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A SYNOPSIS OF THE GENUS BRAYA (BRASSICACEAE)

IHSAN A. AL-SHEHBAZ1,2 AND DMITRY A. GERMAN3

Abstract. Synonymy, typification, distribution, and key to the 23 species of Braya are given, along with an updated generic description. The new species B. sichuanaica is described and illustrated. The new combinations B. fengii, B. parvia, B. piaszecki, B. qingshuiheense, and B. stignatosa are proposed. A list of taxa excluded from Braya is given, along with their current generic and tribal placements. The following taxa are lectotypified: Beketovia tianschanica, Braya aenea var. multicaulis, B. aenea var. simplicior, B. pectinata, B. purpurascens var. longisiliquosa, B. rosea var. angustifolia, B. tibetica var. breviscapa, B. versicolor, Erysimum pamiricum, E. stigmatosum, Pilosella richardsonii, Sisymbrium nanum var. leiocarpum, and Torularia humilis pro. venusta. Previous designations are narrowed for Arabis sinuata, Braya aenea, B. rosea, B. thomsonii, and B. tibetica.

Keywords. Cruciferae, Euclidieae, Neotorularia, Eurasia, North America, typification

Braya Sternb. & Hoppe (Brassicaceae or Cruciferae) is distributed primarily in the alpine and subarctic regions of Eurasia and North America. There is a lack of agreement among various authors on the total number of species in the genus, and estimates within the past decade varied from six (Appel & Al-Shehbaz, 2003), to 17 (Harris, 2010), to 25 species (Al-Shehbaz, 2012). This major discrepancy reflects the lack of a comprehensive study of the genus. Except for the long-outdated account of Schulz (1924), the genus has not previously been studied on a worldwide basis. The North American species were subjected to more studies (e.g., Fernald, 1918; Abbe, 1948; Rollins, 1953; Böcher, 1956, 1973; Harris, 1985, 2006a, 2006b, 2010) than were their congeners of the Old World, especially Asia.

Perhaps one source of taxonomic difficulty in Braya is the excessive recognition of taxa, and the International Plant Names Index (IPNI) lists some 105 unique records at the species, subspecies, and varietal ranks. Of these, 16 are accepted herein as species, 37 are excluded and currently placed in 18 genera of ten tribes (see below), 51 are synonymized in Braya, and three (discussed under B. humilis) are considered of doubtful status. Another factor is the difficulty in delimiting Braya from its closest relative Neotorularia Hedge & J. Léonard due to substantially overlapping characters. Although molecular data (Warwick et al., 2004; German et al., 2009) showed that the two genera are distinct members of the tribe Euclidieae, more work is needed to resolve the boundaries of polyphyletic Neotorularia.

Half of the species of Braya have siliques, and this fruit type is a reliable feature that readily distinguishes the genus from Neotorularia, which exclusively has silique fruits. However, Braya species that produce siliques can be separated from Neotorularia by their usually perennial (vs. annual) duration, slender and relatively long (vs. usually short and stout) fruiting pedicels narrower than (vs. usually as wide as) the fruit, usually basally bracteate (vs. ebracteate) racemes, straight or slightly curved (vs. often twisted or strongly curved) fruits, and 2-lobed or less often entire (vs. entire) stigmas.

The present synopsis accounts for all names in Braya (excluding forms), and also provides the basis for two major works currently in progress, the World Flora Online and the Brassicaceae database (Brassibase) in Heidelberg University (see Koch et al., 2012; Kiefer et al., 2014).

The taxonomic status of all infraspecific taxa, including 16 not listed in IPNI and excluding all forms, are dealt with and typified, and an updated generic description and key to all species are given.

Unless otherwise indicated, type specimens and/or images of all taxa included in this work were examined by one or both of us.


We are grateful to David E. Boufford (A) for allowing us to study his recent collections of Chinese Brassicaceae, to Barbara Thiers (NY) and Anthony R. Brach (A and GH) for locating type collections, to Libing Zhang (MO) for helping with localities in China and publication dates of Chinese journals, to Tatiana V. Shulikina (MO) for helping Al-Shehbaz with Russian text, to Barbara Helltenthal (NDG) for sending images of the type collection of Braya pectinata Greene, and to Gustavo A. Romero and Deborah Smiley for their editorial advice. Partial funding for this research was supported by the United States National Science Foundation grant DEB-1252905 to Al-Shehbaz and by the DFG priority program 1529 “Adaptomics” to German, for which they are profoundly grateful. We are grateful to the directors, curators, and collection managers of A, AA, ALTB, B, BAA, BAB, BACP, BH, BM, BRNM, BRNU, CAS, CDBA, CONC, DAO, DS, E, FI, FRU, G, GH, GOET, H, HAL, HEID, HIP, HNW, JE, K, KFTA, KUN, KW, LE, LIL, LP, M, MHA, MO, MSB, MW, NAS, NS, NSK, NY, OSBU, P, PE, POM, PR, PRC, RM, S, SI, SZ, TASH, TK, UC, UPS, US, W, WU, XIA, XJBI, XJU, and Z for sending loans and/or allowing us study their collections of Braya.

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Herbs perennial or rarely annual, with simple to many-branched caudices, sometimes scapose and/or forming cushions. Trichomes simple and/or stalked to subsessile, submalpighiaceous, forked, subdendritic, or stellate. Multicellular glands absent. Stems erect to ascending or rarely decumbent, simple or branched basally, leafy or leafless, unarmed. Basal leaves petiolate, rosulate, simple, margin entire or dentate, rarely pinnately lobed, pinnatisect, or subpinnate, petiolar bases persistent; cauline leaves absent or few to several, sessile or nearly so, not auriculate at base, margin similar to basal leaves. Racemes few to many flowered, ebracteate or bracteate basally or throughout, corymbose, elongated or not elongated in fruit; racemes bracteate throughout, or few to several, sessile or rarely 1(–3)-leaved. Sepals ovate to oblong, free or rarely united, deciduous or persistent, erect, equal, base of inner pair not saccate; petals white, pink, or purple, rarely yellow, erect at base with flaring blade, slightly to distinctly longer than sepals; blade obovate to oblanceolate, apex obtuse to rounded; claw often slightly differentiated from blade, shorter than sepals, glabrous, entire; stamens 6, slightly exserted, erect, tetradyadous; filaments wingless, unappendaged, glabrous, free, dilated at base; anthers ovate or oblong, not apiculate at apex; nectar glands 4, lateral, 1 on each side of lateral stamens; median glands absent; ovules 4–28 per ovary; placental parietal. Fruits dehiscent, capsular siliques or silicles, linear, oblong, lanceolate, ellipsoid, ovoid, or globose, terete or slightly latiseptate, not inflated, unsegmented; valves papery, with a distinct midvein, glabrous or pubescent, not keeled, smooth or torulose, wingless, unappendaged; gynophore absent; replum rounded, visible; septum complete, membranous, usually translucent, veinless; style obsolete or short and to 1.2(−2.5) mm, cylindric, persistent, glabrous; stigma capitate, entire or slightly 2-lobed, lobes free, not recurved, unappendaged. Seeds uniseriate or biseriate, wingless, oblong or ovoid, plump; seed coat minutely reticulate, not mucilaginous when wet; cotyledons incumbent or rarely obliquely so. \( x = 7 \)

As delimited herein, Braya consists of 23 instead of the 25 species estimated by Al-Shehbaz (2012). The difference is the reduction of some of the species to synonymy based on the examination of substantial material, including types.

### Key to the species of Braya

1a. Fruits linear, rarely linear-oblong ................................................................. 2
1b. Fruits globose, ovoid, ellipsoid, oblong, or lanceolate ................................... 15
2a. Sepals united ............................................................................................. 15
2b. Sepals free ................................................................................................ 3
3a. Plants scapose or subscapose; stems simple or rarely branched, leafless or rarely 1(–3)-leaved ........................................................................... 4
3b. Plants not scapose; stems usually branched, more than 3-leaved ........................................................................... 9
4a. Fruits oblong-linear, to 7 time longer than broad ........................................... 5
4b. Fruits linear, usually more than 7 times longer than broad .............................. 7
5a. Raceme capitate in fruit; fruits recurved at apex (4–7 times in B. alpina) .......... B. thomsonii
5b. Raceme elongated in fruit; fruits not recurved at apex ................................. 6
6a. Seeds biseriate throughout; Alaska, Canada, Russian Far East ................. B. glabella
6b. Seeds often biseriate only proximally, distally (or throughout) subbiseriate to almost uniseriate; Siberia, Central Asia, Himalayas . . . . B. rosea
7a. Style (0.5–)0.9–1.2 mm in fruit; petals 4–6 mm; Mongolia, Russia (Siberia, Far East) ........................................... B. siliquosa
7b. Style 0.1–0.5 mm in fruit; petals 2.5–3.5(−4) mm; Europe ................................ 8
8a. Fruits 8–15 × 0.9–1.3 mm, 9–12 times longer than wide; ovules 20–28 per ovary; Greenland, Norway, Sweden ........................................... B. linearis
8b. Fruits 5–11 × 1–1.7 mm, 4–7 times longer than wide; ovules 12–18 per ovary; Alps of Austria and Italy ........................................... B. alpina
9a. All leaves pinnatisect to subpinnate; petioles long ciliate with subsetose simple trichomes to 1.2 mm ........................................... B. siliquosa
9b. At least some leaves entire, dentate, or pinnatifid; petioles not ciliate or rarely short ciliate with non-setose trichomes ............... 10
10a. Petals 1–2.5 × 0.5–0.9(−1.1) mm; fruits 5–10(−12) mm, widest and biseriately seeded basally ........................................... B. parvula
10b. Petals 2.5–10 × 0.7–6 mm; fruits 9–35 mm, uniformly wide and uniseriately seeded basally ........................................... 11
11a. Fruits pinnatus; stigma distinctly wider than style, oftenensely recurved with lobed recurves ........................................... B. stigmatosa
11b. Fruits straight; stigma narrower than or about as wide as style, entire or with non-recurred lobes ........................................... 12
12a. Petals 6–9(–10) × (3)–3.5–6 mm, purple or rarely lavender; leaves pinnatifid or sinuate-pinnatifid; plants with thick, woody caudex ........................................... B. fennii
12b. Petals (2.5–)3–5(–5.5) × (0.7)–1–2(–3) mm, white, lavender, or rarely purple; leaves entire, dentate, or sinuate, rarely pinnatifid; caudex slender or poorly developed ........................................... 13
13a. Cotyledons obliquely incumbent; fruits latiseptate or slightly flattened; stigma 2-lobed ........................................... B. piasezkii
13b. Cotyledons incumbent; fruits terete; stigma entire or 2-lobed ................................ 14
14a. Fruiting racemes with straight rachis; stigma entire; basal leaves entire or dentate, not pinnatifid ........................................... B. humilis
14b. Fruiting racemes with flexuous rachis; stigma strongly 2-lobed; basal leaves pinnatifid ........................................... B. qingshuiheense
15a. (1b) Flowers yellow .............................................................................. 16
15b. Flowers white, pink, lavender, rose, or purple ........................................... 17
16a. Fruits torulose, 6–8(–14) × 1–1.2 mm, 5–8(–11) times longer than broad; racemes ebracteate or basally bracteate, elongated in fruit ........................................... B. pamirica
16b. Fruits smooth, rarely torulose, 3–4.5(–5) × 1.8–2 mm, 1.8–2.5 times longer than broad; racemes bracteate throughout, not elongated in fruit ........................................... B. scharnhorstii
KEY TO THE SPECIES OF Braya cont.

17a. Trichomes exclusively simple; ovary 4–8-ovuled. ................................................................. B. forrestii
17b. At least some trichomes branched; ovary 10–30-ovuled ........................................................ 18

18a. Racemes bracteate throughout; fruits basally biseriate, distally uniseriate ............................ B. parvula
18b. Racemes ebracteate; fruits usually uniformly either uniseriate or biseriate .............................. 19

19a. Fruits globose to broadly ovoid, 1–2 times longer than broad .............................................. 20
19b. Fruits narrowly ovoid, ellipsoid, lanceolate, to oblanceolate, more than twice longer than broad ............................................................................................................................. 23

20a. Fruits 1–2 mm wide; raceme not elongated in fruit; China, India, Pakistan .......................... B. tibetica
20b. Fruits (1.2–)3–5 mm wide; raceme elongated or not in fruit; Canada, Russia, Central Asia, U.S.A. (Alaska) ................................................................. B. pilosa

21a. Style 1.2–2(–2.5) mm in fruit; petals 4.5–6.5 × 3–5 mm ........................................................ B. thorild-wulffii
21b. Style 0.1–0.7(–1) mm in fruit; petals 2–3.7 × 1–1.5 mm ........................................................... B. rosea

22a. Fruits 3–5 mm wide; basal leaves spatulate to narrowly so; Russia (Siberia), Central Asia .................. B. fernaldii
22b. Fruits 1.2–2 mm wide; basal leaves linear to linear-oblanceolate; Russia (Siberia), Central Asia .............................. B. pilosa

23a. Fruit replum not expanded at base; ovules 16–24 per ovary .............................................. B. pilosa
23b. Fruit replum expanded at base; ovules 10–16 per ovary ..................................................... B. rosea


Distribution: Austria, Italy.


Distribution: China (SE Tibet, Yunnan).

When Phaeochnychium fengii was described (Al-Shehbaz, 2000a), no fruiting material was available, and its generic relationship was not entirely clear. However, the availability of additional material with young fruits amply demonstrate that the affinity of this species is with Braya humilis, especially for having linear, terete fruits with submalpighiaceous trichomes and basally bracteate racemes. All other species of Phaeochnychium O. E. Schulz sensu Al-Shehbaz (2000a) have recently been transferred by Yue et al. (2008) and German & Al-Shehbaz (2010) to Solms-Laubachia Muschl.

Braya fernaldii differs from B. humilis by having thick and woody (vs. slender and non-woody) caudex, pinnatifid to sinuate-pinnatifid (vs. entire to dentate or rarely sinuate) basal leaves, purple or rarely lavender (vs. white, rarely lavender or purple) flowers, larger petals 6–9(–10) × (3–)3.5–5(–6) mm (vs. (2.5–)3–5(–5.5) × (0.7–)1–2(–2.5) mm), and 2-lobed (vs. entire or rarely slightly lobed) stigmas. The presence of simple trichomes in B. fengii varies a great deal from being restricted to the basal leaves to being widespread to the inflorescence, sepalas, and sometimes fruits. By contrast, typical B. humilis either lacks the simple trichomes or have them restricted to petioles of lowermost and basal leaves.

Schulz (1931) cited two syntypes (Rock 17190 and Rock 17374) for Torularia humilis prol. venusta. The most complete specimen is designated herein as the lectotype.


Distribution: Bhutan, China (Sichuan, Xizang, Yunnan).

Braya fernaldii is anomalous in Braya for having exclusively simple trichomes, whereas all other species of
the genus have one or more type of branched trichomes in addition sometimes to simple ones. Warwick et al. (2004) showed that B. forrestii clearly falls in a clade sister to the rest of Braya. Based on that finding, Al-Shehbaz et al. (2004) suggested that the species perhaps ought to be placed in a genus of its own. Without detailed molecular studies on this species and other genera closely related to Braya, we prefer to tentatively retain the species in this genus.


**Braya aenea** subsp. **pseudoaenea** V. V. Petrovsky, Arkhiches. Fl. SSSR 7: 49. 1975. TYPE: RUSSIA. Southeast part of Chukotka peninsula, shore of Senyavin strait, vicinities of Yanrakynnot near the mouth of the river Marich, 22 July 1972, V. V. Razzhivin & B. A. Yurtsev SG 72-33 (Holotype: LE; Isotypes: 3 at LE).

**Distribution:** Canada (Alberta, British Columbia, Northwest Territories, Nunavut, Quebec, Yukon), U.S.A. (Alaska, Colorado, Montana, Wyoming), Russia (Wrangel Island, East Chukotka).


**Pilosella richardsonii** Rydb., Torreya 7(8): 159. 1907; **Braya richardsonii** (Rydb.) Fernald, Rhodora 20: 203. 1919; **B. humilis** subsp. **richardsonii** (Rydb.) Hultén, Ark. Bot., n.s. 7(1): 66. 1968. TYPE: [CANADA. Northwest Territories], about Mackenzie River, from lat. 60° to 68°, 1935 (Lectotype designated by Dorofeyev in German (2005: 255); LE).


*Arabidopsis trichocarpa* R. F. Huang, Fl. Qinghaiica 1: 247. 1988; *Neotorularia trichocarpa* (Böcher) B. humilis (var. interior) Böcher. Braya humilis is by far the most variable and widespread species in the genus, and the variation covers almost every aspect of morphology. It appears that the main sources of variation are the presence of different breeding systems, hybridization, and polyploidy (e.g., 4x, 6x, 8x, and 10x based on x = 7), which lead various authors to recognize several species, subspecies, and varieties in the complex (Harris, 2006a). Plants corresponding best to the type collections from the Altai Mountains (see also discussion under *B. fengii*) have white, small petals rarely to 5.5 × 2.5 mm, terete fruits with exclusively submalpighiaceous trichomes, entire stigmas narrower than the style, and leaves with predominantly submalpighiaceous and 3-fid trichomes and rarely some simple trichomes, especially along the petioles of basal and lowermost cauline leaves. The greatest variability occurs in the Himalayas, where lavender or purplish flowers are more common than white, and the presence of simple trichomes tends to be quite variable and ranges from the lower parts of the plant all the way up to the sepal and sometimes fruits. Flower size in the species is also most variable in the Himalayas, and some forms approach the smallest flower size of *B. fengii*. The cause of this variation is unclear, and extensive cytological and breeding experiments are needed to elucidate the sources of this complexity. Plants with preponderance of simple trichomes are extremely rare and only in one case (*Rock 14131*) at GH had we examined a mixed collection of a typical *B. humilis* plant mounted with another having almost exclusively simple trichomes.

Harris (2006b) divided the North American populations of *Braya humilis* into four subspecies, including subsp. *humilis*. While his subs. *ellesmerensis* J. G. Harris is distinctive and should merit recognition, the status of the sterile subs. *maccallae* J. G. Harris and subs. *porsildii* J. G. Harris requires further study, especially in connection with the extensively widespread and far more variable Asian representatives of the species. Without such a thorough study, it would be meaningless to recognize infraspecific taxa in a small portion of the species range and ignore the vast territory it occupies in Asia, especially the Himalayas. It is beyond the scope of this study to deal with the North American infraspecific taxa, and the interested reader should consult the Panarctic Flora website (http://nhm2.uio.no/paf/flora#paf-670903) and Harris (2006b, 2010).

*Torularia grubovii* was separated from *B. humilis* by having numerous rosette leaves and higher percentage of simple and long-stalked forked (instead of sessile to subsessile) trichomes (Botschantzev, 1975). Indument variability in *B. humilis* is discussed above and number of rosette leaves also varies greatly and cannot be used as reliable character for maintaining the former a distinct species.

*Neotorularia mongolica* was distinguished from *B. humilis* by being annual [vs. perennial] with usually entire [vs. predominantly sinuate-dentate] leaves, yellow petals 5.5 mm long [vs. white to pink or purplish petals (2.5–)3–5–(5.5) mm], style of equal width to [vs. slightly narrower than] the stigma, and opaque [vs. translucent] septum (Botschantzev & Gubanov, 1988). Despite these apparently convincing differences, they only partly work at best. Thus, life form in *B. humilis* is flexible and being usually perennial...
it can flower during the first season. Variability of leaf shape and margin was well illustrated by Berkutenko (1977), and her observations are supported by our study. Furthermore, while in the isotype of *N. mongolica* most leaves are entire to subentire, the holotype has profoundly dentate leaves. Style of equal width with the stigma is another character rather typical for *B. humilis* and the petals 5.5 mm long found in *N. mongolica* corresponds the upper limit of petal size of *B. humilis* which varies a great deal within the species. Yellow petals is a unique feature unknown in *B. humilis* and related species, and it might justify some distinctness of *N. mongolica*. However, petals of the type gathering are white with pink claws and only youngest flowers are very pale yellowish. It is highly desirable to have fresh material to resolve the status of *N. mongolica*, but with the currently available single collection (two specimens) and taking into consideration the overall similarity with *B. humilis* in all other characters, we refrain from recognizing *N. mongolica*.

The holotype of *Neotorularia mongolica* in MW is with a printed label “Isotypus” while the isotype in LE bears the label “Typus.” Furthermore, the latter is reported as holotype in the catalogue of type specimens of LE (Buzunova, 2000), and Gubanov (2002) mentioned that MW was wrongly indicated in the protologue as the place of deposition of the type instead of LE and that the specimen in MW is an isotype. However, this change is in conflict with ICN Art. 9.1, Note 1 (McNeill et al., 2012) and cannot be accepted; thus, the specimen in MW is holotype, as stated in the protologue, and that in LE is an isotype.


**Distribution:** Greenland, Norway, Sweden.


**Distribution:** Canada (Newfoundland).


1–2.5 × 0.5–0.9(–1.1) mm (vs. (2.5–)3–(5–)5 × (0.7–)1–2 (–2.5) mm), fruits basally biseriate (vs. uniseriate), usually shorter (vs. longer) than 1 cm, and widest (vs. narrower) at 1–2.5 × 0.5–0.9(–1.1) mm (vs. (2.5–)3–5(–5.5) × (0.7–)1–2 & Leningrad) 44: 1488. 1959; Neotorularia piasezkii (Maxim.) Botsch., Bot. Zhurn. (Moscow & Leningrad) 73: 1188. 1988. (comb. invalid., no basionym cited); (Maxim.) Botsch., Bot. Zhurn. (Moscow & Leningrad) 44: 1488. 1959; Neotorularia piasezkii (Maxim.) Botsch., Bot. Zhurn. (Moscow & Leningrad).


Distribution: China (Beijing, Gansu, Hebei, Shanxi, Tibet).

Braya piasezkii is easily distinguished from B. humilis by having obliquely incumbent (vs. incumbent) cotyledons, horizontally spreading (vs. ascending to erect) fruits and fruiting pedicels, latiseptate to slightly flattened (vs. terete) fruits, and 2-lobed (vs. entire) stigmas usually slightly wider (vs. narrower) than style. Both species and B. stigmatosa have similar petal size (3–5 × 1–2.5 mm), but they differ from the last species by their straight (vs. tortuose) fruits.

The illustration of Braya piasezkii (as Arabis) in plate 12 of Maximowicz (1889a) corresponds very well to the description, but the illustration is not sufficient to establish whether or not they are conspecific.


Braya pilosa was considered by Harris (2006a, 2010) to be restricted to the type locality, but the species range was expanded in the Panarctic Flora to cover the larger territories listed above. Forms outside the type area of locality seem to have somewhat shorter styles, and further studies are needed to firmly establish whether or not they are conspecific.


Distribution (circumpolar): Canada (British Columbia, Northwest Territories, Nunavut), U.S.A. (Alaska), Norway, Russia (Far East, NE European part, Siberia), Svalbard (Spitzbergen).

The taxonomic status of Braya purpurascens varied from treating it as a synonym of B. glabella (Harris, 1985; Rollins, 1993), as a subspecies of the latter (Harris, 2006b, 2010), or as a distinct species (Schulz, 1924; Vassilezenko, 1939; Ball, 1993; Jalas & Suominen, 1994; Czerepanov, 1995). Although molecular data (Warwick et al., 2004) showed that the two species are similar in their ITS sequences, it is clear that they are reproductively isolated in areas of sympatry, as evidenced from field observation reported in the Panarctic Flora. (http://nhm2.uio.no/paf/flora#paf-670903). We prefer to follow that latter conclusion and maintain both taxa as independent species.

The differences between Braya purpurascens s. str. and subsp. prostrata rests solely on quantitative and continuous characters and may not justify the division of the species into infraspecific taxa.


Distribution: China (Nei Mongol).

Braya qingshuiheense resembles B. humilis in flower and fruit size, the overall habit, and trichomes type. It is readily distinguished from the latter by the characters listed in the key above.


**Distribution:** China (Xinjiang), Kyrgyzstan.


**Distribution:** China (Xinjiang), Kyrgyzstan.

18. **Braya sichuana** Al-Shehbaz, sp. nov. TYPE: CHINA. Sichuan, Jiulong Xian, Tanggu Xiang, NW of the city of Jiulong at Wuxu Hai (Wuxu Lake) Scenic Area, gentle to steep slopes and adjacent limestone cliffs and sand scree slopes, 29°8′14″N, 101°24′47″E, 3,665–4,460 m, 4 August 2010, D. E. Boufford, L. Y. Chen, J. L. Dong, X. H. Li and J. P. Yue 42622 (Holotype: A; Isotype: MO). Fig. 1.

**Herbs** perennial; caudex simple, slender, covered with some leaf remnants of previous years. **Stems** erect to ascending, single to several from caudex, simple or rarely branched, 4–12 cm, pubescent throughout with minutely stalked, submalpighiaceous trichomes 0.2–0.7 mm. **Basal leaves** rosulate, pinnatisect to subpectinate, 1–1.5 cm, sparsely pubescent with stalked, 2- or 3-forked trichomes mixed with submalpighiaceous ones; petiole 5–10 mm, ciliate with subentose simple trichomes 0.7–1.2 mm; lateral lobes 2–4, ovate to oblong, 0.7–2 × 0.2–0.7 mm, proximal lobes smallest; terminal lobe larger than lateral ones, oblong to oblanceolate; cauleine leaves similar to basal, progressively smaller upwards. **Raceme** 7–20-flowered, elongated in fruit; rachis straight, pubescent as stem; fruiting pedicels 2.5–6 mm, narrower than fruit, divaricate to horizontal, straight or recurved, pubescent as stem, lowermost bracteate. **Flowers** not seen. **Fruits** linear, terete, sessile, torulose, 10–17 × 0.7–0.9 mm, straight or arcuate, pubescent with
Figure 1. *Braya sichuanica* Al-Shehbaz. **A**, plant; **B**, basal leaf; **C**, fruit and fruiting pedicel. Bars = 1 cm (A); 5 mm (B); 2 mm (C). Drawn by Al-Shehbaz from the isotype (MO).
subsessile, submalpighiaceous trichomes variable in length; septum membranous; style 0.5–1 mm; stigma 2-lobed, lobes opposite replum. Seeds and ovules 18–26 per ovary, uniseriate, oblong, brown, 0.8–1 x ca. 0.4 mm; cotyledons incumbent.

**Distribution:** China (Sichuan). Known only from the type collection.

**Braya sichuanica** is allied to the *B. humilis* relatives that have linear, terete fruits pubescent with submalpighiaceous trichomes, basally bracteate racemes, and leafy stems. From these and the remainder of the genus, the species is easily distinguished by the finely pinnatisect to subpectinate basal leaves with petioles long ciliate with subsetose simple trichomes to 1.2 mm.


**Distribution:** Mongolia, Russia (Siberia, Far East).

Previous records of *B. siliquosa* from Kazakhstan are based on misidentified plants of *B. rosea* (German, 2003).


**Sisymbrium piazezkii** Maxim., Bull. Acad. Petersb. 26: 421. 1880; *S. humile* C. A. Mey. var. piazezkii (Maxim.) Maxim., Enum. Pl. Mongol. 1: 62. 1889; *Hesperis piazezkii* (Maxim.) Kuntze, Revis. Gen. Pl. 935. 1891; *Torularia humilis* (C. A. Mey.) O. E. Schulz prol. piazezkii (Maxim.) O. E. Schulz in Engler, Pflanzenreich IV. 105(Heft 86): 226. 1924; *T. maximowiczii* Botsch., Bot. Zhurn. (Moscow & Leningrad) 44: 1488. 1959, non *T. piazezkii* (Maxim.) Botsch., Bot. Zhurn. (Moscow & Leningrad) 44: 1488. 1959; *T. maximowiczii* (Botsch.) H. L. Yang, Acta Phytotax. Sin. 19: 243. 1981; *Neotorularia maximowiczii* (Botsch.) Botsch., Bot. Zhurn. (Moscow & Leningrad) 73: 1188. 1988; *Malcolmia perennans* Maxim., Fl. Tangut. 5: 168. 1861. TYPE: [CHINA]. Tibet, Piti, 4 September 1847, 12,000–13,000 ft [3,658–3,962 m], T. Thomson s.n. (lectotype partially designated by Jafri (1973: 261) as type and completed herein: K; Isolectotypes: B, K). Two sheets of this type collection are at K; the one annotated by Jafri as the lectotype. The three plants on the upper part of lectotype sheet belong to this taxon and perfectly match the original description; the six rossetes in the envelope represent *Aphragmus oxycarpus* infected with rust, and the plant to the lower right is sterile and may not be *Braya*.

**Distribution:** China (Beijing, Gansu, Hebei, Henan, Nei Mongol, Ningxia, Qinghai, Shanxi, Shaanxi, Sichuan).

Maximowicz (1880) simultaneously described *Sisymbrium piazezkii* and *Arabis piazezkii* and compared them with *Sisymbrium humile* (herein *Braya humilis*). He maintained *A. piazezkii* in a later publication (Maximowicz, 1889b) but apparently was uncertain of the status of *S. piazezkii* because he treated it as a variety of *S. humile* (Maximowicz, 1889b), as a synonym of the latter (Maximowicz, 1889c), or replaced it with *Malcolmia perennans* (1889a). The lack of consistency in Maximowicz’s work regarding *S. piazezkii* caused further confusion later on. Subsequent taxonomic treatments varied from recognizing both *A. piazezkii* and *S. piazezkii* as distinct species of illegitimate later homonym *Torularia* O. E. Schulz (Botschantzev, 1959), as two species of *Neotorularia* (Botschantzev & Gabunov, 1988), as an infraspecific taxon, “prol. piazezkii” of *T. humilis* (Schulz, 1924), or as synonyms of *N. humilis* (Jafri, 1956; Zhou et al., 2001).

Schulz (1924) placed both *Erysimum stigmatosum* and *E. alyssoides* Franch. under the synonomy of *Braya* (as *Torularia* *humilis*). The type collection of *E. alyssoides* has not yet been found in P, but four syntypes of *E. stigmatosum* exist, and the most fragmentary of which (P-0083640) was annotated by A. Polatscheck in 1983 as the lectotype. However, that lectotypification has never been published.

**Braya stigmatosa** resembles *B. humilis* in having terete fruits, incumbent cotyledons, comparable petal size, and similar indumentum. It is readily distinguished by its tortuose (vs. straight) fruits and prominently 2-lobed (vs. entire) stigmas.

**Braya stigmatosa** exhibits substantial variation in stigma size and the development of its lobes. However, the stigmas are always distinctly wider than the style, compared to those of *B. humilis*, which are usually entire and narrower than style. Plants described by Maximowicz (1880, 1889a) as *Sisymbrium piazezkii* and *Malcolmia perennans*, respectively, have stigmas emarginate though wider than the style. However, the development of prominently 2-lobed stigmas are found throughout the species range. The occurrence of tortuose linear fruits in *Braya* is unique to *B. stigmatosa*, including *S. piazezkii*.

Previous records of *B. stigmatosa* (as *Torularia maximowiczii* or *Neotorularia maximowiczii*) from Mongolia are based on misidentified plants of *B. humilis* (German, 2001).

21. **Braya thomsonii** Hook.f., J. Proc. Linn. Soc., Bot. 5: 168. 1861. TYPE: [CHINA]. Tibet, Piti, 4 September 1847, 12,000–13,000 ft [3,658–3,962 m], T. Thomson s.n. (lectotype partially designated by Jafri (1973: 261) as type and completed herein: K; Isolectotypes: B, K). Two sheets of this type collection are at K; the one annotated by J. D. Hooker as *Braya thomsonii* is taken here as the lectotype. The three plants on the upper part of lectotype sheet belong to this taxon and perfectly match the original description; the six rossetes in the envelope represent *Aphragmus oxycarpus* infected with rust, and the plant to the lower right is sterile and may not be *Braya*.

**Distribution:** China (Tibet).


The presence vs. absence of trichomes on part or whole plant in the Brassicaceae does not necessarily justify the division of species into infraspecific taxa, especially if used alone. This difference can be controlled by a simple Mendelian inheritance (Rollins, 1958). Therefore, in the absence of other morphological differences we are reluctant to recognize subsp. *glabrata* and reduce herein to synonymy.


*Braya sinuata* Maxim., Fl. Tangut. 69, t. 28 figs. 24–33. 1889. TYPE: [CHINA. Tibet]. Keria jugum, 10,500–13,000' s.m. [3,200–3,962 m] in campis lapidosis, frequens, 3–15 July 1885, *N. M. Przewalski* 175 (Holotype: LE).


*Distribution:* China (Qinghai, Tibet (Xizang), Xinjiang), India, Pakistan.

**TAXA EXCLUDED FROM *BRAYA***

The following 36 names are excluded from *Braya* and assigned to 18 genera of ten tribes. Names in boldface are the currently accepted placements of the excluded *Braya* taxa, and their tribal assignments are given between square brackets [ ] at the end of each entry.


**Literature Cited**


PAYPAYROLA ARENAECA (VIOlaceae). A NEW SPECIES WITH AN UNUSUAL LIFE-FORM FROM A WHITE SAND SAVANNA IN THE AMAZON RIVER BASIN OF VENEZUELA

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Abstract. A new species of Paypayrola from a white sand savanna in the San Miguel river basin, a tributary of the lower Guainía river in Amazonas State, Venezuela, is described, illustrated, and its relationships with putatively allied species are discussed. This new species differs from all others in the genus in its small habit and aggregate life-form. The flowers are similar to those of P. confertiflora and P. blanchetiana but are intermediate in size and the petals are pink- or red-tinged. The phytogeography of white sand savannas is briefly discussed and a key and a synopsis of the known species of Paypayrola are presented in two appendices. Leaf structure and histology were studied using both light and scanning electron microscopy and a chemical test showed a positive reaction to aluminum accumulation in leaf tissues. However, it was not possible to ascertain if levels of aluminum accumulation exceeded what was present in the substrate.

Resumen. Se describe y se ilustra una nueva especie de Paypayrola de una sabana de arena blanca de la cuenca del río San Miguel, un afluente del bajo río Guainía, estado Amazonas, Venezuela, se discuten sus relaciones con las especies putativamente aliadas. Esta nueva especie es similar a P. confertiflora y P. blanchetiana, pero difiere en su pequeño hábito, los tallos agregados y las flores más pequeñas, con los pétalos rosados a rojo palidos. Se discute brevemente la fitogeografía de las sabanas de arena blanca y se presentan una clave y una sinopsis del género en dos apéndices. Se estudiaron la estructura y la histología de la hoja usando microscopía de luz y electrónica de barrido y un ensayo mostró una reacción positiva de acumulación de aluminio en los tejidos de las hojas. Sin embargo, no fue posible comprobar si los niveles de aluminio acumulado excedían a los que estaban presentes en el substrato.

Keywords: Aluminum, Guayana, leaf structure, upper Rio Negro basin, Violaceae, white sand habitats

Paypayrola Aubl. (Violaceae) is a neotropical genus comprising approximately eight to ten species of small trees or shrubs (Fernández del Valle, 2005; Wahlert et al., 2014; Ballard et al., 2014; see appendices I–II herein). The cosmopolitan Violaceae includes about 24 genera (Munzinger and Ballard, 2003; Ballard et al., 2014); Paypayrola has been treated as Violoideae, Rinoreeae, Paypayrolinae, based on the classification system proposed by Hecking (1988) and subsequently improved by other authors (e.g., Ballard et al., 2014). Some of this classification has not been supported by recent molecular phylogenies of Violaceae (Wahlert et al., 2014), and results are not congruent for Paypayrolinae (Amphirrhox Spreng., Hekkingia H. E. Ballard, and Paypayrola; Tokuoda, 2008; Wahlert et al., 2014). Tokuoda (2008) inferred that some morphological characters traditionally used to characterize taxonomic groups may be plesiomorphic or autopomorphic.

Paypayrola is characterized by a nearly actinomorphic corolla and staminal glands that are never elaborated into prolongednectaries (characters that defined tribe Rinoreae); one petal slightly to distinctly shaped from the others, a fused staminal tube (characters of Paypayrolinae); subsessile flowers, with pedicel bracts and bracteoles early deciduous, anthers with an obsolete dorsal connective appendage, and smooth capsules (Munzinger and Ballard, 2003; Ballard et al., 2014). Species of Paypayrola are restricted to South America, where they are common in lowland moist forest formations. Most species occur in the Amazon Basin and on the Guiana Shield. One species (P. confertiflora Tul.), however, has apparently been collected in Panama (Tropicos, 2014).


Several novelties to science (e.g., Cleistes sp. nov. and Coryanthes sp. nov., Orchidaceae) and for the flora of Venezuela (e.g., Caraipa valioi Paula, Calophyllaceae; Douradoa consimilis Sleumer, Olacaceae; Galeandra pubicentrum C. Schweinf., Orchidaceae; Mezlil aura caatingae van der Werff, Lauraceae; and Gleasonia auapensiis Ducke, Rubiaceae) recently have been collected along the San Miguel river, a tributary of the Guainía river and therefore of the upper Rio Negro in the Amazon river basin, including the new species of Paypayrola we describe herein. One of us (L.M.C.) also conducted a leaf structure and histology study, as well as Chenery’s (1948) test to detect the presence of aluminum, using leaf samples from the type collection (Romero et al. 3154, GH).

The authors are grateful to B. Angell for the line drawing, herbaria TFAV and VEN for their logistic support, and C, G, GH, K, NY, P, PORT, R, VEN for making access to their collections possible. J. Cammarata, D. Cavaliere, and K, Watson are thanked for their technical assistance. We are also grateful to the D.E.A. Amazonas of the Venezuelan Ministerio del Poder Popular para el Ambiente (currently part of the Ministerio del Poder Popular para Ecossocialismo, Hábitat y Vivienda), and the citizens of Maroa for their support, particularly the Sandalio family. Harvey Ballard helped composing the diagnosis. Field work could not have been completed without the help of Carlos Gómez or the generous financial support of the Orchid Society of Arizona (to G.A.R.-G.).

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Materials and Methods

Specimens from the following herbaria were examined: GH, NY, PORT, TFAV, VEN, and from plants.jstor.org in the JSTOR Portal (courtesy of JSTOR, 2014). The description of vegetative parts is based on herbarium material; that of the inflorescence and flowers based on alcohol-preserved material.

For scanning electron microscopy (SEM), samples from the type collection were coated with gold palladium in a Hummer 6.2 sputtering system (Anatech U.S.A., Union City, California). Observations were made at 10 kV using a JEOL JSM-5410LV SEM (JEOL, Tokyo, Japan).

For light microscope observations, leaf tissue from the type collection was rehydrated using either a 5% aqueous solution of Aerosol® OT (Fisher Scientific Inc., USA; Ayensu, 1967) or Contrad® 70 (Decon Labs, Inc., PA; Schmid and Turner, 1977). A leaf was softened in a 5% NaOH solution, cleared with Stockwell’s bleach (Johansen, 1940; Schmid, 1977) and stained with safranin (50:50 water: ethyl alcohol solution). Medial and basal leaf sections were embedded using standard methods for Paraplast+ (McCormick Scientific™, Leica Biosystems), trans sectioned (t.s.) at 12 μm thickness, and stained with safranin and astra blue (Roeser, 1972). For additional histochemical observations, sections were stained with Sudan IV for suberin and cutin (Johansen, 1940) and ruthenium red for mucilage (Gregory and Bass, 1989). Leaf architecture terminology follows Hickey (1979) and Wilkinson (1979). All images were edited using Photoshop CS4 (©Adobe Systems Inc.).

Chenery’s (1948) aluminon test was employed to detect aluminum in leaves from the type collection. Several species of Rapateaceae (Monotrema aemulans Körn, Campbell et al. 648 (NY), Stegolepis humilis Steyerm. (Huber et al. 8080, NY), Stegolepis sp. Campbell et al. 797, NY), from genera known to accumulate aluminum (Chenery, 1949), were also tested for comparison. Two hundred μl of the resulting solutions and control were dispensed onto bibulous paper for color comparisons. Color profiles were quantified in Photoshop CS4.

Taxonomy

Paypayrola arenacea Aymard & G. A. Romero sp. nov., Fig. 1–2.

The new species differs from all others in the genus in its small habit and presence of a lignotuber; the flowers are intermediate in size between those of Paypayrola conferiflora Tul. and P. blanchetiana Tul., and the petals are pink- or red-tinged. Paypayrola arenacea resembles P. longifolia Tul., with which it shares lanceolate to elliptic-lanceolate leaves with a long-attenuate base, however, P. arenacea differs from the latter in its small habit and shorter petioles, leaves, and petals.

TYPE: VENEZUELA. Amazonas: Municipio Autónomo Maroa, riberas del río ("caño") San Miguel, transecto entre la orilla del río, caatinga y sabana amazónica, aguas abajo de Limoncito, detrás de un punto habitado pero abandonado recientemente, la sabana con vegetación típica y con pequeños arbustos; arbusto de hasta 0.75 m, flores blancas, localmente frecuente, aprox. 2˚43’N, 67˚33’O, 120 m, 22 julio 2013, G. A. Romero & C. Gómez 4113 (GH, NY, PORT, TFAV, VEN). Additional specimen examined: VENEZUELA. Same locality as the type, arbusto de 30–50 cm de altura, from genera known to accumulate aluminum (Chenery, 1949), were also tested for comparison. Two hundred μl of the resulting solutions and control were dispensed onto bibulous paper for color comparisons. Color profiles were quantified in Photoshop CS4.

Etymology: From the Latin arenaceus, of sand, in reference to the sandy soils where the species was collected.

Distribution: Known from two separate collections made in the type locality. However, the new species most likely occurs in nearby white sand savannas elsewhere in the San Miguel river basin and perhaps in similar habitats in Brazil, Colombia, and Peru.

Additional specimen examined: VENEZUELA. Same locality as the type, arbusto de 30–50 cm de altura, from genera known to accumulate aluminum (Chenery, 1949), were also tested for comparison. Two hundred μl of the resulting solutions and control were dispensed onto bibulous paper for color comparisons. Color profiles were quantified in Photoshop CS4.

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Figure 1. *Paypayrola arenacea* Aymard & G. A. Romero. A, views of a flowering stem showing a detail of the petiole insertion; B, inflorescences; C, flower bud; D, flower; E, petals; F, stamens, adaxial and abaxial views; G, gynoecium. Drawing by B. Angell based on the holotype and Romero & Gómez 4113 (GH, K, TFA V, VEN).
Figure 2. *Paypayrola arenacea* Aymard & G. A. Romero. A, flowering branch in situ; B, close-up of flowers, from below; C, a clump of *P. arenacea in situ*, note the stature of *Pachira amazonica* (A. Robyns) W. A. Alverson (Bombacaceae) at the right (the pruner shown is a Felco® model F-6); D, an individual “plantlet” from the clump shown in C. Photographs by G. A. Romero based on *Romero & Gómez 4113* (GH, K, TFA V, VEN).
Habitat: This new species was found growing in scrub-savanna locally called “Sabanas de arena blanca” (Spanish), further south “campina de solo arenoso” (Portuguese; Anderson, 1981; Lisbôa, 1975) or “Campinarana graminea lenhosa” (Portuguese; Pombo de Souza, 2012). This type of vegetation mainly occurs in the black water drainages of the Rio Negro and Guainía rivers in Venezuela (Amazonas state), Colombia (Guainía, Vaupés, and Vichada departments), Brazil (Amazonas, Pará, and Roraima states), and as far south as the Peruvian Amazon at the Jenaro Herrera district and the Allpahuayo-Mishana Reserve, near Iquitos, where apparently similar plant communities are known as “Varillalles” and “Chamizales” (Revilla, 1974; García-Villacorta et al. 2003). In addition, these communities go farther south in Brazil, in Acre and Rondônia (“Chapada de Parecis;” Prance, 2001). In Venezuela, white-sand savannas also are found, from north to south, in the Samariapo, Sipapo, Ucata, and Atabapo river basins, and most likely farther north in the states of Amazonas, Apure, and, Bolívar, as suggested by the presence of plant species found only in this particular habitat.

Leaf Structure and Histology

Leaf symmetric, narrow elliptic to narrow oblong in outline, apex acute, rarely obtuse, midvein often extended beyond the lamina and spine-like. Margin entire, revolute, most strongly so at the base. Venation brochidodromous, primary vein straight, secondary veins diverging at 60–70°; tertiary veins transverse ramified within the secondary veins, percurrent arches towards the margin, higher order venation random reticulate, veinlets multi-branched. Surface glabrous, cuticle slightly thicker adaxially. Cuticle and portion of anticlinal epidermal cell walls deeply stained with Sudan black B. Adaxial epidermal cells undulate in surface view (Fig. 3), columnar in t.s. (Fig. 4A), rounded to angular in outline, interior periclinal wall thicker than the others and deeply stained with Astra blue (Fig. 4A, B); abaxial epidermal cells wider than tall in t.s., irregularly oblate to pyriform in outline, interior periclinal wall thickened; hypostomatic, stoma irregularly distributed, not on the midvein, in t.s. guard cells shorter than or equal in height to the adjacent epidermal cells, cuticular ledges not seen, stoma laterocytic, subsidiary cells 2–4, unequal. Mesophyll well differentiated, palisade parenchyma bilayered (Fig. 4A), external layer dense, interrupted by a tapering band of 1–5 layers of collenchyma above and below the midvein, and a single layer at the margin, internal palisade layer loose, spongy parenchyma with some peg cells. Midvein slightly to prominently raised above the adaxial surface, more pronouncedly so abaxially, elliptic in t.s., bundle nearly concentric, amphicribal, external phloem interrupted by xylem, xylem with tracheary idioblasts (Fig. 4B), surrounded by a sheath of sclerenchyma, sheath to 4 cells wide. Smaller veins collateral, with or without some peripheral sclerenchyma.

Rehydration and subsequent treatment relaxed the enrolled margin of the sectioned leaves (Fig. 4A). Leaf sections stained with ruthenium red did not exhibit a positive result for polysaccharide mucilage.

The aluminum solution prepared with leaf tissue of Paypayrola arenacea exhibited a moderate color change compared to Rapateaceae, indicating the presence of this element. Violaceae are reported to accumulate aluminum (Chenery, 1948), nickel (Peterson, 1983), heavy metal waste (Jędrzejczyk et al., 2002), as well as hyperaccumulate aluminum (Jansen et al., 2002) and nickel (Fernando et al., 2014). Plants are considered hyperaccumulators when the concentration of aluminum exceeds 1000 ppm in herbaceous tissue (Jansen et al., 2002). Species in the genera of Rapateaceae that we tested are reported to

![Figure 3](https://via.placeholder.com/150) Abaxial leaf surface of Paypayrola arenacea Aymard & G. A. Romero. A, scattered distribution of stoma (note the presence of stoma on secondary veins but not on the midvein); B, detail of the stomata apparatus and undulate epidermal cells.
Figure 4. Leaves of *Paypayrola arenacea* Aymard & G. A. Romero. A, cross section showing the leaf margin; B, midvein; C, venation.
have 123–15000 ppm of aluminum (Chenery, 1949). The lamina in Paypayrola arenacea is a yellow-green color that is associated with aluminum accumulation (Chenery, 1948). Our test for this mineral in leaves of P. arenacea was positive; however, without quantitative testing it isn’t possible to ascertain if levels of aluminum accumulation exceed that of the soil (i.e., hyperaccumulation; see Jansen et al., 2002). It is of interest to note that Chenery (1949) found different levels of aluminum in samples of different maturity in the one species examined in replicate (Rapatea paludosa Aubl.); however, it was not indicated if these were from the same individual or even from the same soil.

**Discussion**

**Paypayrola arenacea** is remarkable in the genus for its small stature and smaller leaves. Fertile individuals seen in the type locality did not even reach 1.0 m in height, although sterile individuals found near the type locality, along a savanna-caatinga ecotone were up to 1.5–1.7 m tall. The reduced vegetative parts and the white flowers easily distinguish this new species from all others of Paypayrola (see appendices I and II). **Paypayrola arenacea** differs further in having brochidodromus vs. eucamptodromous venation sometimes with a few brochidodromus veins distally, and ramified tertiary venation vs. tertiary veins rarely branched.

This new species exhibits a steep angle of leaf insertion (Fig. 1A, 2A, C, D), a mechanism that is common in open-canopied vegetation in the region that minimizes exposure to intense insolation (Medina et al., 1990). Havran and Ballard (unpublished, cited in Ballard, 2014) suggest the number of palisade parenchyma layers in some *Viola* is correlated to light exposure.

**Paypayrola arenacea** leaves were covered by a thick cuticle, had slightly recessed guard cells, and increased palisade parenchyma, although other xeromorphic anatomical features (Esau, 1965: 429), such as mesophyll sclerenchyma not associated with the vascular bundles (Dickison, 2002: 312) were not present. In some Violaceae inner epidermal cell walls secrete mucilage, not detected here. Mucilage produced in quantity may function in water storage enabling plants to endure drought (Roth and Lindorf, 1991). Plants subjected to fluctuating inundation and dry periods may exhibit a structural combination of characters associated with both xerophytism and hydrophytism (e.g., *Equisetum*, see Foster and Gifford, 1988: 189; *Abolboda*, Campbell, 2004). We suggest that the leaf structure and stunted plant size (see Prance and Schubart, 1978; Klinge and Medina, 1979; Anderson, 1981), and presence of a lignotuber (see Fahn and Cutler, 1992; Fig. 1A, 2D) are adaptations to both limited water availability and oligotrophic soils (Seddon, 1974; Medina et al., 1990). Resprouting from lignotubers or xylodizia is a adaptation to fire-prone habitats in Australia (especially Myrtaceae; Burrows, 2013) and cerrado vegetation (Appessato da Gloria and Cury, 2011; Frisby et al. 2013; Many xerophytic characteristics can also result from insufficient nutrients, particularly N and P (Medina et al., 1990; Fahn and Cutler, 1992: 136). The leaf margin in some dried specimens of Paypayrola appears to be thickened, but not enrolled as in *P. arenacea*, where it is most prominent at the lamina base (see Wilkinson, 1979) and is underlain by a narrow layer of mechanical tissue. We did not observe any mites (Chevalier and Chesnais, 1941; Jacobs, 1966; Stace, 1965) or fungi inhabiting the leaf surface; however, further observations are warranted to determine if the enroll functions as a domatium. In Violaceae domatia are known in Rinorea (Ballard et al., 2014).

White sand savannas can be small to large (up to hundreds of hectares) patches of herbaceous vegetation, most often found near black water rivers, which can be partially or completely flooded during the peak of the rainy season (June–August in the northern hemisphere). These savannas are surrounded by Amazonian caatinga, bana, or sometimes by terra firme forest (Klinge et al. 1977; Prance 1996). The soils are deep sandy spodosols or quartzitaments, a very acidic parent material characterized by a subsurface accumulation of humus that is complexed with aluminium and iron (Herrera, 1979; Schargel et al., 2000). As in banas, this unique vegetation could be considered the ultimate seral state in reduction of biomass, caused by extreme levels of nutrient deficiency, periodic fires, and unfavorable soil-water conditions (Huber, 1995a, b; Klinge and Cuevas, 2000). The most profound climatic event in South America occurred during the Last Glacial Maximum (LGM), ca. 18000 years ago. There is evidence for a decline in precipitation and a decrease in temperature of up to 5 °C in some parts of this continent (Bush et al., 2004); climate was dry and cool, inducing a high degree of aridity in this region (van der Hammen and Hooghiemstra, 2000; Hooghiemstra et al., 2002). Some authors have used this evidence to suggest that large tracks of Amazonian forests were largely converted into savannas during the glacial periods. Pennington et al. (2000) proposed that much of the current extent of the Amazonian forest in the LGM was occupied by the now geographically restricted seasonally dry tropical forests and, in several areas of the Amazon basin, forest vegetation changed perhaps into present day savanna and others types of deciduous, scrubby vegetation (van der Hammen and Absy, 1994; Pessenda et al., 2004; Mayle et al., 2007). Nonetheless, others authors find no evidence for a widespread transition from forests to a woodland savanna system either in the paleoecological record (Colinvaux et al., 2000) or in modelling studies (Cowling et al., 2001). The pollen record suggests that glacial-age Amazonian forests, with their mix of currently Andean and lowland Amazonian taxa, have no modern analogues (Mayle et al., 2009).

Amazonian oligotrophic white sand savannas are characterized by many species only known from this particular habitat, but unlike others tropical savannas they harbor relatively few taxa of Poaceae (i.e., *Axonopus casiquiarensis* Davids., *A. schultesii* G. A. Black, *Paspalum...
tillettii Davids and Zuloaga, and Steyermarkochloa angustifolia (Spreng.) Judz.). Other remarkable examples of the unique white sand savanna flora are: Gonglyolepis martiana (Baker) Steyerm. & Cuatrec. (Asteraceae), Schefflera pimicinchensis Maguire, Steyerm. & Frodin, and S. spruceana (Seem.) Maguire, Steyerm. & Frodin (Araliaceae), Pitcairnia juncoidea L. B. Sm. (Bromeliaceae), Terminalia yapacana Maguire (Combretaceae), Blepharandra angustifolia (Kunth) W. R. Anderson (Malpighiaceae), Comolia prostrata Wurdack (Melastomataceae), Duckeella adolphii Porto & Brade (Orchidaceae), Cybianthus reticulatus (Benth. ex Mez) G. Agostini (Primulaceae), and Polygala sanariapoana Steyerm. (Polygalaceae).

Other families with species endemic to white sand savannas are Araceae, Cyperaceae, Eriocaulaceae, Euphorbiaceae, Gentianaceae, Haemodoraceae, Lentibulariaceae, Rupataceae, and Xyridaceae. Other cases of “dwarfism” are known in plant species that grow in white sand savannas, such as Himanthus semilunatus Himatanthus that grows in white sand savannas, such as Araceae, Cyperaceae, Eriocaulaceae, Euphorbiaceae, and Xyridaceae. Other remarkable examples are Araceae, Cyperaceae, Eriocaulaceae, Euphorbiaceae, Gentianaceae, Haemodoraceae, Lentibulariaceae, Rupataceae, and Xyridaceae. The unusual habit of Paypayrola arenacea is, to our knowledge, unique in woody Violaceae. What appears to be individual stems, as evidenced by a tap root, occur aggregated in isolated clumps, slightly elevated above the savanna (Fig. 2C). One of these clumps was excavated and it revealed a truncated stem without connection to other nearby clumps (Fig. 2D). The isolated plants form several woody stems branching near ground level from a nodular tuber atop a tap root. Plants inhabiting upper Rio Negro savannas are adapted to poor and acidic soils that can be periodically flooded; some species produce a greater below ground biomass relative to above ground (Campbell, 2004); however, the possible cause and selective advantage for the habit of P. arenacea warrant further study. Morphologically, Paypayrola arenacea does not appear to have close allies: its small vegetative size and its life-form easily distinguish it from all the other species in the genus. (see key to species in Appendix I.)

**LITERATURE CITED**


APPENDIX I

KEY TO THE SPECIES OF PAYPAYROLA

The authors could not locate the type of *Wibelia brasiliensis* Spreng., the base name of *Paypayrola brasiliensis* (Spreng.) Steud. (see APPENDIX II) and the original description of this species is quite succinct (“*P. pedunculis rameis unifloris aggregatis, foliis oblongis scabris, laciniiis calycinic obtusis. Hab. Brasilis*”). Furthermore, we did not find any herbarium material referable to *Paypayrola brasiliensis*, which is lamentably excluded from the key. In writing the key, we struggled to find characters differentiating *Paypayrola blanchetiana* from *P. hulkiana*, which appear to the closely related.

1. Leaves lanceolate to elliptic-lanceolate, base long-attenuate .............................................. 2
2. Shrubs to small trees, petiole >5 mm long, leaf blade 16–30 cm long ......................................................... 3
3. Leaves elliptic to obovate-lanceolate, petiole >12 mm; rachis elongate, inflorescence congested ....................... 6
4. Flowers slender, 10–15 mm long; petals linear ........................................................................... 5
3. Leaves elliptic to obovate-elliptic, petiole 5–9 mm; rachis shortened, inflorescence congested ....................... 5
5. Leaves lanceolate-oblong; inflorescence 3–6 cm long, connective apex present ........................................ 6
6. Leaves 6–10 wide, apex acute; ovary ovate-linear ................................................................. 1.0
1. Leaves ovate, obovate, or oblong-lanceolate, base rounded, cuneate, or short-attenuate ........................................ 4
4(1). Flowers robust, 15–30 mm long, petals ovate ............................................................
2. Suffrutices, petiole <4 mm long; leaf blade 3.5–8.0 cm long ........................................................ 3
3. Leaves obovate to obovate-lanceolate, petiole >12 mm; rachis elongate, inflorescence loose ....................... 3
6. Leaves 4–6 cm wide, apex long-acuminate; ovary conical ................................................................. 1.0
6. Leaves 6–10 cm wide, apex long-acuminate; ovary conical ................................................................. 1.0
APPENDIX II

A SYNOPSIS OF PAYPAYROLA


*Paypayrola brasiliensis* (Spreng.) Steud., Nomencl. Systemat., ed. 2. ii. 280. 1841.

Basionym: *Wibelia brasiliensis* Spreng., Neue Entdeck. Pflanzenk. 3: 63. 1822. TYPE: BRAZIL. Without locality, date, or collector [type not located].


In the original description, L. R. Tulasne compared *Paypayrola ventricosa* to *P. grandiflora*. Smith and Fernández-Pérez (1954) relegated the former to the synonymy of *P. grandiflora*. An examination of the syntypes and isosyntypes of *P. ventricosa* at P indeed show large, robust flowers. According to an annotation of W. H. A. Hekking attached to the holotype of *P. glazioviana* at P, dated 31 January 1996, this name is a taxonomic synonym of *P. grandiflora*.


*Paypayrola hulkiana* Pulle, Recueil Trav. Bot. Néerl. 9: 155. 1912. TYPE: SURINAM. In forests in the upper Gran Rio [“In Wäldern am oberen Gran Rio”], 8 September 1910, ca. 200 m, J. F. Hulck 248 [Syntype, not seen]; 25 September 1910, ca. 350 m, J. F. Hulck 296 [syntype, not seen].

Epidendrum L. is one of the largest genera among flowering plants, encompassing over 1500 species in the Neotropics (Hágsater, 1985). At present, ca. 400 species in the genus have been recorded as to occur in Ecuador, being 210 (= 52 %) of those endemic to the country (Dodson in Jorgensen & León, 1999; Valencia et al., 2011).

Red-flowered species in Epidendrum are known for having a distinctive distribution pattern in the Andes (e.g., the Elongatum subgroup; Hágsater, 2013); furthermore, no species of the genus bearing red flowers was previously known from lowland Ecuador. During field work in a foggy, very dry, and disturbed coastal forest in the lowlands of Manabí Province in western Ecuador, a red-flowered epiphytic Epidendrum with distinctive floral features called our attention, and it is here described and illustrated as a new species.

**Epidendrum aromoense** X. Cornejo & E. Hágsater, sp. nov.

**TYPE:** Ecuador. Manabí: El Aromo, a disturbed very dry coastal forest, ca. 200 m, 7 March 2014 (fl), X. Cornejo, M. Gallardo & V. Solórzano 8601 (holotype, GUAY; digital photos at AMO, GUAY), Fig. 1–3.

**Diagnosis:** Similar to *Epidendrum tulcanense* Hágsater & Dodson but the callus of the lip orange, concave within, 5-tuberculate, 2 globose processes, 2 outer, smaller flat growths, and an apical-V shaped protuberance like the bow of a ship, the apex acute, versus the massive, white callus, formed by nine unequal tubercles, four basal ones and the main structure formed by five sub-equal tubercles.

Epiphytic, caespitose, sympodial, erect herb, ca. 60 cm tall. *Roots* 1–1.5 mm in diameter, fleshy. *Stems* ca. 25 × 0.5 cm, simple, cane-like, terete, thin, straight. *Leaves* 7–12, distributed throughout the stem, alternate, sub-erect; sheaths 1.5–2.1 × 0.4–0.5 cm, tubular, minutely striated when dry; blade 5.5–8.5 × 1.4–2 cm, coriaceous, smooth, the lower leaves lanceolate-oblong, the upper leaves oblong, about 3 to 5 times longer than wide, apex broadly obtuse at upper leaves, slightly bilobed, margin entire. *Spathe* lacking. *Inflorescence* ca. 36 cm long, apical, racemose; peduncle 28.5 cm long, elongate, terete, thin, straight, nearly totally covered by ca. 8 acute, tubular sheaths, 3.3–4.3 × 0.3 cm; rachis ca. 7.5 cm long, terete, thin. *Flowers* 30–40, successive, ca. 18 open at one time, non-resupinate, red (*lacquer red*), the callus orange (yellow in photos). *Floral bracts* 1.5–4.5 mm long, much shorter than the ovary, triangular-lanceolate, acuminate, gradually shorter towards the apex of the rachis. *Ovary* 13–17 mm long, terete, thin, arching towards the apex, smooth. *Sepals* ca. 9 × 3 mm, spreading, free, elliptic, sometimes oblique, minutely apiculate, 5-veined, margin entire, spreading. *Petals* 7–8 × 2 mm, spreading, free, ob lanceolate, papillose, cuneate towards the base, obtuse towards the apex, 4– 5-veined.

The senior author wishes to thank Natalie Pyrooz, an associate field researcher of the California Academy of Sciences, for the drawings of *E. aromoense*.

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Figure 1. *Epidendrum aromoense*. A, epiphytic habit and disturbed habitat; B, stem and leaf bases; C, inflorescence. Photograph by X. Cornejo based on Cornejo et al. 8601 (GUAY), the holotype.
Lip 8–10 × 3–4 mm, united to the column, 3-lobed, base deeply cordate, distal margins laciniate; callus concave within, 5-tuberculate, 2 globose processes, 2 outer, smaller flat growths, and an apical-V shaped protuberance like the bow of a ship, the apex acute; lateral lobes ca. 2 × 2 mm, dolabriform; mid-lobe 3–4 × 4 mm, rather acutely dentate to somewhat flabellate, forming two divaricate lobes, apex emarginate. Column 5 mm long, straight, thin, without wings, papillose mainly towards the apex. Clinandrium hood reduced, margin minutely dentate. Anther obovoid, acute, 3-celled, densely papillose. Pollinia 3, ca. 0.8 × 0.2 mm, oblancoate, elongate, laterally compressed, slightly unequal, papillose. Rostellum apical, slit. Lateral lobes of the stigma small. Nectary penetrating nearly 1/2 the ovary. Capsule not seen.

Habitat and distribution: Known only from the seasonally foggy very dry coastal forests of El Aromo and Montecristi, located ca. 20 km apart from each other in the Province of Manabí in western Ecuador, at ca. 200 m. The disturbed habitat in which Epidendrum aromoense occurs is characterized by an annual average temperature of 25°C, annual average relative humidity of 78%, average precipitation of 250 mm per year, and high exposure to sun’s UV rays (Weatherbase, 2014). In these harsh weather conditions, the moisture provided by seasonal and nocturnal fog undoubtedly plays a critical role in those xerophytic areas allowing the establishment of populations of this as well as other epiphytic endemics such as the recently described and sympatric Anthurium aromoense Croat (Araceae), also collected by the first author in the same area (Croat et al., 2013).

Conservation status: The localities where Epidendrum aromoense does occur are threatened by the advance of agricultural frontier or forest conversion to cattle farms and other land use. Therefore, the status of endangered, EN B1ab(iii) (IUCN, 2001) is assigned to this species.

Uses: Epidendrum aromoense as well as another recently described species from the same habitat, Anthurium aromoense, become adapted in cultivation with little care within few weeks. These species have been successfully planted as ornamentals by the senior author in hot and humid cities such as Manta and Guayaquil.

Phenology: Epidendrum aromoense has been observed with flowers during February and March. It is unknown if flowers are also produced during some of the remaining months of the year.

Etymology: The specific epithet refers to El Aromo, the locality where the new species was found.

Paratypes: ECUADOR. Manabí: Slopes of Montecristi, L. Besse 134 (QCA, SEL); same locality, C. Luer 1472 (SEL). Specimens seen but not studied in detail.

The type specimen had only three pollinia, which is unusual for this group of species, the normal number being four. The authors were not able to study this character in the proposed paratypes.

Epidendrum aromoense belongs to the Secundum group, Elongatum subgroup which is recognized by the caespitose habit, simple stems, leaves oblong-lanceolate, coriaceous, bilobed and elongate peduncle of the erect, pluriracemose inflorescence, the flowers non-resupinate, the callus complicated, plurituberculate. The species is recognized by the successive, lacquer-red flowers, the orange callus, sepals about 9 mm long, the petals somewhat smaller than the sepals, oblancoate, the lip square in outline, deeply 3-lobed, the lateral lobes dolabiform, terminating in a pair of divari-cate, narrow, triangular, acute, bifurcate teeth, the lateral lobes clearly separate and never overlapping with the mid-lobe when spread, and the mid-lobe rather acutely dentate to somewhat flabellate, bilobed and distinctively divaricate; callus concave within, 5-tuberculate, 2 globose processes, 2 outer, smaller flat growths, and an apical-V shaped protuberance like the bow of a ship, the apex acute.
The distinctive pattern of distribution, that is, restricted to the lowlands of central-western Ecuador (versus Andean) makes an easy differentiation for *E. aromoense* in comparison to the remaining red-flowered species in the subgroup. Similar red-flowered species are: *Epidendrum tulcanense* Hágsater & Dodson has also red flowers but it is distinguished by the large white massive callus, formed by nine unequal tubercles: four basal ones and the main structure formed by five sub-equal tubercles. *Epidendrum laurelense* Hágsater & Dodson, that differ from *E. aromoense* by the carmine-red flowers on a much more open raceme, with a massive white callus formed by a semicircular sulcate, marginally plurilobulate fleshy plate, found between Tulcán and Maldonado, on the border between Ecuador and Colombia, on roadsides and rocks in wet forest between at around 2000 to 2500 m above sea level. *Epidendrum coroicoënse* Schltr. is another species similar to *E. aromoense* by the lacquer-red flowers; however, the former species is known from southern Peru and western Bolivia, along the upper Amazon slope of the Cordillera Oriental of the Andes, and differ from *E. aromoense* by the narrow leaves about 6–7 times longer than wide, the petals wider than the sepals, elliptic-sub-orbicular, the lip bearing lateral lobes overlapping with the mid-lobe when spread; and callus 5-tuberculate with two basal and three apical tubercles, and without keels. *Epidendrum portokalium* Hágsater & Dodson is another species with red flowers that resembles *E. aromoense*, but it is found on the Amazon slopes of the Andes in central Ecuador, and differs from *E. aromoense* by the callus unequally 7-tuberculed (with four basal tubercles and three apical ones).

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CAPPARIDA스트럼 TAFALLANUM (CAPPARACEAE),
A NEW SPECIES FROM THE NORTHWESTERN
ANDEAN SLOPES OF ECUADOR

XAVIER CORNEJO,1,2 HUGH H. ILTIS,3 AND CARLOS E. CERÓN4

Abstract. Capparidastrum tafallanum a new species of Capparaceae from the wet forests of Andean slopes at northwestern Ecuador is
here described and illustrated. The status of endangered, EN B1ab(iii), is assigned to this taxonomic novelty.

Resumen. Se describe e ilustra Capparidastrum tafallanum, una nueva especie de Capparaceae de los bosques muy húmedos de las
estribaciones andinas del noroccidente de Ecuador. A esta nueva especie se asigna el estatus En Peligro, EN B1ab(iii).

Keywords: Capparaceae, Capparidastrum tafallanum, Ecuador, endemic

Capparidastrum Hutch., a Neotropical genus of
Capparaceae, comprises 19 species ranging from southern
Mexico to northern Argentina (Cornejo, 2008, 2010).
During the revision of Capparaceae for Flora of Ecuador,
the following new species was found:

Capparidastrum tafallanum X. Cornejo, Iltis & C. Cerón,
sp. nov. TYPE: ECUADOR. Pichincha: cantón Quito,
Parroquia suburbana Nanegalito, cuenca del Río Pachijal,
sector Rancho Buitrón, 78°43’W, 0°02’N, 1330–1450
m, 13 May 1999 (fl), C. Cerón 38069 (Holotype: QAP
[00027340!]; Isotypes to be distributed). Fig. 1.

Species nova affinis Capparidastrum bonifazianum
(Cornejo & Iltis) Cornejo & Iltis et C. megalospermum
Cornejo & Iltis, a qua differt sepalis grandioribus, nectariis,
filamentiis et ginophoriis minoribus.

Diagnosis: Treelet or tree to 25 m tall and 41 cm or more
dbh, glabrous throughout. Stipules narrowly-triangular, ca.
1.5 × 0.6 mm. Leaves unequal in size; blades coriaceous,
ove to elliptic or ovate-oblong, 11.5–32 × 6–17 cm,
broadly obtuse to rounded at base, usually acuminate at
apex, dark green above, pale green beneath; main lateral
veins ca. 8 to 11 on each side; petioles 1–15 cm, the
pulvinus 5–10 mm, dark brown to blackish. Inflorescence
terminal, erect racemes; peduncles ca. 3 cm, the terminal
flower-bearing portion of the axis ca. 4 cm; floral bracts
triangular to linear, minute, deciduous; pedicels 4–5.5
mm. Flower buds just preceding anthesis broadly ovate to
elliptic, ca. 16 × 12–14 mm. Floral nectaries ca. 2–3 × 3–5
mm, white (fresh), dark brown to blackish (dried). Sepals
ovate to deltoid to semiorbicular, ca. 10 × 5–7 mm, broadly
divergent at anthesis, greenish without, white-hyaline
and shallowly erosive-ciliolate at margins. Petals broadly
ovate to elliptic, ca. 15–18 × 10–13 mm, somewhat fleshy,
divergent, forming a teacup-shaped corolla at anthesis,
subsessile at base, broadly rounded at apex, cream to white
within, creamish without, more or less entire, minutely and
irregularly erosive-denticulate at the margins. Stamens ca.
40; filaments 2–3 cm; anthers ca. 5 mm, dorsifixed on the
basal third. Gynophore ca. 3 cm long. Ovary oblongoid, ca.
4–5 × 1 mm, green (fresh); stigma truncate to hemispherical
(fresh). Infructescence and fruits not seen.

Habitat and distribution: Capparidastrum tafallanum
is known only from two collections gathered ca. 6 km from
each other, between 1400–1700 m, in the basin of Río
Pachijal. The habitat is a secondary wet forest located at the
Andean slopes of northwestern Ecuador.

Conservation status: The localities where Capparidastrum tafallanum does occur are threatened by
fragmentation and massive deforestation mainly due to the
advance of agricultural frontier or forest conversion to cattle
farms and other land use. Therefore, according to IUCN
guidelines the status of endangered, EN B1ab(iii) (IUCN,
2012), is here assigned to this species.

Uses: As the sweet pulp of the fruits is occasionally eaten
by humans as well as by wild mammals (Cerón 38069,
Cevallos et al. 2457); it is most likely that Pre-Hispanic
gatherers also ate the fruits of this new species.

Phenology: Capparidastrum tafallanum bear flowers
during May through June. Similar to the morphologically
closely related species C. bonifazianum, C. megalospermum
and C. macrophyllum, it is most likely that the flowers are
ephemeral and nocturnal. The pollinators are unknown.

Local name: Chirimoya de monte (Spanish, Cerón
38069).

Etymology: This new species is named to honor Juan José
Tafalla y Nabasques (1755–1811), a Spanish pharmacist
from Navarra, and a leader of the first expedition that
documented the plant species from Ecuador. His historical
collections, often unfairly attributed to Hipólito Ruiz or
José Pavón, who never visited Ecuador (e.g., the type of
Capparis didymobotrys), and the corresponding color plates

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Figure 1. Capparidastrum tafallanum: A, flowerbud preceding anthesis; B, inflorescences; C, branch and leaves. Based on Cerón 38069 (QAP [00027340]), the holotype.
prepared from plants in situ, remained forgotten in MA (Spain) herbarium for approximately 200 years. Tafalla’s manuscripts, collections, and plates were rediscovered and finally edited and published in Flora Huayaquilensis (Estrella, 1989); a masterpiece of plants of the Guayaquil region written in a 19th century style.

**Additional specimens examined:** ECUADOR. Pichincha: cantón Quito, Parroquia Nanegalito, cuenca del Río Pachijal, sector Rancho Buitrón, 78°46’W, 0°02’N, 1340–1600 m, *M. Cevallos et al. 2457* (QAP); same locality, *M. Cevallos et al. 95* (QAP).

*Capparidastrum tafallanum* is assigned to *Capparidastrum* subgen. *pulviniglans* Cornejo & Iltis based on the absence of indument; large leaves with elongate petioles, often of unequal lengths; the absence of a hypanthium, with petals divergent at anthesis; and fleshy floral nectaries that are rounded, and cushion shaped (Cornejo and Iltis, 2008).

*Capparidastrum tafallanum* has flowers with a short gynophore and filaments of 2–3 cm, similar in length to those of the South American *C. osmanthum* (Diels) Cornejo & Iltis. However, measurements of several floral elements of *C. tafallanum* largely differs from those of *C. osmanthum*, such as flower bud sizes preceding anthesis (ca. 16 vs. 6–12 mm long), pedicels (4–5.5 vs. 2–4 cm long), sepals (ca. 10 x 5–7 vs. 1–3.5 x 1.5 mm), petals (ca. 15–18 x 10–13 vs. 9–13 x 5–8 mm), anthers (ca. 5 mm vs. 1.5–2.5 mm long), and ovaries (ca. 4–5 vs. ca. 2 mm long). Vegetatively, *C. tafallanum* resembles *C. bonifazianum* from western Ecuador and southwestern Colombia. However, the former species differs from *C. bonifazianum* by the distinctively larger sepals (ca. 10 vs. 4–6 mm long), the narrower floral nectaries (3–5 vs. 5–8 mm wide), the shorter filaments (2–3 vs. 5.5–8 mm long), shorter gynophore (ca. 3 vs. 6–8 cm long), and it occurs at a higher elevation (1330–1600 m vs. 0–850 m). *Capparidastrum tafallanum* is also similar to *C. macrophyllum*, but the former species differs from the latter by the shorter gynophore (ca. 3 vs. 7–12 cm long), shorter filaments (ca. 2–3 × 5.5–10 cm), fewer stamens (ca. 40 vs. 80–130), and the different pattern of distribution, separated by the Andean chain (western Ecuador vs. widely distributed in Amazonia to premonotane slopes of the northern Andes in Venezuela and Colombia). *Capparidastrum tafallanum* also resembles *C. megalospermum*, a species restricted to the wet forests of northwestern Ecuador and southwestern Colombia, but this new species is easily distinguished by the distinctive shorter gynophore (ca. 3 vs. ca. 8 cm) and different altitudinal pattern of distribution (1330–1600 m vs. 0–500 m).

**LITERATURE CITED**


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**ALIAE LEPANTHES MACHOGAFFENSES (ORCHIDACEAE: PLEUROTHALLIDINAE)**

**FRANCO PUPULIN**1–4 AND **DIEGO BOGARÍN**1,5

**Abstract.** Two new species of *Lepanthes* are described and illustrated. *Lepanthes elvirae* is reminiscent of *L. estrellensis* in the large size of the flower and the broad and rounded laminae of the lip, but can be distinguished from the latter by the glabrous sheaths of the ramicaul, the petals with lobes distinctly different in size and the lobes of the lip held subparallel to the column. *Lepanthes queveriensis* is most similar to *L. cribbii*, from which it differs by the inflorescence sub equal to longer than the leaf, the margins of the sepals entire, the shorter body of the lip, provided with two hemielliptic, low, and the rectangular, straight appendix of the lip. Considerations on orchid diversity in unexplored regions of Costa Rica are presented.

**Keywords:** Orchidaceae, *Lepanthes*, new species, Costa Rica, Cordillera de Talamanca, species diversity

The region of Macho Gaff, close to the northernmost end of the Cordillera de Talamanca in Costa Rica, represents an interesting example of how orchid diversity in biologically rich countries is still far from being entirely apprehended. Included in the large area protected by the Tapantí–Machizo de la Muerte National Park, Macho Gaff is located only seventeen kilometers from the center of the ancient capital of Costa Rica, Cartago, and it is relatively close to agricultural lands that have been severely cleared in the second half of the nineteenth century. The partial exploration of Macho Gaff primary forest is actually just a consequence of its random privilege of possessing two different trails that run to the Macho River from the northeastern and southern hills. Thousands of square kilometers of virgin oak forests with similar characteristics, with their intricate system of valleys and rivers, expand uninterrupted from here to the province of Chiriquí in Panama, almost two hundred kilometers to the southeast, crossing the continental division to embrace the two slopes. Even though most of these areas are completely inaccessible, they are probably as rich as Macho Gaff in orchid diversity. For what concerns the genus *Lepanthes* Swartz (1788), we can also estimate that the levels of endemism are likely comparable, with most of the species restricted in distribution to a few tens of square kilometers.

We first explored the region of Macho Gaff in 2008, taking a road that starts from the watershed of the Cordillera de Talamanca close to Paso Macho (Macho Gaff), at about 2400 m elevation, and later goes down toward Queverí, becoming a steep trail crossing the Macho river some 400 meters below (Fig. 1). We discovered several new species of *Lepanthes* during our first visit, conducted along a practically linear transect of about four km through pristine forest, three of which were described the following year, namely *L. gratiosa* Pupulin & D. Jiménez, *L. machogaffensis* Pupulin & D. Jiménez and *L. pelvis* Pupulin & D. Jiménez (in Pupulin et al., 2009). From the same area, *Lepanthes arenasiana* Bogarín & M. Fernández (Bogarín and Fernández, 2010) was described one year later. At least two other species from the same collection seem to be different from any other known taxa and are actually under study (Bogarín and Pupulin, in prep.).

In January of 2014, we visited the region again, entering the protected area from the north, along the unpaved road running from Queverí to the swinging bridge over the Río Macho. Here we made a second linear transect of about two km, beginning at 2200 m elevation and descending 200 meters to the edge of the Macho river (Fig 1). Along the trail, we found large populations of *L. pelvis* and *L. machogaffensis*, together with *L. gratiosa*, *L. cf. cascajalensis* Ames (1923), *L. tipulifera* Reichenbach f. (1866), *L. latisepala* Ames & C. Schweinfurth (Ames and Schweinfurth, 1930), *L. ciliisepala* Schltr. (Schlechter, 1923) and two unknown species, that we describe herein as new to science.

Including the two species presented here, we have a total of six to eight new species of the genus *Lepanthes* found in two random adjacent transects, totaling six kilometers in length, in the lower montane rain forest of the Talamanca range. One could only speculate about how many thousands of possible transects like this could be traced in the mountainous region of eastern Costa Rica, and how many unknown species of *Lepanthes* and other groups of Orchidaceae with diminutive plants are yet to be discovered.

We wish to thank the scientific services of Ministerio del Ambiente y Energía (MINAE) and Sistema Nacional de Áreas de Conservación (SINAC) of Costa Rica, for issuing the scientific permit R-SINAC-DE-077 under which wild specimens treated in this study were collected. Fabricio Carbonell Torres of ACLA-P for granting access to the Parque Nacional Tapantí (PNT) and for his interest in the development of orchid research at Tapantí. To Carl Luer, who created the fundamental framework that allows comparing species of *Lepanthes*. Melissa Díaz and Melanía Fernández helped with fieldwork and logistics. The present paper is part of the Project 814-BO-052, “Flora Costaricensis: taxonomía y filogenia de la subtribu Pleurothallidinae (Orchidaceae) en Costa Rica” supported by the Vice-President of Research, University of Costa Rica.

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**Lepanthes elvirae** Pupulin, sp. nov.

**TYPE:** COSTA RICA. Cartago: Paraíso, Orosi, Queverí, Finca Durman, Tapanti-Macizo de La Muerte National Park, road to the swinging bridge over the Río Macho, 9°43'46.71"N, 83°51'27.53"W, 2115 m, lower montane rain forest, epiphytic in secondary mature vegetation with remnants of primary vegetation, 21 January 2014, flowered in cultivation under accession number JBL-30025, prepared 2 May 2014, F. Pupulin, D. Bogarin, M. Díaz & M. Fernández 8355 (holotype, JBL; isotypes, JBL). Fig. 2–3.

Flore magnitudine pro genere magna, labelli laminis latis rotundatisque petalis gracilis discrepantibus, Lepanthes elvirae primo adspectu Lepanthi estrellensi Ames similium est, sed vaginis ramicaulium glabris (vs. breviter muricatibus), lobis petalorum inter eos magnitudine distincte dissimilibus (vs. subequales), lobulis labelli columnae subparallelis portatis (vs. perpendiculis) ab ea plerumque recedit.

In the large size of the flower and the broad and rounded laminae of the lip, contrasting with the slender sepals, *L. elvirae* is reminiscent of *L. estrellensis* Ames, from which it mainly differs by the glabrous sheaths of the ramicaul (vs. shortly muricate), the petals with lobes distinctly different in size (vs. subequal) and the lobes of the lip held subparallel to the column (vs. perpendicular).

Epiphytic, cespitose, spreading to pendent herb to 11 cm tall. Roots filiform, flexuous, to 1 mm in diameter. Ramicauls slender, horizontal-arched, rarely suberect, 2.2–7.2 cm long, covered by 4–8, closely adpressed, ribbed, glabrous (microscopically ciliate along the ribs), pale brown sheets, dilated at apex into an obliquely lanceolate ostia, ciliate along the margins, 2.5 × 1.2 mm. Leaf broadly elliptic, thin, flat, pale green, 2.1–3.9 × 1.5–2.0 cm, the base rounded, abruptly contracted into a short, conuplicate petiole, the apex obtusely shortly cuspidate, excise, with the tip of the central vein protruding abaxially within the sinus. Inflorescence produced on top of and exceeding the leaf, successively few-flowered (at least to 5), the pedicel slender, terete, to 2.7 cm long, covered with two tightly adpressed, tubular, sparsely muricate, acute bracts; the rachis fractiflex, to 9 mm long; floral bracts broadly lanceolate, acute, sparsely muricate, 1.2-2.0 mm long. Flowers comparatively large for the size of the plant, the sepals white to pale greenish yellow, hyaline, the petals pale yellow, flushed with red in the basal part, the lip pale yellow, flushed with red in the basal part, the column and the anther white. Dorsal sepal broadly ovate, shortly cuspidate, 3-veined, slightly convex, 6.4–6.7 × 5.2–5.5 mm, connate with the lateral sepals for about 2 mm. Lateral sepals asymmetrically ovate, 2-veined, the shortly cuspidate apices divergent, connate at the base for about 3 mm. Petals transversely bilobed, 1.5–1.7 × 5.0–5.2 mm, erect to incurved in natural position, the upper lobe larger, 1.5–1.7 × 4.0 mm, oblong, subfalcate to falcate, diverging above, rounded; the lower lobe smaller, 1.2 × 2.5 mm, triangular-oblong, rounded. Lip bilobed, broadly reniform in general outline, 3.0 × 3.7 mm, the lobes elliptic, rounded at the base, incurved at the subacute apices, suberect, the basal margins completely encircling the column; connective trapezoidal, deeply incised in front, the margins of the sinus finely pubescent; appendix external, rectangular, reflexed. Column terete, broadened at the subspherical apex, 3 mm long, the anther dorsal, the stigma apical. Anther cap cucullate, ovate, 2-celled, about 0.5 mm long. Pollinia 2, obpyriform, the basal portion attenuate-filamentous; viscidium rounded, yellowish brown, apical.
Figure 2. *Lepanthes elvirae* Pupulin. A, habit; B, flower; C, dissected perianth; D, ovary, column and lip, lateral view; E, lip, spread; F, pollinarium and anther cap. Drawn by D. Bogarin and F. Pupulin from the holotype.
Figure 3. Flower variation in *L. elvirae*. A, Pupulin 8555 (JBL); B, Pupulin 8553 (JBL); C, Pupulin 8572 (JBL); D, Pupulin 8581 (JBL). Photographs by F. Pupulin.

**Distribution:** Known only from Costa Rica, where it has been found along the Caribbean slopes of the Cordillera de Talamanca’s northernmost range.

**Habitat and ecology:** Lepanthes elvirae inhabits the wet premontane forests of the Cordillera de Talamanca in Costa Rica, where the only known population was found in the Caribbean watershed of the chain, at about 2100 meters of elevation. Lepanthes elvirae is one of the species apparently suited to occupy the shaded and constantly wet canopy understory in dense vegetation, where the reduced air movement reduces the loss of water by transpiration. Lepanthes species of this “forest group” are commonly characterized by soft-herbaceous instead of coriaceous leaves, very prone to tissue dehydration under suboptimal conditions. Flowering of L. elvirae has been recorded in cultivation from February to August, but new flowers are probably produced in succession year-round.

**Eponymy:** Named after the senior author’s wife, Elvira Salas-Pupulin, to acknowledge her continuous support in research and in life.

New species of Lepanthes are frequently described on the sole basis of morphological features’ unique combinations, in both vegetative habit and flower shape. In general, these combinations easily distinguish Lepanthes species from each other and, in a few cases, enable recognition of species-groups whose members are probably close relatives (see, for example, Pupulin and Bogarín, 2010; Pupulin et al., 2010; Bogarín et al., 2012; Pupulin and Bogarín, in press). Nevertheless, the lack of both a larger genetic sampling in this hyper-diverse genus of probably more than thousand species, and of a finer resolution of the internal relationships, obscures in many cases the phylogenetic affinities of the new proposed taxa. Lepanthes elvirae is no exception. The glabrous ramicauls and the soft-herbaceous leaves are commonly observed in several Lepanthes groups adapted to the wet conditions of the lower canopy in pristine, dense forests, while the flower shape is reminiscent of L. estrellensis resembling both its rounded flower and the broad laminae of its labellum. Its affinities, as in most species of Lepanthes, are therefore purely speculative.

**Lepanthes queveriensis** Bogarín & Pupulin, sp. nov.

**TYPE:** COSTA RICA. Cartago: Paraíso, Orosi, Queverí, Finca Durman, Parque Nacional Tapanti-Macizo de La Muerte, camino al puente de hamaca sobre el Río Macho, 9°43'46.71"N, 83°51'27.53"W, 2115 m, epífitas en rámitas delgadas de Ocotea sp. (Lauraceae) en bosque pluvial montano bajo, 21 Enero 2014, D. Bogarín 10843, M. Díaz, M. Fernández & F. Pupulin (holotype, USJ). Fig. 4–5.

Species nova Lepanthi cribbii Pupulin plerunque similis, inflorescensia folio subequalis vel longiore (vs. brevior), marginibus sepalorum integris (vs. breviter ciliatis), corolla brevi duabus lamellis pronis semiplaniflitis munito (vs. corpum elongatum lamellis destitutum), labelli appendicis rectangulis rectaqua (vs. digitatum, reflexum) ab ea differt.

The new species is most similar to L. cribbii Pupulin, from which it differs by the inflorescence sub equal to longer than the leaf (vs. shorter), the margins of the sepals entire (vs. shortly ciliate), the shorter body of the lip, provided with 2 hemi-elliptic, low flaps (vs. body longer, bare), and the rectangular, straight appendix of the lip (vs. digitate, reflexed).

Epiphytic, cespitose, spreading to pendant herb to 7 cm tall. Roots filiform, flexuous, to 0.5 mm in diameter. Ramicauls slender, pendent, 1.4–4.5 cm long, covered by 5–9, closely adpressed, ribbed, minutely ciliate-muricate, brown sheets, dilated at apex into an obliquely lanceolate, acuminate ostia, ciliate along the margins, 2.5 × 1.5 mm. Leaf ovate, subcoriaceous, flat, grayish green, 1.1–2.4 × 0.5–1.2 cm, the base rounded, gradually contracted into a short, conduplicate petiole, the apex cuspidate-acute, excise, with the tip of the central vein protruding abaxially within the sinus. Inflorescence produced on top of and subequal to slightly exceeding the leaf, successively many-flowered (at least to 14), the pedicel slender, terete, to 2 cm long, covered with two tightly adpressed, lanceolate, acute bracts; the rachis fraxintflex, to 14 mm long; floral bracts lanceolate, acute, sparsely muricate, 0.7–0.9 mm long. Pedicel terete, 2 mm long. Ovary terete, to 1.5 mm long. Flowers comparatively large for the size of the plant, the sepals pale greenish yellow to yellow, hyaline, sometimes suffused with rose-purple particularly along the veins (the dorsal sepal almost entirely rose-purple, the lateral sepals yellow in the labeller half), the petals bright yellow, the upper lobes flushed with red almost to the apex, the lower lobes flushed at the base in the labeller side, the lip bright yellow, blotted with red at the base of the lobes, the column red-violet, the anther white. Dorsal sepal triangular-lanceolate, acuminate-attenuate, 3-veined, slightly convex, 7.2–7.5 × 3.2–3.4 mm, connate with the lateral sepals for about 1 mm. Lateral sepals triangular-lanceolate, subfalcate, acuminate-attenuate, 2-veined, connate at the base for about 1 mm. Petals transversely bilobed, 0.7 × 4.0 mm, erect, the upper lobe broader, 0.7 × 2.0 mm, oblanceolate, rounded; the lower lobe 0.4 × 1.8 mm, ligate-subfalcate, minutely rounded. Lip bilobed, broadly H-shaped in general outline, 1.3 × 1.9 mm, the lobes narrowly elliptic-subfalcate, rounded at the base, incurved at the minutely rounded, tomentose apices, erect, the basal margins completely encircling the column; connective short, transversely rectangular, emarginate in front, the frontal margin long-pubescent; the disc provided with two hemi-elliptic, diverging, low flaps, extending over...
Figure 4. *Lepanthes queveriensis* Bogarín & Pupulin. A, habit; B, flower; C, dissected perianth; D, ovary, column and lip, three-quarters view; E, lip, spread; F, pollinarium and anther cap. Drawn by D. Bogarín and F. Pupulin from the holotype.
the margin of the connective; appendix external, ligulate-subcylindric, sparsely hairy, slightly bent. Column terete, broadened at apex, ca. 2 mm long, the anther and the stigma apical. Anther cap cucullate, sub orbicular, 2-celled, about 0.5 mm long. Pollinia 2, obpyriform, the basal portion attenuate-subfilamentous; viscidium ovate, yellowish brown, apical.


Distribution: Known only from the northern end of the Cordillera de Talamanca in Costa Rica, where it has been collected in the Caribbean watershed.

Habitat and ecology: Epiphytic on twigs of Ocotea sp. (Lauraceae) in understory vegetation. Plants were found growing with L. cascajalensis and L. pelvis. Flowering of cultivated plants has been recorded from January to July, but successive flowering is probably done year-round.

Etymology: Named after the locality of Queverí, at the northern end of the trail Queverí–Macho Gaff. Queverí is a tributary of the Macho River. It is an indigenous Cabécar dialect probably meaning “the river of the brother.”

Lepanthes queveriensis is apparently related to the group of L. cribbii Pupulin (in Pupulin & Bogarín, 2004) / L. falx-bellica Pupulin & Bogarín (Pupulin and Bogarín, 2011) / L. mentosa Luer (Luer, 1987) / L. monteverdensis Luer (Luer, 1987), all characterized by the glabrous sheaths of the ramicaul, the ovate leaves, the narrow petals with subequal upper and lower lobes, and the rounded lateral lobes of the lip flanking the column to the apex and almost hiding it in lateral view. The new species differs from the other members of this eminently Costa Rican group by the inflorescences that reach the apex of the leaf, and distinctly surpass it when old, while they are shorter than the leaf in the other species. Furthermore, the margins of the sepals are ciliate in L. cribbii and L. falx-bellica, and irregularly dentate-erose in L. mentosa and L. monteverdensis, whilst in L. queveriensis they are entire.

To facilitate species comparisons, the protologues and digital images and/or illustrations of the types, as well as photographs of living flowers and botanical illustrations of the taxa discussed in the present paper, are available for download through the “List of species” page of the Epidendra website, http://www.epidendra.org/taxones/index.html (Epidendra, 2014).
LITERATURE CITED


**ONOSMA HAWRAMANENSIS** (BORAGINACEAE), A NEW SPECIES FROM KURDISTAN, IRAQ

**SAMAN A. AHMAD**

**Abstract.** *Onosma hawramanensis* from Kurdistan, Iraq, is described and illustrated. Its relationship and distinguishing characters from nearest relatives in southwestern Asia are discussed. It is easily distinguished by the combination of setae with basal tubercles sparsely pubescent with small simple trichomes, and the non-accrescent fruiting calyx; the yellow corolla, pubescent outside and glabrous inside, the sparsely pubescent nectar annulus at the base of the corolla tube; the linear anthers, free at the base and bidentate at the apex; and glabrous, glossy, broadly ovoid fruits with the surface slightly reticulate.

**Keywords:** Boraginaceae, Iraq, Kurdistan, *Onosma*

The author conducted extensive floristic fieldwork in Hawraman Mountains (Kurdistan, Iraq) as part of his Ph.D. research during the years 2011–2013. This mountain series is part of the Zagros Range, located along the Iraqi-Iranian borders some 50 km E of Sulaimani City. Several novelties, such as *Ferula shehbaziana* S.A.Ahmad (Ahmad, 2013), *Petrorhagia sarbaghiae* S.A.Ahmad (Ahmad, 2014a), *Scrophularia sulaimanica* S.A.Ahmad (Ahmad, 2014b), and the novelty described below, as well as 18 species new to the flora of Iraq (Ahmad, 2014c), were discovered while conducting this fieldwork.

*Onosma hawramanensis* S.A.Ahmad, sp. nov. TYPE: IRAQ. Kurdistan, Sulaimani Province, Rangin Mt., subalpine rocky grassland, 2004 m, 35˚21'20"N, 46˚05'10"E, 8 June 2012, Saman A. Ahmad 12-997 (Holotype: SUFA; Isotype: SUFA). Fig. 1.

*Herbs* perennial, canescent, woody at base. *Stems* 20–30 cm, several branched at base, few branched distally, hispid, with spreading white trichomes 1–2 mm, dark brown after bark peeling off. *Basal leaves* and lowermost cauline ones soon withered; middle leaves broadly elliptic, 3–4 × 1.5–2 cm, sessile, base cuneate, margin entire, apex subacute, densely pubescent with ascending trichomes to 2 mm and with sparsely pubescent tuberculate base with simple trichomes; uppermost leaves elliptic-ob lanceolate, smaller. *Inflorescence* dense, scorioid, 5–10-flowered; bracts lanceolate, 10–20 × 2–5 mm; flowering pedicels 1–2 mm, slightly elongated and 3–4 mm in fruit. *Calyx* ca. 10 mm in flower, 12–15 mm in fruit, not accrescent, united at base, densely white pubescent with trichomes to 2 mm; corolla yellow, tubular, 13–15 mm, slightly expanded at apex, pubescent outside, glabrous inside; teeth broadly triangular, ca. 1.5 × 1.5 mm; nectar annulus poorly developed, sparsely pubescent; filaments ca. 4 mm, inserted at middle of corolla tube, not expanded at base; anthers free, linear, 6–7 mm, sagittate at base, sterile apex bidentate, to 1.5 mm. *Fruits* 5.5 × 3.5–4 mm, broadly ovoid, glossy, slightly reticulate, straight, glabrous, carinate adaxially, slightly so abaxially, apex straight, flattened.

*Onosma* L. is a large and complex genus represented in Turkey by 88 species (Riedl, 1978) and Southwest Asia, especially the Flora Iranica area by 58 species (Riedl, 1967). The genus is represented in Kurdistan Iraq by 32 species, including the novelty described above.

*Onosma hawramanensis* is known only from the type gathering collected in the Rangin Mountain, a range that has never been explored botanically before. It is easily distinguished from related species in Iraq and neighboring countries by the perennial habit, the broadly elliptic cauline leaves, leaves with setae, the setae with basal tubercles sparsely pubescent with small simple trichomes, the basally united calyx not accrescent after flowering; yellow corolla pubescent outside and glabrous inside, broadly triangular corolla lobes, and sparsely pubescent nectar annulus at base of corolla tube; filaments inserted at middle of corolla tube, linear anthers free at base and bidentate at apex; and broadly ovoid, glabrous and glossy fruits 5.5 × 3.5–4 mm, with an slightly reticulate surface.

**LITERATURE CITED**


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Figure 1. *Onosma hawramanensis*. **A**, plant; **B**, part of inflorescence.
Gustavo A. Romero-González2 and Carlos Gómez3

Abstract. A new species of Galeandra from the state of Apure, Venezuela, is described and illustrated. The new species, *in vivo*, is easily distinguished by its unpleasant fragrance that reminds one of the smell emitted by the American roach, and in the herbarium by a set of unique morphological characters. We also present miscellaneous herbarium notes on *Galeandra* and a bilingual key to identify the species of the genus found in Venezuela.

Resumen. Se describe y se ilustra una nueva especie de *Galeandra* del estado Apure, Venezuela. La nueva especie, *in vivo*, se distingue fácilmente por su fragancia desagradable que recuerda a la cucaracha americana y, en el herbario, por una serie de caracteres morfológicos únicos. También se presentan notas misceláneas sobre el género *Galeandra* y una clave bilingüe para identificar las especies presentes en Venezuela.

Keywords: Amazonas, Galeandra, Orchidaceae, Periplaneta, Venezuela

*Galeandra* Lindl. is restricted to the Americas, where it is found from Florida and the West Indies to southern Brazil and Argentina (Monteiro et al. in Pridgeon et al., 2009: 29). Recent publications place this genus in Catasetinae (Romero-González and Pridgeon in Pridgeon et al., 2009: 11–12; Monteiro et al., 2010; Batista et al., 2014). It includes some 69 described taxa (IPNI, 2014), of which 39 binomials are currently accepted (Plant List, 2014); the actual number of species is uncertain. The genus is most diverse in the Amazon and Orinoco River basins, with only six species in Central America and Mexico (one undescribed) and one in Florida and the West Indies.

The genus was first documented by Alexander Rodrigues Ferreira (1756–1815) and his team during their expedition to the Rio Negro in the 1780s. At least one of the unpublished drawings from this expedition, preserved in the Fundação Biblioteca Nacional (Brazil) dated 1785 (“Do Rio Negro”; mss1255473; Biblioteca Nacional Digital Brasil, Fundação Biblioteca Nacional (Brazil) dated 1785 (“Do Rio Negro”); ms1255473; Biblioteca Nacional Digital Brasil, 2014) represents what would be described as *Galeandra devoniana* R.H. Schomb. ex Lindl. some 50 years later (Fig. 1). Nonetheless, the first published record was by Francis Bauer (1758–1840) in his famous work *Illustrations of Orchidaceous Plants* (in installments between 1830 and 1838; *Galeandra* in part II, Genera plate VIII, 1832; Bauer, 1830–1838). The description of *Galeandra* is attributed to Lindley, but the book to Bauer and Lindley. Therefore, the authorship of the genus *Galeandra* can be as simple as “Lindl.” or as convoluted as “Lindl. in F. A. Bauer and Lindl.”

A phylogenetic study of *Galeandra* (Monteiro et al., 2010) revealed two clades sister to *Galeandra devoniana* (one of the showiest species, bearing articulate leaves; Fig. 1); one clade includes all the terrestrial species, bearing non-articulate leaves, the other all the epiphytic ones, bearing articulate leaves. Incidentally, *Tupacamaria* Archila, recently proposed to include the clade of *Galeandra* with all the terrestrial species (Archila, 2008, 2013), is phylogenetically untenable because it renders *Galeandra* paraphyletic (i.e., *Tupacamaria* is imbedded in *Galeandra* as elucidated by Monteiro et al., 2010).

Eleven species of *Galeandra* have been documented in Venezuela (Romero-González, 2003), mostly south of the Orinoco river. Here we describe and illustrate a new epiphytic species from the Sinaruco river, Apure state. This showy species is easily distinguished *in vivo* by its unpleasant odor that reminds one of the smell emitted by the American roach, and in the herbarium by a set of unique characters. We also present miscellaneous herbarium notes on *Galeandra* and a bilingual key to identify the species found in Venezuela.

We are grateful to Bobbi Angell and Natalie Warford (R.I.P.) for the excellent drawings, to Bruno Manara for his help selecting the specific epithet of the new species, to the staff and curators of K, MO, NY, PORT, VEN, and particularly TFAV for their assistance with loans and visits, to the DEA-Amazonas of Ministerio del Poder Popular para el Ambiente de Venezuela (currently part of Ministerio del Poder Popular para Ecosocialismo, Hábitat y Vivienda) for their logistic support, to Irina Ferreras and Daniel Santamaria for their invaluable help in the herbarium, to Francisco Urbani and Leonardo Venegas for geographical information, to Germán Carnevali and William Cetzal for comments, and to the Orchid Society of Arizona (O.S.A.) for its generous financial support (to G.A.R.-G.). Field work on the San Miguel river and the Cariche mountains in June 2009 could not have been completed without the help of Carlos and Oscar Gómez, Demetrio Aragua, Emiro Yuriyuri, Pascual Garrido, and José Miguel Aragua†, to whom this article is dedicated.

1Previous articles in this series were Romero-González and Batista (2009), Romero-González et al. (2010a, b), Romero-González and Meneguzzo (2012), and Romero-González et al. (2013a, b).
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Galeandra blattiodora

G.A.Romero & C.Gómez, sp. nov.

TYPE: VENEZUELA. Apure: río Sinaruco, Ex Hort. Carlos Gómez, flowering 10 December 2005, sub G. A. Romero & C. Gómez 3522 (Holotype: TFAV; Isotype: AMES [flower in spirit], VEN [dry flowers]). Fig. 2–4.

The new species is similar to Galeandra magnicolumna G.A.Romero & Warford, but differs in vivo in the fetid, unpleasant odor of the flowers, which reminds one of a place heavily infested by the American roach, Periplaneta americana L. (versus a sweet, pleasant fragrance), and in herbarium specimens by the absence of pubescence on the labellum and column (versus densely pubescent), and the short, conical anther (versus elongate, clavate).

Epiphytic herbs, pseudobulbs of up to 10 internodes, narrowly fusiform, up to 42 cm high to the base of the inflorescence, up to 2.0 cm in diameter at its thickest point. Leaves dark green, stiff, 3-veined, articulate, linear lanceolate, up to 32 cm long × 1.5 cm wide, the sheaths and lower portions of the blade with small red spots and red pigment at the articulation, present when plants first flower, shed as the flowering season progresses. Inflorescence a spike, occasionally with 1 or 2 branches in robust plants, with up to 15 flowers borne in succession, 1–3 at a time, the base covered with papyraceous, narrowly lanceolate bracts, 4.0 cm long × 0.4 cm wide, decreasing in size toward the apex of the peduncle, the peduncle up to 18 cm long; rachis up to 10 cm long; floral bracts lanceolate, 0.7 cm long × 0.2 cm wide at the base. Ovary pedicellate, olive green, 2.5 cm long, 1.5 mm in diameter at the widest point. Flowers overall light lime green, the margins of the sepals and petals slightly brownish red, the margins of labellum and especially the apex white, the column and the anther light lime green. Dorsal sepal narrowly obovate, 2.0–2.3 cm long, 0.6 cm wide, lateral sepals falcate, 2.0–2.3 cm long, 0.6 cm wide. Petals narrowly obovate, 2.0 cm long, 0.7 cm wide. Labellum (including spur) 8.0 cm long, 4.0 cm wide at the apex when spread; spur, to the base of the column, 5.5 cm long, lined with short trichomes; labellum disk with five conspicuous keels (Fig. 2–3). Column 1.2 cm long through the axis, winged, the ventral surface naked except for two tufts of multicellular trichomes at each side of the base (the trichomes similar to the ones inside the spur), strongly concave below the stigma, wings curving outward then inward, with a lateral span of 6–7 mm, the margins of the clinandrium fringed. Rostellum horseshoe-shaped. Anther beaked, 4.0–4.5 mm long, 2.8–3.2 mm wide at the base, the base scrotiform, the tip 3 mm long, conical. Pollinarium with viscidium, stipe, and two pollinia; viscidium and stipe hippocrepiform, firm, minutely celled, elastic (the viscidium hidden on the inner margin of the stipe), 6.5 mm high, 5.8 mm wide; pollinia juxtaposed, sulcate, ovoid-globose, 1.9 mm long, 1.2 mm wide.
Figure 2. Galeandra blattiodora G.A.Romero & C.Gómez. A, views of the flower and labellum; B, views of the column; C, views of the anther; D, views of the pollinarium and pollinium. Drawn by Bobbi Angell based on photographs and material preserved in alcohol of an Isotype (G. A. Romero & Gómez 3522, AMES).
Etymology: Derived from Blattidae, the name designating the family encompassing most of the common household roaches, including the American cockroach, *Periplaneta americana*; and the Latin *odor*, smell, scent, in reference to the odor emitted by the flowers of the new species, similar to the fetid, disagreeable odor of a place infested by the American cockroach.

Additional material examined: [Municipio Pedro Camejo, Parque Nacional Santos Luzardo], laguna la Guacharaca, ca. 14 km due W of the northern end of the Galeras of Cinaruco; 6°42’N, 67°27’W; elev. 70 m. Low gallery forest surrounding the laguna. Epiphyte, perianth green, the upper part of the lip white, 24 February 1979, G. Davidse & A. C. González 15706A (VEN [No. 167368], MO [No. 2705767]); same locality, 40 m, bosque inundable al borde de la laguna, suelo limoso con alto contenido de materia orgánica, epífita, pétalos verdosos, labelo blanco cremoso, 31 February 1989, T. Ruiz, R. Gómez, R. Smith, R. Winfield y O. Díaz 4428 (MY [not seen], VEN [271922]).

*Galeandra blattiodora* is closely related to *G. magnicolumna* G.A.Romero & Warford (Fig. 5–6). However, it differs from the latter in the fetid fragrance, the absence of trichomes on the labellum and the ventrum of the column, and in the shape of the anther (see key below).

The unpleasant odor of the flowers of the new species is most peculiar (calling it a “fragrance” would be a contradiction in terms!). Plants first flowered in the garden of one of the authors (C.G.), where they continued to flower December–March, maintaining their foul fragrance while the plants survived in cultivation for three years. The pheromone of *Periplaneta americana* is Periplanone B (Sass, 1983), a compound not known in any orchid floral scent (Kaiser, 1993). It, however, would not be unexpected in Orchidaceae where floral scents range from exquisite to the smell of death (van der Niet et al., 2011) or even feces (the compound Skatole, an indole that occurs naturally in mammal feces, is a minor component of many orchid fragrances [Kaiser, 1993] and an active attractant to several species of euglossine bees; Romero-González, unpublished data).

Based on the overall size of the flowers, *Galeandra blattiodora* is most likely pollinated by a species of *Eulaema* Lepeletier, as is *G. magnicolumna* (Romero and Warford, 1995).

The additional specimens cited here were originally referred to *Galeandra magnicolumna* (Romero and Warford, 1995). Flowers of one of the specimens (*Davidse & González 15706A*, MO) were re-examined and they are unequivocally referable to *G. blattiodora*. We refer the second specimen, *Ruiz et al. 4428*, to the same species, given that it was collected in the same general locality.
Figure 5. Galeandra magnicolumna G.A. Romero & Warford. Views of the labellum. Drawn from hydrated, herbarium material by Natalie Warford based on G. Escobar 866 (AMES).
Figure 6. Galeandra magnicolumna G.A. Romero & Warford. Views of the column. Drawn from hydrated, herbarium material by Natalie Warford based on G. Escobar 866 (AMES).
**Herbarium notes**


A second specimen of this apparently rare species, known only from the type collection, was brought to our attention:

VENEZUELA. Bolívar, Municipio Piar, bajo Caroní, sector Cerro Morichito, morichal, 7˚53’01.2”N, 63˚00’11.6”O, 100–130 m, hierba flores moradas, poco frecuente, 24 June 2006, W. Díaz & A. Pérez 8347 (VEN [393337]).


Synonym: **Galeandra schunkii** V.P. Castro & Chiron, TYPE: BRAZIL. Espíritu Santo: Município de Marechal Floriano, 500–600 m, “environ 70 km du littorial, floraison en culture en juin 2008,” V. P. Castro 106 (Holotype: SP, not seen), **syn. nov.**

The authors of *G. schunkii* compared their new species to *G. dives* Rchb.f. and *G. stangeana* Rchb.f. (Castro Neto and Chiron, 2009), two distantly related species, instead of *G. claesii* (Cogniaux, 1893a,b), from which it is morphologically undistinguishable.


As circumscribed by Romero-González (2005), this terrestrial, showy species, is locally frequent in many localities in the eastern (Carnevalu et al., 2007) and western Guayana Shield (e.g., *Cabrera* 2358, COL). However, it is apparently rare elsewhere and, it has not been collected in Venezuela since 1927, in Colombia since 1889, or in Panamá since 1960. The population in Carabobo state, Venezuela, is probably extirpated, because the area has been heavily disturbed (c.f., Magallanes, 2005), although the one in Trujillo, in “cerro El Baño,” near a popular thermal spring (Urbani, 1991), may still survive. The status of the populations in Sierra de Santa Marta, Colombia, and Panama is unknown.


We recently collected this species along the Guainía river, a tributary of the Río Negro and therefore of the Amazon river. It appears to be the same species that G. C. K. Dunsterville drew from cerro Moriche, along río Manapiare, a tributary of the Ventuari river in the Orinoco river basin (Dunsterville and Garay, 1966: 110–111, 1979: 323; Romero-González and Carnevali, 2000: 341).


During the June 2009 field trip to the Cariche mountains (Romero-González, 2009), we also collected a specimen of *Galeandra pubicentrum*, the first record of this species for Venezuela (Romero-González and Gómez, 2009).

VENEZUELA. Amazonas: Municipio Autómomo Maroa, cuenca del río San Miguel, alto Mee, entre el campamento base y el desecho, hierba epífita, flores amarillo-verdosas, ápice del labelo blanco, con una mancha roja en el ápice, ápice de la antera marrón rojizo, 18 junio 2009, *G. A. Romero, C. Gómez, O. Gómez, J. M. Aragua & D. Aragua* 4055 (TFAY). Fig. 9–10.

Here we also reproduce an excellent drawing of the type of *Galeandra pubicentrum* at AMES (Fig. 11).

The following is a bilingual key that can be used to identify species of *Galeandra* from Venezuela and surrounding areas in Brazil, Colombia, and Guyana. Authors are cited for species hitherto not cited in the text.
KEY TO THE SPECIES OF GALEANDRA FOUND IN VENEZUELA

1a. Plants terrestrial, without evident pseudobulbs [plantas terrestres, sin pseudobulbos evidentes] ................................... 2
1b. Plants epiphytic, with conspicuous pseudobulbs [plantas epífitas, con pseudobulbos evidentes] ................................... 4

2a. Plants found in shady habitats, below the canopy of forests; when in flower, leafless; inflorescence appearing to be produced directly from the surface of the substrate [plantas de bosque, de ambientes sombreados, cuando en flor, sin hojas, inflorescencia pareciera surgir directamente de la superficie del substrato] ............................ G. beyrichii Rchb.f.
2b. Plants found in open, sunny habitats; when in flower, with 1 or 2 green leaves; inflorescence produced from the base of the upper most leaf [plantas de ambientes soleados, cuando en flor, con 1 ó 2 hojas verdes, la inflorescencia surge de la base de la hoja apical] ............. 3

3a. Labellum entire [labelo enterol] .......................................................... G. carnevaliana
3b. Labellum conspicuously trilobate [labelo conspicuasmente trilobulado] ......................................................... G. juncea

4a. Flowers with a recurved spur [flores con el espolón recurvado] .......................................................... G. devoniana
4b. Flowers with a straight spur [flores con el espolón recto] .................................................................. 5

5a. Labellum with 2 high, conspicuous keels, diminishing in size towards the base, apex of the labellum colored deep purple, labellum and column without trichomes [labelo con dos quillas conspicuas, que disminuyen en tamaño hacia la base; ápice del labelo púrpura intenso, labelo y columna sin tricomas] .......................................................... G. duidensis Garay & G.A.Romero
5b. Labellum with 3–5 conspicuous keels or, if 2 present, low and inconspicuous; apex of the labellum not colored deep purple, labellum and column with or without trichomes [labelo con 3–5 quillas o, si hay dos presentes, inconspicuas; ápice del labelo sin color púrpura intenso, labelo y columna con o sin tricomas] ........................................................................... 6
6a. Labellum with two inconspicuous keels, labellum and column without trichomes [labelo con dos quillas inconspícuas, labelo y columna sin tricomas] .......................................................... G. badia Garay & G.A.Romero
6b. Labellum with 3–5 conspicuous keels, labellum and column with or without trichomes [labelo con 3–5 quillas conspicuas, labelo y columna con o sin tricomas] .......................................................... 7
7a. Labellum with 3 or 4 keels; spur nearly as long or slightly longer than the lamina of the labellum [labelo con 3 ó 4 quillas; espolón casi tan largo como la lámina del labelo] ........................................................................... 8
7b. Labellum with 3–5 keels; spur 1.5–2.0 times as long or longer than the lamina of the labellum [labelo con 3–5 quillas; espolón al menos 1.5–2.0 veces o más largo que que lámina del labelo] .......................................................... 10

8a. Labellum with 4 keels, the two outer ones conspicuously larger than the inner ones, labellum and column without trichomes [labelo con 4 quillas, las exteriores conspicuamente más elevadas que las interiores, columna sin tricomas] ................................................. G. minax
8b. Labellum with 3 keels, column conspicuously pubescent [labelo con tres quillas, columna conspicuamente pubescente] .................. 9
9a. Labellum apex, beyond the keels, with short trichomes, barely extending beyond the disk; labellum obtuse to rounded [labelo, en el ápice, más allá de las quillas, con tricomas cortos, que no llegan al ápice obtuso del labelo] .......................................................... G. stangeana Rchb.f.
9b. Labellum apex, beyond the keels, with long trichomes, extending almost to the margin, labellum deeply emarginate [labelo, en el ápice, más allá de las quillas, con tricomas largos, que se extienden casi al ápice; labelo profundamente emarginado] ............. G. pubicentrum

10a. Labellum with 3 keels; labellum and column conspicuously pubescent; column 4–5 mm wide [labelo con tres quillas; labelo y columna conspicuamente pubescentes; columna de 4–5 mm de largo] .......................... G. macroplectra G.A.Romero & Warford
10b. Labellum with 5 keels, labellum and column conspicuously pubescent or not, column 6–7 mm wide [labelo con 5 quillas, labelo y columna conspicuamente pubescente o no; columna de 6–7 cm de largo] .......................................................... 11
11a. Fragrance sweet, agreeable; labellum, including the spur, light to strongly flush with pink; labellum disk and ventrum of the column conspicuously pubescent; anther 6–7 mm long, clavate, the tip, in vivo, deep maroon [fragancia dulce, agradable; labelo, incluyendo el espolón, ligera o fuertemente teñido de rosado; labelo y ventro de la columna conspicuamente pubescente; antera 6–7 mm de largo, clavada, el ápice, in vivo, de color rojo-vino intenso] .......................................................... G. magnicolumna G.A.Romero & Warford
11b. Fragrance fetid, disagreeable; labellum, including the spur, white to greenish-white; labellum disk without trichomes, ventrum of the column with only isolated trichomes at the sides of the base; anther 4.0–4.5 mm long, conical, the tip, in vivo, yellowish green [fragancia desagradable; labelo, incluyendo el espolón, blanco o blanco-verdoso; disco del labelo sin tricomas, ventro de la columna con sólo tricomas aislados en el margen de la base; antera 4.0–4.5 mm de largo, cónica, la punta, in vivo, amarillo verdoso] ............. G. blattiodora
Figure 7. Galeandra minax Rchb.f. Side views of the flowers. Photographs by G. A. Romero-González based on Romero et al. 4056 (TFAV).
Figure 8. *Galeandra minax* Rchb.f. Above and front view of the flower. Photographs by G. A. Romero-González based on *Romero et al.* 4056 (TFAV).
Figure 9. Galeandra pubicentrum C. Schweinf. Photographs by G. A. Romero-González based on Romero et al. 4055 (TFAV).
Figure 10. *Galeandra pubicentrum* C. Schweinf. **A**, habit; **B**, detail of the pseudobulb; **C**, flower in side view; **D**, details of the labellum; **E**, views of the column; **F**, views of the anther; **G**, views of the pollinarium. Drawing by Bobbi Angell based on Romero et al. 4055 (TFAV).
Figure 11. Galeandra pubicentrum C.Schweinf. Drawing by Natalie Warford based on the holotype, Klug 10095 (Holotype: AMES).
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TWO NEW SPECIES OF FRELZIERA (PENTAPHYLACACEAE) FROM COSTA RICA

Daniel Santamaría-Aguilar,1,2 Alex K. Monro,3 Quirico Jiménez-Madrigal,4 and Laura P. Lagomarsino5

Abstract. Two new species of Freziera endemic to Costa Rica, F. tarariae from the Cordillera de Talamanca and F. bradleyi from the Cordillera Central are described and illustrated. Their distribution, phenology, habitat, and relationship to allied species are discussed.

Resumen. Se describen e ilustran dos nuevas especies de Freziera endémicas de Costa Rica: Freziera tarariae de la Cordillera de Talamanca y Freziera bradleyi de la Cordillera Central. Se discuten sus afinidades, distribución, fenología y hábitat.

Keywords: Cordillera Central, Ericales, Mesoamerica, Talamanca, Theaceae

Freziera Willd. (Pentaphylacaceae) is a genus of ca. 57 trees and shrubs distributed from Mexico to Bolivia and in the Antilles, with the highest species diversity in the Andes mountains of western South America (Mabberley, 2008; Weitzman, 1987; Weitzman et al., 2004). Including the species described here, ten species of Freziera are known from Mesoamerica, eight of which occur in Costa Rica. Most Mesoamerican species are restricted to cloud forests, where they are associated with disturbed habitats including roadsides, steep slopes, and mountain peaks.

Species of Freziera are characterized by simple, alternate, distichously arranged leaves, usually with serrate margins. Leaves begin in a rolled terminal bud, and in some cases a vernation scar or line remains on the undersurface of the leaf lamina at maturity. At senescence, the leaves turn red. The flowers are 5-merous with an urceolate corolla with pale petals that are connate or free at their base. The pedicels have a pair of bracteoles at their apex. The fruit is a berry bearing many foveolate seeds.

During the preparation of the treatment of Freziera for the Manual de Plantas de Costa Rica, two undescribed species, commonly misidentified as Symlocos Jacq. (Symlocaceae), were encountered. These are described herein.

Materials and Methods

Herbarium specimens, including types, were examined at A, BM, CAY, CR, F, GH, INB, LPB, LSCR, MO, MOL, NY, PMA, SCZ and USM (herbarium abbreviation follows Thiers, 2014); images from the Global Plants Initiative website (http://plants.jstor.org/) were also consulted. Flowers were rehydrated in a solution of ammonia hydroxide for one day and then placed in water until they were sufficiently soft and pliable to be examined under a dissecting microscope. After study, flowers were dried and returned to the herbarium sheet. Material was examined under a Leica StereoZoom 5 binocular microscope.

Taxonomy

Freziera bradleyi D. Santam. & Q. Jiménez, sp. nov.

TYPE: COSTA RICA. Heredia: Barva, Cordillera Volcánica Central, Parque Nacional Braulio Carrillo, Volcán Barva, sendero Laguna Copey, 10°08'20"N, 84°05'40"W, 2500 m, 07 November 1989 (cfl), G. Rivera 133 (Holotype: INB [1001570472]; Isotypes: INB, MO [1622285]). Fig. 1.

Freziera bradleyi is most similar to F. forerorum A. H. Gentry from which it can be distinguished by the petiolate (versus sessile) leaves with fewer secondary veins and longer bracts, which together with the bracteoles, bear setae (versus absent).

Shrubs or trees, 3–9 m tall; leaf bearing branches cylindrical to weakly angulate in cross-section, straight, papillose and weakly striate, the bark of the twigs pale brown to reddish-brown, sericeous or glabrescent, golden or pale brown, hairs 0.5–1.5 mm, lenticels elliptic to round, white; terminal bud conuplicate-involute 2.6–5.5 cm long, sericeous, hairs 0.4–1.1 mm. Leaves petiolate, petiole

We thank A, BM, CAY, CR, F, GH, INB, LPB, MO, MOL, NY, PMA, SCZ, and USM for access to their collections, Claudia Aragón for her illustrations, Fabio Carbonell-Torres and his team of the La Amistad-Pacífico (ACLA-P) Conservation Area for their help in making collections of F. tarariae, Carlos Godínez and his family for assistance with fieldwork, and Frank González for logistical support in the field. In addition, the senior author would like to thank the Missouri Botanical Garden and an Elizabeth E. Bascom Grant for supporting a visit to MO, Barry Hammel for help in preparing this manuscript, Kanchi Gandhi for nomenclatural advice, David E. Boufford for his helpful comments, and the curators and staff in the Harvard University Herbaria for their support and hospitality. We are also grateful to the Natural History Museum (London) Collections Enhancement Fund for funding a fieldtrip to the Talamanca Mountains.

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Figure 1. *Freziera bradleyi* D. Santam. & Q. Jiménez. A, branch with flowers and leaves showing venation patterns, with detail of the leaf margin and hairs on the abaxial surface; B, bracts with the margin with small setae; C, inflorescence. A from G. Varela 155; B and C from the holotype. Drawing by Claudia Aragón-Quesada.
0.3–0.8 cm long, abaxially rounded, adaxially caniculate, weakly winged, the wings usually erect or involucrate without setae on their margins, sericeous or glabrescent, hairs golden or pale brown, hairs 0.3–1 mm; colletor 1, in petiole base or absent; lamina 8.2–19.5 × 2.5–7.1 cm, elliptic, base cuneate, weakly revolute and symmetrical to markedly asymmetrical and lobed (one side sagittate, the lobe overlapping petiole), margin serrate, with 48–54 teeth per side, each tooth with a black, curved caducous seta, apex long acuminate to cuspidate, coriaceous, adaxial surface strigose-sericeous to glabrescent, hairs <0.1 mm long, abaxial surface sparsely substrigose-sericeous, hairs <0.5 mm long; midrib weakly elevated, crest- or thread-like, strigose-sericeous to pilose, glabrescent; with a black, straight or curved terminal seta, adaxial surface strigose, hairs 0.2–0.5 mm; bracteoles 2, persistent, opposite or subopposite, at apex of pedicel, 4.5–5.2 × 2.7–4 mm, unequal, broadly ovate to deltate, margin with small setae below midpoint, apex acute to mucronate, outer surface strigose-sericeous, hairs 0.2–0.8 mm, inner surface glabrous; sepals 5, imbricate; outer sepals 5–6.1 × 4–4.5 mm, abaxially strigose-sericeous, margins with small setae below midpoint; inner sepals obovate or more or less deltate, 4.2–4.9 × 3–3.2 mm, glabrescent or strigose, abaxially pubescent on central portion, margins entire, ciliate, apex acuminate or rounded; petals 5, 4.1–7 × 3–3.5 mm, white, free, ovoid to oblong-elliptic, margins entire, apex rounded. Staminate flowers: stamens 29 or 30, ± uniseriate, free, unequal, filaments 0.4–1.8 mm long, flat or rounded, anthers 1–1.5 mm long, ovoid-lanceolate, base weakly cordate or truncate, apex apiculate. Pistillate flowers: gynoecium narrowly ellipsoid to conical, ca. 3.8 mm long, glabrous, ovary 4-locular, stigma 4-lobed. Fruit ca. 8 × 6 mm, globose to ovoid, walls ca. 0.2 mm thick, green when immature; seeds 135–150 per fruit, 0.5–1 mm long, reddish brown, foveolate.

**Etymology:** It is an honor to dedicate this species to a great friend, botanist, and founder of the herbarium at George Mason University, Dr. Ted Ray Bradley (1940–). Bradley’s support of the first author during his formative years at INBio is greatly appreciated and acknowledged. Bradley has also greatly contributed to the botanical community in Costa Rica via several years of volunteer work in the herbarium at INBio.

**Distribution and Habitat:** Endemic to Costa Rica, where it is found in cloud and oak forests on the Pacific slopes of the Continental Divide of the Volcán Barva sector of Braulio Carrillo National Park, Cordillera Central at 1800–2500 m.

**Phenology:** Collected with staminate flowers in November, pistillate flowers in August, and fruit from June to August.

**Discussion:** Freziera bradleyi is known from only three collections, but is easily recognized among Costa Rican species by its subsessile leaves with weakly asymmetrical laminae (one side ca 0.5 cm broader than the other), very asymmetrical leaf base and long acuminate or cuspidate apex. Freziera bradleyi is also unique among Costa Rican Freziera for bearing small setae on its bracts, bracteoles and outer sepals. Freziera bradleyi is most similar to the Bolivian *F. angulosa* Tul and *F. forerorum* A. H. Gentry from the border between Panama and Colombia. It is distinguished from them by stem, leaf, bract and bracteole morphology, as summarized in Table 1.

**Additional specimens examined:** COSTA RICA. Heredia: Cantón de Barva. Parque Nacional Braulio Carrillo, Cordillera Volcánica Central, around the Barva research station, Paso Llano, Sacramento y Quebrada Honda, 10°09'00"N, 84°09'00"W, 1800 m, 15 August 1990 (♀ fl, fr). B. Apú 160 (INB, MO); Parque Nacional Braulio Carrillo, Estación Barva, 10°07'22"N, 84°27'15"W, 2300 m, 26 June 1990 (fr). G. Varela 155 (CR, INB, MO).

**Table 1.** Comparison of distinguishing characters of *Freziera bradleyi*, *F. angulosa*, and *F. forerorum*.

<table>
<thead>
<tr>
<th>CHARACTER</th>
<th><strong>F. bradleyi</strong></th>
<th><strong>F. angulosa</strong></th>
<th><strong>F. forerorum</strong></th>
</tr>
</thead>
<tbody>
<tr>
<td>Leaf-bearing stems</td>
<td>cylindrical to weakly angular in cross-section, sericeous to glabrescent</td>
<td>flattened in cross-section, glabrous or sericeous</td>
<td>strongly angular in cross-section, glabrous</td>
</tr>
<tr>
<td>Laminae dimensions</td>
<td>8.2–19.5 × 2.5–7.1 cm</td>
<td>15.5–18 × 6.7–7.4 cm</td>
<td>8–18 × 1.8–5.2 cm*</td>
</tr>
<tr>
<td>Secondary venation</td>
<td>15–18 pairs</td>
<td>20–33 pairs</td>
<td>20–30 pairs</td>
</tr>
<tr>
<td>Petiole</td>
<td>0.3–0.8 cm long</td>
<td>sessile or 0.5 cm long</td>
<td>sessile</td>
</tr>
<tr>
<td>Leaf margins</td>
<td>serrate with 48–54 teeth per side</td>
<td>lightly serrulate, with 60–116 teeth per side</td>
<td>serrulate with 54–95 teeth per side</td>
</tr>
<tr>
<td>Leaf apex</td>
<td>long-acuminate to cuspidate</td>
<td>acuminate to apiculate</td>
<td>acuminate</td>
</tr>
<tr>
<td>Bract and bracteole margin setae</td>
<td>present</td>
<td>absent</td>
<td>absent</td>
</tr>
<tr>
<td>Bracts</td>
<td>3–5.8 mm, margin with small setae</td>
<td>2–3 mm, margin entire</td>
<td>to 1 mm, margin entire</td>
</tr>
</tbody>
</table>

* * information from protologue
Figure 2. Freziella tarariae Q. Jiménez, D. Santam. & A.K. Monro. A, branch with floral buds and immature fruit, with detail of midrib with hairs on the abaxial surface; B, fruit. Drawing by Claudia Aragón-Quesada based on the holotype.

Freziera tarariae most closely resembles F. reticulata Bonpl., from which it can be distinguished by its stem which is round (versus square) in cross section, long acuminate (versus acute) leaf apex and gold or copper-gold, shiny (versus ferruginous and matte) pubescence on the abaxial surface of the laminae.

Shrubs or trees, 3–12 m tall; leaf-bearing branches rounded to weakly angulate in cross-section, occasionally zig-zag, papillate; bark of twigs dark reddish brown or almost black, densely ferruginous, golden or pale brown, sometimes whitish gray, tomentose to glabrescent, hairs 0.5–2.5 mm long, lenticels sparse, round to elliptic, white; terminal bud conduplicate-involute, 3.8–6.3 cm long, densely ferruginous-tomentose, hairs >1 mm long. Leaves petiolate; petiole 0.5–2.5 cm long, usually winged, when winged, the wings involucrate or erect, occasionally bearing black setae on their margins, the setae erect or weakly curved, adaxially caniculate, abaxially rounded, densely ferruginous-tomentose to strigose, golden, pale brown or whitish gray, hairs 0.1–2 mm long; colleter 1, in the petiole base, or absent; laminae (8–) 11.7–16.6 (–21) × (3.8–) 3.8–5.6 (–6.5) cm, oblong-elliptic, base cuneate to rounded, not revolute, weakly asymmetrical, margin strongly serrate with ca. 24–43 teeth per side, each tooth bearing a terminal black, curved caducous seta, apex long acuminate, coriaceous, adaxial surface subsericeous-tomentose to glabrescent, hairs <0.1 mm long, abaxial surface tomentose to pilose, occasionally subsericeous, hairs 0.5–3 mm; midrib on abaxial surface elevated and round in cross section, midrib on adaxial surface planar or weakly sulcate, tomentose to pilose, secondary veins 9–18 pairs, rounded in cross-section on abaxial surface, weakly impressed on adaxial surface, tertiary venation reticulate, prominent and raised on abaxial surface. Inflorescences fasciculate, bearing 1–5 flowers per axil. Flowers pedicellate, pedicel 1–5 (–9) mm long, erect, cylindrical, densely sericeous, hairs 0.5–1 mm; bracts ca. 2–3.3 × 1–1.5 mm, triangular to obovate-lanceolate, margins entire, apex acute or acuminate, without setae, outer surface densely sericeous, inner surface glabrous; bracteoles 2, persistent, opposite or subopposite, at apex of pedicel, 2.3–4 × 0.8–4 mm, unequal, broadly obovate or triangular, margin entire, apex acute or rounded, abaxial surface densely sericeous or tomentulose, hairs 0.4–0.6 mm, adaxial surface glabrous; sepals 5, imbricate, outer sepals 3.1–4 ×
3.9 (–5) mm, densely sericeous or sericeous-tomentulose outside, margins entire; inner sepal 3–4 × 3–4.1 mm, glabrescent or strigose, pubescent only across central external portion, margins entire, ciliate, ovate or broadly ovate, apex acute to rounded; petals 5, 6–6.2 × 2.5–3.5 mm, white or yellowish cream lightly flushed red, free or weakly connate toward base, ovate or oblong-elliptic, margins entire, apiculate or rounded.

Staminate flowers: stamens 18–20, ± uniseriate, free or weakly adnate to base of petals, unequal, filaments 1–2 mm long, flat, anthers 1–2.1 mm long, ovoid-lanceolate, base subcordate, apex apiculate. Pistillate flowers: gynoecium globose to conical, ca. 10 mm long, glabrous, locules 2–4, stigma 3- or 4-lobulate. Fruit 9–10 × 5–7 mm, ovoid or globose, walls ca. 1.1 mm thick, green when immature, deep purple when mature; seeds ca. 65–180 per fruit, ca. 0.8–1 mm long, dark reddish brown, foveolate.

Etymology: The specific epithet refers to the type locality, Cerros Tararia, Cordillera de Talamanca, Limón, Costa Rica.

Distribution and Habitat: Endemic to Costa Rica, where it is found in cloud, elfin, and oak forests at elevations of (2200–) 2400–2900 m on the Caribbean slopes of the Talamanca mountains in La Esperanza del Guarco del Parque Nacional Tapanti-Macizo de La Muerte and the Valle del Silencio sectors on the flanks of rocky outcrops which make up the Cerros Tararia. Within the La Amistad International Park Freziera tarariae is associated with trees of Clusia L., Myrsine L., Podocarpus L’Hér. ex Pers., and Drimys granadensis L.f. Freziera tarariae is known from few localities, where it has been observed at the edge of trails in oak forests and in early successional vegetation. It is likely that Freziera tarariae also occurs in northern Panama within the Bocas del Toro sectors of the La Amistad International Park, though it has yet to be collected there.

Phenology: Collected with staminate flowers in September, pistillate flowers in February, April and September, and fruit in February.

Discussion: Freziera tarariae is distinctive among Freziera in leaf and fruit morphology. The lower surface of the leaf lamina has distinct, raised tertiary veins, the leaf apex is long acuminate and the petioles are usually winged, the wings occasionally bearing black, erect or weakly curved setae. Additionally, dense ferruginous-tomentose pubescence on the leaves and young stems gives the abaxial surface of the dried leaves a shiny copper-gold appearance. The fruit wall is relatively thick (ca. 1.1 mm). While these morphologies are usually constant, G. Davidse et al. 29054 is unusual in having larger leaf laminae with much longer apices (2.5–3.5 cm long) and margins with more conspicuous teeth.

Freziera tarariae has frequently been misidentified as the widespread F. candicans Tul., from which it can be distinguished by the smaller leaf laminae with entire to subentire margins, abaxial copper-gold pubescence, less apparent secondary and tertiary venation, and unwinged petioles, or the wing very short. See Table 2.

Freziera tarariae, however, most closely resembles F. reticulata Bonpl. from Colombia and Ecuador, with which it shares leaves that are densely pubescent abaxially, with strongly impressed, reticulate venation and prominently serrate margins. For differences between these species see Table 2.

Additional specimens examined: COSTA RICA. Cartago: El Guarco, Tapanti-Macizo de La Muerte National Park, catchment of Río Reventazón, to the left-hand side at the cross-roads on the path to towers 21 and 22, 09°41’35"N, 83°52’03"W, 2800–2900 m, 01 September 2011 (st). D. Santamaria & L. Lagomarsino 8983 (GH, INB, MO); El Guarco, Tapanti-Macizo de La Muerte National Park, catchment of Río Reventazón, to the left-hand side at the

<table>
<thead>
<tr>
<th>Character</th>
<th>F. TARARIAE</th>
<th>F. CANDICANS</th>
<th>F. RETICULATA</th>
</tr>
</thead>
<tbody>
<tr>
<td>Leaf-bearing branch</td>
<td>rounded to weakly angulate</td>
<td>rounded or square</td>
<td>square</td>
</tr>
<tr>
<td>Lamina dimensions (8–) 11.7–16.6 (21) × (2.3–) 3.8–5.6 (6.5) cm</td>
<td>7–14.1 × 2.8–4.6 cm</td>
<td>14.2–22.1 × 7.3–9.3 cm</td>
<td></td>
</tr>
<tr>
<td>Leaf margin</td>
<td>strongly serrate</td>
<td>entire, sinuous to serrulate</td>
<td>strongly serrate</td>
</tr>
<tr>
<td>Leaf apex</td>
<td>long acuminate</td>
<td>acuminate</td>
<td>acute</td>
</tr>
<tr>
<td>Petiole 0.5–2 (2.4) cm; usually winged</td>
<td>0.5–1.8 cm; unwinged or the wing very short</td>
<td>1.6–2.7 cm; winged</td>
<td></td>
</tr>
<tr>
<td>Abaxial lamina pubescence</td>
<td>ferruginous, golden or pale brown copper-gold</td>
<td>silver, gold or whitish</td>
<td>ferruginous</td>
</tr>
<tr>
<td>Adaxial venation</td>
<td>prominent, raised</td>
<td>flat or slightly raised</td>
<td>prominent, raised</td>
</tr>
<tr>
<td>Length of inflorescence bract relative to pedicel shorter</td>
<td>shorter or equal</td>
<td>equal or longer</td>
<td></td>
</tr>
<tr>
<td>Fruit diameter</td>
<td>5–7 mm</td>
<td>5–9 mm</td>
<td>7–11 mm</td>
</tr>
</tbody>
</table>
cross-roads on the path to towers 21 and 22, 09°41'35"N, 83°52'03"W, 2800–2900 m, 01 September 2011 (♂ fl), D. Santamaria & L. Lagomarsino 8984 (BM, CR, GH, INB, K, MO, NY, US); El Guarco, Tapantí-Macizo de La Muerte National Park, catchment of Río Reventazón, La Esperanza del Guarco, 09°41'35"N, 83°52'03"W, 2800–2900 m, 15 May 2004 (but fl), R. Kriebel 4683 (GH, INB); El Guarco, Tapantí-Macizo de La Muerte National Park, catchment of Río Reventazón, La Esperanza del Guarco, 09°41'35"N, 83°52'03"W, 2840 m, 21 April 1999 (fl, fr), M. Alfaro 124 (INB); Cantón Cartago, Cuenca del Reventazón, Río Queveri, camino al ICE, 09°42'50"N, 83°50'10"W, 2200 m, 22 April 1998 (fl, fr) E. Alfaro 1545 (CR, INB, MO).

Limón. Talamanca, Bratsi, Cordillera de Talamanca. La Amistad International Park, secondary peak of Cerros Tararias minor, 09°08'53"N, 082°57'55"W, 2650 m, 14 February 2012 (but fl), D. Santamaría et al. 9162 (BM, GH, INB, K, MO, NY); Talamanca, Bratsi, Cordillera de Talamanca. La Amistad International Park, secondary peak of Cerros Tararias minor, 09°08'53"N, 082°57'55"W, 2650 m, 14 February 2012 (♀ fl, fr), D. Santamaría et al. 9167 (BM, CR, GH, INB, K, MO, NY); Cordillera de Talamanca, Atlantic slope, unnamed cordillera between the Río Terbi and the Río Siní, 09°11'00"N, 82°58'30"W, 2400–2750 m, 13 September 1984 (but fl), G. Davidse et al. 29054 (CR, GH).

Literature cited


In a recent monograph of *Macrocarpaea* Gilg from Ecuador (Grant, 2014), seven new species were indicated. Five of these species are formally described here including *M. catherineae* J.R. Grant, *M. cortinae* J.R. Grant, *M. illuminata* J.R. Grant, *M. pacifica* J.R. Grant, and *M. umbellata* Weaver & J.R. Grant. This study has been prepared within a broader context to prepare a full monograph of the genus (Grant, 2003, 2004, 2005, 2007, 2008, 2011, 2014; Grant and Struwe, 2001, 2003; Grant and Trunz, 2011; Grant and Weaver, 2003).

1. *Macrocarpaea catherineae* J.R. Grant, sp. nov. TYPE: ECUADOR. Zamora-Chinchipe: Road from Chuchumbeza, Quimi and Tundayme towards the Condor Mirador, 16 km from end of road at Military camp “Condor Mirador,” 03°36′32.7″S, 078°28′18.3″W, 1059 m, 15 February 2011, *Grant, J.R. & J. Vieu 11-4695* (Holotype: NY; isotypes MO, NEU, QCA, QCNE); *Quimi and Tundayme towards the Condor Mirador, 16 km from end of road at Military camp “Condor Mirador,” 03°36′32.7″S, 078°28′18.3″W, 1059 m, 15 February 2011, Grant, J.R. & J. Vieu 11-4695*.

*Macrocarpaea catherineae* is a new species endemic to the Cordillera del Condor that differs from the widespread *Macrocarpaea micrantha* in being an unbranched shrub with larger and broader leaves that are smooth, coriaceous and yellowish green in color.

Unbranched shrub to small tree, 2–3 m tall, glabrous throughout. **Stems** terete to quadangular, hollow, 5–7 mm in diameter just below the inflorescence. **Leaves** ovate to elliptic, long-petiolate, 11–28 cm long. **Petioles** 10–60 mm, slender with slight vagination, interpetiolar ridge 1–2 mm. **Blades** 10–22 × 5–11 cm, entire, not revolute, yellowish green with slightly impressed veins above, and slightly raised veins below, glabrous above and below, thin coriaceous; base aequilateral to oblique, rounded to cuneate; apex acuminate. **Inflorescence** a much diffusely branched open thyrsus 25–36 cm long; branches 10–24 cm long, 5–9 flowered per branch. **Bracts** ovate to elliptic, sessile to petiolar, 5–87 × 2.5–40 mm; base aequilateral to oblique, rounded to cuneate; apex acute to acuminate; bract petioles 0–6 mm. **Flowers** pedicellate, erect to slightly spreading; pedicels 15–20 mm long; bracteoles linear to lanceolate, 2–8 × 0.25–0.5. **Calyx** campanulate, 6–9 × 5–6 mm, glabrous, smooth, green, ecarinate, ovate; calyx lobes 3–4 × 3–4 mm, rounded to obtuse. **Corolla** unknown. **Capsules** ellipsoidal 29–35 × 6–7 mm, smooth to faintly ribbed, erect; style remnant 7–12 mm long. **Seeds** “Perimetrically winged type,” flattened, roughly 3–4 sided in outline, yet appearing as myriads of different puzzle pieces, 0.5–1.0 × 0.4–0.8 mm, bicolored, testa tan to dark orange, wings translucent cream, testa reticulate, wings ribbed.

**Distribution and habitat:** *Macrocarpaea catherineae* occurs on the Cordillera del Condor in southern Ecuador.

**Eponymy:** Named for Belgian Catherine Vits, renowned ornithologist and owner of the fabulous Copalinga Eclocodge in Zamora, Ecuador. http://www.copalinga.com

**Additional specimens examined:** ECUADOR. Zamora-Chinchipe: Région de la Cordillera del Cóndor, vertiente occidental, Cantón El Panguí, parroquia Tundayme, Valle del Río Quimi, Bosque húmedo premontano, arbustivo de 3 m de alto, flores campanulares color blanco-crema, 03°35′05″S, 078°27′07″W, 900 m, 8 July 2007, *Quizhpe, W. & F. Luisier 2007* (MO, QCNE); El Panguí, Cordiller del Cóndor, vertiente occidental, cuenca del Río Quimi, zona de la futura mina de cobre de la compañía EcuadorCorriente, Formación rocosa areniscosa, suelo arenoso, bosque muy húmedo montano bajo y bosque arbustivo. Arbusto de 304 m, hojas carnosas, flores con pecíolos amarillos, 03°34′55″S, 078°26′10″W, 1400–1670 m, 19 March 2006, *Quizhpe, W. & F. Luisier 2006* (MO, QCNE); Cordiller del Cóndor, vertiente occidental, cuenca del Río Quimi, zona de la futura mina de cobre de la compañía EcuadorCorriente, 03°34′55″S, 078°26′10″W, 1400–1670 m, 19 March 2006, *Quizhpe, W. & F. Luisier 2018* (LOJA, QCNE).


1 Laboratoire de Botanique évolutive, Institut de Biologie, Université de Neuchâtel, rue Émile-Argand 11, Unimail, 2000 Neuchâtel, Switzerland; jason.grant@unine.ch

Figure 1. *Macrocarpaea pacifica* (A–D) and *M. catherineae* (E–G). A, lower leaf; B, flowering stem; C, bud; D, fruiting stem; E, lower leaves; F, fruiting stem; G, capsule. A–D drawn from *Grant 4704* (3 unmounted sheets), E–G from *Grant 4695* (unmounted specimens).
Macrocarpaea catherineae belongs to a group of closely related species restricted to the Amotape-Huancabamba zone including *M. catherineae*, *M. claireae*, *M. dies-viridis*, *M. illuminata*, *M. lenae*, *M. micrantha*, *M. pacifica*, *M. quishpei*, and *M. xerantifulva*. *Macrocarpaea catherineae* is immediately recognized as distinct from the other species in this complex by its smooth, coriaceous and yellowish green leaves. It is sympatric with *M. micrantha* and *M. opulenta*, and may be confused with *M. micrantha* in the field (yet this species is a much-branched plant with thin leaves). The yellowish-green color and coriaceous texture of the leaves of *M. catherineae* is also reminiscent of roadside populations of *M. xerantifulva*.

2. **Macrocarpaea cortinae** J.R. Grant, sp. nov. TYPE: ECUADOR. Sucumbios: 4 km N of Rio Chigual ridge at km 44 from Lumbaqui, 00°16'46.7"N, 77°27'39.6"W, 767 m, 7 February 2013, Grant, J.R & J. Cortina 13-5116 (Holotype: NY; isotypes G, MO, NEU, QCA, QCNE). Fig. 2.A—F, 3, 4.

*Macrocarpaea cortinae* is a new species from northern Ecuador and southern Colombia that differs from *Macrocarpaea pringleana* in having stouter more compact cymes composed of flowers with shorter pedicels, leaves that dry almost translucent thin, and calyces with an orange coloration of the dorsal side of the lobes. Unbranched shrub to tree 1–5 m tall, glabrous throughout. Stems terete below to quadrangular above, hollow, 6–12 mm in diameter just below the inflorescence. Leaves ovate to ovate-elliptic, sessile to long-petiolate, (16)21–47 cm long. Petioles 0–60 mm, slender with very slight vagination; interpetiolar ridge 1–2 mm. Blades 16–41 × 9–20 cm, entire, not revolute, bright green, with slightly impressed veins above, and slightly raised veins below, glabrous above and below, papery thin; blade base aequilateral to slightly oblique, cuneate to attenuate and slightly vagination; interpetiolar ridge 1–2 mm.

**Distribution and habitat:** *Macrocarpaea cortinae* occurs on Amazon-facing slopes of the Andes in northern Ecuador (Napo and Sucumbios) and southern Colombia (Caquetá, Nariño, and Putumayo).

**Eponymy:** Named for Swiss Jimmy Cortina (1986-), co-collector of the type.

**Additional specimens examined:** ECUADOR. Napo: Valle alto del Río Quijos, 5 km al Sur de Cuyuya, Finca Agroecologica Antisana, 00°28’S, 078°03’W, 2850, 16 June 1998, Vargas, H. et al. 1851 (MO, NY, QCNE). Sucumbios: Río Bermejo to Cerro Sur Pax, Cofan community of Alto Bermejo, access from Bermejo oil field of Pozo 1, NW between Lumbaqui and Cascales, vicinity of Vista Camp, 00°18’13.8”N, 77°24’32.0”W, 100–1200 m, 29 July 2001, Aguida, R. et al. 1204 (F); Sinangoe Station, Río Cuconcho Chico, affluent of Río Due, SW of Puerto Libre, NW of Lumbaqui, access trail from Río Sieguyo, vicinity of Cuconcho beach camp, 00°07’48.5”N, 77°33’19.9”W, 940–1000 m, 8 August 2001, Aguida, R. et al. 1585 (F); Gonzalo Pizarro Cantón, Parroquia Reventador, 1800 m, 23 May 1990, Cerón, C. & Ayala 9988 (MO, QCNE); 13 km NW of La Bonita on road towards Santa Barbara, 00°32’14.7”N, 77°31’53.6”W, 2016 m, 7 February 2013, Grant, J.R & J. Cortina 13-5114 (NY); 6 km south of La Bonita, 00°27’21.1”N, 77°32’20.8”W, 1903 m, 7 February 2013, Grant, J.R & J. Cortina 13-5115 (NY). COLOMBIA. Caquetá: Comisaría del Caquetá, Cordillera Oriental, vertiente oriental, Sucre, orillas del Río Hacha, matorrales, 1000 m, 3 April 1940, Cuatrecasas, J. 9034 (COL [2 sheets], US); San José de la Fragua, Serranía de Los Churumbelos, Vereda Las Palmas, parte alta de Río Yuruyaco, 01°20’55”N, 76°6’11”W, 900 m, 20 September 2000, Mendosa, H. et al. 9173 (FMB). Nariño: Muníc. Barbacoas, Bermejo, access from Bermejo oil field of Pozo 1, NW between Lumbaqui and Cascales, vicinity of Vista Camp, 00°18’13.8”N, 77°24’32.0”W, 100–1200 m, 29 July 2001, Aguida, R. et al. 1204 (F); Sinangoe Station, Río Cuconcho Chico, affluent of Río Due, SW of Puerto Libre, NW of Lumbaqui, access trail from Río Sieguyo, vicinity of Cuconcho beach camp, 00°07’48.5”N, 77°33’19.9”W, 940–1000 m, 8 August 2001, Aguida, R. et al. 1585 (F); Gonzalo Pizarro Cantón, Parroquia Reventador, 1800 m, 23 May 1990, Cerón, C. & Ayala 9988 (MO, QCNE); 13 km NW of La Bonita on road towards Santa Barbara, 00°32’14.7”N, 77°31’53.6”W, 2016 m, 7 February 2013, Grant, J.R & J. Cortina 13-5114 (NY); 6 km south of La Bonita, 00°27’21.1”N, 77°32’20.8”W, 1903 m, 7 February 2013, Grant, J.R & J. Cortina 13-5115 (NY).
Figure 2. *Macrocarpaea cortinae*. A, lower leaf; B, habit of flowering stem; C, flower, face view, and flower and bud, side view; D, corolla l.s; E, calyx and pistil, l.s of same; F, infructescence. All drawn from Grant 5116 (unmounted specimens, pickles and photos).
Figure 3. *Macrocarpaea cortinae*. Habit of flowering plant with co-collector of the type, Jimmy Cortina.
Figure 4. *Macrocarpaea cortinae*. Branch of the inflorescence, notice orange coloration on the dorsal portion of each calyx lobe.
Macrocarpaea cortinae belongs to a species complex comprising four species, two of which occur on Pacific-facing slopes of the Andes (M. sodiroana and M. umbellata), and two on Amazon-facing slopes of the Andes (M. pringleana and M. cortinae). The main character that united this group are leaves that are generally long-decurrent on the petiole, but the group is also strongly supported by molecular characters (Vieu & Grant in prep). The leaves of M. cortinae have perhaps the shortest petioles in the group, being generally decurrent to the base of the petiole. Macrocarpaea cortinae is most closely related to M. pringleana yet it is unique in having an orange coloration on the dorsal side of the calyx lobes, still faintly visible on herbarium specimens.

3. Macrocarpaea illuminata J.R. Grant, sp. nov. TYPE: ECUADOR. Zamora-Chinchipe: Cordillera del Condor region, from the road from Zumbi to Paquisha, 8 km south on the road towards Guayzimi, (just W of Paquisha), 03°58′02.1″S, 079°41′09.9″W, 910 m, 11 Feb 2011, Grant, J.R., B. Angell, W. Grant & V. Trunz 09-4560 (Holotype: NY; isotypes G, MO, NEU, QCA, QCNE). Fig. 5. A–E.

Macrocarpaea illuminata is a new species from lowlands areas in the Cordillera del Condor region of southern Ecuador that differs from Macrocarpaea dies-viridis which occurs at higher elevations in the same area in being shorter, entirely glabrous, with a slightly smaller calyx (7–8 × 6–7 mm vs 7–10 × 7–9 mm) and shorter calyx lobes (2–4 × 2 mm vs. 3–5 × 4–5 mm).

Unbranched shrub to small tree 2–3 m tall, glabrous throughout. Stems terete to slightly quadrangular, hollow, 4–8 in diameter just below the inflorescence. Leaves ovate to elliptic, long-petiolate, 26–42 cm long; petioles 40–60 mm, slender with slight vagination; interpetiolar ridge 1–3 mm high. Blades 22–36 × 9–25 mm, entire, not revolute, dark green, with slightly impressed veins above, and slightly raised veins below, glabrous above and below, papery thin; blade base aequilateral to oblique, rounded to cuneate and slightly decurrent on the petiole; blade apex acute to acuminate. Inflorescence a much branched open thyrsus 40+ cm high; branches 6–30 cm long; 5–9 flowered per branch. Bracts ovate to lanceolate, sessile to short-petiolate, 10–75 × 4–50; base aequilateral to oblique, rounded to cuneate; apex acute to acuminate; bract petioles 0–5 mm. Flowers pedicellate, erect to spreading; pedicels 8–24 mm long; bracteoles linear to lanceolate, 1–4 × 0.25–0.5 mm. Calyx campanulate, 7–8 × 6–7 mm, glabrous, green, ecarinate; ovate to rotund; calyx lobes 2–4 × 2 mm, rounded to obtuse. Corolla funnel-shaped, 38–40 mm long, 18–20 mm wide at the apex of the lobe, yellow, smooth; corolla lobes ovate 11–13 × 9–12, apex obtuse to rounded. Stamens 21–28 mm long; filaments 18–23 mm long, filiform, flattened; anthers ovate, 3–5 × 1.5–2.5 mm, sagittate, versatile; pollen glabra-type. Pistil 25–28 mm long; ovary 5–6 × 2–3 mm; style 18–19 × 0.5; stigma lobes spathulate, 2–3 × 1–2 mm. Capsules ellipsoidal, 32–40 × 8–10 mm, smooth to faintly ribbed, faint-orangeish tan, erect to slightly spreading; style remnant 1–3 mm long. Seeds “Perimetrically winged type,” flattened, roughly 3–4 sided in outline, yet appearing as myriads of different puzzle pieces, 0.9–1.0 × 0.9–1.0 mm, bicolored, testa tan, wings straw-colored, testa reticulate, wings ribbed.

Distribution and habitat: Macrocarpaea illuminata occurs on the Cordillera del Condor in southern Ecuador.

Etymology: From the Latin, illuminata.

Additional specimens examined: ECUADOR. Zamora-Chinchipe: Cordillera del Condor, 9.3 km E of Paquisha (measured from the church in the central square), 1394 m, 7 January 2008, Grant, J.R., C. Agier, C. Arnold & M.L. Cheung 08-4529 (G, LOJA, MO, NY); Cordillera del Condor region, from the road from Zumbi to Paquisha, 8 km south on the road towards Guayzimi, (just W of Paquisha), 03°58′05.5″S, 078°41′13.3″W, 1022 m, 25 January 2009, Grant, J.R., B. Angell, W. Grant & V. Trunz 09-4560 (NY).

Macrocarpaea illuminata belongs to a group of closely related species restricted to the Amotape-Huancabamba zone including M. catherineae, M. claireae, M. dies-viridis, M. illuminata, M. lenae, M. micrantha, M. pacifica, M. quispeii, and M. xerantifulva. Macrocarpaea illuminata and M. dies-viridis represent one of the most complicated and cryptic species pairs in southern Ecuador. Indeed my original description of M. dies-viridis was partially based on specimens from both of these species. However, after multiple collection trips to the region, the differences between the two species became clear. M. illuminata is shorter, glabrous, and lowland, while M. dies-viridis is taller, with puberulent calyces, and occurs at higher elevations. The characters of the calyx are diagnostic where M. illuminata has a smaller calyx (7–8 × 6–7 mm vs. 7–10 × 7–9 mm), the difference mainly in the shorter calyx lobes (2–4 × 2 mm vs. 3–5 × 4–5 mm). The two species are well distinguished on molecular characters.

4. Macrocarpaea pacifica J.R. Grant, sp. nov. TYPE: ECUADOR. El Oro: Piñas, Bosque Protector Buenaventura, Fundación de Conservación Jocotoco, 03°39′02.4″S, 079°44′53.0″W, 925 m, 16 February 2011, Grant, J.R. & J. Vieu 11-4704 (Holotype: NY; isotypes G, MO, NEU, QCA, QCNE). Fig. 1. A–D.

Macrocarpaea pacifica is a new species from Pacific-facing slopes of the Andes in southern Ecuador that differs from Macrocarpaea lenae of Amazon-facing slopes in having slightly spiculate calyces and leaves that are decurrent on the petiole.

Unbranched shrub to small tree 1.5–2.5 m tall, glabrous throughout. Stems terete to slightly quadrangular, solid to hollow, 5–12 mm in diameter just below the inflorescence. Leaves ovate to oval, 28–39 × 13–23 cm, long-petiolate, 30–46 cm long. Petioles 20–70 mm long, slender with slight vagination; interpetiolar ridge 1–2 mm. Blades 28–39 × 13–23 cm, entire, not revolute, dark green, with slightly impressed veins above, and slightly raised veins below, glabrous above and below, papery thin; leaf base aequilateral to slightly oblique, cuneate to attenuate and decurrent on the petiole; leaf apex acute to acuminate. Inflorescence a much branched open thyrsus 60+ cm high; branches 20–50
Figure 5. *Macrocarpaea illuminata*. A, habit of flowering stem; B, cyme; C, bud; D, flower; E, dissected flower. A drawn from *Grant 4687 (NY)*, B–E from *Grant 4650 (NY)*.
cm long; 7–15 flowered per branch. **Bracts** ovate to oval, short-petiolate, 18–300 × 5–130 mm; base aequilateral to slightly oblique, cuneate to attenuate and decurrent on the petiole; apex acute to acuminate; bract petioles 2–20 mm. **Flowers** pedicellate, erect to spreading; pedicels 17–25 mm long; bracteoles linear to lanceolate to ovate, 3–13 × 1–4 mm. Calyx campanulate, 6–9 × 6–9 mm, slightly spiculate to glabrous, dark green, ecarinate, ovate; calyx lobes 3–4 × 4.5–5.0 mm, rounded to obtuse. **Corolla** unknown. **Capsules** ellipsoidal, 28–35 × 6–8 mm, smooth to ribbed, faintly impressed veins above, and slightly raised veins below, glabrous above and below, papery thin to nearly coriaceous; leaf base aequilateral to slightly oblique, cuneate to attenuate and decurrent on the petiole to the base of the leaf; leaf apex acuminate. **Inflorescence** a much branched open thyrsie 50+ cm high, branches 8–40 cm long; 5–12 flowered per branch. **Bracts** ovate to lanceolate, sessile to short-petiolate, 8–130 × 2–75 mm; bract base aequilateral to oblique, cuneate to rounded; bract apex acuminate; bract petioles 0–5 mm. **Flowers** pedicellate, erect; pedicels 8–28 mm long; bracteoles inconspicuous, linear to lanceolate, 1–8 × 0.5–2.0 mm. Calyx campanulate, 6–10 × 6–8 mm, glabrous, smooth, green, ecarinate, ovate; calyx lobes 3–5 × 4–6 mm, obtuse to rounded. **Corolla** funnel-shaped, 27–36 mm long, 12–20 mm wide at the apex of the tube, yellow, smooth; corolla lobes ovate to elliptic, 7–11 × 6–7 mm, obtuse to rounded. **Stamens** 20–25 mm long; filaments 16–20 mm long, filiform, flattened; anthers elliptic to oblong, 4–5 × 1.5–2.0 mm, sagittate, versatile; pollen glabra-type. **Pistil** 28–34 mm long; ovary 8–9 × 2–3 mm; style 17–21 mm long; stigma lobes spathulate, 3–4 × 2.0–2.5 mm. **Capsules** shaped like an elephant’s tusk (that is, linear-long to narrowly ellipsoidal yet always arched upwards), (10)30–37 × 6–12 mm, smooth to ribbed, chestnut-tan, erect to slightly spreading; style remnant 4–11 mm. **Seeds** “Perimetrically winged type,” flattened, roughly 3–4 sided in outline, yet appearing as myriads of different puzzle pieces, 0.4–0.7 × 0.5–1.0 mm, bicolored, testa tan, wings straw-colored, testa reticulate, wings ribbed.

**Distribution and habitat:** *Macrocarpaea pacifica* occurs on Pacific-facing slopes of the Andes in El Oro province in southern Ecuador. It is the southernmost species of *Macrocarpaea* on Pacific-facing slopes of the Andes; all other species are located much further north, for example *M. sodiroana* M. gattaca, and *M. umbellata* on Pacific slopes from near Quito northwards, and *M. lenae* in overall shape and form, including calyces that dry dark green (to nearly black in *M. lenae*), and leaves that are generally more congested, and shorter pedicels.

Unbranched **shrub** to tree 1–5 m, glabrous throughout. **Stems** terete to slightly quadrangular above, hollow, 6–14 mm in diameter just below inflorescence. **Leaves** ovate, elliptic, rhombic, to nearly obovate, sessile to long-petiolate, 13–59 cm long. **Petioles** 0–90 mm, slender with very slight vagination; interpetiolar ridge 1–5 mm. **Blades** 13–59 × 6–26 cm, entire, not revolute, dark green, with slightly impressed veins above, and slightly raised veins below, glabrous above and below, papery thin to nearly coriaceous; leaf base aequilateral to slightly oblique, cuneate to attenuate and decurrent on the petiole to the base of the leaf; leaf apex acuminate. **Inflorescence** a much branched open thyrsie 50+ cm high, branches 8–40 cm long; 5–12 flowered per branch. **Bracts** ovate to lanceolate, sessile to short-petiolate, 8–130 × 2–75 mm; bract base aequilateral to oblique, cuneate to rounded; bract apex acuminate; bract petioles 0–5 mm. **Flowers** pedicellate, erect; pedicels 8–28 mm long; bracteoles inconspicuous, linear to lanceolate, 1–8 × 0.5–2.0 mm. Calyx campanulate, 6–10 × 6–8 mm, glabrous, smooth, green, ecarinate, ovate; calyx lobes 3–5 × 4–6 mm, obtuse to rounded. **Corolla** funnel-shaped, 27–36 mm long, 12–20 mm wide at the apex of the tube, yellow, smooth; corolla lobes ovate to elliptic, 7–11 × 6–7 mm, obtuse to rounded. **Stamens** 20–25 mm long; filaments 16–20 mm long, filiform, flattened; anthers elliptic to oblong, 4–5 × 1.5–2.0 mm, sagittate, versatile; pollen glabra-type. **Pistil** 28–34 mm long; ovary 8–9 × 2–3 mm; style 17–21 mm long; stigma lobes spathulate, 3–4 × 2.0–2.5 mm. **Capsules** shaped like an elephant’s tusk (that is, linear-long to narrowly ellipsoidal yet always arched upwards), (10)30–37 × 6–12 mm, smooth to ribbed, chestnut-tan, erect to slightly spreading; style remnant 4–11 mm. **Seeds** “Perimetrically winged type,” flattened, roughly 3–4 sided in outline, yet appearing as myriads of different puzzle pieces, 0.4–0.7 × 0.5–1.0 mm, bicolored, testa orangish-brown, wings straw-colored; testa reticulate, wings ribbed.

**Distribution and habitat:** *Macrocarpaea umbellata* occurs on Pacific-facing slopes of the Cordillera Occidental in eastern Colombia and northern Ecuador that differs from Ecuadorian *Macrocarpaea sodiroana* in leaves that are larger, thinner-textured, with less prominent venation, long-attenuate at the base and long-acuminate at the apex, cymes that are generally more congested, and shorter pedicels.

Additional **specimens examined:** COLOMBIA. **Mutis** 334 (US). Cauca: Santa Martha, Bota Cauca, en la via Mocoa-Pitalito, ca. 5 km del puente del Rio Caquetá, 1100 m, 25 January 1990, Ramos, J.E. et al. 2501 (CUVC, MO, U); Mun. Santa Rosa, Corregimiento Descanse, Vereda Genova, en cercanía de la quebrada La Isla, Finca La Isla, 1100 m,
Figure 6. *Macrocarpaea umbellata*. **A**, leaf; **B**, habit of fruiting stem; **C**, fruit; **D**, flowering stem; **E**, flower. **A**–**E** drawn from Cuatrecasas 14986 (US), **B**–**C** from Madison et al. 4795 (F), and **D**–**E** from Croat 38605 (MO).
Macrocarpaea umbellata belongs to a group of closely related species with leaves that are generally long-decurrent on the petiole including *M. cortinae*, *M. pringleana*, *M. stenophylla*, and *M. umbellata*. It can be easily identified by its large thin leaves with a sessile to long-attenuate base and acuminate apex, cymes congested so as to form sub-umbels of flowers, squat and deeply cleft calyces, extremely reduced bracteoles. *Macrocarpaea umbellata* has previously been identified as *M. sodiroana*, which is now recognized as a narrow endemic of Pichincha, Ecuador (Grant 2003; 2014). The two species are similar in their general leaf morphology and inflorescence architecture, but *M. umbellata* differs in leaves that are larger, thinner-textured, with less prominent venation, long-attenuate at the base and long-acuminate at the apex, cymes that are generally more congested, and shorter pedicels.


This is the first report of *Macrocarpaea stenophylla* in Ecuador, or even on the Cordillera del Condor. It was previously only known from the Chachapoyas region of northern Peru, but this range extension is not surprising since other species known best from northern Peru have been found here recently. At 30-50 cm tall, *Macrocarpaea stenophylla* is perhaps the shortest of all species in the genus, other than its most closely related species of similar stature, *M. wurdackii* of northern Peru. It was collected in low scrub vegetation on summits of the Cordillera del Condor that have been burned, so it is possible that larger plants may occur outside of burned areas.

It was first thought that these collections represented a new species provisionally called *M. "lilliputiana"* (Grant 2014). However, subsequent morphological studies indicate this the material falls within the currently understood circumscription of *M. stenophylla*, as is the same case of *M. "zumbae"* for *M. harlingii* (Fig. 7 A–D). *Macrocarpaea stenophylla* is part of a group of closely related group with smooth leathery leaves where the secondary leaf veins are absent or scarcely visible including *M. abiseo*, *M. harlingii*, and *M. pajonalis*. In Ecuador, *M. stenophylla* is superficially similar to *M. subsessilis* that prospers and resprouts on burned slopes of the Yangana-Cerro Toledo road. *Macrocarpaea stenophylla* can be differentiated from *M. subsessilis* in its shorter leaves (2–5 vs. 2.5-9.0 cm), much smaller calyx (6–8 mm vs. 8–13 mm), and shorter capsules (10–13 vs. 11–15 mm).

**Additional specimens examined:** ECUADOR. Zamora-Chinchipe: Paquisha Cantón, Cordillera del Cóndor, Machinaza plateau summit area, adjacent to obelisk-shaped border marker, at end of trail from upper Paquisha military post, precisely on Ecuador-Peru border, nearly level sandstone plateau with low scrub vegetation, charred stems and regrowth indicate that area was burned about 15 years previously, small shrub or subshrub, 30-50 cm tall, growing on bare sandstone rock plateaux, 03°53’50”S, 078°28’49”W, 2420 m, 15 March 2008, Neill, D. & W. Quinze 16113 (MO, NY). Paquisha Cantón, Cordillera del Cóndor, the Machinaza plateau, one of the highest-elevation Hollín sandstone plateaux in the Condór region, about 500 m west of the Ecuador-Peru international border, near end of trail from Paquisha Alto military post. Bare sandstone substrate, or quartzite sand derived therefrom, very nutrient poor. Dwarf scrub vegetation, dominated by shrubs to about 1.5 m tall, with occasional small tree to 4 m tall. Vegetation recovering slowly from an extensive burn about 20 years previously, with charred woody stems in abundance on ground, 03°54’06”S, 078°28’57”W, 2315 m, 23 June 2009, Neill, D. & C. Kajekai 16910 (LOJA, MO, QCNE).
Figure 7. *Macrocarpaea harlingii* (A–D) and *M. stenophylla* (E–G). A, habit of flowering stem; B, lower leaf; C, flower and bud, side view; D, pistil and calyx; E, habit; F, bud and flower with bracts; G, capsule with bracts. A–D from Grant 4669 (pickles and 2 sheets), E–F from Neill & Quizhpe 16113 (unmounted specimen), G from Neill & Kajekai 16910 (MO).
Literature cited


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Three new species of *Macrocarpaea* Gilg from Peru are described and illustrated, one based on a single specimen from a poorly known locality, and two from recently collected material that have been sequenced and included in a new molecular phylogeny of the genus (Vieu and Grant in prep.). This paper continues a series of studies in preparation of a full monograph (Grant, 2003, 2004, 2005, 2007, 2008, 2011, 2014; Grant and Struwe, 2001, 2003; Grant and Trunz 2011; Grant and Weaver, 2003).

1. *Macrocarpaea abiseo* J.R. Grant, sp. nov. TYPE: PERU. San Martín: Dist. Huallaga, Valley of Rio Apisconco, 30 km above Jucushamba, 7˚55’S, 77˚10’W, 3000 m, 4 September 1965, A.C. Hamilton & P.M. Holligan 688 (Holotype K).

*Macrocarpaea abiseo* is a new species from Amazon-facing slopes of the Andes in central Peru that differs from *Macrocarpaea pajonalis* in having slightly visible secondary veins on its leaves, spicate calyces, and flowers that are less nodding.

*Shrub* glabrous to hyaline spiculate, especially spiculate on petioles, bracteoles, and calyces which are covered with short simple hairs. *Stems* terete to slightly quadrangular, solid, 4–5 mm in diameter just below the inflorescence. *Leaves* oval to ovate, sessile to short-petiolate, 3.0–8.5 cm long. *Petioles* 0–10 mm, robust with slight vagination one quarter the length of the petiole; interpetiolar ridge 2–3 mm. *Blades* 3.0–7.5 × 1.5–5.0 mm, entire, revolute, dark above, lighter below, glabrous, thick, leathery-coriaceous, midrib thick, secondary veins slightly visible either above or below; leaf base aequilateral, cuneate; leaf apex obtuse to rounded. *Inflorescence* a few branched short compact thyrse, 10–14 cm high; branches 3–5 cm long; 5–8 flowers per branch. *Bracts* oval to obovate, sessile to short-petiolate, 8–20 × 4–16 mm; bract base aequilateral, cuneate; bract apex obtuse to rounded; bract petioles 0–2 mm. *Flowers* pedicellate, erect; pedicels 5–8; bracteoles inconspicuous and scabrous, linear to triangular, 1.0–2.5 × 0.5–1.0 mm. *Calyx* campanulate, 6–8 × 5–6 mm, hyaline spicate, faintly rugose, ecarinate, reniform to ovate; calyx lobes 1–2 × 2.5–3.0 mm, rounded. *Corolla* funnel-shaped, 28–33 mm long, 12–15 mm wide at the apex of the tube, yellow, smooth; corolla lobes ovate, 7–8 × 6–7 mm, obtuse to rounded. *Stamens* 15–20 mm long; filaments 10–15 mm long, filiform, flattened; anthers elliptic to sagittate, 5 × 1.5–2.0 mm, sagittate, versatile; pollen glabra-type. *Pistil* 26–28 mm long; ovary 6.5–7.0 × 2–3; style 17–18 × 0.5–0.75 mm; stigma lobes spathulate, 2.5–3.0 × 2 mm. Capsules and seeds unknown.

**Distribution and habitat:** *Macrocarpaea abiseo* occurs on Amazon-facing slopes of the Andes in central Peru. Since this area has been little explored, it is not surprising there are novelties in the region. The only other species of *Macrocarpaea* known from this area is *Macrocarpaea gran-pajatena* J.R. Grant.

**Etymology:** Named for Parque Nacional del Río Abiseo in Peru, where it occurs.

*Macrocarpaea abiseo* has thick leathery leaves with scarcely visible secondary veins. It appears to belong to a group of species from southern Ecuador and Peru with these characteristics including *M. harlingii*, *M. loranthisoides*, *M. luya*, *M. pajonalis*, and *M. stenophylla*. It may be most closely related to *M. pajonalis*, a common species of the Oxapampa and Huánuco region of Pasco and Huánuco in central Peru. However, *M. abiseo* has more visible secondary veins on its leaves, hispid calyces, and flowers that are less nodding. *Macrocarpaea pajonalis* is always completely glabrous. Additional collections from the Oxapampa region that may eventually be attributed to *M. abiseo* are Perea 694, Valenzuela 13762, van der Werff 22970. These were collected within the general distribution of *M. pajonalis*, but at higher elevations.


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2. *Macrocarpaea felicitata* J.R. Grant & J. Vieu, sp. nov.

**TYPE:** PERU. Pasco: Dist. Oxapampa, bosque primario y de arenisca, 10°40'36"S, 075°18'55"W, 2400 m, arbolito 4 m, flores amarillo-verdosas, 21 February 2006, *R.* Rojas, A. Peña, J. Mateo, & C. Rojas 3935 (Holotype: MO; Isotype: NY). Fig. 2.

*Macrocarpaea felicitata* is a new species from Amazon-facing slopes of the Andes in central Peru that differs from *Macrocarpaea stenophylla* in being a 4 m tall tree with a large panicle of trumpet-shaped corollas and hispid to spiculate calyces.

Small tree to 6 m, hyaline hispid to spiculate with short simple hairs on stems, petioles, leaves, inflorescences, bracts and calyces. **Stems** terete to slightly quadrangular, solid to hollow, 7–10 mm in diameter just below the inflorescence. **Leaves** oval to broadly elliptic, petiolate, 45 cm long. **Pedicel** 6 mm long, robust with strong open vagination one half the length of the petiole; intepetiolar ridge 1–3 mm high. **Blade** 39 × 22 cm, entire, dark green, with slightly impressed veins above, and slightly raised veins below, hyaline hispid to spiculate throughout especially along veins on lower surface, papery thin; leaf base aequilateral, oblique, to cuneate; leaf apex obtuse to acute. **Inflorescence** a much branched open thyrs 29–36+ cm high; branches 10–25 cm long; 5–10 flowered per branch. **Bracts** ovate, oval, elliptic, to narrowly oblanceolate, sessile to petiolate, 12–190 × 2–100 mm; bract base aequilateral to oblique, cuneate, rounded to short attenuate; bract apex acute to obtuse; bract petioles 0–25 mm long. **Flowers** pedicellate, spreading; pedicel 9–26 mm long, linear to lanceolate; bracteoles 1.5–12 × 0.5–2.0 mm.

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**Figure 1.** *Macrocarpaea abiseo*. A, habit of flowering stem; B, detail of stem nodes; C, bud; D, open corolla; E, immature fruit. All drawn from Hamilton & Holligan 688 (K).
Figure 2. *Macrocarpaea felicitata*. A, lower leaf; B, habit of flowering stem; C, bud and pistil in calyx. A from Vieu et al. JVII (NY), B–E from Rojas et al. 3935 (MO).
Calyx campanulate, 8–11 × 5–6 mm long, hyaline hispid to spicate with short simple hairs, ecarinate; calyx lobes ovate to reniform, 1.5–2.0 × 2–3 mm, rounded to obtuse, the edges slightly fimbriate. Corolla funnel-shaped, 57–63 mm long, 23–30 mm wide at the apex of the tube, greenish-yellow, smooth; corolla lobes ovate to elliptic, 11–18 × 7–14 mm, apex obtuse to rounded. Stamens 43–48 mm long; filaments 38–42 mm long, filiform, flattened; anthers elliptic to sagittate, 5–6 × 1.5–3 mm, sagittate, versatile; pollen glabra-type. Pistil 60–62 mm long; ovary 8–11 × 3–4 mm; style 45–47 × 1 mm; stigma lobes spathulate to oblong, 5–6 × 1.0–2.5 mm. Capsules and seeds unknown.

**Distribution and habitat:** Macrocarpaea felicitata occurs in primary to secondary forests on Amazon-facing slopes of the Andes on the Cordillera Central in central Peru near Oxaapampa. This is the area where Macrocarpaea is currently best understood in Peru. There are ample herbarium collections of all the species, which was useful in discriminating *M. felicitata* from the known taxa. The region has an impressive number of at least nine overlapping species including *M. revoluta* J.R. Grant, *M. ostentans* J.R. Grant, *M. wallnoeferi* J.R. Grant, *M. tahuantinsuyuan* J.R. Grant, *M. viscosa* (Ruiz & Pavon) Gilg, and *M. chthonotropa* J.R. Grant. *Macrocarpaea felicitata* can be easily identified within this group in having small (5 mm long) puberulent hairy calyces.

**Etymology:** From the Latin, *felicitata.*


3. *Macrocarpaea huamantanga* J.R. Grant & J. Vieu, sp. nov. **TYPE:** PERU. Cajamarca: Distrito de Jaén, caserio San Jose, camino hasta la catarata “del velo de la novia,” Bosque de Huamantanga, 5°42.370 S, 78°57.106 W, 2223 m, 21 February 2012, J. Vieu & D. Desrousseaux 43 [DNA voucher = JV47] (Holotype: NY; Isotype: MO). Fig. 3.

*Macrocarpaea huamantanga* is a new species closely related to *M. chthonotropa,* yet differs in having generally oblanceolate leaves, a large paniculate inflorescence with comparatively small flowers, and an urceolate-campanulate calyx with thickened calyx lobes and a thickened area at the base between each calyx lobe.

**Tree** to 4 m, glabrous throughout. Stems terete to slightly quadrangular above, hollow, 7–13 mm in diameter just below the inflorescence. Leaves elliptic, oblong, ovate to obovate, short-petiolate, 36–40 cm long. Petioles 20–30 mm long, robust with strong open vagination one-third the length of the petiole; interpetiolar ridge 2–3 mm. Blades 36–37 × 11–17 cm, entire, not revolute, dark above and conspicuously lighter below, with slightly impressed veins above, and slightly raised veins below, glabrous above and below, papery thin; leaf base aequilateral to oblique, cuneate, decurrent on the petiole to the base of the leaf; leaf apex acute to acuminate. Inflorescence a much branched open thryse 50+ cm; branches 34–40 cm long; 5–15 flowered per branch. Bracts elliptic, oblong, ovate to oblanceolate, sessile to short-petiolate, 10–220 × 4–70 mm; bract base aequilateral to oblique, cuneate, decurrent on the petiole to the base of the bract; bract apex acuminate; bract petiole 0–10 mm long. Flowers pedicellate, erect; pedicels 8–22 mm long; bracteoles inconspicuous and scabrous, linear, triangular to ovate, 1–10 × 1–3 mm. Calyx campanulate to urceolate, 5–7 × 6–7 mm, glabrous, rugose, ecarinate, but calyx lobes thickened dorsally, and thickened basally between each calyx lobe; calyx lobes ovate, 2.4 × 2–4 mm, acute to obtuse. Corolla funnel-shaped, 28–38 mm long, 10–15 mm wide at the apex of the tube, yellow, smooth; corolla lobes ovate, 8–11 × 6–7 mm, apex obtuse to rounded. Stamens 20–23; filaments 16–18 filiform, flattened; anthers elliptic to oblong, 4–5 × 2 mm, sagittate, versatile; pollen glabra-type. Pistil 30–32 mm long; ovary 5–7 × 1–3 mm; style 21–22 × 0.5–1.0 mm; stigma lobes spathulate, 3–4 × 1–2. Capsules ellipsoidal to linear-long, 24–26 × 7–9 mm, smooth to faintly ribbed, faint-orangish tan, erect to slightly spreading. Seeds “Perimetrically winged type,” flattened, roughly 3-4 sided in outline, yet appearing as myriads of different puzzle pieces, straw-colored, testa reticulate, wings ribbed.

**Distribution and habitat:** Macrocarpaea huamantanga occurs in the understory of primary forest of the Andes of Cajamarca in northern Peru.

**Etymology:** Named for its locality at Bosque de Huamantanga, Jaén, Cajamarca.

**Additional specimens examined:** PERU. Cajamarca: Distrito de Jaén, camino hasta la catarata “del velo de la novia,” Bosque de Huamantanga, 5°42.370 S, 78°57.106 W, 2223 m, 21 February 2012, J. Vieu & D. Desrousseaux 42 [DNA voucher = JV45], and 44 [DNA voucher = JV48] (NY).

*Macrocarpaea huamantanga* is most closely related to *M. chthonotropa* as can be seen in both morphology as well as in DNA sequences. It is distinct in having generally oblanceolate leaves, a large paniculate inflorescence with comparatively small flowers, and an urceolate-campanulate calyx with thickened calyx lobes, and a thickened area at the base between each calyx lobe.
Figure 3. *Macrocarpaea huamantanga*. A, lower leaf and habit of flowering stem; B, bud; C, pistil in calyx. All drawn from *Vieu & D. Desrousseaux* 43 (NY).


SORBUS ULLLEUNGENSIS, A NEW ENDEMIC SPECIES ON ULLLEUNG ISLAND, KOREA

CHIN-SUNG CHANG1,2 AND HEE YOUNG GIL1

Abstract. Plants that have been treated as Sorbus commixta on Ulleung Island, Korea, show morphological variability and their taxonomy is unclear. We extensively studied the morphology of wild populations of these plants and found that they can be distinguished from S. commixta by their larger fruits and flowers and wider inflorescences. Here we describe and illustrate them and propose them as representing a new species, S. ulleungensis. An updated key to the five Korean species of Sorbus including the new species is provided.

Keywords: new species, Sorbus commixta, Sorbus pohuashanensis, Ulleung rowan, Ulleung island

Sorbus L. (Rosaceae) comprises approximately 100 species of deciduous trees and shrubs widely distributed throughout northern hemisphere (Krüssmann, 1984; Ohwi, 1984; Robertson et al., 2010; Lu and Sponberg, 2003; McAllister, 2005). The main centers of diversity for the genus are in China, northern Myanmar, and the eastern Himalayas (McAllister, 2005). Recent study (McAllister, 2005) treated Sorbus in a narrower sense (sensu stricto) to include only the pinnate-leaved species, raising several of the simple leaved species to generic rank. As treated in its broad sense (sensu lato), Sorbus alnifolia (subgenus Aria) is included in the genus Sorbus here. Therefore, four species, S. pohuashanensis (Hance) Hedl., S. commixta Hedl., S. sambucifolia (Cham.& Schldl.) M. Roem, and S. alnifolia (Siebold & Zucc.) K. Koch are known from the Korean peninsula (Lee, 1980; Chang et al., 2011).

Ulleung Island, a volcanic, pentagonally shaped island about 10 km in diameter, is located about 150 km from the Korean mainland. The island, formed during the late Tertiary period and surrounded by rocky cliffs, is well known for its unique flora numbering about 180 woody species, including several endemics (Lee and Joo, 1958). The one species of Sorbus on Ulleung Island has long been recognized as S. commixta Hedl. (Lee, 1980). However, Nitzelius (1989), during his expedition to Ulleung Island in 1976, first raised the question of its status due to the large size of most of its morphological characters. Nitzelius called a clone of the Ulleung rowan “Dodong” and propagated and distributed it throughout northern hemisphere (Krüssmann, 1984; Ohwi, 1984; Robertson et al., 2010; Lu and Sponberg, 2003; McAllister, 2005). Recent study (McAllister, 2005) treated Sorbus in a narrower sense (sensu stricto) to include only the pinnate-leaved species, raising several of the simple leaved species to generic rank. As treated in its broad sense (sensu lato), Sorbus alnifolia (subgenus Aria) is included in the genus Sorbus here. Therefore, four species, S. pohuashanensis (Hance) Hedl., S. commixta Hedl., S. sambucifolia (Cham.& Schldl.) M. Roem, and S. alnifolia (Siebold & Zucc.) K. Koch are known from the Korean peninsula (Lee, 1980; Chang et al., 2011).

Ulleung Island, a volcanic, pentagonally shaped island about 10 km in diameter, is located about 150 km from the Korean mainland. The island, formed during the late Tertiary period and surrounded by rocky cliffs, is well known for its unique flora numbering about 180 woody species, including several endemics (Lee and Joo, 1958). The one species of Sorbus on Ulleung Island has long been recognized as S. commixta Hedl. (Lee, 1980). However, Nitzelius (1989), during his expedition to Ulleung Island in 1976, first raised the question of its status due to the large size of most of its morphological characters. Nitzelius called a clone of the Ulleung rowan “Dodong” and propagated and distributed it in Europe because of its great value to landscape architecture (Nitzelius, 1989).

When field work was undertaken in Ulleung Island over several years, the larger fruits and flowers having several distinctive vegetative characters were noticed on the Ulleung rowan in comparison with the closely related S. commixta. An examination of herbarium material and field collections of Sorbus L. on Korea’s Ulleung Island suggested that a description of a new taxon similar to S. pohuashanensis (Hance) Hedl. and S. commixta Hedl. was required.

Previously recognized endemic taxa, Fagus multinervis Nakai, Cotoneaster wilsonii Nakai, Acer takesimense Nakai, and Acer okamotoanum Nakai on Ulleung Island are currently treated as F. engleriana Seemen ex Diels, C. multiflorus Bunge of central China, Acer pseudosieboldianum (Pax) Kom., and Acer pictum Thunb., respectively (Chang and Jeon, 2003, Chang, 1992, Chang et al., 2011). On the other hand, Tsuga on Ulleung Island was shown to be more closely related to T. diversifolia (Maxim.) Mast. of northern Japan, rather than to T. sieboldii Carriere of southeastern Japan (Havill et al., 2008). Also, Prunus takesimense Nakai and Sambucus racemosa subsp. pendula (Nakai) H. I. Lim and Chin S. Chang on Ulleung Island have been reported as distinctive endemic subspecies on this island (Chang, 1992; Chang et al., 2004; Lim et al., 2009). Recent studies (Koji et al. 2012, Stussey et al., 2006) showed that examination of an anagenetically derived endemic species on Ulleung Island reveals genetic variation equal or nearly equal to that of its continental progenitor.

The primary objective of this research was to define the phenetic relationships among the different morphological entities of the S. pohuashanensis, S. commixta and Ulleung island individuals. Individuals of Sorbus on Ulleung island were studied to determine if their morphological differentiation from the related taxa warranted specific taxonomic recognition.

Materials and Methods

Mature leaves were collected from many places in South Korea from 2010 to 2012. Three hundred and ninety one individuals were sampled for fruits, flowers and leaves from individuals from Ulleung Island (59 individuals), S. pohuashanensis (182), and S. commixta (150) were collected and measured for characters. Herbarium specimens from the material collected were stored at SNUA. In addition, herbarium specimens of S. commixta from Japan (48) and S. pohuashanensis from China (70) (from TI, MAK, TUS and PE) were selected to represent the entire geographical...
range and to reflect the morphological variability present within each taxon. Previous studies suggested that *S. pohuashanensis* in Korea is considered to be a past hybrid originating between *S. commixta* and *S. wilsoniana* in China, thus this taxon is excluded for morphological analysis here.

Characters selected for analysis included those most frequently utilized in keys and diagnoses. Criteria classically used in the literature (Lu and Sponberg, 2003; McAllister, 2005) to distinguish among taxa concerned include the length of leaflet, number of leaflets, width of inflorescence and fruit size. Since flowering or fruit specimens were not available to measure the width of floral tube, length of pistil, length of seed, and width of seed, only living collections of *S. pohuashanensis*, *S. commixta* and Ulleung individuals from Korea were selected and measured. For leaf measurements a “typical,” usually the largest, measurable leaf, was selected. The initial data matrices were constructed from 19 vegetative and fruit characters including one ratio (Table 1).

Morphological variation within and among taxa was assessed using univariate statistics (mean, maximum, minimum) and multivariate morphometric analyses (principal components analysis: PCA). The PCAs and univariate statistics were produced with XLSTAT (version 2011.1.04) and R (version 2.15.2). A correlation matrix was generated using selected significant characters along with the univariate and analysis of variance (ANOVA). Also, bivariate scatter diagrams were performed and each characters associated with individuals of several OTUs were plotted here.

**Results and Discussion**

For fruit with leaf characters the first three PCA axes accounted only for 62.6% of the total variance: PC (principal component) 1 had the highest loadings for leaf length (character 1), terminal leaflet length (character 2), terminal leaflet width (character 3), petiole length of terminal leaflet (character 6), petiole length (character 8), toothed length of middle leaflet (character 14), length of corymb (character 15), diameter of corymb (character 16); PC2 had the highest loadings for angle of terminal leaflet apex (character 10); Angle of terminal leaflet base (character 12); PC3 had the highest loadings for ratio of toothed length/leaflet length of middle leaflet (character 19).

PC 1 vs. PC 3 provided better separation of the Chinese *S. pohuashanensis* from other taxa, while PC 1 versus PC 2 revealed separation of *S. commixta* from individuals of the Ulleung rowan. It was clear that there was minimal overlap in the clusters of individuals of the Ulleung rowan and *S. commixta*. The characters that contributed most to the separation were the leaf length, the number of leaflets (11–13 versus 13–15), corymb width, and fruit width (6–7 mm versus 9–10 mm) (Fig. 1). Also, it differs from *S. commixta* in having a wide calyx-tube, long pistil, and large seed (Fig. 1) and has more carpels (3–4 versus 4–5). This new species can be consistently distinguished from the related taxa in characters of leaf length, number of leaflets, corymb width, fruit width (Fig. 1). In general, large flowers and fruits can be considered characters of great taxonomic value to distinguish the Ulleung individuals (Table 2).

Bivariate analysis demonstrated that width of inflorescence and size of fruit between Ulleung individuals and the other related taxa emerged as the most distinct (Fig. 2). Also, its habit is more likely to be a large tree with dark gray

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**Table 1.** Morphological characters for pomes and leaves of the *Sorbus commixta* complex used in the principal components analysis. Units of measurement are given in parentheses.

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<td>2. Terminal leaflet length (mm)</td>
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<td>3. Terminal leaflet width (mm)</td>
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<td>4. Middle leaflet length (mm)</td>
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<td>5. Middle leaflet width (mm)</td>
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<tr>
<td>6. Petiole length of terminal leaflet (mm)</td>
<td></td>
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<td>7. Rachis length (mm)</td>
<td></td>
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<td>8. Petiole length (mm)</td>
<td></td>
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<tr>
<td>9. Number of leaflets</td>
<td></td>
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<tr>
<td>10. Angle of leaflet apex, terminal leaflet (°)</td>
<td></td>
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<tr>
<td>11. Angle of leaflet apex, middle leaflet (°)</td>
<td></td>
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<tr>
<td>12. Angle of leaflet base, terminal leaflet (°)</td>
<td></td>
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<tr>
<td>13. Number of middle leaflet’s teeth</td>
<td></td>
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<tr>
<td>14. Toothed length, middle leaflet (mm)</td>
<td></td>
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<tr>
<td>15. Length of corymb (mm)</td>
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<tr>
<td>16. Diameter of corymb (mm)</td>
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<tr>
<td>17. Length of pome (mm)</td>
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<tr>
<td>18. Diameter of pome (mm)</td>
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<tr>
<td>19. Ratio of toothed length/leaflet length, middle leaflet</td>
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**Table 2.** Comparisons of three taxa, *Sorbus pohuashanensis*, *S. commixta*, and *S. ulleungensis* in terms of seven morphological characters.

<table>
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<tr>
<th>Characters</th>
<th><em>S. pohuashanensis</em></th>
<th><em>S. commixta</em></th>
<th><em>S. ulleungensis</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Habits</td>
<td>Shrub to small tree</td>
<td>Shrub to small tree</td>
<td>Large tree</td>
</tr>
<tr>
<td>Leaf length (cm)</td>
<td>(11.0) 14.0–18.7 (25.0)</td>
<td>(10.2) 14.4–20.4 (30.3)</td>
<td>(16.7) 22.5–25.3 (31.3)</td>
</tr>
<tr>
<td>Inflorescence width (mm)</td>
<td>(63) 100–122 (160)</td>
<td>(50) 85–115 (154)</td>
<td>(90) 130–160 (235)</td>
</tr>
<tr>
<td>Flower diameter (mm)</td>
<td>(8) 9–11 (13)</td>
<td>(7) 8–10 (13)</td>
<td>(10) 12–14 (16)</td>
</tr>
<tr>
<td>Fruit length (mm)</td>
<td>(4.7) 6.0–7.1 (8.9)</td>
<td>(4.4) 6.2–7.1 (8.2)</td>
<td>(7.6) 9.0–10.5 (12.2)</td>
</tr>
<tr>
<td>Fruit width (mm)</td>
<td>(4.4) 6.5–7.9 (9.7)</td>
<td>(5.2) 6.4–7.2 (8.7)</td>
<td>(8.2) 9.2–10.6 (12.9)</td>
</tr>
<tr>
<td>Number of carpels</td>
<td>(2) 3–4 (5)</td>
<td>(2) 3–4 (5)</td>
<td>(3) 4–5 (6)</td>
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</tbody>
</table>
Figure 1. Univariate statistics with the minimum and maximum values for the discriminating characters for *Sorbus pohuashanensis* (SPK), *S. commixta* (SCK and SCJ; Korean and Japanese individuals), and *S. ulleungensis* (SU). A, leaf length (mm); B, number of leaflets; C, calyx tube width (mm); D, inflorescence diameter (mm); E, flower diameter (mm); F, fruit width (mm); G, petal length (mm); H, seed length (mm).
Figure 2. Bivariate scatter diagrams using 327 specimens for the discriminating characters for Sorbus ulleungensis (SU) and the other related taxa (S. commixta and S. pohuashanensis) A, inflorescence vs. flower diameter (mm); B, leaf length vs. petal length (mm).
outer bark, whereas *S. commixta* and *S. pohuashanensis* are shrubby to small but sometimes large trees with light gray bark. The results of current analysis indicate that Ulleung individuals and others were distinct in morphological aspects. No strong discontinuities, however, existed among taxa of *S. commixta* and *S. pohuashanensis* in the Korean peninsula [In a plot of PC 1, PC 2, and PC 3, OTUs from *S. pohuashanensis* in the Korean peninsula occupied the central area of the plot and overlapped with many individuals from *S. commixta* (Fig. 3). Univariate statistics (Fig. 1), in addition to the minimum and maximum values for many characters, showed that values overlapped extensively for these taxa. These are believed to have originated by ancient hybridization between *S. commixta* from Japan and *S. wilsoniana* C.K. Schneid. from China based on flavonoids and morphology (Gil, 2013). In fact, *S. pohuashanensis* in the Korean peninsula has a very high level of morphological variation, which is more closely related to *S. commixta*. The morphological and chemical relationship between these two taxa will be presented as a separate study.

*Sorbus ulleungensis* grows in deciduous forest montane forests at elevations of 300–980 m with *Fagus engleriana* Seemen ex Diels, *Acer pseudosieboldianum* (Pax) Kom., *Acer pictum* var. *mono* (Maxim.) Maxim. ex Franch., and *Tilia amurensis* Rupr. (Kim et al., 2003). Several hundred individuals of this species are usually found within this island. The new taxon is compared to *S. commixta* and *S. pohuashanensis* in Table 2. The specimen collected by Nakai cited under *Sorbus commixta* f. *rufohirtella* Nakai is described as a new form because of the presence of leaflet reddish hairs below on midrib unlike tufts of soft reddish hairs on leaflet midrib in other individuals. It is known that leaflets of *S. commixta* in Japan and southern Korea are glabrous to glabrate on lower surfaces, while those of *S. pohuashanensis* in Northeastern China and the putative hybrid in Korean peninsula are hairy on lower surface, which may be an important key character. *S. commixta* f. *rufohirtella*, which was not found anywhere in Island Ulleung seemed to be a unique form of this described new species. We have not found this form of this species thus far, and excluded it as a synonym of this new species.
**Taxonomy**

*SORBUS ULEUNGENSIS* Chin S. Chang, *sp. nov.* **TYPE:** KOREA. Gyeongsangbuk-do: Ulleung-gun, Ulleung-eup, Jeodong-ri, Naesujeon observatory, along trail, mixed broadleaf forest, on roadside, natural habitat, 37˚30’45.9”N, 130˚54’29.2”E, alt. 370 m, 9 September 2011, *H.Y. Gil 736* (Holotype: SNUA [90590]; Isotype: A). Figs. 4–5.

*Arbores insignes, ad 20 m altae; cortex adultus fissuris verticalibus percursus; stipulae membranaceae, deciduae; foliola 13–15; flores 12–14 mm longi, fructus 9–10.5 mm longi.*

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**Figure 4. Sorbus ulleungensis** Chin S. Chang. A, plant; B, fruit; C, seed. (Holotype: *H.Y. Gil 073*, SNUA).
Figure 5. A holotype of *Sorbus ulleungensis* Chin S. Chang, *sp. nov.* (SNUA).
veins 15–21 on each side of midvein. Inflorescence to (8.0–)9.8–10.6–(14.4) cm long, (9.0–)13.0–16.0–(23.5) cm wide, corymbose. Flowers to (1.0–)1.2–1.4 (1.6) cm diam., crowded, fragrant. Sepals triangular, green. Petals 5–6 mm long, 4–5 mm wide, broadly elliptic, white. Fruits glossy, yellowish-orange or orange to red, subglobose to globose, (7.5–)9.0–10.5–(12.0) mm long, (8.0–)9.2–10.6–(13.0) mm wide. Calyx somewhat fleshy. Carpels 3–5–(6), semi-inferior, white hairy. Styles (3–)4–5–(6), to 3 mm, distantly inserted. Stamens 20, 4 mm long; anthers yellow. Seeds light brown to brown, to 4.1 × 2.1 mm, up to 12 per fruit. A sexual diploid (2n = 34) species.

Additional specimens examined: KOREA. Gyeongsangbuk-do: Ulleung-gun, Ulleung-eup: Jeodong-ri, along trail of “Naesujeon old path” (from Naesujeon to Seommok), alt. 260–420m. 17 May 2011, H.Y. Gil 0063 (SNUA); Jeodong-ri, along trail of “Naesujeon old path” (from Naesujeon to Seommok), alt. 260–420m. 9 Sept. 2011, H.Y. Gil 0763 (SNUA); Jeodong-ri, E slope of Mt. Seongin, along summit trail, 270–320m, ca. 500m from Bonggae waterfall entrance. 20 May 2011, H.Y. Gil 0143 (SNUA); Jeodong-ri, E slope of Mt. Seongin, along summit trail, alt. 270–320m, ca. 500m from Bonggae waterfall entrance. 9 September 2011, H.Y. Gil 0719 (SNUA); mountain trail (Bonggae waterfall), along the creek, eastern part of island, 28 June 1986, C.S. Chang et al. 088 (A); Jeodong-ri, Naesujeon observatory, along trail, alt. 340–440m. 9 September 2011, H.Y. Gil 0731 (SNUA); Dodong-ri, Mt. Seongin, from Naribunj (N slope) via summit to Dodong village (S slope), alt. 310m. 18 May 2011, H.Y. Gil 0099 (SNUA); Dodong-ri, ridge E. of Dodong. 19 October 1989, S. G. March et al. 338 (SNUA); Dodong-ri. 29 September 2010, H. J. Eom 0477 (SNUA); Sadong-ri, 100m, volcanic mountain peak, 19 May 1989, S. G. March et al. 44 (SNUA); Seo-myeon: Taeha-ri, along the trail of ‘Taeaharyeong’[(from Golgaeol (a stream) to Guam village, Namseo-ri], alt. 120–430m. 19 May 2011, H.Y. Gil 0114 (SNUA); Taeha-ri, Taeha elementary school-Taeharyeong-Tsuga diversifolia community-Taeha elementary school, alt. 439m. 27 September 2010, H.J. Eom et al. 0445 (SNUA); Buk-myeon, alt. 410m. 21 May 1989, S. G. March et al. 63 (SNUA); Na-ri, Naribunj (basin). 28 September 2010, H.J. Eom et al. 0450 (SNUA); Ooryong-too (Degelet Island) al t. 0.920m, 2 June, 1917, E. H. Wilson 8553 (A); Ooryong-too (Degelet Island), al t. 0.920m, 31 May, 1917, E. H. Wilson 8553 (A); Naridong, 31 May, 1917, T. Nakai s.n. (TI); Ulleungdo, K. Okamoto s.n. (TI); Sang-bong, 2 June, 1917, T. Nakai s.n. (TI); Sang-bong, 23 May, 1916, alt. 900m, T. Ishidoya s.n. (TI); Ulleungdo, 19 August, 1938, R. Toyama, s.n. (KYO).

Distribution: Ulleung Island, endemic to Korea. Very common in the whole island at 300–980 m. The total number of individuals on the island was estimated at 2,000–2,500 (Fig. 6).

Habitat: On steep cliff slopes or rocks and mountain woodlands.

Korean name: U-san-ma-ga-mok.

English common name: Ulleung rowan.

Flowering: Early May to mid-June.

Etymology: The specific epithet, “ulleungensis,” is based on the name of the location where the new species is found.

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**Figure 6.** Distribution of *Sorbus ulleungensis* on Ulleung Island of Korea.
**Key to Sorbus Ulleungensis and Other Sorbus Taxa in Korea**

1a. Leaves simple; styles 2 ................................................................. *S. alnifolia*

1b. Leaves pinnately compound; styles 3–4 or 5 ............................... *S. alnifolia*

2a. Styles 5; leaflets 3–5(6) paired; fruit 10 mm in diameter; small shrub (<2m); inflorescences loosely flowered (<10) .......... *S. sambucifolia*

2b. Styles 3–4; leaflets 4–7 paired; fruit 4–7 mm in diameter; small tree (>2m); inflorescences densely flowered (20–30) .............. *S. sambucifolia*

3a. Winter buds densely covered with white hairs, non glutinous; leaflet lower surface pubescent with white hairs; stipules herbaceous, fan-shaped and persistent; from northeastern China, far eastern mainland Russia, and northern Korea (Mt. Baekdu) .................. *S. pohuashanensis*

3b. Winter buds glabrous or occasionally covered with brown or white hairs or glabrous, glutinous; leaflet lower surface glabrous, pubescent with yellowish brown hairs only when young; stipules membranous and deciduous; from Japan, Russia (Sachalin Island), and Korea (excluding Ulleung Island) ........................................... *S. commixta*

4a. Flower diameter 8–11 mm; fruit diameter 6.4–7.9 mm; leaflets 9–13; style 3–4; bark light gray; from Japan, Russia (Sachalin Island), and northeastern China, far eastern mainland Russia, and northern Korea (Mt. Baekdu) ................. *S. commixta*

4b. Flower diameter 12–14 mm; fruit diameter 9.0–10.5 mm; leaflets 13–15; styles 3–5; bark dark brown; from Ulleung Island. *S. ulleungensis*

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