

The rise of *Cynometra* (Leguminosae) and the fall of *Maniltoa*: a generic re-circumscription and the addition of 4 new species

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Abstract

Cynometra L. is a genus of ca. 85 species of shrubs to large trees. It is amongst the largest genera in the legume subfamily Detarioideae and one of the few with a pantropical distribution. Perhaps due to this wide distribution and high diversity, systematists and taxonomists have struggled with the classification of *Cynometra* and its close ally, the genus *Maniltoa* Scheff. Recent phylogenetic studies have shown that many of the African species are more closely related to other genera and that the genus *Maniltoa* is nested within a clade of Indo-Pacific *Cynometra*. Here, I present an emended circumscription of *Cynometra* that excludes the African species defined by jointed pedicels and dehiscent fruits and includes the species formerly recognised in *Maniltoa*. New combinations in *Cynometra* are also provided for those species that require them. Additionally, four new species of Neotropical *Cynometra* are described and illustrated: *Cynometra cerebriformis* **sp. nov.** from the lower Rio Trombetas in Brazil; *Cynometra duyerrii* **sp. nov.** from the Darien gap region of Panama; *C. tumbesiana* **sp. nov.** from the dry tropical forests of Ecuador and Peru; and *C. steyermarkii* **sp. nov.** from the foothills of the western Cordillera de la Costa in Venezuela.

Keywords

Cynometra L, Detarioideae, Leguminosae, *Maniltoa* Scheff, new species, taxonomy

Introduction

The genus *Cynometra* L. (Leguminosae) has a broad tropical distribution, is relatively species rich and many of its species are poorly represented in herbaria. The approximately 85 species of trees and (some) shrubs in the genus are spread somewhat evenly amongst four regions (Figure 1): the Neotropics (from southern Mexico and the Caribbean to northern Argentina; Dwyer 1958, Sprada Tavares and da Silva 1992), mainland tropical Africa (equatorial forest belt; Léonard 1951), Madagascar and the Comoros Islands (Du Puy et al. 2002) and the Indo-Pacific (extending from the Western Ghats eastward to Fiji; Knaap-van Meeuwen 1970, Smith 1985). Perhaps unsurprisingly, the genus has long troubled taxonomists and systematists who have struggled with its diversity in several attempts to revise and classify regional groupings of the species (Léonard 1951, Dwyer 1958, Knaap-van Meeuwen 1970). Further, its relationship to the much smaller Pacific genus *Maniltoa* Scheff. has remained equivocal. Several important phylogenetic studies of the Caesalpinioideae sensu lato suggested that *Cynometra* was not monophyletic (Bruneau et al. 2001, 2008). More recent studies, with greater taxonomic sampling, have provided additional evidence that the genus is polyphyletic and, furthermore, that one of the lineages is paraphyletic with respect to *Maniltoa* (Mackinder et al. 2013, Radosavljevic et al. 2017, de la Estrella et al. 2018). In order for the classification of *Cynometra* to reflect a monophyletic taxon, a new genus circumscription must be provided and *Maniltoa* should be subsumed into *Cynometra*. In addition, during the course of herbarium study and fieldwork, several undescribed species were revealed. Those species are here described. This paper is divided into three parts: I. A new circumscription of the genus *Cynometra*; II. The transfer of all species of *Maniltoa* into *Cynometra*; and III. Description of four new species of *Cynometra*.

Materials and methods

The following herbaria allowed the author to study their collections in person or provided loans: A, ATH, BM, BRI, CANB, F, IAN, INPA, K, MG, MO, NY, P, RB, SING and US. Morphological characters were assessed and measured from herbarium material. Flowers and immature fruit were rehydrated in warm Pohl's solution (Pohl 1965) prior to dissection and measurement. Other characters were measured directly from the herbarium specimens. For the new species from Ecuador, flower colour, habit and habitat information were taken from label data and field observations by Gwilym Lewis and Bente Klitgaard (pers. comm.); for the other three species, these features were described from label data. Reproductive status is indicated with the following abbreviations (alone or in combination): fl, flowering; fr, fruiting; im, immature; st, sterile. Illustrations were made at the National Museum of Natural History, Washington DC, USA by Mattias S. Lanás (*Cynometra steyermarkii*), Katherine Rudebusch (*C. tumbesiana*) and Alice Tangerini (*C. cerebriformis* and

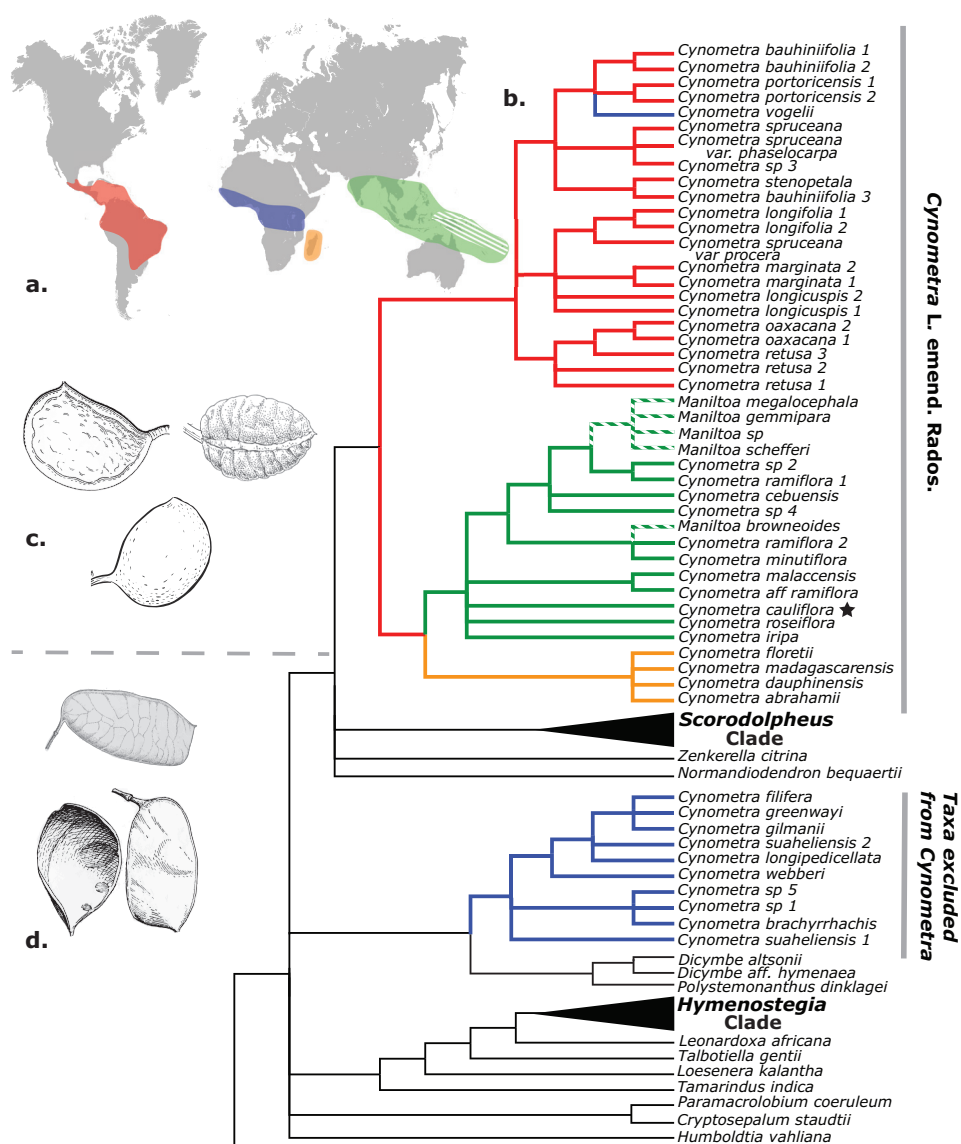


Figure 1. **A** Map showing global distribution of *Cynometra* and *Maniltoa* (white hatching) **B** ML majority rules consensus tree from Radosavljevic et al. (2017) with branches coloured by species distributions. Star indicates type species of *Cynometra* **C** indehiscent fruits typical of *Cynometra* as circumscribed here; **D** dehiscent fruits typical of those species formerly included in *Cynometra*, but excluded by the new circumscription.

C. dwyerii) from herbarium specimens. Two of the new species are described based on a single collection: in both cases, the taxa are morphologically and geographically distinct and, after extensive herbarium study, the author is confident that the available material, while limited, is sufficient to distinguish two new entities at the species level.

Part I: A new circumscription of the genus

Linnaeus established the genus *Cynometra* and included two species from south-east Asia in the first edition of *Species Plantarum*, *Cynometra cauliflora* L. and *C. ramiflora* L. (Linnaeus, 1753). This original concept of *Cynometra* was of a genus distinguished by compound leaves, four reflexed sepals, five equal petals and by single-seeded, indehiscent pods with thick and tuberculate valves (Linnaeus' description does not explicitly mention 'indehiscent pods', but it is a character present in both of his original species). For nearly the next century, this circumscription was generally followed by taxonomists around the world. The limits of the genus were first expanded by the publication of two new species from the Indo-Pacific region: *Cynometra polyandra* Roxb., described in 1820 from Indian material and *Cynometra grandiflora* A.Gray, described in 1854 from Fijian specimens. These species differed most notably from the traditional understanding of *Cynometra* by having more numerous stamens (35–40 in *C. grandiflora* and approximately 50 in *C. polyandra*; Roxburgh 1820, Gray 1854). Bentham (1865a) later described the African species *C. floribunda* Benth. and *C. laxiflora* Benth., species with large, petaloid bracteoles and only two showy petals which he placed in a new subgenus, *Hymenostegia* (the fruit of the two species also differs from *Cynometra*, but these were unknown at the time). Scheffer (1876) established the segregate genus *Maniltoa* after viewing collections from New Guinea; believing the material to be conspecific, he included a single species, *Maniltoa grandiflora* (A.Gray) Scheff. (based on *Cynometra grandiflora* A.Gray). While the most apparent difference between the new genus *Maniltoa* and typical *Cynometra* was the number of stamens, Scheffer (1876) argued that the genus was distinct based on the size of the flowers, the number of seeds, caducous filiform stipules, the presence of a tendril terminating the leaf rachis and bracts subtending each pedicel in the inflorescence. He does not include or reference *C. polyandra*, another polyandrous species. *Maniltoa* was not universally accepted at first and Taubert's (1894) treatment of the Leguminosae for Engler's *Die Natürlichen Pflanzenfamilien* treated *Maniltoa* as a section of *Cynometra* (along with the sections *Eucynometra*, *Hymenostegia* and *Pseudocynometra*). A few years later, however, Harms (1897) broke apart this broad concept of *Cynometra*. He elevated *Hymenostegia* to the rank of genus and restored *Maniltoa* by combining it with section *Pseudocynometra* (consisting of a single species, *C. polyandra*) on the basis of greater stamen number and the presence of prominent buds enclosed in imbricate scarious bract scales (Harms 1897, 1902, 1919). This understanding of *Cynometra* and *Maniltoa* in the Indo-Pacific was further refined by Knaap-Van Meeuwen (1970) who sought to better define the limits between the two genera – she again placed greatest significance on the stamen number, placing those with 8–13 stamens in *Cynometra* and those with 15–80 in *Maniltoa*. While many authors have followed this delimitation (Verdcourt 1979; Hou et al 1996), some have continued to question the distinction of the two genera (Soerianegara 1993; Pan et al. 2010).

In Africa, misunderstanding of the delimitation of *Cynometra* persisted, even after Harm's (1897) treatment and the turn of the century marked the beginning of a period of rapid taxonomic expansion in both the number of species and, consequently, the characters describing the generic limits of *Cynometra*. As explained (in great detail) by Léonard (1951), the first few species described in Africa generally matched the Linnaean concept (e.g. *Cynometra vogelii* Hook.f. in 1849 from Nigeria; *C. mannii* Oliv. in 1871 from Cameroon). However, with the description of *Cynometra sessiliflora* Harms, Harms (1899) expanded the understanding of *Cynometra* to include species with five erect sepals (instead of four reflexed sepals) and, most importantly for the continued confusion regarding the genus, dehiscent pods with thin, flat valves. Not long after, the publication of *Cynometra alexandri* C.H. Wright, *C. gillettii* De Wild., *C. laurentii* De Wild., *C. lujae* De Wild., *C. oddonii* De Wild. and *C. pedicellata* De Wild. added more species with five sepals and dehiscent fruits and further expanded the genus to include species with an intrastaminal disc and numerous ovules (Wright 1902; De Wildeman 1904, 1905, 1906, 1907). Harms (1907) also continued to expand the generic conception of *Cynometra* in Africa to include species with alternate leaflets, distichous flowers and a stipe fused with the receptacle wall when he described *C. leptantha* Harms, *C. multijuga* Harms and *C. pierreana* Harms. *Cynometra brachyura* Harms, expanded the genus to again include species with only two petals (Harms 1913). As a result, species with all manner of combinations of these characters were placed in *Cynometra* (see Baker 1930 and Pellegrin 1949). While many taxonomists, working in Africa, noted the heterogeneity of the genus, it was not until Léonard undertook a thorough and careful revision of the African species that a coherent circumscription of *Cynometra* began to emerge (Baker 1930; Lebrun 1933; Aubréville 1936; Léonard 1951, 1957).

Léonard's work (1951, 1957) was a major advancement in revising the boundaries of *Cynometra* and its allies in Africa, which had become so broad as to make genera nearly indistinguishable. Léonard (1951) removed from *Cynometra* any taxa with the stipe of the ovary adnate to the hypanthium or eccentrically inserted (species with a free, central stipe but alternate leaflets with translucent dots were moved to *Gilletiodendron* Vermoesen). To accommodate his revised concept of the genus, Léonard (1951, 1957) described a new genus, *Lebruni dendron* J. Léonard, resurrected the genera *Gilletiodendron* Vermoesen and *Zenkerella* Taub. and transferred numerous species out of *Cynometra* and into the genera *Hymenostegia* (Benth.) Harms, *Plagiosiphon* Harms, *Schotia* Jacq. and *Scorodophloeus* Harms. He placed the remaining *Cynometra* into three informal groups; they share a centrally inserted stipe, opposite leaflets, five equal petals and imbricate sepals, but differ notably in characters such as inflorescence structure, presence or absence of a staminal disc, presence or absence of foliar glands and fruit shape and dehiscence. Léonard (1951) acknowledged that the genus remained heterogeneous – the species of 'group one' resembled 'typical *Cynometra*', but the others were possibly misplaced. Later, he further assessed the genera of African Amherstieae and Cynometreae, revising the tribal and generic limits using characters from germination

mode, seedling architecture and wood structure, amongst others. (Léonard 1957). A thorough examination of the genus *Cynometra*, unfortunately, was not included in that otherwise exhaustive study. Léonard and others recognised that, as contemporarily circumscribed, the genus was likely polyphyletic and would require further revisionary studies at a global scale (Aubréville 1968, 1970; Breteler 1996; Léonard 1996).

An early morphological cladistic analysis by Temu (1990) provided the first phylogenetic evidence for the non-monophyly of African *Cynometra*. The results showed two distinct clades of *Cynometra* in tropical Africa, one of which included *Maniltoa*. Later morphological and molecular phylogenetic analyses, albeit with limited sampling of *Cynometra* and *Maniltoa*, also found no evidence to support monophyly of *Cynometra* and suggested that it may be paraphyletic with respect to *Maniltoa* (Bruneau et al. 2001, 2008). More recent studies which included a greater taxon sampling from *Cynometra* and *Maniltoa* have found support for two clades of *Cynometra*, one consisting of exclusively East African species and the other containing species from the rest of the genus plus *Maniltoa* (Mackinder et al. 2013; Radosavljevic et al. 2017; de la Estrella et al. 2018). Radosavljevic et al. (2017), which featured 47 accessions from 36 species of *Cynometra* and *Maniltoa*, recovered two strongly supported clades of *Cynometra* sensu lato, which are each diagnosed by several morphological characters (Figure 1). One clade (*Cynometra* clade A of Radosavljevic et al. 2017) is comprised of exclusively east African species and is grouped as sister to a clade composed of *Dicymbe* Spruce ex Benth. and *Polystemonanthus* Harms with strong support. The other clade, which includes the type species *Cynometra cauliflora* L., contains *Cynometra* species from the Neotropics, the remaining Afrotropical species and the Indo-Pacific species (*Cynometra* clade B of Radosavljevic et al. 2017). *Maniltoa* is nested within clade B and is also recovered as non-monophyletic. This clade of *Cynometra* and *Maniltoa* is placed in a clade with *Zenkerella* Taub., *Normandi dendron* J. Léonard and the *Scorodophloeus* clade, again with strong support. The species of *Cynometra* clade A are characterised by the absence of foliar extra-floral nectaries, paniculate inflorescences (with two exceptions), articulated pedicels, a well-developed intrastaminal disc, 2–4 ovules and dehiscent fruit. *Cynometra* clade B is characterised by the presence of foliar extra-floral nectaries (in most species), racemose inflorescences, simple pedicels, the absence of an intrastaminal disc, 1–2 ovules and indehiscent fruit. The species of *Cynometra* clade A correspond to Léonard's (1951) groups 2 and 3 while *Cynometra* clade B, which contains the generic type *Cynometra cauliflora* L., corresponds to group 1. Léonard (1951, 1996) predicted as much; he referred to group 1 as 'typical *Cynometra*' and believed that *Cynometra alexandri* and *C. hankei* Harms were likely misplaced. De la Estrella et al. (2018), who sampled broadly across Detarioideae, placed *Cynometra* and *Maniltoa* in a re-circumscribed Amherstieae.

To reconcile the discrepancy between the current classification of *Cynometra* and *Maniltoa* and our understanding of their evolutionary relationships, I present here an emended generic circumscription of *Cynometra* that excludes the species of *Cynometra* clade A and includes the species formerly placed in *Maniltoa*. A treatment that proposes a new genus for the species of *Cynometra* clade A is in preparation.

Taxonomic treatment

Cynometra L. Sp. Pl. 1:382. 1753.

Syn. *Iripa* Adans., Fam. 2: 508. 1763. *Cynomora* R.Hedw. Gen. Pl. [R. Hedwig]. 1806.

Type. *Cynometra cauliflora* L. (lectotype, designated by A.S. Hitchcock, in Hitchcock and Green 1959, pg. 152)

Metrocynia Thouars, Gen. Nov. Madagasc. 22. 1806. Type. *Metrocynia commersoniana* DC.

Maniltoa Scheff., Ann. Jard. Bot. Buitenzorg 1: 20. 1876. Type. *Cynometra grandiflora* A.Gray.

Schizosiphon K.Schum., Fl. Kais. Wilh. Land 101. 1889. *Schizoscyphus* K.Schum ex Taubert, *nom. superfl.* Bot. Centralbl. 41: 265. 1890. Type. *Schizosiphon rosea* K. Schum.

Pseudocynometra Kuntze in Post & Kuntze, Lex. Gen. Phan. Phan. 464. 1903. Type. *Cynometra polyandra* Roxb.

Trees or shrubs (infrequent), evergreen (rarely deciduous), buttressed or not, growth flush-wise, new growth flaccid and whitish or reddish at emergence, becoming green with maturity, vegetative buds covered in a series of imbricate scales. *Stipules* lateral, free, linear or filamentous, early caducous, scars typically not visible on mature growth.

Leaves pulvinate, petiolate, rachis (if present) terete or caniculate, often terminating in a filiform outgrowth, axes glabrous or pubescent, paripinnate with 1–16 pairs of opposite leaflets (rarely unifoliolate); leaflets petiolulate but sometimes appearing sessile because of decurrent lamina, blade lanceolate, ovate, elliptic, oblong, obovate, oblanceolate or trapeziform, symmetrical to strongly asymmetrical, glabrous or sparsely pubescent abaxially, glabrous adaxially (rarely with sparse pubescence along midvein), margins entire, apex broadly obtuse to acuminate, retuse or emarginate, mucronate, base oblique, distal margin decurrent to petiolule; laminar nectaries usually present, abaxial, submarginal, embedded in laminar surface, shallow, without noticeably raised edges. **Inflorescences** axillary or ramiflorous (rarely cauliflorous), racemose, 1–2(–3), per axil, buds enclosed by imbricate bracts, appearing conical, ovoid or cigar-shaped in silhouette; pedicels simple (not articulated), filamentous in anthesis, accrescent and lignified in fruit; bracts enclosing inflorescence during development prior to emergence, imbricate, distichous, deciduous or persistent; bracteoles not enclosing buds, paired, inserted along proximal half of pedicel, opposite or subopposite, caducous.

Flowers bisexual, actinomorphic; hypanthium present (sometimes indistinct), either turbinate-campanulate and short or tubular and partially to completely enveloping ovary; disc absent; sepals (3–)4(–5), reflexed at anthesis, unequal, deltoid, ovate, elliptic or oblong; petals 5, crumpled or smooth, incurved, erect or horizontal, equal, linear, oblong, or oblanceolate, with rounded or acute apices; stamens (8–)10–80, filaments free or briefly connate basally; anthers dorsifixed, versatile, longitudinally dehiscent; ovary inserted +/- centrally, occasionally eccentric, free, short-stipitate or subsessile, pubescence varied but rarely glabrous, light green or pinkish, often turning red post anthesis, ovules 1 (2); style eccentric, glabrous; stigma capitate. **Legumes**

indehiscent, splitting along suture after germination due to action of emerging shoot, orbicular to oblong, often laterally compressed, smooth to deeply fissured, often apiculate (in some taxa only when immature), valves 0.5–4.0 mm thick, cork-like in several species, remaining attached to cotyledons during and after germination. **Seeds** 1–2, enclosed in fruit until germination. **Seedling** germination epigeal.

The emended description above reflects the merger of *Maniltoa* and *Cynometra* s.s. and the exclusion of the east African taxa with dehiscent pods, paniculate inflorescences and articulated pedicels (Tables 1, 2). While many taxa in the former *Maniltoa* are no doubt distinctive and, in many cases, striking when compared to the more unassuming *Cynometra*, a close examination of their morphological characteristics reveals a strong similarity. The number of stamens has been perhaps the most distinctive and most often cited character separating the two genera. *Cynometra* has long been known to have only 10 stamens, while *Maniltoa* has been traditionally treated as having anywhere from 15–80 stamens. Indeed, this proliferation in stamen number is rare in the Detarioideae. However, a closer look at the Indo-Pacific *Cynometra* reveals several examples of species which regularly have as few as eight stamens (*Cynometra glomerulata* Gagnep.) or as many as 12 (*Cynometra katikii* Verdc.) and some with variation across the range within a species (8–10 stamens in *Cynometra cauliflora* L. and 10–15 stamens in *Cynometra ramiflora* L.; Knaap-van Meeuwen 1970, Verdcourt 1979). So, while the majority of species, placed within *Cynometra*, do have 10 stamens, there is lability amongst this trait in the taxa of the region.

Several other characteristics of *Maniltoa* that supposedly distinguish it from *Cynometra* are also incorrect. The first is the presence of conspicuous ‘bract covered’ vegetative and reproductive buds (Scheffer 1876, Harms 1902, 1919). In some species of *Maniltoa*, these buds can be many centimetres long and several centimetres in diameter. The scales themselves are often tan or brown, but can be whitish or pinkish and are often covered with parallel striations running longitudinally along the surface. These types of buds are also present in *Cynometra*, although they are much smaller, in some cases only 4 or 5 mm long. Likewise, the scales are similar in shape, vestiture and surface texture. Another general characteristic used to separate the two genera has been the sturdiness of the inflorescence rachis in *Maniltoa* (Knaap-van Meeuwen 1970). However, this is likely related to the overall general difference in size of the flowers and inflorescence between the two genera: *Maniltoa* tend to have larger buds, bracts, inflorescences and individual flowers. The larger inflorescences of the *Maniltoa* species may be an adaptation to mammal pollination as there are reports of marsupials and bats visiting the flowers of *Maniltoa* species in Australia and the Pacific Islands (Marshall 1985, Endress 1994). Scheffer (1876) cited the presence of a tendril terminating the leaf rachis as a distinguishing character of *Maniltoa*, but Dwyer (1958) notes that this trait is present in several *Cynometra*. Finally, differences in wood anatomy given by Knaap-van Meeuwen (1970) have been found to be insufficiently distinct from one another and overlapping in range (Soerianegara 1993; Pan et al. 2010).

The most clearly distinguishing feature of the newly emended *Cynometra* with respect to the taxa here excluded (*Cynometra* clade A) is the indehiscent pod. Indeed, if one examines the taxa misplaced in *Cynometra* over the years, they nearly all share the characteristic of dehiscent pods. Unfortunately, Linnaeus makes no mention of the

Table 1. Species excluded from *Cynometra*. Distributions correspond to regions given in text. Species may occupy only a part of the overall region. MTA = mainland tropical Africa.

Species	Distribution
<i>Cynometra alexandri</i> C.H. Wright	MTA
<i>Cynometra ananta</i> Hutch. & Dalziel	MTA
<i>Cynometra brachyrrhachis</i> Harms	MTA
<i>Cynometra engleri</i> Harms	MTA
<i>Cynometra filifera</i> Harms	MTA
<i>Cynometra fischeri</i> Baker f.	MTA
<i>Cynometra gillettii</i> De Wild.	MTA
<i>Cynometra gillmanii</i> J. Léonard	MTA
<i>Cynometra greenwayi</i> Brenan	MTA
<i>Cynometra hankei</i> Harms	MTA
<i>Cynometra leonensis</i> Hutch. & Dalziel	MTA
<i>Cynometra longipedicellata</i> Harms	MTA
<i>Cynometra lujae</i> De Wild.	MTA
<i>Cynometra nyangensis</i> Pellegr.	MTA
<i>Cynometra oddonii</i> De Wild.	MTA
<i>Cynometra palustris</i> J. Léonard	MTA
<i>Cynometra pedicellata</i> De Wild.	MTA
<i>Cynometra sessiliflora</i> Harms	MTA
<i>Cynometra suaheliensis</i> (Taub.) Baker f.	MTA
<i>Cynometra ulugurensis</i> Harms	MTA
<i>Cynometra webberi</i> Baker f.	MTA

nature of the pods' dehiscence. Likewise, subsequent treatments were vague. Bentham (1865b), Taubert (1894) and Harms (1897) all described the pods as 'two-valved' without further elaboration. Léonard (1951) and Aubréville (1968, 1970) cite the pods of 'typical *Cynometra*' as dehiscent or indehiscent, likely owing to the fruit of *Cynometra mannii*, the valves of which are not dehiscent but, upon pressing and drying, often split and rupture in several places along axes roughly perpendicular to the sutures. A similar occurrence is observed in the Neotropical species *Cynometra baubiniifolia* Benth. When Harms (1899) described *C. sessiliflora*, he set a precedent regarding the pod characters that contributed to the imprecise delimitation of *Cynometra* and subsequently led to the taxonomic confusion surrounding *Cynometra* in Africa.

With this new circumscription, the two genera are united and share radially symmetric flowers, bract covered buds (with bracts persisting on the inflorescence), flowers with early caducous bracteoles not enveloping the flowers and indehiscent fruits (which may play a role in dispersal as many taxa are associated with alluvial habitats or appear as drift 'fruit' in coastal environments; Ridley 1930, Léonard 1951, Clarke et al. 2001, Tomlinson 2016). The new classification changes the overall distribution of the taxa. Prior to this, *Cynometra* was a genus with its diversity distributed somewhat evenly across the American, African and Asian tropics. However, with the exclusion of many of the African species and the inclusion of the former *Maniltoa*, *Cynometra* is now a genus whose primary centre of diversity is the Indo-Pacific region, with a secondary centre in the Neotropics and the majority of Afrotropic taxa restricted to Madagascar.

Table 2. Accepted species of *Cynometra*. Taxonomy follows: Knaap Van-Meeuwen 1970; Léonard 1951; Dwyer 1958. New combinations and new species presented in text are not included. Distributions correspond to regions given above. Species may occupy only a part of the overall region. COM = Comoros Islands; INP = Indo-Pacific; MAD = Madagascar; MTA = mainland tropical Africa; NEO = Neotropics.

Species	Distribution	Species	Distribution
<i>Cynometra abrahamii</i> Du Puy & R.Rabev.	MAD	<i>Cynometra longifolia</i> Huber	NEO
<i>Cynometra americana</i> Vogel	NEO	<i>Cynometra lukei</i> Beentje	MTA
<i>Cynometra ankaranensis</i> Dupuy & R.Rabev.	MAD	<i>Cynometra hyallii</i> Baker	MAD
<i>Cynometra aurita</i> R.Vig.	MAD	<i>Cynometra macrocarpa</i> A.S.Tav.	NEO
<i>Cynometra baubiniifolia</i> Benth.	NEO	<i>Cynometra madagascariensis</i> Baill.	MAD
<i>Cynometra beddomei</i> Prain	INP	<i>Cynometra malaccensis</i> Meeuwen	INP
<i>Cynometra bourdillonii</i> Gamble	INP	<i>Cynometra mannii</i> Oliv.	MTA
<i>Cynometra brachymischa</i> Harms	INP	<i>Cynometra marginata</i> Benth.	NEO
<i>Cynometra capuronii</i> Du Puy & R.Rabev.	MAD	<i>Cynometra marleneae</i> A.S.Tav.	NEO
<i>Cynometra cauliflora</i> L.	INP	<i>Cynometra mayottensis</i> Labat & O.Pascal	COM
<i>Cynometra cloiselii</i> Drake	MAD	<i>Cynometra megalophylla</i> Harms	MTA
<i>Cynometra commersoniana</i> Baill.	MAD	<i>Cynometra microflora</i> R.S.Cowan	NEO
<i>Cynometra congensis</i> De Wild.	MTA	<i>Cynometra minutiflora</i> F.Muell.	INP
<i>Cynometra copelandii</i> (Elmer) Elmer	INP	<i>Cynometra mirabilis</i> Meeuwen	INP
<i>Cynometra craibii</i> Gagnep.	INP	<i>Cynometra novoguineensis</i> Merr. & L.M.Perry	INP
<i>Cynometra crassifolia</i> Benth.	NEO	<i>Cynometra oaxacana</i> Brandegees	NEO
<i>Cynometra cubensis</i> A.Rich.	NEO	<i>Cynometra parvifolia</i> Tul.	NEO
<i>Cynometra cuneata</i> Tul.	NEO	<i>Cynometra pervilleana</i> Baill.	MAD
<i>Cynometra dauphinensis</i> Dupuy & R.Rabev.	MAD	<i>Cynometra polyandra</i> Roxb.	INP
<i>Cynometra dongnaiensis</i> Pierre	INP	<i>Cynometra portoricensis</i> Krug & Urb.	NEO
<i>Cynometra duckei</i> Dwyer	NEO	<i>Cynometra ramiflora</i> L.	INP
<i>Cynometra elmeri</i> Merr.	INP	<i>Cynometra retusa</i> Britton & Rose	NEO
<i>Cynometra falcata</i> A.Gray	INP	<i>Cynometra sakalava</i> Du Puy & R.Rabev.	MAD
<i>Cynometra fissicuspis</i> (Pittier) Pittier	NEO	<i>Cynometra sanagaensis</i> Aubrev.	MTA
<i>Cynometra floretii</i> Labat & O.Pascal	COM	<i>Cynometra schlechteri</i> Harms	MTA
<i>Cynometra glomerulata</i> Gagnep.	INP	<i>Cynometra schottiana</i> Hochr.	NEO
<i>Cynometra grandiflora</i> A.Gray	INP	<i>Cynometra simplicifolia</i> Harms	INP
<i>Cynometra hemitomophylla</i> (Donn.Sm.) Rose	NEO	<i>Cynometra spruceana</i> Benth.	NEO
<i>Cynometra hondurensis</i> Dwyer	NEO	<i>Cynometra stenopetala</i> Dwyer	NEO
<i>Cynometra hostmanniana</i> Tul.	NEO	<i>Cynometra travancorica</i> Bedd.	INP
<i>Cynometra humboldtiana</i> Stergios	NEO	<i>Cynometra trinitensis</i> Oliv.	NEO
<i>Cynometra insularis</i> A.C.Sm.	INP	<i>Cynometra vogelii</i> Hook.f.	MTA
<i>Cynometra iripa</i> Kostel.	INP	<i>Cynometra warburgii</i> Harms	INP
<i>Cynometra katikii</i> Verdc.	INP	<i>Cynometra whitfordii</i> Elmer	INP
<i>Cynometra letestui</i> (Pelleg.) J.Léonard	MTA	<i>Cynometra yokotai</i> Kaneh.	INP
<i>Cynometra longicuspis</i> Ducke	NEO	<i>Cynometra zeylanica</i> Kosterm.	INP

Part II: Reduction of *Maniltoa* into *Cynometra*

The generic rearrangements require new combinations to reflect the merging of *Maniltoa* into *Cynometra*. For *Maniltoa*, in most cases, the taxonomy proposed by Knaap-van Meeuwen (1970) has been followed, but for some species limits, the interpretations of Verdcourt (1979) have been followed; such deviations are noted. Species, for which a combination already exists in *Cynometra*, are not listed (Knaap-van Meeuwen 1970). In total, 18 new combinations and one new name are proposed. A lectotype is designated for *Maniltoa megalcephala* Harms and a neotype is designated for *Maniltoa peekelii* Harms.

1. *Cynometra basifoliola* (Verdc.) Rados., comb. nov.

urn:lsid:ipni.org:names:77199243-1

Basionym. *Maniltoa basifoliola* Verdc., Kew Bull. 37: 129. 1982. Type. PAPUA NEW GUINEA. Madang province: Madang subprovince [district], cleared area utilized as a gravel pit on north side of Madang Usino Highway on banks of Gogol River, 145 37 E, 05 15 S, 100 m alt., 25 April 1979, *S.H. Somer & P. Katik LAE 75185* (holotype: K; isotypes: BM, L, M).

Notes. The arrangement of leaflets for which this species is named (i.e. the basal-most pair of leaflets inserted just above petiole and separated from terminal pair of leaflets by a relatively long rachis) is unusual amongst the species that were formerly included in *Maniltoa*; however some species of *Cynometra* have a similar arrangement (e.g. *Cynometra sakalava* Du Puy & R.Rabev from Madagascar).

2. *Cynometra brassii* (Merr. & L.M.Perry) Rados., comb. nov.

urn:lsid:ipni.org:names:77199244-1

Basionym. *Maniltoa brassii* Merr. & L.M.Perry, J. Arnold Arbor. 23: 398. 1942. Type. BRITISH NEW GUINEA [PAPUA NEW GUINEA]. Central Division: U-uma River, 14 May 1926, [fl., imm. fr.], *L. J. Brass 1428*, (holotype: A; isotype: K).

Notes. The protologue lists the collection year as 1928, however 1926 appears to be the correct date. While the label affixed to the holotype does list the collection date as “14 May 1928”, this appears to be a transcription error. The handwritten slip attached to the holotype, presumably filled out by the collector Brass, gives the date as “14/5/26”. Additionally, the printed label is titled “Arnold Arboretum Expedition, 1925–1926”. The label on the isotype also has the collection date as 14 May 1926.

3. *Cynometra browneoides* (Harms) Rados., comb. nov.

urn:lsid:ipni.org:names:77199245-1

Basionym. *Maniltoa browneoides* Harms, Notizbl. Königl. Bot. Gart. Berlin 3: 190. 1902. Synonym. *Pseudocynometra browneoides* (Harms) Kuntze, Deutsche Bot. Monatsschr. 21: 173. 1903. Type. [INDONESIA]. Java. [West Java: Bogor Botanic Gardens], 1880–1882, [fl.], *H. O. Forbes 1204a* (holotype: B, destroyed; isotype: BM).

Synonym. *Maniltoa gemmipara* Scheff. ex Backer, Voorl. Schoolfl. Java 104: in clavi. 1908. Type. [INDONESIA]. Cultivated at Weltevreden (Djakarta), 1908, *Backer s.n.* (holotype: L, fide Knaap-van Meeuwen 1970).

Notes. According to Knaap-van Meeuwen (1970, p. 42), the type material for *Maniltoa browneoides* came from a cultivated specimen grown at Bogor Botanical Gar-

dens from seeds or seedlings collected by Forbes on New Guinea, however no citation is given as the source for this information. The holotype for *M. gemmipara* is listed as being at Leiden by Knaap-van Meeuwen, however there are no specimens there annotated as such. There are two specimens, however, from Java collected in 1908 that seem to match the details in the protologue. These are filed as *M. gemmipara* and have the registration numbers L.3886447 and L.3886448.

4. *Cynometra cynometroides* (Merr. & L.M.Perry) Rados., comb. nov.

urn:lsid:ipni.org:names:77199246-1

Basionym. *Maniltoa cynometroides* Merr. & L.M.Perry, J. Arnold Arbor. 23: 398. 1942. Type. BRITISH NEW GUINEA [PAPUA NEW GUINEA]. Palmer River, 2 mi. below junction Black River, 100m alt., Jun 1936, [fr], *L. J. Brass 6903* (holotype: A; isotypes: BM, BO, BRI, L).

5. *Cynometra fortuna-tironis* (Verdc.) Rados., comb. nov.

urn:lsid:ipni.org:names:77199247-1

Basionym. *Maniltoa fortuna-tironis* Verdc., Kew Bull. 32 (1): 243. 1977. Type. PAPUA NEW GUINEA. Central District [Central Province]: Rouna Falls area, forest by tributary of R. Laloki, 300 m alt., 2 Jan. 1976, *B. Verdcourt, C.R. Huxley, & Dodd 4899* (holotype: K; isotypes: LAE, UPNG).

6. *Cynometra lenticellata* (C.T.White) Rados., comb. nov.

urn:lsid:ipni.org:names:77199248-1

Basionym. *Maniltoa lenticellata* C.T.White, J. Arnold Arbor. 8: 130. 1927. Type. PAPUA [PAPUA NEW GUINEA]. Northern Division: Sageri, July 1922, [fl], *C. E. Lane-Poole 203* (holotype: BRI; isotype: A).

7. *Cynometra lenticellata* var. *villosa* (Verdc.) Rados., comb. nov.

urn:lsid:ipni.org:names:77199249-1

Basionym. *Maniltoa lenticellata* var. *villosa* Verdc., Kew Bull. 32 (1): 241. 1977. Type. TERRITORY OF NEW GUINEA [PAPUA NEW GUINEA]. Morobe district [Morobe province]: Lae subdistrict [Lae district], Kassam Pass, 6°20'S, 146°00'E, 3500 ft alt., [fl], *J.S. Womersley & J. Vandenberg NGF 37192* (holotype: LAE; isotypes: A, BISH, BO, BRI, CANB, K, L, NSW, PNH, SING, UPNG, US)

8. *Cynometra mariettae* (van Meeuwen) Rados., comb. nov.

urn:lsid:ipni.org:names:77199250-1

Basionym. *Maniltoa mariettae* van Meeuwen, Blumea 18 (1): 37. 1970. Type. TERRITORY OF NEW GUINEA [PAPUA NEW GUINEA]. Morobe District [Morobe Province]: Yalu, 6°36'S, 146°52'E, 50 ft alt., Jul 1944, [fl], *C.T. White, H.E. Dadswell, & L.S. Smith*, NGF 1661 (holotype: BRI; isotype: CANB).

9. *Cynometra megalcephala* (Harms) Rados., comb. nov.

urn:lsid:ipni.org:names:77199251-1

Basionym. *Maniltoa megalcephala* Harms, Bot. Jahrb. Syst. 55 (1): 52. 1917. Type. NORDÖSTLICH NEU-GUINEA [PAPUA NEW GUINEA]. Sepik area, 1912–1913, *C. L. Ledermann* 7857, 7895, 10616 (syntypes: B, destroyed). PAPUA NEW GUINEA. Sepik area, *Harms, Bot. Jahrb. Syst. 55 (1): 53, tab. 2. 1917.* (lectotype, here designated)

Notes. All three syntypes cited in Harms' original description were destroyed and no isotypes have been located. Therefore plate 2 (tab. 2) from Harms 1917 is designated as the lectotype (Figure 2).

10. *Cynometra minor* (A.C.Sm.) Rados., comb. nov.

urn:lsid:ipni.org:names:77199252-1

Basionym. *Maniltoa minor* A.C.Sm., Sargentia 1: 37. 1942. Type. FIJI. Lau Province: Moala Island, near Maloku, 20–24 Mar 1934, [fl], *A.C. Smith* 1333 (holotype: GH; isotype: BISH, K, NY, S, WIS, US).

11. *Cynometra plurijuga* (Merr. & L.M.Perry) Rados., comb. nov.

urn:lsid:ipni.org:names:77199253-1

Basionym. *Maniltoa plurijuga* Merr. & L.M.Perry, J. Arnold Arbor. 23: 398. 1942. Type. NETHERLANDS NEW GUINEA [INDONESIA]. [Papua:] 2 km southwest of Bernhard Camp, Idenburg River, 650 m alt., 3 April 1939, *L.J. Brass & C. Versteegh* 13539 (holotype: A; isotype: BO, BRI, L).

12. *Cynometra psilogyne* (Harms) Rados., comb. nov.

urn:lsid:ipni.org:names:77199254-1

Basionym. *Maniltoa psilogyne* Harms, Bot. Jahrb. Syst. 55 (1): 50. 1917. Type. KAISER-WILHELMSLAND [Papua New Guinea]. At Kaulo, ca. 250 m alt., 1 December 1907, *R. Schlechter* 16934 (holotype: B; isotypes: A, E, G, K, L, S, Z).

13. *Cynometra rosea* (K.Schum.) Rados., comb. nov.

urn:lsid:ipni.org:names:77199255-1

Basionym. *Schizosiphon roseus* K.Schum., Fl. Kais. Wilh. Land 101. 1889. Syn. *Schizoscyphus roseus* (K.Schum.) Warb., *nom superfl.*, Bot. Jahrb. Syst. 13: 331. 1891. *Maniltoa rosea* (K.Schum.) Meeuwen, Blumea 18: 35. 1970. Type. KAISER-WILHELMSLAND [PAPUA NEW GUINEA]. Astrolabebay, Im Hochwalde von Constantinshafen, July [1886–1887], *Hollrung* 492 (holotype: B, destroyed; isotypes not found). PAPUA NEW GUINEA. Madang Province: Madang District, Naikum, Josephstaal, 04°45'30"S, 145°00'30"E, 1 Sept. 1958, *K.J. White NGF 10226* (neotype, designated by Knaap-van Meeuwen 1970, p. 35: K; isoneotypes: BRI, CANB).

Maniltoa urophylla Harms, Bot. Jahrb. 55: 51. 1917. Type. NORDÖSTLICH NEU-GUINEA [PAPUA NEW GUINEA]. Kameelsrücken, lager G, 6–900 m, Sept. 1912, *C. L. Ledermann 8848* (holotype: B, destroyed; isotypes: WRSL, LE, not located).

Notes. I agree with Verdcourt (1979) that this synonymy is questionable. However, with the original type material destroyed and to avoid creating an unnecessary new combination, I have elected to follow Knaap-van Meeuwen's treatment here.

14. *Cynometra schefferi* (K.Sch.) Rados., comb. nov.

urn:lsid:ipni.org:names:77199256-1

Basionym. *Maniltoa schefferi* K.Sch., Fl. Kais. Wilh. Land 10. 1889. Syn. *Pseudocynometra schefferi* Kuntze, Deutsche Bot. Monatsschr. 21: 173. 1903. Type. PAPUA NEW GUINEA. Dore, *Teysmann s.n.* (lectotype, designated by Knaap-van Meeuwen 1970, p. 45: L).

Maniltoa hollrungii Harms, Notizbl. Königl. Bot. Gart. Berlin 3: 189. 1902. Syn. *Pseudocynometra hollrungii* Kuntze, Deutsche Bot. Monatsschr. 21: 173. 1903. Type. KAISER-WILHELMSLAND [PAPUA NEW GUINEA]. Augusta-Station, Aug. 1887, *Hollrung* 689 (holotype: B, destroyed; isotypes not found).

15. *Cynometra schefferi* var. *peekelii* (Harms) Rados., comb. nov.

urn:lsid:ipni.org:names:77199257-1

Basionym. *Maniltoa peekelii* Harms, Bot. Jahrb. Syst. 55 (1): 50. 1917. Syn. *Maniltoa schefferi* var. *peekelii* (Harms) Verdc. Type. [PAPUA NEW GUINEA]. Neu-Mecklenburg (New Ireland): Lemakot, Garamate, Strandebene, July 1912, *G. Peekel 841* (holotype: B, destroyed). PAPUA NEW GUINEA. New Ireland District [Province]: [Island of New Ireland], Kavieng Sub-District [District], ca. 26 miles from Kavieng, inland from Lavongai, 2°46'S, 151°2'E, 0 m alt., 24 Jan. 1967, *M.J.E. Coode, T. Crolepy, & P. Katik NGF 29604* (neotype, here designated: K; isoneotypes: A, CANB, L, LAE).

Note. When Verdcourt (1977) published the above name at a new rank, he did not name a neotype. He did cite several representative specimens and specifically men-

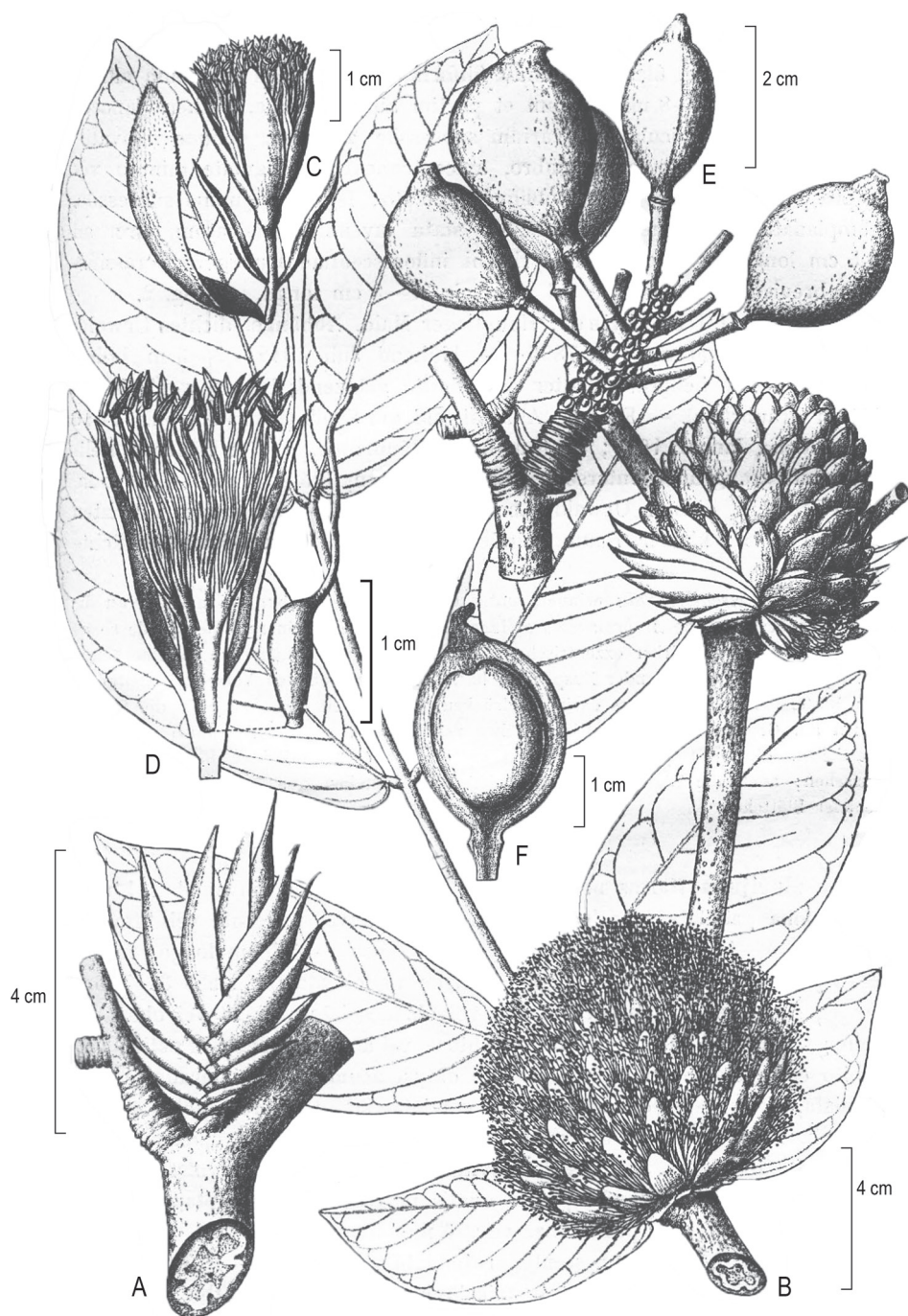


Figure 2. Illustration of *Maniltoa megalocephala* Harms, reproduced from protologue and designated here as the lectotype.

tioned Coode et al NGF 29604 as a specimen he was certain belonged to this species. Given that it is well represented in herbaria and was collected near the original type locality, this specimen has been chosen as the neotype.

16. *Cynometra steenisii* (van Meeuwen) Rados., comb. nov.

urn:lsid:ipni.org:names:77199258-1

Basionym. *Maniltoa steenisii* van Meeuwen, *Blumea* 18 (1): 40. 1970. Type. TERRITORY OF PAPUA [PAPUA NEW GUINEA]. Northern District [Northern Province]: Tufi subdistrict, near Budi Barracks, 9°32'S, 148°58'E, 75 m alt., 26 August 1954, *R.D. Hoogland 4581* (holotype: CANB).

Notes. Knaap-van Meeuwen incorrectly cites the holotype as being housed in BRI.

17. *Cynometra steenisii* var. *rodneyensis* (Verdc.) Rados., comb. nov.

urn:lsid:ipni.org:names:77199266-1

Basionym. *Maniltoa steensisii* var. *rodneyensis* Verdc., *Kew Bull.* 32 (1): 241. 1977. Type. TERRITORY OF PAPUA [PAPUA NEW GUINEA]. Central District [Central Province]: Abau Subdistrict [Abau District], Cape Rodney, Mori River, 200 ft alt., 20 June 1968, *E. E. Henty NGF 38561* (holotype: LAE; isotypes: A, BISH, BO, BRI, CANB, K, L, NSW, SING).

18. *Cynometra vestita* (A.C.Sm.) Rados., comb. nov.

urn:lsid:ipni.org:names:77199267-1

Basionym. *Maniltoa vestita* A.C.Sm., *J. Arnold Arbor.* 31: 170. 1950. Type. FIJI. Vanua Levu. Mathuata [Macuata] province: east of Lambasa [Labasa], on the southern slopes of Mt Numbuiloa, 3 Nov 1947, [fl], *A.C. Smith 6442* (holotype: A; isotypes: BISH, BRI, K, L, LE, NY, P, S, US).

19. *Cynometra vitiensis* Rados., nom. nov.

urn:lsid:ipni.org:names:77199269-1

Basionym. *Maniltoa floribunda* A.C.Sm., *J. Arnold Arbor.* 31: 169. 1950, non *Cynometra floribunda* Benth, *Trans Linn. Soc. London* 25: 318. 1865. Type. FIJI. Viti Levu. Nandronga-Navosa Province: southern slopes of Nausori Highlands, in drainage of Namosi Creek above Tumbenasolo, 300–400 m alt., 29 May 1947, *A.C. Smith 4588* (holotype: A; isotypes: BISH, BRI, K, L, LE, NY, P, S, US).

Notes. This species is named after the nation of Fiji, where it is endemic, but somewhat common and widespread, occurring on at least six islands (Smith 1985).

Part III: Four new species of *Cynometra*

A monograph of the Neotropical species of *Cynometra* was published by Dwyer (1958), but it was limited by the lack of fertile material. In the intervening decades, however, many new collections have been made, particularly in the Amazon basin, the centre of diversity of the genus in the New World. This has made revisionary work more feasible and uncovered previously undocumented diversity. In the context of the ongoing taxonomic and phylogenetic studies, several new species have been discovered in existing herbarium collections. Four new species are described below: *Cynometra cerebriformis* sp. nov. from the lower Rio Trombetas in Para State, Brazil; *Cynometra dwyerii* sp. nov. from the Darien gap region of Panama; *C. tumbesiana* sp. nov. from the dry tropical forests of Ecuador and Peru; and *C. steyermarkii* sp. nov. from the foothills of the western Cordillera de la Costa in Venezuela (Figure 3).

1. *Cynometra cerebriformis* Rados., sp. nov.

urn:lsid:ipni.org:names:77199270-1

Figures 4, 5

Type. BRAZIL. Pará: [Mun. Oriximiná] Rio Trombetas, near Cachoeira Porteira, 24 May 1974, [fl.], D. G. Campbell et al., P22338 (holotype US; isotype F, INPA, MO, NY).

Description. *Tree* to 20 m tall; bark not seen; branchlets rough, lenticels prominent, bud scale scars partially encircling stems near base, new growth with short scattered pubescence, glabrous or nearly so at maturity. *Stipules* not seen. *Leaves* bifoliate, pulvinate, axes glabrous or with sparse pubescence concentrated on adaxial surfaces; petioles 3.0–4.0 mm long, 1.0 mm wide, transversely corrugated; petiolules 0.5–1.0 mm long, 0.5 mm wide, transversely corrugated; leaflets appearing sessile, coriaceous, obelliptic to obovate, asymmetric, primary vein eccentric, proximal side 2.0–2.7 times wider than distal, 3.1–4.5 cm long, 1.1–1.9 cm wide, abaxial surface with scattered raised areas both surfaces glabrous, primary venation pinnate, secondary venation brochidodromous-eucamptodromous, 3–4 basal acrodromous veins, decurrent to primary vein, prominent abaxially, their course barely visible adaxially, tertiary venation difficult to discern on either surface even under magnification, margins entire, apex acute, usually short acuminate (acumen to 4.0 mm), retuse, mucronate, base oblique, acute, distal side narrowly cuneate with margin nearly parallel to midvein for 8.0–10.0 mm, proximal side convex, decurrent to petiolule, laminar glands absent. *Inflorescence* an axillary raceme, (1–)2 per axil, bracteate, axes ferrugino-pilose; peduncle 1.0–2.0 mm, rachis 2.0–5.0 mm long, flowers spirally arranged, 2–10 per raceme; pedicels 7.0–10.0 mm and filamentous in anthesis, to 18.0 mm and accrescent in fruit; bracts subtending individual flowers, scale-like, quickly deciduous, brown, broadly elliptical to deltoid, strongly convex 1.5–2.5 mm long, 1.0–1.5 mm wide, striate, abaxial surface pubescent, pubescence denser at base and along margins, glabrous adaxially; bracteoles not seen. *Flowers* bisexual, radially symmetric, pentamerous, delicate; hypanthium cupular, 0.7–1.0 mm deep,

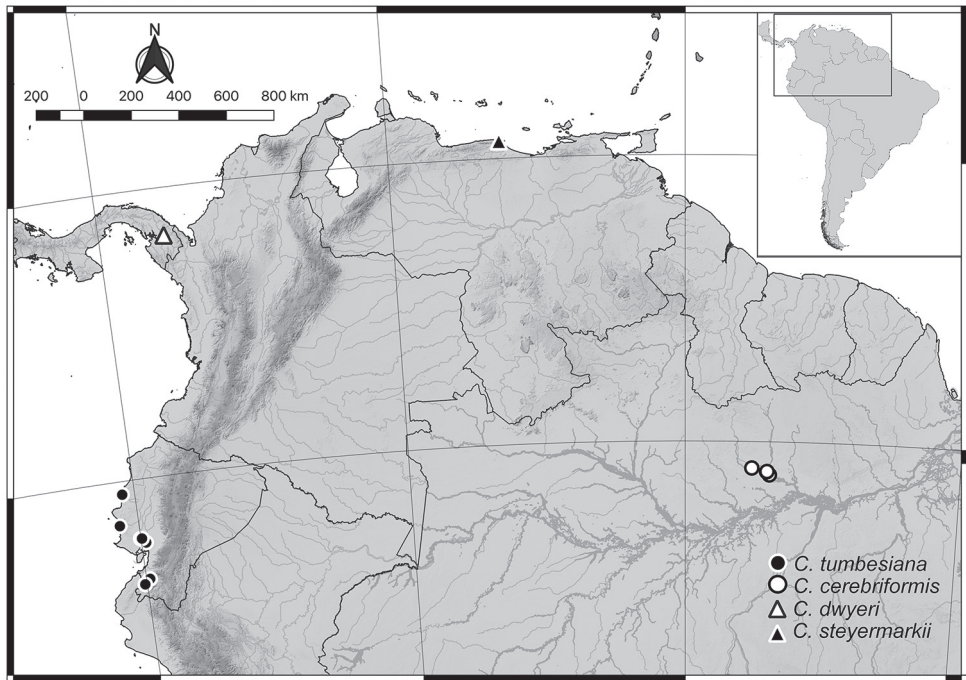


Figure 3. Distribution of *Cynometra cerebriformis*, *C. dwyeri*, *C. steyermarkii* and *C. tumbesiana*.

surrounding basal portion of ovary, fleshy, abaxial surface pubescent, adaxial surface glabrous; sepals 4, imbricate, reflexed, abaxial and adaxial sepals larger than lateral, greenish-white, petaloid, oblong to elliptic, apices acute to rounded, 3.0–4.0 mm long, 1.0–2.0 mm wide, pubescence on abaxial surface near apex, with faint parallel venation; petals 5, equal, white, crumpled texture, curving inwards, oblanceolate, 4.0–5.0 mm long, 1.0–1.5 mm wide, adaxial surface with minute appressed hairs, pinnate venation; stamens 10, filaments free, subequal, 7.0–8.5 mm long, anthers dorsifixed, versatile, longitudinal dehiscence, ellipsoid, to 1.0 mm long, glabrous; ovary centrally inserted, free, stipitate, obliquely elliptical, 2.5–3.0 mm long, 1.5–2.0 mm wide, tomentose, stipe 0.5 mm, style apical, 2.0–2.5 mm long, glabrous, eccentric, curving downwards, stigma capitate. **Legume** indehiscent, oblate, rugose, apiculate when immature, 14.2–17.5 mm long, 7.1–9.2 mm wide, 12.1–13.9 mm thick, valves pubescent, wall of pericarp up to 2.5 mm thick, brown. **Seeds** 1 per pod, filling locule, dark brown.

Distribution and ecology. Currently, this species appears restricted to the Trombetas River Basin of Para State, Brazil. However, it is quite possible that the range is more extensive given that the species occurs in seasonally flooded forests and the genus is known for water dispersed fruits (Ridley 1930, Clarke et al. 2001, Tomlinson 2016). Little else is known about this taxon.

Phenology. Flowering specimens have been collected in May. Fruiting specimens have been collected in June and August.

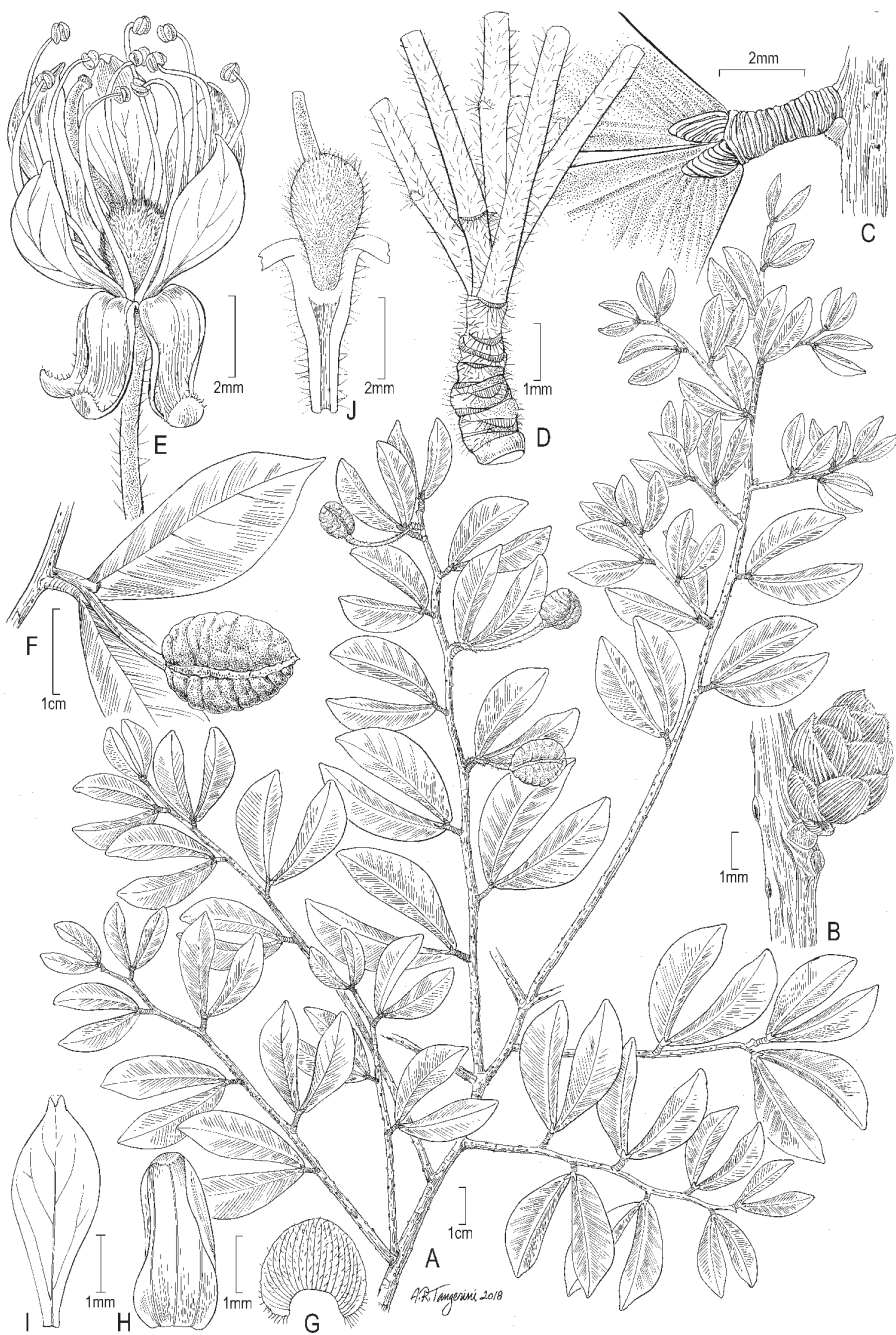


Figure 4. Illustration of *Cynometra cerebriformis*. **A** Habit **B** bud with imbricate bracts **C** leaf base showing corrugated petiole and petiolule **D** inflorescence rachis showing bract scars on main axis and remnants of bracteoles on pedicels **E** flower **F** infructescence with single pod **G** bract **H** sepal **I** petal **J** longitudinal section of hypanthium and receptacle; sepals, petals and stamens removed. **A–E, G–J** Campbell *et al.* P22338, US **F** G. Martinelli 7016, US.

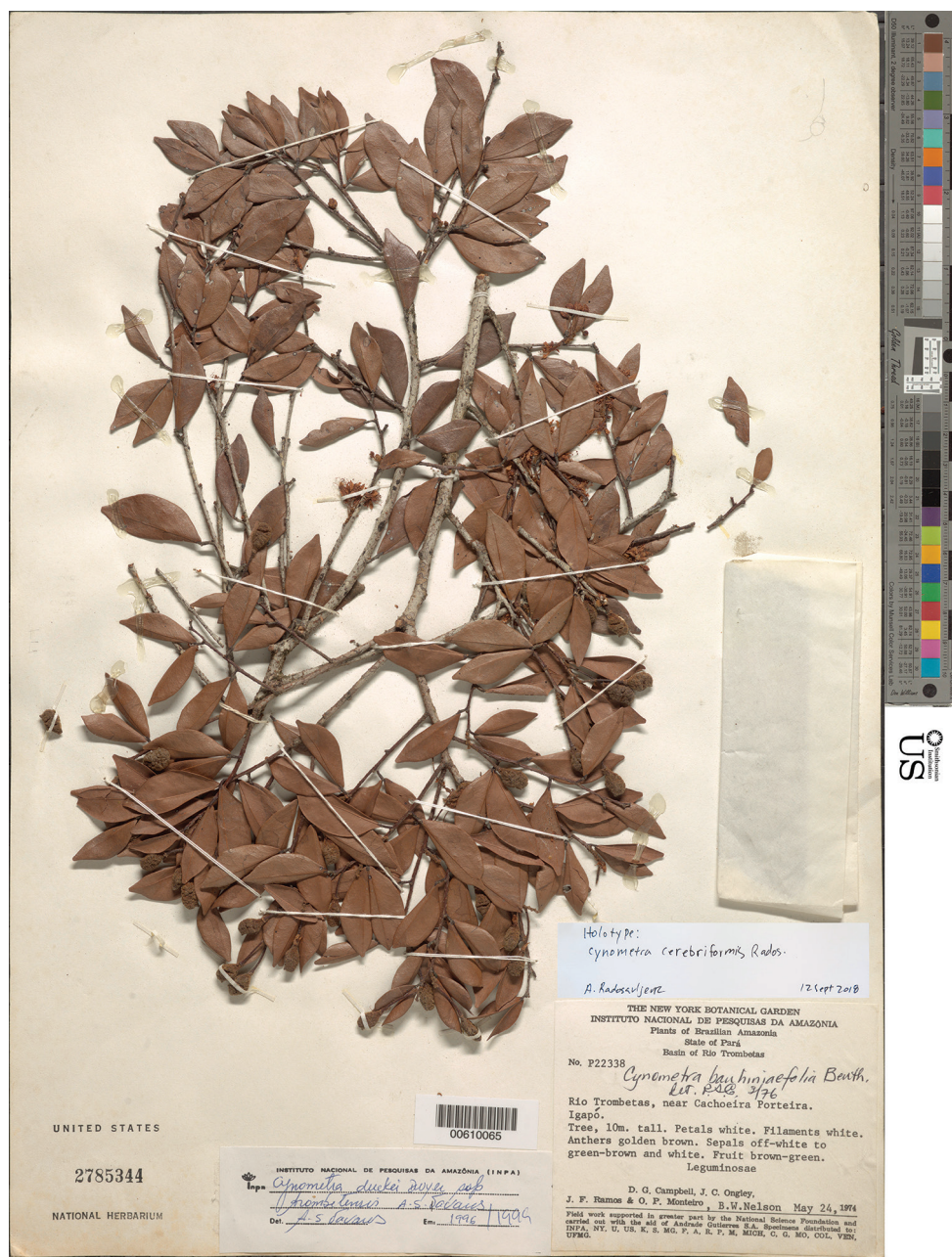


Figure 5. Photograph of the holotype of *Cynometra cerebriiformis* (Campbell et al. P22338, US).

Etymology. *Cynometra cerebriiformis* is named after the brain-like appearance of the mature fruit.

Additional specimens examined. BRAZIL. Pará: Município Oriximiná: Rio Trombetas shore, Porteira cemetery, 3 Jun 1974 [im fr], D. G. Campbell et al. P22510

(INPA, NY, US); Margem direita do Rio Mapuera, entre as Cach[oeira] Paraíso Grande e Maracajá, Área do reservatório da 2ª etapa, 00°58'S, 57°35'W, 12 Aug 1986 [im fr], *C.A. Cid Ferreira et al.* 7659 (INPA, NY); Rio Trombetas, river banks downriver from Cachoeira Porteira, N to NE bank (Between C.P. and IBDF Reveral – Lago do Jacaré), 17 Jun 1980 [fr], *C. Davidson & G. Martinelli* 10324 (INPA, NY, US); Rio Trombetas, margem esq. entre o Lago Jacaré e Cachoeira Porteira, 70 m alt., 17 Jun 1980 [fr], *G. Martinelli* 7016 (INPA, NY, RB).

Notes. This taxon has been collected in the areas around Santarem and Oriximiná in Para, Brazil. Many of the specimens have been annotated by Adalea Sprada Tavares as *Cynometra duckei* ssp. *trombetensis*, but I can find no record of publication and several of the specimens thus annotated are assigned to different taxa in her unpublished thesis (Sprada Tavares 1987). The available material of *C. duckei* is limited and only a few fruiting specimens exist. While a case can be made that *C. duckei* shares certain vegetative traits with *C. cerebriformis* (prominent lenticels, the smoothness of the adaxial surface of the leaflets), it also shares characteristics with several other taxa, including *C. spruceana* var. *spruceana* (long pedicels, leaflet shape) and *C. marginata* var. *laevis* (smooth leaflet surface, nearly sessile leaflets). In light of the characters separating *C. cerebriformis* from other taxa (see below), the author has opted to describe this taxon at the species level.

Cynometra cerebriformis differs from *C. duckei* primarily in the shape of the leaflets. *Cynometra cerebriformis* differs from *C. spruceana* var. *spruceana* in several ways. The leaflets of *C. cerebriformis* are generally smaller than those of *C. spruceana* var. *spruceana* and the surface is nearly smooth, while the secondary veins are quite obvious in *C. spruceana*. *Cynometra cerebriformis* also lacks the basal laminar gland present in *C. spruceana* and many other *Cynometra* taxa. Finally, the fruit of *C. spruceana* is approximately 1.5×–2.5× larger than the fruit of *C. cerebriformis* and the valves are smooth to slightly rugulose, lacking the strongly rugose surface of *C. cerebriformis*.

Cynometra cerebriformis differs from *C. marginata* var. *laevis* by having an acute leaflet base, short acumen and oblate rugose fruit; *C. marginata* var. *laevis* has an obtuse leaflet base, long acumen and a globose fruit with a prominent raised suture ridge.

2. *Cynometra dwyerii* Rados., sp. nov.

urn:lsid:ipni.org:names:77199272-1

Figures 6, 7

Type. PANAMA. Darién [now Comarca Emberá-Wounaan]: vicinity of Campamento Buena Vista, Río Chucunaque above confluence with Río Tuquesa, [08°23'N, 77°47'W] 5 July 1959, [fr.], *W. L. Stern* 941 (holotype US; isotype MO).

Description. *Tree* to approximately 20 m tall; bark not seen; branchlets lenticellate, pubescent when young, becoming glabrous with age. *Stipules* not seen. *Leaves* bifoliolate, axes pubescent, transversely corrugated; petioles 4.5–5.5 mm long; petiolules 1.0–1.5 mm long, inconspicuous, leaflets appearing sessile; leaflets narrowly obovate to obovate, occasionally sub-trapeziform, strongly asymmetric, primary vein

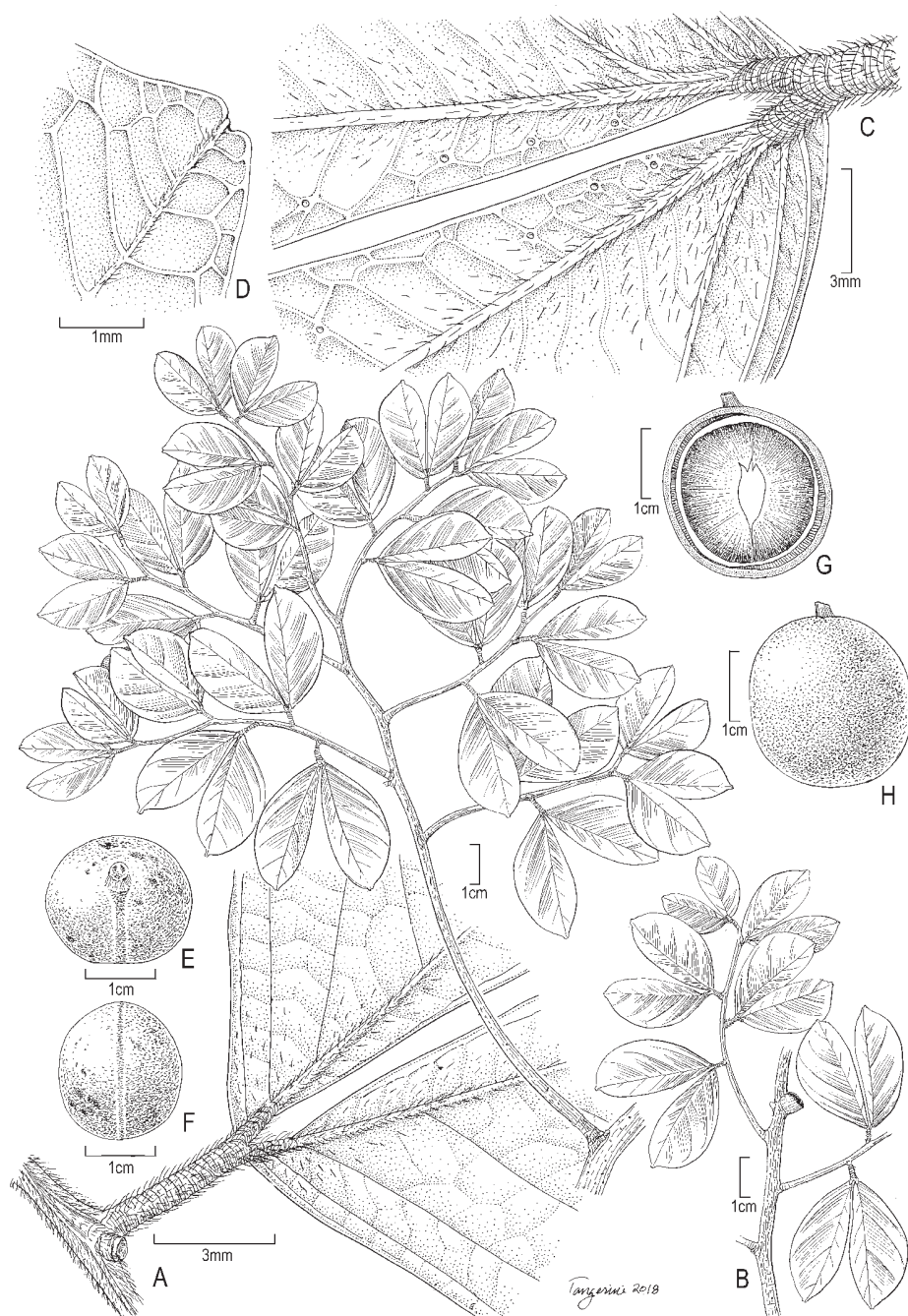


Figure 6. Illustration of *Cynometra duyerii*. **A** Leaf base (adaxial surface) showing corrugated petiole and pubescence along midrib **B** habit **C** leaf base (abaxial surface) showing basal acrodromous veins arising from leaflet pulvinus and laminar glands **D** leaflet apex (abaxial surface) **E** Dissected fruit, proximal surface **F** dissected fruit, distal surface **G** longitudinal section of fruit with single seed **H** reconstruction of fruit. **A–H** Stern et al. 941, US.



Figure 7. Photograph of the holotype of *Cynometra dwyerii* (Stern et al. 941, US).

eccentric, proximal side 2.8–3.7 times wider than distal, 3.1–3.9 cm long, 1.4–1.9 cm wide, thin, abaxial surface sparsely pubescent, more so on midvein and major secondaries, adaxial surface with pubescence restricted primarily to midvein, occasional hairs scattered on lamina, primary venation pinnate, secondary venation brochidodromous-eucamptodromous, 2(–3) basal acrodromous veins, decurrent to primary, prominent abaxially, only slightly less so adaxially, tertiary venation visible on both surfaces at 10× magnification, margins entire, apex acute, weakly acuminate (to 2.0 mm), retuse, mucronate, base oblique, acute, distal side narrowly cuneate, proximal side slightly concave to cuneate, decurrent to petiolule, laminar glands present, 3–6 per leaflet, arranged in a row approximately halfway between margin and midvein, restricted to distal portion of lamina, typically adjacent to tertiary veins, crateriform, less than 1.0 mm in diameter. **Inflorescences** not seen, position inferred as axillary from remnant of peduncle. **Flowers** not seen. **Legume** indehiscent, roughly globose, to 4.7 cm in diameter, surface of valves rugulose, wall of pericarp up to 3.0 mm thick, deep brown colour at maturity. **Seeds** 1 per pod, filling entire cavity, dark brown.

Distribution and ecology. Known only from the type locality in the Darien Gap region of Panama; the area where the type was collected is primarily lowland moist tropical forest.

Phenology. The type was collected with mature fruit in July.

Etymology. The specific epithet honours the contributions of Dr. John Dwyer, who published the first monograph of the Neotropical species of *Cynometra*.

Note. This species is known only from the type collection, however the combination of vegetative characters and fruit morphology make it clearly distinct from other *Cynometra* species. Superficially, this species resembles *C. baubiniifolia*, given its small leaflets with prominent secondary venation. However, the pubescence and arrangement of laminar glands clearly distinguish it from other Neotropical species of *Cynometra*, which usually have just a single, basal laminar gland. In fact, the combination of bifoliolate leaves with small leaflets and several submarginal laminar glands is unique across the entire genus. When these characters are combined with the large, globose fruit, it is clear that this is a distinct species.

Additional specimens examined. None.

3. *Cynometra steyermarkii* Rados., sp. nov.

urn:lsid:ipni.org:names:77199276-1

Figures 8–10

Type. VENEZUELA. Miranda: Distrito Brión, Selva siempre verde a lo largo de la quebrada afluente del río Aricagua, 3.9 km oeste del Pueblo Seco, 1.6 km oeste de Aricagua, 75 m alt., 24–25 March 1973, [fl, fr], J. A. Steyermark & V. Carreño Espinoza, 106937 (holotype: US; isotypes: F, VEN *n.v.*).

Description. **Tree** to 25 m tall; bark not seen, sapwood reddish; branchlets glabrous, lenticellate. **Stipules** not seen. **Leaves** bifoliolate, axes glabrous; petioles 6.5–

9.0 mm long, 2.0 mm wide, transversely corrugated; petiolules 2.0–3.0 mm long, 1.0 mm wide, transversely corrugated; leaflets, coriaceous, elliptic to slightly obovate, asymmetric, primary vein eccentric, proximal side 2.3–3.1 times wider than distal, 5.7–7.1 cm long, 2.7–3.6 cm wide, discolorous, abaxial and adaxial surface glabrous, primary venation pinnate, secondary venation brochidodromous-eucamptodromous, 2(–3) basal acrodromous veins, decurrent to primary vein, prominent abaxially, slightly raised adaxially, tertiary venation visible on abaxial surface without magnification, margins entire, apex obtuse, usually rounded but occasionally acuminate (to 3.0 mm), retuse, mucronate, base oblique, acute, distal side strongly cuneate, proximal concave to convex, decurrent to petiolule, single laminar gland present on some leaflets, abaxial, near basal margin of proximal lamina and insertion point of petiolule, typically adjacent to tertiary veins, crateriform, 0.5 mm in diameter. **Inflorescence** an axillary raceme, bracteate, axes densely ferrugino-puberulent; peduncle together with rachis to 6.0 mm long, flowers spirally arranged, 15 per raceme; pedicels 5.5–6.0 mm, pubescent, accrescent in fruit; bracts subtending individual flowers, scale-like, deciduous, lustrous, brown, broadly elliptical, strongly convex 1.0–2.0 mm long, 1.5–2.5 mm wide, striate, abaxial surface with appressed pubescence along medial surface and along margins, glabrous adaxially; bracteoles paired, inserted near base of pedicel, subopposite, linear to oblanceolate, 2.5–3.0 mm long, 0.75 mm wide, acute at apex, densely pubescent on abaxial surface, less so adaxially. **Flowers** bisexual, radially symmetric, pentamerous, delicate; hypanthium much reduced, less than 0.5 mm deep, with a few scattered hairs on abaxial and adaxial surface; sepals 4, imbricate, reflexed, slightly unequal, white, petaloid, oblong to obovate, 2.5–3.5 mm long, 1.0–1.5 mm wide, faintly striate, appressed pubescence on abaxial surface near insertion point and along central axis; petals 5, equal, white, oblanceolate, 3.5–4.5 mm long, 1.0–1.5 mm wide, pinnate venation; stamens 10, filaments appearing free but possibly connate for approximately 0.25 mm at base, subequal, 4.0–5.5 mm long, anthers dorsifixed, versatile, longitudinal dehiscence, ellipsoid, to 0.75 mm long, glabrous; ovary centrally inserted, free, sessile, obliquely elliptical, 2.5–4.0 mm long, 1.5–3.0 mm wide, pubescent at base and along suture, becoming glabrous with age, style apical, 1.5–2.5 mm long, glabrous, eccentric, stigma capitate. **Legume** indehiscent, globose, shortly apiculate (to 0.75 mm), 1.5 cm in diameter, surface of granulose, with very short pubescence, wall of pericarp up to 2.0 mm thick, brown. **Seeds** 1 per pod (1 ovule per ovary based on dissections), dark brown.

Distribution and ecology. Known from a single collection made in Miranda State, Venezuela. The species was collected growing along a small stream in the foothills of the Cordillera de la Costa at approximately 75 m above sea level. While much of this region is covered in xeric shrublands and thorn forests, this site corresponds to a low gallery forest growing along a tributary of the Río Aricagua.

Phenology. The type material was collected at the end of March with late flowers and nearly mature fruit.

Etymology. The specific epithet honours Dr. Julian A. Steyermark, the collector of the type material and a prolific collector of neotropical plants. Over the course of his



Figure 8. Illustration of *Cynometra steyermarkii*. **A** Habit, flowering branch **B** habit, fruiting branch **C** leaf base, showing basal acrodromous veins arising from leaflet pulvinus **D** inflorescence rachis, showing bracts and bracteoles; pedicels removed to show structure **E** buds with imbricate bracts **F** flower **G** bract **H** bracteoles **I** sepals **J** petal **K** longitudinal section of flower showing single ovule and much reduced hypanthium; sepals, petals and stamens removed. **A–K** Steyermark *et al.* 106937, US.



Figure 9. Photograph of the holotype of *Cynometra steyermarkii*, sheet one of two (Steyermark et al. 106937, US).

career, he made over 130,000 collections and greatly advanced our knowledge of the Venezuelan flora.

Additional specimens examined. None.

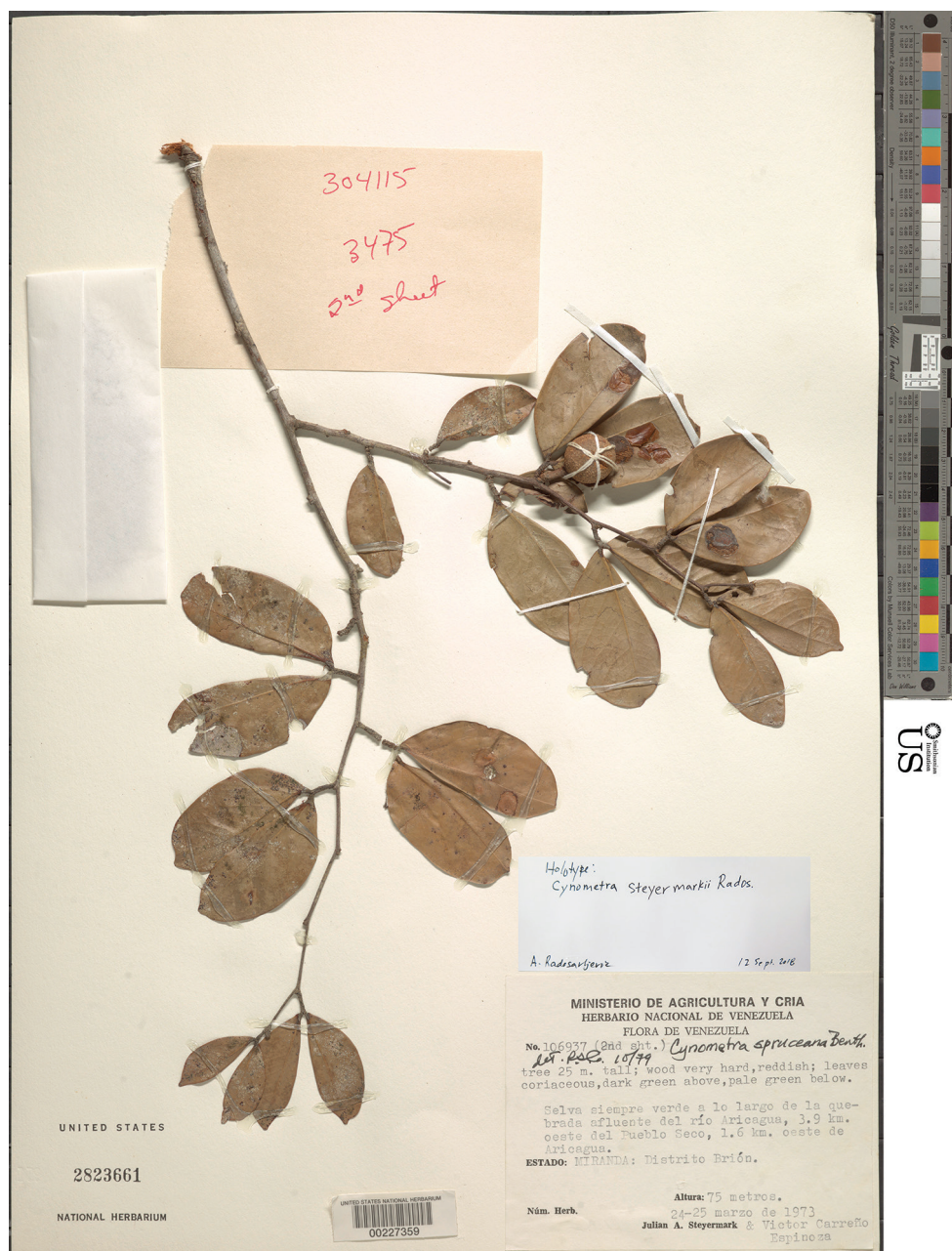


Figure 10. Photograph of the holotype of *Cynometra steyermarkii*, sheet two of two (Steyermark et al. 106937, US).

Notes. *Cynometra steyermarkii* is the only confirmed species of *Cynometra* known from the forests of the Cordillera de la Costa in northern Venezuela and one of two species of Venezuelan *Cynometra* growing outside of the Guayana region. Henri Pittier

(1926) published an account of a *Cynometra* growing in the hills outside of Caracas, *Cynometra sphaerocarpa* Pittier, for his *Manual de las plantas usuales de Venezuela*. While the description is valid, according to the rules of nomenclature in effect at the time, he failed to designate a type or list any collections that may correspond to this taxon. In his 1958 revision, Dwyer was unable to locate any material that could be assigned to this taxon and pointed out the limited utility of Pittier's description – 'Las hojas inequilaterales, lanceadas, largamente atenuadas y glabras... Los frutos son subglobosos, de 3.5–4 cm. de diametro y contienen una sola semilla [Leaflets asymmetric, lanceolate, largely attenuate and glabrous. The fruits are sub-globose, 3.5–4 cm in diameter, and contain a single seed].' – which could very well describe any number of *Cynometra* species, including *C. steyermarkii*. A full set of Pittier's duplicates from this publication should be deposited in the United States National Herbarium (US), but after exhaustive searches in the US collections and a study of both Pittier's archives and the museum registrar's records, I was unable to find any material that could be attributable to *C. sphaerocarpa*. Curators at Herbario Nacional de Venezuela graciously searched through material housed there, but were also unsuccessful. While it is possible that *C. steyermarkii* and *C. sphaerocarpa* are the same taxon, without Pittier's original material, it is impossible to know for sure. Rather than leave this unresolved, it is more useful to describe a new species with good type material.

This species bears a resemblance to *Cynometra spruceana* var. *phaselocarpa* Benth. owing to the obtuse nature of the leaf apices. However, *C. steyermarkii* often has slightly acuminate apices. Furthermore, both the rachis and pedicels of the inflorescence are much shorter in *C. steyermarkii* than in typical *C. spruceana* var. *phaselocarpa*.

4. *Cynometra tumbesiana* Rados., sp. nov.

urn:lsid:ipni.org:names:77199277-1

Figures 11, 12

Type. ECUADOR. El Oro: Bosque Petrificado Puyango, dirt track from information centre towards the camping area near Río Puyango, 03°52'30"S, 80°05'01"W, 450 m alt., 6 May 1997 [fl], *B.B. Klitgaard et al.* 507, (holotype K; isotype AAU n.v., LOJA n.v., NY, QCNE n.v., US).

Description. *Tree* 10–25 m tall; bark grey-brown, lenticellate, inner bark red; branchlets with short pubescence when young, becoming glabrous with age. *Stipules* not seen. *Leaves* bifoliate, axes ferrugino-puberulent when young, glabrous when mature; petioles 4.5–6.5 mm long, transversely corrugated; petiolules 1.5–2.0 mm long, inconspicuous; leaflets oblong-ovate to elliptic to oblong-obovate, occasionally slightly falcate or sub-trapeziform, strongly asymmetric, primary vein eccentric, proximal side 1.8–2.5 times wider than distal, 4.1–7.9 cm long, 2.5–3.3 cm wide, discolorous, abaxial surface sparsely pubescent on midvein, secondary veins and along basal margin, adaxial surface glabrous, primary venation pinnate, secondary venation brochidodromous-eucamptodromous, 2–3 (–4) basal acrodromous veins, decurrent to

primary vein, prominent abaxially, flush to slightly raised adaxially, tertiary venation visible on abaxial surface at 10× magnification, margins entire, apex acute, acuminate (to 6.0 mm), retuse, mucronate, base oblique, distal side acute, convex to cuneate, proximal side obtuse, concave to rounded, decurrent to petiolule, single laminar gland present, abaxial, near basal margin of proximal lamina and insertion point of petiolule, typically adjacent to tertiary veins, crateriform, 1.0 mm in diameter. **Inflorescence** a cluster of (1–)2–3 axillary racemes, bracteate, axes ferrugino-puberulent at base, hairs becoming scattered at distal end; peduncle together with rachis 4.5–8.0 mm long, flowers spirally arranged, 12–20 per raceme; pedicels 5.0–9.0 mm, pubescent initially but soon glabrescent, accrescent in fruit; bracts subtending individual flowers, scale-like, deciduous, leaving behind a lunate scar on the rachis, lustrous, brown, broadly elliptical, strongly convex 1.5–2.5 mm long, 1.5–2.5 mm wide, striate, abaxial surface with scattered appressed pubescence at apex and along margins, glabrous adaxially; paired bracteoles inserted 0.5–1.0 mm from base of pedicel, subopposite, oblong-lanceolate, 2.0–2.5 mm long, 1.0 mm wide, convex at apex, pubescent along margins and medial abaxial surface. **Flowers** bisexual, radially symmetric, pentamerous, delicate; hypanthium cupular, 1.0–1.5 mm deep, fleshy, with a few scattered hairs on abaxial and adaxial surface; sepals 4, imbricate, reflexed, unequal, adaxial sepal usually 2 times as wide as the others, white, petaloid, broadly ovate to elliptical, 3.0–4.5 mm long, 1.5–4.0 mm wide, striate, scattered pubescence at base; petals 5, erect, equal to subequal, white, spathulate to oblanceolate, 3.5–5.5 mm long, 1.0–2.0 mm wide, glabrous but with a tuft of hair at base of claw; stamens 10, filaments free, subequal, 5.5–7.5 mm long, white, anthers dorsifixed, versatile, longitudinal dehiscence, suborbicular, to 1.5 mm long, yellow-orange, glabrous; ovary centrally inserted in hypanthium, free, stipitate, obliquely elliptical, 4.0–5.0 mm long, 2.0–2.5 mm wide, densely pilose, stipe 0.5–1.0 mm long, style apical, 3.0–4.0 mm long, glabrous, eccentric, geniculate, stigma capitate. **Legume** indehiscent, oblong, weakly apiculate, slightly compressed, up to 5.2 cm long, 4.0 cm wide, 3.9 cm thick, surface of valves finely textured, granulose, wall of pericarp up to 4.0 mm thick, deep brown colour at maturity. **Seeds** 1 per pod, filling entire cavity, dark brown.

Distribution and ecology. *Cynometra tumbesiana* occurs in the seasonally dry tropical forests of western and southern Ecuador and north-western Peru (a single collection) at elevations between 100–800 m (Figure 3). These habitats are severely threatened regionally and globally due to extensive human modification of the landscape and, as a result, this species now exists primarily as isolated fragments. While *C. tumbesiana* is locally abundant at a few sites, it is currently known from less than 10 localities, several of which are within 5 km of each other.

Phenology. Flowering specimens have been collected in May and December to January; fruiting specimens have been collected in August and January to February. *Cynometra tumbesiana* is one of the few woody taxa in the dry forests that retain their leaves during the dry season.

Etymology. The specific epithet refers to the Tumbes region, where the type specimen was collected and where many of the known localities occur.

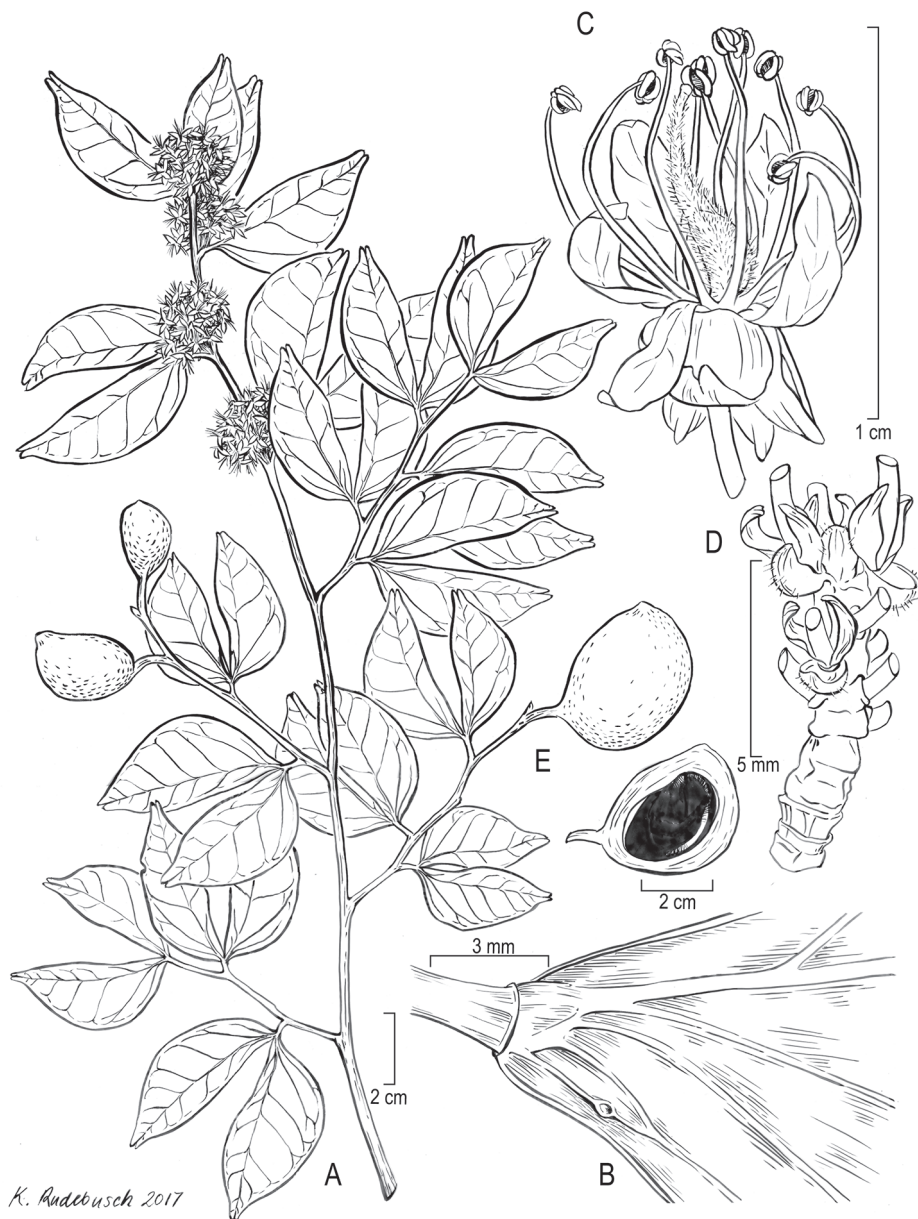


Figure 11. Illustration of *Cynometra tumbesiana*. **A** Habit **B** leaflet base, showing laminar gland **C** flower **D** inflorescence rachis, showing bracts and bracteoles; pedicels removed to show structure **E** fruit, dissected to show single seed filling entire cavity. **A–D** Klitgaard *et al.* 507, K; **B** Neill & Núñez 10453, US.

Additional specimens examined. ECUADOR. El Oro: Bosque Petrificado Puyango, dirt track from information centre towards the camping area near Río Puyango, 03°52'30"S, 80°05'01"W, 450 m alt., 23 Aug 1996 [fr], B.B. Klitgaard *et al.* 325 (AAU

n.v., K, LOJA n.v., NY, QCNE n.v.); 26 Feb 1997 [fr], *B.B. Klitgaard et al.* 424 (AAU n.v., K, LOJA n.v., NY, QCNE n.v.). [Piñas]: Piedras, about 3 km. along new trail, 18 Jun 1943 [st], *E.L. Little, Jr.* 6622 (US). **Guayas:** [without specific locality] 2 Feb 1962 [fr], *A.J. Gilmartin* 551 (US). Guayaquil: Bosque Protector Cerro Blanco, 15 km west of Guayaquil, summit area of Cerro Blanco, 2°10'S, 79°58'W, 370 m alt., 27 Feb 1996 [fr], *D. Neill & T. Núñez* 10453 (MO, US); Bosque Protector Cerro Blanco, along road from visitor centre to “Cusumbo Top”, 80, 01 W, 2 10 S, 400 m alt., 7 Aug 1996 [im fr], *D. Neill, T. Núñez & J. Machuca* 10636 (MO); Bosque Protector Cerro Blanco, carretera a Salinas, km 15, 2°10'S, 79°58'W, 400 m alt., 21–25 Jan 1992 [fr], *D. Rubio & Galo Tipaz* 2365 (MO). Isidro Ayora: Reserva Ecológica Manglares Churute, carretera Guayaquil–Puerto Inca, sector norte del Cerro Masvale, 2°20'S, 79°50'W, 200–300 m alt., May 1993 [fl], *T. Núñez & A. Hernández* 147 (MO). **Manabi:** [Puerto López]: Estero Perro Muerto, Machalilla National Park, below San Sebastian, 1°36'S, 80°42'W, 400–420 m alt., 23 Jan 1991 [fl], *A. Gentry & C. Josse* 72677 (MO); [San Vicente]: [hacienda] El Recreo, [fl], *H.F.A. von Eggers* 15752 (US). **PERU. Tumbes:** Zarumilla: Dtto. Matapalo, Campo Verde a 68 km de. Tumbes, 700–800 m alt., 24 Dec 1967 [fr], *J. Schunke* V. 2411 (F, NY, US).

Notes. This species, restricted to the few remaining fragments of dry tropical forest in western Ecuador and the Tumbes region of Peru, has been mistakenly referred to as *Cynometra crassifolia* Benth. for many years. However, closer examination shows it to be quite distinct from this taxon. The type specimen of *C. crassifolia* was collected in Brazil by Portuguese naturalist Alexandre Rodrigues Ferreira during his exploration of the Amazonian region of Brazil from 1783–1792. His collections, along with many others housed at Lisbon, were expropriated by Étienne Geoffroy Saint-Hilaire and transferred to Paris during Napoleon's occupation of Portugal. There, it was seen by George Bentham, who described *Cynometra crassifolia* in 1840. The primary differences between *C. tumbesiana* and *C. crassifolia* are found in the inflorescences: the racemes of *C. crassifolia* have larger flowers, longer pedicels and a more robust pedicel and rachis, but fewer individual flowers than those of *C. tumbesiana*. The flowers of *C. tumbesiana* are indeed relatively small compared to the other neotropical *Cynometra* species, though they are densely clustered on the short rachis of the inflorescence. The leaflets of *C. tumbesiana* are also less distinctly acuminate than those of *C. crassifolia* and have a less obtuse base; the base of the leaflet in *C. crassifolia* can appear to be almost truncate.

Some taxonomists have placed the Ecuadoran *Cynometra* within *C. bauhiniifolia* Benth., with a few treating *C. crassifolia* as a synonym of *C. bauhiniifolia* (Neill et al. 1999). In the first case, while *C. tumbesiana* does bear a passing resemblance to some forms of *C. bauhiniifolia*, the pod of *C. bauhiniifolia* is many times smaller and the surface of the valves is corky and deeply rugose. In the latter case, it is difficult to find justification for synonymising the two with the exception that *C. bauhiniifolia* has been a dumping ground for hard to place taxa within the genus and does occasionally occur in drier habitats. The leaflets, inflorescences and fruits all differ. Instead, the type material of *C. crassifolia* seems to be very similar to *C. longicuspis* Ducke, a widespread species from the moist lowland forests of Brazil.



Figure 12. Photograph of the holotype of *Cynometra tumesiana* (Klitgaard et al. 507, K).

Cynometra tumbesiana is morphologically and ecologically similar to *C. oaxacana* Brandege from western and southern Mexico. The two can be distinguished by the narrower and more acuminate leaflets and larger fruits in *C. tumbesiana*. The inflorescences of *C. oaxacana* are also slightly more robust and have a more obvious pubescence. Both species are found in dry habitats (uncommon amongst the neotropical species of *Cynometra*), though *C. tumbesiana* is found in much drier sites.

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Dichotomous keys to the species of *Solanum* L. (Solanaceae) in continental Africa, Madagascar (incl. the Indian Ocean islands), Macaronesia and the Cape Verde Islands

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Abstract

Solanum L. (Solanaceae) is one of the largest genera of angiosperms and presents difficulties in identification due to lack of regional keys to all groups. Here we provide keys to all 135 species of *Solanum* native and naturalised in Africa (as defined by World Geographical Scheme for Recording Plant Distributions): continental Africa, Madagascar (incl. the Indian Ocean islands of Mauritius, La Réunion, the Comoros and the Seychelles), Macaronesia and the Cape Verde Islands. Some of these have previously been published in the context of monographic works, but here we include all taxa. The paper is designed to be used in conjunction with the web resource Solanaceae Source (www.solanaceaesource.org) and hyperlinks provide access to online descriptions, synonymy and images (where available) of each species. All taxa treated and specimens seen are included in searchable Suppl. material 1, 2.

Keywords

Africa, Aldabra, Azores, Canary Islands, Cape Verde, Comoros, cultivated plants, identification, keys, Madagascar, Madeira, Mauritius, La Réunion, Seychelles, *Solanum*, weeds

Introduction

Solanum L. (Solanaceae) is one of the largest of angiosperm genera (Frodin 2004) with ca. 1,200 species distributed worldwide with species on all continents except Antarctica. The greatest species diversity in the genus occurs in the Neotropics (see Bohs 2005), but significant diversity also occurs in the Old World, with Africa and Australia particularly important areas for diversification (see Vorontsova and Knapp 2016; Echeverría-Londoño et al. 2018). Due to its large number of species and the number of introductions and cultivated taxa, *Solanum* is often an identification challenge for non-specialists. Recent completion of several large monographic treatments of the *Solanum* of Africa (e.g. Vorontsova and Knapp 2016; Knapp and Vorontsova 2016; Särkinen et al. 2018) as part of the US National Science Foundation funded Planetary Biodiversity Inventory project “PBI *Solanum*” means we can now provide keys for the genus across the continent and for adjacent islands such as Madagascar and Macaronesia. Some of these have been published in the Open Access literature (e.g. Knapp 2013; Knapp and Vorontsova 2016; Särkinen et al. 2018), but the largest of these, treating the spiny solanums (Vorontsova and Knapp 2016) is not. Several species that are either naturalised (e.g. members of the *Brevantherum* Clade) or cultivated (tree tomatoes, pepinos, potatoes and tomatoes) in the region are also not treated as part of these monographic treatments, although complete species descriptions and photographs are provided on the web resource Solanaceae Source (www.solanaceaesource.org).

Here we provide dichotomous keys that include all groups and species (native, naturalised and widely cultivated; see Table 1 for species list) of *Solanum* occurring in continental Africa, Madagascar (incl. the Indian Ocean islands of Mauritius, La Réunion, the Comoros, and the Seychelles), Macaronesia and the Cape Verde Islands to facilitate identification across the region. Taxa occurring in each country in the region are shown in Table 2 and a map of *Solanum* diversity (all taxa) is presented in Figure 1. Keys to individual groups are also provided for the 135 *Solanum* species occurring in the region (see Table 1 and Appendix 1 for a species list). We hope that these keys will encourage collection and documentation of *Solanum* across Africa and uncover new distributions and perhaps new species for the region.

Materials and methods

We modified keys from published monographs for groups of *Solanum* from the botanical continent “Africa” as defined in the World Geographical Scheme for Recording Plant Distributions (WGSRPD; Brummitt 2001). This corresponds basically to the countries of the continent of Africa, but excludes the Sinai Peninsula (politically part of Egypt and in WGSRPD part of Western Asia). It also includes islands grouped as Macaronesia (Azores, Canary Islands, Madeira and the Cape Verde Islands) and Madagascar and other Indian Ocean islands east to Rodrigues.

We assessed distribution using the published monographs, with additional data points added from subsequent herbarium visits. All specimens seen for these keys can be seen in the Supplemental File and in the dataset published on the NHM Data Portal (<https://doi.org/10.5519/0042549>). For descriptions of the taxa, users are referred to the original publications or the Solanaceae Source website (www.solanaceaesource.org), where all species treated here are described and synonymy listed.

To access descriptions on the Solanaceae Source website, begin by typing the species name in the search box in the upper right-hand part of the screen banner (tick the option “Taxonomy” below the box); when the correct name you are searching for appears, select it, then push the “Search” button to the right of the search box (if you do not push the “Search” button, nothing will happen). You will be taken to the species page, where images and synonyms appear on the opening page; to access descriptions, click on the “Description” tab where information can be obtained. Up-to-date specimen details are not currently available on the website but can be found as described above.

Keys

Solanum can be divided into 13 major clades or monophyletic groups (Bohs 2005; Weese and Bohs 2007; Särkinen et al. 2013; see Figures 2 and 3 for photographs illustrating representative morphology of these groups in Africa). The largest monophyletic clade is the Leptostemonum clade, or the “spiny solanums”, which comprises approximately half of the species diversity of the genus; divisions within that clade have been defined by Stern et al. (2011), Vorontsova et al. (2013) and Aubriot et al. (2016). This group is rapidly diversifying in the Old World (Echeverría-Londoño et al. 2018), with most taxa occurring in the Old World belonging to a single monophyletic group. Previous treatments (e.g. Whalen 1984; Jaeger 1985; Jaeger and Hepper 1986) had suggested the African taxa were members of, or closely related to New World groups. More information on the phylogenetic relationships of African and Asian members of the Leptostemonum Clade can be found in Vorontsova et al. (2013) and Aubriot et al. (2016). Other clades with significant species diversity in Africa (as defined here) are the African non-spiny (ANS) and Normania Clades (both endemic to the region; see Bohs and Olmstead 2001) and the Morelloid Clade (with a number of widespread weedy taxa, see Särkinen et al. 2018). Other clades such as the Geminata, Brevantherum and Potato Clades are represented only by introduced or cultivated species. The Dulcamaroid Clade has a single species native to Mediterranean northern Africa and Macaronesia and two cultivated taxa that can become naturalised (Knapp 2013). In order to facilitate identification and to assist with the discovery of novelties from the region, we provide a key to the major groups (clades) of *Solanum* following the most recent phylogeny of the genus (Särkinen et al. 2013) and additional dichotomous keys to the species within each group. Groups are ordered as they occur as branches in the phylogeny of Särkinen et al. (2013).

Table 1. The 135 species of *Solanum* (native, naturalised and widely cultivated) occurring in Africa as defined by Brummitt (2001), with their places of original publication and clade membership as currently understood (Major Clades sensu Bohs 2005; minor clades are divisions within these sensu Bohs 2007; Stern et al. 2011; Vorontsova et al. 2103; Särkinen et al. 2015, 2018; Aubriot et al. 2016; Tepe et al. 2016).

Species	Place of original publication	Major Clade	Minor clade
<i>Solanum aculeastrum</i> Dunal	Prodr. [A. P. de Candolle] 13(1): 366. 1852.	Leptostemonum	Old World-Africa
<i>Solanum aculeatissimum</i> Jacq.	Collectanea [Jacquin] 1: 100. 1787 [‘1786’].	Leptostemonum	Acanthophora
<i>Solanum adoense</i> Hochst. ex A.Rich.	Tent. Fl. Abyss. 2: 105. 1850 [1851].	Leptostemonum	Old World-Africa
<i>Solanum aethiopicum</i> L.	Cent. Pl. 2: 10. 1756.	Leptostemonum	Old World-Africa
<i>Solanum africanum</i> Mill.	Gard. Dict. ed. 8, no. 26. 1768.	African non-spiny (ANS)	
<i>Solanum agnewiorum</i> Voronts.	Phytotaxa 10: 32. 2010.	Leptostemonum	Old World-Africa
<i>Solanum agrarium</i> Sendtn.	Fl. Bras. (Martius) 10: 68, fig. 5, 32–33. 1846.	Leptostemonum	Gardneri
<i>Solanum aldabrense</i> C.H.Wright	Kew Bull. 1894: 149. 1894.	Leptostemonum	Old World
<i>Solanum americanum</i> Mill.	Gard. Dict. ed. 8, no. 5. 1768.	Morelloid	Black nightshade
<i>Solanum anguivi</i> Lam.	Tabl. Encycl. 2: 23. 1794.	Leptostemonum	Old World-Africa
<i>Solanum anomalum</i> Thonn.	Beskr. Guin. Pl. 126 1827.	Leptostemonum	Old World-Africa
<i>Solanum arundo</i> Mattei	Boll. Reale Orto Bot. Giardino Colon. Palermo 7: 188. 1908.	Leptostemonum	Old World-Africa
<i>Solanum atropurpureum</i> Schrank	Syll. Ratisb. 1: 200. 1824.	Leptostemonum	Acanthophora
<i>Solanum aureitomentosum</i> Bitter	Repert. Spec. Nov. Regni Veg. 11: 18. 1912.	Leptostemonum	Old World-Africa
<i>Solanum batoides</i> D’Arcy & Rakot.	Fl. Madag., Fam. 176: 75. 1994.	Leptostemonum	Old World-Madagascar
<i>Solanum betaceum</i> Cav.	Anales Hist. Nat. 1: 44. 1799.	Cyphomandra	Pachyphylla
<i>Solanum betroka</i> D’Arcy & Rakot.	Fl. Madag., Fam. 176: 77. 1994.	African non-spiny (ANS)	
<i>Solanum bumeliifolium</i> Dunal	Prodr. [A. P. de Candolle] 13(1): 292. 1852.	Leptostemonum	Old World-Madagascar
<i>Solanum burchellii</i> Dunal	Prodr. [A. P. de Candolle] 13(1): 291. 1852.	Leptostemonum	Old World-Africa
<i>Solanum campylacanthum</i> Hochst. ex A.Rich.	Tent. Fl. Abyss. 2: 102. 1850.	Leptostemonum	Old World-Africa
<i>Solanum capense</i> L.	Syst. ed. 10: 935. 1759.	Leptostemonum	Old World-Africa
<i>Solanum capsicoides</i> All.	Auct. Syn. Meth. Stirp. Hort. Regii Taur. 64. 1773.	Leptostemonum	Acanthophora
<i>Solanum catombelense</i> Peyr.	Sitzungsber. Kaiserl. Akad. Wiss., Math.-Naturwiss. Cl. 38: 576. 1860.	Leptostemonum	Old World-Africa
<i>Solanum cerasiferum</i> Dunal	Prodr. [A. P. de Candolle] 13(1): 365. 1852.	Leptostemonum	Old World-Africa
<i>Solanum chenopodioides</i> Lam.	Tabl. Encycl. 2: 18. 1794.	Morelloid	Black nightshade
<i>Solanum chrysotrichum</i> Schldtl.	Linnaea 19: 304. 1847.	Leptostemonum	Torva
<i>Solanum coagulans</i> Forssk.	Fl. Aegypt.-Arab. 47. 1775.	Leptostemonum	Old World-Africa
<i>Solanum cordatum</i> Forssk.	Fl. Aegypt.-Arab. 47. 1775.	Leptostemonum	[not assigned]
<i>Solanum croatii</i> D’Arcy & R.C.Keating	Phytologia 34: 282. 1976.	Leptostemonum	Old World-Madagascar
<i>Solanum cyaneopurpureum</i> De Wild.	Pl. Bequaert. 1: 425. 1922.	Leptostemonum	Old World-Africa
<i>Solanum cymbalariaefolium</i> Chiov.	Boll. Soc. Bot. Ital. 1925: 107. 1925.	Leptostemonum	Old World-Africa
<i>Solanum dasyphyllum</i> Schumach. & Thonn.	Beskr. Guin. Pl. 126 [146]. 1827.	Leptostemonum	Old World-Africa
<i>Solanum dennekenense</i> Dammer	Bot. Jahrb. Syst. 38: 57. 1905.	Leptostemonum	Old World-Africa
<i>Solanum diphyllum</i> L.	Sp. Pl. 184. 1753.	Geminata	
<i>Solanum elaeagnifolium</i> Cav.	Icon. 3: 22, tab. 243. 1795.	Leptostemonum	Elaeagnifolium
<i>Solanum erianthum</i> D.Don	Prodr. Fl. Nep. 96. 1825.	Brevantherum	
<i>Solanum erythracanthum</i> Dunal	Prodr. [A. P. de Candolle] 13(1): 201. 1852.	Leptostemonum	Old World-Madagascar
<i>Solanum forskalii</i> Dunal	Hist. Nat. Solanum 237. 1813.	Leptostemonum	Old World-Africa
<i>Solanum giganteum</i> Jacq.	Collectanea [Jacquin] 4: 125. 1791.	Leptostemonum	Old World-Africa

Species	Place of original publication	Major Clade	Minor clade
<i>Solanum glabratum</i> Dunal	Hist. Nat. Solanum 240. 1813.	Leptostemonum	Old World-Africa
<i>Solanum goetzei</i> Dammer	Bot. Jahrb. Syst. 28: 473. 1900.	Leptostemonum	Old World-Africa
<i>Solanum guineense</i> L.	Sp. Pl. 184. 1753.	African non-spiny (ANS)	
<i>Solanum hastifolium</i> Hochst. ex Dunal	Prodr. [A. P. de Candolle] 13(1): 284. 1852.	Leptostemonum	Old World-Africa
<i>Solanum heinianum</i> D'Arcy & R.C.Keating	Phytologia 34: 282. 1976.	Leptostemonum	Old World-Madagascar
<i>Solanum herculeum</i> Bohs	Plant Syst. Evol. 228: 44. 2001.	Normania	
<i>Solanum humblotii</i> Dammer	Bot. Jahrb. Syst. 38: 184. 1906.	African non-spiny (ANS)	
<i>Solanum humile</i> Lam.	Tabl. Encycl. 2: 23. 1794.	Leptostemonum	Old World-Africa
<i>Solanum imamense</i> Dunal	Prodr. [A. P. de Candolle] 13(1): 85. 1852.	African non-spiny (ANS)	
<i>Solanum inaequinadians</i> Werderm.	Notizbl. Bot. Gart. Berlin-Dahlem 12: 90. 1934.	Leptostemonum	Old World-Africa
<i>Solanum incanum</i> L.	Sp. Pl. 188. 1753.	Leptostemonum	Old World-Africa
<i>Solanum insanum</i> L.	Mant. 1: 46. 1767.	Leptostemonum	Old World-Tropical Asia
<i>Solanum ivohibe</i> D'Arcy & Rakot.	Fl. Madag., Fam. 176: 97. 1994.	African non-spiny (ANS)	
<i>Solanum jubae</i> Bitter	Bot. Jahrb. Syst. 54: 501. 1917.	Leptostemonum	Old World-Africa
<i>Solanum laciniatum</i> Aiton	Hort. Kew. ed. 1, 1: 247. 1789.	Archaeosolanum	
<i>Solanum lamprocarpum</i> Bitter	Repert. Spec. Nov. Regni Veg. Beih. 16: 107. 1923.	Leptostemonum	Old World-Africa
<i>Solanum lanzae</i> J.-P.Lebrun & Stork	Candollea 50: 217. 1995.	Leptostemonum	Old World-Africa
<i>Solanum lichtensteinii</i> Willd.	Enum. Pl. (Willdenow) 1: 238. 1809.	Leptostemonum	Old World-Africa
<i>Solanum lidii</i> Sunding	Blyttia 24: 368. 1966.	Leptostemonum	Old World
<i>Solanum linnaeanum</i> Hepper & P.-M.L. Jaeger	Kew Bull. 41: 435. 1986.	Leptostemonum	Old World-Africa
<i>Solanum litoraneum</i> A.E.Gonç.	Kew Bull. 52(3): 703. 1997.	Leptostemonum	Old World-Africa
<i>Solanum lycopersicum</i> L.	Sp. Pl. 185. 1753.	Potato	Tomato
<i>Solanum macracanthum</i> A.Rich.	Tent. Fl. Abyss. 2: 106. 1850.	Leptostemonum	Old World-Africa
<i>Solanum macrocarpon</i> L.	Mant. Pl. Altera: 205. 1771.	Leptostemonum	Old World-Africa
<i>Solanum macrothyrsus</i> Dammer	Bot. Jahrb. Syst. 38: 185. 1906.	African non-spiny (ANS)	
<i>Solanum madagascariense</i> Dunal	Prodr. [A. P. de Candolle] 13(1): 99. 1852.	African non-spiny (ANS)	
<i>Solanum mahoriense</i> D'Arcy & Rakot.	Ann. Missouri Bot. Gard. 73: 498. 1986.	Leptostemonum	Old World-Madagascar
<i>Solanum malindiense</i> Voronts.	Syst. Bot. 35: 904. 2010.	Leptostemonum	Old World-Africa
<i>Solanum mammosum</i> L.	Sp. Pl. 187. 1753.	Leptostemonum	Acanthophora
<i>Solanum marginatum</i> L.f.	Suppl. 147. 1781.	Leptostemonum	Old World-Africa
<i>Solanum mauense</i> Bitter	Repert. Spec. Nov. Regni Veg. Beih. 16: 42. 1923.	Leptostemonum	Old World-Africa
<i>Solanum mauritianum</i> Scop.	Delic. Fl. Faun. Insubr. 3: 16. 1788.	Brevantherum	
<i>Solanum melastomoides</i> C.H.Wright	Bull. Misc. Inform. Kew 1894: 128. 1894.	Leptostemonum	Old World-Africa
<i>Solanum melongena</i> L.	Sp. Pl. 186. 1753.	Leptostemonum	Old World-Tropical Asia
<i>Solanum memphiticum</i> J.F.Gmel.	Syst. Nat., ed. 13[bis] 2(1): 385. 1791	Morelloid	Black nightshade
<i>Solanum muricatum</i> Aiton	Hort. Kew, ed. 1, 1: 250. 1789.	Potato	Basarthrum
<i>Solanum myxotrichum</i> Baker	J. Linn. Soc., Bot. 21: 426. 1885.	Leptostemonum	Old World-Madagascar
<i>Solanum myrsinoides</i> D'Arcy & Rakot.	Fl. Madag., Fam. 176: 115. 1994.	African non-spiny (ANS)	
<i>Solanum nava</i> Webb & Berthel.	Phyt. Canar. 2. 3(3): 123. 1845.	Normania	

Species	Place of original publication	Major Clade	Minor clade
<i>Solanum nigriviolaceum</i> Bitter	Repert. Spec. Nov. Regni Veg. Beih. 16: 163. 1923.	Leptostemonum	Old World-Africa
<i>Solanum nigrum</i> L.	Sp. Pl. 186. 1753.	Morelloid	Black nightshade
<i>Solanum nitidibaccatum</i> Bitter	Repert. Spec. Nov. Regni Veg. 11: 208. 1912.	Morelloid	Black nightshade
<i>Solanum pampaninii</i> Chiov.	Res. Sci. Somalia Ital. 1: 128. 1916.	Leptostemonum	Old World-Africa
<i>Solanum pauperum</i> C.H.Wright	Bull. Misc. Inform. Kew 1894: 127. 1894.	Leptostemonum	Old World-Africa
<i>Solanum pectinatum</i> Dunal	Prodr. [A. P. de Candolle] 13(1): 250. 1852.	Leptostemonum	Lasiocarpa
<i>Solanum phoxocarpum</i> Voronts.	Syst. Bot. 35: 903. 2010.	Leptostemonum	Old World-Africa
<i>Solanum pimpinellifolium</i> L.	Cent. Pl. 1: 8. 1755.	Potato	Tomato
<i>Solanum polhillii</i> Voronts.	Syst. Bot. 35: 902. 2010.	Leptostemonum	Old World-Africa
<i>Solanum pseudospinosum</i> C.H.Wright	Fl. Trop. Afr. [Oliver et al.] 4, 2: 220. 1906.	Morelloid	Black nightshade
<i>Solanum pyracanthos</i> Lam.	Tabl. Encycl. 2: 21. 1794.	Leptostemonum	Old World-Madagascar
<i>Solanum retroflexum</i> Dunal	Prodr. [A. P. de Candolle] 13(1): 50. 1852.	Morelloid	Black nightshade
<i>Solanum richardii</i> Dunal	Encycl. [J. Lamarck & al.] Suppl. 3: 775. 1814.	Leptostemonum	Old World-Africa
<i>Solanum rigidum</i> Lam.	Tabl. Encycl. 2: 23. 1794.	Leptostemonum	Old World-Africa
<i>Solanum robustum</i> H.L.Wendl.	Flora 27: 784. 1844.	Leptostemonum	Erythrotrichum
<i>Solanum rubetorum</i> Dunal	Prodr. [A. P. de Candolle] 13(1): 304. 1852.	Leptostemonum	Old World-Africa
<i>Solanum runsoriense</i> C.H.Wright	Uganda Prot. (H.H.Johnston) 1: 326. 1902.	African non-spiny (ANS)	
<i>Solanum ruvu</i> Voronts.	J. E. Afr. Nat. Hist. 99: 230. (2010) 2011.	Leptostemonum	Old World-Africa
<i>Solanum sambiranense</i> D'Arcy & Rakot.	Fl. Madag., Fam. 176: 123. 1994.	African non-spiny (ANS)	
<i>Solanum sarrachoides</i> Sendtn.	Fl. Bras. (Martius) 10: 18, tab. 1, fig. 1-8. 1846.	Morelloid	Black nightshade
<i>Solanum scabrum</i> Mill.	Gard. Dict. ed. 8, no. 6. 1768.	Morelloid	Black nightshade
<i>Solanum schimperianum</i> Hochst. ex A.Rich.	Tent. Fl. Abyss. 2: 98. 1850.	Leptostemonum	Old World-Africa
<i>Solanum schliebenii</i> Werderm.	Notizbl. Bot. Gart. Berlin-Dahlem 12: 92. 1934.	Leptostemonum	Old World-Africa
<i>Solanum schumannianum</i> Dammer	Pflanzenw. Ost-Afrikas C (Engler): 352. 1895.	Leptostemonum	Old World-Africa
<i>Solanum setaceum</i> Dammer	Pflanzenw. Ost-Afrikas C (Engler): 33. 1895.	Leptostemonum	Old World-Africa
<i>Solanum sisymbriifolium</i> Lam.	Tabl. Encycl. 2: 25. 1794.	Leptostemonum	Sisymbriifolium
<i>Solanum sodomaeodes</i> Kuntze	Revis. Gen. Pl. 3(3): 227. 1898.	Leptostemonum	Old World-Africa
<i>Solanum somalense</i> Franch.	Sert. Somal. 47. 1882.	Leptostemonum	Old World-Africa
<i>Solanum stipitatosellatum</i> Dammer	Abh. Königl. Akad. Wiss. Berlin 1894: 63. 1894.	Leptostemonum	Old World-Africa
<i>Solanum supinum</i> Dunal	Prodr. [A. P. de Candolle] 13(1): 289. 1852.	Leptostemonum	Old World-Africa
<i>Solanum taitense</i> Vatke	Linnaea 43: 327. 1882.	Leptostemonum	Old World-Africa
<i>Solanum tarderemotum</i> Bitter	Repert. Spec. Nov. Regni Veg. 10: 547. 1912.	Morelloid	Black nightshade
<i>Solanum terminale</i> Forssk.	Fl. Aegypt.-Arab. 45. 1775.	African non-spiny (ANS)	
<i>Solanum tettense</i> Klotzsch	Naturw. Reise Mossambique (Peters) 1: 237. 1861.	Leptostemonum	Old World-Africa
<i>Solanum thomsonii</i> C.H.Wright	Fl. Trop. Afr. [Oliver et al.] 4, 2: 217. 1906.	Leptostemonum	Old World-Africa
<i>Solanum tolianae</i> D'Arcy & Rakot.	Ann. Missouri Bot. Gard. 76: 351. 1989.	Leptostemonum	Old World-Madagascar
<i>Solanum tomentosum</i> L.	Sp. Pl. 188. 1753.	Leptostemonum	Old World-Africa
<i>Solanum torreanum</i> A.E.Gonç.	Kew Bull., 52(3): 706. 1997.	Leptostemonum	Old World-Africa
<i>Solanum torvum</i> Sw.	Prodr. [O. P. Swartz] 47. 1788.	Leptostemonum	Torva
<i>Solanum trichopetiolatum</i> D'Arcy & Rakot.	Fl. Madag., Fam. 176: 130. 1994.	African non-spiny (ANS)	
<i>Solanum triflorum</i> Nutt.	Gen. N. Amer. Pl. 1: 128. 1818.	Morelloid	

Species	Place of original publication	Major Clade	Minor clade
<i>Solanum trisetum</i> Dunal	Prodr. [A. P. de Candolle] 13(1): 36. 1852.	Normania	
<i>Solanum truncicola</i> Bitter	Bot. Jahrb. Syst. 54: 435. 1917.	African non-spiny (ANS)	
<i>Solanum tuberosum</i> L.	Sp. Pl. 185. 1753.	Potato	Petota
<i>Solanum umalilaense</i> Manoko	PhytoKeys 16: 67. 2012.	Morelloid	Black nightshade
<i>Solanum umtuma</i> Voronts. & S.Knapp	PhytoKeys 8: 4. 2012.	Leptostemonum	Old World-Africa
<i>Solanum usambarens</i> Bitter & Dammer	Repert. Spec. Nov. Regni Veg. Beih. 16: 40. 1923.	Leptostemonum	Old World-Africa
<i>Solanum usaramense</i> Dammer	Pflanzenw. Ost-Afrikas C (Engler): 353. 1895.	Leptostemonum	Old World-Africa
<i>Solanum vespertilio</i> Aiton	Hort. Kew. ed. 1, 1: 252. 1789.	Leptostemonum	Old World
<i>Solanum viarium</i> Dunal	Prodr. [A. P. de Candolle] 13(1): 240. 1852.	Leptostemonum	Acanthophora
<i>Solanum villosum</i> Mill.	Gard. Dict. ed. 8, no. 2. 1768.	Morelloid	Black nightshade
<i>Solanum violaceum</i> Ortega	Nov. Pl. Descr. Dec. 56. 1798.	Leptostemonum	Old World-Tropical Asia
<i>Solanum virginianum</i> L.	Sp. Pl. 187. 1753.	Leptostemonum	Old World-Tropical Asia
<i>Solanum wendlandii</i> Hook.f.	Bot. Mag. 113: tab. 6914. 1887.	Wendlandii-Allophyllum	
<i>Solanum wittei</i> Robyns	Bull. Jard. Bot. État Bruxelles 17: 82. 1943.	Leptostemonum	Old World-Africa
<i>Solanum wrightii</i> Benth.	Fl. Hongk. 243. 1861.	Leptostemonum	Androceras-Crinitum
<i>Solanum zanzibarens</i> Vatke	Linnaea 43: 326. 1882.	Leptostemonum	Old World-Africa

Table 2. Country distribution of *Solanum* species in Africa (as defined here); introduced (incl. cultivated) species in brackets (epithet); taxa not included in the keys because they are known from a singleton cultivated specimen, are in *italic* type. All records based on specimens examined by the authors with verified identities. The status of *S. torvum* is not completely clear, but it is most likely to be introduced from the New World, so is treated as that here; *S. americanum*, on the other hand, appears to have a worldwide distribution, so is treated as native. The occurrence of *S. rigidum* in Senegal is doubtful, the specimen is very old and the label may be in error. Cultivated plants are often not collected, so the absence of records of commonly cultivated crops (e.g. *S. lycopersicum*, *S. macrocarpon*, *S. tuberosum*) should not be interpreted as lack of occurrence, merely as lack of collections. *Solanum diphyllum* was recorded from Egypt by Fawzi and Habeeb (2016) with a verifiable photograph; this Mexican species is widely cultivated and easily naturalised and is likely to be spreading around the Mediterranean.

Country	Species
Algeria	<i>herculeum</i> , <i>linnaeanum</i> , <i>nigrum</i> , <i>villosum</i>
Angola	<i>aculeastrum</i> , (<i>aculeatissimum</i>), <i>aethiopicum</i> , <i>americanum</i> , <i>anguivi</i> , <i>anomalum</i> , <i>auweitomentosum</i> , (<i>betaceum</i>), <i>campylacanthum</i> , <i>capsicoides</i> , <i>catombelense</i> , <i>dasyphyllum</i> , <i>humile</i> , <i>lichtensteinii</i> , (<i>lycopersicum</i>), <i>macrocarpon</i> , <i>mammosum</i> , (<i>mauritanium</i>), <i>pauperum</i> , <i>scabrum</i> , <i>tarderemotum</i> , <i>terminale</i> , <i>tettense</i> , <i>villosum</i>
Azores	(<i>linnaeanum</i>), (<i>chenopodioides</i>), (<i>chrysotrichum</i>), (<i>nava?</i>), <i>nigrum</i> , (<i>maritimum</i>), (<i>pseudocapsicum</i>), <i>villosum</i>
Benin	<i>anguivi</i> , <i>anomalum</i> , <i>incanum</i> , <i>scabrum</i> , (<i>torvum</i>)
Botswana	<i>campylacanthum</i> , <i>catombelense</i> , <i>lichtensteinii</i> , <i>retroflexum</i> , <i>scabrum</i> , <i>supinum</i> , <i>tarderemotum</i> , <i>tettense</i> , <i>villosum</i>
Burkina Faso	<i>cerasiferum</i> , <i>dasyphyllum</i> , <i>incanum</i> , <i>scabrum</i>
Burundi	<i>aculeastrum</i> , <i>anguivi</i> , <i>campylacanthum</i> , <i>cyaneopurpureum</i> , <i>dasyphyllum</i> , <i>mammosum</i> , <i>memphiticum</i> , <i>tarderemotum</i> , <i>terminale</i> , <i>villosum</i>
Cabo Verde	(<i>agrarium</i>), <i>americanum</i> , (<i>lycopersicum</i>), <i>nigrum</i> , <i>rigidum</i> , <i>scabrum</i> , <i>tarderemotum</i> , (<i>torvum</i>)
Cameroon	<i>aculeastrum</i> , (<i>aculeatissimum</i>), <i>aethiopicum</i> , <i>americanum</i> , <i>anguivi</i> , <i>anomalum</i> , <i>cerasiferum</i> , <i>dasyphyllum</i> , (<i>erianthum</i>), <i>giganteum</i> , (<i>lycopersicum</i>), <i>macrocarpon</i> , (<i>mauritanium</i>), (<i>melongena</i>), <i>pseudospinosum</i> , <i>scabrum</i> , <i>tarderemotum</i> , <i>terminale</i> , (<i>torvum</i>), (<i>wendlandii</i>), (<i>wrightii</i>)

Country	Species
Canary Islands (Spain)	<i>americanum</i> , (<i>laxum</i>), (<i>lycopersicum</i>), (<i>mauritanium</i>), <i>nava</i> , <i>nigrum</i> , (<i>pseudocapsicum</i>), (<i>robustum</i>), <i>vespertilio</i> , (<i>wendlandii</i>)
Central African Republic (CAR)	<i>aculeastrum</i> , (<i>aculeatissimum</i>), <i>anguivi</i> , <i>cerasiferum</i> , <i>dasyphyllum</i> , <i>giganteum</i> , (<i>lycopersicum</i>), <i>macrocarpon</i> , <i>scabrum</i> , (<i>seaforthianum</i>), <i>terminale</i> , (<i>torvum</i>), (<i>wrightii</i>)
Chad	<i>cerasiferum</i> , <i>forskalii</i> , <i>incanum</i> , <i>tarderemotum</i> , <i>villosum</i>
Comoros (incl. Mayotte)	<i>americanum</i> , <i>macrothyrsus</i> , <i>richardii</i> , <i>scabrum</i> , <i>tarderemotum</i> , <i>terminale</i> , (<i>torvum</i>)
Democratic Republic of the Congo	<i>aculeastrum</i> , (<i>aculeatissimum</i>), <i>aethiopicum</i> , <i>anomalum</i> , <i>aureitomentosum</i> , <i>campylacanthum</i> , <i>cerasiferum</i> , (<i>chrysotrichum</i>), <i>cyaneopurpureum</i> , <i>dasyphyllum</i> , <i>giganteum</i> , <i>lichtensteinii</i> , (<i>lycopersicum</i>), <i>macrocarpon</i> , (<i>mammosum</i>), (<i>mauritanium</i>), (<i>melongena</i>), <i>memphiticum</i> , <i>richardii</i> , <i>runsoriense</i> , <i>scabrum</i> , (<i>seaforthianum</i>), <i>tarderemotum</i> , <i>terminale</i> , <i>tettense</i> , (<i>torvum</i>), (<i>viarum</i>), <i>wittei</i> , (<i>wrightii</i>)
Republic of the Congo	<i>aculeastrum</i> , <i>anomalum</i> , <i>dasyphyllum</i> , (<i>lycopersicum</i>), <i>terminale</i> , (<i>torvum</i>)
Cote d'Ivoire	(<i>aculeatissimum</i>), <i>americanum</i> , <i>anguivi</i> , <i>anomalum</i> , <i>cerasiferum</i> , <i>dasyphyllum</i> , (<i>lycopersicum</i>), <i>scabrum</i> , <i>terminale</i> , (<i>torvum</i>)
Djibouti	<i>somalense</i>
Egypt (incl. Hala'ib triangle)*	<i>coagulans</i> , (<i>diphyllum</i>), <i>dulcamara</i> , <i>elaegnifolium</i> , <i>forskalii</i> , <i>incanum</i> , (<i>lycopersicum</i>), <i>macrocarpon</i> , (<i>melongena</i>), <i>memphiticum</i> , <i>nigrum</i> , <i>scabrum</i> , (<i>torvum</i>), <i>villosum</i> , <i>virginianum</i> , (<i>wendlandii</i>), (<i>wrightii</i>)
Equatorial Guinea	(<i>aculeatissimum</i>), <i>aethiopicum</i> , <i>americanum</i> , <i>anguivi</i> , <i>dasyphyllum</i> , <i>giganteum</i> , (<i>lycopersicum</i>), <i>pseudospinosum</i> , <i>scabrum</i> , <i>terminale</i> , (<i>torvum</i>)
Eritrea	<i>adoense</i> , <i>americanum</i> , <i>anguivi</i> , <i>campylacanthum</i> , <i>cerasiferum</i> , <i>coagulans</i> , <i>dasyphyllum</i> , <i>forskalii</i> , <i>glabratum</i> , <i>incanum</i> , (<i>lycopersicum</i>), <i>macracanthum</i> , <i>marginatum</i> , <i>melastomoides</i> , (<i>melongena</i>), <i>memphiticum</i> , <i>muricatum</i> , <i>scabrum</i> , <i>schimperianum</i> , <i>somalense</i> , <i>tarderemotum</i> , <i>terminale</i> , <i>villosum</i>
Ethiopia	(<i>aculeatissimum</i>), <i>adoense</i> , <i>americanum</i> , <i>anguivi</i> , <i>arundo</i> , <i>campylacanthum</i> , <i>capsicoides</i> , <i>cerasiferum</i> , <i>coagulans</i> , <i>cordatum</i> , <i>dennekense</i> , <i>forskalii</i> , <i>giganteum</i> , <i>glabratum</i> , <i>hastifolium</i> , <i>hirtulum</i> , <i>incanum</i> , <i>jubae</i> , <i>lanzae</i> , (<i>lycopersicum</i>), <i>macracanthum</i> , <i>macrocarpon</i> , <i>marginatum</i> , <i>melastomoides</i> , <i>memphiticum</i> , <i>muricatum</i> , <i>pampaninii</i> , <i>runsoriense</i> , <i>schimperianum</i> , <i>somalense</i> , <i>tarderemotum</i> , <i>terminale</i> , <i>tettense</i> , <i>villosum</i> , (<i>wrightii</i>)
Gabon	<i>aethiopicum</i> , <i>americanum</i> , <i>anguivi</i> , <i>anomalum</i> , <i>dasyphyllum</i> , <i>giganteum</i> , <i>macrocarpon</i> , <i>scabrum</i> , <i>terminale</i> , (<i>torvum</i>), (<i>wrightii</i>)
Gambia	<i>americanum</i> , <i>anguivi</i> , <i>cerasiferum</i> , <i>dasyphyllum</i>
Ghana	(<i>aculeatissimum</i>), <i>americanum</i> , <i>anguivi</i> , <i>anomalum</i> , <i>capsicoides</i> , <i>dasyphyllum</i> , (<i>erianthum</i>), <i>incanum</i> , <i>macrocarpon</i> , (<i>melongena</i>), <i>scabrum</i> , <i>tarderemotum</i> , <i>terminale</i> , (<i>torvum</i>), (<i>wrightii</i>)
Guinea	(<i>aculeatissimum</i>), <i>anguivi</i> , (<i>erianthum</i>), <i>scabrum</i> , <i>tarderemotum</i> , <i>terminale</i> , (<i>torvum</i>), (<i>wrightii</i>)
Guinea-Bissau	<i>americanum</i> , <i>anguivi</i> , <i>cerasiferum</i> , <i>dasyphyllum</i> , <i>terminale</i>
Kenya	<i>aculeastrum</i> , (<i>aculeatissimum</i>), <i>aethiopicum</i> , <i>agneviorum</i> , <i>americanum</i> , <i>anguivi</i> , <i>arundo</i> , (<i>betaceum</i>), <i>campylacanthum</i> , <i>coagulans</i> , <i>cordatum</i> , <i>dasyphyllum</i> , <i>dennekense</i> , <i>forskalii</i> , <i>giganteum</i> , <i>goetzei</i> , <i>hastifolium</i> , <i>incanum</i> , <i>jubae</i> , <i>lanzae</i> , (<i>laxum</i>), (<i>lycopersicum</i>), <i>macrocarpon</i> , <i>malindiense</i> , <i>mammosum</i> , <i>mauense</i> , (<i>mauritanium</i>), <i>melastomoides</i> , (<i>melongena</i>), <i>nigriviolaceum</i> , <i>pampaninii</i> , <i>phoxocarpum</i> , <i>polhillii</i> , (<i>pseudocapsicum</i>), <i>richardii</i> , <i>runsoriense</i> , <i>schumannianum</i> , (<i>seaforthianum</i>), <i>setaceum</i> , <i>sisymbriifolium</i> , <i>somalense</i> , <i>stipitatostellatum</i> , <i>taitense</i> , <i>tarderemotum</i> , <i>terminale</i> , <i>tettense</i> , (<i>tuberosum</i>), <i>usambarense</i> , <i>usaramense</i> , <i>villosum</i> , (<i>wendlandii</i>), (<i>wrightii</i>), <i>zanzibarense</i>
Lesotho	(<i>aculeatissimum</i>), (<i>chenopodioides</i>), <i>lichtensteinii</i> , <i>retroflexum</i> , <i>scabrum</i> , <i>sodomeodes</i> , <i>tarderemotum</i>
Liberia	(<i>aculeatissimum</i>), <i>americanum</i> , <i>anguivi</i> , <i>anomalum</i> , <i>dasyphyllum</i> , (<i>lycopersicum</i>), (<i>mauritanium</i>), <i>scabrum</i> , <i>terminale</i> , (<i>torvum</i>)
Libya	<i>linnaeanum</i> , <i>nigrum</i> , <i>villosum</i> , <i>virginianum</i>
Madagascar	<i>aethiopicum</i> , <i>americanum</i> , <i>anguivi</i> , <i>batoides</i> , (<i>betaceum</i>), <i>betroka</i> , <i>bumelifolium</i> , <i>croatii</i> , <i>erythmacanthum</i> , <i>heinianum</i> , <i>humblotii</i> , <i>imamense</i> , <i>insanum</i> , <i>ivohibe</i> , (<i>lycopersicum</i>), <i>macrocarpon</i> , <i>madagascariense</i> , <i>mahoriense</i> , (<i>mauritanium</i>), (<i>melongena</i>), <i>myoxotrichum</i> , <i>mysinoides</i> , (<i>pseudocapsicum</i>), <i>pyracanthos</i> , <i>richardii</i> , <i>sambiranense</i> , <i>scabrum</i> , (<i>seaforthianum</i>), <i>tarderemotum</i> , <i>toliaraea</i> , (<i>torvum</i>), <i>trichopetiolum</i> , <i>truncicola</i> , (<i>tuberosum</i>), <i>violaceum</i>
Madeira (Portugal)	(<i>chenopodioides</i>), <i>dulcamara</i> , (<i>laxum</i>), <i>linnaeanum</i> , (<i>lycopersicum</i>), <i>marginatum</i> , <i>nigrum</i> , (<i>pseudocapsicum</i>), <i>trisectum</i> , <i>villosum</i>
Malawi	<i>aculeastrum</i> , (<i>aculeatissimum</i>), <i>aethiopicum</i> , <i>americanum</i> , <i>anguivi</i> , <i>aureitomentosum</i> , <i>campylacanthum</i> , (<i>chrysotrichum</i>), <i>dasyphyllum</i> , <i>giganteum</i> , <i>goetzei</i> , <i>lichtensteinii</i> , <i>macrocarpon</i> , <i>retroflexum</i> , <i>richardii</i> , <i>scabrum</i> , <i>schumannianum</i> , (<i>seaforthianum</i>), <i>tarderemotum</i> , <i>terminale</i> , <i>tettense</i> , (<i>torvum</i>), <i>villosum</i> , (<i>wendlandii</i>), (<i>wrightii</i>)
Mali	<i>cerasiferum</i> , <i>dasyphyllum</i> , <i>forskalii</i> , <i>incanum</i> , (<i>lycopersicum</i>), <i>tarderemotum</i>

Country	Species
Mauritania	<i>dasyphyllum</i> , <i>scabrum</i> , <i>villosum</i>
Mauritius (incl. La Réunion)	<i>americanum</i> , (<i>anguivi</i>), (<i>chenopodioides</i>), <i>erythracanthum</i> , <i>insanum</i> , (<i>lycopersicum</i>), (<i>mauritanum</i>), (<i>melongena</i>), <i>richardii</i> , <i>tarderemotum</i> , (<i>torvum</i>), <i>violaceum</i>
Morocco	<i>dulcamara</i> , <i>elaeagnifolium</i> , <i>forskalii</i> , <i>berculeum</i> , (<i>laciniatum</i>), <i>linnaeanum</i> , <i>nigrum</i> , <i>triflorum</i> , <i>villosum</i>
Mozambique	<i>aculeastrum</i> , (<i>aculeatissimum</i>), <i>aethiopicum</i> , <i>americanum</i> , <i>anguivi</i> , <i>aureitomentosum</i> , <i>campylacanthum</i> , <i>catombelense</i> , <i>dasyphyllum</i> , <i>giganteum</i> , <i>goetzei</i> , <i>lamprocarpum</i> , <i>lichtensteini</i> , <i>linnaeanum</i> , <i>litoraneum</i> , <i>retroflexum</i> , <i>richardii</i> , <i>scabrum</i> , <i>stipitatostellatum</i> , <i>tarderemotum</i> , <i>tettense</i> , <i>torreanum</i> , (<i>torvum</i>), <i>usaramense</i> , (<i>viarum</i>), <i>villosum</i> , <i>zanzibarens</i>
Namibia	<i>burchellii</i> , <i>campylacanthum</i> , <i>capense</i> , <i>catombelense</i> , <i>elaeagnifolium</i> , <i>numile</i> , <i>lichtensteini</i> , (<i>lycopersicum</i>), <i>pimpinellifolium</i> , <i>retroflexum</i> , <i>scabrum</i> , (<i>seaforthianum</i>), <i>supinum</i> , <i>tarderemotum</i> , <i>tettense</i>
Niger	<i>anguivi</i> , <i>forskalii</i> , <i>incanum</i> , (<i>lycopersicum</i>), <i>villosum</i>
Nigeria	<i>aculeastrum</i> , (<i>aculeatissimum</i>), <i>aethiopicum</i> , <i>americanum</i> , <i>anguivi</i> , <i>anomalum</i> , <i>cerasiferum</i> , <i>dasyphyllum</i> , (<i>erianthum</i>), <i>giganteum</i> , <i>incanum</i> , (<i>lycopersicum</i>), <i>macrocarpon</i> , <i>melongena</i> , <i>scabrum</i> , <i>terminale</i> , (<i>torvum</i>), <i>villosum</i> , (<i>wrightii</i>)
Rwanda	<i>aculeastrum</i> , (<i>aculeatissimum</i>), <i>anguivi</i> , <i>campylacanthum</i> , <i>cyaneopurpureum</i> , <i>dasyphyllum</i> , <i>giganteum</i> , <i>tarderemotum</i> , <i>terminale</i> , <i>wittei</i>
São Tome e Principe	<i>americanum</i> , <i>capsicoides</i> , (<i>melongena</i>), <i>scabrum</i> , <i>terminale</i>
Senegal	<i>anguivi</i> , <i>cerasiferum</i> , <i>forskalii</i> , <i>incanum</i> , (<i>lycopersicum</i>), <i>rigidum</i> ?, <i>scabrum</i> , <i>tarderemotum</i>
Seychelles	<i>aldabrense</i> , <i>americanum</i> , <i>scabrum</i>
Sierra Leone	<i>aculeatissimum</i> , <i>americanum</i> , <i>anguivi</i> , <i>capsicoides</i> , <i>dasyphyllum</i> , (<i>erianthum</i>), (<i>lycopersicum</i>), <i>macrocarpon</i> , (<i>melongena</i>), <i>scabrum</i> , <i>tarderemotum</i> , <i>terminale</i> , (<i>torvum</i>), (<i>wrightii</i>)
Somalia	<i>arundo</i> , <i>campylacanthum</i> , <i>coagulans</i> , <i>cordatum</i> , <i>cymbalariifolium</i> , <i>dasyphyllum</i> , <i>dennekense</i> , <i>forskalii</i> , <i>glabratum</i> , <i>hastifolium</i> , <i>incanum</i> , <i>jubae</i> , <i>melastomoides</i> , (<i>melongena</i>), <i>memphiticum</i> , <i>pampaninii</i> , <i>schimperianum</i> , <i>somalense</i> , <i>tarderemotum</i> , <i>tettense</i> , <i>villosum</i>
South Africa	<i>aculeastrum</i> , (<i>aculeatissimum</i>), <i>africanum</i> , <i>americanum</i> , <i>anguivi</i> , <i>burchellii</i> , <i>campylacanthum</i> , <i>capense</i> , <i>catombelense</i> , (<i>chenopodioides</i>), (<i>chrysotrichum</i>), <i>dasyphyllum</i> , <i>elaeagnifolium</i> , <i>giganteum</i> , <i>guineense</i> , <i>humile</i> , (<i>laxum</i>), <i>lichtensteini</i> , <i>linnaeanum</i> , (<i>mauritanum</i>), (<i>pseudocapsicum</i>), <i>retroflexum</i> , <i>rubetorum</i> , (<i>sarachooides</i>), (<i>seaforthianum</i>), <i>sisymbriifolium</i> , <i>sodomeodes</i> , <i>supinum</i> , <i>tarderemotum</i> , <i>terminale</i> , <i>tettense</i> , <i>tomentosum</i> , <i>torreanum</i> , (<i>torvum</i>), <i>triflorum</i> , (<i>viarum</i>), (<i>wrightii</i>)
South Sudan	<i>aculeastrum</i> , (<i>aculeatissimum</i>), <i>aethiopicum</i> , <i>anguivi</i> , <i>campylacanthum</i> , <i>cerasiferum</i> , <i>coagulans</i> , <i>dasyphyllum</i> , <i>giganteum</i> , <i>hastifolium</i> , <i>scabrum</i> , <i>tarderemotum</i> , <i>terminale</i>
Sudan (incl. Hala'ib triangle)*	<i>aculeastrum</i> , <i>adoense</i> , <i>aethiopicum</i> , <i>campylacanthum</i> , <i>cerasiferum</i> , <i>coagulans</i> , <i>forskalii</i> , <i>hastifolium</i> , <i>incanum</i> , <i>macrocarpon</i> , <i>memphiticum</i> , <i>nigrum</i> , <i>scabrum</i> , <i>schimperianum</i> , <i>somalense</i> , <i>tarderemotum</i> , <i>villosum</i>
Swaziland	<i>aculeastrum</i> , <i>campylacanthum</i> , <i>catombelense</i> , <i>retroflexum</i> , (<i>robustum</i>), (<i>seaforthianum</i>), <i>sisymbriifolium</i> , <i>torreanum</i>
Tanzania	<i>aculeastrum</i> , (<i>aculeatissimum</i>), <i>americanum</i> , <i>anguivi</i> , <i>arundo</i> , (<i>atropurpureum</i>), <i>aureitomentosum</i> , (<i>betaceum</i>), <i>campylacanthum</i> , <i>coagulans</i> , <i>cyaneopurpureum</i> , <i>dasyphyllum</i> , <i>dennekense</i> , <i>giganteum</i> , <i>goetzei</i> , <i>hastifolium</i> , <i>inaequiradians</i> , <i>lamprocarpum</i> , <i>lanzae</i> , <i>lichtensteini</i> , (<i>lycopersicum</i>), <i>macrocarpon</i> , <i>mauense</i> , (<i>melongena</i>), <i>memphiticum</i> , (<i>pectinatum</i>), <i>phoxocarpum</i> , <i>polhillii</i> , <i>richardii</i> , (<i>robustum</i>), <i>scabrum</i> , <i>schliebenii</i> , <i>schumannianum</i> , (<i>seaforthianum</i>), <i>setaceum</i> , <i>stipitatostellatum</i> , <i>taitense</i> , <i>tarderemotum</i> , <i>terminale</i> , <i>tettense</i> , <i>thomsonii</i> , (<i>tuberosum</i>), <i>umalilaense</i> , <i>usambarens</i> , <i>usaramense</i> , <i>villosum</i> , (<i>wendlandii</i>), <i>wittei</i> , (<i>wrightii</i>), <i>zanzibarens</i>
Togo	(<i>aculeatissimum</i>), <i>aethiopicum</i> , <i>americanum</i> , <i>anguivi</i> , <i>anomalum</i> , (<i>melongena</i>), <i>scabrum</i> , <i>terminale</i> , (<i>torvum</i>)
Tunisia	<i>linnaeanum</i> , (<i>lycopersicum</i>), <i>nigrum</i> , <i>triflorum</i> , <i>villosum</i>
Uganda	<i>aculeastrum</i> , (<i>aculeatissimum</i>), <i>aethiopicum</i> , <i>americanum</i> , <i>anguivi</i> , (<i>betaceum</i>), <i>campylacanthum</i> , <i>cerasiferum</i> , <i>coagulans</i> , <i>cyaneopurpureum</i> , <i>dasyphyllum</i> , <i>giganteum</i> , <i>hastifolium</i> , <i>lanzae</i> , <i>macrocarpon</i> , <i>mammosum</i> , <i>mauense</i> , <i>mauritanum</i> , <i>memphiticum</i> , <i>runsoriense</i> , <i>scabrum</i> , <i>schumannianum</i> , (<i>seaforthianum</i>), <i>tarderemotum</i> , <i>terminale</i> , <i>tettense</i> , <i>villosum</i> , <i>wittei</i> , (<i>wrightii</i>)
Western Sahara	<i>villosum</i>
Zambia	(<i>aculeatissimum</i>), <i>americanum</i> , <i>anguivi</i> , <i>aureitomentosum</i> , <i>campylacanthum</i> , (<i>chrysotrichum</i>), <i>goetzei</i> , <i>lichtensteini</i> , (<i>lycopersicum</i>), <i>retroflexum</i> , <i>richardii</i> , <i>scabrum</i> , (<i>seaforthianum</i>), <i>tarderemotum</i> , <i>terminale</i> , <i>tettense</i> , (<i>torvum</i>), (<i>tuberosum</i>), <i>villosum</i> , (<i>wendlandii</i>), (<i>wrightii</i>)
Zimbabwe	<i>aculeastrum</i> , (<i>aculeatissimum</i>), <i>anguivi</i> , <i>aureitomentosum</i> , (<i>betaceum</i>), <i>campylacanthum</i> , <i>catombelense</i> , <i>giganteum</i> , <i>lichtensteini</i> , <i>linnaeanum</i> , (<i>mauritanum</i>), <i>retroflexum</i> , <i>richardii</i> , <i>scabrum</i> , (<i>seaforthianum</i>), <i>tarderemotum</i> , <i>terminale</i> , <i>villosum</i> , (<i>wendlandii</i>)

*Possession of the area known as the Hala'ib triangle is disputed between Egypt and Sudan, species occurring there are listed under both countries.

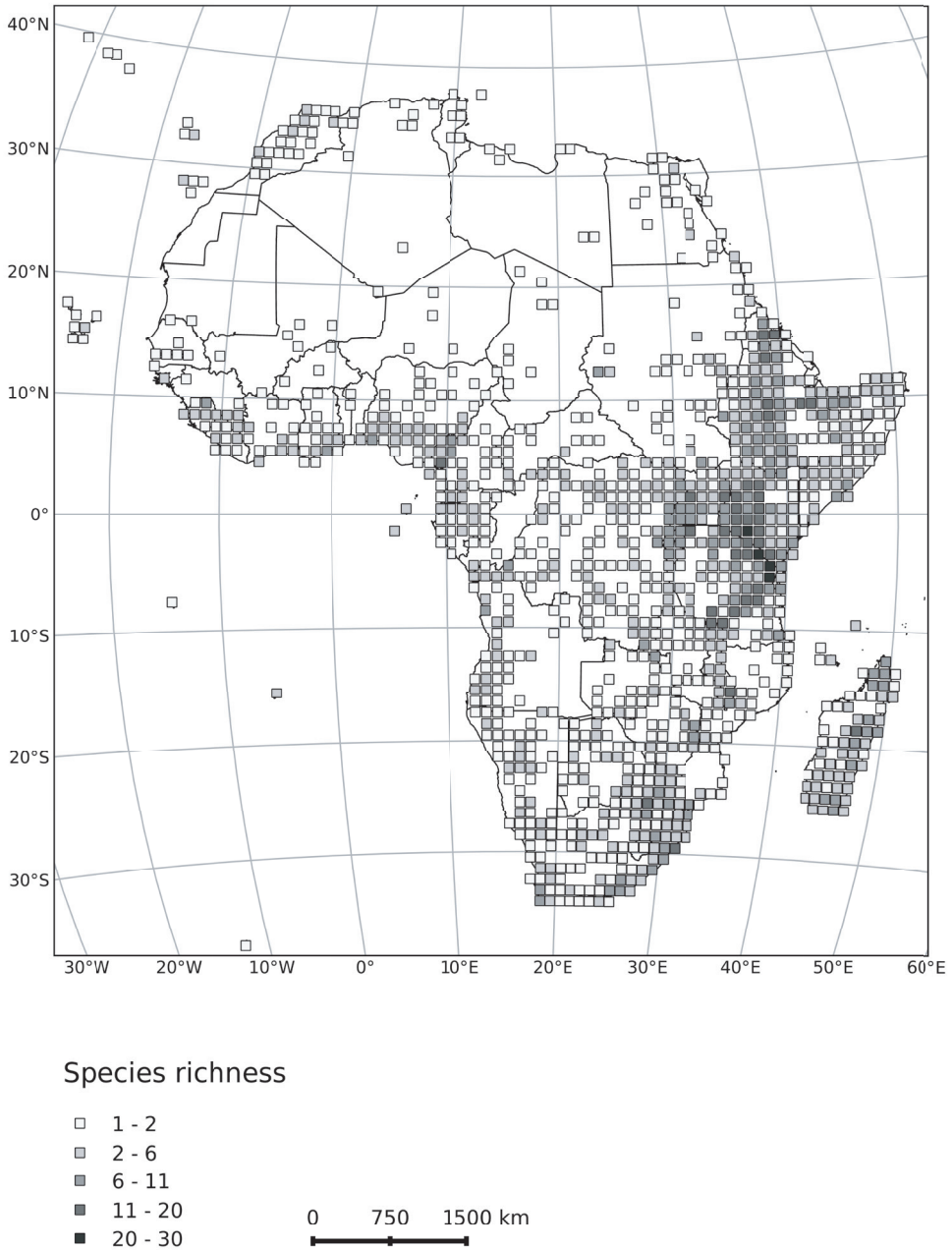


Figure 1. Heat map of *Solanum* diversity in Africa. Darker degree squares indicate greater species richness. The middle to high elevation regions of eastern Africa (Kenya/Tanzania) have the highest high species diversity, followed by secondary areas of species richness in the Ethiopian plateaus, dry areas of central Madagascar, South Africa and the area around Mount Cameroon. We have not analysed how collecting effort has influenced these patterns, but it is likely to be important. As the *Leptostemonum* Clade has the largest number of species in Africa, diversity in that clade drives species richness overall (see Vorontsova and Knapp 2016, figure 2). Map prepared by Sarah Ficinski.

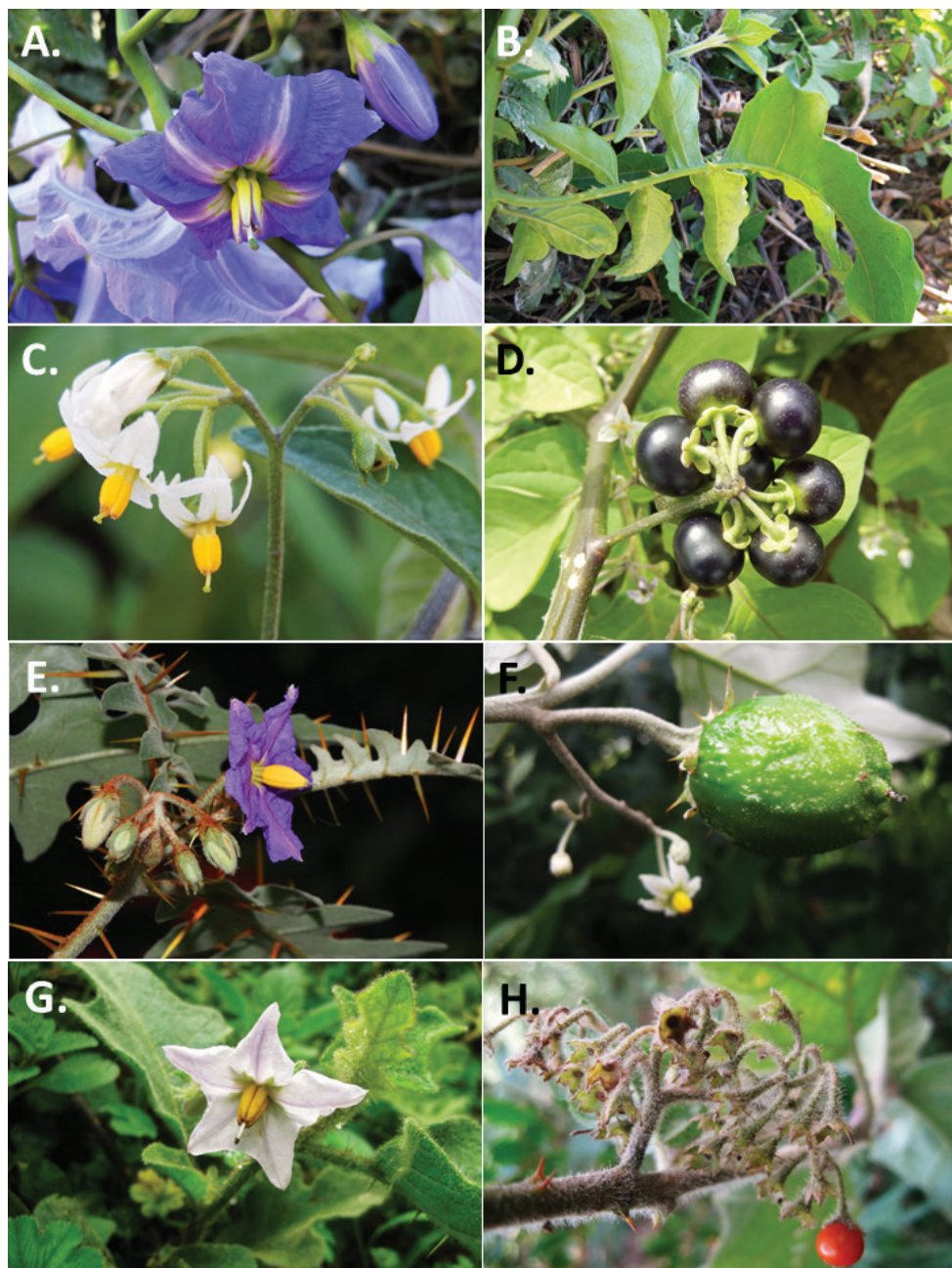


Figure 2. **A, B** *Solanum wendlandii* Hook.f. (Allophyllum-Wendlandii Clade) **C** *Solanum tarderemotum* Bitter (Morelloid Clade) **D** *Solanum scabrum* Mill. (Morelloid Clade) **E** *Solanum pyracanthos* Lam. (Leptostemonum Clade) **F** *Solanum aculeastrum* Dunal (Leptostemonum Clade) **G** *Solanum nigriviolaceum* Bitter (Leptostemonum Clade) **H** *Solanum usambarense* Bitter & Dammer (Leptostemonum Clade). Photos **A, B, F, G, H** by M.S. Vorontsova **C, D, E** by S. Knapp.

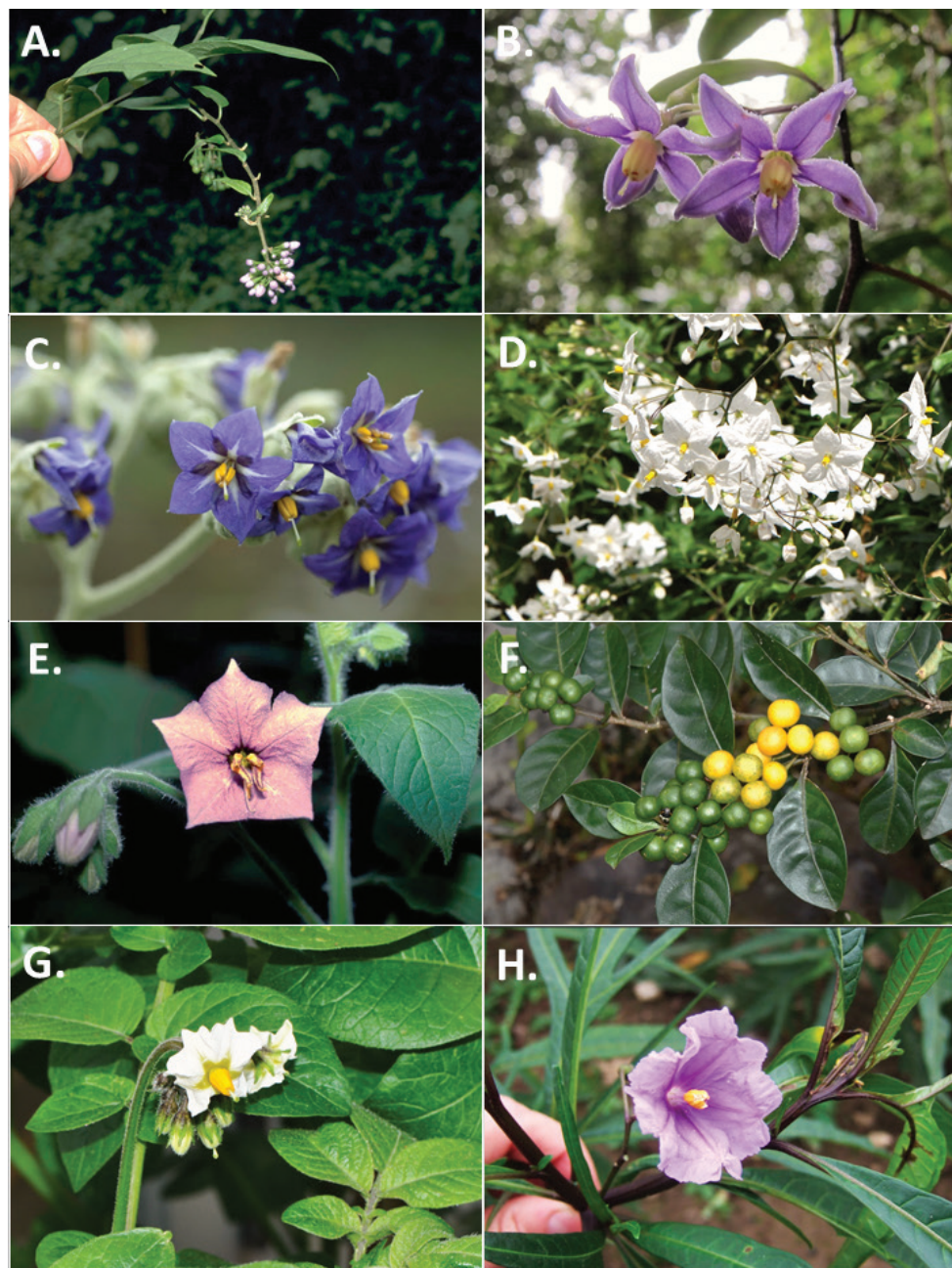


Figure 3. **A** *Solanum terminale* Forssk. (African non-spiny Clade) **B** *Solanum madagascariense* Dunal (African non-spiny Clade) **C** *Solanum mauritianum* Scop. (Brevantherum Clade) **D** *Solanum laxum* Spreng. (Dulcamaroid Clade) **E** *Solanum trisetum* Dunal (Normania Clade) **F** *Solanum diphyllum* L. (Geminata Clade) **G** *Solanum tuberosum* L. (Potato Clade) **H** *Solanum laciniatum* Aiton (Archaeosolanum Clade). Photos **A, C, D, E, F, G, H** by S. Knapp **B** by M.S. Vorontsova.

Four species have been recorded from this area, for which we have only seen single specimens, all of which are cultivated and not naturalised. *Solanum laciniatum* Aiton (Archaeosolanum Clade), the kangaroo apple from Australia and New Zealand, has been recorded from Morocco, *S. agrarium* Sendtn. (Leptostemonum Clade, section *Acanthophora* Dunal sensu Nee 1979) from Brazil has only recently been collected in the Cape Verde Islands and *S. atropurpureum* Schrank (Leptostemonum Clade, section *Acanthophora* Dunal sensu Nee 1979) from Brazil and *S. pectinatum* Dunal (Leptostemonum Clade, section *Lasiocarpa* Dunal sensu Whalen et al. 1981) from Mexico have been recorded from Tanzania in a botanical garden. These singletons have been included in Table 1, but not in the keys below; descriptions should be checked if identification is ambiguous.

Each species name is hyperlinked to its page on Solanaceae Source (www.solanaceae-source.org) where photographs (if available), descriptions and other information can be found. An expanded key to all of the thirteen major clades of *Solanum* worldwide is in preparation (R. Hilgenhof and T. Särkinen, pers. comm.). Instructions on how to use Solanaceae source are included in the Materials and Methods.

Key to the groups of *Solanum* in continental Africa, Madagascar (incl. the islands of Réunion, the Comoros and the Seychelles), Macaronesia and the Cape Verde Islands

- 1a Trichomes of stems and leaves stellate or echinoid.....**2**
- 1b Trichomes of stems and leaves simple (unbranched) or dendritically branched, never stellate or echinoid.....**3**
- 2a Anthers ellipsoid in outline; inflorescences many times branched; branching dichasial; stems without prickles**Key 6. Brevantherum Clade**
- 2b Anthers tapering in outline; inflorescences branched or unbranched; branching monochasial; stems with or without prickles
..... **Key 7. Leptostemonum Clade**
- 3a Shrubs, small trees or woody vines**4**
- 3b Herbs or if plants woody, only at the base; never true vines, occasionally scandent**9**
- 4a Stems with hooked prickles; anthers tapering.....
..... ***Solanum wendlandii* Hook.f. (Wendlandii-Allophyllum Clade)**
- 4b Stems without prickles; anthers ellipsoid.....**5**
- 5a Small trees with foetid cordate leaves; flowers waxy pink or greenish white; anther connectives enlarged; fruit a large turbinate berry with fleshy pulp; cultivated tree tomato
..... ***Solanum betaceum* Cav. (Pachyphylla [Cyphomandra] Clade)**
- 5b Shrubs or woody vines; leaves, flowers and anther connectives not as above .
..... **6**

- 6a Small shrubs with paired (geminate) leaves; flowers nodding, white; fruit held on erect pedicels, orange; cultivated or occasionally naturalised in northern Africa.....7
- 6b Woody vines or scandent shrubs; leaves, flowers and fruit not as above; continental Africa, Madagascar; or cultivated8
- 7a Leaves lanceolate, with at least some branched trichomes on new growth; leaves of a pair more or less the same shape; inflorescence usually with 2 flowers; berry dark orange; cultivated “Jerusalem cherry”
..... ***Solanum pseudocapsicum* L. (Geminata Clade)**
- 7b Leaves ovate or elliptic, completely glabrous; leaves of a pair markedly different in shape; inflorescence with more than 2 flowers; berry pale orange; only recorded from Egypt ***Solanum diphyllum* L. (Geminata Clade)**
- 8a Base of pedicel enclosed in a small sleeve of rhachis tissue usually more than 0.5 mm long; Mediterranean northern Africa; Macaronesia; if in other parts of Africa, cultivated..... **Key 3. Dulcamaroid Clade**
- 8b Base of pedicel peg-like, sometimes enclosed in a small sleeve of rhachis tissue, if so the sleeve less than 0.5 mm long; Continental tropical Africa; Madagascar; native plants **Key 1. African non-spiny (ANS) Clade**
- 9a Leaves pinnate or deeply pinnatifid..... 11
- 9b Leaves simple (at most the margins toothed) or at most ternate 12
- 10a Fleshy prostrate herbs; leaves pinnatifid, the leaflets not distinct; inflorescences unbranched..... ***Solanum triflorum* Nutt. (Morelloid Clade)**
- 10b Spreading herbs or herbaceous scramblers, not fleshy; leaves pinnate with distinct leaflets; inflorescences branched or less often unbranched.....
..... **Key 5. Potato Clade**
- 11a Anthers dimorphic, of different sizes and two of the five with horn-like projections; Macaronesia and northern Africa **Key 2. Normania Clade**
- 11b Anthers equal in size and shape, if unequal only slightly so; widespread or cultivated..... 12
- 12a Trichomes simple with a single long terminal cell (bayonet hairs); fruit a large greenish berry with purple stripes (more than 3 cm diameter), with abundant solid mesocarp; herbaceous vine.....
..... ***Solanum muricatum* Aiton (Potato Clade)**
- 12b Trichomes simple or branched; fruit variously coloured (usually less than 1 cm in diameter), with juicy mesocarp; annual or short-lived perennial herbs
..... **Key 4. Morelloid Clade**

KEY 1. AFRICAN NON-SPINY (ANS) CLADE (descriptions Knapp and Vorontsova 2016)

- 1a Leaves glabrous on both surfaces.....2
- 1b Leaves with at least some pubescence on either surface (this sometimes sparse along veins and midrib) 10

- 2a Inflorescence few-flowered, unbranched (at most furcate in *Solanum betroka*) ..3
- 2b Inflorescence many flowered, usually many times branched5
- 3a Flowers appearing fasciculate and axillary; corolla usually somewhat campanulate; fruit orange; South Africa*Solanum guineense* L.
- 3b Flowers not appearing fasciculate; corolla stellate, the petals spreading or reflexed; fruit colour green, black or not known, never orange; Madagascar4
- 4a Leaves clustered on short shoots; calyx lobes deltate, not divided to base; dry forests *Solanum betroka* D'Arcy & Rakot.
- 4b Leaves not clustered on short shoots; calyx lobes long triangular, divided to the base; wet forests *Solanum truncicola* D'Arcy & Rakot.
- 5a Flowers or fruits (or pedicel scars) in tightly packed groups on individual branches (these sometimes very short and the inflorescence appearing spicate)..... *Solanum terminale* Forssk.
- 5b Flowers spaced on the open inflorescence, often unevenly so6
- 6a Leaves clustered on short shoots..... *Solanum betroka* D'Arcy & Rakot.
- 6b Leaves spaced along the stem7
- 7a Anthers opening by pores that elongate with age; mountains of continental Africa..... *Solanum runsoriense* C.H.Wright
- 7b Anthers opening by delineated pores that do not elongate with age; Madagascar8
- 8a Leaves fleshy, thick and coriaceous, the venation not visible in dry specimens; fruit with thick pericarp (woody?) *Solanum myrsinoides* D'Arcy & Rakot.
- 8b Leaves membranous to coriaceous, not markedly thick and fleshy, the venation visible in dry specimens; fruit with thin pericarp, the seeds visible through the berry wall9
- 9a Petioles with long, simple trichomes (these not extending to the lamina); seeds 4–8 per berry; inflorescence axis thin and delicate..... *Solanum trichopetiolatum* D'Arcy & Rakot.
- 9b Petioles glabrous or with minute dendritic trichomes; seeds 20–40 per berry; inflorescence axis robust..... *Solanum madagascariense* Dunal
- 10a Leaf trichomes simple (unbranched)11
- 10b Leaf trichomes branched (dendritic to echinoid).....16
- 11a Inflorescence axis unbranched, the flowers closely spaced.....12
- 11b Inflorescence axis branched, often many times so.....13
- 12a Leaves clustered along stem; fruit orange; South Africa *Solanum guineense* L.
- 12b Leaves spaced along shoots; fruit purple or black; Madagascar *Solanum truncicola* D'Arcy & Rakot.
- 13a Flowers or fruits (or pedicel scars) in tightly packed groups on individual branches (these sometimes very short and the inflorescence appearing spicate)..... *Solanum terminale* Forssk.
- 13b Flowers spaced on the open inflorescence, often unevenly so14

- 14a Stems strongly quadrangular; at least some leaves with shallow lobes; plants of seashore and dune habitats..... ***Solanum africanum* Mill.**
- 14b Stems terete; leaves not lobed; plants of forests and forest edges **15**
- 15a Leaf pubescence very sparse, confined to the midrib or near the petiole; flowers not heterostylous; Madagascar ... ***Solanum trichopetiolatum* D’Arcy & Rakot.**
- 15a Leaf pubescence variable, not very sparse, along veins and lamina; flowers heterostylous; mountains of continental Africa
..... ***Solanum runsoriense* C.H.Wright**
- 16a Abaxial leaf surfaces with tufts of trichomes in the vein axils (domatia)..... **17**
- 16b Abaxial leaf surfaces with trichomes on lamina and/or along veins, not with prominent tufts in the vein axils (domatia) **19**
- 17a Inflorescence many times branched, open and with many flowers (more than 20); calyx lobes broadly deltate; petioles to 4 cm long, thin and flexuous; Mayotte (Comoros) ***Solanum macrothyrsum* Dammer**
- 17b Inflorescence furcate, more congested and with fewer flowers (fewer than 20); calyx lobes deltate; petioles to 2.5 cm long, thicker; Madagascar **18**
- 18a Calyx lobes 0.8–2 mm long; inflorescences with 10–16 flowers
..... ***Solanum ivobibe* D’Arcy & Rakot.**
- 18b Calyx lobes 4–6 mm long; inflorescences with 3–10 flowers
..... ***Solanum sambiranense* D’Arcy & Rakot.**
- 19a Abaxial leaf surfaces evenly pubescent on veins and lamina **20**
- 19b Abaxial leaf surfaces pubescent only along the veins and midrib, the trichomes not extending to the lamina **22**
- 20a Anther pores lengthening to slits with age; flowers heterostylous; leaves evenly distributed along branches; mountains of continental Africa.....
..... ***Solanum runsoriense* C.H.Wright**
- 20b Anther pores not lengthening to slit with age; flowers not heterostylous; leaves usually at least somewhat clustered on short shoots; Madagascar **21**
- 21a Leaves densely pubescent with golden (when dry) loosely dendritic trichomes; flowers more than 2 cm in diameter; anthers 4–6 mm long; widespread in Madagascar ***Solanum imamense* Dunal**
- 21b Leaves sparsely pubescent with white (when dry) congested dendritic trichomes; flowers 2 cm in diameter or less; anthers 3.5–4 mm long; dry forests of southern Madagascar ***Solanum betroka* D’Arcy & Rakot.**
- 22a Inflorescence unbranched, with few flowers; pedicels 1.8–4.5 cm long
..... ***Solanum humblotii* Bitter**
- 22b Inflorescence many times branched, with many flowers; pedicels 0.8–1.2 cm long **23**
- 23a Anther pores lengthening to slits with age; flowers heterostylous; pedicels with pubescence like the inflorescence rhachis; mountains of continental Africa ***Solanum runsoriense* C.H.Wright**
- 23b Anther pores not lengthening to slit with age; flowers not heterostylous; pedicels always glabrous; Madagascar..... ***Solanum madagascariense* Dunal**

KEY 2. NORMANIA CLADE (descriptions on Solanaceae Source)

- 1a Leaves shallowly lobed, pubescent with long, tangled eglandular trichomes; anthers tapering, horned near the base, tightly connivent; seeds more than 5 mm long; fruit a dry berry; Mediterranean ***Solanum herculeum* Bohs**
- 1b Leaves simple or ternate, glabrous or pubescent, but the trichomes not long and tangled, glandular; anthers markedly horned, spreading; seeds less than or equal to 5 mm long; fruit a brightly coloured, juicy berry; laurisylva forest in Macaronesia..... **2**
- 2a Leaves simple or ternate, the base truncate or cordate if leaves unlobed; anthers yellow, horned in lower third; berry bright red; Madeira ***Solanum trisectum* Dunal**
- 2b Leaves simple, the base cordate; anthers black, horned about halfway up from the base; berry orange or red; Tenerife, Canary Islands..... ***Solanum nava* Webb & Berthel.**

KEY 3. DULCAMAROID clade (descriptions in Knapp 2013 and on Solanaceae Source)

- 1a Buds turbinate and strongly pointed; petals strongly reflexed, with shiny green dots at the base of each; anthers tightly connivent with “glue”; fruit a shiny red berry, often ellipsoid; native plants in Mediterranean northern Africa..... ***Solanum dulcamara* L.**
- 1b Buds rounded, often somewhat inflated; petals spreading, without shiny green dots; anthers not tightly connivent with “glue”; fruit red or black, globose; cultivated plants, occasionally naturalised throughout the region **2**
- 2a Flowers white; anthers on equal filaments; leaves with axillary tufts of trichomes on the lower surfaces (domatia), usually simple, occasionally pinnatifid; berry (very rarely) black ***Solanum laxum* Spreng.**
- 2b Flowers purple; one filament slightly longer than the other 4; leaves completely glabrous, pinnatifid, rarely simple; berry bright shiny red ***Solanum seafortianum* Andrews**

KEY 4. MORELLOID CLADE (descriptions in Särkinen et al. 2018 and on Solanaceae Source)

- 1a Leaves shallowly to deeply pinnatifid ***Solanum triflorum* Nutt.**
- 1b Leaves entire to sinuate-dentate **2**
- 2a Glandular trichomes present (e.g. along stems, petioles and leaves), plants usually sticky to touch when fresh..... **3**
- 2b Glandular trichomes absent (e.g. along stems, petioles and leaves), plants not sticky to touch when fresh **14**
- 3a Anthers less than 1.8 mm long..... **4**

- 3b Anthers more than or equal to 1.8 mm long.....7
- 4a Inflorescences with 10–40 flowers; pedicels spaced 1–2 mm apart, sharply bent at the base (near articulation point) in flower and fruit
..... ***Solanum tarderemotum* Bitter**
- 4b Inflorescences with 2–5(-10) flowers; pedicels spaced 0–1 mm apart, nodding, erect or spreading in flower and fruit, reflexed and slightly curved in some species in fruit but never in flower5
- 5a Calyx lobes 1–1.5 mm long in flower; fruiting calyces not accrescent, the tube remaining 1–1.7 mm long and lobes 1–1.5 mm long; fruit black when ripe, not markedly shiny, with a glaucous cast..... ***Solanum retroflexum* Dunal**
- 5b Calyx lobes 1.5–2.5 mm long in flower; fruiting calyces accrescent, the tube 3–4 mm long and lobes 2.5–8.0 mm long; fruit green when ripe, shiny6
- 6a Leaf bases attenuate to cuneate; inflorescences mostly intermodal, with 4–8(-10) flowers; pedicels spaced 0.3–1 mm apart; calyx lobes 1.7–2.5 mm long; corollas with yellow-green central eye with black-purple V-shaped margins; anthers 1.0–1.4 mm long; berries dark green to green-brown marbled with white lines, becoming usually translucent and glossy, lower half of berries covered with enlarged calyces but berry mostly visible; seeds brown; stone cells (1-)2–3, these 0.5 mm in diameter; northern Africa
..... ***Solanum nitidibaccatum* Bitter**
- 6b Leaf bases truncate; inflorescences mostly leaf-opposed, with 2–5(-7) flowers; pedicels spaced 0(-1) mm apart; calyx lobes 1.5–2.0 mm long; corolla with yellow-green or translucent basal star without black-purple colouration; anthers 1.2–2.0 mm long; berries pale green, shiny becoming dull, opaque, usually completely enveloped by enlarged calyces; seeds pale yellow; stone cells 4–6, these (0.5-)0.8–1 mm in diameter; only known from South Africa
..... ***Solanum sarrachoides* Sendtn.**
- 7a Anthers more than or equal to 2.8 mm long.....8
- 7b Anthers less than 2.8 mm long.....9
- 8a Inflorescences with bracteoles present in most individuals; buds narrowly ellipsoid; corolla deeply stellate, the lobes narrowly lanceolate; berries with more than 30 stone cells ***Solanum triflorum* Nutt.**
- 8b Inflorescences never with bracteoles; buds globose, ovoid or narrowly ellipsoid; corolla rotate-stellate, the lobes long- triangular with rounded tips; berries with (0-)2–4 stone cells ***Solanum memphiticum* Forssk.**
- 9a Calyx lobes appressed to spreading in fruit, never strongly reflexed10
- 9b Calyx lobes strongly reflexed in fruit12
- 10a Calyx accrescent in fruit, calyx tube 3–4 mm long and lobes 2.5–8 mm long
..... ***Solanum sarrachoides* Sendtn.**
- 10b Calyx not accrescent in fruit, calyx tube 1–2 mm long and lobes 1–1.5 mm long11

- 11a Buds ellipsoid; calyx tube 1.5–2.0 mm long, lobes 1–1.5 mm long, elongate-deltate with rounded tips; fruiting pedicels persist when fruits mature and fall off; Cameroon line (Cameroon and Equatorial Guinea), above 2,000 m elevation ***Solanum pseudospinosum* C.H.Wright**
- 11b Buds subglobose; calyx tube 0.8–1.0 mm long, lobes 0.5–0.8 mm long, triangular with rounded to acute tips; fruiting pedicels generally do not persist and fall off with maturing fruits; in continental Africa only in South Africa and around the Mediterranean..... ***Solanum nigrum* L.**
- 12a Leaves rhomboidal to lanceolate; filaments 1.2–1.5 mm long, anthers 1.3–1.8(-2) mm long; seeds 1.6–1.8 mm long and 1.3–1.5 mm wide..... ***Solanum retroflexum* Dunal**
- 12b Leaves broadly to narrowly ovate to elliptic; filaments 0.5–1.3 mm long; anthers 1.8–2.5 mm long; seeds 1.8–2.2 mm long and 1.5–1.7 mm wide **13**
- 13a Calyx with broad and relatively transparent sinuses, lobes elliptic to triangular, rounded at tip; free part of the filaments 1.0–1.3 mm long; mature berries slightly ellipsoid, shiny yellow, orange or red; stone cells always absent ***Solanum villosum* Mill.**
- 13b Calyx with narrow, sharp triangular sinuses, lobes deltate with acute or rounded tips; free part of the filaments 0.5–0.7 mm long; mature berries round, dull black or green; stone cells 0–4; in Africa only in South Africa and around the Mediterranean ***Solanum nigrum* L.**
- 14a Anthers less than 1.8 mm long..... **15**
- 14b Anthers more than or equal to 1.8 mm long..... **17**
- 15a Pedicels spaced 1–2 mm apart, pedicels sharply bent at the base (near the articulation point) in flower and fruit ***Solanum tarderemotum* Bitter**
- 15b Pedicels spaced 0–0.5 mm apart, pedicels nodding, erect or spreading in flower and fruit..... **16**
- 16a Leaves with entire margins, occasionally sinuate-dentate; calyx lobes 0.3–0.5 mm long in flower, 1(-2) mm in fruit; mature fruits black, the surface very shiny..... ***Solanum americanum* Mill.**
- 16b Leaves shallowly toothed, occasionally entire; calyx lobes 1.0–1.5 mm long in flower, 1.5–2 mm in fruit; mature fruits purple-black or green, the surface dull ***Solanum retroflexum* Dunal**
- 17a Anthers less than 2.8 mm long..... **18**
- 17b Anthers more than or equal to 2.8 mm long **27**
- 18a Berries without stone cells..... **19**
- 18b Berries with 2–22 stone cells..... **24**
- 19a Pedicels persisting and not dropping with mature fruits; calyx lobes in fruit mostly strongly reflexed **20**
- 19b Pedicels dropping with mature fruits; calyx lobes in fruit appressed to slightly spreading, rarely strongly reflexed **22**

- 20a Leaves rhomboidal to lanceolate; filaments 1.2–1.5 mm long, anthers 1.3–1.8(-2) mm long; seeds 1.6–1.8 mm long and 1.3–1.5 mm wide.....
..... ***Solanum retroflexum* Dunal**
- 20b Leaves broadly to narrowly ovate to elliptic; filaments 0.5–1.3 mm long; anthers 1.8–2.5 mm long; seeds 1.8–2.2 mm long and 1.5–1.7 mm wide **21**
- 21a Calyx with broad and relatively transparent sinuses, lobes elliptic to triangular, rounded at tip; filaments 1.0–1.3 mm long; mature berries slightly ellipsoid, shiny yellow, orange or red; stone cells always absent
..... ***Solanum villosum* Mill.**
- 21b Calyx with narrow, sharp triangular sinuses, lobes deltate with acute tips; filaments 0.5–0.7 mm long; mature berries round, dull black or green; stone cells generally absent (2–4 stone cells common in Asian material)
..... ***Solanum nigrum* L.**
- 22a Buds elongate-oblong; fruiting peduncles strongly deflexed at the base (bent downwards at junction with the stem) ***Solanum chenopodioides* Lam.**
- 22b Buds ellipsoid to subglobose; fruiting peduncles straight or ascending **23**
- 23a Pedicels spaced 1–2 mm apart, sharply bent at the base (near the articulation point) in flower and fruit; seeds 1.5–2 mm long and 1–1.5 mm wide
..... ***Solanum tarderemotum* Bitter**
- 23b Pedicels spaced 0–0.7 mm apart, straight, spreading or reflexed in flower and fruit; seeds 1.8–2 mm long and 1.5–1.6 mm wide ***Solanum nigrum* L.**
- 24a Prostrate herb; leaves narrowly elliptic to lanceolate, base strongly attenuate; inflorescences with 1–5 flowers; pedicels stout and spreading; calyx lobes linear-oblong with rounded apices; mountains of Ethiopia
..... ***Solanum hirtulum* C.H.Wright**
- 24b Upright or spreading herb; leaves broadly ovate to elliptic, base acuminate, acute, obtuse, truncate to abruptly attenuate; inflorescences with 2–40 flowers; pedicels thinner, spreading to strongly reflexed; calyx lobes triangular, broadly deltoid or ovate with acute to rounded apices **25**
- 25a Pedicels strongly bent downwards at the base (near articulation point) in flower and fruit ***Solanum tarderemotum* Bitter**
- 25b Pedicels spreading, stout or pendent in flower, occasionally recurved in fruit but never strongly bent downwards at the base **26**
- 26a Inflorescences unbranched or more often branched, often with small leaves (bracteoles?); calyx lobes broadly deltate to mere enations of the rim; style exserted 1.0–1.5 mm beyond anther cone; mature berries 3–4(-5) mm in diameter, dull yellowish brown ***Solanum umalilaense* Manoko**
- 26b Inflorescences unbranched, never with small leaves; calyx lobes triangular; style exserted 0–1 mm beyond anther cone; mature berries 6–10 mm in diameter, dull black ***Solanum nigrum* L.**
- 27a Inflorescences with bracteoles present in most individuals; buds narrowly elliptic; berries with more than 30 stone cells ***Solanum triflorum* Nutt.**
- 27b Inflorescences never with bracteoles; buds globose, ovoid or narrowly ellipsoid; berries with 0–14 stone cells **28**

- 28a Berries with 2–14 stone cells; leaf base strongly attenuate ***Solanum hirtulum* C.H.Wright**
- 28b Berries without stone cells; leaf base not strongly attenuate.....**29**
- 29a Buds elongate-oblong; calyx lobes broadly deltate to triangular with acute tips; fruiting peduncles strongly bent at the base near junction with the stem; fruiting pedicels thin, reflexed and slightly recurved; seeds 1.2–1.4 mm long and 1.0–1.2 mm wide.....***Solanum chenopodioides* Lam.**
- 29b Buds globose-subglobose; calyx lobes broadly deltate with rounded tips; fruiting peduncles straight; fruiting pedicels stout, erect and spreading; seeds 2–2.8 mm long and 1.5–1.8 mm wide***Solanum scabrum* Mill.**

KEY 5. POTATO CLADE (descriptions on Solanaceae Source)

- 1a Flowers yellow; anthers tightly connivent and tapering to a beak-like tip; fruit a bright red berry; cultivated tomatoes**2**
- 1b Flowers white or purple; anthers ellipsoid, not tapering to a beak-like tip; fruit green or whitish green (often with purple stripes).....**3**
- 2a Corolla lobes deltate to triangular; anther cone stout, the style included; berry usually more than 1 cm in diameter (often much larger), fewer than 20 per infructescence; leaflets with serrate margins; cultivated tomato ***Solanum lycopersicum* L.**
- 2b Corolla lobes narrowly triangular; anther cone long and narrow, the style exserted; berry less than 1 cm in diameter, more than 20 per infructescence; leaflets with entire margins; cultivated currant tomato ***Solanum pimpinellifolium* L.**
- 3a Leaves at most ternate, usually simple; fruit a berry more than 3 cm in diameter; plant not bearing underground tubers; cultivated pepino ***Solanum muricatum* Aiton**
- 3b Leaves pinnate; fruit a berry less than 3 cm in diameter; plant bearing underground tubers; cultivated potato ***Solanum tuberosum* L.**

KEY 6. BREVANTHERUM CLADE (descriptions on Solanaceae Source)

- 1a Young flower buds turbinate; calyx densely pubescent within over entire surface; young stems sulcate; axillary leaves absent..... ***Solanum erianthum* D.Don**
- 1b Young flower buds oblong to orbicular; calyx lobes pubescent within only in distal quarter; young stems terete; axillary leaves common ***Solanum mauritianum* Scop.**

KEY 7. LEPTOSTEMONUM CLADE (descriptions in Vorontsova and Knapp 2016 and on Solanaceae Source)

- 1a Young stems and petioles noticeably winged; mature fruit densely pubescent; invasive plant in Tanzanian highlands and South Africa ***Solanum robustum* H.Wendl.**
- 1b Young stems and petioles not markedly winged (terete or slightly ridged); mature fruit glabrous; native or invasive, widespread..... **2**
- 2a Flowers with stamens of differing lengths (due either to unequal anthers or unequal filaments or both); arid eastern and north-eastern Africa **3**
- 2b Flowers with all stamens equal in length; widespread **8**
- 3a Corolla strongly zygomorphic, with the two lower lobes much larger; flowers often enantiostylous; Canary Islands **4**
- 3b Corolla only weakly zygomorphic, the lower lobes somewhat but not markedly larger; flowers not enantiostylous; continental Africa **5**
- 4a Leaves narrowly elliptic to lanceolate; calyx lobes linear and awn-like; corolla always 5-merous; ripe berry orange; Gran Canaria ... ***Solanum lidii* Sunding**
- 4b Leaves ovate; calyx lobes linear; corolla often 4-merous; ripe berry yellow or yellowish green; Tenerife and Gran Canaria ***Solanum vespertilio* Aiton**
- 5a Leaves orbicular to reniform, 1.2–2.5 cm long, wider than long; petioles longer than leaves; rare in north-eastern Somalia..... ***Solanum cymbalariifolium* Chiov.**
- 5b Leaves ovate to elliptic or lanceolate, 2–14 cm long, longer than wide; petioles shorter than leaves; arid eastern and north-eastern Africa **6**
- 6a Stem prickles dense, acicular, less than 0.5 mm wide at base, pale yellow; fruit fully concealed by the accrescent calyx ***Solanum coagulans* Forssk.**
- 6b Stem prickles absent or sparse, if present wider than 1 mm at base, yellow to orange or brown; fruit at least partly exposed..... **7**
- 7a Leaves subentire to lobed; anthers of equal length; seeds very dark brown to almost black..... ***Solanum melastomoides* C.H.Wright**
- 7b Leaves entire; one anther much longer than the others; seeds dull yellow to orange-brown ***Solanum somalense* Franch.**
- 8a Flower one per inflorescence, peduncle and rhachis absent; corolla pentagonal, lobed for 1/4–1/3 of the way to the base, 0.9–1.3 cm in diameter; southern Africa..... ***Solanum supinum* Dunal**
- 8b Flower usually more than one per inflorescence, peduncle and/or rhachis present in at least some inflorescences; corolla usually stellate, lobed for more than 1/3 of the way to the base or, if lobed, for 1/4–1/3 of the way to the base then corolla of long-styled flowers broader than 1.3 cm in diameter; widespread.... **9**
- 9a Trichomes on young stems and adaxial (upper) surfaces of the leaves simple only, never stellate..... **10**
- 9b Trichomes on young stems and adaxial (upper) surfaces of the leaves stellate... **13**

- 10a Flowers pale bluish purple; anthers 8–12.5 mm; fruit globose or extended into a “nipple” ***Solanum mammosum* L.**
- 10b Flowers white or greenish white; anthers 5–7.5 mm; fruit globose **11**
- 11a No stellate hairs anywhere on the plant; fruit bright orange at maturity; seeds winged, 4–6 mm long..... ***Solanum capsicoides* All.**
- 11b Stellate hairs almost always present on the abaxial (lower) surface of the leaves; fruit yellow at maturity; seeds not winged, 1.8–2.8 mm long..... **12**
- 12a Leaf lobes 2–3 pairs, extending 1/3–1/2 distance to the midvein; calyx lobes 5–6.5 mm long, often caudate ***Solanum aculeatissimum* Jacq.**
- 12b Leaf lobes 3–5 pairs, extending less than 1/3 of the distance to the midvein; calyx lobes 0.8–2 mm long, acute ***Solanum viarum* Dunal**
- 13a Leaves entire, 3–10 times longer than wide; shrubs erect, 1–6 m tall; stem trichomes with partly fused rays; southern Madagascar **14**
- 13b Leaves entire or lobed, 1–3(8) times longer than wide; shrubs erect, scandent or climbing, 0.2–6 m tall; if leaves entire and more than 3 times longer than wide, then shrub less than 1 m tall and not in southern Madagascar; stem trichomes with free rays **16**
- 14a Leaves 9–13(20) cm long; corolla 2–3.1 cm in diameter; juvenile branches with dark red prickles; south-eastern Madagascar
..... ***Solanum croatii* D’Arcy & Keating**
- 14b Leaves 1.5–7 cm long; corolla 1–2 cm in diameter; juvenile branches with grey-brown or red-brown prickles; south-western Madagascar **15**
- 15a Leaf blades 3–7 cm long, concolorous to weakly discolorous, yellow-green ...
..... ***Solanum bumeliifolium* Dunal**
- 15b Leaf blades 1.5–3(4) cm long, strongly discolorous, green-brown adaxially and glaucous abaxially..... ***Solanum heinianum* D’Arcy & Keating**
- 16a Prickles and leaf venation noticeably dark orange to red, contrasting with the yellow-green to red-green leaf surface; southern Madagascar
..... ***Solanum pyracanthos* Lam.**
- 16b Prickles and leaf venation not a contrasting colour, yellow to green or red-brown; widespread or naturalised..... **17**
- 17a Mature fruit green, never developing to bright yellow, orange or red; plants weakly andromonoecious; fruits 1–1.5 cm in diameter **18**
- 17b Mature fruit yellow, orange or red; plants hermaphroditic or andromonoecious, fruits 0.5–6 cm in diameter, if andromonoecious, then fruits more than 1.5 cm in diameter..... **19**
- 18a Shrub to tree 1.5–9 m tall; young stems and leaves densely ferruginous pubescent; trichomes on the inflorescences and pedicels not glandular; prickles straight to slightly curved..... ***Solanum chrysotrichum* Schltdl.**
- 18b Shrub to 3 m; young stems and leaves pubescent green to brownish; trichomes on the inflorescences and pedicels glandular; prickles curved.....
..... ***Solanum torvum* Sw.**

- 19a Mature fruit yellow or greenish yellow, 1.5–5(6) cm in diameter; corolla on long-styled flowers (1.3)2–6 cm in diameter; plants mostly andromonoecious **20**
- 19b Mature fruit orange to red, 0.5–1.2(1.7) cm in diameter; if mature fruit orange (1)1.5–2.5(5) cm in diameter, the plant cultivated; corolla on long-styled flowers 0.8–3 cm in diameter; plants mostly hermaphroditic **45**
- 20a Cultivated tree 5–10 m tall with copious flowers; corolla bright purple aging to white with both colours usually present in an inflorescence, 5.5–8 cm in diameter ***Solanum wrightii* Benth.**
- 20b Wild plants or cultivated vegetables, less than 6 m tall; corolla white to mauve or purple with the colour constant within each individual, 1.6–6 cm in diameter **21**
- 21a Petiole usually decurrent, leaf bases attenuate (cuneate); trichomes on abaxial leaf surface (if present) stalked with 4(5) rays **22**
- 21b Petiole never decurrent, leaf bases cordate to cuneate; trichomes on abaxial leaf surface (if present) sessile or stalked with 6–16 rays **23**
- 22a Plant clearly stellate-pubescent and armed, drying yellow-green to red-brown; wild plant ***Solanum dasyphyllum* Schumach. & Thonn.**
- 22b Plant usually glabrous and unarmed, drying a distinctive red-brown colour; cultivated plant ***Solanum macrocarpon* L.**
- 23a Climbers or scandent plants **24**
- 23b Plants erect or rarely semi-scandent **27**
- 24a Prickles on young stems straight **25**
- 24b Prickles on young stems strongly curved **26**
- 25a Prickles pale straw-yellow, to 20 mm long; petiole with sessile stellate trichomes; corolla ca. 2.5 cm in diameter; style strongly curved; Mediterranean northern Africa (adventive from Asia) ***Solanum virginianum* L.**
- 25b Prickles yellow (but not straw-coloured) or brown; petiole trichomes usually stalked; corolla 3.5–5 cm in diameter; style straight; southern Kenya ***Solanum nigriviolaceum* Bitter**
- 26a Corolla white, 1.3–1.6 cm in diameter; seeds 5.5–6 mm long; Kenyan mountains ***Solanum agnewiorum* Voronts.**
- 26b Corolla mauve to purple, 3.5–6 cm in diameter; seeds 3–4 mm long; eastern and southern Africa, Madagascar ***Solanum richardii* Dunal**
- 27a Calyx inflated, fully covering the berry at maturity; young stems densely covered with straight prickles; northern Madagascar ***Solanum maboriense* D'Arcy & Rakot.**
- 27b Calyx not inflated, the berry exposed at maturity; young stems prickly or unarmed; widespread **28**
- 28a Corolla lobed for more than half way to the base; shrubs or trees up to 6 m; variety of habitats **29**
- 28b Corolla lobed for half way to the base or less; small shrubs up to 2 m; weeds of open arid environments or cultivated crops; relatives of the eggplant **35**

- 29a Leaves 8–18 cm long, strongly discolorous; young fruits plain green; seeds 3.5–4.5 mm long; wet upland habitats.....**30**
- 29a Leaves 2–8 cm long, concolorous or sometimes discolorous; young fruits striped in different shades of green; seeds 2.2–3.5 mm long; arid upland or lowland habitats.....**32**
- 30a Fruit globose, never apiculate, 1.4–1.7 cm in diameter, 4–10 per infructescence; young stems with yellow (when dry) long-stalked trichomes, the stalks 1–3 mm.....***Solanum thomsonii* C.H.Wright**
- 30b Fruit turbinate or cone-shaped, sometimes globose, usually somewhat apiculate, 2.8–5 x 1.8–4.5 cm, 1–3(5) per infructescence; young stems usually lacking long-stalked yellow (when dry) trichomes.....**31**
- 31a Fruit distinctly turbinate or cone-shaped, 2.8–3.7 x 1.8–2.2 cm; leaves on fertile branches elliptic and subentire, 6–8 x 2.5–4 cm, ca. 2.5 times longer than wide; 2100–3000 m elevation.....***Solanum phoxocarpum* Voronts.**
- 31b Fruit globose, usually somewhat apiculate, 3–5 x 2–4.5 cm; leaves on fertile branches ovate(elliptic) and lobed(subentire), 8–15 x 6–12 cm, 1.5–2 times longer than wide; 1200–2100(3200) m elevation***Solanum aculeastrum* Dunal**
- 32a Prickles straight or occasionally curved; petioles 1/3–2/3 as long as the leaf blades.....***Solanum polhillii* Voronts.**
- 32b Prickles on young stems strongly curved; petioles less than 1/3 of the leaf blade length**33**
- 33a Leaves entire, densely stellate-pubescent on both sides; eastern and north-eastern African highlands.....***Solanum dennekense* Dammer**
- 33b Leaves lobed, adaxially glabrescent; eastern and north-eastern Africa**34**
- 34a Leaves 2–4 cm long; curved prickles on young stems 5–10 mm long; eastern and north-eastern Africa***Solanum arundo* Matthei**
- 34b Leaves 6–8 cm long; curved prickles on young stems 1–3 mm long; coastal Kenya, rare***Solanum malindiense* Voronts.**
- 35a Fruit with soft pericarp, in a variety of shapes and colours, edible; common fasciation in the flowers (e.g. increase in the number of flower parts up to 8), inflated ovaries; cultivated species***Solanum melongena* L.**
- 35a Fruit spherical, yellow, with comparatively hard pericarp, not edible; flowers 5-merous; wild plants**36**
- 36a Leaves lobed with primary and secondary lobes, the primary lobes extending 2/3–3/4 of the distance to the midvein and secondary lobes always present; southern Africa and northern African coasts around the Mediterranean.....***Solanum linnaeanum* Hepper & P.M.-L.Jaeger**
- 36b Leaves entire or lobed, lobes extending up to 2/3 of the distance to the midvein, secondary lobes usually not present; widespread**37**

- 37a Leaf margins and venation nearly white and contrasting with greenish red-brown adaxial leaf surface; trichomes on the abaxial surface of the leaves with 10–17 rays; Ethiopian highlands..... ***Solanum marginatum* L.f.**
- 37b Leaf margins and venation the same colour as the rest of the leaf blade; trichomes on the abaxial surface of the leaves with 5–12(15) rays; widespread **38**
- 38a Leaf lobes apically obtuse to acute, sometimes rounded, sometimes with secondary lobes; lobes 1/4–2/3 of the distance to the midvein; leaves and young stems glabrescent to moderately pubescent **39**
- 38b Leaf lobes apically rounded, sometimes obtuse, never with secondary lobes; lobes up to 1/3(1/2) of the distance to the midvein; leaves and young stems usually densely pubescent **41**
- 39a Calyx lobes on long-styled flowers 7–10 mm long, ovate and foliaceous, apically obtuse; South Africa..... ***Solanum umtuma* Voronts. & S.Knapp**
- 39b Calyx lobes on long-styled flowers 4–7 mm long, deltate or long-triangular apically acuminate; northern Africa and Cape Verde Islands **40**
- 40a Calyx lobes on long-styled flowers 4–7 mm long, deltate, ca. 1/6 as long as the fruit at maturity; continental Africa north of the equator.....
..... ***Solanum cerasiferum* Dunal**
- 40b Calyx lobes on long-styled flowers 6–7 mm long, long triangular, 1/2 to 1/3 as long as the fruit at maturity; Cape Verde Islands (Senegal?).....
..... ***Solanum rigidum* Lam.**
- 41a Prickles straight; corolla on long-styled flowers 1.8–2.5 cm in diameter; anthers ca. 4.5 mm long; Madagascar; Mauritius, Réunion
..... ***Solanum insanum* L.**
- 41b Prickles curved or straight; corolla on long-styled flowers 2.5–4.5 cm in diameter; anthers 5–9 mm long; widespread **42**
- 42a Leaves usually entire, sometimes lobed; trichomes on the abaxial leaf surface sessile or with stalks up to 0.1 mm long; fruits 1.5–3 cm diameter
..... ***Solanum campylacanthum* Hochst. ex A.Rich.**
- 42b Leaves lobed; trichomes on the abaxial leaf surface with stalks up to 0.5(1) mm long; fruits 2.5–4.5 cm diameter **43**
- 43a Leaves velvety red-brown adaxially; calyx lobes on long-styled flowers ovate to oblong, foliaceous, 7–10 mm long..... ***Solanum aureitomentosum* Bitter**
- 43b Leaves yellow-green to green-brown adaxially; calyx lobes on long-styled flowers deltate, usually not foliaceous, 2.5–6 mm long..... **44**
- 44a Leaves concolorous to weakly discolorous, indumentum yellowish; leaves ca. 1.5 times longer than wide; young stems terete to angular; north-eastern Africa
..... ***Solanum incanum* L.**
- 44b Leaves strongly discolorous, indumentum dirty greenish brown adaxially and whitish yellow abaxially; leaves 1.5–2.5 times longer than wide; young stems with somewhat raised longitudinal ridges; southern Africa.....
..... ***Solanum lichtensteinii* Willd.**

- 45a Leaves on fertile branches with distinct lobes, at least some of the lobes longer than 1/4 of the distance from the midvein to the leaf edge.....46
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Supplementary material 1

List of *Solanum* species occurring in Africa as defined in this paper

Authors: Sandra Knapp, Maria S. Vorontsova, Tiina Särkinen

Data type: species data

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Link: <https://doi.org/10.3897/phytokeys.127.34326.suppl1>

Supplementary material 2

Specimens examined by the authors for the preparation of these keys

Authors: Sandra Knapp, Maria S. Vorontsova, Tiina Särkinen

Data type: species data

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Five new species of the genus *Primulina* (Gesneriaceae) from Limestone Areas of Guangxi Zhuangzu Autonomous Region, China

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Abstract

Five new species of *Primulina* (Gesneriaceae) are described and illustrated here, namely *P. purpureokylin* F. Wen, Yi Huang & W. Chuen Chou, *P. persica* F. Wen, Yi Huang & W. Chuen Chou, *P. cerina* F. Wen, Yi Huang & W. Chuen Chou, *P. niveolanosa* F. Wen, S. Li & W. Chuen Chou and *P. leiyyi* F. Wen, Z.B. Xin & W. Chuen Chou. The characteristic traits of these species, together with photographs, detailed descriptions, notes on etymology, distribution, and habitat, as well as comparisons with morphologically similar species, are provided.

Keywords

Biodiversity, flora of Guangxi, karst, lithophilic plant, new taxon, taxonomy

Introduction

The genus *Primulina sensu lato*, as a group, is representative of the rich diversity of Chinese Gesneriaceae. The tropical and subtropical karst limestone mountainous areas of Guangxi, China, are the centers of species diversity and differentiation of this genus. As

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of the end of June 2017, the accepted and published species of *Primulina* from China had already reached 180 (including infraspecific taxa). Among them, 115 species (more than 63%) are confirmed and recorded from Guangxi Zhuangzu Autonomous Region (Guangxi for short) (Xu et al. 2017). Recently, an additional 16 new taxa of *Primulina* from China were published. By the end of January 2019, at least 196 species of *Primulina* were recorded from China (Wen et al. 2019). Many new taxa of *Primulina* from South and Southwest China are being discovered and published. After reviewing the genus *Primulina* and collating the new taxa for about two years (2017–2018), we discovered that there were a total of 11 new taxa from Guangxi. They are *P. lutescens* B. Pan & H. S. Ma (Ma et al. 2017), *P. albicalyx* B. Pan & Li H. Yang (Yang and Pan 2017), *P. curvituba* B. Pan, L.H. Yang & M. Kang (Yang et al. 2017), *P. dichroantha* F. Wen, Y.G. Wei & S.B. Zhou (Wu et al. 2017), *P. yandongensis* Ying Qin & Yan Liu (Qin et al. 2018), *P. hiemalis* Xin Hong & F. Wen, *P. davidioides* F. Wen & Xin Hong (Hong et al. 2018b), *P. zhoui* F. Wen & Z.B. Xin, *P. huangii* F. Wen & Z.B. Xin (Xin et al. 2018), *P. cangwuensis* X. Hong & F. Wen (Hong et al. 2018a), *P. hochiensis* (C.C. Huang & X.X. Chen) Mich. Möller & A. Weber var. *ovata* L.H. Yang, H.H. Kong & M. Kang (Yang et al. 2019). Guangxi is located in southern China. Most of the province originates from erosion of a limestone plateau and has a subtropical monsoon-affected climate. Several new species of Gesneriaceae have been discovered and published in recent years from this region. We suspect that more new taxa of *Primulina*, and even Gesneriaceae, are still to be found here.

The Guangxi Institute of Botany continues to support the Gesneriad Conservation Center of China (GCCC) and the Guilin Botanical Garden, CAS, in carrying out the investigations of Gesneriaceae diversity in S & SW China in recent years. Since 2015, the GCCC has been introducing, conserving, and propagating a large number of *Primulina* plants from S and SW China and N Vietnam. Many *Primulina* species from the Guangxi area are new to science, and waiting to be further studied. After careful study of both relevant specimens and taxonomic publications from the adjacent regions (Wang et al. 1990, 1998; Li and Wang 2005; Wei et al. 2010; Weber et al. 2011; Möller et al. 2016; Xu et al. 2017), we concluded that these plants represent five new species of *Primulina*. Descriptions, figures, and photos of these plants are presented here, as are morphological characters which are compared with those of closely related species.

Taxonomic treatment

***Primulina purpureokylin* F.Wen, Yi Huang & W.Chuen Chou, sp. nov.**

urn:lsid:ipni.org:names:77199643-1

Fig. 1

Diagnosis. *Primulina purpureokylin* most resembles *P. leprosa* (Yan Liu & W.B. Xu) W.B. Xu & K.F. Chung (Fig. 6 A) (Xu et al. 2010, 2012) in having similarly purple indumentum on both surfaces of the leaf blade, but differs in having fewer leaves (4–6

in *P. purpureokylin* vs 5–12 in *P. leprosa*; same order as following), smaller leaf blade size ($2\text{--}6.5 \times 1.5\text{--}3.5$ cm vs. $6\text{--}13 \times 4\text{--}8$ cm), bracts shape (linear or linear-lanceolate vs broadly ovate), corolla color (pinkish purple vs. yellow) and length (1.5–1.8 cm long vs. ca. 2.3 cm long), staminodes number (2 vs 3) and indumentum of style (nearly glabrous vs glandular-pubescent).

Type. CHINA. Pingguo County, Xin'an Town, Gusha village, $23^{\circ}16'N$, $107^{\circ}29'E$, 200 m a.s.l., growing on the surface and crevices of moist limestone rocks at the bottom of cliffs, 3 Apr 2018, *Chou Wei Chuen et al. CWC171116-01* (holotype: IBK!, isotype: IBK!).

Description. Perennial herbs. Rhizome subterete, 1–1.5 cm long, 5–10 mm in diameter. Leaves 4–6, all basal, opposite pairs; petiole compressed, cross section semi-elliptic, 1.5–2.5 cm long, 0.6–1.1 cm wide, shortly reddish purple to purplish brown strigose on both surfaces; blades dark green to purplish green, coriaceous or stiffly chartaceous, obliquely ovate, elliptic to broadly oblong-ovate, left-right asymmetric or symmetric, $2\text{--}6.5 \times 1.5\text{--}3.5$ cm, upper surface distinctly bullate, cuneate at base, commonly symmetric, occasionally oblique, margin entire, obtuse or rounded at apex, with erect reddish purple pubescence on both surfaces, margins with ciliate, pubescence 0.5–1 mm long, lateral veins 3 or 4 on each side, impressed adaxially and prominent abaxially. Cymes axillary, 2–4, 1- or 2-branched or single, 1- or 2–4-flowered on one cyme; peduncle 5.5–14.5 cm long, slender, 1–1.2 mm in diam., erect white glandular-pubescent; bracts 2, opposite, purplish green, linear or linear-lanceolate, ca. 6×1.5 mm, margin entire, acute at apex, sparsely purple puberulent outside, glabrous inside. Bracteoles 2, opposite, shape, hairs and color same as bracts but obviously smaller, ca. 3×0.8 mm. Pedicel 1–1.6 cm long, 0.8–1 mm in diam. Calyx 5-parted near to the base, lobes narrowly lanceolate-linear, $3\text{--}4 \times 0.8\text{--}1$ mm, margin entire, acute at apex, spreading white pubescent outside, glabrous nearly inside. Corolla pinkish purple, within 8–10 longitudinal dark purple stripes from corolla throat to the bottom of corolla tube, 1.5–1.8 cm long, spreading glandular puberulent outside, glabrous inside; tube tubular, pink, 8–9 mm long, 5–6 mm in diameter in medium, 5.5–6.5 mm in diam. at the mouth; limb distinctly 2-lipped, dark pink to purplish pink, adaxial lip 2-lobed to the middle, lobes ovate or nearly oblong, ca. 5×3 mm, obtuse to rounded at apex, with 2 or 3 deep purple lines inside; abaxial lip 3-lobed over the middle, two lateral lobes in apparently obliquely oblong, the central one zygomorphic, oblong, ca. 7×4 mm, rounded at apex. Stamens 2, adnate to ca. 5.5 mm above the base of the corolla tube; filaments white, geniculate at the middle, ca. 5.5 mm long, glabrous; anthers pale brown to purplish brown, subreniform, slightly contracted in the middle, ca. 1 mm long, glabrous. Staminodes 2, translucent, 0.8–1 mm long, glabrous, adnate to ca. 5 mm above the base of the corolla tube. Disc annular, ca. 0.7 mm high, margin entire. Pistil 1–1.1 cm long, ovary yellowish brown, linear, ca. 5 mm long, 0.8–1 mm in diam., glandular-puberulent; style white to translucent, 5–6 mm long, nearly glabrous; stigma obtrapeziform, ca. 0.9 mm long, apex 2-lobed. Capsule glabrous, valvate dehiscence when mature, 1.5–2 cm long.

Phenology. Flowering in Nov., fruiting time in Dec.

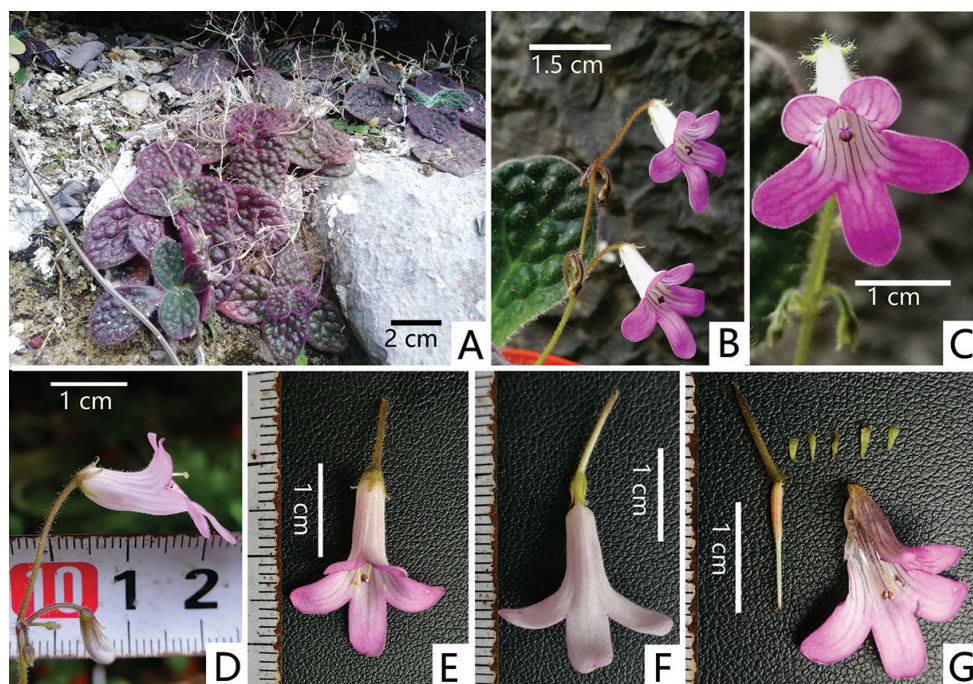


Figure 1. *Primulina purpureokylin* F.Wen, Yi Huang & W.Chuen Chou sp. nov. **A** habit **B** cyme **C** frontal view of corolla **D** lateral view of corolla **E** dorsal view of corolla **F** ventral view of corolla **G** opened corolla for showing stamens, with pistil and calyx. Photographed by Wei-Chuen Chou and Yi Huang, charted by Wen-Hua Xu.

Etymology. The specific epithet, ‘*purpureokylin*’, consists of two parts. The first part of the scientific epithet is “*purpure-*”, means purple. It refers to the upper faces of the leaf blades which are covered in purple pubescent-hairs. The second half of the epithet, “*kylin*”, refers to one of the auspicious animals in the traditional culture of China. Because the interesting and beautiful leaves are full of purple-hairs, bubbles on the surface appear as if covered with the purple squamae of Kylin. The Chinese name is “Zí Lín Bào Chūn Jù Tǎi” (紫麟报春苣苔).

Distribution and habitat. *Primulina purpureokylin* is currently known only from the type locality. Only a single population with ca. 100 individuals was discovered and confirmed. The species is only known growing on the surface and crevices of wet limestone rocks at the bottom of cliffs in Pingguo County, Guangxi, China.

Provisional IUCN conservation assessment. Along with the further field investigations for the current survival situation of *Primulina purpureokylin*, the extinction risk of this species is rising because of over-harvesting by local plant collectors. Over-exploited because of its beauty, this unpublished species is on the brink of extinction. Although more surveys are needed to clarify its conservation status, the provisional conservation status is Critically Endangered CR B2ab (iii, v) according to the IUCN red list criteria (IUCN 2012).

***Primulina persica* F.Wen, Yi Huang & W.Chuen Chou, sp. nov.**

urn:lsid:ipni.org:names:77199644-1

Fig. 2

Diagnosis. *Primulina persica* most closely resembles *P. gongchengensis* Y.S. Huang & Yan Liu (Fig. 6 B) (Huang et al. 2012) in having similarly shaped leaf blades. It differs from the latter by having a different indumentum on both surfaces of the leaf blades (densely eglandular-pubescent in *P. persica* vs densely glandular-pubescent in *P. gongchengensis*; same order as following), margin of leaf blade (irregularly serrate in different numbers vs. repand or crenate), smaller bracts ($6-7 \times 1.5-2$ mm vs. $10-20 \times 2-3.5$ mm) and bracts shape (linear vs. narrowly rhombic to oblong), the indumentum of calyx lobes inside (glabrous vs sparsely glandular-pubescent) and shorter corolla length (7.5–10 mm long vs. 22–28 mm long).

Type. CHINA. Yangshuo County, Gaotian Town, Lexiang village, $24^{\circ}42'N$, $110^{\circ}30'E$, 124 m a.s.l., growing on the surface of tufa and crevices of moist rocks on a cliff of a limestone hill, 3 Apr 2018, *Chou Wei Chuen et al. CWC171116-01* (holotype: IBK!, isotypes: IBK!)

Description. Perennial herbs. Rhizome subterete, 5–6 cm long, 8–10 mm in diam. Leaves 6–10, crowded at apex of rhizome, petiolate; petiole cylindrical, upper slightly smaller and the bottom slightly inflated but the base slightly applanate, 8–15 cm long, 6–8 mm in diam. at base, densely eglandular-pubescent; leaf blade herbaceous, rhomboid-ovate or elliptic, $6-11 \times 5-9.5$ cm, apex acute, obtuse or slightly round, base cordate, broadly cuneate to cordate, slightly inequilateral, margin irregularly serrate in different numbers, densely pubescent on both surfaces, lateral veins 2 or 3 on each side, impressed adaxially and prominent abaxially. Cymes 4–10, 1–3-branched, 12–30-flowered; peduncle 12–20 cm long, 2–2.5 mm across, densely glandular-pubescent; pedicel 1–3 cm long, densely glandular-pubescent; bracts opposite, linear, $6-7 \times 1.5-2$ mm, margin entire, apex acute, adaxially glandular-puberulent, abaxially nearly glabrous. Calyx 5-parted nearly to base, lobes narrowly lanceolate, $4.5-5.5 \times$ ca. 1 mm, margin entire and ciliolate, outside densely glandular-pubescent, inside glabrous. Corolla pinkish, fuchsia to pale purple, 7.5–10 mm long, 4–4.5 mm in diam. at mouth, outside glandular-puberulent; tube short, 5.5–6.5 mm long, ca. 4.5 mm in diam. in middle, tube base slightly swollen, ca. 2 mm in diam. at base; limb distinctly 2-lipped, adaxial lip 2-lobed to more than the middle, lobes oblong, apex round, $3.2-3.8 \times 2.5-3$ mm, abaxial lip 3-lobed to more than the middle, lobes oblong, apex round, $4.5-5.2 \times 3.3-3.6$ mm. Stamens 2, adnate to 2.5 mm above corolla tube base, filaments 4–4.5 mm long, curved at middle, anthers elliptic or reniform, ca. 1.5 mm long, glabrous; staminodes 3, lateral ones 0.8–1 mm long, adnate to 1.8–2 mm above corolla tube base; middle one 0.5 mm long, adnate to ca. 1.3 mm above corolla tube base. Disc annular, ca. 0.6 mm in height, margin entire. Pistil 6.5–7.5 mm long, ovary ovoid, ca. $2.5 \times 1.3-1.5$ mm, glandular-puberulent; style indumentum same as ovary, 4–5 mm long, ca. 0.5 mm in diam. in the middle; stigma obtrapeziform, ca. 0.8 mm long, apex 2-lobed. Capsule ovoid, ca. 8 mm long, valvate dehiscence when mature, outside pubescent.

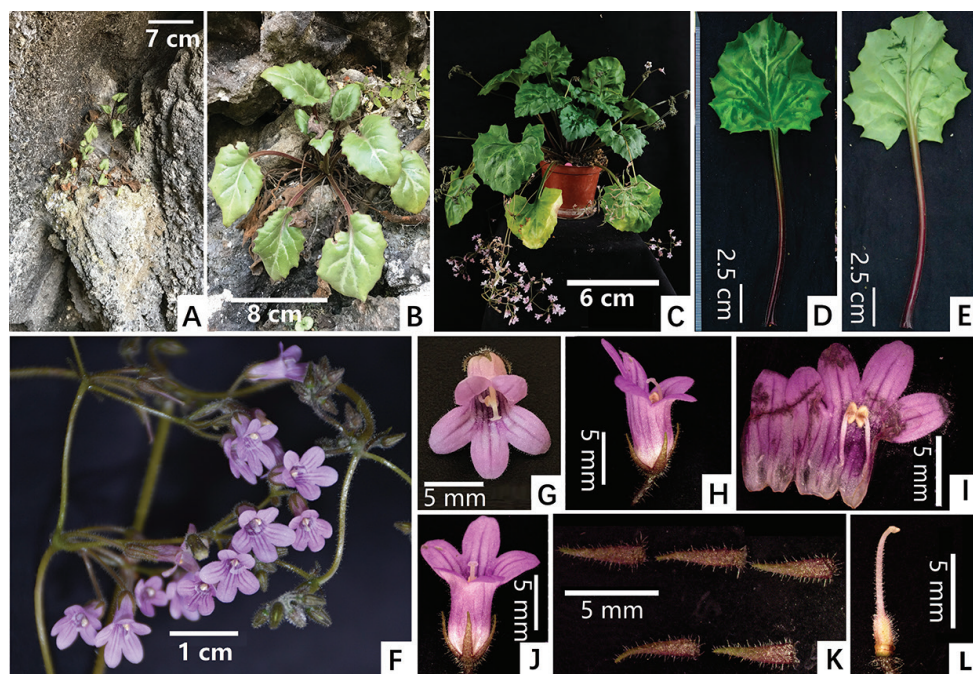


Figure 2. *Primulina persica* F.Wen, Yi Huang & W.Chuen Chou sp. nov. **A** habitat **B** habit **C** plant in flower, cultivated in GCCC **D** adaxial surface of leaf **E** abaxial surface of leaf **F** cyme and flowers **G** front view of corolla **H** lateral view of corolla **I** opened corolla for showing stamens **J** dorsal view of corolla **K** adaxial surface of calyx lobes **L** pistil. Photographed by Fang Wen, charted by Wen-Hua Xu.

Phenology. Flowering from May to June; fruiting from June to August.

Etymology. The specific epithet, ‘*persica*’, refers to the color of its flower, a vivid and bright peach. The Chinese name is “Tāo Hóng Xiǎo Huā Jù Tái” (桃红小花苣苔).

Distribution and habitat. *Primulina persica* is currently known only from the type locality and only about 50 individuals were confirmed. All individuals are growing on the surface of tufa and wet crevices of moist rocks on the cliff of a limestone hill in Yangshuo, Guangxi, China. There are no accompanying plants except for some ferns.

Provisional IUCN conservation assessment. The original habitat of this species was almost destroyed because of road building in 2013; it directly resulted in a single small population with no more than 50 surviving individuals. We hope we can find more populations in the future through field surveys. The habitat of *Primulina persica* is likely to be subjected to human activities because the survival population grows in cracks of a limestone cliff by the side of the road. Thus, based on currently available information, *P. persica* should be considered as ‘Critically Endangered’ (CR): B1+2ab(V); C2b, following the IUCN categories and criteria (IUCN 2012).

***Primulina cerina* F.Wen, Yi Huang & W.Chuen Chou, sp. nov.**

urn:lsid:ipni.org:names:77199645-1

Fig. 3

Diagnosis. *Primulina cerina* most closely resembles *P. renifolia* (D. Fang & D.H. Qin) J.M. Li & Y.Z. Wang (Fig. 6 C) (Fang and Qin 2004, Wang et al. 2011, Weber et al. 2011) in having similarly shaped leaf blades, but differs in their indumentum of the peduncle (densely erectly eglandular-puberulent in *P. cerina* vs spreading white pubescent and glandular puberulent in *P. renifolia*; same order as following), corolla tube shape (tubular, abaxially straight and not swollen vs. obliquely campanulate, abaxially swollen), corolla color (beige to pale yellow mixed slightly reddish brown vs. pale purple to purple inside longitudinally purple lines), indumentum of filaments (glabrous vs glabrous but base glandular puberulent), the indumentum of calyx lobes inside (glabrous vs sparsely glandular-pubescent) and stigma shape (obtrapeziform and 2-lobed vs obliquely hippocrepiform but unlobed).

Type. CHINA. Yizhou city, Beiya Town, Xiaozhudong village, 24°22'N, 108°23'E, 220 m a.s.l., only known from crevices of moist rock surfaces at the entrances of a big limestone cave, 3 Apr 2018, *Chou Wei Chuen et al. CWC171116-01* (holotype: IBK!, isotypes: IBK!)

Description. Perennial herbs. Rhizome small and short, indistinctive but nearly cylindrical, 3–8 mm long, 2–3 mm in diam. Leaves numerous, 8–20 or more, all basal, petiolate; petiole pale brownish purple to dark brownish purple, cylindrical, 7.5–12 cm long, 3–3.2 mm in diam., extremely short puberulent to nearly glabrous; leaf blade dark green, slightly fleshy to thickly chartaceous, herbaceous when dried, nearly rounded to cordate rounded, 3–5.5 × 3.5–5.5 cm, apex obtuse to rounded, base cordate to deeply cordate, margin undulant to crenate; lateral veins 3–4 on each side, slightly impressed adaxially and apparently prominent abaxially. Cymes 8–16, 1–3-branched, 16–30-flowered per cyme; peduncle 8–15 cm long, ca. 2.5 mm in diam., densely erectly eglandular-puberulent; pedicel 5–10 mm long, ca. 1 mm in diam., indumentum same as pedicel; bracts 2, opposite, brownish purple, linear to oblanceolate, 5–12 × 1–4 mm, margin entire to inconspicuously dentate, apex acuminate to acute, adaxially very shortly puberulent, abaxially nearly glabrous. Calyx 5-parted nearly to base, lobes brownish purple, narrowly lanceolate, 3–4 × ca. 1 mm, margin entire, outside sparsely extremely short puberulent, inside nearly glabrous. Corolla beige to pale yellow mixed slightly reddish brown, 1.8–2 cm long, 4–5 mm in diam. at mouth, outside sparsely eglandular-puberulent to nearly glabrous, inside glabrous; tube tubular, 1.5–1.8 cm long, 3.5–4 mm in diam. at the middle, tube base slightly constricted, 1–1.5 mm in diam. at base; limb distinctly 2-lipped, adaxial lip 2-lobed to base, lobes oblong, apex rounded, 2.5–3 × 2–2.5 mm, abaxial lip 3-lobed to over middle, lobes oblong, apex rounded, ca. 3.5 × 3 mm. Stamens 2, adnate to ca. 3 mm above corolla tube base, filaments ca. 6 mm long, curved at middle, anthers elliptic or reniform, ca. 1.8 mm long, glabrous; staminodes 2, extremely small and inconspicuous, punctate, ca. 0.05 mm

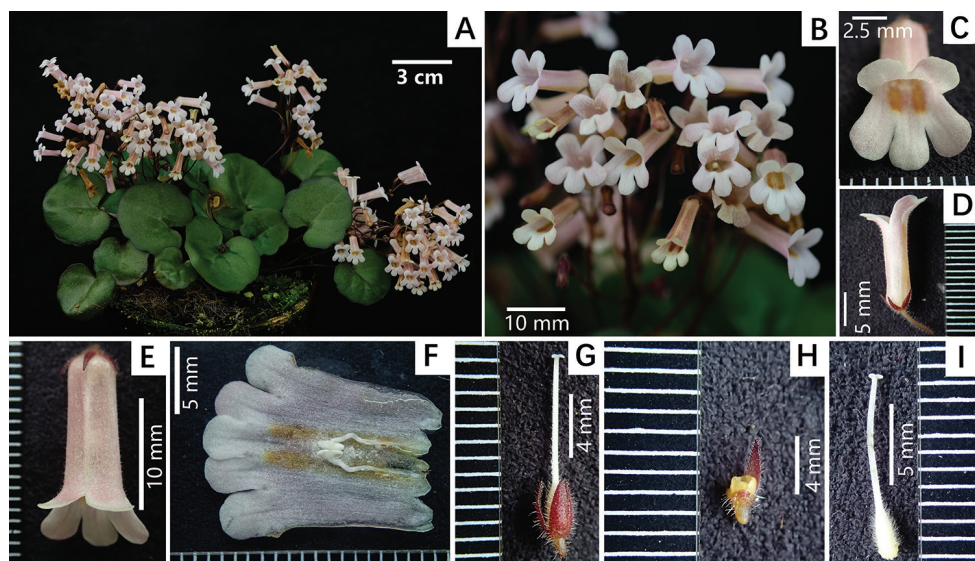


Figure 3. *Primulina cerina* F.Wen, Yi Huang & W.Chuen Chou sp. nov. **A** plant in flower, cultivated in GCCC **B** cyme with flowers **C** front view of corolla **D** lateral view of corolla **E** dorsal view of corolla **F** opened corolla for showing stamens **G** pistil and calyx lobes for showing their adaxial surfaces **H** disc and one of calyx lobes for showing its abaxial surface **I** pistil without calyx lobes for showing ovary and style and their indumentum. Photographed by Fang Wen, charted by Wen-Hua Xu.

long, adnate to corolla tube base. Disc annular, ca. 0.9 mm in height, margin entire to sinuate. Pistil 10.5–11 mm long, ovary ovoid, ca. 2.5×1 mm, densely eglandular-puberulent; style ca. 8 mm long, ca. 0.2 mm in diam. at the middle, the lower part of style sparsely eglandular- and glandular-puberulent but the upper half part of style nearly glabrous; stigma obtrapeziform, ca. 0.5 mm long, apex 2-lobed. Capsule ovoid, valvate dehiscence when mature, $4\text{--}4.5 \times$ ca. 3 mm.

Phenology. Flowering from April to May; fruiting from June to July.

Etymology. The specific epithet, ‘*cerina*’, refers to the special color of the flowers; ‘*cerina*’ is derived from the Latin, ‘*cerinus*’, meaning dark yellow or sulfur yellow, but mixed with a little pale reddish brown. The color seems like the hue of the natural brimstone (sulphur) ore. The Chinese name is “Àn Lú Sè Xiǎo Huā Jù Tǎi” (暗疏色小花苣苔).

Distribution and habitat. *Primulina cerina* is currently known only from the type locality. The species grows in the crevices of rocks with wet surfaces at the entrances of a large limestone cave in Yizhou, Guangxi, China.

Provisional IUCN conservation assessment. *Primulina cerina* is rarer than the species mentioned above, *P. persica*. At present, only a single population with ca. 20 individuals is known, counted and confirmed from 2016 to 2018. Although the type locality is in an outlying mountain area and surrounded by limestone forest, this species should be assessed as ‘Critically Endangered, CR B2a+C2a(i,ii)+D’, given the few known individuals and a single population based on the IUCN categories and criteria (IUCN 2012).

***Primulina niveolanosa* F.Wen, S. Li & W.Chuen Chou, sp. nov.**

urn:lsid:ipni.org:names:77199646-1

Fig. 4

Diagnosis. *Primulina niveolanosa* most closely resembles *P. repanda* (W.T. Wang) Y.Z. Wang (Fig. 6 D) (Wang 1981, Wang et al. 2011, Weber et al. 2011) in having similarly shaped leaf blades, but differs in their indumentum of the leaf blades (both surfaces spreading densely long white villous to lanate in *P. niveolanosa* vs. appressed puberulent to villous in *P. repanda*; same order as following), number of bracts (3, whorled vs. 2, opposite), shape of bracts (narrowly oblong to broadly oblanceolate vs. lanceolate-linear to subulate), shape of calyx lobes (linear to narrowly oblanceolate vs. narrowly triangular), corolla length (1.5–1.8 cm long vs. ca. 8 mm long).

Type. CHINA. Yizhou city, Beiya Town, Jiucui village, 24°24'N, 108°24'E, 181 m a.s.l., growing on the surface of a moist cliff at the edge of a village, 3 Apr 2018, *Chou Wei Chuen et al. CWC171116-01* (holotype: IBK!, isotypes: IBK!)

Description. Perennial herbs. Rhizome cylindrical, 3–15 mm long, 1.5–3 mm in diam. Leaves numerous, 16–40 or more, all basal, petiolate; petiole green, oblong-oblate, 4–8 cm long, 6–15 mm in diam., spreading appressed white pubescent to lanate; leaf blade pale green to green, fleshy to thickly chartaceous, herbaceous when dried, narrowly oblong, narrowly oblanceolate to oblong-elliptic, 5–10 × 2.5–4.5 cm, apex obtuse and occasionally rounded, base gradually attenuated to form petiole, margin entire, undulate to crenate, both surfaces densely villous to lanate with long, spreading white hairs, lateral veins 4 or 5 on each side, slightly impressed adaxially and apparently prominent abaxially. Cymes axillary, 6–12 per plant, 2–4-branched, 16–36-flowered per cyme; peduncle 15–25 cm long, 2.5–3.5 mm in diam., green, densely white villous and lanose; bracts 3, whorled, brownish green, margin entire to undulate, apex acuminate to acute, adaxially white pubescent, abaxially nearly glabrous, lateral ones bigger, ca. 15 × 6 mm, narrowly oblong to broadly oblanceolate, central one smaller, ca. 15 × 3.5 mm; pedicel 1–1.5 cm long, ca. 1 mm in diam., indumentum same as pedicel; pedicel green, 1–2.5 cm long, 1–1.5 mm in diam., densely white pubescent. Calyx 5-parted nearly to base, lobes green to brownish green, linear to narrowly oblanceolate, 5–7 × ca. 2 mm, margin entire, outside white puberulent, inside nearly glabrous. Corolla pale pink to white, inside with two dark pink to pinkish orange stripes, 1.5–1.8 cm long, 5–7.5 mm in diam. at mouth, outside and inside glabrous; tube infundibular, pale pink, 1.1–1.3 cm long, 4.5–5.5 mm in diam. at the middle, 1.3–1.8 mm in diam. at base; limb distinctly 2-lipped, adaxial lip 2-lobed to over middle, lobes oblong to rounded, apex rounded, 3.5–4 × ca. 4 mm, abaxial lip 3-lobed to over middle, lobes oblong to rounded, apex rounded, 4–4.5 × ca. 4 mm. Stamens 2, adnate to ca. 1.8–2.2 mm above corolla tube base, filaments 1.8–2.3 mm long, geniculate at 1/3 from the bottom, glabrous, anthers elliptic or reniform, ca. 1 mm long, ca. 0.5 mm in diam. per anther, white beard; staminodes 3, glabrous, lateral ones adnate to 1.7–2 mm above corolla tube base, white to translucent, ca. 2 mm long, apex capitate, central one adnate to ca. 1.6 mm above corolla tube base, capitate. Disc annu-

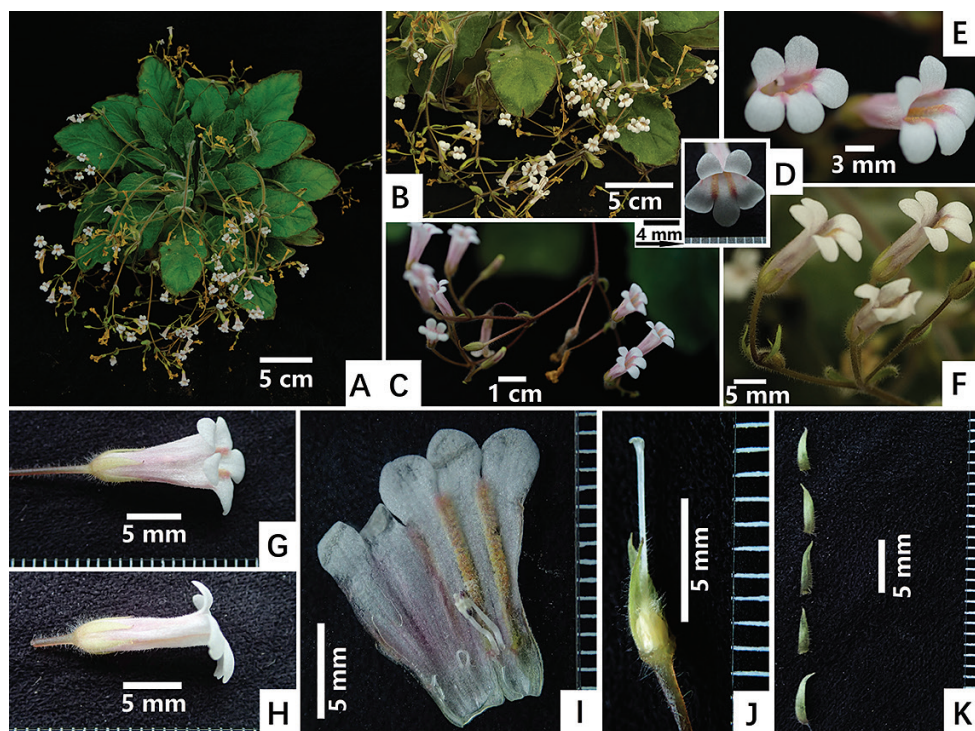


Figure 4. *Primulina niveolanosa* F.Wen, S. Li & W.Chuen sp. nov. **A** plant in flower, cultivated in GCCC **B** cyme with flowers **C** close look of cyme and flowers **D** front view of corolla **E** lateral view of corolla **F** lateral view of corolla, bracts and bracteoles **G** dorsal view of corolla **H** lateral view of corolla with scale **I** opened corolla for showing stamens and staminodes **J** pistil with two calyx lobes for showing ovary and style and their indumentum **K** adaxial surface of calyx lobes. Photographed by Fang Wen, charted by Wen-Hua Xu.

lar, glabrous, ca. 0.6 mm in height, margin entire to sinuate. Pistil ca. 8 mm long, ovary ovoid, ca. 2×1.3 mm, densely eglandular lanose; style ca. 6 mm long, ca. 0.3 mm in diam. at the middle, the lower part of style sparsely eglandular-puberulent but the upper half part of style nearly glabrous; stigma obtrapeziform, ca. 0.5 mm long, apex 2-lobed. Capsule ovoid, glabrous, valvate dehiscence when mature, $4\text{--}4.5 \times$ ca. 3 mm.

Phenology. Flowering from March to April; fruiting from April to May.

Etymology. The specific epithet, '*niveolanosa*', consists of two parts. The first part of "*niveo*", comes from the Latin word, '*niveus*', and means as white as snow, or snow-white; the second half, '*lanosa*', is from the Latin, '*lanosus, lani-*', meaning with lanose or villous hairs. Thus, the scientific name refers to the plants seemingly covered with snow because of the indumentum of snowy lanose hairs. The Chinese name is "Mián Máo Xiǎo Huā Jù Tái" (绵毛小花苣苔).

Distribution and habitat. *Primulina niveolanosa* is currently known only from the type locality: a single population with ca. 100 individuals, and although it might be endangered, more surveys are needed to clarify its conservation status. The species is only known growing on the surface of a moist cliff along the edge of a village.

Provisional IUCN conservation assessment. About 100 mature individuals have been recorded and confirmed, growing on a wet rock surface under evergreen broad-leaved forest on a limestone hill. Because the local government of Yizhou city is planning to develop a scenic spot project at this place, the habitat of this new species is likely to be subjected to human activities. Thus, based on currently available information, *P. niveolanosa* should be considered as ‘Critically Endangered’ (CR): B1+2ab(V); C2b, following the IUCN categories and criteria (IUCN 2012).

***Primulina leiyyi* F.Wen, Z.B. Xin & W.Chuen Chou, sp. nov.**

urn:lsid:ipni.org:names:77199647-1

Fig. 5

Diagnosis. *Primulina leiyyi* most closely resembles *P. longgangensis* (W.T. Wang) Yan Liu & Y.Z. Wang (Fig. 6 E) (Wang and Huang 1982, Wang et al. 2011, Weber et al. 2011) in having similarly shaped leaf blades, but differs in their indumentum of young stems (sparsely appressed hazel pubescent in *P. leiyyi* vs. nearly glabrous in *P. longgangensis*; same order as following), shape of bracts (elliptic to cymbiform vs. linear to lanceolate or obovate), indumentum of corolla (outside sparsely glandular-puberulent, inside glabrous vs. outside glabrous to puberulent, inside puberulent or glabrous below stamens), pistil length (1.8–2.0 cm long vs. ca. 2.8 cm long) and capsule length (4.8–5.5 cm long vs. 1.6–2.5 cm long)

Type. CHINA. Nanning city, Suxu Town, Shibaluohandong village, 22°32'N, 108°3'E, 150 m a.s.l., growing on the top of limestone cliff near road, 3 Apr 2018, *Lei YuYang et al. LYY181208-01* (holotype: IBK!, isotypes: IBK!)

Description. Perennial herbs. Rhizome cylindrical, the long rhizome up to 50 cm long or longer and branched repeatedly after several years of growth, 5–6 mm in diam.; branch up to 8–15 cm long, sparsely appressed hazel pubescent when young, gradually glabrous when mature. Leaves ternate, occasionally opposite, subsessile to sessile; leaf blade fleshy to thickly herbaceous when fresh, hard chartaceous when dried, often asymmetric, obliquely oblanceolate to broadly ensiform, 6.5–16 × 1.5–2.5 cm, apex acuminate to acute, base narrowly cuneate, gradually attenuated to be petiole, margin entire, adaxially and abaxially densely appressed pubescent and strigose, lateral veins 4 or 5 on each side, slightly impressed adaxially and apparently prominent abaxially. Inflorescences axillary, cymes 2–6 on the near top of every branch, 1-branched, (1)2–6-flowered per cyme; peduncle reddish brown, 3–7.5 cm long, 1–1.5 mm in diam., densely spreading eglandular-pubescent; bracts 2, opposite, green to yellowish green, elliptic to cymbiform, 1.2–2.3 cm × 3–6.5 mm, margin entire, apex acuminate to acute, adaxially and abaxially densely appressed pubescent; pedicel reddish brown, 2–3 cm long, ca. 1 mm in diam., indumentum same as peduncle. Calyx 5-parted to base, lobes reddish brown, narrowly lanceolate-linear to linear, ca. 8 × 0.3 mm, margin entire, outside densely puberulent, inside nearly glabrous. Corolla dark pink to purplish pink, ca. 3.5 cm long, 11–12.5 mm in diam. at mouth, outside sparsely

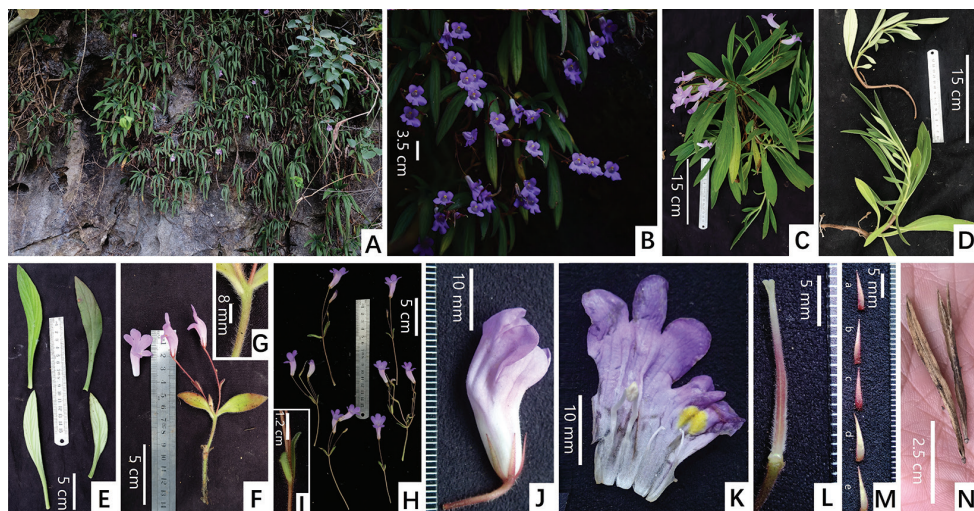


Figure 5. *Primulina leiyyi* F.Wen, Z.B. Xin & W.Chuen sp. nov. **A** habit **B** cyme and flowers **C** plant in flower collected in the field **D** extended branches after growing for one or some years **E** adaxial and abaxial view of leaf blades **F** cyme with one flower near top of stem **G** pubescent hairs on the surface of stem **H** different cymes with variable numbers of flowers **I** bracts **J** lateral view of bud **K** opened corolla for showing stamens and staminodes **L** pistil without calyx lobes **M** adaxial surfaces of calyx lobes **N** mature capsules. Photographed by Fang Wen, charted by Wen-Hua Xu.

glandular-puberulent, inside glabrous; tube tubular, 2.4–2.8 cm long, 3–3.5 mm in diam. at the middle, tube slightly upswept, base gradually constricted, 2.5–3.5 mm in diam. at base; limb distinctly 2-lipped, adaxial lip 2-lobed to over middle, slightly obliquely oblong, apex rounded, 4.5–5.5 × 3.8–4.5 mm, abaxial lip 3-lobed to about middle, lateral ones slightly obliquely oblong, 6.5–7.5 × ca. 4.5 mm, central one oblong, apex rounded, 7.5–8 × 6.5–7 mm, mm. Stamens 2, adnate to ca. 7 mm above corolla tube base, filaments white, 8–9 mm long, geniculate at middle, anthers white, reniform to fusiform, ca. 3 mm long, nearly glabrous; staminodes 3, lateral translucent to white, ones adnate to 6.2–6.5 mm above corolla tube base, 4–4.5 mm long, apex capitate, central one adnate to 4.8–5 mm above corolla tube base, small, punctate, ca. 1 mm long. Disc annular, white, 0.8–1 mm in height, margin entire. Pistil 1.8–2.0 cm long, ovary reddish brown, cylindric, 9–10 mm long, 1–1.3 mm in diam., densely white glandular-puberulent; style 9–10 mm long, 0.6–0.7 mm in diam., pale reddish brown from base to middle, white from middle to top, densely glandular-puberulent; stigma obtrapeziform, ca. 1.2 mm long, apex 2-lobed, lobes truncate. Capsule linear, valvate dehiscence and glabrous when mature, 4.8–5.5 cm × 2.2–2.5 mm.

Phenology. Flowering from November to the beginning of December; fruiting in January of the next year.

Etymology. The new species is named after Mr. Yu-Yang Lei, who first discovered and collected this rare species and who accompanied us on a number of subsequent field expeditions in Nanning, Guangxi. The Chinese name is “Léi Shì Bào Chūn Jù Tái” (雷氏报春苣苔).

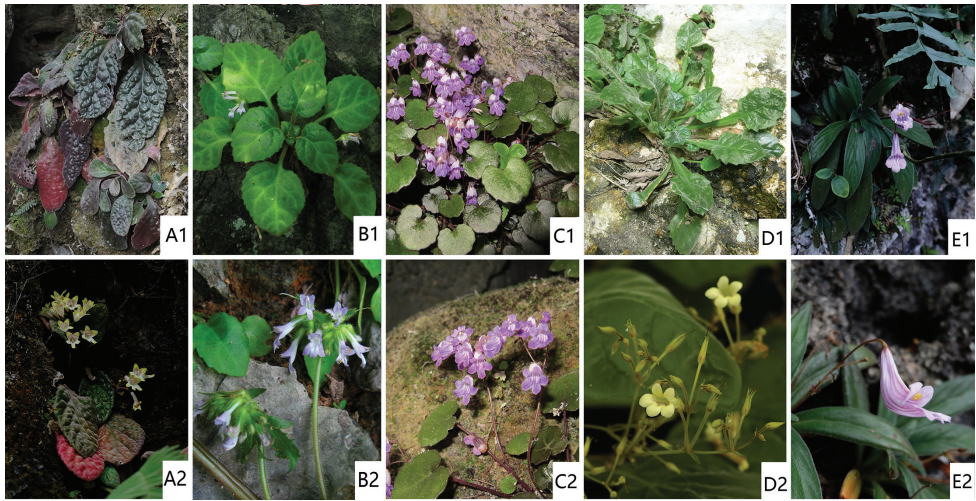


Figure 6. The morphologically similar congeners of the five new species of *Primulina* **1** habit **2** flowers. **A** *P. leprosa*, the congener of *P. purpureokylin* **B** *P. gongchengensis*, the congener of *P. persica* **C** *P. renifolia*, the congener of *P. cerina* **D** *P. repanda*, the congener of *P. niveolana* **E** *P. longgangensis*, the congener of *P. leiyyi*. Photographed by Fang Wen, charted by Wen-Hua Xu.

Distribution and habitat. It is currently known only from the type locality in a single population with ca. 100 individuals. Although it might be endangered, more surveys are needed to clarify its conservation status. The species is only known growing on the surface of wet rocks on the limestone hills along the edges of village roads.

Provisional IUCN conservation assessment. We carefully explored the type locality on five visits over a period of three years. *Primulina leiyyi* appears to be restricted to limestone hills surrounding Shibaluohandong village, Suxu Town, Nanning city. Although the habitats are very near to densely populated areas and are easily threatened by human activities, this species is common and locally abundant on limestone hills. Using the IUCN Red List categories (IUCN 2012), a provisional conservation status of Least Concern (LC), is assessed for this species.

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Three new species of *Lachemilla* (Rosaceae) from South America

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Abstract

Three new species of *Lachemilla* (Rosaceae), two from Colombia and one from Peru, are described and illustrated. *Lachemilla rothmaleriana* is characterized by its stout stems, sericeous-villous indumentum, and wide ascending sheaths with trilobate lateral lobes. *Lachemilla argentea* presents a unique combination of tripartite basal leaves with an adaxial silvery villous indumentum, and decumbent branches with verticillate lobed sheaths. Finally, *Lachemilla cyanea* has distinctly basal reniform leaves with a blue-green color and hirsute pubescence. Phylogenetic analyses of the nuclear ribosomal cistron and multiple regions of the plastid genome revealed the allopolyploid origin of the three new taxa.

Resumen

Tres nuevas especies de *Lachemilla* (Rosaceae), dos de Colombia y una de Perú, se describen e ilustran. *Lachemilla rothmaleriana* se caracteriza por tener tallos robustos, indumento sericeo-viloso, y verticilos anchos ascendentes con lóbulos laterales trilobados. *Lachemilla argentea* presenta una combinación única de hojas basales tripartitas con indumento viloso plateado en el haz y ramas decumbentes con verticilos lobulados. Finalmente, *Lachemilla cyanea* presenta hojas basales distintivas de forma reniforme, color azul-verdoso y pubescencia hirsuta. Análisis filogenéticos del cistrón ribosomal nuclear y múltiples regiones del genoma cloroplástico revelaron el origen aloploiploide de los tres nuevos taxones.

Keywords

Allopolyploidy, Colombia, *Lachemilla*, new species, páramo, Peru, Rosaceae

* These authors contributed equally to this work

Introduction

The genus *Lachemilla* (Focke) Rydb. is a morphologically diverse group that includes perennial herbs, subshrubs, and dwarf shrubs (Romoleroux 1996, 2004; Gaviria 1997). *Lachemilla* is distributed in the neotropical mountains from Mexico to Argentina and Chile, between 2,200 m and 5,000 m (Romoleroux 1996, 2004; Gaviria 1997), and it is especially common and diverse in the high elevation ecosystems of the Northern Andes where this group has undergone a rapid ecological radiation associated with the most recent Andean orogeny (Romoleroux 2004; Morales-Briones et al. 2018a).

The taxonomy of *Lachemilla* has proven challenging (e.g., Perry 1929; Rothmaler 1935a, 1935b, 1937), and although more recent regional treatments have reviewed this group (Gaviria 1997; Romoleroux 2004; Barrie 2015), the complex morphology of *Lachemilla* has obscured species boundaries and morphological subdivisions. Additionally, recent attention to the systematics of *Lachemilla* has resulted in the description of several new species (Romoleroux 2009; Romoleroux and Morales-Briones 2012; Morales-Briones 2016), but a comprehensive monographic revision of the genus is still needed (Romoleroux and Morales-Briones in prep.).

Based on molecular phylogenetic evidence, Morales-Briones et al. (2018a) proposed the recognition of 61 species of *Lachemilla* separated into four well-supported lineages that are somewhat congruent with previously morphology-based classification systems (Perry 1929; Rothmaler 1937). The Tripartite clade includes herbs with ascending and procumbent stems and tripartite leaves. The Verticillate clade includes subshrubs with erect or decumbent stems and reduced leaves that fuse with the stipules to form verticillate sheaths. The Pinnate clade comprises species with repent or decumbent stems and pinnate or bipinnatifid basal leaves. Finally, the Orbiculate clade encompasses species with a stoloniferous habit and palmately lobed leaves, and, it has been established that the Orbiculate clade is of ancient hybrid origin (Morales-Briones et al. 2018b). Moreover, Morales-Briones and Tank (2019a), using copies (or ribotypes) of the nuclear ribosomal (nrDNA) cistron and multiple regions of the plastid genome (cpDNA), showed that at least 30 species of *Lachemilla* are allopolyploids, and that this condition is widespread among the four main clades of this group.

Here, we describe and illustrate three new species of *Lachemilla*, two from Colombia and one from Peru, and using a phylogenetic approach, we show evidence that these new species are of allopolyploid origin.

Materials and methods

Phylogenetic analyses

We used previously published datasets from Morales-Briones and Tank (2019b) from the nrDNA cistron and 45 regions of cpDNA for *Lachemilla*, and included 68 samples representing 48 species of *Lachemilla*, seven samples of the three new taxa, and four outgroups (Appendix 1). DNA extraction, amplification and sequencing were

carried out as described in Morales-Briones and Tank (2019a). Molecular datasets from Morales-Briones and Tank (2019a) and data for the new taxa presented here were generated simultaneously. Data processing and ribotype selection was performed as described in Morales-Briones and Tank (2019a). The three regions of the nrDNA (ETS, ITS1, and ITS2) were concatenated, and the 45 regions of the cpDNA were concatenated as well. Phylogenetic analyses of the nrDNA and cpDNA matrices were carried out independently to avoid conflicting phylogenetic signal due to widespread cytonuclear discordance in *Lachemilla* produced by polyploidy and ancient hybridization (Morales-Briones et al. 2018a, 2018b). Maximum likelihood (ML) analyses were conducted with RAxML v8.2.10 (Stamatakis 2014) using a GTRGAMMA model, 100 searches for the best tree, and clade support was assessed with 1,000 bootstrap replicates summarized using transfer bootstrap expectation (TBE; Lemoine et al. 2018). Bayesian inferences (BI) were performed with MrBayes v3.2.6 (Ronquist et al. 2012) on the CIPRES portal (Miller et al. 2010). Analyses consisted of two independent runs with four Markov Chain Monte Carlo (MCMC) chains for 20 million generations with trees sampled every 20,000th generation and allowing sampling across the entire substitution rate model space using reversible-jump Markov Chain Monte Carlo (rjMCMC) (nst = mixed) and rate variation set to GAMMA. Parameter estimate convergence of the independent MCMC runs was assessed by analyzing plots of all parameters and the $-\ln L$ after reaching an ESS (effective-sample size) ≥ 200 using Tracer v1.6 (Rambaut et al. 2014). A 50% majority rule consensus tree was generated and posterior probabilities (PP) were calculated after removing the first 25% of sampled trees. Alignments and phylogenetic trees are available at TreeBASE (<http://purl.org/phylo/treebase/phyloids/study/TB2:S24437>).

Taxonomic analyses

Morphological characters were studied using dried herbarium specimens of *Lachemilla* deposited in ANDES, CAS, COL, F, HUT, HAO, ID, JE, MEXU, MO, NY, QCA, TEX, and USM. Additionally, we reviewed species descriptions and types to determine the existence of the new taxa. The conservation status of the new species was evaluated using the guidelines of the International Union for Conservation of Nature (IUCN 2017).

Results and discussion

Phylogenetic analyses

The final cpDNA concatenated matrix included 65 sequences representing 47 species of *Lachemilla* and four outgroup species, and had an aligned length of 22,000 bp. The ML and BI analyses recovered the same overall topology (Fig. 1). The four major clades within *Lachemilla* are the same as in previous phylogenetic analyses of the genus (Morales-Briones et al. 2018a; Morales-Briones and Tank 2019a). The samples of

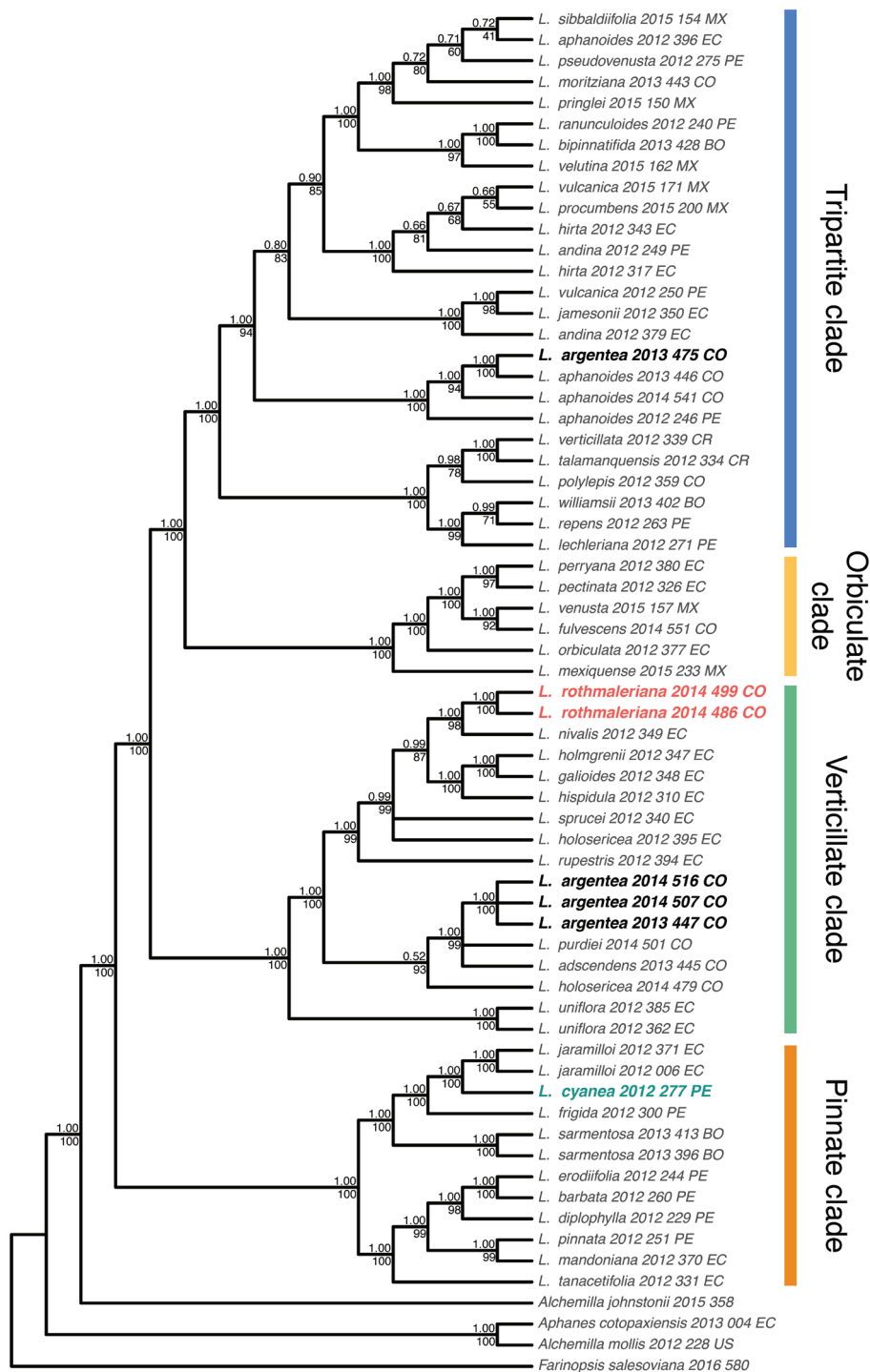


Figure 1. Bayesian 50% majority rule consensus tree of the cpDNA dataset. Posterior probabilities and transfer bootstrap expectation support values are shown above and below the branches, respectively.

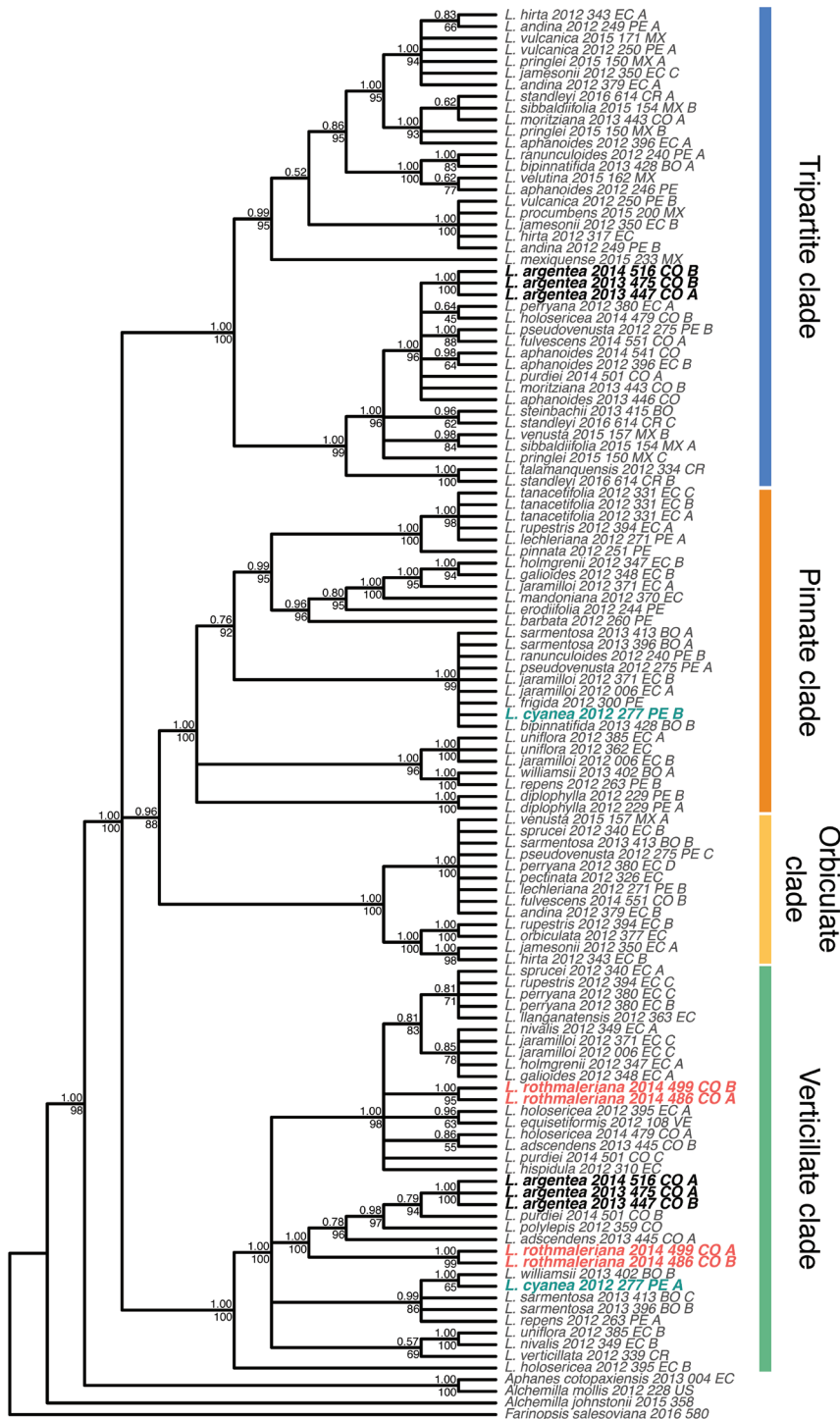


Figure 2. Bayesian 50% majority rule consensus tree of the nrDNA dataset. Posterior probabilities and transfer bootstrap expectation support values are shown above and below the branches, respectively.

L. rothmaleriana form a clade (TBE = 100, PP = 1.0) and are placed as sister to *L. nivalis* (Kunth) Rothm. in the Verticillate clade. *Lachemilla cyanea* is placed in the clade (TBE = 100, PP = 1.0) composed of *L. frigida* (Wedd.) Rothm. and *L. jaramilloi* Romol. & D.F. Morales-B. (a known allopolyploid species) within the Pinnate clade. *Lachemilla argentea* is placed in two major clades. Three samples form a clade (TBE = 100, PP = 1.0) that is placed along other allopolyploid species (*L. purdiei* (L.M. Perry) Rothm., *L. adscendens* (Rothm.) Rothm. and *L. holosericea* (L.M. Perry) Rothm.) within the Verticillate clade. The remaining sample (2013_475_CO) is placed within a clade composed of only samples of *L. aphanoides* (Mutis ex L. f.) Rothm. within the Tripartite clade.

The final nrDNA concatenated alignment included 121 sequences representing 51 species of *Lachemilla* and four outgroup species, and had aligned length of 1038 bp. The ML and BI analyses also recovered the same overall topology (Fig. 2). As in the cpDNA analyses, the four major clades within *Lachemilla* are the same as in previous studies (Morales-Briones et al. 2018a; Morales-Briones and Tank 2019a). *Lachemilla rothmaleriana* showed the presence of two ribotypes within the Verticillate clade. One of the ribotypes is placed as sister (TBE = 100, PP = 1.00) to a clade composed of *L. adscendens*, *L. polylepis* (Wedd.) Rothm., *L. purdiei*, and *L. argentea*. The second copy is placed within a clade (TBE = 98, PP = 0.91) that includes several species with verticillate sheaths along the entire stem, like *L. hispidula* (L.M. Perry) Rothm., *L. equisetiformis* (Trevir.) Rothm., and *L. nivalis*, and several allopolyploid species (e.g. *L. adscendens*, *L. holosericea*, *L. sprucei* (L.M. Perry) Rothm.), but the resolution within this clade is rather uncertain. *Lachemilla cyanea* also presents two ribotype copies. One copy, as in the cpDNA tree, is placed in the clade (TBE = 100, PP = 0.99) composed of *L. frigida* and its allopolyploid species (e.g. *L. jaramilloi*, *L. sarmentosa* (L.M. Perry) Rothm.) within the Pinnate clade. The other ribotype is placed within a clade (TBE = 86, PP = 0.99) composed only of allopolyploid species (*L. williamsii* (L.M. Perry) Rothm., *L. repens* (C. Presl) Rothm., and *L. sarmentosa*) within the Verticillate clade. All samples of *L. argentea* also have two ribotypes. The first is placed in the Tripartite clade along several allopolyploid species that involve *L. aphanoides* as one parental species (e.g. *L. pseudovenusta*, *L. fulvescens* (L.M. Perry) Rothm., *L. purdiei*, *L. perryana* (Rothm.) Rothm.). The second copy is placed as sister (TBE = 84, PP = 0.79) to the allopolyploid species *L. purdiei* in the Verticillate clade.

Previous phylogenetic analysis of *Lachemilla* have shown that allopolyploidy is common in this group with at least 30 species confirmed to be of allopolyploid origin (Morales-Briones and Tank 2019a). Here we show that the three new taxa of *Lachemilla* described here are also allopolyploids. *Lachemilla rothmaleriana* appears to be an allopolyploid of two different species within the Verticillate clade. Based on the cpDNA tree we can determine that *L. nivalis* might be the maternal lineage, while the paternal lineage seems to be the same as in the allopolyploids *L. adscendens*, *L. purdiei* and *L. argentea*, all from Colombia. From the nrDNA tree we can see that the paternal species is either extinct or unsampled. Morphologically, *L. rothmaleriana* presents the main characteristic of the Verticillate clade, which is the presence of reduced leaves that fuse with the stipules to form verticillate sheaths, but this new taxon is distinguished mainly by

the presence of wide ascending sheaths with trilobate lateral lobes and a dense sericeous-villous indumentum (see Taxonomic treatment for details). The presence of divided lobes is a characteristic of other species of the Verticillate clade that are now known to be of hybrid origin, like *L. adscendens* and *L. sprucei* (Morales-Briones and Tank 2019a).

Lachemilla argentea is also an allopolyploid species of two major clades. The cpDNA tree shows that three of the four samples have the maternal lineage from the Verticillate clade, while for one sample (2013_475_CO) the maternal lineage is *L. aphanoides* in the Tripartite clade. The nrDNA data shows that the paternal lineage of *L. argentea* is in the Tripartite clade, except for 2013_475_CO which has an extinct or unsampled parental lineage in the Verticillate clade. Although the sample 2013_475_CO is monophyletic with the other samples of this species for both ribotypes in the nrDNA, the different position in the cpDNA tree is clear evidence that the parental contribution in the formation of allopolyploid species in *Lachemilla* can work in both directions, as well as the recurrent origin of allopolyploids, which has also been previously shown for this group (Morales-Briones and Tank 2019a), and is known for other related groups in Rosaceae, like *Fragaria* (Dillenberger et al. 2018). The basal tripartite leaves of *Lachemilla argentea* are characteristic of the Tripartite clade, but its decumbent branches with verticillate lobed sheaths resemble the Verticillate clade (see Taxonomic treatment for details).

Finally, *L. cyanea* also shows evidence of an allopolyploid origin between two major clades. The maternal species appears to be *L. frigida* in the Pinnate clade, which is also the maternal lineage of *L. jaramilloi* (Morales-Briones and Tank 2019a), with which *L. cyanea* also shares a rosette habit (see Taxonomic treatment for details). The paternal lineage appears to be the same as in the allopolyploid and morphologically similar species *L. williamsii*, *L. repens*, and *L. sarmentosa* in the Verticillate clade, where the parental lineage of these species has been shown likely to be extinct (Morales-Briones and Tank 2019a). Interestingly, these three similar species are hybrids of three different major clades (Pinnate, Verticillate, and Tripartite; Morales-Briones et al. 2018a). Given its tripartite leaf and glomerulate inflorescence (see Taxonomic treatment for details), *L. cyanea* also shares characteristics with the Tripartite clade, but we were not able to obtain evidence of this from the nrDNA tree, which can be explained by omission nrDNA copies during bioinformatic processing of the PCR amplicon pools as seen in other species of *Lachemilla* (Morales-Briones and Tank 2019a).

Taxonomic treatment

***Lachemilla rothmaleriana* D.F.Morales-B. & Romol., sp. nov.**

urn:lsid:ipni.org:names:77199640-1

Figs 3–5

Diagnosis. *Lachemilla rothmaleriana* differs from *L. hispidula* (L.M. Perry) Rothm. and *L. nivalis* (Kunth) Rothm. by its stout stems, sericeous-villous indumentum, wide ascending sheaths with trilobate lateral lobes, and a turbinate-campanulate hypanthium.

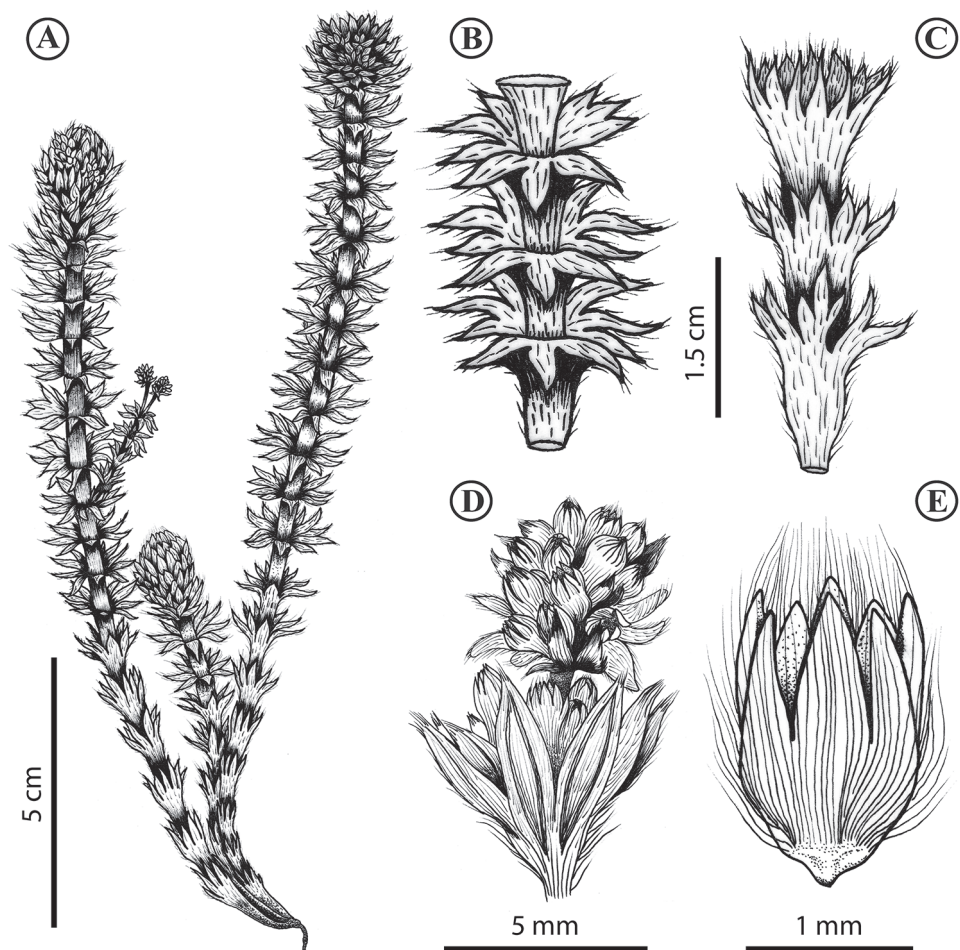


Figure 3. *Lachemilla rothmaleriana*. **A** Habit **B** stem, apical leaves **C** stem, basal leaves **D** flowering branch **E** flower. Illustration by S. Cordero.

Type. COLOMBIA. Boyacá: Duitama. Road to páramo de la Rusia, 22 km from Duitama, before ‘fábrica de arepas Buenos Aires’, 5.92656N, 73.08826W, alt. 3650 m, 24 September 2013, *Morales-Briones D.F. & Uribe-Convers S.* 506. (holotype: ID!, isotypes: ANDES!, QCA!).

Description. Ascendent subshrubs; stems erect to slightly decumbent, up to 22–27 cm long, robust, densely sericeous-villous, branched at apex. Basal stipules usually caducous, if present 5–6 mm long, adnate to the petiole at base, free at apex, entirely membranous, brown. Basal leaves usually caducous, if present 3–6-lobed, 4–6 × 3–6 mm; basal petiole 3–4 mm long. Distal leaves reduced, adnate, and connate to the distal stipules forming verticillate, lobed sheaths; sheath lobes 7–8, ascending to spreading at maturity, lanceolate, one lobe 3–5 lobate, lobes (4) 6–8 × 1–2 (4) mm, (2/3 of the entire sheath length), chartaceous, margin revolute, lower surface appressed

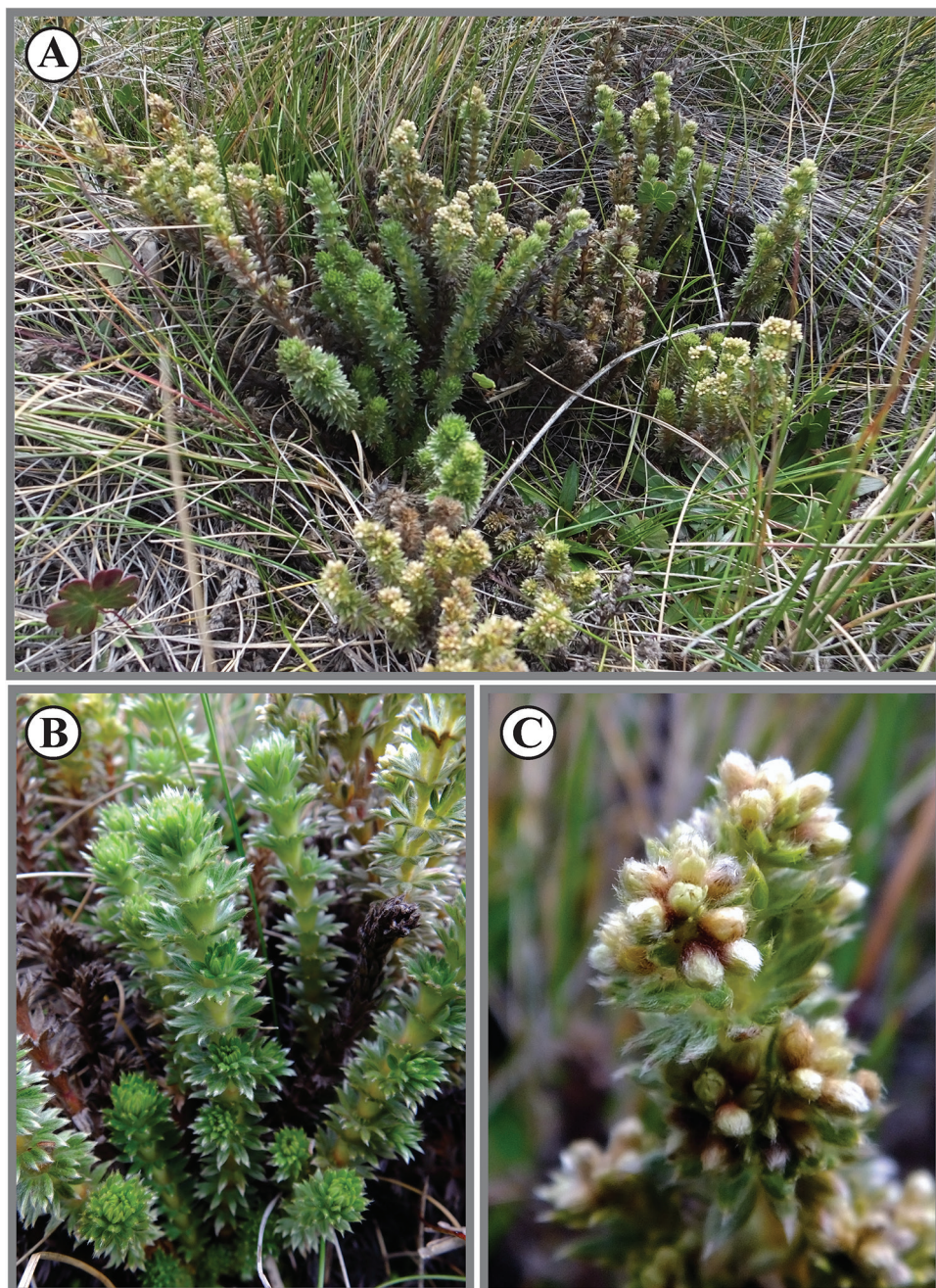


Figure 4. *Lachemilla rothmaleriana*. **A** Habit **B** stems **C** flowering branch.

sericeous-villous to villous, upper surface sericeous-villous to glabrescent. Inflorescences terminal or axilar \pm glomerulate cymes; floral bracts lobed, ascending; 8–10 flowers per inflorescence; pedicels 0.3–0.4 mm long, pilose. Flowers 1.5–2.5 mm long; hypan-



Figure 5. *Lachemilla rothmaleriana*. Isotype collection: Morales-Briones D.F. & Uribe-Convers S. 506. (QCA).

thium turbinate-campanulate, brown-reddish at base, pilose-sericeous outside slightly glabrescent at base, glabrous within; 4 episepals and 4 sepals connivent to \pm straight, abaxially sericeous, adaxially glabrous; episepals narrowly ovate, $0.8\text{--}1 \times 0.2\text{--}0.3$ mm,

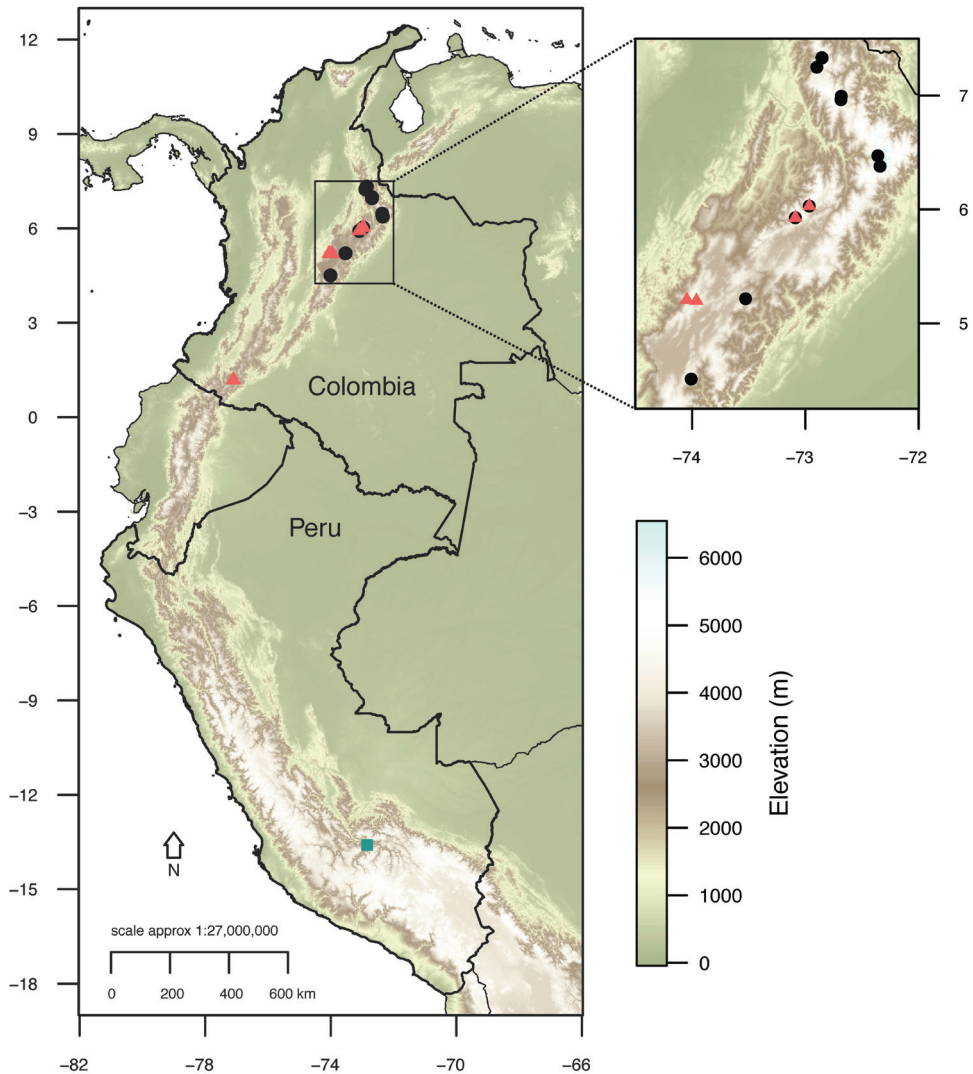


Figure 6. Geographic distribution of *Lachemilla rothmaleriana* (red triangles), *L. argentea* (black circles), and *L. cyanea* (cyan rectangle).

apex acute; sepals ovate, $0.5\text{--}1 \times 0.4\text{--}0.5$ mm, apex \pm acute; stamens 2 adnate to the floral disc; carpels 2 (3), stigma clavate. Two achenes $0.8\text{--}0.9 \times \text{ca. } 0.5$ mm, subovoid.

Distribution and ecology. *Lachemilla rothmaleriana* has a scattered distribution in the northcentral region of the Cordillera Oriental and in the southern part of the Cordillera Central of the Colombian Andes, between 3250 and 3768 m (Fig. 6). This species is mainly found in páramos dominated by bunchgrasses (*Agrostis*, *Calamagrostis*, *Chusquea*) and lives in sympatry with *L. hipidula*, *L. nivalis*, and *L. purdiei*. Flowering and fruiting collections dated from the months of January, May, September, and December.

Etymology. The specific epithet honors Prof. Dr. Werner Rothmaler (1908–1962), a German botanist who studied *Lachemilla* in detail and described over 20 species of this genus.

Conservation status. *Lachemilla rothmaleriana* is known only from the three localities that are zones impacted by human activities, including conversion to agriculture. Following the IUCN (2017) guidelines, based on the reduced geographic distribution and altered land use at the type locality, this species should be categorized as vulnerable (VU).

Additional specimens examined. COLOMBIA. Putumayo: Comisaria del Putumayo, Alta cuenca del río Putumayo, filo de Cordillera entre El Encano y Sibundoy, páramo de San Antonio del Bordoncillo, 1.18333N, 77.1000W, alt. 3250 m, 4 January 1941, *Cuatrecasas J. 11761* (COL, F, JE frag.). **Santander:** Páramo del Consuelo, Belén, Vereda de San José, 18 km from Belén on road to Encino, 6.02920N, 72.96523W, alt. 3768 m, 23 September, 2013, *Morales-Briones D.F. & Uribe-Convers S. 492* (ANDES, ID, QCA).

Notes. *Lachemilla rothmaleriana* resembles *L. hispidula* and *L. nivalis* by its habit and erect stems with reduced leaves that fuse with the stipules to form verticillate sheaths, but differs by having trilobate lateral lobes. Additionally, *L. hispidula* has an overall hispid pubescence, while *L. rothmaleriana* has a characteristic sericeous-villous indumentum. Moreover, *L. rothmaleriana* has a turbinate-campanulate hypanthium with pilose-sericeous pubescence, while *L. hispidula* has a globose-campanulate hypanthium with pilose-hirsute pubescence. *Lachemilla nivalis* has a hypanthium with similar indumentum but its shape is only slightly campanulate. In the shape of sheath lobes, *L. rothmaleriana* somewhat resembles *L. galioides* (Benth.) Rothm., but the latter has slender stems, broader sheath lobes, and villous-hispid indumentum.

***Lachemilla argentea* D.F.Morales-B. & Romol., sp. nov.**

urn:lsid:ipni.org:names:77199641-1

Figs 7–9

Diagnosis. *Lachemilla argentea* differs from *L. holmgrenii* Rothm. and *L. adscendens* (Rothm.) Rothm. by its herbaceous habit with decumbent branches, conspicuous basal reniform tripartite leaves with an adaxial silvery villous pubescence, and a turbinate to urceolate hypanthium with pilose-sericeous pubescence.

Type. COLOMBIA. Bogotá, Distrito Capital: Páramo de Cruz Verde. Path to Laguna El Verjón, 4.56102N, 74.02172W, alt. 3495 m, 26 September 2013, *Morales-Briones D.F. & Uribe-Convers S. 523* (holotype: ID!, isotypes: ANDES!, QCA!).

Description. Decumbent herbs; branches decumbent up to 12 cm long, sericeous-villous. Basal stipules 5–10 mm long, adnate to the petiole, sparsely villous, membranous, brown at base, free at apex. Basal leaves tri-parted, blade reniform in outline, 6–7 (–10) × 7.5–10 (–1.3) mm, 3 lobes, chartaceous, slightly plicate, lobes unequally obovate-rhomboid, margin dentate-incised, teeth 3–6 on each of the lobes, lower sur-

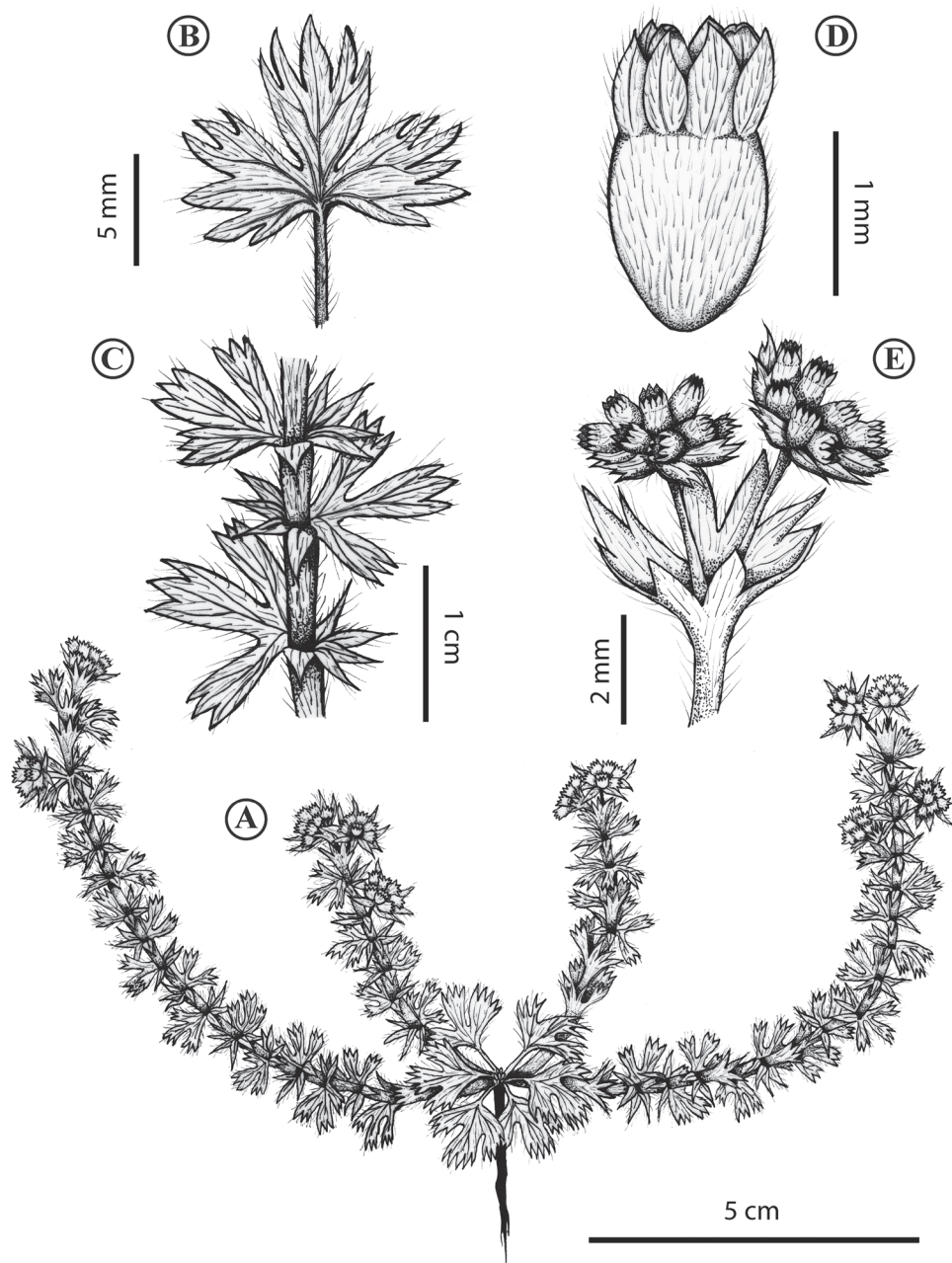


Figure 7. *Lchemilla argentea*. **A** Habit **B** basal leaf **C** stem, apical leaves **D** flower **E** flowering branch. Illustration by C. Rodríguez.

face sparsely sericeous-villous, upper surface villous; basal petiole 5–12 mm long. Distal stipules and distal leaves reduced adnate and connate, forming verticillate lobed sheaths; sheath lobes 6–10 ascending or slightly spreading; lobes $4\text{--}7 \times 1.5\text{--}3$ mm,

lanceolate, entire or trilobed, decreasing in size. Inflorescences axilar or terminal glomerulate cymes, flowers aggregate at the distal part. Floral bracts 2–4 mm long, free, incised, and ascending; 3–7 flowers per inflorescence; pedicels 0.5–1 mm long, slightly pilose. Flowers 2–2.5 mm long; hypanthium turbinate to urceolate, green or reddish, pilose-sericeous outside, glabrous within; 4 episepals and 4 sepals green or slightly reddish, straight, abaxially pilose-sericeous, adaxially glabrous; episepals triangular, 0.7–0.8 × 0.4–0.5 mm, apex acute; sepals triangular-ovate, 0.75–0.85 × 0.5–0.6 mm, apex acute; stamens 2 adnate to the floral disc; carpels 2–3, stigma clavate. Two achenes, ca. 1–1.5 × 0.6–0.8 mm, globose-ovoid.

Additional specimens examined. **COLOMBIA.** **Bogotá, Distrito Capital:** Páramo de Cruz Verde, Bogotá-Choachí road, km 11.2, alt. 3257 m, 1 May 1972, *Cleef A. 3330A* (COL). **Bogotá, Distrito Capital:** Páramo de Cruz Verde, path to Laguna El Verjón, 4.56102N, 74.02172W, alt. 3495 m, 26 September 2013, *Morales-Briones D.F. & Uribe-Convers S. 522* (ANDES, ID, QCA). **Boyacá:** Güicán, Sierra Nevada del Cocuy, road to the small house, in 'Lagunilla' area, towards to Pulpito del Diablo, 6.37906N, 72.33995W, alt. 3950 m, 18 September 2013, *Morales-Briones D.F. et al. 476* (ANDES, ID, QCA). **Boyacá:** Duitama, road to Páramo de la Rusia, 22 km from Duitama, before 'fábrica de arepas Buenos Aires', 5.92656N, 73.08826W, alt. 3650 m, 24 September 2013, *Morales-Briones D.F. & Uribe-Convers S. 507* (ANDES, ID, QCA). **Boyacá:** Belén, Vereda de San José, Páramo del Consuelo, 18 km from Belén, on the way to Encino, 6.02920N, 72.96523W, alt. 3768 m, 23 September 2013, *Morales-Briones D.F. & Uribe-Convers S. 499* (ANDES, ID, QCA). **Boyacá:** Páramo de Pisba, Socha-La Punta road, km 72, near to M.O.P campsite. El Cadillal, stony slope, alt. 3500 m, 8 June 1972, *Cleef A. 4235* (COL). **Boyacá:** Páramo NW of Belén, Vereda S. José de la Montaña, Alto de las Cruces and surroundings, alt. 3790 m, 24 February 1972, *Cleef A. 1756* (COL). **Boyacá:** Páramo de Pisva, Socha-La Punta road, km 61, 5.6 km east of Los Pinos, Alto de Granados, alt. 3635 m, 12 June 1972, *Cleef A. 445813* (COL). **Boyacá:** Páramo de Pisva, flank SW of Morros de S. Gabriel, 2 km SW of Laguna Batanera, alt. 3670 m, 18 June 1972, *Cleef A. 4702A* (COL). **Cundinamarca:** Villa Pinzón, Páramo de Guachenque. Entrance to the Laguna del Valle and surroundings of Laguna del Mapa, 5.21641N, 73.52675W, alt. 3346 m, 25 September 2013, *Morales-Briones D.F. & Uribe-Convers S. 514* (ANDES, ID, QCA). **Cundinamarca:** Páramo de Palacio, 18 km from the road, alt. 3485 m, 16 December 1971, *Cleef A. 327* (COL). **Santander:** Vetás, road to the Laguna Pajaritos, at the entrance of private property, 7.33349N, 72.85373W, alt. 3539 m, 14 September 2013, *Morales-Briones D.F. et al. 437* (ANDES, ID, QCA). **Santander:** Vetás, road to Laguna Pajaritos, 7.33086N, 72.85106W, alt. 3585 m, 14 September 2013 *Morales-Briones et al. D.F. 440* (ANDES, ID, QCA). **Santander:** Páramo de Almorzadero, road Presidente-Cerrito, km 98, 6.99470N, 72.68187W, alt. 3567 m, 16 September 2013, *Morales-Briones D.F. et al. 458* (ANDES, ID, QCA). **Santander:** Páramo de Almorzadero, road Presidente-Cerrito, km 98, 6.96333N, 72.68488W, alt. 3801 m, 16 September 2013, *Morales-Briones D.F. & Uribe-Convers S. 459* (ANDES, ID, QCA).

Mixed specimens examined. the following specimens are collections with two different species under the same number, one (a) correspond to *L. argentea*. **Boyacá:**

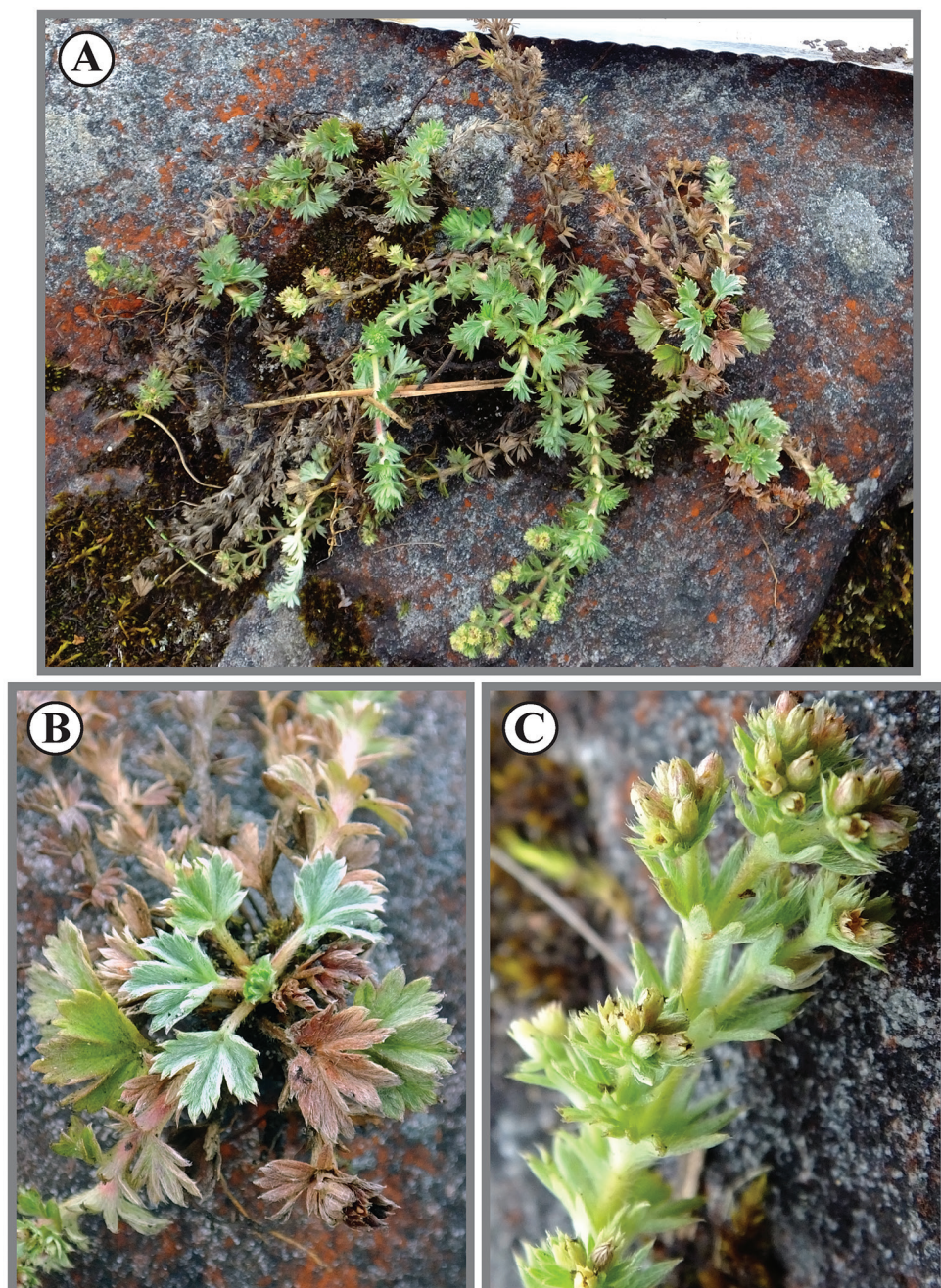


Figure 8. *Lachemilla argentea*. **A** Habit **B** basal leaves **C** flowering branch.

Páramo de Pisva, Alto de Granados, 5 km E of Los Pinos, alt. 3735m, 15 June 1972, Cleef A. 4593A (a) (COL). **Boyacá:** Güicán Sierra Nevada del Cocuy, after Cabañas Kanwara, 17.7 km from 'water plant', Lomas Las Pajas, 6.47093N, 72.35934W,

alt. 4105 m, 17 September 2013, *Morales-Briones D.F. & Uribe-Convers S.* 473 (a) (ANDES, ID, QCA). **Santander:** Páramo de Santurbán, Berlín, 7 km from Vetás, 7.24935N, 72.89784W, alt. 3567 m, 13 September 2013, *Morales-Briones D.F. et al.* 431 (a) (ANDES, ID, QCA).

Deviating specimens examined. The following specimens have similar habit, leaf shape, and pubescence to *L. argentea*, but they only differ in having glabrous flowers. These specimens may represent only a variety of *L. argentea*, but they are maintained here as uncertain taxa until more material is available or can be included in phylogenetic analyses. **Boyacá:** Páramo NW of Belén, Quebrada Minas. Hoya CLLA, Slopes N of Valle Lajas, alt. 3835m, 2 March 1973, *Cleef A. 2119A* (COL). **Boyacá:** Páramo de Pisva, Road Socha-La Punta, km 61.5, 6 km E from Los Pinos Alto de Granados, alt. 3630 m, 14 June 1972, *Cleef A. 4545* (COL). **Cundinamarca:** Páramo de Palacio aprox. 1 km E from ‘la mina de cal’, alt. 3853 m, 19 May 1972, *Cleef A. 3853A* (COL). **Quindío/Tolima:** Paramillo of Quindío and Páramo de Tolima. 13 km from Valle de Cocora. 4.64433N, 75.43060W, alt. 3645 m, 4 October 2013, *Morales-Briones D.F. et al.* 543 (ANDES, ID, QCA). **Santander:** Vetás, road to Laguna Pajaritos, 7.33086N, 72.85106W, alt. 3585 m, 14 September 2013, *Morales-Briones D.F. et al.* 439 (ANDES, ID, QCA).

Distribution and ecology. *Lachemilla argentea* is distributed in the central northern (primarily) regions of the Cordillera Oriental between 3275 and 3735 m (Fig. 6). This species occurs in humid and very humid páramos dominated by grasses, shrubs, and dwarf shrubs. *Lachemilla argentea* can be found living in sympatry with multiple species of *Lachemilla*, including *L. aphanoides*, *L. hispidula*, *L. nivalis*, *L. mandoniana* (Wedd.) Rothm., *L. purdiei*, and *L. vulcanica* (Schltdl. & Cham.) Rydb. Flowering and fruiting collections dated from the months of February, May, June, and September.

Etymology. The specific epithet refers to the silvery aspect of the basal leaves.

Conservation status. *Lachemilla argentea* is a common element throughout its distributional range, and occurs in several well-conserved areas. Following the IUCN (2017) guidelines, we consider this species is not at risk and should be categorized as least concern (LC). Nonetheless, the rapid deterioration and conversion to agriculture of proximate areas where *L. argentea* occurs may put this species at some threat in the near future.

Notes. *Lachemilla argentea* resembles *L. holmgrenii* and *L. adscendens* by having basal tripartite leaves and stem leaves fused to the stipules forming verticillate sheaths with one tripartite lobe that is larger than the remaining lobes, but differs in having an herbaceous habit with decumbent branches, while the other two species are subshrubs with suberect to ascending branches. Furthermore, *L. argentea* has conspicuous basal reniform tripartite leaves with an adaxial silvery villous pubescence, while *L. holmgrenii* and *L. adscendens* have smaller hirsute leaves. These species also vary in the number of sheath lobes; *L. argentea* has 6–10 ascending or slightly spreading lobes, while *L. holmgrenii* and *L. adscendens* have 5–7 loosely ascending to reflexed lobes, and eight erecto-patent lobes, respectively. By having conspicuous basal leaves, *L. argentea* also resembles *L. sprucei*, but the latter is a subshrub with suberect stems and coriaceous 5-parted basal leaves, in addition to distinct 3-parted distal leaves.



Figure 9. *Lchemilla argentea*. Isotype collection: Morales-Briones D.F. & Uribe-Convers S. 523 (QCA).

Key to *Lachemilla rothmaleriana*, *L. argentea*, and similar species of the Verticillate clade from Colombia

Notes. Includes species with stem leaves fused to the stipules forming verticillate sheaths (sect. *Nivales* and sect. *Subnivales*; *sensu* Rothmaler 1935a). Accepted taxa and synonymy follows Morales-Briones et al. (2018a). Adapted in part from Perry (1929) and Romoleroux (2004).

- 1 Subshrubs with erect or decumbent stems; basal leaves caducous or sessile when present; stem leaves reduced, with the adnate stipule forming verticillate sheaths along the entire stem **2**
- Herbs with procumbent or decumbent stems, or subshrubs with suberect or \pm decumbent stems; basal leaves petiolate; lower stem leaves subequal to or often longer than the stipules, 3-parted or 3-lobed, uppermost stem leaves reduced, with the adnate stipule forming verticillate sheaths **8**
- 2 Outer surface of sheath lobes glabrous or puberulent; lobes 4–6 **3**
- Outer surface of sheath lobes conspicuously pubescent; lobes 4–15 **4**
- 3 Outer surface of sheath lobes glabrous and reticulate, margins strongly revolute .
..... ***L. equisetiformis***
- Outer surface of sheath lobes hispidulous and not reticulate, margins revolute at apex ***L. ericoides***
- 4 Plants pilose, villous or sericeous; sheath lobes laxly ascending to erect, basal leaves mainly caducous **5**
- Plants hispid, hirsute or villous; sheath lobes widely spreading to abruptly reflexed; basal leaves usually present (except in *L. verticillata*) **6**
- 5 Stems sparsely villous, pilose to glabrescent, or sericeous; sheath lobes 10–15, linear to linear-lanceolate, all lobes entire ***L. nivalis***
- Stems densely sericeous-villous; sheath lobes 7–8, lanceolate, one lobe 3–5 lobate ***L. rothmaleriana***
- 6 Sheath lobes 7–8 (10); stems villous; sepals and episepals divergent and equal in length; hypanthium villous ***L. verticillata***
- Sheath lobes 9–13; stems hispid or hirsute; sepals and episepals connivent, episepals usually a little shorter than the sepals **7**
- 7 Plant copiously hirsute; sheath lobes reflexed; hypanthium glabrous ... ***L. galioides***
- Plant sparsely hispid; sheath lobes spreading; hypanthium glabrous or pubescent
..... ***L. hispidula***
- 8 Caespitose herbs; stems procumbent or slightly decumbent, multiple branched and rooting **9**
- Herbs or subshrubs; stems suberect or \pm decumbent, not branched and not rooting **10**
- 9 Flowers ca. 2–2.5 mm long, hypanthium campanulate, appressed villous, carpels 5–10; stigma clavate ***L. holosericea***
- Flowers ca. 3.5 mm long, hypanthium globose-urceolate, sericeous-villous, carpels 5; stigma subclavate ***L. purdiei***

- 10 Basal leaves 5-parted, coriaceous; flowers ca. 2.5–3.5 long; carpels 5–6... *L. sprucei*
- Basal leaves 3-parted, not coriaceous; flowers ca. 2–2.5 long; carpels 2–4..... **11**
- 11 Herbs, sericeous-villous; stems decumbent; sheath lobes 6–10, ascending or slightly spreading *L. argentea*
- Subshrubs, villous or hirsute; stems suberect or ascending, sheath lobes 5–8, loosely ascending to reflex **12**
- 12 Stems suberect; sheath lobes 5–7; hypanthium campanulate-globose; carpels 2–3 *L. holmgrenii*
- Stems ascending; sheath lobes 8; hypanthium globose-urceolate; carpels 3–4.....
..... *L. adscendens*

***Lachemilla cyanea* D.F.Morales-B. & Romol., sp. nov.**

urn:lsid:ipni.org:names:77199642-1

Figs 10–12

Diagnosis. *Lachemilla cyanea* differs from *L. ranunculoides* (L.M. Perry) Rothm. and *L. williamsii* (L.M. Perry) Rothm by its hirsute pubescence, reniform basal leaves that have a blue-green color, and turbinate-campanulate hypanthium.

Type. PERU. Apurímac: Abancay Province, road Abancay - Cuzco, 23 km from Abancay, 13.59722S, 72.84083W, alt. 3423 m, 25 June 2012, *Morales-Briones D.F. & Uribe-Convers S. 246*, (holotype: ID!, isotypes: HAO!, QCA!).

Description. Rosette herbs up to 10 cm long, branches decumbent, sparsely hirsute. Basal stipules 10 mm long, adnate to the petiole, sparsely hirsute, membranaceous, brown at base, free at apex. Basal leaves tri-parted, blade reniform in outline, 17–20 × 25–26 mm, 3 lobes, chartaceous, slightly plicate, lobes unequally obovate-rhomboid, lateral lobes divided the length 1/2 of the blade, margin dentate-incised, teeth 8–10 on each of the lobes, lower and upper surface sparsely hirsute-villous; basal petiole 12–20 mm long. Distal stipules 7–8 mm long, connate and adnate to the petiole at base, free and incised at apex, leaf-like in texture. Distal leaves tri-parted, 8–10 × 8–12 mm, lobes obovate-rhomboid, decreasing in size; distal petiole 1–2.5 mm long. Inflorescences axilar or terminal glomerulate cymes, flowers aggregate at the distal part. Floral bracts 1–2 mm long, free, incised, and ascending to slightly spreading; 2–6 flowers per inflorescence; pedicels 0.6–1 mm long, sericeous. Flowers 2–2.5 mm long; hypanthium turbinate-campanulate, green, glabrous outside and within; 4 episepals and sepals green to reddish at apex, straight, abaxially and adaxially glabrous; episepals triangular, 0.7–0.8 × 0.3–0.4 mm, apex acute; sepals triangular-ovate, 0.7–0.8 × 0.5 mm, apex acute; stamens 2 adnate to the floral disc; carpels 2, stigma clavate. Two achenes, ca. 1 × 0.7–0.8 mm, globose-ovoid.

Distribution and ecology. *Lachemilla cyanea* is only known from the Province of Abancay in the Department of Apurímac at ca. 3420 m in southern Peru (Fig. 6). This species occurs in the transition zone between the montane forest and the high-elevation grassland dominated by dwarf shrubs and herbs. This species lives in sympatry with *L. aphanoides* and *L. fulvescens*. It was collected in flower and fruit in late June.

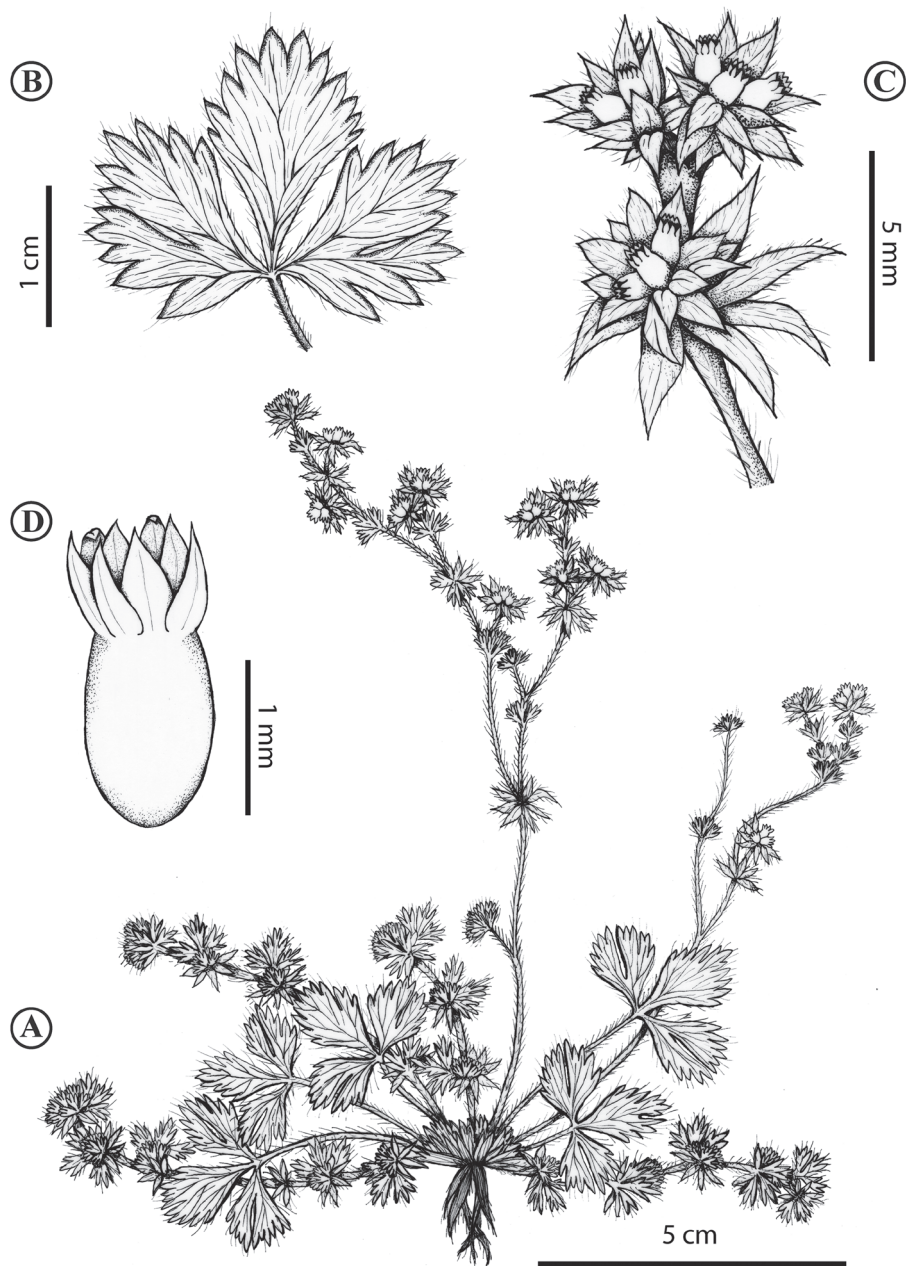


Figure 10. *Lachemilla cyanea*. **A** Habit **B** basal leaf **C** flowering branch **D** flower. Illustration by C. Rodríguez.

Etymology. The specific epithet refers to the blue-green color of the leaves.

Conservation status. *Lachemilla cyanea* is only known from the type locality in a zone severely impacted by human activities, including conversion to agriculture. Fol-

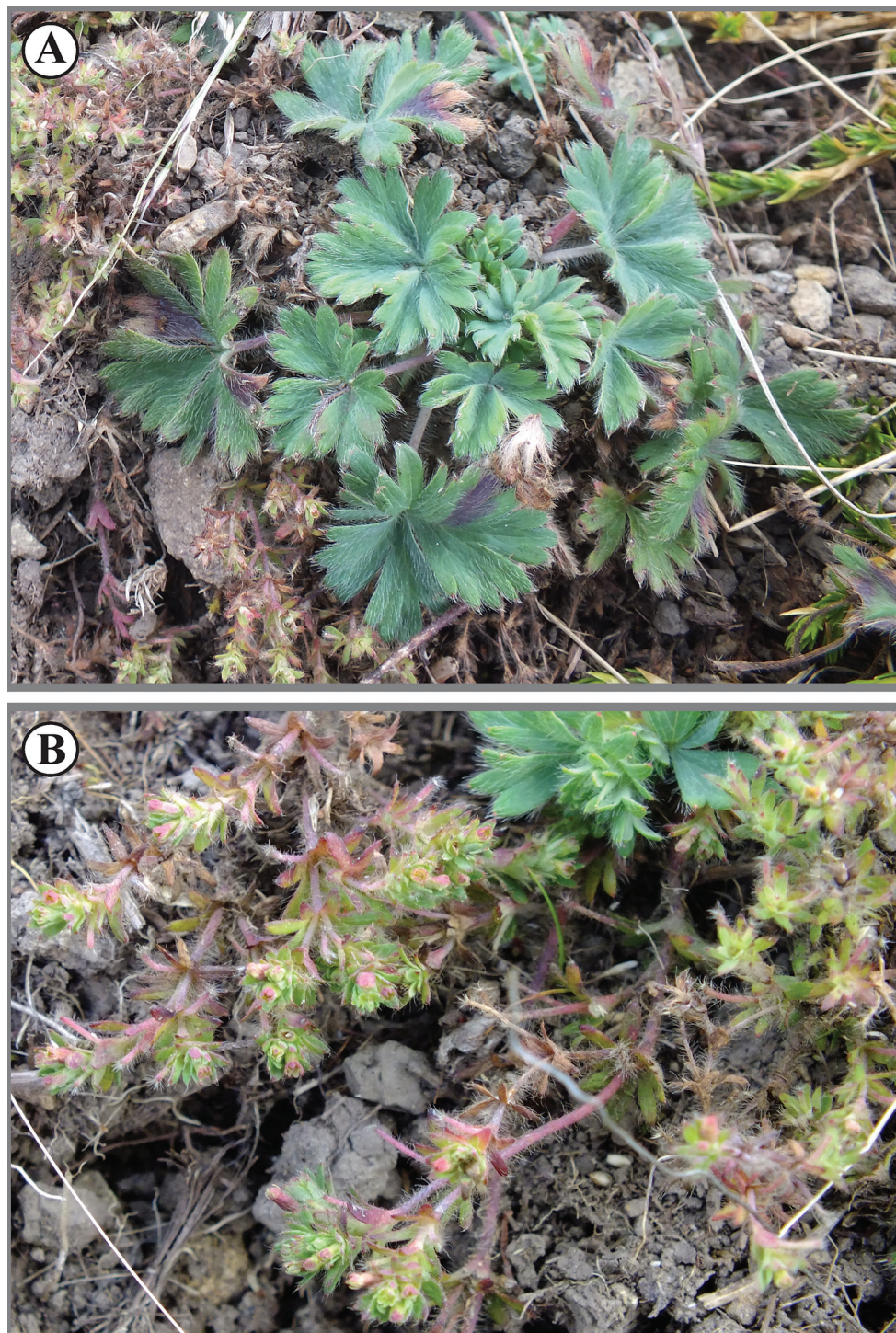


Figure 11. *Lachemilla cyanea*. **A** Habit **B** flowering branch.



Figure 12. *Lachenilla cyanea*. Isotype collection: Morales-Briones D.F. & Uribe-Convers S. 246 (QCA).

lowing the IUCN (2017) guidelines, based on the reduced geographic distribution and altered land use at the type locality, this species should be categorized as endangered (EN), at least until other populations are discovered.

Notes. *Lachemilla cyanea* resembles *L. ranunculoides* in habit and glabrous flower, but differs in the reniform shape of the basal leaves in contrast to the orbicular-ovate shape of the latter. Moreover, *L. cyanea* has a turbinate-campanulate hypanthium while *L. ranunculoides* has an oblong-ventricose hypanthium. *Lachemilla cyanea* also resembles *L. aphanoides* in the tripartite basal leaves and glomerulate inflorescence, but differs in the rosette habit and decumbent branches, in contrast to the erect stems of *L. aphanoides*. *Lachemilla cyanea* is also similar to *L. williamsii* in habit, but the former has an overall hirsute pubescence and glabrous flowers with strictly two stamens, while the latter has a general villous pubescence, and villous flowers with up to four stamens (a characteristic only known in *L. williamsii*).

Key to *Lachemilla cyanea* and similar species from the Central Andes

Notes. Includes species with a general prostrate habit, tripartite basal leaves, and mainly glomerulate inflorescences (series *Aphanoides*, subseries 2; *sensu* Perry 1929). Accepted taxa and synonymy follows Morales-Briones et al. (2018a). Adapted from Perry (1929).

- 1 Herbs with creeping stems, mat-forming; lateral segments of the leaves entire; inflorescences loosely dichotomous; stipules entirely membranaceous.....***L. rupestris***
- Herbs with prostrate or loosely decumbent stems, villous or hirsute; lateral segments of the leaves variously lobed; inflorescences glomerulate cymes; stipules herbaceous at least at apex.....**2**
- 2 Basal leaves lobes acute; flowers ca. 3 mm long, hirsute-villous to sericeous; stamens 2–4.....***L. williamsii***
- Basal leaves lobes obtuse; flowers ca. 2–2.5 mm long, glabrous or with scattering hairs on the hypanthium lobes; stamens 2.....**3**
- 3 Plants densely sericeous-villous; sepals oblong-ovate.....***L. grisebachiana***
- Plants hirsute or glabrate; sepals ovate.....**4**
- 4 Basal leaves subreniform; cauline leaves mainly subsessile; episepals reduced or absent; carpels 1–2.....***L. frigida***
- Basal leaves orbicular or reniform; cauline leaves mainly petiolate; episepals conspicuous, carpels 2–4.....**5**
- 5 Basal leaf blade reniform; hypanthium turbinate-campanulate; carpels 2.....***L. cyanea***
- Basal leaf blade orbicular; hypanthium oblong-ventricose; carpels 2–4.....***L. ranunculoides***

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Appendix I

Species and vouchers used in the phylogenetic analyses. Arranged by *species name* and authority, DNA number, and *collector and number* (herbarium code).

Outgroup: *Alchemilla johnstonii* Oliv.: 2015_358, B. Gehrke 364 (UZH). *Alchemilla mollis* (Buser) Rothm.: 2012_228_US, D.F. Morales-Briones 687 (ID). *Aphanes cotopaxiensis* Romol. & Frost-Ols.: 2013_004_EC, D.F. Morales-Briones 276 (ID). *Farinopsis salesoviana* (Stephan) Chrtek & Soják: 2016_580, B. Bartholomew 8364 (MO). **Ingroup:** *Lachemilla adscendens* (Rothm.) Rothm.: 2013_445_CO, D.F. Morales-Briones & S. Uribe-Convers 429A (ID). *Lachemilla andina* (L.M. Perry) Rothm.: 2012_249_PE, D.F. Morales-Briones & S. Uribe-Convers 218 (ID); 2012_379_EC, D.F. Morales-Briones et al. 122 (QCA). *Lachemilla aphanoides* (Mutis ex L. f.) Rothm.: 2012_246_PE, D.F. Morales-Briones & S. Uribe-Convers 215 (ID); 2012_396_EC, D.F. Morales-Briones et al. 115 (QCA); 2013_446_CO, D.F. Morales-Briones & S. Uribe-Convers 430 (ID); 2014_541_CO, D.F. Morales-Briones & S. Uribe-Convers 550 (ID). *Lachemilla argentea* D.F. Morales-B. & Romol.: 2013_447_CO, D.F. Morales-Briones et al. 431 (ID); 2013_475_CO, D.F. Morales-Briones et al. 459 (ID); 2014_507_CO, D.F. Morales-Briones & S. Uribe-Convers 514 (ID); 2014_516_CO, D.F. Morales-Briones & S. Uribe-Convers 523 (ID). *Lachemilla barbata* (C. Presl) Rothm.: 2012_260_PE, D.F. Morales-Briones & S. Uribe-Convers 229 (ID). *Lachemilla bipinnatifida* (L.M. Perry) Rothm.: 2013_428_BO, D.F. Morales-Briones et al. 326 (ID). *Lachemilla cyanea* D.F. Morales-B. & Romol.: 2012_277_PE, D.F. Morales-Briones & S. Uribe-Convers 246 (ID). *Lachemilla diplophylla* (Diels) Rothm.: 2012_229_PE, D.F. Morales-Briones & S. Uribe-Convers 198 (ID). *Lachemilla equisetiformis* (Trevir.) Rothm.: 2012_108_VE, A.J.P. Martin 740 (QCA). *Lachemilla erodiifolia* (Wedd.) Rothm.: 2012_244_PE, D.F. Morales-Briones & S. Uribe-Convers 213 (ID). *Lachemilla frigida* (Wedd.) Rothm.: 2012_300_PE, D.F. Morales-Briones & S. Uribe-Convers 269 (ID). *Lachemilla fulvescens* (L.M. Perry) Rothm.: 2014_551_CO, D.F. Morales-Briones & S. Uribe-Convers 560 (ID). *Lachemilla galioides* (Benth.) Rothm.: 2012_348_EC, K. Romoleroux et al. 4403 (QCA). *Lachemilla hirta* (L.M. Perry) Rothm.: 2012_317_EC, K. Romoleroux et al. 4588 (QCA); 2012_343_EC, K. Romoleroux et al. 4389 (QCA). *Lachemilla hispidula* (L.M. Perry) Rothm.: 2012_310_EC, K. Romoleroux et al. 4470 (QCA). *Lachemilla holmgrenii* Rothm.: 2012_347_EC, K. Romoleroux et al. 4397 (QCA). *Lachemilla holosericea* (L.M. Perry) Rothm.: 2012_395_EC, D.F. Morales-Briones & K. Romoleroux 161 (QCA); 2014_479_CO, D.F. Morales-Briones et al. 485 (ID). *Lachemilla jamesonii* (L.M. Perry) Rothm.: 2012_350_EC, K. Romoleroux et al. 4387 (QCA). *Lachemilla jaramilloi* Romol. & D.F. Morales-B.: 2012_006_EC, D.F. Morales-Briones & S. Uribe-Convers 193 (ID); 2012_371_EC, D.F. Morales-Briones et al. 115 (QCA). *Lachemilla lechleriana* (Griseb.) Rothm.: 2012_271_PE, D.F. Morales-Briones & S. Uribe-Convers 240 (ID). *Lachemilla llanganatensis* Romol.: 2012_363_EC, D.F. Morales-Briones et al. 105 (QCA). *Lachemilla mandoniana* (Wedd.) Rothm.:

2012_370_EC, D.F. Morales-Briones et al. 114 (QCA). ***Lachemilla mexiquense*** D.F. Morales-B.: 2015_233_MX, D.F. Morales-Briones & P. Tenorio-Lezama 683 (ID). ***Lachemilla moritziana*** Dammer: 2013_443_CO, D.F. Morales-Briones & S. Uribe-Convers 427 (ID). ***Lachemilla nivalis*** (Kunth) Rothm.: 2012_349_EC, D.F. Morales-Briones & M.F. Latorre-Barragán 11 (QCA). ***Lachemilla orbiculata*** (Ruiz & Pav.) Rydb.: 2012_377_EC, D.F. Morales-Briones et al. 121 (QCA). ***Lachemilla pectinata*** (Kunth) Rothm.: 2012_326_EC, K. Romoleroux et al. 4706 (QCA). ***Lachemilla perryana*** (Rothm.) Rothm.: 2012_380_EC, D.F. Morales-Briones et al. 123 (QCA). ***Lachemilla pinnata*** (Ruiz & Pav.) Rothm.: 2012_251_PE, D.F. Morales-Briones & S. Uribe-Convers 220 (ID). ***Lachemilla polylepis*** (Wedd.) Rothm.: 2012_359_CO, P. Sklenář FAA652 (PRC). ***Lachemilla pringlei*** Rydb.: 2015_150_MX, D.F. Morales-Briones & P. Tenorio-Lezama 595 (ID). ***Lachemilla procumbens*** (Rose) Rydb.: 2015_200_MX, D.F. Morales-Briones & P. Tenorio-Lezama 648 (ID). ***Lachemilla pseudovenusta*** (Rothm.) Rothm.: 2012_275_PE, D.F. Morales-Briones & S. Uribe-Convers 244 (ID). ***Lachemilla purdiei*** (L.M. Perry) Rothm.: 2014_501_CO, D.F. Morales-Briones & S. Uribe-Convers 508 (ID). ***Lachemilla ranunculoides*** (L.M. Perry) Rothm.: 2012_240_PE, D.F. Morales-Briones & S. Uribe-Convers 209 (ID). ***Lachemilla repens*** (C. Presl) Rothm.: 2012_263_PE, D.F. Morales-Briones & S. Uribe-Convers 232 (ID). ***Lachemilla rothmaleriana*** D.F. Morales-B. & Romol.: 2014_486_CO, D.F. Morales-Briones & S. Uribe-Convers 492 (ID); 2014_499_CO, D.F. Morales-Briones & S. Uribe-Convers 506 (ID). ***Lachemilla rupestris*** (Kunth) Rothm.: 2012_394_EC, D.F. Morales-Briones et al. 157 (QCA). ***Lachemilla sarmentosa*** (L.M. Perry) Rothm.: 2013_396_BO, D.F. Morales-Briones et al. 292 (ID); 2013_413_BO, D.F. Morales-Briones et al. 309 (ID). ***Lachemilla siboldiifolia*** (Kunth) Rydb.: 2015_154_MX, D.F. Morales-Briones & P. Tenorio-Lezama 599 (ID). ***Lachemilla sprucei*** (L.M. Perry) Rothm.: 2012_340_EC, K. Romoleroux et al. 4474 (QCA). ***Lachemilla standleyi*** (L.M. Perry) Rothm.: 2016_614_CR, K. Romoleroux et al. 5023 (QCA). ***Lachemilla steinbachii*** Rothm.: 2013_415_BO, D.F. Morales-Briones et al. 311 (ID). ***Lachemilla talamanquensis*** Romol. & D.F. Morales-B.: 2012_334_CR, K. Romoleroux et al. 5008 (QCA). ***Lachemilla tanacetifolia*** Rothm.: 2012_331_EC, K. Romoleroux et al. 4396 (QCA). ***Lachemilla uniflora*** Maguire: 2012_362_EC, D.F. Morales-Briones et al. 75 (QCA); 2012_385_EC, D.F. Morales-Briones et al. 130 (QCA). ***Lachemilla velutina*** (S. Watson) Rydb.: 2015_162_MX, D.F. Morales-Briones & P. Tenorio-Lezama 607 (ID). ***Lachemilla venusta*** (Schltdl. & Cham.) Rydb.: 2015_157_MX, D.F. Morales-Briones & P. Tenorio-Lezama 602 (ID). ***Lachemilla verticillata*** (Fielding & Gardner) Rothm.: 2012_339_CR, K. Romoleroux et al. 5007 (QCA). ***Lachemilla vulcanica*** (Schltdl. & Cham.) Rydb.: 2012_250_PE, D.F. Morales-Briones & S. Uribe-Convers 219 (ID); 2015_171_MX, D.F. Morales-Briones & P. Tenorio-Lezama 617 (ID). ***Lachemilla wiliamsii*** (L.M. Perry) Rothm.: 2013_402_BO, D.F. Morales-Briones et al. 298 (ID).

Recircumscription of *Bredia* and resurrection of *Tashiroea* (Sonerileae, Melastomataceae) with description of a new species *T. villosa*

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Abstract

Bredia (Melastomataceae) is an Asian genus that extends from central and southern mainland China to Taiwan and the Ryukyu islands. Molecular phylogenetic analyses reveal that the type of *Bredia* is nested in a clade of 20 species, while *Tashiroea*, a genus previously synonymized in *Bredia*, falls in another distantly related clade of 10 species. Our morphological survey shows that the two clades can be distinguished by several diagnostic features including leaf indumentum, texture, leaf surface sculpture under SEM, presence/absence of yellowish uniseriate trichomes, and capsule morphology. Based on molecular and morphological evidence, *Bredia* is recircumscribed and *Tashiroea* is resurrected. Description and a list of species are provided for the two genera with the description of a new species, *T. villosa*.

Keywords

Bredia, *Tashiroea*, Sonerileae, Melastomataceae, morphology, taxonomy

Introduction

Bredia Blume (Sonerileae, Melastomataceae) was originally described based on *B. hirsuta* Blume (Blume 1849), a species in Taiwan and the Ryukyu islands. Later, Ito and Matsumura (1899) established another genus, *Tashiroea* Matsumura, to accommodate two new species, *T. yaeyamensis* Matsum. and *T. okinawensis* Matsum., also discovered

in the Ryukyus. Diels (1924, 1932) recognized both genera. He added one Chinese species to *Tashiroea* and expanded *Bredia* by describing new species and transferring species from *Blastus* Lour., *Otanthera* Blume and *Fordiophyton* Stapf into *Bredia*. Li (1944) followed Diels's concept of *Bredia* but considered *Tashiroea* to be included within the limits of *Bredia*. He therefore synonymized *Tashiroea*, accommodating its three species within *Bredia* section *Tashiroea* (Li 1944). With additional descriptions of new species and transfers of other species (Hooker 1871; Cogniaux 1891; Diels 1924, 1932; Ohwi 1936; Li 1944, 1945; Lauener 1972; Chen 1984a; Yeh et al. 2008; Zhao et al. 2017; Zhou et al. 2018), *Bredia* as currently circumscribed comprises 18–22 species according to different species delimitations (e.g. Chen 1984b; Chen and Renner 2007), and occurs from northern Vietnam and southern mainland China to Taiwan and the Ryukyu islands.

The generic circumscription of *Bredia* has long been problematic. *Bredia* is morphologically closely related to *Phyllagathis* Blume (Blume 1849; Ito and Matsumura 1899; Li 1944; Chen 1984a; Hansen 1992; Chen and Renner 2007), another Asian genus with overlapping geographical range. Delimitation of the two genera was traditionally based on staminal morphology (equal or only slightly unequal, isomorphic vs. dimorphic, subequal, or distinctly unequal stamens), which is rather obscure when species with subequal stamens are concerned. The vague generic boundary is reflected in the taxonomic history of some species that have been moved back and forth between the two genera by different authors (Diels 1932; Merrill and Chun 1940; Li 1944; Chen 1979, 1984b; Hansen 1992; Chen and Renner 2007) and also in two phylogenetic studies based on very limited taxon sampling (Zeng et al. 2016; Zhou et al. 2018).

A recent molecular phylogenetic study, with extensive sampling of *Bredia* (19 species) and *Phyllagathis* (35 species), has shed new light on their generic delimitation (Zhou et al. 2019). Staminal characters traditionally used to separate *Bredia* and *Phyllagathis* were shown to be highly homoplasious (Zhou et al. 2019). Both genera as currently defined are not monophyletic. To facilitate discussion, we reconstructed a phylogenetic tree using the combined dataset (nrITS and chloroplast *trnV-trnM*) published in Zhou et al. (2019) plus eight newly sequenced species (see methods). As shown in Fig. 1, *Bredia hirsuta*, the type of *Bredia* is clustered within a clade of 20 species, viz. 13 of *Bredia* and seven of *Phyllagathis*, (hereafter referred to as the *Bredia* clade), whereas the two species originally published in *Tashiroea*, *B. yaeyamensis* (Matsum.) H.L. Li (= *T. yaeyamensis*) and *B. okinawensis* (Matsum.) H.L. Li (= *T. okinawensis*), fall in another clade comprising the new species, seven species of *Bredia* and two of *Phyllagathis* (hereafter referred to as the *Tashiroea* clade). The *Bredia* clade is close to *Blastus*, *Fordiophyton* and *Plagiopetalum* Rehder, while the *Tashiroea* clade is most closely related to *Scorpiothyrsus* H.L. Li and *Driessenia axantha* Korth. (Fig. 1). These findings are strongly corroborated by our chloroplast phylogenomic analyses (unpublished), indicating that the *Tashiroea* clade is an independent lineage distantly related to the *Bredia* clade. The same conclusion is also reached in a recently published study, although based on limited sampling of species (Kokubugata et al. 2019). Continued use of the non-monophyletic *Bredia* may hinder further study of this group and cause problems in describing new species, which has led us to update its circumscription.

In this paper, we revisited the morphological characters of the *Bredia* and *Tashiroea* clades in search of possible diagnostic characters. The results are presented below. Based on molecular and morphological evidence, *Bredia* is recircumscribed and *Tashiroea* is resurrected. Descriptions and a list of species are provided for the two genera with the description of a new species *T. villosa*. Thirteen new combinations are made.

Methods

Molecular experiments and phylogenetic analysis

Eight newly sequenced species were added to the combined dataset (nrITS and chloroplast *trnV-trnM*) published in Zhou et al. (2019), including *Driessenia glanduligera* Stapf, *D. phasmolacuna* C.W. Lin, *Phyllagathis hispidissima* (C. Chen) C. Chen, *P. tentaculifera* C. Hansen, *Scorpiothyrus shangszeensis* C. Chen, *Bredia okinawensis* (= *Tashiroea okinawensis*), *B. yunnanensis* (H. Lév.) Diels, and a new species *T. villosa*. All molecular experiments and phylogenetic analysis using bayesian inference and maximum likelihood methods followed Zhou et al. (2019). A complete list of the taxa sampled in this study, their collection localities, voucher information, and GenBank accession numbers are provided in Suppl. material 1: Table S1.

Morphological comparison

All species of the *Bredia* clade (20 species) and the *Tashiroea* clade (10 species) were examined, including *B. changii* W.Y. Zhao, X.H. Zhan & W.B. Liao, *B. dulanica* C.L. Yeh, S.W. Chung & T.C. Hsu, *B. esquirolii* (H. Lév.) Lauener, *B. gibba* Ohwi, *B. hirsuta*, *B. longiloba* (Hand.-Mazz.) Diels, *B. microphylla* H.L. Li, *B. oldhamii* Hook. f., *B. repens* R.C. Zhou, Q.J. Zhou & Ying Liu, *B. rotundifolia* Yan Liu & C.H. Ou, *B. tuberculata* (Guillaumin) Diels, *B. yunnanensis*, *P. fordii* (Hance) C.Chen, *P. gracilis* (Hand.-Mazz.) C. Chen, *P. guidongensis* K.M. Liu & J. Tian, *P. latispala* C. Chen, *P. longearistata* C. Chen, *P. longiradiosa* C. Chen, *P. plagiopetala* C. Chen and *P. velutina* (Diels) C. Chen from the former clade, and *B. amoena* Diels, *B. biglandularis* C. Chen, *B. okinawensis* (= *T. okinawensis*), *B. quadrangularis* Cogn., *B. sessilifolia* H.L. Li, *B. sinensis* (Diels) H.L. Li (= *T. sinensis* Diels), *B. yaeyamensis* (= *T. yaeyamensis*), *P. nudipes* C. Chen, *P. oligotricha* Merr. and the new species *T. villosa* from the latter clade. Their habit, indumentum, shape and texture of the leaves, leaf surface sculpture under scanning electronic microscope (SEM), inflorescence type, stamen morphology, capsule morphology, habitat preference and geographical distribution were recorded. Data were obtained via field, herbarium and literature surveys as well as by observing living plants in the facilities of Sun Yat-sen University. Specimens of the two clades (GXMG, GXMI, HNNU, IBG, IBK, IBSC, JJE, KUN, NAS, PE, SYS) or their high-resolution photos (A, BM, CSFI, E, HAST, K, KYO, MO, NTUF, NY, PH, TAI, TAIF, TI, UC,

WU) were examined. Habit, shape and texture of the leaves, and inflorescence type were obtained via visual observation. Stamen morphology and capsule morphology were determined by stereomicroscopic (Leica S8APO) examination, leaf epidermal features by desktop SEM (Phenom Pro), and indumentum by both equipment. During observation using Phenom Pro, fresh or dried tissues were directly mounted on stubs and examined without further processing. We failed to obtain the materials of two species recorded in *Bredia*, namely *B. laisherana* C.L. Yeh & C.R. Yeh and *B. violacea* H.L. Li, which were therefore not included in our molecular phylogenetic study. For the two species, we examined their protologue, images of herbarium specimens and color photos from the author of *B. laisherana*. Species circumscriptions basically follow Chen (1984b). Description of the capsule morphology mainly follows Hansen (1992), while the description of one type of trichomes (sessile glands with thin-walled heads) was taken from Wurdack (1986).

Taxonomy

Diels published several names in Melastomataceae in 1924 and 1932. Although he designated type specimens, he did not specify the place of deposition for them in the protologue. Even if we assume the holotypes existed in the Berlin herbarium (where Diels worked), they were probably destroyed during the Second World War. Therefore, we follow McNeill (2014) and designate lectotypes for those taxa according to the stipulations of Art. 9.12, 9.22 and 9.23 of the Code (Turland et al. 2018). Diels (1932) also lectotypified two names, *Barthea cavaleriei* H. Lév. and *Fordiophyton tuberculatum* Guillaumin, without citing the herbaria where they were housed. For *Barthea cavaleriei*, only one specimen of the gathering designated by Diels is known and is in the Royal Botanic Garden Edinburgh herbarium (E). We accept it as the lectotype of this name and cite the page number of Diels's lectotypification. For *Fordiophyton tuberculatum*, multiple specimens of the gathering designated by Diels (1932) are mixtures of more than one taxon. Based on Art. 9.17 (Turland et al. 2018), a lectotype corresponding most closely with the original description is designated for this name. *Tashiroea*, *T. yaeyamensis* and *T. okinawensis* were described simultaneously without designation of a type (Ito and Matsumura 1899). We also lectotypify these names here according to Art. 8.1, 8.2, 10.1, and 10.2 (Turland et al. 2018). In general, we select the herbarium sheet with the best-preserved leaves and flowers for lectotypification. Detailed reasoning where the choice may not be obvious is provided at the end of the taxon being discussed.

Results

The combined dataset contained 1768 characters. The phylogenetic tree resulted from ML analysis is shown in Fig. 1 with PP and ML bootstrap support values (BS) indicated at nodes. Phylogenetic relationships within Sonerileae/Dissochaeteae are near-

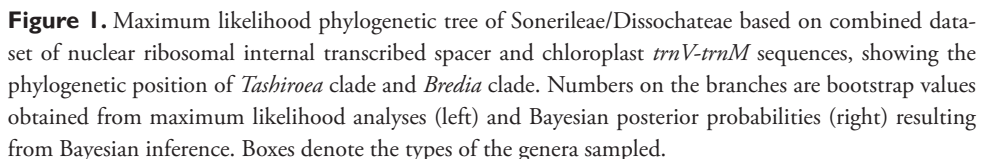


Table 1. Comparison of the *Tashiroea* clade and the *Bredia* clade. Potential diagnostic characteristics are indicated in bold.

	<i>Tashiroea</i> clade	<i>Bredia</i> clade
Habit	Shrubs or shrublets	Shrubs, shrublets or herbs
Indumentum of mature leaf	Glabrous, rarely pubescent and villous (<i>T. villosa</i>)	Sparsely to densely puberulous or strigose
Leaf texture	Stiffly papery to leathery	Papery, rarely submembranous
Leaf surface sculpture	Furrowed, rarely not (<i>T. villosa</i>)	Not furrowed
Leaf shape	Lanceolate, ovate, elliptic or suborbicular	Lanceolate, ovate, cordate, oblong, elliptic, ovate-orbicular
Leaf base	Cuneate, obtuse, rounded, or subcordate	Cuneate, obtuse, rounded, often cordate
Leaf veins	3–5	5–11, rarely 3 (<i>B. guidongensis</i>)
Leaf margin	Entire to serrulate	Entire to serrulate
Indumentum	Sessile gland with thin-walled head; multiseriate trichomes with glandular head or not; appressed uniseriate trichomes with glandular head; yellowish uniseriate trichomes	Sessile gland with thin-walled head; multiseriate trichomes with glandular head or not; appressed or spreading uniseriate trichomes with glandular head or not
Inflorescence	Cymose, cymose panicle	Cymose, umbellate, or cymose panicle
Stamens	Dimorphic and isomorphic	Dimorphic and isomorphic
Staminal appendage of dimorphic stamens	Gibbose, tuberculate or spurred at the base of anthers in shorter stamens; connectives decurrent and prolonged, gibbose or tuberculate dorsally in longer stamens	Gibbose, tuberculate or spurred at the base of anthers in shorter stamens; connectives decurrent and prolonged, gibbose, tuberculate, or spurred ventrally in longer stamens
Staminal appendage of isomorphic stamens	Slightly gibbose ventrally at the base of the anthers, spurred dorsally	Gibbose or tuberculate at the base of the anthers, sometimes short spurred dorsally
Ovary top at anthesis	Slightly crowned or uncrowned	Crowned
Capsule	Ovary crown usually evanescent, capsule uncrowned with rounded or 4-humped top; or ovary crown persistent and enlarged, enclosing an obpyramidal space (in <i>T. nudipes</i> and <i>T. oligotricha</i>)	Ovary crown persistent and enlarged, enclosing an inverted frustum-shaped depression at capsule top
Habitat	Open or dense forests, slopes, stream banks, alt. 50–2300 m	In forest or along forest margin, stream banks, damp places, alt. 100–2500 m
Distribution	South eastern mainland China, Taiwan, Ryukyu Islands	Central and south mainland China, Taiwan, Ryukyu Islands

ly identical to those reported in Zhou et al. (2019). Both *Tashiroea* clade (PP=1.00; BS=100%) and *Bredia* clade (PP=1.00; BS=98%) are well resolved. Among the newly sequenced species, *B. okinawensis* (= *T. okinawensis*) and the new species *T. villosa* are nested in the *Tashiroea* clade, while *B. yunnanensis* is grouped in the *Bredia* clade.

Characters of the *Tashiroea* clade (10 species) and the *Bredia* clade (20 species) are summarized in Table 1. Species of the two clades are shrubs or shrublets, except that the latter clade includes some herbs. The mature leaves of species in *Tashiroea* clade are usually glabrous, stiffly papery to leathery and exhibit furrowed surface sculpture under SEM (Figs 2, 4 A–B, D), except that those of the new species *T. villosa* are densely pubescent and villous and without furrowed surface sculpture (Fig. 4C). The mature leaves of species in the *Bredia* clade are usually puberulous and papery and without furrowed surface sculpture (Figs 3, 4 E–L). Species in both clades have sessile glands and



Figure 2. Leaf morphology of the *Tashiroea* clade. **A** *T. amoena* (Y. Liu 571) **B** *T. biglandularis* (Y. Liu 553) **C** *T. nudipes* (Y. Liu 435) **D** *T. oligotricha* (Y. Liu 468) **E** *T. okinawensis* (Y. Liu 636) **F** *T. quadrangularis* (Y. Liu 585) **G** *T. sessilifolia* (Y. Liu 540) **H** *T. yaeyamensis* (Y. Liu 631).

uniseriate/multiseriate trichomes with or without glandular heads (Fig. 5A–C, E–H). Yellowish uniseriate trichomes (branched or unbranched) (Fig. 5D), are present only in the *Tashiroea* clade, where they occur on apical and axillary buds and sometimes on young leaves and branches (Fig. 5M–P). Both clades are quite variable in terms of leaf



Figure 3. Leaf morphology of the *Bredia* clade. **A** *B. changii* (Y. Liu 548) **B** *B. guidongensis* (Y. Liu 472) **C** *B. hirsuta* (Y. Liu 634) **D** *B. longiradiosa* var. *pulchella* (Y. Liu 485) **E** *B. microphylla* (Y. Liu 551) **F** *B. plagiopetala* (Y. Liu 460) **G** *B. tuberculata* (Y. Liu 629) **H** *B. yunnanensis* (Y. Liu 627).

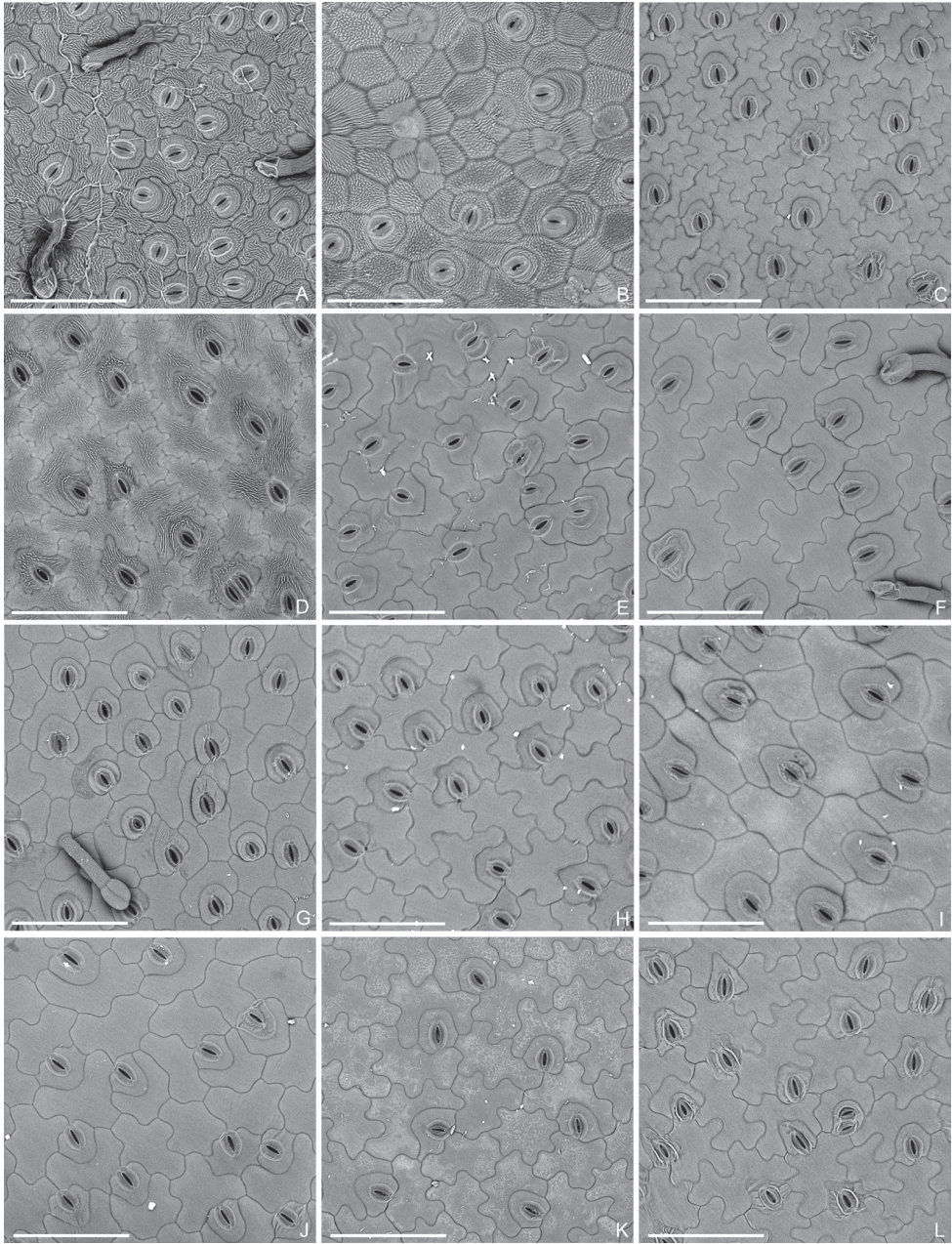


Figure 4. Scanning electron micrographs of lower epidermis. **A–D** *Tashiroea* clade, showing presence of furrowed surface sculpture: **A** *T. amoena* (Y. Liu 571) **B** *T. nudipes* (Y. Liu 435) **C** *T. villosa* (Y. Liu 568) **D** *T. yaeyamensis* (Y. Liu 631) **E–L** *Bredia* clade, showing absence of furrowed surface sculpture **E** *B. dulanica* (Y. Liu 565) **F** *B. gibba* (Y. Liu 566) **G** *B. gracilis* (Y. Liu 457) **H** *B. hirsuta* (Y. Liu 563) **I** *B. longiradiosa* var. *pulchella* (Y. Liu 485) **J** *B. repens* (Y. Liu 558) **K** *B. tuberculata* (Y. Liu 629) **L** *B. yunnanensis* (Y. Liu 627). Scale bars: 100 μ m.

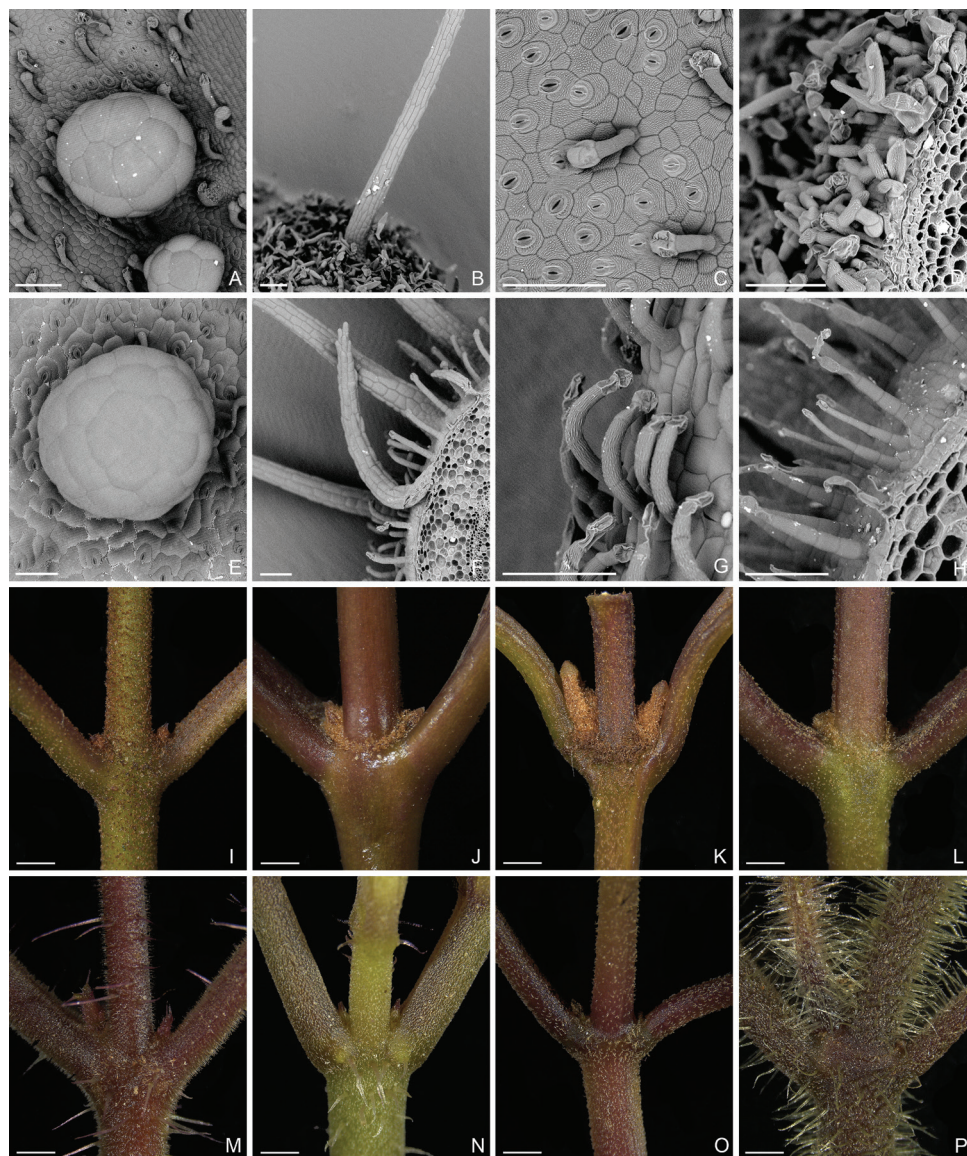


Figure 5. Trichomes in the *Tashiroea* clade and the *Bredia* clade. **A–D** Micrographs of trichomes in the *Tashiroea* clade: **A** sessile gland with thin-walled head in *T. nudipes* (Y. Liu 435) **B** multiserial trichomes in *T. amoena* (Y. Liu 571) **C** appressed uniseriate trichomes with glandular heads in *T. nudipes* (Y. Liu 435) **D** yellowish uniseriate trichomes (branched or unbranched) in *T. quadrangularis* (Y. Liu 585). **E–H** Micrographs of trichomes in the *Bredia* clade: **E** sessile gland with thin-walled head in *B. longiradiosa* var. *pulchella* (Y. Liu 485) **F** multiserial trichomes in *B. repens* (Y. Liu 558) **G** appressed uniseriate trichomes with glandular heads in *B. gibba* (Y. Liu 566) **H** spreading uniseriate trichomes in *B. hirsuta* (Y. Liu 563). **I–L** Stereoscopic images of the *Tashiroea* clade, showing buds covered in yellowish uniseriate trichomes: **I** *T. amoena* (Y. Liu 571) **J** *T. nudipes* (Y. Liu 435) **K** *T. quadrangularis* (Y. Liu 585) **L** *T. yaeyamensis* (Y. Liu 631). **M–P** Stereoscopic images of the *Bredia* clade, showing buds without yellowish uniseriate trichomes: **M** *B. dulanica* (Y. Liu 565) **N** *B. gibba* (Y. Liu 566) **O** *B. gracilis* (Y. Liu 457) **P** *B. yunnanensis* (Y. Liu 627). Scale bars: 100 µm (**A–H**); 1 mm (**I–P**).

shape (lanceolate to suborbicular), leaf base (cuneate to cordate), inflorescence type (cymose to cymose panicle), stamen morphology (dimorphic to isomorphic), and staminal appendages (gibbose, tuberculate, or spurred) (Figs 2–3, 6–7). An ovary crown is present in most species of the *Tashiroea* clade at anthesis (Fig. 8A–D), but is usually evanescent, resulting in uncrowned capsules (Fig. 8I–K). Exceptions are two species traditionally placed in *Phyllagathis*. Their crowns are persistent and enlarged, forming crowned capsules with an obpyramidal depression at the top (Fig. 8L). In species of the *Bredia* clade, an ovary crown is present at anthesis (Fig. 8E–H), and persistent and enlarged in old capsule, enclosing an inverted frustum-shaped depression (Fig. 8M–P).

Field and literature surveys revealed that species of both *Tashiroea* clade and *Bredia* clade prefer shaded or moist habitats in forests or along forest margin, often along stream banks, from 50 m to 2500 m alt. The *Tashiroea* clade occurs in southeastern mainland China and the Ryukyu islands, while the *Bredia* clade, aside from the above areas, also extends to the central and southwestern Chinese provinces of Guizhou, Hubei, Chongqing, Sichuan and Yunnan.

Of the two species without molecular data, *B. laisherana* is endemic to Taiwan and *B. violacea* occurs in northern Vietnam. The former species has glabrous stems and leaves, and uncrowned ovaries and capsules (Yeh et al. 2008), occurring in dense forests, while the latter has puberulous stems, leaves and inflorescences but no habitat record is available.

Discussion

Morphological comparison

Species of the *Tashiroea* clade and *Bredia* clade are similar in habit, habitat preference, most indumentum types, and in having lanceolate, ovate to suborbicular leaves, a cuneate to cordate leaf base, cymose to cymose panicles, dimorphic or isomorphic stamens, and gibbose, tuberculate, or spurred staminal appendages (Figs 2–3, 5–7). Additionally, their range of distribution partly overlaps in southeastern mainland China, and the Ryukyu islands. Therefore, it is quite understandable that Li (1944) considered *Tashiroea* to be congeneric with *Bredia*, where he placed it in synonymy.

However, our survey of morphological characters has shown that the two clades can be distinguished by several diagnostic features, including leaf indumentum, texture, leaf surface sculpture under SEM, presence/absence of yellowish uniseriate trichomes, and capsule morphology. Species of the *Tashiroea* clade differ from those of the *Bredia* clade by the glabrous, stiffly papery to leathery mature leaves with furrowed surface sculpture under SEM (vs. puberulous and papery, without furrowed sculpture) (Figs 2–4), the presence of yellowish uniseriate trichomes on buds (vs. absence) (Fig. 5), and usually uncrowned capsules with a rounded or 4-humped apex, or rarely crowned with an obpyramidal apical depression (vs. capsules crowned, with an inverted frustum-shaped depression) (Fig. 8). *Tashiroea villosa*, the only exception in the *Tashiroea* clade with densely hairy leaves and without furrowed surface sculpture,

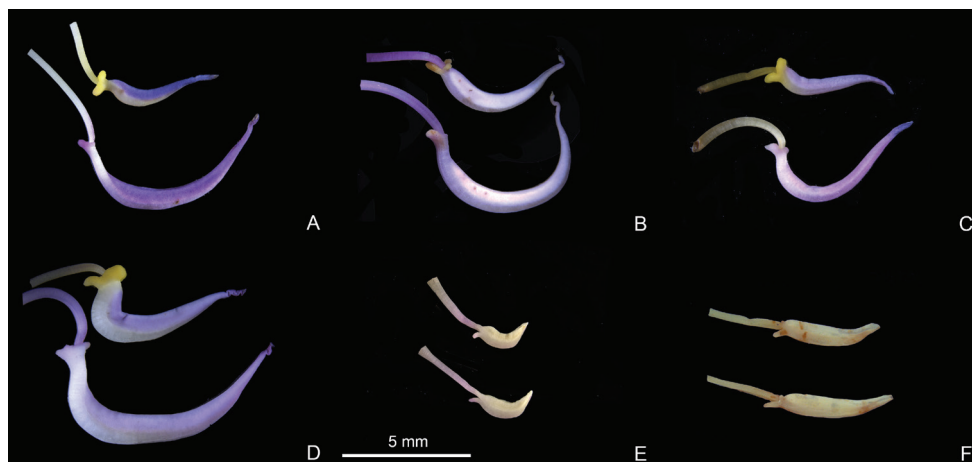


Figure 6. Stamen morphology in the *Tashiroea* clade. **A–D** Dimorphic stamens: **A** *T. amoena* (Y. Liu 571) **B** *T. quadrangularis* (Y. Liu 585) **C** *T. biglandularis* (Y. Liu 553) **D** *T. sinensis* (Y. Liu 569). **E–F** Isomorphic stamens: **E** *T. nudipes* (Y. Liu 435) **F** *T. oligotricha* (Y. Liu 468). Scale bar: 5 mm.

nevertheless has yellowish uniseriate trichomes on buds and uncrowned capsules with a 4-humped apex characteristic of this clade. At least some of the above differences, such as indumentum and capsule morphology, had long been noticed by previous authors. Li (1944) established section *Tashiroea* in *Bredia*, whereas Hansen (1992) divided *Bredia* into four groups of species, placing *Tashiroea* in a separate group.

The two clades are also morphologically distinguishable from their close relatives. Phylogenetic analyses showed that the *Tashiroea* clade is most closely related to *Scorpiothyrus* and *Driessenia axantha* while *Bredia* clade is closest to *Blastus*, *Fordiophyton*, and *Plagiopetalum* (Fig. 1). Species in the *Tashiroea* clade differ from *Scorpiothyrus* in the 3–5-veined leaves (vs. 7–9-veined), from *Driessenia axantha* in inflorescence terminal (vs. axillary), and from both in inflorescence cymose to cymose panicles (vs. often scorpioid cymose panicles), and ventrally gibbose or tuberculate anthers (vs. 2-setose or 2 band-shaped ventral appendages). The *Bredia* clade is easily distinguished from *Blastus* by having two whorls of stamens (vs. one), from *Fordiophyton* by ventrally appendaged anthers (vs. unappendaged) and the capsule crown usually exserted from the calyx (vs. not exserted), and from *Plagiopetalum* by appendaged anthers and crowned capsules (vs. unappendaged and uncrowned).

Species without molecular data

Two species previously placed in *Bredia* were not sampled in the molecular phylogenetic studies: *B. laisherana* from Taiwan and *B. violacea* from north Vietnam. *Bredia laisherana* was initially identified as *B. quadrangularis* by Yeh and Yeh (2006) and was later published as a new species (Yeh et al. 2008). It has glabrous stems and leaves, and uncrowned ovaries and capsules (Yeh et al. 2008), which are characteristic of the *Tashiroea* clade. *Bredia vio-*

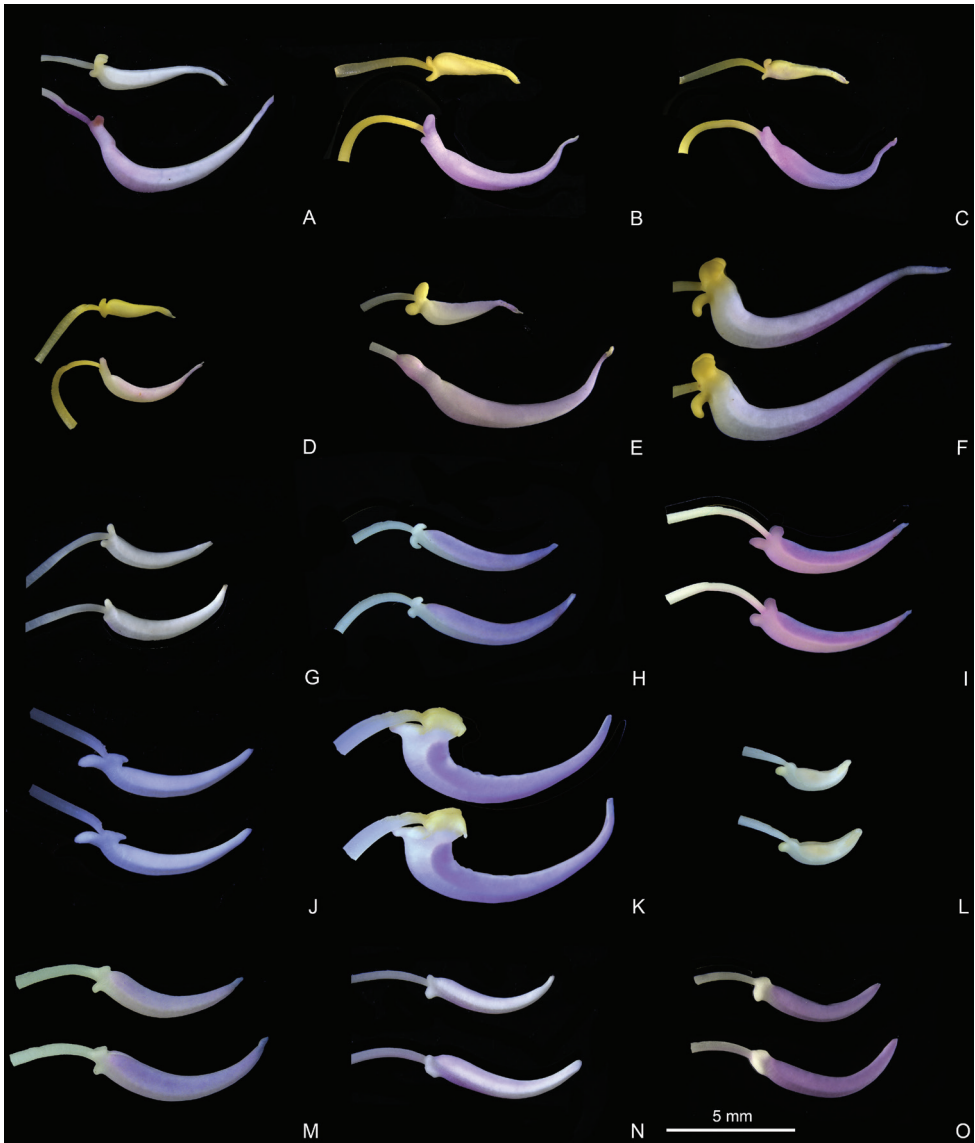


Figure 7. Stamen morphology in the *Bredia* clade. **A–E** Dimorphic stamens: **A** *B. esquirolii* (Y. Liu 587) **B** *B. hirsuta* (Y. Liu 563) **C** *B. hirsuta* var. *scandens* (Y. Liu 539) **D** *B. rotundifolia* (Y. Liu 538) **E** *B. tuberculata* (Y. Liu 629). **F–O** Isomorphic stamens: **F** *B. fordii* (Y. Liu 444) **G** *B. fordii* var. *micrantha* (Y. Liu 580) **H** *B. gracilis* (Y. Liu 457) **I** *B. guidongensis* (Y. Liu 472) **J** *B. longearistata* (Y. Liu 496) **K** *B. longiradiosa* var. *pulchella* (Y. Liu 485) **L** *B. microphylla* (Y. Liu 551) **M** *B. plagiopetala* (Y. Liu 460) **N** *B. repens* (Y. Liu 558) **O** *B. yunnanensis* (Y. Liu 627). Scale bar: 5 mm.

lacea has puberulous stems, leaves and inflorescences (Li 1945). Li (1945) noted that the general appearance and inflorescence characters of *B. violacea* closely resembled those of *B. hirsuta* (type of *Bredia*). Morphological characters therefore suggest that *B. laisherana* belongs to the *Tashiroea* clade, and *B. violacea* to the *Bredia* clade.

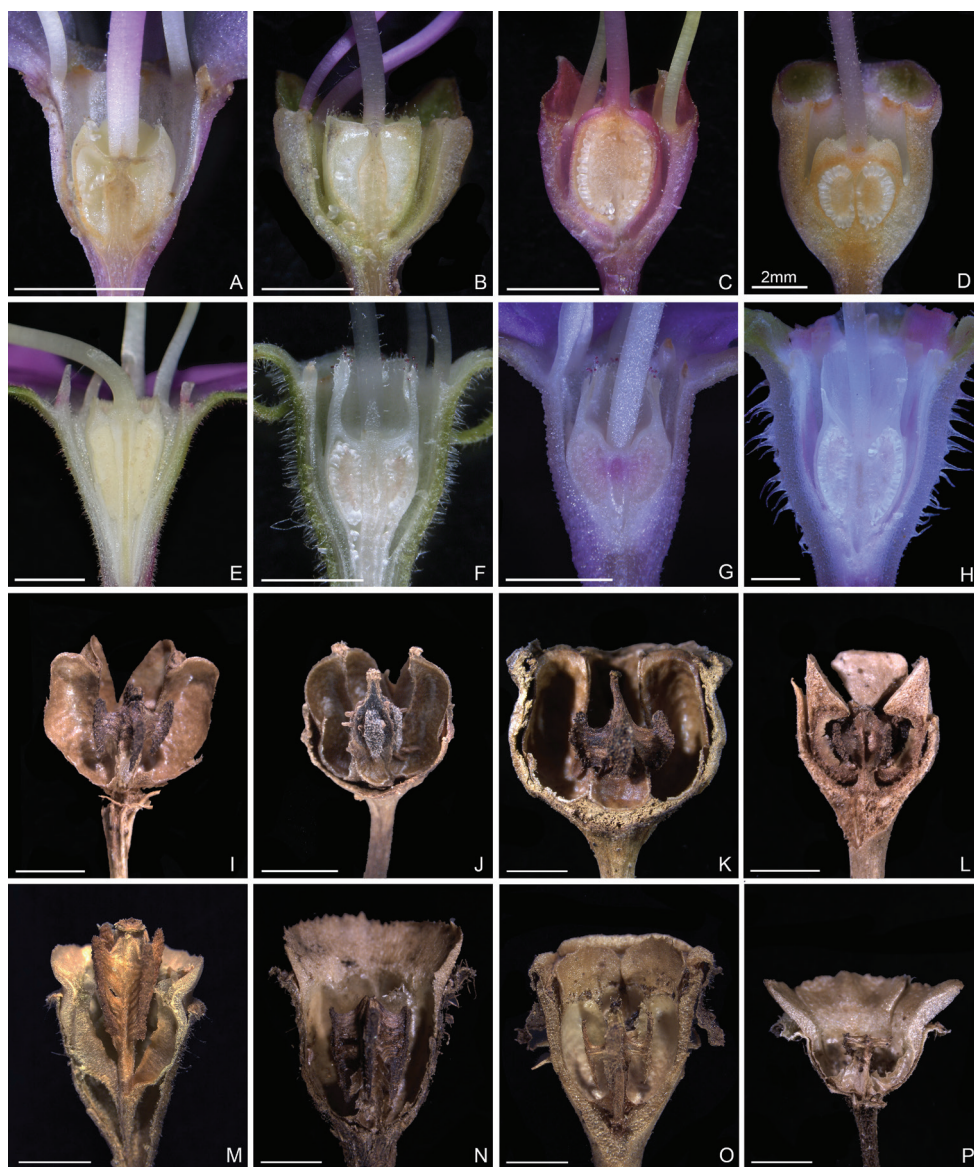


Figure 8. Longitudinal section of ovary (A–H) and old fruit (I–P). **A–D** *Tashiroea* clade, crowned or uncrowned ovaries at anthesis: **A** *T. amoena* (Y. Liu 571) **B** *T. quadrangularis* (Y. Liu 585) **C** *T. biglandularis* (Y. Liu 553) **D** *T. sinensis* (Y. Liu 569). **E–H** *Bredia* clade, crowned ovaries at anthesis: **E** *B. hirsuta* (Y. Liu 563) **F** *B. fordii* var. *micrantha* (Y. Liu 580) **G** *B. plagiopetala* (Y. Liu 459) **H** *B. longiradiosa* var. *pulchella* (Y. Liu 485). **I–L** *Tashiroea* clade, uncrowned, rarely crowned capsules: **I** *T. amoena* (Y. Liu 571) **J** *T. biglandularis* (Y. Liu 553) **K** *T. sinensis* (Y. Liu 569) **L** *T. oligotricha* (Y. Liu 468). **M–P** *Bredia* clade, crowned capsules: **M** *B. dulanica* (Y. Liu 565) **N** *B. fordii* (Y. Liu 444) **O** *B. latispala* (Y. Liu 557) **P** *B. repens* (Y. Liu 558). Scale bars: 2 mm.

Conclusion

Morphological evidence and molecular phylogenetic data confirmed that the *Tashiroea* clade and the *Bredia* clade represent two distantly related lineages morphologically well differentiated from each other and from their possible relatives. We therefore resurrect the generic name *Tashiroea* Matsum for the former clade and redefine *Bredia* Blume to include the latter. For the species lack of molecular data, we place *B. laisherana* and *B. violacea* in *Tashiroea* and *Bredia* respectively based on morphology. Species circumscriptions basically follow Chen (1984b). A revision at the species level will be dealt with in another study.

Taxonomy

***Tashiroea* Matsum., J. Coll. Sci. Imp. Univ. Tokyo 12: 489. 1899, emend. R.C. Zhou & Ying Liu**

Lectotype. *Tashiroea yaeyamensis* Matsum., J. Coll. Sci. Imp. Univ. Tokyo 12: 489. 1899. (Designated here)

Description. Shrubs or shrublets, erect, rarely creeping in the lower parts. Stems terete or slightly 4-sided, glabrous or glabrescent, rarely densely hairy (in *T. villosa*), terminal and axillary buds pubescent with yellowish uniseriate branched trichomes. Leaves petiolate; leaf blade lanceolate, ovate, elliptic, rarely suborbicular, stiffly papery to leathery, glabrescent when mature, rarely hairy (in *T. villosa*), secondary veins 1 or 2 on each side of midvein, margin remotely serrulate, or almost entire. Inflorescences terminal, few-flowered cymes to cymose panicles; bract minute, rarely to 1–2 cm long (in *T. villosa*), usually caducous. Flowers 4-merous. Hypanthium campanulate, rarely funnel shaped. Calyx lobes repand, crenate or triangular. Petals pink or purplish red, ovate, oblong to suborbicular, more or less oblique, apex acute or acuminate. Stamens 8, unequal or subequal; filaments filiform; anthers dimorphic or isomorphic, subulate to oblong-linear, gibbose, tuberculate or spurred at base, sometime unappendaged adaxially. Ovary half inferior, slightly crowned or uncrowned, ovoid-globular or turbinate, 4-celled. Style filiform; stigma apiculate. Capsule cup-shaped or subglobular, more or less 4-sided, woody, uncrowned, apex rounded or 4-humped, or crown persistent and enlarged, enclosing an obpyramidal space (in *T. nudipes* and *T. oligotricha*). Seeds numerous, minute, cuneate, densely granulate. (Figs 2, 6, 5A–D, I–L, 8A–D, I–L)

Distribution. Eleven species, eight in southeastern mainland China (Anhui, Fujian, Guangdong, Guangxi, Guizhou, Hunan, Jiangxi, Zhejiang), one in Taiwan, and two in the Ryukyus (Fig. 9).

Ito and Matsumura (1899) established *Tashiroea* based on *T. yaeyamensis* and *T. okinawensis* without designating a type. The original materials of both species conform to the protologue of *Tashiroea*. We designate *T. yaeyamensis* as the type of *Tashiroea* because this species bears much larger leaves and more flowers than *T. okinawensis*, which may facilitate future molecular and/or morphological analysis of the type materials.

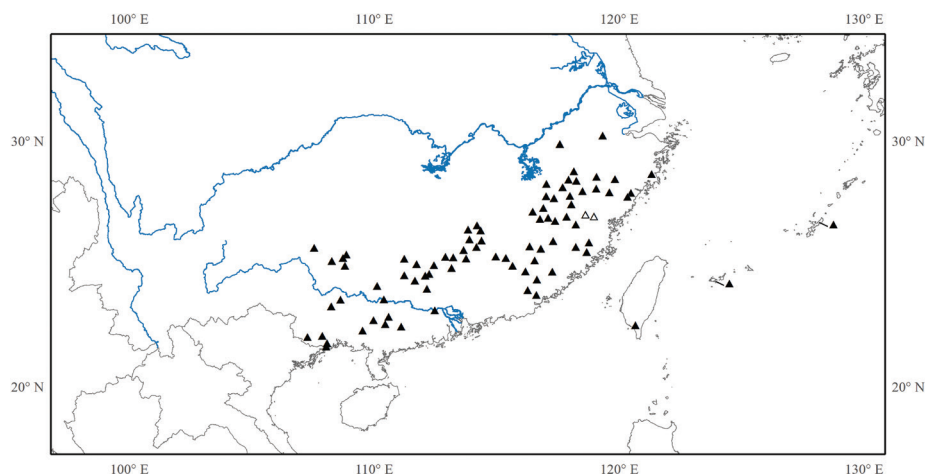


Figure 9. Distribution of *Tashiroea*. Hollow triangles indicate the locations of *Tashiroea villosa*.

Species included in *Tashiroea*:

***Tashiroea amoena* (Diels) R.C.Zhou & Ying Liu, comb. nov.**

urn:lsid:ipni.org:names:77199697-1

Bredia amoena Diels, Notizbl. Bot. Gart. Berlin-Dahlem 9(83): 197–198. 1924 (Basionym). Type: China. Zhejiang: Yentang, 16 Aug 1920, H.H. Hu 30 (lectotype, designated here: A! [A00071979]; isolectotype: UC! [UC231837]).

Bredia chinensis Merr., J. Arnold Arbor. 8(1): 11–12. 1927. Type: China. Zhejiang: Yentang, 16 Aug 1920, H.H. Hu 30 (holotype: UC! [UC231837]; isotype: A! [A00071979]).

Bredia pricei F.P. Metcalf, Lingnan Sci. J. 12: 153–154. 1933. Type: China. W.R. Price 1200A (K! [K001325176]).

***Tashiroea biglandularis* (C. Chen) R.C.Zhou & Ying Liu, comb. nov.**

urn:lsid:ipni.org:names:77199698-1

Bredia biglandularis C. Chen, Bull. Bot. Res., Harbin 4(3): 39. 1984 (Basionym). Type: China. Guangxi: Dongxing, Lu-bao-shan, 2 Oct 1976, T. Fang 1519 (holotype: GXMI! [GXMI050232]).

***Tashiroea laisherana* (C.L. Yeh & C.R. Yeh) R.C.Zhou & Ying Liu, comb. nov.**

urn:lsid:ipni.org:names:77199699-1

Bredia laisherana C.L. Yeh & C.R. Yeh, Edinburgh J. Bot. 65(3): 400 (–403; figs 3, 4C–D). 2008 (Basionym). Type: Taiwan, Pingtung, Mt Laisher, on the ridge of a mountain and steep valley and in a dense cloudy forest, 1600–1800 m, 15 Sept 2005, C.L. Yeh & C.R. Yeh 33 (holotype: PPI 065514).

***Tashiroea nudipes* (C. Chen) R.C.Zhou & Ying Liu, comb. nov.**

urn:lsid:ipni.org:names:77199700-1

Phyllagathis nudipes C. Chen, Bull. Bot. Res., Harbin 4(3): 47. 1984 (Basionym). Type: China. Guangdong: Ruyuan, Wuzhi Shan, 21 May 1973, Guangdong73-101 (holotype: IBSC! [IBSC0003997]).

***Tashiroea okinawensis* Matsum., J. Coll. Sci. Imp. Univ. Tokyo 12: 490. 1899.**

Bredia okinawensis (Matsum.) H.L. Li, J. Arnold Arbor. 25: 21. 1944.

Type. Japan. Okinawa: in montosis tractus Kunchan, Apr 1887, Y. Tashiro (5) (lectotype, designated here: TI! [TI00002346]). Additional syntypes: Japan. Okinawa: S. Tanaka 216 (TI! [TI00002347]), Matsumura (TI! [TI00002348]).

***Tashiroea oligotricha* (Merr.) R.C.Zhou & Ying Liu, comb. nov.**

urn:lsid:ipni.org:names:77199701-1

Phyllagathis oligotricha Merr. Sunyatsenia 1: 74. 1930 (Basionym). Type: China. Guangdong: Lok Chang, 8 Jun 1929, Tso 21016 (holotype: NY! [NY00273007]; isotypes: IBSC! [IBSC0003939, IBSC0003940]).

Phyllagathis anisophylla Diels, Bot. Jahrb. Syst. 65(2–3): 115. 1932. Type: China. Hunan, no precise location, 1926, Hunan Museum 60 (lectotype, designated here: IBSC! [IBSC0003938]; isolectotypes: IBSC! [IBSC0003936, IBSC0003937]).

***Tashiroea quadrangularis* (Cogn.) R.C.Zhou & Ying Liu, comb. nov.**

urn:lsid:ipni.org:names:77199702-1

Bredia quadrangularis Cogn. Monogr. Phan. 7: 473–474. 1891 (Basionym). Type: South China. Seemann s.n. (LE).

***Tashiroea sessilifolia* (H.L. Li) R.C.Zhou & Ying Liu, comb. nov.**

urn:lsid:ipni.org:names:77199703-1

Bredia sessilifolia H.L. Li, J. Arnold Arbor. 25: 22. 1944 (Basionym). Type: China. Guangxi: Shang-sze District, Shih Wan Tai Shan, Tang Lung Village, 25 Sept 1934, W. T. Tsang 24346 (holotype: A! [A00071991]; isotype: IBSC! [IBSC0003956]).

Tashiroea sinensis* Diels, Notizbl. Bot. Gart. Berlin-Dahlem 9: 198. 1924.Bredia sinensis* (Diels) H.L. Li, J. Arnold Arbor. 25: 22. 1944.*Bredia glabra* Merr., J. Arnold Arbor. 8: 12. 1927. Type: China. Zhejiang: Pinyong Xian, 11 Jul 1924, Ling Kan 7333 (holotype UC! [UC252284]).**Type.** China. Fujian: Chung-an District, 27 Jul 1921, H.H. Hu 1343 (lectotype, designated here: A! [A00073233]).***Tashiroea yaeyamensis* Matsum., J. Coll. Sci. Imp. Univ. Tokyo 12: 489. 1899.***Bredia yaeyamensis* (Matsum.) H.L. Li, J. Arnold Arbor. 25: 21. 1944.*Tashiroea yaeyamensis* var. *tanakaea* Matsum., J. Coll. Sci. Imp. Univ. Tokyo 12: 490. 1899. Type: Okinawa: Yaeyama archipelago, Jul 1890, S. Tanaka 344 (holotype: TI! [TI00002345]).**Type.** Japan. Okinawa: Iriomote 1890, S. Tanaka 345 (lectotype, designated here: TI! [TI00002344]). Additional syntype: Japan. Okinawa: in Yaeyama, Aug 1887, Tashiro (TI! [TI00002343]).***Tashiroea villosa* X.X.Su, sp. nov.**

urn:lsid:ipni.org:names:77199704-1

Figures 10, 11, 12A–B

Type. China. Fujian: Pingnan County, Lingxia Town, 1000 m, 16 Jul 2017, Y. Liu 568 (holotype: A!; isotype: SYS!).**Diagnosis.** Resembles *T. amoena* in height, leaf size and shape, inflorescence and stamen morphology, while differing from the latter in the dense indumentum covering the whole plant and much larger bracts.**Description.** Shrubs or shrublets, 20–60 (–90) cm tall. Stem, leaves, peduncles, bracts, pedicels and hypanthium densely pubescent and villous with multiseriate or sometimes uniseriate glandular or non-glandular trichomes. Stems cylindrical, branchlets slightly 4-sided, sometimes rubescent. Leaves opposite; petiole 1.2–4.5 cm long; leaf blade ovate to ovate-elliptic, 4.2–12 × 1.8–6 cm, papery, abaxial surface pale green, adaxial surface green, secondary veins 3 on each side of midvein, base cordate to rounded, margin ciliate and inconspicuously serrulate, apex acuminate or short acuminate. Inflorescences terminal, cymose, 7–14 × 3.5–6.5 cm, bracts 9–19 × 5–8 mm, deciduous or sometimes persist till anthesis. Pedicels 1–3 mm. Hypanthium short campanulate, 4-sided, 3–5 mm long, calyx lobes broadly triangular, 1 mm long, apex acute. Petals purplish pink or pink, ovate to ovate-oblong, 7–10 × 3.5–5 mm, slightly oblique, apex acute. Stamens 8, dimorphic, unequal. Longer stamens antesealous, ca. 15 mm long; anthers



Figure 10. Line illustration of *Tashiroea villosa* (A–G), all from Y. Liu 568. **A** Habit **B** Flower (side view) **C** Longitudinal section of flower, showing slightly crowned ovary **D** Dimorphic stamens **E** Capsule (side view) **F** Capsule (longitudinal section) **G** Capsule (top view). Scale bar: 1 cm (**A**).



Figure 11. Y. Liu 568 (A) collected from Lingxia, Pingnan County, Fujian, China, holotype of *Tashiroea villosa*.

lanceolate, ca. 8 mm long, geniculate; connective decurrent, slightly prolonged, forming a short spur dorsally. Shorter stamens antepetalous, ca. 8 mm long, anthers lanceolate, ca. 4 mm long, base gibbose ventrally and forming a short spur dorsally. Ovary half inferior,



Figure 12. *Tashiroea villosa* (A–B) and *T. amoena* (C–D). **A** Habit **B** Inflorescence showing large bracts **C** Habit **D** Inflorescence showing minute bracts. Photographed by Xiang-xiu Su (A, C) and Ying Liu (B, D).

locules 4, apex slightly 4-lobed, margin ciliate with glandular trichomes. Style ca. 0.6 cm long, puberulous with glandular trichomes basally. Capsule cup-shaped; hypanthium ca. 4×3.5 mm long; placental column distally entire, placentas non-thready. Seeds numerous, minute, cuneate, granulate. Flowering July–August, fruiting August–October.

Etymology. The specific epithet refers to the dense pubescent and villous indumentum.

Distribution and ecology. *Tashiroea villosa* is currently known from Pingnan, Jianou and Jianyang, northern Fujian, China (Fig. 9). It often grows in grasses and bushes along streamside at elevations of 900–1400 m.

Notes. *Tashiroea villosa* is discovered by Mr. Xiang-xiu Su. He is an amateur collector in Fujian who had made an important contribution to the description of this new species. We therefore include him as the author of this name. *Tashiroea villosa* is the sole species currently known in *Tashiroea* with densely puberulous and villous leaves (vs. glabrous) and smooth leaf surface sculpture (vs. furrowed). It is morphologically and phylogenetically closest to *T. amoena*. The two species are similar in height, leaf size and shape, inflorescence and stamen morphology. *Tashiroea villosa* is distinct from *T. amoena* in the dense indumentum covering the whole plant (vs. petioles and

inflorescences pubescent or sometimes glabrescent) and much larger bracts (9–19 × 5–8 mm vs. 1–2 × 1 mm) in the florescence (Fig. 12). Geographically, *T. amoena* is widely distributed in southeastern China (Anhui, Fujian, Zhejiang, Jiangxi, Guangxi), whereas *T. villosa* occurs in northern Fujian where both species occur. Nevertheless, they have not been found to co-occur within the same habitat.

***Bredia* Blume, Mus. Bot. 1: 25. 1849, emend. R.C. Zhou & Ying Liu**

Type. *Bredia hirsuta* Blume, Mus. Bot. 1(2): 25. f. 4. 1849.

Description. Shrubs, shrublets or herbs, erect, ascending or creeping. Stems terete or more or less 4-sided, sparsely to densely puberulous, rarely glabrescent. Leaves petiolate; leaf blade ovate, cordate, oblong, elliptic, ovate-orbicular, rarely lanceolate, papery, rarely submembranous, sparsely to densely puberulous or strigose, secondary veins 2–5 on each side of midvein, margin serrulate or entire. Inflorescences terminal, umbellate, cymes or cymose panicles. Flowers 4-merous. Hypanthium funnel shaped to campanulate. Calyx lobes conspicuous, linear-lanceolate to triangular. Petals pink or purplish red, ovate to oblong, more or less oblique, apex acute or acuminate. Stamens 8, unequal or subequal; filaments filiform; anthers dimorphic or isomorphic, subulate to oblong-linear, gibbose, tuberculate or spurred at base, rarely unappendaged abaxially. Ovary half inferior, crowned, ovoid, 4-celled. Style filiform; stigma apiculate. Capsule turbinate to cup-shaped, more or less 4-sided, crown persistent and enlarged, enclosing an inverted frustum-shaped depression at capsule apex. Seed numerous, minute, cuneate, densely granulate. (Figs 3, 7, 5E–H, M–P, 8E–H, M–P)

Distribution. Twenty-one species: 15 in central and southern mainland China (Fujian, Guangdong, Guangxi, Guizhou, Hubei, Hunan, Jiangxi, Sichuan, Chongqing, Yunnan, Zhejiang), one in north Vietnam, five in Taiwan and one extending to the Ryukyu islands (Fig. 13).

Species included in *Bredia*:

***Bredia changii* W.Y. Zhao, X.H. Zhan & W.B. Liao, Phytotaxa 307(1): 36–42.**

Type. China. Jiangxi: Chongyi County, Niedu Town, 579 m, 1 Aug 2016, W. Y. Zhao et al. LXP-13-22114 (holotype: SYS!; isotype: IBSC!).

***Bredia dulanica* C.L. Yeh, S.W. Chung & T.C. Hsu, Edinburgh J. Bot. 65(3): 395, 399 (figs 2, 4A–B). 2008.**

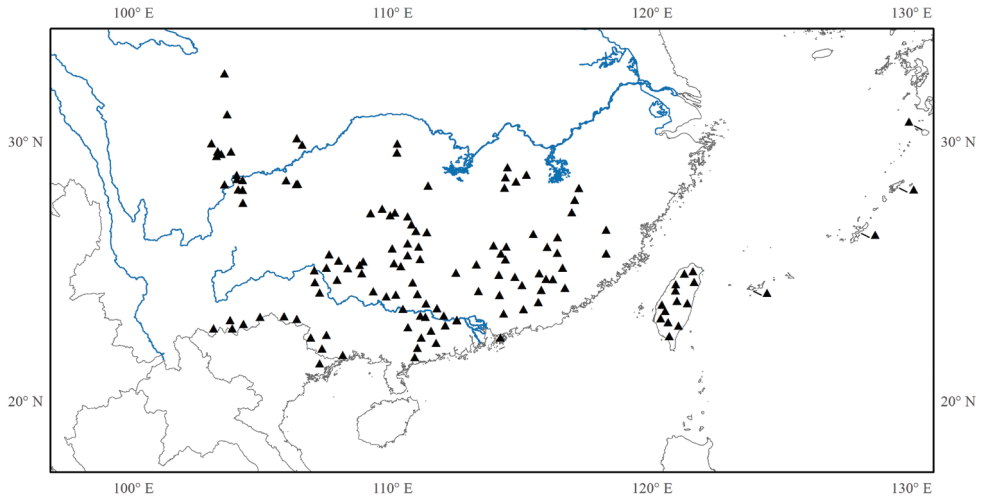


Figure 13. Distribution of *Bredia*.

Type. Taiwan, Taitung, Mt Dulan, on the ridge of a mountain, 1000–1200 m, 14 Oct 2007, S.W. Chung, T.C. Hsu & C.R. Yeh 16 (holotype: TAIF! [TAIF348619]; isotypes: TAIF! [TAIF348620, TAIF348621, TAIF348622]).

***Bredia esquirolii* (H. Lév.) Lauener, Notes Roy. Bot. Gard. Edinburgh 31(3): 398–399. 1972.**

Barthea esquirolii H. Lév., Repert. Spec. Nov. Regni Veg. 11(301–303): 494. 1913 (Basionym). Type: China. Guizhou: Tchai-choui-ho, July 1909, Esquirol 1581 (holotype: E! [E00090793]).

Bredia cordata H.L. Li, J. Arnold Arbor. 25(1): 24–25. 1944. Type: China. Sichuan: Ya-an, dense forest shade, 686 m, 30 Jul 1939. C. Y. Chiao 1205 (holotype: A! [A00071982]).

Bredia esquirolii var. *cordata* (H.L. Li) C. Chen, Bull. Bot. Res., Harbin 4(3): 40. 1984.

***Bredia fordii* (Hance) Diels, Bot. Jahrb. Syst. 65(2–3): 110. 1932.**

Otanthera fordii Hance, J. Bot. 19: 47. 1881 (Basionym). Type: China. Hong Kong, Jul 1880, C. Ford. herb no. 21099 (lectotype, designated here: BM! [BM000629024]; isolectotype BM! [BM000629025]).

Phyllagathis fordii (Hance) C. Chen, Bull. Bot. Res., Harbin 4(3): 50. 1984.

Bredia sepalsosa Diels, 65(2–3): 109–110. 1932. Type: China. Guangxi: Yao shan, 1928, S.S. Sin & K.K. Whang 648 (lectotype, designated here: IBSC! [IBSC0003942]).

***Bredia fordii* var. *micrantha* (C. Chen) R.C.Zhou & Ying Liu, comb. nov.**

urn:lsid:ipni.org:names:77199705-1

Phyllagathis fordii var. *micrantha* C. Chen, Bull. Bot. Res., Harbin 4(3): 50–51. 1984 (Basionym). Type: China. Guizhou: Dushan, in convallibus montanis, 600 m, 22 Aug 1930, Y. Tsiang 6563 (holotype: IBSC! [IBSC0003995]; isotypes: NAS! [NAS00052126] PE! [PE00782806, PE00782810]).

***Bredia gibba* Ohwi, J. Jap. Bot. 12(6): 385–386. 1936.**

Bredia penduliflora S.S. Ying, Quart. J. Chin. Forest. 6(1): 167. 1972. Type: Taiwan, Sakanyalan-Tawu, 10 Oct 1972, S.S. Ying 1517 (lectotype, designated here: NTUF! [F00004987]; isolectotypes: NTUF! [F00004986, F00004989, F00004990, F00004991, F00004992, F00004993]).

Type. Taiwan. Pingtung, Sungshan, J. Ohwi s.n. (holotype: KYO! [KYO00022400]).

***Bredia gracilis* (Hand.-Mazz.) Diels, Bot. Jahrb. Syst. 65(2–3): 110. 1932.**

Fordiophyton gracile Hand.-Mazz., Akad. Wiss. Wien, Math.-Naturwiss. Kl., Anz. 63: 3, 10. 1926 (Basionym). Type: China. Hunan: Heng Shan, Wukang, 1150–1300 m, 4–8 Aug 1918, Hand.-Mazz. 12380 (holotype: WU! [WU0059491]; isotypes: A! [A00055337] E! [E00090795]).

Phyllagathis gracilis (Hand.-Mazz.) C. Chen, Bull. Bot. Res., Harbin 4(3): 51. 1984.

***Bredia guidongensis* (K.M. Liu & J. Tian) R.C.Zhou & Ying Liu, comb. nov.**

urn:lsid:ipni.org:names:77199706-1

Phyllagathis guidongensis K.M. Liu & J. Tian, Phytotaxa 263(1): 58–62 (Basionym). Type: China. Hunan: Guidong County, Pule Town, 970 m, 3 Jul 2013, K.M. Liu, R.Y. Yi & L. Peng 24147 (holotype: HNNU; isotypes: HNNU CSFI).

***Bredia hirsuta* Blume, Mus. Bot. 1(2): 25. f. 4. 1849.**

Type. Japan. K. Ito s.n. (lectotype, designated here: L! [L0170980]).

In the protologue, Blume (1849) cited no specimen but the name “*Rhexia fasi-kan*” (should be *Rhexia hasikan*, see below) attached to a specimen from Von Siebold’s herbarium. Ohba and Akiyama (pers. comm.) discovered one sheet with the name “*Rhexia hasikan*” in the herbarium in Leiden (L0170980). The sheet contains two col-

lections, a smaller one covered by paper on the upper part and a larger one with four branches on the middle and lower part. According to Ohba (pers. comm.), the epithet “hasikan” comes from the Japanese name of *B. hirsuta*, viz. “Hashikan-boku”. This sheet is regarded as the type material of *B. hirsuta*. We here designate the larger collection on the sheet as the lectotype of *B. hirsuta*.

***Bredia hirsuta* var. *scandens* Ito & Matsum., J. Coll. Sci. Imp. Univ. Tokyo 12: 487. 1898.**

Bredia scandens (Ito & Matsum.) Hayata. J. Coll. Sci. Imp. Univ. Tokyo 30(1): 114. 1911.

Type. Taiwan, inter Suiteiryō et Niki, C. Owatari, Jan 1898 (the date “1896” cited in the protologue is probably erroneous) (lectotype, designated here: TI! [TI00002337]; isolectotype: TI!, [TI00002339]).

***Bredia latisejala* (C. Chen) R.C.Zhou & Ying Liu, comb. nov.**
urn:lsid:ipni.org:names:77199707-1

Phyllagathis latisejala C. Chen, Bull. Bot. Res., Harbin 4(3): 53–54. 1984 (Basionym).
Type: China. Hubei: Hefeng, ad pedes montis calcareo, 18 Sept 1958, H.J. Li 6451 (holotype: IBSC! [IBSC0003996]; isotype: PE! [PE00025692]).

***Bredia longearistata* (C. Chen) R.C.Zhou & Ying Liu, comb. nov.**
urn:lsid:ipni.org:names:77199708-1

Phyllagathis longearistata C. Chen, Bull. Bot. Res., Harbin 4(3): 52–53. 1984 (Basionym). Type: China. Guangxi: Hechi, prope rivulos in convallibus montanis, 19 May 1928, L.H. Chun 91861 (holotype: IBK! [IBK00190677]; isotype: IBK! [IBK00190678]).

***Bredia longiloba* (Hand.-Mazz.) Diels, Bot. Jahrb. Syst. 65(2–3): 111. 1933.**

Fordiophyton gracile var. *longilobum* Hand.-Mazz., Akad. Wiss. Wien, Math.-Naturwiss. Kl., Anz. 63: 3, 10. 1926 (Basionym). Type: China. Jiangxi: between Ningdu and Ki-an, T.H. Wang 493 (holotype: WU! [WU0059490]).

***Bredia longiradiosa* C. Chen ex Govaerts, World Checkl. Seed Pl. 2(1): 13. 1996.**

Phyllagathis longiradosa C. Chen, Bull. Bot. Res., Harbin 4(3): 51. 1984 (Basionym).

Type: Based on *Barthea cavaleriei* H. Lév.

Barthea cavaleriei H. Lév., Repert. Spec. Nov. Regni Veg. 8(160–162): 61. 1910. Type: China. Guizhou: near Mou-you-sé, J. Cavalerie 1552 (lectotype, designated by Diels 1932, pg. 110: E! [E00090789]).

Fordiophyton cavaleriei (H. Lév.) Guillaumin, Bull. Soc. Bot. France 60: 275. 1913.

Bredia cavaleriei (H. Lév.) Diels, Bot. Jahrb. Syst. 65(2–3): 110. 1932.

Bredia longiradosa C. Chen, Fl. Yunnan 2: 105, f. 27, 1–5. 1979. nom. inval. (reference to place of publication of basionym not provided).

***Bredia longiradosa* var. *pulchella* (C. Chen) R.C.Zhou & Ying Liu, comb. nov.**
urn:lsid:ipni.org:names:77199709-1

Phyllagathis longiradosa var. *pulchella* C. Chen, Bull. Bot. Res., Harbin 4(3): 52. 1984 (Basionym). Type: China. Guangxi: Daxin, Longjin, 4 May 1959, F.F. Huang 3596 (holotype: GXMI! [GXMI050237]).

Notes. Three gatherings were cited in the protologue of *Barthea cavaleriei*, viz. Cavalerie 1552, Esquirol 1581 and Esquirol 215, without designation of a type. Two of the syntypes, Esquirol 1581 and 215 were later cited as the types of *Barthea esquirolii* H. Lév. (1913) and *Barthea blinii* H. Lév. (1913), respectively. Guillaumin (1913) transferred *Barthea cavaleriei* to *Fordiophyton* citing only Cavalerie 1552 under the new combination *F. cavaleriei* (H. Lév.) Guillaumin. Diels (1932) formally designated Cavalerie 1552 as the lectotype and published a new combination *Bredia cavaleriei* (H. Lév.) Diels. However, this name is an illegitimate later homonym of *B. cavaleriei* H. Lév. & Vaniot (see Art. 53.1). Chen (1979) published the replacement name *B. longiradosa* C. Chen for this species, but he did not provide a full reference of the basionym, which makes the name invalid (see Art. 41.1). Chen (1984b) subsequently transferred the species to *Phyllagathis*. As the epithet *cavaleriei* is also not available in *Phyllagathis*, a new name *P. longiradosa* C. Chen was published together with the description of a new variety, *P. longiradosa* var. *pulchella* C. Chen. There are three effectively published names for this species in *Bredia*. With *B. cavaleriei* (H. Lév.) Diels illegitimate and *B. longiradosa* C. Chen invalid, the only legitimate name, *B. longiradosa* C. Chen ex Govaerts is adopted as the correct name for this species.

***Bredia microphylla* H.L. Li, J. Arnold Arbor. 25(1): 23. 1944.**

Type. China. Guangxi: Guilin District, Chi-fen Shan, Xichang Cun and vicinity, W.T. Tsang 28432 (holotype: A! [A00071988]; isotype: IBSC! [IBSC0003950]).

***Bredia oldhamii* Hook. f., Icon. Pl. 11: 68, pl. 1085. 1871.**

Bredia oldhamii var. *ovata* Ohwi, J. Jap. Bot. 12(9): 661–662. 1936. Type: Taiwan, Taitung, in open forest, forest margin, 100–1200 m, J. Ohwi 425 (holotype: KYO).

Type. Taiwan, near Tamsuy, Jan 1864, R. Oldham 118 (holotype: K! [K000978944]; isotype: GH! [GH00071989] P! [P02274733] US! [US00120439]).

***Bredia plagiopetala* (C. Chen) R.C.Zhou & Ying Liu, comb. nov.**

urn:lsid:ipni.org:names:77199710-1

Phyllagathis plagiopetala C. Chen, Bull. Bot. Res., Harbin 4(3): 44–45. 1984 (Basionym). Type: China. Hunan: Xinning, Ziyun Shan, in dense silvis apice montium, 800 m, 11 Jul 1959, P.C. Tam 63423 (holotype: IBK! [IBK00127587]).

***Bredia repens* R.C. Zhou, Q.J. Zhou & Ying Liu, Syst. Bot. 43(2): 549. 2018.**

Type. China. Hunan: Sangzhi County, from Shayuan to Nanmuping village, 430–470 m, 11 Nov 2016, Y. Liu 558 (holotype: SYS!; isotypes: A! SYS!).

***Bredia rotundifolia* Yan Liu & C.H. Ou, Quart. J. Chin. Forest. 9(2): 118, f. 1. 1976.**

Type. Taiwan, Chiayi, Juili, Ou 2869 (holotype: NCUF).

***Bredia tuberculata* (Guillaumin) Diels, Bot. Jahrb. Syst. 65(2–3): 111. 1932.**

Fordiophyton tuberculatum Guillaumin, Notul. Syst. (Paris) 2(11): 326. 1913 (Basionym). Type: China. Yunnan: Tchen fong chan, Delavay 5053 (lectotype, designated here: E! [E00285959]; isolectotypes: P! [P02274731], P! [P02274729] individual on the right side of the sheet).

Bredia omeiensis H.L. Li, J. Arnold Arbor. 25(1): 24. 1944. Type: China. Sichuan: Emei Shan, 1100 m, 21 Aug 1937, Y.S. Liu 1080 (holotype: A! [A00071990]; isotype: LBG! [LBG00089612]).

Notes. Three gatherings were cited in the protologue of *Fordiophyton tuberculatum*, viz. Delavay 5053, Ducloux 2192 and Wilson 4906. Diels (1932) designated Delavay 5053 as the type without citing a specific herbarium. We located four duplicates of Delavay 5053 (E00285959, P02274729, P02274730, P02274731). Close examination of the specimens revealed that this gathering is a mixture of *B. tuberculata* and *B. yunnanensis*. Individuals on E00285959, P02274731 and the one on the right side of P02274729

conform to the protologue of *B. tuberculata* in the adaxially white punctate leaves and unequal and dimorphic stamens. The remaining four individuals (three on P02274730 and one on the left side of P02274729) conform to the holotype of *B. yunnanensis* in the absence of white spots on their leaves and the subequal and isomorphic stamens. According to Art. 9.11, 9.12, 9.14, and 9.17 (Turland et al. 2018), the lectotypification by Diels should be accepted and further narrowed to a single specimen that corresponds most closely with the original description. We therefore designate E00285959 as the lectotype as it conforms to the description and contains many well-preserved leaves and flowers.

***Bredia violacea* H.L. Li, J. Arnold Arbor. 26(1): 120. 1945.**

Type. Vietnam. Tonkin: Tian-yen, Ho Yung Shan & vicinity, 13 Oct–22 Nov 1940, W.T. Tsang 30751 (holotype: A! [A00071992]).

***Bredia velutina* Diels, Bot. Jahrb. Syst. 65(2–3): 109. 1932.**

Phyllagathis velutina (Diels) C. Chen, Bull. Bot. Res., Harbin 4(3): 51. 1984.

Type. China. Yunnan: Mengzi, 1000–2300 m, A. Henry 13479 (lectotype, designated here: K! [K000867582]; isolectotypes: A! [A00055334] NY! [NY00221472]).

***Bredia yunnanensis* (H. Lév.) Diels, Bot. Jahrb. Syst. 65(2–3): 111. 1932.**

Blastus yunnanensis H. Lév., Repert. Spec. Nov. Regni Veg. 11(286–290): 300–301. 1912 (Basionym). Type: China. Yunnan: Vallée de Long-Ky, pied des rochers humides, 700 m, Aug 1911, Maire s.n. (holotype: E! [E00285956]).

Blastus mairei H. Lév., Repert. Spec. Nov. Regni Veg. 11(286–290): 300. 1912. Type: China. Yunnan: Bord des eaux, Vallée de Long-Ky, 700 m, Jul 1911, Maire s.n. (holotype: E! [00285957]).

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Supplementary material I

Table S1. Source of materials studied and GenBank accession numbers for nrITS and chloroplast intergenic spacer *trnV-trnM*

Authors: Qiu-Jie Zhou, Jin-Hong Dai, Che-Wei Lin, Tetsuo Denda, Ren-Chao Zhou, Ying Liu

Data type: molecular data

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