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

by

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Resumen


En esta revisión taxonómica de Ceiba, que incluye el género Chorisia, se reconocen 17 especies, siete de las cuales se agrupan en el complejo C. insignis. Se describe una nueva especie, C. lupuna P.E. Gibbs & Semir, del Perú, que pertenece al complejo de C. insignis, así como una nueva subespecie, C. aesculifolia subsp. parvifolia (Rose) P.E. Gibbs & Semir. Se incluyen mapas de distribución de 16 especies (aunque en el caso de C. pentandra solo se representa su distribución americana) y se dibujan detalles diagnósticos de seis especies.

Palabras clave: Bombaceae, Chorisia, Ceiba, Sudamérica.

Abstract


In this taxonomic revision of Ceiba Mill. (in which we include Chorisia Kunth) we recognize 17 species, seven of which we group in the C. insignis species aggregate. One new species is described, C. lupuna P.E. Gibbs & Semir from Peru, which is referred to the C. insignis agg., and one new subspecies, C. aesculifolia subsp. parvifolia (Rose) P.E. Gibbs & Semir is recognized. Distribution maps are provided for 16 species (that for C. pentandra is restricted to the New World), and six species are illustrated.

Key words: Bombaceae, Chorisia, Ceiba, South America.

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 **Lycnophora** 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 **RAVENNA** (1998). The principle objective of **RAVENNA** (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 Ravenna (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.

**RAVENNA** (1988) claimed that **GIBBS & AL.** (1988) “believed that *Ch. crispiflora* HBK, *Ch. speciosa* St. Hil., Juss. & Camb., *Ch. ventricosa* Nees & Mart., *Ch. integrifolia* 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 habit, 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. integrifolia* 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...”.
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 aesculefolium, Bombax erianthos (as E. leiantherum) and Bombax pentandrum (as E. anfractuosum). To these latter genera, NEES & 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 Spirotherca 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 chodatti. 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. aesculefolia, 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 diminutive 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. schotii*) 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. glaziovii* 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. schotii*.

**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
C. pentandra s.l. of 2n = 72-88, from prove-
nances in Jamaica, Guyana, W Africa and In-
donesia. All counts were with root tip materi-
eal, either from acetocarmine squash prepara-
tions, or haematoxylin stained sections. Da Cruz (GIBBS & AI, 1988), using aceto-orcein
squash preparations of anther material, estab-
lished chromosome numbers of n = 43 for
Ceiba insignis, C. erianthos, C. glaziovii,
C. jasminodora, C. pentandra, C. pubiflora
and C. speciosa. Interestingly, da Cruz noted
that root tips of germinating seeds of
C. speciosa gave counts of In = 69-87 showing that
aneusomatic divisions may occur, and per-
haps explaining the cytological variation re-
ported by BAKER & BAKER (1968). These con-
sistent counts of n = 43 for Ceiba species,
contrasted with counts of n = 46 for Pachira
aquatica Aubl., n = 44 for Bombax longiflo-
rum (Mart. & Zucc.) K. Schum. and n = 46 for
Spirotheca passifloroides Cuatrec.

REPRODUCTIVE BIOLOGY

Most Ceiba species have nocturnal anthe-
sis and C. pentandra (GRIBEL et 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. in-
signis, C. samauma, C. ventricosa, and
C. trischistandra, but field observations are
lacking. C. erianthos and C. glaziovii have
particularly copious nectar. C. chodati also
has crepuscular anthesis but with sparse nect-
ar, and is probably pollinated by sphingid moths (we have seen sphingids visiting flow-
ers 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 butter-
flies which beat their wings against the an-
thers or stigma as they probe between the sta-
minal appendages for nectar. Hummingbirds
are frequent but ineffective visitors to this
species since they do not touch the anthers/ stigmas. However, C. pubiflora, with its re-
supinate 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 poten-
tially bat-pollinated species.

The Bombacaceae present a cluster of taxa
[see GIBBS & BIANCHI (1999) for review] with
late-acting self-incompatibility (LSI) sensu
SEAVEY & BAWA (1986). In this system, self-
ed flowers uniformly fail to form fruits al-
though self pollen tubes grow to the ovary and
penetrate ovules. In the genus Ceiba, LSI
has been studied in the species C. chodati
and C. speciosa (GIBBS & BIANCHI, 1993) and
C. pentandra (GRIBEL et al., 1999).

HABITAT

Most species of Ceiba are restricted to sea-
onally dry woodlands, including C. erian-
thos, 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. pubi-
flora seems to have a marked but not exclu-
sive preference for calcareous soils in its dis-
tribution from Mato Grosso Sul to the caatin-
gas 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 val-
leys, whilst C. pentandra seems to be able to occupy
both dry seasonal forest and humid river val-
leys, 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 tol-
erance 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 com-
mented: “it is a common constituent of the
gallery forests which line the river banks as
these lead out from the true forest into the sa-
vanna 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)

**Chorisia** Kunth in Humb., Bonpl. & Kunth, Nov. Gen. Sp. 5: 295 (1822)

**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 usually glabrous, occasionally sparsely simple or stellate hairy. Inflorescences in few-flowered fascicles or flowers solitary, with very caducous bracts and bracteoles. Flowers 18-145 mm, with 5 usually spreading or sometimes 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 connate 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 magenta 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, sometimes 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 staminal 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 upper part of the common filament, whereas in *C. soluta* it occurs just above the staminal appendages. The ovary superior, usually pyriform, five loculate-carpellate, with axile placentation and many ovules. Style usually slender, white and glabrous (hairy in *C. samauma*), terminating in a globose somewhat lobed stigma, which may be white to red. Fruit an elongate capsule with the seeds embedded in dense cotton-downy fibres originating 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 staminal tube giving rise initially to 5 filaments, which further subdivide to give 3 free filaments ............................................................................. 12. *C. trichistandra*
   - 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 appendages ................................................................. 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, becoming glabrous above .................................................. 14. *C. samauma*
   - Anthers sinuous with undulate thecae; style entirely glabrous .............................................. 6
6. Petals 65-90 x 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 .................... 10. C. erianthos

- Petals 170-190 x 15 mm, narrowly oblong, with short, brownish sericeous hairs exteriorly; lower staminal tube 80-100 mm, slender, sparsely hairy .................. 15. C. schottii

7. Leaves 3-foliolate; petals 18-25 mm; lower staminal column terminating in a disc-like staminal appendage giving rise to 5 free, 8-12 mm stamen filaments ........... 11. C. jasminodora

- Leaves mostly 5-7 foliolate; petals 50 mm or more; lower staminal column terminating in scale-like or corona-like staminal appendages, giving rise to an upper staminal tube, or 5 free staminal filaments, of 50 mm or more ........... 8

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)

- Flower with 5 free filaments arising from a 10-50 mm lower tube ......................... 9

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

- Lower staminal tube bearing 5 short, usually bifid, appendages which close off the lower corolla; petals erect or spreading .................. 10

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

- Flower with petals spreading, white or pale pink to pink-lilac, distally with carmine flecks or striations which may fuse below; stamen filaments white, anthers sinuous; stigma white to pale pink ........................................ 11

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

- Petals white distally, dark livid towards the base internally; stamens spreading; with nocturnal flowering .................. 9. C. glaziovii

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. Staminial appendages, when present, vacuolarized.

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 x 17-50 mm, oblongate or elliptical, with apex acuminate, margin entire or variously denticate, glabrous, petiolules 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 x 17-25 mm, campanulate, lobed, glabrous externally, usually densely villous within. Petals 60-130 x 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 ellipsoidal-pyriform capsule, c. 10-15 x 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 “Pleistocenic Arc” of seasonal woodlands as defined by Prado & Gibbs (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 corona-like staminal appendages of the C. insignis agg. but either immediately, or some 5-10 mm above the corona, five separate staminal filaments 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 ........................................... 7. *C. pubiflora*
   - Stamens above the staminal appendages united into a tube which has a collar of 5 sinuous, anthers (occasionally this tube with some fissure 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 spatulate 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-cresate 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 spatulate or broadly oblong, usually more than 15 mm wide, margin only slightly undulate .................. 3. *C. speciosa*
   - Staminal tube below the staminal appendages sericeous; petals narrowly oblong, usually less than 15 mm wide, with markedly undulate-cresate 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 Jaen, in fruticetis et fruticibus peraltis arboribusque compositis in altitudine 900 msm”

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

Trees c. 10 m, usually with aculeate trunk. Leaflets somewhat coriaceous, entire or dent-iculate. Pedicels 15-25 mm long. Petals 90-120 × 22-25 mm, spathulate to narrowly ob-long, 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. Stama-nal 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 Martin) (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 Maraión, 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 Passo de Pucara-Las Huertas-Passo de Matara-Passo de Cavico-Sonanga-Chamaya-Choros (5°52’S, 78°40’W)-Tomependa-Rio Chin-chipe to Río Maraión.

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 hesita-tion 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 Bon-pland’s notes on this taxon.

Based on specimens from the the Chama-ya-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 local-ities but added a Spruce collection from Tara-poto, some 250 km to the East, in San Martin 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 rosei" 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-
Chorisia integrifolia is another problematical taxon. Ulbrich described his species as having ‘white 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: Chamay 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 dissimilis quidem ab speciebus gregis “Ceiba insignis aggr.” –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 sericeus, drying brownish with whitish pubescence. Staminatal 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 lupuna: “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 domos 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 chartaceous, usually serrate. Pedicels 10-15 mm long rather stout. Petals 70-105 x 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 cinerous 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 x 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* observed by us in SE Brazil comprise a series of forest papilionid butterflies which alight on the flower and probe between the corollal lobes for the rather sparse nectar available at the base of the petals. Most of these butterflies, e.g. *Battus polydamas* (Roths. & Jord.), *Papilio anchisiades* (Roths. & Jord.), *P. thoas* (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**


4. **Ceiba crispiflora** (Kunth) Ravenna, Oni-ra 3: 45 (1998)

*Chorisia crispiflora* Kunth in Humb., Bonpl. & Kunth, Nov. Gen. Sp. 5, 297, tab. 485 fig. 2 (1822)

**Ind. loc.:** “In Brasilia legit Cel. Langsdorffius”

**Type:** Brazil. Mandioca, *Langsdorff* s.n. (lectotype, here designated, P! [herb. Humboldt & Bonpland])

Tree 10 m or more with sometimes swollen, aculate trunk. Leaflets denticulate. Pedicels 15-23 mm long. Petals c. 8.5 x 6-10 mm, very narrowly oblong, margin markedly undulate-crespatate, sericeous externally, glabrous internally, dark pinkish-magenta with few striations distally, yellowish at the base. Staminode column c. 15 mm to the apex. Flowers February-March. Mata Atlântica and coastal restinga. Brazil (near Rio de Janeiro). Cited further [cf. Santos (1967)] south but probably for cultivated material.

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

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-crespatate petals. Indeed, the flowers of *C. crispiflora* resemble what might be expected in a hybrid between *C. speciosa x C. ventricosa*, but we have absolutely no evidence of such hybrid status.

**Examined specimens**


5. **Ceiba ventricosa** (Nees & Mart.) Ravenna, Onira 3: 45 (1998)


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

**Ind. loc.:** “In sylvis, Cascam late cingentibus, inter Rio das Contas et Tiquirica, fluviis prope a loco, quem Cabeça do Boi incolae voeant. Martio mense flores deiecti terrain ad arboris radices tegebant. Princeps Max- im Neov.”

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

*Ind. loc.*: "Bahia, rodovia Itabuna-Ilheus, beira da estrada"

*Type*: Brazil. Bahia, Rodovia 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 x 8-10 mm, narrowly oblong with a markedly undulate-crespat 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, Espirito Santo, E Minas Gerais, Pernambuco, Paraiba) (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 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 synonym of *C. crispiflora* by SCHUMANN (1886) in Marius’ *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 NEES & 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. Hassler 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 x 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-the-cate, sinuous, pale yellowish anthers, occasionally splitting distally to give 5 short filaments and separate anthers. Stigma pinkish-
red. Fruit an elongate-pyiform capsule 15-18 x 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 pallid 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 misidentification of exsiccata of C. chodatii from Argentina, Bolivia, Brazil and Paraguay as Chorisia insignis Kunth.

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, Pl!)

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!)


Ind. loc.: “Arboreal caatinga near Jaiba, middle São Francisco river region, northern Minas Gerais”

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

Trees with sometimes ventricose, aculeate trunk. Leaflets somewhat chartaceous, usually serrate. Pedicels 5-10 mm long. Petals 47-85 x 20-25 mm, initially somewhat erect, subsequtentially spreading, obovate-oblong, margin somewhat undulate, sericeous externally, glabrous internally, uniformly pale pink with sparse dark flecks, or deep pink-lilac with conspicuous carmine striations
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, sinusuous 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 (Missiones), Paraguay, Centre-West Brazil from Corumbá to NE Minas Gerais, extending to Bahia and Espírito Santo (fig. 1).


Flowers rather variable in size, and also include forms ranging from pale pink petal with very 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. jabai-bana 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. jai-bana, and also had the opportunity to study some 11 carefully annotated collections of Ceiba trees recently made at our suggestion in the Montes Claros-Jaiba-Janauba area of Minas Gerais by E.R. Salviani and J. Dutilh. 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. jaibana 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. jaibana 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 Porterieinha, 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. jaibana 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.
8. **Ceiba boliviana** Britton & Baker f., J. Bot. 34: 175 (1896)

*Ind. loc.:* “Hab. Bolivia”

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

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

*Ind. loc.:* “Hab. Vicinnis Sorata ad radicam Catarguata in scopulis. Prov. Larecaja, Bolivia, G. Mandon 825; alt 2550 m.”


*Xylon tunariensis* Kuntze, Rev. Gen. Pl. 3(2): 23 (1898); *Ceiba tunariensis* (Kuntze) K. Schum., Just’s Bot. Jahrb. 26: 343 (1900)

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

*Type:* Bolivia. Tunari, O. Kuntze s.n. (lectotype, here designated, NY digital image!)

*Chorisia grandiflora* Rusby, nom. nud.

Trees c. 10 m with usually with swollen, aculate trunk. Leaves 5-7 foliolate, petiolo 35-135 mm; leaflets 95-110 × 35-50 mm, oblongolate, denticulate, glabrous, with petiolo 5-10 mm long. Flowers axillary, borne singly or in fascicles. Pedicels c. 12 mm long, stout. Calyx 32-40 × 20-23 mm, broadly campanulate, lobed. Petals 75-110 × 25-35 mm, held erect and so flower rather campanulate, broadly spathulate, 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 x 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. MACBRIDE (1956) in his Flora of Peru, identified specimens of *C. boliviana*: Weberbauer 5874 and Vargas 7195, as *Ceiba pubiflora*.

Field observations by Nee & Solomon (1964) note that “at 12.35 pm flowers open but old and falling, with an unpleasant smell, probably bat-pollinated”.

Examined specimens

**BOLIVIA. CHUQUISACA: Tarabuco-Zudanez, J.R. Wood 8007 (K), Vila-Vila, Sucre, IV-1933. Cardenas 543 (NY). COCHABAMBA: Chulumaní, 28-VI-1961, L.G. Holliday 20 (K). Comarapa, Sorata, Fries 1924 (S). Km 186 on Cochabamba-Sta. Cruz highway. 20-IV-1963, D. & V. Ugent 5106 (WIS). La Paz: Coroico, 10 km hacia Caranavi, S Beck 1777 (MO). 10 km SW of Yolosa, on road to Chusipata. J. Solomon & M. Wehling 7220 (K); ibidem, 12°53'S, 20-28 mm, campanulate, glabrous, with petiololes 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 x 25 mm, spathulate, 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 ellipsoidal capsule, c. 8-12 x 5-9 cm.

Flowering July-September. Dry woodlands (Caatinga). NE Brazil (Bahia, Pernambuco, Paraiba, Ceará) (fig. 4).

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

The specimen Glaziou 18145a, cited by Kunze 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.

Examined specimens


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

The specimen Glaziou 18145a, cited by Kunze 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 eriantha** (Cav.) K. Schum. in Mart. (ed.), Fl. Bras. 12(3): 211 (1886)

*Bombax erianthos* Cav., Diss. 5: 294, tab. 152

*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, *Commerson 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 foliolate, petioles 45-120 mm long; leaflets 34-85 × 16-40 mm, chartaceous, oblanceolate, apex acute, mucronate, glabrous petiololes 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-villous externally, glabrous internally, with sparse carmine striations distally, becoming uniformly carmine towards the base. Lower staminal 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 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 specimens of C. glaziovii.

Examined specimens


Illustrations. Santos (1969, fig. 5; Lorenzi (1998: 43).

Fig. 5.—*Ceiba jasminodora* (Semir 10929, UEC): a) branch with leaves; b) flower at anthesis; c) androecium. *C. samambua* (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 x 6 mm, campanulate, glabrous-puberulent externally. Petals 18-25 x 7 mm, cream, markedly reflexed. Stamen 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 x 5 cm.

Flowering April-July. Campo rupestre (rocky upland vegetation). Brazil, endemic to the southern Serra de Espinhaco 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 x 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 petiolules 2-3 mm long. Flowers axillary, solitary or fascicles of 2-3. Pedicels 10-30 mm long. Calyx 23-30 x 20-26 mm, broadly campanulate, four lobed, glabrous or finely velutinous, crimson. Petals c. 45-60 x 23 mm, narrowly oblong 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, monothecate, anfractuose anthers. Ovary pyriform, with style bearing the stigma usually above the level of the anthers. Fruit elongate-ellipsoidal capsule c. 12 x 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 stamen 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.” C. 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-


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- alt. 70 hex.”

Type: Colombia. without locality, Humboldt & Bonpland s.n. (lectotype, here designated, P!)


Ind. loc.: “Crescit prope Cumana (Nova Andalusia)”

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 ob lanceolate, base cuneate to somewhat truncate, apex acuminate, margin entire or obscurely denti-club, 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. Stamenal 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 anthers. Fruit ellipsoidal to pyriform capsule 15-18 × 8-10 cm.

Flowering August to September. Distribution effectively pan-tropical but almost certainly introduced in Asia and the Pacific, although probably native, at least in part, in W Africa (cf. Baker, 1965). We have not attempted 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 concluded 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 narrowly 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. indica (DC) Bakh. (= var. pentandra) for the asiatic 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-

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Fig. 6.—Distribution map of *Ceiba pentandra* (New World only).
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 oblanceolate leaves which taper to short, 2-5 mm petiolules, and which correspond to *Bombax mombopersonse* (again represented by a sterile *Humboldt & Bonpland* specimen at P) and characterised by, e.g. *Gentry & Renteria 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 2 mm which terminates abruptly to give a truncate ledge from which the free filaments arise. Examples occur in both S America and the Caribbean, e.g. *Little 9431* (Colombia) and *Bodin 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 has certainly influenced its distribution and possibly some morphological attributes, we prefer 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 Gribe & 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.

Examinined specimens

**Central America**


Panama. "Plants of Panama" sin loc., 1892, S. Hayes s.n. (E).

**Caribbean Islands**


SOUTH AMERICA


II. Ceiba sect. Campylanthera (Schott & Endl.) K. Schum. in Mart. (ed.), Fl. Bras. 12(3): 207 (1886)

Campylanthera Schott & Endl., Melet. Bot.: 35 (1832)
Type: Lectotype, here designated, C. samauma (Mart. & Zucc.) K. Schum.

Pollen grains distinctly oblate with distinctly protruding equatorial caps and either pili/clavae or with striate muri. Staminal appendages usually absent, when present, not vascularized.


Ind. loc.: “Habitat in sylvis primaevis densis usimis udis semipinete rore humentibus fluvios Japará, Madeira et Solimões”

Type: Brazil. Amazonas, Rio Negro, ad margines Japuri, prope São João de Principe, Martius 3048 (lectotype, here designated, M; isotypes, F-photo! MO-photo! NY-photo! P-photo!)

Ceiba burchellii K. Schum. in Mart. (ed.), Fl. Bras. 12(3): 211 (1886)
Fig. 7.—Distribution map of *Ceiba samauma*.

*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-oblancoellate, 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. Staminodal tube basally 35-80 mm, dividing without the presence of staminodial appendages or swelling to give 5 filaments 45-90 mm, bearing short setae but appearing glabrous, with long, up to 18 mm orange, anfractuose anthers. Ovary subglobose, with a long slender style which is densely hairy as it emerges from the staminal tube, becoming glabrous distally, stigma shortly 5-lobed. Borne at same level or somewhat above anthers. Fruit ellipsoid–pyriform capsule 15-18 x 8 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


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

Type: Mexico. Yucatán. Mérida, Schott s.n. (lectotype, here designated, BM!)

Trees c. 8 m with aculeate trunk and branches, spines on younger branches c. 0.5 mm, black, only slightly curved. Leaves 3-7 foliolate, petiole c. 60 mm long; leaflets 50-100 x 19-30 mm, entire, coriaceous, oblonglunate 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 x 8-10 mm, rather cylindrical (c. 3x longer than broad), glabrous, only slightly curved. Leaves 3-7 foliolate, petiole c. 60 mm long; leaflets 50-100 x 19-30 mm, entire, coriaceous, oblonglunate 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 x 8-10 mm, rather cylindrical (c. 3x longer than broad), glabrous, only slightly curved.
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)


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 oblanceolate or obovate, apex acuminate, margin denticulate to serrate, glabrescent or uniformly finely hairy with stellate and simple hairs, or hairs restricted to nerves, petiolule 3-12 mm long. Flowers usually borne
singly, petals markedly reflexed. Pedicels 10-20 mm long, stout. Calyx 17-45 x 15-30 mm, funnelform to broadly campanulate, 4-5 lobed, glabrous or with fine hairs. Petals 100-130 x 14-25 mm, narrowly oblong, 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 x 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. There are certainly striking differences in petal size and shape (particularly whether the apex is rounded or acute), and degree of exsertion of the stamens, and also pubescence (used to delimit *C. tomentosa* but note that e.g. *Hinton 13878* has young leaves with simple and stellate hairs, but older leaves only with sparse hairs on the midrib). However, we have been unable to correlate any character differences consistently with distribution patterns.

Again the fact that *C. aesculifolia* usually flowers in a leafless state, with nocturnal anthesis (*Bullock 1583* comments anthesis at 20.15 h) and bat pollination (*Baker & al., 1971*), means that most flowers are collected the following day as they are wilting. As a consequence, the quality of some of the herbarium material available is of limited value. This is a group where field studies, or the collection of carefully annotated leaf and flowering specimens, with photographs, may yet reveal variation within *C. aesculifolia* s.l. which merits recognition at species level.

1. Leaflets 30-100 x 18-40 mm, acuminate ................. a. subsp. *aesculifolia*

- Leaflets 20-40 x 13-18 mm, obscurely mucronate ................. b. subsp. *parvifolia*

a. subsp. *aesculifolia*


*Ind. loc.*: “Hacienda San Miguel (F). Perhaps the same that was collected by Mocino & 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!)


*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*”


*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 × 18-40 mm, acuminate elliptical to narrowly oblong-elliptical, with denticulate to serrate margin and acute apex, usually gl abrous or with sparse simple or stellate hairs.

Flowering March to July [but occasional specimens from diverse localities, e.g. Puebla (Dunn & Dunn 18741), Michoacan (Ittis & 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 we refer to C. aesculifolia. Eriodendron acuminatum was described from a fruiting specimen, and flowering characters were derived from Sessé & Moñino, 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. It has never been collected in flower. It is likely to be near C. tomentosum and with this material in hand it is difficult to separate them. The flowers may well show specific differences”.

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


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”


Leaves 5-7 foliolate. Petioles 25-35 mm, petiolules, leaflets 20-40 x 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!)

Tall trees with aculeate trunk and flattish, spreading crown. Leaves described as digitate, but not seen by us. Pedicel very stout, 10 mm long. Calyx also very robust, c. 30 x 30 mm, orange-brown hairy without, very densely villous pubescent within. Petals c. 140 x 35 mm, spathulate, with a white inner surface, and golden brown hairy externally, reflexed and curling back. Staminal tube c. 20 mm, with a corona of five, bifid, densely hairy scales, with (10)15 slender, free filaments, c. 105 mm, each bearing a c. 7 mm anfractuose monothecate anther. Ovary c. 8 mm, pyriform, with a long, slender style which exceeds the level of the anthers by 10 mm or so, but the form of the stigma unknown. Fruit not seen.

Flowering February. Dry woodland. Apparently endemic to Guatemala (fig. 8).

Until the recent collection by Hughes & al. 1690, this 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 caribaea** (DC.) A. Chev., Rev. Int. Bot. Appl. Agric. Trop. 17: 266 (1937) [*Eriodendron anfractusom var. caribaeum DC.*] = *Ceiba pentandra* according to BAKHUIZEN VAN DEN BRINK (1924) and BAKER (1965)

**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 candollea* (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 distinice 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”.

Excluded or doubtful names


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


**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*.


**Neusa Diniz da Cruz** was involved in early cytological and reproductive biology studies with *Chorisia-Ceiba* species. Neusa always avoided the taxonomic part, but she understood the taxonomic process and her common sense opinions from the sidelines were much missed as this work progressed. The late Al Gentry provided photographs and comments in letters which gave us important insights into *C. insignis*, *C. lupuna* and *C. boliviensis*. Julie Dutfield was always ready to provide the second author with field transport, or to include the search for ceibas in her own field expeditions. Also to Dr Piet Stoffelen for checking for the presence of a Von Wied collection of *C. ventricosa* at BR. We thank Dr Salvador Talavera for a critical reading of the draft mss., and also the editor and anonymous referees for numerous textual improvements, and Rodrigo Tavera for preparation of the illustrations. Finally, the first author is indebted to Kirsten Llamas, who by repeatedly sending him photos of ceibas cultivated in Florida to identify, made him feel that his knowledge of these taxa was actually of some use, and stimulated the final push to complete this revision. Also to Dick Brummitt and Gwilym Lewis at RBG Kew, for patiently supplying bibliographic information, and to the Brazilian Conselho Nacional de Desenvolvimento Cientifico e Tecnologico for the award of a visiting research fellowship which allowed final stages of this study to be completed.

**ACKNOWLEDGEMENTS**

We thank the Directors and Curators who have loaned specimens or permitted visits to their herbaria. The first author is especially grateful to the curators of F, MO and NY for showing endless patience and courtesy with loans retained over far too many years. Our late dear friend and colleague

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Edited by Carlos Aedo
Aceptado para publicación: 28-V-2003