Revision of Ancylobotrys Pierre

Series of Revisions of Apocynaceae XXXVII

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Abstract

Monograph of *Ancylobotrys*, a genus counting 7 species of the *Apocynaceae-Plumerioideae-Carisseae-Landolphiinae* restricted to Africa. A key to the species is presented. All 7 species are described in detail, illustrated and maps depict the geographical distribution.

Introduction

The present paper is a monographic revision of the genus *Ancylobotrys*. The study is based mainly on herbarium material, but in addition the second author has had the opportunity of observing living plants in the wild of 4 of the 7 species maintained here.

It has been possible to trace almost all type specimens of the names and synonyms discussed in the present revision.

Geographical distribution

The genus *Ancylobotrys* comprises 7 species, which are all restricted to Africa. Six of them occur only on the the continent. One of them, *A. petersiana*, known on the eastern part of the continent from Somalia to South Africa, also occurs in the Comoro Islands and Madagascar, but in the latter country it is restricted to the coastal dunes mainly near Majunga.

The most widespread species is *A. amoena*, known from almost all tropical regions of continental Africa. This is followed by *A. scandens* represented from Liberia to Zaire and Angola and *A. petersiana* metioned above.

The areas of the four other species are much smaller, *A. robusta* is represented from the Cross River State in Nigeria to Zaire, *A. pyriformis* from the Cross River State in Nigeria to Gabon, *A. tayloris* occurs near the coast from Kenya to northern Mozambique and on the Mt Mulanje in Malawi, while *A. capensis* is only known from southern Africa.

Relationships with other genera

Ancylobotrys belongs to the subtribe *Landolphiinae* of the tribe *Carisseae* of the subfamily *Plumerioideae*. It is most closely related to *Landolphia*, from which it can be distinguished most easily by two characters: the inflorescence is tendril-like contrary to fairly densely cymose and the fruits are softly pubescent rather than glabrous.

The genus can be distinguished from the other ones of the subtribe as is shown in the key to the genera of this subtribe published by Persoon et al. (1992).

Reference

Persoon, J.G.M., F.J.H. van Dilst, R.P. Kuijpers, A.J.M. Leeuwenberg and G.J.A. Vonk. 1992. The African species of Landolphia P. Beauv. Series of revisions of Apocynaceae XXXIV. Wageningen Agric. Univ. Pap. 92-2: 1-232.

Orthography of the genus name

Pierre erroneously wrote the genus name as *Ancylobothrys*, this spelling has been followed until Huber (Fl. W. Trop. Afr. 2nd ed. 2. 1963) corrected it. The name has been derived from two Greek words: ἀγκύλη, ancyla, hook, and βότρυς, botrys, grape. For this genus Huber fortunately was not obliged to accept the earlier misspellings as in the case of *Rauvolfia* (named after Rauwolf).

Systematic part

Ancylobotrys Pierre, Bull. Soc. Linn. Paris sér. 2: 91. 1898; Hua, Bull. Mus. Nat. Hist. Nat. 5: 186. 1899; Pichon, Mém. IFAN 35: 272. 1953 (all three as *Ancylobothrys*); Huber in Fl. W. Trop. Afr. 2nd ed. 2: 60. 1963; Persoon et al., Wageningen Agric. Univ. Pap. 92.2: 5. 1992.

Sarmentose shrubs or lianas, at least partly with a rusty-brown indumentum, with large curled terminal tendrils, which could be at the same time inflorescences. Branchlets terete. Stipules absent. *Leaves* opposite, petiolate, entire. *Inflorescence* terminal, tendril-like, lax, except for the last ramifications where flowers are usually sessile. *Flowers* sweet-scented. *Sepals* green, often seemingly rusty-brown by indumentum, usually without colleters. *Corolla* white or nearly so; tube narrow, often thickened above the stamens, glabrous or pubescent outside; lobes ciliate at both sides, with longer hairs at side covered in bud. *Stamens* deeply included, inserted 0.1—0.35 of the length of the corolla tube from the base; anthers narrowly triangular, cordate at the base, keeled along the back, glabrous. *Pistil*: ovary hairy, unilocular, abruptly narrowed into the style; pistil head of a subglobose or cylindrical stigmatic basal part and a bilobed stigmoid apex. *Fruit* a berry, yellow to red, globose or pear-shaped or nearly so, rounded at the apex, softly velutinous; wall without sclereid cell-layer. *Seed* with horny endosperm, surrounding the embryo. Embryo almost touching the edges of the seed; cotyledons large, membranaceous, undulate; rootlet about 1.5 × 1 mm.

The genus counts 7 species in tropical Africa, one of which occurs also in the Comoro Islands and in NE Madagascar mainly near Majunga.

Uses: The fruits of all species are edible, especially those of *A. capensis* are appreciated; they taste like apricots.

Key to the species

1. Secondary veins curved, forming an angle of 45–60° with the costa 2
   Secondary veins more or less straight, forming an angle with the costa of 60–90° or less (*A. amoena* which has tomentose branchlets) 3
2. Petiole 12–26 mm long; leaf blade acuminate at the apex, with 5–12 pairs of secondary veins; corolla tube 0.9–2.1 × as long as the lobes, 10.5–20 mm long. From Cameroun and Gabon to Zaire and Zambia ..... **5. A. robusta**
   Petiole 6–10 mm long; leaf blade rounded or obtuse at the apex, with 4–9 pairs of secondary veins; corolla tube 0.3–0.8 × as long as the lobes, 8.5–13 mm long. Kenya to South Africa, Comoro Islands and Madagascar ..... **3. A. petersiana**
3. Corolla tube glabrous or sparsely short-pubescent outside, 1.4–3.8 × as long as the lobes, 17.5–43.5 mm long; corolla 33–59 mm long in the mature bud; secondary leaf veins forming an angle of 60–90° with the costa; branchlets rather densely more or less appressedly short-pubescent. Liberia to Zaire and Angola ..... **6. A. scandens**
   Corolla tube pubescent, often even densely so outside, 0.5–1.4 × as long as the lobes, 7.7–18 mm long; corolla 18–35 mm long in the mature bud; secondary leaf veins forming various angles with the costa, less than 60° only in *A. amoena* which has almost tomentose branchlets 4
4. Corolla lobes with same often dense pubescence outside as tube; secondary leaf veins in 8–16 pairs and forming an angle of 70–90° with the costa. Nigeria to Gabon ..... **4. A. pyriformis**
   Corolla lobes glabrous to minutely pubescent and tube often densely pubescent outside; secondary leaf veins in 7–14 pairs and forming an angle of 45–70° with the costa, leaves acuminate and branchlets almost tomentose (*A. amoena*), otherwise forming an angle of 70–90° with the costa (only in 8–16 pairs when leaves rounded or obtuse, *A. capensis*) 5
5. Leaf blades 0.8–4.5 cm long, usually rounded or obtuse at the apex; secondary veins in 8–16 pairs. SE and S Africa ..... **2. A. capensis**
   Leaf blades 6.7–12 cm long and acuminate at the apex, if only 4 cm long then secondary leaf veins in 19–40 pairs 6
6. Branchlets glabrous or minutely pubescent; secondary leaf veins in 19–40 pairs, forming an angle of 70–90° with the costa. Kenya and Tanzania ..... **7. A. tayloris**
   Branchlets almost tomentose; secondary leaf veins in 7–14 pairs, forming an angle of 45–70° with the costa. Tropical Africa ..... **1. A. amoena**

1. Ancylobotrys amoena Hua, Bull. Mus. Nat. Hist. Nat. 5: 186. 1899; Pichon, Mém. IFAN 35: 274, pl. 17. 1–2. 1953. **Fig. 1, p. 6; map 1 p. 7**

Type: Guinea, Kankan, Upper Niger R., near Kouroussa, Paroisse 24 (P, holotype; isotype K; phot. of holotype B, K, MO, NY).

Homotypic synonyms: *Landolphia amoena* (Hua) Hua & A.Chev. in Morot, Journ. Bot. 15: 8. 1901. *Pacouria amoena* (Hua) Pichon, Mém. Mus. Nat. Hist.

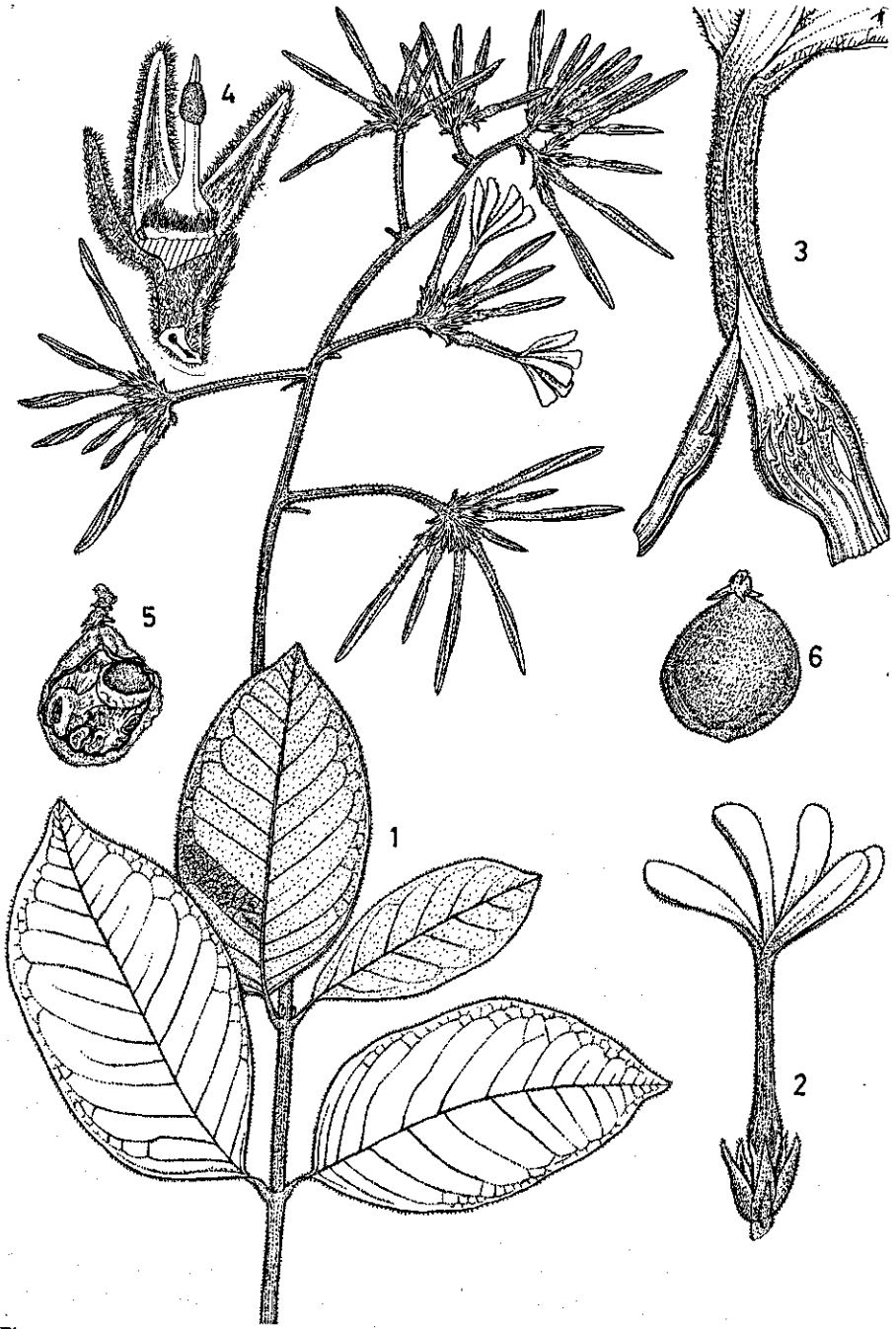
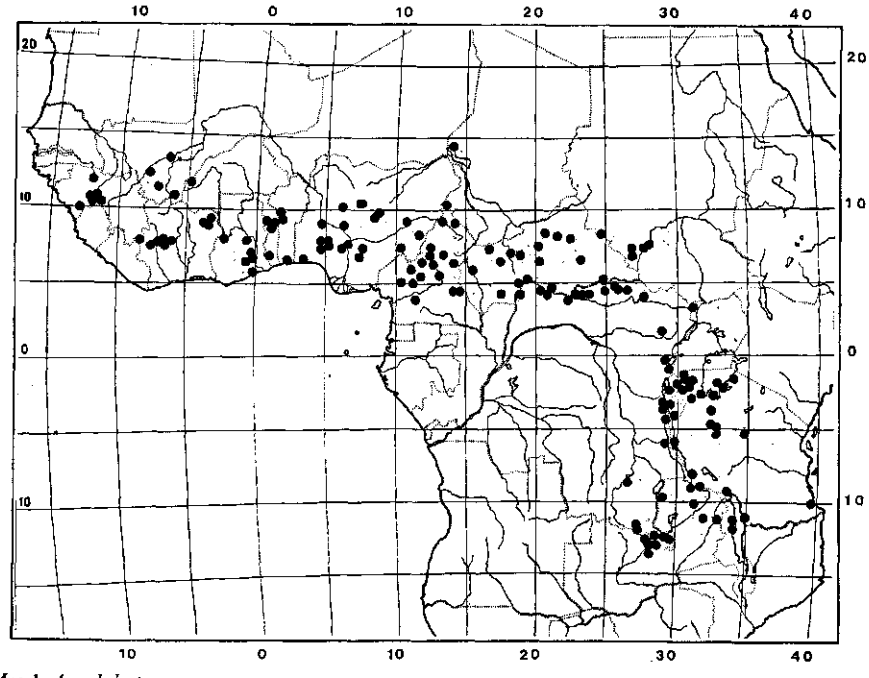


Fig. 1. *Ancylobotrys amoena*. 1, habit (× 2/3); 2, flower (× 2); 3, corolla with tube partly opened (× 4); 4, calyx with pistil (× 6); 5, longitudinal section of dried fruit (× 2/3); 6, fruit (× 2/3). 1–4 from Asongany 598; 5 from Bridson 239; 6 from Troupin 4157.



MAP 1. *Ancylobotrys amoena*.

Nat. sér. 2. 24: 144. 1948.

Heterotypic synonyms: *Landolphia scandens* var. *ferruginea* Hall. f., Jahrb. Hamb. Wiss. Anst. 170, Beih. 3: 80. 1900. Type Tanzania, T8, Lake Malawi, Kanda Peninsula, Goetze 884 (K, lectotype, designated here; isolectotypes BR, E). Homotypic synonym: *L. ferruginea* (Hall. f.) Stapf in Fl. Trop. Afr. 4. 1: 46. 1902.

L. scandens var. *rigida* Hall. f., op. cit. 81. Type: Tanzania, T1, Karagwe, Scott Elliot 8167 (K, lectotype, designated here).

L. scandens var. *schweinfurthiana* Hall. f., l.c. Type: Sudan, Djurland, Sériba d'Agat, Wau R., Schweinfurth 1685 (K, lectotype, designated here; isolectotype P). Homotypic synonyms: *L. petersiana* var. *schweinfurthiana* (Hall. f.) Stapf in op. cit. 48. *P. petersiana* var. *schweinfurthiana* (Hall. f.) S. Moore, Journ. Linn. Soc. Bot. 37: 180. 1905.

L. nitida Lebrun & Taton, Expl. Parc. Nat. Kagera 105. 1948. Type: Rwanda, Rwabiega (= Ryabega), Lebrun 9820 (BR, holotype; isotypes K, P).

Scrambling shrub or liana climbing up to at least 10 m high. Branchlets densely brown-pubescent to almost tomentose. *Leaves*: petiole densely pubescent, (1.1–)5–13 mm long; blade thinly coriaceous even when fresh, elliptic or ovate, sometimes oblong, 1.6–2.4 × as long as wide, 6.7–11.6 × 2.8–7 cm, acuminate at the apex with an up to 10 mm long acumen, cuneate at the base, sometimes decurrent into the petiole, glabrous to minutely pubescent on both sides, with 7–14 pairs of conspicuous more or less straight to slightly curved secondary veins, forming an

angle of 45–70° with the costa; tertiary venation reticulate. *Inflorescences* 10–38 × 5–17 cm, with 5–11 cymes, each cyme with up to about 25 flowers; peduncle 4–18 cm long, densely pubescent; pedicels about 1 mm long, densely pubescent; bracts sepal-like, densely pubescent outside, 1.7–2 mm long, persistent, with or without colleters at both sides of the base. *Sepals* connate at the base for up to 0.8 mm, narrowly triangular to ovate, 1.5–2.9 × as long as wide, 2.5–5 × 1–2 mm, acute or obtuse at the apex, densely pubescent outside, ciliate, glabrous inside. *Corolla* white or pinkish, especially at the tube, 19.5–35 mm long in the mature bud and forming a narrowly ovoid to oblong head, pubescent, often densely so outside, from 1.5–3.5 mm above the base to the base of the lobes, indumentum less dense towards the apex; tube thin to thick, usually somewhat thickened above the anthers, 3.5–7.1 × as long as the sepals, 0.9–1.4 × as long as the lobes, 11.2–18 mm long, contracted at the base and 1.4–1.9 mm wide, widened above to 1.8–3 mm wide which is 4.2–5 mm above the base (0.3–0.4 of the tube length), contracted again just above the anthers and 0.9–1.9 mm wide, abruptly widened at the throat, inside minutely pilose around the stamens, rarely glabrous, throat glabrous; lobes narrowly elliptic, rarely oblong, 0.7–1.1 × as long as the tube, 2.4–5.7 × as long as wide, 8.5–20.5 × 2.7–5 mm, obtuse at the apex, glabrous on both sides, sometimes minutely pubescent outside. *Stamens* with apex 6.2–12.7 mm below mouth of corolla tube (0.5–0.7 of the tube length), inserted 0.2–0.3 of the tube length, (at 2.7–3.9 mm from the base), (the base of the anthers 3.2–4.3 mm above the base of the tube); filaments glabrous, 0.6–1 mm long; anthers 1.8–3.2 × as long as the filaments, 3–4.3(–5.3) × as long as wide, 1.6–2 × (0.3–)0.4–0.6 mm, apex acuminate and sterile for up to 0.2 mm. *Pistil* 3.5–4.5 mm long, with apex 1.1–2.2 mm below apices of anthers; ovary subglobose, 0.6–1.3 × 0.9–1.6 × 0.9–1.6 mm, appressed-pubescent, often densely so; style glabrous, cylindrical, not or sometimes slightly thickened at the apex, 1.5–2.1 × 0.2–0.4 mm; pistil head: basal part cylindrical, 0.7–1.2 × 0.5–0.6 mm and upper part conical, 0.4–1 × 0.3–0.6 mm. Placentas with 40–50 ovules. *Fruit* yellow to red, globose or slightly pear-shaped, 1.5–2 cm in diameter, 1–4-seeded. *Seeds* 7–10 × 7–10 × 3 mm.

DISTRIBUTION: Tropical Africa.

ECOLOGY: Secondary forest and gallery forest in woodland. Alt. 0–2400 m. Flowering in West Africa west of Nigeria mainly from November to February, in Nigeria and countries eastwards to Uganda from December to May, in Rwanda and Tanzania scattered over the year, and in southern Zaire, Zambia, Malawi and Zimbabwe mainly from July to September. Fruiting from the same months to one year later; in the latter case flowers and ripe fruits on the same branch.

Geographical selection of the approximately 300 specimens examined:

GUINEA. Labé: Fouta Dallon, near Mali, Lisowski 51575 (BR, POZG). Kindia: Kindia, Chevalier 13158 (P); near Dalaba, Lisowski 60265 (BR); ibid., Malaisse 2629 (BR); between Diaguissa and Boulivel, Chevalier 12415 (P); Diaguissa, Chevalier 18006 (P, WAG); Mamou, Boué 11 (G). Kankan: Kouroussa, Chevalier 384 (BR, G, K, P, WAG); ibid., Upper Niger R., Paroisse 24 (K, P, type; phot. of

K sheet B, BR, K, MO, NY); 4 km N of Kankan, Lisowski 55122 (K, POZG). Nzérékoré: Mt Nimba, Adam 25228 (MO).

Mali. Near Bamako, Roberty 10389 (G); Mono, Doudou, Chevalier 432 (P, WAG); Lobougoula, Anonym. S 326 (P); between Kangala and Kindali, Chevalier 861 (P).

Ivory Coast. 5 km NW of Duékoué, Leeuwenberg 3879 (B, K, P, WAG); Upper Sassandra R., between Koualé and Kouroukoro, Chevalier 21753 (P); Séguéla, Garnier 39 (K); Rocher d'Issia, Roberty 13832 (G, Z); ibid., J. de Wilde 833 (WAG); Mankono, Chevalier 21914 (P); 30 km N of Gawi, Comoe R., Geerling & Bokdam 1924 (BR, C, LG, MO, WAG); 15 km SW of Seye, Geerling & Bokdam 2058 (BR, K, MO, WAG); Téhini, Oldeman 365 (BR, K, WAG).

Burkina Faso. between Sikasso and Bobo-Dioulasso, Vuillet 559 (P).

Ghana. Brong-Ahafo: Wenchi area, top of Banda ridge, Morton GC 25280 (K); Prang, Vigne 1577 (K, P). Eastern: E.P. Mpraeso, Enti FH 6506 (B, K, P); between Dodowa and Aburi, Morton GC 6350 (K, WAG); NE of Dodowa, Leeuwenberg 11916 (WAG); Akwapim, W.H. Johnson 782 (K). Volta: Toga Mt, Morton A 3555 (K); near Amedzofe, Morton GC 9391 (K).

Togo. Sokodé Bafilo, near Péwa, Hakki et al. 242 (K, P, WAG); Bassar, Ern 2644 (B, K); near Sokodé, Brunel 7156 (B); N of Kpalimé, Hakki et al. 793 (B).

Benin. near Ouidah, Adjanohoun 216 (K); Djougou, Chevalier 23921 (P); Mt Atacora, Chevalier 24051 (P).

Nigeria. Lagos: near Isahin R., Rowland 20 (K). Ondo: Isua District, Olorunfemi & Fagbemi FHI 70714 (K, WAG); Ikare District, Ipe, Daramola & Ihe BO 413 in FHI 86359 (MO, WAG). Oyo: between Nkata and Ayo, Unwin 2 (K, P, Z). Kwara: Lokoja District, between Lampese and Ibillo, Soladoye et al. BO 374 (MO, WAG); Lokoja, Dalziel 98 (K); Oke-Opin, Ajayi FHI 19294 (K); Jebba, Meikle 1005 (K). Niger: Kpashimi F.R., Eimunjeze & Adebusuyi FHI 66323 (K, WAG); near Kayara, Meikle 1371 (B, BR, K, P). Kaduna: Kan Gimi, Keay FHI 22960 (K). Plateau: Naraguta F.R., Olorunfemi FHI 55684 (K, P); Kirimi, Sharland 1211 (K); Assob Hill, 55 km S of Jos, Wit 1340 (WAG). Benue: Ankpa District, Acharane F.R. Okafur FHI 36870 (K); between Idah and Nsukka, Latilo FHI 47699 (K). Gongola: Moakam R., between Serti and Gashaka, Latilo & Daramola FHI 34454 (K, P, WAG); Sanlingbe, Hepper 1555 (BR, K, P, S); Gangoro F.R., Chapman 4161 (K).

Cameroun. Nord: between Mogodé and Rhoumsiki, Geerling 5664 (P, WAG); Sanguere, 22 km S of Garoua, Fotius 2551 (P); Langoy, 60 km SW of Tcholliré, Fotius 2578 (P); Tchabal Mts, 50 km WSW of Tignéré, Satabié 636 (P, WAG); ca 5 km S of Ngaoundéré, Breteler 312 (BR, K, LISC, P, WAG); 10 km S of Ngaoundéré, Wakwa, Leeuwenberg 7660 (BR, K, LISC, MO, P, WAG); Galim, Saxer 365 (K); Mbella Assom, 41 km E of Tibati, Asonganyi 598 (YA); Labaré, Ledermann 2530 (K); near Banyo, Biholong 190 (BR, K, P, WAG); between Foumban and Banyo, Jacques Félix 3275 (P). Ouest: 6 km NE of Banganté, W. de Wilde 2578a (P, WAG). Centre-Sud: near Nyanbingi, 30 km SW of Linte, Nkongmeneck 338 (WAG); Mt Yangba, 42 km NNE of Bafia, Letouzey 7849 (P, WAG); Mts Ngole, N of Banda, Raynal 10728 (P); Lom and Djerem Rivers confluence, Mildbraed 8501 (HBG). Est: between Kongolo and Mbussa, Mildbraed 9116 (K); Mt Pandi, 30 km NW of Batouri, Letouzey 4743 (BR, K, P, WAG); Mt Nion, 15 km ESE of Batouri, Letouzey 4619 (P, WAG).

Central African Republic. Nana-Mambéré: Bouar, Mildbraed 9444 (K). Lobaye: Bambari, Mbokou R., Tisserant 579 (BM, P). Kemo-Gribingui: Yamberé R., Chevalier 6055 (P, Z); Tomi R., near Fort de Possel, Chevalier 5377 (BM, COI, P). Bamingui-Bangoran: Kaga Pongourou, Chevalier 6558 (P, WAG); near Balidja, Chevalier 6678 (P); Ndellé, Chevalier 7143 (P, W, Z), 7402 (BR, G, K, L, P); between Ouadda and Ndellé, Chevalier 400 (P). Ouham: Boguila Region, Fay et al. 5136 (K); Bossangoa, Fay 5135 (K); Mt Kadé, Lenfant 1119 (P). Gribingui: Gribingui, Chevalier 6488 (P). Ouaka: near Kuduko, 20 km N of Moroubas, Tisserant 1810 (BM, GH, P, WAG). Basse-Kotto: Fay 2144 (K). Haut-Kotto: Ouadda, Dybowski 8b (P); near Mouka, 65 km S of Yalinga, Le Testu 2800 (BM, BR). Haut-Mboumou: 21 km W of Zemio, along road to Rafaï, Descoings 12400 (P).

Chad. Lac: Kouloa, Chevalier 8306 (BM, COI, W, WAG).

Zaire. Equateur: Zongo, Evrard 2575 (BR, WAG); Banzyville (= Mobayi), Lebrun 2100 (BR, K); km 30 Mobayi-Yakoma Road, Germain 8541 (BR, K, M); Lower Uele R., Bomu, De Wulf 168 (BR). Haut-Zaire: Monga, Uele-Tumbiri, Lebrun 2330 (BR, K); Mt Kundugu, near Masabe, Lisowski 50166 (BR) = Lejoley 4137 (BR); between Bondo and Lebo, Germain 775 (BR, K); between Lilèko and Basoko, J. Louis 11407 (BR, C, F, NY, S); Tiligba, Piedboeuf 202bis (MO, WAG); near Pengbele, Boutique 172 (BR, WAG); Tukpwo, Gérard 4126 (BR, WAG); Gwane, Lebrun 2875 (BR, K); between

Digba and Bokoyo, Piedboeuf 213 (BR); between Doruma and Niangara, Lebrun 3181 (BR); near Nduye, Lisowski 42748 (POZG). Kivu: near Lubero, Humbert 8744 (B, BR, P); Kabasha, de Witte 1141 (BR, K, P); Kiliba R., Rusizi Plain, Germain 6753 (BR, P); between Uvira and Mbaraka, Germain 7037 (BR, P). Shaba: Albertville (= Kalemie), De Giorgi 1 (BR); Upemba Nat. Park, de Witte 3009 (BR, MO, P, WAG); Mt Kaponda, Quarré 518 (BR, K, MO); Kasapa, Malaisse 9111 (BR, MO, WAG); near Mokambo, Breyne 4445 (BR); near Kabunda, Lisowski 60263 (BR).

Rwanda. near Uwinka, Troupin 11355 (BR, LG); Kagera (= Akagera) Nat. Park, Troupin 7451 (BR, LG, NY); ibid., Bridson 239 (BR, K, WAG); near Nyagatare, Troupin 4157 (BR, K, WAG); Ryabega, Lebrun 9820 (BR, K, P, type of *Landolphia nitida*); Rusumo, Raynal 20685 (BR, K, P, WAG).

Burundi. km 8 Kimina-Gakara Road, Reekmans 5572 (BR, K, LG, MO, WAG); Kwitaba, Reekmans 6533 (K, LG).

Sudan. Bahr al Ghazal: NW of Said Bundas, Hoyle 495 (BM); Sériba d'Agat, Wau R., Schweinfurth 1685 (K, P, lectotype of *Landolphia scandens* var. *schweinfurthiana*); Ngwolina, SW of Wau, Hoyle 367 (BM); W side of Pongo, H. Brown 17 (K); near Badiri's, H. Brown 14 (BM, K); Busseri R., New Mill, Turner 131 (K).

Uganda. Koboko, Eggeling 1838 (in herb. 1658) (BR, K); sin. loc., Bagshawe 205 (BM).

Tanzania. T1: Karagwe, Scott Elliot 8167 (BM, K, lectotype of *Landolphia scandens* var. *rigida*); Bukoba District, Ford 655 (K); Rubondo Island, FitzGibbon & Barcock 79 (K, WAG); Buruma, Tanner 4351 (BR, K, UC); Bwiru Parish, Tanner 610 (B, BR, K, LISC, MICH, NY, S, UC, WAG); Karumo, Burtt 6486 (BM, BR, K, P); Nyabekwabi, Tanner 4301 (BR, K, MO, UC). T4: Mkweni, Glover 236 (K); Ulyankulu, Procter 2094 (BR, K); Tabora, Lindeman 357 (BM, EA); between Pasagulu and Musenabantu, Harley 9223 (B, BR, K); Mahali Mts, Newbould & Jefford 2559 (BR, K); Kwihala, Peter 35330 (B, WAG); Kirambo, Richards 18753 (BR, K). T5: near Maw Hills, Burtt 5226 (BR, K). T7: Kyimbila District, Stolz 1712 (A, BM, BR, C, K, MO, PRE, UPS, Z). T8: Kanda Peninsula, Goetze 884 (BM, BR, E, K, lectotype of *Landolphia scandens* var. *ferruginea*); 40 km W of Lindi, Schlieben 5357 p.p. (B partly; other sheets probably all belonging to *A. petersiana*).

Zambia. Northern: Abercorn (= Mbala) District, 8 km from Kawimbe, near Tanzanian border, Richards 12912 (BR, K, SRGH); Sunzu Mt, Richards 13165 (BR, K, SRGH); Kasama District, Robinson 3814 (K, M, SRGH); Mwenge, Greenway & Trapnell 5740 (K); 16 km N of Isoka, Lawson 1245 (K). Lupala: Kawambwa, Fanshawe 3536 (BR, K). Copperbelt: Ndola District, Fanshawe 1389 (B, BR, K, LISC, S); Ndola, Greenway & Miller 5676 (K); Nkana, Holmes 754 (BR, K, MO, SRGH); Luano, Brenan & Greenway 8006 (BR, K); Bwana Mkubwa, Fries 390 (UPS), 391 (UPS).

Malawi. Northern: Chitipa District, 64 km W of Karonga, Songa stream, Pawek 12147 (K); 16 km S of Nkhata Bay Road, Pawek 10429 (K, SRGH, WAG); Nkwati For., Pawek 13141A (BR, K, MO, UC, WAG), 13141B (K, MO, UC, WAG).

2. Ancylobotrys capensis (Oliv.) Pichon, Mém. IFAN. 35: 297, pl. 19. 4–5. 1953.

Fig. 2, p. 11; map 2, p. 12

Basionym: *Landolphia capensis* Oliv. in Hooker Ic. 13: t. 1228. 1877.

Type: South Africa, Transvaal, W. of Pretoria, McLea 3098 (K, lectotype, designated by Pichon).

Homotypic synonym: *Pacouria capensis* (Oliv.) S. Moore, Journ. Bot. 41: 403. 1903.

Lianescent shrub mostly about 0.50 m high. Branches lenticellate; branchlets densely rusty-brown-pubescent. *Leaves*: petiole pubescent, 2–8 mm long, with colleters in the axils; blade coriaceous even when fresh, elliptic or narrowly so, or somewhat obovate, occasionally suborbicular, 1.3–3.1 × as long as wide, 0.8–4.5 × 0.5–2.4 cm, rounded or obtuse, rarely in some leaves acute or retuse, cuneate at the base or decurrent into the petiole, glabrous or pubescent on both sides, beneath pubescent especially on the veins, with 8–16 pairs of straight con-

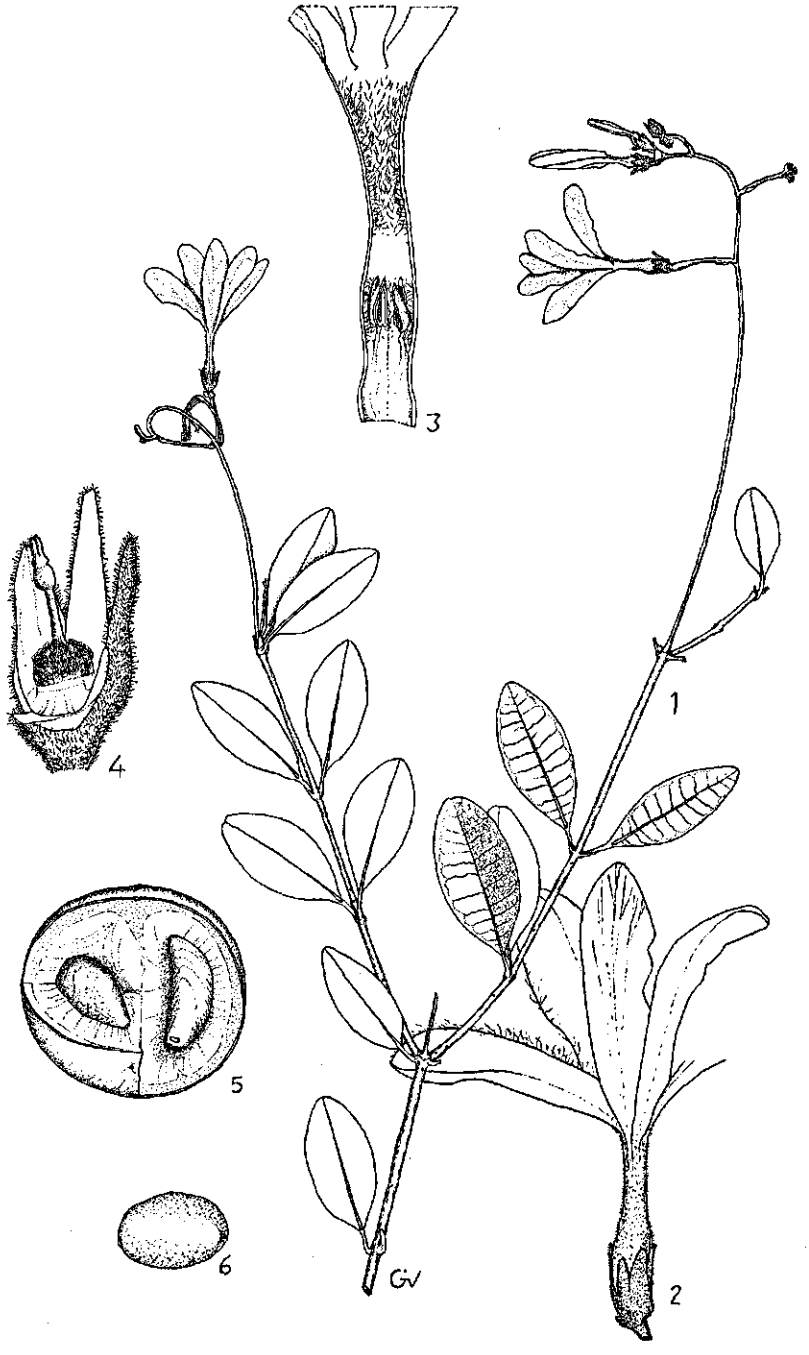
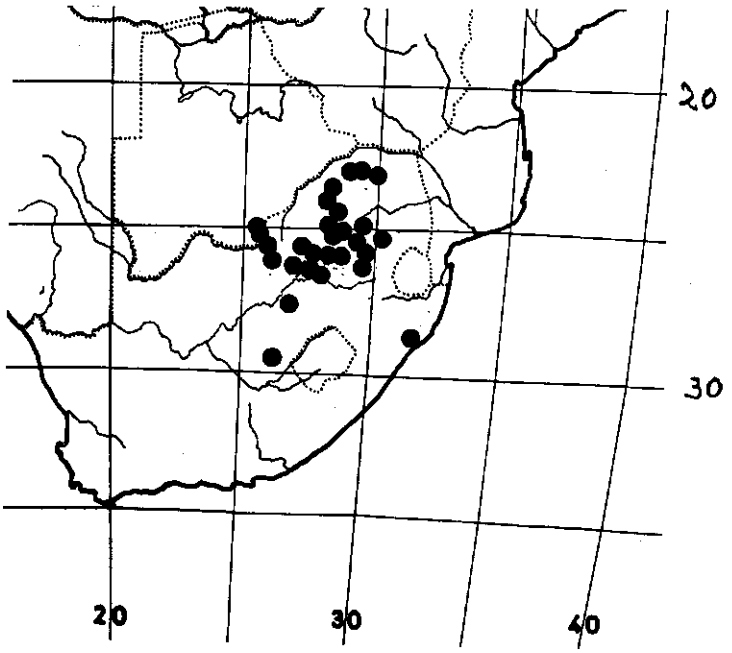


Fig. 2. *Ancylobotrys capensis*. 1, habit (× 2/3); 2, flower (× 2); 3, opened corolla (× 4); 4, opened calyx with pistil (× 6); 5, opened fruit (× 2/3); 6, seed (× 2/3). 1–4 from Hansen 3219; 5–6 from Leeuwenberg 12388.



MAP 2. *Ancylobotrys capensis.*

spicuous secondary veins forming an angle of 70–90° with the costa; tertiary venation inconspicuous above, reticulate and conspicuous beneath. *Inflorescence* 4–15 × 3–8 cm, with 1–5 cymes, each cyme with up to 10 flowers; peduncle 1–14 cm long, pubescent; pedicels 1–4 mm long, densely pubescent; bracts sepal-like, pubescent, 2–5 mm long, persistent, without colleters. *Sepals* connate at the base for up to 1 mm, triangular, 1.2–4.5 × as long as wide, 1.9–7.5 × 0.8–2.7 mm, obtuse or rounded, sometimes truncate or acute at the apex, densely pubescent outside, glabrous inside, sometimes minutely pubescent at the apex. *Corolla* white, sometimes tinged with pink, 18–25 mm long in the mature bud and forming a more or less oblong head 0.6–0.7 of the bud-length, pubescent outside from 1.8–3.5 mm above the base to the base of the lobes; tube thin, not thickened above the anthers, 2–4.1 × as long as the sepals, 0.5–1 × as long as the lobes, 7.7–12 mm long, contracted at the base and 1–1.9 mm wide, widened above to 1.9–2.8 mm, 3.5–4.5 mm above the base (about 0.4 of the tube length), contracted again just above the anthers to 1–2 mm wide, rather abruptly widened at the throat, with two pilose belts inside, one starting 1.7–2.7 mm and ending 4.1–5.5 mm above the base of the tube, and one starting 5–7.6 mm and ending 6.5–7.4 mm above the base or at the base of the lobes, indumentum in the throat somewhat more dense; lobes narrowly elliptic or oblong, 2.6–4.8 × as long as wide, 9–20 × 3–5 mm, rounded or obtuse at the apex, slightly curved inwards at the left side, glabrous outside, sometimes minutely pubescent at the parts not covered in bud, glabrous inside. *Stamens* with apex 2.7–7 mm below mouth of corolla tube (0.4–0.6 of the tube length), inserted

2.2–3 mm from the base of the tube (the base of the anthers 2.8–3.8 mm above the base of the tube); filaments glabrous or minutely pilose inside, glabrous outside, 0.2–1 mm long; anthers 1.8–9.5 × as long as the filaments, 3–10 × as long as wide, 1.8–2 × 0.2–0.6 mm, apex acuminate and sterile for 0.1–0.3 mm. *Pistil* 3–3.8 mm long, with apex 1–1.7 mm below apices of anthers; ovary subglobose or cylindrical, 0.6–1.1 × 0.8–1.3 × 0.8–1.3 mm, densely pubescent; style glabrous, cylindrical, not thickened at the apex, 0.9–1.4 × 0.2–0.4 mm; pistil head: basal part ovoid or nearly so, 0.5–1 × 0.4–0.7 mm, apical part 0.5–1 × 0.4–0.5 mm. Placentas with 8–20 ovules. *Fruit* orange, subglobose, 3–6 cm in diameter, subtended by the persistent calyx; pulp orange. *Seeds* more or less ellipsoid, 12–24 × 16 × 7–9 mm. Embryo: cotyledons elliptic, 20 × 14 mm; rootlet 1.5 × 1 mm.

DISTRIBUTION: Southern Africa.

ECOLOGY: Dry rocky grasslands or bushlands. Alt. 800–1900 m. Flowering from September to December, occasionally in May and June; fruiting from about November onwards.

Geographical selection of the approximately 90 specimens examined:

BOTSWANA. Ootse Mts, Hansen 3219 (C, K); Mannyelanong Hill, 32 km SW of Gaborone, Mott 384 (K, MO, SRGH); Lobatsi, Hillary & Robertson 539 (PRE); ibid., Boschwelatton, McConnell SRGH 68918 (K, SRGH).

SOUTH AFRICA: Transvaal: 13 km N of Louis Trichardt, van Vuuren 1285 (G); 67 km W of Louis Trichardt, Schlieben 7523 (A, B, BR, F, G, HBG, K, M, NY, UC, US); near Mt Blaauwberg, Pole-Evans 894 (S); km 43 Nijlstroom-Vaalwater Road, Leeuwenberg 10915 (WAG); Waterberg, Road to Sandpoort, Smuts & Gillett 3346 (STE); N of Warmbaths, Sidey 3022 (F, S); Vaalwater, Farm Driefontein, Westfall 1522 (K, WAG); Reneke or Ottoshoop, Tuck 4 (K, paratype); Brits District, Jacksonstuin, van Vuuren 207 (K); Rustenburg, Galpin 11520 (BM, K); Magaliesberg, Burke 404 (BM), 405 (K, paratype); Pretoria, near Aapies R., Rehmann 4295 (BM, K, Z); Brummeria, Leeuwenberg 10890 (WAG); ibid., Merxmüller 56 (BR, LISU, M, W); ibid., le Roux 6 (K, MO); N of Pretoria, Scott Elliot 1404 (E); Rietendale, Lanjouw 764 (BR, U); Meyerspark, Leeuwenberg 12388 (WAG); Meintjes Kop, Lansdell 16076 (UPS); W of Pretoria, McLea 3098 (BM, K, lectotype); Hartebees Poortdam, Breyne 5265 (BR); Premier mine, Rogers 25220 (G, S); Ventersdorp District, L.E. Taylor 5082 (STE); near Heidelberg, Schlechter 3523 (B, BR, L, Z); ibid., Thode STE 2671 (STE); S of Heidelberg, M.C. Gillett 4610 (BM, K, LD); Johannesburg, Moss 2703 (BM, Z); ibid., Neethling STE 11451 (STE); between Potchefstroom and Johannesburg, Wall 29 Sept. 1938 (S); Potchefstroom, Hafström & Acock 1108 (S); Losberg, Elandsfontein, Theron 1001 (P); Middelburg District, Waterval, Kleinhoonte 629 (L); Olifantsrivier, Rudatis STE 20184 (STE); ibid., Farm Slaghoek, Mogg et al. 22478 (K); Steenkampsberg, Rudatis STE 13313 (STE). Orange Free State: De Kroon, Putterill 16144 (BR); Ons Rus, near Bloemfontein, M.C. Gillett 172 (K). Natal: Zululand, Santa Lucia, Germain 1516 (BR).

3. Ancylobotrys petersiana (Klotzsch) Pierre, Bull. Soc. Linn. Paris sér. 2: 91. 1898; Pichon, Mém IFAN 35: 290, pl. 21. 1–3. 1953. **Fig. 3, p. 14; map 3, p.15**

Basionym: *Willughbeia petersiana* Klotzsch in Peters, Nat. Reise Mossamb. Bot. 1: 281. 1862.

Types: Mozambique, Sofala, Sena, Peters s.n. (B†, holotype); Niassa, Antonio Enes (= Angoche), Gomes e Sousa 4856 (K, neotype, designated here; isoneotypes COI, PRE, WAG).

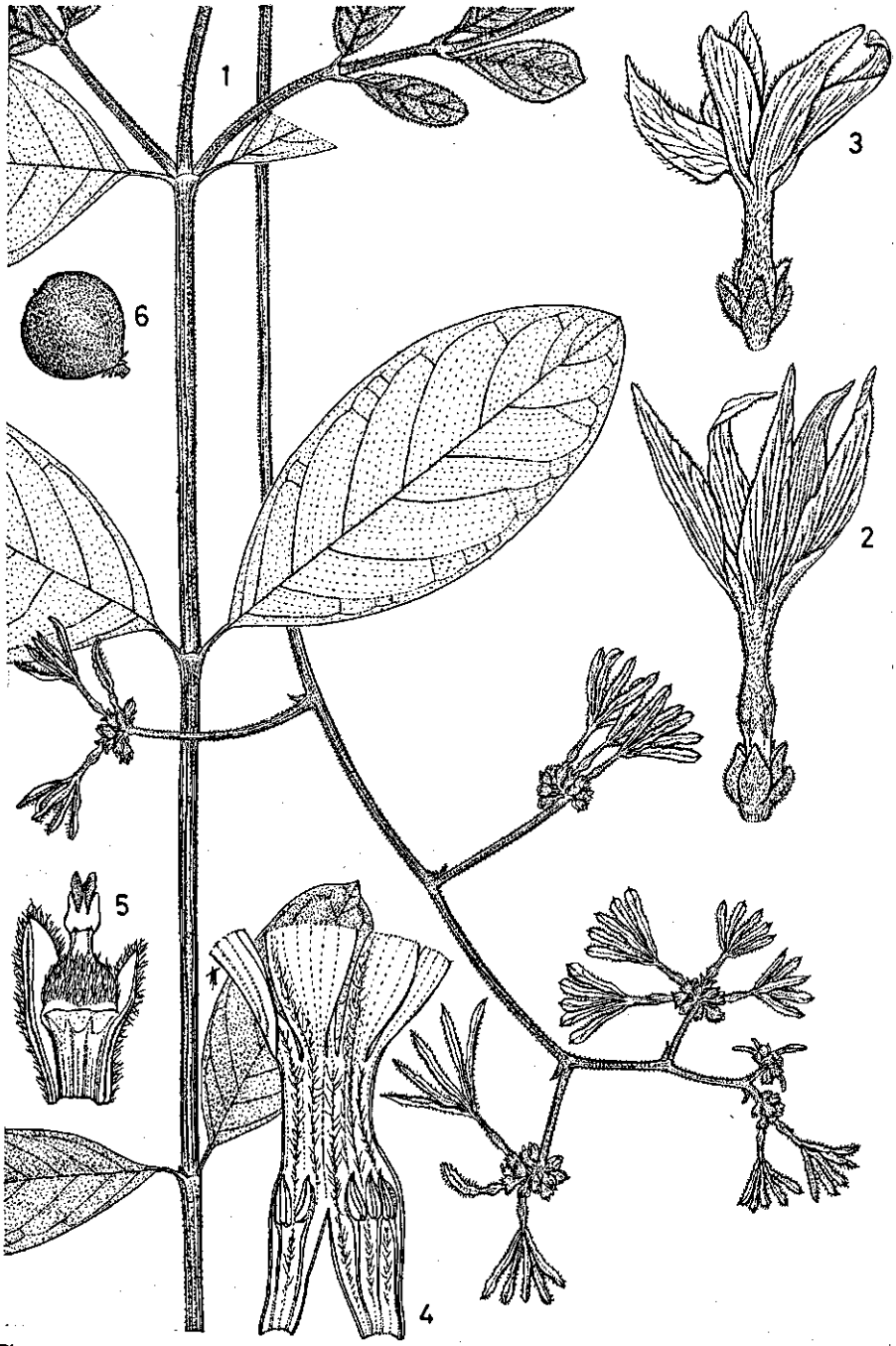
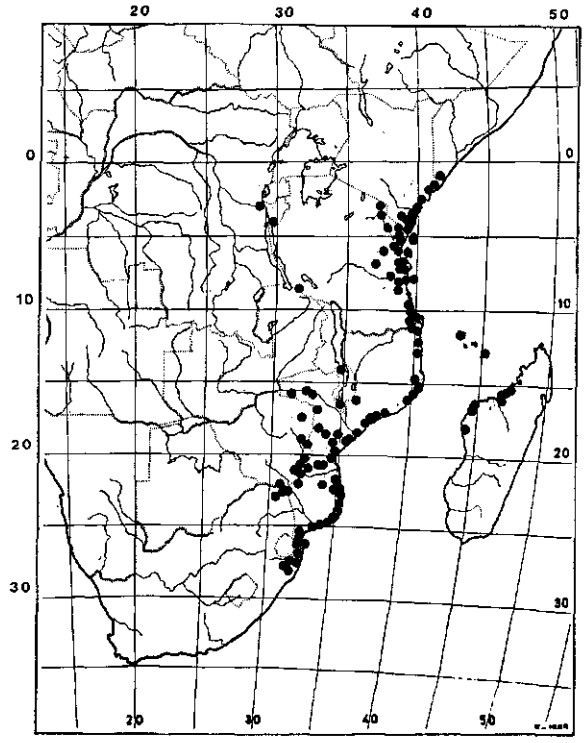


Fig. 3. *Ancylobotrys petersiana*. 1, habit (× 2/3); 2-3, flowers (× 2); 4, opened corolla (× 4); 5, opened calyx with pistil (× 6); 6, fruit (× 2/3). 1–2 and 4–5 from Mendonça 976; 3 from Torre 3839; 6 from Tanner 3439.



MAP 3. *Ancylobotrys petersiana.*

Homotypic synonyms: *Landolphia petersiana* (Klotzsch) Dyer, Report. Roy. Gard. Kew 1880: 42. 1881. *L. scandens* var. *petersiana* (Klotzsch) Hall. f., Jahrb. Hamb. Wiss. Anst. 17, Beih. 3: 82. 1900. *Pacouria petersiana* (Klotzsch) S. Moore, Journ. Linn. Soc. Bot. 37: 180. 1905.

Heterotypic synonyms: *W. sennensis* Klotzsch, l.c. Type: Mozambique, Sofala, Sena, Peters s.n. (B†, holotype). Homotypic synonym: *L. sennensis* (Klotzsch) K. Schum. in Engler, Pflanzenw. Ost-Afr. B: 453. 1895.

L. monteiroi N.E. Br in Monteiro, Delagoa Bay 161, 163, 178. 1891; Dyer ex Stapf, Kew Bull. 1907: 51. 1907. Type: Mozambique, Maputo, Delagoa Bay, Monteiro 37 (K, holotype).

L. angustifolia K. Schum. ex Engl., Abh. Kön. Akad. Wiss. Berlin, Phys.-Math. 1: 34. 1894; K. Schumann, Notizbl. Bot. Gart. Berlin 1: 25. 1895. Type: Tanzania, T3, Mizozue (= Misoswe), Holst 2220 (B†, holotype; K, lectotype, designated here (was isotype); isotypes, COI, HBG, M, phot. of lectotype B, MO, NY). Homotypic synonym: *L. scandens* var. *angustifolia* (K. Schum. ex Engl.) Hall. f., op. cit. 84; *L. petersiana* var. *angustifolia* (K. Schum. ex Engl.) Stapf in Fl. Trop. Afr. 4. 1: 48. 1902. *Pacouria angustifolia* (K. Schum. ex Engl.) O. Kuntze, Deutsche Bot. Monatsschr. 21: 173. 1903.

L. petersiana var. *rotundifolia* Dew., Ann. Soc. Sci. Brux. 19: II, 122. 1895.

Type: Tanzania, Zanzibar, Joblonsky 23 (P, holotype). Homotypic synonym: *A. rotundifolia* (Dew.) Pierre, op. cit. 92. *L. scandens* var. *rotundifolia* (Dew) Hall. f., op. cit. 82.

L. scandens var. *stuhlmannii* Hall. f., op. cit. 83. Type: Tanzania, T3, Amboni, Holst 2563 (B†, holotype; HBG, lectotype, designated here; isolectotypes COI, K, M, W, Z).

L. petersiana var. *rufa* Stapf, l.c. Type; Malawi, sin. loc., Buchanan 437 (K, lectotype).

L. petersiana var. *tubeufii* Busse ex Stapf in op. cit. 49. Type: Tanzania, sin. loc., Busse 1051 (G, lectotype, designated here (was isotype); isotypes B, HBG). Homotypic synonym: *L. scandens* var. *tubeufii* (Busse ex Stapf) Busse in Engler, Bot. Jahrb. 32: 171. 1902.

Scrambling shrub or liana climbing up to at least 5 m high. Trunk 2–5 cm in diameter; bark pale grey-brown, shallowly and longitudinally fissured. Branches dark brown to grey, with many lenticels; branchlets densely rusty-brown-pubescent. *Leaves*: petiole glabrous to pubescent, 6–10 mm long, with colleters in the axils; blade coriaceous when dried, elliptic, sometimes suborbicular or obovate, 1.5–2.4 × as long as wide, 4.5–9.3 × 2.2–4.4 cm, retuse to slightly acuminate at the apex, never with clear acumen, cuneate at the base, sometimes rounded or decurrent into the petiole, glabrous to minutely pubescent on both sides, then especially so on the costa, with 4–9 pairs of curved conspicuous secondary veins, forming an angle of 45–60° with the costa; tertiary venation reticulate, prominent beneath. *Inflorescences* 7.5–36.5 × 3.5–13.5 cm, with 2–6 cymes, each cyme with up to 20 flowers; peduncle 4.5–24.5 cm long, pubescent; pedicels 1–2 mm long, densely pubescent; bracts sepal-like, triangular, densely pubescent outside, glabrous or minutely pubescent inside, obtuse at the apex, 1.4–2.2 mm long, persistent, without colleters. *Sepals* connate at the base for up to 0.7 mm, triangular or narrowly so, sometimes ovate, 1.1–3.3 × as long as wide, 1.7–3.9 × 0.9–2 mm, acute or obtuse at the apex, densely pubescent outside, glabrous or pubescent inside, then especially so near the midrib, persistent, without colleters. *Corolla* white or cream, often pinkisk at tube, 20–37.5 mm long in the mature bud and forming an attenuate head 0.5–0.7 of the bud-length, almost glabrous to pubescent outside, pubescent inside in a belt from 2–5.5 mm above the base to the base of the lobes and pilose near the mouth; tube rather thin, not thickened or slightly so above the anthers, 3.4–5.3 × as long as the sepals, 0.3–0.8 × as long as the lobes, 8.5–13 mm long, contracted at the base and 1–2 mm wide, widened above to 1.4–2.5 mm wide 2.5–5 mm above the base (0.3–0.4 of the tube length), contracted again just above the anthers to 0.8–1.5 mm wide, fairly abruptly widened at the throat; lobes narrowly elliptic to oblong, 3.7–10.7 × as long as wide, 11–35 × 2–4.5 mm, obtuse or acute at the apex, glabrous on both sides. *Stamens* with apex 4.6–7.2 mm below mouth of corolla tube (0.5–0.6 of the tube length), inserted 1.8–3 mm from the base of the tube (the base of the anthers 2.1–3.8 mm above the base of the tube); filaments glabrous or pilose inside, glabrous outside, 0.4–1 mm long; anthers 2–5 × as long as the filaments, 3.8–8 × as long as wide, 1.4–2.1 × 0.2–0.5 mm, apex acuminate and

sterile for up to 0.2 mm. *Pistil* 2.2–3.8 mm long, with apex 1.2–2.2 mm below apices of anthers; ovary subglobose, 0.6–1.2 × 0.8–1.3 × 0.8–1.3 mm, densely appressed-pubescent; style glabrous, cylindrical, not thickened at the apex, 0.3–1.4 × 0.2–0.4 mm; pistil head: basal part cylindrical or nearly so, 0.6–1.1 × 0.5–0.7 mm, apical part 0.3–0.7 × 0.3–0.5 mm. Placentas with 25–50 ovules. *Fruit* yellow or orange, globose to slightly pear-shaped, 25–50 mm in diameter, about 5–20-seeded. *Seed* ovoid or ellipsoid, laterally compressed, 10–18 × 6–10 × 5–6 mm.

DISTRIBUTION: From Somalia to South Africa, Comoro Islands and NE Madagascar mainly near Majunga.

ECOLOGY: Light forest, bush in dune vegetation or on rocky hills. Alt. 0–1300 m. In Madagascar only on coastal dunes. Flowering almost exclusively from August to December and fruiting probably mainly January to March. Only in Kenya and Tanzania flowering and fruiting scattered over the year.

Geographical selection of the approximately 400 specimens examined:

ZAIRE. Kivu: Kigogo, Yamada 400 (WAG).

BURUNDI. Rumonge, Reekmans 1442 (BR, LG, M), 3535 (BR, LG, MO).

SOMALIA. Jubbada Hoose: Badada, Senni 552 (FI); 17 km W of Badada, on road to Kolbio, J.B. Gillet et al. 25152 (K).

KENYA. K1/7: Marrarani, Boni For., Gillespie 386 (FI, K). K7: Lamu District, Kiangwe, Battiscombe 230 (K); Tana River District, Karawa, 48 km S of Garsen, Polhill & Paulo 631 (B, BR, K); Kilifi District, Sakadi, 6 km N of Malindi, Polhill & Paulo 680 (B, BR, K, UPS); Mombasa, Ruspoli 542 (FI); Dasenyi Hill, near Maungu, Bally 12704 (G, K); 4 km W of Ganze, Reitsma 209 (WAG); near Taru, Drummond & Hemsley 4207 (K); ca 3 km SW of Jilore, Spjut & Ensor 2708 (K, UC); Arabuko-Sokoke F.R., Beentje 2286 (WAG); ibid., Faden 74/1254 (K, MO, WAG); Bome R., Kässner 315 (BM, K); Kwale District, near Kwale, Magogo 1241 (BR, K); Shimba Hills, W.E. Taylor anno 1887 (BM); between Umba and Mwena, Drummond & Hemsley 3848 (BR, FI, K).

TANZANIA. T1: Ukerewe, Conrads 439 (FI). T2: Kilimanjaro, Johnston s.n. (BM); Rau For., Moshi, Swynnerton 946 (K). T3: near Umba, Grote Mar. 1915 (B); near Muheza, Archbold 1389 (MO); Kigaraze Hill, Peter 56998 (B, WAG); E Usambara, Bwiti, Peter 57042 (B); W Usambara, Makuyuni District, Koritschoner 1141 (K); Maramba, Peter 57023 (B, WAG); Handeni District, Kwamkono, Archblod 2739 (K, WAG); Msubugwe F.R., Mgaza 547 (K); Mkaramo, Pangani District, Tanner 2561 (K, MICH, NY, UC); Mizozue (= Misoswe), Holst 2220 (COI, HBG, K, M, type of *L. angustifolia*; phot of K sheet B, BR, MO, NY); Tanga, Volkens 173 (BM, G, K, paratype of *Landolphia scandens* var. *stuhlmannii*); Amboni, Holst 2563 (COI, HBG, K, M, W, Z, lectotype of *L. scandens* var. *stuhlmannii*); ibid., Hepper & Field 5523 (K); 20 km NW of Pangani, along road to Muheza, Leeuwenberg 10828 (WAG); Mvumoni Parish, Tanner 3439 (BR, K, MICH, NY, UC, WAG); Bushiri, Faulkner 561 (BR, FI, K, P, S). T4: 8-9 km W from Sumbawanga-Mbala Road, Gereau 4992 (WAG). T6: Kilosa, Swynnerton 4006 (K), 4007 (K); Turiani, Semsei 1409 (BR, K); Morogoro, E.A. Bruce 860 (BM, BR, K, P); Bana F.R., Shabani 108 (K); Usaromo, between Nsua and Bagalla, Peter 31890 (B, WAG); Kibaha, Flock 1000 (S); Mbagala, Shabani 300 (BR, K); Uluguru Mts, Schlieben 3824 (B, BR, K, LISC, M, MA); near Toga, Peter 57002 (B, WAG); Mtanza, Musk 130 (K); Mafia Island, Wallace 698 (K). T7: Kidatu, Mhoro 398 (UPS). T8: Kingupira, Vollesen 4318 (C); 40 km W of Lindi, Lutamba Lake, Schlieben 5357 p.p. (B p.p., BM, G, K, LISC, MO, S, see also *A. amoena*); Tendaguru, Migeod 1053 (BM); Naleindele, Mtwara District, Fison 159 (K); Mtonge, Lindi, Gillman 1162 (K); Newala-Mtwara Road, Richards 17771 (K). Pemba: Mvumoni, Vaughan 369 (BM); Kengeja, R.O. Williams 142 (BR, K); Makongwe Island, Greenway 2734 (K); Paza Island, SW of Pemba, Greenway 1396 (K). Zanzibar: Joblonsky 23 (P, type of *L. petersiana* var. *rotundifolia*), Sacleux 324 (P), Stuhlmann 340 (HBG), 352

(HBG), 475 (HBG, paratype of *L. scandens* var. *stuhlmannii*), 828 (HBG, paratype of *L. scandens* var. *stuhlmannii*), Vaughan 68 (BM); Chukwani, R.O. Williams 112 (BR, K); Mazizini, Faulkner 2423 (B, BR, K). Sin. loc., Busse 1051 (B, G, HBG, type of *L. petersiana* var. *tubeufii*).

MALAWI. Southern: Mangochi- Monkey Bay Road, Salubeni et al. 2643 (MO); near Chikwawa Boma, Salubeni 126 (MAL, SRGH). Sin. loc., Buchanan 437 (BM, K, lectotype of *L. petersiana* var. *rufa*).

MOZAMBIQUE. Cabo Delgado: Palma, Torre & Paiva 12106 (LISC); Nangade Region, Mendonça 976 (LISC); Mtamba, 3 km from Mocimboa, Stocks 61 (K, P, Z); near Mocojo, Stocks 18 (K, Z); Porto Amélia (= Pemba), Mafumo 7 (LMU, MO, WAG). Nampula: Monapo, 2 km from Itoculo, Torre & Paiva 9364 (LISC); Monapo, Groenendijk et al. 979 (K, WAG); Mossuril, de Koning et al. 9690 (K, WAG); Bajone, Barbosa & Carvalho 4285 (G); Mogincual, Torre & Paiva 11447 (LISC); Antonio Enes (= Angoche), Gomes e Sousa 4856 (COI, K, PRE, WAG, neotype), 4870 (K, PRE), 4872 (K, PRE). Zambézia: Milange, Torre & Correia 15848 (LISC); Namacura, km 7 of road to Maganja da Costa, Torre & Correia 14078 (LISC); Maganja da Costa, Andrada 1926 (COI, LISC); Pebane, Munch 256 (K, SRGH); 32 km N of Quelimane, Wild 5863 (BR, K, LISC, MO, SRGH); Nhandoa, Le Testu 832 (BM, P); Chinde, Amico & Buvazzano 403 (FI), 410 (FI); ibid., Le Testu 301 (BM, BR); Boa Vista, Le Testu 302 (P); Luabo R., Kirk 27 (K). Sofala: Inhaminga, Macedo 2466 (WAG); Congone, Zambezi R. mouth, Kirk 309 (K); 47 km S of Muda, Methuen 226 (K); E of Beira, Leach 11260 (BM, K, MO, PRE, SRGH); Mossurizi, W.H. Johnson 89 (K); Barada, Methuen 254 (K); Madanda For., Dawe 458 (K); between Inharingua and Chiloane, W.H. Johnson 17 (K). Manica: Jête, Kirk Dec. 1858 (K). Tete: near Songo, Macedo 4797 (LISC, LMU); Chicoa, Torre & Correia 13896 (LISC); Cabora Bassa, Torre et al. 18912 (LISC); Mazoe R., Whellan SRGH 21889 (K, SRGH). Inhambane: Govuro, Correia & Marques 3269 (LMU, WAG); between Mabote and Mambone, Mendonça 1975 (LISC); Bazaruto Island, Mogg 28451 (K, LISC, LMU, PRE, SRGH); Magarugue Island, Guy SRGH 155425 (LMU, SRGH); between Vilanculos and Massinga, Torre 3839 (LISC); Pomene, P.C.M. Jansen et al. 7518 (K, WAG); Massinga, Gomes e Sousa 1910 (BR, K); 24 km E of Inhambane, along road to Velho, Estevam, Gomes e Sousa 2008 (K, LISC); between Inharrime and Maxine, D'Orey 8 (LISC); Zavala, Moura et al. 299 (LISC, WAG). Gaza: Guijá, road to Pafuri, Barbosa & Lemos 8167 (COI, LISC); Xai-Xai, de Koning 7800 (BR, K, WAG); Chidenguel, Pedro & Pedrogão 1726 (LMU); near Sepúlveda, Balsinhas 1368 (LISC, WAG); Chirindzena, Nuvunga et al. 365 (BM, BR, K). Maputo: Lourenço Marques (= Maputo), Schlechter 11628 (BM, BR, G, HBG, K, P, WAG, Z); Marracuéne, Barbosa & Lemos 8668 (COI, K, LISC, SRGH); Delagoa Bay, Junod 282 (G, Z); ibid., Kirk s.n. (K); ibid., Monteiro 37 (K, P, type of *Landolphia monteiroi*); Inhaca Island, Mogg 28384 (K, PRE, SRGH); Polana, Balsinhas 627 (K, LISC, PRE); Bela Vista (= Matutuine), Balsinhas 1422 (LISC, WAG).

ZIMBABWE. Mashonaland East: Mutoko, T. Müller & Burrows 943 (K, SRGH). Manicaland: Umtali (= Mutate) District, Chase 4161 (BM, BR, COI, K, LISC, MO, PRE, SRGH), 4678 (BM, BR, COI, LISC, MO, PRE, S, SRGH), 7203 (BM, K, LD, LISC, MO, PRE, SRGH); Birchenough Bridge, Ball 1041 (SRGH); Chipinga District, Goodier 123 (K, PRE, SRGH); Chisumbanje, Pope et al. 1487 (B, C, K, MO, SRGH); Lower Sabi R., Wild 2358 (K, SRGH). Victoria: Chief Chitsa's Village, Chase 2410 (BM, K, LISC, SRGH); Gona re Zhou, Mavi 1278 (B, S, SRGH); Chiturupadzi, Mavi 240 (BR, LISC, SRGH).

SOUTH AFRICA. Transvaal: Punda Maria (= Punda Milia), van der Schijf 939 (K); 12 km S of Punda Milia, Codd & Dyer 4592 (K). Natal: 10 km S of Maputo, Moll 4710 (K); near Kosi Nat. Res., Edwards 2548 (K); Ubombo Region, Goodman 313 (E); Sordwana Bay Nat. Park, Koutnik 1220 (MO); ibid., Stephen et al. 1089 (K); Nongoma, Gerstner 146 (K); Hlabisa, Codd 2015 (K).

COMORO ISLANDS. Grand Comore: Humblot 1458 (P, W); Niamaony, Floret 790 (MO, P, WAG). Mayotte: Boivin 3200 (P); Dzoumogné, Pobéguin 45 (P); Biré, Humblot 1146 (=146) (K, P, W); Combani, Humblot 334 (= 1334) (BM, K, LG, P, W).

MADAGASCAR. Majunga, Perrier de la Bâthie 12317 (P); ibid., Ankatsepe, Perrier de la Bâthie 8946 (P); Antsanitia For. Stat., Boiteau 1073 (K, MO, P, WAG); near Boina, Perrier de la Bâthie 8199 (P); Cap Saint André, Perrier de la Bâthie 8198 (P); Besalampy, Decary 8003 (C, P); near Maintirano, Decary 8266 (BM, P, US), 15558 (K, P, WAG).

CULT. Mauritius, Commerson s.n. (P). Sri Lanka, Peradenya Bot. Garden, Trimen Apr. 1884 (K).

4. **Ancylobotrys pyriformis** Pierre, Bull. Soc. Linn. Paris sér. 2: 127 1899; Pichon, Mém IFAN 35: 280. 1953, partly, as for type only. **Fig. 4, p. 19; map 4, p. 20**

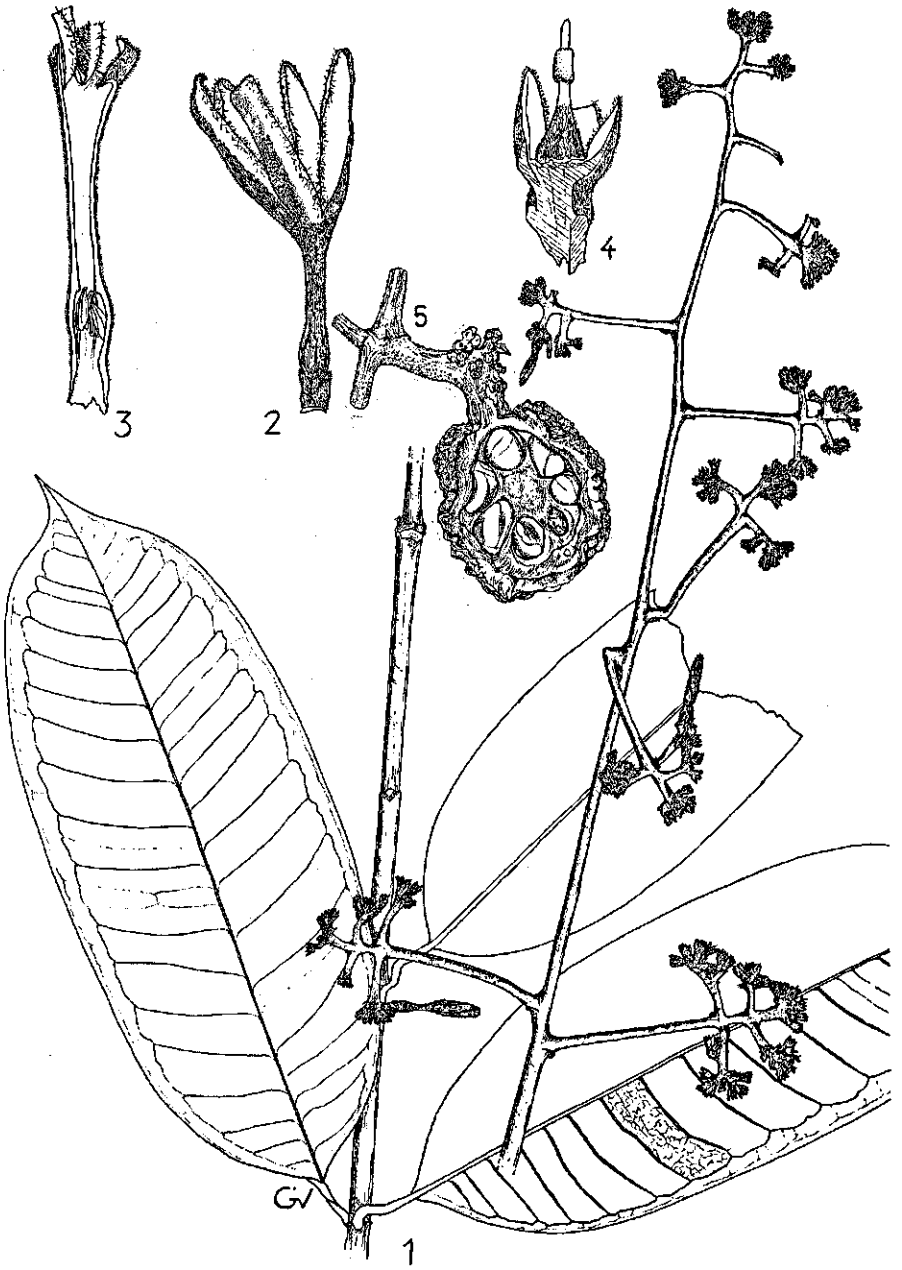
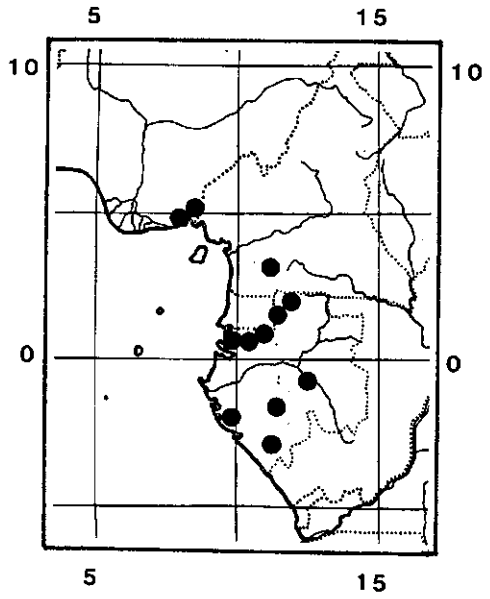


Fig. 4. *Ancylobotrys pyriformis*. 1, habit (× 2/3); 2, flower (× 2); 3, opened corolla tube (× 4); 4, opened calyx with pistil (× 6); 5, opened dried fruit (× 2/3). 1 and 4 from Le Testu 6054; 2 from Le Testu 9511; 3 from Le Testu 9294; 5 from Letouzey 11402.



MAP 4. *Ancylobotrys pyriformis.*

Type: Gabon, Estuaire, near Libreville, Klaine 1401 (P, holotype; isotypes BR, K; phot. of K sheet B, BR, MO, NY).

Homotypic synonym: *Pacouria pyriformis* (Pierre) Pichon, Mém. Mus. Nat. Hist. Nat. sér. 2. 24: 144. 1948.

Heterotypic synonyms: *A. trichantha* Pichon, Mém. IFAN 35: 299, pl 19. 6–8. 1953, **syn. nov.** Type: Ogooué-Lolo, Gabon, Comi, Lastoursville region, Le Testu 8255 (P, holotype; isotypes BM, MO).

A. gabonensis Pichon, op. cit. 299, pl. 20, **syn. nov.** Type: Gabon, Woleu-Ntem, Oyem, Le Testu 9294 (P, holotype: isotypes BM, BR, GH, K, LISC, MO, WAG).

Large liana climbing up to 30 m high in trees. Branches dark brown, lenticellate; branchlets densely pubesecent. *Leaves*: petiole 8–20 mm long, glabrous to pubescent; blade coriaceous even when fresh, elliptic to oblong, 1.9–2.5 × as long as wide, 7.5–20 × 3.5–9 cm, usually short-acuminate at the apex, acumen 3–13 mm long, acute, cuneate at the base, somewhat revolute at the margin, glabrous on both sides, with 8–16 pairs of straight to slightly curved secondary veins, forming an angle of 70–90°, anastomosing at the apex, among 2 secondary veins 0–2 more or less straight less conspicuous ones; tertiary venation reticulate. *Inflorescences* up to 49 × 12 cm, with about 10 cymes, each cyme up to approximately 50-flowered. Peduncle 9.5–14 cm long, puberulous, glabrescent; pedicels 0–2 mm long, densely pubescent; bracts sepal-like, densely pubescent, 1–1.5 mm long, persistent, sometimes with colleters at both sides of the base. *Sepals* connate at the base for up to 0.3 mm, triangular, 0.9–1.8 × as long as wide, 1.2–2 × 1–1.6 mm, obtuse or acute at the apex, densely pubescent outside, ciliate, glabrous inside, with or without up to

20 colleters alternating with them. *Corolla* white, 20–30 mm long in the mature bud, densely pubescent outside; tube rather thick, thickened above the anthers, 5–7 × as long as the sepals, 0.7–0.9 × as long as the lobes, 9.5–15 mm long, contracted at the base and 1.1–1.5 mm wide, widened above to 1.5–3.6 mm wide 3–4.5 mm above the base (about 0.3 of the tube length), contracted again above the anthers to 1–2.7 mm wide, abruptly widened at the throat, with a pilose belt inside from between the anthers (1.9–2.8 mm above the base) to just above them (3.4–4.5 mm above the base) or the base of the lobes, indumentum less dense towards the lobes; lobes narrowly elliptic to narrowly obovate, 1.1–1.4 × as long as the tube, 3.2–4 × as long as wide, 12–20 × 3.5–5 mm, rounded or obtuse at the apex, densely pubescent outside at the parts not covered in bud, glabrous to pilose outside at the parts covered in bud, glabrous or minutely pilose inside. *Stamens* with apex 5.5–9 mm below mouth of corolla tube (about 0.6 of the tube length), inserted about 0.2 of the length of the tube (at 1.9–2.5 mm from the base), (the base of the anthers 2.4–2.8 mm above the base of the tube); filaments glabrous, 0.6–1.1 mm long; anthers 1.3–2 × as long as the filaments, 3–6.5 × as long as wide, 1.2–2 × 0.2–0.7 mm, apex acute, sometimes minutely retuse, rarely acuminate and then for 0.2 mm sterile. *Pistil* 2.4–5.1 mm long, with apex 0.2–1.5 mm below apices of anthers; ovary conical to almost ovoid, 0.8–1.2 × 0.9–1.4 × 0.9–1.4 mm, densely puberulous; style glabrous, cylindrical, 0.2–1.9 × 0.2–0.4 mm; pistil head: basal part ovoid or cylindrical, 0.5–1.2 × 0.4–0.6 mm, apical part conical, 0.6–1.6 × 0.3–0.5 mm. Placentas with 25–40 ovules. *Fruit* yellow, globose or pear-shaped, 7–15 cm in diameter, 4–20-seeded. *Seeds* irregularly ellipsoid, 19–26 × 16–19 × 10–13 mm. Embryo: cotyledons more or less elliptic, 17–25 × 15–16 mm, undulate; rootlet 1 × 1 mm.

DISTRIBUTION: Nigeria, Cameroun and Gabon.

ECOLOGY: Rain forest. Flowering and fruiting from June to March. The fruits probably need a year to develop and mature.

Specimens examined:

NIGERIA. Cross River State, Eket, Talbot 3119 (BM, K, Z); Awi-Odukpani Road, Onochie & Jones FHI 55237 (K).

CAMEROUN. Centre-Sud: Nkolemana, Letouzey 11402 (BR, K, P, WAG).

GABON. Estuaire:, near Libreville, Klaine 1401 (BR, K, P, type; phot. of K sheet B, BR, MO, NY); 7 km E of Mvoum, A.M. Louis et al. 266 (WAG). Woleu-Ntem: Cristal Mts, Tchimbélé, Wieringa 977 (WAG, fruit only); 30 km E of Abanga R., Leeuwenberg & Persoon 13550 (BR, WAG); Oyem, Le Testu 9294 (BM, BR, GH, K, LISC, MO, P, WAG, type of *A. gabonensis*), 9511 (B, BM, BR, GH, K, LISC, MO, P, WAG, paratype of *A. gabonensis*). Ogooué-Maritime: Rabi, Wieringa & van der Poll 1380 (WAG). Ngounié: Mogoumou, Le Testu 6054 (BM, BR, GH, LISC, MO, P, WAG, paratype of *A. gabonensis*). Ogooué-Lolo: Comi, Lastoursville Region, Le Testu 8255 (BM, MO, P, type of *A. trichantha*). Nyanga: 45 km SW of Ndendé, near road to Tchibanga, A.M. Louis et al. 1177 (WAG).

CULT. Gabon, Libreville, Chevalier 4410 (P).

Notes. Pichon confused the type of *A. pyriformis* with that of *A. robusta*. It turned out, that all specimens he cited except the type of *A. pyriformis* do not be-

long there, but to *A. robusta*. The specimens he cited as *A. gabonensis* belong here and therefore the latter name has been reduced to synonymy in this publication. The last synonym *A. trichantha* has been based on a specimen of which the flowers are somewhat larger than those of the other specimens named *A. pyriformis* here. As it fits perfectly in the species as for all characters, *A. trichantha* is also reduced to a synonym.

5. Ancylobotrys robusta Pierre, Bull. Soc. Linn. Paris sér. 2: 128. 1899. Type: Equatorial Guinea, Rio Muni, Mann 1764 (P, holotype: isotype K).

Fig. 5, p. 23; map 5, p. 24

Homotypic synonyms: *Landolphia robusta* (Pierre) Stapf in Fl. Trop. Afr. 4. 1: 43. 1902. *Pacouria robusta* (Pierre) Pichon, Mém. Mus. Nat. Hist. Nat. sér. 2. 24: 144. 1948.

Liana climbing up to at least 30 m high. Trunk 2–8 cm in diameter; bark rather rough, shallowly and longitudinally fissured, about 5 mm thick. Branches brown, lenticellate; branchlets densely rusty-brown-pubescent. *Leaves*: petiole puberulous, sometimes glabrous beneath, 12–26 mm long, with conspicuous colleters in the axils; blade coriaceous even when fresh, usually ovate, sometimes elliptic or oblong, 1.5–2.9 × as long as wide, 8–21 × 4–8 cm, acuminate at the apex, acumen 4–17 mm long, cuneate to truncate at the base, glabrous to minutely pubescent on both sides, with 5–12 pairs of conspicuous secondary veins, forming an angle of 45–60° with the costa; tertiary venation reticulate. *Inflorescences* 16–43 × 6–14 cm, with 8–12 cymes, each cyme with up to about 60 flowers; peduncle 7–19 cm long, puberulous or pubescent; pedicels 1–3 mm long, densely pubescent; bracts sepal-like, densely pubescent, about 1 mm long, persistent, usually with colleters at the base. *Sepals* connate at the base for up to 0.3 mm, triangular to ovate, 1–2.7 × as long as wide, 1.2–3.7 × 0.8–2 mm, acute to truncate at the apex, densely rusty-brown-pubescent outside, ciliate, glabrous inside. *Corolla* white or yellow, often with a pinkish tube, 16.5–30.5 mm long in the mature bud, forming an attenuate head 0.4–0.6 of the bud length, glabrous to pubescent outside; tube rather thin, sometimes slightly thickened above the anthers, 4.1–8.7 × as long as the sepals, 0.9–2.1 × as long as the lobes, 10.5–20 mm long, contracted at the base and 1–1.6 mm wide, widened above to 1.5–2.5 mm wide 3–4.5 mm above the base (0.2–0.4 of the tube length), contracted again at the throat to 0.5–1.3 mm wide, abruptly widened at the throat, glabrous inside, sometimes with a minute pilose belt from behind the anthers (2.5–4 mm above the base) to 4–9.5 mm above the base of the tube, indumentum less dense towards the apex, throat glabrous; lobes narrowly ovate to oblong, 0.5–1.1 × as long as the tube, 3.5–6 × as long as wide, 8.5–14 × 1.5–4 mm, obtuse or rounded at the apex, glabrous on both sides. *Stamens* with apex 6.2–14 mm below mouth of corolla tube, (at 0.6–0.8 of the tube length), inserted 0.1–0.2 of the length of the corolla tube, (at 1.9–2.8 mm from the base); anthers 2.5–3.5 mm above the base of the tube); filaments glabrous, 0.6–1.2 mm long; anthers 1.2–2.3 × as long as the filaments, 2.3–7 × as long as wide, 1.1–1.5 × 0.2–0.6 mm, apex acuminate or acute and sterile for up to 0.1 mm. *Pistil*

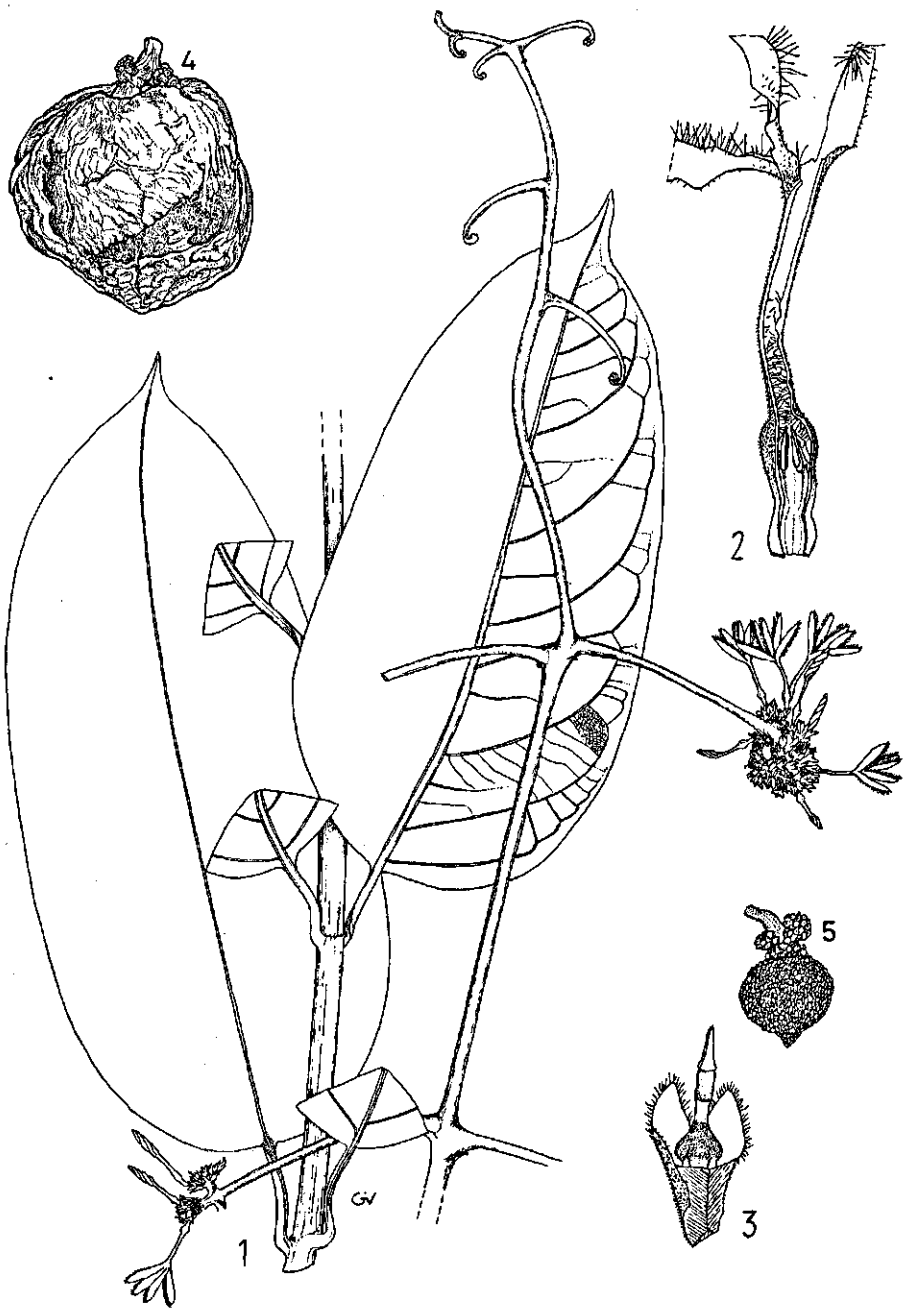
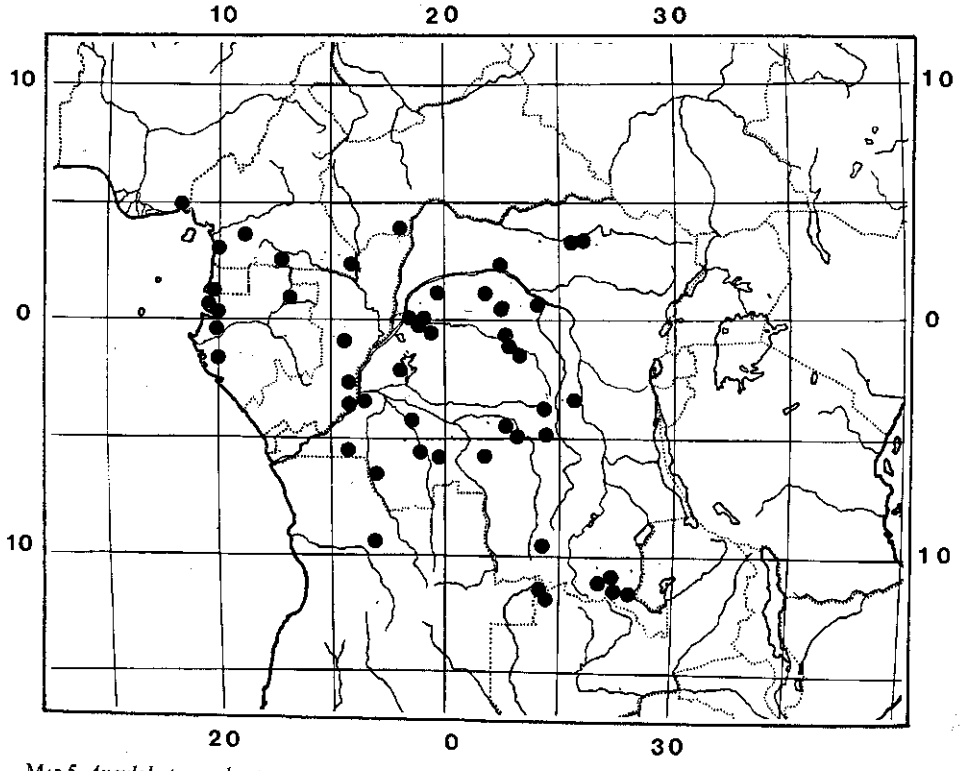


Fig. 5. *Ancylobotrys robusta*. 1, habit (× 2/3); 2, opened corolla (× 4); 3, opened calyx with pistil (× 6); 4, dried fruit (× 2/3); 5, dried immature fruit (× 2/3). 1–3 from J. Louis 9465; 4 from J. Louis 2637; 5 from Koufani 163.



MAP 5. *Ancylobotrys robusta*.

2.8–3.3 mm long, with apex 1.1–1.7 mm below apices of anthers; ovary ovoid or nearly so, 0.9–1.2 × 0.8–1.8 × 0.8–1.8 mm, appressed-puberulous or densely so; style glabrous, cylindrical, not thickened at the apex, 0.4–0.9 × 0.2–0.4 mm; pistil head: basal part cylindrical, 0.6–0.9 × 0.3–0.6 mm, upper part conical, 0.5–0.9 × 0.2–0.5 mm. Placentas with 25–50 ovules. *Fruit* orange, subglobose, 3–6 cm in diameter, truncate at the base, more or less ridged at the apex, smooth to somewhat warty, lenticellate, subtended by the persistent calyx, ca 10–40-seeded. *Seed* ellipsoid, 10–13 × 8–11 × 3–5 mm.

DISTRIBUTION: Cameroun to Zaire.

ECOLOGY: Forests. Alt. 0–1200 m. Flowering and fruiting scattered over the year with peaks in flowering June-July and November-December.

Geographical selection of the approximately 110 specimens examined:

CAMEROUN. Centre Sud: 9 km N of Kribi, Bos 4985 (BR, LD, M, WAG); 9 km SW of Yaoundé, Breteler 1596 (WAG); near Akonetye, S of Ebolowa, Koufani 163 (P, WAG). Est: 45 km S of Lindjombo, Sangha R., Harris & Fay 1574 (K).

EQUATORIAL GUINEA. Rio Muni, Mann 1764 (K, P, type).

GABON. Estuaire: near Libreville, Klaine 1400 (P), 1503 (P); Acondjo, Chevalier 27107 (P); 5 km N

of Ndouaniang, Wilks 971 (WAG). Ogooué-Maritime: Mvouma, between Bokoïo et Mouenda, Arsandeau 15 June 1920 (P). Ogooué-Ivindo: Babiel-Sud, Bos et al. 10720 (BR, WAG).

CONGO. Cuvette: km 46 Edou-Boundji Road, Descoings 8107 (P). Plateaux: Ngo For., Makany 1820 (P). Pool: Batéké Plateau, Sita 2724 (P).

CENTRAL AFRICAN REPUBLIC. Lobaye: Boukoko, Tisserant 2123 (BM, BR, GH, P), 2293 (BM, P, WAG).

ZAIRE. Bas Zaire: Kimbuba, Callens 4578 (BR). Bandundu: near Ila, Anonym. 12 Mar. 1907 (BR); Ngandju-Sedec, Vermoesen 2422 (BR, K); Madibi, Sapin 28 June 1906 (BR); Kasongo Luna, Vanderyst 17567 (BR); Lutshima, Sapin July 1907 (BR); Bienge, Sapin Oct. 1907 (BR). Equateur: Eala, J. Louis 1933 (B, BR, K, P); ibid., Staner 1423 (BR, K, P); Ingende, Goosens 6029 (BR); Djoa, Evrard 4093 (BR, K); Bala Lundji, Pynaert 267 (BR); Basankusu, L. Dubois 440 (BR); Bodala, Coulon 4 (BR); Bumba, Pynaert 83 (BR); Djolu, Evrard 5766 (BR, K); Mondombe, Evrard 5557 (BR); ibid., Jespersen 42 (BR): Balanga, zone d'Ikela, Bermejo 124 (BR). Haut-Zaire: Yangambi, J. Louis 2637 (BR, K), 9465 (BR, MO), 15600 (BR, NY, US); Bambesa, Gérard 4914 (BR, WAG); Bambili, Anonym. anno 1906 (BR). Kasai Occidental: Kafulumba, Sapin 5 Jan. 1907 (BR). Kasai Oriental: Bena-Dibele, E. & M. Laurent 1 Dec. 1903 (BR); Mununga, Sapin Oct. 1906 (BR); Katako Kombe, Claessens 432 (BR); near Lubefu, Lescrauwaet anno 1907 (BR). Kivu: Elundu, Kibombo, Gaillez 304 (BR). Shaba: Dilolo, Young 246 (A, BM, BR, NY, S, Z); Mapanda, Desenfans 1967 (BR); Likasi Road, Ritschaert 1710 (BR, K); Luiswishi, Malaisse 9894 (BR); ibid., Lisowski 90141 (BR).

ANGOLA. Sin. loc., Lynes 349b (BR). Malaje: Quela, von Nolde 761 (BM).

ZAMBIA. North-Western: Mwinilunga District, ca 6 km N of Kalene Hill Mission, Edwards 793 (BR, K, P, SRGH); Lisombo R., 15 km SW of same mission, Drummond & Williamson 9479 (K, SRGH); Matochi Farm Road, 24 km from Mwinilunga, Duff 191 (K).

CULT. Gabon, Libreville, Chevalier 26747 (P), 26827 (P).

Note. *A. robusta* is reinstated here as a distinct species (see note with *A. pyriformis*).

6. **Ancylobotrys scandens** (Schum. & Thonn.) Pichon, Mém. IFAN 35: 286, pl. 18. 4. 1953. **Fig. 6, p. 26; map 6, p. 27**

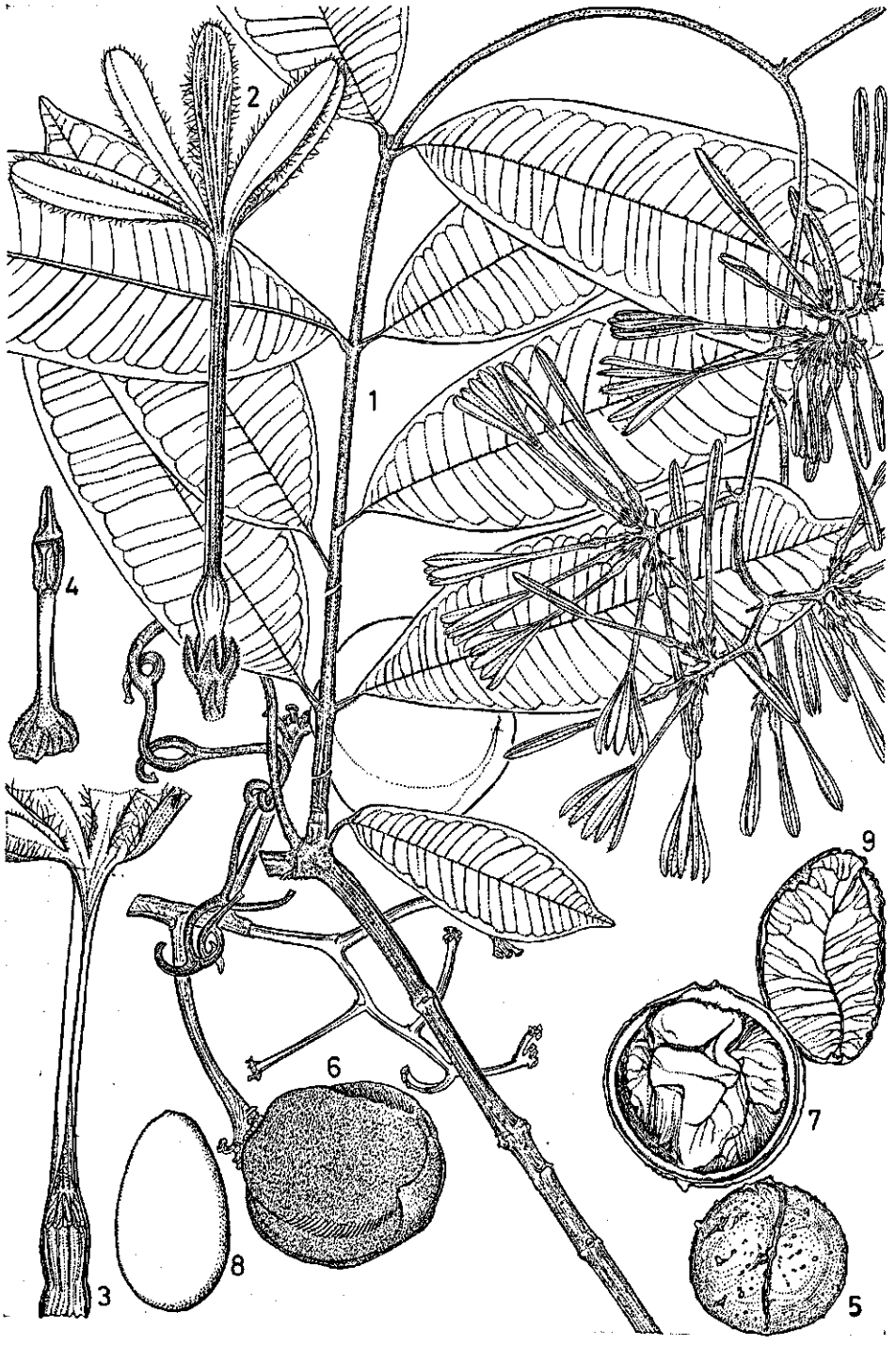
Basionym: *Strychnos scandens* Schum. & Thonn., Beskr. Guin. Pl. 147. 1827. Type: Ghana, Eastern, Akwapim, Thonning 281 (C-THONN, holotype; isotypes G, P-JU).

Homotypic synonyms: *Landolphia scandens* (Schum. & Thonn.) Didrichs., Vidensk. Meddel. Naturh. Foren Kjöbenhavn 1853: 190. 1854. *Pacouria scandens* (Schum. & Thonn.) Pichon, Mém, Mus. Nat. Hist. Nat. sér. 2. 24: 144. 1948.

Heterotypic synonyms: *Landolphia petersiana* var. *crassifolia* K. Schum. in Engler, Bot. Jahrb. 15: 408. 1893. Type: Angola, Cuanza Norte, Golungo Alto, Welwitsch 5927 (BM, lectotype, designated here; isolectotypes C, COI, G, K, MO, P). Homotypic synonyms: *L. welwitschii* Dyer fide Stapf ex De Wild. & Th. Dur. Ann. Mus. Congo sér. 3. 1: 146. 1901. *Pacouria crassifolia* (K. Schum.) Hiern, Cat. Afr. Pl. Welw. 1: 663. 1898. *A. mammosa* var. *crassifolia* (K. Schum.) Pierre, Bull. Soc. Linn. Paris sér. 2: 92. 1898.

L. petersiana var. *mucronata* Dew., Ann. Soc. Sci. Brux. 19: 122. 1895. Type: Gabon, Bonando Plain, Duparquet l, anno 1864 (P, holotype). Homotypic synonym: *A. mammosa* var. *mucronata* (Dew.) Pierre. l.c.

L. scandens var. *coriacea* Hall. f., Jahrb. Hamb. Wiss. Anst. 17, Beih. 3: 81. 1900. Type: Gabon, Estuaire, near Libreville, Klaine 591 (P, lectotype, designated here (was isotype); isotypes BR, K).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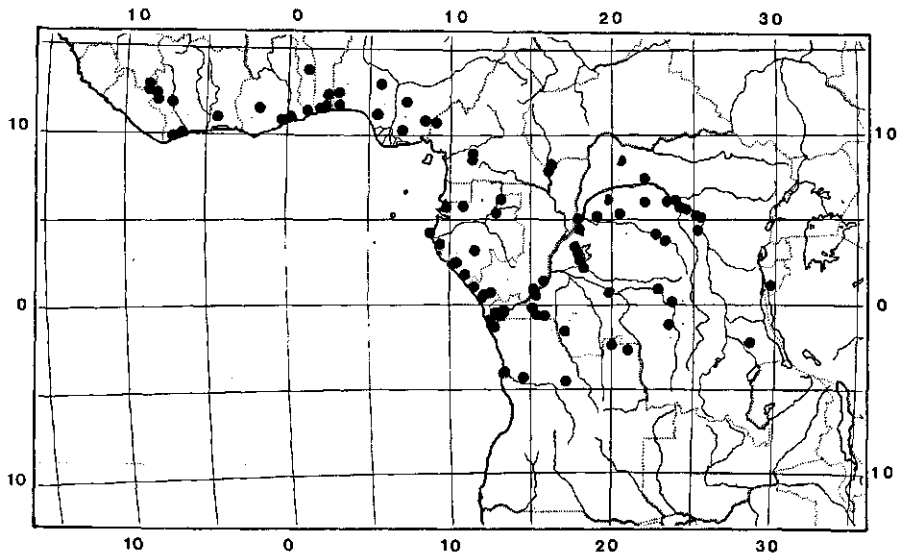


MAP 6, *Ancylobotrys scandens*.

L. echinata A. Chev., Mém. Soc. Bot. Fr. 8: 45. 1908. Type: Congo, Pool, Brazzaville, Chevallier 4286 (P, lectotype, designated here). Homotypic synonym: *P. echinata* (A. Chev.) Pichon l.c.

L. scandens var. *floribunda* Pellegr., Mém. Soc. Linn. Norm. sér. 2. Bot. 1. 3: 24. 1928. Type: Gabon, Nyanga, Tchibanga, Le Testu 1438 (P, holotype: isotypes BM, K, LISC, MO). Homotypic synonym: *P. scandens* var. *floribunda* (Pellegr.) Pichon, l.c.

A. brevituba Pichon, Mém. IFAN 35: 283, pl. 17. 5–6. 1953, **syn. nov.** Type: Benin, Kétou Forest, Le Testu 110 (P, holotype, isotype BM).

Sarmentose shrub or liana climbing up to at least 12 m high. Trunk 2–5 cm in diameter; bark rather smooth, lenticellate. Branches brown, lenticellate; branchlets densely pubescent with rather short hairs. *Leaves*: petiole 4–15 mm long, pubescent, with colleters in the axils; blade coriaceous even when fresh, usually elliptic or narrowly so, sometimes ovate or oblong, 1.9–3.2 × as long as wide, 6.5–17.5 × 2.6–7 cm, acuminate at the apex, cuneate, sometimes rounded at the base, glabrous on both sides, with 10–17 pairs of more or less straight conspicuous secondary veins, forming an angle of 60–90° with the costa; often alternated by less conspicuous ones; tertiary venation reticulate. *Inflorescences* 9–25 × 4–15 cm, with 4–8 cymes, each cyme with up to about 30 flowers; peduncle 4–14.5 cm long,

Fig. 6. *Ancylobotrys scandens*. 1, habit (× 2/3); 2, flower (× 2); 3, opened corolla (× 2); 4, pistil (× 6); 5, bottom of ovary (× 6); 6, fruit (× 2/3); 7, longitudinal section of fruit (× 2/3); 8, seed (× 2); 9, embryo on half of endosperm (× 2). 1–4 from J. Louis 11491; 5 and 7–9 from Breteler 2882; 6 from J.W.A. Jansen 1816.

pubescent; pedicels up to about 2.5 mm long, densely pubescent; bracts sepal-like, densely pubescent, up to 1.5 mm long, persistent, usually with colleters at the base. *Sepals* up to 0.5 mm connate at the base, narrowly triangular to ovate, 0.7–3.2 × as long as wide, 0.6–3.5 × 0.8–1.5 mm, obtuse, sometimes acute at the apex, densely pubescent outside, glabrous inside, sometimes with colleters at the base, alternating with them. *Corolla* white, sometimes tinged with pink, 33–59 mm long in the mature bud and forming a more or less oblong head 0.2–0.4 of the bud length, glabrous or sparsely short-pubescent; tube thin, not thickened above the anthers, 8.1–32.4 × as long as the sepals, 1.4–3.8 × as long as the lobes, 17.5–43.5 mm long, contracted at the base and 1–2 mm wide, widened above at insertion of anthers and widest 4.3–7.5 mm above the base (0.1–0.3 of the tube length) to 1.7–3 mm wide, contracted again just above the anthers to 0.6–1.7 mm wide, fairly abruptly widened at the throat, with a pilose belt inside from between the anthers which is 3.2–8.5 mm above the base, to 6.5–16 mm above the base of the tube, throat glabrous; lobes narrowly elliptic to oblong, 2.4–5.8 × as long as wide, 7–19 × 1.9–5 mm, obtuse at the apex, slightly curved inwards at the left side, glabrous on both sides. *Stamens* with apex 14–33 mm below mouth of corolla tube (0.7–0.9 of the tube length), inserted 3.2–6.5 mm from the base of the tube (the base of the anthers 3.7–7 mm above the base of the tube); filaments glabrous or minutely pilose inside, glabrous outside, 0.5–1 mm long; anthers 1.9–4.6 × as long as the filaments, 3.4–4.8 × as long as wide, 1.6–2.3 × 0.4–0.5 mm, apex acuminate and sterile for up to 0.2 mm. *Pistil* 4.2–6.5 mm long, with apex 0.8–1.8 mm below apices of anthers; ovary almost ovoid to subglobose, 0.7–1.2 × 1–1.8 × 1–1.8 mm, densely pubescent; style glabrous, cylindrical, not thickened at the apex, 1.5–2.4 × 0.2–0.4 mm; pistil head: basal part cylindrical to subglobose, 0.9–1.3 × 0.5–0.7 mm, apical part 0.7–1.2 × 0.2–0.5 mm. Placentas with 35–50 ovules. *Fruit* yellow, orange, or red, subglobose, 2–5 cm in diameter, cuneate to truncate at the base, sometimes minutely warty, subtended by the persistent calyx, about 2–40-seeded. *Seeds* more or less ellipsoid, smooth, 8–14 × 5–8 × 4–5 mm. Embryo: cotyledons 12 × 8 mm, slightly undulate; rootlet about 1 × 1 mm.

DISTRIBUTION: West and Central Africa.

ECOLOGY: Forest or gallery forest. Alt. 0–1400 m. Flowering and fruiting probably scattered over the year, in West Africa probably mainly from January to March.

Geographical selection of the approximately 230 specimens examined:

GUINEA. Nzérékoré: Nimba Mts base, Schnell 1860 (P).

LIBERIA. Yéképa, Adam 25182 (MO); Nimba Mts, J.W.A. Jansen 1816 (WAG).

IVORY COAST. 2 km E of Danané, Leeuwenberg 2993 (BR, K, L, UC, WAG); midlle Sassandra R. basin, Guidéko, Chevalier 16478 (P); Sassandra, near Longa, de Koning 2688 (WAG); 5 km W of bifurcation to Grand Béréby in Tabou-San Pedro Road, Leeuwenberg 12318 (WAG); 13 km from km 26 Sassandra-San Pedro Road to Monogaga, Leeuwenberg 12330 (WAG); Bouroukrou, Chevalier 16682 (P).

GHANA. Eastern: Akwapim, Thonning 281 (C-THONN, G, P-JU, type); Kwaobenya, Akwapim, Irvine 1545 (K); Aburi Scarp, Enti FH 7574 (B, K, P, WAG); Legon Hill, Adams 3656 (K); Krobo plains, W.H. Johnson 494 (K). Ashanti: Bosumtwe Range F.R., Hall & Abbew GC 44142 (WAG).

TOGO. near Lomé, Warnecke 252 (BM, BR, E, G, K, L, M, P); Cabolé (= Kambolé), Annet 66 (P).

BENIN. near Ouidah, Chevalier 23456 (P); Allada de Torricada, Estève in Le Testu 169 (BM); Adjara, Chevalier 22742 (P); Cohoué, between Porto-Novo Lagoon and the coast, Chevalier 22790 (P); Adja Ouéré, Le Testu 112 (A, BM, BR, K, MO, P, S, UC); Kétou For., Le Testu 110 (BM, P, type of *A. brevituba*).

NIGERIA. Lagos: Lagos, Dalziel 1104 (E, K, M). Oyo: Asaka Division, Ibuya, Unwin 14 (K, P). Ogun: Abeokuta, van Meer & Redhead 745 (WAG). Bendel State: Benin City, Unwin 28 in Chevalier 15140 (P). Anambra: Nsukka District, Ubukpa For., Emwigbon & Anyandiegwu FHI 72924 (K, WAG). Imo: Umudike, Ariwaodo 1280 (K, LISC).

CAMEROUN. Sud-Ouest: 40 km W of Mamfé, road to Calabar, Letouzey 13555 (BR, K, P, WAG). Centre-Sud: Nkolfeb Hill, Mbaminkom Mts, Dang 666 (P, WAG); Nkolbisson, 7 km W of Yaoundé, Breteler 2882 (A, BR, K, LISC, M, P, WAG); Yaoundé, Jacques Félix 5072 (P).

CENTRAL AFRICAN REPUBLIC. Sangha: 25 km ESE of Bayanga, Dzanga-Sangha Res., Carroll 80 (WAG); ibid. Harris & Fay 948 (K, WAG).

GABON. Estuaire: near Libreville, Klaine 29 (K, P), 411 (P), 591 (BR, K, P, type of *Landolphia scandens* var. *coriacea*), 1089 (BR, P); ibid., Reitsma 796 (WAG); ibid., Thollon 156 (P); Cap Esterias, N. Hallé 809 (P). Woleu-Netem: 8 km E of Médouneu, Leeuwenberg 12531 (WAG). Ogooué-Ivindo: Belinga, Gentry 33570 (MO); Makokou, Caballé 305 (WAG); ibid., Florence 2000 (P). Ogooué-Maritime: Cap Lopez, Chalot 58 (P); Fernan Vaz, Leroy Sept. 1894 (P); Gamba, Wieringa & van der Poll 1371 (WAG). Ngounié: between Mouila and Yono, Breteler et al. 8148 (WAG). Nyanga: Panga, Le Testu 1775 (BM, BR, G, K, LISC, MO, P); ibid., J. de Wilde et al. 9260 (WAG); Mayumba, A.M. Louis 2220 (WAG); Tchibanga, Le Testu 1438 (BM, K, LISC, MO, P, type of *L. scandens* var. *floribunda*). Bonando Plain (not localized), Duparquet 1 (P, type of *L. petersiana* var. *mucronata*).

CONGO. Badondo Kouilou: Numbi R., Trochain 10236 (P); Kouilou Region, Moutsamboté & Dowsett-Lemaire 4501 (BR, WAG); Tchissanga, Dowsett-Lemaire 1400 (BR, WAG); Loango, Lecomte B 70 (P); between Djéno and the Cabinda border, Farron 4777 (P, WAG). Pool: Batéké Plateau, km 46 Maloukou-Maès Road, Sita 2726 (P); Brazzaville, Chevalier 4286 (P, lectotype of *L. echinata*), 11266 (P, paratype of *L. echinata*).

ZAIRE. Bas-Zaire: Moanda, Gillet 4032 (BR); ibid., Vanderyst 27837 (BR); Poiti-Tshoa Road, Dewèvre 393 (BR); Tshikay and Matemba Plateaux, Boma-Banana Road, Wagemans 1345 (BR, WAG); Kanzi, Nsimundele 785 (BR); Luki, Breyne 3808 (BR, WAG); ibid., Toussaint 121 (BR, K, P); Gimbi, Toussaint 602 (BR); Benga, Kisantu, Callens 4334 (BR, NY); Kimvula-Ngidinga Road, Callens 3834 (BR, NY); between Kimvula and Kimbuka, Callens 3864 (BR). Kinshasa: Ndjili, Evrard 6527 (BR, MO). Bandundu: near Pelende, Callens 4769 (BR); between Selenge and Lukolela, Goosens 5096 (BR); Ibali, E. & M. Laurent 4 Nov. 1903 (BR); Ganda For., Body anno 1906 (BR); Bokoro, Jans 719 (BR); Lubue, Gentil 46 (BR). Equateur: Irebu, M. Laurent 636 (BR); near Eala, Nannan 42 (BM, BR); Eala, Staner 1467 (BR, MO, P); ibid., Ruki R., J. Léonard 804 (BR, K); Djoa, Evrard 4108 (BR); Basankusu, Evrard 4749 (BR); Gbo-Sasa, Evrard 362 (BR); Yambata, Vermoesen 13 (BR); Baringa R., Yala, Bruneel 31 (BR); Wamba, Nsola 1257 (BR); near Mondombe, Jespersen 10 (BR); Yasala-Yetsi Road, Evrard 5228 (BR). Haut-Zaire: Basoko, E. & M. Laurent 18 Jan. 1904 (BR); Limbutu, M. Laurent 976 (BR); Yangambi, J. Louis 11491 (BM, BR, C, FI, K, NY, P); 10 km W of Kisangani, Bokdam 3261 (WAG); Kisangani, Mangobo, Lisowski 47406 (BR); 10 km NW of Wanie-Rukula, Lisowski 17307 (BR). Kasai Oriental: Bena Dibele, Flamigni 30 (BR); Kasongo Batetela, Sapin 20 Oct. 1906 (BR); Miabi, Liben 1969 (BR, WAG). Kivu: Makuta, km 13 Buniakiri-Tshigoma Road, Pierlot 2875 (BR, WAG); Viega, Maniema, Lebrun 5818 (BR, K).

BURUNDI. Kigwena, Reekmans 22 Oct. 1976 (FI).

ANGOLA. Zaire: Sumba Peco, Gossweiler 8697 (BM, K). Bengo: Luanda, Cazengo, Gossweiler 575, anno 1903 (BM, K), anno 1903 (LISJC, P). Cuanza Norte: Golungo Alto, Gossweiler 4402 (BM, K), 4414 (BM, COI, K), 4738 (BM, COI, K); ibid., Welwitsch 5927 (BM, C, COI, G, K, MO, P, type of *Landolphia welwitschii* and lectotype of *L. petersiana* var. *crassifolia*); near Salazar (= Dalatando), M. da Silva 2207 (LISC), 2435 (LISC). Malanje: Quela Mts, von Nolde 783 (BM, COI). Lunda Norte: Lovua R., Marques 230 (COI, LISU); Dundo, Luachima R., Gossweiler 13583 (B, BM, K, P, US).

CULT. Netherlands, Wageningen, de Bruijn 2094 (WAG). Zaire, Equateur, Eala, Corbisier-Baland 1282 (BR).

Note. The type of *A. brevituba* falls with all of its characters perfectly within the variation of *A. scandens*. Therefore it is not maintained here as a distinct species.

7. Ancylobotrys tayloris (Stapf) Pichon, Mém. IFAN 35: 284, pl. 18. 1–3. 1953.
Fig. 7, p. 31; map 7 p. 32

Basionym: *Landolphia tayloris* Stapf in Fl. Trop. Afr. 4. 1: 45. 1902.

Type: Kenya: K7, Rabai Hills, Fimboni, W.E. Taylor Nov. 1885 (BM, holotype).

Heterotypic synonym: *Landolphia pachyphylla* Stapf, l.c. Type: Malawi, sin. loc., Buchanan 140 (BM, holotype; isotype E).

Climbing shrub or liana climbing up to 20 m high in trees. Branches dark brown, lenticellate; branchlets dark brown-pubescent. *Leaves*: petiole 5–8 mm long, glabrous to puberulous, with colleters in the axils; blade coriaceous when dried, elliptic or narrowly so, 2–3.4 × as long as wide, 4–11.8 × 1.7–5 cm, acuminate at the apex with an up to 17 mm long acumen, cuneate at the base, glabrous on both sides, with 19–40 pairs of more or less straight conspicuous secondary veins, forming an angle of 60–90° with the costa, often alternated by less conspicuous ones; tertiary venation reticulate beneath, inconspicuous above. *Inflorescences* 9–32 × 4.5–10 cm, with 5–9 cymes, each cyme with up to about 30 flowers; peduncle 4–12.5 cm long, pubescent or minutely so; pedicels about 1 mm long, densely pubescent; bracts up to about 2.5 mm long, sepal-like, persistent. *Sepals* connate at the base for up to 0.7 mm, triangular or sometimes ovate, 1.6–3.4 × as long as wide, 1.6–3.1 × 0.7–1.8 mm, obtuse or acute at the apex, densely pubescent outside, glabrous inside, usually without colleters. *Corolla* white, 18–26.5 mm long in the mature bud and forming an attenuate head 0.6 of the bud length, pubescent outside; tube thin, not thickened above the anthers, 2.7–6.1 × as long as the sepals, 0.5–0.8 × as long as the lobes, 8–12.2 mm long, contracted at the base and 1–1.3 mm wide, widened above and widest 3–3.7 mm above the base (0.3–0.4 of the tube length) to 1.5–2 mm wide, contracted again just above the anthers to 0.8–1.3 mm wide, fairly abruptly widened at the throat, with a pilose belt inside from between the anthers which is 2–3.8 mm above the base, to 5.8–8 mm above the base of the tube or sometimes to the base of the lobes, throat usually glabrous, sometimes minutely pilose; lobes narrowly triangular to narrowly elliptic, 2.1–8.5 × as long as wide, 10–20 × 2–5 mm, obtuse at the apex, glabrous on both sides. *Stamens* with apex 4–7.8 mm below mouth of corolla tube (0.5–0.6 of the tube length), inserted 2–2.9 mm from the base of the tube (the base of the anthers 2.5–3.2 mm above the base of the tube); filaments glabrous or sometimes minutely pilose inside, glabrous outside, 0.4–0.6 mm long; anthers 2.4–3.3 × as long as the filaments, 4–7.5 × as long as wide, 1.2–1.5 × 0.2–0.3 mm, apex acuminate and sterile for 0.1 mm. *Pistil* 2.5–2.9 mm long; with apex 1.2–1.5 mm below apices of anthers; ovary more or less superior, subglobose to slightly cylindrical, 0.5–0.8 × 0.7–0.8 × 0.7–0.8 mm, densely appressed-pubescent; style glabrous, cylindrical, not thickened at the apex, 0.6–0.8 × 0.2 mm; pistil head: basal part more or less cylindrical, 0.8–1 × 0.3–0.4 mm, apical part 0.2–0.6 × 0.2–0.3 mm.

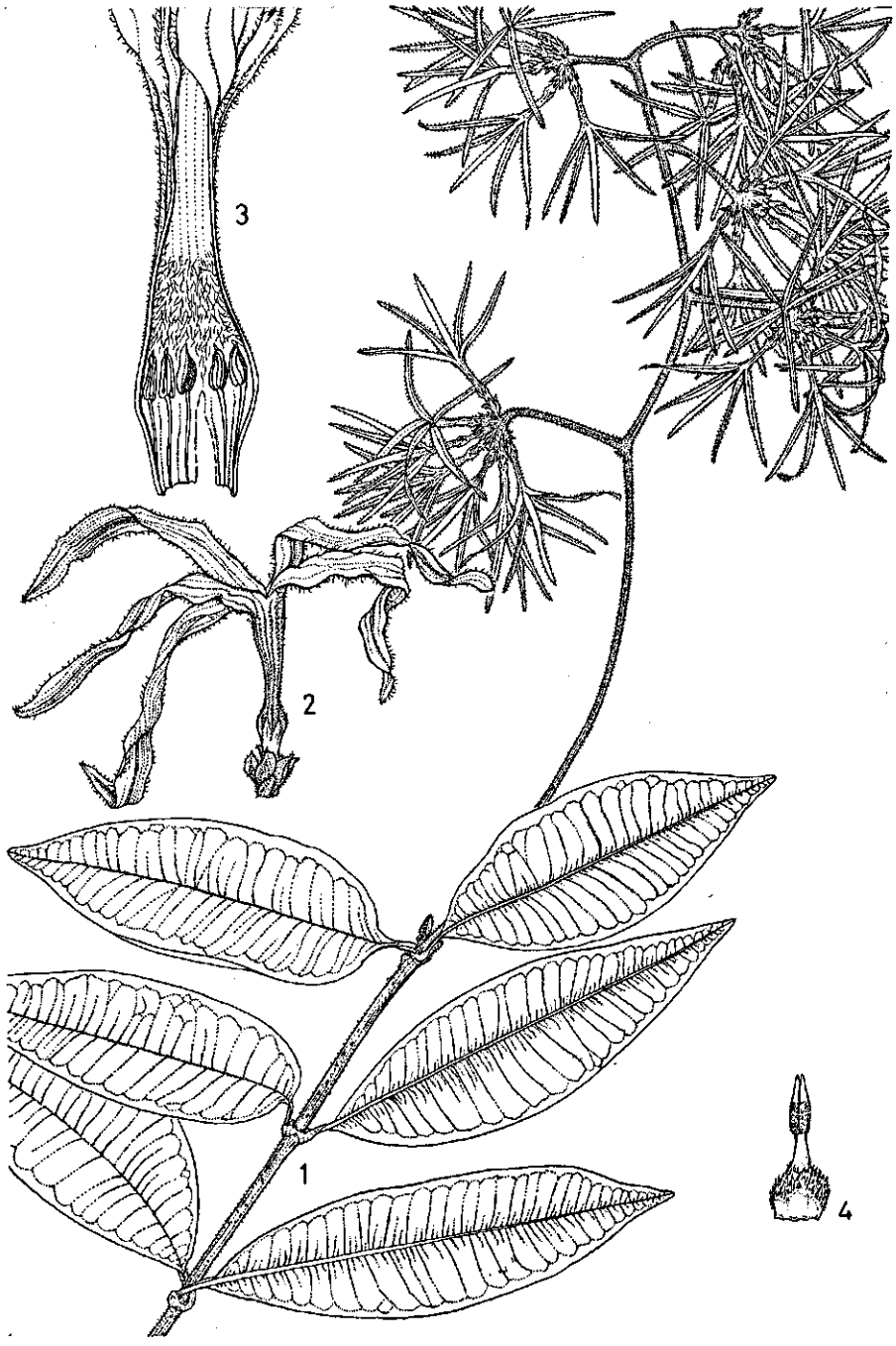
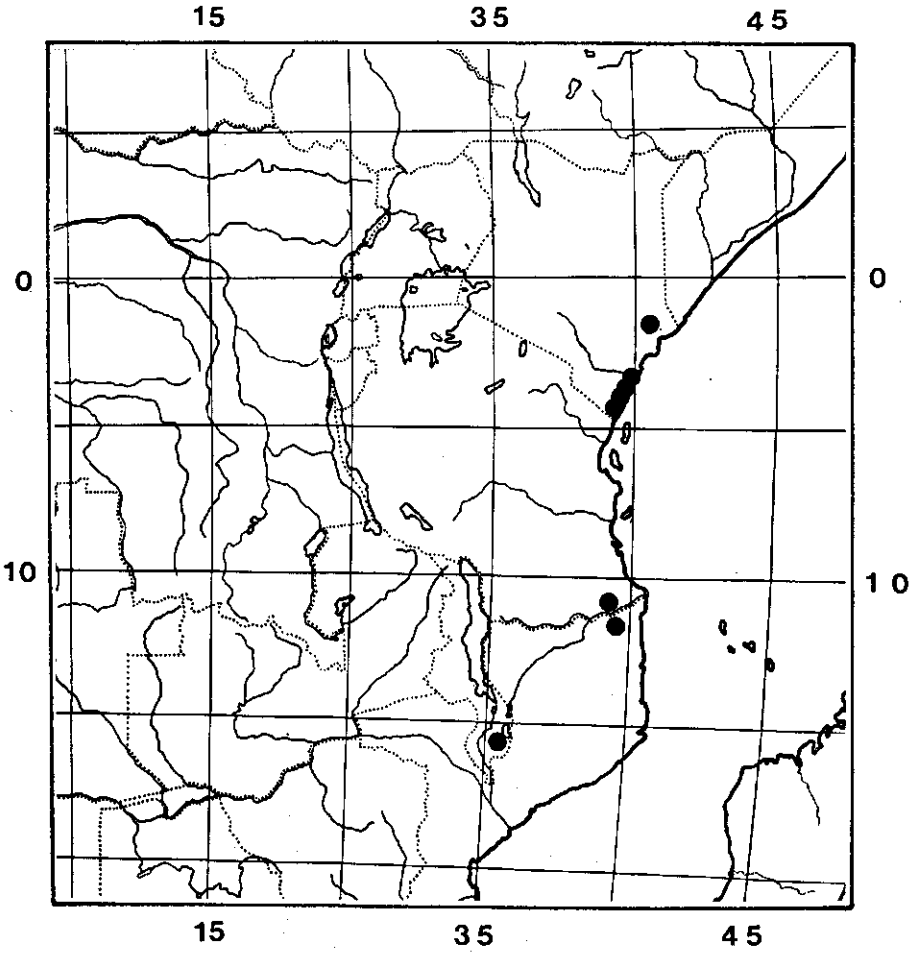


Fig. 7. *Ancylobotrys tayloris*. 1, habit (× 2/3); 2, flower (× 2); 3, opened corolla (× 4); 4, pistil (× 6). 1 from Chapman 8914; 2–4 from Reitsma 505.



MAP 7. *Ancylobotrys tayloris*.

Placentas with 15–35 ovules. *Fruit* yellow, subglobose, 4 cm in diameter (teste Gardner 1462A).

DISTRIBUTION: Kenya, Tanzania and Malawi.

ECOLOGY: Light forest with *Cynometra* or bush. Alt. 0–1000 m. Flowering from August to December.

Specimens examined:

KENYA. K4: N of Mombasa, Whyte anno 1902 (BM, K, MO, P). K7: Kilifi District, S of Jilore, Spjut & Ensor 2614 (K, UC); W of Kakuyuni, ca 16 km W of Malindi, Spjut 3939 (BR, K, UC); ca 7 km E of Vitengeni, Reitsma 505 (WAG); Arabuko For., Brenan et al. 14686 (K, WAG); ibid., Scott Elliot 93 (K); Rabai Hills, Fimboni, W.E. Taylor Nov. 1885 (BM, type); Kwale, Graham 1647 (K, NY), 1648

(NY); Shimba Hills, Gardner 1462A (K); Buda Mafisini For., 13 km WSW of Ganzi, Drummond & Hemsley 3935 (BR, K).

TANZANIA. Sin. loc., Busse 664 (EA). T8: Newala, Hay 73 (K).

MALAWI. Sin. loc., Buchanan 140 (BM, E, type of *Landolphia pachyphylla*); Southern: Mulanje Region, Machemba Hill, Patel & Morris 1552 (K, MO); Mt Mulanje massif, Michesi Mt, Chapman 8914 (K, MO).

MOZAMBIQUE. Niassa: Macondes, Mueda, Mendonça 959 (LISC).

Nomen nudum

A. mammosa Pierre, Bull. Soc. Linn. Paris sér. 2: 92. 1898. = *A. scandens* (Schum. & Thonn.)Pichon.

Excluded species

Ancylobotrys (?) *reticulata* (Hall.f.) Pichon, Mém. IFAN 35: 300. 1953. = *Landolphia reticulata* Hall.f., see Persoon et al., Wageningen Agric. Univ. Pap. 92. 2: 169, fig. 36, map 40. 1992.

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A, B, BM, BR, C, COI, E, EA, FI, G, GH, HBG, K, L, LD, LG, LISC, LISJC, LISU, LMU, M, MA, MAL, MICH, MO, NY, P, POZG, PRE, S, SRGH, STE, U, UC, UPS, US, W, WAG, YA, Z.

Grateful thanks go to Miss Yuen Fang Tan for preparing the excellent drawings and to Prof. dr. L.J.G. van der Maesen for correcting the English text.

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Ancylobotrys amoena (am), *A. capensis* (ca), *A. petersiana* (pe), *A. pyriformis* (py), *A. robusta* (ro), *A. scandens* (sc) and *A. tayloris* (ta).

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Nannan, 42 (sc).
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Okafor, J.C., FHI 36870, 54634 (am).
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Olorunfemi, J., FHI 24414, 55684, 70714 (am).
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Taxa of the Apocynaceae above the genus level

Series of Apocynaceae XXXVIII

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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
Apocynoideae
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-

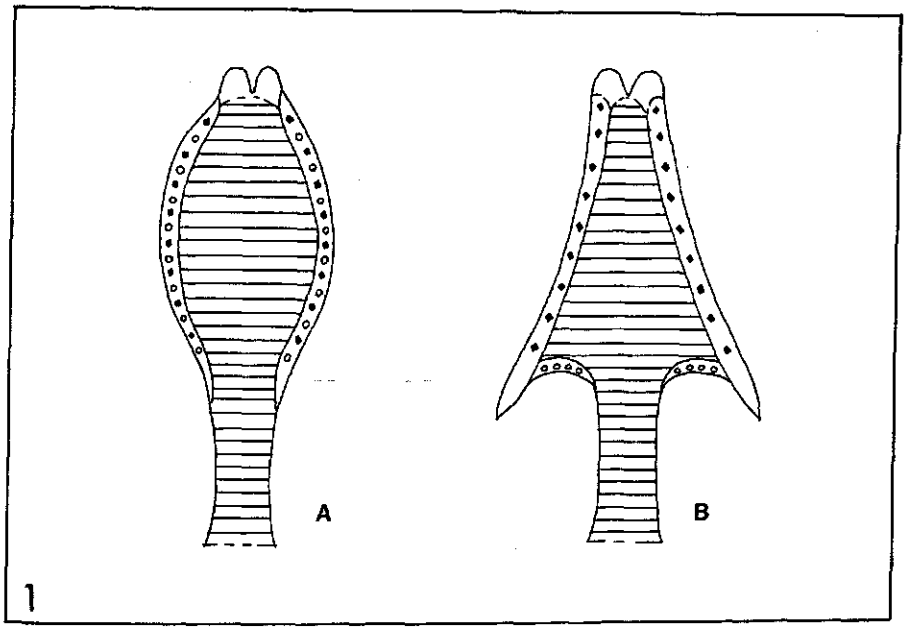


Fig. 1. Apocynaceae pistil heads according to Schick (1980, 1982), adapted from the original figure. A. *Plumeria*-type; B. *Allamanda-Nerium*-type. O - receptive surface ; ♦ - tissue producing adhesive matter.

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.

l). 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.

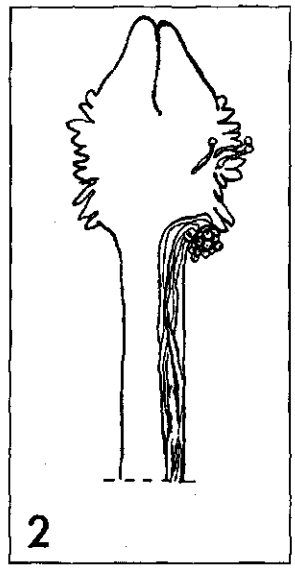


Fig. 2. Pistil head of *Alstonia boonei*.

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.

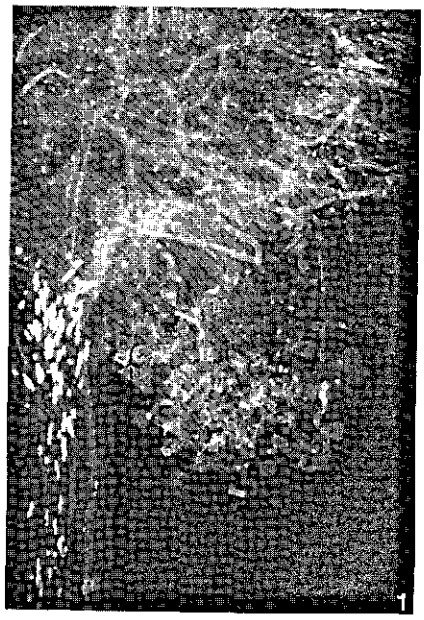


Photo 1. *Catharanthus roseus* pollen tubes originating from pollen grains attached just below the lower hair whorl (top of photograph).

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

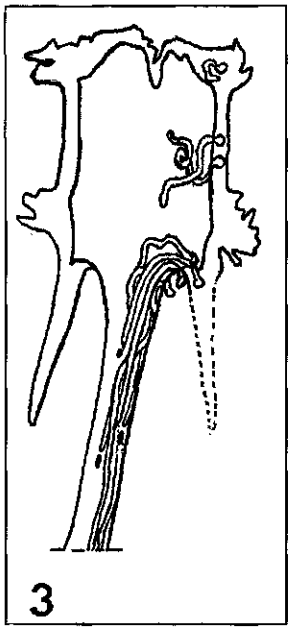


Fig. 3. Pollen germinating on pistil head of *Catharanthus roseus*. Some pollen tubes halted in the style by callose.

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.

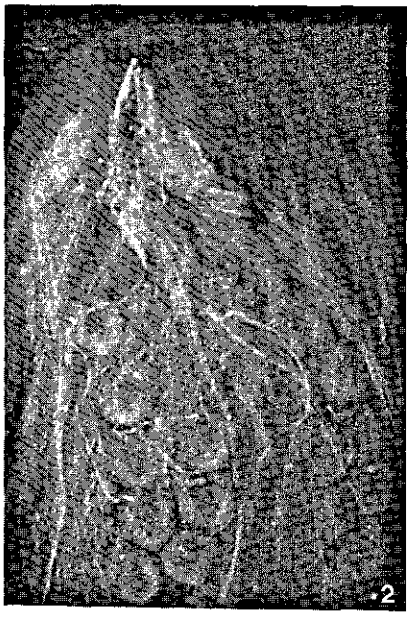


Photo 2. Pollen tubes in ovarium of *Catharanthus roseus*.

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

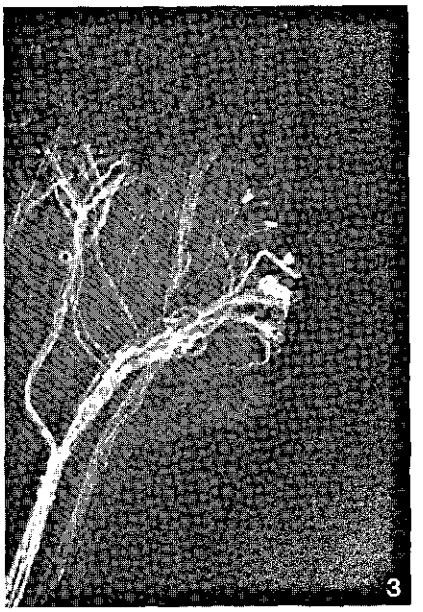


Photo 3. *Tabernaemontana pandacacqui* pollen grains germinated on pistil head and growth of pollen tubes in style. No pollen germinating on stigmoidal apex.

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).

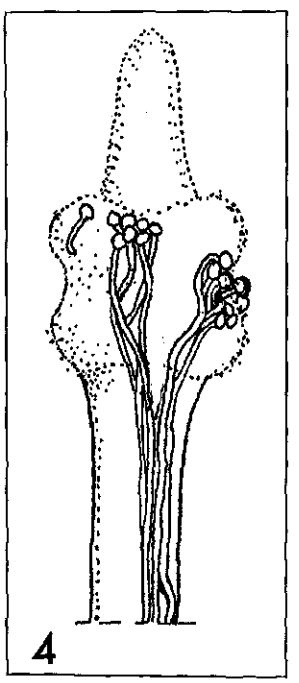
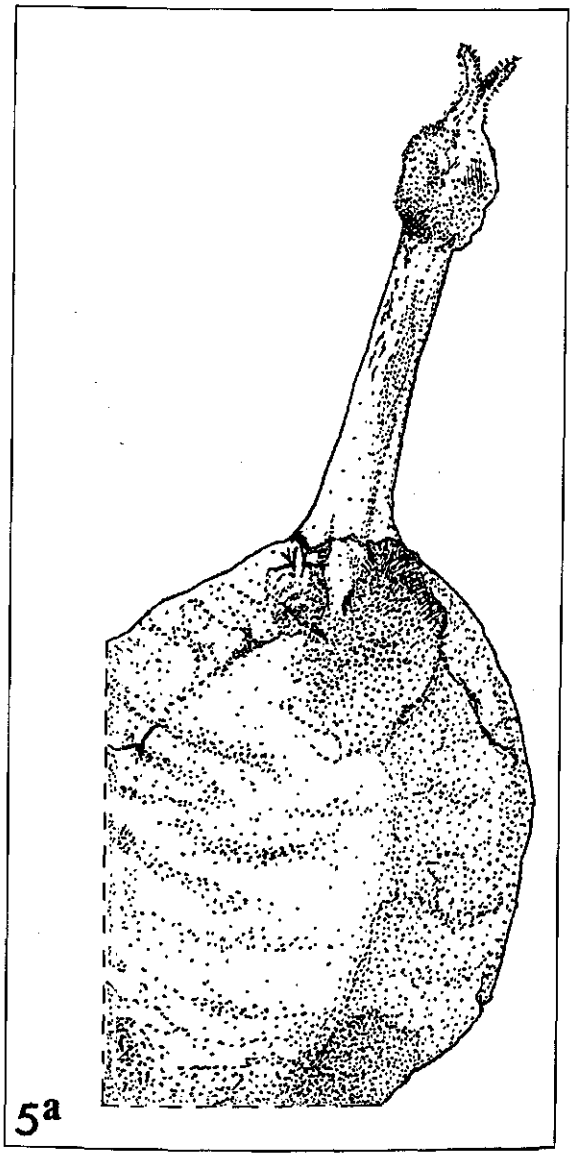


Fig. 4. Schematical representation of Photo 3, *Tabernaemontana pandacacqui*.

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.



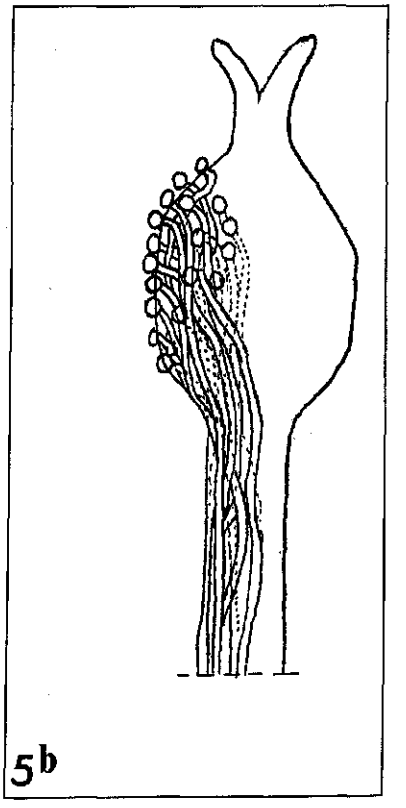


Fig. 5. *Tabernaemontana pandacacqui* pistil head and schematical representation of pollen germination (only shown for one side of pistil head).

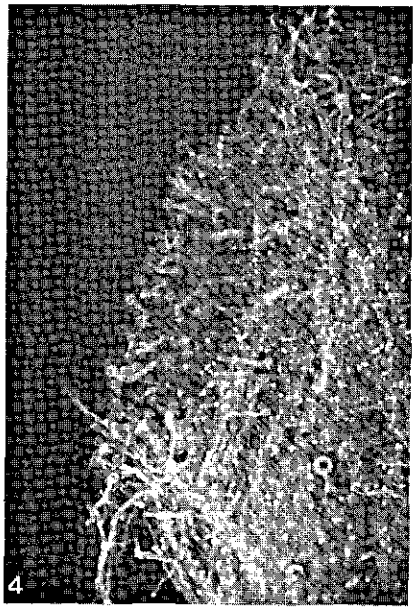


Photo 4. *Tabernaemontana sphaerocarpa* germinated pollen. The ellipsoid part of the pistil head is pollinated entirely and pollen germinates all around.

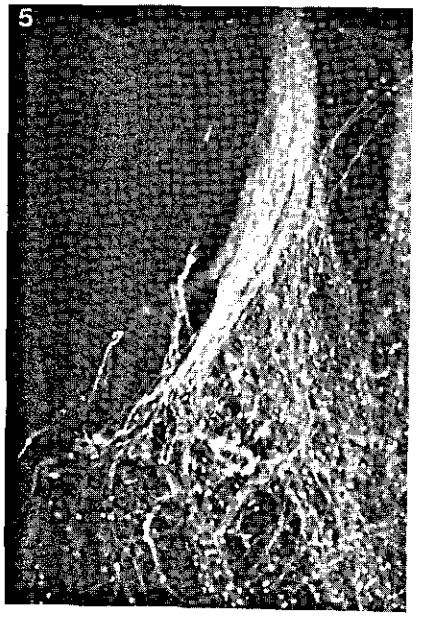


Photo 5. *Tabernaemontana sphaerocarpa* growth of pollen tubes in the style.

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.

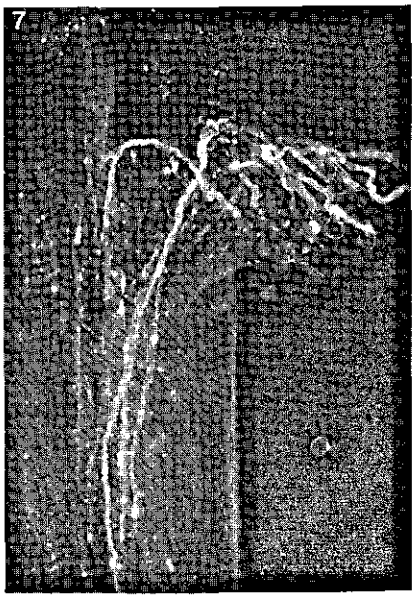


Photo 7. *Vinca minor* pistil head with pollen germinated just below the lower whorl of hairs.

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.

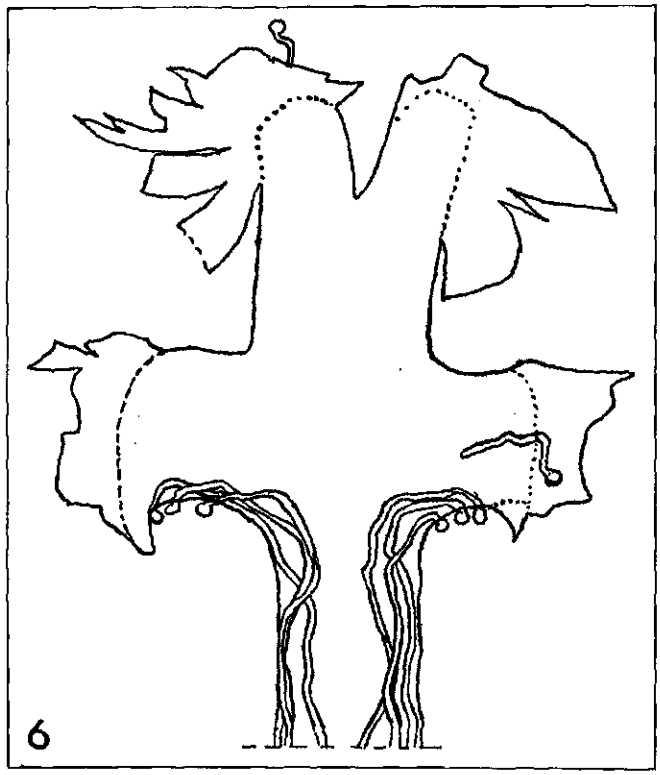


Fig. 6. *Vinca minor*, pollen germinated just below the lower hair whorl on the stigmatic surface.

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

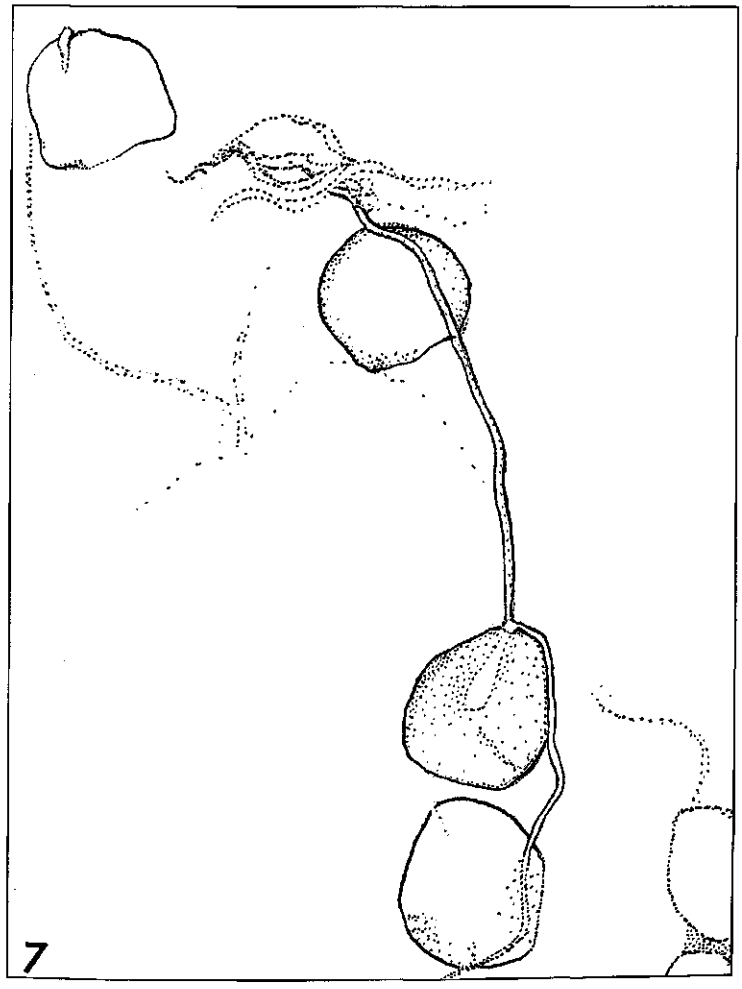


Fig. 7. See Photo 8, pollen tube penetrating ovules of *Vinca minor*.

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. 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.

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