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A PROPOSAL TO UNITE THE GENERA CHORISIA KUNTH AND CEIBA MILLER (BOMBACACEAE)

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ABSTRACT: Criteria used to distinguish the genera *Chorisia* Kunth and *Ceiba* Miller are shown to be unsatisfactory and new evidence from cytology, palynology and experimental pollination studies support the view that these genera should be united under *Ceiba*. A new combination *Ceiba insignis* (Kunth) Gibbs & Semir is proposed.

These observations on the limits of *Ceiba* and allied genera stem from studies on species of *Chorisia*, *Ceiba* and *Spirotheca* which we have intermittently carried out over a number of years. Although this work has been largely based on herbarium material, our understanding of some species has been greatly enhanced by the opportunity to study living trees of a number of Brazilian species which form a part of the collection at the Horticultural Section of the Experimental Station of the Instituto Agronômico at Campinas. The main results of our taxonomic studies are intended as a contribution to the Flora Neotropica series of monographs, and detailed results of cytological and breeding system studies will also be published elsewhere. Here we simply present aspects of our work which have a bearing on our proposal to realign generic limits in this group.

The generic name *Ceiba* [Ceyba] was first employed by Oviedo y Valdez (1535) and derives from an Amerindian name. It was used subsequently by Plumier (1703:42). *Ceiba* was first validly published by Miller (1754) but like other genera in this work Miller's priority was overlooked until Druce (1913). The first specific name currently accepted in *Ceiba* was published as *Bombax pentandrum* by Linnaeus (1753) under that author's wide interpretation of the genus *Bombax*, and although *B. pentandrum* L. was transferred to *Ceiba* by Gaertner (1791) the generic name *Ceiba* was ignored by most authors until the work of Schumann (1886, 1890).

Kunth (1822) described the genus *Chorisia* for two species, *Chorisia insignis* from Peru and *Ch. crispiflora* from E Brazil. In the same work, Kunth (1822) treated *Bombax* in 'sections' with '(a) filamenta quinque (Bombax)' for his new species *Bombax aesculifolium* from Mexico, and '(b) filamenta creberrima (Ceiba)' for two other species with multiple staminal filaments. In contrast to these taxa, species of the new genus *Chorisia* were distinguished by complete fusion of the staminal filaments to form a tube around the style: '...Tubus staminens duplex; interior tenuis, elongatus, teres, apice antherifer; exterior brevis interiori adnatus, apice decemlobus, lobis patentibus, sterilibus. Antherae 10, summo tubo externae adnatae...'.

De Candolle (1824) took a rather different view since he restricted *Bombax* to seven species with numerous stamens and described a new

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genus *Eriodendron* (with *Ceiba* Plum. as a synonym) for species with five stamens united at their base into a tube. De Candolle referred Kunth's *Bombax aesculifolium* to this new genus, together with two 'new' species, *E. leiantherum* DC. (*Bombax erianthos* Cav.) and *E. anfractuosum* DC. (*Bombax pentrandrum* L.). The genus *Chorisia* was maintained with two species as recognized by Kunth (1822).

Further botanical exploration in Brazil produced a number of new species. Martius & Zuccarini (1825) added *Eriodendron samauma* and St Hilaire (1828) described *Chorisia speciosa*, *Eriodendron jasminodorum* and *E. pubiflorum*. A number of additional generic names were subsequently proposed by diverse authors, notably by Schott & Endlicher (1832) with *Campylanthera* (a monotypic genus to contain *Eriodendron samauma*) and *Erione* (comprising *Erione jasminodorum*).

None of these taxa received wide acceptance, however, and the modern mould for this group of Bombacaceous genera derives from the treatment by Schumann in Martius' *Flora brasiliensis* (1886) and, particularly, the same author's account in Engler & Prantl's *Pflanzenfamilien* (1890). In the latter work, Schumann recognized the tribe Adansoniae Bentham as comprising four genera, *Adansonia*, *Bombax*, *Chorisia* and *Ceiba*. *Bombax* sensu Schumann was a very broad concept and the genus has been split by more recent authors to recognize *Pachira* Aubl., *Eriotheca* Schott & Endl., *Pseudobombax* Dugard and *Pochota* Goyena (syn. *Bombacopsis* Pitt.)*. *Ceiba* as recognized by Schumann included three sections: Sect. I. *Campylanthera* with four species from tropical America including *C. pentandra* and *C. samauma*; Sect. II. *Eriodendron* with two rather disparate species from E Brazil, *Ceiba rivieri* (Decne.) Schum. and *C. erianthos* (Cav.) Schum.; and Sect. III. *Erione* with *C. rosea* (Seem.) Schum. from Central America and *C. pubiflora* (St Hil.) Schum. and *C. jasminodora* (St Hil.) Schum. from Central Brazil. *Chorisia* was distinguished by the presence of an entire staminal tube.

It is of interest to note that in this classification Schumann radically changed the concept of *Eriodendron* by excluding all but one of the species originally included in this genus by De Candolle and by adding *Ceiba rivieri*, an epiphytic species with red flowers and tetrathecate anthers. Schumann's interpretation of *Ceiba* and *Chorisia* was essentially accepted by subsequent authors, who described new species in these genera, with the exception of the following:

(a) Ulbrich (1913) transferred *Ceiba rivieri* to a new genus *Spirotheca* in which he also included a new species, *S. salmonea* from Peru. Cuatrecasas (1954a & b) accepted the genus *Spirotheca* Ulbrich and enlarged it by four new species, *S. michaeli*, *S. rhodostyla*, *S. rimbachii* and *S. passifloroides* and one new combination *S. allenii* (Woodson) Cuatr.

Our own studies on *Spirotheca* are not yet complete but these species seem to form a coherent group united by the presence of semi-versatile, partially spiralled, tetrathecate anthers, small pleurotreme pollen grains with well-differentiated but scarcely protruding equatorial caps, and an epiphytic 'strangler' habit. *Spirotheca* was accepted by Santos (1964, 1969) but rejected by McBride (1956) and Robyns (1964). We are in agreement with Ulbrich (1913) and recognize the genus.

*See Stevens (1987).

(b) Dawson (1944) drew attention to the fact that *Ceiba pubiflora* (St Hil.) Schum. was essentially similar to *Chorisia speciosa* and *Ch. insignis*. All these species have a lower staminal tube surmounted by staminodial appendages. In *Ce. pubiflora* this tube divides above into five free staminal filaments whereas in the Chorisias there is an upper, entire staminal tube.

To resolve this obviously anomalous situation Dawson (*op. cit.*) redefined *Chorisia vis a vis Ceiba* on the presence of the staminodial ring or corona in *Chorisia* and its absence in *Ceiba*, and *Ce. pubiflora* was transferred to the genus *Chorisia*. Santos (1964) accepted Dawson's criterion and drew attention to the fact that another *Ceiba* species, *Ce. glaziovii* (Kuntze) Schum., also combined a staminodial corona with free stamen filaments and she effected the transfer of this species also to *Chorisia*.

Our studies on the species of *Ceiba* and *Chorisia* have led us to the conclusion that the separateness of these genera cannot be sustained, even on the basis of traditional characters, and data from new parameters such as pollen, chromosome number and pollination experiments support this view.

The staminal column in Ceiba and Chorisia

The staminal column, with associated staminodial appendages or corona where present, is illustrated for seven species of *Ceiba* and *Chorisia* in Fig. 1a–g. If two extreme conditions are compared, e.g. *Chorisia insignis* (Fig. 1f) and *Ceiba samauma* (Fig. 1b), one can understand why Kunth (1822) considered it necessary to describe the new genus *Chorisia*. However, when the entire sequence of species is considered there is no such clear-cut distinction and the following intergradations should be emphasized:

(a) The extent of fusion of the upper (inner) staminal column in different flowers of the same tree of *Chorisia speciosa* in SE Brazil can be quite variable, ranging from entirely fused (the commonest condition) to 2–5 stamens with free filaments for one third to half the length of the tube (Fig. 2). Likewise, some flowers of *Ceiba/Chorisia pubiflora* have the five 'free' stamens partly fused to form a short tube above the staminodia (see illustrations of these species in Santos, 1964). Indeed, since the degree of staminal fusion is the only separating character, maintenance of *Chorisia speciosa* and *Chorisia pubiflora* as distinct species is not tenable (see below also); obviously this applies even more strongly to their separation in genera as recently proposed by Bernardini (1984).

(b) The staminodial appendages in *Chorisia insignis*, *Ch. speciosa*, and *Ceiba/Chorisia pubiflora* consist of five bifid projections which effectively close off the lower part of the flower enclosed by the cup-like calyx, and thus limits access to the nectar. In SE Brazil the flowers are commonly pinkish-magenta, diurnal, present sparse nectar, and are visited by humming birds and butterflies, but are probably only effectively pollinated by certain species of the latter which continue to beat their wings (against anthers or stigma) whilst inserting their proboscises between successive inter-staminodial apertures. In this species, the lower staminal tube, surrounding the ovary, contains five groups of tripartite

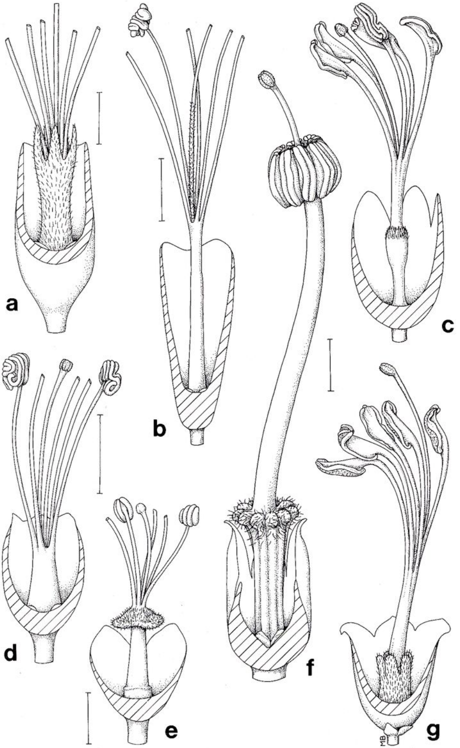

FIG. 1. The staminal column and the presence or absence of staminodial appendages in various *Ceiba* and *Chorisia* species: a, *Ceiba aesculifolia*; b, *Ce. samauma*; c, *Ce. erianthos*; d, *Ce. pentandra*; e, *Ce. jasminodora*; f, *Chorisia insignis*; g, *Ch. glaziovii*. Scale bars: a–d, f–g = 10mm; e = 5mm.

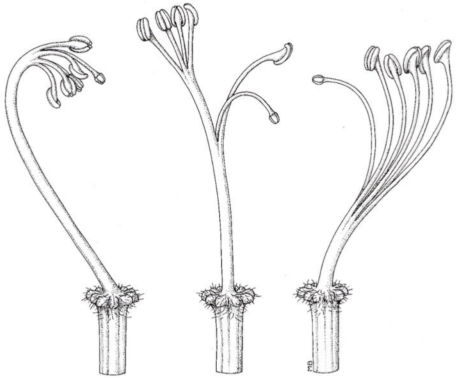

FIG. 2. The staminal column, with varying degrees of free filaments, in flowers of *Chorisia speciosa.*

vascular traces. As these ascend to the region of the staminodial appendages the outer traces of each group deflect and loop into each staminodium prior to rejoining the central trace and continuing to ascend the 'inner' staminal tube (see also Van Heel, 1966).

In *Ceiba/Chorisia glaziovii* only five entire staminodia form the corona which is less distinct and rather hidden by shaggy hairs (Fig. 1g). However, the looped vasculature in the staminodia seems to be the same as that in *Chorisia insignis*, as is their function in closing off the nectary. This species, however, has white, nocturnal flowers with copious nectar and is probably pollinated by bats and perhaps moths. Another species, *Ceiba erianthos* Schumann, has flowers which closely resemble those of *Ch. glaziovii* (also white and nocturnal) to such an extent that as noted by Santos (1964) herbarium specimens of the two can only be distinguished with difficulty; the petals of *Ce. erianthos* usually have a shaggy, white-lanate indumentum, in contrast to the rather appressed sericeous-villous pubescence of *Ch. glaziovii.* More strikingly, *Ce. erianthos* lacks the staminodial appendages of *Ch. glaziovii*, although this not immediately obvious since the staminal tube of the former is distinctly swollen in the same region and may possess incipient lobes with dense tufts of hairs (Fig. 1c; see also the excellent illustrations in Santos, 1964).

Thus, the situation of *Ceiba erianthos* and *Ceiba/Chorisia glaziovii* rather parallels that of *Chorisia speciosa-Ceiba pubiflora*, with one species referred to *Ceiba* and the other to *Chorisia*, except that in this case it is the presence of staminodial appendages *versus* a hair-tufted staminal tube swelling which scarcely seems to warrant generic segregation.

(c) Staminodial appendages are found in some other species of *Ceiba* in the traditional sense. *Ceiba jasminodora* (Fig. 1e), a rather diminutive treelet from rocky upland areas in Minas Gerais state, Brazil, has a short, 6–7mm staminal tube which surrounds the ovary and is capped by a disc-like staminodial appendage, which has vascular loops, and from which the five free staminal filaments arise. *Ceiba aesculifolia* (Kunth) Britten & Baker from Mexico (Fig. 1a) has a staminal tube of c.30mm which gives rise to five free filaments of c.90mm. At the apex of the tube, alternating with the filaments, there are five hairy staminodial appendages which may reach 8mm in length. Despite their conspicuousness in some specimens these appendages do not appear to take a loop vascular trace. In other species (*Ceiba pentandra*, *C. schottii* and *C. samauma*), there is no staminodial development.

There is thus no clear-cut distinction between *Ceiba* and *Chorisia* on the basis of either free versus fused staminal filaments, or presence of absence of staminodial appendages.

Pollen morphology in Ceiba and Chorisia

Palynological surveys of the Bombacaceae by Erdtman (1952)*, Sharma (1970) and Moreira (1960) each include details of one or two *Ceiba/Chorisia* species, but more extensive data are provided by Fuchs (1967) and a recent detailed study of the family by Nilsson & Robyns (1986).

Fuchs made an extensive survey by means of light microscopy of acetolysed grains which included eight species of *Campylanthera* (the splinter genus, originally monotypic, described for *Ceiba samauma* by Schott & Endlicher, 1832), eight species of *Ceiba*, seven species of *Chorisia*, and four species of *Spirotheca*. Surprisingly, the actual species studied were not fully listed and this, together with the lack of references to voucher material and the fact that the results are presented in a very concise, summarized form, unfortunately limits the value of this work. It is interesting to note, however, that Fuchs preferred to revive the genus *Campylanthera* for *S. samauma* and allied species because, as he commented: 'The genus *Ceiba sensu lato* includes two groups of species which are clearly different in their palynomorphology. The type species of *Campylanthera* belongs to one group, the type species of *Ceiba*, *C. pentandra*, to the other'. Similarly, for the genus *Chorisia* he noted: '*Chorisia soluta* J. D. Smith seems to belong to the genus *Campylanthera* as defined by us, according to palynomorphological characters. The remaining species of *Chorisia* do not seem separated from species of *Ceiba sensu stricto* on palynomorphological grounds'.

Nilsson & Robyns (1986) have provided a comprehensive palynological account of the Bombacaceae by means of light- and scanning electron

*The specimen 'Mexico, *Gaumer* 694' cited as *C. aesculifolia* as a pollen voucher by Erdtman (1952:75–76, fig. 33B) is actually *C. schottii*.

microscopy of representative taxa which included four species of *Ceiba*, five species of *Chorisia* and five species of *Spirotheca*. These authors opted for a rather narrow classificatory view of this clearly eurypalynous family and recognized 11 pollen types, some of which are further subdivided to give a total of 20 pollen groups. Within this classification, all *Chorisia* species were grouped as the '*Chorisia* type', three *Ceiba* species (*C. boliviana* Britten & Baker, *C. pentandra* and *C. trichistandra* (Gray) Bakh.) were grouped as the '*Ceiba* type' whilst *Ceiba samauma* was referred to the '*Bombax* type-*Neobuchia* subtype', and the five *Spirotheca* species were referred to the '*Bombax* type-*Bombax* subtype'.

A feature of this classification is that species of a number of genera are dispersed in different pollen types, e.g. *Bombacopsis* species occur in three pollen subtypes, *Quararibea* species are distributed between two pollen types and six subtypes, and pollen from different collections of the species *Pachira aquatica* was placed in two subtypes. Another aspect is that a number of the pollen types recognized by these authors appear to be rather arbitrarily designated points on a morphological continuum. This seems to apply particularly to the '*Ceiba*-', '*Chorisia*-' and '*Ochroma*-' pollen types (Nilsson & Robyns, *op. cit.*, pp. 11–12, figs. 11–13).

In Fig. 3a–i we present scanning electron micrographs for nine species of *Ceiba* and *Chorisia*. It can readily be seen that, although there is a degree of pollen heterogeneity, the pollen types do not support the traditional split between *Ceiba* and *Chorisia*. Rather, as emphasized by Fuchs (1967), the major divide lies between *Ceiba aesculifolia*, *Ce. schotti* and *Ce. samauma*, with distinctly oblate grains, c.$50 \times 90 \mu m$, with strikingly protruding equatorial caps and either striate mural processes in *Ce. aesculifolia* (which is perhaps referable to the *Bombax* subtype of Nilsson & Robyns, 1986) or with free standing pila/clavae in *Ce. samauma* and *Ce. schottii* (the *Neobuchia* subtype of Nilsson & Robyns, 1986) *versus* the remaining species. The latter comprise *Chorisia insignis*, (together with *Ch. speciosa* and *Ch. pubiflora* which have identical pollen), *Ceiba/Chorisia glaziovii* and *Ce. jasminodora*, which have peritreme grains, c.$40 \times 55 \mu m$, with high, simple or branched bacula supporting rather delicate, sinuous muri (i.e. the *Chorisia* type of Nilsson & Robyns, 1986), and the rather similar *Ceiba pentandra*, *Ce. erianthos* and *Ce. trichistandra* with peritreme to suboblate grains with low to medium height bacula supporting rather robust muri (i.e. the *Ceiba* type of Nilsson & Robyns, 1986).

CHROMOSOME NUMBERS

Virtually the only extensive list of chromosome numbers available for the family Bombacaceae is that by Baker & Baker (1968) which includes some 26 counts for several varieties of *Ceiba pentandra* which have the range $2n = 72$, 74, 75, 76, 80 & 88, and a single count for *Chorisia speciosa* of $2n = 72$. The *Ce. pentandra* counts derive from mainly African cultivars with others from Guyana and Indonesia, whilst that for *Ch. speciosa* is from a tree cultivated at the Jardin d'Essai, Hamma, Algeria. All these counts were obtained from mitotic figures of root-tip squashes or paraffin sections.

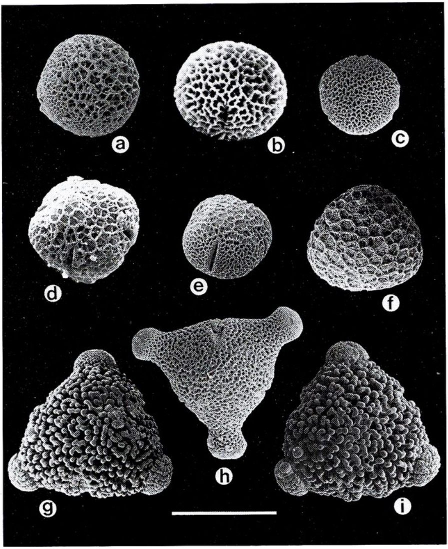

FIG. 3. Scanning electron micrographs of pollen of some *Ceiba* and *Chorisia* species: a, *Chorisia glaziovii*; b, *Ch. insignis*; c, *Ceiba jasminodora*; d, *Ce. trichistandra*; e, *Ce. erianthos*; f, *Ce. pentandra*; g, *Ce. schottii*; h, *Ce. aesculifolia*; i, *Ce. samauma*. Scale bar = 50μm.

In our studies of *Ceiba* and *Chorisia* species N. D. da Cruz has prepared chromosome counts from meiosis in pollen mother cells for a number of Brazilian species together with some counts from other Bombacaceous genera (Cruz *et al.*, in preparation). These studies have established that the chromosome number n = 43 occurs uniformly in *Chorisia insignis*, *Ch. speciosa*, *Ceiba/Chorisia glaziovii*, *Ceiba/Chorisia pubiflora*, *Ceiba erianthos*, *Ce. jasminodora* and *Ce. pentandra*. Interestingly, in root-tip squashes of germinating seeds of *Chorisia speciosa* chromosome numbers ranging from 2n = 69–87 were obtained, showing that aneusomatic divisions may occur and this, perhaps, explains the numbers obtained by Baker & Baker (1968). Also of interest is the fact that the other genera for which counts are available are all characterized by different numbers: *Pachira aquatica* n = 46, *Pseudobombax longiflorum* n = 44, and *Spirotheca passifloroides* n = 46. Also, Maglio *et al.* (1984) have studied meiosis in pollen mother cells of *Eriotheca* and report *E. gracilipes* with n = 48 and *E. pubescens* with n = 135.

Interspecific fertility studies

We have also initiated a series of studies on the breeding systems of *Ceiba* and *Chorisia* species at the Experimental Station at Campinas. A series of self-, intraspecific and interspecific controlled pollinations were carried out with various species. Some of the pollinated flowers were left to observe fruit-set, but the pistils of others were fixed after 24–72 hours and examined for pollen germination and pollen-tube growth by means of fluorescence microscopy. These studies are still in progress and the results will be published elsewhere but the following observations are of interest to the question of generic limits:

(a) *Chorisia insignis*, *Ch. speciosa* and *Ceiba/Chorisia pubiflora* are completely interfertile and cross-pollinations yield fully viable seed from which we have hybrid trees in cultivation. Whilst such cross-fertility is clearly not necessarily an absolute criterion of specific status, these data, together with the lack of sustainable morphological criteria, lead us to consider that these taxa form a single species aggregate (the *Ceiba insignis* complex—see below) within which the possible delimitation of component species, subspecies or varieties requires further detailed studies.

(b) Interspecific pollinations with pollen of either *Chorisia insignis* or *Ch. speciosa* on stigmas of flowers of *Ceiba/Chorisia glaziovii* result in prolific pollen tube growth to the ovules. The majority of such cross-pollinated flowers dropped after 3–4 days but a few persisted to produce fruits of c.3cm before these too were aborted.

(c) Reciprocal interspecific cross-pollinations between *Chorisia speciosa* and *Ceiba erianthos* also result in pollen germination on the stigma and some pollen tubes penetrate as far as the ovary where the tubes were seen to penetrate the ovules. The majority of such pollinated flowers dropped after 3–4 days, but a small number produced fruits with viable seeds.

These levels of interspecific fertility emphasize, on the one hand, the weak differentiation between the components of the *insignis* aggregate, and since these have been considered members of two genera, the desirability of treating all the taxa concerned within a single genus. The degree of compatibility shown in (b) and (c) also provide evidence of the close relationship of the species involved.

All of the above lines of evidence indicate that the distinction between *Ceiba* and *Chorisia*, either as established by Schumann (1886) or as redefined by Dawson (1944), cannot be maintained. Rather, two different assemblages of species emerge: one comprises *Ceiba erianthos*, *C. jasminodora*, *C. pentandra* and *C. trichistandra* together with the *Chorisia insignis* group (*Ch. insignis*, *Ch. pubiflora* and *Ch. speciosa*) and *Ch. glaziovii*. This assemblage contains the type species of the genus *Ceiba*, *C. pentandra* (see Nicolson, 1979) and so must be referred to this genus. The other group consists of *Ceiba aesculifolia* from Mexico to Nicaragua (which actually involves another rather polymorphic assemblage—see synopsis below), the closely related *C. parvifolia* Rose, and what seem to be a vicariant pair of species, *C. schottii* from Mexico–Guatemala and *C. samauma* from Amazonian S America. The latter taxon is the type species of the genus *Campylanthera* Schott & Endl. so that a case could be made for reviving this genus as suggested by Fuchs (1967) on palynological grounds. However, such a treatment does ignore floral similarities, and we are also acutely aware that our studies on this group are biased towards those Brazilian taxa for which we have had access to living specimens. Rather than attempt to split off *Campylanthera* again at this stage we prefer to await the outcome of future cytological and, hopefully, pollination biology data from some species of this group. For the present our proposal is to unite all of these species under *Ceiba* and acknowledge the pollen heterogeneity by recognizing two sections, as follows.

Ceiba Miller, Gard. Dict., Abridg. Ed. 4 1:[287] (1754).
Type species: *Ceiba pentandra* (L.) Gaertner, Fruct., 2:244, tab. 133 (1791).

Section **Ceiba**.

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

This section includes, in addition to the type species, *C. erianthos* (Cav.) Schum., *C. glaziovii* (Kuntze) Schum., *C. trichistandra* (Gray) Bakh., *C. jasminodora* (St Hil.) Schum., *C. boliviana* Britten & Baker, and also the following new combination:

Ceiba insignis (Kunth) Gibbs & Semir, **comb. nov.**
Basionym: *Chorisia insignis* Kunth in Humboldt, Bonpland & Kunth, Nov. Gen. et Spec. 5:297 (1822).

Ceiba insignis represents a polymorphic complex or perhaps an aggregate species with an extensive distribution in South America including NE & SE Brazil in the east, the central Brazilian plateau, Paraguay and Argentine Chaco, and in the west, dry valley habitats in the Andes of Ecuador, Peru and N Argentina. Our detailed studies on this complex are not yet complete, but it appears likely that all other species of *Chorisia*, i.e. *Ch. crispiflora* Kunth, *Ch. incana* Robyns, *Ch. integrifolia* Ulbr., *Ch. speciosa* St Hil. and *Ch. ventricosa* Nees & Mart. are referable to it. 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.

Section **Campylanthera** (Schott & Endl.) Schumann in C. Martius (ed.) Flora brasiliensis 12(3):207.

Pollen grains distinctly oblate with distinctly protruding equatorial caps and either pili/clavae or with striate muri. Staminodial appendages usually absent; when present, not vascularized, and the result of splitting of the staminal tube.

Type species: *C. samauma* (Mart. & Zucc.) Schum.

Other species which belong to this section are *C. schottii* Britten & Baker, *C. parvifolia* Rose, and another species complex, *C. aesculifolia* (Kunth) Britten & Baker, which includes *C. acuminata* (Watson) Rose, *C. grandiflora* Rose, *C. pallida* Rose, *C. soluta* J. D. Smith and *C. tomentosa* Rose.

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