RESEARCH ARTICLE



Recircumscription and taxonomic revision of Siderasis, with comments on the systematics of subtribe Dichorisandrinae (Commelinaceae)

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Abstract

A new circumscription and a total of six microendemic species, four of them new to science, are herein presented for *Siderasis*, based on field and herbaria studies, and cultivated material. We provide an identification key to the species and a distribution map, description, comments, conservation assessment, and illustration for each species. Also, we present an emended key to the genera of subtribe Dichorisandrinae, and comments on the morphology and systematics of the subtribe.

Keywords

Atlantic Forest, Brazil, Commelinales, Neotropical flora, spiderwort, Tradescantieae

Introduction

Siderasis Raf. is currently applied to a small genus of neotropical Commelinaceae, comprising only two microendemic species, restricted to the Atlantic Forest of Southeastern Brazil (Pellegrini 2017). It was originally described by Rafinesque (1836), together with several other small genera, in order to better organize the many species misplaced in

Commelina L. and Tradescantia L. Rafinesque (1836) mentioned a possible affinity between Siderasis, Callisia Loefl. and Etheosanthes Raf. (= Belosynapsis Hassk.), and considered Siderasis not at all similar to Tradescantia; but gave no explanation for any of these statements. He also considered T. fuscata Lodd. a synonym of his newly described S. acaulis Raf., which was characterized by its rusty hirsute indumentum covering the entire plant, short stems, flowers emerging from the roots, petals basally connate, dimorphic stamens varying from four to six, and gynoecium 2-3-locular [sic]. After Rafinesque's publication, Siderasis was completely overlooked by all Commelinaceae specialists for the next 120 years (Moore 1956). In the meantime, Hasskarl (1869) described the new genus Pyrrheima Hassk. following his discussions with Schlechtendal during the Botany Meeting in Amsterdam in April of 1865. Hasskarl and Schlechtendal believed that Pyrrheima diverged greatly from Tradescantia and Tinantia Scheidw. due to its non-tubular perianth, six equal and fertile stamens, and lunate anther sacs, and thus merited distinct generic status. Clarke (1881), in his monograph for Commelinaceae, accepted Pyrrheima, including only P. loddigesii Hassk., and reducing P. minus Hassk. to a variety of it. Brückner (1930), noticing that P. loddigesii was an unnecessary replacement name for T. fuscata, made the new combination P. fuscata (Lodd.) G.Brückn., but was unsure if Siderasis and Pyrrheima were indeed congeneric. This was later confirmed by Moore (1956), when he merged the two by transferring *P. fuscata* to *Siderasis*.

After further period of neglect, the genus was placed in subtribe Dichorisandrinae (Faden and Hunt 1991), along with its sister-genus Dichorisandra J.C.Mikan, Cochliostema Lem., Geogenanthus Ule, and Plowmanianthus Faden & C.R.Hardy (Faden and Hunt 1991; Hardy 2001; Evans et al. 2003; Hardy and Faden 2004). However, resolution of the relationships within the group remains elusive. While it appears certain that Siderasis is proximally related to Dichorisandra, the subtribe as a whole has been recovered as paraphyletic in most molecular and morphological phylogenies to date. Two separate clades are recovered with one containing *Dichorisandra* and *Siderasis* (i.e. subtribe Dichorisandrinae s.s), while the remaining three genera (Geogenanthus and Cochliostema+Plowmanianthus) are recovered as one of the early-diverging clades in tribe Tradescantieae (Hardy 2001; Evans et al. 2003; Wade et al. 2006; Zuiderveen et al. 2011; Hertweck and Pires 2014; Pellegrini 2017; Pellegrini et al., in prep.). Siderasis has hitherto been characterized by the rusty to bright red hirsute indumentum covering the entire plant (except the petals and androecium), its ebracteolate cincinni, filaments three to four times longer than the anthers, anthers with rimose dehiscence (Hardy and Faden 2004), and exarillate seeds (Faden 1998).

Composition of the genus itself also remains unclear with Faden and Hunt (1991) mentioning two *Siderasis* species, while Faden (1998) mentions two to three species. Barreto (1997), in a survey of the Commelinaceae native to Brazil accepts only *S. fuscata* and reaffirmed *Siderasis* as a monospecific genus. Pellegrini (2017) recently described a new species of *Siderasis*, and provided important information regarding inflorescence and seed morphology in the genus. Clearly, further studies were still necessary to solve the ongoing issues (Pellegrini et al. 2013), and with this in mind recent field and herbaria studies have been undertaken to shed further light on this genus. In an

attempt to clarify the taxonomy and systematics of neotropical Commelinaceae, and as part of the authors' ongoing studies in subtribe Dichorisandrinae (Hardy and Faden 2004; Aona et al. 2012; Aona et al. 2016; Pellegrini and Almeida 2016; Pellegrini 2017), we recircumscribe and revise *Siderasis*, with the description of four new species. We also provide detailed comments on the morphology and systematics of subtribe Dichorisandrinae *s.l.*

Methods

The description of the species, phenology and illustrations were based on herbaria (A, ALCB, B, BHCB, BHZB, BM, BOTU, BRIT, C, CAL, CEPEC, CESJ, CGE, CNMT, CVRD, ESA, F, FCAB, FLOR, FURB, G, GUA, HAMAB, HAS, HB, HBR, HRB, HRCB, HSTM, HUEFS, HUFSJ, HURB, IAC, ICN, INPA, K, L, MBM, MBML, MG, MO, MY, NY, P, PMSP, PORT, R, RB, RFA, RFFP, SP, SPF, U, UEC, UPCB, US, and WAG; herbaria acronyms according to Thiers, continuously updated), spirit, fresh, and cultivated material. Specimens of Siderasis albofasciata M.Pell., S. almeidae M.Pell. & Faden sp. nov., and S. fuscata were kept in cultivation at the greenhouse of the Jardim Botânico do Rio de Janeiro, in order to observe, photograph, and analyze fresh flowers, fruits, and seeds as well as other phenological data. Fresh specimens, field notes, photographs, and specimens for cultivation were gathered during several field trips across the Brazilian Atlantic Forest, from the states of Sergipe to Rio Grande do Sul, between 2008–2016. Field data and description of S. medusoides M.Pell. & Faden sp. nov., and S. zorzanellii M.Pell. & Faden sp. nov. were complemented with notes, photographs and spirit samples kindly provided by the collectors. Fertile specimens were deposited in RB, and whenever possible duplicates were sent to US. Indumentum and shape terminology follows Radford et al. (1974); the inflorescence and general morphology terminology follows Weberling (1965, 1989) and Panigo et al. (2011); the fruit terminology follows Spjut (1994); and the seed terminology follows Faden (1991). The conservation assessments followed the recommendations of "IUCN Red List Categories and Criteria, Version 3.1" (IUCN 2001). GeoCAT (Bachman et al. 2011) was used for calculating the Extent of Occurrence (EOO) and the Area of Occurrence (AOO). The distribution of the species is based on herbaria materials, field data, and literature. The classification of vegetation patterns follows IBGE (2012).

Results

In the present study, we accept six species of *Siderasis*, with four of them newly described here. All species in the genus are microendemics, restricted to the Atlantic Forest of eastern Brazil. Both *Dichorisandra* and *Siderasis* share considerable variation in growth form, inflorescence architecture and androecium arrangement, which may have hindered the emergence of a stable taxonomy. Due to the variation and peculiar morphology of the newly described species, especially the two climbing species, *Siderasis* is recircumscribed below. The genus can be distinguished from the remaining Dichorisandrinae *s.l.* based on floral morphology, especially androecium and microstigmatic morphology. An updated identification key for the genera of Dichorisandrinae *s.l.* is presented, along with comments on the morphology of *Siderasis* compared to the remaining genera of the subtribe.

Emended key to the genera of Dichorisandrinae s.l. (modified from Hardy and Faden 2004)

Petals with glabrous margins, rarely ciliate with non-moniliform hairs; fila-1 ments glabrous, anther sacs not appressed to each other (if appressed, anther sacs not semicircular); capsules thick-walled; seeds arillate2 Petals with margins fringed with moniliform hairs; filaments bearded with moniliform hairs, rarely glabrous, anther sacs appressed to each other; cap-2. Stamens 5-6, staminodes sometimes present; anthers basifixed, anthers sacs parallel, elongate, 3 to 4 times longer than the filaments, connectives inconspicuous, dehiscence poricidal or introrsely rimose, but functionally poricidal; stigmatic papillae multicellular, completely concealing the stylar canal Dichorisandra J.C.Mikan (Fig. 1D-L) Stamens 6, staminodes absent; anthers dorsifixed, anther sacs divergent, semicircular, 3 to 4 times shorter than the filaments, connectives expanded, dehiscence extrorsely rimose; stigmatic papillae unicellular, restricted to margins of the stigma and leaving the stylar canal evident 3. Dracaenoid herbs; roots with terminal tubers; shoots determinate; inflorescences borne at the lower nodes below the leaves; pedicel with glandular hairs, stamens 5-6, all fertile, stigmas never fringed with moniliform hairs Rosette herbs; roots without terminal tubers; shoots indeterminate; inflorescences borne among the leaves; pedicels with eglandular hairs, fertile stamens 3, on the upper half of the flower, staminodes 3 (sometimes microscopic), on the lower half of the flower, stigmas commonly marginally fringed with moniliform hairs......4 Tank-forming or creeping rosettes, epiphytes, rarely terrestrial; inflorescence a 4. many-branched thyrse, with alternate or verticillate cincinni, cincinni bracts showy; fertile anthers spirally-coiled, hidden within a hood-like structure; testa smooth, sticky when hydrated...... Cochliostema Lem. (Fig. 1M) Rosettes not tank-forming, terrestrial; inflorescence reduced to a solitary pedunculate cincinnus, cincinnus bract inconspicuous; fertile anthers semicircular, not hidden within a hood-like structure; testa rugose to foveolate, farinose Plowmanianthus Faden & C.R.Hardy (Fig. 10)



Figure I. Floral morphology of subtribe Dichorisandrinae s.l. A-C Siderasis Raf. emend M.Pell. & Faden:
A S. fuscata (Lodd.) H.E.Moore B S. albofasciata M.Pell. C S. zorzanellii M.Pell. & Faden. D-L Dichorisandra J.C.Mikan: D D. acaulis Cogn. E D. hexandra (Aubl.) C.B.Clarke F D. thyrsiflora J.C.Mikan G D. paranaënsis D.Maia et al. H D. nana Aona & M.C.E.Amaral I D. incurva Mart. J D. penduliflora Kunth K D. sagittata Aona & M.C.E.Amaral L D. radicalis Nees & Mart. M Cochliostema odoratissimum Lem. N Geogenanthus rhizanthus (Ule) G.Brückn. O Plowmanianthus panamensis Faden & C.R.Hardy. Photographs A-B, D-G, J by M.O.O. Pellegrini, C by J.P.F. Zorzanelli, H by V. Bittrich, I by G.H. Shimizu, K by J.L. Costa-Lima, L by M.A.N. Coelho, M by R. Moran, N by D. Scherberich, and O by C.R. Hardy.

Siderasis Raf., Fl. Tellur. 3: 67. 1837, emend. M.Pell. & Faden

Pyrrheima Hassk., Flora 52: 366. 1869, nom. illeg. Type species (designated here). P. loddigesii Hassk., nom. illeg. [≡ S. fuscata (Lodd.) H.E.Moore].

Type species. *Siderasis acaulis* Raf. $[\equiv S. fuscata$ (Lodd.) H.E.Moore].

Description. Herbs or vines, perennial, with a definite base, terrestrial or rupicolous. Roots thin, fibrous, sometimes forming terminal, small, fusiform to oblongoid tubers. Rhizomes present or not, if present short, shallowly to deeply buried in the ground, rarely only covered by leaf litter. Subterraneous stems present or not, when present buried deep in the soil, unbranched, produced directly from the short rhizome; internodes moderately elongate to elongate. Aerial stems with determinate or indeterminate growth, elongated or short to inconspicuous, densely branched or unbranched, when densely branched primary shoot determinate or not, when present secondary shoots determinate; internodes inconspicuous to weakly elongate, or elongate; flagelliform-shoots (ramets) present or not, if present produced after the fertile period, forming a new rosette at the apex, axillary, unbranched, internodes elongate. *Leaves* spirally-alternate or distichously-alternate, congested at the apex of the stems forming a rosette or evenly distributed along the secondary branches, sessile to subpetiolate or petiolate, sheathing at the base, ptyxis involute; blades membranous to chartaceous or succulent, base symmetric or slightly to completely asymmetric, margins slightly revolute to flat, apex curved or straight. Synflorescence composed of a solitary main florescence or with 1–7 coflorescences. *Main florescence (inflorescence)* a thyrse, terminal or apparently so, rarely axillary, a many-branched, pedunculate thyrse, with alternate cincinni or reduced to a solitary pedunculate cincinnus; basal bract sessile or amplexicaulous or sheathing; cincinni bracts sessile or amplexicaulous; cincinni pedunculate, 1-many-flowered; bracteoles present or not. Flowers bisexual or staminate, actinomorphic or zygomorphic, chasmogamous, flat, pedicellate or sessile; pedicels erect during pre-anthesis and anthesis, erect or deflexed post-anthesis, generally elongating in fruit; sepals 3, unequal, free, membranous or fleshy, persistent and accrescent in fruit, the uppermost external, broader than the others, sometimes also shorter than the others; petals 3, deliquescent, free, margins entire to irregularly lacerated, glabrous, rarely ciliated with non-moniliform hairs, apex entire to irregularly lacerated, subequal, the lowermost either broader or longer than the others; stamens 6, equal or unequal, straight or curved upwards, filaments free, glabrous, straight or sigmoid, anthers dorsifixed, extrorsely rimose, anther sacs semicircular, divergent, pollen white, connectives expanded, quadrangular to rectangular; ovary sessile, globose to broadly oblongoid to ellipsoid in outline, trigonous with obtuse to round angles in cross-section, densely hirsute or lanate or velutine, 3-locular, locules equal, 3-6-ovulate, ovules hemianatropous, biseriate to partially uniseriate; style terminal, straight or curved upwards; stigma annular-truncate or annular-capitate, marginally papillate leaving the stylar canal evident, papillae unicellular. *Capsules* loculicidal, thick-walled, 3-valved, globose or subglobose to broadly ellipsoid to broadly oblongoid to oblongoid

in outline, trigonous with obtuse to round angles in cross-section, smooth to sparsely reticulate, apiculate due to persistent style base. *Seeds* (1-)3-6 per locule, arillate, obconic to ellipsoid, dorsiventrally compressed, ventrally slightly flattened or with a mild ridge, testa foveolate or rugose; hilum C-shaped, in a shallow depression; embryotega semidorsal or semilateral, relatively inconspicuous, without a prominent apicule; aril cream-colored to hyaline, slightly to completely translucent, thick or inconspicuous.

Etymology. *Siderasis* was named in allusion to the peculiar red to bright-red hairs that cover almost the entire plant, but especially the leaves. However, only *S. fuscata* possesses the aforementioned hairs, and all of the remaining species possess leaf blades covered by hyaline to light brown, rarely rusty hairs.

Habitat, distribution and ecology. *Siderasis* is endemic to the Atlantic Forest domain in coastal Brazil, occurring in the states of Bahia, Espírito Santo, and Rio de Janeiro (Fig. 2). More specifically, *Siderasis* is restricted to the Central Corridor of the Atlantic Forest, growing in remnants of semideciduous forests associated with inselbergs, between 90–1350 m above sea level. The genus is composed exclusively by microendemic species distributed in very small and fragmented subpopulations, susceptible to deforestation and illegal collection of specimens for ornamental purposes.

Biogeography. Since most phylogenies for Commelinaceae corroborate the paraphyly of Dichorisandrinae (Evans et al. 2000, 2003; Hardy 2001; Wade et al. 2006; Zuiderveen et al. 2011; Hertweck and Pires 2014; Pellegrini et al., in prep.), we can hypothesize on the independent diversification of these lineages from a biogeographical point of view. The clade composed by Cochliostema, Geogenanthus, and Plowmanianthus is consistently recovered as the second lineage to diverge in tribe Tradescantieae, following the diversion of subtribe Streptoliriinae (Evans et al. 2003; Wade et al. 2006; Zuiderveen et al. 2011; Hertweck and Pires 2014; Pellegrini et al., in prep.). The ancestor of this lineage probably originated in the Amazon Basin, and posteriorly diversified in the Guyana Shield, northern Andes, and Central America reaching Costa Rica (Hardy 2001; Hardy and Faden 2004). On the other hand, the clade composed by Dichorisandra and Siderasis is recovered as the third lineage to diverge in Tradescantieae (Evans et al. 2003; Wade et al. 2006; Zuiderveen et al. 2011; Hertweck and Pires 2014; Pellegrini et al., in prep.). The ancestor of this clade probably originated and diversified in the Atlantic Forest domain, since it is the center of diversity of both genera. Subsequently, the ancestors of various Dichorisandra lineages might have dispersed, more than once, diversifying in the Amazon Basin through gallery forests in the Cerrado domain.

Growth form and leaf morphology. *Siderasis* possesses two clearly differentiated growth patterns: (1) rosette herbs, generally with very short internodes, and spirally-alternate, symmetrical leaves (Fig. 3A–B); (2) climbing vines, with elongated internodes, and distichously-alternate, asymmetrical leaves (Fig. 3C–D). The rosette habit has hitherto been the only one recognized in the genus. Faden (1998) mentioned the existence of a climbing species in the genus, but due to the synoptic nature of that publication, no further remarks were made on the subject. The climbing habit is relatively uncommon in the family, but found in the closely related *Dichorisandra*. However, in *Dichorisandra* the plants tend to lean on nearby trees and shrubs, later producing



Figure 2. Distribution map of *Siderasis* Raf. *emend.* M.Pell. & Faden. Blue circles– *S. albofasciata*; Blue triangles– *S. almeidae*; Red circles– *S. fuscata*; Red triangles– *S. medusoides*; Blue square– *S. spectabilis*; Red Square– *S. zorzanellii*; BA– state of Bahia; ES– estate of Espírito Santo; RJ– estate of Rio de Janeiro.

pendant branches, or even growing completely intertwined with more robust shrubs (Fig. 3E–F). In *Siderasis*, the primary branch grows at the base of a tree (Fig. 3C), posteriorly spirally ascending around the trunk, and finally producing the flowering secondary branches (Fig. 3D). In the remaining genera of Dichorisandrinae, growth form is stable, with almost no variation within each genus. In *Cochliostema*, the plants tend to be tank-forming rosette herbs, but creeping individuals are also known in *C*.



Figure 3. Growth forms in Dichorisandrinae *s.s.* **A–D** *Siderasis* Raf. emend. M.Pell. & Faden: **A** rosette habit of *S. fuscata* (Lodd.) H.E.Moore **B** rosette habit with flagelliform-shoots of *S. albofasciata* M.Pell. **C** habit of an immature, still prostrate, individual of *S. zorzanellii* M.Pell. & Faden. **D** habit of a mature individual of *S. zorzanellii* spirally ascending a tree. **E–F** *Dichorisandra hexandra* (Aubl.) C.B.Clarke: **E** intertwined habit **F** decumbent stem apex, bearing flowers and fruits. Photographs **A–B, E–F** by M.O.O. Pellegrini, **C–D** by J.P.F. Zorzanelli.

velutinum Read (Hardy 2001). In *Geogenanthus*, the plants always possess a dracaenoid habit, with leaves congested at the apex (Hardy 2001). In *Plowmanianthus*, the plants are always rosette herbs with very short stems (Hardy and Faden 2004).

Considerable variation in leaf morphology occurs in *Siderasis*, with leaves ranging from: (1) sessile to subpetiolate (Fig. 3B–D); (2) truly petiolate, as in *S. fuscata* (Fig. 3A, 8C). Truly petiolate leaves are extremely rare in Commelinaceae, being recorded only in a handful of species restricted to the peculiar-looking subtribe Streptoliriinae, mostly comprised of vining plants (Pellegrini and Faden, pers. observ.). Phyllotaxy in *Siderasis* can range from distichous to spirally-alternate, the arrangement being correlated to symmetry of the leaf blades.

Inflorescence morphology. In all Dichorisandra and two species of Siderasis (i.e. S. spectabilis and S. zorzanellii), the main florescence is a many-branched, pedunculate, terminal or axillary thyrse with alternate cincinni, each cincinnus being multiflowered. In the remaining species of Siderasis (i.e. S. albofasciata, S. almeidae, S. fuscata and S. medusoides), the main florescence is composed of a thyrse reduced to a solitary cincinnus, as described in Pellegrini (2017; Fig. 4A). These reduced thyrsi are arranged into a synflorescence that may contain up to seven coflorescences. The center of the mature Siderasis rosette may contain several terminal or apparently terminal synflorescences. In Dichorisandra and the two climbing species of Siderasis, the main axis of the inflorescence is usually well developed, thus producing a typical looking thyrse (Fig. 4B). Nevertheless, the inflorescences may also be extremely reduced in some species (i.e. D. acaulis group), due to the shortening of the inflorescence's internodes (Pellegrini and Almeida 2016). The cincinni are also very short (i.e. sessile to subsessile), being enclosed by the leaf sheaths and not obvious at first glance (Pellegrini and Almeida 2016). The flowers are peculiarly long-pedicellate, giving the impression that all flowers emerge directly from the apex of the stems (Pellegrini and Almeida 2016; Fig. 4C). Despite the extreme reduction and superficial similarity, this inflorescence pattern differs from the one found in the rosette species of Siderasis, since it still is a many-branched thyrse. In Plowmanianthus the main florescence is also reduced to a solitary cincinnus. Nonetheless, coflorescences only develop after the main florescence has failed to develop or set fruit, and the cincinni from the primary and secondary thyrsi are morphologically distinct (Hardy and Faden 2004). In Geogenanthus the inflorescences are always born at the base of the plant, near the ground. Aside from that, the main florescence is a pedunculate, fascicle-like thyrse, with (1-)2-4-several alternate cincinni (Hardy 2001). Finally, in Cochliostema the main florescence is a many-branched, pedunculate, axillary thyrse, with alternate to verticillate cincinni, each cincinnus being multi-flowered and subtended by showy and cucullate spathaceous bracts (Hardy and Stevenson 2000; Hardy 2001).

Floral symmetry. Two distinct floral patterns can be observed in different species of *Siderasis*: (1) flowers are always bisexual, actinomorphic, having 6 equal stamens arranged cyclically around the ovary, with straight filaments (Fig. 1A–B); (2) flowers bisexual or staminate, zygomorphic, having 6 unequal stamens curved upwards, with sigmoid filaments (Fig. 1C). Furthermore, in the zygomorphic staminate flowers, the lower antepetalous stamen is longer, and is arranged and curved in the same way as the



Figure 4. Inflorescence architecture in Dichorisandrinae *s.s.* **A** diagram of the basic *Siderasis* Raf. emend M.Pell. & Faden inflorescence type, consisting of a thyrse reduced to a solitary cincinnus **B** diagram of the basic *Dichorisandra* inflorescence type (also characteristic of *S. spectabilis* and *S. zorzanellii*), consisting of a many-branched thyrse with alternate, many-flowered cincinni **C** diagram of the basic *D. acaulis* species group inflorescence type, where the main florescence axis and cincinni axis are greatly reduced, and the pedicels are peculiarly elongated. **P** = prophyll; **pB** = peduncle bract on main synflorescence axis; * = aborted or dormant apex of main inflorescence axis (usually not observed); **B** = cincinnus bract; **b** = bracteole; **f** = flower; **1°bud** = bud terminating cincinnus; **2°bud** = bud in axil of peduncle bract with potential to develop into a secondary thyrse (coflorescence); Modified from Pellegrini (2017).

style in bisexual flowers. The first flower morph is very similar to that found in the *D. acaulis* group (Pellegrini and Almeida 2016; Fig. 1D), while the second is equivalent to that of the *D. hexandra* and *D. incurva* groups (Fig. 1E, I). In *Dichorisandra*, flower symmetry is generally influenced by the positioning of the stamens, rather than by the relationship of stamens and staminodes. Actinomorphic flowers can be found not only in the *D. acaulis* group (Fig. 1D), but also in a group of still-undescribed species from the Guyana Shield (Faden and Pellegrini, pers. observ.). In all remaining species groups in *Dichorisandra*, the flowers are clearly zygomorphic, either due to the number of stamens, their size and/or position. In the *D. thyrsiflora* group, the androecium is generally composed of six fertile stamens, four of them curved towards the center of the flower, and the two lower lateral ones curved towards their opposing sides (Fig. 1F). An exception can be noticed in *D. paranaënsis* D.Maia et al. (Fig. 1G) and *D. nana* Aona & M.C.E.Amaral (Fig. 1H). In *D. paranaënsis* the stamens are curved upwards, varying from five fertile stamens with a staminode (present or not) to six fertile stamens, and introrsely rimose anthers. On the other hand, in *D. nana* the six fertile stamens are curved

upwards, and possess poricidal anthers. In the *D. incurva* (Fig. 1I), *D. penduliflora* (Fig. 1J), *D. leucophthalmos* (Fig. 1K), and *D. radicalis* groups (Fig. 1L), the androecium is composed of five stamens (generally with an upper staminode; notice the filiform staminode in Fig. 1L), rarely six fertile stamens, curved upwards, and with introrsely rimose anthers. In the *D. incurva* and *D. leucophthalmos* groups, the anthers are always yellow (Figs. 1I, K), while in the *D. penduliflora* and *D. radicalis* groups, the anthers are white, generally with the anther sacs partially to totally colored in blue, pink or purple (Figs. 1J, L). The remaining genera of Dichorisandrinae possess strongly zygomorphic flowers, especially due to the position and/or number of stamens: (1) 5–6 dimorphic, free and fertile stamens in *Geogenanthus* (Hardy 2001; Fig. 1N); (2) 3 stamens in the upper side of the flower, fused in a hood-like structure, and 3 lower staminodes (the middle one microscopic) in *Cochliostema* (Hardy 2001; Fig. 1M); (3) and 3 free to partially fused stamens in the upper side of the flower, and 7 lower staminodes (generally all of them microscopic) in *Plowmanianthus* (Hardy and Faden 2004; Fig. 1O).

Androecium and gynoecium morphology. The anthers in *Siderasis* are dorsifixed, with extrorsely rimose dehiscence, two times wider than long, three to four times shorter than the filaments, with semicircular, divergent anthers sacs, and expanded connectives (Fig. 1A–C). In *Dichorisandra* the anthers are basifixed, with poricidal or introrsely rimose (but functionally poricidal) dehiscence, three to four times longer than wide, and three to four times longer than the filaments, rarely equal to the filaments, with elongate, parallel anther sacs, and inconspicuous connectives (Aona 2008; Figs. 1D–L). In *Cochliostema, Geogenanthus* and *Plowmanianthus* the anthers vary from dorsifixed to basifixed, with extrorsely rimose dehiscence, as wide as long to two times shorter than the filaments, with semicircular to spirally-coiled, appressed anther sacs, and inconspicuous connectives (Hardy and Stevenson 2000; Hardy 2001; Hardy and Faden 2004; Figs. 1M–O).

The gynoecium is fairly homogeneous in Dichorisandrinae *s.l.*, with all genera having sessile, 3-locular ovaries, with all locules fertile, ovules hemianatropous, biseriate to partially uniseriate, style terminal, straight or bent at the apex, stigma annular-truncate to annular-capitate, peripherally ciliate with moniliform hairs (i.e. *Cochliostema* and *Plowmanianthus*) or not (i.e. *Dichorisandra*, *Geogenanthus* and *Siderasis*). In *Siderasis*, the stigmatic papillae are unicellular, and restricted to the margins of the stigma, leaving the stylar canal evident (Owens and Kimmins 1981). On the other hand, in *Dichorisandra*, the stigmatic papillae are multicellular, and evenly distributed on the stigma, completely concealing the stylar canal (Owens and Kimmins 1981).

Fruit and seed morphology. The capsules of *Dichorisandra* and *Siderasis* can be differentiated from capsules of other Commelinaceae by their thick and tough walls. In Commelinaceae the fruits are commonly (1–)2–3-locular, thin walled, septicidal capsules (Faden 1998). *Dichorisandra* and *Siderasis* possess 3-locular, 3-valvar capsules, and arillate seeds. The aril in *Dichorisandra* is generally opaque (rarely hyaline), usually thick (rarely inconspicuous), and colored from white to grayish or bright orange (rarely colorless) (Fig. 5A–B). Whereas the aril in *Siderasis* can be hyaline to slightly hyaline, inconspicuous or thick, and cream-colored to colorless (Fig. 5C–D).



Figure 5. Aril morphology in Dichorisandrinae s.s. A–B Dichorisandra J.C.Mikan: A D. thyrsiflora J.C.Mikan B D. hexandra (Aubl.) C.B.Clarke. C–D Siderasis Raf. emend. M.Pell. & Faden: C S. fuscata (Lodd.) H.E.Moore D S. albofasciata M.Pell. Photographs by M.O.O. Pellegrini.

The seeds in both genera are very similar in gross morphology, varying in shape from obconic to ellipsoid to quadrangular; in ornamentation from foveolate to scrobiculate to rugose, with a semilateral to semidorsal embryotega, and with a C-shaped hilum. In *Cochliostema, Geogenanthus* and *Plowmanianthus* the capsules are thinwalled, 3-locular, 3-valvar, and with exarillate seeds. In *Cochliostema* the capsules are narrowly cylindrical, and the seeds vary from subcylindrical to narrowly oblongoid, with a smooth testa that becomes sticky when hydrated, semidorsal embryotega, and a linear hilum with curved edges. In *Geogenanthus* and *Plowmanianthus* the capsules are fusiform to ellipsoid, the seeds range from reniform to ellipsoid, with rugose to foveolate, farinose testa, lateral embryotega, and a C-shaped hilum (Hardy 2001; Hardy and Faden 2004).

In *Dichorisandra* and *Siderasis* capsule and seed morphology differences may have great taxonomic potential. In *Dichorisandra*, many of the aforementioned species groups display characteristic capsule and seed morphology, as exemplified in the *D. acaulis* group by Pellegrini and Almeida (2016). In the *D. thyrsiflora* group, capsule morphology can easily differentiate most known species, based on shape, coloration, texture and pubescence (Pellegrini, pers. observ.). In *Siderasis*, capsule morphology shows a similar potential, with the fruits of *S. zorzanellii* being completely deviant in shape, texture and pubescence from the remaining species. Unfortunately, since the fruits of *S. spectabilis* are still unknown, it is impossible to know if this change in capsule morphology is correlated to the change in habit from rosette to vining herbs. *Siderasis fuscata* possesses unique seed morphology, being the only known species with an inconspicuous and hyaline aril, testa light gray to gray, and foveolate. Field expeditions focused on collecting fruit and seed samples of all species of *Siderasis* could be of great taxonomic value. It is possible that most, if not all, presently accepted species could be differentiated based exclusively on fruit and seed morphology.

Reproductive biology. Little is known regarding the floral biology of subtribe Dichorisandrinae, although this subtribe possesses the greatest range in inflorescence architecture and floral patterns in the family. In *Siderasis* the anthers are always extrorsely rimose, but apart from the floral specialization (i.e. zygomorphic, bisexual

or staminate flowers, and unequal and sigmoid stamens) in the two climbing species and the petals with margins ciliated with non-moniliform hairs, a character unique in the family, in S. spectabilis, the flowers are relatively unspecialized. Dichorisandra possesses a wide variation in flower morphology and androecium arrangement. Its flowers can range from actinomorphic to zygomorphic, the stamens can vary from (5-)6, sometimes with the upper stamen reduced to a staminode in some species. The filaments can be either straight, slightly sigmoid or slightly twisted depending on their position in the flower, while the anthers can be introrsely rimose and functionally poricidal or truly poricidal (Aona 2008; Fig. 1D-L). On the other hand, in Cochliostema, Geogenanthus and Plowmanianthus, the flowers are highly specialized, being zygomorphic (in all genera), scented (in *Cochliostema*), with a high frequency of cleistogamous flowers (in *Plowmanianthus*), petals and stigma fringed with moniliform hairs (fringed petals in all genera, stigma fringed exclusively in Cochliostema and Plowmanianthus), filaments bearded with moniliform hairs (in all genera), functionally poricidal androecium (in Cochliostema, due to the hood-like structure enclosing the anthers), and curved to spirally-coiled anthers (in all genera) (Hardy and Stevenson 2000; Hardy 2001; Hardy and Faden 2004; Fig. 1M-O). Only three species of *Dichorisandra* have had their reproductive biology investigated, presenting typical buzz-pollination, performed by bumblebees (Apidae) and/or sweatbees (Halictidae) (D. thyrsiflora, Boaventura and Matthes 1987; D. hexandra and D. incurva, Sigrist and Sazima 2015). Information regarding flower visitation in Cochliostema, Geogenanthus, and *Plowmanianthus* is completely lacking from the available literature. During our field studies and while observing the Siderasis specimens grown at the greenhouse of Jardim Botânico do Rio de Janeiro, the first author has observed flowers of S. albofasciata, S. almeidae, and S. fuscata being visited by stingless honey bees (Apidae, tribe Meliponini). Siderasis medusoides was not seen in the field, but high-resolution photographs sent by one of the collectors clearly show several small ants walking around the flowers and cincinni (Fig. 9C). The bees might either represent pollen robbers or potential pollinators, but the presence of the ants is hard to explain, since nectaries are unknown for Commelinaceae (Faden 1992, 1998). Further studies on the reproductive biology of Siderasis are clearly needed.

Aside from the peculiar floral diversity, Dichorisandrinae *s.l.* has two genera (out of five) and the majority of species in the family with arillate seeds (Pellegrini 2017). Nonetheless, no study has ever focused on vector-mediated (i.e. zoo-choric) seed dispersal in the family. In *Dichorisandra*, the seeds in the *D. hexandra* group are most certainly dispersed by birds (Faden 1992), due to the plants vining habit (Fig. 3E), which help in displaying the seeds, covered by an orange to bright orange, thick and opaque aril (Fig. 5B). The seeds in the *D. thyrsiflora* group are covered by a thick and opaque, white to cream-colored aril (Fig. 5A), and are generally easy to see in the field, due to the plants high stature (Pellegrini pers. observ.). Nonetheless, these species lack the characteristic colors that are generally associated with bird pollination/dispersal (i.e. pink, red, orange and yellow; Fleming and Estrada 1993), always present in the *D. hexandra* group. The species in the *D. acaulis* group possess seeds also covered by a thick and opaque,

white aril, lacking the visual attraction associated with bird dispersal, and also lack an elevated display, since they are always shorter than 1 m long (Pellegrini and Almeida 2016). These seeds might be dispersed by ants, or by small terrestrial vertebrates (e.g. small rodents), instead of being dispersed by birds, as hypothesized for other species of *Dichorisandra*. The seeds from the rosette species of *Siderasis* have similar morphological and ecological features to the species from the *D. acaulis* group. These species also have small stature and seeds with hyaline and inconspicuous, or cream-colored, slightly translucent, thick arils (Fig. 5C–D), being most probably dispersed by animals similar to the ones dispersing the seeds of the species in the *D. acaulis* group.

From a phylogenetic point of view, it seems that vector-mediated seed dispersal has evolved several times in the family: (1) arillate seeds are recorded for Dichorisandra and Siderasis in Dichorisandrinae, Amischotolype Hassk., Coleotrype C.B.Clarke and Porandra Hong in Coleotrypinae (Pellegrini 2017), and Spatholirion Ridl. in Streptoliriinae (Thitimetharoch 2004); (2) appendaged seeds are recorded for at least two separate lineages in tribe Commelineae (i.e. some species of Commelina L. and Murdannia Royle; Pellegrini et al. 2016); (3) truly fleshy fruits are known only from *Palisota* Rchb. ex Endl. (Faden 1998); (4) in Tradescantia zanonia (L.) Sw. the fleshy sepals cover the indehiscent fruit at post-anthesis, producing a sweet and atro-vinaceous berry-like fruit, dispersed by birds (Pellegrini, obs. pers.); (5) in Pollia Thunb. the fruits are dry, crustaceous and indehiscent, and due to their vibrant colors (metallic blue to shiny black) mimic real berries (Faden 1978); (6) in some Commelina (i.e. the species originally placed under Phaeosphaerion Hassk. and Commelinopsis Pichon) the fruits are morphologically similar to those of *Pollia*, being also crustaceous, but either dehiscent or indehiscent (Faden and Hunt 1987); (7) and sticky capsules covered by a mixture of hook and minute glandular hairs, in *Rhopalephora* Hassk. (Pellegrini et al., in prep.). Nonetheless, further investigations are needed to better understand the ecology and evolution of vector-mediated seed dispersal in Commelinaceae.

Key to the species of Siderasis

ciliate with non-moniliform hairs; northern montane Rio de Janeiro state Inflorescences axillary in older primary branches and/or terminal in the secondary branches; flowers 0.7-0.9 cm diameter, petals white, margins glabrous; southern montane Espírito Santo stateSiderasis zorzanellii M.Pell. & Faden (Fig. 1C, 3B-C & 12) 3. Leaves petiolate, indumentum bright red to red, hirsute on both sides; bracteoles absent; capsules ellipsoid to fusiform, greenish brown with 3 atro-vinaceous stripes; seeds grey to light grey, testa foveolate, aril hyaline and inconspicuous; coastal Rio de Janeiro state Leaves sessile to subpetiolate, indumentum rusty to light brown to hyaline, adaxially hispid, abaxially hispid to lanate; bracteoles present; capsules oblongoid to broadly oblongoid to subglobose, green; seeds medium to dark brown, testa rugose, aril cream-colored, slightly translucent and thick; Bahia 4. Rosettes forming flagelliform-shoots; leaves adaxially dark green with a thin white to silvery line along the midvein; flowers pedicellate, petals with white proximal third, anthers purple to bluish purple; capsules with elongated pedicels up to 7.2 mm long; central montane Espírito Santo state Rosettes not forming flagelliform-shoots; leaves adaxially uniformly green to dark green; flowers sessile, petals evenly colored, anthers white; capsules with elongated pedicels shorter than 2.2 mm long......5 5. Aerial stems with elongate internodes; leaves covered with light brown to rusty hairs, midvein shallowly canaliculate; cincinni compact, straight; sepals fleshy, internally lilac to purple, petals rhomboid to broadly obtrullate, ovary densely lanate; southern Bahia state Aerial stems with inconspicuous internodes; leaves covered with hyaline hairs, midvein deeply canaliculate; cincinni elongated, tangled; sepals membranous, internally light green, petals obovate to spatulate, ovary hispid; northern lowland Espírito Santo state...... Siderasis medusoides M.Pell. & Faden (Fig. 9)

1. *Siderasis albofasciata* **M.Pell., Nordic J. Bot. 35(1): 30. 2017.** Figs 1B, 2, 6

Type. BRAZIL. Espírito Santo: Santa Teresa, Alto do Julião, Fazenda Novo Triunfo, property of Mrs. Florinda, gallery forest with rocky formations, above the dam, fl., fr., 18 Apr 2013, M.O.O. Pellegrini et al. 337 (holotype: RB barcode RB00813532!; isotype: US!).

Description. *Herbs* ca. 10 cm tall, rhizomatous, terrestrial or rupicolous. *Roots* with terminal tubers present. *Rhizomes* buried deep in the ground. *Subterraneous*

stems with internodes moderately elongate, vinaceous, sparsely lanate, hairs light brown to hyaline. Aerial stems short to inconspicuous, unbranched; internodes inconspicuous to weakly elongate, vinaceous, lanate, hairs light brown to hyaline; flagelliform-shoots (ramets) present. Leaves spirally-alternate, forming a rosette at the apex of the aerial stems, sessile to subpetiolate; sheaths 0.7-1.3 cm long, vinaceous, with or without green spots, lanate, hairs light brown to rusty; subpetiole 1-2.7 cm long to inconspicuous, D-shaped in cross section, canaliculate, dark green to vinaceous, hispid, hairs light brown to hyaline; blade (4.5-4.8-)10-15.8 × (3.1-3.5-)4.4-7.2 cm, elliptic to obovate, rarely lanceolate, succulent, adaxially dark green, with a thin white stripe along the midvein, hispid, hairs light brown to hyaline, abaxially vinaceous to atro-vinaceous, lanate, hairs light brown, base slightly subcordate to cuneate, vinaceous, margins vinaceous, slightly revolute, apex acute, straight to curved downwards; midvein adaxially inconspicuous, slightly impressed, abaxially prominent, obtuse, secondary veins 3–5, inconspicuous in both faces, becoming more evident when dry. Synflorescence composed of a solitary main florescence with 1-2 coflorescences. Main florescence (inflorescence) reduced to a solitary pedunculate cincinnus, terminal or apparently so; basal bract $11.3-13.4 \times 4.8-7.8$ mm, triangular, slightly cymbiform, amplexicaulous, vinaceous, hispid, hairs rusty, opaque at the base and margins; inflorescence main axis 2.1-4.4 cm long, vinaceous, densely hispid, hairs rusty to brown; cincinni bract 3.3-6 × 2.2-4.6 mm, triangular, amplexicaulous, vinaceous, hispid, hairs rusty; cincinni (3–)5–8-flowered, peduncles 0.8–1.6 cm long, vinaceous, densely hispid, hairs rusty to brown, reflexed in fruit; bracteoles 2.9-4.4 × 2.8-3.2 mm, broadly ovate to depressed ovate, sessile, revolute, vinaceous to pinkish purple, sparsely hispid, hairs rusty, apex rounded to truncate. Flowers bisexual, actinomorphic, 2.3–2.8 cm diameter, pedicellate; pedicel 1–7.2 mm long, white to light green, hispid, hairs rusty, reflexed and slightly elongate in fruit; floral buds $0.7-1.6 \times 0.3-0.6$ cm, ellipsoid to narrowly obovoid, light green, apex obtuse; sepals $0.9-1.1 \times 0.4-0.7$ cm, narrowly ovate to elliptic, membranous, white to light green on both sides, externally sparsely hispid, hairs hyaline to rusty, rusty in fruit, internally glabrous, margin hyaline, apex obtuse, slightly purple; petals $1.3-1.6 \times 1-1.2$ cm, broadly ovate to broadly elliptic, bluish lilac to bluish purple, proximal third white, base cuneate, margin entire, apex obtuse to rounded, sometimes irregularly lacerated; stamens equal, filaments 5-7.1 mm long, straight, white, terminal third purple to bluish purple, anthers $1.5-2.2 \times 1.3-2$ mm, anther sacs purple to bluish purple, connectives quadrangular, purple; ovary $1.5-2 \times 1.5-2$ mm, globose, white, densely hispid, hairs hyaline, style 4.1–6.3 mm long, straight, white, terminal third purple to bluish purple; stigma annular-truncate, purple to bluish purple, papillate. Capsules $1-1.3 \times 0.7-0.9$ cm, subglobose to broadly oblongoid in outline, smooth, green, when mature light brown, hispid, hairs rusty. Seeds 3.3-5.2 × 2.4-2.9 mm, obconic to ellipsoid, medium to dark brown, testa rugose; hilum approximately 1/2 the length of the seed; embryotega semilateral; aril cream-colored, slightly translucent, thick.

Specimens seen. BRAZIL. Espírito Santo: Fundão, Alto Piaba, cultivado na casa de epífitas do MBML, fl., 13 Sep 1989, W. Boone 1349 (MBML); A.P.A. do Goiapaba-açú, Piabas, propriedade de Albino Casimiro, fl., 8 Nov 2007, A.P. Fontana & K.A.



Figure 6. *Siderasis albofasciata* M.Pell. **A** habit, showing the well-defined white stripe along the midvein of the leaves and the flagelliform-shoots with terminal rosettes **B** detail of the abaxial side of the leaf, showing the light-brown lanate indumentum **C** detail of the adaxial side of the leaf, showing the light-brown hispid indumentum **D** detail of the inflorescence, showing the solitary cincinnus **E** flower **F** detail of the androecium and the gynoecium **G** detail of the capsules, the left one immature with evident accrescent sepals and the right one mature **H** detail of an open capsule, showing the biseriate to partially uniseriate, arillate seeds **I** dorsal view of a seed, showing the semi-lateral embryotega and the cream-colored, slightly translucent and thick aril. Photograph **F** by L. Kollmann, remaining by M.O.O. Pellegrini.

Brahim 2827 (MBML, RB). Santa Teresa, Alto do Julião, propriedade de João Luiz Rodrigues de Souza, fl., 23 Feb 2007, A.P. Fontana & K.A. Brahim 2975 (MBML, RB); Cabeceira do 25 de Julho, Julião, fl., 10 Nov 2007, L. Kollmann et al. 11839 (MBML).

Etymology. The epithet means "white-striped", making reference to the thin and always present, white to silver stripe along the midvein of this species' leaves.

Distribution and habitat. *Siderasis albofasciata* is known exclusively from the municipalities of Santa Teresa and Fundão, state of Espírito Santo (Fig. 2). It occurs in the understory of evergreen forests, in shady areas with shallow and rocky soil, with great leaf-litter accumulation.

Phenology. It blooms from November to February. This species was collected in fruit in April, when mature and immature capsules were seen.

Conservation status. According to Pellegrini (2017), *S. albofasciata* should be considered as Critically Endangered [CR, B1ac(ii, iii, iv)+B2ab(ii, iii, iv)+C2a(i)].

Affinities. Siderasis albofasciata is similar to S. fuscata due to its leaves being of a different color along the midvein of the adaxial side, abaxially vinaceous, and inflorescences covered with rusty hairs. However, S. albofasciata can be readily differentiated by its sessile to subpetiolate leaves covered by hyaline to light brown indumentum (vs. petiolate leaves with bright red to red indumentum, in S. fuscata), a well-defined white stripe along the midvein on the adaxial side of the blade (vs. sometimes blotched silver to metallic light green), main axis of the synflorescence elongate (vs. inconspicuous), bracteoles present (vs. bracteoles absent), cincinni (3–)5–8-flowered [vs. 1-3(-4)-flowered], anthers purple, filaments and style apically purple (vs. androecium and gynoecium completely white), testa brown and rugose (vs. grey to light grey and foveolate), and aril cream-colored, thick and slightly hyaline (vs. aril colorless and inconspicuous). It is also similar to S. almeidae and S. medusoides due to the leaf blades adaxially hispid, abaxially lanate, and presence of bracteoles in the cincinni. Siderasis albofasciata can be easily differentiated from all the accepted species in the genus by the peculiar coloration pattern in its androecium and gynoecium.

Furthermore, *S. albofasciata* produces unique axillary flagelliform-shoots after its flowering period. Each flagelliform-shoot is homologous to a daughter ramet, consisting of an extremely elongate stem, that may or not develop leaf blades (sometimes the blades are very reduced or absent), and a terminal rosette that roots after it touches the soil. This clonal propagation strategy gives this species a chandelier appearance, similar to many epiphytic bromeliads. This clonal propagation strategy is unique within sub-tribe Dichorisandrinae (Pellegrini 2017).

2. Siderasis almeidae M.Pell. & Faden, sp. nov.

urn:lsid:ipni.org:names:77164153-1 Figs 2, 7

Diagnosis. Similar to *S. fuscata* due to its rusty indumentum in the leaves, lilac to purple rhomboid petals and white anthers. Also, similar to *S. albofasciata* due to its sessile to subpetiolate leaves, blades adaxially hispid and abaxially lanate, present bracteoles, and



Figure 7. *Siderasis almeidae* M.Pell. & Faden. **A** habit, showing a fertile rosette **B** detail of the elongated aerial stem, showing the rusty internodes and leaf-sheaths **C** detail of the lanate indumentum on the abaxial side of the leaf blade **D** detail of the hispid indumentum on the adaxial side of the leaf blade **E** detail of the inflorescence, showing the contracted cincinnus and some floral buds **F** front view of a flower, showing the fleshy and internally purple sepals, and the lanate ovary. Photographs **A**, **F** by M.A.N. Coelho, remaining photographs by M.O.O. Pellegrini.

purple filaments and style. Nevertheless, *Siderasis almeidae* is peculiar in lacking terminal tubers in the roots, subterraneous stems, and having aerial stems elongate and trailing in the leaf litter, leaves entirely green, fleshy showy sepals, and a densely lanate ovary.

Type. BRAZIL. Bahia: Itamarajú, Fazenda Pau Brasil, caminho para o Monte Pescoço, fl., 19 Nov 2015, M.O.O. Pellegrini & R.F. Almeida 493 (holotype: RB barcode RB01132619!; isotype: US!).

Description. Herbs ca. 20-45 cm tall, terrestrial. Roots thin, fibrous, terminal tubers absent. Rhizomes only covered by leaf litter. Subterraneous stems absent. Aerial stems trailing, only covered by leaf litter, unbranched to little branched, produced directly from the short rhizome; internodes elongate, green, sparsely lanate, becoming glabrous at age, hairs light brown to rusty; flagelliform-shoots (ramets) absent. Leaves spirally-alternate, forming a rosette at the apex of the stems, sessile to subpetiolate; sheaths 1.5-3.2 cm long, green, lanate, margin densely lanate, hairs light brown to rusty; subpetiole 0.8-4.6 cm long to inconspicuous, D-shaped in cross section, canaliculate, green, hispid, margin densely lanate, hairs light brown to rusty; blades 12.6-25.7 × 4-9.1 cm, succulent, elliptic or narrowly obovate to obovate, base cuneate, margins green, slightly revolute, densely lanate, apex acute, curved downwards, adaxially green to dark green, hispid, hairs light brown to rusty, abaxially light green, lanate, light brown to hairs rusty; midvein adaxially inconspicuous to conspicuous, slightly impressed, abaxially prominent, obtuse, secondary veins 6-8 pairs, adaxially conspicuous, slightly impressed, abaxially slightly prominent, becoming more evident adaxially when dry. Synflorescence composed of a solitary main florescence, or with 1-3(-5)coflorescences. Main florescence (inflorescence) reduced to a solitary pedunculate cincinnus; basal bract triangular, 2.4-4.6 × 1.1-2.2 cm, slightly cymbiform, amplexicaulous, green, hispid, hairs rusty, opaque at the base and margins; inflorescence main axis 2.2–8.6 mm long, green, densely hispid, hairs rusty; cincinni bract $1.1-3.6 \times 0.4-1.4$ cm, narrowly triangular, amplexicaulous, green, hispid, hairs rusty, apex acuminate; cincinni 5–11-flowered, peduncles 0.7–1.8 cm long, green, densely hispid, hairs rusty, reflexed in fruit; bracteoles 7.4–15.3 × 3.8–7.4 mm, broadly triangular, sessile, revolute, green at pre-anthesis, becoming purple at anthesis, hispid to densely hispid, hairs rusty, apex acuminate. *Flowers* bisexual, actinomorphic, 1.6–2.2 cm diameter, sessile; pedicel inconspicuous at anthesis, elongated in fruit, 0.8-2.2 mm long; floral buds 5.7-7.6 × 4.6–6.5 mm, broadly ellipsoid to broadly obovoid, green, apex obtuse to truncate; sepals $6.8-10.9 \times 2.3-5.9$ mm, ovate to broadly ovate, fleshy, externally green, densely hispid, hairs rusty, internally lilac to purple, glabrous, margins hyaline to hyaline lilac, apex acute; petals $8-18.2 \times 6.4-8.1$ mm, rhomboid to broadly obtrullate, purple to bluish purple, base cuneate, margin entire, rarely irregularly lacerated, apex obtuse to rounded; stamens equal, filaments 2.4-4.8 mm long, straight, lilac to purple, anthers $0.7-2.3 \times 0.7-1.9$ mm, anther sacs white, connectives quadrangular, white; ovary $1.8-2.9 \times 1.2-2.1$ mm, broadly oblongoid, white, densely lanate, hairs hyaline, style 3.6-4.8 mm long, straight, purple; stigma annular-truncate, purple, papillate. Capsules (immature) 5.7-6.8 × 5.9-7.2 mm, subglobose to broadly oblongoid in outline, smooth, green, when mature light brown, hispid, hairs rusty. Seeds unknown.

Specimens seen (paratypes). BRAZIL. Bahia: Itamarajú, ca. 2 km da Estrada BR-101 ao S de Itamarajú, fl., 5 Apr 1971, T.S. Santos 1559 (CEPEC, K); Fazenda Pau Brasil, ca. 5 km ao NW de Itamarajú, 17°1' S 39°33' W, fl., fr., 19 Sep 1978, S.A. Mori et al. 10730 (CEPEC, K, NY, RB, US); fl., 31 Oct 1979, L.A. Mattos Silva & H.S. Brito 692 (CEPEC, K, US). Prado, rod. BA-001, a 61 km ao N de Alcobaça, fl., 19 Mar 1978, S.A. Mori et al. 9739 (CEPEC, RB); km 21 of road from Itamarajú to Prado, forest on N side near logging operation, fl., 9 Feb 1993, J.A. Kallunki & J.R. Pirani 474 (NY, SPF).

Etymology. The epithet honors Brazilian botanist Rafael Felipe de Almeida, a prominent specialist in Malpighiaceae, contributor in the studies of Commelinaceae, husband of the first author, and co-collector of the holotype, for his unmeasurable support in the field and in my research.

Distribution and habitat. *Siderasis almeidae* is confined to the municipalities of Itamarajú and Prado, Bahia (Fig. 2). It occurs in the "mata higrófila" vegetation with emerging rocky formations, in shady and moist areas. In the type locality, the subpopulations were found growing in great accumulations of leaf litter, among dense clusters of Marantaceae. The area is greatly disturbed, and within private property.

Phenology. It was found in bloom from September to April, beginning to fruit in September, but mature fruits are unknown.

Conservation status. *Siderasis almeidae* has considerably narrow EOO (ca. 180.390 km²) and AOO (ca. 2800 km²). Most of the known collections were made in the type locality, in a small forest patch inside a private cattle farm. None of the known subpopulations is protected by a conservation unit, and the southern region of Bahia has few undisturbed areas of Atlantic Forest, being subjected to ongoing deforestation, cattle breeding, and several crops. The subpopulations of *S. almeidae* are small to medium-sized (with ca. 20 individuals), but mainly composed of clonal individuals. Thus, following the IUCN (2001) criteria, we suggest *S. almeidae* to be considered Critically Endangered [CR, A2abcd+B2ab(i, ii, iii, iv, v)+C1].

Affinities. Siderasis almeidae is similar to S. fuscata due to their rusty indumentum covering the leaf blades, inflorescences and sepals, lilac to purple petals, and white anthers. It is also similar to S. albofasciata due to its sessile to subpetiolate leaves, present bracteoles, and purple filaments and style. Furthermore, S. almeidae is similar to S. medusoides, due to their sessile flowers, purple filaments and style, and white anthers.

3. *Siderasis fuscata* (Lodd.) H.E.Moore, Baileya 4: 28. 1956. Figs 1A, 2, 8

Pyrrheima fuscatum (Lodd.) Backer, Handb. Fl. Java 3: 37. 1924.

Pyrrheima loddigesii var. *minus* (Hassk.) C.B.Clarke in Candolle & Candolle, Monogr. Phan. 3: 272. 1881.

Pyrrheima loddigesii Hassk., Flora 52: 367. 1869, nom. illeg.

Pyrrheima minus Hassk., Flora 52: 368. 1869. Holotype. BRAZIL. Rio de Janeiro. Rio de Janeiro, Corcovado, fl., s.dat., C. Gaudichaud 137 (P barcode P01799823!).

Tradescantia hirsutissima Pohl *ex* Seub., *in* Martius, Fl. bras. 3(1): 254. 1855, pro. syn. *Siderasis acaulis* Raf., Fl. Tellur. 3: 67. 1837, nom. illeg.

Tradescantia fuscata Lodd., Bot. Cab. 4: t. 374. 1820. Lectotype (designated by Pellegrini 2017). [illustration] Original parchment plate of "The Botanical Cabinet" at the British Museum Library and later published in Loddiges, Bot. Cab. 4: t. 374. 1820. Epitype (designated by Pellegrini 2017). BRAZIL. Rio de Janeiro. Rio de Janeiro, Floresta da Tijuca, FEEMA, Parque Nacional da Tijuca, fl., fr., 7 Nov 2012, M.O.O. Pellegrini 217 (RB barcode RB01093071!).

Description. Herbs ca. 20-30 cm tall, terrestrial. Roots thin, fibrous, terminal tubers present. Rhizomes buried deep in the ground. Subterraneous stems with internodes elongate, brownish vinaceous to vinaceous with white spots, hirsute, hairs reddish brown. Aerial stems short to inconspicuous, unbranched; internodes weakly to moderately elongate, vinaceous with white spots, hirsute, hairs reddish brown; flagelliformshoots (ramets) absent. *Leaves* spirally-alternate, forming a rosette at the apex of the aerial stems, petiolate; sheaths 1-1.5 cm long, hirsute, hairs dark red; petiole 2.7-9.6(-11.4) cm long, terete, canaliculate, C-shaped in cross section, succulent, green to dark green with dense vinaceous spots, spots sometimes covering almost all the petiole, hirsute, hairs red to dark red; blade $(4.8-5.6-)7.8-21.1(-23.6) \times (2-)3-9.6$ cm, succulent, elliptic to obovate to broadly obovate, rarely lanceolate, base cuneate, margins green, flat, densely hirsute, apex acute to obtuse or rounded, slightly curved downwards, adaxially dark green, with a silver to light green, blotched silver to metallic light green along the midvein or not, abaxially light green, with dense vinaceous spots or not; midvein conspicuous, adaxially impressed, abaxially prominent, obtuse, secondary veins 3–6 pairs, adaxially conspicuous, impressed, abaxially inconspicuous, becoming more evident on both sides when dry. Synflorescence composed of a solitary main florescence, or with (1-)2-6(-7) coflorescences. Main florescence (inflorescence) reduced to a solitary pedunculate cincinnus; basal bract $1.5-2.2 \times 0.3-1$ cm, triangular, cymbiform, dorsally keeled, light pink, hirsute, hairs rusty to dark red, hyaline at the base and margins, apex acuminate; inflorescence main axis inconspicuous; cincinni bract $0.8-2 \times 0.2-0.9$ cm, triangular, slightly cymbiform, amplexicaulous, pink to vinaceous, hirsute along the midvein, hairs red, base hyaline, margins light brown to golden, glabrous, hyaline, apex acuminate; cincinni 1-3(-4)-flowered, peduncle 1.3-7.4 cm long, light brown, hirsute, hairs red, reflexed in fruit, more rarely also spirallycoiled in fruit; bracteoles absent. *Flowers* bisexual, actinomorphic, 2–2.8 cm diameter, pedicellate; pedicel 1-5.6 mm long, light brown, hirsute, hairs red, reflexed and elongate in fruit; floral buds $0.8-1.2 \times 0.4-0.6$ cm, ovoid, light brown to light pink, apex acuminate; sepals $0.8-1.4 \times 0.3-0.8$ cm, ovate to triangular, membranous, externally light brown, hirsute, hairs red, internally pink to vinaceous, glabrous, margin hyaline, apex acuminate; petals $1.2-1.6 \times 1.2-1.5$ cm, rhomboid to broadly obtrullate, rarely orbicular, pale lilac to lilac, proximal third gradually white, base cuneate, margin en-



Figure 8. *Siderasis fuscata* (Lodd.) H.E.Moore. **A** habit, showing a mature rosette and green leaves **B** detail of leaf with a silvery blotch along the midvein **C** detail of the canaliculate petiole, showing the rusty hairs **D** detail of the bright-red hirsute indumentum **E** upper view of a fertile rosette, showing many lilac flowers open at the same time **F** front view of a pale-lilac flower, showing the lacerated petals and completely white androecium and gynoecium **G** detail of the androecium and the gynoecium **H** detail of a mature capsule, showing the atro-vinaceous longitudinal stripes **I** detail of an open capsule, showing the biseriate to partially uniseriate, inconspicuously arillate seeds, with grey foveolate testa. Photographs by M.O.O. Pellegrini.

tire, sometimes irregularly lacerated, glabrous, apex obtuse to rounded, sometimes irregularly lacerated; stamens equal, filaments 3.5-6.3 mm long, straight, white, anthers $1.5-2.1 \times 3-4.2$ mm, anther sacs white, connectives quadrangular, white; ovary glo-

bose, $2.9-3.7 \times 2.3-3.2$ mm, white, densely hirsute, hairs white at base, gradually becoming rusty, then dark red terminally, style 3.1-4.4 mm long, straight, white; stigma annular-truncate, white, papillate. **Capsules** ellipsoid to fusiform in outline, $1.1-1.6 \times 0.5-0.8$ cm, smooth, light greenish brown with minute purple spots near the base and 3 longitudinal atro-vinaceous stripes along the septa, when mature light brown with 3 longitudinal black stripes along the septa, hirsute, hairs red. **Seeds** obconic to ellipsoid, dorsoventrally compressed, ventrally slightly ridged, $2.9-4.4 \times 2.9-3.6$ mm, grey to light grey, testa foveolate, ventral face slightly cleft on the side towards the embryotega; hilum longer than $\frac{1}{2}$ the length of the seed; embryotega semilateral; aril hyaline, inconspicuous.

Specimens examined. BRAZIL. Rio de Janeiro: Niterói, Itaipu, P.E. Serra da Tiririca, Alto Mourão, fl., 15 Jan 1982, V.F. Ferreira et al. 2104 (RB); divisa entre os municípios de Niterói e Maricá, entre Itacoatiara e Itaipuaçu, Alto Mourão, fl., 11 Sep 2007, A.A.M. Barros & M. Pontes 3127 (RFFP). Rio de Janeiro, s.loc., fl., s.dat., Mr. Boag s.n. (K barcode K001190685); s.loc., fl., s.dat., Mrs. Graham s.n. (K barcode K001190684); s.loc., fl., 1816–1821, A. Saint-Hilaire A/683 (P); s.loc., fl., fr., 1832, Riedel s.n. (P barcodes P01730357, P01730358); Corcovado, fl., fr., 1831-1833, C. Gaudichaud 337 (P 3 ex); fl., Jul 1837, G. Gardner 847 (K barcode K001190683); Cova da Onça, fl., 15 Aug 1861, A.M. Glaziou 527 (NY, P); fl., 17 Aug 1869, A.M. Glaziou 4285 (P 2 ex); fl., Jul 1878, J. Miers 3534 (K, P); fl., fr., 5 Dec 1889, P. Schwacke 6699 (RB); fl., 5 May 1892, A. Ducke s.n. (RB 64); Tijuca, rio Trapicheiros (Fábrica da Cheetos), fl., Nov 1925, J.S. Kuhlmann s.n. (RB 19282, U barcode U1210766); fl., fr., 4 Mar 1943, A.P. Duarte & C.T. Rizzini 8 (RB); fl., 6 Nov 1944, P. Occhioni 50 (RB); Parque Natural da Tijuca, Matas do Pai Ricardo, fl., 29 Oct 1975, D.S. Araújo et al. 883 (GUA); fl., 30 Oct 2013, M.O.O. Pellegrini 404 (RB); fl., 15 Nov 2013, L.S.B. Calazans & R.T. Valadares 234 (RB); road to Vista Chinesa, next to the Biological Station, fl., 18 Aug 1960, C. Angeli 230 (GUA); Setor das Paineiras, next to Pedra do Beijo, fl., 15 Nov 1965, J.P.P. Carauta 286 (GUA); road to Vista Chinesa, fl., fr., 31 Oct 1969, J.P.P. Carauta 923 (GUA); Santa Cruz, fl., 6 Jul 1972, E. Lagasa s.n. (HB 71875); Pedra da Gávea, fl., 13 Jul 1966, D. Sucre 1304c (HB, RB); Alto da Boa Vista, Morro Queimado, next to the FEEMA building, fl., 26 Oct 2000, F. Pinheiro et al. 557 (HB); Estrada da Guanabara, Parque Lage, 25 Jan 1968, fl., D. Sucre 2161 (RB); Reserva Florestal do Jardim Botânico, fl., 19 Jan 1969, D. Sucre & P.J.J. Braga 4472 (RB); fl., 22 Dec 1971, D. Sucre 8152 (RB); Matas da Lagoinha, fl., 18 September 1946, P. Occhioni 692 (RB); fl., 6 Mar 1978, V.F. Ferreira et al. 256 (RB); fl., 11 Nov 1946, P. Occhioni 781 (RFA); brook trail between Paineiras and Jardim Botânico, fl., 4 Dec 1928, L.B. Smith s.n. (US barcode US1540545).

Specimens examined (cultivated). ENGLAND. Greater London: London, Royal Botanic Gardens, Kew, cultivated at the Nepenthes House, Kew, fl., 1908, s. leg. s.n. (K); fl., fr., Jun 1879, N.L. Brown s.n. (K); fl., 1967, Mason 458/61 (K); fl., 9 Jul 1974, Jodrell Laboratory s.n. (K 458-61-45801).

Etymology. The epithet "*fuscata*" means dark-colored, in allusion to the red to bright red hairs that cover almost the entire plant, in opposition to the normally hyaline hairs in most Commelinaceae. **Distribution and habitat.** *Siderasis fuscata* is endemic to the municipalities of Rio de Janeiro (with several localities inside Floresta da Tijuca) and Niterói (with just one locality, Alto Mourão), in the Rio de Janeiro state (Fig. 2). It occurs in the vegetation on hillsides (mata de encosta) near the littoral, in shady areas with shallow and rocky soil.

Phenology. It blooms from August to May and fruits from January to May, although fructification seems to be an uncommon event since few fruiting specimens were seen or collected.

Common name. "violeta-silvestre", "orelha-de-urso", "pelo-de-urso", "trapoerabapeluda", "brown spiderwort", "bear ears".

Conservation status. *Siderasis fuscata* is one of the few Commelinaceae included in the *Lista da Flora Brasileira Ameaçada de Extinção* (List of the Threatened Brazilian Flora; Fundação Biodiversitas 2009) and in the *Lista Oficial das Espécies da Flora Brasileira Ameaçadas de Extinção* (Official List of the Threatened Species of the Brazilian Flora; MMA 2008), at both lists classified as Data Deficient (DD). In the recently published Commelinaceae chapter of the *Livro Vermelho da Flora do Brasil* (Red Book of the Brazilian Flora; Aona-Pinheiro et al. 2013), *S. fuscata* is classified as Endangered (EN) by the authors, based on existing published data.

The subpopulation from Niterói is disjunct from the others in Rio de Janeiro, due to the urban area of both cities. It possesses a considerably small EOO (ca. 7000 km²), with the population being severely fragmented. Despite all the extant subpopulations being inside conservation units (i.e. Parque Nacional da Tijuca and Parque Estadual Serra da Tiririca), they are considerably small, composed mainly of clonal individuals, with no more than 30 mature individuals. Only a small number of fertile individuals can be found during the flowering season in each population, and very few fruits are produced. All these areas are extremely susceptible to real-estate development, deforestation, and have many invasive species, with areas like Parque Estadual Serra da Tiririca being especially affected by human-related forest fires. The subpopulations from Pedra da Gávea and Corcovado are probably extinct, or nearly so, since no recent collection in either areas is known by the authors. A total of 250 mature individuals is estimated for the overall population, based on our field observations. Added to the above factors, S. fuscata is appreciated as an ornamental plant all over the world due to its exotic foliage and beautiful flowers, so the few known extant subpopulations are also a target of illegal collection for exotic plant growers from all over the world. Thus, following the IUCN criteria (2001), we suggest S. fuscata be considered Critically Endangered [CR, A2abcde+B1ab(i,ii,iii,iv,v)+B2a(i, ii)+ C2a(i)+D2].

Affinities. Siderasis fuscata is similar to S. albofasciata in their variegated leaf blades, and similar to S. almeidae and S. medusoides in their white anthers. Nevertheless, it can be readily distinguished from all species of Siderasis by its petiolate leaves, red to bright red indumentum covering almost the entire plant (vs. sessile to subsessile leaves, light brown to hyaline indumentum), cincinni without bracteoles (vs. bracteoles present), acuminate flower buds and sepals (vs. obtuse to rounded), androecium and gynoecium completely white (vs. androecium and gynoecium partially bluish, lilac or purple), ovary and capsules hirsute (vs. velutine, hispid or lanate), seeds with light grey to grey and foveolate testa (vs. medium to dark brown and rugose or scrobiculate testa), and hyaline and inconspicuous aril (vs. aril cream-colored, slightly translucent and thick).

4. *Siderasis medusoides* **M.Pell. & Faden, sp. nov.** urn:lsid:ipni.org:names:77164154-1

Figs 2, 9

Diagnosis. Similar to *S. almeidae* due to its sessile to subpetiolate, entirely green leaves, present bracteoles, sessile flowers, purple filaments and style combined with white anthers, and oblongoid to broadly oblongoid capsules. *Siderasis medusoides* is distinct due to its membranous leaves, elongate and tangled cincinni, small flowers, and purple to dark blue and elliptic to narrowly obovate or spatulate petals.

Type. BRAZIL. Espírito Santo: Marilândia, perímetro urbano, na Estrada para São Pedro, fragment de floresta junto a uma serraria de madeira, a ca. 100 m do portão da serraria, em encosta de morro, 19°24'30.5"S 40°32'1.8"W, fl., fr., 20 Jan 2011, P. Fiaschi et al. 3489 (holotype: SPF barcode SPF200900!; isotype: MBML barcode MBML42135!).

Description. Herbs ca. 5-10 cm tall, rhizomatous, terrestrial. Roots with terminal tubers present. Rhizomes shallowly buried in the ground. Subterraneous stems short to inconspicuous, unbranched, dark green to vinaceous to brown, sparsely lanate, hairs light brown to hyaline. Aerial stems short to inconspicuous, unbranched; internodes inconspicuous to weakly elongate, green, lanate, hairs light brown to hyaline; flagelliform-shoots (ramets) absent. *Leaves* spirally-alternate, forming a rosette; sheaths 0.8–1.4 cm long, hispid, hairs hyaline to light brown; subpetiole 0.4–4.6 cm long to inconspicuous, D-shaped in cross section, canaliculate, dark green to vinaceous, hispid, hairs light brown to hyaline; blades 10-24.4 × 5.9-11.2 cm, elliptic to broadly elliptic, membranous, adaxially dark green, hispid, hairs light brown to hyaline, abaxially green to vinaceous, hispid to lanate, hairs light brown to hyaline, base cuneate, margins green, revolute, lanate, hairs light brown to hyaline, apex obtuse, rarely acute, straight; midvein conspicuous, adaxially impressed, abaxially prominent, acute, secondary veins 2-7 pairs, inconspicuous on both sides, becoming more conspicuous on both sides when dry. Synflorescence composed of a solitary main florescence, or with 1-15 coflorescences. Main florescence (inflorescence) reduced to a solitary pedunculate cincinnus; basal bract 7.6-10.4 × 4.6-6.2 cm, broadly elliptic to broadly ovate, slightly cymbiform, amplexicaulous, green, sparsely hispid, hairs rusty, opaque at the base and margins; inflorescence main axis 2.3-4.8 cm long, green, densely hispid, hairs rusty; cincinni bract ovate, amplexicaulous, 2.4-4.9 × 1.5-4 mm, green, hispid, hairs rusty, apex acute; cincinni (5–)8–26-flowered, peduncles 5.6–12.7 mm long, green, densely hispid, hairs rusty, reflexed in fruit; bracteoles $0.9-1.5 \times 0.8-1.3$ mm, broadly triangular, sessile, flat, green, hispid, hairs rusty, apex obtuse. *Flowers* bisexual, actinomorphic, 0.9–1.2 cm diameter, sessile; pedicel inconspicuous, elongate in fruit, 1–2.2 mm long, green, hispid, hairs light brown to rusty; floral buds $2.6-5.4 \times 2-3.7$ mm, broadly ellipsoid to broadly obovoid, light green, apex obtuse to truncate; sepals $3.7-6.7 \times$ 2.2-3.6 mm, elliptic to obovate, the uppermost external and broader than the others, membranous, externally light green to green, sparsely hispid, hairs light brown to rusty, internally light green, purple towards the apex, glabrous, margin hyaline, apex obtuse; petals $4.4-10.1 \times 1.9-6.7$ mm, elliptic to narrowly obovate to spatulate, the lowermost



Figure 9. *Siderasis medusoides* M.Pell. & Faden. **A** habit, showing a fertile rosette **B** detail of the synflorescence, showing the elongated and tangled cincinni **C** front view of a flower, showing small ants near the flower center **D** detail of the capsule. Photographs by P. Fiaschi.

usually broader than the others, bluish purple to dark blue, margin entire to irregularly lacerated, apex obtuse to round, irregularly lacerated; stamens 6, equal, filaments 2.6–3.4 mm long, bluish purple to dark purple, anthers $0.8-1 \times 1-1.3$ mm, anther sacs semicircular, divergent, white, connectives quadrangular, white; ovary broadly oblongoid, $1.2-1.9 \times 1-1.5$ mm, white, densely hispid, hairs white; style 1.3-4.7 mm long, straight, bluish purple to dark blue, lilac at the terminal end; stigma annular-truncate, lilac to white, papillate. *Capsules* $6.8-9.4 \times 6.7-7.8$ mm, oblongoid to broadly oblongoid, smooth, green, hispid, hairs rusty. *Seeds* $3.6-4.1 \times 2.6-3.2$ mm, obconic to ellipsoid, medium to dark brown, testa rugose; hilum longer than $\frac{1}{2}$ the length of the seed; embryotega semilateral; aril cream-colored, slightly translucent, thick.

Specimens seen (paratypes). BRAZIL. Espírito Santo: Marilândia, rodovia Marilândia-Rio Bananal, ca. 1 km N de Marilândia, remanescente de floresta junto a Cerâmica Floresta, fl., 6 Dec 1994, J.R. Pirani et al. 3421 (NY, SPF); Liberdade, propriedade de Deoclécio Lorenccini, 19°21' 7" S 40°30' 51" W, fl., fr., 22 Mar 2007, V. Demuner et al. 3429 (HERB, MBML); propriedade de Sônia e Reinaldo Bautz, 19°20' 8" S 40°32' 8" W, fl., 10 Dec 2007, V. Demuner et al. 4682 (MBML). Santa Leopoldina, Colina Verde (Morro do Agudo), propriedade de Israel Elias Ramos, trilha da casa, 20°6' 12" S 40°26' 34" W, fl fr., 13 Mar 2007, V. Demuner et al. 3118 (MBML).

Etymology. The epithet alludes to the extremely elongated cincinni, common in mature individuals of this species, due to their resemblance to the snakes that composed the hair of Medusa, one of the three Gorgon sisters from Greek mythology.

Distribution and habitat. *Siderasis medusoides* is known from the municipalities of Marilândia and Santa Leopoldina, in the state of Espírito Santo (Fig. 2). It grows in lowland Atlantic Forest, in shady and moist areas with great leaf litter accumulation, 90–550 m above the sea level.

Phenology. It blooms from December to March and fruits between January and March.

Conservation status. *Siderasis medusoides* possesses narrow EOO (ca. 11037 km²) and AOO (ca. 2000 km²), and based solely on distribution data should be treated as Endangered (EN). Nonetheless, it is known from only five collections in three different localities. They were made within urban areas, and these localities have suffered greatly with direct anthropic influence and deforestation in recent years. We have made several attempts to recollect *S. medusoides*, but they were all unsuccessful. Thus, we suggest that *S. medusoides* be considered Critically Endangered [CR, A2abcd+B2ab(i, ii, iii, iv)+C1+C2b+D2].

Affinities. Siderasis medusoides is similar to S. almeidae and S. albofasciata, due to their sessile to subpetiolate leaves, inflorescence with elongate main axis, bracteolate cincinni, sessile flowers, and purple filaments and style combined with white anthers. Nevertheless, it can be easily differentiated from S. almeidae by its inconspicuous sub-terraneous and aerial stems (vs. subterraneous stems absent and aerial stems elongate, in S. almeidae), membranous leaves appressed against the soil (vs. succulent and ascending), membranous and internally light green sepals (vs. fleshy and internally lilac to purple), narrowly obovate to spatulate petals (vs. rhomboid to broadly obtrullate), and hispid ovary (vs. lanate). It can be differentiated from S. albofasciata by lacking flagelliform-shoots (vs. flagelliform-shoots produced after the fertile period, in S. albofasciata), concolorous and membranous leaves (vs. adaxially variegated, abaxially vinaceous, succulent leaves), petals entirely purple to bluish purple). Siderasis medusoides is peculiar due to its membranous leaves appressed to the soil, tangled and elongate cincinni, small flowers, and narrow petals.

5. Siderasis spectabilis M.Pell. & Faden, sp. nov.

urn:lsid:ipni.org:names:77164155-1 Figs 2, 10, 11

Diagnosis. Very distinctive due to its vining habit, distichously-alternate leaves, blades asymmetric at base, main florescence a many-branched thyrse, with alternate cincinni, flowers zygomorphic, bisexual or staminate, stamens unequal, curved upwards, sigmoid filaments, and capsules globose and shallowly foveolate. It can be differentiated from *S. zorzanellii* by its membranous and velutine leaves, inflorescences always terminal in the secondary branches, petals dark mauve to vinaceous, rarely light pink or white, with margins ciliate with non-moniliform hairs.

Type. Brazil. Rio de Janeiro: Santa Maria Madalena, morro atrás do Horto Santos Lima (sede do Parque Estadual do Desengano), fl., 19 Jan 1957, L.E. Mello-Filho 1172 (holotype: R barcode R000103716!; isotypes: RB!, SPF!, US!).

Description. Vines ca. 0.5-3 m tall, terrestrial. Roots unknown. Rhizomes unknown. Subterraneous stems unknown. Aerial stems twining, primary stem indefinite, densely branched, internodes elongate, 2.2–6.5 cm long, green, minutely velutine on both sides, hairs hyaline to light brown; secondary branches definite, unbranched, ca. 17–25 cm long, internodes elongate, 1.1–2.3 cm long, green, minutely velutine on both sides, hairs hyaline to light brown. Leaves distichously-alternate, evenly distributed along the secondary branches, sessile; sheaths 0.7–2 cm long, green to vinaceous, minutely velutine, with a line of eglandular hairs opposite the leaf above, margins setose, hairs hyaline to light brown; subpetiole 1.1-3.3 mm long to inconspicuous, C-shaped in section, canaliculate, membranous, green to dark green, minutely velutine on both sides, hairs hyaline to light brown; blades $4.6-11.8 \times 1.6-2.5$ cm, linear elliptic or linear lanceolate or linear oblong, membranous, adaxially dark green to green, becoming dark brown when dry, abaxially light green to green, becoming greyish green to olive-green when dry, minutely velutine on both sides, hairs hyaline to light brown, base slightly asymmetric to asymmetric, cuneate to narrowly rounded, margins vinaceous, flat, minutely velutine, hairs hyaline to light brown, apex acuminate to caudate, straight; midvein conspicuous, impressed adaxially, prominent, obtuse abaxially, secondary veins (3-)4-5 pairs, slightly conspicuous on both sides, becoming more evident when dry. Synflorescence composed of a solitary main florescence. Main florescence (inflorescence) a pedunculate, many-branched thyrse, with alternate cincinni, terminal in the secondary branches; basal bract leaf-like, amplexicaulous to sheathing, sheaths 1.2-4.8 mm long, minutely velutine, margins of the sheaths densely setose, blades $3.9-6.7 \times 0.5-1.1$ cm, green to dark green, minutely velutine on both sides, base opaque, margins minutely velutine, apex acuminate to caudate, hairs hyaline to light brown; peduncle 1-1.3 cm long, green, minutely velutine, hairs hyaline to light brown; cincinni bract $3.2-10.6 \times 0.8-1.2$ mm, linear triangular, mauve to vinaceous, minutely velutine on both sides, base truncate, margin sparsely setose, apex acuminate to caudate, hairs hyaline to light brown; cincinni 14–17 per thyrse, 3-8-flowered, peduncles 1.4-7.2 mm long, light green to pink, minutely velutine,

hairs hyaline to light brown, erect in fruit; bracteoles $1.8-2.2 \times 0.8-1.2$ mm, ovate to broadly ovate, flat, cream-colored densely covered with vinaceous to pinkish purple spots to completely mauve to vinaceous, minutely velutine on both sides or only along the midvein, base rounded, margin hyaline, sparsely ciliate, apex hyaline, acute to obtuse, hairs hyaline to light brown. *Flowers* bisexual or staminate, zygomorphic, 1-1.3 cm diameter, pedicellate; pedicel 0.5–0.7 mm long, medium to dark mauve, sparsely minutely velutine, hairs hyaline to light brown, patent and slightly elongate in fruit; floral buds $3.5-4.4 \times 2.4-3.8$ mm, broadly ellipsoid to broadly obovoid, vinaceous to dark vinaceous, apex truncate; sepals $4.8-5.2 \times 2-2.6$ mm, narrowly ovate to elliptic, cymbiform, unequal, the uppermost external, broader and shorter than the others, fleshy, vinaceous to dark vinaceous, externally sparsely minutely velutine, hairs hyaline to light brown, internally glabrous, margin hyaline, glabrous to sparsely minutely velutine, hairs hyaline, apex obtuse, slightly purple; petals 5.1–6.3 × 2.8–3.6 mm, trullate to obovate, the lowermost narrower than the others, dark mauve to vinaceous, rarely light pink or white, base cuneate, margin entire, ciliate with dark mauve, eglandular, non-moniliform, uniseriate hairs, apex obtuse to rounded; stamens 6, unequal, the anterior longer than the posterior ones, curved upwards, filaments 1.8-4.6 mm long, sigmoid, white, terminal third dark mauve, anthers $1.2-1.4 \times 0.8-1$ mm, anther sacs dark mauve, connectives quadrangular in the shorter stamens and rectangular in the longer, dark mauve to purple; ovary 1.7-1.9 × 1-1.4 mm, ellipsoid to broadly ellipsoid, white, velutine, hairs hyaline, style 3.2-4 mm long, curved upward at the apex, white to pink, terminal third dark mauve; stigma annular-capitate, mauve to pink, papillate. *Capsules* and *Seeds* unknown.

Specimens seen (paratypes). BRAZIL. Rio de Janeiro: Santa Maria Madalena, morro atrás do Horto Santos Lima (sede do Parque Estadual do Desengano), fl., 19 Jan 1957, L.E. Mello-Filho 1162 (R, RB, US); fl., 19 Jan 1957, L.E. Mello-Filho 1171 (R, RB, US).

Etymology. The epithet means "admirable, remarkable, spectacular", in allusion to its distinctive growth form, small flowers with a peculiar coloration, and the unique petal margins ciliate with non-moniliform hairs.

Distribution and habitat. *Siderasis spectabilis* is confined to the type locality, in the native vegetation of the Horto Santos Lima (currently the headquarters of the Desengano State Park), in Santa Maria Madalena, state of Rio de Janeiro (Fig. 2). Nothing is known about this species habitat, since the original labels give no information on the area and all field expeditions to recollect this plant have been unsuccessful.

Phenology. Since all known collections were done on the same day, *S. spectabilis* is only known to bloom during January. Fruits and seeds are unknown for this species.

Conservation status. Due to the complete lack of information on the distribution, ecology and lack of any collections aside from the type specimens, according to the criteria proposed by IUCN (2001), *S. spectabilis* should be considered Data Deficient (DD), until new collections and data become available.

Affinities. *Siderasis spectabilis* is morphologically closely related to *S. zorzanellii*, but *S. spectabilis* can be easily differentiated due to its inflorescences being always ter-



Figure 10. Holotype of *Siderasis spectabilis* M.Pell. & Faden. Image courtesy of the Museu Nacional, Rio de Janeiro, Brazil.



Figure 11. Line drawings of *Siderasis spectabilis* M.Pell. & Faden. **A** bracteole **B** front view of a bisexual flower, showing the petals ciliate with non-moniliform hairs **C** detail of the petal margin, showing the non-moniliform hairs **D** lower stamen, showing the rectangular anther connective **E** upper stamen, showing the quadrangular anther connective **F** Detail of the gynoecium, showing the velutine ovary and bent style. Line drawings by M.O.O. Pellegrini.

minal in the secondary branches (vs. axillary in the primary branches or terminal in the secondary branches, in S. zorzanellii), and petals dark mauve to vinaceous, rarely light pink or white, and margins ciliate with non-moniliform hairs (vs. white and glabrous margins). All studied specimens were in excellent condition, and color of most organs could be easily described. Regarding color pattern in the androecium and gynoecium, S. spectabilis is similar to S. albofasciata. These are the only two species in the genus to present the upper third of filaments and style, and the anthers in the same color as the petals, contrasting greatly with the white base of filaments and style, and the white ovary of other species. Nevertheless, both species can be easily differentiated using vegetative or reproductive characters. One specimen (L.E. Mello-Filho 1171) is peculiar in being the only specimen with light-colored flowers. In the label, it is described by the collector as possessing white flowers. Nonetheless, while analyzing the duplicates available at R, RB, SPF and US, we noticed that a few flowers possessed pale pink pigment (particularly noticeable in the petals and stamens). We believe that these specimens might represent albino or semialbino individuals, and thus merit no taxonomic status, especially since they were collected at the same place and date as the remaining darkflowered specimens.

Aona (2008), in her unpublished Ph.D. thesis, lists one of the paratypes of *S. spect-abilis* under *Dichorisandra incurva* Mart. This is justified by her due to the specimens climbing habit, decumbent apical branches, distichously-alternate and sessile leaves, inflorescence composed of a pedunculate, many-branched thyrse, with alternate cincinni, and "white" [sic] flowers. Nevertheless, *S. spectabilis* can be easily differentiated by its erect inflorescences (*vs.* pendant to curved downwards, hence the name, in *D. incurva*),

flower buds broadly ellipsoid to broadly obovoid, with truncate apex (*vs.* ellipsoid, with acute apex), sepals fleshy (*vs.* membranous), petals dark mauve to vinaceous, rarely light pink or white, with margins ciliate with non-moniliform hairs (*vs.* white with glabrous margins), stamens 6, anthers dorsifixed, 3 to 4 times shorter than the filaments, dehiscent by extrorse slits, and anther sacs divergent, semicircular, and expanded connectives (*vs.* stamens 6 or 5 + the upper one modified into a staminode, anthers basifixed, 3 to 4 times longer than the filaments, dehiscent by introrse slits, but functionally poricidal, anthers sacs parallel, elongate, and inconspicuous connectives). All these floral characters can be easily observed with the dissection of mature flower buds in herbarium specimens. The floral morphology of *D. incurva* is illustrated in Fig. 1I.

6. Siderasis zorzanellii M.Pell. & Faden, sp. nov.

urn:lsid:ipni.org:names:77164156-1 Figs 1A, 2, 3B–C, 12

Diagnosis. Similar to *S. spectabilis* due to its vining habit, distichously-alternate leaves, blades asymmetric at base, main florescence a many-branched thyrse, with alternate cincinni, flowers bisexual or staminate, zygomorphic, stamens unequal, curved upwards and sigmoid filaments. It can be differentiated from by its chartaceous and sparsely velutine leaves, inflorescences axillary in the primary branches or terminal in the secondary branches, and petals white with glabrous margins.

Type. Brazil. Espírito Santo: Iúna, Serra do Valentim, ao lado do transecto 1, 20.4989°S, 41.4725°W, fl., 27 Mar 2014, J.P.F. Zorzanelli 969 (holotype: RB!; isotype: VIES!).

Description. Vines ca. 0.5-3 m tall, terrestrial. Roots thin, fibrous, terminal tubers present, fusiform. Rhizomes buried deep in the ground. Subterraneous stems inconspicuous. Aerial stems twining, primary stem indefinite, densely branched, internodes elongate, 4.3–10.6 cm long, green, minutely velutine on both sides, hairs hyaline to light brown; secondary branches definite, unbranched, (6.4-8-)15-34 cm long, internodes elongate, 2–2.3 cm long, green, minutely velutine on both sides, hairs hyaline to light brown. Leaves distichously-alternate, evenly distributed along the secondary branches, sessile; sheaths 2-2.7 cm long, green to brown, minutely velutine, with a line of eglandular hairs opposite the leaf above, margins setose to densely setose, hairs hyaline to light brown; subpetiole 2.9–3.5 mm long to inconspicuous, C-shaped in section, canaliculate, membranous, green to dark green, minutely velutine on both sides, hairs hyaline to light brown; blades 5.1–12.7 × 1.1–2.8 cm, linear elliptic to linear lanceolate, chartaceous, adaxially dark green to green, becoming dark brown when dry, abaxially light green to green, becoming greyish green to olive-green when dry, sparsely minutely velutine on both sides, hairs hyaline to light brown, base slightly asymmetric to asymmetric, cuneate to narrowly rounded, margins green to vinaceous, flat, glabrous, apex acuminate to caudate, straight; midvein conspicuous, impressed adaxially, prominent, obtuse abaxially, secondary veins 2-3 pairs, inconspicuous on both sides, becoming more evident when

dry. Synflorescence composed of a solitary main florescence. Main florescence (inflorescence) a pedunculate, many-branched thyrse, with alternate cincinni, axillary in the primary branches or terminal in the secondary branches; basal bract reduced, rarely leaflike, sessile, $1.7-2 \times 0.2-0.4$ cm, green, minutely velutine on both sides, base opaque, margins minutely velutine, apex caudate, hairs hyaline; peduncle 0.9-1.2 cm long, light green to green, minutely velutine hairs hyaline; cincinni bract linear triangular, 3-15.3 × 1.4–1.8 mm, green to brown, minutely velutine on both sides, base truncate, margin velutine, setose only at base, apex acuminate to caudate, hairs hyaline; cincinni 14-19 per thyrse, (1–)2–5-flowered, peduncles 1.2–5.3 mm long, white to pink, minutely velutine, hairs hyaline, erect in fruit; bracteoles ovate to broadly ovate, flat, $1-1.7 \times 0.8-1.3$ mm, vinaceous to brown, minutely velutine, base rounded, margin hyaline, ciliate, apex hyaline, acute to obtuse, hairs hyaline. *Flowers* bisexual or staminate, zygomorphic, 0.7-0.9 cm diameter, pedicellate; pedicel 1.2-2.8 mm long, white, minutely velutine, hairs hyaline, patent and slightly elongate in fruit; floral buds 3.6–4.9 × 2.2–4.1 mm, broadly obovoid to subglobose, white, apex truncate to rounded, green; sepals $3.6-4 \times 1.5-2.1$ mm, narrowly ovate to elliptic, cymbiform, unequal, the uppermost external, broader and shorter than the others, fleshy, white, externally minutely velutine, hairs hyaline, internally glabrous, margin hyaline, glabrous to sparsely velutine, hairs hyaline, apex obtuse, green; petals $3.7-4.5 \times 2.7-3.4$ mm, trullate to obovate, the lowermost narrower than the others, white, base cuneate, margin entire, glabrous, apex obtuse to rounded; stamens 6, unequal, the anterior longer than the posterior, curved upwards, filaments 1.3–4.2 mm long, sigmoid, white, anthers $0.7-0.9 \times 0.7-1$ mm, anther sacs white, connectives quadrangular in the shorter stamens and rectangular in the longer, white; ovary $1.5-1.7 \times 1.1-1.2$ mm, ellipsoid, white, velutine, hairs hyaline, style 2.7-3.2 mm long, curved upward at the apex, white; stigma annular-capitate, papillate, white. Capsules $0.9-1.3 \times 0.8-1.2$ cm, subglobose to globose, green, sparsely reticulate, sparsely velutine, hairs hyaline. Seeds $3.6-3.9 \times 2.9-3.2$ mm, obconic to ellipsoid, medium to dark brown, testa scrobiculate; hilum longer than 1/2 the length of the seed; embryotega semidorsal; aril cream-colored, slightly translucent, thick.

Specimens seen (paratypes). BRAZIL. Espírito Santo: Iúna, Serra do Valentim, trilha do Sr. Aristides, próximo à borda da mata, fl., 27 Jan 2012, J.P.F. Zorzanelli et al. 328 (VIES); floresta do Sr. Aristides, próximo à borda da vegetação, antes da primeira subida íngreme da trilha, fl., 15 Dec 2015, J.P.F. Zorzanelli 1391 (RB, VIES); floresta do Sr. Aristides, próximo ao início do zigue-zague da trilha, 20°21' 56" S 41°28' 26" W, fr., 31 Mar 2016, J.P.F. Zorzanelli 1505 (RB, VIES).

Etymology. The epithet honors the collector of the type specimens, João Paulo Fernandes Zorzanelli, Brazilian botanist and dear friend of the authors. JPFZ is an active and prominent collector in the state of Espírito Santo, with collections currently focused on Serra do Valentim, the type locality of *S. zorzanellii*.

Distribution and habitat. *Siderasis zorzanellii* is confined to the municipality of Iúna, Espírito Santo (Fig. 2). It occurs in the "Floresta Ombrófila Densa Montana" vegetation, at 1200–1350 m above the sea level, generally near disturbed sites, being less frequent in well-preserved areas. This could be related to its climbing habit and



Figure 12. *Siderasis zorzanellii* M.Pell. & Faden. **A** habit, showing an immature individual **B** habit, showing a mature individual spirally ascending a tree **C** detail of a secondary branch, showing distichously-alternate, asymmetric leaves **D** detail of an axillary inflorescence, in the primary branch **E** detail of a terminal inflorescence, at pre-anthesis, in a secondary branch **F** detail of a terminal inflorescence, at anthesis, in a secondary branch, showing an open male flower **G** side view of a male flower, showing the unequal and sigmoid stamens **H** side view of a post-anthesis bisexual flower, showing the bent style **I** detail of the inflorescence bearing two mature capsules **J** dorsal and ventral view of the seeds, showing the rugose testa, cleft towards the semidorsal embryotega, and the C-shaped hilum. Photographs by J.P.F. Zorzanelli.
the need of more sunlight exposure then the rosette species of the genus. This pattern is common in other liana and vine groups, such as Bignoniaceae, Malpighiaceae, and Sapindaceae (Acevedo-Rodríguez, pers. comm.), especially evident in big families such as Asteraceae, where the primarily climbing genus *Mikania* Willd. is almost exclusively found at the edge of forests, along trails, and in disturbed areas (Oliveira 2015).

Phenology. It was found in bloom from December to March and in fruit in March.

Conservation status. *Siderasis zorzanellii* is very narrowly distributed, with an EOO of ca. 7.779 km² and an AOO of ca. 300 km². The subpopulations are small, with no more than 10 mature individuals each. Unlike for the rosette species in the genus, it is still uncertain if the two climbing species reproduce vegetatively through cloning. Flowering seems to be frequent, although fruits have been collected only once. Thus, following the recommendations from IUCN (2001), *S. zorzanellii* should be considered Critically Endangered [CR, A2abde+B1ab(iii, iv, v)+ B2ab(iii, iv, v)+C2a(ii)+D1+D2].

Affinities. Siderasis zorzanellii is morphologically similar to S. spectabilis. Nevertheless, both species can be differentiated based on consistency of the leaf blades (chartaceous in S. zorzanellii vs. membranous in S. spectabilis), density of their pubescence (sparsely minutely velutine vs. minutely velutine), position of the inflorescences (terminal in the secondary branches or axillary in the older nodes of the primary branches vs. exclusively terminal in the primary branches), floral morphology (flowers 0.7–0.9 cm diameter, petals white, margins glabrous vs. flowers 1–1.3 cm diameter, petals dark mauve to vinaceous, rarely light pink or white, margins ciliate with non-moniliform hairs), and by their disjunct distribution (southern montane Espírito Santo state vs. northern montane Rio de Janeiro state).

Final remarks

The present work adds four new species to *Siderasis*, along with the addition of new morphological characters that help clarify the circumscription of the group. *Siderasis* Raf. *emend.* M.Pell. & Faden may be uniquely characterized as comprising small perennial rosette herbs or robust perennial vines, with shoots determinate or indeterminate, leaves spirally- or distichously-alternate. The inflorescences are terminal or axillary, either a many-branched thyrse with alternate cincinni or reduced to a solitary cincinnus, cincinni always several-flowered. The flowers are chasmogamous, bisexual or male, actinomorphic or zygomorphic, and petals with glabrous margins or ciliated with non-moniliform hairs. The androecium is composed of 6 fertile stamens, filaments straight or sigmoid, anthers dorsifixed and extrorsely rimose, anther sacs semicircular, divergent, connectives expanded and quadrangular. In the gynoecium, the stigma is annular-truncate or annular-capitate, marginally papillate with unicellular papillae restricted to the margin of the stigmatic regions. Also, similar to *Dichorisan-dra*, the capsules are thick-walled, and the seeds are arillate, biseriate to partially uniseriate, with semidorsal or semilateral embryotega, and a C-shaped hilum. All species

accepted by us are easily diagnosed by a unique and constant combination of morphological character states. Furthermore, each species can be easily separated based on their geographical distribution, since they are microendemics, with non-overlapping distribution areas (Fig. 2).

As indicated by several systematic studies in Commelinaceae (Evans et al. 2000, 2003; Hardy 2001; Wade et al. 2006; Zuiderveen et al. 2011; Hertweck and Pires 2014) and by the morphological evidence presented here and by Pellegrini (2017), the need to recircumscribe subtribe Dichorisandrinae is pressing. Aside from the cytological character of x=19 large chromosomes described by Jones and Jopling (1972) and hypothesized by Faden and Hunt (1991), no macro or micromorphological synapomorphies were found so far for subtribe Dichorisandrinae in its current circumscription. On the other hand, if subtribe Dichorisandrinae is recircumscribed to exclusively contain Dichorisandra and Siderasis, Dichorisandrinae s.s. can be easily morphologically characterized by its thick-walled capsules, the biseriate to partially uniseriate arillate seeds, semidorsal to semilateral embryotega, and C-shaped hilum. The lineage composed by Geogenanthus(Cochliostema+Plowmanianthus) needs to be formally recognized as a subtribe, and can be easily circumscribed by its petals with marginally fringed with moniliform hairs, and anthers sacs curved to spirally-coiled and appressed to each other. Phylogenetic studies using both nuclear and chloroplast sequences seem promising in elucidating phylogenetic incongruences in Commelinaceae (e.g. Burns et al. 2011). However, most phylogenetic in the family so far completely disregard morphological data, with the exception of Evans et al. (2000, 2003). Studies focusing on the systematics and recircumscription of Dichorisandrinae are currently being conducted, combining morphological and molecular data (Pellegrini et al., in prep.), and should shed some light on the evolution of the reproductive biology in the family.

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References

- Aona LYS (2008) Revisão taxonômica e análise cladística do gênero *Dichorisandra* J.C.Mikan (Commelinaceae). PhD Thesis, Instituto de Biologia, Universidade Estadual de Campinas, Campinas, São Paulo.
- Aona LYS, Faden RB, Amaral MCE (2012) Five new species of *Dichorisandra* J.C.Mikan (Commelinaceae) from Bahia State, Brazil. Kew Bulletin 66: 1–13.
- Aona LYS, Faden RB, Bittrich V, Amaral MCE (2016) Four new species of *Dichorisandra* (Commelinaceae) endemic from Bahia State, Brazil. Brittonia 68(1): 61–73. https://doi. org/10.1007/s12228-015-9397-x
- Aona-Pinheiro LYS, Pellegrini MOO, Valente ASM, Maurenza D, Kutschenko DC, Reis Júnior JS, Abreu MB (2013) Commelinaceae. In: Martinelli G, Moraes MA (Eds) Livro Vermelho da Flora do Brasil. Andrea Jakobsson Estúdio, Instituto de Pesquisas Jardim Botânico do Rio de Janeiro, Rio de Janeiro, 454–457.
- Bachman S, Moat J, Hill AW, Torre J, Scott B (2011) Supporting Red List threat assessments with GeoCAT: geospatial conservation assessment tool. In: Smith V, Penev L (Eds) e-Infrastructures for data publishing in biodiversity science. ZooKeys 150: 117–126. https://doi. org/10.3897/zookeys.150.2109
- Barreto RC (1997) Levantamento das espécies de Commelinaceae R.Br. nativas do Brasil. PhD Thesis, Instituto de Biociências, Universidade de São Paulo, São Paulo.
- Boaventura YMS, Matthes LAF (1987) Aspectos da biologia da reprodução em plantas ornamentais cultivadas no estado de São Paulo I: *Dichorisandra thyrsiflora* J.C.Mikan (Commelinaceae). Acta Botânica Brasílica 1(2): 189–199. https://doi.org/10.1590/S0102-33061987000200007
- Brückner G (1930) Commelinaceae. In: Engler HGA, Prantl KAE (Eds) Die natürlichen Pflanzenfamilien (Ed. 2). Engelmann, Leipzig, 159–181.
- Burns JH, Faden RB, Steppan SJ (2011). Phylogenetic Studies in the Commelinaceae subfamily Commelinoideae inferred from nuclear ribosomal and chloroplast DNA sequences. Systematic Botany 36(2): 268–276. https://doi.org/10.1600/036364411X569471
- Clarke CB (1881) Commelinaceae. In: De Candolle ALPP, De Candolle ACP (Eds) Monographiae Phanerogamarum, vol. 3. Sumptibus G. Masson, Paris, 113–324. [t. I–VIII]
- Evans TM, Faden RB, Simpson MG, Sytsma KJ (2000) Phylogenetic relationships in the Commelinaceae: I. A cladistic analysis of morphological data. Systematic Botany 25: 668–691. https://doi.org/10.2307/2666727
- Evans TM, Sytsma KJ, Faden RB, Givnish TJ (2003) Phylogenetic relationships in the Commelinaceae: II. A cladistic analysis of rbcL sequences and morphology. Systematic Botany 28: 270–292.
- Faden RB (1978) *Pollia* Thunb. (Commelinaceae): The first generic record from the New World. Annals of the Missouri Botanical Garden 65(2): 676–680. https://doi.org/10.2307/2398866
- Faden RB (1991) The morphology and taxonomy of *Aneilema* R.Brown (Commelinaceae). Smithsonian Contributions to Botany 76. Washington, DC, 181 pp.
- Faden RB (1992) Floral attraction and floral hairs in the Commelinaceae. Annals of the Missouri Botanical Garden 79(1): 46–52. https://doi.org/10.2307/2399808

- Faden RB (1998) Commelinaceae. In: Kubitzki K (Ed.) The families and genera of vascular plants, vol. 4. Springer Verlag. Berlin, 109–128. https://doi.org/10.1007/978-3-662-03531-3_12
- Faden RB, Hunt DR (1987) Reunion of *Phaeosphaerion* and *Commelinopsis* with *Commelina* (Commelinaceae). Annals of the Missouri Botanical Garden 74(1): 121–122. https://doi.org/10.2307/2399267
- Faden RB, Hunt DR (1991) The Classification of the Commelinaceae. Taxon 40(1): 19–31. https://doi.org/10.2307/1222918
- Fleming TH, Estrada A (1993) Frugivory and seed dispersal: Ecological and evolutionary aspects. Kluwer Academic Publishers, Dordrecht, 392 pp. https://doi.org/10.1007/978-94-011-1749-4
- Hardy CR, Stevenson DW (2000) Development of the gametophytes, flower, and floral vasculature in *Cochliostema odoratissimum* (Commelinaceae). Botanical Journal of the Linnean Society 134: 131–157. https://doi.org/10.1111/j.1095-8339.2000.tb02348.x
- Hardy CR (2001) Systematics of *Cochliostema*, *Geogenanthus*, and an undescribed genus in the spiderwort family, Commelinaceae. PhD Thesis, Cornell University, Ithaca, New York.
- Hardy CR, Faden RB (2004) *Plowmanianthus*, a new genus of Commelinaceae with five new species from Tropical America. Systematic Botany 29(2): 316–333. https://doi. org/10.1600/036364404774195511
- Hasskarl JC (1869) Ueber *Pyrrheima* Hasskl., eine nueu Gattung der Commelinaceae. Flora 52: 366–368.
- Hertweck KL, Pires JC (2014) Systematics and evolution of inflorescence structure in the *Tradescantia* alliance (Commelinaceae). Systematic Botany 39(1): 105–116. https://doi. org/10.1600/036364414X677991
- IBGE [Instituto Brasileiro de Geografia e Estatística] (2012) Manual Técnico da vegetação Brasileira: sistema fitogeográfico, inventário das formações florestais e campestres, técnicas e manejo de coleções botânicas, procedimentos para mapeamentos, ed. 2, vol. 1. IBGE, Rio de Janeiro, 272 pp.
- IUCN (2001) The IUCN red list of threatened species, version 2010.4. IUCN Red List Unit, Cambridge, UK. http://www.iucnredlist.org/ [accessed: 3.27.2017]
- Jones K, Jopling C (1972) Chromosomes and the classification of the Commelinaceae. Botanical Journal of the Linnean Society 64: 129–162. https://doi.org/10.1111/j.1095-8339.1972. tb00929.x
- Loddiges CL (1820) The Botanical Cabinet: consisting of coloured delineations of plants from all countries. 4: t. 374.
- Moore HE (1956). Siderasis fuscata. Baileya 4: 28-30.
- Owens SJ, Kimmins FM (1981) Stigma morphology in Commelinaceae. Annals of Botany 47(6): 771–783. https://doi.org/10.1093/oxfordjournals.aob.a086076
- Panigo E, Ramos J, Lucero L, Perreta M, Vegetti A (2011) The inflorescence in Commelinaceae. Flora 206(4): 294–299. ttps://doi.org/10.1016/j.flora.2010.07.003
- Pellegrini MOO (2017) Siderasis albofasciata sp. nov. (Commelinaceae), endemic to the state of Espírito Santo, Brazil, and the typification of S. fuscata. Nordic Journal of Botany 35(1): 29–37. https://doi.org/10.1111/njb.01267

- Pellegrini MOO, Almeida RF (2016) Rediscovery, identity and typification of *Dichorisandra picta* (Commelinaceae) and comments on the short-stemmed *Dichorisandra* species. Phytotaxa 245(2): 107–118. https://doi.org/10.11646/phytotaxa.245.2.2
- Pellegrini MOO, Aona-Pinheiro LYS, Forzza RC (2013) Taxonomy and conservation status of *Tripogandra warmingiana* (Seub.) Handlos (Commelinaceae), a previously obscure taxon from Brazil. Phytotaxa 91(2): 39–49. https://doi.org/10.11646/phytotaxa.91.2.2
- Pellegrini MOO, Faden RB, Almeida RF (2016) Taxonomic revision of Neotropical Murdannia Royle (Commelinaceae). PhytoKeys 74: 35–78. https://doi.org/10.3897/phytokeys.74.9835
- Rafinesque CS (1836[1837]) Flora Telluriana, vol. 3. H. Probasco, Philadelphia, 135 pp.
- Sigrist MR, Sazima M (2015) Phenology, reproductive biology and diversity of buzzing bees of sympatric *Dichorisandra* species (Commelinaceae): breeding system and performance of pollinators. Plant Systematics and Evolution 301(3): 1005–1015. https://doi.org/10.1007/ s00606-014-1131-8
- Spjut RW (1994) A systematic treatment of fruit types. The New York Botanical Garden, New York, USA, 1–181.
- Thiers B (continually updated) Index Herbariorum: A global directory of public herbaria and associated staff. New York Botanical Gardens' Virtual Herbarium. http://sweetgun.nybg. org/ih/ [accessed: 2.12.2017]
- Thitimetharoch T (2004) Taxonomic studies of the family Commelinaceae in Thailand. PhD thesis, Khon Kaen University, India.
- Wade DW, Evans TM, Faden RB (2006) Subtribal relationships in tribe Tradescantieae (Commelinaceae) based on molecular and morphological data. Aliso 22(1): 520–526. https:// doi.org/10.5642/aliso.20062201.40
- Weberling F (1965) Typology of inflorescences. Botanical Journal of the Linnean Society 59: 15–221. https://doi.org/10.1111/j.1095-8339.1965.tb00058.x
- Weberling F (1989) Morphology of flowers and inflorescences. Cambridge University Press, Cambridge, 348 pp.
- Zuiderveen GH, Evans TM, Faden RB (2011) A phylogenetic analysis of the African plant genus Palisota (family Commelinaceae) based on chloroplast DNA sequences. Grand Valley State University, Honors Projects: Paper 65. http://scholarworks.gvsu.edu/honorsprojects/65

RESEARCH ARTICLE



Study of the leaf anatomy in cross-section in the Iberian species of *Festuca* L. (Poaceae) and its systematic significance

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Abstract

A study of the leaf anatomy in the species of the genus *Festuca* present in the Iberian Peninsula was made. A total of 68 taxa were included and 15 characters were measured in leaf cross-section. The major anatomical features of each taxonomic group were characterized, and some variability was observed in the taxa. The anatomical patterns observed were compared and discussed with the relationships suggested by the molecular analyses. The leaf outline, the presence or absence of complete girders, and the development degree of the bulliform cells were the main characters to differentiate among fescue species of the fine-leaved clade and those of the broad-leaved clade. The most useful character to segregate species groups within the different taxonomic sections was the arrangement of the sclerenchyma, and a remarkable variability of this character was found in the species of *Festuca* section *Festuca*, especially in those located in other lineages, and only some taxa could be anatomically differentiated at species level based on a set of non-taxative characters. The discordant pattern observed in *F. henriquesii*, a species traditionally included in *Festuca* sect. *Festuca* that shared anatomical features with the species of "*F. rubra* complex", suggests its possible inclusion in the sect. *Aulaxyper* pending further taxonomic and phylogenetic analyses.

Keywords

Festuca, Iberian Peninsula, leaf anatomy, sclerenchyma arrangement

Introduction

Festuca L. is one of the largest genera within the family Poaceae with more than 450 species mostly distributed in the temperate and alpine zones of both hemispheres (Watson and Dallwitz 1992; Clayton et al. 2006 onwards). Some fescue species are economically important worldwide for their forage value (e.g., *Festuca arundinacea* Schreb.), as well as for their use in turfs (e.g., *F. rubra* L.), gardening (e.g., *F. glauca* Vill.), and soil fixation (e.g., *F. ovina* L.).

The Iberian Peninsula has been considered one of the main speciation centres of the genus *Festuca* (Saint-Yves 1930), with about 100 taxa (between 70 and 80 species) organized in ten sections and three subgenera (Cebolla and Rivas Ponce 2003a; Devesa et al. 2013). It comprises rhizomatous and cespitose perennial species, both diploid and polyploid (up to 12x = 84 chromosomes; Fuente et al. 2001; Loureiro et al. 2007), capable of growing in a wide variety of environments and habitats (Kerguélen and Plonka 1989). Many of them are endemic species adapted to high mountain conditions (e.g., *F. indigesta* Boiss. and *F. pseudeskia* Boiss.), but they also grow in wet pastures (many species of the "*F. rubra* complex"), river areas, and forest edges [e.g., *F. gigantea* (L.) Vill.], and on coastal rocky cliffs and fixed coastal dunes, being able to tolerate high environmental salt levels [e.g., *F. vasconcensis* (Markgr.-Dann.) Auquier & Kerguélen and *F. juncifolia* Chaub.].

The phylogenetic analyses based on nuclear and chloroplast markers suggest that *Festuca* is a paraphyletic genus which should include other genera that were previously treated independently, such as *Lolium* L. and *Vulpia* C.C. Gmel. among others (e.g., Charmet et al. 1997; Torrecilla and Catalán 2002; Catalán et al. 2004; Inda et al. 2008). The fescue species are subdivided into two well supported clades: the "broad-leaved" and the "fine-leaved", named so for the leaf shape of the species included in them. In general terms, the broad-leaved fescues have flat leaves, convolute or inrolled vernation, and the fine-leaved fescues have conduplicate or infolded leaves, and acicular, setaceous, or filiform innovation leaf blades (Catalán et al. 2007), although there are several exceptions (Namaganda and Lye 2008).

In the Iberian territory, the broad-leaved clade comprises the sects. *Schedonorus* (P. Beauv.) W.D.J. Koch (4 species), and *Plantynia* (Dumort.) Tzvelev (1 species) from subgenus *Schedonorus* (P. Beauv.) Peterm., the sect. *Phaeochloa* Griseb. (2 species) from subgenus *Drymanthele* Krecz. & Bobrov, and the sects. *Subbulbosae* Nyman ex Hack. (3 species), *Scariosae* Hack. (1 species), *Pseudoscariosa* Krivot. (1 species), and *Lojaconoa* Catalán & Joch. Müll. (2 species) from subgenus *Festuca*. The fine-leaved clade includes the sects. *Eskia* Willk. (5 species), and the more recently diverged sects. *Festuca* (subsections *Festuca* and *Exaratae* St.-Yves; ca. 45 species) and *Aulaxyper* Dumort. (ca. 15 species), all of them belonging to the subgenus *Festuca*. According to the molecular data, some species conventionally classified within sects. *Festuca* and *Aulaxyper* fall outside the clades that include their respective type species (Catalán et al. 2007), but the interspecific relations within those clades are not resolved or are poorly supported (Torrecilla et al. 2004).

The taxonomy of this genus is very complex due to the great morphological similarity between species and the high degree of overlap in the ranges of variation. The shortage of diagnostic morphological characters has favoured the study of complementary characters in order to clarify the taxonomic relationships between species and allow their correct identification. Anatomical features of the leaf blades in cross-section and those related to the micro-morphology of epidermal surfaces have been the main supplementary tools to add to the morphological characters used to characterize Festuca (e.g., Metcalfe 1960; Ellis 1976, 1979, 1986; Namaganda et al. 2009) and other genera of difficult taxonomy within the Poaceae family (e.g., López and Devesa 1991; Pimentel and Sahuquillo 2003; Kuzmanović et al. 2009; Gennaro et al. 2010; Ortúñez and Fuente 2010; Ortúñez and Cano-Ruiz 2013). Since Hackel (1882), leaf anatomy has been considered of taxonomic interest in the genus, and characters such as the outline of the leaf cross-section, the arrangement of sclerenchyma in relation to the vascular bundles, and the number of ribs and furrows are used around the world in combination with other morphological characters (e.g., Saint-Yves 1909; Metcalfe 1960; Ellis 1976; Markgraf-Dannenberg 1980; Kerguélen and Plonka 1989; Portal 1996; Clayton and Renvoize 1986; Fuente and Ortúñez 1998). The leaf anatomy has been especially investigated within the fineleaved fescues clade, with a more complex taxonomy than the broad-leaved clade, and many taxa have been described or segregated mainly based on those anatomical characters (Namaganda et al. 2009).

Despite the extensive use of the leaf anatomy in *Festuca* and the importance of its systematics, many studies have evaluated environmental influences on the anatomical characters. Several authors have pointed out its restricted taxonomic value in *Festuca* (Connor 1960; Kjellqvist 1961; Aiken et al. 1985; Aiken and Consaul 1995; Ramesar-Fortner et al. 1995) and other grasses (Ruiz-Téllez et al. 1998; Giełwanowska et al. 2005; Kuzmanović et al. 2012; Olsen et al. 2013) because some features may be affected by ecological factors and by phenotype plasticity. However, although the identification of *Festuca* species using only anatomical variables is complex, most authors agree that it would reduce the possibilities of error and improve the separation of several similar taxa which were indistinguishable based on the morphology of vegetative and reproductive organs (Aiken et al. 1985).

In the Iberian Peninsula, leaf anatomy studies have usually been partial, accompanying species descriptions or in the treatments of regional Floras, and generally corresponding to iconographic details and diagrams or drawings of leaf cross-sections (e.g., Aizpuru et al. 1997; Fuente et al. 1997; Bolòs and Vigo 2001; Catalán 2009). On the occasion of the taxonomic study of the genus *Festuca* in the framework of the *Flora iberica* Project (Castroviejo et al. 1986–2017), the cross-section leaf anatomy of most species currently recognized for this territory have been analysed. In this work, we aim at improving our anatomical knowledge about the genus, and compare the leaf anatomy patterns with the latest molecular phylogenies.

Material and methods

We analysed leaf sections in cross view of 68 Iberian taxa belonging to the subgenera *Festuca, Drymanthele*, and *Schedonorus* of the genus *Festuca*. Exceptionally, apart from the Iberian material, material from the French Pyrenees and from Andorra was selected. The species included and their nomenclature followed Devesa et al. (2013). The identification of the specimens was performed according to local Floras and monographs (Markgraf-Dannenberg 1980; Kerguélen and Plonka 1989; Fuente and Ortúñez 1998). Anatomical observations were based mainly on herbarium specimens from ABH, BC, COFC, FCO, GDAC, HUAL, MA, MAF, MGC, JACA, SANT and SEV (acronyms according to Thiers 2017), and also from fresh material collected in the field during the years 2012–2016 (specimens deposited in the COFC herbarium). About 400 preparations were made (several per individual). The list of plants examined anatomically, localities, and authorship of the species are given in Suppl. material 1.

Free-hand cross-sections of the penultimate innovation leaf blades were made directly on fresh or dry material, and subsequently hydrated in water, following the framework proposed by López and Devesa (1991). The cross-sections were mounted in 50% lactic acid, which helped to clear the cells. Observations and measurements were taken using a Motic BA300 light microscope equipped with an ocular micrometer. Photographs of leaf cross-sections were obtained using a Moticam 2500 digital microscope camera, and edited with Motic Images Plus 2.0 software.

The leaf anatomical characters observed were compiled from those mentioned in the literature on genus *Festuca*, as the outline, the pattern of abaxial and adaxial sclerenchyma arrangement, length, width (when the leaves are flat, the width was measured as the sum of the two hemilimbs), thickness at the midrib, number of vascular bundles, number of ribs, and number of bulliform cells (viewed in the grooves contiguous to the median rib). Other additional characters were added for anatomical characterization of the species, such as median vascular bundle diameter/maximum size, number of outer and inner bundle sheath cells, sclerenchyma thickness at the midrib, trichome density of the adaxial surface (glabrous, sparsely aculeate, or densely aculeate) and its length, and length and width of abaxial and adaxial epidermal cells (referred to the cell lumen from the lateral side). The terminology for the anatomical characters was based on Ellis (1976) and Metcalfe (1960). The main characters studied and positions of measurements made on each cross-section are illustrated in Fig. 1, and the main types of arrangement of sclerenchyma in Fig. 2.

Results and discussion

The studied anatomical characters in leaf cross view are summarized in Table 1. The species were grouped by subgenera and taxonomic sections according to traditional classification (Devesa et al. 2013), and subsequently were ordered by anatomical affinities. The lineage in which the fine-leaved species is located based on nuclear ITS and



Figure 1. Main characters observed in the leaf cross-sections and abbreviations. Lines in grey indicate measures: **I** length (only in species with conduplicate blades) **2** maximum width **3** thickness of the blade at the midrib **4** maximum size/diameter of the median vascular bundle (**MVB**) **5** length × width of abaxial epidermal cells (**AbEC**). **6** length × width of adaxial epidermal cells (**AbEC**). Sclerenchyma (**SCL**); vascular bundles (**VB's**); ribs (**R**); trichomes (**TRI**); outer bundle sheath cells (**OBS**); and inner bundle sheath cells (**IBS**).



Figure 2. Major types of arrangement of sclerenchyma found in the leaf cross-sections. In conduplicate leaf blades: A continuous ring B interrupted continuous ring C forming abaxial strands and an adaxial strand on the median rib D with an abaxial girder at the median vascular bundle. In flat leaf blades: E complete (abaxial and adaxial) girder at the first vascular bundles, abaxial girder at the second vascular bundles, third vascular bundles without associated sclerenchyma.

cells of out 3). Abbrevi lleaves. Abbi NP, not pr chyma only girder of scl bundles (in by sclerench adaxial site. numbers in	er bunc ations er bunc reviatio cesent; ć in cer lerench broad- broad- nyma ii section parent	Ille shear in the c ons in the strand thral vas tyma at tyma at tyma at tyma at the ce in the ce in the ce in the ses in	th; IBS , cell uutline: U, 1 te sclerenchy, d ds, but not first order v species); * ii ntral vascul ntral vascul at cleat	is of inner bu U-shaped; V yma pattern: in contact w le (in fine-le vascular bun ndicate girdé ar bundle; n z:; A , sparsel) zmmon valu	, V-shap , V-shap , V-shap , C, cont , ith the , v-shap ,	eath. Al oed; Y, Y, Y, Y bundle bundle ecies); I girder c girder c trension tra. Abb tra. C, gl cter pre-	Y-shaped; Y-shaped; t Ci, conti sheath; G MB, prese of sclerenc of sclerenc or colour or eviations abrous. N :sence.	F, flat: r, rc F, flat: r, rc nuous ring , girders. Si arce of gird hyma at see hyma at see cless cells ne in the bull úmbers in '	ade or lines aude or lines sometimes ib-indices er of sclere cond order ar of the v iform cells square braa	indicate results of the second	ne-leave s, s, strai thicken location only in - bundle undles. loped; u loped; u cates nu	ad clade; Bl , ight; a , angl ed, broken c ed, broken c of the gird lateral vascu s; 3 , girder s; 3 , girder d d , undevelc umber of str	broad-lee broad-lee ed; IL, ir er: MVBs er: MVBs er: MVBs er so r scheren ns in the ped. Abb	aved clade; J interruptee presence or chyma at th OBS/IBS: i creviations i reviations i rands plus g	L, lineage eaves; CL, lineage d, never in f girder of leaved spe leaved spe leaved spe ird order , OBS intu n the trich n the trich	(see Fig. (see Fig. cauline strands; scleren- cies); 1, vascular vascular vascular omes of omes of ters and
										-			-		-	,
Таха	Clade, lineage	Outline	Abaxial sclerenchyma pattern	Adaxial sclerenchyma pattern (in ribs)	Vascular bundles number	Ribs number	Length (mm)	Width (mm)	Thickness at the mid- rib (mm)	MVB max. size (µm)	OBS/ IBS number	Sclerenchyma thickness at the midrib (µm)	Bulliform cells number	Adaxial site trichomes (µm)	Abaxial epidermal cells, L × W (µm)	Adaxial epider- mal cells, L × W (µm)
A. SUBGENU	IS FESTU	JCA														
Sect. Festuca																
F. hystrix	H	Ur	C	S[1]	3	1	0.44-0.60	0.52-0.70	0.33-0.44	70-87.5	12–16/ 19–22	37.5-75	3(5), ud	E, 12.5–37.5 (67.5)	7.5-20 × 5-10	7.5–12.5 × 5
F. reverchonii	H	Ur	C (Ci)	S[1]	6	1	0.32-0.46	0.30-0.46	0.19-0.25	70-77.5	13–15/ 20–25	10-20	5(6), ud	E, 15–37.5	7.5–12.5 × 5–7.5	7.5–12.5 × 5–10
F. airoides	H	Ur-e	U	NP or S[1]	5-7	1	0.54-0.68	0.37-0.52	0.24-0.30	67.50-80	10–13/ 21–23	12.5–50	3(4), ud	E(A), 15–47.5	7.5-15 × 5-10	7.5–12.5 × 5–10
F. niphobia	H	Ue	U	NP or S[1]	(5)7	1	0.56-0.75	0.43-0.50	0.27-0.32	67.5–85	12–13/ 19–23	27.5-42.5	3, ud	E, 17.5–50	7.5–12.5 × 7.5–12.5	7.5–12.5 × 2.5–7.5
F. brigantina subsp. brigantina	E	Ue	U	NP	5-7	1	0.60-0.91	0.44-0.69	0.31-0.39	72.5-100	8–15/ 18–24	22.5-67.5	4–5, ud	E, 10–87.5	10–27.5 × 7.5–15	7.5-17.5 × 5-10
F. gracilior	E	Uerr	C (Ci)	NP	~	1–3	0.52-0.73 (0.80)	0.32-0.54	0.19-0.28	62.5-85	11–13/ 19–23	27.5-60	3–5, ud	E, 10–50	12.5–20 × 7.5–12.5	5-12.5 × 5-7.5
F. michaelis	FI	Vs or Ue	C (Ci)	NP	7	(1)3	0.64-0.93	0.49-0.65	0.28-0.36	77.5- 112.5	9–12/ 19–24	12.5–52.5	3, ud	E, 15–75 (112.5)	12.5–25 × 7.5–17.5	7.5–15 × 5–10
F. valentina	H	Ue-r	υ	NP or S[1–3]	5-7	3(5)	0.72-0.80 (1.05)	0.51-0.74	0.30-0.47	82.5- 112.5	9-14/ 19-25	50-82.5	3-4(5), ud	E, 15–95	7.5–27.5 × 5–15	7.5–15 × 5–10

xial Adaxial epider- srmal mal cells, L × W (µm) (µm)	$-20 \times 7.5 - 12.5$ 12.5 $\times 5 - 10$	2.5 × 7.5–12.5 12.5 × 2.5–7.5	17.5 × 12.5–20 × -15 5–7.5	$\begin{array}{c c} -20 \times & 10 \\ -17.5 & 7.5 \\ -10 \end{array}$	15 × 7.5-15 × 12.5 5-10	22.5 × 7.5–15 × -20 5–12.5	25 × 10–17.5 × -20 5–10	$\begin{array}{c c} 20 \times \\ -20 \end{array} \times \begin{array}{c} 7.5 - 12.5 \\ \times (5) 7.5 - \\ 10 \end{array}$	$-25 \times 10-15 \times -20 7.5-10$	15 × 7.5–17.5 12.5 × 5–10	-17.5 12.5 $-20 \times$ -12.5 5 -7.5	-15 × 5-12.5 × 5-15	-25 × 7.5-15 × -15 5-10	-37.5 7.5-17.5 -32.5 × 5-12.5	7.5 × 10–20 × -25 5–17.5	35 × 12.5–25 × -25 × 7.5–20	
al site Abi omes cells n) W (5-40 12.5 7.5-	-87.5 5-11 7.5-	-75.0 7.5-1 7.5	5-75 12.5 7.5-	-100 7.5-	$-122.5 \begin{array}{ c c c c c c c c c c c c c c c c c c c$	112.5 10- (0) 7.5	5-75 10- 0) 7.5	-87.5 12.5- 10-	-125 10- 8) 7.5-	$-100 \frac{12.5}{\times 7.5}$	-55 7.5-	-82.5 12.5 7.5	-125 17.5 × 15	-55 <u>15-</u> 3	-37.5 15- 10	
m Adaxia tricho er (µn	d E, 22.	d E, 25-	E, 25.0	ud E, 12.	d E, 25-	d E, 27.5-	d E, 15– (125	E, 27.: (15	d E, 25-	d E, 45- (15	d E, 32.5	d E, 10	d E, 12.5	d E, 50-	d E, 10	d E, 15–	
a Bullifor t cells numbe	3-4, u	3-5, u	3, ud	2-3(4),	3-6, u	3-5, u	3-5, u	3, ud	3-5, u	3-5, u	4-6, u	3-7, u	3-6, u	3-4, u	3-5, u	4-6, u	
Sclerenchym thickness at the midrib (µm)	15-55	42.5-82.5	37.5-67.5	20-57.5	25-70	12.5-97.5	20-50	22.5-32.5	25–80	62.5-87.5	37.5–50	75-175	30-60	40-50	15-30	12.5–25	
OBS/ IBS number	7–13/ 16–27	11-17/ 20-24	11–12/ 20–24	9-16/ 19-24	8-13/ 19-27	7–17/ 21–28	9-14/ 19-24	8–12/ 19–23	10–15/ 20–26	13–15/ 20–26	10–16/ 20–26	11–14/ 19–22	11–14/ 27–30	11-12/ 24	8–13/ 19–25	69/ 1620	
MVB max. size (µm)	65-107.5	77.5- 87.5	75.0- 82.5	65–100	70-115	70-152.5	85.0- 155.0	75-112.5	95–125	117.5- 130	80–107 (125)	62.5- 72.5	95-117.5	85-107.5	85-115	65–90 (100)	
Thickness at the mid- rib (mm)	0.20-0.33	0.30-0.41 (0.43)	0.31-0.36	0.25-0.36	0.31 - 0.43 (0.50)	0.26-0.55 (0.60)	0.32 - 0.49 (0.53)	0.31-0.41	0.33-0.44 (0.50)	0.35-0.57	0.38–0.67	0.28-0.38	0.31-0.34	0.30-0.36	0.35-0.45	0.26-0.35 (0.48)	
Width (mm)	0.42-0.69	0.50-0.68 (0.81)	0.58-0.69	(0.34) 0.44-0.50	(0.50) 0.61-0.89	0.54-0.88	(0.53) 0.57-0.94	0.61-0.95	(0.57) 0.72–0.90	0.75-1.11	0.69-1.02	0.52-0.66	0.63-0.89	0.55-0.76	0.66-0.85	0.40-0.61 (0.87)	
Length (mm)	0.54-0.86	0.51-0.84 (0.90)	0.73-0.84	0.52-0.73 (0.81)	(0.60) 0.69-1.17	0.66–1.20 (1.41)	0.67-1.34	0.90-1.15	0.80-1.18	0.80-1.52	0.70-1.1 (1.3)	0.45-0.58	(0.87)0.91– 1.06	0.79–1.15	0.75-0.97	0.46-0.62 (0.94)	
Ribs number	1–3	1–3	3	1	1-3(5)	1-3(5)	1-3(5)	1–3	1–3	(1)3(5)	3	3(4)	3	1–3	1	1	
Vascular bundles number	(6)2	~	~	5-7	7(8)	(5)6-9 (10)	6-7	~	6-2	7–9(11)	5-7(9)	~	(8)	7(10)	5-7	3-5	
Adaxial sclerenchyma pattern (in ribs)	NP	NP or S[1–3]	S[3] (NP)	NP or S[1]	NP or S[1–2]	NP or S[1–3]	NP or S[1–3]	NP	NP	NP or S[1–3]	S[3]	S[1-3]	NP	NP	NP	NP	
Abaxial sclerenchyma pattern	C (Ci)	U	U	C (Ci)	U	U	U	C (Gi)	υ	υ	U	C, Ci, S[(3)5–7] or S+G _{MVB}	C (Ci)	C (Ci)	U	Ci or S[3–6]	
Outline	Vsor Ue	Ue-r	Ue	Ue	Ue	Ue	Ue	Ue or Vs	Ue or Vs	Ue	Ur	Ur-s	Ue	Ue	Ue-r	Ue-r	
Clade, lineage	H	H	H	H	H	H	H	H	H	H	H	Н, L3	H	H	H	E	
Taxa	F. ochroleuca	F. longiauricu- lata	F. vettonica	F. aragonensis	F. carpetana	F. summilusi- tana	F. gredensis	F. altopyr- enaica	F. yvesü	F. indigesta	F. segimonensis	F. clementei	F. liviensis	F. glauca	F. vasconcensis	F. brigantina subsp. actiophyta	

Taxa	Clade, lineage	Outline	Abaxial sclerenchyma pattern	Adaxial sclerenchyma pattern (in ribs)	Vascular bundles number	Ribs number	Length (mm)	Width (mm)	Thickness at the mid- rib (mm)	MVB max. size (µm)	OBS/ IBS number	Scherenchyma thickness at the midrib (µm)	Bulliform cells number	Adaxial site trichomes (µm)	Abaxial epidermal cells, L × W (µm)	Adaxial epider- mal cells, L × W (µm)
F. rivas- martinezii	H	Ue or Vs	S[3] (C)	NP	7(9)	3	0.70-1.02	0.60-0.90	0.25-0.44	85-117.5	$\begin{array}{c} 11-22/\\ 21-33\\ (37) \end{array}$	35-60(95)	3–5, ud	E, (10)15– 115	15-22.5 × 7.5-20	5-12.5 × 5-10
<i>F. marginata</i> subsp. <i>andres-</i> <i>molinae</i>	H	Ue Vs or Y	S[3] (C)	NP	7	(1)3	0.50-0.85	0.33–0.56	0.22-0.36	70-95	10–11/ 20–27	40-85	(1)3, ud	E, 10–60	15–22.5 × 7.5–10	5–12.5 × 7.5–10
F. marginata subsp. mar- ginata	E	Ue, Vs or Y	S	NP	7(9)	(1)3	0.60-1.05	0.37-0.63	0.27-0.39	77.5- 112.5	13–14/ 22–30	37.5-112.5	3-4, ud	E, (15)20– 42.5	15-25 × 7.5-15	5-12.5 × 5-7.5
F. frigida	Н	Ue or V	S[3]	NP	3	1	0.40-0.54	0.30-0.46	0.20-0.29	52.5- 62.5	9–10/ 18–20	12.5-17.5	2—4, ud	A, 25–37.5	10–20 × 7.5–12.5	7.5–12.5 × 5–12.5
F. alpina	E	$\underset{V_{S_{(a)}}}{\text{Ue or}}$	S[3]	NP	3-4	1–3	0.45	0.36	0.20	57.5	12/ 17–20	30	4–5, ud	A, 25–37.5	15-20 (22.5) × 10-15	7.5–12.5 × 7.5– 12.5
F. glacialis	Н	Ue	S[3-5(7)]	NP	3-5	1–3	0.34-0.62	(0.24) 0.32-0.46	0.16-0.28	52.5- 82.5	9–13/ 14–22	15-25	4–6, ud	E, 10–72.5	15–22.5 × 7.5–15	7.5–12.5 × 5–10
F. plicata	Fl, L3	Va	S or S+G _{MVB} [5(6)]	NP or S[1]	3(4)	1(2)	0.47–0.54	0.40-0.51	0.29-0.36	57.5- 67.5	8–10/ 16–20	25-107.5	3-4, ud	A, 17.5–58	15-27.5 × 7.5-12.5 (20)	7.5–20 × 5–12.5
F. capillifolia	Fl, L3	Ua	S+G _{MVB} (S) [7(9)]	NP or S[1–3]	5-7	1–3	0.35-0.61	0.43-0.59	0.19-0.30	67.5–75	10-13 (16)/ 15-23	25-142.5	3, ud	E, 50–77 (110)	22.5–30 × 12.5–32.5	7.5–10 × 5–12.5
F. ampla	Fl, L2	Ue–r or Ua	G _{VB} [7–9]	S[3–5]	(6)7(8)	(4)5	(0.44)0.52- 0.78	0.50-0.8 (0.9)	0.21 - 0.32 (0.34)	72.5- 112.5	9–12 (16)/ 17–23	45-120	3–6, ud	E(A), 17.5–55	12.5–32.5 × 10–25	$10-25 \times 10-20$
F. querana	Fl, L2	Ue or Vs	$S+G_{LVB}[5]$	NP	7–9(10)	3	0.72-1.01	0.41-0.55	0.20-0.35	80–92.5	12–13/ 22–23	50-70	4–5, ud	E or A, 15–30	12.5–17.5 × 7.5–12.5	7.5–15 × 7.5–12.5
F. borderei	Fl, L3	$\underset{VS_{(a)}}{\text{Ue or}}$	S+G _{MVB} [7–9]	NP (S[1])	6-7	5	0.66-0.96	0.55-0.73	0.24-0.35	62.5–85	10–14/ 22–24	87.5–125	4-7, ud	E, 32.5–87.5	12.5-25 × 7.5-15 (22.5)	7.5–15 × 5–10
F. henriquesii	H	F(V)	S[(3)5–7(8)]	S[5-7]	7–9(15)	5-7(9)		2.0–3.36	0.31-0.44	100-120	14–16/ 21–29	32.5–37.5	6, d	G or A, 22.5–30	10–20(25) × 10–17.5	7.5–17.5 × 7.5–15 (17.5)
Sect. Aulaxyper																

Taxa	Clade, lineage	Outline	Abaxial sclerenchyma pattern	Adaxial sclerenchyma pattern (in ribs)	Vascular bundles number	Ribs number	Length (mm)	Width (mm)	Thickness at the mid- rib (mm)	MVB max. size (µm)	OBS/ IBS number	Scherenchyma thickness at the midrib (µm)	Bulliform cells number	Adaxial site trichomes (µm)	Abaxial epidermal cells, L × W (µm)	Adaxial epider- mal cells, L × W (µm)
<i>E. rubra</i> subsp. rubra	H	Vs	S[7(10)]	NP	5-7(8)	3-5(6)	0.55-1.25	0.40–0.75 (1.3)	0.25-0.42	67.5- 102.5	9–10/ 18–20	15-72.5	4–6, ud	E, 22.5– 55(105)	15–32.5 × 12.5–30	$\frac{10-22.5 \times}{10-22.5}$ (27.5)
<i>F. rubra s</i> ubsp. juncea	E	Va	S[5–7]	NP or S[1]	(6)7	3-5	0.79–1.08	0.54-0.81	0.37-0.45	92.5– 112.5	10–12/ 17–22	100-132.5	3–7, ud	A or E, 12.5–37.5	17.5–25 × 12.5–22.5	10-22.5 × 7.5-17.5
<i>F. rubra</i> subsp. <i>pruinosa</i>	н	Vs-a (U)	S[7]	ďN	5(7)	3	(0.71) 0.78 -1	0.58-0.75	0.35-0.56	77.5–105	8-12/ 18-25	37.5–125	4–5, ud	E, 15–37.5	17.5–35 × 17.5–37.5	7.5–17.5 × 5–17.5
F. iberica	н	Vs	S[5-7]	ďN	(3)5(7)	(1)3	0.36-0.63 (0.71)	0.33-0.52	0.19-0.34	62.5-85	9–12/ 17–22	30-50(100)	3–5, ud	E, (10)20– 75(125)	17.5–27.5 × 10–22.5	10–17.5 × 7.5–20
F. trichophylla	H	Vs	S[(6)7]	NP	(4)5	1–3	0.47-0.57	0.33–0.49	0.24-0.30	57.5–90	9–12/ 15–19	50-62.5	3–5, ud	E, 25– 62.5(107.5)	$17.5-32.5 \\ \times 12.5-35 \\ (42.5)$	7.5–17.5 × 7.5–15
E rivularis	H	Vs	S[5-7(8)]	NP	5-7	3(5)	0.61-1.06	0.55-0.90	0.29-0.50	85–92.5	9–12/ 17–21	14-20	3–5, ud	E, (18)25– 100(120)	$15-30 \times 12.5-25$ (37.5)	10–25 × 7.5–30
F. nigrescens	E	Vs	S[(6)7]	ΔŊ	5(6)	3	(0.42)0.59– 0.80	0.38-0.60	0.20-0.35	62.5- 77.5	8-9/ 17-19	35-77.5	4–5, ud	E(A), (10)20- 37.5	$15-30 \times 12.5-20$	7.5–17.5 × 7.5–20
F. nevadensis	H	Λ	S[(5)7–9]	S[5–7]	7(9)	5-7(8)	(0.65)0.75 - 1.30	0.74-1.25	0.23-0.45	82.5-120	9–13/ 16–21	50-120	3–5, ud	E, (20)42.5- 125 (158)	20-40 × 12.5-37.5	12.5–22.5 × 7.5–15
F. rothmaleri	H	>	S[8-10]	NP	6-7	5-7	(0.56)0.79– 1.07	0.41–0.85	(0.22)0.33– 0.37	80-95	9–11/ 18–22	50-100	6–7, ud	E, (13)25– 75(113)	12.5–30 × 12.5–27.5	7.5-17.5 ×7.5- 22.5
F. pyrenaica	Fl, L3	Vs	S[9(11)]	NP or S[3]	7(9)	5(7)	0.57-0.92	0.52-0.61	0.17-0.25	57.5-75	9–10/ 15–21	22.5–25	3-4, ud	E, 15–37.5	12.5-20 × 10-20	7.5-15 (17.5) × 5-15
F. juncifolia	н	Ur–a	C or S[(6)7] (G _{MVR})	S[3–5]	7	3-5	0.67–0.98 (1.55)	0.61-0.86	0.31-0.39 (0.47)	85-100	9–12/ 18–22	47.5–52.5	3–5, ud	E, 12.5–85	12.5–30 × 17.5–32.5	7.5–17.5 × 5–17.5
F. heterophylla		IL. Va	S[5]	NP	3	1	0.36-0.39	0.34-0.41	0.23-0.26	47.5- 67.5	nd/ 14–18	15-27.5	4–5, ud	A, 17.5–37.5	12.5–5 × 5–12.5	7.5–15 × 5–10
subsp. <i>hetero-</i> phylla	E	CL. F	S[9]	NP	7	Ś		2.32	0.16	85	nd/ 18	35-50	4-5, d	E, 10–102.5	12.5–30 × 10–20	$10-15 \times 10-12.5$ (20)
F. heterophylla		IL. Va	S[(6)7]	NP	5-7	3	0.64-0.68	0.53-0.61	0.27-0.31	75-82.5	8-10/ 19-21	32.5-37.5	3–5, ud	A, 10–25	12.5–25 × 10–17.5	7.5–15 × 7.5–15
blanquetii	=	CL. F	S[9]	NP	10	9–10		3.43	0.33	92.5	9/ 20	22.5	4–5, d	A, 12.5–14 (G)	17.5–27.5 × 12.5–15	7.5-20 × 5-20
Sect. Eskia																

Taxa	Clade, lineage	Outline	Abaxial sclerenchyma pattern	Adaxial sclerenchyma pattern (in ribs)	Vascular bundles number	Ribs number	Length (mm)	Width (mm)	Thickness at the mid- rib (mm)	MVB max. size (µm)	OBS/ IBS number	Sclerenchyma thickness at the midrib (µm)	Bulliform cells number	Adaxial site trichomes (µm)	Abaxial epidermal cells, L × W (µm)	Adaxial epider- mal cells, L × W (µm)
F. eskia	E	Ue (F)	U	S[(6)7–13]	10-13 (17)	7–11 (13)	(0.75)0.89- 1.10 (1.47)	0.72 - 1.02 (3.23)	0.27-0.38	80-102.5	10–13/ 17–22	30-75	3–5, ud	E, (13)20–65 (70)	$7.5-20 \times 5-12.5$	7.5–12.5 × 5–10
F. × picoeuro- peana	H	Ue-a	С	S[3-5(7)]	7(9)	3-5(7)	0.57-0.87	0.55-0.73	0.25-0.33	72.5- 87.5	8-14/ 17-21	35-47.5	3–7, ud	E, 20–52.5	$5-20 \times 5-15$	5-10 × 5-7.5
F. burnatii	E	Ue	C, Ci or S[7]	S[4–5(6)]	(5)7(9)	4-5(6)	(0.38)0.47- 0.80 (0.90)	0.32-0.60	(0.19)0.26– 0.32 (0.47)	57.5–8	7–10/ 13–16	20-62.5	3–5, ud	E, (17.5)22.5- 57.5	17.5–30 × 10–17.5	7.5-12.5 × 7.5-10
F. elegans	E	Ue	U	NP	2	1	0.47-0.67 (0.70)	0.40-0.53	0.18-0.26 (0.30)	112.5-170	11–15/ 21–34	12.5–25	3-4, ud	E, (15)35–70	10–17.5 × 7.5–17.5	7.5-12.5 × 5-10
F. gautieri	H	Ua	C, Ci or S[7–9]	NP	5-7	1	0.44-0.67	0.53-0.60	0.28-0.46	72.5- 92.5	9-14/ 17-24	25-75	4–7, ud	E, (10)20– 42.5(47)	$12.5-20 \times 10-20$	5-10 × 5-7.5
Sect. Subbulbo.	ae															
F. baetica	Bl	Ur	(Ci or Ci+) $G_{1,2}$ (S ₃)	ج	17–23	3	1.03–1.66	0.99–1.64	0.49-0.74	142.5- 200	18–25/ 30–36	105-232.5	4–7, d	E, 7.5– 27.5(32)	10–22.5 × 5–10	7.5–15 × 5–15
F. paniculata s.l.	Bl	Ur (Vs or F)	$(C \text{ or } Ci+) \\ G^{(*)}_{1} + S_{2,3}$	$G^*_{1}(S_{2,3})$	13-20	3-9	1.0–2.14	0.95-1.96 (4.18)	0.35-0.53	90-132.5	13–15/ 20–30	50-150	4–10, d or ud	A, (7)10– 22(30)	15–32.5 × 7.5–25	7.5-17.5 × 7.5- 17.5
F. durandoi	Bl	Ur or Vs	S[10–13]	NP or S[1–2]	11-13	1–3	0.66-0.89	0.66-0.95	0.29-0.36	75–92.5	11–12/ 19–22	47.5-62.5	4–7, d or ud	A, 7.5– 27.5(G)	15-27.5 × 10-25	5- 17.5 × 7.5-15
Sect. Lojaconou																
F. coerulescens	Bl	F	$G_{1,2,3}$	$G_{1,2,3}$	10-14	8-12		1.67–2.25	0.20-0.26	90-110	i/ 18–22	27.5-42.5	4–7, d	G or A, 5–12.5	7.5–17.5 × 10–17.5	7.5–12.5 × 7.5–15
F. patula	Bl	ц	$G_{1,2} + S_3$	$G_1 + S_{2,3}$	12-17	11–16		(1.57)2.22– 4.46	0.15-0.35	75-107.5	i/ 20–21	20-50	49, d	G	25–47.5 (57.5) × 17.5–42.5	10–20 × 7.5–17.5
Sect. Scariosae																
F. scariosa	Bl	Ur (F)	$C(Gi)+G_{1,2,3}$	$\mathrm{G}^*_{1,2}$	14–19	11-15	(0.74)0.89- 1.67	0.97–2.39	0.37-0.54	117.5- 132.5	14–16 (i)/ 26–30	75-112.5	4–7, d or ud	A(E), 20– 37.5(38)	7.5–15 × 2.5–10	5-12.5 × 5-10
Sect. Pseudosca.	riosa															
F. pseudeskia	BI	Ur (F)	$G^{(*)}_{1,2}(G_3)$	$G^*_{1,2}$	15–18	58(9)	1.23–2.32	1.12–2.37 (2.72)	0.41-0.63	85-112.5	8–13/ 19–27	185–225	4–5, d or ud	E, 25–42.5	10–15 × 7.5–12.5	7.5–17.5 × 5–7.5

Taxa	Clade, lineage	Outline	Abaxial sclerenchyma pattern	Adaxial sclerenchyma pattern (in ribs)	Vascular bundles number	Ribs number	Length (mm)	Width (mm)	Thickness at the mid- rib (mm)	MVB max. size (µm)	OBS/ IBS number	Scienchyma thickness at the midrib (µm)	Bulliform cells number	Adaxial site trichomes (µm)	Abaxial epidermal cells, L × W (µm)	Adaxial epider- mal cells, L × W (µm)
B. SUBGENU	S DRYM	tANTHEL	E													
Sect. Phaeochlo	a															
F. altisima	Bl	ц	$G_{1,2,3}$	$G_{1,2,3}$	25-32	23–30		5.44-10.16	0.12-0.27	87.5- 92.5	i/ 18–22	22.5-47.5	5, d	G(A), 15–30	7.5–17.5 × 12.5–27.5	5-7.5 × 7.5-15
F. lasto	Bl	ц	$G_{1,2,3}$	$G_{1,2,3}$	40-45	39-44		10.13–16.58 (20)	(0.20)0.26- 0.38	105 - 137.5	i/22–29	52.5–95	5-7, d	A, 7.5–45	$10-15 \times 10-22.5$	7.5–15 × 10–17.5
C. SUBGENL	IS SCHE.	DONORI	SC													
Sect. Schedonor	511															
F. mediter- ranea	Bl	ц	G_1+S_2	$S^{*}_{1,2}$	7–20	(7)12- 18		(1)1.24- 7.09	0.23-0.34	82.5-110	11–17/ 18–25	57.5-80	(3)5–7, d	A, 15–37.5	$10-15 \times 20-25$	12.5-22.5 × 17.5-25
F interrupta	Bl	щ	$G_{1,2}+S_3$	$G^*_{1,2}$	12-20	10–19		1.76–6.48	0.31-0.39	95-125	13–16/ 24–25	77.5–105	6 - 8, d	G or A, 30–42.5	10–15 × 12.5–22.5	12.5–22.5 × 12.5– 27.5
F. arundinacea	Bl	ц	$G_{1,2}(S_3)$	$G_{1}^{*} + S_{2}(S_{3})$	13-17	11-15		4.30-12	0.23-0.28 (0.37)	95-130	12–15/ 22–24	62.5-75	59, d	G(A), 25-42.5	12.5–22.5 × 17.5–25	12.5–27.5 × 12.5–25
Sect. Plantynia																
F. gigantea	Bl	ц	$G_{1,2,3}$	$G_{1,2,3}$	29–35	29–31		13-14.13	0.30-0.32	100-120	i/ 20–23	82.5-117.5	5-6, d	G(A), 22.5–30	$12.5-30 \times 17.5-30$ 17.5-30 (37.5)	$12.5-20 \times 12.5-30$ (37.5)

Study of the leaf anatomy in cross-section in the Iberian species of *Festuca*

chloroplast *trn*L and *trn*L-F markers has been added when the molecular classification differs from the conventional one (Torrecilla and Catalán 2002; Torrecilla et al. 2004; Catalán et al. 2006, 2007; Nova et al. 2006; Inda et al. 2008). The main anatomical patterns found are discussed in relation to the two large clades recognized in molecular analyses within genus (*Festuca* s.str.) (Fig. 3): broad-leaved taxa and fine-leaved taxa (e.g., Charmet et al. 1997; Catalán et al. 2004; Inda et al. 2008). Illustrations of a selection of leaf cross-sections are provided in Figs 4–9.

Leaf anatomy in the Festuca species of the fine-leaved clade

The fine-leaved fescues (see Fig. 3) present the outline of the blade in the transverse section usually conduplicate (from U- to V- or Y-shaped) and they usually do not exceed 1.5 mm in length, except for *F. henriquesii* and some rare forms of *F. eskia* with flat leaves (up to 3.3 mm wide). The sclerenchyma may be arranged in a continuous ring or forming strands that occasionally contact with the median or lateral vascular bundles, but never forming complete (abaxial and adaxial) sclerenchyma girders. The bulliform cells located in the intercostal zones are inconspicuous, and may even be absent (Table 1A, Figs 4–7).

This group comprises 3 taxonomic sections (sects. *Festuca*, *Aulaxyper*, and *Eskia*) which have been segregated into 4 different lineages according to the molecular phylogenies (e.g., Torrecilla et al. 2004; see Fig. 3). In those analyses, the location of some species from sects. *Festuca* (subsects. *Festuca* and *Exaratae*) and *Aulaxyper* differs slightly with the conventional classification (Fig. 3).

Festuca sect. Festuca

The sect. *Festuca* (34 species analysed) in its traditional circumscription has the most diversity in anatomical features among the fine-leaved species. Three main patterns were observed regarding the arrangement of the sclerenchyma. The first pattern arranges sclerenchyma in a continuous ring, sometimes interrupted by just a few cells. The second pattern presents the sclerenchyma arranged in strands at the margins and midrib, rarely opposite the vascular bundles. The third pattern shows strands opposite the vascular bundles, frequently contacting the median or lateral vascular bundles (namely abaxial girder).

In the first pattern, the leaf is always conduplicate, often U-shaped and from elliptic to orbicular in outline, and may present from 3 to 9 (rarely 11) vascular bundles and from 1 to 3 (rarely 5) inconspicuous, slightly rounded ribs, with or without adaxial sclerenchyma strands (Table 1A, Fig. 4A–G). This is the most frequent anatomical model among the species of the sect. *Festuca* (subsect. *Festuca*) that dominate in high mountain pastures (about 21 species), although it is also present in the coastal taxa *F. vasconcensis*, *F. glauca*, and *F. brigantina* subsp. *actiophyta* (Table 1A).



Figure 3. Simplified cladogram showing the major supraspecific relations in *Festuca* s.str., based and adapted on phylogenetic trees from Catalán et al. (2004), and Inda et al. (2008). Main leaf anatomical patterns are exemplified in each line evolutive. Abbreviations: L1, lineage 1; L2, lineage 2; and L3, lineage 3. Asterisks indicate sections which have been included in other subgenera by several authors (sect. *Phaeochloa* in the subgenus *Drymanthele*, and sects. *Schedonorus* and *Plantynia* in the subgenus *Schedonorus*).

Traditionally, the species of sect. Festuca with this anatomical pattern have been included within the broad "F. ovina complex", which in turn includes groups of species with greater or lesser taxonomic difficulty (cf. Cebolla and Rivas Ponce 1999; Foggi et al. 2006; Pyke 2013; López et al. 2016). As in most species of the sect. Festuca, they have intravaginal innovations and sheaths usually open, as well as great morphological similarity. Almost all of these species grow in places that are dry, windswept, and nutrient deficient. They share a set of anatomical xeromorphic features such as strongly conduplicate leaves, of greater diameter in cross-section, highly developed sclerenchyma on the abaxial face, thick cell walls and abundant cutinization, small-sized lumen of the epidermal cells, bulliform cells barely visible or very small and relatively undifferentiated from the rest, and high density of trichomes on the adaxial face (Fig. 4). Many studies have indicated that the thickness of the sclerenchyma, and sometimes its arrangement and distribution, may vary depending on the environmental conditions, age and development of the leaf (Aiken and Consaul 1995). The sclerenchymatous protection may have played a major role in the survival of many grass species in such extreme ecological environments, since it confers mechanical support and protection, and contribute to rolling or folding of leaves, reducing water loss in drought conditions (Wrobel et al. 2007). The amount of basal sclerenchyma (maximum values of sclerenchyma found in F. valentina, F. longiauriculata, F. indigesta, and F. summilusitana), pubes-



Figure 4. Leaf cross-sections of the *Festuca* sect. *Festuca* species from lineage 1. A *F. hystrix* B *F. reverchonii* C *F. segimonensis* D *F. indigesta* E *F. michaelis* F *F. glauca* G *F. vasconcensis* H *F. brigantina* subsp. *actiophyta* (the arrow indicates inflated adaxial epidermal cells) I *F. marginata* subsp. *andres-molinae* J *F. rivas-martinezii* K *F. frigida* L *F. alpina* M *F. glacialis.* Scale bars: 0.2 mm.

cence, and the size of the trichomes (maximum density and values in *F. summilusitana*, *F. gredensis*, *F. indigesta*, and *F. glauca*) are characters with high variability at intra- and inter-species levels, and could be a response to micro-environmental differences, therefore those have been considered just as descriptive characters (Connor 1960; Aiken and Consaul 1995; Ramesar-Fortner et al. 1995).

The length of the leaf section and the number of vascular bundles and ribs facilitated species distinction such as F. hystrix and F. reverchonii, the species of this group with the smallest diameters, characterized by having 3 vascular bundles and 1 median rib with sclerenchyma (Table 1A, Fig. 4A, B). These two species also present unique morphological characters within Festuca sect. Festuca such as the apex of the leaf being noticeably flattened in the first, and helicoid and scabrous leaves in the latter (Ortúñez et al. 1995). The remaining species show a considerable overlap of these characters which hampers the identification based solely on their leaf anatomy (Table 1A). For example, anatomy was useless to discriminate the species of the most complex groups within the sect. Festuca, as seen in the species studied of the "F. inops group" (F. michaelis, F. inops, and F. valentina), and for the species of the "F. indigesta group" (e.g., F. indigesta, F. summilusitana, F. gredensis, and F. yvesii, among others) (Table 1A). Within the latter group, only for *F. segimonensis* the leaf anatomy helped in its identification as the taxon has a more or less orbicular outline and presents adaxial sclerenchyma strands on its 3 ribs, which are more pronounced (with somewhat compressed bases) than in the other species (Fig. 4C).

Coastal species tend to have the largest abaxial epidermal cells (most visible in *F. glauca*; Fig. 4F), although with overlapping and not significant values. Generally, their subepidermal cells on the adaxial face are more or less inflated, which is a highly variable character even within the same population but that has been used by Fuente and Ortúñez (1998) to distinguish between *F. vasconcensis* (Fig. 4G) and other species. This character is also observed in *F. brigantina* subsp. *actiophyta* (absent in *F. brigantina* subsp. *brigantina*), another coastal taxon that was described from ultrabasic rocks of the northwest Iberian Peninsula (cf. Gutiérrez Villarías et al. 1997) and which is variable in the sclerenchyma arrangement (Table 1A, Fig. 4H). In this sense, it has been noted that, in addition to thick adaxial epidermis, plants growing near the sea present other adaptations against water loss under conditions of salt stress such as more-developed bulliform cells and atypical vascular bundles (Giełwanowska et al. 2005), although these characters were not observed in this study.

The molecular analyses group together all the species of sect. *Festuca* with continuous (or more or less interrupted) sclerenchyma within the first lineage of the fineleaved clade (mostly subsect. *Festuca* species) (Fig. 3). Only *F. clementei* (Fig. 5F), a species that may have both continuous and discontinuous sclerenchyma, falls into lineage 3 together with the species of *Festuca* subsect. *Exaratae* and others close taxa (Fig. 3). Interestingly, in this species, the basal sclerenchyma is thicker and occasionally contacts the median vascular bundle (Table 1A), an anatomical feature that also appears in other phylogenetically related species (see below).

In the second pattern within sect. Festuca, the strands never make contact with the vascular bundles, and two variants can be recognized. The first variant is characterized by 3 strands of sclerenchyma, two marginal (apical in the cross-section) and one at midrib (basal in the cross-section), sometimes even visible externally on the leaf. The leaves are conduplicate, with elliptical cross-section, or in a V- or Y-shape, from 0.5 to 1 mm in length, with 7 (rarely 9) vascular bundles and 3 (more rarely 1) ribs without adaxial sclerenchyma strands (Table 1A). This pattern is present in *F. marginata* subsp. alopecuroides, F. marginata subsp. and res-molinae, F. marginata subsp. marginata, and F. rivas-martinezii which have traditionally been included in the "F. marginata group" (Fig. 4I, J). They are distributed over the centre, east, and northeast of the Iberian Peninsula, and some reach France. Some anatomical characters have been used in the taxonomy of this group such the ribs shape, which varies between rounded to more rarely truncate, and does not discriminate among these taxa, and the decurrence of the sclerenchyma strands (Kerguélen and Plonka 1989; Cebolla and Rivas Ponce 2003b). In the species studied, the arrangement of the marginal strands is very variable but that of the basal strand has taxonomic utility (although its observation requires some practice). It is decurrent in F. marginata subsp. alopecuroides and F. rivas-martinezii (Fig. 4]), and truncate and no decurrent in *F. marginata* subsp. marginata and *F. marginata* subsp. andres-molinae (Fig. 4I). Very rarely, the sclerenchyma was found to be continuous (Table 1A), making it very difficult in these cases to identify them from other "F. ovina complex" species. The species that share this anatomical pattern are included in lineage 1 of the fine-leaved clade (Festuca subsect. Festuca; Fig. 3). The AFLP and RADP markers seem to group these species together, although the trnL chloroplast marker does not discriminate affinities (Nova et al. 2006). In the second variant, the sclerenchyma may be arranged on the margins and the midrib, or also occasionally opposite some vascular bundles (Fig. 4K-M). The leaves are also conduplicate, but differ from the previous variant because the length of the leaf section is much smaller (0.34–0.62 mm), there are fewer vascular bundles (3 to 5), and the sclerenchyma strands are usually thinner, in addition to the adaxial trichomes being less abundant (Table 1A). This leaf model is that presented by the "F. alpina group" species which live in the alpine or subalpine habitats of the north (F. alpina and F. glacialis) and southeast (F. frigida) of the Iberian Peninsula. They are characterized by their small size, flexible leaves, and short panicles with few spikelets (López et al. 2016). The three species are phylogenetically very close (Catalán et al. 2007), and appear grouped within the lineage 1 (Festuca subsect. Festuca; Fig. 3).

In the third pattern, the sclerenchyma is opposite the vascular bundles, and frequently with an abaxial girder on the medial or lateral vascular bundle (Fig. 5A–E). This group includes species with anatomical characteristics intermediate between those of the previous species (lineage 1) and those of lineage 2 (mostly sect. *Aulaxyper* species, see below and Fig. 3). The majority of these species have a conduplicate leaf, and many of them are easily recognizable by their anatomy (Table 1A), an example being *F. plicata* (Fig. 5E) which has a trigonal or rhombic outline. *Festuca capillifolia* (Fig. 5D) presents an angular (polygonal) outline and differs from anatomically similar spe-



Figure 5. Leaf cross-sections of the *Festuca* sect. *Festuca* species from lineage 2: **A** *F. querana* **B** *F. ampla*; from lineage 3: **C** *F. borderei* **D** *F. capillifolia* **E** *F. plicata* **F** *F. clementei*; and unknown: **G** *F. henriquesii*. Scale bars: 0.2 mm.

cies such as F. ampla (Fig. 5B) because it does not present adaxial sclerenchyma on all of its ribs. Festuca querana (Fig. 5A) has a smooth outline and presents a more developed lateral abaxial sclerenchyma than the other species, even making contact with the vascular bundles, and neither does it present sclerenchyma on the ribs. The leaf anatomy of *F. borderei* (Fig. 5C) is similar to the previous species but it has a greater number of strands that in no case or very rarely contact the lateral vascular bundles and neither fuse abaxially. Interestingly, these anatomically heterogeneous species with unique anatomical patterns fall into a different clade from that formed by most species of sect. Festuca in the molecular trees (Catalán et al. 2004). Thus, F. capillifolia and F. borderei, which were already separated from the rest in the subsect. Exaratae due to morphological differences in their leaf sheaths (Saint-Yves 1922), are also differentiated in molecular phylogenies, being placed in a basal position (lineage 3) with respect to subsect. Festuca (lineage 1) and sect. Aulaxyper (lineage 2) (see Fig. 3). Festuca plicata seems to be more related to some species of the genus Vulpia and to the two previous species than to the rest of the species of subsect. Festuca (Catalán et al. 2004). Finally, F. ampla and F. querana are grouped together with the species of sect. Aulaxyper (Catalán et al. 2004; Nova et al. 2006), with which they share some anatomical characteristics.

Within this section, only one species, *F. henriquesii* (Table 1A, Fig. 5G), has a flat (or very broad V-shaped) leaf, with adaxial and abaxial strands on the margins and at the level of the vascular bundles which they do not make contact. Although there are no data on the phylogenetic relationships of this species, its leaf anatomy and some morphological characters such as closed leaf sheaths (Fuente and Ortúñez 1995) make it seem to be more related to the species of sect. *Aulaxyper* than those of sect. *Festuca*.

Festuca sect. Aulaxyper

Almost all the species of this section (10 species analysed) share a pattern of abaxial sclerenchyma distribution of the leaves in strands opposite each of the vascular bundles, and at the leaf margins (Fig. 6). Although not very frequent, some species may present adaxial sclerenchyma on the ribs, which are well defined in this group. The leaves are frequently conduplicate, and exceptionally the cauline leaves may be flat (Table 1A). Only in *F. juncifolia* (Fig. 6A), a species that grows in the dunes and coastal sands in the north of the Iberian Peninsula, the abaxial strands frequently make contact forming a continuous or slightly disrupted ring. In most species, the leaf section has a polygonal outline (e.g., *F. iberica* and *F. nigrescens*; Fig. 6F, G), sometimes carinate (e.g., *F. rivularis* and *F. heterophylla*; Fig. 6C, H1, I), although with a great diversity of forms transitioning towards V-shaped (e.g., *F. rothmaleri* and *F. nevadensis*; Fig. 6D, E), and more rarely orbicular (*F. juncifolia*; Fig. 6A) or obovoid (some forms of *F. rubra* subsp. *pruinosa*, a species that is highly polymorphous in outline; Fig. 6B).

The only Iberian species of the genus with leaf dimorphism is *F. heterophylla* s.l., in which the cauline leaves are flat (Fig. 6H2) but those of the innovations are conduplicate and very narrow (especially in the subsp. *heterophylla*) (Fig. 6H1, I). In general, in the species of this section the abaxial epidermis cells are larger than those of the sect. *Festuca* (especially those in lineage 1), although variation in size was observed throughout the leaf cross-section, with greater values in the sides of the keel (remarkably in *F. rivularis*; Fig. 6). In addition, some of them are easily recognizable by their scalloped abaxial surface seen in cross-section (e.g., *F. iberica* and *F. trichophylla*; detail in Fig. 6F vs. not scalloped in Fig. 6D). In relation to the adaxial epidermis cells, it stands out that they are inflated in almost all the species of sect. *Aulaxyper* (Fig. 6, detail in Fig. 6H1), not only the coastal species as was the case in sect. *Festuca*. The thickness of the sclerenchyma strands, which has in some cases been used to separate some species (*F. nigrescens* vs. *F. iberica*), was found to be a very variable character, calling into question the taxonomic value that it had been given (Table 1A, Fig. 6F, G).

The species of sect. *Aulaxyper* ("*F. rubra* complex") are characterized morphologically by their extravaginal innovations, with reddish-brown closed leaf sheath, generally fibrous (Hackel 1882). Most species live in woodland and meadows, on wet soils, and many are widely distributed throughout central, northern, and southwestern Europe (Markgraf-Dannenberg 1980). All the species of this group with the exception of



Figure 6. Leaf cross-sections of Iberian species of the *Festuca* sect. Aulaxyper from lineage 2: A *F. junci*folia B *F. rubra* subsp. pruinosa C *F. rivularis* D *F. rothmaleri* (in detail abaxial surface not scalloped) E *F.* nevadensis F *F. iberica* (in detail scalloped abaxial surface) G *F. nigrescens* H *F. heterophylla* subsp. braunblanquetii (H1 innovation leaf, in detail inflated adaxial epidermal cells; H2 cauline leaf) I *F. heterophylla* subsp. heterophylla (innovation leaf); and from lineage 3: J *F. pyrenaica*. Scale bars: 0.2 mm.

F. pyrenaica (lineage 3) fall into lineage 2 (see Fig. 3), although, as also is the case in the sect. *Festuca*, the phylogenetic relationships between the species are not well defined. In *F. pyrenaica* the outline is elliptical or obovate, and neither does it present a girder in the median vascular bundle (Fig. 6J).

Festuca sect. Eskia

The most frequent anatomical model for the species of this section is the sclerenchyma arranged in a continuous ring (Fig. 7A–E1), sometimes interrupted or forming irregular and decurrent strands as in *F. burnatii* (Fig. 7C), and only in *F. gautieri* might the sclerenchyma be continuous or arranged in well-defined or decurrent strands at the level of the vascular bundles (Fig. 7E2). The leaves are strongly conduplicate, although occasionally an individual of *F. eskia* was detected with more or less flat leaves (Fig. 7A2), both in the shoots from the sterile innovations and in the cauline leaves. This type of leaf was found in a plant that was growing in grassy and wet pastureland under the shelter of a rock, so it is possible that these variations are the result of phenotypic plasticity strongly influenced by environmental conditions. In fact, some *Festuca* species which have strongly folded leaves in dry places have been observed to have more or less flat leaves in moist conditions (Aiken et al. 1985).

In general, the sect. Eskia includes species with an outline that is elliptical (F. elegans; Fig. 7D), more or less obovate (F eskia and F burnatii; Fig. 7A1, C), sometimes slightly angular (F. × picoeuropeana; Fig. 7B), or markedly polygonal (F. gautieri; Fig. 7E1, E2), especially in those with sclerenchyma arranged in strands. In this sense, it has been shown that leaves with a more continuous sclerenchyma on the abaxial surface usually present a rounded and smooth outline, whereas those with sclerenchyma in strands have a more angular outline (Aiken and Consaul 1995). The largest leaf cross-section sizes are reached by *F. eskia* followed by *F. × picoeuropeana* and *F. burnatii*, while *F. gautieri* and *F. elegans* presented the smallest sizes (Table 1A). All of them have usually small-sized epidermal cells and abundant adaxial trichomes. They are glabrous on the abaxial surface, except F. elegans that is scabrous and also has a larger median vascular bundle diameter in proportion to the cross-section length (Fig. 7D, Table 1A). Section Eskia comprises species that share many anatomical features with the sect. Festuca but they are morphologically segregated from that section because they present broadly scarious lemmas and glumes and because of the shape of the ligule (Willkomm 1861; Fuente and Ortúñez 2001). The species of sect. Eskia inhabit alpine and subalpine pastures of the north of the Iberian Peninsula, being able to extend into the French Pyrenees, as well as in the mountains of the centre, northwest, and south of the Iberian Peninsula (Ortúñez and Fuente 2004; Torrecilla et al. 2013).

Anatomically, the $F \times picoeuropeana$ hybrid shares intermediate anatomical characters with its parents, *F. eskia* and *F. gautieri*, mainly those referring to the outline, shape and number of ribs, and number of vascular bundles (Fig. 7B). Representatives from *Festuca* sect. *Eskia* were resolved as basal of the fine-leaved clade (Torrecilla et al. 2003, 2013).



Figure 7. Leaf cross-sections of the *Festuca* sect. *Eskia* species. **A** *F. eskia* (A1 conduplicate leaf, A2 flat leaf) **B** F × *picoeuropeana* **C** F *burnatii* **D** F *elegans* **E** F *gautieri* (**E1** sclerenchyma in continuous ring, **E2** in strands). Scale bars: 0.2 mm (**A–E**), and 0.3 mm (**A2**).

Leaf anatomy in the Festuca species of the broad-leaved clade

The broad-leaved taxa show two models of leaf cross-section: from narrowly flat (up to 2.4 mm wide, rarely reach 4 mm) to more generally conduplicate innovation leaf blades (up to 2.3 mm length) in the species of the sects. *Subbulbosae, Scariosae* and *Pseudoscariosa* (subgen. *Festuca*; Table 1A, Fig. 8); or completely flat (up to ca. 17 mm wide), with the leaves being more or less rolled up in prefoliation or under conditions of water stress (very visible especially in herbarium specimen sheets), as in the sects. *Lojaconoa* (subgen. *Festuca*; Table 1A, Fig. 9), *Phaeochloa* (subgen. *Drymanthele*; Table 1B), and sects. *Schedonorus* and *Plantynia* (subgen. *Schedonorus*; Table 1C).

Species of this clade present complete girders that extend from the vascular bundles to both the abaxial and the adaxial epidermis (except in *F. durandoi*), which can contact the abaxial face with a continuous or discontinuous ring. The girders may consist only of small sclerenchyma cells with thickened and lignified walls, sometimes interrupting the outer bundle sheath, or the outer sheath may possess girder-like extensions contacting with the sclerenchyma tissue, on both the abaxial and the adaxial faces. The density and size of the adaxial trichomes are less than in the fine-leaved fescues, particularly marked in the species with a completely flat leaf section where they may be glabrous or present small and very scattered aculei (Table 1). Noticeable in most species is the presence of large, highly developed bulliform cells in the intercostal spaces, making the leaf blade unfold (see exceptions in sects. *Subbulbosae, Scariosae* and *Pseudoscariosa*). In this great clade, 7 lineages are recognized that correspond to 7 well-defined taxonomic sections (Fig. 3), which have been distributed in three different subgenera.



Figure 8. Leaf cross-sections of the *Festuca* sects. *Pseudoscariosa* (**A**), *Scariosae* (**B**) and *Subbulbosae* (**C–E**) species. **A** *F. pseudeskia* (**A1** conduplicate leaf, arrow pointing to the colourless cells; **A2** flat leaf) **B** *F. scariosa* (**B1** conduplicate leaf, **B2** flat leaf) **C** *F. baetica* (arrow pointing to the colourless cells) **D** *F. paniculata* s.l. (**D1** subsp. *multispiculata*, **D2** subsp. *fontqueri*, **D3** subsp. *paui*, **D4** subsp. *longiglumis*) **E** *F. durandoi*. Scale bars: 0.3 mm (**A–E**), and 0.4 mm (**D4**).



Figure 9. Leaf cross-sections of the *Festuca* sects. *Lojaconoa* (**A–B**), *Schedonorus* (**C–E**), and *Phaeochloa* (**F–G**) species. **A** *F. patula* **B** *F. coerulescens* (arrow pointing to the sclerenchyma interrupting the cells of the outer median vascular bundle sheath) **C** *F. interrupta* (**CI** inrolled leaf, **C2** flat leaf) **D** *F. arundinacea* (arrow pointing to the bulliform cells) **E** *F. mediterranea* (**EI** mature leaf, **E2** inmature leaf) **F** *F. altissima* **G** *F. lasto.* Scale bars: 0.4 mm (**A–E**), 0.5 mm (**F**), and 0.6 mm (**G**).

Festuca sects. Scariosae and Pseudoscariosa

The sects. Scariosae (F. scariosa) and Pseudoscariosa (F. pseudeskia) have very similar anatomical patterns (Fig. 3). The leaves are more or less conduplicate, although sometimes they can have very extended blades and be almost flat, with the midrib only slightly differentiated (Fig. 8). They are characterized by the presence of adaxial and/ or abaxial sclerenchyma girders (usually T-shaped on the adaxial side) in the first-order and second-order vascular bundles, associated with extensions of the bundle sheath composed of large, thin-walled, colourless cells of the same size as or larger than the outer bundle sheath cells, and girders or strands facing the third-order vascular bundles only on the abaxial face, or sometimes without sclerenchyma. The girders may finish in a sclerenchyma ring as in F. scariosa (Fig. 8B), or not as in F. pseudeskia (Fig. 8A). In cross-section, both species present deep heteromorphic furrows, rounded or sometimes truncate or slightly triangular. Bulliform cells are less developed in the conduplicate forms of these sections (Fig. 8A1, B1), sometimes unnoticeable, whereas they are far more developed in the extended or more or less flat forms (Fig. 8A2, B2). Epidermal cells are small in both species, especially those on the abaxial face in F. scariosa, most likely due to the presence of the continuous ring and a strongly cuticularized epidermis. They grow in the south and southeast of the Iberian Peninsula, and present mixed shoots and short rhizomes (Fuente and Ortúñez 2001). Given their morphological characteristics, both taxonomic sections have been included within the broad subgenus *Festuca*, although phylogenetic reconstructions show that they are more related to species of the sect. Phaeochloa (e.g., Torrecilla et al. 2003; Fig. 3), with which, however, they show major anatomical differences (Fig. 9, see below).

Festuca sect. Subbulbosae

The anatomical model of the species of the sect. *Subbulbosae* hardly differs from the previous ones, except that complete girders (T-shaped and usually with colourless cells towards the adaxial epidermis) are only found in the main vascular bundles and are usually absent in the secondary vascular bundles (Fig. 8C–E). Anatomical differences have been found between species with regard to the arrangement of the sclerenchyma and the form and number of ribs (Fig. 8C–E). Some variations of *F. paniculata* s.l. have been found and these may correspond to different infraspecific categories (Fig. 8D1–D4). One variant is characterized by a flat section, a great number of vascular bundles, with complete girders in the first- and second-order vascular bundles, and strands in those of third-order, which never end in a ring on the abaxial face, and that could correspond with *F. paniculata* subsp. *longiglumis* (Fig. 8D4), the only subspecies of the "*F. paniculata* group" for which completely flat leaves have been described. More frequent is the variant characterized by having conduplicate (U- or V-shaped) leaves, whose arrangement of the abaxial sclerenchyma may be in the form of a continuous band (*F. paniculata* subsp. *multispiculata*; Fig. 8D1), an almost continuous band with

the base of the girders swollen (*F. baetica*; Fig. 8C), or in strands which confluent with the first-order vascular bundles (*F. paniculata* subsp. *fontqueri* and *F. paniculata* subsp. *paui*; Fig. 8D2, D3, respectively). *Festuca durandoi* (Fig. 8E) differs from all the foregoing species in that it presents neither complete sclerenchyma girders nor adaxial girders, and it have underdeveloped strands, generally smaller leaf length and width, and lateral ribs absent or inconspicuous.

The sect. *Subbulbosae* was also traditionally included in the subgenus *Festuca*, being characterized by the presence of intravaginal innovations, leaves with swollen bases that confer a sub-bulbous appearance, and split sheaths. However, phylogenetically it is located in the same clade as the sects. *Plantynia* and *Schedonorus* with which it has evident anatomical differences (Torrecilla and Catalán 2002).

Festuca sect. Lojaconoa

The leaf model of sect. *Lojaconoa (F. patula* and *F. coerulescens*) shares many characteristics with the rest of the taxonomic sections with flat leaves (Fig. 3, Table 1B, C). *Festuca patula* (Fig. 9A) only presents girders in the primary and secondary vascular bundles, and has a greater number of vascular bundles. Its adaxial surface is almost smooth with the intercostal spaces defined only by the bulliform cells, and the midrib projects abaxially. *Festuca coerulescens* (Fig. 9B) presents complete girders in all its vascular bundles, and generally has fewer vascular bundles and ribs, the latter being truncate and with relatively pronounced intercostal spaces. In both, the sclerenchyma girders interrupt the outer first-order bundle sheath cells in the adaxial and abaxial surfaces, and are not associated with colourless cells. These may sometimes be present but only associated with lower order vascular bundles towards the adaxial face. In addition, the epidermal cells are clearly visible on the abaxial face, which is glabrous or slightly aculeate. They are the only species of the subgenus *Festuca* with totally flat leaf blades, and are characterized morphologically by basally swollen leaf sheaths (Müller and Catalán 2006).

Festuca sect. Phaeochloa

The anatomical pattern presented by the species of this section (*F. altissima* and *F. lasto*) is quite homogeneous (Fig. 9F, G), although with variability in width, and numbers of ribs and vascular bundles. In both, the sclerenchyma forms complete girders in all the vascular bundles and interrupts the outer bundle sheath cells in the adaxial and abaxial surfaces (Table 1B). They are two of the species with the greatest leaf widths of the entire genus (*F. lasto* is the largest of the genus with up to 16.6 mm, rarely 20 mm), and have practically smooth adaxial surfaces since the intercostal spaces defined by the bulliform cells are weakly or not at all developed. The bulliform cells are clearly visible, as in all the species with flat leaves of this clade. *Festuca lasto* grows in the south of the

Iberian Peninsula, while *F. altissima* inhabits wet zones of the north of this territory, and extends over Europe (Devesa et al. 2013). Both species are elsewhere characterized morphologically by extravaginal innovations and absence of auricles (Hackel 1882; Clayton and Renvoize 1986), and are included in the subgenus *Drymanthele*.

Festuca sects. Plantynia and Schedonorus

In the species of these sections, the leaves are flat, with more or less open or fully expanded hemilimbs (Table 1C, Fig. 9). Only F. interrupta may have convolute leaves more or less inrolling from one margin (Fig. 9C). No clear anatomical models associated with these taxonomic sections can be appreciated. The species of the sect. Schedonorus (F. interrupta, F. arundinacea and F. mediterranea; Fig. 9C-E) only have complete girders in the primary and secondary vascular bundles. In addition, the sclerenchyma makes contact with adaxial extensions of colourless cells in the median vascular bundle, sometimes also in the abaxial site (seen in *E arundinacea*). The ribs are well defined in all of these species, from truncate to rounded in *F. arundinacea* (Fig. 9D) and *F. interrupta*, in which they are peculiarly heteromorphic in size and form (Fig. 9C), while in *F. mediterranea* they range from rounded to triangular (Fig. 9E). In *F. gigantea* (sect. *Plantynia*), the girders are complete in all the vascular bundles and the outer sheath is interrupted, and the ribs are rounded or truncate. Of these species, F. arundinacea and *F. gigantea* have the largest leaf widths (up to 12 mm and 14 mm, respectively), while *F. interrupta* and *F. mediterranea* have the smallest (up to 6.5 mm and 7.1 mm, respectively). The bulliform cells appear markedly larger and inflated, and arranged in a fan shape in the intercostal areas in all of these species. The adaxial surface may be glabrous or slightly aculeate. All these species have been integrated into the subgenus Schedonorus (Inda et al. 2014), and are characterized morphologically by having sterile extravaginal shoots with cataphylls and clasping falcate auricles.

Conclusion and final remarks

Leaf anatomy as seen in cross-section has certain limitations for the delimitation of species, although it has taxonomic value for the separation of some groups. How useful anatomical characters is closely related to the taxonomic level that one wants to discriminate. Thus, the anatomical differences between the species of the two major clades are evident, and there are many features that distinguish them. Fine-leaved fescues usually present strongly folded leaves, rarely flat, with continuous sclerenchyma or strands, but never forming complete girders nor having colourless cells associated with the girders, and with bulliform cells that are relatively unpronounced. Fescues of the broad-leaved clade may present a leaf blade from convolute to fully folded, almost always with sclerenchyma girders associated with colourless cells, and highly developed bulliform cells.

Within the fine-leaved fescues clade, the character that most discriminates the taxonomic sections, the groups of species, and the species, is the arrangement of the sclerenchyma. Its analysis in species whose phylogenetic placement puts them in different lineages than what had been expected according to traditional taxonomy affects the previously recognized anatomical models, especially for the sects. *Festuca* and *Aulaxyper*. In species of the sect. *Festuca* included in lineage 1 (Fig. 3) and in the sect. *Eskia*, the leaves generally present smooth outlines, and there predominates a continuous or continuous-interrupted arrangement of the sclerenchyma, more rarely in strands in the margins and the midrib or opposite the vascular bundles. In contrast, in species of the sect. *Festuca* included in lineage 2 (Fig. 3), the leaves have angular outlines, and there predominates discontinuous sclerenchyma opposite the vascular bundles.

The length and width of the leaf cross-section, and the number of vascular bundles and ribs overlap in most species of this clade, although they are useful for the differentiation of some taxa within the same taxonomic section and/or lineage. Only *F. henriquesii*, a species traditionally placed in the sect. *Festuca*, has a flat or a wide V-shaped leaf, and its pattern is very different from that typical of species of lineages 1 or 3 (Fig. 3). The arrangement of the sclerenchyma into strands without forming complete girders, the presence of developed ribs, and the number of vascular bundles suggest a greater affinity with the species of the sect. *Aulaxyper*, in which there are species whose leaf cross-sections present extended arms (*F. nevadensis* and *F. rothmaleri*) or are flat in their cauline leaves (*F. heterophylla*).

Species can neither be distinguished nor grouped together by the remaining characters studied, since they overlap to a great extent (especially in the number of outer/ inner bundle sheaths cells, and the number of bulliform cells), and many of the variations found (e.g., thickness of the sclerenchyma, and abundance and length of the trichomes) may be responses to environmental conditions. The size of the lumen of the epidermal cells may be useful to differentiate certain species (*F. glauca, F. vasconcensis, F. brigantina* subsp. *actiophyta, F. iberica*, and *F. trichophylla*), although some heterogeneity was found. Also, a major intraspecific variability was found, especially in the sclerenchyma pattern and the degree of folding of the leaf, which is particularly striking in *F. eskia*.

In the species of the broad-leaved clade, some anatomical features are associated with the shape of the leaf, which may be conduplicate or totally flat. The variations observed affect the size, the presence of girders, their arrangement relative to the vascular bundles, the presence of colourless cells, and the development and shape of the ribs. Thus, the species of the sects. *Scariosae, Pseudoscariosa,* and *Subbulbosae* are anatomically the most similar, but they are very different from those of the sect. *Lojaconoa* which has been included within the same subgenus *Festuca.* All except those of the sect. *Lojaconoa* which has been included girders, and a major overlap in the numbers of vascular bundles and ribs. The main differences between them have to do with the arrangement of the sclerenchyma with respect to the vascular bundles, and the presence of a ring that may or may not be continuous. *Festuca durandoi* is the species that is anatomically farthest from the rest of this group, it being the only one that has no complete sclerenchyma girders. In the remaining sections of the broad-leaved clade, the species have flat leaves and greater leaf width and numbers of vascular bundles and ribs, and some of them

may be recognized by the ribs being absent or poorly developed (*F. altissima*, *F. lasto*, and *F. patula*) or by whether or not the sclerenchyma contacts the outer bundle sheath towards the adaxial face.

The leaf anatomy has, on the one hand, a clear practical interest from an ecological and agronomic point of view for the early recognition (e.g., vegetative stages) of many species of *Festuca*. From a systematic view, anatomical patterns reinforce the morphological and molecular delimitation of some taxonomic sections or groups of taxa, although some of these patterns or models may appear in different sections or be very different in closely related sections. It would be interesting to assess anatomically all genera currently included in the genus *Festuca* s.l. (e.g., *Vulpia, Wangenheimia, Ctenopsis, Lolium* and *Castellia*, among others), whose leaf anatomy is less known because it is not a diagnostic character in their taxonomy, with the aim of exploring the global anatomical diversity patterns in the different lineages.

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References

- Aiken SG, Darbyshire SJ, Lefkovitch LP (1985) Restricted taxonomic value of leaf sections in Canadian narrow-leaved *Festuca* (Poaceae). Canadian Journal of Botany 63: 995–1007. https://doi.org/10.1139/b85-135
- Aiken SG, Consaul LL (1995) Leaf cross sections and phytogeography: A potent combination for identifying members of *Festuca* subgg. *Festuca* and *Leucopoa* (Poaceae), occurring in North America. American Journal of Botany 82: 1287–1299. https://doi.org/10.2307/2446252
- Aizpuru I, Aseginolaza C, Uribe-Echebarría PM, Urrutia P (1997) Catálogo florístico del País Vasco y territorios limítrofes. Itinera Geobotanica 10: 183–233.
- Bolòs O, Vigo J (2001) Festuca. In Flora dels Països Catalans 4: 329-358. Barcelona.
- Castroviejo, S. (1986-2017) Flora iberica. Real Jardín Botánico, CSIC, Madrid.
- Catalán P, Torrecilla P, López JA, Olmstead RG (2004) Phylogeny of the festucoid grasses of subtribe Loliinae and allies (Poaceae, Pooideae) inferred from ITS and trnL-F sequences. Molecular Phylogenetics and Evolution 31: 517–541. https://doi.org/10.1016/j. ympev.2003.08.025
- Catalán P, Torrecilla P, López Rodriguez JA, Müller J (2006) Molecular evolutionary rates shed new lights on the relationships of *Festuca*, *Lolium*, *Vulpia* and related grasses (Loliinae, Pooideae, Poaceae). Current taxonomic research on the British & European Flora. Botanical Society of the British Isles. Conference report 25: 45–70.

- Catalán P, Torrecilla P, López-Rodríguez JA, Müller J, Stace CA (2007) A systematic approach to subtribe Loliinae (Poaceae, Pooideae) based on phylogenetic evidence. Aliso 23: 380– 405. https://doi.org/10.5642/aliso.20072301.31
- Catalán P (2009) *Festuca* L. In Blanca G, Cabezudo B, Cueto M, Fernández López C, Morales Torres C (eds.) Flora Vascular de Andalucía Oriental 1: 298–310. Consejería de Medio Ambiente, Junta de Andalucía. Sevilla.
- Cebolla Lozano C, Rivas Ponce MA (1999) *Festuca indigesta* Boiss. subsp. *lagascae* Cebolla et Rivas Ponce subsp. *nova* et ses relations avec le complexe *Festuca indigesta* Boiss. Criteres utilises lors de son etude taxonomique. Flora Mediterranea 9: 131–146.
- Cebolla C, Rivas Ponce MA (2003a) Catálogo del género *Festuca* L. (Poaceae) en la Península Ibérica. Candollea 58(1): 189–213.
- Cebolla C, Rivas Ponce MA (2003b). Contribución al conocimiento del género *Festuca* L. en el noreste de Cataluña (Gerona, España). Acta Botanica Barcinonensia 49: 39–50.
- Charmet G, Ravel C, Balfourier F (1997) Phylogenetic analysis in the *Festuca-Lolium* complex using molecular markers and ITS rDNA. Theoretical and Applied Genetics 94: 1038–1046. https://doi.org/10.1007/s001220050512
- Clayton WD, Renvoize SA (1986) Genera Gramineum: Grasses of the World. Genera graminum. Grasses of the world. HMSO Books. London.
- Clayton WD, Vorontsova MS, Harman KT, Williamson H (2006 onwards) GrassBase -The Online World Grass Flora. London The Board of Trustees, Royal Botanic Gardens, Kew. http://www.kew.org/data/grasses-db.html [accessed 10 February 2017].
- Connor HE (1960) Variation in leaf anatomy in *Festuca* novae-zelandiae (Hack.) Cockayne and *F. matthewsu* (Hack.) Cheeseman. New Zealand Journal of Botany 3: 468–509.
- Devesa JA, Catalán P, Müller J, Cebolla C, Ortúñez E (2013) Checklist de *Festuca* L. (Poaceae) en la Península Ibérica. Lagascalia 33: 183–274.
- Ellis RP (1976) A procedure for standardizing comparative leaf anatomy in the Poaceae. I. The leaf-blade as viewed in transverse section. Bothalia 12: 65–109. https://doi.org/10.4102/abc.v12i1.1382
- Ellis RP (1979) A procedure for standardizing comparative leaf anatomy in the Poaceae. II. The epidermis as seen in surface view. Bothalia 12: 641–671. https://doi.org/10.4102/abc. v12i4.1441
- Ellis RP (1986) A review of comparative leaf blade anatomy in the systematics of the Poaceae: the past 25 years. In Soderstrom TR, Hilu KW, Campbell CS, Barkworth ME (eds) Grass systematics and evolution. Smithsonian Institution Press, Washington D.C., 3–10 pp.
- Foggi B, Gherardi ME, Signorini MA, Rossi G, Bruschi P (2006) *Festuca inops* and *Festuca gracilior* (Poaceae): are they two different species?. Botanical Journal of the Linnean Society 151: 239–258. https://doi.org/10.1111/j.1095-8339.2006.00496.x
- Fuente V, Ortúñez E (1995) Festuca henriquesii Hackel y Festuca ampla Hackel en la Península Ibérica. Studia Botanica 14: 129–141.
- Fuente V, Ortúñez E, Ferrero L (1997) Contribución al conocimiento del género Festuca L. (Poaceae) en el País Vasco y Sistema Ibérico septentrional (Península Ibérica). Itinera Geobotanica 10: 317–351.
- Fuente V, Ortúñez E (1998) Biosistemática de la sección *Festuca* del género *Festuca* L. (Poaceae) en la Península Ibérica. EUA. Madrid, 126 pp.

- Fuente V, Ortúñez E (2001) Festuca sect. Eskia (Poaceae) in the Iberian Peninsula. Folia Geobotanica 36: 385–421. https://doi.org/10.1007/BF02899988
- Fuente V, Ferrero L, Ortúñez E (2001) Chromosome counts in the genus *Festuca* L. section *Festuca* (Poaceae) in the Iberian Peninsula. Botanical Journal of the Linnean Society 137: 385–398. https://doi.org/10.1111/j.1095-8339.2001.tb02333.x
- Gennaro DD, Morrone O (2010) Anatomía foliar de *Sacciolepis* Nash (Poaceae). Candollea 65(2): 197–210. https://doi.org/10.15553/c2010v652a3
- Giełwanowska I, Szczuka E, Bednara J, Gorecki R (2005) Anatomical features and ultrastructure of *Deschampsia antarctica* (Poaceae) leaves from different growing habitats. Annals of Botany 96: 1109–1119. https://doi.org/10.1093/aob/mci262
- Gutiérrez Villarías I, Romero MI, Soñora X, Homet J (1997) A new subspecies of *Festuca brigantina* (Marckgr.-Dann.) Markgr.-Dann. Botanical Journal of the Linnean Society 123: 249–255. https://doi.org/10.1111/j.1095-8339.1997.tb01417.x
- Hackel E (1882) Monographia Festucarum Europaerum. T. Fischer. Kassel & Berlin, 216 pp.
- Inda LA, Segarra-Morales JG, Müller J, Peterson PM, Catalán P (2008) Dated historical biogeography of the temperate Loliinae (Poaceae, Poideae) grasses in the Northern and southern hemispheres. Molecular Phylogenetics and Evolution 46: 932–957. https://doi. org/10.1016/j.ympev.2007.11.022
- Inda LA, Sanmartín I, Buerki S, Catalán P (2014) Mediterranean origin and Miocene–Holocene Old World diversification of meadow fescues and ryegrasses (*Festuca* subgenus *Schedonorus* and *Lolium*). Journal of Biogeography 41: 600–614. https://doi.org/10.1111/ jbi.12211
- Kerguélen M, Plonka F (1989) Les *Festuca* de la flore de France (Corse comprise). Bulletin de la Société Botanique du Centre-Ouest: Nouvelle Serie: Numero Special. Niort, 10.
- Kjellqvist E (1961) Studies in *Festuca rubra* L., 1. Influence of environment. Botaniska Notiser 114: 403–408.
- Kuzmanović N, Šinžar-Sekulić J, Lakušić D (2009) Leaf anatomy of the Sesleria rigida Heuffel ex Reichenb. (Poaceae) in Serbia. Botanica Serbica 33: 51–67.
- Kuzmanović N, Šinžar-Sekulić J, Lakušić D (2012) Ecologically determined variation in leaf anatomical traits of *Sesleria rigida* (Poaceae) in Serbia-multivariate morphometric evidence. Folia Geobotanica 47(1): 41–57. https://doi.org/10.1007/s12224-011-9104-y
- López J, Devesa JA (1991) Contribución al conocimiento de la anatomía foliar de las Aveneae (Poaceae, Pooideae) del centro-oeste de España. Anales del Jardín Botánico de Madrid 48(2): 171–187.
- López E, Martínez-Sagarra G, Devesa JA (2016) Estudio taxonómico del complejo *Festuca alpina* (Poaceae, Pooideae) en la Península Ibérica. Acta Botanica Malacitana 41:19–31.
- Loureiro J, Kopecký D, Castro S, Santos C, Silveira P (2007) Flow cytometric and cytogenetic analices of Iberian Peninsula *Festuca* spp. Plant Systematics and Evolution 269(1): 89–105. https://doi.org/10.1007/s00606-007-0564-8
- Markgraf-Dannenberg I (1980) Festuca L. In: Tutin TG, Heywood VH, Burgess NA, Moore DM, Valentine DH, Walters SM, Webb DA (Eds) Flora Europaea V: 125–154. Cambridge University Press, Cambridge.
- Metcalfe CR (1960) Anatomy of the Monocotyledons: Gramineae I. Clarendon Press, Oxford.
- Müller J, Catalán P (2006) Notes on the infrageneric classification of *Festuca* L.(Gramineae). Taxon 55: 139–144. https://doi.org/10.2307/25065535
- Namaganda M, Lye KA (2008) A taxonomic comparison between tropical African and related European broad-leaved species of *Festuca* L. (Poaceae). South African Journal of Botany 74(2): 295–305. https://doi.org/10.1016/j.sajb.2007.12.005
- Namaganda M, Krekling T, Lye KA (2009) Leaf anatomical characteristics of Ugandan species of *Festuca* L. (Poaceae). South African Journal of Botany 75(1): 52–59. https://doi. org/10.1016/j.sajb.2008.07.004
- Nova PJ, Cruz M, Monte JV, Soler C (2006) Genetic relationships within and among Iberian fescues (*Festuca* L.) based on PCR-amplified markers. Genome 49(9): 1170–1183. https:// doi.org/10.1139/g06-077
- Olsen JT, Caudle KL, Johnson LC, Baer SG, Maricle BR (2013) Environmental and genetic variation in leaf anatomy among populations of *Andropogon gerardii* (Poaceae) along a precipitation gradient. American Journal of Botany 100(10): 1957–1968. https://doi.org/10.3732/ajb.1200628
- Ortúñez E, Fuente V (2004) Chromosome counts in the genus *Festuca* section *Eskia* (Poaceae) in the Iberian Peninsula. Botanical journal of the Linnean Society 146: 331–337. https://doi.org/10.1111/j.1095-8339.2004.00320.x
- Ortúñez E, Fuente V (2010) Epidermal micromorphology of the genus *Festuca* L. (Poaceae) in the Iberian Peninsula. Plant Systematics and Evolution 284(3): 201–218. https://doi. org/10.1007/s00606-009-0248-7
- Ortúñez E, Cano-Ruiz J (2013) Epidermal micromorphology of the genus *Festuca* L. subgenus *Festuca* (Poaceae). Plant Systematics and Evolution 299(8): 1471–1483. https://doi. org/10.1007/s00606-013-0809-7
- Ortúñez E, Palacio C, Fuente V (1995) *Festuca hystrix* Boiss. y *Festuca reverchonii* Hackel en la Península Ibérica. Acta Botanica Malacitana 20: 51–60.
- Pimentel M, Sahuquillo E (2003) Study of the leaf anatomy of the Iberian species of genus *Anthoxanthum* (Poaceae). Bocconea 16(2): 683–689.
- Portal R (1996) *Festuca* du Massif Central. Guide pratique pour leur étude. Published by the author, Vals-près-le-Puy, France.
- Pyke S (2013) Fescues of the Intravaginal group of *Festuca* L. section *Festuca* in the lowland and montane areas of the northeastern Iberian Peninsula. Collectanea Botanica 32: 43–57. https://doi.org/10.3989/collectbot.2013.v32.005
- Ramesar-Fortner NS, Dengler NG, Aiken SG (1995) Phenotypic plasticity in leaves of four species of arctic *Festuca* (Poaceae). Canadian Journal of Botany 73: 1810–1823. https:// doi.org/10.1139/b95-192
- Ruiz-Téllez T, Devesa JA, López J (1998) Anatomical plasticity in species of *Deschampsia* P. Beauv. (Poaceae) in SW Europe (Iberian Peninsula). Acta Botanica Gallica 145(4): 281– 305. https://doi.org/10.1080/12538078.1998.10516308
- Saint-Yves A (1909) Le *Festuca ovina* subsp. *Hackelli* St-Y. subsp. Nov. et le groupe *indigesta*. Bulletin de la Société Botanique de France 56(5): 356–367. https://doi.org/10.1080/003 78941.1909.10831423
- Saint-Yves A (1922) Les Festuca de l'Afrique du Nord et des Iies Atlantiques. Candollea 1, 1.

- Saint-Yves A (1930) Aperçu sur la distribution géographique des *Festuca* Subgen. *Eu-Festuca*. Candollea 4: 146–165.
- Thiers B (2017) Index Herbariorum: A global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. http://sweetgum.nybg.org/ science/ih/ [10 January 2017].
- Torrecilla P, Catalán P (2002) Phylogeny of broad-leaved and fine-leaved *Festuca* lineages (Poaceae) based on nuclear ITS sequences. Systematic Botany 27: 241–251.
- Torrecilla P, López-Rodríguez JA, Stančik D, Catalán P (2003) Systematics of *Festuca* L. Sects. *Eskia* Willk., *Pseudatropis* Kriv., *Amphigenes* (Janka) Tzvel., *Pseudoscariosa* Kriv. and *Scariosa* Hack. based on analysis of morphological characters and DNA sequences. Plant Systematics and Evolution 239(1): 113–139. https://doi.org/10.1007/s00606-002-0265-2
- Torrecilla P, López-Rodríguez JA, Catalán P (2004) Phylogentetic relationships of *Vulpia* and related genera (Poeae, Poaceae) based on analysis of its and trnL-F sequences. Annals of the Missouri Botanical Garden 91: 124–158.
- Torrecilla P, Acedo C, Marques I, Diaz-Perez AJ, Lopez-Rodriguez JA, Mirones V, Sus A, Llamas F, Alonso A, Perez-Collazos E, Viruel J, Sahuquillo Sancho MD, Komac B, Manso JA, Segarra-Moragues JG, Draper D, Villar L, Catalan P (2013) Morphometric and molecular variation in concert: taxonomy and genetics of the reticulate Pyrenean and Iberian alpine spiny fescues (*Festuca eskia* complex Poaceae). Botanical Journal of the Linnean Society 173(4): 676–706. https://doi.org/10.1111/boj.12103
- Watson L, Dallwitz MJ (1992) The grass genera of the world. CAB International, Wallingford.
- Willkomm M (1861) Poaceae. In: Willkomm M, Lange J (Eds) Prodromus Florae Hispanicae Stuttgartiae. Vol. 1, 33–118.
- Wrobel C, Coulman BE, Smith DL (2007) An investigation into the anatomical differences between flat and folded leaves in reed canarygrass (*Phalaris arundinacea* L.). Canadian journal of plant science 88: 339-342. https://doi.org/10.4141/CJPS07025

Supplementary material I

Additional information

Authors: Gloria Martínez-Sagarra, Pilar Abad, Juan Antonio Devesa

- Data type: species data
- Explanation note: List of taxa and localities of herbarium specimens used for the leaf cross-section anatomical study. Subgenera and taxonomic sections are arranged as in Table 1, and the taxa appear in alphabetical order within each section.
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- Link: https://doi.org/10.3897/phytokeys.83.13746.suppl1

RESEARCH ARTICLE



Stipa pennata subsp. ceynowae (Poaceae, Pooideae), a new taxon from Central Europe

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Abstract

Based on numerical analyses of macromorphological characters, scanning electron microscopy observation of leaves and lemma micromorphology, as well as field observations, *Stipa pennata* subsp. *ceynowae* was described here as a new taxon from Poland. It differs from the most similar *S. pennata* subsp. *pennata* and *S. borysthenica* mainly by its longer ligules of vegetative shoots. The affinities of this taxon are discussed and a morphological comparison with related species is provided. Illustrations and images of the micromorphological structures, as well as information about its distribution, habitat and conservation status are given.

Keywords

feather grasses, micromorphology, numerical analyses, Poland, taxonomy

Introduction

Stipa Linnaeus (1753) is one of the largest genera in the family Poaceae, subfamily Pooideae (Soreng et al. 2015). In the narrow approach, it comprises over 150 species distributed in open grasslands and steppes, with the highest species diversity in the warm temperate regions of the Old World (Roshevitz 1934, Tzvelev 1968, 1976, Bor 1970, Martinovský 1980, Freitag 1985, Wu and Phillips 2006, Nobis 2013). New species of *Stipa* continue to be described. For instance, in the last twenty years, over thirty

species have been described from such countries as Morocco, Spain, Italy, Turkey, Kazakhstan, Kyrgyzstan, Tajikistan, Mongolia, Bhutan, India and China (e.g. Kotukhov 1998a, 1998b, Noltie 1999, Vázquez and Ramos 2007, Vázquez et al. 2009, Nobis 2013, 2014a, Vázquez and Gutiérrez 2011, Zhao and Guo 2011, Cataldo et al. 2012, Tzvelev 2012, 2014, Nobis et al. 2013, 2016a). At the same time, there are also still many unresolved taxonomic problems within the different sections and taxonomic complexes of this genus.

One of the numerous and taxonomically problematic sections in the genus Stipa is the nominal section, which comprises (depending on the approach) from 15 to 55 species (Smirnov 1925, Martinovský 1965, 1970, 1977, 1980, Klokov and Osychnyuk 1976, Tzvelev 1976, 1986, Freitag 1985, Vazquez and Gutierrez 2011, Gonzalo et al. 2013, Nobis et al. 2016b). In Central Europe (including Czech Republic, Germany, Poland, Slovakia, Hungary and Austria), the section Stipa is represented by about 10 taxa: S. bavarica Martinovský and Scholz (1968), S. borysthenica Klokov ex Prokudin (1951), S. dasyphylla (Cernjaev ex Lindemann 1882) Trautvetter (1884), S. eriocaulis Borbás (1878) subsp. eriocaulis, S. eriocaulis subsp. austriaca (Beck von Mannagetta 1890) Martinovský (1965), S. pennata Linnaeus (1753), S. pulcherrima Koch (1848), S. styriaca Martinovský (1970), S. tirsa Steven (1857) and S. zalesskii Wilensky ex Smirnov (1925) (conf. Martinovský 1980, Tzvelev 1986, Conert 1998, Marhold and Hindák 1998, Danihelka et al. 2012). In Poland, there are only four species from the above-mentioned section, namely: S. borysthenica, S. pennata, S. pulcherrima and S. eriocaulis, all of them reaching here the northwestern limit of their general range (Ceynowa-Giełdon 1976, Ceynowa-Giełdon et al. 2014a, 2014b, Nobis 2014b, Nobis et al. 2017). The section Stipa can be divided into many critical groups of closely related and morphologically similar taxa. One example is the group that includes Stipa pennata, a species which over the years has undergone numerous changes. Before Freitag (1985) chose a lectotype from the original material studied by Linnaeus, the name S. pennata was regularly used by various authors to identify different species. The most correct seems to be Mansfeld's (1939) assumption of the synonymization of S. joannis Čelakovský (1884) with S. pennata. Furthermore, some authors distinguished within the group a number of species and many units of lower rank (Klokov and Osychnyuk 1976, Tzvelev 1976, 2006, Martinovský 1977, 1980), whereas others distinguished a single species and several taxa of lower rank (Freitag 1985).

In our work within the *S. pennata* group, we included taxa previously classified in the series *Penicilliferae* Martinovský (1976) and characterized by having leaves with apical tassel, ventral line of hairs terminating below the top of lemma, dorsal line free and longer than the subdorsal ones. Within series *Penicilliferae*, Martinovský (1977) recognized four species: *S. joannis* (= *S. pennata*), *S. borysthenica, S. styriaca* Martinovský (1970) and *S. danubialis* Dihoru and Roman (1969). *Stipa styriaca* and *S. danubialis* are endemic species (Martinovský 1977) respectively for Austria and Romania. There are five additional taxa from Asia that fit the criteria for incorporation to ser. *Penicilliferae* (sect. *Stipa*): *S. kirghisorum* Smirnov (1925), *S. turkestanica* Hackel (1906) subsp. *turkestanica, S. turkestanica* subsp. *trichoides* (Smirnov 1925) Tzvelev (1974), *S. macroglossa* Smirnov (1924) subsp. *macroglossa* and *S. macroglossa* subsp. *kazachstanica* (Kotukhov 1994) Nobis (2013). Taxonomic revision as well as macroand micromorphological variation of those aforementioned taxa have recently been presented by Nobis et al. (2016b).

During the taxonomic revision of the central European representatives of the *Stipa pennata* group, we came across herbarium specimens from Folusz near Szubin in Poland that greatly differ from the hitherto known species. On the basis of these sheets, Ceynowa-Giełdon (1976) distinguished *Stipa joannis* var. *cujavica*. Unfortunately, the name of this taxon was not validly published because the author provided only its brief description in Polish with no references to the type and place of its preservation. The aim of our study was to examine distinctiveness of individuals from Folusz in relation to other Central European taxa from *S. pennata* group by using multivariate morphometric analysis.

Materials and methods

Over 500 herbarium sheets with specimens from the *Stipa pennata* group deposited at B, FRU, GAT, GOET, JE, KFTA, KHOR, KRA, KRAM, LE, LECB, M, MSB, MW, NY, PE, POZ, SZUB, PR, PRC, TAD, TASH, TK, TRN, UPS, W, WA, WU were examined (acronyms by Thiers 2016). The morphological characteristics of the vegetative and generative structures were examined on well-developed specimens. For numerical analysis, we selected 177 herbarium sheets (67 of *Stipa borysthenica*, 104 of *Stipa pennata*, and 6 of *Stipa* from Folusz). A list of the morphological characteristics used in analyses is presented in Table 1. Measurements were taken using a Nikon SMZ800 stereo microscope.

In accordance with the assumption of numerical taxonomy (Sokal and Sneath 1963), each specimen was treated as an Operational Taxonomic Unit (OTU). For testing the normal distribution of each characteristic, the Lilliefors and Shapiro-Wilk statistical tests were performed. Those that did not fulfill the criterion of normality were log-transformed. Next, the Pearson correlation coefficient was calculated; the characteristics in which a strong correlation was found (>0.9) were excluded from further analyses. To illustrate the relationship between the studied taxa and also to select the features that best describe the existing variability, a Principal Component Analysis (PCA) was conducted using all quantitative characteristics. According to the Kaiser criterion, factors with eigenvalues >1 were chosen (Kaiser 1960) and characteristics with the highest factor loadings of the first three principal components ($r \ge 0.60$) were determined. Subsequently, descriptive statistics of characters for all recognized taxa were calculated. Levene's test was using to assess the equality of variances. To reveal significant differences between means of particular characters across all examined taxa, one-way analysis of variance (ANOVA) and nonparametric Kruskal-Wallis test followed by Tukey's HSD test or multiple comparison test were calculated. All statistical analyses and calculations were performed using Statistica software, version 10 (Statsoft Inc. 2011).

Abbreviation	Character
AL	length of anthecium (mm)
AwnL	length of awn (mm)
CL	length of callus (mm)
Col ₁ L	length of lower segment of awn (mm)
Col ₂ L	length of middle segment of awn (mm)
CRL	length of peripheral ring of callus base (mm)
CRW	width of peripheral ring of callus base (mm)
DDL	distance from the end of dorsal line of hairs to the top of anthecium (mm)
DVL	distance from the end of ventral line of hairs to the top of anthecium (mm)
LigC	length of ligules of the middle cauline leaves (mm)
LigIV	length of ligules of the internal vegetative shoots (mm)
LC	length of culm (mm)
LCL	length of upper cauline leaves (mm)
LP	length of panicle
LV	length of vegetative shoots (mm)
NF	number of flowers in panicle
SL/ColL	ratio length of seta to the sum of length of lower and middle segment of the awn
WA	width of anthecium (mm)

Table 1. Morphological characters used in the present analyses, involving *Stipa pennata* group.

For observations in a scanning electron microscope, samples were coated with gold using a JFC-1100E Ion sputter manufactured by JEOL, then observed and photographed using a Hitachi S-4700 scanning electron microscope (SEM). The methods and terminology were adopted from Thomasson (1978, 1981), Ellis (1979), Snow (1996) and Nobis (2013, 2014a).

Results

Numerical analysis

The result of the Principal Component Analysis (PCA) revealed twelve characteristics with high factor loadings ($r\geq0.6$) on the first three principal components. Together, the first three components accounted for 57.71% of the total variation. The first two components explained respectively 27.85% and 21.48% of the total variation (Table 2). The scatterplot of the first two axes showed three group of points (Figure 1). Seven characteristics, including AL, CL, CRL, LCL, LigC, LP, and NF, displayed the highest correlations with the first axis, grouping specimens of *Stipa borysthenica* on the left and *S. pennata* on the right side. The remaining characteristics (AwnL, Col₁L, LC, LigIV, LV) highly influenced the second axis, separating specimens representing *Stipa* from Folusz.

Table 2. Results of numerical analysis involving *Stipa pennata* group. Principal component analysis (PCA): factor loadings for 18 characters, eigenvalues and percent variation. The highest factor loadings (\geq 0.6) are bolded. One-way ANOVA: F and p values for characters with normal distribution. Kruskal-Wallis test: H and p values for characters with non-normal distribution. The highest F/H values are bolded. For characters abbreviations see Table 1.

	PC 1	PC 2	PC 3	ANOVA	
Character addreviation				F/H	р
AL	- 0. 77	0.24	0.33	20.28	0.000
AwnL	-0.41	0.68	-0.04	19.01	0.000
CL	-0.81	-0.34	0.27	248.95	0.000
Col ₁ L	0.23	0.72	0.41	47.26	0.000
Col,L	-0.24	0.58	0.45	15.27	0.001
CRL	-0.62	-0.07	0.21	53.73	0.000
CRW	0.55	0.37	-0.16	64.72	0.000
DDL	-0.50	0.48	0.13	15.29	0.001
DVL	-0.21	0.19	0.38	7.20	0.027
LC	-0.38	0.65	-0.39	64.24	0.000
LCL	-0.62	-0.36	-0.01	17.41	0.000
LigC	-0.66	-0.14	-0.13	113.10	0.000
LigIV	-0.37	0.60	-0.16	118.02	0.000
LP	-0.76	-0.33	-0.11	100.61	0.000
LV	-0.23	0.74	-0.34	28.80	0.000
NF	-0.67	-0.35	-0.03	79.41	0.000
SL/ColL	-0.57	-0.16	-0.57	11.76	0.001
WA	-0.11	0.48	-0.29	21.46	0.000
Eigenvalue	5.01	3.87	1.51		
Percent variation (%)	27.85	21.48	8.38		

The results of the one-way ANOVA/Kruskal-Wallis test revealed significant differences in all examined characters (Table 2). The results of the post hoc tests (Tukey's HSD test for variables with normal distribution and multiple comparison tests for characters with non-normal distribution) are presented in Table 3. The ranges of variability of the most important characteristics of the designated morphological groups corresponding to the two examined taxa and the population from Folusz are presented in Table 4.

Scanning microscope observation

The results of SEM observations showed that the general patterns of the lemma micromorphology of *Stipa* from Folusz are typical for the genus *Stipa* (cf. Barkworth and Everett 1987, Nobis 2013, Nobis et al. 2013, 2016b) (Figure 2). Fundamental (long) cells are elongated, rectangular to a more or less square in shape. The side walls of long cells are raised and undulate, but often hidden under a thick layer of wax that hin-



Figure 1. Biplot of principal component analysis (PCA) performed on 18 characters.

ders observation. Silica bodies are quite common, reniform to oblong or ovate, while cork cells are sparse or absent. Hooks are frequent, oriented towards the lemma apex, whereas prickles are completely absent. Lemma apex is glabrous (Figure 2A–D).

The adaxial surface of leaves of the vegetative shoots is ribbed and densely covered by short prickles, long cells and silica bodies (Figure 2E). Whereas the abaxial surface is dominated by long cells with admixtures of silica bodies and sparsely distributed prickles (Figure 2F).

Taxonomic treatment

Conducted analysis clearly indicated that specimens from Folusz represents a new taxon, which is described below.



Figure 2. SEM morphology of *Stipa* from Folusz. **A** Structure of lemma – superior view **B** Structure of lemma – lateral view **C** Callus **D** Top of anthecium **E** Adaxial surface of vegetative leaves **F** Abaxial surface of vegetative leaves. Abbreviations: h = hook, l = long cell, sb = silica body.

Stipa pennata subsp. ceynowae Klichowska & M.Nobis, subsp. nov.

urn:lsid:ipni.org:names:77164173-1 Figures 2, 3, 4, 5

Diagnosis. *Stipa pennata* subsp. *ceynowae* is most similar to *S. pennata* subsp. *pennata* from which differs mainly in longer ligules of internal leaves of vegetative shoots (3.2–)4.1–5.2(–6.7) mm vs. (1.0–)1.3–2.2(–3.6) mm and lemmas with a somewhat longer awn (305–)328–412(–442) mm vs. (228–)283–340(–408) mm respectively.

Table 3. Results of post-hoc tests. Tukey's HSD test for characters with normal distribution, multiple comparison tests for characters with non-normal distribution. + – statistically significant, p < 0.05; ns – not significant. *Stipa pennata* – pe, *Stipa borysthenica* – bo, *Stipa* from Folusz – F. For characters abbreviations see Table 1.

Character	pe-bo	pe-F	bo-F
AL	+	+	ns
AwnL	ns	+	+
CL	+	+	+
Col ₁ L	+	+	+
Col ₂ L	ns	+	+
CRL	+	+	ns
CRW	+	ns	+
DDL	ns	+	+
DVL	ns	ns	ns
LigC	+	+	ns
LigIV	ns	+	+
LC	ns	+	+
LCL	+	+	ns
LP	+	ns	ns
LV	+	+	+
NF	+	ns	ns
SL/ColL	+	ns	ns
WA	+	+	+
Number of significance differences	12	13	10

Table 4. Main morphological differences among selected members of *Stipa pennata* group. Measurements are given in millimeters.

Taxon	S. borysthenica	S. pennata subsp. ceynowae	S. pennata subsp. pennata
Character		1 1 2	
Anthecium length	(15.7–)17.00–18.9(–20.4)	(17.4–)18.1–19.9(–20.0)	(14.25–)15.9–18.0(–19.8)
Awn length	(225–)279–334(–396)	(305–)328–412(–442)	(228–)283–340(–408)
Callus length	(3.4–)3.7–4.2(–4.6)	(3.1–)3.3–3.8	(2.4–)2.8–3.25(–3.75)
Column length	(43–)57–69(–59)	81-91(-94)	(55–)64–78(–93)
Ligules of the middle cauline leaves length	(1.2–)2.2–4.2(–6.3)	(2.6–)2.8–4.3(–4.4)	(0.4-)1-2.5(-4.0)
Ligules of internal vegetative shoots length	(0.9–)1.3–2.2(–3.4)	(3.2–)4.1–5.2(–6.7)	(1.0–)1.3–2.2(–3.6)
Uppermost cauline leaves length	(22–)36–62(–125)	(16–)27–38(–69)	(4-)10-22(-40)
Shape of callus base	Cuneate	Piriformis	Piriformis



Figure 3. *Stipa pennata* subsp. *ceynowae* from Folusz near Szubin (Poland). **A** Map of distribution in Poland, red dot – locality of population **B** Photograph of habitat.

Type. POLAND. Folusz koło Szubina, zarośla na wydmie [Folusz near Szubin, scrub on the dune], 5 July 1962, *Ceynowa-Giełdon s.n.* (holotype TRN!, isotype KRA 0451189!).

Description. Plant perennial, densely tufted, with a few culms and numerous vegetative shoots. Culms (56-)84-95(-99) cm tall, 3-4-noded, glabrous at nodes and slightly scabrous to more or less densely pubescent below them. Leaves of vegetative shoots: sheaths of external leaves shortly pilose to scabrous, of internal leaves scabrous to almost glabrous; ligules membranous, acute or slightly obtuse, with very short cilia at the apex and shortly setulose on the back, of external leaves (1.0-)1.1-2.1(-2.7) mm long, of internal leaves (3.2-)4.1-5.2(-6.7) mm long; blades convolute, green to pale green, (73-)81-97(-107) cm long, (0.5-)0.7-0.8(-1.0) mm in diameter, abaxial surface from scabrous, covered by short spinules (on external leaves) to slightly scabrous or almost smooth, with spinules almost confined to the margins of leaf blades (on internal leaves), adaxial surface always covered by short prickles less than 0.1 mm long, juvenile leaves usually with an apical tassel of hairs up to 2 mm long. Cauline leaves: sheaths smooth to slightly scabrous (usually in upper part of sheath); ligules of the middle cauline leaves (2.6-)2.8-4.3(-4.4) mm long, slightly acute or obtuse, at the apex with very short cilia, and with short bristles on the back; blades convolute, green or pale green, the uppermost one (1.6-)2.7-3.8(-6.9) cm long, abaxial surface scabrous. Panicle 10-11(-14.5) cm long, contracted, with 8-10 spikelets; branches scabrous or with short hairs 0.2-0.5(-0.8) mm long. Glumes subequal, 56-64 mm long, narrowly lanceolate. Anthecium (17.4–)18.1–20.0 mm long and 1.0–1.25 mm wide; callus (3.1-)3.3-3.8 mm long, with hairs (1.6-)1.7-2.1(-2.4) mm long in ventral part and (1.0-)1.1-1.4 mm long in dorsal; foot of callus curved, peripheral ring flattened $0.9-0.95 \times 0.3-0.35$ mm; lemma straw-coloured, with 7 lines of hairs, dorsal and subdorsal lines slightly fused at the base, ventral line with (0.5–)0.6–0.8 mm long hairs, terminating at 1/2-2/3 of lemma length about 4.5-5.8(-6.4) mm below the top of lemma; dorsal line with (0.4-)0.5-0.6 mm long hairs, terminating at 1/3 of lemma



Figure 4. *Stipa pennata* subsp. *ceynowae* based on the holotype. **A** Panicle with upper cauline leaves **B** Awn with glabrous column and pilose seta **C** Anthecium **D** External (the lower) and internal (the upper) ligules of the vegetative leaves **E** Apex of juvenile leaves with an apical tassel of hairs.

Stipe permete L. subsp. ceynowee Klichowske & H. Nodis Holotypus ! subsp. nov. rev. E. Kkichowske & H. Abdis	
Stipo jonnis Celak. Rev. Waldemar Heise Jagiellonian University, Cracow, Poland 19 March 2009 Zielnik Zakładu Systematyki i Geografii Roślin Dalwerzytetu Mikołaja Kopernika w Toruniu <u>Stapow jewance Caymen Sustan</u> <u>Miejscowośk</u> Zołum <u>Inaw Swistana</u> <u>Dala 5. Jil 1962</u> <u>Dala 5. Jil 1962</u> <u>Dala 5. Jil 1962</u>	2001 - 1 - 1 - 2 - 1 - 1 - 2 - 1 - 1 - 2 - 1 - 2 - 1 - 2 - 2

Figure 5. Holotype of *Stipa pennata* subsp. *ceynowae*.

length, about (9.1-)9.5-11.0(-11.1) mm below the top; awn (305-)328-412(-442) mm long, bigeniculate; column smooth and glabrous, twisted, straw-coloured or slightly green, 0.5-0.6 mm wide near base, 81-91(-94) mm long with the lower segment of column (63-)65-69(-70) mm long and the upper (19-)22-24 mm long; seta (222-)247-318(-354) mm long, pilose, with 5.2-6.0 mm long hairs, gradually decreasing in length towards apex; palea straw-coloured equaling lemma in length. Caryopsis ca.12 mm long.

Etymology. The name of taxon honors the collector—Prof. Mirosława Ceynowa-Giełdon, who first noted the distinctiveness of *Stipa* individuals from Folusz.

Distribution and habitat. *Stipa pennata* subsp. *ceynowae* is an endemic taxon, known only from Folusz settlement near Szubin in Kuyavia region (northern Poland). It grows on a dune hill surrounded by wet meadows occurring in the Gąsawka River Valley. The subspecies occurs on small fragment of dry, sandy grassland adjoining oak and pine stands. At the locality, the following species grow together with *Stipa: Achillea pannonica* Scheele, *Asperula tinctoria* L., *Avenula pratensis* (L.) Dumort., *Betula pendula* Roth, *Calamagrostis epigejos* (L.) Roth, *Carex praecox* Schreb., *Dianthus carthusianorum* L., *Euphorbia cyparissias* L., *Festuca trachyphylla* (Hack.) Krajina, *Filipendula vulgaris* Moench, *Galium verum* L., *Geranium sanguineum* L., *Peucedanum oreoselinum* (L.) Moench, *Poa pratensis* L., *Polygonatum odoratum* (Mill.) Druce, *Vincetoxicum hirun-dinaria* Medik.

Phenology. Flowering period: May–June.

Conservation status. *Stipa pennata* is a species protected in Poland (Regulation of the Minister of the environment dated October 9, 2014) as well as it was included in the Polish red data book of plants (Ceynowa-Giełdon et al. 2014b). The only known locality of *S. pennata* subsp. *ceynowae* was partly destroyed by the extraction of sand (up to the mid-1950s) and the subsequent afforestation of pine and birch trees carried out in the 1990s (Ceynowa-Giełdon 2001, Nienartowicz et al. 2014). Currently, *S. pennata* subsp. *ceynowae* should be considered as a critically endangered (CR) species—to date, only several flowering individuals have survived (tufts with 8, 10, 11 and 14 culms), occupying a very small area of dry grassland. Lack of grazing has resulted in increased ground cover by layer of "steppe felt", which hamper seeds germination and seedlings growth. Also, tree seedlings pose a threat by shading the grasslands. Similarly, as in the case of other dry grassland species— survival depends on the preservation of suitable habitat conditions, which can be achieved through active protection. Due to the extremely small size of the population, it seems reasonable to apply the methods of *ex situ* conservation, including *in vitro* propagation.

Additional specimens studied (paratypes). POLAND. Folusz, 16 Jun 1959, *Michalska and Bohr s.n.* (TRN!); Folusz koło Szubina nad Gąsawką, na wydmie, wśród łąk [Folusz near Szubin on the Gąsawka River, on a dune, among meadows], 13 Jun 1972, *Ceynowa-Giełdon s.n.* (TRN!)×4; North Poland, Kuyavian-Pomeranian Voivodeship, Folusz near Szubin by the Gąsawka River; xerothermic grassland on a sandy dune, 3 Jun 2014, *Klichowska s.n.* (KRA 0451190!).

Discussion

Ceynowa-Giełdon (1976) distinguished Stipa joannis var. cujavica (nom. inval.) based on the longer hairless part of the awn, longer vegetative leaves and longer upper cauline leaves than in the case of the typical variety. Although the Principal Component Analysis supports the usefulness of these characteristics (Table 2), their larger size can also be found in individuals of S. pennata subsp. pennata and, after examining a great number of individuals, they seem to be insufficient to distinguish this taxon based on its description. According to our results, the internal vegetative leaves (Figure 4D) in specimens of S. pennata subsp. ceynowae have distinctly longer ligules (usually 4.1-5.2 mm in length) than the other closely related species from Poland, namely S. borysthenica and S. pennata subsp. pennata (in both cases, usually reaching of 1.3-2.2 mm in length; Table 4). Our research carried out on a large number of herbarium specimens (from the geographical range of these taxa), as well as on the findings of other authors (Bor 1970, Tzvelev 1976, Martinovský 1977, 1980, Conert 1998, Gonzalo et al. 2013, Nobis et al. 2016b), confirm that all known taxa closely related with S. pennata do not have such long ligules of their vegetative shoots. Ligules of a similar length or even longer are observed in other species of the section Stipa occurring in Central Asia, namely: S. turkestanica subsp. turkestanica, S. macroglossa subsp. macroglossa and S. macroglossa subsp. kazachstanica (Gonzalo et al. 2013, Nobis et al. 2016b). However, S. pennata subsp. ceynowae cannot be confused with any of them due to its definitely longer anthecium, callus, awn, culm and vegetative leaves, as well as to its distribution, limited only to Central Europe.

Stipa kirghisorum, is another species that is morphologically similar to both S. pennata subsp. pennata and S. pennata subsp. ceynowae. However, S. kirghisorum differs from the two above-mentioned taxa by the strongly scabrous abaxial surface of leaves of the vegetative shoots, shorter anthecium (13.1-)14.5-16.0(-17.8) mm and ventral line of hairs terminating (0.5-)1.4-3.1(-4.6) mm below the top of the lemma, as well as its general range that is limited to the Central Asia (Nobis et al. 2016b).

Stipa pennata subsp. ceynowae is somewhat similar to two other European species from ser. Penicillifera. First is S. styriaca that is also characterized by having long awn up to 445 mm and anthecium 17.5–21.5 mm, but in contrast to S. pennata subsp. ceynowae it has densely pubescent leaf sheaths (with 0.2–0.8 mm hairs) (Martinovský 1977). The second species is S. danubialis that differs from Stipa pennata subsp. ceynowae by having pilose column (lower part of awn) and anthecium 23–25 mm long (Martinovský 1977).

Due to its long awn, *Stipa pennata* subsp. *ceynowae* could be also confused with *S. pulcherrima* that occurs in Central Europe too. However, it can easily be distinguished by its ventral lines of hairs terminating at 1/2–2/3 of lemma length, shorter anthecium (17.4–20.0 mm) and longer ligules on vegetative shoots, while *S. pulcherrima* is characterized by ventral lines reaching the base of the awn, anthecium 18–25 mm long and ligules of the vegetative shoots not exceeding 2 mm long (Martinovský 1980, Nobis 2014b).

The results of ANOVA and post-hoc tests confirm separateness of the taxon from Folusz (Tables 2, 3). *Stipa pennata* subsp. *ceynowae* differs from *S. pennata* subsp. *pennata* and from *S. borysthenica* in a statistically significant way by 13 and 10 characters respectively (Table 3).

A key to identification of feather grasses (Stipa) in Poland

1	Awns scabrous throughoutS. capillata
_	Awn smooth in the lower pat and plumose in the upper2
2	Ventral line of hairs on lemma not reaching the base of awn, ending (1.0–)3.0–
	6.0(-7.9) mm below the top; dorsal line only in lower 1/4 of its length fused
	with subdorsal ones
_	Ventral line of hairs on lemma reaching the base of awn; dorsal line at least in
	3/4 of its length fused with subdorsal ones
3	Blade of uppermost cauline leaf (22-)36-62(-125) mm long; floret callus
	(3.4–)3.7–4.2(–4.6) mm, straight to slightly curved, callus base cuneate
_	Blade of uppermost cauline leaf (4–)10–24(–69) mm long; floret callus (2.4–
)2.8–3.3(–3.8) mm long, curved, callus base piriform
4	Ligules of internal leaves of vegetative shoots (1.0–)1.3–2.2(–3.6) mm long;
	column of awn (55-)64-78(-93) mm long; blade of uppermost cauline
	leaves (4–)10–22(–40) mm longS. pennata subsp. pennata
_	Ligules of internal leaves of vegetative shoots (3.2–)4.1–5.2(–6.7) mm long,
	column of awn 81-91(-94) mm long; blade of uppermost cauline leaves
	(16–)27–38(–69) mm long
5	Leaves of the vegetative shoots distinctly scabrous; anthecium (18.1-)20.6-
	22.8(-24.6) mm long; floret callus (3.7-)4.4-5.1(-5.8) mm long; awn (277-
)328–394(–463) mm long
_	Leaves of the vegetative shoots glabrous and smooth to very slightly scabrous
	especially in their lower part; anthecium (15.0-)16.3-18.7(-20.7) mm long;
	floret callus (3.4-)3.6-4.4(-5.0) mm long; awn (218-)228-269(-312) mm
	long S. eriocaulis

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References

- Barkworth ME, Everett J (1987) Evolution in the Stipeae: identification and relationships of its monophyletic taxa. In: Soderstrom TR, Hilu KW, Campbell CS, Barkworth ME (Eds) Grass systematics and evolution. Smithsonian Institution Press, Washington, DC, 251–264.
- Beck-Mannagetta G (1890) Flora von Nieder-Österreich. Druck und Verlag von Carl Gerold's Sohn, Wien, 889 pp.
- Bor NL (1970) Graminae. In: Rechinger KH (Ed.) Flora Iranica, 70. Academische Druck-und Verlagsanstalt, Graz-Austria, 1–573. [72 tables]
- Borbás V (1878) Floristicai közlemények a magy. tud. akadémia által támogatott botanikai kutatásaimból. Mathematikai és Természettudományi Közlemények 15: 265–371.
- Cataldo D, Giardina SA, Moraldo B, Raimondo FM (2012) *Stipa valdemonensis* (Poaceae), a new species from Sicily. Plant Biosystems 146: 658–663. http://dx.doi.org/10.1080/112 63504.2012.700961
- Čelakovský LF (1884) Nachtragliches über *Stipa tirsa* Steven. Oesterreichische Botanische Zeitschrift. Gemeinnütziges Organ für Botanik 34: 318–321.
- Ceynowa-Giełdon M (1976) Ostnice sekcji Pennatae w Polsce. Rozprawy Uniwersytetu Mikołaja Kopernika, Toruń, 99 pp.
- Ceynowa-Giełdon M (2001) *Stipa joannis* Čelak. Ostnica Jana. In: Kaźmierczakowa R, Zarzycki K (Eds) Polska Czerwona Księga Roślin. Paprotniki i rośliny kwiatowe. W. Szafer Institute of Botany, Polish Academy of Science, Kraków, 260–261.
- Ceynowa-Giełdon M, Nobis M, Barańska K (2014a) Stipa borysthenica Klokov ex Prokudin Ostnica piaskowa. In: Kaźmierczakowa R, Zarzycki K, Mirek Z (Eds) Polska czerwona księga roślin: paprotniki i rośliny kwiatowe (ed. 3). Instytut Ochrony Przyrody. Polska Akademia Nauk, Kraków, 656–658.
- Ceynowa-Giełdon M, Nobis M, Rutkowski L (2014b) *Stipa pennata* L. Ostnica piórkowata. In: Kaźmierczakowa R, Zarzycki K, Mirek Z (Eds) Polska czerwona księga roślin: paprotniki i rośliny kwiatowe (ed. 3). Instytut Ochrony Przyrody. Polska Akademia Nauk, Kraków, 651–654.
- Conert HJ [Ed.] (1998) Gustav Hegi Illustrierte Flora von Mitteleuropa, 1(3), Spermatophyta: Angiospermae: Monocotyledones 1(2) Poaceae. Parey Buchverlag, Berlin, 897 pp.
- Danihelka J, Chrtek Jr J, Kaplan Z (2012) Checklist of vascular plants of the Czech Republic. Preslia 84: 647–811.
- Dihoru GH, Roman N (1969) Une nouvelle espece du genre *Stipa*. Revue Roumaine de Biologie, Série Botanique 14(1): 21–27.

- Ellis RP (1979) A procedure for standardizing comparative leaf anatomy in the Poaceae. II. The epidermis as seen in surface view. Bothalia 12: 641–671. https://doi.org/10.4102/abc.v12i4.1441
- Freitag H (1985) The genus *Stipa* (Gramineae) in southwest and south Asia. Notes from the Royal Botanical Garden, Edinburgh 42: 355–489.
- Gonzalo R, Aedo C, García MA (2013) Taxonomic revision of the Eurasian *Stipa* subsections *Stipa* and *Tirsae* (Poaceae). Systematic Botany 38: 344–378. https://doi.org/10.1600/03636-4413X6666615
- Hackel E (1906) Gramineae novae turkestanicae. Trudy Imperatorskago S.-Peterburgskago Botaničeskago Sada 26: 53–60.
- Kaiser HF (1960) The application of electronic computers to factor analysis. Educational and Psychological Measurement 20: 141–151. https://doi.org/10.1177/001316446002000116
- Klokov M, Osychnyuk V (1976) Stipae Ucrainicae. Novosti Sistematiki Vysshik i nizshikh rastenii Kiev 1975: 7–91.
- Koch K (1848) Beitrage zu einer Flora des Orients. Linnaea 21: 289–736.
- Kotukhov YuA (1994) Novye vidy roda Stipa (Poaceae) iz yuzhnogo Altaya, Saura i Tarbagataya [New species of the genus Stipa (Poaceae) from south Altai, Saur and Tarbagatai]. Botanicheskii Zhurnal 79: 101–106.
- Kotukhov YuA (1998a) New species of grasses (Poaceae) from south Altai, Saur and Tarbagatai. Turczaninowia 1(1): 7–21.
- Kotukhov YuA (1998b) New species of the genus *Stipa* L. (Poaceae) from western Kazakhstan. Turczaninowia 1(2): 9–15.
- Lindemann E (1882) Flora Chersonensis, 2. Odessae, 329 pp.
- Linnaeus C (1753) Species Plantarum, 1. L. Salvii, Holmiae, Stockholm, 1–560. http://dx.doi. org/10.5962/bhl.title.669
- Mansfeld R (1939) Zur Nomenklatur der Farn- und Blütenplflanzen Deutschlands. VII. Feddes Repertorium. Zeitschrift für Botanische Taxonomie und Geobotanik 47: 263–287.
- Marhold K, Hindák F (1998) Zoznam nižších a vyšších rastlín Slovenska Checklist of nonvascular and vascular plants of Slovakia. Veda, VSAV, Bratislava.
- Martinovský JO (1965) Kavyly serie Pulcherrimae na Slovensku. Biológia: 498–510.
- Martinovský JO (1970) Über drei neue Stipa Sippen aus dem Verwandtschaftskreis Stipa joannis s. l. XXII. Beitrag zur Kenntnis der Stipa-Sippen. Oesterreichische Botanische Zeitschrift 118: 171–181. https://doi.org/10.1007/BF01373228
- Martinovský JO (1976) Neue *Stipa*–Sippen und einige Ergänzungen der früher beschriebenen *Stipa*–taxa. Preslia 48: 186–188.
- Martinovský JO (1977) Clavis analytica nec non descriptions breves taxorum generis *Stipa* in Europa centrali provenientium. Preslia 49: 97–113.
- Martinovský JO (1980) Stipa L. In: Tutin TG, Heywood VH, Burges NA, Moore DM, Valentine DH, Walters SM, Webb DA (Eds) Flora Europaea, 5. Cambridge University Press, Cambridge, 247–252.
- Martinovský JO, Scholz H (1968) Stipa bavarica: Eine Neue Federgrasart. XIII. Beitrag Zur Kenntnis Der Europäischen Federgrassippen (Stipa bavarica: A new species of feathergrass). Willdenowia 4(3): 317–324.
- Nienartowicz A, Kamiński D, Kunz M, Deptuła M, Adamska E (2014) Changes in the plant cover of the dune hill in Folusz near Szubin (NW Poland) between 1959 and 2013: the

problem of preservation of xerothermic grasslands in the agricultural landscape. Ecological Questions 20: 23–38. http://dx.doi.org/10.12775/EQ.2014.013

- Nobis M (2013) Taxonomic revision of the *Stipa lipskyi* group (Poaceae: *Stipa* section *Smirno-via*) in the Pamir Alai and Tian-Shan Mountains. Plant Systematics and Evolution 299: 1307–1354. http://dx.doi.org/10.1007/s00606-013-0799-5
- Nobis M (2014a) Taxonomic revision of the Central Asian *Stipa tianschanica* complex (Poaceae) with particular reference to the epidermal micromorphology of the lemma. Folia Geobotanica 49: 283–308. http://dx.doi.org/10.1007/s12224-013-9164-2
- Nobis M (2014b) *Stipa pulcherrima* K. Koch. In: Kaźmierczakowa R, Zarzycki K, Mirek Z (Eds) Polska czerwona księga roślin: paprotniki i rośliny kwiatowe, ed. 3. Instytut Ochrony Przyrody. Polska Akademia Nauk, Kraków, 654–656.
- Nobis M, Erst A, Nowak A, Shaulo D, Olonova M, Kotukhov Yu, Király G, Ebel AL, Kushunina M, Nobis A, Piwowarczyk R, Sukhorukov AP, Verloove F, Zalewska-Gałosz J, Burri JF, Caković D, Jędrzejczak E, Jogan N, Klichowska E, Pliszko A, Popovich AV, Stešević D, Šilc U, Tupitsyna N, Vasjukov VM, Wang W, Werner P, Wolanin MN, Wolanin MM, Xiang KL (2017) Contribution to the flora of Asian and European countries: new national and regional vascular plant records, 6. Botany Letters 164: 23–45. http://dx.doi.org/10.1080/23818107.2016.1273134
- Nobis M, Klichowska E, Nowak A, Gudkova PD, Rola K (2016b) Multivariate morphometric analysis of the *Stipa turkestanica* group (Poaceae). Plant Systematics and Evolution 302: 137–153. http://dx.doi.org/10.1007/s00606-015-1243-9
- Nobis M, Nobis A, Klichowska E, Nowak A, Nowak S, Gudkova PD (2016a) *Stipa dickorei* sp. nov. (Poaceae), three new records and a checklist of feather grasses of China. Phytotaxa 267(1): 29–39. http://dx.doi.org/10.11646/phytotaxa.267.1.3
- Nobis M, Nowak A, Nobis A (2013) Stipa zeravshanica sp. nov. (Poaceae), an endemic species from rocky walls of the western Pamir Alai Mountains (middle Asia). Nordic Journal of Botany 31: 666–675. http://dx.doi.org/10.1111/j.1756-1051.2013.00184.x
- Noltie HJ (1999) Notes relating to the flora of Bhutan: XXXVIII. Gramineae I, tribe Stipeae. Edinburgh Journal of Botany 56: 285–292. https://doi.org/10.1017/S0960428600001141
- Prokudin GN (1951) Zlaki [Gramineae]. In: Stankov SS (Ed.) Flora Kryma, 1(4). Gosudarstwennoe Izdatel'stvo Sel'skokhozyaistvennoi literatury, Moscow, 1–153.
- Roshevitz RYu (1934) *Stipa* L. In: Komarov VL (Ed.) Flora SSSR, 2. Editio Academiae Scientiarum URSS, Leningrad, 79–112 and 740–741.
- Regulation of the Minister of the Environment (2014) Regulation of the Minister of the Environment dated October 9, 2014, on the protection of the species of plants. Journal of Laws, item 1409.
- Smirnov PA (1924) Stipa macroglossa P.A. Smirnow sp.n. Botaniceskie Materialy Gerbariya Glavnogo Botanicheskogo Sada RSFSR 5: 47–48. https://doi.org/10.1002/ fedr.19250210806
- Smirnov PA (1925) Die neuen russischen Stipa-Pennata-Arten. Repertorium Novarum Specierum Regni Vegetabilis 21: 231–235.
- Snow N (1996) The phylogenetic utility of lemmatal micromorphology in *Leptochloa* s.l. and related genera in subtribe Eleusininae (Poaceae, Chloridoideae, Eragrostideae). Annals of the Missouri Botanical Garden 83: 504–529. https://doi.org/10.2307/2399991
- Sokal RR, Sneath PH (1963) Principles of numerical taxonomy. Freeman WH, San Francisco, 359 pp.

- Soreng RJ, Peterson PM, Romschenko K, Davidse G, Zuloaga FO, Judziewicz EJ, Filgueiras TS, Davis JI, Morrone O (2015) A worldwide phylogenetic classification of the Poaceae (Gramineae). Journal of Systematics and Evolution 53(2): 117–137. https://doi. org/10.1111/jse.12150
- StatSoft Inc. (2011) STATISTICA (data analysis software system), version 10.
- Steven C (1857) Verzeichniss der auf der taurischen Halbinsel wildwachsenden pflanzen. Bulletin de la Société impériale des naturalistes de Moscou 30(3): 65–133.
- Thiers B (2016) Index Herbariorum: A global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. http://sweetgum.nybg.org/ih/
- Thomasson JR (1978) Epidermal patterns of the lemma in some fossil and living grasses and their phylogenetic significance. Science 199: 975–977. https://doi.org/10.1126/science.199.4332.975
- Thomasson JR (1981) Micromorphology of the lemma in *Stipa robusta* and *Stipa viridula* (Gramineae: Stipeae): taxonomic significance. Southwest Naturalist 26: 211–214. https://doi.org/10.2307/3671126
- Trautvetter E (1884) Incrementa florae phaenogamae rossicae. Trudy Imperatorskago S.-Peterburgskago Botaniceskago Sada 9: 1–415.
- Tzvelev NN (1968) Zlaki (Gramineae). In: Grubov VI (Ed.) Rastieniya Centralnoi Azii. Po materialam Botanicheskogo Instituta im. Komarova VL (Plantae Asiae Centralis, secus materies Instituti botanici nomine Komarovii VL), 4. Nauka, Leningrad, 1–243 and 12 maps.
- Tzvelev NN (1974) Zametki o tribe Stipae Dum. semejstva zlakov (Poaceae) v SSSR—Notulae de tribu Stipae Dum. (fam. Poaceae) in URSS. Novosti Sistematiki Vysshikh Rastenii 11: 4–21.
- Tzvelev NN (1976) Zlaki SSSR. Nauka, Leningrad, 1–788.
- Tzvelev NN (1986) On the feather-grasse (*Stipa* L., Gramineae) in the Ukraine. Byuletin Moskovskogo Obschestva Ispytatelei Prirody. Otdel Biologicheskii 91(1): 116–124.
- Tzvelev NN (2006) Stipa L. In: Takhtajan AL (Ed.) Caucasian flora conspectus, 2. Saint-Petersburg University Press, Petersburg, 348–356.
- Tzvelev NN (2012) Notes on the tribe Stipeae Dumort. (Poaceae). Novosti Sistematiki Vysshikh Rastenii 43: 20–29.
- Tzvelev NN (2014) On some hybridogenous taxa in the genus *Stipa* L. (Poaceae). Novosti Sistematiki Vysshikh Rastenii 45: 5–8.
- Vázquez FM, Ramos S (2007) Two new taxa and a new combination for Stipa (Gramineae: Stipeae) in Tunisia. Botanical Journal of the Linnean Society 153: 439–444. https://doi. org/10.1111/j.1095-8339.2007.00625.x
- Vázquez FM, Gutièrrez M (2011) Classification of species of *Stipa* with awns having plumose distal segments. Telopea 13: 155–176. https://doi.org/10.7751/telopea20116012
- Vázquez FM, Perez-Chiscano JL, Gutiérrez M, Ramos S (2009) A new species of *Stipa* sect. *Leiostipa* (Poaceae) from SW Spain. Willdenowia 39: 261–264. http://dx.doi.org/10.3372/ wi.39.39204
- Wu ZL, Phillips SM (2006) Tribe Stipae. In: Wu ZY, Raven PH, Hong DY (Eds) Flora of China (Poaceae), 22. Science Press, Beijing and Missouri Botanical Garden Press, St. Louis, 188–212.
- Zhao LQ, Guo K (2011) *Stipa albasiensis* (Poaceae), a new species from Inner Mongolia, China. Annales Botanici Fennici 48: 522–524. http://dx.doi.org/10.5735/085.048.0615

RESEARCH ARTICLE



Premna bhamoensis (Lamiaceae, Premnoideae), a new species from Kachin State, northeastern Myanmar

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Abstract

In the present study, we describe and illustrate a new species, *Premna bhamoensis* Y. T. Tan & B. Li (Lamiaceae), from Myanmar. In the 1980s, this species was transplanted from Bhamo County in northeastern Myanmar to the Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences. The species shows striking morphological similarity to *P. menglaensis* B. Li, and thus, has been misidentified as the latter for a long period of time. However, morphological comparison revealed that *P. bhamoensis* is distinct from *P. menglaensis* in many aspects. Moreover, literature survey and specimen examinations also indicated that *P. bhamoensis* is undoubtedly different from all seven known congenetic species recorded from Kachin State, Myanmar, and a key for their identification has been provided in this paper.

Keywords

China, morphology, Myanmar, Premna menglaensis, Xishuangbanna Tropical Botanical Garden

Introduction

The genus *Premna* L. is one of the largest woody genera belonging to the mint family, consisting of approximately 200 species distributed mainly in the Old World tropics and subtropics (Verdcourt 1992, Harley et al. 2004). The genus was first described by Linnaeus (1771), on the basis of two species, *P. serratifolia* L. and *P. integrifolia* L.,

which are now treated as a single species (de Kok 2013). It was traditionally placed in the subfamily Viticoideae Briq. (Briquet 1897, Chen and Gilbert 1994, Harley et al. 2004), but was recently transferred to the newly established subfamily Premnoideae B. Li, R.G. Olmstead & P.D. Cantino (Li et al. 2016).

With 46 species recognized in China, Premna is the fifth largest genus in Lamiaceae flora of China (Chen and Gilbert 1994, Li and Hedge 1994). In June 2011, a field survey was carried out to investigate the biodiversity of Premna in Yunnan Province, southwestern China. When visiting the Xishuangbanna Tropical Botanical Garden (XTBG), Chinese Academy of Sciences (CAS), the authors found a rare Premna shrub in the fruiting stage (Figure 1), which was being cultivated in the C20 region of the garden, and was labeled as "Premna laevigata C. Y. Wu" ($\equiv P.$ menglaensis B. Li, after Li et al. 2013). Superficially, the plant strongly resembles P. menglaensis in having a climbing habit, ovate-oblong to elliptic leaves, and a congested pyramidshaped thyrse (Figure 2), but differs noticeably in having densely pubescent branchlets and petioles, and lips of fruiting calyces distinctly 2- or 3-lobed. Many more differences between this plant and P. menglaensis were discovered during the flowering stage, whose observations were taken during the month of May 2012. This analysis indicated that the plant probably represented a new species. In order to verify the information about the origin of this putative new species, we examined the XTBG introduction records and found that this plant was introduced from Bhamo County, Kachin State of northeastern Myanmar in the 1980s. However, precise location data and the collection date had not been recorded. During the period from 2011 to 2016, the first author has visited Kachin State many times, but the plant was not found in this area. Further examination of literature and specimens revealed that seven Premna species have been recorded from Kachin State, viz., P. barbata Wall. ex Schauer, P. bengalensis C.B. Clarke, P. khasiana C.B. Clarke, P. pinguis C.B. Clarke, P. pyramidata Wall. ex Schauer, P. racemosa Wall. ex Schauer, and P. scandens Roxb. (Kress et al. 2003). However, none of them is morphologically similar to the putative new species. Therefore, it is confirmed that this species of *Premna* is new to science, and thus, we describe and illustrate it in this study.

Methods

Morphological observations of the new species were carried out based on living plants as well as dry specimens, during the period from 2011 to 2016. Measurements were made using a ruler and a micrometer. Both herbarium and fresh specimens of *P. menglaensis* were examined under a stereo dissecting microscope (StereoZoom[®] Leica S8 APO, © Leica Microsystems 2017). The conservation status of the new species was evaluated based on the guidelines of the International Union for Conservation of Nature (IUCN 2012). A distribution map was prepared using data obtained from our field observations, herbarium specimens and relevant literature (extrapolated or approximated with respect to a few old or vaguely specified localities).

Taxonomy

Premna bhamoensis Y.T. Tan & B. Li, sp. nov.

urn:lsid:ipni.org:names:77164217-1 Figures 1, 2A–C, 3

Diagnosis. The species is most similar in morphology to *P. menglaensis* B. Li, but differs from the latter in having branchlets and petioles densely tomentose (vs. glabrous or glabrescent), leaf blades papery with minute pubescence (vs. leathery and glabrous), flowers green to greenish yellow (vs. red flowers), calyces slightly 2-lipped with five equal lobes (vs. calyces distinctly 2-lipped with entire or minute emarginate lips), and stamens exserted from corolla (vs. included).

Type. MYANMAR. Kachin State, Bhamo County, voucher from a cultivated plant at the Xishuangbanna Tropical Botanical Garden, Menglun Town, Mengla County, Yunnan Province, Alt. 550 m, 21.404408N, 101.152401E, 10 June 2011, *B. Li LB0399* (fruiting branches) (holotype: IBSC!; isotypes: IBSC!, JXAU!, HITBC!).

Description. Woody shrubs, climbing. Branches brown, terete, with an interpetiolar ridge and sparse small yellow elliptic lenticels, sparsely and minutely pubescent to glabrescent. Branchlets grayish to brownish, densely tomentose, without bracts at the base. *Leaves* simple, opposite-decussate, ovate-oblong to elliptic, papery, $9.0-17 \times 4.5-7.5$ cm, apex long caudate to caudate-acuminate, base cuneate, subrounded to slightly cordate, margin entire; adaxial surface subglabrous except minutely hirsute on veins; abaxial surface densely pubescent with sparse, yellowish-brown glands; veins 4-8 pairs, abaxially raised and adaxially slightly compressed, secondary veins curved and jointed near margin; petiole 1.5-4.5 cm long, furrowed on upper part, densely yellowishbrown pubescent. Inflorescences terminal, mostly pyramid-shaped thyrse, densely dusty brownish-yellow pubescent, 4.0–7.5 cm long; peduncles 1.5–2.5 cm long; bracts ovatelanceolate to lanceolate-linear, 0.6-1.2 cm long, easily deciduous; bracteoles linear or lanceolate-linear, 1.0-2.5 mm long; pedicels 0.5-1.5 mm long. Calyx campanulate, 2.5–3.0 mm long, slightly 2-lipped with five equal lobes, apex acute, outside minutely brownish pubescent with brown glands; fruiting calyx distinctly 2-lipped with one lip 2-lobed and another 3-lobed, apex obtuse to subrounded. Corolla green to greenish yellow, 2-lipped, 4.5-5.5 mm long; tube 2.5-3.0 mm long, outside glabrous, inside densely white villose around throat; upper lip 1-lobed, entire, broadly oblong-obovate, obovate, concave, apex subrounded, outside glabrous or slightly pubescent; lower lip 3-lobed, middle lobe rounded to obovate, lateral lobes broadly oblong-ovate or ovate. Stamens 4, didynamous, filaments greenish-white, glabrous, slightly exserted; anther white. Ovary obovoid, 1.0-1.5 mm long, minutely pubescent and golden glandular near the apex; style white, slender, 3.5–4.5 mm long. Fruits drupaceous, purplish dark brown, obovoid to obovoid-ellipsoid, 7.0-8.0 × 4.5-5.5 mm, sparsely dusty pubescent and glandular.

Phenology. Flower buds were observed in early April. Flowering was observedfrom mid-May to early June and fruiting from late May to late June.



Figure I. *Premna bhamoensis* Y. T. Tan & B. Li, sp. nov. **A** habit **B** a branchlet with ovate-oblong to elliptic leaves **C** branchlet and petioles covered by dense brownish pubescences **D** abaxial surface of leaf blade.

Distribution. Per the introduction record, *P. bhamoensis* is originally collected from northeastern Myanmar, but currently known only from the cultivated type in the Xishuangbanna Tropical Botanical Garden (Figure 4). Based on our experience in examination of Asian *Premna* specimens, we suspect that the species is probably endemic to Kachin State of Myanmar and distributed in a very small area.

Etymology. The specific epithet of this new species, "*bhamoensis*", is derived from the name of the locality, Bhamo County, from where the species was originally collected.

Preliminary conservation status. Since we have neither rediscovered the wild population of *P. bhamoensis* in Myanmar, nor identified any other specimens in the herbarium, very few details about its natural distribution and/or population status are currently known. Therefore, the information is inadequate to assess the species' risk of extinction, whether directly or indirectly. In accordance with the IUCN Red List Categories (IUCN 2012), we propose to temporarily list the species as a taxon under



Figure 2. Morphological comparison between *Premna bhamoensis* (**A–C**) and *P. menglaensis* (**a–c**). **A, a** branchlets with inflorescences **B, b** inflorescences, flowers and calyces (in the blank circle) **C, c** fruitescences and fruits (arrow show fruiting calyx).

the Data Deficient (DD) category. Further field surveys in northeastern Myanmar are needed to gain more information on its abundance and/or distribution.

Other specimen examined. MYANMAR. Kachin State, Bhamo County, voucher from a cultivated plant at the Xishuangbanna Tropical Botanical Garden, Menglun Town, Mengla County, Yunnan Province, Alt. 550 m, 21.404408N, 101.152401E, 31 May 2012, *Y. H. Tan 120* [flowering branches] (XTBG!).

Note. Among the seven *Premna* species recorded in the flora of Kachin State, Myanmar (Kress et al. 2003), *P. pyramidata* (= *P. tomentosa* Willd.) and *P. bengalensis* have



Figure 3. Line drawing of *Premna bhamoensis* Y. T. Tan & B. Li, sp. nov. **A** abranchlets with inflorescence **B** inflorescence **C** fruitescence **D** corolla **E** calyx in flowering (left) and fruiting (right) **F** fruit.



Figure 4. Distribution map of *Premna bhamoensis* (green circle showing the type locality and red circle for the cultivated cite) and *P. menglaensis* (orange star).

dense stellate hairs on branchlets, leaves, and petioles, *P. racemosa* (= *P. interrupta* Wall. ex Schauer) has spikelike inflorescences, and *P. scandens* is a large and glabrous vine. Thus, these four species are quite distinct from *P. bhamoensis*. *P. barbata* and *P. khasiana* both have bracts at the base of branchlets, whereas such bracts are absent in *P. bhamoensis*. *P. pinguis* differs from *P. bhamoensis* in having ovate leaves with strongly serrulate margins, and branches without interpetiolar ridges. All these differences make *P. bhamoensis* a distinct *Premna* species in Myanmar. A key to the *Premna* species in Kachin State of Myanmar is provided below.

Among the Asian *Premna*, *P. menglaensis*, as the introduction label indicated, is the species showing the maximum level of similarity to *P. bhamoensis*. Both are climbing shrubs with ovate-oblong to elliptic leaves, and congested pyramid-shaped inflorescences. However, *P. bhamoensis* can be easily distinguished from *P. menglaensis* on the basis of the differences observed in a number of traits, e.g., branchlets and petioles (densely pubescent vs. glabrous or glabrescent), leaf blades (papery and mi-

nutely pubescent vs. leathery and glabrous), flower color (green to greenish yellow vs. red), calyx shape (slightly 2-lipped with five equal lobes vs. distinctly 2-lipped with entire or minute emarginate lips), stamens length (exserted from corolla vs. included) (Figure 2). *P. bhamoensis* also resembles *P. fulva* Craib in having a climbing habit, dense indumentum on branchlets and petioles, green to greenish yellow flowers, and calyces with five lobes, but clearly differs in leaf shape (ovate-oblong to elliptic with entire margins vs. ovate to subrounded with serrate margins) and inflorescence type (congested pyramid-shaped thyrse vs. flat-topped corymbose cyme) (Chen and Gilbert 1994, Tan and Li 2016). Besides, branchlets, petioles, leaf blades, and inflorescences of *P. fulva* are densely covered with long, spreading, golden-brown hairs, which are different from the hairs found on *P. bhamoensis*.

A key to the species of Premna in Kachin State of Myanmar

1	Inflorescences spikelike	P. interrupta
_	Inflorescences compound cymes	2
2	Branchlets, leaves, and petioles covering dense stellate hairs	
_	Branchlets, leaves, and petioles glabrous or covering other typ	e of hairs 4
3	Leaf blades ovate to ovate-oblong; cymes in a lax conical panicle.	P. tomentosa
_	Leaf blades elliptic to oblong-lanceolate; cymes in a lax flat-topp	ed corymbs
		P. bengalensis
4	Vines; branches and leaves glabrous	P. scandens
_	Trees, erect or climbing shrubs; branches and leaves pubescent	5
5	Base of branchlets surrounded by bracts	6
_	Base of branchlets without bracts	7
6	Corymbs ca. 15 cm in diameter, peduncles slender; leaf blades	turn brownish
	black when dry	P. khasiana
_	Corymbs ca. 4 cm in diameter, peduncles robust; leaf blades br	ownish yellow
	when dry	P. barbata
7	Leaves margins strongly serrulate; branches without interpetio	lar ridges
		P. pinguis
_	Leavesmargins entirely; branches with interpetiolar ridges	P. bhamoensis

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References

- Briquet J (1897) Verbenaceae. In: Engler A, Prantl K (Eds) Die Natürlichen Pflanzenfamilien, Teil 4, Abt. 3a. Engelmann, Leipzig, 132–182.
- Chen SL, Gilbert MG (1994) *Premna*. In: Wu CY, Raven PH (Eds) Flora of China, Vol. 17. Science Press, Beijing & Missouri Botanical Garden Press, St. Louis, 16–27.
- Harley RM, Atkins S, Budantsey AL, Cantino PD, Conn BJ, Grayer R, Harley MM, de Kok RPJ, Krestovskaja T, Morales R, Paton AJ, Ryding O, Upson T (2004)Labiatae. In: Kubitzki K, Kadereit JW (Eds) Families and genera of vascular plants. Flowering plants. Dicotyledons – Lamiales (except Acanthaceae including Avicenniaceae), Vol. 7. Springer, Berlin, 167–275. https://doi.org/10.1007/978-3-642-18617-2_11
- IUCN (2012) IUCN Red List Categories and Criteria, Version 3.1 (2nd edn). Gland and Cambridge, 32 pp.
- de Kok RPJ (2013) The genus *Premna* L. (Lamiaceae) in the *Flora Malesiana* area. Kew Bulletin 68: 55–84. https://doi.org/10.1007/s12225-013-9433-5
- Kress WJ, DeFilipps RA, Farr E, Yin Yin Kyi D (2003) A checklist of the trees, shrubs, herbs, and climbers of Myanmar (revised from the original works by JH Lace, R. Rodger, HG Hundley and U Chit Ko Ko on the "List of trees, shrubs, herbs and principal climbers etc. recorded from Burma"). Contributions from the United States National Herbarium 45: 1–590.
- Li B, Tan Y, Zhang ZY, Zhang DX (2013) Premna menglaensis, a new name for Premna laevigata C. Y. Wu (Lamiaceae). Phytotaxa 153: 58–59. https://doi.org/10.11646/phytotaxa.153.1.4
- Li B, Cantino PD, Olmstead RG, Bramley GLC, Xiang CL, Ma ZH, Tan YH, Zhang DX (2016) A large-scale chloroplast phylogeny of the Lamiaceae sheds new light on its subfamilial classification. Scientific Reports 6: 34343. https://doi.org/10.1038/srep34343
- Li HW, Hedge IC (1994) Lamiaceae. In: Wu CY, Raven PH (Eds) Flora of China, Vol. 17. Science Press, Beijing & Missouri Botanical Garden Press, St. Louis, 269–291.
- Linnaeus C (1771) Mantissa Plantarum. Salvius, Stockholm, 587 pp.
- Tan Y, Li B (2014) Taxonomic studies on the genus Premna (Lamiaceae) in China—I: the identities of *P. fulva* and *P. tapintzeana*. Phytotaxa 173: 207–216. https://doi.org/10.11646/ phytotaxa.173.3.3
- Verdcourt B (1992) Verbenaceae. In: Polhill RM (Ed.) Flora of tropical east Africa. Balkema, Rotterdam, 1–156.

RESEARCH ARTICLE



Craterispermum capitatum and C. gabonicum (Rubiaceae): two new species from the Lower Guinean and Congolian Domains

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Abstract

Craterispermum capitatum and *C. gabonicum*, two new species of Rubiaceae, are described from the Lower Guinea and Congolian Domains. Detailed descriptions and distribution maps are provided for each species, their conservation status is assessed and their taxonomic affinities are discussed. *Craterispermum gabonicum* is unique within the genus because of the strong dimorphism in brevistylous and longistylous flowers and inflorescences. We hypothesize that this species shows some form of dioecy. The distribution of *C. capitatum* shows a wide disjunction: the species is present in the Lower Guinean and Congolian Domains but absent from Gabon and South Cameroon. An identification key for the *Craterispermum* species present in the Lower Guinean and Congolian Domains is given.

Résumé

Craterispermum capitatum et *C. gabonicum*, deux nouvelles espèces de la famille des Rubiaceae, des Domaines Bas Guinéen et Congolais sont décrites. Des descriptions détaillées et des cartes de distribution sont données pour chacune des espèces, leur statut de conservation est évalué et leurs affinités taxonomiques discutée. *Craterispermum gabonicum* est unique dans le genre en raison d'un dimorphisme avéré entre les fleurs, mais aussi les inflorescences brévistyles et longistyles. L'hypothèse de l'existence d'une tendance vers la dioécie chez cette espèce est émise. La distribution *C. capitatum* présente une importante disjonction: l'espèce est présente dans les Domaines Bas Guinéen et Congolais, mais absente au Gabon et au sud du Cameroun. Une clé d'identification pour les espèces de *Craterispermum* présentes dans les Domaines Bas Guinéen et Congolais est donnée.

Keywords

Rubiaceae, Craterispermum, C. capitatum, C. gabonicum, dimorphic inflorescences and flowers, dioecy, heterostyly, Cameroon, Gabon, Nigeria, Congo, DR Congo

Introduction

The genus *Craterispermum* Benth. (Rubiaceae, subfamily Rubioideae) is distributed in tropical Africa, Madagascar and the Seychelles (Robbrecht 1988, Taedoumg et al. 2011, Taedoumg and Hamon 2013; De Block and Randriamboavonjy 2015). *Craterispermum* species are shrubs or small trees with axillary or supra-axillary inflorescences, paired at the nodes and often condensed. The flowers are few to many per inflorescence, small, heterostylous and white. The ovary is bilocular with a single, apically attached, pendulous ovule in each locule. One ovule aborts and the fleshy fruit contains a single seed, shaped like an asymmetrical shallow or deep bowl. The seed has a peculiar, discontinuous seed coat, comprised of isolated cells with ring-like thickenings (Igersheim 1992). Raphides are present in all plant tissues in the genus. *Craterispermum* species have been shown to accumulate aluminium in leaves and stem tissue (Jansen et al. 2000); the leaves dry pale yellow or green, which is typical for aluminium accumulating species.

According to Anderson (1973), there are probably more heterostylous species in the Rubiaceae than in all other angiosperm families put together. In the genus *Craterispermum* heterostyly was often overlooked and plants with different floral morphs were sometimes described as separate species. For example, the type of *C. congolanum* De Wild. & Th. Dur. is just the brevistylous morph of *C. angustifolium* De Wild. & Th. Dur. De Wildeman, 1924 was one of the first to notice that some described species were just different morphs of heterostylous species. In *Craterispermum* and in other heterostylous Rubiaceae species (e.g. *Psychotria* L.), thrum flowers characteristically have included styles and exserted anthers; pin flowers have exserted styles and included anthers (complete heterostyly) (Robbrecht 1988).

Craterispermum is easily recognized at the genus level, but many of the species look similar and identification at the species level is difficult (Verdcourt 1973, Taedoumg et al. 2011). Herbarium material of *Craterispermum* is often poor, generally carrying only residual inflorescences. Because of the compact structure of the inflorescences, flowers and fruits fall easily during collecting, pressing, drying and mounting. Moreover, flowers are short-lived and ripe fruits do not remain on the plant for long (Taedoumg et al. 2011). The above-mentioned reasons make *Craterispermum* species challenging to describe.

The examination of the available herbarium material allowed us to highlight the existence of several new species. Hitherto, we have described five species from continental Africa (Taedoumg et al. 2011; Taedoumg and Hamon 2013). The present paper describes two further species from Cameroon, Gabon, Nigeria, Congo and the Democratic Republic of Congo. An identification key for the *Craterispermum* species present in the Lower Guinean and Congolian Domains is also given.

Methods

Herbarium material of the following institutions was studied: BR, BRLU, G, K, MO, P, WAG and YA. Descriptive terminology follows Robbrecht (1988) and Anonymous (1962). Phytogeographical terminology follows White (1979). Measurements and other given details are based on the study of herbarium specimens, using a Leica MZ95 stereomicroscope, and data derived from field notes. In the descriptions and key, inflorescence size does not include the corollas, and given colours (except flower colour) are for dried material. Inflorescences are described as uniflorous (one flower only), pauciflorous (2 to 9 flowers) or multiflorous (10 to up to 50 flowers). Flowering and fruiting periods are given as cited on the collector's labels.

Specimens are cited per country, alphabetically by first collector. All cited specimens have been seen. Coordinates are given to minute-level for each specimen. In the specimen citations "sl" and "sd" indicate that collection locality and date, respectively, are missing on the herbarium label. The conservation status was assessed by applying the IUCN Red List Category criteria (IUCN 2012) using the Geospatial Conservation Assessment Tools in GeoCAT (Bachman et al. 2011). The key covers the countries Nigeria, Cameroon, Equatorial Guinea, Gabon, Congo and D.R.Congo.

Taxonomic treatment

Craterispermum capitatum Taedoumg & De Block, sp. nov. urn:lsid:ipni.org:names:77164218-1 Figs 1, 2

Diagnosis. Resembling *C. robbrechtianum* Taedoumg & Sonké, 2011 by the coriaceous leaves, the obscure intersecondary venation especially in fresh condition and the ovoid shape of the young fruits, but differing from this species by the capitate structure of the inflorescence (vs branched and subcapitate in *C. robbrechtianum*), the ovoid shape of its fruits at maturity (vs asymmetrically subglobular), the granular texture of the young branches (vs smooth), and the leaf blades generally glossy above in dry condition (vs dull).

Type. DEMOCRATIC REPUBLIC OF THE CONGO. Yangambi, à 6,5 km au NW du Poste, 0°46'N, 24°27'E, 470 m, 6 March 1937 (fr), *J.L.P. Louis 3440* (holo-type BR [000008055132])

Shrub or treelet up to 8 m tall; all vegetative and reproductive parts glabrous externally. Stems pale grey, ca. 10 cm in diameter; young branches grayish to brownish, often granular in outlook, often with more or less quadrangular sections, generally canaliculate near the final nodes. Stipules persistent, sheath 1–3 mm long, truncate to subtruncate or rarely with short awn ca. 0.5 mm long. Leaves petiolate; petioles canaliculate, 10–17 mm long; leaf blades narrowly elliptic or narrowly oblong to obovate, $8-20.5 \times 3-7$ cm, coriaceous, green, greenish brown or gold green and glossy above,



Figure 1. Craterispermum capitatum. A Longistylous flower B Node with stipules and inflorescences (only one shown) C Node with infrutescence with young fruits D Young fruit. A from Trochain 8306 (P)
B from Richards 3382 (MO) C, D from Louis 9162 (BR). Drawn by Antonio Fernandez.

paler green below; base cuneate; apex acuminate, acumen 7–10 mm long; margins somewhat revolute; midrib prominent below; secondary nerves 8–9 pairs, somewhat prominent on both surfaces, intersecondary venation obscure on both surfaces, almost invisible in fresh condition. Inflorescences supra-axillary, borne 1–5 mm above the nodes, erect, capitate, $4-9 \times 1.8-4$ mm, pauciflorous to multiflorus; peduncle flattened, 1.5–7 mm long; bracts and bracteoles broadly triangular, 1–1.6 mm and ca. 0.8 mm long respectively, apex obtuse or truncate, margins sometimes bearing sparse

colleters. Flowers presumed heterostylous (but only longistylous morph known), 5-merous, sessile. Longistylous flowers: Calyx greenish white; tube 0.5–0.7 mm long, subtruncate or with short, obtuse teeth ca. 0.3 mm long, margins sometimes sparsely bearing colleters. Corolla white; tube narrowly cylindrical, 4–5 mm long, sparsely to densely pubescent in the throat and upper quarter inside; lobes ca. 2.5 mm long, glabrous or sparsely pubescent in the basal half inside, tips acute. Stamens inserted below the level of the throat, only apices exserted from corolla tube at anthesis; anthers ca. 1.1 mm long, white; filaments ca. 0.2 mm long. Ovary ca. 1.1 mm long, greenish white. Style and stigma exserted from the corolla tube at anthesis, ca. 6 mm long, glabrous; stigma bilobed, stigmatic lobes ca. 1.4 mm long. Infrutescences carrying (2–)4–10 fruits. Fruits sessile, ovoid, 8–10 mm diam., successively green, whitish green and dark violet at maturity.

Taxonomic affinities. This species is morphologically close to *C. robbrechtianum* because of its coriaceous leaves, its obscure intersecondary venation especially in fresh material, the length of its peduncles and the shape of its young fruits. However, it differs from this species by the capitate structure of its inflorescence (vs branched and subcapitate in *C. robbrechtianum*), the ovoid shape of its fruits at maturity (vs asymetrically subglobular in *C. robbrechtianum*), the granular texture of the young branches (vs smooth in *C. robbrechtianum*), and its leaf blades generally glossy above in dry condition (vs dull in *C. robbrechtianum*). In addition, fruiting herbarium specimens tend to retain more fruits [(2–)4–10 fruits] (vs ca. 1–2 fruits in *C. robbrechtianum*).

The specimens of *C. capitatum* studied were almost all previously identified as *C. cerinanthum* Hiern. But this species clearly differs from *C. capitatum* by its relatively long pedunculate, branched and lax inflorescences.

Phenology. Flowers: March - May (Nigeria), July (Cameroon); October (Republic of the Congo); Fruits: March - May, September - December (Democratic Republic of the Congo); April (Nigeria).

Distribution and habitat. *Craterispermum capitatum* is known from Western Cameroon, the Democratic Republic of the Congo, South-Eastern Nigeria and the Republic of the Congo. It grows in semi-deciduous primary and secondary forest between 0 and 470 m elevation (Fig. 2).

Vernacular name and uses. Democratic Republic of the Congo - Botele bo lokonda (Turumbu); Djeli na Kupi (-). Leaves are used as fetish to avoid panthers.

Preliminary conservation status. IUCN status:—Vulnerable: VU B2b(iii). The extent of occurrence (EOO) of *C. capitatum* is 1,134.21 km², and its area of occupancy (AOO) is 52 km² using a cell width of 2 km. The species is distributed in 7 subpopulations, 2 of which are located in protected areas: the Omo-Oluwa-Shasha Forest Reserve located in Ondo State in Nigeria and the Korup National Park in Cameroon and Cross River National Park in Nigeria, which are in fact contiguous. Habitat loss outside the protected areas is a serious threat for *C. capitatum*, but loss of forest is also documented for the Omo-Oluwa-Shasha Forest Reserve and the Cross River National Park in Nigeria (Ite 1997; Adedeji and Adeofun 2014).



Figure 2. Distribution map of Craterispermum capitatum.

Field study is required to fully assess the AOO of *C. capitatum* and, given the fact that the Democratic Republic of the Congo is not well collected, the number of locations for the species is likely to increase.

Etymology. The name of the species was chosen because of the capitate structure of its inflorescences.

Critical notes. The distribution of *C. capitatum* is atypical because of its absence in the South of Cameroon and in Gabon. While rare, several other Rubiaceae species show distribution patterns with a similar macro-disjunction, notably *Hymenocoleus rotundifolius* (A. Chev. ex Hepper) Robbr. (Robbrecht 1996) and *Ixora brachypoda* DC. (De Block 1998). The reason of this atypical distribution is not yet clearly determined, but in this case, it is probable that the continuous humid forest in southern Cameroon and Gabon is not an ideal habitat for *C. capitatum*, which occurs mostly in more semideciduous forests.

Additional specimens examined (paratypes). CAMEROON: NE corner of Korup National Park, near Baro Village, 5°16'N, 9°11'E, 200 m, 24 March 1984 (fl), *D.W. Thomas 3358* (MO, WAG). **REPUBLIC OF THE CONGO:** M'Boku-COFORIC, Forêt du Mayumbe, 4°15'S, 13°29'E, 8 October 1950 (fl), *J. Trochain 8306* (P). **NIGE-RIA:** South-West, Shasha Forest Reserve, 1/4 mile SW of Osho enclave, 7°5'N, 4°30'E, 1 April 1946 (fl bud), *A.D.P. Jones FHI 17233* (BM, K, P); Omo and Shara Forest Reserve, about 1/2 mile SW of Osho enclave, site of E.B.3L., 7°0'N, 4°15'E, 3 April
1946 (fr), A.P.D. Jones & C.F. Onochie FHI 17352 (K, P); Omo Forest Reserve, 3 km S of Aberu, 10 km S of Omo Sawmill, 7°0'N, 4°15'E, 14 May 1980 (fl), E. Pilz 2455 (MO); Ogun, Omo Forest Reserve, 3 km S of Aberu, 10 km S of Omo Sawmill, 7°0'N, 4°15'E, 17 May 1980 (fl), E. Pilz 2530 (MO, WAG); Ijebu Province, Shasha Forest Reserve, 7°5'N, 4°30'E, 4 March 1935 (fl), P.W. Richards 3192 (BM, MO); Ijebu Province, Shasha Forest Reserve, 7°5'N, 4°30'E, 22 April 1935 (fr), P.W. Richards 3382, (BM, MO); Ijebu Province, Shasha Forest Reserve, 7°5'N, 4°30'E, 12 April 1935 (fr), R. Ross 210 (BM, MO); Oban, 5°19'N, 8°34'E, 1911 (fr), P.A. Talbot 208 (BM); South Eastern State, Ekinta River Forest Reserve, about 20 km ENE of Calabar, 5°0'N, 8°30'E, 1 April 1971 (fr), P.P.C. Van Meer 1113A (WAG); South Eastern State, Ekinta River Forest Reserve, about 20 km ENE of Calabar, 5°0'N, 8°30'E, 2 April 1971 (fl, fr), P.P.C. Van Meer 1124 (WAG); South Eastern State, Oban Group Forest Reserve, West block, between pillar 59 and 60, Kwa River, 5°9'N, 8°28'E, 150 m, 14 April 1971 (fr), P.P.C. Van Meer 1450 (WAG). DEMOCRATIC REPUBLIC OF THE CONGO: route Mabana km 3, terr. Maluku, 4°3'S, 15°33'E, 27 November 1970 (fr), H. Breyne 982 (BR); Sualempu, 12 km de Bita, 4°16'S, 15°48'E, 24 March 1971 (fr), H. Breyne 2125 (BR); sl, 1921 (fr), J. Claessens 644 (BR); Bokolongo-Djoa, terr. Bolomba, 0°12'N, 19°21'E, 27 February 1958 (fr), C. Evrard 3569 (BR); Djoa (territoire Bolomba), 0°8'N, 19°16'E, 17 May 1958 (fr), C. Evrard 4075 (BR); Djoa, terr. Bolomba, 0°8'N, 19°16'E, 15 October 1958 (fr), C. Evrard 5014 (BR); Bankaie, terr. Inongo 2°22'S, 18°25'E, 9 September 1953 (fr), G. Gilbert 14772 (BR); Yangambi, plateau de la Luweo, 0°46'N, 24°27'E, 470 m, 30 April 1938 (fr), J. Louis 9162 (BR).

Craterispermum gabonicum Taedoumg & De Block, sp. nov.

urn:lsid:ipni.org:names:77164219-1 Figs 3, 4

Diagnosis. Resembling *C. ledermannii* K. Krause, 1912 because of the large leaves and the often robust peduncles, but differing from this species by the subcapitate inflorescences (vs branched in *C. ledermannii*), the notable dimorphism between flowers and inflorescences of the different flower morphs, the secondary nerves clearly ascending and forming acute angles with the midrib (vs secondary nerves more or less perpendicular to the midrib).

Type. GABON. Ogooué-Maritime: Rabi-Kounga, ca. 4 km N of Shell-camp, 1°55'S, 9°52'E, 19 September 1992 (fl), *J.J. Wieringa & J.B. Epoma 1611* (holotype WAG [WAG0233599], isotype WAG [WAG0233600]).

Shrub or treelet, 1.5–9 m tall; all vegetative and reproductive parts glabrous externally. Stems brownish, ca. 8 cm in diameter; young branches greenish or grayish, somewhat granular in outlook. Stipules persistent, sheath 2–7 mm long, keeled, subtruncate or with short awn <1 mm long. Leaves petiolate; petioles canaliculate, 7–19 mm long; leaf blades narrowly elliptic or narrowly obovate, more rarely elliptic or obovate, $10.5-24 \times 4.4-7.2$ cm, coriaceous, brownish or yellowish green and gene-



Figure 3. Craterispermum gabonicum. A Flowering branch (brevistylous morph) B Node with stipules and young inflorescences C Inflorescence (longistylous morph) D Inflorescence (corollas fallen) (brevistylous morph) E Bracteole (brevistylous morph) F Bracteole (longistylous morph) G Corolla (longistylous morph)
H Longitudinal section of corolla (longistylous morph) I Corolla (brevistylous morph) J Longitudinal section of corolla (brevistylous morph) K Tip of corolla lobe showing subapical spike-like protuberance L Calyx (longistylous morph) M Calyx (brevistylous morph) N Immature fruit. A–B, D–E, G–H, M from Wieringa 1611 (WAG), C, F, I–K, L from Issembe 244 (WAG), N from Breteler 10979 (WAG). Drawn by Marijke Meersman.

rally dull above, paler green or brown below; base cuneate; apex acuminate, acumen 8–16 mm long; margins not revolute; midrib prominent below; secondary nerves 6–9 pairs, clearly ascending and forming acute angles with midrib, obscure on both surfaces; intersecondary venation moderately prominent above, obscure on lower surface, obscure to almost invisible on both surfaces in fresh condition. Inflorescences axillary to supra-axillary, borne up to 7.5 mm above the nodes, erect, subcapitate to capitate, $4-19 \times 5-20$ mm; peduncle subcylindrical to flattened (up to 3.5 mm wide), robust, 1.5-4.5(-7) mm long. Inflorescences completely covered by imbricate outer bracts when young, medium green to greenish white (somewhat resembling an immature fruit); brevistylous and longistylous inflorescences dimorphous: brevistylous inflorescences very congested, 11.5–19 × 7.5–20 mm, pauciflorous to multiflorous; bracts and bracteoles broadly triangular or ovate, $6-8 \times 5-8$ mm and 6×3 mm respectively with rounded or rarely subtruncate apex and margins sometimes bearing sparse colleters; longistylous inflorescences less congested, 4-7 × 5.2-9.1 mm, pauciflorous; bracts and bracteoles broadly triangular, ca. $2 \times 1.5-2$ mm and $0.7-2 \times 1-2$ mm respectively with rounded or truncate apex and margins sometimes bearing sparse colleters. Flowers heterostylous, 5-merous, sessile; ovary and calyx pale green or whitish, somewhat violet tinged; corolla narrowly cylindrical, white; anthers and filaments white or whitish violet. Brevistylous flowers: Calyx with tube (1.5-)3-5 mm long, sometimes bearing sparse colleters at the base inside; lobes (0.3-0.6)-1.5 mm long, apex acute, obtuse or rounded, margins sometimes bearing sparse colleters. Corolla with tube 6-12 mm long, pubescent in the throat and upper half inside; lobes 3-6 mm long, covered with short hairs at the base inside, tips acute. Stamens inserted ca. 2 mm below the level of the throat, completely exserted from or only bases included in corolla tube at anthesis; anthers 1.1-3 mm long; filaments 1-2.5 mm long. Ovary 0.5-1.2 mm long. Style and stigma included in corolla tube at anthesis, 4–7.5 mm long; stigma bilobed, stigmatic lobes 1.5-2 mm long. Longistylous flowers: Calyx with tube 1-1.5 mm long; lobes triangular, 0.5-0.7 mm long sometimes bearing sparse colleters at the base inside. Corolla with tube 4–5 mm long, pubescent in the throat and upper third inside; lobes 3.5-4 mm long, densely pubescent at the base inside, tips acute. Stamens inserted ca. 2 mm below the level of the throat; completely included in the corolla tube or only the apices exserted at anthesis; anthers 1.8–2 mm long; filaments <0.5 mm long. Ovary ca. 1.2 mm long. Style and stigma exserted from the corolla tube at anthesis, ca. 7.5 mm long; stigma bilobed, stigmatic lobes ca. 1.5 mm long. Fruits sessile, urceolate, ca. 16×8 mm, colour at maturity unknown.

Taxonomic affinities. This species is atypical in the genus because of the flower and inflorescence dimorphism. However, it somewhat resembles *C. ledermannii* because of the large leaf blades and the often robust peduncles. It differs from this species by its subcapitate inflorescences (vs mostly branched in *C. ledermannii*), its secondary nerves clearly ascending and forming acute angles with the midrib (vs more or less perpendicular to the midrib in *C. ledermannii*) and by the fact that its inflorescences are completely covered by imbricate outer bracts when young (somewhat resembling an immature fruit) (vs never completely covered in *C. ledermannii*).



Figure 4. Distribution map of Craterispermum gabonicum.

Phenology. Flowers: March-May and August-November. Fruits: February, April and August-December.

Distribution and habitat. *Craterispermum gabonicum* is endemic to Gabon. It grows in primary forest but also in humid secondary forest between 150 and 400 m elevation (Fig. 4).

Vernacular names and uses. Unknown.

Preliminary conservation status. IUCN status:—Vulnerable: VU B2(iii). The extent of occurrence (EOO) of *C. gabonicum* is 80,847.46 km², and its area of occupancy (AOO) is 60 km² using a cell width of 2 km. The species is distributed in 7 or 8 subpopulations, 2 of which are located in protected areas: in Wonga Wongué Forest Reserve in Ogooué-Maritime Division and on the edge of the Loango National Park in West Gabon. The Wonga Wongué Forest Reserve is subject, these last years, to a very strong pressure from uncontrolled anthropomorphic activities (illegal exploitation of the resources as well as degradation of the ecosystems as a result of oil exploitation). Habitat loss outside and inside the protected areas is a serious threat for *C. gabonicum*.

Etymology. This species is named after the country to which it is currently endemic.

Critical notes. Within this species flowers and inflorescences are very variable in shape and size, more so than in other species of the genus. This variability seems to be *a priori* correlated with the heterostyly, which is present in all species of the genus.

However, *C. gabonicum* does not only show the reciprocal stigma and anther position and the pollen dimorphism typical for heterostylous species and present in all continental African *Craterispermum*, but a further dimorphism occurs at flower and at inflorescence level. The corolla tube of brevistylous flowers is longer and wider than that of longistylous flowers (6–12 mm × ca. 3 vs $4-5 \times 1.5-2$ mm) (Fig. 3 H–I, K–L). Brevistylous flowers generally also have longer and wider calyx tubes than longistylous flowers [(1.5–)3–5 mm vs 1–2 mm long) (Fig. 3J–G). Except for the length of the filaments, possible size differences in anthers and stigmatic lobes could not conclusively be observed. In regard to the inflorescences, those with brevistylous flowers comprise more flowers than those with longistylous ones (multiflorous vs pauciflorous, respectively)(Fig. 3C–D). Furthermore, bracts and bracteoles are larger in inflorescences with brevistylous flowers than in inflorescences with longistylous flowers (6–8 × 5–8 mm and ca. 6 × 3 mm respectively vs ca. 2 × 1.5–2 mm and 0.7–2 × 1–2 mm) (Fig. 3E–F).

These differences in size are unknown in heterostylous species but are typical for certain dioecious ones (Pailler et al. 1998; Lantz and Bremer 2004; Mouly and Achille 2007). In several plant groups dioecy has been shown to have evolved from heterostyly, with the functionally male flowers derived from the brevistylous and the functionally female flowers from the longistylous morphs (Beach and Bawa 1980). This is also the case for certain Rubiaceae species, such as Chassalia corallioides (Cordem.) Verdc. (Pailler et al. 1998) and Mussaenda parviflora Miq. (Naiki and Kato 1999). The size difference in flowers and inflorescences observed in C. gabonicum is also reported from certain dioecious species. Fewer flowers per inflorescence are found in individuals with female flowers than in individuals with male flowers in dioecious species of the tribe Vanguerieae (Lantz and Bremer 2004; Mouly and Achille 2007). Also, in certain dioecious species, such as Chassalia corallioides (Pailler et al. 1998) male flowers have longer corolla tubes than female flowers. We therefore suggest that a trend towards functional dioecy could be the explanation for the dimorphism in flowers and inflorescences in C. gabonicum, with the flowers being morphologically heterostylous but functionally dioecious or evolving towards this condition.

It is very difficult to verify this hypothesis without field studies, especially since mature flowers of both morphs and mature fruits are rare on the available herbarium material and no fixed flower material was available for detailed morphological and anatomical studies. With hardly any fruit set, it is impossible to know whether only one (brevistylous) or both morphs set fruit. Furthermore, both morphs produce viable pollen (based on morphological characters) although anthers are somewhat larger and pollen more abundant in the brevistylous morph. While the calyx tube is much longer in the brevistylous morph, this is not the case for the ovaries, which rather are somewhat reduced. All ovaries of brevistylous flowers contained ovules, but these too seemed somewhat reduced in size. Because of the lack of available plant material with mature flowers and fruits, it is impossible to demonstrate with certainty the hypothesis stated here that dioecy in some form is present in *C. gabonicum*. The species would certainly be an ideal species for field studies focusing on breeding system and reproductive ecology.

Additional specimens examined (paratypes). GABON: Ogooé-Maritime, Toucan, 1°47'S, 9°53'E, 29 May 2002 (fl bud), H.P. Bourobou Bourobou, G. Niang-Essouma & T. Nzabi 623 (K, MO, P, WAG); 50 km SE of Lambaréné, 1°4'S, 10°30'E, 30 September 1968 (fl), F.J. Breteler 5747 (BR, K, MO, WAG); Rabi, 1°55'S, 9°50'E, 24 March 1990 (st), J. Breteler & C.C.H. Jongkind, J. Wieringa & J.M. Moussavou 9437 (BR, WAG); about 30 km E of Lastoursville, 0°40'S, 13°00'E, 20 November 1991 (fl bud), F. J. Breteler & C.C.H. Jongkind 10609 (WAG); 5-30 km NNW of Ndjolé, 0°5'S, 10°45'E, 21 April 1992 (f bud, fr), F.J. Breteler, C.C.H Jongkind. & J. Wieringa 10979 (WAG); Moyen-Ogooué, ca. 20-30 km NNW of Ndjolé, 0°3'S, 10°45'E, 1 October 1994 (fl), F.J. Breteler, B.J.M. Breteler & Klein Breteler 13110 (WAG); Ogooué-Maritime, Rabi-Kounga, route Divangui, 1°54'S, 9°46'E, 14 July 1998 (fl bud), F.J. Breteler, I.M. Moussavou, J. Nang & O. Pascal 14428 (WAG); Rabi 51, 1°55'S, 9°53'E, 1 March 2007 (st), J. Choo 1042 (BR); about 30 km NW of Doussala, in the direction of Bongo, 2°38'S, 11°38'E, 16 March 1988 (fl), J.J.F.E. De Wilde & C.C.H. Jongkind 9392 (BR, K, MO, WAG); Abanga, chantier C.E.T.A. 0°12'S, 10°11'E, 3 June 1963 (st), N. Hallé 2170 (P); Moyen-Ogooué, Camp Mboumi, 0°25'S, 10°50'E, 1 September 1999 (fl), Y. Issembe 244 (WAG); Concession Murel & Prom près du Lac Ezanga, 1°5'S, 10°13'E, 51 m, 24 November 2013 (st), O. Lachenaud, D. Ikabanga, E. Akouangou, J.Y. Serein, E. Bidault, Y. Issembe, A. Boupoya & J.D.D. Kaparadi 1609 (BRLU); 2 km SE of Forestry Camp Waka, situated ca. 32 km SE of Sindara, Waka River basin, 1°14'S, 10°53'E, 10 December 1983 (fr), A.M. Louis, F. Breteler & J. De Bruijn 1248 (WAG); Rabi (parcelle Smithsonian) code dans la parcelle: CRATGF, 1°55'S, 9°52'E, 30m, 18 March 2011 (st), D. Nguema, H. Memiague, P. Bissiemou, E. Mounoumou, G. Moussavou, L. Tchignoumba, D. Bikissa & M.W. Mbanding 1311 (BRLU); chantier CEB, ca. 50 km SW of Doussala, 2°36'S, 10°35'E, 21 August 1985 (fl, fr), J.M. Reitsma & B. Reitsma 1342 (BR, WAG); at logging site of CBG, ca. 5 km beyond checkpoint Divangui, 1°50'S, 10°0'E, 29 October 1990 (fr), I. Van Nek 152 (WAG); Nyanga, Moukalaba Doudou National Park, 2°44'S, 10°30'E, 20 February 2004 (fl, fr), J. van Valkenburg, L. Ngok Banak, Y. Issembé & T. Nzabi 2872 (BR, K, WAG); Moyen-Ogooué, Ezanga, Layon D ouest, 1°5'S, 10°14'E, sd (fl) C.M. Wilks 2466 (WAG).

Identification key of the species of *Craterispermum* present in the Lower Guinean and Congolian Domains

- Bracteoles 3–6 mm long, long aristate; peduncles 1–5 mm long2
 Bracteoles shorter, 0.3–2(–6) mm long, broadly triangular, ovate or subtrun-
- 2 Stipules 5–11 mm long, with short and broadly triangular tips, 1–3(–4.5) mm long; 5–6 pairs of secondary veins; flowers 5-merous; calyx lobes equal; tertiary and higher order venation laxly and irregularly reticulate; leaf blades 11–25.5 × 4–8 cm *C. aristatum* Wernham (SW Cameroon, SE Nigeria)

Stipules 5-16 mm long, with long and narrowly triangular tips, 4-13 mm long; 10–12 pairs of secondary veins; flowers 4-merous; calyx lobes unequal; tertiary and higher order venation closely and more or less regularly reticulate; leaf blades 6.7–14 × 2–4.8 cm C. sonkeanum Taedoumg & Hamon (Equatorial Guinea, Gabon) 3 Tertiary and especially quaternary venation obscure on both surfaces and/or very lax in fresh condition; leaf blades always coriaceous.......4 Tertiary and quaternary venation conspicuous on both surfaces; leaf blades 4 Twigs decurrently ridged, peduncles often slender, 4-150 mm long, erect or curved, fruits red at maturity...... C. inquisitorium Wernh (Cabinda, Congo, Democratic Republic of the Congo, Gabon) Twigs not decurrently ridged, peduncles stout, (0.6–)2–23 mm long, always erect, fruits violet or dark blue to black at maturity......5 5 Inflorescences subcapitate and completely covered by imbricate outer bracts (somewhat resembling an immature fruit) when young, secondary nerves clearly ascending and forming acute angles with the midrib; bracts overlapping one another at least at the base; bracts and bracteoles $6-8 \times 5-8$ mm and 6×3 mm respectively in brevistylous morph and ca. 2×1.5 –2 mm and $0.7-2 \times 1-2$ mm respectively in longistylous morph; corolla tube 6–12 mm and 4-5 mm long for brevistylous and longistylous flowers respectively...... Inflorescences mostly branched and not completely covered by the outer bracts when young, secondary nerves more or less perpendicular to the midrib; bracts not overlapping one another; bracts and bracteoles ca. 1-4 and ca. 1-2 mm long respectively, not differing between morphs; corolla tube 4–8.5 long mm in both morphs6 6 Bracts and bracteoles ca. 4 mm and ca. 2 mm long, respectively; inflorescences 6-90 mm long, moderately to very compact, subcapitate or consisting of 2 branches, each up to 60 mm long; peduncle 1.1–26 mm long; leaf blades $7-35 \times 2.5-13.5$ cm; corolla tube 6-8.5 mm long; calyx tube 1-1.3 mm long C. ledermannii K.Krause (Cameroon, Equatorial Guinea, Gabon) Bracts and bracteoles more or less equal, 1-1.5 mm long; inflorescences 2.2-20 mm long, very compact, capitate, subcapitate or consisting of 2-3 branches, each 4.5–15 mm long; peduncle (0.6-)2-7 mm long; leaf blades $6-23 \times 1.5-8$ cm; corolla tube ca. 4 mm long; calyx tube 0.4-0.7 mm long.....7 7 Inflorescences consisting of 2-3 branches or subcapitate, each 4.5-15 mm long; fruits urceolate to subglobose at maturity, usually wider at the base than at the tip; leaf blades generally not glossy above; young twigs often smooth, always cylindrical; fruits sessile or very rarely shortly pedicellate (pedicels ca. 2 mm) C. robbrechtianum Taedoumg & Sonké (Cameroon, Gabon)

-	Inflorescences capitate; fruits ovoid at maturity; leaf blades usually glossy
	above; young twigs often granular in outlook; often quadrangular and cana-
	liculate near nodes; fruits sessile C. capitatum Taedoumg & De Block
	(SW Cameroon, Congo, Democratic Republic of the Congo, SE Nigeria)
8	Stipules with conspicuous narrowly triangular tips, tip 1.5–8 mm long; fruits
	pedicellate; venation more or less regularly reticulate with secondary veins
	parallel between them and more or less perpendicular to midrib9
_	Stipules with more ovate and short tips, tip not exceeding ca. 1 mm long;
	fruits sessile; venation irregularly reticulate with secondary veins not perpen-
	dicular to midrib11
9	Stipules persistent; leaf blades papyraceous, 3.3–11 × 0.9–3.5 cm; fruits shortly
	pedicellate, pedicels 1-1.5 mm long; inflorescences with 1-4 flowers; peduncles
	0.5-4.5 mm long; inter-secondary and tertiary venation parallel and more or less
	perpendicular to midrib
	<i>C. parvifolium</i> Taedoumg & Sonké (Cameroon, Equatorial Guinea, Gabon)
_	Stipules caducous; leaf blades coriaceous or subcoriaceous, $5-25 \times 1.9-7.5$
	cm; fruits long pedicellate, pedicels 2.5-9 mm long; inflorescences 3- to sev-
	eral-flowered; peduncles 0.5-9 mm long; intersecondary and tertiary vena-
	tion not as above10
10	Twigs decurrently ridged but otherwise smooth; 6-12 pairs of secondary veins,
	leaf blades 5–15 × 1.7–5.3 cm; peduncles 4–9 mm long <i>C. caudatum</i> Hutch
	(Cameroon, Gabon, Guinea Conakry, Ghana, Ivory Coast, Nigeria, Senegal)
_	Twigs not decurrently ridged with surface granular; 14–16 pairs of secondary
	veins; leaf blades $8.5-25 \times 3.2-7.5$ cm; peduncles $0.5-5$ mm long
	C. deblockianum Taedoumg & Hamon (Gabon)
11	Stipules caducous; inflorescences sessile, subcapitate; leaves subcoriaceous,
	margins revolute when dry; tertiary and higher order venation closely reticu-
	late; young twigs with bark quickly woody, folded longitudinally and more
	or less corky in dry condition
	<i>C. rumpianum</i> Taedoumg & Hamon (SW Cameroon)
-	Stipules persistent; inflorescences pedunculate, branched or subcapitate espe-
	cially in young stage; leaves coriaceous or papyraceous, margins not revolute
	when dry; tertiary and higher order venation closely or laxly reticulate; young
	twigs not as above
12	Peduncles (7-)10-20 mm long, slender, leaf blades papyraceous to rarely
	subcoriaceous, tertiary venation and higher laxly reticulate; inflorescences
	2-3-branched, rarely subcapitate especially at young stage; bracteoles and
	flowers laxly placed; branches (1.5-)4.5-21 mm long; acumen 7-18 mm
	long C. cerinanthum Hiern (Cameroon, Congo, DR
	Congo, Gabon, Equatorial Guinea (Annobon), Nigeria, Principe, Sao Tomé)
-	Peduncles 1.4-7(-10) mm long; stout, leaf blades subcoriaceous to coriaceous;
	tertiary venation and higher densely reticulate; inflorescences subcapitate, rarely
	shortly 2-branched [<4(4.9) mm long each]; bracteoles and flowers very con-

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References

- Adedeji OH, Adeofun CO (2014) Spatial Pattern of Land Cover Change Using remotely Sensed Imagery and GIS: A Case Study of Omo-Shasha-Oluwa Forest Reserve, SW Nigeria (1986–2002). Journal of Geographic Information System 6: 375–385. https://doi. org/10.4236/jgis.2014.64033
- Anonymous (1962) Systematics Association Comittee for descriptive biological terminology. II. Terminology of simple symmetrical plane shapes (chart 1). Taxon 11: 145–156. https:// doi.org/10.2307/1216718
- Anderson WR (1973) A morphological hypothesis for the origin of heterostyly in the Rubiaceae. Taxon 22: 537–542. https://doi.org/10.2307/1218628
- Bachman S, Moat J, Hill AW, de la Torre J, Scott B (2011) Supporting Red List threat assessments with GeoCAT: geospatial conservation assessment tool. In: Smith V, Penev L (Eds) e-Infrastructures for data publishing in biodiversity science. ZooKeys 150: 117–126. https://doi.org/10.3897/zookeys.150.2109
- Beach JH, Bawa KS (1980) Role of pollinators in the evolution of dioecy from distyly. Evolution 34: 1138–1142. https://doi.org/10.1111/j.1558-5646.1980.tb04055.x
- De Block P (1998) The African species of *Ixora* (Rubiaceae Pavetteae). Opera Botanica, Belgica 9: 1–218.
- De Block P, Randriamboavonjy T (2015) Three new species of *Craterispermum* (Rubiaceae) from Madagascar. Phytotaxa 206(1): 79–89. https://doi.org/10.11646/phytotaxa.206.1.11
- De Wildeman E (1923) Etudes sur les récoltes botaniques du Dr J. Bequaert (1913–1915). Plantae Bequaertianae II, 570 pp.
- Igersheim A (1992) The ovary, fruit and seed development of *Craterispermum*. Belgian Journal of Botany 125: 101–113.

- Ite UE (1997) Small Farmers and Forest Loss in Cross River National Park, Nigeria. The Geographical Journal 163: 47–56. https://doi.org/10.2307/3059685
- IUCN (2012) Red List Categories and Criteria: Version 3.1. Second edition. IUCN Species Survival Commission. IUCN, Gland and Cambridge, 34 pp.
- Jansen S, Robbrecht E, Beeckman H, Smets E (2000) Aluminium accumulation in leaves of Rubiaceae: systematic and phylogenetic implications. International Association of Wood Anatomists Journal 95: 91–101. https://doi.org/10.1006/anbo.1999.1000
- Lantz H, Bremer B (2004) Phylogeny inferred from morphology and DNA data: characterizing well-supported groups in Vanguerieae (Rubiaceae). Botanical Journal of the Linnean Society 146: 257–283. https://doi.org/10.1111/j.1095-8339.2004.00338.x
- Moat J (2007) Conservation assessment tools extension for ArcView 3.x, version 1.2. GIS Unit, Royal Botanic Gardens, Kew. http://www.rbgkew.org.uk/gis/cats
- MoulyA, AchilleF (2007) Theenigmatic *Rhopalobrachiumfragrans*transferred to *Cyclophyllum* (Rubiaceae). Systematic Botany 32: 883–887. https://doi.org/10.1600/036364407783390746
- Naiki A, Kato M (1999) Pollination system and evolution of dioecy from distyly in *Mussaen-da parviflora* (Rubiaceae). Plant Species Biology 14: 217–227. https://doi.org/10.1046/j.1442-1984.1999.00021.x
- Pailler T, Humeau L, Figier J, Thompson JD (1998) Reproductive trait variation in the functionally dioecious and morphologically heterostylous island endemic *Chassalia corallioides* (Rubiaceae). Biological Journal of the Linnean Society 64: 297–313. https://doi.org/10.11-11/j.1095-8312.1998.tb00335.x
- Robbrecht E (1988) Tropical woody Rubiaceae. Characteristics, features and progressions. Contribution to a new subfamilial classification. Opera Botanica Belgica, 1271 pp.
- Robbrecht E (1996) Geography of African Rubiaceae with reference to glacial rain forest refuges. In: van der Maesen LJG, van der Burgt XM, van Medenbach de Rooy JM (Eds) The biodiversity of African Plants. Proceedings Symposium 'Glacial forest refuges' at the XIVth AETFAT Congress (Wageningen 1994), 564–581. https://doi.org/10.1007/978-94-009-0285-5_71
- Taedoumg H, De Block P, Hamon P, Sonké B (2011) Craterispermum parvifolium and C. robbrechtianum spp. nov. (Rubiaceae) from west central Africa. Nordic Journal of Botany 29: 700–707. https://doi.org/10.1111/j.1756-1051.2011.01297.x
- Taedoumg H, Hamon P (2013) Three new *Craterispermum* from the Lower Guinea Domain. Blumea 57: 236–242. https://doi.org/10.3767/000651913X663776
- Verdcourt B (1973) The identity of the common East African species of *Craterispermum* Benth. (Rubiaceae) with some other notes on the genus. Kew Bulletin 28: 433–431. https://doi. org/10.2307/4108887
- White F (1979) The Guineo-congolian Region and its relationships to other phytochoria. Bulletin du Jardin Botanique National de Belgique 49: 11–55. https://doi.org/10.2307/3667815

RESEARCH ARTICLE



Melicope stonei, section Pelea (Rutaceae), a new species from Kaua'i, Hawaiian Islands: with notes on its distribution, ecology, conservation status, and phylogenetic placement

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Abstract

Melicope stonei K.R. Wood, Appelhans & W.L. Wagner (section *Pelea*, Rutaceae), a new endemic tree species from Kaua'i, Hawaiian Islands, is described and illustrated with notes on its distribution, ecology, conservation status, and phylogenetic placement. The new species differs from its Hawaiian congeners by its unique combination of distinct carpels and ramiflorous inflorescences arising on stems below the leaves; plants monoecious; leaf blades $(5-)8-30 \times (4-)6-11$ cm, with abaxial surface densely tomentose, especially along midribs; and very long petioles of up to 9 cm. Since its discovery in 1988, 94 individuals have been documented and are confined to a 1.5 km² region of unique high canopy mesic forest. *Melicope stonei* represents a new Critically Endangered (CR) single island endemic species on Kaua'i.

Keywords

Rutaceae, *Melicope, M.* section *Pelea*, new species, conservation, Hawaiian Islands, Kaua'i, Critically Endangered

Introduction

The genus Melicope J.R. Forst. & G. Forst. consists of ca. 235 species of shrubs and trees with a distribution that ranges from the Malagasy and Indo-Himalayan regions in the east to the Hawaiian and Marguesan Islands in the west and from Nepal, southern China, Taiwan and the Japanese Ogasawara Islands in the north to New Zealand and Australia in the south (Hartley 2001, Appelhans et al. 2014a, Wood et al. 2016a). With the inclusion of *Melicope stonei* K.R. Wood, Appelhans & W.L. Wagner, the total number of recognized Melicope reported for the Hawaiian Islands totals 50 endemic species, making Melicope the most species-rich radiation of woody plants throughout the archipelago (Hillebrand 1888, Hartley and Stone 1989, Wagner et al. 1999, Wood et al. 2016a). Molecular phylogenetic studies indicate that the Hawaiian species arose from a single introduction, and that the Hawaiian genus *Platydesma* H. Mann is nested within Melicope section Pelea (A. Gray) Hook. f. as sister to the Hawaiian species of Melicope (Harbaugh et al. 2009, Appelhans et al. 2014b, c). To preserve the monophyly of Melicope sect. Pelea, Platydesma must be merged with Melicope and when those new combinations are validly published, Hawaiian Melicope will then be increased by an additional four species.

In the most current systematic revision by Hartley (2001) *Melicope* was subdivided into four sections: *Lepta* (Lour.) T.G. Hartley; *Melicope*; *Pelea*; and *Vitiflorae* T.G. Hartley. Only sect. *Lepta* proved to be a monophyletic group in a recent molecular study (Appelhans et al. 2014b). All Hawaiian species of *Melicope* are members of sect. *Pelea*, which consists of 86 species almost exclusively restricted to Melanesia and the Pacific region. *Pelea* previously was recognized at the genus rank with the Hawaiian species subdivided into four sections in the revision by Stone (1969): *Apocarpa* B.C. Stone; *Cubicarpa* B.C. Stone; *Megacarpa* B.C. Stone; and *Pelea* (Wagner et al. 1999). The classification needs to be revised since the sectional classification of Hartley (2001) would require the Hawaiian groups to be treated as subsections if it is appropriate to continue recognizing them at all. Within these four Hawaiian groups only the Hawaiian group proved to be monophyletic (Appelhans et al. 2014c).

Methods

All measurements were taken from dried herbarium specimens and field notes and are presented in the descriptions as follows: length \times width, followed by units of measurements (mm or cm). The authors have examined all specimens cited. The extent of occurrence and area of occupancy for *Melicope stonei* was calculated by using ArcMap 10.2 in relation to coordinates recorded while collecting herbarium specimens or making field observations.

Taxonomic treatment

Melicope stonei K.R.Wood, Appelhans & W.L.Wagner, sp. nov.

urn:lsid:ipni.org:names:77164681-1 Figs 1, 2A–F

Diagnosis. Differs from Hawaiian congeners by its combination of distinct carpels and ramiflorous inflorescence; plants monoecious; leaf blades $(5-)8-30 \times (4-)6-11$ cm, with abaxial surface tomentose, especially along midribs; and very long petioles of up to 9 cm.

Type. United States of America. Hawaiian Islands, Kaua'i: Waimea District, Mākaha Valley, *Metrosideros-Acacia* montane mesic forest, 22°7'1.8258"N; 159°40'45.534"W, 997 m elev., 24 Jan 2016, *K. R. Wood & Kahekili Lee 16727* (holotype: PTBG-073080!; isotypes: BISH!, K!, MO!, NY!, UC!, US!).

Description. Trees (3-)5-12 m tall, trunks up to 25 cm diameter, bark smooth, mottled gray to light brown, new growth and young branchlets tomentose, yellowtan, glabrate in age. *Leaves* opposite, unifoliolate, coriaceous, the blade ovate, oblongovate, oblong-elliptic, or oblong-lanceolate, $(5-)8-30 \times (4-)6-11$ cm, margin entire, base rounded, apex obtuse to acute, occasionally rounded, secondary veins 7-15 pairs, connected by an arched vein 5–20 mm from margin, higher order venation reticulate, adaxial surface glabrous, abaxial surface densely tomentose, yellow-tan, rarely glabrate, with midrib and secondary veins densely tomentose, interspersed villous, the midrib sometimes also long-villous or woolly along the sides; petiole shallowly canaliculate, (2.5-)3.5-9.0 cm long, puberulent to tomentose. *Inflorescences* in axillary and ramiflorous, fasciculate cymes to 22 mm long, peduncles 1-5(-10) mm long, short-villous, pedicles 1-4 mm, short-villous, bracteoles deltoid-ovate, 1-2 mm long, densely shortvillous. Flowers male or female, plants monoecious, 3-5(-7), sepals deltoid-ovate, naviculate, $2.5-3.0 \times 1.5-2.0$ mm, densely short-villous externally, glabrous internally, tip acute, persistent in fruit; petals whitish green, ovate, tip acute, slightly thickened and hooked inward, 3.5×2.5 mm, densely short-villous externally, glabrous internally; stamens 8, filaments glabrous, papillose on distal half, antisepalous ones ca. 4 mm long in male flowers (1.5 mm in female flowers), antipetalous ones 3 mm long (1.5 mm in female flowers), anthers ca. 1 mm long, all with pollen in male flowers, (0.6-0.7 mm long in female, apparently sterile); nectary disk glabrous; ovary glabrous; gynoecium 1×2 mm, style including stigma 1 mm long in male flowers (1.5 mm in female), glabrous, stigmas capitate, 4-lobed, papillose, 0.5 mm wide. Capsules medium to dark green when fresh, irregularly pusticulate, 5-9 × 15-21 mm, of 4 distinct follicles, slightly ascending, occasionally 1 or more abortive, exocarp glabrous, glandular punctate, endocarp glabrous. Seeds 1-2 per carpel, ovoid, 6-8 mm long.

Phenology. *Melicope stonei* has been observed with flower buds in January, May, and September, and with both flower and fruit during January, February, and July.



Figure I. Melicope stonei K.R. Wood, Appelhans & W.L. Wagner. A Flowering branch B Adaxial leaf surface near margin toward apex C Abaxial leaf surface near margin toward apex D Ramiflorous inflorescence arising below leaves on stem E Female flower, lateral view F Immature fruit and flowers G Dehisced fruit, showing seeds. A-C from Wagner & Wood 6891 (US) D from Wood 8431 (US) E from Wood 15101 (PTBG)
F from Wood & Lee 16729 (photo) G from Lorence et al. 6454 (photo) (Illustration by Alice Tangerini).

Etymology. We are pleased to name *Melicope stonei* in honor of Benjamin Clemens Masterman Stone, British-American botanist, born in Shanghai, China in1933 and passed in 1994 while working at the Philippine National Museum on the Flora of the Philippines Project. He contributed over 300 publications to science during his career, including taxonomic monographs of Hawaiian *Pelea* (Stone 1969) and *Platydesma* (Stone 1962). For all his contributions, especially his keen insights into Hawaiian *Melicope*, we gratefully extend him due recognition.

Specimens examined. United States. Hawaiian Islands, Kaua'i: Waimea District, Ku'ia, upper headwater gulch, 1027 m elev., 03 Sep 2015, K. R. Wood, S. Perlman, S. Walsh, M. Query 16579 (PTBG); Miloli'i ridge road, Mahanaloa, 933 m elev., 06 Nov 2008, C. Trauernicht & N. Tangalin 617 (PTBG); Mahanaloa, 1055 m elev., 21 Oct 2015, S. Walsh & A. Williams 136 (PTBG); Pa'aiki-Mahanaloa flats, 1036 m elev., 07 Oct 2001, K. R. Wood 9128 (BISH, PTBG); Pa'aiki-Mahanaloa flats, 991 m elev., 04 Mar 2001, K. R. Wood & M. LeGrande 8879 (PTBG); Pa'aiki-Mahanaloa flats, 1000 m elev., 14 Dec 1994, K. R. Wood 3840 (PTBG, US); Pa'aiki-Mahanaloa flats, 1000 m elev., 24 Feb 1999, K. R. Wood 7696 (PTBG); Pa'aiki-Mahanaloa flats, 1000 m elev., 24 Feb 1999, K. R. Wood & R. Aguraiuja 7697 (BISH, CANB, MO, NY, PTBG, US); Pa'aiki-Mahanaloa flats, 1015 m elev., 06 May 2000, K. R. Wood 8432 (BISH, NY, PTBG, US); Pa'aiki-Mahanaloa flats, 1015 m elev., 06 May 2000, K. R. Wood 8433 (PTBG, US); Mākaha Ridge Road, down .8 mi to 988 m elev., north side of road, just inside forest, 970 m elev., 7 Feb 1988, D. Lorence, G. Lorence & E. Crum 5779 (PTBG); loc. cit., 970 m elev., 2 Jan 1989; D. Lorence, T. Flynn & Smith 6316 (PTBG); loc. cit., 970 m elev., 1 Mar 1989, T. Flynn & Decker 3280 (AD, BISH, F, MO, MU, PTBG, US); loc. cit., 970 m elev., 31 May 1990, D. Lorence et al. 6449 (PTBG); loc. cit., 920 m elev., 25 Feb 2000, W. Wagner & K. R. Wood 6891 (PTBG); south side of Mākaha road, 988 m elev., 06 May 2000, K. R. Wood 8430 (PTBG); loc. cit., 988 m elev., 06 May 2000, K. R. Wood 8431 (PTBG, US); loc. cit., 991 m elev., 21 Jul 2012, K. R. Wood & T. Bierly 15104.02 (PTBG); loc. cit., 997 m elev., 24 Jan 2016, K. R. Wood & K. Lee 16726 (BISH, PTBG); loc. cit., 997 m elev., 24 Jan 2016, K. R. Wood, K. Lee 16727 (PTBG); loc. cit., 997 m elev., Jan 2016, K. R. Wood, S. Perlman & R. Aguraiuja 16729 (BISH, PTBG, US); loc. cit., 997 m elev., K. R. Wood & K. Lee 16728 (BISH, K, MO, NY, PTBG, UC, US); loc. cit., 997 m elev., 28 Jan 2016, K. R. Wood, S. Perlman & R. Aguraiuja 16730 (PTBG, US); loc. cit., 997 m elev., 28 Jan 2016, K. R. Wood, S. Perlman & R. Aguraiuja 16731 (BISH, PTBG, US); loc. cit., 997 m elev., 28 Jan 2016, K. R. Wood, S. Perlman & R. Aguraiuja 16732 (BISH, PTBG, UC, US); Mākaha, forests around dividing ridge between upper north and south fork, 1037 m elev., 18 Feb 2016, K. R. Wood & S. Perlman 16741 (PTBG); Nu'ololo, north facing slopes above northern branch, 1097 m elev., 18 Jul 2012, K. R. Wood, M. Query & M. Kirkpatrick 15101 (BISH, K, MBK, MO, NY, P, PTBG, UC, US); Nu'ololo, north of trail, headwaters of central Nu'ololo stream, 1061 m, 3 Oct 2012, K. R. Wood, M. Kirkpatrick & M. Query 15267 (BISH, PTBG, US); Nu'ololo, 1052 m elev., 02 Jan 2013, K. R. Wood & M. Kirkpatrick 15319 (BISH, PTBG); Nu'ololo, 1049 m elev., 02 Jan 2013, K. R. Wood & M. Kirkpatrick 15320 (BISH, NY,



Figure 2. *Melicope stonei* K.R. Wood, Appelhans & W.L. Wagner. A Male flower, lateral view with sepals and petals cut away to show antisepalous and antipetalous stamens B Male flower, top view C Female flower, lateral view with sepals and petals cut away to show staminodes and pistil D Female flower, top view E-F abaxial leaf surface along midvein of *M. stonei* showing variability of leaf vestiture G *Melicope barbigera* A. Gray abaxial leaf surface along midvein A–D from *Wood 15101* (PTBG) E from *Wagner & Wood 6891* (US) F from *Wood 8432* (US) G from *Wagner & Wood 6896* (US) (Illustration by Alice Tangerini).

PTBG, UC, US); Nu'ololo, 1085 m elev., K. R. Wood, M. Kirkpatrick & S. Perlman 15560 (PTBG); Nu'ololo, 1027 m elev., Jul 2013, K. R. Wood, M. Kirkpatrick & S. Perlman 15562 (PTBG); Nu'ololo, 1052 m elev., 12 Sep 2013, K. R. Wood & W. Kishida 15667 (PTBG); Nu'ololo, 1036 m elev., 12 Sep 2013, K. R. Wood & W. Kishida 15668 (PTBG); Nu'ololo, 1061 m elev., 28 Sep 2013, K. R. Wood & M. Query 15671 (PTBG); Nu'ololo, 1073 m elev., 22 Jul 2014, K. R. Wood, M. Kirkpatrick, S. Perlman & R. Aguraiuja 16001 (PTBG); loc. cit., 1073 m elev., 22 Jul 2014, K. R. Wood, M. Kirkpatrick, S. Perlman & R. Aguraiuja 16002 (PTBG).

Distribution, ecology, and threats. *Melicope stonei* is endemic to Kaua'i, oldest of the high Hawaiian Islands at 5.1 million years, with an area of ca. 1430 km² (Sakai et al. 2002), and maximum elevation of 1598 m at the summit of Kawaikini. Floristically, Kaua'i has the phenomenal distinction of having the highest level of plant diversity of all the Hawaiian Islands, which includes 249 single island endemic (SIE) taxa, 232 of which are flowering plants, and the remaining 17 being unique fern taxa (Palmer 2003, Wagner et al. 2012, Vernon and Ranker 2013, Ranker 2016, Wood et al. 2016b).



Figure 3. Map of Kaua'i, Hawaiian Islands, with polygon indicating distribution of *Melicope stonei* in the Köke'e forests.

Earliest known collections of *Melicope stonei* were made by David Lorence and Timothy Flynn (National Tropical Botanical Garden) as far back as February of 1988 within the forests of Mākaha Valley, Kaua'i. Over the past 29 years, 94 trees have been mapped by local botanists, with colonies extending into several valleys to the north of Mākaha, namely Ku'ia, Miloli'i, Mahanaloa, Nu'ololo, and Pa'aiki (Figure 3). *Melicope stonei* has a very narrow elevational range of 988 to 1097 m and a precariously small extent of occurrence of 1.5 km². Rich forest habitats still flourish in adjacent lower and higher elevational regions, yet it is evident that *M. stonei* prefers very tall (15–20 m) old growth *Metrosideros polymorpha* Gaudich. (Myrtaceae)- *Acacia koa* A. Gray (Fabaceae) mixed mesic forest with the occasional co-dominant *Alphitonia ponderosa* Hillebr. (Rhamnaceae). This plant community type only occurs on Kaua'i and is exceedingly limited with some of the finest examples occurring around the forested flats of Kōke'e State Park above Pa'aiki, Mahanaloa, and Nu'ololo. In these forests, *M. stonei* reaches heights of 10–12 m and is associated with a wide diversity of other tall understory trees such as *Bobea brevipes* A. Gray (Rubiaceae), *Cryptocarya mannii* Hillebr. (Lauraceae), *Dodonaea viscosa* Jacq. (Sapindaceae), *Kadua affinis* DC. (Rubiaceae), *Melicope barbigera* A. Gray, *Myrsine lanaiensis* Hillebr. (Primulaceae), *Nestegis sandwicensis* (A. Gray) O. Deg., I. Deg. & L.A.S. Johnson (Oleaceae), *Planchonella sandwicensis* (A. Gray) Pierre (Sapotaceae), *Polyscias kavaiensis* (H. Mann) Lowry & G.M. Plunkett and *P. waimeae* (Wawra) Lowry & G.M. Plunkett (Araliaceae), *Psychotria mariniana* (Cham. & Schltdl.) Fosberg (Rubiaceae), *Santalum pyrularium* Hook. & Arn. (Santalaceae), *Syzygium sandwicensis* (A. Gray) Nied. (Myrtaceae), *Xylosma hawaiiense* Seem. (Salicaceae), and *Zanthoxylum dipetalum* H. Mann (Rutaceae).

Interspersed below this community's canopy are rich assemblages of medium statured trees that include Antidesma platyphylla H. Mann var. hillebrandii Pax & Hoffm. (Phyllanthaceae), Chrysodracon aurea (H. Mann) P.-L. Lu & Morden (Asparagaceae), Claoxylon sandwicense Müll. Arg. (Euphorbiaceae), Coprosma foliosa A. Gray and C. waimeae Wawra (Rubiaceae), Cyanea leptostegia A. Gray (Campanulaceae), Elaeocarpus bifidus Hook. & Arn. (Elaeocarpaceae), Labordia helleri Sherff (Loganiaceae), Myrsine alyxifolia Hosaka, Pittosporum kauaiense Hillebr. (Pittosporaceae), Platydesma rostrata Hillebr. and P. spathulata (Rutaceae), Psychotria greenwelliae Fosberg, Psydrax odorata (G. Forst.) A.C. Sm. & S.P. Darwin (both Rubiaceae), Sophora chrysophylla (Salisb.) Seem. (Fabaceae), Streblus pendulinus (Endl.) F. Muell. (Moraceae), and Wikstroemia furcata (Hillebr.) Rock (Thymelaeaceae).

Common shrubs and smaller tree components are *Leptecophylla tameiameiae* (Cham. & Schlecht.) C.M. Weiller (Epacridaceae), *Lysimachia kalalauensis* Skottsb. (Primulaceae), *Melicope anisata* (H. Mann) T.G. Hartley & B.C. Stone, *M. feddei* (H. Lév.) T.G. Hartley & B.C. Stone, *M. ovata* (H. St. John & E.P. Hume) T.G. Hartley & B.C. Stone, and *M. peduncularis* (H. Lév.) T.G. Hartley & B.C. Stone.

Associated sedges (Cyperaceae) include *Carex meyenii* Nees, *C. wahuensis* C.A. Mey., and *Gahnia beecheyi* H. Mann, grasses (Poaceae) are *Eragrostis grandis* Hillebr., *E. variabilis* (Gaudich.) Steud., and *Panicum nephelophilum* Gaudich., and additional associated vegetation includes the herbaceous *Dianella sandwicensis* Hook. & Arn. (Xanthorrhoeaceae), and vines of *Alyxia stellata* (J.R. & G. Forst.) Roem. & Schult. (Apocynaceae), and *Smilax melastomifolia* Sm. (Smilacaceae).

Common to occasional pteridophytes of this habitat are Asplenium normale D. Don (Aspleniaceae) Adenophorus tamariscinus (Kaulf.) Hook. & Grev. and A. tripinnatifidus Gaudich. (Polypodiaceae), Cibotium nealiae O. Deg. (Cibotiaceae), Coniogramme pilosa (Brack.) Hieron. (Pteridaceae), Diplazium sandwicensis (A. DC.) Fosberg (Athyriaceae), Doodia kunthiana Gaudich. (Blechnaceae), Dryopteris glabra (Brack.) Kuntze, and D. unidentata (Hook. & Arn.) C. Chr. (Dryopteridaceae), Elaphoglossum paleaceum (Hook. & Grev.) Sledge (Dryopteridaceae), Microlepia strigosa (Thunb.) C. Presl (Dennstaedtiaceae), and Odontosoria chinensis (L.) J. Sm. (Lindsaeaceae). Threats to *Melicope stonei* include habitat degradation by introduced pigs (*Sus scrofa* L.) and mule deer (*Odocoileus hemionus* Rafinesque), predation of seeds by rats (*Rattus rattus* L. and *R. exulans* Peale), environmental events such as hurricanes, fire (mostly by humans), and competition with invasive non-native plant species, including *Adiantum hispidulum* Sw. (Pteridaceae), *Blechnum appendiculatum* Willd. (Blechnaceae), *Corynocarpus laevigatus* J.R. Forst. & G. Forst. (Corynocarpaceae), *Erigeron karvinskianus* DC. (Asteraceae), *Grevillea robusta* A. Cunn. ex R. Br. (Proteaceae), *Hedychium gardnerianum* Ker Gawl. (Zingiberaceae), *Kalanchoe pinnata* (Lam.) Pres. (Crassulaceae), *Lantana camara* L. (Verbenaceae), *Lophospermum confertus* (R. Br.) P.G. Wilson & J.T. Waterhouse (Myrtaceae), *Morella faya* (Ait.) Wilbur (Myricaceae), *Setaria parviflora* (Poir.) Kerguélen (Poaceae), and *Sphaeropteris cooperi* (Hook. ex F. Muell.) R.M. Tryon (Cyatheaceae) all of which possess the ability to spread rapidly and cover effectively large areas (Smith 1985).

Conservation status. *IUCN Red List Category.* When evaluated using the World Conservation Union (IUCN) criteria for endangerment (IUCN 2001), *Melicope stonei* falls into the Critically Endangered (CR) category, which designates this species as facing a very high risk of extinction in the wild. Our formal evaluation can be summarized by the following IUCN hierarchical alphanumeric ranking system of criteria and subcriteria: CR B1ab(i,ii,iii,iv,v)+2ab(i,ii,iii,iv,v); C2a(i); which reflects a severely limited Extent of Occurrence (EOO) and Area of Occupancy (AOO) of less than 1.5 km² and a wild population of less than 100 individuals with all facing a continuing decline in their area of extent and quality of habitat (see Distribution, ecology, and threats). Seeds from several individuals of *M. stonei* have been collected and submitted to the NTBG Horticultural Department for cultivation.

Morphology, related taxa, and phylogenetic placement. Melicope stonei stands apart from all other described Hawaiian Melicope species by its combination of being large monoecious trees up to 12 m tall with distinct carpels and short-villous ramiflorous inflorescences. There are three other Hawaiian species that usually have ramiflorous cymes arising on stems below the leaves, namely M. clusiifolia (A. Gray) T.G. Hartley & B.C. Stone from Kaua'i, O'ahu, Moloka'i, Lana'i, Maui, and Hawai'i, M. haleakalae (B.C. Stone) T.G. Hartley & B.C. Stone from Maui, and *M. waialealae* (Wawra) T.G. Hartley & B.C. Stone from Kaua'i, yet they differ from *M. stonei* in having leaves in whorls of 4-8 with abaxial surface glabrous or with some hairs on midrib or sometimes loosely villous throughout the surface, and having carpels connate at their base or nearly throughout their length in fruit (as compared to M. stonei having leaves opposite with abaxial surface densely tomentose and with carpels distinct in fruit). Other Hawaiian species that may occasionally have the cymes arising below the leaves include M. ovata from Kaua'i, M. pseudoanisata (Rock) T.G. Hartley & B.C. Stone, from Maui and Hawai'i, and M. quadrangularis (H. St. John & E.P. Hume) T.G. Hartley & B.C. Stone, also from Kaua'i. The latter two differ with carpels connate and leaves glabrous or with some hairs on midrib (Wagner et al. 1999), and the former, M. ovata, lacks the

short-villous peduncles, pedicels, sepals, and petals found on *M. stonei*. Morphologically, these species have little else in common with *M. stonei*.

In habit *Melicope stonei* appears most similar to trees of *M. barbigera* from Kaua'i and *M. knudsenii* (Hillebr.) T.G. Hartley & B.C. Stone from Kaua'i and Maui, both of which can reach heights of 12 m. *Melicope barbigera* differs from *M. stonei* in having new growth grayish appressed puberulent; slightly folded leaves with waxy scurf and commonly having abaxial leaf surface densely long-villous along each side of midrib (Fig. 2G); cymes axillary, not ramiflorous; peduncles 20–25 mm long; nectary disk and ovary puberulent (as compared to *M. stonei* with new growth tomentose, yellow-tan; leaves neither folded nor having a waxy scurf, rarely with abaxial surface densely long-villous along each side of midrib (Fig. 2E–F); cymes axillary and ramiflorous; peduncles 1–5(–10) mm long; with nectary disk and ovary glabrous). *Melicope knudsenii* differs in having leaf bases weakly cordate; flowers perfect or unisexual, (3–)20–200; cymes axillary, not ramiflorous; and peduncles (10–)30–60 mm long; (as compared to *M. stonei* with leaf bases rounded; flowers male or female, plants monoecious, 3–5(–7); cymes axillary and ramiflorous; and peduncles 1–5(–10) mm long) (Wagner et al. 1999).

Four specimens of *Melicope stonei* (*Wagner & Wood 6891; Wood 7696; Wood & Aguraiuja 7697; Wood, Query & Kirkpatrick 15101*) have been included in phylogenetic analyses of Hawaiian *Melicope* (Harbaugh et al. 2009; Appelhans et al. 2014b,c) and they all represent paratypes of this new species. The specimens were labeled as *M. knudsenii* in these studies according to their original conferred determination. Phylogenetic analyses showed that the former section *Apocarpa* is paraphyletic with respect to the former section *Pelea* (unpublished results) and that *M. stonei* forms a clade with the "*Apocarpa*" species *M. adscendens* and *M. ovata* (Fig. 4). The monophyly of this clade is supported by posterior probability (1.00pp) and bootstrap (98bs) values and the three species, of which three to four specimens have been sampled, were resolved as monophyletic entities (Appelhans et al. 2014c; Fig. 4).

Melicope adscendens (H. St. John & E.P. Hume) T.G. Hartley & B.C. Stone, from Maui, and the previously mentioned *M. ovata* from Kaua'i, which are the closest relatives of *M. stonei*, (Appelhans et al. 2014c; Fig. 4) do not have clear morphological similarities with the new species. While *M. stonei* is a tall tree, *M. adscendens* is a sprawling shrub and *M. ovata* is a shrub or small tree with sprawling branches. *Melicope adscendens* has considerably smaller leaves $1.5-6.5 \times 1-4$ cm and does not have a densely tomentose abaxial leaf surface, being minutely puberulent, becoming glabrate (as compared to *M. stonei* with leaves $(5-)8-30 \times (4-)6-11$ cm with densely tomentose abaxial leaf surface). *Melicope ovata* has sepals glabrous or sparsely minutely ciliate externally, and petals glabrous externally (Wagner et al. 1999), (as compared to *M. stonei* with sepals and petals densely short-villous externally).

A striking character of *Melicope stonei* is the ramiflorous inflorescences, which it most notably shares with *M. clusiifolia*, *M. haleakalae*, *M. ovata*, *M. pseudoanisata*, *M. quadrangularis*, and *M. waialealae*, and can occur on rare occasions with other Hawaiian *Melicope*. This character is homoplasious and has evolved probably three or four times in Hawaiian *Melicope*: once in *M. stonei* and *M. ovata* of the *Apocarpa* group,



Figure 4. Phylogenetic placement of *Melicope stonei* K.R. Wood, Appelhans & W.L. Wagner based on four nuclear and two plastid markers (modified from Appelhans et al. 2014c). The phylogenetic tree only shows the Hawaiian radiation of *Melicope*. The terms *Apocarpa*, *Cubicarpa*, *Megacarpa* and *Pelea* refer to the former Hawaiian sections of *Melicope/Pelea* (Hartley & Stone 1989). The support values are displayed above the branches and the first value represents the Bayesian posterior probability values (pp), followed by the bootstrap values (bs) from the Maximum Likelihood analysis.

once in the ancestor of *M. clusiifolia*, *M. haleakalae* and *M. waialealae*, who form the monophyletic *Pelea* group (Appelhans et al. 2014c; Fig. 4), and once or twice in the ancestor(s) of *M. pseudoanisata* and *M. quadrangularis*, which are part of an unresolved group of species belonging to the intermixed former sections *Cubicarpa* and *Megacarpa* (unpublished results; Fig 4).

Morphologically, *Melicope stonei* is most similar to *M. barbigera* and the Kaua'i population of *M. knudsenii* (see above). *Melicope knudsenii* has been shown to be polyphyletic and the Maui form does not belong to this group (Appelhans et al. 2014c; Fig. 4). As a result, a future publication is now in preparation which will resurrect the Maui form (i.e., *M. multiflora* Rock) as a species distinct from the Kaua'i *M. knudsenii*. While *M. barbigera* and the Kaua'i form of *M. knudsenii* are resolved as immediate sisters in the phylogenetic analyses, *M. stonei* is not closely related to them and belongs to another clade of the paraphyletic *Apocarpa* group (Appelhans et al. 2014c; Fig. 4). It should be noted that the variable abaxial midrib pubescence of *M. stonei* ranging from villous on the sides to uniform pubescence (Fig. 2E–F) could represent natural

variability or may suggest possible undetected hybridization between *M. stonei* and *M. barbigera*. Other putative *Apocarpa* hybrids collected and observed in the Kōke'e forests of Kaua'i include: *M. barbigera* × *M. haupuensis* (H. St. John) T.G. Harley & B.C. Stone (i.e., *Wood & Query 14696* [PTBG]) observed around Awa'awapuhi and Honopū (825–1050 m); *M. haupuensis* × *M. pallida* (Hillebr.) T.G. Harley & B.C. Stone (i.e., *Wood et al. 7725* [PTBG]) around Awa'awapuhi (1050 m); and *M. ovata* × *M. stonei* (i.e., *Wood 17237* [BISH, K, MO, NY, PTBG, UC, US], *Wood 17245* [BISH, PTBG, UC, US], *Wood 17246* [BISH, PTBG, US]), in the valleys of Mākaha to Nu'ololo (988–1097 m).

Insert for existing key to Hawaiian Melicope

To accommodate *Melicope stonei*, the following couplets can be inserted into the existing key to Hawaiian *Melicope* (treated as *Pelea*) by Stone, Wagner, and Herbst (in Wagner et al. 1999, p. 1178) (Note: K=Kaua'i; O=O'ahu; WM=West Maui).

1	Carpels distinct in fruit; leaves opposite or rarely ternate2
1'	Carpels connate at least at base in fruit; the capsules 4-lobed; leaves opposite
	or whorled
2(1)	Endocarp pubescent, at least along suture
2'	Endocarp glabrous
6(2)	Leaves ternate; new growth black-resinous and minutely puberulent; exocarp gla-
	brous and somewhat glaucous, especially when immature; K, OM. pallida
6'	Leaves opposite; new growth not black-resinous, but puberulent or tomen-
	tose; exocarp glabrous or puberulent, but never glaucous7
7(6)	Abaxial leaf surface densely long-villous or tomentose in a line along each
	side of midrib and sometimes on the midrib itself, the surface away from
	midrib densely to loosely pubescent or tomentose, some hairs tending to fall
	off with age
7'	Abaxial leaf surface glabrous to densely tomentose or puberulent, sometimes
	more densely so toward midrib, but not long-villous in a line along each side
	of midrib
7a(7)	Midrib glabrous or nearly so other than long-villous hairs along sides; K
7a'	Midrib pubescent and also long-villous or tomentose along sides; KM. stonei
8(7)	Exocarp minutely puberulent throughout with short, erect, white hairs, be-
	coming yellowish in dry specimens; O, WM M. elliptica
8'	Exocarp glabrous or minutely appressed puberulent near suture
9(8)	Abaxial leaf surface densely tomentose or densely puberulent with strongly
	appressed, extremely fine hairs
9'	Abaxial leaf surface glabrous or densely puberulent when young, becoming
	sparsely so or glabrate with age

10(9)	Shrubs or trees to 3 m tall; leaves 1.5-5 cm wide; abaxial leaf surface densely
	puberulent with strongly appressed extremely fine hairs mixed with white waxy
	scurf; petioles 10-22 mm long; pedicels 5-10 mm long; O M. makahae
10'	Large trees to 12 m tall; leaves (4–)6–11 cm wide; abaxial leaf surface densely
	tomentose without white waxy scurf; petioles 20-90 mm long; pedicels 1-5
	mm long10a
10a(10)	Leaf base weakly cordate; flowers (3-)20-200; cymes axillary, not ramiflor-
	ous; peduncles (10–)30–60 mm long; K, EM M. knudsenii
10a'	Leaf base rounded; flowers 3-5(-7); cymes axillary and ramiflorous; pedun-
	cles 1–5(–10) mm long; K

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References

- Appelhans MS, Wagner WL, Wood KR (2014a) *Melicope balgooyi* Appelhans, W.L. Wagner & K.R. Wood, a new species and new record in *Melicope* section *Melicope* (Rutaceae) for the Austral Islands. PhytoKeys 39: 77–86. https://doi.org/10.3897/phytokeys.39.7691
- Appelhans MS, Wen J, Wagner WL (2014b) A molecular phylogeny of *Acronychia*, *Euodia*, *Melicope* and relatives (Rutaceae) reveals polyphyletic genera and key innovations for species richness. Molecular Phylogenetics and Evolution 79: 54–68. https://doi.org/10.1016/j. ympev.2014.06.014
- Appelhans MS, Wen J, Wood KR, Allan GJ, Zimmer EA, Wagner WL (2014c) Molecular phylogenetic analysis of Hawaiian Rutaceae (*Melicope, Platydesma* and *Zanthoxylum*) and their different colonization patterns. Botanical Journal of the Linnean Society 174: 425–448. https://doi.org/10.1111/boj.12123
- Harbaugh DT, Wagner WL, Allan GJ, Zimmer EA (2009) The Hawaiian Archipelago is a stepping stone for dispersal in the Pacific: an example from the plant genus *Melicope*

(Rutaceae). Journal of Biogeography 36: 230–241. https://doi.org/10.1111/j.1365-2699.2008.02008.x

- Hartley TG (2001) On the Taxonomy and Biogeography of *Euodia* and *Melicope* (Rutaceae). Allertonia 8(1), National Tropical Botanical Garden, Lawa'i, Kaua'i, Hawaii.
- Hartley TG, Stone BC (1989) Reduction of *Pelea* with new combinations in *Melicope* (Rutaceae). Taxon 38: 119–123. https://doi.org/10.2307/1220910
- Hillebrand W (1888) Flora of the Hawaiian Islands: a description of their phanerogams and vascular cryptogams. B. Westermann & Co., New York, 673 pp.
- Palmer DD (2003) Hawai'i's ferns and fern allies. University of Hawaii Press, Honolulu.
- Ranker TA (2016) What do we know about Hawaiian ferns and lycophytes? Journal of Systematics and Evolution 54: 626–637. https://doi.org/10.1111/jse.12213
- Sakai AK, Wagner WL, Mehrhoff LA (2002) Patterns of endangerment in the Hawaiian flora. Systematic Biology 51: 276–302. https://doi.org/10.1080/10635150252899770
- Smith CW (1985) Impact of alien plants on Hawai'i's native biota. In: Stone CP, Scott JM (Eds) Hawai'i's Terrestrial Ecosystems: Preservation and Management. Cooperative National Park Resources Studies Unit, University of Hawaii, Manoa, 180–250.
- Stone BC (1962) A monograph of the genus *Platydesma* (Rutaceae). Journal of the Arnold Arboretum 43: 410–427.
- Stone BC (1969) The Genus Pelea A. Gray (Rutaceae: Evodineae) A Taxonomic Monograph (Studies in the Hawaiian Rutaceae, 10) Phanerogamarum Monographiae Tomus III Verlag Von J. Cramer.
- Vernon AL, Ranker TA (2013) Current status of the ferns and lycophytes of the Hawaiian Islands. American Fern Journal 103: 59–111. https://doi.org/10.1640/0002-8444-103.2.59
- Wagner WL, Herbst DR, Sohmer SH (1999) Manual of the flowering plants of Hawai'i, revised edition with supplement by Wagner WL & Herbst DR. University of Hawaii Press, 1855–1918. [Bishop Museum Special Publication 97]
- Wagner WL, Herbst DR, Khan N, Flynn T (2012) Hawaiian vascular plant updates: a supplement to the Manual of the Flowering Plants of Hawai'i and Hawai'i's Ferns and Fern Allies, version 1.3. http://botany.si.edu/pacificislandbiodiversity/hawaiianflora
- Wood KR, Appelhans MS, Wagner WL (2016a) Melicope oppenheimeri, section Pelea (Rutaceae), a new species form West Maui, Hawaiian Islands: with notes on its ecology, conservation, and phylogenetic placement, PhytoKeys 69: 51–64. https://doi.org/10.3897/ phytokeys.69.8844
- Wood KR, Lorence DH, Kiehn M (2016b) Coprosma kawaikiniensis (Rubiaceae) a new species from the Dubautia-Sadleria shrubland-fernland community on Kaua'i, Hawaiian Islands. PhytoKeys 60: 21–32. https://doi.org/10.3897/phytokeys.60.6406