Studies in Annonaceae. IV

A taxonomic revision of *Tetrameranthus* R.E. Fries

by L.Y.Th. Westra[1]

Institute of Systematic Botany, Utrecht, the Netherlands

Communicated by Prof. F.A. Stafleu at the meeting of May 20, 1985

SUMMARY

The small genus *Tetrameranthus* R.E. Fries, occurring in the Amazon region, is revised. Two new species are described, in addition to the three already known. Available data still indicate that this genus belongs in Annonaceae, but takes up an isolated position within that family.

INTRODUCTION AND TAXONOMIC HISTORY

The neotropical genus *Tetrameranthus* was described by R.E. Fries (1939) with the only species *T. duckei* R.E. Fries, based on, among others, the unusual phyllotaxis: leaves in a spiral instead of in two rows, the presence of four bracts verticillately placed under the articulation of the flower stalk, and, above all, the perianth consisting of 4 sepals and 2 whorls of 4 petals each. The position of this peculiar genus is discussed by Fries in that paper; Fries places *Tetrameranthus* in an isolated position within the Annonaceae.

Two more species were added in later years, viz. *T. macrocarpus* R.E. Fries from Southeastern Colombia (Fries 1956), and *T. laomae* D. Simpson from Eastern Peru (Simpson 1975). More material was collected too, largely around Manaus: all referable to *T. duckei*. Outside Manaus, relatively few collections were made up until this day. Therefore *Tetrameranthus*, as a whole, must be regarded as a rarity.

The isolated position of this genus within the family was even more em-

[1] L.Y.Th. Westra is the author of all chapters for which no further authorship is indicated.

phasized by Fries in placing it as the only member in a tribe Tetramerantheae in subfamily Annonoideae (beside Uvarieae and Unoneae) (Fries 1959).

The generic name is composed of the Ancient Greek word elements "tetra" (four), "meros" (part), and "anthos" (flower), referring to the four-parted flowers.

SCOPE OF THE PRESENT PAPER

This paper adds to the already existing data-set on *Tetrameranthus* in describing two new species, and compiling data on wood and leaf anatomy, pollen morphology, flower ecology, geography, and economic use. It does not deal with problems concerning relationship, other than presenting mere facts. A cladistic analysis will be presented in a following paper.

NOTES ON MORPHOLOGY

Vegetative part

Tetrameranthus is a genus of shrubs to (sometimes apparently large) trees.

The leaves, in their shape, conform to the general pattern in Annonaceae: they are simple, undivided, entire, pinnately veined, symmetrical, and lack stipules. They are generally of moderate to fairly large size (greatest length: ±30 cm), with a l/w ratio commonly between 2:1 and 3.5:1. The placement of the leaves, in a spiral, is another matter: Annonaceae, almost without exception, have the leaves in two alternate rows (Fries 1959, p. 8).

Leaves are mostly found not farther away than about 10 cm from the growing point of the branchlet; beyond that, they are shed. This gives many specimens of *Tetrameranthus* a Sapotaceous-like look.

Inflorescences

Inflorescences in *Tetrameranthus* are truly axillary. They apparently appear at variable time intervals. In *T. duckei, T. macrocarpus,* and *T. pachycarpus* inflorescences are usually seen singly, in one of the leaf axils of a branchlet. In *T. umbellatus* inflorescences tend to develop from all or most leaf axils, as the leaves are growing, too. The same is sometimes also observed in *T. laomae.*

As for the structure of the inflorescence in Annonaceae in general, the reader is referred to publications by Fries (1919, 1959). *Tetrameranthus* conforms to Fries's type 1 (1959, p. 13) in that it has a primary flower stalk which carries bracts below the articulation, but no bracts beyond it. The articulation is suprabasal, situated in the lower half of the stalk; only in *T. laomae* it is basal or almost so. Immediately below the articulation, there are 4 small bracts in a verticil. These bracts drop before or (immediately) after the flowering period. In *T. laomae*, together with the (almost) basal position of the articulation, only 3 bracts could be observed. It does not seem unlikely that this lower number of bracts in *T. laomae* is due to reduction, along with shortening of of the lower part of the flower stalk as evidenced by the (almost) basal articulation in this species.

In *T. umbellatus* from the axil of each bract a lateral flower may develop. This leads to pleiochasial umbels with up to 5 flowers in that species. The (up to) four second-order flower stalks have a basal articulation, and lack bracts. In other species development of second-order flowers, as a rule, does not take place, and the inflorescences remain single-flowered. Only in *T. duckei* development of one lateral flower has been observed as an exception.

In the present treatment the term peduncle is applied to the part of the first-order flower stalk from the base to the verticil of bracts. The remaining part of the first-order flower stalk is referred to as pedicel. The term pedicel is also applied to the second-order flower stalks.

Flowers (Plate 1; Plate 2: fig. 1)

The perianth consists of three whorls, one whorl of sepals, two whorls of petals: the usual configuration in Annonaceae. Unusual, however, is the fact that all whorls are tetramerous instead of trimerous (next to tetramerous flowers, trimerous or pentamerous flowers are occasionally met with in *Tetrameranthus*).

The sepals are small in relation to the petals. They are free or connate just at the base (this is not always easy to observe). The aestivation is imbricate: this can only be observed in very young buds, as the sepals soon spread. The sepals drop after flowering.

The petals are rather fleshy (though in *T. laomae* and *T. umbellatus* probably somewhat less so than in the other three species). In *T. duckei* they are curved in the living condition, giving the open flower a more or less bowl-shaped appearance, as is clearly seen from photographs taken by Webber (1981). The petals are adorned with a callus or callus-like tissue at the base on the inner side: this is an area which is devoid of indument, and often shows longitudinal furrowing in some degree. In pickled material of *T. duckei*, and also on the photographs by Webber, this callus appears as a protruding hump, particularly on the inner petals where it is even larger than on the outer petals. In the other species the callus is smaller in relation to the size of the whole petal than in *T. duckei*. The shape could not be studied properly due to lack of pickled material.

The function of the callus on the petals might be that of an osmophore: this is yet open for investigation. Although Webber observed a (strong) odour emitted by flowers of *T. duckei*, he makes no mention of the callus as a possible source. It should immediately be added, however, that Webber observed that odour emission continued, albeit much weaker, also after dropping of the petals.

The convex torus bears stamens in spiral arrangement, and a mostly rather small number of free carpels in the center. The stamens are mostly numerous, with short filamental part, a thick connective capped by a massive, more or less conical or flat, apical prolongation, and an extrorse to latrorse anther. The carpels contain two, lateral, superposed ovules, and have on top a sessile stigma which varies from trilobed to an irregularly lobed disc.

Fruits (Plates 2: figs. 2, 3a, 3b, 4a, 4b, 5)

The carpels grow into free monocarps, though usually part of them abort before reaching maturity. The ellipsoid to oblongoid monocarps are fleshly, indehiscent, and two-seeded or, due to abortion of one ovule, one-seeded. The seeds are laterally attached, one near the base, the second higher up, and are ascending. The two seeds (if both are developed) thereby are obliquely superposed, which gives two-seeded monocarps a characteristic appearance in particular due to the constriction between the two seeds. Only in *T. pachycarpus* this oblique constriction is not evident. In this species the thick, ellipsoid monocarps probably have the thickest wall of all fruits known in this genus so far.

The seeds are quite large in relation to the fruit body; they are slightly compressed dorsiventrally, and possess ruminations in the shape of fairly numerous lamellae protruding from the seed coat into the interior almost to the middle.

Indument

The indument of *Tetrameranthus* consists of stellate tufts of up to, mostly, 10 trichomes. There is no other genus in the Neotropics with this type of indument in all species (in *e.g. Annona, Rollinia*, similar stellate tufts may be found in a small percentage of the species only; in *Duquetia* most species have scales, rather than stellate tufts).

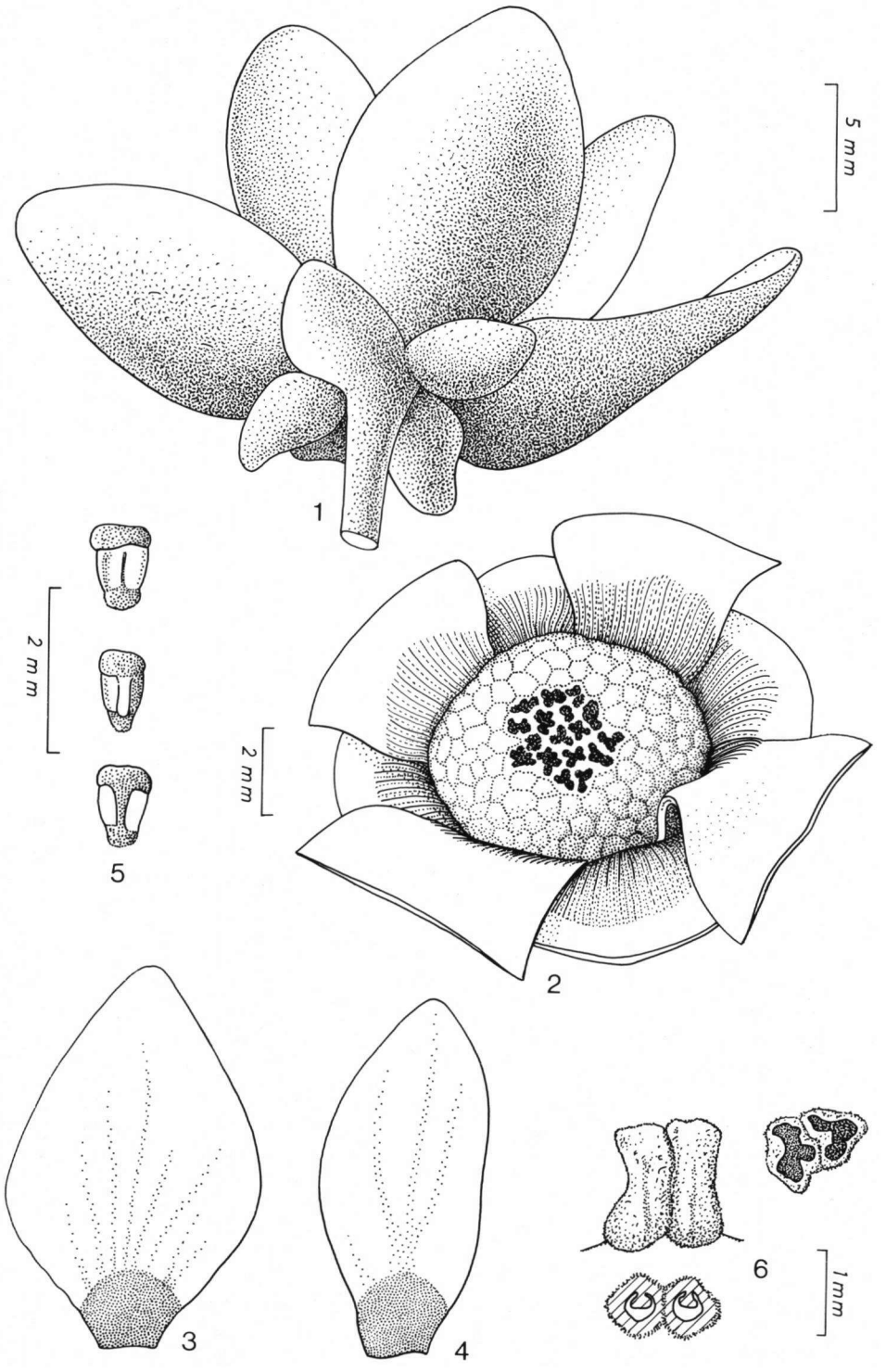
Indument in *Tetrameranthus* is found especially on young vegetative parts and inflorescences. Some of it persists on the primary vein, and to a lesser extent on the secondary veins, of the leaves mainly on the abaxial side, and on petioles and branchlets in the foliated zone. In *T. umbellatus* tufts are also found diffusely spread over the leaf surface, especially on the abaxial side. In *T. laomae*, too, scattered tufts may be spotted on the abaxial leaf surface.

Floral parts, with the exception of the callus area on petals mentioned above, and stamens, are usually covered with a dense indument.

Carpels, when enlarging into monocarps, quickly become glabrous.

The trichome length on vegetative parts (except in very young stage, and persisting near axils) commonly does not exceed 0.1 mm in *T. laomae* and *T. umbellatus*: these two species are easily recognized by the minute tufts as compared to the other three, where considerably longer (to 0.5 mm, occasionally even more) and stiffer trichomes are found. Trichomes on inflorescences and flower parts may atteign a somewhat larger average size than those on vegetative parts (this, however, has not been established with accuracy yet).

Plate 1. *Tetrameranthus umbellatus* (*Tunqui 62*, U): fig. 1, flower seen from the outside; fig. 2, center of flower; fig. 3, outer petal - inner (= adaxial) side; fig. 4, inner petal - inner (= adaxial) side; fig. 5, (top:) stamen - abaxial view, (middle:) same - lateral view, (bottom:) same - adaxial view; fig. 6, (upper left:) two carpels - abaxial view, (right:) same - top view, (lower left:) same in cross section.


5 mm
1
2 mm
5
2 mm
2
3
4
6
1 mm

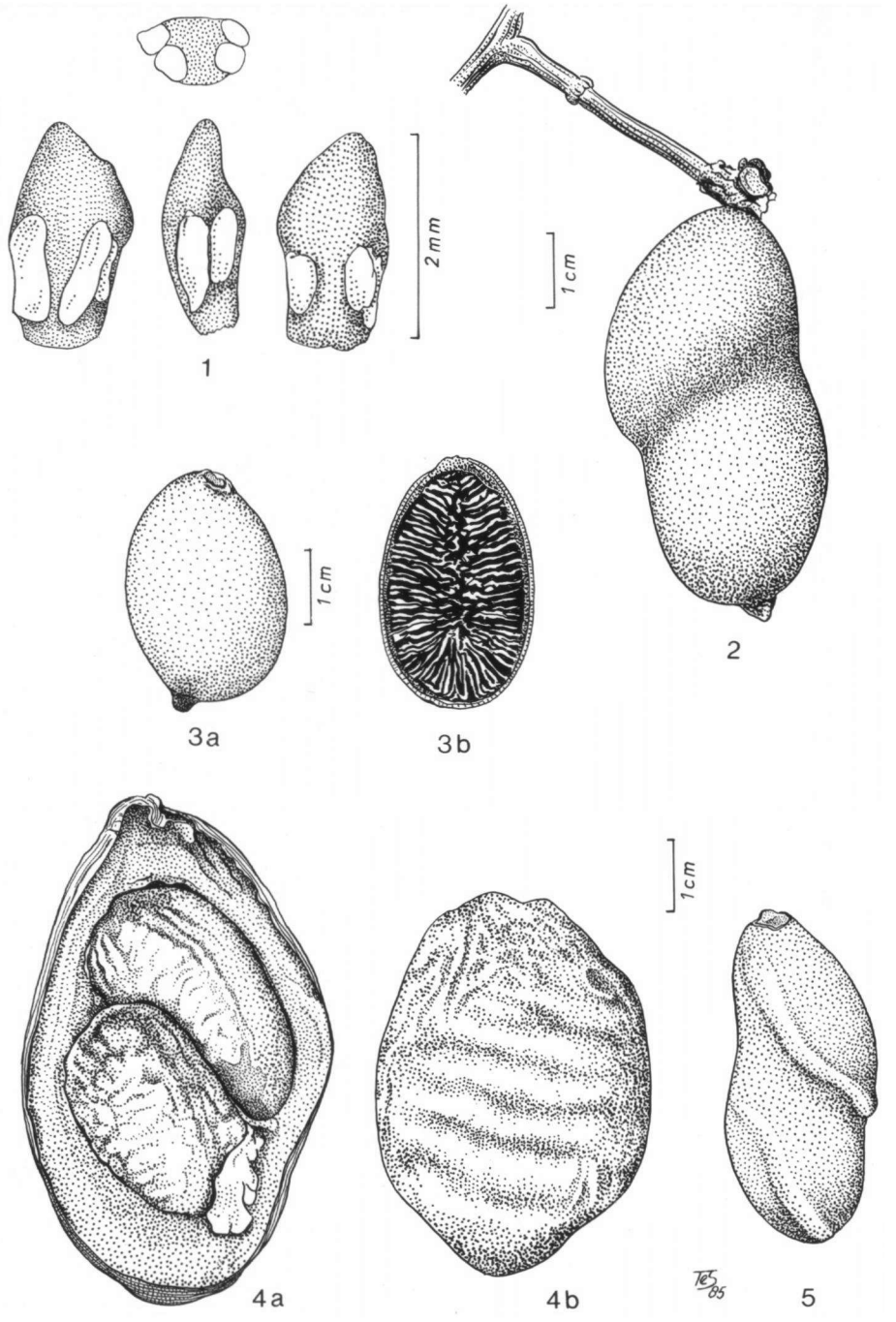


Plate 2. *Tetrameranthus pachycarpus* (*Klug 1216*, NY): fig. 1, (left:) stamen - abaxial view, (middle, below:) same - lateral view, (right:) same - adaxial view, (middle, above:) same in cross section. *T. duckei* (*Rodrigues 8742*, INPA): fig. 2, two-seeded monocarp attached; (*Rodrigues & Coêlho 3835*, U): fig. 3a, one-seeded monocarp; (*Morawetz et al. 21-9883*, WU): fig. 3b, seed in longitudinal section.

T. pachycarpus (*Foster 4271*, NY): fig. 4a, two-seeded monocarp cut open; fig. 4b, two-seeded monocarp seen from outside.

T. umbellatus (*Huashikat 613*, U): fig. 5, two-seeded monocarp.

WOOD ANATOMY

by B.J.H. ter Welle (Utrecht)

Material studied

T. duckei: Brazil. Amazonas: near Manaus, *L. Coêlho s.n. (INPA 69232)* (wood coll. nr. INPA X 7328, Uw 26746), *D. Coêlho s.n.* (wood coll, nr. INPA X7330, Uw 26747).

Description (Plate 3: figs. 1, 2, 3)

Growth rings absent.

Vessels diffuse, solitary (10%) and in radial chains and occasionally in irregular clusters of 2-4(-8), 5 (1-11) per sq. mm, round, oval or occasionally angular, walls 4-6 μm, diameter 107-122 (84-168) μm, vessel member length 557-683 (400-810) μm. Perforations simple. Intervascular pits alternate, polygonal to round, 6-7 μm. Vessel-ray pits and vessel-parenchyma pits as the intervascular pits, sometimes elongated, half bordered.

Fibres non-septate, diameter up to 15 μm, walls 6-10(-12) μm. Pits indistinctly bordered, equally frequent on the radial and tangential walls, 6-7 μm. Length 1760 (1240-2230) μm, F/V ratio 2.55-3.16.

Rays heterogeneous, with very few uniseriates, and mostly 5-8-seriate, composed of weakly procumbent, procumbent, and some square cells. Especially on the tangential section, the ray cells vary in size. Height of the multiseriate rays up to 103-111 cells (= 4300-5000) μm, and 240 to 260 μm wide; 3 (2-5) per mm.

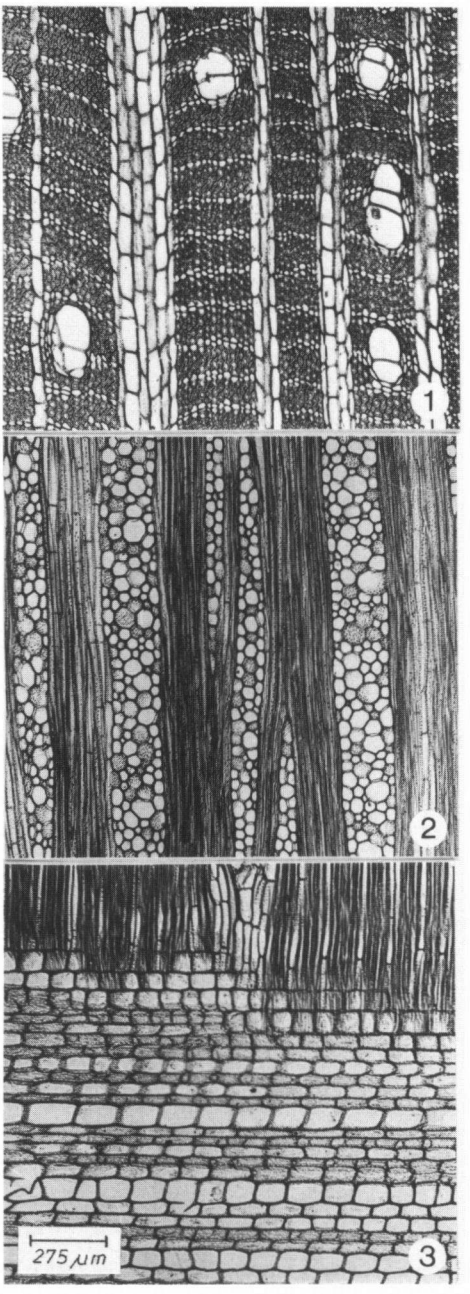
Parenchyma in apotracheal, continuous, concentric tangential bands, 1-2 cells wide, with 4-6 fibres between two bands. Number of bands 7-8 per mm. Vasicentric parenchyma always present, varying from scanty to a complete sheath of one cell wide. Length of the parenchyma strands 2-4 cells, 530 to 674 (400-810) μm.

DISCUSSION

Tetrameranthus shows well-developed continuous concentric tangential bands of apotracheal parenchyma, so characteristic for Annonaceae. This important wood anatomical character, therefore, supports inclusion of this genus within the family.

Tetrameranthus, besides these apotracheal bands, also possesses paratracheal vasicentric parenchyma. This combination it shares with about 1/3 of the genera in Annonaceae. In addition, *Tetrameranthus* has rays up to 5000 μm high: this combination of high rays with the parenchyma distribution just mentioned is rarely found within the family (Ter Welle 1984[a]).

In conclusion: wood anatomy shows that *Tetrameranthus* is definitely Annonaceous. Within that family, it is characterized by a rare, but not unique combination of character states. Therefore, from the wood anatomical viewpoint, *Tetrameranthus* does not stand in such an isolated position as it does in its gross morphology (Vander Wijk & Canright 1956; Ter Welle & Van Rooden 1982; Ter Welle 1984[b]).



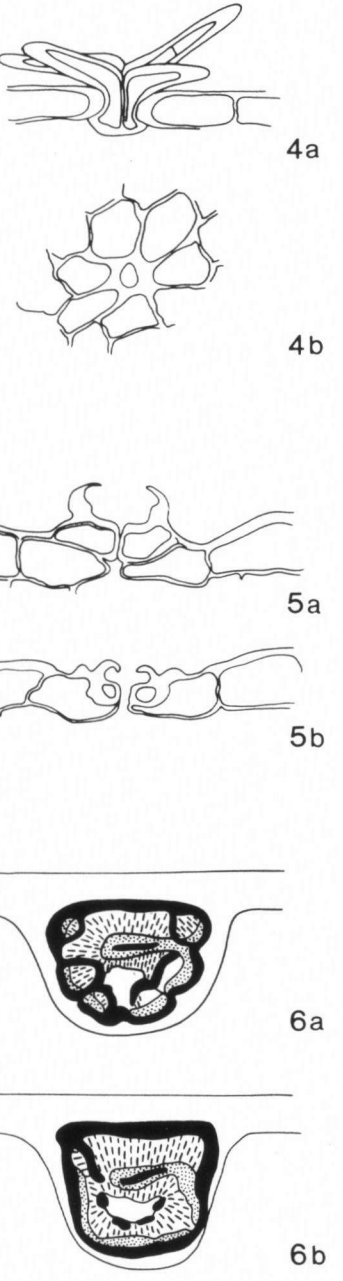


Plate 3. Anatomical features of *Tetrameranthus*: fig. 1, wood of *T. duckei* (Uw 26747) in transverse section; fig. 2, same in tangential section; fig. 3, same in radial section; fig. 4a, stellate tuft as seen in transverse section on abaxial leaf side of *T. duckei* (*Steyermark & Bunting 102721*); fig. 4b, remnant of trichome base in surface view of same; fig. 5a, stoma in transverse section in *T. umbellatus* (*Tunqui 62*); fig. 5b, stoma in transverse section in *T. duckei* (*Liesner 8598*); figs. 6a and 6b, schematical drawings of primary vein in transverse section - black = sclerenchyma, dotted = phloem, striped = xylem.

LEAF ANATOMY

by A.K. van Setten & J. Koek-Noorman (Utrecht)

Material studied

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

The generic description is based upon four samples of *T. duckei (Liesner, 7590, 8598; Rodrigues 8742; Steyermark & Bunting 102721)*, and one sample each of *T. laomae (Gentry et al. 41743)*, *T. pachycarpus (Foster 4271)*, and *T. umbellatus (Tunqui 62)*. *T. macrocarpus*, unfortunately, could not be included because of scarcity of material.

Description (Plate 3: figs. 4a, 4b, 5a, 5b, 6a, 6b)

1. In surface view:

Indument present along the primary vein on the abaxial and on the adaxial side, in *T. laomae* and *T. umbellatus* also diffusely spread over the abaxial surface; easily coming off (scars easily discernible by the heavily cutinized part of the bordering cell walls); consisting of tufts of 2–10(–20) uniseriate, 1–2-celled trichomes (fig. 4a).

Unspecialized epidermal cells polygonal, isodiametric to oval, but elongated and parallel above primary and secondary veins, adaxially 30–75 × 20–45 μm,

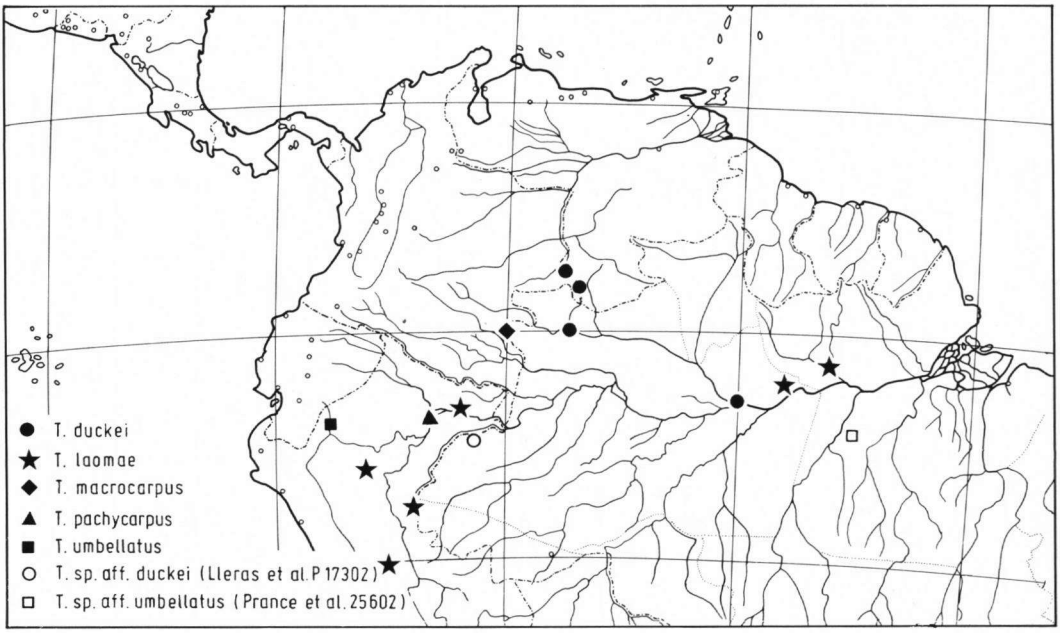


Plate 4. Distribution map of *Tetrameranthus*.

abaxially 35–80 × 20–50 μm. The anticlinal cell walls on both surfaces straight to slightly curved.

Stomata exclusively abaxial, paracytic with 2(–4) subsidiary cells, 30–45 μm long.

2. In transverse section:

Lamina dorsiventral.

Cuticle adaxially 4–8 μm, abaxially 1–4 μm thick.

Unspecialized epidermal cells adaxially in 1–3 layers, 20–40 μm thick, abaxially one-layered, 8–15 μm thick.

Stomata on the same level as the unspecialized cells or slightly sunken, with prominent outer ledges (figs. 5a, 5b).

Mesophyll composed of 1–3 layers of palisade parenchyma and 4–8 layers of compact to rather loosely packed sponge parenchyma.

Astrosclereids occur as a non-continuous layer under the epidermis both adaxially and abaxially, and also in palisade parenchyma and sponge parenchyma.

Oil cells are found in the palisade parenchyma, and occasionally in the transitional zone between palisade parenchyma and sponge parenchyma.

Primary vein with one vascular bundle surrounded by a continuous sclerenchymatous sheath. The vascular tissue is always complex, consisting of one xylem body surrounding a wide parenchymatic central part; abaxially, a continuous or interrupted phloem cap surrounds the xylem: islands of phloem and sclerenchyma are included in the xylem body (figs. 6a, 6b).

The vascular bundle is accompanied by few to many stone cells. In most specimens, a narrow zone of flattened parenchymatic cells is found around the vascular bundle.

Smallest veins surrounded by narrow sclerenchymatic sheaths, sometimes connected with astrosclereids.

Petiole with a 5–12 μm thick cuticle, with many vascular bundles, these bundles separate or confluent, wholly or in part surrounded by sclerenchyma caps.

Ground tissue with few to many druses and oil cells, and with many stone cells.

DISCUSSION

The studied samples match well with other Annonaceae, as known from own studies and from literature. All character states found in the specimens of *Tetrameranthus*, have also been recorded for other Annonaceae, although some features are rather rare, or are restricted almost exclusively to African or Asiatic genera. The samples of *Tetrameranthus* are, furthermore, alike in nearly all features which are considered to have diagnostic or taxonomic value on the generic level (Van Setten & Koek-Noorman in prep.). Features which are often mentioned in this respect, are trichome types, structure of vascular bundles in the primary vein, and crystal types in epidermal cells.

The trichome type found in *Tetrameranthus*: stellate tufts, although reported to occur in several African and Asiatic genera (*e.g.* Roth 1981), is rather uncommon among neotropical Annonaceae (see also paragraph on indument in section on morphology in the present paper).

The complex structure of the vascular tissue of the primary vein in *Tetrameranthus* is unique within the neotropical genera; the closest match is

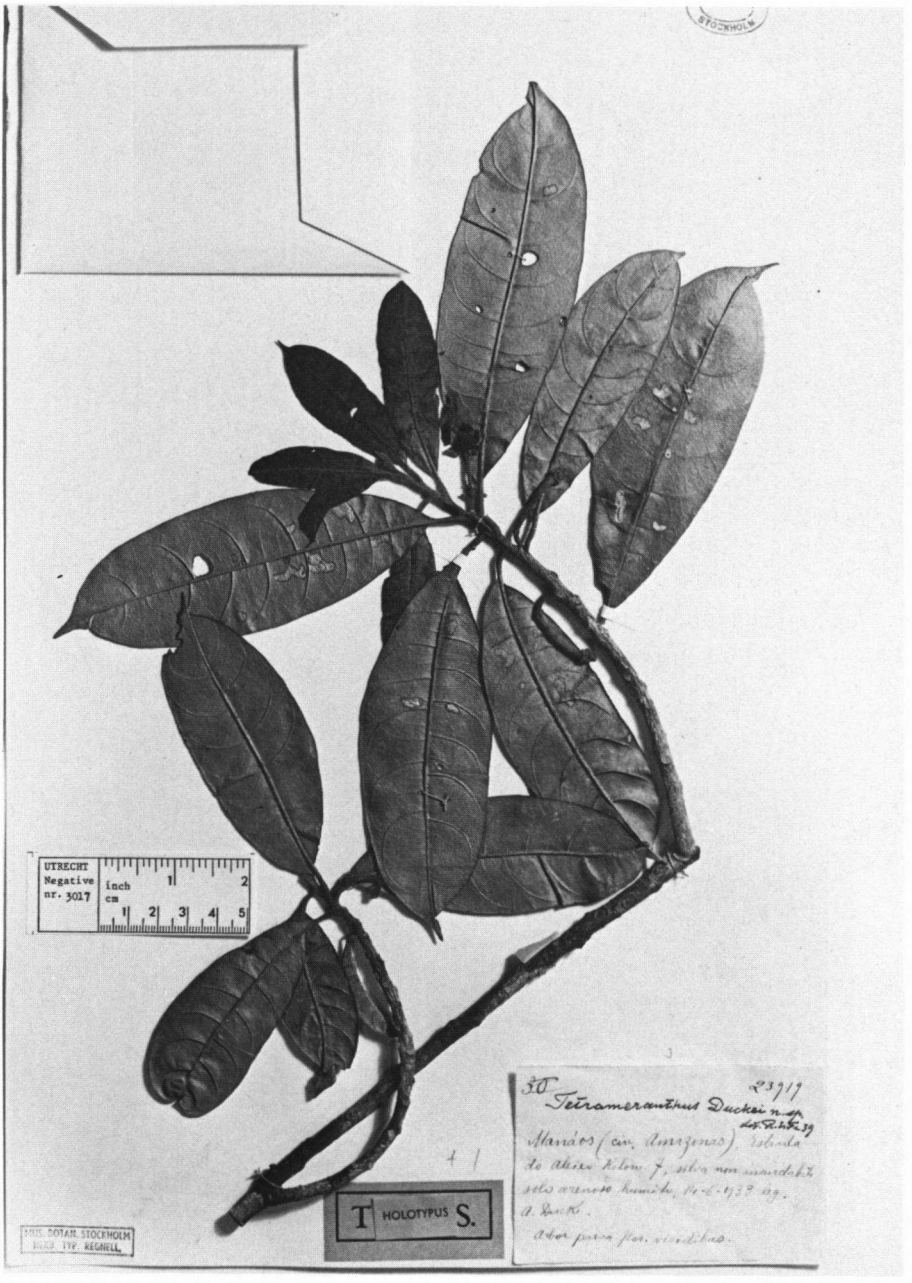


Plate 5. *Tetrameranthus duckei*, holotype specimen (*Ducke s.n.* = *RB 23919*, S).

Melodorum (Jovet-Ast 1942). Jovet-Ast lists *Bocageopsis* in the same category. The samples of *Bocageopsis* studied by us largely confirm this, although the vascular structure of the primary vein is less complex than in *Tetrameranthus* (Van Setten & Koek-Noorman in prep.).

In three specimens of *Tetrameranthus* crystal sand is found in epidermal cells. Other types of crystals commonly found in Annonaceae, viz. druses and

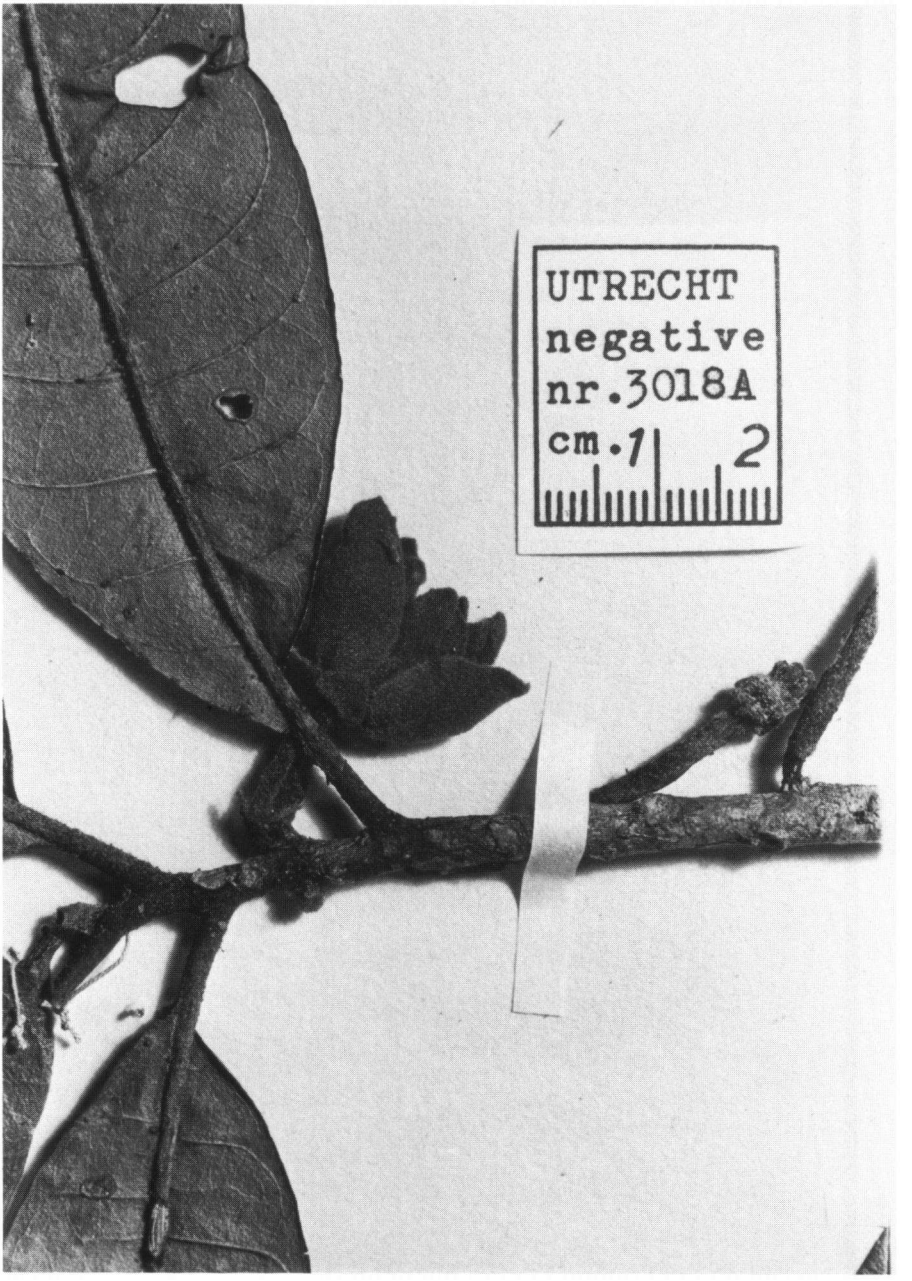


Plate 6. *Tetrameranthus duckei*, detail of isotype specimen (*Ducke s.n.* = *RB 23919*, S).

rhombic crystals, are lacking in *Tetrameranthus*. Crystal sand, on the other hand, is also met with in a few species of various genera, viz. *Annona, Bocageopsis, Duguetia, Rollinia,* and *Rolliniopsis.*

Van Setten and Koek-Noorman found that sclereids are present in many neotropical genera, though not necessarily in every species within these genera. These sclereids, depending upon the genus, are either astrosclereids or

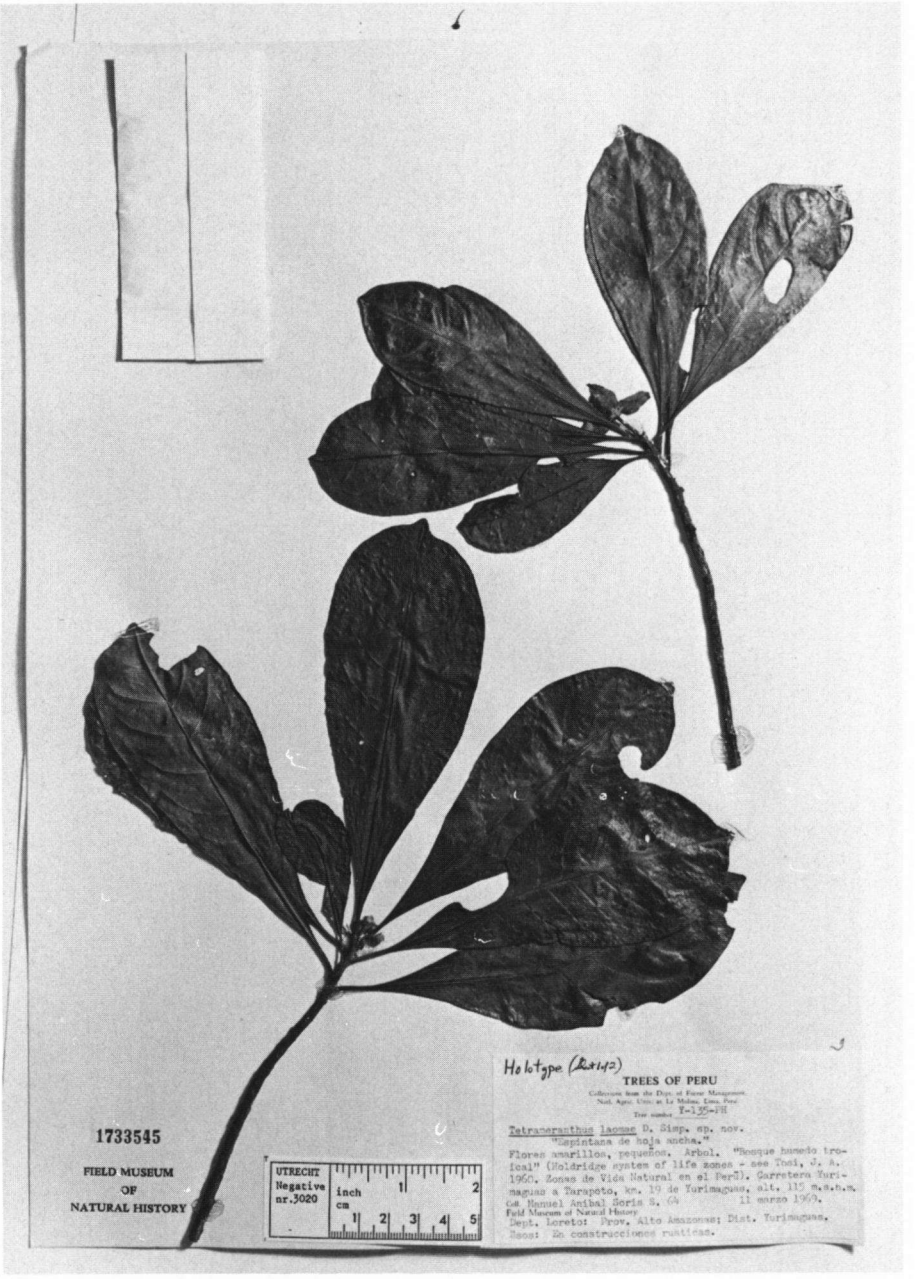


Plate 7. *Tetrameranthus laomae*, holotype specimen, first sheet (*Soria S. 64*, F).

osteosclereids; only in the large genus *Guatteria* both types of sclereids are present. *Tetrameranthus* possesses astrosclereids, along with *Anaxagorea, Annona, Desmopsis, Heteropetalum*, and *Guatteria* in part.

A multi-layered (adaxial) epidermis, such as found in *Tetrameranthus*, is frequently found in the neotropical representatives of the genera *Annona, Guatteria*, and *Xylopia*, too. However, it was never found in all specimens of a

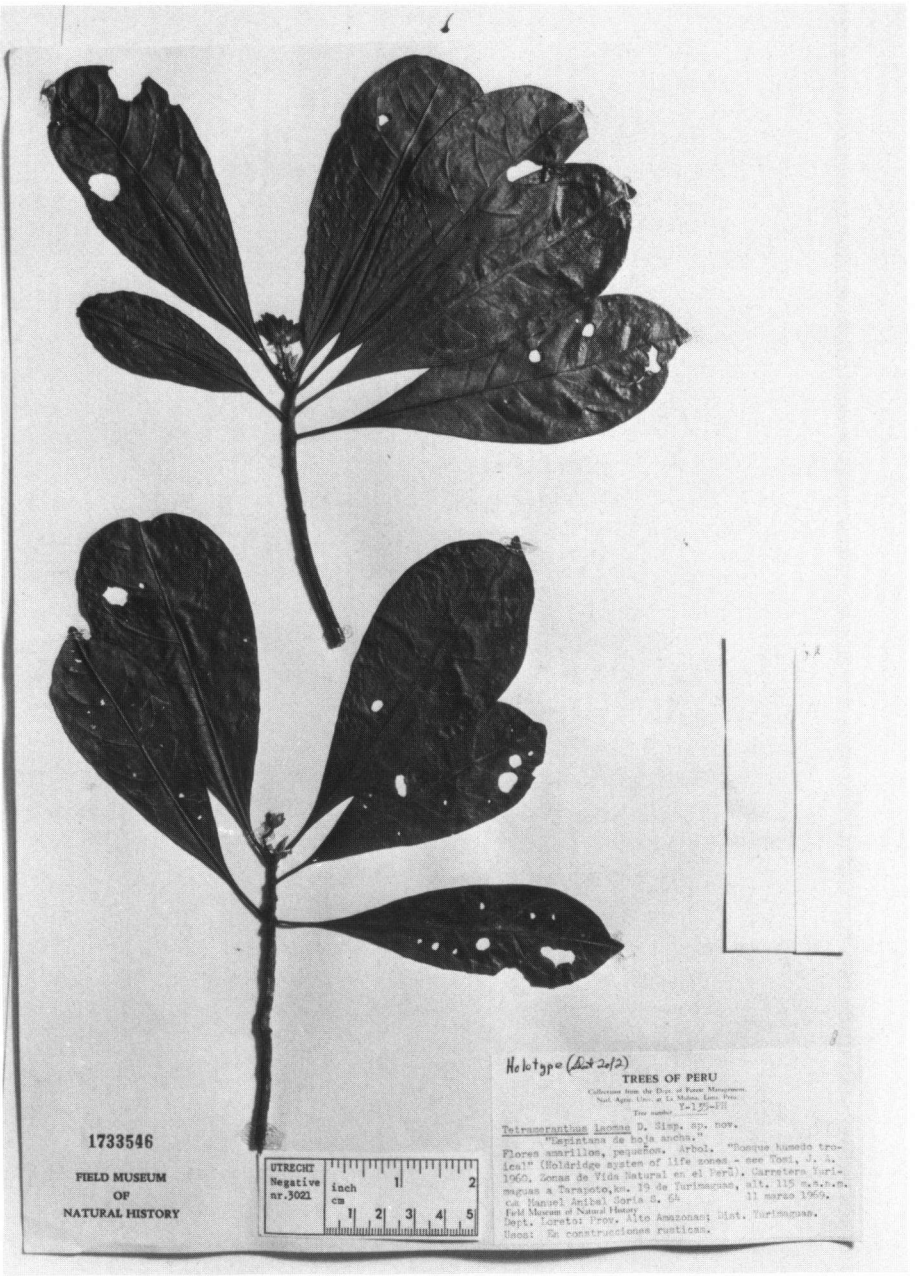


Plate 8. *Tetrameranthus laomae*, holotype specimen, second sheet (*Soria S. 64*, F).

genus examined by us. The presence of a one-layered epidermis in one specimen (out of four) of *T. duckei*, therefore, does not change our impression that *Tetrameranthus* has a very homogeneous leaf anatomy.

Summarizing, we can state that the leaf anatomy supports placing *Tetrameranthus* in Annonaceae. *Tetrameranthus*, however, can easily be recognized by the complex vascular bundle in the primary vein in combination

Plate 9. *Tetrameranthus laomae*, detail of holotype specimen, second sheet (*Soria S. 64*, F).

with the stellate tufts of trichomes, epidermal crystals (if present) in the form of crystal sand, and the presence of astrosclereids in the mesophyll.

POLLEN MORPHOLOGY

The first light microscope studies, on pollen of *T. macrocarpus*, were carried out by Walker, as part of his extensive survey of the family (Walker 1971). This

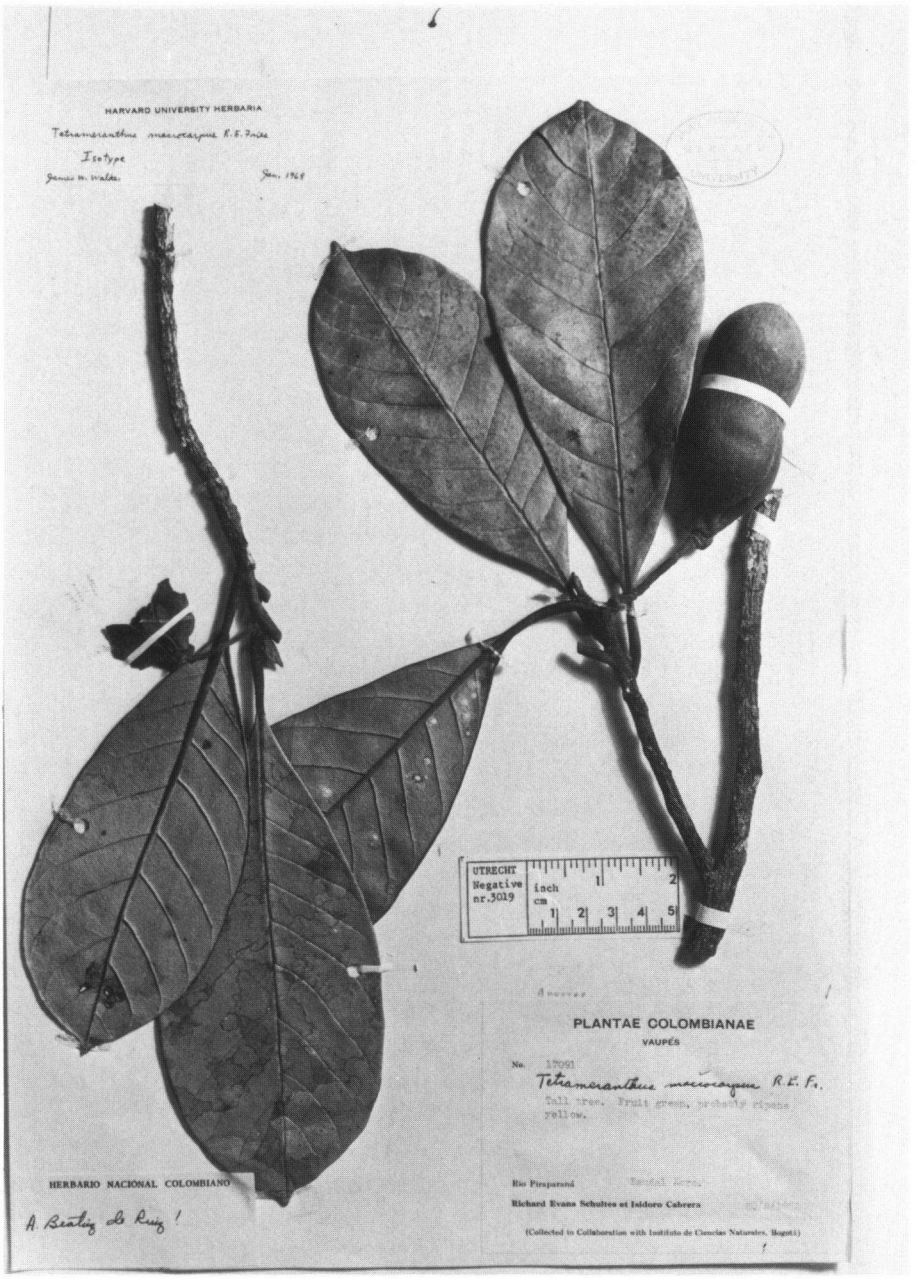


Plate 10. *Tetrameranthus macrocarpus*, isotype specimen (*Schultes & Cabrera 17091*, GH).

pollen was found to be inaperturate, with a high degree of psilateness as remarkable feature. In Walker's "informal infrafamiliar" (palynological) classification of the Annonaceae, *Tetrameranthus* is placed in the *Uvaria* tribe of the *Malmea* subfamily, together with *Desmopsis, Stenanona, Duguetia*, and many other genera both from the New and the Old World (Walker l.c., p. 24).

A micromorphological and ultrastructural investigation of pollen of *T.*

Plate 11. *Tetrameranthus macrocarpus*, detail of isotype specimen (*Schultes & Cabrera 17091*, GH).

duckei was recently carried out by Hesse & Waha (1984). Each pollen grain in this species, in contrast to Walker's findings for *T. macrocarpus*, appears to have a single, rounded aperture. Before acetolysis the surface around this aperture is covered with thread-like material and consists of smooth, rounded verrucae. In contrast, the circular aperture region differs significantly in its sculpturing with small globular elements but without verrucae. With the excep-

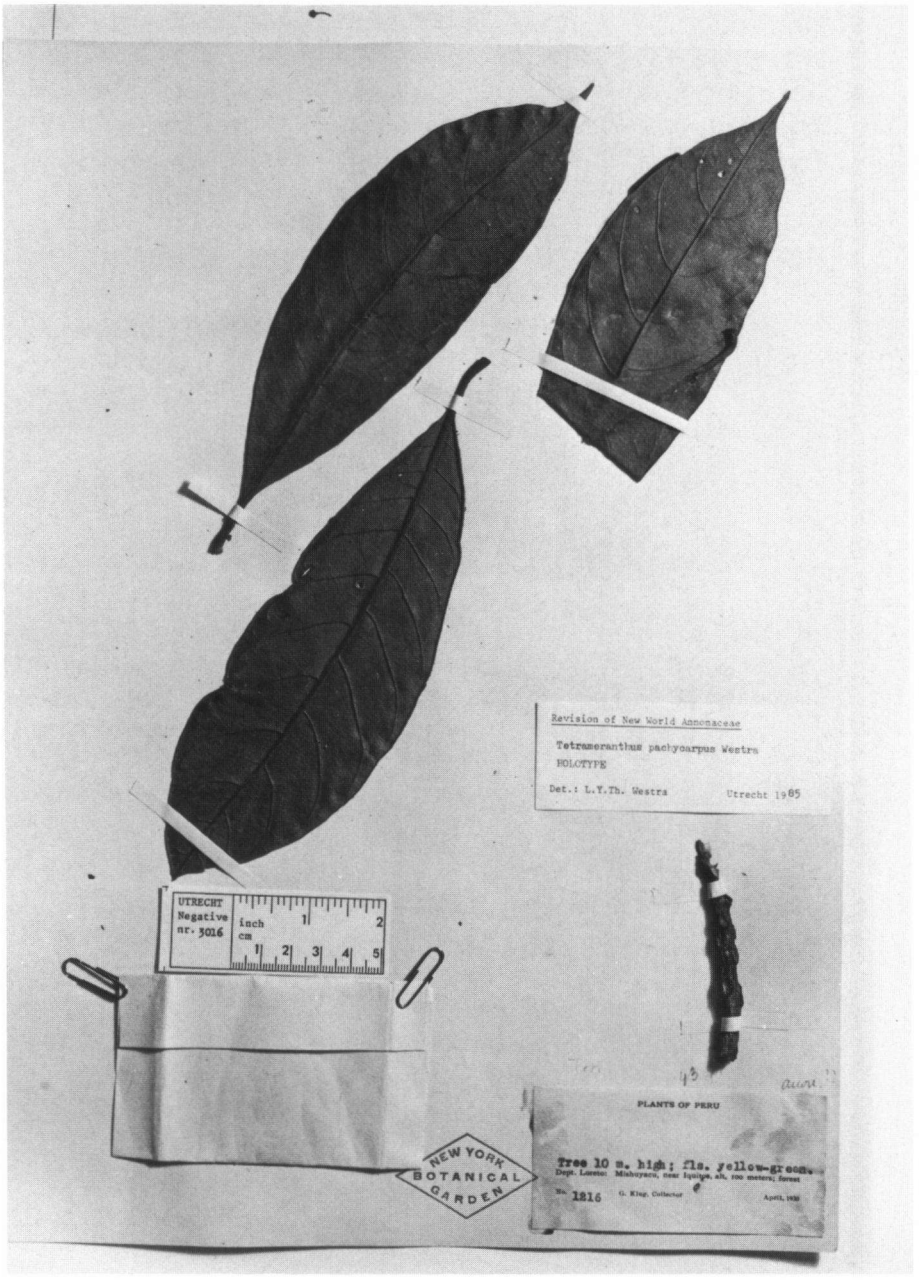


Plate 12. *Tetrameranthus pachycarpus*, holotype specimen (*Klug 1216*, NY).

tion of the placement of the aperture, the pollen grains seem to lack polarity. It is uncertain if the aperture (it could be classified as an abbreviated sulcus) is proximal or distal.

Ultrathin sections made by these authors reveal a thick, heterogeneous intine which is significantly thicker than the exine. The intine consists of two strata with different electron-densities. Beside this, local thickenings of the outer in-

Plate 13. *Tetrameranthus pachycarpus*, detail of holotype specimen (*Klug 1216*, NY).

tine layer are found. The exine is usually formed by a thick outer and a thin, mostly lamellated layer. The outer layer forms a homogeneous smooth tectum (*sensu* Le Thomas 1981) in the extra-aperture region and lacks structural and sculptural elements, while the inner layer always consists of several (two or more) continuous, unfolded, thin lamellae. A foot-layer *sensu* Le Thomas is lacking, but these lamellae could also be interpreted as a special feature of a

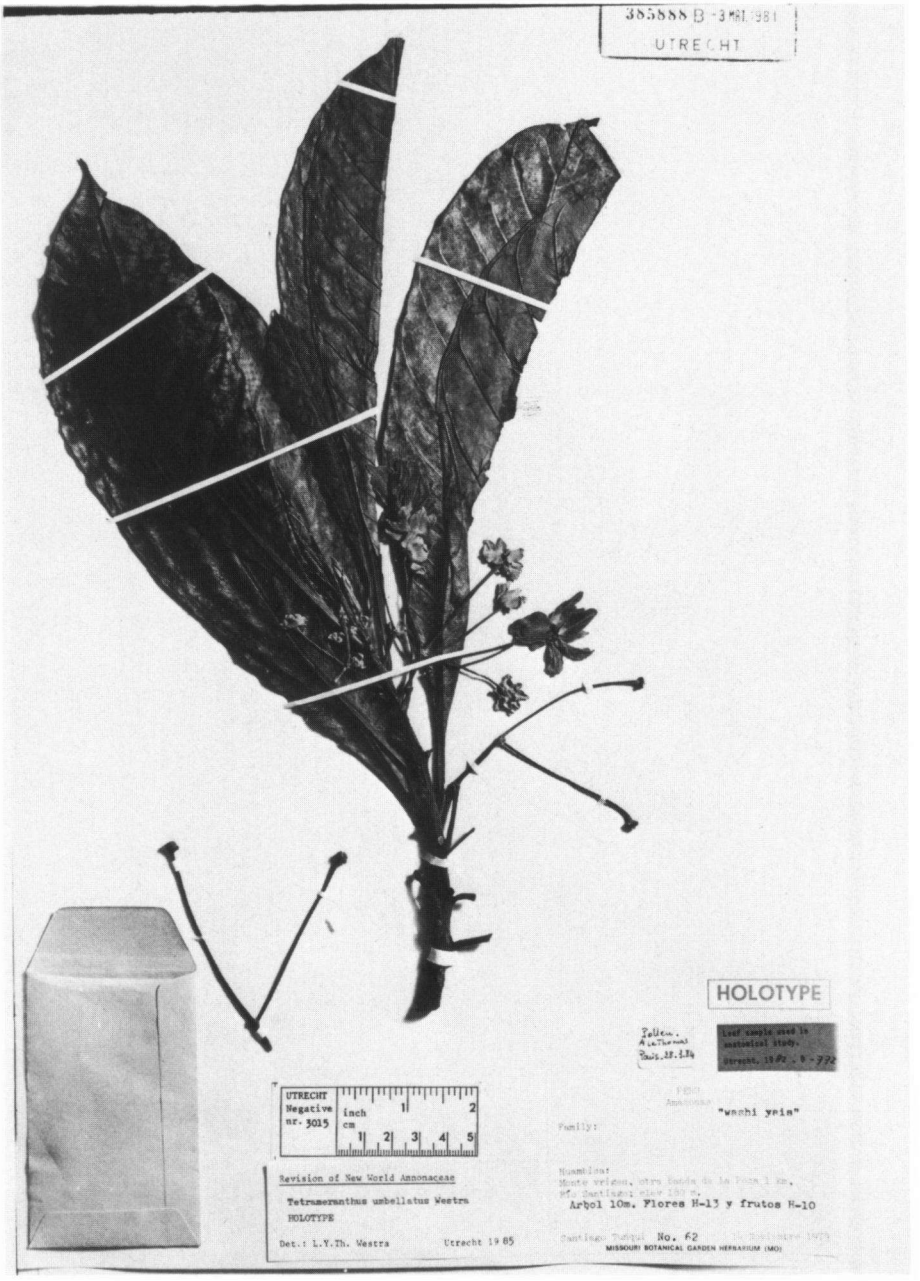


Plate 14. *Tetrameranthus umbellatus*, holotype specimen (*Tunqui 62*, U).

foot-layer. The homogeneous tectum of the extra-aperture region becomes isolated into globular elements in the aperture region; they are located on the outer face of the exine lamellae. Sometimes similar exine globules also appear on the inner face of the exine lamellae in the extra-aperture region. The results of this investigation, too: particularly the unfoliated basal exine lamellae, the exine globules inside the lamellae, and the partial intine thickenings - not

Plate 15. *Tetrameranthus umbellatus*, detail of holotype specimen (*Tunqui 62*, U).

paralleled in other Annonaceous genera –, show that *Tetrameranthus* takes up an isolated position within the Annonaceae.

FLOWER ECOLOGY

Extensive field observations on flowers of *Tetrameranthus duckei* were made by Webber in the region of Manaus (Webber 1981).

The flowering period covers about three days. The flowers, which are facing downwards, are protogynous, and the stigmas remain receptive for about 30 hours. The petals are not closed, except in young bud stage; the colour of the petals during the flowering period is yellowish.

In the first day the stamens are light cream-coloured. The stigmas are greenish in colour, and the stigmatic surface is covered with a slimy and viscous secretion. Odour is imperceptible, and no visitors are seen.

In the second day the petals unfold more and more, until about 16.00 hrs. The flowers now emit a musky odour, and the first visitors, Curculionid beetles, are present. In the course of the day the colour of the stigmas changes slightly (eventually, the stigmas become maroon). Towards noon the stamens change in colour to maroon, and become separated from each other. Now the anthers dehisce. Curculionidae walk over the stamens and the stigmas. In the course of the afternoon pollen becomes liberated, and visiting beetles crawl among the stamens eating pollen. Few Meliponidae are now also visiting the flower. In late afternoon the petals drop, whereas the odour then is very intense and can be perceived over a great distance. Towards the evening the odour diminishes again, but the Curculionids remain among the stamens.

In the third day there is a weak odour, and the visitors are still among the stamens. Later on during the morning the odour dissipates totally, and the Curculionids leave the flower.

The time lapse observed between pollination and fruit setting is about 90 days.

An experiment on self-pollination proved negative: none of six isolated flowers set fruit.

From these observations the Curculionidae emerge as pollinators of *T. duckei*. Numbers between 5 and 7 individuals on a flower were frequently encountered. Other visitors, like the Meliponidae already mentioned, probably do not play a role in pollination. Dipters (Drosophilidae) were observed visiting the flowers at night. Besides the pollinating beetles, Chrysomelid beetles were seen. They were eating buds and petals of flowers just becoming mature without, however, having access to the reproductive organs. Their activity largely was during the night, and rarely in the morning.

While *T. duckei* apparently is pollinated by beetles, the permanently open flowers do not exhibit the specialized type of beetle pollination observed in *e.g. Guatteria, Duguetia, Xylopia, Annona*, and *Porcelia* in which a pollination chamber is formed (Gottsberger, 1970, 1977).

There are no data on other species of *Tetrameranthus*.

GEOGRAPHICAL DISTRIBUTION AND ECOLOGY (Plate 4)

To judge from the small number of collections, *Tetrameranthus* as a whole can be considered as a rarity. *T. macrocarpus, T. pachycarpus*, and *T. umbellatus*, so far, each are known only from a small area, all situated in the western part of the Amazon drainage system (*T. macrocarpus* has been collected only once!). *T. duckei* now is known from two quite disjunct areas, *i.e.* around Manaus, Brazil, and in the vicinity of San Carlos de Río Negro in Southern Venezuela. Out of the species described up to and including this paper, only *T. laomae* is known to occur in a large area in the Amazon basin. The only place where the genus is found in larger numbers is the region around Manaus, where *T. duckei* appears to be fairly common.

T. duckei is a shrub to small tree found in savanna shrub vegetation, low forest, secondary vegetation, etc. Other species, as far as known, are (much) larger forest trees.

USES AND VERNACULAR NAMES

There is only one report that (wood of) *T. laomae* is used in construction work on farms. No other uses are known so far.

The following vernacular names are reported:
Banayo (Venezuela. Amazonas, *T. duckei*)
Cuchara (Venezuela. Amazonas, *T. duckei*)
Envira (Brazil. Amazonas, *T. duckei*)
Envireira (Brazil. Amazonas, *T. duckei*)
Palo de Cuchara (Venezuela. Amazonas, *T. duckei*)
Washi yais or Washi yéis (Peru. Amazonas, *T. umbellatus*)
Yaú (Peru. Amazonas, *T. umbellatus*).

SYSTEMATIC TREATMENT

Tetrameranthus R.E. Fries, Acta Horti Berg. **12**(3): 554. fig. 41. 1939; R.E. Fries in Engler & Prantl, Nat. Pflanzenfam., ed. 2, **17aII**: 166. fig. 38. 1959. – Type: *Tetrameranthus duckei* R.E. Fries.

Shrubs or trees. Branchlets terete to more or less angular in very young stage, internodes (2–)5–10 mm long, hirsute, pubescent, or puberulous, to densely so, becoming glabrous. Leaves in a spiral, simple, entire, concolorous, petiolate, estipulate, often crowded at the end of the branchlets in a way more or less reminiscent of Sapotaceae. Petioles mostly 10–30 mm long, slightly thickened toward base to uniform in diameter throughout, terete with the adaxial side more or less flattened to slightly canaliculate. Lamina mostly elliptic, narrowly elliptic, elliptic-obovate or narrowly elliptic-obovate, membranaceous to coriaceous, base cuneate to narrowly cuneate, apex acute to (abruptly, shortly) acuminate, the very apex, however, often obtuse or rounded, upper side hirsute, puberulous, to glabrous, on primary vein, otherwise mostly glabrous, lower side hirsute, pubescent, or puberulous, on primary vein, sparsely hirsute, pubescent, or puberulous, on secondary veins, to glabrous elsewhere, primary

vein impressed to slightly prominent above, prominent below, secondary veins straight to more or less curved, varying from 6–20 on either side of primary vein, impressed to more or less prominent above, prominent below, angle with primary vein mostly 50°–80°, not loop-forming to loop-forming at acute to right (or obtuse) angles, loops indistinct to distinct, the smallest distance between loops and margin < 1–5 mm, tertiary veins parallel to reticulate, flat and inconspicuous to prominulous above, prominulous to prominent below.

Indument of vegetative parts consisting of stellate tufts of 2–10(–20) trichomes > 0.1–0.5(–10) mm long.

Inflorescences axillary, single-flowered to pleiochasially umbellate, flower-stalk of first order articulate in the lower half, the articulation mostly suprabasal, to almost basal (one species), with 4 (or less) small, narrow bracts just below the articulation, caducous before or after flowering, flower-stalks (up to 4) of second order articulate at the base, and without bracts. Part of flower-stalk between the base and the verticil of bracts referred to as peduncle, the upper part, and the flower-stalks of second order, referred to as pedicel. Pedicles slightly elongating in fruit, both peduncle and pedicels thickening in fruit.

Indument of inflorescence parts, including outer side of sepals and petals, consisting of tufts similar to those of vegetative parts, though with sometimes slightly larger trichomes.

Flowers medium-sized; perianth normally tetramerous, consisting of one whorl of sepals and two whorls of petals. Sepals imbricate, free to connate just at the base, small in relation to the petals, dropping after flowering, of about equal length and width to slightly longer than wide. Petals imbricate, fleshy, the inner side with a callus or callus-like area of varying dimensions at the base. Outer petals mostly elliptic, ovate, or obovate. Inner petals generally somewhat smaller and narrower, and with slightly larger callus (or callus-like area), than the outer petals. Torus convex. Androecium acyclic; stamens mostly numerous (ca. 25 and up – more precise numbers to be established yet for *T. laomae* and *T. macrocarpus*), free, short and stout, the filamental part (as far as seen) < 1 mm long, apical prolongation of connective conical (to acuminate) or flat, anther extrorse to latrorse. Gynoecium apocarpous, carpels few to fairly numerous (4–17 observed), ellipsoid to oblongoid, stigma sessile, more or less lobed, ovules 2, lateral, superposed.

Monocarps free, moderate-sized to fairly large (to ca. 8 cm long, in dried condition!), fleshy, ellipsoid to oblongoid, often with an oblique constriction between the seeds (two-seeded ones), shortly stipitate to sessile, with a short, blunt beak to round at the apex, indehiscent; seeds 1 or 2, ascending and (when 2) obliquely superposed, slightly compressed dorsiventrally, ellipsoid, the surface smooth to more or less rugulose, the vascular bundle flat to slightly protruding.

KEY TO SPECIES OF *TETRAMERANTHUS*

1. Primary vein of leaves prominent to flat above. Stellate tufts minute, with trichomes mostly ≦0.1 mm long. Apical prolongation of connective flat 2
– Primary vein of leaves impressed above. Stellate tufts with trichomes >0.2 mm long. Apical prolongation of connective conical 3
2. Inflorescences umbellate with (up to) 5 flowers. Peduncle manifest, ≧15 mm long ..... *T. umbellatus*
– Inflorescences single-flowered. Peduncle rudimentary, <0.1 mm long ..... *T. laomae*
3. Callus area on inner side of petals mostly ≦3 mm long, *i.e.* <1/6 of total length of petal. Fruits with inconspicuous constriction (two-seeded specimens)..... *T. pachycarpus*
– Callus area on inner side of petals >4 mm long, *i.e.* ≧1/6 of total length of petal. Fruits with obvious oblique constriction (two-seeded specimens)..... 4
4. Fruits ≧3.5 cm in diam. Tree ..... *T. macrocarpus*
Fruits ≦2.5 cm in diam. Shrub to small tree..... *T. duckei*

1. **Tetrameranthus duckei** R.E. Fries, Acta Horti Berg. 12(3): 557. fig. 41. 1939. – Type: *Ducke s.n. (RB 23919).* Brazil. Amazonas: Manaus, Estrada do Aleixo, km 7, non-inundated forest, wet sandy soil, 14 Jun 1933, fl (holotype, S; isotype, S). Plates 5, 6.

Small tree to ca. 5 m tall. Branchlets 2–3 mm in diam. shortly below the apex, 3–5 mm in diam. in older part, terete, internodes 5–15 mm long, young parts hirsute to densely hirsute. Petioles 10–30(–40) mm long, (1–)1.5–3(–4) mm in diam., slightly thickened towards base, terete, slightly canaliculate above, hirsute to sparsely hirsute (becoming glabrous). Lamina elliptic to narrowly elliptic or obovate, (7–)10–25(–30) cm long, (2.5–)3.5–10(–11) cm wide, thinly coriaceous to coriaceous, sparsely hirsute on larger veins, otherwise glabrous below, sparsely hirsute on primary vein, otherwise glabrous above, base cuneate to narrowly cuneate, apex more or less abruptly acuminate, the very apex acute to rounded; primary vein impressed above, prominent below; secondary veins straight to more or less curved, ca. (8–)10–12 on either side of primary vein, more or less impressed above, prominent below, angles with primary vein (45°–)60°–80°(–90°), loop-forming at acute angles, loops distinct to indistinct, smallest distance between loops and margin 1.5–5 mm; tertiary veins parallel to reticulate, flat and inconspicuous to prominulous above, prominent below.

Indument of vegetative parts consisting of light brown stellate tufts with trichomes up to 0.5(–1.0) mm long.

Inflorescences one-flowered, rarely with more than one flower. Peduncle 5–12(–18) mm long, 1.5 mm in diam. when in flower, to 3 mm in diam. when in fruit, & becoming more or less swollen at the apex, hirsute to densely hirsute, becoming glabrous in age. Pedicel 10–20(–25) mm long, 1.5 mm in diam. when in flower, to 35(–40) mm long and to 3 mm in diam. when in fruit, densely hirsute, becoming glabrous in age. Bracts 4, linear-subulate, (2–)3–6 mm long, densely hirsute, caducous after flowering.

Indument of inflorescence parts consisting of tufts similar to those of vegetative parts.

Flowers green, (turning) to yellow (*in vivo*), with (strong) musky odour, or

strong fragrance of anise (*one report, referring to flower?*). Sepals elliptic to obovate, free, 5–7 mm long, 4 mm wide, thinly carnose, obtuse to rounded at the apex, densely hirsute on the outer side, inner side glabrous. Outer petals ovate, 20–25 mm long, 9–12 mm wide, carnose, obtuse at the apex, inner side with longitudinally plurisulcate callus at the base 5–6 mm long and extending across the whole width. Inner petals narrowly ovate, 15–20 mm long, 6–9 mm wide, carnose, more or less contracted at the base, apex more or less incurved, obtuse to acute, inner side with similar, but larger, callus at the base 7–8(–10) mm long. Both outer and inner petals densely pubescent to hirsute on both sides except for the callus, stellate hairs as mentioned before. Torus convex. Stamens ca. 50–90, 2–2.5 mm long, 1–1.2 mm wide and almost as thick, glabrous, filamental part 0.2–0.5 mm long, anthers extrorse to latrorse, locules 0.8–1.0 mm long, apical appendage of connective conical to acuminate, more or less curved toward the center, 1.0–1.5 mm long, ± 1 mm thick at base. Carpels 5–10, ellipsoid, ca. 1.5 mm long, densely pubescent, stigma sessile, more or less trilobed to irregularly lobed.

Monocarps ellipsoid to oblongoid, one-seeded or two-seeded and then with an oblique constriction, one-seeded to ca. 4.5 cm long and two-seeded to ca. 6.5 cm long, to 2.5 cm in diam., sessile to shortly stipitate, with a thick, blunt beak at the apex, glabrous. Seeds to 30 mm long, 20 mm wide.

Specimens examined: BRAZIL. Amazonas: Manaus [and surroundings], 21 Mar 1958, *Centro de Pesquisas Florestais, personnel of, INPA 6232* fr (INPA, S), 9 Mar 1956, *Chagas s.n.* fl (S), 26 Mar 1956, *L. Coêlho s.n. (INPA 3673)* fr (S), 1 May 1942, *Ducke 1908* fl (F, NY), 16 Jul 1937, *Ducke s.n. (RB 35313)* fl (S), 20 Sep 1957, *Ferreira 79/57* fl (S), 9 Aug 1983, *Morawetz et al. 21–9883* fl (WU), 23 Aug 1983, *Morawetz et al. 21–23883* fl (WU), 19 Aug 1983, *Morawetz et al. 22–19883* st (WU), 12 Sep 1983, *Morawetz et al. 24–12983* fl (WU), 26 Dec 1982, *Plowman et al. 12647* fr (U: distributed from NY), 19 Oct 1967, *Prance et al. 2721* fl (INPA, NY, US), 21 Dec 1966, *Prance et al. 3816* fr (NY, US), 17 Mar 1967, *Prance et al. 4679* fr (NY, US), 4 Jul 1961, *Rodrigues & L. Coêlho 2937* fl (U), 28 Jul 1961, *Rodrigues & Chagas 3068-A* fl (U), 17 Oct 1961, *Rodrigues & Lima 3454* st (U), 7 Dec 1961, *Rodrigues & D. Coêlho 3839* fr (U), 10 Feb 1970, *Rodrigues 8742* fr (INPA), 31 Jul 1980, *Webber 162* fl (U), 22 Jul 1980, *Webber 163* fl (U); mouth of Rio Uaupés, Feb 1959, *Pires et al. 7473* fr (S).

COLOMBIA. Vaupés: Puerto Colombia (opposite Venezuelan town of Maroa) and vicinity, alt. ca. 800–850 ft., Oct 31-Nov 2 1952, *Schultes et al. 18157* fr (US).

VENEZUELA. Amazonas: San Carlos de Río Negro [and surroundings], 17 Apr 1979, *Liesner 6744* fr (U: distributed from MO), 20 May 1979, *Liesner 7590* fr (U: distributed from MO), 22 Jan 1980, *Liesner 8598* fl (U: distributed from MO), 28 Jan 1980, *Liesner 8838* fr (U: distributed from MO), 17–18 Apr 1970, *Steyermark & Bunting 102721* fr (NY, US).

Distribution: Manaus and surroundings, Upper Río Negro region. Shrubs to small trees probably with preference for (white) sand.

Discussion: *T. duckei*, as far as now known, occurs in two disjunct and rather restricted regions. See, however, also remarks under "Unidentified specimens".

The population around Manaus looks quite homogeneous, whereas material collected near San Carlos de Río Negro shows more variation. The noticeable differences between the two populations are given in the following table.

Manaus	Upper Río Negro
Leaves mostly not exceeding 20 cm in length.	Leaves up to 25(–30) cm long.
Tertiary veins often inconspicuous above.	Tertiary veins (mostly) prominulous above.
Pedicel mostly not longer than 15 mm when in flower, to 25 mm when in fruit.	Pedicel to 20 mm (or more) long when in flower, to 35 mm (or more) long when in fruit.

There is, however, considerable overlap in variation range, which does not permit to grant formal taxonomic status to these two groups.

2. **Tetrameranthus laomae** D. Simpson, Phytologia **30**(5): 309. 1975. – Type: *Soria S. 64*. Peru. Loreto: Prov. Alto Amazonas: Distr. Yurimaguas, road from Yurimaguas to Tarapoto, km 19 from Yurimaguas, alt. 115 m, 11 Mar 1969, fl (holotype, F). Plates 7, 8, 9.

Tree up to about 25 m tall, 30 cm in diam. Branchlets 1–2 mm in diam. shortly below the apex, 3–4 mm in diam. in older part, terete, internodes 2–5(–10) mm long, young parts puberulous. Petioles 10–15 mm long, 1(–1.5) mm in diam., terete to more or less flattened, puberulous. Lamina obovate to narrowly obovate. (4.5–)7–15 cm long, (2–)2.5–5.5 cm wide, membranaceous to chartaceous, sparsely puberulous on primary vein, otherwise very sparsely puberulous to glabrous both below and above, base narrowly cuneate, the very base attenuate and decurrent along the petiole, apex acute to abruptly acuminate, the very apex acute to obtuse; primary vein slightly prominent above, prominent below; secondary veins straight to more or less curved, ca. (6–)7–9(–10) on either side of primary vein, more or less prominent above, clearly prominent below, angles with primary vein 60°–70°, not loop-forming to loop-forming at (mostly) acute angles, loops mostly indistinct, smallest distance between loops and margin 2–4 mm; tertiary veins (mostly) reticulate, also more or less tending to form intersecondary veins, prominulous on both sides.

Indument of vegetative parts consisting of tiny whitish (or light olive-green) stellate tufts with trichomes (mostly) not exceeding 0.1 mm in length.

Inflorescences one-flowered, sessile (peduncle 0–< 1 mm long). Pedicel to ca. 15 mm long, 1 mm in diam. when in flower, to 25 mm long and 3 mm in diam. when in fruit, puberulous, becoming glabrous. Bracts 3 (always?), narrowly triangular, to 1 mm long, densely puberulous on the outer side, caducous after flowering.

Indument of inflorescence parts consisting of tufts similar to those of vegetative parts.

Flowers yellow (*in vivo*). Sepals broadly elliptic to oblong, free, to 2.5 mm long, 2 mm wide, obtuse to rounded at the apex, densely puberulous on the outer side. Outer petals ovate-elliptic, 10–16 mm long, 5–8 mm wide, acute to obtuse at the apex. Inner petals narrowly elliptic, 8–11 mm long, 3–4 mm wide, acute at the apex. Both outer and inner petals puberulous on both sides, but glabrous at the base on the inner side; stellate hairs as mentioned before. Stamens with "connective expanded and flat on top" [Simpson]. Carpels "8, densely pilose, stigmas sessile" [Simpson].

Monocarps ellipsoid to oblongoid, mostly (?) two-seeded and with an oblique constriction, to 4.5 cm long and to 2 cm in diam., shortly stipitate (to almost sessile), (mostly) round at the apex, orange (*in vivo*). Seeds to 25 mm long, 20 mm wide.

Specimens examined: BRAZIL. Acre: vicinity of Serra da Moa, forest on terra firme, 22 Apr 1971, *Prance et al. 12236* fl (U: distributed from NY). Amazonas: Mun. Itapiranga, Rio Uatumã, right margin, above confluence of Rio Uatumã with Rio Pitinga, forest on river margin, sandy soil, 26 Aug. 1979, *Cid et al. 824* fr (U: distributed from NY). Pará: Mun. Oriximiná, Rio Trombetas, Lago Maincoé, 8 km NE of Mineração Santo Patricia, campina, alt. 80 m, 8 Jul 1980, *Martinelli 7338* fr (U: distributed from NY).

PERU. Loreto: Prov. Maynas: Guarnicion Pijuayal, near Pebas, alt. ca. 130 m, 7 Sep 1978, *Díaz et al. 571* fr (MO). Pasco: Prov. Oxapampa: Cabeza de Mono, Río Iscozacin, Palcazu Valley, sandy river terraces (tree plot), alt. 320 m, 9 Jun 1983, *Gentry et al. 41743* fr (U: distributed from MO).

Distribution: Of rare occurrence throughout Peruvian and Brazilian Amazonia.

Discussion: *T. laomae* is easily recognized by the strongly reduced peduncle; vegetatively, it much resembles *T. umbellatus*.

3. **Tetrameranthus macrocarpus** R.E. Fries, Ark. Bot. Ser. 2, **3**(18): 603. plate 4. 1956. – Type. *Schultes & Cabrera 17091*. Colombia. Vaupés: Río Piraparaná, Raudal Koro, 30 Aug 1952, fl, fr (holotype, S; isotypes, GH, U). Plates 10, 11.

Shrub to tall tree. Branchlets 3–4 mm in diam. shortly below the apex, 5–6 mm in older part, terete, internodes 5–8 mm long, young parts hirsute to densely hirsute. Petioles 20–30 mm long, 3–4 mm in diam., slightly thickened towards base, terete, scarcely flattened above, hirsute, (soon) becoming glabrous. Lamina elliptic to obovate, (13–)14–20 cm long, 5.5–8 cm wide, coriaceous, hirsute to sparsely hirsute on primary vein, sparsely hirsute on secondary veins, otherwise glabrous below, glabrous above, base cuneate to narrowly cuneate, apex acute to shortly and abruptly acuminate, the very apex acute to obtuse; primary vein impressed above, prominent below; secondary veins straight to more or less curved, ca. 9–11 on either side of primary vein, impress-

ed above, prominent below, angles with primary vein 50°–60°, not loop-forming to loop-forming at acute angles, loops mostly indistinct, smallest distance between loops and margin 1–2 mm; tertiary veins more or less parallel to reticulate, mostly flat and inconspicuous above, slightly prominulous below.

Indument of vegetative parts consisting of light brown stellate tufts with trichomes up to 0.4(–0.7) mm long.

Inflorescences one-flowered. Peduncle to 5 mm (?) long, 2–2.5 mm in diam. when in flower, to 5 mm in diam. when in fruit, hirsute, becoming glabrous in age. Pedicel 25–30 mm long, 2 mm in diam. when in flower, to 3 mm in diam. when in fruit, hirsute, becoming glabrous in age. Bracts 4, triangular to narrowly triangular, ca. 2 mm long, hirsute, caducous after flowering.

Indument of inflorescence parts consisting of stellate tufts with rays generally up to 0.3 mm long.

Sepals broadly triangular-ovate, connate just at the base, 3–4 mm long and wide, obtuse to rounded at the apex, pubescent to densely pubescent on the outer side, inner side glabrous. Outer petals elliptic, 25–30 mm long, 12–15 mm wide, narrowed at the base into a more or less distinct claw, acute to obtuse at the apex, glandular area covering inner side of claw, to ca. 5 mm long. Inner petals 20–25 mm long, otherwise (largely) similar to outer petals. Stamens "numerous, 3 mm long, apical appendage of connective with conical prolongation" [R.E. Fries]. Carpels "4 (always?), short-cylindrical, 3 mm long, hirsute, stigma disk-shaped" [R.E. Fries].

Monocarps ellipsoid to oblongoid, one-seeded or two-seeded and then with an oblique constriction, one-seeded to ca. 6 cm long, two-seeded to ca. 8 cm long, to 3.5 (–4) cm in diam., more or less narrowed into a short stipe, round at the apex, glabrous. Seeds to 35 mm long, 28 mm wide.

Distribution: Only known from the type collection.

4. **Tetrameranthus pachycarpus** Westra, sp. nov. – Type. *Klug 1216*. Peru. Loreto: Mishuyacu, near Iquitos, alt. 100 m, Apr 1930, fl (holotype, NY; isotype, U). Plate 2: fig. 1; Plates 12, 13.

Arbor ad 25 m alta. Folia elliptica, anguste elliptica, vel – obovata, 17–22 cm longa et 5–10 cm lata, coriacea, costa supra impressa, subtus prominente, venis secundariis utroque latere c. 10–15.

Flores singuli axillares pedunculo 4–5 mm longo pedicelloque 10–15 longo suffulti, bracteis mox caducis. Sepala late elliptica, 3–4 mm longa et lata. Petala exteriora elliptica vel oblonga, basi intus callosa. Petala interiora anguste elliptica vel oblonga, petalis exterioribus paullo angustiora, basi intus callosa. Stamina 25–30, filamento brevissimo, anthera latrorsa, appendice connectivi plusminusve conico. Carpella 4–8, stigmate irregulariter lobato.

Monocarpia (plerumque) ellipsoidea, seminibus 1 vel 2, constrictione inconspicua, ad ca. 7 cm longa et c. 4 cm in diametro.

Tree to 25 m tall. Branchlets 2–4 mm in diam. shortly below the apex, to 6 mm in diam. in older part, terete, internodes 5–10 mm long, young parts pubes-

cent to densely pubescent to -hirsute. Petioles 20–30 mm long, 2–4 mm in diam., slightly thickened towards base, terete, more or less flattened above, pubescent to hirsute, becoming glabrous. Lamina elliptic, elliptic-obovate, to narrowly elliptic or narrowly elliptic-obovate, 17–22 cm long, 5–10 cm wide, coriaceous, pubescent to sparsely pubescent on larger veins, otherwise very sparsely pubescent to glabrous below, pubescent to almost glabrous on the primary vein, otherwise glabrous above, base cuneate to narrowly cuneate, apex acute to acuminate, the very apex obtuse to rounded; primary vein impressed above, prominent below; secondary veins straight to (mostly) more or less curved, ca. 10–15 on either side of primary vein, impressed above, prominent below, angles with primary vein 60°–70°(–80°), not loop-forming or loop-forming at acute to right angles, loops indistinct to distinct, smallest distance between loops and margin 2–3 mm, tertiary veins parallel to more or less reticulate, flat and inconspicuous to slightly prominulous above, prominulous below.

Indument of vegetative parts consisting of light brown stellate tufts with trichomes up to 0.3(–1.0) mm long.

Inflorescences one-flowered. Peduncle 4–5 mm long, 1.5–2 mm in diam. when in flower, to 5 mm in diam. when in fruit, pubescent to densely pubescent, becoming glabrous in age. Pedicel 10–15 mm long, 1.5–2 mm in diam. when in flower, to 25 mm long, 3–4 mm in diam. when in fruit, pubescent to densely pubescent, becoming glabrous in age. Bracts (probably) 4, (narrowly) triangular, ca. 2 mm long, densely pubescent, caducous (before flowering).

Indument of inflorescence parts consisting of tufts (largely) similar to those of vegetative parts.

Flowers yellow-green (*in vivo*). Sepals broadly elliptic, connate just at the base (?), 3–4 mm long and wide, acute to obtuse at the apex, densely pubescent on the outer side, inner side glabrous. Outer petals (narrowly) elliptic to oblong, to 35 mm long and 16 mm wide, somewhat narrowed at the base, obtuse to rounded at the apex, callus area on inner side to (2–)3 mm long. Inner petals narrowly elliptic to oblong, somewhat smaller than outer petals, acute (to obtuse) at the apex, callus area on inner side to 3(–4) mm long. Stamens 25–30, ca. 2 mm long, 1 mm wide, glabrous, filamental part 0.3–0.5 mm long, anthers latrorse, locules 0.5–0.8 mm long, apical appendage of connective more or less conical, more or less curved towards the center. Carpels 4–8, ellipsoid, ca. 2 mm long, densely pubescent, stigma sessile, irregularly lobed.

Monocarps (mostly) ellipsoid, one- or two-seeded, oblique constriction (in two-seeded fruits) rather inconspicuous, to ca. 7 cm long and ca. 4 cm in diam. Seeds to 40 mm long, 28 mm wide.

Specimens examined: PERU. Loreto: Prov. Maynas: Mishana (Iquitos), alt. 100 m, 12 Aug 1978, *Ayala 1564* fr (AMAZ); Mishana, Río Nanay, alt. ca. 140 m, 14 Aug 1978, *Díaz et al. 404* fr (MO); Callicebus Biological Res. 4 km S of Mishana, 30 km SW of Iquitos, 26 Aug 1978, *Foster 4271* fr (F, U); Mishana, Río Nanay halfway between Iquitos and Santa Maria de Nanay, Tree Plot ca. 1 km N of Campamento 1, Tree # 436, alt. 140 m, 10 jan 1983, *Gentry et al. 39313* fr (U: distributed from MO).

Distribution: Vicinity of Iquitos, Peru; in forest at low altitudes, on white sand.

Discussion: The fruit of *T. pachycarpus*, with an (in two-seeded fruits) inconspicuous lateral constriction, and a very thick wall, is quite unlike the fruit of any *Tetrameranthus* species seen so far. Otherwise, this species much resembles *T. macrocarpus*, and possibly is closely related to it.

Note: one flower of the type collection is 5-merous. One collector mentions transparent resin.

5. **Tetrameranthus umbellatus** Westra, sp. nov. - Type. *Tunqui 62*. Peru. Amazonas: Río Santiago, Huambisa, other side of La Poza 1 km, alt. 180 m, 14 Nov 1979, fl (holotype, U; isotype, MO). Plates 1, 14, 15.

Arbor ad 15 m alta. Folia anguste elliptica ad ovata, 15–30 cm longa et 4–9 cm lata, basi anguste cuneata in petiolum plerumque 20–25 mm longum decurrentia, costa supra plana vel leviter impressa, subtus prominente, venis secundariis utroque latere plerumque 15–18.

Flores 5 in umbellis in axillis foliorum, pedunculis 15–25 mm longis et pedicellis 40–70 mm longis, bracteis mox caducis. Sepala triangularia-ovata ad ovata, basi ipsa connata, ad 4 mm longa. Petala exteriora ovata-elliptica, 16–20 mm longa, 9–12 mm lata, basi intus callosa. Petala interiora anguste elliptica, 13–17 mm longa, 6–7 mm lata, basi intus callosa. Stamina c. 80–90, filamento brevissimo, anthera latrorsa vel plusminusve extrorsa, appendice connectivi pulviniformi. Carpella 17 (quoad florem visum), stigmate trilobato vel irregulariter lobato.

Monocarpia (ellipsoidea vel) oblongoidea, seminibus 1 vel 2, oblique constricta, ad 4.5 cm longa et 2 cm in diametro.

Tree to about 15 m tall. Branchlets to ca. 4 mm thick shortly below the apex, 5–7 mm in diam. in older part, more or less angular below the apex, becoming terete when older, internodes 5–10 mm long, young parts puberulous to densely puberulous. Petioles (10–)20–25 mm long, 1.5–3 mm in diam., flattened to slightly canaliculate above, puberulous to densely puberulous (becoming glabrous). Lamina narrowly elliptic-ovate, 15–30 cm long, 4–9 cm wide, chartaceous, puberulous to sparsely puberulous on primary vein, otherwise sparsely puberulous to (nearly) glabrous below, puberulous to nearly glabrous on primary vein, otherwise (very) sparsely puberulous to glabrous above, base narrowly cuneate, decurrent along the petiole, apex acute to more or less abruptly and shortly acuminate; primary vein flat to slightly impressed above, prominent below; secondary veins mostly straight, to slightly curved, ca. (13–)15–18(–20) on either side of primary vein, slightly impressed to slightly prominulous above, prominent below, angles with primary vein 50°–70°, loopforming at (acute to) right to obtuse angles, loops mostly distinct, smallest distance between loops and margin 0.5–2 mm; tertiary veins parallel to more or less reticulate, flat and inconspicuous to prominulous above, prominent below.

Indument of vegetative parts consisting of tiny whitish stellate tufts with trichomes (mostly) not exceeding 0.1 mm in length.

Inflorescences (up to) 5-flowered umbels often arising from every axil. Peduncle 15–25 mm long, to 1.5(–2) mm in diam. when in flower, to 3(–4) mm in diam. when in fruit, puberulous to densely puberulous, becoming glabrous in age. Pedicels 40–70 mm long, 1.0–1.2(–1.5) mm in diam. when in flower, to 3(–3.5) mm in diam. when in fruit, puberulous to densely puberulous, becoming glabrous in age. Bracts (4) oblong, 4–5 mm long, (broadly) obtuse at the apex, densely puberulous on the outer side, caducous before flowering.

Indument of inflorescence parts consisting of tufts similar to those of vegetative parts.

Sepals broadly triangular-ovate to ovate, connate just at the base, to 4 mm long, 3–5 mm wide, obtuse to rounded at the apex, densely puberulous on the outer side, the inner side puberulous to densely puberulous, but glabrous at the base. Outer petals ovate-elliptic, 16–20 mm long, 9–12 mm wide, subacute to obtuse at the apex, with 11–13 more or less prominulous veins, inner side callose at the base. Inner petals narrowly elliptic, 13–17 mm long, 6–7 mm wide, obtuse to rounded at the apex, with 5 prominulous veins, inner side callose at the base, the callus slightly larger than that of the outer petals. Both outer and inner petals puberulous to densely puberulous on both sides except for the base on the inner side, where glabrous. Stamens ca. 80–90, 0.7–1.0 mm long, 0.5–0.7 mm thick, glabrous, filamental part 0.2–0.3 mm long, apical appendage of connective cushion-shaped, flat, 0.2 mm high. Carpels 17 (in the flower examined), oblongoid, slightly constricted between ovary and stylar part, 1.5 mm long, densely pubescent, stigma trilobed to irregularly lobed.[1]

Monocarps (ellipsoid to) oblongoid, one-seeded to (mostly) two-seeded and with an oblique constriction, to 4.5 cm long and to 2 cm in diam., almost sessile, mostly round at the apex, glabrous. Seeds to 25 mm long, 18 mm wide.

Specimens examined: PERU, Amazonas: Río Santiago, 2 km below Community of Caterpiza, Trocha de Mitayar, east side of Quebrada Caterpiza, 13 Sep 1979, *Huashikat 613* fl, fr (MO, U), Quebrada Sasa, Monte Numi, alt. 600 m, 25 Aug 1975, *Kayap 2015* fr (MO, U).

Distribution: State of Amazonas, Peru.

Discussion: *T. umbellatus* is remarkable because in this species leaf axils carry small umbels instead of solitary flowers.

UNIDENTIFIED SPECIMENS

Prance et al. 25602. Brazil. Pará: BR 163, Cuiabá-Santarém Highway, km 1225, forest on terra firme, 21 Nov. 1977, fr (U: distributed from NY).

Tree 20 m × 15 cm diam. A fruiting collection, much like *T. umbellatus*, but different from it by the much shorter (≦ 5 mm) petioles.

Lleras et al. P17302. Brazil. Amazonas: Rio Javari, behind Estirão de Equador, primary forest on terra firme, 11 Aug 1973, fl (U: distributed from NY).

[1] The flower dissected was not fully mature. Measurements of stamens and carpels, therefore, may require modification at a later time.

Treelet 6 m tall. Flowers green. A flowering collection resembling *T. duckei*, but distinct by longer pedicels (35–40 mm long vs. up to 25 mm in *T. duckei*), and broadly ovate, broader outer petals (ca. 15 mm wide, vs. ovate outer petals to 12 mm wide in *T. duckei*). It is difficult to judge, having only one collection at hand from a region well away from either of the two distribution centers of *T. duckei*, whether this falls within the variability range of *T. duckei* or whether it is an undescribed taxon.

ACKNOWLEDGEMENTS

Many thanks are due to Dr. P.J.M. Maas and Dr. J. Koek-Noorman for critically reading the manuscript. Thanks are also extended to Mrs. A.K. van Setten and Ing. B.J.H. ter Welle for their stimulating help and advise.

The author also wishes to thank Prof. Dr. G. Gottsberger, Giessen, for a fruitful discussion on flower pollination. Prof. Gottsberger also was so kind to provide a copy of Webber's thesis concerning observations on pollination in *Tetrameranthus duckei*, and to lend a colour slide, taken by Webber, of a mature flower of that species.

Thanks are also due to Dr. W. Morawetz, Vienna, for providing pickled flowers of *T. duckei*, and for lending his own colour slides of the inflorescence of *T. duckei*.

The author is much indebted to the curators of the following herbaria, from which material was received on loan: AMAZ, F, GH, INPA, MO, NY, S, US, WU.

Finally, thanks go to Mr. W. Driehuis and Mr. P.C. Postema for the time and care they spent in administration of loans and making photographs of type sheets, and, last but not least, to Mr. H. Rypkema and Mr. T. Schipper for making the drawings.

REFERENCES

Fries, R.E. – Studien über die Blütenstandsverhältnisse bei der Familie Anonaceae. – Acta Horti Berg. **6**(6), 3–48 (1919).

Fries, R.E. – Revision der Arten einiger Annonaceen-Gattungen. V. – Acta Horti Berg. **12**(3), 554–558, Fig. 41 (1939).

Fries, R.E. – New species of Annonaceae from the Upper Amazon Basin. – Ark. Bot. Ser. 2, **3**(18), 603–604 (1956).

Fries, R.E. – Annonaceae. – In Engler, A. & Prantl, K. (eds.): Die natürlichen Pflanzenfamilien, ed. 2, **17aII**, 44, 166–167, Fig. 38 (1959).

Gentry, A. – Flora Neotropica news. – Taxon **33**, 355–358 (1984).

Gottsberger, G. – Beiträge zur Biologie von Annonaceen-Blüten. – Österr. Bot. Z. **118**, 237–279 (1970).

Gottsberger, G. – Some aspects of beetle pollination in the evolution of flowering plants. – Plant. Syst. Evol., Suppl. **1**, 211–226 (1977).

Hesse, M., and M. Waha – Sporoderm characters of *Tetrameranthus duckei* (Annonaceae) and their systematic implications. – Plant. Syst. Evol. **147**, 323–326 (1984).

Jovet-Ast, S. – Recherches sur les Annonacées d'Indochine. – Mém. Mus. Natl. Hist. Nat., Nouvelle série **16**, 125–308 (1942).

Le Thomas, A. – Ultrastructural characters of pollen grains of African Annonaceae and their significance for the phylogeny of primitive angiosperms. – Pollen & Spores **22**, 265–342, and **23**, 5–36 (1981).

Roth, J.L. – Epidermal studies in the Annonaceae and related families. – Thesis, Indiana University, 1981.

Van Setten, A.K. and J. Koek-Noorman - Studies in Annonaceae. V. A leaf anatomical survey of genera of Annonaceae in the Neotropics. - In preparation.
Simpson, D.R. - New species from South America. II. - Phytologia **30**, 309-310 (1975).
Vander Wijk, R.W. and J.E. Canright - The anatomy and relationships of the Annonaceae. - Trop. Woods **104**, 1-24 (1956).
Walker, J.W. - - Pollen morphology, phytogeography, and phylogeny of the Annonaceae. - Contr. Gray Herb. **202**, 3-130 (for *Tetrameranthus*, see p. 17, 19, 24, 40, 46, 49, 52), Plate 7, Fig. 11 (1971).
Webber, A.C. - Biologia floral de algumas Annonaceae na região de Manaus AM. - Thesis, Instituto Nacional de Pesquisas da Amazônia and Fundação Universidade do Amazonas, 1981.
Ter Welle, B.J.H.. - Variation and diversity in the Annonaceae. - Proceedings PRWAC, Tsukuba, Japan, 1984a.
Ter Welle, B.J.H. - Wood anatomy. - In Maas, P.J.M. & Westra, L.Y.Th. (eds.): Studies in Annonaceae. II. A monograph of the genus *Anaxagorea* A. St. Hil. Part. 1. - Bot. Jahrb. Syst. **105**, 82-84 (1984b).

NUMERICAL LIST OF TAXA

1. *Tetrameranthus duckei* R.E. Fries
2. *Tetrameranthus laomae* D. Simpson
3. *Tetrameranthus macrocarpus* R.E. Fries
4. *Tetrameranthus pachycarpus* Westra
5. *Tetrameranthus umbellatus* Westra

INDEX OF EXSICCATA

Note 1: Co-collectors who, at one time or another, cooperated in a given collector's number series, are mostly not mentioned separately. Instead, in such cases the principal collector with the addition *et al.* is listed. An entry like *Rodrigues, W., et al.*, therefore, may include both collections made by *W. Rodrigues* alone and collections by *W. Rodrigues* together with one or more other collectors.
Note 2: As regards citation of institutional collection numbers, guidelines for collection numbering and citation in monographs by A. Gentry (1984) have been followed. In cases where both an individual and an institutional collection number are mentioned on the label, only the individual number is mentioned here.

Ayala, F., 1564 (4).
Centro de Pesquisas Florestais, personnel of, INPA 6232 (1).
Chagas, J., s.n. (1).
Cid, C.A., et al. 824 (2).
Coêlho, D., s.n. (wood sample seen only INPA X7330, Uw 26747).
Coêlho, L., s.n. (INPA 3673) (1), *s.n. (INPA 69232)* (wood sample seen only INPA X7328, Uw 26746).
Díaz, S., et al. 404 (4); *571* (2).
Ducke, A., 1908 (1); *s.n. (RB 23919)* (1); *s.n. (RB 35313)* (1).
Ferreira, E., 79/57 (1).
Foster, R.B., 4271 (4).
Gentry, A., et al. 39313 (4); *41743* (2).
Huashikat, V., 613 (5).
Kayap, R., 2015 (5).
Klug, G., 1216 (4).
Liesner, R.L., 6744 (1); *7590* (1); *8598* (1); *8838* (1).
Lleras, E., et al. P17302 (see "Unidentified specimens").
Martinelli, G., 7338 (2).
Morawetz, W., et al. 21-9883 (1); *21-23883* (1); *22-19883* (1); *24-12983* (1).
Pires, J.M., et al. 7473 (1).
Plowman, T., et al. 12647 (1).
Prance, G.T., et al. 2721 (1); *3816* (1); *4679* (1); *12236* (2); *25602* (see "Unidentified specimens").
Rodrigues, W., et al. 2937 (1); *3068-A* (1); *3454* (1); *3839* (1); *8742* (1).
Schultes, R.E., & Cabrera, I., 17091 (3); *18157* (1).
Soria, S., M.A., 64 (2).
Steyermark, J.A., & Bunting, G., 102721 (1).
Tunqui, S., 62 (5).
Webber, A.C., 162 (1); *163* (1).