

# STUDIES IN ARTOCARPUS AND ALLIED GENERA, V. A REVISION OF PARARTOCARPUS AND HULLETTIA

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**Parartocarpus** Baillon, *Adansonia* 11: 294. 1875; Benth. & Hook. f. *Gen. Pl.* 3: 375. 1880; Becc. *For. Borneo*, 632. 1902, *Webbia* 5: 559. 1923; Renner, *Bot. Jahrb.* 39: 361. 1907; Backer, *Beknopte Fl. Java* 6: 12. 1948; Jarrett, *Jour. Arnold Arb.* 40: 9, 11. fig. 2, *a-f*, fig. 3, *g-i*. 1959. TYPE SPECIES: *Parartocarpus beccarianus* Baillon (= *P. venenosus* (Zoll. & Mor.) Becc.).

*Gymnartocarpus* Boerl. *Ic. Bogor.* 1: 73. *t.* 24, 25. 1897, *Handl. Fl. Ned. Ind.* 3: 335, 371. 1900; Koord. & Val. *Bijdr. Boomsoort. Java* 11: 28. 1906; Koord. *Exkursionsfl. Java* 2: 96. 1912, "*Gymnoartocarpus*." TYPE SPECIES: *Gymnartocarpus venenosa* (Zoll. & Mor.) Boerl. (= *Parartocarpus venenosus* (Zoll. & Mor.) Becc.).

Medium to large trees. *Leaves* spirally arranged, simple, entire, penninerved, thinly to thickly coriaceous, glabrous to pubescent; epidermal gland-hairs superficial, long-stalked, heads cylindric, unicellular; spongy mesophyll compact, without resin-cells; juvenile leaves elongate. *Stipules* simple, axillary, nonamplexicaul, the apex entire or bifid, scar intrapetiole.

*Inflorescences* unisexual, rarely bisexual, capitate, head globose at anthesis, becoming shallowly lobed in syncarp, pedunculate, solitary or paired in leaf-axils; stamens or ovaries sunken in numerous cavities closely set over the entire surface of the receptacle; receptacle armoured from numerous, closely set, indurated, spinous, conical, obtuse or truncate processes (perianth segments or interfloral bracts ?), those surrounding the openings connate basally in groups of 2-4 around each aperture, those covering the intervening surface free; basal involucre of 3-4(-8) deltoid or ovate bracts present, sometimes obsolete. *At anthesis*: anthers or stigmas exserted between the connate processes; *male head* with 1-3 stamens in each cavity, the filaments free or united, anthers 2-3 mm. long, short-exserted; *female head* with the ovaries solitary in each cavity, unilocular, the style apical with a short-exserted, lanceolate or fimbriate stigma, the ovule subapical. *Mature syncarp* formed by the enlargement of the entire female head, with (1-)3 to many flowers forming fruit; mature ovary thick-walled, with a firm exocarp finally decaying and leaving the stony endocarp, the style lateral, the seed large, attached laterally, testa membranous with a thickened apical cap, the embryo curved, the cotyledons incumbent, unequal, the inner one smaller, the appressed faces at an angle of 90° to the median plane of the ovary, the large, straight radicle directed upwards at the hilum with the tip enclosed in a little remaining endosperm; germination epigeal.



DISTRIBUTION: peninsular Siam, Malaysia (except the Moluccas and the Lesser Sunda Islands), Solomon Islands.

The genus *Parartocarpus*, in which two species are recognized in this revision, has capitate, armoured inflorescences which have frequently been confused with the inflorescences of *Artocarpus*. The characters distinguishing the two genera have been discussed fully in the introductory paper of this series (Jour. Arnold Arb. 40: 1-29. 1950; keys to the genera on page 26) and they will therefore be recapitulated only briefly here. The inflorescences of *Parartocarpus* differ from those of *Artocarpus* in having a usually well-developed involucre of 3-4(-8) basal bracts and in having the stamens or ovaries enclosed in what are considered to be cavities of the receptacle (formed chiefly by intercalary growth in the walls separating them), rather than enclosed in perianths. The surface of the receptacle is covered by solid, indurated (sessile) processes which vary in shape from cylindric and truncate to spinous and which bear a superficial resemblance to the indurated, tubular, perforate, free perianth apices of *Artocarpus* sect. *Duricarpus*. Many of the processes are connate, either at the base only or for nearly their whole length, in groups of 2-4 around the openings of the receptacular cavities, with the stamens or stigmas exerted between them at anthesis. The processes covering the intervening surface are free but are otherwise identical in appearance to those surrounding the apertures. These processes may represent fertile and sterile perianths respectively, but, taking into account their similarity to the indurated heads of the interfloral bracts in some species of the related, though less reduced, African genus *Treculia*, it is possible that they are secondarily modified interfloral bracts.

The leaves in *Parartocarpus* are spirally arranged as in *Artocarpus* subg. *Artocarpus*, but the stipules are nonamplexicaul and they are not paired as in *Artocarpus*, but are simple and axillary, each being formed from a pair of stipules fused along the intrapetiolar margins.

The generico-specific description of *Parartocarpus beccarianus* was published by Baillon in 1875 and was based on a Beccari collection from Borneo bearing male inflorescences. These were rather poorly preserved and Baillon described them erroneously as being covered by stamens intermixed with [stalked] bracts having obtuse, somewhat thickened heads. He stated that *Parartocarpus* differed from *Artocarpus* in having a basal involucre, in the lack of perianths, and in the nature of the stipules. (But he apparently compared the last only with the amplexicaul stipules of subg. *Artocarpus*, since he described them, in contrast, as lateral and nonamplexicaul which, if correct, would have corresponded with the condition present in subg. *Pseudojaca*.)

The genus was described again as *Gymnartocarpus* by Boerlage in 1897 with a single species, *G. venenosa*, based on *Artocarpus venenosa* Zoll. & Mor. from Java. The latter was published in 1845 and is the earliest account of a species of *Parartocarpus*. Boerlage described the stamens and ovaries in *Gymnartocarpus* as being enclosed in cavities of the re-



ceptacle, and he regarded the processes on the surface as representing bracteoles, not observing any fusion between them. He distinguished the genus from *Artocarpus* by the absence of perianths and the different form of the interfloral bracts. On the basis of Baillon's description he also separated it from *Parartocarpus*. He did not comment on the stipules or on the involucre, but the latter appears, from the plates, not to have been well developed in his material.

Several further species that must be referred to *Parartocarpus* had meanwhile been described under *Artocarpus*. *Artocarpus tylophylla* Miq. (1859) and *A. cerifera* Miq. (1867) were both described from Java and were reduced to *Gymnartocarpus venenosa* by Boerlage in 1897. *Artocarpus riedelii* Miq. (1867), from Celebes, and *A. involucrata* Schum. (1889), from New Guinea, were transferred to *Parartocarpus* in 1907 and 1900, respectively. In describing *Artocarpus bracteata* from Malacca and *A. forbesii* from Perak and Sumatra, King (1888, 1889) mistook the spinous processes on the syncarp for the perforate perianth apices of *Artocarpus*, and the discordant stipular characters were the cause of his rejection of Trécul's subgenera in *Artocarpus* when revising the species of "British India" (i.e., India, Pakistan, Ceylon, Burma and Malaya), as explained in an earlier paper (Jour. Arnold Arb. 40: 123. 1959). King made no mention of *Parartocarpus* and Baillon's description may not have been available to him.

In 1902 Beccari, in an appendix to his *Nelle Foreste di Borneo* (reprinted in *Webbia* 5: 550-565. 1923), discussed the inflorescence structure of *Parartocarpus* and listed seven species in the genus: *P. beccarianus* Baill., *P. venenosus* (Zoll. & Mor.) Becc. (*Artocarpus venenosa* Zoll. & Mor., *Gymnartocarpus venenosa* (Zoll. & Mor.) Boerl., *Artocarpus forbesii* King), *P. bracteatus* (King) Becc. (*Artocarpus bracteata* King), *P. borneensis* Becc., *P. excelsa* Becc. (also from Borneo), *P. papuana* Becc. and *P. involucrata* (K. Schum.) Schum. & Lauterb. He reduced *Gymnartocarpus* to *Parartocarpus*, removed King's two wrongly placed species to the correct genus, and described three new species. He minimized the differences between *Artocarpus* and *Parartocarpus*, stating that the only distinguishing character was the presence of an involucre in the latter. He regarded the stamens and ovaries in *Parartocarpus* as being enclosed in perianths which were tubular and laterally fused with each other below, but free and 2-3-fid above. The "sterile" processes he thought were sterile perianths, but he also apparently regarded them as equivalent to the interfloral bracts of *Artocarpus*. In considering this structure as similar to that found in *Artocarpus* he failed to recognize significant differences that exist between the genera, regardless of the morphological interpretation of the inflorescences in *Parartocarpus*. In *Artocarpus* the 2-4-fid or -partite male perianths enclosing the stamens are always completely free from each other. The tubular and perforate female perianths are frequently connate only in a peripheral layer forming an external wall to the syncarp, while they remain free in the proximal region containing the ovaries. Thus each ovary is separated from the next by two perianth



walls instead of the single (receptacular) wall found in *Parartocarpus*.

J. J. Smith, in describing *Gymnartocarpus triandra* in 1922 (transferred by him to *Parartocarpus* in 1924) apparently took the same view of the inflorescence structure as Beccari. He was the first author to describe the stipules correctly as connate and intrapetiolar.

The two species recognized in this revision are *Parartocarpus bracteatus*, showing little variation and confined to Western Malaysia, and the variable *P. venenosus*, the distribution of which corresponds to that of the genus, extending beyond Malaysia to peninsular Siam and the Solomon Islands. Four fairly distinct subspecies are here distinguished within the latter and the three that are additional to the type subspecies correspond to the three new species described by Beccari in 1902. For one of these (*P. excelsus*) King's species, *Artocarpus forbesii*, is taken as the basionym for the subspecific epithet.<sup>1</sup> The remaining specific names mentioned above, with the addition of *Artocarpus woodii* described by Merrill in 1908 (transferred to *Gymnartocarpus* in 1921 and to *Parartocarpus* in 1923), are distributed in synonymy among the various subspecies of *Parartocarpus venenosus*.

A few comments on the inflorescences in *Parartocarpus* may be added here. The male and female heads are indistinguishable externally before anthesis, in contrast to *Artocarpus* in which they usually differ in shape. The fusion of some of the processes is only conspicuous in the female head, especially at maturity, although it may be established by cutting transverse sections through the bases of the processes in the male head. While the inflorescences are normally unisexual, heads are found in which male and female flowers occur on different areas of the receptacle, but only very rarely intermingled. The involucre, again, is normally well developed, but in *P. venenosus* the bracts may be indistinct and merged into an annulus at the base of the inflorescence. Both *Parartocarpus* and *Hullettia* are unusual among the Moraceae in that the anthers are extrorse.

*Parartocarpus* has copious latex which is poisonous (unlike that of *Artocarpus*) and is used as an arrow poison. The ripe fruits are, however, frequently described as being edible, although the young seeds are stated to be poisonous. The bark on the trunk is very distinctive through the presence of abundant, large, pustular lenticels.

#### KEY TO THE SPECIES OF PARARTOCARPUS

Leaves having 11–15 pairs of lateral veins, rufous pubescent beneath with the intercostals distinctly prominent, 5–10 on each side of midrib; processes on the syncarp spinous, the bases  $\pm$  bulbous, on inflorescences at anthesis narrowly spinous, c.  $3 \times 1$  mm.; involucre bracts 5–10 mm. long. . . . 1. *P. bracteatus*.

Leaves having 6–15 pairs of lateral veins, thinly pubescent to glabrous beneath with the intercostals not or shallowly prominent, fewer; processes on the syn-

<sup>1</sup> It should be noted that in the introductory paper this was referred to as a distinct species within *Parartocarpus*; it is now considered that the taxon can be recognized only at the subspecific level.



carp truncate to spinous, the bases not bulbous, on inflorescences at anthesis truncate to acute, never narrowly spinous; involucre bracts to 5 mm. long.  
 ..... 2. *P. venenosus*.

1. *Parartocarpus bracteatus* (King) Becc. For. Borneo, 632. 1902, "*bracteata*"; Renner, Bot. Jahrb. 39: 362. 1907.

*Artocarpus bracteata* King in Hook. f. Fl. Brit. Ind. 5: 540. 1888, et in Ann. Bot. Gard. Calcutta 2: 7. 1889, pro parte quoad *t. 1B*, syncarpium solum, et spec. Griffith 4663; Ridley Fl. Malay Penin. 3: 352. 1924. Syntypes, Malacca, Griffith 4663, Maingay 2411 (*Kew Distrib.* 1476) (CAL); lectotype, Griffith 4663 (CAL).

*Artocarpus rufescens* auct. non Miq., Kurz, For. Fl. Burma 2: 431. 1877.

Trees, height to 45 m., buttressed or not, bark grey, smooth, with very large lenticels. Twigs 5–8 mm. thick, rugose, densely rufous pubescent. Stipules 5–10 mm. long, broadly lanceolate, rufous pubescent. Leaves 10–28 × 6–14 cm., obovate-oblong, obtuse or short-acuminate, base rounded or shallowly cordate, margin entire; venation prominent beneath; glabrous or nearly so above, except the short-pubescent main veins, rufous pubescent beneath; lateral veins 11–15 pairs, curved, basal 2 or 3 pairs slightly crowded; intercostals numerous, usually parallel; dark green, drying yellowish to purplish brown above, red-brown beneath; petiole 20–35 mm. long.

Inflorescences solitary in leaf-axils. At anthesis: male head 25–35 mm. across, globose, echinate from closely set, rigid, spinous, often slightly curved processes c. 3 × 1 mm.; stamens 2 in each cavity, to 8 mm. long, filaments free or united at the base, anthers oblong, apiculate, 2.5–3 mm. long; basal involucre of 3 ovate, concave, rufous-pubescent bracts, 5–10 × 5–10 mm.; peduncle 20–35 × 2–3 mm., rufous pubescent; female head echinate as in male head, many of the processes basally connate in groups of 2–4 with a lanceolate style exerted to 3 mm. between the free apices. Syncarp to 9 cm. across, subglobose, shallowly lobed, drying red-brown, echinate from closely set, rigid, spinous processes, many connate in groups of 2–4, those on the lobes ± bulbous below, 6–8 × 2–5 mm., the rest slender; wall c. 2 mm. thick; "seeds" (pericarps with a thick, stony endocarp) numerous, ellipsoid, 15 × 12 mm.; core c. 40 mm. across; involucre as in male head; peduncle 40–55 × 5 mm., rufous pubescent.

VERNACULAR NAME: *ipoh*, Malaya (cf. *Antiaris toxicaria* Lesch.).  
 USES: the latex is used as an arrow poison.

DISTRIBUTION: in evergreen forest to 2000 ft.; Malaya, Sumatra, Banka, Borneo.

Malaya. SELANGOR. Bukit Cheraka For. Res., Walton KEP 28387 (KEP, infl.); Kuala Lumpur, Ginting Simpah, KEP 64942, 71252 (KEP, ♀); Sungei Lalang Kajang, Symington CF 22967 (SING). NEGRI SEMBILAN. Senawang Reserve, Yakim CF 507 (K, KEP, ♂). MALACCA. Alvins 465 (SING), Maingay 2411 (*Kew Distrib.* 1476), 1867–8 (GH, K, ♂); Bukit Kemuning, Derry 1022 (SING);



between Ching and Roombiya, *Griffith 4663*, 1842 and 1845 (CAL, K, L, P, U, ♂, mixed, ♀). PENANG. *Curtis*, March 1893 (SING, ♂, ♀). SINGAPORE. Chanchu Kang, *Ridley 4128* (CAL, SING); MacRitchie reservoir, *Sinclair SFN 39426* (L, SING, ♀); Mandai road, *Nur*, Oct. 1917 (SING, ♀); Serangoon road, *Ridley 8408* (K, ♀); Tanjong Kling, *Corner*, March 1938 (SING). PULAU TIOMAN. Ayer Surin, *Henderson SFN 21692* (BM, BO, K, SING, infl.).

**Sumatra.** TAPANULI. Barus, Penkalan Tapus, *bb 29549* (A, BO, L). EAST COAST. Huta Padang, near Kisarin, *Krukoff 327* (BO, SING). PALEMBANG. Banjuasin, Bajunglintjir, *NIFS T 761* (BO, L, ♀); Lematang Ilir, Gunong Megang, *NIFS T 816* (BO, L, ♂); Lematang Ilir, Semangus, *bb 32216* (BO, L, SING); Lematang Ilir, Tandjong, *NIFS T 645* (BO, infl.); Rawas, *Grashoff 1001* (BO, L, ♀). BANKA. Blinju, *Berkhout 151*, *Grashoff 90* (BO).

**Borneo.** EAST AND NORTHEAST BORNEO. Balikpapan: Pemaluan, *bb 24741*, *24753* (A, BO, L); Sungei Warin region, *Kostermans 4303* (K, L, ♀). Berouw: Inaran, *bb 12173* (BO). E. Kutei: Loa Djanan, w. of Samarinda, *Kostermans 6550* (BO, K, L, ♂, mixed). W. Kutei: Mendom, Sungei Alan-Klindjang, *bb 29257* (A, BO, L). BRITISH NORTH BORNEO. Bukit Garam, near Kinabatangan river, *Wood A 4659* (A, KEP, L, SING, infl.).

In publishing the description of *Artocarpus bracteata*, King cited two collections, *Griffith Kew Distrib. 4663* and *Maingay Kew Distrib. 1476*, both from Malacca. While the first of these collections is *Parartocarpus bracteatus* as here understood, the second is a mixture of this species and *Artocarpus rigidus* ssp. *rigidus*, owing to the allocation of the same Kew Distribution number to two different collections. At Kew there are under the number 1476 a sheet of *Parartocarpus bracteatus* bearing Maingay's own number 2411 and a sheet of *Artocarpus rigidus* with his number 2414. Duplicates distributed under the number 1476 consist at Calcutta and Leiden of *A. rigidus* and at the Gray Herbarium of *Parartocarpus bracteatus*. Although King at some period annotated the Kew specimens correctly, he appears to have drawn up his description from the material at Calcutta, namely the Griffith specimen consisting of detached leaves, a small portion of twig, and a mature syncarp of *Parartocarpus bracteatus*, and the Maingay specimen which was a sterile shoot of *Artocarpus rigidus*. The vegetative characters are a mixture of the two species, and the twigs are described as annulate (as in *Artocarpus* subg. *Artocarpus*). The plate is also a mixture, since comparison with these specimens shows that the artist drew the syncarp of *Griffith 4663* as if attached to the shoot of *Maingay 1476*. The confusion in the type material, the description, and the plate has not been noted previously, and King's specific epithet has always been applied to this species of *Parartocarpus*.

Kurz incorrectly identified this species with *Artocarpus rufescens* Miq. (= *A. dadah* Miq.) and included it under that name in his *Forest Flora of British Burma* (1877), presumably because on *Griffith 4663* at Calcutta the provenance is given as Burma. This is certainly an error, since no other collections have been seen from farther north than Penang and the Kew specimen has notes by Griffith stating that it was collected in Malacca. King corrected Kurz's identification in 1888 and gave the distribution as Malacca only.



The collection made by Curtis in Penang which is cited above resembles *Parartocarpus bracteatus* in the shape and venation of the leaves, but is anomalous in that the shoot is subglabrous except for the youngest parts, and the processes on both male and female inflorescences are much shorter than is usual in this species. In the male head they are shortly conical and in the syncarp they are obtuse with a small, acute umbo. In the absence of other, similar collections this specimen is not treated as distinct, but it would be of interest to have further material from Penang.

2. *Parartocarpus venenosus* (Zoll. & Mor.) Becc. For. Borneo, 632. 1902.

Trees, height to 35 m., not or scarcely buttressed, bark yellow to grey-brown, with numerous large lenticels. *Twigs* 3–7 mm. thick, rugose, appressed pubescent to puberulent, glabrescent or not. *Stipules* to 3 mm. long, deltoid, appressed pubescent. *Leaves* 4.5–23(–30)  $\times$  3–10 cm., obovate-oblong to obovate- or oblanceolate-elliptic, obtuse to short-acuminate, base rounded or cuneate, varying auriculate, margin entire; main veins prominent beneath, reticulum not or shallowly so; glabrous or nearly so above, thinly pubescent to glabrous beneath; lateral veins 6–15 pairs, curved; intercostals few, not parallel; dark green above, paler beneath, drying grey-green to purplish brown above, yellow-green to red-brown beneath; petiole 15–45 mm. long.

*Inflorescences* solitary in leaf-axils. *At anthesis: male head* 15–30 mm. across, globose, covered by closely set, indurated, conical, obtuse, umbonate or truncate processes, 1–1.5  $\times$  1–1.5 mm.; stamens 1–3 in each cavity, to 4.5 mm. long, filaments united for half to nearly all their length, anthers oblong, obtuse or apiculate, 2–2.5 mm. long; basal involucre of 3–4(–8) deltoid, short-pubescent to glabrous bracts, to 5  $\times$  5 mm.; peduncle 12–60  $\times$  2–3 mm., short-pubescent to glabrous, often somewhat thickened below the involucre, sometimes markedly so, the involucre reduced to an annulus; *female head*, surface as male head, many of the processes basally connate (often inconspicuously so) in groups of 2–4 with a lanceolate or fimbriate style exerted to 0.5–1.5 mm. between the free apices. *Syncarp* to 18 cm. across, subglobose, shallowly, sometimes markedly, lobed, brown, covered by closely set, indurated, spinous, umbonate, obtuse or truncate processes, many often clearly connate in groups of 2–4, those on the lobes 1–10  $\times$  2–5 mm., the rest smaller; wall 3–5 mm. thick; “seeds” (pericarps with a thick, stony endocarp) (1–)3 to many, ellipsoid, 15–30  $\times$  13–20 mm.; core c. 30 mm. across; involucre as in male head; peduncle 30–100  $\times$  c. 5 mm., short-pubescent to glabrous.

USES: the latex is used as arrow poison; the ripe fruit is said to be edible, but unripe seeds are poisonous.

DISTRIBUTION: peninsular Siam, Malaya, Sumatra, Simalur, Enggano, Riouw-Lingga Archipelago, Borneo, Java, Philippine Islands, Celebes, New Guinea, Bismarck Archipelago, Aru Islands, Solomon Islands.



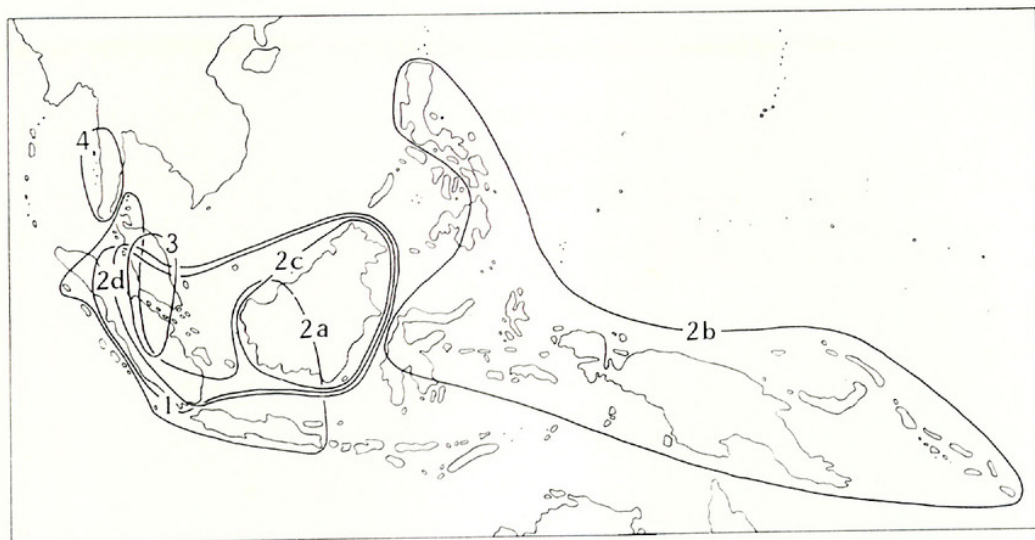


FIG. 20. Distribution of the species of *PARARTOCARPUS* and *HULLETTIA*. 1, *Parartocarpus bracteatus*; 2, *P. venenosus*, a, ssp. *venenosus*, b, ssp. *papuanus*, c, ssp. *borneensis*, d, ssp. *forbesii*; 3, *Hullettia dumosa*; 4, *H. griffithiana*.

*Parartocarpus venenosus* has the widest range of any species within the group of genera under study and extends over the whole of Malaysia and the Solomon Islands, though it is apparently absent from the Moluccas and the Lesser Sunda Islands. Within this area, it shows considerable variation and four subspecies are recognized here with a geographical and ecological basis.

The greatest variation is found in the shape of the processes on the syncarp. They range from broadly truncate, so that the syncarp surface appears tessellated, to spinuous so that the fruit is echinate. The processes enlarge during the maturation of the syncarp by intercalary growth at the base, and it is perhaps due to this that they are particularly subject to variation in shape. In two of the subspecies, ssp. *venenosus* and ssp. *papuanus*, the syncarp is usually tessellated, whereas in the other two, ssp. *borneensis* and ssp. *forbesii*, it is characteristically spinuous. However, specimens bearing syncarps having a knobbly surface, with processes of intermediate shape, are found which are referable on their vegetative characters to both ssp. *venenosus* and ssp. *forbesii*. The vegetative distinctions between the four taxa lie in slight differences in indumentum, leaf shape and size, and number and prominence of the lateral veins, as may be seen from the key to the subspecies. The peduncles in ssp. *forbesii* are also rather shorter than in the other subspecies.

These taxa are not absolutely separable, but most of the collections seen can be assigned to one or another without difficulty. In view of their fairly clear geographical and ecological separation, recognition at the subspecific level would seem to be justified. The distribution of ssp. *forbesii* is of particular interest in that it appears to be almost completely confined to peat-swamp forest. Very few other species of this group of genera are found in this habitat, apparently because they require fairly good drainage.



## KEY TO THE SUBSPECIES OF PARARTOCARPUS VENENOSUS

1. Peduncles glabrous, the male 12–35 mm., the female 30–40 mm. long; syncarp processes umbonate to spinous; leaves usually to less than 12 cm. long, thickly coriaceous, glabrous, obovate-elliptic, base cuneate, with 6–10 pairs lateral veins. . . . . ssp. *forbesii*.
1. Peduncles glabrous to pubescent, the male 25–60 mm., the female 35–100 mm. long; syncarp processes truncate to spinous; leaves larger, or obovate-oblong and usually puberulent.
  2. Leaves usually less than 12 cm. long, lateral veins 8–11 pairs, distinctly prominent beneath, reticulum shallowly so; syncarp processes spinous. . . . . ssp. *borneensis*.
  2. Leaves usually more than 12 cm. long, lateral veins 6–15 pairs, less prominent, reticulum not or scarcely so; syncarp processes truncate or obtuse.
    3. Shoot appressed-pubescent to subglabrous; leaves obovate-oblong to obovate-elliptic, base cuneate or rounded, lateral 8–15 pairs, usually drying red-brown. . . . . ssp. *venenosus*.
    3. Shoot glabrous or nearly so; leaves obovate-elliptic, apex often rather broadly rounded, lateral veins 6–10 pairs, usually drying greyish to yellowish green. . . . . ssp. *papuanus*.

ssp. *venenosus*

*Artocarpus venenosa* Zoll. & Mor. Natuur- en Geneesk. Arch. Neerl.-Ind. 2: 213. 1845, Flora 30: 471. 1847; Miq. in Zoll. Syst. Verz. Ind. Archip. 2: 89, 95. 1854; Miq. Fl. Ind. Bat. 1(2): 289. 1859. Holotype, Java, Zollinger 2371 (P); isotypes (BM, BO, P).

*Artocarpus venenosa* Zoll. var. *tylophylla* Miq. in Zoll. Syst. Verz. Ind. Archip. 2: 89, 95. 1854. Holotype, Java, Zollinger 2983 (P); isotypes (BM, L, P, U).

*Artocarpus tylophylla* Miq. Fl. Ind. Bat. 1(2): 289. 1859.

*Artocarpus callophylla* Zoll. & Mor. in Teysm. & Binnend. Cat. Hort. Bog. 85. 1866, nomen nudum.

*Artocarpus cerifera* Miq. Ann. Mus. Lugd.-Bat. 3: 212. 1867. Holotype, Java, Blume 2145 (L).

*Parartocarpus beccarianus* Baillon, Adansonia 11: 294. 1875; Becc. For. Borneo, 632. 1902; Renner, Bot. Jahrb. 39: 363. 1907. Holotype, Sarawak, Beccari PB 2557 (P); isotypes (A, K).

*Gymnartocarpus venenosa* Boerl. Ic. Bogor. 1: 73. t. 24, 25. 1897; Koord. & Val. Bijdr. Boomsoort. Java 11: 28. 1906.

*Radermachia cerifera* Blume ex Boerl. Ic. Bogor. 1: 73. 1897, pro syn. *Gymnartocarpus venenosa*.

*Parartocarpus venenosus* (Zoll. & Mor.) Becc. For. Borneo, 632. 1902, "venenosa"; Renner, Bot. Jahrb. 39: 362. 1907; Backer, Beknopte Fl. Java 6: 12. 1948.

Twigs, lower surface of leaves, peduncles and involucre bracts appressed pubescent or puberulent, glabrescent or not. Leaves to 12–23(–30) × 5–10 cm., obovate-oblong to obovate-elliptic, varying to oblanceolate-oblong or oblanceolate-elliptic, base rounded or cuneate; main veins promi-



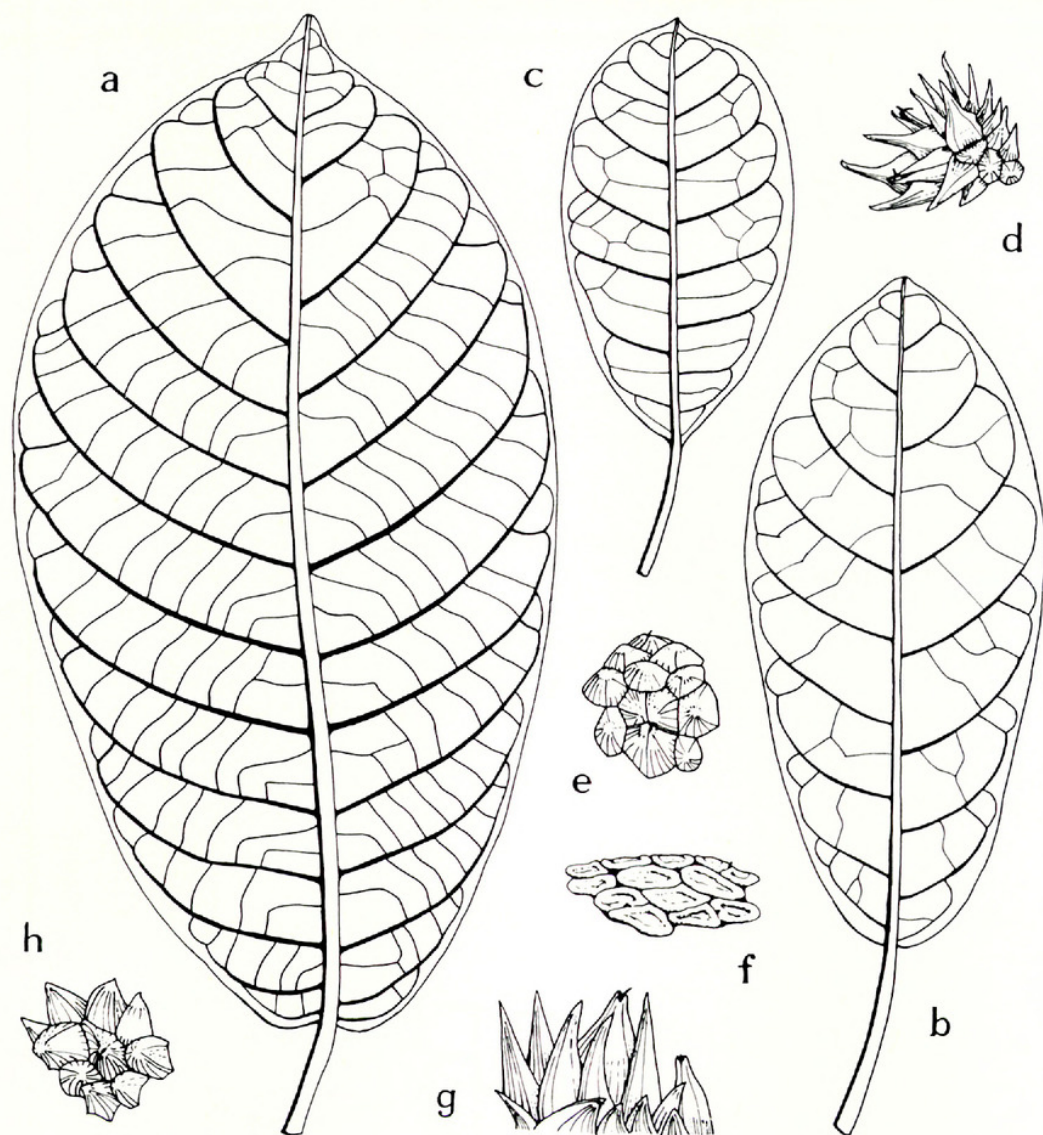


FIG. 21. Leaves and syncarp surface in *Parartocarpus*. a-c, Leaves ( $\times \frac{1}{2}$ ): a, *P. bracteatus*; b, c, *P. venenosus*, b, ssp. *venenosus*, c, ssp. *forbesii*. d-h, Surface of the mature syncarp (approx.  $\times 1$ ): d, *P. bracteatus*; e-h, *P. venenosus*, e, ssp. *venenosus*, f, ssp. *papuanus*, g, h, ssp. *forbesii*.

nent beneath, reticulum not or scarcely so; lateral veins 8-15 pairs. *Male head*, peduncle c. 30-60 mm. long. *Syncarp* with obtuse, or truncate and often depressed processes; peduncle c. 40-100 mm. long.

VERNACULAR NAMES: *bulu ongko* (Sundanese), *purut* (Javanese), Java.

DISTRIBUTION: in evergreen and mixed forest to 3000 ft., tolerating a short dry season; peninsular Siam, northern Malaya, Sumatra, Simalur, Enggano, Java.

Peninsular Siam. Islands off e. coast: Kaw Pa-ngan, *Put* 1256 (BM, ♂); Kaw Samui, *Put* 844 (BM, ♀); Kaw Tao, *Kerr* 12771 (BM, ♂, ♀). Malaya. PROV. WELLESLEY. Bukit Juru For. Res., *KEP* 9831 (KEP), 9843 (KEP, ♀), *Durant*



KEP 9840 (KEP). LANGKAWI ISLANDS. Langkawi, Gunong Raya, *Abdullah* KEP 42014 (KEP).

Sumatra. TAPANULI. Sibolga: Aek Labuan Talang, *bb* 19303 (BO); Kuala Badung, *bb* 19335 (A, BO). INDRAGIRI. Danau Mengkuang, *bb* 27558 (A, BO, L). SIMALUR. *Achmad* 155 (BO, L, ♂), 920 (BO, K, L, ♀); Landschap Tapah, Defajan, *Achmad* 1604 (BO, L). ENGGANO. Bua Bua, *Lütjeharms* 4258 (A, BO, K, L, P), 4464 (A, BO, K, L, P, infl.). BORNEO. SARAWAK. *Beccari* PB 2557 (A, K, P, ♂).

Java. *Blume* 2145 (L, ♂); between Mt. Smeru and Mt. Kelut, *Blume* HB 7314 (BO). WEST JAVA. Bantam: Gunong Karang, Tjimanuk, *Koorders* 8686 (BO, K, L), 40107 (BO, L); Menes, *Backer* 7063 (BO, ♂, ♀); Tjimara Ujung, Gunong Rompong, *Koorders* 8685 (BO, K, L). Batavia: Gunong Salak, *Koorders* 24444 (BO), 33285 (BO, L); Tjiampea, *Koorders* 30362, 30363 (BO). Buitenzorg: Djasinga, *De Voogd*, April 1941 (BO, K, L); Handjere, *NIFS* Ja 6816 (K, L); Natuur Monument, Dungus Iwul, *NIFS* Ja 1961 (BO); Pasir Pogor, *Bakhuizen van den Brink* 8017 (BO). Preanger: Palabuanratu, *Koorders* 5246 (BO, L), 8684 (BO, K, L, P, ♀), 8688 (BO, infl.), 12357 (BO, L, ♀), 42907 (BO, ♀); Tjilumpang, near Tjidadap, *Winckel* 1912 (BO). CENTRAL JAVA. Banjumas: Pringombo, Bandjarnegara, *Koorders* 8695 (BO, K, L, ♀). Pekalongan: Batu Kumpas, *NIFS* s.n. (BO). EAST JAVA. Besuki: Banjuwangi, *Koorders* 8028 (BO), 8680 (BO, L, P), 8681, 8682 (BO, L), 8683 (BO, K, L, P); Tjuramanis, *Koorders* 21066, 21406 (BO), 21407 (BO, K, L, infl.), 22238 (L), 38336 (BO, ♂). Madiun: Gunong Willis, Ngebel, *Koorders* 38756 (BO, K, L, P, ♂, ♀). Pasuran: Tangkil-Zuidergebergte, *Koorders* 22441 (BO, L), 23891 (BO, K, L, P, SING, U). Probolinggo: Malang, *Zollinger* 2371, Oct. 1844 (BM, BO, L, P, ♀). NUSA KAMBANGAN. *Koorders* 8694, 20225 (BO, L), 24126 (A, BO, K, L, ♀), 24627, 24640, 24728, 24729 (BO, L), 27036 (BO, L, ♂). Cultivated. JAVA. Bogor: Hort. Bot., *Teysmann*, 1860 (L), *Zollinger* 2983 (BM, L, P, U, ♀); Hort. Bot., cult. sub VIII B 1a, *Forman* 60, *Sutrisno* 78 (K, ♀).

The type subspecies of *Parartocarpus venenosus* shows some variation in the outline of the leaves and rather more in the shape of the processes on the syncarp. The leaves are, however, characteristically obovate-oblong with a somewhat acute apex, and persistently puberulent beneath, at least on the main veins. The leaves are usually larger and more thinly coriaceous than in either ssp. *borneensis* or ssp. *forbesii*. The venation is less prominent than in the former and the syncarp processes are never spinous.

The type collection of *Parartocarpus beccarianus*, *Beccari* PB 2557, has small, thinly coriaceous, narrowly obovate-oblong leaves (to  $12 \times 4$  cm.), which are puberulent beneath, but lack a prominent reticulum. The male inflorescences have processes with obtuse apices and the syncarp (presumably at Florence) is described by Beccari in 1902 as having the surface tessellate from the depressed pyramidal apices of the "polygonal scales" or perianth apices. Except in the rather small size of the leaves, the collection agrees with *P. venenosus*, *sensu stricto*, rather than with ssp. *borneensis* or ssp. *forbesii*.

ssp. *papuanus* (Becc.) Jarrett, stat. nov.

*Artocarpus riedelii* Miq. Ann. Mus. Lugd.-Bat. 3: 213. 1867. Syntypes, Celebes,



- Manado, *Teysmann* HB 5778 (U), *De Vriese* s.n. (L); lectotype, *Teysmann* HB 5778 (U).
- Artocarpus involucrata* K. Schum. in Schum. & Hollrung, Fl. Kais. Wilhelms Land, 39. 1889. Holotype, northeast New Guinea, *Hollrung* 522 (B); isotype (BO).
- Parartocarpus involucrata* (K. Schum.) Warb. ex Schum. & Lauterb. Fl. Deutsch. Schutzgeb. Südsee, 267. 1900; Becc. For. Borneo, 632. 1902; Renner, Bot. Jahrb. 39: 363. 1907; Lauterb. ibid. 62: 303. 1928; Diels, ibid. 67: 174. 1935; White, Jour. Arnold Arb. 31: 82. 1950.
- Parartocarpus papuana* Becc. For. Borneo, 633. 1902, non S. Moore, 1923. Holotype, New Guinea, Vogelkop, *Beccari* PP 719 (FI); isotype (FI).
- Parartocarpus riedelii* Warb. ex Renner, Bot. Jahrb. 39: 362. 1907.
- Artocarpus woodii* Merr. Philip. Jour. Sci. Bot. 3: 221. 1908; Elmer, Leaflet. Philip. Bot. 2: 623. 1909. Holotype, Mindanao, *Merrill* 5259 (PNH, destroyed); isotypes (L, P); lectotype (P).
- Gymnartocarpus woodii* (Merr.) Merr. Philip. Jour. Sci. 18: 52. 1921; Brown, Bull. Bur. For. Philip. 22(2): 270. fig. 19. 1921.
- Parartocarpus woodii* (Merr.) Merr. Enum. Philip. Pl. 2: 39. 1923.
- Artocarpus venenosa* Zoll & Mor., Schum. Notizbl. Bot. Gart. Berlin 1: 48. 1895.

Twigs, lower surface of leaves, peduncles and involucre bracts appressed pubescent or puberulent, soon glabrescent except often the involucre. Leaves to  $12-23 \times 5-10$  cm., obovate-elliptic, varying to oblanceolate-elliptic or obovate-oblong, base cuneate, varying to rounded or auriculate; main veins prominent beneath, reticulum not or scarcely so; lateral veins 6-10 pairs. Male head, peduncle c. 25-35 mm. long. Syncarp with truncate, often depressed processes; peduncle 35-70 mm. long.

DISTRIBUTION: in evergreen forest to 2000 ft.; Philippine Islands, Celebes, New Guinea, Bismarck Archipelago, Aru Islands, Solomon Islands.

**Philippines.** LUZON. Cagayan: *Klemme* FB 6650 (US, ♀). Isabela: San Marino, *Ramos & Edano* BS 47015 (BM, SING, ♀), 47176 (SING). Quezon: Baler, mountains e. of Castillo river, *Quisumbing* PNH 2518 (A, PNH, ♀). Bataan: *Alvarez* FB 12942 (P, US, ♀), *Curran* FB 17584 (BM, BO, L, US, ♂). Rizal: *Maneja* FB 23961 (P, US, ♀); Orind, *Loher* 6946 (K, infl.). Laguna: *Tamesis* FB 11993 (L, P, US, ♀); Calauan, *McGregor* BS 12392 (BM, P, ♀); Mt. Maquiling, *Forestry School* FB 20140 (BM, L, P, US, ♂), *Ramos* 1044 (U, US, ♂, ♀), *Villamil* FB 20394 (US, ♀), *Whitford* FB 19729 (BM, ♀); Mt. Maquiling, Los Banos, *Elmer* 18291 (A, BM, K, L, P, ♂); San Antonio, *Ramos* BS 15051 (P). Camarines: *Alvarez* FB 21453 (BM, P, US, ♀), 23748 (A, BO, ♀), *Hsia* FB 21107 (US, infl.); Camarines Sur, *Ahern* 41 (BO, US, infl.), *Alambra* FB 28088 (A, P, ♀). Albay: Rapu-Rapu Island, *Vidal* 3837 (A, K, ♀). Sorsogon: Irosin, Mt. Bulusan, *Elmer* 14650 (A, BM, K, L, ♀). SAMAR. *Sherfese et al.* FB 21084 (US, ♀). LEYTE. Dagami, *Ramos* BS 15184 (K, US, ♂, ♀). MINDANAO. Surigao: *Ramos & Pascasio* BS 34684 (A, P, ♀). Dinagat Island: *Ramos & Pascasio* BS 32540 (A, ♀). Bucas Grande Island: *Merrill* 5259, Oct. 1906 (L, P), *Ramos & Pascasio* BS 35056 (BO, L, infl.), 35092 (A, K, US, ♀).

**Celebes.** NORTH PENINSULA. Manado, *DeVriese* (L); Manado, Ratahan, *Teysmann* HB 5778 (BO, L, U); Minahassa, *Koorders* 19050 (BO, ♂), 19315 (BO, L). CENTRAL CELEBES. Malili: Kawata, *NIFS Cel./II-409* no. 10 (BO, K,



L, ♂); Lawoli, *bb* 23251 (BO); Usu, *NIFS Cel./II-324* (A, L, SING), 409 no. 409 (BO, L, ♂); Mantano Meer, *Kjellberg* 2805 (BO, ♀). Masamba, Mina, *bb* 24504 (BO, L, SING).

**New Guinea.** VOGELKOP. Bomberai: Fakfak, *Lundquist* 266 (L); Rauna, *bb* 22536 (BO). Inanwatan, *bb* 32657 (BO, L). Manokwari: Andai, *Beccari PP* 719, 1872 (FI, ♂, ♀); Momi, *bb* 33492 (BO, L); Oransbari, *Brouwer BW* 2584 (L); Warnapi, *Kostermans* 408 (BO, K, L). Sorong: Warsamson, 25 km. e. of Sorong, *Schram BW* 2923, 5949 (L). DUTCH NORTH NEW GUINEA. Hollandia: *Versteeg BW* 4825 (L, ♂, ♀); Holtekang, *Schram BW* 1508 (L); Idenburg river, Bernhard Camp, *Brass* 13547 (A, infl.), *Brass & Versteegh* 13547A (A, ♀); Tami, *Schram BW* 2723 (K, L, ♀); mouth of Tami river, *Schram BW* 2678 (K, L, infl.), 2811 (K, L, infl.), 2812 (L, infl.), *Versteegh BW* 3805 (L). DUTCH SOUTH NEW GUINEA. Merauke, Bot river, halfway between Bupul and Lake Wam, *Van Royen* 4737 (K, L). PAPUA. Central Division: Koitaki, *Carr* 12623 (A, BM, K, SING, ♂, ♀). Northern Division: Hydrographers Range foothills, *Hoogland* 3855 (A, BM, L, ♀). Western Division: Lake Daviumbu, Middle Fly river, *Brass* 7476 (A, L, ♂). MANDATED TERRITORY OF NEW GUINEA. Madang District: Constantinhafen, *Hollrung* 522, Feb. 1887 (B, BO, ♂); Gogol valley, hills ne. of Mawan village, *Hoogland* 4891 (K, ♀); Ramu valley, c. 5 mi. se. of Faita airstrip, *Saunders* 274, 539 (L). Morobe District: near Finschhafen, *Hellwig* 286 (SING); Umboi Island, *White NGF* 9646 (K, ♀). Sepik District: *Leder-mann*, 1912-13 (SING). NEW BRITAIN. West Nanakai, Gorea village, near Cape Hoskins, *Floyd* 6448 (K, ♂). SCHOUTEN ISLANDS. Biak, *bb* 30684 (BO, K), 30830 (BO, L, SING). JAPEN. *bb* 30281 (BO, L, SING); Mentebu, *bb* 30228 (A, BO, L, SING, ♀); Rendawaja, *Malinka BW* 7014 (L). SALAWATI. Kaloal, *Koster BW* 4243 (L). ARU ISLANDS. Kobraor: Dosinamalu, *bb* 25319 (A, BO, L, SING, infl.), *Buwalda* 5096 (A, K, L, SING, infl.). Trangan: Lutor, *Beccari*, June 1873 (FI, ♂); Ngaibor, *bb* 25453 (A, BO, SING, ♀), *Buwalda* 5420 (A, K, L, PNH).

**Solomon Islands.** BOUGAINVILLE. Buin, Marmaromino, *Kajewski* 2199 (A, K, infl.). TREASURY ISLAND. *Guppy* 55 (K, infl.). SANTA ISABEL. Kalina bay, *Walker BSIP* 238A (A, K, ♀). GUADALCANAL. Beaufort river, Kambou river, *Walker BSIP* 238 (A, K, ♀).

Although ssp. *papuanus* is widely distributed, it is rather constant in its characters. It is nearest to ssp. *venenosus* but is distinguished by the consistently subglabrous mature shoot and by the rather few lateral veins and broadly rounded apex of the leaves, which usually dry yellowish or greyish green. The syncarp is apparently always tessellate.

ssp. *borneensis* (Becc.) Jarrett, stat. nov.

*Parartocarpus borneensis* Becc. For. Borneo, 634. 1902; Renner, Bot. Jahrb. 39: 362. 1907. Holotype, Sarawak, *Beccari PB* 2005 (FI); isotypes (FI, K).

Twigs, lower surface of leaves, peduncles and involucre bracts appressed pubescent when young, usually persistently puberulent. *Leaves* to 8.5-12 × 5-7 cm., obovate-oblong, base rounded or broadly cuneate; main veins distinctly prominent beneath, reticulum shallowly so; lateral veins 8-11 pairs. *Male head*, peduncle 25-35 mm. long. *Syncarp* with spinous processes; peduncle 40-80 mm. long.



DISTRIBUTION: in evergreen forest on sand or loam to 200 (–1200) ft. in low undulating or hilly country; Borneo.

**Borneo.** SARAWAK. Mt. Mattang, Vallombrosa, *Beccari PB 2005*, June 1866 (K, FI, ♀); Sungei Semenggoh For. Res., *Wyatt-Smith KEP 79306* (K, L, ♀). BRUNEI. Andulau For. Res., *Ashton BRUN 585* (K, KEP, L, ♀), *Smythies et al. SAN 17500* (K, KEP, L, ♂), *Wyatt-Smith KEP 80076* (KEP, ♀). EAST AND NORTHEAST BORNEO. Central Kutei: Belajan river region, *Kostermans 10258* (K, ♀). W. Kutei: Longbleh, *bb 16047, 16054* (A, BO, L); Mujup, *bb 16782* (A, BO, L, infl.); near Tandjong Isui, *Endert 1898* (K, L). Tidung: Birik, *bb 17930* (A, BO, L, SING, ♂). BRITISH NORTH BORNEO. Kabili-Sepilok For. Res., *Enggoh KEP 48779* (KEP, ♂). LABUAN. *Motley 254* (K, infl.).

This subspecies is readily distinguished by the consistently spinous syncarp and the small, obovate-oblong, rather thickly coriaceous, usually thinly pubescent leaves with rather prominent venation.

ssp. *forbesii* (King) Jarrett, Jour. Arnold Arb. 41: 137. 1960.

*Artocarpus forbesii* King in Hook. f. Fl. Brit. Ind. 5: 539. 1888; King, Ann. Bot. Gard. Calcutta 2: 7. t. 1A. 1889; Ridley, Fl. Malay Penin. 3: 352. 1924; Moore, Jour. Bot. 63, Suppl. 112. 1925. Syntypes, Malaya, *King 10829* (CAL, not seen; duplicates examined, K, P), Sumatra, *Forbes 3080* (CAL, not seen; duplicates examined, BM, L).

*Parartocarpus excelsa* Becc. For. Borneo, 634. 1902; Renner, Bot. Jahrb. 39: 363. 1907. Holotype, Sarawak, *Beccari PB 673* (FI); isotypes (A, BM, FI, K).

*Gymnartocarpus triandra* J. J. Smith, Bull. Jard. Bot. Buitenzorg III. 4: 233. t. 6–8. 1922. Syntypes, Sumatra, *Beguin 316, 536, 583, Grashoff 798* (BO); lectotype *Beguin 583* (BO).

*Parartocarpus triandra* J. J. Smith, Bull. Jard. Bot. Buitenzorg III. 6: 80. 1924; Browne, For. Trees Sarawak, 357. 1955.

Twigs, and involucre bracts appressed pubescent or puberulent, soon glabrescent. Leaves to 8–13 × 4–6 cm., obovate-elliptic, base cuneate; main veins prominent beneath, reticulum not or scarcely so; lateral veins 6–10 pairs. Male head, peduncle 12–35 mm. long. Syncarp with spinous or umbonate processes; peduncle 30–40 mm. long.

VERNACULAR NAME: *tenggajun* (Malay), Sumatra, Borneo.

DISTRIBUTION: in evergreen forest to 2500 ft., usually in low-lying peat-swamp forest; western and southern Malaya, eastern and southern Sumatra, Riouw-Lingga Archipelago, Borneo.

**Malaya.** PERAK. Ulu Bubong, *King 10829*, Aug. 1886 (K, P, ♀). JOHORE. 8th mile Kota Tinggi-Mawai road, *Corner*, Feb. 1935 (SING); Gunong Pantai, *Corner*, Jan. 1937 (SING); Pengkalan Raja, *Ngadiman SFN 36661, 36682* (SING, ♀); Sungei Kayu, Mawai-Jemalaung road, *Kiah SFN 32185* (K, SING, ♀). PENANG. Ayer Hitam For. Res., *Strugnell KEP 49702* (KEP, ♀). SINGAPORE. Jurong, *Corner SFN 21845* (A, BM, BO, K, SING, ♂, ♀), *28147* (K, SING); 15th mile Jurong, *Corner SFN 26194* (A, K, SING, infl.).

**Sumatra.** EAST COAST. Asahan, Masihi For. Res., *Krukoff 4124* (A, BO, L,



SING, ♀); Benkalis, Sengoro, *Beguin* 536 (BO); Benkalis, Sungei Missigit, *Beguin* 583 (BO, L, ♂, ♀); Benkalis, Tamansari, *Beguin* 316 (BO, L, ♀); Labuan Batu, Sungei Palas, *bb* 10642 (BO); P. Mendal, Kelumang, *bb* 12472 (BO, SING, infl.); P. Tebing Tinggi, *bb* 12926 (BO, infl.). INDRAGIRI. Belimbing, *bb* 28537 (A, BO, L); P. Gelang, *bb* 29150 (A, BO, L). PALEMBANG. Banjuasin and Kubustreken, *Grashoff* 798 (BO, L, ♂); Muara Mengkulem, River Rawas, *Forbes* 3080, 1880 (BM, L, ♀). RIOUW-LINGGA ARCHIP. Karimon: Rutan, Simulur, *bb* 6303 (BO). P. Sinkep: Manggu, Ketjil, *bb* 5366 (BO, infl.).

**Borneo.** SARAWAK. Binatang, Surong, Daro For. Res., *Tahir* 9715 (K, L, infl.); near Kuching, *Beccari* PB 673, Nov. 1865 (A, BM, FI, K, ♂). BRUNEI. Sebatu-Arur Mangan watershed, *Ashton* BRUN 348 (K, KEP, ♀). WEST BORNEO. Kubu, Baru, Telok Meranti, *bb* 8041 (BO); Sambas, Paloh, *bb* 13891 (BO, ♀); Simpang, Djenu, *bb* 12699 (BO). SOUTH AND SOUTHEAST BORNEO. Lower Dajak, Danau Rawah, *bb* 13483 (BO); Sampit, Sungei Kereng Bindjai, Sabangau, *bb* 7941 (BO). BRITISH NORTH BORNEO. Tambunan, *Wyatt-Smith* KEP 80436 (K, KEP, infl.). P. NUNUKAN. *Kostermans* 8664 (K, L, ♀); S. Simengkadu, *Meijer* B 2372 (K, KEP, ♀).

This subspecies may be distinguished from the type and from ssp. *borneensis* by the obovate leaves, the consistently subglabrous adult shoot, and the shorter peduncles. The syncarp processes are rather variable in shape, overlapping those of both these entities. However, as noted above, the ecological preferences of ssp. *forbesii* seem to be quite distinct from those of the other subspecies. From ssp. *papuanus*, ssp. *forbesii* may be distinguished by the smaller, more thickly coriaceous leaves drying red-brown, and by the syncarp processes. *Artocarpus forbesii* was reduced by Beccari to *Parartocarpus venenosus* in 1902, and King's epithet has not been taken up previously in the latter genus, most specimens having been determined as *P. triandra* J. J. Smith.

#### SPECIES EXCLUDENDAE

PARARTOCARPUS PAPUANA S. Moore, Jour. Bot. 61, Suppl. 52. 1923, non Becc., 1902 = *Prainea papuana* Becc. For. Borneo, 635. 1902.

PARARTOCARPUS sp., Benth. & Hook. f. Gen. Pl. 3: 375. 1880 (*Beccari* PB 667) = *Prainea frutescens* Becc. For. Borneo, 635. 1902.

*Hullettia* King in Hook. f. Fl. Brit. Ind. 5: 547. 1888; King, Ann. Bot. Gard. Calcutta 5(2): 163. *t.* 197. 1896; Engler & Prantl, Nat. Pflanzenfam. Nachträge II-IV. 122. 1897; Boerl. Handl. Fl. Ned. Ind. 3: 338, 372. 1900; Ridley, Fl. Malay Penin. 3: 358. 1924; Jarrett, Jour. Arnold Arb. 40: 9, 11. *fig.* 2, *g-k*, *fig.* 3, *j-l*. 1959. LECTOTYPE SPECIES: *Hullettia griffithiana* (Kurz) King.

*Kurzia* King in Hook. f. Fl. Brit. Ind. 5: 479. 1888, in clavis.

Shrubs to small trees. *Leaves* spirally arranged, simple, entire, penninerved, thinly to thickly coriaceous, lower epidermis with numerous cells having strongly thickened, pitted walls and bearing hairs or not, the lower



surface hence hispid-pubescent, scabrid or smooth, minutely punctate beneath in sicco from the whitish stomata; epidermal gland-hairs superficial, long-stalked, heads globose, unicellular; spongy mesophyll compact, without resin-cells; juvenile leaves elongate. *Stipules* paired, linear, lateral, scars small, round.

*Inflorescences* unisexual, capitate, head pulvinate or obconical at anthesis, becoming subglobose in syncarp, pedunculate, solitary or paired in leaf-axils; stamens or ovaries sunken in cavities closely set on the upper surface of the receptacle; receptacle naked (perianths and interfloral bracts lacking), fleshy; involucre of 3–6 obtuse to lanceolate, fleshy, flattened bracts present. *At anthesis*: anthers or stigmas exerted through perforations in the upper surface of the receptacle; involucre marginal; *male head* with up to 30 flowers; stamens paired in each cavity with the filaments partially or almost completely united, anthers 0.7–1 mm. long, long-exserted; *female head* with up to 6 flowers, ovaries solitary in each cavity, unilocular, the style apical with a short-exserted, capitate stigma, the ovule apical. *Mature syncarp* formed by the enlargement of the entire female head, with 2–6 flowers forming fruit and completely filling the receptacle; involucre equatorial or becoming sub-basal through the greater expansion of the upper surface of the receptacle; mature ovary pergamentaceous, scar left by the style apical, the seed large, attached apically, testa membranous except the thickened apical cap, endosperm none, embryo straight, orientation longitudinal, cotyledons equal, appressed faces at an angle of 0–90° to median plane of ovary, radicle and plumule small, basal.

DISTRIBUTION: southern Tenasserim and peninsular Siam, Malaya, Sumatra (Indragiri).

The genus *Hullettia* was described by King in 1888 with the two species recognized in the present revision, namely, a species from Tenasserim based on the wrongly assigned *Dorstenia griffithiana* Kurz, and a new species from Malaya, *Hullettia dumosa* King. The new genus appeared in the key to the Urticaceae in the *Flora of British India* as "*Kurzia*," but, finding that this name was preoccupied [by the algal genus *Kurzia* Martius, *Flora* 53: 417. 1870], King changed it in the systematic treatment to *Hullettia*, after R. W. Hullett, a schoolmaster in Singapore who served on the Gardens Committee there. In 1896 King published a somewhat more detailed account, with a plate of *H. dumosa*, in "A Century of New and Rare Indian Plants." As with *Prainea*, which he described in the same works, King wrongly stated that the ovule was basal and erect and hence that the position of *Hullettia* was in the tribe Conocephaleae (= subfamily Conocephaloideae). It was rejected from this group by Renner in his study of the leaf anatomy of the Artocarpoideae and Conocephaloideae, but he omitted the genus as being of doubtful affinity (*Bot. Jahrb.* 39: 419. 1907). *Hullettia* has otherwise been mentioned only in the *Nachträge* to the *Natürlichen Pflanzenfamilien* (1897), in the floras of Boerlage (1900) and Ridley (1924), and in Burkill's *Dictionary* (1935).



The morphology of the inflorescences has been discussed in the introductory paper of this series (Jour. Arnold Arb. 40: 1-29. 1959). The attachment of the ovule has been found to be apical in the two species both at anthesis and at maturity, which indicates (with the erect stamens) that *Hullettia* is related to the genera at present placed in the Artocarpoideae. The capitate inflorescences resemble those of *Parartocarpus* in being clearly involucrate (with fleshy marginal to sub-basal bracts) and in having the stamens and ovaries apparently enclosed in cavities of the receptacle rather than in perianths. Externally, however, the inflorescences of the two genera have a very different aspect, since those of *Parartocarpus* are armoured from indurated processes, whereas those of *Hullettia* have a smooth, fleshy, pubescent surface, with perforations leading to the receptacular cavities. Perianths and interfloral bracts appear to be entirely absent in the latter genus.

The mature syncarp of *Hullettia* differs internally from that of *Parartocarpus* in having pergamentaceous, not indurated, pericarps, and straight, rather folded embryos. However, the testa has a well-developed, thickened cap occupying an apical position in the pericarp, as in *Parartocarpus*. The tips of the cotyledons lie in contact with this cap, which may be compared with the similar thickening of the testa in *Prainea*. The latter, however, is basal (corresponding with the sub-basal attachment of the mature seed) and the orientation of the embryo relative to the pericarp is the reverse of that found in *Hullettia*, the radicle being apical.

It should be noted that this view of the inflorescence structure of *Hullettia* is in complete accord with the account of "*Dorstenia* sp." given by Griffith (published in 1854), on which *Dorstenia griffithiana* Kurz (= *Hullettia griffithiana* (Kurz) King) was largely based. Griffith apparently dissected fresh inflorescences and the details given by him of the pericarps and seeds support the present description, which is based on an examination of dried syncarps (boiled up in water) of both species. King, on the other hand, regarded the stamens and ovaries as being enclosed in tubular perianths, which were connate with each other and the receptacle. However, as in *Parartocarpus*, no sign of fusion between adjacent perianths has been found in the walls separating the receptacular cavities. In view of the other characters indicating an affinity between the genera, it seems more probable that the inflorescence structure of *Hullettia* is homologous with that of *Parartocarpus*. In the latter the walls have been shown to be largely, if not wholly, of intercalary origin. No material has been available for the study of development in *Hullettia* and it is possible that vestiges of perianths, indistinguishable at later stages, are incorporated in the surface of the receptacle.

The leaves of *Parartocarpus* and *Hullettia* agree in having long-stalked, superficial gland-hairs with unicellular heads. As was noted in the introductory paper, *Hullettia* is distinguished by the numerous enlarged cells with strongly thickened, pitted walls in the lower epidermis. However, it should be observed that the minutely punctate appearance of the under



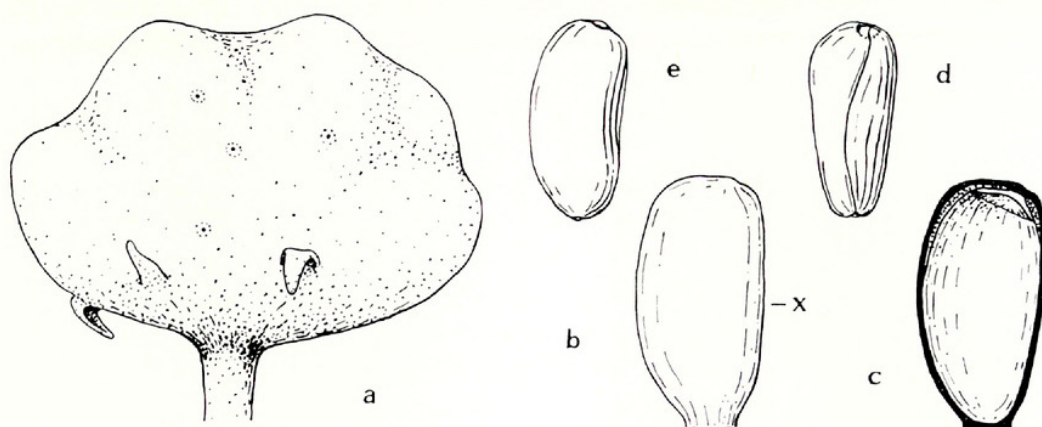


FIG. 22. The syncarp in *Hullettia griffithiana*: a, entire head; b, pericarp, side view; c, pericarp cut in median plane and embryo removed; d, embryo from same view; e, embryo seen from "x" (all approx.  $\times 1$ ).

surface of the leaves when dry is due, not to these cells, as was stated there, but to the whitish guard cells of the stomata.

The distribution of *Hullettia* as a genus is very limited. *Hullettia griffithiana* is known from southern Tenasserim and peninsular Siam, while *H. dumosa* occurs quite widely in Malaya and has recently been collected in central Sumatra. Both species may well be more common than is indicated by the number of collections, since they are small trees or shrubs which are probably relatively inconspicuous except at the time of fruiting. The fleshy, orange syncarps presumably attract arboreal mammals or birds in the same way as the fruits of those species of *Artocarpus* that have fleshy syncarps. The two species in the genus are readily separated on inflorescence characters, especially those of the mature syncarp. The vegetative characters show some overlapping, but there is usually no difficulty in assigning sterile collections to one or other of the species.

#### KEY TO THE SPECIES OF HULLETTIA

Male head c. 10 mm. across, peduncle to 20 mm.; syncarp with obtuse to obsolete involucre bracts, peduncle to 45(–55) mm.; leaves smooth to scabrid beneath, base cuneate to rounded, petiole to 50 mm. .... 1. *H. dumosa*.

Male head to 7 mm. across, peduncle 25–45 mm.; syncarp with lanceolate involucre bracts, peduncle c. 75 mm.; leaves hispid-pubescent to scabrid beneath, base narrowly and abruptly rounded or auriculate, petiole to 18 mm. .... 2. *H. griffithiana*.

1. *Hullettia dumosa* King in Hook. f. Fl. Brit. Ind. 5: 547. 1888; King, Ann. Bot. Gard. Calcutta 5(2): 163. t. 197. 1896; Ridley, Fl. Malay Penin. 3: 358. 1924; Burkill, Dict. 1202. 1935. Syntypes, Perak, King 3959, *Scortechini s.n.* (CAL, not seen; duplicates examined, K).

Shrubs or small trees, height to 10 m. Twigs 3–6 mm. thick, acutely rugose, thinly pubescent to subglabrous, hairs pale yellow, subappressed.



*Stipules* 3–10(–15)  $\times$  c. 1 mm., puberulent. *Leaves* 10–40  $\times$  4–12 cm., elliptic to oblong- or obovate-elliptic, rarely oblanceolate-elliptic, with an acumen to 2.5 cm. long, base cuneate to rounded, margin entire; main veins prominent beneath, reticulum less so; smooth on both surfaces or scabrid beneath; lateral veins 8–12(–15) pairs, curved; intercostals few, often one median between and parallel to the lateral veins, mid-green, drying greyish to yellowish green, paler beneath and minutely punctate, venation straw-coloured; petiole 10–35(–50) mm. long.

*Inflorescences* solitary or paired in leaf-axils. *At anthesis: male head* c. 10 mm. across, obconical or pulvinate, short-pubescent, with c. 4 marginal, subacute, fleshy, involucre bracts, c. 3  $\times$  5 mm.; stamens 3 mm. long, paired, filaments united to just below anthers, anther-cells oblong, 1 mm. long; peduncle 10–20  $\times$  1 mm., short-pubescent, often enlarging gradually into receptacle; *female head* with clavate stigmas exerted 0.5 mm. through perforations in the surface. *Syncarp* to 5.5 cm. across, depressed globose, orange with orange-yellow flesh, drying olive-brown, with surface smooth, velutinous, with c. 4 equatorial to sub-basal, obtuse, fleshy, involucre bracts to 3  $\times$  12 mm., often nearly obsolete; wall c. 2 mm. thick; “seeds” (pergamentaceous pericarps) 2–5, ellipsoid, 22  $\times$  11 mm.; peduncle 15–45(–55)  $\times$  1.5 mm., short-pubescent.

DISTRIBUTION: in forest to 6700 ft.; Malaya, Sumatra (Indragiri).

**Malaya.** PERAK. *Scortechini* 656 (K), [*Scortechini*] s.n. (K, ♀); Batu Kuran, Curtis, 1892 (SING); Bujong malacca, Curtis, 1892 (SING), Ridley 9617 (SING, ♀); Gunong Batu Puteh, Wray, 1888 (BM, SING, ♂); Gunong Kerbau, Robinson, Mar. 1913 (K, ♂, ♀); Kota Lama, Kuala Kangsar, Haniff SFN 16040 (SING); Larut, King 2405 (BM, infl.), 3959, Mar. 1883 (K, ♀); 11th mile from Tapah, Haniff SFN 14283 (SING); Ulu Bubong, King 10427 (BM, K, ♀). TRENGGANU. Bukit Kajang, Kemaman, Corner, Nov. 1935 (SING). PAHANG. Fraser's Hill, Corner SFN 33206 (A, K, SING, ♂); Telom, Ridley 13788 (BM, SING, ♂); Temerloh, Titi Bungor, Henderson SFN 10543, 10629 (SING, infl.). SELANGOR. Kepong, For. Res. Inst. plantations, Kochummen KEP 78955 (K, ♀); Klang Gates, Hume 7231 (SING), Ridley, Jan. 1921 (K, SING, ♀); Kuala Lumpur, Curtis 2404 (SING, ♀); Simpang, Ridley 15603 (BM, K, ♀); Sunenyih, Hume 8205 (SING); Sungei Buluk, Ridley 13343 (BM, K, SING, infl.); Sungei Lalang Kajang, Symington CF 24185 (SING, infl.). NEGRI SEMBILAN. Gunong Angsi, Nur SFN 11569 (K, SING, ♀). MALACCA. Mt. Ophir, Cameron, Nov. 1941 (SING, ♀), Lobb (GH, infl.). Sumatra. INDRAGIRI. Taluk region, near bivac Dewan, Meijer 4281 (CGE, ♂, ♀). **Cultivated.** MALAYA. Singapore, Hort. Bot., Hassan, May 1927 (SING, infl.).

2. *Hullettia griffithiana* (Kurz) King in Hook. f. Fl. Brit. Ind. 5: 547. 1888; King, Ann. Bot. Gard. Calcutta 5(2): 163. 1896.

*Dorstenia* sp., Griffith, Not. Pl. Asiat. 4: 403. 1854.

*Dorstenia griffithiana* Kurz, Jour. Asiat. Soc. Bengal 42: 104. 1873, For. Fl. Burma 2: 462. 1877. Syntypes, Tenasserim, Griffith 929 (*Kew Distrib.* 4676) (K), Helfer 4676/1 (CAL, not seen; duplicates examined, GH, K); lectotype, Griffith 929 (K).



Shrubs or small trees, height to 7 m. *Twigs* 4–5 mm. thick, acutely rugose, thinly to moderately pubescent, hairs pale yellow, subappressed. *Stipules* 6–10  $\times$  1 mm., indumentum as twigs. *Leaves* (12–)16–35  $\times$  4.5–9 cm., oblanceolate- to obovate-elliptic, often narrowly so, acuminate, base narrowly and abruptly rounded, or auriculate, the auricles sometimes joined across the petiole, margin entire; main veins prominent beneath, reticulum less so; glabrous above, moderately to sparsely short hispid-pubescent beneath; lateral veins 11–16 pairs, curved; intercostals few, often one median between and parallel to the lateral veins; drying greyish to yellowish green, paler beneath and minutely punctate, venation straw-coloured; petiole 10–18 mm. long.

*Inflorescences* solitary or paired in leaf-axils. *At anthesis: male head* 4–7 mm. across, pulvinate, short-pubescent, with c. 4 marginal, acute, fleshy, involucre bracts, c. 1.5  $\times$  1 mm.; stamens 3 mm. long, paired, filaments united for half their length, anther-cells oblong, 0.7 mm. long; peduncle (? 20–)28–45  $\times$  1 mm., short-pubescent; *female head*. . . *Syncarp* to 4.5 cm. across, depressed globose, drying olive-brown, the surface smooth, velutinous, with 4–6 equatorial to sub-basal, lanceolate, fleshy, involucre bracts to 6  $\times$  3 mm.; wall c. 2 mm. thick; “seeds” (pergamentaceous pericarps) c. 4–6, ellipsoid, 22  $\times$  12 mm.; peduncle 75  $\times$  1.5 mm., short-pubescent.

DISTRIBUTION: to 200 ft.; southern Tenasserim and peninsular Siam.

**Lower Burma.** TENASSERIM. *Helper* 4676/1 (GH, K, ♂). Mergui: Madamacca Island, *Griffith* 929 (*Kew Distrib.* 4676), Jan. 1835 (K, ♀); Mergui Island, *Proudlock* 52 (BM, K, SING, ♂, ♀), 61 (BM, K, ♀); Tenasserim River, Kanaung-gyi, *Parkinson* 1978 (K, ♂). **Peninsular Siam.** Klong Bagatac, *Kloss* 6564 (K, ♂); Koh Khan, Kopah, *Haniff SFN* 2991 (SING, ♂); Tasau, *Kloss* 6826 (K, ♂).

It has been noted above that *Hullettia griffithiana* was first described, as *Dorstenia* sp., by Griffith, who stated that he had collected his material in the Mergui Archipelago in January 1835. There is a specimen with mature syncarps at Kew, presumably representing this collection, which bears Griffith's number 929 and the Kew Distribution number 4676. The latter was not listed in J. D. Hooker's *Catalogue of the plants distributed at the Royal Gardens, Kew, from the Herbaria of Griffith, Falconer, and Helper* (1865), which indicates, according to the preface, that there were no duplicates. Kurz's description of *Dorstenia griffithiana* was mainly abbreviated from that of Griffith, which he cited, but he made slight changes in the details of the leaves and added their measurements. Although he did not quote any specimens, it may be assumed that the collection available to him in Calcutta was *Helper Kew Distrib.* 4676/1, since this was listed by Hooker (and hence distributed in 1862–3) and was mentioned by King in his second account of *Hullettia* (1896). This collection, which bears immature male inflorescences, must have been made in the period 1837 to 1839, when Helper was in Tenasserim, and thus it was not the earliest collection of *Hullettia griffithiana*, as stated by King in 1896. It is con-



cluded that both the Griffith and Helfer collections should be regarded as the syntypes of *Dorstenia griffithiana*; the former is chosen as the lectotype, since Griffith's account provided the chief part of Kurz's description.

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Jarrett, Frances M. 1960. "Studies in Artocarpus and Allied Genera, V. A Revision of Paratocarpus and Hullettia." *Journal of the Arnold Arboretum* 41(3), 320–340. <https://doi.org/10.5962/p.324670>.

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