THE NERIEAE (APOCYNACEAE—APOCYNOIDEAE)

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ABSTRACT

The genera of tribe Nerieae of Apocynaceae are surveyed here and the relationships of the tribe within the family are evaluated. Recent monographic work in the tribe enabled the author to update taxonomic approaches since Pichon (1950) made the last survey. Original observations on the pollen morphology of the genera by S. Nilsson, Swedish Natural History Museum, Stockholm, are appended to this paper.

RÉSUMÉ

L'auteur étudie les genres de la tribu des Nerieae des Apocynacées et évalue les relations de la tribu au sein de la famille. Un travail monographique récent sur la tribu a permit à l'auteur de mettre à jour les approches taxonomiques depuis la dernière étude de Pichon (1950). Les observations inédites par S. Nilsson du Muséum d'Histoire Naturelle Suédois à Stockholm sur la morphologie des pollens des genres sont jointes à cet article.

The Apocynaceae have long been divided into two subfamilies, Plumerioideae and Apocynoideae (Echitoideae). Pichon (1947) added a third, the Cerberioideae, a segregate of Plumerioideae—a situation which I have provisionally accepted. These subfamilies were in turn divided into tribes and subtribes. Comparative studies have shown that the subdivision of the Plumerioideae is much more natural than that of the Apocynoideae.

Although the Apocynoideae is a coherent grouping, it has so far proved very difficult to devise a satisfactory and practicable subdivision for it. Pichon (1950) had little confidence in early classifications of the subfamily, although, like his predecessors, he seems to have preferred a more or less artificial treatment. He recognized four tribes in Apocynoideae—Echiteae, Nerieae, Apocyneae, and Ichnocarpeae—each of which was further divided into a number of subtribes. However, none of these can be maintained as delimited by Pichon. For example, there appears to be a greater degree of similarity between *Echites* and *Rhodocalyx* of the Echiteae and *Mandevilla* and *Mesechites* of the Ichnocarpeae than is evident from his classification.

Nevertheless, the Nerieae, dealt with in detail here, are maintained largely as proposed by Pichon except for the following changes: *Dewevrella* is transferred to Parsonsiineae (Echiteae). *Amphineurion* is treated as a synonym of *Aganosma*. De Candolle (1844) regarded *Amphineurion* as a section of *Aganosma*, but Pichon raised it to generic rank and in his arrangement included *Aganosma* in the Echitinae. Further, because of its conspicuous resemblance to *Beaumontia*, it may well be that *Amalocalyx* (Echiteae—Amalocalycinae, according to Pichon) ought to be moved to the Nerieae.

Pichon's system is artificial, because he used the shape and the indumentum of the area where the connectives cohere with the head of the pistil as the only character to distinguish the four tribes of his Apocynoideae. That the Nerieae is the most satisfactorily defined tribe of the Apocynoideae only becomes evident after combinations of characters are taken into account.

Pichon divided the Nerieae into nine subtribes (Table 1), but it is certain that not all of these can be maintained. Indeed, it is questionable whether the Nerieae ought to be divided into subtribes at all.

Connections can be seen between certain groups of genera. Thus *Adenium* has flowers that resemble those of *Nerium*, especially in the corona and in the long bristly appendages at the apices of the anthers.

Wrightia, *Pleioceras*, and *Stephanostema* can also be grouped together, as they have a corona (deeply incised in the first two and almost entire in the last one), more or less bifurcate ramification, and a similarly shaped corolla. There is, in addition, the resemblance shown by *Beaumontia* and *Vallaris* to *Wrightia*, in particular to those of its species with a broad corolla and thick-walled fruits. *Strophanthus*, with comparable

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TABLE 1. Pichon's treatment of the Nerieae compared with the arrangement proposed here.

Pichon (1950)	Leeuwenberg (1988)
Nerieae	Nerieae
1. Neriinae (as Amphineuriinae)	*Adenium* (5; Afr., Arab.; Plaizier, 1980)
Amphineurion (= *Aganosma*)	*Nerium* (1; Medit. to China; Leeuwenberg, 1984)
Pottsia	*Strophanthus* (38; Afr., As.; Beentje, 1982)
Dewevrella (to Parsonsiinae)	*Wrightia* (23; Afr., As.; Ngan, 1965)
Isonema	*Pleioceras* (5; Afr.; Barink, 1983)
Nerium	*Stephanostema* (1; Afr.; Barink, 1983)
2. Beaumontiinae	*Beaumontia* (9; As.; Rudjiman, 1986)
Vallaris	*Vallaris* (3; As.; Rudjiman, 1982)
Parabeaumontia (= *Vallaris*)	*Vallariopsis* (1; As.; Rudjiman, 1986)
Muantum (= *Beaumontia*)	*Kibatalia* (15; As.; Rudjiman, 1986)
Beaumontia	*Malouetia* (ca. 15; Afr., S. Amer.; Van der Ploeg, 1984, 1985; Fallen, unpubl.)
3. Strophantinae	*Allowoodsonia* (1; Pacif.; Fallen; unpubl.)
Christya (= *Strophanthus*)	*Funtumia* (2; Afr.; Zwetsloot, 1981)
Roupellina (= *Strophanthus*)	*Mascarenhasia* (ca. 10; Afr., Mad.; Markgraf, 1976)
Strophanthus	*Farquharia* (1; Afr.; Zwetsloot, 1981)
4. Mascarenhasiinae	*Alafia* (ca. 25; Afr., Mad.; Pichon, 1954)
Mascarenhasia	*Isonema* (3; Afr.; Van der Ploeg, 1983)
Echitella (= *Mascarenhasia*)	*Pottsia* (3; As.; Tsiang & Li, 1977)
5. Alafiinae	
Alafia	
Aladenia (= *Farquharia*)	
6. Kibataliinae	
Funtumia	
Kibatalia	
7. Wrightiinae	
Wrightia	
Wallida (= *Wrightia*)	
Scleranthera (= *Wrightia*)	
Pleioceras	
Stephanostema	
8. Malouetiinae	
Malouetia	
Malouetiella (= *Malouetia*) (Pichon, 1952)	
9. Adeniinae	
Adenium	
Vallariopsis not included.	
Allowoodsonia not mentioned.	

fruits and flowers with a corona, also belongs here.

A third group comprises *Kibatalia, Funtumia, Mascarenhasia, Malouetia,* and *Allowoodsonia.* These five genera probably all conform to the model of Koriba when in the flowering stage. *Funtumia,* however, matches the model of Prévost in the juvenile stage. This has still to be investigated for the other four genera. The coriaceous leaves, small stunted inflorescences, and fleshy corollas can make it difficult to distinguish these genera from each other. Within the group, *Malouetia* and *Allowoodsonia* are so close in all their characters, including those of the seeds (the only ones without a coma in the whole of the Apocynoideae), that the two should probably be united. *Kibatalia* differs from them only in the rostrum and coma of the seeds.

Farquharia and *Alafia,* large lianes with coriaceous leaves, exhibit similarity in their flowers and fruits, and they therefore form a fourth group within the Nerieae.

Of the three genera not yet mentioned, *Vallariopsis, Isonema,* and *Pottsia,* it is mainly *Vallariopsis* that shows connections with other genera. Thus, its flowers resemble those of *Kibatalia, Allowoodsonia,* and *Malouetia,* and to a lesser extent those of *Vallaris, Isonema,* and *Pottsia.*

The four groups outlined above could, if necessary, be distinguished as the subtribes Neriinae, Wrightiinae, Kibataliinae, and Alafiinae, but they are difficult to define.

Strophanthus gratus has flowers reminiscent of *Adenium* and *Nerium* in their corolla and corona. The corona and syncarpous fruits of *Nerium* have their counterparts in several *Wrightia* species. The model of Leeuwenberg has been recognized in species of *Nerium, Strophanthus boivinii,* and *Wrightia.* The seeds of *Beaumontia* resemble those of *Isonema* and *Pottsia.* In addition, the flowers of *Isonema* bear lateral appendages on the corolla lobes and, in this respect, are like those of *Mascarenhasia.* The remarkable long, slender, rostrate seeds of *Strophanthus,* with a coma on the rostrum, are also found in *Funtumia* and *Kibatalia.* On the other hand, the seeds of *Adenium* and *Farquharia* have basal and apical comas that are persistent, while in *Strophanthus, Funtumia,* and *Isonema* the second coma is deciduous.

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Appendix

Pollen Description of Apocynaceae–Apocynoideae–Nerieae[2]

Pollen grains usually spheroidal, 3(–4)-porate, exceptionally polypantoporate (*Vallariopsis*); exine smooth, perforated, often densely spaced towards the apertures; pores provided with thickened margin; inner exine consisting of globular or irregular elongated elements that are free or partly fused.

The exine fine structure varies among the taxa investigated with five or possibly six types:

(1) Exine stratified into tectum, a distinct central granular-columellate stratum and a basal stratum (sole, foot layer), endexine obsolete; the sole appears fragmented towards the pores (*Adenium obesum*). In *Vallaris solanacea* the granular stratum, when discernible, is displaced proximally towards the laminated sole.

(2) Exine with a relatively thick tectum, a distinct granular stratum more proximally located than in previous type, an unevenly thickened, partly discontinuous sole, fragmented near the apertures and possibly subtended by a thin, indistinct endexine (*Nerium oleander*).

(3) Exine stratified into tectum, a thin indistinct granular stratum subtended by a sole to which granules or knoblike elements are attached; near the apertures only granules (*Pleioceras barteri*).

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(4) Exine unstratified, with or without a central commissural line; inner face consists of small and large granules (*Farquharia elliptica, Funtumia africana, Kibatalia gitingensis, Mascarenhasia arborescens* var. *boivinii, Strophanthus gratus,* and *Wrightia pubescens*).

(5) Exine consists of an outer tectal stratum towards which free or fused rounded-elongated elements appear piled up (*Alafia lucida*).

The above arbitrary groups are not sharply delimited from each other, in particular group 4 from groups 3 and 5, respectively. From the complete exine in *Adenium* there is a series of transitional exine structures to the tectal-granular exine of *Alafia.*

Out of the remaining genera (pollen grains seen in LM or SEM only) it is only *Vallariopsis* that markedly deviates from all others by being poly-panto-porate. Pollen morphology does not reveal any evidence as to the position and interrelationships of *Allowoodsiana, Beaumontia, Isonema, Malouetia* (*Malouetiella*), *Pottsia,* and *Stephanostema.* Nor does it support the removal of *Amphineuron* and *Dewevrella* from the Nerieae.

Pollen morphologically, *Adenium* and *Nerium* appear related. *Wrightia* and *Strophanthus* appear related more to *Kibatalia, Funtamia, Mascarenhasia,* etc. than to *Pleioceras. Vallaris* shows certain similarity to *Adenium*; *Vallariopsis* is unique within the Nerieae. *Farquharia* appears closer to *Kibatalia, Funtumia,* etc., than to *Alafia.*