



Taxonomy “under construction”: advances in the systematics of Apocynaceae, with emphasis on the Brazilian Asclepiadoideae

Taxonomia “em obras”: avanços na sistemática de Apocynaceae, com ênfase nas Asclepiadoideae brasileiras

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Abstract

The Apocynaceae comprise approximately 5,000 species and are widely distributed. The family belongs to the Gentianales and can be easily recognized by the presence of latex and a style-head derived from the fusion of two carpels at the apex of the styles. The largest subfamily in Apocynaceae is Asclepiadoideae. Treated as the Asclepiadaceae for almost two centuries, it comprises about 3,000 species and is defined by stamens with bisporangiate anthers and pollen transferred in specialized units called pollinaria. Since the 19th century, floristic studies and taxonomic monographs have significantly contributed to the taxonomy of Brazilian Asclepiadoideae. Nevertheless, advances in understanding the internal relationships in the subfamily were not done until this millennium, with the popularization of phylogenetic studies based on molecular data and powerful computer analyses. Advances in the systematics of Apocynaceae have provided new interpretations on the morphological evolution and biogeography of the family and have led to important changes in its classification. Nevertheless, several taxonomic rearrangements are still needed and it can be said that the taxonomy of Apocynaceae is “under construction”. In this article, the major taxonomic changes in the family are reviewed, with special attention given to the systematics of Neotropical groups. A cladogram of the Apocynaceae is presented, which highlights the phylogenetic position of the Brazilian genera and their diversity in number of native species. The main studies and the diversity of Asclepiadoideae in Brazil are summarized and perspectives for future research on the subfamily are presented.

Key words: Asclepiadaceae, Brazil, molecular data, morphological evolution, phylogeny.

Resumo

As Apocynaceae compreendem aproximadamente 5.000 espécies e estão amplamente distribuídas. Pertencem às Gentianales e podem ser facilmente reconhecidas pela presença de látex e por uma cabeça estilar derivada da fusão dos dois carpelos no ápice do estilete. Asclepiadoideae é a sua maior subfamília. Tratada por quase dois séculos em Asclepiadaceae, ela inclui aproximadamente 3.000 espécies e é definida pelos estames com anteras bisporangíadas e pólen transferido em unidades especializadas denominadas polinários. Desde o século XIX, trabalhos florísticos e revisões taxonômicas têm contribuído significativamente para a taxonomia das Asclepiadoideae no Brasil. No entanto, foi apenas a partir deste milênio que estudos filogenéticos, principalmente com base em dados moleculares e um arsenal robusto de análises computacionais, propiciaram avanços significativos para a compreensão das relações internas na subfamília. Avanços na sistemática de Apocynaceae têm gerado novas interpretações sobre evolução morfológica e biogeografia e promovido mudanças substanciais na classificação da família. Vários arranjos taxonômicos ainda são necessários e pode-se dizer que a taxonomia de Apocynaceae encontra-se “em obras”. Neste artigo, são revisadas as principais mudanças taxonômicas na família, com atenção especial para a sistemática dos grupos neotropicais. É apresentado um cladograma das Apocynaceae salientando a posição filogenética dos gêneros brasileiros e sua diversidade em número de espécies nativas. Os principais estudos e a diversidade de Asclepiadoideae no Brasil são sintetizados e perspectivas para futuras pesquisas na subfamília são apresentadas.

Palavras-chave: Asclepiadaceae, Brasil, dados moleculares, evolução morfológica, filogenia.

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Introduction

Apocynaceae belongs to the Gentianales, an order of (eu)Asteridae, with five families: Apocynaceae, Gelseminaceae, Gentianaceae, Loganiaceae, and Rubiaceae (APG III 2009). With about 5,000 species, it is one of the ten largest families of angiosperms, and also one of the most popular, due to the traditional widespread use of some of its species as ornamental plants (e.g., *Allamanda cathartica* L., *Catharanthus roseus* (L.) G. Don, *Nerium oleander* L., *Plumeria rubra* L., *Thevetia peruviana* (Pers.) K. Schum.). Several species are rich in chemical compounds (e.g., *Rauvolfia* spp.), others provide hardwood (e.g., *Aspidosperma* spp.), and only a few are fruit species (*Couma rigida* Müll. Arg., known as *mucugê*, and *Hancornia speciosa* Gomes, known as *mangaba*). They show variable habit, from magna trees to climbing vines or small herbs, including some succulent ones (Stapeliinae, paleotropical). Yet, they can be easily recognized by the presence of latex and by a bicarpelar gynoeceum, in almost all cases separated at the ovary level, but distally merging to form an organ called the style-head. The carpels are usually separated at the apex, forming the apical appendices, sometimes inconspicuous. The lineage showed a gradual increase in the synorganization of the floral structures, leading to gynostegium formation, derived from the post-genital merging of the stamens to the style-head, and culminating in the formation of the pollinaria, specialized pollen units characteristic of the subfamilies Asclepiadoideae, Secamonoideae, and Periplocoideae (Rapini 2004).

Although it was initially recognized as “Apocyna” by Adanson, in 1763, Apocynaceae was formally established as “Apocineae” by Jussieu (1789), a work that marks the beginning of valid supra-specific names for spermatophytes (International Code of Botanical Nomenclature, Art. 13.1; McNeill *et al.* 2006). Subsequently, the group was divided by Brown (1810) into two families of similar sizes and easily distinguished by the presence (Asclepiadaceae *s.l.*) or absence (Apocynaceae *s.str.*) of pollinaria. Almost a century later, Schlechter (1905) subdivided Brown’s Asclepiadaceae *s.l.* into two families, Periplocaceae (absent in the Neotropics), with spatulate pollinaria, and Asclepiadaceae *s.str.*, with bifurcated pollinaria. A fourth alternative, considering Periplocaceae in Apocynaceae *s.str.*, was also suggested, approximating it either to

Rauvolfioideae (“Plumerioideae”; Schumann 1895; Wanntorp 1988) or Apocynoideae (Nilsson *et al.* 1993). Despite these taxonomic divisions, the proximity between these groups has never been questioned, and when recognized, these families were frequently classified in a category immediately above, such as Rosatti’s (1989) suborder Apocynineae.

With the diffusion of the phylogenetic principles for classification (e.g., Backlund & Bremer 1998), and the perception that the differences between Asclepiadaceae and Apocynaceae *s.str.* represent arbitrary limits in the morphological gradation between these families (e.g., Safwat 1962; Endress & Bruyns 2000), a broader concept came to be followed by most authors (e.g., APG III 2009; Reveal & Chase 2011). The adoption of Apocynaceae *s.l.* rather than Asclepiadaceae is not the result of findings revealed only by molecular data, or generated only by computationally sophisticated phylogenetic analyses. More than that, this comprehensive circumscription portrays the change in the concept of taxonomic grouping adopted in botany, especially after the 1990s, and arises as a strategy so the paraphyletic group Apocynaceae *s.str.* does not have to be recognized (Goyder 1999; Rapini 2000).

This essay aims to synthesize the advances in the systematics of Apocynaceae, focusing mainly on phylogenetic studies and the incorporation of its results on the taxonomy of the family. Special attention will be given to studies on Asclepiadoideae and its implications for the systematics of Neotropical groups. Firstly, the general phylogenetic structure of Apocynaceae will be presented, showing the relationship among its main groups and discussing the main conceptual changes in the internal classification of the family. Once the position of Asclepiadoideae in Apocynaceae is contextualized, phylogenetic studies on the subfamily will be addressed, pointing out the most important advances in the taxonomy of the group. The recent monographic and floristic studies which assisted the compilation of the list containing almost 400 species of Asclepiadoideae of Brazil (Rapini *et al.* 2010a) are indicated, and perspectives for future taxonomic studies in the subfamily will be presented.

Apocynaceae systematics

Jussieu (1789) described Apocynaceae (“Apocineae”) with 24 genera subdivided in three groups, essentially defined by fruit characteristics

(berry-like or bifollicular) and seeds (with or without coma). Brown's (1810) contribution increased the number of genera to 53, and today they reach almost 400; the increase in the number of species in these last 200 years was even greater, leaping from 169 to more than 5,000 (Endress 2004). In the Neotropical Region, the family is represented by nearly 100 genera and 1,500 species (Rapini 2004), approximately 70% of the genera and half of these species being native to Brazil (Rapini *et al.* 2009; Koch & Rapini 2011).

Five subfamilies are today included in Apocynaceae (*e.g.*, Endress & Bruyns 2000; Endress *et al.* 2007): Rauvolfioideae (cosmopolitan; 10 tribes/83 genera), Apocynoideae (cosmopolitan; 8 tribes/80 genera), Periplocoideae (Old World; 33 genera), Secamonoideae (Old World; 8 genera), and Asclepiadoideae (cosmopolitan; 4 tribes/172 genera); the first two subfamilies are paraphyletic, while the last three are monophyletic. Rauvolfioideae consists of the basal grade of the family, while Apocynoideae forms a more derived grade, from which Periplocoideae, Secamonoideae, and Asclepiadoideae emerge. Secamonoideae and Asclepiadoideae form a clade (Asclepiadaceae *s.str.*), but the position of Periplocoideae is uncertain. This last subfamily has appeared in different positions in the APSA clade, which includes Apocynoideae, Periplocoideae, Secamonoideae, and Asclepiadoideae, but its proximity to "Asclepiadaceae *s.str.*" is unlikely, since Secamonoideae and Asclepiadoideae seem to be more closely related to the African tribe Baisseeae of Apocynoideae (Sennblad & Bremer 1996, 2000, 2002; Sennblad *et al.* 1998; Potgieter & Albert 2001; Livshultz *et al.* 2007; Simões *et al.* 2007; Livshultz 2010; Fig. 1).

The use of molecular data in phylogenetic analyses of Apocynaceae (*e.g.*, Potgieter & Albert 2001; Simões *et al.* 2007) was crucial to reveal the artificiality of many Rauvolfioideae tribes traditionally defined based on fruit and seed morphology. The gynoecium, free at the ovary level, emerged as a synapomorphy of Apocynaceae, derived from the syncarpy that characterizes the other Gentianales. This interpretation was confirmed by the positions of Aspidospermeae and Alstonieae, together forming the basal grade of Apocynaceae (Simões *et al.* 2007). The congenital syncarpy of the ovary is a derived and homoplastic condition, and not a symplesiomorphy of the family. Similarly, the fleshy and indehiscent

fruits arised many times in the evolution of Apocynaceae (Potgieter & Albert 2001; Simões *et al.* 2007). Taxonomically, these findings had direct impact on the circumscription of Carisseae (*sensu* Leeuwenberg 1994), leading to its disintegration in four tribes (Carisseae *s.str.*, Hunterieae, Melodineae, and Willughbeieae; Endress *et al.* 2007). Carisseae, traditionally regarded as the most basal tribe of Apocynaceae *s.str.*, was reduced to two genera only, *Acokanthera* G. Don and *Carissa* L., and began to be recognized as the most derived tribe (Carisseae *s.str.*) of Rauvolfioideae, raising as sister group of the APSA clade. Among the three tribes segregated from Carisseae *s.l.*, only Willughbeieae has representatives in the New World. It appears in a clade with Vinceae and Tabernaemontanae (divided into Tabernaemontaninae and Ambelaniinae; Simões *et al.* 2010), both also having representatives in the New World as well as in the Old World (for a general description of these relationships, please see Fig. 1).

Although fruits and seeds vary amongst the members of Rauvolfioideae, they are conservative in the APSA clade, which helps to define the lineage morphologically. The group has been recognized by the presence of bifollicular fruits and comose seeds since Jussieu (1789), although these characteristics appear independently in groups of Rauvolfioideae, such as bifollicular fruits in Plumerieae and Vinceae and comose seeds in Alstonieae. Other diagnostic characteristics have also been pointed out to define the APSA clade, such as corolla with dextrorse prefoliation, lignified and partially sterile anthers, gynostegium formation, porate pollen grains, and production of cardenolides and steroidal (but not indole) alkaloids (Livshultz *et al.* 2007, and references cited). Wrightieae (*sensu* Leeuwenberg 1994) traditionally considered as the most basal tribe of Apocynoideae, was found to be paraphyletic (Sennblad & Bremer 1996; Sennblad *et al.* 1998), and most of its genera were distributed in Wrightieae *s.str.* (reduced to three genera only), Nerieae, and Malouetieae (Endress *et al.* 2007), three tribes that form together the basal grade of APSA. Wrightieae *s.str.* is the most basal tribe of the APSA clade, which is coherent with the retention of some plesiomorphies in the group, such as sinistrorse prefoliation and seeds with chalazal coma only, being dextrorse prefoliation and micropylar coma probably synapomorphies of its sister group. Except for this grade, the APSA

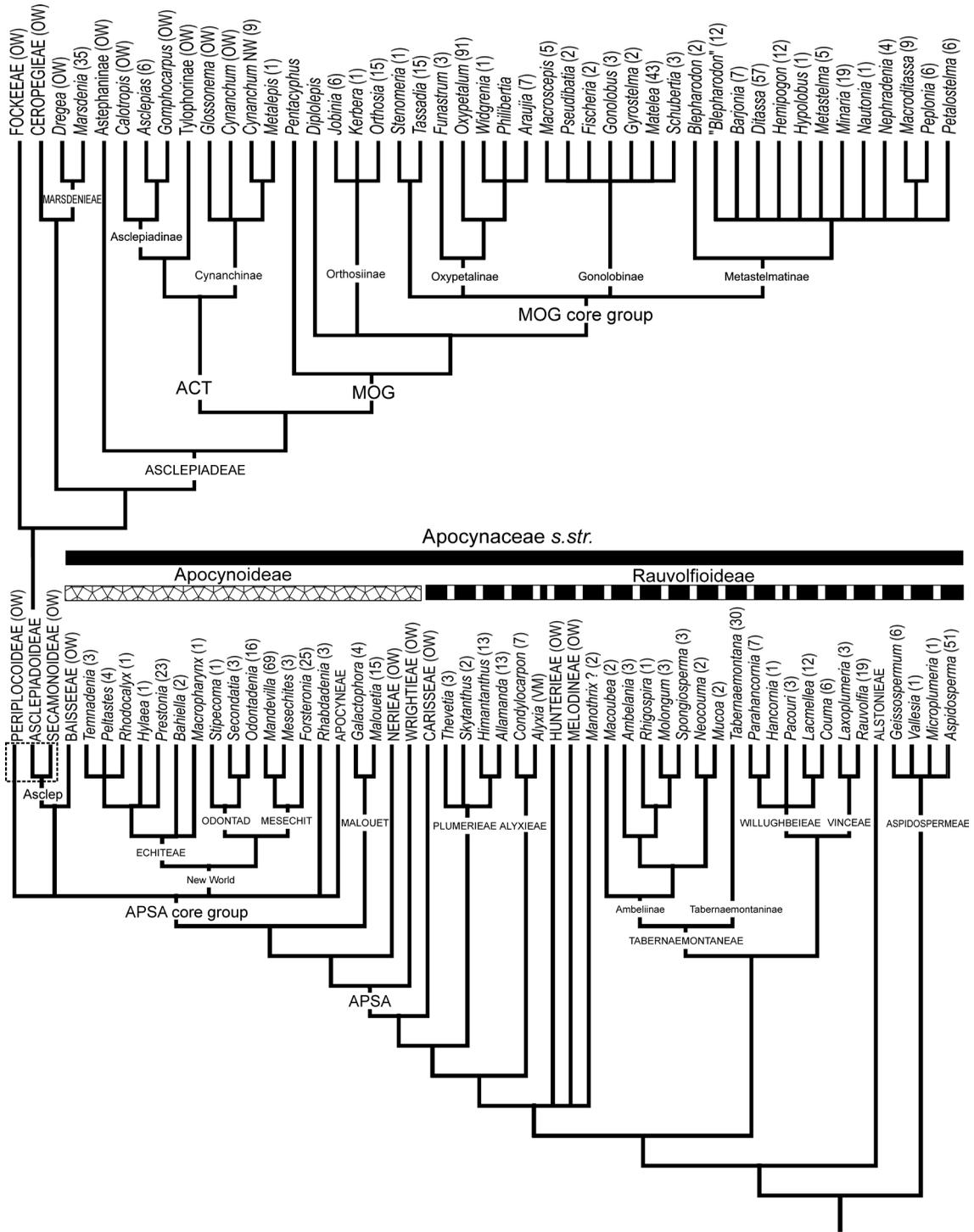


Figure 1 – Reconstructed phylogenetic hypothesis based on the studies discussed in this work. Terminals represented in Brazil are at genus level (except Asclepiadoideae, which is presented in detail above), with the number of species (Koch & Rapini 2011) between parentheses. Names of tribes and subfamilies are in capital letters. The traced rectangle shows the Asclepiadaceae *s.l.*; ACT (Asclepiadinae, Cynanchinae, and Tylophorinae), APSA (Apocynoideae, Periplocoideae, Secamonoideae, and Asclepiadoideae), Asclep (Asclepiadaceae *s.str.*), MALOUET (Malouetieae), MESECHIT (Mesechiteae), MOG (Metastelmatinae, Oxypetalinae, and Gonolobinae), ODONTAD (Odontadenieae), OW (Old World). The position of *Manothryx* is uncertain among lineages and tribes of the Rauvolfoideae grade.

core group can be divided into six main lineages: 1) Apocynae, an essentially Asian tribe, but including the North American genus *Apocynum* L.; 2) *Rhabdadenia* Müll. Arg., a Neotropical genus; 3) a clade including Echiteae, Odontadeniae, and Mesechiteae, predominantly from the New World, but with a relatively recent dispersion to the Old World; 4) Baisseeae, an African tribe; 5) “Asclepiadoideae *s.str.*”, forming a clade with Baisseeae; and, 6) Periplocoideae, a subfamily exclusive to the Old World (Livshultz *et al.* 2007; Livshultz 2010; Fig. 1).

The relationships in the clade of the New World (clade 3 above) were investigated in more detail for the tribe Mesechiteae (Simões *et al.* 2004, 2006), which led to significant modifications in its circumscription: *Secondatia* A. DC. and *Galactophora* Woodson were excluded, the first being transferred to Odontadeniae, and the second to Malouetieae, while *Forsteronia* G. Mey., previously in Apocynae, was incorporated into Mesechiteae (Endress *et al.* 2007). The tribe came to be recognized by the colleters on the adaxial side of the leaf, cordate to truncate anthers, style-head with five longitudinal ribs and cellular fusion of anthers to the style-head (Simões *et al.*, 2004). Its largest genus, *Mandevilla* Lindl. (120 species), was extended to include the South American genera *Macrosiphonia* Müll. Arg. and *Quiotania* Zarucchi, and the North American genera *Telosiphonia* (Woodson) Henrickson. As they are both (sub)shrubs, with woolly leaves and white flowers with a long, narrow tube, *Macrosiphonia* and *Telosiphonia*, in spite of being geographically apart, had been considered as co-generic by Woodson (1933). Analyses with molecular data, however, have shown that these groups correspond to lineages that appeared independently within *Mandevilla*, representing a fine example of convergence, possibly associated with the occupation of open, dry habitats and hawkmoth pollination (Simões *et al.* 2006).

Asclepiadoideae

Asclepiadoideae represents the largest APSA clade. The subfamily includes about 3,000 species and 170 genera, representing an extremely successful lineage when compared to its sister group Secamonoideae, with only 180 species and eight genera (Meve 2002; Endress *et al.* 2007). Five tribes were recognized by Liede & Albers (1994) in Asclepiadoideae: Fockeeae (Old

World), Asclepiadeae (cosmopolitan), Gonolobeae (New World; presently, Gonolobinae, subtribe of Asclepiadeae), Marsdenieae (cosmopolitan), and Stapelieae (Old World; currently Ceropegieae). Subsequently, the Asclepiadeae genera were classified into five subtribes (Liede 1997a): Astephanineae (paleotropical), Asclepiadineae (cosmopolitan), Glossonematineae (Paleotropical), Oxyptelinae (Neotropical), and Gonolobinae (Neotropical), establishing an updated database for a more objective evaluation of the taxonomy of the group. Based on the phylogenetic results, especially with molecular data, it was found that some of these subtribes were not monophyletic (for a comparison between the pre-cladistic classifications and the first phylogenetic results in the subfamily, see Rapini *et al.* 2003). The incorporation of these new findings in the taxonomy of Asclepiadoideae required a number of rearrangements, producing a classification with eight subtribes (Endress *et al.* 2007). The subtribe Tylophorinae was created, consisting of nine genera, most of them taken from Astephanineae, which was reduced to only three genera. Metastelmatinae, which presented a wide distribution and included more than 30 genera, is now restricted to 14 American genera; the rest of the subtribe was mostly segregated to compose Cynanchinae. Glossonematinae was also included in Cynanchinae, forming a subtribe predominantly from the Old World, with 14 genera. Finally, Orthosiinae was created from three American genera, also segregated from Metastelmatinae.

The first phylogenetic analyses including Asclepiadoideae focused mainly on the relationships among the subfamilies of Apocynaceae (discussed in the Introduction). Few representatives of the group were sampled, and as a consequence, the results were of limited scope for internal relationships in Asclepiadoideae. More representative analyses of the subfamily were carried out with morphological data focused mainly on groups of the Old World (Liede 1994, 1996a, 1997b). Until the 1990s, the taxonomic studies carried out in the Americas had primarily focused on elaborating a classification system for identification at the species level, and many genera were defined artificially, especially based on corona morphology and/or on the type of inflorescence (Rapini 2002). The first study that broke away from that taxonomic pragmatism in Brazil was carried out with the species from the Espinhaço Range, in the state of Minas Gerais (Rapini *et al.* 2001). Albeit without objective

phylogenetic analyses, groups were limited based on morphological affinities which supposedly would reflect phylogenetic relationships, and therefore, represented grouping hypotheses that could be evaluated from a cladistic point of view. In less than 10 years, however, about 25% of the species from that survey have already had their classification changed, and approximately 10% of the species found in the whole Espinhaço Range, in Minas Gerais and Bahia states, are still in need of taxonomic modifications, waiting for more accurate phylogenetic results to direct them (Rapini 2010a).

Neotropical groups were given more significant representation in phylogenetic studies with the popularization of phylogenetic analyses with molecular data. The plastid markers *rbcL*, *matK*, and *trnL-F* (*trnL* intron and *trnL-F* intergenic spacer) were the most used at this stage, and the first truly representative phylogenetic analysis of the Neotropical groups (65 species and 26 genera) used only the last one (Rapini *et al.* 2003; see also for a list of the first phylogenetic studies in the subfamily). This study was followed by one (Liede-Schumann *et al.* 2005) including *trnT-F* (*trnT-L* and *trnL-F* spacers with the *trnL* intron between them) and *rps16*, and another one (Rapini *et al.* 2006) including *trnT-L*, *rps16*, *matK*, and *trnS-G* regions. The reason for this preference for plastid markers is simple: the most used nuclear markers for phylogenetic studies of plants (*e.g.*, ITS, but also *LEAFY*) present polymorphic paralogs in many Neotropical species of Asclepiadoideae, requiring cloning (Rapini *et al.* 2006; Krings *et al.* 2008). The nuclear ribosomal DNA ITS, for instance, is easily amplified and presents high substitution rates in Asclepiadoideae, so it is appropriate for analyses at the genus level. However, the recurring presence of polymorphisms in this marker puts its phylogenetic information in doubt, as its phylogeny may not reflect that of the detainers, leading to distorted conclusions about relationships in the group (Alvarez & Wendel 2003; Feliner & Rosselló 2007).

Today, it is possible to have a more consistent view of the phylogenetic structure of Asclepiadoideae and understand the position of the Neotropical groups in this context. Fockeeae is the most basal tribe of the subfamily, including only two genera of the Old World, *Fockea* Endl. and *Cibirhiza* Bruyns. Its position is justified by pollinaria morphology: absence of caudicles (or very reduced ones), pollinia with no external wall, and pollen in tetrads, characteristics considered

to be intermediate between Secamonoideae and Asclepiadoideae (Kunze *et al.* 1994; Endress & Bruyns 2000; Endress & Stevens 2001). This relationship has also been confirmed in phylogenetic studies with molecular data (*e.g.*, Sennblad & Bremer 2000, 2002; Fishbein 2001; Potgieter & Albert 2001; Rapini *et al.* 2003; Lahaye *et al.* 2007). The other Asclepiadoideae plants are divided into two clades basically defined by the position of the pollinia: Asclepiadeae (cosmopolitan), with pendent pollinia, and a clade with erect pollinia, consisted of Ceropegieae (Old World only) and Marsdenieae (cosmopolitan). Although species in Tylophorinae and Gonolobinae show horizontal pollinia, which may be interpreted as an intermediate between Asclepiadeae and Marsdenieae, the position of these groups in Asclepiadeae has been confirmed based on molecular data (Liede *et al.* 2002; Rapini *et al.* 2003; Liede-Schumann *et al.* 2005). In the clade with erect pollinia, only Ceropegieae is divided into subtribes: Anisotomiinae, Heterostemminae, Leptadeniinae, and Stapeliinae (Endress *et al.* 2007), which is supported by phylogenetic results with *trnT-F* data (Meve & Liede 2004). In Asclepiadeae, Astephaninae is the most basal subtribe; the remainder of the tribe can be divided into two clades: one exclusively from the New World, predominantly consisting of representatives of the subtribes Metastelmatinae, Oxypetalinae, and Gonolobinae (Clade MOG), and the other predominantly from the Old World, consisting of the subtribes Asclepiadinae, Cynanchinae, and Tylophorinae (Clade ACT) (Rapini *et al.* 2003; Fig. 1).

Asclepiadoideae of the New World

The Neotropical species of Asclepiadoideae are divided into four main lineages, which reached the New World at different moments and probably by different routes (Rapini *et al.* 2007). The clade MOG seems to have colonized the Americas by transoceanic dispersion, from Africa to South America, and it is the oldest and also the largest lineage in the Americas, including about 750 species. Besides the three subtribes that form the MOG core group, the clade includes Orthosiinae and the genera *Diplolepis* R. Br. (Argentina and Chile) and *Pentacyphus* Schltr. (Colombia, Ecuador, and Peru), the last one being its most basal genus (Liede-Schumann *et al.* 2005). The relationship between *Diplolepis*, Orthosiinae, and the MOG core group is not settled (Liede-Schumann *et al.* 2005; Hechem *et al.* 2011) and, in the core

group, the relationship between Metastelmatinae, Oxypetalinae, and Gonolobinae, and the position of *Tassadia* Decne. (together with *Stenomeria* Turcz.) among them is also uncertain (Liede-Schumann *et al.* 2005; Rapini *et al.* 2006; Fig. 1).

The second lineage of Asclepiadoideae to arrive in the New World was *Cynanchum* L. subgenus *Melichampia* (A. Gray) Woodson. It belongs to Cynanchinae, and is placed in a clade which is predominantly from the Old World. It has only 23 species and is divided into two main clades, one predominantly South-American (section *Roulinia* (Decne.) Sundell) and the other North-American (section *Melichampia* (A. Gray) Sundell), both showing relatively slow diversification (Rapini *et al.* 2007). The third lineage to colonize the New World was *Asclepias* L. The genus includes about 125 species (Woodson 1954), considering only the American ones, and most of them are concentrated in North America. The lineage is placed in a predominantly African clade of Asclepiadinae (Goyder *et al.* 2007), from which it would have emerged, possibly reaching North America via the Bering Strait (Rapini *et al.* 2007). The last lineage to come into the New World was *Marsdenia* R. Br. It has about 70 Neotropical species and forms a clade nested in the Paleotropical Mardenieae (e.g. Rapini *et al.* 2003). This is the only Asclepiadoideae lineage with erect pollinia in the Americas, where it was marked by rapid diversification (Rapini *et al.* 2007).

MOG is certainly the most interesting and promising clade for students of the Asclepiadoideae in the Neotropics. It belongs exclusively to the New World, has a huge diversity, and its internal relationships are complex, hard to define based on morphological or molecular characteristics. Most of the new findings provided by recent phylogenetic studies on the subfamily are directly related to the circumscription of Metastelmatinae. The delimitation of *Sarcostemma* R. Br. is a good example of how difficult it is to recover historical relationships among the members of MOG. Holm (1950) has adopted a Pantropical concept for the genus, including the American genera *Cystostemma* E. Fourn., *Funastrum* E. Fourn., *Pentacyphus*, and *Philibertia* Kunth in its synonymy. In spite of the fragility of the first phylogenetic studies, both with morphological (Liede 1996b) and molecular data (*trnL-F*; Liede & Täuber 2000), it was clear that *Sarcostemma*, as it was delimited, would not be monophyletic. The species of the Old World

are placed in a clade with *Cynanchum* and similar genera, while species of the New World form a paraphyletic group, justifying the recognition of different genera. Phylogenetic studies with more terminals and/or more molecular markers (e.g., Liede & Täuber 2002; Rapini *et al.* 2003, 2006; Liede-Schumann *et al.* 2005) demonstrated that *Sarcostemma* species from the Old World emerge in Cynanchinae and, today, are placed in *Cynanchum*, while the American species belong to the MOG clade, *Pentacyphus* diverging right from its basis, and *Funastrum* and *Philibertia* appearing in Oxypetalinae, the first as a basal genus, and the second as a more derived genus in the subtribe (Fig. 1). *Cystostemma*, on the other hand, was regarded as a synonym of *Funastrum* (*Cystostemma glandulosum* E. Fourn. = *Funastrum flavum* (Decne.) Schltr.).

Phylogenetic studies (Liede-Schumann *et al.* 2005) have also demonstrated that the tribe Orthosieae consisted of five genera of Asclepiadeae, therefore the tribe category would not be appropriate for the taxon. Even worse, these genera are not closely related phylogenetically: *Orthosia* Decne. and *Jobinia* Müll. Arg. are not in the MOG core group and belong to the subtribe Orthosiinae, while *Peplonia* Decne. and *Gonioanthea* Malme form a clade in Metastelmatinae, being closely related to *Macroditassa* Malme (Silva 2010; Fig. 1). *Peplonia* was regarded as a monospecific genus due to its double corona, with the external segments merging almost to the apex, forming a tube. This characteristic of the genera highlighted an autapomorphy of the species and did not establish any phylogenetic relationship. The merger of *Peplonia* and *Gonioanthea* then resulted in a monophyletic taxon with six species distributed in the eastern part of Brazil, especially in the Atlantic Forest, and characterized by a twining habit and axillary inflorescences, generally opposite (Rapini *et al.* 2004).

Another new taxonomic finding presented by phylogenetic studies on Asclepiadoideae was the creation of the genera *Minaria* T.U.P. Konno & Rapini. Analyses with plastid markers (Rapini *et al.* 2006) have confirmed the existence of a clade consisted of subshrubs with very small leaves diverging at the initial evolution of Metastelmatinae. Most species are confined to small areas of “campos rupestres” in the Espinhaço Range, mainly in its Minas Gerais portion (Konno *et al.* 2006). Its

subshrub habit must have persisted in association with the occupation of open habitats, while its floral plasticity may have evolved stochastically and/or associated with the diversity of available pollinators in small, isolated populations of the Espinhaço Range. Such combination of factors must have made *Minaria* become a lineage which can be recognized by vegetative characters, but is cryptic in relation to floral characters traditionally used in the taxonomy of the family, including species with double corona and even species without corona. Species previously classified in phylogenetically distant genera, such as *Ditassa* R. Br. (Metastelmatinae) and *Astephanus* R. Br. (Astephaninae), were included in this genus. Yet, the circumscription of *Minaria* is not complete, as *Barjonia harleyi* Fontella & Marquete and *Hemipogon harleyi* (Fontella) Goyder, two species endemic to the Bahia portion of Espinhaço Range, are nested in species of *Minaria* from the Minas Gerais portion, and will also be transferred to this genus (Silva 2008, 2010). This relationship had already been suggested for *B. harleyi* (Konno *et al.* 2006), but it is surprising for *H. harleyi*, a rare species that is rather discrepant with the rest of the genus by having twining habit, linear leaves, and flowers with conspicuously rostrate gynostegium, which is why it was originally described in *Melinia* Decne. (= *Philibertia*, Oxypetalinae). *Hemipogon harleyi* affinities could only be detected from molecular studies, which once more proves the power of this data source and the sensitivity of the analyses in recovering the evolutionary history of plants.

The delimitation of many genera of the MOG clade is still being evaluated, and its taxonomy will still be considerably modified in order to clearly and accurately define the phylogenetic relationships among its members. Besides *Ditassa*, genus from which *Minaria* was segregated (although its circumscription will still be amended to a considerable extent), other genera have been shown inadequate from the phylogenetic systematics point of view: *Blepharodon* Decne. is an example. *Blepharodon lineare* (Decne.) Decne., the type species of the genus, appears as a sister group of the other Metastelmatinae, forming a clade with only *B. ampliflorum* E. Fourn. The other species from the genus (“*Blepharodon*”), however, appear in the Metastelmatinae core group; therefore, they will have to be transferred to another genus (or other genera) (Rapini *et al.* 2006; Rapini 2010a;

Silva 2010). Conflicts between phylogenetic results and taxonomic classification are not exclusive to Metastelmatinae. In Oxypetalinae, *Schistogyne* Hook. & Arn. emerges in the *Oxypetalum* core group, while *Morrenia* Lindl. emerges amongst the species of *Araujia* Brot. (Liede-Schumann *et al.* 2005; Farinaccio 2007). In both cases, these relationships could be morphologically found, which supported the synonymies of *Schistogyne* and *Morrenia* in *Oxypetalum* and *Araujia*, respectively (Rapini *et al.* 2011). In Gonolobinae, the situation is more complex, and the relationships less resolved. The delimitation of *Gonolobus* Michx. was confirmed by molecular data, and the laminar dorsal appendix of the anthers seems to represent a synapomorphy of the genus (Krings *et al.* 2008), as originally defined by Woodson (1941). However, the circumscription of *Matelea* Aubl. remains obscure, perpetuating discussions on whether small genera synonymized in *Matelea* should be reestablished.

Asclepiadoideae in Brazil

South America is one of the main centres of Asclepiadoideae diversity, and Brazil emerges as one of the countries with the highest number of species of the subfamily in the Neotropics. Most of these species were described in the 19th century, especially by Descaigne (1844: 92 species) and Fournier (1885: 184 species). During the 20th century, taxonomic studies on the group were basically dominated by two researchers, G.O.A. Malme, in the first half of the century, and J. Fontella Pereira, in the second. They were responsible for the description of several new species, but also recognized many synonyms, helping to stabilize the number of species in the group (Rapini *et al.* 2005). In the last five years, a subtribe (Orthosiinae; Liede-Schumann *et al.* 2005), a genus (*Minaria*; Konno *et al.* 2006), 10 species and more than 30 new combinations in the subfamily were proposed for Brazilian Asclepiadoideae, bringing together the knowledge of more than 10 researchers, Brazilian and foreign, which demonstrates a decentralization of the studies on the group. Many species are still being described, mainly in less explored areas, such as is the case of the Caatinga (*e.g.*, Rapini & Fontella-Pereira 2011).

Some genera represented in Brazil have synopses, taxonomic reviews or representative surveys for the country done in the last 50 years:

*Asclepias*¹ (12 South-American species, including assumed hybrids; Bollwinckel 1969), *Barjonia* Decne. (5 species²; Marquete 1979), *Blepharodon*³ (7 species for Brazil; Fontella-Pereira & Marquete 1973; and 11 species; Morillo 1976), *Cynanchum*⁴ (5 species, as “*Telminostelma*”, in Fontella-Pereira & Schwarz 1981; 11 species, as *Cynanchum* subgenus *Mellichampia*, in Sundell 1981), *Ditassa* (50 species for Brazil; Konno 2005), *Fischeria* DC. (6 species; Murphy 1986), *Jobinia* (5 species for Brazil; Schwarz & Fontella-Pereira 1995), *Macroditassa*⁵ (11 species for Brazil; Fontella-Pereira & Ferreira, 2005), *Minaria*⁶ (19 species; Konno 2005; Konno *et al.* 2006), *Morrenia* (= *Araujia*, 8 species; Goyder 2003), *Oxypetalum* (124 South American species and 90 Brazilian species; Farinaccio 2007), *Peplonia* (6 species; Rapini *et al.* 2004), and *Tassadia* (17 species⁷; Fontella-Pereira 1977); finally, the review of *Orthosia* is in progress (about 40 species; Liede-Schumann & Meve 2008). In the last decade, relatively comprehensive inventories (as “Asclepiadaceae” or as part of Apocynaceae *s.l.*) were also concluded, highlighting the floras of Cadeia do Espinhaço of Minas Gerais (99 species; Rapini *et al.* 2001), later also including the Bahia portion (133 species; Rapini 2010a; for pictures of most of this diversity, see Rapini 2010b), from Santa Catarina (51 species; Fontella-Pereira *et al.* 2004), from São Paulo (83 species; Fontella-Pereira 2005), and from Distrito Federal (40 species; Fontella-Pereira *et al.* 2003), besides the lists from the Northeast (65 species; Mezabarba *et*

al. 2006), from Caatinga (67 species; Rapini 2006; this number has doubled; data under preparation) and from the Atlantic Forest (213 species; Rapini & Fontella-Pereira 2009). The North Region possibly represents the largest gap in our knowledge of Brazilian flora, and with Asclepiadoideae, it is not different. Except for the catalogue of species from Acre (15 species only; Hansen *et al.* 2009), recent surveys in the region are scarce. The taxonomy of the group is even more difficult in the North because of its border with other countries, which increases the chance of having species shared with other different and little known floras, such as those from Colombia, Venezuela, and Bolivia.

In spite of the numerous gaps, the taxonomic and floristic advances achieved in the last decades have enabled the composition of a list of species of Asclepiadoideae from Brazil (Rapini *et al.* 2010a, updated in Koch & Rapini 2011), bringing together 32 genera and 392 native species; *Oxypetalum* (91 species), *Ditassa* (57), *Matelea* (43), and *Marsdenia* (35) are the largest genera in number of species, while *Kerbera* E. Fourn. (*K. eichleri* E. Fourn.), *Hypolobus* E. Fourn. (*H. infractus* E. Fourn.), and *Nautonia* Decne. (*N. nummularia* Decne.) are monotypic (Fig. 1). This diversity represents 10% of the entire subfamily, and is much greater than that found in other megadiverse countries of Latin America, such as Peru (105 species; Brako & Zarucchi 1993) and/or countries with great territorial extension, such as Argentina (145 species; Ezcurra 1999) and Mexico (288 species; Juárez-Jaimes *et al.* 2007).

Most of these species are endemic to Brazil, and many have quite limited distribution; at least one fifth of them (76 species) is restricted to areas of less than 10,000 km² (Rapini *et al.* 2009). The Espinhaço Range, including the states of Minas Gerais and Bahia, stands out by having a great diversity of Asclepiadoideae, with high rates of endemism, especially in its Minas Gerais portion (Rapini *et al.* 2001, 2002; Rapini 2010a,b). A total of 133 species of Asclepiadoideae are registered in the Espinhaço Range, which corresponds to more than 30% of the species registered for Brazil, and about 30% (42 species) of them are endemic, which corresponds to 10% of the Brazilian species of the subfamily (Rapini 2010a). Some species with sparse distribution had not been collected for more than a century. In Serra do Cipó, the collections of *Minaria hemipogonoides* (E. Fourn.) T.U.P. Konno & Rapini, in 2008, and, especially, of *Hemipogon abietoides* E. Fourn.,

¹ The genus is predominantly North American, but Goyder (2009) has adopted a more comprehensive circumscription, also including African species.

² Nowadays, *B. chloraefolia* Decne. is not considered synonymous with *B. erecta* (Vell.) K. Schum., while *B. harleyi*, described after the review, shall be transferred to *Minaria*.

³ This genus shall be reduced to only two species, *B. lineare* and *B. ampliflorum* (eventually considered synonymus; *e.g.*, Morillo 1976).

⁴ Some Neotropical species traditionally addressed in *Cynanchum* (Cynanchinae) belong to the clade MOG, as *C. morrenioides* Goyder, which emerges as a sister group of the other Orthosiinae and shall be treated as a monotypic genus (Liede & Meve, under review), and many species recently transferred to *Diplolepis* (Hechem *et al.* 2011).

⁵ Some species of the genus, including the type species, form a grade in relation to *Peplonia*, and the synonymization of *Macroditassa* under *Peplonia* is being proposed (Silva *et al.*, under review).

⁶ *Barjonia harleyi* and *Hemipogon harleyi* shall be transferred to this genus (Silva *et al.*, under review).

⁷ After the genus review, eight species have been incorporated to *Tassadia*, four new ones, including *T. rizzoana* Fontella, from Tocantins; *Tassadia subulata* (Vell.) Fontella & E.A. Schwarz, however, was included in the synonymy of *Orthosia scoparia* (Nutt.) Liede & Meve.

in 2007 and 2008, deserve special attention. Both species had not been collected for more than a century, and the latter species was known only from its type collection, collected by Riedel during the expedition led by Baron Langsdorff, who crossed the mountains of Lapinha in January 1825, returning from Diamantina (Rapini *et al.* 2010b). Also particularly noteworthy was the recent collection of *Nephradenia filipes* Malme from the steep walls of the canyons of Chapada dos Guimarães, in the state of Mato Grosso. The species, collected by Malme in 1894 and described by himself in 1900, was also known only from its type collection, and was rediscovered in 2009, next to *Rauvolfia anomala* Rapini & Koch, a recently described species (Rapini *et al.* 2010c).

Implications for Taxonomic Studies

Most species of Apocynaceae were described in the 19th century, but until the 1990s, the taxonomy of the family did not reflect the phylogenetic relationships of its representatives. With the advent of cladistics and analyses statistically more robust, many inconsistencies between phylogenetic results and the taxonomy of Apocynaceae were evidenced. The use of molecular data, especially plastid markers, and more powerful methods to detect phylogenetic evidence were crucial to reveal relationships that had gone unnoticed by taxonomists. Characteristics regarded as diagnostic for the classification of Apocynaceae, such as fruit and seed for recognition of tribes, for instance, have been debunked; new interpretations for the morphological evolution of the family have arisen, and together with them, taxonomic rearrangements at different levels. From the beginning of the millennium, the species of the New World have been sampled more often in phylogenetic studies, which made the detection of Neotropical lineages possible, as well as the definition of phylogenetic studies directed specifically to South American groups.

The phylogenetic studies on Asclepiadoideae have boosted taxonomic changes, especially at subtribe and genus levels. Yet, there are some obstacles for a complete understanding of the relationships in the subfamily. The group presents a great morphological diversity where homoplasies are common, making it hard to detect morphological synapomorphies useful for taxon definition. The Neotropical lineages are relatively recent, and except for *Cynanchum* subg.

Mellichampia, marked by rapid diversification (Rapini *et al.* 2007). Therefore, finding molecular markers capable of detecting accurate phylogenetic signal to recover the hierarchical structure of these groups is not an easy task. Some inconsistencies have been pointed out by the phylogenetic studies, but a new classification could not always be proposed with certainty, whether due to lack of representatives or to low resolution and/or lack of statistical support for the results (e.g., Silva *et al.*, under review). Thus, it can be said that the taxonomy of Neotropical Asclepiadoideae (and Apocynaceae in general) is “under construction”. Every scholar of the group, when defining their object of study, must be aware of the taxonomic instability the group faces and be prepared for its possible implications.

The importance of monographs and taxonomic reviews is undeniable, but the fragility observed in the delimitation of several genera and the urgent need for new taxonomic arrangements in Asclepiadoideae makes the moment inappropriate for extensive reviews. Still, synopses that help identify species and point out its distribution accurately shall guide more detailed studies and represent important stages for new advances in Asclepiadoideae systematics. Small genera (up to 10 species), still confusing and concentrated in Brazil, such as *Nephradenia* Decne. and *Petalostelma* E. Fourn., can offer great subjects for Scientific Initiation and Master’s course theses. In this sense, *Marsdenia* offers promising perspectives for mid-term studies. A taxonomic synopsis of the genus for Brazil would be convenient, and phylogenetic studies of intercontinental scope would aid a better understanding of the position of Neotropical species, as well as the relationships among them. On the other hand, other genera, especially *Matelea*, with wide diversity concentrated in northern South America and complex taxonomy, may be inappropriate for projects with strict deadlines. Biogeographical and phylogeographical studies would also help elucidate Asclepiadoideae systematics, especially when associated with studies on reproductive biology and pollination. This mixture of approaches, if properly applied, could help decode affinities and taxonomic boundaries among close related species or species with questionable delimitation, such as *Blepharodon lineare*, *Minaria cordata* (Turcz.) T.U.P. Konno & Rapini, *Oxypetalum insigne* (Decne.) Malme, and *O. strictum* Mart.

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