Apocynaceae: Brown and now

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Abstract

Endress, Mary (Institute of Systematic Botany; University of Zurich; Zollikerstrasse 107; 8008 Zurich, Switzerland) 2004. Apocynaceae: Brown and now. Telopea *10(2): 525–541.* Robert Brown was one of the most important contributors to our understanding of the Apocynaceae sens. lat. He had the prescience to recognise that the asclepiads were more advanced than the Apocynaceae sens. strict., and that together they form a natural series. He chose to split the asclepiads out of Jussieu's Apocineae, and recognised them as a separate family, Asclepiadaceae, on the basis of practicality. Today, following cladistic procedure, the Apocynaceae and Asclepiadaceae are mostly again united into a single family, with five subfamilies recognised: Rauvolfioideae, Apocynoideae, Periplocoideae, Secamonoideae and Asclepiadoideae. That Brown's subfamilial classification of the traditional Asclepiadaceae has endured time and cladistics, is a legacy to his sagacity and outstanding skill as a microscopist. Currently, higher level classification in the family is focused mainly on better understanding generic relationships and refining tribal concepts. The great increase in material collected and corresponding increase in the number of known taxa has helped taxonomists to circumscribe natural groups. But the greatest impact has come from the use of phylogenetic methods, especially because they have demonstrated the many instances of parallelisms, which were not recognised as such in traditional classifications. The asclepiads are more homogeneous than are the Apocynaceae sens. strict., and the tribes more clearly defined. Uncertainty still exists as to whether the traditional Asclepiadaceae form a monophyletic group, or if the Periplocoideae are more closely related to the Apocynoideae in the Apocynaceae sens. strict. than they are to the Secamonoideae and Asclepiadoideae. The recognition of four tribes (Fockeeae, Marsdenieae, Ceropegieae and Asclepiadeae) within the Asclepiadoideae is well supported; in addition, great strides have been made in recent years towards a subtribal classification within the tribe Asclepiadeae. Within the Apocynaceae sens. strict., the Rauvolfioideae are especially heterogeneous and have been correspondingly difficult to divide into natural tribes. In the more specialised subfamily, Apocynoideae, on the other hand, genera are much more closely related, and this has proved to be a stumbling block of a different sort for taxonomists, with genera sometimes being differentiated based on whimsical (often 'absence of') characters. In both subfamilies of the Apocynaceae sens. strict., much systematic work remains to be done.

Introduction

Robert Brown was one of the most influential people in the classification of the Apocynaceae sens. lat. He described more than 40 genera in the family, the great majority of which are still valid today. He segregated the asclepiads out of Jussieu's Apocineae and recognised them as a separate family, which was distinguished by having the pollen coalesced into masses or pollinia and attached to a translator. One of his most significant contributions was his subdivision of the asclepiads into three groups based mainly on the number of pollinia per flower and the type of translator. In Brown's time only 53 genera and some 170 species were known in the Apocynaceae and Asclepiadaceae combined. Today, nearly 200 years later, the Apocynaceae sens. lat. has grown to 395 genera and some 5100 species (Meve 2002, Endress, unpub. data). Brown's three groups are still recognised as the subfamilies Periplocoideae, Secamonoideae and Asclepiadoideae. Since the Apocynaceae sens. strict. are paraphyletic without the Asclepiadaceae, the tendency today is to recognise them as one family. In addition, it is uncertain whether the traditional Asclepiadaceae are a monophyletic group. Many characters have evolved in parallel at various hierarchical levels, the extent of which has only become apparent with the widespread use of phylogenetic analyses, mainly of molecular data.

Then: Jussieu and Brown

Robert Brown's interest in the Apocynaceae began in 1800, when he was 27 years old. He had just been commissioned by Sir Joseph Banks as naturalist aboard the *Investigator*, the ship captained by Matthew Flinders, which was to circumnavigate Australia (Mabberley 1985). The trip turned into an odyssey of nearly five years. Even before they reached Australia, Brown came into contact with some of the most complex flowers in the asclepiads, when the ship stopped on the way at the Cape of Good Hope in South Africa. One can imagine his fascination with the bizarre Ceropegieae they collected near Table Mountain, which Brown had time to study at length for the next five months until they reached Australia. The Investigator landed first at King George Sound, and then proceeded clockwise around Australia, stopping at various spots along the way (Mabberley 1985). The localities in Australia where Apocynaceae were collected during the *Flinders* Expedition included the Isles of St. Francis (S. A.), Mornington Peninsula and King Island in the the Bass Strait, Port Jackson, Fraser Island, and Moreton Bay (Brisbane). But the great majority were collected in the North, west of Cape York Peninsula, on the mainland as well as islands in the Gulf of Carpentaria.

The chance to see exotic plants in their natural habitat and to study the flowers at length and have them illustrated in great detail by Ferdinand Bauer during the Flinders voyage must have been a great inspiration to Brown. In two important papers – the *Prodromus Florae Novae Hollandiae* (Brown 1810a) and *On the Asclepiadeae* (Brown 1810b) he published on more than 50 genera in Apocynaceae sens. lat., 40 of which were new. In the first of these papers, 14 new genera were described based on plants collected in Australia – ten in Asclepiadeae and four in Apocyneae. Of the 40 new genera Brown described, almost all are still recognised today. (Table 1). *On the Asclepiadeae* (Brown 1810b) contained accounts of a total of 53 genera and 169 species: 38 genera in the Asclepiadeae, and 15 in the Apocyneae. Brown only misplaced one genus, *Cryptolepis*, which has translators so small even he didn't see them, and thus placed it in the Apocyneae, instead of the Asclepiadeae. His *Prodromus* (Brown 1810a) unexpectedly came out a week before *On The Asclepiadeae* (Brown 1810b). So, although the more detailed descriptions are in the latter paper, the type description of the 14 genera indicated in Table 1, as well as those of a number of species (Forster 1991, Forster & Williams 1996, Forster et al. 1996), is in the former.

In *On the Asclepiadeae* Brown (1810b) split the Asclepiadeae out of Jussieu's Apocineae and treated them as separate families. In systematics articles today one often reads that the Apocynaceae is monophyletic if circumscribed in the sense of Jussieu — that is, including the Asclepiadaceae (e.g., Wanntorp 1988, Judd et al. 1994, Civeyrel et al. 1998, Sennblad & Bremer 1996, 2000, Endress & Bruyns 2000, Potgieter & Albert 2001) . Since it was Robert Brown who divided them, one could get the impression that Jussieu was correct, and Brown made a mistake when he separated out the asclepiads as their own family. This is a very naive interpretation of the events. But to understand this, one must take into account what was known about the family as it was circumscribed at the time.

In 1810 the family Apocineae, as circumscribed by Jussieu (1789), contained only 24 genera. These were divided into three groups, based on gynoecium, fruit and seed characters (Table 2). Between his two families Apocineae and Sapotae, Jussieu appended an assemblage of genera, which he described as: genera with an affinity to

Table 1. Genera of Apocynaceae first described by Robert Brown.

Alstonia R. Br., Asclepiadeae 64, *nom. cons.* (RAU)
Balfouria R. Br., Prodr. 467, *nom. rej.* = Wrightia R. Br. (APO)
Wrightia R. Br., Prodr. 467, (APO)
Holarrhena R. Br., Asclepiadeae 51, (APO)
Isonema R. Br., Asclepiadeae 52 (APO)
Ichnocarpus R. Br., Asclepiadeae 50, *nom. cons.* (APO)
Parsonsia R. Br., Prodr. 465, *nom. cons.* (APO)
Lyonsia R. Br., Prodr. 466, *nom. rej.* = Parsonsia R. Br. (APO)
Prestonia R. Br., Asclepiadeae 58, *nom. cons.* (APO)
Cryptolepis R. Br., Asclepiadeae 58 (PER)
Cryptostegia R. Br., Bot. Reg. 5, t. 435 (PER)
Gymnanthera R. Br., Prodr. PER
Secamone R. Br., Prodr. 464 (SEC)
Hoya R. Br., Prodr. 459 (ASC)
Dischidia R. Br., Prodr. 461 (ASC)
Marsdenia R. Br., Prodr. 460 (ASC)
Gymnema R. Br., Prodr. 461 (ASC)
Sarcolobus R. Br., Asclepiadeae 23 (ASC)
Caralluma R. Br., Asclepiadeae 14 (ASC)
Huernia R. Br., Asclepiadeae 11 (ASC)
Leptadenia R. Br., Asclepiadeae 23 (ASC)
Piaranthus R. Br., Asclepiadeae 12 (ASC)
Microstemma R. Br., Prodr. 459 *nom. rej.* = Brachystelma Sims (ASC)
Astephanus R. Br., Asclepiadeae 43 (ASC)
Calotropis R. Br., Asclepiadeae 28 (ASC)
Diplolepis R. Br., Asclepiadeae 30 (ASC)
Ditassa R. Br., Asclepiadeae 41 (ASC)
Eustegia R. Br., Asclepiadeae 40 (ASC)
Sarcostemma R. Br., Prodr. 463 (ASC)
Gomphocarpus R. Br., Asclepiadeae 26 (ASC)
Holostemma R. Br., Asclepiadeae 31 (ASC)
Kanahia R. Br., Asclepiadeae 28 (ASC)
Metaplexis R. Br., Asclepiadeae 37 (ASC)
Metastelma R. Br., Asclepiadeae 41 (ASC)
Microloma R. Br., Asclepiadeae 42 (ASC)
Oxypetalum R. Br., Asclepiadeae 30 (ASC)
Oxystelma R. Br., Prodr. 462 (ASC)
Tylophora R. Br., Prodr. 460 (ASC)
Daemia R. Br., Asclepiadeae 39 *nom. rej.* = Pergularia L. (ASC)
Xysmalobium R. Br., Asclepiadeae 27 (ASC)

Names in **bold** are based on plants collected in Australia during Flinders' circumnavigation of the continent. Three-letter acronyms refer to subfamilial position following Endress and Bruyns (2000): APO = Apocynoideae; ASC = Asclepiadoideae; PER = Periplocoideae; RAU = Rauvolfioideae; SEC = Secamonoideae.

Apocyneae, but not lactiferous. Of the five genera included in this assemblage, three (*Strychnos, Fagraea* and *Gelsemium*) are still considered to be among the close relatives of Apocynaceae.

Table 2. Jussieu's Classification of Apocineae (1789).

JUSSIEU'S APOCINEAE (1789)

GROUP 1 (Ovary of 2 free carpels, fruit bifollicular, and seeds without a coma)

1. Vinca L.
2. Matelea Aubl.
3. Ochrosia Juss.
4. Tabernaemontana L.
5. Cameraria L.
6. Plumeria L.

GROUP 2 (Ovary of 2 free carpels, fruits bifollicular, seeds with a coma)

7. Nerium L.
8. Echites P. Browne
9. Ceropegia L.
10. Pergularia L.
11. Stapelia L.
12. Periploca L.
13. Apocynum L.
14. Cynanchum L.
15. Asclepias L.

GROUP 3 (Ovary of 2 fused carpels, fruits baccate or rarely capsular, seeds without a coma)

16. Ambelania Aubl.
17. Pacouria Aubl.
18. Allamanda L.
19. Melodinus J.R. & G. Forster
20. *Gynopogon* J.R. Forst. & G. Forst. *nom. rej.* (= Alyxia Banks ex R. Br.)
21. Rauvolfia L.
22. *Ophioxylon* L. *nom. rej.* (= Rauvolfia L.)
23. Cerbera L.
24. Carissa L.

In Jussieu's classification there is a major split between Group 1 and 3 on the one hand, and Group 2 on the other. The taxa in Groups 1 and 3 almost always have corolla lobes contorted to the left, anthers free from the style-head and non-comose seeds. They constitute the Rauvolfioideae in modern classifications. The taxa in Group 2, in contrast, almost always have corolla lobes contorted to the right, anthers postgenitally united with the style-head (forming a gynostegium) and comose seeds. They represent all the other subfamilies in modern classifications: Apocynoideae, Periplocoideae, Secamonoideae and Asclepiadoideae.

Figure 1 shows Jussieu's three Groups where they would come out based on current information. Whereas Group 2 is natural, Groups 1 and 3 are intermixed and thus artificial. It is interesting that Jussieu included *Matelea* in Group 1. This genus is clearly a member of Group 2, and its inclusion elsewhere suggests that the seed depicted in Aublet (1775) belonged to one of the riparian species adapted to water dispersal, in which the seed coma has been lost.

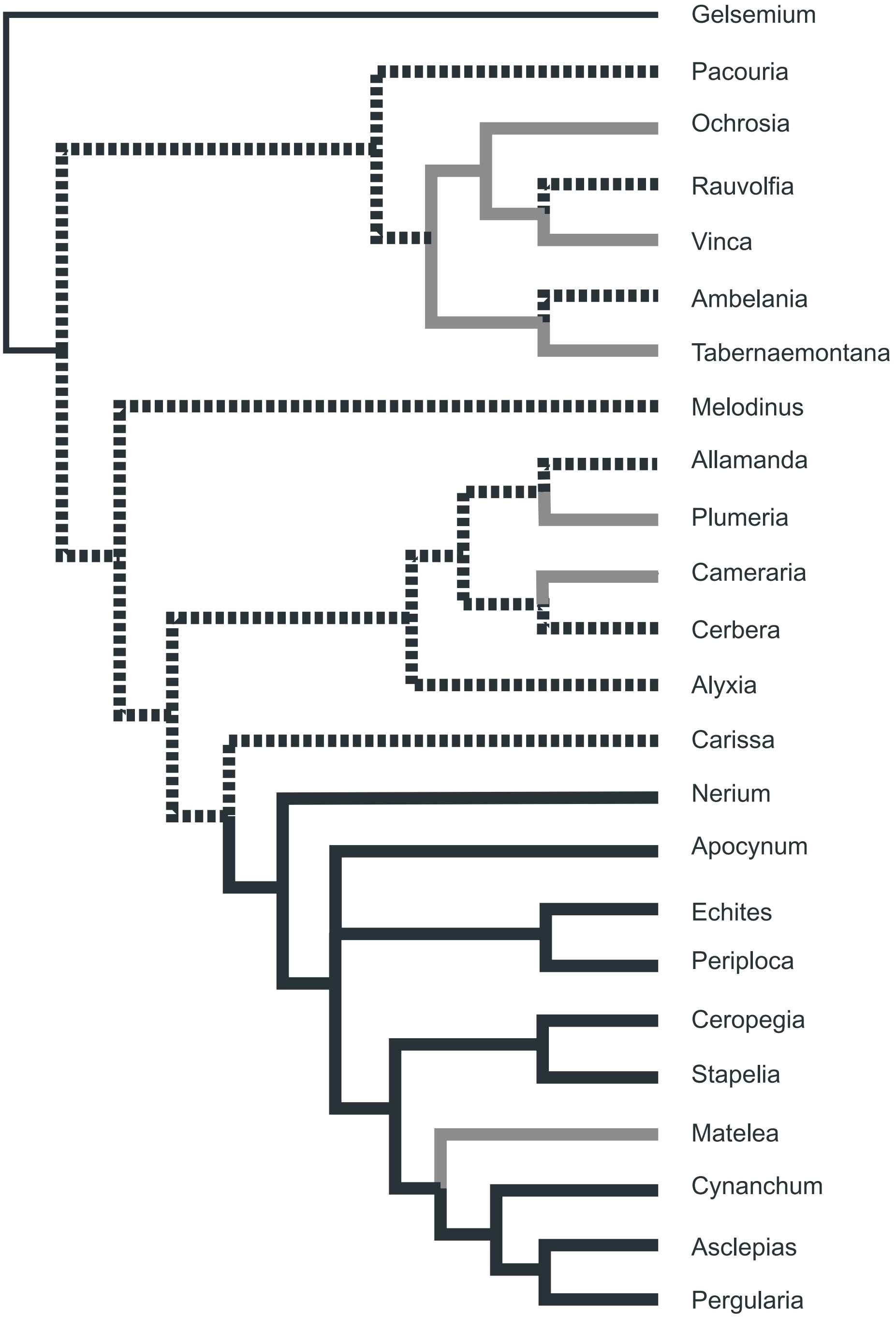

Fig. 1. Jussieu's three groups of Apocineae, with the taxa shown where they would come out based on current data. Group 1: grey; Group 2: black; Group 3: interrupted line; outgroup: thin black line.

Brown was fascinated by complex flowers, so he concentrated on Jussieu's Group 2, which contains the most complicated flowers in the family. He was an outstanding microscopist, and did meticulous studies of various developmental stages of the flowers of *Asclepias*. He was the first to realise that the pollinia are produced in the anthers, and only secondarily come into contact with the translator produced by the style-head (Brown 1833). Up until then, it was believed that the pollinia were produced by the style-head.

Brown realised that there were substantial differences among the genera included in Jussieu's group 2. His keen eye discerned and recognised the significance of the different types of pollen presentation and transfer in this assemblage of taxa, and he used this knowledge to order them in a logical fashion. First he excluded the genera that didn't belong, and then elevated Group 2 to a separate family, which he called the Asclepiadeae. He did this based on what he called the'essential character' of the Asclepiadeae: that they have pollen coalesced into masses (pollinia) and that these pollinia are attached to a translator, whereas in the Apocyneae pollen is in single grains. (Definitions for the terminology of some of the key characters found only in Apocynaceae sens. lat. is given in Endress 1994, 2003.)

Brown's greatest contribution to the family, however, was his subfamilial classification within the asclepiads. Because of his careful, detailed studies of the flowers, he had the insight to recognise the meaningful characters to define his infrafamilial groups.The result was a natural classification, recognising three groups, which are given subfamilial status today (Fig. 2):

The 'Asclepiadeae verae'. Pollen is in pollinia. Each anther has two pollen sacs and thus two pollinia. One pollinium each from a theca of two adjacent anthers are attached to a clamp-like translator. This group is known today as the Asclepiadoideae.

An unnamed group, which contained only the genus *Secamone*. Pollen is in pollinia. Each anther has four pollen sacs and thus produces four pollinia. Two pollinia each from a theca of two adjacent anthers are attached to a clamp-like translator. This group is known today as the Secamonoideae.

The 'Periploceae'. Pollen is in tetrads (or rarely in pollinia). Each anther has four pollen sacs. The tetrads (or two pollinia each) from a theca of two adjacent anthers are shed onto a sticky spoon-like translator. This group is known today as the Periplocoideae.

Now: Grades, Clades and Monophyly

Today, in the Apocynaceae sens. lat. (the Apocynaceae and Asclepiadaceae combined), we estimate there are around 395 genera and some 5100 species. This is more than seven times the number of genera and 30 times the number of species known to Brown in 1810. Despite this significant increase in the number of recognised taxa, the names of most of the genera of Apocynaceae described by Brown are still valid. Of the 40 new genera described by him, only four have been put into synonymy to date (see Fig 1). More significant, however is the endurance of his subfamilial classification within the asclepiads. Today, more than 200 years later, the same three groups, defined using Brown's criteria, represent monophyletic groups and are given subfamilial status. Fig. 3 shows a DNA-generated tree, based on the cholorplast gene *mat*K (taken from Fishbein 2001) with Brown's subfamilies Periplocoideae, Secamonoideae, and Asclepiadoideae mapped on. Brown's accuracy in recognising these three main groups within the asclepiads is quite remarkable, especially when one takes into account the microscope he used at the time, and that he had so few specimens upon which to base his subfamilies.

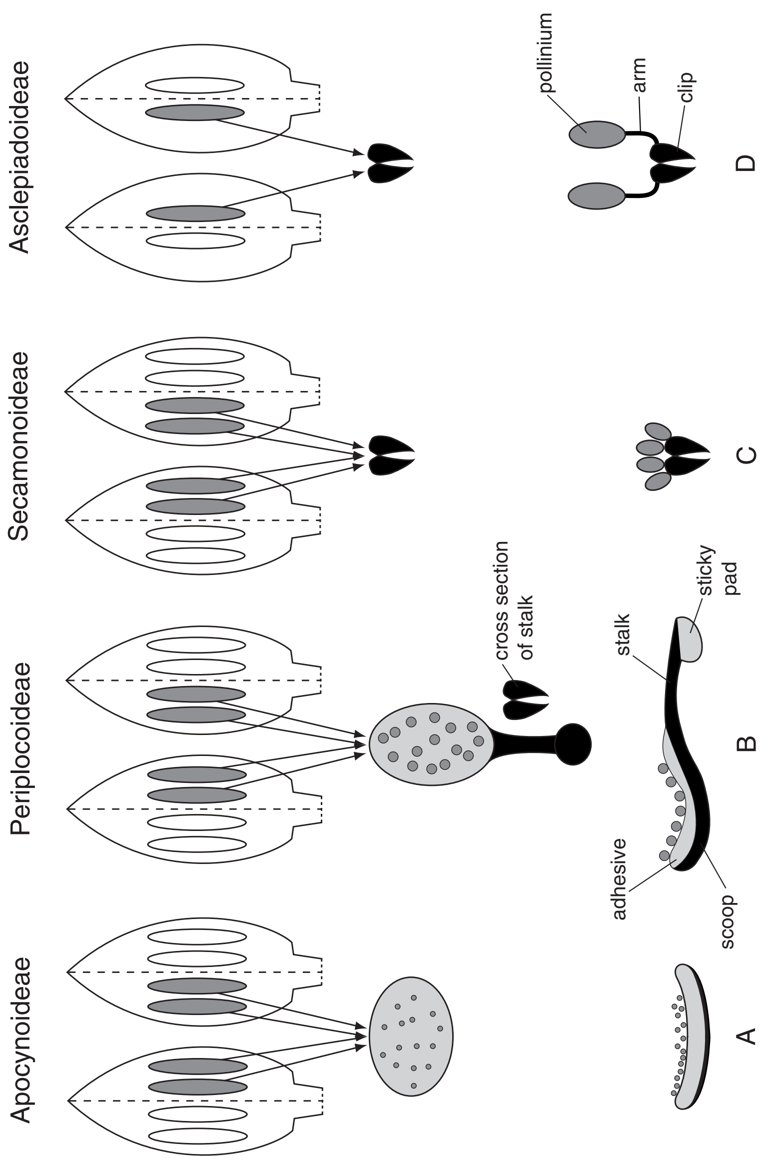

Fig. 2. Key characters of the three subfamilies of Robert Brown's Asclepiadeae: translators and pollen masses. Apocynoideae (Apocynaceae sens. strict.) are also shown for comparison. Transition series does not necessarily imply straight-line evolution, only evolutionary stages. A, Apocynoideae: the pollen grains of one theca (containing two pollen sacs) each of two adjacent anthers are shed onto an undifferentiated glob of adhesive situated between two anthers; B, Periplocoideae: the pollen tetrads of one theca (containing two pollen sacs) each of two adjacent anthers is shed onto the adhesive-lined scoop of a morphologically differentiated translator; C, Secamonoideae: the pollen content of one theca (containing two pollen sacs) each of two adjacent anthers is coalesced into pollinia, which become stuck to the dorsal surface of a clip-type translator; D, Asclepiadoideae: the pollen content of one theca (containing one pollen sac) each of two adjacent anthers is coalesced into pollinia, which become stuck to a slender arm attached to the clip-type translator. Pollen: dark grey; black: secretions that are rigid at maturity; light grey: secretions that remain frothy, viscid or tacky at maturity. This figure was first published in Endress (2003), and is reproduced here with permission.

The most dramatic changes in our concepts of the family have occurred within the past ten years, however, and have been brought about by the boom of cladistics and phylogenetic reconstruction, which have changed forever the way we do systematics. Nowadays we strive for monophyletic groups in classification. Since the Apocynaceae sens. strict. are paraphyletic without the Asclepiadaceae, most specialists in the group now unite them into one family, as this is the most straightforward way to achieve a monophyletic group (Goyder 1999, 2001, Endress & Bruyns 2000, Endress & Stevens 2001, Endress 2003). The most recent unified classification is that of Endress and Bruyns (2000), which recognised five subfamilies. This classification was slightly modified by recognition of the tribe Fockeeae by Endress and Stevens (2001) (Table 3): Brown's subfamilies Periplocoideae, Secamonoideae and Asclepiadoideae from the traditional Asclepiadaceae, and in Apocynaceae sens. strict., Rauvolfioideae and Apocynoideae. These last two subfamilies were already recognised in the Apocynaceae by Schumann (1895), although he used the names Plumerioideae and Echitoideae for them, respectively. The main characters used to circumscribe the two subfamilies in the classification are the same as those used by Schumann (1895), and correspond to the major split already present, as mentioned above, in the classification by Jussieu (1789). Thus, there is nothing revolutionary about the circumscription of the subfamilies in the classification by Endress and Bruyns.

Table 3. Classification following Endress and Bruyns (2000), as modified in Endress and Stevens (2001).

APOCYNACEAE sens. lat.
RAUVOLFIOIDEAE Kostel.
Alstonieae G. Don
Vinceae Duby
Willughbeieae A. DC.
Tabernaemontaneae G. Don
Melodineae G. Don
Hunterieae Miers
Plumerieae E. Mey.
Carisseae Dumort.
Alyxieae G. Don
APOCYNOIDEAE Burnett
Wrightieae G. Don
Malouetieae Müll.-Arg.
Apocyneae Rchb.
Mesechiteae Miers
Echiteae Bartl.
PERIPLOCOIDEAE R. Br. ex Endl.
SECAMONOIDEAE Endl.
ASCLEPIADOIDEAE R. Br. ex Burnett
Fockeeae Kunze, Meve & Liede
Marsdenieae Benth.
Ceropegieae Orb.
Asclepiadeae (R. Br.) Duby

Another thing that has changed is that the monophyly of the traditional Asclepiadaceae (the Periplocoideae, Secamonoideae and Asclepiadoideae as a natural unit) is no longer indisputable. The tree shown in Fig. 3 includes only two taxa of the Apocynaceae sens. strict., neither of them from the tribe Echiteae (a tribe of the higher Apocynoideae), which some recent analyses (e.g. Sennblad & Bremer 2000) suggest may include some of the closest relatives of the asclepiads. Based on results from the taxa analysed to date, in order to achieve a monophyletic Asclepiadaceae like that shown in Fig. 3, one has to 'not include' critical taxa of the higher Apocynoideae and/or further manipulate the data.

When critical taxa from higher Apocynoideae (Apocyneae and/or Echiteae) are included in the analysis, monophyly of the traditional Asclepiadaceae is equivocal. Figure 4 is a simplified reconstruction of a tree published by Sennblad and Bremer (2000) based on *rbcL* data, which included 77 genera: 53 Apocynaceae and 24 Asclepiadaceae. The relationships shown here are from a combinable component consensus tree from a successive weighting analysis. Noteworthy is that *Periploca* and *Mondia*, both members of the Periplocoideae, form a clade together with *Parsonsia* and *Prestonia*, two genera of Echiteae (Apocynoideae). In addition, *Baissea*, a member of Apocyneae, another tribe of the higher Apocynoideae, is intercalated between Secamonoideae and Asclepiadoideae.

Without successive weighting, relationships among the subfamilies are less clear-cut. The summarised form of the strict consensus tree from the unweighted parsimony analysis from two studies based on cpDNA is shown in Fig. 5. Tree A shows the strict consensus of the tree in Fig. 4 without successive weighting. Except for the basalmost genera, all Apocynoideae, Secamonoideae and Asclepiadoideae form a polytomy (modified from Sennblad & Bremer 2000). Tree B is a summarised form of the strict consensus tree from the unweighted parsimony analysis published by Potgieter and Albert (2001) based on the *trn*L intron and *trn*L-F spacer and six propagule characters. This study is the largest molecular analysis of Apocynaceae sens. lat. to date, and included 117 genera: 72 Apocynaceae sens. strict. (including several taxa of the crucial higher Apocynoideae) and 45 Asclepiadaceae in the traditional sense. *Wrightia* is at the base of the Apocynoideae, and sister to all other Apocynoideae, Periplocoideae, Secamonoideae and Asclepiadoideae. The bulk of the Apocynoideae form a polytomy, in which the Periplocoideae is nested. The crown clade is composed of another group of genera from the tribe Apocyneae (*Urceola, Apocynum, Beaumontia, Trachelospermum* and *Chonemorpha*), which is sister to a clade composed of two subclades: one containing the genus *Baissea*, and the other all the Secamonoideae + Asclepiadoideae (modified from Potgieter & Albert 2001). Results such as those by Sennblad and Bremer (2000) and Potgieter and Albert (2001) are indications that the systematic position of Periplocoideae is still very much unresolved. Nor do we know how to interpret the position of *Baissea.*

The relationship of Secamonoideae to Asclepiadoideae and the relationships among tribes currently recognised in the Asclepiadoideae can be seen in Fig. 3. Secamonoideae, which contains only eight genera (Klackenberg 2001) and is not divided into tribes, comes out fairly consistently as sister to the Asclepiadoideae, if taxon sampling is sufficient (see e.g. Potgieter & Albert 2001). If, with more thorough sampling, it is shown that the unexpected position of *Baissea* in recent analyses is an artifact, Secamonoideae could be reduced to a tribe of the Asclepiadoideae. Based on cladistics alone, there would be nothing to refute this. Considering the degree of the differences in floral structure, however, it is questionable whether including Secamoneae as a tribe of Asclepiadoideae is desirable.

Another thing that has changed significantly since Brown's time, is that we now have a better idea of the tribal relationships within the subfamily Asclepiadoideae. This is

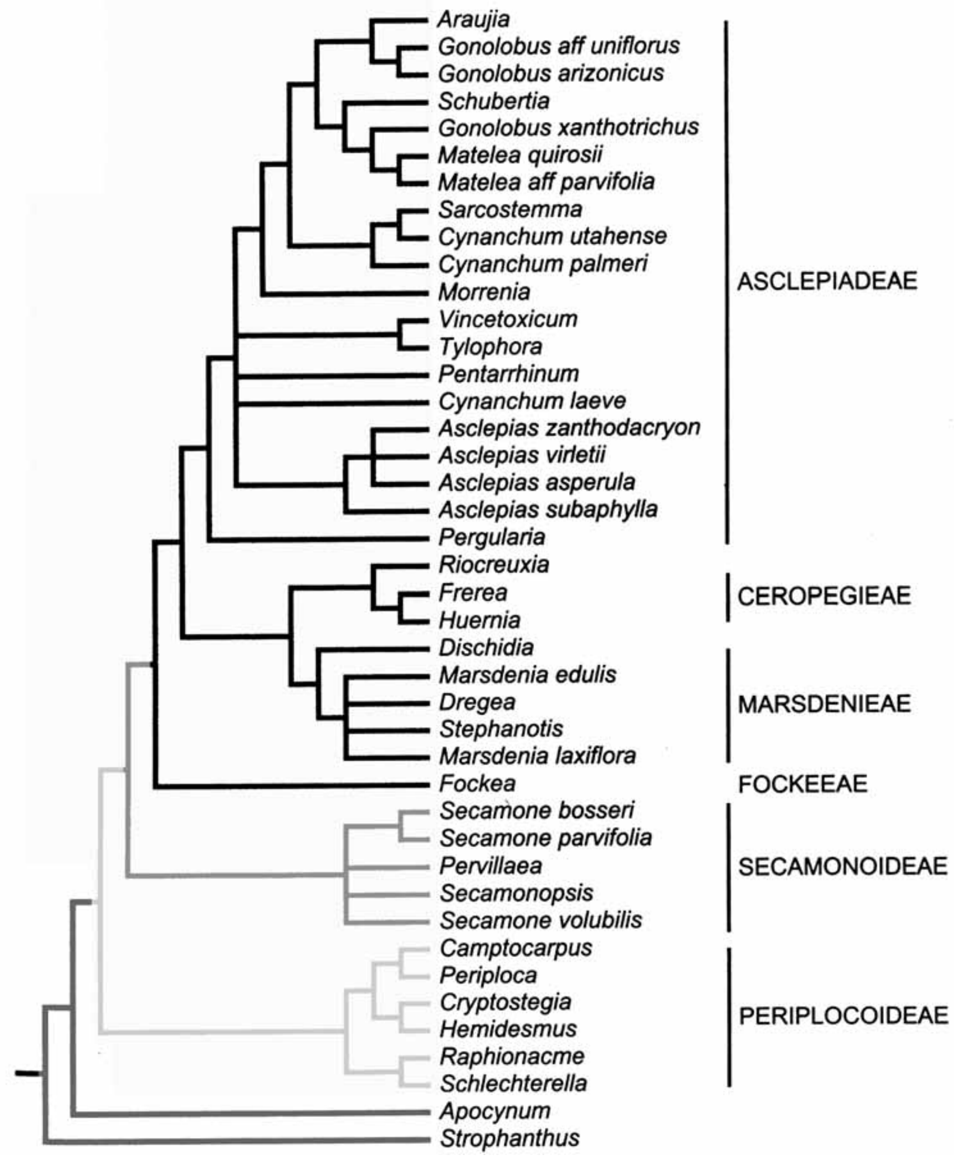

Fig.3. Tree based on maximum parsimony analysis of partial and complete *mat*K sequences published in Fishbein (2001), with Robert Brown's three subfamilies mapped onto it. Periplocoideae: light grey; Secamonoideae: medium grey; Asclepiadoideae, showing the tribes Fockeeae, Marsdenieae, Ceropegieae and Asclepiadeae: black; outgroup (Apocynoideae): dark grey. The traditional Asclepiadaceae is monophyletic.

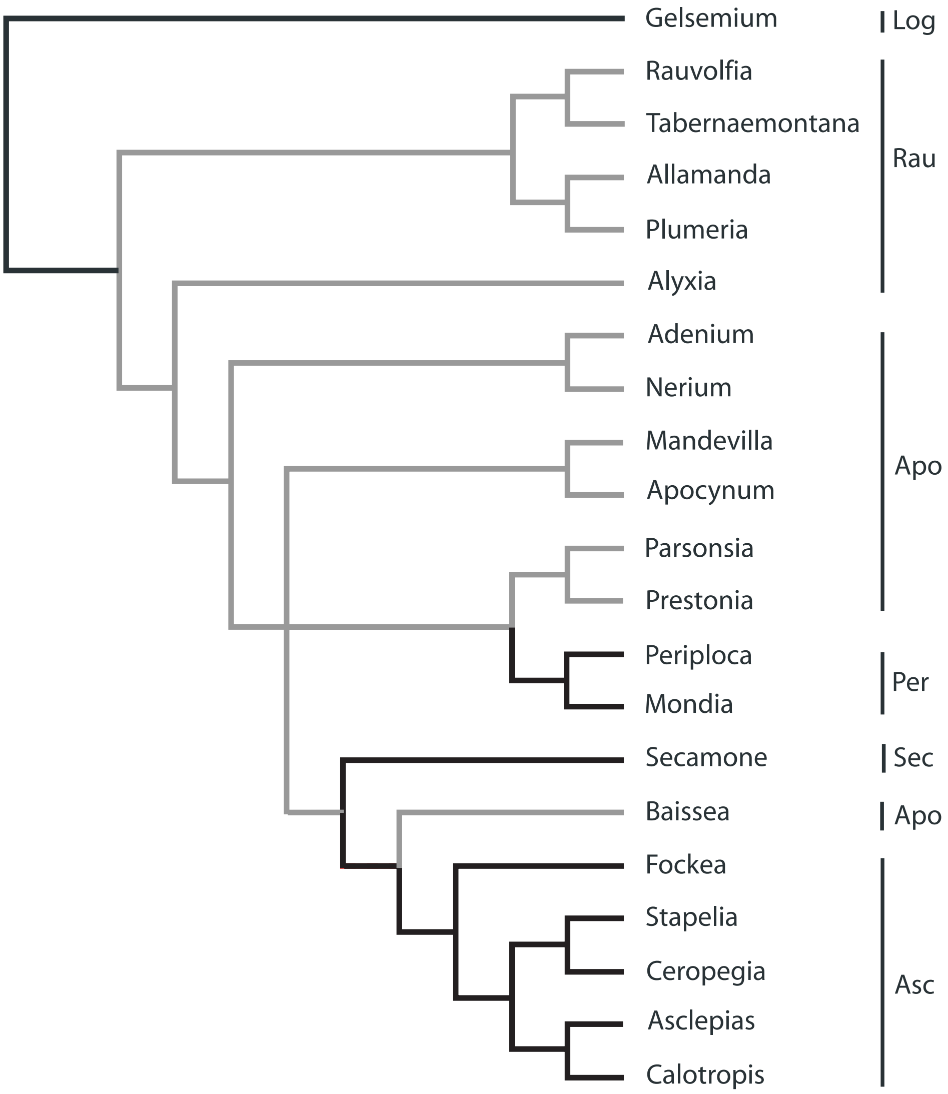

Fig. 4. Simplified reconstruction of the phylogenetic tree of Apocynaceae sens. lat. by Sennblad and Bremer (2000) based on the cholorplast gene *rbc*L with *Gelsemium* (Loganiaceae) as outgroup. 1) The three clades at the apex form an unresolved polytomy; 2) Periplocoideae are sister to *Parsonsia* and *Prestonia* of tribe Echiteae, Apocynoideae, rather than to Secamonoideae + Asclepiadoideae, suggesting that Periplocoideae and Secamonoideae + Asclepiadoideae may not be a natural group; 3) *Baissea* of tribe Apocyneae, Apocynoideae is intercalated between Secamonoideae and Asclepiadoideae, questioning monophyly even within Secamonoideae + Asclepiadoideae. Traditional Apocynaceae: grey; traditional Asclepiadaceae: black.

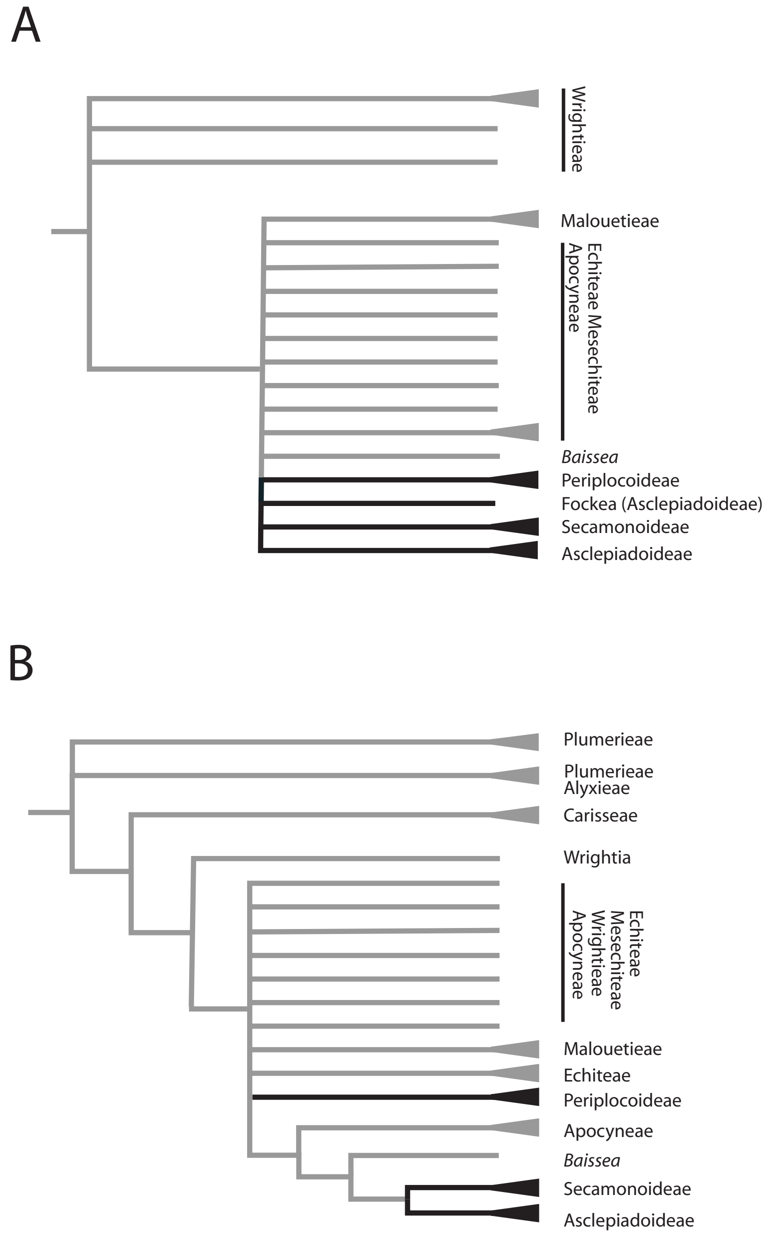

Fig. 5. Summarised form of the strict consensus tree from the unweighted parsimony analysis from two cpDNA studies. **A**. Tree based on *rbc*L. The Rauvolfioideae (lower part of the tree) is not shown. Except for the basalmost genera, all Apocynoideae form a polytomy, in which Periplocoideae is nested (modified from Sennblad & Bremer 2000). **B.** Tree based on the *trn*L intron and *trn*L-F spacer and six propagule characters. Except for three of the more advanced tribes of the Rauvolfioideae, the lower part of the tree is not shown. Except for *Wrightia*, at the base, the bulk of the Apocynoideae form a polytomy, in which the Periplocoideae are nested. The crown clade is composed of another group of genera of the tribe Apocyneae, which is sister to the genus *Baissea* on the one hand and the Secamonoideae + Asclepiadoideae on the other (modified from Potgieter & Albert 2001). Traditional Apocynaceae: grey; traditional Asclepiadaceae: black.

partly due to the additional material that has accumulated since then. But the bulk of the new information on relationships among genera is due to the use of DNA data, especially because it has repeatedly revealed convergences that were not realised as such in earlier classifications. This has led to a much more natural delimitation of tribes. Within the Asclepiadoideae four tribes are currently recognised: Fockeeae, Marsdenieae, Ceropegieae and Asclepiadeae (Endress & Stevens 2001). Fockeeae are the basalmost tribe. They contain only two genera – *Fockea* and *Cibirhiza* – and are sister to all the rest of the Asclepiadoideae. The basal position of the Fockeeae is well supported by both morphological as well as molecular data (Kunze 1993, 1994, 1996; Civeyrel et al. 1998, Potgieter & Albert 2001, Verhoeven et al. 2003). The Fockeeae exhibit some unusual ('primitive') features, not found in other Asclepiadoideae, but which are more reminiscent of Secamonoideae (Kunze et al. 1994, Verhoeven et al. 2003). Fockeeae are followed by a major dichotomy, in which all other taxa of the Asclepiadoideae are included. One clade is composed of the Marsdenieae and Ceropegieae (Stapelieae in earlier classifications); the other is comprised of only the large tribe Asclepiadeae (including the taxa, formerly treated as a separate tribe – Gonolobeae) (Bruyns & Forster 1991, Sennblad & Bremer 2000, Fishbein 2001, Potgieter & Albert 2001). Within the ca. 140 currently recognised genera of the Asclepiadeae, work towards a subtribal classification continues to be refined, especially by Sigrid Liede and collaborators. Currently some six subtribes are recognised, though at present taxonomy in the tribe is in a state of flux, and there remains much to do (Liede 1996, 1997, 2001; Liede & Täuber 2000; Liede et al. 2002).

Currently, our ideas about the direction of evolution within the Asclepiadoideae are more or less the reverse of Schumann's (1895), who considered the taxa with pendant pollinia to be less specialised, whereas those with erect pollinia were said to be the 'crowning glory' of the entire family. This interpretation was questioned as early as 1922 by Demeter, based on detailed floral developmental studies of various taxa, and later by Safwat (1962) and Wanntorp (1988). All tribes except Asclepiadeae have erect pollinia. Pendant pollinia are interpreted as an apomorphy and derived state of the tribe Asclepiadeae.

The systematic history of the Apocynaceae sens. lat. is characterised by major categories having repeatedly been based mainly on one or two, easy-to-determine characters – even when other characters suggested that this might not be the best choice. In the Asclepiadoideae, the orientation of the pollinia and the type of corona are the two most important characters that have been used to define tribes (Schumann 1895, Woodson 1941). We have been exceedingly lazy – continuing to use the easy characters, even after there were hints that they might result in artificial groups. A good example of how this illogical clinging to simplistic characters has led us astray is the genus *Astephanus*. Basically, this genus came to be defined by the lack of a staminal corona. As Liede (2001) demonstrated, this condition has apparently arisen at least twice independently in the tribe Asclepiadeae alone. Similarly, *Tylophora* was long included in the Marsdenieae because of the orientation of the pollinia, even though there were other morphological characters, which suggested that it was better placed near *Vincetoxicum* in the Asclepiadeae (Kunze 1996, Liede 1996, Swarpuanandan et al. 1996), a position which has since been confirmed with molecular data (Sennblad & Bremer 2000, Civeyrel & Rowe 2001, Fishbein 2001, Liede 2001).

Within the Apocynaceae sens. strict., the Rauvolfioideae (Plumerioideae in earlier classifications) has almost always been considered to be the more more ancestral, and the Apocynoideae (Echitoideae in earlier classifications) the more derived subfamily. Only Woodson (1930), basing his hypothesis on the assumption that apocarpy is more primitive than syncarpy, considered the Rauvolfioideae to be the more derived subfamily. Morphological characters within the Apocynaceae sens. strict. are much more heterogeneous than in the asclepiads. In the basalmost subfamily, Rauvolfioideae, earlier classifications were almost always based mainly on a few easy to see fruit and seed characters. If the fruit was an indehiscent drupe the plant belonged to the Alyxieae; if it is was an indehiscent berry it was a Carisseae; and if it was dehiscent and had winged seeds, it was a Plumerieae (Pichon 1948, 1949, Leeuwenberg 1994). All of these tribes have now been shown to be polyphyletic (Potgieter & Albert 2001). Selective pressure for dispersal optimisation, means that ovary walls, and even more so, seed surfaces, are evolutionarily remarkably plastic, making them especially poor choices as defining characters for higher taxonomic categories. In addition, syncarpy and thus the taxa with indehiscent berry fruits ('Carisseae') were considered to be 'primitive' in all traditional classifications (e.g. Schumann 1895, Pichon 1948, Leeuwenberg 1994). But results from molecular analyses suggest that the basalmost taxa are more likely those with dehiscent follicles and wind-dispersed seeds (Endress et al. 1996, Potgieter & Albert 2001; but see also Sennblad & Bremer 2000), whereas *Carissa* and *Acokanthera* come out as the most advanced taxa of the Rauvolfioideae in the analysis by Potgieter and Albert (2001). The 'Carisseae' as circumscribed by e.g. Pichon (1948) or Leeuwenberg (1994) are dispersed among three clades in recent molecular analyses (Sennblad & Bremer 2000, Potgieter & Albert 2001), and this division has been followed through in the classification by Endress & Bruyns (2000), with the taxa distributed among four recircumscribed tribes: Willughbeieae, Melodinae, Hunterieae, and Carisseae.

In the more evolved subfamily of the Apocynaceae sens. strict., Apocynoideae, the situation is similar. Results of a combined morphological-molecular analysis (Sennblad et al. 1998) suggest that within the subfamily all the tribes as circumscribed by Leeuwenberg (1994) are not monophyletic. Where morphological differences supported the molecular findings, these were followed through in the classification of Endress and Bruyns (2000) by recognition of the tribe Malouetieae. Because the study of Sennblad et al. (1998) focused only on the basal region of the Apocynoideae, relationships among and within the more advanced tribes of the Apocynoideae (Apocyneae, Mesechiteae, and Echiteae) remain unresolved. To date, all molecular phylogenies of Apocynaceae sens. lat. have been based on chloroplast DNA (*rbc*L, *mat*K, *trn*L), either singly, combined, or in conjunction with a morphological dataset. The two largest studies in the family (Sennblad & Bremer 2000, Potgieter & Albert 2001) suggest that these genes are evolving too slowly to be used alone for sorting out relationships within Apocynoideae. The next logical step is to sequence nuclear genes and combine them with the data from chloroplast DNA. Independent studies, based on previously untried genetic regions, as well as morphological characters, are currently underway, which we hope will help resolve the relationships within the Apocynoideae, including the systematic position of the Periplocoideae. Until more reliable data are available, no satisfactory tribal circumscription within the Apocynoideae is possible.

Even though the tribes within them continue to be refined, both Rauvolfioideae and Apocynoideae are a grade, rather than a clade. Based on current phylogenetic reconstructions, in order to make monophyletic groups in the Apocynaceae sens. strict., one would have to describe a number of additional subfamilies (Sennblad & Bremer 1996, Civeyrel et al 1998, Potgieter & Albert 2001). But to do so at this point would be premature. There are still several areas where relationships are uncertain or where branch support is too low to be useful as the basis for a classification. Once additional genetic regions have been analysed, we should have a better idea of how to proceed. Especially when things are in such a state of flux, it seems best to improve the classification stepwise, as sufficient support is available. The unconventional classification suggested by Sennblad and Bremer (2002), which includes 21 tribes and four rankless taxa, is thought-provoking, if perhaps not palatable for botanists 'in the trenches'.

Conclusions

1. Robert Brown had a major impact on the classification of the Apocynaceae, especially in the asclepiads. Most of the new genera he described are still in use today. Due to his extraordinary skill as a microscopist and unquenchable desire to understand how complex flowers function, he was able to distinguish the meaningful characters and thus established a subfamilial classification for the traditional Asclepiadaceae that has stood the test of time and cladistics.

2. There has been a manifold increase in the number of known species in the family in the past 200 years. New species are described regularly, and new genera are still being discovered in the tropics of both the Old and New World (Forster 1990, Forster et al. 1997, Zarucchi 1991, Middleton 1995, 1996, Morales 1999, Bruyns 2000). The most profound changes in the family since Brown's time, however, are due to the molecular revolution, which brought to light convergences of characters strongly influenced by ecological factors, which were not obvious using traditional methods. This has resulted in the recircumscription of most tribes in the family, in some cases radically so.

3. We've still got a lot of work to do! Additional studies need to be done in order to come up with satisfactory tribal and subtribal limits in the Rauvolfioideae, Apocynoideae and Asclepiadeae, and we need to explain the anomalous placement of *Baissea* and the Periplocoideae, as well as refine groupings within the Asclepiadeae. When selecting taxa for studies to test the monophyly of the traditional Asclepiadaceae, a sufficient number of taxa of the higher apocynoid tribes should be included in order to make the results meaningful. And authors should have the courage to show the strict consensus tree from the unweighted parsimony analysis. A monophyletic Asclepiadaceae has little meaning if it was only achieved by leaving out critical taxa.

4. Finally, did Robert Brown err when he segregated the Asclepiadeae out of Jussieu's Apocyneae? In the Introduction to *On The Asclepiadeae* he explains his reasons for doing so: "It is true that to the experienced observer, it may still be practicable to refer the greater part, perhaps the whole, of these plants to their proper places in a natural series; but it is, I apprehend, no longer so, to distinguish the two orders by definitions derived from the usual source. ... As, however, both of these families are already too extensive, it becomes expedient rather to attempt their subdivision into smaller groups... .' Thus it is clear that Brown was aware that the Apocyneae and Asclepiadeae form a natural series, but he chose to divide them, because he felt it the more practical way to handle the group. His only mistake, then, was that he was not a cladist. But since he wrote these words more than 100 years before cladistics was invented, I think one can forgive him this indiscretion.

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