of the two sulculi; sometimes the ring furrow seems less developed at the connection point (Fig. 14), consistent with its putative origin by the fusion of two sulculi. Although Mols *et al.* (2004*a*) regarded the pollen of *Marsypopetalum pallidum* and *P. littoralis* as inaperturate, the latter is actually disulculate with two 'cryptoapertures' (*sensu* Punt *et al.*, 2007; R.W.J.M. van der Ham, pers. comm.). The pollen of *P. crassa* is clearly disulculate (Fig. 16); it is therefore likely that disulculate pollen is common to all members of Clade IV and its sister clade, *Trivalvaria*, although not necessarily synapomorphic since such pollen appears to be widespread within the miliusoid clade (Waha & Hesse, 1988; Waha & Morawetz, 1988; Chaowasku *et al.*, 2008).

The morphological data are therefore congruent with the results of the phylogenetic study, although unequivocal identification of synapomorphies is precluded by inadequate resolution of the phylogeny. The molecular phylogeny, however, provides strong support for the recognition of Clade IV as a distinct genus, and the nomenclatural transfer of the five *Polyalthia* species included in Clade IV into *Marsypopetalum* is therefore proposed. The following nomenclatural list includes all species names within the more broadly delimited genus *Marsypopetalum*, including five new nomenclatural combinations.

### ***Marsypopetalum*** Scheff., *Tijdschr. Nederl. Ind*. 31: 342 (1870).

Type: *Marsypopetalum pallidum* (Blume) Kurz, *J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist.* **43**, 201 (1874).

Small treelets to medium-sized trees. Branches dark brown, glabrous or glabrescent. Leaves coriaceous, oblong to oblong-lanceolate; secondary veins straight, anastomosing 3–8 mm away from the leaf margin, forming prominent arcuate brochidodromous loops; leaf margin sometimes recurved. Flowers bisexual, solitary, extra-axillary; pedicels very short, *c.* 1 cm long; sepals 3, valvate; petals in two series, valvate, thick and fleshy; outer whorl sometimes inwardly curved; inner whorl always inwardly curved, enclosing the reproductive organs; carpels numerous; stigma capitate, pilose; ovule 1, basal; stamens numerous with truncate or reduced connectives. Fruit apocarpous; torus not much enlarged, depressed, somewhat globose; monocarps numerous, ovoid, oblong, or ellipsoid. Seeds 1 per monocarp, basal, vertical, ovoid, ellipsoid or fusiform.

### ***Marsypopetalum crassum*** (R. Parker) B. Xue & R.M.K. Saunders, comb. nov.

Basionym: *Polyalthia crassa* R. Parker, *Indian Forester* **55**, 375 (1929).

### ***Marsypopetalum littorale*** (Blume) B. Xue & R.M.K. Saunders, comb. nov.

Basionym: *Guatteria littoralis* Blume, *Fl. Javae* [*Anon.*] **30–31**, 99, fig. 49A (1830).
Additional homotypic synonyms: *Monoon littorale* (Blume) Miq., Ann. Mus. Bot. Lugduno-Batavum **2**, 19 (1865); *Polyalthia littoralis* (Blume) Boerl., *Cat. Plant. Phan.* **1**, 34 (1899).
*Polyalthia littoralis* (Blume) Boerl. var. *daclacensis* Bân, *Thu'c vật chí Việt Nam* **1**, 102 (2000).
*Polyalthia zhui* X.L. Hou & S.J. Li, *Novon* **14**, 173–175 (2004). [Listed as a synonym of *Polyalthia littoralis* by Li & Gilbert (in press). We furthermore sequenced the *matK* region for one of the paratypes of *P. zhui* from Hainan (*Liang 66102*), and found it to be identical to a collection from Java (*Rastini 153*)]

### ***Marsypopetalum lucidum*** (Merr.) B. Xue & R.M.K. Saunders, comb. nov.

Basionym: *Polyalthia lucida* Merr., *Philipp. J. Sci.*, *C* **10**, 249–250 (1915).

### ***Marsypopetalum modestum*** (Pierre) B. Xue & R.M.K. Saunders, comb. nov.

Basionym: *Unona modesta* Pierre, *Fl. Forest. Cochinch.* **2**, fig. 28A, C (1881).
Additional homotypic synonyms: *Polyalthia modesta* (Pierre) Finet & Gagnep., *Bull. Soc. Bot. France* **53**, *Mém.* **4**, 89–90 (1906).
? *Unona concinna* Pierre, *Fl. Forest. Cochinch.* **2**, fig. 28B (1881). [The protologue of *Unona concinna* (Pierre, 1881) was based on fruiting material. Fruit morphology is variable within *Marsypopetalum* species (van Heusden, 1992), and unequivocal determination of the taxonomic affinities of the name *U. concinna* is therefore difficult. We tentatively list the name *U. concinna* as a synonym of *M. modestum* in accordance with Pierre (1881), Finet & Gagnepain (1906) and Craib (1925), who all highlighted morphological similarities with '*Polyalthia modesta*']

### ***Marsypopetalum pallidum*** (Blume) Kurz, *J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist.* **43**, 201 (1874).

Basionym: *Guatteria pallida* Blume, *Fl. Javae* [*Anon.*] **21–22**, 20 (1830).

Additional homotypic synonyms: *Monoon pallidum* (Blume) Miq., *Ann. Mus. Bot. Lugduno-Batavum* **2**, 19 (1865).

*Marsypopetalum ceratosanthes* Scheff., *Natuurk. Tijdschr. Ned.-Indië* **31**, 343 (1870), nom. illeg. [Synonymy with *Guatteria pallida* first recognized by Scheffer (1870)]

***Marsypopetalum triste*** (Pierre) B. Xue & R.M.K. Saunders, comb. nov.

Basionym: *Unona tristis* Pierre, *Fl. Forest. Cochinch.* **2**, fig. 27 (1881).

Additional homotypic synonyms: *Polyalthia tristis* (Pierre) Finet & Gagnep., *Bull. Soc. Bot. France* **53**, *Mém.* **4**, 90 (1906); *Polyalthia littoralis* (Blume) Boerl. var. *tristis* (Pierre) Bân, *Novit. Syst. Plant. Vasc.* **11**, 190 (1974).

## Acknowledgements

Financial support was provided by a grant from the Hong Kong Research Grants Council (HKU 775009M), awarded to RMKS. We are grateful to: the directors and curators of IBSC, K, L, NY, P and SING herbaria for loan of (or access to) their collections and/or for providing leaf samples for DNA extraction; Piya Chalermglin, Wang Ruijiang and Laura Wong for collecting fresh plant material; Jim Doyle and Raymond van der Ham for their discussions regarding the interpretation of pollen apertures; Simon Gardner and Piya Chalermglin for permission to use their photographs; Vatsala Mirnaalini for drawing Fig. 3; Jim Doyle and David Johnson for their comments on the manuscript; and Laura Wong for general technical assistance.

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**Associate Editor: Charlie E. Jarvis**