



A new species of *Ceiba* (Malvaceae, Bombacoideae), previously confused with *Ceiba speciosa*

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Abstract

Based on the review of herbarium specimens, geo-referenced live images, and field observations, a new species of the genus *Ceiba* (Malvaceae) is described. *Ceiba camba*, the new species, has previously been confused with other species in the *Ceiba insignis* complex, specially with *C. speciosa*, and went undifferentiated despite having a wide distribution in the lowlands of central-western South America and being quite common. However, the new species here described shows clear visible morphological differences from *C. speciosa* and the other members of the genus. The main similarities and differences with other morphologically and geographically close species of the *C. insignis* complex (*C. chodatii*, *C. crispiflora*, *C. insignis*, *C. lupuna*, *C. pubiflora*, *C. speciosa*) are discussed.

Key words: Chiquitania, pink bottle tree, Southwest Amazon, floss silk tree, toborochi

Resumen

A partir de la revisión de muestras de herbario, imágenes en vivo georeferenciadas y observaciones en campo, se describe una nueva especie del género *Ceiba* (Malvaceae) perteneciente al complejo de *Ceiba insignis*. *Ceiba camba*, la nueva especie, hasta ahora ha sido confundida con otras del complejo *Ceiba insignis*, especialmente *C. speciosa*, y pasó desapercibida pese a contar con una amplia distribución en las tierras bajas de Sudamérica centroccidental y ser bastante común. Sin embargo, la nueva especie descrita aquí muestra claras diferencias morfológicas visibles con *C. speciosa* y los otros miembros del género. Se discuten las principales similitudes y diferencias con otras especies del complejo *C. insignis* (*C. chodatii*, *C. crispiflora*, *C. insignis*, *C. lupuna*, *C. pubiflora*, *C. speciosa*) morfológica y geográficamente cercanas.

Palabras clave: árbol botella rosado, Chiquitania, Sudoeste Amazonia, árbol de seda, toborochi

Introduction

The contemporary species of the genus *Ceiba* Mill. (1754, s.p.) were initially divided into three taxa (*Ceiba*, *Chorisia* Kunth (1822, 295) and *Eriodendron* DC. (1824: 479)) according to the presence of staminal appendages, the degree of fusion of the stamens and the swelling of the trunk. However, the differences proved inconsistent and species previously belonging to *Chorisia* and *Eriodendron* were integrated into the genus *Ceiba* (Gibbs & Semir 2003; Carvalho-Sobrinho *et al.* 2016; Pezzini *et al.* 2021) which currently includes 18 accepted species, considering the 19 listed by the POWO (2023), but excluding *Ceiba salmonea* (Ulbr.) (Bakh. (1924: 198) which has been synonymized with *Spirotheca rosea* (Seem.) P.E.Gibbs & W.S.Alverson (2006, 253) (Gibbs & Alverson 2006; Carvalho-Sobrinho *et al.* 2016; Pezzini *et al.* 2021).

Within the genus, Gibbs & Semir (2003) recognized a set of seven species—*Ceiba chodatii* (Hassl.) Ravenna (1998: 44), *C. crispiflora* (Kunth) Ravenna (1998: 45), *C. insignis* (Kunth) (P.E.Gibbs & Semir (1988: 134), *C. lupuna*

P.E.Gibbs & Semir (2003: 270), *C. pubiflora* (A.St.-Hil.) K.Schum. (1886: 213), *C. speciosa* (A.St.-Hil., A.Juss. & Cambess.) Ravenna (1998: 46) and *C. ventricosa* (Nees & Mart.) Ravenna (1998: 47)—with characteristics very similar to each other and sometimes difficult to differentiate, which they group in a species complex around *C. insignis*. Later, Pezzini *et al.* (2021) based on the results of molecular studies propose the inclusion of three species—*C. boliviana* Britten & Baker f. (1896: 174), *C. erianthos* (Cav.) K.Schum. (1886: 211) and *C. rubriflora* Carv.-Sobr. & L.P.Queiroz (2008: 649)—in the *C. insignis* complex *sensu* Gibbs & Semir (2003). So far, the *C. insignis* complex comprises these 10 previously listed species.

Species of the *Ceiba insignis* complex are naturally distributed in the tropical and subtropical regions of South America, mostly in the seasonally dry and semi-deciduous forests that extend along the Pleistocene arc from Ecuador in the northwest, through Peru, Bolivia, Paraguay, northern Argentina as far south as Tucumán, and then up through northern Uruguay to northeastern Brazil. However, two species—*C. speciosa sensu* Gibbs & Semir (2003) and *C. lupuna*—are also found in more humid habitats such as the riparian forests of western and southwestern Amazon (Gibbs & Semir 2003; Pezzini *et al.* 2021).

The present taxonomic treatment proposes an additional species of the genus *Ceiba*, belonging to the *C. insignis* complex, so far erroneously identified as *C. speciosa*. Our hypothesis is based on the observation of morphological characters of floral and foliar structures, as well as distributional and ecological characteristics, which clearly differentiate the individuals of this new species from those belonging to *C. speciosa* with which they have been confused until now.

Material and methods

The identification of diagnostic characters and the description of the new species were made based on herbarium specimens, *in situ* observations, and georeferenced photographs. Botanical specimens, represented by own gatherings and herbarium specimens, were mainly used to analyze characters related to structure, shape, and morphometry. Additionally, *in situ* observations and live photographs were used to analyze traits related mainly, but not exclusively, to coloration. Patterns were identified to define the non-morphological characteristics of the new species from data from all sources, such as date, location and habitat type, among others. The analyses related to the locality and the map of recorded occurrences, were performed using the software Qgis (version 3.20) for the visualization of various thematic maps (Navarro & Ferreira 2009; Olson *et al.* 2001; others). A cluster analysis by similarity of the visible morphological characters of the floral structures was carried out with the maximum distance or farthest neighbor (complete) method and rectilinear distance (“Manhattan”) (Palacio *et al.* 2020) using the statistical software Rstudio (version 2021.09.2; Build 382). For the definition of morphological characters and their states, the method proposed by Sereno (2007) was followed. The character statements used for the cluster analysis and the included species are presented in Annex B. In the analysis of diagnostic characters, geographic distribution areas, and grouping by morphological similarity (cluster analysis), specimens of other species of the *Ceiba insignis* complex (*C. boliviana*, *C. chodatii*, *C. crispiflora*, *C. erianthos*, *C. insignis*, *C. lupuna*, *C. pubiflora*, *C. speciosa*, *C. rubriflora*, and *C. ventricosa*), and also of *C. glaziovii* (Kuntze) K.Schum. (1900: 343), *C. pentandra* (L.) Gaertn. (1791: 244), *C. samauma* K.Schum. (1886: 210) and *C. trischistandra* Bakh. (1924: 196) as outgroups, were included among the examined material (herbarium specimens listed in Annex A and live photographs listed in Annex B). To reduce distortions in the results, reports from possibly cultivated specimens were excluded in the locality-dependent analyses and those with uncertain morphological character states were excluded in the similarity cluster analysis.

The examined botanical material, both in physical and as digitized images, are deposited in the herbaria ASU, B, BM, F, H, L, LPB, M, MO, NY, O, P, U, UF, UNOP, US, USZ, W, WAG, Z (Thiers 2022); and in the case of digitized images, they were accessed through GBIF (2022). The iNaturalist (2022) database was used as source of live photographs, along with our own field images or those provided by collaborators.

Results

Ceiba camba Drawert, Angulo & Catari, *sp. nov.* (Figures 1, 2 & 3)

Type:—BOLIVIA. Santa Cruz, Provincia Obispo Santistevan, Municipio Montero: at 0.3 km E of Puente Eisenhower/Puente de la Amistad, on small dirt road ca. 0.2 km N from the Montero-Buena Vista highway (“carretera nueva a Cochabamba”), 17°19′09″ S, 63°19′18″ W, 10 May 2007, *M.H. Nee 55409* (holotype, here designated: USZ!, isotypes COL, CTES, K, LPB, MEXU, MO, NSW, NY, US).

It differs from all species of the genus *Ceiba* by the combination of short and winged petiolules; calyx cylindrical to elongated-campanulate; petals distally pale pink to magenta and basally white to deep yellow; 5 lobed staminal appendages, lobes bifid, scarcely pilose to pilose and whitish, yellow to pinkish; stamens fused into staminal tube; and stigma deep red to carmine.

Tree, deciduous, 20–30 m tall when mature; trunk conical, pachycaulous, usually ventricose in the basal section, up to 2 m diameter at breast height and with low buttresses; bark in juveniles green, turning gray to dark gray and often developing green striations, especially in juveniles usually covered with conoidal aculei up to 25 mm, regularly scattered and extending to the main branches; canopy generally open with erect-patent branches. *Leaves* alternate, palmately compound with (3–) 5 (–7) leaflets, usually the two posterior ones smaller than the anterior ones; petioles 30–150 mm long, the petiolules short, not more than 12–15 mm long, marginate-winged; leaflets 43–125 mm × 18–52 mm, with length/width (l/w) ratio about (1.4–) 2.3 (–3.1), elliptic to oblanceolate or even slightly obovate, the base attenuate to cuneate and apex acute to acuminate, pinnatinerved, the margin medially and distally dentate and usually entire at basal section, the upper surface dark green, the lower face paler. *Inflorescences* of few-flowered fascicles or of single flowers. *Flowers* stellate, 75–120 mm long when extended; peduncle 8–25 mm long; calyx 16–26 mm tall × 8–13 mm diameter, gamosepalous with 3–5 lobes, tubular to slightly elongate-campanulate, green to yellowish green; corolla dialipetalous, actinomorphic and pentamerous; petals 70–90 mm × 15–35 mm, with ca. 4 (2.5–5.1) l/w ratio, spatulate to oblanceolate, slightly arched from base, the margin undulate, abaxially sericeous, whitish pink to pale pink and basally usually white, adaxially glabrous, distally deep pink to pale pink, or even white with faint pink only on the margins, basal third to half yellow to ivory, usually with some irregular longitudinal deep pink to red lines in some cases concentrated near the base to form an inverted “V”, in senescent flowers the color intensity of petals gradually reduced and a brown spot arising from the base, the base usually becoming whitish; androecium with stamens fused into a staminal tube 58–78 mm in total length, basal section below staminal appendages 13–21 mm long × 3.1–5 mm diameter, glabrous and caniculate, staminal appendages 5, 2.1–5.5 mm high, scarcely pilose to pilose, strongly bi-lobed, forming usually an asymmetrical crown, yellow to ivory and sometimes pink towards apex, with whitish trichomes, the staminal tube above the staminal appendages 42–56 mm long × 1.8–2.7 mm diameter, pink to white, usually lightening towards the base, slightly curved with concrescent filaments up to the apex, the anthers welded into a collar 6.3–8.4 mm high × 5–8 mm diameter, and rarely split at the apex; pollen white to ivory; gynoecium with subglobose semi-inferior ovary 4–9.6 mm high × 2.7–4.4 mm diameter; style white, extending 5.7–13 mm above the anther collar; stigma globose and velutinous red to crimson. *Fruit* a capsule 100–200 mm long × 50–120 mm diameter, the shape variable, usually ellipsoid to pyriform, green to dark green, with 5 valves; endocarp with trichomes forming dense white cottony filling in which the seeds embedded. *Seeds* 4–8 mm diameter, spheroid, slightly prolate and mamelonate, dark brown to chestnut-colored.

Paratypes:—BOLIVIA. **Beni:** Prov. Ballivián, Mun. San Borja, serranía Pilon Lajas carretera Yucumo-Quiquibey 13 km al suroeste de Yucumo, [15°17′26″ S, 67°04′25″ W], 400 m, 08 May 1991, *T. Killeen 3260* (LPB, MO image!, USZ!); Prov. Vaca Díez, Tumi Chucua, 30 km S of Riberalta along the Río Beni, 11°08′ S, 66°10′ W, 210 m, 15 May 1982, *J.C. Solomon 7604* (F image!). **La Paz:** Prov. Larecaja, Guanay, [15°28′59″ S, 67°52′59″ W], 2000 ft. [609.6 m], October 1885, *H.H. Rusby 661* (US image!). **Santa Cruz:** Prov. Andrés Báñez, Mun. La Guardia, along new highway from Santa Cruz to Abapó, 5 km S of Río Peji bridge, 18°01′ S, 63°12′ W, 500 m, 02 May 1991, *M.H. Nee 49222* (USZ!); along Brecha 7, 3.1 km E of the Santa Cruz-Abapo highway, 18°08′12.8″ S, 63°09′38.2″ W, 455 m, 13 May 2007, *M.H. Nee, D. McClelland & S. Stern 55426* (US image!); [ex Prov. Cercado], Mun. Santa Cruz de la Sierra, Quinta de Santa Cruz, [17°42′ S, 63°12′ W], 450 m, 31 May 1925, *J. Steinbach 7129* (BM image!); J. Botanique de Santa Cruz de la Sierra [Jardín Botánico antiguo], [17°47′08″ S, 63°13′29″ W], 18 May 1978, *J.P. Ybert 639* (P image!); Santa Cruz de la Sierra, 22 April 1979, *A. Krapovickas & A. Schinini 35189* (F image!); Santa Cruz [de la Sierra], 07 June 1989, *C. Orellana-Soto 4* (USZ!); Santa Cruz de la Sierra, Avenida Piraí, W side of city of Santa Cruz [de la Sierra], [17°46′48″ S, 63°12′00″ W], 420 m, 14 May 1991, *M.H. Nee 40440* (NY image!); Santa Cruz de la



FIGURE 1. *Ceiba camba*. Isotype (M.H. Nee 55409, NY 02684187). The New York Botanical Garden (licensed under CC BY 4.0).

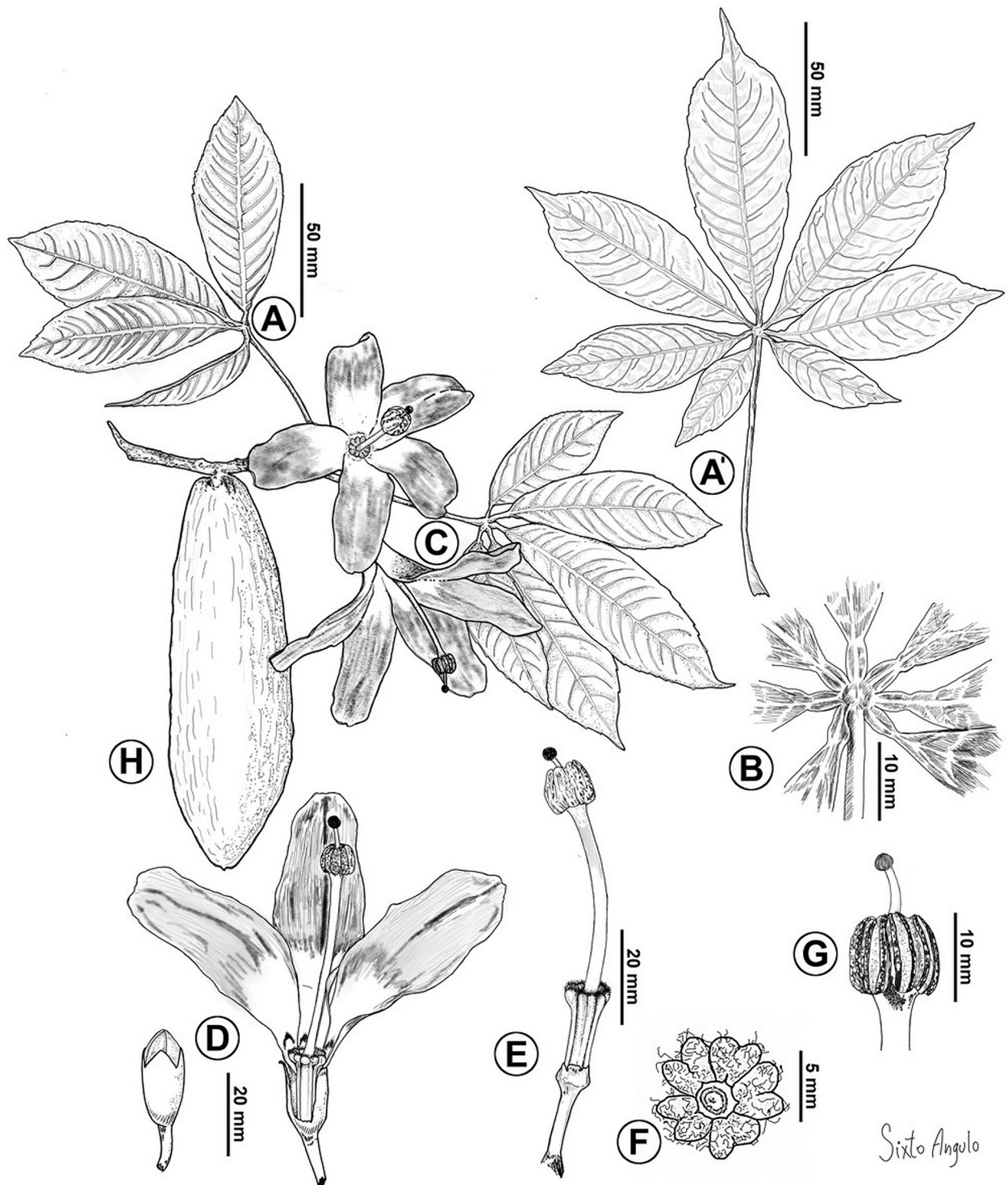


FIGURE 2. *Ceiba camba*. **A:** Leaves. **B:** Detail of petiolules. **C:** Flowers at anthesis. **D:** Flower-bud and flower. **E:** Staminal column and appendages. **F:** Staminal appendages, upper view. **G:** Collar of anthers, style and stigma. Based on paratype (A.A. Angulo et al. 5, USZ). Drawings by Sixto Angulo.

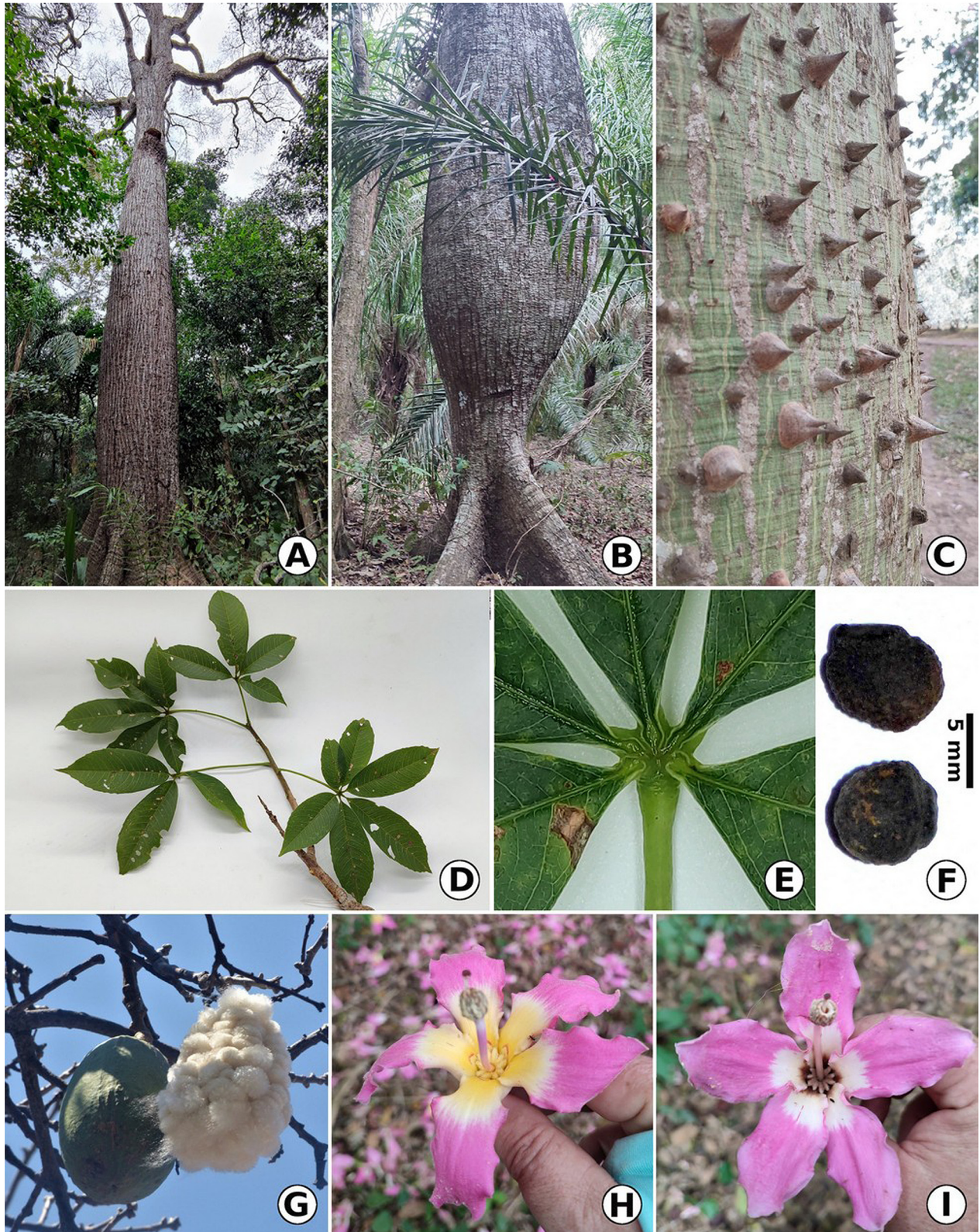


FIGURE 3. *Ceiba camba*. **A:** Trunk in humid habitat (A.A. Angulo et al. 1, paratype, USZ). **B:** Trunk in dry habitat (A.A. Angulo et al. 3, paratype, USZ). **C:** Detail of bark and prickles. **D:** Branch with leaves of 3, 4, 5 and 6 leaflets (A.A. Angulo et al. 5, paratype, USZ). **E:** Detail of petiolules. **F:** Seeds. **G:** Fruit and open capsule. **H:** Flower (A.A. Angulo et al. 5, paratype, USZ). **I:** Senescent flower (A.A. Angulo et al. 5, paratype, USZ). Photos: A.A. Angulo (D, F, G), J.C. Catari (A, B, I) & H.A. Drawert (C, E, H).

Sierra, alrededores de la Plaza 24 de Septiembre, [17°47'00" S, 63°10'55" W], 420 m, 11 March 1995, *A. Jiménez, M. Villegas & M. Menacho 1* (USZ!); Santa Cruz de la Sierra, Plazuela Blacutt, from 1–2 blocks south of Irala Ave. on Velarde Ave., [17°47' S, 63°10' W], 400 m, 10 April 1995, *J.R. Abbott 16568* (UF image!, USZ!); Santa Cruz de la Sierra, campus universitario facultad de veterinaria, 17°46' S, 63°11' W, 400 m, 29 March 1996, *M. Menacho & A. Jiménez 781* (USZ!); Prov. Ichilo, Buena Vista, cultivated on main plaza, 17°27' S, 63°40' W, 375 m, 26 May 1991, *M.H. Nee 40575* (NY image!, USZ!); cultivated on the main plaza, 17°27' S, 63°40' W, 375 m, 27 May 1991, *M.H. Nee 40576* (NY image!); Prov. Sara, Mun. Santa Rosa del Sara, Propiedad Juan Deriba aprox. 4.4 km al este de Santa Rosa, 17°07'12" S, 63°33'40" W, 260 m, 30 May 2022, *A.A. Angulo, J.C. Catari & H.A. Drawert 1* (USZ!); Propiedad Juan Deriba aprox. 4.6 km al este de Santa Rosa, 17°06'49" S, 63°33'29" W, 252 m, 30 May 2022, *A.A. Angulo, J.C. Catari & H.A. Drawert 2* (USZ!); Propiedad Juan Deriba aprox. 4.9 km al este de Santa Rosa, 17°06'44" S, 63°33'17" W, 285 m, 30 May 2022, *A.A. Angulo, J.C. Catari & H.A. Drawert 3* (USZ!); Propiedad Juan Deriba aprox. 5.5 km al este de Santa Rosa, 17°07'01" S, 63°33'02" W, 274 m, 30 May 2022, *A.A. Angulo, J.C. Catari & H.A. Drawert 4* (USZ!); Santa Rosa, ca. 150 m al este del Estadio Municipal, 17°06'41" S, 63°35'39" W, 277 m, 31 May 2022, *A.A. Angulo, J.C. Catari & H.A. Drawert 5* (USZ!); Prov. Velasco, Mun. San Ignacio de Velasco, en el pueblo en la plaza, [16°22'26" S, 60°57'37" W], 30 April 1986, *S.G. Beck & R. Seidel 12433* (US image!); Reserva forestal Bajo Paraguá, Laja Granítica, 14°32'20" S, 61°30'00" W, 250–500 m, 12 May 1994, *T. Killeen 6303* (USZ!); Prov. Warnes, Mun. Warnes, pampa de Viru Viru a 17 km de Santa Cruz de la Sierra, aeropuerto Int. de Viru-Viru, 17°39'46" S, 63°69'24" W, 30 April 1995, *M. Menacho & J. Balcazar 733* (USZ!). BRAZIL. **Mato Grosso:** Mun. Barra dos Bugres, Serra das Araras, Fazenda Currupira, 15°10' S, 56°51' W, 17 May 1998, *B. Dubs 2346* (E, K, MBM, S, U image!, Z); Cotriguaçu, road Cotriguaçu to Juruena, 18 km S of Cotriguaçu, [15°10' S, 56°51' W], 26 May 1998, *B. Dubs 2443* (E, S, Z image!); Mun. Jauru, Rodovia Jauru-Araputanga próximo ao km 30, [15°27'19" S, 58°38'59" W], 6 May 1995, *G. Hatschbach et al. 62447* (US image!). **Rondônia:** Mun. Ji-Paraná, Linha 56 a 45 km da cidade, [10°52'45" S, 61°56'57" W], 4 May 1987, *C.A. Cid Ferreira 9024* (NY image!); Mun. Ouro Preto do Oeste, Estrada para o morro da Embratel, pista sul de vôo de Paraclaide, 10°43'16.8" S, 62°13'24.9" W, 4 June 2015, *H. Medeiros et al. 1768* (NY image!); Mun. Presidente Medici, BR 364, rodovia Cuiabá-Porto Velho, km 300, estrada para Alvorada do Oeste, km 24, linha 110, 11°12' S, 62°63' W, 28 June 1984, *C.A. Cid Ferreira et al. 4868* (NY image!). PERÚ. **Madre de Dios:** Prov. Tahuamanu, Distr. Iñapari, Rio Acre, [10°56' S, 69°57' W], May 1911, *E.H.G. Ule 9597* (L image!).

Phenology:—With flower buds in February to May and flowers in anthesis from March to June at beginning of the dry season. Capsules open and disperse seeds from June to September. Leaves usually drop shortly before and/or at the beginning of flowering.

Distribution and habitat:—The species is reported from the lowlands of the departments of Beni, Pando and Santa Cruz in eastern Bolivia, the states of Rondônia and Matto Grosso in central-western Brazil, and the department of Madre de Dios in southeastern Peru (Fig. 4). It inhabits humid to sub-humid and often seasonally dry, semi-deciduous to evergreen forests in the southern portion of the southwestern Amazon moist forests and northern Chiquitano dry forests (Olson *et al.* 2001), mainly in transitional ecosystems between the two biomes. According to the biogeographic classification of Navarro & Ferreira (2009) for Bolivia, the species is found throughout the Benianian province (“Beniana”); in the Chiquitano-Crucenian (“Chiquitano Cruceño”) and Chiquitanian transitional to Amazonian (“Chiquitano transicional a la Amazonía”) sectors of the Western Cerradense (“Cerradense Occidental”) province; the sectors Pre-Andean of northern Bolivia and southern Peru (“Preandino del Norte de Bolivia y Sur de Perú”), Heath and lower Madidi (“Health y bajo Madidi”), and Acre and Madre de Dios (“Acre y Madre de Dios”) of the Southwestern Amazonian (“Amazónica Suroccidental”) province; and the Guaporé and upper Madeira sectors of the Central-Southern Amazonian (“Amazónica Centro-Suereña”) province.

Etymology:—The specific epithet “*camba*” is a noun used as a demonym to refer to the inhabitants of the eastern lowlands in Bolivia, mainly in the departments of Santa Cruz, Beni and Pando, and largely coincides with the distribution of the species.

Conservation status:—The species is relatively extensively distributed in western and central South America, where it is abundant in some localities. The extent of occurrence (EOO) of the species, calculated from the analyzed data in this description, is approximately of 1000000 km². There are stable natural populations within several protected areas in Bolivia, and possibly also in Brazil. It is also widely cultivated in urban and peri-urban areas because of its ornamental qualities, even outside its natural range.

Although there are anthropogenic pressures, such as the expansion of agricultural frontiers and changes in land cover, that can locally impact population sizes, *Ceiba camba* thrives in areas that have experienced some degree of ecological degradation. Furthermore, the species exhibits a remarkable resilience to forest fires, a major threat to biodiversity within its distribution range. Although *C. camba* holds cultural and ornamental value, it currently lacks economic significance as a timber resource, thus mitigating risks associated with logging and illegal trade.

Therefore, according to the International Union for Conservation of Nature (IUCN) categories and criteria (IUCN Standards and Petitions Subcommittee 2022), *Ceiba camba* should be classified as of “Lower Concern” (LC) since it does not meet any of the criteria for inclusion in a threatened category (Critically Endangered, Endangered or Vulnerable).

Taxonomic observations:—Similar to *Ceiba speciosa* and *C. crispiflora* in color of petals; but differs in light (whitish, yellow to pink) and never dark (red to crimson) color of staminal appendages, dark (red to crimson) and never light (pale red to white) color of stigma, cylindrical to elongate-campanulate (*vs.* globular-campanulate) calyx, and short and winged (*vs.* long) petiolule (Fig. 5). Similar to *C. lupuna* in color of stigma and basal section of petals, but differs in distal petal color (pink to deep pink *vs.* red) and petal shape (spatulate to obovate, 15–35 mm wide with slightly undulate margin *vs.* narrowly oblong to elongate-spatulate, 14–18 mm wide with markedly undulate margin) and the color and pubescence of staminal appendages (whitish, yellow to pink and sparsely pilose to pilose *vs.* dark red and densely pilose) (Fig. 5). Similar to *C. chodatii* and *C. insignis* in color of staminal appendages but differs in that they are sparsely pilose to pilose and not glabrous to sparsely pilose; also differs by cylindrical to elongate-campanulate shape of calyx rather than campanulate to globose, and petals externally sericeous rather than sericeous to villous, distally pink to deep pink *vs.* white, ivory to pale pink or yellow. It differs from *C. boliviana* and *C. pubiflora* by filaments fused in staminal tube and anthers in collar (rarely slightly fissured), and never free filaments and separate anthers.

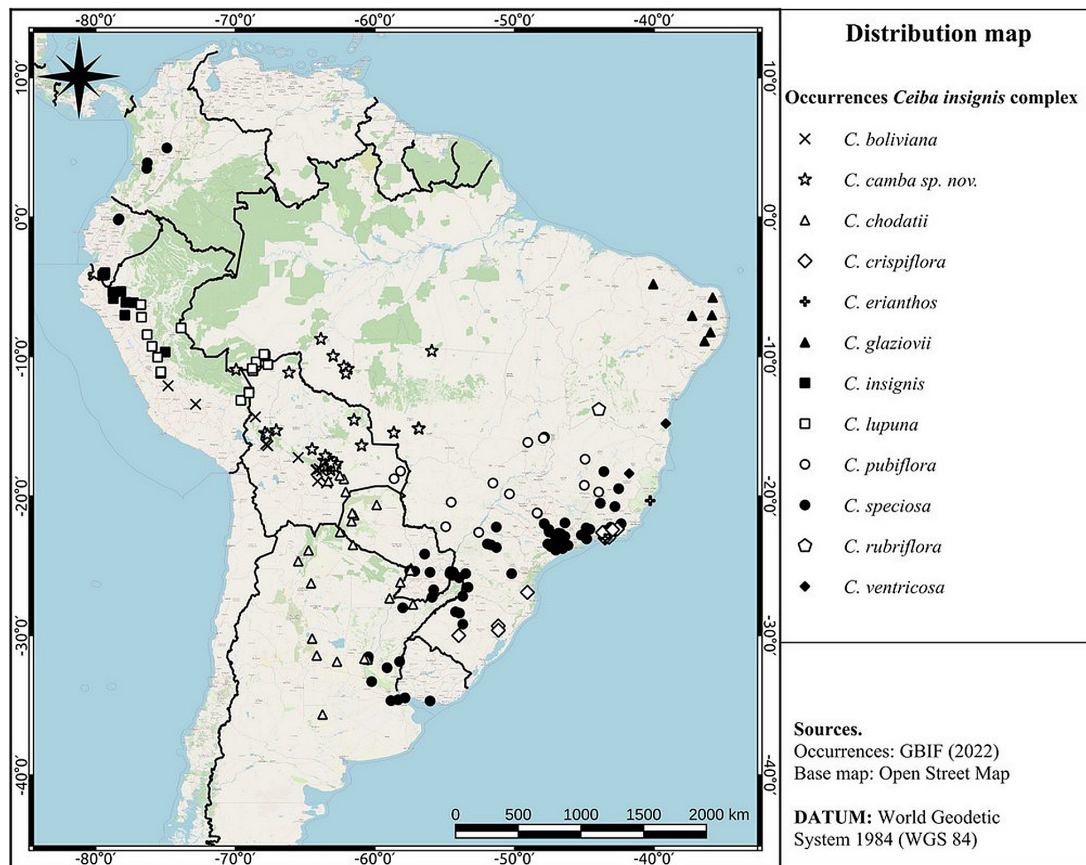


FIGURE 4. Distribution map of autochthonous occurrences of *Ceiba insignis* complex species.

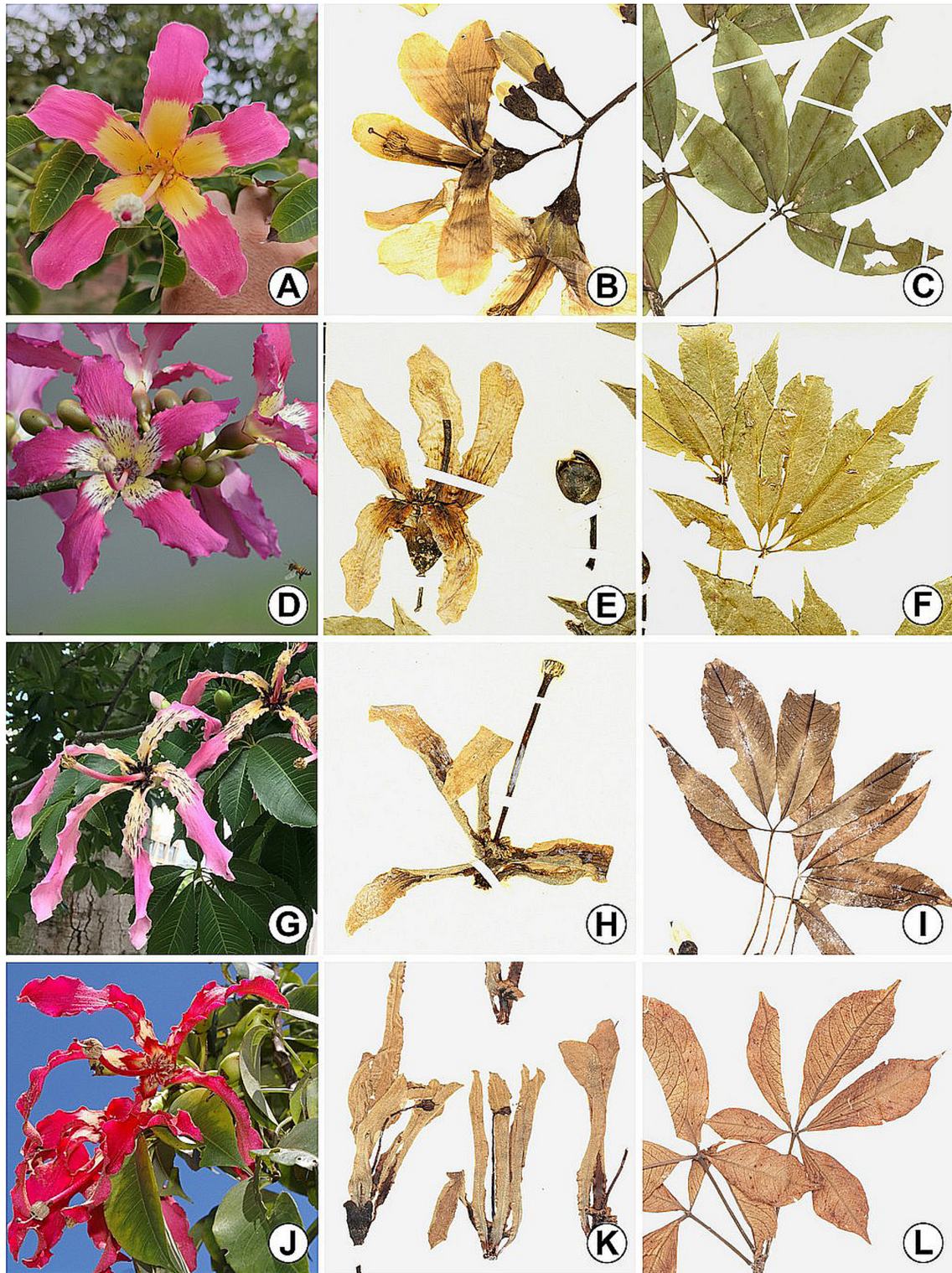


FIGURE 5. Comparison of flowers and leaves of *Ceiba camba* (A: Paratype designed here, A.A. Angulo et al. 2, USZ. B: Paratype designed here, M.H. Nee 40440, NY. C: Isotype, designed here, M.H. Nee 55409, US.); *C. speciosa* (D: iNaturalist 111017339. E: and F: Lectotype designed by Gibbs & Semir 2003, A. de Saint-Hilaire [s.n.], P.); *C. crispiflora* (G: www.tropplants.com. H: Lectotype designed by Gibbs & Semir 2003, G.H. Langsdorff [s.n.], P. I: Paratype designed by Gibbs & Semir 2003, C.M. Viera 544, NY); and *C. lupuna* (J: R. Vásquez et al. 35772, MO. K: Holotype designed by Gibbs & Semir 2003, J. Schunke V. 5326, MO. L: Paratype designed by Gibbs & Semir 2003, C.A. Cid et al. 10234, NY). Photographs by H.A. Drawert (A), The New York Botanical Garden (B, I, L, licensed under CC BY 4.0), Smithsonian Institution (C, licensed under CC0 1.0), C. Mermelstein (D, licensed under CC BY-NC 4.0), Muséum national d'Histoire naturelle, Paris (E, F, H, licensed under CC BY 4.0), M.C. Gaston (G), Missouri Botanical Garden (J, K, licensed under CC BY-NC-SA 3.0).

Discussion

Species of the *Ceiba insignis* complex in general present high intraspecific morphological plasticity and high interspecific morphological affinity (Gibbs & Semir 2003; Perrotta *et al.* 2007; Lozano & Zapater 2018; Pezzini *et al.* 2021). This often makes their correct identification difficult. Taxonomic boundaries within *Ceiba* sometimes become tenuous, even more so if we consider that the species of the complex are inter-fertile and can produce fertile hybrids, which opens up an almost infinite range of individual morphological characteristics, especially in floral structures (Gibbs & Semir 2003; De Egea *et al.* 2012; Lozano & Zapater 2018; Pezzini *et al.* 2021). In addition, some key characters for identification are often lost during the process of botanical material preparation or specimens are incomplete (Gibbs & Semir 2003). All this implies that non-floral characteristics, and even non-morphological traits, are helpful in delimiting the species of this complex, especially when there are shared and/or very similar morphological characters in the floral structures. Thus, leaf and non-morphological characteristics such as biogeographic and habitat attributes proved to be very useful in delimiting this new species within the *C. insignis* complex.

The distribution range of *Ceiba camba* is clearly disjunct from that of *C. speciosa* with which it was confused so far, and these species do not meet geographically (Fig. 4). While the species described here inhabits mainly moist to subhumid and seasonally dry semi-deciduous to evergreen forests of central-western and central South America, *C. speciosa* is found mainly in moist to subhumid deciduous to semi-deciduous forests in the southern region of the Atlantic Forest at the eastern side of the continent. The two species are separated by a wide area inhabited in the northern section by *C. pubiflora* and in the southern by *C. chodatii*. Furthermore, considering the predominant orography in the distribution area of both species, it is very likely that the references made to the presence of *C. speciosa* in humid environments (Gibbs & Semir 2003; Pezzini *et al.* 2021) are mainly based on occurrences of *C. camba* widely distributed in the Moxos plains (“Llanos de Moxos”), and not of *C. speciosa* which is mostly found in an undulating and better drained landscape.

There exists a population of *Ceiba* aff. *speciosa* in the montane forests of Ecuador and Colombia (iNaturalist 2022; Orrell & Informatics Office 2022) that is completely isolated and distant from the distribution range of *C. speciosa*. Further studies are needed to rule out an anthropogenic origin or the existence of a cryptic species. Additionally, this population is also separated from *C. camba* by a wide area occupied by other species of the *C. insignis* complex (i.e. *C. insignis* and *C. lupuna*).

Other species with which the species described here has been confused in the past are *Ceiba insignis*, which has historically been problematic (Gibbs & Semir 2003), and *C. lupuna*. Although flower colors are generally distinctly different in fresh samples (petals distally white to pale pink in *C. insignis* and deep red in *C. lupuna*), there is some similarity in the shapes of floral structures and in the leaves with short, winged petiolules in all three species. This can lead to confusion in herbarium preparations where the colors have disappeared or which do not include mature flowers, and which also do not indicate in the label a description of the live colors of the floral structures. Confusion can also occur in fresh samples when petal coloration is atypical and very close to that typical of one of the other species; for example, specimens of *C. camba* with almost white or reddish-pink petals, which, although very rare, are within the range of morphological plasticity of the species. However, besides non-morphological differences such as inhabited ecosystem and distribution area, according to the redescription by Gibbs & Semir (2003), the new species differs from *C. insignis* by a more cylindrical to elongate-campanulate rather than campanulate to globose calyx, petals externally glabrous to sericeous rather than sericeous to villous, and subtly more pubescence of the staminal appendages against sparse or no pubescence; whereas from *C. lupuna* it can be differentiated because the latter has narrower petals with markedly undulate margin and densely pilose, dark red staminal appendages, as described by Gibbs & Semir (2003).

Cluster analysis by similarity of visible morphological characters of floral structures, which did not include *Ceiba insignis*, *C. rubriflora* and *C. ventricosa* due to a lack of live photographs with which to evaluate them, indicates that *C. camba* would be very close to *C. lupuna*, and both would form a parallel clade to *C. crispiflora* and *C. speciosa* (Fig. 6). Furthermore, according to the results of phylogenetic analyses of DNA sequences performed by Pezzini *et al.* (2021), which does not include *C. camba* and *C. chodatii*, there is a greater genetic affinity of *C. lupuna* with *C. pubiflora* and *C. insignis* than with *C. crispiflora* or *C. speciosa*. Therefore, the phylogenetic position of *C. camba* with respect to the other species of the *C. insignis* complex is for now still uncertain, but we hypothesize that the species could be part of a clade composed of *C. lupuna*, *C. insignis* and *C. pubiflora* within the maximum clade credibility tree presented by Pezzini *et al.* (2021).

Alverson (2014) treated *Ceiba camba* under the name *C. speciosa*, only commenting (in translation) that the species is “part of the *C. insignis* complex and frequently so identified when sterile.” Nee (2008), for the Parque

Nacional Amboró region, treated two species of *Ceiba*, *C. boliviana* and *C. camba*, the latter also under the name of *C. speciosa*, and did not address differences between the populations in Brazil and those in Bolivia (pers. comm., 2022). In a recent overview of the genus *Ceiba* in Bolivia, Melgar *et al.* (2021) included *C. insignis* and *C. speciosa* as species present in the country. However, the figures accompanying the text of *C. speciosa*, and the indicated examined material (that was also examined for this work) showed the diagnostic characters that indisputably permits identifying it as *C. camba*. The report of *C. insignis* is based on the occurrence of only one cultivated specimen within the urban area of the city of Santa Cruz de la Sierra, which probably corresponds to a hybrid of *C. camba* with *C. chodatii*. We were able to confirm *in situ* that the specimen even on the same branch carries flowers with characteristics of both the new species, although of very pale color, and of *C. chodatii*, very similar to those presented by Melgar *et al.* (2021) in their figure 5D (see also the flowers in the background) as of the latter species. Furthermore, in the description they indicate “petals [...] 5–8 × 2–3 cm, externally sericeous or glabrous” and “appendicular lobes [...] somewhat pubescent”, characteristics that deviate from those indicated by Gibbs & Semir (2003) for *C. insignis* (petals 90–120 mm long, externally sericeous to villous and staminal appendages glabrous to sparsely hairy) and, except for petal coloration, agree more closely with those of the species described in this paper. Unfortunately, we were unable to examine the supporting herbarium material on which Melgar *et al.* (2021) relied to state the presence of *C. insignis* in Bolivia, as we were unable to access it at “Germán Coimbra Sanz” Herbarium [not indexed by Thiers (2022)] where it should be deposited.

With the description of *C. camba* the number of species of the genus *Ceiba* increases to 19 and the number of species of the *C. insignis* complex to 11, comprising the seven species originally included by Gibbs & Semir (2003), the three added by Pezzini *et al.* (2021) and the new species described here.

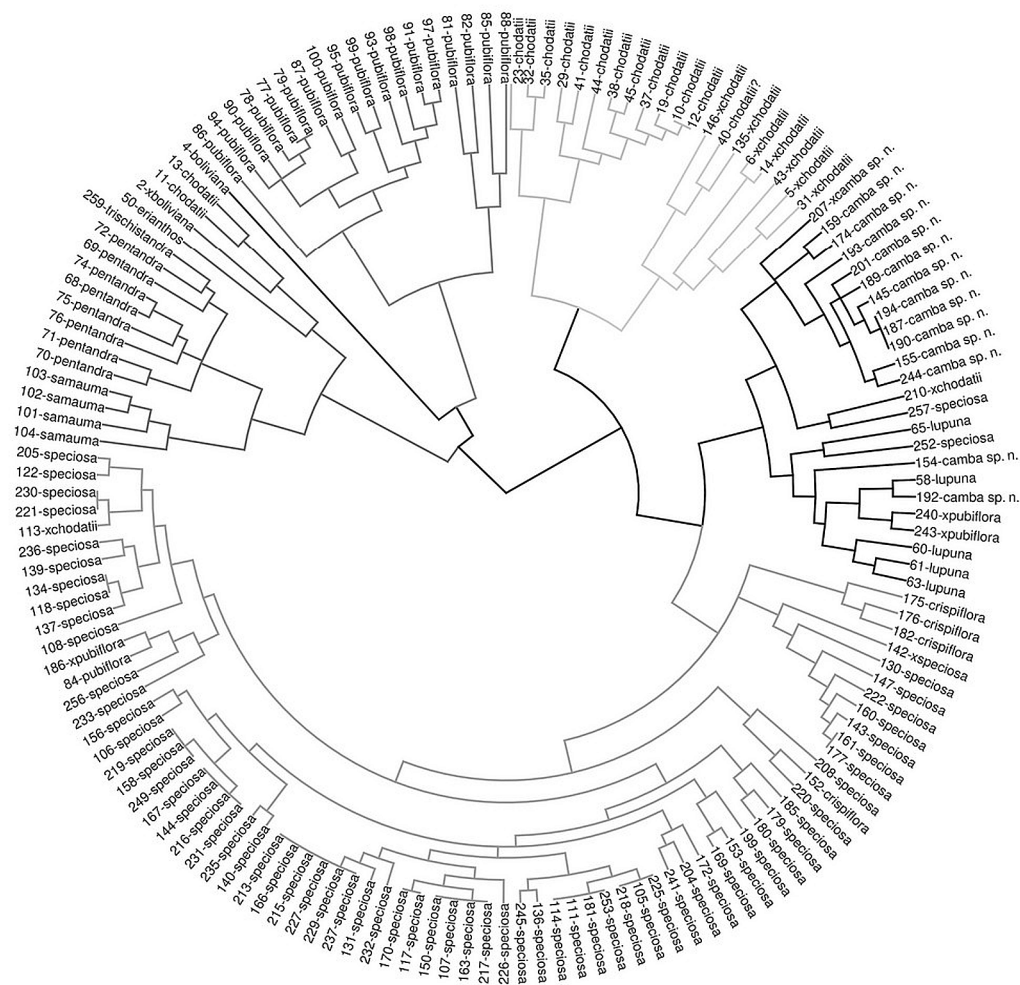


FIGURE 6. Dendrogram resulting from the analysis of hierarchical clusters by morphological characters affinity between some species of *Ceiba*.

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