

ANATOMICAL CONTRIBUTIONS TO PLANT TAXONOMY II¹

The affinities of *Hua* Pierre and *Afrostryrax* Perkins et Gilg

P. BAAS

Rijksherbarium, Leiden

CONTENTS

Summary	161
Introduction	161
Techniques	163
Materials	163
Synopsis of the family Huaceae	163
Results and Discussion	164
Taxonomical and macromorphological notes	164
Ovary, fruit and seed anatomy	165
Pollen morphology	166
Vegetative anatomy	167
<i>Hua</i>	167
<i>Afrostryrax</i>	172
The Halphen reaction	179
Discussion of some of the characters of Huaceae	179
<i>Hua</i> and <i>Afrostryrax</i> as related genera of the family Huaceae	182
Huaceae compared with other plant groups	183
Perkins' and Chevalier's view: Styracaceae and related families	183
Hallier's and Hutchinson's suggestions: Linaceae s.l. and Malpighiales	184
Pierre's view: Sterculiaceae and other Malvales	185
General Conclusions	190
Acknowledgements	190
References	191
Index to original observations in other families	192

SUMMARY

Vegetative anatomy, fruit and seed structure, and pollen morphology of *Hua* and *Afrostryrax* (tropical West and Central Africa) are described in detail. The two genera have many anatomical characters in common (see anatomical family diagnosis on p. 182) but are sufficiently different from other families to justify the existence of the family *Huaceae*. Some characteristic features are discussed and the results of comparisons with representatives of about 50 families are reported. *Afrostryrax* is not related to *Styracaceae*, nor is *Hua* to *Erythroxylaceae* as had been suggested in the past. *Sterculiaceae* and *Bombacaceae* appear to have the highest number of characters in common with *Huaceae* of all the families compared. This supports the inclusion of *Huaceae* in the *Malvales* as advocated previously by several authors. Some original observations on the anatomy of a few of the families compared are included in the comparative part.

INTRODUCTION

The two genera *Hua* and *Afrostryrax* from tropical West and Central Africa consist of shrubs or trees which are used by the local population as a spice because of the strong

¹) Part I was published in *Blumea* 18: 369—391, 1970.

garlic flavour of their young leaves, bark and seeds (Mildbraed 1913, Walker & Sillans 1961, Germain 1963).

Their taxonomic history is rather confused. They have been considered to be closely related to each other by several authors, whilst others maintain that they should be placed in families of different orders.

Hua was described from the Congo by Pierre in 1906 as a member of *Sterculiaceae*. Features aberrant for the family induced him to create a new tribe *Huaeae*. The external morphology was amply illustrated and showed the peculiar more or less peltate and clawed petals, the 4-celled anthers and the unilocular ovary with one basal ovule.

Afrostryax was first described from the Cameroons by Perkins et Gilg (1909), who placed this genus in *Styracaceae* in a new subfamily *Afrostryacoideae*, being the only *Styracaceae* representative on the African continent. Features in common with *Styracaceae* such as resemblance in seed structure and stellate indumentum were emphasized and Perkins exemplified the isolated position within the family by the calyx, fused in bud and opening with irregular lobes, the free fleshy petals, the unilocular ovary with 6 basal ovules and the garlic smell of all parts of the plant (see also Perkins 1928).

Mildbraed (1913) was the first to advocate the affinities of *Afrostryax* with *Hua* in a paper on garlic barks of West Africa. He furthermore added the important observation that *Afrostryax* has early caducous stipules, which made a close relationship with the exstipular *Styracaceae* more unlikely. In spite of the unilocular ovary with basal ovule(s) he regarded it to be more closely related to *Sterculiaceae* than any other plant group. Hallier f. (1923) also indicated the affinities of *Hua* with *Afrostryax* when he commented: 'Sie (Marquesia Gilg) scheint mit *Monotes* A. DC, *Afrostryax* Perk. et Gilg und *Hua* Pierre eine kleine Afrikanische Pflanzengruppe zu bilden welche die Linaceen-Houmiereen mit den Tiliaceen und Dipterocarpaceen verbindet.' The Rijksherbarium contains a sheet (Zenker 3992) of *Afrostryax kamerunensis* with a note by Hallier f. '*Huae arcte affinis*'. This suggestion was supported by Van Steenis and Bakhuizen van den Brink Jr. (1967), who also advocated a Sterculiaceae affinity for *Hua* and *Afrostryax*.

Chevalier (1947) formally erected the family '*Huaceae*' in which he included the two genera. Because of 'une parenté évidente' with *Styracaceae* he placed the family in *Ebenales*, adding that *Hua* and *Afrostryax* constitute the ancestors of present day *Styracaceae* from Asia and America. He also mentioned some points in common with *Sterculiaceae*, however. Shaw (1966, in Willis: Addenda XXI) also stressed the probable affinities of *Afrostryax* with *Hua*, but concluded that 'Pierre and De Wildeman's original suggestion of a Sterculiaceae affinity for *Hua* is almost certainly correct'.

Different views came from Hutchinson (1959), who reserved the family rank for *Hua* (*Huaceae*) in his *Malpighiales* close to *Erythroxylaceae*, and maintained that *Afrostryax* differs widely from *Hua* and should be retained in *Styracaceae*. W. Robyns (1958) in revising *Afrostryax* for the Congo, also arrived at the conclusion that this genus should be kept in *Styracaceae* and that affinities with *Hua* are unlikely. Accordingly Germain (1963) only considered *Hua* in his treatment of *Huaceae* in the Flore du Congo du Rwanda et du Burundi.

Apart from the mutual affinities between *Hua* and *Afrostryax*, the affinities with other families remained controversial and enigmatic. Edlin (1935) in revising certain groups of *Malvales* expelled *Hua* from that order because it showed 'no affinities whatsoever.' Cronquist (1968) and Takhtajan (1969) admitted that the affinities of *Huaceae* are still obscure. Krause (1915) in Engler and Prantl's *Nachträge IV* recognized Pierre's tribe *Huaeae*, but Engler and Gilg (1919) placed both *Hua* and *Afrostryax* in *Styracaceae*. In the new Engler Syllabus (1964) both the relationships between *Hua* and *Afrostryax* and their affinities to *Styracaceae* are said to be uncertain.

The anatomy of both *Hua* and *Afrostryrax* has received little attention so far. Perkins (1909) stated only: 'Die anatomische Befund spricht weder für noch gegen eine Zugehörigkeit von *Styracaceae*, so dasz ich hier nicht näher darauf eingehen möchte.' Dehay (1941) briefly described the petiole of *Hua*. Mildbraed (1913: 557) gave a detailed description of the bark of *Afrostryrax lepidophyllus*. We owe to Normand and Chatelet (1955) a description of the wood of that species. They mentioned the great differences between the woods of *Styracaceae* and *Afrostryrax* and suggested a provisional placement near *Sterculiaceae*, stressing the need of a profound study of *Huaceae* in order to gain more insight into their affinities. Lebacqz and Dechamps (1964) included *Hua gabonii* in their codified description of the woods of Central Africa. Their list of characters selected for identification purposes does not allow, however, a detailed comparison with the available data on *Afrostryrax lepidophyllus*.

A comprehensive study of the anatomy of both genera was undertaken in order to employ anatomical characters reliably in a discussion of both the mutual affinities and the relationships with other plant groups. For this purpose it was found necessary to make a study of leaf, twig, bark and wood anatomy, as well as of pollen, seed and fruit structure. A chemical test for the presence of cyclopropene containing fatty acids (Halphen reaction) was also carried out. Other chemotaxonomic work is reported by Beijersbergen in the present issue.

TECHNIQUES

Techniques employed in the anatomical studies of vegetative parts, flowers, fruits, and seeds are the same as described before (Baas, 1970). Scanning Electron Microscope (S.E.M.) studies were carried out with the Cambridge instrument ('Stereoscan') of the Department of Microscopy T.N.O., Delft, using gold coated herbarium specimens. In order to reveal the surface structure of stomata, the scales of *Afrostryrax lepidophyllus* were stripped off with adhesive tape. Pollen preparations were made by acetolysing entire flowers in the usual way. The Halphen reaction was carried out on endosperm extracts by Dr. H. W. L. Ruigrok from the Lab. voor Experimentele Plantensystematiek, Leiden, according to a recipe from the Nederlandse Farmacopee 1966: 447.

MATERIALS

Through the courtesy of the Director of the Herbarium at Brussels, the Keeper of the Jodrell Laboratory, Royal Botanic Gardens Kew, the Forest Products Research Laboratory at Princes Risborough, Ir. J. J. Bos and Ir. F. J. Breteler (Wageningen), Mr. J. Brookman-Amissah of the Department of Forestry, Ghana, Mr. R. Dechamps of the Musée Royal de l'Afrique Centrale, Tervuren, Belgium, I obtained a wealth of herbarium material, wood samples, and some pickled material of flowers and fruits. Some of the wood samples were especially collected for this study by Bos, Breteler and Brookman-Amissah. Specimens studied will be listed under the different headings of the descriptive part. Most of the herbarium material used is from Brussels; Bos and Breteler collections are at Wageningen.

SYNOPSIS OF THE FAMILY HUACEAE

Anticipating the results of this study a short description of the family *Huaceae*, consisting of *Hua* and *Afrostryrax*, is given.

Trees or shrubs with simple, entire, alternate, stipulate leaves. Flowers actinomorphic,

in axillary few-flowered fascicles or solitary. Calyx either valvate and 5-merous or fused in bud and opening with 3—5 irregular lobes. Petals 5, free, with very short or long claws. Stamens 10, 1-seriate, of equal length, anthers 4-celled. Ovary superior, unilocular with 1 or (5) 6 basal, erect, anatropous ovule(s) and a short conical style. Fruit a dehiscent or indehiscent capsule. Seed 1 (or 2), with copious endosperm. Embryo straight with obovate cotyledons.

RESULTS AND DISCUSSIONS

Taxonomical and macromorphological notes

In the past 5 specific names have been proposed: *Hua gabonii* Pierre ex De Wildeman, *H. parvifolia* Engl. et Krause (1911), *Afrostryrax kamerunensis* Perk. et Gilg (1909), *A. lepidophyllus* Mildbr., and *A. macranthus* Mildbr. (1913).

H. parvifolia has been reduced to *H. gabonii* by Germain (1963) apparently because size and shape of the leaves show a continuous range of variation in *Hua*.

A. macranthus, described by Mildbraed from the Cameroons, agrees according to the description fully with *A. kamerunensis* except for its narrower leaves, larger flowers, and denser indumentum of pedicel and calyx. As for the leaf shapes and sizes I found a considerable range of variation in specimens which belonged undoubtedly to *A. kamerunensis*. This character is therefore not valid in distinguishing *A. macranthus* from *A. kamerunensis* and it is possible that, like *Hua parvifolia*, *A. macranthus* should be reduced. W. Robyns (1958: 96) also mentioned that '*A. macranthus* semble a peine distincte de *A. kamerunensis*'.

The presence of early caducous stipules in *Afrostryrax* was first reported by Mildbraed. Chevalier and W. Robyns were unable to discover any stipules in the herbarium material they studied. Of *A. lepidophyllus* I found a specimen (Congo, Gilbert 10508) with conspicuous lanceolate stipules on a young shoot. The scars left by the stipules in *Afrostryrax* are inconspicuous indeed, but their presence in young shoots is indicated by the nodal anatomy of older twigs where short stretches of vascular tissue split off from each of the lateral nodal bundles to supply the early caducous stipules. There are therefore no reasons to doubt Mildbraed's observations.

Glandular structures on the leaves of *Afrostryrax* have been reported by Normand and Chatelet (1955) and Robyns (1958). Chevalier (1947) recorded them for the sepals of *Hua*. The anatomical structure of the glands as described on p. 178 applies essentially to all glands independent of where they occur. In the limited material of flowers and fruits investigated these glands were found in *Hua* as circular, slightly raised disks along the margins of the sepals. I observed a circular thickening around the basis of a developing seed in *Hua*, composed of an epidermis with palisade-like cells and parenchyma. This thickening might also be glandular. In *Afrostryrax* glands can be found as raised disks on the margins of the petals and on the inner surface of the calyx, mostly overlying the five major vascular bundles. On the leaves these glands have a different distribution in each species. *Hua* has more or less crateriform circular glands scattered on the lower leaf surface (Plate II: 3 & 4), their occurrence being most frequent near the leaf base. In *Afrostryrax kamerunensis* the glands are oblong-oval structures along the leaf margin, again most numerous towards the base (Plate II: 6). In *A. lepidophyllus* the occurrence of glands is not a constant character. If present they may be found on the abaxial or adaxial surface of the leaf or along the leaf margin, in each case near the base of the leaf.

One of the striking differences between *Hua* and *Afrostryrax* lies in the shape of the petals. In *Hua* these are long clawed, with a hirsute \pm peltate lamina. The petals of

Afrostyrax are not conspicuously clawed but they too consist of two parts: a very short and rather broad base supporting an obovate lamina. The petals of several *Buettnerioideae* of the *Sterculiaceae* (see Leinfellner, 1960) recall those of *Hua* and *Afrostyrax*.

Ovary, Fruit and Seed Anatomy

Hua gabonii

Material: Congo, *Donis 3121* (dried fruit), *Louis 7287* (pickled material of immature fruit).

Pericarp glabrous, *c.* 0.7 mm thick. Epidermis and subsequent parenchyma layers (*c.* 3) followed by zone of thick-walled densely pitted stone cells (brachysclereids). Inner part parenchymatous and constituting the bulk of the pericarp, supplied with collateral vascular bundles. Testa 3-layered, *c.* 0.5 mm thick, developing from two integuments, the outer integument giving rise to the outer parenchymatous testa, covered with thin-walled simple unicellular hairs and traversed by numerous centric (amphicribal) vascular bundles. Outer epidermis of inner integument developing into lignified palisade cells with thick densely pitted walls; cells *c.* 250 μ tall; some cells divided into a broad and short inner and a longer and narrower outer cell. Remainder of testa parenchymatous, compressed in mature seed. Perisperm present in mature seed as very thin layer of compressed parenchyma cells. Endosperm copious, composed of cells rich in starch grains and minute oil droplets. Embryo straight with two flat obovate cotyledons (6 \times 5 mm), adpressed to each other.

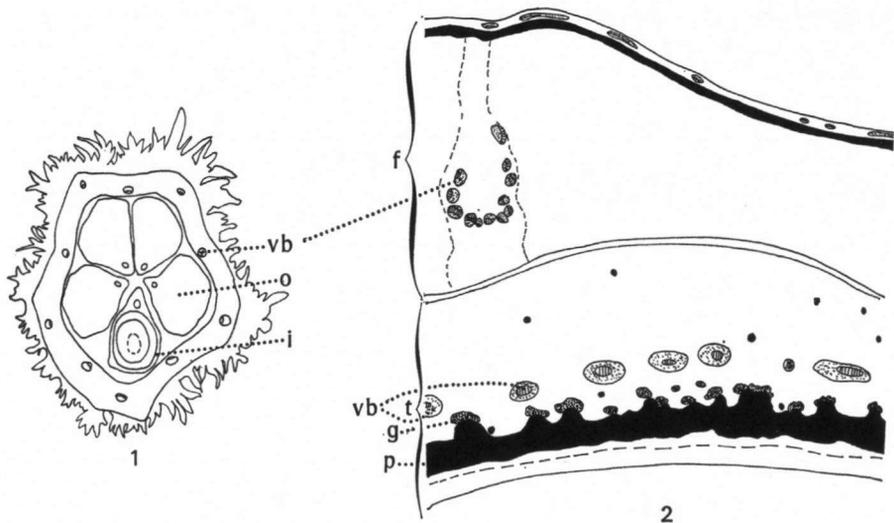
Afrostyrax kamerunensis (Fig. 1 & 2, Plate II: 1)

Material: Congo, *Gillardin 176* (dried flower), *Louis 13877* (pickled flowers), *Louis 7287* (pickled fruit).

Ovary pentagonal in transverse section, densely covered with stellate hairs. Ovary wall supplied with 10 vascular bundles, all \pm collateral in *Louis 13877* (fig. 1), only 5 collateral in *Gillardin 176*, the 5 bundles at the corners of the ovary as seen in transverse section with 2 lateral xylem poles (fused lateral bundles of 5-carpellate ovary?). Ovules 5 or 6, erect on a central basal placenta, anatropous, bitegmic, with adaxial raphe and abaxial micropyle. Pericarp densely covered with stellate hairs, *c.* 2 mm thick, interspersed with vascular bundles on both outer and inner parenchymatous parts (fig. 2). Layer of brachysclereids and inner part of pericarp as in *Hua*; vascular tissue more elaborate and complex, however (fig. 2). Testa 3-layered as in *Hua*, *c.* 2.5 mm thick, glabrous; outer parenchymatous tissue traversed by amphicribal vascular bundles, *c.* 2 mm thick, parenchyma cells opposite ridges of palisade layer with brown contents. Palisade layer of tall thick-walled and densely pitted cells (*c.* 200 μ tall), with narrow ridges and broad furrows in sectional view (fig. 2; Plate I: 1), and with reticulate sculpturing in surface view. Inner testa wholly parenchymatous; layers close to endosperm compressed. Remainder of seed as in *Hua*.

Afrostyrax lepidophyllus

The anatomy of fruit and seed has not been studied in this species. As seen with a stereomicroscope (magnification \times 50) the structure is basically similar to that in *A. kamerunensis* except for a much thinner testa and the absence of a reticulate sculpturing in the palisade layer.



Figs 1 and 2. *Afrostryax kamerunensis*. — 1. transverse section of ovary, $\times 50$. — 2. section of pericarp and testa, $\times 17$. — f: fruit wall; g: groups of cells with dark contents; i: integument; o: ovule; p: palisade layer; t: testa; vb: vascular bundle. Phloem dotted, sclerenchyma black, xylem hatched.

Pollen morphology

Hua gabonii (Plate I: 1, 2, 3 & 4)

Material: Congo, *Klaine 2895, Louis 2914, Robyns 1441*.

Grains single, oblate, equatorial outline triangular to semitriangular, diameter 36–49 (mean 43) μ . 3-, rarely 2-porate. Pores circular to oval (c. 3–5 μ in diameter), mainly endexinous, surrounded by annular thickening of endexine, virtually closed by ektexine and with an operculum of variable size. Endexine c. 1.5 μ , near pores 2.5–4 μ thick, sometimes differentiated into a thin inner and a thicker outer layer. Ektexine c. 1 μ thick, composed of a layer of short, densely spaced columellae and a tectum. Tectum surface finely verrucate to areolate. Areolae c. 0.5–1.5 μ in diameter.

Afrostryax lepidophyllus (Plate I: 7)

Material: Congo, *Evrard 4221, Gilbert 10221, Louis 13883*.

Grains as in *Hua* but smaller and with thinner exine layers. Oblate to suboblate, diameter 27–33 (mean 31) μ . Pores 2.5 \times 3–3 \times 4 μ . Operculae often indistinct. Endexine c. 0.5 μ , near pores c. 1 μ thick. Ektexine c. 0.5 μ thick, almost homogeneous in optical section. Surface pattern very finely scabrate.

Afrostryax kamerunensis (Plate I: 5 & 6)

Material: Cameroons, *Zenker 3922*; Congo, *Gillardin 176*.

As in *A. lepidophyllus*. Endexine near pores 1–1.5 μ thick. Ektexine 0.5–1 μ thick.

Note. Acetolysed grains of *Hua* and *Afrostryrax* often show folds in a regular triangular arrangement on one or sometimes both sides of the equator (Plate I). For *Hua* similar structures have been interpreted as colpi by Oltman (1971), who investigated one sample from the Congo. His illustration is indeed suggestive of colpi, but in most grains I investigated, I found these structures less conspicuous and without 'smooth colpus membranes'. Moreover, they are absent from a considerable number of grains (see e.g. Plate I: 4) or are more irregularly arranged. Regular folds of the type as in *Huaceae* are of common occurrence in triplicate oblate grains (Mr. J. Muller, private communication).

Vegetative anatomy

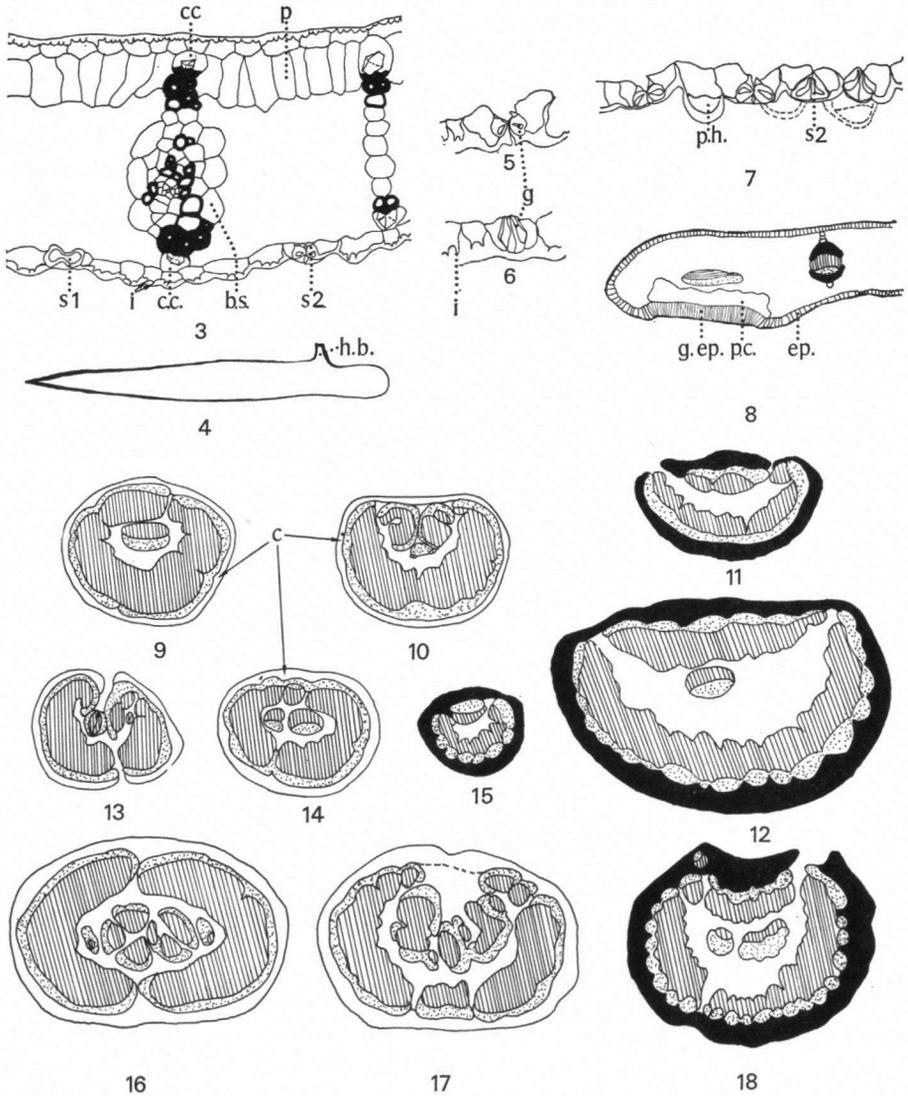
Hua gabonii

Leaf (Fig. 3, 4, 5, 6, 9, 10, 11 & 12, Plate I: 8, II: 3 & 4, III: 1 & 2).

Material: Congo, Gillardin 355, Gillet s.n., Louis 930.

In surface view. Unicellular adpressed *hairs* infrequently present on abaxial surface, mostly branched with one short thin-walled and one long thick-walled arm (fig. 4). Stellate to peltate hairs very rarely present near leaf base. *Wax* present as small particles on the cuticle (Plate III: 2). *Epidermal cells* of adaxial surface rectangular to polygonal; anticlinal walls sinuous at high focus and \pm straight at low focus. Outer walls with pit-like cavities between anticlinal wall undulations due to invaginations of the cell lumina into the inner part of the walls. Unspecialized cells of abaxial epidermis similar but with pit-like structures present in the entire outer wall (Plate III: 1); anticlinal walls \pm straight; periclinal outer walls lowly papillate as seen with S.E.M. (Plate III: 2). Cells overlying major veins \pm square to rectangular, arranged in rows. *Stomata* confined to abaxial surface, abundant in areolae and over minor veins, scanty over midrib and major veins, paracytic with \pm rectangular to high dome-shaped subsidiary cells and narrow guard cells. Subsidiary cells and guard cells devoid of pit-like structures. Guard cells with so-called T-piece at poles (see Stace, 1965; Plate III: 1). Diameter perpendicular to the pore 8—10 μ . *Stomata* overlying major veins and midrib often of deviating types. *Venation pattern* (as seen in cleared leaves and paradermal sections) reticulate with for the greater part entirely closed, square to rectangular areolae, resulting in a characteristic regular pattern (Plate II: 3). Circular crateriform *glands* present in varying number on adaxial surface, most frequently near leaf base (Plate II: 3 & 4).

In transverse section. *Cuticle* c. 1 μ thick. *Epidermal cells* square to flattened, adaxial cells of about the same size as unspecialized cells of abaxial side or slightly smaller. Outer walls of abaxial epidermal cells convex to lowly papillate. For pit-like structures see above and fig. 3, 5 & 6. Outer wall thickness 4—5 μ . *Stomata* \pm in one plane with other cells, with well developed outer and inner cuticular ledges (fig. 5). Guard cells with lumina that are slit-like in polar transverse section (fig. 6), triangular in median transverse section and dumbbell-shaped in sections parallel to the pore (fig. 3). *Mesophyll* composed of one layer of short palisade cells, and fairly compact 'spongy' tissue of about 4 layers of isodiametric, rounded, very slightly lobed cells. *Midrib* (fig. 11 & 12) with slightly convex adaxial surface and strongly convex abaxial surface, supplied with an abaxial crescentiform vascular system and an almost flat adaxial vascular system, forming together an almost closed cylinder sometimes enclosing an extra medullary bundle (fig. 12). Whole vascular system sheathed by several layers of thick-walled sclerenchyma fibres. Ground tissue of midrib parenchymatous, unligified at periphery, ligified in 'pith'



Figs. 3—6. *Hua gabonii*, transverse section of lamina. 3. general view, spongy tissue omitted, $\times 290$; 4. unicellular hair, $\times 290$; 5. median transverse section of stoma, $\times 440$; 6. polar transverse section of stoma, $\times 440$. — 7. *Afrostyrax lepidophyllus*, transverse section of abaxial epidermis, $\times 440$. — 8. *A. kamerunensis*, transverse section of base of lamina through gland, $\times 50$. — Figs. 9—18. Vascular systems of petiole and midrib (all $\times 50$). 9, 13 and 16 through base of petiole; 10, 14 and 17 through distal end of petiole; 11, 12, 15 and 18 through midrib. 9—12. *Hua gabonii* (9—11. Gillet s.n.; 12. Gillardin 355). 13—15 *A. kamerunensis*. 16—18. *A. lepidophyllus*. — c: collenchyma; c.c.: cristarque cell; b.s.: bundle sheath; g. ep.: epidermis of gland; i: pit-like invaginations of lumen into cell wall; ep.: epidermis; p: palisade chlorenchyma; p.c.: densely pitted cells; p.h.: papilla-like hair; s₁: stoma sectioned parallel to the pore; s₂: stoma sectioned perpendicular to the pore. Phloem dotted, sclerenchyma black, xylem hatched.

enclosed by vascular system. Lateral veins with single collateral bundles. Veins ranging between the following types: 1) minute veinlets composed of a vertical row of 3 or 4 lignified elongated parenchyma cells; 2) minor veins composed of several xylem elements accompanied by ab- and adaxial girders of lignified parenchyma cells with each a small fibre strand and an ordinary parenchyma cell or cristarque cell (defined as cells with a partially thickened and lignified wall containing one or more crystals) linking the fibre strands to the epidermis (fig. 3), and 3) larger veins with well developed xylem and phloem portions separated from abaxial and adaxial sclerenchyma strands by lignified parenchyma; the whole system again linked to the epidermis by ordinary parenchyma cells or cristarque cells (fig. 3). Bundle sheaths hardly or not differentiated. Fibres of strands accompanying vascular system often branched at junction of different veinlets. *Petiole* \pm cylindrical; in transverse section through distal end (fig. 10) supplied with large abaxial crescentiform strand accompanied by two adaxial bundles, at base of petiole (fig. 9) with vascular cylinder enclosing one or two medullary bundles. Vascular system sheathed by collenchyma. *Cristarque cells* with rhomboidal crystals, present in ground tissue of petiole as scattered idioblasts (Plate I: 8), in phloem rays of petiole and in sub-epidermal cells opposite veins (see above). *Glands* similar in anatomy to those described on p. 178 for *Afrostryrax kamerunensis*.

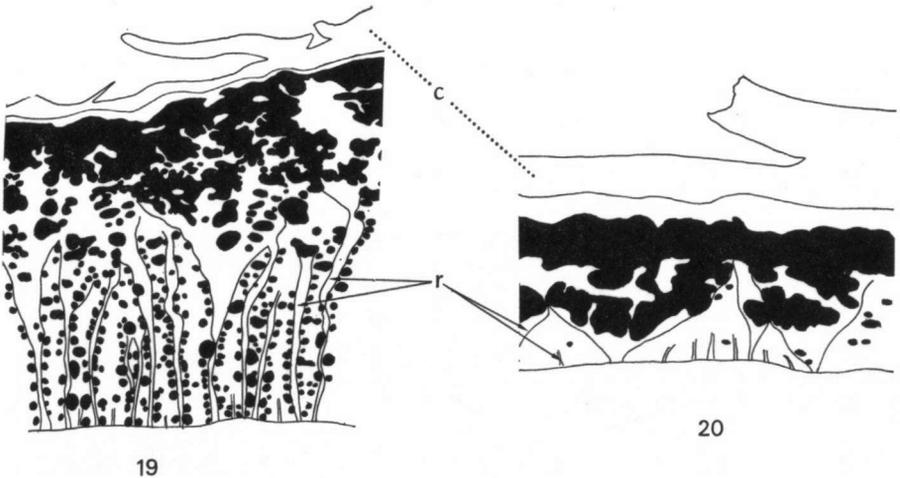
Axis (Table I)

Material: Congo, *Gillardin 355*, *Gillet s.n.*, *Louis 930*. Young twigs 1–4 mm in diameter and twig of 10 mm diameter.

Young twigs rounded-rectangular, older twigs terete. Unicellular hairs as on leaf, infrequent. *Epidermis* of \pm cubical, axially slightly elongated cells, lost in twigs thicker than 3 mm. *Hypoderm* differentiated only in *Gillardin 355*, consisting of cells with adaxially thickened and lignified walls. *Cork* arising in subepidermal layer, composed of cells which are rectangular in transverse and radial section and pentagonal or hexagonal in tangential section, with thickened inner walls. Several cork cells with brown contents. *Cortex* of 5–8 layers of parenchyma cells interspersed with idioblastic cristarque cells (frequency variable). *Endodermis* only distinguishable by a higher proportion of cristarque cells in this layer, followed by a *perivascular cylinder* of a mixture of fibres and brachysclereids, many of the latter crystalliferous. Secondary *phloem* composed of sieve tubes, companion cells, and parenchyma cells, traversed by narrow and broad rays; the latter more or less triangular and for a large part composed of sclerified cells. *Secondary xylem*: *Growth rings* poorly defined or absent. *Vessels* diffuse, mostly solitary but also in radial multiples of 2 or 3, typically more numerous in regions between the corners of the rectangular pith than in regions facing these corners (this only applies to vessel frequency in first formed secondary xylem, not in more peripheral parts of thicker twigs). Vessels round to oval in transverse section, mean tangential diameter of first formed vessels 26–30 μ , mean vessel member length 630 and 640 μ (see also table I). Perforations simple in oblique end walls, except for very scanty scalariform perforation plates in some first formed secondary xylem vessels. Lateral wall pits opposite to alternate, round, oval, or transversely much elongated with horizontal to oblique slit-like apertures; vessel—parenchyma and vessel—ray pits sometimes unilaterally compound. Round pits *c.* 2–3 μ in diameter. Vessel contents absent. *Tracheids* in association with vessel multiples, infrequently present. *Fibres* constituting ground tissue of secondary xylem, with thick walls and minutely bordered to simple pits. *Parenchyma* mainly paratracheal in short irregular bands in first formed secondary xylem; in later formed wood more regularly banded.

TABLE I: Vessel member length in *Hua* and *Afrostryax* (in μ).

Material	twigs		near pith of trunks		peripheral wood (at least 2.5 cm from pith)	
	mean	range	mean	range	mean	range
<i>Hua gabonii</i>						
Gillet s.n.	640	210—860				
Louis 930	630	390—920				
Breteler 6677, upper part of stem			860	560—1130	940	620—1280
ibid. middle part			780	410—960	860	570—1340
ibid. basal part			820	370—1130	880	670—1550
Dechamps 172					750	520—1150
Dechamps 296					740	460—860
Dechamps 363					640	310—800
<i>Afrostryax lepidophyllus</i>						
Devred 2661	430	170—740				
Brookman Amisshah s.n. G.C. 5773			650	390—950	730	580—1030
					770	520—1080
<i>Afrostryax kamerunensis</i>						
Evrard 2838	570	410—750				
Gillardin 176	470	190—720				
Louis 5611	670	460—930	(peripheral part of twig, 1 cm in \varnothing)			
Bos 7155			770	540—1030	620	110—1130
Bos 7287			830	520—1140	710	520—930
Bos 7205			730	540—1080	720	460—1130



Figs 19 and 20. Transverse sections of bark, $\times 17$. — 19. *Afrostryax lepidophyllus*. — 20. *Hua gabonii*. — c: cork; r: rays. Sclerenchyma (stone cells and/or fibres) black.

Rays 12—17/mm at periphery of secondary xylem of material investigated, of two distinct sizes: narrow, mainly uniseriate rays of upright cells, and broad, very tall rays, heterogeneous, composed of square central and upright marginal cells; some sheath cells of central ray portions also upright. *Primary xylem* present in 4 major bundles at corners of the quadrangular pith with a varying number of smaller bundles in between. *Node* trilacunar with one major median bundle and two smaller lateral bundles, split off the vascular cylinder. Lateral bundles forked to supply stipules with one vascular strand each. *Pith* quadrangular in transverse section, composed of parenchyma cells which are isodiametric and polygonal in transverse, rectangular in longitudinal section; cell walls lignified in older twigs. Solitary rhomboidal *crystals* present in varying amounts in cells of cortex, perivascular sclerenchyma, phloem, secondary xylem rays, and pith. The crystalliferous cells include unligified or ligified parenchyma cells, stone cells and cristarque cells. Many of the crystalliferous cells of the pith in longitudinal pairs due to subdivision of a pith cell by a thin transverse wall, and with unilateral lignified wall thickening: 'chambered cristarque cells'.

Bark (Fig. 20)

Material: Gabon, *Breteler 6677* (from stem of c. 5 cm diameter).

General features. Colour very light brownish grey; c. 1—2 mm thick; outer surface partly smooth, partly with narrow longitudinal cracks in periderm.

Microscopic features. *Cork* of many layers of flattened cells with faintly thickened and lignified inner tangential walls, some of the cork cells with brown contents. *Cortex* as in young twigs. *Perivascular cylinder* of mainly brachysclereids and less numerous fibres well developed, c. 0.5 mm thick. Secondary *phloem* of sieve tubes, companion cells, parenchyma, cristarque cells, and small stone cell groups, traversed by narrow and broad rays. Broad rays triangular in transverse section, with strongly sclerified parts obscuring the dilatation pattern of the rays (fig. 20). Solitary rhomboidal *crystals* present in cristarque cells and parenchyma cells of cortex and phloem and in some brachysclereids of the perivascular cylinder and rays. Smaller crystals present in some of the cork cells. Very irregular clusters of variable size also infrequently present in cortex and phloem.

Wood (Plate IV: 1 & 2, Table I)

Material: Gabon, *Breteler 6677* (basal, middle and upper part of stem c. 5 cm in diameter and 1.4 m long); Congo, *Dechamps 172, 296 & 363 ex Tervuren* (samples from thicker stems).

General features. Wood heavy and hard. Colour light brownish yellow. Growth rings faintly demarcated at irregular intervals. Vessels, broad rays, and numerous tangential parenchyma bands visible to the naked eye. Heartwood brown, poorly demarcated from sapwood.

Microscopic features. *Growth rings* indistinct. *Vessels* diffuse, 9—16/mm² in mature wood samples, 32/mm² in periphery of small stem from *Breteler 6677*; solitary and in radial multiples or clusters of 2—5. Ratio solitary vessels to vessel groups ranging from 4:1 (small trunk) — 1:2 (generally 1:1). Vessels round to oval in transverse section (radially elongated); mean tangential diameter 110—165 μ in mature wood, 75 μ in *Breteler 6677*, radial diameter up to 280 μ; walls 4—8 μ thick, mean vessel member length 640—750 μ for mature wood, 860—940 μ for *Breteler 6677* (Table I). Perforations simple in horizontal to slightly oblique end walls. Lateral wall pits alternate. Intervessel

pits round to polygonal, 5–9 μ in diameter with slit-like and \pm horizontal apertures, mostly enclosed within the pit borders, occasionally extending over several pits (coalescent), giving the impression of being vested in vessels with contents. Vessel—ray and vessel—parenchyma pits similar but half bordered, sometimes slightly smaller and occasionally unilaterally compound. *Tyloses* absent. Solid amorphous light brown contents present in some of the heartwood vessels. *Vascular tracheids* associated with some of the vessel multiples, sparsely present. Ground tissue composed of thick-walled fibres with few simple pits which are mainly confined to the radial walls; some minute pit borders present in *Breteler 6677*. Fibres arranged in radial rows which are disturbed by intrusive growth, hexagonal to rounded in transverse section, diameter 20–30 μ , walls 5–15 μ thick; lumina very narrow, mean length 1760–1950 μ . *Parenchyma* in tangential more or less continuous bands in which the vessels are (mostly completely) embedded (confluent paratracheal), bands 1–3 (or 4) cells wide and at variable distance (100–350 μ) from each other; subsequent bands linked through paratracheal parenchyma of some of the radial vessel multiples. Parenchyma strands of 6–12 (mostly 8) cells. *Rays* 9–11/mm, of two distinct sizes: narrow rays 1- or 2 (or 3)-seriate, (1–)3–20 cells high, composed of square to upright cells and broad rays (4 or) 5–15-seriate, up to 3 mm high, composed of mainly procumbent cells with square to upright marginal cells; some square to upright sheath cells also present. Chambered crystalliferous cells in various frequencies present in parenchyma bands, confined to strands touching on fibres. Only part of the cells of a parenchyma strand subdivided into chambers, each with a solitary rhomboidal crystal and wall thickening where touching on the fibres. Prismatic crystals also infrequently present in ray cells. *Silica bodies* absent.

Afrostryax lepidophyllus

Description gives only points of difference with *Hua*.

Leaf (Fig. 16, 17 & 18, Plate II: 2 & 5, III: 3 & 4)

Material: Congo, *Devred 2661*, *Gilbert 10508*, *Louis 350*.

In surface view. Peltate scales covering abaxial surface, with several-celled stalk inserted between a rosette of 6–8 small, often cutinized cells (Plate III: 3 & 4). Scale cells long and fusiform, not subdivided, attached to each other for more than half of their lengths (Plate II: 2). Diameter of scales 120–260 μ . Stellate hairs present on petiole. Short dome-shaped 2- or 3-cellular hairs resembling papillae also present on abaxial surface (Plate III: 4). *Wax* absent. *Epidermal cells* of adaxial surface rectangular to polygonal with anticlinal walls slightly sinuous at high focus and straight at low focus. Outer walls without pit-like structures. Cells overlying veins as in *Hua*. Epidermis of abaxial surface almost entirely composed of specialized cells apart from cells overlying major veins which are similar to those of the adaxial surface. Remainder composed of short papilla-like hairs, scales, subsidiary cells and guard cells of stomata. *Stomata* raised above abaxial leaf surface, very numerous in areolae and over minor veins, scanty over midrib and major veins, paracytic with crescentiform subsidiary cells (Plate III: 3) and low dome-shaped guard cells. T-piece at poles of guard cells inconspicuous. Lumina of guard cells as in *Hua* (fig. 7). Diameter perpendicular to the pore 9–11 μ . *Venation pattern* as in *Hua* (Plate II: 5) but areolae slightly smaller. Glands often absent, if present confined to basal part of lamina as smooth circular or oval areas on abaxial or adaxial surface or along the leaf margin.

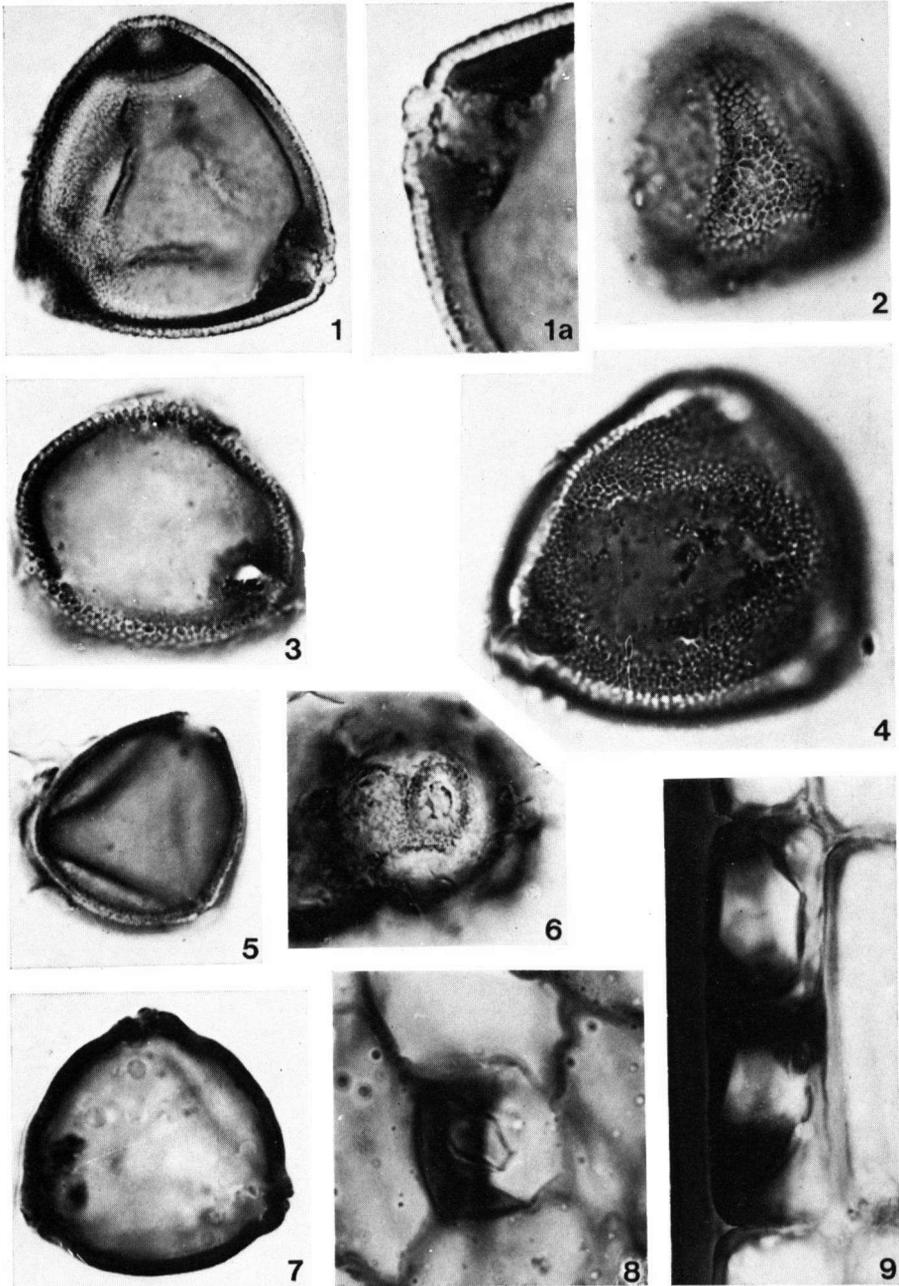


Plate I. 1—4. *Hua gabonii*. — 1. *Klaine 2859*, pollen grain in optical section, x 1000; 1a. *ibid.*, showing pore, operculum and exine layers, x 2000; 2. *Robyns 1441*, polar view showing areolate pattern, x 1000; 3. *ibid.*, poral view, x 1000; 4. *ibid.*, grain without folds in exine, x 1000. — 5 and 6. *Afrostryax kamerunensis*. — 5. *Zenker 3922*, pollen grain in optical section, x 1000; 6. *Gillardii 176*, poral view, x 1000. — 7. *A. lepidophyllus*, *Louis 13883*, pollen grain in optical section showing operculae. — 8. *H. gabonii*, cristaque cell from ground tissue of petiole, x 840. — 9. *A. lepidophyllus*, crystalliferous axial wood parenchyma cells, x 840.

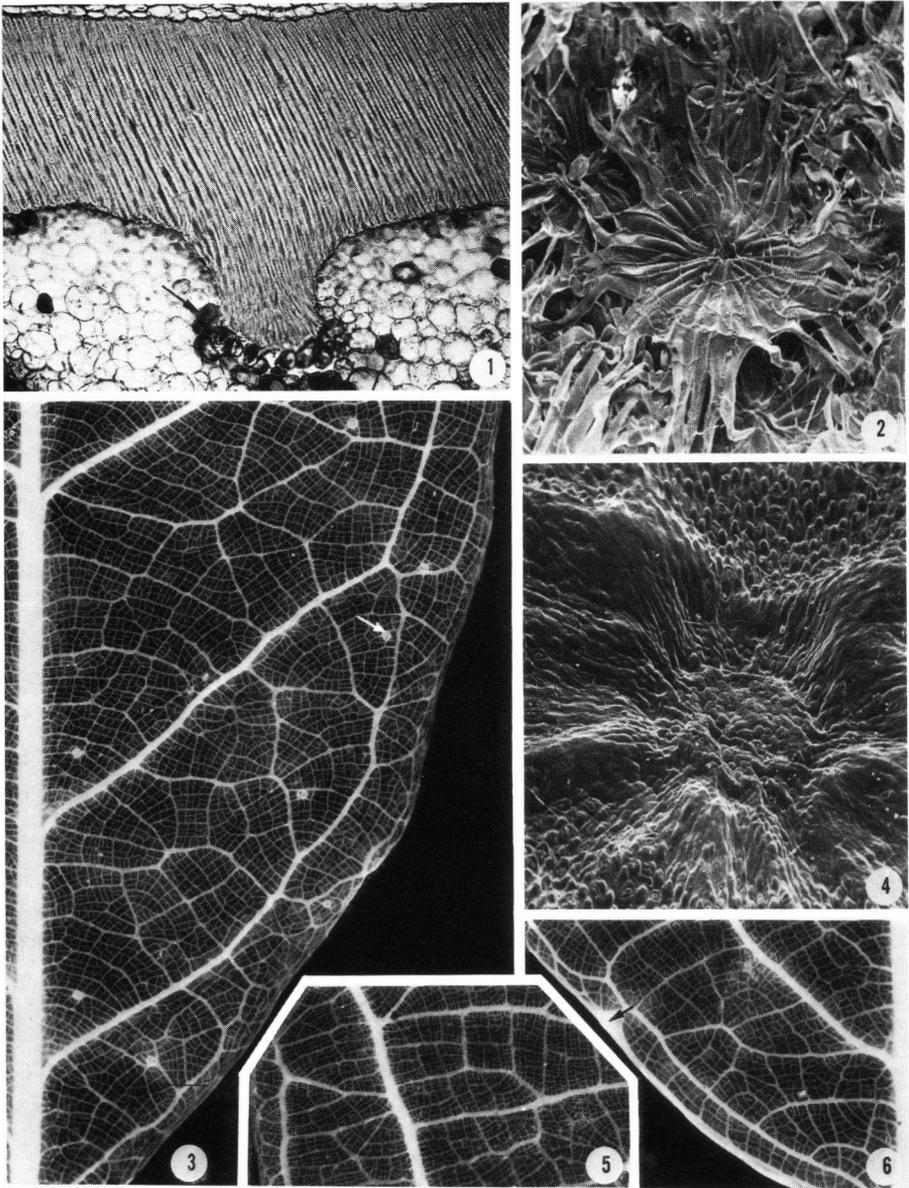


Plate II. 1. *Afrostryax kamerunensis*, section of testa showing palisade layer and cells with dark contents (arrow) in outer testa, x 100. — 2. *Afrostryax lepidophyllus*, leaf scale partly covered with fungal hyphae, S.E.M., x 150. — 3 and 4. *Hua gabonii*. — 3. cleared leaf showing venation and glands (arrow), x 6; 4. detail of crateriform gland, S.E.M., x 100. — 5. *A. lepidophyllus*, cleared leaf, x 6. — 6. *A. kamerunensis*, cleared leaf with marginal gland (arrow), x 6.

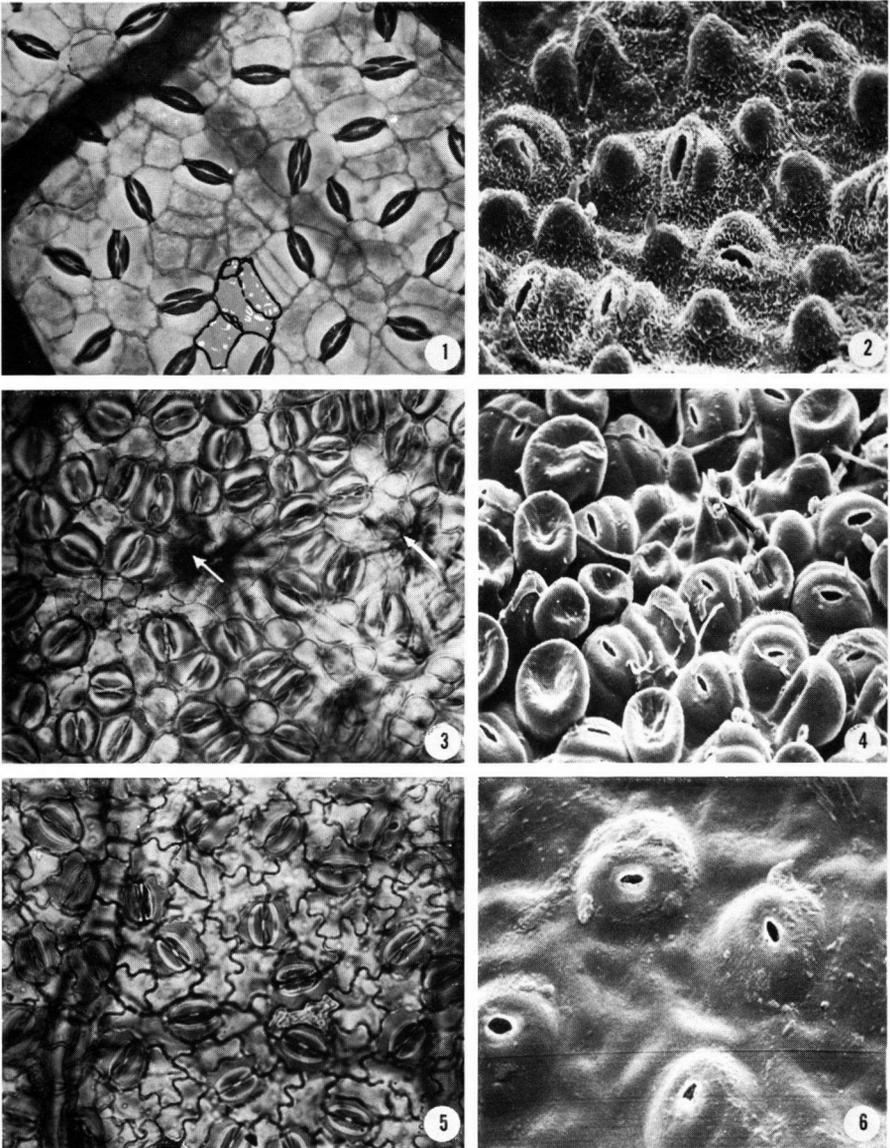


Plate III. Abaxial epidermis as seen with the light microscope (1, 3 and 5; all $\times 420$) and the Scanning Electron Microscope (2 and 4, $\times 500$; 6, $\times 750$). — 1 and 2. *Hua gabonii*; note pit-like structures in unspecialized epidermal cells (partly retouched) in 1, and wax particles in 2. — 3 and 4. *Afrostryax lepidophyllus*; note hair bases (arrows). Fungal hyphae present in 4. — 5 and 6. *A. kamerunensis*.

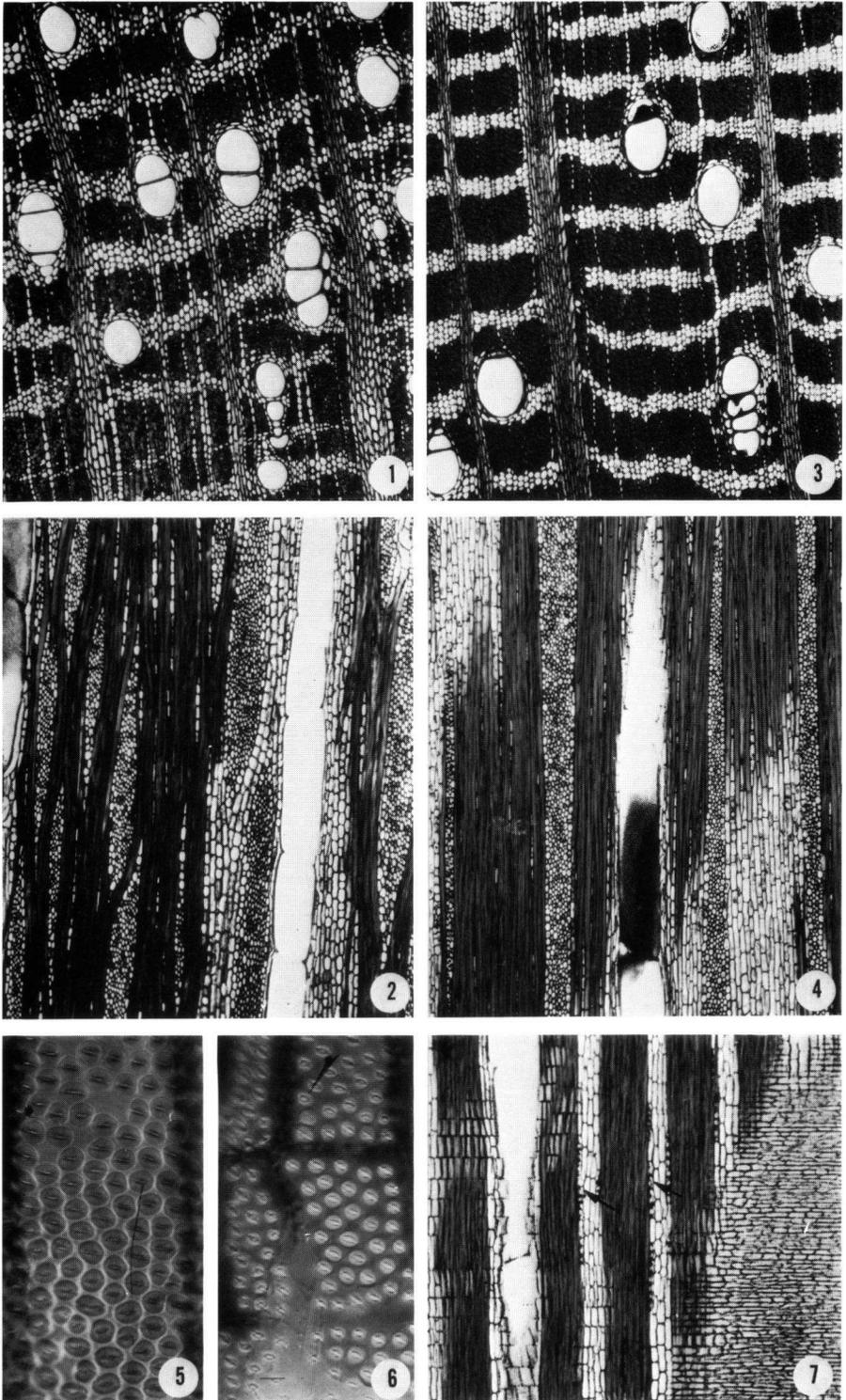


Plate IV. Wood anatomy of *Hua gabonii* (1 and 2) and *Afrostryrax lepidophyllus* (3—7). 1, 2, 3, 4 and 7, x 42; 5 and 6, x 420. — 5. intervessel pits. — 6. vessel—ray pits. — Note crystalliferous parenchyma cells (arrows) in radial section (7).

In transverse section. Cuticle less than $1\ \mu$ thick. Epidermal cells of adaxial surface \pm square, those of adaxial surface papillose or specialized in another way (see above and fig. 7) and smaller than adaxial cells. Outer wall thickness *c.* $2\ \mu$. Guard cells of stomata slightly raised over subsidiary cells; stomatal complex like in *Hua* for other characters (fig. 7). Mesophyll composed of 1 or 2 layers of tall palisade cells, and loose to fairly compact spongy tissue of \pm isodiametric slightly lobed cells. Midrib shallowly grooved or almost flat adaxially, strongly raised above abaxial surface, supplied with a flattened cylindrical vascular system enclosing 2 or 3 medullary bundles; for the rest as in *Hua* (fig. 18). Major lateral veins also provided with a vascular cylinder. Veins of higher order essentially similar to those of *Hua* but differing in the following characters: 1) adaxial girders linking sclerenchyma strands with epidermis taller and composed of several cells of narrow diameter, some of which are cristarque; 2) bundle sheath fairly conspicuous, often containing cristarque cells with the lignified wall thickenings on the side of contact with the vascular bundle. Petiole more or less as in *Hua*, degree of complexity of vascularization variable, e.g. like in fig. 16 and 17. Cristarque cells present in ground tissue of petiole and midrib as scattered idioblasts, in phloem rays of petiole, and in lamina in bundle sheaths and adaxial and abaxial girders linking sclerenchyma strands with the epidermis. Crystals rhomboidal or of irregular shapes, more rarely clustered, mostly confined to cristarque cells. Glands if present similar in anatomy to those of *A. kamerunensis* (p. 178).

Axis (Table I)

Material: Congo, *Devred 2661*, *Louis 350*. Twigs 4 and 7 mm in diameter.

Stellate hairs (of the same type as on the leaves of *A. kamerunensis*) present on young twig. Epidermis, cork, cortex and perivascular cylinder as in *Hua*, tangential wall thickenings of cork cells confined to inner cell layers of periderm, however. Broad rays in secondary phloem not sclerified, accompanied on both sides by groups of fibres surrounded by a sheath of cristarque cells. Secondary xylem \pm as in *Hua*. Vessel multiples of up to 10; frequency of vessels in first formed secondary xylem independent of position with regard to quadrangular pith, mean tangential diameter of first formed vessels 30 and 33 μ , mean vessel member length 430 μ (*Devred 2661*). Mean fibre length 950 μ (*Devred 2661*). Parenchyma more abundant than in *Hua*. Rays 12 and 16/mm respectively.

Bark (Fig. 19)

Material: Congo, *Michelson 281*; Ghana, *Brookman Amisshah s.n.* (bark of young stems *c.* 5 cm in diameter).

General features. Colour light green to brownish grey; *c.* 1—3 mm thick. See also Mildbraed (1913).

Microscopic features. Cork as in *Hua* but adaxial wall thickenings confined to inner cell layers. Some parenchyma cells of secondary phloem with brown contents. Groups of 2—10 fibres sheathed by strands of chambered cristarque cells lining the borders of the broad rays (fig. 19).

Wood (Plate I: 9; IV: 3, 4, 5, 6 and 7, Table I)

Material: Ghana, *Brookman Amisshah s.n.* (stem 5 cm in diameter), Ghana Forest Dept. G.C. 5773, sample from mature tree.

General features. Colour somewhat darker than in *Hua*; growth rings and heartwood not differentiated in material investigated.

Microscopic features. *Vessels* 11 and 12/mm², ratio solitary vessels to vessel groups 2 : 1 (small stem) and 1 : 1 (mature wood), mean tangential diameter 80 μ (small stem) and 145 μ ; radial diameter up to 220 μ , mean member length 730 and 770 μ (Table I). *Vessel contents* infrequently present, also in peripheral secondary xylem. Mean *fibre* length 1890 (small stem) and 2260 μ . In G.C. 5773 peripheral zone with extremely abundant parenchyma noted. *Rays* c. 11/mm, broad rays up to 4.5 mm tall and up to 10 cells wide.

Afrostyrax kamerunensis

Description gives only points of difference with *A. lepidophyllus*.

Leaf (Fig. 8, 13, 14 & 15, Plate II: 6; III: 5 & 6)

Material: Congo, *Evrard 2838*, *Gillardin 176*.

In surface view. Stellate *hairs* (occasionally tending to peltate scales) scarce on adaxial side of leaf base and petiole. Papillae and papilla-like hairs absent. Unspecialized *epidermal cells* with markedly sinuous anticlinal walls (Plate II: 5). Outer anticlinal walls of subsidiary cells also sinuous. Diameter of *stomata* perpendicular to the pore 9–12 μ . *Venation pattern* with more open veinlet endings than in *A. lepidophyllus* (Plate II: 6). *Glands* confined to leaf margin and narrowly oval in outline, mostly larger than those of *A. lepidophyllus* and *Hua*.

In transverse section. *Stomata* in about the same plane as other epidermal cells. Major lateral *veins* only provided with a single vascular bundle. Parenchymatous girders of minor veins shorter than in *A. lepidophyllus* due to the leaf being thinner and containing less cell layers in the *mesophyll*. Bundle sheaths without cristarque cells. Vascular system of *petiole* less complex (fig. 13 & 14). *Glands* similar to those of *Hua* and *A. lepidophyllus*, composed of palisade-like thin-walled epidermis cells. Tissue underlying glandular epidermis composed of several layers of densely packed cells with lignified abundantly pitted walls (fig. 8).

Axis (Table I)

Material: Congo, *Evrard 2838*, *Gillardin 176* and *Louis 5611*. Twigs of 1.5–8 mm in diameter.

In most details similar to *A. lepidophyllus*. Mean *vessel* member length 470–670 μ . Only in *Gillardin 176* few scalariform perforation plates noted.

Bark

Material: Cameroons: *Bos 7155* and *7287* (barks of young trunks, 5 cm in diameter).

Bos 7287 similar in most details to *A. lepidophyllus*; *Bos 7155* exhibiting far less fibre groups in the secondary phloem and therefore resembling the bark of the *Hua* material studied. The amount of differentiated sclerenchyma might be a matter of developmental stage, in spite of the fact that all material studied had approximately the same diameter. More material of *Hua* should be studied in order to assess whether fibre groups differentiate in more mature bark.

Wood (Table I)

Material: Cameroons, *Bos* 7155 (young stem, 5 cm in diameter, sections and macerations), *Bos* 7205 and 7287 (stems 5 cm in diameter, macerations only).

Agrees with *A. lepidophyllus* (young stem, *Brookman Amissah s.n.*) in almost all details. Mean vessel member length 780 μ . Mean fibre length 1720 μ . Peripheral zone with abundant parenchyma (as in *A. lepidophyllus*: G.C. 5773). Rays c. 13/mm, broad rays up to 4 mm high and up to 8 cells wide; in peripheral zone with abundant parenchyma much broader due to conversion of fusiform initials into ray initials.

The Halphen reaction

Material: *Hua gabonii*, Cameroons, seeds collected by the local population for flavouring food (legit *Bretelel*); *Afrostryrax lepidophyllus*, Ghana, *Flora of Gold Coast* 5818 (Coll. *Andoh*).

The Halphen reaction was negative.

Discussion of some of the characters of Huaceae

Ovary. The 5-merous structure of the unilocular ovary in *Afrostryrax* is revealed by its supply of 10 vascular bundles, five of which to be interpreted as fused lateral bundles. In a young ovary of *Hua* I could only trace 3 vascular bundles all on one side of the pentagonal ovary. However, the dehiscence of *Hua* fruits with five valves also suggests a 5-merous structural basis of the ovary. These considerations are of taxonomic importance for comparisons of *Hua* and *Afrostryrax* with putative relatives, since they remove objections against affinities with families showing a 5-carpellary ovary.

Ovule and Seed structure. Bitegmic ovules of which the outer epidermis of the inner integument develops into a sclerenchymatous palisade layer occur in a number of families (Netolitzky), among which are the major families of the *Malvales*. In comparing the seed anatomy of *Hua* and *Afrostryrax* with descriptions by Vaughan (1970) of oil seeds from 50 different families, closest resemblance was found in the seed structure of *Sterculia* (p. 245 l.c.). The layer of palisade cells in *Sterculia*, like in other *Malvales*, exhibits a zone where the lumina of the cells are wider than elsewhere. This zone is absent, however, in the seed of *Hua* and of *Afrostryrax*. The seed structure of *Ricinus* (*Euphorbiaceae*) is also quite *Huaceae*-like. It differs, however, in the presence of vascular tissue in the inner parenchymatous layers of the testa, instead of in the outer layers as is the case in *Hua* and *Afrostryrax*. Unfortunately our knowledge of seed anatomy is still very fragmentary and the use of anatomical characters of the seed for taxonomic purposes can only yield additional suggestions for affinities. If sufficiently known they can serve as well as any other character complex in confirming or denying relationships (see e.g. p. 184 of this paper where *Irvingia* is excluded as a close relative, amongst others because of its seed anatomy).

Pollen morphology. The grains of *Huaceae*, characterized by their three pores, usually provided with operculae and a finely verrucate to scabrate ektexine sculpturing are sufficiently distinct and unusual to offer a character complex of taxonomic significance. In the comparative part pollen characters will be included in the discussion of some putative relatives. Comparisons with pollen from other families have been very limited.

In studying Erdtman's descriptions of representatives of a great number of families, some striking similarities were found with the triporate grains of *Helicteres* (*Sterculiaceae*). In pollen slides, the grains of this genus were also found to have endexinous apertures and an annular endexinous thickening near the pores. Operculae are, however, not differentiated and the tectum is slightly different. No very striking resemblance was found with pollen types of other families described by Erdtman, but conclusions on the grounds of palynology offered here are only tentative because of the very incomplete comparison.

Oltmann recently reported on the pollen morphology of *Hua*, but I disagree with his view that, in addition to the three porate apertures, the grains show six colpi (see p. 167). This also implies that I do not see any reason to link *Huaceae* with *Olacaceae*, as was tentatively suggested by Oltmann. Neither the pollen morphology of this family as described by Erdtman, nor floral morphology or wood and leaf anatomy lend support to this view.

Indument. Edlin (1935) based his exclusion of *Hua* from *Malvales* partly on the simple hairs of *Hua* as contrasted with the typically stellate indumentum of representatives of the *Malvales*. This argument becomes invalid after the observation of some stellate hairs on the leaves of *Hua* (see p. 167) and the abundant occurrence of this hair type in *Afrostryax kamerunensis*. Scales of the type encountered in *A. lepidophyllus* would also be in line with Malvalian affinities, since the *Durioneae* of the *Bombacaceae* and some other *Malvales* exhibit a similar indumentum. The unicellular hairs of *Hua* with one very short and one long arm are similar to those reported by Heinzlmann and Howard for *Icacinaeae*, who called them Icacinaeous hairs because they were typical for a majority of representatives of this family. This hair type also occurs in *Malpighiaceae* and some other families (Metcalf and Chalk; Uphof et al.) where it is intermediate between simple and 2-armed types also occurring in those families.

Glands. Extra floral nectaries have been recorded for 25 families by Metcalfe and Chalk. Those of *Bombacaceae*, *Malvaceae*, and *Sterculiaceae* are different from the glands in *Huaceae*, since they are formed by assemblages of trichomes (see also Schnell, et al.). The glands of *Hua* and *Afrostryax* recall those of *Dipterocarpaceae*, *Euphorbiaceae*, *Malpighiaceae*, *Passifloraceae*, and *Rosaceae* (Schnell et al.) in their anatomy. The haphazard occurrence of these glands throughout the Dicotyledons suggests that they are of restricted taxonomic value in discussions on relationships of higher taxa. However, their structure and occurrence in *Hua* and *Afrostryax* support the mutual affinities between the two genera.

Venation pattern. The very regular venation pattern in the leaves with rectangular areolae, almost all completely surrounded by veinlets, is a very striking character of both *Hua* and *Afrostryax*. In making miscellaneous comparisons and going through Ettinghausen's classical works (1858, 1861) on venation patterns, I could not find any taxon exhibiting the same regular meshwork. The closest approximation was found in *Theobroma* and *Scaphopetalum* of the *Sterculiaceae*. However, there are far more open vein endings and the areolae are larger and have more irregular shapes in these genera than in *Hua* and *Afrostryax*.

Stomata and other epidermal characters. The potentialities and limitations of both light microscopy and scanning electron microscopy for the studies of epidermal structure are well illustrated by Plate III: 1—6. Features such as anticlinal wall undulations, pit-like structures (in *Hua*), and arrangement of subsidiary cells are clearly demonstrated with

light microscopy but do not or hardly show up in S.E.M. studies. On the other hand, the presence of waxy particles in *Hua* could not be demonstrated light-microscopically. The presence of wax was only assessed after the S.E.M. work had revealed the particles (Plate III: 2), by applying local heat to the leaf surface after which a shining patch of melted and resolidified wax became visible.

The taxonomic significance of the type of stomata for comparing taxa of higher rank remains uncertain. In many cases our knowledge is only limited to a few representatives of a given family and for many families several types have been recorded (see also p. 189).

Petiole anatomy and cristarque cells. The similar complex petiole vasculature in both *Hua* and *Afrostryrax* provides an additional argument to regard these two genera as mutually closely related. There are several families in which a more or less similar type of petiole anatomy occurs. Amongst those are *Bombacaceae*, *Sterculiaceae*, and *Tiliaceae* of the *Malvales* (Dehay, 1941; Havez; Herlemont). Mucilage canals almost always present in the petiole of members of those families are, however, absent from *Huaceae*.

Although the cristarque cells of *Hua* and *Afrostryrax* occur in different parts of the plant, they are most conspicuous in the petiole. Metcalfe and Chalk list cristarque cells for only three families: *Melastomataceae*, *Ochnaceae*, and *Scytopetalaceae*. In the course of my studies I also found them in *Bombacaceae* (*Coelostegia*, see Baas 1972), *Irvingiaceae* (or *Irvingioideae* of *Ixonanthaceae*: *Irvingia* and *Klainedoxa*), and *Pandaceae* (*Panda*). Probably they are of more common occurrence than is known at present. Yet their restricted occurrence remains of diagnostic value, and if sufficiently substantiated by other characters their presence in two different taxa may provide additional evidence for mutual relationships as between *Hua* and *Afrostryrax*.

Bark anatomy. The dilatating rays of the bark of *Hua* and *Afrostryrax* are a notable character. Zahur (1959) recorded dilatating rays for 26 families out of 85 investigated. The triangular rays are in *Bombacaceae*, *Malvaceae*, *Sterculiaceae*, and *Tiliaceae* always accompanied by a conspicuous stratification into fibrous and non-fibrous portions of the remainder of the bark tissue and in this respect *Huaceae* differ from these *Malvales*. Moreover, mucilage canals, generally present in Malvalian barks (not in *Elaeocarpaceae* and *Scytopetalaceae*, however) are absent in *Hua* and *Afrostryrax*.

Wood anatomy, vessel member length. The woods of *Hua* and *Afrostryrax* are more or less identical anatomically. They combine some specialized features such as simple vessel perforations, libriform fibres, and confluent parenchyma, with less advanced characters such as heterogeneous rays, long parenchyma strands, and vessel members which are of medium length or moderately long. In table I the measurements for vessel member length are given. Two points are of interest here: firstly that the vessel members of twigs are generally shorter than those of first formed secondary xylem of trunks and, secondly, that in *Afrostryrax kamerunensis* (Bos 7155, 7205 and 7287) the peripheral vessel members of the more mature wood are shorter than the first formed secondary xylem vessel members near the pith. This is a reversal of the trend, always reported in literature, that vessel member length increases from the pith outwards (Bailey and Tupper, and many others). In this respect it is also noteworthy that in peripheral young stem wood of *Hua gabonii* (Breteler 6677) vessel members were found to be considerably longer than in more mature samples (Dechamps 172, 296 and 363). The significance of the great variation in vessel member length in *Huaceae* is not yet fully understood. On some herbarium labels the growth habit of *Hua* and *Afrostryrax* is described as liana-like and the variable

habit of the two genera might account for part of the great plasticity in vessel member length.

The combination of xylem characters of *Hua* and *Afrostryax* plays an important part in the comparative section of this paper, because of the well established taxonomic value of wood anatomical features and the large body of information readily available on this subject for other plant groups.

The Halphen reaction. The negative result of the Halphen reaction for *Hua* and *Afrostryax* has no implications of taxonomic importance. If the outcome had been positive, a very strong indication of Malvalian affinity would have been given (Hegnauer, 1964: 286). The negative result does, however, not imply that *Huaceae* are not related to *Malvales*, since a number of undisputed Malvalian plants also lack the cyclopropene containing fatty acids in their seeds (Blackwell et al.) and are therefore negative for the Halphen reaction (Ivanow, 1927).

Hua and Afrostryax as related genera of the family Huaceae

From the descriptive part an overwhelming resemblance between *Hua* and *Afrostryax* becomes apparent. Apart from the fundamental agreement in macromorphological characters such as the alternate stipulate leaves, 5-merous perianth, 8—10 stamens with 4-celled anthers, unilocular ovary with basal ovule(s) etc., a great number of microscopical characters are shared by both genera.

The more striking shared anatomical characters, constituting at the same time an anatomical diagnosis of *Huaceae*, are the following:

Fruit wall with outer and inner parenchymatous layers separated from each other by a layer of brachysclereids (stone cells). Outer *testa* parenchymatous, supplied with vascular bundles. Inner *testa* with an outer sclerenchymatous palisade layer. *Pollen* triporate and operculate. *Stomata* paracytic. *Petiole* supplied with \pm cylindrical vascular system enclosing medullary bundle(s). *Venation pattern* of regularly arranged veinlets enclosing rectangular areolae. *Leaf glands* with palisade-like epidermis mostly present. *Cristarque cells* present. *Node* 3-trace, 3-lacunar. Solid perivascular sclerenchyma ring present in axis. *Bark* with narrow and broad triangular rays. *Wood* composed of vessels with simple perforations and alternate wall pitting, libriform fibres, banded paratracheal parenchyma and heterogeneous broad and narrow rays.

On the grounds of these shared characters, most of which are by no means of general occurrence within the Dicotyledons, *Hua* and *Afrostryax* must be regarded as closely related to each other. The anatomical resemblance in for instance fruit-, leaf-, and wood anatomy is much greater than often encountered between two genera of — on other grounds — well established mutual affinity. The views of those authors who maintain that *Hua* and *Afrostryax* belong to different families and even orders (Hutchinson; Robyns) must therefore be rejected. Mildbraed's, Hallier's, Chevalier's and Van Steenis' and Bakhuizen van den Brink's suggestions with regard to mutual relationships of the two genera are sufficiently proved by the anatomical evidence.

The differences in external morphology as listed by Chevalier together with those found in anatomical structure can be profitably used for diagnostic purposes. These differences concern type of indumentum, shape of epidermal cells (anticlinal wall undulations), girders of veinlets, and other minor characters (see descriptive part, p. 165—179).

Huaceae compared with other plant groups

In the following a summary will be given of comparisons made with the aid of data from literature and numerous personal observations of representatives of about 50 dicotyledonous families. All families, in the past suggested by several authors as possible relatives, were included and the comparisons were extended to all families of the order to which these families belonged (following the systems of both Hutchinson (1959) and Engler's Syllabus. Some families sharing striking anatomical features with *Hua* and *Afrostryrax* were also compared. From the families compared, only those groups with at least a sensible claim for affinity will be discussed in this paper. Families which have been loosely brought into connection with *Hua* and *Afrostryrax*, as for instance *Icacinaceae*, *Olacaceae* and *Opiliaceae* (Chevalier) have been considered but they offer too little resemblance to be elaborately discussed. Comparisons with data from literature have often been restricted to textbooks like Engler's Syllabus (1964), Erdtman (1952), Hutchinson (1959), Metcalfe and Chalk (1950), Netolitzky (1926), Solereder (1899, 1908) and Vaughan (1970). Additional anatomical monographic treatments have also been consulted. As far as possible the comparisons have been extended to microscopical slides of leaves, twigs, and wood from representatives of the families concerned. The slide collections of the Jodrell Laboratory, Kew; the Forest Products Laboratories at Princes Risborough; the Forestry School at Oxford; the Institute for systematic Botany, Utrecht, and the Rijks-herbarium, Leiden, have been extensively consulted for this purpose.

As with all comparative studies based on microscopical characters, conclusions cannot be definite, since the majority of species and a considerable number of genera, particularly from the large families, have never been studied. It can only be hoped that in considering both anatomical characters and macromorphological features these gaps in our knowledge will be more or less compensated for.

I have often used family names for disputed small groups. This has been done for practical reasons only and does not reflect any personal opinion about the family rank of these groups.

Perkins' and Chevalier's View: *Styracaceae* and related families.

Perkins (1909) and Chevalier were struck by the resemblance of the seed structure and the stellate indumentum of *Afrostryrax kamerunensis* with that of *Styracaceae*, and therefore put the genus into that family. The number of characters in *Huaceae*, differing from those in *Styracaceae* is, however, substantial. The differences listed below remove any ground for regarding *Afrostryrax* or *Huaceae* as a whole to be related to *Styracaceae*.

<i>Huaceae</i>	<i>Styracaceae</i>
Stipules present	Stipules absent
Corolla choripetalous	Corolla sympetalous
Pollen 3-porate	Pollen 3-colporate
Stomata paracytic	Stomata anomocytic
Venation pattern with rectangular areolae	Venation pattern different
Petiole vasculature complex	Petiole vasculature relatively simple
Node trilacunar	Node unilacunar
Cristarque cells present	Cristarque cells absent
Cork arising in subepidermis	Cork arising in pericycle

Vessel perforations simple
Xylem parenchyma banded

Vessel perforations mainly scalariform
Xylem parenchyma diffuse or in narrow
lines

Styracaceae are in most systems included in *Ebenales* together with *Sapotaceae*, *Sarcospermataceae*, *Ebenaceae*, *Lissocarpaceae*, *Symplocaceae*, and *Hoplostigmataceae* (Engler's Syllabus). Hutchinson maintains a smaller order *Styracales*. Neither the gross morphological characters nor the anatomical structure of the representatives of those families recall *Huaceae*, so that affinities with *Ebenales* s.l. are most unlikely.

Hallier's and Hutchinson's suggestions: *Linaceae* s.l. and *Malpighiales*.

Hallier's brief statement that together with *Monotes* and *Marquesia*, *Hua* and *Afrostryrax* are more or less intermediate between *Linaceae* s.l. (*Houmiriaceae*), and *Dipterocarpaceae* and *Tiliaceae*, and Hutchinson's placement of *Hua* near *Erythroxyloaceae*, both imply an affinity of *Huaceae* with a group of families included in the *Malpighiales* by Hutchinson and in the *Geraniales* in Engler's Syllabus. A brief summary of elaborate comparisons made with all families included in the *Malpighiales* by Hutchinson is given below.

Malpighiaceae do not recall *Huaceae* in their external morphology; differences in anatomy may be exemplified by the simple vasculature of the petiole, the arrangement of xylem parenchyma, and the usually narrow rays in *Malpighiaceae*. *Houmiriaceae* differ substantially from *Huaceae* in their floral characters; their anomocytic or diacytic stomata, secondary xylem with scalariform vessel perforations and fibre tracheids also provide evidence that the two families are not mutually related.

Linaceae s.s. (excluding *Ixonanthaceae*, *Ctenolophonaceae*, *Houmiriaceae* etc.) show a number of differences in both floral structure and vegetative anatomy. The most important anatomical criteria by which the family can be distinguished from *Huaceae* are the relatively simple petiole vascularization and the occurrence of fibre-tracheids in the secondary xylem. The parenchyma distribution and ray structure are also never quite as in *Huaceae*, though *Hugonia* shows some superficial histological resemblance in its wood. The pollen grains of *Linaceae* are very different from those of *Huaceae*.

Irvingiaceae, included in *Ixonanthaceae* or even in *Simaroubaceae* (*Rutales*) by several authors, have flowers which do not resemble those of *Huaceae*; their vegetative anatomy, however, offers a great number of characters in common: cristarque cells occur in *Irvingia malayana* Oliver (original observation), stomata are also paracytic, and the wood of *Irvingia* and *Klainedoxa* resembles that of *Huaceae* quite strongly, except for the absence of very broad rays such as occur in *Hua* and *Afrostryrax* (see Webber). Major differences of *Irvingiaceae* with *Huaceae* are the absence of medullary vascular bundles in the petiole, the 3-colporate pollen grains, and the arrangement of tissues in the testa (Vaughan).

Ledocarpaceae, usually included in *Geraniaceae*, do not recall *Huaceae* in floral, pollen, and vegetative anatomical characters.

Erythroxyloaceae, stated by Hutchinson to be the closest relative to be found for *Hua* not only differs from the latter genus and *Afrostryrax* in a number of floral characters, but also lack any resemblance in vegetative anatomy. *Erythroxyloaceae* do not have a closed vascular cylinder with medullary bundles in the petiole, they possess cortical bundles in the axis, and have a different type of parenchyma distribution, ray structure, and vessel—ray pitting in the secondary xylem. The pollen is also very different.

Ctenolophonaceae, often included in *Linaceae* but very different from that family in wood anatomy and pollen type (Metcalfe and Chalk; Erdtman), have primitive xylem

characters such as scalariform vessel perforations and fibre-tracheids. No characters from vegetative anatomy, nor from floral morphology recall *Huaceae*.

Lepidobotryaceae are anatomically very imperfectly known. The description given by Metcalfe and Chalk (1950) does not recall *Huaceae*, nor do external morphological characters. *Balanitaceae* also differ widely in gross leaf and flower morphology. The wood is also different in its storied parenchyma and exclusively broad rays. *Zygophyllaceae* have anisocytic stomata, wood with generally storied structure, fibre-tracheids, and narrow homogeneous rays, and show many differences in external morphology with *Huaceae* as well.

The *Malpighiales*, as understood by Hutchinson and discussed above in relation to *Huaceae*, present anatomically a very heterogeneous assemblage and it is therefore impossible to deny any affinities with the order on the grounds of anatomical characters. Each family considered separately, however, is sufficiently different from *Huaceae* to deny close affinity. It is significant in this respect to stress that *Erythroxylaceae*, placed close to *Hua* by Hutchinson, show no affinities in anatomical structure at all. *Irvingiaceae*, treated in another order (*Rutales*) by other authors, show some rather striking resemblances in leaf and wood anatomy. The great differences in external morphology, seed anatomy, and pollen type, however, suggest incidental convergence of some characters rather than phylogenetic relationship.

Following the system given in Engler's Syllabus, Hallier's and Hutchinson's suggestions would also validate a comparison with *Limnanthaceae*, *Oxalidaceae*, *Geraniaceae*, *Tropaeolaceae*, *Euphorbiaceae*, and *Daphniphyllaceae*, all included in *Geraniales*. Such comparisons are however, beyond the intentions of the two latter authors, and discussions of the results from these comparisons will therefore be very limited. *Limnanthaceae*, *Oxalidaceae*, *Geraniaceae* and *Tropaeolaceae* are very unlike *Huaceae*; the same applies to *Daphniphyllaceae* which are characterized by a primitive wood structure. It is difficult to deny any relationships with *Euphorbiaceae* on the grounds of anatomical characters because this family is very heterogeneous in both leaf and wood anatomy. Several characters that occur regularly in *Euphorbiaceae* like the type of glands, petiole vascularization (Dehay 1935), and seed anatomy are shared by *Hua* and *Afrostryax*. Wood anatomical characters of *Huaceae* if taken one by one, can be retraced in different genera of the *Euphorbiaceae*, but a similar over-all histology has not been encountered in any representative of the latter family. Differences in wood anatomy taken together with the great differences in floral morphology therefore invalidate a close relationship between the two families.

Hallier's further suggestion of a relationship of *Hua* and *Afrostryax* with *Marquesia* and *Monotes* of the *Dipterocarpaceae* is not supported by anatomical characters such as the uniseriate rays and the parenchyma distribution in the wood of the latter genera (Bancroft). The pollen of *Monotes* with its colporate apertures is also different. Characters of other *Dipterocarpaceae* also do not recall *Huaceae*. Possible connections with *Tiliaceae*, implied in Hallier's suggestion, will be discussed on p. 188.

Summing up, only two families from *Malpighiales* as conceived by Hutchinson or from *Geraniales* as treated in the Engler's Syllabus, viz. *Euphorbiaceae* and *Irvingiaceae*, show a number of striking characters shared with *Huaceae*. The characters in common are, however, outweighed by points of difference, so that a close phylogenetic relationship seems most unlikely (see also table II).

Pierre's view: *Sterculiaceae* and other *Malvales*.

Pierre's original placement of *Hua* in *Sterculiaceae*, and the suggestion repeatedly put forward from that time, of a Sterculiaceous affinity for *Hua* and *Afrostryax* (Mildbraed,

TABEL II: Occurrence of some characters of Huaceae in other families, mainly Malvales.

Characters of Huaceae	Family	n	Number of shared characters
	Bombacaceae	15	6 (11)
	Cochlospermaceae	15	3
	Elaeocarpaceae	15	3 (6)
	Malvaceae	15	4 (7)
	Sphaerosepalaceae	15	3 (5)
	Sarcolaenaceae	14	2 (4)
	Scytopetalaceae	15	5
	Sterculiaceae	15	6 (13)
	Tiliaceae	15	5 (6)
	Euphorbiaceae	15	4 (8)
	Irvingiaceae	14	5 (6)
ovary unilocular			—
placentation basal			—
ovule bitegmic and seed with palisade layer			+
pollen triporate			(+)
scales or star-shaped hairs			+
stomata paracytic			(+)
venation pattern			—
crystal cells			(+)
petiole vasculature			+
mucilage cavities absent			—
dilatating bark rays			+
libriform fibres			+
parenchyma paratracheally banded			(+)
broad and narrow rays			(+)
chambered crystalliferous cells			+

— = character absent; + = character present in most representatives of the family; (+) = character present in a few representatives only; ± = tendency to be similar in this character; ? = no data available. n = number of characters recorded. Under 'number of shared characters' the figure between brackets represents the total number of +, (+) and ± characters.

1913; Normand and Chatelet, 1955, and Van Steenis and Bakhuizen van den Brink, 1967) induced me to make elaborate comparisons of *Huaceae* with *Sterculiaceae* and other *Malvales*. *Malvales* are taken here in the broadest sense, including *Bombacaceae*, *Dirachmaceae*, *Elaeocarpaceae*, *Malvaceae*, *Peridaceae*, *Sarcolaenaceae* (= *Chlaenaceae*), *Scytopetalaceae*, *Sterculiaceae*, and *Tiliaceae*, together with *Cochlospermaceae* and *Sphaerosepalaceae* (= *Rhopalocarpaceae*) which have been linked with *Malvales* in recent years (Capuron, 1962; Huard, 1965; Keating 1968, 1970). This concept of the order *Malvales* does not reflect any personal opinions but has been adopted for practical reasons in order to avoid the possibility that a putative relative of *Huaceae* might be missed out from the comparisons.

Elaeocarpaceae show a great number of differences in external morphology from *Huaceae*. Anatomically they do not recall *Huaceae* either. Paracytic stomata have not been recorded for the family and the parenchyma distribution in the wood is never in confluent bands. The pollen is also different.

Scytopetalaceae, again very different in external morphological characters, differ from *Huaceae* anatomically by the anisocytic stomata (original observation), the simple petiole vasculature, the sclereids in the leaf mesophyll, the occurrence of both scalariform and simple vessel perforation plates in the mature wood, the large and simple vessel—ray pits, and the axial parenchyma distribution in narrow lines. However, one very unusual character, the presence of cristarque cells, is shared by the two families.

Sphaerosepalaceae (= *Rhopalocarpaceae*) have been described anatomically by Boureau and by Huard, who considered them to be closely related to *Malvales*, particularly *Sterculiaceae*. In order to extend Huard's observations on leaf anatomy of the family some original observations were made on material of *Dialyceras parvifolium* R. Cap. (18126 S.F.), *Rhopalocarpus louvellii* (Danguy) Cap. (27563 S.F.), *R. lucides* Boj. (*Lam & Meeuse* 6116), and *R. triplinervius* Baill. (22963 S.F.) all from the Rijksherbarium. It appeared that the petiole anatomy shows an even greater range of vascular patterns than in the material described by Huard. *R. triplinervius* shows a closed vascular ring including three concentric (amphivasal) medullary bundles in a horizontal plane whilst the other species investigated by Huard and me have a closed or strongly incurved vascular strand without additional bundles. Stomata, imperfectly described by Huard, were found to be distinctly anisocytic in *Dialyceras parvifolium* and predominantly anomocytic (occasionally tending to anisocytic) in *Rhopalocarpus*. The seed structure of *Rhopalocarpus* (Capuron), though complex through rumination, is fundamentally similar to that in *Huaceae*, having a parenchymatous outer testa supplied with vascular bundles separated from the inner soft tissue by a layer of thick-walled sclerenchymatous palisade cells. Though I could not study the ontogeny in *Rhopalocarpus*, it seems likely that this palisade layer also originated from the outer epidermis of the inner integument, because of its position within the testa.

The wood of *Sphaerosepalaceae* (Boureau; Huard) is rather similar to that of *Scytopetalaceae* (e.g. narrow wavy parenchyma bands) and does therefore not recall that of *Huaceae*. The differences between *Sphaerosepalaceae* and *Huaceae* in both floral structure and vegetative anatomy suggest therefore the absence of close affinities between the two families. It may be mentioned in passing, that the original observation on the anatomy of *Sphaerosepalaceae* mentioned above, support Huard's and Capuron's view of a Malvalian affinity of that family.

Dirachma, formerly included in *Geraniaceae* but raised to family rank by Hutchinson and placed in his *Tiliales*, is at present under my investigation. Neither its floral morphology nor its leaf or wood anatomy recall *Huaceae*.

Peridiscaceae, recognized by Hutchinson as a distinct family in his *Tiliales*, are also very different in external morphology and vegetative anatomy (e.g. in wood with scalariform vessel perforations). *Peridiscus* and *Whittonia*, their constituent genera, are often regarded as related to *Flacourtiaceae* (Sandwith; Metcalfe).

Cochlospermaceae, treated by several authors as belonging to the *Parietales*, *Bixales*, or *Violales*, have been investigated in detail by Keating (1968, 1970) who regarded them as more closely related to *Sterculiaceae* and *Tiliaceae* than to *Cistaceae*, *Flacourtiaceae*, and *Violaceae*. Characters such as anisocytic stomata, the presence of mucilage canals, wood with very short elements, and apotracheal very thin-walled parenchyma, together with gross morphology exclude close relationships of this family with *Huaceae*.

Sarcolaenaceae (= *Chlaenaceae*), a family of much disputed affinities (Capuron, 1970, Cavaco, 1952 and the literature cited by them) differs from *Huaceae* in several characters of floral morphology. Anatomically the anomocytic stomata, the presence of mucilage cells, and the wood with diffuse apotracheal parenchyma and exclusively solitary vessels and uniseriate rays, do also not indicate a close relationship with *Huaceae*. The anatomy

of the petiole and midrib is, however, very similar to that in *Hua* and *Afrostryax* (Dehay 1957). The indumentum may consist of various hair types and also recalls *Huaceae*. Cavaco (1950) illustrated a *Hua*-like 2-armed hair, and the peltate scales recall those of *Afrostryax lepidophyllus*.

With *Tiliaceae*, *Bombacaceae*, *Sterculiaceae*, and *Malvaceae* we arrive at a group of *Malvales* anatomically characterized by the presence of mucilage cells or cavities and stratified secondary phloem with triangular broad rays. This typically Malvalian character complex is also present in *Cochlospermaceae* and *Sphaerosepalaceae* but is absent from *Elaeocarpaceae*, *Dirachmaceae*, and *Scytotetalaceae*. For *Peridiscaceae* and *Sarcoalaenaceae* no data are available. *Huaceae* differ from the former undisputed Malvalian families in the absence of mucilage cells or cavities and also lack a stratification of the phloem into soft and fibrous portions. The dilatation in the broad phloem rays is, however, like that in the majority of *Malvales*.

Tiliaceae are recorded by Metcalfe and Chalk as having anomocytic stomata. The wood anatomy of the family is rather variable and accordingly it is possible to find many of the characters of *Huaceae* wood also in scattered members of the *Tiliaceae* a combination of broadly banded paratracheal parenchyma, very broad and narrow rays has, however, not been encountered in the latter family. The anatomy of the petiole also varies considerably within *Tiliaceae* but closed vascular cylinders with included medullary bundles as in *Huaceae* do occur in many representatives (Herlemont).

In *Bombacaceae* the anatomy of the petiole and the presence of peltate scales in several genera recall *Huaceae*. The stomata are recorded as predominantly anisocytic (Inamdar and Chohan; Baas, 1972) in the few taxa investigated, but anomocytic and paracytic types also occur, even in the same specimens. In *Catostemma* they are exclusively paracytic (Fryns-Claessens and Van Cotthem). In *Coelostegia* I found cristarque cells of the same type as in *Huaceae* (Baas, 1972). The wood anatomy of *Bombacaceae* is different from that in *Huaceae* because it either shows a storied structure, tile cells, or a parenchyma distribution in very narrow lines, or a combination of these characters. The general histology in *Catostemma* and to a lesser extent in *Scleronema* recalls *Huaceae*, however. *Catostemma* wood differs from the latter in its large vessel parenchyma pits, scarcity of narrow rays, and the length of the parenchyma strands (4 cells). In *Scleronema* not all the parenchyma is banded but it is also partly in thin vasicentric sheaths, and the vessel—parenchyma pitting is large and simple. *Bombacaceae* seeds have, as those of *Huaceae*, a palisade layer corresponding to the outer epidermis of the inner integument; this layer, however, shows a light line due to local widening of the lumina. *Bombacaceae* are eurypalynous but the pollen of some representatives faintly recalls *Huaceae* (Fuchs). Though the floral characters, particularly of the ovary, are not suggestive of close affinities of *Bombacaceae* with *Huaceae* a substantial number of characters are shared by some representatives of *Bombacaceae* and *Huaceae* (table II) which might indicate a remote phylogenetic relationship.

Malvaceae have many anatomical characters in common with *Bombacaceae* and therefore provide no new clues in the discussion of affinities of *Huaceae*. Where *Malvaceae* deviate from *Bombacaceae* both in floral characters and vegetative anatomy, this usually concerns features which indicate that, if related at all, the *Malvaceae* are more remote from *Huaceae* than are *Bombacaceae*.

Sterculiaceae, most frequently mentioned as possible relatives of *Huaceae*, differ together with the three above mentioned families in bark anatomy, presence of mucilaginous elements, and merousness of the ovary, from *Hua* and *Afrostryax*. There is a noteworthy exception in *Sterculiaceae*, however. The ovary of *Waltheria* is unilocular and has two

lateral ovules of which the lower one is in an almost basal position and develops into the only seed (Hallé). I have suggested (p. 179) that the unilocular ovary in *Huaceae* can be interpreted as a 5-carpellary structure. This would remove objections to linking *Hua* and *Afrostryrax* with families where the gynoeceum is usually 5-merous like *Sterculiaceae*. Peculiar petals like those in *Hua* occur in many *Buettnerieae* (Leinfellner). The seed anatomy of some commercially important *Sterculiaceae* is fairly well known (Vaughan, and literature cited therein) and the structure of the testa is essentially similar to that of *Huaceae* (p. 179). The pollen of *Helicteres* (*Sterc.*) is also in some respects similar to that of *Huaceae* (p. 180). Stomata of *Sterculiaceae* are imperfectly known, but are on record as predominantly anisocytic. Paracytic stomata occur, however, in *Reevesia*. Scales as in *Afrostryrax lepidophyllus* occur in many *Sterculiaceae* taxa. Mucilage cells and cavities are recorded as being absent in some species of *Sterculiaceae* by Solereder (1899 and 1908). The petiole in many *Sterculiaceae* has a vascular supply which is very similar to that in *Huaceae* (Dehay, 1941). A venation pattern more or less like that of *Hua* and *Afrostryrax* has been encountered in *Scaphopetalum* and slightly less so in *Theobroma* (p. 180).

The wood anatomy of most *Sterculiaceae* is different from that of *Huaceae* because of the occurrence of a storied structure in most of the genera, or of the presence of tile cells in the rays. Parenchyma distribution and ray structure are extremely variable within the family, and *Hua* and *Afrostryrax* could fall within the range of variation as far as these characters are concerned (Chattaway; Metcalfe and Chalk). Parenchyma strands of up to 8 cells or more are, however, most uncommon within *Sterculiaceae*. Chattaway has described the structure of the chambered crystalliferous cells in *Sterculieae* and recorded the occurrence of extra wall thickenings, similar to those in *Huaceae*. Lateral vessel wall pitting of *Huaceae* also agrees with that in most *Sterculiaceae*. In conclusion, the wood anatomy of *Huaceae* agrees fairly well with that of some *Sterculiaceae* (including *Buettnerieae*) but it has retained more primitive characters like the rudimentary scalariform perforations in the first formed secondary xylem, the longer vessel members in mature wood, and the parenchyma strands of more cells. Highly specialized features, such as tile cells and storied structure present in *Sterculiaceae* but absent from *Huaceae*, also favour this conclusion.

It is no coincidence that in this part comparisons of *Huaceae* with *Sterculiaceae* have been more elaborate than with any other family. This is because in this family one can find the highest number of characters shared with *Huaceae*. It should be stressed here, however, that the characters in common are by no means of constant occurrence in all members of *Sterculiaceae* and that they are scattered over different representatives of the family. Hence it is impossible to indicate a group within *Sterculiaceae* to which *Huaceae* are most closely related.

In table II some selected characters are listed for families which might claim some affinity on the grounds of the comparisons discussed above. *Sterculiaceae* rank highest in the number of characters shared with *Huaceae*. However, it is obvious that *Huaceae* are different from this family in a number of other characters such as its free basal placentation, absence of mucilage cavities, its unstratified phloem, and the typically longer vessel members and xylem parenchyma strands. These differences and the fact that no representatives of *Sterculiaceae* could be found where most of the shared characters occurred in combination, convinced me that *Huaceae* form a distinct family. The occurrence of some other characters, typical for *Huaceae*, in the remaining *Malvales*, e.g. cristarque cells in *Bombacaceae* and *Scytopetalaceae*, paracytic stomata in *Catostemma*, \pm basal ovules in *Sphaerosepalaceae*, the absence of mucilage cavities in a Malvalian family like *Elaeocarpaceae* etc. etc., support the inclusion of *Hua* and *Afrostryrax* in *Malvales s.l.*

In comparing *Huaceae* with a number of families from different orders which suggested themselves because of the occurrence of one or two characters in common (see p. 179—182) no group was found with a better coincidence of shared features than the families listed in table II or discussed in the foregoing comparative part. It is also because of these negative reasons that I propose to keep *Huaceae* within the order *Malvales*, in spite of the considerable differences that separate *Hua* and *Afrostryax* from each of its constituent families.

GENERAL CONCLUSIONS

Vegetative anatomy, fruit and seed anatomy, and pollen morphology clearly demonstrate that *Hua* and *Afrostryax* are closely related genera, definitely belonging to the same family. These microscopical character complexes make it also possible to deny relationships with *Styracaceae* and *Erythroxylaceae* and several other families suggested by different authors as close relatives. No family could be found with enough micro- and macro-morphological characters in common with *Hua* and *Afrostryax* to justify the inclusion of the two genera in such a family. Of all the plant groups compared, *Sterculiaceae* show most resemblance with *Huaceae*. Several unusual characters of *Huaceae* occur; moreover, in some other scattered representatives of the *Malvales*. These resemblances suggest a fairly loose Malvalian affinity. As with the inclusion in this order of other, slightly aberrant families such as *Cochlospermaceae*, *Sarcolaenaceae*, *Scytopetalaceae*, and *Sphaerosepalaceae*, the boundaries of *Malvales* become vaguer through the addition of taxa with new characters more typical for other plant groups. A more positive conclusion on the relationships of *Huaceae* will not depend on the study of more material of *Hua* and *Afrostryax* but on the availability of more comparable data from other plant groups of the Dicotyledons.

ACKNOWLEDGEMENTS

This subject was suggested by Dr. C. R. Metcalfe (Kew) following an enquiry from Dr. R. Melville about the anatomical affinities of *Hua*. After a preliminary study of leaf and twig material the former concluded that the anatomical evidence pointed rather vaguely to an affinity of *Hua* with *Sterculiaceae*, although he hesitated to place it there unless the exomorphic characters lent strong support (quoted from a letter to Dr. Melville, February, 1968). I am greatly indebted to Dr. Metcalfe for putting this information at my disposal. It is noteworthy that even after much more material has been studied, my rather vague conclusions can hardly be more positive than his tentative suggestion.

Thanks are due to those institutions and persons who provided material of *Hua* and *Afrostryax* or gave access to their slide collections (see p. 163, 183). Helpful discussions with Dr. W. A. van Heel (floral anatomy), Mr. J. Muller (palynology), Dr. N. Parameswaran (Hamburg, bark anatomy) and Dr. L. Rüffle (Berlin, leaf venation) are gratefully acknowledged. Miss D. M. Catling, (London) kindly sectioned part of the wood samples, and Dr. H. W. L. Ruigrok carried out the Halphen reaction. I am particularly indebted to Mr. J. Isings of the Microscopy Department T.N.O., Delft, for giving access to the Scanning Electron Microscope and to Miss R. Hooftman for operating the instrument. This study was carried out under the supervision of Prof. Dr. C. G. G. J. van Steenis. Thanks are due to him, Prof. Dr. W. K. H. Karstens, and Mr. H. K. Airy Shaw for critically reading the manuscript.

REFERENCES

- BAAS, P. 1970. Anatomical contributions to plant taxonomy I. Floral and vegetative anatomy of *Eliaea* from Madagascar and *Cratoxylum* from Indo-Malesia (Guttiferae). *Blumea* 18: 369—391.
- 1972. The vegetative anatomy of *Kostermansia malayana* Soegeng. *Reinwardtia* 8: 335—344.
- BAILLY, I. W., & W. W. TUPPER. 1918. Size variations in tracheary cells, I. *Proc. Amer. Acad. Arts Sci.* 54: 149—204.
- BANCROFT, H. 1935. Material of *Marquesia acuminata* from Northern Rhodesia. *Kew Bull.* 10: 559—568.
- BEIJERSBERGEN, A. 1972. Note on the chemotaxonomy of Huaceae. *Blumea* 20: 160.
- BLACKWELL, J., J. A. CORNELIUS & T. W. HAMMONDS. 1966. Examination of *Theobroma cacao* fat for the presence of cyclopropanoid acids. *Chemistry and Industry* 1966: 769.
- BOURBAU, E. 1958. Contribution à l'étude anatomique des espèces actuelles de Ropalocarpaceae. *Bull. Mus. Nat. Hist. Nat.* 30: 213—221.
- CAPURON, R. 1962. Révision des Rhopalocarpaceae. *Adansonia* 2: 228—267.
- 1970. Observations sur les Sarcolaenacées. *Adansonia* 10: 247—265.
- CAVACO, A. 1950. Sur une espèce nouvelle de Sarcolaena (Chlaenaceae) et sur sa structure vasculaire foliaire. *Bull. Soc. Bot. Fr.* 97: 95—97.
- 1952. Recherches sur les Chlaenaceae, famille endémique de Madagascar. *Mém. Inst. Sci. Madag. sér. B*, 4: 59—92.
- CHATTAWAY, M. M. 1937. The wood anatomy of the family Sterculiaceae. *Philos. Trans. Roy. Soc.* 228: 313—366.
- CHEVALIER, A. 1947. La famille des Huacaceae et ses affinités. *Rev. Int. Bot. Appl. Agric. Trop.* 27 (No. 291—292): 26—29.
- CRONQUIST, A. 1968. The evolution and classification of flowering plants.
- DEHAY, CH. 1935. L'Appareil libéro-ligneux des Euphorbiacées. *Ann. Sci. Nat. b. sér.* 10, 17: 147—290.
- 1941. L'Appareil libéro-ligneux foliaire des Sterculiacées. *Ann. Sci. Nat. b. sér.* 11, 2: 45—131.
- 1957. Anatomie comparée de la feuille des Chlaenacées. *Mém. Inst. Sci. Madag. sér. B*, 8: 145—203.
- EDLIN, H. L. 1935. A critical revision of certain taxonomic groups of the Malvales I. *New Phytol.* 34: 1—20.
- ENGLER, A. (ed. H. Melchior) 1964. *Syllabus der Pflanzenfamilien*, 12th ed.
- & E. GILG, 1919. *Syllabus der Pflanzenfamilien*, 7th ed.
- & K. KRAUSE. 1911. *Sterculiaceae africanae* V. *Bot. Jahrb.* 45: 338—339.
- ERDTMAN, G. 1952. Pollen morphology and plant taxonomy; Angiosperms.
- ETTINGHOUSEN, C. VON. 1858. Ueber die Nervation der Bombaceen. *Denkschr. Math. Nat. Classe Kaiserl. Akad. Wiss.* 14.
- 1861. Die Blatt-Skelette der Dikotyledonen.
- FRYNS-CLAESSENS, E., & W. VAN COTTHEM, 1966. Blijft *Catostemma* een Bombacaceae? *Natuurwet. Tijdschr.* 48: 45—50.
- FUCHS, H. P. 1967. Pollen morphology of the family Bombacaceae. *Rev. Palaeobot. Palyn.* 3: 119—132.
- GERMAIN, R. 1963. Huaceae, in *Flora du Congo, du Rwanda et du Burundi* X: 317—319.
- HALLÉ, N. 1961. *Sterculiaceae*, in *Flora du Gabon* No. 2.
- HALLIER, H. 1923. Beiträge zur Kenntnis der Linaceae. *Beih. Bot. Centralblatt* 39: 1—178.
- HAVEZ, J. M. 1950. L'Appareil libéro-ligneux foliaire des Bombacées. Thesis, Lille.
- HEGNAUER, R. 1964. Chemotaxonomie der Pflanzen 3: 284—288.
- HERLEMONT, R. J. H. 1951. Les Tiliacées d'Indochine. Etude d'anatomie et d'histologie comparées de la feuille. Thesis, Lille.
- HEINZELMANN, C. E., & R. A. HOWARD, 1948. The comparative morphology of the Icacinaceae V. The pubescence and the crystals. *Amer. J. Bot.* 35: 42—52.
- HUARD, J. 1965. Anatomie des Rhopalocarpaceae. *Adansonia* 5: 103—123.
- HUTCHINSON, J. 1959. The families of flowering plants. 2nd ed.
- INAMDAR, J. A., & A. J. CHOCHAN. 1969. Epidermal structure and stomatal development in some Malvaceae and Bombacaceae. *Ann. Bot. (N.S.)* 33: 865—878.
- IVANOV, S. 1927. Die Halphenische Reaktion auf Baumwollensamenöl als allgemeine Reaktion für Öle der Familien Malvaceae, Tiliaceae und Bombacaceae. *Ber. Deutsch. Bot. Ges.* 45: 588—591.
- KEATING, R. C. 1968. Comparative morphology of Cochlospermaceae I. Synopsis of the family and wood anatomy. *Phytomorph.* 18: 379—392.
- 1970. Ibid. II. Anatomy of the young vegetative shoot. *Amer. J. Bot.* 57: 889—898.
- KRAUSE, K. 1915. in *Engl. & Prantl, Natürl. Pflanzenfamilien. Nachträge* IV: 201.
- LEBACQ, L., & R. DECHAMPS. 1964. Essais d'identification anatomique des bois de l'Afrique Centrale. *Kon. Mus. Midden Afrika. Ann. IN-8° Econ. Wetensch. Nr.* 3.
- LEINFELNER, W. 1960. Zur Entwicklungsgeschichte der Kronblätter der Sterculiaceae—Buettneriaceae. *Öst. Bot. Zeitschr.* 107: 153—176.

- METCALFE, C. R. 1962. Notes on the systematic anatomy of *Whittonia* and *Peridiscus*. *Kew Bull.* 15: 472—475.
- & L. CHALK. 1950. Anatomy of the Dicotyledons.
- MILDBRAED, J. 1913. Ueber die Gattungen *Afrostryrax* Perk et Gilg und *Hua Pierre* und die 'Knoblauch-Rinden' Westafrikas. *Bot. Jahrb.* 49: 552—559.
- NEDERLANDSE FARMACOPÉE, 1966. 6de Uitgave, 2e druk.
- NETOLITZKY, F. 1926. Anatomie der Angiospermen-Samen. In K. Linsbauer, *Handbuch der Pflanzen-anatomie* X.
- NORMAND, D., & R. CHATELET. 1955. Sur le bois de quatre espèces Africaines. *J. d'Agric. Trop. Bot. Appl.* 11: 19—27.
- OLTMANN, O. 1971. Pollenmorphologisch-systematische Untersuchungen innerhalb der Geraniales. *Diss. Bot.* 11.
- PERKINS, J. 1909. Eine neue Gattung der Styracaceae aus dem tropischen Afrika. *Bot. Jahrb.* 43: 214—217.
- 1928. Uebersicht über die Gattungen der Styracaceae.
- PIERRE, L. 1906. in E. de Wildeman, *Flore du Bas- et du Moyen Congo I. Ann. Mus. Congo sér. 5, I: 288.*
- ROBYNS, W. 1958. Le genre *Afrostryrax* Perk. et Gilg au Congo Belge. *Bull. Soc. Roy. Bot. Belg.* 91: 93—98.
- SANDWITH, N. Y. 1962. Contributions to the Flora of Tropical America 69. A new genus of Peridiscaceae. *Kew Bull.* 15: 467—471.
- SHAW, H. K. A. 1966. in J. C. Willis, *A dictionary of flowering plants and ferns.* 7th ed.
- SCHNELL, R., G. CUSSET & M. QUENUM. 1963. Contribution à l'étude des glandes extra-florales chez quelques groupes de plantes tropicales. *Rev. Gén. Bot.* 70: 269—342.
- SOLBERGER, H. 1899 & 1908. Systematische Anatomie der Dicotyledonen (& Ergänzungsband).
- STACE, C. A. 1965. Cuticular Studies as an aid to Plant Taxonomy. *Bull. Brit. Mus. (Nat. Hist.) Bot.* 4—1: 44.
- STEENS, C. G. J. VAN, & R. C. BAKHUIZEN VAN DEN BRINK. 1967. Miscellaneous botanical notes XVI. *Bot. Jahrb.* 86: 393.
- TAKHTAJAN, A. 1969. Flowering plants, origin and dispersal.
- UPHOF, J. C. TH., K. HUMMEL & K. STAESCHE. 1962. Plant hairs; in W. Zimmermann & P. G. Ozenda, *Handbuch der Pflanzenanatomie*, 2nd. ed. IV, 5.
- VAUGHAN, J. G. 1970. The structure and utilization of oil seeds.
- WALKER, A., & R. SILLANS. 1961. Les plantes utiles du Gabon. *Enc. Biol.* 56: 203.
- WEBBER, I. E. 1936. Systematic anatomy of the Simarubaceae. *Amer. J. Bot.* 23: 577—587.
- ZAHUR, M. S. 1955. Comparative study of secondary phloem of 423 species of woody Dicotyledons belonging to 85 families. *Cornell Univ. Agric. Exp. Sta. Mem.* 358.

INDEX TO ORIGINAL OBSERVATIONS IN OTHER FAMILIES

Irvingiaceae	181, 184
Pandaceae	181
Scytopetalaceae	187
Sphaerosepalaceae	187
Sterculiaceae	180, 189