

Phylogenetic evidence reshapes the taxonomy of Cacao and its allies (*Theobroma* and *Herrania*; Malvaceae, Byttnerioideae)

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Abstract

Theobroma (Malvaceae, Byttnerioideae), the cacao genus, has a taxonomic history spanning over two centuries. Currently, it comprises 23 species of trees from lowland forests from the Tropical Americas. *Herrania*, a closely related genus described later, includes 17 additional species commonly referred to as “wild cacaos.” Phylogenetic relationships and morphological circumscriptions between *Theobroma* and *Herrania* have been the subject of debate. While *Herrania* has traditionally been treated as a separate genus based on evident morphological differences in leaf and petal features, it shares similarities with *Theobroma* in terms of habit, inflorescence, and fruit types. Recent phylogenetic evidence, incorporating a broader taxonomic sampling and a total-evidence analysis, suggested that *Theobroma* is paraphyletic, with *Herrania* nested within it. This finding supports the restoration of a classical circumscription of *Theobroma* wherein *Herrania* is considered a section of the former genus. Here, we provide a detailed account of the taxonomic history at infrageneric levels and propose one new subsection, two names at new ranks (to better allocate the diversity within *T. sect. Herrania*), and nine new combinations encompassing this expanded circumscription of *Theobroma*. In our study, we delimit *Theobroma* with forty species divided into six sections: *T. sect. Glossopetalum* (14 spp.), *T. sect. Herrania* (17 spp.), *T. sect. Oreanthes* (5 spp.), *T. sect. Rhytidocarpus* (1 sp.), *T. sect. Telmatocarpus* (2 spp.), and *T. sect. Theobroma* (1 sp.). Furthermore, we recognize three subsections within *T. sect. Herrania*. Alongside these newly proposed changes, we present a section-level identification key and provide diagnostic characters for each taxon.

Keywords Amazonia · Malvales · Neotropical region · South America · Central America · infrageneric descriptions

Introduction

Theobroma L. (Malvaceae, Byttnerioideae) has a botanical history spanning two centuries. Comprising 23 species of understory trees native to Neotropical forests (Cuatrecasas, 1964; Colli-Silva & Pirani, 2020; Santamaría-Aguilar et al., 2023), mostly from lowland areas, *Theobroma* stands out from other Malvaceae for its baccate fruits with axial placentation and large brownish seeds. *Theobroma* species also

hold immense cultural, economic, and culinary significance. Notably, the seeds of its most renowned species, the cacao tree (*T. cacao* L.), are the source of chocolate, a globally cherished food. In fact, the cultural history of cacao dates back to ancient Mesoamerican civilizations, where it was considered a divine gift (hence the genus name assigned by Linnaeus, which means “food of the gods”) and used in various rituals and ceremonies (Coe & Coe, 2013). In modern times, the global chocolate industry has become a multi-billion-dollar

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enterprise, supporting livelihoods in numerous cocoa-producing regions around the world (Sahagún et al., 2018).

A closely related genus, *Herrania* Goudot (Goudot, 1844) includes 17 species also known as “wild cacao” (Schultes, 1958). Morphologically, *Herrania* shares traits with species of *Theobroma* with regard to the understory tree habit, cauliflory, and complex flower structure, featuring unguiculate and cucullate petals and a staminal tube with alternating stamens and staminodes. As in *Theobroma*, these staminodes are often petaloid, and are interspersed between groups of fertile stamens arranged in dyads, triads, or tetrads, connected by the filament, resulting in what is commonly referred to as “2–3–4-antheriferous” stamens (Schumann, 1886; 1895; Schultes, 1958; Cuatrecasas, 1964). Furthermore, both *Theobroma* and *Herrania* exhibit baccate fruits (see Roth, 1977), usually spherical, conical, or cylindrical, with diverse epicarp ornamentation.

The name *Theobroma* was first mentioned by Linnaeus in his *Genera Plantarum* (1737: 350). Subsequently, Linnaeus (1738: 379), recognized two species with the phrase names “*Theobroma foliis integerrimis*” and “*Theobroma foliis serratis*.” These polynomials were repeated later in Linnaeus’s *Species Plantarum* (1753: 782) when he published the binomials *T. cacao* L. and *T. guazuma* L. (= *Guazuma ulmifolia* Lam.), respectively. The genus *Herrania* was later described by Goudot (1844). Based on collections initially assigned to *Theobroma* (or *Abroma* Jacq.), Goudot emphasized that his new genus represented an intermediate between *Guazuma* Mill. and *Theobroma*,

resembling the former in the disposition of the stamens in the staminal tube but differing from it in fruit form. Moreover, *Herrania* diverged from *Theobroma* in sepal count, stamen arrangement, seed characteristics, and cotyledon appearance, despite having a very similar fruit.

Bernoulli’s (1869) monograph on *Theobroma* was the first to propose an infrageneric classification. Bernoulli created five sections (Table 1), which have formed the basis for subsequent classifications of the genus (e.g., Schumann, 1886, 1895; Pittier, 1930). Schumann (1886, 1895) considered *Herrania* to be a section of *Theobroma*, and thus proposed *T. sect. Bubroma* K.Schum., while also recognizing *T. sect. Eutheobroma* (invalid name; see below). Pittier (1930) reduced in rank Bernoulli’s (1869) sections, which he considered to be subsections (Table 1). Schumann and Pittier’s systems both strongly relied on stamen arrangement, whether in dyads or triads, a common feature in *Theobroma* but variable in *Herrania*, where triads or tetrads can appear in the same flower. Thus, *T. sect. Eutheobroma* [sic] encompassed species with stamens in dyads, while *T. sect. Bubroma* consisted of species with stamens in triads. Pittier’s (1930) subsections were based on staminode morphology, distinguishing between linear and expanded forms, as well as petal attributes.

In the 20th century, Schultes (1958) and Cuatrecasas (1964) established the current taxonomy and nomenclature of *Herrania* and *Theobroma*, both maintaining *Herrania* as a separate genus. Cuatrecasas (1964) provided detailed insights into the nomenclatural status of *Theobroma* at

Table 1 Comparison of the main classification systems for *Theobroma* L. and *Herrania* Goudot, as described by various authors, in relation to the classification presented in this study.

Bernoulli (1869); Goudot (1844)	Schumann (1886); Schumann (1895); Pittier (1930)	Schultes (1958); Cuatrecasas (1964)	This work
<i>Theobroma</i> L.	<i>Theobroma</i> L.	<i>Theobroma</i> L.	<i>Theobroma</i> L.
Sect. <i>Cacao</i> Bernoulli, nom. illeg.	Sect. <i>Eutheobroma</i> K.Schum. nom. inval. Subsect. <i>Cacao</i> (Bernoulli) Pittier, nom. illeg.	Sect. <i>Theobroma</i>	Sect. <i>Theobroma</i>
Sect. <i>Rhytidocarpus</i> Bernoulli	Subsect. <i>Rhytidocarpus</i> (Bernoulli) Pittier Sect. <i>Bubroma</i> K.Schum.	Sect. <i>Rhytidocarpus</i> Bernoulli	Sect. <i>Rhytidocarpus</i> Bernoulli
Sect. <i>Telmatocarpus</i> Bernoulli	Subsect. <i>Telmatocarpus</i> (Bernoulli) Pittier	Sect. <i>Telmatocarpus</i> Bernoulli	Sect. <i>Telmatocarpus</i> Bernoulli
Sect. <i>Oreanthes</i> Bernoulli	Subsect. <i>Oreanthes</i> (Bernoulli) Pittier	Sect. <i>Oreanthes</i> Bernoulli	Sect. <i>Oreanthes</i> Bernoulli
Sect. <i>Glossopetalum</i> Bernoulli	Subsect. <i>Glossopetalum</i> (Bernoulli) Pittier	Sect. <i>Glossopetalum</i> Bernoulli Sect. <i>Andropetalum</i> Cuatrec.	Sect. <i>Glossopetalum</i> Bernoulli
<i>Herrania</i> Goudot	Sect. <i>Herrania</i> (Goudot) K.Schum.	<i>Herrania</i> Goudot Sect. <i>Herrania</i> (Goudot) K.Schum.	Sect. <i>Herrania</i> (Goudot) K.Schum. Subsect. <i>Herrania</i> (Goudot) Colli-Silva, stat. nov. Subsect. <i>Dugandia</i> Colli-Silva, subsect. nov.
		Sect. <i>Subcymbicalyx</i> R.E.Schult.	Subsect. <i>Subcymbicalyx</i> (R.E.Schult.) Colli-Silva, stat. nov.

infrageneric levels, including the designation of types for several of the recognized sections. Bernoulli's sections were retained by Cuatrecasas, but Schultes (1958) introduced two new sections within *Herrania* sensu Goudot (1844): *H. sect. Herrania* and *H. sect. Subcymbicalyx* R.E.Schult. The former section encompassed species having a patelliform calyx, while the latter included species with a cupuliform one. Branch architecture and seed germination played significant roles in infrageneric classification, particularly for *Theobroma* (Ducke, 1940; Cuatrecasas, 1964).

With the advent of molecular phylogenetics, the monophyly of *Theobroma* and *Herrania* became uncertain due to limited sampling and low branch support (Whitlock & Baum, 1999; Sousa Silva & Figueira, 2005; Borrone et al., 2007; Richardson et al., 2015). Paraphyly has been observed in certain sections, such as *T. sect. Glossopetalum* Bernoulli and *H. sect. Subcymbicalyx* (Sousa Silva & Figueira, 2005; Borrone et al., 2007). A recent study (Bossa-Castro et al., 2024) presented a new phylogeny based on the sampling of nearly all species of *Theobroma* and *Herrania*, using both morphological and molecular (nuclear) datasets, the latter consisting of *WRKY* transcription-factor gene sequences. This study concluded that *Theobroma* is paraphyletic with regard to *Herrania*, a result that had strong branch support. The study also confirmed the monophyly of most sections described by Bernoulli (1869) and Cuatrecasas (1964). *Herrania sect. Subcymbicalyx* sensu Schultes (1958), however, was not confirmed, but instead is paraphyletic.

When treated as separate genera, *Theobroma* and *Herrania* exhibit notable morphological differences, including branch architecture (sympodial in *Theobroma* vs. monopodial in *Herrania*), leaf blade division (simple in *Theobroma* vs. palmately compound in *Herrania*), petiole length (<3 cm long in *Theobroma* vs. >10 cm long in *Herrania*), and petal ligule length (not more than 2× the petal claw length in *Theobroma* vs. more than 2× in *Herrania*). However, the new phylogeny presented by Bossa-Castro et al. (2024), along with earlier circumscriptions proposed by Schumann (1886; 1895), Pittier (1930), and Ducke (1940, 1953) for *Theobroma* sensu lato (including *Herrania*), gained support over the scenario suggested by Schultes (1958) and Cuatrecasas (1964). Notably, both *Theobroma* and *Herrania* share common morphological features, such as strongly cucullate and relatively thick petals (although plesiomorphic or apomorphic conditions of this feature remain unclear), staminodes (present in both genera, ranging from linear to petaloid but never bifid as seen in *Guazuma*, another closely related genus), and the unique baccate fruit characterized by a mesocarp divided into two portions by a parenchymatic, which consists of a multiseriate layer of sclerenchyma cells that separates the outer and the inner portion of the mesocarp (see Roth, 1977).

Additional diagnostic features apparently unique to *Theobroma* + *Herrania*, not found in close relatives, include

wood anatomical characteristics (presence of small, bordered pits, mostly solitary vessels, and non-storied rays, as opposed to irregularly storied rays in *Guazuma*), seed and cotyledon characteristics (purplish seeds with folded and corrugated cotyledons), and chromosome numbers, which are identical in both groups ($2n = 20$) (Cuatrecasas, 1964). Moreover, successful hybridizations between species of *Theobroma* and *Herrania* have been reported (Addison & Tavares, 1952; Ascenso, 1964; Sousa Silva et al., 2004). The evolution of selected morphological characters within *Theobroma* is discussed by Bossa-Castro et al. (2024), where they suggest that *Herrania* species would represent extreme cases of flower evolution with elongated petal ligules and strongly ridged fruits. Cauliflory would also have been evolved from an exclusively ramiflorous condition in early-diverging lineages of *Theobroma* (as a plesiomorphic condition) towards an exclusively cauliflorous condition observed in *T. sect. Herrania* (Goudot) K.Schum. and *T. sect. Oreanthes* Bernoulli.

The present study proposes an infrageneric classification that re-establishes *Theobroma* sensu lato, in which *Herrania* is included as a section of *Theobroma*. This decision is based on newly available evidence and considers previous authors who considered *Herrania* congeneric with *Theobroma* solely based on morphology (Schumann, 1886, 1895; Pittier, 1930; Ducke, 1940, 1953) and on the comparison of the morphological features described above. Figure 1 summarizes the main changes under the new phylogenetic framework derived from the study of Bossa-Castro et al. (2024).

Materials & Methods

Leaf terminology follows the framework established by Ellis et al. (2009), while descriptions of flower and fruit morphology drew from the works of Roth (1977), and Weberling (1989). For precise terminology concerning the petal ligules of *Theobroma* and *Herrania*, we followed Schultes (1958) and Cuatrecasas (1964). The leaves in *Theobroma* sensu lato exhibit two main forms: they are either simple or palmately compound. Additionally, we categorized leaf(-let) margins as either untoothed—characterized by a lack of vascularized projections or teeth along the edge—or toothed, indicating the presence of vascularized projections. Within the toothed-margin category, we further distinguished whether the veins reached the margin of the leaf or protrude beyond it. Lastly, we treated the petals as unguiculate structures, comprising a lower expanded and cucullate portion defined as the claw, and an upper, filiform segment referred to as the ligule. The proportions of claw length with respect to the ligule length (i.e., the number of times the ligule is longer than

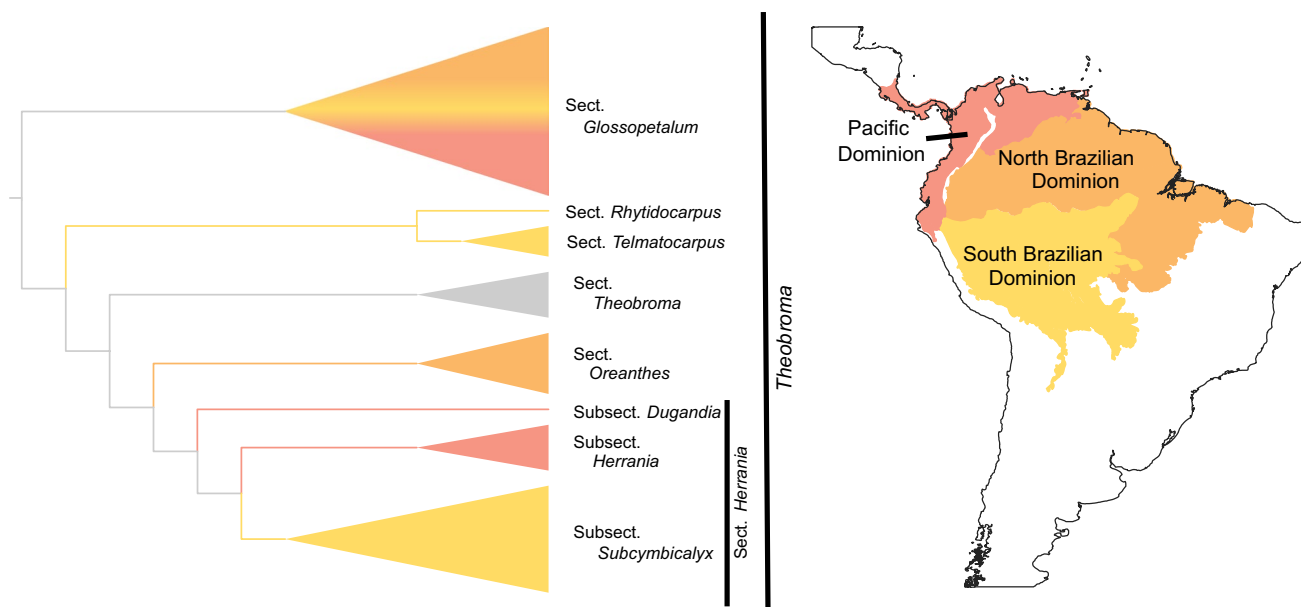


Fig. 1 A new infrageneric classification of *Theobroma* L., including *Herrania* Goudot as a section of *Theobroma*, based on phylogenetic evidence from the study of Bossa-Castro et al. (2024). The left panel illustrates the phylogeny, showing the sections and subsections of *Theobroma* with their respective distributions (roughly simplified for visualization) colored and depicted in the map on the right. The color-coded areas represent major biogeographical regions following Morrone (2014) bioregionalization of the Neotropical region. A minor correction has been made to the caption, changing “Boreal Brazilian Dominion” (sensu Morrone, 2014) to “North Brazilian Dominion” to better reflect this location. *Theobroma* sect. *Glossopetalum* is represented as a gradient of colors because it is distributed across all these areas, while *T.* sect. *Theobroma* (consisting of the single species *T. cacao*) is depicted in gray due to the presence of numerous introduced populations in Tropical Americas with uncertain origin. Inner branches with unclear ancestral range were also colored in gray.

the claw) were also significant features that aid in distinguishing taxa at various ranks within our classification framework. Additionally, we considered petal venation, specifically the number of veins vascularizing the claw, as another important feature for infrageneric classification.

Taxonomic Treatment

Theobroma L., Sp. Pl. 782. [1 May] (1753). TYPE (designated by Hitchcock & Green, 1929: 177): *Theobroma cacao* L. *Cacao* Mill., Gard. Dict. Abr. ed. 4: s.p. (1754). TYPE: Not designated.

Herrania Goudot, Ann. Sci. Nat. Bot., sér. 3, 2: 230 (1844). TYPE (designated by Schultes, 1953: 77): *Herrania albiflora* Goudot.

Lightia R.H.Schomb., Rep. Brit. Assoc. Advancem. Sci. 1844(2): 71 (1845). TYPE: *Lightia lemniscata* R.H.Schomb.

Brotobroma H.Karst. & Triana, Nuev. Jen. Esp. 11 (1854). TYPE: *Brotobroma aspera* H.Karst. & Triana.

Tribroma O.F.Cook, J. Washington Acad. Sci. 5: 288 (1915). TYPE: *Tribroma bicolor* O.F.Cook.

Diagnostic comments. *Theobroma* sensu lato is characterized by flowers with unguiculate and deeply cucullate petals divided into two portions: a lower expanded petal claw and an upper linear to filiform ligule. The stamens are grouped in dyads, triads, or tetrads, with one cluster of staminodes between each stamen group, forming a staminal tube. The baccate fruit has a fibrous outer pericarp and pulpy internal portions, separated by a multiseriate layer of sclerenchyma cells (see Roth, 1977). The seeds are purplish with folded and deeply corrugated cotyledons, and the chromosome number is $2n = 20$.

Under this broadened circumscription, the number of *Theobroma* species increases from 23 to 40, distributed across six sections: *T.* sect. *Glossopetalum* (14 spp.), *T.* sect. *Herrania* (17 spp.), *T.* sect. *Oreanthes* (5 spp.), *T.* sect. *Rhytidocarpus* Bernoulli (1 sp.), *T.* sect. *Telmatocarpus* Bernoulli (2 spp.), and *T.* sect. *Theobroma* (1 sp.) (Table 1). An identification key for the sections and subsections of *Theobroma* sensu lato is provided below, to better demonstrate the morphological and geographic features that are common to the species. A comprehensive taxonomic revision, accounting for synonyms and infraspecific taxonomy, is currently being prepared.

Key to the sections and subsections of *Theobroma sensu lato*

1. Trees with monopodial growth; leaves palmately-compound; petioles >3 cm long; stipules >1.5 cm long; inflorescences cauliflorous, usually 5–10-many-flowered; calyx 3-merous, crimson to purplish, exceptionally ochraceous or ferruginous or cream; petal ligules filiform, at least 2× longer than the claw; fruit epicarp irregularly 10-ridged, usually yellowish-green when ripe.....*T. sect. Herrania*
2. Leaflets ovate, leaflet base convex, margin entire; petals with 7 veins; staminodes lanceolate.....*T. subject. Dugandia*
2. Leaflets elliptic-oblong, obovate or lobate, exceptionally ovate, leaflet base decurrent, straight or cuneate, usually with the secondary veins protruding beyond the leaf margin; petals with 4–6-veins, rarely 7-veined.
 3. Leaflet margin usually partially to entirely toothed, veins protruding beyond the leaf margin, forming conspicuous apicules >2 mm long; inflorescences 10-many-flowered; corolla usually glabrous to sparsely pubescent; petal ligules >10× longer than the petal claw. Mostly from the Amazon Basin.....*T. subject. Subcymbicalyx*
 3. Leaflet margin untoothed, exceptionally toothed at the apex, veins protruding beyond the leaf margin, but forming apicules <2 mm long; inflorescences 4–10- or many-flowered; corolla sparsely pubescent, rarely glabrous; petal ligules <10× longer than the petal claw. Mostly from the Pacific Dominion (sensu Morrone, 2014), northern South America to Panama.....*T. subject. Herrania*
1. Trees with sympodial growth; leaves simple; petioles <3 cm long; stipules <1.5 cm long; inflorescences cauliflorous or ramiflorous, few- or 10-many-flowered; calyx 3–5-merous, ochraceous to ferruginous, occasionally crimson to purplish; petal ligules widened and expanded, up to 2× longer than the claw; fruit epicarp smooth or 5-ridged, usually ochraceous to ferruginous when ripe.
 4. Leaves pulvinate, glabrous abaxially, brochidodromous; calyx yellowish green externally; petals purplish, pink to light red, yellow or crimson; corolla glabrous; fruit epicarp glabrous, variously shaped.....*T. sect. Theobroma*
 4. Leaves not pulvinate, pubescent abaxially, eucamptodromous to craspedodromous; calyx purplish or ochraceous to ferruginous externally; corolla pubescent, exceptionally glabrous; fruit epicarp smooth or deeply ridged, pubescent.
 5. Petals crimson, orange to yellow, 7-more-veined, petal ligules almost equal to or longer than the petal claws; staminodes petaloid, elliptic-ovate; fruit epicarp smooth, rugose, not ridged.....*T. sect. Glossopetalum*
 5. Petals crimson to purplish, 3–6-veined; petal ligules shorter than petal claws in length; staminodes filiform to lanceolate; fruit 5–10-ridged.
 6. Leaf acumen up to 10× longer than leaf blade length; inflorescences few-flowered; petals orbicular, 4–6-veined, <7 cm diam; fruit orbicular, shortly 5–10-ridged; germination hypogeal.....*T. sect. Telmatocarpus*
 6. Leaf acumen always >10× longer than leaf blade length. Inflorescences many-flowered; petals 1–3-veined; fruit sub-orbicular to cylindrical, 5–10-ridged, epicarp smooth or tuberculate, usually >7 cm diam; germination epigeal.
 7. Leaves widely ovate, base cordate, 3-nerved. Inflorescences ramiflorous, 4–10-flowered; petals crimson to purplish, petal claws 1–2-nerved; fruit markedly tuberculate, 10-ridged, glabrous, yellowish-green when ripe.....*T. sect. Rhytidocarpus*
 7. Leaves elliptic-ovate to elliptic-oblong, base rounded, 1–2-nerved; inflorescences cauliflorous, 1–3-flowered or 10-more-flowered; petals pinkish to crimson; petal claws 3-more-nerved; fruit smooth to slightly 5-ridged, not tuberculate, densely pubescent, ochraceous to ferruginous when ripe.....*T. sect. Oreanthes*

1. *Theobroma sect. Theobroma*

Theobroma sect. Cacao (Mill.) Bernoulli, Uebersicht Theobroma 6 (1869), *nom. illeg.* *Theobroma* subsect. *Cacao* (Mill.) Pittier, Rev. Int. Bot. Appl. Agric. Trop. 10(110): 779 (1930). TYPE: Not designated.

Theobroma sect. Eutheobroma K.Schum. in Martius, Fl. Bras. 12(3): 70 (1886), *nom. inval.*

Diagnostic comments. Leaves simple, pulvinate, glabrous abaxially, brochidodromous; calyx yellowish-green externally, petals purplish, pink to light red, yellow, or crimson;

corolla glabrous; fruit variously shaped, slightly ridged depending on the cultivar, epicarp glabrous. One species:

1.1. *Theobroma cacao* L., Sp. Pl. 782 (1753).

2. *Theobroma sect. Telmatocarpus* Bernoulli, Uebersicht Theobroma 11 (1869). *Theobroma* subsect. *Telmatocarpus* (Bernoulli) Pittier, Rev. Int. Bot. Appl. Agric. Trop. 10(110): 779 (1930). TYPE: *Theobroma microcarpum* Mart.

Diagnostic comments. Leaves simple, acumen less than 10× longer than the leaf-blade length; inflorescences

few-flowered; petals with 4 or more veins, petal ligules almost lacking; germination hypogeal. Two species:

2.1. *Theobroma gileri* Cuatrec., Rev. Int. Bot. Appl. Agr. Trop. 33(373–374): 562, t. 1 (1953).

2.2. *Theobroma microcarpum* Mart. in Buchner, Repert. Pharm. 35: 24 (1830) (“*microcarpa*”).

3. *Theobroma* sect. *Rhytidocarpus* Bernoulli, Uebersicht *Theobroma* 9 (1869). *Theobroma* subsect. *Rhytidocarpus* (Bernoulli) Pittier, Rev. Int. Bot. Appl. Agric. Trop. 10(110): 779 (1930). TYPE (designated by Cuatrecasas, 1964: 458): *Theobroma bicolor* Bonpl.

Diagnostic comments. Leaves simple, cordate at the base, less than 10× longer than leaf-blade length; petals and staminodes pink to light red, petals with 1–2 veins; fruit epicarp irregularly and prominently tuberculate. One species:

3.1. *Theobroma bicolor* Bonpl., Pl. Aequinoct. 1(4): 104, t. 30 (1806 [1808]).

4. *Theobroma* sect. *Oreanthes* Bernoulli, Uebersicht *Theobroma* 7 (1869) (“*Oreanthes*”). *Theobroma* subsect. *Oreanthes* (Bernoulli) Pittier, Rev. Int. Bot. Appl. Agric. Trop. 10(110): 779 (1930). TYPE (designated by Cuatrecasas, 1964: 467): *Theobroma speciosum* Willd. ex Spreng.

Diagnostic comments. Leaves simple, acumen more than 10× longer than leaf-blade length; inflorescences many-flowered; petals with 1–3 veins, petal ligules sessile and large; germination epigeal. Five species:

4.1. *Theobroma bernoullii* Pittier, Repert. Spec. Nov. Regni Veg. 13: 319 (1914) (“*Bernoullii*”).

4.2. *Theobroma glaucum* H.Karst., Linnaea 28(4): 447 (1857 [1856]).

4.3. *Theobroma speciosum* Willd. ex Spreng., Syst. Veg. 3: 332 (1826).

4.4. *Theobroma sylvestre* (Aubl.) Mart. in Buchner, Repert. Pharm. 35: 24 (1830).

4.5. *Theobroma velutinum* Benoist, Bull. Mus. Hist. Nat. Paris 27: 113 (1921).

5. *Theobroma* sect. *Glossopetalum* Bernoulli, Uebersicht *Theobroma* 11 (1869). *Theobroma* subsect. *Glossopetalum* (Bernoulli) Pittier, Rev. Int. Bot. Appl.

Agric. Trop. 10(110): 779 (1930). TYPE: *Theobroma angustifolium* DC. (**here designated**). **Note:** Although Cuatrecasas (1964: 526) stated that the type of this section was *Theobroma grandiflorum* DC., this species was not one of the species included by Bernoulli (1869) and cannot serve as type of this name.

Theobroma sect. *Bubroma* K. Schum., in Engler & Prantl, Nat. Pflanzenfam. 3(6): 89 (1890). TYPE: *Theobroma angustifolium* DC. (**here designated**).

Theobroma sect. *Andropetalum* Cuatrec., Contr. U.S. Natl. Herb. 35(6): 579 (1964), **syn. nov.** TYPE: *Theobroma mammosum* Cuatrec. & J.León

Diagnostic comments. Leaves simple; inflorescences 1–3–10-flowered, exceptionally 11–many-flowered; petals crimson, with 7–many veins, petal ligules almost equal to or longer than the petal claw; staminodes elliptic or ovate; fruit smooth or rugose, exceptionally tuberculate. Fourteen species:

5.1. *Theobroma angustifolium* DC., Prodr. 1: 484 (1924).

5.2. *Theobroma canumanense* J.M.Pires & R.L.Frões ex Cuatrec., Contr. U.S. Natl. Herb. 35(6): 577, fig. 43 (1964).

5.3. *Theobroma chocoense* Cuatrec., Contr. U.S. Natl. Herb. 35(6): 543 (1964).

5.4. *Theobroma cirmolinae* Cuatrec., Notas Fl. Colombiana 6: 5, Figs. 1–5 (1944).

5.5. *Theobroma flaviflorum* Aguilar & D.Santam., Syst. Bot. 48(2): 315, Figs. 1, 2, 3A, 4R, 7T (2023).

5.6. *Theobroma grandiflorum* (Willd. ex Spreng.) K.Schum. in Martius, Fl. Bras. 12(3): 76, t. 17 (1886).

5.7. *Theobroma hylaeum* Cuatrec., Contr. U.S. Natl. Herb. 35(6): 570, Figs. 25F, 39D (1964).

5.8. *Theobroma mammosum* Cuatr & J.León, Bol. Técn. Inst. Interamer. Ci. Agric. 2: 1, Figs. 1–7 (1949).

5.9. *Theobroma nemorale* Cuatrec., Revista Acad. Colomb. Ci. Exact. 8(32): 487, Fig. 4 (1952).

5.10. *Theobroma obovatum* Klotzsch ex Bernoulli, Uebersicht *Theobroma* 14, t. 7, Fig. 3 (1869).

5.11. *Theobroma simiarum* Donn.Sm., Bot. Gaz. 25(3): 145 (1898).

5.12. *Theobroma sinuosum* Pav. ex Huber, Bull. Herb. Boissier, sér. 2, 6: 274 (1906).

5.13. *Theobroma stipulatum* Cuatrec., Fieldiana, Bot. 27(1): 84, Fig. 7 (1950).

5.14. *Theobroma subincanum* Mart. in Buchner, Repert. Pharm. 35: 23 (1830).

6. *Theobroma* sect. *Herrania* (Goudot) K.Schum. in Martius, Fl. Bras. 12(3): 70 (1886). *Herrania* Goudot, Ann. Sci. Nat., Bot., sér. 3, 2: 230 (1844). TYPE: *Herrania albiflora* Goudot. *Theobroma albiflorum* (Goudot) De Wild.

Diagnostic comments. Trees with monopodial growth; leaves palmately-compound, petioles more than 3 cm long; stipules more than 1.5 cm long; inflorescences cauliflorous, usually 5–10–more-flowered; calyx 3-merous, crimson to purplish, exceptionally ochraceous or ferruginous, or cream; petal ligules filiform, at least 2× longer than the petal claw; fruit epicarp deeply 10-ridged, usually yellowish-green when ripe.

In order to enrich the differentiation among various groups within *T.* sect. *Herrania*, and considering the presence of both morphological and geographical distinctions, we have classified the diversity of *T.* sect. *Herrania* in three subsections:

6.1. *Theobroma* subsect. *Dugandia* Colli-Silva, **subject. nov.** TYPE: *Theobroma dugandii* (García-Barr.) Colli-Silva.

Diagnostic comments. Leaflets ovate, base shape convex, veins touching but not extending beyond the leaf margin; petals with 7 veins; staminodes lanceolate. One species:

6.1.1. *Theobroma dugandii* (García-Barr.) Colli-Silva, **comb. nov.** *Herrania dugandii* García-Barr., *Caldasia* 1(2): 59, Fig. 3 [*“Dugandii”*] (1941).

6.2. *Theobroma* subsect. *Subcymbicalyx* (R.E.Schult.) Colli-Silva, **stat. nov.** *Herrania* sect. *Subcymbicalyx* R.E.Schult., J. Arnold Arbor. 39: 229 (1958). TYPE (designated by Schultes, 1958: 229): *Herrania nitida* (Poepp.) R.E.Schult. *Theobroma asperum* (H.Karst. & Triana) K.Schum. ex C.J.J.Hall.

Diagnostic comments. Leaflet margin usually toothed (throughout or only at the apex), veins extending beyond the leaf margin, forming apicules >2 mm long; inflorescences 10-many-flowered; corolla usually glabrous to

sparsely pubescent; petal ligules more than 10× longer than the petal claw. Six species:

6.2.1. *Theobroma asperum* (H.Karst. & Triana) K.Schum. ex C.J.J.Hall., *Cacao*, ed. 2, 49 (1932) (*“aspera”*). **Note:** The name *Theobroma nitidum* (Poepp.) K.Schum., in Mart. Fl. Bras. 12(3): 71 (1886), *nom. illeg.* [*non Theobroma nitidum* Bernoulli, Ueberischt *Theobroma*: 15 (1869)] is originally based on *Abroma nitida* Poepp., Nov. Gen. Sp. Pl. 3: 74 (1845). However, it cannot be utilized because this combination is a later homonym to *Theobroma nitidum* Bernoulli. Schultes (1958: 257) tentatively proposed the combination to *Herrania nitida* (Poepp.) R.E.Schult., but according to the findings of this study, the correct nomenclature for this species is as described herein. A comprehensive nomenclatural conspectus will be included in an ongoing taxonomic treatment that we are currently preparing.

6.2.2. *Theobroma cuatrecasianum* (García-Barr.) Colli-Silva, **comb. nov.** *Herrania cuatrecasiana* García-Barr., *Caldasia* 1(2): 57, t. 2. (*“Cuatrecasana”*) (1941).

6.2.3. *Theobroma kanukuense* (R.E.Schult.) Colli-Silva, **comb. nov.** *Herrania kanukuensis* R.E.Schult., *Caldasia* 2(6): 11 (1943).

6.2.4. *Theobroma mariae* (Mart.) K.Schum. in Martius, Fl. Bras. 12(3): 71 (1886).

6.2.5. *Theobroma nycterodendron* (R.E.Schult.) Colli-Silva, **comb. nov.** *Herrania nycterodendron* R.E.Schult., *Caldasia* 2(6): 21 (1943).

6.2.6. *Theobroma tomentellum* (R.E.Schult.) Colli-Silva, **comb. nov.** *Herrania tomentella* R.E.Schult., Bot. Mus. Leaflet. 16(8): 213, t. 32 (1954).

6.3. *Theobroma* subsect. *Herrania* (Goudot) Colli-Silva, **stat. nov.** *Herrania* Goudot, Ann. Sci. Nat., Bot., sér. 3, 2: 230 (1844). TYPE: *Herrania albiflora* Goudot. *Theobroma albiflorum* (Goudot) De Wild.

Diagnostic comments. Leaflet margin untoothed, exceptionally partially toothed, veins extending beyond the leaf margin, forming small apicules, <2 mm long; corolla sparsely pubescent, seldom glabrous; petal ligules less than 10× longer than the petal claw. Ten species:

6.3.1. *Theobroma albiflorum* (Goudot) De Wild., Pl. Trop. Gr. Cult. 90 (1902).

- 6.3.2. *Theobroma balaense*** (P.Preuss) De Wild., Pl. Trop. Gr. Cult. 89 (1902).
- 6.3.3. *Theobroma breviligulatum*** (R.E.Schult.) Colli-Silva, **comb. nov.** *Herrania breviligulata* R.E.Schult., *Caldasia* 1(4): 20, figs. s.n. [p. 21], 5 (1942).
- 6.3.4. *Theobroma camargoanum*** (R.E.Schult.) Ducke, Bol. Técn. Inst. Agron. N. 28: 15, tt. 29, 32 (1954).
- 6.3.5. *Theobroma kofanorum*** (R.E.Schult.) Colli-Silva, **comb. nov.** *Herrania kofanorum* R.E.Schult., Bot. Mus. Leaflet. 14(5): 126, tt. 28, 34 (1950).
- 6.3.6. *Theobroma laciniifolium*** (Goudot ex Triana & Planch.) De Wild., Pl. Trop. Gr. Cult. 90 (“*laciniifolium*”) (1902).
- 6.3.7. *Theobroma lemniscatum*** (R.H.Schomb.) Colli-Silva, **comb. nov.** *Lightia lemniscata* R.H.Schomb., Rep. Brit. Assoc. Advancem. Sci. 1844(2): 71 (1845). *Herrania lemniscata* (R.H.Schomb.) R.E.Schult. *Caldasia* 2(6): 13 (1943).
- 6.3.8. *Theobroma pulcherrimum*** (Goudot) De Wild., Pl. Trop. Gr. Cult. 89 (1902).
- 6.3.9. *Theobroma purpureum*** Pittier, Repert. Spec. Nov. Regni Veg. 13: 319 (1914).
- 6.3.10. *Theobroma umbraticum*** (R.E.Schult.) Colli-Silva, **comb. nov.** *Herrania umbratica* R.E.Schult., *Caldasia* 2(8): 261, t. s.n. [p. 263] (1943).

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Declarations

Competing interests

The authors have no competing interests to declare that are relevant to the content of this article.

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