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## Studies in the Cleomaceae II: *Cleome boliviensis*, a New, Spiny, Large-Flowered Andean Species

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**ABSTRACT.** *Cleome boliviensis* Iltis, a large-flowered new species of the speciose, mostly spiny section *Tarenaya* (Rafinesque) Iltis [validated here], is described, illustrated, and its relationship to other species discussed. This xerophytic subshrub, widespread and common in the Andes of southern Peru and Bolivia (and becoming weedy in adjacent Amazonian lowlands), differs from the allopatric, more eastern, lowland, annual *C. hassleriana* by its more or less perennial habit, whitish to pinkish white flowers, finely glandular-pubescent fruits, and smaller seeds with abundant, minute (use 20× lens), oil-containing, light-refracting, caruncular bulliform cells. These densely cover the flat seed faces and often the mouth of the seed “cleft,” and appear to be related to dispersal by ants. At the edge of its range, the new species seems to hybridize with other species of section *Tarenaya*, such as *C. parviflora* and long-fruited *C. spinosa* s.l. recently introduced from northeastern Brazil. Myrmecochory in the Cleomaceae is discussed and appears to have arisen independently several times.

**RESUMEN.** Se describe e ilustra *Cleome boliviensis* Iltis (Cleomaceae), una nueva especie de flores grandes, perteneciente a la sección *Tarenaya* (Rafinesque) Iltis, una sección con numerosas especies en su mayoría espinosas; se discute su relación con otras especies afines. Es un subarbolito xerofítico, ampliamente distribuido en los Andes del sur de Perú y de Bolivia (llega a ser una maleza adventicia en áreas bajas aledañas de la Amazonía), difiere de la especie alopatrica *C. hassleriana* por su hábito más o menos perenne, flores blanquecinas hasta rosado blanquecinas, por sus frutos finamente pubescente-glandulares y semillas más pequeñas con abundantes diminutas (use una lupa de 20 ×) células carunculares buliformes, que contienen aceites y reflejan la luz. Éstas cubren densamente las caras aplanadas de las semillas y a menudo la boca de la “escotadura” de la semilla y sugieren la dispersión por hormigas. En el límite de su distribución geográfica, esta especie parece formar híbridos con otras especies de la sect. *Tarenaya* como *C. parviflora* y *C. spinosa* s.l., una especie de fruto

largo de reciente introducción en el nororiente de Brasil. Se discute la mirmecocoria en las Cleomaceae que parece haber evolucionado varias veces, independientemente.

**Key words:** Andean biogeography, ant-dispersal, Bolivia, Cleomaceae, *Cleome* sect. *Tarenaya*, myrmecochory.

Throughout extensive montane and submontane areas of Bolivia and adjoining southern Peru (Fig. 3) there grows a common large-flowered, very spiny, shrubby *Cleome*, one of the more than 40 members of the speciose, mostly spiny, almost exclusively New World *Cleome* sect. *Tarenaya* (see below and Jacobs, 1960; Iltis, 1952, 1967). Though this strikingly beautiful species is represented by many herbarium collections and has long been recognized as distinct (Iltis, 1952, 1967), it lacks a properly published binomial.

**Cleome** sect. **Tarenaya** (Rafinesque) Iltis, comb. et stat. nov. Basionym: *Tarenaya* Rafinesque, Sylva Telluriana 111. 1838. TYPE: *Tarenaya spinosa* (Jacquin) Rafinesque = *Cleome spinosa* Jacquin.

Mostly annual herbs, usually glandular pubescent, often with epidermis-derived paired spines or thorns in the stipular position at the base of the multifoliolate, palmately compound leaves, with many-flowered bracteate inflorescences, flowers with 6 stamens, elongate gynophores and many-seeded siliques, the seeds with a deep hollow cleft chamber closed on all sides by distinct cleft membranes from embryo vertex to seed mouth (Iltis et al., in prep.).

A group of ca. 40 New World species and one West African (Iltis, 1967).

The above change in status, made previously informally by Jacobs (*Flora Malesiana* 1 6(1): 100, 1960), is herewith validated.

The forthcoming enumeration of the Bolivian flora by the Missouri Botanical Garden and the National Herbarium of Bolivia and of the genus *Cle-*



ome for Bolivia by Lupita Sánchez (Sánchez, in prep.) necessitates its formal publication as:

***Cleome boliviensis*** Ilitis, sp. nov. TYPE: Bolivia.

La Paz: "Plantae Andium Boliviensium, Prov. Larecaja, vicinus Sorata, Challapampa, ad rivium, in schistosis, Reg.[ion] temp[lada], 2600 m, Sept. 1857–Jan. 1858," *G. Mandon* 938 (holotype, WIS; isotypes, BM, F, G, GH, K, LE, LPB, NY, P, PR, S, W). Figures 1–4.

Haec species a *Cleome hassleriana* et *C. spinosa* habitu suffruticoso perenni (vel annuo?), capsula glanduloso-puberula, seminibus minoribus cellulis bulliformibus caruncularibus membranas fissurales omnino obtegentibus atque floribus albidis vel albido-roseis distinguitur.

Erect, herbaceous to suffruticose, much-branched, ill-smelling, coarse, perennial, spiny herbs or subshrubs, (0.5–)1–1.6(–2.2) m tall, to 2 m across, densely viscid glandular-pilose to -hirsute generally, the hairs rather short and stiff and frequently intermixed with many scattered spinules, these often also gland-tipped; stems spiny and densely glandular-pubescent, with the paired, stout "stipular" spines 3–6 mm long, 2–6 mm wide at the base (where often glandular pubescent), divergent at 90° to ± recurved. Major leaves 5- to 7-foliolate, on petioles 2–9 cm long, prominently armed with ascending or divergent prickles and spines (Fig. 1); leaflets narrowly elliptic to oblanceolate-elliptic, broadly acute to acuminate at the tip, attenuate to the base, 6–15(–30) × 2–8(–10) cm, rarely larger on vigorous young shoots, often somewhat conduplicate, entire (but microscopically serrulate, the denticulations scarcely more than gland-tipped hairs), glandular-pubescent and somewhat scabrous, rarely subglabrous above, glandular hirsute-pilose beneath, particularly along the midrib and prominent veins; lateral veins on each side of the midrib 8 to 12. Racemes often very dense, elongating to 40 cm or more by the time they have finished blooming, the primary ones each with up to 200 or more flowers opening acropetally (i.e., estimated by counting the persistent floral bracts), but with only ca. 20 to 40 buds and 3 to 5(to 10) open flowers at any one time at the apex; floral bracts 1-foliolate (or the lowest flowers frequently subtended by 3-foliolate bracts or rarely full-sized leaves), narrowly to broadly ovate- to oblong-elliptic, acute to obtuse at the tip, cuneate to rounded or subcordate at the base, mostly 6–15 × 4–12 mm, their 1–8 mm long petioles frequently subtended by a pair of minute prickles. Flowers on pedicels (13–)22–32(–41) mm long; sepals narrowly lanceolate, acute, 6–10 × 2–3 mm, soon deciduous, densely glandular-pubescent throughout, es-

pecially toward the tip, the glands often mostly sessile or subsessile; petals spatulate, 24–35 × 4–10 mm, showy, basically mostly white, but often variously flushed with lilac or pale pink, or rarely dark blood red to a rich pinkish purple, glabrous or rarely with a few scattered glandular hairs on the back and top when in bud, the blade obovate-elliptic, rounded, gradually attenuate to the slender claw, the claw 1/3 to 2/3 as long; disk (androgynophore) slightly fleshy, conic, 3–4(–5) mm long; stamens 6, the filaments glabrous, 50–70 mm long, red, reddish violet, purple, or deep maroon, the anthers (7–)9–13 mm long; ovary cylindric to fusiform, 10–13 × 1 mm, finely and densely glandular-pubescent; gynophore 4–7 cm long, glabrous, and together at least initially with pedicel and silique often strongly arching upward at 45°. Mature siliques oblong to cylindric, sometimes somewhat clavate (i.e., wider toward the tip), broadly acute to rounded at the apex, obtuse to long-attenuate at the base, (4–)5–8(–9) × 0.5–0.8 cm, usually stout with the valves firm to somewhat lignified, and with the evenly smooth to scaberrulous and continuous (never torulose) surface ± sparsely and minutely glandular-puberulent (the relatively large glands sessile or subsessile on short stalks); stigma capitate, sessile or subsessile; gynophore glabrous, stout, straight, (35–)50–95 mm long; androgynophore 3–6 mm long; pedicel (15–)25–40(–47) mm long, divergent to stiffly ascending and continuous with the gynophore and silique, often arching upward together; seeds often many, 100 to 400 or more per silique, reniform-sub spherical or -obovoid, very small, 1.5–1.9 × 1.4–1.7 × 1.1–1.3 mm, brown to dark brown or almost black when mature, smooth or essentially so, finely longitudinally striate, the internal cleft cavity oblong to obovate in cross section, narrowed toward the vertex, relatively small; seed cleft-membranes (i.e., on the 2 ± grooved or flat sides of the seed connecting the two curved ends, or "claws") totally covered over by ± densely aggregated, small (use 20× lens), varnished, light-reflecting, oil-containing, bulliform cells which may spread into, and completely occlude, the mouth of the cleft and spill over onto the surrounding testa, and sometimes even onto the back of the seed, forming a densely caruncular surface (see below and Fig. 2); claws subequal, the radicular claw considerably longer.  $2n = 20$ .

*Habitat and distribution.* Foothills and mountains of southern Peru and Bolivia (Fig. 3), at elevations of (250–)1700–2800(–3500) m, on open, dry, stony slopes among scattered shrubs, in rocky beds of dried-up mountain streams, and along





Figure 1. *Cleome boliviensis* Iltis. —A. Habit, with characteristic ascending young siliques. —B. Petiole with spines mostly at right angles or somewhat antrorse. A, B based on *Ugent 5112*. Drawing by Kandis Elliot.

shrubby, moist riversides, from “bosques montañosos [cloud forests] con muchas epfitas” down to transitional humid savannas, in open sandy soils and arid waste places, rocky roadsides and fields,

at lower elevations weedy and adventive in fields and along roads, rarely cultivated for its showy flowers in gardens.

*Phenology.* Flowering and fruiting intermittent-



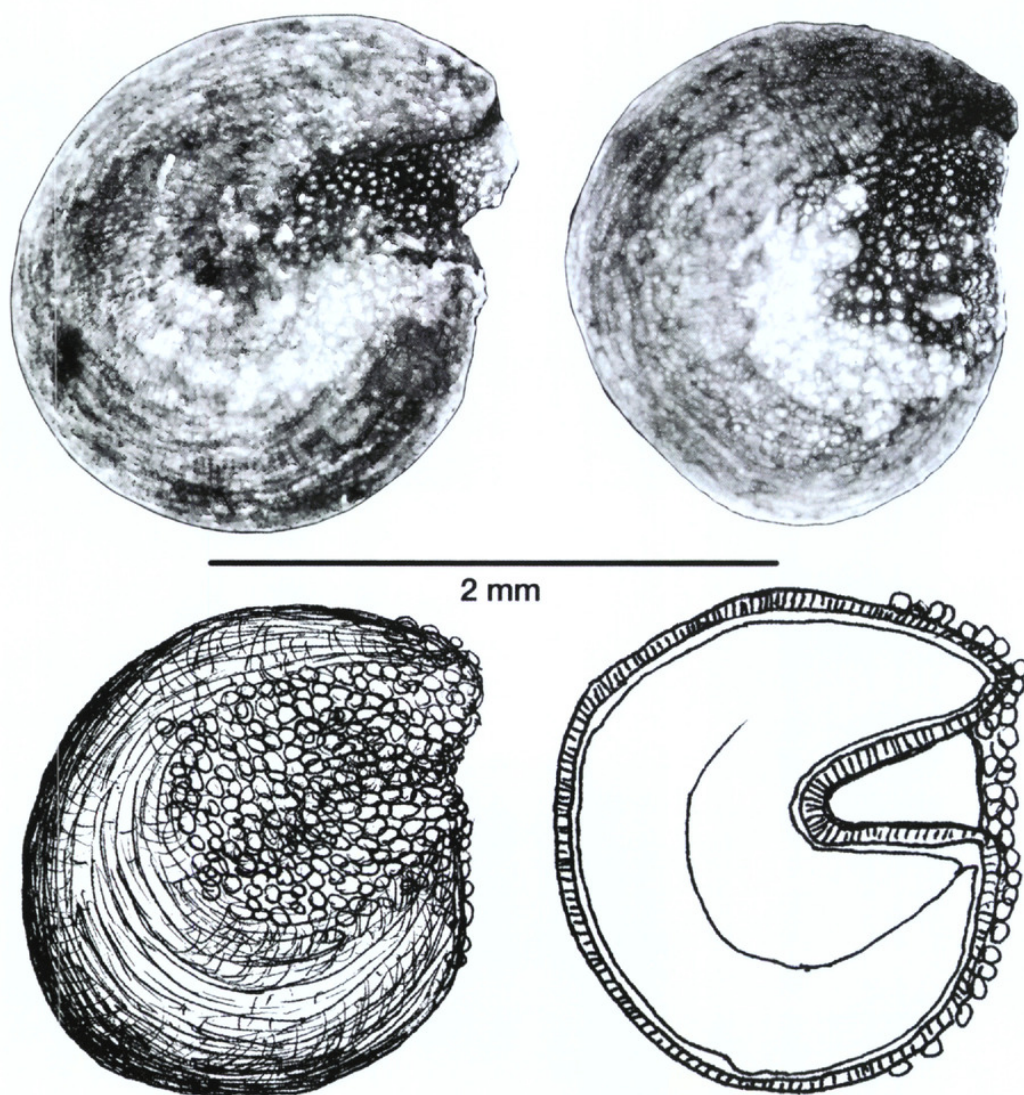


Figure 2. Four assorted seeds of *Cleome boliviensis* showing characteristic oil-filled bulliform cells in seed cleft and on seed faces, each from a different specimen. Drawing by the author.

ly throughout the year but apparently mostly from October to July.

**Vernacular names and uses.** Peru. Cuzco: “*Quichita*” (McCarroll 59), as a “remedy for pains of rheumatism.” BOLIVIA. Cochabamba: “*Khichita*” (Baer 223), reported simply as “medicinal,” and “*Kichita*” (Ugent 4593), where “the leaves when crumpled and stuffed into the ear are said to cure earaches” [see Ilitis, 1960: 289, for similar reports from Africa, where the mustard-oil-containing, acrid leaf juices, seeds, or whole seed pods of the nearly pantropic weedy *Cleome gynandra* (L.) L. are placed into the ear canal to dissolve ear wax, and where poultices of the leaves or fruits are applied for various purposes, including to relieve the pain of rheumatism].

*Cleome boliviensis* is a common and widespread, mostly low-to-mid-elevation Andean xerophyte, with a modern range that evidently now heavily reflects human influence. Not only is it often weedy,

but in Bolivia (Saravia 11156) and in Argentina (Pederson 177) it is reportedly cultivated as an ornamental in gardens for its “fine pink flowers” (Bolivia, Brooke 5018). E. K. Balls (ex sched.) made the following field observations on *C. boliviensis* in Bolivia: “Bushy shrubs to 5 ft. tall and 6 ft. or more through. Leaves sticky, with an unpleasant smell, stems hairy and woody, usually red. Flowers pink with deep maroon stamens.” The showy flowers must make this a beautiful species, though the abundant spines might well discourage garden cultivation.

**Relationships.** *Cleome boliviensis* is one of a half dozen or more segregates of the old “*C. spinosa*” s.l. complex to which all of the larger-flowered, 5- to 9-foliolate, spiny *Cleome* plants had been referred previous to my Ph.D. thesis (Ilitis, 1952). Of the South American taxa, it is apparently most closely related to the commonly cultivated, sometimes adventive *C. hassleriana* Chodat, the



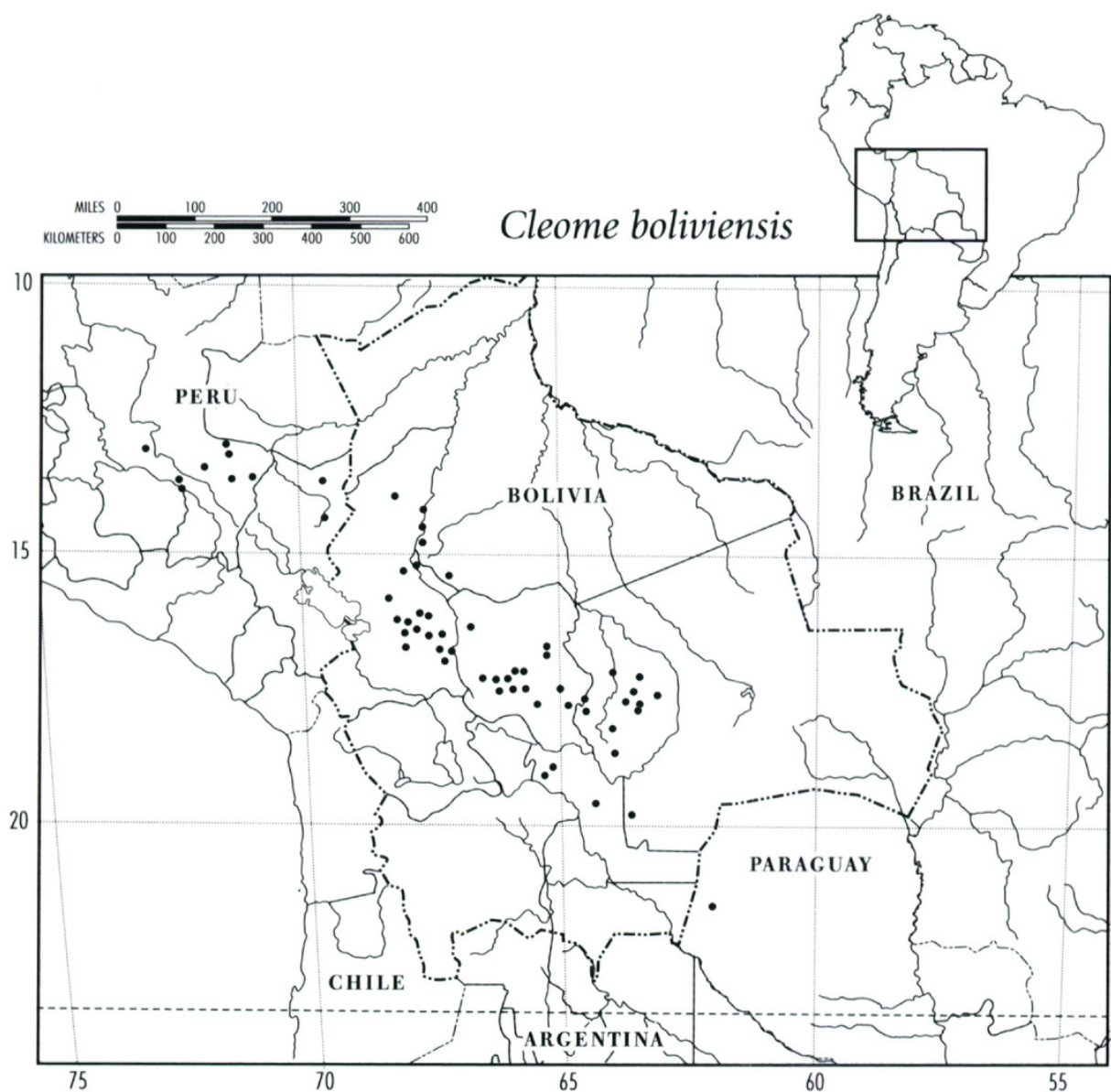


Figure 3. *Cleome boliviensis*: geographic distribution. (The location of Fiebrig 1375, “Alto Paraguay 21°S,” is questionable.)

“Pink Queen,” “Spider Flower,” or “*C. spinosa*” of American gardens, an allopatric native of swamps and riversides from northeastern Argentina and Uruguay to southeastern Brazil (Minas Gerais), and perhaps even to the extremely rare, giant-flowered, also allopatric *C. lilloi* S. A. Gómez (Gómez, 1953), native to the lowland swamps of the Chaco, from northern Argentina to Bolivia and Paraguay (Iltis, 1967, 1998). Very spiny specimens of *C. hassleriana* can be nearly indistinguishable from *C. boliviensis*, but have, as a rule, fewer spines and less pubescence, 5 to 9 thinner, larger and more pointed, long-acuminate leaflets, deeper-colored pink to purple flowers (except for an occasional cultivated albino), and are less-branched, more herbaceous, annuals. Most significantly, *C. hassleriana* has totally glabrous petals, ovaries, and fruits, and larger

seeds (mostly 2–2.3 mm) that always lack the minute oil-inflated bulliform cells on the cleft-membranes (use 20× lens) that are so characteristic of *C. boliviensis*. In contrast to the lowland, riverine *C. hassleriana*, *Cleome boliviensis* is a much more xeromorphic perennial or short-lived shrub of the seasonally dry Bolivian and southern Peruvian mountains, glandular throughout, including the siliques, though it, too, may grow on streamsides or sometimes, at lower elevations, as a weed in wet ditches.

SOME *CLEOME* PROBLEMS IN BOLIVIA

Bolivian species with which *Cleome boliviensis* may be confused, especially when in flower, include the following:

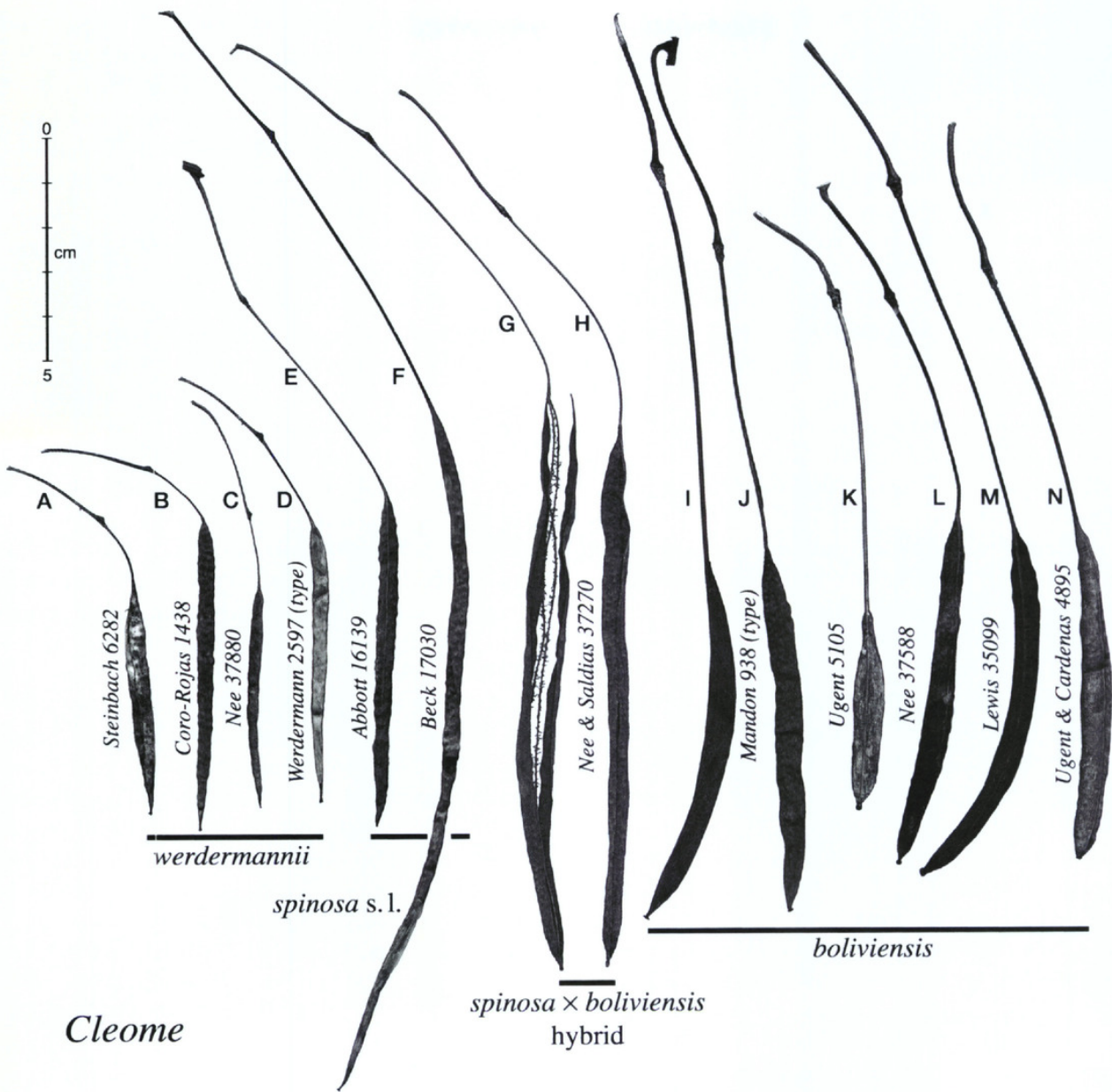


Figure 4. *Cleome boliviensis* and related Bolivian taxa: mature siliques, each showing (from top) pedicel, receptacle, gynophore, and silique [all to same scale; siliques from asterisked (\*) herbarium]: *Cleome werdermannii* Ernst. —A. Steinbach 6282 (A, G-DEL, K\*), Santa Cruz, Cercado. —B. Coro-Rojas 1438 (LPB, WIS\*), Tarija, Bermejos. —C. Nee 37880 (CAS, K, LIL, MA, MO, NY, WIS\*), Santa Cruz, W-side of the city. —D. Werdermann 2597 (B, MO\*, S), Santa Cruz, Misiones Guarayos. —E. *Cleome spinosa* s.l., Abbott 16139 (BEREA, MO, USZ, WIS\*), from San José de Chiquitos, a peculiar population of *C. spinosa* with strigose, eglandular pubescence (see text). —F. *Cleome spinosa* s.l., Beck 17030 (LBP, WIS\*), Pando, Cobija, a weedy recent introduction into Amazonian lowlands (see text). —G, H. Hybrid or introgressant of *Cleome boliviensis* with *C. spinosa* s.l., Nee & Saldias 37270 (NY, WIS\*). I–N. *Cleome boliviensis* (see text; for all, WIS\*). —I, J. Mandon 938 (the holotype). —K. Ugent 5105. —L. Nee 37588. —M. Lewis 35099. —N. Ugent & Cárdenas 4895.

1. The rather uncommon white-flowered and spiny *Cleome werdermannii* Ernst is a Bolivian endemic of low and mid elevations (300–1600 m) that has small, essentially glabrous, smooth and narrow siliques (Fig. 4A–D), long-attenuate from far below the middle, that are sharply deflexed on a quite short, ± curved, gynophore (only 12–25 mm long). Its slightly tubercled seeds are somewhat larger than those of *C. boliviensis* and lack caruncular,

bulliform cells. *Cleome werdermannii* is evidently related to the widespread, polymorphic *C. spinosa* s.l. complex, perhaps to some Central American types, and does not seem to introgress with *C. boliviensis*.

2. White-flowered *Cleome spinosa* of certain common, long-fruited, and torulose phenotypes of northeastern and central Brazil have recently become introduced in forested Amazonian lowlands



near the Brazilian border [e.g., Bolivia: Pando, Cobija, *Beck 17030* (LPB, WIS), *Fernández-Casas 8053* (MA, MO, NY, photocopies WIS)]. Aside from the enormously long fruits, to 15–17 cm (Fig. 4F), they differ in their larger seeds devoid of minute bulliform caruncular cells.

2a. One collection each from the Bolivian Departments of Santa Cruz (*Nee & Saldias 37270*, NY, WIS; Fig. 4G, H) and Cochabamba (*Holliday 67*, K) suggests interspecific hybridization with *C. boliviensis* by repeated putative backcrossing to these long-fruited *C. spinosa* phenotypes. The first of these, a glabrous specimen, has the long (13–14 cm), hanging siliques (Fig. 4G, H) typical of the Brazilian *C. spinosa* mentioned above, yet has seeds with abundant caruncular bulliform cells typical of *C. boliviensis*.

3. Some sporadic and puzzling specimens from northwestern Peru and southeastern Ecuador are problematic [e.g., Peru: Department Tumbes, Zarumilla, quebrada Faical, *D. R. Simpson & Schunke 559* (F, NY, US); Dept. La Libertad, Trujillo, Barrazu, *A. Sagastegui 7879* (GH, F, K, MO, NY). Ecuador: Prov. El Oro, Zaruma, El Calvario, *C. Bonifaz & X. Cornejo 3686* (GUAY, WIS); Prov. Loja, Macara, *G. Harling & L. Andersson 22539* (GB, WIS); Zambi, *F. Vivar 2816* (AAU, LOJA, photocopy WIS)]. They grow in irrigation ditches and nearby desert areas, edges of towns and waste places, and have in the past been misidentified by me as *Cleome boliviensis*. With better recent collections available, it became clear that most lacked the distinctive caruncular bulliform cells on their seeds, but that others had eglandular hispid pubescence mixed with shorter, glandular hairs unique in the polymorphic *C. spinosa* complex. These may thus represent a local variant ecotype or mutant rarely collected and as yet unnamed (Iltis & Cornejo, unpublished), while others may yet prove to be *C. boliviensis* or weedy *C. spinosa* or *C. hassleriana* Chodat, recently introduced near Guayaquil, Ecuador, or simply the variable offspring of a hybrid swarm between these species.

4. Two separate collections with very similar pubescence, cited in detail below (*Abbott 16139* and *Jardin & Mamani 3698*), have recently turned up far away in eastern Bolivia, both from San José de Chiquitos, growing in roadside ditches and marshy areas. This old, small town, a railroad stop in a vast, arid plain, is, according to Michael Nee (pers. comm.), characterized by a hot and seasonally dry climate resembling somewhat that of the forested coastal plain to the west and north of Guayaquil, Ecuador. Superficially, these plants look like hundreds of other *C. spinosa* collections, were it not for

their unique, dense, closely appressed, strigose and totally eglandular pubescence, one that somewhat resembles that of the Pacific coastal plain desert plants mentioned above, but even more so, especially on the young inflorescences and sepals. In addition, Abbott's collection has mature siliques (Fig. 4E) with seeds 2.3 mm in diameter, which distinguish themselves by a pronounced scruffiness of relatively large, dried and collapsed blisters on their backs, much larger and more pronounced than those sometimes found on the seeds of *Cleome spinosa*, and quite unlike the minute ones on the seeds of *C. boliviensis*. Are these distinctive plants indeed recent weedy immigrants from the Peruvian coast, or in fact members of a local autochthonous endemic that, geographically and ecologically isolated, speciated allopatrically in this ecotonal border town between the *Chaco* (mineral-rich, recent alluvial soils derived from the Andes) and the *Cerrado* (nutrient-poor soils derived in situ from the pre-Cambrian Brazilian shield; Michael Nee, pers. comm.)? Whether endemic or not, these are questions that need, above all, intense fieldwork and many additional collections to be answered. [Bolivia: Santa Cruz, Chiquitos Province: suffrutescent herb to ca. 2 m tall, petals light whitish purple, filaments purple (siliques 6–7.5 cm long, narrowly torulose, on slender gynophores 5–6 cm long), San José de Chiquitos, ca. 3 km W of town square; roadside ditch and marshy area, 17°49'S, 60°44'W, ca. 500 m, 6 Feb. 1995 (fl, fr), *Abbott 16139* (BEREA, MO, USZ, WIS); hierba de 1.5 m, flores blancas-rosadas claro con olor dulce, 2 km E de San José de Chiquitos, yendo hacia Roboré del pozo del agua con *Ludwigia*, *Tessaria* [*integrifolia*], suelos arcillosos, 18°19'S, 60°63'W, 200 m, 15 Nov. 1996 (fl), *Jardin & Mamani 3698* (MO, WIS)].

5. Finally, I have seen a half dozen perplexing collections of *Cleome boliviensis* from Madre de Dios in southern Peru [e.g., *Plowman & Davis 5088* (WIS)], which have narrower, somewhat torulose siliques and smaller white flowers, thus resembling *C. parviflora* HBK subsp. *psoraleifolia* (DC.) Iltis (based on *C. psoraleifolia* DC., Prodr. 1: 239. 1824), yet have very small seeds (1.5 × 1.4 mm) with well-developed bulliform cells. That most of them are reported as weedy suggests hybridization with *C. boliviensis*, a problem that, like many others here, needs study.

#### BIOGEOGRAPHY AND TAXONOMY

The three large-flowered southern South American endemics, *Cleome hassleriana*, *C. lilloi*, and *C. boliviensis*, constitute a series of geographically re-



placing ranges from southeastern Brazil, Paraguay, and northeastern Argentina west to southern Bolivia and Peru (Iltis, 1967: 961, fig. 6; Iltis, 1998: 438, fig. 5) and suggest a clade that evolved from a single southern South American ancestor by allopatric speciation. Furthermore, this clade seems to be ancestral to two other, geographically very distant and highly restricted, local endemics: the annual swamp-dwelling *Cleome chapalaensis* Iltis (Iltis, 1998) of the Lago Chapala basin of southwestern Mexico (*Cleome "pringlei"* [ined.] of Iltis, 1967: 961, fig. 6); and the extremely rare local endemic of the Dominican Republic, *Cleome dominicensis* Iltis (a renaming of *Cleome erosa* Urban, 1912, not *Cleoma erosa* (Nuttall) Eaton, 1836, which is *Polanisia erosa* (Nuttall) Iltis, 1958; cf. Iltis, 1958). Since both species grow in wet habitats similar to those of *C. hassleriana* and *C. liloi* and at geographically equivalent latitudes but north of the equator, one may assume that they developed their macro-disjunctions by avian long-distance dispersal (Carlquist, 1966, 1981; Iltis, 1967; Raven, 1963), a view supported by recent molecular analysis (Sánchez, 2002).

Whether the West African swamp and riverside *Cleome afrospina* Iltis (Iltis, 1967), the only indigenous Old World species of section *Tarenaya*, is derived from the same New World clade or another, closely related one (e.g., *C. trachycarpa* Klotzsch ex Eichler), again no doubt by avian long-distance dispersal (Iltis, 1967), awaits future molecular studies. In any case, *C. hassleriana*, *C. boliviensis*, and *C. chapalaensis* all have the same number of chromosomes ( $n = 10$ ,  $2n = 20$ ), as does the polymorphic *C. spinosa* s.l. of Central America, the West Indies, and South America north of Bolivia (Kawano & Kowal in Iltis, 1998; Costa e Silva, 2000; Iltis, Kawano, Kowal, Pazy & Pzywara, unpublished). Yet only *C. boliviensis*, among all these taxa, exhibits the unique glistening bulliform cells on its small seeds (see below), a specialization putatively related to dispersal by ants, and one suggesting autochthonous evolution in situ of this interesting species.

#### ANTS, ARILS, AND SEED STRUCTURE IN THE CLEOMACEAE

Seed structure in the Cleomaceae is of great diagnostic value (Iltis, 1952, 1967; Ruiz-Zapata & Escala, 1995; Ruiz-Zapata, 1995; Sánchez, 2002), and myrmecochory, suggested by the presence of usually oily appendages as food for ants, is of special interest.

Various specializations for ant dispersal are

found in the seeds of several groups of Cleomaceae. Some are related to each other, others not, these evidently having arisen independently at least seven times: (1) Small, light-reflecting, oil-containing, inflated caruncular cells at the mouth of the seed cleft and on the cleft membranes, one of the main diagnostic characters of *C. boliviensis*, suggest that these seeds are ant dispersed. (2) The cluster of some five taxa centering on *Cleome rosea* Vahl s.l. (Iltis, 1952; Costa e Silva, 2000; Iltis, in prep.), a group of ca. seven eastern Brazilian taxa that vary from spinose to, rarely, unarmed, and form a closely interrelated complex in section *Tarenaya* only distantly related to *C. boliviensis*, have bulliform cells on the strongly transversely rugose seeds, that, somewhat different from those of *C. boliviensis*, most probably arose independently by convergent evolution. (3) Bulliform cells almost identical to those that cover the cleft membranes connecting the two seed claws of *C. boliviensis* occur only in one other annual species of *Cleome*, a member of a group of three ebracteate unarmed species, probably belonging to *Tarenaya* (Iltis, 1952), namely the glabrous, spineless *C. paludosa* Willdenow ex Eichler of lowland northern Argentina, Uruguay, and southern Brazil, this surely again a case of convergent evolution. To prove the point, and most curiously, such cells are totally lacking in its closely related sister taxon, the common and weedy annual *C. serrata* Jacquin of Central America, the West Indies, and northern South America, a species which, except for the total absence of bulliform cells on its seeds, differs from its southern South American relative only by the lack of an elongated gynophore (Iltis, 1952, 2001). (4) Quite different and more prominent are the large, white, spongy funicular arils, so-called elaiosomes (Bresinsky, 1963), which occur in the spiny, weedy, and widespread tropical American *C. aculeata* L. of section *Tarenaya* s.l. and its several tropical South American relatives (Iltis, 1952; Ruiz-Zapata & Escala, 1995; Ruiz-Zapata & Iltis, 1998; Costa e Silva & Iltis, in prep.). (5) Independently evolved, although similar in appearance, are the white arils of the unarmed, weedy Old World *C. rutidosperma* DC. of section *Rutidosperma* Iltis (Iltis, 1960: 287, fig. 1; Jacobs, 1960; Ruiz-Zapata & Escala, 1995), which unlike the New World *aculeata* group has a quite open seed cleft. (6) Similar to the spongy funicular arils of *C. aculeata*, but undoubtedly independently evolved as well, and for the third time, are the generically characteristic and prominent funicular arils of the 26 species (Cochrane, 1997) of the annual to perennial, herbaceous to woody New World genus *Podandroyne* Ducke (Woodson,



1948; Iltis & Cochrane, 1989; Cochrane, 1977, 1978, 1997), which may have had their origin in (7) the quite inconspicuous small (funicular?) aril that projects from the very tip of the radicular claw of the seeds of the widespread, low-elevation annual *C. pilosa* Bentham, which, it so happens, is clearly related, albeit distantly, to *Podandrogynae* (Iltis, 1952; Iltis et al., 2005; Iltis & Cochrane, 1989; Ruiz-Zapata & Iltis, 1998: 151) as verified by morphological assessments and recent molecular studies (Hall et al., 2002: 1830; Sánchez, 2002).

**Paratypes.** ARGENTINA. **Corrientes:** Parque Dutre., *Pedersen* 177 (P) [probably cultivated in a city park]. BOLIVIA. Prov. unknown: Vinto, *W. M. A. Brooke* 5018 (BM, F). **Beni:** Distr. Ballivian, Serranía de Pilón Lajas, Bosque Montañoso, al borde de camino, San Borja, 75 km hacia La Paz, *St. G. Beck* 6987 (WIS); La Cumbre, *Beck* 13251 (WIS); vertiente oriental, 21 km de Yucumo, *D. N. Smith, G. Quintana & V. García* 13202 (LPB, MO, WIS). **Chuquisaca:** Distr. Oropeza, rocky roadside, base of cliff, 16 km NE of Sucre on Aiquile Rd., *D. Ugent & M. Cárdenas* 4895 (IBUG, MY, QCA, WIS); Distr. Tomina, Musuru (16 km de Padilla), rumbo a Monteagudo, *C. Saravia* 11156 (CTES); Sucre, open, stony, dry slopes, *E. K. Balls* 6187 (DAB, E, K, NA, UC, US); des ravine de Velco mayo [sic! = Pilcomayo?] près Chuquisaca, *A. D'Orbigny s.n.* (P); Distr. B. Baletto, 700 m N of town square of Nuevo Mundo, on road to Villa Serano, then 300 m left (downhill) of road, *D. M. Spooner, R. G. van der Berg & M. L. Ugarte* 6786 (WIS). **Cochabamba:** Cervecería Colón, Cochabamba, in a stony bed of a mountain stream, *Balls* 6205 (E, UC, US); Tunari, *K. Graf* 521 (NY); 20 km E of Cochabamba, among stones, thickets on riverbank, *W. J. Eyerdam* 24752 (F, K, NA); 2 km N of Cochabamba, *Ugent* 4593 (P, U, US, WIS); Tiquipaya, 10 km N of Cochabamba, *Ugent* 5003 (LIL, UC, WIS); Distr. Carrasco, Cochabamba 142 km from Cochabamba at Santa Cruz, *Beck* 6830 (WIS); roadside thickets, km 180 on Cochabamba–Sta. Cruz road between Duraznillo & Challuani, *Ugent* 5105 (G, K, NY, UC, US, WIS); rock wall crevice, Tuti-mayo, 25 km E of Cochabamba, *Ugent* 4643 (GH, K, SMF, WIS); Río Mizque, Mizque [riverside thickets], *C. Troll* 1464 (B, M); Tako-Tako near Mizque, *Brooke* 5916 (BM, F, NY); stony valley near stream, Cochabamba, *T. G. Tutin* 1612 (MO); Liriumi, *R. Scolnik & R. Luti* 599 (SI, WIS); Distr. Ayopaya, cuenca Río Tambillo, Independencia, *R. Baar* 223 (LPB, WIS); San Benito, 44 km de Cochabamba a Sta. Cruz, *J. Fernández-Casas* 7721 (MA, MO, NY); La Maica, *M. Cárdenas* 3440 (S, US); Prov. Carrasco al borde de camino y de las chacras, Cochabamba, km 142 hacia Sta. Cruz, Prov. Carrasco, *Beck* 6830 (WIS); valle de Cochabamba, *J. Steinbach* 8741 (BM, F, G, GH, IM, K, M, NY, PH, S, U, UC, US, Z); Tunari, *R. F. Steinbach* 117 (DAV, GH, MO, NY, UC, WIS); progeny of seeds collected in Cochabamba (grown in Washington, D.C.), *R. M. King & L. E. Bishop* 7716 (B, IBUG, K, MARACAY, MEXU, QCNE, TEX, UB, US, USM, WIS); Cochabamba, *O. Buchtien* 2371 (NY, US); Pairumani, *Musch* 16 (SI). **La Paz:** Abel Iturralde Distr., lado de carretera en la banda del Río Tekeje, a 10 km de Ixiamas, Ixiamas Tacana, *G. Bourdy* 2771 (IRD, LPB, UMSA, WIS); delta que forman el arroyo Arana y el Río Tuichi, pozo Yariapo X-1, *B. Kuno* 353 (LPB, WIS); Distr. Inquisivi, Inquisivi, 3 km hacia Circuata, *Beck* 4477 (WIS); 4 km SE of Inquisivi, *M. Nee*

37588 (NY, WIS), *M. Lewis* 35099 (LPB, MO, WIS); Río Sara at Rancho Cuesta Sara, Inquisivi, *Lewis* 882007 (LPB, MO, WIS); Distr. Nord-Yungas, Milliquaya, *Buchtien* 4330 (US); Hacienda “El Choro,” Coripata, *Buchtien* 8092 (NY, US); Isapuri, *D. E. Williams* 684 (NY, US); Río Palca valley, Mt. Illimani, *B. Julio* 110 (C, US); Coroico, *J. Solomon, B. Stein & M. Uehling* 12066 (MO, WIS 2 sheets); forest edge on bank of Río Beni, 20 km upstream from Rurrenabaque, *L. G. Holliday* 60, 67 (K); Rurrenabaque, mossy boulders near river, *D. C. Daly et al.* 6638 (NY, WIS); Reyes, Rurrenabaque, Río Beni, *Fleischman* 476 (S); brecha 22, heliport 14, Río Tuichi, *A. Fournet* 489 (WIS); 12 km along Río Santa Bárbara, below Yolosa, rd. to Caranavi, *Solomon* 8898 (MO, WIS); Distr. Sud-Yungas, Arroyo San Antonio, bajando la Concesión Tropical (ribera del río), Alto Beni, *E. Vargas, R. Seidel & L. Cruz* 2230-A (LPB, WIS); Inicua, *O. M. R. (ERTS)* 373 (WIS); rd. to Chulumani, 23 km E of Unduavi, *T. B. Croat* 51534 (MO, WIS); El Chaco, Valle de Unduavi, *A. Lourteig* 2625 (P); Cañamina, *H. H. Rusby* 66 (BKL, NY); Valle del Río Unduavi de la escuela de Sirupaya por abajo *R. Seidel & E. Richter* 1250 (WIS); Sirupaya near Yanacachi, *Buchtien* 566 (F, G, GH, NY, US, W); Cotaña, am Illimani, *Buchtien* 3173 (NY, US); dry rocky soil on roadside 21 km W of Puente Villa & 26 km E of Unduavi, *C. Davidson* 5003 (RSA); Puente Villa 2 km arriba del Río Tamanpaya, *Beck* 17781 (LPB, WIS); rd. to Puente Villa, 5 km W of Chulumani, *D. M. Spooner, R. G. van den Berg & W. García* 6734 (LPB, WIS); lowland forest along Río Satar-iapo, 12 km SW of Ixiamas, *A. Gentry & R. Foster* 70883 (WIS); [probably La Paz] Yungas, 1890, *M. Bang* 485 (C, G, LD, LE, LIL, M, MO, NDG, NY, PH, R, US, W, WIS, Z). **Santa Cruz:** roadside between Santa Cruz–Cochabamba, km 240, *W. J. Badcock* 468 (K [an exceptionally spiny plant]); Manuel Maria Caballero Distr., ladera con bosques ralo, cerca de Comarapa en dirección a Epizana, *Fernández-Casas* 7901 (MA, MO, NY); Bachraender [borders of creek], Samaipata, *C. Troll* 1063 (B); bosque montañoso con poco influencia humana, Prov. Cordillera, Carapari-cito, 40 km de Camiri, *R. de Michel* 181 (WIS); 35 km de Camiri, *Michel* 65 (WIS); Distr. Vallegrande, low, semi-deciduous forest, 10 km E of Guadalupe, valley of Río Piraymiri, “Juntas de Guaricongas,” *M. Nee, P. Bettella & M. Saldías* 36194 (LPB, NY, WIS); 5 km WNW of Comarapa on road to Catalinas, *D. Ugent & V. Ugent* 5112 (B, UC, WIS). **Sara** [now Prov. Ichilo]: Cerro de Amboró, playitas arenosas del Yráma, *J. Steinbach* 2971 (GH, LIL, NY, SI); San Ignacio, *J. Steinbach* 3537 (G, GH, K, LIL, SI); Distr. Ichilo, Parque Nacional Amboró, tropical evergreen forest, sandy edges of Río Saguayo, 1 km downstream from Quebrada Yapojé, *Nee* 38152 (NY, WIS); evergreen tropical lowland forest along Río Moile, opposite Campamento Moile, 6 km SW of Villa San German, *M. Nee & E. Chávez* 51613 (NY, WIS); Río Saguayo, *Nee & Saldías* 37270 (NY, WIS). PARAGUAY. **Chaco:** Alto Paraguay, *Fiebrig* 1375 (Z) [this location is questionable]. PERU. **Cuzco:** Distr. Cuzco, Camisea, Campamento Armihuari, *P. Acevedo-Rdgz.* 9230 (NY, US, WIS); Anta, El Chaccan, *Brunel* 584 (MO, WIS); Cillapuy, El Chaccan, *Brunel* 359 (MO); Distr. Convención, Amaibamba, Liucumayo, *C. Vargas* 4562 (WIS); Distr. Echarate, Armihuari Well Site, *P. Núñez & Beltrán* 19863 (US, WIS); Distr. Paucartambo, Atalaya, hillside & riverside, jet. Río Carbón with Río Madre de Dios, *R. Foster* 3037 (US); abierta pedregoso, Pilcapata, La Raya, *Vargas* 11320 (CUZ, WIS); arenoso, cerca al río, Atalaya-Kosñipata, *Vargas* 13987 (WIS); Distr. Quispicanchis, Tío-San Pedro, *Vargas* 9730



(A, CUZ, WIS); ruderal, Chili-Chili, *Marin* 2436 (LIL); borde camino, en lugares abicotos, Murayaca, Marcapata, *Vargas* 3756 (LIL, MO); Quince Mil, *Vargas* 7772 (MO). **Madre de Dios:** Distr. Manu, rd. from Shintuya to Salvación, *T. Plowman & E. W. Davis* 5088 (GH). **Puno:** Distr. Sandia, Sandia, *L. Hoogte & C. Roersch* 3447 (MO); trail from Aricoma Pass to Sto. Domingo, *D. McCarroll* 59 (CUZ, MICH).

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