Classification of Apocynaceae s.l. According to a New Approach Combining Linnaean and Phylogenetic Taxonomy

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Abstract.— A new approach to a nomenclatural system, including elements from both Linnaean and phylogenetic nomenclature, is proposed. It is compatible with the existing Linnaean system, including "standard names" corresponding to principal and secondary ranks, and uses a variant of the definitions from the Phylocode system. A new infrafamilial classification, using this nomenclatural approach, of the Apocynaceae s.l. (i.e., including the Asclepiadaceae) based mainly on analyses of *rbc*L and *ndh*F data is discussed. Twenty-one tribes and four rankless taxa are defined. [Apocynaceae s.l.; classification; Linnaean nomenclature; *ndh*F; nomenclature; phylogenetic nomenclature; phylogeny; *rbc*L.]

Discussion about different nomenclature systems in recent literature has been intense (e.g., de Queiroz and Gauthier, 1992, 1994; Schander and Thollesson, 1995; Bryant, 1996, 1997; de Queiroz, 1996, 1997a; Liden and Oxelman, 1996; Reveal, 1996; Cantino et al., 1997; Liden et al., 1997; Moore, 1998; Schander, 1998; Sereno, 1999). A new nomenclature system, termed the Phylocode or phylogenetic taxonomy (de Queiroz and Gauthier, 1992; Cantino and de Queiroz, 2000) has been proposed, challenging the traditionally used "Linnaean system" (e.g., Greuter et al., 1994). Applications of phylogenetic taxonomy to plant systematics include, for example, classifications of the Lamiaceae (Cantino et al., 1997), Ericaceae (Kron, 1997), Malvaceae (Baum et al., 1998), and Scrophulariaceae (Olmstead et al., 2001).

In the Linnaean system, nomenclature and classification (circumscription) are not strongly coupled. Named taxa are fixed to two reference points: the type (type genus/species or, in the case of species, type specimen) and the rank; the only mandatory rank is genus (Greuter et al., 1994; in practice, further ranks are often treated as mandatory). An exact circumscription of the taxon is not required; the only restriction is that a taxon cannot include another taxon with the same or higher rank. Nevertheless, a list of included taxa is often added in classifications of taxa above species level.

The Phylocode system aims at explicitly binding names to specific clades; the name of a taxon is tightly coupled to a specific clade (or a specific ancestor) through a definition. Three different kinds of definitions (node-based, stem-based, and apomorphy-based; e.g., de Queiroz and Gauthier, 1992; Cantino and de Queiroz, 2000) have been proposed. Because the Phylocode system abandons ranks, it is (with its present description) incompatible with the Linnaean system.

Both systems have certain advantages as a communication tool in biology: The Linnaean system has a more stable set of names in use (but the exact circumscriptions of their corresponding taxa may vary), whereas the phylogenetic system provides more exact definitions, thus reducing instability caused by subjective changes in taxon circumscriptions (e.g., splitters and lumpers). In addition, the principal ranks of the Linnaean system provide universal standard names that are important, for example, for textbooks, databases, and floras.

We propose a compromise approach that combines the advantages of the two systems. It is compatible with the system presently in use—the Linnaean system—in using a system of hierarchic standard names (compare with "primary ranks" in the Linnaean system) and types, but it also adopts a variant of the definitions from the phylogenetic system to reduce the impact of subjective changes in circumscriptions. Because the main aim with the present study is to present a new tribal classification of the angiosperm family Apocynaceae s.l., we will mainly concern

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ourselves with family/tribal-level plant classification. Likewise, our use of the term the Linnaean system mainly refers to the International Code of Botanical Nomenclature (ICBN; Greuter et al., 1994). We will not discuss species-level nomenclature, nor that of extinct taxa (see, e.g., de Queiroz and Gauthier, 1992; Eriksson et al., 1998; Mishler, 1999).

The Apocynaceae s.l. belong to the order Gentianales and have a mainly pantropical/subtropical distribution, with a few temperate representatives. The family comprises many well-known ornamentals such as *Nerium* (oleander) and *Hoya* (wax flower). The plants are typically laticiferous and produce various alkaloids and cardenolides, some of which have medical properties. The most well-known example is *Catharanthus* (rose periwinkle), which contains vinblastine and vincristine, compounds now used worldwide to treat childhood leukemia.

The family Asclepiadaceae was segregated from the Apocynaceae s.l. by Brown (1810). Although some authors have questioned this separation (e.g., Demeter, 1922; Safwat, 1962; Judd et al., 1994; Struwe et al., 1994), most classifications subsequent to that of Brown have followed his "two-family" treatment. Molecular studies of the Apocynaceae s.l. (Sennblad and Bremer, 1996; Civeyrel et al., 1998; Potgieter and Albert, 2001) have indicated that the Asclepiadaceae form a subclade of the Apocynaceae s.str., thus rendering the Apocynaceae s.str. nonmonophyletic. These studies also indicated major problems with the infrafamilial classification in the two families. A detailed discussion of different classifications of the Apocynaceae s.str. and the Asclepiadaceae is given in Sennblad and Bremer (1996), and only a short review will be given here, concentrating on the most recent classifications and results from molecular studies.

Since the classification of Schumann (1895), the Apocynaceae have traditionally been divided into two subfamilies, the Plumerioideae and the Apocynoideae, and approximately into 12 tribes and 27 subtribes (Pichon, 1948a,b,c, 1950; Leeuwenberg, 1994a). The studies by Sennblad and Bremer (1996) and Endress et al. (1996) showed that both the Plumerioideae and Apocynoideae are nonmonophyletic. Four of the tribes of the Plumerioideae have been shown to be nonmonophyletic (Endress et al., 1996;

Sennblad and Bremer, 1996; Civeyrel et al., 1998; Potgieter and Albert, 2001), three tribes were monogeneric, and the monophyly of one tribe has not been evaluated. The study of Sennblad et al. (1998) was aimed mainly at the tribe Wrightieae (Apocynoideae) sensu Leeuwenberg (1994a) but also included representatives of the other tribes of the Apocynoideae, as well as of the Asclepiadaceae. Sennblad et al. showed that none of the described tribes within the Apocynoideae is monophyletic and suggested a reclassification of the Wrightieae sensu Leeuwenberg (1994a) into the Wrightieae, the Nerieae, and the Malouetieae.

The infrafamilial classification of Asclepiadaceae proposed by Brown (1810) when describing the family has been followed by most subsequent authors (Liede and Albers, 1994) and comprises three subfamilies, of which the Periplocoideae and Secamonoideae are monotribal and the Asclepiadoideae usually comprise five tribes. An exception from this traditional view is the classification of Swarupanandan et al. (1996), which reduced the number of tribes of the Asclepiadoideae to two and included the Secamonoideae as a third tribe in the Asclepiadoideae. Furthermore, a revision of the Periplocoideae by Venter and Verhoeven (1997) recognizes three tribes in this subfamily. The monophyly of the Asclepiadaceae is uncertain; in the study of Sennblad and Bremer (1996), however, the subfamily Periplocoideae, itself monophyletic, did not form a monophyletic group with the other two subfamilies (sensu Liede and Albers, 1994), whereas in the study of Civeyrel et al. (1998) the three subfamilies did form a monophyletic group. The study of Civeyrel et al. (1998) also indicated that the traditional Secamonoideae is monophyletic with a position as sister to Asclepiadoideae (see also Sennblad and Bremer, 1996; Potgieter and Albert, 2001). The traditional Asclepiadoideae receive good support (Sennblad and Bremer, 1996; Civeyrel et al., 1998; Potgieter and Albert, 2001). Of the tribes of the Asclepiadoideae in the classification of Liede and Albers (1994), Asclepiadeae and Marsdenieae have been shown to be nonmonophyletic.

The findings of the molecular studies indicated above and also from a previous version of this paper (included in the Ph.D. thesis of B.S., 1997; see also Sennblad and Bremer,

2000) were summarized and developed further by use of morphology in the most recent classification of the Apocynaceae s.l. by Endress and Bruyns (2000). The five traditional subfamilies were kept, but 19 newly recircumscribed tribes were also recognized (see Table 1).

However, the results of the present study indicate that although the classification of Endress and Bruyns (2000) are a major advance in making the classification congruent with current best estimates of phylogeny, problematic cases still need revision. Furthermore, for many of the recognized tribes, taxon sampling for molecular data is weak and the morphological homologies in these groups are difficult to interpret (Endress and Bruyns, 2000). Further rearrangements of tribal circumscription will almost certainly be needed in the future.

The Apocynaceae s.l. may thus provide a suitable test for the classification system proposed in this study. We therefore propose a new classification of the Apocynaceae based mainly on an *rbc*L analysis that includes extended taxon sampling as well as additional data from length variation of *rbc*L in its 3′-end and downstream. Certain relationships of special interest have been tested with a smaller data set for the subfamily Apocynoideae and the traditional Asclepiadaceae, including additional nucleotide sequences of the chloroplast gene *ndh*F. This gene often has a greater substitution rate than *rbc*L (see Olmstead and Sweere, 1994; Kim and Jansen, 1995) and may therefore form a complement to *rbc*L when the latter proves too conserved. We have used only the 3′ region of the gene because that region appears to show the most variability (see Kim and Jansen, 1995). Furthermore, results from other recent molecular studies have also been taken into account in the classification.

MATERIALS AND METHODS

We sampled 77 representatives of the Apocynaceae s.l. (Table 1). All subfamilies and tribes of the classification of Endress and Bruyns (2000) are represented in the analysis. *Gelsemium* Juss. and *Mostuea* Didr. of the Gelsemiaceae were chosen as outgroup taxa, because they were indicated to be the closest

TABLE 1. Classification of the Apocynaceae s.l. and sampling of taxa. Classification are according to Endress and Bruyns (2000).

RAUVOLFIOIDEAE

Alstonieae
Alstonia R.Br.
Aspidosperma Mart. et Zucc.
Vallesia Ruiz et Pav.

Vinceae
Catharanthus G. Don
Kopsia Blume
Ochrosia Juss.
Rauvolfia L.
Vinca L.

Willughbeieae
Ancylobotrys Pierre
Dictyophleba Pierre
Vahadenia Stapf

Tabernaemontaneae
Carvalhoa K. Schum.
Molongum Pichon
Schizozygia Baill.
Tabernaemontana L.
Tabernanthe Baill.

Melodineae
Craspidospermum A.DC.
Diplorhynchus Ficalho et Hiern
Melodinus J.R. Forst. et G. Forst.

Hunterieae
Picralima Pierre
Pleiocarpa Benth.

Plumerieae
Allamanda L.
Anechites Griseb.
Cameraria L.
Cerbera L.
Plumeria L.
Thevetia Adans.

Carisseae
Acokanthera G. Don
Carissa L.

Alyxieae
Alyxia R.Br.
Chilocarpus Blume
Lepinia Decne.

APOCYNOIDEAE

Wrightieae
Adenium Roem. et Schult.
Nerium L.
Stephanostema K. Schum.
Strophanthus DC.
Wrightia R.Br.

Malouetieae
Funtumia Stapf
Holarrhena R.Br.
Kibatalia G.Don
Mascarenhasia A.DC.
Pachypodium Lindl.

Apocyneae
Aganosma (Blume) G. Don
Apocynum L.
Baissea A.DC.
Beaumontia Wall.
Trachelospermum Lem.

Mesechiteae
Mandevilla Lindl.
Mesechites Müll.-Arg.

Echiteae
Parsonsia R.Br.
Peltastes Woodson
Prestonia R.Br.
Rhabdadenia Müll.-Arg.

PERIPLOCOIDEAE

Mondia Skeels
Parquetina Baill.
Pentopetia Decne.

Periploca L.
Petopentia Bullock
Tacazzea Decne.

SECAMONOIDEAE

Secamone R.Br

ASCLEPIADOIDEAE

Marsdenieae
Fockea Endl.
Hoya R.Br.
Micholitzia N.E.Br.
Stephanotis Thouars

Ceropegieae
Ceropegia L.
Stapelia L.

Asclepiadeae
Araujia Brot.
Asclepias L.
Calotropis R.Br.
Orthosia Decne.
Fischeria DC.
Matelea Aubl.
Schizostephanus Benth. et Hook. f.
Tweedia Hook. et Arn.
Tylophora R.Br.
Vincetoxicum Wolf

sister group to the Apocynaceae s.l. in the recent analysis of Gentianales by Backlund et al. (2000).

Forty-one new sequences of *rbc*L are published in this study; *rbc*L sequences for the outgroup taxa and for 35 ingroup taxa were published previously (Table 2). For *ndh*F, the 3′ region of the gene was sequenced for 18 taxa, representing the traditional Apocynoideae and Asclepiadaceae. Total DNA was extracted from fresh leaves or herbarium material by using the methods of Saghai-Maroof et al. (1984) and Doyle and Doyle (1987). The extractions were purified by ultracentrifugation in CsCl gradients or ethanol precipitation. Additional purification with the Qiaquick PCR purification kit (Qiagen Inc.) was performed in cases with problematic polymerase chain reaction (PCR) amplification. Double-stranded DNA was amplified by PCR by using Taq polymerase kit (Promega Corp.). Synthetic PCR primer sequences for *rbc*L were taken from Olmstead et al. (1992); *ndh*F primers were taken from Olmstead and Sweere (1994) and Oxelman et al. (1999). In cases where PCR amplification proved difficult, a PCR reaction using Taq extender PCR additive (Stratagene Inc.) was performed, following the protocol provided by the supplier. A second round of PCR, with only one of the primers, was performed to obtain single-stranded DNA (Kaltenboeck et al., 1992). Single-stranded DNA was sequenced manually (Sanger et al., 1977) by using internal primers designed for *rbc*L by G. Zurawski (DNAX Research Institute) and for *ndh*F by Olmstead and Sweere (1994) and Oxelman et al. (1999).

The length of the sequences of *rbc*L, excluding the 26 first nucleotides, but including positions just downstream from the gene, obtained in this study varied between 1,411 and 1,509 nt. For all taxa except *Parsonsia*, the sequence includes the stop codon. In positions 27–1,425, no structural mutations occur in *rbc*L. Alignment of this part of the gene is thus very simple. However, after position 1,425, that is, just before the typical position of the stop codon, gaps of different sizes occur, complicating alignment. Similarly, gaps occur in the coding region of the *ndh*F sequences. Because of these alignment problems, the sequences were truncated 23 bases before the typical position of the stop codon in Apocynaceae s.l. The reading frame was inferred through comparisons with complete Apocynaceae *ndh*F-sequences from the study of Backlund et al. (2000).

Multiple sequence alignment was made by hand to reduce the number of gaps while increasing the percentage similarity. We used the criteria of Golenberg et al. (1993) with minor modifications.

Two cladistic analyses were performed. The data matrix for the first analysis covered all included taxa and comprised characters corresponding to the nucleotide positions 27–1,425 of the *rbc*L gene and characters corresponding to gaps and informative nucleotide positions downstream of position 1,425. EMBL database accession numbers for *rbc*L sequences are given in Table 2. Only parsimony informative characters were analyzed.

The second analysis was of a subset of the taxa included in the first analysis and includes 18 genera representing the Apocynoideae sensu Leeuwenberg (1994a) and the traditional Asclepiadaceae. The data matrix consisted of two submatrices. One submatrix comprised positions 27–1,425 of the *rbc*L gene. The second submatrix comprised 733 aligned nucleotide positions from the 3′ region of *ndh*F. EMBL database accession numbers for the *ndh*F sequences are given in Table 2. Only parsimony informative characters were analyzed.

The cladistic analyses were performed using PAUP 4.0b2 (Swofford, 1998). An initial heuristic search (PAUP settings: HSEARCH [ADDSEQ = RANDOM NREPS = 200 SWAP = TBR]; other options with default settings) with all characters given a unit weight was followed by a successive weighting analysis (Farris, 1969, 1989) also using heuristic searches (PAUP settings: HSEARCH [ADDSEQ = RANDOM NREPS = 10 SWAP = TBR]; other options with default settings) and characters reweighted according to their rescaled consistency index.

Bootstrap frequencies (Felsenstein, 1985) were calculated with 10,000 replicates on the unit-weighted (*uwboot*) and successive weighted (*swboot*) data matrices (PAUP settings: BOOTSTRAP [NREPS = 10,000 METHOD = HEURISTIC CONLEVEL = 50] [/ADDSEQ = RANDOM NREPS = 1 SWAP = SPR NOMULPARS]; other options with default settings).

To simplify the discussion of the results, we used a rough scale of the relative support

TABLE 2.   Vouchers and EMBL accession numbers for sequences published in this study. For previously published sequences and for sequences from previously published voucher specimens, the reference is given.

Taxon	Voucher/source[b]	EMBL number rbcL/ndhF
Acokanthera oblongifolia (Hochst.) Codd	Sennblad and Bremer, 1996	X91758/-
Adenium obesum (Forssk.) Roem. et Schult.	Sennblad et al., 1998	AJ002880/AJ420130
Aganosma marginata (Roxb.) G. Don	Ryding 490, UPS	AJ419730/-
Allamanda cathartica L.	Sennblad and Bremer, 1996	X91759/-
Alstonia scholaris R.Br.	Sennblad and Bremer, 1996	X91760/-
Alyxia ruscifolia R.Br.	Sennblad 236, UPS	AJ419731/-
Ancylobotrys petersiana Pierre	Sennblad 201, UPS	AJ419732/-
Anechites nerium Urb.	Bremer et al. 3,386, UPS	AJ419733/-
Apocynum cannabinum L.	Sennblad and Bremer, 1996	X91761/AJ420113
Araujia hortorum E. Fourn.	Bremer 3,006, UPS	AJ419734/-
Asclepias curassavica L.	Sennblad and Bremer, 1996	X91774/-
Aspidosperma triternatum Rojas Acosta	Bremer 3,029, UPS	AJ419735/-
Baissea leonensis Benth.	Sennblad et al., 1998, Yallah 112, UPS[a]	AJ002881/AJ420114
Beaumontia grandiflora Wall.	Sennblad et al., 1998	AJ002882/AJ420115
Calotropis procera (Aiton) W.T. Aiton	Sennblad 222, UPS	AJ419736/-
Cameraria latifolia L.	Houghton 1,085, FTG	AJ419737/-
Carissa bispinosa (L.) Merxm.	Sennblad 235, UPS	AJ419738/-
Carvalhoa campanulata K. Schum.	Sennblad 217, UPS	AJ419739/-
Catharanthus roseus G. Don	Sennblad and Bremer, 1996	X91757/-
Cerbera venenifera Steud.	No voucher	AJ419740/-
Ceropegia woodii Schltr.	Sennblad and Bremer, 1996	X91775/-
Chilocarpus suaveolens Blume	Endress et al., 1996	X92445/-
Fockea multiflora K. Schum.	Specks 248, cult, MSTR[c]	AJ419741/-
Craspidospermum verticillatum Bojer	Pettersson and Nilsson 742	AJ419742/-
Dictyophleba lucida Pierre	Sennblad and Bremer, 1996	X91762/-
Diplorhynchus condylocarpon (Müll.-Arg.) Pichon	Sennblad 203, UPS	AJ419743/-
Fischeria stellata (Vell.) E. Fourn.	Clark and Watt 793, UPS	AJ419744/-
Funtumia elastica Stapf	Sennblad et al., 1998	AJ002884/-
Gelsemium sempervirens Aiton	Olmstead et al., 1993	L14397/-
Holarrhena pubescens G. Don	Sennblad et al., 1998	AJ002884/-
Hoya bella Hook.	Sennblad and Bremer, 1996	X91776/-
Kibatalia gitingense (Elmer) Woodson	Liede 3,268, Z	AJ419745/-
Kopsia fruticosa A.DC.	Sennblad and Bremer, 1996	X91763/-
Lepinia taitensis Decne.	Perlman 15071, NTBG	AJ419746/-
Mandevilla sanderi (Hemsl.) Woodson	Sennblad and Bremer, 1996	X91764/AJ420116
Mascarenhasia arborescens A.DC.	Sennblad et al., 1998	AJ002885/AJ420117
Matelea hirsuta (Vahl) Woodson	Sennblad 263, UPS	AJ419747/-
Melodinus monogynus Roxb.	Sennblad 261, UPS	AJ419748/-
Mesechites trifida Müll.-Arg.	Bremer et al. 3,351, UPS	AJ419749/-
Micholitzia obcordata N.E.Br.	Bremer 3,010, UPS	AJ419750/-
Molongum laxum (Benth.) Pichon	Sennblad and Bremer, 1996	X91765/-
Mondia ecornuta (N.E.Br.) Bullock	Sennblad 215, UPS	AJ419751/-
Mostuea brunonis Didr.	Olmstead et al., 1993	L14404/-
Nerium oleander L.	Sennblad 265, UPS	AJ002886/AJ420118
Ochrosia coccinea Miq.	v. d. Laan 389, WAG	AJ419752/-
Orthosia serpyllifolia Decne.	Bremer et al. 3,372, UPS	AJ419753/-
Pachypodium lamerei Drake	Sennblad et al., 1998	AJ002887/AJ420119
Parquetina nigrescens (Afzel.) Bullock	Sennblad and Bremer, 1996	X91777/-
Parsonsia heterophylla A. Cunn.	Sennblad et al., 1998	AJ002888/-
Peltastes peltatum (Vell.) Woodson	Sennblad 262, UPS	AJ419754/-
Pentopetia sp.	No voucher	AJ419755/-
Periploca graeca L.	Sennblad et al., 1998	AJ002889/AJ420120
Petopentia natalensis (Schltr) Bullock	Sennblad 237[a] and s.n. cult. MSTR	AJ419756/AJ420121
Picralima nitida T. et H. Dur.	Sennblad and Bremer, 1996	X91766/-
Pleiocarpa mutica Benth.	Bremer 3,017, UPS	AJ419757/-
Plumeria inodora Jacq.	Sennblad and Bremer, 1996	X91767/-
Prestonia quinquangularis Spreng.	Sennblad and Bremer, 1996	X91768/AJ420122
Rauvolfia mannii Stapf	Sennblad and Bremer, 1996	X91769/-
Rhabdadenia biflora Müll.-Arg.	Zona 616, FTG	AJ419759/AJ420123
Schizostephanus alatus K. Schum.	Cult. MSTR	AJ419758/-
Schizozygia coffaeoides Baill.	Sennblad 207, UPS	AJ419760/-
Secamone afzelii (Schult.) K. Schum.	Sennblad and Bremer, 1996	X91779/AJ420124

TABLE 2. Continued

Taxon	Voucher/source	EMBL number rbcL/ndhF
Secamone geayi Constatin et Gallaud	Civeyrel 1,200, LC	AJ419761/-
Stapelia leendertziae N.E.Br.	Sennblad and Bremer, 1996	X91778/-
Stephanotis floribunda Brongn.	Sennblad 256, UPS	AJ419762/AJ420125
Stephanostema stenocarpum K. Schum.	Sennblad and Bremer, 1996	X91770/AJ420126
Strophanthus eminii Pax	Sennblad and Bremer, 1996	X91771/AJ420127
Tabernaemontana divaricata Roem. et Schult.	Sennblad and Bremer, 1996	X91772/-
Tabernanthe iboga Baill.	Leeuwenberg 12544, WAG	AJ419763/-
Tacazzea apiculata Oliver	Venter 9,188, cult. MSTR	AJ419764/-
Thevetia peruviana (Pers.) K. Schum.	Sennblad and Bremer, 1996	X91773/-
Trachelospermum jasminoides (Lindl.) Lem.	Sennblad et al., 1998	AJ002890/AJ420128
Tweedia coerulea Sweet	Sennblad 254, UPS	AJ419765/-
Tylophora sylvatica Decne.	Sennblad and Bremer, 1996	X91789/-
Vahadenia caillei (A.Chev.) Hutch. et Dalziel	Leeuwenberg 12,275, WAG	AJ419766/-
Vallesia antillana Woodson	Meagher 966, FTG	AJ419767/-
Vinca minor L.	Sennblad 230, UPS	AJ419768/-
Vincetoxicum hirundinaria Medik.	Sennblad 257, UPS	AJ419769/-
Wrightia arborea (Dennst.) Mabb.	Sennblad et al., 1998	AJ002891/AJ420129

[a] Voucher for *rbc*L sequence only.

[b] Herbarium abbreviations are according to Index Herbariorum, except LC = Private herbarium of Laure Civeyrel.

[c] This specimen was originally determined as *Cibirhiza albersiana* in Kunze et al. (1994), but has recently been redetermined as *Fockea multiflora* K. Schum. (Verhoeven et al., 2002).

of the clades in the successive weighting analysis: Clades with a successive weighted bootstrap >63% were considered well supported, those with a successive weighted bootstrap >85% were considered strongly supported. In a theoretical context, a clade supported by one uncontradicted character corresponds to a bootstrap support of 63%, and a clade supported by two uncontradicted characters to 85% (Harshman, 1994; Farris et al., 1996). Here, however, this scale merely relates to the support distribution within the analysis.

RESULTS

The unit weight analysis of the complete *rbc*L data set (237 characters total; 2.14% of the cells were scored as missing data) resulted in 19,003 trees 828 steps long, with a consistency index (ci) = 0.378, and a retention index (ri) = 0.678. The consensus tree from the successive weighting analysis of 252 most-parsimonious trees (each 177.3 steps long, $ci = 0.661$, $ri = 0.880$) is presented in Figure 1. The length of these trees with unit weight characters is 830 steps; thus these trees are not identical to any of the most-parsimonious trees from the unit weight analysis. Branches not present in the strict consensus tree from the unit weight analysis are indicated on the combinable consensus tree from the successive weighting analysis (Fig. 1). The unit weight analysis of the combined set of the *rbc*L and *ndh*F data (153 characters total; 0.43% of the cells were scored as missing data) resulted in four trees 345 steps long ($ci = 0.539$, $ri = 0.482$). The successive weighting analysis gave three trees 97.8 steps long ($ci = 0.840$, $ri = 0.849$). The strict consensus tree of the successive weighting analysis is presented in Figure 2. These trees are one step longer with unit weights than the trees from the unit weight analysis. Unless otherwise stated, the following discussion refers to the successive weighting analyses of the complete *rbc*L data set.

Investigating the justification of a priori weighting (Sennblad and Bremer, 2000), we made some additional analyses of our *rbc*L data set, including tests for base composition bias and rate heterogeneity. This did not produce significantly different results, and all well-supported groups were congruent with those of the present study. The general structure and the well-supported groups of the resulting trees (Figs. 1 and 2) are to a large degree congruent with the molecular studies of Sennblad and Bremer (1996), which are based on *rbc*L data; of Civeyrel et al. (1998), based mainly on *mat*K sequence data; and of Potgieter and Albert (2001), based mainly on *trn*L–F data. Although there are differences in the weakly supported relationships among the well-supported groups, in particular the exact position of the
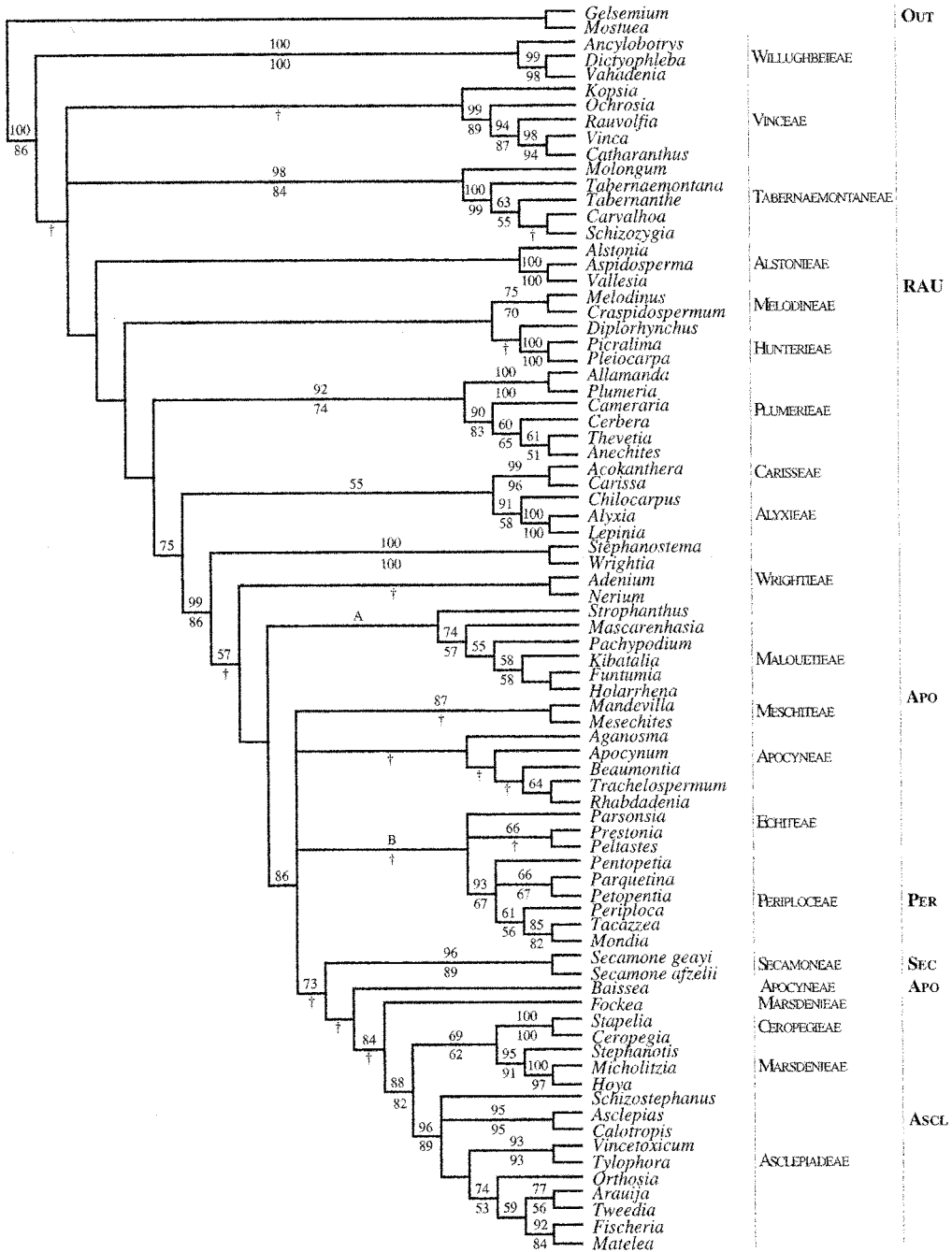
FIGURE 1. Combinable component consensus tree of the 252 most-parsimonious trees from the successive weighting analysis of the complete *rbc*L data set. Subfamilial and tribal classification is according to Endress and Bruyns (2000). For subfamilies, a three-letter code is used: RAU, APO, PER, SEC, and ASC denote Rauvolfioideae, Apocynoideae, Periplocoideae, Secamonoideae, and Asclepiadoideae, respectively; OUT denotes the outgroup. Numbers below branches are unit-weighted bootstrap values; successive weighted bootstrap values are indicated above branches. Branches not present in the strict consensus tree from the unit weight analysis are indicated with a cross (†). For branches marked A or B, the frequencies in the combinable component consensus are 95% or 50%, respectively; all other branches have 100% frequency.
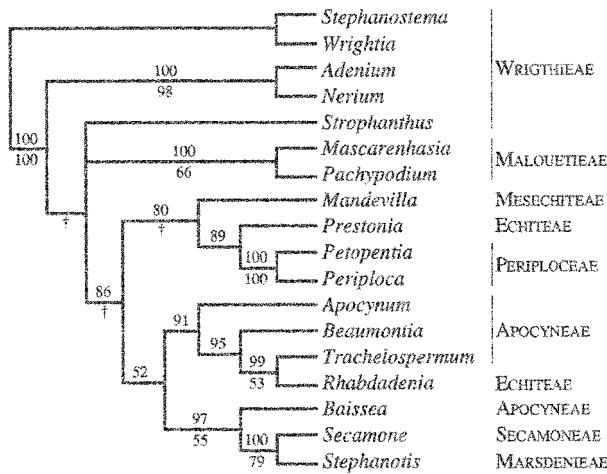
FIGURE 2. Strict consensus tree from the successive weighting analysis of the combined *ndh*F and *rbc*L data set. Tribal classification sensu Endress and Bruyns (2000) is indicated. Numbers below branches are unit-weighted bootstrap values, whereas successive weighted bootstrap values are indicated above branches. Branches not present in the strict consensus tree from the unit weight analysis are indicated with a cross (†).

Periplocoideae and of the root of the ingroup, all well-supported groups in our analysis are congruent with those studies. The combined analysis using data from *rbc*L- and *mat*K-sequences and floral and pollen morphology in the study of the Apocynaceae s.str. by Endress et al. (1996), and the analysis of Sennblad et al. (1998) of the tribe Wrightieae sensu Leeuwenberg (1994a) and related taxa, using *rbc*L and morphological data, are largely congruent with the result from the present study. Furthermore, preliminary results from collaborative studies by Sennblad et al. (aimed at the traditional Apocynoideae and Asclepiadaceae, pers. comm.) and Endress et al. (aimed at the traditional Alyxieae, pers. comm.) based on combined analysis of several molecular and morphological datasets are also congruent with our results.

Support is good for the split between the ingroup and the two outgroup taxa, *Gelsemium* and *Mostuea* ($uwboot = 96\%$, $swboot = 100\%$). Thus, the initial assumption of monophyly of the Apocynaceae s.l. is not violated. Conforming to earlier studies (e.g., Sennblad and Bremer, 1996; Civeyrel et al., 1998; Sennblad et al., 1998; Potgieter and Albert, 2001), the traditional Asclepiadaceae are nested within the traditional subfamily Apocynoideae (e.g., sensu Endress and Bruyns, 2000).

The Apocynoideae–Asclepiadaceae clade, which is strongly supported ($uwboot = 86\%$, $swboot = 99\%$), is in turn nested within the subfamily Rauvolfioideae sensu Endress and Bruyns (2000).

Comparison of our results to the most recent classifications of the Apocynaceae Endress and Bruyns (2000; see Table 1 and Fig. 1), shows that, although their circumscription of the subfamilies Periplocoideae, Secamonoideae, and Asclepiadoideae are monophyletic in our analysis, their subfamilies Rauvolfioideae and Apocynoideae are nonmonophyletic. Similarly, the tribes of the Rauvolfioideae except Melodineae are monophyletic, but three of the tribes of the Apocynoideae—the Apocyneae, the Echiteae, and the Wrightieae—are nonmonophyletic. Of the tribes of the Asclepiadoideae, the Ceropegieae and Asclepiadeae are monophyletic. The position of *Fockea* as sister to the rest of the Asclepiadoideae renders the Marsdenieae nonmonophyletic. All the included Periplocoideae taxa belong to the tribe Periploceae sensu Venter and Verhoeven (1997), except *Pentopetia*, which they placed in the tribe Cryptolepideae. Given this unresolved position of *Pentopetia*, the monophyly of these tribes cannot be evaluated; however, the reduction of *Parquetina* to synonymy with *Periploca*, proposed by Venter and Verhoeven (1997), is not supported by the present study.

DISCUSSION

One of the most important tasks for a nomenclature system is to provide a stable means to communicate classifications (which we here will understand as representing phylogenetic relationships). Although both the Linnaean and the Phylocode systems are able to communicate phylogenies, they are sensitive to changes in phylogenetic hypotheses, which in both systems will demand taxonomic changes. In addition, the Linnaean system is subject to a potential instability relating to subjective changes in circumscription, that is, lumpers and splitters may refer to different groups of organisms by the same name (see de Queiroz and Gauthier, 1992). For many taxa, a consensus circumscription has eventually been established, but for other groups this is still a problem. A current example of this from Apocynaceae is the genus *Tabernaemontana* sensu Leeuwenberg (1991, 1994b), which in the classification of Allorge (1985) is split into eight genera. The Phylocode system was designed to avoid this problem; by use of strict definitions of taxa, subjective changes in circumscription are avoided.

However, this rigidity in definitions leads to a potential instability and high turnover of names associated with a group of nested taxa. Relatively small changes in phylogenetic views, e.g., when a defining taxon, "specifier," receives a less nested position, may cause some (or all) of these nested names to become synonymous (e.g., de Queiroz and Gauthier, 1994; Bryant, 1996; Liden and Oxelman, 1996; Sereno, 1999). The junior synonyms should, according to the Phylocode, be rejected, and new names may then be needed for the new system of nested clades (de Queiroz and Gauthier, 1994). The names associated with this group of taxa are, thus, replaced by new names. This can be especially problematic when careless definitions have been made, as have been noted by Schander and Thollesson (1995) and Cantino et al. (1997) among others. Consider a hypothetical worst-case example: The Asclepiadaceae were traditionally considered as separate from Apocynaceae. A stem-based definition of Apocynaceae reflecting this view could be the largest clade that includes *Apocynum* but not *Asclepias*. On the present tree, such a definition would limit the Apocynaceae to be synonymous with the tribe Apocyneae, and a new name would be needed for the taxon corresponding to the current view of Apocynaceae (e.g., sensu Endress and Bruyns, 2000). A node-based definition would handle this particular problem but may have other problems, as illustrated here with another hypothetical worst-case scenario: Early classifications of the Apocynaceae included *Plocosperma* Benth. A node-based definition representing this view could have included as reference taxa, say, *Apocynum* and *Plocosperma*. The recently proposed position of *Plocosperma* close to the Boraginaceae (Backlund et al., 2000) would with this definition have made Apocynaceae a very large taxon (containing at least both Gentianales and Boraginales), possibly synonymous with (a hypothetical definition of) the informal taxon Euasterids II (Bremer et al., 1998), and again a new name for the Apocynaceae sensu Endress and Bruyns (2000; i.e., excluding *Plocosperma*) would have been needed. Because the Linnaean system allows recircumscription of synonymous names, the potential turnover in the set of names in use is reduced with this system (albeit at the expense of allowing subjectivity). Additionally, the ranks of the Linnaean system provide a set of names that work as relatively stable universal standard names in communication; note that equal ranks does not guarantee comparable evolutionary units, however. Continuity in usage of names is important, for example, in journals, literature databases, floras, teaching, and inventory work, and the need for such continuity has been recognized by proponents of both nomenclature systems (de Queiroz and Gauthier, 1992; Greuter et al., 1994; Reveal, 1996).

We propose a compromise approach that uses solutions relating to these aspects from both systems, concentrating mainly on botanical classification of extant plant taxa at the tribal and familial levels and only considering monophyletic taxa. We recommend a system that uses "standard names," (i.e., universally used communication units at convenient hierarchical levels), such as those provided by the principal ranks of the Linnaean system (Greuter et al., 1994), but in which sensitivity toward subjective changes in circumscription is reduced. One way to do this is to adopt the definitions of the phylogenetic system but use constraints similar

to those that apply between ranks in the Linnaean system. To reduce sensitivity toward changes in phylogenetic hypotheses (Schander and Thollesson, 1995; Bryant, 1996, 1997; Cantino et al., 1997; Moore, 1998), we propose using combined node + stem-based definitions that will provoke explicit incompatibilities between taxa in case of unfortunate changes in circumscription (de Queiroz, 1996, has proposed a similar type of definition for designating nonmonophyletic taxa; somewhat similar variants are also discussed in the Phylocode). A node-based part of the definition provides a minimal circumscription, whereas a stem-based part provides boundaries to competing taxa (maximal circumscription). If, on a particular phylogeny, the minimal (monophyletic) circumscriptions of competing taxa are overlapping, then the two taxa are incompatible. To make this meaningful, at least two taxa should be included in the node-based part of the definition; this will also avoid unnecessary monotypic taxa. This incompatibility will provide an objective point when nomenclatural reconsideration is needed. Returning to the first of our examples above, node + stem-based definitions of the Apocynaceae and Asclepiadaceae could be as follows:

> The family Apocynaceae is the most inclusive clade in the order Gentianales, including the type specimens of *Apocynum* and *Dictyophleba*, but not the taxa Asclepiadaceae [, Gentianaceae, Rubiaceae . . .]

and

> The family Asclepiadaceae is the most inclusive clade in the order Gentianales, including the type specimens of *Asclepias* and *Periploca*, but not the taxa Apocynaceae [, Gentianaceae, Rubiaceae . . .]

On the tree in Figure 1, these two definitions are mutually exclusive, and a decision on which name to keep must be made. Minimizing the number of classificatory changes should take precedence in this decision. The reason for this is to avoid the large, inconvenient "standard name" changes that could result from relatively small rearrangements. Rejected names are then ignored when occurring in definitions of other taxa. This is because the reference taxa in the stem-based part of the definitions are "defined" taxa rather than physical types (thus, reliance on defined reference taxa, which has been criticized for stem-based definitions by Sereno, 1999, is what we aim for; on the other hand,

the explicit reference of type specimens in the minimum circumscription provided by the node-based part of the definitions circumvents the tautology problem raised by Bryant, 1996). In the current example, this would mean that regardless of which name of Apocynaceae and Asclepiadaceae is rejected, the other will be defined as corresponding to the Apocynaceae sensu Endress and Bruyns (2000). The choice will therefore simply be which name to keep. In this case, because Apocynaceae has priority under the Linnaean system, we would choose to keep Apocynaceae to promote consistency with the current system. Nevertheless, outside these recommendations, choices of what names to choose will probably to a certain degree be arbitrary. We also propose that the rejected name should be reinstated with an emended definition if appropriate, to potentially allow for more stability in the set of names in use. Thus, in our second example above, a node + stem-based definition reflecting the inclusion of Plocosperma in Apocynaceae (e.g., by exchanging *Dictyophleba* for *Plocosperma* in the definition above) would presumably be incongruent with the definition of Gentianales as well as the definitions of Rubiaceae, Gentianaceae, and so forth, and therefore would be rejected. In such a case, where the only real change is in the position of a single taxon, a reinstatement of the Apocynaceae with an emended definition is motivated. However, a drawback is that this may also introduce elements of subjectivity in the circumscriptions of taxa.

Not all named clades need to be provided with standard names. In fact, for the purpose of a universal set used in journals, databases, and so forth, it may suffice to use standard names corresponding to the principal ranks of the Linnaean system (Greuter et al., 1994), such as species, genus, family, and order. Nevertheless, to provide compatibility with the present system, we suggest that additional names corresponding to commonly used secondary ranks (e.g., tribes) may be recognized. The hierarchical level of a standard name needs to be indicated. This does not imply that taxa of the same hierarchical level are comparable evolutionary units but simply indicates the hierarchical level of a taxon relative to nested taxa. Because such misinterpretations will in any case be difficult to prohibit, one may as well provide compatibility with the present Linnaean

system by using the names of the Linnaean ranks (e.g., species, genus, tribe, family, order) to indicate hierarchical level. The principle of exhaustive subsidiary taxa is not accepted, so redundant taxa need not be recognized. Other, "nonstandard," taxa could be defined by using Phylocode definitions—that is, without the restraints discussed for standard taxa above.

One advantage of the described system is that utilizing the correspondence between the standard names and Linnaean ranks allows the system to be largely compatible with the established Linnaean system. A change of system could therefore be gradual, with the two systems coexisting during a conversion time (see e.g., de Quieroz, 1997b).

Even though the node + stem-based definitions reduce the sensitivity towards changes in circumscriptions, they may still be sensitive toward "unfortunate" or "bad" definitions (see e.g., Cantino et al., 1997; Cantino and de Queiroz, 2000). Many of the recommendations for such things as choices of reference taxa (specifiers) in phylogenetic definitions are applicable also to the node + stem-based definitions (e.g., Schander and Thollesson, 1995; Bryant, 1996; Cantino et al., 1997; Sereno, 1999). Most likely the compromise system described above will have several further problems, and we hope that this paper will invite further discussion on the subject.

A New Classification of the Apocynaceae s.l.

Our results indicate that some problematic taxa remain in the classification of Endress and Bruyns (2000). Monophyly for two of the subfamilies and five of the tribes is called into question. If other recent molecular studies (e.g., Potgieter and Albert, 2001) are taken into consideration, a further four tribes (Alstonieae, Alyxieae, Plumerieae, and Vinceae) may be nonmonophyletic. This can in some cases be simply analysis artifacts, but as Endress and Bruyns (2000) themselves point out, their classification is to be considered preliminary. Insufficient taxon sampling in molecular studies and difficult homology decisions relating to morphological characters make the circumscription of many of the tribes, for example, in the Apocynoideae sensu Endress and Bruyns (2000), uncertain. There is, thus, risk for future rearrangements in many of the tribes. A classification using

node + stem-based definitions may be able to subsume such rearrangements without numerous explicit recircumscriptions. We will here use the result from the present study as a basis to propose such a classification of the Apocynaceae s.l.

Our aim is to base taxa on clades that are well supported. A second aim is to make our classification compatible with the current system. We will therefore primarily recognize nonoverlapping tribes that are valid under the Linnaean system. We will further adopt the principle of nested referencing (as suggested by Lee, 1999, and Sereno, 1999) from the Linnaean system. Thus, the first reference taxon in the node-based part of the definition is the primary type, which corresponds to the Linnaean type used for the name of the taxon. Instead of the (optional) enumeration of subsumed taxa of a lower rank (e.g., genera or subtribes), we will include node + stem-based definitions as discussed above. Citations to primary types of reference taxa, in node-based part of definitions, are also nested, and thus refer to "the type specimen of the type species of the type genus . . . of the defined taxon." A problem is that the relationships between the tribes are weakly supported. This may lead to very cumbersome definitions, enumerating all competing tribes in the stem-based part of the definition (e.g., Moore, 1998). One way to reduce this problem is to define intermediate, well-supported, taxa and use them as competing taxa. We therefore will further recognize four nonstandard taxa (note that an assignment of "nonstandard" taxa does not imply less reliability; standard names relate to communication purposes only). The taxa discussed are indicated in Figure 3. We will discuss the tree from the top of Figure 3, starting with the taxa of the traditional Plumerioideae. Tribes and subtribes given in parentheses in the text refer to the classifications of Endress and Bruyns (2000); in other cases, our classification is implied. For some tribes we have chosen a name with priority under Linnaean system that implies inclusion of a genus not sampled in the present study. For all but one (Willughbeieae) of these cases, additional molecular or morphological phylogenetic analyses support the inclusion of the genus. Even if too uncertain definitions should be avoided, this is less critical with node + stem-based definitions. In the case of Willughbeieae, we have decided, from
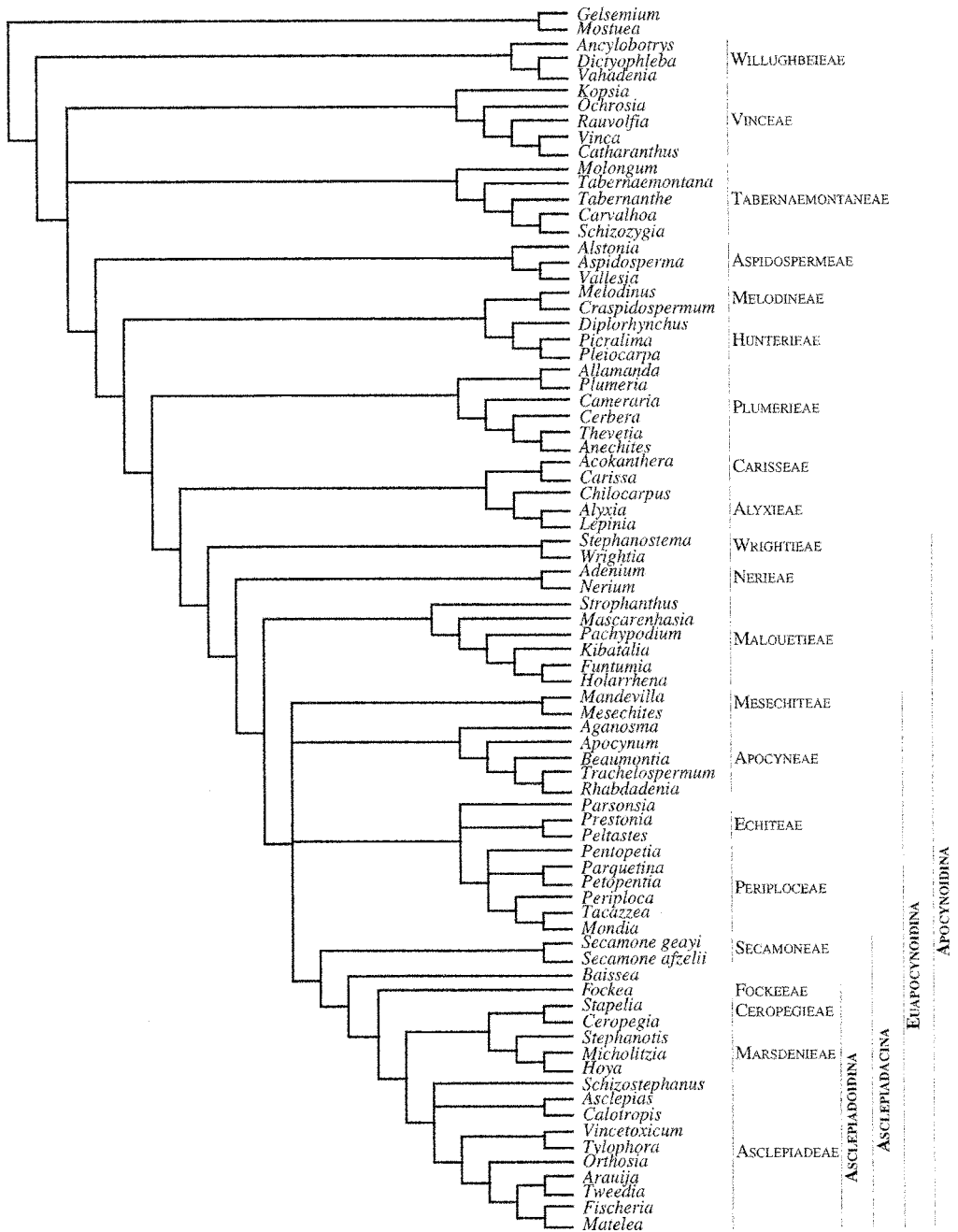
FIGURE 3. The tribal reclassification discussed in the text indicated on the combinable component consensus tree from the successive weighting analysis of the complete *rbc*L data set. Four nonstandard taxa—Apocynoidina, Euapocynoidina, Asclepiadacina, and Asclepiadoidina—are also indicated.

discussions with a morphological expert (M. Endress, pers. comm.), that morphological support exists for including *Willughbeia* Roxb. in Willughbeieae. If this is correct, the definition given below will be valid; if it is not, our system allows redefinition of the taxon. We have also tried to provide comments on potential morphological characters taken from literature for the different taxa recognized. However, we have not

performed any morphological analysis, but rely on information external to this study for these comments. In most cases we can therefore not identify synapomorphies for the taxa.

TAXONOMIC TREATMENT
Tribus Willughbeieae A.DC.

The *Ancylobotrys*, *Dictyophleba*, and *Vahadenia* clade is strongly supported (*uwboot* and *swboot* = 100%) and corresponds to the Willughbeieae of Endress and Bruyns (2000). The present sampling contains closely related genera that have been traditionally kept together. *Landolphia* P. Beauv. s.l. includes all these taxa (e.g., Schumann, 1895). In addition to the taxa sampled here, the study of Potgieter and Albert (2001) supports the inclusion of *Couma* Aubl., *Lacmellea* H. Karst., *Pacouria* Aubl., and *Saba* (Pichon) Pichon in this clade. Plants in this clade all have a gynoecium that is congenitally syncarpous and indehiscent and that contains a fleshy pulp including numerous seeds with copious horny endosperm (Fallen, 1986; Persoon et al., 1992). This probably constitutes synapomorphies for this clade (M. Endress, pers. comm.), although not unambiguously; for example, syncarpy is paralleled in Carisseae. We will therefore assume that the reference genus *Willughbeia* is included in this tribe.

Definition.—Tribe Willughbeieae is the most inclusive clade that includes the primary types of *Willughbeia* and *Dictyophleba* but not Alyxieae, Aspidospermeae, Carisseae, Hunterieae, Melodineae, Plumerieae, Tabernaemontaneae, Vinceae, or Apocynoidina.

Tribus Vinceae Bartl.

Ochrosia, *Rauvolfia*, *Vinca*, and *Catharanthus* (all Vinceae) form a strongly supported clade (*uwboot* = 89%, *swboot* = 99%). The association between *Rauvolfia* and *Catharanthus* was indicated by Sennblad and Bremer (1996). The study of Potgieter and Albert (2001) supports inclusion of the genera *Laxoplumeria* Markgr., *Neisosperma* Raf., and *Tonduzia* Pittier, previously classified with *Aspidosperma*. The Vinceae contain both herbaceous and fruticose taxa. The fruits are apocarpous, but whereas the fruits of *Catharanthus, Laxoplumeria, Neisosperma, Tonduzia*, and *Vinca* have dry fruit walls, the fruits of *Ochrosia* and *Rauvolfia* are drupes. Plants in Vinceae share a similar type of style head (i.e., the apical enlarged part of the style), with a stigmatic hollow and upper and lower hair wreaths (except in some species of *Ochrosia*), the presence of a nectar disk, and a linear hilum on the seed (Pichon, 1948b). On the present tree, Vinceae also include *Kopsia*; however, this position of *Kopsia* is very weakly supported (see also Sennblad and Bremer, 1996).

Definition.—Tribe Vinceae is the most inclusive clade that includes the primary types of *Vinca* and *Rauvolfia* but not Alyxieae, Aspidospermeae, Carisseae, Hunterieae, Melodineae, Plumerieae, Tabernaemontaneae, Willughbeieae, or Apocynoidina.

Tribus Tabernaemontaneae G. Don

The strongly supported association between *Tabernaemontana, Tabernanthe, Carvalhoa, Schizozygia*, and *Molongum* (Tabernaemontaneae; *uwboot* = 84%, *swboot* = 98%) has been suggested previously (Boiteau et al., 1978; Fallen, 1986; Endress et al., 1996; Sennblad and Bremer, 1996). Inclusion of taxa traditionally associated with *Tabernaemontana* (e.g., *Voacanga* Thouars and *Callichilia* Stapf; see also Tabernaemontaneae sensu Leeuwenberg, 1994a) and *Macoubea* Aubl. is supported by the analysis of Potgieter and Albert (2001). The taxa share sclerenchymatic anthers, free from the style head, and a characteristic band of heavily cutinized cells at the insertion on the staminal rib (Endress et al., 1996). The taxa traditionally associated with *Tabernaemontana* are characterized by their apocarpous fruits with arillate seeds, whereas genera associated with *Molongum* (Ambelanieae sensu Leeuwenberg, 1994a) have syncarpous fruits and lack an arillus. However, *Macoubea* forms a link between the two, having a syncarpous fruit with arillate seeds (Zarucchi et al., 1995).

Definition.—Tribe Tabernaemontaneae is the most inclusive clade that includes the primary types of *Tabernaemontana* and *Schizozygia* but not Alyxieae, Aspidospermeae, Carisseae, Hunterieae, Melodineae, Plumerieae, Vinceae, Willughbeieae, or Apocynoidina.

Tribus Aspidospermeae Miers

Aspidosperma and *Vallesia* (Aspidospermeae) form a strongly supported clade (*uwboot* and *swboot* = 100%) first suggested in Sennblad (1997; see also Sennblad and

Bremer, 2000). Subsequently, *Geissospermum* Allemão, *Haplophyton* A.DC., *Microplumeria* Baill., and *Strempeliopsis* Benth. were indicated to belong to this clade (Potgieter and Albert, 2001). The Aspidospermeae have simple style heads, lacking both stigmatic hollow and upper hair wreath, and have apocarpous fruits with variation in fleshiness and sclerification. *Alstonia* has traditionally been placed in the Plumerieae. Because its seeds have a hairy margin, it has been suggested to form a link to subfamily Apocynoideae. This was contradicted by Sennblad and Bremer's study (1996), however, where *Alstonia* was placed in an isolated position as the sister group to the rest of the Apocynaceae s.l. Here it groups with Aspidospermeae Sensu Endress and Bruyns (2000). However, this association is very weakly supported (*uwboot* and *swboot* < 50%), and in other recent studies Aspidospermeae and *Alstonia* do not form a clade (Potgieter and Albert, 2001). Because of this, we do not use it as a reference taxon in the definition. Thus, although the Aspidospermeae include *Alstonia* on the present tree, some other position of Alstonia can be accommodated without amending the definition.

Definition.—Tribe Aspidospermeae is the most inclusive clade that includes the primary types of *Aspidosperma* and *Vallesia* but not Alyxieae, Carisseae, Hunterieae, Melodineae, Plumerieae, Tabernaemontaneae, Vinceae, Willughbeieae, or Apocynoidina.

Tribus Melodineae G. Don

The well-supported association between *Melodinus* and *Craspidospermum* (*uwboot* = 70%, *swboot* = 75%) was first reported by Sennblad (1997; see also Sennblad and Bremer, 2000) and has subsequently been reflected in the tribe Melodineae sensu Endress and Bruyns (2000; their inclusion of *Diplorhynchus*, however, is not supported). *Craspidospermum*, although its fruit is dry and dehiscent as opposed to the indehiscent fruits of *Melodinus*, was noted by Pichon (1948b) to present several characters of the Carisseae, such as stamens inserted near the base of the corolla tube and a syncarpous ovary. In particular, Pichon found the very dense suprastaminal indumentum type reminiscent of *Melodinus*. From his descriptions

of the two genera (Pichon, 1948a,b), the following similarities also emerge: presence of a stipular line, pollen in tetrads, and a punctiform hilum.

Definition.—Tribe Melodineae is the most inclusive clade that includes the primary types of *Melodinus* and *Craspidospermum* but not Alyxieae, Aspidospermeae, Carisseae, Hunterieae, Plumerieae, Tabernaemontaneae, Vinceae, Willughbeieae, or Apocynoidina.

Tribus Hunterieae K. Schum.

The *Picralima* and *Pleiocarpa* clade is strongly supported (*uwboot* and *swboot* = 100%) and corresponds to the subtribe Hunterieae sensu Endress and Bruyns (2000). The study of Potgieter and Albert (2001) also supports the inclusion of *Hunteria* Roxb. These taxa are characterized by apocarpous, sometimes pluricarpous, ovaries and fleshy, fibrous fruit walls (Omino, 1996). *Diplorhynchus* (Melodineae) is here weakly associated (*uwboot* and *swboot* < 50%) with the Pleiocarpeae. It shares a few similarities, such as stipular lines and a style head without a stigmatic hollow and hair wreaths, but also has differences, such as a dry dehiscent fruit. With the present definition, *Diplorhynchus* will tentatively be included in the Hunterieae.

Definition.—Tribe Hunterieae is the most inclusive clade that includes the primary types of *Hunteria* and *Picralima* but not Alyxieae, Aspidospermeae, Carisseae, Melodineae, Plumerieae, Tabernaemontaneae, Vinceae, Willughbeieae, or Apocynoidina.

Tribus Plumerieae Endl.

The strongly supported relationship (*uwboot* and *swboot* = 100%) between *Allamanda* and *Plumeria* corresponds to earlier studies (Endress et al., 1996; Sennblad and Bremer, 1996; Civeyrel et al., 1998; Potgieter and Albert, 2001). In all earlier treatments, *Allamanda* has had uncertain relationships. The association with *Plumeria* finds support in pollen morphology, such as perforate mesocolpial depressions and similar inner exine pattern. The two genera also contain secoiridoids rather than the indole alkaloids and cardenolides that are common in the traditional Plumerioideae (Endress et al., 1996). *Cameraria*, *Cerbera*, and *Thevetia* form a strongly supported association

($uwboot = 83\%$, $swboot = 91\%$) with *Anechites*, which has been suggested by Fallen (1983). This association was based mainly on the latrorse/sublatrorse anthers and the broad style head with large apical appendages and stigmatic hollow. The study by Potgieter and Albert (2001) suggested a further inclusion of *Cerberiopsis* Viell. Ex. Pancher & Sébert and *Skytanthus* Meyen in this tribe. These taxa form a well-supported clade with *Plumeria* and *Allamanda*, which corresponds to the Plumerieae sensu Endress and Bruyns (2000). Characters supporting this relationship are the presence of infrastaminal as well as suprastaminal appendages (not present in *Anechites* and *Plumeria*) and winged seeds (not present in *Anechites*) (Endress et al., 1996).

Definition.—Tribe Plumerieae is the most inclusive clade that includes the primary types of *Plumeria* and *Allamanda* but not Alyxieae, Aspidospermeae, Carisseae, Hunterieae, Melodineae, Tabernaemontaneae, Vinceae, Willughbeieae, or Apocynoidina.

Tribus Carisseae Dumort.

Acokanthera and *Carissa* (both Carisseae) are traditionally joined and are sometimes even treated as one genus (e.g., Pichon, 1948a). In the present study they form a strongly supported clade ($uwboot = 96\%$, $swboot = 99\%$). Among the characters supporting this tribe are syncarpous fruits without axile placentation and endocracks on the inner exine of the pollen (Endress et al., 1996).

Definition.—Tribe Carisseae is the most inclusive clade that includes the primary types of *Carissa* and *Acokanthera* but not Alyxieae, Aspidospermeae, Hunterieae, Melodineae, Plumerieae, Tabernaemontaneae, Vinceae, Willughbeieae, or Apocynoidina.

Tribus Alyxieae G. Don

Chilocarpus has been a genus with uncertain affinities. In Endress et al. (1996), it was the sister taxon to the Apocynoideae. Here it is associated with *Alyxia* and *Lepinia* in a clade corresponding to the Alyxieae sensu Endress and Bruyns (2000). This clade is strongly supported with successive weighted bootstrap ($swboot = 91\%$), but not with unit-weighted bootstrap support ($uwboot = 58\%$); such clades will henceforth be termed moderately well supported clades.

A further inclusion of *Condylocarpon* Desf., *Lepiniopsis* Valeton, and Plectaneia Thouars was indicated by Potgieter and Albert (2001). The constituent taxa are the only Apocynaceae taxa outside the Apocynoidina that have porate pollen.

Definition.—Tribe Alyxieae is the most inclusive clade that includes the primary types of *Alyxia* and *Lepinia* but not Aspidospermeae, Carisseae, Hunterieae, Melodineae, Plumerieae, Tabernaemontaneae, Vinceae, Willughbeieae, or Apocynoidina.

APOCYNOIDINA

On the present tree, the traditional subfamily Apocynoideae includes all subfamilies (Periplocoideae, Secamonoideae, and Asclepiadoideae) of the Asclepiadaceae sensu Liede and Albers (1994). All of these taxa are established names, and selecting one as a subfamily at the expense of the others might be considered unfortunate from different points of view. We have here chosen not to recognize subfamilies; instead, we will define the traditional Apocynoideae, Asclepiadaceae, and Asclepiadoideae as nonstandard taxa. The correspondence to the traditional taxa will be indicated in the names by replacing the suffix -eae with a neutral suffix -ina (Kron, 1997). We will also, for practical reasons, recognize as a nonstandard taxon the informal group euapocynoids, suggested by Sennblad et al. (1998).

The taxa of the traditional Apocynoideae and Asclepiadaceae ($uwboot = 86\%$, $swboot = 99\%$) clade will in many cases be more difficult to safely delimit to tribes, because many of the groups in this clade have weak or no support (although preliminary results from an unpublished collaborative study by Sennblad et al. indicate additional support for the tribes discussed below). The tribal and subtribal classification of the traditional Apocynoideae has been shown to be problematic (Leeuwenberg, 1994a; Endress and Bruyns, 2000). The circumscription of tribes for these taxa might therefore in some cases be preliminary.

In all following taxa, the basal part of the anther connective, called the retinacle, is adnate to the style head.

Definition.—Apocynoidina are the most inclusive clade that includes the primary types of *Apocynum* and *Wrightia* but not Alyxieae, Aspidospermeae, Carisseae,

Hunterieae, Melodineae, Plumerieae, Tabernaemontaneae, Vinceae, or Willughbeieae.

Tribus Wrightieae G. Don

The *Stephanostema* and *Wrightia* (both Wrightieae) clade is strongly supported (*uwboot* and *swboot* = 100%) and corresponds to the Wrightieae sensu Sennblad et al. (1998), who also suggested an inclusion of *Pleioceras* Baill. The tribe could be characterized by a combination of synapomorphic and plesiomorphic characters, for example presence of a chalazal and absence of micropylar coma, left contorted aestivation, and absence of air spaces in the anthers (1998).

Definition.—Tribe Wrightieae is the most inclusive clade in the Apocynoidina that includes the primary types of *Wrightia* and *Stephanostema* but not Malouetieae, Nerieae, or Euapocynoidina.

Tribus Nerieae (Benth.) M. Pichon

Adenium, Nerium, and *Strophanthus* (all Wrightieae) constituted the Nerieae in Sennblad et al. (1998); however, the clade received weak support. Here *Adenium* and *Nerium* form a clade that is absent in half of the most-parsimonious trees in the complete *rbc*L analysis but is strongly supported in the combined *ndh*F and *rbc*L analysis (*uwboot* = 98%, *swboot* = 99%). *Strophanthus* groups with the *Mascarenhasia, Pachypodium, Kibatalia, Funtumia,* and *Holarrhena* clade, which corresponds to the Malouetieae sensu Sennblad et al. (1998). This position of *Strophanthus* is, however, weakly supported (*uwboot* and *swboot* < 50%) and is not present in the combined *ndh*F and *rbc*L tree. Furthermore, certain morphological characters (unfused slits in the corolla tube and an apical anther appendage) indicate a position closer to the Nerieae (Sennblad et al., 1998).

Definition.—Tribe Nerieae is the most inclusive clade in the Apocynoidina that includes the primary types of *Nerium* and *Adenium* but not Malouetieae, Wrightieae, or Euapocynoidina.

Tribus Malouetieae Müll-Arg.

The association of *Mascarenhasia, Pachypodium, Kibatalia, Funtumia,* and *Holarrhena* (all Wrightieae) is moderately well supported in the complete *rbc*L analysis (*uwboot* = 57%, *swboot* = 74%), whereas the corresponding clade is well supported in the combined *rbc*L and *ndh*F analysis (*uwboot* = 66%, *swboot* = 100%). On the basis of identified synapomorphies (presence of calcium oxalate crystals in the stomium of the anthers, absence of interpetal vein, sessile filaments, and absence of air spaces in the anthers), Sennblad et al. (1998) predicted an inclusion of *Alafia* Thouars, *Kibatalia,* and *Malouetia* A.DC. in the tribe. The inclusion of *Kibatalia* is strongly supported in this study. Following these suggestions, we will here assume the inclusion of the reference genus *Malouetia* in this tribe. (The definition below will include *Strophanthus* on the present tree, but see comments under Nerieae.)

Definition.—Tribe Malouetieae is the most inclusive clade in the Apocynoidina that included the primary types of *Malouetia* and *Funtumia* but not Nerieae, Wrightieae, or Euapocynoidina.

EUAPOCYNOIDINA

In all the remaining representatives of the Apocynoideae sensu Endress and Bruyns (2000), that is, *Mandevilla, Mesechites, Aganosma, Apocynum, Trachelospermum, Rhabdadenia, Beaumontia, Parsonsia,* and *Prestonia,* the anthers are adnate to the style head both by the retinacle and by the thecae. These taxa together with the taxa of the traditional Asclepiadaceae form a moderately supported clade (*uwboot* < 50%, *swboot* = 86%) that corresponds to the informal taxon euapocynoids sensu Sennblad et al. (1998).

Definition.—Euapocynoidina are the most inclusive clade that includes the primary types of *Apocynum* and *Echites* but not Malouetieae, Wrightieae, or Nerieae.

Tribus Mesechiteae Miers

Mandevilla and *Mesechites* (both Mesechiteae) form a moderately supported clade (*uwboot* < 50%, *swboot* = 87%), equivalent to the Mesechiteae. This tribe could be characterized by anthers with obtuse, truncated tails and a retinacle lacking hairs, and also a strongly pentagonal style head with a stigmatic hollow.

Definition.—Tribe Mesechiteae is the most inclusive clade in the Euapocynoidina that includes the primary types of *Mesechites* and *Mandevilla* but not Apocyneae, Echiteae, Periploceae, or Asclepiadacina.

Tribus Apocyneae Bercht. et J. Presl.

Aganosma, *Apocynum*, *Beaumontia*, and *Trachelospermum* (Apocyneae) form a weakly supported clade with *Rhabdadenia* (Echiteae) (*uwboot* and *swboot* < 50%) in the complete *rbc*L analysis, whereas the corresponding clade in the combined *ndh*F and *rbc*L analysis gains a little better support (*uwboot* < 50%, *swboot* = 91%). Likewise, this clade (with the inclusion of *Chonemorpha* G. Don) is weakly supported in Potgieter and Albert (2001). Potential characterizing traits could be a style head without stigmatic hollow in combination with thecae that are adnate to the style head (Sennblad et al., 1998).

Definition.—Tribe Apocyneae is the most inclusive clade in the Euapocynoidina that includes the primary types of *Apocynum* and *Trachelospermum* but not Echiteae, Mesechiteae, Periploceae, or Asclepiadacina.

Tribus Echiteae Bartl.

Parsonsia, *Peltastes*, and *Prestonia* (all Echiteae) form a moderately supported or unsupported clade with the Periplocoideae representatives of the study (*uwboot* and *swboot* < 50%, and *uwboot* < 50%, *swboot* = 89% in the complete *rbc*L and the combined *rbc*L and *ndh*F analysis, respectively). In the study of Sennblad et al. (1998), *Prestonia* and *Parsonsia* formed a weakly supported clade, and in the study of Potgieter and Albert (2001), inclusion of both *Parsonsia* and *Echites* P. Browne in the Echiteae is supported. Parsonsia and Echiteae also share certain characters, such as a horseshoe-shaped retinacle and a style head with stigmatic hollow (see Sennblad et al., 1998).

Definition.—Tribe Echiteae is the most inclusive clade in the Euapocynoidina that includes the primary types of *Echites* and *Prestonia* but not Apocyneae, Mesechiteae, Periploceae, or Asclepiadacina.

Tribus Periploceae Bartl.

The representatives of the Periplocoideae sensu Endress and Bruyns (2000)—*Pentopetia*, *Parquetina*, *Petopentia*, *Periploca*, *Tacazzea*, and *Mondia*—group together in a well-supported clade (*uwboot* = 67%, *swboot* = 93%). The monophyly of the traditional periplocoid taxa is also supported in earlier studies that included a wider or different sampling (Civeyrel et al., 1998;

Potgieter and Albert, 2001). The taxa of the traditional Asclepiadaceae have "translators," structures related to pollination specialization. In the Periploceae, the pollen is deposited as tetrads in a spoon-like translator with an adhesive disc.

Definition.—Tribe Periploceae is the most inclusive clade in the Euapocynoidina that includes the primary types of *Periploca* and *Pentopetia* but not Apocyneae, Echiteae, Mesechiteae, or Asclepiadacina.

ASCLEPIADACINA

The taxa of the Asclepiadoideae sensu Liede and Albers (1994) form a clade together with the two *Secamone* species and *Baissea* (Apocyneae; *uwboot* < 50%, *swboot* = 73%). The exclusion of Periploceae (traditionally associated with this clade; see Civeyrel et al., 1998) from this taxon is weakly supported. Therefore, Periploceae is not included as a reference taxon in the stem-based part of the definition of the Asclepiadacina, thus leaving open the possibility for a later inclusion of this taxon. In the Asclepiadacina (except *Baissea*) the pollen is agglutinated into pollinia that are connected to a clasping translator.

Definition.—Asclepiadacina are the most inclusive monophyletic clade in the Euapocynoidina that includes the primary types of *Asclepias* and *Secamoneae* but not Apocyneae, Echiteae, or Mesechiteae.

Tribus Secamoneae G. Don

The tribe Secamoneae sensu Bruyns (*uwboot* = 89%, *swboot* = 96%) is monophyletic in the present analysis. However, because representatives from only one of the constituent genera are included, monophyly is not well tested, but the study of Civeyrel et al. (1998), which included a larger number of taxa, including *Pervillea* Decne., showed that monophyly of the tribe was supported. The traditional character for this tribe is four pollinia per translator.

Definition.—Tribe Secamoneae is the most inclusive clade in the Asclepiadacina that includes the primary types of *Secamone* and *Pervillea* but not Asclepioidina or *Baissea*.

Baissea

The position of *Baissea* corresponds with that in the study of Sennblad et al. (1998)

and is also supported by the combined *ndh*F and *rbc*L analysis (*uwboot* = 55%, *swboot* = 97%). The unexpected position of the Baissea (first suggested in Sennblad, 1997, see also Sennblad and Bremer, 2000) nested within the traditional Asclepiadaceae prompted us to verify the *rbc*L sequence by resequencing; the results turned out to be identical. Furthermore, in the study of Potgieter and Albert (2001), based on *trn*L–F data, an independent extraction (but sampled from the same specimen) placed *Baissea* in the same position. No obvious characters connect *Baissea* to the traditional Asclepiadoideae and Secamonoideae, but suggestive qualities may be the tendencies of the stamens to have dorsal staminal appendages, of the style to have elongated apices (compare certain *Secamone*), and of the bulbs or ridges to be below or at the filament insertions of certain species (suggesting a basal tube). Translators of a very simple type are also found in *Baissea*. Because of its uncertain position, there are no obvious sister groups to *Baissea*. Also, to avoid monotypic taxa, we do not assign *Baissea* to a tribe (the principle of exhaustive subsidiary taxa is not followed).

ASCLEPIADOIDINA

The genera of the traditional Asclepioideae form a moderately supported clade (*uwboot* = 58%, *swboot* = 84%), which will here be treated as a nonstandard taxon. The traditional characters for the Asclepiadoideae are clasping translators with two pollinia per translator.

Definition.—Asclepiadoidina are the most inclusive clade that includes the primary types of *Asclepias* and *Fockea* but not Secamoneae.

Tribus Fockeeae Kunze et al.

Fockea (Marsdenieae) has been placed with *Cibirhiza* Endl. in the tribe Fockeeae. In this analysis *Fockea* is the sister group to the rest of the Asclepiadoideae (*uwboot* = 58%, *swboot* = 84%). This position is similar to the position of *Fockea* in the studies by Civeyrel et al. (1998) and Potgieter and Albert (2001). Inclusion of the tribe Fockeeae (Kunze et al., 1994) in the Marsdenieae (Endress and Bruyns, 2000) is thus not supported.

Definition.—Tribe Fockeeae is the most inclusive clade in the Asclepiadoidina that includes the primary types of *Fockea* and *Fockea* but not Ceropegieae, Marsdenieae, or Asclepiadeae.

Tribus Ceropegieae Decne.

The tribe Ceropegieae sensu Endress and Bruyns (2000) is represented by *Stapelia* and *Ceropegia* and is very strongly supported (*uwboot* and *swboot* = 100%). This traditional group is strongly supported by morphology, and the inclusion of further traditional stapeliad taxa is indicated in Potgieter and Albers (2001).

Definition.—Tribe Ceropegieae is the most inclusive clade in the Asclepiadoidina that includes the primary types of *Stapelia* and *Ceropegia* but not Asclepiadeae, Fockeeae, or Marsdenieae.

Tribus Marsdenieae Benth.

Stephanotis, *Micholitzia*, and *Hoya* represent the tribe Marsdenieae sensu Endress and Bruyns (2000) and form a very well supported clade (*uwboot* = 91%, *swboot* = 95%). The position of *Fockea* as sister group to the rest of the Asclepiadoidina makes the Marsdenieae sensu Endress and Bruyns (2000) nonmonophyletic. *Stephanotis* is most likely congeneric with, or sister to, *Marsdenia* R.Br., which we therefore will assume to be included in the tribe. The study of Potgieter and Albers (2001) supports further inclusion of *Dischidia* R.Br., *Dregea* E. Mey., and *Telosma* Coville.

Definition.—Tribe Marsdenieae is the most inclusive clade in the Asclepiadoidina that includes the primary types of *Marsdenia* and *Hoya* but not Asclepiadeae, Fockeeae, or Ceropegieae.

Tribus Asclepiadeae (R. BR.) Duby

Schizostephanus, *Asclepias*, *Calotropis*, *Vincetoxicum*, *Tylophora*, *Orthosia*, *Araujia*, *Tweedia*, *Fischeria*, and *Matelea* form a strongly supported clade (*uwboot* = 89, *swboot* = 96) corresponding to Asclepiadeae sensu Endress and Bruyns (2000). The inclusion of *Tylophora* and the traditional Gonolobeae (here represented by *Fischeria* and *Matelea*) in the Asclepiadeae (e.g., Liede, 1996; Sennblad and Bremer, 1996, 2000; Swarupanandan et al., 1996; Civeyrel et al., 1998; Endress and Bruyns, 2000; Potgieter and Albert, 2001) is thus supported. The studies of Civeyrel et al. (1998)

and Potgieter and Albert (2001) also indicate support for inclusion of other traditional Asclepiadeae taxa.

Definition.—Tribe Asclepiadeae is the most inclusive clade in the Asclepiadoidina that includes the primary types of *Asclepias* and *Matelea* but not Fockeeae, Marsdenieae, or Ceropegieae.

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