Taxa of the Apocynaceae above the genus level

Series of Apocynaceae
XXXVIII

A.J.M. Leeuwenberg
Abstract

The systematic position and nomenclature of the 12 tribes and 27 subtribes maintained here is treated for the two subfamilies of the Apocynaceae, the Plumerioideae and the Apocynoideae, the only ones kept up in this paper. In Apocynoideae the framework is less definite than was possible for the Plumerioideae.

Introduction

Since the family of Apocynaceae Juss. (1789) was founded, little dispute rose about its delimitation. Any controversy disappeared completely when Leenhouts (1963) moved Neuburgia to the Loganiaceae.

The family is generally subdivided into two subfamilies, the Plumerioideae and the Apocynoideae, a system followed here. These two subfamilies have exceptions in almost all of their characters but in combination the characters are quite diagnostic.

Table 1. Diagnostic characters of the subfamilies of Apocynaceae

<table>
<thead>
<tr>
<th>Plumerioideae</th>
<th>Apocynoideae</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aestivation usually to the left.</td>
<td>Aestivation usually to the right.</td>
</tr>
<tr>
<td>Anthers entirely fertile or only</td>
<td>Anthers mostly fertile only near the apex,</td>
</tr>
<tr>
<td>sterile at the acumen or macro,</td>
<td>usually coherent with the pistil head.</td>
</tr>
<tr>
<td>mostly free from the pistil head</td>
<td>Fruit capsular, mostly apocarpous, of two folli-</td>
</tr>
<tr>
<td>Fruit baccate or capsular,</td>
<td>cles. Seed generally with coma; endosperm pre-</td>
</tr>
<tr>
<td>syncarpous or apocarpous</td>
<td>sent, not ruminate.</td>
</tr>
<tr>
<td>Seed generally without coma;</td>
<td>Glycosides often present.</td>
</tr>
<tr>
<td>endosperm sometimes absent,</td>
<td></td>
</tr>
<tr>
<td>ruminate or not.</td>
<td></td>
</tr>
<tr>
<td>Indole alkaloids often present</td>
<td></td>
</tr>
</tbody>
</table>

Some exceptions are:

- Aestivation to the right in several species of Alstonia, Carissa and Tabernaemontana; in Callichita subsessilis and Schizozygia coffeoides
- Anthers coherent with the pistil head in Voacanga and Allamanda
- Seeds with coma occur in Alstonia.

<table>
<thead>
<tr>
<th>Apocynoideae</th>
</tr>
</thead>
<tbody>
<tr>
<td>Anthers free from the pistil head and almost</td>
</tr>
<tr>
<td>completely fertile in Holarrhena, and more or</td>
</tr>
<tr>
<td>less free from the pistil head in Nerium.</td>
</tr>
<tr>
<td>Seeds without coma only in Malouetia and Allowoodsonia.</td>
</tr>
</tbody>
</table>

Tribes and subtribes in the Apocynaceae

Pichon was the last author who made a commented survey of the entire family. For that purpose he coined many tribes and subtribes with descriptions in French. For most genera his comments were preliminary but he also made valuable revisions of some genera. His untimely death in 1954 made completion of his work impossible. Up to then Pichon devoted approximately 40 publications to Apocy-
naceae. Since then more monographic revisions were produced by several authors, including more elaborate field studies. It is remarkable that the additional information confirms most of Pichon’s conclusions in the taxonomy of the Plumerioideae, but it is still impossible at this point to reach a satisfactory arrangement of the genera placed in the Apocynoideae. The Plumerioideae are subdivided here into 9 tribes, 7 of which were also accepted as such by Pichon. The Macoubeeae were distinguished by Boiteau & Sastre (1975) and the Cerberae were a subfamily with Pichon. The delimitation of these 9 taxa, tribes in this publication, has hardly changed since Pichon and Boiteau (1950, 1975). As for the Apocynoideae many changes are proposed; none of the tribes is similar to those of Pichon. After elaborate critical remarks on the arrangements of Bentham & Hooker f. (1876) and K. Schumann (1895), Pichon made arrangements that may be even more artificial. His most important character, the “rétilacle” (way of coherence of anthers and pistil head), is difficult to observe. Pichon exaggerated its importance, and placed several genera resembling each other in several characters far apart, e.g. Odontadenia in Apocynae and Mandevilla in Ichnocarpeae, Micrechites (at present even a synonym of Ichnocarpus) in Echiteae and the related Ichnocarpus in Ichnocarpeae.

The subdivision of the Plumerioideae into tribes and subtribes is first of all based on characters of fruits and seeds.

Syncarpous fruits are the rule in Carisseae, only the genera in its subtribe Pleiocarpinae are exceptions. Conform to its name Pleiocarpa may even have more than 2 carpels. Multi-carpellate fruits are a great exception in the family. This character is otherwise only known in the genera Lepinia and Lepiniopsis of the Alyxieae-Alyxiinae.

The Carissinae may be the subtribe with the most plesiomorphous characters, as the pistil head is often a plain stigma (receptive all over) and the pistil length varies more or less independently from that of the stamens. A pistil head with a non-receptive stigmoid apex and a true stigma at the base is the rule in the family. In general the great variation in shape of the pistil head, even within a single genus, makes it almost impossible to use it for classification.

The four following subtribes have plants that are usually lianescent with large many-seeded berries. The Melodininae and Leuconotidinae have no tendrils and are distinguished first of all by the corona present in the former and absent in the latter. The Landophiinae and Willughbeiniae have large curled terminal tendrils and display the model of Korba, if they are lianescent. They are closely allied not only by the fruits and the tendrils not known elsewhere in the family, but also by many characters of the flowers. Their difference lies in the endosperm, thick and horny in the Landophiinae; and thin and flimsy in the Willughbeiniae. These two subtribes therefore may be united, if the value of the distinctive characters is compared with those in the Leuconotidinae. Endosperm is present only in the genus Cyclocotyla, which is well placed in the Leuconotidinae because of its other characters.

The last three subtribes of the Carisseae, the Pleiocarpinae, Lacmelliinae and Couminae, shrubs or trees, have many flower characters in common with the Landophiinae.
The second tribe in Plumerioideae, the Chilocarpeae, is characterized by the 1-celled ovaries, baccate bivalved fruits, arils and seeds with a deep hilar groove and ruminate endosperm. These plants are lianescent.

The Ambelaniiaceae, shrubs or trees, have 2-celled ovaries, indehiscent fruits, no arils and seeds without hilar groove and non-ruminate endosperm.

The fruits of Macoubeeae are apocarpous, fleshy and indehiscent and the seeds lack the aril and the hilar groove, and the endosperm is not ruminate. As for the flowers, they very much resemble the Couminae.

The Tabernaemontaneae usually have apocarpous, dehiscent, mostly fleshy fruits, but syncarp is known in some genera, e.g. Voacanga and Tabernanthe. The fruits of Tabernanthe iboga are even halfway 1-celled and indehiscent. The seeds are surrounded by an aril and have a deep hilar groove and ruminate endosperm. The Tabernaemontaneae were raised to the level of subfamily by Stapf (1902), an opinion at first embraced by Pichon (1949, p. 212) and rejected at the end of the same paper (p. 238). However, it is interesting to see that it is well housed in the Plumerioideae at the tribal level. Apocarpous fruits are the rule not only in the Tabernaemontaneae but also in the Macoubeeae and Plumerieae. Tabernanthe iboga has the halfway unilocular ovaries in common with the Landolphiinae. The presence of the aril, the deep hilar groove in the seeds and the ruminate endosperm are shared by the Chilocarpeae and the Tabernaemontaneae. Ruminate endosperm is otherwise known from Rhazya, Plumerieae, Catharanthinae and Alyxieae-Alyxinae. Two genera of the Tabernaemontaneae, Schizozygia and Tabernaemontana (some species) have dry follicles, by which they more or less resemble almost all Plumerieae. The Plumerieae in their turn house one genus, Geissospermum, with fleshy follicles. In most subtribes of the Plumerieae the seeds are winged. In this respect they show a slight resemblance with the last three tribes of the Plumerioideae.

The first subtribe of the Plumerieae, the Aspidospermatinae are characterized by the similarities in the flowers, and, except for Geissospermum, by the often thick-walled bivalved oblique mericarps and the flat seeds often winged all around.

The Craspidospermatinae are close to Aspidospermatinae for the similar flowers, but the fruits are generally more slender, and the wings of the seeds are often smaller and mostly less distinct from the grain.

The Plumerieae have mostly robust cylindrical follicles, which may even be cucumber-like, they possess winged seeds and large sometimes waxy flowers, e.g. in the well-known ornamental Plumeria rubra.

The Alstonieae are the only Plumerioideae of which seeds with coma are known. The fruits usually are long slender follicles.

The Catharanthinae are a more or less artificial rest-group in the Plumerieae. The shortish follicles either contain winged or non-winged seeds.

The Alyxieae are mainly characterized by the drupes containing mostly flat seeds. The relatively slight differences between its subtribes are not easily described in a concise way.

The eighth tribe, the Cerbereae, resemble the Alyxieae by the flat seeds enclosed in indehiscent fruits. The fruits of the Cerbereae, however, are drupaceous as in the
Afyxieae in Thevetia and Cerbera, and samaroid in the three other genera. The pistil head is broad. The obscure corona lobes and the broad pistil head inspired Pichon (1948) to place the five genera housed here in a separate subfamily. However, after some hesitation, it is decided here to place these 5 genera in a tribe on the basis of their fruit and seed characters. The anthers strikingly resemble those of the Carisseae.

The Allamandeae are easily characterized by their mostly subglobose 1-celled usually prickly capsules containing flat seeds winged all around. Moreover, the large corolla has small corona lobes just above the deeply included stamens and the anthers are coherent with the pistil head. Winged seeds are common in Plumerieae, prickles on fruits are known of some Tabernaemontaneae, corona lobes of Melodininae and Cerberae and coherence between anthers and pistil head of Voacanga (Tabernaemontaneae). The last mentioned character is the rule in the Apocynoidea and therefore it may introduce the reader to this, the second and last subfamily of the Apocynaceae.

The Apocynoideae genera are so closely interrelated, that it is probably impossible to place them into distinct tribes or subtribes. It proved difficult at present to define the 3 subtribes maintained here. The genera of each subtribe share certain characters, but it was impossible to build a set of characters to distinguish the tribes from each other. Nevertheless, in the Wrightiieae a reasonable stability is obtained since most of its genera have recently been revised monograpically. They are maintained here in almost the same delimitation as with Pichon. The only changes are the removal of Amphineurion (reduced to the synonymy of Aganosma) and the moving of Dewevrella, Pottsia and Isonema to the Echiteae-Parsonsiinae. The Echiteae and Apocyneae are only partly as with Pichon and they share the genera he placed in his fourth tribe, the Ichnocarpeae, not maintained here.

The names of the tribes and subtribes were always chosen from the earliest found in literature. If they appeared in these publications at another level than they are maintained here, the author who changed the level is mentioned as combiner, although in most cases the basionyms were omitted.

This survey is partly preliminary, especially in the Apocynoideae. The author respects with gratitude the opinions of the following authors: M.E. Endress-Fallen (remarks on taxonomic position of Holarrhena, Carruthersia and Spirolobium), P.I. Forster (reduction of Micrechites to the synonymy of Ichnocarpus), A.H. Gentry (reduction of Tonduzia to the synonymy of Alstonia), P.T. Li (reduction of Parabarism, Chunechites and Xylohabitopsis as synonyms of Ecdysanthera and of Poacynum as a synonym of Apocynum), D.J. Middleton (reduction of Urmaria to the synonymy of Willughbeia, reduction of Rhynchodia to the synonymy of Chonemorpha and preparation of the reduction of Ecdysanthera, Hymenolophus, Nouetia, Xylohabitaria and perhaps also Valariopsis to the synonymy of several other genera), J.G.M. Persoon (reduction of Anthoclitandra and Aphanostylis to synonymy of Landolphia), Rudjiman (classification of the Wrightiieae) and J.L. Zarucchi (Ambelanieae).
Table 2. Conspectus of the tribes and subtribes of *Apocynaceae*, with their genera, the number of species therein and their general distribution. Abbreviations are self-explanatory.

<table>
<thead>
<tr>
<th>Tribe/Subtribe</th>
<th>Genera</th>
<th>Species</th>
<th>Distribution</th>
</tr>
</thead>
<tbody>
<tr>
<td>Apocynaceae</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Plumerioideae</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1. Carisseae</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1.1. Carissinae</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Carissa</td>
<td>20</td>
<td>Afr + As</td>
<td></td>
</tr>
<tr>
<td>Acokanthera</td>
<td>5</td>
<td>Afr</td>
<td></td>
</tr>
<tr>
<td>1.2. Melodininae</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Melodinus</td>
<td>45</td>
<td>As + Oc</td>
<td></td>
</tr>
<tr>
<td>1.3. Landolphiinae</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Landolphia</td>
<td>60</td>
<td>Afr</td>
<td></td>
</tr>
<tr>
<td>Chamaecitrandra</td>
<td>1</td>
<td>Afr</td>
<td></td>
</tr>
<tr>
<td>Cithandra</td>
<td>1</td>
<td>Afr</td>
<td></td>
</tr>
<tr>
<td>Orthopicia</td>
<td>6</td>
<td>Afr</td>
<td></td>
</tr>
<tr>
<td>Pacouria</td>
<td>2</td>
<td>Afr</td>
<td></td>
</tr>
<tr>
<td>Dictyophleba</td>
<td>5</td>
<td>Afr</td>
<td></td>
</tr>
<tr>
<td>Vahadania</td>
<td>2</td>
<td>Afr</td>
<td></td>
</tr>
<tr>
<td>Ancylobotrys</td>
<td>7</td>
<td>Afr</td>
<td></td>
</tr>
<tr>
<td>Saba</td>
<td>3</td>
<td>Afr</td>
<td></td>
</tr>
<tr>
<td>1.4. Willughbeinae</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cylindropsis</td>
<td>1</td>
<td>Afr</td>
<td></td>
</tr>
<tr>
<td>Willughbea</td>
<td>15</td>
<td>As</td>
<td></td>
</tr>
<tr>
<td>1.5. Leucodontinae</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bousigonia</td>
<td>2</td>
<td>As</td>
<td></td>
</tr>
<tr>
<td>Leuconotis</td>
<td>7</td>
<td>As</td>
<td></td>
</tr>
<tr>
<td>Cyclocotyla</td>
<td>1</td>
<td>Afr</td>
<td></td>
</tr>
<tr>
<td>1.6. Pleiocarpinae</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Picralina</td>
<td>1</td>
<td>Afr</td>
<td></td>
</tr>
<tr>
<td>Hunteria</td>
<td>10</td>
<td>Afr + As</td>
<td></td>
</tr>
<tr>
<td>Pleiocarpa</td>
<td>7</td>
<td>Afr</td>
<td></td>
</tr>
<tr>
<td>1.7. Lacmelleinae</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lacmellea</td>
<td>15</td>
<td>Am</td>
<td></td>
</tr>
<tr>
<td>Hancornia</td>
<td>4</td>
<td>Am</td>
<td></td>
</tr>
<tr>
<td>1.8. Coumineae</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Parahancornia</td>
<td>6</td>
<td>Am</td>
<td></td>
</tr>
<tr>
<td>Couma</td>
<td>6</td>
<td>Am</td>
<td></td>
</tr>
<tr>
<td>2. Chilocarpae</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chilocarpus</td>
<td>15</td>
<td>As</td>
<td></td>
</tr>
<tr>
<td>3. Ambelanicea</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ambelania</td>
<td>3</td>
<td>Am</td>
<td></td>
</tr>
<tr>
<td>Mucoa</td>
<td>2</td>
<td>Am</td>
<td></td>
</tr>
<tr>
<td>Spongiosperma</td>
<td>6</td>
<td>Am</td>
<td></td>
</tr>
<tr>
<td>Molongum</td>
<td>3</td>
<td>Am</td>
<td></td>
</tr>
<tr>
<td>Rhigosperma</td>
<td>1</td>
<td>Am</td>
<td></td>
</tr>
<tr>
<td>Neocouma</td>
<td>2</td>
<td>Am</td>
<td></td>
</tr>
<tr>
<td>4. Macoubeea</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Macouba</td>
<td>2</td>
<td>Am</td>
<td></td>
</tr>
<tr>
<td>5. Tabernaemontaneae</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Voacanga</td>
<td>12</td>
<td>Afr + As</td>
<td></td>
</tr>
<tr>
<td>Tabernaemontana</td>
<td>99</td>
<td>trop</td>
<td></td>
</tr>
<tr>
<td>Tabernanthe</td>
<td>2</td>
<td>Afr</td>
<td></td>
</tr>
<tr>
<td>Carvalhoa</td>
<td>1</td>
<td>Afr</td>
<td></td>
</tr>
<tr>
<td>Plumeriinae</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>6.1. Aspidospermatinae</td>
<td></td>
<td></td>
<td>As + Oc</td>
</tr>
<tr>
<td>6.2. Craspidospermatinae</td>
<td></td>
<td></td>
<td>As + Oc</td>
</tr>
<tr>
<td>6.3. Plumerinae</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>6.4. Alstoninae</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>6.5. Catharanthinae</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>7. Alyxiaceae</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>7.1. Condylocarpinae</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>7.2. Rauvolfiinae</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>7.3. Alyxiinae</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>7.4. Kopsiinae</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>7.5. Ochrosiinae</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>8. Cerbereae</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Thevetia 8 Am
Cerbera 4 Seych - Oc
Cerberiopsis 2 N Cal
Cameraria 2 W I
Skytanthus 2 Am
9. Allamandaceae
Allamanda 14 Am
Apocynoideae
10. Echiteae
10.1. Echitinae
Secondatia 6 Am
Odontadenia 20 Am
Mesechites 12 Am
Mandevilla 150 Am
Macroispophia 10 Am
Elytropus 1 Am
Themnadenia 4 Am
Macrophyryn 2 Am
Asketanthera 4 Am
Fernaldia 4 Am
Neobracea 4 Am
Prestonia 35 Am
Rhodocalyx 1 Am
Lauberia 4 Am
Echites 6 Am
Thysanthera 1 USA
Trachelospermum 15 Am + As
Valariopsis 1 As
Aganosma 10 As
Chonemorpha 10 As
Amalocalyx 1 As
Angadenia 2 Am
Pentalinon 2 Am
Rhabdadenia 4 Am
Galactophora 6 Am
Salpinctes 1 Am
Cycladenia 1 Am
Peltastes 6 Am
Stipecoma 1 Am
10.2. Parsonsiinae
Delphyodon 1 N Guin
Grissea 1 Indon
Parsonsi 50 As + Oc
Dewevrella 1 Afr
Thenardia 4 Mex
Artia 4 As + Oc
Pottsia 2 As
Isonema 3 Afr
10.3. Pachypodinae
Pachypodium 17 Afr
11. Wrightiae
11.1. Neriiinae
Adenium 5 Afr + Arab
Nerium 1 Medit - Him
11.2. Wrightiinae
Wrightia 23 Afr + As
Pleioceras 5 Afr
Stephanostema 1 Afr
Spirolobium 1 As
Tinturnabularia 1 Am
Beaumontia 9 As
Vallaris 3 As
Strophianthus 38 Afr + As
11.3. Malouetiinae
Kibatilia 15 As
Funtumia 2 Afr
Mascarenhasia 10 Afr
Malouetia 30 Am + Afr
Allowoodsonia 1 Oc
11.4. Alafiinae
Holarrhena 4 Afr + As
Carruthersia 4 As + Oc
Alafia 30 Afr
Farquharia 1 Afr
12. Apocynineae
12.1. Apocyninae
Apocynum 9 N Hem
12.2. Ichnocarpinae
Anodendron 15 As
Urecola 25 As
Parameria 4 As
Agnanocerion 1 As
Ichnocarpus 12 As + Aus
I xo d en er i um 1 As
Epygynum 10 As
Eu corymbia 1 As
Parepygynum 1 As
Papuechites 2 As
Cleghornia 4 As
Sindechites 2 As
Motandra 3 Afr
Forsteronia 40 Am
Baissea 18 Afr
Oncinotis 7 Afr

Diagnoses of tribes and subtribes of Apocynaceae Juss., Gen. 143. 1789.
Plumeriodeae K. Schum. in Engler & Prantl, Nat. Planzenf. 4:2: 122. 1895, partly, excl. Chaetosos (= Parsonsiinae), Neuburgia (Loganiaceae), Stepanhostegia, Holarrhena and Ceratitis (Asclepiadaceae).
1. Tribe Carisseae Endl., Gen. Pl. 578. 1838, partly, excl. Ambelania, Collopho-
ra (= Couma), Couma, Chilocarpus and Allamanda.

Woody plants. Leaves opposite or sometimes whorled. Corolla hypocrateriform or urceolate; lobes overlapping to the left or sometimes to the right. Stamens usually inserted in the upper half of the corolla tube; anthers completely fertile. Ovary syncarpous or only in Pleiocarpinae apocarpous. Fruit mostly a syncarpous berry. Endosperm mostly present, not ruminate.

1.1. Subtribe Carissinae A. DC., Prod. 8: 324. 1844 (as Eucarisseae), partly, as for Carissa.

Woody plants, often with straight spines. Leaves opposite or sometimes whorled. Corolla hypocrateriform, without corona; lobes overlapping to the left or to the right. Stamens inserted in the upper half of the corolla tube. Ovary 2-celled. Fruit a berry with 1-8 seeds. Seed with endosperm.


Unarmed climbers or shrubs. Leaves opposite. Corolla hypocrateriform, with corona; lobes overlapping to the left. Stamens inserted on various levels. Ovary 2-celled. Fruit a berry with many seeds. Seed with endosperm.

1.3. Subtribe Landolphiinae K. Schum., op. cit. 127, partly, as for Landolphia, Carpodinus (= Landolphia) and Clitandra.

Unarmed woody climbers with large curled terminal tendrils or less often rhizomatous pyrophytic shrubs. Leaves opposite. Corolla hypocrateriform or more or less urceolate, without corona; lobes overlapping to the left. Stamens inserted mostly above the middle of the corolla tube. Ovary usually halfway 1- and halfway 2-celled. Fruit a berry, mostly with many seeds. Seed with thick horny endosperm.

1.4. Subtribe Willughbeiinae A. DC., op. cit. 318, partly, as for Willughbeia.

Unarmed woody climbers with large curled terminal tendrils. Leaves opposite. Corolla hypocrateriform or urceolate, without corona; lobes overlapping to the left. Stamens inserted mostly in the lower half of the corolla tube. Ovary 1-celled, with 2 parietal placentas. Seed with thin flimsy endosperm.


Type genus: Leuconotis Jack

Unarmed woody climbers without tendrils. Leaves opposite. Flowers only in Leuconotis 4-merous. Corolla hypocrateriform to almost saucer-shaped, without corona. Stamens inserted at or below the middle of the corolla tube. Ovary 1- or 2-celled. Fruit a many-seeded berry. Seeds with or without endosperm.

1.6. Subtribe Pleiocarpinae (K. Schum.) Pichon, op. cit. 158. Basionym: Pleiocarpaceae K. Schum., op. cit. 133 (as tribe), the latter partly, as for Pleiocarpa.

Unarmed shrubs or small trees. Leaves opposite. Corolla hypocrateriform, without corona. Stamens inserted above the middle of the corolla tube. Ovary of two or more separate carpels. Fruit of two or more indehiscent fleshy mericarps. Seed with endosperm.

Wageningen Agric. Univ. Papers 94-3 (1994)
1.7. Subtribe Lacmelliinae Pichon, op. cit. 133, with French description; ex Leeuwenberg, subtribus nova.


Type genus: Lacmellea Karst.

Trees or shrubs, sometimes armed with thick prickles on trunk and/or thick branches. Leaves opposite. Corolla hypocrateriform, without corona; lobes overlapping to the left. Stamens inserted just below the corolla mouth and included. Ovary 2-celled. Fruit a berry, mostly with few, often only one seed. Seed with endosperm.

1.8. Subtribe Couminae Pichon, op. cit. 123, with French description; ex Leeuwenberg, subtribus nova.


Type genus: Couma Aubl.

Unarmed trees or shrubs. Leaves whorled or opposite. Corolla without corona; tube cylindrical; lobes overlapping to the left. Stamens inserted around the middle of the corolla tube, included. Ovary 1-celled with 2 parietal placentas fused at the apex. Fruit a many-seeded berry. Seed with endosperm.


Type genus: Chilocarpus Bl.

Lianas without tendrils. Leaves opposite. Corolla without corona; tube cylindrical; lobes overlapping to the left. Stamens included. Ovary syncarpous, 2-celled. Fruit berry-like, variously shaped, bivalved. Seed with deep hilar groove, ruminate endosperm and aril.


Unarmed trees. Leaves opposite. Corolla hypocrateriform; lobes overlapping to the left. Stamens inserted at about one quarter from the base of the corolla tube. Ovary of 2 separate carpels. Fruit of 2 fleshy subglobose dehiscent mericarps with many seeds, often only one of them developing. Seed without aril, without hilar groove; endosperm not ruminate.

5. Tribe Tabernaemontaneae G. Don, Gen. Syst. 4: 70, 87. 1837, partly excl. Cameraria, Vahea (= Landolphia), Plumeria, Vinca and Catharanthus.

Shrubs or trees, repeatedly dichotomously branched with two inflorescences.
(one of which is often absent) in the forks. Especially in American species one of the branches may be missing as well; this is never the case for the entire plant. Only Calocrater is seemingly unbranched, as in almost all cases each branch bears one branchlet with a single pair of leaves and one inflorescence at the apex. Leaves opposite. Corolla without corona; tube cylindrical or nearly so; lobes mostly overlapping to the left. Stamens included or exserted; anthers mostly acuminate or mucronate at the apex, with 2 fertile tails or cordate at the base. Ovary of two separate or sometimes fused carpels, in the latter case mostly halfway 1- and halfway 2-celled. Fruit mostly of two separate, usually fleshy generally dehiscent mericarps. Aril present. Seed with a deep hilar groove and ruminate endosperm.


Mostly woody plants. Leaves opposite, verticillate or sometimes alternate. Corolla mostly without corona (present only in Vinca); tube cylindrical or infundibuliform; lobes mostly overlapping to the left. Stamens included; anthers often sterile at the apex, mostly subcordate at the base. Ovary of two separate carpels. Fruit mostly dry and follicular (baccate only in Geissospermum). Seeds usually winged, sometimes with coma.


Woody plants. Leaves opposite, alternate or verticillate. Corolla tube cylindrical or nearly so; lobes overlapping to the left. Stamens included. Ovary of 2 separate carpels. Fruit of 2 separate mericarps; mericarps mostly dry and then seeds flat and winged. Seed not winged only in Geissospermum; endosperm thin, not ruminate.

6.2. Subtribe Craspidospermatinae A. DC., op. cit. 323 (as Craspidospermeae).

Woody plants. Leaves opposite or verticillate. Corolla tube cylindrical or nearly so; lobes overlapping to the left. Stamens included. Ovary 2-celled or of 2 separate carpels. Fruit a bivalved capsule or of 2 dry follicles. Seed flat, winged; endosperm mostly thin, not ruminate.

6.3. Subtribe Plumeriinae Pichon, op. cit. 207, with French description; ex Leeuwenberg, subtribus nova.

Shrubs or trees. Leaves alternate. Corolla salverform or infundibuliform; lobes overlapping to the left. Stamens deeply included, inserted low down in the corolla tube. Ovary of 2 separate carpels. Fruit of 2 dry follicles basally united, robust, not yet known of Mortoniella. Seeds winged; endosperm thin, not ruminate.

6.4. Subtribe Alstoniinae (G. Don) K. Schum., op. cit. 135, partly, as for Alstonia. Basionym: Alstoniaceae G. Don, op. cit. 70, 86, as tribe.

Trees or shrubs. Leaves whorled or opposite. Corolla hypocrateriform; lobes overlapping to the left or to the right. Stamens included. Ovary of 2 separate carpels. Fruit of 2 long basally usually united follicles. Seed with 2 comas, one at
the apex and one at the base, ciliate all around or winged; endosperm rather thin, not or slightly ruminate.


Herbs or undershrubs. Leaves opposite, alternate or subverticillate. Corolla hypocrateriform, only in Vinca with corona; lobes overlapping to the left. Stamens inserted at or above the middle of the corolla tube, mostly barely included. Ovary of 2 separate mericarps. Fruit of 2 dry follicles, dehiscent with an adaxial slit. Seed winged or not; endosperm ruminate only in Rhazya.

7. Tribe Alyxieae G. Don, op. cit. 70, 96.

Woody plants. Leaves opposite, whorled or sometimes alternate. Corolla with mostly cylindrical tube, without corona; lobes overlapping to the left or to the right. Stamens included or exserted. Ovary of 2, less often 3-5 separate or partly fused carpels. Fruit drupaceous. Seed mostly flat, with endosperm.

7.1 Subtribe Condylocarpinae Pichon, op. cit. 173, with French description; ex Leeuwenberg, subtribus nova.


Type genus: Condylocarpon Desf.


Shrubs or trees. Leaves whorled or opposite. Corolla often slightly zygomorphic; lobes overlapping to the left. Stamens inserted in the upper half of the corolla tube, mostly included. Ovary of 2 separate carpels. Fruit of 2 drupaceous mericarps, one of which often not developing, sometimes partly fused or moniliform and each mericarp containing several drupes; mesocarp fleshy. Seed flat, without hilar groove; endosperm not ruminate.

7.3. Subtribe Alyxiinae Pichon, op. cit. 164, with French description; ex Leeuwenberg, subtribus nova.


Type genus: Alyxia Banks ex R.Br.

Woody plants. Leaves whorled, opposite or alternate. Corolla hypocrateriform; lobes overlapping to the left or to the right. Stamens inserted at or above the middle of the corolla tube, included. Ovary of 2-5 free or partly united carpels. Fruit apocarpous and of 2 mericarps containing a single drupe or moniliform and containing several drupes, or of 3-5 completely or almost completely fused carpels each containing 0-1 drupes; mesocarp fleshy, or fibrous, in Lepinia each mericarp has an
elongate stipe; the 3-5 mericarps united at the apex. Seeds not winged, with a deep hilar groove; endosperm ruminate.

7.4. Subtribe Kopsiinae (G. Don) Leeuwenberg, stat. nov. Basionym: Kopsieae G. Don, op. cit. 70, 100, as tribe, partly, excl. of Ochrosia and Calpicarpum (lectotypified by Boiteau, Adansonia sér. 2. 14: 495. 1974, with C. oppositifolium (Lam.) Boiteau (= Ochrosia oppositifolia (Lam.) K. Schum.)).

Shrubs or trees. Leaves opposite or alternate. Corolla hypocrateriform; lobes overlapping to the left or to the right. Stamens inserted in the upper half of the corolla tube, included. Ovary of 2 separate carpels. Fruit of 2 separate mericarps, often only one of which developing, 1-2-seeded; mesocarp fibrous. Seed not or slightly flattened, not winged, without hilar groove; endosperm absent.

7.5. Subtribe Ochrosiinae Pichon, op. cit. 169, with French description; ex Boiteau, l.c.

Trees or shrubs. Leaves whorled or opposite. Corolla tube cylindrical or nearly so; lobes overlapping to the right. Stamens inserted at or above the middle of the corolla tube. Ovary of 2 mostly free carpels. Fruit of 2 mostly free subglobose or ovoid mericarps; mesocarp fibrous. Seed winged or nearly so, without hilar groove; endosperm not ruminate.

8. Tribe Cerbereae (Benth. & Hook. f.) Leeuwenberg, stat. nov. Basionym: Cerberinae Benth. & Hook. f., op. cit. 685 (as subtribe Cerbereae), partly as for Thevetia, Cerbera, Cameraria and Skytanthus.

Woody plants. Leaves alternate or opposite. Corolla hypocrateriform or infundibuliform, with or without 5 small corona lobes; corolla lobes overlapping to the left. Stamens included; anthers sterile at the apex. Ovary of 2 separate carpels. Fruit of 2 separate or sometimes connate mericarps; mericarps subglobose or rhomboid drupes with fibrous or fleshy mesocarp, samaroid or follicular. Seed flat, shortly winged or nearly so; endosperm not ruminate, thin in samaroid fruits.

9. Tribe Allamandeae G. Don, op. cit. 71, 102 (as Allamandieae).

Shrubs, trees or climbers. Leaves verticillate, opposite or near inflorescences sometimes alternate. Corolla infundibuliform, with small corona lobes; corolla lobes overlapping to the left. Stamens deeply included; anthers triangular, sagittate at the base, coherent with the pistil head. Ovary 1-celled, with 2 parietal placentas. Fruit a subglobose or ellipsoid bivalved capsule, mostly with prickles, many-seeded. Seed flat, obovate or suborbicular, winged all around; endosperm rather thin, not ruminate, sometimes absent.

Apocynoideae

10. Tribe Echiteae G. Don, op. cit. 69, 72, partly, as for Echites, Chonemorpha, Aganosma, Pachypodium, Parsonsia, Helygia (= Parsonsia), Lyonsia (= Parsonsia), Thenardia, Prestonia and Haemodictyon (= Prestonia).

Woody or herbaceous plants. Leaves opposite or sometimes alternate. Corolla hypocrateriform or infundibuliform, sometimes with small corona lobes; corolla lobes overlapping to the right. Stamens included or exserted. Ovary of 2 separate or less often united carpels. Fruit of two separate or less often united mericarps, follicular. Seed narrow, with a terminal coma; endosperm thin, not ruminate.
10.1. Subtribe **Echitinae** Benth. & Hook. f., op. cit. 688 (as *Euechitideae*), partly, as for *Stipecoma, Echites, Laseguea* (= *Mandevilla*), *Rhodocalyx, Macrosiphonia, Dipladenia* (= *Mandevilla*), *Mandevilla, Rhabdadena, Urechites* (= *Pentalinon*), *Cycladenia* and *Elytropus*.

Woody climbers, shrubs or tuber-bearing herbs. Leaves opposite. Corolla hypocrateriform or infundibuliform, mostly with a narrow basal part and widened at or near the insertion of the stamens, sometimes with a corona. Stamens usually deeply included. Ovary of 2 separate carpels. Fruit of 2 mostly slender follicles. Seed with coma.

10.2. Subtribe **Parsonsiinae** (A. DC.) Benth. & Hook. f., op. cit. 687 (as *Parsonsieae*, partly, as for *Lyonsia* (= *Parsonsia*), *Parsonsia, Pottsia* and *Isonema*. Basionym: *Parsonieae* A. DC., op. cit. 399, as tribe, partly as for *Parsonsia*.

Woody climbers. Leaves opposite. Corolla tube mostly short, cylindrical or nearly so; lobes overlapping to the right or in *Parsonsia* valvate. Stamens usually clearly exserted and with long filaments. Ovary of 2 separate or united carpels. Follicles separate or united. Seed with coma.


Succulent trees or shrubs, cactus-like, armed with straight spines in groups of 2 or 3. Leaves alternate. Corolla hypocrateriform, less often campanulate or infundibuliform, without corona; lobes overlapping to the right. Stamens included or exserted. Ovary of 2 separate carpels. Fruit of 2 separate often robust follicles. Seed flattened, with an apical coma; endosperm thin.


Unarmed woody plants. Leaves opposite, verticillate or sometimes alternate. Corolla variously shaped, with or without corona; lobes overlapping to the right or to the left. Stamens included or exserted. Ovary of 2 separate or united carpels. Fruit follicular, dry. Seed usually with an apical coma; endosperm not ruminate.


Shrubs or trees, often succulent. Leaves verticillate or alternate. Corolla infundibuliform or hypocrateriform, with a corona; lobes overlapping to the right. Stamens mostly barely included; anthers with long apical bristly appendages. Ovary of 2 separate or united carpels. Fruit follicular. Seed flat, with 1 or 2 comas.

11.2. Subtribe **Wrightiinae** Pichon, op. cit. 72, with French description; ex Leeuwenberg, *subtribus nova*.


Type genus: *Wrightia* R.Br.

Woody plants. Leaves opposite or verticillate. Corolla variously shaped, with or
without corona; lobes overlapping to the right or to the left. Stamens included or exserted. Ovary of 2 separate or united carpels. Follicles free or completely or partly united, not known of *Tintanabularia*. Seed narrow, often rostrate, with an apical and sometimes also deciduous basal coma.


Woody plants. Leaves opposite. Corolla hypocrateriform or nearly so, with or without a small corona; lobes overlapping to the right. Stamens included or exserted. Ovary of 2 separate carpels. Fruit of 2 follicles, usually connate at the base, unknown of *Vallariopsis*. Seed narrow, with an apical coma, absent only in *Allowoodsonia* and most species of *Malouetia*; endosperm often thin.

11.4. Subtribe *Alafiinae* Pichon, op. cit. 67, with French description; ex Leeuwenberg, *subtribus nova*.


Type genus: *Alafia* Thou.

Woody plants. Leaves opposite. Corolla hypocrateriform, without corona; lobes overlapping to the right. Stamens included; anthers almost entirely or only near the apex fertile. Ovary of 2 separate or sometimes united carpels. Follicles mostly connate only at the base. Seed narrow, with an apical coma, in *Farquharia* also a basal coma; endosperm often thin.


Type genus: *Apocynum* L.

Unarmed woody climbers, shrubs, herbs or undershrubs. Leaves opposite or sometimes verticillate or alternate. Corolla variously shaped, with or without corona; lobes mostly overlapping to the right. Ovary of 2 separate or less often connate carpels. Fruit of 2 dry follicles, free or connate. Seed with apical coma; endosperm not ruminated.

12.1. Subtribe *Apocynininae* Pichon, op. cit. 94, with French description; ex Leeuwenberg, *subtribus nova*.


Type genus: *Apocynum* L.

Herbs or undershrubs. Leaves opposite or alternate. Corolla campanulate, without corona; lobes overlapping to the right. Stamens inserted near the corolla base, included or exserted. Ovary of 2 separate carpels. Follicles slender, cylindrical. Seed ellipsoid or nearly so.


Lianas or shrubs. Leaves opposite or sometimes verticillate. Corolla with or
without corona; tube cylindrical, infundibuliform or urceolate; lobes overlapping to the right or sometimes (in Parameria and Parepigynum) to the left. Stamens included or exserted. Ovary of 2 separate or sometimes connate carpels. Seed narrow.

Important references


Pollination of Apocynaceae

P. Albers & L.J.G. van der Maesen

Department of Plant Taxonomy, Wageningen Agricultural University,
P.O. Box 8010, 6700 ED Wageningen, the Netherlands
Abstract

Pollination of a number of Apocynaceae species was studied by fluorescence microscopy of alcohol specimens mainly from Africa and Indonesia, showing growth of pollen tubes or absence thereof, and by field observations in Ivory Coast. The receptive surface of the pistil is predictable from its morphology. The flowers are visited by many insects and nectar-stealing birds, that do not pollinate; pollination is carried out by insects with long mouth parts, such as butterflies, bees, bumble bees and perhaps some wasps. Insect species have been determined up to family or species.

Introduction

Because of the very particular morphology of the flowers, pollination in Apocynaceae has often been questioned (Allorge, 1976). Nevertheless relatively little is known about plant-pollinator relations in this plant family. Vogel (1954), in his study on South American Flora, showed that flowers can be distinguished as ‘butterfly-flowers’, ‘bee-flowers’ etc. on the basis of general morphology, colour, and symmetry. The shape of flowers provides useful information about pollinators, and allows prudent speculations about these agents, but as a single character flower shape does not tell us anything about the mutual adaptation of plant and fauna, and the importance of visitors of flowers with regard to pollination and fertilization. The most important source of information remains detailed observation of visiting fauna, e.g. insects, on flowers (Faegri & van der Pijl, 1979). This kind of research is time consuming, needs patience and hence field observations are hardly available (Rowley, 1980).

Not every visitor of flowers necessarily induces pollination, and not every pollination leads to fertilization; self-incompatibility is common in Apocynaceae (Rowley, 1980). The flower shape of Apocynaceae is indicative for the pollination mechanism, and one could select certain insects as potential pollinators. Waddington (1976) observed many insects on Apocynum sibiricum, but only butterflies were potential pollinators. In Nerium oleander small insects, such as Cochliomyia hominivorax and C. macellaria (Diptera-Oestridae) were captured by the flower, but these did not play a role in pollination (Broce & Ideker, 1978). Of course suppositions are prone to mistakes: some flower visitors may erroneously be disregarded as pollinators, for instance because they do not belong to the usual group of pollinators, or because their size is too small (Faegri & van der Pijl, 1979).

Self-pollination is rare in Apocynaceae. Wrightia tinctoria has completely hermaphroditic flowers, honey bees (Apis spp.) induce pollination without touching pollen or stigma (Reddi et al., 1979). Kessel & Shih (1974; in Allorge, 1976) report autogamy in Catharanthus roseus. Allorge (1976) observed germination of pollen tubes after artificial pollination on the top of the clavuncula (we prefer the term
pistil head) at the level of the stigmoidal apex, and supposes a natural form of self-pollination. Often self-pollination has been considered as the most likely mechanism, because the anthers burst open introrsely, and the pollen reaches the top of the pistil head (Miers, 1878; in Allorge, 1976). However, if the top of the pistil head is not receptive, the pollen will not germinate there. Moreover, pollen tubes penetrating in receptive surfaces may be halted by callose plugs in the style, and self-fertilization may no longer be obvious.

As well as in Catharanthus roseus, Allorge also observed germination of pollen near the stigmoidal apex in species of Ochrosia, Melodinus and Nerium. She cautiously concluded, that the real stigmatic surface is positioned near the stigmoidal apex (appendices clavonculaires). This conclusion is based on few data, and information on the experiments is lacking. Schick (1982) opposes this conclusion on the basis of some more data.

The pollination mechanism has been described a few times, particularly in Nerium oleander L. (Pagen, 1987). If the flower morphology of other genera is similar to Nerium, the pollination mechanism may also be supposed to be similar (see Rowley, 1980, for Adenium).

Flower morphology in Apocynaceae has been described in detail, taking into account taxonomy and floral biology (Allorge, 1976): the differences between flowers of Plumeroideae and Tabernaemontanoideae are considered so fundamental, that the latter taxon can stand as a subfamily rather than as a tribe (Tabernaemontaneae) in Plumeroideae. Plumeroideae are usually autogamous, and rarely need specialized insects to stimulate pollination, while Tabernaemontanoideae are exclusively allogamous and entomogamous. This conclusion is mainly based on floral morphology: few field observations can back these differences.

Schick (1980, 1982) distinguishes two types of Apocynaceae pistil-heads: the Plumeria-type and the Allamanda-Nerium-type (Fig. 1). The Plumeria-type pistil-head is conical and little developed, the Allamanda-Nerium-type is more advanced; and has the following parts: stigmoid apex, upper whorl of hairs, cylindric part, lower whorl of hairs, and basal stigma. In the genus Tabernaemontana both types are observed, e.g. the Plumeria-type is found in Tabernaemontana sphaerocarpa and T. pandacaqui, and the Allamanda-Nerium type in T. crassa and T. pachysiphon (see Leeuwenberg 1991).

Schick also observed pollination of Vinca minor by Apis mellifera (as mellifica). The results of earlier research do not give an unambiguous picture of pollination in Apocynaceae, often it is not clear whether autogamy or allogamy is the case. For both flower types the stigmatic surface is indicated, but even this is not unambiguous. Schick (1982) continues in describing five more detailed pistil head types, but we prefer to maintain the two general shapes in the description of the observed species.

Artificial pollination over the entire pistil head can show where pollen germi-
Fig. 1. Apocynaceae pistil heads according to Schick (1980, 1982), adapted from the original figure. A. Plumeria-type; B. Allamanda-Nerium-type. O - receptive surface; • - tissue producing adhesive matter.

nates, but evades the influence of the pollination mechanism: it may not have biological significance.

The purpose of this study was to gain more insight in the pollination of Apocynaceae. At first the growth of pollen tubes in flowers pollinated under natural conditions was observed. For this purpose flowers, collected from nature, fixed in FAA and preserved in alcohol, were used. Next, observations were carried out in nature, to obtain an inventory of (insect) species visiting Apocynaceae flowers that can be indicated as potential pollinators. Hopefully this may be followed by more entomological research.

Material and methods

Localization of the receptive surface

In order to localize the receptive tissue several species of Apocynaceae were observed. Flowers of the spirit collections of the Herbarium Vadense (Dept. of Plant Taxonomy, Wageningen Agricultural University) were used, as well as live material from the tropical glasshouse and the Botanical Gardens of Wageningen (Table
Table 1. Species of Apocynaceae studied for germination of pollen tubes. Spirit material of various collections of the Herbarium Vadense (WAG). 1-5 preparations per species.

<table>
<thead>
<tr>
<th>Species</th>
<th>Collnr</th>
<th>Origin</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alafia lucida*</td>
<td>Leeuwenb.8650</td>
<td>Cameroun</td>
</tr>
<tr>
<td>Alafia multiflora*</td>
<td>de Koning 6225</td>
<td>Ivory Coast</td>
</tr>
<tr>
<td>Alstonia boonei</td>
<td>de Wit 2352</td>
<td>Nigeria</td>
</tr>
<tr>
<td>-do-</td>
<td>Leeuwenb.11602</td>
<td>Ghana</td>
</tr>
<tr>
<td>-do-</td>
<td>Albers 18</td>
<td>Ivory Coast</td>
</tr>
<tr>
<td>Amsonia orientalis</td>
<td>Leeuwenb.12125</td>
<td>Ivory Coast</td>
</tr>
<tr>
<td>-do-</td>
<td>Albers 30</td>
<td>Ivory Coast</td>
</tr>
<tr>
<td>Catharanthus roseus</td>
<td>Leeuwenb.12125</td>
<td>Ivory Coast</td>
</tr>
<tr>
<td>-do-</td>
<td>Albers 30</td>
<td>Ivory Coast</td>
</tr>
<tr>
<td>C. trichophyllus*</td>
<td>Zwetsloot 5</td>
<td>Greenhouse</td>
</tr>
<tr>
<td>Funtumia africana*</td>
<td>Beentje 276</td>
<td>Ivory Coast</td>
</tr>
<tr>
<td>Isonema smeathmannii*</td>
<td>de Kruif 787</td>
<td>Ivory Coast</td>
</tr>
<tr>
<td>Mascarenhasia arborescens*</td>
<td>de Koning 4796</td>
<td>Ivory Coast</td>
</tr>
<tr>
<td>Oncinotis glabrata*</td>
<td>Barrink 68</td>
<td>Greenhouse</td>
</tr>
<tr>
<td>Oncinotis pontyi*</td>
<td>Leeuwenb.11952</td>
<td>Ivory Coast</td>
</tr>
<tr>
<td>Pleioceras barteri*</td>
<td>Leeuwenb.11907</td>
<td>Ivory Coast</td>
</tr>
<tr>
<td>Rauvolfia mombasiana*</td>
<td>Leeuwenb.13853</td>
<td>Ivory Coast</td>
</tr>
<tr>
<td>Strophanthus hispidus</td>
<td>Leeuwenb.13255</td>
<td>Indonesia</td>
</tr>
<tr>
<td>-do-</td>
<td>Leeuwenb.13853</td>
<td>Indonesia</td>
</tr>
<tr>
<td>Strophanthus sarmentosus</td>
<td>Leeuwenb.13255</td>
<td>Indonesia</td>
</tr>
<tr>
<td>Tabernaemontana undulata*</td>
<td>Fe 9929</td>
<td>French Guyana</td>
</tr>
<tr>
<td>Vinca minor</td>
<td>Leeuwenb.9472</td>
<td>Bot. Gdn WAG</td>
</tr>
<tr>
<td>Voacanga africana</td>
<td>vdMaesen 5980</td>
<td>Cameroun</td>
</tr>
<tr>
<td>Voacanga grandifolia*</td>
<td></td>
<td>Indonesia</td>
</tr>
</tbody>
</table>

*) Species not referred to in the text; did not show pollen or germination of pollen in the inspected flowers.

1). All but the glasshouse flowers were considered to be pollinated in a natural way, if at all. No hand pollination was carried out.

To observe the pollen tubes a squash technique was combined with anilin staining:
- fresh material was rinsed in water and ethanol 70%
- flowers were kept 1 hr in 1 N NaOH at 60°C
- rinsed with water
- anilin stained for 45-60 min. (7 g K3PO4·3H2O + 2 g anilin per l)
- pistil heads were put on an object slide in a drop of glycerin and squashed under a cover plate. The preparations were observed with a Zeiss Standard WL microscope with UV light (Pagen, 1987).

Callose present in the walls of the pollen tubes and absent in the surrounding tissue, takes up anilin selectively. UV light distinguishes the pollen tubes, as anilin

Wageningen Agric. Univ. Papers 94-3 (1994)
fluoresces, from the style tissue. The locations where pollen germinates successfully, and the tubes penetrate the style, are considered receptive in nature too. Only in a few cases the pollen tubes could be followed into the ovaries or ovules. In this study the resulting fertilization has not been considered, as it is depending on more factors than germination of pollen tubes alone. The results are recorded in photographs, illustrations and descriptions of those cases where pollen germination was successful.

Pollination and insect visitors of flowers

An initial inventory of the potential pollinators was carried out in Ivory Coast between 30 November, 1989, and 30 January, 1990. The Medicinal Plants Garden of the I.I.R.S.D.A. (Institut International de Recherche Scientifique de Adiopodoumé), the former O.R.S.T.O.M., 17 km W of Abidjan, provided many fully-grown Apocynaceae for observation. Other plants of the family are scattered over the campus. Some data originate from plants in the Wageningen Botanic Gardens.

Insects visiting flowers were caught to enable identification and later verification. The activity of the insects and the size of their mouth parts were decisive to establish a role in pollination. The insect specimens are conserved in the Museum of the Department of Entomology, Wageningen Agricultural University. Voucher specimens of the plants are deposited in the Herbarium Vadense. Some flowers were covered in bud stage to check autogamy.

Results

Allamanda cathartica (PA 36)

Ornamental, introduced from America. Flowering throughout the year, planted around IIRSDA. Visitors: none observed in Ivory Coast.

Alstonia boonei (PA 18, 31)

Tall tree, scattered over the IIRSDA campus, flowering short periods late November-early December when trees are fully grown, fruiting from December onwards.

Receptive surface: in the extant alcohol collection only incomplete germination of pollen was observed in the upper corona. Later, in the Ivory Coast flowers were actively pollinated particularly by honey bees (Apis mellifera). The preparations show the receptive surface (Fig. 2). The pistil head is differentiated towards the Allamanda-Nerium-type, and has a similar receptive surface.
Visitors: *Apis mellifera* (PA 11, 12, 15). Take-up of honey was clearly observed. Solitary bees (Apidae, PA 17) are probably also pollinators, pollen was present on the mouth parts, which are similar to those of the honey bee. Butterflies also qualify as pollinators, but could not be captured because of the great height of the trees. Only *Hypolimnas missipus* (Nymphalidae, PA 41) could be determined as a pollinator through photography and capture in a trap.

Further observations: Eumenidae (Vespoidea, PA 10); *Acraea circeis* (Lepidoptera, PA 16); Lycidae (Coleoptera, PA 18).

**Amsonia orientalis** (= *Rhazyra orientalis*) & **A. angustifolia**

Flowering May, June, July in the Wageningen Arboretum.

Despite the large number of developed fruits none of the observed and stained pistils appeared pollinated. The pistil head is quite far differentiated and of the Al-lamanda-Nerium-type.

Visitors include bumble bees (*Bombus terrestris*, Hymenoptera, Apoidea) on *Amsonia orientalis*. A few inflorescences of both species were covered with mosquito-netting cloth bags to check autogamy: none of the flowers produced fruits as compared to about 80% in the controls.

**Catharanthus roseus** (= *Vinca rosea*) (PA 20, 30)

Ornamental, distributed all over the tropics, originally from Madagascar. Planted on IIRSDA campus. Herb or undershrub with white or pink flowers, in leaf axils.
Fruits as long as the leaves, ca 3 cm. Flowering throughout the year. Observed population flowering and fruiting November through January.

Receptive surface: See Photo 1. The whorl of hairs obscures the germinating pollen. Pollen seems to germinate also between the hairs of the lower whorl. Despite malformation due to the squash technique the pollen tubes in the style clearly originate from the area immediately below the whorl of hair where a large amount of pollen is present. This agrees with a receptive surface as detailed in Fig. 1 and 3.

A large portion of the pollen tubes has not advanced, as can be seen by callose plugs. Many tubes, however, reach the ovary and the ovules, as is visible on Photo 2.

Visitors: the Lepidoptera *Papilio demodocus*, Papilionidae (not caught), *Acraea egina*, Nymphalidae (PA 20), and various Pieridae. Other insects occurring on *C. roseus* included many orders, e.g. Hymenoptera: *Anthrosephalus sp.*. *Brachymeria sp.* (Chalcididae), 2 Pteromalidae spp., an Eurytomidae sp., 2 Apidae spp., and 5 Typhlidae (Myziniinae) spp., 4 Heteroptera, 1 Homoptera, 36 Diptera and 7 Coleoptera specimens.

Pollination was not observed, nevertheless fruits set for 100%. The flower of *C. roseus* has a very long corolla tube, which may be inaccessible for many insects; in any case it seems unlikely that any of the insect species caught on the plants acts as pollinator.

Six flowering branches in the bud stage were covered with mosquito netting to check the effect of possible nocturnal pollination. Open flowers were removed, the
covers were left for 3 weeks. Except for a plant in poorer condition all flowers (12, 12, 5 and 6 respectively) set fruit, and no difference with non-covered plants was seen.
**Hunteria eburnea** (PA 21, 29)

Small tree, ca 5 m with small flowers of 1 cm diameter. Planted in Medicinal Garden, IIRSDA. Flowering from November to April. Indigenous in Ivory Coast.

Receptive surface: no alcohol material available, not collected in Ivory Coast because of the low fertilization percentage and complete absence of pollinating insects. The chance of finding pollinated pistils appears very small in Ivory Coast.

Visitors: no visiting insects were observed.

**Strophanthus gratus** (PA 25)

Liana, to 3 m high with large purplish pink flowers. Flowering in January and February. The observed plants did not produce fruits. The ovaries were deformed considerably. Planted in Medicinal Garden, IIRSDA. Origin Ivory Coast, indigenous in Tropical Africa.

Visitors: *S. gratus* did not attract flying insects, but in the flowers often beetles of the Nitidulidae (PA 34) were found, often in considerable numbers.

**Strophanthus hispidus** (PA 23, 24)

Liana, to 3 m, planted in the IIRSDA Medicinal Garden, growing on trellis. Indigenous in Ivory Coast.

Flowering in January, fruiting from January onwards.

Receptive surface: none of the spirit samples contained pollen.

Visitors: *Ypthima cf. asterope*, Nymphalidae (PA 14, 32), *Planema camerunica*, Nymphalidae (PA 31) and *Acraea pentapolis* (PA 30) were caught on the flowers while *Acraea sp. (A. egina?)* was observed, but none of these Lepidoptera acted as pollinators: their tongues did not enter the corolla tube.

Two Hymenoptera, a Scolidae (PA 27) and an Apidae (solitary bee, PA 28) were acting as pollinators, other hymenopterous visitors were determined as Vespoidae (PA 29, 33).

**Tabernaemontana pandacaqui**

Pistil heads of *Tabernaemontana pandacaqui* vary in shape, mainly due to differences in hairiness. During anthesis a lower and an upper whorl of hairs can be distinguished. Later, when the corolla is shed (the style remains), the whorls of hair can remain less clear, while appreciable individual differences exist between flowers. When both whorls are present, the pistil head may appear developed toward
the Allamanda-Nerium type; nevertheless the preparations clearly show that pollen can germinate on the entire surface of the pistil head (Plumeria-type). The stigmatical apex is free of pollen (Photo 3, Fig. 4).
**Tabernaemontana sphaerocarpa**

Receptive surface: the pistil head is entirely covered with hairs but no separate whorls of long hairs can be seen (Fig. 5): the Plumeria-type. Germination of pollen takes place on the entire surface of the cylindric part of the pistil head, the apex remains free of pollen (Photo 6). The growth of the pollen tubes is abundant, many reach the ovary (Photo 5). The receptive surface hence conforms with the Plumeria-type.

*Fig. 5. Tabernaemontana panda-cacqui pistil head and schematical representation of pollen germination (only shown for one side of pistil head).*
Vinca minor

Receptive surface: the pistil head conforms to the Allamanda-Nerium-type (Fig. 6). Germination of pollen and penetration of the pollen tubes is localised below the lower hair ray. Pollen that reaches the lower hair ray itself often germinates, but
Visitors: Darwin (in Schick 1982) and Schick (1982) reported that honey bees (\textit{Apis} spp.) pollinate the flowers. Observations in the Wageningen Arboretum could not corroborate these reports.

\textit{Wageningen Agric. Univ. Papers 94-3 (1994)}
Fig. 6. *Vinca minor*, pollen germinated just below the lower hair whorl on the stigmatic surface.

Photo 8. *Vinca minor* pollen tube penetrating ovules in ovary.
Voacanga africana (PA 52)

Small tree, ca 5 m, planted in the Medicinal Garden of the IIRSDA. Flowering from January to June.

Receptive surface: the preparations obscured the pistil heads, and despite the presence of pollen, the receptive surface could not be discerned. The tissue darkened under influence of the NaOH used. The pistil head is of the Allamanda-Nerium type.

Visitors: the birds Nectarinia cuprea and N. chloropygia, and possibly a third
species, *N. coccinigaster*, regularly visited the flowers obviously to extract nectar. The birds do not seem to act as pollinators, as they steal the nectar and damage the flowers. Two potential pollinating Lepidoptera are *Apphocalcia iphis* (Hesperiidae, PA 40) and *Hypolimnas missippus* (Nymphalidae, PA 41).

**Discussion**

*Receptive surface of pistil heads*

The morphology of the apocynaceous pistil heads predicts quite well the location of the receptive surface, as the observations show. The Plumeria and the Alamannda-Nerium type suffice to classify the studied, mainly West-African species, possibly a more detailed grouping is needed when more species are investigated.

**Pollinators**

Pistil head morphology also predicts quite well the type of pollinator. Especially for *Alstonia boonei* and *Amsonia orientalis* the length of the mouth parts of the visiting insects agrees well with the length of the corolla tube. Both trees are frequently visited, and *Amsonia orientalis* fertilization is very successful, ca 80% of the flowers produces a fruit.

Insects of many orders visit Apocynaceae flowers. Some have no role in pollination, as they are not adapted to exploit nectar or pollen offered by the flowers. The observed Heteroptera, Diptera and Coleoptera belong to this group of insects.

**Heteroptera**

Predatory insects, such as bugs on *Catharanthus roseus* may (accidentally) be present to prey on other visiting insects.

**Diptera**

Flies are attracted by other food sources on the plants or are accidental visitors. Their morphology makes pollination unlikely, and the broad spectrum of their food sources excludes an important role in pollination. Flies have not been observed in the flowers, but always on the plants, and near or on the inflorescences of e.g. *Vocalanga africana*. Flowers of *V. africana* produce a sickly odour.

**Coleoptera**

Beetles were observed on *Catharanthus roseus*, *Alstonia boonei* and in the flowers of *Strophantus gratus*. In *S. gratus* flowers many Nitidulidae beetles live on tissue, nectar and pollen, but the abnormal development of the fruits shows the negative results of their activity (Richards & Davies, 1977; Grassé, 1949). A role
as pollinator appears absent. The Nitidulidae were restricted to *S. gratus*, no other Apocynaceae nearby carried these beetles, so they are very specific to their host.

**Hymenoptera, Vespoida**

Wasps generally are unreliable pollinators, just as flies (Faegri & van der Pijl, 1979). Their food mainly consists of animal protein. Some Vespoid wasps have been observed on *Strophanthus hispidus*, they penetrated the flowers, their behaviour coincided with that of the usual pollinators, so these Vespoida are potential pollinators.

**Lepidoptera and Hymenoptera as pollinators**

As pollinators insects of these two orders are the most successful. In Apocynaceae the pollination mechanism, particularly of the species with more derived flower types, seems only to work if insects have adequate mouth parts or tongue and sufficient force to penetrate the flowers to obtain nectar (Schick, 1982; Pagen, 1987). Honey bees are important pollinators, as they have to forage for large colonies, and hence visit many flowers. Their ability to recognize flowers is strongly developed. Even though Apocynaceae flowers are not typical bee-flowers, which employ the hairy abdomen and legs of the bees, transfer of pollen can be effectuated through the mouth parts, which are hairy too. Pollen transfer in Apocynaceae will usually be restricted to transfer by mouth parts.

Honey bees and butterflies were observed in large numbers on *Alstonia boonei*. As most flowers were situated rather high, close observation was quite difficult, the insects caught therefore did not well represent the arthropod fauna on this tree. One solitary bee had pollen on its mouth parts, pollen was not seen on other insects, and further study is needed. The fruit set in *A. boonei* is low, as also observed in *Apocynum sibiricum* by Waddington (1976), apparently because of the low chance of pollen transfer with mouth parts, however, it is very likely that insects (especially butterflies) are pollinating agents.

Self-pollination is rare in Apocynaceae. *Wrightia tinctoria* (Reddi et al. 1979) is such an exception. *Catharanthus roseus* is autogamous too (Kessel & Shih, 1974; in Allorge, 1976; and Schick, 1980; these authors consider the entire pistil head to be receptive). The population in Adiopodoumé apparently needs no specific pollinators, as the bagging experiment also indicated. Squash preparations of flowers from Sassandra, Ivory Coast, point to insects as pollinating agents, as pollen clearly germinated on the stigma where only butterfly and moth tongues could have reached. Butterflies and moths are the most likely pollinators, as the long corolla tubes require long mouth parts. Also in Madagascar and Indonesia butterflies visited *Catharanthus* flowers (Leeuwenberg, pers. comm.) but spirit samples of these flowers did not contain germinated pollen, although fruit set was very high. Both allogamy and autogamy seem therefore possible in *C. roseus*. *Ansonia orientalis* and *A. angustifolia* basically show the same situation.

In *Ansonia orientalis* the bumble bee *Bombus terrestris* was very active. Cov-
ered inflorescences did not set fruit at all, insect pollinators are therefore very success­ful, and autogamy seems unlikely.

Birds

The honey birds (Nectarinidae) form the last group of animals observed on Apocynaceae species, in this case on *Voacanga africana*. The birds steal away the nectar before the insects visit later on the day (as also observed by e.g. Winkler, 1917). The nectar is removed with the bills penetrating the flower tubes from above. The flowers are damaged to some degree and a role in pollination seems unlikely. *Voacanga africana* does not have the typical features of a ‘bird flower’ as defined by Faegri & van der Pijl (1971): vivid colours, often scarlet with contrasting parrot colours, absence of odour, a deep tube or spur, wider than in butterfly flowers.

Conclusions

The hypotheses drawn from several earlier observations in literature could be confirmed. The following statements hold true for the studied species:

- The location of the receptive surface is predictable from the morphology of the pistil head, and agrees with one or the other of the two types recognized by Schick (1980).
- Apocynaceae flowers are visited by many insects from many orders, which do not necessarily play a role in pollination.
- Pollination is carried out by insects with long mouth parts, e.g. butterflies, bees, bumble bees and possibly some species of wasps.

The conclusions have to remain broad, as the observations were fragmentary due to limitations in time, locations and available species. Apocynaceae offer good opportunities to study insect-flower relations and their co-evolution. More widespread inventories are needed in the near future. So far the data present are too limited to generalize, but this study contributed to remedy part of our lack of knowledge of the pollination biology of Apocynaceae.

Acknowledgements

The first author is grateful to all persons who facilitated his research, carried out for his MSc. degree. Dr. A.J.M. Leeuwenberg guided the work, mr. J. van de Vooren taught him the use of the Fluorescence Microscope and the preparations of the slides, Ir. F. Vooren guided his stay in Ivory Coast. Mr. Y. Jongema, collection conservator, helped with the work at the Department of Entomology. The second author assisted with guidance, preparation of the report and the English version thereof.
Literature


