

MOLECULAR PHYLOGENETIC ANALYSIS OF PHYLLANTHACEAE (PHYLLANTHOIDEAE PRO PARTE, EUPHORBIACEAE SENSU LATO) USING PLASTID *RBCL* DNA SEQUENCES¹

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Analysis of plastid *rbcl* DNA sequence data of the pantropical family Phyllanthaceae (Malpighiales) and related biovulate lineages of Euphorbiaceae sensu lato is presented. Sampling for this study includes representatives of all 10 tribes and 51 of the 60 genera attributed to Euphorbiaceae-Phyllanthoideae. *Centroplacus* and Putranjivaceae (Phyllanthoideae-Drypeteae) containing a paraphyletic *Drypetes* are excluded from Phyllanthaceae. *Croizatia*, previously thought to be a “basal” member of Euphorbiaceae-Oldfieldioideae (Picrodendraceae), falls within Phyllanthaceae. Phyllanthaceae with the mentioned adjustments form a monophyletic group consisting of two sister clades that mostly correspond to the distribution of tanniniferous leaf epidermal cells and inflorescence structure. With the exception of bigeneric Hymenocardiaceae and monotypic Bischofiaceae, none of the current Phyllanthoideae (Phyllanthaceae) tribal circumscriptions are supported by *rbcl*. *Antidesma*, *Bischofia*, *Hymenocardia*, *Martretia*, and *Uapaca*, all of which have previously been placed in monogeneric families, are confirmed as members of Phyllanthaceae. *Savia* is polyphyletic, and *Cleistanthus* appears paraphyletic. Paraphyly of *Phyllanthus* is also indicated, but this pattern lacks bootstrap support. Morphological characters are discussed and mapped for inflorescence structure, tanniniferous epidermal cells, breeding system, and fruit and embryo type. A table summarizes the main characters of six euphorbiaceous lineages.

Key words: *Centroplacus*; Euphorbiaceae; Malpighiales; molecular phylogenetics; morphology; Pandaceae; Phyllanthaceae; Phyllanthoideae; Putranjivaceae.

Euphorbiaceae sensu lato (s.l.) are a diverse, economically important, pantropical family of ca. 340 genera (including 8000–9000 species). The circumscription, classification, and affinities of the group have long been controversial (reviewed by Webster, 1987). The heterogeneity of Euphorbiaceae s.l. is reflected in a long history of attempts to dismember the family, and at least 20 segregates have been proposed (Webster, 1987). Corner (1976) and Huber (1991) advocated a split of uniovulate Euphorbiaceae from the biovulate taxa based on seed coat characters. A notable, recent attempt by Meeuse (1990) pro-

posed the recognition of 10 segregate families. The current inclusive sensu lato circumscription of the family and infra-familial classification was developed by Webster (1975, 1994b) and extended by Radcliffe-Smith (2001).

The most fundamental division in Euphorbiaceae s.l. is based on ovule number with a grouping of two biovulate subfamilies (Phyllanthoideae and Oldfieldioideae) and three uniovulate ones (Acalyphoideae, Crotonoideae, and Euphorbioideae). This binary division was conceptually provided by de Jussieu (1823, 1824) and considered the “first great advance in taxonomic insight” for the family (Webster, 1987, p. 23). Separation of Phyllanthoideae, and with limited data Oldfieldioideae, from uniovulates is supported by seed-protein serological data (Vogel, 1986; Jensen et al., 1994), lack of phorbol ester bioactivity (Beutler et al., 1996), predominantly ecarunculate seeds (present in most Oldfieldioideae), and derivation of cyanogenic glycosides from tyrosine (Hegnauer, 1977; Seigler, 1994). The biovulate subfamilies lack latex and laticifers (but see Balaji et al., 1996) although those are by no means ubiquitous in the uniovulates.

Chase et al. (1993) were the first to show the potential polyphyletic nature of Euphorbiaceae s.l. using molecular data that placed two taxa within the subclade of “rosid I” (= eurosid I sensu APG) later circumscribed as Malpighiales (APG, 1998). Their sampling included only two widely divergent species, uniovulate *Euphorbia polychroma* A. Kern. (Euphorbiaceae sensu stricto [s.s.]) and biovulate *Drypetes roxburghii*

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(Wall.) Hurus. (= *Putranjiva roxburghii* Wall.; Putranjivaceae), which presented the prospect that the nonsister placement was either an evolutionary reality or a study artifact of inadequate sampling and/or suboptimal analysis of a large data set. Other studies (Conti et al., 1996; Koontz and Soltis, 1999; Setoguchi et al., 1999; Schwarzbach and Ricklefs, 2000) using these initial two sequences have shown concordance with the basic eurousid I topology.

Phylogenetic hypotheses about the family have been further advanced with additional taxon sampling (Wurdack and Chase, 1996; Fay et al., 1997; Litt and Chase, 1999; Savolainen et al., 2000b; Chase et al., 2002) and additional genes (Soltis et al., 1997, 2000; Savolainen et al., 2000a; Tokuoka and Tobe, 2002; Wurdack, 2002; Davis and Chase, 2004). The original APG system (1998) reclassified Euphorbiaceae s.l. into three lineages, Euphorbiaceae, Putranjivaceae (from Phyllanthoideae tribe Drypeteae), and Pandaceae (from Acalyphoideae tribe Galearieae). Savolainen et al. (2000b) continued the dismemberment by removing the two remaining biovulate lineages, Phyllanthaceae (from Phyllanthoideae excluding tribe Drypeteae) and Picrodendraceae (as Pseudanthaceae; from Oldfieldioideae), and leaving Euphorbiaceae s.s. comprised of the remaining uniovulates (excluding tribe Galearieae = Pandaceae).

Following these changes, APG II (2003) recognized three biovulate and two uniovulate families from Euphorbiaceae s.l. All five family-level monophyletic groups remain more or less closely related within Malpighiales. However, even with additional sampling of taxa and/or genes, there are notably few bootstrap supported associations (i.e., >50%) for the segregate families either among themselves or with any of the other families of Malpighiales (see Savolainen et al., 2000a, b; Soltis et al., 2000, 2003; Wurdack, 2002; Davis and Chase, 2004). The Neotropical ditypic genus *Paradrypetes*, previously considered a "basal" member of Oldfieldioideae (Levin and Simpson, 1994a), is also a separate lineage (Wurdack and Chase, 1999) allied with Rhizophoraceae (Wurdack, 2002). It is aberrant in possessing raphides, colleters, and epipetiolar inflorescences.

The focus of this paper is Phyllanthaceae, the largest of the biovulate lineages. The systematics of the family are presently inferred to coincide with that of Phyllanthoideae (excluding Putranjivaceae). The recognition of Phyllanthoideae or its segregates at the family level has had a long, tumultuous history (Webster, 1987) that well predates the recent molecular-based reevaluation of the question. Phyllanthoideae span the morphological and chemical diversity of Euphorbiaceae s.l. Their distribution is also pantropical, although they include fewer temperate taxa than Euphorbiaceae s.s. In contrast, they lack worldwide economic plants as present in Euphorbiaceae s.s. A number of taxa are regionally cultivated for their fleshy edible fruits [e.g., *Phyllanthus acidus* (L.) Skeels, *P. emblica* L., *Baccaurea* spp., *Antidesma* spp.], provide timber, or show medicinal promise (Rizk, 1987; Calixto et al., 1998).

Phyllanthoideae have a limited diversity of floral bauplan, notably lacking extreme floral reductions as, e.g., in uniovulate *Euphorbia* s.l., with the exception of *Uapaca*. They also lack specialized pollinator adaptations such as brightly colored flowers or zygomorphy, but *Glochidion* and *Phyllanthus* subgenus *Gomphidium* have an apparently species-specific obligate mutualistic relationship with their pollinators (Kato et al., 2003; Kawakita and Kato, 2004). Instead, they present innumerable small variations on reproductive organs, especially an-

droecial and glandular elaborations. Their fossil record has been claimed to date back to the Upper Cretaceous based on wood (reviewed by Prakash et al., 1986). Wheeler (1991, p. 663) stated that the "phyllanthoid structural pattern is one of the earliest known for dicotyledonous woods," although it is generalized and not unique to any single extant family. Fruits compared to *Phyllanthus* are known from the Miocene (Nambudiri and Binda, 1989; Mai, 1996), and Phyllanthaceae appear well diversified by the Eocene from pollen evidence (Muller, 1981; Gruas-Cavagnetto and Köhler, 1992).

Phyllanthoideae have been considered the most primitive subfamily of Euphorbiaceae s.l., from which the others are derived or to which they are sister (Webster, 1994a). Simpson and Levin (1994) suggested the subfamily was paraphyletic and united by plesiomorphic characters. Webster (1994b) classified Phyllanthoideae into eight tribes with 60 genera (including two, *Centroplacus* and *Meborea*, incertae sedis) and ca. 2200 species. He also suggested that *Tacarcuna* belongs in Phyllanthoideae, although placed incertae sedis for the entire family. *Tacarcuna* was described nearly concurrently with Webster's system (1994b); it was at the time poorly known and originally incorrectly described as uniovulate.

Radcliffe-Smith's (2001) classification includes 10 tribes for 60 genera and closely follows that of Webster (1994b). It has detailed descriptions of genera and suprageneric taxa but provides few systematic innovations besides recognizing two monotypic tribes (Centroplacaceae and Martretieae) for previously unplaced genera (*Centroplacus* and *Martretia*, respectively), submerging *Meborea* in *Phyllanthus* and placing *Tacarcuna* as incertae sedis for Phyllanthoideae. He failed to take notice of the exclusion of *Phyllanoa* as belonging to Violaceae (Hayden and Hayden, 1996b). Two additional genera, *Distichirhops* and *Nothobaccaurea* (presumably related to *Baccaurea*), have been recently described (Haegens, 2000). *Dicoelia*, previously aberrant in Euphorbiaceae s.s., or sometimes considered close to Pandaceae, and *Lingelsheimia* (= *Aerisilvaea* = *Danguyodrypetes*) that has been included in tribe Drypeteae (= Putranjivaceae sensu APG) have recently been found to be members of Phyllanthaceae (Katriarachchi et al., 2004a).

Evolutionary relationships among Phyllanthoideae were first depicted in intuitive phylograms by Pax (1924). Webster (1984a) appears to have been the first to conduct a cladistic analysis of any Phyllanthaceae (and any Euphorbiaceae) in his revision of *Flueggea*. Levin's (1986b) work on Phyllanthoideae is the broadest published study to date and also groundbreaking in its demonstration of the utility of foliar morphology in resolving relationships. The few other morphological phylogenetic studies are on the *Baccaurea* alliance (Haegens, 2000) and limited sampling of Phyllanthaceae as outgroups for Oldfieldioideae (Picrodendraceae) (Levin and Simpson, 1994a) and Celastraceae (Simmons and Hedin, 1999). Surveys of wood anatomy (Menega, 1987), pollen (Punt, 1962; Köhler, 1965), seed-coat structure (Stuppy, 1996; Tokuoka and Tobe, 1999a, 2001), and additional work on leaf venation (Klucking, 1998) have identified putatively significant systematic characters that have yet to be put in a phylogenetic framework.

No published molecular systematic study has yet focused solely on Phyllanthaceae. The sampling for explicit higher-level studies has included a total of six exemplars using *rbcL* (Fay et al., 1997; Litt and Chase, 1999; Savolainen et al., 2000b; Chase et al., 2002). No Phyllanthaceae are present in angiosperm-wide multi-gene phylogenetic studies (e.g., Sa-

volainen et al., 2000a; Soltis et al., 2000, 2003) or gene-content surveys (e.g., Adams et al., 2002). This demonstrates limitations with exemplar sampling for poorly known polyphyletic groups. Källersjö et al. (1998) used limited unpublished data generated early in this study, but only generalized trees were presented.

To evaluate relationships at the generic level, the commonly used *rbcL* gene is well suited for higher-level intrafamilial questions (i.e., Bremer et al., 1995; Plunkett et al., 1996; Cameron et al., 2001). The large existing database of *rbcL* sequences makes this gene the locus of choice for evaluating taxa of uncertain affinity and the monophyly of families (i.e., Chase et al., 2002). We acknowledge the preliminary nature of this study because of the limitations of sampling with only a single gene. This study was undertaken to evaluate the circumscription of Phyllanthaceae and monophyly of suprageneric taxa described in current Phyllanthoideae classification schemes, elucidate patterns of intrafamilial relationships, examine the evolution of selected morphological characters, and provide a broad framework for more detailed, future studies. We have refrained from proposing a formal phylogenetic classification of Phyllanthaceae based solely on the analysis of *rbcL* sequence data. We do, however, wish to highlight well-defined groups that could be incorporated in such a system and the putative morphological synapomorphies characters that appear to support them.

MATERIALS AND METHODS

Taxon sampling—Taxa, voucher information, and GenBank numbers for all 110 *rbcL* sequences are available in the Appendix (see Supplemental Data accompanying the online version of this article). Eighty-nine sequences are previously unpublished, and six additional Phyllanthaceae sequences, originally generated for this investigation, have been published elsewhere (Fay et al., 1997; Savolainen et al., 2000b; Chase et al., 2002). Sampling included all 10 tribes and 51 of the 60 genera of Phyllanthoideae sensu Radcliffe-Smith (2001). A partial sequence of *Celianella* was obtained during manuscript revisions. Potentially the most significant taxa not sampled here as a result of lack of adequate material include *Ashtonia*, *Dicoelia*, *Lingelsheimia*, *Protomegabaria*, and *Richeriella*. Outgroups were chosen based on larger phylogenetic analyses (Chase et al., 1993; Savolainen et al., 2000a, b; Soltis et al., 2000; Wurdack, 2002) on subsets of the 500+ members of Malpighiales for which *rbcL* sequences are presently available. Biovulate Euphorbiaceae are clearly polyphyletic (Fig. 1a in Chase et al., 2002) and lack bootstrap-supported sister relationships, making the choice of malpighialean outgroups somewhat arbitrary on the basis of molecular evidence. Picodendraceae are probably the best outgroup choice for Phyllanthaceae (see Discussion; Wurdack, 2002; Fig. 4 in Davis and Chase, 2004). Given the low bootstrap support for a sister relationship of Phyllanthaceae and Picodendraceae, and the need to encompass all euphorbiaceous lineages, multiple outgroups were chosen. These included Euphorbiaceae s.s., Humiriaceae, Irvingiaceae, Lophopyxidaceae, Pandaceae, Picodendraceae, and Putranjivaceae. Humiriaceae seem particularly useful for malpighialean lineages that lack supported sister groups due to their low levels of molecular divergence (see Fig. 1b in Chase et al., 2002). An analysis including representatives of all biovulate lineages allows taxa to group with individual clades and readily reveals misclassified taxa either by exclusion or emerging phylogenetic patterns.

Laboratory methods—Samples and data were gathered over nine years and were subject to a diverse array of evolving methods and technologies. DNA extraction, polymerase chain reaction (PCR), and sequencing methods largely followed Chase et al. (2002) or Wurdack (2002). Recent extractions involving about half of the accessions (and nearly all herbarium material) have been made using the DNeasy Plant Mini Kit (Qiagen, Valencia, California, USA) following tissue disruption of 0.5–1 cm² of leaf tissue in a FastPrep FP-120

bead mill using lysing matrix “A” tubes containing one ceramic bead and garnet sand (Qbiogene, Carlsbad, California, USA). DNA extractions followed manufacturer’s protocols with the modification of buffer API lysis conditions by the addition of 0.4–0.7 mg of PCR-grade proteinase K (Roche, Indianapolis, Indiana, USA), 6.5% 2-mercaptoethanol or 15 mg dithiothreitol, and incubation at 42°C for 12–48 h on a rocking platform. This mini-prep method is primarily designed for herbarium material and minimizes sample mass and contamination risks. The addition of *N*-phenacylthiazolium bromide (PTB; Poinar et al., 1998) or 4,5-phenacyldimethylthiazolium chloride appeared helpful for recalcitrant herbarium material. Many Phyllanthaceae (especially Flueggeinae and *Leptopus*) were mucilaginous and difficult to extract. *Jablonskia* contained a potent PCR inhibitor that was removed by centrifugal ultrafiltration with Ultrafree-MC (100 000 nominal molecular weight limit; Millipore, Billerica, Massachusetts, USA) following the manufacturer’s directions.

The *rbcL* exon was amplified as one piece using primers 1F and 1368R/1460R (or variants) or as two overlapping fragments using combinations 1F-724R and 636F-1460R (For primer information, see Appendix 2 in Supplemental Data accompanying online version of this article.). Three noncontiguous fragments of *Tacarcuna* from a highly degraded sample were generated using 1F-367R, 636F-854R, and 1024F-1368R. PCR products were purified and directly sequenced for both strands. For 17 taxa, *rbcL* sequences were obtained by radioactive, manual-sequencing methods using eight primers (1F, 234F, 424F, 633F, 878F, 286R, 346R, 895R, 1460R). Autoradiograms were read by eye and recorded by hand.

The remaining sequences were more recently generated by fluorescent sequencing on ABI Prism 373A or 377XL automated sequencers (Applied Biosystems, Foster City, California, USA) with dye-terminator ABI Prism Ready Reaction mix and typically using four primers (or any additional amplification primers). Sequences were assembled and edited in Sequencher 3.1.1 (Gene Codes, Ann Arbor, Michigan, USA). Significant missing data are in *Celianella*, *Maesobotrya* sp., *Tacarcuna*, and *Uapaca* sp.

Data analysis—Sequences were aligned by eye (no indels present), and bases 1–30 that formed the primer-binding region most inclusive of all 1F primer variants used were excluded to reduce missing data. Maximum parsimony searches were conducted using PAUP* 4.0b10-Altivec (Swofford, 2003) with 1000 replicates of random taxon addition, equal weights, and unordered characters (Fitch parsimony; Fitch, 1971), and tree bisection-reconnection (TBR) branch swapping with 10 trees held at each step (MulTrees, saving multiple equally short trees, on) to save time swapping on large numbers of suboptimal trees. The resulting trees, including multiple minimal-length trees, were used as starting trees in another round of TBR and a maximum tree limit of 20 000. Branches with a minimum length of zero were collapsed. Uninformative characters were included in analyses except, as noted, for the calculation of alternative tree statistics. Tree statistics included the consistency index (CI; Kluge and Farris, 1969), retention index (RI; Farris, 1989), and rescaled consistency index (RC; Farris, 1989). Partitioned analyses were conducted of 5′ and 3′ halves (or in the case of *Tacarcuna*, each of the three noncontiguous fragments was examined) of *rbcL* corresponding to primer pairs used for amplifying degraded samples. Incongruent positions between these separate searches could be evidence of chimeric sequences composed of data derived from different taxa (many taxa were amplified in two pieces using the internal primers described earlier, which could result in a contaminating sequence being preferentially amplified if the desired template DNA was highly degraded, as is often the case with herbarium DNA). Relative support for clades was evaluated using the bootstrap (Felsenstein, 1985). For the bootstrap, 1000 replicates were performed using TBR swapping with each replicate consisting of five random taxon additions, holding 10 trees at each step and saving no more than 10 trees (nchuck = 10, chuckscore = 1) per iteration. Bootstrap percentages are described as high (85–100%), moderate (75–84%) or low (50–74%). Tree and character manipulations were carried out in MacClade 4.0 (Maddison and Maddison, 2000). These included translations to amino acids to check for internal stop codons (none found).

RESULTS

No unusual amino acid substitutions (i.e., substitutions not tabulated in Fig. 4 of Kellogg and Juliano, 1997) were detected at the RuBisCo active site or other conserved residues noted by Kellogg and Juliano (1997). Putranjivaceae (including *Drypetes*, *Putranjiva*, and *Sibangea*) contains a suite of unusual synapomorphies (Y-33, W-248, Q-440, K-447, N-453), but these amino acid differences do not affect major structural functions and do not appear to be coordinated changes (see examples in Kellogg and Juliano, 1997). The stop codon TGA (vs. TAA in all other Phyllanthaceae except as noted later) was present in *Breynia*, *Phyllanthus flagelliformis* Müll. Arg., *P. fluitans* Benth., *P. liebmannianus* Müll. Arg. subsp. *platylepis* (Small) G. L. Webster, and *Reverchonnia* but otherwise absent in Phyllanthaceae and rare in Malpighiales. This is the result of a duplication within the 3' terminus of the gene where bases 1397–1428 have been shifted to 1422–1453 following a 25-base pair (bp) duplication (e.g., positions 1397–1421 and 1422–1446 form tandem paralogs, shifting the otherwise conserved TAA stop codon into the flanking noncoding region but resulting in a new stop codon that terminates the gene at the typical 1428 bases). One additional predicted amino acid beyond the usual malpighialean 475 is present in *Phyllanthus nutans* Sw. (I-476) and *Spondianthus* (K-476). *Andrachne microphylla* (Lam.) Baill. and *Andrachne telephioides* L. contain three additional amino acids (V-476, V-477, L-478). Four species, each represented by two sequences from separate accessions, have variation. Raw data were verified for *Disco-carpus* (one base difference) and the Kenyan *Heywoodia* (AY663587). It is unknown if error or genuine polymorphism contributes to *Breynia*, *Putranjiva roxburghii*, and the other *Heywoodia* sequence differences. The two *Poranthera huegelii* Klotzsch sequences were identical as were *Leptopus chinensis* (Bunge) Pojark. and *L. colchicus* (Fisch. & C. A. Mey. ex Boiss.) Pojark.

The 109-sequence (76 Phyllanthaceae before the inclusion of *Celianella*) *rbcL* matrix contained 1398 characters (1.74% missing or ambiguous cells) of which 464 (365, Phyllanthaceae only) were variable and 359 (266, Phyllanthaceae only) potentially parsimony informative. Phylogenetic analysis yielded the upper limit of 20 000 most parsimonious trees (MPT) of length 1633 steps, CI = 0.39 (0.34 excluding uninformative characters), RC = 0.30 (0.27 excluding uninformative), and RI = 0.77. The strict consensus with bootstrap percentages (≥ 50) is shown in Fig. 1 and a single most parsimonious tree in Fig. 2. A reduced sampling containing only Phyllanthaceae + Picrodendraceae (removing all unresolved outgroup taxa, especially Putranjivaceae) did not produce less than the tree limit of 20 000 MPT (results not shown). The partitioned analyses (i.e., the two halves of *rbcL*) did not detect any bootstrap-supported (BP > 50) incongruence.

The three families (Phyllanthaceae, Picrodendraceae, and Putranjivaceae) of biovulate Euphorbiaceae s.l. sensu APG II as well as Pandaceae + *Centroplacus* were recovered in the strict consensus tree (Fig. 1). Monophyly of Phyllanthaceae received low support (BP 73). Phyllanthoideae sensu Webster (1994b) are polyphyletic due to the inclusion of *Centroplacus* (although its sister position to Pandaceae has BP < 50) and *Drypetes*, *Putranjiva*, and *Sibangea* (Putranjivaceae), and the exclusion of *Croizatia* (Oldfieldioideae). Phyllanthaceae are resolved into two well-supported sister clades (BP 91 and 98, respectively), hereby designated the fasciculate and tannini-

ferous clades. These names refer to different inflorescence types (axillary fascicles vs. elongate), and the absence and presence of tanniferous epidermal cells. With the exception of bigeneric Hymenocardieae *rbcL* does not support the monophyly of any of the current tribes in Phyllanthoideae (Phyllanthaceae) (Webster, 1994b).

The fasciculate clade (BP 91) contains *Heywoodia* and five supported subclades. Subclade F1 (BP 100) includes Phyllanthaceae subtribe Flueggeinae plus *Savia bahamensis* Britton (Wielandieae). Subclade F2 (BP 95) unites 10 genera from four phyllanthoid tribes (Amanoeae, Brideliaceae, Phyllanthaceae, and Wielandieae), oldfieldioid *Croizatia*, and incertae sedis *Tacarcuna*. This subclade includes *Savia* section *Savia*, thereby making that genus biphyletic. *Cleistanthus* (Brideliaceae) is paraphyletic in a well-supported subclade (BP 99) together with *Bridelia* (Brideliaceae), *Pentabrachion* (Amanoeae), and *Pseudolachnostylis* (Phyllanthaceae). The strongly supported subclade F3 (BP 99) contains four genera from three subtribes of tribe Phyllanthaceae, *Actephila* (Wielandieae), and *Poranthera*, the only member of Antidesmeae to fall outside the tanniferous clade. The anomalous position of "*Poranthera* sp." embedded in Euphorbiaceae s.s. in Chase et al. (2002) is based on a misidentified collection. *Chase 2162* is correctly *Monotaxis megacarpa* F. Muell. (Euphorbiaceae s.s.) and excluded in favor of new accessions of authentic *Poranthera*. All Wielandieae from the western Indian Ocean region (Malagassia) are found in subclade F4 (BP 100). *Astrocasia* and *Chascotheca* form a well-supported sister group (subclade F5; BP 100). *Heywoodia* (subclade F6) does not have supported relationships. The tanniferous clade (BP 98) includes all members of Antidesmeae except *Poranthera*, as well as Bischofieae, Hymenocardieae, and Martretieae. The Antidesmeae subtribes Antidesminae (including Hymenocardieae and Martretieae) and Scepinae each form well-supported (BP 90+) subclades (T1 and T2, respectively). *Bischofia*, *Jablonskia* + *Celianella* (the latter not shown), *Spondianthus*, and *Uapaca* mostly lack supported sister groups, although they are resolved in the strict consensus (Fig. 1) and *Spondianthus* + *Bischofia* is weakly supported (BP 50).

DISCUSSION

Affinities and circumscription of Phyllanthaceae—Based on molecular data with limited exemplar sampling, the Angiosperm Phylogeny Group II (APG, 2003) recognized three segregate families (Phyllanthaceae, Picrodendraceae, and Putranjivaceae) of biovulate Euphorbiaceae s.l. Until now, delimitation of these families has relied on inferences from previous sensu lato classifications (e.g., Webster, 1994b; Radcliffe-Smith, 2001). Our analyses recover all three families for which circumscription is largely in accordance with that predicted from the morphologically based classifications. Due to the focus of this paper on Phyllanthaceae and the resulting limited outgroup sampling, a close relationship among these families should not be inferred by proximity in our trees. Additional sampling and analyses of more genes have so far only modestly improved support for deep branches along the spine of Malpighiales phylogenies. Three-gene analyses (*atpB*, *rbcL*, 18S rDNA; Wurdack, 2002) recovered Phyllanthaceae + Picrodendraceae in the strict consensus, but this sister relationship received no support (BP < 50). These same analyses have low support for Phyllanthaceae but strong support for each of its two main clades. Davis and Chase (2004) found weak sup-

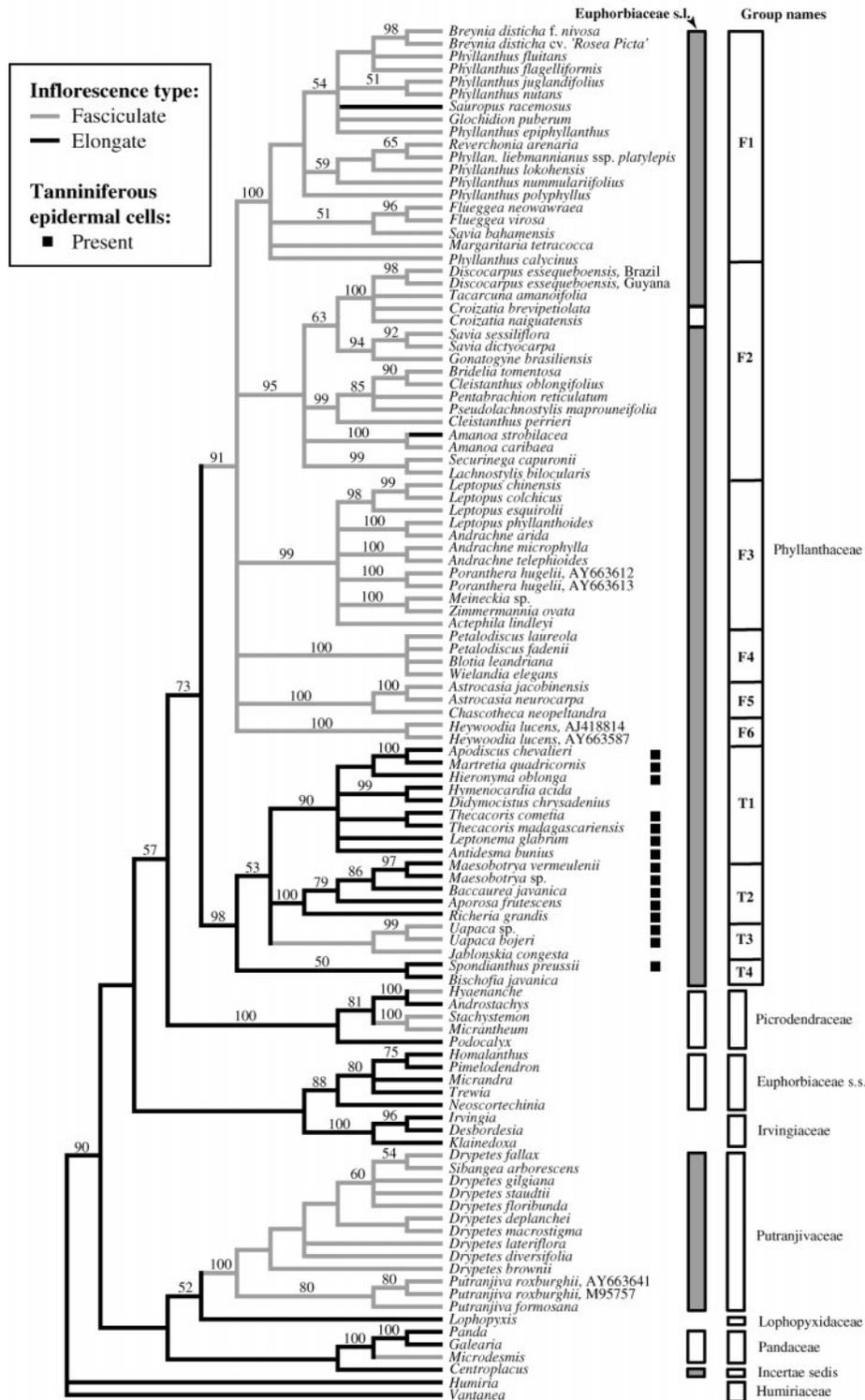


Fig. 1. Strict consensus of 20 000 minimal length trees resulting from parsimony analysis of 109 *rbcL* sequences of Malpighiales. The numbers above the branches are bootstrap percentages $\geq 50\%$. The inner bar indicates Euphorbiaceae s.l. of Webster (1994b) and Radcliffe-Smith (2001) with Phyllanthoideae shaded. The outer bar indicating group names has families sensu APG II (2003) overlain with Phyllanthaceae subclade designation used here (F = fasciculate; T = tanniniferous). Inflorescence type and the presence of tanniniferous leaf epidermal cells are mapped according to the legend.

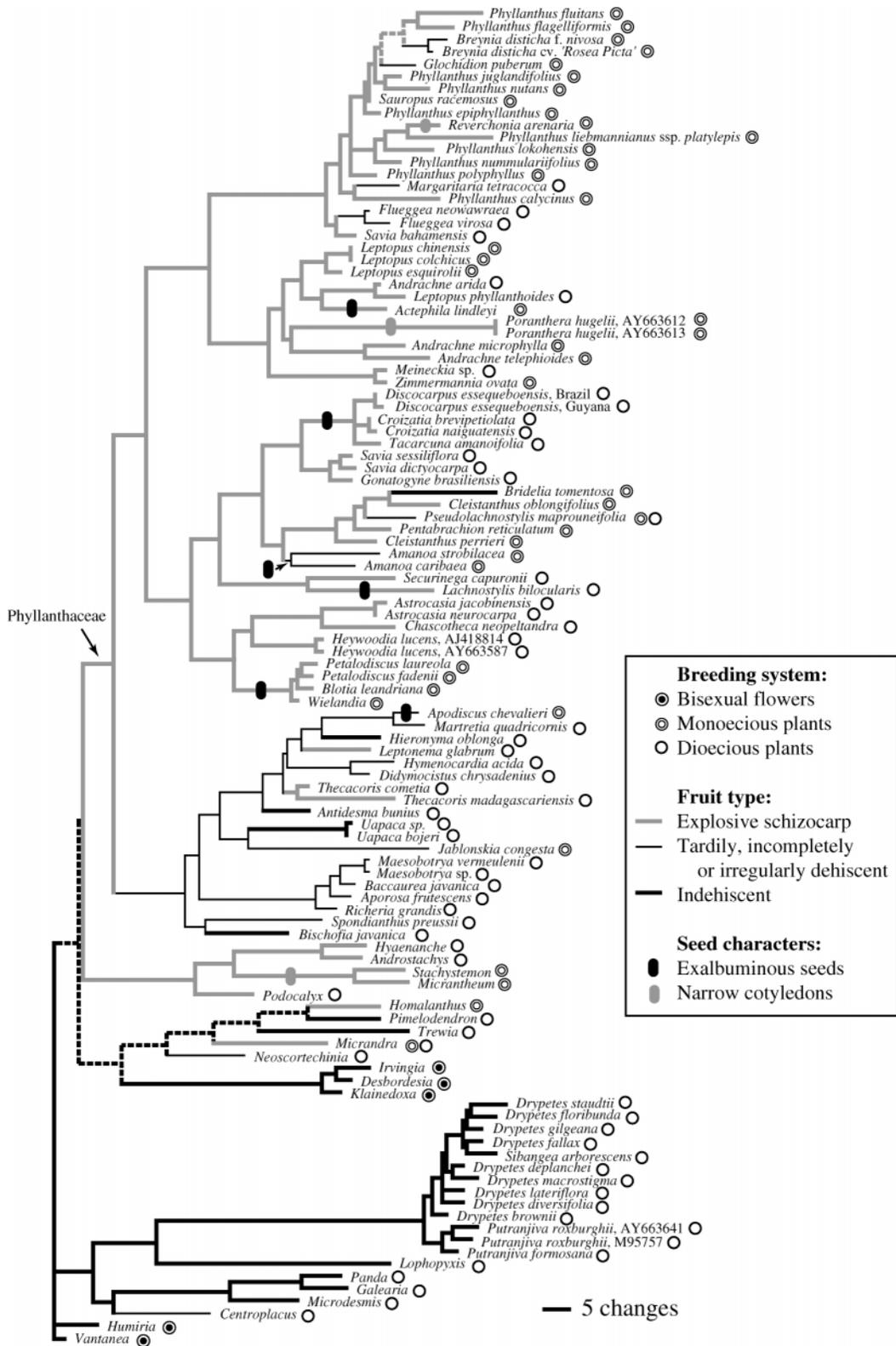


Fig. 2. Phylogram of one of 20 000 minimal length trees. Breeding system, fruit type, and seed characters are mapped according to the legend. Dashed branches are equivocal. The branches leading to Euphorbiaceae s.s. are equivocal if the family is constrained to be plesiomorphically schizocarpous but otherwise would be indehiscent with ACCTRAN optimization.

port (BP 53) for Phyllanthaceae + Picrodendraceae using combined *ndhF*, *rbcL*, and *PHYC* (although BP < 50 in separate plastid and nuclear analyses) and their strong support for Phyllanthaceae (BP 98) reflects sampling only two members of the fasciculate clade that in our analyses also receives strong support (BP 91).

Picrodendraceae differ from Phyllanthaceae in pollen characters (Levin and Simpson, 1994a), notably the echinate pollen exine first used by Köhler (1965) to distinguish the group (as Oldfieldioideae) and more than three pollen apertures. Pollen with spinose sculpturing (e.g., in *Amanoa* and *Securinega*) or more than three apertures (e.g., in *Phyllanthus*) rarely occurs in Phyllanthaceae and appears to be the result of convergence (Levin and Simpson, 1994a; Simpson and Levin, 1994). Additionally, Phyllanthaceae are ecarunculate (but see Stuppy, 1996, for *Celianella*) and frequently have petals, whereas Picrodendraceae are apetalous and usually have carunculate seeds. Compound leaves are common in Picrodendraceae but in Phyllanthaceae are restricted to *Bischofia javanica* Blume (Table 1).

Embryological evidence (e.g., two ovules per locule) may unite Phyllanthaceae + Picrodendraceae (PO-group, Sutter and Endress, 1995; D. Sutter, University of Zurich, Zurich, Switzerland, personal communication). Ovule number must be used with care and in some cases, scrutinized from an anatomical-developmental standpoint. Many biovulate taxa appear uniovulate in fruit (e.g., *Antidesma*, *Spondianthus*, *Tacarcuna*, *Wielandia*) from the abortion of one of the paired ovules. Some taxa may have carried this further and secondarily lost an ovule although they have not been investigated for embryological vestiges at early stages. These include uniovulate *Scagea*, which was placed in the biovulate Oldfieldioideae. *Pseudanthus ovalifolius* F. Muell., from the same subfamily, is the only uniovulate species in an otherwise biovulate genus (Halford and Henderson, 2003). This is also implicit in the proposed general derivation of uniovulates from ancestral biovulates noted earlier (Webster, 1994a).

Sutter and Endress (1995) noted a suite of gynoecial similarities (potential synapomorphies) between uni- and biovulate Euphorbiaceae s.l., including an extended nucellar beak, divided styles often with a ventral furrow, epitropous ovules, obturators present, carunculate seeds (usually lacking in Phyllanthaceae), unicellular-papillate stigmas, and often trimerous gynoecia. A nucellar beak, epitropous ovules, and obturator may in combination be unique to Euphorbiaceae s.s., Phyllanthaceae, and Picrodendraceae. The schizocarp with complex explosive dehiscence in these three lineages could also be synapomorphic and adaptively related to the embryology (Berg, 1975; but see also Webster's [1994a] critique). It is unclear whether these complex characters have evolved multiple times or whether they have been lost in some families that are related to and possibly interdigitated with Euphorbiaceae s.l. that formerly had them (i.e., become secondarily indehiscent).

Excluded taxa—The third biovulate lineage, Putranjivaceae, appears more distantly related to the other former members of Phyllanthoideae as suggested by embryological evidence (Tokuoka and Tobe, 1999b), especially the lack of a nucellar beak. It has been primarily united with Phyllanthoideae based on characters that could be interpreted as plesiomorphic. The unusual sieve-element plastid type (PICs) recorded for *Drypetes* and *Bischofia* but no other Phyllanthaceae (Behnke, 1981) was erroneous (H.-D. Behnke, Heidelberg

University, personal communication). Both *Drypetes* and all 31 examined species of Euphorbiaceae s.l. have S-type plastids (H.-D. Behnke, unpublished data), as have 16 other malpighialelean families. An exception is Rhizophoraceae sensu APG II (including Erythroxylaceae), which have the PVc type. Despite the extremely limited phytochemical knowledge of the family, the presence of mustard oils (glucosinolates) in Putranjivaceae has been unduly emphasized for systematic comparisons, usually with Brassicales (Rodman et al., 1993, 1996; Seigler, 1994). Putranjivaceae share $n = 20$ (Hans, 1973, with probably erroneous counts; see Chattopadhyay and Sharma, 1988), whereas Phyllanthaceae have predominantly $x = 13$ (see later).

Large-scale *rbcL* analyses (Savolainen et al., 2000a, b; Wurdack, 2002) place Irvingiaceae and Putranjivaceae as sisters, whereas small-scale *rbcL* analyses (i.e., as shown here) and data from other genes (18S rDNA, *atpB*, and combined with *rbcL*; Wurdack, 2002) support a relationship of Putranjivaceae to monotypic Lophopyxidaceae. All three families are isolated lineages, and Putranjivaceae is the most divergent member in this analysis (see Fig. 2). *Lophopyxis maingayi* Hook. f. has a scandent habit with tendrils and anomalous secondary growth, petals, and dry, winged fruits. Putranjivaceae, in contrast, are strictly shrubby or arborescent, apetalous, and drupaceous. Characters consistent with common ancestry include leaves with theoid teeth, dioecy, and many floral features such as pentamerous flowers with a disc, styles separate or nearly so, and two pendulous apical-axile anatropous ovules per locule (each with an obturator), one of which aborts during the development of the indehiscent fruit.

Putranjiva and *Sibangea* closely resemble the large pantropical genus *Drypetes*, and their generic distinctiveness has been questioned (Webster, 1994b). In our analyses, relationships within Putranjivaceae are poorly resolved. It is indicated that *Sibangea* nests within a paraphyletic *Drypetes* and should be subsumed under that genus. This is concordant with the subtle generic differences given by Radcliffe-Smith (1978, 2001) and Webster (1994b). In *Sibangea*, the pistillate sepals are open in bud and persistent in fruit, whereas in *Drypetes* they are imbricate and deciduous. The pistillate sepals are narrow and therefore do not overlap as in regular *Drypetes* flowers. Pax and Hoffmann (1922) included *Sibangea* in *Drypetes* section *Hemicyclia*. *Sibangea arborescens* Oliv. from Gabon belongs to a poorly supported clade also containing four *Drypetes* species from West Africa (two each of section *Sphragidia* and *Stemonodiscus*, respectively) which is in turn sister to two Australasian species, *D. deplanchei* (Brongn. & Gris) Merr. and *D. macrostigma* J. J. Sm. The three Neotropical species, *D. lateriflora* (Sw.) Urb., *D. diversifolia* Krug & Urb., and *D. brownii* Standl., do not resolve as a monophyletic group. *Drypetes lateriflora* is the only New World member of section *Oligandrae*, and the remaining Neotropical species belong to section *Drypetes* (Webster, 1967), which also has Old World representatives. The sectional classification used in the latest revision of the entire genus (Pax and Hoffmann, 1922) is not concordant with our results and is in need of reevaluation.

The small Asian genus *Putranjiva* is sister to *Drypetes* including *Sibangea* but this relationship lacks bootstrap support. Differential characters between *Putranjiva* and *Drypetes* lie in leaf venation, absence/presence of a floral disc, number of stamens, and shape of stigmas. The topology of Putranjivaceae presented here indicates a potentially complex biogeographic

history as only c. 20 of c. 200 *Drypetes* species are Neotropical (G. Levin, Center for Biodiversity, Illinois Natural History Survey, personal communication). The inclusion of more species, especially southern Asian *Drypetes*, and the use of more rapidly evolving molecular markers is called for.

Lingelsheimia (not sampled here), a small poorly known Afromalagasy genus, has been placed in tribe Drypeteae (Webster, 1994b; Radcliffe-Smith, 2001). It is anomalous in Putranjivaceae but not Phyllanthaceae based on seed coat data (Tokuoka and Tobe, 2001) and leaf morphology (Levin, 1986b). The genus has been confirmed as member of Phyllanthaceae (Katriarachchi et al., 2004a).

The affinities of *Centroplacus* (reviewed by Radcliffe-Smith, 2001) have been thought to be with Celastraceae, Flacourtiaceae, Pandaceae, or most recently Phyllanthaceae. The APG II (APG, 2003) highlighted this wandering affiliation by considering it incertae sedis. Radcliffe-Smith (2001) returned to the views of Pax and Hoffmann (1931) by including *Centroplacus* in Phyllanthoideae, but his placement in a monotypic tribe Centroplacaceae at the end of the subfamily did little to further clarify relationships. Pollen morphology (Punt, 1962; Köhler, 1965) excluded the genus from biovulate Euphorbiaceae and indicated a relationship with Acalyphoideae tribe Galearieae (= Pandaceae). Seed coat data have been interpreted controversially. Stuppy (1996) excluded *Centroplacus* from biovulate Euphorbiaceae, whereas Tokuoka and Tobe (2001) found no reason to separate it from Phyllanthaceae. Comparative seed coat studies with Pandaceae have not been published.

Our analyses place *Centroplacus* outside of Phyllanthaceae as the unsupported (BP < 50) sister to uniovulate Pandaceae. Airy Shaw (in Willis, 1966) put *Centroplacus* in Pandaceae, an affinity recently accepted by Takhtajan (1997) and Govaerts et al. (2000). *Centroplacus* differs from Pandaceae in, e.g., possessing two ovules per locule (vs. one), dehiscent fruits (vs. drupaceous), and carunculate seeds (vs. ecarunculate) (Table 1).

Relationships in Phyllanthaceae—The *rbcl* tree (Fig. 1) strongly supports relationships in Phyllanthaceae that are substantially different from those suggested in previous classifications. Seed coat data (Tokuoka and Tobe, 2001) are partly congruent with these results, and exotegmens with ribbon-like cells appear plesiomorphic for the family. Wood anatomy (*Aporosa* vs. *Glochidion* types; Metcalfe and Chalk, 1950; Mennega, 1987) does not correlate well with the major clades recovered, although it has mainly been approached from a typological rather than a phylogenetic perspective and needs to be reconsidered. Vegetative anatomy (e.g., Gaucher, 1902) indicates coherence within the tanniferous (T1–T4) clade and within the Flueggeinae (F1) clade but provides no further characters uniting major groups recognized here. This corresponds with Pax and Hoffmann's (1931) statement that anatomical data generally do not support delimitation of major groups but are often useful for defining smaller taxonomic units. The occurrence of tanniferous epidermal cells in one of the major phyllanthoid clades recovered here, however, shows that a thorough examination of morphological/anatomical characters may still yield more significant indicators of phylogenetic relationships. In considering cytological data (reviewed by Hans, 1973, but see critique by Webster, 1994a, on the partly erroneous conclusions; also Urbatsch et al., 1975; Tammaro and Pogliani, 1977; Humphries et al., 1978; Gill et al., 1981; Pod-

lech, 1986; Rossignol et al., 1987) in relation to our results, $x = 13$ appears to be the base chromosome number for the family.

Phyllanthaceae are resolved into two well-supported sister clades corresponding to the distribution of tanniferous epidermal cells and to inflorescence types. The inflorescence type is used here as in the second couplet of Webster's tribal key (1994b, p. 35): axillary clusters with "inflorescence axes usually less than 1 cm long" vs. "spicate or racemose" inflorescences with axes usually over 1 cm long. The clade with contracted inflorescence axes and lacking tanniferous cells is earlier designated as the fasciculate clade comprising subclades F1–F6, and its sister clade with predominantly elongated inflorescence axes is earlier designated as the tanniferous clade comprising subclades T1–T4. These two clades could prove a logical subfamilial division, although they presently lack uncontradicted morphological distinctions.

The clustered vs. elongated appearance of the inflorescence was noted by Bentham and Hooker (1880) and later adopted in major classifications to delimit the core of the tanniferous clade (Pax and Hoffmann, 1922, as Antidesmineae; Webster, 1994b, as Antidesmeae + Hymenocardieae). Exceptions are in the tanniferous clade subclade T3 with contracted inflorescences and in the fasciculate clade the rare occurrence of (possibly secondarily) elongated inflorescences (i.e., *Amanoa strobilacea* Müll. Arg., *Sauropus racemosus* Beille). Axillary fasciculate inflorescences are sometimes concentrated at the tips of the branches and subtended by much-reduced foliage leaves (e.g., in some species of *Amanoa*, *Bridelia*, *Petalodiscus*, and *Poranthera*). In these cases the subtending leaves resemble regular foliage leaves in all but size and have normal stipules. Bracts subtending flowers in elongated inflorescences of the tanniferous clade are clearly differentiated from the foliage leaves and lack stipules. No systematic study (although Webster [1956–1958] discussed variation and issues in *Phyllanthus*) of inflorescence morphology in Phyllanthaceae has yet been undertaken to establish homology of the inflorescence types.

The fasciculate clade—The first major clade of Phyllanthaceae includes members with axillary, fasciculate clusters of flowers and no tanniferous epidermal cells in leaves. Tannin deposits, but not the enlarged idioblastic leaf epidermal cells characteristic of most of the tanniferous clade (see Levin, 1986a), have been detected in the leaves of *Discocarpus* (Hayden and Hayden, 1996a; not reported by Levin, 1986a) and the leaves and stems of some *Phyllanthus* species (Webster, 1956–1958).

Subclade F1—Phyllanthaceae subtribe Flueggeinae + *Savia bahamensis* (Wielandiaeae) are strongly supported (BP 100) but include only few supported internal relationships. Members of this subclade contain securinine alkaloids that are synthesized by a unique pathway and not found in other plants (Seigler, 1994 and references therein). *Savia* is not monophyletic, and it would appear that *Savia* section *Heterosavia* belongs in Flueggeinae (F1) and *Savia* section *Savia* belongs to subclade F2 with other elements of Wielandiaeae. The morphological differences between the two sections of *Savia* are slight (P. Hoffmann, unpublished manuscript), but pollen of *Savia* section *Heterosavia* is aberrant in Wielandiaeae (Punt, 1962; Köhler, 1965). The generic identity of *Flueggea neowawraea* W. J. Hayden, a nearly extinct Hawaiian tree superficially resem-

TABLE 1. Characters of the major lineages of Euphorbiaceae s.l. (character states in brackets are rare). *Paradrypeetes* not included here. Numbers of taxa mainly from Radcliffe-Smith (2001), modified using more recent literature.

Character	Phyllanthaceae	Picrodendraceae	Putranjivaceae	Pandaceae	<i>Centroplacus</i>	Euphorbiaceae s.s.
Numbers of taxa (genera/species)	59/c. 2000	24/c. 80	3/c. 200	3/15–20	1/1	246/c. 6300
Breeding system	Monoecious or dioecious	Dioecious or monoecious	Dioecious or monoecious	Dioecious	Dioecious	Monoecious or dioecious
Life form	Trees, shrubs, herbs (or climbers, aquatics)	Trees or shrubs	Trees or shrubs	Trees or shrubs	Trees	Trees, shrubs, herbs (or climbers, succulents, geophytes)
Indumentum	Simple (or stellate, lepidote)	Simple	Simple	Simple	Simple	Simple, stellate (or lepidote, T-shaped, stinging)
Latex and laticifers	Absent	Absent	Absent	Absent	Absent	Present or absent
Leaf arrangement	Alternate, spiral (or opposite)	Alternate, opposite or whorled	Alternate	Alternate	Alternate	Alternate (or opposite, whorled or spiral)
Stipules	Present (or absent)	Present or absent	Present	Present	Present	Present or absent
Leaves (division)	Simple (or pinnately compound)	Simple or palmately compound	Simple	Simple	Simple	Simple or palmately compound
Leaf margin	Entire (or subentire, toothed in <i>Bischofia</i>)	Entire or toothed	Entire or toothed	Entire or toothed	Obscurely toothed	Entire or toothed
Venation	Penninerved	Penninerved (or palminerved)	Penninerved	Penninerved	Penninerved	Penninerved or palminerved
Foliar glands	Absent (or present)	Absent (or present)	Absent	Absent	Absent	Absent or present
Inflorescence position	Terminal, axillary, cauline	Axillary or terminal	Axillary or cauline	Terminal, axillary, cauline	Axillary	Axillary, terminal (or leaf-opposed, cauline)
Inflorescence type	Fasciculate (or raceme-like)	Fasciculate or raceme-like	Fasciculate	Fasciculate or thyrsoid	Paniculate	Fasciculate, raceme-like, thyrsoid, paniculate
Sepals	Free or connate	Free	Free to partially connate	Free or connate	Free	Free to connate
Petals	Present or absent	Absent	Absent	Present	Present in staminate, absent in pistillate flowers	Present or absent
Floral disc	Present (or absent)	Present or absent	Present (or absent)	Absent	Present	Present or absent
Staminate disc, position	Extra- or interstaminal (or stamens inserted in cavities of disc, <i>Celianella</i> and <i>Reverchonnia</i> with central disc)	Central or interstaminal (or stamens inserted in cavities of disc)	Central	—	Extrastaminal	Extra- or interstaminal (or central)
Stamens, number	2–35	(2–)4–55(–∞)	2–20(–50)	5, 10, or 15	5	1–∞
Stamens, fusion	Free or connate	Free (or partially connate)	Free (or subconnate)	Free	Free	Free, connate or branched
Anthers	Extrorse or introrse	Extrorse (or introrse)	Extrorse or introrse	Introrse	Introrse	Extrorse or introrse
Pollen, shape	Oblate to prolate	Spheroidal to suboblate	Prolate (to spheroidal)	Subspheroidal	Oblate-spheroidal	Prolate to oblate
Pollen apertures	3–4-colporate (to pantosyncolporate with up to 60 apertures)	4–8-colporate or pantoporate (up to 60 apertures)	3-colporate	3-colporate	3-colporate	(2–)3(–6)-colporate or -colpate, -porate or inaperturate
Pollen, exine	Smooth, reticulate (or echinate)	Echinate to verruculose	Smooth	Often finely reticulate	Smooth	Tectate-perforate, reticulate, punctate, rugulose, echinate, clavate, intectate

TABLE 1. Continued.

Character	Phyllanthaceae	Picrodendraceae	Putranjivaceae	Pandaceae	<i>Centroplocus</i>	Euphorbiaceae s.s.
Pistillode	Present or absent	Present or absent	Absent (or present)	Present	Present	Present or absent
Ovary, no. of locules	(1–)2–5(–15)	2–5	1–4	2–5	3	(1–)2–5(–20)
Ovules/locule	2	2(1)	2	1	2	1
Ovule orientation	Ana- or hemitropous	Anatropous	Anatropous	Ana- or orthotropous	Anatropous	Anatropous
Obturator	Present	Present	Present	Absent	Absent	Present
Fruit	Dehiscent (explosive) or indehiscent	Dehiscent (explosive) or indehiscent	Indehiscent (drupe)	Indehiscent (drupe)	Dry dehiscent (not explosive)	Dehiscent (explosive) or indehiscent
Seeds	Ecarunculate (or carunculate)	Carunculate or ecarunculate	Ecarunculate	Ecarunculate	Carunculate	Carunculate or ecarunculate
Endosperm in mature seed	Copious (or absent)	Copious (or absent)	Copious	Copious	Copious	Copious (or absent)

bling and at one time transferred to *Drypetes*, is in agreement with the findings of Hayden (1987).

Phyllanthus with over 800 species (Govaerts et al., 2000) is the most species-rich genus of Phyllanthaceae. It has a diversity of growth forms (annual, arborescent, aquatic, pachycaulous, and phyllocladous), chromosome numbers, and pollen types rivalling that of any genus of flowering plants. Webster's ongoing treatment (1956–1958, 1967, 1970, 1986, 2001, 2002, 2003; Webster and Airy Shaw, 1971; Webster and Carpenter, 2002a, b) of *Phyllanthus* includes a broad circumscription (subsuming numerous segregate genera) and the creation of a more natural but complex infrageneric classification of 10 subgenera and over 30 sections based on branching patterns and pollen types in addition to floral characters. The 10 *Phyllanthus* species sampled include three species with spiral phyllotaxy (*P. liebmannianus* subsp. *platylepis* and *P. calycinus* Labill. from subgenus *Isocladus*; *P. nutans* from subgenus *Xylophylla*), two highly specialized phyllocladous species (*P. epiphyllanthus* L. from subgenus *Xylophylla* and *P. flagelliformis* from subgenus *Phyllanthus*), and the odd plagiotropic aquatic *P. fluitans* that was classified by Brunel (1987) in subgenus *Phyllanthus*. The other four species belonging to subgenera *Embllica* (*P. polyphyllus* Willd.), *Kirganelia* (*P. nummulariifolius* Poir.), *Phyllanthus* (*P. lokohensis* Leandri), and *Xylophylla* (*P. juglandifolius* Willd.) have typical “phyllanthoid” branching (see Webster, 1956–1958) with spirally arranged, deciduous, floriferous short-shoots, resembling compound leaves, borne on cataphyllous, indeterminate long-shoots.

The *Phyllanthus* species do not form a monophyletic group with *rbcl* data, but the sampling is poor considering the species richness of the genus. At face value, the strict consensus indicates complex patterns of habit evolution and biogeography in *Phyllanthus*. Morphological specialization has created classification difficulties, and it is not unusual for problems to occur when there is such diversity in form. *Phyllanthus* resembles the other large euphorbiaceae genera, *Euphorbia* s.l. (see Steinmann and Porter, 2002) and *Croton* s.l. (also probably polyphyletic; Wurdack, 2002; P. Berry et al., unpublished data), in which paraphyletic genera have been formed by recognition of specialized lineages, leaving a rump of more plesiomorphic species in the parent genus. It is clear that further work on *Phyllanthus* will not only require more rapidly evolving genes with greater numbers of variable positions but also more extensive sampling from Flueggeinae. As noted in the Results, an unusual and perhaps synapomorphic 3'-duplication

unites *Breynia*, *Phyllanthus flagelliformis*, *P. fluitans*, *P. liebmannianus* subsp. *platylepis*, and *Reverchonnia*. There is no support (BP < 50) for this grouping and alternative relationships (although partly united in two separate, poorly supported groups) are present in the strict consensus tree. The two phyllocladous species sampled are from two proposed independent origins of the growth form (Webster, 1956–1958), as suggested by their classification in different subgenera and recent pollen investigations (Webster and Carpenter, 2002a). *Phyllanthus fluitans* is the only fully aquatic Euphorbiaceae s.l. The plant is a free-floater resembling *Salvinia*, with which it sometimes grows, and is becoming popular in the commercial aquarium market. In the Adams consensus tree (not shown but see Fig. 2) it is sister to the phyllocladous *P. flagelliformis*.

According to our results, the sand dune annual *Reverchonnia*, revised by Webster and Miller (1963), does not warrant generic status but rather represents a highly specialized *Phyllanthus*. The main generic characters of *Reverchonnia* are a central staminate disc, otherwise unknown in Phyllanthaceae, and the narrow cotyledon shape. The latter is shared with *Poranthera* and unrelated taxa of ericoid habit in Euphorbiaceae s.s. and Picrodendraceae that were classified in a series “Stenolobae” apart from all other Euphorbiaceae s.l. by Müller (1866). The distribution of this character (Fig. 2) suggests pleiotropic effects associated with extremely reduced leaves. The chromosome number in *Reverchonnia* is $2n = 16$. This is rare in Phyllanthaceae but corresponds with *Phyllanthus* section *Isocladus* (containing *Phyllanthus liebmannianus*), which, like *Reverchonnia*, is characterized by the lack of phyllanthoid branching typical for most other Flueggeinae (Webster and Miller, 1963). Pollen of *Reverchonnia* has been reported from the Eocene of France (Gruas-Cavagnetto and Köhler, 1992), suggesting its present limited North American distribution is relictual.

Subclade F2—The next subclade (F2 of Fig. 1) contains four genera of Wielandieae, as well as Amanoeae, Brideliaceae, *Croizatia* (Oldfieldioideae), *Tacarcuna* (incertae sedis), and one member of Phyllanthaceae (*Securinega*). They share petaliferous flowers except for *Pseudolachnostylis*, *Securinega*, and perhaps *Tacarcuna*. In addition, the mitochondrial *cox1* intron is absent in this clade, whereas all other Phyllanthaceae sampled possess it (Wurdack, 2002). Wielandieae have been considered the “basal” tribe of Phyllanthoideae and of probable paraphyletic circumscription (Webster, 1994b) and in our analysis fall in four of the five fasciculate-clade lineages.

Subclade F2 contains four supported groups including a

weakly supported (BP 63) strictly New World subclade with *Croizatia* + *Discocarpus* + *Tacarcuna* and *Gonatogyne* + *Savia* section *Savia*. There are two strongly supported Old World groups, one comprising *Bridelia*, *Cleistanthus*, *Pentabrachion*, and *Pseudolachnostylis*, and the other, strictly African group, including *Lachnostylis* and *Securinega*. The fourth group consists of *Amanoa*, the only genus in this clade with a trans-Atlantic disjunction. Neotropical *A. caribaea* Krug & Urb. and African *A. strobilacea* Müll. Arg. are strongly supported (BP 100) as monophyletic. *Amanoa* shares sclerified walls of the leaf epidermis with *Discocarpus* (Rothauscher, 1896; Gaucher, 1902; Hayden, 1980; Levin, 1986a; Hayden and Hayden, 1996a), although this character was homoplasious in phylogenetic reconstructions using leaf morphological data (Levin, 1986b).

Croizatia contains five species of Neotropical shrubs that closely resemble members of Wielandieae. The genus has been classified as the first branching lineage of Oldfieldioideae (Picrodendraceae), principally on shared echinate pollen even though it represented a discordant element in possessing petals, tri-aperturate pollen, and ecarunculate seeds lacking endosperm (Webster et al., 1987; Levin and Simpson, 1994a). Cladistic analyses of Oldfieldioideae by Levin and Simpson (1994a) showed an unstable placement of *Croizatia* when using palynological characters alone vs. when combined with morphology, suggesting conflicting signal from homoplasious characters (e.g., foot-layer structure). Echinate pollen has been derived elsewhere in Phyllanthaceae (*Amanoa*, *Securinega*). In the case of *Amanoa*, the echinae appear clearly homoplasious and are not supracteal but derived from columellae of intecate pollen (Levin and Simpson, 1994a).

Two species of *Croizatia* were sequenced (one nucleotide difference) for confirmation of the unexpected placement in Phyllanthaceae in a strongly supported heterogeneous clade containing *Discocarpus* and *Tacarcuna*. *Croizatia* is monophyletic in the Adams consensus tree (not shown). The lack of resolution in the strict consensus may be attributed to missing data in *Tacarcuna* and low levels of sequence divergence. Placement of *Croizatia* with Phyllanthaceae has been supported by analyses of other sequence data (18S, *atpB*, *trnL-F*, *nad1*; Wurdack, 2002). Dorr (1999) reviewed the disposition of monotypic *Pseudosagotia* and proposed a new combination, *Croizatia brevipetiolata* (Secco) Dorr, which is here supported based on sequence data. Species delimitation among the similar-looking species of *Croizatia* remains poorly understood and needs to be reevaluated in light of numerous new collections.

Tacarcuna contains three poorly known species of Neotropical trees. The genus resembles other Wielandieae, but this affinity was initially obscured by being incorrectly described (Huft, 1989) as uniovulate. Subsequent observation has shown this to be by abortion and the undeveloped second ovule is sometimes even persistent on the columella of dehiscent fruits (K. J. Wurdack, personal observation). *Tacarcuna* shares with *Croizatia* and *Discocarpus* (illustrated by Stuppy, 1996) large embryos with thin, contorted cotyledons that fill the seed and lack (or nearly so) endosperm in the mature seed. It does not appear to have distinct petals that are usually present in members of subclade F2 but are highly reduced in *Croizatia* and *Discocarpus*. Huft (1989) originally interpreted the flowers as containing a disc and a perianth of five sepals (*T. gentryi* Huft) or three sepals and three petals (*T. amanoifolia* Huft, *T. tachirensis* Huft). In the latter case, the perianth parts are poorly

differentiated despite the positional distinctiveness of the two whorls and are persistent in fruit (K. J. Wurdack, personal observation). The previously unrecorded high stamen number in *T. amanoifolia* (14–19, among the highest in Phyllanthaceae) suggests this taxon is derived. Most members of subclade F2 (including *T. gentryi*) have only five stamens. Although we saw no evidence of chimerism or contamination, given the degraded nature of the DNA sample, additional data for *Tacarcuna* are desirable to confirm our results.

Lachnostylis (South Africa) and *Discocarpus* (northern South America) have been suggested to represent a vicariant pair (Bentham and Hooker, 1880; Webster, 1994a) and even treated as synonymous by Pax and Hoffmann (1922, 1931). A close relationship is not supported by our data, although it has recently been reaffirmed morphologically, and an affiliation with the poorly known *Chonocentrum* dismissed (Hayden and Hayden, 1996a, b). *Lachnostylis* has a strongly supported (BP 94) relationship with the Madagascan *Securinega capuronii* Leandri despite little morphological resemblance between the genera. As with *Savia* and *Andrachne* (see later), *Securinega* has had considerable flux in generic delimitation. The broad circumscription of Pax and Hoffmann (1931) has been reduced with the removal of *Flueggea* (Webster, 1984a), *Jablonskia* (Webster, 1984b), and *Meineckia* (Webster, 1965), leaving a core Malagassian group characterized by distinctive spiny pollen and smooth seeds.

The Brazilian monotypic genus *Gonatogyne* has been included as a section of *Savia* by Pax and Hoffmann (1922, 1931) in a treatment adopting the widest circumscription of *Savia*, including *Petalodiscus* and species of *Andrachne* and *Leptopus*. The same authors reinstated *Gonatogyne* at generic rank after examining more material (Pax and Hoffmann, 1933). In our analysis, *Gonatogyne* is sister to *Savia* section *Savia* (for *Savia* section *Heterosavia* see subclade F1). Morphological characters shared between *Gonatogyne* and *Savia* section *Savia* are the terete (vs. adaxially channeled in section *Heterosavia*) petiole, articulated pistillate pedicel, caducous perianth in fruit, and distally narrow columella. Differences between *Gonatogyne* and *Savia* lie in the shape of the floral disc, style division, fusion of the androecium, petiolar vascularization, and fruit dehiscence (P. Hoffmann, unpublished manuscript).

Due to their valvate sepals, *Bridelia* and *Cleistanthus* were united in tribe Bridelieae. This tribe was juxtaposed with tribe Phyllanthaeae containing all other phyllanthoid genera except *Poranthera* in most pre-Websterian classifications of Euphorbiaceae (Müller, 1866; Jablonszky, 1915; Pax and Hoffmann, 1922, 1931). The importance of this character was contested by Baillon (1873), who went so far as to include *Bridelia*, *Cleistanthus*, *Gonatogyne*, and *Pentabrachion* in *Amanoa*, which in turn, he considered to be closely related to *Lachnostylis*. Webster (1975, 1994b) took an intermediate view and maintained tribe Bridelieae in Phyllanthaceae using calyx aestivation as a key differential character. Our results show that this character has at most generic value in Phyllanthaceae.

Genera of subclade F2 are linked by pollen morphology. The *Amanoa* type of Köhler (1965) united *Amanoa*, *Bridelia*, *Cleistanthus*, *Pentabrachion*, and *Pseudolachnostylis* and that of Punt (1962) included *Amanoa*, *Pentabrachion*, and *Pseudolachnostylis*. Gaucher (1902) noted the similarity of *Pseudolachnostylis* and *Lachnostylis* with regards to vegetative anatomy, calling the former a xeromorphic version of the latter. Many *Cleistanthus* spp., *Bridelia*, and monotypic *Penta-*

brachion share conspicuous parallel (percurrent or scalariform) tertiary leaf venation, whereas other genera of this subclade have mostly reticulate tertiary venation. Vestured pits have been reported from *Bridelia* and *Cleistanthus* but not other Euphorbiaceae s.l. (reviewed by Jansen et al., 2001).

The main distinction previously drawn between *Bridelia* and *Cleistanthus* lies in fruit morphology. *Bridelia* has one- to two-locular drupes or rarely capsules, whereas *Cleistanthus* has three-locular dehiscent capsules (Jablonszky, 1915; Webster, 1994b). We found this to be oversimplified as it ignores the trend towards drupaceous fruits in *Cleistanthus* section *Chartacei*, e.g., *C. megacarpus* C. B. Rob. with tardily dehiscent to nearly indehiscent fruits (P. Hoffmann, personal observation). The two *Cleistanthus* species sampled represent sections *Chartacei* Jabl. [*C. oblongifolius* (Roxb.) Müll. Arg.] and *Cleistanthus* (*C. perrieri* Leandri). Members of the latter section seem to have exclusively explosive schizocarps. Given the paraphyly of *Cleistanthus* in our phylogenetic study, more sampling and a careful study of reproductive characters such as sepal aestivation, locule number, and fruit type, as well as leaf venation (Levin, 1986a), are needed to reevaluate generic boundaries.

Subclade F3—*Actephila*, *Andrachne*, *Leptopus*, *Meineckia*, *Poranthera*, and *Zimmermannia* form a strongly supported clade (BP 99) in this analysis, mixing two tribes and four subtribes. *Poranthera* was classified in series “*Stenolobeae*” with other unrelated ericoid Euphorbiaceae s.l. by Müller (1866) apart from tribes Phyllanthaceae and Brideliaceae, which formed Pax and Hoffmann’s (1931) subfamily Phyllanthoideae. Bentham (1873, 1878) and Bentham and Hooker (1880) also adopted this concept. In contrast, Baillon (1858) did not attach the same importance to cotyledon shape and placed *Poranthera* next to *Andrachne*, a view initially shared by Webster (1975) and vindicated by our results. Based on palynological evidence, there has been conflicting placement of *Poranthera* near *Andrachne* or *Antidesma* (subclade T1). Punt (1962) placed it in his *Andrachne* subtype with *Actephila*, *Andrachne*, and *Leptopus*, whereas Köhler (1965) placed it next to his *Antidesma* type suggesting a remote relationship to *Andrachne* and allies. The affiliation with *Antidesma* was ultimately preferred by Webster (1994b).

Poranthera is unique in Phyllanthaceae in having poricidal anthers. The ericoid leaves lack tanniferous epidermal cells (Levin, 1986a), contradicting Webster’s placement in the tanniferous clade near *Antidesma*. Inflorescences of *Poranthera* have been described by many authors as racemose (Müller, 1866; Bentham and Hooker, 1880; Grüning, 1913; Webster, 1994b; Radcliffe-Smith, 2001). Only Baillon (1858) saw a gradual transformation of foliage leaves into bracts. Allan (1961, p. 346) recorded the flowers of *P. microphylla* Brogn. as in the “axils of uppermost lvs, in few-fl’d cymes to solitary.” The New Zealand endemic *Poranthera alpina* Cheeseman [often segregated as monotypic *Oreoporanthera alpina* (Cheeseman) Hutch.] has solitary flowers in the upper leaf axils (Grüning, 1913; Allan, 1961; Radcliffe-Smith, 2001). Our observations agree with those of Baillon and Allan in that *Poranthera* flowers are solitary or arranged in highly contracted fascicles in the axils of stipulate foliage leaves. These leaves are slightly reduced in size, and the flowers or inflorescences are apically densely crowded so as to resemble terminal racemes. Placement of *Poranthera* in the fasciculate clade is concordant with these findings. *Poranthera* is the most

divergent terminal (see Fig. 2) in Phyllanthaceae, indicating that molecular evolution has been in step with the highly derived morphology of this genus. The two accessions of *Poranthera huegellii* Klotzsch have identical *rbcL* sequences but differ at five sites (0.84% divergence) in ITS (K. J. Wurdack, unpublished data).

The remaining five genera in subclade F3 have been separated in classifications, but there are some characters linking *Actephila* with *Leptopus* and *Andrachne*, such as prolate pollen, enlarged pistillate sepals, and presence of petals. This group has also been identified by Punt (1962) and Köhler (1965) based on pollen morphology, juxtaposed with the *Zimmermannia* pollen type, which was separated due to verrucate exine sculpture. Webster’s (1994b) disjunct placement of *Andrachne* (Phyllanthaceae subtribe Andrachninae), *Leptopus* (subtribe Leptopinae), *Meineckia*, *Zimmermannia*, and unsampled *Zimmermanniopsis* (all subtribe Pseudolachnostylidinae) emphasized ovule attachment and presence/absence of petals. Hemitropous ovules in subtribes Andrachninae and Flueggeinae are shown to be homoplasious by our results.

Our results do not support a wider concept of *Andrachne* s.l. (Müller, 1866; Bentham and Hooker, 1880; Pax and Hoffmann, 1922, 1931; Hoffmann, 1994, 2000), despite bringing together its core elements. *Leptopus chinensis* (eastern and southern China) and *L. colchicus* (southern trans-Caucasia) have identical *rbcL* sequences despite their considerable geographic disjunction. This is corroborated by the lack of differential morphological characters (P. Hoffmann and M. Vorontsova, Royal Botanic Gardens, personal observation). The affiliation of the relictual xerophyllous shrub *Andrachne arida* (Warnock & M. C. Johnst.) G. L. Webster with *Leptopus* as suggested by Hoffmann (1994) is strongly supported in these analyses and brings together the only two North American taxa. The two species of *Andrachne* s.s., one Mediterranean (*A. telephioides* L.) and the other American [*A. microphylla* (Lam.) Baill.], represent biogeographically and palynologically (see El-Ghazaly and Raj, 1986) widely separated taxa. Taxonomic decisions regarding the generic boundaries in subclade F3 await the future sampling of *Leptopus diplosperrmus* (Airy Shaw) G. L. Webster (= *Chorisandrachne diplosperrma* Airy Shaw) and *Andrachne* section *Pseudophyllanthus*.

The taxonomic status of *Zimmermannia* and *Meineckia* needs further investigation. Brunel (1987) and Radcliffe-Smith (1997) subsumed *Zimmermannia* under *Meineckia* as *Meineckia* section *Zimmermannia*. Shortly after, Radcliffe-Smith (2001) reverted to the narrow generic circumscription of Webster (1994b). In our analyses, the sister relationship of *Meineckia* and *Zimmermannia* receives strong support (BP 100). The enigmatic Madagascan *Z. decaryi* (Leandri) G. L. Webster (not sampled) appears to be intermediate, but pollen morphology of the two genera differs considerably (Poole, 1981).

Subclade F4—This strongly supported grouping contains all sampled members of Wielandieae from the western Indian Ocean region, often referred to at least partially as *Savia* (Webster, 1994b; Radcliffe-Smith, 2001). *Wielandia elegans* is conspicuous in having perfectly pentamerous flowers but is otherwise similar to *Petalodiscus* with predominantly trimerous ovaries (Hoffmann and McPherson, in press). No further resolution is obtained with *rbcL*. Shared characters of this clade are cyclocytic stomata, spheroidal to oblate pollen grains, monoecy, flowers always petaliferous in both sexes, petals usually much larger than sepals, and exalbuminous seeds with

massive or plicate cotyledons. The wood of *Petalodiscus* (as *Blotia*) has been considered among the most primitive of all Euphorbiaceae s.l. (Mennega, 1987; Hayden et al., 1993).

Subclade F5—This Neotropical subclade contains *Chascotheca* as the strongly supported (BP 100) sister to *Astrocasia*, a relationship that has never before been suggested. These two genera have been recognized only in the last century, and many characters have not yet been explored, especially for *Chascotheca*. *Chascotheca* is a monotypic genus from Cuba and Hispaniola. Pax and Hoffmann (1931) included it in *Securinega* section *Colmeiroa* (now *Flueggea*) together with *Flueggea tinctoria* (L.) G. L. Webster (as *Securinega buxifolia*). Webster (1975) classified it in Phyllanthaceae-Securineginae and later (1994b) in Phyllanthaceae-Pseudolachnositylinae.

Astrocasia was first classified in Wielandieae (Webster, 1975, 1992). Pollen (Punt, 1962; Köhler, 1965) and leaf (Levin, 1986a) morphological results, as well as wood anatomy (Mennega, 1987) led Webster (1994b) to place it closer to *Phyllanthus* in creating the monogeneric Phyllanthaceae-Astrocasinae. *Astrocasia jacobinensis* (Müll. Arg.) G. L. Webster from eastern Brazil (disjunct in Bolivia) is geographically isolated from the Mexican center of generic distribution and has distinctive staminate flowers, but its transfer from *Phyllanthus* (Webster, 1992) is supported by our data.

There are substantial differences but also similarities between *Astrocasia* and *Chascotheca* with regards to generative morphology. *Chascotheca* differs from *Astrocasia* in having persistent pistillate sepals (vs. caducous). *Chascotheca* is apetalous, whereas the petals of *Astrocasia* are among the most conspicuous in Phyllanthaceae. The androecium of *Chascotheca* is only basally fused (anthers dehiscing longitudinally), that of *Astrocasia* is highly connate (anthers dehiscing horizontally), and the number of stamens is reduced from five to three in some species of *Astrocasia*. Regarding seed morphology, the curvature of the dorsal side together with the convex raphe and the expanded chalaza of *Chascotheca* seeds result in the chalazal depression being visible in dorsal view ("dorsal chalaza" in Webster, 1994b). Morphologically the chalaza is, in fact, basal rather than dorsal, and the seed is anatropous with a slight tendency towards campylotropy (W. Stuppy, Royal Botanic Gardens, personal communication). Seeds of *Astrocasia* are either comparatively unremarkable with a typical \pm level basal chalaza visible in ventral view [*A. peltata* Standl., *A. tremula* (Griseb.) G. L. Webster] or with a peculiar chalazal projection, also visible in ventral view [*A. jacobinensis*, *A. neurocarpa* (Müll. Arg.) I. M. Johnst. ex Standl.]. Seed coat anatomical data place the genera in different groups (Stuppy, 1996; Tokuoka and Tobe, 2001).

Overall distribution, ecology, and morphology of the two genera, on the other hand, show some striking similarities. Distribution appears to be allopatric, overlapping only in the Cuban province of Oriente. Both genera have a strong preference for coastal limestone. They share a strongly imbricate pentamerous calyx, a floral disc in both sexes, extrorse anthers, and a pistillode. *Chascotheca* and at least two *Astrocasia* species share dilated stigmas, and the dehiscent fruits of both genera are conspicuously veined. The most unusual shared character must be the peltate leaf base, here probably recorded for the first time in *Chascotheca* (although minimally peltate and easily overlooked). Peltate leaf bases are rare in Phyllanthaceae, known outside subclade F5 in African *Heywoodia* (see discussion of subclade F6), which also occupies a pre-

sumed isolated position in this analysis. This is a potential synapomorphy for F5 + F6. The character is also found in unrelated *Meineckia peltata* (Hutch.) G. L. Webster from Madagascar and *Phyllanthus peltatus* Guillaumin from New Caledonia. Taxa with peltate leaves from other euphorbiaceous lineages are known in *Androstachys* (Picrodendraceae), *Doroxylon*, *Homalanthus*, *Macaranga*, *Mallotus*, *Ricinus*, and *Sumbaviopsis* (all Euphorbiaceae s.s.).

Subclade F6—*Heywoodia*, a monotypic African genus with a discontinuous distribution, has been placed as the first genus in the intuitively ordered classifications of Webster (1994b) and Radcliffe-Smith (2001). Webster (1975, 1994b, p. 36) consistently placed it in Wielandieae and remarked that the genus "appears to me as perhaps the nearest in morphological characters to the hypothetical ancestor of the family." *Heywoodia* has a poorly differentiated perianth (inner parts larger and more delicate than outer parts), which has been interpreted as consisting of eight sepals (Sim, 1907; Pax and Hoffmann, 1922), six sepals (Milne-Redhead, 1957 [pistillate flowers]), or three sepals and five petals (Hutchinson, 1922 [staminate flowers]; Radcliffe-Smith, 2001). The latter also postulated two bracteoles in the pistillate flower, and we confirmed that the two lower perianth parts are inserted at different heights (P. Hoffmann, personal observation).

Pollen morphology also isolates *Heywoodia* in Phyllanthaceae; Köhler (1965) considered it aberrant in his *Drypetes* type, whereas Punt (1962) cited a monotypic *Heywoodia* pollen type. Vegetatively, *Heywoodia* is striking in having strongly peltate leaves in seedlings and basally attached leaves in flowering shoots. *Heywoodia* was placed with *Drypetes* and *Lingelsheimia* in subtribe Drypetinae by Pax and Hoffmann (1922, 1931) based on their interpretation of the staminate disc as central, whereas Radcliffe-Smith (2001, p. 6) described it "peripheral, invaginated amongst the filaments of the outer staminal whorl." Our results show *Heywoodia* clearly distinct from *Drypetes* and its close relatives (we were unable to sample *Lingelsheimia*). The *rbcL* sequence variation between the two *Heywoodia* accessions may reflect populational disjunction, but the provenance of the cultivated South African tree is unknown.

The tanniferous clade—The second major Phyllanthaceae clade includes tribes Bischofieae, Hymenocardieae, Martretieae, and Antidesmeae (excluding *Poranthera*). In addition to elongate inflorescence axes (except *Jablonskia* and *Uapaca*), members of this group are mostly dioecious, lack petals (except *Spondianthus* and *Thecacoris*), have tanniferous leaf epidermal cells (mapped in Fig. 1; Levin, 1986a), and tardily dehiscent to indehiscent fruits (except *Leptonema* and *Thecacoris*). Gaucher (1902) reported tanniferous epidermal cells in *Bischofia* and *Hymenocardia* in the tanniferous clade and *Breynia disticha* J. R. Forst. in the fasciculate clade (F1). Rothduscher (1896) found sausage-shaped, slightly branched, enlarged cells with yellowish content in *Bischofia javanica*. All three genera were reported to lack tanniferous cells by Levin (1986a). Mucilaginous cells in the leaf epidermis are also common (found in *Antidesma*, *Aporosa*, *Baccaurea*, *Hieronoma*, *Hymenocardia*, *Jablonskia*, and *Richeria*; Rothduscher, 1896), but this character is shared with the fasciculate taxa *Actephila*, *Andrachne* (except *A. ovalis* [Sond.] Müll. Arg. of section *Pseudophyllanthus*), and *Flueggea* (as *Securinega*).

The overwhelming majority of genera in this clade are dioecious, the exceptions being *Apodiscus* and *Jablonskia*. Dioecy was found to be strictly maintained in a 2-yr population study of *Aporosa* and *Baccaurea* spp. (subclade T2; Thomas and LaFrankie, 1993). Dioecy is known in the fasciculate clade as are examples of sex switching (Borges et al., 1997) or the occurrence of sporadic pistillate flowers on “staminate” plants [e.g., *Leptopus phyllanthoides* (Nutt.) G. L. Webster, K. J. Wurdack, personal observation; *Phyllanthus*, Webster, 1956–1958]. Rare occurrences of monoecious specimens in *Bischofia* and *Thecacoris* are recorded by Radcliffe-Smith (2001). In a sample of over 7500 examined herbarium specimens of *Antidesma*, only two were found to be monoecious (Hoffmann, in press). Other floral variants, such as presence of staminodes and additional ovaries, occurred more frequently than monoecy (P. Hoffmann, personal observation). *Antidesma acuminatum* Wight, for example, was described with bisexual flowers but seems to be only an aberrant specimen of *A. montanum* Blume.

Although members of a predominantly dioecious genus, *Aporosa hermaphrodita* Airy Shaw and *A. heterodoxa* Airy Shaw are described as consistently having bisexual flowers (Airy Shaw, 1971). In addition to those, *A. brevicaudata* Pax & K. Hoffm. and *A. egreria* Airy Shaw were described from fruiting material only but have subsequently been found to also have bisexual flowers (Schot, in press). All four species are restricted to New Guinea or the Solomon Islands. It is not known whether the flowers are functionally hermaphroditic, and some of the stamens are malformed. Other “stamens” have normally dehiscent anthers containing pollen. The position of *Aporosa* in our analysis marks this as an autapomorphy. The exceptional occurrence of hermaphroditic flowers in the otherwise unisexual Euphorbiaceae s.l. has been known for a long time and was discussed, e.g., by de Jussieu (1823) in *Jatropha* and *Phyllanthus* and by Baillon (1858) in *Aparisthium*, *Breynia*, *Cleistanthus*, *Chrozophora*, *Mercurialis*, *Phylla*, *Phyllanthus*, *Ricinus*, *Suregada*, and *Trigonostemon* (as *Clutia*).

Subclade T1—The first tanniniferous clade confirms Webster’s classification (1994b) by uniting all four genera of Antidesmeae-Antidesminae included in this study, plus *Apodiscus* (Antidesmeae-Scepiniae), *Martretia* (Martretieae), and *Hymenocardia* + *Didymocistus* (Hymenocardieae). This grouping is further supported by the presence of the unique alkaloid antidesmone in *Antidesma*, *Hieronyma*, and *Thecacoris*, which is absent in *Aporosa*, *Maesobotrya*, and *Uapaca* (Buske et al., 2002). Genera included in this clade share a more-or-less pronounced peculiar anther morphology. In *Martretia*, *Didymocistus*, and *Hymenocardia*, the connective is of normal size, but the thecae are at least partly free of it. The anthers of *Antidesma*, *Hieronyma*, and *Thecacoris* closely resemble one another. In these three genera, the thecae are completely separated by an enlarged connective from which they hang in bud where the connective may have a protective function. At anthesis, the thecae are turned upward to expose the pollen. The separation of the thecae is extreme in *Apodiscus* and *Leptonema* in which each theca is narrowed basally and separately joined to the filament, giving the impression of a split filament. Separate thecae are known in some Euphorbiaceae s.s. (e.g., *Acalypha*, *Amperea*, *Claoxylon*, *Mareya*, and *Monotaxis*) but are rare in Phyllanthaceae. They seem to be limited to this subclade with few exceptions such as *Aporosa subcaudata*

Merr. (subclade T2), *Celianella* (subclade T3, not shown), and Neotropical *Phyllanthus* section *Phyllanthus* subsection *Clausenii* (subclade F1).

Subclade T1 alone in the tanniniferous clade contains taxa with typical explosive euphorbiaceous schizocarps (*Thecacoris* and *Leptonema*). All other genera are either indehiscent or tardily or irregularly dehiscent. Many tardily or irregularly dehiscent taxa in both the tanniniferous (*Aporosa*, *Ashtonia*, *Baccaurea*, *Jablonskia*, *Maesobotrya*, and *Richeria*) and fasciculate (*Glochidion* and *Margaritaria*) clades feature development of a sarcotesta. Explosive schizocarps are predominant in the fasciculate clade (indehiscent fruits occur rarely in subclades F1 and F2; see Fig. 2). A homology assessment of both dehiscent and indehiscent fruits is clearly needed.

The genus *Apodiscus* is aberrant in the tanniniferous clade because of its monoecy and exalbuminous seeds. Inflorescence, flower, and fruit characters, on the other hand, agree with its position in our analysis. The humerate fruits of *Apodiscus* approach the unusual fruit shapes of *Martretia* and *Didymocistus*.

The placement of *Martretia* in subclade T1 proposes a solution to a long-standing enigma in Euphorbiaceae systematics. This monotypic African genus with anomalous false-partitioned fruit and atriate-apertured pollen has been subjected to wide-ranging classification. Léonard (1989) reviewed the taxonomy of *Martretia* and agreed with the general consensus of placement in Phyllanthoideae, although isolated in a monotypic tribe. Meeuse (1990) proposed a radical placement in Euphorbiaceae s.s. (Acalyphoideae), in part because of the erroneous belief that it possessed a caruncle (ecarunculate fide Stuppy, 1996; Radcliffe-Smith, 2001) and because of its unusual pollen. A detailed examination of the pollen has shown connections with biovulate Euphorbiaceae (Lobreau-Callen and Suarez-Cervera, 1989). Webster (1994b) considered the genus incertae sedis within Euphorbiaceae s.l., but recently it was again placed in Phyllanthoideae as monotypic tribe Martretieae (Radcliffe-Smith, 2001). Its placement in our analyses with members of Antidesmeae-Antidesminae vindicates the affinities proposed by Beille (1908) and Pax and Hoffmann (1922, 1931), who placed *Martretia* in Phyllanthées Antidesmiées and Phyllanthées-Antidesminae, respectively. Mennega (1987) found anatomical similarities in wood between *Martretia* and *Aporosa*. Tanniniferous epidermal cells have not been reported for *Martretia* (Levin, 1986a).

The seeds of *Martretia* contain a large embryo (shaped like that of the majority of Phyllanthaceae) but only a thin layer of endosperm, whereas its sister taxon *Apodiscus* is exalbuminous. *Hieronyma* is an unsupported sister group to *Apodiscus* + *Martretia*. Morphologically most similar to *Antidesma*, *Hieronyma* has a similar fleshy embryo of average size and shape with moderately developed endosperm. Endosperm reduction appears to have occurred independently several times in Phyllanthaceae (Fig. 2). Exalbuminous seeds occur in *Amanoa*, *Croizatia*, *Discocarpus*, *Lachnostylis*, *Tacarcuna* (subclade F2), *Actephila* pro parte (F3), *Blotia* + *Petalodiscus* + *Wielandia* (F4), and *Apodiscus* (T1). The condition is rare in the remainder of Euphorbiaceae s.l., found only in *Picrodendron* (Picrodendraceae), and in *Elaterospermum*, *Syndyphyllum*, and *Trigonopleura* (Euphorbiaceae s.s.).

Molecular data support a sister relationship for *Hymenocardia* and *Didymocistus* and placement of this clade within Antidesmeae, resolving another long-standing enigma in Euphorbiaceae systematics. *Didymocistus* is a relatively recently de-

scribed monotypic Amazonian genus placed in Aporoseae in an earlier version of Webster's classification (1975). Only recently has it been dissociated from that group and linked with *Hymenocardia* based on pollen and trichome similarities (Levin and Simpson, 1994b; Webster, 1994b). The unusual punctiform scales appear to have secretory function based on their structure (Levin and Simpson, 1994b) and in the leaf epidermis of *Hymenocardia* are probably what Gaucher (1902) reported as multicellular, tanniniferous glands. Their secretory nature has been confirmed by P. Mahlberg (Indiana University, personal communication). Wood anatomical characters (Mennega, 1987) do not support this relationship apart from absence of parenchyma, a character that is present in several unrelated taxa.

Hymenocardia, with a suite of wind adaptations including amentiferous staminate inflorescences, smooth porate pollen, and compressed bilobate samaroid fruits, is aberrant enough to have been proposed as a monotypic family, Hymenocardiaceae (e.g., Léonard and Mosango, 1985), or monotypic tribe, Hymenocardiaceae (e.g., Webster, 1975). Generally, *Hymenocardia* has been considered to occupy an isolated position in Phyllanthoideae (Radcliffe-Smith, 1987), although it was recently associated with Oldfieldioideae on palynological grounds (Lobreau-Callen and Suarez-Cervera, 1994). *Hymenocardia* and *Didymocistus* lack tanniniferous leaf epidermal cells (Levin, 1986a) and share a tanniniferous endotegmic seed coat (unique in Euphorbiaceae s.l.), for which type V classification supports placement in Antidesmeae (Tokuoka and Tobe, 2001). Both genera share bilocular fruits that loculicidally disarticulate as two indehiscent cocci, unlike other Phyllanthaceae fruits which are (sub-) drupaceous, baccate, or explosive schizocarps. Abiotic dispersal of *Didymocistus* may be by water (saccate nature of the fruit and occurrence along rivers) and *Hymenocardia* by air. Although all *Hymenocardia* fruits are compressed, there is specific variation in wing development with wingless (*H. heudelotii* Planch. ex Müll. Arg., *H. punctata* Wall. ex Lindl.), double winged (*H. acida* Tul.), or cyclicly winged (*H. ulmoides* Oliv.) species. This wing variation is reminiscent of members of Juglandaceae, and developmental studies are called for coupled with a species-level phylogeny.

Monophyly of the two sampled species of *Thecacoris* receives no support (BP < 50) with *rbcL*, although they were recovered as a sister pair in the strict consensus. This may indicate a greater level of divergence between the two species groups sometimes recognized at generic level as *Cyathogyne* and *Thecacoris* (e.g., Pax and Hoffmann, 1922; Léonard, 1995), which are both represented in our sampling.

Antidesma was segregated in the monogeneric Stilaginaceae and allied with Icacinaceae by Airy Shaw (in Willis, 1966). Although its fruits bear an uncanny resemblance to those of *Rhyticaryum* (Icacinaceae), floral morphology and pollen and wood anatomy support placement in Phyllanthaceae (Radcliffe-Smith, 1987; Hoffmann, in press).

Subclade T2—This clade corresponds to tribe Aporoseae (excluding *Didymocistus* in subclade T1) in Webster's first family classification (1975) or Antidesmeae-Scepiniae (excluding *Apodiscus* [T1] and *Jablonskia* [T4]) in Webster's most recent classification (1994b). The main body of Scepiniae is formed by the large Asian and Australasian genera *Aporosa* and *Baccaurea*. *Baccaurea* is the largest Phyllanthaceae genus to have been recently revised taxonomically (Haegens, 2000).

In the same publication, two new genera, *Distichirhops* and *Nothobaccaurea* (both not sampled), were described to accommodate a handful of aberrant species. *Richeria* is the only Neotropical member of this subclade and is moderately supported as sister to the other genera. Levin (1986b) recovered a subclade of the same composition as T2 with cladistic analysis of foliar morphology. Synapomorphies include marginal glands (otherwise only present in *Bischofia* and the incompletely known *Antidesma vaccinioides* Airy Shaw), anisocytic rather than paracytic stomata, and enlarged epidermal tanniniferous cells (Levin, 1986a, b).

Subclade T3—The association of *Jablonskia* and *Uapaca* may be spurious, although they do share reduced, bracteate inflorescences. *Uapaca* has only recently been associated with Antidesmeae (Webster, 1994b) following foliar morphological studies (Levin, 1986a, b). This genus had previously been regarded as the monogeneric family Uapacaceae (Airy Shaw, 1965; Meeuse, 1990) although Baillon (1858), Müller (1866), and Pax and Hoffmann (1922, 1931) had placed it without doubt in biovulate Euphorbiaceae. The reason for its recognition at family rank lies in its dense, clustered unisexual inflorescences that are subtended by involucre bracts so as to resemble single flowers. This syndrome is unique in Phyllanthaceae but also known from *Dalechampia*, *Pera*, and tribe Euphorbieae (e.g., cyathia), all of which belong in Euphorbiaceae s.s. and are each independent derivations of bisexual (sometimes secondarily unisexual) pseudanthia (Wurdack, 2002). Pollinator specialization and coevolution is known to occur in *Dalechampia* (Armbruster, 1984) but not the other pseudanthial taxa including *Uapaca*, which has generalized reproductive ecology (Ngulube et al., 1998).

Jablonskia is a monotypic genus, widespread in northern South America, which was recently recognized by Webster (1984b) after long being a discordant element in *Securinea*. It differs from all other Antidesmeae in being monoecious and having fasciculate inflorescences; it was placed in this tribe mainly on account of pollen (Punt, 1962; Webster, 1984b) and wood (Mennega, 1984, 1987) studies. Levin (1986a) found the leaves of *Jablonskia* consistent with members of Antidesmeae and did not observe tanniniferous cells.

A partial *rbcL* sequence for the Guyana Highland endemic *Celianella* obtained during our final manuscript revisions places it as the strongly supported sister to *Jablonskia* (not shown). *Celianella* has complex staminate inflorescences with distinctly pedunculate clusters of subsessile flowers surrounded by bracteoles that could, at least in bud or after flowering, be mistaken for sepals. This is similar to *Uapaca* if much less pronounced. The partial inflorescences with contracted axes in *Celianella* are subtended by partly fused involucre bracts. A close relationship between these two genera was suggested by wood anatomy (Mennega, 1984) and pollen morphology (Webster, 1984b). This connection was eventually dismissed by Webster (1984b) because *Celianella* is dioecious, has pendulous anthers, a strongly accrescent pistillate calyx, solitary seeds in each locule, and embryos with radicles much shorter than the cotyledons, as well as mistakenly interpreted as having racemose, pedicellate staminate flowers. Seed characters placed *Celianella* in the same group as *Jablonskia* and other tanniniferous and fasciculate genera in the study of Tokuoka and Tobe (2002), whereas *Celianella* was associated with *Antidesma*, *Hyeronima*, *Thecacoris*, and *Uapaca* by Stuppy

(1996) who regarded *Jablonskia* as incertae sedis because of its lack of synapomorphic seed characters.

Subclade T4—This subclade contains monotypic *Bischofia* and *Spondianthus* in a weakly supported (BP 50) sister relationship. *Bischofia javanica* (sometimes treated as two species) is a wide-ranging, invasive Asian tree with trifoliolate leaves bearing theoid teeth. Airy Shaw (1965) proposed monotypic Bischofiaceae to accommodate the taxon near the vegetatively similar Staphyleaceae. The affinities of *Bischofia* have since been generally accepted to lie with Phyllanthoideae as confirmed by embryological, leaf anatomical, and wood evidence (Bhatnagar and Kapil, 1973; Levin, 1986a; Mennega, 1987; Tokuoka and Tobe, 2001).

The well-supported placement within Phyllanthaceae provides little insight into the origin of its compound leaves, which are unique in Phyllanthaceae. Airy Shaw (1967), noting the longer terminal petiolule and a penta-foliolate pinnate leaf mutant, considered them to be of pinnate and not palmate derivation and thus unprecedented in Euphorbiaceae s.l. Despite Airy Shaw's conclusions (1967) drawn from limited teratological evidence, leaf mutants are equivocal and on a single tree can come in a wide range of pinnate, palmate, and mixed multifoliolate forms (K. J. Wurdack, personal observation). More revealing are the unequal lengths of all three petiolules and the location of two pairs of minute glandular stipels—one pair on the petiole (at junction with lateral petiolules) and the other at the summit of the terminal petiolule (base of terminal leaflet). Leaf developmental studies are called for.

Bischofia has several other features that have been considered unusual or unique in Phyllanthaceae. For example, the leaves bear marsupiform acaridomatia that functionally host mites (Rozario, 1995; K. J. Wurdack, personal observation). These are not unique as suggested by Levin (1986a) but have a convergent gain in *Antidesma* (subclade T1). *Antidesma pulvinatum* Hillebr. has inhabited acaridomatia (Pemberton and Turner, 1989; P. Hoffmann, personal observation), and domatia are consistently present in several other species of *Antidesma* (Hoffmann, in press). Domatia also occur in some *Cleistanthus* spp. (G. McPherson, Missouri Botanical Garden, personal communication) in subclade F2. It is possible that the epidermal idioblastic secretory cells in *Bischofia* (Levin, 1986a and references therein) are homologous to tanniferous cells that characterize most of this clade.

Bischofia is also unique in Phyllanthaceae in possessing eight instead of four hypocotylary vascular bundles (Verdus, 1976). Among Phyllanthaceae as circumscribed here, Levin (1986a) found theoid teeth to be present only in *Bischofia*, although he suggested that the marginal glands present in Aporo-seae (noted earlier) might be their remnants. Cytologically *Bischofia* is $n = 98$, which suggests derivation from a dysploid gain followed by polyploidization of $x = 14$, instead of direct polyploidization from $x = 7$ as hypothesized by Hans (1973). Given the morphological and phylogenetic isolation of *Bischofia*, this probably was an old event. *Bischofia* pollen has been reported for the Eocene of France (Gruas-Cavagnetto and Köhler, 1992).

Spondianthus contains a single, variable, widespread, tropical African species (revised by Léonard and Nkounkou, 1989) that has always been associated with Antidesmeae. Its isolated position in phylogenetic analyses, both here and in Levin (1986b), was only recently emphasized in classifications, first as a monotypic tribe Spondiantheae (Webster, 1975) and later

as subtribe Antidesmeae-Spondianthinae (Webster, 1994b). Webster (1994b), on the tribal reduction, noted foliar characters (Levin, 1986b) and pollen (Köhler, 1965). Levin (1986b) suggested that it is the plesiomorphic sister group of the clade containing Antidesmeae, Aporo-seae, and Uapaceae. *Spondianthus* is strongly toxic, containing fluoroacetic acid (Hegnauer, 1989; Neuwinger, 1994) and, besides *Uapaca*, is the only taxon with resinous exudate in Phyllanthaceae. The first several nodes of the tanniferous clade require more genes for robust phylogenetic hypotheses.

Conclusions—Analysis of *rbcL* sequence data has resolved problems of circumscription and composition of Phyllanthaceae, as well as provided a good indication of major supra-generic groupings. The largest grouping (fasciculate and tanniferous clades) is also supported by two independent morphological characters, even though there are exceptions that may be due to our limited knowledge of some taxa and generally of organ homology in Phyllanthaceae. The groups recovered within these two clades (subclades F1–F6 and T1–T4) are correlated with much of the palynological, seed anatomical, and leaf morphological data. Floral and fruit characters are often found to be homoplasious. Certain taxa (e.g., *Martretia*, *Poranthera*) have morphological modifications that have previously obscured their relationships. Nevertheless, several suprageneric taxa of Webster's most recent classification are, if somewhat modified, recovered in the analysis.

Support for many clades with *rbcL* alone is not sufficient to present a revised tribal classification here. Further studies using a number of different genetic markers (Katriarachchi et al., 2004a; Samuel et al., in press) confirm the clades found here and will provide a firm base for a family classification that better reflects phylogenetic relationships. More extensive taxon sampling will clarify generic boundaries in subclades F1 (Katriarachchi et al., 2004b), F2, and F3.

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