

A revision of *Lissocarpa* BENTH. (Ebenaceae subfam. Lissocarpoideae (GILG in ENGLER) B.WALLN.)

B. Wallnöfer*

With a contribution on its pollen morphology by H. Halbritter

Abstract

In the course of a revision of the neotropical Ebenaceae for "Flora Neotropica" and some other regional floras, specimens of *Lissocarpa* from ca. 40 herbaria have been studied. Currently, the genus comprises 8 species, distributed in northern and western South America. Full descriptions, including illustrations of species, a key for identification, distribution maps and a list of exsiccates are provided. This revision is further complemented with data pertaining to vegetative morphology and anatomy, flachnektarien (extrafloral nectaries), inflorescence and flower structure, pollen morphology (contributed by H. Halbritter), fruits and seeds, seedlings, ecology, and phylogenetic affinities. The former family Lissocarpaceae is here transferred to the Ebenaceae as its new subfamily Lissocarpoideae. A new section, *Enho*, and the species *Lissocarpa kating*, *L. ronliesneri* and *L. uyat*, are here described as new.

Key words: Ebenaceae, Lissocarpaceae, Lissocarpoideae, *Lissocarpa*, *Lissocarpa* section *Enho*, taxonomy, revision, new species, *Lissocarpa kating*, *Lissocarpa ronliesneri*, *Lissocarpa uyat*, Flora of South America.

Zusammenfassung

Im Rahmen einer Revision der neotropischen Ebenaceae für "Flora Neotropica" und einige andere Regionalfloras wurden Belege von *Lissocarpa* aus rund 40 Herbarien eingehend studiert. Die Gattung umfasst derzeit 8 Arten, die im nördlichen und westlichen Südamerika beheimatet sind. Beschreibungen und Abbildungen aller Arten, ein Bestimmungsschlüssel, Verbreitungskarten und eine Liste der Exsiccata werden präsentiert. Vorgelegt wird auch eine Zusammenfassung der relevanten Daten betreffend vegetative Morphologie und Anatomie, Flachnektarien (extraflorale Nektarien), Infloreszenz- und Blütenstruktur, Pollen (beigesteuert von H. Halbritter), Früchte und Samen, Keimlinge, Ökologie und Verwandtschaftsverhältnisse. Die frühere Familie Lissocarpaceae wird hier als neue Unterfamilie Lissocarpoideae zu den Ebenaceae gestellt. Die Sektion *Enho*, sowie die folgenden Arten werden hier erstmals beschrieben: *Lissocarpa kating*, *L. ronliesneri* und *L. uyat*.

Introduction, historical overview, and affinities

The genus *Lissocarpa* is native to northern and western South America. The name of the genus was coined by BENTHAM (1876), based on two collections gathered by Spruce (numbers 3108 and 3504) in southern Venezuela, but he did not assign a specific epithet to them. The first species (*L. benthamii*) was later named by GÜRKE (1891), and independently, also by BAILLON (1892). Another species (*L. tetramera*), occurring in Bolivia, first described as a member of the genus *Diospyros* by RUSBY (1896), has

* Dr. Bruno Wallnöfer, Naturhistorisches Museum Wien, Botanische Abteilung, Burgring 7, Postfach 417, A-1014 Wien, Austria; (e-mail: bruno.wallnoefer@nhm-wien.ac.at).

recently been transferred to *Lissocarpa* by BERRY (1999). The third species (*L. guianensis*), collected in Guyana, was described by GLEASON (1926). *L. stenocarpa*, occurring on slopes of the Tepui (table mountains) in southern Venezuela, has been made known to science by STEYERMARK in 1987. So far, *L. jensonii*, growing in the lowland rain forests of northeastern Peru, was the latest new species to be published (VÁSQUEZ 1993). In the present paper, *L. kating* (occurring in southeastern Colombia, northwestern Brazil, and northeastern Peru), *L. ronliesneri* (southern Ecuador), and *L. uyat* (northern Peru) are described as new to science.

The systematic placement of *Lissocarpa* has been controversial since the beginning. The first specimens, collected by R. Spruce, were distributed to various herbaria with the provisional determination "Ebenacea gen. nov.". Several years before the genus *Lissocarpa* was described, W. P. Hiern, the monographer of the Ebenaceae [for this see HIERN 1873], studied some of these sheets in the herbaria at K and BR and annotated them with pencil as: "Styracacea (?) – W. P. H.". When BENTHAM (1876) first described the genus, he accommodated it within the Styracaceae, an opinion in which he was followed also by GÜRKE (1891). OLIVER (1895), on the other hand, suggested again a relationship with the Ebenaceae, and in her monograph of the Styracaceae, PERKINS (1907) finally excluded *Lissocarpa* from that family. GILG (1908) after having discussed its affinities, later (GILG 1924) formally transferred it into its own family Lissocarpaceae. And until recently, most subsequent authors, such as HUTCHINSON (1959, 1967), NG (1971, 1991), CRONQUIST (1981), WHITE (1981), FRANCESCHI (1993), and TAKHTAJAN (1997), all accepted GILG's judgment, keeping this family as a member of the order Ebenales (with the exception of HUTCHINSON, who positioned it into the order Styracales). NG (1971, 1991) and FRANCESCHI (1993) even pointed out that Lissocarpaceae are the closest living relatives of Ebenaceae. GENTRY (1993) and VÁSQUEZ (1997) treated *Lissocarpa* as a member of the Ebenaceae.

Meantime, new results, based on modern molecular techniques, showed that the Ebenales are not a natural order (MORTON et al. 1997; SOLTIS et al. 1997, 2000; NANDI et al. 1998). It also became evident that the family status of the Lissocarpaceae has to be denied and that the genus *Lissocarpa* has to be included in the monophyletic Ebenaceae, a family which has now to be placed within the expanded order of the Ericales (BERRY et al. 2001; ANDERBERG et al. 2002; BREMER et al. 2002; APG II 2003). However, on account of the remarkable differences, especially in floral characters (see next paragraph), between *Lissocarpa* on the one hand, and *Diospyros* and *Euclea* on the other, the former (*Lissocarpa*) is here placed into its own subfamily. This transfer, as well as some other new results presented in this revision will, unfortunately, be missing in WALLNÖFER (2004a, b), because these manuscripts had been submitted for publication long ago already and can not be updated anymore.

In its vegetative parts, *Lissocarpa* shares various characters with *Diospyros* and *Euclea*, such as, e.g., the black color of roots and bark, the presence of flachnektarien (extrafloral nectaries) on abaxial sides of leaves, the persistent calyx, unisexual flowers, biovulate carpels with pendulous ovules (placentation apical), and wood anatomy (see also the comparative tables in NG 1991; WALLNÖFER 2001). However, a remarkable difference is the general absence of any indumentum in *Lissocarpa* (except on stigmas). Even more striking are divergences in inflorescence structure and among floral organs,

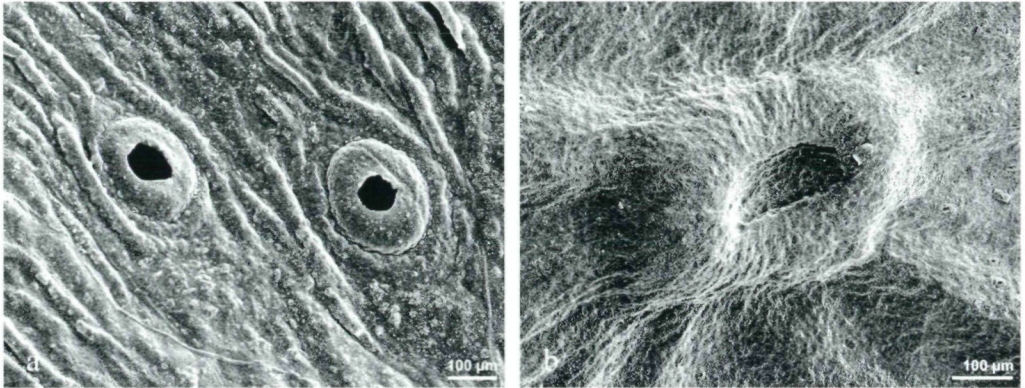


Fig. 1. **a:** Stomata of *Lissocarpa kating* (from Prance et al. 23855); **b:** flachnektarium (extrafloral nectarium) of *L. kating* (from Vásquez & Ortiz-Gentry 25233). [photographs: H. Halbritter].

such as inflorescences indeterminate (v. determinate in *Diospyros* and *Euclea*), ovary inferior (v. superior), bracteoles subopposite at the base of the ovary (v. bracteoles clearly alternate and somewhat distant from the ovary), corolla in species of section *Lissocarpa* with a corona (v. corolla always without a corona), carpels undivided (v. carpels divided in most species, into two locules, by a false, longitudinal septum).

Vegetative anatomy

In *Lissocarpa*, flachnektarien (extrafloral nectaries; see Fig. 1b) which are round, or slightly elongated and patelliform in shape, occur on abaxial leaf surfaces, scattered near the base, the apex, the margins, or near the midvein, and less frequently on other parts of the lamina. Their light brown margins are somewhat thickened and raised, and the centers usually slightly sunken, brown, or often black. Although somewhat smaller (usually not exceeding 0.6 mm), these nectaries have the same appearance than those occurring on leaves of most species of *Diospyros* (for the latter compare CONTRERAS & LERSTEN 1984).

According to SCHADEL & DICKISON (1979), stomata are anomocytic and occur only on abaxial leaf surfaces (see Fig. 1a). Diffuse vesiculose sclereids are present in the petiole and mesophyll of leaves. The vasculature of the petioles forms an arc with outwardly curved ends. The marginal, ultimate venation is fimbriate. The leaf anatomy of *L. tetramera* (at the time still known as *Diospyros tetramera*) is described by BUSCH (1913).

Wood anatomy

Anatomically, the wood of *Lissocarpa* is very similar to that of Ebenaceae, except for the rays (best observed in tangential wood sections) which are predominantly longer than 1 mm. NG (1971: p. 81, fig. 2.4, fig. 2.8; 1991), and DICKISON & PHEND (1985: fig. 4 - 6) describe it as follows: vessels solitary and in radial multiples of 2 - 9 cells, with simple, and less frequently, scalariform perforation plates; pits small (mostly 4 (- 8) µm

in diameter) between vessels, as well as between ray cells or parenchyma and vessels; parenchyma predominantly apotracheal, present as scattered cells and in uniseriate lines, tending to form vasicentric sheaths around the vessels; imperforate tracheary elements of the libriform fiber type; rays heterocellular, 1 - 2 cells wide, predominantly more than 1 mm long; fibers without spiral thickenings.

Vegetative morphology

The species of *Lissocarpa* are treelets or trees up to 20 (- 28) m tall and with a dbh up to 25 cm. The architectural tree-model (for this topic see HALLÉ et al. 1978) to which these species conform, has not yet been determined. But, from what can be observed on herbarium specimens, the growth mode is basically sympodial. New shoots always originate from lateral buds. The branching pattern of twigs is discussed in the following chapter on the structure of inflorescences.

The roots of *Lissocarpa* seem to be black (as seen on a seedling of *L. guianensis*; herbarium specimen: Forest Dep. Brit. Guiana 6066 = Fanshawe F2919), most probably in all species, as is also the case in many species of *Diospyros*. The bark of trunks (although not documented for all species on the corresponding herbarium labels, but most probably similar in all species) is usually hard, brittle, black or blackish, and charcoal-like, as in many species of *Diospyros*. In some species of *Lissocarpa*, the inner bark of the trunks is reported to be yellow, or brownish yellow, the sapwood light yellow to whitish (dark yellow after exposure to air), and the heart-wood gamboge-yellow, or dark to nearly black. Young twigs of several species show characteristic, longitudinal, slightly to conspicuously raised, paired ridges running down from both sides of each petiole into the axil of the next but one petiole. The bark of twigs of all species is soon cracking up by many longitudinal, usually black fissures with slightly raised margins. For the first few years the unruptured parts of the bark usually remain covered with the grayish remnants of the epidermis, and later become increasingly black or blackish.

Although unknown as to its chemical nature, the black substances in roots and bark of *Lissocarpa* (according to HEGNAUER 1962 -1992, the genus has not yet been investigated with respect to its chemical constituents) are most probably, like in *Diospyros*, a product of the decomposition of naphthoquinones. These substances may also be important components of the dense layers of minute, white crystals which occasionally cover young petioles and other juvenile parts of twigs on some herbarium specimens of some species of *Lissocarpa* and *Diospyros*.

Branching patterns of twigs and inflorescence structure

After a period of rest, two types of new shoots (short- and long-shoots) are developed in a sympodial manner, from dorsiventrally compressed buds in, or some millimeters above (supra-axillary) the axils of leaves. A few cataphylls (probably bud scales) persist for a while at the base of the new shoots. Long-shoots are generated in distal parts of the branching system, or wherever a leader-twigg has been lost, whereas short-shoots (racemose inflorescences) are formed on the somewhat more proximal parts.

Long-shoots (Fig. 15a) and short-shoots (Figs. 8b, 15b, 21b) are structurally alike, with, however, only the former being long-lived and continuing elongation for several centimeters, or up to 2 - 3 decimeters, finally ending in an apical (terminal), vegetative bud which becomes crooked and is shed soon after shoot growth stops. Subsequent, new long-shoots are usually generated from one of the more proximal buds. Near their base, the long-shoots often (but not always!) bear a few, in most species single flowers in the axils of spaced bracts (Fig. 15a). A few centimeters away from the base of these shoots, small leaves are developed which sometimes also bear flowers in their axils. Towards twig apices, leaves rapidly increase to more or less full size and usually remain destitute of flowers in their axils. During the following growth period, short-shoots (inflorescences) may be generated in the axils of these leaves. On some herbarium specimens (of e.g., *L. tetramera*), older twigs, composed of a succession of several long-shoots, each with a few, old, persistent pedicels in their proximal part, can be seen. Instead of being solitary as in other species, flowers produced on the proximal part of new long-shoots seem always to be grouped 2 or up to 4 together in *L. uyat*, *L. jensonii*, and *L. ronliesneri* (but much more herbarium material is needed to study this in detail!).

Short-shoots (Figs. 8b, 15b, 21b) are always associated with flowers, in fact they represent short inflorescences (racemes) with up to 15 (very rarely up to 50) mm long axes. Two to ten flowers are usually arranged along these axes, in the axils of small bracts. Distally, the short-shoots (racemes) always end in a vegetative bud which is often somewhat hidden between bracts and persistent pedicels, and is often shed very soon. Short-shoots usually die off after fruiting. On rare occasions, after damage or loss of the twig leaders, nearby short-shoots still in the process of growth may be transformed into long-shoots. *L. guianensis* and *L. kating* regularly develop more than one short-shoot (raceme) in the same leaf axil, or even dense clusters of them on (or in the vicinity of) older, already leafless nodes (Fig. 12). The former species has also been reported to be sometimes cauliflorous (Stoffers et al. 111), or to develop flowers "fascicled on stem" (Forest Dep. Brit. Guiana 3290).

Sexual polymorphism

Erroneously, flowers of *Lissocarpa* have been, and still are assumed by many authors, to be hermaphroditic. NG (1971, 1991) first pointed out that they are in fact unisexual, and postulated that the plants are probably dioecious. Unfortunately, in the course of the present revision, it was not possible to study the sexual polymorphism more in detail, due to the circumstance that specimens with flowers are generally underrepresented in herbaria, and dry flowers are usually available only in small numbers. According to own observations made on herbarium specimens, whether *Lissocarpa* is dioecious or monoecious, and whether self-pollination may occur or not, are still open questions. Astonishingly, however, many of the flowers analyzed were found to be completely sterile, with anthers devoid of pollen and collapsed, and ovaries without locules. As nothing is known about the pollination and breeding system of *Lissocarpa*, the function of these sterile flowers can not yet be interpreted.

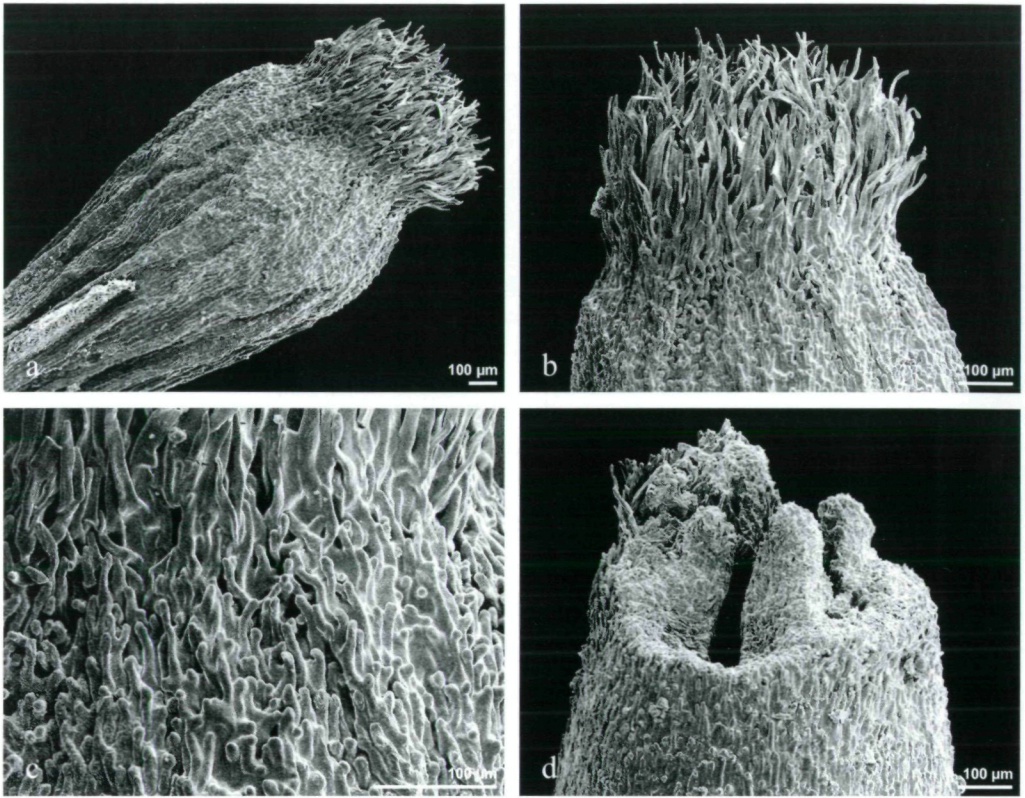


Fig. 2. Style and stigma of *Lissocarpa*. **a - c**: *L. kating* (from Werff et al. 9825): **a**: distal, clavate part of the style; **b**: stigma; **c**: surface of the style near the stigma; **d**: stigma of *L. benthamii* after loss of most of the hair-like appendages (from Castillo 6884). [photographs: H. Halbritter].

Floral biology

Concerning the type collection of *L. guianensis*, GLEASON (1926) wrote: "It [the tree] was in full bloom, that is, the twigs were crowded with unopened flower-buds and the ground beneath was carpeted with fallen corollas. No open corollas were observed on the tree. They are pure white, not 'sordide lutei' as stated by Bentham ...". The label of the collection Maas & Westra 3999 indicates for *L. guianensis*: "corolla light cream, fragrant; open corollas gathered from the ground, no open flowers on branches at moment of collecting around the middle of the day"; Tutin 78 informs for the same species: "flowers opening at night"; Vásquez et al. 26053 mention for *L. uyat*: "botones verdes (pocas flores blancas)"; and Werff et al. 9825 report for *L. kating*: "the corollas fell very soon after opening". It is quite obvious from all this information that the anthesis of the fragrant (according to Maas & Westra 3999 and Werff et al. 9825), and usually white flowers of *Lissocarpa* is nocturnal, as it is in many rainforest-species of *Diospyros* (WALLNÖFER 2001). The flowers are then shed the same night. Nothing is known to date concerning pollination and pollinators.

The lobes of the very remarkable corona (Figs. 10, 11b, 15c) of species in section *Lissocarpa* are most probably derived from stamens, being alternate to the true stamens (or staminodes in female or sterile flowers). Although the fact would still have to be ascertained, they could serve as osmophores ("fragrance-dispenser"). Chambers occupying the whole interior of the distal, clavate part of styles (Fig. 2a) are filled with a dark brown, oily, or resinous substance which is still fluid even on very old herbarium material. Obviously, these chemical compounds play a particular role in the flower biology and pollination of *Lissocarpa*. Anthers seem to produce only little amounts of pollen, and have been found already in a dehisced state in some flower buds (? self-pollination?). In other flowers, on the other hand, the anthers seem not to dehisce at all, and thus do not seem to be able to release the more or less deformed or somewhat flattened pollen (Fig. 3c). Further studies, to be carried out on living plants in their natural habitat, are essential to ascertain and interpret all these observations made only on herbarium material.

Gynoecium, embryology and seed

In its structure, the gynoecium of *Lissocarpa* is quite similar to that of the rest of Ebenaceae, except that the ovary is inferior, and false (secondary) septa are not developed (NG 1971, 1991). Each of the four locules bears a pair of ovules, both attached near the apex of the locule. The four locules all open into a common styler passage. The ovules are pendulous, oblong, anatropous, with the raphe descending on the outer side. The vascular system of the seed consists of one vein, descending from the placenta to the chalaza, which sends 6 - 12 branches back up to the apex. These branches are visible as prominently raised, longitudinal ridges on the seed surface (NG 1971; WHITE 1981; compare also Fig. 13c). As in Ebenaceae, the radicle of the embryo is pointing towards the apex of the locule ("radicle superior").

Pollen morphology

By H. Halbritter*

Overview of the data available from the literature: The pollen grains are suboblate to oblate-spheroidal, or somewhat flattened, with three tenuimarginate pores, about 7 μm wide (ERDTMAN 1971). According to NG (1971; see also WHITE 1981), the sculpturing of the surface is prominently reticulate. This circumstance is, however, confirmed, neither by MORTON & DICKISON (1992), nor by FRANCESCHI (1993). According to MORTON & DICKISON (1992), the pollen possesses an essentially complete tectum with a fossulate to somewhat rugulate sculpturing. FRANCESCHI (1993) describes the pollen as having two to four pores and a complete, homogenous, granulate and undulate tectum. The sexine is thinner than the nexine and baculate (ERDTMAN 1971). According to NG (1971), sizes of pollen grains range from 46×53 to $65 \times 70 \mu\text{m}$ (p/e 0.9 - 0.7).

* DDr. Heidemarie Halbritter, Institut für Botanik der Universität Wien, Rennweg 14, A-1030 Wien, Austria.

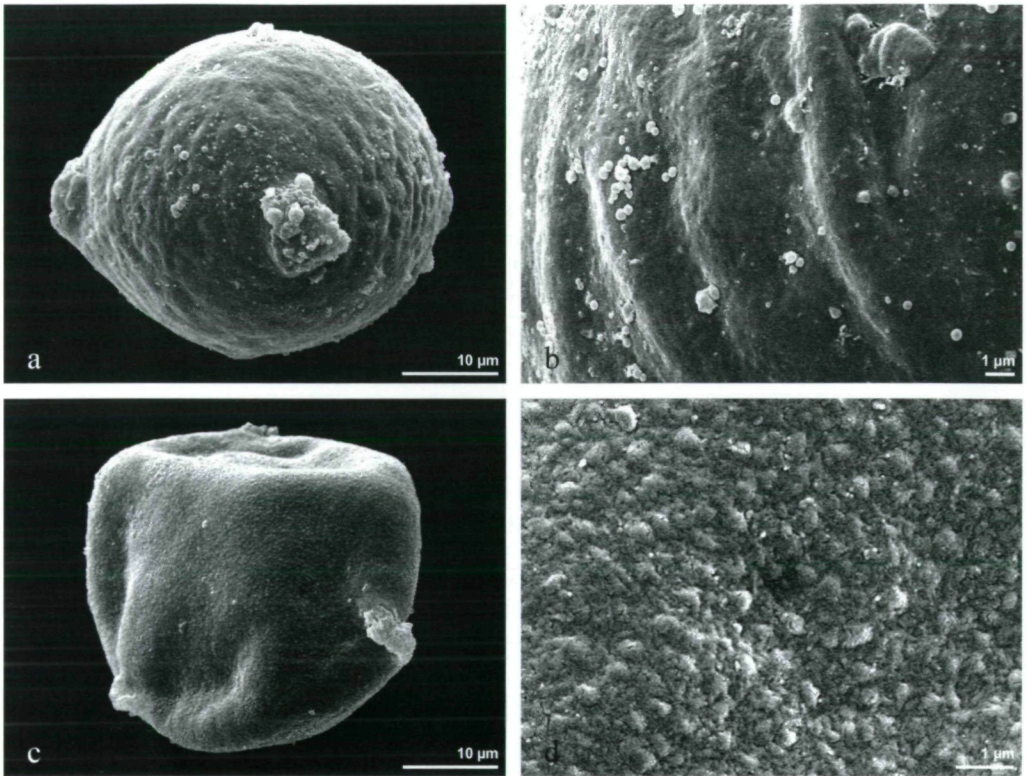


Fig. 3. Pollen of *Lissocarpa*. **a - b**: *L. kating* (from Prance et al. 23855): **a**: equatorial view; **b**: psilate, undulating surface at the equator; **c - d**: *L. tetramera* (from Bang 1681): **c**: oblique polar view (the pollen grain is slightly collapsed); **d**: finely structured, warty and perforated pollen surface.

In the course of the present investigation, pollen, taken from herbarium material of the following species, was investigated for the first time with a scanning electron microscope (SEM): *Lissocarpa guianensis* (Stoffers et al. 111), *L. kating* (Prance et al. 23855, Vasquez et al. 26053), and *L. tetramera* (Bang 1681).

Method: After having been rehydrated and critical point dried, pollen was investigated on a JEOL T300 scanning electron microscope.

Results: The pollen grains (Fig. 3) are 40 - 50 µm in diameter, 3-porate (exceptionally 4-porate), psilate, and slightly oblate to spheroidal. The pores are situated at the equator and are indistinctly delimited (tenuimarginate). The ornamentation consists of fine granules, warty elements and perforations. High magnifications show a very finely structured, warty surface with perforations in *L. tetramera* (Fig. 3d), and a more finely granulate surface in *L. guianensis*. In *L. kating*, the psilate tectum is undulating in the equatorial region (Fig. 3b). These undulating structures have probably been interpreted as "prominent reticulate sculpturing" by NG (1971; see also WHITE 1981), or as "fossulate to somewhat rugulate sculpturing" by MORTON & DICKISON (1992).

A final judgment about pollen shape, size and sculpturing would have to be based on fresh pollen material, but also on TEM investigations.

Ethnobotany

According to SCHULTES & RAFFAUF (1990), along the upper Rio Negro of Brazil, the leaves of *L. benthamii* (voucher: Schultes & López 9905) are "boiled in water to prepare a bath for washing resistant ulcers", and are said to have been used also as a minor fish poison. According to the collection Henkel & Chin 524, *L. guianensis* is also used medicinally, but no further details are available.

Distribution, habitat and ecology

Lissocarpa is only known from South America (Figs. 4, 5) and has been collected in Bolivia, northwestern Brazil, Colombia, Ecuador, Guyana, Peru, and Venezuela. Two of its species are characteristic elements of the specialized vegetation occurring in non-flooded, white-sand areas (with soils extremely low in nutrients) in Guyana (*L. guianensis*) and western Amazonia (*L. kating*). Another species (*L. benthamii*) occurs in seasonally flooded areas along or near black-water rivers in southern Venezuela, and adjacent Brazil and Colombia. Four species (*L. ronliesneri*, *L. stenocarpa*, *L. tetramera*, and *L. uyat*) grow in montane or cloud forests of Bolivia, Ecuador, Peru, and Venezuela. *L. jensonii* occurs in northeastern Peru, on clay soils in non-flooded lowland rainforests, and in southwestern Colombia in a mountainous area at 1230 meters. (For more details, see below, following the descriptions of the single species.)

Taxonomy

Ebenaceae GÜRKE subfam. Lissocarpoideae (GILG in ENGLER) B.WALLN., comb. et stat.n.

≡ Lissocarpaceae GILG in ENGLER, Syllabus, ed. 9 & 10: 324 (1924), nom.cons. (see: GREUTER et al. 2000: 135).

Type genus: *Lissocarpa* BENTH. in BENTH. & HOOK. f.

Description: as for the genus.

***Lissocarpa* BENTH. in BENTH. & HOOK. f., Gen. pl. 2 (2): 671 (1876).**

Type species: *Lissocarpa benthamii* GÜRKE, Nat. Pflanzenfam. IV.1: 180 (1891).

Treelets, small or, less frequently, medium tall trees without latex, glabrous on all organs (except on stigmas); roots probably black in all species; small stilt roots sometimes present; bark black, blackish or dark gray, hard, brittle, charcoal-like, smooth, or rough or grooved vertically; sapwood light yellow to whitish, darker after air exposure, without odor; heart-wood gamboge-yellow, or dark to nearly black; twigs terete or subterete, with or without wing-like longitudinal ridges; bark soon bloating and cracking up by longitudinal, black fissures; still entire parts of the bark of older twigs at first often

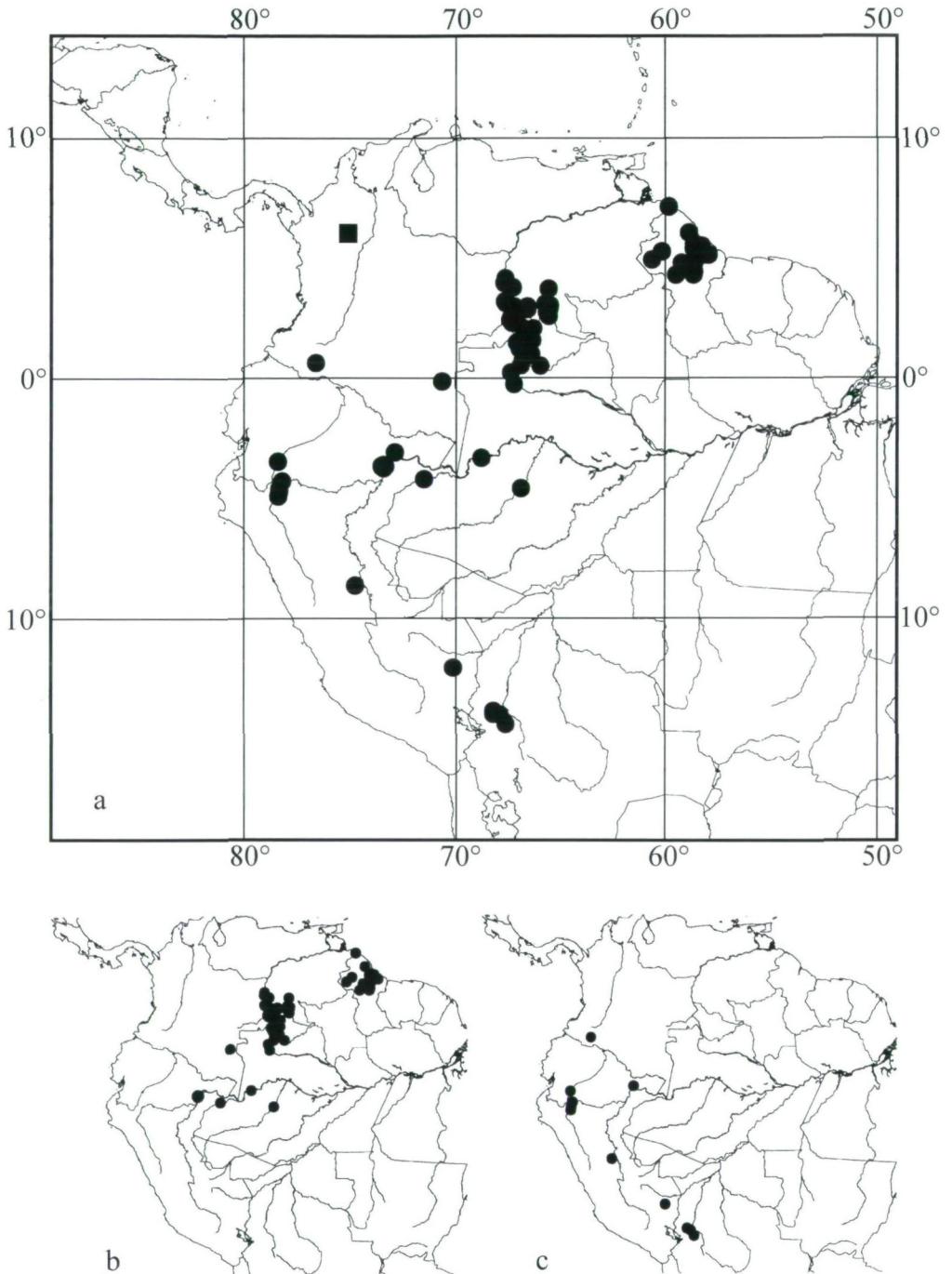


Fig. 4. Distribution of *Lissocarpa*. a: the genus as a whole (■: added in proof, see note on last page of this revision); b: section *Lissocarpa*; c: section *Enho*.

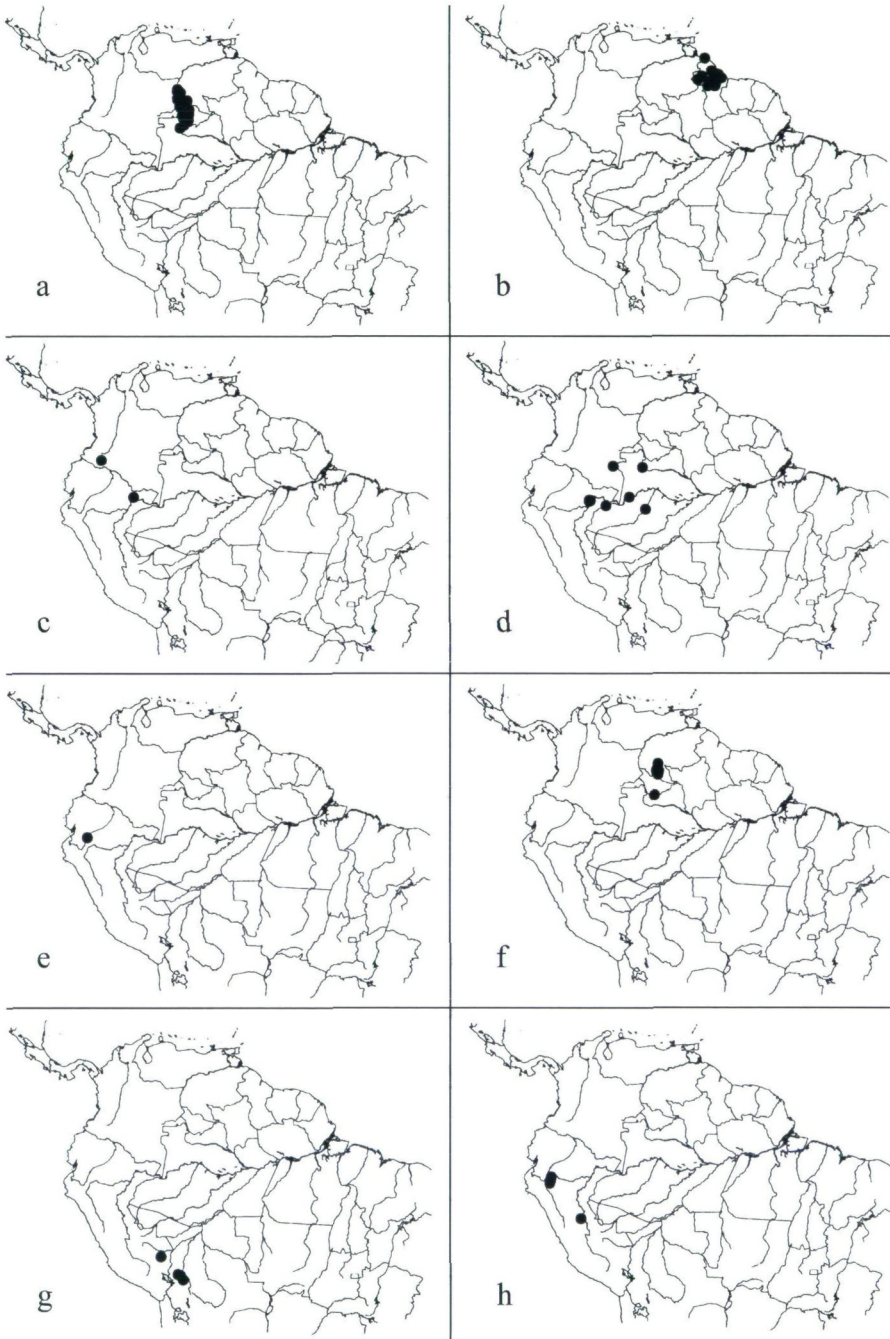
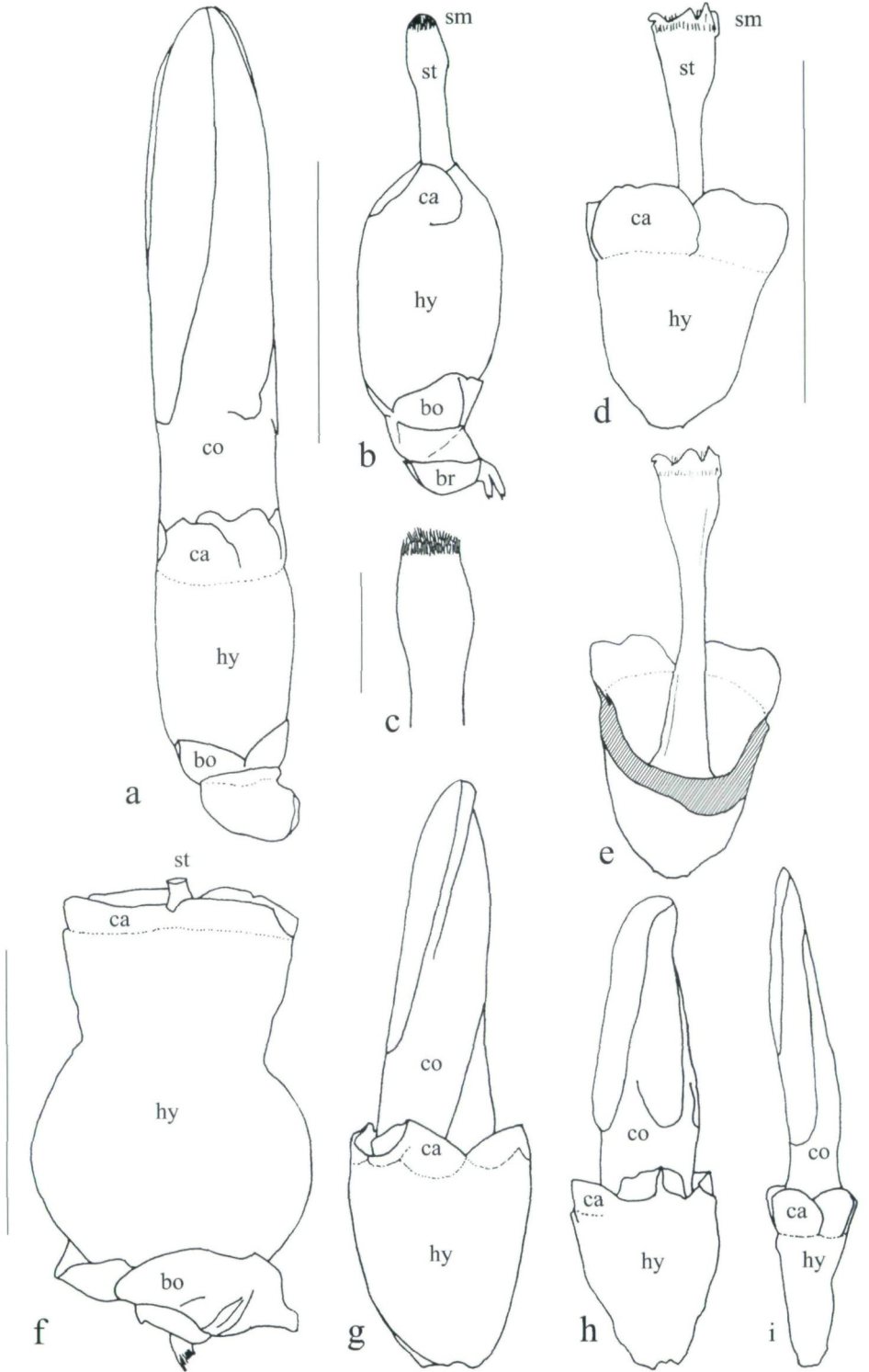


Fig. 5. Distribution of: **a:** *Lissocarpa benthamii*; **b:** *L. guianensis*; **c:** *L. jensonii*; **d:** *L. kating*; **e:** *L. ronliesneri*; **f:** *L. stenocarpa*; **g:** *L. tetramera*; **h:** *L. uyat*.

covered with the partially peeling off, gray remnants of the epidermis, later becoming grayish brown to black; buds dorsiventrally flattened, brownish to black, the apical ones soon aborted after termination of growth; new axes developed from lateral buds (growth sympodial); **leaves** alternate, simple, exstipulate, petiolate or nearly sessile, finely and pinnately veined (venation brochidodromous); lamina usually broadly lanceolate to elliptic; leaf margins entire, usually revolute when dry, notably thickened in some species; leaf apex acute to shortly acuminate (and in this case with a short drip tip), rarely obtuse or rounded; base of the lamina attenuate or rounded, tapering ridge-like into the petiole; flachnektarien (extrafloral nectaries, Fig. 1b) on abaxial leaf surfaces round or less frequently elliptic, 0.2 - 0.6 mm in diameter, with a strongly raised margin and a sunken center (patelliform), the younger ones usually drying light brown, the older ones black; midvein prominent or sunken adaxially, strongly prominent and often triangular in cross section abaxially; secondary veins straight, or less frequently slightly curved; intersecondary veins 1 - 3 in-between and only slightly shorter and thinner than the secondary veins; **flowers** axillary, solitary along the proximal part of long-shoots (Fig. 15a), or 2 - 10 together on lateral, 2 - 15 mm long, inflorescence-like short-shoots (Figs. 8b, 15b, 21b) which are terminating in a soon aborting bud; flowers sessile or shortly pedicellate, actinomorphic, epigynous, 4-merous (very rarely 5-merous), unisexual (apart from many completely sterile flowers); flower bract (Fig. 6b) small and inconspicuous; pedicel persistent, articulated above the bracteoles; bracteoles 2 (Figs. 6a - b, 6f), much larger than the bract, wider than long, subopposite, subtending the hypanthium; hypanthium on the inside crateriform (Fig. 6e); calyx lobes 4 (Fig. 6), attached in an erect position to the distal border of the hypanthium, usually dextrorsely contorted, sometimes imbricate, obtuse, rounded, broadly truncate or slightly emarginate distally, with fimbriate, or slightly erose, or entire margins, persistent but not enlarging with the fruit; corolla (Fig. 10) sympetalous, isomerous with the calyx, white at anthesis in most species, firm and somewhat fleshy when alive, very hard, brittle and black when dry (leathery, with organs persistently sticking together when rehydrated); corolla lobes contorted dextrorsely (the uncovered part of the lobe is always to the right, when seen from the adaxial side), often slightly asymmetrical; tube prominent; corona (Figs. 10, 11b, 15c) most probably absent in all species of section *Enho* (4 species), present in species of section *Lissocarpa* (4 species), consisting of 8 sinistrorsely contorted lobes, most probably derived from stamens; corona lobes flat, exerted for half of their length, widest somewhat below the rounded or acute apex, connate near their base and forming a short tube adnate to the corolla tube near its middle, more or less flexed towards the corolla distally, alternate with respect to the stamens and staminodes; stamens (in male flowers) 8, included, free abaxially, adnate to the corolla tube only below its middle; filaments very short; anthers linear, erect, basifixed, with a short apiculate-prolonged con-

Fig. 6. **a - c:** *Lissocarpa guianensis* (from Stoffers et al. 111, alcohol-preserved material): **a:** flower bud; **b:** flower after anthesis, corolla already shed; **c:** clavate, distal part of the style with stigma; **d - e:** *L. kating* (from Prance et al. 23855): flower after anthesis, corolla already shed (**e:** hatched area indicates the cut of the removed part); **f:** flower after anthesis (corolla already shed) of *L. ronliesneri* (from Miranda et al. 160); **g:** flower bud of *L. uyat* (from Vásquez 27599); **h:** flower bud of *L. tetramera* (from Bang 1681); **i:** flower bud of *L. stenocarpa* (from Liesner 24878). – **bo:** bracteoles, **br:** bract, **ca:** calyx lobes, **co:** corolla, **hy:** hypanthium, **sm:** stigma, **st:** style; bar = 1 cm: a - b, d - e, and i; 5 mm: f - h; 1 mm: c.



nective, 2-thecal, 4-sporangiate, dehiscing by longitudinal slits; pollen 3-porate (Fig. 3); staminodes (in female or sterile flowers) 8, resembling stamens although anthers collapsed, flat, devoid of pollen, adnate on their abaxial side for their whole length to the corolla tube and to the corona tube respectively, except for the apical part of the connective; ovary inferior (axis forming a hypanthium, see Fig. 6), 4-carpellate, syncarpous, 4-locular; ovary of the male and sterile flowers without locules; stylodia as numerous as carpels, fully connate, forming a terminal style; the latter markedly enlarged basally, narrowed towards the middle, clavate near the apex (Fig. 6); clavate part of the style (Figs. 2a, 6c) containing chambers filled with an oily, or resinous, dark brown substance; stigma densely covered with hair-like appendages (Fig. 2b), concealing the shallowly 4-lobed apex (Fig. 2d); carpels biovulate, with apical placentation, not bisected by a false (secondary), longitudinal septum (as is the case in most other Ebenaceae); **fruit** representing an ellipsoidal-fusiform, less frequently ellipsoidal, ovoid, or subglobose berry with persistent, not accrescent calyx lobes at the apex; fruit wall thin, fleshy, pink or red at maturity (at least in some species) when alive; seeds (Figs. 13c, 17d) only 1 - 2 per fruit, rarely more (others aborting), pendulous, with a vascular system consisting of 6 - 12 branches visible as longitudinal ridges; hilum relatively small, apical; testa smooth, thin, coriaceous; endosperm horny, abundant, smooth; embryo upside-down (radicle superior), straight, with two small foliaceous cotyledons and a strongly developed radicle.

Key to species

- 1 Midvein of leaves raised adaxially (sometimes flattened near the base); calyx teeth wider than long, emarginate or broadly rounded distally, markedly overlapping on their sides, fimbriate on the margins; corona (Figs. 10, 11b, 15c) present; (section *Lissocarpa*) 2
- 1* Midvein of leaves impressed adaxially; calyx teeth more or less triangular (broadly truncate in *L. ronliesneri*), barely or not overlapping on their sides, not fimbriate on the margins; corona absent; (section *Enho*) 5
- 2 Youngest twigs drying gray-green, very much resembling the characteristic twigs of *Heisteria* (Olacaceae); tertiary and ultimate venation densely crowded, well visible and raised on both sides of the lamina, predominantly oriented subparallel to the secondary veins (Fig. 13a); – white-sand areas (caatinga) on terra-firme (not subject to periodical inundation) in lowlands of central and western Amazonia
..... *L. kating*
- 2* Not as above 3
- 3 Corolla lobes up to 16 mm long; fruits up to 40 mm long; leaves often up to 20 (- 30) cm long, and up to 8 (- 11) cm wide; – swamp forests drained by black-water rivers and white-sand areas in lowlands in Guyana *L. guianensis*
- 3* Corolla lobes and fruits usually much smaller; leaves predominantly smaller 4
- 4 Surfaces of the lamina differing in color when dry; tertiary venation obscure adaxially (Fig. 8a); twig around the petiole-base not markedly thickened; pedicels 1 - 2 mm long; corolla lobes longer than 9 mm [flowers not seen at anthesis]; – lowland forests in periodically inundated areas (igapós) along black-water rivers within the upper Rio Orinoco and Rio Negro drainage *L. benthamii*
- 4* Both surfaces of the lamina the same color when dry; tertiary venation well visible adaxially; twig markedly thickened around the petiole-base (Figs. 15a - b);

- pedicels 2 - 4 mm long; corolla lobes at anthesis ca. 6.5 mm long; – cloud forests on slopes and ridges of Tepui (table mountains) in southern Venezuela
..... *L. stenocarpa*
- 5 Midvein on its adaxial side slightly impressed (more or less flat distally) and well visible; – montane forests in SE-Peru and NW-Bolivia *L. tetramera*
- 5* Midvein markedly or strongly (hidden in a deep groove) impressed adaxially 6
- 6 Leaves oblong, with marginal vein not notably thickened distally; immature fruits up to 3.5 cm long and 1.8 cm wide when dry; – lowlands in northern Peru, and mountainous area in southwestern Colombia *L. jensonii*
- 6* Leaves lanceolate or broadly lanceolate, with marginal vein notably thickened distally; ripe fruits up to 2.5 cm long and ca. 1 cm wide when dry [fruits of *L. ronliesneri* not seen] 7
- 7 Midvein strongly impressed, and hidden in a deep groove adaxially; subopposite bracteoles at the base of the hypanthium slightly keeled along the midvein; calyx teeth triangular (Fig. 6g), 0.5 - 0.8 mm long, and 1.5 mm wide; – montane forests in northern Peru *L. uyat*
- 7* Midvein moderately impressed, and well visible adaxially; subopposite bracteoles at the base of the hypanthium not keeled along the midvein; calyx truncate over most of its width (Fig. 6f), 0.2 (!) mm long, and 2 mm wide; – montane forests in southern Ecuador *L. ronliesneri*

Lissocarpa BENTH. in BENTH. & HOOK. f., sectio *Lissocarpa*

Type species: same as for the genus.

Note: For characters see the 'key to species'. This section comprises the following species: *L. benthamii*, *L. guianensis*, *L. kating*, and *L. stenocarpa*. For distribution see Fig. 4b.

Lissocarpa benthamii GÜRKE, Nat. Pflanzenfam. IV.1: 180 (1891); [Figs. 2d, 7 - 8].

≡ *Lissocarpa benthamii* BAILL., Hist. pl. 11: 460 (1892), nom. illeg.

Typus: Venezuela, Amazonas, San Carlos, ad rivuli ostiam inundatum, [1°55' N, 67°4' W]¹, (fl)², Oct. 1853, **R. Spruce 3108** [holo(?)type: B (destroyed, photo F: 4276 at F, G, MO, NY); lectotype: K (designated by WHITE 1981: 330), isolectotypes: BR, C, F, G, G-DC, GOET, K, NY, P 2×, W 2×]³ "arbor parva 18 ped., anguste ramosissima; flores sordide lutei; fructus rubii carnosuli"; on the original label as: "Ebenacea gen. nov."

Note: GÜRKE (1891) did not cite any specimens in the short protologue of his *L. benthamii*. Of the two sole collections (Spruce 3108 and 3504; both also cited by BENTHAM 1876) available at the time, a duplicate of Spruce 3108, was certainly present in Berlin,

¹ Coordinates given in brackets have been determined during this revision.

² Abbreviations: defl = deflorate; fl = flowering; flbuds = with flower buds; fr = fruiting; st = sterile; yfr = with young fruits.

³ Acronyms of herbaria according to HOLMGREN & HOLMGREN (2003); abbreviations: n.v. = non vidi (= not seen); 2× = 2 sheets.

as can be concluded from the presence of a photo of it in the photo-negative collection at the Field Museum in Chicago. Whether the collection Spruce 3504 was also present in Berlin or, whether GÜRKE had an occasion to study duplicates of it somewhere else, is not known. Whatever the case, a photographic negative of a duplicate of the latter collection which may have been kept at Berlin, is lacking in the Field Museum in Chicago. Since also the Lissocarpaceae in the Berlin herbarium were destroyed during World War II, it can now not be established anymore, whether the duplicates of both collections, Spruce 3108 and 3504, represent syntypes, or whether the former must be regarded as the sole type collection.

Treelet or tree 2 - 14 m tall; trunk cylindrical, observed destitute of branches for its lower half, circumference up to 1.1 m; bark dark or grayish, thin, smooth or rough; phloem yellowish; sapwood light yellow to whitish, darker after air exposure; heartwood thin, dark to nearly black; crown dense; twigs subterete; bark dark brown to brownish black, smooth, with a pair of longitudinal ridges running down from both sides of each petiole into the axil of the next but one petiole; bark soon bloating and cracking up by longitudinal, black fissures with slightly raised margins; still intact parts of the bark of older twigs covered with the gray remnants of the epidermis, later on grayish brown to blackish; buds brownish; **leaves:** petioles (2 -) 5 - 10 (- 12) mm long, 1 - 2 mm thick, drying brown or black, usually transversally shriveled, with a quite flat longitudinal groove adaxially; lamina lanceolate to broadly lanceolate (broadest near middle), sometimes elliptic or ovate, rarely oblong, (5 -) 10 - 18 (- 20) cm long, (1.8 -) 3 - 6 (- 7.5) cm wide, somewhat coriaceous; adaxial side gray-brown to dark brown, often irregularly spotted red-brown to blackish, and slightly shiny when dry, dark green when alive; abaxial side lighter brown and dull when dry, light green when alive; leaf apex acute to short acuminate, rarely obtuse, with a drip tip up to 1 cm long; base of the lamina attenuate, abruptly attenuate or rounded; leaf margins not thickened; extrafloral nectaries on abaxial leaf surfaces 0.3 - 0.4 mm in diameter, frequent near the margins, scattered near the base and the apex, rarely present in the central part of the lamina; midvein more or less flat and 0.5 - 1 mm wide near the base of the lamina, in the more distal parts prominent, semi-circular in cross section, adaxially sometimes slightly longitudinally shriveled when dry, strongly prominent abaxially, and there on the distal half of the lamina triangular in cross section; secondary veins ca. 10 per side, slightly raised on both sides of the lamina; tertiary veins obscure, only slightly prominent on both sides of the lamina, often flat abaxially; quaternary veins hardly visible and nearly flat on both sides of the lamina; **flowers** solitary on the proximal part of young long-shoots, or on up to 7-flowered short-shoots (inflorescences, Fig. 8b), with up to 15 mm long, ca. 1 mm thick axes; pedicels 1 - 2 mm long, ca. 0.8 mm thick, blackish; subopposite bracteoles at the base of the hypanthium ca. 2.5 mm long, ca. 4 mm wide, fimbriate on their margins, rounded or obtuse distally; anthetic flowers not available for study; longest flower buds ca. 2 cm long, pale green when alive; hypanthium 4 - 5 mm long, 2 - 4 mm wide, with scattered, appressed, oblong, papilla-like structures adaxially (inside); calyx lobes blackish when dry, dextrorsely contorted, 1 - 1.5 mm long, 1.5 - 3 mm wide, rounded, truncate or slightly emarginate distally, fimbriate on their margins; corolla white or yellowish (turning into the latter color probably after anthesis) when alive, blackish when dry; corolla tube ca. 6 mm long, 3 mm wide distally, 1 mm wide basally; corolla lobes ca. 9 mm long, ca. 5 mm wide, rounded apically, fimbriate on their margins; tube of the



Fig. 7. Lectotype of *Lissocarpa benthamii* GÜRKE.

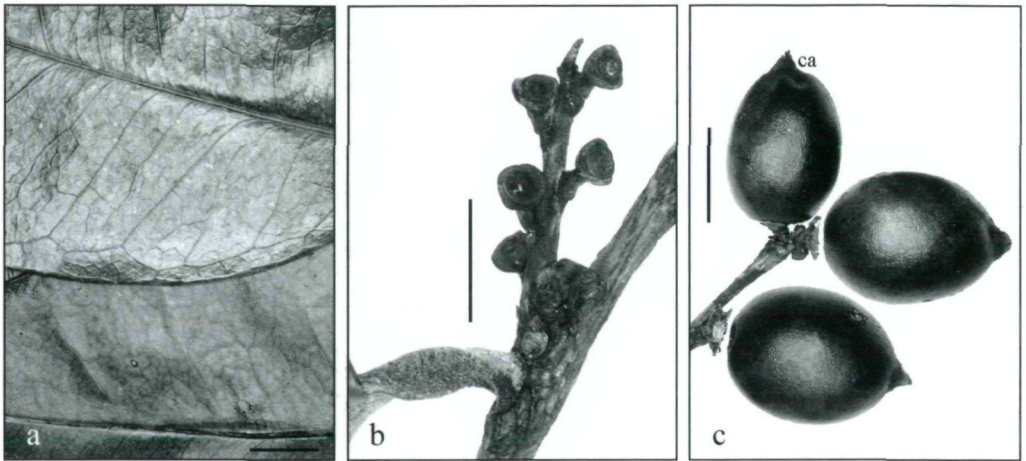


Fig. 8. *Lissocarpa benthamii*. **a**: adaxial (on top) and abaxial (bottom) leaf surface (from Liesner 7285); **b**: short shoot (inflorescence) with abscised flowers (from Aymard et al. 6460); **c**: fruits (from Clark 7456), (ca: calyx lobes); bar = 1 cm: a, c; 5 mm: b.

corona ca. 1 - 3 mm long, adnate to the corolla tube at ca. 2 mm above its base; lobes of the corona broadly lanceolate, ca. 4 mm long, 1.5 mm wide, obtuse distally; stamens not available for study; staminodes 4 mm long; filaments ca. 1 mm long; aborted anthers ca. 3 mm long, ca. 0.5 mm wide, flat; style ca. 7 mm long, the uppermost millimeter below the stigma clavate; **fruits**: pedicels ca. 1 mm long and thick; living fruits green when unripe, later on changing colors to mottled olive, yellowish, orange-brown to red-orange, finally red to bright red when ripe; dry fruits (Fig. 8c) ellipsoidal-fusiform, less frequently ellipsoidal, up to 30 mm long, and ca. 18 mm wide, 1 - 2 (- 4)-seeded; fruit surface brown to dark brown or blackish-brown, smooth, without or only with few large wrinkles; outer layer of the fruit quite firm when dry; calyx lobes erect, fitting tightly together around the broad, obconical base of the broken style; seeds 10 - 20 mm long, ca. 7 mm wide, brown to blackish when dry, with ca. 8 longitudinal, salient veins, and with a wrinkled surface.

Figures: twig with flowers, various floral details, fruit, seed (OLIVER 1895; same drawings also used in HUTCHINSON 1959); twig with fruits (BERRY 2001).

Vernacular names: "arrendajo" (Liesner 7285), "mâmokoÿoma" (Stergios & Aymard 9076), "palo de carbón" (Clark 7456, 7550; Clark & Maquirino 7988; BERRY 2001), "palo de lameya" (BERRY 2001), "palo de payema" (Williams 14756), "simure" (Liesner 6734, 7144; BERRY 2001), "pau amarelo" (OLIVEIRA & DALY 2001, but see also the remark under *L. kating*).

Distribution, habitat, ecology, and phenology: This species is known from Brazil (northern Amazonas), Colombia (Guainía), and Venezuela (Amazonas), where it grows at elevations between 80 and 160 meters (Fig. 5a), along or near black-water rivers (bosques bajos de rebalse en las orillas) in seasonally flooded, usually "low and open" forests. Frequently (but not always), it is found in special, primary woodlands characteristic of podsolized white-sand soils extremely poor in nutrients (HUBER 1995: 113 - 115). This

kind of vegetation is called "caatinga amazonica", "campinarana", "campina" (PIRES & PRANCE 1985; ANDERSON 1981), "pseudo-caatinga" (SCHNELL 1987) or "Rio Negro caatinga" (HUBER 1995). For further details concerning this vegetation type, see also KLINGE & MEDINA (1979). HUBER (1995: 137) reports *Lissocarpa* also from a characteristic, seasonally flooded, riparian scrub (locally called "boyal"), growing along black-water rivers and not associated with white-sand soils. *L. benthamii* has been collected in flower from October to November, and in fruit from January to July.

Specimens examined: **Colombia**, **Guainía**, ca. 5 km N of Boca de Casiquiare (where Rios Negro, Guainía & Casiquiare join), mouth of Caño, S side of Caño, 120 m, 1°57' N, 67°7' W, 7 m tall open forest adjacent to mouth of Caño, (fr), 5 Feb. 1980, **R.L. Liesner & H. Clark 9076** [MO, NY], "6 m tree; fruit orangish brown"; – same area, date (fr), and collectors, **9083** [MO, NY], "4 m tree; fruit brown".

Venezuela, **Amazonas**, Mun. Autana, confluencia de los ríos Sipapo y Orinoco, margen derecha desde Isla Ratón hacia Boca del Cuao, 4°54' - 5°3' N, 67°34' - 46' W, en bosque inundable, (flbuds), 22 Sept. 1996, **A. Castillo 4081** [MO n.v. (digital photo seen)], "árbol de 8 m de alto; flores amarillas; cáliz verde; yemas amarillo-verdoso"; – same area, entre Boca de Cuao y Piedra Chamii, (fr), 13 May 1998, **A. Castillo 5795** [MO], "árbol 6 m; frutos inmaduros verdes-anaranjados y rojos al madurar"; – same area, 225 m, (flbuds), 18 Aug. 1997, **A. Castillo 5419** [MO n.v. (digital photo seen)], "árbol sumergido de 6 m de alto; yemas florales verdes"; – Río Sipapo, bordeando hacia Cerro Pelota, margen izquierdo, [4°46' N, 67°43' W], (fl), 17 Oct. 1999, **A. Castillo 6884** [MO], "árbol de 14 m de alto; flores blanco verdoso; frutos inmaduros verdes y rojos; semillas con arillo blanco"; – same area, cerca de Cerro Pelota, 242 m, 4°53'06" N, 67°42'55" W, (fr), 19 Feb. 2001, **A. Castillo & B. Camaripano 8286** [MO n.v. (digital photo seen)], "árbol de 18 m de alto; frutos verdes, inmaduros"; – Dept. Atures, Río Sipapo, entre el Salto Remo y Morichito, frente al campamento Salto Remo, 120 m, 4°34' N, 67°18' W, bosque de ladera, (fr), Jun. 1989, **E. Foldats & J. Velazco 9614** [MO, NY], "arbolito ca. 7 m, abundante; fruto maduro se torna rojizo"; – Dpto. Casiquiare, Río Atabapo, desde San Fernando de Atabapo hasta 12 km río arriba, 110 m, [3°55' N, 67°41' W], bosques bajos de rebalse en la orilla y alrededores del Río Atabapo, (yfr), 14 Jan. 1988, **G. Aymard, B. Stergios & N. Cuello 6460** [FHO, HBG, MER n.v., MO, NY], "árbol; frutos verdes"; – Dept. Atabapo, ca. 20 km S of San Fernando de Atabapo on the eastern bank of the Río Atabapo, ca. 95 m, 3°50' N, 67°39' W, inundated caatinga on white sand on river bank, (fr), 29 Apr. 1979, **G. Davidse, O. Huber & S.S. Tillett 16855** [FHO, MO, NY], "slender treelet 4 m tall; fruit red, 2-seeded"; – upper porcion of Caño Caname, ca. 100 m, 3°40' N, 67°13' W, low forest on sandy river bank, (fr), 3 May 1979, **G. Davidse, O. Huber & S.S. Tillett 17124** [FHO, MO], "shrub 2 m; fruit green"; – along Yapacana caño [=? Caño Yagua] from laguna to mouth, 125 m, [3°40' N, 66°35' W], (fr), 21 Mar. 1953, **B. Maguire & J.J. Wurdack 34618** [FHO, MO, NY], "small tree"; – ribera inundada del Caño Yagua, frente al cerro Cucurital, al nor-este [correct is: SE] del Cerro Yapacana, formación de matorral alto inundable, 120 m, 3°33' N, 66°36' W, ribera inundada, (fr), 24 May 1981, **F. Guánchez 1205** [MER n.v., MY n.v. (photocopy seen)], "arbolito de unos 5 - 6 m de alto, parcialmente sumergido; aislado y frecuente en toda la ribera; frutos verde pálido cuando inmaduros, rojos cuando maduros, de 2.3 cm de largo × 1.3 cm de diámetro; arilo verde intenso; endosperma blanco cristalino; hojas papiráceas, algo quebradizas"; – bajo Caño Yagua, cerca de su desembocadura en el Río Orinoco, 120 m, 3°32' N, 66°46' W, bosque ribereño del bajo caño, (yfr), 15 Jan. 1979, **O. Huber 3084** [FHO], "árbol torcido de unos 4 m; con copa densa; fruto ovalado, verde, rojo cuando maduro, ca. 1.5 cm de largo y 0.5 - 0.8 cm de diam.; haz verde oscuro, envés verde claro"; – Río Temi below Laja Inunda, ca. 110 m, 3°9'51" N, 67°23'11" W, seasonally flooded forest along black-water río, (yfr), 10 Feb. 1997, **P.E. Berry, L. Brako & D.K. Berry 6536** [MO], "tree 5 m; fruits green to orange-red"; – Río Temi below Sejal, 110 m, 3°2'56" N, 67°25'59" W, seasonally flooded forest along black-water río, (fl), 19 Nov. 1996, **P.E. Berry & J. Rosales 6412** [MO, W], "tree 6 m; flowers white; fruits green"; – Río Temi between Budare and Yavita, ca. 110 m, 2°52' - 55' N, 67°18' - 27' W, flooded riparian forest along black-water río, (yfr), 26 Nov. 1995, **P.E. Berry, R. Duno & G. Romero 5678** [MO], "tree 7 m; fruits green"; – Dept. Casiquiare, Caño "San Miguel", 160 m, ca. 2°40' N, 66°50' W, arbustales ("bayales") con bosques bajos de rebalse en planicie aluvial, (fr), 22 Apr. 1991, **G. Aymard 9210** [MO, NY], "árbol 5 m; frutos amarillos"; – Capihua [? = Capibara], Alto Casiquiare, 120 m, [2°38' N, 66°19' W], selva rebalsera, (fr), 6 Feb. 1942, **L. Williams 15729** [F], "arbusto alto o árbol de 6 - 8 m; tronco inclinado, redondo, 12 cm de diam.; corteza algo delgada, grisacea; corteza algo áspera y el liber [phloem] amarillento; albura [sapwood] de color amarillo quemado y el duramen [heartwood] mas oscuro; corona de forma irregular y las ramas colgantes; fruto

rosado fuerte a colorado, ovoideo"; – Bajo Chimoni, [2°5' N, 66°22' W], selvas pluviales de rebalse (aguas negras), (fr), 18 Feb. - 4 Mar. 1986, **B. Stergios & G. Aymard 9194** [NY], "arbolito ca. 5 m; frutos verde-rojo"; – Solano, Bajo Casiquiare, 100 m, [1°58' N, 66°57' W], selva alta, tupida de rebalsas, (fr), 12 Mar. 1942, **L. Williams 14756** [F, NY], "árbol de 10 - 12 m; tronco redondo, derecho, 15 cm de diam., sin ramas por la mitad o mas; corteza de color oscuro algo lisa y delgada; albura [sapwood] de color amarillo canario a blanquecino, cambiando a mas oscuro al exponerse al aire, y el duramen [heartwood] delgado, de color oscuro casi negro; con copa algo frondosa, de hojas gruesas; fruto ovoideo 2.5 cm de largo, de color castaño claro y algo lustroso, solitario o en pares"; vern. name: "Palo de Payema"; – Dpto. Río Negro, Río Casiquiare entre Guachapita y El Porvenir, [1°58' N, 66°40' W], selvas pluviales en los alrededores de las orillas del río, (fr), 15 Apr. 1985, **B. Stergios, G. Aymard & L. Nico 8156** [MO], "arbolito ca. 4 m con frutos anaranjados"; – in Guainia ripis (label of duplicates: "prope San Carlos ad Río Negro superiorem Brasiliae borealis et in terris vicinis Venezuelanis", or (at W): "ad flum. Guiaime [= Guainia] v. Río Negro supra ortum flum. Casiquiare"), [1°55' N, 67°4' W], (fl, fr), May 1854, **R. Spruce 3504** [syntypes (?): K 2x, P 2x, W], "arbor tenuis 20 pedalis; corolla luteola; fructus coccineus siccusculcus"; – 1 to 6 km N of San Carlos de Río Negro, ca. 20 km S of confluence of Río Negro and Brazo Casiquiare, 120 m, 1°56' N, 67°3' W, along the river, (fr), 2 May 1979, **R.L. Liesner 7144** [MO], "5 m tree; fruit red"; vern. name: "simure"; – [San Carlos] between airstrip and river, ca. 20 km S of confluence of Río Negro and Brazo Casiquiare, 120 m, 1°56' N, 67°3' W, between airstrip and river, edge of forest, (fr), 8 May 1979, **R.L. Liesner 7285** [FHO, MO], "5 m tree; fruit red"; vern. name: "arrendajo"; – directly S and SW of San Carlos de Negro, ca. 20 km S of confluence of Río Negro and Brazo Casiquiare, 120 m, [1°55' N, 67°3' W], forest and cleared area, (fr), 17 Apr. 1979, **R.L. Liesner 6734** [FHO, MO], "5 m tree; fruit red"; vern. name: "simure (es una clase de majagua)"; – 0 to 1 km SE of San Carlos de Río Negro, 120 m, [1°54' N, 67°3' W], seasonally flooded forest, (fr), 25 Jan. 1980, **R.L. Liesner 8692** [MO, NY], "4 m tree; fruit greenish yellow"; – same area, date (flbuds, fr), and collector, **8706** [LL, MO, NY], "6 m tree; flower bud pale green; fruit greenish brown, becoming greenish brown or red when larger"; – Río Pasimoni, entre la boca y la piedra Gavilán, [1°50' N, 66°40' W], selvas pluviales de rebalse, (yfr), 18 Feb. - 4 Mar. 1986, **B. Stergios & G. Aymard 9076** [MO 2x], "arbolito ca. 5 m; frutos verde-rojizo"; vern. name: "Mâmokoÿoma"; – Pacimoni [=Pasimoni], [1°45' N, 66°35' W], (fl), s.d., **R. Spruce s.n.** [K], "a small tree of 18 ft., had only this solitary ramulus in flower"; – Río Pasimoni a altura de Buridajao [= Boridahari], [1°45' N, 66°33' W], selvas pluviales y área perturbado (conuco), (fr), 10/22 Feb. 1989, **B. Stergios, K. Kubitzki, G. Aymard & E. Melgueiro 13320** [HBG 2x, NY], "arbolito de 5 m; frutos verdes hasta naranjados"; – Río Casiquiare, Río Pacimoni [= Pasimoni], between Caño Arapacua and Caño Boridahari, 120 m, [1°40' N, 66°35' W], (fr), 7 Apr. 1953, **B. Maguire & J.J. Wurdack 34907** [FHO, MO, K, NY], "small tree; occasional"; – Dept. Río Negro, Río Pasimoni, between its mouth and its junction with the Río Baria and the Río Yatua, 80 m, 1°27' - 53' N, 66°32' - 35' W, inundated forest along river margin, (fr), 23/25 Jul. 1984, **G. Davidse 27839** [FHO, MO], "tree 8 m; fruit bright red"; – San Carlos de Río Negro, ca. 20 km S of confluence of Río Negro and Brazo Casiquiare, near Caño Cuweje ± 32 km S of San Carlos, 119 m, [1°40' N, 66°58' W], rebalse (igapó) forests; average rainfall 3400 - 3600 mm/year, (fr), 20 Mar. 1980, **H.L. Clark 7456** [MO, NY], "small tree; fruit pale green to red-orange to mottled olive"; vern. name: "palo de carbón (PM)"; – same area, (fr), 4 Apr. 1980, **H.L. Clark & P. Maquirino 7484** [MO, NY], "small tree; fruit red, ovoid"; – same area, (fr), 8 May 1980, **H.L. Clark & P. Maquirino 7988** [MO, NY], "small tree 7 m, 7.2 cm dbh"; vern. name: "palo de carbón (PM)"; – same area, 0 - 5 km N of Caño Cuweje, ± 30 km S of San Carlos, [1°40' N, 66°58' W], same habitat, (fr), 2 May 1980, **H.L. Clark 7550** [FHO, NY, US], "small tree 5 m high; fruit pale green to mottled olive, mature fruit red"; vern. name: "palo de carbón (PM)"; – Caño Adabo, ca. 25 km S of San Carlos de Río Negro, near Río Negro, 120 m, [1°40' N, 66°58' W], rebalse (seasonally flooded forest), (fr), 27 Jan. 1980, **R.L. Liesner 8632** [MO, NY, VEN n.v.], "8 m tree; fruit dark green"; – Dpto. Río Negro, márgenes del Río Varía, 90 m, 1°25' N, 66°24' W, márgenes del río, (fr), Apr. 1991, **J. Velazco 1890** [MO], "árbol 6 m; frutos color rojo cuando maduros".

Brazil, Amazonas, Río Negro, Cucuí, [1°10' N, 66°50' W], (fr), 25 Apr. 1975, **O.C. Nascimento, J.M. Pires & L. Coradin 186** [INPA, MO], "arvore de 13 m e 1,1 m de circ."; – upper Río Negro basin, Uanadona [= Ilha Uevadon], near mouth of Río Dimiti [= Demiti], [0°53' N, 66°55' W], (fr), 10 May 1948, **R.E. Schultes & F. López 9905** [NY]; – Mun. São Gabriel da Cachoeira, Río Negro, Río Cubate, tributary of Río Içana, 10 min. by motorboat from mouth, 0°33' N, 67°23' W, high caatinga; rare in open, disturbed area near seasonally inundated "campina", (fl), 4 Nov. 1987, **D.C. Daly, C.F. Sá & J. Ramos 5586** [K, MO, NY], "shrub or small tree 3.5 m; few flowers; buds and corolla white".

Lissocarpa guianensis GLEASON, Bull. Torrey Bot. Club 53 (5): 296 - 297 (1926); [Figs. 6a - c, 9 - 11].

Typus: Guyana, Cuyuni-Mazaruni, Essequibo River, at Butukari [= Butakari], [5°45' N, 58°37' W], dense upland forest, (fl), 20/21 Jul. 1921, **H.A. Gleason 724** [holotype: NY, isotypes: GH n.v., K, US], "small tree 25 - 30 ft".

Treelet or tree 2.5 - 25 m tall, up to 25 cm in diameter; stilt roots small; trunk slightly furrowed; bark hard, brittle, smooth or grooved vertically, black or blackish, charcoal-like; wood light yellow, soon becoming dark yellow on exposure to air; heart-wood gamboge-yellow; seedlings (Forest Dep. Brit. Guiana 6066 [= D.B. Fanshawe F2919]) with black roots; hypocotyl dark brown when dry; cotyledons opposite, nearly sessile, 5.8 - 6.5 cm long, 3 - 3.5 cm wide; shoot with some small cataphylls near the cotyledonar node, and with 1 - 2 alternate, a little larger cataphylls 0.3 - 2 cm above this node; first regular leaves alternate, ca. 8 cm long and 2.5 cm wide; twigs of the tree terete; young bark dark brown to black, shriveled longitudinally, brown inside; bark of older twigs usually gray to gray-brown, covered by the light gray remnants of the epidermis, soon cracking up by longitudinal, black fissures with slightly raised margins; old bark usually more or less black; buds black; leaf primordia on twig apices glabrous, black, with brown, erose margins; **leaves:** petioles (4 -) 6 - 10 (- 15) mm long, 1.8 - 3 mm thick, drying brown or black, slightly thickened, smooth, or shriveled longitudinally or transversally, and with a longitudinal groove adaxially; lamina broadly lanceolate to elliptic (broadest near middle), rarely ovate or oblong, (5.5 -) 12 - 20 (- 30) cm long, (2.4 -) 5 - 8 (- 11) cm wide, brown on both sides (the youngest ones drying black), slightly shiny adaxially, dull abaxially when dry, slightly coriaceous (very stiff, or leathery and supple when alive); leaf apex acute to shortly acuminate, either with a drip tip 0.5 - 1.5 cm long, or sometimes obtuse or rounded; base of the lamina attenuate or rounded; leaf margins not thickened; flachnektarien (extrafloral nectaries) on abaxial leaf surfaces 0.2 - 0.4 mm in diameter, usually light brown, frequent near margins and the apex, very scattered near the base, rarely present in the central part of the lamina; midvein on its adaxial side prominent (but area along the midvein somewhat sunken compared to the rest of lamina), semicircular in cross section, near base 1.5 mm wide, and somewhat shriveled when dry, abaxially strongly prominent, semicircular or especially distally slightly triangular in cross section; secondary veins ca. 10 per side, raised on both sides of the lamina; tertiary veins slightly prominent on both sides of the lamina; quaternary veins hardly visible and nearly flat on both sides of the lamina; **flowers** solitary on the proximal part of young long-shoots or on up to 4-flowered short-shoots (inflorescences), the latter either solitary in the leaf axils of younger twigs, or more or less densely crowded on the already leafless nodes of older twigs, (flowers also said to be cauliflorous [Stoffers et al. 111], or "fascicled on stem" [Forest Dep. Brit. Guiana 3290]); inflorescence axes up to 10 mm long, 0.8 - 1 mm thick; flowers (material preserved in alcohol, from Stoffers et al. 111, was analyzed) fragrant, opening at night; flower buds (Fig. 6a) up to 2.5 cm long; bract, pedicel, bracteoles, hypanthium, and calyx lobes light green (or partly yellow-green) when alive, blackish when dry; bract 1 mm long, 2 mm wide; pedicels 2.5 - 3 mm long (on solitary flowers up to 6 mm long), ca. 0.8 mm thick; subopposite bracteoles (Fig. 6a) at the base of the hypanthium 2.5 mm long, ca. 5 mm wide, obtuse distally, finely fimbriate on their margins; hypanthium 4 - 6 mm long, 3 - 4.5 mm

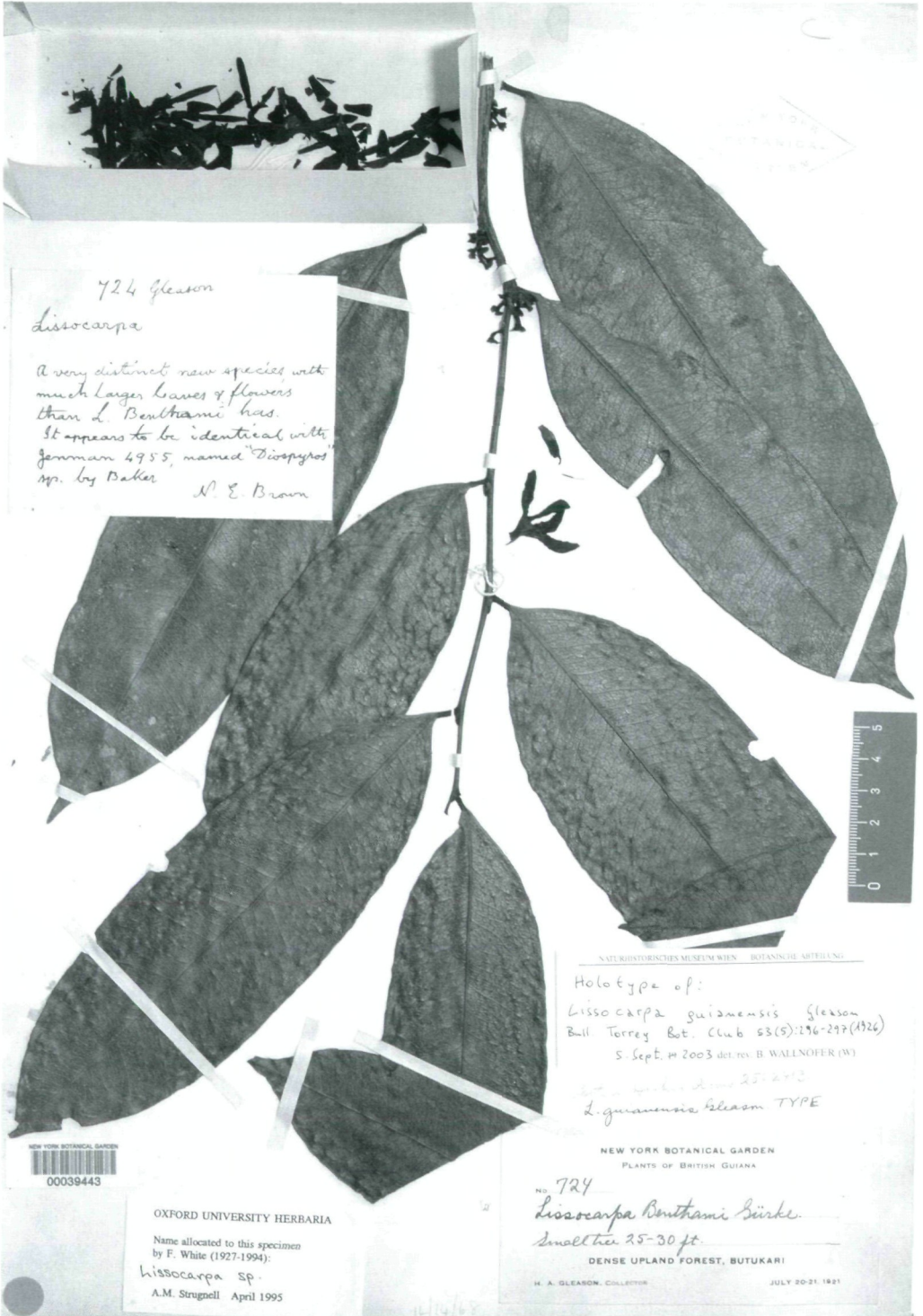


Fig. 9. Holotype of *Lissocarpa guianensis* GLEASON.

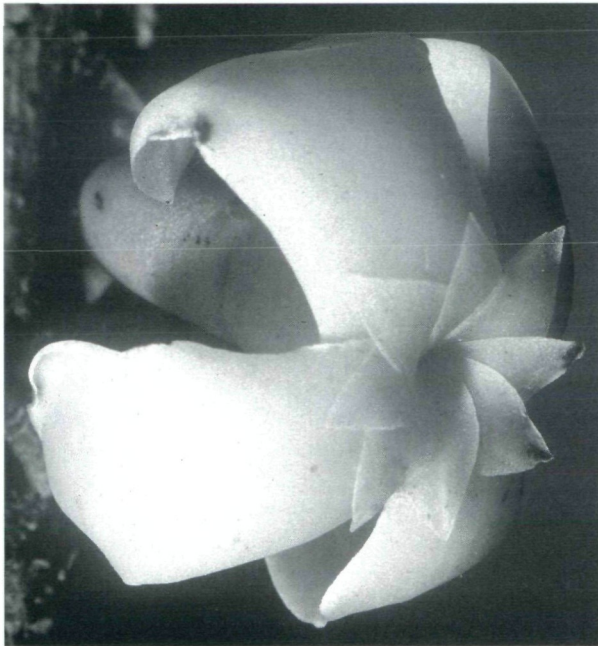
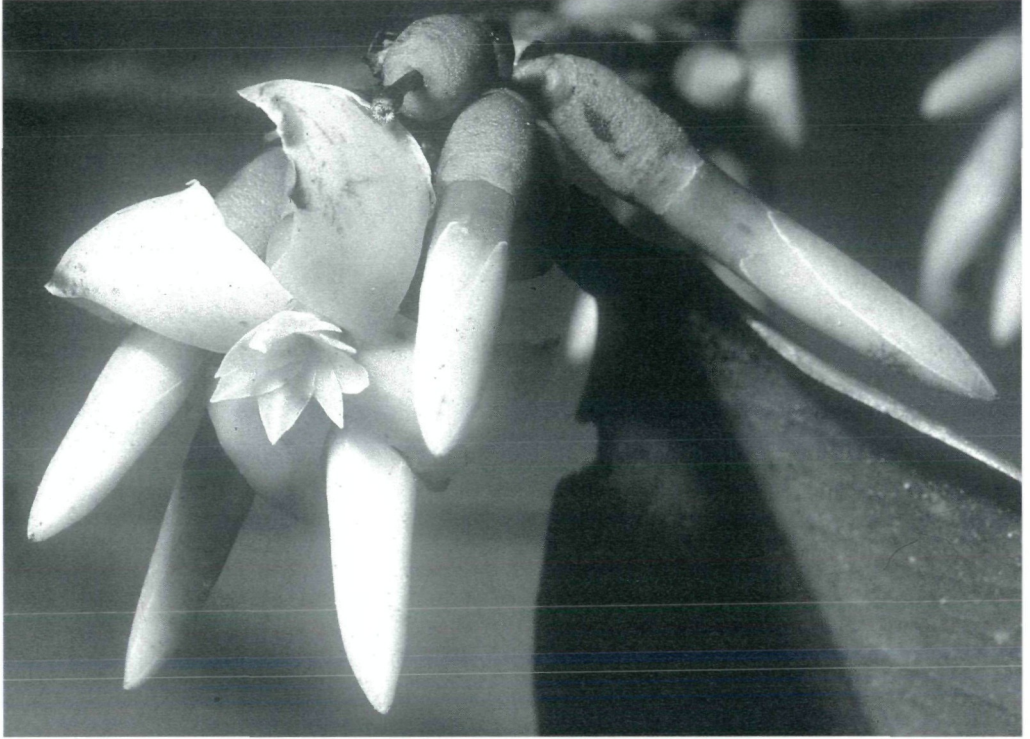


Fig. 10. Flowers of *Lissocarpa guianensis* (Guyana, along the road from Mabura Hill Township to Kurupukari, 5 Oct. 1988; photos: L.Y.T. Westra [U]).

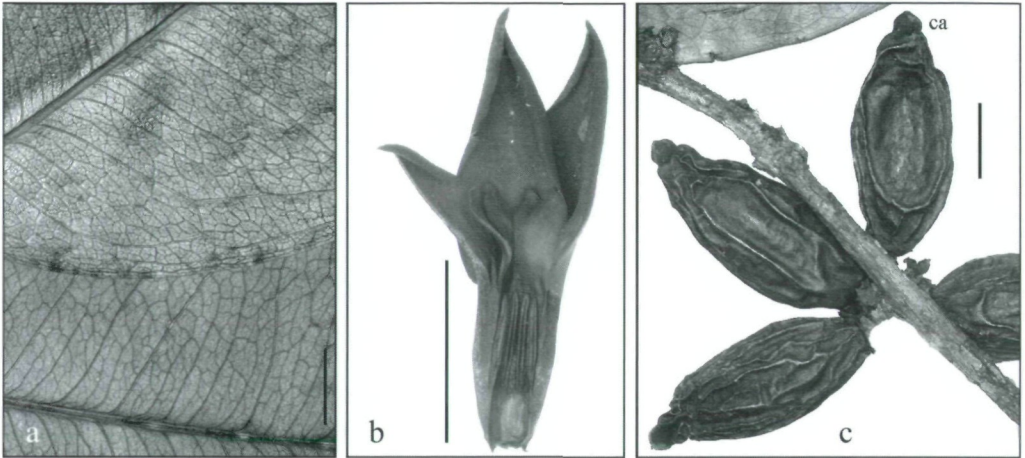


Fig. 11. *Lissocarpa guianensis*. **a**: adaxial (on top) and abaxial (bottom) leaf surface (from Maas & Westra 3999); **b**: dissected corolla showing the stamens and the corona lobes (from Stoffers et al. 111, alcohol-preserved material); **c**: fruits (from Ek et al. 1084), (ca: calyx lobes); bar = 1 cm.

wide; calyx lobes (Fig. 6a) 1.5 - 2 mm long and ca. 3 wide, more or less emarginate distally, finely fimbriate on their margins; flower buds with a pale green corolla when young, later on (shortly before anthesis) with a light green corolla tube and white corolla teeth; corolla (Fig. 10) 23 mm long at anthesis, stiff and waxy when alive; corolla tube 10 mm long, basally 2.5 mm, distally 4.5 mm wide; corolla lobes 16 mm long, ovate, 8 mm wide, gradually narrowing into the acute or obtuse apex, white and strongly bent towards the hypanthium at anthesis, later on light cream, cream or pale yellow when alive, black and hard when dry; tube of the corona short, adnate to the corolla tube at 5 mm above its base; lobes of the corona (Fig. 10) white when alive, contorted, patent or appressed to the corolla at anthesis, 10 mm long, the upper 5 mm exserted, lanceolate, 2.5 mm wide, acute distally; stamens (Fig. 11b) adnate to the corolla tube at 3.5 mm above its base, white when alive; filaments ca. 0.5 mm long; anthers linear, 5 mm long, 0.8 mm wide, obtuse distally; style (Fig. 6b) 5 mm long, 0.8 mm wide in its lower half, in the distal third clavate and up to 1 mm wide; **fruits**: pedicels ca. 2 mm long and 3 mm thick; living fruits first green, later yellow, finally pink and glossy when ripe, brown to dark brown or blackish-brown when dry, 1 - 4 developing per infructescence, ellipsoid-fusiform, up to 3 - 4 cm long and 1.4 - 1.8 cm wide when dry, 1 - 2-seeded; fruit surface smooth, usually with prominent, long and thin (sometimes also larger), longitudinal wrinkles when dry (Fig. 11c); outer layer of the fruit relatively fragile, ca. 0.5 mm thick when dry; calyx lobes erect, fitting tightly together around the broad, obconical base of the broken style; seeds 1.5 - 2.7 cm long, ca. 0.9 cm wide, ellipsoidal when solitary, flattened on one side when more than one per fruit, thickened and light brown on both ends, with ca. 7 - 8 light brown, longitudinal, salient, often branched veins; seed surface between the veins dark brown when dry, finely wrinkled; endosperm ivory-colored, hard.

Figures: anatomical wood sections (DICKISON & PHEND 1985: fig. 4 - 6); transverse sections of petiole and midrib, leaf venation (SCHADEL & DICKISON 1979: pl. 1: B, pl. 5: B,

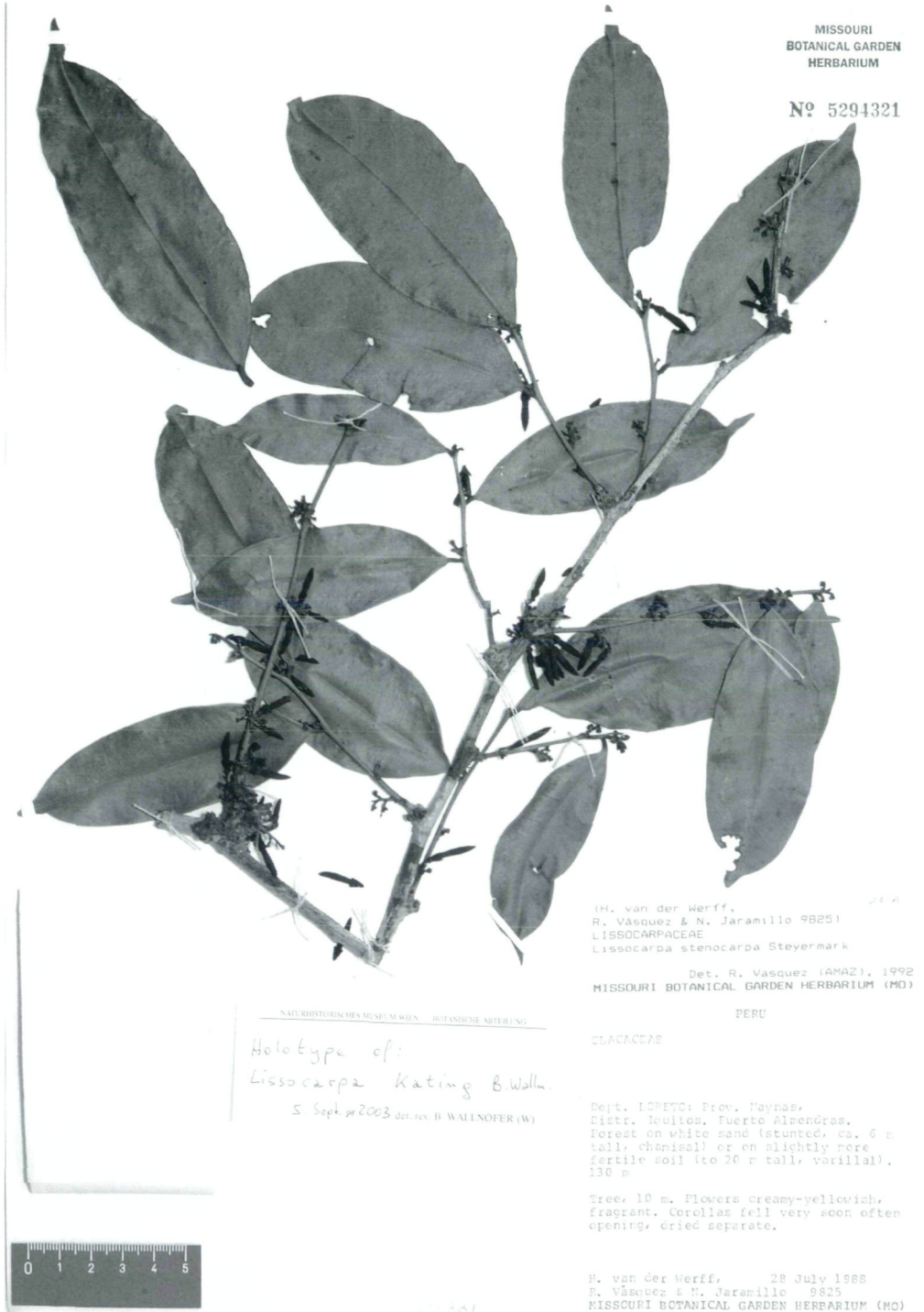
respectively); secondary xylem in transverse section, wood in transverse, tangential and radial sections, pollen (NG 1971: p. 81, fig. 2.4, fig. 2.8, respectively); fruit (ROOSMALEN 1985: plate 102: fig. 4).

Vernacular names: According to 13 of the herbarium-labels seen, it is called "barabara" ("bara bara", "bara-bara") by the Arawak-Indians, a name which is also used by them for 5 species of *Diospyros* (*D. dichroa*, *D. carbonaria*, *D. cayennensis*, *D. guianensis*, and *D. lissocarpoides*). Additional names are "Kerecanaoballi" [Arawak] (Jenman 4955; cited also in KLOOSTER et al. 2003), "Hill Bara-bara" (Hohenkerk 532), "Barabara" (SANDWITH 1931; ROOSMALEN 1985; EK & VAN DER HOUT 1997; KLOOSTER et al. 2003), and "Charcoal" (EK & VAN DER HOUT 1997).

Distribution, habitat, ecology, and phenology: This species is only known from Guyana (Fig. 5b), where it grows at elevations from sea-level up to ca. 550 meters, in usually (exclusively?) non-flooded white-sand areas, and in swamp forests drained by black-water rivers. According to herbarium labels, it has been collected in the following vegetation types: "Mora-forest" (Maas & Westra 3999), "Mora-morabukea forest" (Sandwith 363; see also SANDWITH 1931), "Dicymbe forest on white sand" (Forest Dep. Brit. Guiana 5521), "Clump Wallaba" (Tutin 213, Forest Dep. Brit. Guiana 890), "Wallaba forest" (Forest Dep. Brit. Guiana 3405, Davis 165), "dense riverine forests with *Mora excelsa*, *Pterocarpus*, *Aspidosperma*, and *Terminalia*" (Henkel & Chin 524), "forest on bauxitic sands with greenheart (*Ocotea rodiei*) and kakaralli (*Lecythis* sp.)" (Pipoly & Boyan 8932), and "forest dominated by *Eperua falcata*" (Maas et al. 7137). EK & VAN DER HOUT (1997) report this species from "Greenheart [Lauraceae: *Chlorocardium rodiei*] dominated mixed rain forests". For further details concerning these vegetation types, see COOPER (1979) and the chapter on ecology in STEEGE (1990). This species has been collected in flower in May and from July to November, and in fruit in March, April, June, and from September to December. According to long-time phenological observations compiled by STEEGE & PERSAUD (1993), it flowers in April and from July to December (main floral activity between September and November), and is in fruit in January, February, and from April to July.

Specimens examined: **Guyana, Barima-Waini**, Northwest District, Barima River, 8°20' N, 59°50' W, (fr), 19/22 Mar. 1923, **J.S. de la Cruz 3356** [paratypes: F, GH n.v., MO, NY, PH], "8 ft. tall"; – **Pomeroon-Supenaam**, Pomeroon river watershed, Kurishi creek, 6 km S confl. Arapiaco and Tapakuma rivers, 0 - 10 m, 7°10' N, 58°42' W, mixed evergreen forest to 35 m; white sand; forest with Wallaba, Greenheart, Bulletwood, *Licania*, Lecythidaceae, (fl), 21 Sept. 1992, **B. Hoffman & L. Roberts 2775** [MO n.v. (digital photo seen), U], "tree 7 m × 3 cm; corolla yellow"; – **Cuyuni-Mazaruni**, upper Mazaruni River, ca. 60°10' W [6°15' N, 60°10' W], (fl), 22 Sept. - 6 Oct. 1922, **J.S. de la Cruz 3076** [paratypes: F, GH n.v., MO, NY, PH]; – Mazaruni Station [now called "Penal Settlement"], [6°24' N, 58°40' W], (st), s.d., **Forest Dep. Brit. Guiana 6066** (= **D.B. Fanshawe F2919**) [K], "seedlings of barabara 6 months old from the forest nursery"; – same area, in mixed forest, (fl), 25 Sept. 1937, **N.Y. Sandwith 1590** [G 2×, K 2×, NY, U], "small tree c. 50 ft. high and 4 in. diam.; heart-wood gamboge-yellow; bark blackish; petals cream, recurved"; vern. name: "barabara (Arawak)"; – same area, swamp forest near a creek, (fl), 12 May 1933, **T.G. Tutin 78** [K, U], "tree ca. 40 ft. high, 6 in. diam.; bark black, smooth; trunk slightly furrowed, stilt roots small; flowers waxy, opening at night"; vern. name: "bara-bara"; – Mazaruni River, Kalakoon [= Kalakun], [6°24' N, 58°39' W], (flbuds), Nov. 1886, **G.S. Jenman 2407** [K]; – Pakaraima Mts., Kamarang, 450 - 550 m, 5°52' N, 60°38' W, Mora-forest just N of Kamarang, (fl), 11 Nov. 1979, **P.J.M. Maas & L.Y.T. Westra 3999** [AAU, F, K, MO, NY, P, S n.v., U, Z], "tree ca. 20 - 25 m tall, 20 cm diam.; wood light yellow, soon becoming dark yellow on exposure by cutting; calyx and bracts light green; corolla light cream, fragrant (open corollas gathered from the ground, no open flowers on branches at moment of collecting around the mid-

dle of the day); wood sample: U-24830"; – Mazaruni-Kuribrong divide, inspections camp 8, [5°43' N, 59°13' W], on white sand; associated with "clump-wallaba"; plentiful in sandy swamps, (fl), 28 Oct. 1926, **Forest Dep. Brit. Guiana 890** [FHO, K], "small tree; bark hard, black, grooved vertically, well numerous well marked fissures; flowers white"; vern. name: "barabara (Arawak)"; – 90 mls. Bartica-Potaro Road, [ca. 5°25' N, 59°1' W], from Dicymbe forest on white sand, (yfr), 28 Oct. 1947, **Forest Dep. Brit. Guiana 5521** (= **D.B. Fanshawe F2722**) [K], "40' tree 6" dia.; leaves leathery, supple; young fruit bunched in axils, sessile, ovoid, glabrous"; vern. name: "Barabara"; – ca. 83 miles, Bartica-Potaro road, ca. 400 ft., [ca. 5°30' N, 58°59' W], Clump Wallaba, (fr), 21 Jun. 1933, **T.G. Tutin 213** [K, U, US n.v.], "fruit yellow"; vern. name: "Bara-bara"; – Essequibo Island-West Demerara, lower 7 km of Kerite [= Keriti] Creek, trib. on W bank of Essequibo R., 1 km N of Goldmine settlement, 0 - 15 m, 6°32' N, 58°39' W, stream 75 m wide at mouth, narrowing rapidly; dense riverine forests: *Mora excelsa*, *Pterocarpus*, *Aspidosperma*, *Terminalia*, (yfr), 18 Dec. 1992, **T.W. Henkel & M. Chin 524** [MO, US n.v.], "tree 5 m; fruit yellow with persistent style, ovate 0.7 cm × 0.5 cm"; vern. name: "Bara Bara", use: "used medicinally"; – Essequibo River, Makauria Creek [= Makouria Creek], [6°28' N, 58°35' W], (fl), 17 Sept. 1940, **Forest Dep. Brit. Guiana 3290** (= **D.B. Fanshawe F554**) [K, NY, OXF/FHO (wood no. 13275)], "40' tree, 6" diam., with brittle, charcoal-like outer bark; leaves very stiff and leathery; flowers fascicled on stem, white; calyx unlobed; corolla tubular, stiff, waxen, convolute in bud; stamens whorled, white"; vern. name: "barabara"; – County Essequibo, Essequibo River, Monkey creek grant, Auarika [?], [6°25' N, 58°24' W], (fr), 19 Mar. 1910, **L.S. Hohenkerk 532 (128)** [K (+ carp.), U], vern. name: "Hill Bara-bara (Arawak)"; – Demerara-Mahaica, Hyde Park near Georgetown, [6°30' N, 58°16' W], sandhill in forest, (fl), Sept. 1924, **A.C. Persaud 154** [paratypes: F, K, NY], "tree; flowers white"; – same area, (fr), Sept. 1924, **A.C. Persaud 155** [F, K, NY]; – County Demerara, Demerara River, Mablissa [= Moblissa] Creek, [6°5' N, 58°17' W], (fr), 1 Mar. 1910, **C.W. Anderson 532a** (Field No. 77) [K], vern. name: "barabara (Arawak)"; – Mahaica-Berbice, nr. St. Francis, Mahaicony River, [6°6' N, 57°57' W], understory in Wallaba forest, (fr), Mar. 1967, **D.H. Davis 165** [K, NY], "tree 12 m; fruits green"; vern. name: "barabarra"; – Upper Demerara-Berbice, Essequibo River, Siba Creek [= Seba Creek near "Mazaruni Station" what is now called "Penal Settlement"], [6°13' N, 58°31' W], Wallaba forest, (fr), 3 Apr. 1941, **Forest Dep. Brit. Guiana 3405** (= **D.B. Fanshawe F669**) [K (+ carp.), NY], "35' tree, 4" diam.; with blk., charcoal-like bark; leaves leathery; fruit green, pink when ripe, glossy, oblong-pointed, mucronate"; vern. name: "barabara"; – Essequibo river, Moraballi creek, near Bartica, near sea-level, [6°12' N, 58°34' W], in Mora-morabukea forest, overhanging the camp, (fl, fr), 1 Oct. 1929, **N.Y. Sandwith 363** [INPA, K 2x, NY, P, U], "middle-sized tree 60 - 70 ft high; bark blackish; fl. cream; young fruit green"; vern. name: "barabara (Arawak)"; – same area, in mixed forest, (yfr), 26 Oct. 1929, **N.Y. Sandwith 525** [K, NY, U], "tree 78 ft. high, 6.5 in. diam.; bark blackish; wood a very distinct gamboge colour; fl. cream"; vern. name: "barabara (Arawak)"; – Upper Demerara Region, Mabura Hill, 50 m, 5°25' N, 58°40' W, medium tall forest to 25 m tall; white sand mixed with brown sand in spots, (fr), 21 Apr. 1989, **W. Hahn 5832** [NY, U], "treelet to 6 m; fruits yellowish-green"; – same area, forest on bauxitic sands; greenheart (*Ocotea rodiei*) and kakaralli (*Lecythis* sp.); numerous lianas, (fr), 19 Nov. 1986, **J.J. Pipoly & R. Boyan 8932** [MO, US n.v.], "treelet 3 m; fruit yellow"; – Mabura Hill region, near field-station, [5°20' N, 58°40' W], white sand; large gap, (fr), 3 Jun. 1994, **R.C. Ek, L. Brouwer & V. Jetten 1084** [NY, U 2x], "tree up to 6 m"; – Mabura Hill area, 150 - 200 m, 5°20' N, 58°40' W, swamp forest on sandy loam, (fr), 5 Jun. 1986, **J.J. Pipoly 7543** [CAY n.v., F, MO n.v. (digital photo seen), NY, U], "tree 12 m × 25 cm; calyx and corolla green; fruit yellow"; – near Mabura Hill sawmill, 5°19' N, 58°38' W, in disturbed and/or secondary vegetation on white sand, (fl), 29 Oct. 1982, **A.L. Stoffers, A.R.A. Görts-van Rijn, B.J.H. ter Welle & K.J. Bonsen 111** [CAY, F, K, MO, NY, U], "tree to 12 m tall; wood yellow; flowers cauliflorous or axillary, 4-merous; calyx yellow-green, coronate; corolla pale yellow, lobes contorted; flowers in spirit; wood sample: UW 30084"; – Mabura Hill, at km 14 on Kurupukari main road, 5°10' N, 58°40' W, forest on white sand dominated by *Eperua falcata*, roadside, (fl), 24 Aug. 1988, **P.J.M. Maas, J. Koek-Noorman, B.J.H. ter Welle & L.Y.T. Westra 7137** [CAY, K, MO, NY, U, WIS n.v.], "tree 8 m tall, 10 cm dbh; wood yellow; bark black; leaves coriaceous; calyx pale green; corolla (in bud) pale green; wood sample: Uw 32434"; – Potaro-Siparuni, Kaieteur Plateau [ca. 5°10' N, 59°30' W], wallaba forest, on savanna, (fr), 11 May 1944, **B. Maguire & D.B. Fanshawe 23381** [GH n.v., U] "occasional; 7 m tree, 10 cm diam.; fr. conical, whitish, thinly fleshy"; – exact collecting site unknown: Demerara, (fl), s.d., **Parker 280** [K], "Loranthus demerara - Demy no. 280 - Parker"; – Demerara R., (fl), Nov. 1888 or 1889, **G.S. Jenman 4955** [K, U], vern. name: "Kerecanaoballi".



MISSOURI
BOTANICAL GARDEN
HERBARIUM

Nº 5294321

(H. van der Werff,
R. Vásquez & N. Jaramillo 9825)
LISSOCARPACEAE
Lissocarpa stenocarpa Steyermark

Det. R. Vásquez (AMA2), 1992
MISSOURI BOTANICAL GARDEN HERBARIUM (MO)

PERU

ELACACEAE

SAURHISTORISCHES MUSEUM WIEN - BOTANISCHE ABTEILUNG
Holotype of:
Lissocarpa kating B. Walln.
5 Sept. 192003 det. rev. B. WALLNÖFER (W)

Dept. ILOPETO: Prov. Moynas,
Dist. Huilcas, Fuerte Alpendres,
Forest on white sand (stunted, ca. 6 m
tall, chusilla) or on slightly more
fertile soil (to 20 m tall, varilla),
130 m

Tree, 10 m. Flowers creamy-yellowish,
fragrant. Corollas fell very soon often
opening, dried separate.

H. van der Werff, 28 July 1988
R. Vásquez & N. Jaramillo 9825
MISSOURI BOTANICAL GARDEN HERBARIUM (MO)

Fig. 12. Holotype of *Lissocarpa kating* B. WALLN.

***Lissocarpa kating* B.WALLN., sp.n.;** [Figs. 1, 2a - c, 3a - b, 6d - e, 12 - 13].

Diagnosis: Arbor 3 - 18 (- 28) m alta; diameter trunci 2,5 - 25 cm; ramuli juvenilissimes laeves, in statu sicco griseo-virides maxime similiter ramulis generis *Heisteria*; petioli (1 -) 4 - 6 (- 10) mm longi; laminae foliorum (3 -) 9 - 15 (- 20) cm longae et (1,2 -) 3,5 - 5,5 (- 9,7) cm latae, ellipticae, chartaceae, ambis lateribus concolores et cum nervatione optime visibili; nervo medio supra prominente; tubus corollae 5 - 9 mm longus; lobis calicis 4, latoribus quam longis, distaliter emarginatis; lobi corollae 8 - 13 mm longi, 6 - 8 mm lati; corona presens; fructus subglobosi, 2,3 - 2,8 cm longi, 1,4 cm diametientes; habitat in silvis supra arenam albam nominatis "caatinga".

Typus: Peru, Dept. Loreto, Prov. Maynas, Distr. Iquitos, Puerto Almendras, 130 m, [3°49' S, 73°22' W], forest on white sand (stunted, ca. 6 m tall, chamisal) or on slightly more fertile soil (to 20 m tall, varillal), (fl), 28 Jul. 1988, **H. van der Werff, R. Vásquez & N. Jaramillo 9825** [holotype: MO; isotypes: AMAZ n.v., USM n.v.], "tree 10 m; flowers creamy-yellowish, fragrant; corollas fell very soon after opening, dried separate".

Treelet or tree 3 - 18 (- 28) m tall (already flowering, when only 3 m high), 2.5 - 25 cm dbh; outer bark hard, tough, black, the inner yellow or brownish yellow, without odor, presence of some orange sap reported by Ruokolainen et al. 1944; twigs terete, the youngest drying greenish-gray (very much resembling the characteristic bark of *Heisteria*, except for alcohol-treated or badly dried herbarium specimens), smooth and destitute of any ridges; bark of young twigs becoming increasingly covered with irregularly enlarging black spots and stripes; bark of older twigs soon completely black, partially covered with dark gray remnants of the epidermis, bloating and cracking up by longitudinal, black fissures with slightly raised margins; buds brownish, later on black; **leaves:** petioles (1 -) 4 - 6 (- 10) mm long, 1.5 - 2 (- 3) mm thick, drying greenish-gray, brownish or black, smooth or slightly shriveled longitudinally especially on their abaxial side, and with a quite flat longitudinal groove adaxially; lamina broadly lanceolate or elliptic (broadest near middle), sometimes oblong, rarely obovate (3 -) 9 - 15 (- 20) cm long, (1.2 -) 3.5 - 5.5 (- 9.7) cm wide, chartaceous, gray-green on both surfaces, slightly shiny adaxially, dull abaxially when dry; leaf apex short acuminate, with a drip tip 0.5 - 1.5 (- 2) cm long; base of the lamina attenuate; leaf margins not thickened; flachnektarien (extrafloral nectaries) on abaxial leaf surfaces 0.2 - 0.5 mm in diameter (Fig. 1b), frequent near the base, scattered along the midvein, along margins and near the apex; midvein prominent on both sides of the lamina, widened, flat or semicircular in cross section and, when dry, somewhat longitudinally shriveled adaxially (area along the midvein somewhat sunken compared to the rest of lamina), semicircular in cross section abaxially; secondary veins ca. 10 per side, prominent adaxially, slightly prominent abaxially; tertiary veins slightly prominent on both sides of the lamina; quaternary veins only hardly visible adaxially; **flowers** solitary on the proximal part of young long-shoots or on up to 5-flowered short-shoots (inflorescences), the latter either solitary in the leaf axils of younger twigs, or more or less densely crowded on the already leafless nodes of older twigs; inflorescence axes up to 10 (- 50) mm long, ca. 0.8 mm thick; pedicels (1 -) 1.5 - 2 (- 3) mm long, 0.5 - 1 mm thick, blackish; subopposite bracteoles at the base of the hypanthium ca. 1.5 (- 2) mm long, ca. 2 mm wide, fimbriate on their margins, rounded or obtuse distally; hypanthium (Figs. 6d - e) 3 - 4 mm long, 2 - 3 mm wide, with scat-

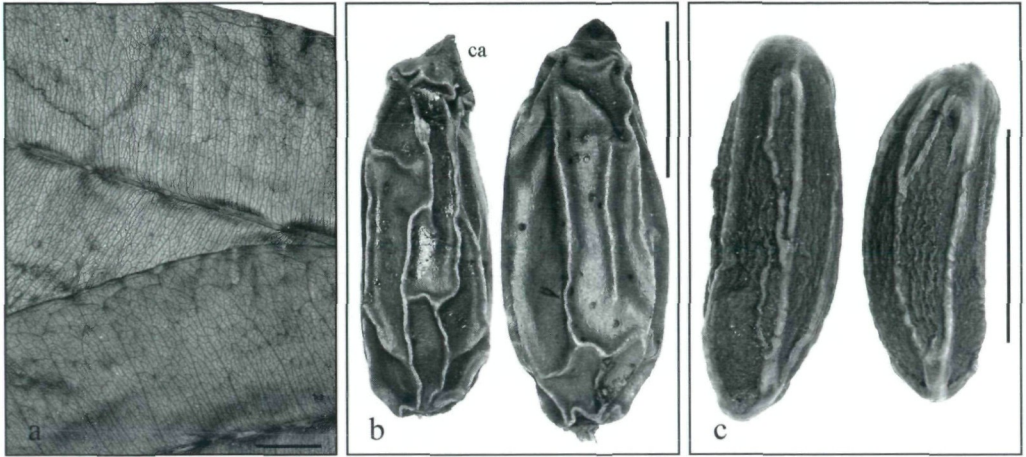


Fig. 13. *Lissocarpa kating*. **a**: adaxial (on top) and abaxial (bottom) leaf surface (from Vásquez et al. 17922); **b**: fruits (ca: calyx lobes), and **c**: seeds (from Schultes & Cabrera 13486); bar = 1 cm.

tered, appressed, oblong, papilla-like structures adaxially (inside); calyx lobes green when alive, blackish when dry, dextrorsely contorted, 1.5 - 2 mm long, 3 - 3.5 mm wide, truncate and emarginate distally, fimbriate on their margins; corolla greenish-yellow in bud, fragrant and white at anthesis, subsequently (?) becoming creamy-yellowish or pale yellow when alive, blackish when dry; corolla tube 5 - 9 mm long, basally 2 - 3 mm, distally 4 mm wide; corolla lobes more or less elliptic (sometimes asymmetrical and differing in width on the same flower, e.g., in Vasquez et al. 8064), 8 - 13 mm long, 6 - 8 mm wide, obtuse or broadly rounded distally; tube of the corona 1 - 2 mm long, adnate to the corolla tube at 3 - 5 mm above its base; lobes of the corona lanceolate to broadly lanceolate, 3 - 5 mm long, the upper part exserted, 1.5 - 2 mm wide, obtuse distally; stamens 4 - 5 mm long, free, adnate to the corolla tube at 3 - 4 mm above its base; filaments 1 mm long; anthers ca. 3.5 mm long, 0.8 mm wide; staminodes ca. 5 mm long; filaments 1 mm long; aborted anthers ca. 3.5 mm long, ca. 0.5 mm wide, flat; thecae collapsed; style 10 mm long, markedly enlarged basally, narrowing towards the middle, clavate at the apex (Fig. 2a); stigma cushion-like, densely covered with hair-like appendages (Fig. 2b); **fruits**: pedicels 3 mm long and 1.5 mm thick; living fruits green when unripe, later on changing colors to yellow and orange, finally to red when ripe; dry fruits ellipsoidal-fusiform, less frequently ellipsoidal, 2.3 - 2.8 cm long, 1.4 cm wide (Fig. 13b); fruit surface brown, smooth, with few, large wrinkles when dry; calyx lobes erect, fitting tight together around the broad obconical base of the broken style; seeds (Fig. 13c) 14 - 18 mm long, 6 - 9 mm wide, dark brown when dry, 1 - 2 per fruit, with ca. 6 - 8 longitudinal, lighter brown, salient veins; seed surface finely shriveled.

This species seems to be closely related to *L. guianensis* from Guyana, with which it shares the following features: midvein raised and widened adaxially; inflorescences usually crowded on the leafless nodes of older twigs. *L. kating* shows a remarkable variation in the flowers size (Prance et al. 23855: flower buds including hypanthium up to 23 mm long!).

Etymology: The name has been coined arbitrarily (see: GREUTER et al. 2000: Art. 23.2), but it seems to have a pleasant, exotic (non-European) sound.

Vernacular name: "pau amarelo" – RODRIGUES (1961) ascribes this name to *L. benthamii*. However, a herbarium collection gathered in the area studied by him, belongs to *L. kating* (Rodrigues 913, see below). It is not clear whether this vernacular name applies to both species or only to one of them (see also the remark under *L. benthamii*).

Distribution, habitat, ecology, and phenology: This species is known from Brazil (Amazonas), Colombia (Vaupés), and Perú (Loreto), where it grows at elevations between 90 and 250 meters (Fig. 5d), in primary, non-flooded ("terra-firme") rain forests, frequently on white-sand soils extremely poor in nutrients. This characteristic Amazon, white-sand woodland is called "caatinga amazonica", "campinarana", "campina" (PIRES & PRANCE 1985; ANDERSON 1981), "pseudo-caatinga" (SCHNELL 1987) or "Rio Negro caatinga" (HUBER 1995) in Brazil, and "Varillal" and "Chamizal" (ENCARNACIÓN 1985; RUOKOLAINEN & TUOMISTO 1993; VÁSQUEZ MARTÍNEZ & PHILLIPS 2000) in Perú. According to specifications on herbarium labels, the vegetation on the collecting sites is often open, stunted, reaching only a few meters in height or, as in other cases, forming a closed canopy up to 25 m in height. Less frequently, this species was collected on lateritic or sandy clay soils. The vegetation at the collection site "Ilha das Flôres" on the upper Rio Negro is described in detail by RODRIGUES (1961). In flower, this species has been collected between May and October (two collections with deflorated specimens gathered in December), and in fruit from January to October.

Specimens examined: **Colombia, Vaupés, Río Apaporis, Cachivera de Jirijirimo y alrededores, ca. 250 m, [0°8' N, 70°39' W], edge of savannah, (fr), 7 Jul. 1951, R.E. Schultes & I. Cabrera 12949 [U], "tree 10 m";** – same area, (fr), 12 Aug. 1951, same collectors **13516 [U], "30 feet tall; fruits red";** – Raudal de Jirijirimo, [0°8' N, 70°39' W], (fr), 8 Jul. 1951, same collectors, **13486 [K, MO, NY, U], "tree 50 ft. tall; fruit reddish".**

Brazil, Amazonas, Alto Rio Negro, Ilha das Flôres, [0°1' N, 67°14' W], catinga arenosa, (fr), 17 Feb. 1959, W. Rodrigues 913 [INPA], "arvore grande; frutos verdes"; – same area, (fr), 20 Feb. 1959, **P. Cavalcante 666 [INPA];** – São Paulo de Olivença, Rio Solimões (Amazonas), [3°27' S, 68°48' W], in silva "catinga"; mata de terra firme, alta, silicosa (catinga), (fl), 5 Oct. 1931, **A. Ducke 24567 [G, INPA, K, P, U], "arbor parva; flor. albis, odoratis";** – same area, silva "catinga", (fr), 25 Jan. 1937, **A. Ducke 5199 [G, K, P, U], "arbor parva; fr. rubris";** – same area, caatinga, (fl), 15 Oct. 1942, **A. Ducke 1117 [K, MO, NY], "arvore pequena; flor branca; abundancia: frequente";** – same area, caatingas, (fl, fr), 3 May 1945, **R.L. de Fróes 20587 [K, NY], "arbusto 3 m";** – same area, mata caatinga, (fr), 3 May 1945, **R.L. de Fróes 20588 [K, NY], "arbusto 3 m";** – same area, caatinga aberta, (fr), 18 Apr. 1945, **R.L. de Fróes 20732 [K, NY], "arbusto";** – Rio Javari, 180 miles above mouth, below Estirão do Equador, [4°27' S, 71°30' W], forest on terra firme, (fl), 17 Oct. 1976, **G.T. Prance, R.J. Hill, T.D. Pennington & J.M. Ramos 23855 [F, K, MO n.v. (digital photo seen), NY, U], "treelet 8 m × 6 cm diam.; corolla pale yellow";** – Carauri [= Carauari], Poço Juruá I, [4°53' S, 66°54' W], mata de terra firme; solo argiloso, (st), Jul. 1980, **A.S.L. da Silva, N.A. Rosa & R.P. Bahia 1017 [MG], "arvore 14 m × 54 cm circ."**

Perú, Loreto, Prov. Maynas, Mishana, 130 m, [3°53' S, 73°29' W], bosque primario, (fl), 21 Jul. 1984, R. Vásquez, N. Jaramillo & G. Criollo 5308 [AMAZ n.v., FHO, MO, USM n.v.], "árbol 12 m; flores verdosas"; – River Nanay, close to the village of Mishana, [3°52' S, 73°29' W], in the first non-flooded terrace from the present flood plain; adjacent to the second terrace; soil sandy clay; drainage imperfect, small depressions gather rain water; forest with *Mauritia* and *Jessenia* palms, (st), 4 Jun. 1990, **K. Ruokolainen, H. Tuomisto, M. García, R. Ríos, A. Torres & J. Ruiz 1389 [TUR], "dbh 10 cm; tough bark, outer part black, inner yellow";** – same locality, date (st), and collectors, **1463 [AMAZ n.v., TUR], "height 15 m, dbh**

11 cm; no latex; outer bark black, inner yellow, no odor"; – same locality, in the second non-flooded terrace from the present flood plain; on a plateau-like top of a c. 10 m high hill; white-sand forest, closed canopy at c. 25 m, (st), 14 Jun. 1990, same collectors, **1646** [AMAZ n.v., TUR], "height 15 m, dbh 10 cm; no latex; outer bark black, hard; inner yellow, no odor"; – same locality, (st), 15 Jun. 1990, same collectors, **1725** [TUR], "height 7.5 m, dbh 3 cm; no latex; outer bark hard, black, inner yellow; no odor"; – same locality, date (st), and collectors, **1736** [TUR], "height 13 m, dbh 10 cm; no latex; outer bark hard, black; inner brownish yellow, no odor"; – same locality, date (st), and collectors, **1742** [TUR], "height 4 m, dbh 7 cm; outer bark black, inner yellow; skew; length of trunk 12 m"; – same locality, (st), 17 Jun. 1990, same collectors, **1853** [TUR], "height 5 m, dbh 3 cm; hard bark, outer part black, inner yellow, no odor"; – same locality, (st), 18 Jun. 1990, same collectors, **1944** [TUR], "height 15 m, dbh 23 cm; some orange sap; hard and black outer bark, inner yellow; no odor"; – ca. 2 km S of the village of Mishana at Río Nanay, 100 - 150 m, [3°53' S, 73°29' W], primary rain forest on a poorly drained plateau with white-sand soil, (st), 13 Nov. 1991, same collectors, **2928** [TUR], "height 8 m, dbh 4 cm"; – Mishana, Río Nanay, halfway between Iquitos and Santa María de Nanay, ca. 140 m, 3°50' S, 73°30' W, upland white sand, (st), 22 Mar. 1979, **A.H. Gentry, C. Díaz, J. Aronson & N. Jaramillo 26022** [AMAZ n.v., MO, USM n.v.], "treelet 1" dbh, sterile; bent petioles"; – same area, ca. 150 m, upland forest on white sand, (st), 24 Mar. 1979, **A.H. Gentry, J. Aronson, C. Díaz & N. Jaramillo 26158** [AMAZ n.v., MO, USM n.v.], "tree 21 cm dbh"; – same locality, date (st), and collectors, **26163** [AMAZ n.v., MO, USM n.v.], "treelet 1" dbh"; – Allpahuayo (Km 25, carretera Iquitos-Nauta), Estación Experimental del Instituto de Investigaciones de la Amazonia Peruana [= Estación IIAP], [3°53' S, 73°25' W], bosque primario, (yfr), 19 Oct. 1984, **R. Vásquez & G. Criollo 5778** [AMAZ n.v., MO, USM n.v.], "árbol 10 m; frutos verdes"; – same area, (fr), 29 Jan. 1985, **R. Vásquez, N. Jaramillo & J. Ruiz 6193** [AMAZ n.v., NY 2x, MO, USM n.v.], "árbol 12 m; frutos verdes"; – same area, 150 m, (fr), 5 Jun. 1985, **R. Vásquez, J. Ruiz & N. Jaramillo 6546** [AAU, F, NY], "arbusto 4 m; frutos anaranjados"; – same area, 130 m, forest on lateritic soil and white sand, (fl), 24 Aug. 1988, **H. van der Werff, R. Vásquez & N. Jaramillo 10250** [AMAZ n.v., MO, USM n.v.], "tree 8 m; buds green"; – same area, 220 m, bosque primario en suelos de arena blanca, (fl), 19 Sept. 1990, **J.J. Pipoly, R. Vásquez, N. Jaramillo & R. Ortíz 12205** [AMAZ n.v., MO, USM n.v.], "árbol de 18 m × 25; cáliz verde; corola verde-amarillenta en botón, blanca en antesis"; – same area, 150 - 180 m, bosque primario; vegetación sobre suelo arcillo-arenoso, con dominancia de arena blanca, en las elevaciones del terreno y de arcilla en los declives; estrato inferior sin dominancia observándose *Lepidocaryum tessmannii* y *Scheelea morenii*; buen drenaje, pequeñas ondulaciones del terreno, (defl), Dec. 1990, **R. Vásquez M. & N. Jaramillo 15447** [AMAZ n.v., MO, USM n.v.], "árbol 12 m × 12.6 cm"; – same locality, date (st), and collectors, **15470** [AMAZ n.v., MO, USM n.v.], "árbol 12 m × 15.6 cm"; – same locality, bosque primario, con suelos de arena blanca "varillal", (st), 28 May 1991, **R. Vásquez & N. Jaramillo 16659** [AMAZ n.v., MO, USM n.v.], "árbol 6 m × 5.2 cm DAP"; – same area, Inventario Permanente, 150 m, (st), 21 Mar. 1992, **R. Vásquez, S.A. Vásquez & N. Jaramillo 17922** [MO], "arbolito 4 m × 2.5 cm DAP"; – same area, 140 m, 3°57'19" S, 73°25'47" W, bosque primario; sobre arena blanca; Varillal alto seco, (fr), 23 Apr. 1997, **R. Vásquez, O. Phillips, R. Rojas & A. Peña 23435** [MO (4x unmounted), W], "árbol 15.0 cm DAP × 28 m; frutos amarillos"; – same area, (defl), 28 Dec. 1997, **R. Vásquez & R. Ortiz-Gentry 25233** [MO], "árbol 12 m"; – Distrito Iquitos, carretera de Peña Negra, 2 km from Quisto Cocha, 17 km from Iquitos, [3°51' S, 73°20' W], sandy uplands, (fr), 30 Mar. 1979, **M. Rimachi Y. 4365** [AMAZ n.v., MO, USM n.v., WIS n.v.], "12 m; fruit green"; – side road off road to Peña Negra, ca. 5 km beyond jct., [3°50' S, 73°21' W], upland forest over sand, (fr), 25 May 1978, **S. McDaniel, M.Y. Rimachi, W. Holmes & J. Bruza 21628** [BR 2x, MO, NY], "tree 10 m; fruit red"; – Distrito Iquitos, Puerto Almendras, 122 m, [3°49' S, 73°22' W], bosque primario; suelo de arena blanca; varillal, no inundable, (st), 17 Jan. 1993, **C. Grández, N. Jaramillo et al. 5549** [MO], "arbusto 4 m, 10.9 cm DAP"; – same locality, bosque primario, (fl), 2 Oct. 1986, **R. Vásquez, N. Arévalo, P. Bardales & N. Jaramillo 8064** [F, MO, NY, TEX], "arbusto 4 m; flores blancas, olor de rosas"; – same locality, bosque primario; suelo de arena blanca, (fl), 30 Sept. 1987, **R. Vásquez & N. Jaramillo 9659** [MO, USM n.v.], "árbol 8 m; flores amarillas"; – Prov. Maynas, Caserío Nina Rummy [= Minarumi], Río Nanay, 123 m, 3°48' S, 73°25' W, bosque primario en estudio integral, suelos de diferentes caracterizaciones no inundables, (st), 13 Jan. 1986, **J. Ruiz 758** [AMAZ n.v., MO], "árbol estéril"; – Manfinfa [locality not traced] on the upper Río Nanay, (fl), 29 Jun. 1929, **L. Williams 1120** [F], "small tree".

Lissocarpa stenocarpa STEYERM., Ann. Missouri Bot. Gard. 74 (1): 104 - 105 (1987); [Figs. 6i, 14 - 15].

Typus: Venezuela, Territorio Federal Amazonas, Dept. Atabapo, Cerro Marahuaca, riverine forest upstream from "Sima Camp", along branch of Caño Negro, south-central portion of meseta, 1140 m, 3°43' N, 65°31' W, (fl, fr), 28 Feb. / 1 Mar. 1985, **J.A. Steyermark & B. Holst 130880** [holotype: MO, isotypes: NY, U, US, VEN n.v.], "tree 10 m; leaves subcoriaceous, dark green above, pale green below; corolla green; fruit yellow green" (The specimen at US has flower buds and young fruits, whereas the others possess only fruits).

Treelet or tree 2 - 10 m tall, 5 - 10 cm in diameter; bark dark gray to black; wood yellowish; twigs terete, the youngest smooth and destitute of any ridges, drying brownish or black; bark of younger twigs covered with the whitish-gray or dirty-gray, partially exfoliating remnants of the epidermis, soon cracking up by longitudinal, black fissures with slightly raised margins; older bark of twigs increasingly losing the epidermis and subsequently becoming nearly black; **leaves:** twig-area around the petiole-base thickened and swelled (Figs. 15a - b), markedly visible as a step (superficially resembling a leaf scar) on dry, in general strongly shrunken petioles; petioles (3 -) 6 - 10 mm long, 1 - 2.5 mm thick, drying blackish, shriveled especially on abaxial sides when dry, with a longitudinal groove adaxially; lamina broadly lanceolate (broadest near middle), less frequently elliptic, (4.5 -) 8 - 14 (- 17) cm long, (1.5 -) 2.5 - 4.5 (- 8.3) cm wide, subcoriaceous, stiff, brittle, slightly revolute, lustrous, dark green adaxially, pale green abaxially when alive, and, when dry, greenish-gray, gray-brown to blackish-brown and sometimes slightly shiny adaxially, brownish to dark brown and dull abaxially; leaf apex long acuminate (drip tip), rarely acute or obtuse; base of the lamina attenuate, rarely rounded; leaf margins not thickened; flachnektarien (extrafloral nectaries) on abaxial leaf surfaces 0.2 - 0.5 mm in diameter, scattered all over the lamina, but more frequent near the base, the apex and the margins; midvein light green and sharply prominent on both surfaces when alive, prominent on both sides of the lamina when dry, semicircular (or somewhat flattened) in cross section and more or less longitudinally shriveled adaxially, triangular in cross section abaxially when dry; secondary veins ca. 7 - 9 per side, slightly prominent on both sides of the lamina; tertiary veins slightly prominent on both sides of the lamina; quaternary veins in general hardly visible; **flowers** (Figs. 6i, 15a - c) usually solitary on proximal parts of young long-shoots (Fig. 15a), or less often on up to 5-flowered short-shoots (inflorescences) with ca. 2 mm long, 0.8 mm thick axes (Fig. 15b); pedicels 2 - 4 mm long, 0.3 - 0.5 mm thick, black; subopposite bracteoles at the base of the hypanthium 1 - 1.5 (- 3) mm long, 1 (- 3) mm wide, fimbriate on their margins, obtuse distally; hypanthium 3 - 4 mm long, 1.5 - 2 mm wide; calyx lobes black when dry, 1.2 - 1.5 (- 2.5) mm long, 2 mm wide, rounded or slightly emarginate distally, fimbriate on their margins; corolla green in bud, later on whitish, yellowish or cream colored when alive, black when dry; corolla tube 5 mm long, basally 1 mm, distally 2 mm wide; corolla lobes (at anthesis) ovate, 6.5 mm long, 2.5 - 3 mm wide, acute distally; tube of the corona ca. 2 mm long, adnate to the corolla tube in approximately its middle; lobes of the corona narrowly triangular, 4 mm long, 0.8 mm wide, the upper 3 mm exerted from the corolla tube, acute and slightly papillose distally; stamens not available for study; staminodes ca. 3 mm long; filaments and aborted, flat anthers not distinguishable; style (of a sterile flower) ca. 5 mm long, clavate and 0.8 mm wide below the apex;

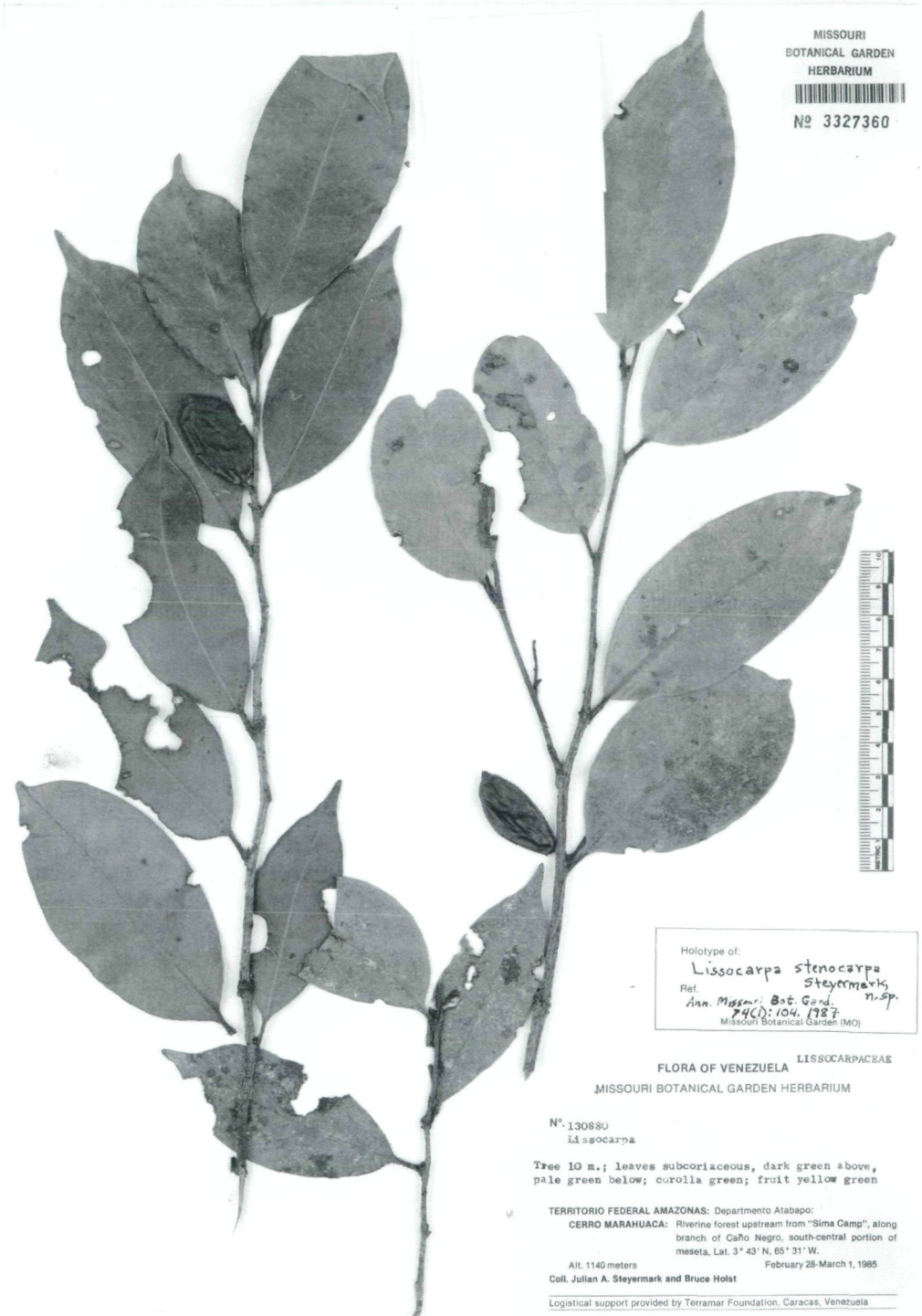


Fig. 14. Holotype of *Lissocarpa stenocarpa* STEYERM. (photo courtesy of the Missouri Bot. Gard.).

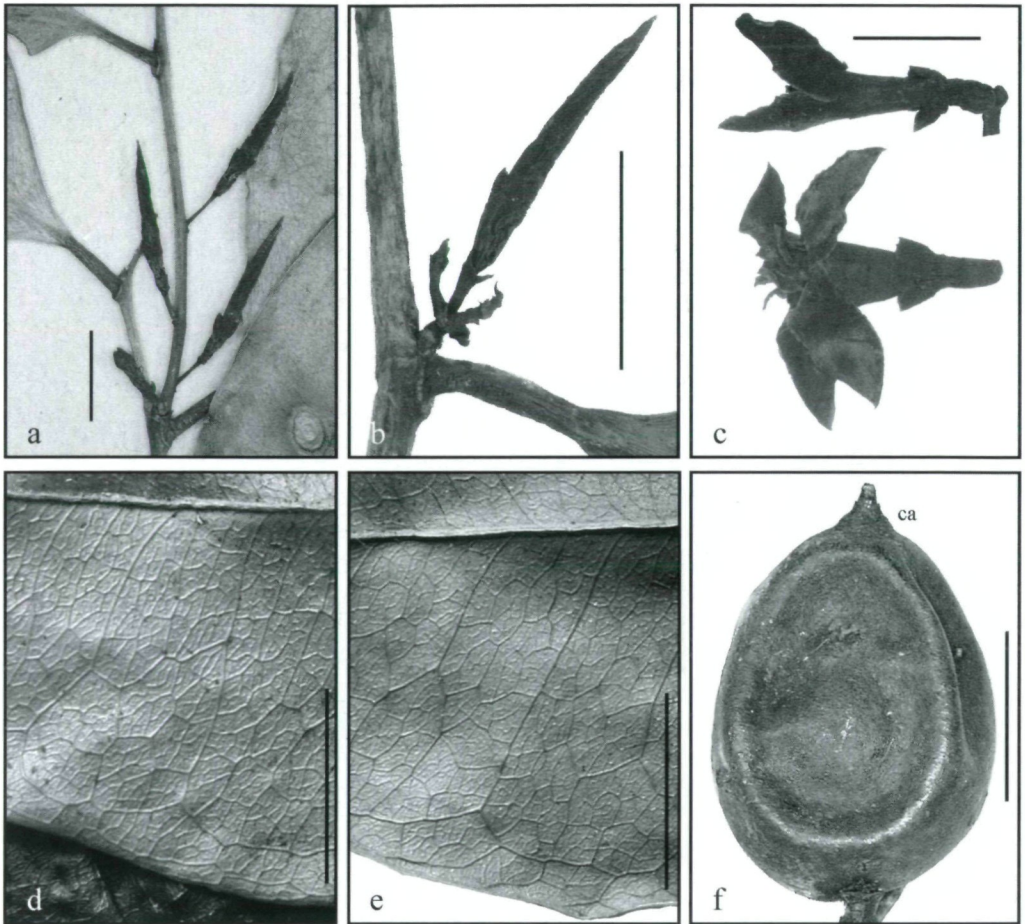


Fig. 15. *Lissocarpa stenocarpa*. **a**: long shoot with basal flowers, and **b**: short shoot (inflorescence) (from Liesner 24878); **c**: flowers at anthesis (from Liesner 25094); **d**: adaxial, and **e**: abaxial leaf surface (from Liesner 24878); **f**: fruit (from Maguire et al. 29964), (ca: calyx lobes); bar = 1 cm: a - b, and d - f; 5 mm: c.

stigma densely covered with a tuft of hair-like appendages; **fruits**: pedicels 1 - 2 mm thick; living fruits green or yellow green when unripe, later on orange-red or reddish orange and sublustrous, dark brown to blackish when dry, ellipsoidal-fusiform, ovoid or subglobose (Fig. 15f), 2 - 3.5 cm long, 1.4 - 2 cm wide, smooth, with few large wrinkles when dry; pulp yellow, 3 - 4 mm thick when alive; seed medium brown, with translucent white endosperm when alive; calyx lobes erect, fitting tight together around the broad, obconical base of the broken style; seeds 1 per fruit, ellipsoidal, 13 - 16 mm long, 8 - 9 mm wide, blackish when dry, thickened on the two ends, with 5 - 8 longitudinal, sometimes branched, brown, salient veins.

Note: Two collections (Nee 31144, 31189) gathered on the Cerro de la Neblina (the southernmost known locality of this species) possess some exceptionally large (up to 17 cm long and 8.3 cm wide), elliptic leaves which may represent atypical shadow-

leaves. The isotype of *L. stenocarpa*, kept at NY, shows quite similar, although smaller leaves. Unfortunately, to date, neither flowers nor ripe fruits have been collected from plants growing at that remote site. Since these two collections do not show any additional discriminating features, they can so far not be attributed to a different species.

Distribution, habitat, ecology, and phenology: This species is only known from Venezuela (Amazonas), growing at elevations between 1000 and 1800 meters (Fig. 5f), in cloud forests, in riverine forests, and in medium tall, moist forests on ridges, slopes and escarpments of the Tepui (table mountains). It has been collected in flower in February, March and October, and in fruit in February, March, October and December.

Specimens examined: **Venezuela, Amazonas,** Cerro Parú, base of escarpment southward from Camp 2 km, 1800 m, [4°30' N, 65°35' W], "talus forest", (fr), 12 Feb. 1951, **R.S. Cowan & J.J. Wurdack 31413** [NY], "tree 4 m; fruit green; frequent"; – Cerro Huachamacari, Río Cunucunuma, Camp II to Culebra, [3°47' N, 65°45' W], in moist forest below Camp II, (fr), 20/21 Dec. 1950, **B. Maguire, R.S. Cowan & J.J. Wurdack 29964** [F, K, MY n.v., NY 2×], "slender tree 8 m; flowers yellowish; fruit orange-red"; – Dept. Atabapo, Cerro Marahuaca, "Sima" area, slopes, 1200 m, 3°43' N, 65°30' W, medium height forest, (flbuds), 16 Oct. 1988, **R.L. Liesner 24878** [FHO, MO, SEL n.v., W ex SEL], "3 m tree; buds whitish"; – same area, (fl, fr), 18 Oct. 1988, **R.L. Liesner 25052** [MO], "4 m tree; fruits reddish orange; buds yellowish"; – same area, (flbuds), 19 Oct. 1988, **R.L. Liesner 25094** [MO], "2 m shrub; flowers cream color, parted regular"; – in saddle between Duida and Marahuaca near base of Duida, 1000 m, 3°34' N, 65°32' W, medium height forest, (flbuds), 26 Oct. 1988, **R.L. Liesner 25402** [FHO, MO], "4 m tree; flowers yellowish"; – slopes of Mount Duida, Aguita, 3800 ft., [3°25' N, 65°40' W], (fr), Aug. 1928 / Apr. 1929, **G.H.H. Tate 925** [US]; – Cerro Duida, inmediatamente al N de La Esmeralda (03°10' N, 65°31' W [correct is: 3°13' N, 65°34' W]), en el alto Río Orinoco, Estación D11, (al NNO del "Savana Hills Camp" de Tate), ca. 1200 m, in forest, (fr), 01/07 Feb. 1975, **S.S. Tillett 752-278** [K, VEN n.v. (cited in BERRY 1999)], "tree 3 - 4 m tall; bark dark gray to black; leaf stiff, brittle, slightly revolute, lustrous dark green above, beneath matte medium green, the midvein light green and sharply prominent both surfaces; fruit sublustrous medium slightly orange-red; flesh yellow, 3 - 4 mm thick; seed medium brown with translucent white endosperm; the fruit ovoid, 2 - 3 × 1.5 cm"; – Dpto. Río Negro, Cerro de la Neblina, Camp XI, 6.5 km NNE of Pico Phelps (= Neblina), cloud forest on ridges and slopes 1 km N of the camp, 1300 m, 00°52' N, 65°58'50" W, (fr), 28 Feb. 1985, **M. Nee 31189** [F, MO, NY, RSA n.v., U, US n.v., VEN n.v.], "tree 8 m tall, 10 cm diam.; fruit green"; – same locality, (yfr), 26 Feb. 1985, **M. Nee 31144** [MO, NA n.v., NY n.v., VEN n.v.], "treelet 4 m, 5 cm in diam.; wood yellowish; fruit green".

Lissocarpa BENTH. in BENTH. & HOOK. f., sectio *Enho* B.WALLN., sect.n.

Diagnosis: Nervo medio foliis supra impresso; lobis calicis triangularibus, distaliter nunquam emarginatis; corona absens.

Type species: *Lissocarpa uyat* B.WALLN., described in the present publication.

Note: For diagnostic characters, see the 'key to species'. This section comprises the following species: *L. jensonii*, *L. ronliesneri*, *L. tetramera*, and *L. uyat*, all restricted to the eastern slopes of the Andes between southern Colombia and northwestern Bolivia, and to the Amazonian lowland of northern Peru (see Fig. 4c).

Lissocarpa jensonii VÁSQUEZ, Novon 3 (2): 211 - 212, fig. 1 (1993); [Figs. 16 - 17].

Typus: Perú, Loreto, Maynas Province, Distrito de Las Amazonas, Quebrada Sucusari, Explornapo Camp, 140 m, 3°20' S, 72°55' W [correct is: 3°12' S, 72°53' W], bosque primario, suelo arcilloso, con buen drenaje, (fr), 13 Apr. 1991, **R. Vásquez & N. Jaramillo**

MISSOURI
BOTANICAL GARDEN
HERBARIUM

Nº 5301073



(R. Vásquez & N. Jaramillo 1598a)
LISSOCARPACEAE *L. jensonii*
Lissocarpa jensonii R. Vásquez

Det. R. Vásquez (AMAZ), 1992

MISSOURI BOTANICAL GARDEN HERBARIUM (MO)

PERU

EBENACEAE

LORETO; Maynas Province
Los Amazonas; Quebrada Susuari; Explor
Napo Camp, Bosque primario, suelo
arcilloso, con buen drenaje. 140 m
03°20'S 72°55'W

Arbol 18 m X 12 cm DAP, frutos verdes.

13 abril 1991

R. Vásquez & N. Jaramillo 1598A
Collected under the auspices of the John
D. and Catherine T. MacArthur Foundation
MISSOURI BOTANICAL GARDEN HERBARIUM (MO)

NATURHISTORISCHES MUSEUM WIEN - BOTANISCHE ABTEILUNG

Lectotype of:

Lissocarpa jensonii Vásquez
Novon 3(2): 211-212 (1993)

5. Sept. 192003 det. rev. B. WALLNOFFER (W)



Fig. 16. Lectotype of *Lissocarpa jensonii* VÁSQUEZ.

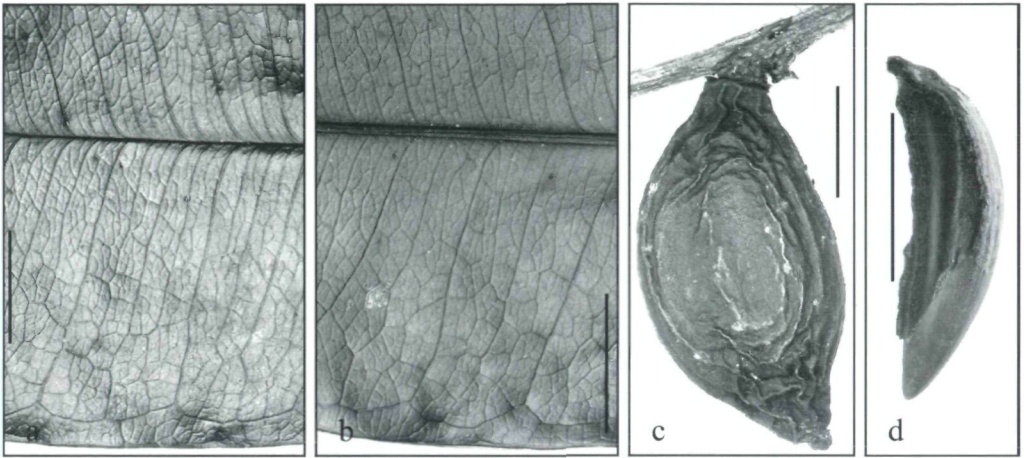


Fig. 17. *Lissocarpa jensonii*. **a**: adaxial, and **b**: abaxial leaf surface (from Vásquez & Jaramillo 15984); **c**: fruit (from Vásquez et al. 16814); **d**: seed (from Vásquez & Jaramillo 15984); bar = 1 cm.

15984 [lectotype (here selected): MO, isotypes: AMAZ n.v., USM n.v., 12 further duplicates (not seen) to be distributed], "árbol 18 m × 12 cm DAP; frutos verdes".

Note: In the protologue (VÁSQUEZ 1993), the holotype is stated to be deposited at MO. This specimen, however, has been untraceable for several years now, a circumstance ("not found") already reported by BERRY (1999). The databases at MO indicate that 13 duplicates of the type collection had arrived there at the time. Recently, despite several inquiries for the holotype, I only received on loan from MO a single sheet from this collection (the only one seen by me to date), and this is marked as isotype. Since Vásquez most probably never marked any one of the duplicates as holotype, the above mentioned sheet is here selected as lectotype.

Treelet or tree 15 - 18 m tall, dbh 10 - 12 cm; twigs subterete, with a pair of wing-like, longitudinal ridges running down from both sides of each petiole into the axil of the next but one petiole; young bark dark brown, slightly exfoliating, soon cracking up by short, longitudinal, blackish fissures; **leaves**: petioles 1 - 2 mm long, 1.5 - 2 mm thick, drying black, slightly shriveled and exfoliating, with a quite flat longitudinal groove adaxially; lamina oblong (broadly lanceolate in the smallest leaf), (7.5 -) 10 - 17 cm long, 3.2 - 5.4 cm wide, chartaceous, drying blackish and slightly shiny adaxially, dark brown and dull abaxially; leaf apex acute; base of the lamina attenuate; leaf margins not thickened, strongly revolute at the base of the lamina, slightly revolute elsewhere when dry; flachnektarien (extrafloral nectaries) on abaxial leaf surfaces 0.3 - 0.4 mm in diameter, frequent near the base and along the midvein towards the apex, scattered in the central part of the lamina, missing on the margins; midvein markedly sunken in the proximal two thirds of the lamina, becoming increasingly shallow and flat towards the leaf apex adaxially, prominent (semicircular in cross section proximally, strongly keeled from the middle towards the leaf apex) and dark brown abaxially; secondary veins ca. 20 per side, raised on both sides of the lamina; tertiary veins prominent, and quaternary veins slightly prominent on both sides of the lamina; **flowers** not available for study, arranged (according to the persistent pedicels) on 2-flowered, slightly supra-axillary short-shoots

(inflorescences) with extremely short axes (thus the persistent pedicels appearing to be paired in the leaf axils); old pedicels 1.5 - 2 mm long, 1.5 mm thick, black; subopposite bracteoles at the base of the hypanthium ca. 1.5 mm long, ca. 2 mm wide, keeled along the midvein, black, with entire margins; **fruits** (Fig. 17c) nearly sessile (with pedicels 1.5 mm long and up to 4 mm thick), green at first, red when ripe, drying black, ellipsoidal-fusiform, up to 3.5 cm long and 1.8 cm wide when still unripe, smooth, with few weak longitudinal folds when dry, usually only one fruit developed per infructescence; fruit wall 0.5 - 1 mm thick and black when dry; calyx lobes and distal part of the hypanthium forming a small, inside crateriform crown, ca. 2 mm high and 2.5 mm wide; calyx lobes oriented parallel to the fruit axis, minute, 0.5 mm long and 1.5 mm wide; a broken fruit in the capsule of the lectotype sheet developed only three locules, one of which is 1-seeded and the other two each 2-seeded (as can be concluded from the scars where seeds had been attached); seeds 1.8 - 2.2 × 0.5 - 0.8 × 0.4 - 0.5 cm, shaped like the segments of peeled oranges (Fig. 17d), and covered by a dark brown testa with basally branched and slightly curved veins; endosperm ivory-colored, hard.

Figures: twig, leaves, fruit, seed, VÁSQUEZ (1993, 1997: 893).

Distribution, habitat, ecology, and phenology: This species is only known from three fruiting collections gathered in the department Loreto in northern Perú, and in the department Putumayo in southwestern Colombia (Fig. 5c). In Perú it grows at an elevation of 140 meters, on clay soils in non-flooded ("tierra-firme") primary rain forests (VÁSQUEZ 1993, 1997). In Colombia it was found in a mountainous area at 1230 meters. It was collected in fruit in April, June and July.

Specimens examined: **Colombia**, Putumayo, Mocoa Municipio, zona montañosa de la vereda Medio Afan, camino Medio Afan-Churumbelo, ca. 2.5 horas de Mocoa hacia el oriente, 1230 m, [ca. 1°9' N, 76°35' W], (fr), 26 Jul. 1990, **L. Garcia et al. 58a** [MO n.v. (digital photos seen)], "arbusto; frutos rojos sin exudado".

Perú, Dept. Loreto, Maynas Province, Distr. Las Amazonas, Explor Napo Camp (Sucusari), 140 m, 3°15' S, 72°54' W [correct is: 3°12' S, 72°53' W], bosque primario, (fr), 24 Jun. 1991, **R. Vásquez, J. Rios T., W. Pariona & N. Jaramillo 16814** [paratypes: AMAZ n.v., MO, USM n.v., 9 further duplicates (not seen) to be distributed], "árbol 15 m × 10 cm DAP; frutos verdes".

***Lissocarpa ronliesneri* B.WALLN., sp.n.**; [Figs. 6f, 18 - 19].

Diagnosis: Differt a *L. uyat* characteribus sequentibus: frutex 4 m altus; ramuli juveniles in statu sicco nigri; laminae foliorum 6 - 11 cm longae et 2,2 - 4,4 cm latae, coriaceae; nervo medio supra impresso et late exarato; prophylla subopposita nec dorsaliter carinata, cum apice rotundata; lobi calicis valde truncati, 0,2 (!) mm longi et 2 mm lati.

Typus: Ecuador, Cantón Zamora-Chinchipec, El Pangui, Cordillera del Cóndor, cerca del destacamento militar Cóndor Mirador en la frontera Ecuador-Perú, 1800 m, 3°38'08" S, 78°23'22" W, bosque montano sobre roca arenisca, (yfr), 15 Dec. 2000, **L. Miranda & Grupo de Post-Grado MO-QCNE 160** [holotype: W; isotypes: MO n.v. (digital photo seen), QCNE n.v., + 1 unmounted specimen at MO n.v. (digital photo seen)], "arbusto de 4 m; fruto cápsula café".

Treelet 4 m tall; twigs subterete, with only faint longitudinal ridges (youngest shoots not available for study); young bark black, cracking up by short, longitudinal, brown fissures; **leaves**: petioles 1 - 2 mm long, ca. 2 mm thick, drying black, somewhat shriv-



NATURHISTORISCHES MUSEUM WIEN BOTANISCHE ABTEILUNG

Holotype of:
Lissocarpa ronliesneri B. Walln.

5. Sept. 2003 det./rev. B. WALLNÖFER (W)

ECUADOR

LISSOCARPACEAE
Lissocarpa

Zamora-Chinchipec: El Pangui

Cordillera del Condor. Bosque
montano sobre roca arenisca, cerca del
destacamento militar Condor Mirador,
en la frontera Ecuador-Perú.
03°38'08"S 078°23'22"W 1800 m

Arbusto de 4 m. Fruto cápsula café.
15 diciembre 2000

Lider Miranda &
Grupo de Post-Grado MD-QCNE 160
MISSOURI BOTANICAL GARDEN HERBARIUM (MO)

Fig. 18. Holotype of *Lissocarpa ronliesneri* B. WALLN.

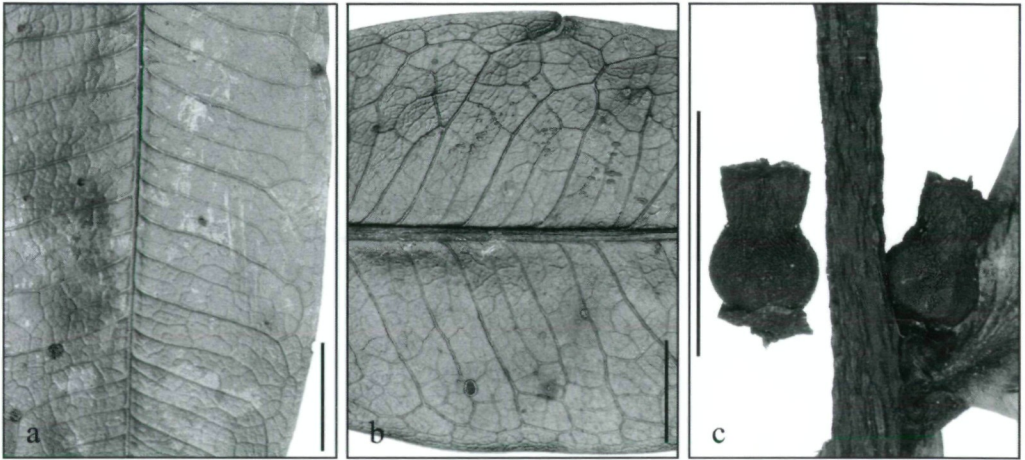
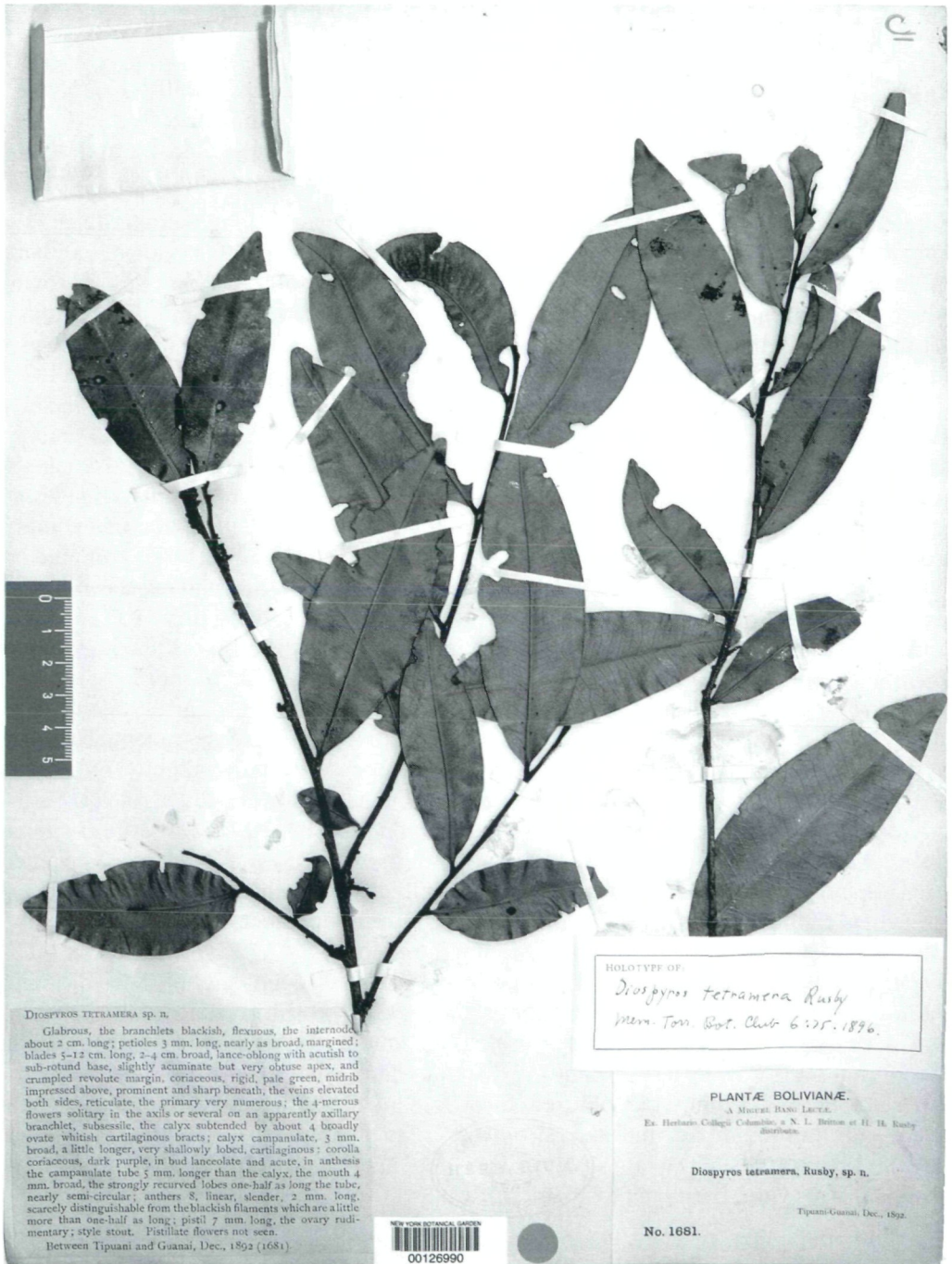


Fig. 19. *Lissocarpa ronliesneri*. **a**: adaxial, and **b**: abaxial leaf surface, **c**: juvenile fruits (all from Miranda et al. 160); bar = 1 cm.

eled, with a flat longitudinal groove adaxially; lamina broadly lanceolate (broadest near middle), less frequently elliptic or rarely slightly ovate, (4.7 -) 7 - 11 cm long, (2.2 -) 3 - 4.9 cm wide, coriaceous, drying greenish-gray adaxially, dark brown abaxially; leaf apex acute; base of the lamina attenuate; leaf margins notably thickened distally, otherwise flat or slightly revolute; flachnektarien (extrafloral nectaries) on abaxial leaf surfaces as in *L. uyat*, but more raised than in the latter, present especially near the base, or in the central part of the proximal half of the lamina; midvein on its adaxial side brown to light brown, nearly flat distally, markedly sunken in the proximal three quarters of the lamina (forming a wide furrow), on its abaxial side prominent, strongly keeled in the distal two thirds, dark brown and shriveled longitudinally; secondary veins ca. 13 per side, raised on both sides of the lamina; tertiary veins prominent on both sides of the lamina; quaternary veins hardly discernible adaxially, better visible abaxially; **flowers** not available for study, arranged (according to the persistent pedicels) on 2-flowered short-shoots (inflorescences) with extremely short axes (thus the persistent pedicels appearing to be paired in the leaf axils); young **fruits** (only two available for study, see Figs. 6f, 19c) dark brown when alive, black when dry, with pedicels ca. 1 mm long, ca. 1.5 mm thick, black; subopposite bracteoles at the base of the hypanthium 2 mm long, ca. 4 mm wide, semicircular, not keeled along the midvein, black, with entire margins; hypanthium 6.5 mm long (proximal, subglobose part 4 mm, and distal, conical part 2 mm long), 5 mm wide; calyx lobes black when dry, only 0.2 mm long, 2 mm wide, truncate over most of the width; margins entire, not fimbriate; mature fruits and seeds not available for study.

Etymology: This species is dedicated to Ron Liesner (MO), who identified many undetermined collections as pertaining to the genus *Lissocarpa*.

Distribution, habitat, ecology, and phenology: This imperfectly known species is only represented by the type collection, gathered in southern Ecuador, near the border to Perú (Fig. 5e), where it grows on sandstone in primary mountain forests at 1800 meter. It was collected in December, with fruits in a very young stage.

**DIOSPYROS TETRAMERA** sp. n.

Glabrous, the branchlets blackish, flexuous, the internode about 2 cm. long; petioles 3 mm. long, nearly as broad, margined; blades 5-12 cm. long, 2-4 cm. broad, lance-oblong with acutish to sub-rotund base, slightly acuminate but very obtuse apex, and crumpled revolute margin, coriaceous, rigid, pale green, midrib impressed above, prominent and sharp beneath; the veins elevated both sides, reticulate, the primary very numerous; the 4-merous flowers solitary in the axils or several on an apparently axillary branchlet, subsessile, the calyx subtended by about 4 broadly ovate whitish cartilaginous bracts; calyx campanulate, 3 mm. broad, a little longer, very shallowly lobed, cartilaginous; corolla coriaceous, dark purple, in bud lanceolate and acute, in anthesis the campanulate tube 5 mm. longer than the calyx, the mouth 4 mm. broad, the strongly recurved lobes one-half as long as the tube, nearly semi-circular; anthers 8, linear, slender, 2 mm. long, scarcely distinguishable from the blackish filaments which are a little more than one-half as long; pistil 7 mm. long, the ovary rudimentary; style stout. Pistillate flowers not seen.

Between Tipuani and Guanani, Dec., 1892 (1681).

HOLOTYPE OF:

Diospyros tetramera Rusby
Mem. Tom. Bot. Club 6: 25. 1896.

PLANTAE BOLIVIANÆ.

A. MURRAY BASS, LECTOR.
Ex. Herbario Collegii Columbiæ, a N. L. Britton et H. H. Rusby
distributæ.

Diospyros tetramera, Rusby, sp. n.

Tipuani-Guanani, Dec., 1892.

No. 1681.



Fig. 20. Holotype of *Lissocarpa tetramera* (RUSBY) P.E.BERRY.

***Lissocarpa tetramera* (RUSBY) P.E.BERRY**, Brittonia 51 (2): 214 (1999); [Figs. 3c - d, 6h, 20 - 21].

≡ *Diospyros tetramera* RUSBY, Mem. Torrey Bot. Club 6: 75 (1896).

Typus: Bolivia, La Paz, between Tipuani and Guanai [= Guanay], [15°30' S, 67°55' W], (fl), Dec. 1892, **M. Bang 1681** [holotype: NY (the specimen belonged to the former "Herbarium, Columbia College, New York"), isotypes: A, BM, E, FHO (fragm.), G 2×, GH, K 2×, LE, M, MICH, MO, NY, US, W, Z]; – RUSBY (1896): "corolla dark purple".

Treelet 3 m, or tree 10 - 15 m tall; twigs subterete, with a pair of longitudinal ridges running down from both sides of each petiole into the axil of the next but one petiole; bark of younger twigs black, wrinkled longitudinally when dry, soon cracking up by brownish to gray, elliptic, salient, lenticell-like structures, which develop into longitudinal fissures with slightly raised margins on older twigs; twig apices black, strongly angular in cross section, sometimes with superficial, transversal fissures; **leaves:** petioles (1 -) 2 - 3 mm long, 1.5 mm thick, drying brown to black, thickened, usually transversally shriveled especially on abaxial side, with a longitudinal groove adaxially; lamina broadly lanceolate (broadest near middle), sometimes slightly ovate (1 -) 4 - 11.5 cm long, (0.6 -) 1.5 - 3.2 (- 4.3) cm wide, chartaceous, brown and usually dull on both sides of the lamina when dry; leaf apex acute; base of the lamina attenuate; leaf margins notably thickened, or flat, near base revolute; flachnektarien (extrafloral nectaries) on abaxial leaf surfaces ca. 0.5 mm in diameter, scattered along the lower half of the midvein (sometimes even on the midvein itself), usually missing on other parts of the lamina; midvein slightly sunken but clearly visible (more or less flat distally) on adaxial side, on abaxial side prominent (triangular in cross section, but somewhat rounded proximally and more or less flat distally); secondary and intersecondary veins hardly distinguishable, 20 - 25 per side, slightly prominent adaxially, somewhat more prominent abaxially; tertiary veins slightly visible, flat to slightly prominent adaxially, slightly prominent abaxially; quaternary veins slightly visible only abaxially; **flowers** (Figs. 6h, 21c) solitary on the proximal part of young long-shoots or on up to ca. 10-flowered short-shoots (inflorescences, see Fig. 21b) with 4 - 10 (- 15) mm long, ca. 1 mm thick axes; pedicels 0.3 - 0.5 mm long (flowers nearly sessile), 1 mm thick, blackish; subopposite bracteoles at the base of the hypanthium 1.5 mm long, ca. 2 mm wide, obtuse, slightly keeled along the midvein, with entire margins; hypanthium 3 mm long, 2 - 2.5 mm wide; calyx lobes blackish when dry, 0.3 - 0.5 mm long, 1.8 mm wide, obtuse and slightly keeled (along the midvein) distally; margins entire or slightly erose, not fimbriate; corolla green in bud, according to RUSBY (1896) dark purple [after anthesis?], blackish when dry; corolla tube 5 mm long, basally 1.5 mm, distally 3 mm wide; corolla lobes more or less elliptic, 5 mm long, 4.5 mm wide, obtuse; corona absent; stamens 3 mm long, free, adnate to the corolla tube at 1.5 mm above its base; filaments ca. 0.5 mm long; anthers ca. 2.5 mm long, ca. 0.3 mm wide; style 6.5 mm long, at the base 1 mm wide; stigma 1 mm long, 0.8 mm wide; **fruits** not available for study.

Distribution, habitat, ecology, and phenology: This species is known from southeastern Perú (Puno) and northwestern Bolivia (La Paz), where it grows in moist montane forests at elevations between 800 and 1500 meters (Fig. 5g). It has been collected with flower buds in October and November, and flowering in December.

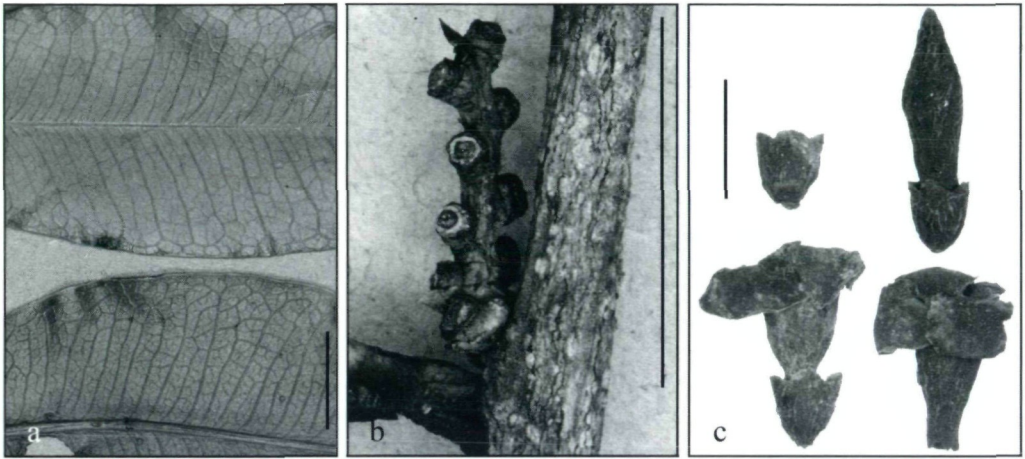


Fig. 21. *Lissocarpa tetramera*. **a**: adaxial (on top) and abaxial (bottom) leaf surface (from Bang 1681); **b**: short shoot (inflorescence) with abscised flowers (from Krukoff 11072); **c**: flowers (from Bang 1681, holotype); bar = 1 cm: a - b; 5 mm: c.

Specimens examined: **Perú, Puno**, Prov. Carabaya, cabeceras del Río Candamo, 800 - 850 m, 13°18' S, 70°7' W, bosque montano en la cima de colina, (flbuds), 14 Nov. 1996, **F. Cornejo V. & A. Balarezo 2689** [MO], "10 m"; - same locality, (st), 16 Nov. 1996, same collectors, **2734** [MO n.v. (digital photo seen)], "8 m".

Bolivia, La Paz, Prov. of Larecaja, Copacabana (about 10 km S of Mapiri), 850 - 950 m, [15°20' S, 68°13' W], (flbuds), 8 Oct. - 15 Nov. 1939, **B.A. Krukoff 11012** [F, G-DEL, K 2×, MO, NY, S, U, UC, US], "tree 50 ft. high"; - same area and date, (flbuds), **B.A. Krukoff 11072** [F, G 4×, GH n.v., K 2×, LP, MG n.v., MO n.v. (digital photo seen), NY, U], "tree 45 ft. high"; - Prov. Nor Yungas, 13.7 km NW of San Pedro on road through Incahuara-Mejillones, trail to 12 de Octubre, 1500 m, 15°58' S, 67°37' W, moist montane forest, (fl), 7 Dec. 1985, **J.C. Solomon 14872** [FHO, MO (3× not mounted), W], "treelet 3 m; corollas green".

Lissocarpa uyat **B.WALLN.**, sp.n.; [Figs. 6g, 22 - 23].

Diagnosis: Arbor 2,5 - 16 m alta; ramuli juvenilissimes in statu sicco fuscii, duabus angulis alatis decurrentibus a petiolo usque ad axillam folii suprajuxti; petioli 0,5 - 2 (- 3) mm longi; laminae foliorum (2 -) 8 - 15 (- 18) cm longae et (1 -) 2 - 5 (- 7,3) cm latae, ellipticae vel latae lanceolatae, leviter coriacea; nervo medio supra valde impresso et peranguste exarato; prophylla subopposita dorsaliter carinata; lobis calicis 4, triangularibus, distaliter numquam emarginatis; tubus alabastrarum corollae circiter 4,5 mm longus; lobi corollae 8,5 mm longi; corona absens; fructus ellipsoideo-fusifformes, 1,8 - 2,5 cm longi, ca. 1 cm diametientes.

Typus: Peru, Amazonas, Bagua Province, Distrito Imaza, Cerros de Putuim, 350 m, 5°03'20" S, 78°20'23" W, bosque primario, (fr), 15 Jun. 1996, **R. Vásquez, A. Vásquez, L. Dekantai & M. Chuintam 21186** [holotype: W; isotype: MO n.v.], "arbusto 6 m; frutos negros".

Treelet (flowering at this stage already) or tree 2.5 - 16 m tall; twigs subterete, with a pair of well developed, longitudinal ridges running down from both sides of each petiole into the axil of the next but one petiole; young bark dark brown, later on blackish, soon

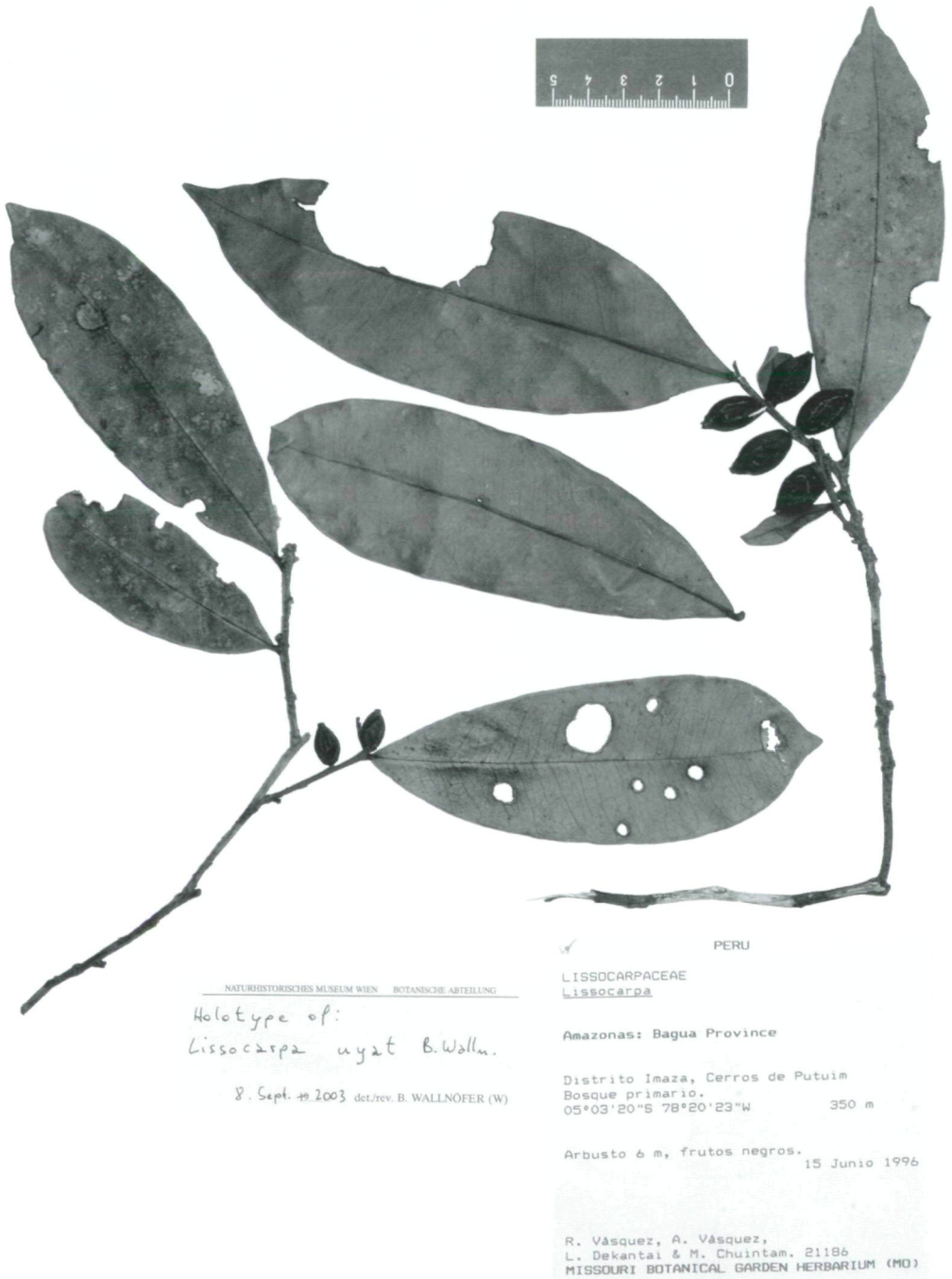


Fig. 22. Holotype of *Lissocarpa uyat* B. WALLN.

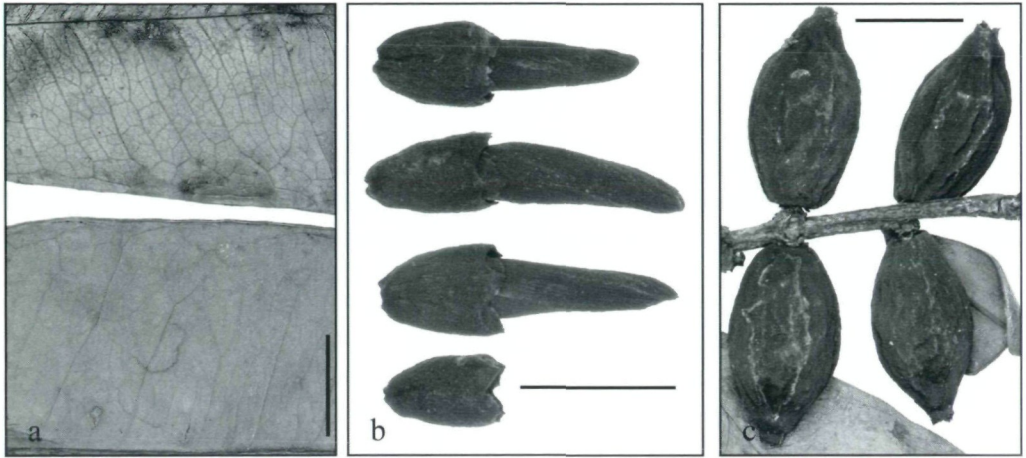


Fig. 23. *Lissocarpa uyat*. **a**: adaxial (on top) and abaxial (bottom) leaf surface (from Vásquez et al. 21186); **b**: flower buds (from Vásquez 27599); **c**: fruits (from Vásquez et al. 21186); bar = 1 cm: a and c; 5 mm: b.

cracking up by short, longitudinal, brown fissures; buds often somewhat displaced (above the axils); **leaves**: petioles 0.5 - 2 (- 3) mm long, 1 - 2 mm thick, drying brown or black, slightly shriveled, with a quite flat longitudinal groove adaxially; the youngest leaves drying black; lamina broadly lanceolate or elliptic (broadest near the middle), (2 -) 8 - 15 (- 18) cm long, (1 -) 2 - 5 (- 7.3) cm wide, slightly coriaceous, drying dark gray, or blackish brown adaxially, brown to dark brown abaxially; leaf apex acute or slightly acuminate, with a drip tip up to 0.5 cm long; base of the lamina attenuate or rounded, sometimes very slightly cordate, especially in nearly sessile leaves; leaf margins notably thickened, in particular distally, otherwise flat or slightly revolute; flachnektarien (extrafloral nectaries) on abaxial leaf surfaces 0.4 - 0.6 mm in diameter, scattered along the midvein and in the central part of the lamina, less frequent near the base, the apex and the margins; midvein on its adaxial side markedly sunken in the proximal two thirds of the lamina (forming a very narrow furrow), becoming increasingly shallow and flat towards the leaf apex, on its abaxial side prominent, more or less strongly, or distally often only slightly keeled, dark brown and shriveled longitudinally; secondary veins ca. 15 per side, raised on both sides of the lamina; tertiary veins prominent adaxially, only slightly prominent abaxially; quaternary veins slightly prominent or flat adaxially, flat and hardly discernible abaxially; **flowers** (Figs. 6g, 23b) usually never solitary on long-shoots, always on 2 - 4-flowered, slightly supra-axillary short-shoots (inflorescences) with up to 3 mm long, ca. 1.5 mm thick axes; pedicels ca. 0.3 mm long (flowers nearly sessile), ca. 1 mm thick, blackish; subopposite bracteoles at the base of the hypanthium 1.5 mm long, 1.5 - 2 mm wide, slightly keeled along the midvein, with entire margins, obtuse distally; hypanthium 3.5 mm long, 2.5 mm wide; calyx lobes blackish when dry, triangular, 0.5 - 0.8 mm long, 1.5 mm wide, obtuse distally; margins entire or slightly erose, not fimbriate; flower buds green when alive, black when dry; corolla white, drying black; anthetic flowers not available for study; corolla buds up to 13 mm long, somewhat longitudinally striate; corolla tube of older buds 4.5 mm long, basally 1 mm, distally 2 mm wide; corolla lobes 8.5 mm long; corona absent; stamens

4 mm long, free, adnate to the corolla tube at 2 mm above its base; filaments 1 mm long, 0.25 mm wide; anthers 3 mm long, 0.3 mm wide; style 7 mm long; stigma ca. 0.8 mm long; **fruits** (Fig. 23c) 1 - 2 developing per infructescence, nearly sessile, green when unripe, red when ripe (said to be black in Vásquez et al. 21186), drying black, ellipsoidal-fusiform, 1.8 - 2.5 cm long and ca. 1 cm wide at maturity when dry, smooth, with few large longitudinal folds; fruit wall 0.5 mm thick, black when dry; calyx lobes oriented parallel to the fruit axis, forming together with the distal part of the hypanthium a small, inside crateriform crown ca. 1 mm high and 2 mm wide; seeds 2 per fruit, ca. 13 mm long, ca. 5 mm wide, ca. 3 mm thick, brown to blackish when dry, with 5 - 8 longitudinal, slightly salient, to some degree branching, brown veins and a thickened brown area around the hilum; seed surface wrinkled.

Etymology: The name has been coined arbitrarily (see: GREUTER et al. 2000: Art. 23.2), but it seems to have a pleasant, exotic (non-European) sound.

Distribution, habitat, ecology, and phenology: This species is known from northern Perú (Departamento Amazonas), where it grows on rocky soils in primary rain forests, on the local sandstone mountains at elevations between 350 and 1100 meters (Fig. 5h). According to specifications on herbarium labels, the sites are covered with a thick, spongy layer of organic material and roots (called "campau" or "campou"). The collection Vásquez et al. 26053 was gathered among vegetation only about 2 meters tall (called "Uwejush"). This species has been collected with flowers in February and June, and in fruit in January, June, and September.

Lissocarpa is also known by an only sterile collection (Dudley 13073) from the department Huánuco in central Peru, which is here provisionally ascribed to *L. uyat*. Fertile material is needed to ascertain or confirm the identity of this apparently isolated population.

Specimens examined: **Perú, Amazonas**, Condorcanqui Province, Distrito El Cenepa, Comunidad de Tutino, Cerro Tutino, 600 m, 4°33'50" S, 78°12'15" W, bosque primario sobre arenisca; suelo cubierto por un manto esponjoso de raíces Campau, (fr), 24 Jun. 1997, **R. Vásquez, A. Peña, E. Chávez, E. Quiaco & A. Ampam 24129** [MO n.v., W], "arbusto 4 m; frutos rojos"; - Bagua District, Distrito Imaza, Comunidad Aguaruna de Putuim, 780 m, 4°55' S, 78°19' W, bosque primario, sobre roca arenisca y abundante material orgánico, "campau", (fr), 13 Jun. 1996, **E. Rodríguez R., P. Atamain & E. Chavez-Aguash 989** [MO n.v., W], "árbol ca. 8 m; frutos rojos"; - same locality, date (fl), and collectors, **1002** [MO n.v., W], "árbol ca. 5 m; flores verdes"; - comunidad Aguaruna Putuim, Anexo de Yamayakat, zonas altas de Putuim "campou", 240 degrees SW de Putuim (285 degrees SW de Yamaykat), 700 - 750 m, [4°59' S, 78°19' W], (fr), 22 Jan. 1996, **C. Díaz, H. Osoreo, H. Díaz & D. Díaz 7746A** [HUT n.v., MO, USM n.v., W], "árbol 16 m; frutos verde-rojizos"; - same area, zona de colinas altas 24 SW de Putuim, 700 - 820 m, [4°59' S, 78°19' W], suelos rocosos con abundante materia orgánica a modo de colchón ("Campou"), (fr), 23 Sept. 1994, **C. Díaz, A. Peña & P. Atamain 7220** [MO n.v., W], "árbol 14 m; frutos rojos"; - same area and habitat, 600 m, (fr), 25 Sept. 1994, **C. Díaz, A. Peña & P. Atamain 7235** [MO n.v., W], "arbusto hemi-epífito; frutos inmaduros verdes, maduros rojos"; - Cerros de Putuim, 350 m, 5°03'20" S, 78°20'23" W, bosque primario, (fl), 15 Jun. 1996, **R. Vásquez, A. Vásquez, L. Dekantai & M. Chuintam 21181** [MO n.v., W], "arbusto 3 m; botones verdes"; - Imaza, Tayu Mujaji, comunidad nativa de Wawas, 1100 m, 5°15' S, 78°22' W, bosque primario; "vegetación de 2 m, de alto promedio, (Uwejush)", (fl), 7 Feb. 1999, **R. Vásquez, C. Vargas, J. Yactayo & E. Palomino 26053** [MO n.v., W], "arbusto 2.5 m; botones verdes (pocas flores blancas)"; - same area, 900 - 1030 m, 5°15'56" S, 78°22'07" W, bosque primario, sobre roca de arenisca y un manto esponjoso de raíces y hojarasca en descomposición, (flbuds), 17 Feb. 2002, **R. Vásquez 27599** [MO n.v., W], "arbolito 3 m; botones verdes"; - **Dept. Huánuco**, southwestern slope of the Rio Lullapichis watershed, on the ascent of Cerros del Sira, at Camp 3 (Laguna), ca. 1290 m, 9°26' S, 74°45' W, in dense cloud forest, (st), 22 Jul. 1969, **T.R. Dudley 13073** [NA, photo at W], "many-stemmed shrub, 6 - 8 ft. tall; rounded, dense; stems purple-blackish".

List of exsiccatae

Abbreviations in parenthesis: **b** = *L. benthamii*; **g** = *L. guianensis*; **j** = *L. jensonii*; **k** = *L. kating*; **r** = *L. ronliesneri*; **s** = *L. stenocarpa*; **t** = *L. tetramera*; **u** = *L. wyat*.

- Anderson, C.W. **532a** (g)
 Aymard, G. **9210** (b)
 Aymard, G. et al. **6460** (b)
 Bang, M. **1681** (t)
 Berry, P.E. & Rosales, J. **6412** (b)
 Berry, P.E. et al. **5678** (b); **6536** (b)
 Castillo, A. **4081** (b); **5419** (b); **5795** (b); **6884** (b)
 Castillo, A. & Camaripano, B. **8286** (b)
 Cavalcante, P. **666** (k)
 Clark, H.L. **7456** (b); **7550** (b)
 Clark, H.L. & Maquirino, P. **7484** (b); **7988** (b)
 Cornejo V., F. & Balarezo, A. **2689** (t); **2734** (t)
 Cowan, R.S. & Wurdack, J.J. **31413** (s)
 Cruz, J.S. de la, **3076** (g); **3356** (g)
 Daly, D.C. et al. **5586** (b)
 Davidse, G. **27839** (b)
 Davidse, G. et al. **16855** (b); **17124** (b)
 Davis, D.H. **165** (g)
 Diaz, C. et al. **7220** (u); **7235** (u); **7746A** (u)
 Ducke, A. **1117** (k); **5199** (k); **24567** (k)
 Dudley, T.R. **13073** (aff. u)
 Ek, R.C. et al. **1084** (g)
 Fanshawe, D.B. **F554** (g); **F669** (g); **F2722** (g); **F2919** (g)
 Foldats, E. & Velazco, J. **9614** (b)
 Forest Dep. Brit. Guiana **890** (g); **3290** (g); **3405** (g); **5521** (g); **6066** (g)
 Fróes, R.L. de, **20587** (k); **20588** (k); **20732** (k)
 Garcia, L. et al. **58a** (j)
 Gentry, A.H. et al. **26022** (k); **26158** (k); **26163** (k)
 Gleason, H.A. **724** (g)
 Grández, C. et al. **5549** (k)
 Guánchez, F. **1205** (b)
 Hahn, W. **5832** (g)
 Henkel, T.W. & Chin, M. **524** (g)
 Hoffman, B. & Roberts, L. **2775** (g)
 Hohenkerk, L.S. **532** (g)
 Huber, O. **3084** (b)
 Jenman, G.S. **2407** (g); **4955** (g)
 Krukoff, B.A. **11012** (t); **11072** (t)
 Liesner, R.L. **6734** (b); **7144** (b); **7285** (b); **8632** (b); **8692** (b); **8706** (b); **24878** (s); **25052** (s); **25094** (s); **25402** (s)
 Liesner, R.L. & Clark, H. **9076** (b); **9083** (b)
 Maas, P.J.M. & Westra, L.Y.T. **3999** (g)
 Maas, P.J.M. et al. **7137** (g)
 Maguire, B. & Fanshawe, D.B. **23381** (g)
 Maguire, B. & Wurdack, J.J. **34618** (b); **34907** (b)
 Maguire, B. et al. **29964** (s)
 McDaniel, S. et al. **21628** (k)
 Miranda, L. et al. **160** (r)
 Nascimento, O.C. et al. **186** (b)
 Nee, M. **31144** (s); **31189** (s)
 Parker **280** (g)
 Persaud, A.C. **154** (g); **155** (g)
 Pipoly, J.J. **7543** (g)
 Pipoly, J.J. & Boyan, R. **8932** (g)
 Pipoly, J.J. et al. **12205** (k)
 Prance, G.T. et al. **23855** (k)
 Rimachi Y., M. **4365** (k)
 Rodrigues, W. **913** (k)
 Rodriguez R., E. et al. **989** (u); **1002** (u)
 Ruíz, J. **758** (k)
 Ruokolainen, K. et al. **1389** (k); **1463** (k); **1646** (k); **1725** (k); **1736** (k); **1742** (k); **1853** (k); **1944** (k); **2928** (k)
 Sandwith, N.Y. **363** (g); **525** (g); **1590** (g)
 Schultes, R.E. & Cabrera, I. **12949** (k); **13486** (k); **13516** (k)
 Schultes, R.E. & López, F. **9905** (b)
 Silva, A.S.L. da, et al. **1017** (k)
 Solomon, J.C. **14872** (t)
 Spruce, R. **3108** (b); **3504** (b); **s.n.** (b)
 Stergios, B. & Aymard, G. **9076** (b); **9194** (b)
 Stergios, B. et al. **8156** (b); **13320** (b)
 Steyermark, J.A. & Holst, B. **130880** (s)
 Stoffers, A.L. et al. **111** (g)
 Tate, G.H.H. **925** (s)
 Tillett, S.S. **752-278** (s)
 Tutin, T.G. **78** (g); **213** (g)
 Vásquez, R. **27599** (u)
 Vásquez, R. & Criollo, G. **5778** (k)
 Vásquez, R. & Jaramillo, N. **9659** (k); **15447** (k); **15470** (k); **15984** (j); **16659** (k)
 Vásquez, R. & Ortiz-Gentry, R. **25233** (k)
 Vásquez, R. et al. **5308** (k); **6193** (k); **6546** (k); **8064** (k); **16814** (j); **17922** (k); **21181** (u); **21186** (u); **23435** (k); **24129** (u); **26053** (u)
 Velazco, J. **1890** (b)
 Werff, H. van der, et al. **9825** (k); **10250** (k)
 Williams, L. **1120** (k); **14756** (b); **15729** (b)

Acknowledgements

I wish to thank Ron Liesner (MO) for identifying many undetermined collections as pertaining to the genus *Lissocarpa*; Heimo Rainer (WU) for helping to prepare the photos and distribution maps; Lubbert Y. T. Westra (U) for permission to publish photos of the flowers of *L. guianensis*; Heidemarie Halbritter and Andrea Frosch-Radivo (both WU) for preparing the raster electronic photos; Friedrich Lauria (W) and Walter Till (WU) for critically reading the manuscript, and the latter also for correcting the Latin diagnosis; Marion J. Jansen-Jacobs (U) and Otto Huber (Meran) for helping to locate some collecting places in Guyana and Venezuela; Mary Merello, Kristin Pierce and Fred Keusenkothen (all MO) for preparing and sending me photos of some herbarium specimens; and finally Wolfgang Reichmann (Vienna) for editing one photo. I am grateful to the directors and curators of ca. 40 herbaria who kindly made their herbarium material available to me for study.

References

- ANDERBERG A.A., RYDIN C. & KÄLLERSJÖ M., 2002: Phylogenetic relationships in the order Ericales s.l.: analyses of molecular data from five genes from the plastid and mitochondrial genomes. – *Amer. J. Bot.* 89 (4): 677-687.
- ANDERSON A.B., 1981: White-sand vegetation of Brazilian Amazonia. – *Biotropica* 13: 199-210.
- APG II, 2003: An update of the Angiosperm phylogeny group classification for the orders and families of flowering plants: APG II. – *Bot. J. Linn. Soc.* 141: 399-436.
- BAILLON H., 1892: Histoire des plantes. Vol. 11. – Paris: Librairie Hachette & Cie.
- BENTHAM G., 1876: Styraceae. – In: BENTHAM G. & HOOKER J.D. (eds.): *Genera plantarum*. Vol. 2: 666-671. – London: Reeve & Co. and Williams & Norgate.
- BERRY P.E., 1999: A synopsis of the family Lissocarpaceae. – *Brittonia* 51: 214-216.
- BERRY P.E., 2001: Lissocarpaceae. – In: BERRY P.E., YATSKIEVYCH K. & HOLST B.K. (eds.): *Flora of the Venezuelan Guayana*. Vol. 6: 19-20. – St. Louis: Missouri Botanical Garden Press.
- BERRY P.E., SAVOLAINEN V., SYTSMA K.J., HALL J.C. & CHASE M.W., 2001: *Lissocarpa* is sister to *Diospyros* (Ebenaceae). – *Kew Bull.* 56: 725-729.
- BREMER B., BREMER K., HEIDARI N., ERIXON P., OLMSTEAD R.G., ANDERBERG A.A., KÄLLERSJÖ M. & BARKHORDARIAN E., 2002: Phylogenetics of asterids based on 3 coding and 3 non-coding chloroplast DNA markers and the utility of non-coding DNA at higher taxonomic levels. – *Molecular Phylogenetics and Evolution* 24 (2): 274-301.
- BUSCH P., 1913: Anatomisch-systematische Untersuchung der Gattung *Diospyros*. – Crefeld: Wilhelm Greven; 95 pp.
- CONTRERAS L.S. & LERSTEN N.R., 1984: Extrafloral nectaries in Ebenaceae: anatomy, morphology, and distribution. – *Amer. J. Bot.* 71: 865-872.
- COOPER A., 1979: Muri and white sand savannah in Guyana, Surinam and French Guiana. – In: SPECHT R.L. (ed.): *Heathlands and related shrublands*. – *Ecosyst. World* 9A: 471-481.
- CRONQUIST A., 1981: An integrated system of classification of flowering plants. – New York: Columbia University Press.
- DICKISON W.C. & PHEND K.D., 1985: Wood anatomy of the Styracaceae: Evolutionary and ecological considerations. – *I.A.W.A. Bull., n.s.*, 6: 3-22.
- EK R.C. & VAN DER HOUT P., 1997: Botanical diversity of Greenheart dominated mixed rain forest near Mabura Hill, Guyana. – In: Ek R.C.: *Botanical diversity in the tropical rain forest of Guyana*: 91-142. – *Tropenbos-Guyana Series* 4: 1-237.
- ENCARNACIÓN F., 1985: Introducción a la flora y vegetación de la Amazonia peruana: estado actual de los estudios, medio natural y ensayo de una clave de determinación de las formaciones vegetales en la llanura amazónica. – *Candollea* 40: 237-252.
- ERDTMAN G., 1971: Pollen morphology and plant taxonomy. Vol. 1: 155-156. – New York: Hafner Publishing Company.
- FRANCESCHI D. DE, 1993: Phylogénie des Ebénales: analyse de l'ordre et origine biogéographique des espèces indiennes. – *Publications du département d'écologie, Institut Français de Pondichery* 33: 1-153 (+ annexe A-E, + 61 planches).

- GENTRY A.H., 1993: A field guide to the families and genera of woody plants of northwest South America. – Washington, DC: Conservation International. [reissued in 1996]
- GILG E., 1908: Die systematische Stellung der Gattung *Hoplostigma* und einiger anderer zweifelhafter Gattungen. – Bot. Jahrb. Syst. 40, Beiblatt 93: 76-84.
- GILG E., 1924: Lissocarpaceae. – In: ENGLER A.: Syllabus der Pflanzenfamilien, ed. 9 & 10: 324. – Berlin: Gebrüder Borntraeger.
- GLEASON H.A., 1926: Studies on the flora of northern South America - IX. – Bull. Torrey Bot. Club 53: 289-301.
- GREUTER W. et al., 2000: International Code of Botanical Nomenclature. – Regnum Veg. 138.
- GÜRKE M., 1891: Styracaceae. – In: ENGLER A. (ed.): Die natürlichen Pflanzenfamilien IV/1: 172-180. – Leipzig: Verlag von Wilhelm Engelmann.
- HALLÉ F., OLDEMAN R.A.A. & TOMLINSON P.B., 1978: Tropical trees and forests. – Berlin, Heidelberg, New York: Springer Verlag.
- HEGNAUER R., 1962-1992: Chemotaxonomie der Pflanzen. Vol. 1-10. – Basel: Birkhäuser.
- HIERN W.P., 1873: A monograph of Ebenaceae. – Trans. Cambridge Philos. Soc. 12 (1): 27-300 (+ XI plates).
- HOLMGREN P.K. & HOLMGREN N.H., 2003: Index Herbariorum. – <http://www.nybg.org/bsci/ih/ih.html>.
- HUBER O., 1995: Vegetation. – In: BERRY P.E., HOLST B.K. & YATSKIEVYCH K. (eds.): Flora of the Venezuelan Guayana. Vol. 1: 97-160. – St. Louis: Missouri Botanical Garden.
- HUTCHINSON J., 1959: The families of flowering plants. Dicotyledons. Vol. 1. – Oxford: Clarendon Press.
- HUTCHINSON J., 1967: The genera of flowering plants (Angiospermae). Dicotyledones. Vol. 2. – Oxford: Clarendon Press.
- KLINGE H. & MEDINA E., 1979: Rio Negro caatingas and campinas, Amazonas states of Venezuela and Brazil. – In: SPECHT R.L. (ed.): Heathlands and related shrublands. – Ecosyst. World 9A: 483-488.
- KLOOSTER C.I.E.A. VAN'T, LINDEMAN J.C. & JANSEN-JACOBS M.J., 2003: Index of vernacular plant names of Suriname. – Blumea, Suppl. 15: 322 pp.
- MORTON C.M. & DICKISON W.C., 1992: Comparative pollen morphology of the Styracaceae. – Grana 31: 1-15.
- MORTON C.M., CHASE M.W., KRON K.A. & SWENSEN S.M., 1997: A molecular evaluation of the monophyly of the order Ebenales based upon *rbcL* sequence data. – Syst. Bot. 21: 567-586.
- NANDI O.I., CHASE M.W. & ENDRESS P.K., 1998: A combined cladistic analysis of angiosperms using *rbcL* and non-molecular data sets. – Ann. Missouri Bot. Gard. 85: 137-212.
- NG F.S.P., 1971: A taxonomic study of the Ebenaceae with special reference to Malesia. – Thesis at the University of Oxford, 221 pp., (microfilmed by British Lending Library Division: no. D 183904).
- NG F.S.P., 1991: The relationships of the Sapotaceae within the Ebenales. – In: PENNINGTON T.D.: The genera of Sapotaceae: 1-13. – Kew: Royal Botanic Gardens & New York: New York Botanical Garden.
- OLIVEIRA A.A. DE & DALY D.C. (eds.), 2001: Florestas do Rio Negro. – São Paulo: Companhia das Letras & Bronx, NY: New York Botanical Garden, 339 pp.
- OLIVER D., 1895: *Lissocarpa benthamii* GÜRKE. – Hooker's Icon. Pl. 25: pl. 2413.
- PERKINS J., 1907: Styracaceae. – In: ENGLER A. (ed.): Das Pflanzenreich IV.241: 1-111. – Leipzig: Engelmann.
- PIRES J.M. & PRANCE G.T., 1985: The vegetation types of the Brazilian Amazon. – In: PRANCE G.T. & LOVEJOY T.E. (eds.): Key environments: Amazonia: 109-145 – Oxford: Pergamon Press.

- RODRIGUES W.A., 1961: Aspectos fitossociológicos das catingas do Rio Negro. – Bol. Mus. Paraense Emílio Goeldi, N. S., Bot. 15: 1-41 (+ 7 tab., 2 photos).
- ROOSMALEN M.G.M. VAN, 1985: Fruits of the Guianan flora. – Utrecht: Institute of Systematic Botany, University of Utrecht.
- RUOKOLAINEN H. & TUOMISTO H., 1993: La vegetación de terrenos no inundables (tierra firme) en la selva baja de la Amazonia Peruana. – In: KALLIOLA R., PUHAKKA M. & DANJOY W. (eds.): Amazonia Peruana. Vegetación húmeda tropical en el llano subandino: 139-153. – Jyväskylä: PAUT & ONERN.
- RUSBY H.H., 1896: On the collections of Mr. Miguel Bang in Bolivia. Part III. – Mem. Torrey Bot. Club 6: 1-130.
- SANDWITH N.Y., 1931: Contributions to the flora of tropical America: VIII. – Bull. Misc. Inform. 1931: 467-492.
- SCHNELL R., 1987: La flore et la végétation de l'Amérique tropicale. Vol. 1-2. – Paris: Masson.
- SCHADEL W.E. & DICKISON W.C., 1979: Leaf anatomy and venation patterns of the Styracaceae. – J. Arnold Arbor. 60: 8-37.
- SCHULTES R.E. & RAFFAUF R.F., 1990: The healing forest. – Portland: Dioscorides Press.
- SOLTIS D.E. et al., 1997: Angiosperm phylogeny inferred from 18S ribosomal DNA sequences. – Ann. Missouri Bot. Gard. 84: 1-49.
- SOLTIS D.E. et al., 2000: Angiosperm phylogeny inferred from 18S rDNA, *rbcl*, and *atpB* sequences. – Bot. J. Linn. Soc. 133: 381-461.
- STEEGE H. TER, 1990: A monograph of wallaba, mora and greenheart. – Tropenbos Technical Series 5. Ede: The Tropenbos Foundation.
- STEEGE H. TER & PERSAUD C.A., 1993: The phenology of guyanese timber species: a compilation of a century of observations. – In: STEEGE H. TER: Patterns in tropical rain forest in Guyana: 17-45. – Tropenbos Series 3. Wageningen: The Tropenbos Foundation.
- STEYERMARK J.A., 1987: Flora of the Venezuelan Guayana - II. – Ann. Missouri Bot. Gard. 74: 85-116.
- TAKHTAJAN A., 1997: Diversity and classification of flowering plants. – New York: Columbia University Press.
- VÁSQUEZ R., 1993: Una nueva *Lissocarpa* (Ebenaceae) de la Amazonia Peruana. – Novon 3: 211-212.
- VÁSQUEZ M., R., 1997: Flórmula de las Reservas Biológicas de Iquitos, Perú. – Monogr. Syst. Bot. Missouri Bot. Gard. 63: 1046 pp.
- VÁSQUEZ MARTÍNEZ R. & PHILLIPS O.L., 2000: Allpahuayo: floristics, structure, and dynamics of a high-diversity forest in Amazonian Peru. – Ann. Missouri Bot. Gard. 87: 499-527.
- WALLNÖFER B., 2001: The biology and systematics of Ebenaceae: a review. – Ann. Naturhist. Mus. Wien, B, 103: 485-512.
- WALLNÖFER B., 2004a: Lissocarpaceae. – In: KUBITZKI K. (ed.): The families and genera of vascular plants. Vol. 6: 236-238. – Berlin, Heidelberg: Springer Verlag.
- WALLNÖFER B., 2004b: Ebenaceae. – In: KUBITZKI K. (ed.): The families and genera of vascular plants. Vol. 6: 125-130. – Berlin, Heidelberg: Springer Verlag.
- WHITE F., 1981: Lissocarpaceae. – In: MAGUIRE B. & collaborators: The botany of the Guayana Highland - Part XI. – Mem. New York Bot. Gard. 32: 329-330.

Note added in proof: Recently (January 2004), Jorge Andrés Pérez-Zabala sent me some digital photos of material of Ebenaceae (*Diospyros* and *Lissocarpa*) kept in the herbarium of Medellín (MEDEL) in Colombia. Among them, surprisingly, also of a recently gathered (still unlabeled) collection of *Lissocarpa* in fruit from: Antioquia, area around Anorí, 800 m, 7°15' N, 75°10' W (no further data available at the moment). This collection represents the first record for this genus (section *Enho*, most probably) in northern Colombia (see Fig. 4), but cannot be identified at species level from the two photographs alone.

ZOBODAT - www.zobodat.at

Zoologisch-Botanische Datenbank/Zoological-Botanical Database

Digitale Literatur/Digital Literature

Zeitschrift/Journal: [Annalen des Naturhistorischen Museums in Wien](#)

Jahr/Year: 2004

Band/Volume: [105B](#)

Autor(en)/Author(s): Wallnöfer Bruno

Artikel/Article: [A revision of Lissocarpa BENTH. \(Ebenaceae subfam. Lissocarpoideae \(Gilg in Engler\) B. Walln.\) \(With a contribution on its pollen morphology by H. Halbritter\). 515-564](#)