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Taxa of the Apocynaceae above the genus level

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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*

Plumerioideae	**Apocynoideae**
Aestivation usually to the left.	Aestivation usually to the right.
Anthers entirely fertile or only sterile at the acumen or mucro, mostly free from the pistil head	Anthers mostly fertile only near the apex, usually coherent with the pistil head.
Fruit baccate or capsular, syncarpous or apocarpous	Fruit capsular, mostly apocarpous, of two follicles. Seed generally with coma; endosperm present, not ruminate.
Seed generally without coma; endosperm sometimes absent, ruminate or not.	
Indole alkaloids often present	Glycosides often present.

Some exceptions are:

Aestivation to the right in several species of *Alstonia, Carissa* and *Tabernaemontana;* in *Callichilia subsessilis* and *Schizozygia coffeoides*	Aestivation to the left in *Pleioceras, Stephanostema* and *Wrightia.*
Anthers coherent with the pistil head in *Voacanga* and *Allamanda*	Anthers free from the pistil head and almost completely fertile in *Holarrhena,* and more or less free from the pistil head in *Nerium.*
Seeds with coma occur in *Alstonia.*	Seeds without coma only in *Malouetia* and *Allowoodsonia.*

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 *Cerbereae* 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 "rétinacle" (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 *Apocyneae* 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 *Willughbeiinae* have large curled terminal tendrils and display the model of Koriba, 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 *Landolphiinae*; and thin and flimsy in the *Willughbeiinae*. 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 *Landolphiinae*.

The second tribe in *Plumeroideae*, 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 *Ambelanieae*, 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* ususally have apocarpous, dehiscent, mostly fleshy fruits, but syncarpy 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-Alyxiinae*. 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

Alyxieae 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 *Cerbereae* and coherence between anthers and pistil head of *Voacanga (Tabernaemontaneae)*. The last mentioned character is the rule in the *Apocynoideae* 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 *Wrightieae* 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 *Parabarium*, *Chunechites* and *Xylinobariopsis* as synonyms of *Ecdysanthera* and of *Poacynum* as a synonym of *Apocynum*), D.J. Middleton (reduction of *Urnularia* to the synonymy of of *Willughbeia*, reduction of *Rhynchodia* to the synonymy of *Chonemorpha* and preparation of the reduction of *Ecdysanthera*, *Hymenolophus*, *Nouetia*, *Xylinobaria* 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 *Wrightieae*) 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.

- Apocynaceae
  - Plumerioideae
    - 1. **Carisseae**
      - 1.1. *Carissinae*
      - Carissa 20 Afr + As
      - Acokanthera 5 Afr
      - 1.2. *Melodininae*
      - Melodinus 45 As + Oc
      - 1.3. *Landolphiinae*
      - Landolphia 60 Afr
      - Chamaeclitandra 1 Afr
      - Clitandra 1 Afr
      - Orthopichonia 6 Afr
      - Pacouria 2 Am
      - Dictyophleba 5 Afr
      - Vahadenia 2 Afr
      - Ancylobotrys 7 Afr
      - Saba 3 Afr
      - 1.4. *Willughbeiinae*
      - Cylindropsis 1 Afr
      - Willughbeia 15 As
      - 1.5. *Leuconotidinae*
      - Bousigonia 2 As
      - Leuconotis 7 As
      - Cyclocotyla 1 Afr
      - 1.6. *Pleiocarpinae*
      - Picralima 1 Afr
      - Hunteria 10 Afr + As
      - Pleiocarpa 7 Afr
      - 1.7. *Lacmelleinae*
      - Lacmellea 15 Am
      - Hancornia 4 Am
      - 1.8. *Couminae*
      - Parahancornia 6 Am
      - Couma 6 Am
    - 2. **Chilocarpeae**
      - Chilocarpus 15 As
    - 3. **Ambelanieae**
      - Ambelania 3 Am
      - Mucoa 2 Am
      - Spongiosperma 6 Am
      - Molongum 3 Am
      - Rhigospira 1 Am
      - Neocouma 2 Am
    - 4. **Macoubeea**
      - Macoubea 2 Am
    - 5. **Tabernaemontaneae**
      - Voacanga 12 Afr + As
      - Tabernaemontana 99 trop
      - Tabernanthe 2 Afr
      - Carvalhoa 1 Afr
      - Schizozygia 1 Afr
      - Calocrater 1 Afr
      - Callichilia 7 Afr
      - Stemmadenia 10 Am
      - Crioceras 1 Afr
    - 6. **Plumerieae**
      - 6.1. *Aspidospermatinae*
      - Geissospermum 5 Am
      - Microplumeria 1 Am
      - Laxoplumeria 3 Am
      - Aspidosperma 70 Am
      - Pycnobotrya 1 Afr
      - Diplorhynchus 1 Afr
      - 6.2. *Craspidospermatinae*
      - Craspidospermum 1 Mad
      - Stephanostegia 5 Mad
      - Dyera 2 As
      - Kamettia 1 As
      - Gonioma 2 Afr
      - Strempeliopsis 2 Am
      - Plectaneia 6 Mad
      - 6.3. *Plumeriinae*
      - Himatanthus 13 Am
      - Plumeria 8 Am
      - Mortoniella 1 Am
      - 6.4. *Alstoniinae*
      - Alstonia 40 trop
      - Haplophyton 1 Am
      - 6.5. *Catharanthinae*
      - Rhazya 1 M East
      - Amsonia 19 Am + As
      - Catharanthus 8 Mad + Ind
      - Vinca 5 Eur + M East
    - 7. **Alyxieae**
      - 7.1. *Condylocarpinae*
      - Condylocarpon 7 Am
      - Anechites 1 Am
      - 7.2. *Rauvolfiinae*
      - Rauvolfia 60 trop
      - Petchia 1 Sri Lanka
      - Cabucala 12 Mad
      - 7.3. *Alyxiinae*
      - Alyxia 90 As + Oc
      - Lepinia 4 Oc
      - Lepiniopsis 2 As + Oc
      - 7.4. *Kopsiinae*
      - Vallesia 5 Am
      - Kopsia 20 As
      - 7.5. *Ochrosiinae*
      - Ochrosia 25 Masc - Oc
    - 8. **Cerbereae**

- Thevetia 8 Am
- Cerbera 4 Seych - Oc
- Cerberiopsis 2 N Cal
- Cameraria 2 W I
- Skytanthus 2 Am
- 9. **Allamandeae**
  - Allamanda 14 Am

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- 10. **Echiteae**
  - 10.1. *Echitinae*
    - Secondatia 6 Am
    - Odontadenia 20 Am
    - Mesechites 12 Am
    - Mandevilla 150 Am
    - Macrosiphonia 10 Am
    - Elytropus 1 Am
    - Themnadenia 4 Am
    - Macropharynx 2 Am
    - Asketanthera 4 Am
    - Fernaldia 4 Am
    - Neobracea 4 Am
    - Prestonia 35 Am
    - Rhodocalyx 1 Am
    - Laubertia 4 Am
    - Echites 6 Am
    - Thyrsanthella 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. *Parsoniinae*
    - Delphyodon 1 N Guin
    - Grissea 1 Indon
    - Parsonsia 50 As + Oc
    - Dewevrella 1 Afr
    - Thenardia 4 Mex
    - Artia 4 As + Oc
    - Pottsia 2 As
    - Isonema 3 Afr
  - 10.3. *Pachypodiinae*
    - Pachypodium 17 Afr
- 11. **Wrightieae**
  - 11.1. *Neriinae*
    - Adenium 5 Afr + Arab
    - Nerium 1 Medit - Him
  - 11.2. *Wrightiinae*
    - Wrightia 23 Afr + As
    - Pleioceras 5 Afr
    - Stephanostema 1 Afr
    - Spirolobium 1 As
    - Tintanabularia 1 Am
    - Beaumontia 9 As
    - Vallaris 3 As
    - Strophanthus 38 Afr + As
  - 11.3. *Malouetiinae*
    - Kibatalia 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. **Apocynyneae**
  - 12.1. *Apocyninae*
    - Apocynum 9 N Hem
  - 12.2. *Ichnocarpinae*
    - Anodendron 15 As
    - Urceola 25 As
    - Parameria 4 As
    - Aganonerion 1 As
    - Ichnocarpus 12 As + Aus
  - Ixodenerium 1 As
  - Epigynum 10 As
  - Eucorymbia 1 As
  - Parepigynum 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 (= Parsonsia), 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.

1.2. Subtribe **Melodininae** (G.Don) K. Schum., op. cit. 122. Basionym: *Melodineae* G. Don, Gen. Syst. 4: 71, 101. 1837, as tribe. Both partly, as for *Melodinus.*

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.

1.5. Subtribe **Leuconotidinae** Pichon, Mém. Mus. Nat. Hist. Nat. sér. 2. 24: 155. 1948, with French description; ex Leeuwenberg, **subtribus nova.**

Lianae follis oppositis. Corolla tubo cylindraceo vel fere cylindraceo. Stamina plerumque medio corollae tubi inserta.

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: *Pleiocarpeae* 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.

1.7. Subtribe **Lacmelliinae** Pichon, op. cit. 133, with French description; ex Leeuwenberg, **subtribus nova**.

Arbores vel frutices foliis oppositis. Corolla hypocrateriformis. Stamina apice corollae tubi inserta. Ovarium biloculare. Bacca saepe monosperma.

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**.

Arbores vel frutices foliis verticillatis vel oppositis. Corolla tubo cylindraceo. Stamina fere medio corollae tubi inserta inclusa. Fructus baccatus polyspermus.

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.

2.2. Tribe **Chilocarpeae** Pichon, Bull. Mus. Paris sér 2. 21: 143. 1949, in key in French; ex Leeuwenberg, **tribus nova**.

Lianae foliis oppositis. Corolla sine corona, tubo cylindraceo. Stamina medio corollae tubi inserta. Ovarium uniculare placentibus duabus parietalibus. Fructus baccatus bivalvis.

Type genus: *Chilocarpus* Bl.

Lianas without tendrils. Leaves opposite. Corolla without corona; tube cylindrical; lobes overlapping to the left. Stamens inserted in the middle of the corolla tube. Ovary 1-celled, with 2 parietal placentas. Fruit berry-like, variously shaped, bivalved. Seed with deep hilar groove, ruminate endosperm and aril.

3. Tribe **Ambelanieae** Pichon, Mém. Mus. Nat. Hist. Nat. sér 2. 24: 165. 1948, partly, excl. *Macoubea*, with French description; ex Boiteau & Sastre, Adansonia sér. 2. 18: 276. 1978.

Shrubs or trees. Leaves opposite. Corolla without corona, tube cylindrical; lobes overlapping to the left. Stamens included. Ovary syncarpous, 2-celled. Fruit a many-seeded berry. Aril absent. Seed generally plano-convex; endosperm not ruminate.

4. Tribe **Macoubeeae** Boiteau & Sastre, Adansonia sér. 2. 15: 244. 1975.

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.

6. Tribe **Plumerieae** Endl., op. cit. 581, partly, excl. *Hunteria, Urceola, Tabernaemontana, Voacanga* and *Orchipeda* (= *Voacanga*).

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.

6.1. Subtribe **Aspidospermatinae** Pichon, Mém. Mus. Nat. Hist. Nat. sér. 2. 27: 195. 1949, with French description; ex Leeuwenberg & Van der Ploeg, Meded. Landbouwhogesch. Wageningen 83. 4: 13. 1983.

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**.

Frutices ver arbores foliis alternis. Corollae lobi sinistrorsi. Stamina basi corollae inserta. Ovarium carpellis duabus separatis. Fructus capsularis. Semina alata.

Type genus: *Plumeria* L.

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: *Alstonieae* 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.

6.5. Subtribe **Catharanthinae** Pichon, op. cit. 237; ex Boiteau, Fl. Nouv. Caled. 10: 8. 1981. Basionym: *Lochnerinae* Pichon, op. cit. 200, with French description.

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**.

Scandentes foliis oppositis vel verticillatis. Corolla tubo fere cylindraceo. Stamina inclusa. Ovarium carpellis duabus separatis. Fructus drupaceus. Semina angusta.

Type genus: *Condylocarpon* Desf.

Lianas. Leaves opposite or verticillate. Corolla tube almost cylindrical; lobes overlapping to the left. Stamens included. Ovary of 2 separate carpels. Fruit of 2 separate mericarps; mericarps flat, with one drupe or moniliform and with several drupes. Seed not winged, fusiform or nearly so, in *Condylocarpon* with a deep hilar groove and with ruminate endosperm.

7.2. Subtribe **Rauvolfiinae** Benth & Hook. f., Gen. Pl. 2: 684. 1876 (as *Rauwolfieae*), partly as for *Rauvolfia*.

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**.

Lignosae foliis verticillatis, oppositis vel alternis. Corolla hypocrateriformis. Stamina medio vel supra medium corollae tubi inserta, inclusa. Ovarium carpellis 2-5. Fructus drupaceus. Semina non alata.

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; 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*, *Rhabdadenia*, *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.

10.3 Subtribe **Pachypodiinae** Pichon, Mém. Mus. Nat. Hist. Nat. sér. 2B. Bot. 1: 45. 1950, with French description; ex Leeuwenberg, **subtribus nova**.

Arbores vel frutices cactiformae spinis armatae. Folia alterna. Corolla hypocrateriformis, campanulata vel infundibuliformis, sine corona. Stamina inclusa vel exserta. Ovarium carpellis duabus separatis. Fructus capsularis. Semina pappo ornata.

Type genus: *Pachypodium* Lindl.

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.

11. Tribe **Wrightieae** G. Don, op. cit. 70, 85. *Nerieae* Benth. & Hook. f., op. cit. 688.

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.

11.1. Subtribe **Neriinae** Boiteau, Fl. Nouv. Caled. 10: 9. 1981.

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**.

Lignosae foliis oppositis vel verticillatis. Corolla saepe corona suffulta, lobis dextrorsis vel sinistrorsis. Stamina inclusa vel exserta. Semina pappo ornata.

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.

11.3 Subtribe **Malouetiinae** (Muell. Arg.) Pichon, op. cit. 75. Basionym: *Malouetieae* Muell. Arg. in Martius, Fl. Bras. 6.1: 6. 1860 (as tribe).

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.**

Lignosae foliis oppositis. Corolla hypocrateriformis sine corona, lobis dextrorsis. Stamina inclusa. Ovarium carpellis duabus plerumque liberis. Semina pappo ornata.

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.

12. Tribe **Apocyneae** Allorge, Compt. Rend. Soc. Biogéogr. 57: 115. 1981, nomen (as *Apocynae*); ex Leeuwenberg, **tribus nova.**

Plantae lignosae vel herbaceae foliis oppositis, verticillatis vel alternis. Corolla saepe corona suffulta. Fructus capsularis. Semina pappo ornata.

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 ruminate.

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

Herbae vel suffrutices foliis oppositis vel alternis. Corolla campanulata, sine corona, lobis dextrorsis. Stamina basi corollae inserta. Ovarium carpellis liberis. Semen pappo ornatum.

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.

12.2. Subtribe **Ichnocarpinae** (Benth. & Hook. f.) Allorge, l.c. Basionym: *Ichnocarpeae* Benth. & Hook. f., op. cit. 688, as tribe, partly, excl. *Apocynum*.

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.

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Pollination of Apocynaceae

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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 *Cochliomya 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-

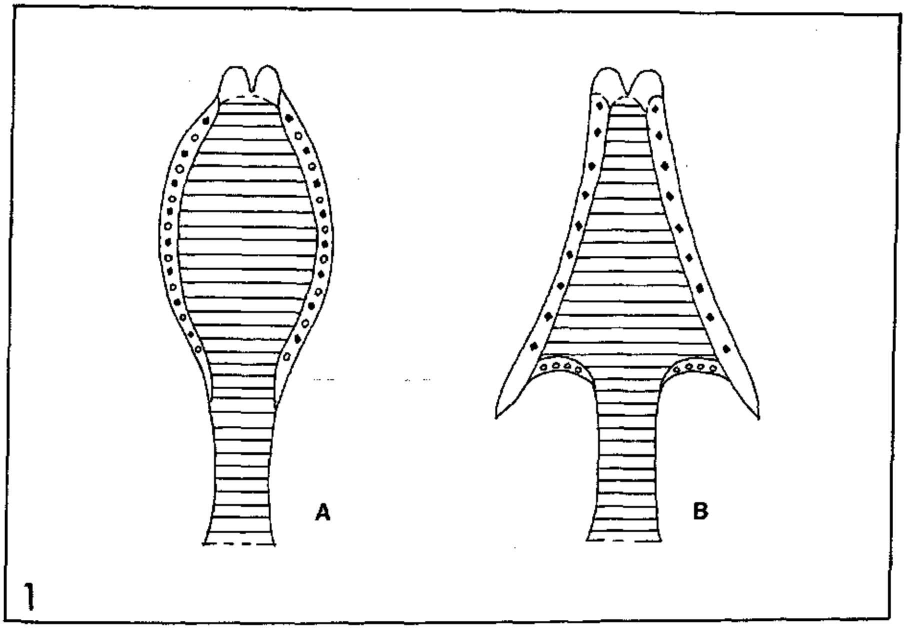

Fig. 1. Apocynaceae pistil heads according to Schick (1980, 1982), adapted from the original figure. A. *Plumeria*-type; B. *Allamanda-Nerium*-type. O - receptive surface ; ◆ - tissue producing adhesive matter.

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.

Species	Coll.nr	Origin
Alafia lucida*	Leeuwenb.8650	Cameroun
Alafia multiflora*	de Koning 6225	Ivory Coast
Alstonia boonei	de Wit 2352	Nigeria
-do-	Leeuwenb.11602	Ghana
-do-	Albers 18	Ivory Coast
Amsonia orientalis		Bot.Gdn WAG
Catharanthus roseus	Leeuwenb.12125	Ivory Coast
-do-	Albers 30	Ivory Coast
C. trichophyllus*		Greenhouse
Funtumia africana*	Zwetsloot 5	Ivory Coast
Isonema smeathmannii*	Beentje 276	Ivory Coast
Mascarenhasia arborescens*		Greenhouse
Oncinotis glabrata*	de Kruif 787	Cameroun
Oncinotis pontyi*	de Koning 4796	Ivory Coast
Pleioceras barteri*	Barrink 68	Ivory Coast
Rauvolfia mombasiana*		Greenhouse
Strophanthus hispidus	de Koning 5509	Ivory Coast
-do-	Leeuwenb.11918	Ghana
Strophanthus sarmentosus	Leeuwenb.11907	Ghana
-do-	Leeuwenb.11952	Ghana
Tabernaemontana pandacaqui	Leeuwenb.13853	Indonesia
Tabernaemontana sphaerocarpa	Leeuwenb.13255	Indonesia
Tabernaemontana undulata*	Fe 9929	French Guyana
Vinca minor		Bot. Gdn WAG
Voacanga africana	Leeuwenb.9472	Cameroun
Voacanga grandifolia*	vdMaesen 5980	Indonesia

*) 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 1n NaOH at 60 C
- rinsed with water
- anilin stained for 45-60 min. (7 g $K_3PO_4.3H_2O$ + 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 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.

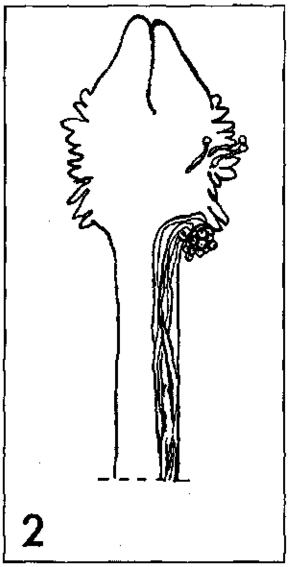

Fig. 2. Pistil head of *Alstonia boonei.*

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 (= Rhazya 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 Allamanda-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.

Photo 1. *Catharanthus roseus* pollen tubes originating from pollen grains attached just below the lower hair whorl (top of photograph).

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 Typhiidae (Myzininae) 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

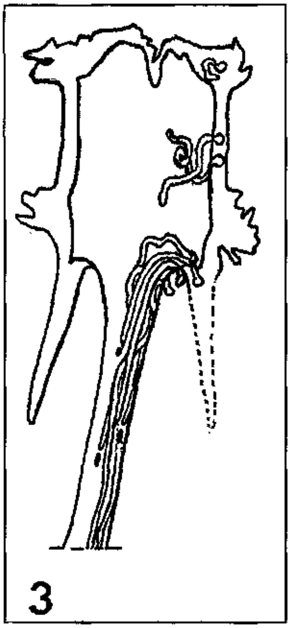

Fig. 3. Pollen germinating on pistil head of *Catharanthus roseus*. Some pollen tubes halted in the style by callose.

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.

Photo 2. Pollen tubes in ovarium of *Catharanthus roseus*.

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

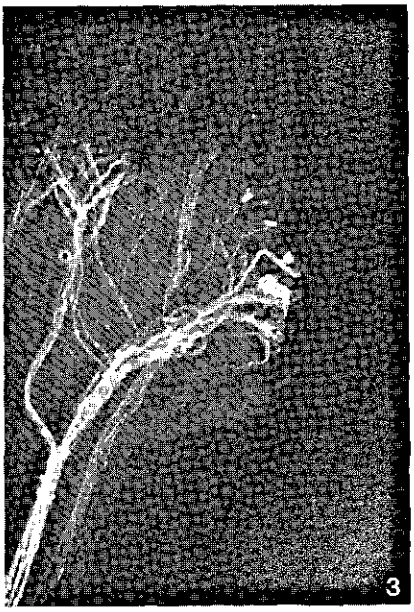

Photo 3. *Tabernaemontana pandacacqui* pollen grains germinated on pistil head and growth of pollen tubes in style. No pollen germinating on stigmoidal apex.

the Allamanda-Nerium type; nevertheless the preparations clearly show that pollen can germinate on the entire surface of the pistil head (Plumeria-type). The stigmoidal apex is free of pollen (Photo 3, Fig. 4).

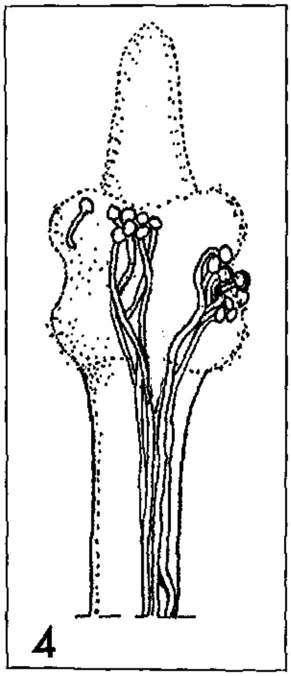

Fig. 4. Schematical representation of Photo 3, *Tabernaemontana pandacacqui*.

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.

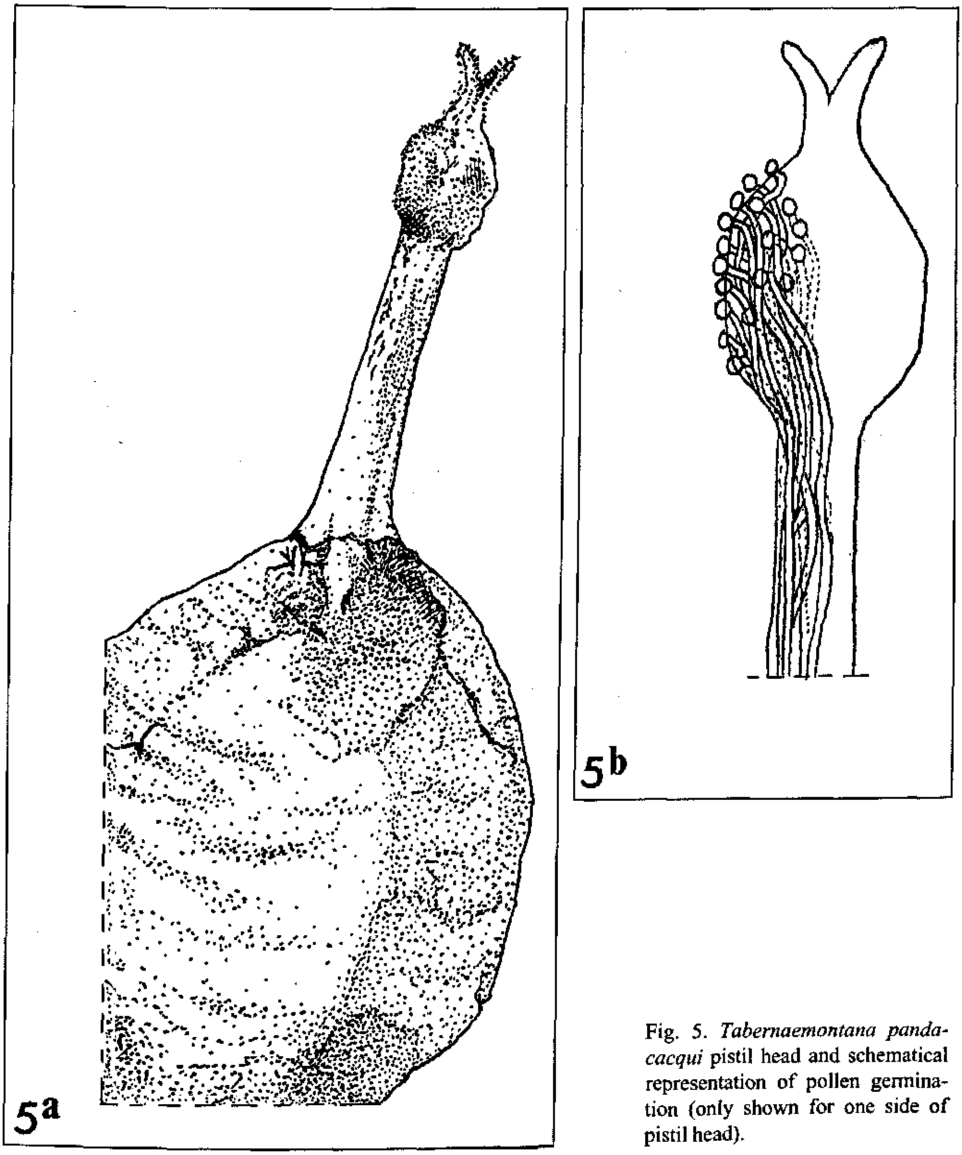

Fig. 5. *Tabernaemontana pandacacqui* pistil head and schematical representation of pollen germination (only shown for one side of pistil head).

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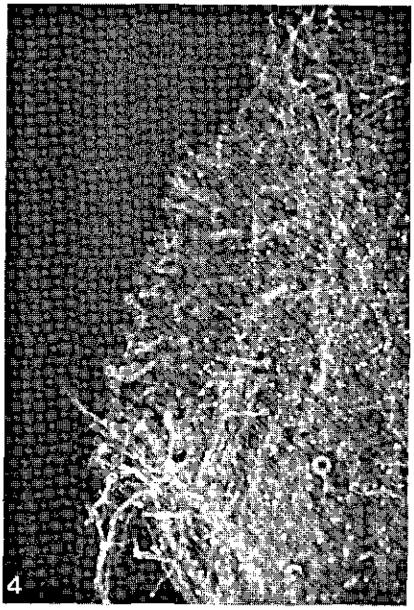

Photo 4. *Tabernaemontana sphaerocarpa* germinated pollen. The ellipsoid part of the pistil head is pollinated entirely and pollen germinates all around.

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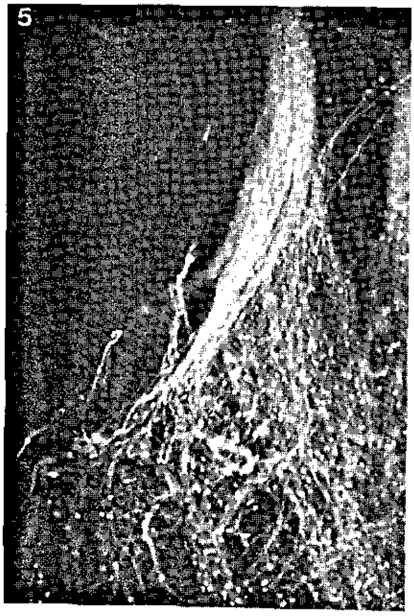

Photo 5. *Tabernaemontana sphaerocarpa* growth of pollen tubes in the style.

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

Photo 6. *Tabernaemontana sphaerocarpa* stigmoidal apex free of pollen grains.

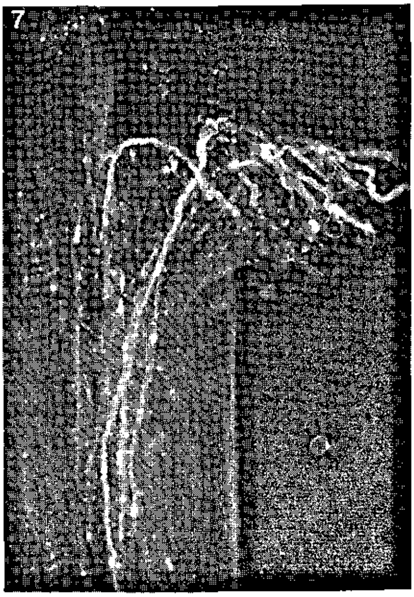

Photo 7. *Vinca minor* pistil head with pollen germinated just below the lower whorl of hairs.

ceases growth very soon. See photo 7 and Fig. 6. Photo 8 and Fig. 7 show a pollen tube reaching an ovule in the ovary.

Visitors: Darwin (in Schick 1982) and Schick (1982) reported that honey bees (*Apis* spp.) pollinate the flowers. Observations in the Wageningen Arboretum could not corroborate these reports.

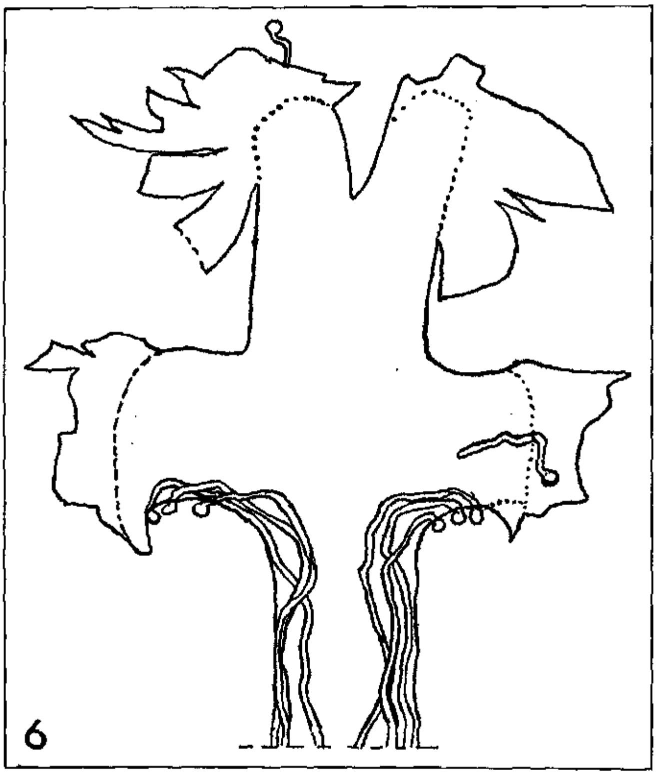

Fig. 6. *Vinca minor,* pollen germinated just below the lower hair whorl on the stigmatic surface.

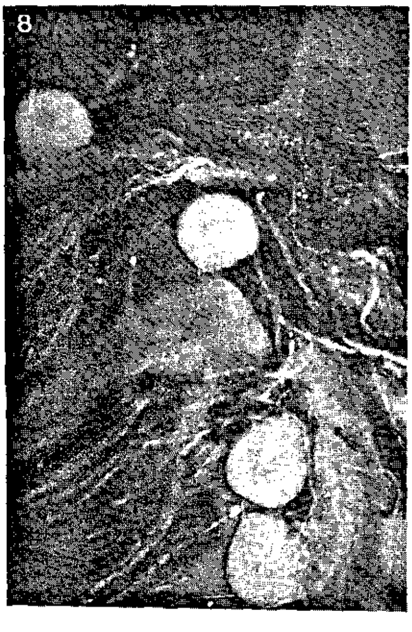

Photo 8. *Vinca minor* pollen tube penetrating ovules in ovary.

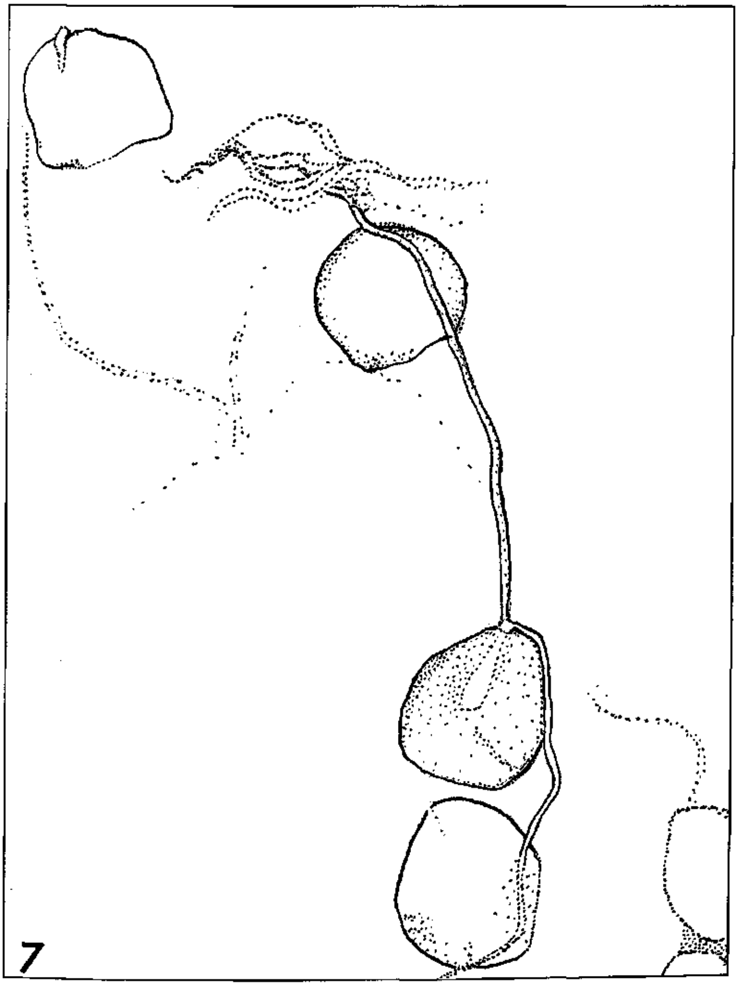

Fig. 7. See Photo 8, pollen tube penetrating ovules of *Vinca minor*.

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 Allamanda-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. *Voacanga africana*. Flowers of *V. africana* produce a sickly odour.

Coleoptera

Beetles were observed on *Catharanthus roseus*, *Alstonia boonei* and in the flowers of *Strophanthus 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, Vespoidea

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 Vespoidea 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*. *Amsonia orientalis* and *A. angustifolia* basically show the same situation.

In *Amsonia orientalis* the bumble bee *Bombus terrestris* was very active. Covered 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

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