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A TAXONOMIC REVISION OF THE GENUS CEIBA MILL. (BOMBACACEAE)

by
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INTRODUCTION

This revision of the genus Ceiba represents the tardy completion of taxonomic studies we initiated with the genus Chorisia in the early 1980s. At that time our main research interest was in the breeding system of Chorisia speciosa and related species, and our taxonomic enquiry began because of doubts we had concerning the identity of pale yellow flowered trees listed as “Chorisia insignis HBK” in cultivation at the horticultural section of the Experimental Station of the Instituto Agronômico (Fazenda Santa Eliza), Campinas (São Paulo). We did not solve this particular problem until much later but sporadic taxonomic studies with herbarium material and species represented in the splendid collection of trees of known provenance at the Fazenda Santa Eliza led to a gradual understanding of this group, and our conviction that the genus Chorisia should be merged with Ceiba (cf. Gibbs & al., 1988). However, our taxonomic research with Ceiba went into abeyance for a
number of years whilst the first author was involved with studies on the reproductive biology of species of the Brazilian cerrado and Argentine Chaco vegetation, and second author undertook a doctoral thesis on the genus *Lycchnophora* Mart. (Asteraceae).

Fortunately, over the intervening years, with one notable exception, few other people have taken an interest in the taxonomy of species of *Ceiba* or *Chorisia*, despite the great beauty of the flowers of these trees, and some confusion concerning their identity. The exception was a paper by Ravena (1998). The principle objective of Ravena (1998) was to accept Gibbs, Semir and da Cruz’s view that *Chorisia* should be merged with *Ceiba*, and then to effect all possible recombinations of *Chorisia* species under *Ceiba*. No attempt was made to study type material of the species of *Chorisia* to be recombined, and unsurprisingly, of the seven new combinations effected in this paper, two were superfluous. In addition, two new species were proposed by Ravena (both rejected in the present revision), together with an unworkable key which purported to identify five of the 10 species considered in his study. Why the key was restricted to just these five taxa was not explained. The paper was produced in the author’s own xeroxed series ‘Onira Botanical Leaflets’ rather than published in a peer-reviewed journal, and so is difficult to access, but since care was taken to ensure that copies were sent to some major botanical institutions, e.g. Royal Botanic Gardens, Kew, effective publication was achieved.

Ravena (1988) claimed that Gibbs & al. (1988) “believed that *Ch. crispiflora* HBK, *Ch. speciosa* St. Hil., Juss. & Camb., *Ch. ventricosa* Nees & Mart., *Ch. integriifolia* Ulbr. and *Ch. incana* Rob. are referable to *Ch. insignis*. The writer’s own experience with living material of these and other species in their native habitat, cannot allow him to accept Gibbs & al. opinion”. This implies we treated all of these taxa as synonyms of *Chorisia insignis*, which in this paper we recombined as *Ceiba insignis*. In fact we commented that these species “form a polymorphic complex or aggregate species... Our detailed studies are not yet complete but it appears that all other species of *Chorisia... are referable to it*” [i.e. to such a species aggregate]. Mindful of the adage “fools rush in where angels fear to tread”, we concluded: “Whether any of these taxa can be maintained at a specific or subspecific level must await the outcome of our analysis of the *Ceiba insignis* complex.” In the event, we recognize here the *Ceiba insignis* aggregate with seven component species, including a new species *C. lupuna*, and we treat *Ch. integriifolia* as a synonym of *C. insignis* s.s., and *Ch. incana* as a synonym of *C. ventricosa*.

Gibbs & al. (1988) provided a taxonomic history of the genera *Ceiba* and *Chorisia*, and a discussion of their alleged differential characters, particularly the nature of the stamen tube, which led us to believe that *Chorisia* should not be separated from *Ceiba*. To provide an introduction to this revision, we here include a summary of the views put forward in that earlier publication.

Although used by Plumier (1703: 42), Miller (1754) provided the first valid publication of the generic name *Ceiba*, but this was overlooked until Druce (1913). As clarified by Nicolson (1979), the type species of this genus is *Ceiba pentandra* (L.) Gaertn. (1791), first published as *Bombax pentandrum* L. (1753). The generic names *Bombax*, and subsequently *Chorisia*, prevailed for this group until *Ceiba* was re-established by Schumann (1886, 1890). Thus, Kunth (1822), working with the Humboldt and Bonpland collections, recognised two “sections” in *Bombax*: “filamente quinque” for his *Bombax aesculifolia*, and “filamenta creberrima (*Ceiba*)” for two other species with multiple stamens, Kunth (1822) also described the genus *Chorisia* for two species, *Ch. insignis* and *Ch. crispiflora*, with complete fusion of the functional staminal filaments to give a tube around the style, but he recognized that this was a complex structure: “…*tubus staminens duplex; interior tenuis, elongatus, teres, apice antherifer; exterior brevis, interior adnatus, apice decimolobus, lobis patentibus, sterilibus. Antherae 10, sumo tubo externae adnatae...*”.

**Ch. speciosa**
De Candolle (1824) retained Bombax for seven species with multiple stamens, and Chorisia for Kunth’s two species, but he described the genus Eriodendron (with Ceiba Plum. as a synonym) for species with five free staminal filaments united at their base into a tube, to which he referred Bombax aesculfolium, Bombax erianthos (as E. leiantherum) and Bombax pentandra (as E. anfractuosum). To these latter genera, Neess & Martius (1823) added Chorisia ventricosa, Martius & Zuccarini (1826) Eriodendron samauma, and Saint Hilaire (1828) described Chorisia speciosa, Eriodendron pubiflora and E. jasminodora.

Additional generic names were subsequently proposed by diverse authors but none received widespread acceptance, and the modern view of Ceiba and related genera was cast by Schumann in his treatment of the group for Martius’s Flora brasiliensis (1886) and subsequently his monograph in Engler and Prantl’s Pflanzenfamilien (1890). In the tribe Adansoniae Benth., Schumann recognized four genera: Adansonia, Bombax, Chorisia and Ceiba. The broadly based Bombax recognized here was subsequently split by various authors, most notably by Robyns (1963). Schumann (1890) recognized Ceiba with three sections: sect. Campylanthera with four species from tropical America including C. samauma and C. pentandra, sect. Eriodendron, with one very different species, C. rivieri (now at Spirothera), and sect. Erione, again with a disparate group of taxa including C. rosea from C America, and C. pubiflora and C. jasminodora from Brazil. Except for recognition of the genus Spirotheca by Ulbrich (1914), which involved the transfer of Ceiba rivieri to this new genus, Schumann’s view of the genera Ceiba and Chorisia has remained essentially intact until the proposal to unite these genera by Gibbs & al. (1988).

Our reasons for this proposal are discussed in detail in the paper cited above. Essentially they are based on the fact that the diagnostic character between Chorisia vs. Ceiba, viz. that species of the former have a lower staminal tube with a corona-like structure of staminal appendages, and with the upper staminal filaments fused to form a tube, whilst species of Ceiba, lack such appendages and divide to give 5 filaments, in fact breaks down with intermediate conditions. Strictly applied, the distinction between Chorisia and Ceiba leads to such species as Chorisia speciosa and the closely related (and interfertile) Ceiba pubiflora, and similarly, Chorisia glaziovii and the closely related Ceiba erianthos, being placed in separate genera, as Dawson (1944) and Santos (1964) noted. We have also produced fertile hybrids between Ceiba erianthos × Chorisia speciosa and C. erianthos × Chorisia chodatii. Again as discussed by Gibbs & al. (1988), pollen morphology divides these taxa not according to Chorisia vs. Ceiba, but a large group of both these genera, with essentially peritreme grains, are distinct from some four or so species with distinctly oblate grains. We used this striking pollen difference to recognize two sections with the united genus Ceiba.

The taxonomy of Ceiba presents some special problems. Most species flower in the leafless condition so that many specimens are either of flowers or leaves. Many Ceibas are large forest trees with flowers of difficult access, so that often specimens have been prepared from old fallen flowers collected on the forest floor. Moreover, since many species have crepuscular or nocturnal anthesis, so that flowers collected after midday the following day are already entering senescence. Add to which most species have fleshy flowers with delicate colour variations which, if not dried carefully, e.g. using aluminum corrugates and heated presses, lose their colour and partially their form. These comments are not made to excuse poor taxonomy, but rather to plead for careful future collecting with this group, and to stress the value of colour photos, and perhaps to justify the rather broad approach we have taken with several species, e.g. C. aesculifolia, and C. pentandra. It will be surprising if our treatment will represent the last word on these taxa.
MATERIALS AND METHODS

This revision is based on herbarium specimens from the following herbaria: BAB, BAF, BHCB, BRAD, CAS, CEN, CEPEC, COL, CPAP, DS, E, EAC, ESA, F, FHO, G, GUA, HUEFS, HXBH, INPA, IPA, K, LIL, LL, MBM, MO, NY, OXF P, R, RB, S, SJRP, SP, SPF, TEX, U, UEC, US, WIS, although we have not necessarily seen all material in any particular herbarium. Where possible we have also studied species either in the field (C. glaziovii, C. jasminodora, C. pubiflora, C. speciosa), or in arboreta (C. erianthos, C. samauma).

MORPHOLOGY

Growth habit

All ceibas are trees, commonly 5–20 m but in some species with imposing height, e.g. *Ceiba pentandra*, at 30–50 m, is a canopy emergent of the *varzea* forest in Amazonian Brazil and riverine forest in W Africa. This species may also present well developed buttresses. At the other extreme, *C. jasminodora* is often encountered as a treelet of 1.5–2 m in upland, rocky campo rupestre habitats in Minas Gerais. Most ceibas present aculeate spines on trunk and branches, and in some species (particularly *C. chodatii, C. pubiflora, C. speciosa* of the *C. insignis* agg.) the trunk may be markedly ventricose (hence the common names barriguda, palo borracho) but individuals of the same species may vary with respect to spines and trunk form.

Leaves

All species have digitate leaves, commonly 5–7 foliolate, usually with a long, slender petiole and diminuitive petiolules, commonly more or less lanceolate, chartaceous to coriaceous, with margin entire or dentate. Serration of the margin may be variable within species, but is consistent in e.g. the aptly named *C. aesculifolia*, and consistently absent in e.g. *C. erianthos, C. jasminodora, C. samauma* and *C. schottii*. Again, *C. jasminodora* is distinctive in having 3-foliolate leaves, usually with a distinct mucron. Indumentum, when present, of simple or stellate hairs, sometimes varying between individuals of the same species.

Calyx

Usually more or less campanulate, robust to fleshy, usually glabrous externally (with few exceptions, particularly some specimens of *C. aesculifolia* and *C. soluta*) and densely villous within, opening to give 4-5 irregular lobes. Dispersed nectaries are distributed on the inner surface of the calyx.

Corolla

Commonly with 5 rather fleshy, more or less linear-oblong to spatulate petals which may be held erect to give a funnelform (*C. chodatii*) or more or less campanulate (*C. boliviana*) flower, but in most species with petals spreading, and in some e.g. *C. jasminodora, C. aesculifolia*, markedly reflexed.

Petal colour and markings are important characters in this genus, although usually lost with herbarium specimens (for which, in many cases, the flowers have been collected after having fallen to the ground), and sparingly commented upon by collectors, making colour photographs invaluable for understanding the species. A common feature is for the petal limb, whether white, ivory or pink to magenta in colour, to have distally sparse dark, usually deep carmine, flecks or striations, which may merge below, but with the claw pale yellow. Thus, *C. boliviana* has strikingly profuse and anastamosing carmine striations on a white-pink petal background, whilst *C. pubiflora* is very variable in this respect, ranging from delicate pale pink petals with few flecks, to dense pink-lilac with many dark striations which may merge below. The ivory–pale yellow petals of *C. chodatii* present very few flecks. The white petals of *C. glaziovii* present variable carmine flecks or striations, whilst the whitish petals of *C. erianthos* have a conspicuous central carmine zone. The petals of our new species *C. lupuna* are a uniformly dense red, with the usual yel-
low claw, whilst those of the morphologically rather similar *C. speciosa* and *C. crispiflora* have magenta petals with sparse carmine flecks or striations. In old or badly pressed specimens, *Ceiba* flowers of diverse species appear yellowish brown with dark brown markings, and the yellow claw becomes white.

In most species, the petals are shortly sericeous pubescent externally and mostly glabrous within, although the distal inner surface may also have hairs, especially towards the margins. In the species of sect. *Campylanthera* (the *C. aesculifolia* complex, *C. schottii*) this external pubescence has a tan colour, whilst in *C. erianthos* and *C. boliviana* the petals are notably white villous-tomentose externally.

**Androecium**

The androecium in *Ceiba* species provides important characters. Superficially, in most species, seemingly five stamens are united by their filaments to form a lower tube, which surrounds the pistil, and which then splits to give five separate filaments and anthers. The situation is structurally much more complex, and reflects the amazing diversity of stamen filament-anther fission and fusion in the Malvales as partially documented in the study by Van Heel (1966).

Based on histological sections and cleared tissues (clearing the androecium with concentrated KOH-fuchsin solution, which provides translucent tissues with deeply staining veins, was particularly helpful) our interpretation of the androecium in *Ceiba* species is as follows. Two whorls with (internally) 5 and (externally) 10 filaments are present. In the lower staminal tube which is present in all species, these are represented by 15 vascular traces in five groups of three. In species of the *C. insignis* agg., which possess a distinct “corona-like” whorl of five bifid, staminal appendages, each appendage receives a curved deviation of the outer two vascular traces, which then rejoin the central traces to ascend the upper staminal tube, and enter the collar of “five” seemingly bithecate anthers. These actually derive from 15 monothecal anthers, each with the interior thecum reduced to connective tissue. In species which have five free stamen filaments above the level of the staminal appendages (or the vestiges of these), each filament presents three fused vascular traces, and an “anther” with two functional thecae, again with the central thecum reduced to connective tissue. In *C. trischistandra*, the triple nature of the staminal filaments is revealed as each “filament” finally divides to furnish three monothecate anthers. In *C. soluta* such fission extends to the level of the staminal “corona” to give 15 staminal filaments, although the actual number seems to be variable in the few specimens available.

In *C. glazioui* the staminal appendages are not bifid, whilst in *C. erianthos* they are represented merely by a hairy swelling, as Santos (1964) noted and illustrated. In other species of sect. *Ceiba*, the staminal appendages may form a disc-like structure (*C. jasminodora*), or a truncate ledge (*C. pentandra*). In species of sect. *Campylanthera*, the staminal appendages in *C. aesculifolia* and *C. soluta* lack a vascular loop, and are absent (or represented by an “articulation”) in *C. schottii*.

**Fruit and seeds**

In all species the fruit is a rotund to ellipsoidal, 5-valvate capsule, with a mostly smooth exterior, and in which the endocarp develops into a white cotton-fibered mass (hence common names “painera”, “pochote”) which surrounds the many seeds. When the capsule valves fall away, this cottony kapok aids in the wind dispersal of the entangled seeds. Seeds are round to pyriform to reniform, usually largish, 5-10 mm, with testa dark brown to black, with matt to smooth surface.

**Cytology**

Baker & Baker (1968) reported chromosome numbers for diverse genera of the Bombacaceae, including *Chorisia speciosa* (= *Ceiba speciosa*) with 2n = 72, and 26 counts for
**REPRODUCTIVE BIOLOGY**

Most Ceiba species have nocturnal anthesis and *C. pentandra* (GRIBEL & al., 1999) and *C. erianthos* (observations by J. Semir) are known to be bat-pollinated. This also likely to be the case in *C. glaziovii, C. boliviana, C. insignis, C. samauma, C. ventricosa*, and *C. trischistandra*, but field observations are lacking. *C. erianthos* and *C. glaziovii* have particularly copious nectar. *C. chodatii* also has crepuscular anthesis but with sparse nectar, and is probably pollinated by sphingid moths (we have seen sphingids visiting flowers of cultivated trees in Rosario, Argentina), as may be the case with *C. jasminodora* and *C. schottii. C. speciosa* (and probably *C. crispiflora*) is pollinated by diurnal butterflies which beat their wings against the anthers or stigma as they probe between the staminal appendages for nectar. Hummingbirds are frequent but ineffective visitors to this species since they do not touch the anthers/ stigma. However, *C. pubiflora*, with its resupinate anthers and somewhat more copious nectar, seems to be adapted for pollination by humming birds, which are certainly frequent visitors to its flowers. It is notable that the corona-like staminal appendages, when they occur, serve to restrict access to the nectar. Thus they are present in all moth, butterfly or hummingbird pollinated species, but absent or reduced in most, but not all, bat or potentially bat-pollinated species.

The Bombacaceae present a cluster of taxa [see Gibb & Bianchi (1999) for review] with late-acting self-incompatibility (LSI) *sensu* Seavey & Bawa (1986). In this system, selfed flowers uniformly fail to form fruits although self pollen tubes grow to the ovary and penetrate ovules. In the genus *Ceiba*, LSI has been studied in the species *C. chodatii* and *C. speciosa* (Gibbs & Bianchi, 1993) and *C. pentandra* (GRIBEL & al., 1999).

**HABITAT**

Most species of *Ceiba* are restricted to seasonally dry woodlands, including *C. erianthos*, which occurs in the coastal restinga of SE Brazil, but almost always associated with rocky outcrops, as is *C. jasminodora* in the “campos rupestres” of Minas Gerais. *C. pubiflora* seems to have a marked but not exclusive preference for calcareous soils in its distribution from Mato Grosso Sul to the caatingas of northern Minas Gerais and Bahia. However, some species, such as *C. samauma* and *C. speciosa*, seem to be able to occupy both dry seasonal forest and humid river valleys, whilst *C. pentandra* shows even greater tolerance, occurring in seasonally flooded lowland forest in Amazonia, but also in mesic habitats in Central America. This same tolerance seems to apply to *C. pentandra* in West Africa, where Baker (1965) reported it to be rare in evergreen rain forest but very common in moist, semideciduous forests, and commented: “it is a common constituent of the gallery forests which line the river banks as these lead out from the true forest into the savanna woodlands and the true savannas”. As far as we are aware, only *C. lupuna* occurs exclusively in humid forest.
TAXONOMY

Ceiba Mill., Gard. Dict. Abr. ed. 4 (1754)
Eriodendron DC., Prodr. 1: 479 (1824)
Xylon Kuntze, Revis. Gen. Pl. 1: 74 (1891)
Xylum T. Post & Kuntze, Lex. Gen. Phan., Prosp. 598 (1903)

Type: Ceiba pentandra (L.) Gaertn. (lectotype, designated by Nicolson, 1979).

Trees, in some species of considerable size, and sometimes with a ventricose trunk, both
trunk and branches often with stout aculeate
spines. Leaves alternate, compound-digitate,
with a longish petiole, with 3-5(8) leaflets;
leaflets elliptic, lanceolate, or oblanceolate,
serrate or entire, usually attenuate, acute to
acuminate, rarely obtuse; both surfaces usual-
ly glabrous, occasionally sparsely simple or
stellate hairy. Inflorescences in few-flowered
fascicles or flowers solitary, with very ca-
ducous bracts and bracteoles. Flowers 18-
145 mm, with 5 usually spreading or some-
times funnelform or campanulate petals.
Pedicels usually stout. Calyx thick-fleshy,
campanulate, opening irregularly to give 3-5
lobes, externally usually glabrous, internally
densely villous-pubescent, with dispersed
nectaries over the internal surface. Petals con-
nate to the staminal tube at the base, usually
oblong-spathulate, with entire or undulate
margin, usually mostly glabrous internally,
sparsely to densely whitish to brownish
sericeous externally, white to pinkish to ma-
genata or red, usually with the claw yellowish,
limb with inner surface frequently blotched
with carmine striations. Staminal filaments
fused to form a tube around the ovary, some-
times with a corona-like whorl of staminal
appendages. Staminal tube usually dividing
to give five free filaments; but in some species
these filaments remain fused above the stami-
nal appendages to give an upper staminal tube
(insignis agg.), whilst in two species, the five
initial filaments split to give three filaments
terminating in monothecate anthers: in
C. trichistandra this division occurs in the up-
per part of the common filament, whereas in
C. soluta it occurs just above the staminal
appendages. The ovary superior, usually pyri-
form, five loculate-carpellate, with axile pla-
centation and many ovules. Style usually
slender, white and glabrous (hairy in C. sa-
mauma), terminating in a globose somewhat
lobed stigma, which may be white to red.
Fruit an elongate capsule with the seeds em-
bedded in dense cotton-downy fibres origi-
nating from the endocarp. Seeds large, 5-
10 mm, roundish to pyriform to reniform,
dark brownish–black.

Three species occur in Mexico and Central
America, and 13 species are distributed in
South America. C. pentandra is the only
species which extends outwith South-Central
America and the Caribbean Islands, occurring
in W Africa, where it is probably native, and
also in India, SE Asia and the Pacific, to
which areas it was most likely introduced by
man.

KEY TO SPECIES OF CEIBA

1. Flowers with 10-15 free staminal filaments,
variously united below .................................. 2
   - Flowers with 5 free staminal filaments, united
   below, or all filaments fused for their entire
   length (occasionally some fission terminally) to
   form a tube ..................................................... 3

2. Calyx crimson, with whitish hairs; short stami-
nal tube giving rise initially to 5 filaments,
which further subdivide to give 3 free filaments
 ..................................................... 12. C. trischistandra
   - Calyx greenish brown, with orange-brown
   hairs; short staminal tube bearing 10-15 slender
   staminal filaments .................................. 17. C. soluta

3. Lower staminal tube lacking appendages ...... 4
   - Lower staminal tube with appendages in the
   form of a disc, or 5 very hairy linear scales, or a
   corona-like whorl of 5 (usually bifid) short ap-
   pendages ................................................ 7

4. Petals less than 50 mm; staminal column 5-
14 mm .................................. 13. C. pentandra
   - Petals more than 65-220 mm; staminal column
10-100 mm ..................................................... 5

5. Anthers markedly anfractuose; style densely
hairy as it emerges from staminal tube, becom-
ing glabrous above .......... 14. C. samauma
   - Anthers sinuous with undulate thecae; style en-
tirely glabrous ................................................ 6
6. Petals 65-90 × 18-22 mm, broadly spatulate, with dense, white-lanate exterior; lower staminal column 10-20 mm, rather swollen below the 5 free filaments, densely hairy .................

8. Flower with fused staminal filaments which form a tube terminating in a collar of 5 anthers (occasionally some terminal fission of this tube) ............ C. insignis agg. (key at page 267)

9. Lower staminal tube bearing 5 densely hairy scale-like appendages; petals usually markedly reflexed ......................... 16. C. aesculifolia

10. Flower more or less campanulate with petals held erect; petals whitish coloured with dense dark red reticulating striations; stamen filaments deep red, anthers anfractuose; stigma deep red ................... 8. C. boliviana

11. Petals pale pinkish, or pink-lilac, distally with sparse to marked dark carmine coloured striations which may fuse below; stamens resupinate; with diurnal flowering .................. 7. C. pubiflora

TYPE: lectotype, here designated, C. pubiflora (A. St.-Hil.) K. Schum.

Pollen peritreme, spherical to oblate-spheroidal with medium to high, simple or branched bacula supporting sinuous muri. Staminal appendages, when present, vascularized.

**Ceiba insignis** aggregate species

Trees c. 12 m or more with sometimes swollen, usually aculeate trunk. Leaves 5-7 foliolate, petiole 35-80 mm long; leaflets 35-110 × 17-50 mm, oblanceolate or elliptical, with apex acuminate, margin entire or variously denticulate, glabrous, petiololes 5-15 mm long. Inflorescence essentially corymbose but with flowers borne in fascicles, or pairs, or singly towards the ends of young branches. Pedicels 5-20 mm long. Calyx 20-30 × 17-25 mm, campanulate, lobed, glabrous externally, usually densely villous within. Petals 60-130 × 6-27 mm, narrowly spatulate to narrowly oblong, usually softly hairy externally, glabrous or nearly so internally, whitish or flushed pink, or magenta to deep red distally, often with darker flecks or striations, and yellow towards the base. Stamens with a basal tube which surrounds the ovary, 10-15 mm long, with a 5 lobed staminal appendages which close the ‘throat’ of the corolla, the lobes bifid, glabrous to densely hairy, and then a staminal tube extending some 40-100 mm, bearing a collar of 5, 2-thecate, sinuous, usually pale yellowish anthers (except C. pubiflora which has 5 free filaments). Ovary superior to slightly inferior, subglobose to pyriform, glabrous, with style usually exerted by some 3-5 mm (occasionally up to 15 mm) above the anthers and with a white or reddish, globose stigma. Fruit and ellipsoid-pyriform capsule, c. 10-15 × 8-10 cm.

We group the following sequence of seven species in an aggregate species sensu Heywood (1963): ‘... the aggregate is a device employed to group together for convenience a number of species (binomials). The component binomials are in taxonomic terms close-
ly related and difficult to discriminate. Their distinguishing characters, although less pronounced and perhaps fewer in number than those which serve to distinguish between other species, are, however, constant and the species appear to be effectively isolated from one another. With one exception, the component species of the *C. insignis* agg. are characterized by the presence of an entire staminal tube which terminates in a collar of anthers.

Species of this aggregate extend in a more or less U-shaped arc of semi-deciduous vegetation from NE–SE–SW Brazil, Paraguay, the Argentine piedmont area as far south as Tucumán, Bolivia, and NW Peru to S Ecuador. This kind of distribution parallels that of the “Pleistocene Arc” of seasonal woodlands as defined by Prado & Gibb (1993), Pennington & al. (2000), but with the complication that whilst most of the species of the *C. insignis* agg., e.g. *C. insignis* s.s., *C. chodatii*, *C. incana* and *C. pubiflora*, and *C. ventricosa* are certainly restricted to seasonally dry habitats, the widely distributed *C. speciosa* and also *C. lupuna*, can be found in moist riverine forest in Peru and in W Brazil (Acre, Rondônia).

One species referred to this aggregate, *C. pubiflora*, has free stamens. This species occurs from Paraguay to centre-west-NE Brazil (Mato Grosso, Goiás to Minas Gerais and Bahia), especially on calcareous soils. *Ceiba pubiflora* shares the prominent coronal-like staminal appendages of the *C. insignis* agg. but either immediately, or some 5-10 mm above the corona, five separate stamens diverge. It is likely that all members of the *C. insignis* aggregate are interfertile. Certainly *C. speciosa* × *C. chodatii* form fertile hybrids, some of which are commonly cultivated as street trees in Argentina, and *C. pubiflora* × *C. speciosa* can also cross. Moreover, occasional specimens of *C. speciosa* and *C. chodatii* are encountered with flowers with the upper staminal tube partially split to give five filaments with separate anthers. However, it is notable that the component species diverge in timing of anthesis, and as a consequence, pollinator type.

**KEY TO SPECIES OF **Ceiba insignis agg.**

1. Stamens with 5 free, usually resupinate filaments arising directly from, or some 5-10 mm above, the staminal appendages:................. 2
   - Stamens above the staminal appendages united into a tube which has a collar of 5 sinuous, anthers (occasionally this tube has some fusion distally and so anthers free) .................. 2
2. Petals ivory to pale yellow, whitish, or white suffused pink: .......................................................... 3
   - Petals deep pink-magenta, or red, at least distally ............................................................... 5
3. Flower rather funnel-form with ivory-pale yellow petals held erect, staminal appendages whitish, glabrous ......................... 6. *C. chodatii*
   - Flower rather stellate with the white to white-pinkish petals spreading, staminal appendages usually hairy ...................... 4
4. Petals narrowly spathulate or oblong, with only slightly undulate margin, white to suffused pink distally, yellowish towards the base; staminal tube below the staminal appendages pale and glabrous, staminal appendages white or reddish, glabrous to sparsely hairy. 1. *C. insignis*
   - Petals narrowly oblong with markedly undulate-crespate margin, whitish with dark reddish flecks distally, these merging towards the base; lower staminal tube reddish and cinerous sericeous, staminal appendages dark red, densely hairy ......................... 5. *C. ventricosa*
5. Petals uniformly deep red distally, pale yellow at the base .................................................. 2. *C. lupuna*
   - Petals deep pink-magenta distally, with many dark red striations mid-length, pale yellow towards the base ...................... 6
6. Staminal tube below the staminal appendages glabrous; petals rather spathulate or broadly oblong, usually more than 15 mm wide, margin only slightly undulate .................. 3. *C. speciosa*
   - Staminal tube below the staminal appendages serrate; petals narrowly oblong, usually less than 15 mm wide, with markedly undulate-crespate margin ......................... 4. *C. crispiflora*


Ind. loc. : “Crescit ad ripam flumis Amazonum prope Tomependa, Chamaya etc.”
Type: Peru? specimen without locality, Humboldt & Bonpland s.n. (lectotype, here designated, P!)


Ind. loc.: “Peru. Cajamarca: near Jaén, in fruticetis et fruticibus peraltis arboribusque parvis compositis in altitudine 900 msn”

Type: Peru. Cajamarca, Jaén, IV-1912, Weberbauer 6195 (lectotype, here designated, US-digital image!)

Trees c. 10 m, usually with aculate trunk. Leaflets somewhat coriaceous, entire or dentate. Pedicels 15-25 mm long. Petals 90-120 × 22-25 mm, spathulate to narrowly oblong, with only slightly undulate margin, white sericeous to villous externally, glabrous internally, white to pale pink, sometimes with occasional dark reddish striations, with a yellowish zone from mid-length to the base. Staminal tube glabrous below the appendages; the appendage lobes whitish or orange-red, glabrous to sparsely hairy, upper staminal tube glabrous, flushed pink, sometimes splitting distally to give 5 short filaments. Stigma red. Fruit ellipsoidal or pyriform capsule.

Flowering May-July(October). Dry valleys with semi-deciduous woodland. S Ecuador (Loja) and N Peru (Amazonas, Cajamarca, Piura, and San Martín) (fig. 1).

This species has a problematical history, not least because in 1900 Hicken identified trees of C. chodatii cultivated at La Recoleta in Buenos Aires as Chorisia insignis HBK, and largely as a consequence, the name C. insignis has been widely given to specimens collected in Argentina, Bolivia and Peru as well as to cultivated trees, giving rise to considerable taxonomic confusion. We here identify C. insignis s.s. with a white-pinkish flowered species of dry, deciduous woodland in NW Peru-Ecuador. We base our view on the following considerations.

Rather than cite type material, Kunth (1822) simply gave a terse summary of the distribution of known localities and collections: “Crescit ad ripam flumis Amazonum prope Tomependa, Chamaya etc”. Chamaya, (5°44'S, 78°39'W) in N Peru, is near the junction of the river Chamaya with the river Marañón, somewhat between Jaén and Pucara, the latter both dry woodland areas. Tomependa has never been precisely located, but SANDWITH (1968), in his account of the Humboldt and Bonpland travel itinaries, listed it in their sequence of travels between Paso de Pucara–Las Huertas–Passo de Matara–Passo de Cavico–Sonanga–Chamaya–Choros (5°52'S, 78°40’W)–Tomependa–Río Chinchipe to Río Marañón.

In the Humboldt and Bonpland collections at P there is only one specimen referable to C. insignis which surprisingly does not have a locality but simply bears (apparently in Kunth’s hand by comparison with examples in BURDET, 1976, p. 145) the name “Chorisia insignis”. It is very likely that this specimen in Paris, which has the flower dissected with calyx, staminal tube and individual petals displayed, as well as leaves, provided the basis for the illustration of Chorisia insignis of the protologue, and we therefore have no hesitation in choosing it as the lectotype of C. insignis. However, from the reference to a fruit in his description, Kunth evidently also had access to either additional specimens, or to Bonpland’s notes on this taxon.

Based on specimens from the the Chama-Tomependa area, C. insignis is a species of semi-deciduous woodlands in dry valleys which has whitish-pink flushed flowers. SCHUMANN (1886), in his description of Chorisia insignis in Martius’ Flora Brasiliensis, repeated the Chamaya and Tomependa localities but added a Spruce collection from Tarapoto, some 250 km to the East, in San Martín province. Since duplicates of this collection were widely distributed, it comprises an important source for C. insignis s.s. but cannot of course be considered as type material. Despite its location in the upper valley of the Río Huallaga, the Tarapoto area is a noted enclave of savanna vegetation where even some Brazilian cerrado species are found (pers. comm., T.R. Pennington) so that it is perhaps not surprising that C. insignis, essentially a dry woodland species of the W side of the
Marañón river system, also occurs there. The Spruce 3928 Tarapoto specimen at K has a more extensive label than most duplicates of this collection, and states “flores rosee” and that the plants occurred in “praeraptis saxosis”. Although some labels refer to the flowers of *C. insignis* from Ecuador and Peru as simply ‘white’, the photos of this species by Lewis (collection Lewis & al. 3308, near Catamayo, Ecuador), and also that of Gentry (Gentry & al. 22688 near Pucara, in NW Peru) show petals with a distinct pinkish tinge. There is no great problem therefore in including the Spruce Tarapoto collection in *C. insignis* s.s., despite its occurrence at a site well to the E of the Marañón river, and reference to ‘pink’ flowers.

In Ravena’s (1998) key to five species of *Ceiba*, *C. insignis* was keyed out together with *C. speciosa* as: “Corolla pink to bright purple-pink”, and then distinguished from *C. speciosa* with a series of vegetative charac-
ters ranging from mature tree height 45 m (in-signis) vs. 25 m (speciosa), and “thorns not perfectly conical, oblique or curved, 30-55 mm, leaf margins repand, or teeth diminutive, less than 1 mm. Anthers 4-5 mm” (insignis) vs. “thorns perpendicular to bark surface, perfectly conical, 8-15 mm. Leaflets coarsely dentate, teeth oblique 1-3 mm. Anthers 7-8 mm.” (speciosa). This interpretation of C. insignis is obviously at variance with that outlined above. However, since no exsiccatas were cited it is difficult to understand Ravenna’s concept of this species.

Chorisia integrifolia is another problematical taxon. Ulbrich described his species as having ‘white-pinkish flowers’, and the type specimen is a Weberbauer collection from near Jaén (Catamarca), which is close to the type locality of C. insignis at Chamaya, and other localities of ‘white-pinkish flowered’ C. insignis collections at Pucara by Gentry. Ulbrich’s insistence on the diagnostic entire-margined leaves for his C. integrifolia is unhelpful since entire to minutely denticulate margined leaves are common in C. insignis s.s. and other taxa of this aggregate. We therefore refer Chorisia integrifolia to C. insignis s.s.

RAVENNA (1998) reported seeing trees of C. integrifolia between Pucara and Jaén but was apparently unaware that this locality is close to the type locality of C. insignis, or that this latter species is also characteristic of the “dry montane plains of the province of Jaen” to which he refers C. integrifolia. Unfortunately, RAVENNA (1998) did not include C. integrifolia in his key to species of the C. insignis group, so that his interpretation of this species is again uncertain.

Ulbrich also subsequently identified a collection by Raimondi from Junín: Chanchamayo to his C. integrifolia. Whilst this specimen certainly has entire-margined leaves, the narrow petals with undulate margins are similar to those of the red-flowered C. lupuna (see below), and the locality on the Rio Mantaro is also in accord with this. We therefore refer this Raimondi specimen to C. lupuna.

It seems likely that C. insignis flowers open at dusk (various photos show pollen dusted on the inner surface of the petals indicating pollen liberation before petal opening) and if so with crepuscular or nocturnal pollinators, but no collection details or field observations are available.

Examined specimens


2. Ceiba lupuna P.E. Gibbs & Semir, sp. nov.

Type: Peru. San Martín, Mariscal Cáceres, Uchiza, 28-III-1972, J.V. Schunke 5326 (holotype, MO!; isotypes, F! G!, NY!, P!, WIS!)

Species quoad characteres praecipuos non dissimiátis quidem ab speciebus gregis “Ceiba insignis agg.” —praesertimque speciebus C. crispifolia et C. ventricosa, petalis angustissimis atque margine undulatis insuperque tubo inferiore staminali piloso aliquando— sed ab speciebus omnibus generis Ceiba floribus aperte rubris modo mirabili differens!

Trees up to 50 m, canopy emergents, trunk and branches usually with blackish aculeate spines. Leaflets somewhat coriaceous, margin entire or denticulate. Pedicels 15-25 mm long, slender. Petals 50-100 x 14-18 mm, narrowly oblong, with markedly undulate margin, deep red distally, pale yellow, speckled red towards the base, externally sericous, drying brownish with whitish pubescence. Staminal tube below the appendages 10-14 mm, glabrous or sparsely sericeous, at least along
the nerves, appendix lobes dark red, densely hairy. Fruit not seen.

Flowering May-June. Humid forest valleys. Gentry (in litt.) indicated that this red-flowered taxon is restricted to nutrient poor soils (see below). Central and E Peru, SE Ecuador (Napo), and W Brazil (Acre, Rondônia) (fig. 1).

In an exchange of letters, the late Al Gentry made the following comments concerning the red-flowered Chorisia which we have here described as Ceiba lapuna: “My big problem concerns what name to put on the red-flowered Chorisia that is common around Pucallpa in Amazonian Peru. We have two species of Chorisia growing sympatrically in this area. One has bright magenta flowers with rather sericeous petals and I am assuming this is correctly called C. insignis HBK [C. speciosa on our interpretation]. The other has bright red flowers, black spines on the trunk and has petals when dried more wooly-tan-nish pubescent outside". Another letter commented: “I recall once flying from Puerto Bermudez to Pucallpa and in the area near Puerto Bermudez seeing both red and pink Chorisia. Nearer Pucallpa there was only the red flowered ones”. And with regard to ecology of these taxa Gentry noted: “My guess is that the red and pink flowered species sort themselves out according to soil fertility more than precipitation. The pink flowered form grows in rich soil forests and the red flowered form in more highly leached forests on lateritic soils”. This species, with deep red flowers, is most likely to have diurnal anthesis but pollinator type unknown.

Examined specimens


Chorisia speciosa A. St.-Hil. in A. St.-Hil., A. Juss. & Cambess., Pl. Usuel. Bras., tab. 43 (1827)

Ind. loc.: “In sylvis primaevis provinciarum Rio de Janeiro et Minas Gerais haud infrequens, visa quoque in campis juxta urbem Barbacena, nec nunquam etiam prope donos sativa”

Type: Brazil. Province de Minas Gerais, Saint Hilaire s.n. (lectotype, here designated, P!)

Trees 10-20 m, usually with somewhat swollen, aculeate trunk. Leaflets rather char-taceous, usually serrate. Pedicels 10-15 mm long rather stout. Petals 70-105 × 25-35 mm, spatulate to oblong, externally sericeous, internally glabrous, margin somewhat undulate, dark pink-magenta distally, usually with dark striations midlength, base white to yellow. Staminal tube to the appendages glabrous, appendage lobes usually dark reddish, densely cinereous hairy, sometimes pinkish and glabrous; upper staminal tube white flushed pink, sometimes splitting distally to give 5 short filaments. Stigma white or pinkish. Fruit an ellipsoidal to pyriform capsule, c. 12-18 × 9-12 cm.

Flowering January-May. Dry semi-deciduous woodland and wet forest. An extensive area from NE and SE Brazil and also W Brazil, N Argentina, Paraguay, Bolivia, S and C Peru (fig. 1). This species is also widely cultivated in Argentina and Brazil as an ornamental.

Illustrations. Santos (1964: 168 tab. 3),

Flowers begin to open at sunrise, and in SE Brazil the early arrival of many honey bees often results in the anthers being cleaned out of pollen by around 10 am and so the flowers are rendered sterile. The effective pollinators of *C. speciosa* (Roths. & Jord.) include butterflies, bees, and hummingbirds. Most of these butterflies, e.g. *Battus polydamas* (Roths. & Jord.), *Papilio anchiadise* (Roths. & Jord.), *P. thoa* (Roths. & Jord.), continue to flutter their wings as they probe the flower, such that these contact either the collar of anthers or stigma. *C. speciosa* flowers are also visited by humming birds, which mostly fail to contact the anthers, and nocturnal visits by large *Phyllostomatus hastatus* bats have also been reported by TADDEI (1977).

Examined specimens


Blanca, 10-IV-1933, M. Koscinski 6354 (SP). Serra de Caracol, 10-II-1874, G. Mosén 1123 (S).


Illustrations. SANTOS (1967: 9 fig. 2), SANTOS (1969, fig. 4).


Bombax ventricosa Arruda in H. Kost., Trav. Brazil: 489 (1816), nom. nud.


Very similar to C. speciosa in most features, but the narrow, markedly undulate margined petals, and pubescent lower staminal tube, resemble C. ventricosa (see below). Apparently restricted to Atlantic forest and restinga around Rio de Janeiro and so partially sympatric with C. speciosa. DE CANDOLLE (1824: 480) treated C. ventricosa (see below) as a synonym of C. crispiflora, which is not surprising since both species have narrow, undulate-crepeate petals. Indeed, the flowers of C. crispiflora resemble what might be expected in a hybrid between C. speciosa × C. ventricosa, but we have absolutely no evidence of such hybrid status.

Examined specimens


Type: Brazil. Bahia, inter Río das Contas et Tiquirica, fluvios prope a loco, quem Cabeça do Boi incolae vocant. Martio mense flores deiecti terram ad arboris radices tegebant. Princeps Maximim Neov.”

Type: Brazil. Bahia, inter Rio das Contas et Tiquirica, Maximillian von Wied s.n. (no original material located at BR) [Bahia, Rio Jequitinonha, Itapebi, 17-IV-1971, T.S. dos Santos 1579 (neotype, here designated, NY!; isotypes, CEPEC! UEC!)]

Type: Brazil. Bahia, Rodavia Itabuna-Ilhéus, IV-1965, Belém & Magalhães s.n. (holotype, BR; isotype, MO!)

Trees 10 m or more with swollen, aculeate trunk. Leaflets somewhat chartaceous, glabrous, usually entire, sometimes obscurely denticulate. Pedicels c. 20-30 mm long. Petals c. 60 × 8-10 mm, narrowly oblong with a markedly undulate-crespite margin, externally sericeous, internally glabrous, white to cream, with sparse dark reddish flecks distally, these merging more uniformly towards the base, becoming chocolate-brown in old flowers and dried specimens. Staminal column densely reddish-sericeous up to and including the 5 staminal appendages which are prominently bifid, then a glabrous, whitish staminal tube to the 5 sinuous anthers. Stigma somewhat 5-lobed, white. Fruit not seen.

Flowering February-April. Dry semi-deciduous woodland. Brazil (Bahia, Espírito Santo, E Minas Gerais, Pernambuco, Paraíba) (fig. 1).

Illustrations. ROBYNS (1967: 185 fig. 1).

Harley (in litt.) notes that Prince Maximilian von Wied probably travelled upstream from near Jequié, on the Rio de Contas and headed north, spending the night at the locality Cabeça de Boi (which no longer exists) and then another night near where he probably collected Chorisia ventricosa, before reaching Santa Inês on the Rio Jiquirica (= Tiquirica).

Although the natural vegetation is much devastated today, this is an area of deciduous dry forest. Since no specimen of Chorisia ventricosa has been located in the von Wied herbarium at BR, we choose as an epitype for this species dos Santos 1579.

ROBYNS (1967) described his Chorisia incana apparently unaware of the previously described Chorisia ventricosa, perhaps because this latter species was treated as a synonm of C. crispiflora by SCHUMANN (1886) in Martius’ Flora Brasiliensis. The similarity between these two species is particularly marked in herbarium specimens which have lost flower colour. Given differences in artistic style, the illustration of C. incana (ROBYNS, 1967) is remarkably similar to that of C. ventricosa in NEE & MARTIUS (1823, tab. 9).

Presumably with its pallid flowers, C. ventricosa is another species with crepuscular anthesis and nocturnal pollinators.

Examined specimens


Ind. loc.: “In campis Santa Elisa (Chaco septentrionalis), April”

Type: Paraguay. Chaco septentrionalis, in campis Santa Elisa, Rojas s.n., herb. Hassl. 2849 (lectotype, here designated, G!)

Tree c. 12 m or more with swollen, sometimes aculeate trunk. Leaflets somewhat coriaceous, denticulate. Pedicels 8-20 mm long. Petals 83-130 × 20-27 mm, usually held erect and so flower more or less funnel-form, spathulate, softly hairy externally, glabrous internally, ivory to pale yellow, occasionally with some crimson flecks. Stamens with a glabrous basal tube, 10-15 mm, staminal appendages pale white-yellow, glabrous, upper staminal tube white with a collar of 5, 2-thecate, sinuous, pale yellowish anthers, occasionally splitting distally to give 5 short filaments and separate anthers. Stigma pinkish-
red. Fruit an elongate-pyriform capsule 15-18 × 8-10 cm.

Flowering February to May. Dry, seasonal woodland. Paraguay, Bolivia and piedmont mountains of W Argentina (fig. 1).

**Illustrations:** DIGILIO & LEGNAME (1906: 76, sub C. insignis); BERNARDINI (1984: 35 fig. 10, sub C. insignis).

Cultivated trees in Campinas (Brazil) and Rosario (Argentina), the latter possibly of hybrid origin, open their flowers in the late afternoon, and it is likely that *C. chodatii*, with its erect pulilld colored petals is another species with crepuscular-nocturnal pollinators. However, given that the species has a distribution largely outwith that of flower-visiting bats, and the nectar supply is sparse, these are likely to sphingid moths.

As noted above, Hicken in 1900 identified cultivated trees of *C. chodatii* from La Recoleta, Buenos Aires as *C. insignis* Kunth, and this initiated a long period of misidentifica-

Examined specimens


7. **Ceiba pubiflora** (A. St.-Hil.) K. Schum. in Mart. (ed.), Fl. Bras. 12(3): 213 (1886)

**Eriodendron pubiflorum** A. St.-Hil., Fl. Bras. Merid. 1: 266 (1828); *Chorisia pubiflora* (A. St.-Hil.) G. Dawson, Revista Argent. Agron. 2 (1): 3 (1944)

**Ind. loc.:** “Prope praesidiolum vulgo Quartel de Texeira (Minas Novas)”

**Type:** Brazil. Minas Gerais, prope praesidiolum vulgo Quartel de Texeira, Minas Novas, Saint Hilaire s.n. (lectotype, here designated, P!)


**Ind. loc.:** “Paraguay, Cordillera de Altos”

**Type:** Paraguay. Cordillera de Altos, VIII-1902, K. Fiebrig 3 (lectotype, here designated E!; isolecotypes, F!, G!, NY photo!, MO! SI!)

**Ceiba jaibana** Ravenna, Onira 3(15): 48 (1998)

**Ind. loc.:** “Arboreal caantinga near Jaiba, mid-dle São Francisco river region, northern Minas Gerais”

**Type:** Brazil. Minas Gerais, Jaiba, 16 May 1985, Pedralli & al. s.n. (holotype, HXBH!)

Trees with sometimes ventricose, aculate trunk. Leaflets somewhat chartaceous, usually serrate. Pedicels 5-10 mm long. Petals 47-85 × 20-25 mm, initially somewhat erect, subsequently spreading, obovate-oblong, margin somewhat undulate, sericeous exter-

which may coalesce midlength. Staminal column glabrous, 10-15 mm long; staminal appendages pink-yellowish, glabrous, with five bifid lobes; above the appendages the column divides either immediately, or at c. 5-10 mm, into 5 usually strongly resupinate, white filaments which have large, sinuous anthers. Stigma white. Fruit a somewhat rotund to ellipsoidal capsule, 10-15 × 8-10 cm.

Flowering February-May. Semi-deciduous woodlands, particularly on calcareous soils. Argentina (Misiones), Paraguay, Centre-West Brazil from Corumbá to NE Minas Gerais, extending to Bahia and Espírito Santo (fig. 1).

Illustrations. Santos (1964: 169 tab. 4), Bernardini (1984: 33 fig. 9), Lorenzi (1998: 46); the photo on page 42, labelled C. boliviana, depicts a dark pink form of C. pubiflora (fig. 2).

Flowers rather variable in size, and also include forms ranging from pale pink petal with few striations, to others flushed dark pink-lilac and with distinct dark, wine-coloured striations which tend to coalesce. C. pubiflora has diurnal anthesis. Flowers on trees in Bahia, and also in cultivation in São Paulo, were observed to be frequently visited, and so probably pollinated, by humming birds.

Ravena (1998) described his C. jabiana with entire margined leaflets, and pink, 7-8 cm flowers with petals externally tomentose. The important details of the androecium were described as: “Columna staminum circ. 30 mm longa, laevis, ad basin 3 mm lata, apicem versus sensim angustiora. Filamenta oblique patentia, 13-15 mm longa. Antherae oblongae, modice flexuosae, 9-10 mm longae, 1.5-1.8 mm latae”.

We have studied the type material of C. jabiana, and also had the opportunity to study some 11 carefully annotated collections of Ceiba trees recently made at our suggestion in the Montes Claros-Jaíba-Janaúba area of Minas Gerais by E.R. Salviani and J. Dutíl. The holotype consists of a twig with a single, broken flower, with two remaining stamens. The petals are similar to those of C. pubiflora, but the basal staminal tube does not have a collar of staminal appendages as occurs in that species, but rather a swelling, thus resembling C. erianthos. The paratype has leaves with an entire margin and an open fruit with kapok. It does not convincingly appear to correspond to the same plant as the holotypus, but could well be a specimen of C. pubiflora.

It is curious, and perhaps significant, that Ravena (1998), in making his comparisons between C. jabiana and diverse Ceiba species, did not comment on the common occurrence of C. pubiflora in this caatinga-like area of N Minas Gerais. In view of the (a) general similarity of the fragmentary type material of C. jabiana to C. pubiflora, with the exception of enigmatic lack of staminal appendages in the solitary flower available; (b) also taking in to account that flower size in C. pubiflora can be variable—it is notable that flowers of the collection of this species by Pirani & al. 4276 from Porteirinha, a locality only some 30 km from the Jaiba area, are particularly small in size, but otherwise in accord with C. pubiflora, and (c) the general prevalence of C. pubiflora in the Jaiba area, we conclude that C. jabiana is in fact a synonym of C. pubiflora.

Examined specimens


Fig. 2.—Ceiba pubiflora (Pott, Cunha & Tavares 2799, E): a) branch with leaves and floral bud; b) flower at anthesis; c) androecium. *Ceiba boliviana* (Nee 34329, E): d) branch with leaves; e) flower at anthesis; f) androecium; g) stigma.
Côrrego ..., and so flower rather campanulate, broadly spathulate, externally densely sericeous-villous, internally glabrous, white-

8. Ceiba boliviana Britten & Baker f., J. Bot. 34: 175 (1896)

Ind. loc.: “Hab. Bolivia”

Type: Bolivia. Vil. Cochabambina, 1891, A.M. Bang 1154 (lectotype, here designated, BM!; isolecotypes, E!, G!, MO!, NY!, US!, W!)

C. moldoni Britten & Baker f., J. Bot. 34: 175 (1896)

Ind. loc.: “Hab. Viciniss Sorata ad radicum collis Catarguata in scopulis. Prov. Larecaja, Bolivia, G. Mandon 825; alt 2550 m.”

Type: Bolivia. Larecaja, vic. Sorata, Catarguata, 3-VI-1860, Mandon 825 (lectotype, here designated, NY!; isolecotypes, G!, P!, F photo!, MO!)

Xylon tunariensis Kuntze, Rev. Gen. Pl. 3(2): 23 (1889); Ceiba tunariensis (Kuntze) K. Schum., Just’s Bot. Jahresber. 26: 343 (1900)

Ind. loc.: “Bolivia: Tunarigebirge 1300 m”

Type: Bolivia. Tunari, vic. Catarguata, 3-VI-1860, Mandon 825 (lectotype, here designated, NY!; isolecotypes, G!, P!, F photo!, MO!)

Chorisia grandiflora Rusby, nom. nud.

Trees c. 10 m with usually with swollen, aculeate trunk. Leaves 5-7 foliolate, petioles 35-135 mm; leaflets 95-110 × 35-50 mm, ob lanceolate, denticulate, glabrous, with peti- oles 5-10 mm long. Flowers axillary, borne singly or in fascicles. Pedicels c. 12 mm long, held erect and so flower rather campanulate, broadly spatulate, externally densely sericeous-villous, internally glabrous, white-
pinkish, with many conspicuous dark red striations. Staminal column 20-40 mm up to appendages which have 5 glabrous bifid lobes, the column then continuing for some 3-15 mm before dividing to 5 red filaments which bear versatile, anfractuose anthers. Ovary pyriform, with slender style bearing the red globose stigma well beyond the anthers. Fruit an ellipsoidal to pyriform capsule, 15–18 × 10-15 cm.

Flowering (January)March-April. Woodlands in dry valleys. Bolivia and S Peru (fig. 3).

Illustrations. Fig. 2.

BRITTEN & BAKER (1896) distinguished *C. mandoni* from *C. boliviana* with the former having more leaflets (6-7 vs. 3-4) which are slightly more long petiolulate and with more marked serrations, and the staminal appendages much nearer the apex of the staminal tube rather than near the centre as in *C. boliviana*. However, in material seen by us these characters are variable, sometimes between flowers of the same specimen, and so are unreliable to delimit species. The description of

Fig. 3.—Distribution map of Ceiba boliviana and C. trischistandra.
KUNTZE’S (1898) Xylon tunariensis, particularly the anfractuose anthers and Bolivian provenance, accord with C. boliviana.

C. boliviana resembles species of the C. insignis aggregate, but the usually large, robust, campanulate flowers, with densely white-hairy, whitish-pinkish coloured petals that have prominent anastomosing dark reddish striations, and the red stamen filaments with anfractuose anthers are very distinctive.

Examined specimens


Trees usually 10-15 m, with swollen, aculeate trunk. Leaves 4-7 foliolate, petioles 60-90 mm long; leaflets 50-130 × 30-60 mm, chartaceous, elliptic-oblanceolate, denticulate, especially distally, acuminate, glabrous, with petiolules 2-4 mm long. Flowers in fascicles of three or solitary. Pedicels 6-10 mm long. Calyx 20-28 mm, campanulate, glabrous, with 3-5 lobes. Petals c. 65 × 25 mm, spatulate, spreading, white, externally villous, internally glabrous basally, hairy distally, sometimes with magenta striations towards the base. Staminal tube 10-50 mm, 5 entire appendages, all covered with dense hairs; tube continuing above the appendages for 3-20 mm and then dividing into 5 spreading, white filaments which terminate in yellow, sinuous anthers. Ovary subglobose, with the slender style terminating in a white globose stigma a little above the anthers. Fruit elongate to subglobose, with an unpleasant smell, such that bat pollination is likely, although observations are lacking.

Examined specimens


Illustrations. SANTOS (1964: 170 fig. 5), LORENZI (1998: 45).

The specimen Glaziou 18145a, cited by Kuntze for his Xylon glaziovii, was collected from a tree cultivated in Rio de Janeiro, which, according to the label, apparently originated from a tree cultivated in Ipiranga, São Paulo. Confusingly, Glaziou (1913) cited his 18145a for both C. glaziovii and C. erianthos.

Ceiba glaziovii has a crepuscular-nocturnal anthesis and the flowers possess copious nectar, such that bat pollination is likely, although observations are lacking.

10. **Ceiba erianthos** (Cav.) K. Schum. in Mart. (ed.), Fl. Bras. 12(3): 211 (1886)

*Bombax erianthos* Cav., Diss. 5: 294, tab. 152 fig. 1 (1788); *Xylon erianthos* (Cav.) Kuntze, Revis. Gen. Pl. 1: 75 (1891); *Eriodendron leiantherum* DC., Prodr. 1: 479 (1824), nom. illeg.

*Ind. loc.:* "Habitat in Brasilia prope S. Sebastianum. Commersonius reperit. V. S. unicum exemplar apud D. de Jussieu".

*Type:* Brazil. Prope S. Sebastianum, Commersonius s.n. (lectotype, here designated, P-Juss.)
Trees around 10 m with aculeate trunk and branches including young flowering branches which bear dense, small, aculeate spines. Leaves 5-7 foliulate, petioles 45-120 mm long; leaflets 34-85 × 16-40 mm, chartaceous, oblanceolate, apex acute, mucronate, glabrous petiolules c. 5 mm long. Flowers axillary, borne singly or in fascicles. Pedicels c. 20-25 mm long, stout. Calyx 20-30 × 11-14 mm, broadly campanulate, glabrous externally. Petals 65-90 × 18-22 mm, more or less spathulate, white, densely lanate-villosus externally, glabrous internally, with sparse carmine striations distally, becoming uniformly carmine towards the base. Lower staminodal tube c. 10 mm, densely hairy and with a swelling but no staminal appendages, continuing united for c. 15 mm and then dividing into 5 filaments which bear elongate sinuate anthers. Ovary subglobose, with slender mucron c. 3 mm, glabrous, with petiolules 3-5 mm long. Flowers borne with very slender mucron c. 3 mm, glabrous, with petiolules 3-5 mm long. Flowers axillary, borne singly or in fascicles. Pedicels c. 20-25 mm long, stout. Calyx 20-30 × 11-14 mm, broadly campanulate, glabrous externally. Petals 65-90 × 18-22 mm, more or less spathulate, white, densely lanate-villosus externally, glabrous internally, with sparse carmine striations distally, becoming uniformly carmine towards the base. Lower staminodal tube c. 10 mm, densely hairy and with a swelling but no staminal appendages, continuing united for c. 15 mm and then dividing into 5 filaments which bear elongate sinuate anthers. Ovary subglobose, with slender glabrous style bearing a globose, pinkish stigma c. 10 mm or more above level of anthers. Fruit rather narrowly elongate–ellipsoidal capsule, c. 14 × 5 cm.

Flowering March-July. Restinga and dry coastal forest, usually on rocky outcrops. SE and E Brazil (Rio de Janeiro, E Minas Gerais, Espírito Santo and Bahia) (fig. 4).

Illustrations. SANTOS (1969, fig. 5; LORENZI (1998: 43).

Crepuscular anthesis with bat pollination. The densely tomentose petals of this species are distinctive although some care is needed with herbarium material to distinguish from C. glaziovii.

Examined specimens


11. Ceiba jasminodora (A. St.-Hil.) K. Schum. in Mart. (ed.), Fl. Bras. 12: 213 (1886)

Eriodendron jasminodorum A. St.-Hil., Fl. Bras. Merid. 1: 265, tab. 52 (1828)

Ind. loc.: “Minas Gerais: Quartel de San Miguel (Minas Novas)”

Type: Brazil. Minas Gerais, Quartel de San Miguel, Minas Novas. Saint Hilaire s.n. (lectotype, here designated, P!)

Ceiba sipolisi K. Schum. & Schwacke, Bot. Jahrb. Syst. 25, Beibl. 60: 16 (1898)

Ind. loc.: “In Brasiliae civit. Minas Gerais, ad Biribiry prope Diamantina, ab Abbé Sipolisi detecta. Schwacke 8324; Glaziou 18893 et 20206.”

Type: Brazil. Minas Gerais, Glaziou 18893 (lectotype, here designated, P!)

Usually small trees 1-2 m, but around 4 m in cultivation, with aculeate branches. Leaves 3-foliolate, petioles 20-45 mm long; leaflets 55-120 × 36-60 mm, ovate to broadly lanceolate, entire, coriaceous, acute or somewhat rounded, with very slender mucron c. 3 mm, glabrous, with petiolules 3-5 mm long. Flowers borne
Fig. 5.–Ceiba jasminodora (Semir 10929, UEC): a) branch with leaves; b) flower at anthesis; c) androecium. C. samau-
ma (Nee 33868, E): d) branch with leaves; e) androecium; f) detail of median zone of staminal tube; g) stigma.
singly in the axils of leaves. Pedicels 10 mm long, slender. Calyx c. 8 × 6 mm, campanulate, glabrous-puberulent externally. Petals 18-25 × 7 mm, cream, markedly reflexed. Staminal column 6-7 mm, glabrous, with appendages in the form of a sparsely hairy disc which is bordered by dense fringe of hairs; 5 free staminal filaments c. 8-12 mm, bearing small (c. 2.5 mm), anfractuose anthers. Ovary pyriform, with a slender style bearing a white globose stigma at the level of the anthers. Fruit an ellipsoidal capsule c. 8 × 5 cm.

Flowering April-July. Campo rupestre (rocky upland vegetation). Brazil, endemic to the southern Serra de Espinhaço and associated uplands in Minas Gerais (fig. 4).

Illustrations. SANTOS (1964, p. 171, Fig. 6, sub C. sipolisii) (fig. 5).

The small cream flowers of this species may open at dusk, and so probably with moth pollination.

Examined specimens


Ind loc.: “Peru. Garden at Lima (Wilkes Expedition)”

Type: Peru. Cultivated tree in Lima, Wilkes s.n. (lectotype, here designated, US digital image!)

Trees 15-30 m with aculeate trunk. Leaves 5-7 foliolate, petioles 100-180 mm long; leaflets 55-125 × 30-55 mm, coriaceous, broadly oblanceolate to obovate, entire or obscurely denticulate, acute, glabrous or with sparse appressed hairs along midrib extending to the lamina, with petiololes 2-3 mm long. Flowers axillary, solitary or fascicles of 2-3. Pedicels 10-30 mm long. Calyx 23-30 × 20-26 mm, broadly campanulate, four lobed, glabrous or finely velutinous, crimson. Petals c. 45-60 × 23 mm, narrowly obovate to spatulate, densely tomentose externally except at the margins, internally mostly glabrous, white, externally tinged green, somewhat reflexed at anthesis. Stamens arising from a short c. 5 mm hairy collar, initially as 5 filaments, but each splitting for the distal 15 mm into 3 short filaments which terminate in versatile, monocotyle, anfractuose anthers. Ovary pyriform, with style bearing the stigma usually above the level of the anthers. Fruit elongate-ellipsoidal capsule c. 12 × 8 cm.

Flowering April-July. Dry valleys of Pacific coast. S Ecuador and N Peru (fig. 3).

A very striking species with its red calyx, densely white tomentose petals, and further fission of the five staminal filaments. Curiously the original collection of this species was from a cultivated tree in Lima city, and its transference to Ceiba by Bakhuizen Van Den Brink (1924) was also based on flowers from cultivated trees in Java (Indonesia). The species was still unknown in its natural habitat when Macbride (1956), in the Flora of Peru, noted: “Type from a garden in Lima; also in Java, country of origin unknown.” Ceiba trischistandra is another species presumably with crepuscular anthesis and bat pollination.

Examined specimens

ECUADOR. GUAYAS: Capara, 21 km Guayaquil to Dante, C.H. & P.M. Dodson 11322 (MO). Esterosalado, near bridge on highway to Salinas, 12-VI-1955, E. As-
Ceiba pentandra (L.) Gaertn., Fruct. Sem. Pl. 2: 244, t. 133 fig. 1 (1791)

Bombax pentandrum L., Sp. Pl.: 511 (1753);

Ind. loc.: “Habitat in Indiis”
Type: lectotype, designated by NICOLSON (1979), in Rheede, Hort. Malab. 3, tab. 50 (1682)

Bombax mompoxense Kunth in Humb., Bonpl. & Kunth, Nov. Gen. Sp. 5: 300 (1822)

Ind. loc.: “Crescit ad ripam fluminis Magdaleneae, prope Mompax, Nova granatensi-um, alt. 70 hex.”
Type: Colombia. without locality, Humboldt & Bonpland s.n. (lectotype, here designated, P!)


Ind. loc.: “Crescit prope Cumana (Nova An-dalusia)”
Type: Venezuela. Cumaná [added later by another hand], Humboldt & Bonpland s.n. (lectotype, here designated, P!)

Tall emergent trees up to 50 m or more, trunk usually aculeate, sometimes with prominent buttresses. Leaves 5-8 foliolate, petiole c. 120-150 mm long; leaflets 110-200 × 25-50 mm, narrowly elliptical to oblanceolate, base cuneate to somewhat truncate, apex acuminate, margin entire or obscurely dentic-ulate, glabrous, petiolule 5-30 mm long. Flowers fasciculate on the stems. Pedicel c. 20 mm long. Calyx 12-15 × 11-13 mm, campanulate, glabrous. Petals 22-46 × 6-13 mm, white or pinkish, externally densely sericeous sometimes with brownish hairs, sparsely so at the overlapping margins. Stami-nal tube variable: either c. 3.5 mm, with an abrupt, truncate termination, and then with 5 free white or markedly pinkish filaments arising directly or nearly so, or tube tapering for 5-14 mm before splitting into 5 filaments, with no staminodial appendages; anthers small, markedly anfractuose. Ovary pyriform with stigma usually exerted above the an-thers. Fruit ellipsoidal to pyriform capsule 15-18 × 8-10 cm.

Flowering August to September. Distribution effectively pan-tropical but almost cer-tainly introduced in Asia and the Pacific, although probably native, at least in part, in W Africa (cf. BAKER, 1965). We have not at-tempted to study this species in any detail out-with the Americas (fig. 6).

Illustrations. ADAMS (1972: 151, fig. 56); LORENZI (1992: 60).

NICOLSON (1979) provided an extensive commentary on the typification of the genera Bombax, Ceiba and Cochlospermum. He con-cluded that Bombax pentandrum L., which was based on a mixture of (mostly) asiatic but also some New World elements, must be typified by one of the illustrations in Rheede Hort. Malab., and lectotypified this species with figure 50 in this work. The illustration proposed by NICOLSON (1979) clearly depicts flowers of C. pentandra, and a plant with nar-rowly elliptical leaflets, but most leaves have eight (or more) leaflets instead of the 5-7 common in this species.

BAKHUIZEN (1924) provided a detailed synonymy for Ceiba pentandra (L.) Gaertn., and he distinguished two varieties, var. caribaea (DC) Bakh., which included the New World and African forms, and var. indi-ca (DC) Bakh. (= var. pentandra) for the asi-atic plants. However, BAKER (1965) pointed out that most authors who recognize infra-
specific, or even specific, variants for *C. pentandra*, distinguish between the New World and African forms. Both BAKHUIZEN (1924) and BAKER (1965), on the basis of their detailed studies of this taxon, concluded that *C. pentandra* should be recognized as a single rather polymorphic species, a view which we adopt here.

In Amazonian Brazil, *C. pentandra* often occurs as a tall emergent tree of *varzea* vegetation, although it also thrives (sometimes almost certainly as planted specimens) in seasonally dry areas in Central America. This ability to grow both in riverine flood plain conditions and also in mesic, seasonally dry areas is found in some other species of diverse families, e.g. *Triplaris gardneriana* Wedd. (Polygonaceae), *Pachira aquatica* (Bombacaceae) [J. Ratter, pers. comm.].

Even as represented in the in the New World, *C. pentandra* is another very variable *Ceiba* species, possibly with distinct infraspe-

![Fig. 6.–Distribution map of *Ceiba pentandra* (New World only).](image-url)
cific taxa. Plants with ‘typical’ leaves, i.e. narrowly oblong to narrowly elliptical, with distinct petiolules c. 10 mm, which correspond to Bombax cumanense (represented by a sterile specimen in the Humboldt & Bonpland herbarium at P), and which occur in Venezuela, and the Caribbean (e.g. Zanoni & al. 10817 from the Dominican Republic) look rather different from others with oblongate leaves which taper to short, 2-5 mm petiolules, and which correspond to Bombax mopoxense (again represented by a sterile Humboldt & Bonpland specimen at P) and characterised by, e.g. Gentry & Rentería 24534 from the Chocó in Colombia.

And there are also striking differences in petal size and colour (white to distinctly pink), and the size and form of the staminal tube, and whether the free filaments are white or markedly pink. Two kinds of lower staminal tube are found: one has the tube around 6 mm and tapering to the level where the 5 free filaments arise. Examples occur in both S America and the Caribbean, e.g. Little 9431 (Colombia) and Bodim 8005 (Puerto Rico). The other has a much shorter tube, around 2-3 mm which terminates abruptly to give a truncate ledge from which the free filaments arise. This form is mainly restricted to S America, e.g. Froes 1997 (Maranhão, Brazil) and Krukoff 5646 (Acre, Brazil). However, some specimens, e.g. Zanoni 10817 (Dominican Republic) and Hermans 700 (Cuba) combine these features with a short truncate tube from which arises a short tapering tube which then gives rise to the 5 free stamens.

Given the general lack of specimens with both leaves and flowers, and the apparent absence of consistent geographical correlation with e.g. flower size and length of staminal tube, and also recognizing the long anthropomorphic interaction with this species, which we prefer to at this time to maintain a single variable species.

Ceiba pentandra is a species with nocturnal anthesis, copious nectar, and bat pollination. In the Manaus area of central Amazonian Brazil some four species of bats were observed to visit this species (see Gribel, Gribel & al., 1999). In this area, flowers also have diverse diurnal morning visitors (birds, monkeys) seeking residual nectar, but since the styles abscise by 10 am, it is the nocturnal pollinators which produce fruits. Baker & Harris (1964) also reported bat pollination for C. pentandra in W Africa. The nocturnal anthesis, and the imposing height of the trees, means that most herbarium specimens consist of old flowers that have fallen to the ground.

**Examined specimens**

**CENTRAL AMERICA**


COSTA RICA. Guanacaste, Paso Temisque, 8-VIII-1932, H.E. Stork 4011 (NY).

EL SALVADOR. La Libertad, coast road W of [illegible], 28-I-1959, P.H. Allen 7203 (LL).


**Caribbean Islands**


Ind. loc.: “Habitat in provincia Brasiliae Goyaz ad Porto Imperial.”

Type: Brazil. Goyaz, Porto Imperial, Burchell 8514 (lectotype, here designated, NY! F-photo!)

Trees 15 m or more, branches with broad-based spines but usually relatively few on trunk which may be buttressed at the base. Leaves 5 foliolate, petiole c. 50-95 mm long; leaflets 33-120 × 28-55 mm, elliptical-oblong-oblanceolate, apex acuminate, base cuneate, margin entire, glabrous, petiolule 5-7 mm long. Flowers axillary, borne singly or in fascicles, rather funnelform. Pedicel c. 15 mm long, stout. Calyx 43-67 × 17-25 mm, cylindrical-funnelform, with 5 conspicuous teeth up to 9 mm, glabrous externally, densely villous within. Petals 100-220 × 17-22 mm, oblong-spathulate, whitish but with dense
golden brown long sericeous-villous indumentum externally, internally uniformly short sericeous. Staminal tube ... style bearing globose stigma at about same level as anthers. Fruit elongate to ellipsoidal capsule c. 10 × 5 cm.

Flowering December-March (May). Humid and riverine forest. Extending from Bolivia and Peru to Amazonian Brazil (fig. 7).

Illustrations. LORENZI (1998: 44) (fig. 5).

This is a widely distributed and probably under collected species. Flowers have crepuscular anthesis and presumably bat pollinators.

Examined specimens


Examined specimens


Ind. loc.: “Hab. Merida, Yucatan, Schott”

Type: Mexico. Yucatán, Mérida, Ind. loc.: Ceiba annua L. var. mexicana (lectotype, here designated, BM!)

Trees c. 8 m with aculeate trunk and branch-es, spines on younger branches c. 0.5 mm, black, only slightly curved. Leaves 3-7 foli-o-late, petiole c. 60 mm long; leaflets 50-100 × 19-30 mm, entire, coriaceous, ob lanceolate to elliptical, acute, with a small mucron, glabrous, with petiolules 6-10 mm long. Flowers axillary, borne singly or in fascicles. Pedicels 4 mm long or less, stout. Calyx 25-40 × 8-10 mm, rather cylindrical (c. 3× longer than broad), glabrous. Petals 170-190 × c. 15 mm, narrowly oblance, white, densely short hirsute externally, scabrous-glabrous internally. Staminal tube 80-100 mm, long and slender, bearing white silky hairs which are prominent in fresh flowers but less evident in dried material, with no appendages and scarcely inflated below division into 5, c. 70 mm filaments, which bear versatile, non-anfractuose anthers. Ovary pyriform with slender glabrous, style bearing globose stigma at about same level as anthers. Fruit elongate to ellipsoidal capsule c. 10 × 5 cm.
Flowering (June) August-February. Dry woodlands. SW Mexico, Guatemala (fig. 8).

Illustrations. Fig. 9.

A striking species with distinctive entire, mucronate leaflets and cylindrical calyx. Again crepuscular or nocturnal anthesis is likely, and since the petals are held erect, rather than reflexed as in *C. aesculifolia*, perhaps sphingids are the pollinators.

Examined specimens


16. **Ceiba aesculifolia** (Kunth) Britten & Baker, J. Bot. 34: 175 (1896)


*Eriodendron aesculifolium* (Kunth) DC., Prodr.: 479 (1824)

*Bombax axillare* Moç. & Sessé ex DC., Prodr.: 479 (1824), nom. nud.

Ind. loc.: “Crescit prope Campeche, ad litus Nova Hispaniae”

Type: Mexico. Campeche, Humboldt & Bonpland s.n. (lectotype, here designated, P!)

Tree 8-10 m with aculeate trunk. Leaves 5-7 foliolate, petiole 20-120 mm long; leaflets 30-100 × 18-40 mm, elliptical to narrowly ob lanceolate or obovate, apex acuminate, margin denticulate to serrate, glabrescent or uniformly finely hairy with stellate and simple hairs, or hairs restricted to nerves, peti olule 3-12 mm long. Flowers usually borne
singly, petals markedly reflexed. Pedicels 10-20 mm long, stout. Calyx 17-45 × 15-30 mm, funnelform to broadly campanulate, 4-5 lobed, glabrous or with fine hairs. Petals 100-130 × 14-25 mm, narrowly oblanceolate, obovate or somewhat acute, sericeous to coarsely villous externally, glabrous within, white tinged green in colour but hairs may have a tan colour. Lower staminal tube 15-25 mm, hairy, with 5 densely hairy scale-like appendages, giving rise to 5 free filaments which stand erect between the 5 reflexed petals, anthers markedly anfractuose. Fruit ellipsoidal to pyriform capsule, c. 15 × 8 cm.

Flowering March to July (see comments below). Dry hillsides, semi-deciduous woodland. Northern Mexico southwards to Central America (fig. 8).

As recognized here, *C. aesculifolia* is a very variable species which is widely distributed from Campeche to Sonora in Mexico, and Central America. There is wide variation in e.g. calyx size, length of the stamens in comparison with the petals, pubescence, and even flowering time (most examples seen flower between March to July but some August to January flowering specimens have been seen) and one would anticipate that some of the numerous species names which have been published for this group (see synonymy below) may comprise valid taxa.

Type: Mexico. Chihuahua, Hacienda San Miguel, 1885, *E. Palmer s.n.* (lectotype, here designated, US!)

**Eriodendron tomentosum** B.L. Rob., Proc. Amer. Acad. Arts 29: 314 (1894); *Ceiba tomentosa* (B.L. Rob.) Britten & Baker f., J. Bot. 34: 175 (1896)

**Ceiba grandiflora** Rose, Contr. U.S. Natl. Herb. 8: 320 (1905)

1. Leaflets 30-100 × 18-40 mm, acuminate ..........
   - Leaflets 20-40 × 13-18 mm, obscurely mucronate ..........

**a. subsp. aesculifolia**


**Ind. loc.:** “Hacienda San Miguel (F). Perhaps the same that was collected by Moçino & Sessé (Icon t. 94), referred by De Candolle to *Eriodendron aesculifolium* a species from the coast of Campeche”

**Type:** Mexico. Chihuahua, Hacienda San Miguel, 1885, *E. Palmer s.n.* (lectotype, here designated, US!)

*Ceiba pallida* Rose, Contr. U.S. Natl. Herb. 8: 320 (1905)

**Ind. loc.** “In rich valleys and in the mountains about Manzanillo, December 1-31, 1890, *Rose 1050*”

**Type:** Mexico. Colima. Around Manzanillo, 1/31-XII-1890, *Pringle 1050* (lectotype, here designated, US-digital image!)

**a. subsp. parvifolia**

**Eriodendron tomentosum** B.L. Rob., Proc. Amer. Acad. Arts 29: 314 (1894); *Ceiba tomentosa* (B.L. Rob.) Britten & Baker f., J. Bot. 34: 175 (1896)

**Ind. loc.:** “Collected on a barranca near Guadalajara, June 1892 (no. 5300)”

**Type:** Mexico. Jalisco, near Guadalajara, VI-1892, *Pringle 5300* (no original material located)


**Ind. loc.** “In rich valleys and in the mountains about Manzanillo, December 1-31, 1890, *Rose 1050*”

**Type:** Mexico. Colima. Around Manzanillo, 1/31-XII-1890, *Primer 1050* (lectotype, here designated, US-digital image!)

**Ceiba pallida** Rose, Contr. U.S. Natl. Herb. 8: 320 (1905)

**Ind. loc.** “Collected by J.N. Rose and Walter Hough near Cuernavaca, May 27 to 30, 1899 (no. 4337 type) and by C.G. Pringle from the same tree, May 31 1899 (no. 8212)”
Fig. 9.—*Ceiba schotii* (Gaumer, Plantae Yucatanae 694, E): a) leaf; b) flower at anthesis; c) androecium; d) detail of terminal part of staminal tube. *C. aesculifolia* (Pringle, Plantae Mexicanae s.n., E): e) branch with leaves; f) flower at anthesis; g) androecium.
Type: Mexico. Morelos, Near Cuernavaca, 27/30-V-1899, Rose & Hough 4337 (holotype, US!)

Leaflets 30-100 x 18-40 mm, acuminate elliptical to narrowly oblanceolate, with denticulate to serrate margin and acute apex, usually glabrous or with sparse simple or stellate hairs.

Flowering March to July but occasional specimens from diverse localities, e.g. Puebla (Dunn & Dunn 18741), Michoacan (Itis & Doebly 45) flowering September to January. Dry valleys and hillsides. Widespread in Mexico and extending southwards to Belize and Guatemala.

Illustrations. Fig. 9.

Although Pringle 5300, the type of E. tomentosum, has not been located, it is likely to be similar to other collections from this locality, e.g. Pringle 4733 and Pringle 9685, both of which refer to C. asculifolia. Eriodendron acuminatum was described from a fruiting specimen, and flowering characters were derived from Sesse & M Onceño icon 94 (cf. White & al., 1998). Rose (1905), on making the transfer as Ceiba acuminata commented: “Type locality: Hacienda San Miguel, Chihuahua, collected by Dr. E. Palmer. This species known only from the type collection and has never been collected in flower. It must be near C. tomentosum and with this material in hand it is difficult to separate them. The flowers may well show good specific differences”.

Rose (1905) also noted that Pringle 8212 was collected from the same tree as Rose & Hough 4337, the type of Ceiba pulilla.

Examined specimens


Costa Rica. Fincas La Pacífica, 2 miles N of Las Cañas, 8-VI-1971, A. Gentry 6578 (WIS).

C. & W.R. Anderson 2087 (CAS, F).

D.E. Breedlove 20392 (DS).

E. tomentosum (type, US!)

Flowering March to July but occasional specimens from diverse localities, e.g. Puebla (Dunn & Dunn 18741), Michoacan (Itis & Doebly 45) flowering September to January. Dry valleys and hillsides. Widespread in Mexico and extending southwards to Belize and Guatemala.

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Examined specimens


Costa Rica. Fincas La Pacífica, 2 miles N of Las Cañas, 8-VI-1971, A. Gentry 6578 (WIS).

C. & W.R. Anderson 2087 (CAS, F).

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E. tomentosum (type, US!)

Illustrations. Fig. 9.

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Rose (1905) also noted that Pringle 8212 was collected from the same tree as Rose & Hough 4337, the type of Ceiba pulilla.

Examined specimens


Costa Rica. Fincas La Pacífica, 2 miles N of Las Cañas, 8-VI-1971, A. Gentry 6578 (WIS).

C. & W.R. Anderson 2087 (CAS, F).

D.E. Breedlove 20392 (DS).

E. tomentosum (type, US!)

Illustrations. Fig. 9.

Although Pringle 5300, the type of E. tomentosum, has not been located, it is likely to be similar to other collections from this locality, e.g. Pringle 4733 and Pringle 9685, both of which refer to C. asculifolia. Eriodendron acuminatum was described from a fruiting specimen, and flowering characters were derived from Sesse & M Onceño icon 94 (cf. White & al., 1998). Rose (1905), on making the transfer as Ceiba acuminata commented: “Type locality: Hacienda San Miguel, Chihuahua, collected by Dr. E. Palmer. This species known only from the type collection and has never been collected in flower. It must be near C. tomentosum and with this material in hand it is difficult to separate them. The flowers may well show good specific differences”.

Rose (1905) also noted that Pringle 8212 was collected from the same tree as Rose & Hough 4337, the type of Ceiba pulilla.

b. subsp. parvifolia (Rose) P.E. Gibbs & Semir, comb. & stat. nov.

Ceiba parvifolia Rose, Contr. U.S. Natl. Herb. 8: 320 (1905)

Ind. loc.: “Collected by the writer on the dry hills near the little town of Matamoros, Puebla”

Type: Mexico. Puebla, Matamoros, 26-VI-1899, Rose & W. Hough, 4701 (lectotype, here designated, US!) A sterile specimen.

Leaves 5-7 foliolate. Petioles 25-35 mm, petiolules, leaflets 20-40 × 13-18 mm, broadly elliptical to obovate, apex obscurely mucronate, with sparse stellate hairs to glabrescent.

Flowering December-January? Dry valleys. Mexico, apparently restricted to states of Morelos, Puebla and Oaxaca within the general distribution of the larger leaved form.

Many specimens of C. aesculifolia are leafless, and it is not possible to distinguish between the two subspecies on flower alone. The following specimens of C. parvifolia all bear leaves.

Examined specimens


The following specimens have flowers and no leaves, but since they are from Oaxaca and Puebla, and in flower in December to January, they may be examples of subsp. parvifolia.


Chorisia soluta Donn. Sm., Bot. Gaz. 16: 1 (1891)

Ind. loc.: “Shores of Lake Amatitlan, Dept. Amatitlan, alt. 3,900 feet, Feb., 1890, J.D.S.”

Type: Guatemala. Amatitlan, shores of Lake Amatitlan, II-1890, Donnell Smith s.n. (lectotype, here designated, BM!; isolecotype, K!) A remarkable species was only known from the type collection which consists of fallen flowers. The description above is derived partly from that of Donnell Smith, but floral details are mostly from the Hughes specimen. These latter flowers, although evidently larger than the Donnell Smith collection, agree in most respects with type description except in one intriguing detail: the original description for this species refers to...
10-12 filiform staminal filaments, and Donnell Smith further emphasises this point in his additional comments, noting that freshly fallen flowers were the only ones accessible, and that the staminal column “partite to the annulus into double the number of branches is exceptional for the genus”. The type specimen at BM and a duplicate collection at K both have floral fragments with 10 staminal filaments, whereas both flowers of the Hughes & al. 1690 collection seen by us have 15 filaments.

Given the close resemblance of the type specimens of Chorisia soluta to the very variable C. aesculifolia, which also extends to Guatemala, and given the fact that C. aesculifolia also has some very large flowered specimens with a robust calyx, we were initially inclined to treat the type specimen of C. soluta simply as an odd double-filamented variant of C. aesculifolia, especially since it was based on a single tree. This was also the interpretation of STANDLEY & STEYERMARK (1949) who treated Chorisia soluta as a synonym of Ceiba aesculifolia. However, the Hughes & al. 1690 collection shows that other specimens occur with a similarly multi-filamented androecium comparable to the Donnell-Smith collection, although the number of free filaments seems to rather variable. In these circumstances, despite its evident affinity with C. aesculifolia, we maintain Ceiba soluta as a species.

Examined specimens


EXCLUDED OR DOUBTFUL NAMES


Ceiba casearia Medik., Malvenfam.: 16 (1787) = Eriodendron orientale Kurz, which according to BAKER (1965) is Ceiba pentandra


Ceiba microphylla K. Schum. in Mart. (ed.), Fl. Bras. 12(3): 213 (1886). Based on a flowerless specimen. Leaf morphology similar to Spirotheca rivieri (K. Schum.) Ulbr., but the reference to “yellow kapok” may indicate Eriotheca candolleana (K. Schum.) Robyns


Ind. loc.: “On hilly areas of the Piura department, Peru, e.g. on the way to Huancabamba 240–2600 m”

Type: Peru. Piura, in montanibus ad viam Huancabamba, III-1979, Ravenna 2507 (holotype, herb. Ravenna)

Described briefly and rather cryptically from a single specimen as: “Arbor 6-10 m, saepe varie contorta. Truncus distincte ventricosus, inermis, olivaceus vel opace viridis, 1-1.5 m crassus. Rami ample patentes, aculeis conicis 10-20 mm longis, armati. Flores albi. Capsulae et semina ut in C. speciosa”. RAVENNA (1998) further commented: “Trees of this species display rather strange forms, resembling fantastic figures. The short description was taken from the writer’s field notes. Poorness of the type specimen do not help as to its completion. However, the tree habit is so unusual that the species cannot be mistaken for any other”.
There is obviously insufficient data here to determine whether this description is indeed a new taxon of *Ceiba*. Some comment as to whether the staminal tube is entire or with five free filaments would have been helpful. We have not seen the apparently fragmentary type specimen. Pending further collections, we assume, from the locality and description of white flowers, that this material represents rather malformed trees of *C. insignis*, which also occurs in Piura.

**Ceiba phaeosantha** K. Schum. in Mart. (ed.), *Fl. Bras.* 12(3): 214 (1886). Schumann commented “species mihi non visi” and based this species on *Eriodendron phaeosantha* Decne., *J. Soc. Hort. Paris* 4: 90-94 (1870), described from a tree cultivated in Algeria. Description indicates this may be *Ceiba samauna*.


**Ceiba rosea** (Seem.) K. Schum. in Engl. & Prantl Nat. Pflanzenfam. 3(6): 63 (1890) [*Chorisia rosea* Seem., *Bot. Voy. Herald* 84 (1853)]. To be transferred to the genus *Spirotheca*.


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