Studies in Annonaceae. II
A monograph of the genus Anaxagorea A. St. Hil.
Part 1

By

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With 17 figures and 4 tables in the text

Abstract

MAAS, P. J. M. & WESTRA, L. Y. Th.: Studies in Annonaceae. II. A monograph of the genus *Anaxagorea* A. St. Hil., Part 1. — Bot. Jahrb. Syst. 105: 73—134. 1984. — ISSN

Anaxagorea A. St. Hil. is distinct from other Annonaceae by the fruits. Unlike most members of the family, it occurs both in the Neotropics and in the Palaeotropics. Several chapters are devoted to a.o. morphology, anatomy, karyology, palynology, chemistry, pollination and seed dispersal, geography and ecology, economic uses and vernacular names, partly compiled from existing literature or collectors' notes, partly as a result of own investigations. A cladistic analysis of intrageneric relationships is given.

The taxonomic part provides descriptions, synonyms (nomina nuda are not included), dichotomous keys. For practical reasons, separate keys are given for neotropical and palaeotropical taxa. For neotropical species, a synoptic key is also provided. Altogether, 20 neotropical species and 3 palaeotropical species (including 2 varieties) are recognized, and 14 taxa are brought into synonymy. Another two taxa from the Neotropics are apparently new, but are not formally published because of incomplete material, and one palaeotropical species cannot be properly evaluated because of insufficient material. An index to exsiccata is appended.

1. Introduction

Within the family of the Annonaceae, the genus *Anaxagorea* stands out clearly. This is in marked contrast to many other genera in this family. It is one of the relatively few members with dehiscent, pod-like monocarps. The

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0006-8152/84/0105-0073 $ 15.50

majority of representatives of the Annonaceae have either indehiscent monocarps or syncarpous fruits.

Anaxagorea occurs both in the Neotropics and the Palaeotropics (Fig. 8). Most species of *Anaxagorea* occur in the Neotropics, from Guatemala southward to Peru and to Rio de Janeiro in Brazil. A second center is in tropical Asia from, roughly, Sri Lanka to the Philippines and Indonesia. With the exception of the large genera *Annona* and *Xylopia*, genera in Annonaceae, as presently understood, are either neotropical or palaeotropical. The peculiar disjunction in *Anaxagorea* is unparalleled in the Annonaceae, but a similar example can be found in a.o. Magnoliaceae (FRIES 1940, 1959).

If the distribution of *Anaxagorea* draws our attention, the same is true as regards the position of the inflorescence. In classifications of the family, most recently by FRIES (1959), and HUTCHINSON (1964), much emphasis has been laid on the position of the inflorescence: either axillary or leaf-opposed, and genera have been placed in, admittedly rather artificial-looking, groups based a.o. on this character. In *Anaxagorea*, most species have axillary inflorescences. Some, however, have leaf-opposed inflorescences, namely two (or possibly three) species in Asia and one in southeastern Brazil.

Economically, *Anaxagorea* is not very important. Whenever species of *Anaxagorea* are used, it is, among others, as a source of fibres for ropes and the like, and there are also reports on use for various other purposes.

2. Taxonomic history

The first two species referable to *Anaxagorea* were described by DUNAL in his monograph of the family (1817) as *Xylopia prinoides* Dunal and *Xylopia acuminata* Dunal. The genus *Anaxagorea* was published some years later by SAINT-HILAIRE (1825) who, having established that *Xylopia prinoides* Dunal did not match with true *Xylopia* and not with several other genera either, made that species to a genus of its own. The formal new combination was made not by SAINT-HILAIRE but by ALPHONSE DE CANDOLLE (1832), who also transferred *Xylopia acuminata* Dunal to *Anaxagorea.* Shortly before that, *Anaxagorea javanica* Blume (BLUME 1830) was published as the first species from Asia.

Although the geographical disjunction and the discrepancy in the position of the inflorescence are somewhat puzzling aspects, the concept of the genus has never been challenged (FRIES 1940). In 1934, FRIES published a revision of the neotropical species. Up until then and including species newly described in that revision, 18 species from the Neotropics had been described, and 7 species from Asia. Five more species were described by FRIES in later years, as recently as 1957.

In a paper on relationships of the genus, FRIES (1940) suggested a diphyletic origin for New World and Old World *Anaxagorea*. As a logical consequence to this, he placed the Asiatic species in a separate section, *A.* sect. *Rhopalocarpus* (FRIES 1959).

3. Morphology

3.1 Habit

Species of *Anaxagorea* are mostly small trees or shrubs, usually with relatively thin stems. A height over 15 m is attained only by exception, and the diameter goes up to 20(—30)cm at most. The smallest sizes recorded are in *A. luzonensis* of, mostly, 0.3—1.5 m tall, and in *A. floribunda* of ca. 1 m tall.

3.2. Leaves

Leaves conform to the general pattern of the family. They are placed in two alternating rows, simple, estipulate, distinctly petiolate. The petioles are usually not longer than 20 mm, longer than that only by exception (to 45 mm in *A. gigantophylla*). The lamina is generally concolorous or nearly so, except for in *A. macrantha* where the lower side has a waxy appearance. The texture of the lamina varies mostly from chartaceous to thinly coriaceous. The shape of the lamina usually centres around narrowly elliptic, the base is mostly cuneate to obtuse, and symmetrical (manifestly asymmetrical, however, in *A. floribunda*), the apex is usually acuminate to acute. The length of the lamina varies from 5—75 cm, the width from 2—26 cm, the smallest-leaved species is *A. prinoides*, the largest-leaved *A. gigantophylla*. The primary vein is impressed on the upper side in most species, distinctly raised, however, in *A. brachycarpa*, and often slightly raised in *A. rufa*. The number of secondary veins on each side of the primary vein varies from 6—29, the largest number being found in *A. gigantophylla* (17—28) and *A. macrantha* (22—29), the lowest numbers in e.g. *A. panamensis*, *A. prinoides*, *A. javanica*, *A. luzonensis* (all 5-10). The secondary veins form and angle with the primary vein mostly between 55°—75°, the smallest angles are found in *A. rufa* and *A. borneensis* (45°—60°), large angles (up to 80°) a.o. in *A. acuminata*. The secondary veins form loops which vary from indistinct to distinct, sometimes resulting in a marginal vein (e.g. in *A. phaeocarpa* and *A. gigantophylla*). The smallest distance between the loops and the margin varies mostly between 2—10 mm (>10 mm in *A. floribunda*). The secondary veins are slightly impressed to slightly raised on the upper side. The tertiary veins form a more or less distinct reticulum.

3.3. Inflorescence

The flower arrangement in *Anaxagorea* conforms to the rhipidium-pattern of most annonaceous genera (FRIES 1919, 1959). The pedicel has two bracts, one at the base, and the other usually near the flower. The articulation is basal, just above the lower bract. Flowers mostly appear in slow succession, so that only one flower is seen at a time. Rhipidia in most species apparently do not produce many flowers. In some species, such as e.g. *A. javanica,* rhipidia may continue to grow, and produce flowers at intervals for some time. This, then, results in a sympodially elongating rhachis under the pedicel.

Below the pedicel, there usually is a peduncle mostly of few, very short, internodes, less than 5 mm long, but sometimes longer. In many cases, it is practically impossible to distinguish the peduncle from a sympodially elongated rhachis on top of it. For this reason, in descriptions the two together will often be referred to as "peduncle (or sympodial rhachis)".

The peduncle may produce one or more lateral shoots from the axils of the bracts, thereby yielding what may be termed a small condensed panicle of rhipidia. An exceptional species is *A. floribunda* with panicles of this type, but now rather lax by comparison, and with a prolonged period of growth, attaining a length of 20 cm or more.

The pedicels are thickened toward the flower to a greater or lesser extent in all species. They are variable in length, from less than 10 mm, as in e.g. *A. brachycarpa* and *A. brevipes*, to ca. 20 mm (and exceptionally more) in e.g. *A. phaeocarpa* and *A. petiolata.*

The bracts on the peduncle and the basal bract of the pedicel are triangular to elliptic, with a broad base, often caducous.

The upper bract of the pedicel is larger than the lower bract, usually orbicular to broadly elliptic when spread, amplexicaul or almost so, more or less cup-shaped in natural position, more or less reflexed, however, in *A. prinoides.* The upper bract is persistent in a number of species, but early caducous in others.

The inflorescences are axillary in the majority of species, leaf-opposed to terminal, however, in the palaeotropical species *A. javanica, A. luzonensis,* and *A. radiata,* as well as in the neotropical *A. silvatica.* In *A. brevipes,* besides axillary inflorescences, short lateral shoots ending in a terminal inflorescence are regularly seen. Terminal inflorescences are exceptionally also found in *A. dolichocarpa.*

Inflorescences often develop on older branchlets, below the leafy zone, and cauliflory is also seen frequently. In *A. floribunda,* the long, flagelliform inflorescences creep over the ground.

Inflorescences may also develop from one to perhaps several auxiliary buds, for instance in *A. crassipetala* and *A. brevipedicellata.* Sometimes it may become difficult to decide, whether one has a small, very compact panicle in his hands, or an aggregation of several inflorescences from auxiliary buds.

3.4. Flowers

Flower buds

The shape of the flower buds is diagnostically important. Flower buds are globose to ovoid in the majority of species. Conical flower buds are found in Central American species: *A. allenii, A. crassipetala, A. guatemalensis, A. panamensis*, and also in *A. macrantha.*

Flower colour

In the Neotropics, the colour of the flowers ranges from green or white to red, with various colours in between. The outer side of the flowers is often covered with brown indument (e.g. in *A. dolichocarpa*). For the Asiatic species white, greenish-white, to yellow flowers are reported.

Flowers, general

The flowers of *Anaxagorea* conform to the general pattern of the family. They are actinomorphic and bisexual. The perianth is trimerous, and consists of one whorl of sepals and two whorls of petals. The inner whorl of petals is lacking in *A. borneensis* and varieties of *A. javanica.* In *A. javanica* var. *dipetala* the perianth is dimerous. The flowers are usually fleshy, and (probably) mostly do not open widely. The stamens and carpels remain enclosed at least in most species within a cavity formed by the hollow lower parts of the enveloping petals.

Sepals

The sepals are shorter than the outer petals, varying from only slightly shorter to much shorter (the measurements given for *A. floribunda* apply to flowers that apparently were still in bud stage, and need rechecking). They are valvate to manifestly imbricate in young buds; the latter condition is not mentioned by FRIES (1959). They vary from, mostly, chartaceous or subcoriaceous, to membranaceous or thinly herbaceous in some species (notably in *A. angustifolia, A. crassipetala, A. panamensis*). They can be free: in about half of the neotropical species, and in the Asiatic species, or connate at the base: some neotropical species (e.g. *A. gigantophylla*), or connate for the greater part: some neotropical species (e.g. *A. acuminata*). In *A. dolichocarpa* both free and connate sepals are known to occur. Often it is difficult to determine from herbarium material whether sepals are free or connate. This, therefore, needs further study, preferably in the field. The persistence of sepals is also important. In a few species the sepals are caducous before anthesis (*A. manausensis, A. phaeocarpa, A. pachypetala;* occasionally also in *A. acuminata* and *A. doli-*

chocarpa). In other species the sepals drop during or after flowering, whereas there are also species with sepals persistent during fruiting stage. The curvature of the sepals is a further diagnostical feature. In e.g. *A. rufa* and *A. acuminata* sepals are curved upward. Strongly reflexed sepals, on the other hand, are met with in e.g. *A. brachycarpa* and in most of *A. dolichocarpa.* In several species, particularly the ones occurring in Central America, sepals are apically reflexed. The length of the sepals varies from 2—15 mm in the American species, and from 2—6 mm in the Asiatic ones. The shape generally is ovate to broadly ovate. The apex varies from obtuse, acute, to shortly acuminate.

Petals

The petals of both whorls are valvate. The outer petals are fleshy in most species. On the inner side there is a cavity in the basal part, often clearly showing markings of closely appressed stamens. The upper part on the inner side is flat to bifacial (with two plane surfaces meeting at an angle in the middle), to keeled in some species. *A. rufa* and *A. brevipes* have a narrow, knife-like keel; in *A. angustifolia* the keel is somewhat thicker (triangular in cross-section). The outer petals in *A. acuminata* are bifacial with a wing-like margin. The inner petals of most species are almost as long as the outer petals, or only slightly shorter. In some species, especially the ones in Central America: *A. allenii, A. crassipetala, A. guatemalensis, A. panamensis,* the inner petals are markedly shorter than the outer petals, the ratio outer/inner petals approaching 3:2. The inner petals are bifacial (angle is variable) to keeled in all species. Like the outer petals, the inner petals are concave on the inner side in the basal part — again with markings of stamens —, often more markedly so.

Torus

The torus (or floral receptacle) is convex in all species of *Anaxagorea.*

Androecium

As in the majority of genera of Annonaceae, the androecium is acyclic, with free stamens. The innermost stamens in all but two species of *Anaxagorea* are sterile. The presence of staminodes is rather unusual within this family. The number of stamens, including staminodes, varies from about 10, in *A. brevipedicellata* and *A. floribunda,* up to almost 200 in *A. brevipes* and *A. gigantophylla.* The length of the stames varies from about 1.5—6 mm, and the outline from elliptic to narrowly obovate. The apical prolongation of the connective is very variable, sometimes within one species and even within the same flower, from triangular and acute to quadrangular and truncate. The change from stamens into staminodes is not abrupt, but gradual due to the anthers becoming progressively shorter towards the center and finally disappearing altogether. In most species the anthers are extrorse, and they do not exceed the connective in width. In some species, however, the anthers tend towards becoming latrorse, and then they are also broader than the connective. The number of staminodes varies greatly, more or less in accordance with the number of stamens, up to a maximum of about 50. In *A. brevipedicellata* and *A. luzonensis*, there are no staminodes. In some species the apex of the staminodes has a glandular margin: this, as far as could be established, coincides with a large number of stamens in the flower (only *A. angustifolia* remains to be investigated). Generally, there is no great difference in length between stamens and staminodes, the stamens only slightly exceeding the staminodes (or vice versa) at most. In *A. petiolata* in particular, but in some other species too, the stamens are considerably longer than the staminodes. It is notably by this character that *A. petiolata* can be distinguished from *A. dolichocarpa*, which it resembles.

Gynoecium

The gynoecium is apocarpous, the number of carpels varying from 5—45. Each carpel contains two basal or nearly basal ovules. The precise ovule position has been one of the characters, that has led FRIES to some speculations regarding the phylogeny of *Anaxagorea* (FRIES 1940), and perhaps merits further attention. The stigma is capitate to slightly horseshoe-shaped, sessile in most species. In *A. luzonensis* and, more variably so, in *A. javanica* the stigma is more or less stipitate. The stigmatic surface is smooth (papillose), but finely tuberculate in *A. borneensis*.

3.5. Fruits

All or most carpels mature into monocarps usually between 20—40 mm long. The monocarps are clavate or more or less dolabriform, consisting of a stipe-like basal part ca. 10—35 mm long and 1.5—4 mm in diam. in the middle, and a head which varies from subglobose to slightly flattened on the sides. The head has a mostly persistent apical beak variable in lenght usually between >0.5—2 mm, but reaching to 6 mm in some species. The colour of the monocarps is reported as green (in all Asiatic species) to yellow, brown, to reddish.

The two shiny black seeds are in the head of the monocarp, with a size of 7—18 x 5—9 mm. The outer side is convex, the inner side flat; the seeds, before dehiscence, lie with the flat sides closely appressed. Dehiscence is along the ventral suture, and sometimes also along part of the dorsal suture.

3.6. Indument, general

Indument of vegetative parts

Young twigs and petioles are often covered with a more or less dense indument, but often become glabrous rather soon. The indument is often detected not so much by the hairs themselves, which are mostly very small and can only be seen through a powerful hand lens or a dissecting microscope, as by the colour. The colour is usually brown. Only few species are truly glabrous, or almost glabrous, even on young parts (e.g. *A. brachycarpa*, *A. brevipes*). For the indument of leaves, we refer to the next paragraph.

Indument of inflorescences, flowers, fruits

This generally appears similar to that of young twigs. It often is more copious, with a greater tendency toward persistence.

3.7. Indument of leaves

by J. KOEK-NOORMAN (Utrecht)

When looking through previous publications (FRIES 1959, KRAMER 1969, ROTH 1981), one is struck by conflicting data on the presence and structure of leaf trichomes in *Anaxagorea.*

For this reason, a thorough study was made of trichomes on the leaves within the framework of the revision of the genus. Material of all but two species was investigated both with the SEM and with the light microscope. Only *A. manausensis* and *A. macrantha* had to be skipped because of scarcity of material. The full account of this investigation falls outside the scope of the present paper, and will be the subject of a forthcoming publication (KOEK-NOORMAN & BERENDSEN, in prep.), to which the reader may be referred. Here, we will limit ourselves to a general description.

Overall surface appearance

All species have an indument of tiny hairs, but often the leaves are glabrescent. To detect the hairs, a good hand lens is absolutely indispensable. Often, though, the hairs can only be spotted with the aid of powerful dissecting microscope. The indument is nearly always restricted to the lower side of the leaf. The colour of the hairs mostly is brown, dark reddish-brown, to purple.

Individual trichomes

Trichomes in *Anaxagorea* are simple, two- to five-armed, or stellate (Fig. 1). In all cases, they are multicellular. The top-cell is longer and sometimes slightly wider than the basal cells, and is often filled with dark coloured substances. There is no indication, so far, that the top-cell has a secretory function. The branched or stellate hairs are attached to the leaf surface by a thin, one cell wide, stalk mostly consisting of two cells. the basal stalk cell is covered by the

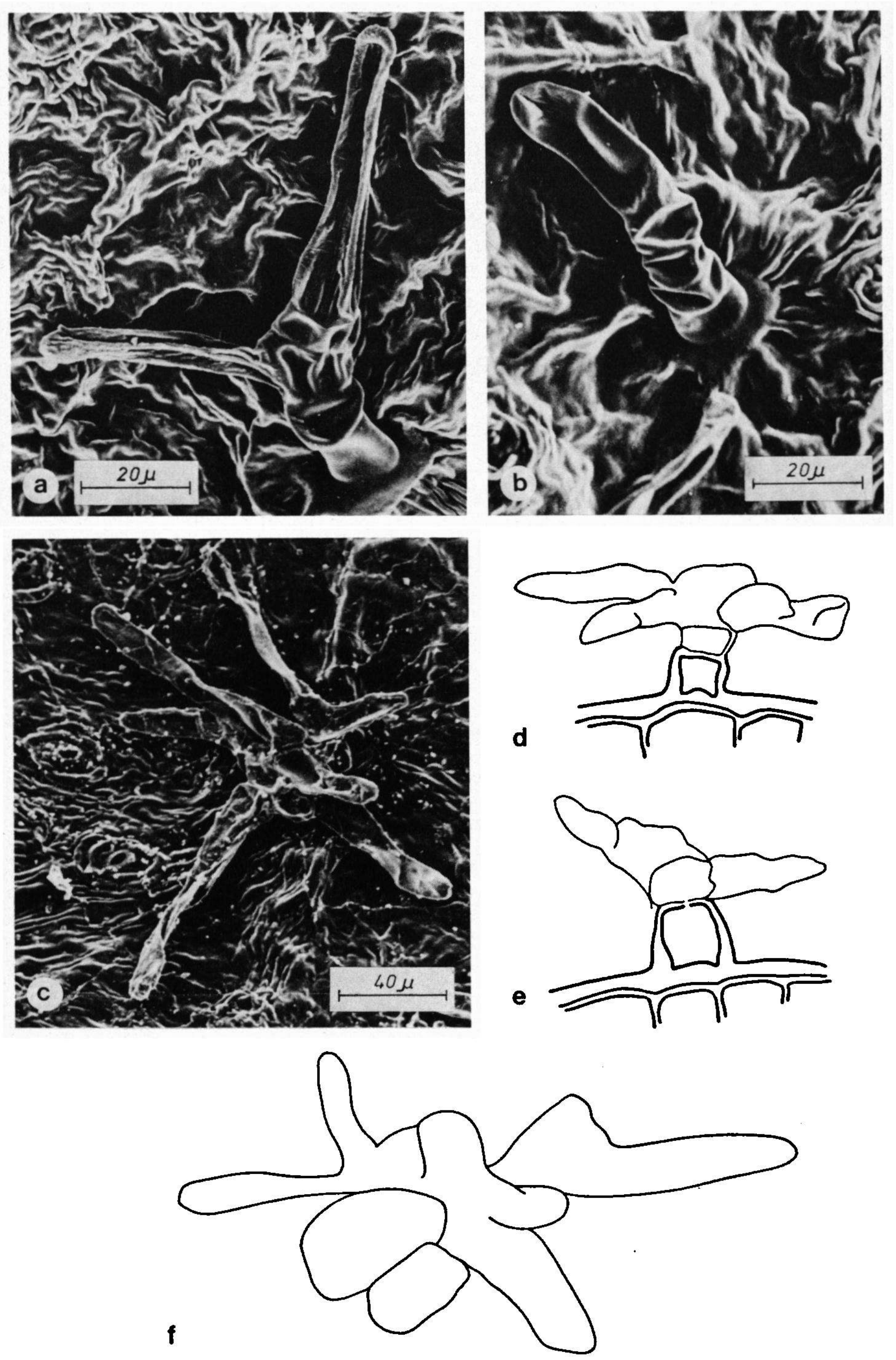


Fig. 1. Hairs of *A. phaeocarpa.* a—c, SEM-photographs; d—f, drawings.

cuticula. The next cell is extremely thin-walled, and is easily damaged; the same applies to the branches. In some instances we had the impression that the branches must have originated as recesses of the top-cell, rather than by cell division. This we could not confirm. It proved often impossible to count the number of cells per branch, because the cell walls are thin and smooth. In spite of some variability in length, width, and number of cells, we may state that the trichomes found in *Anaxagorea* are very homogeneous. The variation is mainly in the number of arms, ranging from one, in unbranched hairs, to 12 in stellate hairs.

Trichome complements

For use of the term "complement", see THEOBALD et al. (1979).

In the palaeotropical species, only unbranched hairs, 3—6-celled, and 70—130 μm long, were found. In the neotropical species, much more variation in trichome complements was seen. In *A. angustifolia* and *A. brachycarpa*, only unbranched trichomes were found. *A. allenii*, *A. crassipetela*, *A. guatemalensis*, and *A. panamensis* had one- to four-armed trichomes. *A. acuminata*, *A. brevipedicellata*, *A. dolichocarpa*, and *A. gigantophylla* had exclusively stellate hairs, i.e. hairs with more than five arms and with a more or less swollen centre. In all species not mentioned, a mixture of unbranched, branched, and stellate hairs appeared to occur.

4. Anatomy

4.1. Wood anatomy

by B. J. H. TER WELLE (Utrecht)

Material studied

Neotropics: *A. acuminata: Irwin et al. 57661* (Uw 21064), *Krukoff 1017* (Uw 19187), *Krukoff 1053* (Uw 19208), *Lindeman 6698* (Uw 4529).

A. brevipes: Krukoff 6820 (Uw 7957), *Morawetz 11-25883* (Uw 29484), *Ll. Williams 849* (Uw 29440).

A. dolichocarpa: Breteler 3760 (Uw 11760), *Daniels & Jonker 1169* (Uw 8621), *Florschütz & Florschütz 1469* (Uw 2031), *Krukoff 4700* (Uw 19575), *Krukoff 5532* (Uw 20017), *Lindeman 4451* (Uw 3117a), *Lindeman 5817* (Uw 3971), *Maguire 24605* (Uw 2564).

A. guatemalensis: Record 41 (Uw 29438).

A. pachypetala: Mathias & Taylor 5389 (Uw 27090).

A. petiolata: A.C. Smith 3192 (Uw 21646).

A. phaeocarpa: W. Rodrigues 2460 (Uw 23646).

Asia: *A. borneensis: Endert 5206, Chew Wee-Lek 648.*

A. javanica: Chan FRI 13337.

A. luzonensis: Bloembergen 4686 (Uw 29433), *De Vogel 3907, Bhargava & Nooteboom 6312.*

A. radiata: Edaño PNH 1508.

The wood samples from the neotropical species vary in diameter from 3 to 10 cm. For the Asiatic species no wood samples proper, i.e. collected from the main stem or the trunk, were available. We had to content ourselves with samples from herbarium sheets. The samples thus obtained had a diameter of at most 1 cm. This means that values obtained from Asiatic specimens, given in the present paper, should be read with caution when compared with values from neotropical specimens.

For most quantitative data lowest and highest values per specimen are given, together with the lowest and highest absolute value found. When two sets of data are given, the first-mentioned set relates to the neotropical specimens and the second set to the Asiatic species (the two sets are separated by a slash).

Description

Growth rings absent or faint, marked by an increase in the number of tangential bands of parenchyma or by zones of fibres with a thicker wall and a smaller lumen than in the rest of the ground tissue.

Vessels diffuse, solitary (10—35 %/17—22 %) and in irregular clusters and occasionally radial chains of 2—8, 8 to 22 (5—23)/14 to 38 (9—41) per sq. mm, (slightly) angular, walls 3 to 6 (2—4) µm, diameter 60 to 107 (50—120)/32 to 64 (24—80) µm, vessel member length 545 to 850 (390—1170)/505 to 725 (420—930) µm. Perforations simple. Intervascular pits alternate, angular, 3—5/2—4 µm/angular to round in Asiatic species. Vessel-ray pits very scarce due to the vessels being in contact with the rays only sporadically; when present identical to the intervascular pits, but half bordered. Vessel-parenchyma pits similar.

Fibres non-septate, diameter 9—33/6—18 µm, walls 3—7/2—6 µm. Pits simple, equally frequent on the radial and tangential walls (or slightly more frequent on the radial walls in neotropical specimens), 3 to 6 µm. Length 1275 to 2040 (875—2580)/1010 to 1460 (1720—1740) µm; F/V ratio 1.90 to 2.40/1.88 to 2.77.

Rays (weakly) heterogeneous, with very few uniseriates, and mostly 5—12/4—8-seriate, composed of procumbent and weakly procumbent and sporadically square cells / in Asiatic specimens some upright cells were also found. Height of the uniseriate rays 6 to 17 cells (= 360—840 µm), 12 to 30 µm wide. Multiseriate rays in neotropical specimens 100 to >200 cells (= 2250—>7000 µm) high /83 to 105 cells (= 2250—3000 µm) high, and 120 to 350/80 to 250 µm wide; 1 to 4 (0—5) per mm.

Parenchyma in apotracheal, continuous, concentric tangential bands, 1 cell (in neotropical specimens occasionally 2 cells) wide, with 1 to 4 fibres between two bands. Number of bands about 13 (10—17)/20—24 per mm. Scanty paratracheal parenchyma occasionally present.

Small druses occur in the rays of all samples except for those of *A. brevipes*, where crystals are lacking.

Discussion

As can be deduced from the description, the specimens studied are very similar. Differences in wood anatomical characters as far as found are largely of a quantitative kind. This could readily be explained by the limited diameter of the wood samples of the Asiatic species. It is far from unlikely that samples of mature wood of Asiatic species will show quantitative values comparable to those of the neotropical species.

The most remarkable character of this genus as a whole is the occurrence of small (ca. 10—15 µm in diameter) druses in the ray cells. Otherwise, it can be said that the genus conforms to the characteristical wood anatomical structure of Annonaceae, i.e. the reticulate pattern formed by the rays, and narrow but numerous axial parenchyma bands.

Crystals are known to be scarce in the Annonaceae (METCALFE & CHALK 1950). Druses have never been described for the wood of taxa of this family, although they usually do occur in the leaves of Annonaceae. After an examination of 300 samples of 65 genera (representing ca. 95 species), no more than two samples, both of *Annona montana* Macfad., were found with only very few druses in the ray cells (TER WELLE, in prep.). The occurrence of druses in *Anaxagorea*, therefore, in both the Asiatic and the neotropical species, sets this genus well apart from other genera in Annonaceae.

4.2. Leaf anatomy

by J. KOEK-NOORMAN (Utrecht)

Material studied

All samples were taken from herbarium sheets. Transverse sections of the lamina including the primary vein were made of the central part of the lamina as well as of the basal part of the petiole. Paradermal sections of the leaf surfaces were also made.

In anticipation of an elaborate survey of the variation of leaf anatomical characters in Annonaceae (VAN SETTEN & KOEK-NOORMAN, in prep.), we will limit ourselves here to a generic description with some preliminary remarks on the systematic value of some features.

Description

1. In surface view:

Indument absent, or present on the abaxial side; when present, consisting of simple hairs, stellate hairs, or both (see Chapter 3.7).

Unspecialized epidermal cells polygonal, adaxial cells 20—65 x 20—40 µm, abaxial cells 25—60 x 15—35 µm. The anticlinal cell walls on the abaxial side are straight to slightly curved in the Asiatic species, distinctly curved in the neotropical species. On the adaxial side, the cell walls in all species are distinctly curved.

Stomata are exclusively abaxial, paracytic with subsidiary cells, length 20—40 µm. Abaxially, striations around stomata and trichome bases are visible in all species. Adaxially, striations occur in the Asiatic species only.

2. In transverse section:

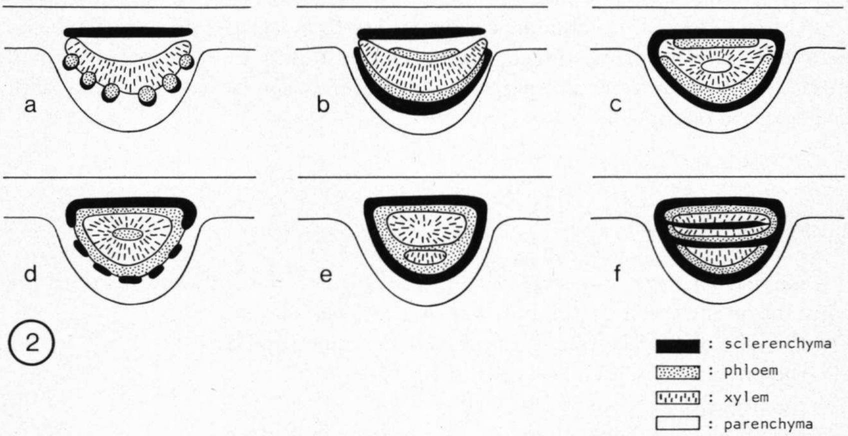
Lamina dorsiventral.

Unspecialized epidermal cells slightly flattened.

Stomata on the same level as the unspecialized cells or slightly sunken, always with pronounced outer ledges covering the stomata.

Mesophyll composed of 1 (sometimes 2) layer(s) of poorly developed palisade parenchyma and loosely packed or compact sponge parenchyma, 5—15 cells thick.

Astrosclereids occur in all neotropical species except *A. silvatica* and *A. prinoides,* either in the palisade parenchyma (*A. brevipes)* or in both sponge parenchyma and palisade parenchyma. They are lacking in the Asiatic species.



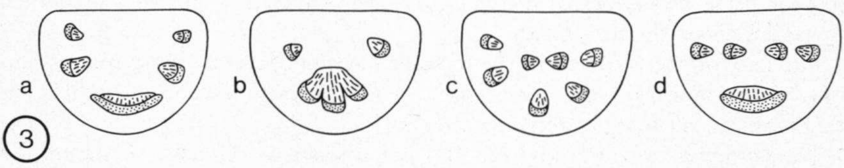


Fig. 2. Transverse sections of primary veins in *Anaxagorea* (schematic). a, *A. silvatica;* b, *A. borneensis;* c, *A. prinoides;* d, *A. acuminata;* e, *A. phaeocarpa;* f, *A. brachycarpa.*

Fig. 3. Transverse sections of petioles in *Anaxagorea* (schematic). a—b, structures found in *A. silvatica* and palaeotropical species; c—d, structures found in Neotropical species, except *A. silvatica.*

Oil cells are encountered in all species with the exception of *A. borneensis*. The oil cells in the Asiatic species and in *A. silvatica* are mainly confined to the sponge parenchyma; in all other neotropical species they occur in both sponge and palisade parenchyma, or in palisade parenchyma only.

Druses occur in the mesophyll of representatives of all species, though not in all specimens studied.

Primary veins with one vascular bundle surrounded by a continuous or interrupted sclerenchyma cap. Two types of vascular bundles are found. In *type 1*, the vascular bundle consists of one kidney-shaped xylem body abaxially accompanied by an U-shaped phloem zone (sometimes with some phloem adaxially, too). This type is found in Asiatic species and in *A. silvatica* (Fig. 2a, b). *Type 2* is found in the other species: a more complex vascular tissue. This is always a variation on the same basal pattern: a circular, continuous or interrupted phloem zone around a xylem body. This zone in some cases is divided into two or more parts by sclerenchyma or phloem tissue (Fig. 2c—f).

Both these primary vein types are highly correlated with two main patterns in the petiole. In the species having *type 1*, the vascular bundles in the petiole are arranged in one arc (Fig. 3a—b). In species with *type 2*, some additional vascular bundles can be found in the center of the petiole (Fig. 3c—d).

Although varying in abundancy, druses are found in the primary veins and petioles of all specimens studied. Stone cells are found in representatives of all species, though not in all specimens (something similar to that seen with druses in the mesophyll).

Discussion

Summarizing, we can state that in *Anaxagorea* the following features are constant on the specific level, but vary on the generic level:

- the type of vascular bundle in primary veins and petioles;
- the presence/absence of oil cells;
- the presence/absence of sclereids;
- the presence/absence of striations on the adaxial surface;
- the presence/absence of distinct curves formed by the anticlinal epidermal cell walls on the adaxial side.

In spite of the variation in the features mentioned above, most species cannot be distinguished from other species with certainty. Exceptions to this are *A. borneensis*, *A. silvatica*, and *A. prinoides*.

A. borneensis can be recognized by the absence of oil cells. *A. silvatica* is the only neotropical species with a primary vein of *type 1*. This species is different from the Asiatic species by the strongly curved anticlinal epidermal cell walls on the abaxial side. *A. prinoides* and *A. silvatica* are the only neotropical species without sclereids in the mesophyll. *A. prinoides*, like other neotropical species, has a primary vein of *type 2*.

The two types of the primary veins and the petioles in general are nearly always constant on the generic level, at least within subgenera: one finds either *type 1* or *type 2*. The occurrence of both *type 1* and *type 2* within *Anaxagorea*, therefore, is suggestive of a subdivision of the genus which goes much towards the two sections actually recognized by FRIES (1959). Only *A. silvatica*, then, would have to move from Sect. *Anaxagorea* to Sect. *Rhopalocarpus*. This is because the structure of primary vein and petiole in *A. silvatica* is highly similar to that in the Asiatic species. It should be brought to attention in this context, that *A. silvatica* also agrees with two of the Asiatic species, viz. *A. javanica* and *A. luzonensis*, in having leaf-opposed (to terminal) inflorescences. Inclusion of *A. silvatica* in sect. *Rhopalocarpus* is not supported, however, by other leaf anatomical features of this species: striations lacking adaxially, strongly curved anticlinal cell walls present, that it has in common with the neotropical species. Another leaf anatomical feature that *A. silvatica* has in common with the Asiatic species: the lack of sclereids, is also found in *A. prinoides*.

5. Leaf surface micromorphology

by W. MORAWETZ (Vienna)

The particular combination of the cuticular folding pattern on the adaxial leaf surface with the cuticular folding pattern on the abaxial surface is characteristic for *Anaxagorea* (15 neotropical and 4 palaeotropical species were examined). In this respect *Anaxagorea* differs remarkably from other annonaceous genera (90 genera have been investigated: MORAWETZ & WAHA 1984).

The type of cuticular folding pattern on the adaxial surface is relatively frequent in the Annonaceae. It occurs in genera supposed to be closely related, *Duckeanthus*, *Goniothalamus*, *Neostenanthera*, *Piptostigma*, and *Xylopia* (all placed in the *Fusaea* subfamily sensu WALKER 1971), as well as unrelated genera like *Enantia*, *Guatteriopsis*, *Isolona*, *Kingstonia*, *Monodora*, *Polyaulax*, and others. The folding pattern on the abaxial surface is, so far, only known from the genus *Anaxagorea*. *Anonidium* shows a few similarities with *Anaxagorea* on the abaxial surface, but the sculpturing of the adaxial side is completely different.

Description

Upper side (Fig. 4a, c):

Epidermal cells tetra- to polygonal; anticlinal boundaries thick, raised, straight to undulate and in some cases consisting of irregular thick spheric warts arranged like a string of pearls; the central cell surface is flat, but in older leaves it is sometimes completely obscured by the very thick anticlinal walls; bundles of parallel thin striae going across the anticlinal boundaries (rare).

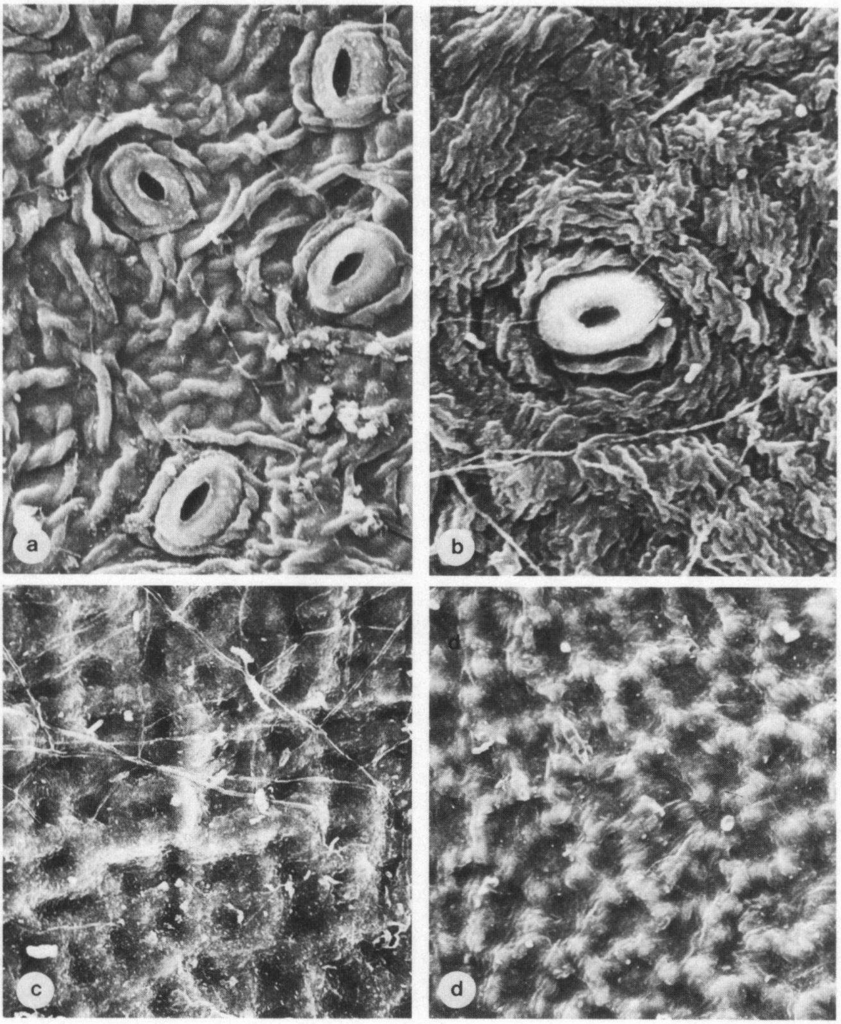


Fig. 4. SEM-photographs of leaf surfaces in *Anaxagorea*. a, *A. allenii (Dressler & Lewis 3713)*, lower side, x400; b, *A. radiata (Santos 4152)*, lower side, x500; c, *A. brevipes (Krukoff 5048)*, upper side, x300; d, *A. borneensis (Clemens 20570)*, upper side, x300.

Lower side (Fig. 4b, d):

Stomata roundish to elliptic, each with a single raised stomatal rim; every stoma surrounded by two to several semicircular, concentric, irregularly folded bundles of thin striae; epidermal surface covered with thick and/or thin randomly orientated, undulate striae; striae few to many, sometimes forming a complicated network across the anticlinal boundaries or ± restricted to convex, raised cells.

6. Karyology

by W. MORAWETZ (Vienna)

The chromosome number 2n = 16 was found in *A. acuminata* (3 individuals, *de Granville 5473* — U), *A. phaeocarpa* (1 individual, *Ehrendorfer 6400—0402* — WU), and *A. javanica* (8 individuals, *Ehrendorfer 03—05* — WU; identical report by OKADA & UEDA 1984). *A. brevipes* has a chromosome number of 2n = 48 (Fig. 5c) (4 individuals, *Morawetz & Coêlho 21-19883* — INPA, U, WU).

Note: The earlier report of 2n = 28 for the above collection of *A. phaeocarpa* (EHRENDORFER et al. 1968, as *A. costaricensis*) was evidently due to a mixing-up with a fixation of *Guatteria*; we re-checked the original fixation and could clearly establish a chromosome complement of 2n = 16.

The appearance of nuclei during the cell-cycle is identical both in the neotropical *A. acuminata* (Fig. 5d) and in the palaeotropical *A. javanica*. The latter is described here in detail (Fig. 5a, b): The 2n-genome lenght of the metaphasic chromosomes is 29.2 µm (s = 5.2; 9 plates measured). The somatic karyotype consists of metacentric to subtelocentric chromosomes of decreasing size from 2.3—1.9 µm to 1.5—1.2 µm. Most of the chromosomes are easily identified during prometaphase by their differing size and their centromere position; fully contracted chromosomes show less differentiation. One of the chromosome pairs bears well-developed satellites, which frequently separate from the chromosomes during prometaphase, or are connected only by a very pale staining chromatin thread to the shorter arm. Similar nucleolus organizing chromosomes also occur in *Annona* species (TANAKA & OKADA 1972, MORAWETZ 1984a). The interphase nuclei have a pale staining reticulate or just punctate euchromatin; there are 10 to 16 large chromocentres which are sometimes supplemented by some small ones. The elongate to roundish chromocentres often have a centromere-like constriction and thread-like appendices (similar to those of *Annona reticulata*: MORAWETZ 1984a). They often appear to be built up heterogeneously: there are dark staining central or terminal parts, while the remainder appears somewhat paler.

The base number in *Anaxagorea* is x = 8. *A. acuminata, A. phaeocarpa* and *A. javanica* are diploids, whereas *A. brevipes* is hexaploid. *A. brevipes*, therefore, is highly derived in this feature; intermediate polyploids may be expected to occur in the Neotropics.

Anaxagorea is placed on the basis of palynological data in the *Fusaea* subfamily sensu WALKER (1971). Our new karyological data are not in conflict with this, as other genera placed here also exhibit x = 8, a.o. *Cananga* (OKADA & UEDA 1984), *Fusaea* (MORAWETZ, unpubl.), *Goniothalamus* (EHRENDORFER et al. 1968, OKADA & UEDA 1984, SAUER & EHRENDORFER 1984, MORAWETZ unpubl.), *Neostenanthera* (MANGENOT & MANGENOT 1962, MORAWETZ unpubl.), and *Xylopia* (MORAWETZ 1984b).

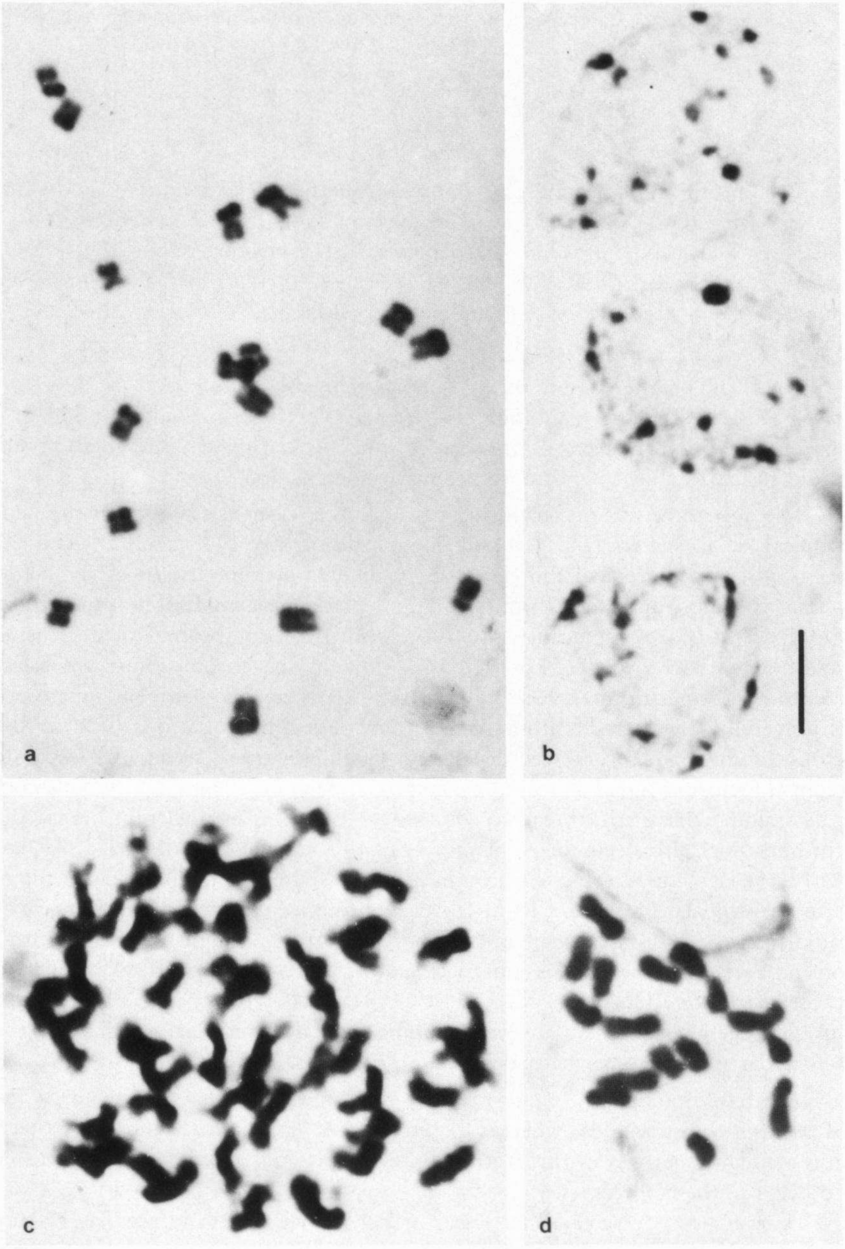


Fig. 5 a—b. *A. javanica*, 2n = 16. a, fully contracted metaphasic chromosomes (pretreated with 8-hydroxiquinoline); b, interphase nuclei, note the big, darkly coloured chromocentres; c, *A. brevipes*, 2n = 48, prometaphasic chromosomes (field fixation); d, *A. acuminata*. 2n = 16, metaphasic chromosomes. All preparations were done by the HCl/Giemsa method; bar (for a—d): 5 µm.

The fact that *Anaxagorea* and *Xylopia* are the only annonaceous genera that occur both in America and in Asia (disjunct and pantropical, respectively), forms an indication of a very early origin and distribution. In contrast, all other genera of Annonaceae are, without exception, confined to one continent or to the Palaeotropics, with many of them endemic to small areas. The occurrence of the base number x = 8 both in *Anaxagorea* and in *Xylopia* (see MORAWETZ 1984b), therefore, could be regarded as an indicator of primitiveness within the family. Possibly, in view of the above, x = 8 could be considered the base number of the Annonaceae.

7. Palynology

by A. LE THOMAS (Paris) & B. LUGARDON (Toulouse)

7.1. Morphology

Pollen with cytoplasm contents, as well as pollen brought into contact with water was studied. The SEM used is at the Laboratoire de Géologie du Muséum d'Histoire naturelle de Paris.

The pollen of *Anaxagorea* is always simple, heteropolar, bilateral, sulcate, the sulcus reaching the extremities of the pollen grain. Under the SEM, the tectum appears totally smooth and continuous, without any perforation (Fig. 6: 1, 3, 4). Like that of the African genus *Meiocarpidium* (LE THOMAS 1981), the pollen of *Anaxagorea* shows the peculiarity of emptying itself of its cytoplasm contents upon contact with water. The cytoplasm is surrounded by the finely granular intine. (*A. prinoides*, Fig. 6: 2)

7.2. Ultrastructure

For the study of the ultrastructure, pollen with cytoplasm contents was fixated with formaldehyde/OsO_4, embedded in Epon, and stained with uranyl acetate/lead citrate. The TEM used is at the Laboratoire de Biologie végétale de l'Université de Toulouse.

In the proximal region, that is, the non-aperturate region of the pollen grain, the exine shows a massive, continuous and homogeneous tectum, traversed by very few and minute perforations (Fig. 7: 1). The infratectal granular layer, rather even in thickness, is constituted by very large granules of variable diameter, mostly agglomerated in larger or smaller clusters of irregular shape, directly connected with the tectum, and with relatively large spaces in between. The basal layer of the exine is formed by a thick, discontinuous (Fig. 7: 3), sinuous foliation connected with the innermost granules of the infratectal layer, and in which no trace of lamellation can be distinguished; exceptionally (Fig. 7: 2) and over a very short distance only, a second thinner foliation is observed detaching from the upper foliation and more or less compressed against the intine.

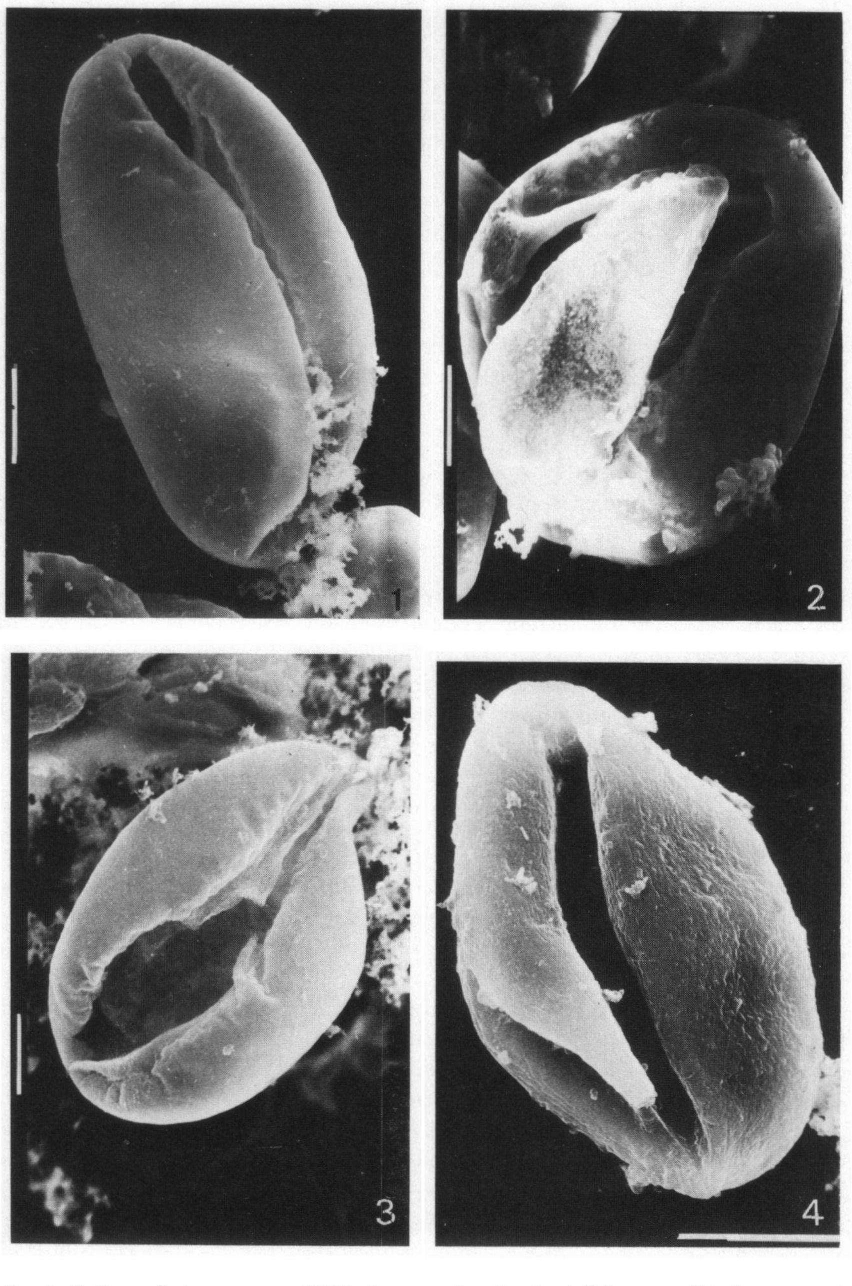


Fig. 6. Pollen of *Anaxagorea*, SEM-photographs. 1, *A. dolichocarpa (Lindeman et al. 706)*; 2, *A. prinoides (Lindeman et al. 713)*; 3, *A. acuminata (Steyermark 94300)*; 4. *A. javanica* var. *javanica (Sinclair 8447)*. White bar = 10 μm.

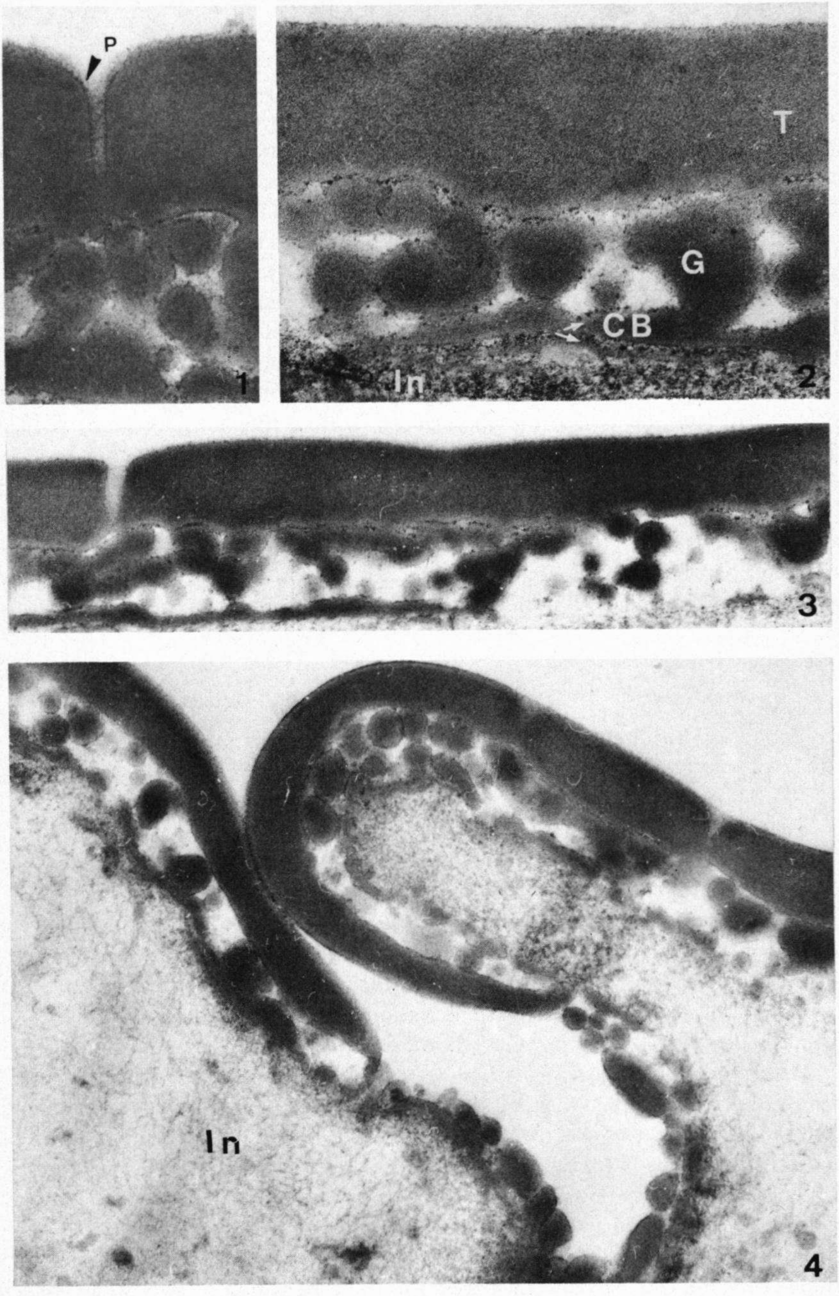


Fig. 7. Pollen of *A. brevipes (Prance et al. 24172)*, TEM-photographs. 1—2, section through exine, proximal region, x 20.000; 3, idem, x 12.000; 4, section through the aperture, x 25.000. p = perforation; T = tectum; G = grains; CB = basal layer ("couche basale" in french); In = intine.

In the distal region (Fig. 7: 4), near the aperture, the granules of the infratectal layer no longer form such conspicuous clusters, become more spaced and reduced in diameter as the tectum becomes thinner. Under the sulcus, there remain only some discontinuous tectal granules, more or less mixed with granules of the infratectal layer. The intine, very thin in the proximal and lateral regions, is considerably thicker at the aperture which is opened in numerous grains.

The morphology of the pollen of *Anaxagorea*, the ornamentation of which is practically smooth, does not permit, as it seems, to make any distinctions on the specific level. The dimensions, though variable according to species (L = 33—60 µm; l = 22—33 µm), are hardly significant considering the very frequent deformation of the pollen of *Anaxagorea*, with a fragile exine in particular. Nevertheless, the ultrastructure of the exine permits to place this type of pollen near the sulcate pollen of the African genus *Meiocarpidium* (LE THOMAS 1981), situating it at the base of the evolutionary series 1 leading to loose, inaperturate tetrads of the *Xylopia* type. This would confirm both the primitive character accorded to the genus *Anaxagorea* by WALKER (1971), and the place given to it by FRIES (1959) in his classification (*Xylopia* group).

8. Chemical studies on the genus Anaxagorea

by A. CAVÉ (Paris) & M. LEBOEUF (Paris)

The genus *Anaxagorea* is one of the chemically least known among the Annonaceae.

Several long-chain polyprenols (C_{45}-C_{70}; mainly the C_{60} compound) were identified in *A. brevipes* (SASAK & CHONJNACKI 1973). The occurrence of cyanogenic glucosides was recorded in *A. luzonensis* (HEGNAUER 1964, GIBBS 1974), and a study was made of the various fatty acids contained in the oil from the seeds of *A. javanica* (GUNSTONE et al. 1972).

A. prinoides and *A. dolichocarpa* were recently studied for their alkaloidal contents (HOCQUEMILLER et al. 1981, RASAMIFAZY 1983). Two aporphinoid bases were identified: the main alkaloid is the known noraporphine asimilobine; the other one is anaxagoreine, a new alcoholic 7-hydroxy noraporphine.

The homogeneity of alkaloidal composition among *Anaxagorea* species may be pointed at. As a matter of fact, in addition to the various parts of *A. prinoides* studied (bark of stem and root, leaves), the two same alkaloids were also found in *A. dolichocarpa* and in material not yet identified of two other species from French Guiana.

It is also of interest to note the presence of a 7-hydroxy aporphine alkaloid within *Anaxagorea* species, as this fact is regarded as an archaic character (URZUA & CASSELS 1978).

9. Pollination and dispersal

by W. MORAWETZ (Vienna)

Field studies were made of *A. brevipes* populations occurring in the vicinity of Manaus, Amazonas, Brazil. This species is a frequent understorey tree up to 8 m tall in some primary forests, and it also occurs in patches of disturbed secondary forest ("capoeira") on sandy and red latosolic soils.

9.1. Pollination

Flowers were found in anthesis before mid-day (10—12 h a.m. observed). The protogynous, pale yellow flowers emit a strong odour somewhat like acetone or overripe tropical fruit. During anthesis, the elongate, thick petals are strongly adpressed, forming a small pollination chamber sensu GOTTSBERGER (1970). A single small beetle was observed once, trapped inside this chamber. This indicates a ± similar cantharophilous pollination mechanism to that found in the genus *Xylopia* (GOTTSBERGER 1970). *A. brevipes* does not appear to have any specific flowering and fruiting season, as vegetative, flowering, and fruiting individuals were found growing close together.

9.2. Seed dispersal

As already indicated by RIDLEY, in his monumental work on plant dispersal (RIDLEY 1930, p. 669), *Anaxagorea* is the only autochorous genus in the Annonaceae. The exploding mechanism is probably identical both in the Asiatic and in the American species (RIDLEY 1930, CORNER 1949). In *A. brevipes* the free carpels mature into characteristic club-shaped monocarps which are coloured bright yellow with red bases and apices. The carpel wall gradually dries out and shrinks. This exerts a certain amount of pressure on the two more or less semi-spheric seeds which lie in the cavity with their flat surfaces together. Two small knobs on the inner side of the small ventral slit prevent a premature liberation of the seeds. When the pressure is high enough, the knobs are pushed away by the rapidly ejected seeds. Under laboratory conditions, the seeds appeared to cover distances up to 6 m. In nature, the seeds are ejected from a height of 6 m or more, and possibly can bridge even longer distances. The extremely hard and smooth seed surface (no epidermal sculpturing, even when seen at a magnification of 20000 x under the SEM) possibly can be correlated with the exploding mechanism.

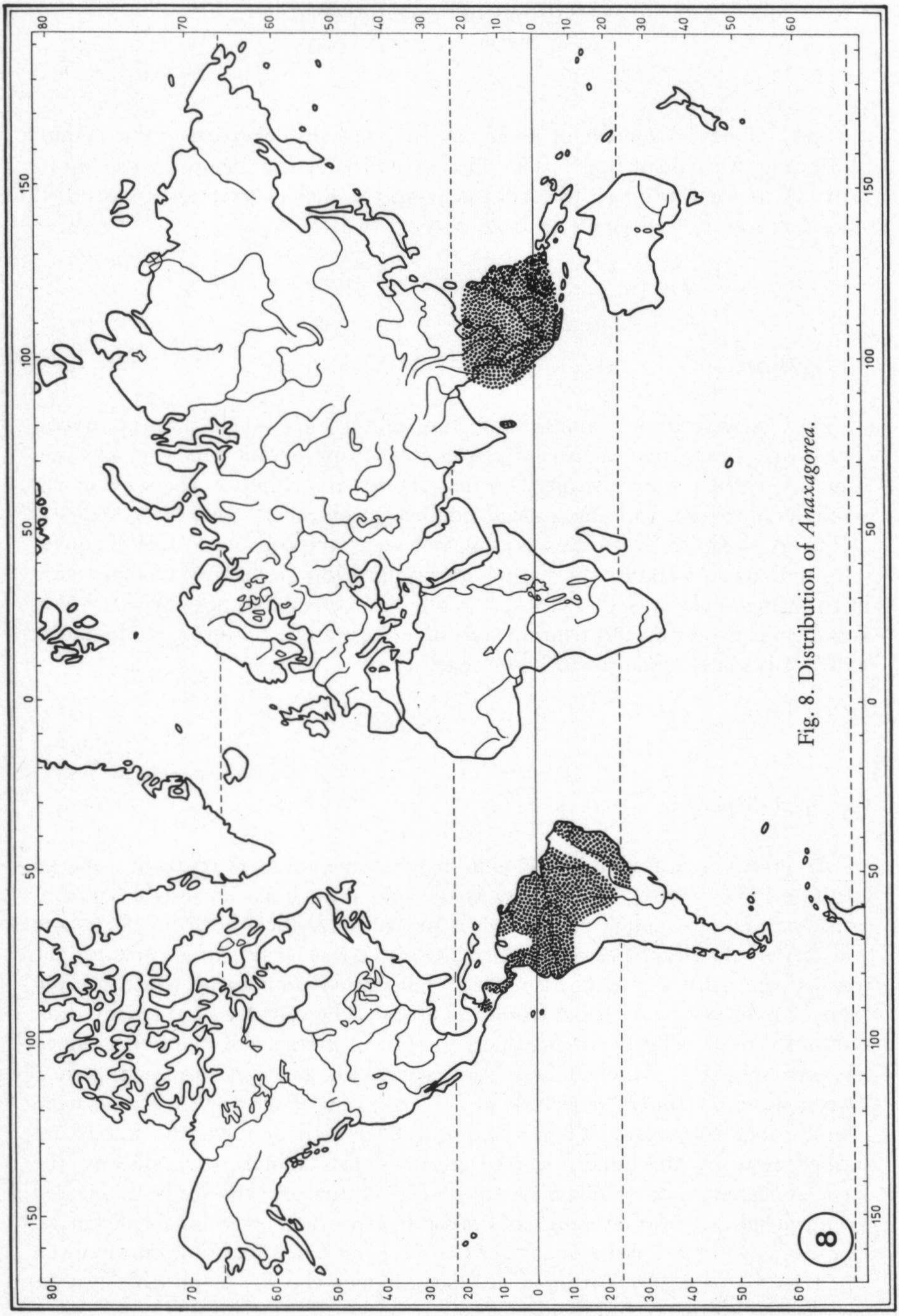


Fig. 8. Distribution of *Anaxagorea.*

10. Geographical distribution and ecology

The remarkable disjunction in the distribution of *Anaxagorea* has already been mentioned in Chapter 1 (see also Fig. 8). In tropical America 20 species, or very likely slightly more, occur, whereas in Asia there are at least 3 species.

In the Neotropics the genus ranges from Guatemala (ca. 17° N) in the North, to halfway down in Peru and to southeastern Brazil (ca. 23° S) in the South. It is known from Trinidad, but not from any of the West Indian islands. The distribution map of neotropical *Anaxagorea* clearly shows two centres of concentration of species (Fig. 9): the Amazon Basin, and adjacent Venezuela and the Guianas, and a second centre in Costa Rica and Panama. Five out of the 20 neotropical species have a large area. These include *A. doli-*

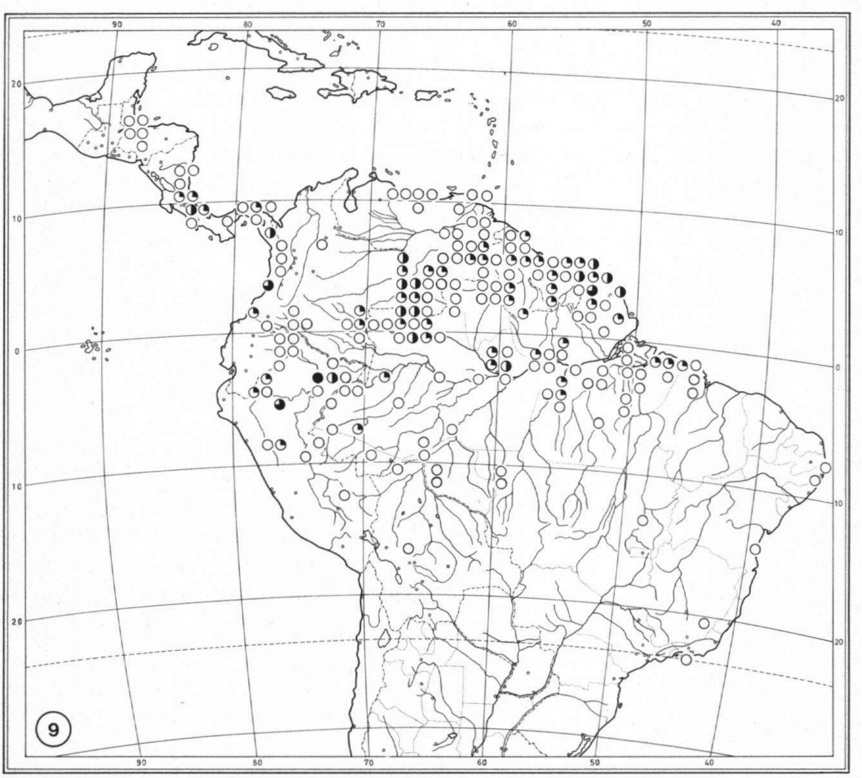


Fig. 9. Distribution of *Anaxagorea* in the Neotropics. One species per square (○); two species per square (◔); three species per square (◑); four species per square (◕); five species per square (●).

chocarpa which is widely distributed throughout tropical South America, and *A. crassipetala* occurring in Central America and western South America. Six neotropical species are known only from a very small area, like *A. floribunda* in northern Peru, and *A. macrantha* and *A. angustifolia*, both in the Upper Rio Negro region in Brazil and bordering Venezuela.

In Asia *Anaxagorea* occurs from Sri Lanka in the West to Southeast Asia, the Philippines, and Indonesia as far as the Moluccas in the East. Two of the Asiatic species are widely distributed, whereas the third, *A. borneensis*, occurs in a restricted area.

Anaxagorea is largely found in lowland rain forest at altitudes between 0—1000 m. *A. silvatica* from Minas Gerais, Brazil, is reported to grow in woods and forest rich in bamboo, however. *A. brevipes* is known to occur not only in primary forest, but also in disturbed secondary forest (see Chapter 9). The first author, during field trips to Guyana and to Venezuela, noted the occurrence of individuals of *Anaxagorea* in dense groups. This phenomenon was also observed by R. B. FOSTER (pers. comm.) on Barro Colorado Island in Panama. A very likely explanation for this is the mode of seed dispersal, by which the seeds are spread explosively over a distance of up to several meters from the parent (see Chapter 9). Only few species have been collected above 1000 m. These include *A. dolichocarpa* and *A. acuminata*, both up to ca. 1300 m. The highest altitude is reached by *A. petiolata*, this species has been found between 400—1500 m.

11. Cladistic relationships in Anaxagorea

by J. KOEK-NOORMAN (Utrecht) & M. ZANDEE (Leiden)

11.1. Introduction

As already pointed out in Chapter 2, the generic delimitation of *Anaxagorea* has never been seriously disputed, contrary to that of numerous other annonaceous genera. The particular shape of the, dehiscent, monocarps clearly distinguishes *Anaxagorea* from all other Annonaceae. This implies that this character state would clearly stand for an autapomorphy in all outgroup comparisons within the Annonaceae. Therefore, the monographic revision of *Anaxagorea* as a monophyletic taxon is justified. The present chapter will deal with considerations about intrageneric affinities.

The geographically separate sections created by FRIES (1940, 1959) are not defined by unique morphological or anatomical character states, as suggested by FRIES. Besides, using the data at hand, we found no other, unambiguous intuitive subdivision. Therefore, in an attempt to resolve the intrageneric relationships, a cladistic analysis was undertaken.

For an elaborate description of outgroup comparison, compatibility analysis, and the concept and methods of the construction of monothetic groups, we refer to De Jong (1980), Meacham (1981), Beckner (1959), Sharrock & Felsenstein (1975), Farris (1978), Hennipman & Roos (1983), and Zandee (1983). Here, we will restrict ourselves to a short survey of the subsequent steps taken using especially the procedures as proposed by Zandee, and a preliminary discussion of the constructed cladograms.

11.2. Construction of the data matrix

The morphological characters selected for our data matrix are represented by only one state in a species. Not all species are characterized by one or more unique character states. In order to make each species appear as a distinct unit in the resulting cladogram, artificial unique characters are introduced.

The 11 characters selected are in part multistate. They were recorded as 28 binary character states (Table 2). Subsequently, a list of partially monothetic subsets (i.e. groups based on unique characters only; Zandee 1983) was made.

Apart from the 22 individual species, 26 subsets were formed. It appeared that these subsets represented much conflicting evidence. The list of subsets served as input for a three-taxon statement permutations + outgroup comparison computer program (Zandee 1983). However, interpretation of the output resulted in cladograms with only two short branches including six species.

Therefore we decided to look for possible sister- and outgroup relations among the strictly monothetic subsets in *Anaxagorea*, i.e. groups of species characterized by a set of both necessary and sufficient character states (i.e. each state is present in all members of the group; each member of the group shows all states of the character state set). These two relations are equivalent. Although this particular combination of states is common to all members of the group and does not occur in any taxon outside the group, it is possible for each separate state to occur in other species outside the groups thus defined (Zandee 1983). Using our data-set, 377 of such sets can be formed. Although, theoretically, one can search for all possible 3-taxon statement permutations, their high number exceeds the available processing capacities.

For this reason we decided to preclude all solutions conflicting with some groups which showed inclusion relations with many groups in the lists of partially and strictly monothetic subsets, and which were also recognized intuitively.

Intuitively, the Central American species *A. allenii* = nr. 2, *A. crassipetala* = nr. 7, *A. guatemalensis* = nr. 11, and *A. panamensis* = nr. 14, are recognized as a "closely related" group. In all cladograms nrs. 2, 7, and 11 are clustered together in a trichotomous arrangement. Species nr. 14 is clustered together with {2+7+11} in combination with nr. 12 only. We decided to accept {2+7+11+12+14} as one taxon.

A. brevipedicellata = nr. 5, and *A. floribunda* = nr. 9, are nearly always found in a trichotomous arrangement with {2+7+11+12+14}. We decided to consider them as another artificial taxon.

Table 1. List of code numbers used in the data matrix of *Anaxagorea*, indicating the respective species.

1. *A. acuminata*
2. *A. allenii*
3. *A. angustifolia*
4. *A. brachycarpa*
5. *A. brevipedicellata*
6. *A. brevipes*
7. *A. crassipetala*
8. *A. dolichocarpa*
9. *A. floribunda*
10. *A. gigantophylla*
11. *A. guatemalensis*
12. *A. macrantha*
13. *A. manausensis*
14. *A. panamensis*
15. *A. pachypetala*
16. *A. petiolata*
17. *A. phaeocarpa*
18. *A. prinoides*
19. *A. rufa*
20. *A. silvatica*
23. *A. borneensis*
24. *A. javanica*
25. *A. luzonensis*

Table 2. List of code numbers used in the data-matrix and cladograms indicating character states.

1. stigma stipitate
2. stigma sessile
3. keel of outer petals broad
4. keel of outer petals narrow or absent
5. outer petals considerably longer than inner petals and sepals
6. sepals considerably shorter than inner and outer petals
7. sepals shorter than inner petals; outer petals considerably longer than inner petals
8. petals and sepals comparable in length
9. flower buds conical
10. flower buds acuminate
11. flower buds ovoid
12. sepals free
13. sepals slightly connate
14. sepals connate
15. sepals fully reflexed
16. sepals apically reflexed
17. sepals curved upwards
18. number of stamina more than 80
19. number of stamina between 25 and 80
20. number of stamina less than 25
21. thecae broader than the connectives
22. connectives broader than the thecae
23. staminodes absent
24. staminodes present
25. staminodes glandular-tipped
26. staminodes not glandular-tipped
27. number of carpels less than 5
28. number of carpels more than 5

A third group, intuitively recognized as such, is formed by *A. dolichocarpa* = nr. 8, *A. gigantophylla* = nr. 10, *A. petiolata* = nr. 16, and *A. acuminata* = nr. 1, with some other species as possible "satellites": *A. brachycarpa* = nr. 4, *A. brevipes* = nr. 6, and *A. rufa* = nr. 19. As a consequence of the repeatedly found cluster {4+8+10+16}, we accepted this group as one unit.

A highly similar pair of species is formed by *A. brevipes* = nr. 6 and *A. rufa* = nr. 19. Among the Asiatic species, *A. javanica* = nr. 24, and *A. luzonensis* = nr. 25, form a closely related pair of species.

As a consequence, a new data-matrix was made, in which the species groups {2+7+11+14+12}, {5+9}, {4+8+10+16}, {6+19}, and {22+23} (see Table 1) were considered as one taxon, characterized by only those binary character states which are present in all participating species. This resulted in a new list with a manageable number of 108 strictly monothetic subsets. (For a list of species and their number used in the analyses, see Table 1).

11.3. Construction of the cladograms

In order to extract cladograms from this list, we applied the concept of "compatibility for groups", slightly deviating from MEACHAM's (1983) "compatibility for characters". In this way we tried to incorporate a taxonomist's idea of correlation (of groups, or characters). We call groups compatible, when their defining character state distributions either include or exclude one another completely. (In this way we preclude the possibility of compatibility between e.g. the strings 111000 and 001111, which, however, satisfy MEACHAM's definition of compatibility.)

From the list with 108 strictly monothetic subsets a (symmetric, binary) compatibility matrix was derived. Here, the ordinal number of each row and column corresponds with the same ordinal number in the list, and therefore with its subsets. All 1-entries in this matrix indicate the compatibility between the corresponding subsets. From this matrix, a search was done for all possible cliques of maximal size; i.e. the largest of those unions of subsets for which all subsets are mutually compatible. The maximum clique size for groups is bounded by the number T of terminal taxa and equals 2T-1 (in this analysis: T = 13).

Although not all cliques were found due to a still imperfect algorithm, the application of this procedure made clear that at least 33 possible alternatives are possible. These cliques defined 33 possible cladograms with the same maximal number (12) of internal nodes (= the same amount of resolution). In the next step, the characters from the list of strictly monothetic sets are added to the branches of the cladogram and subsequently tested for apo- and plesiomorphic condition by means of the outgroup rule (HENNIPMAN & ROOS 1983, DE JONG 1980). In this way, only those cladograms are selected for which the largest number of branches is supported by an apomorphic state. However, the number of branches, supported by a presumed apomorphic character state (and thus the degree of solution of the cladogram) depends on the choice of the outgroup for the genus as a whole. In our opinion, no such choice can presently be made in view of lack of knowledge about generic limits within Annonaceae (see Chapter 1). Besides, for some species some character states are yet unknown. Moreover, in all cases the presupposition of multiple sister group-relations is unavoidable. As a consequence, a final cladistic evaluation of all characters involved in the construction of the cladograms and the selection of the best cladogram are yet regarded premature.

Nevertheless, in spite of this it appears possible, after analysing the 33 cladograms, to select 9 "best" solutions with 9 or 8 internal nodes left. In these cladograms, the main branches are defined by only 5 out of the 11 selected characters. As a result, some groups of species are repeatedly present. Figs. 10 and 11 illustrate two possible "best" cladograms.

The species groups {2+7+11+14+12} and {5+9} are always found clustered together, and united with the group formed by all other species only in the last step.

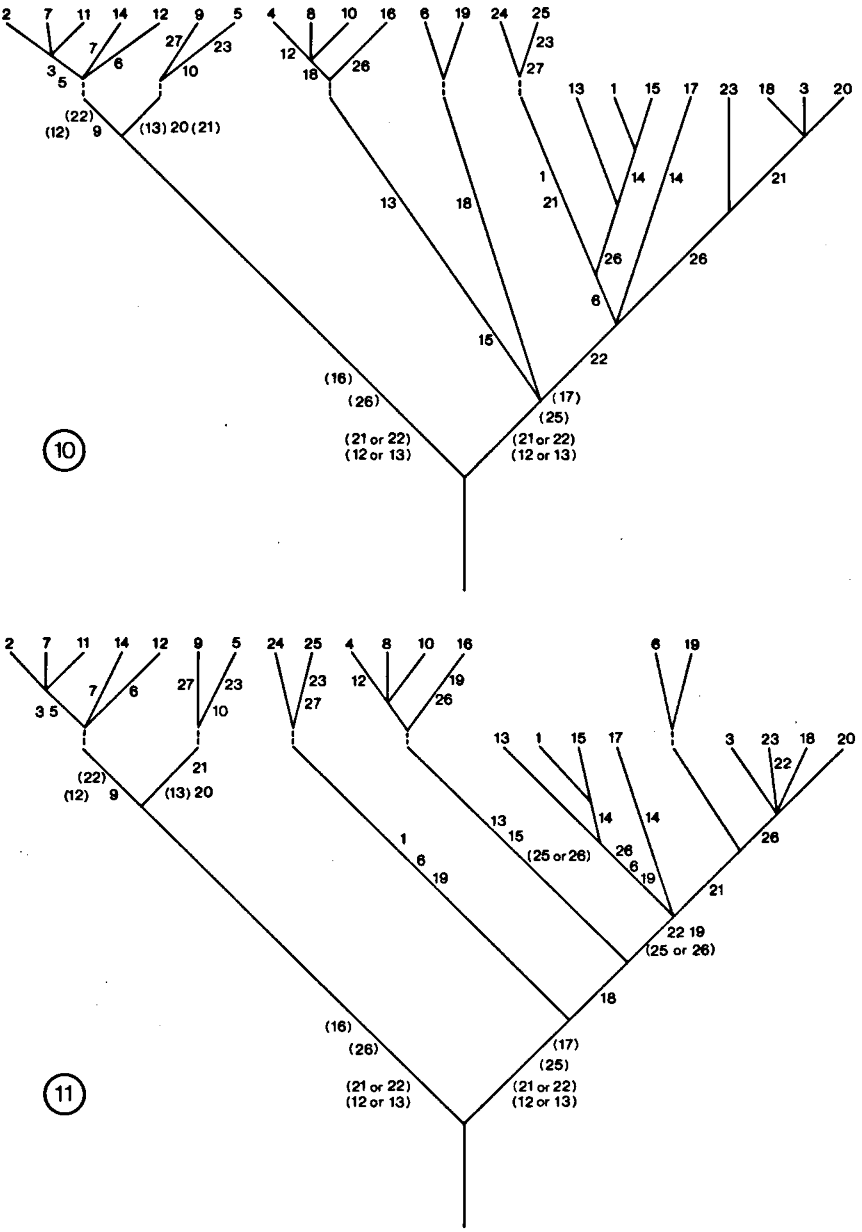


Fig. 10 and 11. Two out of nine possible "best" cladograms, indicating cladogenetic affinities in *Anaxagorea*. The numbers along the branches indicate apomorphic character states. For the numbers between brackets it appeared impossible to decide upon the apo- or plesiomorphic condition of the characters. The numbers terminating the branches indicate the species as numbered in this paper. For explanation with regard to the groups connected with the cladograms by dotted lines, see text.

The species nrs. 1, 13 and 15 are always found together, often united in the next dichotomous or trichotomous step with group {22+23}. A frequently found alternative position for {22+23} is illustrated in Fig. 11.

Species nr. 17 is often found in a trichotomous sistergroup-relation with {22+23+1+13+15} (Fig. 10) or {1+13+15} (Fig. 11), together with a group of species {6+19+3+21+18+20} within which the relationships show much variation; consequently, the species are found in varying dichotomous or trichotomous arrangements.

The five characters involved in the definition of the relationships between these (groups of) species are:

1. the position of the sepals (character state 15—17),
2. the connation of the sepals (12—14),
3. the width of the thecae in relation to the connectives (21—22),
4. the presence of a glandular margin on the apex of the staminodes (25—26), and
5. the number of stamina (18—20).

For each cladogram the application of the outgroup rule dictates the assumption of several character state reversals for the four latter characters. For the first four characters, the apo- vs. plesiomorphic condition in the first dichotomy cannot be deduced from our cladograms because of the lack of a sistergroup and outgroup for *Anaxagorea.*

Decisions concerning apo- vs. plesiomorphic condition of character states in the higher dichotomies are complicated by the fact, that in most groupings in the cladograms there exists more than one state for these character states. Following ARNOLD (1981), in his discussion of possible "pseudoreversal", we accept the presence of completely overlapping distribution patterns as some evidence, that the whole group indicated by the main right branch of the cladograms may be monophyletic.

As far as we know now, glandular-tipped staminodes and wide thecae (i.e. thecae broader than the connective) are not found in other genera, intuitively thought to be possibly related to *Anaxagorea.* The character states for the number of stamina, and the connation of the sepals are all found in other Annonaceae. It is tempting to hypothesize a transformation series for the position of the sepals: curved upwards — apically reflexed — fully reflexed. The cladograms suggest, that the curved-upward position is the apomorphic condition. Either fully reflexed or apically reflexed sepals are plesiomorphic.

The construction of the branches formed by the species {2+7+11+12+14} and {4+8+10+16} as indicated in Fig. 10 and 11, was suggested by the results of the three-taxon statement permutations + outgroup comparison using strictly monothetic subsets. The outgroup rule suggests the apomorphic condition of conical and acuminate flower buds in {2+7+11+12+14}, because of the globose condition in all other species, although a final decision must be postponed pending the choice of a sister group for *Anaxagorea.*

The structure of group {4+8+10+16} has no such consequence for any character.

12. Subdivision of the genus

As indicated before (Chapters 1, 2), *Anaxagorea* is a homogeneous genus. This is confirmed by the wood anatomy (Chapter 4.1). The two sections distinguished by FRIES, i.e. only indicated at first, later formally published (FRIES 1940, 1959), are based on the position of the inflorescence and the shape of the carpel. Sect. *Anaxagorea* has axillary inflorescences and sessile stigmata, whereas sect. *Rhopalocarpus* has leaf-opposed inflorescences and stipitate stigmata (FRIES l.c.).

The trouble is that *A. borneensis* has axillary, rather than leaf-opposed inflorescences. While FRIES, in the case of *A. borneensis*, assumes a terminal position on reduced lateral shoots, it is all the more curious that he apparently did not notice the leaf-opposed inflorescences in *A. silvatica.* Another question is, if the axillary position of the inflorescence in *A. borneensis* should be explained by reduction of lateral shoots, then why not extend this to the neotropical species as well? Moreover, it should be noted that in *A. brevipes* inflorescences of a clearly terminal position regularly occur, and the same is more rarely seen in *A. dolichocarpa*, too. Besides, the stigmata in *A. borneensis* can hardly be termed stipitate. There only remains to be investigated the position of the ovules: subbasal in neotropical species, and truly basal in at least *A. luzonensis and A. javanica* (FRIES 1940). We have not been able to confirm this while dissecting flowers: this should be done by means of good microscope slides.

Contradictions such as appear on the level of the gross morphology, are also evident on the level of the leaf anatomy (Chapter 4.2). We mention here the structure of the primary vein, which places *A. silvatica* next to the Asiatic species, and the absence of oil cells in *A. borneensis* indicating once more the somewhat isolated position of that species.

In view of this, we reject the sections by FRIES, and we do not attempt to come up with an alternative subdivision of the genus. We have tried, however, to arrange *Anaxagorea* species in groups with a certain overall resemblance. The following must be regarded as a memory aid for the time being, and certainly does not pretend to be more than that!

1. *A. allenii, A. crassipetala, A. guatemalensis, A. panamensis,* all occurring in Central America (with only *A. crassipetala* extending into South America), and the South American *A. macrantha.* These species all have flower buds which are conspicuously longer than wide (conical).

2. A large and heterogeneous group perhaps of Amazonian origin including *A. acuminata, A. angustifolia, A. brachycarpa, A. brevipes, A. dolicharpa, A. gigantophylla, A. manausensis, A. pachypetala, A. petiolata, A. phaeocarpa, A. ru-*

fa. These species have flower buds varying from globose to slightly longer than wide (ovoid, ellipsoid).

3. *A. brevipedicellata* and *A. floribunda*, two species from French Guiana and Pará, and from Amazonian Peru respectively. Although vegetatively quite dissimilar, these species might belong together on account of floral characters, perhaps with a link toward the first group.

4. *A. javanica* and *A. luzonensis*, the two most common and widespread species in Asia, characterized by stipitate stigmata (carpels attenuate towards the stigma) and leaf-opposed or terminal inflorescences.

5. *A. silvatica*, an imperfectly known species froim southeastern Brazil which has the leaf-opposed inflorescences in common with the previous group.

6. *A. prinoides*, a species from French Guiana and Amapá in Brazil, which takes up an isolated position.

7. *A. borneensis*, a species from Borneo which also takes up an isolated position.

Groupings of species comparable to these were frequently found in a three-taxon statement permutations + outgroup comparison computer program (see Chapter 10). Two possible cladistic relation schemes for these clusters are provided (Fig. 10, 11). As already explained, these cladistic analyses are to be regarded as provisional. It would be premature to draw conclusions as to the systematics of the genus now.

13. Uses and vernacular names

Anaxagorea, as a whole, is of little economic importance. The following summarizes information from herbarium labels.

1. Bark. This is used for making ropes or bands, but there are also other uses, including medicinal use.

2. Leaves. These possibly are used here and there for medicinal purposes.

3. Wood. This apparently is sometimes used for construction work.

4. Seeds. There is one report on toxic seed.

For the following, all neotropical, species economic uses are reported:

1. *A. acuminata.* In Venezuela, bark is used as a deodorant, rubbed into armpit, with long lasting smell (Amazonas); also, wood is used for construction Work (Monagas). In Guyana, an infusion of bark and wood, or bark boiled to syrup, is used against cough. In Suriname, bark is used for cordage. In Brazil, wood is used for general construction work (Pará).

2. *A. brevipes.* The strong fibers of the bark are used in Amazonas, Venezuela, by natives for head bands or straps for carrying their cargo in their guayare.

Table. 3. List of vernacular names from the Neotropics (the numbers refer to the numbers of the species in the systematic treatment).

Acuanim (Peru. Amazonas, 7)
Apérémoe (Suriname, 8)
Aratiaeum brabo (Brazil. Pernambuco, 8)
Ata (Brazil. Pará, 1)
Bara caspi (Peru, 6)
Black yarri yarri (Guyana, 1)
Boszuurzak (Suriname, 1)
Cara huasca (Peru. Loreto, 8)
Carapipa (Venezuela. Bolívar, 16)
Cará-pi-pok (Venezuela. Bolívar, 8)
Chamuscasaina (Ecuador, 17)
Cuanim vačuána (Peru, Amazonas, 8)
Danta (Venezuela. Yaracuy, 1)
Envira (Brazil. Amazonas, 7, 13)
Envireira (Brazil. Amazonas, Pará, 17)
Espintana (Peru. Loreto, 14)
Fashkechi (Guyana, 1)
Gotoeman Apoeroe lobi (Suriname, 8)
Grootbladige pepre-soutoe (Suriname, 8)
Hicoja blanco (Peru. San Martín, 14)
Invireira (Brazil. Pará, 1)
Jari jari (Suriname, 1, 8)
Karibuyoko (Guyana, 8)
Kéwék-é timé (Suriname, 8)
Kleinbladige pepre-soutoe (Suriname, 1)
Kleinbladige zuurzak (Suriname, 1)
Koeliki kojoko (Suriname, 8)
Kolihi kojoko oniekhar refodikoro (Suriname, 8)
Koyóvi fa?nti (Ecuador, 8)
Kuber=o-keé-ko" (Colombia, 19)
Kulihi kuyoko (Guyana, 8)
Kurekoiyoiko (Suriname, 1)
Kurihi kuryuko (Guyana, 8)
Kurikuruku (Guyana, 8)
Kurikuyefu (Guyana, 1)
Laimtare (Brazil. Roraima, 1)
Lepegasautu (French Guiana, 8)
Majagiúllo (Venezuela. Yaracuy, 1)
Majagua (Venezuela. Amazonas, 1, 4)
Majagua blanca (Venezuela. Amazonas, 4)
Majagua dura (Venezuela. Amazonas, 4)
Majagua hoja fina (Venezuela. Amazonas, 3)
Majagua hoja larga (Venezuela. Amazonas, 19)
Mamayawé (French Guiana, 1, 5, 8)
Murnek-yek (Guyana, 8)
Oreja de burro (Venezuela. Yaracuy, 1)
Palanco (Guatemala. Izabal, 11)
Panta (Suriname, 1, 8)
Paxinho (Brazil. Pernambuco, 8)
Péré inde (Suriname, 8)
Pindahyba (Brazil. Minas Gerais, 20)
Rinoncillo (Venezuela. Miranda, 1)
Saimelukaa (French Guiana, 8, 17)
Socoro jaugera (Panama. Darién, 7)
Soratama (Colombia. Amazonas, 8)
Swamp yarri yarri (Guyana, 8)
Tigua (Venezuela. Monagas, 1)
Wauricoco (Guyana, 1)
Wild yarri yarri (Guyana, 1)
Yara yara (Venezuela, Bolívar, 8, 16)
Yara yara negro (Venezuela. Delta Amacuro, 8)
Yėrika-natna (Venezuela. Amazonas, 1)
Zoutoe hoedoe (Suriname, 8)
Zoutoe nangapepre (Suriname, 8)
Zwampzuurzak (Suriname, 8)

Table 4. List of vernacular names from Asia.

Bagang áso (Philippines, 25)
Berats ayer (Malaya, 24)
Bobonoyang (Philippines, 25)
Bungasi (Malaya, 24)
Cham pun (Thailand, 24)
Chā wūa talông (Thailand, 25)
Chempaka nutan (Borneo, 24)
Chum poon (Thailand, 24)
Dok iho pai (Thailand, 24)
Jagaleg (Philippines, 25)
Kapur (Malaya, 24)
Lampiu (Borneo, 24)
Joemalagi ètem (Sumatra, 24)
Lurat ayer (Malaya, 24)
Malu-itan (Borneo, 24)
Mempisang (Malaya, 24)
Mempulut (Malaya, 24)
Mengapur (Malaya, 24)
Pēngasi (Malaya, 24)
Pun (Thailand, 25)

3. *A. dolichocarpa.* In Guyana, bark is used for rope, and bark fiber is used for carrying baskets; bark is also used for fishing rods, and, after having been burnt, for cleaning teeth. In Suriname, bark fiber is used for carrying baskets; leaves and bark are supposed to be good against headaches. In Ecuador, bark is used as a curare ingredient.

4. *A. pachypetala.* According to one report, the seed is toxic, and the bark is used as an antirheumatic.

5. *A. petiolata.* The bark is reported as strong, rope-like: used for tying and carrying cargoes (Venezuela, Bolívar).

No reports on uses are available from Asia.

14. Systematic treatment

14.1. Description of the genus

Anaxagorea A.F.C.P. de Saint-Hilaire, Nouv. Bull. Sci. Soc. Philom. Paris: 90—91. 1825; Blume, Fl. Javae 2: 64—67. t. 32, 36(A). 1830; A. de Candolle, Mém. Soc. Phys. Génève 5: 211. 1832; Bentham & Hooker, Gen. pl. 1: 25. 1862, & 957. 1867; Baillon, Hist. pl. 1: 213—214, 283. 1868; Prantl in Engler & Prantl, Nat. Pflanzenfam. 3(2): 32—33. 1891; R.O. Williams, Fl. Trinidad & Tobago 1: 17. 1928; R.E. Fries, Acta Horti Berg. 12 (1): 6—27, 215. t. 1, 2. 1934; R.E. Fries, Field Mus. Nat. Hist., Bot. Ser. 13(2): 747—750. 1938; R.E. Fries in Pulle, Fl. Suriname 2(2): 354—356. 1940; R.E. Fries in Engler & Prantl, Nat. Pflanzenfam. ed. 2, 17aII: 117—119. fig. 26. 1959; R.E. Fries, Ann. Missouri Bot. Gard. 49: 194—196. 1962. — Type: *Anaxagorea prinoides* (Dunal) A.DC.

= *Anaxagoraea* Martius in Martius, Fl. bras. 13(1): 40—41. 1841.

= *Rhopalocarpus* Teysmann & Binnendijk ex Miquel, Ann. Mus. Bot. Lugduno-Batavi 2: 22. 1865. — Type: *Rhopalocarpus fruticosus* Teysm. & Binnend. ex Miq. = *Anaxagorea luzonensis* A. Gray. Not *Rhopalocarpus* Bojer, Procès Verbaux Soc. Roy. Hist. Nat. Ile Maurice 149. 1846 (Sphaerosepalaceae).

= *Eburopetalum* Beccari, Nuovo Giorn. Bot. Ital. 3: 181. pl. 2. 1871. — Type: *Eburopetalum borneense* Becc. ≡ *Anaxagorea borneensis* (Becc.) James Sincl.

= *Anaxagorea* sect. *Rhopalocarpus* R.E. Fries in Engler & Prantl, Nat. Pflanzenfam. ed. 2, 17aII: 118. 1959. — Type: *Rhopalocarpus fruticosus* Teysm. & Binnend. ex Miq. = *Anaxagorea luzonensis* A. Gray.

Shrubs to small (occasionally medium-sized) trees. Twigs terete, often densely brownish-puberulous, but frequently soon becoming glabrous. Leaves distichous, simple, entire, estipulate, concolorous (very rarely discolorous), (shortly) petiolate. Lamina most often narrowly elliptic, chartaceous to thinly coriaceous, base cuneate to obtuse (rarely asymmetrical), apex acuminate to acute, upper side glabrous or nearly so, lower side puberulous to glabrous; primary vein impressed on the upper side, rarely raised; secondary veins between 5—30 on each side of the primary vein, angles with primary vein between 55°—80°, indistinctly to distinctly loop-forming, sometimes loops forming a marginal vein; tertiary veins forming a more or less distinct reticulum.

Inflorescences axillary (most species) or leaf-opposed to terminal, often ramiflorous to cauliflorous, rarely flagelliform and creeping over the ground, 1—several-flowered rhipidia or small panicles or clusters of rhipidia, clearly pedunculate or not; pedicels thickened toward the flower, mostly under 20 cm long; lower bracts (also including peduncular bracts) triangular to elliptic, with a broad base, often caducous; upper bract larger than the lower bracts, orbicular to broadly elliptical, amplexicaul or almost so, usually near the flower, caducous or persistent. Flower buds globose, ovoid, to conical. Flowers green, white, yellow, to red (in vivo).

Indument of floral parts (including pedicels) and fruits consisting of usually brownish, microscopical hairs.

Flowers actinomorphic, bisexual, fleshy, mostly not opening widely, trimerous (very rarely dimerous), with one whorl of sepals and two (rarely one) whorls of petals, the stamens and carpels mostly enclosed within a cavity formed by the hollow lower parts of the enveloping petals. Sepals valvate to imbricate, ovate to broadly ovate, free to connate, shorter than the outer petals, chartaceous, subcoriaceous, rarely membranous, caducous before to after anthesis, or persistent, curved upward to reflexed. Petals of both whorls valvate, mostly fleshy, inner side with a cavity in the basal part showing markings of stamens. Outer petals scarcely longer to markedly longer than the inner ones, upper part on inner side flat, bifacial, to keeled. Inner petals bifacial to keeled in upper part. Torus (floral receptacle) convex. Androecium acyclic; stamens free, between 10—200, elliptic to narrowly obovate, apical prolongation of connective triangular to quadrangular, small; anthers mostly extrorse, sometimes more or less latrorse, locules not septate. Innermost stames staminodial (except in two species), staminodes up to 50, with or without a glandular margin at the apex. Gynoecium apocarpous, carpels 5—45, with two (sub-) basal ovules. Stigmata capitate to slightly horseshoe-shaped, sessile in most species, stipitate in some species (Asia), smooth (very rarely finely tuberculate).

Monocarps free, green, yellow, brown, to red (in vivo), clavate to dolabriform, with a stipe-like basal part and a more or less subglobose head with a mostly persistent apical beak usually under 2 mm long. Seeds 2, shiny black, outer side convex, inner side flat, withouth aril. Dehiscence along the ventral suture, and sometimes also along part of the dorsal suture.

Chromosome number $2n = 16$ or 48.

14.2. Neotropical species

by P. J. M. MAAS, L. Y. Th. WESTRA & A. TIMMERMAN (Utrecht)

14.2.1. Key to neotropical species

I. Dichotomous key

1 Inflorescences leaf-opposed or terminal.[1] 2
— Inflorescences axillary, or cauliflorous. 3

2 Upper bract 4 mm below the calyx or more. . . . . 20. *A. silvatica*
— Upper bract 2 mm below the calyx or less. . . . . 6. *A. brevipes*

3 Inflorescences flagelliform, with ramifications ending in rhipidia producing many flowers in succession; the whole becoming 20 cm long or more; leaf bases manifestly asymmetrical. . . . . 9. *A. floribunda*
— Inflorescences rhipidia producing up to ca. 10 flowers in succession, often showing only one flower at a time, or small condensed panicles of rhipidia, the peduncle and sympodial rhachis or ramifications (not including pedicels) not exceeding 3 cm, usually much shorter; leaf bases symmetrical. . . . 4

4 Largest leaves always less than 20 cm long and less than 6 cm wide; pedicels at the insertion of the upper bract less than 1.5 mm in diam., (sub)-glabrous. 5
— Largest leaves mostly more than 20 cm long and/or 6 cm wide (exception: *A. manausensis*); pedicels at the insertion of the upper bract more than 1.5 mm in diam. — if less than 1.5 mm in diam., then densely covered with hairs. 10

5 Primary vein raised on upper side. . . . . 4. *A. brachycarpa*
— Primary vein slightly to manifestly impressed on upper side. 6

6 Pedicels up to 5 mm long. 7
— Pedicels 6 mm long or more. 8

7 Sepals up to 7 mm long and 3.5 mm wide, connate at the base, persistent, the apex acute to acuminate; leaves less than 4 x as long as wide. . . . . 5. *A. brevipedicellata*
— Sepals more than 8 mm long and 5 mm wide, free, caducous after flowering, the apex obtuse; leaves more than 4 x as long as wide. 3. *A. angustifolia*

8 Upper bract up to 5 mm below the calyx; sepals free, caducous after flowering; pedicels mostly up to 17 mm long; number of monocarps from a single flower ca. 5—15. 9
— Upper bract 8 mm or more below the calyx; sepals connate up to about the middle, caducous before flowering; pedicels mostly more than 17 mm long; number of monocarps from a single flower ca. 14—25. . . . . 14. *A. pachypetala*

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[1] Terminal (or seemingly terminal) inflorescences are rarely found in *A. dolichocarpa*, too. When in doubt, consult couplet nr. 13.

9 Flower buds narrowly conical; sepals more than 8 mm long; outer petals 16 mm long or more; pedicels usually longer than 10 mm; beak of monocarps mostly 2 mm long or more. . . . . 15. *A. panamensis*

— Flower buds globose; sepals 7 mm long or less; outer petals up to 11 mm long; pedicels mostly 10 mm long or less; beak of monocarps up to 1 mm long. . . . . 18. *A. prinoides*

10 Flower buds globose or ovoid; beak of monocarps mostly not longer than 2 mm, except for in *A. gigantophylla* up to 4 mm long (monocarps unknown in *A. manausensis*). 11

— Flower buds elongate or (narrowly) conical (flower buds unknown in *A.* spec. *A*); beak of monocarps commonly 2—6 mm long (monocarps unknown in *A. macrantha*). 19

11 Leaves usually more than 35 cm long and 10 cm wide, usually with 18—28 pairs of secondary veins; beak of monocarps usually 1.5—4 mm long. . . . . 10. *A. gigantophylla*

— Leaves usually less than 35 cm long, mostly not exceeding 30 cm, and less than 10 cm wide, with usually less than 18 pairs of secondary veins; beak of monocarps usually 2 mm long or less. 12

12 Primary vein raised on the upper side at least toward the base, or if more or less flat, then broader than 1 mm at least toward the base. 13

— Primary vein more or less impressed on upper side, or if more or less flat, then less than 1 mm broad throughout. 14

13 Leaves puberulous to sparsely puberulous with tiny purplish-red stellate hairs below; petioles, leafy twigs, inflorescence parts, outer side of perianth members, and monocarps densely puberulous; largest leaves usually longer than 30 cm; primary vein flat to slightly raised on upper side. . . . . 19. *A. rufa*

— Vegetative parts glabrous (or almost so), inflorescence parts, perianth members, and monocarps sparsely puberulous to glabrous; leaves mostly up to 25 cm long; primary vein distinctly raised on upper side. . . . . 4. *A. brachycarpa*

14 Sepals free in bud, longer than 6 mm; outer petals with a narrow keel on the inner side; leafy twigs and petioles glabrous or nearly so. . 6. *A. brevipes*

— Sepals connate in bud at least at the base, or if free, then shorter than 4 mm — in case sepals are free and longer than 6 mm (*A. dolichocarpa*, in part), then outer petals without a narrow keel on the inner side; leafy twigs and petioles puberulous to densely puberulous (although sometimes soon glabrescent) 15

15 Secondary veins with loops forming a distinct marginal vein; flower buds frequently distinctly longer than wide; upper bract caducous before flowering. . . . . 17. *A. phaeocarpa*

— Secondary veins with indistinct loops, or with loops not forming a marginal vein (or rarely forming a marginal vein toward the apex only); flower buds not or hardly longer than wide; upper bract mostly caducous after flowering, or persistent. 16

16 Staminodes distinctly shorter than stamens; pedicels mostly 15 mm long or more. . . . . 16. *A. petiolata*

— Staminodes as long as (or slightly longer than) stamens; pedicels mostly not longer than 15 mm. 17

17 Sepals commonly 7 mm long or more, often persistent and becoming reflexed; outer petals mostly 13 mm long or more; secondary veins curved to straight. . . . . 8. *A. dolichocarpa*

— Sepals up to 5 mm long, caducous, or if persistent, then patent to curved upward; outer petals ca. 7—12 mm long; secondary veins usually straight. 18

18 Outer petals bifacial above the middle on the inner side, and with a wing-like margin (best observed on the inner side); sepals connate at least at the base (to above the middle in early bud stage); largest leaves usually longer than 20 cm. . . . . 1. *A. acuminata*

— Outer petals flat in the upper part on the inner side, and without a wing-like margin; sepals free; leaves (mostly) not longer than 17 cm. . . . . 3. *A. manausensis*

19 Combined length of pedicel and peduncle, or distance between flower and base of inflorescence, usually 20 mm or less; upper bract persistent (exception: *A. macrantha*); fruiting floral axis between insertion of calyx and insertion of monocarps less than 3 mm long. 20

— Combined length of pedicel and peduncle, or distance between flower and base of inflorescence, more than 25 mm; upper bract caducous before flowering; fruiting floral axis between insertion of calyx and insertion of monocarps 4 mm long or slightly more. . . . . 22. *A.* spec. *B*

20 Sepals connate at least at the base; pedicels 2 mm in diam. at the base or more; outer petals mostly longer than 20 mm, flat in the upper part on the inner side; petioles more than 4 mm in diam.; secondary veins (in the larger leaves) in more than 20 pairs. . . . . 12. *A. macrantha*

— Sepals free; pedicels less than 2 mm in diam. at the base; outer petals mostly up to 20 mm long, bifacial in the upper third on the inner side; petioles usually less than 4 mm in diam.; secondary veins usually in up to 20 pairs. 21

21 Outer diameter of upper bract 5 mm or more; pedicels more than 2 mm in diam. at the insertion of the upper bract; sepals (mostly) elliptic-ovate. . . . . 2. *A. allenii*

— Outer diameter of upper bract less than 5 mm; pedicels mostly less than 2 mm in diam. at the insertion of the upper bract; sepals (mostly) ovate-triangular. 22

22 Leaves elliptic to narrowly elliptic, the largest width at the middle; number of monocarps from a single flower ca. 10—20. . . 7. *A. crassipetala*

— Leaves obovate to narrowly obovate or elliptic-obovate, the largest width above the middle; number of monocarps from a single flower ca. 5—11. . 23

23 Beak of monocarps less than 5 mm long, forming an angle of (much) more than 90° with the stipe. . . . . 11. *A. guatemalensis*
— Beak of monocarps more than 5 mm long, forming an angle of ca. 90° with the stipe. . . . . 21. *A.* spec. *A.*

II. Synoptic key

Numbers which are underlined, indicate species in which other character states also occur. Numbers for which a given character has not been scored, are placed between brackets.

Flower

1. Flower buds conical: 2 — 7 — 11 — 12 — 15 — 20 — (21) — 22
   (vs. globose, ellipsoid, or ovoid)
2. Sepals shorter than 5 mm: 1 — 5 — 9 — 13 — 14 — (20) — (21)
   Sepals longer than 10 mm: 2 — 6 — 8 — 14— 17 — 19 — (20) — (21)
   (vs. Sepals between 5—10 mm long)
3. Sepals reflexed entirely: 4 — 8 — 10 — 16 — (20) — (21) — (22)
   Sepals apically reflexed: 2 — 5 — 7 — 9 — 11 — 12 — 15 — (20) — (21) — (22)
   (vs. patent or curved upward)
4. Sepals caducous before anthesis: 1 — (2) — (3) — (6) — (7) — 8 — (11) — (12) — 13 — 14 — (15) — 17 — (18) — (20) — (21) — (22)
   Sepals persistent: (2) — (3) — 4 — 5 — (6) — (7) — 8 — 9 — 10 — (11) — (12) — (15) — 16 — (18) — (19) — (20) — (21) — (22)
   (vs. caducous after anthesis)
5. Sepals membranaceous or thinly herbaceous: (1) — (2) — 3 — (4) — (5) — (7) — (8) — (10) — (11) — (12) — (14) — 15 — 18 — (20) — (21) —(22)
   (vs. chartaceous to coriaceous)
6. Outer petals keeled in upper part on inner side: 3 — 4 — 5 — 6 — 8 —15 — 19 — (20) — (21) — (22)
   petals bifacial in upper part on inner side: 1 — 2 — 3 — 4 — 5 —7 — 8 — 11 — 14 — 15 — 16 — (20) — (21) — (22)
   Outer petals flat (to slightly convex or concave) in upper part on inner side: 4 — 8 — 9 — 10 — 12 — 13 — 14 — 15 — 16 — 17 — 18 — (20) — (21) — (22)
7. Outer petals shorter than 12 mm: 1 — 2 — 3 — 4 — 5 — 7 — 8 — 9 —11 — 13 — 14 — 16 — 17 — 18 — 19 — (20) — (21) — (22)
   Outer petals longer than 20 mm: 2 — 8 — 10 — 12 — 15 — (20) — (21) — (22)
   (vs. between 12—20 mm long)
8. Outer petals 1.5—2 x as long as inner petals: 2 — 7 — 11 — 15 — (20) — (21) — (22)
   (vs. 1—1.3 x as long as inner petals)

9. Staminodes absent: 5 — (20) — (21) — (22)
Staminodes more than 20: (3) — 4 — 6 — 8 — 10 — (12) — 17 — 19 —(20) — (21) — (22)
(vs. present, less than 20)
10. Staminodes glandular-tipped (or glandular at either side of the apex): 3 —4 — 6 — 8 — 10 — (12) — 17 — 19 — (20) — (21) — (22)
(vs. not glandular-tipped)
11. Stamens less than ca. 25: 1 — (3) — 5 — 9 — 11 — (12) — 13 — 15 —18 — (20) — (21) — (22)
Stamens more than ca. 80: (3) — 4 — 6 — 8 — 10 — 12 — 17 — 19 —(20) — (21) — (22)
(vs. stamens ca. 25—80)
12. Thecae broader than connective: 3 — 4 — 5 — 6 — 8 — 9 — 10 — 16 — 19 — (20) — (21) — (22)
(vs. connective broader than thecae)
13. Stamens ca. 1.5—2 x as long as staminodes: 4 — 9 — 12 — 16 — (20) — (21) — (22)
(vs. stamens and staminodes ca. equally long)
14. Stamens less than 3 mm long: 1 — 3 — 5 — 7 — 8 — 9 — 11 — 12 —14 — 16 — 17 — (20) — (21) — (22)
(vs. longer than 3 mm)
15. Apical prolongation of stamens 1 mm long or more: 4 — 6 — 10 — 18 — (20) — (21) — (22)
(vs. less than 1 mm long)

Inflorescence

16. Inflorescence terminal or leaf-opposed: 6 — 8 — 20
(vs. axillary)
17. Pedicel shorter than ca. 5 mm: 3 — 4 — 5 — 6 — 8 — 9 — 12 — 19
Pedicel longer than ca. 15 mm: 1 — 7 — 8 — 10 — 13 — 14 — 15 — 16 — 17 — 21 — 22
(vs. ca. 5—15 mm long)
18. Pedicel diameter at insertion of upper bract less than 1.5 mm: 3 — 5 — 14 — 15 — 18
(vs. more than ca. 2 mm)
19. Distance between upper bract and calyx up to 4 mm: 1 — 2 — 3 — 4 — 5 — 6 — 7 — 8 — 9 — 10 — 11 — 12 — 13 — 15 — 17 — 18 — 19 — 21 — 22
Distance between upper bract and calyx more than 5 mm: 1 — 4 — 8 — 10 — 13 — 14 — 16 — 17 — 20
(vs. ca. 4—5 mm)
20. Outer diameter of upper bract up to 4 mm: 1 — 3 — 4 — 5 — 6 — 7 — 8 — 9 — 11 — 13 — 14 — 15 — 16 — 18 — 20 — 21 — (22)

Outer diameter of upper bract more than 6 mm: 2 — 6 — 8 — 10 — 12 — 17 — 19 — (22)
(vs. outer diameter ca. 4—6 mm)

21. Upper bract caducous before anthesis: 4 — 8 — 17 — 19 — 22
Upper bract persistent: 2 — 3 — 5 — 6 — 7 — 8 — 10 — 11 — 15 — 20 — 21
(vs. caducous during or after anthesis)

Leaf

22. Petiole shorter than 10 mm: 1 — 2 — 3 — 4 — 5 — 6 — 7 — 8 — 9 — 11 — 12 — 13 — 14 — 15 — 16 — 17 — 18 — 19 — 20
Petiole longer than 20 mm: 2 — 7 — 8 — 10 — 16 — 17 — 19 — 21 — 22
(vs. ca. 10—20 mm long)

23. Largest lamina length less than 20 cm: 3 — 5 — 13 — 14 — 15 — 18 — 20
Largest lamina length more than 40 cm: 2 — 7 — 8 — 10 — 12 — 19
(vs. ca. 20—40 cm)

24. Largest lamina width less than 6 cm: 3 — 5 — 13 — 14 — 15 — 18 — 20
Largest lamina width more than 10 cm: 1 — 2 — 7 — 8 — 10 — 11 — 12 — 17 — 19 — 21 — 22
(vs. ca. 6—10 cm)

25. Leaf base rounded: 2 — 4 — 6 — 7 — 8 — 9 — 10 — 11 — 16 — 17 — 19 — 22
(vs. acute, cuneate, obtuse)

26. Leaf base (slightly) assymmetrical: 9 — 10 — 19
(vs. symmetrical)

27. Primary vein raised on upper side at least toward the base: 4 — 19
Primary vein flat on upper side: 1 — 2 — 7 — 8 — 11 — 16 — 17 — 19 — 21 — 22
Primary vein impressed on upper side: 1 — 3 — 5 — 6 — 8 — 9 — 10 — 11 — 12 — 13 — 14 — 15 — 16 — 17 — 18 — 20 — 21

28. Secondary veins raised on upper side: 2 — 3 — 4 — 7 — 8 — 14 — 19 — 20 — 21
Secondary veins flat on upper side: 1 — 2 — 4 — 6 — 7 — 8 — 11 — 15 — 16 — 18 — 22
Secondary veins impressed on upper side: 5 — 6 — 9 — 10 — 12 — 13 — 17

29. Secondary veins in less than 10 pairs: 1 — 3 — 4 — 5 — 6 — 8 — 11 — 13 — 14 — 15 — 16 — 18 — 20
(vs. in 10 pairs or more)

30. Secondary veins straight: 1 — 2 — 3 — 4 — 5 — 6 — 7 — 8 — 12 — 13 — 15 — 17 — 21 — (22)
(vs. curved)

31. Secondary veins forming indistinct marginal loops: 1 — 2 — 3 — 5 — 7 — 8 — 11 — 14 — 20 — 21 — 22
Secondary veins forming a marginal vein: 4 — 10 — 17
(vs. distinct loops, but no marginal vein from base to apex)
32. Secondary veins joining at acute angles: 1 — 3 — 4 — 6 — 8 — 11 — 15 — 19 — 20 — (22)
Secondary veins joining at obtuse angles: 4 — 5 — 10 — 14 — 15 — 17 — 18 — (22)
(vs. at right angles)

Provenance

33. Central America: 2 — 7 — 11 — 15 — 17 — 21
Minas Gerais: 20
Guianas, Amapá, Pará, Roraima: 1 — 5 — 6 — 8 — 16 — 17 — 18
Amazonia, Andes: 1 — 3 — 4 — 6 — 7 — 8 — 9 — 10 — 12 — 13 — 14 — 16 — 17 — 19 — 22

14.2.2. Descriptions of neotropical species

1. **Anaxagorea acuminata** (Dunal) A.DC., Mém. Soc. Phys. Genève 5: 211. 1832 (p.p.); Baillon, Hist. pl. 1: 213—214. 1868; Sagot, Ann. Sci. Nat. Bot., Sér. 6 (11): 136. 1881; R.E. Fries, Kongl. Svenska Vetenskapsakad. Handl. 34(5): 25. 1900; R.O. Williams, Fl. Trinidad & Tobago 1: 17. 1928; R.E. Fries, Acta Horti Berg. 12(1): 11. 1934; R.E. Fries in Pulle. Fl. Suriname 2(2): 355. 1940. Fig. 12.

≡ *Xylopia acuminata* Dunal, Monogr. Anonac. 122, t. 16. 1817; A.P. de Candolle, Syst. 1: 501. 1818; A.P. de Candolle, Prodr. 1: 93. 1824 (p.p.) — Type: *Patris s.n.* French Guiana. fr (holotype, G, not seen).

≡ *Xylopicrum acuminatum* (Dunal) O. Kuntze, Revis. gen. pl. 1: 8. 1891.

= *Anaxagorea multiflora* R.E. Fries, Acta Horti Berg. 12(1): 13. 1934. — Type: *Krukoff 1017.* Brazil, Pará: Tapajos River Region, Fordlandia, Sep 1931, fl, fr (holotype, S; isotypes, A, B, BM, G, K, MO, NY, P, U, UC).

Tree or shrub, up to 10(—20) m tall. Leafy twigs 1—6 mm in diam., brown-puberulous (coffee-colour), sometimes glabrescent. Petioles 4—17 mm long, 1—3.5 mm in diam. brown-puberulous. Lamina (narrowly) elliptic to ovate or obovate, 6—36 cm long, 2—12 cm wide, coffee-colour brown-puberulous on lower side, especially near the base, base acute to obtuse, often slightly decurrent, apex acute to acuminate; primary vein slightly impressed to flat on upper side; secondary veins mostly straight, ca. 9—20 on each side of primary vein, flat on upper side, angles with primary vein up to 80°, loop-forming at acute angles, loops rather indistinct, smallest distance between loops and margin 3—9 mm.

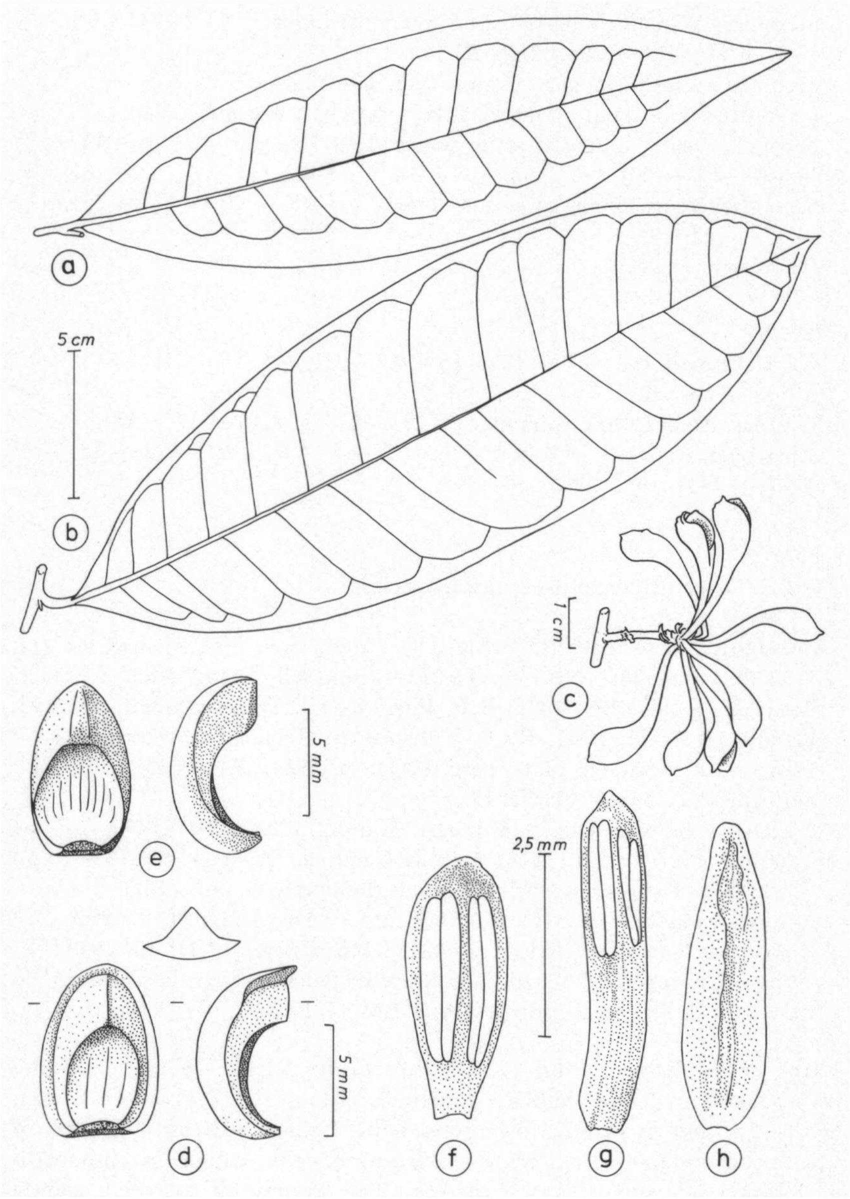

Fig. 12. *A. acuminata* (a, *Gentry & Troth 24816*; b, *Prance et al. 24881;* c, *Lindeman 5260;* d—h, *Krukoff 1017*). a—b, leaves; c, infructescence; d, outer petal, inner side, lateral view, and cross section; e, inner petal, inner side and lateral view; f, outer stamen, also in cross section; g, inner stamen; h, staminode.

Inflorescences axillary, mostly on older parts of branchlets, to cauliflorous, pedunculate to nearly sessile, with 1—several flowers at a time, flowers placed in rhipidium-mode; peduncle (or sympodial rhachis) up to 10(—18) mm long; pedicels 5—19 mm long, (1—)1.5—3 mm thick at the base and 2—3.5(—4) mm thick below the flower; upper bract (1—)2—6.5(—8) mm below the calyx, with an outer diameter of 2.5—5(—5) mm, often caducous after flowering. Flower buds globose, brownish to yellowish (in vivo). Flowers brownish to yellowish, or the inner side cream with pink base, to pale yellow with maroon base (in vivo).

Indument of floral parts: pedicels densely to sparsely brown-puberulous, to glabrescent, outer side of sepals and petals densely to sparsely brown-puberulous, inner side of sepals and petals glabrous.

Sepals connate to above the middle, soon splitting to the base, depressed ovate, (2—)3—5 mm long, 3.5—6 mm wide, acute to subacuminate, to truncate, rarely caducous before flowering, erect. Outer petals elliptic to ovate, 7—12 mm long, 4.2—8 mm wide, obtuse, inner side bifacial above the middle, with a distinct wing-like margin, 2—2.5 mm thick in the upper part. Inner petals elliptic (to obovate), 6.5—11 mm long, 3.5—5 mm wide, obtuse, inner side bifacial above the middle, 2.5—4.5 mm thick in the upper part. Stamens ca. 25—40, 2.8—6.2 mm long, 0.8—1.7 mm wide, thecae 1.7—4.5 mm long, not broader than the connective, apical prolongation of connective to ca 0.5 mm long, truncate, retuse, to subacuminate. Staminodes ca. 5—10, narrowly ovate, 4—6.5 mm long, 1—1.5 mm wide, acute. Carpels ca. 10—40, 2—3.8 mm long.

Monocarps 21—35 mm long, yellow to brown, rarely dark green (in vivo), densely to sparsely brown-puberulous, to glabrescent, stipitate part 12—25 mm long, beak 0.3—1.5 mm long, often caducous. Seeds 9.5—16 x 6—9 mm.

Specimens examined: VENEZUELA. Amazonas: 27 May 1975, *Berry 750* fr (US, VEN); Jan—Feb 1969, *Fariñas 690* fr (NY, VEN); 2 Dec 1975, *Lister 95* (K); 10 Sep 1972, *Lizot 1972-2* fl (VEN); 9 May 1980, *Steyermark et al. 122177* fr (U); 30 Apr—1 May 1972, *Steyermark & Carreño Espinoza 105877* fr (U, US, VEN). Carabobo: 14 Apr 1982, *Liesner & Medina 13623* fr (MO); 7—8 Aug 1965, *Steyermark 94300* fl (NY, S, US); 28 Mar 1966, *Steyermark & Steyermark 95201* fr (NY, S, VEN); Feb 1942 *Tamayo 2208* fl, fr (US, VEN). Distrito Federal: 16 Apr 1967, *Bunting 2061* fr (F, MY). Miranda: 20 Dec 1961, *Agostini 9* fl, fr (VEN); 25 Oct 1956, *Bernardi 5632* fr (NY, VEN); 23 Nov 1956, *Bernardi 5825* fl (NY); 16 Feb 1979, *Gentry & Troth 24816* fr (U); 19—24 Mar 1913, *Pittier 5950* fr (NY, US); 5—7 Apr 1917, *Pittier 7083* fl, fr (GH, M, US, VEN); 23 Nov 1961, *Steyermark 89986* fr (NY, S, US, VEN); 16—17 Mar 1978, *Steyermark & Davidse 116334* fr (MO, NY). Monagas: 24 Aug 1961, *Aristeguieta 4808* fr (NY); 21 Apr 1959, *Buza 7599* fl (NY, US, VEN); 22 Sep 1955, *Wurdack & Monachino 39405* fl, fr (NY, S, VEN). Yaracuy: Jun 1953, *Aristeguieta 1751* fl (VEN); 2 Jul 1953, *Aristeguieta & Pannier 1830* fr (NY, VEN); 4 Mar 1982, *Liesner & Steyermark 12351* fr

(U); 19—20 Jan 1982, *Mori et al. 14669* fr (U); 4 Mar 1971, *R.F. Smith V 6464* fr (VEN); 28 Nov 1971, *Steyermark & Bunting 105284* fr (NY, U); 27—30 Dec 1972, *Steyermark et al. 106765* fr (VEN); 10 Apr 1949, *Trujillo 10* fr (MY).

TRINIDAD. *A. Anderson s.n.* st (BM); Jan 1898, *Dannouse TRIN 5561* (TRIN), *TRIN 6441* fr (K, TRIN); 1899, *Dannouse TRIN 6642* (TRIN); 16 Feb 1901, *Dannouse TRIN 6798* (K, TRIN); 23 Feb 1901, *Dannouse s.n.* fr (NY, TRIN); 1877—1880, *Fendler 216* fr (BM, K); Nov 1847, *Purdie 45* fr (K); *Purdie s.n.* fr (GH, K).

GUYANA. 1919, *Hohenkerk 10* fr (UG); 17 May 1918, *Hohenkerk 35A* fr (K, UG); 28 Feb 1919, *Hohenkerk 35C* (K); 1 Aug 1931, *Forest Dep. Br. Guiana 2107* fl (K); 21 Oct 1931, *Forest Dep. Br. Guiana 2227* fl (K, S); 23 Sep 1952, *Forest Dep. Br. Guiana 7191* fl (NY); 28 Sep 1952, *Forest Dep. Br. Guiana 7235* fl (NY); *7240* fl (NY); Apr 1884, *Jenman 1865* (K); *1866* fl (K, UG); 15—24 Dec 1937, *A.C. Smith 2735* fr (A, F, NY, S, US); 10—20 Jan 1938, *A.C. Smith 2910* fr (A, F, K, NY, S, US).

SURINAME. 5 Dec 1934, *Archer 2860* fr (US); 23 Sep 1901, *Boon 1192* (U); 27 Dec 1954, *Cowan 39015* fr (NY, S, U); 13 Mar 1964, *van Donselaar 1034* fr (U); 8 Sep 1910, *Hulk 246* (U); 1 Aug 1963, *Irwin et al. 54545* fl (F, G, GH, M, NY, S, UC, W); 23 Aug 1963, *Irwin et al. 54999* fl, fr (NY); 26 Aug 1963, *Irwin 55085* fl (F, GH, MO, NY, UC, US); 26 Aug 1963, *Irwin et al. 55095* fr (F, US); 22 Aug 1963, *Irwin et al. 55194* fl, fr (F, MICH, MO, NY, RB, U, US, VEN); 28 Aug 1963, *Irwin et al. 55275* fl (F, FHO, GH, MICH, U, US); 27 Sep 1963 (fr), *Irwin et al. 57661* fr (F, GH, K, NY, S, U, US); 9 Sep 1975, *LBB 15240* (U); 13 Jun 1953, *Lindeman 4068* st (U); 13 Jan 1954, *Lindeman 5260* fr (IJ, U, UC); 22 Nov 1954, *Lindeman 6698* st (U); 17 Dec 1954, *Lindeman 6868* fr (U); 20 Sep 1975, *Lindeman et al. 116* fr (F, K, MO, NY, U); 2 Oct 1975, *Lindeman et al. 670* fl, fr (K, NY, U, Z); 13 Apr 1975, *Maas & Tawjoeran 3178* (U); *Maguire et al. 54108* fr (NY); 13 Oct 1976, *Mori & Bolten 8475* fr (NY); 18 May 1963, *Wessels Boer 1394* fl, fr (C, U, UC, US); *Wullschlaegel 1346* fl, fr (GOET); Oct 1853, *Wullschlaegel 1347* fr (BR).

FRENCH GUIANA. 11 Dec 1954, *Cowan 38432* fr (NY, P, S); 7 Nov 1982, *Fournet 295* fr (U); 10 Aug 1981, *de Granville 4801* fl (P, U); 3 Apr 1983, *de Granville 5473* fr (U); 11 Aug 1966, *Oldeman 2189* fl, fr (CAY); 22 Jan 1970, *Oldeman B-2840* fl, fr (CAY, P, U); 1821, *Perrottet s.n.* (B); *Perrottet s.n.* fr (P); 4 Feb 1981, *Riera 141* st (U); 1855, *Sagot 8* fl, fr (B, BM, BR, G, GOET, K, P, S); 1854, *Sagot 9* fr (K, P).

BRAZIL. Amapá: 24 Aug 1961, *Pires et al. 50477* fl (NY). Amazonas: 16—24 Feb 1946, *Cardona 1382* fr (US, VEN); 25 Feb 1969, *Prance et al. 10232* fr (INPA); 17 Oct 1971, *Prance et al. 15365* fr (MG, VEN); 23 Feb 1977, *Rosa & Cordeiro 1617* fr (MG, NY). Pará: 13 Jul 1980, *Cid et al. 1485* fr (NY); 24 Jul 1980, *Cid et al. 1807* st (NY); 29 Aug 1980, *Cid et al. 1889* fl (NY); Sep 1931, *Krukoff 1053* fr (A, BM, K, NY, P, S, U), *1151* fr (A, K, NY, P, U); 29 Nov 1977, *Prance et al. 25881* fr (U); 18 Nov 1978 , *Silva & Rosario 3815* fr (NY, U). Rio Branco: Oct 1951, *Black 1—13941* fr (S). Roraima: 3 Mar 1979, *Pires et al. 16871* fr (F); 20 Feb 1967, *Prance 4561* fr (F, K, MG, NY, US, VEN); 23 Feb 1967, *Prance 4607* fr (F, INPA, K, NY, S, US, VEN); 17 Jan 1969, *Prance et al. 9339* fr (INPA); 23 Jan 1969, *Prance et al. 9394* fr (INPA); 14 Mar 1971, *Prance et al. 10974* fr (INPA, VEN); 24 Mar 1971, *Prance et al. 11194* fr (INPA, VEN); 2 Dec 1973, *Prance 19957* fl, fr (U). Without locality, 4 Sep 1907, *Ducke MG 8618* fl (MG).

Distribution: (Fig. 36): Northern Venezuela, the Guianas, and the Amazon region, especially the northern part.

Discussion: The shape of the outer petals in *A. acuminata* has not been found in any other member of the genus. Otherwise, *A. acuminata* is often difficult to distinguish from *A. dolichocarpa*, as is explained in the discussion under that species. It should be noted that specimens of *A. acuminata* from northern Venezuela differ more or less from specimens from other regions in often having a thinner indument on vegetative parts, and also by more conspicuous secondary veins, thicker petioles, and larger leaves. The thickest peduncles and pedicels were found in specimens from Brazil.

2. **Anaxagorea allenii** R.E. Fries, Ann. Missouri Bot. Gard. 42: 151. 1955. —Type: *P.H. Allen 2143*. Panama. Canal Zone: Quebrada López, alt. 30 m, 11 Feb 1940 (holotype, MO; isotypes, F, GH, NY, US). Fig. 13.

Tree or shrub, up to 10 m tall. Leafy twigs 1—5 mm in diam., dark brown-puberulous. Petioles 7—20(—27) mm long. 1.5—4 mm in diam., dark brown-puberulous. Lamina narrowly elliptic (to ovate), 15—40 cm long, 3.5—12.5 cm wide, dark brown-puberulous to glabrescent on lower side, base obtuse (to rounded), apex acuminate to acute; primary vein flat on upper side; secondary veins straight, ca. 12—20, flat or slightly raised on upper side, angles with primary vein up to 80°, loop-forming at right angles, loops rather indistinct, smallest distance between loops and margin 2—5 mm.

Inflorescences axillary an older parts of branchlets, to cauliflorous, (mostly short-)pedunculate, 1—several-flowered at a time; peduncle (or sympodial rhachis) up to 10(—14) mm long; pedicels (5—)7—15(—20) mm long, 1—2 mm thick at the base and 3—4.5 mm thick below the flower; upper bract close to the calyx to 3 mm below the calyx, with an outer diameter of 5—9 mm, persistent. Flower buds conical, brownish to cream-white (in vivo). Flowers brown to brownish-yellow, with "fragrance of ripe *Asimina* fruit" (in vivo).

Indument of floral parts: pedicels and outer side of sepals and petals densely to sparsely dark brown-puberulous, inner side of sepals sparsely pale brown-puberulous, inner side of petals densely to sparsely orange-puberulous.

Sepals free, elliptic to broadly ovate, 8—14.5 mm long, 5—10.5 mm wide, rigid, apex acuminate and slightly recurved. Outer petals (narrowly) oblong, 8—17(—25) mm long, 4—6(—8) mm wide, rounded, inner side bifacial in

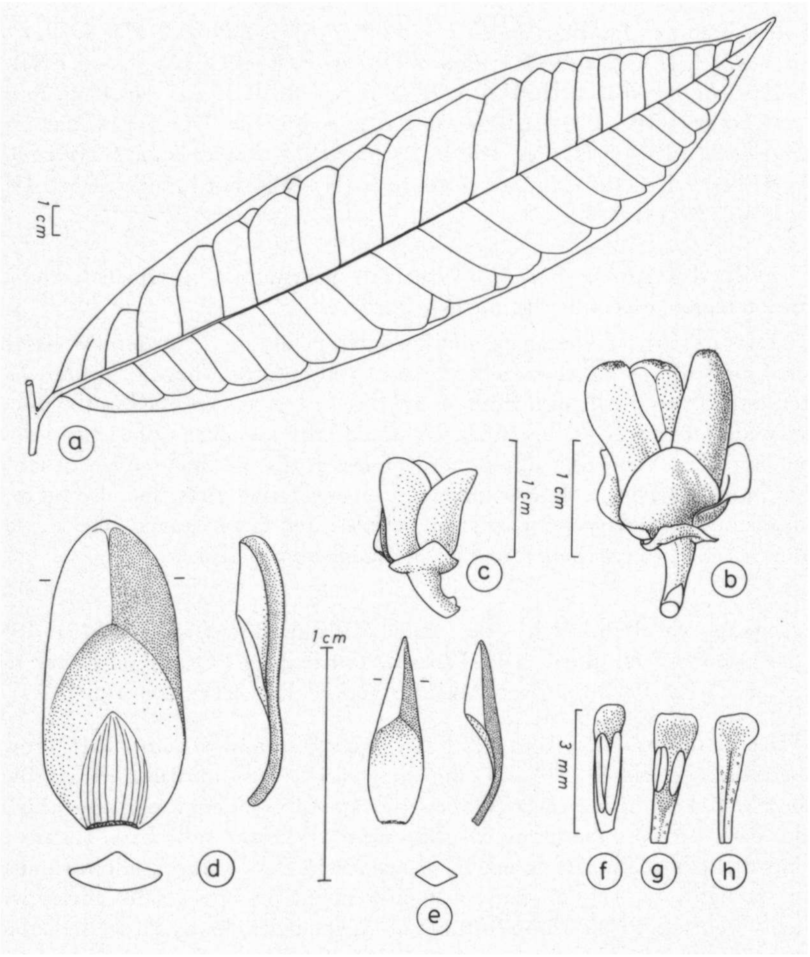

Fig. 13. *A. allenii* (a—c, *Dressler & Lewis 3713;* d—h, *Folsom et al. 2598*). a, leaf; b, flower, showing bracts, sepals, and outer petals; c, flower bud; d, outer petal, inner side, lateral view, and cross section; e, inner petal, inner side, lateral view, and cross section; f, outer stamen; g, inner stamen; h, staminode.

upper third, thickness 2—4 mm. Inner petals narrowly ovate (to ovate), 6—11(—17) mm long, 2—4 mm wide, acute, inner side bifacial in upper third, thickness including keel 1—2 mm. Stamens ca. 50—70, 3.5—5 mm long, 0.7—1.6 mm wide, thecae 1.4—3.2 mm long, not broader than the connective, apical prolongation of connective 0.5—1 mm long, 0.8—1.5 mm wide, truncate to rounded. Staminodes ca. 5—10, narrowly obovate, 3.3—5 mm long, 0.8—1.7 mm wide, truncate to rounded (rarely obtuse). Carpels ca. 5—15, 1.5—4 mm long.

Monocarps (22—)25—33(—40) mm long, green (to dull yellowish-green) (in vivo), stipitate part 14—28 mm long, beak (2.5—)3.5—5 mm long. Seeds 9.5—11 x (5—)6—7 mm.

Specimens examined: PANAMA. Colón: 20 Mar 1969, *Correa & Dressler 1202* fr (MO); 5 Oct 1969, *Dressler & Lewis 3713* fl (U); 19 Dec 1974, *Dressler 4894* fl, fr (DUKE, F, MO); 28 Jan 1969, *Dwyer 8553* fr (F, MO), *8570* fr (MO); 30 Dec 1971, *Dwyer 9381* fr (MO); 11 Dec 1973, *Gentry et al. 8859* fr (MO); 19 Jan 1973, *Kennedy & Foster 2164* fr (MO); 26 Sep 1974, *Mori & Kallunki 2132* fl (MO); 8 Oct 1974, *Mori & Kallunki 3044* fl (U). Panamá: 18 Jul 1974, *Croat 25137* fl (GH, MO); 31 Oct 1974, *Mori & Kallunki 2896* fr (MO); 27 Dec 1974, *Mori & Kallunki 4143* fr (NY); 20 Mar 1975, *Mori & Kallunki 5111* fl (MO); 16 Jan 1974, *Nee & Dressler 9363* fr (MO, US); 28 Mar 1974, *Nee & Tyson 10949* fl (MO), *10978* fl, fr (MO, US), *10994* fl, fr (MO, NY, Z). San Blas: 13 Apr 1977, *Folsom 2598* fl, fr (MO, U).

COLOMBIA. Chocó: 6 Apr 1979, *Forero et al. 4762* fl (MO). Valle: 4 Dec 1981, *Gentry 35260* fr (U); 10 Dec 1981, *Gentry 35533* st (U); 15 Feb 1983, *Gentry et al. 40289* fl (U).

Distribution (Fig. 30): Panama and Pacific side of Colombia. In wet forests at altitudes up to 500 m.

Discussion: *A. allenii* comes closest to *A. crassipetala* and *A. guatemalensis*; it differs from these two species by the larger size of the upper bract and by the shape of the sepals as given in the key. The flowers of *A. allenii* usually are somewhat larger than those of *A. crassipetala* and *A. guatemalensis.*

3. Anaxagorea angustifolia Timmerman in Maas, Timmerman & Westra, Proc. Kon. Ned. Akad. Wetensch., Ser. C, 87 (3): 298. 1984. — Type: *Fróes 22217.* Brazil Amazonas: Rio Negro, Piraiauari, Içana, 24 Apr 1947, fr (holotype, U). Fig. 14.

Shrub or tree, up to 7 m tall. Leafy twigs 0.5—2.5 mm in diam., sparsely puberulous, soon glabrescent. Petioles 3—6 mm long, 1—1.5 mm in diam., sparsely puberulous, soon glabrescent. Lamina narrowly elliptic, 6—16 cm long, 1.5—3.5 cm wide, sparsely blackish red-puberulous on lower side, base acute, slightly decurrent, apex acute to acuminate, margin slightly revolute; primary vein slightly impressed on upper side; secondary veins straight, ca. 9—16 on each side of primary vein, slightly raised on upper side, angles with primary vein up to 80°, loop-forming at acute to right angles, loops rather indistinct, smallest distance between loops and margin 2—4 mm.

Inflorescences axillary, short-pedunculate to nearly sessile, mostly with a single flower at a time; peduncle (or sympodial rhachis) up to 2 mm long; pedicels 3—4.5 mm long, ca. 1 mm thick at the base and 1.5—2 mm thick below the flower; upper bract close to the calyx to 2 mm below the calyx, with an

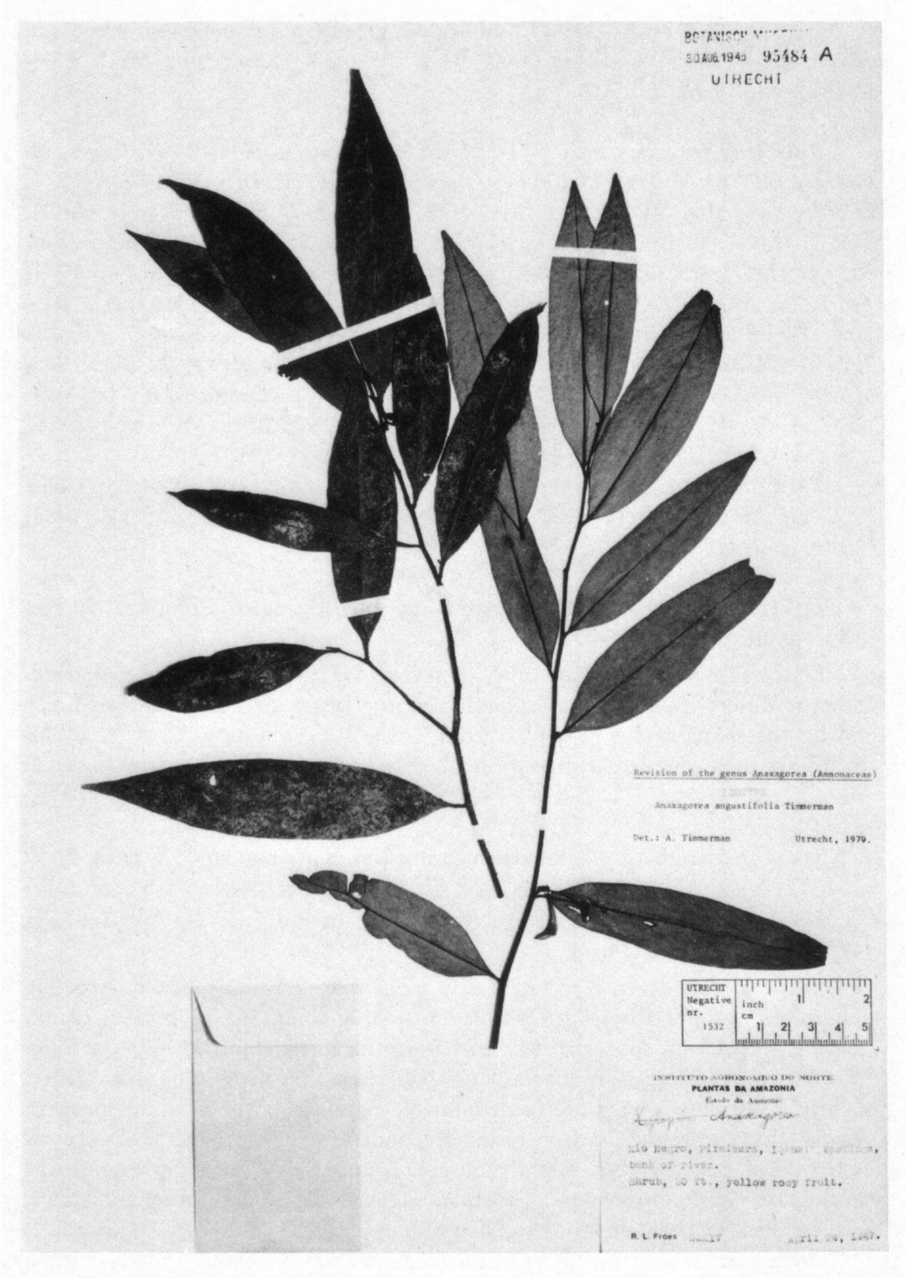

Fig. 14. *A. angustifolia (Fróes 22217).*

outer diameter of 2—3 mm, persistent. Flower buds ovoid to ellipsoid. Flowers yellow (in vivo).

Indument of floral parts: pedicels densely to sparsely reddish- or blackish-puberulous, sepals glabrous except for the apex and margins, petals sparsely creamy-puberulous on the outer side, glabrous on the inner side.

Sepals free, ovate, 8.5—9 mm long, 5.5—6.5 mm wide, obtuse, membranous, erect. Outer petals narrowly elliptic, 10—11 m long 2.5—4 mm wide, obtuse, inner side with thick keel above the basal third, the keel ca. 1 mm wide, part with keel ca. 2.5 mm thick. Inner petals narrowly ovate to narrowly elliptic, 8—10.5 mm long, 1.5—3.1 mm wide, acute, inner side keeled above the middle or basal third, to merely bifacial, part with keel ca. 2 mm thick. Stamens unknown in number, 1.8—2.2 mm long, 0.7—0.8 mm wide, thecae 1.1—1.7 mm long, broader than the connective, apical prolongation of connective 0.2—0.3 mm long, 0.8—0.9 mm wide, truncate. Staminodes unknown in number, narrowly obovate, ca. 2 mm long, ca. 0.8 mm wide, retuse, with glandular tissue at either side of the apex. Carpels ca. 10—15, ca. 2 mm long.

Monocarps 22—23 mm long, yellow to red (in vivo), subglabrous, stipitate part ca. 13 mm long, beak 1—1.5 mm long. Ripe seeds not seen.

Specimens examined: VENEZUELA. Amazonas: 1 to 6 km N of San Carlos de Río Negro, ca. 20 km S of confluence of Río Negro & Brazo Casiquiare, alt. 120 m, 2 May 1979, *Liesner 7157* fl juv, fr (MO).

BRAZIL. Amazonas: Upper Rio Negro, Cucui, 30 Apr 1975, *Cavalcante 3060* fr (INPA, MG); Rio Vaupés, Trovão, 6 Nov 1947, *Pires 856* fl, fr (INPA, NY, P).

Distribution (Fig. 32): Upper Rio Negro region.

Discussion: *A. angustifolia* is clearly distinct from other small-leaved species (*A. brevipedicellata, A. pachypetala, A. panamensis, A. prinoides*) by its comparatively narrow leaves with usually more secondary veins. conspicuously keeled outer petals, and very short (less than 2.5 mm) stamens. The keel on the outer petals is rather broad in comparison with the much more knife-like keel in e.g. *A. brevipes* and *A. rufa.*

4. **Anaxagorea brachycarpa** R.E. Fries, Acta Horti Berg. 12(1): 14. fig. 1a—c. 1934. — Type: *Spruce 3291*, p.p. (see also discussion) Venezuela. Amazonas: region of Río Casiquiare, Río Vasiva, and Río Pacimoni, 1853—1854, fr (holotype, K, not seen; isotypes, B, BM, BR, ECON, G p.p., GH, GOET, MG, NY, P p.p., S). Fig. 15.

= *Anaxagorea brachycarpa* var. *obovata* R.E. Fries, Ark. Bot. 3(18): 599. 1957. — Type: *García-Barriga 14402.* Colombia. Amazonas-Vaupés: Río Apaporis, Jino-Gojé, between Río Piraparaná and Río Popayaká, alt. 250 m, 3—11 Sep 1952, fl (holotype, S; isotype, US).

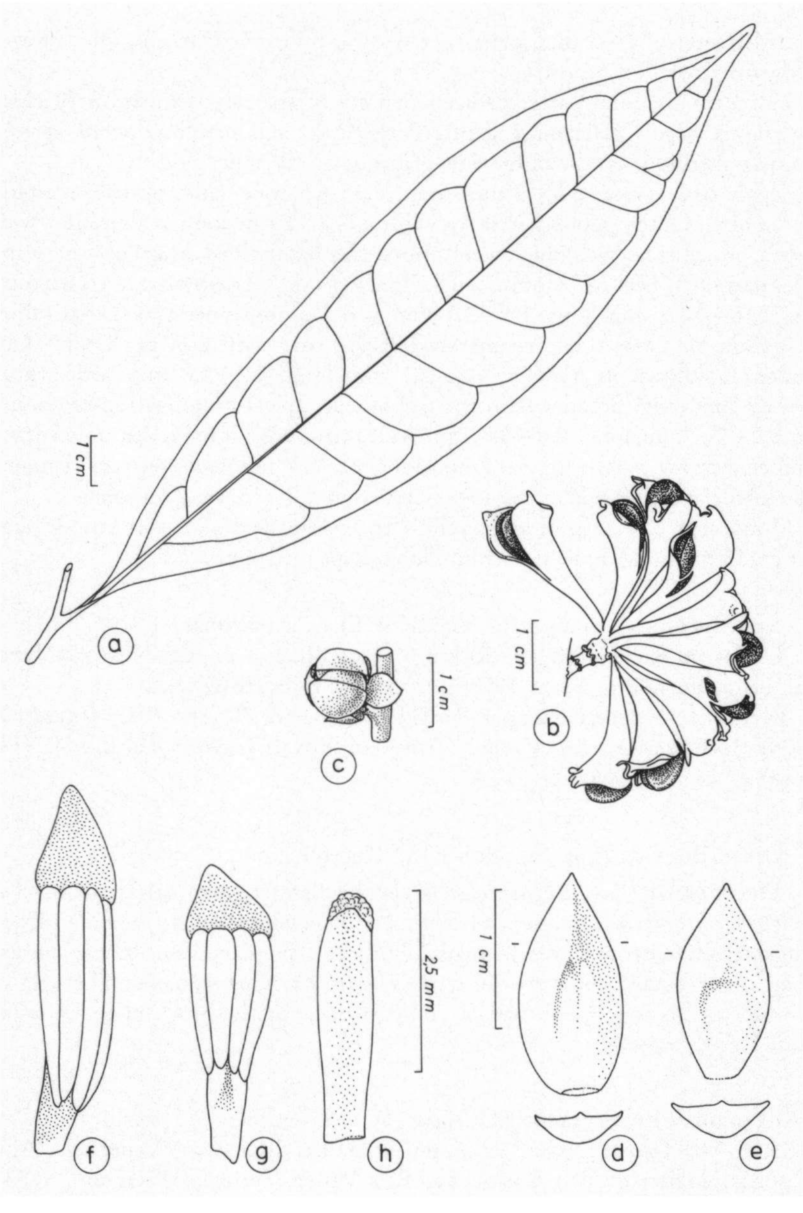

Fig. 15. *A. brachycarpa* (a—b, *Morillo & Hasegawa 5114*; c, *Nascimento 718;* d—h, *Maguire et al. 36789*). a, leaf; b, infructescence; c, flower bud; d, outer petal, inner side and cross section; e, inner petal, inner side and cross section; f, outer stamen; g, inner stamen; h, staminode.

Tree or shrub, up to 8(—15) m tall. Leafy twigs 1—5 mm in diam., glabrous, with yellow cortex. Petioles 5—14 mm long, 1.5—3 mm in diam., glabrous. Lamina narrowly elliptic to obovate, (9—)12—28 cm long, 2—9 cm wide, sparsely dark red-puberulous to glabrescent on lower side, base acute to rounded, decurrent, apex acuminate (the very tip sometimes obtuse); primary vein raised on upper side; secondary veins straight, ca. 8—16, flat to slightly raised on upper side, angles with primary vein up to 75°, loop-forming at acute to obtuse angles, loops distinct, tending to form a marginal vein, smallest distance between loops and margin 2—6 mm.

Inflorescences axillary, mostly on older parts of branchlets, to cauliflorous, mostly short-pedunculate, mostly with a single flower at a time; peduncle (or sympodial rhachis) 1.5—3(—5.5) mm long; pedicels 1.5—3(—8.5) mm long, 1.5—2.5 mm thick at the base and 2—3.5 mm thick below the flower; upper bract 1—2(—6) mm below the calyx, with an outer diameter of 3—4.5 mm, caducous before flowering. Flower buds globose. Flowers yellowish or greenish (in vivo).

Indument of floral parts: pedicels subglabrous, outer side of sepals sparsely reddish-puberulous, inner side of sepals, and petals, subglabrous.

Sepals free, elliptic to transversely ovate-elliptic, 6.5—10 mm long, 5—9.5 mm wide, acute to obtuse, soon reflexed, sometimes persistent. Outer petals elliptic, 10—17 mm long, 5.9—9.3 mm wide, acute, inner side flat, bifacial, to sometimes keeled above the middle, ca. 2.5—3 mm thick at the center. Inner petals elliptic, 8.5—14 mm long, 5—8 mm wide, acute, inner side bifacial to keeled above the middle, ca. 3.5—4 mm thick at the keel. Stamens ca. 100—110, 4—5.2 mm long, 0.8—1.2 mm wide, thecae 1.7—3.2 mm long, broader than the connective, apical prolongation of connective 0.8—1.6 mm long, 1—1.4 mm wide, obtuse. Staminodes ca. 25—30, narrowly oblong to narrowly obovate, 2.7—3.7 mm long, 0.6—0.8 mm wide, obtuse to rounded, apex with a glandular margin. Carpels ca. 15—25, 2.8—3.7 mm long.

Monocarps 21—30 mm long, yellow to green with reddish tinge (in vivo), subglabrous, stipitate part 12—17 mm long, beak 0.8—1.7 mm long. Seeds 11.3—13.5 x 6—8(—9) mm.

Specimens examined: VENEZUELA. Amazonas: 19 Sep 1975, *Berry 1465* fl (MO), *1466* fr (VEN); 6—19 Jul 1969, *Bunting et al. 3804* fr (MY, U); 7 May 1979, *Davidse et al. 17299* fr (MO); Apr 1931, *Holt & Blake 722* fl, fr (B, NY, US); 18 Nov 1977, *Liesner 3621* fr (MO); 5 Apr 1979, *Liesner 6199* fr (MO); 19 Apr 1979, *Liesner 6794* fr (U); 20 May 1979, *Liesner 7577* fr (MO); 14 Dec 1953, *Maguire et al. 36789* fl (NY, S); 22—23 Dec 1947, *Schultes & López 9463* fr (US); 3 May 1970, *Steyermark & Bunting 103039* fr (U); 2 Mar 1942, *Ll. Williams 14580* fr (A, F, S, US, VEN, W); 7 Mar 1942, *Ll. Williams 14673* fl (F, VEN); 29 Jul 1959, *Wurdack & Adderley 43657* fr (NY, S).

PERU. Loreto: 26 Aug 1978, *Foster 4261* fl, fr (U); 29 Nov 1977, *Gentry et al. 21018* fr (MO); 19 Feb 1924, *Kuhlmann 1454* fr (RB, S); Jul 1967, *Martin* *et al. 1655* fl (ECON); 13 Jul 1980, *Vásquez & Jaramillo 218* fr (MO); 9 Dec 1980, *Vásquez et al. 999* fr (MO, U); 2 May 1929, *Ll. Williams 19* st (F).

BRAZIL. Acre: 13 Apr 1971, *Prance et al. 11177* fr (VEN). Amazonas: 24 Oct 1957, *Meijer Drees 35* fl (INPA, S); 17 Oct 1978, *Nascimento 674* st (F); 23 Oct 1979, *Nascimento 718* fr (F); 28 Oct. 1971, *Prance et al. 15635* fl, fr (U).

Distribution (Fig. 30): Upper Amazon Region.

Discussion: The type collection of this species, *Spruce 3291*, appears to be a mixture of *A. brachycarpa* and *A. brevipes*. The following sets are referable to *A. brevipes:* E, F, G p.p., and P p.p.

A. brachycarpa is easily recognized by the leaves with a raised primary vein on the upper side, in combination with the glabrous petioles and young twigs. The cortex of young twigs is often yellow or straw-coloured, rather than dull gray to brown as is more usual in herbarium specimens of *Anaxagorea*.

5. **Anaxagorea brevipedicellata** Timmerman in Maas, Timmerman & Westra, Proc. Kon. Ned. Akad. Wetensch., Ser. C, 87 (3): 299. 1984. — Type: *Campbell et al. P 22258*. Brazil. Pará: Rio Trombetas, km 54 on access road from Cachoeira Porteira to Perimetral do Norte, 24 May 1974, fl (holotype U; isotypes, INPA, K, MEXU, MO, NY, US, VEN). Fig. 16.

Shrub or tree, up to 3(—15) m tall. Leafy twigs 0.5—3.5 mm in diam., reddish brown-puberulous, soon glabrescent. Petioles 2—8 mm long, 1—2 mm in diam., reddish brown-puberulous, soon glabrescent. Lamina (narrowly) elliptic, (5—)8—15(—19) cm long, 2—6 cm wide, sparsely reddish brown-puberulous on lower side, base acute to obtuse (to rounded), apex acuminate to obtuse; primary vein impressed on upper side; secondary veins straight to curved, ca. 6—12 on each side of primary vein, slightly impressed on upper side, angles with primary vein up to 70°, loop-forming at obtuse angles, loops rather indistinct, smallest distance between loops and margin 2—6 mm.

Inflorescences on older branchlets (axillary), cluster-like, sessile or on a short thickened base, or on a peduncle (or sympodial rhachis) up to 13 mm long; pedicels 1.5—3.5 mm long, 0.5—1 mm thick at the base, 1—1.5 mm thick below the flower; upper bract close to the calyx to 1.5 mm below the calyx, apiculate, with an outer diameter of 1—2.5 mm, persistent. Flower buds ovoid, acuminate, dark brown (in vivo). Flowers green to rose or cream (in vivo).

Indument of floral parts: pedicels densely red-brown-puberulous, soon glabrescent; outer side of sepals sparsely red-brown-puberulous, inner side of sepals covered with some hairs with some stellate hairs added at the apex; petals subglabrous.

Sepals connate at the base, ovate to narrowly ovate, 2—6.5 mm long, 1.5—3.3 mm wide, acuminate, soon apically reflexed, persistent. Outer petals ovate (to narrowly ovate), 5—10 mm long, 2—4 m wide, apex long-acuminate and

Fig. 16. *A. brevipedicellata (Campbell et al. P22258).*

slightly recurved, inner side bifacial to sometimes keeled above the middle. Inner petals obovate to elliptic, 4.5—9.5 mm long, 2.3—4 mm wide, inner side bifacial to keeled above the middle, acuminate to obtuse. Stamens ca. 10—11, 1.7—3.5 mm long, 0.6—1.2 mm wide, thecae 0.9—2.7 mm long, broader than the connective, apical prolongation of connective 0.2—0.5 mm long, 0.4—0.6 mm wide, acute, obtuse, or rounded. Staminodes absent. Carpels ca. 10—20, 1.5—2 mm long, reddish (in vivo).

Monocarps 20—25 mm long, reddish (in vivo), subglabrous, stipitate part 13—16 mm long, beak 0.5—0.7 mm long, sometimes caducous. Seeds ca. 9 mm long.

Specimens examined: FRENCH GUIANA. Left bank of Crique Saï (affluent of Fleuve Grand Inini) a little upstream from mouth, 26 Aug 1970, *de Granville 632* fl (CAY); left bank of Fleuve Ouaqui, 5 Jul 1973, *de Granville 1705* fl (CAY, P, U), 9 Jul 1973, *de Granville B-4919* fl (CAY, P, U); Chemin de Emerillons km 10.6, bank of Crique Tamouri, 26 Feb 1974, *Lescure 214* fr (CAY, P, U); left bank of Fleuve Grand Inini on Saut Emerillon, 25 Aug 1970, *Oldeman B-3553* fl (CAY, P).

BRAZIL. Pará: Rio Mapuera 1—2 km upstream from Rio Trombetas, 29 May 1974, *Campbell et al. P22403* fl (U); BR 165, Cuiabá-Santarém Highway km 1305, vicinity of Igarapé José Prêto, 23 Nov 1977, *Prance et al. 25691* fr (U).

Distribution (Fig. 35): French Guiana and State of Pará, Brazil.

Discussion: The small number of stamens and the lack of staminodes are particularly noteworthy features of *A. brevipedicellata*. This species resembles *A. prinoides* both in the vegetative parts and in the fruits. It is clearly distinguished from the latter by the shorter pedicels, acuminate sepals, acuminate outer petals, as well as by the lack of staminodes already mentioned.

6. **Anaxagorea brevipes** Benth., Hooker's J. Bot. Kew Gard. Misc. 5: 8. 1853; R.E. Fries, Acta Horti Berg. 12(1): 14. 1934. — Type: *Spruce 1722.* Brazil. Amazonas: Manaus ("Barra do Rio Negro"), Jul 1851, fr (holotype, K; isotypes, B, BM, ECON, F, G, M, NY, OXF, P).

= *Anaxagorea minor* Diels ex R.E. Fries, Acta Horti Berg. 12(1): 22. fig. 2a—e. 1934; R.E. Fries, Field Mus. Nat. Hist., Bot. Ser. 13(2): 748. 1938. — Type: *Ll. Williams 854.* Peru. Loreto: Río Nanay, near Altura, Jun 1929, fl, fr (holotype, F).

= *Anaxagorea krukoffii* R.E. Fries, Acta Horti Berg. 12(1): 270. 1937. — Type: *Krukoff 5048.* Brazil. Amazonas: near mouth of Rio Embira, tributary of Rio Tarauacá, 28 Jun 1933, fl, fr (holotype, S; isotypes, A, B, BM, F, K, LE, M, MICH, MO, NY, U, UC, US).

Tree or shrub, up to 10(—25) m tall. Leafy twigs 1—6 mm in diam., glabrous. Petioles 3—13 mm long, 1.5—4.5 mm in diam., sparsely reddish-puberulous, soon glabrescent, or glabrous. Lamina (narrowly) elliptic to obovate, 8—27(—35) cm long, 3—10 cm wide, sparsely reddish-puberulous to glabrescent on lower side, base acute to rounded, apex acuminate, margin sometimes revolute; primary vein slightly impressed on upper side; secondary veins curved or straight, ca. 7—15, flat to slightly impressed on upper side, angles with primary vein up to 70°, loop-forming at right to acute angles, loops mostly distinct, especially toward the apex, smallest distance between loops and margin 2—10 mm.

Inflorescences axillary, pedunculate to nearly sessile, or terminal on short lateral shoots, or cauliflorous, mostly with 1—2 flowers at a time; peduncle (or sympodial rhachis) occasionally up to 20 mm long (mostly much shorter!); pedicels 3—11(—15) mm long, 1.5—3 mm thick at the base and 2.5—4 mm thick below the flower; upper bract close to the calyx to 2 mm below the calyx, with an outer diameter of 3—7.5(—9) mm, persistent (or tearing off partially). Flower buds ovoid to globose. Flowers yellow (with red "eye") to cream (or yellow-brown or cream marked with red without) (in vivo).

Indument of floral parts: pedicels sparsely ferrugineous-puberulous (soon glabrescent), outer side of sepals and petals densely ferrugineous-puberulous, inner side of sepals and petals sparsely creamy- or orange-puberulous to glabrous.

Sepals free, ovate to broadly ovate, 6.5—12 mm long, 5—9 mm wide, acute to obtuse, chartaceous to coriaceous, erect. Outer petals ovate to narrowly ovate, 12—17 mm long,. (4.5—)5.8—7.7 mm wide, obtuse, inner side keeled in the upper two-thirds, keel to 0.8—2.5 mm wide, narrowing toward the apex, whole thickness including keel 2.5—4.5 mm. Inner petals ovate to narrowly ovate, 11—16 mm long, 4—7 mm wide, acute, inner side with thick keel above the middle, 3.5—5 mm thick including keel. Stamens ca. 85—125, 3.3—4.5 mm long, 0.6—1 mm wide, thecae 1.4—3 mm long, broader than the connective, apical prolongation of connective 0.5—1.2 mm long, 0.8—1.2 mm wide, rounded to truncate. Staminodes ca. 30—45, narrowly obovate to narrowly elliptic, 3—5.5 mm long, 0.6—1.4 mm wide, rounded to truncate, apex with a glandular margin. Carpels ca. 10—25, 4.5—5 mm long.

Monocarps 20—36 mm long, yellow, yellow with red at the apex and the base, or dark violet (in vivo), subglabrous, stipitate part (13—)17—23 mm long, beak 0.5—2.5 mm long. Seeds 11—16.2 x 5.9—8.5 mm.

Specimens examined: COLOMBIA. Caquetá: 30 Mar 1940, *Cuatrecasas 8908* fr (US), *8915* fr (F). Santander: 25 Aug 1954, *Romero Castañeda 4701* fl (US); 3 Sep 1954, *Romero Castañeda 4817* fr (US).

VENEZUELA. Amazonas: 17 Feb 1951, *Cowan & Wurdack 31530* fr (MICH, NY, S); Jan—Feb 1969, *Fariñas 350* fl (VEN); Jan—Feb 1969, *Fariñas et al. 489* fl, fr (NY, U, VEN); 17 Jan 1979, *O. Huber 3117* fr (VEN); 25

Nov 1948, *Maguire & Politi 27396* fl (NY, S); 14 Jan 1949, *Maguire & Politi 28369* fl, fr (NY, S, US); 8 Feb 1949, *Maguire & Politi 28818* fl, fr (GH, MO, NY, S, U, UC, W); 29 Nov 1950, *Maguire 29792* fl (NY, S); 24 Apr 1968, *Medina 406* fr (VEN); 1853—1854, *Spruce 3291* fr (E, F, G, P); 23 Aug 1944, *Steyermark 57924* fr (F, S); 6 Sep 1944, *Steyermark 58401* st (F); 11 May 1980, *Steyermark et al. 122286* fl (U); Aug 1928—Apr 1929, *G.H.H. Tate 882* fr (NY, P, US). Bolívar: 15 Dec 1941, *Cardona 408* fl, fr (UC, US, VEN); 26 Apr 1966 (fl), *Steyermark & Gibson 95765* fl (NY, US, VEN).

GUYANA. 21—26 Nov 1937, *A.C. Smith 2550* fl, fr (A, K, MO, NY, P, S, U, US); 15—24 Dec 1937, *A.C. Smith 2735* fr (K, S); 8—22 Jan 1938, *A.C. Smith 2867* fr (A, K, NY, S, US).

SURINAME. Jan 1970, *Oldenburger et al. 1171* (U).

ECUADOR. Morona-Santiago: 20 Jun 1980, *Brandbyge & Asanza 32115* fr (AAU, U). Pastaza: 20 Mar 1980, *Holm-Nielsen 22283* st (AAU); 26 Jul 1980, *Øllgaard et al. 35282* fr (AAU).

PERU. Loreto: 16 Jul 1972, *Croat 18202* fr (MO); 18 Jul 1972, *Croat 18242* fr (F, GH, MO, NY, US); 10 Jan 1976, *Gentry et al. 15786* fr (MO, U); 27 May 1978, *Gentry & Jaramillo 22307* fr (MO); 21 Mar 1979, *Gentry et al. 25926* st (U); 23 Mar 1979, *Gentry et al. 26107* st (U), *26115* st (U); 24 Mar 1979, *Gentry et al. 26178* st (U); 21 Jul 1980, *Gentry et al. 28900* fr (MO); 24 Feb 1981, *Gentry et al. 31683* fr (MO); 19 Mar 1982, *Gentry et al. 36480* st (U); 28—30 Aug 1929, *Killip & Smith 28395* fl, fr (F, US), *28599* fr (NY, US), *28610* fl (NY, US); 11 Mar 1974, *McDaniel & Rimachi 18306* fr (MO); 3 May 1977, *Plowman et al. 7193* fr (GH); 26 Oct 1976, *Prance et al. 24122* fl (U); 28 Oct 1976, *Prance et al. 24172* fl, fr (U); 21 Jan 1977, *Rimachi 2772* fr (F, MO); 11 Apr 1964, *Schunke Vigo 6375* fl, fr (F, US); 17 Oct 1980, *Vásquez & Jaramillo 525* fl (MO); Jun 1929, *Ll. Williams 849* fl (B, F, S), *855* fl (F). Madre de Dios: 29 Oct 1979, *Gentry et al. 27330* fl (MO).

BRAZIL. Amazonas: 27 Sep 1973, *Berg et al. P18135* fl, fr (U); 13 Nov 1973, *Berg et al. P19551* fl (U); 14 May 1956, *Chagas INPA 3833* fr (F, INPA, MG, S); 25 Nov 1957, *Chagas INPA 5967* fl (INPA); 8 Aug 1979, *Cid et al. 38* fl, fr (U); 20 Aug 1979, *Cid et al. 549* fl (U); 30 Nov 1955, *Coêlho INPA 3002* fl, fr (INPA, MG); 5 Oct 1931, *Ducke RB 23907* fl (S); 7 Apr 1936, *Ducke RB 29011* fl, fr (RB, S); 19 Oct 1945, *Fróes 21202* fl (F, K, NY, US); 16 Dec 1974, *Gentry & Ramos 13350* fl, fr (INPA, MG, MO, U); 12 Oct—6 Nov 1934, *Krukoff 6820* fl, fr (A, BM, BR, F, K, LE, MICH, MO, NY, S, U, US); 16 Aug 1973, *Lleras et al. P17316* fr (U); 1819—1820, *Martius s.n.* fr (MO); Oct—Nov 1831, *Poeppig 2802* fr (BR, F, P); 12 Oct 1966, *Prance et al. 2633* fl (B, F, GH, INPA, K, NY, S, VEN); 29 Aug 1957, *Rodrigues 590* fl (INPA, S); 17 Oct 1960, *Rodrigues & Chagas 1854* fr (INPA); 21 Dec 1963, *Rodrigues & Coêlho 5633* fr (INPA); 15 Nov 1967, *Rodrigues & Monteiro 8323* fr (INPA); 26 May 1974 (fr), *Rodrigues et al. 9338* (INPA); 11 Nov 1955, *Rodrigues & Coêlho INPA 2880* fl (INPA, MG); 11—14 Apr 1972 *Schultes & Rodrigues 26192A* fr (GH, INPA); 21 Feb 1974, *Steward et al. P20415* fr (U). Pará: 9

Oct 1922, *Ducke RB 17872* fl, fr (S); 17 Sep 1969, *M. Silva & Souza 2637* fl, fr (MG); 15 Jul 1968, *Prance et al. 6040* fr (U).

Distribution (Fig. 33): Colombia, Venezuela, Guyana, Suriname, and throughout the greater part of the Amazon region. Primary and secondary rainforest, shrub savannas, at alt. 100—500 m.

Discussion: Some distinctive features of *A. brevipes* are the glabrous vegetative parts and the free sepals. In addition to characters described above, it should be noted that pedicels are verruculose or wrinkled (at least in herbarium specimens). Inflorescences are sometimes terminal on short axillary shoots, rather than truly axillary. *A. brevipes* much resembles the common and widespread *A. dolichocarpa*; it is distinct from that species a.o. by the erect sepals, the keel on the outer petals, and the apical prolongation of the connective which is about as long as wide.

7. **Anaxagorea crassipetala** Hemsley, Diagn. plant. nov. mexic. 1: 2. 1878; Hemsley, Biol. cent.-amer., Bot. 1: 17. 1879; R.E. Fries, Acta Horti Berg. 12(1): 24. t. 2. 1934. — Type: *R. Tate 3*. Nicaragua. Without locality, 1867—1868, fl, fr (lectotype, K; isolectotype, BM). *Seeman 3*. Nicaragua. Chontales: without precise locality, 1866—1867, fr (syntypes, BM, K, LE). Fig. 17.

= *Anaxagorea clavata* R.E. Fries, Ark. Bot., n.s. 1(6): 342. pl. 7. 1950. — Type: *Cuatrecasas 21275*. Colombia. Valle: Río Calima, Quebrada de la Brea, alt. 20—40 m, 24 May 1946, fl, fr (holotype, S; isotypes, F, US).

Tree or shrub, up to 12(—25) m tall. Leafy twigs 1—5(—9) mm in diam., ferrugineous-puberulous. Petioles 7—20(—25) mm long, 1.5—3 mm in diam., ferrugineous-puberulous. Lamina (narrowly) elliptic to (ob)ovate, (11—)16—40 cm long, 4—14 cm wide, ferrugineous-puberulous to glabrescent on lower side, base obtuse to rounded, apex acuminate to acute; primary vein flat on upper side; secondary veins (straight to) curved, ca. 10—24 on each side of primary vein, flat to slightly raised on upper side, angles with primary vein up to 75°, loop-forming at right angles, loops mostly indistinct, smallest distance between loops and margin 2—5 mm.

Inflorescences axillary, mostly on older parts of branchlets, to cauliflorous, pedunculate to nearly sessile, with 1—several flowers at a time, flowers arranged in rhipidium-mode or clustered; peduncle (or sympodial rhachis) up to 11 mm long; pedicels (6—)8—20 mm long, 1—1.5 mm thick at the base and 2—3.5 mm thick below the flower; upper bract close to the calyx to 5 mm below the calyx, with an outer diameter of (2—)2.5—4.5 mm, persistent. Flower buds conical, green (in vivo). Flowers of various colours, mostly shades of yellow, orange, or brown (in vivo).

Indument of floral parts: pedicels and outer side of sepals and petals densely ferrugineous-puberulous, inner side of sepals and petals densely to sparsely brown-, orange-, or white-puberulous.

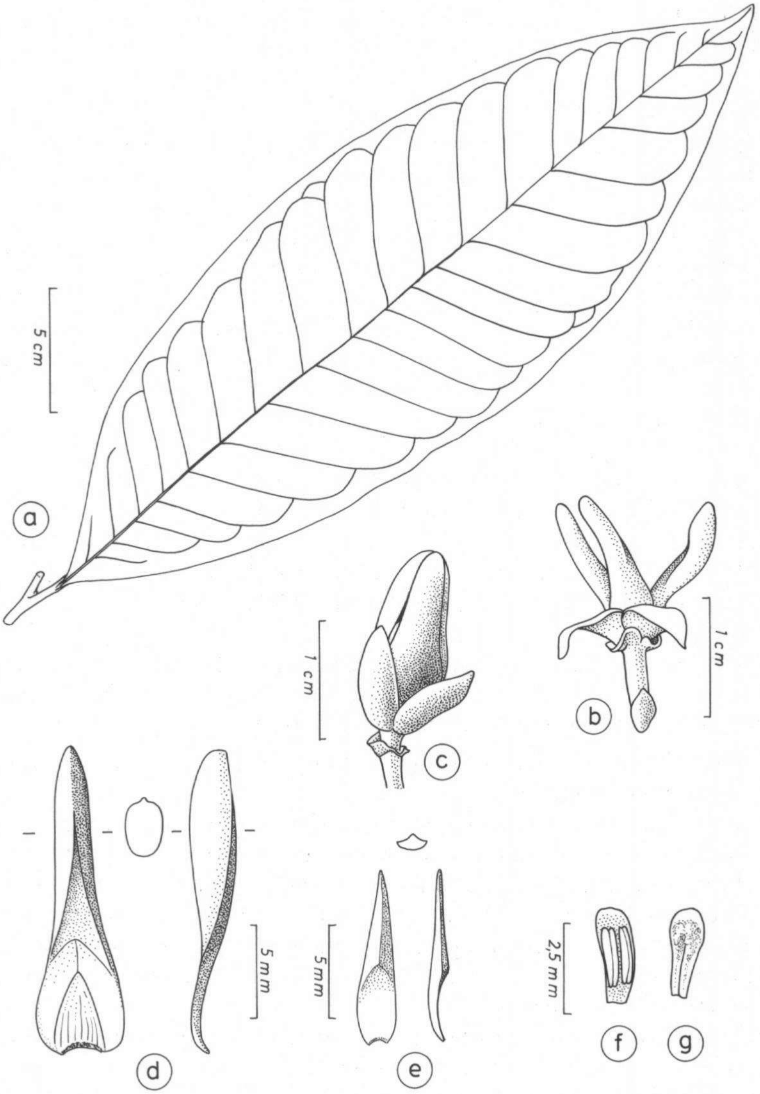

Fig. 17. *A. crassipetala* (a, *Schunke Vigo 10006;* b—c, *Neill 2584;* d—e, *Forero et al. 1285*; f—g, *Duke 5257*). a, leaf; b, flower; c, flower bud; d, outer petal, inner side, lateral view, and cross section; e, inner petal, inner side, lateral view, and cross section; f, stamen; g, staminode.

Sepals free, ovate to triangular, 5.5—10 mm long, 3.5—6 mm wide, apex obtuse to subacute, conspicuously reflexed. Outer petals narrowly ovate, 9—20(—22) mm long, 3.5—6 mm wide, apex obtuse to rounded, inner side bifacial in upper third, thickness of upper part to 6 mm. Inner petals narrowly ovate to narrowly elliptic, rarely narrowly obovate, 6—14 mm long, (1.5—)2—3 mm wide, acute, inner side bifacial above the middle, thickness of upper part to 2 mm. Stamens ca. 35—40, 2.5—3.5 mm long, 0.7—1.2 mm wide, thecae (1—)1.5—2.2 mm long, not broader than the connective, apical prolongation of connective 0.3—0.8 mm long, 0.7—1.2 mm wide, acute, obtuse, truncate, to retuse. Staminodes ca. 10—20, narrowly ovate to narrowly obovate, or narrowly oblong, 2—3 mm long, 0.5—1 mm wide, truncate (to retuse). Carpels ca. 10—20, 2—3.5 mm long.

Monocarps 22—32 mm long, green, greenish-yellow (or reddish-brown) (in vivo), sparsely ferrugineous-puberulous, stipitate part 14—23 mm long, beak (1.5—)2—5 mm long. Seeds 8—12 x 5—7.2 mm.

Specimens examined: NICARAGUA. Chontales: 9 Apr 1961, *Bunting & Licht 1171* fl, fr (F, NY, US); 1893, *Shimek & Smith 414* fr (F). Zelaya: 13 Sep 1977, *Neill 2584* fl (U); 24 Mar 1966, *Proctor et al. 27229* fl, fr (F, IJ, NY, S, US, VEN); 6—7 Nov 1977, *Stevens & Krukoff 5078* fl, fr (MO, U); May 1855, *Wullschlaegel 1783* st (BR).

COSTA RICA. Alajuela: 23 Jun 1966, *Jiménez 4044* fl, fr (BM, CR, MO, NY); 15 Mar 1939, *A. Smith 1816* fr (A, F, MO, NY). Cartago: 5 Feb 1965, *Godfrey 66253* fr (MO). Heredia: 23 Jan 1970, *Bawa 510* (MO); 6 Nov 1968, *Frankie 50 A* fl, fr (MO), *50 C* st (F); 25 Nov 1970, *Hunter ACM 95* fl (CR); 18 Feb 1965, *Jiménez 2911* fr (F); 20 Jan 1966, *Jiménez 3627* fr (CR, F, NY); 30 Mar 1956, *Schubert & Holdridge 1311* fl, fr (US). Limón: 20 Nov 1964, *Little 20076* fr (CR); 19 Feb 1926, *Standley & Valerio 48766* fl (US). Puntarenas: 10 Jul 1977, *Liesner 3210* fl, fr (MO); 13 Jul 1977, *Liesner 3268* fl (MO); 22 Sep 1975, *Poveda et al. s.n.* (CR).

PANAMA. Coclé: Jul 1979, *Antonio 1371* fl (U); 7 Dec 1979, *Antonio 3053* fl (U); 28 Jan 1980, *Antonio 3562* fl (U); 3 Feb 1983, *Davidse & Hamilton 23540* st (MO); 20 Feb 1978, *Hammel 1618* fl (U); 8 Mar 1978, *Hammel 1934* fl, fr (U); 10 Apr 1981, *Sytsma 3920* fr (U). Darién: 26 Jul 1962, *Duke 5257* fl (F, MO); 26 Jul 1967, *Duke 13608* fl, fr (GH, MO, OS, US); 21 Dec 1980, *Hartman 12096* fr (U); 28 Apr 1968, *Kirkbride & Bristan 1508* fl (MO, NY).

COLOMBIA. Chocó: 31 Jan 1967, *Duke 9637* fr (MO, US); 25 Apr 1975, *Forero 1214* fr (NY); 27 Apr 1975, *Forero et al. 1285* fl (MO, NY). Nariño: 23 Nov 1981, *Gentry et al. 34865* fl, fr (MO, U); 20 Jun 1951, *Romero Castañeda 2789* st (F).

PERU. Amazonas: 16 Jul 1974, *Berlin 1612* fr (U). San Martín: 2 Jul 1978, *Plowman & Schunke Vigo 7524* fl (F, NY, U); 13 Nov 1969, *Schunke Vigo 3617* fl (GH); 11 Mar 1978, *Schunke Vigo 10006* fl (U).

Distribution (Fig. 30): Central America from Nicaragua southward, northeastern South America: Pacific side of Colombia as far as Amazonas and San Martín in Peru.

Discussion: *A. crassipetala* comes closest to *A. allenii* and *A. guatemalensis*, see remarks under those species. The apex of the sepals is conspicuously reflexed, to an extent not encountered in either of the other two species.

(Part 2 in the next issue of this journal.)