

Taxonomy of the weed species of the genus *Echinochloa* (Poaceae, Paniceae) in Southwestern Europe: Exploring the confused current state of affairs

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Abstract

The taxonomy of *Echinochloa*, a predominantly tropical to warm-temperate genus of 40–50 species, including some of the world's worst weeds, is still poorly understood. This is because some species, including the extremely widespread *E. crus-galli*, show a wide range of morphological, physiological and ecological variation, in part the result of a complex recent evolutionary history. Furthermore, there is often a dearth of clear distinguishing features among species. The same applies to the species established in Southwestern Europe, where unintentionally introduced populations have now established themselves as important weeds of crops, especially maize and rice. Taxonomic and nomenclatural confusion hampers progress in weed science. In this study, we give an identification key that covers the weedy taxa encountered in Southwestern Europe, followed by notes on taxonomy and nomenclature. Moreover, a lectotype is designated for *Echinochloa frumentacea*. It is argued that current confusion cannot be overcome without including populations of Eastern Asian origin in taxonomic studies and without the joint efforts of experts in the fields of weed science, morphology-based taxonomy, genomics and phylogenetics.

Keywords

Echinochloa, evolutionary history, lectotypification, nomenclature, Poaceae, Southwestern Europe, taxonomy

Introduction

Echinochloa P. Beauv. is a predominantly tropical to warm-temperate genus of 40–50 species that are usually associated with wet or damp places (Michael 2003). *Echinochloa crus-galli* (L.) P. Beauv., by far the most widespread species of the genus, is among the worst weeds worldwide (Holm et al. 1977). However, in Western and Southern Europe, *E. crus-galli* is not the only troublesome species of this genus of Poaceae. Together with several other C_4 grasses of the genera *Digitaria* Haller, *Panicum* L. and *Setaria* P. Beauv., *Echinochloa muricata* (P. Beauv.) Fernald, too, has become a widespread weed, especially in maize fields, in the past few decades (Jauzein and Montégut 1983; Scholz 1995; Hoste 2004). Furthermore, the spread of a few additional taxa of Asian origin in rice fields in the Mediterranean area has increasingly challenged the identification skills of botanists and agronomists (Jauzein 1993; Viggiani and Tabacchi 2017; Martínez-Azorín and Crespo 2021).

The taxonomy of *Echinochloa* is still poorly understood, resulting in strongly diverging interpretations of its classification and nomenclature. These divergent interpretations can be attributed to several reasons, such as the wide range of within-species variation (not in the least in ill-defined and polymorphic *E. crus-galli*), the recurrent absence of unequivocal qualitative and quantitative distinguishing features among species, insufficient joint research by taxonomists and agronomists and the often extended lag time between the introduction of an exotic taxon in a new geographic region and its detection and correct identification by local botanists and weed scientists. As a result of the description of numerous taxa with probably little or no taxonomic value, quite a few species may be overvalued.

In Southwestern Europe, taxonomically widely divergent treatments of the genus *Echinochloa* are available for the British Isles (Hubbard 1968; Cope and Gray 2009; Stace 2019), the Netherlands (Duistermaat 2020), Belgium (Lambinon and Verloove 2012; Verloove 2021), France (Jauzein 1993, 1995; Tison and de Foucault 2014), Central Europe (Conert 1998; Parolly and Rohwer 2019), the Iberian Peninsula (Martínez-Azorín and Crespo 2021) and Italy (Pirola 1965; Pignatti 1982; Viggiani et al. 2003; Banfi 2017; Viggiani and Tabacchi 2017). Nothing better illustrates the confusion and changing views on taxonomy and nomenclature of *Echinochloa* in Southwestern Europe during the past half-century than the five references given for Italy. The tangled web of confusion is also revealed in a quote by Tabacchi et al. (2006) about Early watergrass (*E. oryzoides*) as “never been reported before in Italy,” whereas the species was described (as *Panicum oryzoides*) on the basis of material that was in all likelihood collected in Italy (see below).

In an overview of the weedy species of *Echinochloa* in Southwestern Europe, Carretero (1981) concentrated on presence in rice fields in Italy, Southern France, Spain and Portugal. He mentioned two indigenous species, *E. crus-galli* and *E. colona* (L.) Link, plus three introduced taxa of Asian origin. Two decades later, Costea and Tardif (2002), in a paper on “the most common weedy European *Echinochloa* species,” never mentioned *E. muricata*. However, by then, this American species had been recorded

as a weed from Camargue, France, and Jauzein (1993) urged botanists to be watchful of *E. muricata*, which he warned had recently started spreading quickly in other parts of France. Unfortunately, to date, this species has hardly ever been mentioned in botanical and weed science papers dealing with Southern Europe: although the species is definitely not common, it may have been overlooked. There is also doubt about its status in the British Isles. Cope and Gray (2009) claimed that some races of *E. crus-galli* “have been considered worthy of recognition at species level, but there is no general agreement on this.” *Echinochloa muricata* is not included in the keys by Stace (2019), yet the author observed that some specimens keying out as *E. crus-galli* would belong to *E. muricata* subsp. *microstachya* (Wiegand) Jauzein.

Distinguishing between American *E. muricata* and European *E. crus-galli* based on morphology is relatively easy, yet separating the latter from persistent and morphologically variable *Echinochloa* introduced from Asia and today thriving in rice fields in Southern Europe proves much more difficult. The contrasting treatments of *Echinochloa* in Japanese (Ohwi 1965; Ibaragi 2020) and Chinese (Shouliang 1990; Shouliang and Phillips 2006) floras only accentuates the confusion.

To develop superior control methods in crops, including rice and maize, basic knowledge of the classification, morphology, physiology and ecology of specific weeds is essential (Yabuno 1983). Recent advances in molecular techniques have created new opportunities to study the weedy species of genus *Echinochloa*. New research combining morphological and molecular data has been undertaken with the aim to better understand the species’ classification and establish useful morphological traits that allow weed scientists and farmers to reliably identify the different taxa. To date, it has been shown that *E. muricata* and *E. crus-galli* are clearly distinct (Claerhout et al. 2016); however, studies dealing with the taxa of Asian origin and specifically aspiring to integrate morphological and molecular data have, so far, yielded only limited success (e.g., Yasuda et al. 2002; Yamaguchi et al. 2005; Ruiz-Santaella et al. 2006; Tabacchi et al. 2006; Aoki and Yamaguchi 2008; Lee et al. 2014a, 2014b; Ye et al. 2014; Yasuda and Nakayama 2019). Often with *E. oryzicola* (Vasinger) Vasinger as the exception, matching the data from genetic research with the multitude of names and descriptions from the morphology-based literature remains ridden with difficulties. Nomenclatural confusion resulting in the same name being applied to different taxa in different studies is a source of uncertainty and may render the interpretation of published research results precarious, especially when no herbarium specimens have been deposited (Yamaguchi et al. 2005). Moreover, the naming of specimens based on the two different and widely diverging identification keys from Carretero (1981) and Pignatti (1982) has also not been helpful to link molecular data with morphology-based taxa (Tabacchi et al. 2006; Kaya et al. 2014). Claerhout et al. (2016) warned that using incorrectly identified seeds accessed from institutes or companies in experiments is a potential source of errors. This probably explains the position of ‘*E. muricata*’ among a cluster of *E. crus-galli* accessions in the phylogenetic tree proposed by Lee et al. (2016; fig. 2). For the same reason, an accession from a Spanish rice field (Seville) identified as ‘*E. crus-pavonis*’ (Ruiz-Santaella et al. 2006) seems doubtful as this species

is not mentioned by Martínez-Azorín and Crespo (2021) and is probably not present as a weed in rice fields anywhere in Southern Europe (Michael 1983).

Morphology-based distinguishing traits frequently used in keys and descriptions often find no confirmation in molecular data. An attempt to bridge the gap with a modified “simple and effective morphological key” (Tabacchi et al. 2006) was not convincing and has been replaced later with a highly modified version (Viggiani and Tabacchi 2017). Most of the authors dealing with the problem declare a stalemate and put their hopes in future research. With this paper, we do not have the ambition to resolve the taxonomic and nomenclatural puzzle posed by *Echinochloa* in Southwestern Europe. Instead, our goal is twofold. On the one hand, we present a provisional key that makes it possible to identify the weedy species occurring in Southwestern Europe (from the British Isles to Portugal and Italy); critical comments are added to explain our choice of accepted taxa. On the other hand, we wonder why matching the results of recent molecular studies on *Echinochloa* in Europe and the Far East with those obtained by morphological research is so problem-ridden. The current variation of taxa in the genus *Echinochloa*, including some that were recently inadvertently introduced to Southwestern Europe, is partly the result of a complex evolutionary history, the traces of which are visible in the morphological and genetic characteristics of currently existing taxa. We include the timescales of both geological epochs and human history to frame the future study of the taxonomy and phylogeny of weedy *Echinochloa* in Southwestern Europe.

Result

An identification key for the species of *Echinochloa* in Southwestern Europe

Identification keys for *Echinochloa* in floras or weed science papers are often restricted to a rather small geographical area. Covering a larger area and more taxa may lead to more attention being paid to taxa which, so far, could have been overlooked. As far as the reviewed European literature is concerned, this paper is mainly restricted to Southwestern Europe, roughly stretching from the British Isles in the north to the Iberian Peninsula and Italy in the south. The key should, however, prove useful to identify the established weedy species of the genus *Echinochloa* in most of Europe. Owing to nomenclatural and taxonomic uncertainties, the key is considered provisional; for a different recent interpretation, see Martínez-Azorín and Crespo (2021).

A number of rare casuals that have been reported from Europe in the past, for instance, as wool aliens, have been omitted. These include *Echinochloa inundata* Michael & Vickery and *E. jubata* Stapf from Belgium (Verloove 2021), *E. turneriana* (Domin) J.M.Black from Germany (Conert 1998) and *E. crus-pavonis* (Kunth) Schult., *E. pyramidalis* (Lam.) Hitchc. & Chase (a perennial species) and *E. turneriana* from Great Britain and Ireland (Ryves et al. 1996; Reynolds 2002). Adding these species – the exact identity of some of which requires confirmation – would have made the key

unnecessarily difficult. Moreover, there is currently no indication for these ephemerals establishing as troublesome weeds in crops.

Echinochloa crus-gavonis has been excluded from the key since the records from rice fields in Southern Europe seem to be based on erroneous identifications (Banfi 2017); the photographs given by Viggiani et al. (2003, pages 242–243) show a form of *E. crus-galli* s.l.

Those who run into problems when using the key given below or suspect they are dealing with a species missing from the key are referred to the keys to the annual and perennial species of *Echinochloa* produced by P.W. Michael (1983), with updates, including those from Michael (2019). In Europe, the known weedy species are all annuals.

In combination with the wide variation within individual species, the dearth of strong qualitative and quantitative features precludes easy identification in the genus *Echinochloa*. Within the same inflorescence, the spikelets may show considerable variation. The number, size, position and direction of hairs and bristles is often strongly influenced by competition for space among the closely packed spikelets. The length of the lower glume and the shape of the sterile lemma (occasionally part of them shiny and convex) can be assessed only by examining several spikelets. The length of the spikelet – excluding the awn of the sterile lemma – is an important feature (Michael 1983; Jauzein 1993). Especially when awned or having an elongated tip, measuring the length of the spikelet may prove difficult as deciding where the spikelet passes into the awn is rather arbitrary. The presence of spikelets in which the upper glume has an elongated tip or a short awn (as sometimes occurs in several taxa) renders a correct measurement more uncertain.

- 1 Fertile floret not disarticulating at maturity. Spikelets unawned. Fertile floret and caryopsis markedly humped. Inflorescence compact, usually contracted and with the axis often hardly visible, sometimes with spreading branches (Fig. 1) 2
- 1' Fertile floret disarticulating at maturity. Spikelets awned or not. Fertile floret and caryopsis not markedly humped. Inflorescence not strongly contracted when fully developed, with the axis showing through (but compare with clearly different *E. muricata* var. *wiegandii* when in doubt)..... 3
- 2 Spikelets dark brownish or purplish at maturity (Fig. 2), ca. 3–4 mm long. Caryopsis brownish ***E. esculenta***
- 2' Spikelets pale (yellowish or greenish) at maturity (Fig. 1), ca. 3–3.5 mm long. Caryopsis whitish..... ***E. frumentacea***
- 3 Spikelets < 3 mm long and lower glume ca. 1/2 length of the spikelet, which is always unawned. Axis of the inflorescence branches (almost) without bristles (except at the base). Inflorescence without secondary branches (Fig. 3). Leaves narrow, usually not exceeding 6 mm. Caryopsis whitish..... ***E. colona***
- 3' Spikelets usually ≥ 3 mm long, awned or not. (If spikelet < 3 mm, then lower glume only ca. 1/3 length of the spikelet.) Axis of the inflorescence branches with bristles. Inflorescence often with secondary branches. Leaves usually wider. Caryopsis usually darker, yellowish or brownish 4

- 4 Spikelets ≥ 4 mm long and at least some spikelets with lower glume up to 2/3 length of the spikelet (Fig. 4D). Mature inflorescence more or less erect (Fig. 5). Spikelets unawned or with an awn up to 20 mm long. Caryopsis 2–2.4 mm long. Embryo at least 0.75 to over 0.9 length of the caryopsis. (An obligate weed of rice.) ***E. oryzicola***
- 4' Spikelets ≥ 4 mm long and lower glume not longer than 1/2 length of the spikelet. Mature inflorescence drooping (Fig. 6). Spikelets usually awned, with an awn up to 50 mm long. Caryopsis 2.2–2.8 mm long. Embryo 0.65–0.75(–0.85) length of the caryopsis. (An obligate weed of rice.) ***E. crus-galli* var. *oryzoides***
- 4'' Spikelets ≤ 4 mm long and lower glume usually clearly less than 1/2 length of the spikelet. (If spikelets > 4 mm, see 6, *E. muricata* var. *muricata*. Solely a rare casual?)..... **5**
- 5 Lemma of the fertile floret with a membranous tip that is clearly differentiated from the coriaceous body of the lemma (Fig. 7A); the membranous tip demarcated from the coriaceous body by a line of minute hairs (the latter, however, not or hardly visible with a hand lens). Palea of the fertile floret with a blunt, soft, frayed looking, usually strongly recurved tip (Fig. 7B). Spikelets unawned or awned; awn length extremely variable (up to 40 mm long or more). The leaf subtending the distal inflorescence with the demarcation between blade and sheath more or less semicircular or forming a slightly elongated upside-down U; blade usually patent from the base. (A complex taxon with several difficult-to-distinguish intergrading forms that are not keyed out here; see comments below.) ***E. crus-galli***
- 5' Lemma of the fertile floret with a stiff, smooth tip, not clearly differentiated from the coriaceous body of the lemma (Fig. 8A). Palea of the fertile floret with a stiff, (nearly) straight tip; the tip (in mature florets!) appressed against the lemma (Fig. 8B). Spikelets unawned or awned, with the awn usually shorter than 10 mm (but longer in the rare var. *muricata*). The leaf subtending the distal inflorescence with the demarcation between blade and sheath forming an elongated upside-down U (Fig. 9); blade stiff upright (esp. when short) or recurved higher up (*E. muricata*) **6**
- 6 Spikelets ≤ 3.5 mm long, with strongly spreading papilla-based bristles (which give the spikelet a rugged appearance), unawned or at most with an elongated tip (Fig. 10). Tip of both the lemma and palea of the fertile floret short. Inflorescence often large (not uncommonly > 20 cm long), when mature with widely spreading lower branches ***E. muricata* var. *microstachya***
- 6' Spikelets ≤ 3.5 mm long; the papilla-based bristles not strongly spreading. Numerous spikelets in the inflorescence with a short awn (sometimes up to ca. 10 mm) (Fig. 11). Tip of the palea of the fertile flower fine and elongated, fitting with the elongated tip of the lemma. Inflorescence usually smaller, its branches usually not spreading when mature **var. *wiegandii***
- 6'' Spikelets ≥ 3.5 mm long; numerous spikelets in the inflorescence with a longer awn (up to 16 mm). (Apart from the presence of awns, the rugged spikelets look like a more robust version of var. *microstachya*.) (Probably only a rare casual.) **var. *muricata***

Notes on the species included in the key

***Echinochloa colona* (L.) Link, Hort. Berol. 2: 209. 1833.**

Basionym. *Panicum colonum* L., Syst. Nat. (ed. 10) 2: 870. 1759.

Type. LINN-80.23 (lectotype, designated by Hitchcock 1908). Image available at <http://linnean-online.org/1255/>.

Remarks. *Echinochloa colona* is usually easy to identify, yet care should be taken to distinguish it from forms with small spikelets of *E. crus-galli* (Martínez-Azorín and Crespo 2021). In the Mediterranean region, it occurs as a persistent weed in crop fields; elsewhere, it has only been recorded as a usually ephemeral alien.

***Echinochloa crus-galli* (L.) P. Beauv., Ess. Agrost. 1: 53, 161, 169, pl. 11, f. 2. 1812.**

Basionym. *Panicum crus-galli* L., Sp. Pl. 1: 56. 1753.

Type. Herb. Burser 1: 303, sine dato (UPS).

Notes. There has always been a great deal of confusion about the type; see, e.g., Hitchcock (1908) or Gould et al. (1972). In fact, all original material came from North America and belongs to *E. muricata*; in 1753 *E. crus-galli*, from Eurasia, was not yet a widespread introduced species in North America. Crespo et al. (2020b) formally proposed to conserve the binomial *P. crus-galli* with a conserved type based on the specimen Herb. Burser I: 103 (UPS), the one previously chosen as “lectotype” by Michael (1983).

Echinochloa crus-galli* var. *crus-galli

- = *Echinochloa crus-galli* subsp. *spiralis* (Vasinger) Tzvelev, Zlaki SSSR 662. 1976. Basionym: *Echinochloa spiralis* Vasinger, Flora SSSR 2: 739–740. 1934. Type: Caucasus: Kuban: Krasnodar vic., 28 Oct 1931, *A. V. Vazinger-Alektorova* s.n. (holotype; LE).
- = *Echinochloa crus-galli* var. *praticola* Ohwi, Acta Phytotax. Geobot. 11: 37 1942. Type: Kiushiu, m. Kujusan, *U. Faurie* 2646 (holotype; KYO). Image available at http://www.museum.kyoto-u.ac.jp/collection/PlePlant/PlePlant00001775_1.htm.
- = *Echinochloa crus-galli* var. *hispidula* (Retz.) Honda, Bot. Mag. (Tokyo) 37: 122. 1923. Basionym: *Panicum hispidulum* Retz., Observ. Bot. 5: 18. 1789. Type: India: “India orientali”, without data, *König* s.n. (LD 1219266) (lectotype, designated by Fischer 1932: 71). Image available at <https://plants.jstor.org/stable/10.5555/al.ap.specimen.ld1219266>.
- = *Echinochloa erecta* (Pollacci) Pignatti, Arch. Bot. 15(1): 2. 1955. Basionym: *Panicum erectum* Pollacci, Atti Ist. Bot. Univ. Pavia 13: 228, t. 5. 1908. Type: Italy: Lombardia, Presso Pavia, Oct 1907, *G. Pollacci* s.n. (lectotype, designated by Ardenghi et al. 2015: 135, PAV-Erbario Lombardo “118”, isolectotypes PAV-Erbario Lombardo “121”, “141”, “123”, “137” (2 sheets), “139”, “140”).



Figure 1. Inflorescence of *Echinochloa frumentacea*. (Photograph: Nico Wysmantel).

***Echinochloa crus-galli* var. *oryzoides* (Ard.) Lindm., Svensk Fanerogamflora 69. 1918.**

Basionym. *Panicum oryzoides* Ard., Animadv. Bot. Spec. Alt. 2: 16, pl. 5. 1764.

Type. LINN 80.68. Image available at <https://linnean-online.org/1302/>.

Note. According to Carretero (1981), LINN 80.68 is a plant sent by Arduino to Linnaeus, possibly collected in Italy. It was designated as the lectotype for that name by Crespo et al. (2020a).

Remarks on *E. crus-galli*. *Echinochloa crus-galli* s.l. is taxonomically the most complex *Echinochloa* occurring as a weed in Southwestern Europe. As we understand, this species occurs in a number of varieties, but *E. oryzicola* is not one of them and is accepted as a separate species (see below). As a result of a long and complex evolutionary history, including significant modifications in the recent past (after the introduction of agriculture), the differences among the varieties are often slight. Furthermore, introductions of several taxa as weeds in a range of crops far outside their natural range have contributed to obscuring their original geographical distribution. Rather than aiming at precisely describing the limits and defining features of varieties of *E. crus-galli* occurring in Southwestern Europe, we restrict ourselves primarily to indicating where unsolved problems remain.

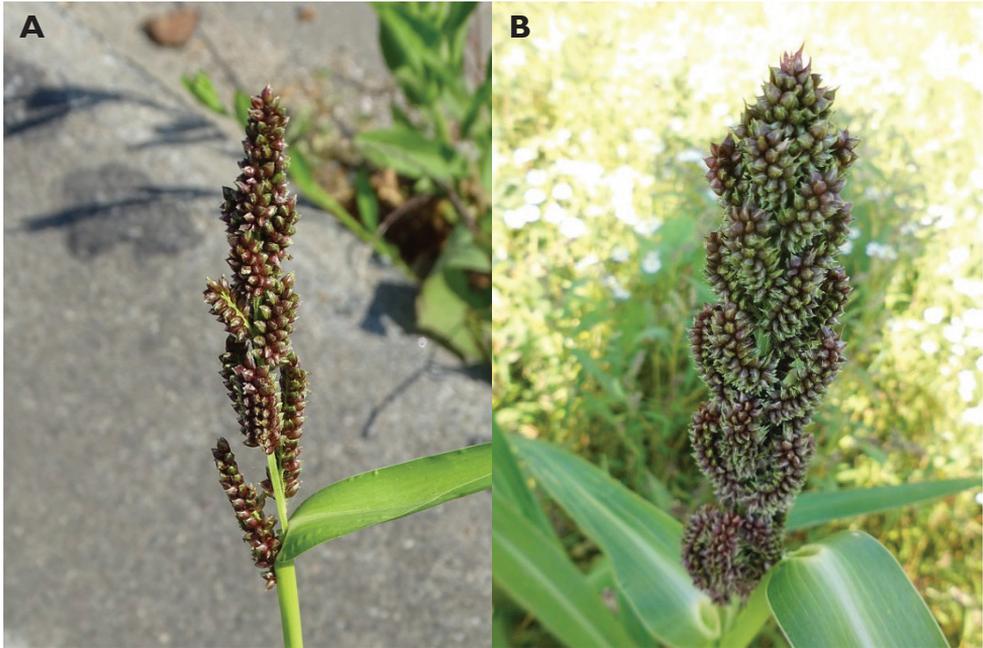


Figure 2. Inflorescences showing the variation of *Echinochloa esculenta*. The apex of the spikelet varies from usually obtuse (A) to less often shortly acute (B). (Photographs: Bart Mortier).

Being extremely polymorphic, numerous varieties of *E. crus-galli* have been described, many of them based on the presence or absence of awns. As the development of awns is influenced by environmental conditions (Michael 1983), the value of varieties or forms based on such characteristics as the presence or absence or the length of awns is quite limited. Inflorescences that develop later in the season frequently differ from the terminal inflorescence. Other characteristics on which the description of varieties has been based include the coloration of the plant (inflorescence, leaves, stem nodes, etc.), structure and position of the inflorescence (erect, bent or nodding; primary branches more or less patent or not, alternately positioned on the main axis or whorled), the arrangement of the spikelets on the branches and the dimensions of the spikelet. The importance of the length of the spikelets is emphasised by Michael (1983), who in his identification key for the annual *Echinochloa* separates the species characterised by spikelets measuring 3–5 mm from those with either shorter or longer spikelets. Applied to specimens collected in Southwestern Europe, the criterion of spikelet length works well to separate only the two rice mimics, *E. crus-galli* var. *oryzoides* (Ard.) Lindm. (syn.: *E. oryzoides* [Ard.] Fritsch) and *E. oryzicola*, from the remaining taxa of *E. crus-galli* s.l. with smaller spikelets.

There is a broad consensus that *E. crus-galli* var. *crus-galli* occurs in large parts of Europe and Asia, but authors differ on how to appropriately define it. Ibaragi (2020) stated that Asian var. *crus-galli* slightly differs from plants in Europe, “but the differ-



Figure 3. Inflorescence of *Echinochloa colona*. (Photograph: Rutger Barendse).

ences are difficult to formally distinguish.” Thus, the need for additional research on the morphological and genetic variation of the type variety throughout its range is evident.

According to Michael (2019), *Echinochloa crus-galli* var. *hispidula* (Retz.) Honda is the appropriate name for *E. crus-galli* with non-pyramidal panicles and usually prominently awned spikelets that are widespread in sub-tropical areas of Japan and Southern China. With slightly larger spikelets than var. *crus-galli*, this taxon is often treated as a separate species, *Echinochloa hispidula* (Retz.) Nees ex Royle; however, Ibaragi (2020) completely ignored it, and Shouliang and Phillips (2006) interpreted it as synonym of var. *crus-galli*. Its extreme variability (Carretero 1981, as *E. hispidula*) makes it hard to distinguish var. *hispidula* from var. *crus-galli*, which is characterised by a usually more or less procumbent habit (the lower nodes often rooting), floppy leaves, the whole plant or parts of it more often than not purple-tinged, erect to strongly bent pyramidal inflorescences with the branches alternately placed or sometimes whorled, with at least the lower branches usually more or less patent, and spikelets with or without awns, the length of the awns and the percentage of awned spikelets within a single inflorescence exhibiting considerable variation (Fig. 12; description based on material from maize fields in Belgium, where var. *hispidula*, a taxon of sub-tropical climates, is considered not established as a persistent weed). If accepted as a separate taxon, the strongly bent inflorescence with appressed branches, the green colour of the plants and the stiffer

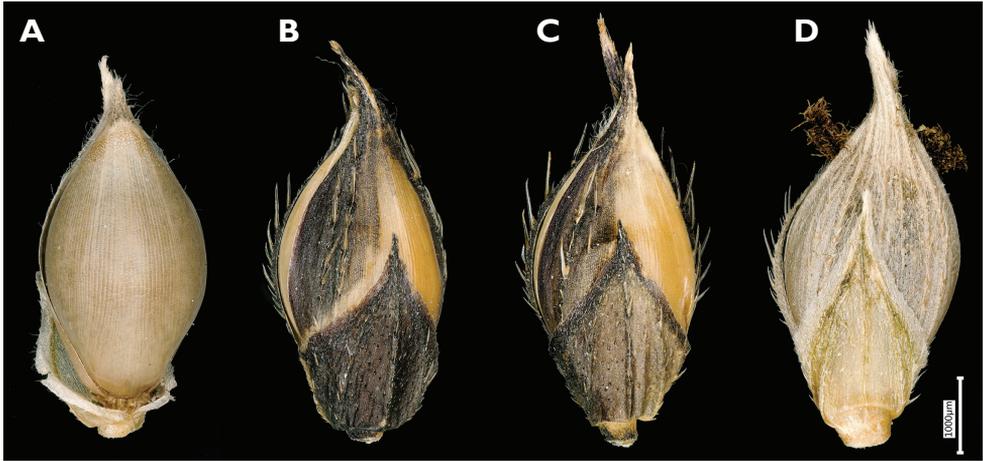


Figure 4. Spikelets of *Echinochloa oryzicola* **A** fertile lemma with the tip differentiated from the coriaceous body of the lemma (upper glume removed) **B, C** two spikelets with convex shiny sterile lemma **D** spikelet with long lower glume and non-shiny sterile lemma. (Photograph: André De Kesel, Meise Botanic Garden).

leaves (the latter two features shared with var. *oryzoides* and *E. oryzicola*) might help to separate *E. hispidula* from *E. crus-galli* var. *crus-galli* (Jauzein 1993). To this could be added the less bristly spikelets of var. *hispidula* (Martínez-Azorín and Crespo 2021). Whether the branches of the inflorescence are whorled or not (Michael 1983) seems to be a less reliable trait to use. The synonymizing of *E. erecta* (Pollacci) Pignatti, characterised by an erect inflorescence, with *E. hispidula* (see, e.g., Ardenghi et al. 2015) underscores the wide morphological variation of *hispidula* and the difficulty to define it as a unit clearly different from the equally variable var. *crus-galli*. Interestingly, the illustration of *E. hispidula* given in Shouliang (1990) shows a spikelet with both the upper glume and lower (sterile) lemma with a short awn, a feature not mentioned in the recent literature; however, apparently, it corresponds with the specification “calycibus hispidis biaristatis” in the original description of the species (Retzius 1789).

Within *E. crus-galli* as interpreted here, var. *oryzoides* is the most easily identified variety, clearly distinguished by the large size of its spikelets. Although the descriptions given in triplet 4 in the key above may suggest otherwise, it is not always easy to distinguish between var. *oryzoides* and *E. oryzicola*; see the discussion about the latter species below. At one time, the name *Echinochloa hostii* (M. Bieb.) Link was used by Italian botanists (Pignatti 1982). Previously, Pirola (1965) merely cited this name as a synonym of *E. crus-galli* subsp. *oryzoides*, but Pignatti (1982) accepted the name at species rank for the taxon that is here named *E. crus-galli* var. *oryzoides*. However, from Pignatti’s identification key, it is clear that the name *E. hostii* was used for the species that today can only be identified as *E. oryzicola*, based on the quite diagnostic glume characteristics. Unfortunately, we were not able to trace type material of *Panicum hostii* M. Bieb. which according to Tsvelev (1984) is preserved in LE. Thus,

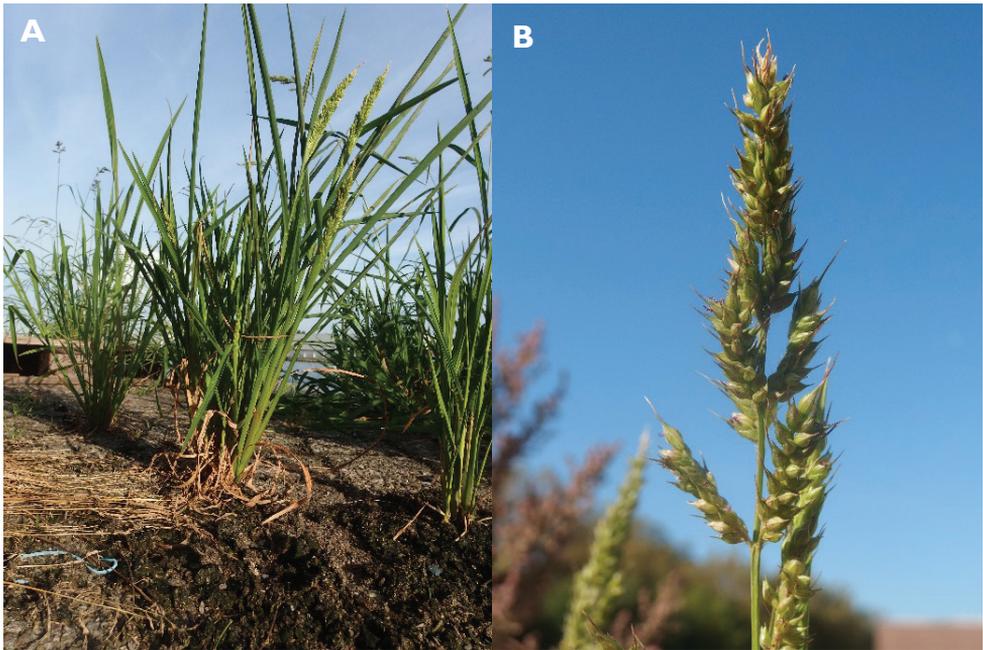


Figure 5. *Echinochloa oryzicola* as an ephemeral casual in the Antwerp port area, Belgium **A** plant with young inflorescences **B** part of an inflorescence with fully developed spikelets. (Photographs: Filip Verloove).

we do not know whether *P. hostii* is indeed identical with *E. crus-galli* var. *oryzoides* as stated by nearly all contemporary authors. Nonetheless, we are certain that the binomial *E. hostii* was wrongly applied by Italian authors (particularly Pignatti 1982) for *E. oryzicola*.

Recently, Martínez-Azorín and Crespo (2021) accepted *E. crus-galli* var. *oryzoides* as a species, just like the similar-looking *E. oryzicola*. The strong similarities shared by these two taxa are explained by a shared ancestor – tetraploid *E. oryzicola* being one of the parent species of hexaploid *E. crus-galli* – and recent convergent evolution as rice mimics derived from *E. oryzicola* and *E. crus-galli* (Fig. 13). This evolutionary trajectory provides an argument for assigning the rank of variety to *E. oryzoides*. Further, it would seem logical to reduce the rice mimic *E. oryzicola* to the rank of variety (provisionally ‘var. *infestans*’ in Fig. 13) as well, but since it is not known whether or how the ‘original’ *E. oryzicola* of pre-agricultural times differed from today’s *E. oryzicola* – because it is now extinct or goes undetected – this is not an option.

Among the forms with small spikelets, subsp. *spiralis* (Vasinger) Tzvelev (no combination available as a variety) and var. *praticola* Ohwi have been mentioned as occurring in Europe. Apparently solely based on the small spikelets, both names were synonymised by Scholz (2002), who noted that subsp. *spiralis* – a taxon with a huge distribution area and possibly indigenous to Europe – and subsp. *crus-galli* are polymorphic and that no sharp distinction between the two is possible solely based on the spikelet length. Martínez-Azorín and Crespo (2021) interpreted var. *praticola* as probably no



Figure 6. Habit of *Echinochloa crus-galli* var. *oryzoides* cultivated from seeds collected in rice, Italy. (Photograph: Maurizio Tabacchi, ISIDRO, Italy).

more than an impoverished form of *E. crus-galli*, and Tison and de Foucault (2014) seriously doubted the taxonomic value of subsp. *spiralis* and var. *praticola*. In Belgium also, *E. crus-galli* with small spikelets has been recorded, but nowhere have such plants been known to establish as noxious weeds.

A rather distinct form of *E. crus-galli* with spikelets ca. 3 mm long or a little longer (somewhat smaller than average var. *crus-galli*) has occasionally been observed in Belgium, including in the border of maize fields where, however, it seems not to establish easily and disappears after only a few years. These plants usually have an erect habit and rather stiff leaves. The inflorescence is erect, with patent branches. The purple-tinged spikelets are usually unawned (but a few spikelets may have a long awn), and some have a glabrous, convex and shiny sterile lemma. The lower leaf sheaths vary from glabrous to densely covered with short retrorse hairs. Scholz (2002) included specimens with small spikelets with a convex, shiny sterile lemma in subsp. *spiralis*, mentioning that the spikelet morphology resembles *Echinochloa glabrescens* Munro ex Hook.f. Another name for *E. glabrescens* is *E. crus-galli* var. *formosensis* Ohwi (Yabuno 1983; Ibaragi 2020); this name was used by Japanese authors for a weed of wetland rice fields. The habitats in which the plants were found in Belgium stand in contrast to those preferred by var. *formosensis* in Japan. Adding to the confusion, the name *E. glabrescens* has also

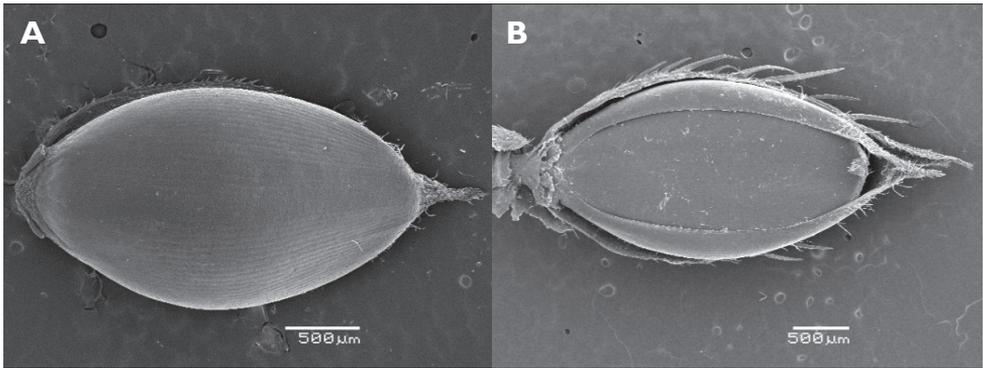


Figure 7. Spikelets of *Echinochloa crus-galli* **A** fertile lemma with the tip differentiated from the coriaceous body of the lemma (upper glume removed) **B** spikelet with tip of the fertile palea frayed and strongly recurved (lower glume and sterile flower removed).

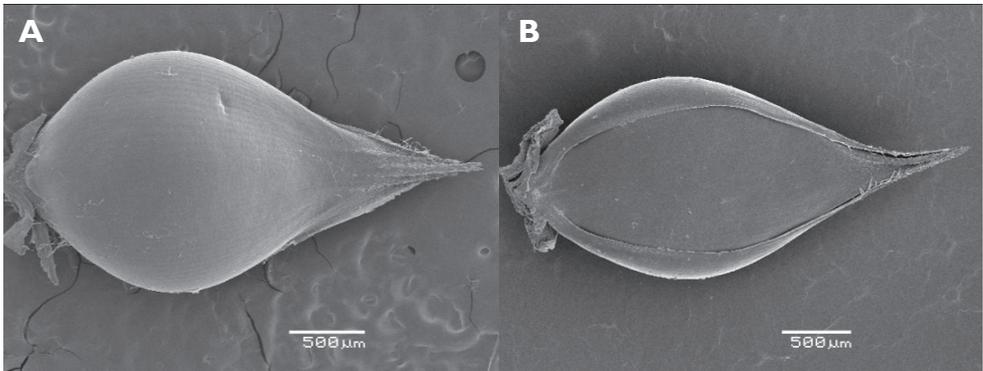


Figure 8. Spikelets of *Echinochloa muricata* **A** fertile lemma with the tip not clearly differentiated from the coriaceous body of the lemma (upper glume removed) **B** spikelet with tip of the fertile palea stiff and straight (lower glume and sterile flower removed).

been applied to plants with spikelets 3.5–5 mm long by Bor (1960), Shouliang and Phillips (2006; as *E. glabrescens* Kossenko) and Xia et al. (2011). *Echinochloa* with small spikelets and a shiny lower lemma collected in Europe requires more study in order to reveal its true identity and its relation with similar taxa having small spikelets in Asia and *E. oryzicola*; see, e.g., Yasuda and Nakayama (2019). Although a quite distinctive feature, the convex and shiny sterile lemma might prove to be of little value taxonomically. Bor (1960) wondered whether the “most peculiar” feature of the indurated sterile lemma in *E. glabrescens* was sufficient to make it a good species, and Yabuno (1966) indicated that in *E. oryzicola*, the convex lemma is a simple dominant characteristic (Fig. 4B, C).

Considering the preceding discussion, we accept, for the present, only few varieties of *E. crus-galli* as occurring in Southwestern Europe. Indigenous and quite variable var. *crus-galli*, usually with a less erect habit and more floppy leaves, is by far the most wide-



Figure 9. *Echinochloa muricata*. The uppermost leaf (or leaves) subtending the distal inflorescence have the demarcation between blade and sheath in the form of an elongated upside-down U. (Photograph: Rutger Barendse).

spread variety, especially towards the north. Part of the variation observed in Europe is perhaps due to the involuntary introduction and establishment of populations of var. *crus-galli*, with slightly different morphological features, from Asia. *Echinochloa crus-galli* var. *oryzoides*, characterised by large spikelets, a more erect habit and stiffer leaves, is a rice mimic in rice fields of Southern Europe. *Echinochloa crus-galli* var. *hispidula*, in some respects resembling var. *crus-galli* and in others var. *oryzoides*, appears to us not to deserve a separate status and is, therefore, included in var. *crus-galli*.

Plants with small spikelets are the most difficult to interpret. Probably representing more than one taxon – quite possibly including taxonomically irrelevant forms of var. *crus-galli* – they require additional study, which will need to include material of Asian origin.

Finally, it can be argued that *Echinochloa esculenta* (A. Braun) H. Scholz, a cultivated taxon derived from *E. crus-galli*, should be included in *E. crus-galli* (Banfi and Galasso 2021). Here, in line with most recent floras, it is pragmatically accepted as a well-defined separate species. However, species rank is justifiable based on morphological features, as the two taxa clearly differ from each other and identification of *E. esculenta* is usually not much of a problem.

***Echinochloa esculenta* (A. Braun) H. Scholz, Taxon 41(3): 523. 1992.**

Basionym. *Panicum esculentum* A. Braun, Index Sem. [Berlin] 1861(App.): 3. 1861.

Type. *Koernicke* s.n., Cult. Hort. Bonn-Poppelsdorf, 28 Oct 1875 (B) (neotype, designated by Scholz 1992: 523). Image available at <https://ww2.bgbm.org/Herbarium/specimen.cfm?Barcode=B100366144>.

Remark. See the combined comments below, under *E. frumentacea*.

***Echinochloa frumentacea* Link, Hort. Berol. 1: 204. 1827.**

Type, lectotype designated here. India, *Roxburgh* s.n. (K000215131, the specimen on the extreme right on the sheet). Image available at <http://specimens.kew.org/herbarium/K000215131>.

Note. The protologue refers to a Roxburgh collection from India (“Roxb. ind. 1. 307. R. S. m. 2. 250. Hab. in India orientali ubi colitur”). The Kew herbarium houses two original but undated Roxburgh collections (sheets K000215131 and K000215132) that can serve for a proper typification. None exactly matches the information provided in the protologue, but since Link described the species in 1827, i.e. well after Roxburgh’s (1751–1815) death, these collections are supposed to have been at his disposal when describing the species. In the apparent absence of other original material, one of the two above-mentioned Kew collections could be chosen as the lectotype for that name. Digital images of both are easily accessible via online resources such as the Kew Herbarium Catalogue, JSTOR or POWO. Sheet K000215131 comprises five stems, four of which have an inflorescence. The extreme left specimen is atypical and might as well represent a different species. The other flowering specimens are representative for the species, and the specimen on the extreme right is here designated as the lectotype for the name *E. frumentacea*. According to Stafleu and Cowan (1983) considerable sets of duplicates of Roxburgh specimens are stored at BM, BR, E, G and LIV. In some of these herbaria isolectotypes could thus be found although a quick online search did not yield further specimens.

Remarks on *E. esculenta* and *E. frumentacea*. *Echinochloa esculenta* (syn.: *E. utilis* Ohwi & Yabuno) and *E. frumentacea* are cultivated species. Neither is considered a persistent weed in Southwestern Europe. Still, they are included in the key since they are the most frequently occurring non-weedy representatives of the genus in Southwestern Europe, frequently recorded as bird-seed aliens in and along the border of crop fields (Hanson and Mason 1985). They look similar, and young specimens can be difficult to identify, yet mature ones are easily distinguished by the colour of the spikelets. In both species, the inflorescence varies. In the more typical specimens, the branches are tightly clustered and appressed against the axis, creating a compact inflorescence. Often, however, the inflorescence is rather lax, with the distal part of the branches somewhat curved towards the axis; such specimens are easily mistaken for an awnless form of *E. crus-galli*. Yabuno (1966) describes the distinct

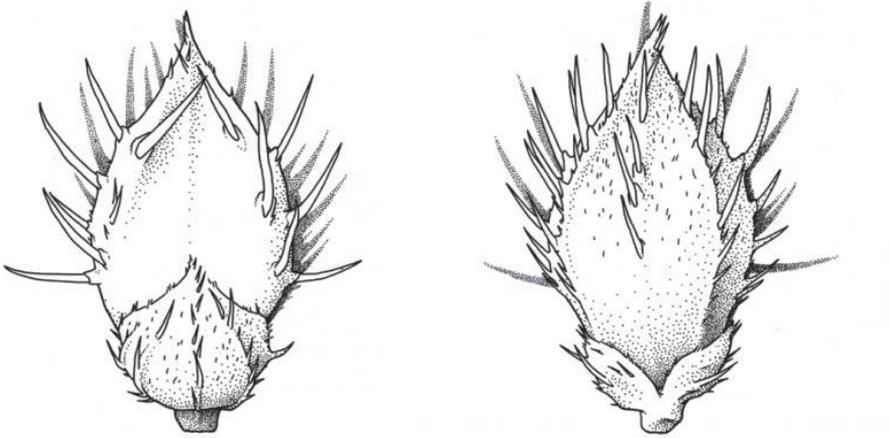


Figure 10. Spikelet of *Echinochloa muricata* var. *microstachya* showing the lower glume and unawned sterile lemma (left) and upper glume (right). Scale bar 1 mm. (Drawing: Sven Bellanger, Meise Botanic Garden).

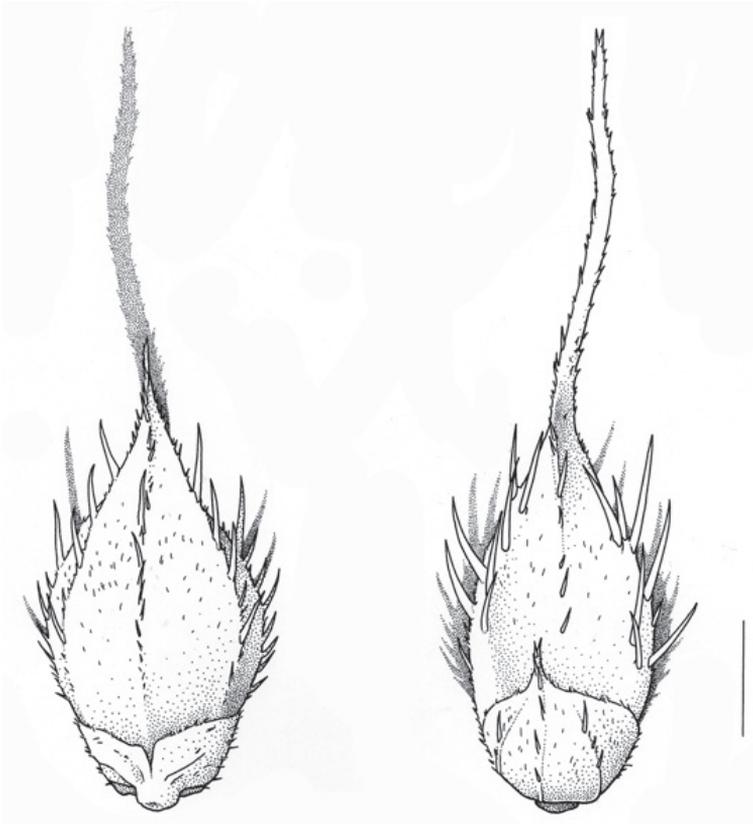


Figure 11. Spikelet of *Echinochloa muricata* var. *wiegandii* showing upper glume (left) and lower glume and awned sterile lemma (right). Scale bar 1 mm. (Drawing: Sven Bellanger, Meise Botanic Garden).



Figure 12. Habit of *Echinochloa crus-galli* var. *crus-galli* growing as a roadside weed, Belgium. Although extremely variable, the usually more or less procumbent habit (the lower nodes often rooting) and the floppy leaves are among the features that distinguish var. *crus-galli* from the obligate rice weeds *E. crus-galli* var. *oryzoides* and *E. oryzicola* which are characterised by a more erect and stiffer habit. (Photograph: Luc Audenaerde).

characteristics of the two species, and recent genetic studies have confirmed that they are quite distinct, *E. esculenta* being derived from *E. crus-galli* and *E. frumentacea* from *E. colona* (Yamaguchi et al. 2005; Ye et al. 2014). There are arguments for reducing these two taxa to variety rank or, following Banfi and Galasso (2021), subspecies rank under *E. crus-galli* and *E. colona*. Yabuno (1966) insinuated that *E. esculenta* shows more variation, and Michael (1983) added that in this species, the spikelets may be awned (although awned spikelets seem to be rare); this reflects the highly polymorphic nature of the parent species.

***Echinochloa muricata* (P. Beauv.) Fernald, Rhodora 17(198): 106. 1915.**

Basionym. *Setaria muricata* P. Beauv., Essai Agrostogr. 51, 170, 178. 1812.

Type. Canada: Quebec Lac Champlain, s.d., A. Michaux s.n. (holotype: P-MICHX, isotype: US-80768).

Echinochloa muricata* var. *muricata

***Echinochloa muricata* var. *microstachya* Wiegand, *Rhodora* 23(267): 58–60. 1921.**

Type (lecto-). USA: New York, Tompkins Co., Ithaca, between Fall Creek, Inlet and city, waste soil, border of west marsh, open alluvial and marshy flats, 19 Jul 1913, *E.L. Palmer* 097 (GH). Image available at <https://s3.amazonaws.com/huhwebimages/755E8AFFFFFF6435/type/full/303931.jpg>.

***Echinochloa muricata* var. *wiegandii* (Fassett) Mohlenbr., III. *Fl. Illinois* (ed. 2) 396. 2001.**

Basionym. *Echinochloa pungens* (Poir.) Rydb. var. *wiegandii* Fassett, *Rhodora* 51(601): 2. 1949.

Type. USA: Oregon, Hayden Island, sandy roadside, *J.C. Nelson* 1974, 8 Sep 1915 (holotype GH). Image available at https://kiki.huh.harvard.edu/databases/specimen_search.php?mode=details&id=126740.

Remarks on *E. muricata*. *Echinochloa muricata* is native to North America. Its status as separate from *E. crus-galli*, which was inadvertently introduced there long ago from Europe, was contested by Hitchcock (1920, 1935, 1950). Hitchcock (1920) rejected the separate status stating that he was unable to distinguish the two species based on the distinguishing features given by Fernald (1915). However, further studies by Wiegand (1921) and especially by Fassett (1949) confirmed the separate status of *E. muricata* (Gould et al. 1972). Probably, largely due to Hitchcock's influential publications, a significant share of American authors have for decades combined native and introduced taxa under *E. crus-galli* in floras and weed-control publications (Maun and Barrett 1986). In the 21st century, some researchers still refer to New World *E. crus-galli* – not to be confused with *E. crus-galli* introduced in North America from Europe – rather than using the name *E. muricata* (Aoki and Yamaguchi 2008). By now, however, molecular research has confirmed *E. muricata* as a separate species, clearly distinct from *E. crus-galli* (Claerhout et al. 2016; Mascanzoni 2018). This should put an end to the confusion that goes back to the days of Linnaeus, as it has been demonstrated that the type specimen of *E. crus-galli* in fact belongs to *E. muricata* (Crespo et al. 2020a).

Echinochloa muricata is a highly variable species, though less so than *E. crus-galli*. This, combined with its resemblance to *E. crus-galli*, has added to the difficulty for agronomists and botanists on both sides of the Atlantic to detect and correctly name its introduced populations. Early records of introduced *E. muricata* from France revealed morphologically very uniform populations (as *E. pungens* [Poir.] Rydb. var. *microstachya* [Wiegand] Fernald & Griscom; Deschatres et al. 1974). This resulted in identification keys that made it harder to correctly identify clearly deviating forms of *E. muricata* that had established in maize fields in Belgium (Hoste 2004).

The European populations of *E. muricata* exhibit only part of the variation found in the natural range of the species. So far, three morphologically distinct

varieties have been recorded from Belgium and France. *Echinochloa muricata* var. *muricata*, with larger spikelets, seems to occur only as an ephemeral alien (Hoste 2004). References to this variety in France require confirmation as they are probably based on misidentifications (Jauzein 1995; Tison and de Foucault 2014). The specimens with smaller spikelets recorded from Belgium are of two clearly different types, apparently with very few intermediates. The characteristics given in the key are mainly based on observations on European-origin plants. Specimens with unawned spikelets with strongly spreading bristles are assigned to var. *microstachya* Wiegand, and those with shortly awned spikelets with more appressed bristles to var. *wiegandii* (Fassett) Mohlenbr.; see Hoste (2004) and Bomble (2016) for illustrations of the inflorescences and spikelets. Genetic research on specimens collected from maize fields in Belgium has resulted in two clusters of *E. muricata* collections (Claerhout et al. 2016). From the study of the morphological features of three of these collections, we tentatively conclude that the two clusters C and D identified by Claerhout et al. (2016) correspond to var. *wiegandii* and var. *microstachya*, respectively (IH, unpublished data). Nonetheless, more genetic studies are needed to confirm whether the three morphologically distinct varieties are indeed genetically well-defined taxa. Both within and outside North America, forms of *E. muricata* with smaller spikelets have shown a stronger tendency to spread as weeds outside their natural range (Dore and McNeill 1980; Michael 2001).

Echinochloa muricata is a species of moist, disturbed sites. It is not an important weed of rice fields (Michael 2001, 2003) and in Europe it mainly occurs as a weed in maize fields (Hoste 2004; Bomble 2016).

***Echinochloa oryzicola* (Vasinger) Vasinger, Fl. SSSR 2: 33. 1934.**

= *Echinochloa phyllopogon* auct., non (Stapf) Stapf ex Kossenko in Botanicheskie Materialy Gerbariia Botanicheskogo Instituta imeni V. L. Komarova Akademii Nauk SSSR 8(12): 208. 1940.

= *E. hostii* auct. ital., non (M. Bieb.) Link, Hort. Berol. 2: 209. 1833.

Basionym. *Panicum oryzicola* Vasinger, Trudy Prikl. Bot. 25(4): 125. 1931.

Type. Vladivostok region, left bank of Santakheza, 4 km east of Lake Hanka, 23 Aug 1928, *A. Venzinger-Alexandrova* (lectotype, designated by Tzvelev 1976: 664, LE01010882). Image available at http://herbariumle.ru/?t=occ&id=15824&rid=image_0036250.

Remarks. Although sometimes included in *E. crus-galli*, several features justify accepting *E. oryzicola* as a separate species. *Echinochloa oryzicola* is tetraploid ($2n = 36$), whereas *E. crus-galli* is hexaploid ($2n = 54$) (Yabuno 1966, 1981). The length of the embryo is a reliable feature to distinguish *E. oryzicola* from *E. crus-galli* var. *oryzoides* (which also has large spikelets) and from specimens of the very poorly defined *E. crus-galli* var. *hispidula*. If carefully applied, the shape of the mature inflorescence and the

length of the lower glume may help separate it from *E. crus-galli* var. *oryzoides*. It is rather surprising that the seemingly distinctive feature of the length of the lower glume is not mentioned in Vasinger's original description (Vasinger in Komarov 1934).

Yabuno (1966) distinguished two morphological forms of *E. oryzicola*: the F-form, in which the lemma of the sterile flower is flat and has a coarse surface texture, and the C-form, in which the lemma is convex, coriaceous and shiny. The latter form has only rarely been recorded from Southwestern Europe. Specimens with spikelets much too small for *E. oryzicola* but with a lemma that morphologically closely resembles Yabuno's C-form have been recorded from Germany (as *E. crus-galli* subsp. *spiralis*; Scholz 2002) and Belgium (IH, unpublished records).

The treatment of the rice mimics *E. oryzicola* and *E. crus-galli* var. *oryzoides* in taxonomic and agronomic publications has been extremely confusing. In the past, the name *E. phyllopogon*, often without author citation and thereby adding to confusion, was used separately for each of the two taxa as well as for both of them together; see, e.g., the shifting interpretation in successive publications by Michael (1983, 1994, 2001) and Yabuno's (1981) discussion of European *E. phyllopogon* as a synonym for *E. oryzicola*. *Echinochloa phyllopogon* is a very confusing name, whose identity has been recently summarised and discussed by Crespo et al. (2020a). Its basionym, *Panicum phyllopogon*, was described by Stapf (1901). The accompanying plate shows a specimen that seems to combine features of at least two species. It was said to have been collected by Arcangeli in rice fields near Pisa (Italy). Arcangeli's herbarium is located in PI and FI, at least for the most part. A targeted search in the Arcangeli Herbarium (PI-ARC) did not yield any *Echinochloa* specimen collected in the rice fields near Pisa (comm. F. Roma-Marzio, 09.2018). In the Herbarium Generale of PI, there is a specimen labelled as *P. phyllopogon*, which was part of Flora Italica Exsiccata. The herbarium label states that this species was collected in Italy for the first time in Novara and that Stapf erroneously indicated it to be from Pisa. In fact, the species was collected by Jacometti near Novara but was originally, erroneously so, attributed to a collection of Arcangeli from near Pisa (comm. N. Ardenghi 10.2018). A lectotype for this name was designated by Kossenko (1940) based on one of Jacometti's collections (K000958854; image available at <http://www.kew.org/herbcatimg/638594.jpg>). This collection includes both vegetative and flowering material that, according to P.W. Michael, refers to two different species. The non-flowering part, with very characteristic hair tufts at the junction of leaf blade and leaf sheath, was said to represent *P. phyllopogon* and was recommended to serve as (second step) lectotypification for that name (Michael 1983). However, the presence or absence of such hair tufts is a non-diagnostic feature that can be observed (although not so frequently) in various species of *Echinochloa*, including *E. oryzicola* and *E. crus-galli* var. *oryzoides*. Since both these taxa occur in the Novara area in Italy, it is impossible to assign Stapf's *P. phyllopogon* to one of these taxa. Therefore, it is a confusing name that should be abandoned. However, lectotypification of *P. phyllopogon* was effected later by Kossenko (1940) himself, though under the combination "*E. phyllopogon* subsp. *stapfiana* Kossenko", a superfluous, illegitimate name that explicitly included the type of the species (subsp. *phyllopogon*). Crespo et al. (2020a) argued this lectotype is to be

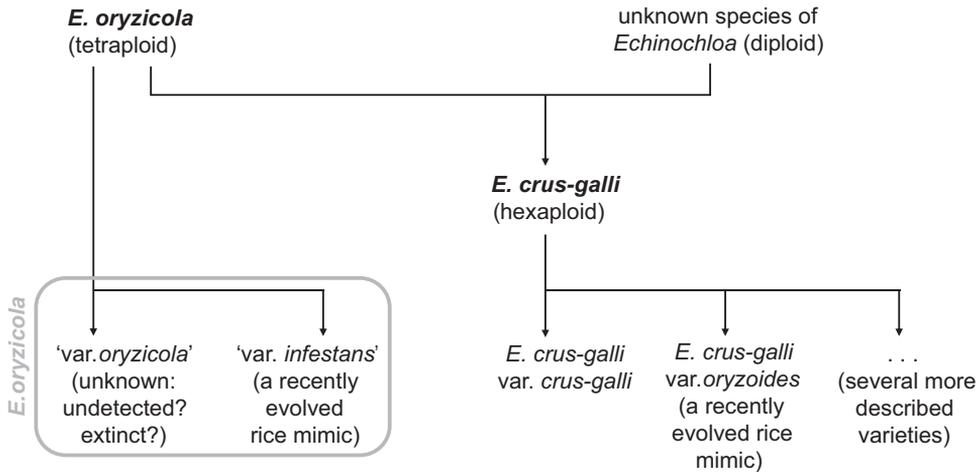


Figure 13. Schematic reconstruction of the evolutionary history of *Echinochloa oryzicola*, *E. crus-galli* and two rice mimics derived thereof. It is hypothesised that the taxon that today is called *E. oryzicola* has only recently evolved from a wild taxon that seems no longer to exist or has not yet been identified. In the absence of information on this original species, it is impossible to distinguish between a long-existing taxon ('var. *oryzicola*') and a recently evolved rice mimic ('var. *infestans*').

followed; this made the later lectotype proposal by Michael (1983) ineffective. Consequently, *E. phyllopogon* should be included as synonymy of *E. oryzoides*, as suggested by Crespo et al. (2020a) and Martínez-Azorín and Crespo (2021).

The separate status of *E. oryzicola* has been corroborated by molecular studies (e.g., Yamaguchi et al. 2005; Ye et al. 2014), although Yasuda and Nakayama (2019) have shown that relying solely on cpDNA may result in misidentification of *E. crus-galli* var. *formosensis* as *E. oryzicola*.

Unfortunately, the structure of the tip of the fertile lemma, which clearly distinguishes *E. crus-galli* from *E. muricata* (Hoste 2004), has received little attention in studies on the weed flora of rice fields in Europe and Asia. In *E. oryzicola*, the tip more closely resembles *E. crus-galli*, although the line of tiny hairs is usually more difficult to see than in *E. crus-galli* (based on specimens from Italian rice fields seen by us; Fig. 4A).

Taxonomy of *Echinochloa*: morphology, genetics and evolutionary history

Defined as “an ubiquitous plant, with variation you can't get your teeth into, which clutters up herbaria” (Anderson 1952), the complex of *Echinochloa crus-galli* and a few closely related taxa fits the definition of a weed perfectly. In the decades after the publication of tentative keys for the annual and perennial species of the genus worldwide (Michael 1983), numerous studies have tried to solve the taxonomic problems relating to this genus. In general, these studies were mostly intended to give an overview of the species that occur in a restricted geographical area (e.g., in country floras) or to help find remedies to lower the impact of *Echinochloa* as noxious weeds in crops (such as rice and maize), which presupposes a correct identification of the taxa involved. Molecular

studies covering a wider range of species are available without, however, linking genetics with morphology; see, e.g., Aoki and Yamaguchi (2008).

So far, *Echinochloa* has not benefitted from the recent revival of interest in botanical monographs, which has primarily been kindled by biodiversity and conservation concerns, especially in the species-rich tropics, rather than by hopes of improving the means to control economically damaging weeds (Grace et al. 2021). However, we believe that a worldwide monograph based on the integration of different scientific expertise including specimen-based taxonomy, genomics and phylogenetics (Muñoz-Rodríguez et al. 2019) is a prerequisite if we are ever to understand the complex taxonomy and evolutionary history and taxonomy of this genus. Once the evolutionary history is better grasped, it will become easier for weed scientists as well as the authors of regional floras to tackle the topics of interest.

The expression ‘evolutionary history’ here refers to more than ‘ancestry of a species’ as routinely used by biologists when describing ‘natural’ events. It also involves human history and the role humans have played, consciously or not, in the origin and evolution of plant species (Russell 2003, 2011). As for *Echinochloa*, a good understanding of what took place in Southeast Asia is essential in order to properly grasp the nature and significance of the diversity of forms displayed by the genus’ representatives in Southwestern Europe. In the latter geographical area, the species under consideration include a single introduced American species (*E. muricata*), the pantropical weed *E. colona* (native to the Old World, possibly including parts of Mediterranean Europe) and the complex of *E. crus-galli* and *E. oryzicola*, originally from Eurasia. Two additional cultivated taxa with non-shattering spikelets (*E. esculenta* and *E. frumentacea*) have both originated in Asia.

Echinochloa muricata exhibits a high degree of variation. Although within North America the distribution of the different forms has been altered as the result of human activities, such as land reclamation (Dore and McNeill 1980), the morphologic and genetic make-up of the species has most likely not strongly been affected by anthropogenic factors. The same can probably be said of polymorphic *E. crus-galli* in Europe. In Southeast Asia, the story is different and more complex. The result of a hybridization event between tetraploid *E. oryzicola* and an unknown diploid species, hexaploid *E. crus-galli* arose around 3.3 million years ago (Ye et al. 2014). *Echinochloa oryzicola* and *E. crus-galli* thus share a number of features, but the latter shows a wider range of morphological variation and ecological tolerances, which may be attributed to the added set of chromosomes (Yabuno 1966). Over time, the natural range of *E. crus-galli* has extended from East Asia to Western Europe, while the natural range of *E. oryzicola* apparently remained restricted to Southeast Asia.

Circa 10 millennia ago, *Echinochloa* spp., along with other wetland grasses such as rice (*Oryza* spp.), was gathered and processed for human consumption in China (Yang et al. 2015). *Echinochloa* fell out of favour when rice gradually evolved into a better-yielding crop (Chang 2000). It persisted, however, as a noxious weed and adapted in response to human activities such as the creation of rice paddies, hand-weeding and the timing of rice harvesting. Over time, *E. crus-galli* developed into a multitude of physiologically, morphologically and genetically different forms, displaying varied life

histories in a range of habitat types (Yabuno 1966; Barrett and Wilson 1981; Yamasue et al. 1989; Fukao et al. 2003). As a result of unintentional selection, *Echinochloa* in rice paddies developed similarities with rice. Along with other features such as a more erect habit, rice mimics are characterised by green seedlings and a green culm base, having lost the anthocyanin pigmentation that is typical for *E. crus-galli* var. *crus-galli*. Judging from the end result, it seems logical to conclude that *E. oryzicola* followed a parallel line of evolution. However, this raises a question. Regarding *E. crus-galli*, both the ancestor (var. *crus-galli*) and the evolved rice mimic (var. *oryzoides*) have been identified, yet in the case of *E. oryzicola* we apparently only know the mimic. Barrett (1983) distinguished between the strategies of the general purpose genotypes (such as var. *crus-galli*) and those of specialised biotic ecotypes (such as the rice mimic var. *oryzoides*). As for the specialised biotic ecotype *E. oryzicola*, no morphologically distinct generalist ancestor has been described. Barrett's nomenclature reflects the shared morphological features of the rice mimics that occur in wetland rice paddies. His *E. crus-galli* var. *oryzicola* included both an early-flowering hexaploid (*E. oryzoides* (Ard.) Fritsch = *E. crus-galli* var. *oryzoides*) and a later-flowering tetraploid (*E. phyllopogon* (Stapf) Koss = *E. oryzicola*). Moreover, Yabuno (1966) described a rice mimic of *E. crus-galli* in upland rice fields; it shares the stiffer plant habit with the mimics from wetland rice paddies.

Echinochloa crus-galli is usually autogamous. When unconsciously transported around the world with rice seed, the introduction of morphologically different forms may, therefore, result in the establishment of seemingly quite distinct taxa (Barrett and Seaman 1980). This, in turn, may lure botanists into describing new species based on material that only poorly represents the range of variation in the area of origin, as illustrated by *Panicum oryzoides* Ard. (syn. *E. crus-galli* var. *oryzoides*; Crespo et al. 2020b) and *P. erectum* Pollacci ('*E. hispidula*'; Ardenghi et al. 2015), both based on materials collected in Italy.

Yamaguchi et al. (2005) stressed the poverty of sequence variations within a complex species such as *E. crus-galli*, despite the fact that the species shows a high morphological diversity, including domesticated forms, non-shattering weedy forms and shattering forms that mimic rice plants. The features of rice mimics, such as green culm base and seedlings, may be of limited value to taxonomists. In rice paddies, plants with red- or purple-tinged seedlings might again re-emerge now that herbicides have replaced hand-weeding. In a genus in which over the last 10 millennia, significant pre-existing morphological variation has been greatly increased due to close association with agriculture, accepting each seemingly well-defined form as a separate taxon may not lead to a satisfactory classification. For weed scientists, less-visible features related to ecological requirements, variation of the life cycle and development of resistance against herbicides may prove more relevant than morphological differences that once originated in a different co-evolutionary setting.

From this short detour into the evolutionary history of *Echinochloa* in Southeast Asia, one can conclude only that the study of the taxonomy of this genus in Europe requires a broader geographical scope. This should be coupled with the consideration of some questions that so far have been insufficiently addressed. The morphological

and genetic variation of *E. crus-galli* var. *crus-galli* within its extensive Old World native range is poorly documented, as are the interactions (occasional cross-pollination of usually autogamous plants) between populations of var. *crus-galli* and those of the derived rice mimics. As for *E. oryzicola*, in the absence of information about its non-mimic ancestor, its evolutionary history is quite obscure. Identifying the unknown diploid parent species that, together with tetraploid *E. oryzicola*, gave rise to *E. crus-galli* would help better understand the species complex of *E. crus-galli* and *E. oryzicola*, including '*E. glabrescens*'.

Embedding these questions in a larger project of a world monograph of *Echinochloa*, the outcome of the collaboration of experts in the fields of taxonomy, genomics and phylogenetics, would enhance our understanding of the affinities between weedy and non-weedy taxa, and between Old and New World species. Moreover, such a project could generate a great deal of knowledge about the evolutionary history of a group of plants that has undergone profound changes resulting from its interactions with humans in the course of the past millennia.

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Primulina nana (Gesneriaceae), a new species from eastern Guangxi, China

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Abstract

Primulina nana C.Xiong, W.C.Chou & F.Wen, a new species of Gesneriaceae from limestone areas of Guangxi, China, is described and illustrated here. It morphologically resembles *P. yangshuoensis* Y.G.Wei & F.Wen in papillose leaf surface, but can be easily distinguished from the latter by noting a combination of characteristics, especially in its leaf blades, leaf blade indumentum characteristic, calyx lobes, corolla and the disc. We found only one population at the type locality, about 200 mature individuals. According to the IUCN Red List Categories and Criteria (Version 3.1), the new species is provisionally assessed as Critically Endangered (CR).

Keywords

Flora of Guangxi, Gesneriaceae, new taxon, *Primulina yangshuoensis*, taxonomy

Introduction

The genus *Primulina* s.l. was redefined in 2011, comprising *Chiritopsis* W.T.Wang, *Wentsaiboea* D.Fang & D.H.Qin (except *W. tiandengensis* Yan Liu & B. Pan) and the large number of species described in *Chirita* sect. *Gibbosaccus* C.B.Clarke

(Wang et al. 2011; Weber et al. 2011). This genus now exhibits the most diversity in the Chinese Gesneriaceae, including approximately 123 species and eight varieties of *Primulina s.l.* after the revision (Wang et al. 2011; Weber et al. 2011). An acceleration of *Primulina* species discovery has been seen over the last decade, with an average of about 10 new species per year. As of February 2022, there were 221 species (excluding infraspecific taxa) (GRC 2022) in this genus. China is the centre of diversity for *Primulina* with at least 204 species and 15 varieties occurring there at present (Wen et al. 2022), especially in limestone areas (Wei 2018; Wen et al. 2019; Ge et al. 2020; Liu et al. 2020; Xin et al. 2020a, b, c, 2021; Zhang et al. 2021). The tropical and subtropical karst limestone mountainous areas of Guangxi, China, are the centres of species diversity and differentiation of this genus (Li et al. 2019).

In October 2021, Y. Huang, a Gesneriaceae enthusiast from Guangxi, found this unknown plant in the wild. One of the authors, W.C. Chou, went to the type locality and collected specimens. Some of the living plants were introduced and cultivated at the Gesneriad Conservation Center of China (GCCC) and the National Gesneriaceae Germplasm Bank for further research. Comparison of the live plants with the type specimens and protologues of all known species of *Primulina* led to the determination that these specimens neither fit the existing protologues nor conform to the type specimens of these species. Nevertheless, the leaves' tiny shape and texture make them very particular and most similar to *P. yangshuoensis* Y.G. Wei & F. Wen (Wen et al. 2012). However, a combination of characteristics easily distinguished it from other species, especially in its leaf blades, leaf blade indumentum, calyx lobes, corolla and the disc characters. We confirmed that it represents a new species of *Primulina* and describe it here.

Taxonomic treatment

Primulina nana C.Xiong, W.C.Chou & F.Wen, sp. nov.

Figs 1, 2A1–F1

urn:lsid:ipni.org:names:77298577-1

Diagnosis. The new species resembles *Primulina yangshuoensis* (Fig. 2A2–F2) in papillose leaf surface, namely numerous single pubescent hair on papilla on surface, but can be easily distinguished from the latter by its leaf blade elliptic to ovate, 1.6–1.8 × 1.1–1.3 cm (vs. broadly ovate-round, subround or round, 3.5–6.5 × 2–4.5 cm); leaf nearly erect semi-transparent papillose-pubescent and white pubescent (vs. densely erect semi-transparent and white multicellular papillose-hispid); peduncle 3–5 cm long (vs. 8–9 cm); calyx lobes with one serration (vs. entire); corolla ca. 1.5 cm long, tube tubular (vs. 2–3 cm, broadly infundibuliform); disc ca. 0.6 mm high (vs. ca. 1 mm). Detailed morphological comparisons with *P. yangshuoensis* are provided in Table 1.

Type. CHINA. Guangxi Zhuangzu Autonomous Region: Wuzhou City, Mengshan County, Xinxu Town, 24°19'N, 110°22'E, altitude ca. 530 m, November 26, 2021, *Chou Wei-Chuen & Huang Yi CWC211126-01* (IBK!)

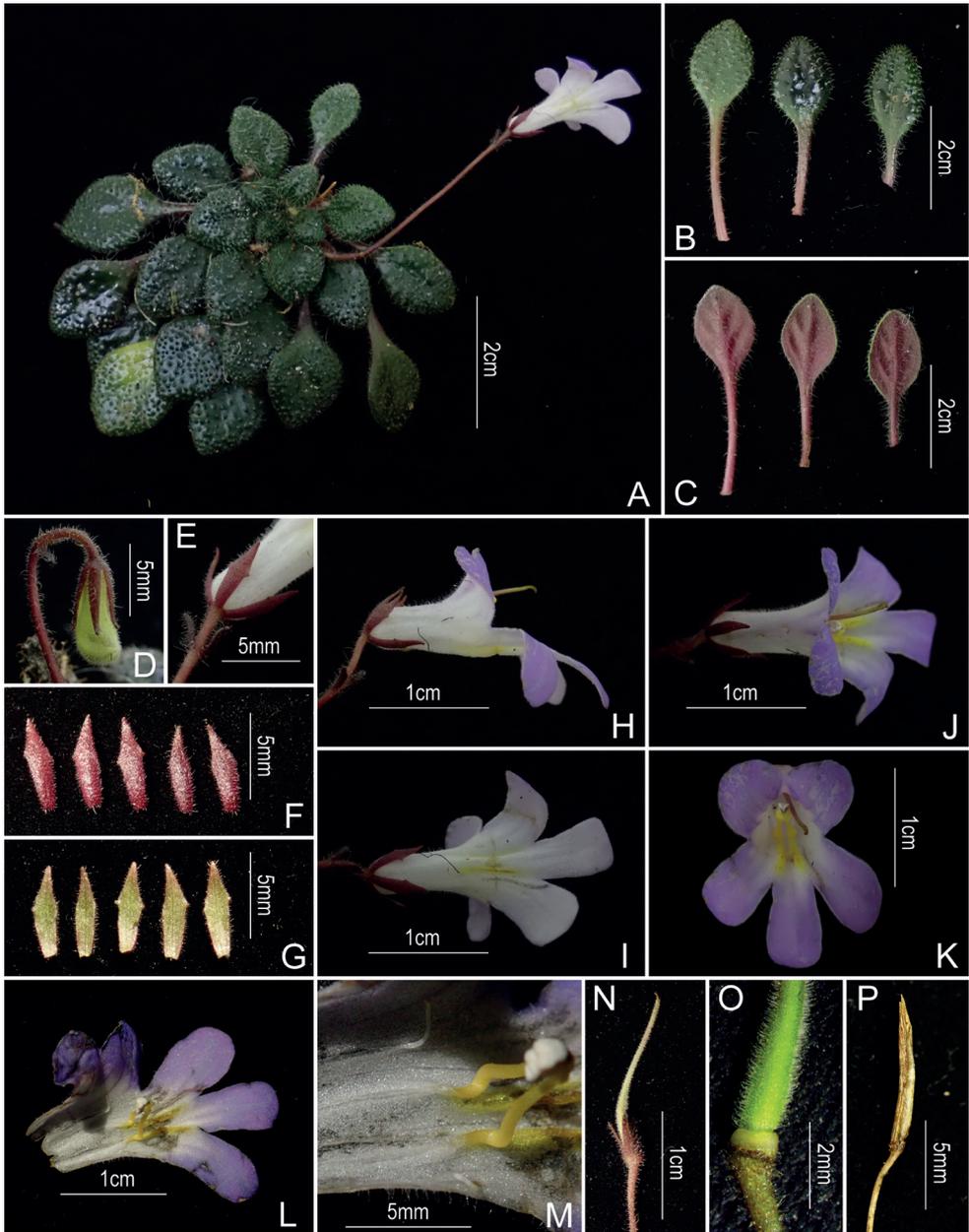


Figure 1. *Primulina nana* sp. nov. **A** habit **B** adaxial side of leaves **C** abaxial side of leaves **D** alabastrum **E** bracts and calyx **F** abaxial side of calyx lobes **G** adaxial side of calyx lobes **H** lateral view of a flower **I** ventral view of a flower **J** top view of a flower **K** front view of a flower showing the internal structure **L** opened corolla **M** stamens and staminodes **N** pistil with calyx **O** disc and ovary **P** capsule. Photographs by Chi Xiong.

Description. Herbs perennial, acaulescent, rhizome subterete, ca. 1.5 cm long, 4–6 mm in diameter, Leaves 14–23, all basal, petiolate; petiole 1–3 cm long, ca. 1.5 mm in diameter, purple, densely pubescent; leaf blade elliptic to ovate, 1.6–1.8 × 1.1–1.3 cm,

leathery, adaxially dark green to purplish-green, nearly erect semi-transparent papillose-puberulent on adaxial surface, 1–2 mm long, abaxially purple, white pubescent, 1–2 mm long, base broadly cuneate, margin entire, apex acute to obtuse, lateral veins inconspicuous, 2–3 on each side. Cymes 2–4, axillary; usually simple, peduncle 3–5 cm long, ca. 0.8 mm in diameter, pubescent; bracts 2, opposite, oblong to linear, 2.5–3 × ca. 1 mm, pubescent on both surfaces, margin entire, apex obtuse. Calyx 5-parted to base, lobes lanceolate, ca. 5 × 1–1.5 mm, nearly equal, outside purple, densely pubescent, inside yellow-green, nearly glabrous, usually with one serrate on the middle of calyx lobe, apex acute. Corolla purple, throat with two yellow stripes inside, ca. 1.5 cm long, outside glandular and eglandular puberulent, inside glabrous, tube tubular and gradually narrowing to the bottom, ca. 1 cm long, orifice 5–6 mm in diameter; limb distinctly 2-lipped, adaxial lip 2-parted to the middle, lobes oblong or round, apex round, 3–4 × 5–6 mm, abaxial lip 3-parted to near the base, lobes oblong, apex round, 6–8 × 4–5 mm. Stamens 2, adnate ca. 8 mm above the corolla base; filaments yellow, ca. 5 mm long, geniculate near the base, glabrous, anthers reniform, slightly constricted at middle, 1.5–2 mm long; staminodes 3, lateral ones linear, glabrous, ca. 3 mm long, apex capitate, glabrous, adnate to ca. 7 mm above the corolla tube base, the central one inconspicuous, adnate near the corolla tube base. Disc annular, ca. 0.6 mm high, margin repand, glabrous. Pistil 1.4–1.6 cm long, ovary 5–6 mm long, ca. 1 mm in diameter, glandular-pubescent; style ca. 1 cm long, 0.6 mm in diameter, glandular-pubescent; stigma obtrapeziform, ca. 1 mm long. Fruit linear, longitudinally dehiscent, 8–9 mm long, ca. 1.5 mm in diameter.

Phenology. Flowering in November, fruiting from December to the following January.

Etymology. The specific epithet ‘*nana*’ is derived from the dwarf plants of the new species compared with that of most other species of *Primulina*.

Vernacular name. 玲珑报春苣苔 (Chinese name); Líng Lóng Bào Chūn Jù Tái (Chinese pronunciation).

Distribution and habitat. *Primulina nana* is only known from the type locality, Xinxu Town, Mengshan County, Wuzhou City, Guangxi, China. It grows on moist, shady limestone rock surfaces, at an elevation of ca. 530 m.

Conservation status. *Primulina nana* is only known from one population of about 200 mature individuals at the type locality. This population has been reduced by 90%

Table 1. Detailed comparison of *Primulina nana* and its relative *P. yangshuoensis*.

Characters	<i>P. nana</i>	<i>P. yangshuoensis</i>
Leaf-blades	elliptic to ovate, 1.6–1.8 × 1.1–1.3 cm	broadly ovate-round, subround or round, 3.5–6.5 × 2–4.5 cm
Leaf indumentum	densely nearly erect semitransparent papillose-puberulent on adaxial surface, 1–2 mm long, abaxially purple, densely white pubescent, 1–2 mm long	densely erect semitransparent or white multicellular papillose-hispid on both surfaces, 0.8–1 cm long on the adaxial surface, 4–5 mm long on the abaxial surface
Peduncle	3–5 cm long	8–9 cm long
Bracts	oblong to linear, 2.5–3 × ca. 1 mm	lanceolate or subulate, 1–2 × 0.3–0.5 mm
Calyx lobes	Usually, one serrate at the middle	entire
Corolla	ca. 1.5 cm long, tube tubular and gradually narrow to the bottom	2–3 cm long, tube broadly infundibuliform
Disc	ca. 0.6 mm high	ca. 1 mm high

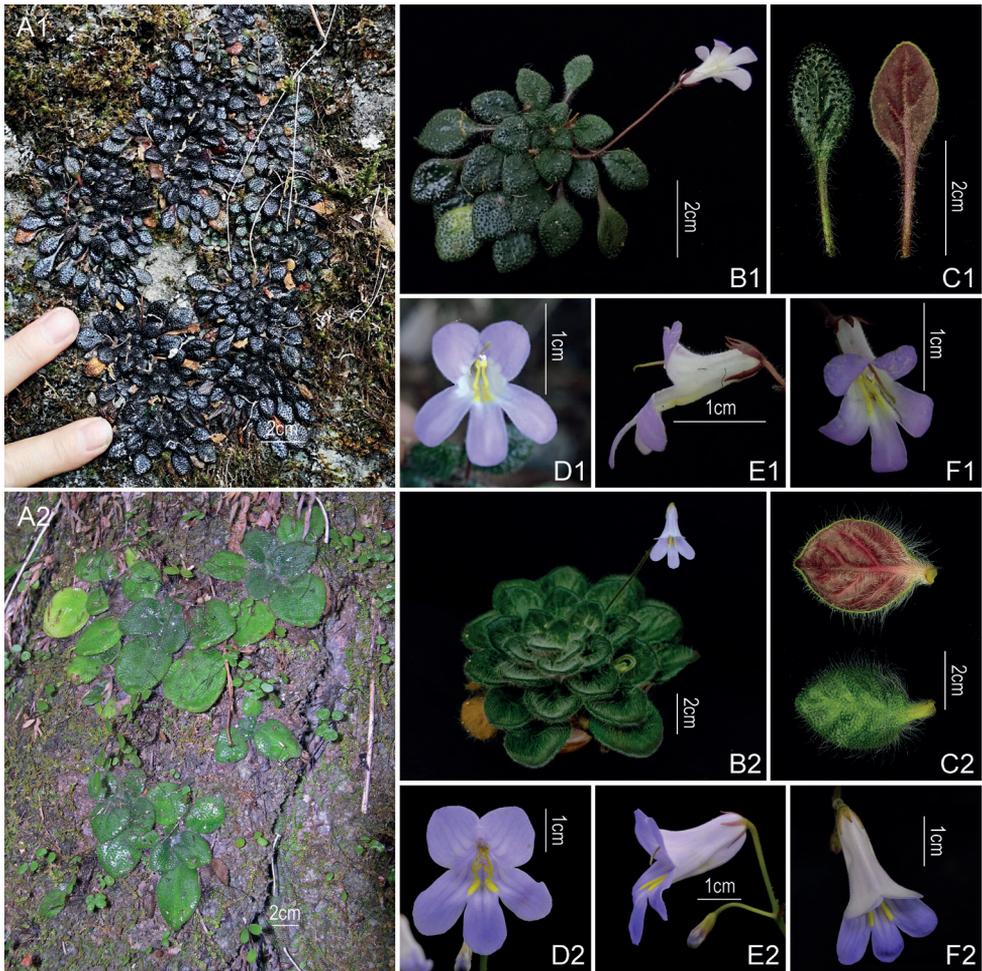


Figure 2. Morphological comparison of *Primulina nana* sp. nov. (1) with *P. yangshuoensis* (2) **A** habitat **B** habit **C** leaf blades **D** front view of flowers **E** lateral view of flowers **F** top view of flowers. **A1** and **D1** photographed by Wei-Chuen Chou; **B1–C1**, **E1–F1**, **C2** photographs by Chi Xiong; **A2–B2** and **D2–F2** photographed by Fang Wen.

from when it was originally found. The EOO and AOO of the new species are about 0.2 km² and 25 m², respectively. Its beautiful flowers, thickened woody rhizomes and shapely leaves, led to over-harvesting by locals, who sold it as an ornamental plant. Thus, following the IUCN Red List Categories and Criteria (IUCN 2019), it is temporarily assessed as Critically Endangered [CR B1ab (iii, v) + B2ab (iii, v)].

Notes. The plant size of *Primulina nana* is dwarf and leaf blade length is less than 2 cm, but length of flowers is about 1.5 cm and the proportion of flowers and leaves is unusual in this genus. These characters differ from other *Primulina* species and can be clearly distinguished from *P. yangshuoensis* in morphological characters (Table 1).

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Didymodon manhanensis (Pottiaceae, Bryophyta), a new species from Inner Mongolia steppe, China and its phylogenetic position, based on molecular data

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Abstract

Inner Mongolia steppe is one of the suitable habitats for *Didymodon* species and a new species, *Didymodon manhanensis* C. Feng & J. Kou from Manhan Mountain in semi-arid region in Inner Mongolia, China is described and illustrated. It is characterised by leaves incurved and slightly twisted when dry, spreading when moist, narrowly lanceolate from an ovate base; subulate and fragile leaf apices; distally bistratose leaf margins that are recurved in proximal 2/3–3/4; excurrent costa with guide cells in 2–3 layers and without ventral stereids; smooth laminal cells and red KOH laminal colour reaction. Our morphological analyses and molecular results, based on DNA sequences of ITS, *rps4* and *trnM-trnV*, confirm that *D. manhanensis* belongs to a group that includes *D. obtusus* J. Kou, X.-M. Shao & C. Feng and *D. daqingii* J. Kou, R.H. Zander & C. Feng. This new species is compared with similar species and its phylogenetic position and ecology are discussed.

Keywords

Asia, Manhan Mountain, phylogenetic analysis, taxonomy

Introduction

Inner Mongolia, situated in Inner Eurasia, is located in the northern part of China and presents a strip distribution from the northeast to the west. The district habitats are temperate continental monsoon climate. The annual mean temperature is 8 °C, which increases from east to west and the annual precipitation is 35–530 mm, which decreases from southeast to northwest (Miao 2017). The area of grassland accounts for 60% of the whole Inner Mongolia and more than one-quarter of the total area of grassland in China. The grassland in Inner Mongolia is divided into three types: meadow steppe formed by, for example, *Stipa baicalensis* Roshev, *Leymus chinensis* (Trin.) Tzvelev; typical steppe formed by, for example, *Stipa grandis* P. Smirn., *Stipa krylovii* Roshev, *Leymus chinensis* (Trin.) Tzvelev and desert steppe formed by, for example, *Stipa klemenzii* Roshev, *Stipa glareosa* P.A. Smirn., *Stipa breviflora* Griseb (Hua et al. 2021). The main vegetation types of the steppes present distinct zonal features (Wu et al. 2005). The Inner Mongolia steppe is a suitable habitat for the *Didymodon* Hedw. species and several new species were recently discovered (e.g. Kou et al. 2016a; Kou et al. 2019; Feng et al. 2022).

The taxonomy of genus *Didymodon* is complicated, involving the differentiation from related genera, such as *Barbula* Hedw. and the circumscriptions of its infrageneric sections (Zander 1993; Zander 2007; Zhang et al. in press). A recent important event associated with *Didymodon s. lat.* was the split of the genus into seven smaller genera: *Aithobryum* R.H. Zander, *Didymodon s. str.*, *Exobryum* R.H. Zander, *Fuscobryum* R.H. Zander, *Geheebia* Schimp., *Trichostomopsis* Card. and *Vinealobryum* R.H. Zander, based on macro-evolutionary analysis and the dissilient genus concept applied (Zander 2013; Zander 2019). Although initially this revolutionary concept was considered unnecessary or unsupported (Blockeel and Kučera 2019), it has later been supported by molecular phylogenetic data, but with some alterations (Jiménez et al. 2022; Zhang et al. in press) and has gained acceptance by some other authors (e.g. Kou and Feng 2018; Osman et al. 2021; Feng et al. 2022). During our continuous investigations of xerophilic mosses, especially Pottiaceae Hampe, in China (e.g. Feng et al. 2016a, b; Kou et al. 2016b, 2018, 2019; Kou and Feng 2018), many specimens have been collected from different provinces. Amongst them, two samples collected from Manhan Mountain in Inner Mongolia of *Didymodon s. lat.* from stony habitats are different from species previously reported in the area (Li et al. 2001). They mostly resemble *Didymodon obtusus* J. Kou, X.-M. Shao & C. Feng. To clarify their taxonomic identity, we conducted phylogenetic analysis and confirm that these samples belong to the genus *Didymodon s. str.* (Zander 2013), but do not match with any species known in the genus. Here, we describe this unknown moss as a new species.

Materials and methods

Morphological observations

Over 3000 specimens of the genus *Didymodon s. lat.* were examined during our revision of Pottiaceae in China. More than 50 field investigations were conducted in past

years and the specimens included in this study were housed in the Herbaria at IFP, KUN and NMAC. Microscopic examinations and measurements were taken with a ZEISS Primo Star light microscope and photomicrographs were obtained with a Canon EOS 70D camera, mounted on this microscope. Specimens were examined in 2% potassium hydroxide (KOH). Three plants were dissected from each collection and, for each shoot, every possible structure from the gametophyte had to be examined and a record kept of what was found for each individual species. Specific morphological and anatomical features of taxonomic importance were assessed mainly following Zander (1993). Leaves were always taken from the upper and middle parts of the stem and cross-sections were made in the middle part of the stem. Measurements of leaf width were taken at the base, mid-leaf and upper part. Cross-sections were made at mid-leaf.

Phylogenetic analyses

To test the phylogenetic position of the new species, two specimens collected from Manhan Mountain were sampled. Due to its great similarity with *D. obtusus* and *Didymodon daqingii* J. Kou, R.H. Zander & C. Feng, the isotypes of the two species were added to the dataset. We employed one nuclear (ITS) and two chloroplast markers (*rps4* and *trnM-trnV*), which had been used successfully in previous phylogenetic studies in *Didymodon* s. lat. and enabled the re-use of earlier results and easier interpretation of new data (Werner et al. 2004, 2005, 2009; Kučera and Ignatov 2015; Kučera et al. 2018; Ronikier et al. 2018; Jiménez et al. 2022; Zhang et al. in press). Phylogenetic trees are created and shown separately. The complete list with sample names and GenBank accession numbers is presented in Tables 1 and 2. DNA extraction, PCR amplification and sequencing procedure followed the protocols described by Wang et al. (2010).

The sequences were aligned by using MAFFT 7.222 (Kazutaka and Daron 2013) and then edited in BioEdit 7.0.1 (Hall 1999). The concatenation of individual *rps4* and *trnM-trnV* fragments was performed by our custom Perl script. Phylogenetic analyses were performed by using the Bayesian Inference (BI) and Maximum Likelihood (ML) methods. MrBayes 3.2.6 (Ronquist et al. 2012) was used for BI analyses under the GTR substitute model. The following was used: two Markov Chain Monte Carlo (MCMC) searches were run for 10 million generations each, with a sampling frequency of 1000. The first 25% of the trees were discarded as burn-in. The convergence between runs in all cases dropped below

Table 1. New sequences used in this study, including taxa vouchers information and GenBank accession numbers.

Species	Voucher information	ITS	<i>rps4</i>	<i>trnM-trnV</i>
<i>Didymodon manhanensis</i> 4	China, Inner Mongolia, Chao Feng 2016060162	OL514237	OL450506	OL450515
<i>Didymodon manhanensis</i> a3	China, Inner Mongolia, Chao Feng 2016060176	OL514238	OL450507	OL450516
<i>Didymodon obtusus</i>	China, Tibet, Xiao-Ming Shao & Jin Kou 20140815037	OL514239	OL450508	OL450517
<i>Didymodon daqingii</i>	China, Inner Mongolia, Chao Feng 20170605032	OL514240	OL450509	OL450518

Table 2. Sequences from GenBank used in this study, including taxa and GenBank accession numbers.

Species	ITS	<i>rps4</i>	<i>trnM-trnV</i>
<i>Acaulon triquetrum</i>	MW398556		
<i>Aloina rigida</i>	MW398549		
<i>Aloinella andina</i>	MW398550		
<i>Andinella churchilliana</i>	MW398720		
<i>Andinella coquimbensis</i>	MW398711		
<i>Andinella elata</i>	MW398708		
<i>Andinella granulosa</i>	MW398714		
<i>Andinella limensis</i>	MW398710		
<i>Andinella oedocostata</i>	MW398733		
<i>Andinella pruinosa</i>	MW398726		
<i>Barbula unguiculata</i>	MW398553	HM147777	JQ890366
<i>Bryoerythrophyllum recurvirostrum</i>	MW398547	JQ890468	JQ890407
<i>Bryoerythrophyllum rubrum</i>	MW398548		
<i>Chenia leptophylla</i>	MW398561		
<i>Cinclidotus riparius</i>	MW398554		
<i>Crossidium squamiferum</i>	MW398558		
<i>Didymodon acutus</i>	AY437111	KP307551	KP307667
<i>Didymodon alpinus</i>	MW398606		
<i>Didymodon andreaeoides</i>	MW398768		
<i>Didymodon anserinocapitatus</i>	MW398649	KP307545	KP307640
<i>Didymodon asperifolius</i>	MW398594	JQ890472	KP307600
<i>Didymodon australasiae</i> (<i>Trichostomum australasiae</i>)	MW398737	KP307571	KP307651
<i>Didymodon brachyphyllum</i> (<i>Vinealobryum brachyphyllum</i>)	MW398817		
<i>Didymodon buckii</i>	MW398578		
<i>Didymodon caboverdeanus</i>	MW398607		
<i>Didymodon californicus</i> (<i>Vinealobryum californicum</i>)	MW398819		
<i>Didymodon canoae</i>	MW398584		
<i>Didymodon cardotii</i>	MW398729		
<i>Didymodon challaensis</i> (<i>Trichostomopsis challaensis</i>)	MW398748		
<i>Didymodon constrictus</i>	MW398613		
<i>Didymodon cordatus</i>	MW398664	KP307564	KP307668
<i>Didymodon ditrichoides</i>	MW398642		
<i>Didymodon eckeliae</i> (<i>Vinealobryum eckeliae</i>)	MW398826		
<i>Didymodon edentulus</i>	MW398685		
<i>Didymodon epapillatus</i>	MW398665		
<i>Didymodon erosodenticulatus</i>	MW398792	MF536597	MF536635
<i>Didymodon erosus</i>	EU835148	MF536609	MF536646
<i>Didymodon fallax</i> (<i>Geheebia fallax</i>)	MW398779	KP307552	KP307663
<i>Didymodon ferrugineus</i> (<i>Geheebia ferruginea</i>)	MW398796	MF536588	MF536625
<i>Didymodon fragilicuspis</i>	KP307482		
<i>Didymodon fuscus</i>	MW398689	KP307537	KP307601
<i>Didymodon</i> aff. <i>fuscus</i>		KP307546	KP307615
<i>Didymodon gaochienii</i>		KP307538	KP307658
<i>Didymodon gelidus</i>	MW398693		
<i>Didymodon giganteus</i>	MW398786	KP307548	KP307669
<i>Didymodon glaucus</i>	MW398612		
<i>Didymodon guangdongensis</i> (<i>Vinealobryum guangdongense</i>)	MW398657		
<i>Didymodon hedyarififormis</i>	MW398582	KP307569	KP307629
<i>Didymodon hengduanensis</i>	MW398629		
<i>Didymodon hegewaldiorum</i>	MW398739		
<i>Didymodon herzogii</i>	MW398746		
<i>Didymodon humboldtii</i>	MW398667		
<i>Didymodon icmadophilus</i>	MW398632	KP307598	KP307604
<i>Didymodon imbricatus</i>	MW398646		

Species	ITS	<i>rps4</i>	<i>trnM-trnV</i>
<i>Didymodon incrassatolimbatius</i>	MW398572		
<i>Didymodon incurvus</i>	MW398680		
<i>Didymodon insulanus</i> (<i>Vinealobryum insulanum</i>)	MW398811		
<i>Didymodon japonicus</i>	MW398757		
<i>Didymodon jimenezii</i>	MW398622		
<i>Didymodon johansenii</i>	MW398589	KP307542	KP307662
<i>Didymodon kunlunensis</i>	MW398610		
<i>Didymodon laevigatus</i>	MW398618		
<i>Didymodon lainzii</i>	MW398575		
<i>Didymodon leskeoides</i> (<i>Geheebia leskeoides</i>)	MW398777	MF536604	MF536642
<i>Didymodon luehmannii</i>	MW398718		
<i>Didymodon luridus</i>	AY437098	MF536587	MF536624
<i>Didymodon maschalogenia</i>	MW398615		
<i>Didymodon maximus</i> (<i>Geheebia maxima</i>)	MW398784	MF536591	MF536628
<i>Didymodon mesopapillosus</i>	MW398758		
<i>Didymodon molendoides</i>	MW398687		
<i>Didymodon mongolicus</i>	KU058175		
<i>Didymodon murrayae</i>	KP307513	KP307563	KP307650
<i>Didymodon nevadensis</i>	MW398730		
<i>Didymodon nicholsonii</i> (<i>Vinealobryum nicholsonii</i>)	MW398808		
<i>Didymodon nigrescens</i>	LC545516	KP307543	KP307611
<i>Didymodon norrisii</i>	MW398830	KP307585	KP307617
<i>Didymodon novae-zelandiae</i>	MW398769		
<i>Didymodon obtusus</i>	MW398666		
<i>Didymodon occidentalis</i>		KP307533	KP307599
<i>Didymodon ochyrarum</i>	MW398763		
<i>Didymodon paramicola</i> (<i>Trichostomopsis paramicola</i>)	MW398740		
<i>Didymodon patagonicus</i>	MW398675		
<i>Didymodon perobtusus</i>	KP307523	KP307539	KP307609
<i>Didymodon revolutus</i> (<i>Husnotiella revoluta</i>)	MW398569	JQ890471	KP307646
<i>Didymodon revolutus</i> var. <i>africanus</i>	MW398568		
<i>Didymodon rigidulus</i>	MW398602	KP307589	KP307647
<i>Didymodon rigidulus</i> var. <i>subulatus</i>	MW398672		
<i>Didymodon rivicola</i>	MW398599	KP30756	KP307607
<i>Didymodon santessoni</i>	MW398705		
<i>Didymodon sicculus</i>	MW398801	MF536606	MF536643
<i>Didymodon sinuosus</i>	MW398567	JQ890476	JQ890410
<i>Didymodon spadiceus</i> (<i>Geheebia spadicea</i>)	MW398795	MF536593	MF536631
<i>Didymodon subandraeoides</i>	AY437108	KP307570	KP307630
<i>Didymodon tectorum</i>	MW398659		
<i>Didymodon tibeticus</i>	MW398638		
<i>Didymodon tomaculosus</i>	AY437114		
<i>Didymodon tophaceus</i>	MW398807	MF536607	MF536644
<i>Didymodon tophaceus</i> var. <i>anatinus</i>		MF536589	MF536626
<i>Didymodon torquatus</i>	MW398719		
<i>Didymodon umbrosus</i> (<i>Trichostomopsis umbrosa</i>)	MW398742		
<i>Didymodon validus</i>	MW398650		
<i>Didymodon vinealis</i> (<i>Vinealobryum vineale</i>)	MW398815	JQ890475	KP307606
<i>Didymodon vinealis</i> var. <i>rubiginosus</i>	MW398822		
<i>Didymodon vulcanicus</i>	MW398636		
<i>Didymodon waymouthii</i>	MW398770		
<i>Didymodon wisselii</i>	MW398655		
<i>Didymodon xanthocarpus</i>	MW398696	KP307534	KP307638
<i>Didymodon zanderi</i>	MW398585	KP307535	KP307621
<i>Dolotortula mnifolia</i>	MW398555		
<i>Erythrophyllopsis andina</i>	MW398546		

Species	ITS	<i>rps4</i>	<i>trnM-trnV</i>
<i>Gertrudiella uncinicoma</i>	MW398698		
<i>Gertrudiella uncinicoma</i> var. <i>serratopungens</i>	MW398701		
<i>Guerramontesia microdonta</i>	MW398543		
<i>Hennediella heimii</i>	GQ339750		
<i>Hennediella polysteta</i>	GQ339759		
<i>Leptodontium excelsum</i>	MW398545		
<i>Microbryum curvicolle</i>		JX679986	JX679936
<i>Microbryum davallianum</i>	MW398557		
<i>Pseudocrossidium hornschiuanum</i>	MW398551	JQ890481	JQ890420
<i>Pseudocrossidium revolutum</i>	MW398552		
<i>Pterygoneurum ovatum</i>	MW398560		
<i>Sagenotortula quitoensis</i>	GQ339761		
<i>Stegonia latifolia</i>	MW398559		
<i>Syntrichia ruralis</i>	MW398564	FJ546412	FJ546412
<i>Tortula muralis</i>	MW398562	JN581679	JQ890421
<i>Tortula subulata</i>	MW398563		
<i>Triquetrella arapilensis</i>	MW398544		
<i>Tridontium tasmanicum</i>	MW398750		

0.01. ML analyses were executed in IQ-TREE 1.6.3 (Nguyen et al. 2014) under the TPM3u+F+R3 (for cpDNA) and TIM3e+I+G4 (for ITS) substitute models, respectively, selected by the ModelFinder programme (Kalyaanamoorthy et al. 2017), based on the Bayesian Information Criterion (BIC) and 1000 fast bootstrapping replicates were used. The final obtained trees were visualised and edited in FigTree v.1.4.0 (Rambaut 2014).

Results

The chloroplast (cp) and ITS alignments comprised 1313 and 1364 nucleotide sites, respectively. The BI and ML phylogenetic trees have a consistent topology, although there are different levels of support depending on the method. Hence, only the topologies with branch lengths from the BI trees are presented, with added support from the ML method on the respective trees (Figs 3–4). Although the inference from analysed chloroplast regions (Fig. 3) and the ITS (Fig. 4) agrees in most aspects, the position of the new species is different between the two above phylogenetic trees and, thus, both of them are reserved. The topology of the ITS dataset shows that *D. manhanensis* is nested within the monophyletic group comprising *Didymodon epapillatus* J. Kou, X.-M. Shao & C. Feng, *Didymodon mongolicus* D.-P. Zhao & T.-R. Zhang, *Didymodon validus* Limpr., *Didymodon wisselii* (Dixon) D.H. Norris & T.J. Kop. and *Vinealobryum guangdongensis* C. Feng & J. Kou and is sister to *D. obtusus*, but with weakly-supported values. In the combined plastid dataset, *D. manhanensis* is nested within the group including *Didymodon cordatus* Jur. and is sister to *D. daqingii* and *Didymodon anserinocapitatus* (X.J. Li) R.H. Zander, with well-supported values.

Discussion

As indicated by Zander (1993), *Didymodon s. lat.* is heterogeneous and could be profitably split. In our phylogenetic analyses, this genus is polyphyletic and its species can be classified within several well-supported monophyletic clades, which correspond to other phylogenetic studies of the genus (Feng et al. 2022; Jiménez et al. 2022; Zhang et al. in press). Our results reveal a close relationship between *D. manhanensis* and two recently-described species in China: *D. daqingii* and *D. obtusus*. Although the latter two species were considered identical by Sollman et al. (2020), they are not closely related in our phylogenetic analyses, based on both ITS and chloroplast data.

Didymodon manhanensis is distinguished from all congeners by the following combination of diagnostic features: leaves incurved and slightly twisted when dry, spreading when moist, narrowly lanceolate from an ovate base; subulate and fragile leaf apices; distally bistratose leaf margins that are recurved in proximal 2/3–3/4; costal guide cells in 2–3 layers and without ventral stereids, smooth laminal cells and red KOH laminal colour reaction. This combination of characters suggests the placement of *D. manhanensis* in the sect. *Didymodon* (Zander 1978, 1993, 1998). Following the recent revolutionary work on the genus *Didymodon s. lat.* by Zander (2013, 2019), morphologically, it belongs in the amended genus *Didymodon s. str.* Its systematic position in *Didymodon s. str.* was also confirmed by our phylogenetic analyses, based on both ITS and chloroplast data.

Chloroplast data support that *D. manhanensis* is closely related to *D. cordatus* and sister to both *D. daqingii* and *D. anserinocapitatus*. However, *D. manhanensis* differs morphologically from *D. cordatus* by the costa with guide cells in 2–3 layers and without ventral stereids and smooth laminal cells. It differs from *D. daqingii* by the leaves that are narrowly lanceolate from an ovate base, smooth laminal cells and red KOH laminal colour reaction; it differs from *D. anserinocapitatus* by the distally bistratose leaf margins and lack of swollen and deciduous leaf apex (Zander 2007). In the ITS analyses, there is successive branching of clades, including *D. obtusus* J. Kou, X.-M. Shao & C. Feng, *D. manhanensis*, *D. epapillatus* J. Kou, X.-M. Shao & C. Feng, *D. mongolicus* D.-P. Zhao & T.-R. Zhang, *D. validus* Limpr., *Vinealobryum guangdongensis* C. Feng & J. Kou and *D. wisselii* (Dixon) D.H. Norris & T.J. Kop. Amongst these species, *D. manhanensis* is most similar to *D. obtusus*, a species that was recently described from Tibet in China (Kou et al. 2018), but the former can be distinguished from the latter by its narrowly lanceolate leaves from an ovate base and spreading when moist, subulate and somewhat fragile leaf apex and unistratose distal lamina.

There are three species distributed in China that have excurrent costa and smooth laminal cells may be confused with the new species. *Didymodon ditrichoides* (Broth.) X.-J. Li & S. He, a species known from North American, Asia (China) and the Atlantic Islands (Iceland) (Li et al. 2001; Zander 2007), differs from the new species by the unistratose leaf margins, costa with 1–2 layers of guide cells and with 0–1 layer of ventral stereids and yellowish KOH laminal colour reaction (Zander 2007).

Didymodon validus Limpr. can be separated from *D. manhanensis* by the twisted and incurved leaves when dry, unistratose leaf margins, costa with 1 layer of guide cells and with 1–3 layers of ventral stereids and yellowish-green KOH laminal colour reaction (Shuayib et al. 2017).

The lanceolate to long-lanceolate leaves with a widely ovate base, distally bistratose leaf margins, excurrent costa and epapillose laminal cells are likewise found in *Didymodon ochyrrarum* J.A.Jiménez & M.J.Cano, a species described from tropical South America (Jiménez and Cano 2019), which may be confused with the new species. However, *D. ochyrrarum* can be separated from *D. manhanensis* by its plane leaf margins, marginal basal cells running up the margin forming a distinctly differentiated area of transversely thick-walled cells and yellowish KOH laminal colour reaction.

Taxonomic treatment

Didymodon manhanensis C. Feng & J. Kou, sp. nov.

Figs 1–2

Chinese name: 蛮汉山对齿藓

Type. CHINA. Inner Mongolia: Ulanqab City, Manhan Mountain, 40°39'19.2931"N, 112°19'36.3792"E, on soil under the grass, elevation 1417 m, 20 June 2016, *Chao Feng 2016060162* (holotype: NMAC!; isotype: MO!).

Diagnosis. It is distinguished from all congeners by the following combination of diagnostic features: leaves incurved and slightly twisted when dry, spreading when moist, narrowly lanceolate from an ovate base; subulate and fragile leaf apices; distally bistratose leaf margins that are recurved in proximal 2/3–3/4; costal guide cells in 2–3 layers and without ventral stereids, smooth laminal cells and red KOH laminal colour reaction.

Description. Plants medium, growing in turfs, green-blackish distally, brown-blackish proximally. Stems very seldom branched, 0.8–1.6 cm in length, not papillose, transverse section rounded to rounded-pentagonal, central strand developed, sclerodermis present, hyalodermis absent; axillary hairs filiform, of 4–8 hyaline cells, the basal cell brown. Leaves crowded on stem, incurved and slightly twisted when dry, spreading when moist, narrowly lanceolate from an ovate base, constricted just above the base, 1.3–2.3 × 0.43–0.55 mm, distal lamina narrowly channelled ventrally; margins plane distally, recurved in proximal 2/3–3/4 of leaf, entire, distal margins bistratose; apex subulate, somewhat fragile; leaf base ovate, not sheathing, not decurrent; costa stout, tapering distally, 57.5–75 µm wide at base, excurrent as a long, thick subula, not spurred, ventral cells of costa in upper middle part of leaf quadrate or subquadrate, smooth, 4 rows of cells across costa ventrally at mid-leaf, dorsal cells of costa in upper middle part of leaf quadrate or subquadrate, smooth, transverse section semi-circular to nearly rounded, epidermis present adaxially and abaxially, not or weakly bulging, ventral stereids absent, guide cells 10–16 in 2–3 layers, 2–4 layers of dorsal stereids, reniform or crescent-shaped, without hydroids; upper laminal cells quadrate

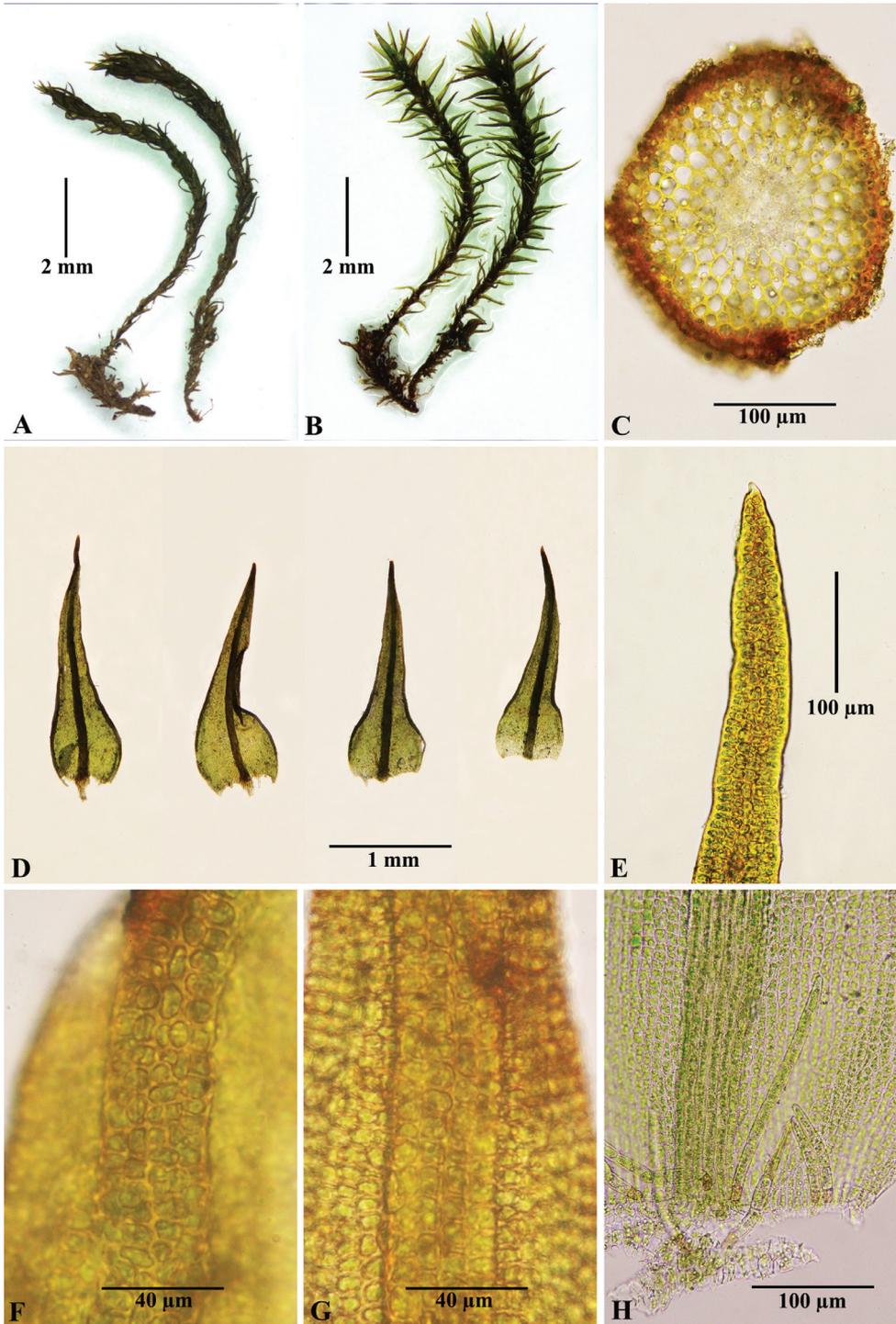


Figure 1. *Didymodon manhanensis* **A** dry plants **B** moist plants **C** cross-section of stem **D** leaves **E** leaf apex **F** upper part of costa (dorsal) **G** upper part of costa (ventral) **H** axillary hairs. Photographed on 21 November 2021 by Chao Feng from the holotype (NMAC!).

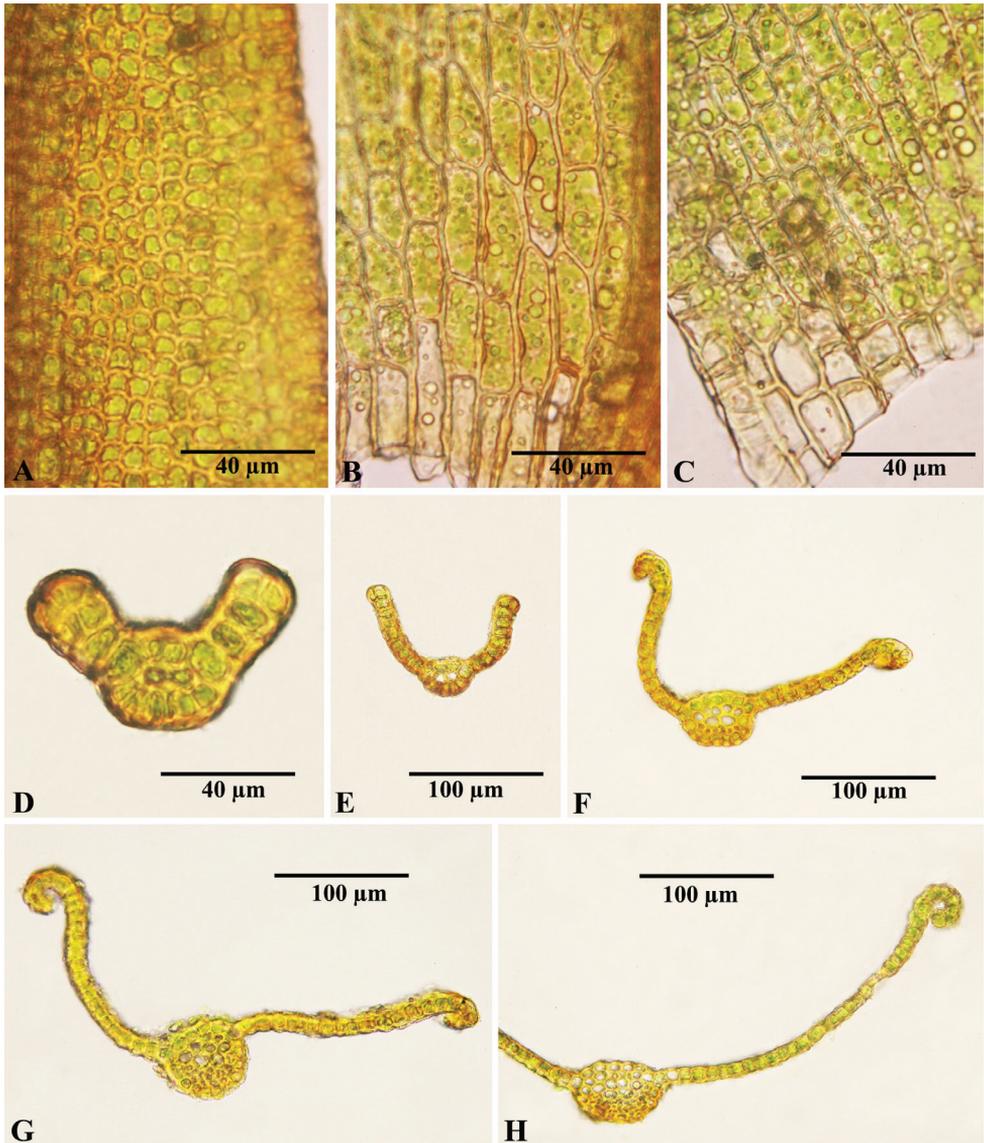


Figure 2. *Didymodon manhanensis* **A** median leaf cells **B** basal juxtacostal cells **C** basal marginal cells; **D–H** cross-sections of leaves, sequentially from apex to base. Photographed on 21 November 2021 by Chao Feng from the holotype (NMAC!).

to rhombic, usually with angular lumens, $7.5\text{--}10 \times 5\text{--}10 \mu\text{m}$, smooth, slightly thick-walled, weakly convex on both surfaces, distal lamina unistratose, basal cells weakly differentiated juxtacostally, rectangular, $12.5\text{--}37.5 \times 5\text{--}7.5 \mu\text{m}$, thin-walled, smooth; basal marginal cells subquadrate or quadrate, $5\text{--}8.75 \times 6.25\text{--}7.5 \mu\text{m}$, with weakly-thickened walls, smooth. Gemmae absent. Dioicous. Sporophytes unknown. KOH laminal colour reaction red.

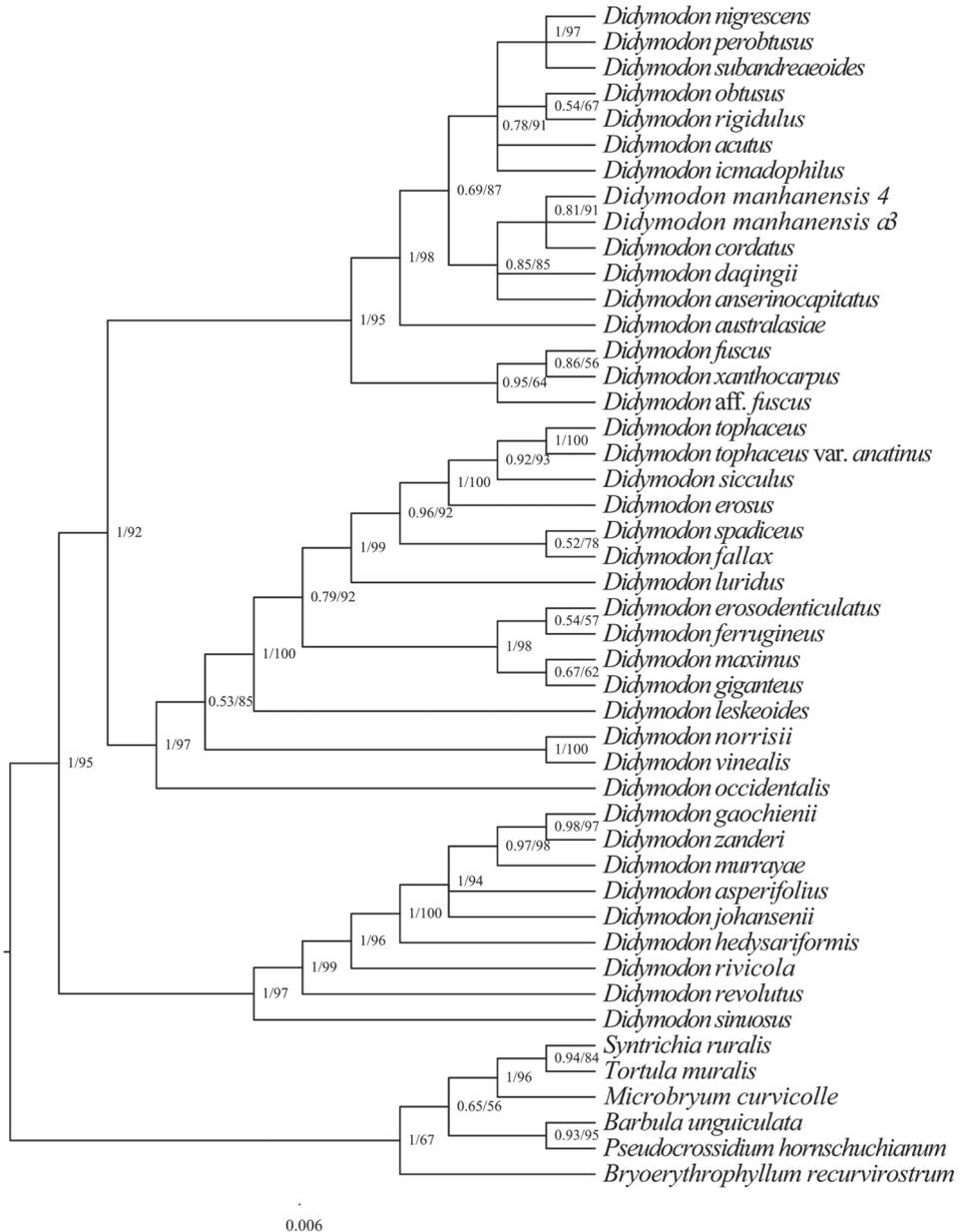


Figure 3. Phylogenetic relationships (50% majority consensus tree) from the Bayesian Inference of the concatenated *rps4* and *trnM-trnV* datasets. Numbers above branches indicate posterior probability from the BI analysis, followed by bootstrap values for the ML analysis.

Additional specimens examined. China INNER MONGOLIA: Ulanqab City, Manhan Mountain, on soil under the grass, 20 June 2016, Chao Feng 2016060176 (NMAC).

Etymology. The specific epithet refers to Manhan Mountain, the type locality.

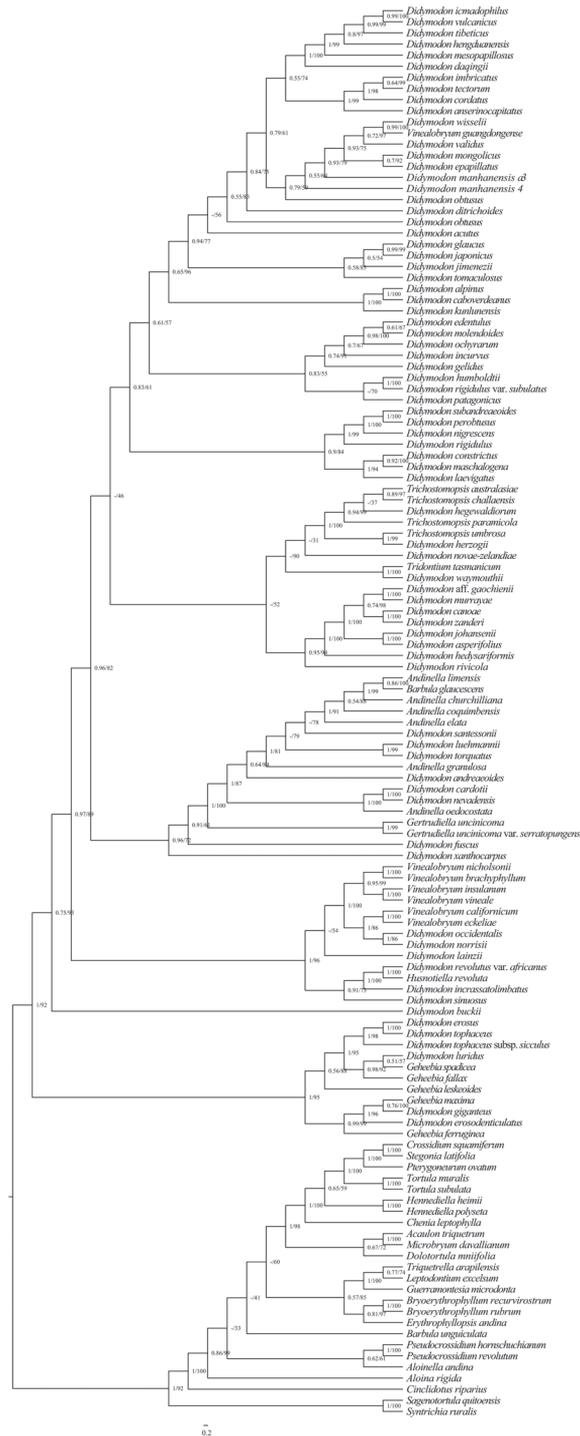


Figure 4. Phylogenetic relationships (50% majority consensus tree) from the Bayesian Inference on the ITS dataset. Numbers above branches indicate posterior probability from the BI analysis, followed by bootstrap values for the ML analysis.

Habitat and distribution. Manhan Mountain is situated in Liangcheng County in the southern section of the Yinshan Mountains in the middle of Inner Mongolia, with an average altitude of approximately 1500 m (Huang et al. 2014). Its soil types are mainly leaching grey, cinnamonic soil (Lyu et al. 2012). The vegetation on Manhan Mountain is typical forest shrub vegetation, including natural forest that consists of *Betula platyphylla* Sukaczew and *Populus davidiana* Dode, plantation that consists of *Larix principis-rupprechtii* Mayr and *Pinus sylvestris* var. *mongolica* Litv., natural shrubs that consists of *Ostryopsis davidiana* Decne., *Spiraea salicifolia* L. and *Rosa davurica* Pall. and the herbaceous plants including *Stipa bungeana* Trin., *Cleistogenes squarrosa* (Trin.) Keng, *Lespedeza bicolor* Turcz., *Carex* spp. and *Leymus chinensis* (Trin.) Tzvelev (Zhang et al. 2017; Li et al. 2021). *Didymodon manhanensis* is currently known only from the type locality at the foot of the Manhan Mountain, north-western Liangcheng County, Inner Mongolia, China, growing on soil under the grass.

Key to species morphologically similar to *D. manhanensis*

- 1 Leaf apices apically swollen as a propagulum..... *D. anserinocapitatus*
- Leaf apices not swollen, usually evenly narrowing 2
- 2 Cells on the upper ventral surface of the costa elongate..... *D. wisselii*
- Cells on the upper ventral surface of the costa quadrate 3
- 3 Laminal cells smooth 4
- Laminal cells papillose 10
- 4 Costa with 2–3 layers of guide cells and without ventral stereids..... 5
- Costa with 1 layer of guide cells and with ventral stereids 6
- 5 Leaves patent to spreading when moist, leaf lamina bistratose..... *D. obtusus*
- Leaves spreading when moist, leaf lamina unistratose..... *D. manhanensis*
- 6 Costa percurrent or ending before the apex..... 7
- Costa long-excurrent..... 8
- 7 Leaf margins bistratose near apex *D. epapillatus*
- Leaf margins unistratose *D. mongolicus*
- 8 Plants flagellate, leaves linear-lanceolate *D. ditrichoides*
- Plants thickly leaved, leaves short-lanceolate to long-lanceolate..... 9
- 9 Leaves appressed when dry..... *D. acutus*
- Leaves twisted or incurved when dry..... *D. validus*
- 10 Leaf margins plane..... *D. tibeticus*
- Leaf margins recurved..... 11
- 11 Costa without ventral stereids 12
- Costa with ventral stereids 13
- 12 Costa excurrent..... *D. daqingii*
- Costa ending below apex *D. imbricatus*
- 13 Marginal basal cells forming a distinctly differentiated area of smooth and transversely thick-walled cells..... *D. hengduanensis*
- Marginal basal cells not forming a distinctly differentiated area..... 14

- 14 Distal laminal cell superficial walls thicker than the internal walls.....*D. mesopapillosus*
 15
- Distal laminal cell superficial walls of same thickness as the internal walls.....
 15
- 15 Laminal cells with low papillae over the transverse walls, which reach the two
 adjacent cells..... 16
- Laminal cells with papillae situated over the lumina..... 17
- 16 Leaves spreading when moist*D. guangdongensis*
 16
- Leaves erect to patent when moist.....*D. vulcanicus*
 16
- 17 Leaf margins recurved in proximal 1/4–3/4*D. icmadophilus*
 17
- Leaf margins strongly recurved or revolute to near apex 18
- 18 Leaf base squared in shape, costa slender.....*D. tectorum*
 18
- Leaf base usually ovate in shape, costa stout.....*D. cordatus*
 18

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Fordiophyton tereticaule (Melastomataceae), a new species from China

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Abstract

A new species, *Fordiophyton tereticaule*, from China, is described and illustrated here based on morphological and molecular evidence. It is morphologically similar to *F. faberi* in having erect stems, slightly oblique and membranous leaf blades, broadly ovate to suborbicular bracts, and oblong petals, but differs by the terete stems, densely puberulous petioles, and elliptic leaf blades. Our phylogenetic analyses based on plastid genome and nrITS data indicate that this new species is clustered with four *Fordiophyton* species of Yunnan but placed far apart from *F. faberi*. An updated key to the genus is also provided.

Keywords

phylogeny, Sonerileae, taxonomy, Yunnan

Introduction

Fordiophyton Stapf, a genus belonging to the tribe Sonerileae of the family Melastomataceae, is endemic to China and Vietnam with 15 species currently known (Chen 1984; Chen and Renner 2007; Ning and Liu 2010; Zeng et al. 2016a, b; Dai et al. 2019; Dai et al. 2020). All species occur in South China except *F. phamhoangii* (V.T.Pham, C.T.Vu & Ranil) T.V.Do & Ying Liu which is endemic to Vietnam. *Fordiophyton faberi* Stapf was designated as the type of *Fordiophyton* (Deng and

Wu 2004). This genus is characterized as usually having raphides, 4-merous flowers and eight distinctly dimorphic and unequal stamens without ventral tubercles or a dorsal spur at the connective base (Deng and Wu 2004; Chen and Renner 2007; Zeng et al. 2016a). Recent phylogenetic studies have shown that *Fordiophyton* is close to *Blastus* Lour. and *Bredia* Blume (Zeng et al. 2016a; Zhou et al. 2019a, b).

During a recent survey in Malipo County, Yunnan Province, China in November 2019, we encountered an interesting *Fordiophyton* species with terete stems. At first glance, it looked like another two species also occurring in Yunnan, viz. *F. faberi* Stapf or *F. strictum* Diels because of its erect stems and membranous leaf blades, but those two species have very different quadrangular stems.

After careful examination of specimens of *Fordiophyton* species from China and Vietnam, and referring to the relevant references (Chen 1984; Pham 2000; Chen and Renner 2007; Ning and Liu 2010; Zeng et al. 2016a, b; Dai et al. 2019; Dai et al. 2020), we were unable to match this unknown species with any previously recorded species. We thus describe it here as a new species. To evaluate its phylogenetic position and relationships with congeneric species, phylogenetic analysis based on plastid genome and nrITS data was performed.

Materials and methods

A total of 43 species from 13 genera (including 14 species of *Fordiophyton*) in the Sonerileae were sampled (Suppl. material 1: Table S1). *Sarcopyramis napalensis* Wall. and *Sonerila cantonensis* Stapf were selected as outgroup taxa according to Zhou et al. (2019a). All the plastid genome and nrITS sequences were downloaded from Genbank except that of this unknown species.

Silica-gel dried leaves of this unknown species were sent to Novogene (Tianjin, China) to extract total genomic DNA for library (350 bp) preparation for genome skimming sequencing. Paired-end (150 bp) sequencing was conducted on Illumina NovaSeq 6000 (San Diego, CA, USA), generating ca. 20 Gb raw data. After quality control of the raw data by fastp v.0.23 (Chen et al. 2018), ca. 6 Gb paired reads were extracted for the plastid and rDNA assembly by GetOrganelle v.1.7 (Jin et al. 2020), and the plastid genome (MK994846) of *F. faberi* and the rDNA (KM117261) of *Wisteria floribunda* (Willd.) DC. were used as the reference. Plastid Genome Annotator (Qu et al. 2019) and Geneious Prime 2019 (<www.geneious.com>) were used for the annotation of the plastid genome. The nrITS sequence of this sample was extracted from the rDNA by Geneious.

All plastid genome sequences were aligned by MAFFT v.7.4 (FFT-NS-i × 1000 strategy) after removing one inverted repeat region of each sample (Katoh and Standley 2013). The nrITS data were aligned in MEGA v.7 using MUSCLE (Edgar 2004; Kumar et al. 2016). Maximum likelihood analyses were conducted by IQTREE v.1.6 using SH-aLRT test and ultrafast bootstrap (UFBoot) feature (–alrt 1000 –bb 1000) on CentOS v.7.6 (Nguyen et al. 2015; Hoang et al. 2018).

Results of phylogenetic analyses

The aligned plastid genome matrix contained 140 425 bp, of which 13 003 bp (9.26%) are variable and 3 790 bp (2.70%) are parsimony informative. The aligned nrITS matrix contained 724 bp, of which 324 bp (44.75%) are variable and 216 bp (29.83%) are parsimony informative. The best-fit model (TVM+F+R3) for plastid genome matrix and best-fit model (GTR+F+I+G4) for nrITS matrix were automatically chosen by IQTREE according to Bayesian Information Criterion. The phylogenetic analysis based on the plastid genome (Fig. 1) indicated that *Fordiophyton* is diphyletic and clustered with *Blastus*, *Bredia* and two species of *Phyllagathis* with weak support (SH-aLRT 76%, UFBoot 49%). Most species of *Fordiophyton* formed a well-resolved clade (Clade A), which includes the type of the genus, while only one species, *F. breviscapum* (Clade B), was placed sister to *Blastus*. Clade A can be further divided into two subclades (A1 and A2) with strong support (SH-aLRT 100%, UFBoot 100%). The unknown species is sister to *F. strictum* and three other *Fordiophyton* species in Subclade A2 with strong support (SH-aLRT 100%, UFBoot 100%). The phylogenetic analysis based on nrITS included all *Fordiophyton* species except *F. damingshanense* S.Y.Liu & X.Q.Ning and *F. degeneratum* (C.Chen) Y.F.Deng & T.L.Wu which supported that *Fordiophyton* is not monophyletic and the unknown species is clustered with four species of Yunnan and one species of Vietnam (Suppl. material 2: Fig. S1).

Discussion

The phylogenetic analyses confirmed that *Fordiophyton* is polyphyletic and consists of two clades (Zhou et al. 2019a, b; Dai et al. 2020). In Clade A, the unknown species was clustered with four other sympatric *Fordiophyton* species from Yunnan in Subclade A2. The forked and curved anther base of the longer stamens seems to be a synapomorphy of this subclade. In contrast, the species in Subclade A1 usually have longer stamens with unforked anther bases and are distributed in Guangdong, with the exception of the widespread *F. faberi* (occurring in almost every province of southern China) which, unusually, has longer stamens with forked anther bases like species in Subclade A2.

Morphologically, the unknown species is more similar to *F. faberi* than any other *Fordiophyton* species in both vegetative and reproductive characters, such as the erect stems, long petioles, slightly oblique and membranous leaf blades, broadly ovate to suborbicular bracts, and non-auriculate base of the calyx lobes. But the phylogenetic analyses revealed the unexpected placement of the unknown species in a different subclade from *F. faberi* (as shown in Fig. 1). A detailed comparison of this unknown species, *F. faberi*, and *F. strictum* (as a representative of species in Subclade A2) is provided in Table 1.

In Clade B, *F. breviscapum* is sister to *Blastus* with strong support (SH-aLRT 100%, UFBoot 100%) but far apart from two species of *Kerriothyrus* C.Hansen Clade (Fig. 1). However, the phylogenetic analysis based on nrITS indicated that it is sister to the *Kerriothyrus* Clade with weak support (Dai et al. 2020; Suppl. material 2: Fig. S1). Further study is needed to resolve the generic assignment of this species.

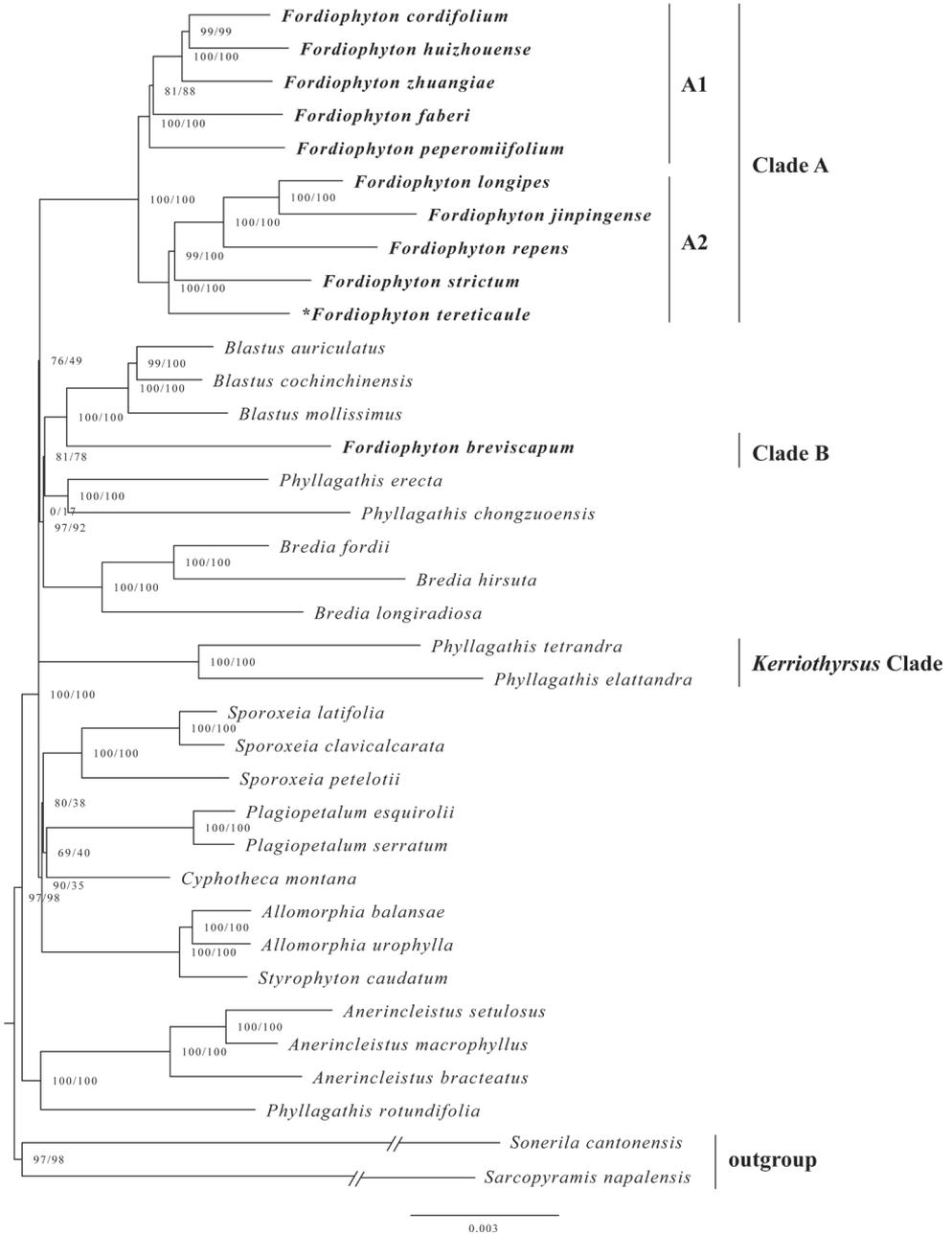


Figure 1. Phylogenetic relationships of Sonerileae based on plastid genome. The numbers near the nodes are the values of the SH-aLRT test (left) and ultrafast bootstrap (right). The unknown species is indicated by an asterisk.

Table 1. Morphological comparison of key features among *Fordiophyton tereticaule*, *F. faberi* and *F. strictum*.

Characters	<i>F. tereticaule</i>	<i>F. faberi</i>	<i>F. strictum</i>
Stem	terete, with dense glandular trichomes and puberulous when young, becoming glabrescent	quadrangular, glabrous	quadrangular, glabrous, usually pilose or setose at nodes
Petioles	1–7 cm long, densely puberulous	1.5–7 cm long, glabrous or shortly setose near leaf blade	usually less than 0.8 cm long, glabrous
Leaf blades	elliptic, slightly oblique	broadly lanceolate, oblong, ovate, or rarely lanceolate, slightly oblique	broadly lanceolate, oblique
Bracts	broadly ovate to suborbicular	broadly ovate to suborbicular	cordate
Calyx lobes	triangular to ovate-triangular without auriculate base	triangular to lanceolate-triangular without auriculate base	broadly ovate-triangular with auriculate base
Longer stamens	anther base lengthened into a forked and curved spur	anther base lengthened into a forked spur	anther base lengthened into a forked and curved spur

Taxonomic treatment

***Fordiophyton tereticaule* S.Jin Zeng & N.H.Xia, sp. nov.**

urn:lsid:ipni.org:names:77298656-1

Figs 2, 3

Verbatim name: 圆茎异药花

Type. CHINA. Yunnan: Wenshan Zhuang and Miao Autonomous Prefecture, Malipo County, Laojunshan Provincial Nature Reserve, elev. 1517 m, 18 September 2020 (fl.), Si-Jin Zeng 4932 (holotype: IBSC!; isotypes: CANT!, KUN!, PE!).

Diagnosis. Similar to *F. faberi* in having erect stems, membranous leaf blades, and oblong petals, but differs by the terete (vs. quadrangular) stems, densely puberulous (vs. green and glabrous or shortly setose near leaf blade base) petioles, and elliptic (vs. broadly lanceolate, oblong, ovate, or rarely lanceolate) leaf blades.

Description. Herbs, 30–100 cm tall. Stems yellowish-green when young, turning red, terete, with dense glandular trichomes and puberulous when young, becoming glabrescent, inflated at the nodes. Leaves in unequal pairs in size; petiole reddish brown, terete, 1–7 cm long, densely puberulous; leaf blade elliptic, slightly oblique, 8–16 × 4–9 cm, membranous, base cordate, apex acuminate to caudate-acuminate, margin inconspicuously serrulate with each tooth bearing a terminal seta, adaxial surface yellowish-green, sparsely puberulous, abaxial surface yellowish-green, densely puberulous on veins; secondary veins 2–3 on each side of midvein, conspicuous; tertiary veins numerous, parallel, connecting with secondary veins. Inflorescences terminal, an umbel-like cyme, sometimes a thyrses, with 6–15 flowers; peduncle usually dull red, terete, 1.3–3.5 cm long, with dense red glandular trichomes; bracts yellowish-green to dull red, imbricate at base of pedicel, broadly ovate to suborbicular, with sparse red glandular trichomes, caducous. Pedicel dull red, terete, 3–5 mm long, with dense red glandular trichomes. Hypanthium scarlet, funnel-form, 6–8 × 3–4

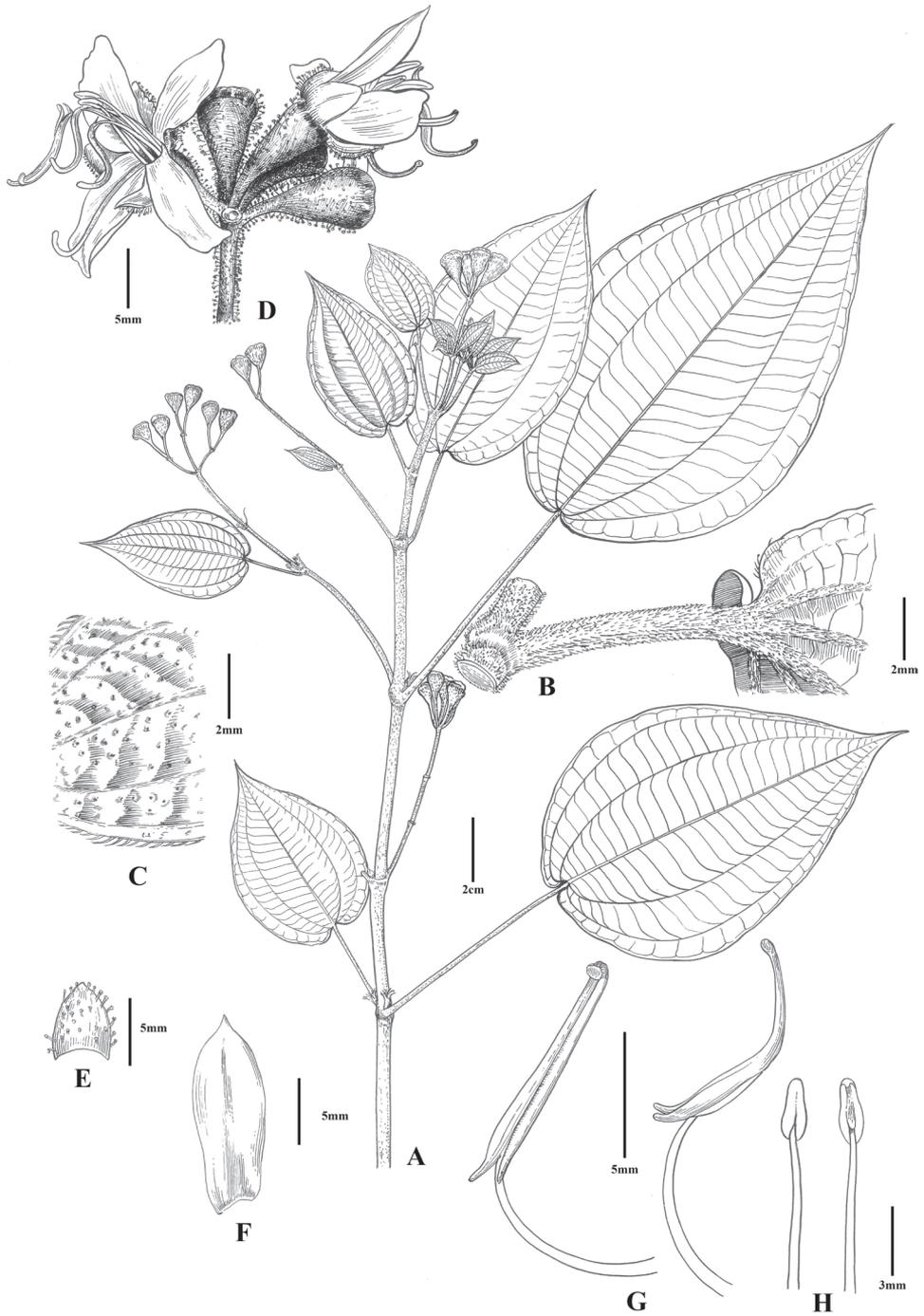


Figure 2. *Fordiophyton tereticaule* S.Jin Zeng & N.H.Xia **A** fruiting branch **B** part of stem with one petiole **C** part of leaf blade, adaxial view **D** cymose inflorescence with opening flowers **E** calyx lobe **F** petal **G** longer stamen, front view (left) and side view (right) **H** shorter stamen, front view (left) and back view (right). Drawn by Ding-Han Cui.

mm, with dense red glandular trichomes. Calyx lobes dull red to scarlet, triangular to ovate-triangular, ca. $5 \times 2\text{--}4$ mm, with sparse red glandular trichomes, apex obtuse to acute, base not auriculate. Petals white to pinkish, oblong, ca. $1.1 \times 0.5\text{--}0.6$ cm, apex oblique with 1 glandular trichome at tip. Stamens 8, 4 longer antisepalous ones and 4 shorter antipetalous ones, arranged in 2 whorls. Antisepalous (longer) stamens 2.0–2.5 cm long; filaments 0.9–1.4 cm; anthers dull red, linear, ca. 1.1 cm long, curved, base lengthened into a forked, curved spur, connective base inflated. Antipetalous (shorter) stamens 0.9–1.2 cm long; filaments 0.6–0.9 cm; anthers yellow, ovoid, ca. 0.3 cm long, straight, connective base slightly inflated. Style 1.7–2.0 cm long, glabrous or with sparse glandular trichomes at base. Ovary half-inferior, ovoid, apex with a membranous crown. Capsule funnel-form, ca. 8×4 mm; placentation axillary, placentas shortly stalked; seeds more than 100, cuneate, less than 2 mm long.

Phenology. Flowering in September–December, fruiting in October–next January.

Distribution and habitat. *Fordiophyton tereticaule* is only known from Malipo County, Yunnan, China. It grows in broad-leaved evergreen forests at elevations of 1260–1540 m.

Etymology. The specific epithet refers to the terete stem.

Additional specimen examined. CHINA. Yunnan: the same locality as above, 1516 m, 28 November 2019, Si-Jin Zeng 898 (paratypes: IBSC!).

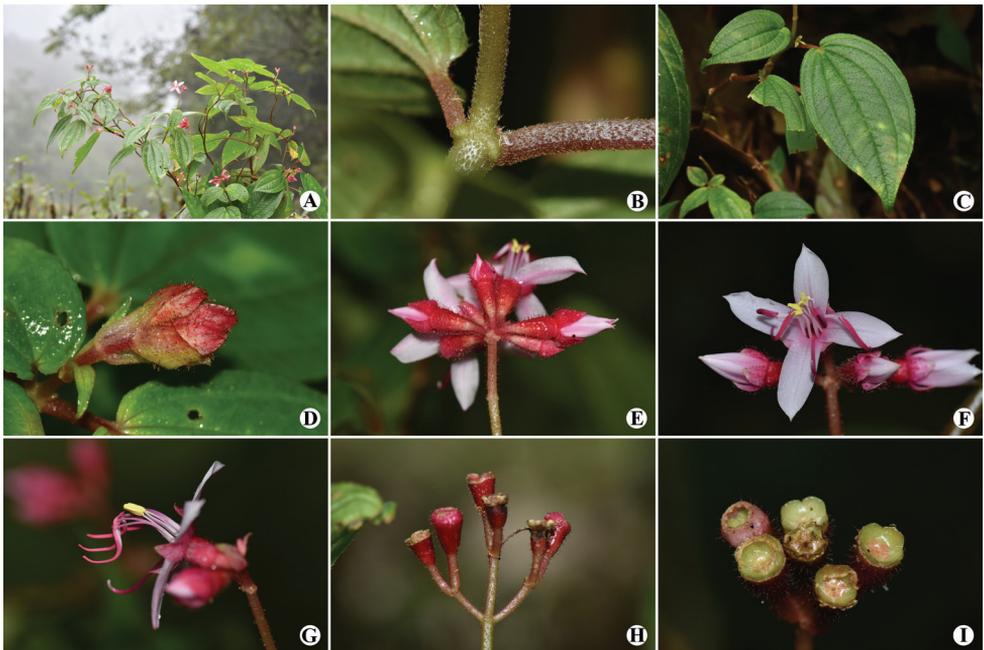


Figure 3. *Fordiophyton tereticaule* S.Jin Zeng & N.H.Xia **A** flowering plants **B** part of stem with a pair of petioles **C** a pair of leaves **D** cymose inflorescence with flower buds **E** cymose inflorescence, oblique view **F** an opening flower, front view **G** an opening flower, side view **H** infructescence, side view **I** young fruits, top view.

Key to the species of *Fordiophyton*

- 1 Internodes of stems indistinct, less than 2 mm 2
- Internodes of stems distinct, more than 5 mm 6
- 2 Stem glabrous; petioles winged..... 3
- Stem densely hirsute or setose; petioles unwinged 4
- 3 Petioles 8–18 cm long; leaf blades ovate or ovate-elliptic, 9–13 × 9–12 cm
..... *F. chenii*
- Petioles 2–4 cm long; leaf blades elliptic, 4–9 × 2–4 cm..... *F. zhuangiae*
- 4 Leaf blades with minute brown glands on both surfaces.....*F. phamhoangii*
- Leaf blades without minute brown glands on both surfaces..... 5
- 5 Adaxial surface of leaf blades glabrous; calyx lobes lanceolate, ca. 6 mm long.....
..... *F. huizhouense*
- Adaxial surface of leaf blades tuberculate; calyx lobes triangular, 1–2 mm long ...
..... *F. peperomiifolium*
- 6 Leaves in a sub-basal rosette 7
- Leaves cauline, not in a rosette 9
- 7 Petioles densely villous *F. jinpingense*
- Petioles glabrous or sparsely glandular-setose..... 8
- 8 Stem winged, glabrous at nodes; petioles glabrous; secondary veins 4 or 5 on each
side of midvein..... *F. cordifolium*
- Stem unwinged, densely spiny at nodes; petioles sparsely glandular-setose; sec-
ondary veins 3 on each side of midvein *F. brevicaule*
- 9 Stem creeping *F. repens*
- Stem erect or at least erect in the upper part..... 10
- 10 Leaves of a pair highly unequal (smaller one less than half of larger one's size);
petioles often less than 1 cm long; base of calyx lobes auriculate.....*F. strictum*
- Leaves of a pair not unequal or only slightly unequal; petioles often more than 2
cm long; base of calyx lobes not auriculate 11
- 11 Plants less than 25 cm tall; anthers of antipetalous stamens greatly reduced or
sterile 12
- Plants more than 30 cm tall; anthers of antipetalous stamens fertile, not greatly
reduced 13
- 12 Stem winged; secondary veins 1 on each side of midvein.....*F. breviscapum*
- Stem unwinged; secondary veins 3 or 4 on each side of midvein.... *F. degeneratum*
- 13 Stem terete; petioles densely puberulous..... *F. tereticaule*
- Stem quadrangular; petioles glabrous or shortly setose near leaf blade base..... 14
- 14 Abaxial surface of leaf blades furfuraceous; peduncle winged..... *F. longipes*
- Abaxial surface of leaf blades glabrous or minutely puberulous; peduncle un-
winged 15
- 15 Inflorescence an umbel-like cyme or a thyrse; anther base of longer stamens not
enlarged *F. faberi*
- Inflorescence a pleiochasium; anther base of longer stamens enlarged.....
.....*F. damingshanense*

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Supplementary material I

Table S1. Vouchers and Genbank accession numbers of the samples used in this study

Authors: Si-Jin Zeng, Yi-Hua Tong, Nian-He Xia

Data type: docx file

Explanation note: Dashes (–) indicate missing data, and asterisks (*) denote the sequence obtained in this study.

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Link: <https://doi.org/10.3897/phytokeys.197.82670.suppl1>

Supplementary material 2

Figure S1. Phylogenetic relationships of Sonerileae based on nrITS

Authors: Si-Jin Zeng, Yi-Hua Tong, Nian-He Xia

Data type: JPG file

Explanation note: The numbers near the nodes are the values of the SH-aLRT test (left) and ultrafast bootstrap (right). The unknown species is indicated by an asterisk.

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Link: <https://doi.org/10.3897/phytokeys.197.82670.suppl2>

Isotrema putalengense, a new species of Aristolochiaceae from northern Vietnam and two new combinations in *Isotrema*

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Abstract

Isotrema putalengense Luu, Q.B.Nguyen & H.C.Nguyen is described as a new species from northern Vietnam. It looks most morphologically like *I. wardianum* but is distinguishable by a combination of different leafy and floral characters. Morphological comparison between the new plant and closest species is provided. In addition, combinations of two recently described *Aristolochia* species are made, namely *Isotrema vuquangense* (T.V.Do) Luu, Q.B.Nguyen & H.C.Nguyen and *Isotrema yachangense* (B.G.Huang, Yan Liu & Y.S.Huang) Luu, Q.B.Nguyen & H.C.Nguyen.

Keywords

Aristolochia, *Isotrema vuquangense*, *Isotrema yachangense*, Pu Ta Leng Mountain, *Siphisia*

Introduction

Isotrema Raf. (Aristolochiaceae) was recently resurrected as a genus independent from *Aristolochia* L. (Zhu et al. 2019a). Species of *Isotrema* are, in fact, those of *Aristolochia* subgenus *Siphisia* (Duch.) O.C.Schmidt (Schmidt 1935) and differ from others of

Aristolochia by having strongly curved perianth, 3-lobed gynostemium, anthers paired on the outer surface of each gynostemium segment, and basipetally dehiscent capsule. This generic concept is followed in many later publications (Li et al. 2019; Zhou et al. 2019; Zhu et al. 2019b, c, d; Cai et al. 2020a; Wang et al. 2020a, b). Although several other authors still prefer assigning their newly described species under *Aristolochia* subgenus *Siphisia* (e.g., Cai et al. 2020b; Luo et al. 2020; Zhou et al. 2020; Do et al. 2021), of which *Isotrema* was accepted as one of the synonyms in the most recent nomenclatural review of *Aristolochia*-related taxa by Ohi-Toma and Murata (2016), the phylogenetic results by Zhu et al. (2019a) appear to be robust because of their extensive samples of Asian species and combination of molecular, chromosomal and morphological data. Therefore, *Isotrema* is followed in this paper.

To date, more than one hundred *Isotrema* species have been reported, including those named under *Aristolochia* (e.g., Liu and Deng 2009; Xu et al. 2011; Yao 2012; Huang et al. 2013; Wu et al. 2013; Do et al. 2014; Lu and Wang 2014; Nguyen et al. 2014; Ohi-Toma et al. 2014; Huang et al. 2015; Wu et al. 2015; Zhu et al. 2015; Do et al. 2016; Do et al. 2017; Do et al. 2018; Zhu et al. 2018; Zhou et al. 2019; Zhu et al. 2019a; Cai et al. 2020a, b; Do et al. 2021). Prior to this paper, 18 *Isotrema* species have been recorded for Vietnam (Lecomte 1909; Schmidt 1935; Pham-hoang 2000; Do et al. 2014; Do et al. 2015a, b; Do et al. 2016; Do et al. 2017; Do and Li 2018; Lai et al. 2019; Do et al. 2021).

During our botanical surveys in Pu Ta Leng Mountain, Lai Chau Province of northern Vietnam in 2020, we encountered a species that looks very much like *I. wardianum* (J.S.Ma) X.X.Zhu, S.Liao & J.S.Ma from China, India and Myanmar (Ma 1989; Zhu et al. 2019a; Wang et al. 2020b). After careful examination of the plant, we concluded it is a new species that is described here. Terminology follows Hou (1984) and Do et al. (2015a).

Taxonomy treatments

Isotrema putalengense Luu, Q.B.Nguyen & H.C.Nguyen, sp. nov.

urn:lsid:ipni.org:names:77298657-1

Fig. 1

Type. VIETNAM. Lai Chau Province, Tam Duong District, Pu Ta Leng Mountain, 22°27'17"N, 103°33'07"E, 2329 m elevation, 14 June 2020, *Nguyen Quoc Binh, Tran Duc Binh, Doan Hoang Son, Nguyen Hieu Cuong SH992* (holotype, VNMN!; isotypes, SGN!, VNMN!).

Diagnosis. The new species is most morphologically similar to *I. wardianum* in the shape of leaves and flowers but differs in having densely brown villous (vs. abaxially light brown villous) bracteoles, flowers on old woody stems (vs. in axils of leafy shoots), basally truncate perianth limb that is ovoid in front view and with purple apex (vs. basally obtuse, oblong in front view and with yellow apex), indistinct (vs. distinct) utricle from lower tube, U-shaped (vs. V-shaped) tube notch and internally black purple (vs. purple) tube.

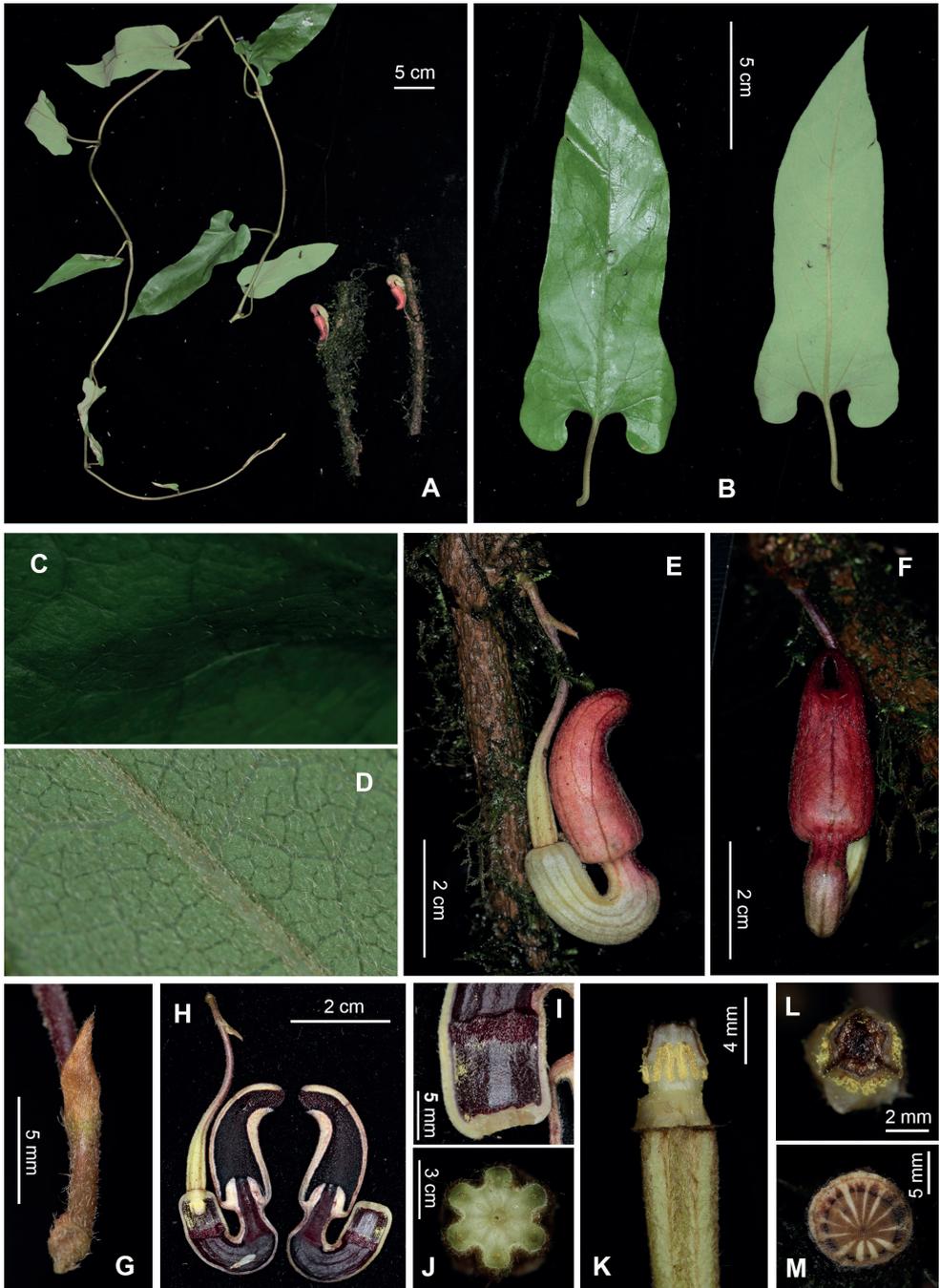


Figure 1. *Isotrema putalengense* Luu, Q.B.Nguyen & H.C.Nguyen **A** habit **B** leaf **C** leaf lamina, adaxial surface **D** leaf lamina, abaxial surface **E** flower, side view **F** flower, front view **G** bracteole **H** perianth, longitudinal dissection **I** utricle, inside **J** ovary, cross section **K** gynostemium, side view **L** stigma, view from above **M** stem, cross section. Photographs by Hieu Cuong Nguyen from *SH992* at the type locality.

Description. Liana perennial, woody. Stems terete, pubescent. Petioles 3–4.5 cm long, densely pubescent; laminas lanceolate to slightly pandurate, 15–20 × 4–6 cm, adaxially sparsely pubescent, abaxially pubescent, margin entire, base auriculate, apex acute; veins palmate, 1 pair from base, lateral veins 3–4-paired; venation slightly adaxially sunken, abaxially prominent. Flowers on old woody stems, solitary; pedicel 2.5–3 cm, densely brown villous; bracteole inserted on basal half of pedicel, triangular, 5–5.5 mm long, 4–5.5 mm wide at base, densely brown villous, persistent. Ovary yellowish, 1.8–2.1 cm, 0.3–0.4 cm in diameter, densely brown villous, 6-ridged. Perianth horseshoe-shaped (in lateral view), 4–4.5 cm high, yellowish to purple, outside densely yellowish to brown hirsute with parallel veins, inside dark purple. Utricle indistinct from the tube, cylindrical, 7–9 mm long, 7–8 mm in diameter, outside light yellow, inside pilose and dark purple. Tube 3.5–4.0 cm, horseshoe-shaped, folded upwards at its middle forming a U-shaped notch, inside glabrous; lower tube 1.7–1.9 cm high and 0.6–0.7 cm in diameter, basally light yellow, apically purple; upper tube 0.6–0.7 cm long and 0.5–0.6 cm in diameter, parallel to the utricle, slightly constricted at the middle, purple; limb cylindrical, ovoid in front view, curved forward, with truncate base, 2.5–2.7 cm long × 1.2–1.3 cm in diameter, inside dark red with dense dark-purple papillae, 3-lobed; lobes widely triangular, 0.5–1.3 mm high × 2–4 mm wide; throat ca. 3–4 mm high × 2 mm wide; annulus hemispherical, 0.5–0.6 cm high × 0.6–0.7 cm in diameter at base. Anthers 6, oblong, 2–2.2 mm long, adnate in 3 pairs to base of gynostemium. Gynostemium 3.5–4 mm long × 3.5–4 mm in diameter, stipitate; stipe ca. 0.5 mm; stigma connate, slightly 3-lobed; lobes (in older state) irregularly toothed. Fruits not seen.

Phenology. Flowering found in June, fruiting unknown.

Etymology. The specific epithet refers to the type locality, Pu Ta Leng Mountain which is part of the Hoang Lien Son Mountain Range and located about 30 km northwest of Vietnam's highest Mt. Fan Si Pan.

Common and vernacular names. Putaleng's pipevine (Vietnamese name: Phòng kỷ Pu Ta Leng).

Distribution and habitat. The new species is currently only known from Pu Ta Leng Mountain (with its highest peak at 3,049 m elevation), Tam Duong District, Lai Chau Province. It grows on humid fertile soils under a closed broadleaved evergreen forest unexplored botanically. There is no data available on the forest cover of the mountain. Our preliminary notes indicate that this forest is dominated by the Fagaceae, Lauraceae, Theaceae, Ericaceae and Magnoliaceae that are common families on the Hoang Lien Son Mountain Range, which is geographically considered part of the southern extension of the Himalayas and phytogeographically located in the Sikang-Yunnan Province (Averyanov et al. 2003).

Preliminary extinction risk assessment. The plant was recorded in a small population with few scattered individuals in a presently unprotected large forest. It may be found in adjacent similar forests on the Hoang Lien Son Mountain Range. Given this fact, it is provisionally assigned as Data Deficient until more information is recorded (IUCN 2012; IUCN Standards and Petitions Committee 2022).

Discussion. *Isotrema putalengense* is most morphologically similar to *I. wardianum* but they have a number of differences as expressed in the diagnosis. Besides, the new

species is also close to *I. utriforme* (S.M.Hwang) X.X.Zhu, S.Liao & J.S.Ma (Hwang 1981; Zhu et al. 2019a) in the shape of leaves and flowers but the latter has glabrous and longer (4–8 cm) petiole, yellow-green flowers borne in axils of leafy shoots, ovate-lanceolate bracteoles inserted above middle of peduncle, short upper tube (3–4 mm), convex annulus, saccate limb with ovate-deltate and erect lobes. The shape of flowers in the new species looks like that in *I. pseudoutriforme* (X.X.Zhu & J.S.Ma) X.X.Zhu, Jun Wang & J.S.Ma and *I. ovatifolium* (S.M.Hwang) X.X.Zhu, S.Liao & J.S.Ma (Hwang 1981; Zhu et al. 2019a, e) but *I. pseudoutriforme* has ovate to narrowly ovate leaves and plain light yellow flowers, uncurved limb forming obtuse angle with upper tuber and ring-like annulus and *I. ovatifolium* has ovate leaves and abaxially densely off-white villous, purple-red flowers in axils of leafy shoots. The key morphological differences between the new species and those closest species are presented in Table 1.

The leaves of the new species resemble those of *I. cucurbitoides* (C.F.Liang) X.X.Zhu, S.Liao & J.S.Ma (Liang 1975; Hwang et al. 2003; Zhu et al. 2019a) and *I. yangii* X.X.Zhu & J.S.Ma (Zhu et al. 2019e; Wang et al. 2020a) but these two species are readily different in a number of characters: *I. cucurbitoides* has leaves with

Table 1. Morphological differences between *Isotrema putalengense* and close species (based on Hwang 1981; Ma 1989; Hwang et al. 2003; Zhu et al. 2019e; Wang et al. 2020b).

Characters	<i>I. putalengense</i>	<i>I. ovatifolium</i>	<i>I. pseudoutriforme</i>	<i>I. utriforme</i>	<i>I. wardianum</i>
Petiole	densely pubescent, 3–4.5 cm long	villous, 3–5 cm long	densely pubescent, 2–5 cm long	glabrous, 4–8 cm long	densely villous, 3–5 cm long
Lamina	lanceolate to slightly pandurate, 15–20 × 4–6 cm, with auriculate base, adaxially sparsely pubescent, abaxially pubescent	ovate, 5–13 × 4–8 cm, with cordate base, abaxially villous, adaxially glabrescent (densely villous when young)	ovate to narrowly ovate, 10–22 × 7–13 cm, with cordate base, adaxially sparsely pubescent, abaxially densely pubescent	ovate-lanceolate, 10–17 × 3–4 cm, with auriculate base, adaxially glabrous	lanceolate, 12–16 × 3–4 cm, with auriculate base, adaxially subglabrous to glabrous
Pedicel	2.5–3 cm long	3–6 cm long	1.8–5 cm long	4–6 cm long	1–2.5 cm long
Bracteoles	triangular, inserted on basal half of pedicel	ovate, inserted on basal 1/2 of pedicel	ovate, inserted on basal half and/or distal half of pedicel	ovate-lanceolate, inserted above distal half of pedicel	ovate, inserted on basal half of pedicel
Flower position	on old woody stems	axillary	axillary, sometimes on stems	axillary	axillary
Perianth limb	cylindric, ovoid in front view, straightly extended from upper tube, purple, 2.5–2.7 cm long × 1.2–1.3 cm in diameter, abaxially densely yellowish to brown hirsute	subcylindric, straightly extended from upper tube, purple-red, 1.5–2.5 cm long × 1–1.5 cm in diameter, abaxially densely off-white villous	cylindric, forming obtuse angle with upper tuber, light yellow, 2–3 cm long × 1–1.7 cm in diameter, abaxially sparsely villous	ovoid, straightly extended from upper tube, yellow-green, 1–2 cm long × ca. 1 cm in widest diameter, abaxially sparsely pilose to glabrous	cylindric, oblong in front view, forming obtuse angle with upper tube, purple with yellow apex, ca. 2.5 cm long × 0.9 cm in diameter, abaxially densely yellow villous
Limb lobes	wide triangle	subrounded or nearly truncate	triangle or wide triangle	ovate-deltate	wide triangle
Perianth throat	ca. 3–4 mm wide	ca. 2.5 mm wide	ca. 6 mm wide	ca. 1 mm wide	ca. 2–3 mm wide
Utricle	indistinct from lower tube, 7–8 mm in diameter, light yellow	indistinct from lower tube, 3–5 mm in diameter, purple-red	indistinct from lower tube, ca. 7–9 mm in diameter, light yellow	indistinct from lower tube, 3–4 mm in diameter, yellow-green	distinct from lower tube, 5 mm in diameter, light yellow
Tube notch	U-shaped	V-shaped	U-shaped	V-shaped	V-shaped
Upper tube	6–7 mm long × 5–6 mm in diameter, purple	ca. 3–5 mm long × 3–4 mm in diameter, purple-red	3–4 mm long × 6–8 mm in diameter, light yellow	ca. 3–5 mm long × 5–6 mm in diameter, yellow-green	ca. 10 mm long × 6 mm in diameter, purple
Annulus	hemispherical	flat	ring-like, raised	convex	hemispherical
Stigma lobes	truncate to slightly obtuse, irregularly toothed	obtuse, entire	round, entire	obtuse, entire	obtuse, entire

7–10 pairs of lateral veins, brownish flowers in axils of leafy shoots, ovate bracteoles, geniculately curved tube, 20 mm long utricle and deeply lobed perianth limb straight extended from upper tube and with 5–7 mm long lanceolate-acuminate lobes while *I. yangii* has leaves with 6–15-pairs of lateral veins, yellowish-white perianth with distinct purple stripes, 25–35 mm long utricles, internally smooth and pinkish or ochre perianth limb that is deeply 3-lobed and straight extended from upper tube and 16–24 mm long limb lobes.

Notably, the notch at the bent perianth tube of *I. putalengense* is obviously U-shaped while it is quite properly V-shaped in the above compared species except *I. pseudoutriforme* where the U-shaped notch is much narrower than that in the new species. Our field observations provisionally indicate that the notch shape is stable in, and could be typical for, *Isotrema* species. This character is more representative on longitudinal dissection of the perianth tube. However, its value as a supplemental taxonomic character for species identification has not been paid attention to in former *Isotrema* studies and needs further examination.

New combinations for some species of *Isotrema*

As a result of their study, Zhu et al. (2019a) has already transferred almost all species of *Aristolochia* subgenus *Siphisia* to *Isotrema*. Another four combinations were made for later described species (Wang et al. 2020a). Following this generic concept, here we propose new combinations for the other taxa of the subgenus that were described recently.

***Isotrema vuquangense* (T.V.Do) Luu, Q.B.Nguyen & H.C.Nguyen, comb. nov.**

urn:lsid:ipni.org:names:77298658-1

≡ *Aristolochia vuquangensis* T.V.Do. Phytotaxa 500 (1): 41. 2021.

Type. VIETNAM. Ha Tinh Province: Vu Quang District, Vu Quang National Park, 1103 m elevation, 18°15.133'N, 105°25.657'E, 30 August 2020, *Do Van Truong* DVT379 (holotype VNMN; isotypes HN, VNMN).

***Isotrema yachangense* (B.G.Huang, Yan Liu & Y.S.Huang) Luu, Q.B.Nguyen & H.C.Nguyen, comb. nov.**

urn:lsid:ipni.org:names:77298659-1

≡ *Aristolochia yachangensis* B.G.Huang, Yan Liu & Y.S.Huang. PhytoKeys 153: 51. 2020.

Type. CHINA. Guangxi Zhuang Autonomous Region: Baise City, Leye County, Huaping Town, Zhongjing (Yachang Orchid National Nature Reserve), 24°49.367'N, 106°24.029'E, 1341 m elevation, 29 July 2019, *Z.C. Lu et al.* 20190729YC4141 (holotype: IBK; isotypes: IBK, GXMG).

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New Species of *Virola* (Myristicaceae) from South America

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Abstract

With about 70 species *Virola*, is the largest genus of Myristicaceae in the Neotropics, the genus ranked in the top ten genera of abundance across Amazonia. Ten new species are proposed in this striking genus, which are described based on morphology, and are illustrated. The new species were discovered thanks to herbarium specimens collected mainly in the 1980s and 1990s when field documentations were more active. The new species come from Colombia (*V. calimensis* **sp. nov.**, *V. cogolloi* **sp. nov.**, *V. excisa* **sp. nov.**, *V. tuckerae* **sp. nov.**), Ecuador (*V. alvaroperezii* **sp. nov.**, *V. bombuscaroensis* **sp. nov.**, *V. calimensis*, *V. excisa*, *V. yasuniana* **sp. nov.**), Peru (*V. aguarunana* **sp. nov.**, *V. cumala* **sp. nov.**, *V. excisa*, *V. parkeri* **sp. nov.**), and Brazil (*V. excisa*, *V. yasuniana*). Additionally, a lectotype is designated for *V. macrocarpa*, a name used to identify some specimens of the new species here described, and *V. kwatae* is reported for the first time for Brazil. We provide a comparison table between the new species and the species that is morphologically close to it, a preliminary list of species for the genus, and notes of how the new species were treated in floras, checklists, or collections that need more study and herbarium specimens.

Keywords

Brazil, Colombia, Ecuador, Herbarium, Magnoliales, Neotropics, nutmeg, Peru, Taxonomy

Introduction

Virola Aubl. (Myristicaceae) is an ecologically and economically important genus of trees in the nutmeg family, Myristicaceae within the order Magnoliales (APG IV 2016). It is the fourth largest genus in Myristicaceae, a pantropical family with 21 genera and nearly 500 species; only three Asian genera, *Horsfieldia* Willd., *Knema* Lour.,

and *Myristica* Gronov., are larger. *Virola* occurs across the wet Neotropics, where it is distributed from Mexico to southern Brazil and in the West Indies [i.e. *V. surinamensis* (Rol. ex Rottb.) Warb.], though it is notably absent from El Salvador (Smith and Wodehouse 1938; Rodrigues 1980; Acevedo-Rodríguez and Strong 2012; Santamaría-Aguilar et al. 2019). Across *Virola*'s ca. 70 species (including those described here), ca. 55 occur in South America (Fig. 1) and 15 in Central America, with just two widespread species [i.e., *V. elongata* (Benth.) Warb., and *V. sebifera* Aubl.] occurring in both (Table 1). The species richness of *Virola* is highest in Amazonia, where it is ranked in the top ten most abundant genera with 35 species (Cardoso et al. 2017). Like other genera that are most species-rich and abundant in Amazonian forests including *Protium* Burm. f. (Burseraceae) (Daly 2020; Daly et al. 2020), a smaller number of species are confined to montane forests, and an even smaller number of species occur in dry areas such as Brazilian (Rodrigues 1980). A few widespread species, including *V. elongata* and *V. sebifera*, can be found across different forest types (Aymard et al. 2020).

Virola is morphologically distinctive on account of its myristicaceous tree architecture model known as “Massart” (Hallé et al. 1978) and sometimes referred to as myristicaceous branching, red exudate, pubescence of dentritic or stellate trichomes on under surface (Aymard et al. 2020), and dehiscent fruit which splits to reveal a seed

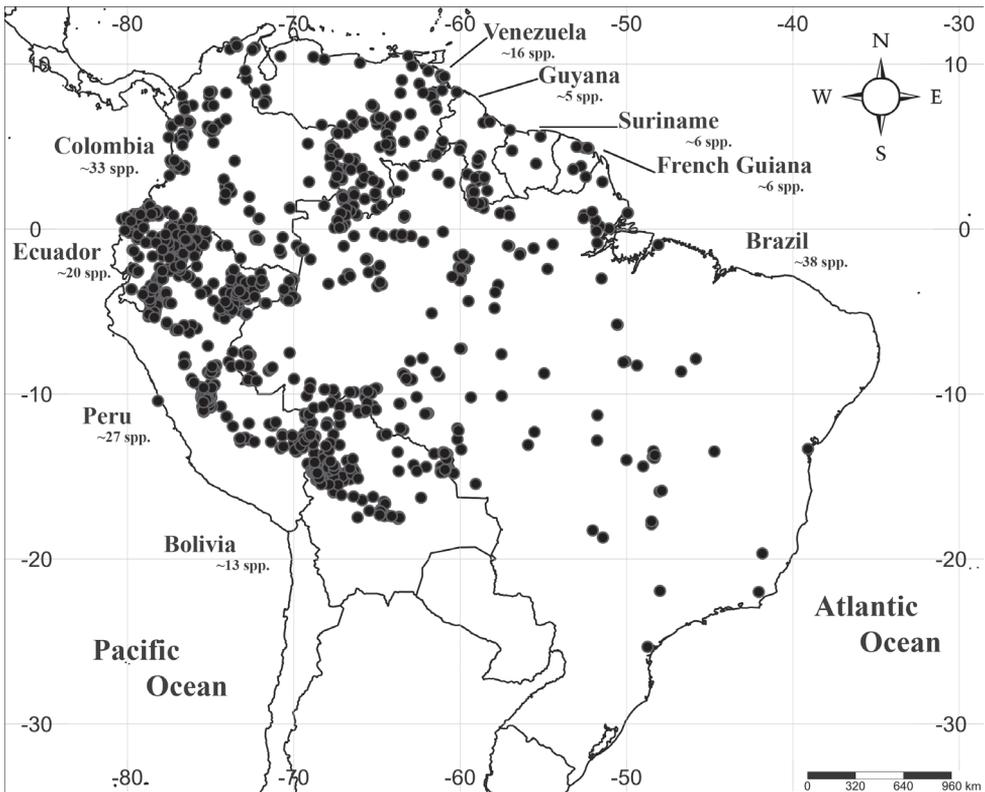


Figure 1. Geographic distribution of *Virola* in South America with number of species per country.

covered by a brightly colored, usually laciniate aril (Figs 2, 3). While *Virola* species tend to be medium to large forest trees, two species [i.e., *V. sessilis* (A. DC.) Warb., *V. subsessilis* (Benth.) Warb.] have an unusually small stature (about 1 to 3 m tall; Fig. 2B). The genus is further characterized by simple, alternate, distichous leaves borne on plagiotropic branches that occasionally have pellucid punctuation (Fig. 2E–G); paniculate staminate inflorescences; ebracteolate, unisexual flowers; a compound androecium with 3 (4–6) anthers fused into a column; and dehiscent fruits that open by two valves that are usually green [e.g., *V. elongata*, *V. obovata* Ducke, *V. sebifera*, and the new species described here] (Fig. 3A–D, F) or yellow [e.g., *V. fosteri* D. Santam., *V. laevigata* Standl., *V. multiflora* (Standl.) A. C. Sm., *V. nobilis* A. C. Sm.] when ripe (Fig. 3J–M), each with a single, arillate seed (Rodrigues 1980; de Wilde 1991; Gentry 1993; Kühn and Kubitzki 1993) (Fig. 3). Among Neotropical Myristicaceae, *Virola* can be vegetatively identified by the combination of its characteristic tree architecture, colored exudate in cut bark or branches, stellate or dendritic trichomes that are often found on young branches, and petioles and leaf blades which display size variation within an individual (see Braga 1992).

Virola is important to indigenous and rural communities for its several ethnobotanical attributes. It can be used as medicine to treat malaria, asthma, rheumatism, tumors of the joints, intestinal worms, skin diseases, erysipelas, hemorrhoids, bucal ulcerations, leishmaniasis, and halitosis; while its wood is used both for construction and paper pulp manufacturing, (Rodrigues 1972, 1980; Lourerio et al. 1989; Plotkin and Schultes 1990; Milliken 1997; Rodrigues et al. 2001). Resin from several species, including *V. calophylla* (Spruce) Warb. and *V. calophylloidea* Markgr., are potent hallucinogens (Schultes 1954). These hallucinogens, commonly ingested as a snuff known as *yakee* and *yato* in Colombia and *paricá*, *kawabó*, *epena* or *nyakwana* in Brazil (Schultes 1969, 1978; Aymard et al. 2020), are central to spiritual ceremonies of various indigenous communities in South America. *Virola* is likely also the source of the powerful hallucinogenic snuff *hakudufha* made by the Yekwana tribe in the upper Orinoco River and other tribes (Schultes 1954). For the elaboration of these snuffs, only the resin is used, or they mix it with the ashes of the leaves of *Justicia pectoralis* Jacq. (Acanthaceae), or ashes of the outer bark of *Duguetia lepidota* (Miq.) Pulle (Annonaceae), *Elizabetha leiogyne* Ducke (Fabaceae), or *Eschweilera itayensis* R. Knuth (Lecythidaceae); the preparation of snuff varies among different indigenous communities (Schultes 1976; Schultes and Raffauf 1994; Milliken et al. 1999).

The genus has also been well-studied by botanists and ecologists as it is a tractable system for studying seed dispersal (e.g., Howe and Vande Kerckhove 1980; Howe 1981, 1993; Queenborough et al. 2007; Ratiarison and Forget 2013; Moreira et al. 2017).

The last complete taxonomic revision of *Virola* was published over 80 years ago by Smith and Wodehouse (1938). This treatment recognized 38 species [including *V. oleifera* (Schott) A. C. Smith, now placed in its own genus *Bicuiba* W. J. de Wilde]. Smith and Wodehouse (1938) divided the genus into six groups: Mollissimae (I), Sebiferae (II), Calophyllae (III), Rugulosae (IV), Surinamenses (V), and Subsessilis (VI). The characters used to delimit these groups included trichome type, degree of

Table 1. List of species of *Virola* in Central and South America, and Antilles. Region: C = Central America; S = South America; A = Antilles; M = Mexico. For the number of species per country in South America see Fig. 1. References next to a country correspond to species for which we have not seen a herbarium specimen for that country.

Species	Country of original material	Region	Distributions
<i>V. aequatorialis</i> Muriel & Balslev. Nordc. J. Bot. 20(4): 443 (–445) (2000).	Ecuador	S	Ecuador.
<i>V. aguarunana</i> D. Santam.	Peru	S	Peru.
<i>V. albidiflora</i> Ducke. J. Wash. Acad. Sci. 26: 259 (1936).	Brazil	S	Colombia (Gradstein 2016), Ecuador, Peru (Vásquez M. et al. 2018), Brazil.
<i>V. allenii</i> D. Santam. & Aguilar. PhytoKeys 134: 14 (2019).	Costa Rica	C	Costa Rica.
<i>V. alvaroperezii</i> D. Santam.	Ecuador	S	Ecuador.
<i>V. amistadensis</i> D. Santam. PhytoKeys 134: 24 (2019).	Panama	C	Costa Rica, Panama.
<i>V. bombuscaroensis</i> D. Santam.	Ecuador	S	Ecuador.
<i>V. caducifolia</i> W. A. Rodrigues. Acta Amazonica 7: 459 (–462) (1977).	Brazil	S	Colombia (Gradstein 2016), Peru (Vásquez M. et al. 2018), Brazil.
<i>V. calimensis</i> D. Santam.	Colombia	S	Colombia, Ecuador
<i>V. calophylla</i> (Spruce) Warb. Nova Acta Acad. Caes. Leop.-Carol. German. Nat. Cur. 68: 231 (1897).	Venezuela	S	Colombia, Ecuador, Peru, Bolivia, Brazil, Venezuela, Guyana, Suriname.
<i>V. calophylloidea</i> Markgr. Repert. Spec. Nov. Regni Veg. 19: 24 (1923).	Brazil	S	Colombia (Aymard C. et al. 2020), Brazil.
<i>V. carinata</i> (Benth.) Warb. Nova Acta Acad. Caes. Leop.-Carol. German. Nat. Cur. 68: 222 (1897). (1897).	Brazil	S	Colombia (Gradstein 2016), Peru (Vásquez M. et al. 2018), Bolivia (Achá & Liesner 2014), Brazil, Venezuela (Aymard C. et al. 2020).
<i>V. chrysocarpa</i> D. Santam. & Aguilar. PhytoKeys 134: 28 (2019).	Costa Rica	C	Costa Rica, Panama.
<i>V. coelboi</i> W. A. Rodrigues. Acta Amazonica 7: 462 (–464) (1977).	Brazil	S	Colombia, Peru, Brazil
<i>V. cogolloi</i> D. Santam.	Colombia	S	Colombia.
<i>V. crebrinervia</i> Ducke. J. Wash. Acad. Sci. 26: 260 (1936).	Brazil	S	Brazil.
<i>V. cumala</i> D. Santam.	Peru	S	Peru.
<i>V. decorticans</i> Ducke. J. Wash. Acad. Sci. 26: 262 (1936).	Brazil	S	Colombia (Gradstein 2016), Peru, Bolivia (Achá & Liesner 2014), Brazil.
<i>V. divergens</i> Ducke. Wash. Acad. Sci. 26: 255 (1936).	Brazil	S	Colombia (Gradstein 2016), Ecuador (Jaramillo et al. 2004), Peru, Brazil.
<i>V. dixonii</i> Little. Phytologia 19: 255 (1970).	Ecuador	S	Colombia, Ecuador.
<i>V. duckei</i> A. C. Sm. Brittonia 2: 487 (1938).	Brazil	S	Colombia, Ecuador, Peru, Bolivia (Achá & Liesner 2014), Brazil, Venezuela (Aymard C. et al. 2007).
<i>V. elongata</i> (Benth.) Warb. Ber. Deutsch. Bot. Ges. 13: 89 (1895). The use of this name should be evaluated in detail, and perhaps some names put in synonymy should be resurrected.		C, S	Panama, Colombia, Ecuador, Peru, Bolivia, Brazil, Venezuela, Guyana, French Guiana, Suriname.
<i>V. excisa</i> D. Santam.	Ecuador	S	Colombia, Ecuador, Peru, Brazil.
<i>V. flexuosa</i> A. C. Sm. Brittonia 2: 151 (1936).	Brazil	S	Colombia, Ecuador, Peru, Bolivia, Brazil.
<i>V. fosteri</i> D. Santam. PhytoKeys 134: 35(2019).	Panama	C	Costa Rica, Panama.
<i>V. gardneri</i> (A. DC.) Warb. Nova Acta Acad. Caes. Leop.-Carol. German. Nat. Cur. 68: 192 (1897).	Brazil	S	Brazil.
<i>V. guatemalensis</i> (Hemsl.) Warb. Nova Acta Acad. Caes. Leop.-Carol. German. Nat. Cur. 68: 220 (1897).	Guatemala	C, M	Mexico, Guatemala, Honduras.
<i>V. guggenheimii</i> W. A. Rodrigues. Acta Amazonica 7: 464 (–467) (1977).	Brazil	S	Brazil.

Species	Country of original material	Region	Distributions
<i>V. koschnyi</i> Warb. Repert. Spec. Nov. Regni Veg. 1: 71 (1905).	Costa Rica	C, M	Mexico, Guatemala, Honduras, Belize, Nicaragua, Costa Rica, Panama.
<i>V. kwatae</i> Sabatier. Adansonia ser. 3, 19: 273 (1997).	French Guiana	S	Brazil, French Guiana.
<i>V. laevigata</i> Standl. Publ. Field Mus. Nat. Hist., Bot. Ser. 4: 209 (1929).	Panama	C	Costa Rica, Panama.
<i>V. lorentensis</i> A. C. Sm. Bull. Torrey Bot. Club 58: 95 (1931).	Peru	C	Colombia, Peru, Bolivia, Brazil, (Achá & Liesner 2014)
<i>V. macrocarpa</i> A. C. Sm. Brittonia 2: 476 (1938).	Colombia	S	Colombia.
<i>V. malmei</i> A. C. Sm. Brittonia 2: 496 (1938).	Brazil	S	Brazil.
<i>V. marleneae</i> W. A. Rodrigues. Acta Amazonica 7: 467 (–469) (1977).	Brazil	S	Colombia, Peru, Brazil.
<i>V. megacarpa</i> A. H. Gentry. Ann. Missouri Bot. Gard. 62: 474 (1975).	Panama	C	Panama.
<i>V. michelii</i> Heckel. Ann. Inst. Bot.-Géol. Colon. Marseille 6: 118 (1898).	French Guiana	S	Colombia (Gradstein 2016), Bolivia (Achá & Liesner 2014), Brazil, Venezuela, Guyana, French Guiana, Suriname.
<i>V. micrantha</i> A. C. Sm. J. Wash. Acad. Sci. 43: 203 (1953).	Colombia	S	Colombia, Venezuela.
<i>V. minutiflora</i> Ducke. J. Wash. Acad. Sci. 26: 259 (1936).	Brazil	S	Peru (Vásquez M. et al. 2018), Brazil, Venezuela (Rodrigues et al. 2001).
<i>V. mollissima</i> (Poepp. ex A. DC.) Warb. Nova Acta Acad. Caes. Leop.-Carol. German. Nat. Cur. 68: 167 (1897).	Peru	S	Colombia, Ecuador (Jaramillo et al. 2004), Peru, Brazil.
<i>V. montana</i> D. Santam. PhytoKeys 134: 52 (2019).	Costa Rica	C	Costa Rica, Panama.
<i>V. multicostata</i> Ducke. J. Wash. Acad. Sci. 26: 261 (1936).	Brazil	S	Colombia (Gradstein 2016), Peru, Brazil, French Guiana (Aymard et al. 2007).
<i>V. multiflora</i> (Standl.) A. C. Sm. Brittonia 2: 499 (1938).	Belize	C	Honduras, Belize, Nicaragua, Costa Rica, Panama.
<i>V. multinervia</i> Ducke. J. Wash. Acad. Sci. 26: 261 (1936).	Brazil	S	Colombia (Gradstein 2016), Ecuador (Jaramillo et al. 2004), Peru (Vásquez M. et al. 2018), Bolivia (Achá & Liesner 2014), Brazil, Venezuela. (Rodrigues 2008).
<i>V. nobilis</i> A. C. Sm. Brittonia 2: 490 (1938).	Panama	C	Costa Rica (cf.), Panama.
<i>V. obovata</i> Ducke. Bol. Técn. Inst. Agron. n. no. 4: 12 (1945).	Brazil	S	Colombia, Peru, Brazil.
<i>V. officinalis</i> Warb. Nova Acta Acad. Caes. Leop.-Carol. German. Nat. Cur. 68: 228 (1897).	Brazil	S	Brazil.
<i>V. otobifolia</i> D. Santam. PhytoKeys 134: 63 (2019).	Panama	C	Panama.
<i>V. parkeri</i> D. Santam. & Lagom.	Peru	S	Peru.
<i>V. parvifolia</i> Ducke. J. Wash. Acad. Sci. 26: 264 (1936).	Brazil	S	Colombia (Gradstein 2016), Brazil, Venezuela.
<i>V. parvusligna</i> Vásquez & L. Valenz. J. Pl. Sci. 10: 28 (2022).	Peru	S	Peru.
<i>V. pavonis</i> (A. DC.) A. C. Sm. Brittonia 2: 504 (1938).	Peru	S	Colombia, Ecuador, Peru, Bolivia (Achá & Liesner 2014), Brazil, Venezuela.
<i>V. peruviana</i> (A. DC.) Warb. Nova Acta Acad. Caes. Leop.-Carol. German. Nat. Cur. 68: 188 (1897).	Peru	S	Colombia, Ecuador, Peru, Bolivia, Brazil.
<i>V. polyneura</i> W.A.Rodrigues. Acta Amazonica 7: 469 (–471) (1977).	Brazil	S	Colombia (Gradstein 2016), Brazil.
<i>V. pseudosebifera</i> Vásquez & Soto-Shareva. Q'Euña 10: 8–11 (2019) [2020].	Peru	S	Peru.
<i>V. reidii</i> Little. Phytologia 19: 258 (1970).	Ecuador	S	Colombia, Ecuador.
<i>V. rugulosa</i> (Spruce) Warb. Nova Acta Acad. Caes. Leop.-Carol. German. Nat. Cur. 68: 227 (1897).	Brazil	S	Brazil, Venezuela.
<i>V. sanguinea</i> D. Santam. J. Bot. Res. Inst. Texas 15(2): 343 (2021).	Honduras	C	Honduras.
<i>V. schultesii</i> A. C. Sm. Amer. J. Bot. 43: 575 (1956).	Colombia	S	Colombia, Venezuela.

Species	Country of original material	Region	Distributions
<i>V. sebifera</i> Aubl. Pl. Guian. 2: 904 (1775).	French Guiana	C, S	Honduras, Nicaragua, Costa Rica, Panama, Colombia, Ecuador, Peru, Bolivia, Brazil, Venezuela, Guyana, French Guiana, Suriname.
<i>V. sessilis</i> (A. DC.) Warb. Nova Acta Acad. Caes. Leop.-Carol. German. Nat. Cur. 68: 190 (1897).	Brazil	S	Brazil.
<i>V. steyermarkii</i> W. A. Rodrigues. Ann. Missouri Bot. Gard. 76: 1164 (1989).	Venezuela	S	Venezuela.
<i>V. subsessilis</i> (Benth.) Warb. Nova Acta Acad. Caes. Leop.-Carol. German. Nat. Cur. 68: 191 (1897).	Brazil	S	Brazil.
<i>V. surinamensis</i> (Rol. ex Rortb.) Warb. Nova Acta Acad. Caes. Leop.-Carol. German. Nat. Cur. 68: 208 (1897).	Suriname	S, A	Colombia, Ecuador, Peru, Bolivia, Brazil, Venezuela, French Guiana, Guyana, Suriname, Antilles.
<i>V. tuckeræ</i> D. Santam. & Lagom.	Colombia	S	Colombia.
<i>V. urbaniana</i> Warb. Nova Acta Acad. Caes. Leop.-Carol. German. Nat. Cur. 68: 168 (1897).	Brazil	S	Brazil.
<i>V. venosa</i> (Benth.) Warb. Nova Acta Acad. Caes. Leop.-Carol. German. Nat. Cur. 68: 224 (1897).	Brazil	S	Brazil, Venezuela, Suriname.
<i>V. weberbaueri</i> Markgr. Notizbl. Bot. Gart. Berlin-Dahlem 9: 965 (1926).	Peru	S	Peru.
<i>V. yasuniána</i> D. Santam.	Ecuador	S	Ecuador, Brazil.

perianth connation, spacing of secondary leaf veins, column shape, and anther apex shape. Since then, 27 binomials of *Virola* have been published (Ducke 1945; Smith 1953, 1956; Williams 1964; Little 1970; Gentry 1975; Rodrigues 1977, 1989; Sabatier 1997; Jaramillo et al. 2000; Santamaría-Aguilar et al. 2019; Vásquez Martínez and Soto Shareva 2020; Vásquez Martínez and Valenzuela Gamarra 2022). Additionally, floristic treatments and/or catalogs have been published for almost all the countries in South America where this genus occurs (Gradstein 2016 [Colombia]; Achá and Liesner 2014 [Bolivia]; Rodrigues 2015; Oliveira 2021 [Brazil]; Jaramillo et al. 2004 [Ecuador]; Mitchell 2002 [central French Guiana]; Aymard et al. 2007 [Guiana Shield]; Vásquez Martínez 2010; Vásquez et al. 2018 [Peru]; Rodrigues 2008; Rodrigues et al. 2001 [Venezuela]; Aymard et al. 2020 [Rio Negro basin: Brazil, Colombia and Venezuela]). Of these, the most comprehensive studies are Ecuador and Brazil, which treated 16 and 35 species, respectively (Rodrigues 1980; Jaramillo et al. 2004). Recent contributions include a vegetative identification key for 25 species of *Virola* (and four additional genera of Myristicaceae) from the Rio Negro basin (Aymard et al. 2020) and a key to the majority (i.e., 34 of 35) of species native to Brazil (Oliveira 2021). Despite its ecological and ethnobotanical importance, the phylogenetic analyses of the genus are limited, with a single well-sampled analysis supporting the resolution of two large subclades, informally called “Multinervae” and “Sebiferae” (Steeves 2011).

During a review of herbarium material from South America as part of the Myristicaceae treatment for “Flora Mesoamericana” (D. Santamaría-Aguilar, in rev.), we found several specimens that we consider fall outside of the morphological species concepts under which they were identified or treated. Most of this material was collected in the 1940s, 1980s, and 1900s, and was identified as *V. calophylla*, *V. macrocarpa* A. C. Sm., *V. obovata* Ducke, *V. peruviana* (A. DC.) Warb., and *V. sebifera*, or *V. multin-*

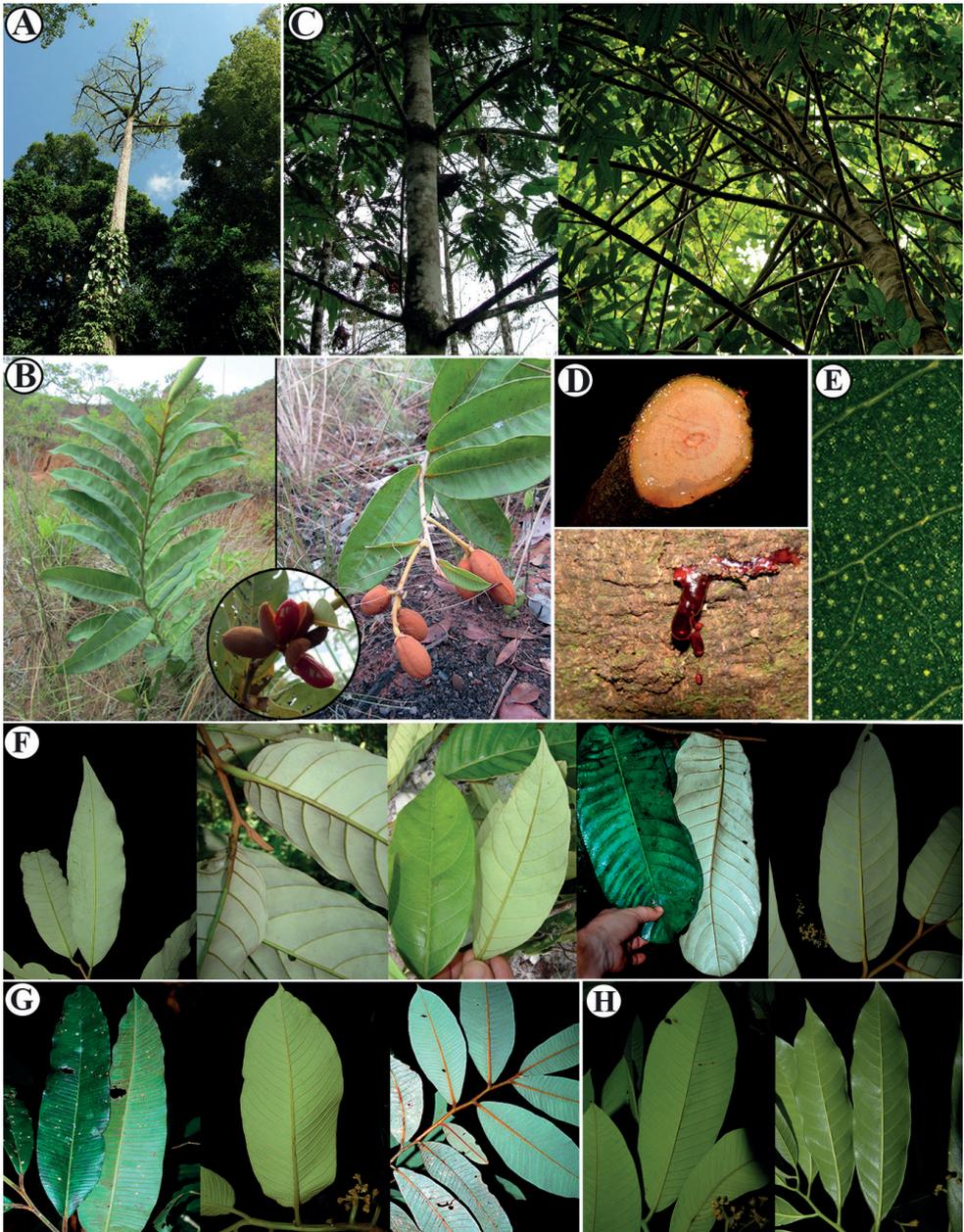


Figure 2. Morphological characters of *Virola* **A** tree habitat of *V. chrysoarpa* **B** shrubby habitat and fruits of *V. sessilis* **C** myristicaceous branching **D** sap on branches (above) and truck (below) **E** leaf punctations **F–H** leaf venations, which correspond to groups Calophyllae, Sebiferae (line **F**; from left to right *V. allenii*, *Virola* spp., *V. calophylla*, *V. sebifera*), Rugulosae (line **G**; *Virola* spp.) and Surinamenses (line **H**; from left to right *V. cf. nobilis*, *V. laevigata*) which correspond to groups of Smith and Wodehouse 1938. Photos by Reinaldo Aguilar (**A**, **D**, **E**, **F** [first and last photo], **G**-right, **H**), Denise Barbosa Silva (**B**), Christopher Davidson (line **F**, second and third photo from left to right), Robin Foster (line **F**, fourth from left to right), **G**-left), and Robbin Moran (**C**).

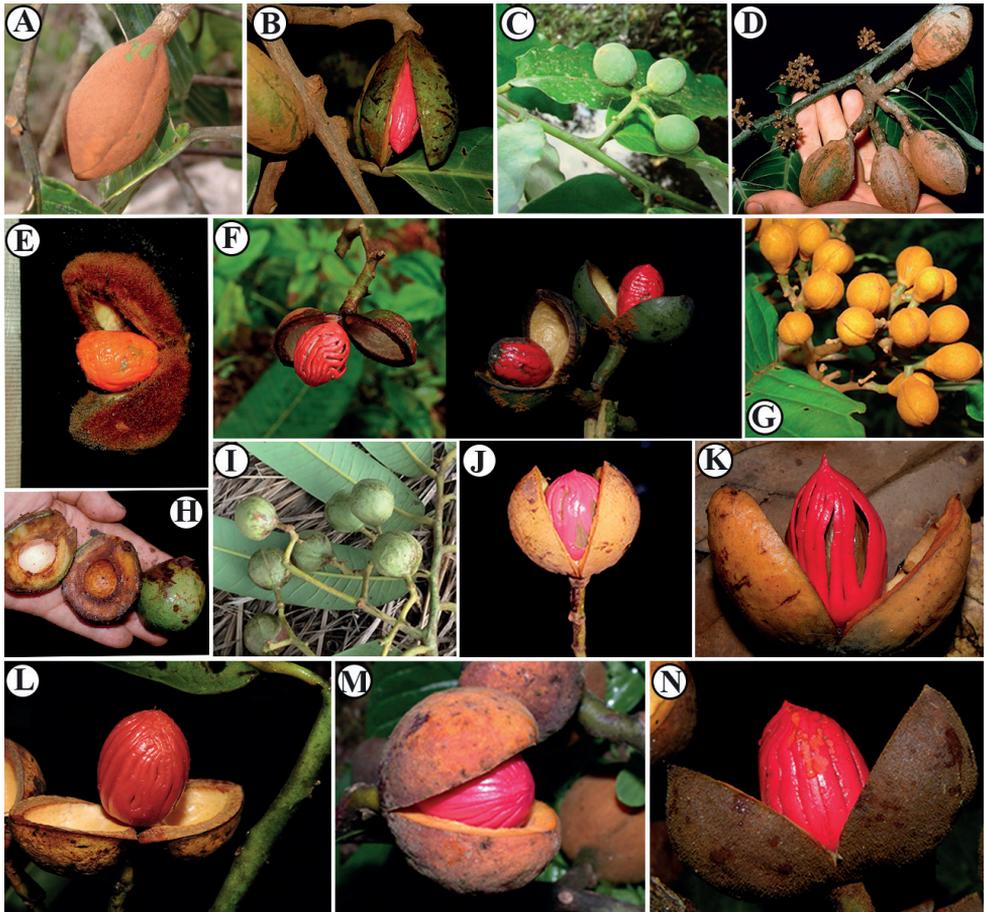


Figure 3. Fruit morphology of *Virola*, note shape, pericarp, indument, and arils. Also see the green color of pericarp, and the minutely pubescent, falling easily as dust (**A–D, F**), and the yellow pericarp (**J–M**) **A** *Virola* sp **B** *V. allenii* **C** *V. elongata* **D** *V. otobifolia* **E** *Virola* sp **F** *V. sebifera* **G** *Virola* sp **H** *Virola* sp **I** *V. surinamensis* **J** *V. fosteri* **K** *V. cf. nobilis* **L** *V. laevigata* **M** *V. koschnyi* **N** *V. chrysoarpa*. Photos by Reinaldo Aguilar (**B, F, K, L, M, N**), Christopher Davidson (**A, C, G**), Robin Foster (**E, H**), Alwyn H. Gentry (**D**), Manuel Morales (**J**), Luiz O. A. Teixeira (**I**).

ervia Ducke. We describe these as new species here. Morphologically, the new species appear similar to the species with which they were previously identified; however, detailed observation of complete specimens (i.e., those in which both flowers and mature fruits are present) reveals clear morphological differences in leaves, trichomes, inflorescences, staminate flowers, and, especially, fruits. It is likely that pistillate flowers are also distinct, although these are infrequent in herbarium specimens. With the exception of *V. cumala*, whose leaves have numerous and close lateral veins and dendritic trichomes, the other new species have leaves with well-separated lateral veins and stellate, sessile trichomes (usually with the central portion darkened) on the abaxial surface of leaf blades (Fig. 4). These characteristics are also shared with *V. allenii* D. Santam. & Aguilar, *V. amistadensis* D. Santam., and *V. otobifolia* D. Santam from Central America.

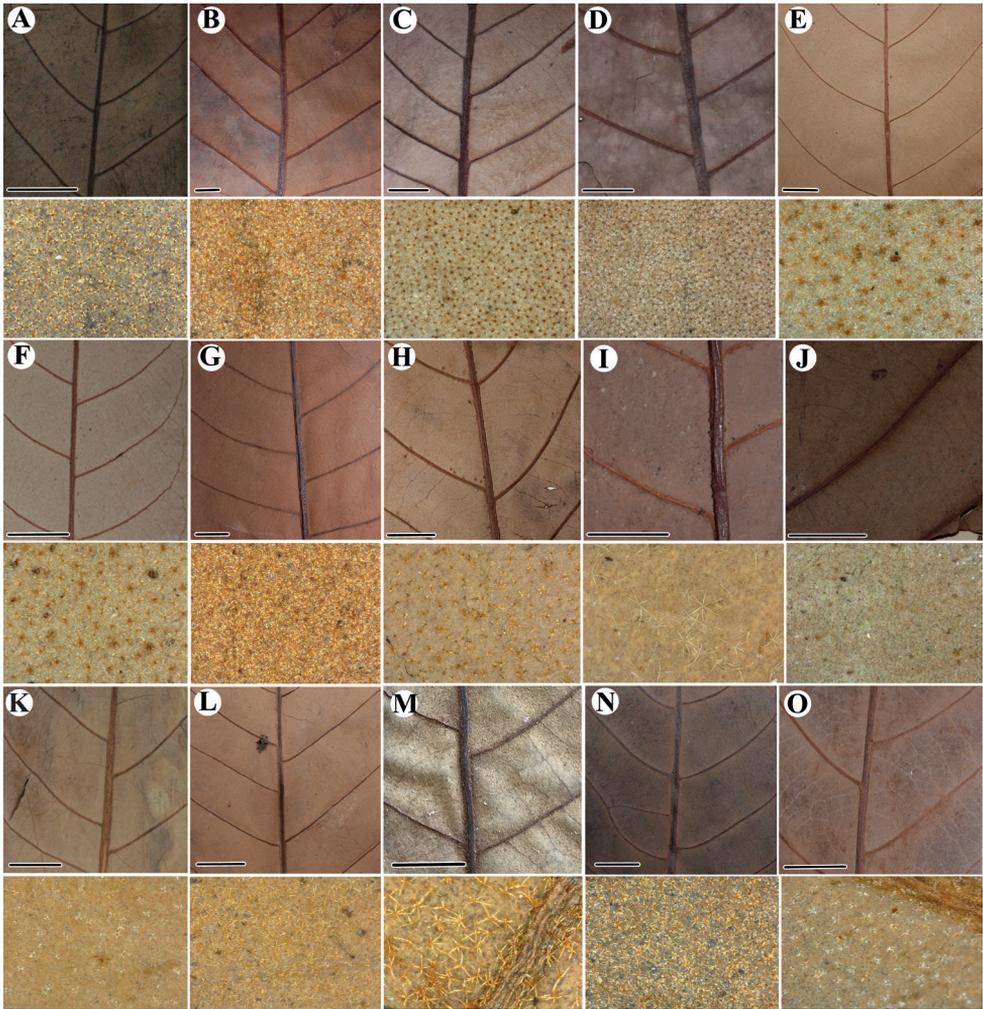


Figure 4. Comparison of pattern of the lateral veins and trichomes on abaxial leaf surface (below) of the newly described species of *Virola* and species that are morphologically similar **A** *Virola aguarunana* (C. Díaz *et al.* 7700A, MO) **B** *V. alvaroperezii* (G. Tipaz *et al.* 1789, MO) **C** *V. bombuscaroensis* (J. Homeier 4507, MO) **D** *V. calimensis* (M. Monsalve 1769, MO) **E** *V. calophylla* (J. E. L. da S. Ribeiro *et al.* 1138, MO) **F** *V. calophylloidea* (C. C. Berg *et al.* P18793, MO) **G** *V. cogolloi* (Á. Cogollo *et al.* 4198, MO) **H** *V. excisa* (C. E. Cerón & F. Hurtado 4147, MO) **I** *V. obovata* (R. Vásquez & N. Jaramillo 3822, MO; below from A. [H.] Gentry & J. Revilla 20448, MO) **J** *V. macrocarpa* (A. E. Lawrence 675, **K** below A. E. Lawrence 675, MO) **K** *V. parkeri* (A. Monteagudo *et al.* 10761, MO; below from M. Huamán *et al.* 334, MO) **L** *V. peruviana* (W. H. Lewis *et al.* 10074, MO) **M** *V. sebifera* (R. Aguilar 2171, MO) **N** *V. tuckerae* (Á. Cogollo *et al.* 4147, MO) **O** *V. yasuniana* (H. Vargas & J. Cerda 678, MO). Scale bars: 1 cm.

Below, we describe 10 new species of *Virola* from Colombia, Ecuador, Peru, and Brazil. This increases the total number of species in *Virola* to *ca.* 70, with 33, 20, 27 and 38 species, respectively, now known from each of these countries. Continued exploration and collection in South America likely will continue to reveal an abundance of new species and new distribution records of *Virola*.

Materials and methods

Approximately 3000 physical herbarium specimens from Meso and South American *Virola* were examined for this study from the following herbaria: COL, CR (including ex INB), JAUM, LSCR, LSU, MO, NO, NY and USJ (acronyms follow Thiers 2021 [continuously updated]), although specimens from MO and NY represent the majority of the material studied. All type specimens, as well as general collections, hosted by virtual herbaria, were consulted, including those maintained by: the Field Museum (F; <http://emuweb.fieldmuseum.org/botany/taxonomic.php>), Instituto Nacional de Pesquisas da Amazônia (INPA; <http://inct.florabrasil.net/en/>), Jardín Botánico Juan María Céspedes (TULV; <https://www.flickr.com/photos/98771984@N05/>), JSTOR Global Plants (<http://plants.jstor.org>), Museum of Natural History, Paris (P; <http://www.mnhn.fr>), Oberösterreichischen Landesmuseums (LI; <https://www.europeana.eu/portal/es>), Refflora Virtual Herbarium (<http://refflora.jbrj.gov.br/refflora/>), species-Link (<https://specieslink.net/>), Smithsonian Institution (US; <https://collections.si.edu/search/>), Universidad Nacional de Colombia (COL; <http://www.biovirtual.unal.edu.co/en/>), Universidad Nacional Autónoma de México (MEXU; <https://datosabiertos.unam.mx/biodiversidad/>) and the National Herbarium of The Netherlands (U; <http://herbarium.naturalis.nl/>).

Species descriptions are based primarily on herbarium specimens. If necessary and material permitted, flowers from herbarium specimens were rehydrated before measurement. A ruler was used to measure leaves and inflorescences; a digital Neiko caliper was used to measure fruits and seeds, as well as the thickness of the twigs, petioles and peduncles; and, finally, flowers, trichomes and thickness of the pericarp were measured with a micrometer calibration tool (1div = 1 mm) under a dissecting stereoscope (Bausch & Lomb).

Specimens cited are listed first by country. Within a country, specimens are listed alphabetically by major division and then alphabetically by department, province or state and, finally, in alphabetical order by the collector's surname. When the coordinates and/or elevation were not included on the herbarium label, but were present in the TROPICOS database, the values from TROPICOS are included. Dot-distribution maps were compiled from studied specimens and generated with SimpleMappr (Shorthouse 2010).

Distribution, habitat, phenological data, common name and uses, flower and fruit colors, habit, bark, and exudate data were obtained from herbarium labels.

In the nomenclatural section for each new species, we cite both accession numbers and barcodes when present.

The preliminary conservation status of each new species was assessed using quantitative criteria recommended by the IUCN Red List (IUCN Standards and Petitions Subcommittee 2014). Georeferenced specimen data were used to determine the area of occupancy (AOO) and the extent of occurrence (EOO), which in turn were used to determine threat status. All analyses were performed in the R package conR (Dauby et al. 2017). When the recommendation differed between AOO and EOO assessments for a given species, we opted to conservatively recommend the more vulnerable status, following Knapp (2013).

Taxonomy

1. *Viola aguarunana* D. Santam., sp. nov.

urn:lsid:ipni.org:names:77298660-1

Type. PERU. Amazonas: Bagua, distrito Imaza, Comunidad Aguaruna Putuim (anexo Yamayakat), zona de colinas altas 24SW de Putuim, [05°00'47"S, 078°23'20"W], 700 m, 22 Sep 1994 (fr), C. Díaz, A. Peña, & P. Ataim 7195 (holotype: MO! [accession 04808693, barcode MO-1405111]; isotypes: UPCB [n.v.]). Fig. 5

Diagnosis. *Viola aguarunana* was mainly confused with *V. calophylla*. Both species share stellate and sessile trichomes and well-separated lateral veins. Morphologically, it differs because the new species has sparsely pubescent abaxial leaf surface (vs. densely pubescent), long staminate perianth ([2–] 2.5–2.7 mm vs. 1–2.1 mm long), and fruits that are covered by a dense layer of trichomes (vs. covered with an inconspicuous layer of trichomes).

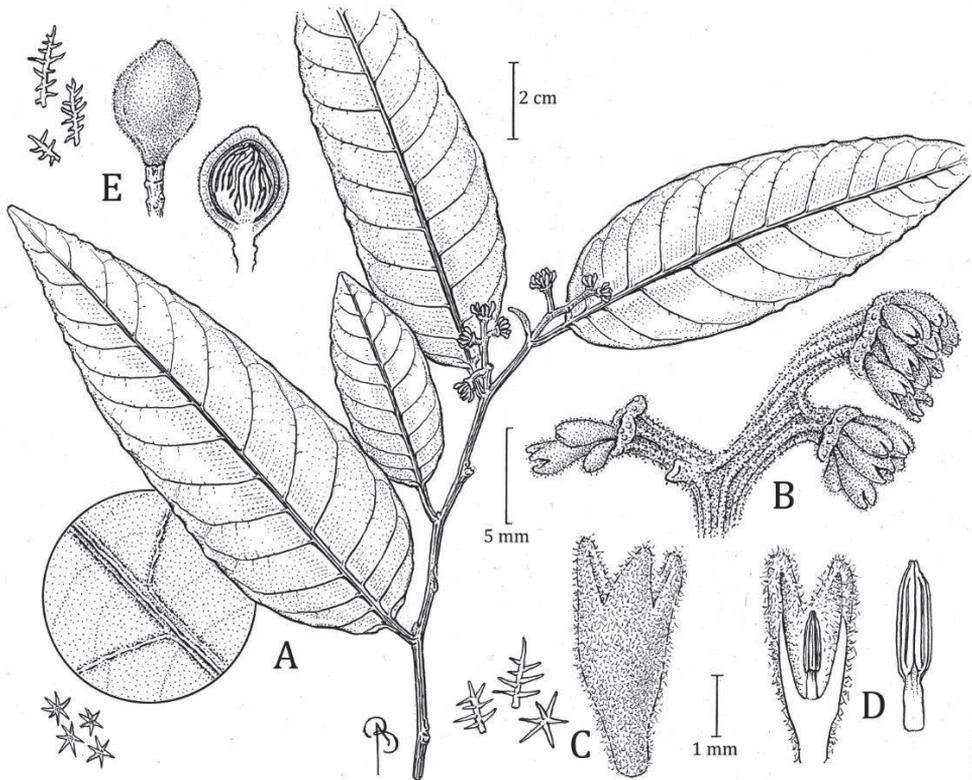


Figure 5. *Viola aguarunana* **A** branch with staminate inflorescence, including detail of abaxial leaf surface **B** partial staminate inflorescence **C** staminate perianth, with detail of trichomes (left) **D** medial sections of staminate perianth, showing the internal surface and androecium, with a closeup of the filament column and anthers (right) **E** fruit with detail of trichomes (left), with open fruit showing lacinate aril. Drawn by Bobbi Angell based on C. Díaz *et al.* 7700A (**A–E**; MO) and C. Díaz *et al.* 7195 (**F**; MO).

Tree 16–20 m tall, diameter and inner bark not described. **Exudate** transparent, oxidizing to red, location of exudate on plant not stated. **Twigs** 0.18–0.27 cm thick, terete to slightly angled, tomentose to puberulent, trichomes dendritic, sessile, brown to ferruginous, sometimes slightly lenticellate. **Leaves** young terminal bud 0.8–1 × 0.16–0.18 cm; petiole 0.9–1.5 (–1.7) × 0.18–0.28 cm, slightly canaliculate, sometimes with very short alate, tomentose, the trichomes dendritic or sometimes stellate; leaf blades (10.7–) 14–22.7 × 4–8.5 cm, oblong-elliptic to ovate; adaxial surface of mature leaves that dry pale to dark brown or blackish, the surface smooth, sometimes shiny, glabrous; abaxial surface dries grayish pale to dark brown, sparsely pubescent, the trichomes stellate or sometimes stellate with dendriform trichomes along the main veins, the stellate trichomes 0.1–0.15 mm diameter, sessile, the central part of the trichome reddish, the branches pale brown-reddish or colorless; lateral veins 13–16 per side, 4–6 per 5 cm, spaced 0.8–1.1 (–1.5) cm, on adaxial side, the same color as the adaxial surface, flat, on abaxial surface raised, laterally compressed, tomentose, arcuate-ascending, slightly anastomosing near the margin and without forming a marked intramarginal vein; tertiary veins slightly visible on both leaf surfaces; midvein adaxially flat to slightly elevated, abaxially raised, rounded, laterally compressed or something triangular, tomentose; base acute to rounded, not revolute, flat; margin flat; apex acuminate. **Staminate inflorescences** 2.2–2.5 cm long, axes flattened, tomentose, the trichomes dendritic, ferruginous; peduncle 0.8–1.1 × 0.1–0.2 cm; main axes with 5 ramifications, the first pair opposite, the others alternate; bracts not seen. **Staminate flowers** (in bud) in dense terminal fascicles of 8–16+ flowers, borne on a receptacle (2–) 3.5–4.5 mm wide; perianth (2–) 2.5–2.7 mm long, obovate, fleshy, brown to brown greenish, connate-connate by 1.3–1.6 mm long, 1.3–1.6 mm long, external surface densely pubescent with ferruginous dendritic trichomes, internal surface moderately pubescent on the lobes; lobes 3, 0.9–1.2 (–1.4) × 0.3–0.8 mm and 0.1–0.2 mm thick, without resinous punctuations when rehydrated; stamens 3, the filament column 0.4–0.5 mm long and ca. 0.2–0.3 mm wide, glabrous, straight or rarely as a bottle shape, not constricted at the apex; anthers 0.6–0.9 mm long and 0.2–0.4 mm wide; apiculus 0.1–0.2 mm long or appearing absent (*R. Rojas et al.* 486), obtuse, connate. **Pistillate inflorescences** and **pistillate flowers** not seen. **Infructescence** 3.4–5 cm long, with 1–2 fruits, peduncle 1.5–2 cm × 0.35–0.46 cm. **Fruits** 2.9–3.5 × 1.8–2.2 cm, green or brown (probably due to pubescence) when fresh, pyriform to subglobose (with narrow base), stipitate, densely tomentose, the trichomes dendritic (ca. 0.2 mm long), ferruginous, and falling easily to the touch as dust, the surface slightly rugose, the line of dehiscence smooth to slightly carinate, the base obtuse, the apex acute to obtuse; pericarp 2–2.5 mm thick; pedicel 0.5–0.6 cm long. **Seed** ca. 2 × 1.6 the testa drying brownish reddish, grooved; aril color when fresh not described, blackish to brownish reddish when dry, the texture dry and thin, lacinate almost to the base, in narrow bands distally.

Distinctive characters. *Viola aguarunana* is recognized by its very short staminate inflorescences (2.2–2.5 cm long) with dense fascicles of flowers, relatively thin perianth that is externally densely pubescent and internally moderately pubescent, and a filament column that is shorter (0.4–0.5 mm long) than the anthers (0.6–0.9 mm

long). It is further distinguished by its pyriform to subglobose fruits covered with ferruginous trichomes (Fig. 6A) that fall easy to the touch and leaf blades usually that are narrow with well-separated later veins and scattered pubescence of stellate and sessile trichomes, on the abaxial surface (Fig. 4A).

Etymology. The specific epithet honors the Aguaruna people, who live in the area where this species was collected.

Distribution. *Virola aguarunana* is known only from the Amazonas Department of Peru (Fig. 18A). This tree has been collected along creek margins on rocky soils with abundant organic material at 700–800 m elevation. The region is also home to other notable species, including many magnoliids— *Compsonura diazii* Janovec (Myristicaceae), *Crematosperma bullatum* Pirie, *Crematosperma yamayakatense* Pirie



Figure 6. Comparison of fruits of newly described *Virola* species, with those species that are morphologically similar to them, noting the shape, indument, a pericarp thickness **A** *V. aguarunana* (C. Díaz et al. 7195, MO) **B** *V. alvaroperezii* (D. Rubio et al. 2205, MO) **C** *V. bombuscaroensis* (J. Homeier 4507, MO) **D** *V. calimensis* (M. Monsalve 158, MO) **E** *V. calophylla* (J. J. Pipoly 15614, MO) **F** *V. calophylloidea* (S. R. Lowrie et al. 54, MO) **G** *V. cogolloi* (D. Cárdenas & E. Alvarez 3239, MO) **H** *V. macrocarpa* (A. E. Lawrence 675, MO) **I** *V. excisa* (W. Palacios 3186, MO) **J** *V. obovata* (R. Vásquez & N. Jaramillo 3822, MO) **K** *V. peruviana* (D. N. Smith & V. García 13841, MO). **L** *V. parkeri* (A. Monteagudo et al. 10761, MO) **M** *V. yasuniana* (Á. Pérez & W. Santillán 4361, MO; right and below from *V. Zak* & S. Espinoza 5149, MO) **N** *V. tuckeræ* (Á. Cogollo et al. 3924, COL). Scale bars: 1 cm.

(Annonaceae), *Ocotea imazensis* van der Werff, *Ocotea leptophylla* van der Werff (Lauraceae)— as well *Dacryodes uruts-kunchae* Daly, M. C. Martínez & D. A. Neill (Burseraceae) and *Quipuanthus epipetricus* Michelang. & C. Ulloa (Melastomataceae), among many others.

Phenology. Staminate buds and flowers of *Viola aguarunana* have been recorded in January, October, and November; pistillate flowers were not seen in the studied material. Fruits have been collected in August and September.

Common name and uses. No common names or uses are mentioned among the herbarium specimens observed.

Preliminary conservation status. *Viola aguarunana* is Endangered following IUCN criteria B1a and B2a. It is known from two localities, has an EOO of 98 km², and an AOO of 12 km². Further justifying this status, this very small distribution is combined with occurrence in areas known to be impacted by forest declines driven by shifting agriculture demands (Antonelli 2022). Of the few species we were able to verify, the most recent was collected in 1997.

Discussion. Most of the specimens of *Viola aguarunana* were previously determined as *V. calophylla* or *V. sebifera*, both widely distributed in South America. The new species shares some characteristics with *V. calophylla*, including a mixture of stellate and sessile trichomes and well-separated lateral veins (a feature shared with *V. sebifera*). However, *V. aguarunana* can be distinguished by its sparsely pubescent abaxial leaf surface (vs. densely pubescent; Fig. 4A, E), longer staminate perianth ([2–] 2.5–2.7 mm vs. 1–2.1 mm long), a filament column that is shorter than the anthers (vs. longer than anthers), and fruits that are covered by a dense layer of trichomes (vs. covered with an inconspicuous layer of trichomes; Fig. 6A, E). *Viola aguarunana* shares the following traits with *V. sebifera*: a filament column that is shorter than the anthers, fruits covered by a dense layer of trichomes, and the same leaf traits as shared with *V. calophylla*. The new species differs from *V. sebifera*, by the sessile trichomes on the abaxial leaf surface (vs. usually pediculate; compare with Fig. 4M) and larger fruits (2.9–3.5 × 1.8–2.2 cm vs. 1–1.9 [–2.1] × 0.7–1.4 [–1.7] cm). Additionally, *V. aguarunana* can be differentiated in both species for its short and narrow staminate inflorescences with flowers borne in dense terminal fascicles. Further, *V. calophylla* and *V. sebifera* tend to have larger leaf blades.

Notes. The only seed that could be measured is from one of the two fruits of the specimen *C. Díaz et al.* 7195 (MO), which is not well preserved. The typical seed size for *V. aguarunana* is likely larger than presented here.

The specimen *D. Neill & Dendrology course students* 15280 (MO; fr), from Cordillera del Cóndor, Zamora-Chinchi, Ecuador may correspond to this species, though it is difficult to tell without flowers.

Specimens examined. PERU. Amazonas: comunidad Aguaruna Putuim, anexo de Yamayakat, 700–750 m, 19 Jan 1996 (♂ fl), *C. Díaz et al.* 7700A (MO!); Comunidad Aguaruna de Wanás (Km 92 Carretera Bagua-Imacita), Cerros Chinim, 700–800 m, 29 Aug 1996 (fr), *C. Díaz et al.* 8054 (F [image!], MO!); Comunidad Aguaruna de Kusú-Listra, Cerro Apág, margen derecha Quebrada Kusú, [05°02'24"S, 078°19'12"W],

550 m, 19 Nov 1996 (fl bud), *C. Díaz et al.* 8086 (MO!); Tayu Mujaji, Comunidad de Wawas, 05°15'25"S, 078°21'41"W, 800 m 25 Oct 1997 (♂ fl bud), *R. Rojas et al.* 486 (MO!).

2. *Virola alvaroperezii* D. Santam., sp. nov.

urn:lsid:ipni.org:names:77298661-1

Type. ECUADOR. **Carchi:** Tulcan Cantón, Parroquia Tobar Donoso, Reserva Indígena Awá, Centro El Baboso, 00°53'N, 078°25'W, 1800 m, 17–27 Aug 1992 (♀ fl and fr), *G. Tipaz, M. Tirado, C. Aulestia, N. Gale & P. Ortiz* 1789 (holotype: MO-2 sheets! [flowers: accession 05005569, barcode MO-1528199; fruits: accession 05005570, barcode MO-1528198]; isotypes: QCNE [n.v.]). Fig. 7

Diagnosis. *Virola alvaroperezii* is more similar to *V. macrocarpa* and *V. otobifolia* from Colombia, Panama, respectively. All these species have relatively large leaf blades and fruits, with lateral veins that are well separated and the abaxial leaf surface covered with stellate, sessile trichomes. Morphologically, it differs from *V. macrocarpa* and *V. otobifolia* by the abaxial leaf surface densely pubescent (vs. sparsely pubescent). Additionally, it differs from *V. macrocarpa* in having lateral veins that are more separated ([2–] 2.4–2.7 cm apart vs. 0.8–1.5 cm apart), and large fruits (4.3–4.5 × 3–3.6 cm vs. 2.7–3.3 × 2–2.3 cm). It differs from *V. otobifolia* by its wide fruit (3–3.6 cm vs. [1.9–] 2.3–2.9) and thin pericarp (2.8 mm vs. [2.7–] 3–4.7 mm).

Tree 30–40 m × 60–70 cm diameter, inner bark and **exudate** not described. **Twigs** 0.37–0.4 cm thick, terete to slightly compressed, inconspicuously pubescent, trichomes dendritic, sessile, ferruginous, without lenticels. **Leaves** young terminal bud not seen; petiole 1.5–2 × 0.34–0.5 cm, terete to slightly canaliculate, sometimes slightly winged, tomentose to tomentulose, the trichomes dendritic; leaf blades 26–28.5 × 12.1–14 cm, widely elliptic; adaxial surface of mature leaves drying brown to brown-olivaceous, the surface smooth, sometimes shiny, glabrous; abaxial surface drying dark brown-reddish to brown-whitish, densely pubescent, the trichomes stellate, ca. 0.1 mm diameter, sessile, the central part of the trichome dark reddish or colorless, the branches brown-reddish or colorless; lateral veins ca. 15, ca. 3 veins per 5 cm, spaced (2–) 2.4–2.7 cm, adaxially the same color as the leaf surface or slightly darker, flat to slightly raised, abaxially brown to blackish, raised, glabrescent above, densely pubescent to the sides, arcuate-ascending distally, slightly anastomosing near the margin and without forming a marked intramarginal vein; tertiary veins lightly visible on both sides, but especially below; midvein adaxially flat to slightly elevated, abaxially raised, rounded, glabrescent to tomentose; base obtuse, not revolute, flat; margin flat; apex absent. **Staminate inflorescence** and **flowers** unknown. **Pistillate inflorescence** ca. 4.2 cm long, axes flattened, tomentose, with trichomes dendritic, ferruginous; peduncle ca. 1.2–1.7 × 0.3–0.35 cm; main axes with 5 ramifications; bracts not seen. **Pistillate flowers** in terminal fascicles of 2–3 flowers, on a receptacle ca. 6 mm wide; perianth ca. 6 mm long, lanceolate, fleshy, brown when fresh, connate by ca. 3–3.2 mm long, external surface densely

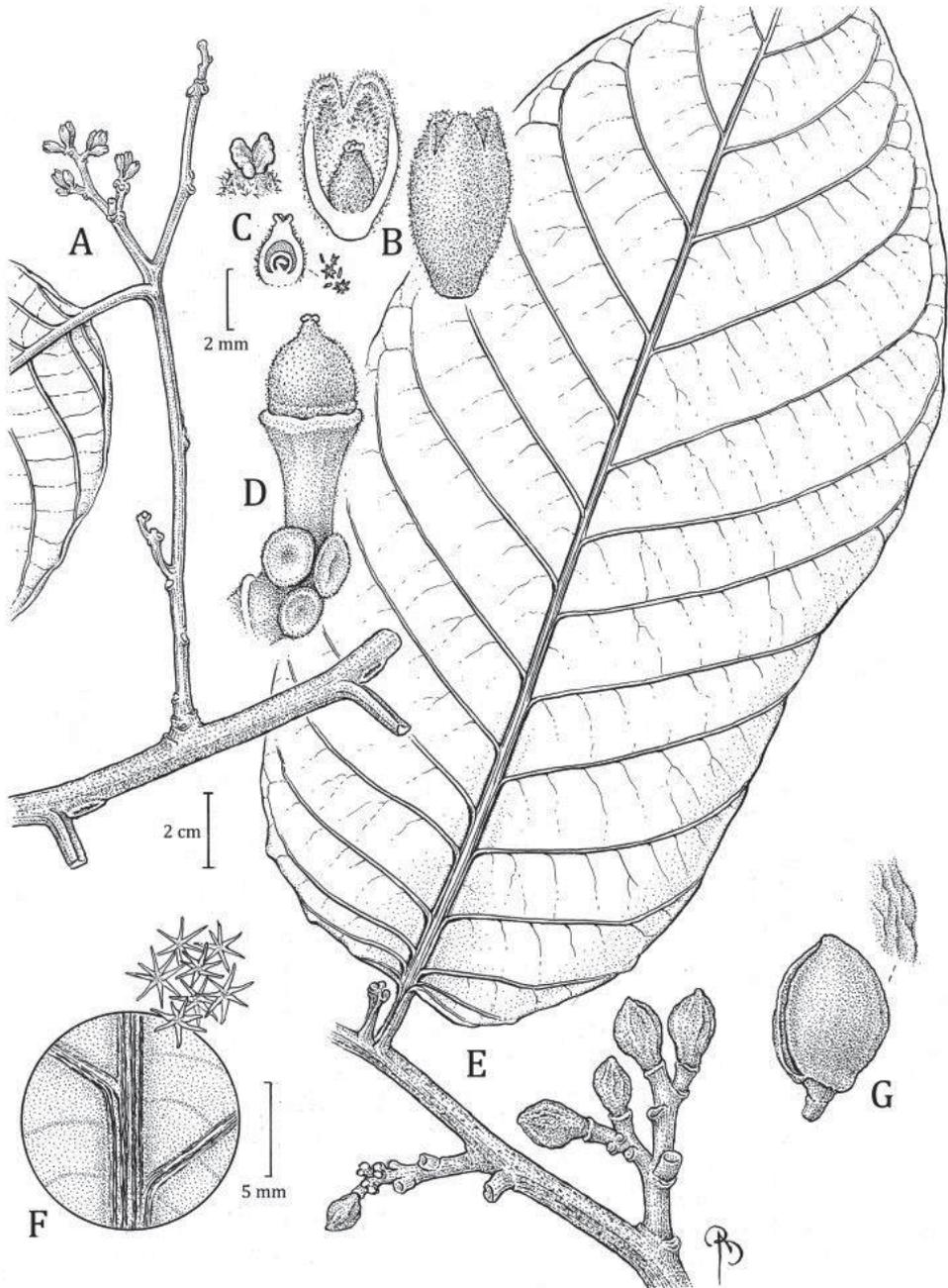


Figure 7. *Viola alvaroperezii* **A** branch with pistillate inflorescence **B** lateral view of pistillate perianth (right), as well as a medial section (left) showing the internal side and gynoecium **C** medial sections of gynoecium, with enlargement of trichomes (right) and stigma (top) **D** lateral view of gynoecium after perianth has fallen **E** leaf blade with infructescence **F** abaxial surface of leaf blade showing the midvein with enlargement of trichomes **G** fruit with detail of indument (right). Drawn by Bobbi Angell based on *G. Tipaz et al.* 1789 (**A–B** MO-05005569), and *G. Tipaz et al.* 1789 (**C–G** MO-05005570).

pubescent with ferruginous and dendritic trichomes, internal surface pubescent (especially on the lobes); lobes 3, ca. 2.8×1.2 – 1.5 mm and ca. 0.5 – 0.6 mm thick, without resinous punctuations when rehydrated; gynoecium ca. 2.5 – 3.1×1.5 – 1.6 mm, conical to subglobose, densely pubescent, the trichomes ferruginous; stigma 2-lobed, ca. 0.5×0.3 mm, erect, flat seen from above, drying blackish, slightly wavy at the margins. **Infructescence** ca. 4.5 cm long, with 1 or 4 fruits in immature infructescence, peduncle ca. 1.5×0.8 cm. **Fruits** 4.3 – 4.5×3 – 3.6 cm, brown when fresh (probably by the indument), ellipsoid, shortly stipitate, densely tomentose, the trichomes dendritic, sessile, ferruginous, not falling to the touch like dust, the surface rugose, the line of dehiscence smooth to faintly carinate, the base obtuse to truncate, the apex obtuse; pericarp 2.8 mm thick; pedicel 0.6 – 1 cm long. **Seed** ca. 2.7×1.6 cm, the testa dark brown to blackish when dry, sulcate; aril described once as red when fresh, dark brown when dry, the texture dry and thin, lacinate almost to the base, in narrow bands distally.

Distinctive characters. *Virola alvaroperezii* is a distinctive species characterized by generally large, wide leaf blades with well-separated lateral veins that are abaxially covered with dense pubescence of stellate, sessile trichomes (Fig. 4B) and large fruits (4.3 – 4.5×3 – 3.6 cm) with thick pericarp (2.8 mm) (Fig. 6B). It is also distinctive for being a large tree (30–40 m tall).

Etymology. It is a great pleasure to dedicate this new species to the Ecuadoran botanist Álvaro Javier Pérez Castañeda. He is an excellent botanist, collector and expert of the flora of Ecuador, especially the flora of Yasuní. Among other contributions, he has described at least 26 from different angiosperm families (e.g., Pérez et al. 2013; Torke and Pérez 2013; Kawasaki and Pérez 2015, 2016) and is coauthor of *Árboles emblemáticos de Yasuní, Ecuador* (Pérez et al. 2014) and the treatment of Myristaceae for the *Flora of Ecuador* (Kawasaki et al. 2019). Pérez Castañeda collected specimens of some of the *Virola* species described here.

Distribution. *Virola alvaroperezii* is known from Carchi and Esmeraldas provinces in Ecuador (Fig. 18A). It grows in primary vegetation in premontane rain and very wet forest from (500–) 1600–1800 m.

Phenology. Only a single studied specimen of *Virola alvaroperezii* has pistillate flowers; it was collected in August. Staminate flowers were not observed in the studied material. Fruits were collected in August and September.

Common name and uses. Guangare macho (Ecuador; *C. Aulestia* & *M. Aulestia* 1017).

Preliminary conservation status. *Virola alvaroperezii* is Endangered following IUCN criteria B1a and B2a. It is known from three localities, has an EOO of 966 km², and an AOO of 12 km². Further justifying this status, this new species occurs in a region of very high rates of deforestation due to agricultural pressures (Kleemann et al. 2022). The only specimens of *V. alvaroperezii* that we were able to verify were collected on the Awá Reserve, and this species may be locally protected by sustainable forestry practices by the Awá indigenous community (Oviedo 2006).

Discussion. Herbarium specimens of *Virola alvaroperezii* have been confused with another montane species, *V. macrocarpa* from Colombia (1100 m elevation). It

could be confused with another Colombian species, *V. cogolloi* (840–1500 m elevation), which is formally described here, as well with *V. otobifolia* D. Santam., recently described from Panama (50–850 m elevation) (Santamaría-Aguilar et al. 2019). All these species have relatively large leaf blades and fruits, with lateral veins that are well separated and the abaxial leaf surface covered with stellate, sessile trichomes. Differences among the three species are summarized in Table 2.

Notes. The holotype deposited at Missouri Botanical Garden (MO) represents a single collection mounted on two sheets that are clearly labeled (i.e., “Sheet 1 of 2” and “Sheet 2 of 2”) as being parts of the same specimen (ICN Art. 8.3; Turland et al. 2018); one of the sheets carries pistillate flowers (MO-05005569) and the other, fruits (MO-05005570).

Leaf size and the number of lateral veins may be higher than presented here, as most of the material examined had broken leaves.

The collection *C. Aulestia* & *M. Aulestia* 1017 (MO) from Esmeraldas Province, Ecuador bears a fruit (possibly immature) that is smaller (ca. 3.7 × 2.6 cm) with thinner pericarp (ca. 2 mm) than other specimens of *V. alvaroperezii*. However, it otherwise matches very well including in its leaf morphology, tall tree habit, and occurrence Río Mira basin; for this reason, it is included in the concept we have adopted, although the fruit measurement is not included in the description.

The fruit specimen *H. Vargas et al.* 4603 (MO, QCNE [image!]), also from Esmeraldas Province, Ecuador, could not be confirmed to the species. It is similar to *V. alvaroperezii* in its leaf morphology (e.g. size, pubescence and trichomes, lateral vein spacing); however, its fruits are rounded and smaller (ca. 3.2–3.3 × 2.6–2.7 mm) with a conspicuous carina.

The two collections of *V. macrocarpa* from Carchi Province that are cited in *Flora of Ecuador* (Jaramillo et al. 2004) correspond to this new species.

Specimens examined. **ECUADOR. Carchi:** Tulcán cantón, Reserva Indígena Awá, Comunidad El Baboso, 12 km al norte de Lita, 00°53'N, 078°20'W, 1600 m, 20 Sep 1991 (fr), *D. Rubio et al.* 2205 (MO!, QCNE [n.v.]). **Esmeraldas:** Reserva Etnica Awá, Parroquia Ricaurte, Centro Pambilar, 01°08'N, 078°36'W, 500 m, 21 Jan 1993 (fr), *C. Aulestia* & *M. Aulestia* 1017 (MO!, QCNE [n.v.]).

Table 2. Comparison of *Virola alvaroperezii*, with *V. cogolloi*, *V. macrocarpa*, and *V. otobifolia*. †From Smith and Wodehouse (1938).

Morphological character	<i>V. alvaroperezii</i>	<i>V. cogolloi</i>	<i>V. macrocarpa</i>	<i>V. otobifolia</i>
Leaf blade size, and pubescence abaxially	26–28.5 × 12.1–14 cm; densely pubescent (Fig. 4B)	25–29.7 × (9.2–) 10.8–15 cm; densely pubescent (Fig. 4G)	20–40 × 7–11 cm [†] ; sparsely pubescent (Fig. 4J)	(14–) 18.2–42.5 × (4.1–) 7.3–14.2 cm; sparsely pubescent
Spaced lateral veins	(2–) 2.4–2.7 cm apart	1.9–2.5 cm apart	0.8–1.5 cm apart	1.7–3 cm apart
Fruit size, and pubescence	4.3–4.5 × 3–3.6 cm; with persistent trichomes (Fig. 6B)	2.7–3.2 × 1.7–2.2 cm; the trichomes do not fall easily like dust (Fig. 6G)	2.7–3.3 × 2–2.3 cm [†] ; with caducous trichomes (Fig. 6H)	(2.7–) 3.5–4.5 × (1.9–) 2.3–2.9 cm; densely tomentose, with persistent trichomes (Fig. 3D)
Pericarp thickness	2.8 mm	1.2–1.6 mm	1.8–3 mm	(2.7–) 3–4.7 mm
Seed	2.7 × 1.6 cm	2.2–2.4 × 1.3–1.4 cm	2.2–2.5 × 1.5–1.7 cm [†]	2.5–2.8 × 1.5–1.7 cm

3. *Virola bombuscaroensis* D. Santam., sp. nov.

urn:lsid:ipni.org:names:77298662-1

Type. ECUADOR. **Zamora-Chinchipe:** PN [Parque Nacional] Podocarpus, Bombuscaro entrance, 04°07'S, 078°58'W, 1350 m, 25 Jan 2011 (fr), *J. Homeier 4507* (holotype: MO! [accession 6863380, barcode MO-3053475]; isotypes: n.v.). Fig. 8

Diagnosis. *Virola bombuscaroensis* differs morphologically from all other species by the combinations of abaxial leaf surface covered by stellate, sessile trichomes, perianth of staminate flowers densely pubescent on both faces, and the column of filaments that has scattered trichomes at the base.

Tree 6–15 m tall, diameter, inner bark and *exudate* not described. **Twigs** 0.43–0.62 cm thick, terete to laterally flattened, tomentose to tomentulose, trichomes dendritic, sessile, ferruginous to whitish, the bark sometimes with small lenticels. **Leaves** young terminal bud 2.5–2.9 × 0.4–0.48 cm, with conspicuous veins; petiole 1.5–2.2 × 0.33–0.5 cm, canaliculate, sometimes very short alate, tomentose, the trichomes dendriform; leaf blades 23.3–30 × 7.1–10.3 cm, ovate; adaxial surface of mature leaves dries brown to olivaceous, glabrous or with very few and scattered trichomes (densely pubescent on new leaves), the surface smooth, sometimes shiny; abaxial surface when drying brown or whitish-grayish, densely pubescent, but inconspicuous to the naked eye, trichomes stellate or sometimes dendriform trichomes along the main veins, the stellate trichomes 0.1–0.2 mm diameter, sessile, the central part of the trichome (usually) reddish and contrasting in color with the hyaline to reddish branches, or the branches the same color as the central part, the dendriform trichomes ca. 0.4 mm long, ferruginous, persistent; lateral veins (13–) 18–23 per side, (3–) 4–5 veins per 5 cm, spaced (0.9–) 1.4–1.8 cm apart, on adaxial surface flat or elevated, the same color as the adaxial leaf surface or a little darker, on abaxial surface raised or flat, rounded or laterally compressed, tomentose to glabrescent, arcuate-ascending, slightly anastomosing near the margin and without forming a very marked intramarginal vein; tertiary veins slightly visible on both sides, more prominent on adaxial side; midvein adaxially slightly elevated, abaxially raised, usually rounded, tomentose; base cordate, not revolute, flat; margin flat to slightly revolute; apex acuminate. **Staminate inflorescences** ca. 5.4 cm long, axes flattened, tomentose, the trichomes dendritic, ca. 0.3–0.4 mm long, ferruginous; peduncle ca. 2 × 0.27 cm; main axes with 5 ramifications, the first pair opposite, the others alternate; bracts not seen. **Staminate flowers** (in bud) in dense terminal fascicles of 13–15+ flowers, on a receptacle 2–2.7 mm wide; perianth 2.8–3.4 mm long, obovoid, fleshy, brown when fresh, connation not seen (young flowers), external surface densely pubescent with ferruginous and dendritic trichomes, internal surface densely pubescent; lobes 3, not measured (young flowers), ca. 0.2 mm thick, without resinous punctuations when rehydrated; stamens 3, the filament column ca. 1.4 mm long, ca. 0.4 mm wide, slightly pubescent at the base, straight to slightly thickened at the base, not constricted at the apex; anthers ca. 0.9 mm long, ca. 0.4 mm wide; apiculus ca. 0.1 mm long, apiculate, separate. **Pistillate inflorescences** and **pistillate flowers** not seen. **Infructescence** 3–3.5 cm long, with 2–6 fruits,

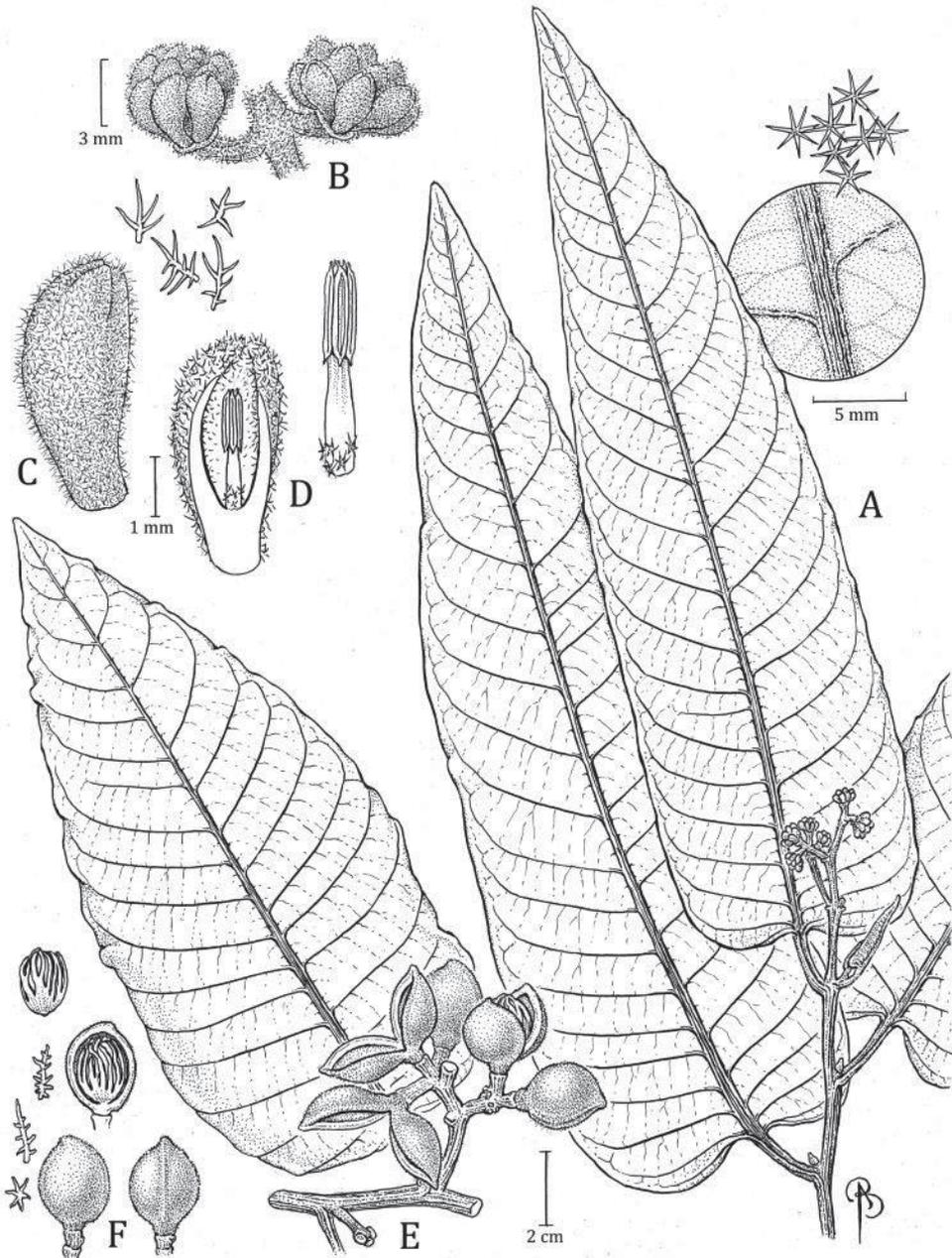


Figure 8. *Virola bombuscaroensis* **A** branch with staminate inflorescence and detail of trichomes on abaxial surface **B** partial staminate inflorescence in bud **C** external surface of staminate perianth (in bud), with detail of trichomes (top right) **D** medial section of staminate perianth showing the internal surface and androecium, with a close-up of the filament column with trichomes at bas and anthers (right) **E** branch with infructescence **F** different views of the fruits, detail of trichomes (left), and open fruit showing the seed with lacinate aril (above). Drawn by Bobbi Angell based on *J. Homeier 1090* (**A–E** MO), and *J. Homeier 4507* (**F–G** MO).

peduncle $1.8\text{--}3 \times 0.43\text{--}0.5$ cm. **Fruits** $2.4 \times 1.8\text{--}1.9$ cm, brown when fresh (probably by the pubescence), globose, stipitate, densely tomentose, the trichomes dendritic, ca. $0.1\text{--}0.3$ mm long, ferruginous, and falling easily to the touch as dust, the surface slightly rugose, the line of dehiscence slightly carinate, but not very conspicuous, the base obtuse, the apex acute to obtuse; pericarp $1.6\text{--}2.2$ mm thick; pedicel $0.5\text{--}0.7$ cm long. **Seed** $1.8\text{--}1.9 \times 1.2\text{--}1.4$ cm, the testa whitish grayish to brownish when dry, grooved; aril color when fresh not described, blackish to brownish red when dry, the texture dry and thin, lacinate almost to the base, in narrow bands distally.

Distinctive characters. *Virola bombuscaroensis* can be recognized by many pubescence characters. Dendritic trichomes cover its branches, petioles, inflorescence axes, and sometimes along the main veins on the abaxial sides of leaves; the abaxial leaf surface always is marked by stellate, sessile trichomes (Fig. 4C); its fruits are covered by ferruginous trichomes that fall very easily to the touch (Fig. 6C); the perianth of staminate flowers is densely pubescent on both sides; and the column of filaments has scattered trichomes at the base. Finally, the filament column is straight, not constricted at the apex, and is longer (ca. 1.4 mm) than the anthers (ca. 0.9 mm).

Etymology. The specific epithet makes reference to the Bombuscaro River in the Podocarpus National Park of southern Ecuador, where most of the collections of this new species were made.

Distribution. *Virola bombuscaroensis* is known only from Ecuador (Zamora-Chinchi Province) (Fig. 18A). It is found in premontane forest at elevations between 1200 to 1350 m, with a single collection from 1930 m in elevation.

Phenology. Staminate flowers of *Virola bombuscaroensis* have been recorded in April and fruits in January. Pistillate flowers were not seen in the studied material.

Common name and uses. None recorded.

Preliminary conservation status. *Virola bombuscaroensis* is Critically Endangered following IUCN criterion B2a. While its very small range from only a single locality justifies this status, *V. bombuscaroensis* benefits from its occurrence in Podocarpus National Park and surrounding areas, which are highly protected within Ecuador (Kleemann et al. 2022).

Discussion. *Virola bombuscaroensis* is difficult to confuse with other species of *Virola* described to date. However, it shares the combination of a cordate leaf base, well-separated lateral veins, sessile trichomes on abaxial leaf surface, and fruits with a conspicuous layer of trichomes with *V. excisa* (described here). Other species with similar leaf morphology, but with fruits with less conspicuous trichomes include: *V. calophylla* (Fig. 6E), *V. peruviana* (Fig. 6K), and *V. schultesii* A. C. Sm.; they can be distinguished by the characters in Table 3.

Other species with similar leaf morphology (i.e., a usually deeply cordate base and well-separated lateral veins) are: *V. divergens* Ducke, *V. mollissima* (Poepp. ex A. DC.) Warb., and *V. sebifera*. However, these species differ in having pediculate trichomes on the abaxial leaf surface (vs. sessile in *V. bombuscaroensis*), internally puberulent staminate perianth (vs. densely pubescent), a glabrous filament column (vs. with scattered trichomes at the base; Fig. 10D) that is shorter (vs. longer) than the anthers. In fruiting

material, *V. divergens*, and *V. mollissima* are covered with a thick layer of long hairs (at least 1.4 mm long) that differ from *V. bombuscaroensis*. While the layer of trichomes on the fruit are somewhat similar to the new species in *V. sebifera*, the fruits are notably smaller (1–1.9 [–2.1] × 0.7–1.4 [–1.7] vs. 2.4 × 1.8–1.9 cm), and *V. sebifera* usually occurs at lower elevations.

Additionally, compared to the species with which it can be confused, *V. bombuscaroensis* tends to have longer staminate inflorescences and more obviously pubescent twigs, petioles, and abaxial leaf surface, very often with dendritic trichomes.

Notes. The specimen *J. Homeier 1090* was cited as *Virola* sp. 1, in *Spermatophyta/Checklist Reserva Biológica San Francisco (Prov. Zamora-Chinchipe, S-Ecuador)* (Homeier and Werner 2007), while *W. Palacios & M. Tirado 13379* was discussed under *V. peruviana* in *Flora of Ecuador* (Jaramillo et al. 2004).

Two collections from Cajamarca Department, Peru collected at 1500–1700 m elevation, *J. Campos & S. Nuñez 4589* (MO!, NY-2 sheets!, UPCB [n.v.]) bearing staminate flowers and *J. Campos & S. Nuñez 4188* (MO, NY, UPCB [n.v.]) bearing an infructescence with very immature fruits, have similar leaf morphology to *V. bombuscaroensis* (i.e., cordate base and abaxial surface with stellate, sessile trichomes). However, these specimens differ in their longer staminate inflorescences (ca. 8 cm vs. ca. 5.4 cm long) and the shorter (ca. 0.4 mm vs. ca. 1.4 mm long), glabrous (vs. pubescent) filament column. Additional, more complete material is needed to assess whether these are conspecific. These specimens have been identified as *V. calophylla* and duplicates may have been distributed under this name.

Table 3. Comparison of *Virola bombuscaroensis* with the morphologically most similar species. †From Smith and Wodehouse (1938); ‡from Smith (1956) (except trichomes on filament column and fruit carina); §from Vásquez Martínez and Soto Shareva (2020).

Morphological character	<i>V. bombuscaroensis</i>	<i>V. calophylla</i>	<i>V. excisa</i>	<i>V. peruviana</i> [†]	<i>V. pseudosebifera</i> [‡]	<i>V. schultesii</i> [§]
Leaf base	Cordate	Usually deeply cordate to truncate (obtuse)	Truncate to subcordate, rarely deeply cordate	Deeply to shallowly cordate	Cordate to rounded	Deeply cordate
# of lateral veins	(13–) 18–23	11–28	(13–) 18–24	17–30	(10–) 12–18	14–19
Perianth staminate long and trichomes inside	2.8–3.4 mm; densely pubescent	1–2.1 mm; glabrescent	1.5–2.8 mm; almost glabrous	2.3–3.2 mm; puberulent	3–3.5 mm; tomentose (in pistillate flowers)	2–2.3 mm long; pubescent
Long filament column, and trichomes	ca. 1.4 mm; slightly pubescent at the base	0.2–0.6 mm; glabrous	(0.4–) 0.5–0.8 mm; glabrous	0.4–0.6 mm; glabrous	0.4–0.7 mm; trichomes not described	0.3–0.4 mm; glabrous
Fruit size, and trichomes	2.4 × 1.8–1.9 cm; densely tomentose, falling easily to the touch as dust (Fig. 6C)	2.5–3 × 1.2–2.5 cm; tomentelous to glabrescent, not falling easily to the touch as dust (Fig. 6E)	2–2.6 × 1.4–1.7 cm; densely tomentose, falling easily to the touch as dust (Fig. 6E)	2–2.8 × 1.5–2.2 cm; glabrescent (Fig. 6K)	2.8–3.6 × 1.8–2.4 cm, densely tomentose	0.8–1.1 × 0.7–1 cm; minutely pubescent, not falling easily to the touch as dust
Carina on the line of dehiscence	Slightly carinate	Carinate	Slightly carinate	Conspicuously carinate	Slightly carinate	Not carinate
Pericarp thick	1.6–2.2 mm	0.5–5 mm	1.5–2.3 mm	0.5–1.5 mm	2–3 mm	0.5 mm

Specimens examined. ECUADOR. **Zamora-Chinchipe:** Area of the Estación Científica San Francisco, road Loja-Zamora, ca 35 km from Loja, 03°58'S, 079°04'W, 1930 m, 6 Apr 2002 (fl ♂), *J. Homeier 1090* (MO!); Zamora cantón, Parque Nacional Podocarpus, guardería Río Bombuscaro, 04°05'S, 078°57'W, 1200 m, [s.d.] Jan 1995 (fr), *W. Palacios & M. Tirado 13379* (MO!, UPCB [n.v.]).

4. *Virola calimensis* D. Santam., sp. nov.

urn:lsid:ipni.org:names:77298663-1

Type. COLOMBIA. **Valle del Cauca:** Bajo Calima, concesión Pulpapel/ Buenaventura, 03°55'N, 077°00'W, 100 m, 03 Aug 1984 (fr), *M. Monsalve 158* (holotype: MO! [accession 3624779, barcode MO-2657915]; isotype: INPA [accession 147738; image!], JAUM [accession 007410]). Fig. 9

Diagnosis. *Virola calimensis* was previously confused with *V. calophylla* and *V. macrocarpa*. Perhaps because of stellate, sessile trichomes and lateral veins that are well separated. Morphologically it differs from *V. calophylla* in having flowers with longer staminate perianth (2.5–3.5 mm vs. 1–2.1 mm), the internal surface densely pubescent (vs. glabrescent), long anthers (0.6–1 [–1.2] mm vs. 0.4–0.5 mm), and large fruits (2.8–3.1 cm long vs. 1.6–1.5 cm). Differs from *V. macrocarpa* in leaf blades abaxially densely pubescent (vs. sparsely pubescent), fruits globose (vs. ellipsoid), shorter (2.8–3.1 cm long vs. [2.7–] 3.5–4.5 cm).

Tree 5–20 or 30 m tall × 25–28 cm in diameter, inner bark described once as brown, cracked, rough. **Exudate** reddish, location of exudate on plant not stated, or described as being present in the inflorescence, but with no information about color. **Twigs** 0.3–0.33 cm thick, terete or slightly compressed, inconspicuously pubescent, trichomes dendritic, sessile, brown reddish, without lenticels. **Leaves** young terminal bud not seen; petiole 1.5–2.4 × 0.22–0.4 cm, slightly canaliculate, sometimes slightly winged, glabrescent, or inconspicuously tomentose to tomentulose, the trichomes dendritic; leaf blades 19–25 × 7.3–11 cm, widely oblong to elliptical; adaxial surface of mature leaves drying brown to olive, the surface smooth, sometimes shiny, glabrous; abaxial surface drying brown reddish to grayish brown, densely pubescent, the trichomes stellate, ca. 0.1 mm diameter, sessile, the central part of the trichome dark reddish, the branches pale reddish; lateral veins ca. 12–13 (*W. Devia 3086*), 3–4 veins per 5 cm, spaced 1.3–2.3 cm apart, flat to slightly raised on adaxial surface, raised on abaxial surface and slightly darker than on adaxial surface, puberulent, densely tomentose to glabrescent above, densely pubescent to the sides, arcuate-ascending distally, slightly anastomosing near the margin and without forming a marked intramarginal vein; tertiary veins slightly visible on both sides; midvein adaxially slightly elevated, abaxially raised, rounded to rectangular, glabrescent to tomentose; base obtuse, not revolute, flat; margin flat; apex acuminate. **Staminate inflorescence** 6–8 cm long, axes flattened, tomentose, with trichomes dendritic, brown-reddish; peduncle 1.3–2.8 × 0.28–0.4 cm; main axes with 5–11 ramifications, the first pair opposite to subopposite, the others alter-

nate; bracts not seen. **Staminate flowers** (in bud) in lax terminal fascicles of 3–5 flowers, on a receptacle 3–5 mm wide; perianth 2.5–3.5 mm long, elongate to rhomboid, fleshy, ferruginous when fresh (probably by the trichomes), connate to 1.1–1.7 mm in length, external surface densely pubescent with ferruginous and dendritic trichomes, internal surface densely pubescent (especially in the lobes) with ferruginous trichomes; lobes 3, 1.3–2 × 0.9–1.5 mm and 0.3–0.7 mm thick, without resinous punctuations when rehydrated; stamens 3, the filament column 0.4–0.6 (–0.8) mm long and 0.2–0.4 mm wide, glabrous, straight, not constricted at the apex; anthers 0.6–1 (–1.2) mm long and 0.2–0.3 mm wide; apiculus 0.1–0.2 mm long, acuminate, slightly separated distally. **Pistillate inflorescence** and **flowers** unknown. **Infructescence** ca. 4.5 cm long, with 2 fruits, peduncle ca. 1.7 × 0.5 cm. **Fruits** ca. 3.3–4.2 × 2.8–3.1 cm, color not

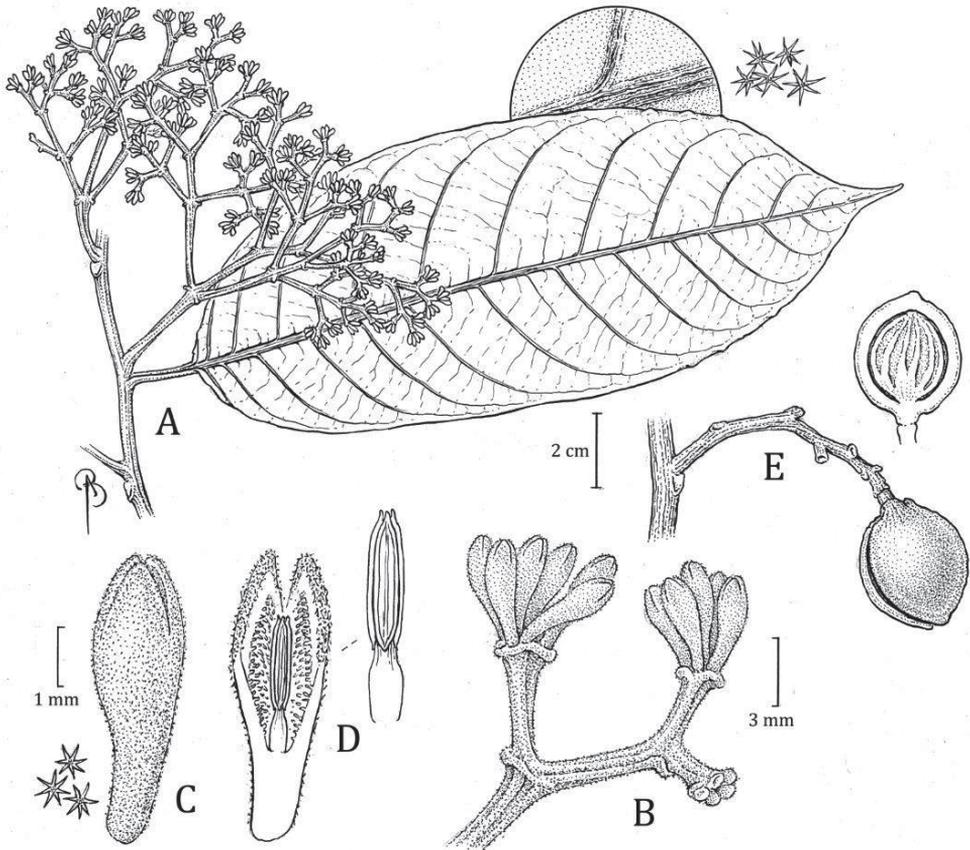


Figure 9. *Virola calimensis* **A** branch with staminate inflorescence and detail of trichomes on abaxial surface **B** closeup of partial staminate inflorescence **C** staminate perianth, with detail of trichomes (left) **D** medial sections of staminate flower showing the internal surface and androecium, with a closeup of filament column and anthers (right) **E** partial infructescence and open fruit (above), showing the seed with lacinate aril. Drawn by Bobbi Angell based on *C. Jativa* & *C. Epling 1143* (**A–D** MO), and *M. Monsalve 158* (**E** MO).

described when fresh, globose, shortly stipitate, densely tomentose, the trichomes dendritic, sessile, ferruginous, the trichomes not falling easily like dust, the surface slightly rugose, the line of dehiscence slightly carinate, the base obtuse, the apex acute; pericarp ca. 3.8–4 mm thick; pedicel ca. 0.6 cm long. **Seed** ca. 2.5 × 2.1 cm, the testa when dry brown reddish, slightly ribbed from the base to the apex; aril color when fresh not described, blackish to brown reddish when dry, the texture dry and thin, lacinate almost to the base, in narrow bands distally.

Distinctive characters. *Virola calimensis* can be recognized by its broad staminate inflorescence, few-flowered inflorescences, elongate to rhomboid, fleshy, densely pubescent perianth, very fleshy filament column and shorter (0.4–0.6 [–0.8] mm long) than the anthers (0.6–1 [–1.2] mm long), and globose, tomentose fruit with trichomes that do not fall easily and with a thick (3.8–4 mm) pericarp (Fig. 6D). Like other species described here, the abaxial side of *V. calimensis*' leaves are covered with stellate, sessile trichomes whose central portion is darker than the branches on their abaxial surfaces. It further has lateral veins that are well separated (1.3–2.3 cm spaced) (Fig. 4D) and a relatively long and thick petiole.

Etymology. The specific epithet of the new species refers to the Bajo Calima region (Valle del Cauca department, Colombia), the region where most specimens of this new species come from.

Distribution. *Virola calimensis* occurs in the Pacific coast of Colombia (Valle del Cauca department) and Ecuador (Esmeraldas province) at elevations ranging from 5 to 260 m (Fig. 18C). According to the field notes of the specimens collected in Colombia (e.g., *M. Monsalve* 158), the species grows in nutrient poor soils with a high concentration of aluminum. See Gentry (1986), Faber-Langendoen and Gentry (1991) and Marcano-Berti and Aymard C. (2021) for more information about this region.

Phenology. Staminate flowers of *Virola calimensis* have been recorded in March, May, June, July, and September. Fruits have been observed in June and August. Pistillate flowers were not seen in the studied material.

Common name and uses. Cuangare (Colombia; *M. Monsalve* 158).

Preliminary conservation status. *Virola calimensis* is Endangered following IUCN criteria B1a and B2a. It is known from three localities, has an EOO of 313 km², and an AOO of 12 km². While its small range justifies this preliminary status, *V. calimensis* benefits from growing in regions with relatively low rates of deforestation compared to the rest of the region (Antonelli 2022), which is in part due to collective land titling by Afro-Colombian communities in Valle del Cauca, Colombia (Vélez et al. 2020) and proximity to the Awá Reserve (Oviedo 2006).

Discussion. Herbarium specimens of *Virola calimensis* were previously identified as *V. calophylla* and/or *V. macrocarpa*. This misidentification was probably due to characteristics shared with *V. calophylla*: stellate, sessile trichomes and lateral veins that are well separated, as well as their lax, few-flowered staminate inflorescences that are relatively wide (these traits are unknown in *V. macrocarpa*). However, *V. calimensis* differs from *V. calophylla* in having fleshier, longer staminate perianth with indument on the internal surface and a filament column that is shorter than the anthers. The new

species also differs in the size and shape of its fruit as compared to *V. calophylla* and *V. macrocarpa*). A summary of the characteristics that differentiate these three species is presented in Table 4, and 5.

Notes. The first collection of *Virola calimensis* was made 76 years ago by José Cuatrecasas (*J. Cuatrecasas 17540*; 5–15 May 1944) in Río Cajambre, Valle del Cauca, Colombia. Six years later, Smith (1950) attributed this Cuatrecasas collection to *V. macrocarpa*, which he used to describe staminate inflorescences; however, he expressed doubt in this and stressed the need for more material, stating that this collection “has leaves considerably smaller, although similar in texture, shape, and indument.” Smith (1950) refers to two additional collections from Colombia with very young inflorescences, which we could not study, as *V. macrocarpa*; these are *J. Cuatrecasas 15596, 16613* (A, F [as Ch]) from the Western Cordillera (1250–1400 m elevations) and Chocó region (5–50 m elevations) respectively.

Walker and Walker (1979; fig. 44) illustrated the pollen of the first collection of this species (again, *J. Cuatrecasas 17540*; 5–15 May 1944), then attributed to *V. macrocarpa*. It was assigned to Pollen Type I (more information can be found in their publication).

The specimens *C. Jativa* & *C. Epling 1143* and *M. Monsalve 158*, mentioned under *V. macrocarpa* in *Flora of Ecuador* (Jaramillo et al. 2004) and *La Familia de Árboles Tropicales Myristicaceae en el Departamento del Valle del Cauca, Colombia* (Taylor and Devia Álvarez 2000) correspond to this new species. The digital images of *W. Devia et al. 5091* (st), *5461* (st), all at TULV, appear to correspond with *V. calimensis* as well.

Specimens examined. COLOMBIA. Valle del Cauca: Bajo Calima, 15–20 m, 28 Jun 1961 (fr), *I. Cabrera 556* (COL);

Table 4. Comparison of *Virola calimensis*, with *V. macrocarpa*. †From Smith and Wodehouse (1938).

Morphological character	<i>V. calimensis</i>	<i>V. macrocarpa</i>
Leaf blades size, and pubescence abaxially	19–25 × 7.3–11 cm; densely pubescent (Fig. 4D)	20–40 × 7–11 cm [†] ; sparsely pubescent (Fig. 4J)
Spaced lateral veins	1.3–2.3 cm apart	1.7–3 cm apart
Fruit shape, and long	Globose, 2.8–3.1 cm (Fig. 6D)	Ellipsoid, (2.7–) 3.5–4.5 cm (Fig. 6H)
Pericarp thickness	ca. 3.8–4 mm	(2.7–) 3–4.7 mm
Seed size	ca. 2.5 × 2.1 cm	2.2–2.5 × 1.5–1.7 cm [†]
Habitat	Lowland rain forest, Colombia (Valle del Cauca), and Ecuador (Esmeraldas), at 20 to 260 m elevation	Montane forests, Andes of Colombia (Boyacá), at 1100 m elevation [†]

Table 5. Comparison of *Virola calimensis*, with *V. calophylla*.

Morphological character	<i>V. calimensis</i>	<i>V. calophylla</i>
Leaf blade size, and base	19–25 × 7.3–11 cm, obtuse	(15–) 20–60 × 10–16 cm; (usually) deeply cordate to truncate (obtuse)
# of lateral veins	ca. 12–13	11–28
Length of staminate inflorescences	6–8 cm	6–30 cm
Staminate perianth long, and internal surface	2.5–3.5 mm; densely pubescent	1–2.1 mm; glabrescent
Long filament column	0.4–0.6 (–0.8) mm	0.2–0.6 mm
Long anthers	0.6–1 (–1.2) mm	0.4–0.5 mm
Fruit size	ca. 3.3–4.2 × 2.8–3.1 cm (Fig. 6D)	2.5–3 × 1.6–1.5 cm (Fig. 6E)

Costa del Pacífico, Río Cajambre, Silva, 5–80 m, 5–15 May 1944 (♂ fl), *J. Cuatrecasas* 17540 (A!, F [image!]); Buenaventura, Carton de Colombia, Vía a Malaga Km. 22, Frente Hans, [03°59'47"N, 076°58'28"W], 20 m, 01 Mar 1990 (fl bud), *W. Devia* 3086 (MO-2 sheets!, TULV [image!], UPCB [n.v.]); Buenaventura [Buenaventura], Canalete, km 28 vía Málaga, 50 m, [s.d.] May 1991 (fr), *W. Devia* 3253 (NY!); Bajo Calima, concesión Pulpapel/ Buenaventura, 03°55'N, 077°00'W, 100 m, 11 Mar 1986 (♂ bud fl), *M. Monsalve* 968 (INPA [image!], MO!); *ibid.*, 22 Sep 1987 (♂ bud fl), *M. Monsalve* 1769 (F [image!], INPA [image!], MO!). **ECUADOR. Esmeraldas:** At Tobar Donoso, junct. of Río San Juan and Río Camumbi, [01°11'24"N, 078°30'30"W], 260 m, 25 Jul 1966 (♂ fl), *C. Jativa* & *C. Epling* 1129 (NY!); *ibid.*, 27 Jul 1966 (♂ fl), *C. Jativa* & *C. Epling* 1143 (MO!, NY!, US [image!]).

5. *Virola cogolloi* D. Santam., sp. nov.

urn:lsid:ipni.org:names:77298664-1

Type. COLOMBIA. Antioquia: Parque Nacional Natural “Las Orquídeas”, Sector Cruces, margen derecha del Río Calles, camino de Cruces hacia Venados, 06°30'N, 076°19'W, 840–870 m, 23 Feb 1989 (♂ fl), *Á. Cogollo* 4198 (holotype: MO! [accession 4235971, barcode MO-2560852]; isotypes: COL [n.v.; accession 333167]). Fig. 10

Diagnosis. *Virola cogolloi* previously confused with *V. macrocarpa* both from Colombian montane forests. These species have similar size and shape of the fruits and abaxial leaf blades with stellate, sessile trichomes. Morphologically, it differs from *V. macrocarpa* in leaf blade densely pubescent abaxially (vs. sparsely pubescent), small fruits (2.7–3.2 cm long vs. [2.7–] 3.5–4.5 cm), cover with persistent trichomes (vs. caducous trichomes), and thinner pericarp (1.9–2.1 mm vs. [2.7–] 3–4.7 mm).

Tree (7–) 14–20 m × (8–) 17–24 cm diameter, inner bark not described. **Exudate** watery, oxidizing reddish, location of exudate on plant not stated. **Twigs** 0.43–0.54 cm thick, terete or laterally compressed, tomentose, trichomes dendritic, sessile, ferruginous, without lenticels on young twigs, but present on mature twigs. **Leaves** young terminal bud 2 × 0.4 cm; petiole 1.7–2.4 × (0.28–) 0.32–0.6 cm, slightly to deeply canaliculate, very often shortly winged, glabrescent to tomentulose, the trichomes dendritic; leaf blades 25–29.7 × (9.2–) 10.8–15 cm, widely elliptical; adaxial surface of mature leaves drying blackish to dark brown, the surface smooth, sometimes shiny, glabrous; abaxial surface drying brown, densely pubescent, the trichomes stellate, ca. 0.1 mm diameter, sessile, the central part of the trichome reddish to dark reddish, the branches reddish to brown-reddish; lateral veins ca. 12–14 per side, 3 veins per 5 cm, spaced 1.9–2.5 cm apart, on adaxial side the same color as the adaxial surface, flat to slightly raised, on abaxial surface blackish, raised, puberulent to glabrescent above, densely pubescent to the sides, arcuate-ascending, slightly anastomosing near the margin and without forming a very marked intramarginal vein; tertiary veins very slightly visible on both sides; midvein adaxially flat to slightly elevated, abaxially raised, rounded to laterally compressed, tomentose to puberulent, more pubescent to the sides; base obtuse, not revolute, flat; margin flat;

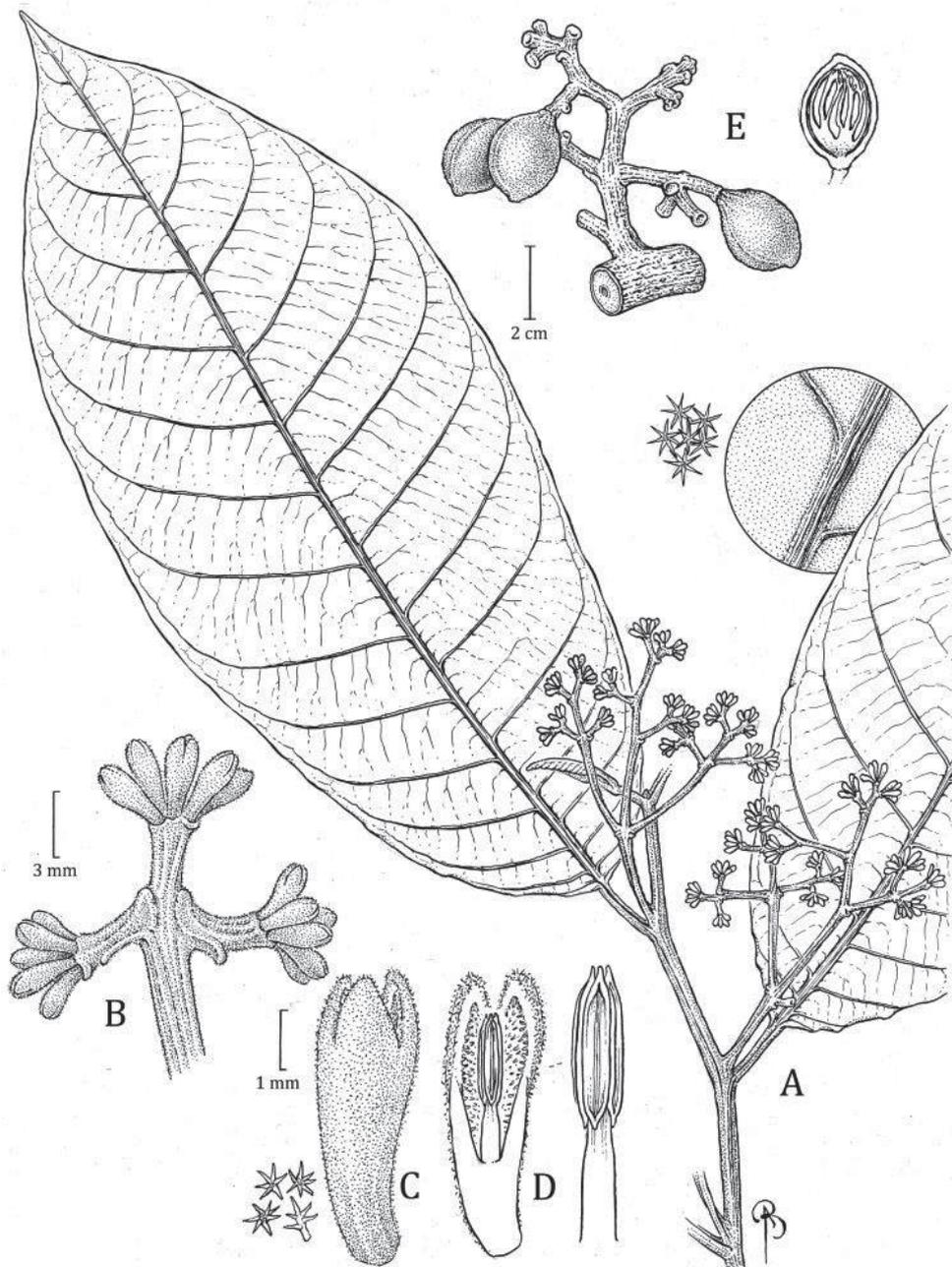


Figure 10. *Virola cogolloi* **A** branch with staminate inflorescence, with detail of trichomes on abaxial surface **B** closeup of partial staminate inflorescence **C** staminate perianth, with detail of trichomes (left) **D** medial sections of staminate flower showing the internal surface and androecium, with a closeup of filament column and anthers (right) **E** partial infructescence and open fruit showing the seed with lacinate aril. Drawn by Bobbi Angell based on *Á. Cogollo* 4198 (**A–D** MO), and *D. Cárdenas & E. Alvarez* 3239 (**E** MO).

apex acute or obtuse. **Staminate inflorescence** 7.5–9 cm long, axes flattened, tomentose, trichomes dendritic, ferruginous; peduncle $2.3\text{--}2.5 \times 0.32\text{--}0.37$ cm; main axis with 4–6 ramifications, the first pair opposite to subopposite, the others alternate; bracts not seen. **Staminate flowers** (in bud) in lax terminal fascicles of 5–8 flowers, on a receptacle 1.6–2 mm wide; perianth 3.5–4.1 mm long, elliptic to elongate, fleshy, yellowish when fresh, connate by 1.5–2.3 mm long, external surface densely pubescent with ferruginous and dendritic trichomes, internal surface densely pubescent (especially in the lobes); lobes 3 (4), $1.8\text{--}2 \times 0.6\text{--}0.9$ (–1.4) mm and $0.2\text{--}0.3$ (–0.5) mm thick, without resinous punctuations when rehydrated; stamens 3, the filament column 1.2–1.4 mm long and $0.2\text{--}0.3$ (–0.5) mm wide, glabrous, straight to bottle-shaped, constricted at the apex; anthers 1.1–1.2 mm long, ca. 0.4 mm wide; apiculus 0.2–0.3 mm long, acuminate, slightly separated distally. **Pistillate inflorescence** and **flowers** unknown. **Infructescence** 6–6.5 cm long, with 1–3 fruits, peduncle $2\text{--}3.4 \times 0.75$ cm. **Fruits** 2.7–3.2 \times 1.7–2.2 cm, when fresh brown or ferruginous (probably by the trichomes), or green and covered with brown trichomes, subglobose to ellipsoid, sessile or shortly stipitate, densely tomentose, persistent, the trichomes dendritic, sessile, ferruginous, the trichomes not falling easily like dust, the surface smooth to slightly rugose, the line of dehiscence smooth, the base obtuse, the apex obtuse to acute; pericarp 1.2–1.6 mm thick on the thinnest side, 1.9–2.1 mm thick on the thickest side; pedicel 0.5–0.8 cm long. **Seed** 2.2–2.4 \times 1.3–1.4 cm, the testa brown to brown reddish when dry, slightly ribbed distally; aril color when fresh described as red or creamy, brown to brown reddish when dry, the texture dry and thin, lacinate almost to the base, in narrow bands distally.

Distinctive characters. *Virola cogolloi* is best distinguished by the combination of its wide leaf blades that are abaxially covered with dense but inconspicuous stellate and sessile trichomes and with lateral veins that are well-separated (Fig. 4G); wide staminate inflorescences with few flowers per fascicle; and staminate flowers with fleshy perianth lobes that are internally covered by a dense layer of trichomes (especially on the lobes) and filament columns that are longer (1.2–1.4 mm long) than the anthers (1.1–1.2 mm long). It is also distinctive for its densely tomentose fruits with relatively thin pericarp (1.2–1.6 mm thick, the thinnest side) (Fig. 6G) and a seed covered by a thin aril that is lacinate almost to the base.

Etymology. The specific epithet honors Álvaro Cogollo Pacheco, the Colombian botanist who collected most known specimens of this new species as well for his valuable contribution to our knowledge of the Colombian flora. We celebrate his important contributions to botany, epitomized by his numerous collections, ~48 of which now represent type specimens (Tropicos 2021). Álvaro is author of the Myristicaceae treatment for the *Catálogo de las Plantas Vasculares de Antioquia* (Cogollo 2011), among others.

Distribution. *Virola cogolloi* is known only from Colombia (Antioquia department) (Fig. 18C). It is found between 840–1500 m elevation in premontane forest in Las Orquídeas National Park in the Western Cordillera of Colombia.

Phenology. Specimens with staminate flowers of *Virola cogolloi* were collected in February and May. Fruits have been observed in February, April to July. Pistillate flowers were not seen in the studied material.

Common name and uses. Sebo (Colombia; *Á. Cogollo et al. 4195*).

Preliminary conservation status. *Virola cogolloi* is Endangered following IUCN criteria B1a and B2a. It is known from three localities, has an EOO of 24 km², and an AOO of 24 km². While *V. cogolloi* benefits from its occurrence within Las Orquídeas National Park, this region (including within the national park) is still vulnerable to deforestation to expand human activities, including agriculture and livestock grazing (González-Caro and Vásquez 2017; Pedraza-Peñalosa 2015).

Discussion. Prior to our study, most of the specimens with fruits of *Virola cogolloi* were identified as *V. macrocarpa*. Both species grow in Colombian montane forests, respectively in the departments of Antioquia (840–1500 m elevation) and Boyacá (1100 m elevation). In addition to a shared habitat, these species have similar size and shape of the fruits and, like other species described here, abaxial leaf blades with stellate, sessile trichomes with a reddish central portion. However, *V. cogolloi* is distinguished by the size of its leaf blades, petiole thickness, separation of the lateral veins, and other features summarized in Table 6.

A second *Virola* species (*V. tuckerae*, formally described below) occurs with *V. cogolloi*. In addition to their similar distributions, these species share leaf blades that are densely pubescent abaxially (Fig. 4G, N). However, *V. tuckerae*, has narrower leaf blades with more lateral veins, a filament column that is shorter than the anthers, and a fruit that is covered by a dense layer of trichomes. A comparison between these two species is presented in Table 7.

Notes. The specimens *Á. Cogollo et al. 4195*, cited as *V. macrocarpa* in Cogollo (2011), and [*Á.*] *Cogollo 3331*, included in Gradstein (2016), both cited as *V. macrocarpa*, correspond with this new species.

Table 6. Comparison of *Virola cogolloi*, with *V. macrocarpa*. †From Smith and Wodehouse (1938).

Morphological character	<i>V. cogolloi</i>	<i>V. macrocarpa</i>
Petiole	1.7–2.4 × (0.28–) 0.32–0.6 cm	1.5–2.3† × 0.18–0.23 cm
Leaf blade size, and pubescence abaxially	25–29.7 × (9.2–) 10.8–15 cm; densely pubescent (Fig. 4G)	20–40 × 7–11 cm†; sparsely pubescent (Fig. 4J)
Spaced lateral veins	1.9–2.5 cm apart	1.7–3 cm apart
Fruit size, and pubescence	2.7–3.2 × 1.7–2.2 cm; with persistent trichomes (Fig. 6G)	(2.7–) 3.5–4.5 × (1.9–) 2.3–2.9 cm; with caducous trichomes (Fig. 6H)
Pericarp thickness	1.9–2.1 mm (on the thickest side)	(2.7–) 3–4.7 mm

Table 7. Comparison of *Virola cogolloi*, with *V. tuckerae*.

Morphological character	<i>V. cogolloi</i>	<i>V. tuckerae</i>
Leaf blade wide	(9.2–) 10.8–15 cm	5–7.2 (–11.7) cm
Lateral veins	ca. 12–14 per side, 3 veins per 5 cm, spaced 1.9–2.5 cm	16–19 per side, 3–4 (–6) veins per 5 cm, spaced 1.1–1.8 (–2.1) cm
Staminate peduncle	2.3–2.5 cm long	0.6–1.8 (–2.8) cm long
Filament column	1.2–1.4 mm long	0.6–0.7 (–0.9) mm long
Anthers	1.1–1.2 mm long	1.2–1.6 mm long
Fruit pubescence	With an inconspicuous layer of trichomes, persistent (Fig. 6G)	With a conspicuous layer of trichomes, caducous, that fall like dust (Fig. 6N)
Pericarp thickness	1.9–2.1 mm (on the thickest side)	ca. 2.4 mm

Specimens examined. **COLOMBIA. Antioquia:** Urrao, Parque Nacional Natural “Las Orquídeas”, Vereda Cruces, camino a Piñares, poco después de la escuela La Esperanza, orilla izquierda del río Calles, 06°28'56"N, 076°19'20"W, 960 m, 5 May 2013 (♂ fl), *J. Betancur et al. 18081* (COL!, NY!); Parque Nacional Natural “Las Orquídeas”, Sector Calles, quebrada La Bironda, 06°31'N, 076°19'W, 1300–1500 m, 02 Apr 1992 (fr), *D. Cárdenas & E. Alvarez 3239* (MO!); Parque Nacional Natural “Las Orquídeas”, Camino a San Mateo, margen izquierda de la Quebrada San Mateo, 06°33'N, 076°19'W, 1060 m, 07 Jun 1988 (fr), *Á. Cogollo et al. 3331* (JAUM!, MO!); Parque Nacional Natural “Las Orquídeas”, sector Venados arriba, margen izquierda del río Venados, 06°34'N, 076°19'W, 1110–1240 m, 27 Jul 1988 (fr imm), *Á. Cogollo et al. 3553* (COL!, JAUM-2 sheets!, MO!); Parque Nacional Natural “Las Orquídeas”, Sector Cruces, margen derecha del río Calles, camino de Cruces hacia Venados, 06°30'N, 076°19'W, 840–870 m, 23 Feb 1989 (fr), *Á. Cogollo et al. 4195* (COL!, JAUM!, MO!); Parque Nacional Natural Las Orquídeas, Vereda Cruces, sitio Piñares, camino a Perdidas, poco después de la escuela La Esperanza, 06°28'35.5"N, 076°19'39.5"W, 980 m, 3 May 2013 (fr), *S. E. Hoyos et al. 2254* (COL!).

6. *Virola cumala* D. Santam., sp. nov.

urn:lsid:ipni.org:names:77298665-1

Type. **PERU. Amazonas:** Bagua, distrito Imaza, Región Nororiental del Marañón, Comunidad de Kampaenza, Ribera de la quebrada Shimutaz, Río Marañón, 04°55'S, 078°19'W, 320 m, 09 Sep 1994 (fr), *N. Jaramillo, R. Apanu, G. Apanu 388* (holotype: MO! [accession 5096935, barcode MO-254989]; isotypes: UPCB [n.v.]). Fig. 11

Diagnosis. *Virola cumala* is most similar to *V. decorticans* and *V. multinervia*; all these species have large leaves, numerous lateral veins, dense indument of dendritic brown to ferruginous trichomes in almost all parts of the plant, and large fruits. Morphologically, it differs from *V. decorticans* in having leaf blade on upper surface glabrous (vs. pubescent), the staminate perianth is subcarnose, without lines or dots (vs. submembranous, and with lines), long filament column (0.5–0.7 mm vs. 0.3–0.4 mm), and anthers (0.7–0.9 mm vs. 0.5–0.6 mm), and narrow fruits (2.3–2.9 cm vs. 1.7–2.2 cm). It differs from *V. multinervia* in the staminate perianth subcarnose (vs. membranous), densely pubescent on all the surface (vs. glabrous or pubescent only at the base and apex), long anthers (0.7–0.9 mm vs. 0.3–0.4 mm), and large fruit (2.3–2.9 cm vs. 1.5–2.5 cm).

Tree 15–35 m × 38 cm diameter; **inner bark** and **exudate** not described. **Twigs** 0.52–1.2 cm thick, laterally flattened to angled, densely tomentose, trichomes dendritic, branched from the base (1–2 mm long) with short lateral branches (0.1–0.2 mm long), brown, sometimes the bark in mature twigs cracks and flakes in small pieces. **Leaves** young terminal bud 2–2.5 × 0.6–2 cm; petiole 0.9–2.2 × 0.43–0.9 cm, strongly canaliculate, densely pubescent, trichomes dendritic; leaf blades 33.1–50.7 (–56.5) × (9.5–) 11.7–15.5 cm, elliptic-oblong to elliptic to obovate, sometimes

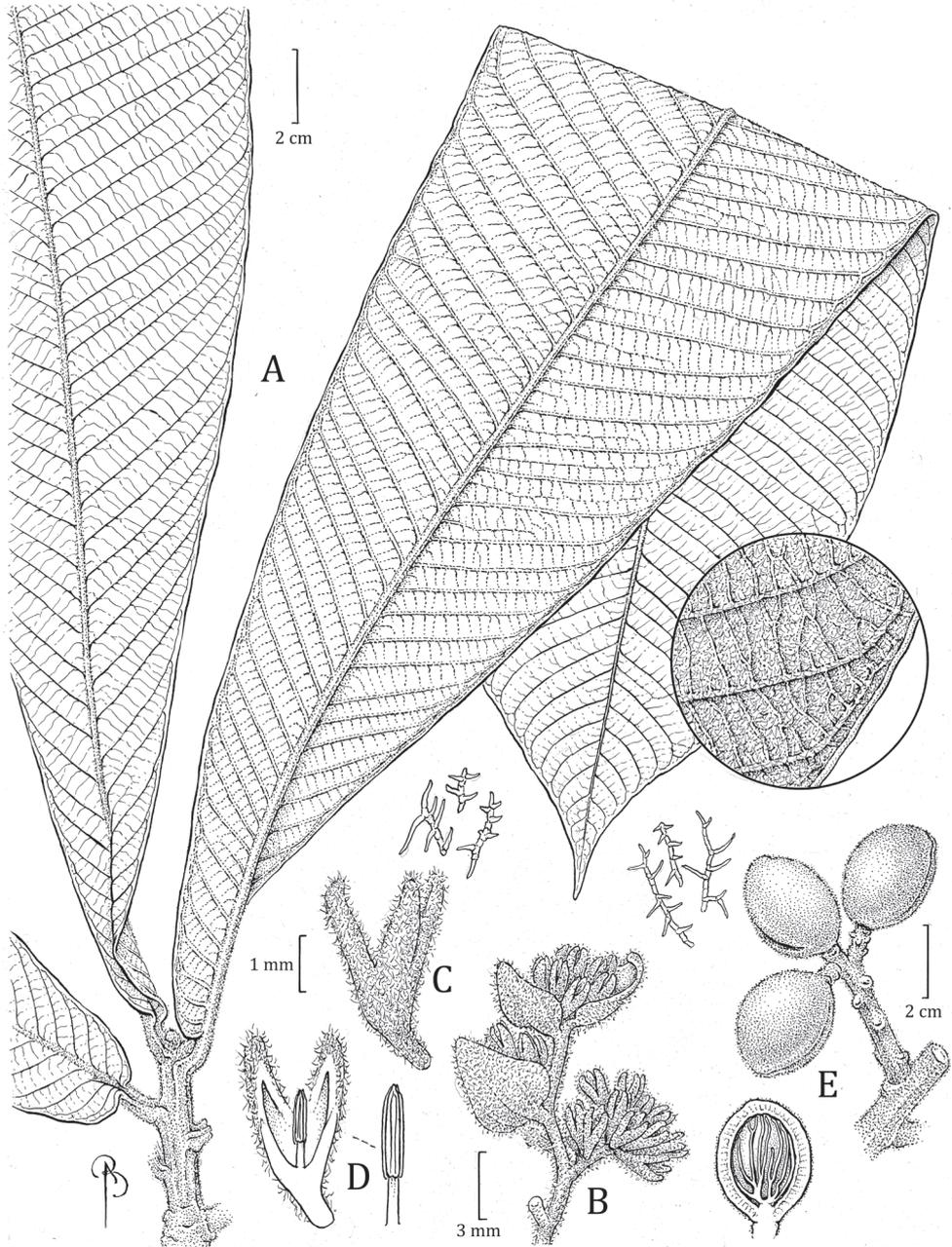


Figure 11. *Virola cumala* **A** branch with leaf blades, with detail of abaxial surface showing trichomes and tertiary venation **B** part of staminate inflorescence **C** lateral view of staminate perianth with detail of trichomes (top) **D** medial section of staminate flower and androecium (right) **E** fruits with detail of trichomes (left), and open fruit showing seed covered with lacinate aril. Drawn by Bobbi Angell based on R. Vásquez & C. A. Grández 17532 (**A–D** MO), and N. Jaramillo *et al.* 388 (**E** MO).

gradually tapering towards the base; adaxial surface of mature leaves (usually) drying brown to dark grayish, glabrous, smooth; abaxial surface drying brown to pale brown, densely pubescent, the trichomes dendritic, yellowish to pale brown, shortly pediculated (branched almost at the base), with 5–8 branches, the branch 0.3–0.7 mm long, persistent; lateral veins 49–65 per side, with 5–7 (–11) veins per 5 cm, spaced 0.4–1.1 cm apart, the same color as the adaxial surface or sometimes slightly contrasting in color, impressed, on abaxial surface the same color as the surface, very conspicuous and raised, slightly straight to arcuate distally, anastomosing very near the margin, forming an intramarginal vein; tertiary veins slightly prominent adaxially, very prominent abaxially; midvein adaxially flat, pubescent, abaxially raised, rounded, pubescent; base cordate to subcordate, not revolute, flat; margin flat; apex acute to cuspidate. **Staminate inflorescences** 7.5–12 cm long, axes slightly flattened at the apex of the defoliated branches, densely pubescent, the trichomes dendritic (1–1.6 mm long), ferruginous; peduncle 1.3–1.5 × 0.34–0.47 cm; bracts 0.4–0.7 × 0.2–0.4 cm, ovate, sometimes triangular, with 3 vertical lines, pubescent on both sides, caducous. **Staminate flower** not very dense, terminal fascicles of 13–21+ flowers, on a receptacle ca. 2 mm wide; pedicel 1.5–2 mm long, pubescent; perianth 2–3 mm long, elongate, subcarinose, brown when fresh, connate to 0.6–1 mm in length, external surface densely pubescent with brown trichomes, internal surface glabrous; lobes 3, 1.1–1.5 × 0.4–0.6 mm, 0.1–0.2 mm thick, without resinous punctuations when rehydrated; stamens 3, the filament column 0.5–0.7 mm long and 0.1–0.2 mm wide, thin, straight, not constricted at the apex; anthers 0.7–0.9 mm long, and ca. 0.2 mm wide; apiculus inconspicuous or obtuse. **Pistillate inflorescences** and **flowers** not seen. **Infructescence** 3.5–5.5 cm long, with 1–3 fruits, peduncle 1–2.7 × 0.4–0.7 cm. **Fruits** 3–3.5 × 2.3–2.9 cm, brown (possibly by the indumentum) when fresh, rounded to ellipsoid, densely and persistently pubescent with a layer of trichomes of 1–2.3 mm thick, the trichomes dendritic, brown to ferruginous, the surface not seen, the line of dehiscence not carinate, the base and apex obtuse; pericarp 3–6 mm thick; pedicel ca. 0.5 mm long. **Seed** (1.9–) 2.3–2.5 × (0.8–) 1.1–1.9 cm, the testa pale brown to brown reddish when dry, grooved (*N. Jaramillo 550*), aril when fresh not described, brown to blackish when dry, the texture dry and thin, lacinate in very narrow bands, almost to the base.

Distinctive characters. The most distinctive characteristic of *Virola cumala* is the dense indument of dendritic brown to ferruginous trichomes that cover almost all parts of the plant. Vegetatively, this species also has large leaves with numerous lateral veins that are prominent (including the tertiary veins, especially below), thick twigs, and bark that sometimes cracks and flakes into small pieces. Further, the staminate flowers have a subcarinose perianth that is densely and uniformly pubescent outside and glabrous inside with narrow lobes, a filament column that is straight and similar in length to the anthers, and large fruits that are covered with a thick layer of trichomes, thick pericarp, and a seed covered by an aril that is lacinate in very narrow bands almost to the base (Fig. 12D).

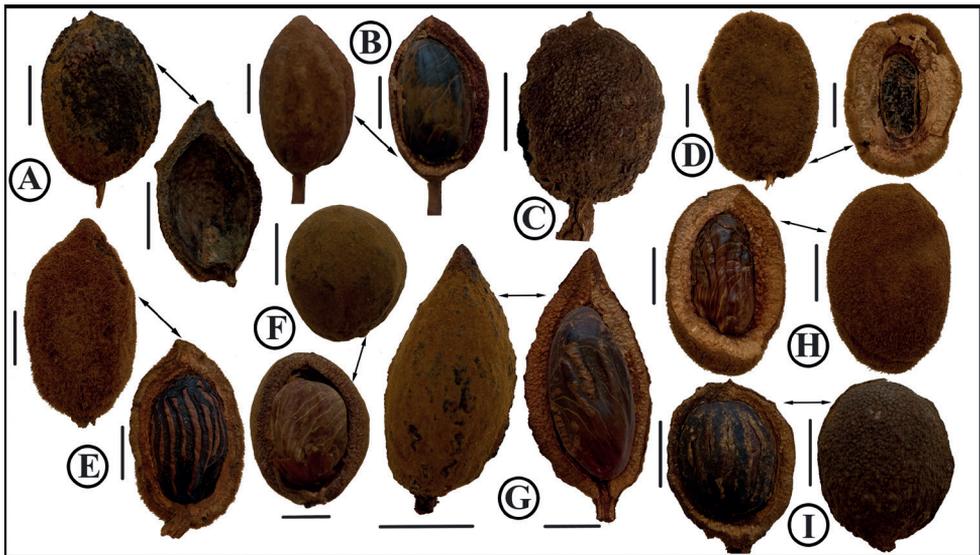


Figure 12. Diversity of fruits from *Virola* species that have numerous and close lateral veins, notice the shape, indument, and pericarp thickness **A** *V. caducifolia* (W. Rodrigues & D. Coêlho 8700, MO) **B** *V. chrysocarpa* (B. Hammel et al. 16864, MO) **C** *V. crebrinervia* (N. A. Rosa 4446, NY) **D** *V. cumala* (C. Grá[n]dez et al. 4919, MO) **E** *V. decorticans* (C. A. Cid Ferreira et al. 9961, MO) **F** *V. koschnyi* (L. D. Gómez et al. 22725, MO) **G** *V. megacarpa* (G. de Nevers 5184, MO) **H** *V. multinervia* (C. A. Sothers & E. D. C. Pereira 1069, MO) **I** *V. multicosta* (R. Vásquez & C. Grández 17507, MO). Scale bars: 1 cm.

Etymology. The specific epithet is taken from the common name on the label of *R. Vásquez & N. Jaramillo* 7879, MO). This common name is often used in Peru to refer to various species of *Virola*, as well to other species in *Otoba* (A. DC.) H. Karst., *Iryanthera* (A. DC.) Warb., and *Osteophloeum* Warb. (e.g. Vásquez Martínez 1997; Zárate-Gómez et al. 2019).

Distribution. *Virola cumala* is known only from Peru (in the Amazonas, Loreto, and Pasco departments) (Fig. 18C). It occurs in primary forests in non-inundated, lateritic soil. It ranges in elevation from 120–320 m, although one collection from Pasco reaches 700–800 m (*H. van der Werff* 20095). It is possible that this species also occurs in Ecuador, as some collections were made close to the border of Peru and Ecuador.

Phenology. Staminate flowers of *Virola cumala* have been recorded in July; pistillate flowers were not seen in the studied material. Fruits have been collected in May, August to October, and December.

Common name and uses. Cumala negra (Peru; *R. Vásquez & N. Jaramillo* 7879, MO).

Preliminary conservation status. *Virola cumala* is Endangered following IUCN criterion B2a. It is known from five localities, has an EOO of 219,024 km², and an AOO of 20 km². Justifying its status, the western Amazonian region where this species occurs is modeled to be modestly impacted by new road construction, a threat that is likely to be superseded by the development of oil palm plantations in the region (Arima 2016).

Discussion. *Virola cumala* is found among a morphological group of ca. 17 species (personal count) that correspond to the group *Rugolosae* of Smith and Wodehouse

(1938). Generally, this group is characterized by leaves with numerous, closely adjacent lateral veins, percurrent tertiary veins that are usually conspicuous, cordate bases, and dendritic trichomes; staminate inflorescences often with large bracts that cover flowers; staminate flowers that are small and usually densely aggregated with membranous to sub membranous perianth, the tube almost split to the base, and a slender filament column. Within this group, the new species is most similar to *V. decorticans* Ducke and *V. multinervia* Ducke, both from South America, and *V. megacarpa* A. H. Gentry from Panama. All four species have large leaves, numerous lateral veins, dense indument of dendritic brown to ferruginous trichomes in almost all parts of the plant, large fruits with a thick layer of trichomes (thin in *V. megacarpa*), and thick pericarp. *Virola cumala* further shares bark that cracks and flakes into small pieces and the thick young terminal bud of leaves. These species are distinguished by the characteristics presented in Table 8.

Virola cumala can be distinguished from other species with numerous lateral and relatively close veins (e.g., *V. caducifolia* W. A. Rodrigues, *V. chrysocarpa* D. Santam. & Aguilar, *V. flexuosa* A. C. Sm., *V. guggenheimii* W. A. Rodrigues, *V. koschnyi* Warb. and *V. polyneura* W. A. Rodrigues) by its fruits: these are large (3–3.5 × 2.3–2.9 cm vs. 1.6–3 × 1.3–2.5 cm), covered with a thick layer of trichomes (vs. tomentose or glabrescent), and have a thick pericarp (3–6 mm vs. 1–4 mm).

The fruits of *Virola divergens*, *V. lorentensis* A. C. Sm., and *V. mollissima* (species of Mollissimae group in Smith and Wodehouse 1938) are also covered by a dense layer of trichomes that is similar to *V. cumala* (cf. Fig. 3E). However, these species have fewer lateral veins (15–30 vs. 49–65), anthers with an apiculate apex (vs. inconspicuous or obtuse), and thin pericarp (0.3–0.7 vs. 3–6 mm).

Notes. The type specimen of *V. cumala* (*N. Jaramillo et al.* 388, MO) was cited as *V. multinervia* in Vásquez et al. (2018). Peruvian specimens identified as *V. multinervia* are very variable, likely representing a combination of misidentifications and undescribed species. Within these, we identified three morphologically distinct groups. The first group corresponds to *V. cumala*. The second, represented by the fruiting specimens *A. H. Gentry et al.* 42594 (MO), *C. Grández et al.* 4929 (MO), *R. Vásquez & C. Grández*

Table 8. Comparison of *Virola cumala*, with three other morphologically closely related *Virola* species. ^{††}From Rodrigues (1980). Perianth information for *V. decorticans* is from *C. Grández et al.* 2525, MO), and fruits from *C. A. Cid Ferreira* 7307, 9961, MO); while those of perianth, filament column and anthers presented for *V. multinervia* are from *C. A. Cid Ferreira et al.* 7537, MO; *W. Rodrigues & D. Coelho* 9617, MO; *J. E. L. S. Ribeiro* 1249, MO; and *W. Thomas et al.* 5239, MO).

Morphological character	<i>V. cumala</i>	<i>V. decorticans</i>	<i>V. megacarpa</i>	<i>V. multinervia</i>
Leaf blade upper surface	Glabrous	Pubescent	Glabrous	Glabrous
No. of lateral veins	49–65	45–60 ^{††}	(32–) 40–50	40–60 ^{††}
Staminate perianth texture, and pubescence on external surface	Subcarnose, without lines or dots, densely pubescent on all the surface	Submembranous, with lines, pubescent	Subcarnose, without lines or dots, densely pubescent on all the surface	Membranous, with lines, glabrous or pubescent only at the base and apex
Filament column length	0.5–0.7 mm	0.3–0.4 mm ^{††}	0.9–1.3 mm	0.3–0.5 mm
Anther length	0.7–0.9 mm	0.5–0.6 mm ^{††}	0.8–0.9 mm	0.3–0.4 mm
Fruit size and apex	3–3.5 × 2.3–2.9 cm, obtuse (Fig. 12D)	2.7–3.5 × 1.7–2.2 cm ^{††} , acute to apiculate (Fig. 12E)	4–5.7 × 2–2.9 cm, acuminate to rostrate (Fig. 12G)	2–3 × 1.5–2.5 cm, apiculate ^{††} (Fig. 12H)
Pericarp thickness	3–6 mm	4–5 mm	3–6 mm	1.5–4 mm

17507 (MO-2 sheets), we tentatively identify as *V. multicosata* Ducke (due to lack of flowers). This group is characterized by scant pubescence covering twigs, petioles, and axes of the infructescence, large leaf-blades (28–37 × 8.1–10 cm) with numerous lateral veins (54–62), the tertiary veins prominent below, and inconspicuously pubescent to glabrescent fruits that are 2.1–2.3 × 1.5–1.8 cm (Fig. 12) with a rugose surface and thin pericarp (1.3–1.5 mm). Finally, the third group is represented by the specimens *A. H. Gentry et al. 19014* (♂ fl.), *A. H. Gentry et al. 21736* (very young fl. bud.; F [image], MO!), and *R. Vásquez & N. Jaramillo 9379* (♀ fl.; MO!). This group is characterized by deciduous (i.e. all leaves fall off the tree), oblong leaves (32.7–44 × 8.5–12.6 cm), brown trichomes that cover the entire plant, staminate inflorescences with bracts that are 0.9–1.5 × 1–1.2 cm, staminate flowers with a ca. 2 mm long perianth which is connate to 0.5 mm in length and densely pubescent externally, glabrous internally, and without dots or lines when rehydrated, perianth lobes that are ca. 1.5 × 0.6 mm, and a filament column ca. 0.4–0.5 mm long with anthers 0.4–0.6 mm long.

Specimens examined. **PERU. Amazonas:** Bagua, distrito Imaza, Región Nororiental del Marañón, Comunidad de Kampaenza, Ribera de la quebrada Shimutaz, Río Marañón, 04°55'S, 078°19'W, 320 m, 10 Oct 1994 (fr), *N. Jaramillo & C. Peas 550* (MO!, UPCB [n.v.]). **Loreto:** Yanamono, Explorama Tourist Camp on Río Amazonas between Indiana and mouth of Río Napo, 03°28'S, 072°48'W, 120 m, 26 July 1980 (♂ fl.), *A. H. Gentry et al. 29027* (INPA [image!], MO!); ExplorNapo Camp (Río Sucusari), 03°15'S, 072°54'W, 140 m, 29 July 1991 (♂ fl.), *R. Vásquez & C. A. Grández 17532* (MEXU [image!], MO-2 sheets); Maynas, IQ [Iquitos]–Nauta, Km 32, 150 m, 20 Aug 1986 (fr), *R. Vásquez & N. Jaramillo 7879* (MO!); Maynas, Distrito Las Amazonas, Explor Napo (Suwzari), 03°20'S, 072°55'W, 124 m, 5 Dec 1992 (fr), *C. Grá[n]dez et al. 4919* (MO!). **Pasco:** Distr. Palcazú, El Paujil, 10°20'12"S, 075°15'39"W, 700–800 m, 13 May 2005 (fr), *H. van der Werff 20095* (F [image!]).

7. *Virola excisa* D. Santam., sp. nov.

urn:lsid:ipni.org:names:77298666-1

Type. **ECUADOR. Pastaza:** Río Curaray, dos horas río abajo del pueblo Curaray, en la boca del Río Namoyacu, 01°24'S, 076°45'W, 275 m, 14–18 Aug 1985 (♂ fl.), *W. Palacios & D. Neill 622* (holotype: MO! [accession 3482884, barcode MO-1565775]; isotype: F [accession 1989048, barcode V0354346F; image!], INPA [accession 147770; image!], NY!, QCA [n.v.]). Fig. 13

Diagnosis. *Virola excisa* is similar to *V. obovata* in the shape of its leaves, which are sparsely stellate and/or dendritic trichomes, or both kinds on abaxial side; staminate flowers with perianth that is nearly glabrous internally and the filament column of similar size to the anthers; and fruits that are covered with a conspicuous layer of ferruginous trichomes. Morphologically, it differs from *V. obovata* in the staminate perianth without resinous punctuations vs. resinous punctuations), long fruits (1.4–1.7 cm vs. 0.8–1 cm), with thick pericarp (1.5–2.3 mm vs. 1–1.2 mm). Given the above mentioned characteristics of leaves and pubescence, *Virola excisa* is similar

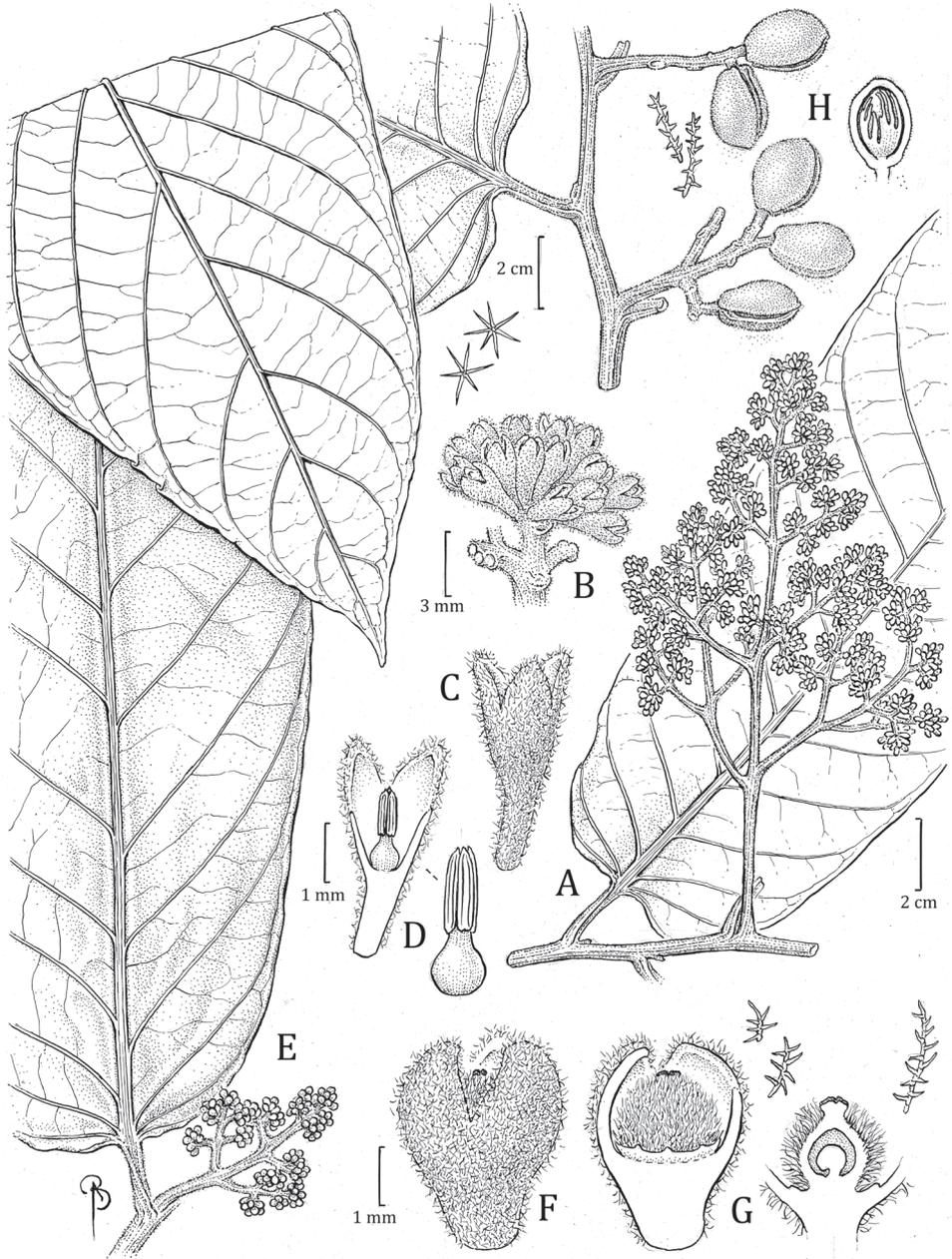


Figure 13. *Viola excisa* **A** branch with staminate inflorescence **B** partial staminate inflorescence **C** staminate perianth **D** medial section of staminate flower and androecium detail (right) **E** branch with pistillate inflorescence, with detail of trichomes on abaxial surface (right) **F** lateral view of perianth (left) and medial section of pistillate flower (right), with enlargement of trichomes on perianth (above right) **G** medial section of pistillate flower, with an enlargement of trichomes on gynoecium (right) **H** branch with fruits, including an enlargement trichomes (middle left), and an open fruit showing seed covered with lacinate aril (right). Drawn by Bobbi Angell based on *W. Palacios & D. Neill 622 (A–D MO)*, *W. Palacios & C. Iguago 4435 (E–G MO)*, and *W. Palacios 3186 (H MO)*.

to *V. peruviana*. But it is distinguished by the fruits densely pubescent at maturity (vs. glabrescent), and slightly carinate (vs. conspicuously carinate).

Tree 8–35 m × 20–40 (–60) cm diameter, inner bark described as grayish and rough. **Exudate** watery, red, or reddish in the trunk or without specifying from where. **Twigs** 0.2–0.47 (–0.55) cm thick, terete, slightly compressed to slightly angulate, tomentose, trichomes dendritic, sessile, ferruginous, without lenticels. **Leaves** young terminal bud 1.2–2.2 × 0.3–0.6 cm; petiole 1.3–2 (–3) × 0.28–0.42 cm, slightly canaliculate and winged, often flattened above, tomentose, sometimes glabrescent, the trichomes dendritic; leaf blades (10.5–) 23.5–46.5 × (6.7–) 9.5–13.5 (–19.7) cm, lanceolate to obovate; adaxial surface of mature leaves usually drying brown to dark brown, the surface smooth, sometimes shiny, glabrous; abaxial surface usually drying white grayish, white brownish to pale brown, sparsely pubescent, the trichomes stellate or sometimes mixture of trichomes stellate and dendritic (especially along the veins), the stellate trichomes ca. 0.1–0.2 mm diameter, sessile, the central part of the trichome pale to dark reddish, sometimes colorless, the branches pale reddish or colorless; lateral veins (13–) 18–24 per side, 3–4 veins per 5 cm, spaced 1.3–2.5 (–3.3) cm, on adaxial side the same color as the adaxial surface, flat to slightly raised, on abaxial surface darker than the surface, slightly raised, glabrescent to scattered pubescent, arcuate-ascending, slightly anastomosing near the margin and without forming a marked intramarginal vein; tertiary veins slightly visible on both sides; midvein adaxially flat to slightly elevated, abaxially raised, rounded, tomentose to puberulent, more pubescent to the sides; base truncate to subcordate, rarely deeply cordate, not revolute, flat; margin flat; apex acute to acuminate. **Staminate inflorescence** 4.5–15.5 cm long, axes flattened, tomentose, with trichomes dendritic (0.2–0.5 mm long), ferruginous; main axes with 9–15 ramifications, the first pair opposite to subopposite, the second and third ramifications sometimes opposite to subopposite, otherwise alternate; peduncle (1.3–) 1.7–4.3 × (0.13–) 0.21–0.3 cm; bracts 2–2.2 × 1–1.6 mm (measured on immature inflorescences). **Staminate flowers** in dense terminal fascicles of 9–25+ flowers, on a receptacle 1.5–1.7 mm wide, sometimes absent; perianth 1.5–2.8 mm long, ovate to obovate, fleshy, cream, yellowish brown, or ferruginous (probably by the trichomes) when fresh, connate 1–1.5 mm long, external surface densely pubescent with ferruginous and dendritic trichomes, internal surface glabrous to almost glabrous; lobes 3, 1–1.1 × 0.5–0.8 mm, and 0.1–0.2 mm thick, without resinous punctuations when rehydrated; stamens 3, the filament column (0.4–) 0.5–0.8 mm long and 0.3–0.4 mm wide, glabrous, fleshy, straight and wide throughout its length, constricted at the apex; anthers 0.5–0.7 mm long, 0.3–0.4 mm wide; apiculus ca. 0.1 mm long, acuminate, separate. **Pistillate inflorescence** 4–7 cm long, axes flattened, tomentose, the trichomes dendritic, ferruginous; peduncle 1.5–4.2 × 0.18–0.46 cm; main axes with 9–10 ramifications, the first and second pair (usually) opposite to subopposite, the other alternate; bracts not seen. **Pistillate flowers** in terminal fascicles of 3–10+ flowers, on a receptacle 2–4 mm wide; perianth 1.7–2.5 mm long (measurement from immature flower), globose, brown when fresh, connation not seen, external surface densely pubescent with ferruginous and dendritic trichomes, internal surface glabrous;

lobes probably 3, not seen properly due to the immaturity of flowers, ca. 0.2–0.3 mm thick, without resinous punctuations when rehydrated; gynoecium 1.1–2 × 1.2–2 mm, globose, densely pubescent, with ferruginous trichomes; stigma 2-lobed, 0.4–0.7 × 0.2 mm, sessile, drying blackish, slightly wavy at the margins. **Infructescence** 3.5–7.5 (–11.5) cm long, with 4–7 fruits, peduncle ca. 1.4–3.5 (–5) × 0.3–0.5 cm. **Fruits** 2–2.6 × 1.4–1.7 cm, when fresh green or brown (the latter probably due to the trichomes) and covered with brown trichomes, ovoid, without stipe, densely tomentose, the trichomes dendritic (0.1–0.4 mm long), sessile, ferruginous, falling very easily like dust, the surface smooth, the line of dehiscence slightly carinate, the base truncate to obtuse, apex acute; pericarp 1.5–2.3 mm thick; pedicel 0.4–0.7 cm long. **Seed** 2–2.3 × 1.1–1.3 cm, the testa drying brown to dark brown, sulcate and bullate; aril when fresh described as red, dark brown, brown-reddish to blackish when dry, the texture dry and thin, laciniate almost to the base, in narrow bands distally.

Distinctive characters. *Virola excisa* can be recognized by its long, lanceolate to obovate leaves that are truncate to subcordate at the base with an underside that is usually white grayish when dry and sparsely pubescent with stellate sessile trichomes (sometimes with dendritic trichomes along the veins) (Fig. 14B); lateral veins that are well separated, with the marginal and tertiary veins not very conspicuous; staminate flowers with the external perianth covered with dense pubescence of dendritic trichomes and a glabrous internal surface, a fleshy filament column that is similar in length ([0.4–] 0.5–0.8 mm long) to the anthers (0.5–0.7 mm long); fruits that are densely pubescent with trichomes that fall easily like dust; and the seed with a bullate, sulcate testa (Fig. 6I). Additionally, herbarium specimens are usually aromatic.

Etymology. The specific epithet of the new species comes from the word *excisus*, meaning cut out (Stearn 1992). The makes reference to the fact that several herbarium specimens of this new species come from felled trees that were killed to make way for oil pipes (e.g. *V. Zak* & *S. Espinoza* 4733, 5149; *F. Hurtado* 2980). This has created irreparable damage to nature, destroying the habitat of this and many other species, potentially paving the path toward their extinction.

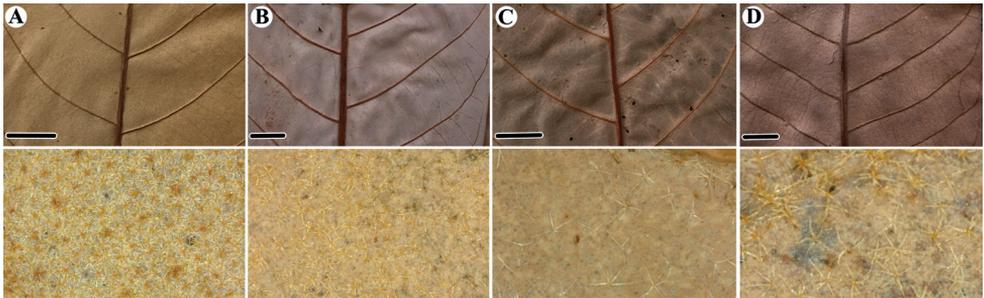


Figure 14. Comparison of abaxial surface, veins, and trichomes of **A** *V. calophylla* **B** *V. excisa* **C** *V. obovata* and **D** *V. peruviana* **A** from J. E. L. S. Ribeiro *et al.* 1138, MO **B** from A. [H.] Gentry & C. Díaz 58536, MO **C** from R. Rueda & J. Ruiz 621, MO **D** from C. A. Grández & A. Chiquispama 1065, MO. Scale bars: 1 cm.

Distribution. *Virola excisa* is known from Colombia (Amazonas, Putumayo departments), Ecuador (Napo, Pastaza, Morona-Santiago provinces), Peru (Amazonas, Huánuco, Loreto, Pasco, Ucayali departments), and Brazil (Acre, Amazonas state) (Fig. 18B), where it occurs in primarily moist tropical forest. Some herbarium labels mention that it grows on hills with red soils, sandy clay soil, near black water or várzea. It ranges in elevation from 130–580 m, with two collections reaching 700 and 830 m.

Phenology. Staminate flowers of *Virola excisa* have been collected in February, May to October, and pistillate flowers in May, July to September. Fruits have been collected in January to April, August to December.

Common name and uses. Common names include in Colombia: sangre de toro (*J. Cuatrecasas* 10653 [F, without common name at COL]). Ecuador: *gomenkowe* (Wao tededo; Pérez et al. 2014), gunhuékonmo (Huaorani; *E. Gudiño et al.* 956), lugumpapu (Huaorani; *D. Rubio & T. Coba* 839), huapa (Quichua; *E. Gudiño et al.* 2139, 2154), numpa tsempu kumpari (Huambisa; *V. Huashikat* 2267, 2322), puca huapa (Quichua; *H. Vargas* 1590), tsempu (Huambisa; *V. Huashikat* 682). Peru: cumala blanca (*[B.] Kröll* 487), sempo (Aguaruna; *J. J. Wurdack* 2272). Brazil: ucuhuba (*[W. A.] Ducke* 396), ucuuba (*M. Silveira et al.* 840), ucuúba da folha grande (*M. Silveira et al.* 718). The trunk of *V. excisa* is used for construction of houses, while the aril attracts birds, rodents, and monkeys (Pérez et al. 2014, as *V. obovata*) or the wood used for firewood (*M. Silveira et al.* 840).

Preliminary conservation status. *Virola excisa* is Not Threatened following IUCN criteria B1a and B2a. It is known from 25 localities, has an EOO of 810,234 km², and an AOO of 112 km². While this species grows in regions of the world that are threatened by human landscape modification (Antonelli 2022), its distribution is wide enough that this species does not need to be considered threatened currently.

Discussion. Of morphology apparent in herbarium specimens, the leaf blades and some flower and fruit features of *V. excisa* are similar to *V. obovata*, and most of the studied specimens were identified as such in *Flora of Ecuador* (Jaramillo et al. 2004). Both species share similarly shaped leaves that appear to be glabrous abaxially, but actually bear sparsely stellate and/or dendritic trichomes, or both kinds; staminate flowers with perianth that is nearly glabrous internally and the filament column of similar size to the anthers; and fruits that are covered with a conspicuous layer of ferruginous trichomes. Despite these morphological similarities, *V. excisa* differs from *V. obovata* in traits related to the leaf base, the perianth of staminate flowers, and fruit, pericarp, and seed size. Differences between these species are summarized in Table 9. In addition to the features in Table 9, there are distinguishing traits that are difficult to describe properly; compared to *V. obovata*, herbarium specimens of *V. excisa* tend to have more elongate leaves and staminate perianth, fruits usually have more conspicuous carina, and trichomes are denser and fall more easily.

Virola excisa resembles *V. calophylla* and especially *V. peruviana* in the shape of its leaves (including the base and lateral vein pattern) and long staminate inflorescences with perianth that is glabrous internally. In addition, *V. calophylla* and the new species have similar fruit morphology (at least when young). *Virola excisa* can be distinguished

Table 9. Comparison of *Virola excisa*, with *V. obovata*.

Morphological character	<i>V. excisa</i>	<i>V. obovata</i>
Leaf blades size, base and shape	(10.5–) 23.5–46.5 × (6.7–) 9.5–13.5 (–19.7) cm; base truncate to subcordate, rarely deeply cordate; lanceolate to obovate	11.5–29.5 (–34) × 6.8–12.5 cm; base attenuate to acute; obovate-elliptic.
Staminate perianth	Without resinous punctuations	With resinous punctuations
Infructescence peduncle	ca. 1.4–3.5 (–5) cm long	0.7–1.3 cm long
Fruits	2–2.6 × 1.4–1.7 cm, without stipe, the base truncate to obtuse (Fig. 6I)	1.3–2.3 × 0.8–1 cm, shortly stipitate, the base rounded (Fig. 6J)
Pericarp thickness	1.5–2.3 mm	1–1.2 mm
Seed	2–2.3 × 1.1–1.3 cm	1.7–1.9 × 0.6–0.7 cm

from *V. calophylla* by its abaxial leaf blades that are sparsely pubescent and puberulent (vs. densely pubescent and appearing squamose; see Fig. 14A), shorter, narrower staminate inflorescences, shorter perianth, and filament column that is similar in length to the anthers (vs. filament column longer than anthers). Immature fruits of *V. calophylla* are densely pubescent (e.g. *D. Daly et al.* 6773, INPA [image!], MO!, NY!) and appear similar to those of *V. excisa*; however, at maturity, its fruits tend to be minutely tomentelous to glabrescent (vs. densely tomentose; see Fig. 6E, I). Additionally, abaxial leaf blades of herbarium specimens of *V. calophylla* tend to be silver to golden.

Virola excisa can distinguished from *V. peruviana* by its staminate flowers with short anthers (0.5–0.7 mm vs. 1.1–1.6 mm long, from Smith and Wodehouse 1938) and fruits that are slightly carinate (vs. conspicuously carinate) and densely pubescent at maturity (vs. glabrescent). For a detailed comparison of the indument and carina of fruits between these two species see Figs 6I, K (fruits) and 14B, D (indument). Although, some specimens of *V. excisa* have a cordate leaf base (e.g. *V. Huashikat* 2267, MO; *D. Rubio & T. Coba* 839, MO), they are never as deeply cordate or as narrow as in *V. peruviana*, whose lobes also sometimes overlap or cover the twig (e.g. *W. H. Lewis et al.* 10074, MO).

Notes. The majority of specimens cited here as *V. excisa*, including the source of illustrations in Pérez et al. (2014) and Jaramillo et al. (2004) were previously identified as *V. obovata*. In addition to the list of paratypes of *V. excisa* below, we provide a list of specimens that correspond to *V. obovata*. Our comparison between these two species is based on these specimens, as well as images of the original material of *V. obovata* collected and described by the Italian-Brazilian botanist, Adolpho Ducke (*A. Ducke* 1509, A, F, IAN, MG, NY!, RB-2 sheets, US-2 sheets).

Specimens examined. **COLOMBIA. Amazonas:** Araracuara, Río Caquetá, margen derecha 3 km arriba de la isla Sumaeta, 00°36'S, 072°10'W, 200–300 m, 31 May 1990 (fl bud), *E. Alvarez et al.* 668 (COAH [n.v.], NY!); Parque Nacional Nataural Amacayacu, 03°47'S, 070°15'W, 200–220, 11 Nov 1991, *J. Pipoly et al.* 15818 (COL!). **Putumayo:** selva higrófila del río Putumayo, Puerto Porvenir, arriba de Puerto Ospina, 230–250 m, 19 Nov 1940 (fr), *J. Cuatrecasas* 10653 (COL!, F [image!]). **ECUADOR. Napo:** Parque Nacional Yasuní, Carretera y Oleoducto de Maxus en construcción,

Km 27, 00°35'S, 076°30'W, 250 m, 4–27 July 1993 (fl bud), *M. Aulestia* 23 (MO!, UPCB [n.v.]); Parque Nacional Yasuní, Pozo petrolero Daimi 2, 00°55'S, 076°11'W, 200 m, 26 May–8 Jun 1988 (♂ fl bud), *C. E. Cerón & F. Hurtado* 3834 (INPA [image!], MEXU [image!], MO!, QCNE [n.v.], US [image!]); *ibid.*, 26 May–8 Jun 1988 (♀ fl bud), *C. E. Cerón & F. Hurtado* 4147 (COL!, INPA [image!], MO!, NY!); Parque Nacional Yasuní, Pozo Petrolero “Amo II” de Conoco, 00°52'S, 076°05'W, 230 m, 11–17 Jan 1988 (fr), *F. Coello* 59 (MO!, NY!); La Joya de los Sachas, Comunidad de Pompeya, lado sur del Río Napo, Campamento de Maxus, Río Jivino, carretera Maxus Km 1–5, 00°25'S, 076°37'W, 220 m, 1–28 Sep 1992 (fr imm), *A. Grijalva & G. Grefa* 115 (MO!, NY!); *ibid.*, 23–29 Nov 1992 (fr), *A. Grijalva et al.* 239 (MO!, QCA [n.v.]); La Joya de los Sachas, Pompeya, 00°25'S, 076°37'W, 250 m, 16–17 Aug 1992 (fr imm), *E. Gudiño* 1677 (COL!, MO!, QCNE [n.v.]); Pompeya, Río Indillama, entre la desembocadura al Napo y el cruce de la carretera de MAXUS, 00°25'S, 076°37'W, 250 m, 13 Dec 1992 (st, fr), *E. Gudiño et al.* 2139 (COL!, LOJA [n.v.], MO!, NY!, QCA [n.v.], UPCB [n.v.]); Pompeya, Carretera MAXUS km 3.9–5.2, 00°25'S, 076°37'W, 250 m, 14–15 Dec 1992 (fr), *E. Gudiño et al.* 2154 (COL!, LOJA [n.v.], MEXU [image!], MO!, QCA [n.v.], QCNE [n.v.]); Estación Experimental INIAP-Payamino, costado oeste del Río Payamino, 5 km al NW de Coca, 00°13'S, 077°10'W, 300 m, 25 Sep 1985 (fr), *D. Neill et al.* 6891 (INPA [image!], MO!, QCA [n.v.]); Maxus petroleum pipeline road, under construction, 2 km south of Río Napo, Comuna Pompeya, 00°30'S, 076°40'W, 220 m, 4 Dec 1992 (♀ fl, fr imm), *D. Neill et al.* 10182 (MO!, NY!); 5 km al Norte de Coca y de la vía Coca-Payamino, Finca Tipán, 00°25'S, 077°00'W, 250 m, 22 Oct 1988 (fr), *W. Palacios* 3186 (INPA [image!], MO!, PMA [image!], QCA [n.v.]); Tena, Estación Biológica Jatun Sacha, 10 km al oeste de la Estación, carretera hacia Tena, 01°03'S, 077°40'W, 500 m, 20 Sep 1989 (♀ fl bud), *W. Palacios & C. Iguago* 4435 (INPA [image!], MO!); Añangu, Parque Nacional Yasuní, 00°31'32"S, 076°23'W, 260–350 m, 30 May–21 Jun 1982 (bud fl), *SEF no. 8934* (NY-2 sheets!); Estación Experimental INIAP-San Carlos, Reserva Florística EL Ahuano, 00°19'S 076°50'W, 250 m, 8 Sep 1986 (fr), *J. Zaruma* 605 (NY!). **Pastaza:** Arajuno, Campamentos temporales 9, 22 y 25, línea propuesta del oleoducto Villano-CPF por ARCO, Km 25 noroeste del pozo Villano 2, 01°27'S, 077°36'W, 700 m, 3–14 Sep 1998 (♂ fl bud), *E. Freire & L. Santi* 3380 (MO!); Pozo petrolero “Moretecocha” de ARCO, 75 km al este de Puyo, 01°34'S, 077°25'W, 580 m, 4–21 Oct 1990 (imm fr), *E. Gudiño et al.* 956 (MO!, QCNE [n.v.]); Pozo petrolero Villano 2 de ARCO, 01°25'S, 077°20'W, 400 m, 1–18 Dec 1991 (fr), *F. Hurtado* 2980 (MO!); Río Capihuari, tributary of Río Pastaza, 02°30'S, 076°50'W, 285 m, 23 July 1980 (bud fl), *B. Ollgaard et al.* 35140 (NY!); Río Curaray, dos horas río abajo del pueblo Curaray, en la boca del Río Namoyacu, 01°24'S, 076°45'W, 275 m, 14–18 Aug 1985 (♂ fl bud), *W. Palacios & D. Neill* 612 (INPA [image!], MO!, QCNE [n.v.]); Pozo Petrolero Villano 2, 01°29'S, 077°27'W, 24 July 1992 (♀ fl bud), *W. Palacios* 10279 (MO!, QCNE [n.v.]); Pozo Petrolero “Danta 2” de UNOCAL, 50 km al sur-sureste de Curaray, 01°47'S, 076°48'W, 365 m, 1–19 Oct 1990 (fr), *D. Rubio & T. Coba* 839 (INPA [image!], MEXU-2 sheets [image!], MO!); Ruta del oleoducto propuesto por ARCO, Villano-La

Independencia, Km 24, 3 km al sur de San Virgilio, 01°24'S, 077°39'W, 830 m, 4 Sep 1997 (♂ fl), *H. Vargas et al. 1590* (MO!, QCNE [n.v.]). **Morona-Santiago:** Pozo petrolero "Garza" de TENNECO, 35 km (aprox.) al noreste de Montalvo, 01°49'S, 076°42'W, 260 m, 2–12 Jul 1989 (♂ fl bud), *V. Zak & S. Espinoza 4733* (INPA [image!], MO!, QCNE [n.v.]); [without province], margen izquierda del río San Miguel, entre Puerto Nuevo y Conejo, 28 Mar 1953 (fr), *G. Gutiérrez 2716* (COL!). **PERU. Amazonas:** Valle del Río Santiago, aprox. 65 km N de Pinglo, quebrada Caterpiza, 2–3 km atrás de la comunidad de Caterpiza, [03°50'00"S, 077°40'00"W], 200 m, 19 Sep 1979 (fr), *V. Huashikat 682* (INPA [image!], MO!); *ibid.*, 15 Mar 1980 (fr), *V. Huashikat 2267* (INPA [n.v.], MO!); *ibid.*, 21 Mar 1980 (fr), *V. Huashikat 2322* (MO!); Condorcanqui, Distrito El Cenepa, Comunidad de Mamayaque, 04°34'49"S, 078°14'01"W, 400 m, 11 Aug 1997 (fr), *R. Rojas et al. 0272* (MO!); Bagua, Rainforest along Río Marañón 2–10 km above mouth of Río Santiago, 250–275 m, 14–15 Oct 1962 (fl), *J. J. Wurdack 2272* (NY!). **Huánuco:** Yuyapichis, Puerto Inca, 00°40'S, 075°02'W, 270 m, 01–15 Jul 1989 (bud fl), [*B.*] *Kröll 476* (NY!); *ibid.*, 1–15 Jul 1989 (bud fl), [*B.*] *Kröll 487* (NY!); *ibid.*, 1–15 Aug 1987 (♀ fl), [*B.*] *Kröll 527* (NY!); *ibid.*, 16–31 Dec 1989 (fr), [without collector name] *Flores & Tello 192* (NY!); *ibid.*, 16–30 Jun 1990 (fl bud), [without collector name] *Flores & Tello 1801* (NY!); *ibid.*, 16–31 Aug 1990 (♀ fl), [without collector name] *Flores & Tello 1995* (NY!); *ibid.*, 1–15 Aug 1987 (♂ fl), [without collector name] *Saito 14* (NY!). **Loreto:** Habanillo, Km 67, carretera Dtto. Iquitos-Nauta, 04°10'S, 073°30'W, 130 m, 03 Jun 1988 (fl bud), *R. Vásquez et al. 10712* (INPA [image!], MO!); Ucayali, vicinity of LSV base camp, Quebrada Shesha, tributary of Río Abajao, ca. 65 km NE of Pucallpa, 08°02'S, 073°55'W, 250 m, 25 Jun 1987 (♂ fl), *A. [H.] Gentry & C. Díaz 58536* (MO!, NY!). **Pasco:** 6 km N of Puente Lorencillo No. 1 on Carretera Marginal, 32 km S of Dantas, 09°56'S, 075°00'W, 350 m, 30 Jun 1987 (st), *A. [H.] Gentry & C. Díaz 58640* (MO!). **Ucayali:** Río Blanco, [not elev.], 30 Jul 1923 (♂ fl), *G. Tessmann 3055* (NY!). **BRAZIL. Acre:** Cruzeiro do Sul, Río Juruá, right margin of Igarapé Viseu, ca. 6 km from left bank of Río Juruá, 08°15'S, 072°44'W, [not elev.], 05 Nov 1991 (fr), *C. A. Cid Ferreira et al. 10586* (NY!, UFACPZ [n.v.], UPCB [n.v.]); Jordão, along Río Jordão, 09°13'28"S, 071°58'26"W, 230–250 m, 06 Feb 2009 (fr), *R. Goldenberg 1316* (NY!, RB [image!]); Porto Acre, Bacia do Rio Purus, Reserva Florestal de Humaitá, margem esquerda do Rio Acre, ca. 4 horas de barco abaixo de Rio Branco, 10°07'S, 069°13'W [not elev.], 03 Nov 1993 (fr), *M. Silveira et al. 718* (INPA [image!], NY, UFACPZ [n.v.]); Sena Madureira, trail from W bank of Río Iaco to Río Purus, 3 km above confluence, [not elev.], 5 Oct 1968 (fr), *G. T. Prance et al. 7862* (F [image!], INPA [image!], NY!, P [image!], U [image!], US [image!]); Tarauacá, 1–3 km east of Río Tarauacá, at Tarauacá, [not elev.], 24 Sep 1968 (fr), *G. T. Prance 7510* (INPA [image!], NY!, US [image!]); Bacia do Río Juruá, Río Tarauacá, 08°27'39"S, 071°22'46"W, [not elev.], 19 Sep 1994 (imm fr), *M. Silveira et al. 840* (INPA [image!], NY!). **Amazonas:** Limoeiro, Est. Ecológica do Juamí Japurá, Río Japurá margem direita abaixo da confluência com Río Puruê, [not elev.], 16 Apr 1986 (fr), *C. A. Cid Ferreira et al. 7240* (NY!, UPCB [n.v.]); Parana do Autaz-Mirim, lago de Cobra, [not elev.], 25 Aug 1973 (♀ fl & imm fr), *C.*

C. Berg et al. P19742 (INPA [image!], NY!, US [image!]); Rio Solimões, loco Bom Futuro (ripa boreali fluvii, super São Paulo de Olivença), [not elev.], 4 Feb 1937 (♂ fl), [*W. A. Ducke 396* (NY!, US [image!]); near mouth of Rio Embira (tributary of Rio Tarauaca), 07°30'S, 070°15'W, [not elev.], 06 Jun 1933 (♂ fl), *B. A. Krukoff 4713* (NY-2 sheets!, US [image!]); Lábrea, trail from W bank of Rio Purus, opposite Labrea, [not elev.], 30 Oct 1968 (fr), *G. T. Prance 8106* (NY!, US [image!]); Rio Purus, Lago Preto, 2 km north of Lábrea, [not elev.], 25 Jun 1971 (bud fl), *G. T. Prance et al. 13692* (NY!, US [image!]).

Specimens examined of *Viola obovata*. **COLOMBIA. Amazonas:** Puerto Nariño, [not elev.], 24 Jul 1965 (♂ fl), *G. Lozano C. et al. 588* (COL!); trapezio Amazónico, entre los ríos Loretoyacu y Hamacayacu, [not elev.], [s.d.] Dec 1945 (fr), *J. M. Duque-Jaramillo 2366* (COL); Araracuara, Pintadillo (frente a la tercer isla), margen izquierda río Caquetá, [not elev.], 14 Apr 1986 (fr), *J. H. Torres et al. 3159* (COL). **PERU. Loreto:** Maynas, Rio Yuvineto, affluent du Putumayo, [not elev.], 06 Feb 1978 (fr), *S. Barrier 549* (NY!); Maynas, near Villa Nueva, Borro Indian village on upper Río Yaguayacu, tributary of Río Ampiyacu, [not elev.], 8 Nov 1977 (fr), *A. [H.] Gentry & J. Revilla 20448* (MO!); Maynas, in vicinity of Mishana, between Río Nanay and Río Itaya, 130 m, 29 Nov 1977 (fr), *A. [H.] Gentry et al. 21006* (MO); Maynas, Mishana, Río Nanay, halfway between Iquitos and Santa María de Nanay, 130 m, [s.d.] 1979 (♂ fl), *R. Ramírez 10* (MO!); Iquitos, Allpahuayo, bosque del Instituto de Investigación de la Amazonía Peruana, km 21 carretera Quistococha-Nauta, [03°58'16"S, 073°25'07"W], [not elev.], 5 Jul 1992 (♂ fl), *R. Rueda & J. Ruiz 621* (MO!); Maynas, Llachapa, (Explor Napo), Río Napo, 130 m, 21 Jan 1983 (fr), *R. Vásquez & N. Jaramillo 3822* (MEXU [image!], MO!, NY!); Iquitos, Allpahuayo, Estación Experimental del Instituto de Investigaciones de la Amazonía Peruana (IIAP), [03°58'16"S, 073°25'07"W], [not elev.], 22 Aug 1990 (imm fr), *R. Vásquez et al. 14250* (MO!).

8. *Viola parkeri* D. Santam. & Lagom., sp. nov.

urn:lsid:ipni.org:names:77298667-1

Type. **PERU. Pasco:** Oxapampa, Dist. Palcazú, Evaluación de los Recursos del Bosque 0.5 ha en la Reserva Comunal Yanasha, Comunidad Nativa Loma Linda-Laguna, Sector Nueva Aldea, 10°23'13"S, 075°05'28"W, 600–620 m, 17 Oct 2005 (fr), *A. Monteagudo, A. Peña, R. Francis, L. Quicha, E. Camavilca & W. G. Camaña 10761* (holotype: MO! [accession 6101576, barcode MO-2134612], isotypes: AMAZ [n.v.], HUT [n.v.], MOL [n.v.], USM [n.v.], US [accession 3558469; image!]). Fig. 15

Diagnosis. *Viola parkeri* morphologically differs from all other species by the combinations of the fruit with a conspicuous “wing” along its dehiscence line, the surface is bullate and inconspicuously pubescent, flowers with the column of filaments shorter (0.2–0.4 mm long) than the anthers (0.5–0.7 mm long), leaf blades covered abaxially with inconspicuous, stellate and sessile trichomes and lateral veins that are evenly spaced.

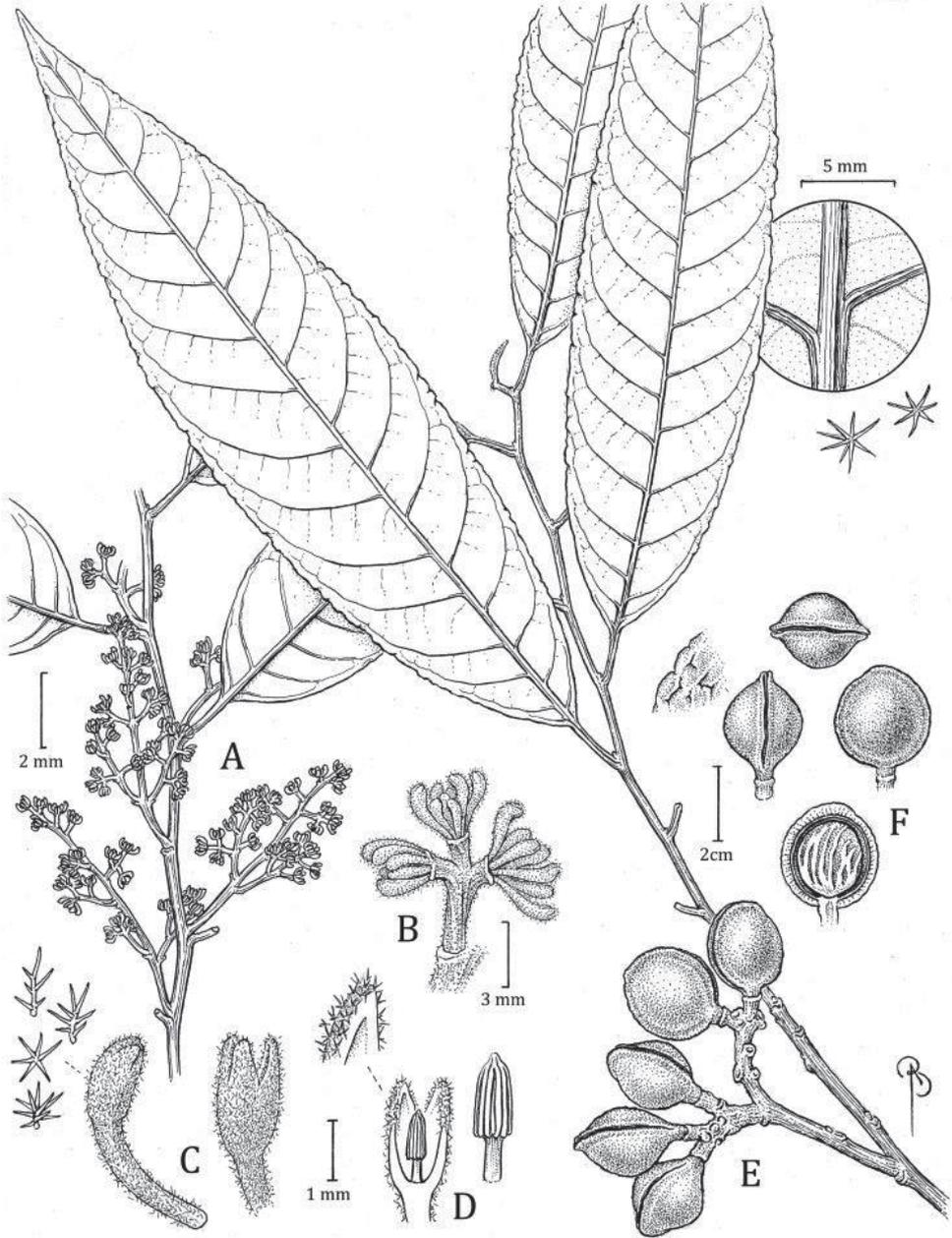


Figure 15. *Virola parkeri* **A** branch with staminate inflorescence **B** part of staminate inflorescence **C** lateral view of staminate perianth with an enlargement of trichomes (left) **D** medial sections of staminate flower, with detail of the lobe with trichomes (above left), and androecium (right) **E** branch with infructescence and detail of abaxial surface of leaf blade showing the midvein with enlargement of trichomes (top right) **F** different views of the fruits, detail of fruit surface (left), and an open fruit showing the seed covered by a laciniate aril (below). Drawn by Bobbi Angell based on *M. Huamán et al.* 334 (**A–D** MO), and *A. Monteagudo et al.* 10761 (**E–F** MO).

Tree 28–35 m tall, diameter, inner bark not described. **Exudate** reddish, location of exudate on plant not stated. **Twigs** 0.2–0.7 cm thick, terete, puberulent to glabrescent, trichomes stellate, sessile, brown-reddish, without lenticels. **Leaves** young terminal bud ca. 1.1×0.2 cm; petiole $1.4\text{--}1.7 \times 0.16\text{--}0.22$ cm, slightly canaliculate, puberulent (especially within the channel) to glabrescent, the trichomes stellate, sometimes with hyaline squamiform structures between the trichomes; leaf blades $19.7\text{--}24 \times 5.2\text{--}6.4$ cm, oblong; adaxial surface of mature leaves drying brown to grayish, glabrous, the surface smooth, sometimes shiny; abaxial surface drying white-grayish to pale brown, sparsely pubescent, the trichomes stellate, ca. 0.1 mm diameter, sessile, the central part of the trichome usually colorless, but sometimes with the central part reddish, the branches colorless; lateral veins 15–17 per side, 4 veins per 5 cm, spaced 1.5–1.7 (–2) cm, on adaxial side flat, the same color as the adaxial surface or a little darker, on abaxial surface slightly raised, tomentose, arcuate-ascending, slightly anastomosing near the margin and without forming a marked intramarginal vein; tertiary veins very slightly visible on both sides; midvein adaxially slightly elevated, immerse in a small channel, abaxially raised, rounded, puberulent to glabrescent, usually with denser pubescence on the sides; base acute, not revolute, flat; margin flat; apex acute. **Staminate inflorescence** 5.8–7 cm long, axes flattened, tomentose, with dendritic trichomes, ferruginous; peduncle $1.5\text{--}1.8 \times 0.18\text{--}0.24$ cm; main axes with 9–10 ramifications, the first pair opposite, subopposite or alternate, the others alternate; bracts not seen. **Staminate flowers** (in bud) in dense terminal fascicles of 10–30+ flowers, on a receptacle 1.5–2.5 mm wide; perianth 1.5–1.8 mm long, ovate to lanceolate, creamy yellow when fresh, connate to ca. 1 mm in length, external surface densely pubescent with ferruginous and dendritic trichomes, internal surface moderately pubescent (especially on the lobes); lobes 3, ca. 0.9×0.5 mm, ca. 0.2 mm thick, without resinous punctuations when rehydrated; stamens 3, the filament column 0.2–0.4 mm long and ca. 0.2–0.3 mm thick, glabrous, straight, constricted to slightly constricted at the apex; anthers 0.5–0.7 mm long, ca. 0.2 mm wide; apiculus ca. 0.8 mm long, acuminate, connate. **Pistillate inflorescences** and **pistillate flowers** not seen. **Infructescence** ca. 2.5 cm long, with 1–5 fruits, peduncle ca. 1×0.6 cm. **Fruits** 3–3.6 \times 2.8–3.1 cm, green when fresh (brown to blackish when dry), oblate, shortly stipitate, very inconspicuously pubescent (not falling like dust), puberulent at the base and sometimes on the carina, the trichomes stellate (sometimes with few dendritic), sessile, ferruginous, the surface bullate, the line of dehiscence winged, the wing ca. 0.4 cm long, the base obtuse, the apex rounded; pericarp ca. 0.3 mm thick (on the thickest side; ca. 0.2 mm thick on the thinnest side); pedicel 0.4–0.6 cm long. **Seed** ca. 1.9×1.6 cm, the testa brown to blackish when dry, smooth; aril color when fresh not described, blackish when dry, the texture dry and thin, lacinate almost to the base, in narrow bands distally.

Distinctive characters. The most striking character of *Virola parkeri* is its fruit, which is reminiscent of Saturn's form: it is oblate with a conspicuous "wing" along its dehiscence line (Fig. 6L, 15F). The fruit is further bullate and inconspicuously pubescent. Other characteristics that distinguish this new species are its leaf blades that are covered abaxially with inconspicuous, usually colorless stellate and sessile trichomes

and lateral veins that are evenly spaced; staminate flowers with perianth that is densely pubescent outside and the inner side moderately pubescent, the lobes are relatively thin, the column of filaments are shorter (0.2–0.4 mm long) than the anthers (0.5–0.7 mm long); and the thin, lacinate aril that covers the seed almost to the base.

Etymology. The specific epithet honors Theodore A. Parker III (1 Apr. 1953–3 Aug. 1993), renowned and talented ornithologist and research associate of the LSU Museum of Natural Science. Parker died in a plane crash on August 3, 1993 while surveying a remote forest in Ecuador, along with three other people: Raul Mortensen (the pilot), Eduardo Aspiazu (ecologist), and Alwyn H. Gentry (botanist). *Virola parkeri* occurs in Peru, a country where Parker spent much of his life studying birds and protecting natural resources. In this country, Parker together with Scott Robinson, established a Big Day record (331 bird species). He also contributed to a field guide to the birds of Peru, an important resource for birdwatching ecotourism. Finally, Parker was part of the Rapid Assessment Program (RAP) at Conservation International, which involved teams of scientists conducting biological surveys in remote areas of the tropics to determine their level of biodiversity and potential for conservation. Thanks to Parker's efforts, Bolivia established Madidi National Park, one of the most important centers for biodiversity.

Distribution. *Virola parkeri* is known only from Peru (Pasco Department) (Fig. 18C). It is found in primary forest between 400 and 620 m in elevation.

Phenology. Staminate flowers and fruits of *Virola parkeri* have been recorded in October. Pistillate flowers were not seen in the studied material.

Common name and uses. Common names include banderín and rrohuatquech (Peru; *M. Huamán et al.* 334). The wood is used in the manufacture of furniture and boxes, and house building (*M. Huamán et al.* 334).

Preliminary conservation status. *Virola parkeri* is Critically Endangered following IUCN criterion B2a. Justifying this status, it is known from only a single specimen, collected in 2008. The only locality of this species is within the Loma Linda community of the Yanesha indigenous community, and so may benefit from an ongoing compensated community-based forest monitoring program (Kowler et al. 2020).

Discussion. *Virola parkeri* is morphologically similar to *V. yasuniana* from Ecuador (which is formally described below) in various leaf traits, including overall shape, trichomes on the abaxial surface, lateral vein separation, and color when dry; additionally, both species share staminate perianth that is moderately pubescent internally and fruits with a markedly carinate dehiscence line, appearing like a wing. Differences among the two species are summarized in Table 10.

Virola parkeri's fruit with a wing-like carina resembles those of *V. peruviana* (see Fig. 6K, L). However, the new species is distinguished from *V. peruviana* in its leaves with acute bases (vs. usually cordate), fewer lateral veins (15–17 vs. 17–30 per side) that are usually more separated (1.5–1.7 [–2] vs. 0.6–1.3 [–1.7] cm), staminate inflorescences that are narrower and shorter, staminate flowers with the filament column shorter than anthers (0.5–0.7 mm vs. 1.1–1.6 mm long; from Smith and Wodehouse 1938), and oblate (vs. ellipsoid) fruits with rounded apex (vs. acute or apiculate).

Table 10. Comparison of *Virola parkeri*, with *V. yasuniana*.

Morphological character	<i>V. parkeri</i>	<i>V. yasuniana</i>
Leaf blade size	19.7–24 × 5.2–6.4 cm	15.7–27.5 × 4.4–6.6 cm
Spaced lateral veins	1.5–1.7 (–2) cm apart	0.9–1.5 (–1.9) cm apart
Staminate perianth lobes	ca. 0.9 × 0.5 mm	0.7–1 × 0.5–0.8 mm
Filament column	0.2–0.4 mm long, and ca. 0.1 mm wide at the base	0.3–0.5 mm long, and ca. 0.2–0.3 mm wide at the base
Anthers long	0.5–0.7 mm	0.5–0.6 mm
Apiculus long	ca. 0.8 mm	ca. 0.1 mm
Fruit size	3–3.6 × 2.8–3.1 cm	3.4–4.2 × 3.1–4 cm
Fruit carina	ca. 0.4 cm long (Fig. 6L)	0.4–0.7 cm long (Fig. 6M)
Seed	ca. 1.9 × 1.6 cm	ca. 2.5 × 1.9 cm

Notes. The type specimen of *Virola parkeri* (A. Montegudo et al. 10761) was previously identified as *Otoba parvifolia* (Markgr.) A. H. Gentry. However, while species of *Otoba* have malpighiaceous trichomes on abaxial leaf surfaces of leaf blades, these trichomes are dendritic or stellate in *Virola*. The other specimen studied (M. Huamán et al. 334) was identified as *V. elongata*. Duplicates may have been distributed under these names.

Specimens examined. PERU. Pasco: Oxapampa, Palcazú, Comunidad Nativa Loma Linda-Laguna, sector Nueva Aldea, Bosque de la Asociación Forestal Yanasha Concoll-Toroñ (AFYCT), 10°21'51"S, 075°03'20"W, 400 m, 16 Oct 2008 (♂ fl), M. Huamán et al. 334 (MO!, P [image!]).

9. *Virola tuckeræ* D. Santam. & Lagom., sp. nov.

urn:lsid:ipni.org:names:77298668-1

Type. COLOMBIA. Antioquia: Las Orquídeas, Vereda Calles, Parque Nacional Natural Las Orquídeas, Quebrada Honda, filo al NW de La Cabaña Calles, Parcela W, subparcelas W 8–W 9, 1300 m, 06°29'N, 076°14'W, 11 Dec 1992 (♂ fl), J. Pipoly, Á. Cogollo, D. Cádenas, M. Villa, O. Alvarez, L. Velez 16962 (holotype: MO! [accession 05011143, barcode MO-2657528], isotypes: not seen). Fig. 16

Diagnosis. *Virola tuckeræ* is similar to *V. cogolloi* in share similar distributions, leaf blades that are densely pubescent abaxially. Morphologically, it differs in having staminate flowers with long filament column (1.2–1.4 mm long vs. 1.1–1.2 mm), fruits with an inconspicuous layer and persistent trichomes (conspicuous layer of trichomes, caducous, that fall like dust). *Virola tuckeræ* previously confused with *V. sebifera*. It differs from these by the staminate flowers with perianth internally densely pubescent (vs. glabrous or almost glabrous), long staminal column (0.6–0.7 [–0.9] mm long vs. 0.2–0.6 mm), and large fruits (2.7 × 2.5 cm vs. 1–1.9 [–2.1]).

Tree (12–) 18–30 m × 17–30.1 cm diameter, inner bark not described. **Exudate** red, location of exudate on plant not stated, or in the fruit hyaline and oxidizing red. **Twigs** 0.21–0.37 cm thick, terete or slightly compressed, tomentose, trichomes dendritic, sessile, ferruginous, without lenticels or lenticels very small and scattered.

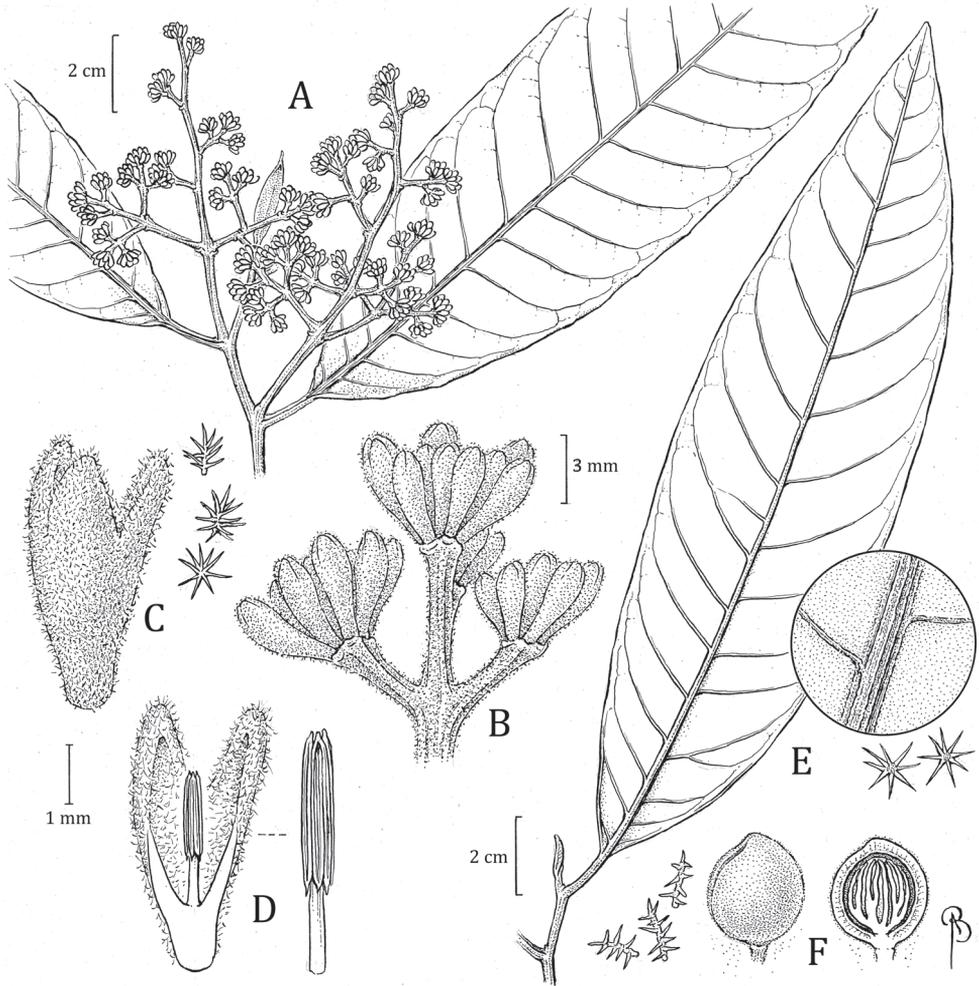


Figure 16. *Virola tuckerae* **A** branch with staminate inflorescence **B** partial staminate inflorescence **C** lateral view of staminate perianth with an enlargement of trichomes (right) **D** medial section of staminate flower and androecium (right) **E** Leaf blade on adaxial side, with detail of petiole and trichomes **F** fruits with detail of trichomes (left) and an open fruit showing seed covered with lacinate aril (right). Drawn by Bobbi Angell based on *J. Pipoly et al.* 16797 (**A–D** MO), and *Á. Cogollo et al.* 4147 (**E–F** MO).

Leaves young terminal bud 1.2–2 × 0.24–0.31 cm; petiole 1.1–1.7 (–2) × 0.23–0.35 (–0.5) cm, slightly canaliculate, not winged or slightly winged (*J. Pipoly et al.* 16805), tomentose, the trichomes dendritic; leaf blades 21–29.5 (–33.5) × 5–7.2 (–11.7) cm, narrowly oblong or rarely elliptical; adaxial surface when drying on mature leaves brown to blackish brown, the surface smooth, sometimes shiny, glabrous; abaxial surface when drying pale brown to grayish brown, densely pubescent, the trichomes stellate, ca. 0.1 mm diameter, sessile, the central part of the trichome pale reddish, sometimes a little darker, the branches pale reddish and not contrasting much in color

with the central part of the trichome; lateral veins 16–19 per side, 3–4 (–6) veins per 5 cm, spaced 1.1–1.8 (–2.1) cm, on adaxial side, the same color as the adaxial surface or slightly darker, flat to slightly raised, on abaxial surface blackish to brown reddish, raised, puberulent to glabrescent above, densely pubescent to the sides, arcuate-ascending distally, slightly anastomosing near the margin and without forming a marked intramarginal vein; tertiary veins very slightly visible on both sides, but especially above; midvein adaxially flat to slightly elevated, abaxially raised, rounded, tomentose to puberulent, more pubescent to the sides; base cuneate, not revolute, flat; margin flat; apex acute. **Staminate inflorescence** 5–9.5 cm long, axes flattened, tomentose, trichomes dendritic, ferruginous; peduncle 0.6–1.8 (–2.8) × 0.2–0.38 cm; main axes with (3–) 5–9 (–12) ramifications, the first pair opposite to subopposite, the others alternate; bracts not seen. **Staminate flowers** (in bud) in dense terminal fascicles of 9–20 flowers, on a receptacle 2–3 mm wide; perianth 3.5–5 mm long, oblong, fleshy, ferruginous when fresh (probably by the trichomes), connate to 1.5–2.5 mm in length, external surface densely pubescent with ferruginous and dendritic trichomes, internal surface densely pubescent (especially in the lobes); lobes 3, 2–2.5 × 1.2–1.7 mm, and 0.2–0.5 mm thick, without resinous punctuations when rehydrate); stamens 3, the filament column 0.6–0.7 (–0.9) mm long and 0.2 mm wide, glabrous, straight or sometimes a little wider at the base, not constricted at the apex; anthers 1.2–1.6 mm long, and 0.2–0.4 mm wide; apiculus 0.1–0.2 mm long, acuminate, slightly separated or connate. **Pistillate inflorescence** and **flowers** unknown. **Infructescence** unknown. **Fruit** 2.7 × 2.5 cm (only one seen, and that immature; *Á. Cogollo et al.* 4147), when fresh green and covered with brown trichomes, globose, densely tomentose, the trichomes dendritic (ca. 0.1–0.2 mm long), sessile, ferruginous, that fall as easily as dust, the surface probably smooth, the line of dehiscence slightly carinate, the base and the apex obtuse; pericarp ca. 2.4 mm thick; pedicel unknown. **Seed** length unknown × ca. 1.4 cm, the testa brown when dry, slightly ribbed distally; aril color not described when fresh, blackish when dry, the texture dry and thin, lacinate almost to the base, in narrow bands distally.

Distinctive characters. *Virola tuckerae* can be recognized by its narrow, oblong leaves with relatively close lateral veins (3–4 [–6] veins per 5 cm) and a cuneate base; its short-pedunculate staminate inflorescence with flowers organized in dense fascicles; its staminate flowers with fleshy perianth that is densely pubescent on both sides and a straight filament column that is shorter (0.6–0.7 [–0.9]) mm long) than the anthers (1.2–1.6 mm long); and its globe fruit that is densely tomentose with dendritic and ferruginous trichomes that fall like dust (Fig. 6N). Like other species described here, the new species is covered with stellate and sessile trichomes on the abaxial side of the leaf blades.

Etymology. It is a pleasure to name a species of *Virola* in honor of Dr. Shirley Cotter Tucker, a botanist, lichenologist, and Professor Emeritus at Louisiana State University (LSU). Despite many challenges she faced as a woman in science, Shirley has had an illustrious career marked by many honors, including a Boyd Professorship, the most prestigious academic rank granted at LSU to internationally renowned scholars.

Shirley is an important leader in botany, and served as president of two of the USA's most prominent botanical societies, the Botanical Society of America and the American Society of Plant Taxonomists. Shirley's intellectual contributions to botany are lasting, providing the foundation framework from which current research on floral morphology and evolution builds. Much of Shirley's academic research (which includes more than 100 published articles) has focused on floral morphology and anatomy, especially of legumes and magnoliids—including studies within Myristicaceae (Armstrong and Tucker 1986), making it particularly special to name a species of *Virola* in her honor. She maintains her passion for lichens into retirement, and actively curates loans of lichen specimens from her home in Santa Barbara, California. The generous philanthropy of Shirley and her late husband, Kenneth Tucker, have greatly benefitted the botanical community. At LSU, where two of the authors work, donations from the Tucker family established the Shirley C. Tucker Endowed Chair in Plant Systematics. The LSU herbarium is named in her honor.

Distribution. *Virola tuckerae* is only known from Antioquia, Colombia (Fig. 18A). It has been collected in premontane wet forest at 1300–1420 m elevation.

Phenology. *Virola tuckerae* was collected with flowers in December and fruit specimens collected in February. Pistillate flowers were not seen in the studied material.

Common name and uses. Sebo cordillero (Colombia; *Á. Cogollo et al.* 4147).

Preliminary conservation status. *Virola tuckerae* is Endangered following IUCN criterion B2a. Justifying this status, it is known from two localities and has an AOO of 4 km². While *V. tuckerae* benefits from its occurrence within Las Orquídeas National Park, this region (including within the national park) is still vulnerable to deforestation to expand human activities, including agriculture and livestock grazing (Pedraza-Peñalosa 2015; González-Caro and Vásquez 2017).

Discussion. All the studied specimens with flowers of *Virola tuckerae* were previously identified as *V. sebifera*, a species that is widely distributed from Central to South America. While *V. sebifera* has variable leaf morphology (i.e., shape, base, apex), it differs from *V. tuckerae* in its long staminate inflorescences (8–23 cm long vs. 5–9.5 cm long), internally glabrous or almost glabrous perianth (vs. densely pubescent), shorter staminal column (0.2–0.6 mm vs. 0.6–0.7 [–0.9] mm long), and smaller fruits (1–1.9 [–2.1] × 0.7–1.4 [–1.7] cm vs. 2.7 × 2.5 cm) that are usually covered by the dense and thick layer of trichomes. While the type of abaxial leaf pubescence is variable in *V. sebifera*, dendritic, pediculate trichomes are common (vs. stellate, sessile trichomes). Further, *V. sebifera* usually occurs at lower elevations.

Virola tuckerae shares similarities with *V. yasuniana*, including its leaf shape, sessile, stellate trichomes on the abaxial leaf surface, and the color of dried herbarium specimens. *Virola yasuniana* is a species primarily from the lowlands of Ecuador (200–480 [1000] m elevations) that is formally described below. However, *V. tuckerae* differs from it in its densely pubescent abaxial leaf surface (vs. sparsely pubescent to glabrescent in *V. yasuniana*) (Fig. 4N, O), staminate flowers with perianth that is densely pubescent internally (vs. moderately pubescent) and long anthers (1.2–1.6 mm vs. 0.5–0.6 mm long), and densely pubescent fruits (vs. puberulent).

Finally, *Virola tuckeræ* and *V. cogolloi*, grow closely in the same region (Urrao, sector Calles, Colombia); the differences and similarities between these species are discussed under *V. cogolloi*.

Notes. As mentioned above, collections with flower have been previously identified as *V. sebifera*. The specimen with fruit (*Á. Cogollo et al. 4147*) was previously identified as *V. elongata*. Duplicates may have been distributed under these names.

Specimens examined. COLOMBIA. **Antioquia:** Parque Nacional Natural Las Orquídeas, Margen derecha del Río Calles y de la quebrada “El Guaguó”, 06°32'N, 076°19'W, 1390–1420 m, 12 Feb 1989 (fr), *Á. Cogollo et al. 3924* (COL!); Urrao, Parque Nacional Natural Las Orquídeas, Margen derecha del Río Calles, 06°32'N, 076°19'W, 1300 m, 21 Feb 1989 (fr), *Á. Cogollo et al. 4147* (COL!, MO!); Urrao, Parque Nacional Natural Las Orquídeas, Vereda Calles Quebrada Honda, filo NW de La Cabaña Calles, 06°29'N, 076°14'W, 1330 m, 8 Dec 1992 (♂ fl), *J. Pipoly et al. 16797* (MO!, NY!); *ibid.*, 8 Dec 1992 (♂ fl), *J. Pipoly et al. 16805* (MO!, NY!); Las Orquídeas, Vereda Calles, filo NW de La Cabaña Calles, 06°29'N, 076°14'W, 1330 m, 10 Dec 1992 (♂ fl), *J. Pipoly et al. 16881* (MO!, NY!); *ibid.*, 10 Dec 1992 (♂ fl), *J. Pipoly et al. 16888* (MO!).

10. *Virola yasuniana* D. Santam., sp. nov.

urn:lsid:ipni.org:names:77298669-1

Type. ECUADOR. **Pastaza:** Pastaza Cantón, Pozo petrolero “Ramírez”, 20 km al sur de la población de Curaray, 300 m, 01°32'S, 076°51'W, 21–28 Feb 1990 (fr), *V. Zak & S. Espinoza 5149* (holotype: MO! [accession 04782630, barcode MO-713299], isotypes: NY!, QCNE [n.v.], US [accession 3625319; image!]). Fig. 17

Diagnosis. *Virola yasuniana* morphologically differ from all others species by the combinations of large fruits (3.4–4.2 × 3.1–4 cm) with very conspicuous wings in the line of dehiscence, staminate flowers, with a filaments column that is wide at the base, constricted at the apex, and usually shorter (0.3–0.5 mm long) than the anthers (0.5–0.6 mm long).

Tree 15–30 m × 30–40 cm diameter, outer bark brown, powdery, rough and thin, inner bark orange-red. **Exudate** translucent on internal bark, or watery reddish or reddish purple, location of exudate on plant not stated. **Twigs** 0.2–0.4 cm thick, terete, puberulent to glabrescent, trichomes stellate, sessile, brown-reddish to whitish, sometimes slightly lenticellate. **Leaves** young terminal bud 1–2 × 0.19–0.28 cm; petiole 1.1–1.7 × 0.15–0.21 cm, canaliculate, sometimes very short alate, puberulent, sometimes tomentose, the trichomes stellate; leaf blades 15.7–27.5 × 4.4–6.6 cm, lanceolate to oblong; adaxial surface when drying on mature leaves pale to dark brown, grayish, or blackish, the surface smooth, sometimes shiny, glabrous; abaxial surface when drying grayish, pale to dark brown, or white-grayish, sparsely pubescent to glabrescent, the trichomes stellate, ca. 0.1 mm diameter, sessile, the central part of the trichome colorless or reddish, the branches brown-reddish or colorless; lateral veins 14–18 per side, 4–5 veins per 5 cm, spaced 0.9–1.5 (–1.9) cm, on adaxial side, the same color

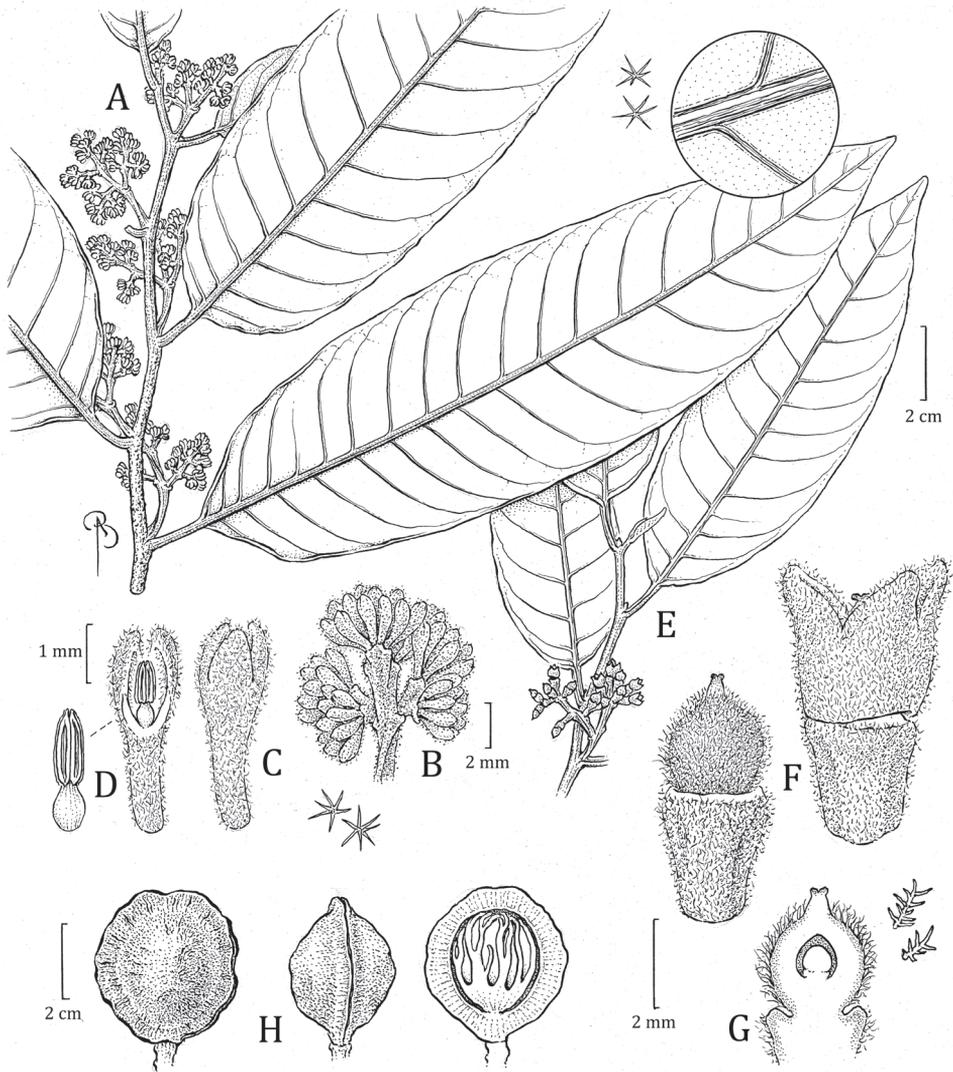


Figure 17. *Virola yasuniana* **A** branch with staminate inflorescence, with detail of midvein and trichomes (upper right) **B** partial staminate inflorescence **C** lateral view of staminate perianth **D** medial section of staminate flower (right) and androecium (left) **E** branch with pistillate inflorescence **F** lateral view perianth (right) of pistillate flower and gynoeceum (left) **G** Medial section of pistillate flower, showing detail of trichomes on gynoeceum (right) **H** different views of the fruits, and an open fruit (right) showing the seed covered by a lacinate aril. Drawn by Bobbi Angell based on *V. Zak & S. Espinoza 5039 (A–D MO)*, *C. Cerón & F. Hurtado 6560 (E–G MO)*; *V. Zak & S. Espinoza 5149 (H MO)*.

as the adaxial surface or a little darker, flat, on abaxial surface slightly raised, glabrous to scattered pubescent, arcuate-ascending, slightly anastomosing near the margin and without forming a very marked intramarginal vein; tertiary veins very slightly visible on both sides; midvein adaxially slightly elevated, abaxially raised, rounded to

triangular, puberulent to glabrescent; base acute, not revolute, flat; margin flat; apex acute. **Staminate inflorescence** 6–6.7 cm long, axes flattened, tomentose, trichomes appressed dendritic, ferruginous; peduncle $1.2\text{--}1.7 \times 0.19\text{--}0.26$ cm; main axes with 6–9 ramifications, the first pair opposite to subopposite, the others alternate; bracts not seen. **Staminate flowers** (in bud) in dense terminal fascicles of 15–25+ flowers, on a receptacle 2.1–3 mm wide; perianth 1.3–1.8 mm long, subglobose to infundibuliform to ovate, subcarnose, brown when fresh, connate to 1.2–1.5 mm in length, external surface densely pubescent with ferruginous and dendritic-stellate trichomes, internal surface moderately pubescent (especially in the lobes); lobes 3, $0.7\text{--}1 \times 0.5\text{--}0.8$ mm, ca. 0.1 mm thick, without resinous punctuations when rehydrated; stamens 3, the filament column 0.3–0.5 mm long, ca. 0.2–0.3 mm wide, glabrous, wide at the base and constricted at the apex; anthers 0.5–0.6 mm long, and 0.3–0.4 mm wide; apiculus ca. 0.1 mm long, acuminate, connate. **Pistillate inflorescence** 2.6–2.9 cm long, axes flattened, tomentose, with trichomes dendritic, ferruginous; peduncle ca. $1 \times 0.2\text{--}0.3$ cm; bracts not seen. **Pistillate flowers** in terminal fascicles of 1–2 flowers, on a receptacle 2.5–3.5 mm wide; perianth ca. 3–3.1 mm long, ovate, subcarnose, brown when fresh, connate by ca. 1.5–2 mm long, external surface densely pubescent with ferruginous and dendritic trichomes, internal surface moderately pubescent (especially in the lobes), sometimes slightly pubescent at the base; lobes 3, ca. $1.3\text{--}1.8 \times 1.1\text{--}1.3$ mm, and ca. 0.1 mm thick; gynoecium ca. $2\text{--}3 \times 1.6\text{--}2.4$ mm, globose, densely pubescent, with ferruginous trichomes; stigma 2-lobed, ca. $0.3\text{--}0.5 \times 0.3$ mm, erect, flat seen from above, drying blackish, slightly wavy at the margins. **Infructescence** 2.3–3.4 cm long, with 1–2 fruits, peduncle $0.7\text{--}1.5 \times 0.34\text{--}0.6$ cm. **Fruits** $3.4\text{--}4.2 \times 3.1\text{--}4$ cm (including wings), green when fresh (blackish when dry), ellipsoid to somewhat flattened (immature), shortly stipitate, puberulent, the trichomes stellate, sessile, ferruginous or whitish and not falling like dust, the surface rugulose, the line of dehiscence winged, the wing 0.4–0.7 cm long, the base rounded to subcordate, the apex rounded; pericarp 1.3 and 2.3 mm thick (measured from two specimens); pedicel 0.7–1 cm long. **Seed** ca. 2.5×1.9 cm, the testa drying dark brown to yellowish, slightly ribbed distally; aril color when fresh described once as red, brown-reddish to blackish when dry, the texture dry and thin, lacinate almost to the base, in narrow bands distally.

Distinctive characters. The very distinctive fruits of *Virola yasuniana*, which are large with very conspicuous wings in the line of dehiscence (Fig. 6M), make it almost impossible to confuse with any other species of *Virola* already described. Other characteristics that distinguish this new species include leaf blades that are abaxially covered with inconspicuous stellate and sessile trichomes, evenly spaced lateral veins that are comparatively spaced, and moderately pubescent internal perianth in staminate flowers, and a filaments column that is wide at the base, constricted at the apex, and usually shorter (0.3–0.5 mm long) than the anthers (0.5–0.6 mm long).

Etymology. The specific epithet refers to Parque Nacional Yasuní, where most of the collections of this new species come from. At present, 2700 vascular plant species are documented from Yasuní, including a high diversity of lianas, epiphytes, and ferns; it is estimated its flora comprises approximately 3213 species; Yasuní is also home to

ca. 1570 species of birds, fishes, mammals, amphibians and reptiles (Bass et al. 2010; Pérez et al. 2014). The description of *Virola yasuniana* is one step closer to a full documentation of this region.

Distribution. *Virola yasuniana* is known from the Napo and Pastaza provinces of Ecuador, where it occurs in primary forests, on hills with red soil, or soils composed of sedimentary rocks. Is also located in Acre state of Brazil, where it grows in terra firme on poorly drained terrace (Fig. 18A). It ranges from 200–480 m in elevation, with a single collection reaching 1000 m (*C. Cerón & F. Hurtado 6560*).

Phenology. Staminate flowers of *Virola yasuniana* have been collected in January, February and November, while pistillate flowers have been collected in April, May, and July. Fruits are known from February, March, June, and September.

Common name and uses. Dobompapoca (Ecuador: Huaorani; *M. Aulestia & O. Gonti 1969*); guapa (Ecuador: Quichua; *C. Cerón & F. Hurtado 6560*). The wood has commercial use (*C. Cerón & F. Hurtado 6560*).

Preliminary Conservation Status. *Virola yasuniana* is Vulnerable following IUCN criterion B2a. It is known from two localities, has an EOO of 117,581 km², and an AOO of 32 km². This species benefits from its occurrence in the Yasuní National Park of Ecuador, which experiences very low rates of deforestation (Bass et al. 2010; van der Hoek 2017), even while the broader region is experiencing land use changes (Heredia-R et al. 2021).

Discussion. It is possible to confuse *Virola yasuniana* with *V. parkeri* from Peru due to their similar leaves (i.e. shape, color when dry, base, venations, and trichomes), staminate perianth that is pubescent on both surfaces, and markedly carinate fruit. Differences among the two species are summarized in Table 11.

Herbarium specimens of *Virola yasuniana* were previously identified as *V. calophylla*, *V. obovata*, or *V. peruviana*, all of which have leaf blades with lateral veins that are well separated and stellate, sessile trichomes on abaxial leaf surface. Additionally, the new species shares fruits with a conspicuous carina with *V. peruviana*. Differences among these species are summarized in Table 10.

Table 11. Comparison of *Virola yasuniana*, with *V. calophylla*, *V. obovata*, and *V. peruviana*. †From Smith and Wodehouse (1938).

Morphological character	<i>V. yasuniana</i>	<i>V. calophylla</i>	<i>V. obovata</i>	<i>V. peruviana</i> †
Leaf blade size, and base	15.7–27.5 × 4.4–6.6 cm; acute	(15–) 20–60 × 10–16 cm; (usually) deeply cordate to truncate (obtruse)	11.5–29.5 (–34) × 6.8–12.5 cm; attenuate to acute	16–35 × 6.5–10.5 cm; shallowly cordate or rounded
# of lateral veins	14–18	11–28	14–19	17–30
Long filament column	0.2–0.4 mm	0.2–0.6 mm	0.4–0.8 mm	0.4–0.6 mm
Long anthers	0.5–0.6 mm	0.4–0.5 mm	0.4–0.6 mm	1.1–1.6 mm
Fruit size, and pubescent	3.4–4.2 × 3.1–4 cm, inconspicuously pubescent	2.5–3 × 1.2–2.5 cm; tomentulose,	1.3–2.3 × 0.8–1 cm, densely pubescent	2–2.8 × 1.5–2.2 cm; glabrescent
Carina on the line of dehiscence	Markedly carinate (Fig. 6M)	Carinate (Fig. 6E)	Not carinate (Fig. 6J)	Conspicuously carinate (Fig. 6K)
Pericarp thick	1.3 and 2.3 mm (just two specimens measured)	0.5–5 mm	1–1.2 mm	0.5–1.5 mm

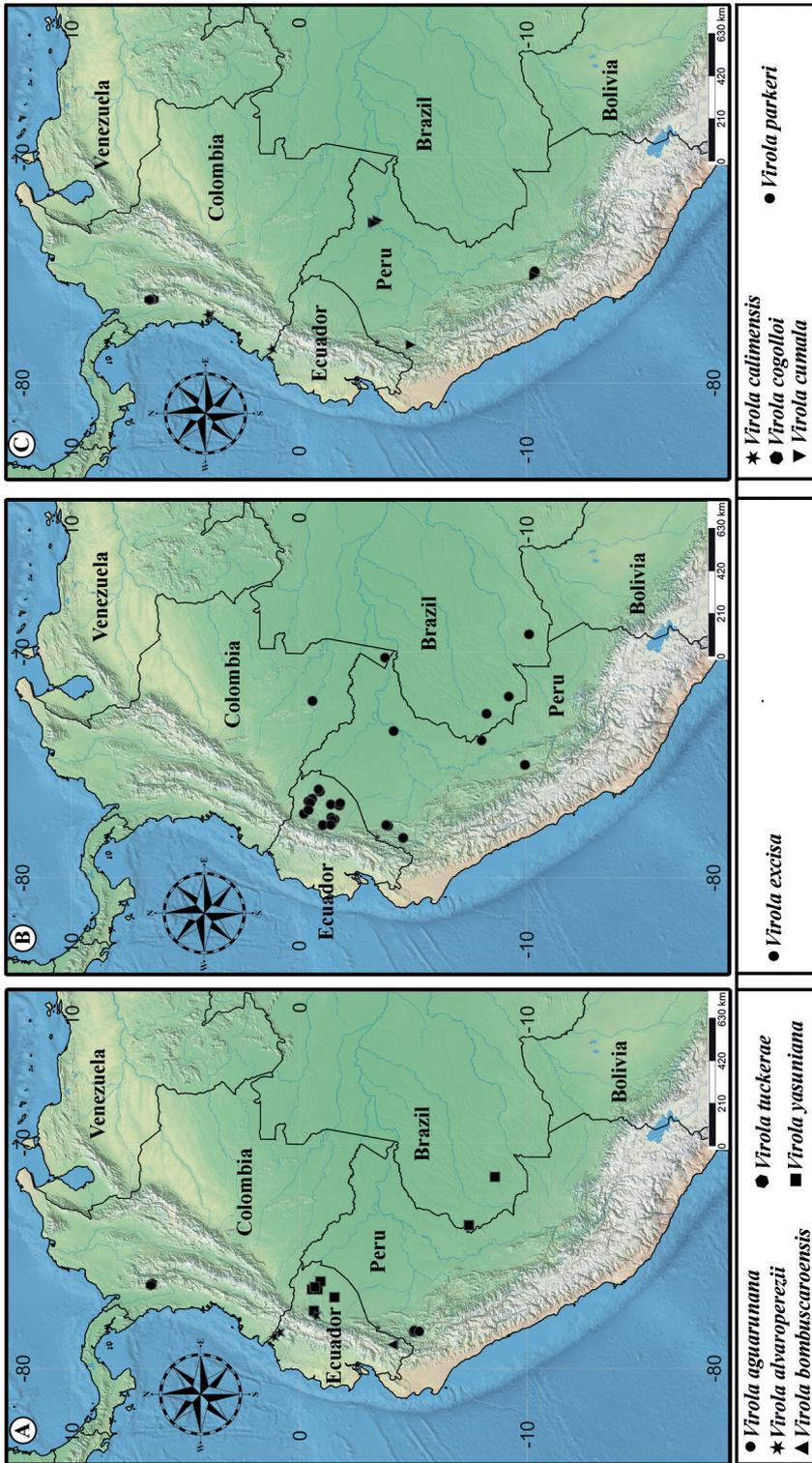


Figure 18. Geographic distribution of the new species of *Virola*.

Notes. Several collections of *Virola yasuniana* were treated as *V. obovata* in *Flora of Ecuador* (H. Vargas & J. Cerda 678, V. Zak & S. Espinoza 4871, 5039, 5049, 5149; Jaramillo et al. 2004). Additionally, studied with “aberrant fruits” that is discussed under *V. peruviana* in *Flora of Ecuador* (Jaramillo et al. 2004) correspond with this new species (C. Cerón & F. Hurtado 6560, M. Aulestia & G. Grefa 247, M. Aulestia & O. Gonti 1969).

Specimens examined. ECUADOR. Napo: Parque Nacional Yasuní, carretera y Oleoducto de Maxus en construcción, Km. 20, 00°33'S, 076°30'W, 250 m, 28–30 Jul 1993 (♀ fl), M. Aulestia & G. Grefa 247 (MO!, UPCB [n.v.]); Parque Nacional Yasuní, Carretera y oleoducto de Maxus en construcción, km 54–58, 00°48'S, 076°30'W, 250 m, 26–30 Sep 1993 (fr), M. Aulestia & N. Andi 783 (MO!, QCNE [n.v.], UPCB [n.v.]); Reserva Etnica Huaorani, carretera y oleoducto de Maxus en construcción Km. 92–96, al norte del Río Yasun, 00°55'S, 076°09'W, 250 m, 20 March 1994 (fr), M. Aulestia & O. Gonti 1969 (MO!, UPCB [n.v.]); Archidona, Carretera Hollín-Loreto, Km 50, comunidad Guagua Sumaco, Faldas al sur del Volcán Sumaco, 00°38'S, 077°27'W, 1000 m, 29 Apr–2 May 1989 (♀ fl), C. Cerón & F. Hurtado 6560 (MO!, NY!); Parque Nacional Yasuni-ECY, Sendero “Napo”- 300 m, 00°40'40"S, 076°23'40"W, 200–300 m, 24 Sep 2009 (fr), Á. Pérez & W. Santillán 4361 (MO!); Parque Nacional Yasuni-ECY, Sendero “Chorongo”- 600 m, 00°40'40"S, 076°23'40"W, 200–300 m, 16 Nov 2009 (fl bud), Á. Pérez & W. Santillán 4402 (MO!); Loreto, 2 Km al oeste del río Tutapishco, 00°36'S, 077°22'W, 480 m, 27 Jan 1996 (♂ fl bud), H. Vargas & J. Cerda 678 (MO!, QCA [image!], UPCB [n.v.]). **Pastaza:** Pozo petrolero “Ramírez”, 20 km al sur de la población de Curaray, [01°32'S, 076°51'W], 300 m, 21–28 Feb 1990 (♂ fl), V. Zak & S. Espinoza 4871 (INPA [image!], MO!, NY!); *ibid.*, 21–28 Feb 1990 (♂ fl), V. Zak & S. Espinoza 5039 (INPA [image!], MO!, NY!, QCNE [n.v.]); *ibid.*, 21–28 Feb 1990 (♂ fl), V. Zak & S. Espinoza 5049 (INPA [image!], MO!, NY!). **BRAZIL. Acre:** Mâncio Lima, Bacia do Alto Juruá, Rio Moa, Parque Nacional da Serra do Divisor, caminho para o rio Anil, 07°26'27"S, 073°39'28"W, [not elev.], 17 Jun 1996 (imm fr), M. Silveira et al. 1374 (NY!, UFACPZ [n.v.], UPCB [n.v.]); Mun. Tarauacá, Basin of Rio Juruá, Rio Tarauacá, right bank, Seringal Tamandaré, Colocação Santa Maria, Praia de Santa Maria, 08°35'12"S, 071°30'57"W, [not elev.], 18 Nov 1995 (♂ fl), D. C. Daly et al. 8594 (NY!, UFACPZ [n.v.], UPCB [n.v.]).

New record

***Virola kwatae* Sabatier. *Adansonia* ser. 3,19: 273. 1997.**

Type. FRENCH GUIANA. Rivère Arataye, Saut Pararé, 31 Jul 1984 [♀ fl & fr], [*D.*/Sabatier 931 (holotype P [barcode P00135215, image!]; isotype CAY, INPA, K [barcode K000575173, image!], MPU [barcode MPU024622, image!], NY! [NY00346038], P-3 sheets [barcodes P00135216, P00135217, P00135218, image!], US [barcode US00623540, image!]).

Distributions. French Guiana and Brazil (Amapá).

Common name. Gaan busi Mulumba (Paramaka; Sabatier 1997). French Guiana: yayamadou, yayamadou montagne (Créole) (Mitchell 2002).

Etymology. The specific epithet alludes to the Spider monkeys, or ateles (*Ateles panisczsis*), locally called kwata, who consume the fruits of this species (Sabatier 1997).

Note. *Virola kwatae* was previously known from French Guiana. However, in a recent study of herbarium specimens at New York Botanical Garden, a collection with fruit made in Amapá state, Brazil was located. To our knowledge this represents the first record of this species among the Flora of Brazil.

Specimens examined. BRAZIL. **Amapá:** Município Macapá, Rio Falsino, approx. 10 km upstream of confluence with Rio Araguari, 00°50'S, 51°45'W, 13 Dec 1984 (fr), *D. C. Daly et al.* 3865 (MO [n.v.], NY!, US [image!]).

Nomenclatural note

Virola macrocarpa A. C. Sm. *Brittonia* 2: 476. 1938.

Type. COLOMBIA. **Boyacá:** [Municipality Muzo] [El Umbo] El Humbo, ca. 130 mi N of Bogotá, alt. ca. 1100 m, 15 Mar. 1933 [fr], *A. E. Lawrence* 675 (holotype: B, destroyed; lectotype, designated here: MO-2 sheets [accession 1068405, 1068404, barcodes MO-100018, MO-100024]; isolectotypes A [barcode 00039901; image!], F-2 sheets [barcodes F0360189F, F0360190F; image!], G-2 sheets [barcodes G00341083, G00341085; image!], K [barcode K000575178; image!], S [S-R-6995], US-2 sheets [barcodes US00098908, US00098909; image!]; photo of the B specimen at P [barcode 02026667; image!]).

Distribution. Endemic to Colombia (Boyacá).

Notes. *Virola macrocarpa* was described by Smith based on a specimen collected by the Scottish immigrant Alexander E. Lawrence in the Andes of Boyacá, Colombia (Smith and Wodehouse 1938). In the protologue, Smith mentions that the type is deposited in the herbarium of the Botanisches Museum, Berlin-Dahlem (B), and F, M, S, US; there are additional, duplicates at A, G, K, and MO. Because the material at B was destroyed during World War II, we designate the material deposited at Missouri Botanical Garden (MO) as lectotype for this name, according to Art. 9.11 of ICN (Turland et al. 2018). This specimen is mounted on two sheets that are properly labelled as being parts of the same specimen (i.e., “Sheet 1 of 2,” “Sheet 2 of 2”) according to ICN Art. 8.3 (Turland et al. 2018). One of these sheets shows the adaxial side of leaves and the infructescence axes (MO-1068404; sheet 1 of 2), while the other (MO-1068405; sheet 2 of 2) includes fragments of both adaxial and abaxial leaf surfaces and a single dehiscent fruit that is attached, with six additional fruits inside the packet. This second sheet is annotated in Smith’s handwriting. These specimens were distributed under the name of *V. sebifera*.

The name *Virola macrocarpa* was applied to collections from Costa Rica and Panama that now correspond to *V. allenii*, *V. amistadensis*, and *V. otobifolia*, as well some collections from Colombia and Ecuador that now correspond to *V. alvaroperezii*, *V. calimensis*, and *V. cogolloi*.

It is important to mention that, following our species concept, this name has been widely used to identify specimens, and is thus frequent in the literature and specimen databases. As circumscribed here, *V. macrocarpa* is known only from the type collection and is restricted to Colombia. We believe that the identity of following and others specimens identified as *V. macrocarpa* should be evaluated when more collections are available, including: *D. Cárdenas et al.* 2772 (fr.; COL, MO); *A. Gentry & E. Rentería* 24055 (fr.; COL, MO), *S. E. Hoyos-Gómez & A. Upegui* 130 (fr.; COL).

Key to *Virola* species with sessile stellate trichomes with darker centers

(*Virola alvaroperezii* and *V. macrocarpa* are not included because staminate flowers are unknown; †from Smith and Wodehouse 1938; §from Carreira 1985).

- 1a Mature leaf blades densely pubescent on abaxial surface (Fig. 4C–G, N)....**2a**
 2a Staminate flowers with the filament column shorter than the anthers **3a**
 3a Leaf blades widely oblong to elliptical (7.3–11 cm wide), base obtuse; staminate inflorescence broadly paniculate; staminate flowers in lax terminal fascicles, the filament column 0.4–0.6 (–0.8) mm long, anthers 0.6–1 (–1.2) mm long; fruits with persistent trichomes; pericarp ca. 3.8–4 mm thick; growing at 20–260 m elevation ***V. calimensis***
 3b Leaf blades narrowly oblong or rarely elliptical (5–7.2 [–11.7] cm wide), base cuneate; staminate inflorescence narrowly paniculate; staminate flowers in dense terminal fascicles, the filament column 0.6–0.7 (–0.9) mm long, anthers 1.2–1.6 mm long; fruits with trichomes that fall like dust; pericarp ca. 2.4 mm thick; growing at 1300–1330 m elevation ***V. tuckeræ***
 2b Staminate flowers with the filament column longer than the anthers **4a**
 4a Abaxial leaf blade surface drying silver to golden (Fig. 4E, F); perianth of staminate flowers 1.2–2.1 mm long, internal surface glabrous to glabrescent **5a**
 5a Staminate inflorescences 12–30 cm long; §pollen subtype *divergens*, type I; fruits 2.5–3 cm long (Fig. 6E); pericarp 2–5 mm thick..... ***V. calophylla***†
 5b Staminate inflorescences 1–4 cm long; §pollen subtype *flexuosa*, type II; fruits 1.8–2.1 cm long (Fig. 6F); pericarp 0.5–0.8 mm thick ***V. calophylloidea***†
 4b Abaxial leaf blade surface drying brown or whitish-grayish (Fig. 4C, G); perianth of staminate flowers 2.8–4.1 mm long, internal surface densely pubescent..... **6a**
 6a Leaf blades with cordate base; staminate inflorescences ca. 5.4 cm long, wide paniculate; staminate flowers in dense terminal fascicles, filament column with scattered trichomes (Fig. 10D); fruits covered with a conspicuous layer of trichomes that fall like dust..... ***V. bombuscaroensis***
 6b Leaf blades with obtuse base; staminate inflorescences 7.5–9 cm long, narrow paniculate; staminate flowers in lax terminal fascicles, filament column

- glabrous; fruits covered with an inconspicuous layer of persistent trichomes .
 ***V. cogolloi***
- 1b Mature leaf blades sparsely pubescent to glabrescent on abaxial surface
 (Fig. 4A, H–K, O) **7a**
- 7a Staminate flowers with the lobes of the perianth glabrous or almost glabrous
 internally **8a**
- 8a Twigs and inflorescence axes covered with appressed trichomes; fruits 2.7–3.5
 long, covered by an inconspicuous layer of trichomes (Fig. 3B); pericarp 3.2–
 3.8 mm thick ***V. allenii***
- 8b Twigs and inflorescence axes covered with erect trichomes; fruits 2–2.6 cm
 long, covered by a conspicuous layer of trichomes (Fig. 6I, J); pericarp 1–2.3
 (–3) mm thick **9a**
- 9a Leaf blades truncate to subcordate at the base; perianth of staminate flowers
 without resinous punctuations when rehydrated; infructescence with pedun-
 cle ca. 1.4–3.5 (–5) cm long; fruits 1.4–1.7 cm wide, without stipe, the base
 truncate to obtuse ***V. excisa***
- 9b Leaf blades attenuate to acute at the base; perianth of staminate flowers with
 resinous punctuations when rehydrated; infructescence with peduncle 0.7–
 1.3 cm long; fruits 0.8–1 cm wide, shortly stipitate, the base rounded
 ***V. obovata***
- 7b Staminate flowers with the lobes of the perianth pubescent internally **10a**
- 10a Staminate inflorescence 2.2–2.5 cm long; fruits covered with a conspicuous
 layer of trichomes (Fig. 6A) ***V. aguarunana***
- 10b Staminate inflorescence 3–9.5 cm long; fruits inconspicuously pubescent
 **11a**
- 11a Leaf blades (6.7–) 9.5–13.5 (–19.7) cm wide; staminate flowers with the fila-
 ment column 0.9–1 mm long ***V. otobifolia***
- 11b Leaf blades 4.4–9.5 (–12.5) cm wide; staminate flowers with the filament
 column 0.2–0.5 mm long **12a**
- 12a Leaf blades elliptical to widely elliptical; staminate flowers in lax terminal
 fascicles; fruits 1.7–2 cm wide, the line of dehiscence slightly carinate
 ***V. amistadensis***
- 12b Leaf blades lanceolate to oblong; staminate flowers in dense terminal fasci-
 cles; fruits 2.8–4 cm wide, the line of dehiscence markedly carinate, like a
 wing **13a**
- 13a Staminate flowers with the filament column ca. 0.1 mm thick at the base, not
 widening at the base (i.e., straight throughout); fruits 3–3.6 × 2.8–3.1 cm,
 oblate, the line of dehiscence with a wing ca. 0.4 cm long ***V. parkeri***
- 13b Staminate flowers with the filament column ca. 0.2–0.3 mm thick at the
 base, widening at the base; fruits 3.4–4.2 × 3.1–4 cm, ellipsoid to somewhat
 flattened, the line of dehiscence with a wing 0.4–0.7 cm long
 ***V. yasuniana***

Key to distinguishing *Virola cumala* from other *Virola* species with leaves with numerous, close lateral veins

(Adapted from Smith and Wodehouse 1938 and Rodrigues 1980; ‡material from Peru quoted here under notes of *V. cumala*).

- 1a Adaxial surface of mature leaf blades pubescent **2a**
 2a Leaf blades 25–60 cm long; staminate perianth submembranous; mature fruits covered by a conspicuous layer of trichomes (Fig. 12E).....
 ***V. decorticans***
- 2b Leaf blades 5–22 (–25.5) cm long; staminate perianth carnose to subcarnose; mature fruits without conspicuous layer of trichomes (glabrescent or densely tomentose to glabrate) (Fig. 12A–C, F, G, I)..... **3a**
 3a Leaf blades with 28–32 lateral veins; staminate inflorescences to 8.5 cm long; staminate flowers with perianth 2–3 mm long; filament column 1.3–1.5 mm long; deciduous during blossom..... ***V. chrysocarpa***
- 3b Leaf blades with 24–58 lateral veins; staminate inflorescences to 14 cm long; staminate flowers with perianth ca. 1–1.5 mm long; filament column 0.3–0.4 mm long; evergreen ***V. guggenheimii***
- 1b Adaxial surface of mature leaf blades glabrous **4a**
 4a Leaf blades with 16–38 lateral veins..... **5a**
 5a Leaf blades on abaxial side densely tomentose, with pediculate, dendritic trichomes; staminate flowers with perianth 2–2.5 mm long, carnose; androecium 1.2–1.6 mm long; fruits on the line of dehiscence smooth or slightly carinate, apex obtuse (Fig. 12F) ***V. koschnyi***
- 5b Leaf blades on abaxial side tomentulose to puberulent, with sessile or shortly pediculate, stellate trichomes; staminate flowers with perianth 1.2–1.8 mm long, membranous to submembranous; androecium 0.8–0.9 mm long; fruits on the line of dehiscence carinate, apex apiculate to acute..... **6a**
 6a Leaf blades with 40–50 lateral veins; staminate inflorescence with 10–15 flowers per fascicle ***V. flexuosa***
- 6b Leaf blades with 30–38 lateral veins; staminate inflorescence with 50–100 flowers per fascicle ***V. minutiflora***
- 4b Leaf blades with (30–) 40–60 lateral veins **7a**
 7a External surface of staminate perianth almost glabrous (pubescent only at base and apex)..... ***V. multinervia***
- 7b External surface of staminate perianth uniformly pubescent (not described for *V. multicostata*) **8a**
 8a Staminate flowers with perianth 2–3 mm long; fruits 3–5.7 cm long, conspicuously pubescent, always present; pericarp 3–6 mm thick..... **9a**
 9a Leaf blades with 49–65 lateral veins; staminate flowers with filament column 0.5–0.7 mm long; fruits rounded to ellipsoid, covered by a conspicuous

- layer of trichomes (1–2.3 mm thick), obtuse at apex (Fig. 12D) *V. cumala*
- 9b Leaf blades with (32–) 40–50 lateral veins; staminate flowers with filament column 0.9–1.3 mm long; fruits ovoid-ellipsoid, covered by an inconspicuous layer of trichomes, acuminate to rostrate at apex (Fig. 12G) *V. megacarpa*
- 8b Staminate flowers with perianth 1–1.5 mm long (not described in *V. polyneura*); fruits 1.4–3 (–3.5) cm long, glabrous or densely tomentellous (if tomentellous, cauduous trichomes soon falling and leaving surface completely glabrous; if conspicuously pubescent, the layer of trichomes falling easily to the touch [*V. crebrinervia*]); pericarp 1–3 (–5) mm thick **10a**
- 10a Abaxial surface of leaf blades glabrous to glabrescent **11a**
- 11a Leaf blades 10–18 (–29) × 2.2–3 (–6) cm, narrowly oblong-lanceolate; fruits 2–3.5 × 1.8–2.5 cm, tomentose (Fig. 12C); pericarp 2–5 mm thick *V. crebrinervia*
- 11b Leaf blades 20–28 × 4–10 cm, elliptic or oblong-elliptic; fruits 2.1–2.3 × 1.5–1.8 cm[‡], glabrous to glabrescent (Fig. 12I); pericarp 1.3–1.5 mm thick[‡] *V. multicosata*
- 10b Abaxial surface of leaf pubescent **12a**
- 12a Leaf blades 10–42 × 3.5–12.5 cm, abaxial surface with sessile trichomes; deciduous in flower *V. caducifolia*
- 12b Leaf blades 5.5–11 × 4–8.5 cm, abaxial surface with pediculate trichomes; evergreen *V. polyneura*

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Johnstonella punensis (Boraginaceae), a new species endemic to the dry Puna of Chile

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Abstract

In an earlier molecular phylogenetic study, a sample of what was originally identified as *Cryptantha hispida* (Boraginaceae) from Chile, grouped with species of the genus *Johnstonella*. This sample was subsequently shown not to be *C. hispida*, but an undescribed species, endemic to the dry Puna of Chile. This new species is described here as *Johnstonella punensis*, along with a key to all South American species of the genus. *Johnstonella punensis* resembles other members of that genus in having an ovate fruit shape, ovate nutlets and a long style that extends beyond the nutlets. It is unusual in the genus in having a non-tuberculate, dimpled to rugulose nutlet surface sculpturing. Its closest relative within the genus is likely the South American *J. diplotricha*.

Resumen

En un estudio filogenético molecular anterior, una muestra que originalmente se identificó como *Cryptantha hispida* (Boraginaceae) de Chile se agrupaba con especies del género *Johnstonella*. Posteriormente se demostró que esta muestra no era *C. hispida* sino una especie no descrita, endémica de la Puna seca de Chile. Esta nueva especie se describe aquí como *Johnstonella punensis*, junto con una clave para todas las especies sudamericanas del género. *Johnstonella punensis* se parece a otros miembros del género por tener un fruto de forma ovada, clusas ovadas y un estilo largo que sobrepasa las clusas. Es inusual en el género que la clusa tenga una superficie no tuberculada, sino que rugulosa formando hoyuelos. Su pariente más cercano dentro del género es probablemente la especie sudamericana *J. diplotricha*.

Keywords

Boraginaceae, Chile, *Cryptantha*, *Johnstonella*, phylogenetics, Puna, taxonomy

Introduction

The genus *Johnstonella* Brand (Boraginaceae s. str., after Chacón et al. 2016 and Luebert et al. 2016) was originally segregated from *Cryptantha* Lehmann ex G.Don and described with two species: *Johnstonella inaequata* (I.M.Johnst.) Brand and *J. racemosa* (A.Gray) Brand, the latter the lectotype of the genus (Simpson et al. 2014). The genus was not accepted by subsequent botanists, however, until the molecular phylogenetic study by Hasenstab-Lehman and Simpson (2012). Their Sanger sequencing-based phylogeny inferred a clade distinct from *Cryptantha* and composed of the two species described by Brand (1925), plus another six species formerly classified in *Cryptantha*. Consequently, these eight sequenced species, plus an additional three based on morphology, were transferred from *Cryptantha* to *Johnstonella* by Hasenstab-Lehman and Simpson (2012). (See Simpson et al. 2019 for a complete listing of *Johnstonella* taxa.) Subsequent high-throughput sequencing-based analyses (Simpson et al. 2017a, Mabry and Simpson 2018) confirmed *Johnstonella* to be a well-supported clade, distinct from *Cryptantha*. However, two taxa previously placed in *Johnstonella* by Hasenstab-Lehman and Simpson (2012), based on morphology or Sanger sequencing data – *J. echinosepala* (J.F.Macbride) Hasenstab & M.G.Simpson and *J. micromeres* (A.Gray) Hasenstab & M.G.Simpson – were found to be nested within *Cryptantha*, based on these two later, more comprehensive molecular phylogenetic studies (see also Simpson and Rebman 2021). New nomenclatural combinations by these workers and by Simpson et al. (2019), plus a recent new species discovery by Hinton and Nesom (2021) has led to the current recognition of 16 total species and three varieties in *Johnstonella*, based either on the cited molecular phylogenetic studies or on comparative morphological similarities (Amsinckiinae Working Group 2022).

In the Simpson et al. (2017a) and Mabry and Simpson (2018) analyses, it was noted that a Chilean species of *Cryptantha* – *C. hispida* (Phil.) Reiche – grouped phylogenetically within *Johnstonella*. This was unexpected given that *Cryptantha hispida* was considered by Johnston (1927), in his revision of the South American *Cryptantha*, to be a close relative of *Cryptantha phaceloides* (Clos) Reiche. In fact, a specimen of the latter species that was included in Simpson et al. (2017a) grouped with strong support within their “*Cryptantha* s.str.” clade. Examination of the fruit morphology of the sequenced sample of *C. hispida* (Teillier 4754; accession number CONC150914; see Fig. 1) clearly demonstrated that it had been misidentified because *C. hispida* has a different nutlet morphology (see Simpson et al. 2019 for images of the type of *C. hispida* and further discussion). The specimen involved did, however, resemble *Johnstonella* taxa in features of the calyx and nutlet shape and in style length, but was also distinct from any known species in nutlet sculpturing.

Methods

As the *Teillier 4754* (CONC150914) sample grouped with strong support phylogenetically within the *Johnstonella* clade in the two cited molecular studies and because of its distinctive nature of nutlet morphology, we thought it a new species. Herbarium specimens at **SGO** were examined in order to ascertain the presence of other specimens of this putative new taxon. Five additional collections that fit the characteristics of the *Teillier 4754* specimen were identified as conspecific. All specimens were studied morphologically and used to create a description and key. Measurements of structures were made with a ruler graduated to 0.1 mm. A type specimen was selected from amongst the **SGO** specimens. Photographic documentation of plant components was made using a Visionary Digital Imaging System photomicroscope or a Nikon Microphot camera attached to an Olympus dissecting microscope. The six total collections of the new taxon were mapped, along with the three other South American species of *Johnstonella*: *J. albida* (Kunth) M.E.Mabry & M.G.Simpson, *J. diplotricha* (Phil.) Hasenstab & M.G.Simpson and *J. parviflora* (Phil.) Hasenstab & M.G.Simpson. The map was created using the BerkeleyMapper tool (https://ucjeps.berkeley.edu/consortium/load_mapper_multi.html) from georeferenced specimen data transcribed or estimated for the six specimens of the new species and from georeferenced specimen data of the other three *Johnstonella* species, the latter derived from records of the Global Biodiversity Information Facility (GBIF.org 2022a, b, c). Aspects of biogeographic regions, after Luebert (2021), were overlain on distribution maps. The morphological and biogeographic differences amongst all four *Johnstonella* species were evaluated, the morphology of *J. albida*, *J. diplotricha* and *J. parviflora* being based on study of specimens listed in Appendix 1. All herbarium acronyms after Thiers (2022).

Results

Based on comparative morphological studies, we feel confident that the six samples studied represent a new species. In addition, these collections have distributions within the same general range in the Atacama Desert in Chile as the original *Teillier 4754* specimen. We describe the new species as follows.

Taxonomic treatment

Johnstonella punensis M.G.Simpson & Muñoz-Schick, sp. nov.

urn:lsid:ipni.org:names:77298802-1

Figs 1–7 (Note: all cited herbarium specimens indicate herbarium accession numbers)

Type. CHILE. Prov. de Antofagasta, Entre Calama y San Pedro de Atacama, Anual, abundante, Expedición al Desierto. 22°41.27'S, 68°28.46'W [estimated from label locality data], 2800 m elevation. 3 January 1944, C. Muñoz 3710 (**holotype:** SGO119165!)

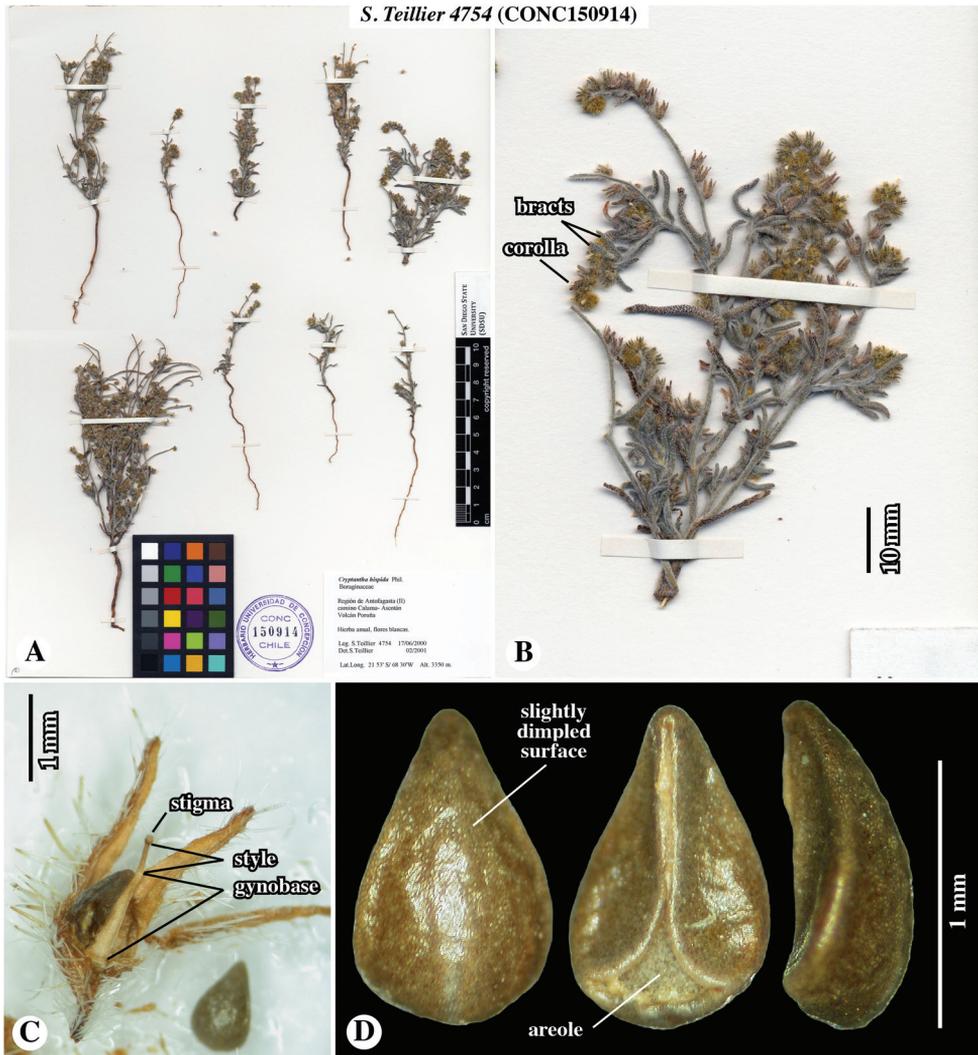


Figure 1. Paratype of *Johnstonella punensis*, sp. nov., Teillier 4754 (CONC150914) [originally identified as *Cryptantha hispida*] **A** whole herbarium sheet **B** close-up of a single plant; note very small corollas and flower bracts **C** close-up fruit; note dense appressed-strigose along margin and spreading-hispid trichomes along mid-rib **D** nutlet in (left to right) dorsal, ventral and lateral views; note slightly dimpled surface.

Diagnosis. *Johnstonella punensis* resembles *J. diplotricha* and *J. parviflora* in having nutlets that are marginally sharp-angled, but differs in having nutlets lacking a lineate-rimmed margin and in having a surface that is dimpled to rugulose, lacking tubercles.

Description. Plants annual herbs, base of plant sometimes woody at maturity, 10–15 cm tall. Root a taproot, not reddish. Stems with primary axis giving rise to secondary branches from base and mid-region, densely appressed-strigose only or appressed-strigose and spreading to inclined-hispidulous, the trichomes whitish

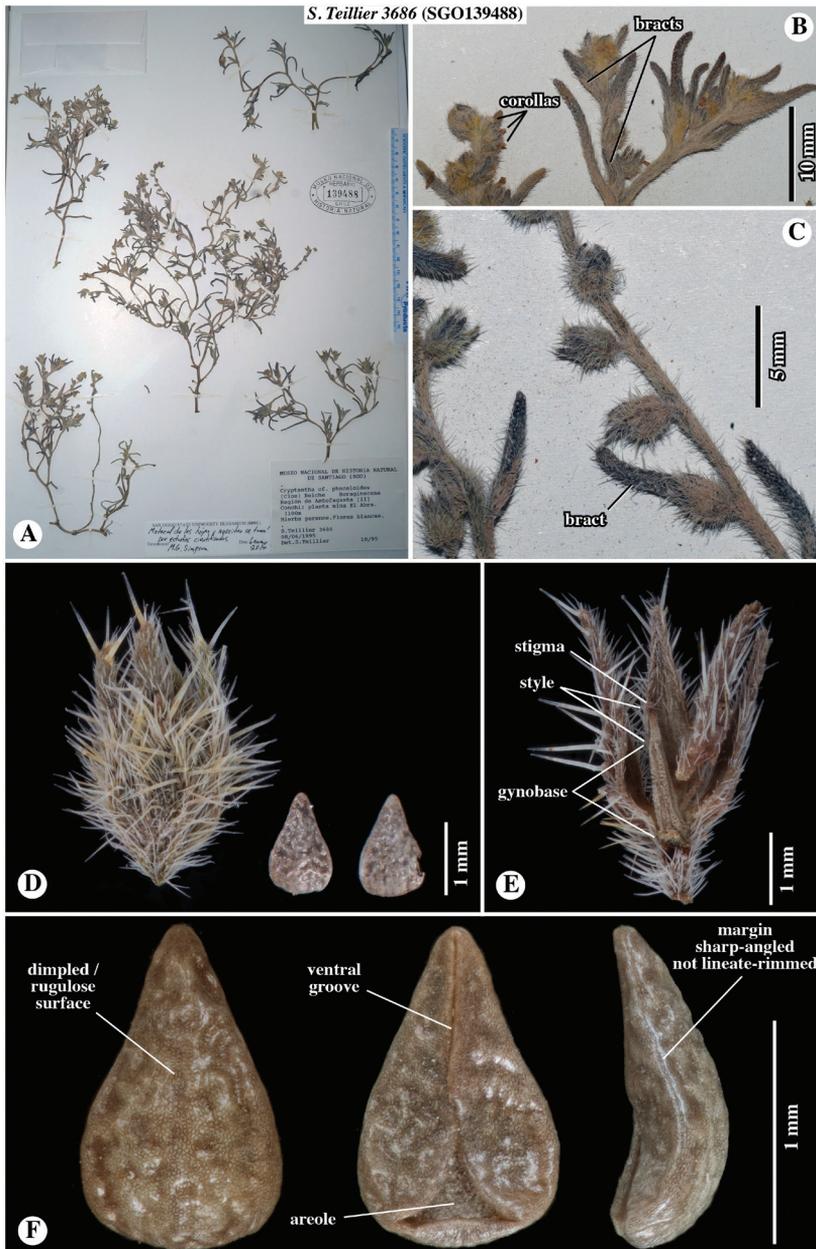


Figure 2. Paratype of *Johnstonella punensis*, sp. nov., Teillier 3686 (SGO139488) [originally identified as *Cryptantha* cf. *phaceloides*] **A** whole herbarium sheet **B** close-up of inflorescences; note very small corollas and flower bracts **C** close-up inflorescence axis and fruits; note dense appressed-strigose and spreading-hispidulous trichomes of axis and note bract subtending lowermost fruit **D** close-up of fruiting calyx, showing short, appressed hirsute trichomes along marginal surface and ascending hispid trichomes along mid-rib, only two nutlets per fruit illustrated **E** fruit opened, showing gynobase, style and stigma **F** nutlet, in (left to right) dorsal, ventral and lateral views; note dimpled surface, narrow ventral groove with triangular areole at base and sharp-angled, but not lineate-rimmed margin.

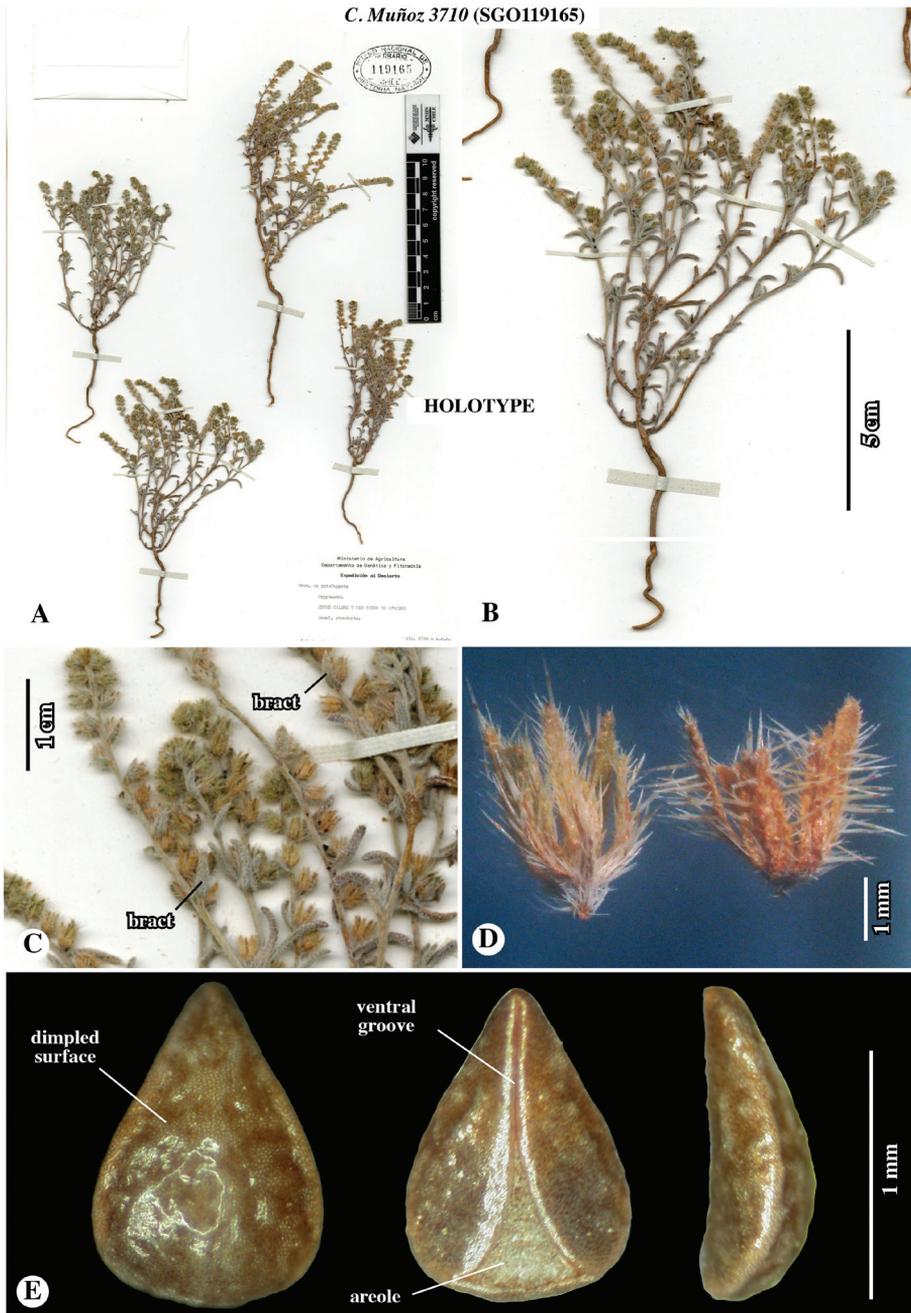


Figure 3. Holotype of *Johnstonella punensis*, sp. nov., C. Muñoz 3710 (SGO119165) [originally identified as *Cryptantha*] **A** whole herbarium sheet **B** close-up of one plant **C** close-up of inflorescence cymules with fruits; note flower bracts **D** close-up of two fruiting calyces, showing short, appressed to ascending hirsute trichomes along marginal surface and ascending to horizontal hispid trichomes along thickened mid-rib **E** nutlet, in dorsal (left), ventral (middle) and lateral (right) views; note dimpled to rugulose surface and narrow ventral groove with triangular areole at base.

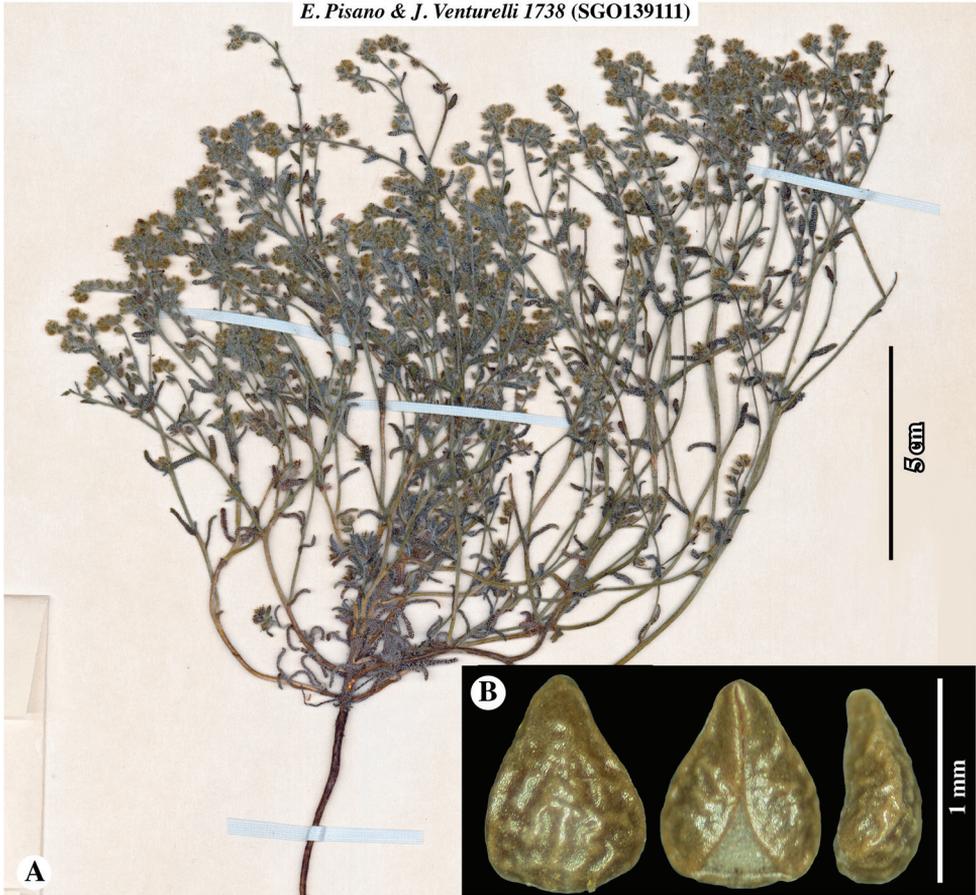


Figure 4. Paratype of *Johnstonella punensis*, sp. nov., *Pisano & Venturrelli 1738 (SGO139111)* **A** plant from herbarium sheet **B** nutlet, in dorsal (left), ventral (middle) and lateral (right) views; note rugulose surface, narrow ventral groove with triangular areole at base and sharp-angled margin.

to greyish, 0.5–1.1 mm long. Leaves alternate, sessile, conduplicate, often recurved, grey-green, 8–13 × 1–2 mm, smaller above and at extreme base, linear to narrowly oblanceolate, entire, apex obtuse to rounded, both surfaces short-hirsute, trichomes ascending, basally white-pustulate on adaxial surface. Inflorescence of ca. 10–20 cymules, terminating upper lateral branches, straight at maturity, cymules 3–7 cm long in fruit, with ca. 10–20 flowers, peduncles 1–2 cm long, fruits erect to ascending, lowest fruits not touching, inflorescence bracts at cymule base and along peduncles, bracts similar to, slightly smaller than vegetative leaves. Flowers mostly, but not all, bracteate, bracts linear to narrowly elliptic, ascending, slightly conduplicate, straight to incurved, 3–10 mm long, decreasing in size towards apex. Pedicels ca. 0.5 mm long. Calyx ovoid, symmetric, ca. 2 mm long in flower, 2.5–3 mm long in fruit, deciduous at maturity, aposepalous, sepals lanceolate, apically narrowly acute, ascending to erect, straight to slightly recurved apically, mid-rib abaxially slightly thickened, margins appressed-hir-

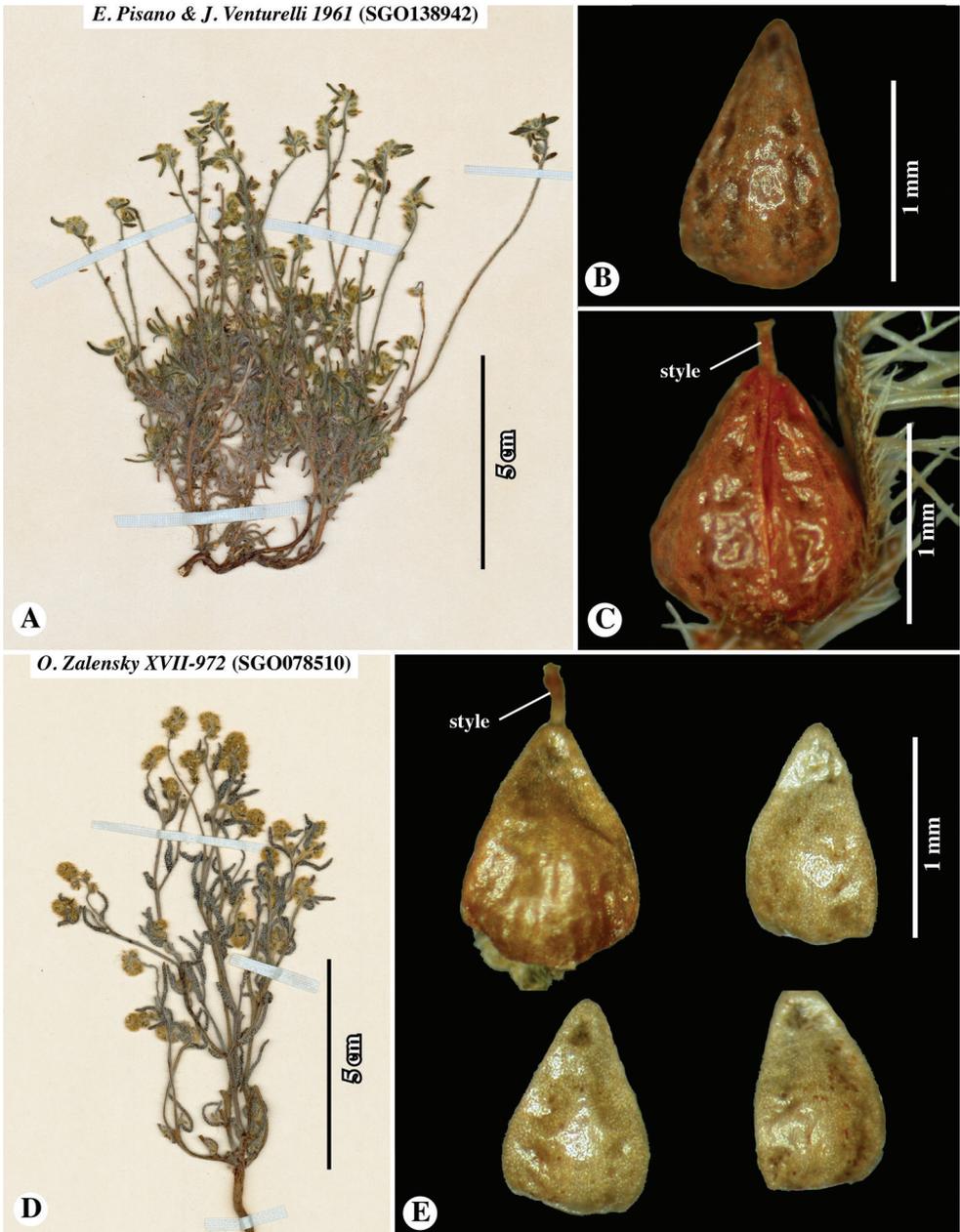


Figure 5. Paratypes of *Johnstonella punensis*, sp. nov. **A–C** Pisano & Venturelli 1961 (SGO138942) **A** plant from herbarium sheet **B** nutlet in dorsal view, showing strongly dimpled surface **C** fruit showing four homomorphic nutlets and elongate style **D–E** Zalensky XVII-972 (SGO078510) **D** plant from herbarium sheet **E** four nutlets of single fruit, dorsal view; note dimpled surface and slight heteromorphism, larger, more adherent nutlet at upper left.

sute, mid-rib inclined to spreading-hispid. Corolla white, rotate to funnellform, tube as long as calyx, limb ca. 1 mm broad. Gynobase 1.1–1.4 mm long, ca. as long as nutlet. Style ca. 0.5 mm long, extending 0.3–0.5 mm beyond nutlet apices. Nutlets 4, brown, erect, 1.1–1.5 × 0.7–0.9 mm, homomorphic or slightly heteromorphic in size only with the abaxial nutlet slightly larger and more adherent to the gynobase, all nutlets brown, generally ovate (length:width ratio ca. 1.3–1.8), very rarely lance-ovate, base rounded, margins sharp-angled but lacking a prominent lineate rim, apex acute, rounded at extreme tip, abaxially convex, adaxially concave-incurved, lacking papillae or tubercles, surface nearly smooth to dimpled or rugulose, spinal ridge absent, attachment scar ventral groove margins abutted or with one side slightly overlapping in upper two-thirds, with an open triangular areole in the lower third, margins laterally bifid at base.

Distribution and habitat. *Johnstonella punensis* is endemic to Chile, ranging in elevation from ca. 2800 to 3420 m. It occurs in the south-western dry Puna region near the eastern margin of the Atacama Desert (biogeographic region after Luebert 2021; see Fig. 6).

Phenology. Based on data from available specimens, *Johnstonella punensis* is reported to flower in January or June, the flowering time presumed to be dependent on precipitation.

Rarity and conservation status. *Johnstonella punensis* is known from only six collections to date. Known populations range from near La Taira (just south of Reserva Nacional Alto Loa) south to near Cuadrilla Díaz (just southwest of Parque Nacional Lullailaco). Based on the paucity of specimens currently known, the species is likely to be deemed Data Deficient, according to guidelines of the IUCN (2022). However, we suspect that this species may qualify as a species of elevated conservation concern (IUCN 2022), because of its relatively narrow geographic range and limited known population sizes.

Etymology. The specific epithet *punensis* means “of the Puna” (the word *puna* derived from Spanish via Quechua, the language of the aboriginal people of that region; Merriam-Webster.com 2022). The epithet highlights the restriction of this new species to the dry Puna biogeographic region (after Luebert 2021; Fig. 6).

Paratypes (arranged chronologically). CHILE. Prov. de Antofagasta, Ascotán, suelos arenosos, graníticos o volcánicos, crece bajo las rocas en lugares protegidos del viento, 21°32.87'S, 68°19.61'W [estimated from label locality data], 3970–4200 m elevation, 23–24 January 1943, *E. Pisano & J. Venturelli 1738 (SGO139111!)*. Prov. de Antofagasta, Socaire, suelo arenoso, en lugares secos entre las piedras, 23°35.42'S, 67°53.49'W [estimated from label locality data], 3000 m elevation, 22 February 1943, *E. Pisano & J. Venturelli 1961 (SGO138942!)*. Prov. de Antofagasta, Depto. El Loa, Valle río Vilama en las pendientes pedregosas en el desierto, 22°55.21'S, 68°11.43'W [estimated from label locality data], 2400 m elevation [estimated from label locality data], 9 June 1968, *O. Zalensky XVII-972 (SGO078510!)*. Región de Antofagasta (II), Conchi: Planta mina El Abra, Hierba perenne, flores blancas. 21°51.82'S, 68°43.11'W [estimated from label locality data], 3100 m elevation, 8 June 1995, *S. Teillier 3686*

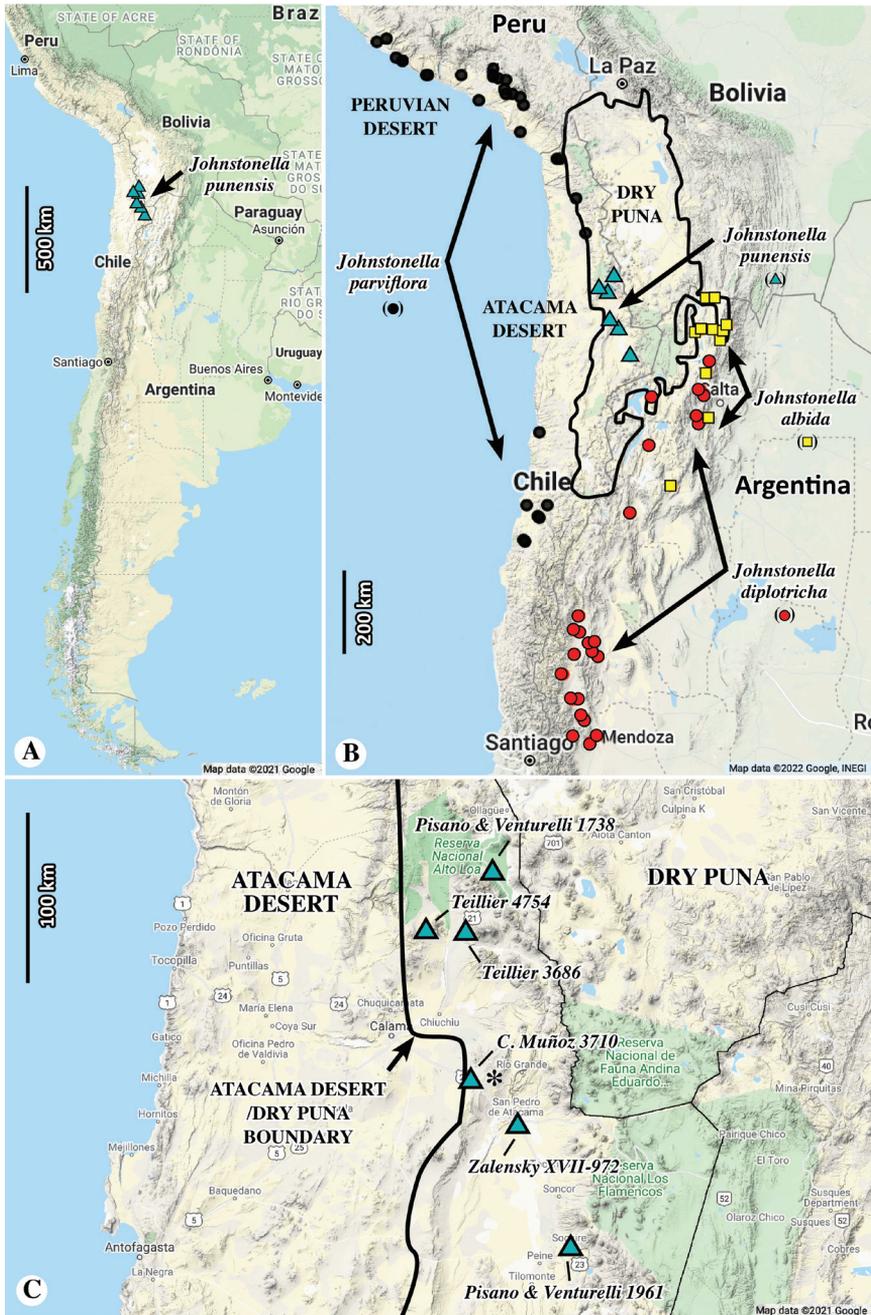


Figure 6. **A** distribution map of six known type collections of *Johnstonella punensis* in South America, endemic to north-eastern Chile **B** distributions of *J. punensis* and of the other three species of South American *Johnstonella*, the latter derived from GBIF.org (2022a, b, c) data; pertinent biogeographic regions of Luebert (2021) are overlain; note restriction of *J. punensis* to the western dry Puna Region **C** close-up of distribution of *J. punensis*, showing localities of six known collections (* = holotype locality); note boundary between Atacama Desert and dry Puna; all maps from Google 2021, INEGI Data.

(SGO139488!). Región de Antofagasta (II), Camino Calama-Ascotán Volcán Poruña, Hierba anual, flores blancas, 21°53'S, 68°30'W, 3420 m elevation, 17 June 2000, S. Teillier 4754 (CONC150914!) [Note: DNA was extracted from leaf material of this specimen for the studies of Simpson et al. (2017a) and Mabry and Simpson (2018)].

Key differentiating *Cryptantha* from *Johnstonella* and separating the species of *Johnstonella* that occur in South America. Note that *J. albida* occurs in both North and South America

- 1 Nutlets 1–4, mostly similar in size and sculpturing, if dissimilar single different nutlet positioned towards inflorescence axis (adaxial), if similar, nutlet margins rounded to sharp-angled and winged, wings lobed; nutlet surfaces smooth or papillate and/or tubercled, if tubercled, tubercles generally not whitish..... ***Cryptantha***
- Nutlets 4, mostly dissimilar in size and/or sculpturing, if dissimilar, single different nutlet positioned away from inflorescence axis (abaxial), if similar, nutlet margins rounded, sharp-angled, lineate-rimmed or narrowly winged with wings not lobed; surfaces densely or sparsely white-tubercled or glabrate, dimpled or rugulose..... **2 (*Johnstonella*)**
- 2 Nutlet surface dimpled to rugulose, lacking tubercles ***Johnstonella punensis***
- Nutlet surface whitish tuberculate..... **3**
- 3 Nutlets widely ovate to deltate, margin irregularly lineate to tuberculate, attachment scar areole extending to 2/3 nutlet length, appearing deeply excavated, Argentina, Mexico, United States ***Johnstonella albida***
- Nutlets ovate, margin with a well-defined lineate rim, attachment scar areole extending to 1/2 nutlet length, moderately deep, not appearing excavated.... **4**
- 4 Calyx in fruit ca. 1.5–2 mm long; nutlets strongly heteromorphic, tuberculate, largest ca. 1 mm long, smallest 0.6–0.8 mm long, Chile, Peru..... ***Johnstonella parviflora***
- Calyx in fruit 2–4 mm long; nutlets homomorphic or slightly heteromorphic, 1.5–2 mm long; Argentina, possibly Chile ***Johnstonella diplotricha***

Discussion

Based on the phylogenetic study of Simpson et al. (2017a), the relationships of *Johnstonella punensis* are equivocal (Fig. 7A). In the analysis of both chloroplast and mitochondrial DNA sequence data, *J. punensis* is sister to the South American *J. diplotricha* (Phil.) Hasenstab & M.G.Simpson with strong support. In these two analyses, *J. diplotricha* and *J. punensis* are together sister to a clade including *J. albida*, which occurs in both North and South America. However, analysis of nuclear ribosomal

DNA sequence data places *J. punensis* in a polytomy with the South American *J. parviflora* (Phil.) Hasenstab & M.G.Simpson and the North American *J. angelica* (I.M.Johnst.) Hasenstab & M.G.Simpson; these last two are sister taxa in both the chloroplast and mitochondrial analyses (Fig. 7A).

Johnstonella punensis and *J. diplotricha* are similar in having homomorphic or slightly heteromorphic nutlets. The two differ in that nutlets of *J. punensis* lack tubercles, having a dimpled to rugulose surface and lack a marginal lineate rim (Fig. 7B–G). Nutlets of *J. diplotricha* are whitish tuberculate and possess a prominent marginal lineate rim (Fig. 7H). In contrast, *J. parviflora* (Fig. 7I) and the North American *J. angelica* (not illustrated) are both generally strongly heteromorphic and are, in fact, quite similar to one another in numerous features (Simpson et al. 2020); both of these species have nutlets that are whitish tuberculate and marginally sharp-angled with a lineate rim. *Johnstonella albida* (Fig. 7J) is rather distinctive morphologically from all other South American species of the genus in having nutlets that are coarsely tuberculate, the tubercles much larger, with a deep attachment scar areole appearing strongly excavated, the scar typically extending to ca. 2/3 to the nutlet apex.

There is some variation in nutlet size and surface sculpturing observed in *J. punensis*, with nutlet length ranging from 1.1–1.5 mm long and surface sculpturing varying from nearly smooth, being only slightly and irregularly dimpled (e.g. Fig. 7E) to prominently dimpled, with irregularly circular, recessed areas (e.g. Fig. 7B–D), to what could be described as rugulose by expansion of the recessed areas (e.g. Fig. 7F–G). We currently believe this is likely natural variation within or between populations.

All known populations of *Johnstonella punensis* occur within what is termed the dry Puna, a biogeographic region of north-eastern Chile, south-western Bolivia and limited areas of extreme north-western Argentina (a component of the western South American Dry Diagonal; see Luebert et al. 2021). By this classification, the dry Puna is just east and northeast of the Atacama Desert of Chile. However, both the Atacama Desert and the region of the dry Puna where *J. punensis* occurs are “hyperarid” with an Aridity Index (AI) of < 0.2 (after Kimura and Moriyama 2019). Germination and growth of *Johnstonella punensis* is dependent on sporadic precipitation associated with a relative increase of summer rainfall in the dry Puna (Luebert 2021). New botanical encounters are not rare in this transition from the desert to the Altiplano highs (e.g. Calvo et al. 2018; Moreira-Muñoz and Muñoz-Schick 2020) and we encourage botanists to continue floristic studies in this harsh but marvellous zone of Chile.

Interestingly, the other South American species of *Johnstonella* occur in biogeographic regions different from that of *J. punensis* (Fig. 6B). *Johnstonella parviflora* is restricted to Chile and Peru in the Atacama and Peruvian desert regions. *Johnstonella diplotricha* is largely restricted to Argentina in the Prepuna Region. Finally, populations of the more distantly related *Johnstonella albida*, which has an American amphitropic disjunction (Guilliams et al. 2017; Simpson et al. 2017b) are restricted to Argentina, largely between the dry Puna, Monte and possibly Prepuna Regions (Luebert et al. 2021).

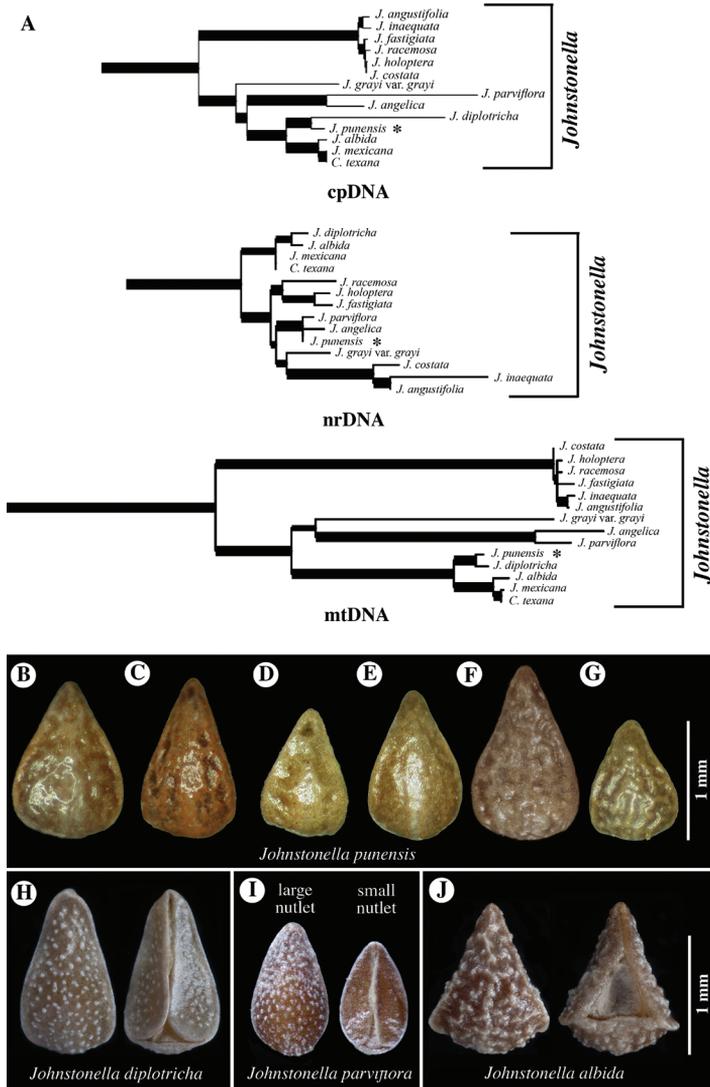


Figure 7. **A** Cladograms of *Johnstonella* clade from Simpson et al. 2017a, showing relationships of *Teillier 4754* (CONC150914) specimen of *J. punensis* (indicated with *) from analyses using sequence data of chloroplast DNA (cpDNA), nuclear ribosomal DNA (nr DNA) and mitochondrial DNA (mtDNA); note that *J. punensis* and *J. diplotricha* are sister taxa in the cpDNA and mtDNA analyses, but that *J. punensis* forms a polytomy with *J. parviflora* and *J. angelica* in the nrDNA analysis **B–J** comparison of nutlet morphology of *Johnstonella* species occurring in South America, all shown at the same scale of magnification **B–G** *Johnstonella punensis*, nutlets dimpled to rugulose, specimen source cited **B** *C. Muñoz 3710* (SGO119165) **C** *Pisano & Venturelli 1961* (SGO138942) **D** *Zalensky XVII-972* (SGO078510) **E** *Teillier 4754* (CONC150914) **F** *Teillier 3686* (SGO139488) **G** *Pisano & Venturelli 1738* (SGO139111); **H** *Johnstonella diplotricha*, nutlets white-tuberculate, generally homomorphic, *Haene 1779* (SI47823) **I** *Johnstonella parviflora*, nutlets white-tuberculate, heteromorphic with one larger (left in dorsal view) and three smaller (one of three at right, ventral view), *M. Muñoz 2715* (MO4317600) **J** *Johnstonella albida*, nutlets coarsely tuberculate, attachment scar deep, appearing excavated, *Kiesling 3589* (SI87780).

Conclusions

This new species was originally detected from the results of molecular phylogenetic analyses, using leaf material removed from an herbarium specimen. Its placement was recognised to be unusual, based on previously published taxonomic concepts (Johnston 1927) and comparisons with herbarium specimens. Luckily, we were able to study fruiting material removed from the sequenced specimen, which allowed us to verify that it was, indeed, misidentified and appeared morphologically unique in its group. Study of additional herbarium collections led to the discovery of another five specimens of this taxon that fit the circumscription here proposed.

The naming of this new species points out that taxa new to science may be “sitting” in herbarium cabinets, waiting to be described (Bowdler 2010). Its discovery highlights the synergistic relationship of molecular phylogenetic analyses and of careful study of morphology from herbarium collections, the latter especially important for plants that are difficult to observe, or even locate, in the field.

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Appendix I

Specimens examined for comparative morphological studies of *Johnstonella*. Listed are collector and collection number, date of collection, and herbarium acronym and accession number.

J. albida: Cabezas 39, February 1975 (SI87779); Cabrera 21483, 21 February 1971 (LP21483); Harbison 1252, 5 June 1903 (SDSU5489); Kelley 1426, 24 June 2007 (SDSU20612); Kiesling 3589, 15 March 1982 (SI87780); Ventura 206, 2 November 1975 (SD99139);

J. diplotricha: Haene 1779, 20 December 1997 (SI47823); Guaglianone 2356, 5 April 1989 (SI87772); Cabrera 31803, 17 February 1980 (SI87773); Mabry 89, 22 December 2014 (SDSU21232).

J. parviflora: Arroyo 84-971, 23 April 1984 (CONC146368); Teillier 4816, 5 July 2000 (CONC150821); M. Muñoz 2715, 19 October 1991 (MO4317600); van der Wurff 20532, 13 Apr 2006 (MO6128118); Moreira 2483, 17 June 2015 (SDSU21343); Teillier 7968, 14 September 2015 (SDSU21478); Simpson 3908, 20 October 2015 (SDSU21627); Simpson 3914, 21 October 2015 (SDSU22982); Böhnert 447, 11 March 2017 (SDSU23445).