A new species of *Cyanea* Gaud. (Lobelioideae, Campanulaceae) from Maui, Hawai`i

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Abstract

*Cyanea heluensis* H. Oppenheimer, *sp. nov.*, a new, narrowly distributed endemic species, is herein described and illustrated with line drawings and digital field photos. It is currently known from a single mature plant and is restricted to the upper Helu planeze on leeward Mauna Kahalawai, West Maui, Hawaiian Islands. It differs from all other species of *Cyanea* Gaudich. with its narrow, shallowly lobed leaves, gently curved muricate corollas, and undulate sepals caducous in fruit. A key to the new species and its congener on Mauna Kahalawai is provided. Its conservation status and efforts to propagate the species are discussed.

Keywords

conservation, Hawaiian Islands, IUCN Red List, Plant Extinction Prevention Program

Introduction

The Hawaiian lobeliods are the largest plant clade restricted to any archipelago, with *Cyanea* being the most species-rich genus within that clade. It is also the largest genus in Hawai`i, and originated from a single introduction of 8–10 Mya (Givnish et al. 2008). As currently circumscribed, the woody lobelioid genus *Cyanea* Gaudich. (including *Rollandia* Gaudich.) comprises 80 species (Oppenheimer and Lorence 2012; Spork-Koehler et al. 2015) all endemic to the Hawaiian Islands where they occur in wet and mesic forests. Most have a very narrow distribution, and are single-island endemics, or restricted to a single volcano. *Cyanea* was first described by Gaudichaud-Beaupré (1829)
based on the type species *C. grimesiana* Gaudich. The genus was later treated in Rock’s (1919) monographic study of the Hawaiian Lobelioideae in which he recognized 52 species in 5 sections. Wimmer (1943) later recognized only 3 sections in his monograph of Campanulaceae. Lammers (1990) revised the Hawaiian members and also recognized 52 species, but stated relationships within *Cyanea* remained poorly understood and consequently did not recognize any formal sections. Givnish et al. (1995) recognized an orange fruited clade and a purple fruited clade. Recent exploration and collecting efforts in poorly explored, often rugged or remote regions in the Hawaiian Islands, continue to yield undescribed species of *Cyanea* (Lammers and Lorence 1993; Lammers 2004; Oppenheimer and Lorence 2012; Spork-Koehler et al. 2015).

In June of 2010, while near the summit of Helu, Mauna Kahalawai (aka West Maui), the author and Jennifer Higashino spotted through binoculars an unusual *Cyanea*. Upon carefully negotiating down the steep, slippery slope and arriving at the plant, it was immediately recognized as distinct from all the other known taxa on Maui by its habit (Fig. 1), and narrow, shallowly lobed and undulate leaf margins. Flower buds were just beginning to emerge in some of the leaf axils (Fig. 1). Return visits to monitor this individual, and to search for others, found the flowers closer to being at full anthesis in September, when the holotype was collected (Fig. 2). Study of this material revealed it to be distinct from all other known species of the genus, herein described.

**Taxonomic treatment**

*Cyanea heluensis* H.Oppenh., sp. nov.
urn:lsid:ipni.org:names:77212950-1

**Diagnosis.** Species allied to *C. asplenifolia* (H. Mann) Hillebr., but differs in its very shallowly lobed leaves (vs. deeply lobed to pinnate-pinnatifid), longer and wider corolla, and larger, undulate sepals (Fig. 3).

**Type.** USA, Hawaiian Islands, west Maui, Lahaina District, slopes of Helu, north side, 4160 ft. (1268 m), H. Oppenheimer, S. Perlman & J.Q.C. Lau #H91007, 8 Sep 2010 (BISH) (Fig. 4).

**Description.** Many-branched, sprawling, decumbent to ascending shrub to 3 m long, stems leaning or tangled in adjacent vegetation, occasionally rooting when in contact with wet soil, very sparingly muricate on the lower trunk, denser on younger stems, leaf scars prominent, nearly orbicular, latex white. Leaves clustered at the ends of the branches, petiolate, chartaceous, dark green above, paler on abaxial surface, midrib usually purple on abaxial surface (live material), blade elliptic to oblanceolate, 26–29 cm long x 4–6 cm wide, apex acuminate, base narrowly cuneate, upper surface mostly glabrous, abaxial surface sparsely pubescent, more so on midrib, margins shallowly and irregularly lobed, the lobes 2–6 mm deep, crenate, undulate, petioles 3–4 cm long, sparsely muricate, pubescent. *Juvenile leaves* weakly (Fig. 4) dimorphic, the lobes more distinct than in adult leaves but cut less than ½ way to midrib, leaf apex rounded.
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Inflorescence axillary, among the lower leaves, peduncles 6–15 mm long, 5–10 flowered, glabrous to sparsely pubescent, bracts caducous (not seen), bracteoles caducous, 1 mm, lanceolate to elliptic, acute, sparsely pubescent. *Pedicels* pubescent, 5–9 mm long, bracteoles usually 1–2 per pedicel, persistent, sparsely pubescent, occurring on basal ¼–1/2 of pedicel. *Calyx* green, the lobes deltate, 4–6 mm long x 2–3 mm wide, margins crenate, undulate, glabrous to sparsely pubescent, purple (most apparent in live material),

*Figure 1. Cyanea heluensis* A habit B close up of flower buds prior to anthesis. Note murications on petioles and corolla. Photos by H. Oppenheimer.
apex acute to short acuminate. *Corolla* white, muricate on corolla lobes especially in bud and distally prior to anthesis, gently curved, 45–55 mm long x 4–5 mm wide, longitudinally pubescent along corolla tube, lobes approximately 1/3 the length of the tube, reflexed, hypanthium 4–5 mm long x 4–5 mm wide, sparsely pubescent. *Berries* small, 5–10 mm, globose, sepals caducous, orange at maturity; *seeds* brown, smooth, round to ellipsoid, < 1 mm.

Figure 2. *Cyanea heluensis* A flowering stem B close-up of flowers. Photos by H. Oppenheimer.
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**Affinities.** Several attempts have been made to divide *Cyanea* into sections (Hillebrand 1888; Rock 1919; Wimmer 1943; Lammers 1990), but none successfully

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**Figure 3.** *Cyanea heluensis*. Leaf (left); flowers (right). Illustration by Anna Palomino. Drawn from *H. Oppenheimer et al. #H91007* (BISH) and field images taken by *H. Oppenheimer.*
arranges the genus into clear-cut phylogenetic entities. Givnish et al. (1995) divides the genus into two distinct clades: one with purple fruits and another with orange fruits. *Cyanea heluensis* belongs to a lineage that includes *C. asplenifolia* (H. Mann) Hillebr., its apparent nearest congener and also endemic to Maui, based on their narrow, gently curved tubular, white corollas with murications, and leaf margins that are shallowly lobed to pinnately divided. In contrast to *C. asplenifolia* with its pinnately divided leaves, *C. heluensis* has narrower leaves very shallowly lobed, longer and wider corollas, and larger, undulate sepals. Although Lammers (1990 p. 445) states

**Figure 4.** *Cyanea heluensis* A seedling at Olinda Rare Plant Facility. Plant is approximately 1 year old. B distribution *Cyanea heluensis* of on Maui, Hawai‘i. Photo by H. Oppenheimer.
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The berries of *C. asplenifolia* are unknown, this species is now known to have bright orange fruits (pers. obs.). A preliminary phylogenomic analysis by Steve Hunter (Univ. Wisconsin, Madison pers. comm.) using whole chloroplast genome sequences (not nuclear sequences) supports *C. heluensis* as being sister to the small clade formed by *C. asplenifolia* and *C. duvalliorum* Lammers & H. Oppenh.

Based partly on Lammers (1990, 2004) and Givnish et al. (1995), the following key will distinguish *Cyanea heluensis* from its congeners on Mauna Kahalawai (West Maui).

1. Fruit purple .......................................................... 2
   – Fruit orange .......................................................... 4
2(1) Corolla pubescent ............................................. *C. obtusa*
   – Corolla glabrous ......................................................... 3
3(2) Inflorescence 6–25 flowered; peduncles 15–240 mm long ................................ *C. angustistifolia*
   – Inflorescence 6–14 flowered; peduncles 10–50 mm long ................................ *C. elliptica*
4(1) All 5 anthers with apical tufts of white hairs .............................................. 5
   – Ventral 2 anthers with apical tufts of white hairs ........................................... 7
5(4) Leaves lobed ......................................................... *C. lobata* subsp. *lobata*
   – Leaves pinnately divided .................................................. 6
6(5) Hypanthium campanulate; dorsal anthers 15–16 mm long ................................ *C. mauiensis*
   – Hypanthium obconic; dorsal anthers 9.5–12 mm long ................................ *C. magnicalyx*
7(4) Corolla laterally compressed ......................................................... *C. scabra*
   – Corolla tubular, round in cross-section .......................................................... 8
8(7) Corolla blackish purple externally, 60–80 mm long, 6–11 mm wide ..................  
   .......................................................................................... *C. macrostegia*
   – Corolla white or white striped with lilac longitudinal lines, 35–55 mm long, 3–5 mm wide .......................................................... 9
9(8) Corolla externally glabrous ......................................................... *C. kauaulaensis*
   – Corolla externally pubescent, sometimes only on longitudinal lines .......... 10
10(9) Plants unbranched or sparingly branched from base, 0.5–1.5 m tall; corolla pubescent, without murications ............................................. *C. kunthiana*
   – Plants branched above base, 1.5–3 m tall; corolla pubescent along longitudinal lines, muricate ................................................. 11
11(10) Leaves pinnately divided, cut ¾ to 7/8 the distance to the midrib ............  
   .......................................................................................... *C. asplenifolia*
   – Leaves shallowly lobed, cut less than ¼ the distance to the midrib .......... *C. heluensis*

**Phenology.** *Cyanea heluensis* has been observed beginning to flower from mid-summer through October, followed by immature, green fruit observed October to December, maturing in early January.

**Etymology.** The specific name honors Helu, a peak on Mauna Kahalawai (aka West Maui Mountains) *Lit.* scratch or count (Pukui et al. 1966); + Latin suffix -ensis, indicating a place of origin or growth.

**Habitat & ecology.** *Cyanea heluensis* occurs in Metrosideros Banks ex Gaertn. Lowland Wet Forest (Wagner et al. 1990). The common associated woody elements are

**Cyanea macrostegia** Hillebr. has been observed infrequently in the general area. *Cyanea elliptica* (Rock) Lammers, *C. kauaulaensis* H. Oppenh. & Lorence, and *C. scabra* Hillebr. occur to the north, along Kaua`ula Stream. These species are nearly 1500 m away and 500 m or more lower in elevation than *C. heluensis* which is located near the ridgetop. Based on genetic analysis and morphology none of these other taxa appear to be potential hybrid parents. The known populations on Mauna Kahalawai of *Cyanea asplenifolia*, one of its two closest relatives, are 3,700 m and over 10,000 m away. Populations on Haleakala, East Maui in Makawao Forest Reserve and Haleakala National Park are 40 kilometers and 70 kilometers to the east. Extant populations of *Cyanea dvalliorum* Lammers & H. Oppenh., the other member of this clade, occur nearly 50 kilometers away on Haleakala. These species are also known to be ornithophilous, and populations and densities of native birds have dramatically declined, it is unlikely *C. heluensis* is of hybrid origin.

Soil is of typical basaltic origin derived from the original shied-building Wailuku Volcanic Series (Stearns and MacDonald 1942) with average annual rainfall approximately 3000 mm. (Giambelluca et al. 1986).

The only known plant occurs in deep shade on the upper rim of the steep south side of the large amphitheater-headed Kaua`ula Valley, with a windward aspect. Recently, several other previously undescribed taxa have been discovered in the area, including *Cyanea kauaulaensis* H. Oppenheimer & Lorence (Oppenheimer and Lorence 2012), *Hibiscadelphus stellatus* H. Oppenheimer, Bustamente & Perlman (Malvaceae) (Oppenheimer et. al. 2014), and *Stenogyne kauaulaensis* K.R. Wood & H. Oppenheimer (Lamiaceae) (Wood and Oppenheimer 2008). Kaua`ula Valley is an important site not only botanically, but economically (as a water source) as well as culturally and spiritually for Native Hawaiians.

**Conservation status.** *Cyanea kauaulaensis* should be considered Critically Endangered due to its limited range, low population numbers, lack of population structure with no seedling recruitment, probable loss and decline of most or all of its avian pollinators and dispersal agents, threats such as landslides and treefall, herbivory by alien slugs and rats, and competition with alien plants such as *Ageratina adenophora* (Sprengel) R.M. King & H. Robinson, *Buddleia asiatica* Loureiro, *Erigeron karvinskianus* DC, *Melinis minutiflora* P. Beauv., *Rubus rosifolius* Smith, and *Tibouchina herbacea* (DC)
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Cogn. When evaluated using the World Conservation Union (IUCN) criteria for endangerment (IUCN 2001), *Cyanea heluensis* easily falls into the Critically Endangered (CR) category, which designates species facing a very high risk of extinction in the wild. The CR designation is met when any of the criteria A to E are met. Both Criterion B1 (Extent of Occupancy or EOO) and B2 (Area of Occupancy or AOO) are met with an EOO of less than 100 km$^2$ and an AOO of less than 10 km$^2$. Criterion D, population size estimated to be fewer than 50 wild individuals is easily met since there is only a single known individual. Criteria A & C address decline in population for which there is no data, although with only a single individual it could reasonably be inferred that this species is in decline. No quantitative analysis predicting the likelihood of extinction (Criterion E) was conducted. The alphanumeric formula CR B1a(1,ii,iv,v)+B2a,b(i,ii,iv,v) represents the current status under IUCN guidelines. Furthermore, *Cyanea heluensis* should be considered by the US Fish & Wildlife Service as a Candidate for listing as Endangered under the Endangered Species Act of 1973, and a Recovery Plan written, funded, and implemented.

**Conservation efforts.** Despite several attempts to locate other populations or individuals elsewhere on Helu and adjacent Kaua`ula and Launiupoko Valleys, including the use of ropes and technical gear, only one single plant has ever been observed. Efforts were made shortly after its discovery to collect mature fruit, including covering flowers with protective nylon mesh bags. These efforts failed due to the predation of the exposed peduncles by non-native slugs (e.g. *Derocerus laevis*). A few short lower branches were collected but only a single one was successfully rooted at the Olinda Rare Plant Facility on Maui, but later died. In 2013, the health and vigor of the plant had declined significantly, but in 2016 it was recovering with new growth and a few new shoots initiated along the main stems. Poor weather prevented helicopter access in late 2017 and early 2018 in attempts to obtain mature fruit. In July of 2018, the plant was showing signs of increased vigor with three ramettes beginning to flower, and several smaller side shoots. Trapping for rats is ongoing, likewise the manual control of weeds. The last flowers of the season and very immature fruit were observed in October of 2018 and October of 2019. A hormone paste was successfully applied in 2018 to the stems to induce branching; three lateral shoots were collected in October of 2019 and sent to the Olinda Rare Plant Facility and Lyon Arboretum Micropropagation Lab on O`ahu. One of these has successfully rooted at Olinda Rare Plant Facility, but the Lyon Arboretum material failed (C. Yamamoto pers. comm.). In January of 2019, a single mature fruit was collected, so resolving which of Givnish’s two clades this new species belongs to. Only a single seed germinated, but it is healthy and continues to grow at the Olinda Rare Plant Facility (Fig. 4) along with the rooted cutting. The Maui Invasive Species Committee (MISC) has been working to control the *Cortaderia jubata* (Lem.) Stapf infestation in adjacent Kaua`ula Valley, and on the surrounding vertical cliffs. The region has for the most part escaped the ravages of introduced feral ungulates due to the extremely rugged topography. However, there has been a small incursion of feral goats and feral pigs approximately 1.5 km to the west and northwest at lower elevation. The Mauna Kahalawai Watershed Partnership (formerly West Maui Mountains Watershed Partnership) has been working to mitigate this incipient yet potentially severe threat.
This new species is a target of the Plant Extinction Prevention Program (PEPP), easily meeting the threshold of 50 wild individuals or less for inclusion. The Program strives to collect seeds or cuttings from every individual plant on the list, with propagation of nursery stock, restoration outplantings into appropriate habitat, and *ex situ* seed storage and living collections being the main goals.

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**References**


An amazing new *Capsicum* (Solanaceae) species from the Andean-Amazonian Piedmont

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Abstract

*Capsicum regale* Barboza & Bohs, *sp. nov.*, a new species from the tropical wet forests of the eastern Andean slopes (Colombia, Ecuador, and Peru) is described and illustrated. This new species belongs to the Andean clade (all species 2n = 26) of *Capsicum* and is similar to *C. longifolium* Barboza & S.Leiva in its glabrescence, calyx morphology, and corolla and seed color but differs in its membranous and elliptic leaves, fleshy calyces, deeper stellate corollas, longer filaments, longer and purple fruiting pedicels, purple berries, and larger seeds. Its chromosome number was counted (2n = 26), a preliminary assessment of conservation status is given and discussed, and an updated identification key to the species of the Andean clade is provided.

Keywords

Andean clade, *Capsicum*, chromosomes, phylogeny, South America, taxonomy

Introduction

*Capsicum* L. (Capsiceae, Solanaceae), the chili pepper genus, consists of approximately 42 species distributed in temperate and tropical Central and South America, Mexico and the West Indies (Barboza et al. 2020). It includes five species cultivated worldwide
as vegetables, spices, and medicines (C. annuum L., C. frutescens L., C. chinense Jacq., C. baccatum L. and C. pubescens Ruiz & Pav.). Capsicum peppers are major crops worldwide, and along with potato, tomato, and eggplant in the genus Solanum L., are amongst the most economically important members of the Solanaceae (Samuels 2015).

The Andes are one of the main centers of diversity for Capsicum, where new species continue to be discovered (Nee et al. 2006; Barboza et al. 2019). Approximately 50% of the species (ca. 20 species) occur in tropical Andean forests or in dry inter-Andean valleys (Barboza et al. in prep.). The tropical montane forest ecoregion is located on the slopes of the Andes extending north to south from southern Colombia, through Ecuador, and into northern Peru (WWF 2020). This region is characterized by a lush vegetation with evergreen seasonal broad-leaved forests and a rich fauna (Stewart et al. 2020; WWF 2020). It is one of the most biologically diverse ecosystems in the world (Gentry 1992; Bruijnzeel et al. 2010; Tapia-Armijos et al. 2015) with a high level of species endemism (Myers et al. 2000). Khoury et al. (2020) have demonstrated that the highlands of Colombia, Ecuador, Peru, and Venezuela represent one of the hotspots for Capsicum that need further investigation in terms of collecting taxa for ex situ conservation of the wild species.

During recent field explorations in the Colombian Cordillera Oriental (Dept. Caquetá), an atypical species of Solanaceae was collected. Despite the presence of several Solanaceae experts in the group, no one was sure what genus it belonged to. Its deeply stellate yellowish corollas, long-exserted stamens, and purple fruits and fruiting pedicels were striking and called to mind some characters of the poorly known genus Cuatresia Hunz., whereas its thick, triangular-compressed, and reflexed calyx appendages resembled those of some Lycianthes (Dunal) Hassler taxa, whose species are not well understood in Colombia. Puzzled, we provisionally named it “Cuatresianthes” and placed some bets on its eventual generic identity. DNA was extracted and sequenced in the Bohs lab from leaf material collected on these field trips. BLAST results indicated that the species belonged not to Cuatresia or Lycianthes, but to Capsicum. A preliminary molecular study placed the collection unequivocally in the Andean clade of Capsicum, but it did not belong to any known species. Through an exhaustive search amongst unidentified Cuatresia collections in herbaria, we found other specimens from Ecuador and Peru that matched our Colombian gatherings. Here, we describe this species as new to science and provide information on its morphology, distribution, karyology and phylogenetic position in the genus Capsicum.

Materials and methods

Two field trips were made in Colombia (Dept. Caquetá) during 2016 and 2019. Fresh material was preserved in 70% alcohol to perform measurements of reproductive organs using a Zeiss Stemi 2000-C stereomicroscope at 6.5–50× magnification. Descriptions were based on living plants observed during field work and examination of digital images of herbarium specimens housed at the following seven herbaria: BM, COAH, COL, F, MO, QCNE, US. Seeds were also examined using scanning electron microscopy (SEM); they were prepared using enzyme etching (Lester and Durrands 1984) to
dissolve outer cell walls, affixed to aluminum stubs with double-sided adhesive tape, coated with gold, and examined using a FE-SEM Sigma (LAMARX, National University of Córdoba, Argentina) microscope.

Information about flower, fruit, and seed color was taken mainly from our own observations in the field and photographs sent by some collectors; we tested pungency in the field on immature and mature fruits.

The distribution map was produced using QGIS 3.8 (QGIS Development Team 2019) and was based on georeferenced data of all the collections analyzed. Conservation status was assessed using IUCN criteria B, geographic range in the form of B1 (EOO: extent of occurrence) and B2 (AOO: area of occupancy) (IUCN 2019). The extent of occurrence and area of occupancy were calculated using the Geospatial Conservation Assessment Tool GeoCAT (Bachman et al. 2011; GeoCAT 2020).

Somatic metaphases were examined in root tip squashes obtained from germinated seeds. The root apices were fixed in 3:1 ethanol: acetic acid mixture for 12 hr after a pretreatment in 2 mM 8-hydroxyquinoline solution for two hr at room temperature and two hr at 4 °C. The material was kept at −20 °C until examination. The root tips were macerated in pectinase-cellulase solution (Moscone et al. 1993), and chromosomes were stained with 4′–6-diamidino-2-phenylindole (DAPI) (Schweizer and Ambros 1994). Metaphase chromosomes were observed and photographed with epifluorescence using an Olympus BX61 microscope equipped with the appropriate filter sets (Olympus, Shinjuku-ku, Tokyo, Japan) and a JAI CV-M4 + CL monochromatic digital camera (JAI, Barrington, N.J., USA). Three individual seeds from the collection Orejuela et al. 3034 were germinated and grown until root tips were produced, and 10 cells from each seedling were studied in metaphases.

Phylogenetic affinities were explored using DNA sequences from four markers, namely: the intergenic spacers \textit{psbA-trnH}, \textit{ndhF-rpl32} and \textit{trnL-trnF} from the plastid genome, and the single-copy nuclear gene \textit{waxy} (GBSSI, granule-bound starch synthase, exons 2 to 10). Representatives of different clades recognized within \textit{Capsicum} and several outgroup species were included. Genomic DNA of \textit{C. regale} was extracted from silica-gel dried leaves using the Qiagen DNeasy Plant mini kit (Qiagen Inc., Valencia, California, EUA) and a modified CTAB protocol. Most sequences included in this study were used in previously published analyses and therefore were retrieved from GenBank, except for a few sequences from outgroup species (see Suppl. material 1: Table S1), for which DNA extracts were already available. Amplification and sequencing protocols for the markers used were as in Carrizo García et al. (2016, 2020) and Barboza et al. (2019). PCR amplicons were sequenced on an automated capillary sequencer [University of Vienna (Vienna, Austria), and the University of Utah HSC Core Research Facility (Salt Lake City, Utah, USA)]. A single concatenated dataset was assembled in MEGA 7 (Kumar et al. 2016). Phylogenetic reconstructions were done using maximum parsimony [MP, in PAUP* 4.0b10 (Swofford 2003)], maximum likelihood [ML, in RAxML v8.2.10 (Stamatakis 2014)] and Bayesian inference [BI, in MrBayes 3.2.2 (Ronquist et al. 2012)] approaches as in Carrizo García et al. (2016, 2020). The GTR+R nucleotide substitution model was selected a priori following the Akaike Information Criteria in jModelTest 2.1.3 (Darriba et al. 2012) for ML and BI analyses.
**Taxonomic treatment**

*Capsicum regale* Barboza & Bohs, sp. nov.
urn:lsid:ipni.org:names:77212951-1
Figs 1–3

**Diagnosis.** *Capsicum regale* is morphologically most similar to *C. longifolium* Barboza & S.Leiva, but the former differs in having membranous and elliptic leaves, fleshy calyces, more deeply stellate corollas, longer filaments, longer and purple fruiting pedicels, dark blue to purple berries, larger seeds, smooth seed coats, and spine-like projections along the seed margins.

**Type.** COLOMBIA. Caquetá: Mun. Florencia, Corregimiento El Caraño, Finca de Don Isauro, camino al río, en interior de bosque fuertemente inclinado, 01°44'10.6"N, 75°40'78.3"W, 1004 m, 22 Aug 2019 (fl, fr), A. Orejuela, L. Bohs, G.E. Barboza, P. González, R. Deanna, J. Urdampilleta, J. Valencia & G. Sierra 3034 (holotype: COL; isotypes: COAH, CORD, HUAZ [to be distributed]).

**Description.** Slender shrubs (1–) 1.8–2.5 (–3) m tall, with the main stem somewhat thick, ca. 0.8 cm in diameter at base, sparsely branched toward apex, the branches dichotomous, weak, spreading horizontally. Stems solid and terete at base, the young stems pale green, glossy, striate, glabrous, the nodes green; bark of older stems dark brown, glabrous; lenticels present. Sympodial units difoliate, geminate, the leaf pairs markedly differing in size. Leaves simple, membranous, slightly discolorous, green adaxially, pale green with the midvein prominent and purple and the secondary veins lilac or green abaxially; adaxial and abaxial surfaces glabrous; major leaves with blades 17–20 (–24) cm long, 4.7–8 (–9.2) cm wide, elliptic, the major veins 6–8 on each side of midvein, the base unequal and attenuate, the margins entire and glabrous, the apex apiculate to long-apiculate; petioles (0.8–) 1.5–2.3 cm long, green adaxially and purple abaxially, glabrous; the minor leaves 2–5 cm long, 1–3 cm wide, ovate, the major veins 3–5 on each side of midvein, the base unequal, the margins entire, glabrous, the apex obtuse; petioles 0–0.4 cm long, green, glabrous. Inflorescence ca. 10 mm long, unbranched or rarely shortly forked, with 5–13 flowers, the axes glabrous; peduncle 0–5.5 mm; rachis 4.5–6 mm long; pedicels 1.2–1.4 cm long, thin, 2–3–edged, erect to spreading, straight, purple to green, glabrous, nearly contiguous, articulated at the base, leaving conspicuous scars. Buds ellipsoid, green. Flowers 5-merous, all perfect. Calyx 2–3 mm long, ca. 2 mm wide, cup-shaped, fleshy, green or greenish purple, the margin truncate, circular in outline, glabrous, the appendages (0–) 4–5, 1–1.8 mm long, 0.8–1.1 mm wide, purple, thick, triangular-compressed, reflexed, inserted very close to the margin. Corolla 7–8 mm long, ca. 10 mm in diameter, deeply stellate, thick, with narrow interpetal tissue, pure yellow or yellow with maroon pigmentation abaxially and greenish yellow with lobes marginally maroon adaxially, glabrous, the tube 2–2.5 mm long, the lobes 5–5.5 mm long, ca. 2 mm wide, triangular, the tips papillose,
Figure 1. *Capsicum regale* Barboza & Bohs. **A** fruiting apical branch **B** unbranched inflorescence **C** flower, in lateral view **D** opened corolla **E** gynoecium **F** fruit. From Orejuela et al. 3034. Drawn by S. Montecchiesi.
Figure 2. **Capsicum regale** Barboza & Bohs. 

A habitat, B apical branch, showing anisophyllous leaf pairs, C abaxial surface of leaf with purple main vein, D forked inflorescence; note the scars of the deciduous flowers, E flower, in lateral view, on a unbranched elongate inflorescence, F, G flowers with and without pigmentation respectively, H–K various stages of fruit maturity, in K mature fruit showing the constriction between the pedicel and the berry (arrow). A–F, H–K from Orejuela et al. 3034 (photos by A. Orejuela, P. Gonzáles, and G. Barboza) G from Hoyos 127 (photo by L. Coca).
the margins with short eglandular trichomes. Stamens subequal, one filament longer than the others; long filament 3.5–4.3 mm long, shorter filaments (2) 3–3.2 mm long, white, glabrous, inserted on the corolla ca. 1 mm from the base, with inconspicuous auricles; anthers ca. 2 mm long, elliptic, not connivent, the thecae lilac or pale bluish, opening into longitudinal slits. Ovary ca. 1.3 mm long, ca. 1 mm in diameter, light green, ovoid, glabrous; nectary ca. 0.4 mm high, paler than the ovary, conspicuous; style 4.3–4.5 mm long, white, clavate, glabrous; stigma ca. 0.1 mm long, ca. 0.8 mm wide, light green, globose or somewhat discoid. Fruit a berry, globose, 6–9 mm in diameter, green when immature, turning nearly white and translucent during transition to maturity, then becoming dark blue to purple when mature, glabrous, non-pungent, the pericarp opaque, without giant cells, the endocarp smooth; stone cells absent; fruiting pedicels ca. 1.8 cm long, 1.8–2 mm in diameter proximally, 2.5–2.6 mm in diameter distally, brilliant dark purple, erect, fleshy, slightly angled and strongly thickened distally; fruiting calyx 3.75–4.25 mm in diameter, persistent, not accrescent, discoid, brilliant purple, with a conspicuous annular constriction at the junction with the swollen pedicel, the appendages reflexed, brilliant purple, fleshy and laterally compressed. Seeds 7–17 per fruit, 2.7–3.4 mm long, 2.2–2.7 mm wide, flattened, C-shaped, black, the seed coat smooth except for small spine-like projections on the seed margin, the cells irregular in shape to polygonal at seed margins, the lateral walls sinuate to straight.

**Distribution.** *Capsicum regale* occurs in southern Colombia, eastern Ecuador, and northern Peru, known mainly on the eastern slopes of the Andes (the Andean-Amazonian Piedmont), between 700–1900 m elevation (Fig. 4).
Ecology. The small populations inhabit the understory of the premontane or montane humid tropical forests of the Amazonian slopes of the Andes.

Phenology. The species has been collected in flower and fruit in April and from August to December.

Etymology. The specific epithet comes from the Latin regalis, royal or regal, referring to the regal, princely, or magnificent appearance of this special plant and also making reference to the royal purple color that suffuses the leaves, fruits, and fruiting pedicels.

Preliminary assessment of conservation status. Assessment using the IUCN Red List Criteria (IUCN 2019) suggests a status of Endangered (EN) B2ab(iii) for C. regale. Although this species has an extent of occurrence (EOO) of 47,806.378 km², its area of occupancy (AOO) is calculated to be 32 km² (criterion B2 < 500 km²), and the habitat quality has experienced a continuing decline, especially associated with fragmentation and deforestation.

Chromosome number. The somatic chromosome number found in C. regale is 2n = 2x = 26 (Fig. 5), as for all of the species of the Andean clade (Scaldaferro and Moscone 2019; Barboza et al. 2019).

Phylogenetic affinities. Capsicum regale is strongly resolved within the Andean clade of Capsicum in all analyses. Within the Andean clade, C. regale is moderately supported in a clade with C. rhomboideum and C. hookerianum. Within this clade, it is weakly supported as sister to C. rhomboideum (Fig. 6).
Specimens examined. COLOMBIA. Caquetá: Mun. Florencia, Corregimiento El Caraño, Km 20, finca Las Brisas, propiedad de Isauro Trujillo, 01°44'11.80"N, 75°40’37.8"W, 1002 m, 7 Oct 2017 (fl, fr), D. Hoyos, E. Trujillo & J. Sánchez 118 (COAH, COL); same locality, 9 Dec 2017 (fl, fr), D. Hoyos, M. Cuellar & F. Vallejo 146 (COL); Finca de don Isauro, camino al río, en interior de bosque fuertemente inclinado, 01°44'01.4"N, 75°40’35.4"W, 1000 m, 16 Apr 2016 (fl, fr), A. Orejuela, L. Bohs, G.E. Barboza, E. Trujillo, J. D. Tovar & J. Castillo 2640 (COL); same locality, 01°44'09.1"N, 75°40’40.3"W, 932 m, 22 Aug 2019 (fl, fr), A. Orejuela, L. Bohs, G.E. Barboza, P. González, R. Deanna, J. Urdampilleta, J. Valencia & G. Sierra 3035 (COL); finca Las Brisas, debajo de la casa, vereda La Cascada, 01°37’5"N, 75°40’50"W, 1000 m, 7 Nov 2015 (fl, fr), D. Sanín 6236 (COL); Mun. San José del Fragua, vereda La Peneya-camino hacia El Jardín, zona amortiguadora PNN Alto Fragua Indi Wasi, 01°17’31"N, 76°08’0.64"W, 700–850 m, 23 Oct 2017 (fl, fr), D. Hoyos et al. 127 (COAH, COL).


Napo: Archidona Cantón, Reserva Ecológica Antisana, Comunidad Shamato, entrada por km 21-Shamato, 00°44’S, 77°48’W, 1700 m, 27 Apr 1998 (fl), J. L. Clark et

PERU. Loreto: Datem del Marañón, Morona District, Pongo Chinim, valley between the eastern and western ridges of the Kampanikis range, ca. 14 km south of the Peru-Ecuador border, 3 Aug 2011 (fl, fr), I. Huamantupa 15251 (V0387079F color photo, F).

Figure 6. Bayesian majority-rule consensus tree of *Capsicum* showing the placement of *C. regale* Barboza & Bohs. The Andean clade is highlighted in colored branches. Support values are indicated by each branch (bootstrap support maximum parsimony/bootstrap support maximum likelihood/posterior probabilities; dashes indicate support values < 50%). Key support values that indicate the position of *C. regale* are shown in bold. Asterisks indicate different resolutions using maximum parsimony.
**Discussion**

*Capsicum regale* belongs to the Andean clade of *Capsicum* (Carrizo García et al. 2016; see below). It is a very striking species due to its unbranched (Figs 1B, 2E, J) or forked inflorescence (Fig. 2D) with 5–13 deciduous flowers on an elongate rachis (Fig. 2D), fleshy and laterally compressed calyx appendages (Fig. 2D, E), deeply stellate corollas (Fig. 2F, G), strongly thickened and brilliant purple fruiting pedicels (Fig. 2H–K), dark blue to purple fruits (Fig. 2J, K), and flattened black seeds with spine-like projections at the margins (Fig. 3). This species is morphologically most similar to *C. longifolium* (Barboza et al. 2019) with which it shares lack of pubescence, multi-flowered inflorescences, yellow corollas, laterally compressed calyx appendages, and black seeds (see contrasting characters in the key below).

*Capsicum regale* possesses unusual characters of the genus. Normally, *Capsicum* species have unbranched inflorescences lacking peduncles, with the flowers solitary or congested on a very short axis. Flowers can be arranged on a short or relatively elongated rachis in a few species, e.g., *C. rhomboideum* (Dunal) Kuntze, *C. coccineum* (Rusby) Hunz., *C. lycianthoides* Bitter (Barboza pers. obs.), *C. longifolium* (Barboza et al. 2019), and *C. regale*, but none of them have short peduncles or forked inflorescences as occurs occasionally in *C. regale*. In most *Capsicum* species the calyx appendages, when present, are usually cylindrical or subulate, and green-colored. It is very rare to find laterally compressed calyx appendages that appear as wing-like structures, as occur in *C. longifolium* (Barboza et al. 2019), in some plants of *C. dimorphum* (Miers) Kuntze (Barboza, pers. obs.), and in *C. regale*. Stellate corollas lobed about halfway to the base are common in the genus; exceptions to this are found in *C. benoistii* Barboza (Barboza et al. 2019) and *C. regale*, both of which have deeply stellate corollas lobed more than halfway to the base. In most *Capsicum* species, the fruiting pedicels and fruiting calyx are generally green or green with purple tones or lines; only *C. caatingae* Barboza & Agra (Carrizo García et al. 2016) and sometimes *C. dimorphum* and *C. geminifolium* (Dammer) Hunz. (Jarret et al. 2019) have pedicels and calyces uniformly violet-colored, while those of *C. regale* are uniformly purple-colored. An unusual constriction at the junction of the thickened fruiting pedicels with the fruiting calyx is clearly evident in *C. regale* (Fig. 2K), a character also present in some other species, i.e., *C. chinense* Jacq. (Baral and Bosland 2004), *C. caatingae* (Carrizo García et al. 2013), *C. minutiflorum* (Rusby) Hunz. (Carrizo García et al. 2016), and *C. lanceolatum* (Greenm.) C.V. Morton & Standl. (Barboza pers. obs.). The dark blue to purple fruits are unique to *C. regale* among the wild *Capsicum* species, which have red, orange-red, or greenish-golden yellow fruits at maturity (Hunziker 2001; Carrizo García et al. 2016).

Carrizo García et al. (2016) were the first to provide an extensive phylogenetic analysis of *Capsicum* using broad sampling of 34 of the approximately 35 species of the genus known at the time. They identified and named 11 well supported clades within *Capsicum*. One of these is the Andean clade, which includes species native to Central America and the Andes in northwestern South America. Morphological characters of the Andean clade species include leaves borne in anisophyllous pairs, flowering pedicels straight (not geniculate), corollas mainly yellow, fruits red to orange-red and non-pungent with the pericarp lacking giant cells, seeds black or blackish-brown,
and chromosome base numbers of \( x = 13 \) (Jarret et al. 2019; Scaldaf erro and Moscone 2019). *Capsicum regale* exhibits all of these characters except for its dark blue or purple fruits and the occasional forked inflorescences, which are not known in any other wild *Capsicum* species. Molecular data from both chloroplast and nuclear regions place *Capsicum regale* within the Andean clade (Fig. 6). Although *C. regale* is morphologically most similar to *C. longifolium*, the combined molecular data places it in a clade with *C. rhomboideum* and *C. hookerianum* with moderate support. Nevertheless, its closest specific affinities need to be further studied using additional data.

*Capsicum regale* inhabits the Andean-Amazonian Piedmont, encompassing the eastern slopes of the Cordillera Oriental from southern Colombia to the Cerros de Kampanquis, the easternmost branch of the Andes in northern Peru. This area is home to a transitional ecosystem with a distinctive vegetation and biodiversity due, in part, to the juxtaposition between the Amazon basin and the Andean forests (Gentry 1992; Pitman et al. 2002); this unique biodiversity is rapidly disappearing due to intense deforestation, clearing, and fragmentation (Pitman et al. 2002; Mulligan 2010; Tapia-Armijos et al. 2015; Alvarez-B et al. 2019). Some localities where *C. regale* has been collected are protected areas (Parque Nacional Natural Alto Fragua Indi Wasi, Colombia; Reserva Ecológica Antisana, Ecuador; Estación Biológica Jatun Sacha, Ecuador), and it is expected that in these reserves it is not under serious threat. Other sites in which it occurs are susceptible to human disturbance such as crop planting and high levels of deforestation; these locations include Correg. Caraño (Caquetá, Colombia, Alvarez-B et al. 2019, our observations), Río Bermejo to Cerro Sur Pax (Sucumbíos, Ecuador, Pitman et al. 2002), and Cuenca del Río Morona, Pongo Chinim (Loreto, Peru, Pitman et al. 2012). In these areas, *C. regale* is considerably threatened, and a conservation strategy is urgently needed to protect these species-rich ecoregions.

### Artificial key to the species of Andean clade of *Capsicum*

1. Flowers solitary, rarely paired; pedicels (15–) 25–43 mm long; calyx with 5 sub-equal reflexed appendages; corolla white or yellowish-white lined with purple; Mesoamerica....................... *C. lanceolatum* (Greenm.) C.V.Morton & Standl.

   - Flowers 2–10 (–13), rarely solitary; pedicels 3–28 mm long; calyx lacking appendages or with up to 10 subequal or unequal, recurved, spreading or erect appendages; corolla pure yellow or yellowish with maroon or purple pigmentation; South America (*C. rhomboideum* also in Mesoamerica) .............................................2

2. Calyx appendages absent, or appearing as 1–3 small 0.5–1.8 mm long mucronate protuberances below the margin, or well-developed, 2–5, triangular-compressed and wing-like, 2–2.5 mm long ..............................................3

   - Calyx appendages (2–) 5–10, subulate or linear-subulate, (0.9–) 2–7 mm long.... 5

3. Plants usually pubescent, rarely glabrescent; flowers up to 5, axillary, the rachis very reduced or lacking; calyx with 0–3 small mucronate appendages 0.5–1.5 mm long .................................................................................. *C. dimorphum* (Miers) Kuntze

   - Plants completely glabrous; flowers 3–13, on a developed rachis; calyx with 2–5 thick triangular-compressed wing-like appendages 1–2.5 mm long.........................4
New Capsicum species from the Andean-Amazonian Piedmont

4 Leaves coriaceous; major leaves narrowly elliptic (ratio length/width 6–10.8); corolla stellate-campanulate, lobed about halfway to base; calyx tube membranous; stamens equal, 2–2.6 mm long; fruits 8–13 mm in diameter, orange at maturity; fruiting pedicels 1–1.6 cm long, green, pendent; fruiting calyx green-purple or green; seeds 1.7–2.3 mm long, 1.7–2.2 mm wide, not flattened, tear drop-shaped, the surface reticulate. 

*C. longifolium* Barboza & S.Leiva

Leaves membranous; major leaves elliptic (ratio length/width 2.5–4); corolla deeply stellate, lobed more than halfway to base; calyx tube fleshy; stamens sub-equal (one longer), (2–) 3–4.3 mm long; fruits 6–9 mm in diameter, dark blue to purple at maturity; fruiting pedicels ca. 1.8 cm long, brilliant dark purple, erect; fruiting calyx entirely brilliant purple; seeds 2.75–3.40 mm long, 2.25–2.70 mm wide, flattened, C-shaped, the surface smooth with small spine-like projections.

*C. regale* Barboza & Bohs

5 Calyx with 8–10 unequal appendages, the longer 4–6 (–7) mm long, the shorter 1.3–4 mm long. 

*C. hookerianum* (Miers) Kuntze

Calyx with 2–5 equal or subequal appendages 0.9–6.5 mm long

6 Flowers 1–3, axillary; corolla long tubular-campanulate, 14.5–17 mm long, the tube 11–12 mm long, the lobes broadly ovate, 3.5–5 mm long, 4.5–5 mm wide; stone cells 2.

*C. piuranum* Barboza & S.Leiva

Flowers (2–) 3–10 (–13), axillary or on a short rachis; corolla deeply stellate or campanulate to broadly campanulate, (6–) 7–15 mm long, the tube 3–12 (–15) mm long, the lobes absent or incipient to well developed, narrowly triangular or ovate to broadly ovate, (3–) 5–9 mm long, 2–5.5 mm wide; stone cells absent or 5–6 (fruits unknown in *C. benoistii*).

*C. benoistii* Barboza

7 Corolla deeply stellate, 12–13 mm long, the lobes narrowly triangular.

*C. benoistii* Barboza

8 Corolla nearly entire, campanulate to broadly campanulate, (6–) 7–15 mm long, the lobes absent or incipient, ovate to broadly ovate.

*Corolla campanulate, stellate in outline, with a thin interpetalar membrane connecting the lobes in the proximal half.*

*C. geminifolium* (Dammer) Hunz.

9 Inflorescence up to 13-flowered; major leaves membranous, (4–) 4.8–12 cm long, 2–5 cm wide, ovate, elliptic, or rhomboid-ovate; corolla 6–9.5 mm long, 8–12 mm in diameter; fruits up to 0.9 cm in diameter, dark red at maturity; stone cells absent; trees or erect shrubs; trichomes simple, branched, and dendritic on the same plant.

*C. rhomboideum* (Dunal) Kuntze

Inflorescences (2–) 3–8 (–10)-flowered; major leaves coriaceous, (10–) 11–22.5 cm long, (3–) 4–8.5 cm wide, ovate to broadly ovate; corolla 8–15 mm long, 15–18 mm in diameter; fruits up to 1.2 cm in diameter, bright orange or red at maturity; stone cells 0–6; scandent or slender shrub or subshrub; mostly glabrous or sparse, simple trichomes present on young stems only.

*C. lycianthoides* Bitter
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References


**Supplementary material I**

**Table S1. Taxa and materials analyzed in the phylogenetic analyses**
Authors: Gloria E. Barboza, Carolina Carrizo García, Marisel Scaldaferrro, Lynn Bohs
Data type: Excel file
Explanation note: Taxa and materials analyzed in the phylogenetic analyses. Position within *Capsicum* (clade) or as outgroup, provenance, voucher specimens, ID in trees, and GenBank accession numbers for each marker analyzed are provided. Sequences retrieved from GenBank are marked with an asterisk. Abbreviations. CGN = Centre for Genetic Resources, Wageningen University, NL. NMCA = College of Agriculture, New Mexico State University, USA. Cult. = cultivated. Authors: Gloria E. Barboza, Carolina Carrizo García, Marisel Scaldaferrro & Lynn Bohs.
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A new species of *Eriotheca* (Malvaceae, Bombacoideae) from coastal areas in northeastern Brazil

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Abstract

A new species of *Eriotheca* (Malvaceae, Bombacoideae) from coastal areas in the northeastern Brazilian states of Alagoas and Bahia is described and illustrated. *Eriotheca alversonii* inhabits Atlantic coastal forest and is found principally on sandy soils in restinga vegetation. It is most similar morphologically to *E. parvifolia*. Both species have 3-foliolate leaves and short petioles on fertile branches, but the new species has smaller flowers, truncate to crenulate calyces, and smaller globose to subglobose capsules. The affinities of *E. alversonii* to morphologically similar species and its phenology are discussed. A distribution map and preliminary assessment of its conservation status are provided.

Keywords

‘Bombacaceae’, ‘embiruçú’, endemism, plant taxonomy, restinga, sandy soils

Introduction

*Eriotheca* Schott & Endl. is one of 17 genera in the Bombacoideae (Malvaceae), a pantropical subfamily that includes ca. 160 species (Carvalho-Sobrinho et al. 2016). *Eriotheca* is restricted to South America (Robyns 1963, 1968, 1979; Robyns and Nilsson 1975, 1981; Fernández-Alonso 1999, 2003) and where it occurs, it is an important ele-
ment in the physiognomy and community structure of both seasonally dry tropical and moist forests (e.g., Macbride 1956; Ferreyra 1986; Linares-Palomino and Ponce Alvarez 2005; Thomas et al. 2008; Pennington et al. 2009). It includes ca. 25 species of which 19 occur in Brazil mainly in cerrado and Atlantic coastal forest (Duarte and Esteves 2011; Carvalho-Sobrinho 2013; Carvalho-Sobrinho et al. 2015; Macedo et al. 2018).

Molecular phylogenetic analyses place *Eriotheca* and *Pachira* Aubl. in a clade characterized by striate seeds (Duarte et al. 2011; Carvalho-Sobrinho et al. 2016), alternate eophylls, lack of prickles on trunks and branches, leaflets with brochidodromous venation (Carvalho-Sobrinho et al. 2016), and only two rows of ovules in the ovary (Franca et al. 2018). These analyses, however, also suggest that *Eriotheca* and *Pachira* as currently circumscribed are not monophyletic, and further molecular and taxonomic sampling is necessary to resolve the relationships between these two genera (Carvalho-Sobrinho et al. 2016). Until such sampling is completed, it would be premature to place *Eriotheca* in synonymy with *Pachira* and as a consequence new species have been described in both genera while maintaining their traditional circumscriptions (Duarte and Esteves 2011; Carvalho-Sobrinho 2013; Carvalho-Sobrinho et al. 2014b, 2015; Macedo et al. 2018).

*Eriotheca* differs in a number of characters from *Pachira*. In addition to the smaller flowers in *Eriotheca* (up to 55 mm long), it also has filaments freely originating from a staminal tube (phalanges are absent), a single whorl in the androecium (Robyns 1963; Carvalho-Sobrinho 2013; Carvalho-Sobrinho et al. 2015), often unilaterally apiculate petals (Robyns 1963), reniform anthers (Carvalho-Sobrinho 2013), a different indumentum on the external surface of the petals, and a glabrous tube (Carvalho-Sobrinho, pers. obs.).

*Eriotheca* is characterized by mostly medium to emergent trees, leaves that are palmately compound with leaflets articulate at the petiole apex, flowers with a persistent calyx that is accrescent in fruit, a receptacle often with external nectaries, an androecium with 18 to 170 stamens and dorsifixed anthers, capsules with copious brown kapok, and numerous, striate seeds usually up to 1 cm in diameter (Robyns 1963). An underground xylopodium-like structure was reported for *E. saxicola* Carv.-Sobr. (Carvalho-Sobrinho 2013). *Eriotheca* flowers are pollinated by bees, bats or hawkmoths (Oliveira et al. 1992; Sazima et al. 1999; MacFarlane et al. 2003).

The taxonomy of *Eriotheca* is challenging because type specimens are often phenomenologically incomplete (cf. Robyns 1963) and affect species circumscriptions because it is difficult to match leaves, flowers, and fruit characters from different specimens (Carvalho-Sobrinho and Queiroz 2008, 2010; Carvalho-Sobrinho et al. 2013a, b, 2014a, b). Identification of *Eriotheca* specimens traditionally has relied largely on floral characters, especially the length of pedicels, flower bud shape, calyx shape and indumentum, petal shape, and staminal tube shape (Robyns 1963). More recently, micromorphological characters from leaves have been used to circumscribe and diagnose species (Duarte and Esteves 2011; Carvalho-Sobrinho et al. 2015) and to elaborate identification keys (Duarte and Esteves 2011), although this innovation has limited applicability in fieldwork or herbarium research.
Ongoing studies on the systematics of Neotropical Bombacoideae (Carvalho-Sobrinho and Queiroz 2008, 2010, 2011; Carvalho-Sobrinho et al. 2009, 2012, 2013a, b, 2014a, b, 2015, 2016; Carvalho-Sobrinho and Dorr 2017) have revealed herbarium specimens of *Eriotheca* from the coastal Atlantic states of Alagoas and Bahia in northeastern Brazil that are noteworthy because their leaves and fruits are smaller than others in the genus. Careful study of these specimens has led to the recognition of a new species, which is described and illustrated here. Notes on this species’ distribution and phenology, comments on morphologically similar species, and a preliminary assessment of its conservation status are provided.

**Material and methods**

This study was based on examination of herbarium collections, field observations, and digital images of specimens. Specimens were studied by visits to or loans from the following herbaria: ALCB, ASE, CEPEC, F, HUEFS, K, MBM, MO, NY, RB, SP, SPF, and US. Images of additional herbarium specimens were studied through the following websites: JSTOR Global Plants (https://plants.jstor.org/) and INCT – Herbário Virtual da Flora e dos Fungos (http://inct.splink.org.br/). Descriptions and measurements are based on dry herbarium specimens. The distribution map was prepared using QGIS v.3.12.2 (QGIS Development Team 2020). A preliminary extinction risk assessment of the new species was made using the IUCN Red List Categories and Criteria (IUCN 2019). Georeferenced specimen data were imported into GeoCAT (Bachman et al. 2011) to estimate the extent of occurrence (EOO) and the area of occupancy (AOO) using 2 × 2 km grid cells.

**Taxonomic treatment**

*Eriotheca alversonii* Carv.-Sobr. & Dorr, sp. nov.

urn:lsid:ipni.org:names:77212952-1

Figs 1, 2

**Diagnosis.** Similar to *Eriotheca parvifolia* (Mart.) A.Robyns in its 3-foliolate, glabrous leaves, and short petioles on fertile branches, but differing in its linear-oblong (vs. large elliptic) flower buds, smaller (3–4 × 3–5 vs. 7 × 8–11 mm) cupuliform (vs. campanulate) calyces with apices truncate to crenulate (vs. mostly 3–5-lobed), fewer stamens (ca. 70 vs. ca. 120), and smaller capsules (15–21 vs. 30–35 mm long).

**Type.** Brazil. Bahia: Maraú, entrada à direita ca. 3 km da entrada da cidade, propriedade particular ‘Espaço 21’, 14°10’27″S, 38°59’53″W, 7 m a.s.l., 08 Jul 2011 (lf, fl buds, fl), J.G. Carvalho-Sobrinho et al. 3126 (holotype: HUEFS).

**Description.** Treelets or more often trees to 20 m tall; trunks to 50 cm dbh; buttresses 40 × 60 cm; branches often blackish in herbarium specimens. Terminal buds
Figure 1. *Eriothea alversonii* **A** flowering branch **B** three-foliolate leaf **C** flower buds and vegetative terminal buds **D** flower bud **E** flower **F, G** petals; adaxial and abaxial views **H** staminal tube **I** ovary **J, K** anthers; undehisced and dehisced **L** stigma **M** fruit. All drawn from the holotype, except for fruit (*L.A. Mattos Silva 1769*). Scale bars: 3 cm (**A, B**); 1 cm (**C, M**); 5 mm (**D–I**); 0.5 mm (**J–L**).
New species of *Eriotheca* from Brazil

often persistent at branch apices, 5–11 mm long, attenuate and falcate apically. Leaves palmately compound; petioles on fertile branches up to 8 mm long (to 20 mm long on vegetative branches); petiolules absent to greatly reduced; leaflets 1–3(–5, in vegetative branches), 15–46(107) × 8–56 mm, coriaceous; proximal leaflets 8–27 mm wide; distal leaflets 8–56 mm wide; leaflet length-to-width ratio (1.5)1.9–2.5(3); leaflets narrowly obovate, elliptic to widely elliptic in fertile branches, rarely obcordate, apices retuse to emarginate, bases cuneate, margin entire, revolute, strongly revolute at base, glabrous on both surfaces, except for sparse microtrichomes on abaxial surface, discolorous, adaxial surface of fresh leaflets dark green and abaxial surface light green, abaxial surface of dry leaflets often reddish-brown, midrib prominent abaxially, secondary veins 7–10, impressed on both surfaces, intersecondary veins impressed on abaxial surface. Inflorescences axillary, 1–6-flowered cymes, borne on younger, terminal often leafy branches; pedicels 10–22 mm long, covered with blackish indumentum; bracteoles caducous. Flowers linear-oblong in bud, ca. 25 mm long; receptacles lacking glands; calyces 3–4 × 3–5 mm, cupuliform, truncate to crenulate, accrescent in fruit, outer surface covered with ferruginous indumentum, blackish when very young; petals 15–23 × 3–6 mm, oblanceolate, unilaterally apiculate, tomentose on both faces, internally with longitudinal lines of longer trichomes (sericeous) on one longitudinal half, whitish when fresh; stamens ca. 70, cream-colored when fresh; staminal tube 5 mm long, oblong, slightly expanded at apex, producing free filaments 11 mm long; ovary subglobose, the style inconspicuously 5–lobed. Capsules 15–21 × 13–20 mm, globose to subglobose, externally inconspicuously 5–lobed. Seeds numerous, 5 mm in diam., pyriform, glabrous.

**Phenology.** Flower buds in June and July, open flowers in August and September and mature fruits in October and December to February.

**Distribution and habitat.** *Eriotheca alversonii* is known from coastal vegetation mainly over quaternary white sand (restinga forest) or less frequently on clay-sandy soils in transitional vegetation between restinga forest and wet dense forest (“floresta ombrófila densa”), in the northeastern states of Alagoas and Bahia, Brazil.

**Conservation status.** *Eriotheca alversonii* is known from 19 collections from six different localities (municipalities). The extent of occurrence (EOO) of this species has been calculated to be 18,466 km², which qualifies the species for the Vulnerable (VU) category, and the area of occupancy (AOO) was estimated to be 28 km², which qualifies it for the Endangered (EN) category (Bachman et al. 2011; IUCN 2019). Based on herbarium specimen labels, three collections of *E. alversonii* were made inside one state-level protected Reserve (APA de Santa Rita) as explicitly stated in collectors’ descriptions, and an additional four collections probably were made inside state- (APA Pratigi and APA Marituba do Peixe) or federal-level (Reserva Extrativista de Canavieiras) protected areas; nevertheless, all these protected areas allow sustainable use of natural resources and none of them are of the highest level of protection (level I or II) described by the IUCN (Dudley 2008). Furthermore, restinga habitat currently is being lost at an accelerated rate due to anthropogenic pressures (Rocha et al. 2007; Pergentino and Landim 2014) and most collections of *E. alversonii* were made on
Figure 2. Distribution map of *Eriotheca alversonii*. Gray-shaded areas represent the original extent of Atlantic forest. State boundaries are indicated by continuous lines. Abbreviations for Brazilian states: AL: Alagoas; BA: Bahia; PE: Pernambuco; SE: Sergipe.

farms. Therefore, due to the rapid rate of deforestation of the much fragmented restinga vegetation and the small AOO (32 km²) of *E. alversonii*, we consider this species to be Endangered (EN category) according to IUCN criteria (IUCN 2019).

**Etymology.** The specific epithet honors the North American botanist Dr. William (‘Bil’) Surprison Alverson (b. 1953) who has contributed greatly to our understanding of the phylogeny and systematics of Neotropical Bombacoideae.


**Discussion**

*Eriotheca alversonii* is characterized by leaves on fertile branches 1–3-foliolate, petioles up to 8 mm long, leaflets coriaceous, elliptic to broadly-elliptic or narrowly obovate, proximal leaflets up to 27 mm wide, flower buds linear-oblong, and small capsules globose to subglobose up to 21 mm long with glabrous valves. On herbarium sheets, specimens are characterized by terminal vegetative buds with attenuate, falcate apices and by leaves on fertile branches often 1–2-foliolate and often reddish-brown on the abaxial surface.

*Eriotheca alversonii* is morphologically similar to *E. parvifolia* – a shrubby species to 2.5 m tall endemic to the arenitic-quartzite rock outcrops in the Espinhaço Mountain Range in the state of Minas Gerais – by the small petioles, the small, narrowly obovate leaflets with retuse to emarginate apices, and the often persistent leaves on fertile branches; furthermore, both species flower from July to September. However, *E. alversonii* differs from *E. parvifolia* in its oblong-linear (vs. large elliptic) flower buds, calyces 3–4 × 3–5 (vs. 7 × 8–11) mm that are cupuliform and truncate to crenu-
late (vs. campanulate and mostly 3–5-lobed), stamens ca. 70 (vs. ca. 120), and capsules 15–21 (vs. 30–35) mm long (Table 1).

Eriotheca alversonii emerged as sister to E. candolleana (K.Schum.) A.Robyns in a multi-locus DNA sequence-based phylogeny (labeled as ‘Eriotheca sp. CS3125’ in Fig. 2B of Carvalho-Sobrinho et al. 2016). It shares with E. candolleana the arborescent habit with a regular, well-defined closed crown (“spherical” sensu Ribeiro et al. 1999) and relatively small leaflets and fruit. However, E. alversonii can be distinguished readily from E. candolleana by 1–3 (vs. 5–9) leaflets that are coriaceous (vs. papyraceous) and glabrous (vs. pubescent with ferrugineous trichomes on the veins abaxially), oblong-linear (vs. globose) flower buds, absence (vs. presence) of glands on the receptacle, and calyces 3–4 × 3–5 (vs. 8–11 × 9–12) mm that are cupuliform (vs. campanulate to tubular), truncate to crenulate (vs. mostly 3–5-lobed), and puberulent to glabrescent (vs. covered with dense ferruginous trichomes). Furthermore, E. alversonii inhabits coastal forest over predominantly sandy soils (restinga) in Alagoas and southern Bahia (i.e., 14°S to 10°S) while E. candolleana inhabits semideciduous forest on the southeastern Atlantic coast from São Paulo to southern Bahia (i.e., 23°S to 17°S) and in the cerrado biome where it reaches 1,200 m in elevation.

Eriotheca alversonii has been frequently misidentified as E. macrophylla – a tree species inhabiting restinga and semideciduous forest in the Atlantic coast of northeastern Brazil – probably because in both species the calyces are cupuliform and the leaflets of the fertile branches are 1.5–2.3× longer than wide. However, E. alversonii can be readily distinguished from E. macrophylla by its terminal, falcate vegetative buds with attenuate apices (vs. straight buds with acute apices), linear-oblong (vs. broadly elliptic

<table>
<thead>
<tr>
<th>Character</th>
<th>E. alversonii</th>
<th>E. macrophylla</th>
<th>E. parvifolia</th>
</tr>
</thead>
<tbody>
<tr>
<td>Leaves on fertile branches</td>
<td>Present</td>
<td>often absent</td>
<td>present</td>
</tr>
<tr>
<td>Petiole length of terminal leaf</td>
<td>up to 8</td>
<td>21–45(-65)</td>
<td>8–26(-37)</td>
</tr>
<tr>
<td>Number of leaflets of terminal leaf</td>
<td>1–3</td>
<td>3(–5)</td>
<td>(2–)13(–5)</td>
</tr>
<tr>
<td>Proximal leaflets width (mm)</td>
<td>8–27</td>
<td>24–66</td>
<td>8–31</td>
</tr>
<tr>
<td>Number of secondary veins</td>
<td>7–10</td>
<td>12–18</td>
<td>14–20</td>
</tr>
<tr>
<td>Inflorescence position</td>
<td>younger, terminal, often leafy branches</td>
<td>old branches often leafless and modified brachyblasts</td>
<td>terminal, leafy branches</td>
</tr>
<tr>
<td>Number of flowers per cyme</td>
<td>1–5</td>
<td>2–7</td>
<td>1–3</td>
</tr>
<tr>
<td>Pedicel length (mm)</td>
<td>10–22</td>
<td>14–25</td>
<td>10–15(-25)</td>
</tr>
<tr>
<td>Flower bud shape</td>
<td>linear-oblong</td>
<td>broadly elliptic</td>
<td>broadly elliptic</td>
</tr>
<tr>
<td>Calyx dimensions (mm)</td>
<td>3–4 × 3–5</td>
<td>5–6 × 7–9</td>
<td>7 × 8–11</td>
</tr>
<tr>
<td>Calyx apex</td>
<td>truncate to crenulate</td>
<td>crenulate</td>
<td>mostly 3–5-lobed</td>
</tr>
<tr>
<td>Calyx shape</td>
<td>cupuliform</td>
<td>cupuliform</td>
<td>campanulate</td>
</tr>
<tr>
<td>Petal dimensions (mm)</td>
<td>15–23 × 3–6</td>
<td>30 × 11</td>
<td>24–31 × 9–15</td>
</tr>
<tr>
<td>Number of stamens</td>
<td>ca. 70</td>
<td>140</td>
<td>125</td>
</tr>
<tr>
<td>Staminial tube length (mm)</td>
<td>4–5</td>
<td>4</td>
<td>5</td>
</tr>
<tr>
<td>Fruit length (mm)</td>
<td>15–21</td>
<td>38–60</td>
<td>27–60</td>
</tr>
<tr>
<td>Fruit shape</td>
<td>globose to subglobose</td>
<td>obovoid</td>
<td>obovoid</td>
</tr>
<tr>
<td>Seed diameter (mm)</td>
<td>4</td>
<td>ca. 10</td>
<td>6–7</td>
</tr>
<tr>
<td>Flowering period</td>
<td>July to September</td>
<td>October to December</td>
<td>July to September</td>
</tr>
<tr>
<td>Fruiting period</td>
<td>August to October and December to February</td>
<td>December to February</td>
<td>October to December</td>
</tr>
</tbody>
</table>
to oblong-obovate) flower buds, smaller calyces (3–4 × 3–5 mm vs. 5–6 × 7–9 mm), smaller petals (19–20 × 4–5 vs. 20–32 × 10–15 mm), fewer stamens (ca. 70 vs. 90–140), and smaller fruit (15–21 mm vs. 38–60 mm long) that are globose to subglobose (vs. obovoid). Moreover, *E. alversonii* is characterized by inflorescences borne on younger terminal and often leafy branches while the inflorescences of *E. macrophylla* are borne on old branches that are often leafless and modified as brachyblasts.

**Acknowledgements**

We thank the curators of the herbaria cited in the text for kindly sending material on loan; Natanael Nascimento for the line drawings; Jefferson Rodrigues Maciel for the map; Mário Terra for help during fieldwork; and PPGBot/UEFS for financial support for the fieldwork; Jacquelyn Kallunki and one anonymous reviewer for valuable suggestions on the manuscript.

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**References**


New species of *Eriotheca* from Brazil


**Appendix I**

Selected herbarium specimens of *Eriotheca macrophylla* and *E. parvifolia* examined for this study.

*Eriotheca macrophylla* (K.Schum.) A.Robyns


Bahia: Ilhéus, on road to Vila Brasil, 10 km West of junction with BA001, the junction ca. 40 km south of Ilhéus, just north of the Rio Acuípe, 15°06’S, 39°04’W, 10 May 1993 (lf, fl), *W. Thomas et al.* 9843 (CEPEC, NY, SP). Itacaré, entre a Praia do Farol e a Praia da Ribeira, 14 Dec 1992 (lf, fl), *A. Amorim et al.* 951 (CEPEC).


**Santa Cruz de Cabrália, Res. Bio. Pau-Brasil, 11 Dec 1971 (lf, fl), *A. Eupunino* 94 (CEPEC).**

Santa Terezinha, 14,5 km na rodovia Elísio Medrado/Sta. Terezinha, Torre da Embratel, ca. 7 km distante do Distr. de Pedra Branca, Serra da Jiboia, 12°51’13”S,
New species of *Eriotheca* from Brazil


*Eriotheca parvifolia* (Mart.) A.Robyns

Hydrostachys flabellifera (Hydrostachyaceae),
a new species from Madagascar

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³ University of Chinese Academy of Sciences, Beijing 100049, China
⁴ Département Flore, Parc Botanique et Zoologique de Tsimbazaza, Antananarivo 101, Madagascar
⁵ Germplasm Bank of Wild Species, Kunming Institute of Botany, Chinese Academy of Sciences, Kunming 650201, China

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Abstract

Hydrostachys flabellifera, a new species of Hydrostachyaceae found in a stream in Manandriana, Madagascar, is described and illustrated herein. It is similar to H. verruculosa and H. laciniata in morphology, but can be distinguished from them by its leaves with sparsely arranged, flabelliform and palmately parted emergences, obvious rachis and the pattern of segments arranged on the male bracts. Molecular phylogenetic analysis of the nuclear ribosomal internal transcribed spacer (ITS) dataset provides a robust support for it as a new species as well.

Keywords

Aquatic plants, Cornales, endemic, new taxa, taxonomy
Introduction

Hydrostachys Thouars (1806: 2) is the sole genus in the family Hydrostachyaceae (Tul.) Engler (1894: 136) with about 22 known species. Fourteen of them are endemic to Madagascar (Phillipson et al. 2018) and the remaining species are native to southern and tropical Africa. Hydrostachys has been used in traditional medicine and probably could be a potential candidate for use in chemotherapy to fight against cancer (Ranarijona et al. 2014). The plants of Hydrostachys, which are aquatic herbs living in fast-moving streams or rivers, are well adapted to turbulent aquatic environments with their roots and discoidal rhizome adhering to the rocks. Hydrostachys are annual or perennial, submerged or partially submerged in the rainy season, flowering in the dry season. Their simple or pinnate leaves emerge from the rhizome, and petiole, rachis and subdivisions are often covered with diverse forms of emergences, including verrucae, scales and lobules (modified leaf blade lobes), which give the plant the appearance of a fern or lycopodium. Hydrostachys are dioecious or seldom monoecious, with highly reduced and unisexual flowers borne on the spike, the spikes usually emerging from the rhizome, sepals and petals are absent; the fruit is a capsule with numerous tiny seeds (Perrier 1952; Cusset 1973; Stannard 1997; Verdcourt 1986; Erbar and Leins 2004).

Hydrostachys are highly modified aquatic plants and the taxonomic placement of this enigmatic genus has confounded botanists for two hundred years. Due to their similar habitat and highly modified morphological characters, the genus was once placed in Podostemaceae (Tulasne 1849). However, this placement was rejected thanks to evidence from embryology, inflorescence morphology (Jäger-Zürn 1965; Rauh and Jäger-Zürn 1966) and biochemistry (Scogin 1992). Phylogenetic studies showed unstable placements, based on different DNA markers and taxon sampling (Les et al. 1997; Soltis et al. 2000; Burleigh et al. 2009). Currently, Hydrostachyaceae is treated as a distinctive family in Cornales with a phylogenetic long branch in most studies (Albach et al. 2001; Xiang et al. 2002; Fan and Xiang 2003; Xiang et al. 2011; Fu et al. 2019). Despite the uncertain placement at the order level, the inter-species identification is much clearer.

During a field investigation in Madagascar in 2017, a Hydrostachys population was found in Manandriana which appeared similar to H. verruculosa A. Juss. (1837: tab. 91) and H. laciniata Warming (1899: 152). However, after carefully comparing the collection with all available specimens of Hydrostachys and consulting relevant literature (Perrier 1952; Cusset 1973), we observed that its leaf structure is different from that of all known species in this genus and that this plant is wholly new to science. Hence, we describe it herein as a new species.

Materials and methods

The description of the new species is based on field notes and observations of field pictures, dried specimens and FAA-fixed (formalin/acetic acid/alcohol) materials. Specimens were collected from Manandriana, Madagascar (20°14’S, 47°06’E) and deposited at the herbaria of Parc Botanique et Zoologique de Tsimbazaza (TAN) and Wuhan Botanical
Hydrostachys flabellifera

Garden, Chinese Academy of Sciences (HIB). Some leaves and spikes were fixed and conserved in formalin/acetic acid/alcohol (FAA) fixatives. Detailed characteristics of the bracts and emergences were observed and measured on the fixed materials by using a stereomicroscope (Nikon Stereo Microscope SMZ25). Terminology was referenced in several books and literature (Perrier 1952; Cusset 1973; Verdcourt 1986; Simpson 2010; Beentje and Williamson 2016). The herbarium abbreviations follow Index Herbariorum (http://sweetgum.nybg.org/science/ih/). Physical specimens of Hydrostachys, deposited at BM, E, K and TAN, were examined. High-resolution digital specimen images from B, BNRH, BR, GH, MA, P and US were checked via JSTOR Global Plants (https://plants.jstor.org) and GBIF (https://www.gbif.org). The distribution map was produced by QGIS3 (available from: https://qgis.org/).

The nuclear ribosomal ITS was used as the DNA marker, with 13 samples included in the phylogenetic analysis. All Hydrostachys sequences were newly generated, while three taxa from Nyssa and one from Triphyophyllum were treated as outgroups. GenBank accession numbers are available in Table 1. Genomic DNA was extracted from dry specimens using Mag-MK Plant Genomic DNA extraction kits (Sangon Biotech, Shanghai). Primers for polymerase chain reactions (PCR) were referred to White et al. (1990). PCR products were sequenced by Sangon Biotech using the 3730xl DNA Analyzer and Geneious v.11.1.5 (available from: http://www.geneious.com/) was used for DNA assembling and manually editing. The dataset was aligned by MAFFT v.7.294 (Katoh and Standley 2013), then trimmed by trimAl v.1.2 (Capella-Gutierrez et al. 2009). The Maximum Likelihood tree was inferred using IQ-TREE v.2.0.6 (Minh et al. 2020) with default parameters and ultrafast bootstrap approximation was assessed with 1000 replicates. The consensus tree was visualised and annotated by ggtree v.2.2.1 (Yu et al. 2017). Dataset, scripts and command lines in the phylogenetic analysis are available in Github (https://github.com/xuzhun1008/Hydrostachys_flabellifera_paper.git).

### Table 1. Taxa included in the phylogenetic analysis.

<table>
<thead>
<tr>
<th>Species</th>
<th>Locality</th>
<th>Voucher</th>
<th>GenBank accession number</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Triphyophyllum peltatum</em> (Hutch. &amp; Dalziel) Airy Shaw</td>
<td>–</td>
<td>TR121</td>
<td>HM204913</td>
</tr>
<tr>
<td><em>Nyssa sylvatica</em> Marshall</td>
<td>–</td>
<td>zhangcq0088</td>
<td>JF977171</td>
</tr>
<tr>
<td><em>Nyssa wenshanensis</em> Fang &amp; Soong</td>
<td>China, Yunnan</td>
<td>S2007041304</td>
<td>JQ280761</td>
</tr>
<tr>
<td><em>Nyssa javanica</em> Wangerin</td>
<td>–</td>
<td>S2007040302</td>
<td>JQ280777</td>
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<tr>
<td><em>Hydrostachys multifida</em> A. Juss.</td>
<td>Madagascar, Boeny, Betseboka</td>
<td>SAJIT3437</td>
<td>MW233025</td>
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<td><em>Hydrostachys longiflora</em> H. Perrier</td>
<td>Madagascar, Analamanga, Antananarivo-Atsimondrano</td>
<td>SAJIT3442</td>
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<td><em>Hydrostachys stolonifera</em> Baker</td>
<td>Madagascar, Vakinankaratra, Antanifotsy</td>
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<td>MW233028</td>
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<td><em>Hydrostachys flabellifera</em> G.W. Hu, Zhun Xu &amp; Q.F. Wang</td>
<td>Madagascar, Amoron’i Mania, Manandriana</td>
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<td><em>Hydrostachys distichophylla</em> var. <em>hildebrandtii</em> (Engl.) C. Cusset</td>
<td>Madagascar, Haute-Matsiatra, Harantena</td>
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<td>Madagascar, Haute-Matsiatra, Ambalavao</td>
<td>SAJIT3498</td>
<td>MW233033</td>
</tr>
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</table>
**Taxonomy**

*Hydrostachys flabellifera* G.W. Hu, Zhun Xu & Q.F. Wang, sp. nov.

urn:lsid:ipni.org:names:77212953-1

Figs 1, 2

**Diagnosis.** *Hydrostachys flabellifera* is similar to *H. verruculosa* and *H. laciniata* in having simple leaves, but it can be easily distinguished from these species by short leaves, 3–12 cm long, the sparsely and spirally-arranged, flabelliform and palmately-parted emergences, the presence of a distinct and thin rachis between emergences and the pattern of segments arranged on the male bracts with acute apex.

**Type.** MADAGASCAR. Fianarantsoa Province: Amoron'i Mania Region, Manandriana District, elev. 1400 m, 20°14’S, 47°06’E, 20 September 2017, Sino-Africa Joint Investigation Team (SAJIT)-003462 (holotype, HIB!, isotypes, HIB!, TAN!)  

**Description.** A hydrophyte herb. Rhizomes discoid, 3–8 mm in diameter; 7–12 leaves emerging from the rhizome. Leaves simple, 3–12 cm long, the upper part slightly curved when rising from water, the base enlarged with stipule; stipule ovoid-elliptical, basal half dorsally attached on petiole, apex sometimes with a tail ca. 1.5 mm; centre bud enclosed by stipules of inner leaves; emergences spirally arranged on rachis and stretching out into loose layers, denser towards the apex of the leaf and gradually reduced to the base. Rachis obvious, 1–2 mm in diameter, white to light green. Petioles indistinct. Emergences (modified leaf blade lobes) 1–6 mm long, flabellate, basal ones reduced into scale-like, upper ones palmately parted, lobes cuneiform, secondly divided into rectangular to linear terminal lobes; the flat of emergences almost perpendicular to the axis; the apex of emergence slightly rolling up, ciliate at the end, cilia gathering into tufts after rising from water; emergences green to mauve at the pinnacle, the rest dark green. Petioles indistinct. Emergences (modified leaf blade lobes) 1–6 mm long, flabellate, basal ones reduced into scale-like, upper ones palmately parted, lobes cuneiform, secondly divided into rectangular to linear terminal lobes; the flat of emergences almost perpendicular to the axis; the apex of emergence slightly rolling up, ciliate at the end, cilia gathering into tufts after rising from water; emergences green to mauve at the pinnacle, the rest dark green. Male spikes 5.4–8.0 cm long, peduncles 4.7–6.2 cm long, covered with few small scale-like emergences. Bracts 1–2.2 mm × 1–2.2 mm, rhombic, dark green; segment I (the terminal segment) acute, flanked by 1–2 tiny lobules on each side; segments II (lobules at the dorsal side of bract) acute or obtuse, 2 rows, each row with 3–5 separated lobules, lobules ca. 0.3 mm high. Stamen sessile, anther oblate, with two divergent thecae dehiscing longitudinally. Female spike not found.

**Etymology.** The epithet refers to the flabellate shape of emergences on leaves.

**Distribution and ecology.** Only one population was found on rocks in a stream in Manandriana, Madagascar (20°14’S, 47°06’E), at an elevation of 1400 m (Fig. 3).

**Conservation status.** *Hydrostachys flabellifera* is currently only known from one location with a very small population. Additionally, all species of *Hydrostachys* are highly dependent on the moving aquatic environment which is threatened by water pollution, natural system modifications, energy production and mining, all of which could drive the taxon to Critically Endangered (CR) or Extinct (EX) in a very short time (IUCN 2020). Following Guidelines for IUCN Red List Categories and Criteria (2020), *H. flabellifera* should be categorised as Vulnerable (VU D2).
Figure 1. *Hydrostachys flabellifera* G.W. Hu, Zhun Xu & Q.F. Wang. A habit B lateral view of stipule and petiole base C ventral view of stipule and petiole base D, E part of the leaf F downside of a leaf emergence G upperside of a leaf emergence H dorsal view of male bract I ventral view of male bract J, K stamen. Drawn by Jing Tian.
Phylogenetic analysis. *Hydrostachys flabellifera* was placed in a robust clade together with *H. stolonifera* and *H. imbricata* (Fig. 4) with a high bootstrap support (BS = 96%), while they share limited morphological characteristics. *H. multifida*, considered as a clade in morphology, is not a monophyletic group, although with low bootstrap support.

Discussion

*Hydrostachys* are mostly annual, only a limited number of species with stolons are perennial (Perrier 1952), like *H. monoica* and *H. stolonifera*. In this case, we did not ob-
serve any structure, like stolons, that could help \textit{H. flabellifera} live for many more years. Therefore, \textit{H. flabellifera} probably is annual, but continuous observation is needed.

\textit{Hydrostachys flabellifera} closely resembles \textit{H. verruculosa} and \textit{H. laciniata} in having simple leaves, but can be easily recognised by several characters. The leaf emergences of the latter two species are densely arranged and overlapping and they constitute a thick cylindrical leaf with indistinct rachis. In contrast, the rachis of \textit{H. flabellifera} are thin and obvious and the emergences stretch out into layers, sparsely arranged and significantly reduced at the lower leaves. Their segments patterns on male bract are also obviously different. \textit{H. laciniata} was once treated as a form of \textit{H. verruculosa} (Perrier 1952) after it was published as a new species (Warming 1899). Cusset (1973)
also recognised it as a distinct species and further presented a diagram to compare it with *H. verruculosa* and that diagram clearly showed the differences in the bracts and the emergences on the leaf. After examining the type specimens of these two species, we accepted the treatment of Cusset (1973) and continued to compare the new species with these two species. Combining with morphology, phylogenetic results also provide solid evidence for the newly-discovered species. *Hydrostachys flabellifera*, *H. stolonifera* and *H. imbricata* form a robust clade, but share limited morphological characters. *H. stolonifera* and *H. imbricata* are much larger than *H. flabellifera* in size and they are definitely different in leaf types. *H. distichophylla* var. *hildebrandtii* is similar to *H. flabellifera* in morphology, but they are located in two distinct clades. The phylogenetic position of *H. flabellifera* would be much clearer when more taxa are included in the analysis. The combined results from phylogenetic analysis and detailed comparisons of morphological characteristics amongst *H. flabellifera*, *H. verruculosa*, *H. laciniata*, *H. distichophylla* var. *distichophylla* and *H. stolonifera* are listed in Table 2.

*Hydrostachys* are adaptable to diverse aquatic environments, from clean mountain streams to muddy rivers. These species can be distinguished by the type of leaves, emergences, spikes, also the bract shape and segments arrangement are valuable identification characteristics. Due to different statuses between fresh plant and pressed specimens, greater attention to detail is needed when comparing and describing these species in different conditions. Based on our empirical research, in some specific cases,
it is tricky to connect the living plant to the corresponding dry specimens. We highly recommend combining field investigations and herbarium examinations to obtain the full knowledge of this aquatic family.

Key to identification of *Hydrostachys* in Madagascar

1. Leaf simple.................................................................2
   - Leaf 1–4-pinnate.........................................................5

2. Cylindrical leaf with emergences densely arranged and overlapped.........3
   - Emergences sparsely arranged and stretched out.....................4

3. Dorsal side of the female bract densely covered with emergences.... *H. verruculosa*
   - Dorsal side of the female bract with bare surface, only few emergences on the top ................................................................. *H. laciniata*

4. Emergences falcate, margin entire .................. *H. distichophylla var. distichophylla*
   - Emergences flabellate, palmotely parted .......................... *H. flabellifera*

5. Plants with stolons; leaf in indefinite growth....................................6
   - Plants without stolon; leaf in definite growth............................7

6. Leaf pinnate or bipinnate, yellowish-white or pale green............... *H. monoica*
   - Leaf tripinnate, moss green or dark moss green .................. *H. stolonifera*
7 Leaf only once pinnate ................................................................. 8
  – Leaf more than once pinnate ...................................................... 11
8 Pinnules bearing long and capillary emergences .................... \textit{H. longifida}
  – Pinnules bearing scale-like emergences ................................ 9
9 Pinnules distantly arranged, terminated with a brush in the rainy season ........
  ........................................................................................................ 11
  – Pinnules closely arranged, without brush at the apex .................. 10
10 Petiole bare at the base, upper part covered with short emergences ... \textit{H. plumosa}
  – Petiole completely covered with imbricata emergences .......... \textit{H. imbricata}
11 The middle of the leaf wider than the base and the top ............ \textit{H. multifida}
  – The base of the leaf wider than the upper .................................. 12
12 Pinnule covered with capillary emergences .................................. 13
  – Pinnule covered with scale-like or irregular emergences ................ 14
13 Leaf divided into 3–5 pinnae; petiole covered with small spatulate emergences ...
  ........................................................................................................ 11
  – Leaf divided into 5–20 pinnae; petiole without obvious emergences but bristles .
14 Leaf large, 3–4-pinnate; rhizome fist-sized; petiole 0.5–1 m long .... \textit{H. decaryi}
  – Leaf short, 1–3-pinnate; rhizome smaller; petiole less than 0.1 m long........... 15
15 Leaf irregularly 1–2-pinnate; petiole and rachis covered with few distant emergences ....................................................... \textit{H. perrieri}
  – Leaf regularly 2–3-pinnate; petiole and rachis densely covered with emergences ...
  ........................................................................................................ \textit{H. fimbriata}

Acknowledgements

We would like to thank the University of Antananarivo and the Parc Botanique et Zoologique de Tsimbazaza for arranging the field expedition and thank Ministère de l’Environnement et du Développement Durable of Madagascar for issuing the research permit (31/17/MEEF/SG/DGF/DSAP/SCB.Re). This work was financially supported by grants from the National Natural Science Foundation of China (31970211) and Sino-Africa Joint Research Center, CAS (SAJC201614). We appreciate Shuai Peng and Cai-Fei Zhang for revising the manuscript and our guides and team members for the assistance in the fieldwork and also appreciate the constructive comments and suggestions from reviewers and editors.

References

Hydrostachys flabellifera


A phylogeny of species near Agrostis supporting the recognition of two new genera, Agrostula and Alpagrostis (Poaceae, Pooideae, Agrostidinae) from Europe

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Abstract
Based on a molecular DNA phylogeny of three plastid (rpl32-trnK, rps16 intron, and rps16-trnK) and nuclear ITS regions investigating 32 species of Agrostidinae, we describe two new genera, Agrostula gen. nov. with a single species and Alpagrostis gen. nov. with four species; provide support for five species in a monophyletic Podagrostis; and include a small sample of 12 species of a monophyletic Agrostis s.s. (including the type and most species of Neoschischkinia), that separates into two clades corresponding to A. subg. Agrostis and A. subg. Vilfa. Agrostula differs from Agrostis in having leaf blades with pillars of sclerenchyma which are continuous between the adaxial and abaxial surface of the blades, dorsally rounded glumes with blunt to truncate and erose to denticulate apices, florets ½ the length of the glumes, lemmas equally wide as long, widest at (or near) apex, apices broadly truncate, irregularly 5 to 7 denticulate to erose, awnless, anthers longer than the lemmas, and rugose-papillose caryopses. Alpagrostis differs from Agrostis in having geniculate basally inserted awns and truncate lemma apices with lateral veins prolonged from the apex in (2)4 setae. The following eight new combinations are made: Agrostula truncatula, Agrostula truncatula subsp. durieui, Alpagrostis alpina, Alpagrostis alpina var. flavescens, Alpagrostis barceloi, Alpagrostis setacea,
Alpagrostis setacea var. flava, and Alpagrostis schleicheri. In addition, we provide a key separating Agrostula and Alpagrostis from Agrostis s.s. and other genera previously considered as synonyms of Agrostis; lectotypify Agrostis alpina Scop., A. schleicheri Jord. & Verl., A. truncatula Parl., and A. truncatula var. durieui Henriq.; and neotypify A. setacea Curtis.

Keywords
Agrostis, Agrostula, Alpagrostis, classification, ITS, Neoschischkinia, plastid DNA sequences, phylogeny, Podagrostis, taxonomy

Introduction

The genus Agrostis L. includes ca. 224 species worldwide and is placed in subtribe Agrostidinae Fr., supersubtribe Agrostidodinae Soreng, tribe Poeae R.Br., and supertribe Poodae L. Liu in subfamily Pooideae Benth. (Soreng et al. 2017). The length of the palea was recognized by Trinius (1820, 1824) as an important character in separating species of Agrostis into two groups, those with short paleas in A. sect. Trichodium (Michx.) Trin. and those with longer paleas in A. sect. Vilfa (Adans.) Roem. & Schult. The term “Trichodium net”, based on observations of the Swedish scientist T. Vester-gren, to describe the lemma epidermis of Agrostis which bear a fine-meshed network when observed under high magnification, is found almost exclusively in those species with short paleas (Björkman 1960).

A detailed review of the infrageneric classification of the Agrostis was given by Björkman (1960) and later summarized in Widén (1971), Romero García et al. (1988a), and Saarela et al. (2017). In the former Soviet Union, Tzvelev (1976, 1983)
Phylogeny and taxonomy of Agrostula and Alpagrostis

recognized four sections in the genus: Agrostis sect. Agrostis (now = A. sect. Vilfa s.s. due to type conservation of Agrostis) containing species with long paleas 1/2–2/3 the length of an usually unawned lemma; A. sect. Pentatherum (Nabel.) Tzvelev with long paleas 2/3–1 the length of a dorsally awned lemma; A. sect. Aegraulus (P. Beauv.) Tzvelev with short paleas <1/3 the length of a dorsally awned lemma, and; A. sect. Trichodium (Michx.) Dumort. with paleas absent or short <1/6 the length of a usually unawned lemma. Romero García et al. (1988a, b) in the Iberian Peninsula divided Agrostis into two subgenera: A. subg. Zingrostis A.T. Romero García, G. Blanca López & C. Morales Torres containing species that have diffuse panicles with widely spreading, capillary and divaricate branches, and paleas 1/2–1 the length of an unawned lemma; and A. subg. Agrostis consisting of three sections, A. sect. Agrostis [= A. sect. Trichodium, A. sect. Aegraulus (P. Beauv.) Tzvelev] with paleas <1/3 the length of the lemma; A. sect. Vilfa with paleas 1/2–2/3 the length of a usually unawned lemma; and A. sect. Aperopsis Asch. & Graeb. [= Neoschischkinia Tzvelev] with paleas <1/6 the length of the awned or unawned lemma, and an annual lifecycle.

Podagrostis (Griseb.) Scribn. & Merr. was initially described as a section of Agrostis (Grisebach 1852) and was recently updated and revised by Sylvester et al. (2019a, b, 2020) to include ten species native to the western hemisphere. Five additional species of Agrostis were transferred into Podagrostis in Sylvester et al. (2020) of which P. bacillata (Hack.) Sylvester & Soreng and P. rosei (Scribn. & Merr.) Sylvester & Soreng are newly included in our molecular analysis using nuclear internal transcribed spacer (ITS) and three plastid DNA (rpl32-trnK, rps16 intron, and rps16-trnK) markers. Previously, P. thurberiana (Hitchc.) Hultén was included in a phylogenetic study based on morphology and three plastid regions, and the taxon was weakly supported as the sister group of a strongly supported Agrostis + Polypogon Desf. clade (Soreng et al. 2007). A limitation of that analysis was that only a single species was included for each of the three genera. No molecular study has included more than two species to test the monophyly of this putative lineage (Saarela et al. 2017). The salient characters separating Podagrostis from Agrostis are: a) floret usually equaling or subequaling the glumes, sometimes slightly shorter but reaching past ¾ the length of the glumes, b) palea well-developed, usually reaching from (2/3) ¾ to almost the apex of the lemma, c) presence of a glabrous or distally hairy rachilla extension emerging from under the base of the palea as a slender short stub up to 1.4 mm long (rudimentary in most florets of P. rosei), and d) lemmas unawned or with a short straight mucro 0.2–0.6 mm long, inserted medially or in the upper half of the lemma, not surpassing the glumes (awn 1.6–2 mm long, inserted in lower 1/3 of lemma, straight or geniculate and usually not surpassing glumes in P. rosei) [Sylvester et al. 2020].

Sáez and Rosselló (2000) described Agrostis barceloi L. Sáez & Rosselló from the northern mountains of Mallorca (Balearic Islands) placing it in the Agrostis alpina Scop. complex along with A. curtisi Kerguélen and A. schleicheri Jord. & Verl. These four species share the following synapomorphies: geniculate basally inserted awns and truncate lemma apices that bare lateral setae (extension of the lateral veins) [Romero
Other species of *Agrostis* with truncate lemma apices include: *A. nebulosa* Boiss. & Reut. [= *Neoschischkinia nebulosa* (Boiss. & Reut.) Tzvelev], *A. reuteri* Boiss., *A. truncatula* Parl. (these three placed in *A. subg. Zingrostis*), *A. pourretii* Willd. (placed in *A. sect. Aperopsis*), and *A. tenerrima* Trin. (placed in *A. sect. Agrostis*) [Romero García et al. 1988a, b].


The main goals of this study were to estimate the phylogenetic relationships of species near or sister to *Agrostis* based on ITS and three plastid DNA regions (*rpl32-trnK*, *rps16* intron, and *rps16-trnK*) for species of *Agrostidinae* and provide names for two clades that align near but not within *Agrostis* s.s. In addition, we provide a key separating *Agrostula*, gen. nov., and *Alpagrostis*, gen. nov., from *Agrostis* s.s. and other genera considered as synonyms of *Agrostis*. We propose lectotypes for *Agrostis alpina*, *A. schleicheri*, *A. truncatula* and *A. truncatula* var. *durieui* Henriq., and a neotype for *A. setacea*.

**Material and methods**

**Phylogenetic analyses**

Detailed methods for DNA extraction, amplification, and sequencing are given in Romaschenko et al. (2012) and Peterson et al. (2014, 2015a, b, 2016). We used Geneious Prime 2020 (Kearse et al. 2012) for contig assembly of bidirectional sequences of *rpl32-trnL*, *rps16* intron, *rps16-trnK*, and ITS regions, and Muscle (Edgar 2004) to align consensus sequences and adjust the final alignment. We identified models of molecular evolution for the cpDNA and nrDNA regions using jModeltest (Posada 2008) and applied maximum-likelihood (ML) and Bayesian searches to infer overall phylogeny. The combined data sets were partitioned in accordance with the number of markers used. Nucleotide substitution models selected by Akaike’s Information Criterion, as implemented in jModelTest v.0.1.1, were specified for each partition (Table 1). The ML analysis was conducted with GARLI 0.951 (Zwickl 2006). The ML bootstrap analysis used 1000 replicates with 10 random addition sequences per replicate. The tree file from the ML result was read into PAUP where the majority-rule consensus tree was constructed. Bayesian posterior probabilities (PP) were estimated using a parallel version of the MrBayes v3.2.7 (Huelsenbeck and Ronquist 2001; Ronquist and Huelsenbeck 2003) where the run of eight Markov chain Monte Carlo iterations was split between an equal number of processors. Bayesian analysis
was initiated with random starting trees and was initially run for four million generations, sampling once per 100 generations. The analysis was run until the value of the standard deviation of split sequences dropped below 0.01 and the potential scale reduction factor was close to or equal to 1.0. The fraction of the sampled values discarded as burn in was set at 0.25.

It is critically important to include the type species of genera and other higher taxa when doing molecular studies to know you are using the name correctly as intended by the original author. The following species are the types of their respective genera and are included in our analyses: *Agrostis canina* L. (type conserved), *Calamagrostis canescens* (Weber) Roth, *Chascolytrum subaristatum* (Lam.) Desv., *Gastridium ventricosum* (Gouan) Schinz & Thell., *Neoschischkinia elegans* (= *Agrostis tenerrima*), *Podagrostis aequivalvis* Trin., and *Triplachne nitens* (Guss.) Link.

Our study was designed to test relationships of three of the four species (*A. alpina*, *A. curtisii*, and *A. schleicheri*) of the *Agrostis alpina* group, all five species that have been attributed to *Neoschischkinia* (*N. elegans*, *N. nebulosa*, *N. pourretii*, *N. reuteri*, and *N. truncatula*), *Podagrostis*, *Gastridium* P. Beauv., *Triplachne* Link, and representative samples of *Agrostis*, *Calamagrostis* Adans., and *Chascolytrum* Desv. All of these genera have been found in a clade in previous molecular analyses and in our unpublished trees investigating a large number of species in *Agrostis*, *Calamagrostis*, *Cinnagrostis* Griseb., and *Koeleria* Pers. (Saarela et al. 2017; Barberá et al. 2019a, b; Peterson et al. 2019). Previous analyses of *Polypogon* found members of the genus nested in a grade within *Agrostis* and there was incongruence between the plastid and nuclear signals (Saarela et al. 2017; Romaschenko et al. unpubl.). We do not address this question here (i.e., *Polypogon* is not included in our sampling) since we lack a large sample of species within *Agrostis* and it is beyond the scope of our study. *Echinopogon caespitosus* C.E. Hubb. in subtribe Echinopogoninae Soreng was chosen as the outgroup since it lies outside of the Agrostidinae, but inside supersubtribe Agrostidodinae (Soreng et al. 2017; Tkach et al. 2020).

**Taxonomy**

Herbarium acronyms follow Index Herbariorum (Thiers, continuously updated). In this treatment glabrous means without pubescence (in the sense of slender, relatively soft hairs). Smooth indicates no prickle-hairs with broad bases and/or hooked or pointed apices (i.e., pubescence can occur on a smooth surface, and a rough or scabrous surface can be glabrous). Specimens in the United States National Herbarium (US) and the Real Jardín Botánico Herbarium (MA) were reviewed for this study, in addition to Romero Zarco (1987), Romero García et al. (1988a, b), Sáez and Rosselló (2000), Clayton et al. (2006), Cope and Gray (2009), and Portal (2009) were consulted during preparation of the descriptions. Beyond types (some only seen in images), only material from herbaria where specimens have been checked and verified by the authors are cited. Parts of the generic key were adapted from Sylvester et al. (2020).
Results

Phylogeny

A total of 176 new sequences from 33 species (48 individuals) are reported in GenBank (Table 1). Total aligned characters for individual regions and other parameters are noted in Table 2. The resulting plastid and ITS topologies were inspected for conflicting nodes (see Fig. 1) with ≥ 80% bootstrap support (BS) and/or posterior probabilities (PP) ≥ 0.95. No supported conflict was found so plastid and ITS sequences were combined.

The ML tree from the combined plastid and ITS regions (Fig. 1) is well resolved (posterior probabilities identified in the Bayesian analysis are included on the ML tree, and most clades include a PP = 1), with strong support (BS ≥ 96–100) for the following clades: two species of *Gastridium*, four accessions of *Triplachne nitens*, an *Agrostis* s.s. clade that includes two subclades A and B, three accessions of *Agrostis truncatula*, and the *Agrostis alpina–A. curtisi–A. schleicheri* clade; moderate support (BS = 84–86%) for seven species of *Calamagrostis* and two species of *Chascolytrum*; and weak support (BS = 57%) for five species of *Podagrostis*. *Chascolytrum* is basal followed by, in order of divergence, a clade with *Agrostis truncatula* sister to *Calamagrostis*, a clade with *Gastridium* sister to *Triplachne* which is sister to the remaining species in the *Agrostis* s.l. clade (PP = 1, BS = 66). In *Agrostis* s.l., *Podagrostis* is sister to the *Agrostis alpina–A. curtisi–A. schleicheri* clade and the *Agrostis* s.s. clade.

Discussion

Our molecular sampling of five species of *Podagrostis* is the largest to date. In an earlier Romaschenko et al. (unpubl.) study of the three species then in the genus, *P. humilis* (Vasey) Björkman exhibited incongruence with the nuclear ITS signal aligning within the *Podagrostis* clade and the plastid signal aligning as sister to *Agrostis* s.s. in a grade with the *Agrostis alpina–A. curtisi–A. schleicheri* clade at the base. The addition of *P. bacillata* and *P. rosei* in our analysis eliminated this anomaly. In an earlier study primarily using different DNA markers with only *P. aequivalvis* and *P. rosei* (as *Agrostis rosei* Scribn. & Merr.), Saarela et al. (2017) found *P. rosei* to be part of a well-supported clade with four Chinese species of *Deyeuxia* Clarion ex P. Beauv. and *Calamagrostis bolanderi* Thurb. + *P. aequivalvis*. Although *C. bolanderi*’s placement in a strongly supported lineage with *P. aequivalvis* provides support for its transfer to *Podagrostis*, we hesitate to include it here because it may represent a separate hybrid between *Podagrostis* and *Calamagrostis* (Sylvester et al. 2020). A robust phylogeny with the inclusion of *P. colombiana* Sylvester & Soreng, *P. excerta* (Swallen) Sylvester & Soreng, *P. liebmannii* (E. Fourn.) Sylvester & Soreng, and *P. trichodes* (Kunth) Sylvester & Soreng is needed, as well as the Asian species of *Deyeuxia* that are allied with the group and are in need of generic realignment.
**Table 1.** Taxon voucher (collector, number, and where the specimen is housed), country of origin, and GenBank accession for DNA sequences of *rps16-trnK, rps16 intron, rpl32-trnL, and ITS* regions; a dash (–) indicates missing data.

<table>
<thead>
<tr>
<th>Taxa</th>
<th>Voucher</th>
<th>Country</th>
<th><em>rps16-trnK</em></th>
<th><em>rps16 intron</em></th>
<th><em>rpl32-trnL</em></th>
<th>ITS</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. <em>Agrostis alpina</em> Scop. (= <em>Alpagrostis alpina</em> (Scop.) P.M. Peterson, Romasch., Soreng &amp; Sylvester)</td>
<td>Soreng 7484, Gillespie &amp; Peterson (US)</td>
<td>Austria, Niederösterreich</td>
<td>MT410018</td>
<td>–</td>
<td>MT409931</td>
<td>MT396529</td>
</tr>
<tr>
<td>3. <em>Agrostis balansae</em> (Boiss.) Tzvelev</td>
<td>Soreng 8967b &amp; Cabi (US)</td>
<td>Turkey, Erzurum</td>
<td>MT410020</td>
<td>MT409979</td>
<td>MT409933</td>
<td>MT396531</td>
</tr>
<tr>
<td>4. <em>Agrostis canina</em> L.</td>
<td>Herrero 1874, Aedo, Azpuru, Alarcón, Aldasoro, Castroviejo, Conti, Estebanez, Güemes, Guillén, Navarro, Pedro, Prunell, Rico, Rodríguez Gracia &amp; Tinti (MA)</td>
<td>Italy, Abruzzo</td>
<td>MT410021</td>
<td>MT409980</td>
<td>MT409934</td>
<td>MT396532</td>
</tr>
<tr>
<td>5. <em>Agrostis capitellaris</em> L.</td>
<td>Aedo 19209 (MA)</td>
<td>France, Landes</td>
<td>MT410022</td>
<td>MT409981</td>
<td>MT409935</td>
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<td>10. <em>Agrostis nebulosa</em> Boiss. &amp; Reut.</td>
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Phylogeny and taxonomy of *Agrostula* and *Alpagrostis*

Affinities of *Agrostis truncatula* are unclear, given the lack of support for its position (PP = 0.52) in the phylogeny sharing a common ancestor with *Calamagrostis* rather than aligning within *Agrostis* s.l. *Agrostis truncatula* has many unique morphological characteristics and differs from other species of *Agrostis* in having the combination of perennial habit, leaf blades with pillars of sclerenchyma that are continuous between the adaxial and abaxial surface of the blades, dorsally rounded glumes with blunt to truncate and erose to denticulate apices, open and diffuse panicles, florets ½ the length of the glumes, lemmas equally wide as long, widest at (or near) apex, apices broadly truncate, irregularly 5 to 7 denticulate to erose, awnless, anthers longer than the lemmas, and rugose-papillose caryopses. We, thus, describe *Agrostula* gen. nov. below based on the single species, *A. truncatula*, with two subspecies. We find no support for recognizing *Neoschischkinia* (Tzvelev 1968; Valdés and Scholz 2006), since four of the five species attributed to the genus align in the *Agrostis* s.s. clade: *A. nebulosa*, *A. reuteri*, and *A. tenerrima* (type of *Neoschischkinia*) in *Agrostis* subg. *Vilfa* (clade B), and *A. pourretii* in *A.* subg. *Agrostis* (clade A); whereas *A. truncatula* is phylogenetically isolated from *Agrostis* (*Agrostula*). All these species exhibit unusual characteristics not commonly found within *Agrostis*, i.e., diffuse, open panicles with divaricate and capillary branches, trapezoid lemmas with truncate apices, and caryopses with transverse furrows. However, without molecular DNA evidence, earlier systematists could not predict the complicated phylogenetic history of *Agrostula truncatula*.

Our rationale for recognizing the *Agrostis alpina* complex in a new genus, *Alpagrostis* gen. nov., is straightforward. Much like *Podagrostis*, there are salient morphological
Figure 1. Maximum-likelihood tree inferred from combined plastid (\textit{rpl32-trnL}, \textit{rps16} intron, \textit{rps16-trnK}) and ITS sequences. Numbers above the branches are posterior probabilities; numbers below the branches are bootstrap values; accessions marked with an asterisk* were formerly included in \textit{Neoschischkinia}; and letters refer to clade A = \textit{Agrostis} subg. \textit{Agrostis} and clade B = \textit{A.} subg. \textit{Vilfa}. Scale bar: 0.002 substitutions per site.
features, i.e., geniculate basally inserted awns and truncate lemma apices with setaceous lateral veins, and there is strong clade support as sister to Agrostis s.s. The branch length of the Alpagrostis clade is moderately long indicating genetic differentiation shared among its members separating it from other clades. Sáez and Rosselló (2000) suggested that Agrostis barceloi, a tetraploid (2n = 28), is closely related to A. schleicheri, a hexaploid (2n = 42), and might have originated by the splitting of the shared ancestral lineage. The morphological features shared by A. barceloi and A. schleicheri suggest they may be derived from the diploids, A. alpina (2n = 14) or A. curtisii (2n = 14) since the former two species are geographically and genetically isolated (Sáez and Rosselló 2000). Massó et al. (2016) surveyed 40 of the 100 known individuals of the extremely narrow endemic, A. barceloi, for allozyme diversity, showing all loci to be monomorphic or with fixed heterozygosity consistent with allopolyploid origin (interspecific hybridization process and subsequent chromosome duplication) [Stebbins 1947; Crawford 1989; Solts and Solts 2000].

The Agrostis s.s. clade is divided into two strongly supported A and B clades that correspond to species that align in the Agrostis subg. Agrostis (clade A) or Agrostis subg. Vilfa (Adans.) Rouy (clade B) [≡ A. sect. Vilfa (Adans.) Roem. & Schult.]. As mentioned in the introduction, palea length is an important character used to separate these two subgenera and all species in clade A have paleas ≤1/3 the length of the lemma as expected, sometimes rudimentary or absent as in e.g. A. mertensii Trin., A. subpatens Hitchc. However, not all species in clade B have paleas ½–2/3 the length of the lemma since A. tenerrima has paleas 1/6 the length of the lemma and only about 0.1 mm long. This is not terribly surprising since hybrids among species of Agrostis are often fertile, and inter-subgeneric hybrids include A. canina × A. stolonifera L., a cross between the type of each subgenus of Agrostis (Widén 1971; Belanger et al. 2003; Watrud et al. 2004). In the future we intend to publish a large phylogeny of Agrostis with a

Table 2. Characteristics of rps16-trnK, rps16 intron, rpl32-trnL, and ITS, and parameters used in Bayesian analyses indicated by Akaike Information Criterion (AIC).

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comprehensive species sampling. In this larger paper we will also address the hybrid origins that complicate species relationships in *Agrostis* s.s. with members of *Polypogon*, *Lachnagrostis* Trin., and *Chaetotropis* Kunth, genera that form a clade sister to or are reticulately intermeshed within *Agrostis* s.s. (Saarela et al. 2017; Soreng et al. 2017: 268).

**Taxonomic treatment**

*Agrostula* P.M. Peterson, Romasch., Soreng & Sylvester, gen. nov.
urn:lsid:ipni.org:names:77212587-1

**Type.** *Agrostis truncatula* Parl.

**Diagnosis.** The one species of *Agrostula* differs from all other species of *Agrostis* by its glumes being dorsally rounded, not keeled, smooth throughout, and with apices blunt to truncate and erose to denticulate. Further differentiation can be made by the combination of perennial habit, leaf blades with pillars of sclerenchyma that are continuous between the adaxial and abaxial surface of the blades, panicles open and diffuse, florets ½ the length of the glumes, lemmas equally wide as long, widest at (or near) apex, apices broadly truncate, irregularly 5 to 7 denticulate to erose, awnless, paleas c. ½ the length of the lemma, anthers longer than the lemma, caryopsis surface rugose-papillose, and its ecology, being found growing in very shallow soils.

**Description.** *Perennials* moderately to densely tufted. *Culms* 10–40 cm tall, erect, arching, or geniculate-ascendant, slender, smooth, usually with 3 or 4 nodes extended above the basal foliage. *Tillers* intravaginal, extravaginal innovations absent. *Leaves* mostly basal, in fascicles of few to many leaves; *sheaths* often as long as or sometimes longer than the internodes, glabrous, smooth; *ligules* 0.5–4 mm long, longer than they are wide in subsp. *truncatula* and shorter than they are wide in subsp. *durieui*, oblong, hyaline, glabrous, smooth, apices truncate to acute, dentate; basal and tiller ligules 0.5–2.5 × 1–2.5 mm; upper culm ligules 3–4 × 1–2.5 mm in subsp. *truncatula*; *blades* flat, conduplicate, or convolute, straight to sometimes recurved after flowering, acute, firm to rigid, glabrous, abaxially scabrous, adaxially scabrous; blades of lower culm and tillers 3–7 cm long, 0.7–2 mm in diameter as flat, folded or rolled; blades of upper culm 1–4 cm long, 0.5–1.2 mm in diameter as flat, folded or rolled. *Inflorescence* c. 2–20 × 2–12 cm, a panicle, diffuse and open, broadly ovoid; *panicle branches* divaricate, capillaceous, with spikelets present only in the distal 1/3–½, glabrous, smooth; *pedicels* generally twice as long as the spikelets or longer, thickened, apices clavate, glabrous, smooth. *Spikelets* 1–1.7 mm long, 1-flowered, disarticulating above the glumes, dorsally compressed or very weakly laterally compressed; *glumes* equal or subequal, ovoid-lanceolate, membranous, 1-veined, the vein inconspicuous, dorsally rounded, smooth throughout, apices truncate to blunt and minutely notched, erose to denticulate; *floret* c. ½ the length of the glumes, sessile; *lemmas* 0.5–0.8 mm long in subsp. *truncatula*
and (0.7–)0.9–1(–1.2) mm long in subsp. *durieui*, broadly ovoid, equally wide as long, widest at (or near) apex, membranous, dorsally rounded, 5-veined, veins usually evident to distinct, with at least the outer veins excurrent, usually glabrous or sometimes pubescent, smooth throughout, apex broadly truncate and denticulate, with the veins terminating in 5 to 7 teeth 1/8–1/5 the length of the lemma, awnless; *paleas* 0.3–0.5 mm long, c. ½ the length of the lemma, glabrous, smooth, apices bifid, denticulate; *calluses* rounded, blunt, glabrous or almost so, abaxially smooth; *rachilla* prolongation absent. *Flowers* perfect; *lodicules* 0.1–0.3 mm long, c. ½ as long as the palea, 2 in number, acute; *anthers* 0.7–1 mm long, 3 in number; *ovaries* glabrous. *Caryopses* 0.8–1.1 mm long, generally longer than the lemmas, only partially concealed at maturity, ellipsoid, surface rugose-papillose, ventrally sulcate, sulcus distinct, almost without rostellum; hilum narrowly elliptic c. 1/6–1/3 the length of the caryopsis; endosperm liquid. 2*n* = 14 + 0–4B (Garde 1951; Björkman 1960; Fernandes and Queiros 1969; Queiros 1974, 1979; Romero García and Blanca López 1988).

**Distribution and ecology.** Iberian Peninsula and northern Africa, distributed in France, Spain, Portugal, and Morocco. Found in Mediterranean, Iberian-Atlantic and cold temperate, often high-elevation, environments of the Pyrenees. Forms part of pioneer grassland species assemblages which grow on very shallow and sandy 'skeleton' soils, apparently reliant on climatic humidity in addition to precipitation for its water supply. Usually flowering from June to July.

**Notes.** *Agrostula truncatula* also differs in its leaf blade anatomy from most other species of *Agrostis* in having pillars of sclerenchyma which are continuous between the adaxial and abaxial surface of the blades. These continuous pillars of sclerenchyma are exceptionally thick and found only on the margins and central vein in subsp. *truncatula*, while subsp. *durieui* has thinner continuous sclerenchyma packets in the margins, central and primary veins (Romero García and Blanca López 1988: fig. 4C–F). Costal cells and intercostal long cells of the abaxial blade surface are also distinct, with *A. truncatula* differing from species of *Agrostis* in the Iberian Peninsula in having paired *s*₂-*z* cells in the costal zone, and *l*₁ type long cells in the intercostal zone (Romero García and Blanca López 1988). Stomata are also apparently absent on the abaxial blade surface, a character found in only a few other species in the Iberian Peninsula, i.e., *Agrostis reuteri* and *Alpagrostis setacea* (Romero García & Blanca López, 1988).

*Agrostula truncatula* (Parl.) P.M. Peterson, Romanch., Soreng & Sylvester, comb. nov. urn:lsid:ipni.org:names:77212590-1

Agrostula truncatula subsp. durieui (Boiss. & Reut. ex Willk.) P.M. Peterson, Romasch., Quintanar, Soreng & Sylvester, comb. nov.
urn:lsid:ipni.org:names:77212591-1


Notes. Romero García et al. (1988a) provide a key to differentiate the two subspecies. The typical subspecies has ligules as long or longer than wide with acute apices, conduplicate leaf blades that recurve at anthesis, and shorter lemmas 0.5–0.8 mm long whereas Agrostula truncatula subsp. durieui has ligules wider than long with truncate apices, flat, rarely conduplicate leaf blades that do not recurve at anthesis, and longer lemmas (0.7–)0.9–1(–1.2) mm long. Portal (2009) treated subsp. durieui as Agrostis durieui for France, and did not recognize A. truncatula as being in France.

Alpagrostis P.M. Peterson, Romasch., Soreng & Sylvester, gen. nov.
urn:lsid:ipni.org:names:77212592-1

Type. Agrostis alpina Scop.

Diagnosis. The species of Alpagrostis differ from Agrostis by a combination of characters in having plants densely tufted with only intravaginal innovations, leaves mainly basal, basal leaf blades involute and setaceous or filiform, conduplicate and acute,
Phylogeny and taxonomy of *Agrostula* and *Alpagrostis*

0.1–1.2 mm in diameter as folded or rolled, ligules longer than they are wide, spikelets generally > 3 mm long, lemma apices truncate with lateral veins prolonged from the apex in 2 (*A. setacea*) or 4 setae 0.1–0.5 mm long, and, crucially, and lemmas with a well-developed awn, 3–7.4 mm long, inserted basally c. 0.1–0.4 mm from the base of the lemma, conspicuously twisted and geniculate.

**Description.** **Perennials,** densely tufted. **Culms** 4–75 cm tall, erect or slightly geniculate at the base, slender, smooth or scabrous in the upper part, usually with 2–3 nodes extended above the basal foliage. **Tillers** intravaginal, extravaginal innovations absent. **Leaves** mostly basal, in fascicles of few to many leaves; **sheaths** shorter than the internodes, glabrous, smooth or scabrous; **ligules** 0.4–5 mm long, longer than they are wide, oblong, hyaline, glabrous, smooth, apices truncate, subacute, acute, entire to dentate; basal and tiller ligules 0.4–3 × 0.15–1.3 mm; upper culm ligules 1.7–5 × 0.7–1.5 mm; **blades** involute and setaceous or filiform and acute, tender to firm, straight to recurved, glabrous, abaxially smooth to scabrous, adaxially scabrous; blades of the lower culms and tillers 2–25 cm long, 0.1–1.2 mm in diameter as folded or rolled; blades of upper culm 1.5–10 cm long, 0.2–1.5 mm in diameter as folded or rolled, generally wider and shorter than tillers. **Inflorescence** (1.5–)2–15 × 0.5–3.5 cm, a panicle, lax and open to loosely to densely contracted and spikelike; **panicle branches** erect, ascendant or patent, with spikelets present from the base to only in the distal ½, glabrous, densely scabrous (or smooth in *A. barceloi*); **pedicels** as long as the spikelets, cylindrical, apices clavate, glabrous, densely scabrous (or smooth in *A. barceloi*). **Spikelets** (2.7 in *A. barceloi*–)3–5.2(–5.5) mm long, 1-flowered, disarticulating above the glumes, weakly laterally compressed; **glumes** unequal, the lower shorter and thinner than the upper, upper glume longer than the length of the floret by c. 0.8–1.9 mm, lanceolate, membranous, glabrous, keel scabrous throughout or in the distal ½, lateral veins smooth or scabrous distally, surfaces smooth or scabrous distally, apices acute or mucronate; lower glume 1-veined; upper glume (1-veined in *A. barceloi*) 3-veined; **floret** sessile, much shorter than the glumes; **lemmas** (1.8 in *A. barceloi*)–2–3.7, lanceolate, membranous, dorsally rounded, 5-veined, veins usually evident to distinct, with at least the outer veins excurrent, glabrous or thinly pubescent at the base with hairs up to 0.4 mm long, surface smooth to densely scabrous with aculeate (thin short stiff) prickles throughout, apex truncate with lateral veins prolonged from the apex in 2 (*A. setacea*) or 4 setae 0.1–0.5 mm long, awned with awn inserted basally c. 0.1–0.4 mm from the base of the lemma (or sometimes in the lower 1/5–1/4 in *A. barceloi*), awn well-developed, 3–7.4 mm long, surpassing the glumes, geniculate in roughly the middle, distinctly twisted proximally with usually at least 2 full twists below the bend, smooth proximally, scabrous distally or for most of the length; **paleas** 0.4–1 mm long, 1/5–1/3 the length of the lemma, glabrous, smooth, apices bifid, dentate, irregularly dentate or emarginate; **calluses** rounded, blunt, pilose, with hairs 0.3–0.7 mm long inserted all around or in 2 lateral tufts, abaxially smooth; **rachilla** prolongation absent. **Flowers** perfect; **lodicules** 0.4–0.6 mm long, ½–2/3 as long as the palea, 2 in number, acute to lanceolate; **anthers** 0.7–2.3 mm long, 3 in number; **ovaries** glabrous. **Caryopses** 1.7–2 mm long, shorter than the lemmas, concealed at maturity, ellipsoid or fusiform, surface smooth (becoming narrow and shriveled with age), ventrally sulcate, sulcus distinct, almost without rostellum; **hilum** 1/6–1/3 length of the caryopsis,
narrowly elliptic; **endosperm** liquid. \(2n = 14\) (In *A. setacea, A. alpina*), 28 (*A. barceloi*), or 42 (*A. schleicheri*) [Frey 1997; Sáez and Rosselló 2000].

**Distribution and ecology.** Europe and Mediterranean. Found in cold temperate, often high-elevation environments, often found growing on nutrient poor soils. Usually flowering from June to August.

**Notes.** All caryopses examined from herbarium specimens had a liquid lipid endosperm or were shriveled with a deep sulcus, implying that fresher specimens likely had a liquid endosperm. *Agrostis* sect. *Bromidium* (Nees & Meyen) E. Desv. shares many characteristics with *Alpagrostis*, such as lemma apices terminating in scabrous setae, well-developed, thickened, twisted and geniculate awns inserted in the lower 1/3 of the lemma, palea < 1/3 the length of the lemma, caryopses with liquid to semi-liquid endosperm. Based on molecular DNA studies, Romaschenko et al. (unpubl.) and Tkach et al. (2020) found *Bromidium* to align within *Agrostis* s.s.

*Alpagrostis barceloi* differs somewhat from the other species in the genus, in terms of the panicle branches and pedicels being smooth, spikelets sometimes being shorter, 1-veined upper glumes, and awn sometimes inserted slightly higher up the lemma.

*Alpagrostis alpina* (Scop.) P.M. Peterson, Romasch., Soreng & Sylvester, comb. nov. urn:lsid:ipni.org:names:77212593-1


*Alpagrostis alpina* var. *flavescens* (Honck.) P.M. Peterson, Romasch., Soreng & Sylvester, comb. nov. urn:lsid:ipni.org:names:77212596-1

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Alpagrostis barceloi (L. Sáez & Rosselló) P.M. Peterson, Romasch., Soreng & Sylvester, comb. nov.
urn:lsid:ipni.org:names:77212597-1


Figure 2. Alpagrostis alpina A, D spikelets B caryopsis C floret E floret, showing dorsal surface. Plant fragments taken from Sain-Lager 3 (US-1628154).
Notes. This species is included in *Alpagrostis* based on its similar morphology, although this needs to be confirmed in molecular analyses. Certain characteristics sometimes differ from the other species in the genus, i.e., spikelets and lemmas sometimes shorter, insertion of the awn sometimes higher on the lemma, panicle branches and pedicels smooth or scaberulous. *Alpagrostis barceloi* shares with other member of the genus, conduplicate leaf blades, truncate lemma apices with setaceous extensions of the lateral veins, and ecologically is a strict orophyte, much like *A. alpina* and *A. schleicheri* (Sáez and Rosselló 2000).

*Alpagrostis setacea* (Poir.) P.M. Peterson, Romasch., Soreng & Sylvester, comb. nov.
urn:lsid:ipni.org:names:77212601-1


Notes. Philipson (1937) mentions “No authentic specimens of Curtis have been preserved. There is one specimen in the British Museum Herbarium, originally from “Curtis’s garden” (BM-001144085), which may be taken as representative of the species.” Philipson was possibly referring to this specimen. On the neotype there are three different collections on the same sheet. The specimen on the upper left of the sheet is BM-001144085 (Fig. 2A).

*Alpagrostis setacea* var. *flava* (Des Moul.) P.M. Peterson, Romasch., Soreng & Sylvester, comb. nov.
urn:lsid:ipni.org:names:77212602-1

Figure 3. Neotype of *Agrostis setacea* Curtis [= *Alpagrostis setacea* (Poir.) P.M. Peterson, Romasch., Soreng & Sylvester] from Curtis’s garden (BM-001144085), upper left hand specimen indicated by A.
Alpagrostis schleicheri (Jord. & Verl.) P.M. Peterson, Romasch., Soreng & Sylvester, comb. nov.
urn:lsid:ipni.org:names:77212600-1


Notes. Jordon (1855) cited the following five collections: the Jura sur le Reculet (Ain), and Mont Ventoux, in August 1841, A. Jordan; Mt. St-Nizier near Grenoble, Verlot; Bex (canton of Vaud), E. Thomas; Mt. St-Nizier near Grenoble, Clement. Also cited is a report of Reuter of his collection from Jura sur le Reculet [P-03161256, image!], and Agrostis filiformis sensu Vill. We select The Verlot 1584 specimen as there are several duplicates, and P-03161255 as the lectotype because that sheet is not mounted with any other collection as the MPU and BM sheets seem to be.

Key to differentiate taxa of Agrostula and Alpagrostis from Agrostis and other genera previously considered as synonyms of Agrostis by Watson and Dallwitz (1992) and Clayton and Renvoize (1986)

1 Spikelets disarticulating below the glumes, the glumes, floret, and part of the pedicel falling together as a unit; glume apices lanceolate or lanceolate-subulate, muticous, mucronate or awned; palea < ½ the length of the lemma ....................
   ..........................................................................................
Pelepogon Desf.

– Spikelets disarticulating above the glumes, the glumes remaining on the inflorescence after the florets have fallen; glumes acute to acuminate, not awned; palea of varying length, absent or rudimentary to equaling the length of the lemma ....... 2

2 Rachilla extension present (cases where it is sometimes rudimentary key both ways), of varying lengths (sometimes very short, and requiring the base of the palea checked closely to distinguish the structure from hairs), glabrous or pilulose to densely pilose; palea well-developed, generally > 2/3 the length of the lemma ........................................................................... 3

– Rachilla extension absent; palea of varying length ........................................ 4
3 Lemmas densely pubescent, with rigid and abundant hairs; callus and rachilla notably hairy; lemmas with a well-developed usually geniculate and twisted awn, > 1 mm long, inserted in the lower or upper half of the lemma, clearly exceeding the glumes; taxa from southern Hemisphere (Australia, Malaysia, New Zealand, South Africa and South America) ...................................................... *Lachnagrostis* Trin.

- Lemmas glabrous; callus and rachilla glabrous or with short hairs emerging from only the rachilla apex and the basal side-ridges of the callus; lemmas unawned or with a short straight awn, usually < 0.5 mm long, inserted in the upper half of the lemma, not or barely exceeding the glumes (awn well-developed, 1.6–2 mm long, inserted in lower 1/3 of lemma, straight or geniculate and usually not surpassing glumes in *Podagrostis rosei* (Scribn. & Merr.) Sylvester & Soreng, but then callus and rachilla glabrous, rachilla very short, < 0.3 mm long, glabrous, plants from Mexico); taxa from North, Central and South America ..........*Podagrostis* (Griseb.) Scribn. & Merr. (in part)

4 Lemma apex terminating in 2 or 4 scabrous setae 0.1–2 mm long; lemma with a well-developed geniculate and twisted awn inserted basally or in the lower 1/3 and surpassing the glumes; paleas < 1/3 the length of the lemma; calluses pilulose or densely tufted; leaf blades often filiform or involute; lemma surfaces pilose (*Bromidium*) or usually glabrous (*Alpagrostis*); caryopses with liquid endosperm becoming narrow and shriveled with age.................................................. 5

- Lemma apex entire or finely dentate with short teeth at the end of each lateral vein; lemmas muticous, with a straight mucron 0.2–1 mm long, or with a long geniculate and twisted awn to 6+ mm long, inserted in the lower, middle or upper 1/3 of the lemma but usually not basally, not surpassing to greatly surpassing the glumes; lemma surface usually glabrous (sometimes pilose e.g. *Agrostis castellana* L.); calluses usually glabrous or with hairs restricted to lateral lines continuous with the basal lemma margins; leaf blades of various forms but less often filiform or involute; caryopsis usually rounded, with hardened endosperm, less often with liquid endosperm ............................................................................................. 6

5 Anthers 0.2–0.7 mm long; lemma surface often pilose; awn inserted in the lower 1/3 but usually not basally; longest setae of lemma apex 0.4–2 mm long; caryopsis thin or with liquid endosperm; leaf blades filiform or flat, generally 1–4 mm diam.; annuals from southern South America.................................................................

- Anthers 0.7–2.3 mm long; lemma surface usually glabrous or pilulose basally; longest setae of lemma apex 0.1–0.5 mm long; awn inserted basally; leaf blades filiform or involute, 0.1–1.5 mm diam. as folded or rolled; perennials of Europe and NW Africa ....... *Alpagrostis* P.M. Peterson, Romasch., Soreng & Sylvester

6 Floret equaling or subequaling the glumes, sometimes slightly shorter but reaching past ¾ the length of the glumes, usually with a short rachilla prolongation emerging behind the palea (sometimes absent in many florets of *P. rosei* and *P. humilis* so check many spikelets); paleas well-developed, usually reaching from (2/3) ¾ to almost
the apex of the lemma; lemmas muticous or with a short straight awn 0.2–0.6 mm long, inserted medially or in the upper half of the lemma, not surpassing the glumes (awn well-developed, 1.6–2 mm long, inserted in lower 1/3 of lemma, straight or geniculate and usually not surpassing glumes in *P. rosei*)

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*Podagrostis* (Griseb.) Scribn. & Merr. (in part)

Floret notably shorter than the glumes, usually 1/3–3/4 the length of the glumes, rarely longer, without a trace of a rachilla prolongation; paleas well-developed, poorly-developed, or absent, when well-developed reaching from ½–¾ the length of the lemma; lemmas muticous, with a short straight awn 0.2–1 mm long, or with a long geniculate and twisted awn to 6+ mm long, inserted basally, medi-

ally or in the upper half of the lemma, not surpassing to greatly surpassing the glumes ............................................................ 7

7 Glumes dorsally rounded, not keeled, smooth throughout, apices blunt to truncate and erose to denticulate; palea c. ½ the length of the lemma; panicles open and diffuse; lemmas equally wide as long, widest at (or near) apex, apices broadly truncate, irregularly 5 to 7 denticulate to erose, awnless; anthers longer than the lemma, caryopsis surface rugose-papillose; perennials; growing from very shallow soils; from the Iberian Peninsula and Northern Africa

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*Agrostula* P.M. Peterson, Romasch., Soreng & Sylvester

Glumes keeled, usually scabrous (at least in part), rarely upper glume smooth throughout, apices obtuse to acute-acuminate, rarely blunt to truncate, rounded to muticous; palea absent or rudimentary to ¾ the length of the lemma; panicles open and diffuse to condensed and spikelike; lemmas usually longer than wide (rarely equally wide as long), usually narrowed towards the apex, apices variable, ranging from somewhat broadly to usually narrowly truncate, usually with 2 to 5 dents (sometimes aristulate), to blunt and entire, awnless or with an awn 0.2–6+ mm long; anthers sometimes longer to usually shorter than the lemma; caryopsis surface usually smooth; perennials or annuals; usually growing from well-developed soils, less often from shallow soils, and generally reliant on soil moisture for their water supply; cosmopolitan

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