



***CEIBA GUARANI* (MALVACEAE, BOMBACOIDEAE), A NEW SPECIES FROM SUB-ANDEAN SOUTHERN BOLIVIA AND THE SIERRAS OF NORTHWESTERN ARGENTINA**

Ceiba guarani (Malvaceae, Bombacoideae), una nueva especie del Subandino sur de Bolivia y las Sierras del noroeste de Argentina

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Summary: Based on observations made during botanical surveys in the southern sub-Andean of Bolivia, analysis of collected material, review of herbarium material and online databases, we determined that the *Ceiba* populations of the xeric Bolivian-Tucuman forests, previously identified as *Ceiba chodatii*, correspond to a new species. Given that the morphological, ecological and distributional characteristics differ from those observed in populations of *C. chodatii*, we propose *Ceiba guarani* *sp. nov.* Our field observations and distribution data from the revised specimens indicate that *C. chodatii* is naturally restricted to the Chaco plains and a strip of the southern Subandean foothills, whereas *Ceiba guarani* is distributed mainly in the Subandean ranges.

Key words: Bolivian-Tucuman forest, Bombacoideae, Chaco, Neotropical flora, Taxonomy.

Resumen: A partir de observaciones hechas durante prospecciones botánicas al Subandino sur de Bolivia, análisis de material colectado, revisión de material de herbarios y bases de datos online, determinamos que las poblaciones de *Ceiba* de los bosques xéricos Boliviano-Tucumano, previamente identificadas como *Ceiba chodatii*, corresponden a una nueva especie. Dado que las características morfológicas, ecológicas y de distribución difieren de lo observado en las poblaciones de *C. chodatii*, se propone *Ceiba guarani* *sp. nov.* Nuestras observaciones de campo y los datos de distribución de los especímenes revisados, indican que *C. chodatii* está naturalmente restringida a las llanuras chaqueñas, y una franja del piedemonte del Subandino sur, en tanto que *Ceiba guarani* se distribuye principalmente en las serranías del Subandino.

Palabras clave: Bombacoideae, Bosque Boliviano-Tucumano, Chaco, Flora Neotropical, Taxonomía.

Introduction

The genus *Ceiba* Mill. (1754: s.p.) within the family Malvaceae Juss. (1789: 271) currently contains 19 recognized species according to Gibbs & Semir (2003), Carvalho-Sobrinho & de Queiroz (2008) and Drawert *et al.* (2024). The proposal made by Gibbs & Semir (2003) included all species of *Eriodendron* DC. (1824: 479) and *Chorisia* Kunth (1822: 295) within *Ceiba*; furthermore, they recognized

two sections [*Campylanthera* (Schott & Endl.) K. Schum., (Martius, 1886: 207) and *Ceiba*] in the genus. These authors highlight that section *Ceiba* contains a group of species that are closely related to each other. They named this group the *Ceiba insignis* (Kunth) P. E. Gibbs & Semir (1988: 134) aggregate (agg.), composed of *C. insignis* Kunth (P. E. Gibbs & Semir, *C. chodatii* (Hassl.) Ravenna (1998: 44), *C. crispiflora* (Kunth) Ravenna (1998: 45), *C. pubiflora* (A. St.-Hil.) K. Schum. (1886:

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213), *C. ventricosa* (Nees & Mart.) Ravenna (1998: 47), *C. speciosa* (A. St.-Hil., A. Juss. & Cambess.) Ravenna (1998: 46) and *C. lupuna* P. E. Gibbs & Semir (2003: 270). Gibbs & Semir (2003) concluded that it is difficult to differentiate between them.

Several researchers have agreed that the recognition of the species within the *C. insignis* agg. is confusing in many cases because of its notorious plasticity and because fertile hybrids are recorded within the group (Perrotta *et al.*, 2007; Lozano & Zapater, 2018; Pezzini *et al.*, 2021). A subsequent analysis by Pezzini *et al.* (2021) analyzed 14 *Ceiba* species with molecular techniques and from the results proposed three clades within the genus *Ceiba*. Pezzini *et al.* (2021) did not include *C. chodatii* in their analysis.

Ceiba chodatii has been thought to be the most common species in the xeric forests of the Chaco plain and the Bolivian-Tucuman xeric forests. However, our results show something different. In field surveys (2015-2022) in the southern sub-Andean and the Chaco plain of Bolivia we found two different populations of *Ceiba*. Both *Ceiba* species have their own characteristics that differ morphologically, ecologically and biogeographically.

The *C. chodatii* populations are widely distributed in the Chaco plains of Bolivia, Paraguay and Argentina, while the other *Ceiba* populations occurring in the mountain ranges and xeric valleys of the southern sub-Andean Bolivia and northern Argentina are a different and undescribed species.

Materials and Methods

Between 2015 and 2021 botanical surveys were carried out along the southern sub-Andean, the Chiquitania, and the Chaco regions in Bolivia. In the years 2021 and 2022, collections of fertile specimens of *Ceiba* were made and georeferenced photographs were taken. The samples were reviewed and compared with other specimens deposited in Bolivian herbaria: German Coimbra S. at the Botanical Garden of Santa Cruz de la Sierra Herbarium (without herbarium acronym), Herbario Nacional Forestal Martín Cardenas

(BOLV), Herbario del Oriente Boliviano (USZ). Online digitized images of herbarium specimens of the following institutions were reviewed: Austroamerican Virtual Herbarium (HVAA), Conservatoire et Jardin botaniques de la Ville de Genève (G), Herbario de Salta (MCNS), Global Biodiversity Information Facility (GBIF), Missouri Botanical Garden (MO), New York Botanical Garden (NY), and the Naturalist Biodiversity Center. In addition, 103 georeferenced photographic records from the iNaturalist platform (2022) were consulted and three photographed specimens were selected for study. We only worked with records and specimens that had floral parts and were in their natural habitat, therefore we eliminated from the analysis all records of photos and specimens that were collected and photographed in cities and towns, or any that had indications of being a cultivated plant.

Results

Ceiba guarani Catari, Angulo & Drawert *sp. nov.* Figs. 1A-D; 3B, E, H; 4A-C-D; 5A-C. *Typus*: BOLIVIA. Tarija: Prov. Gran Chaco, 28.5 km NE of Palos Blancos, along road from Palos Blancos to Villa Montes, 21°21'52"S, 63°38'09"W, 625 m, 23-III-2007, *M. Nee & R. Flores S. 54884* (*holotypus* USZ!; *isotypi* LPB, MO, NY).

Calyx campanulate, 30 to 60 mm long. Petals white to pale yellow and pubescent on the outside. Staminal appendages yellow and slightly pilose. Staminal tube divided in the distal third forming free filaments. Petiolules 6 to 18 mm long.

Tree, deciduous, 10 to 15 m tall at maturity. Trunk pachidactyl, usually ventricose, especially in juvenile stages; bark often with green longitudinal striations and/or covered with conoidal spines extending to main branches. Leaves palmately compound with 5(-7) articulate leaflets; petiole 50-90 mm long; petioles 6-18 mm long; leaflets glabrous, lanceolate to elliptic, usually with margin serrate in apical half, the lamina 50-70 mm long × 30-40 mm wide, the upper side dark green

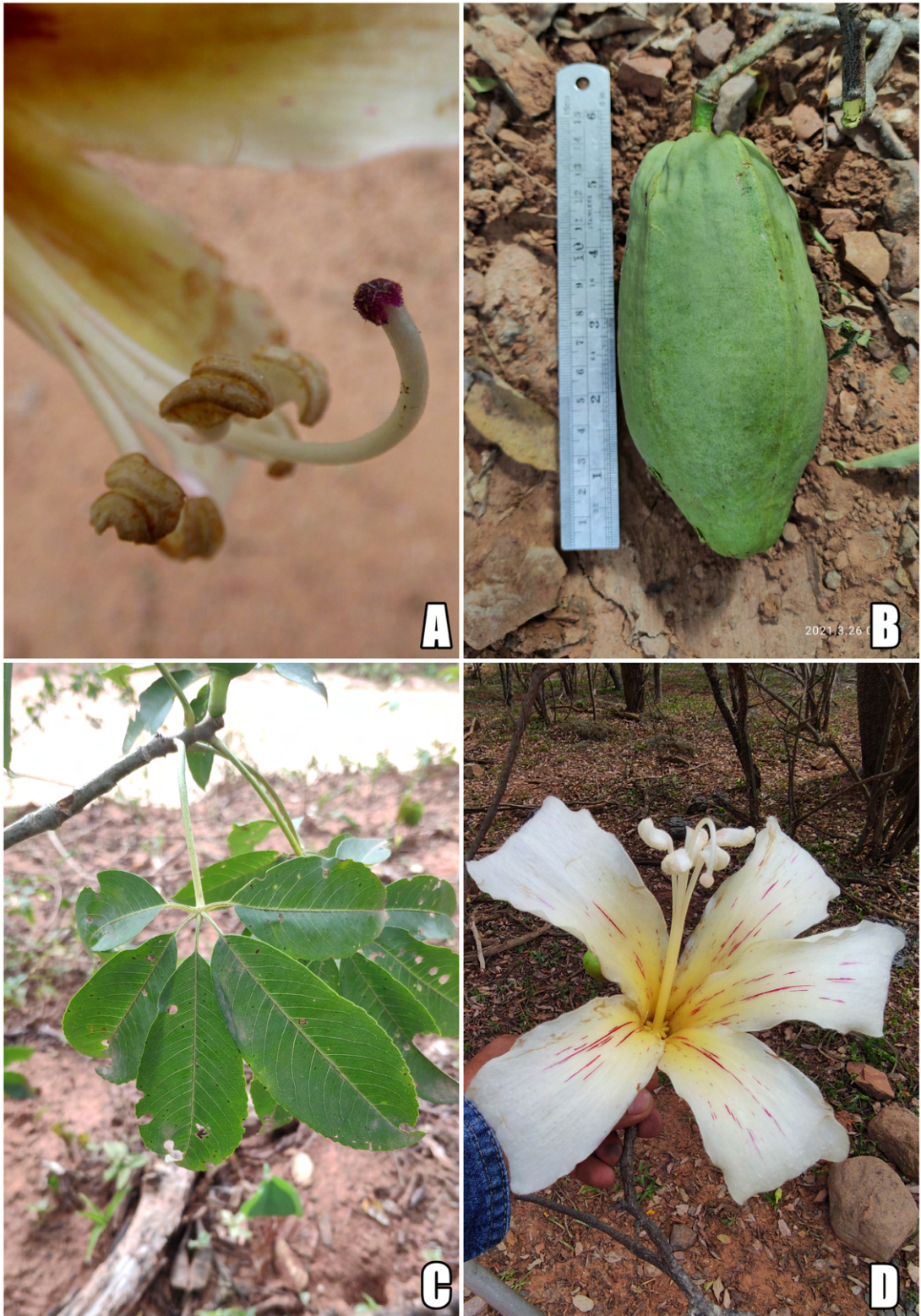


Fig. 1. Taxonomic details of *Ceiba guarani*. A: Detail of stamens and stigma. B: Immature fruit. C: Leaf. D: Flower.

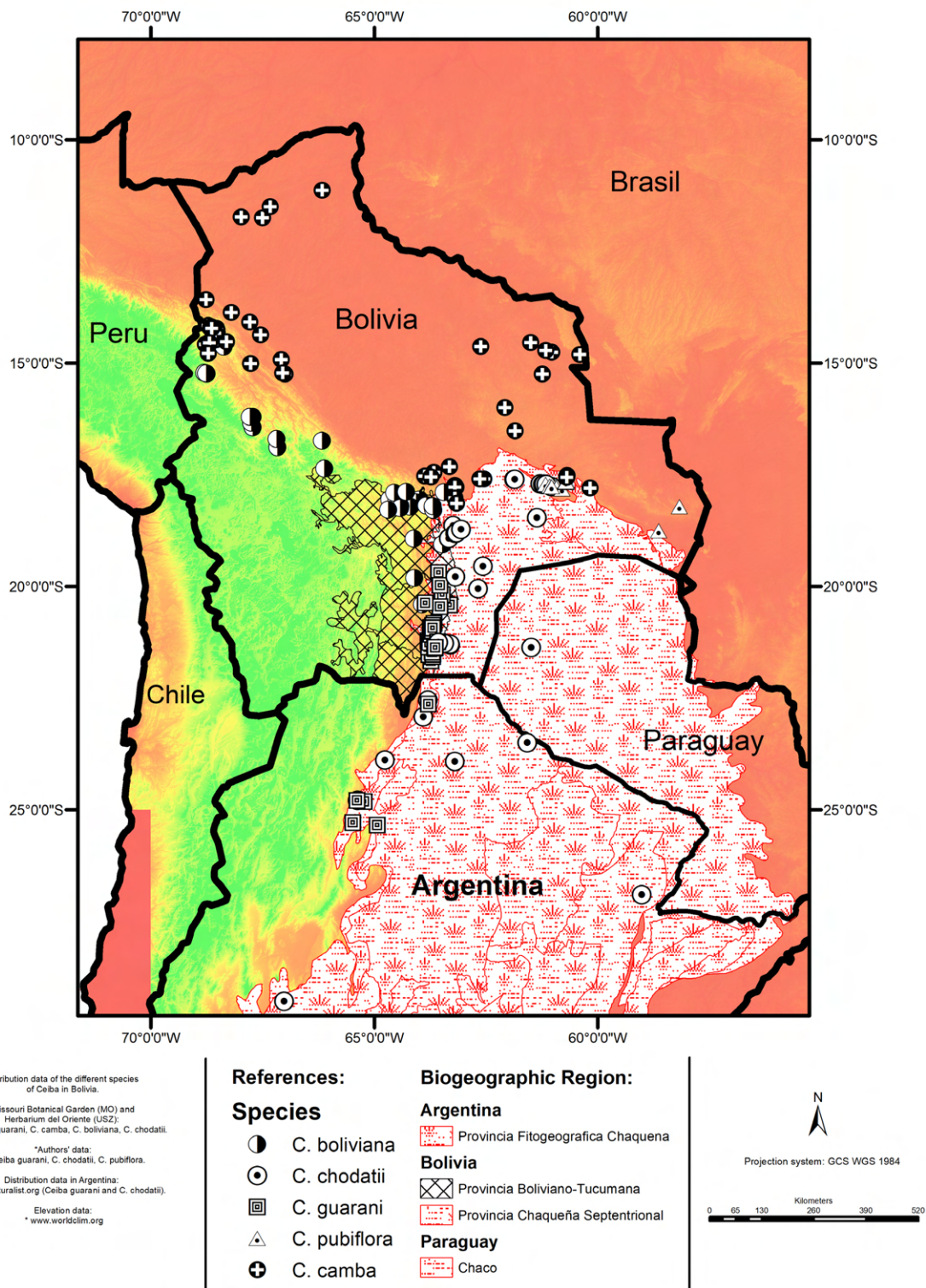


Fig. 2. Distribution map of five species of the *Ceiba insignis* aggregate. The distribution points of *C. guarani* and *C. chodatii* correspond to specimens with visible floral parts collected and observed in Argentina, Bolivia and Paraguay.

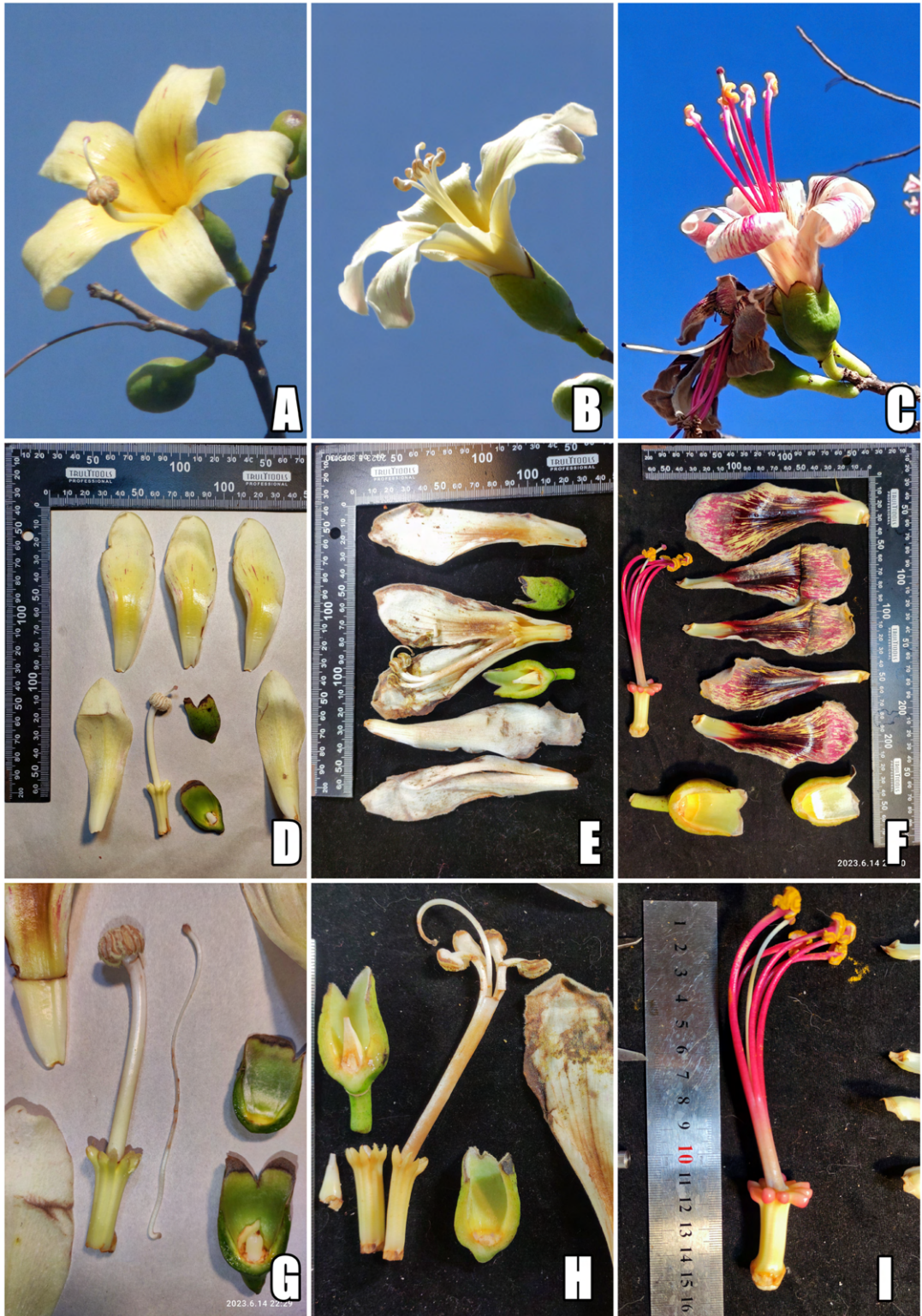


Fig. 3. Morphological differences of flowers between *Ceiba chodatii* (A, D, G), *C. guarani* (B, E, H) and *C. boliviana* (C, F, I).

and underside paler; leaflet apex cuspidate. Inflorescences in few-flowered fascicles or of solitary flowers; flowers axillary, 100-120 mm long; pedicel 10-20 mm long; calyx campanulate to elongate-campanulate, 30-60 mm long and 20-25 mm in diameter, green to yellowish-green, with 1 to 3 deciduous bracts 2-3 mm long; corolla yellowish-white/rosaceous; petals 5, spatulate to obovate, 80-110 mm long \times 20-25 mm at widest point, with smooth to wavy margin, arched from base, the lower surface sericeous to white to creamy white, hairy, the upper surface distally glabrous white to pale ivory with an exceptionally very faint pinkish tinge becoming ivory to pale yellow toward the base and sometimes with some dashed reddish to magenta lines which may or may not be concentrated at the base forming an inverted V-shaped; petals may change color during anthesis until they fade; androecium with stamens white to ivory at base, sometimes turning pinkish distally, fused into a glabrous staminal tube 15-20 mm long below the staminal appendages and extended 50-80 mm above these giving rise to free filaments in their $\frac{1}{2}$ to $\frac{1}{3}$ distal portion (20-40 mm), the 5 bifurcate staminal appendages pubescent to setose, yellow to greenish yellow in the apical zone; anthers sinuous 5-8 mm long; gynoecium with subglobose ovary; style white, extending from the base without fusing to the staminal tube; stigma pink to red, hairy on the apex of the slightly flat style. Fruits ellipsoid, oblong to pyriform capsules up to 170 mm long \times 80 mm in diameter, green to dark green, with 5 valves; seeds reniform to pyriform, dark brown to black.

Paratypes: **BOLIVIA. Chuquisaca:** Prov. Luis Calvo, Mun. Huacaya, 18.3 km in a straight line south of Huacaya on the road to Kumandaroti, 20°53'43"S, 63°41'43"W, 4-IV-2022, *Catari et al.* 2531 (USZ); 14.9 km straight line south of Huacaya on road to Kumandaroti, 20°52'05"S, 63°41'19"W, 4-IV-2022, *Catari et al.* 2532 (USZ). **Santa Cruz:** Prov. Cordillera, Mun. Cuevo, 1.4 km west of Cuevo on road to Boicobo, 20°27'06"S, 63°31'50"W, 5-IV-2022, *Catari et al.* 2533 (USZ). **Tarija:** Prov. Gran Chaco, highway Villamontes-Entre

Ríos, 14 km west of the bridge over Río Pilcomayo, 21°13.77'S, 63°34.46'W, 28-V-2005, *Nee 53186* (LPB, MO, NY, USZ). Prov. O'Connor, Mun. Entre Ríos, 5.8 km straight line northeast of Kumandaroti on road to Huacaya, 21°02'15"S, 63°43'07"W, 4-IV-2022, *Catari et al.* 2528 (USZ); 6.9 km straight line NE of Kumandaroti on road to Huacaya, 21°01'49"S, 63°42'41"W, 4-IV-2022, *Catari et al.* 2529 (USZ); 6 km straight line N of Campamento "El Toro" on road to Huacaya, 20°52'04"S, 63°18'53"W, 11-V-2023, *Catari & Mendez 2600* (USZ); Chigmiano [*sic!*, probably Chiquiacá], 8-III-1904, *Fiebrig 2717* (U). **ARGENTINA. Salta:** Dep. Capital, Barrio 3 Cerritos, sports square, 30-IV-2010, *Almazán 41* (MCNS); Salta, 25-II-1986, *Palaci 405* (MCNS); Ciudad de Salta, 5-III-1991, *Tolaba 79* (MCNS); City of Salta, s. dat., *Zabala 383* (MCNS). Dep. Gral. San Martín, Cpto. Tablillas 3-4 km to the east of Gral. Mosconi, 1-II-1997, *Palma 196* (MCNS); Tartagal, on National route 34, 19-II-2000, *Tolaba 2650* (MCNS). Dep. La Viña, Coronel Moldes, ruta 68, km 123, 1 km west of the road, 1-III-1989, *Novara et al.* 8633 (MCNS).

Etymology: The specific epithet *guarani* is conferred in reference to the Guarani indigenous people. With the name we honor this people who historically and still live in the southern sub-Andean region in the Departments of Chuquisaca, Santa Cruz and Tarija.

Common names: "Luchan" is the local name throughout its area of distribution [localities of Cuevo, Boicobo (Mboicobo), Mbororigua, Igüembe, Huacaya, Kumandaroti, Palos Blancos and Caraparí]. Other names such as "lluchan", "yuchan" and "oroche", however, are of localized use in a few places.

Ecology and distribution: In Bolivia, *C. guarani* is distributed in the mountains, hills, and foothills of the southern sub-Andean of the departments of Santa Cruz, Chuquisaca, and Tarija. The altitudinal range of the population is 800-1400 asl throughout the three departments. In Argentina, the species

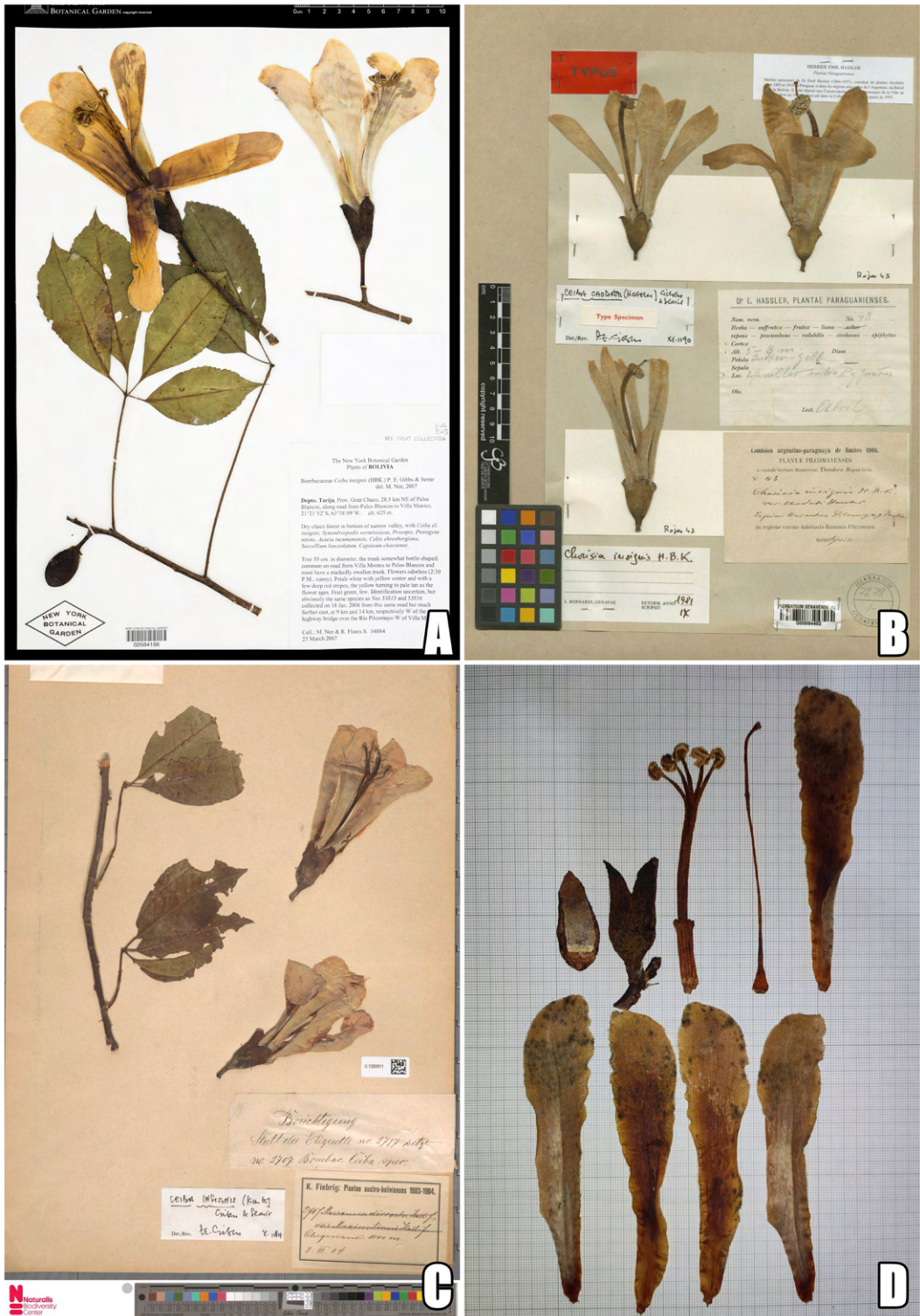


Fig. 4. Specimens considered important for the description of *Ceiba guarani*. A: Bolivia, Nee & Flores 54884 (NY). B: Paraguay, type specimen of *C. chodatii*, Rojas 43 (G). C: Bolivia, K. Fiebrig 2717 (U). D: Bolivia, Catari & Mendez 2600 (USZ).

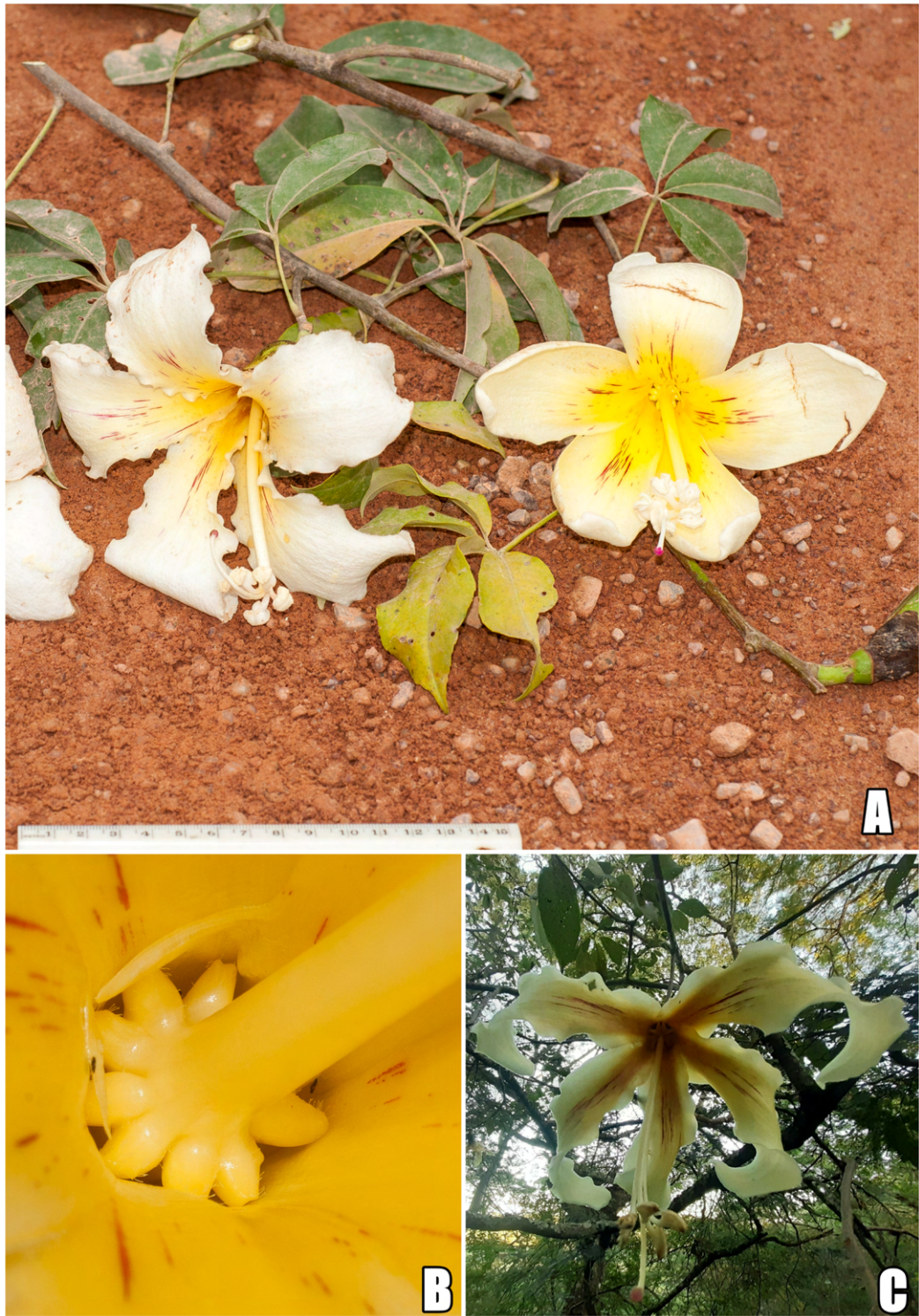


Fig. 5. A: Flowers at different stages of development of *Ceiba guarani*. B: Appendices, in anthesis, photo and collection of *M. Nee & D. Villarroel* 60955. C: “Yuchan”, photo of Oliver Kohler in <https://www.inaturalist.org/observations/109846577>.

is distributed in the northwest of the country, in the province of Salta (Figs. 2 y 6). In this figure, there is an area of potential distribution called Bolivian-Tucuman inter Andean and sub-Andean xerophytic forests and pre-Andean transitional forests of the western northern Chaco of the Pilcomayo-Alto Parapetí biogeographic sector, which belongs to the Bolivian-Tucuman Biogeographic Province of the Andean Biogeographic Region (Navarro & Ferreira, 2009). The bioclimate in its area of distribution corresponds to dry xeric according to Navarro (2002). In the localities recorded for *C. guarani* the annual average precipitation is 500-1100 mm and the annual average temperature has a range of 20-25 °C, following to the WorldClim bioclimatic coverages (Fick & Hijmans, 2017). However, the records of the meteorological station of the National Meteorology and Hydrology Service (SENAMHI) in the town of Huacaya for the years 2018, 2019 and 2020 indicate that in winter the temperature usually drops to 1-3 °C, and in summer the maximum temperatures reach up to 40-42 °C (SENAMHI, 2022).

Observations: The separation of the anthers up to one third of their length in their distal part is the most notorious characteristic to differentiate it from the other species. Figure 3 shows the morphological characteristics of the flowers and leaves that differentiate *C. guarani* from other congeners that are distributed in the sub-Andean mountains of Bolivia and pre-Andean hills in Argentina. Moreover, Table 1 highlights the most notable differences between *C. guarani* and the other species of the *C. insignis* aggregate.

Discussion

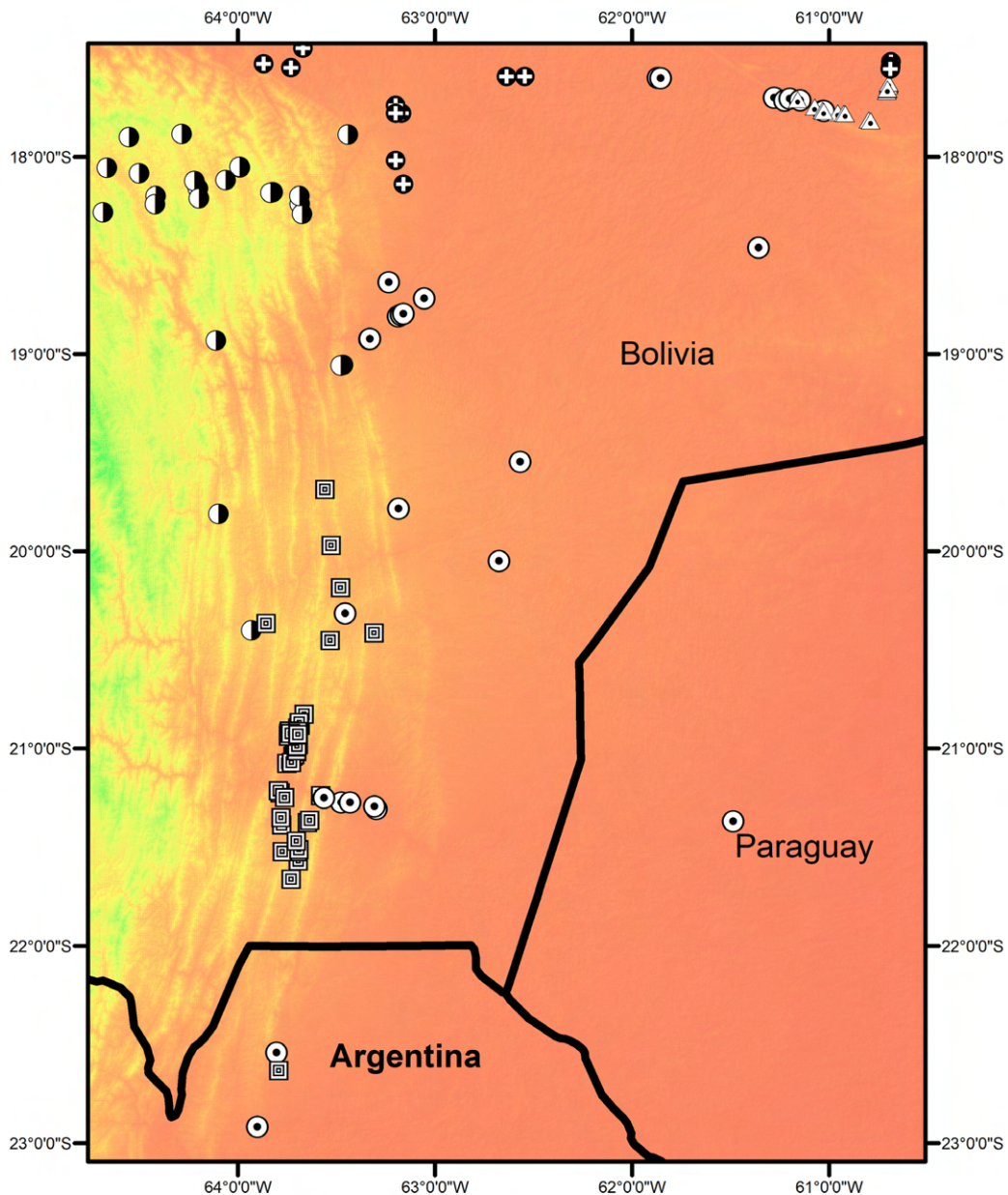
The first herbarium specimen was made by Karl August Gustav Fiebrig, who conducted an expedition to the Andes of southern Bolivia in 1904. In his published notes (Fiebrig, 1911) he mentions a species of Bombacaceae, in the chapter “V. Die Buschwaldformation”, where he writes: *Among the trees there would be a large-flowered bombacee 7-10 m in height (¿Chorisia?).* We conducted a revision of

his collections on the Bionomía (2022) and Herbario Virtual Austral Americano (HVAA, 2022) platforms and found a digitized specimen (*Fiebrig 2717*, U 1380811) collected by K. Fiebrig on March 8, 1904, at the locality with apparent spelling “Chigmiano, 1000 m”. This specimen is identified as *Ceiba insignis* (Kunth) P. E. Gibbs & Semir (Fig. 4C) (Naturalis Biodiversity Center, 2022).

Given the morphological characteristics of the specimen, the location, and the ecology of the locality, we consider that it is actually *C. guarani*. After an intense search for any locality “Chigmiano” in national databases, no match was found with this name or with a similar one. According to the itinerary of his collections in Bolivia, due to the date and altitude described in his notes (Fiebrig, 1911), it is probable that the collection locality is Chiquiacá at 21°51'51”S, 64°07'20”W, ca. 860 asl, a small settlement in a narrow agricultural valley, in the department of Tarija, Prov. O'Connor.

Contemporary botanists, such as Michael Nee, of the New York Botanical Garden, collected in 2005 samples of trees in an ecotone area between the Chaco plain and the Bolivian-Tucuman xeric forests (Pilcomayo River Canyon, Aguara Güe Mountains). The specimen collected under the number *Nee 53185* showed anthers united in a head, typical of *C. chodatii*, while the collection number *Nee 53186*, collected at a distance of 5 km to the west of the previous one, had free filaments and the anthers did not form a head; on the label of # *Nee 53186* he states that it is not *C. boliviana*. *Nee & Flores 54884* (designed here as type of *Ceiba guarani*) collected in 2007 in the valley of the Isiri River at 9 and 14 km respectively from Nee's previous collections, these had the same characteristics as *Nee 53186*. On this occasion he noted on the label: ... *Identification uncertain, but obviously the same species as Nee 53815 and 53816...*

In the review of the *Ceiba* for Bolivia, carried out by Melgar *et al.* (2021) the authors reviewed all the available herbarium specimens, including some of the specimens cited here; however, they did not investigate the morphological differences of the stamens.



Distribution data of the different species of *Ceiba* in Bolivia.
 *Missouri Botanical Garden (MO) and Herbarium del Oriente (USZ):
Ceiba guarani, *C. cambia*, *C. boliviana*, *C. chodatii*.
 *Authors' data:
Ceiba guarani, *C. chodatii*, *C. pubiflora*.
 Distribution data in Argentina:
 * www.inaturalist.org (*Ceiba guarani* and *C. chodatii*).
 Elevation data:
 * www.worldclim.org

References:

Species

- *C. boliviana*
- ⊙ *C. chodatii*
- ⊠ *C. guarani*
- △ *C. pubiflora*
- ⊕ *C. cambia*

Digital Elevation Model

Meters
Value
 High : 8424
 Low : -415

N

Projection system: GCS WGS 1984

Kilometers
 0 15 30 60 90 120

Fig. 6. Distribution map of five species of the *Ceiba insignis* aggregate, with emphasis on Bolivia. The distribution points of *C. guarani* and *C. chodatii* correspond to specimens with visible floral parts collected and observed in Argentina, Bolivia and Paraguay.

Table 1. Morphological differences between *Ceiba guarani* *sp. nov.* and the other species of the *C. insignis* complex

Species	Morphological characters	Notable differences from <i>Ceiba guarani</i> <i>sp. nov.</i>
<i>C. chodatii</i> , <i>C. insignis</i> and <i>C. ventricosa</i>	White to pale yellow flowers	Staminal tube divided into filaments at least in the upper third
<i>C. insignis</i> and <i>C. ventricosa</i>	staminal appendages white, orange, or red	Staminal appendages yellow or greenish yellow
<i>C. chodatii</i> and <i>C. insignis</i>	Staminate appendages glabrous and sparsely hairy	Sparsely hairy staminal appendages
<i>C. boliviana</i> , <i>C. glaziovii</i> and <i>C. pubiflora</i>	Staminal tube divided into free filaments from the base or about 5-10 mm above.	Staminal tube with filaments united from its base up to two thirds of its size and then free until the end
<i>C. boliviana</i> and <i>C. pubiflora</i>	Pale pink to deep pink petals or many dark red streaks	Petals white to pale yellow pale, red lines sometimes with few red
<i>C. boliviana</i> and <i>C. glaziovii</i>	Staminal appendages irregular or entire	Regular bifid staminate appendages
<i>C. boliviana</i>	Calyx globose short (30-40 mm), staminal appendix glabrous, red to dark red	Calyx bell-shaped (30-60 mm), staminal appendages sparsely hairy, staminal tube and filaments yellow
<i>Ceiba insignis</i> complex		Calyx bell-shaped (30-60 mm long), petals white to pale yellow, staminal appendages sparsely hairy yellow, staminate pale yellow, staminal appendages sparsely hairy, and staminal tube divided at the distal part forming free filaments up to one third of their total size

Gibbs & Semir (2003) designate the collection *Rojas s.n.* [35], *herb. Hassler 2849* as a lectotype of *C. chodatii* (one of at least two sheets at G, here reproduced as Fig. 4B) and cite the illustrations by Digilio & Legname (1906: 76); Bernardini (1984: 35). Both references to the illustrations are erroneous, as they actually correspond to Digilio & Legname (1966) and Bernardi (1984), respectively. Although the lectotype and illustrations show that the staminal filaments form a staminal tube and end in a collar of anthers, Gibbs & Semir (2003) include in their description the phrase ... *upper staminal tube white with a collar of 5, 2-thecate, sinuous, pale yellowish anthers, occasionally splitting distally to give 5 short filaments and separate anthers*, which induced all the *Ceiba* trees of the southern sub-Andean of Bolivia and the highlands of northern Argentina that present free filaments in their distal part, to be included within *C. chodatii*.

This discrepancy between the description in Gibbs & Semir (2003) and what is observed in the type material was mentioned by Lozano & Zapater (2018). However, they indicated that it is common for some individuals of *C. chodatii* to present this difference, probably because they reviewed a greater number of samples that came

from the mountains. However, the type material of *C. chodatii* [*Rojas s.n.* (35), *herb. Hassler 2849* (G)] is from Chaco plain ecosystems of Paraguay (*Chaco septentrionalis, in campis Santa Elisa*). Gibbs & Semir (2003) only cited one herbarium sample from Bolivia, and this corresponds to *Weddell s.n.* (P) collected in the year 1846. We searched for the specimen in the online database of the herbarium of the French National Museum of Natural History (P) and no such specimen was found.

Ceiba guarani has its population established in the first foothills of the Andes (800-1200 asl). It contacts the populations of *C. chodatii* in the foothills, in ecotone zones between the Bolivian-Tucuman forests and the Chaco forests, but it has its own morphological, ecological and biogeographical characteristics throughout its distribution area in southern Bolivia and the northern sierras of Argentina (Figs. 1A-D, 2, 3B-E-H, 5A-C). In addition, the region of the upper basins of the Grande and Pilcomayo rivers, where *C. guarani* is distributed in Bolivia, is considered a center of diversity of the Bolivian-Tucuman flora, and has been recognized for its high level of endemism and paleoendemism (Navarro, 2002; López, 2003; Martín *et al.*, 2022).

On the other hand, the typical habitat of *C. chodatii* is found mainly in the Chaco plain and the low sub-Andean foothills (Fig. 2). In this last area both populations intermingle, mainly in the departments of Santa Cruz, Chuquisaca and Tarija (Bolivia), and in the region of Salta (Argentina). The specimens examined from Bolivia and the few records available online for Argentina, indicate that *C. chodatii* would have its potential distribution in the former dry alluvial plains (paleo plains) of the Grande, Parapetí, Pilcomayo and Otuquis rivers in Bolivia. likewise in their respective extensions in Paraguay and Argentina, mainly in areas with a xeric thermotropical bioclimate with a mostly xeric ombrotype (Fig. 6).

Acknowledgements

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